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

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ABSTRACT

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

1. Introduction

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

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

humpback whales could be removing significant amount of biomass from these locally harvested fish populations.

The degree of top-down control that humpback whales exert on local forage fish populations is likely to vary across their range. Humpback whales demonstrate inter-annual fidelity to foraging areas (Baker et al., 2013) and show individual preferences for a particular prey type. By returning each year and focusing their foraging in specific locations whales could exert top down control on some local populations, while other populations remain unaffected. However, the extent of control depends on the size of the prey population (Bax, 1988). Impacts of humpback whale foraging on local populations would be particularly acute when humpback whales exploit forage fish that congregate in predictable locations, as is the case for overwintering herring (Sigler and Csepp, 2007). Humpback whales have been observed foraging on large, dense, overwintering shoals of herring in southeastern Alaska and Prince William Sounds (Boswell et al., 2016; Straley et al., in this issue).

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

2. Methods

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

2.1. Biomass removal model

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

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

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

2.2. Whale abundance

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

$$\sum n_t = \sum \alpha n_{t\ observed} \qquad (2)$$

where α is a coefficient that minimizes

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

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

2.3. Prey selection

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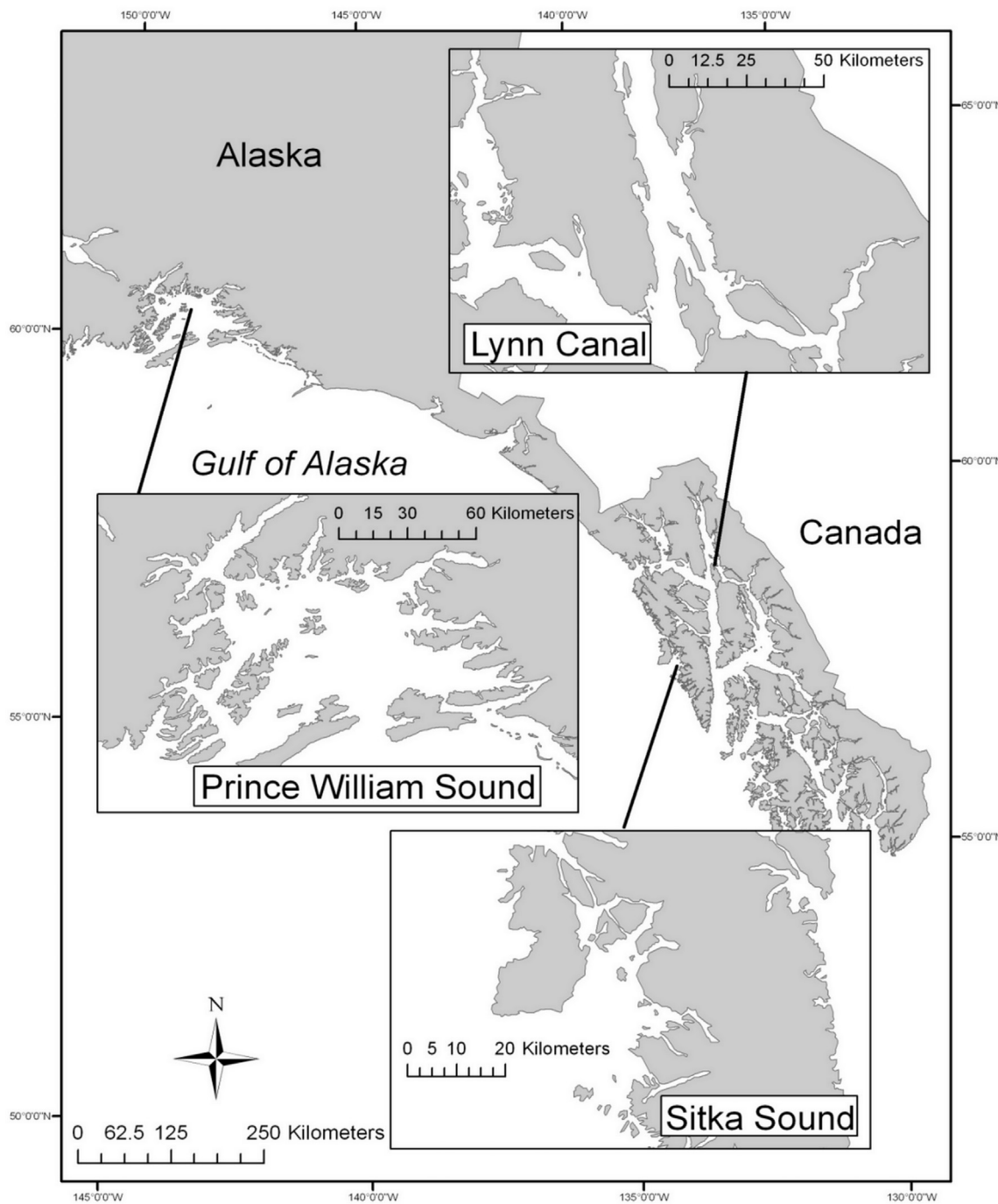
Fig. 1. Location of Lynn Canal, Sitka Sound and Prince William Sound around the periphery of the Gulf of Alaska.

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

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

eating known prey that were consuming herring.

2.4. Energy content of herring

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

given location was randomly selected from the 95% confidence interval for the *t*th day.

2.5. Whale weight

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

$$w_i = \frac{0.0158 L_i^{2.95}}{100} \tag{4}$$

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

2.6. Whale metabolic rate

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

2.7. Herring biomass estimates and predation intensity

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

3. Results

3.1. Whale abundance

Humpback whales were generally most abundant in all locations in the first half of each year's survey from September through December. Timing of peak abundance depended on both year and location. In Sitka Sound the peak abundance of whales was observed in November during the first survey (2007–2008) and in October during the second survey (2008–2009) (Fig. 2). Peak abundance in Lynn Canal tended to be earlier, occurring in September in the first survey and October during the second survey. In Prince William Sound whales remained at high

abundance throughout the fall of the second survey and only began declining after December (Fig. 2). While the daily abundance for first survey in Prince William Sound was not estimated, the largest number of whales was observed in December.

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

3.2. Prey selection

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

3.3. Energy content of herring

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

3.4. Whale metabolic rates and consumption

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

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

Metabolic rate under the low-end model predicts average daily metabolic cost. It estimates metabolic demand from mass using values of 209 and 0.75 for K and β, respectively. The value for K has been adjusted upwards from Kleiber's basal metabolic rate model to reflect
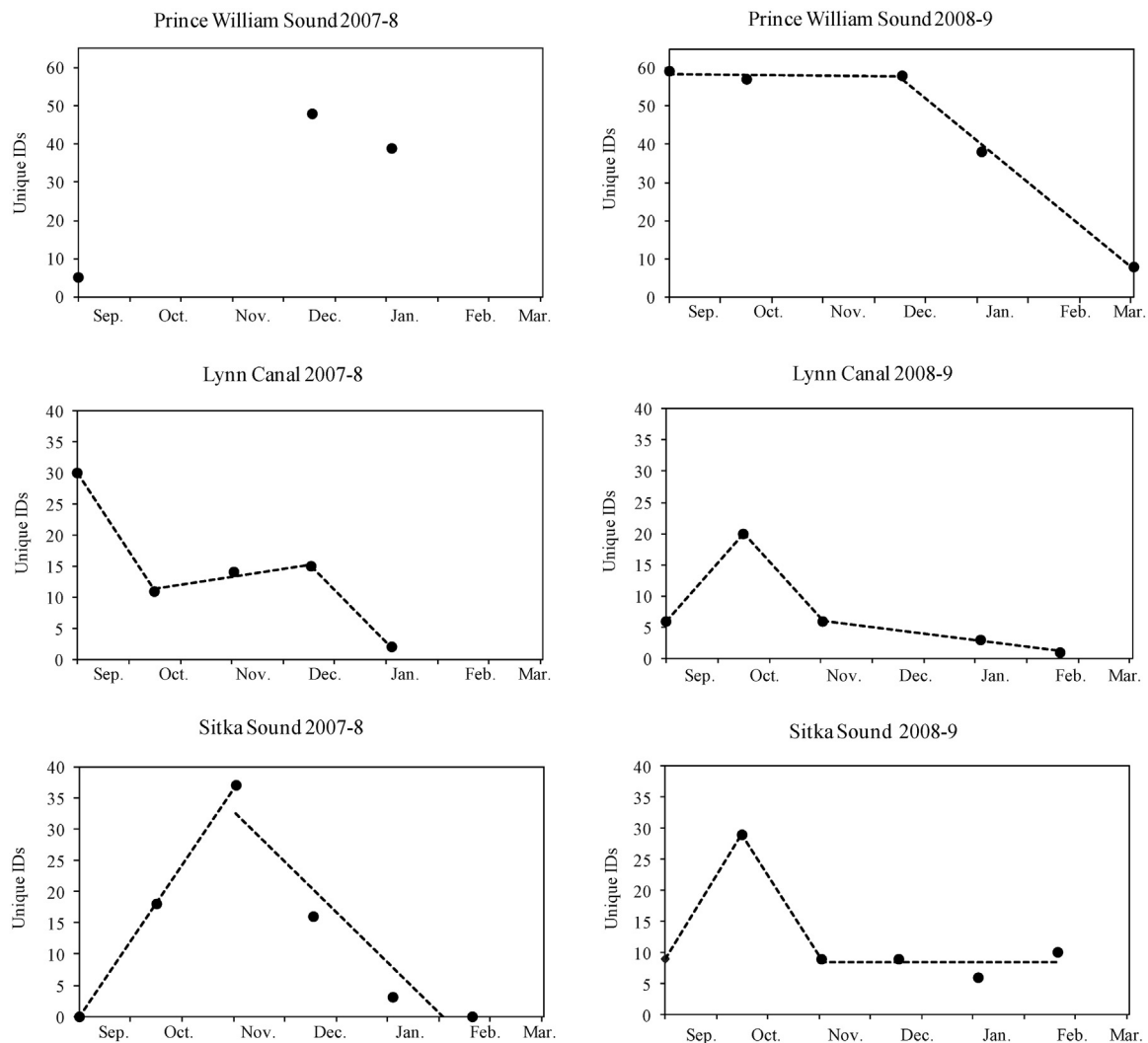
Fig. 2. Daily abundances of humpback whales in Lynn Canal, Sitka Sound and Prince William Sound. The daily abundance for Prince William Sound in 2007–2008 was not estimated because only three surveys were conducted over a limited spatial area. The study period spanned between September 15 (day 1) and March 15 (day 182).

Table 2

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

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

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

the additional cost of activity. The adjustment is based on observations of respiration in captive gray whales (Wahrenbrock et al., 1974). These estimates underestimate demand during winter foraging periods, because humpback whales must secure sufficient energy reserves during to fuel a fast that lasts at least two months (Gabrielle et al., 1996; Mate et al., 1998). During this period humpback whales migrate to their calving grounds, mate and return to the foraging grounds. Some of the

returning females will be accompanied by suckling calves. Thus additional costs not predicted by the low-end model include late-term gestation and lactation.

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

3.5. Predation intensity

In Lynn Canal most of the whale foraging effort on herring was focused on the beginning of the survey period when whales were abundant and herring were relatively scarce. Overall, humpback whales consumed between 732 and 1987 t of herring in 2007–2008 and 501–1335 t in 2008–2009 (Table 2). In November 2007 whales
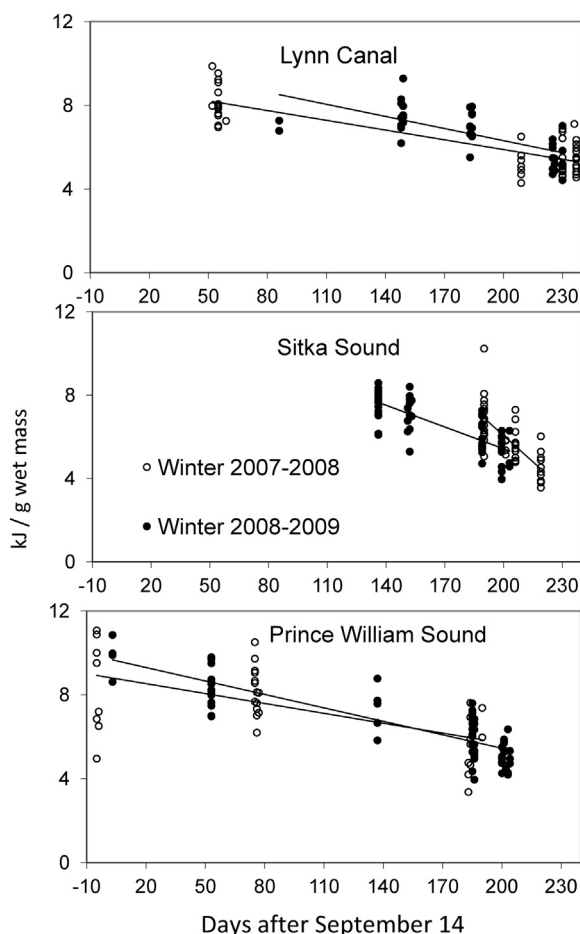
Fig. 3. Energy loss in herring from Lynn Canal, Sitka Sound and Prince William Sound during the winters of 2007–2008 and 2008-009. Elapsed days is the same scale as in Fig. 2.

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

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

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

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

less than the biomass removed in the Sitka Sound sac roe harvest: 14,616 and 15,012 t in 2007 and 2008, respectively (ADFG, 2012)

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

4. Discussion

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

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

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

4.1. Identification of the most appropriate consumption estimate

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

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

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

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

4.2. Impacts of whale predation on Lynn Canal herring

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

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

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

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

4.4. Impacts of whale predation on Sitka Sound herring

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

4.5. Conclusion

By remaining in Alaskan waters during the fall and winter months, humpback whales can exploit large shoals of lipid-rich herring. Late season predation had varying effects on the different herring stocks examined in this study. The shoaling behavior of overwintering and pre-spawning herring in predictable locations increases their vulnerability to humpback whale predation. When these shoals are large relative to the number of whales, then impacts to the local herring stock is minimal. However, when herring abundance is low, their tendency to aggregate continues to make an attractive target for foraging whales. Predation effects on herring can be minimized if the shoaling behavior is delayed until humpback whales begin their winter migration to calving grounds. Thus, the late arrival of herring in Sitka Sound coupled with their large biomass led to a minimal effect of whale predation. This contrasts with Prince William Sound, where there was a significant spatial and temporal match between whales and a depressed herring population. This temporal and spatial match between whales and herring resulted in whales removing a significant proportion of the spawning stock biomass. Therefore, the interplay between herring
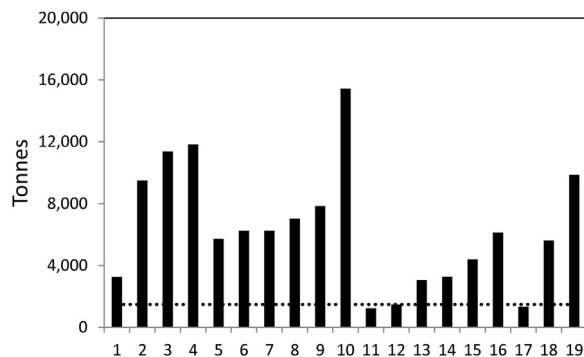
Fig. A1. Estimated total consumption for a single simulation of the winter of 2008–2009 in Prince William Sound using values of K and β found in different reports. The horizontal line depicts the estimate produced by Klieber's (1961) relation for basal metabolic rate. Models are classified as being derived from doubly labeled water isotope ratio studies (DW-IR), ingestion rate allometries (Ingestion), metabolic rate allometries (Kleiber) or alternative approaches (Other). Published models are found in: 1. Nagy et al. (1999) (all mammals), 2. Current pinniped FMRs with walrus, 3. Nagy et al. (1999) (mammalian carnivores), 4. Acquarone et al. (2006), 5. Trites et al. (1997), 6. Armstrong and Siegfried (1991), 7. Sigurjónsson and Víkingsson (1997), 8. Innes et al. (1987), 9. Reilly et al. (2004), 10. Nagy (2001), 11. Boyd (2002). 12. Kleiber (1961), 13. Laidre et al. (2007), 14. Lockyer (1981), 15. Perez and McAlister (1993), 16. Sigurjónsson and Víkingsson (1997), 17. Folkow and Blix (1992), 18. Blix and Folkow (1995), 19. Armstrong and Siegfried (1991).
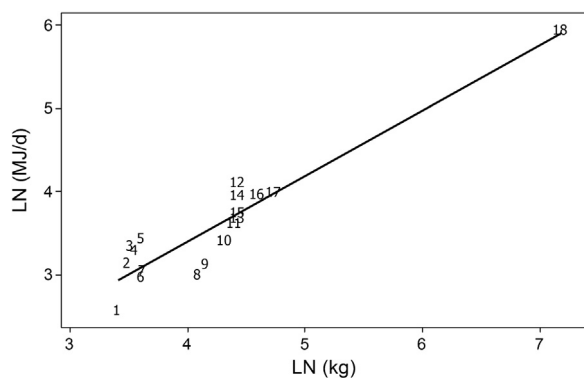
Fig. A2. Comparison (natural log- natural log) of body weights (kg) and current published metabolic (MJ/d0 rates of foraging pinnipeds and walrus based on DW-IR studies. Symbol numbers : 1. Trillmich and Kooyman (2001), 2. Costa and Gentry (1986), 2. Costa et al. (2000), 3. Costa et al. (1989a), 4. Costa et al. (1985), 5. Arnould and Boyd (1996), 6. Costa et al. (1985), 7. Sparling et al. (2008), 8. Costa and Gales (2003), 9. Costa and Gales (2003), 10. Costa et al. (1991), 11. Costa et al. (1989b) Abstract, 12. Costa et al. (1989a), 13. Costa et al. (1985), 14. Costa et al. (1985), 15. Reilly and Fedak (1991), 16. Costa and Gales (2000), 17. Reilly et al. (1996), 18. Acquarone et al. (2006).

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

Appendix A

Rationale for selecting allometric models

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

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

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