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

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ABSTRACT

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

1. Introduction

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

Alaska) and the Northern GOA.

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

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

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

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

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

In this paper, we report on humpback whales in the three areas: PWS, LC, and SS. Specifically, we identified and counted humpback whales in each area during the fall and winter, observed and characterized their feeding behavior, and applied isotopic analyses to

corroborate diet (Witteveen et al., 2009). We documented temporal and spatial patterns of humpback whales and herring to assess how the predator-prey relationship varied demographically.

2. Materials and methods

2.1. Study areas

Located along the perimeter of the GOA, Prince William Sound, Lynn Canal, and Sitka Sound are distinct geographically (Fig. 1) and oceanographically. PWS, the most northern study site (60.5°N 147.0°W), has relatively protected waters characterized by a complex coastline of glacial fjords and islands, with an area of approximately 4500 km². The other study areas are located in Southeast Alaska, which is a mosaic of islands adjacent to the mainland of Canada, deeply incised with glacial fjords, many passageways, and bays. SS is situated mid-way along the outer coast of Baranof Island (57.0°N 135.5°W), encompassing approximately 450 km² and is directly exposed to the elements of the GOA. LC (58.4°N 134.8°W), is a long north-south oriented deep trench located to the north and east of SS in the inside waters of Southeast Alaska. The LC study area encompasses approximately 500 km² and includes the waters of southern LC and the adjacent waters of northern Stephens Passage.

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

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

2.2. Whale survey effort

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

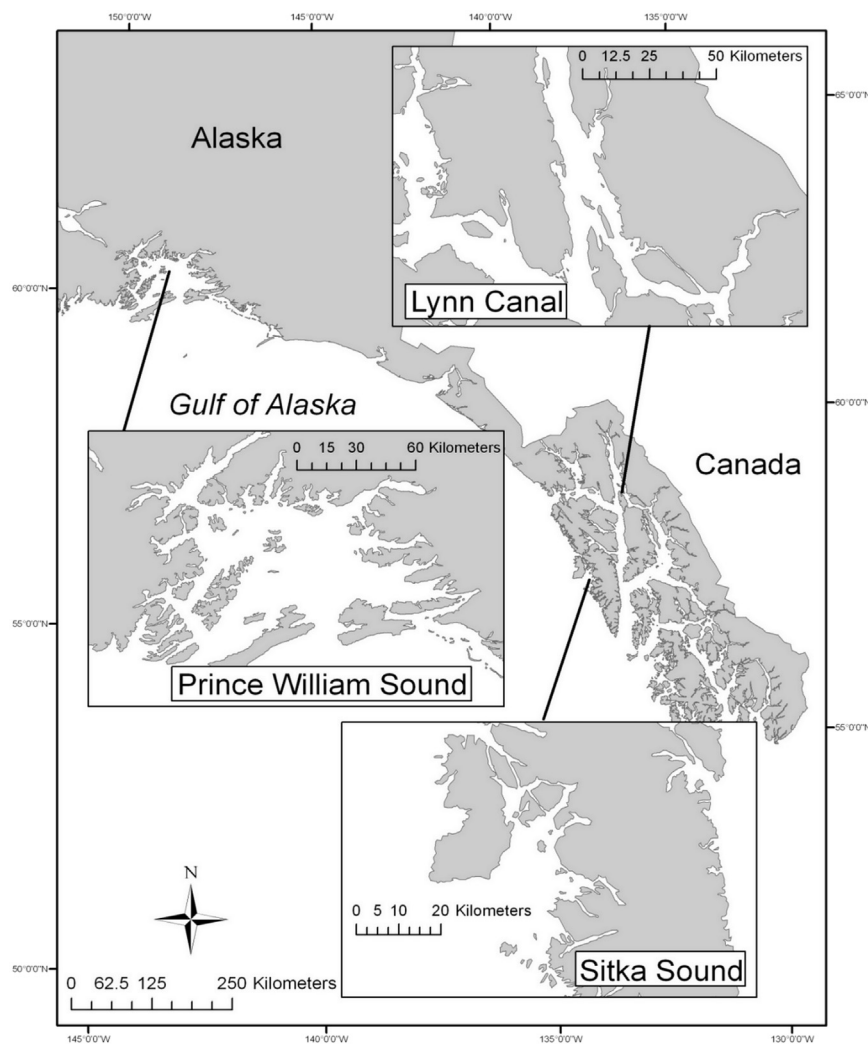


Fig. 1. Locations of the Prince William Sound, Lynn Canal, and Sitka Sound study areas.

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

2.3. Monthly whale observations across the fall and winter seasons

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

2.4. Groups of whales, behavior determination and age class

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

The behavior of each group was recorded. Whale behaviors were recorded as: 1) feeding: defined as diving and surfacing repeatedly in the same area with prey visible on the echosounder or seen within the

water; 2) sleeping: defined as resting or motionless at or just below the surface; 3) traveling: defined as directed swimming in one direction or 4) milling: defined as moving in an unspecified direction, sometimes with an erratic path of travel or circling, giving the appearance searching. Also recorded, if possible, were whale age classes (calf, adult, or juvenile). An adult is a whale over five years old, a calf is a whale less than a year old in close association with the presumed mother, and a juvenile is a whale whose birth year is known and age is 1–5 years old (Clapham, 2009).

2.5. Photo-identification of individual whales

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

2.6. Overwintering whales

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

Table 1

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

a. Prince William Sound. (dash = no survey)										
Effort: Month	Days	km	Hrs	Whale:groups	avg group size	whales counted	photo-identified	unique whales	number unique per year	Total unique whales both years
2007/08										
15 Sep–14 Oct	5	559	48.8	24	1	31	5	5		162(+ 21 calves)
15 Oct–14 Nov	0	–	–	–	–	–	–	–		
15 Nov–14 Dec	8	376	68.0	44	2	106	63	48		
15 Dec–14 Jan	0	–	–	–	–	–	–	–		
15 Jan–14 Feb	5	535	32.3	26	2	42	42	40		
15 Feb–14 Mar	0	–	–	–	–	–	–	–		
Total	18	1470	149.1	94	2	179	110	93	76(+ 5 calves)	
2008/09										
15 Sep–14 Oct	6	763	54.9	26	3	71	79	59		
15 Oct–14 Nov	5	596	42.7	32	4	143	58	57		
15 Nov–14 Dec	7	550	43.2	38	3	95	81	63		
15 Dec–14 Jan	0	–	–	–	–	–	–	–		
15 Jan–14 Feb	5	598	42.3	20	3	58	51	38		
15 Feb–14 Mar	5	618	30.0	5	2	8	8	8		
Total	28	3117	213.0	121	2	375	277	1225	131(+ 16 calves)	
b. Lynn Canal. (dash = no survey)										
Effort: Month	days	km	Hrs	Whale: groups	avg group size	whales counted	photo-identified	unique whales	number unique per year	Total unique whales all years
2007/08										
15 Sep–14 Oct	3	398.2	26.3	47	1	55	44	30		46(+ 6 calves)
15 Oct–14 Nov	4	333.4	35.4	22	1	92	17	13		
15 Nov–14 Dec	3	259.3	15.8	17	1	50	32	19		
15 Dec–14 Jan	2	179.6	9.3	6	1	10	8	6		
15 Jan–14 Feb	0	–	–	–	–	–	–	–		
15 Feb–14 Mar	6	498.2	40.4	1	1	2	0	–		
Total	18	1668.7	127.2	93	1	209	101	68	38(+ 4 calves)	
2008/09										
15 Sep–14 Oct	3	275.9	20.1	19	2	55	34	22		
15 Oct–14 Nov	0	–	–	–	–	–	–	–		
15 Nov–14 Dec	1	142.6	5.7	3	2	7	6	6		
15 Dec–14 Jan	1	85.2	5.0	2	2	3	3	3		
15 Jan–14 Feb	1	100.0	2.3	1	1	1	1	1		
15 Feb–14 Mar	1	8.9	1.5	0	0	0	0	0		
Total	7	612.7	34.7	25	1	66	44	32	22(+ 2 calves)	
c. Sitka Sound. (dash = no survey)										
Effort: Month	days	km	Hrs	Whale: groups	avg group size	whales counted	photo-identified	unique whales	number unique per year	Total unique whales all years
2007/08										
15 Sep–14 Oct	2	64.8	5.5	20	1	20	13	13		68(+ 12 calves)
15 Oct–14 Nov	5	122.2	13.7	33	3	83	64	38		
15 Nov–14 Dec	3	72.2	7.7	16	3	43	22	16		
15 Dec–14 Jan	0	–	–	–	–	–	–	–		
15 Jan–14 Feb	2	53.7	2.7	2	1	2	0	0		
15 Feb–14 Mar	1	40.7	4.1	3	1	2	3	3		
Total	13	353.7	33.7	74	2	150	102	70	44(+ 8 calves)	
2008/09										
15 Sep–14 Oct	3	124.1	13.1	19	3	60	46	28		
15 Oct–14 Nov	3	66.7	9.9	10	2	19	18	13		
15 Nov–14 Dec	1	24.1	2.2	4	1	5	5	5		
15 Dec–14 Jan	5	174.1	13.6	9	2	18	9	9		
15 Jan–14 Feb	4	200.0	8.8	12	2	22	21	10		
15 Feb–14 Mar	3	166.7	8.9	7	2	11	7	6		
Total	19	755.6	56.4	61	2	135	106	71	45(+ 4 calves)	

satellite tag data. Theoretically, humpbacks could reach the breeding area in Hawaii and return to Alaska within 60 days. A small number of whales migrate to Mexico (Calambokidis et al., 2001, 2008) with the transit time unknown, but it is likely similar to Hawaii because the distance is similar (about 4400 km). Our criterion for determining overwintering (i.e. not making an annual migration to a lower latitude

breeding area) was that there would be insufficient time for a whale to make two transits of 30 days each way. Therefore, a whale would need to be sighted at least once in Alaska within 60 consecutive days to preclude two oceanic migrations of 30 days each had not occurred.

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

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

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

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

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

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

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

Table 2

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

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

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

These parameters were estimated by:

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

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

2.8. Numbers of whales and seasonal distribution

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

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

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

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

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

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

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

where α is a coefficient that minimizes

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

2.9. Foraging observations and identification of diet

2.9.1. Whale foraging behavior

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

(ocean bottom) and if prey were observed on the echosounder tracing (Fig. 2a and b). Often other herring predators (sea lions and birds) were present, as well. All whales in a group were presumed to be foraging on the same prey. Other behaviors observed were resting, traveling, and milling, but only foraging behavior was analyzed for the purposes of this paper.

2.9.2. Prey type identification from direct observations

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

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

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

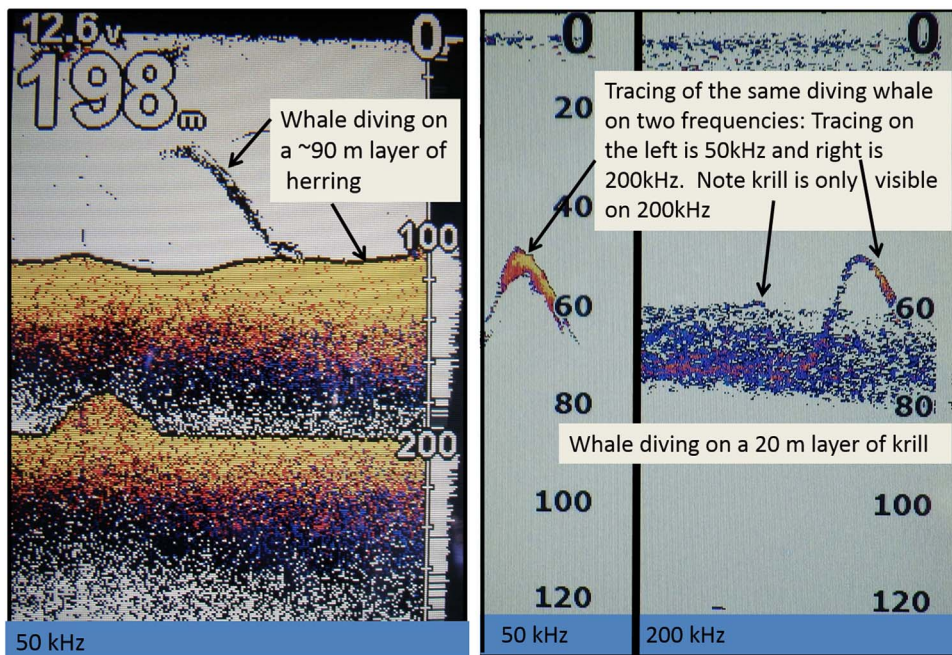


Fig. 2. a. This image is of a Lowrance echo sounder equipped with a 50 kHz transducer used to help identify prey. The tracing shows a 90 m layer of herring almost to the ocean bottom (198 m) with a whale diving into top of the herring. b. The two images show the dual frequency Lowrance echosounder with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

a

b

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

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

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

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

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

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

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

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

2.11. Statistical analysis

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

3. Results

3.1. Whale observations

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

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

3.2. Whales forgoing annual migration, and overwintering in Alaska

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

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

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

3.4. Seasonal trends in peak whale attendance patterns

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

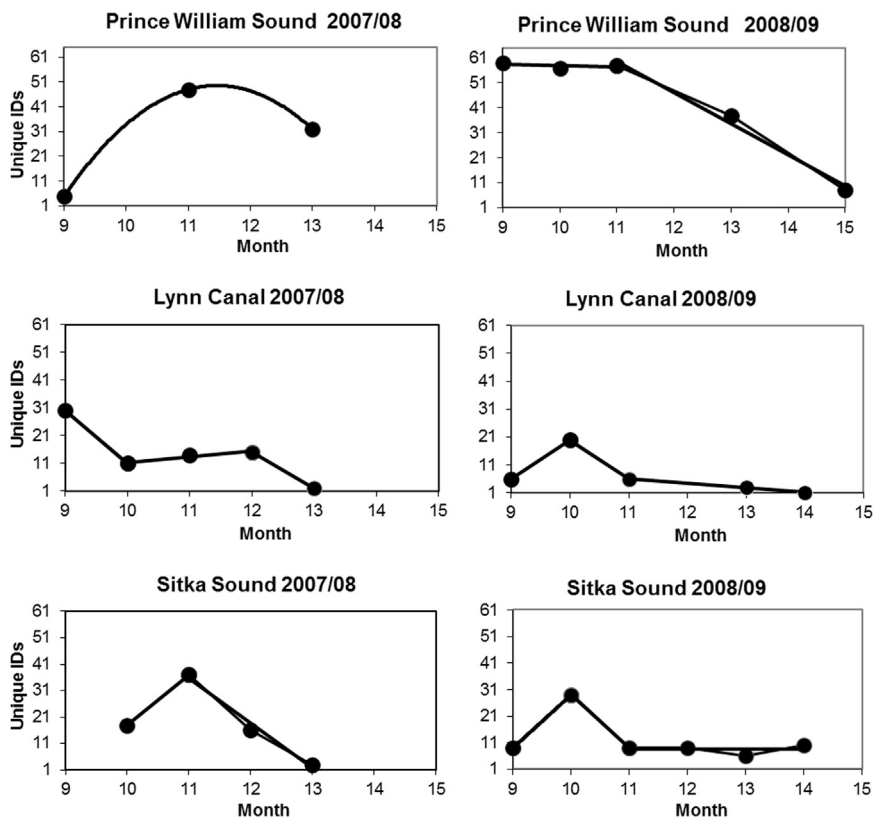


Fig. 3. Late season attendance patterns of humpback whales in Prince William Sound, Lynn Canal and Sitka Sound. Points show the number of unique whales identified in each location during each month from September (month 9) to March (month 15). The attendance pattern for Prince William Sound in 2007/08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

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

3.5. Foraging behavior observations

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

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

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

were observed to prey upon krill, while during the winter, the majority of groups preyed upon herring. The same groups of whales found feeding on krill in the fall were observed feeding on herring in winter.

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

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

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

4. Discussion

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

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

Table 3

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

a. Prince William Sound. (dash = no survey)								
Group behavior	Year	15-Sep	15-Oct	15-Nov	15-Dec	15-Jan	15-Feb	Totals
Feed	2007/08	19	–	30	–	22	–	71
	2008/09	23	23	30	–	13	3	92
	Totals	42	23	60	–	35	3	163
Other	2007/08	5	–	14	–	4	–	23
	2008/09	3	9	8	–	7	2	29
	Totals	8	9	22	–	11	2	52
b. Lynn Canal. (dash = no survey)								
Group behavior	Year	15-Sep	15-Oct	15-Nov	15-Dec	15-Jan	15-Feb	Totals
Feed	2007/08	46	18	9	5	–	0	78
	2008/09	18	–	2	2	1	0	23
	Totals	64	18	11	7	1	0	101
Other	2007/08	1	4	8	1	–	1	15
	2008/09	1	–	1	0	0	0	2
	Totals	2	4	9	1	0	1	17
c. Sitka Sound. (dash = no survey)								
Group behavior	Year	15-Sep	15-Oct	15-Nov	15-Dec	15-Jan	15-Feb	Totals
Feed	2007/08	20	31	16	–	2	3	72
	2008/09	15	10	4	7	12	7	55
	Totals	35	41	20	7	14	10	127
Other	2007/08	0	2	0	–	0	0	2
	2008/09	4	0	0	2	0	0	6
	Totals	4	2	0	2	0	0	8

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

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

resulted in fewer photographs that passed quality codes for the mark-recapture model, leading to an underestimate of abundance. During 2008/09, two more surveys were conducted than for 2007/08, considerably improving the quality and amount of data collected.

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

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

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

Table 4

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

a. Prince William Sound. (dash = no survey)								
Prey	Year	15-Sep	15-Oct	15-Nov	15-Dec	15-Jan	15-Feb	Totals
Herring	2007/08	9	–	5	–	18	0	32
	2008/09	19	21	30	–	12	2	84
Krill	2007/08	1	–	2	–	0	0	3
	2008/09	2	2	0	–	0	0	4
Unknown	2007/08	9	–	23	–	4	0	36
	2008/09	2	0	0	–	1	1	4
Totals		42	23	60	–	35	3	163
b. Lynn Canal. (dash = no survey)								
Prey	Year	15-Sep	15-Oct	15-Nov	15-Dec	15-Jan	15-Feb	Totals
Herring	2007/08	45	17	5	3	0	–	70
	2008/09	18	–	2	2	1	0	23
Krill	2007/08	0	0	2	0	0	–	2
	2008/09	0	–	0	0	0	0	0
Both	2007/08	0	0	1	0	0	–	1
	2008/09	0	–	0	0	0	0	0
Unknown	2007/08	0	1	1	2	0	–	4
	2008/09	1	–	0	0	0	0	1
Totals		64	18	11	7	1	0	101
c. Sitka Sound. (dash = no survey)								
Prey	Year	15-Sep	15-Oct	15-Nov	15-Dec	15-Jan	15-Feb	Totals
Herring	2007/08	0	2	7	–	2	3	14
	2008/09	0	4	4	4	12	7	31
Krill	2007/08	0	24	8	–	0	0	32
	2008/09	15	6	0	0	0	0	21
Both	2007/08	0	0	0	–	0	0	0
	2008/09	0	0	0	3	0	0	3
Unknown	2007/08	20	5	1	–	0	0	26
	2008/09	0	0	0	0	0	0	0
Totals		35	41	20	7	14	10	127

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

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

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

5. Conclusions

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

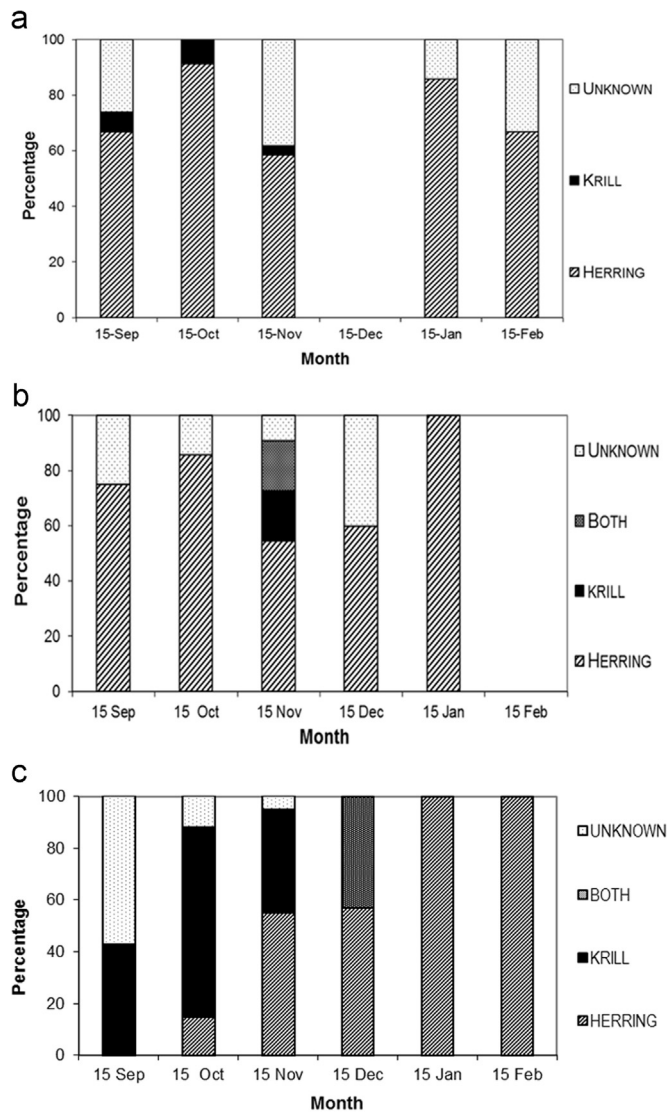


Fig. 4. a. Proportion of prey type observed by groups (N = 163) of foraging humpback whales in Prince William Sound each month during the combined fall and winters, 2007/08 and 2008/09. b. Proportion of prey type observed by groups (N = 101) of foraging humpback whales in Lynn Canal each month during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

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

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

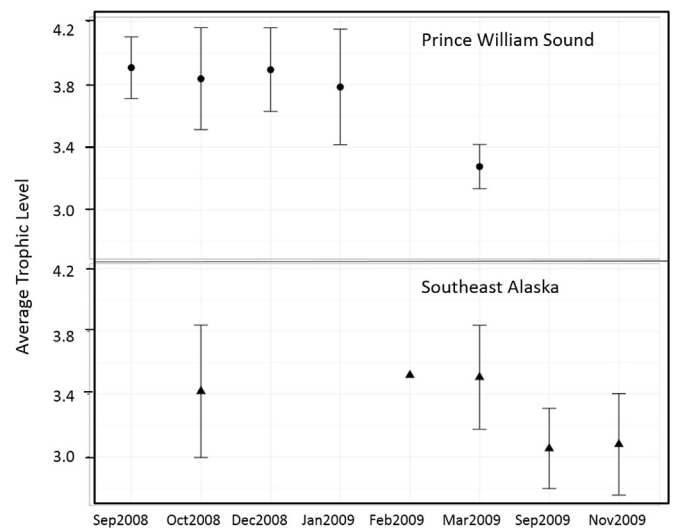


Fig. 5. Trophic level values with standard errors for humpback whales foraging in Prince William Sound (PWS) (n = 42) from the fall and winter 2008/09 and in southeastern Alaska (SEAK) (n = 47) from fall and winter 2008/09 and fall 2009.

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

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

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

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

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

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

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

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

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