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Are spatial and temporal patterns in Lynn Canal overwintering Pacific herring related to top predator activity?

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Abstract: In Southeast Alaska, overwintering Pacific herring (*Clupea pallasii*) form large conspicuous schools that are preyed upon by an abundance of mammalian and avian predators, thus leading to the question of why herring adopt a strategy that appears counterproductive to predator avoidance during these periods. We examined the spatial and temporal dynamics of overwintering Pacific herring and associations with predators through monthly hydroacoustic surveys during two consecutive winters. Large variation was observed through the winter season in herring distribution, school morphology, and density. Herring school characteristics and biomass estimates were negatively correlated with humpback whale (*Megaptera novaeangliae*) abundance patterns during both winters, and as whales departed towards the end of winter, herring distributions shifted from dispersed schools in the water column toward deep, dense schools. We postulate that the schooling patterns observed in Lynn Canal overwintering herring are likely to be mediated by predation threat rather than energetics or feeding activities. An additional consequence of humpback whales dispersing herring in the water column may be an increased threat of predation by other surface-oriented predators.

Résumé : Dans le sud-est de l'Alaska, lors de périodes d'hivernage les harengs du Pacifique (*Clupea pallasii*) se regroupent dans des zones bien précises où ils forment de grands bancs très visibles, prédatés par de nombreuses espèces de mammifères et d'oiseaux marins. Ceci soulève la question de savoir pourquoi les harengs adoptent une telle stratégie qui semble être contre-productive en terme de survie durant ces périodes. Nous avons examiné les comportements de bancs de harengs du Pacifique et leurs relations avec la présence de prédateurs au cours de relevés acoustiques effectués lors de deux hivers consécutifs. Nos résultats démontrent une variation significative des caractéristiques des bancs, ainsi que des biomasses estimées, négativement corrélées avec l'abondance de baleines à bosse (*Megaptera novaeangliae*) au cours des deux hivers. Le départ de ces prédateurs de la zone d'étude est suivi d'un changement de distribution des bancs de harengs passant de dispersés dans la colonne d'eau, à denses et profonds typiques des périodes d'hivernage. Les comportements des harengs du Pacifique observés dans la zone d'étude ne seraient pas induits par des considérations énergétiques ou d'alimentation, mais refléteraient plutôt une réponse directe à la pression de prédation. La présence de baleines à bosse semble forcer les bancs de harengs à se disperser dans la colonne d'eau, avec comme possible conséquence d'augmenter leur vulnérabilité face à d'autres prédateurs de surface.

Introduction

Predator avoidance is the prime explanation for why many pelagic fishes aggregate to form large-scale schools (Magurran 1990; Rieucau et al. 2015a). Although schooling is commonly considered as an adaptive strategy aimed at reducing the risk of predation (Pitcher and Parrish 1993), few studies have examined the functional importance of the observed natural variations in school morphology, internal organization, and behaviour of pelagic schools. Oceanic acoustic surveys have provided valuable observational information that depicts the high degree of plasticity in schooling dynamics and internal structure induced by predation, anthropogenic (e.g., research and fishery vessels), or environmental perturbation (Fréon et al. 1996; Soria et al. 2003; Paramo et al. 2010). Under fluctuating environmental conditions or predation risk, schooling fish face the ceaseless challenge of fine-tuning their schooling tendency to minimize their vulnerability to predation while maximizing fitness gains. Variations in schooling tendency observed in pelagic fishes are thought to reflect changes in fish fitness trade-offs (e.g., feeding, survival, or reproduction). Axelsen et al. (2000) suggested that school formation and density in prespawning Atlantic herring (*Clupea harengus*) are mediated by state-dependent processes that reflect a trade-off primarily between survival and reproduction, with herring aggregating in small isolated and dense schools in the summer. It is also well established that *C. harengus* perform diel vertical migrations. In the winter when fish form dense schools close to the seabed during the day, they swim towards the surface at dusk to aggregate in less dense layers (Mackinson et al. 1999). Avoiding predators is the most commonly invoked driver of herring bottom–surface migration (Misund et al. 1997; Mackinson et al. 1999). Like their Atlantic counterparts, Pacific herring (*Clupea pallasii*) are intrinsically tuned to form small schools in the summer and large, dense schools in the

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Can. J. Fish. Aquat. Sci. Vol. 73, 2016

winter, and their distribution and aggregation dynamics also shift at seasonal and diurnal scales in accordance with their life history and environmental pressures (Mackinson et al. 1999). However, for Pacific herring, shifts at the scale of the school (e.g., behavioural, morphological, or structural) in response to predators are not well understood. It remains unknown whether pelagic schooling fishes, such as Pacific herring, are capable of adaptively adjusting their aggregative tendencies in response to temporal fluctuations in predator abundance.

Recently, Langård et al. (2014) described distributional patterns at the aggregation level in Atlantic herring as a function of physiological state; however, the direct effects of predators were largely unresolved. In addition to the other factors controlling herring distributions (i.e., spawning activity or maturation state), predators likely play an important role in determining how herring schools are distributed and moreover how shifts in their schooling behaviour and dynamics might lead to increased risk of predation by other predators (Nøttestad et al. 2002a). Nonconsumptive predator effects are thought to be equally as important as consumptive effects in structuring ecological processes, and the role of predators acting simply as "agents of fear" can have cascading consequences throughout the ecosystem (Preisser et al. 2005; Wirsing et al. 2008). Developing an understanding of how pelagic fishes modulate their schooling behaviour in response to fluctuations in perceived predation risk will necessitate in situ studies directed at linking variable predation intensity to changes in schooling tendency.

In the waters of Southeast Alaska, Pacific herring predictably coalesce at overwintering grounds and form large (~5 km in length) schools in trenches in which they provision their gonads in preparation for spring spawning (Carlson 1980; Sigler and Csepp 2007). The formation of large, vertically compressed schools is thought to be a predator avoidance strategy (Røttingen et al. 1994; Nøttestad and Axelsen 1999) that confers safety through a numerical dilution of risk (Hamilton 1971; Foster and Treherne 1981; Turner and Pitcher 1986; Landa 1998; Skaret et al. 2003). As noted recently by Langård et al. (2014), few studies have examined prespawning behavioural shifts in herring schools, particularly in response to predator threats. This is of importance in Southeast Alaska because overwintering herring schools begin to form prior to the departure of humpback whales (Megaptera novaeangliae) on their annual migration from northern foraging grounds to southern areas for reproduction (Darling and McSweeney 1985). Krill (Thysanoessa spp. and Euphausia pacifica) and Pacific herring are primary prey species for humpback whales that occupy these regions (Rice et al. 2011), and humpback whales are known to exploit both prey sources while provisioning for their extended fasting during migration and reproduction. The timing of migration to lower latitudes during the fall and winter months varies by individual whale. Although there is a year-round presence of humpback whales on the feeding grounds, the overall abundance and fine-scale distribution changes seasonally (Straley 1990; Pritchett et al. 2007). With increased predator interactions, herring are likely to vary their school dynamics and distribution in accordance with perceived risk and elicit varying strategies to mitigate risk effects (Pitcher and Parrish 1993; Nøttestad and Axelsen 1999), resulting in plasticity in schooling dynamics and state-dependent morphology (Fernö et al. 1998; Langård et al. 2014).

Humpback whales are major predators and consume an average 0.4 t of prey per whale per day (Witteveen 2003). Humpback populations in the Pacific Ocean have increased at a rate of approximately 5% per year with an estimate of nearly 20 000 individuals for the North Pacific (Calambokidis et al. 2008), up from an estimated low of 1500–2000 individuals in the late 1960s. Generally, humpback whales consume many types of prey, including herring, krill, capelin (Mallotus villosus), and Pacific sand lance (Ammodytes hexapterus). As whale numbers increase, their impact on forage species, which are prey for a host of other marine mam-

mals, seabirds, and piscivorous fish, is of considerable interest and may have pronounced ecosystem-level effects (Overholtz and Link 2007).

Here we examine the relationship between two species present during winter months in Southeast Alaska: Pacific herring and one of their primary predators, humpback whales. This study examined whether patterns in herring school distribution, morphology, and density were correlated with changes in humpback whale abundance over the course of the winter. Variation in distribution, intrinsic morphological characteristics (depth, height, volume, and perimeter), and density of herring schools were evaluated during acoustic surveys over two consecutive winters at a prominent overwintering area in Lynn Canal.

Methods

Study area

A region of Lynn Canal in southeastern Alaska was surveyed during two consecutive winters, 2007–2008 and 2008–2009, where large schools of overwintering herring consistently form (Fig. 1). Monthly acoustic surveys were conducted between November and February for herring and between September and February for whales, during the two winter periods and are further detailed below.

Acoustic surveys

To estimate herring biomass and describe patterns in school dynamics, monthly hydroacoustic surveys were planned over a series of 3 consecutive days from November to February during the winters of 2007–2008 and 2008–2009 (Table 1). Given the variable weather conditions, not all surveys were completed across consecutive days. Each survey comprised 13 distinct strata, including two bays of open water, with survey sections ranging from approximately 3 km to 28 km in length. Surveys followed a standardized zig-zag transect line (197 km total length), covering an area of 161 km² (Fig. 1; Table 2). Acoustic data were collected with a calibrated 38 kHz Simrad EK60 split-beam echosounder system with a towfish-mounted transducer deployed at 1 m below the water surface. The echosounder system was calibrated during each survey following the standard sphere method (Foote et al. 1987). All surveys were conducted during daylight hours to account for potential variation due to diel vertical migration behaviour and acoustic intensity (Huse and Korneliussen 2000). Strata description, transect layout, collection parameters, and system setup are described in Sigler and Csepp (2007). The nomenclature for the acoustic variables follows MacLennan et al. (2002). During each survey, water temperature and conductivity were collected throughout the water column at standardized locations using a Sea-Bird 19+ CTD (Sea-Bird Electronics, Inc.) to characterize water chemistry, vertical water column structure, and derive sound speed profiles. Sound speed and absorption coefficients were calculated to account for the effects of temperature and salinity on acoustic transmissions.

Monthly surveys were subdivided into 13 strata (Table 2) within Lynn Canal, where each stratum was generally characterized by similar bathymetry, location, and the presence of Pacific herring. Herring schools were manually identified in the acoustic record and then outlined with a region editor tool in Echoview (version 6.0; Myriax). School-based metrics were derived for all manually identified herring schools using the school detection algorithm (minimum threshold –70 dB, minimum school length 10 m, minimum school height 3 m, vertical linking distance 3 m, and horizontal linking distance 10 m) in Echoview. Herring schools identified along the transects were selected for analysis in Echoview where the echo-integral (Simmonds and MacLennan 2005) was computed for the acoustic backscatter in cells 0.18 km long by 10 m deep, comprising each elementary sampling distance unit. Standard output following echo integration includes the acoustic estimate

Fig. 1. Bathymetry (100 m isobaths) of Lynn Canal region, near Juneau, Alaska (JNU), with acoustic cruise track overlaid (broken lines). Note: inset map is rotated from north.
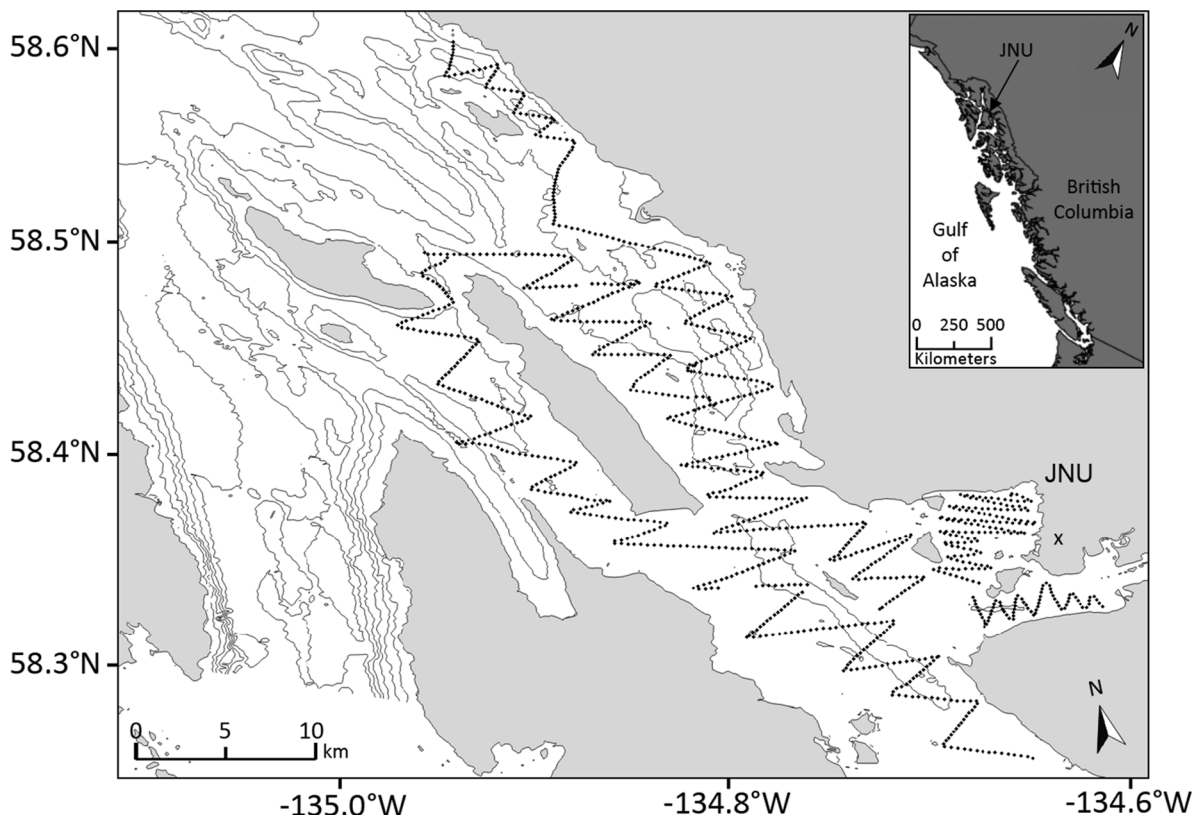

Table 1. Monthly survey efforts conducted in Lynn Canal, Alaska, by survey type.

Month	2007–2008		2008–2009	
	Date	Survey type	Date	Survey type
September	21–23, 28	w	23–24	w
October	18–19	w	3–4, 6, 8	w
November	6–8	a, t, w	3–4	a, w
	10–11, 19	w	8	t
December	5–6	w	10–11, 23	a, t
	20–21	a, w	18	w
	29–30	a		
January	14	a, w	10–11, 14	a, w
February	23–25	a, t, w	3–4, 12	a, t
			8	w

Note: Whale surveys began in September of each winter; however, acoustic surveys did not begin until November of each winter. Survey types were as follows: acoustic (a), trawl (t), whale (w).

Table 2. Strata surveyed during acoustic transects conducted in Lynn Canal with corresponding area (km²) and total transect length (km) used for calculating herring biomass.

Strata	Area (km²)	Transect length (km)
Aaron Island Trench	1.8	5.9
Amalga Trench	22.9	16.1
Auke Bay	7.0	28.3
Benjamin Island Trench	6.2	11.7
Eagle Beach	8.1	9.6
East Portland Island	14.8	9.1
Favorite Channel	23.0	23.3
Fritz Cove	4.5	12.6
Halibut Cove	2.3	2.6
Lena Point	11.0	11.5
Mansfield Peninsula	20.1	21.5
Portland Island Trench	16.9	20.7
Saginaw Channel	22.4	24.4
Total	161.0	197.3

of fish density, s_a (area scattering coefficient; m²·m⁻²). Metrics describing the geometric morphological characteristics of herring schools (i.e., school area (m²); height (m); length (m); perimeter (m), based on the 2D shape of the school in the vertical domain) and volume (m³) were extracted for analysis. In addition, image compactness, a measure of the ratio of the squared school perimeter and school area, was extracted within Echoview. Image compactness values of 1 represent a circle.

Processed echo integration data were used to compensate for effects of acoustic shadowing and extinction on the estimates of herring school biomass and density (Foote 1990; Zhao and Ona 2003; Sigler and Csepp 2007). Following methods described in Sigler and Csepp (2007), we calculated and applied extinction values for each stratum independently. The overall extinction coef-

ficient of 0.97 ± 0.27 was similar to that presented by Sigler and Csepp (2007; 0.94 ± 0.16). Additionally, the mean correction factor applied to adjust acoustic data for effects of extinction (1.78 ± 0.31) was comparable, relative to 1.21 and 1.07 for Ona (2003) and Sigler and Csepp (2007), respectively. Acoustic backscatter data were adjusted (s_{a_ADJ}) following the extinction correction methods. Density estimates were derived by scaling measured acoustic intensity by target strength (TS) values calculated with fish lengths from direct capture methods. Given the effect of depth on TS of herring (Ona 2003; Thomas et al. 2002), we adopted the depth-dependent TS relationship for herring developed by Ona (2003), as

it allowed for greater variation in fish school depth relative to those estimated from Thomas et al. (2002):

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

where L is mean fork length (cm) and Z is mean water depth (m). Following TS calculations, areal estimates of fish density number (number of fish·m⁻²) were derived from the adjusted s_{a_ADJ} values within each elementary sampling distance unit (MacLennan et al. 2002):

(2) $Fish\ density\ (no.\ of\ fish \cdot m^{-2}) = s_{a\_ADJ}/10^{(TS/10)}$

Areal biomass (g·m⁻²) was calculated as the product of fish density and a length–mass relationship derived from herring captured during the study period:

(3) $Mass\ (g) = 8.0\ e^{-7} \cdot L^{3.48}$

where L is fish fork length (cm), and mass is expressed in grams. Total biomass per strata was extrapolated through the product of areal biomass and strata area.

Herring collections

Herring were collected from overwintering schools that were located and identified during acoustic surveys along the transect lines. Collections occurred periodically during each survey to confirm species identification and composition observed in acoustic data and to obtain length frequency distributions and length–mass relationships (Table 1). Herring were collected from multiple schools and strata during each collection period to account for potential size partitioning by habitat. Fish were collected with a mid-water herring rope trawl (Research Nets Inc., Redmond, Washington) towed at approximately 3 knots (1 knot = 1.852 km·h⁻¹) that had a 3.0 m deep by 6.1 m wide opening, with a 0.6 cm mesh cod end liner and 1.5 m² alloy doors. Trawl tow duration was adjusted as necessary to ensure adequate catches for species identification and length frequency samples. Herring fork lengths were measured aboard the vessel, and individual masses were measured upon return to the laboratory.

Whale surveys

Monthly humpback whale abundance was estimated during day-long surveys with a small vessel (<8 m) in Lynn Canal, during the same period for both years of the study, occurring within the same strata as the acoustic surveys, and also following a transect design. To examine abundance patterns of humpback whales in the vicinity of herring schools, whale position data (including group size, whale activity (feeding, milling, resting, surface active, or traveling), prey type (using prey remains, visual observations, scat and acoustic scattering patterns of aggregated prey), and prey depth (estimated from the vessel-based echosounder: Furuno 50 and 200 kHz)) were recorded. We used the unique marking patterns on the ventral side of humpback whale flukes to identify individual whales and maintained photographic records for each individual (Katona et al. 1979). Digital images were collected with Nikon D-300, D-200, and D-70 cameras with a 80–200 mm telephoto lens, and photographs were ranked as good, fair, poor, or of insufficient quality following Straley et al. (2009). Photographs of individuals deemed to be poor or of insufficient quality were specifically excluded from the mark–recapture analysis (described below) to avoid potential bias from matching errors; however, those whales were still included in the total tally of observations. Further, photographs of humpback whale calves were also excluded, because the capture probability for calves is complicated by their co-occurrence with their mothers (and is therefore not

independent), and the probability of recapture in later years can be difficult, as calf flukes tend to change more than adult flukes (Teerlink et al. 2015).

Combining the number of unique individuals (i.e., confirmed identities from photographs) observed in each month, we determined the minimum number of whales present over the course of each winter, which serves as a conservative estimate of total whale abundance. Whale abundance was estimated using a mark–recapture method with the Huggins closed-capture model (Huggins 1989, 1991). All modeling was done in program MARK (White and Burnham 1999). The closed-capture modeling setting was used to directly estimate abundance in each area. Models were structured to consider the population closed during the survey season only. The Huggins-style closed-capture model was chosen because it distinguishes "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 season for a particular area, and it is important that gaps in survey effort are not treated as an absence in humpback whales. The Huggins model estimates account for whales not seen during surveys; hence, it represents an upper limit to the number of whales present. Closed models are generally considered to be robust to variable capture probabilities and permit the estimation of important demographic parameters, namely abundance (Kendall 1999). Further, closed population estimates are based on fewer parameters than open models and can provide more precise estimates of total numbers (White et al. 1982). While open models are robust to estimating critical demographic parameters (i.e., survival, capture probability), in this study we were interested in computing a conservative estimate of abundance. While in Lynn Canal, humpback whales commonly display fidelity to feeding areas; thus, over the relatively short temporal scales of these observations, emigration, immigration, and mortality could be considered negligible (Pollock 1991).
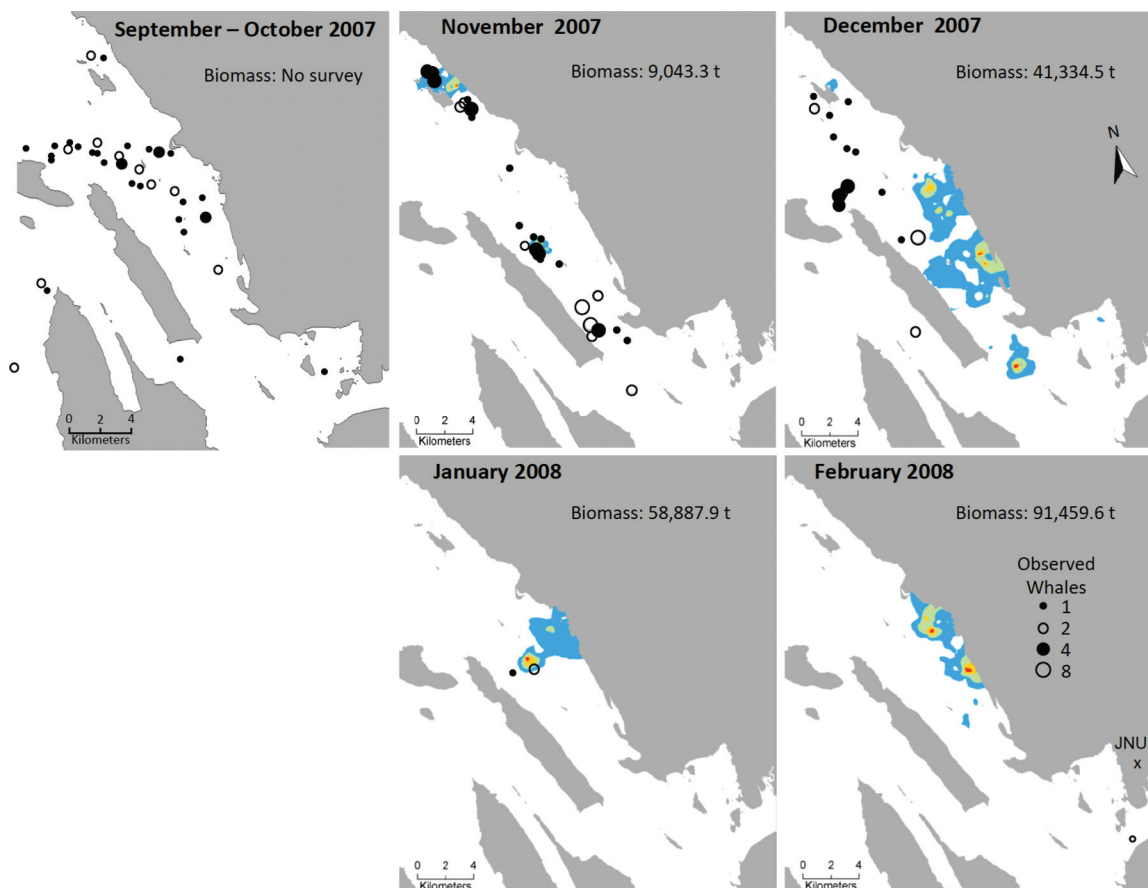
Estimates of the number of unique whales generated from mark–recapture modeling were used to derive an index of whale abundance (hereinafter referred as whale days), which was derived as the cumulative number of whales present on each day summed throughout a month (Rice et al. 2011). Rather than reporting winter trends in whale abundance, we report whale days, which is more representative of the monthly predation pressure on Pacific herring.

Statistical analyses

We examined the spatial and temporal patterns of herring school distribution and morphology through a combination of spatial analysis, analysis of variance (ANOVA) procedures, and linear regressions. We used the inverse distance weighting (IDW) interpolation routine in the Spatial Analyst toolbox in ArcMap (version 9.3.1; ESRI, Redlands, California) to map the spatial distribution of herring density (see above for herring density estimation). To ensure adequate and equal sample size for interpolating herring density, we selected a variable radius to include 20 nearest neighbours in the IDW estimation for each time period. To further allow comparison of interpolated herring density, we selected a constant raster output grid cell size of 250 m × 250 m for all interpolations and time periods (Nye et al. 2009). To evaluate differences in herring density distributions across space and time, interpolations were binned into equal interval bins, each representing 10% of the density distribution for each month. Bins were assigned a colour and mapped to illustrate the spatial distribution contours of herring densities (see Figs. 2 and 3). Contour polygons representing the upper 90th percentile were extracted from interpolated densities to measure the geographic area corresponding to this bin to compare between months in each sampling year.

Many of the geometric morphological variables of interest were highly correlated ($r > 0.75\%$), and therefore, to reduce both dimensionality and address collinearity among variables, a principal component analysis (PCA) was conducted. A suite of morphological

Fig. 2. Winter distribution (2007–2008) of herring schools derived from inverse distance weighting (IDW) analysis. Colour map represents the spatial distribution contours of herring coded by the acoustic estimates of school density (red = area occupied by densities within the first 25%, orange = 50%, green = 90%, and blue = 95%). Total monthly biomass (tonnes) of herring estimated from acoustic surveys is provided for each month. Humpback whale abundance estimates are represented by graduated symbols.

Results

Herring length distributions

Herring lengths collected in Lynn Canal from trawl catches were composed of individuals ranging from 15.5 to 25.6 cm in length with overall mean (±SE) sizes of 19.3 ± 1.6 cm and 18.9 ± 1.1 cm for the winters of 2007–2008 and 2008–2009, respectively. Length-at-age relationships constructed from scale analysis for herring in Lynn Canal indicate that fish within this size range were age 3 to age 8 (Hebert 2013), thus predominantly adults occupying historical prespawning aggregation areas (Carlson 1980; Sigler and Csepp 2007).

Spatial distribution of herring schools

Acoustically derived estimates of Pacific herring biomass increased over the course of the winter, with the lowest biomass occurring during November and the greatest during February for both winters, with December and January being intermediate (Table 4). Coincident with increasing biomass was a broadening of the spatial distribution of herring and increase in school density (Figs. 2 and 3). During the onset of winter in both years, herring schools were distributed across a wide area (November and December) and settled into denser schools (smaller geographic areas) along the eastern margin of the channel (January and February). The geographic area occupied by herring (90th percentile contour) increased by more than a factor of five through the progression of both winters (3.5-fold increase and 14.5-fold increase) for 2007–2008 and 2008–2009, respectively (Figs. 2 and 3). In November 2007, herring schools occupied 121.7 ha (90th percentile

variables (Table 3) was examined in a PCA, and the first two components (explaining greater than 90% of the total variance) were retained and further used to describe the variation in school morphology. Morphological variables and s_a had highly skewed distributions and were therefore $\log_{10}$-transformed prior to analysis. Initially, a mixed effects model was employed to examine the dependency of s_a relative to school morphological variables, with strata included as a random effect to control for spatial variation in herring school distributions. The random effect was later removed for lack of significance and in favour of a more parsimonious model with s_a (m²·m⁻²) as the response variable in a generalized linear model ANOVA (Proc GLM; SAS version 9.3) against whale abundance (whale days) and the principal components (Lemoine et al. 2013). Thus, an ANOVA with a generalized linear model (GLM) was chosen, with each year being analyzed separately to accommodate variation observed in the abundance patterns of whales. Variation in school depth was examined using a GLM, again run separately for each year. The effect of whale abundance (whale days) was examined as an explanatory variable against herring school depth using a GLM, with each year being analyzed separately. Finally, monthly acoustic estimates of herring biomass (tonnes; Table 4) were examined relative to whale abundance ($\log_{10}$ whale days) with linear regression. All statistical tests were considered significant at $\alpha = 0.05$. Results from GLMs are presented following standard nomenclature, including F statistic with factor and model error degrees of freedom; means and standard error are presented from pairwise comparisons, and model significance and variance explained (i.e., r^2) are provided for regression analyses.

Fig. 3. Winter distribution (2008–2009) of herring schools derived from IDW analysis. Colour map represents the spatial distribution contours of herring coded by the acoustic estimates of school density (red = area occupied by densities within the first 25%, orange = 50%, green = 90%, and blue = 95%). Total monthly biomass (tonnes) of herring estimated from acoustic surveys is provided for each month. Humpback whale abundance estimates are represented by graduated symbols.

Table 3. Results of the principal components analysis (PCA) grouping herring school morphological variables into two main principal components: PC1 = broad school shape (area, perimeter, height, and perimeter) and PC2 = image compactness.

	2007–2008		2008–2009	
Variable	PC1	PC2	PC1	PC2
Image compactness	0.12	*0.99*	0.01	*0.97*
Area	*0.98*	0.15	*0.99*	0.08
Height	*0.90*	0.04	*0.89*	−0.27
Length	*0.89*	0.20	*0.83*	0.36
Perimeter	*0.88*	0.47	*0.89*	0.46
Volume	*0.99*	0.10	*0.99*	−0.07
Eigenvalue	4.64	0.98	4.32	1.29
Variance (%)	77.4	16.3	72.1	21.4
Total variance explained (%)	93.7		93.5	

Note: Loadings, eigenvalues, and variance are provided for the two dominant components. Principal component loadings in italics represent major contributions by variables to components.

contour) and increased to 427.0 ha by February 2008. While not as extensive, herring schools occupied 27.8 ha (90th percentile contour) during November 2008 and increased to 402.3 ha by February 2009.

School distributions in the water column

As the spatial extent of herring schools shifted, so too did their position within the water column. Vertical position of detected

Table 4. Winter Pacific herring biomass (tonnes) and "whale days", a cumulative index of humpback whale abundance in Lynn Canal.

Year	Month	Tonnes	SE	Whale days
2007–2008	November	9 043	1 268	690
	December	41 335	2 891	697
	January	58 888	—	134
	February	91 460	14 286	0.0
2008–2009	November	14 560	513	394
	December	34 671	1 712	242
	January	16 828	1 473	151
	February	39 599	3 329	58

Note: During January 2008, herring were only observed in one stratum; therefore, error estimates are not available.

fish schools was strongly correlated with water depth in both years (2007–2008: $F_{[1,239]}$ = 189.77; b_1: 0.87 ± 0.058; 2008–2009: $F_{[1,205]}$ = 212.81; b_1: 0.47 ± 0.1) and increased to deeper depths as winter progressed (Fig. 4). Schools moved from shallower depths in November (2007–2008: 72.8 m; 2008–2009: 70.6 m) to the deepest areas in February (2007–2008: 102.0 m; 2008–2009: 113.21 m; Fig. 5). Variation in school depth relative to water depth was examined for consistency in herring behaviour between years and accounted for greater than 75% of the observed variance, suggesting that as winter progressed in both years, herring schools moved into deeper waters.

Fig. 4. Vertical distribution of herring schools (filled symbols) relative to the mean depth of the water column (open symbols) in which they were detected during the winter season in both years 2007–2008 (left panel) and 2008–2009 (right panel).
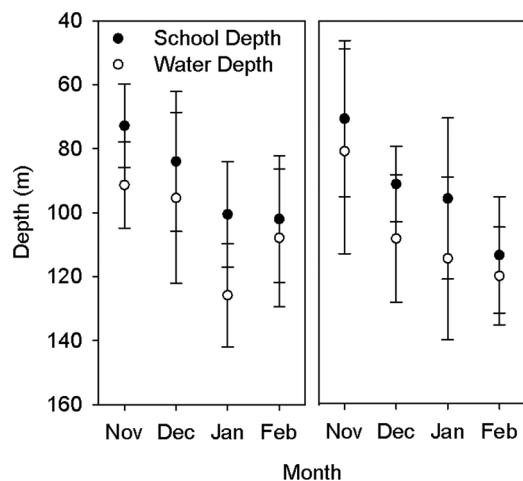
School morphology and density

PCA of the geometric and morphological variables describing herring schools indicated high covariance among the selected variables. Variables with a loading greater than 0.50 were considered to contribute to a PC. The first PC accounted for the majority of the variation explained among variables (2007–2008: 72.1%; 2008–2009: 77.4%), describing the size of herring schools and contained school area, height, length, perimeter, and volume (Table 3). The second PC represented the shape of the schools (2007–2008: 16%; 2008–2009: 21%). Together the two PCs accounted for greater than 93% of the total observed variance, regardless of year. Thus, the PCA was a robust method for reducing the dimensionality used in the linear models while maintaining the informational value of the shape variables.

Results from the GLM indicated that herring school density (s_a) was significantly and inversely related to whale abundance (whale days) and positively related to both PCs in both years (2007–2008: $r^2 = 0.40$, $F_{[3,236]}$, $p < 0.001$; 2008–2009: $r^2 = 0.64$, $F_{[3,202]}$, $p < 0.001$; Table 5). Between the 2 years, s_a increased throughout the progression of winter during both years (Fig. 6), with the 2007–2008 season being characterized, on average, by schools approximately 2.7 times more dense ($1.2 \times 10^{-3} \pm 7.9 \times 10^{-4}$ m²·m⁻²) than 2008–2009 ($4.5 \times 10^{-5} \pm 4.1 \times 10^{-5}$ m²·m⁻²). Interannual variability in school density was consistent (i.e., increasing through winter) albeit with differences in magnitude between years.

Temporal variation in whale abundance and foraging activity

During the winter months, comprising a total of 181 h of surveying (2007–2008: 117 h; 2008–2009: 64 h), 174 whale encounters were tallied, comprising individuals and groups. Of these, 48 individual whales were successfully photo-identified across both winters. Whale group size ranged from 1 to 11 animals, with a mean of 1.8 (SD = 1.4). Based on positive photo-identification, the Huggins closed-capture models estimated 51.6 whales (SE = 6.4, 95% confidence interval 47.4–57.5) for the first year and 35.4 whales (SE = 8.7, 95% confidence interval 30.7–42.5) for the second year. Whale numbers peaked in September during the first year and in October during the second year, prior to the acoustic survey period and before herring moved into the study area (Rice et al. 2011). Monthly estimates of whale days decreased as expected over both winters as whales departed the area, although the magnitude of whale days and the rates of departure were different

(Table 4). In the winter of 2007–2008, whale days were nearly double that of 2008–2009 within the surveyed area in Lynn Canal (Fig. 7). Though whales were more numerous in 2007–2008, they had completely departed the area by February. In contrast, whales lingered into February during 2008–2009.

Of the 174 whale observations, 91 (52.3%) were approached close enough and for sufficient duration to evaluate their activities. Among those, 73 (80.2%) were classified as actively feeding, while 18 (19.8%) were observed performing other activities (e.g., traveling, milling, and surface activity). Targeted prey items were identified in 57 observations. Of these, herring comprised the majority (86.0%) of the targeted prey items. In the remaining cases, unidentified fish species (which may include herring) were noted based on observation of scales floating on the water surface (10.5%), in addition to zooplankton (predominantly euphausiids) that were observed 3.5% of the time.

Relationship of whale abundance and herring biomass and distribution

Whale abundance estimates ($\log_{10}$ whale days) were significantly and negatively related to herring biomass estimates across both years ($p = 0.003$, $r^2 = 0.50$; $b_1 = -3.0 \times 10^{-5} \pm 8.28 \times 10^{-6}$). Similarly, within each year, as whale abundance decreased, herring biomass increased significantly (2007–2008: $p = 0.003$, $r^2 = 0.74$; $b_1 = -4.11 \times 10^{-5} \pm 9.28 \times 10^{-6}$; 2008–2009: $p = 0.042$, $r^2 = 0.68$; $b_1 = -2.44 \times 10^{-5} \pm 8.31 \times 10^{-6}$). A significant negative linear relationship was observed between whale abundance and mean herring school depth and was consistent across both winters (Fig. 7b). When examined separately by year, a negative linear trend was also observed among herring school depth distributions and whale abundance estimates, indicating increasing school depth with decreasing whale abundance through the progression of winter.

Oceanographic properties of the water column

Salinity and temperature were stable through the water column, with well-mixed conditions and low overall variation in vertical profiles from conductivity–temperature–depth casts (Table 6). Conditions were generally consistent through the winter, with salinity varying by less than 2 psu during both winters. Similarly, temperature varied slightly through the water column (<3 °C), with warmest temperatures observed during November (2007–2008: 6.69 ± 0.14 °C, 2008–2009: 6.20 ± 0.26 °C) and coldest temperatures in either February (2007–2008: 3.96 ± 0.05 °C) or January (3.79 ± 0.49 °C).

Discussion

The results of this study reveal a shift in herring school distribution, morphology, and biomass along with simultaneous decreases in whale abundance through the progression of both winters in Lynn Canal. When whale abundance was high during early winter, Pacific herring formed diffuse, pelagic schools spread over a relatively large geographic area. As winter developed, school morphology shifted and density increased as herring moved deeper into the water column, following the departure of foraging humpback whales. Our results also demonstrate that whale abundance and herring biomass estimates were strongly and inversely related, irrespective of year. We found that the progressive departure of humpback whales from Lynn Canal corresponded to shifts toward deeper water where they formed dense overwintering schools, potentially seeking refugia (Mackinson 1999). By examining the possible explanations for the observed changes in overwintering herring distribution and schooling dynamics, and focusing on the main potential factors (energetics, feeding activity, and predator avoidance) ascribed to these patterns, it is plausible that the presence of humpback whales may be responsible for the delay in the formation of deep, dense schools. Accordingly, schooling patterns observed in Lynn Canal overwintering herring may reflect a response to predator activity.

Fig. 5. Example echograms of herring distributions observed at 38 kHz during winter months (November: A and B; February: C and D) in Lynn Canal, Alaska. Depth intervals are displayed at 50 m increments, and horizontal cells are separated by 0.1 nautical mile (1 n.mi. = 1.852 km). The green line represents the bottom detection.
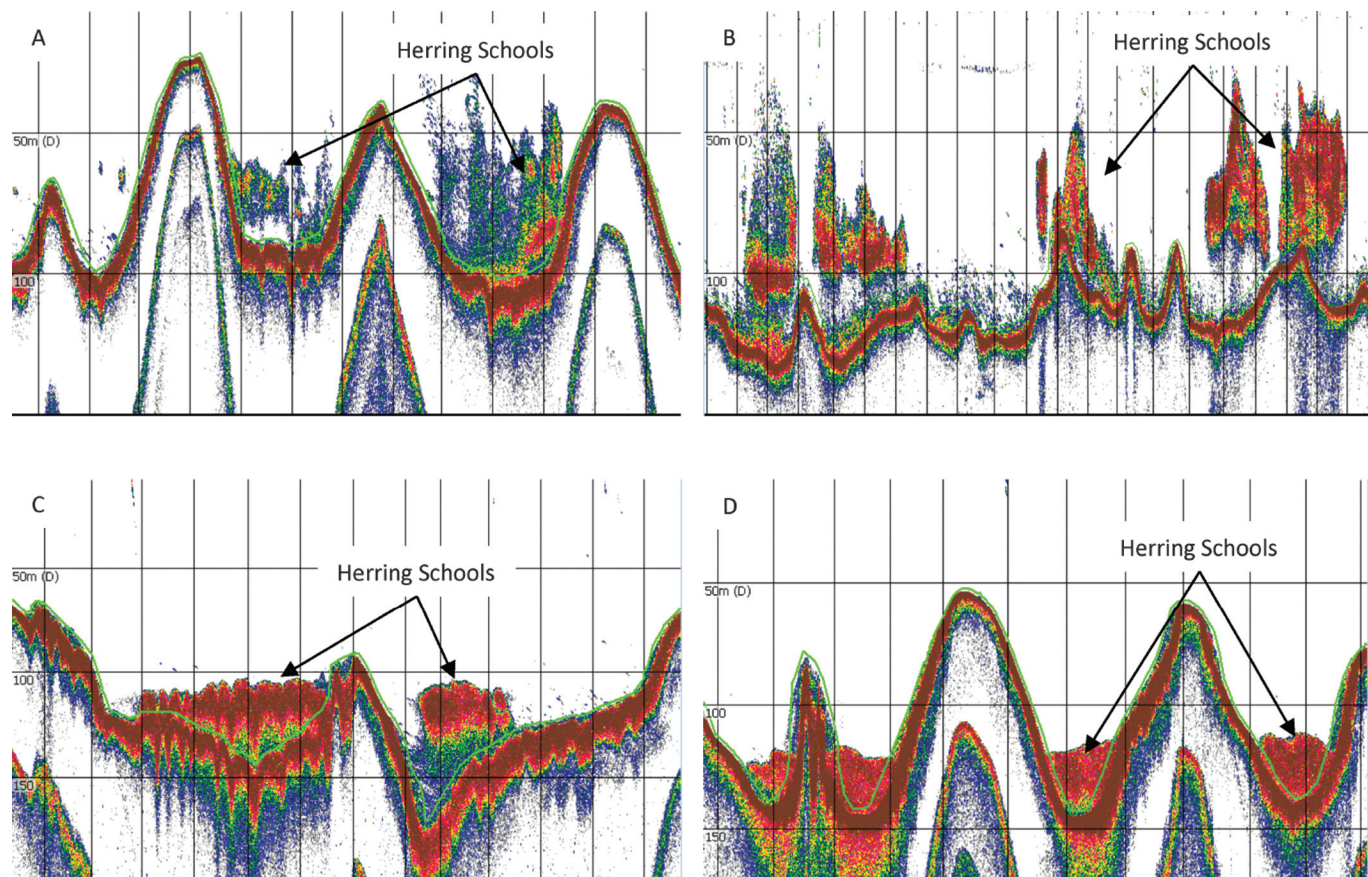

Table 5. Results of generalized linear model investigating the effects of whale abundance and morphological variation on herring school density, $\log_{10}s_a$, for both winter periods surveyed.

| Variable	2007–2008					2008–2009				
	df	F	P	C	SE	df	F	P	C	SE
Whale abundance	1,236	4.69	0.031	−0.058	0.027	1,202	4.33	0.037	−0.24	0.11
PC1	1,236	56.78	<0.001	0.030	0.04	1,202	8.33	<0.001	0.10	0.033
PC2	1,236	100.14	<0.001	0.030	0.04	1,202	325.66	<0.001	0.57	0.031

Note: Principal components 1 and 2 represent variables describing school morphology (refer to Table 4). Whale abundance is derived from mark–recapture model populated by unique identification of humpback whales. Summary statistics include degrees of freedom (df; model, error), F statistic, P value, parameter coefficient (C), and standard error (SE).

Energy conservation is particularly important during winter when feeding opportunities are diminished, yet herring coincidentally incur large energetic demands in preparation for spring spawning. Herring are zooplanktivores and substantially reduce feeding in the winter as a result of decreased food availability (Wing and Reid 1964) while simultaneously provisioning their gonads in preparation for spring spawning. Herring do not normally feed before spawning, but start shortly afterwards (e.g., Huse and Ona 1996; Slotte 1999; Johnsen and Skaret 2008), reflecting a change in fitness trade-off favouring reproductive activity over feeding activity (Nøttestad et al. 1996; Axelsen et al. 2000). Gut content analysis from Lynn Canal indicates that herring feeding is largely negligible during winter months (gut fullness: 0.0%–0.03% wet mass; n = 44; J. Vollenweider unpublished data), while during this period, herring condition significantly decreases with losses up to 66% of lipid and 50% of total energy content owing to the cessation of feeding and concurrent energetic demands of maturation (Slotte 1999; Vollenweider et al. 2011). Further, to date

no studies have reported evidence of differential mortality among age-classes of prespawning Pacific herring in Lynn Canal; thus, the ages 3–8 herring observed in this study are likely subjected to the same energetic and predation pressures. In nonfeeding schools, herring are relaxed from intraspecific competition for food, a situation favouring the formation of large, tightly bound schools (Nøttestad and Axelsen 1999; Rieucau et al. 2015a). Thus, during the overwintering period when whale predation is focused on large, localized schools, herring in Lynn Canal are not yet faced with the additional energetic trade-offs associated with balancing foraging and spawning activities.

In the winter, oceanographic characteristics of the water column in Lynn Canal, such as temperature, were found to be well-mixed and relatively homogeneous, suggesting that shifts observed in herring distributions during winter may not be mediated by access to thermal refuge (Røttingen et al. 1994; Clarke and Johnston 1999) or food availability (Wing and Reid 1964; J. Vollenweider, unpublished data). It is thought that the preferred morphological

Fig. 6. Mean (and standard errors) fish density (s_a) for both winters (2007–2008, filled symbols; 2008–2009, open symbols).
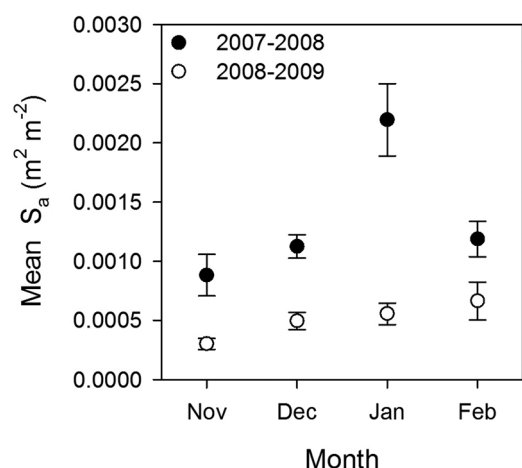
and structural configuration for overwintering herring schools is the formation of deep, densely packed schools, conferring energetic advantages during limited prey availability, as well as offering safety against surface-oriented predators where the trenches serve as spatial refugia for prespawning herring (Mackinson 1999). It is this deep, stable habitat that prespawning herring are known to occupy prior to the spawning season (Carlson 1980). As physostomes, herring must regulate their buoyancy by surfacing to refill their swim bladder. Though the depth at which fatty herring reach neutral buoyancy is controversial, 100 m has been suggested for overwintering Norwegian spring spawning herring (Huse and Ona 1996). Thus, the formation of large overwintering schools at depth may reduce metabolic demand, resulting in an optimal approach for overwintering survival and increased potential for maximizing reproductive investment.

Formation of large, densely packed schools at depth may be a defense against many of herring's predators that are present throughout the winter where increased packing density might favour more efficient collective evasions through an increased collective information transfer process (Handegard et al. 2012; Rieucau et al. 2014). For instance, recent research revealed that dense captive schools of Atlantic herring, with shorter interfish distances, performed stronger collective evasive reactions compared with schools of lower density (Rieucau et al. 2014). It is well understood that school formation enhances safety against predators that consume few fish per feeding event, such as seabirds, pinnipeds, and piscivorous fish. However, in Lynn Canal, herring did not form dense schools despite being in the presence of whales. While deep, dense schooling behaviour may be an effective antipredator defense against the majority of herring predators owing to several antipredator mechanisms, including risk dilution (Hamilton 1971; Pitcher and Parrish 1993), greater threat detection (Magurran et al. 1985), predator confusion (Ioannou et al. 2008), improved information transfer (Foster and Treherne 1981; Handegard et al. 2012), or coordinated evasive maneuvers (Pitcher and Wyche 1983; Nøttestad and Axelsen 1999; Nøttestad et al. 2002b), it may not be an effective strategy against humpback whales in this region where herring are unable to flee by diving deeper.

Response of herring to predators is known to vary with the type of predatory attack (Pitcher et al. 1996) and position in the water column. Overwintering Pacific herring in Lynn Canal are generally found in areas where the bathymetry restricts the lower limits of their depth distribution to approximately 150 m. By occupying deeper water, herring may avoid interactions with shallow-diving, surface-oriented predators (e.g., seabirds and pinnipeds). In particular, Steller sea lions (*Eumetopias jubatus*), which are abundant

in Lynn Canal during winter months (~800 individuals), pose major threats for herring (Womble and Sigler 2006). At deeper depths, predation pressure by piscivorous fish is expected to diminish over the course of winter as walleye pollock (*Gadus chalcogrammus*), Pacific hake (*Merluccius productus*), and arrowtooth flounder (*Atheresthes stomias*) move out of the area and into the Gulf of Alaska to spawn during winter (Csepp et al. 2011). Further, adult walleye pollock are most commonly found at depths ≥180 m, with Pacific hake being often much deeper (≥250 m) (Csepp et al. 2011). Over much of our study area, water depths were too shallow for adult walleye pollock and hake to access their optimal depth ranges and are therefore found in low numbers, if at all, throughout our study area (Sigler and Csepp 2007). Moreover, cold temperatures, such as those encountered in Lynn Canal during winter, have been linked to decreasing foraging activity of predatory groundfish (Stoner et al. 2006). Thus, under most circumstances, herring would be expected to form deep, dense schools where predation pressure is presumably reduced.

During the early part of winter, and despite the abundance of whales and other predators, herring biomass accumulated and schools occupied shallower water. Delayed school formation is not likely due to feeding (Wing and Reid 1964) and appears contrary to the need to avoid surface-oriented predators or minimize energy loss. Surface-oriented predators are highly abundant, particularly Steller sea lions, which optimize their foraging strategies at relatively shallow depths (~50 m) where herring appear to be distributed and in high abundance during the early winter periods (Womble and Sigler 2006; Womble et al. 2009). In contrast, humpback whales routinely forage at depth ranges of 100–300 m (Herman et al. 2007; Witteveen et al. 2008), consuming large numbers of herring in a single event, and can therefore be effective at forcing herring into the upper water column; consequently, herring are not able to find refuge from humpback whale foraging bouts within Lynn Canal.

Despite the obvious differences in foraging methods between odontocetes and mysticetes, with killer whales (*Orcinus orca*) consuming only several individuals per attack while humpback whales are capable of consuming large quantities of herring in a single strike, disruption of deep herring schools appears to be beneficial to both. By herding herring closer to the surface, whales can make shorter dives and consequently optimize their diving energy expenditures with energy consumed. Another potential benefit of shallower feeding could be greater light for visual feeding as posited by Carlson (1980). Overwintering herring are known to school below illuminated depths to avoid predominantly visual predators (Blaxter and Hunter 1982). Humpback whales may also be attracted to large schools within their diving range because such schools would reduce the energy spent searching for and obtaining prey and thus ensure greater capture rate per attack. Thus, if humpback whales are capable of redistributing herring into the water column, they may be an important contributing factor responsible for structuring the schooling dynamics of overwintering herring in Lynn Canal and may further explain why herring consolidate into deeper schools following the departure of humpback whales.

It would be interesting in future studies to test whether, by disrupting the formation of deep overwintering schools, foraging humpback whales may also facilitate opportunistic predation by Steller sea lions, seabirds, and other pelagic predators for which the deep overwintering herring schools would otherwise be relatively inaccessible. Tagging studies of adult female Steller sea lions in Lynn Canal indicate that 80% of their dives are to depths less than 100 m (B. Fadely and M. Lander, NOAA Alaska Fisheries Science Center, USA, personal communication) and show a strong mode at depths of 50–74 m in November and December (2009), coincident with herring depths observed during whale disruptions. Further, sea lion presence was positively correlated to the presence of large herring schools, particularly during peak over-

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Fig. 7. Monthly whale abundance (A) during winter months. Fitted regression between mean monthly herring school depth distribution and whale abundance (B) throughout the study period. Regression (solid line) and 95% confidence interval (broken lines) were fitted to monthly means. Number of observations for each mean are presented in brackets. Error bars represent standard error.
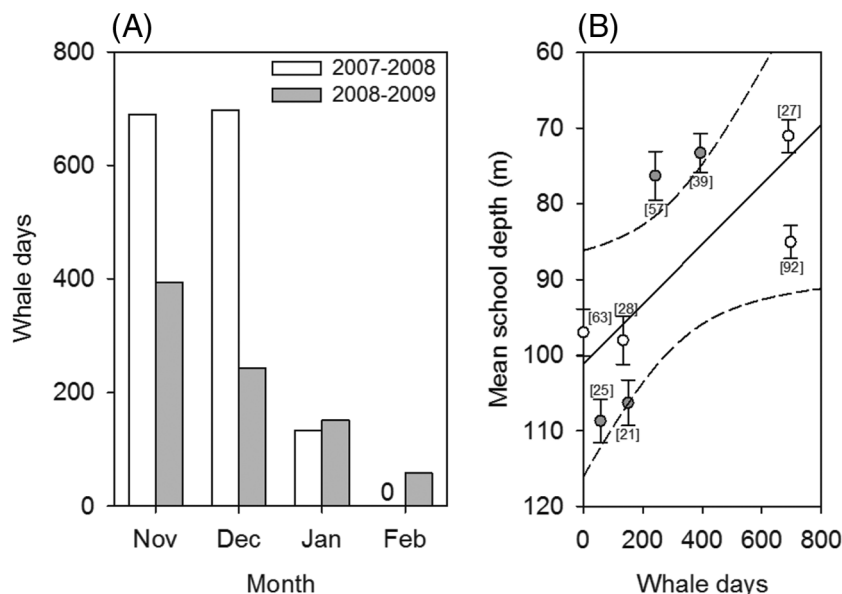

Table 6. Water column structure from conductivity–temperature–depth casts in Lynn Canal during winter months, including mean water column salinity (psu) and temperature (°C).

Month	2007–2008		2008–2009	
	Salinity	Temperature	Salinity	Temperature
November	30.90 (0.95)	6.69 (0.14)	30.40 (0.78)	6.20 (0.26)
December	31.34 (0.63)	5.67 (0.44)	29.86 (1.11)	5.24 (0.88)
January	31.47 (0.02)	4.74 (0.08)	31.71 (0.26)	3.79 (0.49)
February	31.46 (0.16)	3.96 (0.05)	31.20 (0.13)	4.12 (0.11)

Note: Standard deviations of means are presented in parentheses.

wintering months (January and February) (Womble and Sigler 2006; Sigler and Csepp 2007; Womble et al. 2009). Womble et al. (2009) reported herring as the most frequently occurring prey item identified in collected scat samples from sea lion haulouts in Lynn Canal during wintering periods. It is possible, then, that a commensal relationship among humpback whales and secondary predators exists during these winter periods.

Our study provides new insights on the capability of free-ranging schooling prey to assess temporal fluctuations in predation risk and respond accordingly. It is well accepted that aggregated prey achieve safety through grouping (the "safety-in-number" principle) from the interplay of several antipredator mechanisms (e.g., risk dilution, predator detection, and confusion). In addition, collective responsiveness and information transfer are also thought to be important mechanisms enhancing collective antipredatory responses for many grouping prey species, such as the synchronized collective escape reactions performed by large pelagic schools (Treherne and Foster 1981; Herbert-Read et al. 2011; Marras et al. 2012; Handegard et al. 2012). A school's internal organization (e.g., density, alignment between neighbouring fish) has been shown to play an important role in the efficient propagation of predator-related information among individuals enhancing the execution of rapid and coordinated collective reactions (Herbert-Read et al. 2011; Marras et al. 2012; Rieucau et al. 2014). Although collective responses towards predators are thought to yield an important adaptive advantage (Treherne and Foster 1981; Handegard et al. 2012), it remains unresolved whether the observed shifts at the school level (in particular the density and morphological changes) in Lynn Canal

overwintering herring, potentially related to changes in the abundance of top predators (whales), are aimed at promoting efficient collective responsiveness and information transfer among individuals. A recent mesocosm study has shown that captive schooling Atlantic herring are able to perceive local changes in predation risk, displaying stronger collective evasive reactions when exposed to playbacks of killer whale feeding calls (Rieucau et al. 2015b), demonstrating that risk awareness influences collective responsiveness. However, how schooling herring in Lynn Canal assess the level and nature of risk in their surroundings remains unknown. Recent advances in the application of acoustic technology will help to address the limitations present in our data by allowing the scale of focus to simultaneously span both the group- and individual-level responses associated with predator–prey interactions (Gerlotto et al. 2006; Handegard et al. 2012; Holmin et al. 2012; Holmin 2013; Rieucau et al. 2015b).

Answering this question will help understand how Pacific herring cope with fluctuating predation pressure in dynamic natural environments and unravel the selective pressures that have shaped the adaptive properties of large-scale pelagic schools. Moreover, this will provide relevant information to shed light on the processes that underlie the interactions between herring and their primary and secondary predators, as well as on structure food web dynamics in Lynn Canal.

Acknowledgements

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