

'Whale wave': shifting strategies structure the complex use of critical fjord habitat by humpbacks

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ABSTRACT: A decade of visual surveys (2005–2014) revealed that humpbacks *Megaptera novaeangliae* occupy a temperate fjord system in British Columbia, Canada, in a wave pattern that propagates from outer channels in the summer to deep inland channels in late fall. Monte Carlo randomization confirmed this apparent pattern statistically. 'Before' and 'after' shift phases were most evident in July and October, respectively. We hypothesized that the 'whale wave' was being driven by (1) prey following, (2) the tracking of environmental proxies, (3) fine-scale philopatry, or some combination of these three factors. To evaluate these hypotheses, we collected new data in 2015, including visual and hydroacoustic surveys and oceanographic sampling. To both full-season and monthly datasets, we fit generalized additive models (GAMs) in a stepwise procedure, using variable sets that represent our hypotheses. Prey models were generally the worst predictors of humpback distribution, while the most complex habitat models were the best. The Prey model performed best in June but increasingly poorly in remaining months. The performance of all models declined throughout the season, suggesting not only that this whale wave is being driven by needs other than food, but also that untested variable(s) inform late-season distribution. Alternative explanations of the wave include physiological maintenance and social habitat partitioning. Our findings demonstrate that marine predators can use complex spatial strategies not only to navigate vast areas of ocean but also to exploit specific habitats thoroughly. Though annually persistent and specific in structure, the whale wave would go (and has gone) unnoticed in typical marine mammal surveys.

KEY WORDS: Foraging ecology · Habitat use · Habitat modeling · Humpback whale · GAM · First Nation · Physiological maintenance

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INTRODUCTION

As the world's largest predators, the great whales must satisfy superlative energetic needs (Alexander 2005) during brief foraging seasons in which ephemeral prey patches are dispersed across vast areas. Foraging efficacy must be optimized, meaning habitat use must be strategic; cues about prey conditions must be tracked at nested spatial and temporal scales, from transoceanic migration to a single forag-

ing excursion (Ballance et al. 2006, Bailey et al. 2009, Hazen et al. 2009, Benoit-Bird et al. 2013). But whales are more than mouths; foraging must be balanced by other needs (e.g. reproductive, social, and health), and resource space must be navigated based on a combination of continuous habitat sampling (either directly or indirectly through proxies), recent experience (Mayo & Marx 1990, Fauchald 1999), and sheer habit (time-tested heuristics in behavior and distribution that maximize chances of resource

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access; e.g. philopatry). The balance of these strategies is likely species-, context-, and scale-specific (Fauchald 1999, Jaquet & Whitehead 1996, Anderwald et al. 2012). Habitat use is thus a dynamic amalgam of motivations (Manly et al. 2002) that is difficult but necessary to parse in order to identify and protect critical habitats (Bjorge 2001, Cañadas et al. 2005, Guisan & Thuller 2005). Without an understanding of underlying causes, researchers cannot advance beyond descriptions of spatial pattern to tractable accounts of habitat use that describe why a given habitat is important to a predator (Redfern et al. 2006).

The high dimensionality of habitat use is reflected in the prevalence of multivariate cetacean-habitat models. While prey metrics alone can strongly predict whale densities (e.g. Piatt & Methven 1992), many published models are improved by the inclusion of non-prey variables, such as fixed hydrographic data (e.g. seafloor depth) and dynamic water column data (e.g. chlorophyll *a* concentration) (Friedlaender et al. 2006, Benoit-Bird et al. 2013). Meanwhile, many have found significant results without including prey variables at all (e.g. Ferguson et al. 2006, Dalla Rosa et al. 2012, Bombosch et al. 2014). Environmental variables in these models are often assumed to serve as proxies for prey abundance and availability (Redfern et al. 2006), the underlying premise being that the processes and resources that govern prey distribution in turn govern that of whales (Croll et al. 2005). However, the relationships among explanatory variables in a system cannot be disaggregated when only some are sampled, and many of the relationships remain poorly understood (Pershing et al. 2009). Alternative explanations for the importance of non-prey variables, such as the thermal maintenance of epicutaneous algal growth (Boily 1995, Durban & Pitman 2012), are receiving increased attention for certain species. Ultimately, knowledge of which variables to include in a habitat model relies upon hypotheses about the relationships among variables that can only be inspired by close familiarity with the specifics of a system, including the prevalence and persistence of the spatial pattern in question.

Mobile predator habitat use is notoriously difficult to study amid the subtleties and expanse of the open ocean (Block et al. 2011), but equal and unique challenges are present in complex coastal habitats such as fjords. Compared to other coastal zones, fjords are seasonally productive, spatially complex, oceanographically dynamic, and economically valuable (Syvitski et al. 1987). As semi-closed systems in which oceanographic processes are relatively self-contained, fjords are also exciting venues for ecosystem research (Pearson 1989). Overall, they serve as intriguing foraging grounds for large whales (Ware et al. 2011), but the opportunity to study feeding whales in such habitats has only recently become possible as recovering populations in some areas return to pre-whaling coastal habitats.

Industrial whaling severely depleted humpbacks in the coastal fjords of British Columbia (BC), Canada (Ford 2014), but as the North Pacific population recovered, they began returning en force in the last 2 decades (Ashe et al. 2013). Here, we report on a decade of cetacean research within a northern

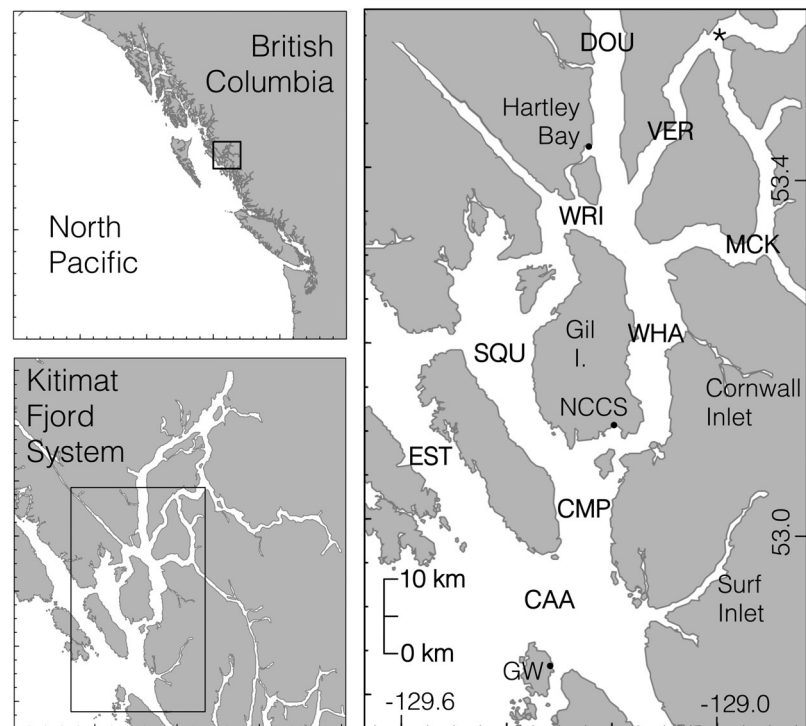


Fig. 1. Study area within the Kitimat Fjord System, within the Gitga'at First Nation territory in British Columbia, Canada. Asterisk (north VER) is treated as the entrance to Gardner Canal for Nearest Inlet variable and as the reference point for Ocean Distance measurements. Primary waterways: CAA: Caa-mano Sound; CMP: Campania Sound; DOU: Douglas Channel; EST: Estevan Sound; MCK: McKay Reach and Ursula Channel; SQU: Squally Channel; VER: Verney Pass; WHA: Whale Channel; WRI: Wright Sound. Research headquarters: NCCS: North Coast Cetacean Society; Hartley Bay: Gitga'at Cetacean Research Program; GW: Gitga'at Guardian Watchmen outcamp

BC fjord system (Fig. 1) proposed as critical habitat for humpback whales *Megaptera novaeangliae* and other marine mammal species (Ashe et al. 2013). Collectively, our sightings suggest that humpbacks occupy this fjord system in a kind of ‘wave’, in which high whale densities propagate from outer channels in summer to deep inner channels in the fall (Fig. 2). If this apparent pattern is real, the ‘whale wave’ would be a rare example of persistent, structured, and complex habitat use that would (1) be an exception to paradigms in the conservation of large marine predators and (2) likely go unnoticed and/or unvetted at the spatio-temporal coverage of typical marine mammal surveys which, given finite resources, tend to prioritize greater spatial range instead of repeated coverage of a restricted site. Furthermore, this novel habitat use strategy may lend insight into the importance of fjord systems to recovering whale populations in BC and elsewhere, as well as the converse: the whales’ ecological importance to fjords, both historical and potential.

Our objective in this study was first to verify the apparent spatial pattern statistically, then to determine the underlying driver(s) of the whale wave. To do so, we designed and launched a new oceanographic survey in 2015 designed to evaluate the following hypotheses of increasing habitat use complexity:

- (1) Prey: Humpbacks are strictly following their prey.
- (2) Proxy: Humpbacks are tracking environmental indicators of prey conditions or other habitat needs.

(3) Habit: Humpbacks are practicing a habit of habitat use, concentrating in certain portions of the fjord system at certain stages of the summer, akin to a fine-scale and timed philopatry.

(4) Prey + Proxy: Distribution is informed by both direct interactions with prey and the tracking of environmental indicators.

(5) Prey + Proxy + Habit: Distribution is informed by all 3 strategies.

MATERIALS AND METHODS

Study area

The study area (1961 km² of water) is located within the Kitimat Fjord System (KFS) of northern mainland BC, centered at 53° N and 129° W (Fig. 1). The KFS contains the marine territory of the Gitga’at First Nation, the confined channel portion of several proposed shipping lanes (e.g. Enbridge 2010), critical habitat for several endangered or threatened species, and Fisheries Management Area (FMA) 6 for the BC coast (Ashe et al. 2013).

This fjord complex extends 140 km inland from the Pacific Coast (Macdonald et al. 1983), nested within the Kitimat Ranges of the Great Bear Rainforest, the largest temperate coastal rainforest in the world (Thomson 1981). An uncommon attribute of this fjord system is its large islands that compartmentalize the fjord into a network of channels. These channels have a typical fjord morphology, with steep bedrock walls and relatively smooth sediment-floored basins separated by high-relief sills (Pickard 1961, Macdonald et al. 1983). Douglas Channel, Gardner Canal, and to a lesser extent Surf and Cornwall Inlets are the primary fjords that feed the system (Pickard 1961).

Spanning the coastal boundary between ocean and the coastal ranges, the KFS is characterized by strong offshore-inshore gradients in climate (Fissel et al. 2010), oceanographic properties (Macdonald et al. 1983), and intertidal ecology (Turner 2003). KFS waters are circulated by a combination of 3 processes: estuarine circulation (forced by freshwater discharge), wind forcing (e.g. katabatic outflows), and tides (Macdonald et al. 1983). The rela-

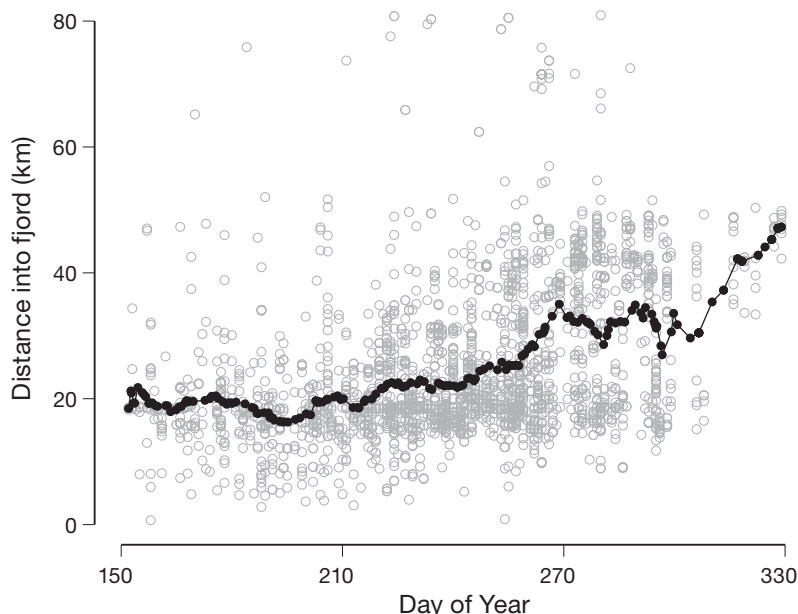


Fig. 2. As summer turns to fall (x-axis), humpback whale *Megaptera novaeangliae* sightings occur increasingly deeper into the Kitimat Fjord System (y-axis). Black line is the running 10 d mean of raw sightings (gray dots, $n = 2527$) from Gitga’at and North Coast Cetacean Society surveys 2004 to 2014

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tive importance of each varies according to location, season, and timescale. Water movements are further influenced by seasonal patterns and punctuated storm events on the adjacent shelf, which are strongest in autumn (Macdonald et al. 1983).

In the spring, seasonally resident humpback whales *Megaptera novaeangliae* migrate to the KFS from tropical Pacific breeding grounds, primarily Hawaii (Ashe et al. 2013). Most leave the KFS by late fall, though our field observations suggest that some individuals may overwinter in protected coastal waters of northern BC. During the summer, these humpbacks feed opportunistically upon euphausiids and small schooling fish. Local net tows indicate that dominant euphausiid species include *Euphausica pacifica*, *Thysanoessa spinifera*, *T. longipes*, and *Tessarabrachion oculatum*, and data on community dynamics are currently being prepared for publication (K. Qualls pers. comm.). Based on field observations and local traditional knowledge, fish prey include herring *Clupea harengus pacifica*, sand lance *Ammodytes hexapterus*, and various species of smelt (f. Osmeridae). In rare years, KFS humpbacks have been observed feeding upon sardine *Sardinops sagax caerulea* (J. Wray, H. Meuter, & C. Picard unpubl. data).

Visual surveys 2005–2014

Over the course of a decade, whale surveys were conducted an average of once per month by 2 collaborative research efforts: the Gitga'at Cetacean Monitoring Program and North Coast Cetacean Society (NCCS) study (Fig. 3), with some differences in methodology and spatial coverage.

Gitga'at surveys were conducted from either a 7 m or 9 m vessel. Nearly all surveys began in Hartley Bay and included the circumnavigation of Gribbell and Gil Islands (Fig. 3). The remainder of the survey route varied according to weather conditions and available daylight. Beginning in 2013, additional surveys focused on the outer channels (primarily Caamano Sound), launching from and ending at a remote outcamp (GW in Fig. 1). Survey routes were recorded manually using GPS. Average survey speed was 38 km h^{-1} .

NCCS surveys were conducted in non-winter months during good weather conditions with visibility greater than 3 nautical miles and sea state no greater than Beaufort 3. All surveys began from the south end of Gil Island (Fig. 3). Surveys were conducted aboard a 7 m vessel at an average speed of 28 km h^{-1} (in 2006,

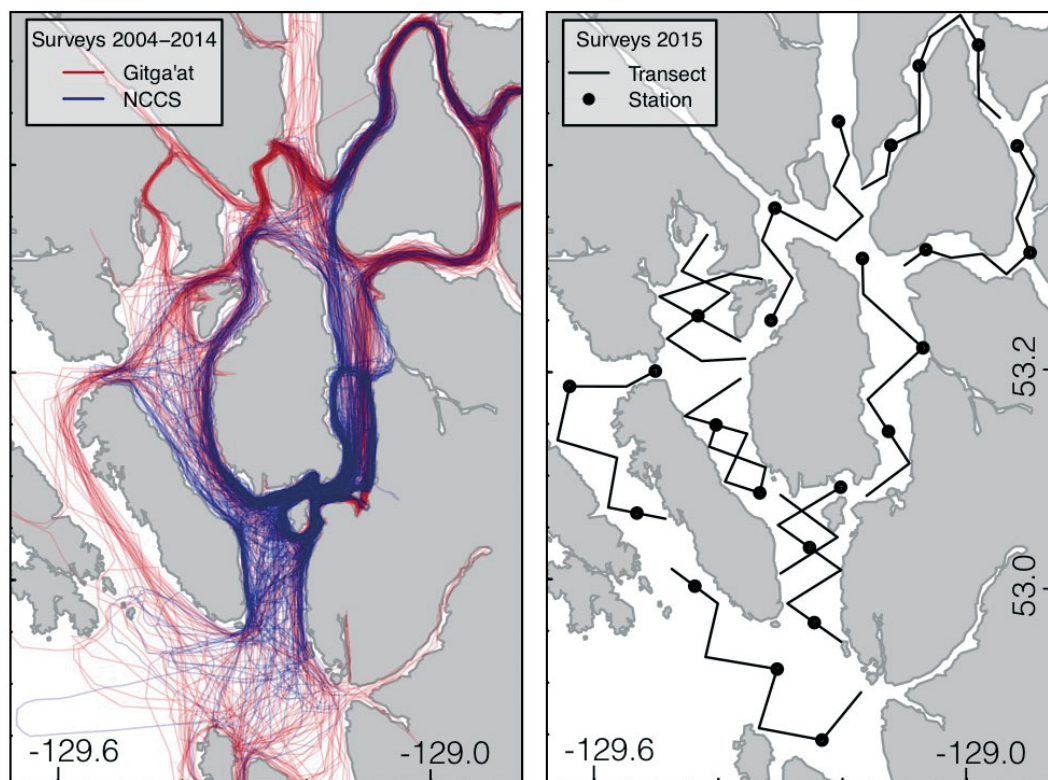


Fig. 3. Left: Survey effort by Gitga'at (red) and NCCS (blue), 2005 to 2014. Right: Sampling plan for 2015 vessel transects (lines) and oceanographic stations (filled circles) in 2015 aboard RV 'Bangarang'

a 8 m vessel was used at 12 km h⁻¹). Regular stops with the engine off were made to listen for blows.

On both platforms, 2 to 3 observers scanned for cues of whale presence such as blows, splashes, flukes, fins, or breaches. Groups were approached slowly in order to estimate group size and record behavior, and GPS location was recorded manually from the vessel's chartplotter. During each encounter, 1 observer would continue scanning for the presence of other whales. An encounter ended when notes on group size and behavior were complete, or within 30 min, at which point the survey would continue along the pre-determined route.

2015 survey efforts

May through September 2015, we conducted concurrent visual and oceanographic surveys aboard the RV 'Bangarang', a 12 m motorsailer with a survey speed of 5 knots, with a team of 3 researchers. We completed monthly surveys of the study area within a target duration of 20 d, during which we visited a grid of stations ($n = 24$), between which we conducted concurrent visual and acoustic transect surveys (Fig. 3).

Visual whale surveys. Monthly surveys were conducted using line-transect sampling methodology (Buckland et al. 2001). Bearing and reticle readings using Fujinon 7 × 50 binoculars, min-max-best group size estimates, and cue behaviors for each sighting were recorded by an observation team from a platform 2 m above sea level. At standard intervals observers rotated between 3 positions, one of which was data entry at the helm. Survey routes were recorded in a data entry software interfaced to a Garmin 441s GPS unit with an external antenna mounted atop the radar tower.

Hydroacoustic data. Hydroacoustic data were collected along survey tracklines with a down-sounding Syqwest Hydrobox echosounder (33 and 200 kHz dual-frequency) to obtain a profile map of the depth, distribution, and patchiness of backscatter down to 300 m, a range that encompasses the maximum dive recorded for humpback whales (Hamilton et al. 1997). The Supplement at www.int-res.com/articles/suppl/m567p211_supp.pdf provides details of echosounder data collection and processing. When odontocetes were seen, the echosounder was turned off to minimize disturbance.

Oceanography. We limited oceanographic variables for our habitat models to surface temperature, surface salinity, and maximum chl *a* concentrations

between the surface and 250 m depth. During transects, surface water temperature and salinity were sampled at 0.3 m depth every 2 s with a Seabird Electronics 45 thermosalinograph (TSG). At each station, we sampled chl *a* with a WetLabs ECO-FL fluorometer mounted to a SBE25plus CTD.

Analysis

Seasonal spatial pattern. A seasonal distribution shift is a pattern in both space and time. Observing it requires (1) the division of the study area into small geographic strata and (2) the division of the year into small temporal blocks. The fjord system is compartmentalized by islands and underwater sills that divide the fjord into discrete channels. We pooled survey effort within these channels into a total of 26 geographic strata in a scheme that balanced spatial resolution against the loss of statistical power with increased strata, making sure to compartmentalize high-effort areas (e.g. thoroughfares, entries to headquarters) from low-effort areas. We aimed for 2 to 4 strata per channel.

The area of viable humpback habitat within each stratum was calculated with a GIS (www.geojson.io) using local knowledge and our combined field experience. In this steep-walled fjord system, humpbacks are commonly seen accessing habitat up to and within the intertidal zones of the area's shoreline. We therefore defined the study area as the waters that humpbacks could easily access at all tides.

Tracks from Gitga'at and NCCS surveys were drawn in a GIS (same as above) based on waypoints and notes taken during the surveys. For each survey, effort (kilometers of trackline surveyed) and humpbacks seen were then totaled within each geographic stratum. Effort and whales were further pooled into monthly bins. From these datasets, humpback density in each month-stratum was calculated as the number of whales seen per kilometer of effort.

We used Monte Carlo randomization in R (R Development Core Team 2013) to test the null hypothesis that, within each geographic stratum, month-to-month differences in observed humpback density were due only to random chance. In effect, we ran 26 randomization tests, one per stratum. Randomization tests are a versatile, valid and relatively intuitive alternative to classical tests when data may not meet parametric assumptions (Manly 1991). Each stratum's randomization entailed 10 000 iterations of the following procedure. All humpbacks seen within a given stratum were totaled across all months and

years. These whales were then randomly redistributed amongst the months during which effort occurred. Redistributed sightings were divided by actual tracklength covered to arrive at a simulated null density for each month. After all iterations were complete, a distribution of null densities was available for each month-stratum. The observed density was then compared to the null distribution to infer statistical significance. The quantile of the null densities that corresponded to the observed density was interpreted as the likelihood that observed density equaled or surpassed that which would be expected by random chance.

Acoustic backscatter. Acoustic backscatter processing is detailed in the Supplement. In summary, the Syqwest Hydrobox outputs a pixelated representation of water column backscatter, where pixel value positively correlated with backscatter. These pixel data were georectified to account for variable vessel speed and were visually scrutinized to ensure all reflections attributable to seafloor, near-surface water bubbles, engine cavitation, sonars of passing ships, and whales were removed. To reduce each frequency further to display only backscatter of probable whale prey, we filtered data based on patch characteristics and overlapping frequencies so that, to the extent possible, 33 kHz backscatter represents small schooling fish, while 200 kHz backscatter represents euphausiids. Deepwater krill imaging and zooplankton tows were used to verify the efficacy of the 200 kHz backscatter processing methods.

Middle-priced echosounders like that used in this study can characterize prey-like backscatter but cannot quantify the biomass of constituent taxa. We developed 3 simple metrics for each filtered frequency, described below and depicted in Fig. S29 in the Supplement. These metrics were cross-checked pairwise for collinearity.

(1) Total backscatter (*T*): The mean sum of pixel values of prey-like backscatter; this is a proxy for the quantity of potential prey available.

(2) Backscatter intensity (*I*): The mean pixel value of prey-like backscatter; this is a proxy that can represent the school density, body size and composition, and/or patch characteristics of potential prey swarms.

(3) Vertical dispersion (*D*): The standard deviation of the depth distribution of prey-like backscatter; this is a proxy for the vertical extent of prey swarms; highly dispersed backscatter may be less ideal for batch-feeding predators such as rorqual whales.

Station interpolation. Within each survey month, chl *a* values from stations were interpolated for each transect centroid using inverse path-weighted dis-

tance, a function that linearly weights combinations of sampled points based on their distance from the interpolation cell, accounting for land obstruction (R package *ipdw*; Stachelek 2015). Interpolation was also used to fill the few gaps in TSG data that were the result of rare priming issues caused by air entering the plumbing during large swells.

Habitat modeling. We used generalized additive models (GAMs) to test for and elucidate relationships between humpbacks, potential prey metrics, and other environmental variables. The GAM is a modeling approach that relates observations (in our case, humpback counts) to predictor variables using non-linear link functions (smoothing or 'spline' functions) without imposing parametric limits on the data (Hastie & Tibshirani 1990). GAMs can accommodate highly nonlinear functional relationships (Zuur et al. 2009). GAMs were built using R package *mgcv* (Wood 2006). Poisson, quasi-Poisson, and negative binomial models were explored (with their default link functions) for modeling humpback counts along transects.

Monthly surveys were split into transects of approximately 5 km length ($n = 216$; after Hedley et al. 1999). This scale was sufficient to minimize autocorrelation between adjacent transects, include a sufficient percentage of humpback sightings, and maintain adequate sample size for modeling. Because the model families tested required us to model whale counts and not densities, the logarithm of transect length was included in models as an offset. An example model, in which humpback counts are modeled by total 200 kHz backscatter and dispersion, would appear as follows in R: `gam(formula = hw ~ offset(log(effort)) + s(T.hi) + s(I.hi), data = data, family = nb, gamma = 1.4)`.

We excluded our third survey (late July) because oceanographic data were not collected, and redundant transects in Squally and Campania were removed to equalize effort among all geographic blocks (Fig. 1). For each 5 km transect, TSG readings were averaged, backscatter metrics were derived, and chl *a* maxima (calculated from fluorescence using SBE laboratory calibrations) were taken from the interpolation cell containing the transect centroid. Whale positions were geo-located using binocular bearing and reticle readings from the observation platform (using R package *bangarang* [Keen 2016] which accounts for horizon obstruction in confined North Pacific channels), and their Euclidean distances to transect centroids were calculated (*swfscMisc*; Archer 2014). Humpbacks and effort (km trackline surveyed) were

totaled in a 2.5 km radius from the centroid of each transect.

We developed sets of candidate models that correspond to our 5 hypotheses (see ‘Introduction’). Prey, Proxy and Habit model candidates were based on non-overlapping sets of explanatory variables (Table 1) that are regularly included within cetacean-habitat models (Reilly 1990, Reilly & Fiedler 1994, Redfern et al. 2006). We developed 1 novel metric, distance to nearest inlet (Inlet), inspired by observations across years of humpback association with the fjord system’s 3 major freshwater inlets (Surf Inlet, Cornwall Inlet, and Gardner Canal; Fig. 1). These waters enter the fjord in tidally mediated flows that can become rapids at peak ebb. In late summer, humpbacks are regularly seen near or among these rapids (Fig. 4). Both Inlet and distance into fjord (Dist) were calculated in R as shortest-path travel routes between points in the Kitimat Fjord System, accounting for winding channels and island obstruction (Keen 2016).

Models for Prey + Proxy and Prey + Proxy + Habit hypotheses were built by pooling their constituent variable sets and adding bivariate interactions that combined variables from separate sets. For models that required position variables, both continuous and

categorical versions were trialed (Table 1). Categorical variables and bivariate interactions (e.g. Lat × Long) are penalized during model selection due to the degrees of freedom they require, but they may best capture the spatiotemporal trend of the wave. All continuous variables were tested for pairwise collinearity with a Pearson’s correlation coefficient cutoff of 0.5 (Zuur et al. 2009). We found that sea surface salinity (SSS) was correlated with distance into fjord and latitude (Pearson’s $r^2 = 0.71$). This reflects the inshore–offshore salinity gradient typical of fjord oceanography. Given the different motivations each variable represents, we kept all 3 variables (SSS, distance into fjord and latitude) and explored results with caution.

Models were evaluated based on the second-order Akaike information criterion (AICc), a metric for model comparison that, like its predecessor AIC, weighs negative-log likelihood against the number of parameters it invokes (Akaike 1974) but more heavily penalizes overfitting and provides bias correction for small sample sizes (Burnham & Anderson 2002). In doing so, AICc selects for models that capture central tendencies most parsimoniously and thus are more predictive than descriptive. Since AICc is a relative measure of fit with no standard scale, Akaike

Table 1. Explanatory variables used in habitat-use models. Model stages are enumerated: 1: Prey; 2: Proxy; 3: Prey + Proxy; 4: Habit; 5: Prey + Proxy + Habit. Each acoustic backscatter ‘Variable’ consists of 2 variables — one for each frequency (*H*: 200 kHz, *L*: 33 kHz). Variable types are continuous (Cont.) or categorical (Cat.)

Variable category	Variable	Symbol	Type	Models	Description
Acoustic backscatter	Total	T_H T_L	Cont.	1, 3, 5	Mean sum of water column pixel values
	Intensity	I_H I_L	Cont.	1, 3, 5	Mean pixel value
	Dispersion	D_H D_L	Cont.	1, 3, 5	Standard deviation of backscatter depth distribution (m)
Oceanography	Nearest inlet	Inlet	Cont.	2, 3, 5	Swimming distance (km) to nearest major inlet
	Sea surface temperature	SST	Cont.	2, 3, 5	Degrees Celsius (°C)
	Sea surface salinity	SSS	Cont.	2, 3, 5	Practical salinity units (psu)
	Chlorophyll <i>a</i> maximum	Chl	Cont.	2, 3, 5	Peak interpolated water column chlorophyll <i>a</i> concentration ($\mu\text{g ml}^{-1}$)
Position	Survey month	Month	Cat.	4, 5	4 levels: June, July, August, September
	Block	Blk	Cat.	4, 5	8 levels (see Fig. 1)
	Day of Year	Day	Cont.	4, 5	
	Position	Lat Long	Cont.	4, 5	Geospatial coordinates (dec. deg.)
	Distance into fjord	Dist	Cont.	4, 5	Swimming distance (km) from the furthest point inland

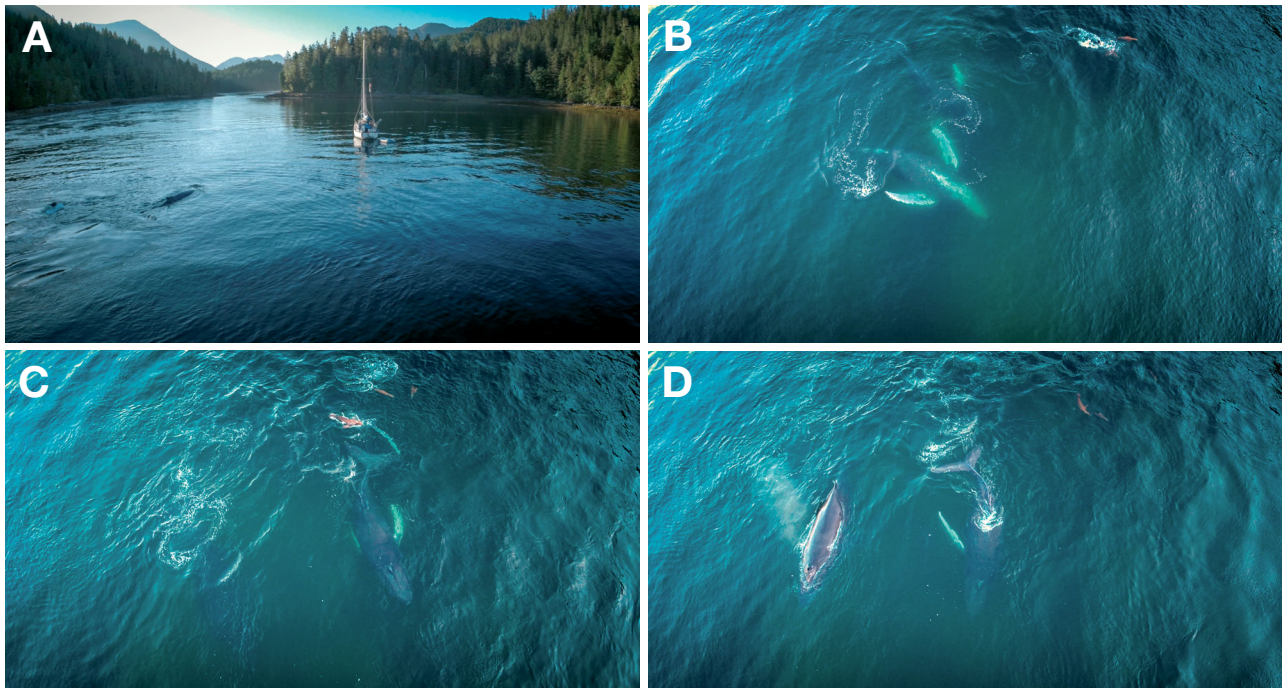


Fig. 4. (A) At peak ebb tide in late August 2015, humpback whales gather at the bottleneck entrance to a large freshwater inlet (Cornwall Inlet) in the study area. Ephemeral but dramatic tidal rapids develop at this site during ebb tides. Coincidentally moored in an adjacent cove just out of the tidal stream, we were able to document this pair and their associated Stellar's sea lions *Eumetopias jubatus* rollicking in the rapids (B) for >1 h, repeatedly practicing contortion maneuvers (C,D). Stills pulled from footage by Luke Padgett, available online at: <https://vimeo.com/154083846> (password: baleen)

weights (w) were also calculated within each model set to compare evidence ratios on a scale from 0 to 1, such that all w for a model set sum to 1 (Burnham & Anderson 2002). When ranked in decreasing order of w , the subset of models whose cumulative w is ≥ 0.95 is called the 95% confidence set. A large 95% set suggests that many variable combinations achieve the same level of parsimony and that there is no clear model choice (Symonds & Moussali 2011). When no single model is clearly the best fit, 95% confidence set is the most transparent way to report results (Symonds & Moussalli 2011).

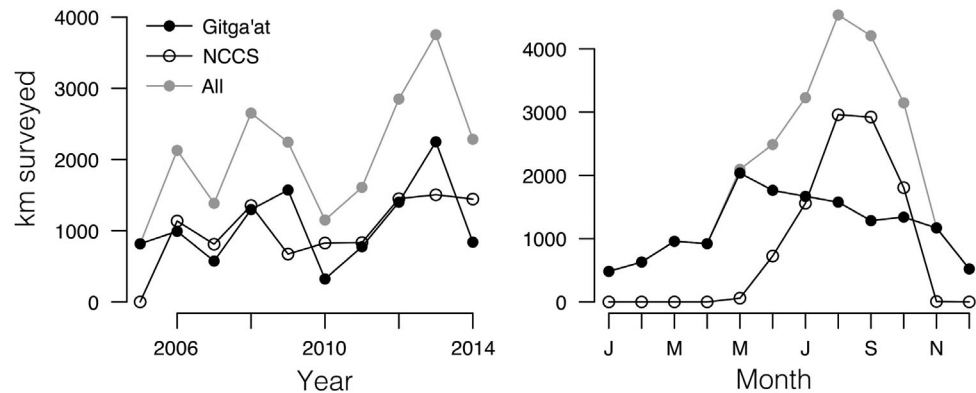
Where possible, we kept candidate model sets 'balanced', such that each variable within a set is used an equal number of times. Given equal representation, each variable's cumulative Akaike weight, summed across all models that include it, can be used as a metric of relative variable importance (RVI; Burnham & Anderson 2002). Interaction terms were not included in balanced sets.

Models were first fit to the full season dataset. Explanatory variables were normalized to a mean of zero, a transformation that preserves variable spread but improves model convergence and facilitates the comparison of effect sizes (Zuur et al. 2009). Proxy

variables (SST, SSS, Chl, Inlet) were normalized across the season, but we opted to normalize backscatter metrics within each month separately. Our rationale was that doing so would (1) reflect the fact that humpbacks are orientating themselves to the best prey conditions available and (2) clarify interpretation of results. We wished for our models to elucidate patterns in humpback habitat use rather than account for trends in explanatory variables.

Models were fit to individual months using the same sets of model candidates. Before fitting, all explanatory variables were normalized within each survey subset. Interaction terms were not used due to reduced sample size, and Day of Year was excluded from the Habit variable set. Prey, Proxy, and Prey + Proxy sets were balanced, and for these stages, we calculated RVI as above. To facilitate results exploration, RVI were also scaled by the most important variable, so that all RVI ranged between 0 and 1. AICc scores were calculated to determine these variable weights but were not used for model selection because AICc could not be compared across models based on different datasets (Burnham & Anderson 2002). Instead, we selected best models based upon minimum prediction error from leave-one-out cross validation, an iterative

Fig. 5. Survey effort (km) by Gitga'at and North Coast Cetacean Society (NCCS) platforms, 2004 to 2014. Left: Annual survey effort (June through November only). Right: Monthly survey effort



routine in which each datum ('test set') is excluded from the data used for model fitting ('training set'); its humpback count is then predicted with the training model (Hastie et al. 2009). The mean squared error (MSE) of predictions, scaled by the mean observation value to account for changes in local humpback abundance and/or group size, provides a metric of model performance across similar datasets (here, survey month), with lower MSE being better.

RESULTS

2005–2014 surveys

Gitga'at effort comprised 182 d spanning all 10 yr of the survey period. NCCS effort (beginning in 2006) comprised a total of 252 d. Effort was concentrated April to November, but occasional opportunistic trips occurred from December to March. In general, survey lengths for both platforms increased during summer months and in the latter years of the study decade (Fig. 5).

Between 2005 and 2014, NCCS and Gitga'at surveys found a total of 4783 humpbacks *Megaptera novaeangliae*. Pooled sightings from all years confirmed that, even after effort-corrected density estimation, the whale wave was strongly apparent (Fig. 6, top). Sightings and effort were also pooled into pairs of years, and spatially stratified density was mapped, confirming that the wave was an annually persistent phenomenon.

The Monte Carlo test found that results were non-random at the 5% significance level in most strata in most months (Fig. 6, bottom). The pattern was most evident in July and October. The test suggested that the move inland actually happens fairly abruptly between August and September. In general, the pattern was more uniformly significant in the interior channels to the northeast of Gil Island. In May, 13 of

14 geographic strata inland of Gil Island had lower observed humpback densities than was expected by random chance, 11 of which were lower than 95% of simulated densities. By September, all 14 strata had higher observed densities than 95% of random trials. The pattern was reversed in the outer channels: in July, 12 out of 13 outer strata had higher humpback densities than 95% of simulated densities, but by October, this number dropped to 3. Of the remaining outer strata, 9 had lower densities than expected by chance, and 5 of these were lower than 95% of simulated densities.

Statistical results broadly supported the existence of a wave of humpback density that propagates from outside to inside waters, but not uniformly so. Notable exceptions to the pattern include certain strata in central and outer waters. The strata at the bottom of Gil Island seemed to have unexpectedly high humpback densities in May, before other outer channels were populated, and onward into the fall when the other adjacent strata had already been cleared out. Based on our field experience, this area appears to be of special importance to resident humpbacks across seasons. Another stratum of interest is the most southeastern in the study area, the sector of Caamano Sound that abuts Laredo Sound and Surf Inlet (1 of the 3 large inlets feeding the fjord system). In all months, this stratum was exceptional, and the pattern coincides with local knowledge about late-fall cetacean activity at the mouth of Surf Inlet.

2015 survey

Visual survey. In 2015, the 5 vessel surveys covered a total of 1653 km of trackline in 5 surveys over 117 d (Table 2). On average, each survey covered 331 km (min. 320, max. 346) in 23 d (min. 16, max. 28). In total, 968 humpbacks were observed, 430 of

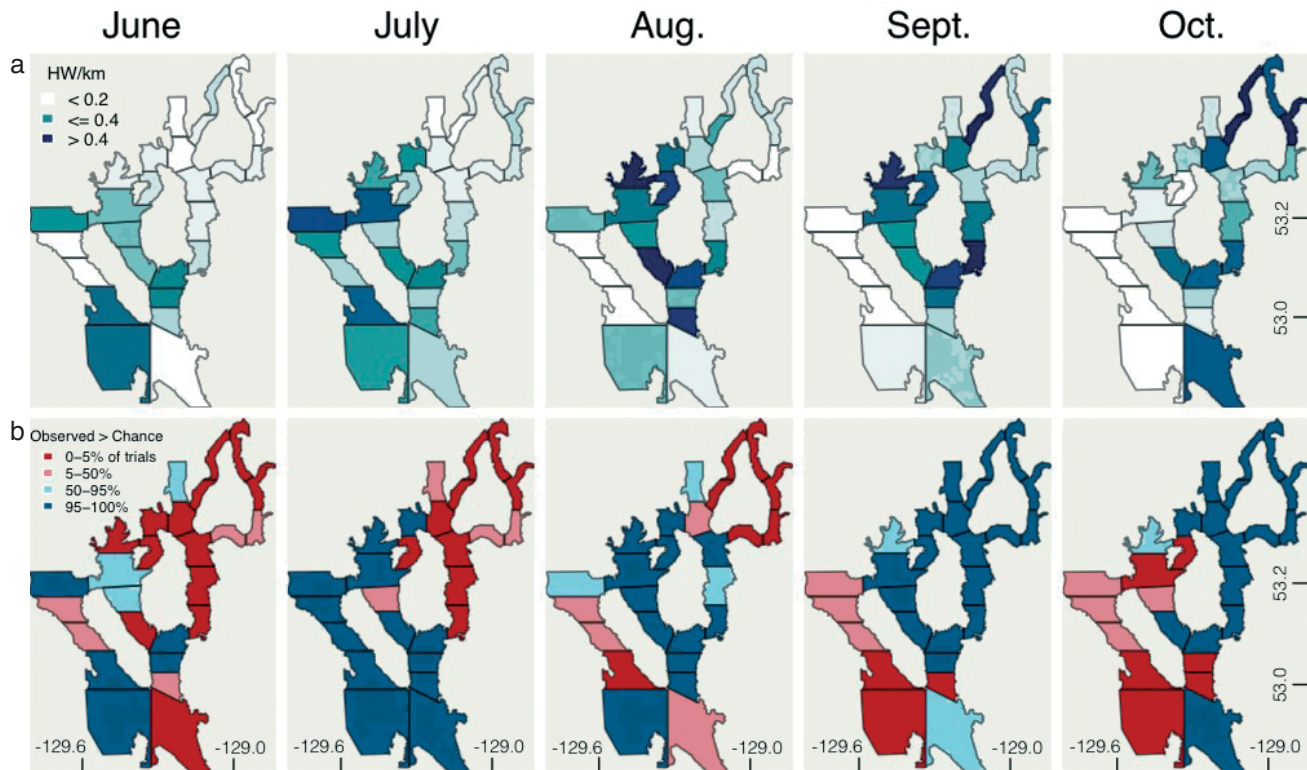


Fig. 6. The 'whale wave' is (a) evident in humpback whale sighting rate (whales per km) estimates and (b) verified by Monte Carlo randomization tests. The 2004 to 2014 surveys from Gitga'at and North Coast Cetacean Society (NCCS) platforms were pooled and then spatially stratified ($n = 26$ strata). Randomization results (b) are color-graded for each stratum as dark red: observed whale sighting rate was lower than at least 95% of the random trials; pink: observed sighting rate was lower than the randomization median; light blue: observed was higher than randomization median; dark blue: observed was higher than 95% of random trials

which were seen during transect effort (in 268 sightings, mean 54 per survey, min. 39, max. 89). Mean group size was 1.6 individuals. While humpbacks were abundant in all survey months, the highest numbers were observed in August. The monthly distribution of these sightings confirms that the whale wave occurred again in 2015 (Fig. 7). As the wave propagated inland, humpback densities also became less concentrated. The most dispersed humpback distribution was observed in September.

Backscatter. For backscatter exploration, we developed both map and profile views (Figs. 8 & 9). Backscatter distribution on both frequencies shifted throughout the summer, but these shifts were neither unidirectional nor simple. Some channels consistently contained krill-like patches (e.g. Squally Channel [SQU]), while others were entirely empty

in some months and full in others (e.g. compare Whale Channel [WHA] month to month in Fig. 9).

Krill-like backscatter (200 kHz) was prevalent throughout the season. Total backscatter was highest in the outer channels during June. In other months, total backscatter remained stable overall, but distribution was patchy and variable. In early summer, most total

Table 2. Monthly oceanographic surveys on the RV 'Bangarang' in 2015, detailing the days of fieldwork within each survey month (Days); the formal transect effort (km); the number (n_b) of 5 km transect bins used in habitat models (late July was excluded from modeling); the average Beaufort sea state conditions (Bft) during the formal effort; the number (n_w) of humpback whales (HW) seen; the average group size during the month (Grp), the mean \pm SD of humpback counts within 5 km transect bins (Mean count), and the percentage of bins with a count of 0 (% 0)

Month	Survey effort				HW sightings			
	Days	km	n_b	Bft	n_w	Grp	Mean count	% 0
May–June	16	320	47	1.6	39	1.538	0.705 ± 1.425	75
June–July	26	335	57	1.3	39	1.744	1.143 ± 2.422	71
Late July	21	346	–	1.4	49	1.714	1.114 ± 1.806	60
August	26	322	59	1.4	89	1.416	1.681 ± 2.587	48
September	28	330	56	1.4	52	1.558	0.853 ± 1.417	62
Total	117	1653	219	–	268	–	1.101 ± 2.005	63

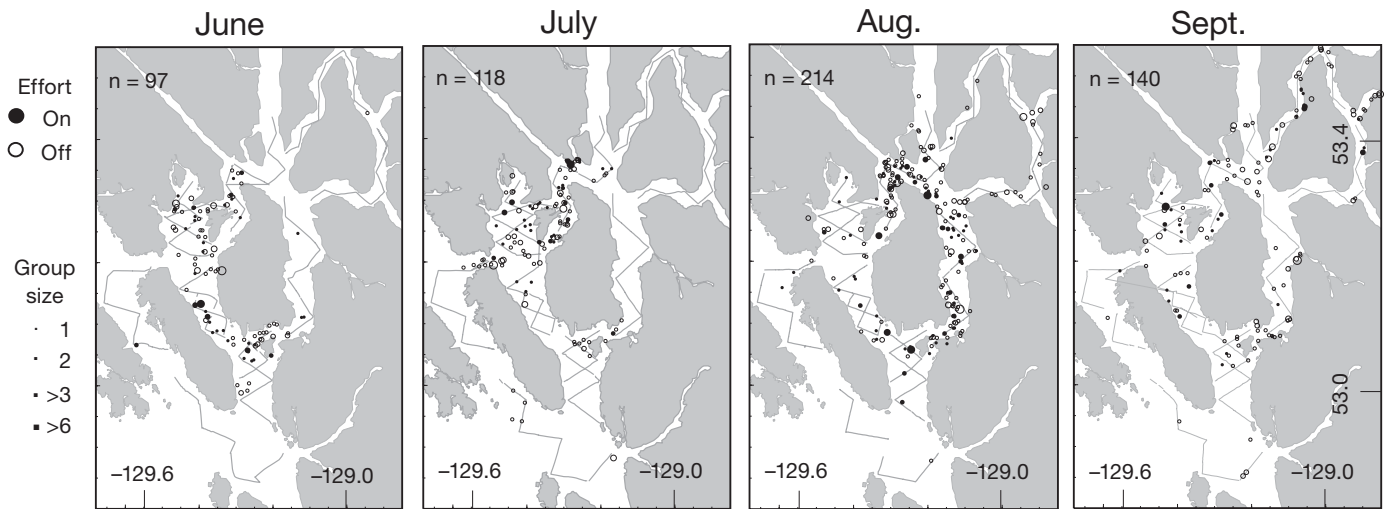


Fig. 7. Humpback whale sightings from the surveys in 2015 aboard RV 'Bangarang'. Circles are scaled positively by group size. Black-filled circles are on-transect sightings; empty circles are sightings during 'casual' or transit effort

backscatter was generally confined to the western half of the study area, in July almost exclusively in north SQU and western Wright Sound. By late summer, areas of high total backscatter had dispersed into multiple channels, including those further inland.

Total fish-like backscatter (33 kHz) declined throughout the summer. The highest readings were in June, also in the outer channels. As total backscatter declined, isolated aggregations of backscatter

developed in all channels with no clear offshore-inshore pattern. One noteworthy exception was a late-season area of high total backscatter in the furthest inland channels of the study area (see Fig. 9, VER block during September). Total backscatter was consistently high in the offshore channel of Caamano Sound (CAA).

Patterns were less obvious in the dispersion and intensity metrics (Fig. S30 in the Supplement). Mean

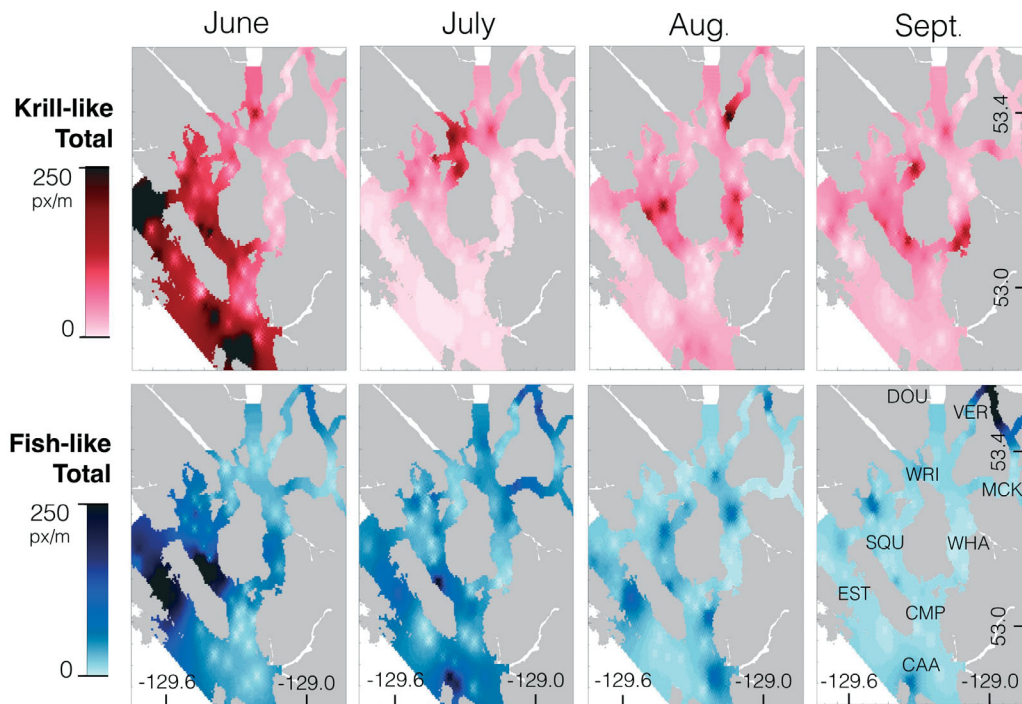


Fig. 8. Total backscatter for both filtered frequencies (pixel m^{-1} ; total pixel values per meter of trackline) interpolated from 5 km bins of trackline within each monthly survey in summer 2015. Color scales range from noise floor to the season's maximum reading. Interpolation was performed using inverse path weighted distance, a function that linearly weights combinations of sampled points based on their distance from the interpolation cell, accounting for land obstruction

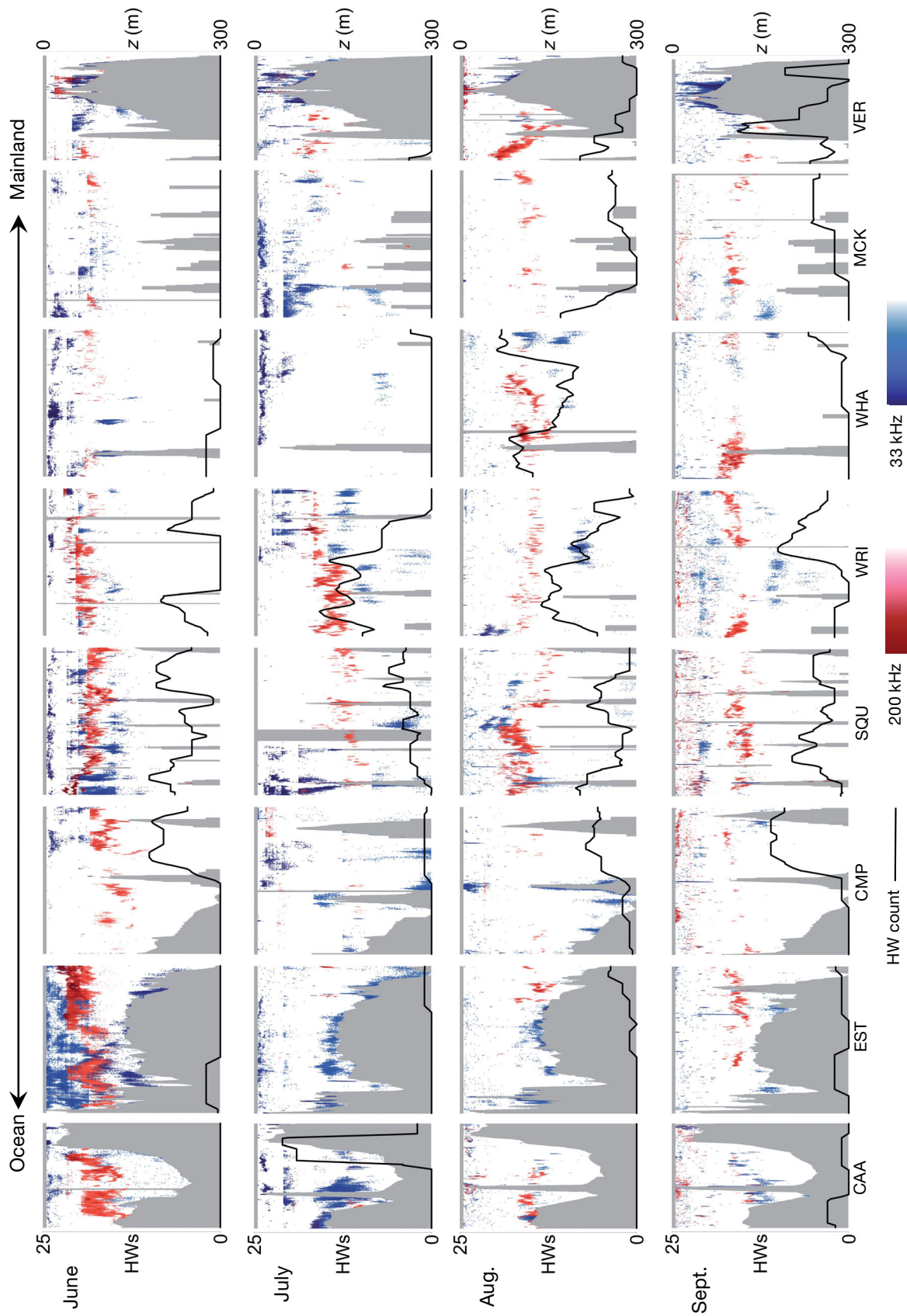


Fig. 9. Spatial association of humpback whale density (HWS, black line) with prey field in 5 surveys in summer 2015. Profiles are transects of discrete waterways arranged roughly from offshore (left) to inshore (right). Profile background is acoustic backscatter (blue: fish-like, 33 kHz; red: krill-like, 200 kHz) from the surface (profile top) down to 300 m (depth, z). Color intensity indicates backscatter strength (deeper/darker colors show stronger backscatter). White is backscatter that did not register above a threshold level. Grey is seafloor and manually removed self-noise. Humpback line is a running mean (~500 m window size) of whales seen within 2.5 km of trackline

intensity was highest overall in June and September, for both frequencies. The only noteworthy pattern in dispersion was for 200 kHz in September: lower values in the inland channels (i.e. tighter scattering layers) than in outer channels, although both areas con-

tained relatively high total 200 kHz backscatter for the month.

Oceanography. Month-to-month sea surface conditions were highly variable (Fig. 10, Table 3). Outer channels were consistently the coolest and most

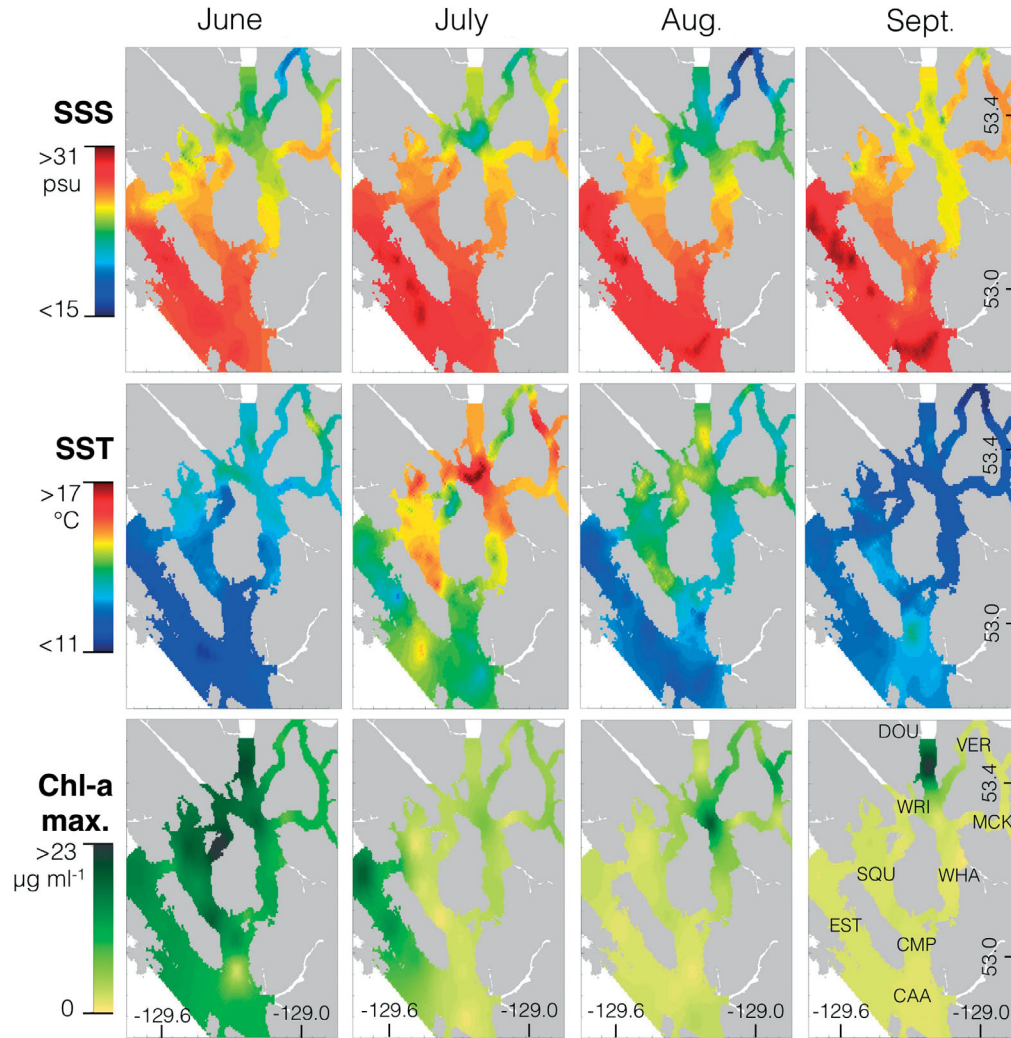


Fig. 10. Near-surface oceanographic variables of the Kitimat Fjord System, summer 2015. Sea surface salinity (SSS, top) and temperature (SST, middle row) were sampled along transects at 0.3 m depth then interpolated (see 'Methods'). Chlorophyll *a* (Chl *a*, bottom) was calculated from fluorescence measurements at station locations ($n = 24$) then interpolated

Table 3. Summary of oceanographic properties sampled in each monthly survey of 2015 aboard RV 'Bangarang'. SSS: sea surface salinity; SST: sea surface temperature (°C); Chl *a*: chlorophyll *a* ($\mu\text{g ml}^{-1}$). Metrics comprise the mean, standard deviation, minimum (Min.) and maximum (Max.). Chl *a* was not sampled in July

Month	SSS				SST (°C)				Chl <i>a</i> ($\mu\text{g ml}^{-1}$)			
	Mean	SD	Min.	Max.	Mean	SD	Min.	Max.	Mean	SD	Min.	Max.
May–Jun	25.70	2.48	15.60	30.67	13.00	1.03	10.35	17.78	14.09	6.57	0.49	28.05
Jun–Jul	26.72	2.47	17.75	31.16	14.67	1.27	11.41	19.05	5.50	4.95	0.95	20.89
Jul	27.84	2.84	17.46	31.68	13.74	1.08	11.16	17.97	–	–	–	–
Aug	25.51	4.02	11.59	31.36	13.54	1.16	11.16	16.63	5.07	5.01	1.01	21.39
Sep	26.92	2.43	19.21	31.73	12.37	0.88	10.48	14.92	3.24	5.14	0.95	27.02

saline; inner channels were typically the freshest but with variable temperatures (SST). Property ranges were widest in July and August for SST (11.41 – 19.05°C) and SSS (11.59 – 31.36), respectively. Waters were warmest in July (mean 14.67°C, max 19.05°C), with isolated areas of warmer surface waters in SQU, Wright Sound, and McKay Reach and Ursula Channel. The offshore-inshore salinity gradient was strongest in August and June but relatively negligible in July and September. The most homogenous surface conditions occurred in September, perhaps due to mixing by the early onset of autumn storms, as did the coolest (mean 12.37°C, min 10.48°C) and most saline measurements (mean 26.92, max. 31.73).

Chlorophyll *a* (Chl) maxima declined throughout the season (Fig. 10, Table 3). June Chl concentrations were much higher in the southwest channels (max. 28.5 $\mu\text{g l}^{-1}$). After June, strong maxima only persisted in isolated hotspots occurring increasingly inland. The largest maxima were found in north SQU in June (above value) and in Douglas Channel (DOU) in September (27.02 $\mu\text{g ml}^{-1}$).

Habitat models

Full season. Superimposing humpback counts upon backscatter data was an important means of visually ground-truthing the modeling process (Fig. 9). We found overdispersion in humpback whale count data, and the negative binomial model was selected over the Poisson and quasi-Poisson models based on visual inspection of quantile-quantile plots. Because residual distributions in negative binomial models are typically non-Gaussian (Hilbe 2011, Zuur et al. 2009), the Anscombe correction was applied to survey cross-

validation residuals (Anscombe 1953). There were 2 accepted algorithms within the literature (McCullagh & Nelder 1989, Choi et al. 2005), so we calculated both. Results were practically identical; those based on the Choi et al. (2005) algorithm are presented here.

The Prey model gave the poorest explanation of humpback distribution (min. AICc = 601; Table 4). All

Table 4. Full season model results for each hypothesis. Data rows summarize the datasets, including sample size (n) and the number of explanatory variables (Vars.) in each stage. Model set summarizes the number of variable combinations fit to the data (Combos), and the subset of those models that are Balanced (equal variable representation). Balanced model sets were used to calculate relative variable importance (RVI) for Prey and Proxy models. 95% Models rows summarize the resulting 95% confidence sets based on Akaike weights: the number of models in each set (n_m), the number of those models that are AICc equivalent (= AICc; within 6 AICc units of the set's minimum AICc, after Hilbe 2011), the minimum AICc in the 95% set (minAICc), and the proportion of null deviance explained by the model (r^2). 95% Vars list the explanatory variables within 95% sets; variables with a '-' were among the candidates; those with ✓ were included (Incl.). Variables used in the model with the lowest AICc are denoted instead with the significance level (p-value) of their smoothing function. When balanced subsets were available, RVI is reported. Bivariate interactions are given their own rows, joined by an 'x'

		Hypothesis					
		Prey		Proxy		Habit	Prey + Proxy
							Prey + Proxy + Habit
Data	n	216		216		216	216
	Vars	6		4		7	12
Model set	Combos	95		39		22	30
	Balanced	51		15		0	0
95% Models	n_m	41		4		1	7
	=AICc	41		4		1	3
	minAICc	601.1		586.6		570.3	579.6
	r^2	0.16		0.35		0.41	0.39
		Incl.	RVI	Incl.	RVI	Incl.	Incl.
95% Vars	T_H	✓	1.00				✓
	T_L	✓	0.76				✓
	D_H	✓	0.61				-
	D_L	✓	0.37				-
	I_H	✓	0.32				-
	I_L	0.1	0.41				-
	$T_H \times D_H$	0.001					✓
	$T_H \times I_H$	✓					-
	$T_H \times V_L$	✓					-
	$D_H \times D_L$	✓					-
	SSS			-	1.00		-
	SST			-	0.16		-
	Chl			✓	0.27		✓
	Inlet			✓	0.40		✓
	SSS \times SST			0.001			0.001
	Chl \times Inlet			✓			✓
	$T_H \times \text{Chl}$						0.01
	$T_H \times \text{Inlet}$						✓
	Lat \times Long					0.001	0.01
	Day of Year					-	0.001

other model stages yielded model fits with lower AICc values and higher proportions of null deviance explained (hereafter represented as r^2 , after Friedlaender et al. 2006), culminating in the Prey + Proxy + Habit model (min. AICc = 554, $r^2 = 0.62$). The best Prey models explained only 16 % of the dataset's null deviance.

Of the 95 candidate Prey models, 41 remained in the 95 % confidence set, all of which were AICc equivalent (i.e. within 6 AICc units for datasets of $n < 256$, Hilbe 2011), a sign of high uncertainty in model selection. Of the 39 Proxy models fitted, 4 AICc-equivalent models remained in the 95 % set (min. AICc = 587, $r^2 = 0.35$). The Prey + Proxy model set, which fit 30 candidates, yielded a 95 % confidence set of 7 models, 3 of which were AICc equivalent (min. AICc = 580, $r^2 = 0.39$). Of 16 candidate models, the 95 % Habit set kept only one (AIC = 560, $r^2 = 0.42$), a good sign of strong support. While the second-best model had considerably worse parsimony (AICc = 571), it is worth noting that this model contained the categorical variable Block, whose 8 levels would have been heavily penalized in an AICc framework. Its low AICc suggests the potential importance of channel-specific patterns in variables and/or humpback distribution. 55 candidate models were passed to the Prey + Proxy + Habit step. The 95 % set contained 8 models, all AICc-equivalent (min. AICc = 553, $r^2 = 0.62$).

Monthly surveys. Based on low importance in full-season fits, backscatter metrics 33 kHz dispersion and 200 kHz intensity were left out of monthly variable sets. Prediction error generally increased throughout the summer (Fig. 11). Prey model performance was relatively poor, but it was not always the worst; in fact, the June Prey model tied for overall lowest prediction error, but its error increased steeply from thereon. In all months but June, the best-fit Prey + Proxy model was the same as the Proxy model (i.e. no backscatter variables were used; Table 5). Habit model performance was sporadic, declining most sharply from August to September. The Prey + Proxy + Habit model was always the best fit. Its prediction error was lowest in July.

Variable importance. Based on the variables present in the full-season 95 % confidence sets (Table 4), Total 200 kHz was the most important backscatter metric, though 200 kHz Dispersion and Total 33 kHz were also used within interaction terms. Total 200 kHz was the only variable to persist in the Prey + Proxy 95 % set, but 200 kHz Dispersion returned in interaction with Total 200 kHz within the overall best-fit model. All 4 oceanographic variables re-

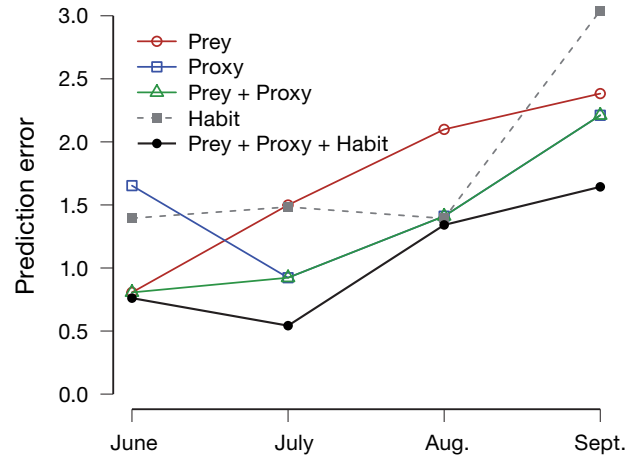


Fig. 11. Prediction errors of the best-fit models for each hypothesis of humpback whale habitat use across monthly surveys in summer 2015. Models were fit to each month separately, with unique sets of variable combinations for each hypothesis (see Table 1). For each survey, prediction error is calculated as the mean square of Anscombe residuals (Choi et al. 2005), scaled by the month's mean humpback count

mained in the 95 % Proxy set. SST and SSS only appeared important when in interaction with each other; the best-fit Proxy model included SST \times SSS only. The best available Habit model included Day of Year and the bivariate interaction Lat \times Long. Similar results were found in RVI weights calculated from balanced subsets of the Prey and Proxy candidates. With interaction terms removed, SSS arose as the most important oceanographic variable by far. This may be more related to its collinearity with latitude (see 'Methods') than its indication of proximity to the fjord's freshwater source. Interestingly, Inlet was the second most important variable in the Proxy models.

Results differed slightly within the best-fit monthly models, in which importance, when inferred from both 95 % sets and RVI, shifted month-to-month (Table 5). Total 200 kHz and dispersion remained the most important backscatter variables, but all months were best-fit by multivariate Prey models. One notable finding was that Total 200 kHz was the most important backscatter metric in June and July, but in the second half of the summer, 200 kHz Dispersion became the most important, possibly suggesting increasing importance of patch characteristics in late season foraging strategy. Except for June, backscatter was entirely absent from Prey + Proxy models, suggesting that oceanographic and position variables held much more explanatory power at the timescale (and sample size) of a single month. One notable discrepancy is that Total 200 kHz was the most important variable in the July Prey + Proxy model ac-

Table 5. Best-fit models for each month (June to September 2015) under each hypothesized model of humpback whale habitat use (Prey, Proxy, etc. in Model column). Performance metrics: Mean square prediction error (Adj. MSE) based on Anscombe residuals (Choi et al. 2005) and scaled by mean humpback count; proportion of null deviance in humpback counts explained by model (r^2); explanatory variables used in candidate models (defined in Table 1). Variables included in the best-fit model are denoted with the significance level (α) of their smoothing function (ns when $p > 0.05$). Variables that were tested but not included in a best-fit model are denoted with '–'. For the first 3 model stages, whose model sets were balanced (equal variable representation), relative variable importance (RVI) is also reported, calculated from Akaike weights and scaled within month-models between 0 and 1. Note that RVI metrics can only be quantitatively compared within model-months

Model	Month	Adj. MSE	r^2		Backscatter				Explanatory variables				Position		
					T_H	T_L	D_H	I_L	Oceanography				Long	Lat	Dist
Prey	J	0.81	0.16	α	–	ns	ns	ns							
				RVI	1.00	0.48	0.55	0.92							
	J	1.50	0.38	α	ns	–	.05	ns							
				RVI	1.00	0.30	0.42	0.23							
	A	2.10	0.19	α	–	0.1	.05	–							
				RVI	0.47	0.73	1.00	0.52							
	S	2.38	0.17	α	ns	ns	ns	ns							
				RVI	0.89	0.60	1.00	0.87							
	Proxy	J	1.65	0.39	α				–	–	0.1	ns			
					RVI				0.31	0.26	1.00	0.24			
		J	0.92	0.56	α				ns	–	ns	.05			
					RVI				0.08	0.27	0.12	1.00			
	A	1.41	0.68	α					.001	–	–	.001			
				RVI					1.00	0.19	0.22	0.85			
	S	2.21	0.16	α					–	ns	ns	ns			
				RVI					0.53	0.63	1.00	0.55			
Prey + Proxy	J	0.81	0.16	α	ns	–	ns	ns	–	–	–	–			
				RVI	0.03	0.01	0.02	0.03	0.31	0.26	1.00	0.24			
	J	0.92	0.56	α	–	–	–	–	ns	–	ns	0.05			
				RVI	1.00	0.30	0.42	0.23	0.04	0.12	0.05	0.46			
	A	1.41	0.68	α	–	–	–	–	0.001	–	–	0.001			
				RVI	0.00	0.00	0.00	0.00	1.00	0.19	0.22	0.85			
	S	2.21	0.16	α	–	–	–	–	–	ns	ns	ns			
				RVI	0.43	0.29	0.48	0.42	0.53	0.63	1.00	0.55			
	Habit	J	1.36	0.41									–	–	ns
		J	1.48	0.37									0.05	–	–
		A	1.39	0.69									0.001	0.001	–
		S	3.04	0.12										ns	–
Prey + Proxy + Habit	J	0.76	0.52		–	–	–	–	ns	–	0.05	–	–	–	ns
	J	0.54	0.48		–	–	–	–	0.1	–	–	–	–	0.05	–
	A	1.34	0.69		–	–	–	–	0.1	–	–	–	0.001	0.001	–
	S	1.64	0.18		–	–	–	–	ns	–	ns	–	–	ns	–

cording to Akaike-based RVI, but residual-based prediction error selected a model with no backscatter metrics whatsoever. On a monthly basis, Chl and SSS were regularly the most important oceanographic variables. Again, geospatial coordinates outperformed distance into fjord as a position metric.

Functional relationships. Inspection of smoothing functions for the variables in the top season models revealed complex interactions between explanatory variables and the linear predictor in some cases (e.g. SST \times SSS, Fig. 12b), but near-linear relationships in others (e.g. Chl in Fig. 12a,e). The large central bulge in the Lat

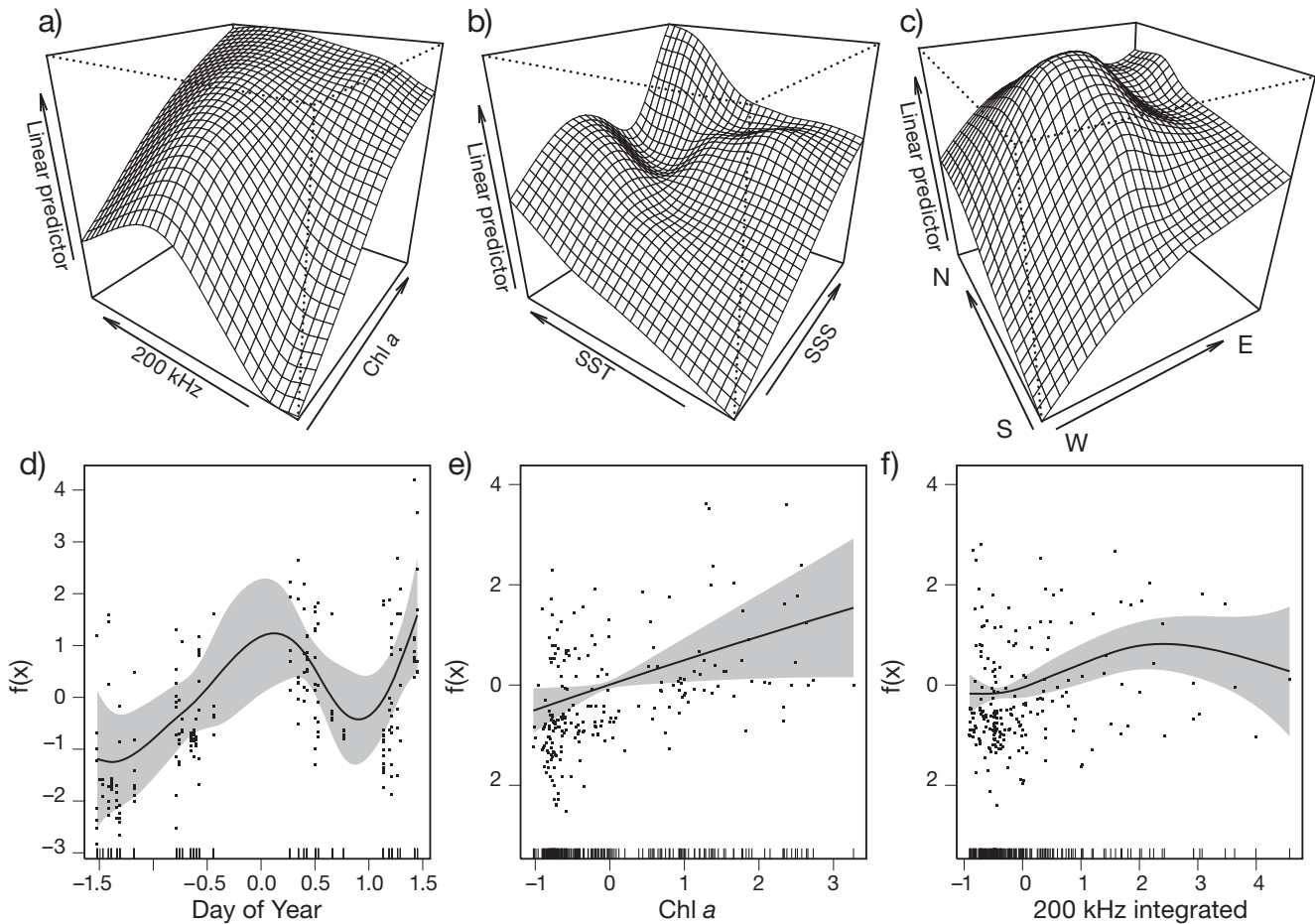


Fig. 12. Smoothing functions of explanatory variables included in the best models fit to the full 2015 dataset. (a–c) Bivariate smoothing functions from the all-round best-fit model (Prey + Proxy + Habit model in Table 4); (d–f) smoothing functions from 2 AICc-equivalent models (within 6 AICc of the minimum AICc; Hilbe 2011) that contained Chl and 200 kHz integrated backscatter in univariate terms, whose plots offer a simpler but related perspective on functional relationships between normalized explanatory variables and the linear predictor of humpback counts (z-axis in 3-D graphs, y-axis in 2-D plots). Plots d–f feature superimposed residuals (dots) and ± 1 standard error bounds (gray shading)

× Long perspective plot corresponds to the position of SQU, which sustained the highest humpback densities throughout the season (Fig. 12c). The Day of Year smoothing function captured the increase in humpback abundance in August (Fig. 12d). The smoothing function for integrated 200 kHz backscatter was a near-sigmoidal curve (Fig. 12f), reminiscent of a Type III functional response (Holling 1965; see ‘Discussion’).

DISCUSSION

Documenting the wave

Ten years of research demonstrated that humpback *Megaptera novaeangliae* densities propagate throughout the Kitimat Fjord System in an offshore-inshore wave as summer turns to fall. Results of our

stratified Monte Carlo procedure were strongly non-random but not absolute. The persistent high-density areas to the southwest of Gil Island (Fig. 6) demonstrate that there are fine-scale deviations from the mesoscale pattern of the wave. Interestingly, another persistent exception to the pattern was the late season hotspot at the entrance of Surf Inlet, one of the 3 major sources of surface freshwater to the outer fjord system (Fig. 1; more on these inlets below).

Habitat models

This study involved (1) long-term, 4-season monitoring that identified spatial pattern and developed hypotheses, followed by (2) new fieldwork dedicated to hypothesis testing. While we recommend this research procedure in general, we acknowledge the

limitations of using a single summer to explain a long-standing pattern. The year 2015 may have been an exceptional year in terms of oceanography that decoupled humpbacks from their typical associations. Indeed, it was in the aftermath of the 'warm blob' and at the onset of an El Niño (Bond et al. 2015, CPC 2016). It is particularly difficult to discount philopatric behavior, which would have been acquired and refined over many years, as any one year may not be optimal.

Nevertheless, our analysis allowed us to compare conventional theories of habitat use strategy against each other, weighing their relative explanatory power on the scale of the full season and from month-to-month. Similar to previous studies (e.g. Friedlaender et al. 2006, Ferguson et al. 2006, Dalla Rosa et al. 2012), the most complex models of habitat use (including both prey, proxy, and habit variables) tended to best explain humpback distributions. Also similar to past findings (e.g. Benoit-Bird et al. 2013) was the importance of multiple prey metrics rather than just backscatter quantity, and there was some indication that as volume declined, the vertical dispersion of remaining backscatter became an increasingly important predictor.

Our most curious results were (1) the generally low importance of prey metrics relative to environment variables, (2) the decline in Prey model rank from first in June to among the worst in remaining months, and (3) the general decline in performance of all models as the season wore on.

Low prey importance. Certain backscatter metrics (particularly Total 200 kHz) were included in many of the best-fit models, but in monthly surveys, their importance was quite low compared to environmental variables. This may reflect reliance upon environmental proxies instead of direct prey sampling at the spatiotemporal scales of our data collection. However, apparently weak whale-prey coupling may also be an artifact of our sampling design. Our study attempted to capture a pattern in both space and time, and it may be that our surveys of the study area were not sufficiently synoptic to capture whale-prey associations. Our instrumentation or backscatter metrics may have inadequately characterized humpback prey, or the measurement scales of our backscatter bins and humpback count radii may have been mismatched; weak results could speak more to analysis design than to ecological patterns (Levin 1992). Many predator-prey association studies have found mixed, highly scale-sensitive results when relying on prey quantity metrics alone (Fauchald 2009). Benoit-Bird et al. (2013) emphasized that observed spatial pattern (or

lack thereof) depends entirely upon what is measured, which is why we included several backscatter metrics. While we were able to use frequency differencing and patch characteristics to roughly distinguish prey type within backscatter patches, our prey metrics may have failed to capture a dimension of prey association related to nutritional differences, if any, in available prey. This has been an important distinction in seabird foraging studies (Hunt et al. 1993).

An issue with an automated approach to the backscatter metric calculation is that our results depend upon the level of refinement and biological relevance of the metrics and filters we developed. However, we stand by our automated analysis on the grounds that (1) manual approaches are subject to human error and not reproducible, and (2) underestimation is more likely than overestimation in automated methods, whereas manually selected patches can incorporate subjective knowledge that increases the risk of positively biased results.

Decline in prey model performance. We offer 5 hypotheses to explain the disproportionate decline in prey model performance throughout the season:

(1) Prey switching: Humpbacks switched to a prey type that was inadequately detected by our echosounder or backscatter metrics, though we cannot guess what that prey type would be, nor did we ever observe any major shifts in foraging style.

(2) Inadequate coverage: Our sampling plan may have been inadequate to detect locally rich but generally sparse backscatter patches of early fall. Indeed, when we broke transect in fall 2015 to approach the whales within inland channels, groups generally behaved as if they were feeding at depth, and the echosounder detected isolated but dense backscatter patches at depth as well (E. Keen unpubl. data).

(3) Satiation: After a winter of fasting, early summer habitat use was 1-dimensional and food-focused. As blubber stores were replenished, whales no longer needed to track the best prey conditions available. Search effort could have relaxed, perhaps falling back on the heuristics of proxies and habit, and other priorities were allowed to inform habitat use (see 'Competition').

(4) Competition: Overall backscatter volume decreased while humpback densities increased, peaking in August. At this time of year, a community of other euphausiivorous predators descends upon the fjord system, including fin whales *Balaenoptera physalus* (Ford 2014, authors' unpubl. data), a variety of seabirds, and salmon. Most of these exhibit preference for outer and central channels (authors' unpubl. data). Intra- and inter-specific competition may have

pushed humpbacks deeper inland and compromised their spatial overlap with prey.

(5) Search shift: While spatial overlap with prey must occur on the smallest scale in order for feeding to occur, mobile oceanic predators must seek out and position themselves for that opportunity by navigating and assessing prey conditions at multiple nested scales in space and time. The scale of apparent spatial association, therefore, may be a moving target. In the abundance of early summer, humpbacks may have been able to find sufficient prey patches without much searching (once they had arrived in the most productive channels). But in the scarcity of autumn, the best foraging strategy may have been to allocate more time and effort to searching, remaining mobile until adequate patches were found. If so, from our trackline perspective, the average humpback would be spatially decoupled from prey-rich areas, but all could still have been engaged in food-driven behavior.

Decline in all models' performance. The growing prediction error in all models throughout the summer suggests that we failed to sample some habitat component that became increasingly important into the fall. Two possible needs that were poorly included in this study are as follows.

(1) Physiological maintenance: 'Nearest inlet' was our only health-related variable, inspired by curious field observations (Fig. 4) and hypotheses from the literature (Boily 1995, Durban & Pitman 2012). Durban & Pitman (2012) hypothesized that physiological maintenance was a driver of baleen whale migration. It seemed possible to us that turbulent mixing zones of fresh, warm water within fjord systems may provide a similar service that prolongs the foraging season; this could also explain why many humpbacks are able to remain in the deep channels of this fjord system long into the fall, possibly overwintering here (J. Wray, H. Meuter & C. Picard unpubl. data). However, inlet importance was mixed according to 95 % model sets and RVI. This hypothesis merits further investigation, given that such inlets are a feature unique to fjord foraging habitats and may suggest the unsung importance of fjords, both historically and into the future, for whale populations.

(2) Social habitat needs: Humpbacks are often philopatric to reliably productive feeding grounds (Fleming & Jackson 2013). However, the foraging season also has a strong social component. Foraging regions tend to correspond to distinct breeding populations (Baker et al. 2013). Field biologists in these feeding grounds often observe complex behavioral transmission (Weinrich et al. 1992), annually persistent social bonds (Ramp et al. 2010), and even song

(Vu et al. 2012). Social interests may gain precedence over foraging as migration and breeding season nears, and the interior channels of the fjord system may be better for socializing in some way. If so, acoustics may be a driving concern for this exceptionally vocal species in this habitat. The steeper walls of bare bedrock and narrow channels of the interior fjords, secluded as they are from major shipping lanes, may offer an attractive acoustic space (Williams et al. 2013). Both social calls and song are common within this fjord system during the late fall (H. Meuter & J. Wray unpubl. data), but further data are needed to test for differences in call rates among channels. An alternative is that the whales found further inland belong to a social network distinct from those loyal to the outer channels, and the apparent wave is in fact a turnover in the resident population with different habitat preferences. Territoriality or inter-group competition may even exacerbate the pattern. Social association analyses based on photo-identification data from our decade of research are forthcoming.

Whale-climate coupling

If the whale wave is a response to changes in prey or their environmental proxies, then its ultimate mechanism is oceanographic. As in most fjord systems, the KFS experiences strong offshore-inshore gradients in oceanography and meteorology driven by seasonal signals in climate and water mixing (Macdonald et al. 1983; Fig. 10). These midsummer gradients may serve as aids to orientation or cues to habitat needs. Gradients are maintained by estuarine circulation, a seaward surface flow of relatively fresh water atop a landward countercurrent at depth (Syvitski et al. 1987). Estuarine flow is governed by snowmelt and, to a lesser degree, seasonal rains (Masson & Cummins 2000). Gradients are disrupted with the onset of fall storms, whose sea waves and strong winds overwhelm estuarine flow and collide with katabatic outflows, inducing vigorous mixing (Thomson 1981, Freeland et al. 1980). By wintertime, KFS waters are relatively homogenous (Macdonald et al. 1983). The breakdown of cue gradients could disperse prey and/or instigate *in situ* prey production deeper inland. In this way, the timing of the whale wave may be coupled to the shifting balance between estuarine circulation and autumn mixing by storms. Both of these processes are governed by climate, including interannual oscillations and long-term trends. If so, whale use of fjord habitats could be particularly sensitive to global trends in climate.

Threshold foraging and ecological role

The season's relationship between humpbacks and krill-like backscatter was muted but sigmoidal (Fig. 12f), suggesting a threshold functional response to prey conditions (Holling 1965). Metabolic and kinematic theory predicts that foraging thresholds are high in large marine predators and have implications for habitat use (Goldbogen et al. 2011). Piatt & Methven (1992) was the first study to document a threshold response in cetaceans (between humpback whales and capelin *Mallotus villosus*). Piatt (1990) observed a similar response to the same prey in common murre *Uria aalge*. Friedlaender et al. (2006), using a GAM framework similar to ours, found a functional relationship between humpbacks and backscatter that was nonlinear but more reminiscent of a saturation response than a sigmoid. Energetic costs of mobility and associated threshold foraging have ecological consequences by reducing the proportion of accessible habitat that is usable, which decouples a predator's trophic impact from its geographic distribution.

Interestingly, the functional relationship with chl *a*, the strongest environmental predictor, was practically linear (Fig. 12e). Its difference from the backscatter sigmoid may reflect nested strategies, in which proxies are used to position for the best probability of prey interactions (higher is always better), while their prey association within those high-probability areas is more discriminating (Fauchald et al. 2000).

As the whales propagate inland, so too does their ecological footprint. Although humpbacks are abundant within the KFS, their trophic impact at any one time is highly localized. Beyond predation and competition, this includes the facilitation of other predators and nutrient redistribution (Roman et al. 2014). Other species may come to coordinate their use of this fjord system accordingly. Habitat use patterns like the whale wave may be a significant medium of 'ecosystem engineering' among large marine predators.

Implications for management

Habitat use inevitably manifests itself as a pattern in both space and time. Like all spatial patterns, it may only be strong, stable, and/or apparent at certain scales (Levin 1992). Others have studied humpbacks in this area without detecting the whale wave (Williams & Thomas 2007, Wheeler et al. 2010,

Gribba & Bailey 2015), and their findings have become the basis for the impact assessment of proposed industrial activities in this fjord system (Williams & O'Hara 2010, Enbridge 2010). Long-lived, mobile predators must be observed across seasons and for many years before strategies and motivations of habitat use can be understood. Where available, research is greatly enhanced by the involvement of local residents who have the familiarity with their home system to interpret observations with unique insight. Our study highlights the value of long-term, local monitoring by indigenous communities and their partnership with non-profit and academic research organizations.

Our findings suggest humpback foraging needs within this fjord system are balanced against interests other than food and that the balance shifts within the foraging season. The annual persistence and statistical strength of the whale wave demonstrate that humpback habitat use can be structured and strategic. It may facilitate the most thorough possible use of a fjord system's resources, provide similar access to other complex systems of BC's fjordland, and accommodate higher densities of humpbacks in the dwindling number of relatively undisturbed coastal foraging grounds of the northeast Pacific than would otherwise be possible. It is likely coordinated to the specific oceanography of the study system, suggesting that local displacement by human impacts may have more consequences than previously supposed. Industrial projects that disrupt habitat continuity, such as shipping lanes, may be particularly detrimental to the integrity of this and other critical habitats. Until sufficiently thorough habitat-use studies have been carried out, irrevocable management decisions should be treated with caution.

Protecting entire species ranges is typically impossible, particularly in the case of mobile oceanic predators such as whales, so we must ask which portions are most important. It is here that the common depiction of mobile predators as masters of foraging improvisation and environmental forensics can be counterproductive for conservation. Though accurate, this picture can be misconstrued as an argument against the protection of specific sites, given that an entire ocean remains available. This outlook ignores the fact, demonstrated by our findings, that mobile marine predators can use complex strategies not only to navigate vast swaths of marine habitat but also to tune into the specific features and attributes of certain areas and to develop spatial strategies that enable their most thorough and efficient use.

Data archive. Keen EM, Wray J, Meuter H, Thompson KL, Barlow JP, Picard CR (2017) Data from: 'Whale Wave': shifting strategies structure the complex use of critical fjord habitat by humpbacks. UC San Diego Library Digital Collections. <http://doi.org/10.6075/J0GT5K3B>

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LITERATURE CITED

- ✦ Akaike H (1974) A new look at the statistical model identification. *IEEE Trans Automat Contr* 19:716–723
- ✦ Alexander RM (2005) Models and the scaling of energy costs for locomotion. *J Exp Biol* 208:1645–1652
- ✦ Anderwald P, Evans PGH, Dyer R, Dale A, Wright PJ, Hoelzel AR (2012) Spatial scale and environmental determinants in minke whale habitat use and foraging. *Mar Ecol Prog Ser* 450:259–274
- Anscombe FJ (1953) Contribution to the discussion of H. Hotelling's paper. *J R Stat Soc B* 15:229–230
- Archer E (2014) swfscMisc v.1.0.3. R package. Available at <https://github.com/EricArcher/swfscMisc>
- ✦ Ashe E, Wray J, Picard CR, Williams R (2013) Abundance and survival of Pacific humpback whales in a proposed critical habitat area. *PLOS ONE* 8:e75228
- Bailey H, Mate BR, Palacios DM, Irvine L, Bograd SJ, Costa DP (2009) Behavioural estimation of blue whale movements in the Northeast Pacific from state-space model analysis of satellite tracks. *Endang Species Res* 10:93–106
- ✦ Baker CS, Steel DJ, Calambokidis J, Falcone E and others (2013) Strong maternal fidelity and natal philopatry shape genetic structure in North Pacific humpback whales. *Mar Ecol Prog Ser* 494:291–306
- ✦ Ballance LT, Pitman RL, Fiedler PC (2006) Oceanographic influences on seabirds and cetaceans of the eastern tropical Pacific: a review. *Prog Oceanogr* 69:360–390
- ✦ Benoit-Bird KJ, Battaile BC, Heppell SA, Hoover B and others (2013) Prey patch patterns predict habitat use by top marine predators with diverse foraging strategies. *PLOS ONE* 8:e53348
- Bjorge A (2001) How persistent are marine mammal habitats in an ocean of variability? In: Evans PGH, Raga JA (eds) *Marine mammals: biology and conservation*. Kluwer Academic/Plenum Publishers, London, p 63–91
- ✦ Block BA, Jonsen ID, Jorgensen SJ, Winship AJ and others (2011) Tracking apex marine predator movements in a dynamic ocean. *Nature* 475:86–90
- ✦ Boily P (1995) Theoretical heat flux in water and habitat selection of phocid seals and beluga whales during the annual molt. *J Theor Biol* 172:235–244
- ✦ Bombosch A, Zitterbart DP, Opzeeland IV, Frickenhaus S, Burkhardt E, Wisz MS, Boebel O (2014) Predictive habitat modeling of humpback (*Megaptera novaeangliae*) and Antarctic minke (*Balaenoptera bonaerensis*) whales in the Southern Ocean as a planning tool for seismic surveys. *Deep-Sea Res* 191:101–114
- ✦ Bond NA, Cronin MF, Freeland H, Mantua N (2015) Causes and impacts of the 2014 warm anomaly in the NE Pacific. *Geophys Res Lett* 42:3414–3420
- Buckland ST, Anderson DR, Burnham KP, Laake JL, Borchers DL, Thomas L (2001) Introduction to distance sampling: estimating abundance of biological populations. Chapman & Hill, New York, NY
- Burnham KP, Anderson DR (2002) Model selection and multimodel inference: a practical information-theoretic approach, 2nd edn. Springer-Verlag, New York, NY
- ✦ Cañadas A, Sagarminaga R, De Stephanis R, Urquiola E, Hammond PS (2005) Habitat preference modelling as a conservation tool: proposals for marine protected areas for cetaceans in southern Spanish waters. *Aquat Conserv* 15:495–521
- ✦ Choi Y, Hongshik H, Chen JJ (2005) Regression trees for analysis of count data with extra Poisson variation. *Comput Stat Data Anal* 49:893–915
- CPC (Climate Prediction Center) (2016) El Niño / Southern Oscillation (ENSO) Diagnostic Discussion. 11 February 2016. Available at www.cpc.ncep.noaa.gov/products/analysis_monitoring/enso_advisory/
- ✦ Croll DA, Marinovic B, Benson S, Chavez FP, Black N, Ternullo R, Tershy BR (2005) From wind to whales: trophic links in a coastal upwelling system. *Mar Ecol Prog Ser* 289:117–130
- ✦ Dalla Rosa L, Ford JKB, Trites AW (2012) Distribution and relative abundance of humpback whales in relation to environmental variables in coastal British Columbia and adjacent waters. *Cont Shelf Res* 36:89–104
- ✦ Durban JW, Pitman RL (2012) Antarctic killer whales make rapid, round-trip movements to subtropical waters: evidence for physiological maintenance migrations? *Biol Lett* 8:274–277
- Enbridge (2010) Volume 8A: overview and general information—marine transportation; Volume 8B: environmental and socio-economic assessment (ESA)—marine transportation. Enbridge Northern Gateway Project Sec. 52 Application. Northern Gateway Pipelines Inc., Calgary
- ✦ Fauchald P (1999) Foraging in a hierarchical patch system. *Am Nat* 153:603–613
- ✦ Fauchald P (2009) Spatial interaction between seabirds and prey: review and synthesis. *Mar Ecol Prog Ser* 391: 139–151
- Fauchald P, Erikstad KE, Skarsfjord H (2000) Scale-dependent predator–prey interactions: the hierarchical spatial distribution of seabirds and prey. *Ecology* 81:773–783
- Ferguson MC, Barlow JP, Reilly SB, Gerrodette T (2006) Predicting Cuvier's (*Ziphius cavirostris*) and Mesoplodon

- beaked whale densities as functions of the environment in the eastern tropical Pacific Ocean. *J Cetacean Res Manag* 7:287–299
- Fissel DB, Borg K, Lemon DD, Birch JR (2010) Marine physical environment. Enbridge Northern Gateway Project. Tech Data Rep, ASL Environmental Sciences, Sidney
- Fleming A, Jackson J (2013) Global review of humpback whales (*Megaptera novaengliae*). NOAA Tech Memo NMFS SWFSC-474
- Ford JKB (2014) Marine mammals of British Columbia. Royal BC Museum, Victoria
- Freeland HJ, Farmer DM, Levings CD (1980) Fjord oceanography. Plenum Press, New York, NY
- ✦ Friedlaender AS, Halpin PN, Qian SS, Lawson GL, Wiebe PH, Thiele D, Read AJ (2006) Whale distribution in relation to prey abundance and oceanographic processes in shelf waters of the Western Antarctic Peninsula. *Mar Ecol Prog Ser* 317:297–310
- ✦ Goldbogen JA, Calambokidis J, Oleson E, Potvin J, Pyenson ND, Schorr G, Shadwick RE (2011) Mechanics, hydrodynamics, and energetics of blue whale lunge feeding: efficiency dependence on krill density. *J Exp Biol* 214: 131–146
- Gribba R, Bailey M (2015) Using fine scale marine mammal distributions to predict potential effects of underwater vessel noise. Society for Marine Mammalogy 21st Biennial, 13–18 Dec 2015, San Francisco, CA
- ✦ Guisan A, Thullier W (2005) Predicting species distribution: offering more than simple habitat models. *Ecol Lett* 8: 993–1009
- Hamilton PK, Stone GS, Martin SM (1997) Note on a deep humpback whale *Megaptera novaengliae* dive near Bermuda. *Bull Mar Sci* 61:491–494
- Hastie TJ, Tibshirani RJ (1990) Generalized additive models. *Monogr Stat Appl Probab* 43
- Hastie TJ, Tibshirani R, Friedman J (2009) The elements of statistical learning: data mining, inference and prediction, 2nd edn. corr. Springer Series in Statistics. Springer, New York, NY
- ✦ Hazen EL, Friedlaender AS, Thompson MA, Ware CR, Weinrich MT, Halpin PN, Wiley DN (2009) Fine-scale prey aggregations and foraging ecology of humpback whales *Megaptera novaengliae*. *Mar Ecol Prog Ser* 395:75–89
- Hedley SL, Buckland ST, Borchers DL (1999) Spatial modelling from line transect data. *J Cetacean Res Manag* 1: 255–264
- Hilbe JM (2011) Negative binomial regression, 2nd edn. Cambridge University Press, Cambridge
- Holling CS (1965) The functional response of predators to prey density and its role in mimicry and population regulation. *Mem Entomol Soc Can* 45:1–60
- Hunt GL Jr, Harrison NM, Piatt JF (1993) Foraging ecology as related to the distribution of planktivorous auklets in the Bering Sea. In: Vermeer K, Briggs KT, Morgan KH, Siegel-Causey D (eds) The status, ecology and conservation of marine birds in the north Pacific. Canadian Wildlife Service Spec Pub, Ottawa
- ✦ Jaquet N, Whitehead H (1996) Scale-dependent correlation of sperm whale distribution with environmental features and productivity in the South Pacific. *Mar Ecol Prog Ser* 135:1–9
- Keen EM (2016) Bangarang. v.1.0.0. R package. Available at <https://github.com/ericmkeen/bangarang>
- ✦ Levin SA (1992) The problem of pattern and scale in ecology. *Ecology* 73:1943–1967
- Macdonald RW, Bornhold BD, Webster I (1983) The Kitimat fjord system: an introduction. In: Macdonald RW (ed) Proceedings of a workshop on the Kitimat marine environment. Can Tech Rep Hydrogr Ocean Sci No. 18. Institute of Ocean Sciences, Sidney, p 2–13
- Manly BFJ (1991) Randomization and Monte Carlo methods in biology. Chapman & Hall, London
- Manly BFJ, McDonald LL, Thomas DL, McDonald TL, Erikson WP (2002) Resource selection by animals: statistical design and analysis for field studies. Kluwer Academic Publishers, Dordrecht
- ✦ Masson D, Cummins PF (2000) Fortnightly modulation of the estuarine circulation in Juan de Fuca Strait. *J Mar Res* 58: 439–463
- ✦ Mayo C, Marx M (1990) Surface foraging behavior of the North Atlantic right whale and associated zooplankton characteristics. *Can J Zool* 68:2214–2220
- McCullagh P, Nelder JA (1989) Generalized linear models, 2nd edn. Chapman & Hall, London
- Pearson TH (1989) Fjordic ecosystems. In: Ray L, Alexander V (eds) Proc Sixth Conf Comité Arctique Int, 13–15 May 1985, Fairbanks, Alaska. Vol 6. Brill Academic Publishers, Leiden
- ✦ Pershing AJ, Record NR, Monger BC, Mayo CA and others (2009) Model-based estimates of right-whale habitat use in the Gulf of Maine. *Mar Ecol Prog Ser* 378:245–257
- Piatt JF (1990) The aggregative response of Common Murres and Atlantic Puffins to schools of capelin. *Stud Avian Biol* 14:36–51
- ✦ Piatt JF, Methven DA (1992) Threshold foraging behavior of baleen whales. *Mar Ecol Prog Ser* 84:205–210
- ✦ Pickard GL (1961) Oceanographic features of inlets in the British Columbia mainland coast. *J Fish Res Board Can* 18:907–999
- R Development Core Team (2013) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, www.R-project.org/
- ✦ Ramp C, Hagen W, Palsboll P, Berube M, Sears R (2010) Age-related multi-year associations in female humpback whales (*Megaptera novaengliae*). *Behav Ecol Sociobiol* 64:1563–1576
- ✦ Redfern JV, Ferguson MC, Becker EA, Hyrenbach KD and others (2006) Techniques for cetacean-habitat modeling. *Mar Ecol Prog Ser* 310:271–295
- ✦ Reilly SB (1990) Seasonal changes in distribution and habitat differences among dolphins in the eastern tropical Pacific. *Mar Ecol Prog Ser* 66:1–11
- Reilly SB, Fiedler PC (1994) Interannual variability of dolphin habitats in the eastern tropical Pacific. I. Research vessel surveys 1986–1990. *Fish Bull* (Wash DC) 92:434–450
- ✦ Roman J, Estes JA, Morissette L, Smith C and others (2014) Whales as marine ecosystem engineers. *Front Ecol Environ* 12:377–385
- Stachelek J (2015) ipdw. v.02-4. R package. Available at <https://github.com/jsta/ipdw>
- ✦ Symonds MRE, Moussalli A (2011) A brief guide to model selection, multimodel inference and model averaging in behavioural ecology using Akaike's information criterion. *Behav Ecol Sociobiol* 65:13–21
- Syvitski JPM, Burrell DC, Skei JM (1987) Fjords: processes and products. Springer-Verlag, New York, NY
- Thomson RE (1981) Oceanography of the British Columbia coast. *Fish Aquat Sci Spec Pub* 56
- ✦ Turner NJ (2003) The ethnobotany of edible seaweed (*Porphyra abbottae* and related species; Rhodophyta: Ban-

- giales) and its use by First Nations on the Pacific Coast of Canada. *Can J Bot* 81:283–293
- ✦ Vu ET, Risch D, Clark CW, Gaylord S and others (2012) Humpback whale song occurs extensively on feeding grounds in the western North Atlantic Ocean. *Aquat Biol* 14:175–183
- ✦ Ware C, Friedlaender AS, Nowacek DP (2011) Shallow and deep lunge feeding of humpback whales in fjords of the West Antarctic Peninsula. *Mar Mamm Sci* 27:587–605
- ✦ Weinrich MT, Schilling MR, Belt CR (1992) Evidence for acquisition of a novel feeding behavior: lobtail feeding in humpback whales, *Megaptera novaeangliae*. *Anim Behav* 44:1059–1107
- Wheeler B, Rambeau A, Zottenberg K (2010) Technical data report: Marine mammals. Enbridge Northern Gateway Project. Stantec, Vancouver
- Williams R, O'Hara P (2010) Modelling ship strike risk to fin, humpback and killer whales in British Columbia, Canada. *J Cetacean Res Manag* 11:1–8
- Williams R, Thomas L (2007) Distribution and abundance of marine mammals in the coastal waters of British Columbia, Canada. *J Cetacean Res Manag* 9:15–28
- Williams R, Clark CW, Ponirakis D, Ashe E (2013) Acoustic quality of critical habitats for three threatened whale populations. *Anim Conserv*. doi:10.1111/acv.12076
- Wood S (2006) Generalized additive models: an introduction with R. Chapman & Hall/CRC Press, Boca Raton, FL
- Zuur AL, Ieno EN, Walker NJ, Saveliev AA, Smith GM (2009) Mixed effects models and extensions in ecology with R. Springer, New York, NY

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