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Distribution, movements and habitat fidelity patterns of Fin Whales (*Balaenoptera physalus*) in Canadian Pacific Waters

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Foreword

This series documents the scientific basis for the evaluation of aquatic resources and ecosystems in Canada. As such, it addresses the issues of the day in the time frames required and the documents it contains are not intended as definitive statements on the subjects addressed but rather as progress reports on ongoing investigations.

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ABSTRACT

Fin Whale distribution and habitat use in northern waters of British Columbia (BC) were investigated using a multi-scale study approach based on data collected by Fisheries and Oceans Canada's Marine Mammal Research Section. Ship-based survey data were used to model Fin Whale distribution as a function of habitat features in Hecate Strait and Queen Charlotte Sound and the results indicate that Moresby Trough and Greater Caamaño Sound were predicted to have the highest densities of whales. Photo-identification data were used to assess movement and site-fidelity of individual Fin Whales, and to estimate abundance. There was little indication of movements between the inshore region of Hecate Strait and Queen Charlotte Sound and the offshore region of Canadian Pacific waters, although there was more photo-identification effort applied to the inshore region. The overall abundance of Fin Whales present in the Hecate Strait and Queen Charlotte Sound region (including Greater Caamaño Sound) at any one time during the study period (2009-2014) was estimated to be 405 Fin Whales (CV = 0.6, 95% CI = 363-469), based on a photo-identification mark-recapture model. Analysis of satellite-linked telemetry tags using State-Space-Switching modelling indicated that tagged Fin Whales (n=19) remained in the area of Hecate Strait and Greater Caamaño Sound for the duration of their tag transmissions and exhibited extended periods of Area-Restricted-Search (ARS) movement behaviour which may represent foraging behaviour. Analysis of satellite-linked dive tags (n=6) indicated that during periods of ARS movement, dives were deeper during the day (70.1 ± 52.1 m SD) than at night (24.9 ± 17.4 m SD) and likely represented foraging behaviour. Tagged Fin Whales, particularly in Caamaño Sound, where most of the dive tags were deployed, dove consistently to depths likely associated with dense day-time zooplankton layers.

INTRODUCTION

Fin Whales, like other large baleen whales, range over vast ocean areas. In the eastern North Pacific, for example, Fin Whales that were marked using 'Discovery' tags during the whaling era often travelled well over 1000 km between where they were marked and where they were killed (Mizroch *et al.* 2009). Fin Whales in the North Pacific were depleted by commercial whaling and their population is considered to be at least 50% below pre-exploitation estimates (COSEWIC 2005; Gregr *et al.* 2006). During the British Columbia whaling era, Fin Whales were considered one of the most abundant large whale species in Canadian waters (Pike and MacAskie 1969). At least 7,605 animals were killed by coastal whalers from 1908 to 1967 (Gregr *et al.* 2000). They are listed as threatened under the Species-at-Risk Act because they have since remained uncommon in BC waters. There are presently no reliable or complete estimates of population abundance in the North Pacific and no estimates for Canadian Pacific waters.

Fin Whales are large-bodied filter-feeders that feed on small prey organisms such as euphausiids, copepods, and small fish. Fin Whales, like other large baleen whales, depend on locating dense aggregations of prey. Estimates made of the energetic costs of lunge feeding demonstrate that net energy return for these animals is highly dependent on the density of prey (Goldbogen *et al.* 2007; Goldbogen *et al.* 2006; Acevedo-Guitierrez *et al.* 2002). Thus, the movements and distribution of these animals are influenced by the distribution of their prey.

Dense patches of zooplankton are the result of oceanographic processes that enhance productivity and (or) serve to aggregate zooplankton prey (Gregr and Trites 2001). These processes create profitable but ephemeral foraging conditions for these large-bodied grazers. In a study of Fin Whale distribution off the West Greenland shelf in relation to physical and biological covariates, Laidre *et al.* (2010) found that Fin Whale density was positively correlated with krill abundance, but only when there was close spatial and temporal proximity (less than a few days) between whale sightings and krill acoustic backscatter volume measurements. In the Gulf of St Lawrence, the distribution of baleen whales was associated with the formation of sea surface temperature (SST) gradients. Thermal fronts are created by tide or wind-induced upwelling, which were hypothesized to either increase productivity, or to herd krill into dense patches. These SST fronts were dynamic and changed over periods of hours or days (Doniol-Valcroze *et al.* 2007).

Key to understanding the ecology of Fin Whales in a region are studies of their movements, the types of habitat with which they are associated, and their behaviour. Studies that collect sighting data from systematic surveys, photo-identifications of individual animals, and movements and dive behaviour from satellite-linked tags, can complement each other and provide important insight into population distribution, size and habitat use.

Sightings collected by systematic methods provide useful spatial information about whale distribution over a broad area; data that can be used to model distribution as a function of habitat predictors to explore patterns of habitat use in a region (Panigada *et al.* 2008, Laidre *et al.* 2010, Dalla Rosa *et al.* 2012). Photo-identification techniques are widely used in the study of cetaceans to estimate their abundance or to investigate movements and site fidelity in populations of Killer Whales, Blue Whales, Fin Whales, and Humpback Whales (Bigg *et al.* 1990; Calambokidis and Barlow 2004; Calambokidis *et al.* 2008a; Calamokidis *et al.* 2009; Ramp *et al.* 2014). Tagging technology for tracking whale movements and dive behaviour has advanced considerably in recent years, particularly with the ability to transmit data signals to satellites. Methods to analyse tracking data have also advanced (Jonsen *et al.* 2005; Bailey *et al.* 2009). Here, we present the results of several analyses to investigate population distribution, size, movements, site fidelity, and behaviour of Fin Whales in British Columbia. Each analysis can be viewed as complimentary to one another at different spatial and temporal scales.

METHODS

Canadian Pacific waters were divided into an offshore and an inshore region (Figure 1A). The western boundary of the inshore region was defined by the 1000m contour along the continental edge from Triangle Island to the northern Canadian border to distinguish the large inshore region of Hecate Strait and Queen Charlotte Sound (including the steep canyon features of western Queen Charlotte Sound), from the deep ocean waters west of the continental shelf, and the generalized 100m contour south of Triangle Island to the southern Canadian border. The 100m depth contour was selected to distinguish inshore from offshore off the west coast of Vancouver Island because the continental slope is more gradual off west coast Vancouver Island than it is to the north. The inshore region was further subdivided into five sub-regions (Figure 1B), primarily for the purpose of examining Photo-ID derived movement information. The sub-regions are:

1. Dixon Entrance,
2. western Hecate Strait and Queen Charlotte Sound,
3. eastern Hecate Strait and Queen Charlotte Sound,
4. Greater Caamaño Sound (includes Caamaño and Campania Sounds and Squally and Whale Channel which comprise Gil Basin (MacDonald *et al.* 1983), and
5. coastal Vancouver Island.

Most research effort has occurred in the area that encompasses 2, 3, and 4.

FIN WHALE DISTRIBUTION AND DENSITY MODELLING

We investigated the distribution of Fin Whales in relation to habitat variables in BC waters using GIS and generalized additive models (GAMs). We used Fin Whale sightings and effort from ship-based surveys and four candidate habitat covariates (depth, slope, X (Easting) and Y (Northing) UTM coordinates).

Ship surveys

Cetacean survey effort and observations were collected using standard line transect sampling data collection procedures during dedicated surveys from 2002 to 2014, primarily from Canadian Coast Guard (CCG) research vessels. Ford *et al.* (2010) provides a full description of the protocol, equipment and ships used. In general, surveys varied from 1 to 3 weeks in duration and were undertaken in all seasons, defined as follows: winter (January-March), spring (April-June), summer (July-September) and fall (October-December). During surveys, dedicated observers followed a scheduled 90 minute shift consisting of two 30-minute rotations of visual observation and one 30-minute rotation of data recording. Observer teams were sufficient in size to allow breaks so as to avoid observer fatigue. At all times, when on effort, two observers were stationed on the observation platform (one on the starboard side, the other on port). The third observer recorded data, including effort information, environmental conditions, and observations relayed by FRS radio from the observers. The position of the ship and its speed were recorded by means of a GPS. Effort was defined as ‘ON’ when observers were on watch, weather was favourable (Beaufort scale < 5 and visibility > 1 nm), and the ship was travelling at > 5 kts. Beginning in 2006, visibility was further classified into *excellent* (clear horizon, excellent lighting), *good* (clear horizon), *fair* (no horizon, > 3 nm visibility), and *poor* (< 3 nm of visibility).

Effort was defined as ‘OFF’ when no observers were available, or when weather deteriorated (sea state > 4, visibility < 3 nm) or when the ship slowed or stopped. When a whale was observed, observers reported the horizontal angle of the sighting from the ship’s heading and the number of reticles below the horizon to the sighting. These two measures are used to estimate the geographic coordinates of the sighting.

Survey Data Processing

Forty-two surveys were candidates for inclusion in an analysis of Fin Whale distribution. Each survey was filtered for effort and sightings based on environmental conditions and details of the sightings. Portions of the survey track and associated sightings when effort was recorded as OFF were excluded. Once filtered the geographic position of each sighting associated with the remaining effort was estimated. First distance to the sighting was calculated based on the following equation:

$$d = \frac{a}{\tan \theta}$$

Where *d* is the distance (m) of the sighting from the ship (position of the observer), *a* is the height of the average observer above sea level (estimated height is known for each ship) and θ is the angle from the observer to the sighting recorded by the observers in reticles below the horizon (radians per reticle are known for the binoculars used). Geographic coordinates for sightings were then calculated using the estimated distance, the geographic coordinates of the ship’s position and the angle of the sighting from the heading of the ship.

Survey Effort

The extent of survey effort associated with survey tracks, was calculated from a buffer based on the estimated maximum sighting distance from the track line for each survey using ArcMap 10.2.2 (ESRI 2014). When visibility was recorded as *excellent or good*, indicating that the horizon was visible, the estimated maximum sighting distances were 3.45 nm (6.40 km) to 7.59 nm (14.05 km) depending on the ship and platform (e.g. bridge or the more elevated Monkey’s Island). If visibility was recorded as *fair* then the visible range, and hence the buffer, was reduced to 3 nm (5.55 km) regardless of ship or platform. A 25 km^2 resolution for our analysis of distribution and density of Fin Whales was deemed to be ecologically reasonable (not too large) for investigating predictive relationships between these large and highly mobile cetaceans and their habitat. We applied a 25 km^2 resolution grid to the entire Canadian Pacific waters and clipped out land from cells adjacent to shore and recalculated the size of the cells. We assigned the buffered effort and associated sightings to these grid cells and calculated the km^2 of survey effort in each grid cell using the tool “insecpolypoly” in the software package Geospatial Modelling Environment (Beyer 2012).

Habitat Variables

We used the bathymetric and slope raster layers of the British Columbia Digital Elevation model (gridded from the 1:25000 Canadian Hydrographic Service bathymetric contours) to calculate summary statistics for depth (m) and slope (degrees) in each grid cell. We calculated mean, maximum, minimum, range, and standard deviation for these two variables using the zonal statistics tool within the Spatial Analyst extension of ESRI ArcMap software (ESRI 2014). We calculated the geographic position at the centre of each cell in units of latitude and longitude, as well as in UTM coordinates. (Table 1). Latitude and longitude were included because they may be proxy for biological or physical property that ultimately affects distribution (Dalla Rosa *et al.* 2012).

Survey Data Selection

We examined the spatial and temporal extent of 42 surveys in three areas, one area was Hecate Strait and Queen Charlotte Sound which was comprised of the sub-regions of eastern Hecate Strait and Queen Charlotte Sound, western Hecate Strait and Queen Charlotte Sound and Greater Caamaño Sound. The other two areas were the sub-region of Dixon Entrance and the offshore region. We had no survey effort for the coastal Vancouver Island region for this analysis. We noted that survey effort was not distributed equally over the coast and that only portions of the coast were surveyed on each cruise, because survey coverage was dependent on the cruise duration, weather and sea conditions, and at times, range restrictions of the ship. Consequently there was considerable variability among surveys. To address this problem, the extent of effort coverage was used to guide the selection of surveys for each of the three area described above. This approach minimized spatial heterogeneity in the analysis which would be difficult to account for in a model of Fin Whale distribution (Zuur *et al.* 2010). It meant, however, that a different selection of surveys would be candidates for each study area. In the Hecate Strait and Queen Charlotte Sound area, all 42 surveys intersected the area to some extent but of these 37 were considered to have sufficient spatial coverage in the study area for inclusion in analysis. There was not sufficient coverage from 17 surveys that intersected the offshore region to proceed with modelling Fin Whale distribution in the offshore region. Although Twenty-three surveys intersected the Dixon Entrance area to some extent, coverage was deemed too heterogeneous to proceed with modelling. Consequently modelling proceeded only with a dataset for the Hecate Strait and Queen Charlotte Sound area (Appendix Figure A1).

After selecting the surveys that would comprise the Hecate Strait and Queen Charlotte Sound dataset, we filtered the data to remove small grid cells. Before filtering, grid cells ranged in size from 0.005 to 25 km^2. We explored the effect of removing small grid cells, by visually inspecting maps using several possible filtering thresholds. Based on this, we removed grid cells (and associated effort and sightings) that were < 11 km^2. This removed cells adjacent to shore – habitat in which Fin Whales would not be expected to occur. Next we filtered survey records to remove survey effort in which less than half of the grid cell had been surveyed. These steps served to reduce the number of zeros in the datasets, resulting from unrealistically low effort in grid cells, and removed the small grid cells (< 11km^2). We noted that removing these grid cells and associated effort did not result in loss of Fin Whale sightings, although this was not a basis for applying these filter thresholds.

Analysis

The Hecate Strait and Queen Charlotte Sound dataset was explored for the presence of outliers using Cleveland dot plots, and assessed for potential collinearity among the covariates via scatterplots and estimation of Pearson correlation coefficients and Variance Inflation Factors. We found Easting UTM (~ Longitude) and Northing UTM (~ Latitude) to be correlated ($r = 0.6$. $p < 0.05$), and based on this we excluded Easting UTM from our models, but retained Northing UTM because of the two, latitude has been described by others as an important proxy for biological or physical properties (Dall Rosa *et al.* 2012). Each covariate was plotted with the response variable (number of whales), to visualize relationships (Zuur *et al.* 2010). Following this, a Generalized Linear Model (GLM) with a poisson distribution, was used to investigate the dispersion characteristic of the model. Based on the findings of this exploration, modelling proceeded using a negative binomial distribution to account for zeros in the response variable. In all models, an offset term was added to account for differences in survey effort ($\log(km^2)$) among grid cells. In the poisson GLM, we also investigated the relationship between each covariate and model residuals to determine if nonlinear relationships were evident (Zuur 2012). Based on this all further candidate models were constructed as Generalized Additive Models (GAM; logarithmic link function) to incorporate the non-linear relationships between Fin Whales and habitat covariates. We constructed GAMs in R using the "mgcv' packaged (Wood 2004). The global GAM model was of the following form:

$$N \sim s(Northing\_utm) + s(slope) + s(depth) + offset(\log(area\_surveyed(km^2)))$$

Model Selection

We selected the best-fit GAM by comparing the AIC scores (Zuur 2012) of the candidate models generated from the global model. We avoided GAM overfitting by incorporating the multiplier gamma=1.4 (Kim and Gu 2004) to inflate the effective degrees of freedom (*e.d.f.*) in the REML score. Once the top-ranked GAMs were selected by AIC, we used the R function "gam.check" (Wood 2011) to determine if there were smoother terms in the model for which *k* (basis dimensions) were potentially too low (Wood 2006). Finally we assessed whether or not there was spatial autocorrelation in model residuals by visually inspecting the distribution of residuals plotted by size over the *x*-*y* coordinates of the study area. We calculated mean ± standard deviation as summary statistics.

FIN WHALE MOVEMENT AND ABUNDANCE BASED ON PHOTO-IDENTIFICATION STUDIES

We applied photo identification techniques to examine site fidelity and movement patterns of Fin Whales among the regions and sub-regions of the study area (Figure 1). Opportunistic photo identification of Fin Whales in BC waters began in 1995, and dedicated studies after 2001 with the formation of the DFO Pacific Cetacean Research Program. Photo-identifications were collected by observers stationed on CCG ships or vessels chartered for cetacean surveys and from small vessels deployed from CCG and charter vessels. Photo-identifications were also collected opportunistically and provided by experienced observers and volunteers. Search effort was focused on locating areas of high concentrations of animals and then on photographing as many of the individuals as possible.

Photo-identification

Fin whales were approached within 30 metres by a research vessel and photographed using digital SLR cameras with telephoto lenses (200-300mm range). The right side of each animal's dorsal fin and flank was photographed, ideally from a position directly perpendicular to the dorsal fin, and parallel to the long axis of the animal. Both left and right sides of each animal were photographed when possible. The geographic coordinates of each encounter were manually recorded, or collected automatically via a GPS linked to the digital SLR. At the completion of each research day, the digital images were examined and the best photograph of each animal from that day was selected. Each of these was called a photo-ID event. At the completion of a field season, all photo-ID events were cross-compared to aggregate photo-IDs of the same animal, and then two experienced photo-identification matchers compared the photo-IDs of each animal to the digital British Columbia Fin Whale catalogue (hereafter referred to as the BCFWC or "catalogue"). Matches were based on a combination of dorsal fin shape, nicks, holes in the fin, and scarring patterns. A match was confirmed by at least two matching features. Animals not found in the catalogue were compared to each other a final time to check for missed within-season matches, and then if no matches were found, the animal was assigned a unique BCFWC ID number. Only right side photographs were selected from the dataset of photo-ID events for analysis. Each photo-ID event was assigned to the region and sub-region where it was collected. Dependent calves were excluded from all analysis because their sightings would not have been independent of their mother's. Furthermore, calves lack identifying scars and have undeveloped fin shapes, and they are, therefore, unlikely to be re-matched correctly in the future.

Discovery Curves

The relationship between the cumulative number of unique individuals encountered over the course of the study (1995-2015) as a function of cumulative effort (in this case the cumulative number of ID events), were plotted for the entire coast, for each region, and for each sub-region.

Site fidelity and Movement

Inter-annual site fidelity and movements was investigated by limiting the dataset to animals that had been photographically documented in two or more years over the entire time series of the catalogue (1995-2015). From this smaller dataset, we calculated the percentage of animals that had returned to only one area and the percentage that had returned to multiple areas. We undertook this analysis at two spatial scales,

1. movement between the offshore region to the inshore region, and
2. movement among the inshore sub-regions.

Mark Recapture Analysis

Photo-identification capture histories of independent (non-calf) individual Fin Whales were used in a mark-recapture analysis to estimate survival and population size in western Hecate Strait and Queen Charlotte Sound, eastern Hecate Strait and Queen Charlotte Sound and Greater Caamaño Sounds (Figure 1B). The photo-ID dataset was limited geographically to photo-ID events collected in these sub-regions and in the years 2009 to 2014 because this represented the data with the highest and most consistent effort. Data were filtered for quality to meet a mark-recapture assumption that each animal had an equal probability of capture and recapture. To assess whether each photographed animal in the dataset would meet this assumption, each photograph (photo-ID event) was reviewed twice by two technicians who ranked each photo independently according to four criteria: proportion of the animal's flank photographed, angle, focus, and exposure, following the methods of Falcone *et al.* (2011). Rankings for each criterion was on a 3-point scale (1 = best, 3 = worst). Animals whose images received a score of 3 on a criterion by both technicians were removed from the dataset. Once the photo-ID dataset was filtered, a capture history, using year as the sampling period, was created for each individual.

Modelling Survival

Apparent survival, which is the product of true survival and the probability that the individual does not permanently leave the study area was estimated using the open population Cormack Jolly Seber (CJS) model (Cormack 1964; Jolly 1965; Seber 1965). This model estimates the apparent survival probability of individuals in the population in the interval between two successive sampling periods for individuals captured in the first year. Recapture probabilities of those individuals in each of the sampling periods were also modeled. During exploration of the dataset it became evident that a large number of individuals had not been recaptured after they were initially marked, a condition termed "transience" in mark-recapture modelling. Transience is the presence of marked and released individuals which then permanently emigrate from the study area and are therefore unavailable for future recapture (Pradel *et al.* 1997). If not accounted for in the CJS model, transience can negatively bias apparent survival estimates. Time-since-marking (TSM) CJS models were run to account for transience. TSM CJS models are a parameterization of the CJS model and estimate apparent survival separately for two "time-since-marking" intervals: the interval immediately following initial marking throughout the study period, and the subsequent intervals after this initial interval. The apparent survival estimates over the initial interval are subject to the negative bias of transience. The apparent survival estimates of the subsequent intervals represent apparent survival of animals recaptured in the study area and are the estimates of interest (Pradel *et al.* 1997). With both sets of “time-since-marking” intervals apparent survival was modeled two ways; varying over time, and as constant. Recapture probabilities were modelled only as varying annually because recapture probabilities are dependent on annual effort, which did vary.

Modelling Abundance

Population abundance estimates were generated using the POPAN parameterization of the open population unconditional Jolly-Seber model (POPAN model) (Schwarz and Arnason 1996). Estimates of apparent survival, recapture probabilities, and probabilities of entry into the population were obtained from the POPAN model. The POPAN model produces an estimate of the super population size which is the number of animals available for capture at any point during the study period, as well as a population abundance at each sampling occasion after the initial sampling period. In the POPAN model, apparent survival was modeled both as varying over time and as a constant, but recapture probabilities were only modeled as varying annually. Probability of entry into the population was modelled to vary with time because there is no biological reason to model it as a constant.

Model Assumptions

The assumptions of these models, as presented in Amstrup *et al.* (2005), are as follows:

1. Every animal alive in the population at a given sampling period has the same probability of being re-sighted (this is limited to marked animals in the conditional CJS model);
2. Every marked animal alive in the population following a sampling period has the same probability of survival to the next sampling period;
3. Marks are neither lost nor overlooked, and are recorded correctly;
4. Sampling periods are instantaneous;
5. All emigration from the sampled area is permanent;
6. The fate of each animal with respect to capture and survival is independent of the fate of any other animal.

Modeling was conducted using the R package ‘RMark’ (Laake 2013) as an interface to the program ‘Mark’ (Version 8) (White and Burnham 1999).

Goodness-of-fit Testing and Mark-Recapture Model Selection

Goodness of fit (GOF) of the mark recapture models was assessed using the program U-CARE, which compares the fit of the data to the fully time dependent CJS model using four different tests (Choquet *et al.* 2005, 2009). In the specific case of the TSM CJS models, GOF was assessed using the sum of three U-CARE tests excluding the fourth test which failed because of transience (Pradel *et al.* 1997). Because there is no means to modify the POPAN JS model to account for transience, a variance inflation factor, was applied to the estimates. The variance inflation factor (Median $\hat{c}$) was calculated for the fully time dependent CJS model and then applied to the POPAN JS estimates (Cooch & White 2002). Model selection was based on comparison of Akaike information criterion scores (Akaike 1973). These were corrected for small sample size for the TSM CJS models (AICc; Hurvich & Tsai 1989). For the POPAN model estimates, quasi-AIC (QAIC; Lebreton *et al.* 1992) values were collected to take into account the variance inflation factor (Median $\hat{c}$) (Burnham and Anderson 2002). Models with AICc score differences of less than two, and with weights greater than 0.9, were considered the ‘best’ model(s)(Burnham and Anderson 2002; Grueber *et al.* 2011).

FIN WHALE MOVEMENT AND DIVE BEHAVIOUR FROM SATELLITE-LINKED TAGS

Satellite Tag Instrument Details

Satellite-linked platform transmitter terminals (PTTs: SPOT5 or SPLASH10; Wildlife Computers, Redmond, WA) were attached to individually identifiable Fin Whales in the vicinity of Caamaño Sound between August and October (2011-2014). These instruments transmitted location, temperature (resolution = 0.05ºC), and depth data (for SPLASH10 only; resolution 0.5 m) via the Argos satellite system and were equipped with a salt-water switch (wet-dry sensor) to delay transmissions until whales were at the surface. PTTs used the Low Impact Minimally Percutaneous External-electronics Transmitter (LIMPET) configuration (Andrews *et al.* 2008), and were attached using sub-dermal barbs near the base of the dorsal fin to maximize the time that tags were exposed for transmitting. PTTs were set to transmit every day between the hours of 2:00-5:00, 11:00-13:00, 16:00-18:00 and 20:00-23:00 UTC in 2011 and 2012; 1:00-3:00, 5:00-7:00, 10:00-13:00, and 17:00-22:00 UTC in 2013, and every hour of the day in 2014. Transmissions were limited to 400 messages per day for all SPOT5, 500 messages for SPLASH10 tags in 2013, and 450 messages for SPLASH10 tags in 2014. Tags were deployed from the bow of a 70 ft steel-hulled sloop, *SV* Achiever, or a 30 ft aluminum motor vessel, *SV* Roller Bay using a pneumatic rifle. Photographs of tagged Fin Whales were taken at the time of deployment to identify each individual from an existing catalogue using unique features of the flank and dorsal fin, including pigmentation, scarring, nicks, and fin shape.

The SPLASH10 tags were programmed to summarize diving behaviour with binning of maximum depth, time at temperature, and time at depth data over six hour periods (01:00–06:59, 07:00–12:59, 13:00–18:59, and 19:00–00:59 GMT). Dive depth was sampled at one second intervals, temperature and the wet/dry sensor was sampled at 10 second intervals, and dives were recorded whenever a whale was submerged at depths of ≥10 m for >30 sec (2013 tag deployments) or >1 min (2014 deployments). Dive shapes were determined using Wildlife Computer’s Dive Analysis Program (DAP, version 3.0, build 299), which assigned dives to “Square”, “U”, or “V” shaped categories depending on the proportion of total dive time that the whale spent at depths ≥80% of the maximum dive depth (i.e., relative bottom time: >50%, 20-50%, and <20%, respectively). Surface durations (i.e., time spent at depths <10 m) were recorded between dives, beginning at the time the wet-dry sensor first read “dry” and ending when the sensor next read “wet” (i.e., when the next dive had begun). We plotted time-depth profiles for the first 24 h of each SPLASH10 tag deployment to assess whether Fin Whales exhibited any atypical dive behaviour patterns as a result of being tagged, with the aim of excluding these portions of each track prior to analysis.

A local ground-based receiving station (Mote; Wildlife Computers) was installed on Campania Island (53.046° N, 129.343° W) in 2014 with the goal of increasing the collection of tag sensor data from the SPLASH10 tags. The number of data messages from the tags that could be received directly by the satellite receiver was limited by satellite coverage. The Mote, on the other hand, could receive messages constantly, thereby boosting the amount of data received, however it could not calculate Doppler locations; which meant although more dive information was be collected there was no boost to the amount of location data.

State-Space Movement Modelling

A Bayesian state-space switching model (SSSM, as described by Jonsen *et al.* 2005) was fitted to the satellite location data (excluding location class “Z”) to take into account error in location estimates, normalize the data so that there were 12 locations per day, and to infer either transiting or area-restricted search (ARS) behaviour from animal movements. ARS behaviour is characterized by decreases in an animal's rate of travel and/or increases in its turning frequency and angle, and is presumed to represent foraging activity, although it could represent other types of behaviour as well, such as socializing (Turchin 1991). Behavioural state (behaviour = 1 for transiting and 2 for ARS) for each location was estimated as the mean value of the Markov Chain Monte Carlo (MCMC) samples, and locations with mean estimates of behaviour <1.25 were assumed to represent transiting, behaviour >1.75 represented ARS, and intermediate behaviour values were considered uncertain. The Argos Kalman filter positioning algorithm (Lopez & Malardé 2011) was applied to the location data. The R package 'bsam' (Jonsen 2014) was used for fitting the hDCRWS model (hierarchical first-difference correlated random walk with switching model) to estimate movement parameters across multiple animals. Estimates were made on aggregated data from multiple animals with the aim of improving the precision of estimates given that some tracks were too short to estimate separately. Track data were split into four groups by year and modelled in R with JAGS (Plummer 2003). Model convergence and sample autocorrelation were assessed by visually inspecting autocorrelation and trace plots.

Fin Whale Dive Behaviour Modelling

For each SPLASH10 tag deployment, we matched the dives with corresponding SSSM behavioural states by associating the start time of each dive with the closest SSSM location. Since modelled locations were estimated every 2 h, each dive was associated with a SSSM position and time that occurred no more than 1 h (half of each SSSM time-step) before or after the dive itself was logged. Dives that occurred >1 h before the first SSSM location or >1 h after the last location in each tag record were discounted from our analysis. We investigated diel patterns of Fin Whale diving behaviour by assigning each SSSM location to either "day" or "night" by relating its time to the timing of nautical dawn (solar elevation < -12°) or dusk (solar elevation ≥ -12°) at that position on that specific day, month and year. Timing of dusk and dawn was calculated using an Excel VBA routine (Pelletier n.d.) based on the implemented a National Oceanic and Atmospheric Administration (NOAA) solar calculator, which calculates the timing of sunrise, sunset, and solar noon, and the solar position for any location on Earth.

To examine differences in Fin Whale diving behaviour between the inshore channels of Caamaño and Campania Sounds versus the open waters of Hecate Strait, we also assigned each dive to one of these two regions based on the position of its corresponding SSSM location. We selected dives associated with locations designated as ARS (i.e., inferred "foraging)") by the SSSM (behaviour > 1.75) for further analysis (N = 7,489 dives). We then examined whether the maximum dive depths (m) of these ARS dives differed with respect to time of day (i.e., day versus night), region (Hecate Strait versus Greater Caamaño Sounds), dive shape (Square, U, or V), or dive duration (min). We also investigated possible relationships between ARS dive durations (min) and the same covariates (plus maximum dive depth (m). Investigation of these relationships was accomplished using Generalized Additive Mixed Models (GAMMs) with Gamma error distributions (logarithmic link function), which we fit by maximum likelihood methods (Laplace approximation) using the R package 'gamm4' (Wood and Scheipl 2014). A random effect of SSSM location ID nested within whale ID (PTT) was included in both models to account for both the repeated association of the same SSSM location with multiple dives in each deployment record, and for within-individual variance in diving behaviour. Prior to modelling, we examined the raw ARS-associated dive data to ensure that it did not contain outliers, collinearity between explanatory covariates, unbalanced categorical covariates, or zero-inflation (Zuur *et al.* 2010). We also used co-plots to assess which interaction terms between covariates should be included in the models. All covariates were centred (means subtracted) and scaled (divided by 1 standard deviation) prior to fitting the GAMMs. We compared each global model with a corresponding null model (without fixed effects) using Akaike's information criterion (AIC) score comparisons. The ability of smoothers to account for non-linear relationships between the GAMM response variable and explanatory covariates was assessed by running a post-hoc Generalized Additive Model (GAM) on the original GAMM residuals as a function of each smooth term. Temporal correlation in model residuals was assessed using an Autocorrelation Function (ACF) plotted in R. Significance of fixed effects were detected using Wald's t-values and associated approximate p-values (α= 0.05) produced by the best-fit GAMMs. GAMM results are reported as model estimates ± standard errors (s.e.).

RESULTS

FIN WHALE DISTRIBUTION AND DENSITY MODELLING

Thirty-seven surveys were selected based on spatial extent of effort in Hecate Strait and Queen Charlotte Sound. Most of the surveys occurred in summer (n=20), (Table 2). All survey effort and sightings were aggregated and analysed as a single dataset (Table 3) because the imbalance in temporal coverage (insufficient data) precluded an analysis of Fin Whale distribution in the study area by either year or season. Visual inspection of the survey sightings by season, however, showed no evidence of a seasonal pattern to the distribution of sightings, which lent support to our choice to aggregate the data.

The top ranked model for Hecate Strait and Queen Charlotte Sound included smoothers for Northing UTM , slope, and depth (Table 4, Table 5). The model predicted mean densities of 0.008 ± 0.020 whales/km^2 (range = 0 to 0.26 whales/km^2) throughout the area comprised of Hecate Strait, Queen Charlotte Sound and Greater Caamaño Sound. Highest densities of Fin Whales were predicted in Moresby Trough (mean = 0.03 ± 0.03 whales/km^2, range = 0 – 0.15 whales/km^2) and in the Greater Caamaño Sound sub-region (mean = 0.03 ± 0.05 whales/km^2, range = 0 – 0.26 whales/km^2), where mean depths were 248 ± 85 m and 259 ± 124 m respectively (Figure 2). The smooth term for slope indicated that Fin Whale density declined when mean slope increased (steeper) beyond about 2˚. The smooth term for depth indicated that Fin Whale density increased with increasing mean depths to about 400 m, after which it leveled out. The smooth term of Northing UTM indicated that Fin Whale density increased slightly from latitude 51˚ to latitude 52.3˚ (Figure 3).

FIN WHALE MOVEMENT AND ABUNDANCE MODELLING FROM PHOTO IDENTIFICATION

During the period 1995-2015, 1549 Fin Whale photo-ID events were collected coast-wide, equating to 681 individual Fin Whales identified in BC waters (Table 6, Figure 4). On a coast-wide basis, the rate of discovery of new animals did not slow over the time series, reflecting the large number of animals that were only seen once in both regions (504 of 681 animals) (Figure 5 and 6). The majority of photo-ID events and unique Fin Whale identifications came from the inshore region (485 of 681 animals) (Figure 7). Inshore regional effort (ID Events) was highest in the Greater Caamaño Sound sub-region. This is due to the year-round presence of the North Coast Cetacean Society in that area and focused photo-ID and satellite tagging efforts by the Cetacean Research Program in recent years. Both Western Hecate Strait and Queen Charlotte Sound, and eastern Hecate Strait and Queen Charlotte Sound sub-regions had less effort than Greater Caamaño Sound, but had higher numbers of individuals identified (Table 7). Only two photo-IDs were obtained from the coastal Vancouver Island sub-region. Greater Caamaño Sound is the only sub-region where the rate of discovery of new individuals slowed significantly during this period (Figure 8).

Site Fidelity and Movement Patterns

Photo-IDs were compared between the inshore and the offshore regions to investigate movements. Only five instances of movement between the regions had occurred during the time series (Table 8). Of these five cases, two were within-season movements, the remaining three cases were resights with four to six-year intervals between sighting events (Figure 9). Photo-identifications were also compared among the inshore sub-regions. Most of the animals photographed in more than one year were photographed in eastern Hecate Strait & Queen Charlotte Sound, western Hecate Strait & Queen Charlotte Sound, and Greater Caamaño Sound sub-regions whereas re-sightings were negligible in Dixon Entrance and coastal Vancouver Island sub-regions(Figure 10). We found moderate site fidelity to sub-regions among the 173 animals that had been photographed in more than one year. Of these animals, 50.8% (n=88) were seen in just one sub-region among years, while the other 50.2% (n=85) were found in multiple sub-regions among years (Table 9).

Population Survival and Abundance Estimation

Apparent Survival

Mark recapture modeling was conducted on the capture histories of 283 individuals over six sampling years (2009-2014). The fully time dependent TSM CJS model fit best (χ^2 = 5.37, df=8, p =0.72). The top ranked model assumed apparent survival varied over time in the initial TSM interval (under the influence of transience), but was constant in the subsequent time since marking intervals (Table 10). Apparent survival was estimated to be 94.5% (95% CI: 58.7-99.5). Recapture probabilities were variable over the time series (Figure 11).

Population Estimate

The fully time dependent CJS model showed a significant lack of fit (χ^2 = 31.11, df=12, p-value=0.002). Lack of fit was likely due to transience as indicated by the significance of the U-CARE direct test for transience (test statistic = 3.89, p-level<0.001). Therefore, Median $\hat{c}$, calculated to be 1.79, was applied to the POPAN model results as a variance inflation factor. The model with the best support assumed that apparent survival was constant, and that recapture probabilities and probabilities of entry were time varying (Table 11). A total of 405 Fin Whales (CV=0.6, 95% CI: 363-469) was estimated, representing the super population, which is defined as the total number of Fin Whales that had occurred in the study area and were available for capture at any time during the study period of 2009 to 2014.

FIN WHALE MOVEMENT AND BEHAVIOUR MODELLING FROM SATELLITE-LINKED TAGS

A total of 19 Fin Whales were tagged with satellite-linked PTTs (7 SPLASH10, 12 SPOT5) during the study period (2011–2014). SPOT5 tags collected an average of 27.6 days (± 17.3 SD; range = 8.1–60.2 days) of location data and SPLASH10 tags collected an average of 11.2 days (± 6.6 SD; range = 3.5–22.8 days) of location and dive data (Table 12). Satellite transmissions were received from most PTTs within 4 hours of deployment, although the first transmissions for PTTs 83620, 83622, 132219, and 142546 were received a minimum of 226, 10, 18 and 10 hours after deployment respectively. This suggests poor satellite coverage for portions of the study area and/or problems with tag placement such that tags failed to clear the water on every surfacing. An average of 29% (± 16 SD; range = 1–56%) of locations for SPOT5 tags and 18% (± 12 SD; range = 5–32) of locations for SPLASH10 tags were of quality 1–3 (≥4 messages, estimated error <1500 m) (Table 12) and the remainder of the locations were of poorer quality.

Placement of PTTs was critical to successfully transmit messages, and in the case of SPLASH10 tags, to ensure accurate recording of dive and surfacing events using the wet-dry sensor. Tags attached lower on the flank of an animal may have failed to rise above the water on every surfacing, causing the wet-dry sensor to continue to read as “wet”. Thus, surfacing events could be missed and erroneously long dive events may have been recorded as a result. For this reason, we excluded all dives recorded by PTT 137684 (FW0184; N = 545), as this tag was placed very low on the whale’s flank and thus incorrectly recorded numerous dives (N = 19) that exceeded the Theoretical Aerobic Dive Limit (TADL) for Fin Whales of 28.6 min (Croll *et al.* 2001). Since Croll *et al.* (2001) determined that maximum dive durations for Fin Whales are typically much shorter than their TADL (59% of TADL), we also excluded 25 dives from the other six SPLASH10 deployments that exceeded 17 min in duration (~60% of TADL), as these were likely due to the wet-dry sensor failing to detect the end of a dive when the tag remained submerged during some surfacings. Once we had excluded the dives recorded by PTT 137684, dives exceeding 60% of TADL, and dives with >1 h of temporal separation from the closest SSSM location, a total of 8,724 dives remained for analysis. Visual inspection of the time-depth profiles for the first 24 h of each PTT deployment revealed no obvious behavioural anomalies as a result of tag attachment.

State-Space Movement Modelling

The switching state-space models had some difficulty distinguishing between the two behavioural modes. There is some overlap in the range of mean autocorrelation in speed and direction (gamma parameters) between the two behavioural states, particularly for 2011 and 2012, but there are clear separations in the parameter values for turning angle (theta) between the two behavioural modes (Table 13). Given the low proportion of good quality location data, short deployment durations, and because Fin Whales did not exhibit a great range in movement behaviour during these relatively short deployments (Figures 12, 13, 14, and 15) there is likely insufficient data to reliably estimate the two behavioural states for 2011 and 2012. An average of 9% of Fin Whale locations were inferred as transiting, 80% as ARS, and 11% as uncertain (Table 14). The SSSM predicted ARS behaviour in both the Greater Caamaño Sound and the Hecate Strait and Queen Charlotte Sound sub-regions (Figures 12, 13, 14, and 15). Some animals with longer deployment durations showed inferred transiting behaviour between Greater Caamaño Sound ARS locations and ARS locations in Hecate Strait and back again. For example, FW0187 (PTT 132220) performed ARS behaviour in the vicinity of the tagging location in Squally Channel (west side of Gil Island) in the Greater Caamaño Sound sub-region, transited south and then west across Hecate Strait, where it performed another bout of ARS behaviour off the east side of Kunghit Island (southern Haida Gwaii) before transiting northeast and then southeast back to Greater Caamaño Sound (Figure 14).

Diving Behaviour

After the dive data were filtered to remove potential wet-dry sensor errors and dives that occurred >1 hr before or after the temporally closest SSSM location, an average of 1454 dives (± 1149.5 SD) remained per SPLASH tag deployment (N = 6; Table 12). Results from the first GAMM (Table 15) indicated that the maximum dive depths (m) of foraging Fin Whales (i.e., dives associated with ARS behaviour states) were predictable as a function of dive duration (min), dive shape, time of day (day versus night), and spatial location (Greater Caamaño Sound versus Hecate Strait and Queen Charlotte Sound sub-regions). All explanatory covariates were significant ($p < 0.05$) and were thus retained in the global model (AIC = 64214.3, logLik = -32096.2, df = 11), which outperformed a null model with an equivalent random effects structure (AIC = 67848.3, logLik = -33920.2, df = 4). The model smoother of dive duration predicted a non-linear relationship with dive depth, such that dive duration increased linearly with depth until reaching durations of approximately 7 min, after which the relationship levelled off and then became negative at dive durations of about 14 min (Figure 16). The decreasing portion of the smoother (indicating that dives with very long durations actually become shallower) could be result of sparse data for these long duration dives (only 29 dives >14 min duration). However, this decreasing portion of the smoother may also be the result of the failure of the wet-dry switch to activate for some surface durations, which could have caused multiple short duration, shallow dives to be erroneously recorded as a single, long duration dive.

One of the most important determinants of maximum dive depth for Fin Whales engaged in ARS behaviour was time of day (-0.365 ± 0.014 s.e., t = -25.802, p < 0.0001). On average, tagged Fin Whales conducted much deeper dives during the day (70.1 ± 52.1 m SD) than they did at night (24.9 ± 17.4 m SD) (Figures 17, 18 &19). During the daytime, maximum depths of ARS-associated dives followed a bimodal distribution with Fin Whales conducting both shallow (<100 m, and typically ~0–5 min in duration) and deep (>100 m, ~5–10 min duration) dive types (Figure 17). At night, Fin Whales only appeared to undertake shallower dives, and very few dives exceeding 100 m were recorded during periods of darkness (Figure 19). All six of the tagged individuals displayed similar differences in dive depth based on time of day (Figure 18). Mean ARS-associated dive depths between Caamaño Sound (55.7 ± 49.2 m SD) and Hecate Strait (58.1 ± 47.9 m SD) were very similar, although the GAMM estimated a significant effect of sub-region on maximum dive depth (Table 15). This significant effect may be the result of unbalanced sampling since more than six times as many dives were logged in Greater Caamaño Sound compared to the Hecate Strait region.

The second GAMM similarly indicated that dive durations (min) of foraging Fin Whales were predictable as a function of dive depth (m), dive shape, time of day, and spatial location. All explanatory covariates of this GAMM were also significant, and thus were retained in the global model (AIC = 25922.8, logLik = -12950.4, df = 11), which also outperformed its null equivalent (AIC = 28939.8, logLik = -14465.9, df = 4). The model smoother for maximum dive depth indicated a non-linear relationship between this covariate and the response variable of dive duration. Dive depth increased linearly with duration until depths of approximately 100 m, at which time the slope of the curve decreased such that dives >100 m increased in duration at a lesser rate (Figure 16). This makes biological sense if Fin Whales are approaching their physiological limits with these deeper, longer dives – if the depth versus duration relationship could be extended further, we would predict it would level off as dive durations approach the TADL for Fin Whales (28.6 min). The average dive duration of foraging Fin Whales was somewhat longer during the day (4.7 ± 2.9 min SD) than at night (3.4 ± 2.5 min SD), probably because deeper (>100 m) dives were so prevalent during daylight hours (Figure 18). Mean ARS-associated dive durations were similar between Greater Caamaño Sound (4.2 ± 2.8 min SD) and Hecate Strait (5.1 ± 3.1 SD) regions, although the GAMM showed a significant effect of region on dive duration (Table 15). This significant effect may also be the result of unbalanced sampling between the two regions, rather than a true regional difference in diving behaviour. Both the depth and duration response GAMMs showed that dive shape was a significant predictor of these two variables, and Square-shaped dives were on average longer (5.1 ± 2.8 min SD) and deeper (65.9 ± 55.3 m SD) than U- (3.3 ± 2.4 min, 51.6 ± 45.9) or V-shaped dives (4.1 ± 2.9 min, 43.9 ± 35.4 m) (Figure 20).

Both GAMMs displayed underdispersion (i.e., observed variability was lower than expected). This underdispersion was likely the result of temporal correlation that was evident in ACF plots of the model residuals (time lags 1–3 showed correlation, lag interval = 2 h).

DISCUSSION

FIN WHALE DISTRIBUTION AND DENSITY MODELLING

Habitat modeling is a useful technique that allows predictions of whale densities as a continuous function of habitat variables, while taking into account the amount of survey effort. Generalized Additive Models (GAM) provide a way to incorporate non-linear relationships between environmental covariates and whale density. The smoothers, when plotted, help to visualize the potential relationship between each covariate and whale distribution in the study area. The best ranked GAM model produced a predicted distribution, that encompassed the distribution of most of the Fin Whale sightings made in the study area and the percent deviance (49%) estimated for the GAM model suggest it is a reasonable fit (Figure 2). The predicted distribution of Fin Whales highlighted the the importance of the Moresby Trough and Greater Caamaño Sound areas. The modelled distribution also encompassed a high proportion of the photo-ID locations (Figure 4). Moresby Trough has been consistently identified in other modelling studies of Fin Whale distribution in Hecate Strait and Queen Charlotte Sound that used different Fin Whale data but similar habitat covariates, including depth to model distribution (Gregr and Trites 2001; Williams and O'Hara 2009; Best *et al.* 2015).

The average Fin Whale density predicted by our model over the entire study area is similar to densities reported by Zerbini *et al.* (2006), in the Gulf of Alaska (0.007 whales/km^2). Williams and Thomas (2007) estimated a density of 0.03 whales/km^2 (CV = 0.46), for a region encompassing Hecate Strait and Queen Charlotte Sound and Dixon Entrance. Best *et al.* (2015) estimated densities ranging from 0.00025 to 0.29 whales/km^2. Our density estimate, averaged over the entire study area, and also calculated for only Moresby Trough and Caamaño Sound, overlaps these estimates.

Moresby Trough and Greater Caamaño Sound had the highest relative predicted densities in the study area, which agreed with the pattern of observations collected during the on-effort portions of the surveys, but is somewhat different than the photo-ID effort. This is likely because photo- IDs were collected from small boats deployed from the survey ship and were constrained by sea conditions and weather, which may contribute to the distribution of photo-ID effort closer to land one either side of the Hecate Strait and Queen Charlotte Sound area.

Depth and slope are frequently reported as covariates in whale distribution models (Gregr and Trites 2001; Panigada *et al.* 2005; 2008; Williams and O'Hara 2009; Best *et al.* 2015). Depth and slope are likely proxies for bathymetric features and oceanographic processes, such as troughs, currents, down-welling and upwelling events (Crawford *et al.* 1995) that may sustain prey because of high nutrient mixing and/or have an aggregating effect, creating dense prey patches that are profitable for Fin Whales to target. In our model, latitude was probably important because Fin Whale sightings were associated with Moresby Trough, a feature that has a strong latitudinal signal because it extends from the southwest to the northeast side of Hecate Strait. The consistency with which Moresby Trough is identified in models, even when they are based on different Fin Whale distribution data and from different periods of time (line transect survey sightings (2004-05) (Williams and O'Hara 2009), line transects survey sightings (2004 to 2008) (Best *et al.* 2015) and whale kill data (1948-1967) (Gregr and Trites 2001), suggests that these processes are strong, consistent and sustain predictable and profitable concentrations of prey that attract Fin Whales.

FIN WHALE MOVEMENT AND ABUNDANCE MODELLING FROM PHOTO IDENTIFICATION

Our mark-recapture modelled estimate of abundance was based on data from years with comparatively high and consistent levels of effort in the study area. Missed photo ID matches, if they occurred, would negatively bias survival estimates in the TSM-CJS model. We minimized the possibility of this effect by using stringent protocols during photo-identification processing and matching. Transience would also tend to negatively bias survival estimates (Ramp *et al.* 2014), but applying the TSM model allowed us to minimize this bias. The resulting estimate of apparent survival of Fin Whales in the combined Hecate Strait and Queen Charlotte Sound and Greater Caamaño Sound region (94.5%) compares well to survival rates estimated for other populations of Fin Whales and Blue Whales based on photo ID mark recapture analyses (Ramp *et al.* 2014; Ramp *et al.* 2006). Abundance estimates can be negatively biased if there is evidence of strong site fidelity which would tend to inflate recapture rates, violating the assumption that animals have an equal probability of being recaptured (Rambeau 2008). Our comparison of photo-IDs among sub-regions of the inshore, indicate only moderate site fidelity to sub-regions and considerable movement amongst the sub-regions, particularly between Eastern Hecate Strait and Queen Charlotte Sound and western Hecate Strait and Queen Charlotte Sound sub-regions. While site-fidelity can negatively bias an abundance estimate, transience can add a positive bias to an abundance estimate (Ramp *et al.* 2014) but we accounted for this with a variance inflation factor in the POPAN model estimate.

Our mark-recapture super population abundance estimate of 405 Fin Whales (%CV 6, 95% CI 363-469) represents the number of animals present in Hecate Strait, Queen Charlotte Sound, and Greater Caamaño Sound during the period of 2009-2014, regardless of whether they were all present in the study area at a given time. Conversely abundance estimates derived from line-transect surveys represent estimates of the number of animals present in a study area at a particular time. For instance, Williams and Thomas (2007) reported an abundance estimate of 496 (%CV 46, 95% CI 202 – 1218) in the region (although including Dixon Entrance) based on line transect surveys made in 2004 and 2005. This number can be interpreted to represent the estimated average number of Fin Whales present in the study area at any time during the given surveys years. Best *et al.* (2015) reported an abundance estimate of 329 Fin Whales in the same region with much narrower confidence intervals (95% CI 274-395), using the Williams and Thomas (2007) dataset plus additional line transect surveys made 2006-2008. Abundance estimates from mark-recapture and line transect surveys are not directly comparable because they measure slightly different things, and in this case, were conducted during different time periods (line transect surveys were made 2004 to 2008 whereas the mark-recapture samples were collected 2009 to 2015). Nonetheless the two estimates suggest that, on average during a line transect year, a high proportion of the super population occupied the Hecate Strait, Queen Charlotte Sound, and Greater Caamaño Sound region (Calambokidis *et al.* 2004).

FIN WHALE MOVEMENT MODELLING FROM SATELLITE-LINKED TAGS

While photo-ID analysis provides insight into large scale movements, State Space modelling of movement data received from tags deployed on individual Fin Whales provides finer scale information about Fin Whale movement and behaviour. None of the animals tagged departed the inshore sub-regions of comprsing Hecate Strait, Queen Charlotte Sound and Greater Caamaño Sound for the period of their tags' transmission (Figure 1). The switching state-space model predicted that Fin Whales engaged in ARS behaviour (presumed foraging) in both the waters of Greater Caamaño Sound and the open waters of Hecate Strait. The greater number of SSSM locations and ARS-associated dives logged in Greater Caamaño Sound compared to Hecate Strait: most likely resulted because tags were first deployed on the whales in Greater

Caamaño Sound. The three SPLASH10 tags with the longest deployment durations, however, showed evidence of tagged Fin Whales transiting from Greater Caamaño Sound to Hecate Strait, and engaging in further ARS behaviour outside the sound. Longer deployment durations will be needed to provide additional information on Fin Whale movements in Hecate Strait and to further explore the possibly of movements from tag deployment locations to other regions. Nonetheless, intense and prolonged ARS behaviour in Greater Caamaño Sound and the associated diving behaviour suggest that this area is an important feeding location for Fin Whales in BC. Hecate Strait is also likely an important feeding area, however, additional longer tag deployments are needed to further resolve which areas of the Strait are used most frequently by foraging Fin Whales. Although the short tag deployment durations and low proportion of high-quality Argos locations presented an analytical challenge, the general movement patterns between Greater Caamaño Sound and Hecate Strait revealed by the SSSM correspond with areas of important habitat identified in the ship survey modelling and photo-ID mark-recapture analyses.

FIN WHALE DIVE BEHAVIOUR MODELLING

ARS-associated dive depths were likely greater during the day than at night due to the diel vertical migration (DVM) patterns of the Fin Whales' planktonic prey (primarily euphausiids; Ford 2014). Zooplankton aggregate at depth during the day as a strategy to avoid visual predators (e.g., planktivorous fish), but migrate toward the surface at dusk to feed (Croxall *et al.* 1985, Hays 2003). This cyclical variation in the vertical distribution of planktonic prey results in deeper daytime foraging dives by baleen whales, with dives becoming increasingly shallower as darkness approaches (Croll *et al.* 1998, Oleson *et al.* 2007, Calambokidis *et al.* 2008b, Nowacek *et al.* 2011). Zooplankton DVM also explains the relationship we found between dive shape, duration, and maximum depth. Square-shaped dives are characterized by a greater proportion of bottom time (>50% of total dive time) than either U- (20–50%) or V-shaped (≤20%) dives. Thus, Fin Whales are extending the relative proportion of bottom-time during square dives, likely as a strategy to maximize their feeding time in the deep-scattering layer, where zooplankton aggregations are densest and lunge-feeding is the most profitable. Square dives made up a slightly higher proportion of overall daytime ARS-associated diving behaviour (45.7%) by Fin Whales, as compared to 38.5% of dives conducted at nighttime.

CONCLUDING REMARKS

Using 3 study approaches and 4 quantitative analyses we have been able to investigate Fin Whale distribution, movements, abundance and behaviour at several different temporal and spatial scales in British Columbia. The Fin Whale distribution model provided a "snap shot" of whale distribution in Hecate Strait, Queen Charlotte Sound and Greater Caamaño Sound highlighting areas of high predicted densities. Photo-ID data provided insight into movements and site fidelity, and it appears that there is little movement or exchange between the inshore and the offshore regions, although most photo-IDs were obtained in the inshore region. Although photo ID effort was imbalanced between the two regions, acoustic studies have indicated that there are two distinct variants of Fin Whale song, (Type 1 and Type 2) in the Northeast Pacific (Koot 2015), which could explain the apparent lack of movement. In British Columbia song Type 2 has been recorded on remote acoustic recorders throughout coastal BC from sheltered inlets and along the shelf edge, but also offshore at Bowie Seamount. The Type 1 song, however, was only heard at offshore and shelf break recording locations. This suggests that there may be two populations; one that occurs primarily in coastal waters, and the other that is distributed offshore (Koot 2015).

Within the inshore region, Photo-ID data also showed that there was only moderate site fidelity, suggesting that Fin Whales moved throughout the Inshore region possibly in search of profitable foraging opportunities. Given their large body size and the energetic costs of lunge feeding, it seems probable that Fin Whales expend considerable time searching to locate dense (i.e., energetically profitable) prey patches. State-space-modelling results illustrated that individual Fin Whales engaged in ARS behaviours, which could represent foraging behaviour, intensively in some areas. ARS behaviour occurred in locations that corresponded to geographical areas predicted to have relatively high densities of Fin Whales by the GAM distribution model. Dive patterns during periods identified as ARS behaviour for individual Fin Whales exhibited distinct differences in dive duration and depth associated with time of day, suggesting that Fin Whales were engaged in foraging during these periods and likely targeting zooplankton prey patches.

Future Analysis

We plan to fit the satellite-linked telemetry tracks as a single hierarchical model for all years to potentially aid in improving the parameter estimates of the SSSM. Future research could also include conducting spatial analyses using SSSM-generated ARS locations to identify potential relationships between environmental characteristics and Fin Whale feeding habitat. Future research could also include extending Fin Whale distribution modelling to incorporate sightings and effort from Photo ID and incorporate more of the ship surveys to model distribution in the other regions of the study area

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TABLES

Table 1. Description of habitat covariates used in the Fin Whale distribution model.

Covariates	Description
Depth	mean depth (m) in the grid cell
Slope	mean slope (˚) in the grid cell
X	Easting UTM coordinate at centre of grid cell (~Longitude)
Y	Northing UTM coordinate at centre of grid cell (Latitude)
effort	Total km^2 of survey effort in the grid cell

Table 2. Surveys used in the Fin Whale distribution model of Hecate Strait and Queen Charlotte Sound.

Survey	Year	Season	Dates
CRP02_01	2002	spring	May 28 to June
CRP02_02	2002	summer	Aug 1 to Aug 7
CRP03_01	2003	spring	May 22 to June 7
CRP03_02	2003	summer	Aug 2 to Aug 8
CRP03_03	2003	summer	Aug 20 to Sept 2
CRP03_04	2003	summer	Aug 31 to Sept
CRP03_05	2003	summer	Aug 29 to Sept 5
CRP04_01	2004	winter	Feb 12 to Feb 29
CRP04_02	2004	spring	May 11 to May 22
CRP04_03	2004	summer	Aug 13 to Aug 18
CRP04_04	2004	fall	Oct 13 to Oct 21
CRP05_01	2005	spring	May 9 to May 22
CRP05_02	2005	summer	Aug 21 to Aug 28
CRP06_01	2006	winter	Jan 3 to Jan 26
CRP06_03	2006	summer	Aug 6 to Aug 13
CRP06_04	2006	fall	Oct 21 to Oct 29
CRP07_02	2007	spring	April 25 to May
CRP07_03	2007	summer	Aug 3 to Aug 12
CRP07_04	2007	fall	Oct 5 to Oct 17
CRP08_01	2008	winter	Mar 4 to Mar 17
CRP08_02	2008	spring	May 5 to May 19
CRP08_03	2008	summer	Aug 13 to Aug 22
CRP09_01	2009	winter	Feb 24 to Mar 9
CRP09_02	2009	summer	July 8 to July 20
CRP09_03	2009	summer	July 25 to July 31
CRP09_04	2009	summer	July 31 to Aug 7
CRP09_05	2009	summer	Aug 8 to Aug 12
CRP10_01	2010	summer	July 11 to July 19
CRP10_02	2010	summer	Aug 3 to Aug 13
CRP11_01	2011	summer	July 21 to July 29
CRP11_02	2011	summer	Aug 3 to Aug 13
CRP12_02	2012	winter	Mar 10 to Mar 19
CRP13_01	2013	winter	Feb 28 to Mar 12
CRP13_02	2013	summer	July 10 to July 22
CRP14_01	2014	winter	Mar 14 to Mar 26
CRP14_04	2014	summer	July 8 to July 21
CRP14_07	2014	fall	Aug 6 to Aug 11

Table 3. Summary of the Hecate Strait and Queen Charlotte Sound dataset.

Study area	Area (km^2)	Effort (km^2)	# of surveys	# sightings	# of whales	Depth (m)	Slope (˚)
Hecate-Queen Charlotte Sound	56,301	555,173	37	266	464	6 – 1,221	0.03 - 22

Table 4. Candidate models for predicting densities of Fin Whales in Hecate Strait and Queen Charlotte Sound, BC (2002-2014). All models included the offset term of logged aggregate effort area (km^2) per grid cell. W_i indicates model weights, with the top-ranked model starred (*).

Candidate GAMs	AIC	∆AIC	W_i
$N \sim s(Northing\_utm) + s(\sqrt{slope}) + s(\sqrt{depth})$	1600.96	0	1
$N \sim s(Northing\_utm) + s(\sqrt{depth})$	1645.51	44.55	0
$N \sim s(\sqrt{depth})$	1678.67	77.71	0
$N \sim 1$	1852.97	252.01	0

Table 5. Negative binomial GAM (log link function) results of top-ranked model for Fin Whale counts (N=266 sightings, 464 individuals; 'Fin Whale' & 'Like Fin Whale') over the 25 km^2 gridded study area of Hecate Strait and Queen Charlotte Sound, with significant relationships starred (*).

Parametric coefficients	**Estimate**	**se**	**z value**	***p*-value**
Intercept	-8.7553	0.2183	-40.11	< 0.001***
Approx. significance of smooth	**e.d.f.**	**Ref.df**	**Chi.sq**	***p*-value**
s(Y_utm)	2.979	3.764	45.38	< 0.001***
s(sqrt.depth)	5.171	6.541	153.37	< 0.001***
s(sqrt.slope)	3.431	4.338	38.87	< 0.001***
R-squared (adjusted)	0.11	-	-	-
-REML score	802.66	-	-	-
Deviance explained	49 %	-	-	-
AIC	1600.96	-	-	-

Table 6. Effort and number of individual Fin Whales photographed annually coast wide and by regions (1995 – 2015). Effort is reported as number of ID Events, number of individuals photographed is reported as number of unique IDs.

Year	Coast-wide #ID. Events	Coast-wide #Unique IDs	Inshore #ID. Events	Inshore #Unique IDs	Offshore #ID. Events	Offshore #Unique IDs
1995	1	1	1	1	-	-
1996	-	-	-	-	-	-
1997	-	-	-	-	-	-
1998	-	-	-	-	-	-
1999	-	-	-	-	-	-
2000	1	1	1	1	-	-
2001	-	-	-	0	-	-
2002	2	2	2	2	-	-
2003	-	-	-	0	-	-
2004	3	3	3	3	-	-
2005	5	5	5	5	-	-
2006	24	23	24	23	-	-
2007	36	29	33	26	3	3
2008	7	7	6	6	1	1
2009	15	14	15	14	-	-
2010	57	41	57	41	-	-
2011	108	68	104	64	4	4
2012	231	150	217	136	14	14
2013	362	203	341	183	21	21
2014	322	180	229	88	93	92
2015	375	270	301	201	74	70
TOTAL	1549	997	1339	794	210	205

Table 7. Effort and number of individuals photographed annually by inshore sub-region (1995 – 2015). Effort is reported as number of ID Events, number of individuals photographed is reported as number of unique IDs.

	Dixon Entrance		western Hecate Strait & Queen Charlotte Sound		Eastern Hecate Strait & Queen Charlotte Sound		Greater Caamaño Sound	
YEAR	#ID Events	#Unique IDs	#ID. Events	#Unique IDs	#ID. Events	#Unique IDs	#ID. Events	#Unique IDs
1995	1	1	-	-	-	-	-	-
1996	-	-	-	-	-	-	-	-
1997	-	-	-	-	-	-	-	-
1998	-	-	-	-	-	-	-	-
1999	-	-	-	-	-	-	-	-
2000	-	-	1	1	-	-	-	-
2001	-	-	-	-	-	-	-	-
2002	-	-	2	2	-	-	-	-
2003	-	-	-	-	-	-	-	-
2004	-	-	3	3	-	-	-	-
2005	1	1	4	4	-	-	-	-
2006	2	2	18	17	-	-	4	4
2007	9	8	20	14	-	-	4	4
2008	3	3	1	1	1	1	1	1
2009	-	-	-	-	-	-	15	14
2010	6	6	8	8	21	21	22	7
2011	30	26	21	19	1	1	50	18
2012	34	30	77	55	40	35	63	23
2013	11	11	55	43	114	99	161	43
2014	5	5	5	5	48	47	171	33
2015	1	1	126	95	99	87	73	28
TOTAL	103	94	341	267	324	291	564	175

Table 8. Summary counts of individual Fin Whales that have been seen either inshore or offshore (on the diagonal), or in both regions (right of the diagonal). Counts in the black text represent totals including all animals seen in the study period (n=681); this includes animals not seen again. Counts in the red text represent totals of animals photographed in more than one year (n=177).

-	Inshore	Offshore
Inshore	480 *(70.5%)* *170 (96.0%)*	5 (0.7%) 3 (1.7%)
Offshore	-	196 *(28.8%)* *4 (2.3%)*

Table 9. Summary counts of individual Fin Whales, in the inshore region, that have been seen in only one sub-region (on the diagonal), or in two sub-regions (right of the diagonal). Counts are of animals photographed in more than one year (n=173). The total sum of this table exceeds the number of unique individuals because some individuals were seen in more than two sub-areas.

-	Dixon Entrance	western Hecate Strait & Queen Charlotte Sound	Eastern Hecate Strait & Queen Charlotte Sound	Greater Caamaño Sound	Coastal Vancouver Island
Dixon Entrance	9 (5.2%)	10 (5.8%)	6 (3.5%)	3 (1.7%)	0 (0%)
West Hecate Strait	-	37 (21.4%)	35 (20.2%)	9 (5.2%)	0 (%)
East Hecate Strait	-	-	29 (16.8%)	38 (22.0%)	2 (1.2%)
Greater Caamaño Sound	-	-	-	13 (7.5%)	0 (%)
Coastal Vancouver Island	-	-	-	-	0 (%)

Table 10. Candidate Cormack Jolly Seber models for estimating apparent survival. Top-ranked model is denoted with #. Model parameters included apparent survival (ϕ) and recapture probability (p). Parameters were modelled to be constant (*) or to vary over time (t). The notation ϕ (x /x) indicates the separate model parameters for each set (group) of time-since-marking estimates – the initial set under the influence of transience, and the second set being the estimates of interest.

Model	Parameters	AICc	ΔAICc	Weight	Deviance
ϕ(*t*/*)*p*(*t*)	11	588.98	0.00	0.92#	58.68
ϕ(*/*)*p*(*t*)	7	594.42	5.43	0.06	72.56
ϕ(*t*/*t*)*p*(*t*)	15	596.85	7.87	0.02	57.92
ϕ(*/*t*)*p*(*t*)	10	600.58	11.6	0.00	72.41

Table 11. Candidate POPAN models for estimating abundance. Top-ranked model denoted by #. Model parameters included apparent survival (ϕ), recapture probability (p), and entry probability (pent). Survival and recapture parameters were modelled as constant (*) or as varying over time (t). Probability of entry into the population was only modelled as varying over time (t).

Model	Parameters	QAICc	ΔAICc	Weight	QDeviance
ϕ(*)*p*(*t*)pent(*t*)	13	377.33	0.00	0.96#	-426.52
ϕ(*t*)*p*(*t*)pent(*t*)	17	384.04	6.71	0.03	-428.39

Table 12. Summary of track and dive behaviour data recorded by SPLASH10 and SPOT5 satellite-linked tags deployed on 19 Fin Whales in the vicinity of Caamaño Sound, British Columbia, between August and October (2011-2014). Number of dives for SPLASH tags refers to the number of dives available for GAMM analysis, after filtering for wet-dry sensor errors (note that PTT 137684 was excluded) and matching to SSSM locations and behaviour states.

Whale ID	Instrument type	PTT ID	Deployment date (GMT)	Track duration (days)	Received locations	Percentage of locations with quality 1-3	Mean number of locations per day	Mean time step (hr)	Number of dives
FW0006	SPOT	83620	11-08-2011	31.4	245	1%	9.1	3.1	-
FW0060	SPOT	83621	11-08-2011	8.1	114	18%	12.7	1.8	-
FW0054	SPOT	83622	10-08-2011	13.0	123	24%	8.8	2.6	-
FW0078	SPOT	83619	17-08-2012	18.7	252	56%	12.6	1.8	-
FW0097	SPOT	110727	17-08-2012	39.9	547	42%	13.3	1.8	-
FW0046	SPOT	110729	18-08-2012	52.8	607	47%	11.7	2.1	-
FW0226	SPOT	110730	23-08-2012	13.8	203	25%	14.5	1.6	-
FW0164	SPOT	127910	20-08-2013	38.4	689	5%	17.2	1.3	-
FW0340	SPOT	127911	10-10-2013	16.5	255	35%	14.2	1.6	-
FW0332	SPOT	127912	16-08-2013	29.2	467	39%	15.1	1.5	-
FW0016	SPLASH	132219	19-08-2013	9.9	215	5%	19.5	1.1	378
FW0187	SPLASH	132220	18-08-2013	13.1	327	22%	23.4	1.0	1210
FW0370	SPOT	133522	18-10-2013	9.5	126	19%	12.6	1.8	-

Whale ID	Instrument type	PTT ID	Deployment date (GMT)	Track duration (days)	Received locations	Percentage of locations with quality 1-3	Mean number of locations per day	Mean time step (hr)	Number of dives
FW0021	SPOT	133523	12-10-2013	60.2	869	32%	14.1	1.7	-
FW0184	SPLASH	137684	16-08-2014	4.5	76	5%	15.2	1.4	(omitted)
FW0029	SPLASH	137685	20-08-2014	14.5	223	32%	13.1	1.6	1982
FW0416	SPLASH	137686	23-08-2014	9.9	210	26%	19.1	1.1	930
FW0162	SPLASH	142546	08-09-2014	22.8	259	6%	10.8	2.1	3521
FW0332	SPLASH	142547	10-09-2014	3.4	69	27%	11.5	1.6	703
-	**-**	**-**	**Mean**	**21.5**	**309**	**25%**	**14.1**	**1.7**	**1454**

Table 13. Posterior medians and 95% credible limits (CL) for parameters estimated from the hierarchical first-difference correlated random walk (hDCRWS) model with switching for each year. Subscripts 1 and 2 index the transiting and ARS behavior modes. The probability of remaining in behavioral mode 1 at time t if in the same behavioral mode at time t – 1 is given by sigma (α), α_1, and α_2 is the probability of switching to behavioural mode 1 at time t if in behavioral mode 2 at time t – 1. The mean autocorrelations in movement speed and direction are given by gamma (γ) and mean turning angle theta (θ) is measured in degrees.

Year	Number of tracks	α_1	α_2	γ_1			γ_2			θ_1			θ_2		
				Median	2.5% CL	97.5% CL	Median	2.5% CL	97.5% CL	Median	2.5% CL	97.5% CL	Median	2.5% CL	97.5% CL
2011	3	0.321	0.011	0.67	0.46	0.94	0.51	0.38	0.62	-4.2	-57.4	54.9	179.5	165.8	192.9
2012	4	0.953	0.007	0.43	0.35	0.52	0.39	0.31	0.45	-25.1	-44.3	-4.7	170.9	157.4	184.7
2013	7	0.942	0.028	0.43	0.33	0.53	0.22	0.12	0.31	4.3	-3.1	12.1	184.9	168.0	202.8
2014	5	0.375	0.064	0.71	0.37	0.96	0.27	0.14	0.40	-17.2	-38.2	2.7	180.0	160.0	202.5

Table 14. Fin Whale SPLASH10 and SPOT5 tag deployments summarized by the percentage of track time spent in the transit behavioural state (b < 1.25), uncertain behavioural state (b ≥ 1.25 and b ≤ 1.75), and the area-restricted search (ARS) behaviour state (b > 1.75).

Whale ID	Instrument type	PTT ID	Deployment date (GMT)	Percentage of track time spent as transit	Percentage of track time spent as uncertain	Percentage of track time spent as ARS
FW0006	SPOT	83620	11-08-2011	0%	0%	100%
FW0060	SPOT	83621	11-08-2011	0%	1%	99%
FW0054	SPOT	83622	10-08-2011	0%	1%	99%
FW0078	SPOT	83619	17-08-2012	18%	2%	80%
FW0097	SPOT	110727	17-08-2012	17%	21%	62%
FW0046	SPOT	110729	18-08-2012	3%	3%	94%
FW0226	SPOT	110730	23-08-2012	0%	0%	100%
FW0164	SPOT	127910	20-08-2013	26%	27%	47%
FW0340	SPOT	127911	10-10-2013	20%	11%	69%
FW0332	SPOT	127912	16-08-2013	11%	14%	75%
FW0016	SPLASH	132219	19-08-2013	26%	45%	29%
FW0187	SPLASH	132220	18-08-2013	28%	17%	55%
FW0370	SPOT	133522	18-10-2013	0%	21%	79%
FW0021	SPOT	133523	12-10-2013	16%	34%	50%

Whale ID	Instrument type	PTT ID	Deployment date (GMT)	Percentage of track time spent as transit	Percentage of track time spent as uncertain	Percentage of track time spent as ARS
FW0184	SPLASH	137684	16-08-2014	0%	4%	96%
FW0029	SPLASH	137685	20-08-2014	1%	5%	94%
FW0416	SPLASH	137686	23-08-2014	1%	6%	93%
FW0162	SPLASH	142546	08-09-2014	1%	4%	95%
FW0332	SPLASH	142547	10-09-2014	0%	2%	98%
-	-	-	**Mean**	**9%**	**11%**	**80%**

Table 15. Model formulae, estimated effect size of fixed parameters (Est.), standard errors (s.e.), and random effect variances (σ^2) and standard deviations (s.d.) for the top-ranked Fin Whale presumed foraging (ARS state) dive behaviour GAMMs (Gamma error distribution with log link function), as selected by AIC comparison. Fixed effects parameters that were modelled using non-linear smoothers are shown in parentheses proceeded by a lower case “s”: e.g., s(duration). Wald t-values and associated p-values indicate that all fixed effects (centred and scaled) are significant predictor variables in both models. For both GAMMs, the (Intercept) parameter corresponds to dive shape 1 (Square).

Response variable: dive depth (m)	Fixed effect levels	Est.	s.e.	*t*	*p*
depth ~ s(duration) + dive shape + time of day + region + duration:time of day	(Intercept)	3.634	0.014	257.569	<0.0001
	dive shape (U)	0.135	0.006	22.519	<0.0001
	dive shape (V)	0.098	0.006	16.48	<0.0001
	time of day	-0.365	0.014	-25.802	<0.0001
	Region	0.068	0.012	5.452	<0.0001
	time of day:duration	-0.149	0.008	-19.644	<0.0001
	Smooth terms	-	e.d.f.	*F*	*p*
	s(duration)	-	6.76	649.9	<0.0001
	Random effect levels	σ^2	s.d.	-	-
	whale ID (PTT)	0	0	-	-

Response variable: dive depth (m)	Fixed effect levels	Est.	s.e.	*t*	*p*
	SSSM location ID	0.090	0.300	-	-
Response variable : dive duration (min)	Fixed effect levels	Est.	s.e.	*t*	*p*
	(Intercept)	1.459	0.031	47.249	<0.0001
	dive shape (U)	-0.139	0.005	-25.297	<0.0001
	dive shape (V)	-0.065	0.006	-11.567	<0.0001
	time of day	0.081	0.014	5.980	<0.0001
	Region	-0.078	0.012	-6.249	<0.0001
duration ~ s(depth) + dive shape + time of day + region + depth:time of day	time of day:depth	0.055	0.007	7.475	<0.0001
	Smooth terms	-	e.d.f.	*F*	*p*
	s(depth)	-	4.165	674.8	<0.0001
	Random effect levels	σ^2	s.d.	-	-
	whale ID (PTT)	0.004	0.063	-	-
	SSSM location ID	0.075	0.274	-	-

FIGURES

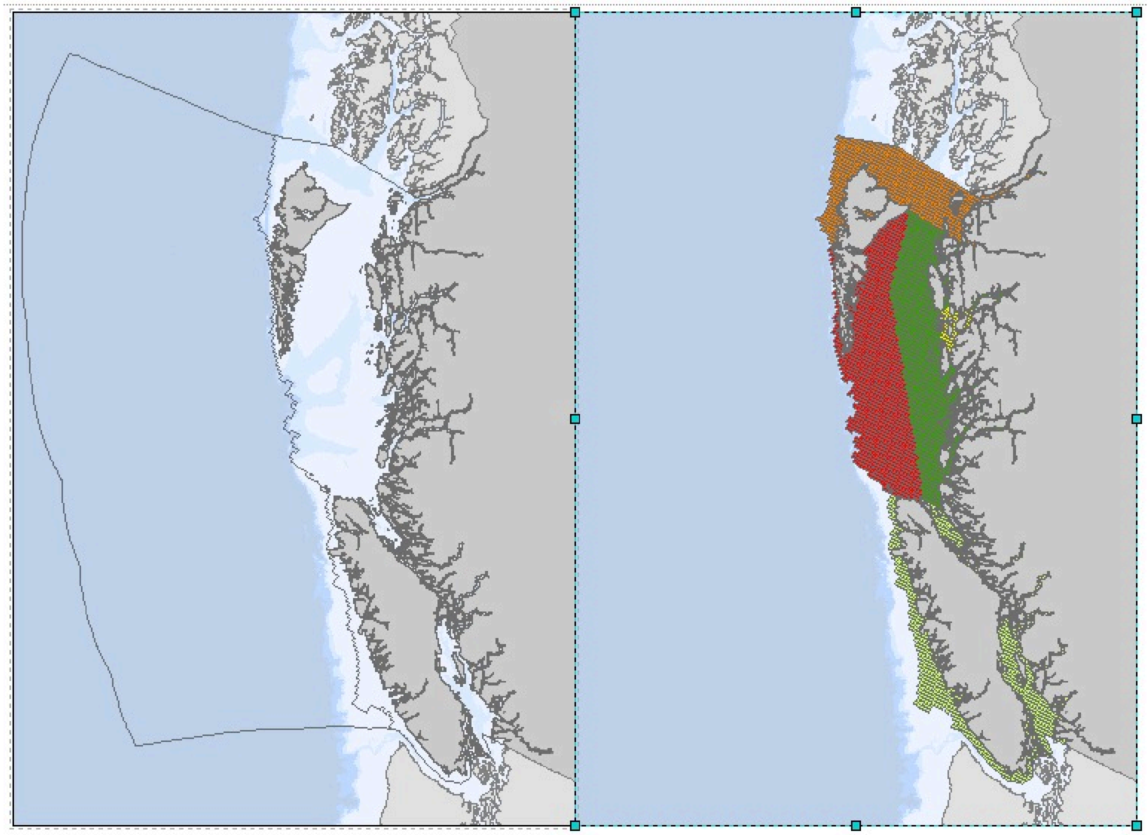

Figure 1: Map of Canadian Pacific waters and study area regions. A. Boundaries of the offshore and the inshore region. Boundary between is the 1000m depth contour from north to the northern tip of Vancouver Island and the 100m depth contour along west coast Vancouver Island. B. Five sub-regions comprising the inshore region. Orange: Dixon Entrance, Green: east Hecate Strait and Queen Charlotte Sound, Red: west Hecate Strait and Queen Charlotte Sound, Yellow: Greater Caamaño Sound, Pale Yellow: coastal Vancouver Island.

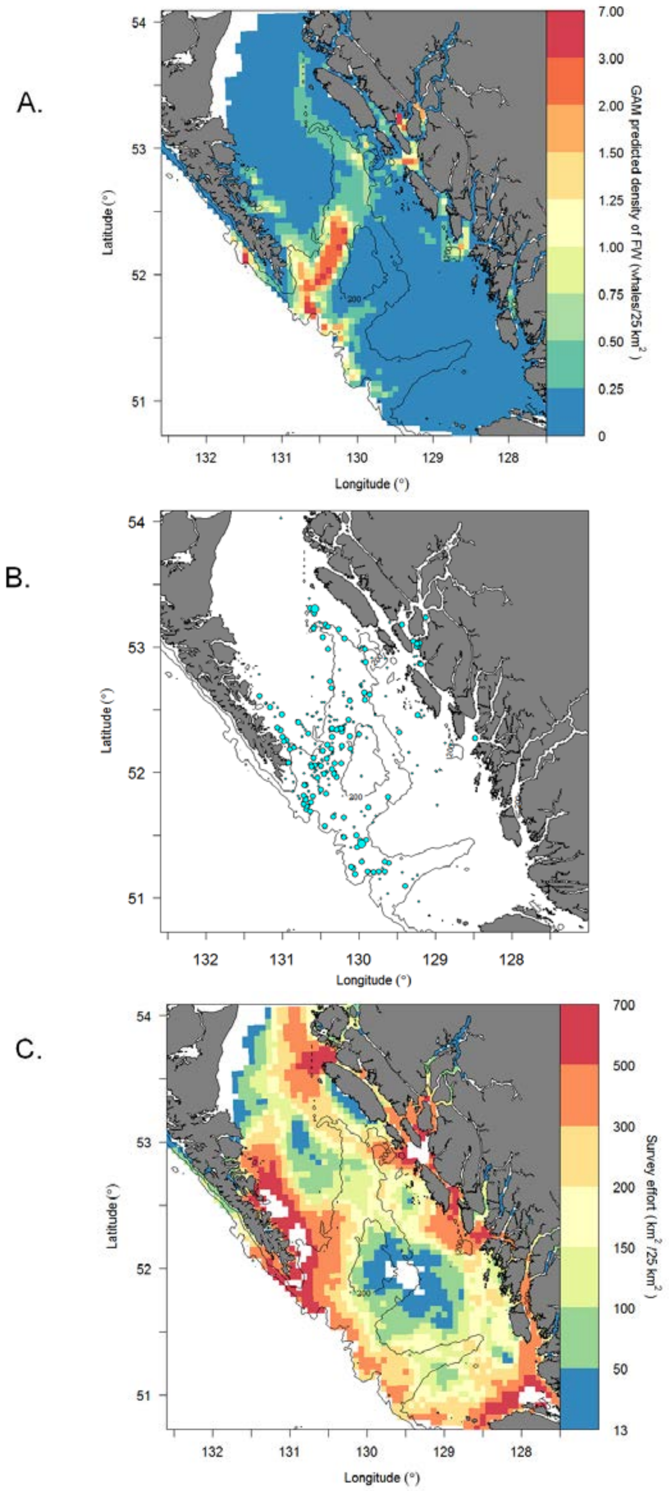

Figure 2: Fin Whale distribution in Hecate Strait and Queen Charlotte Sound A. Model predicted distribution as a function of latitude slope, depth, and B. Fin Whale sightings from 37 surveys used in the model (2002-2014), C. Survey effort expressed as km^2 of effort per 25 km^2 grid cell (2002-2014).

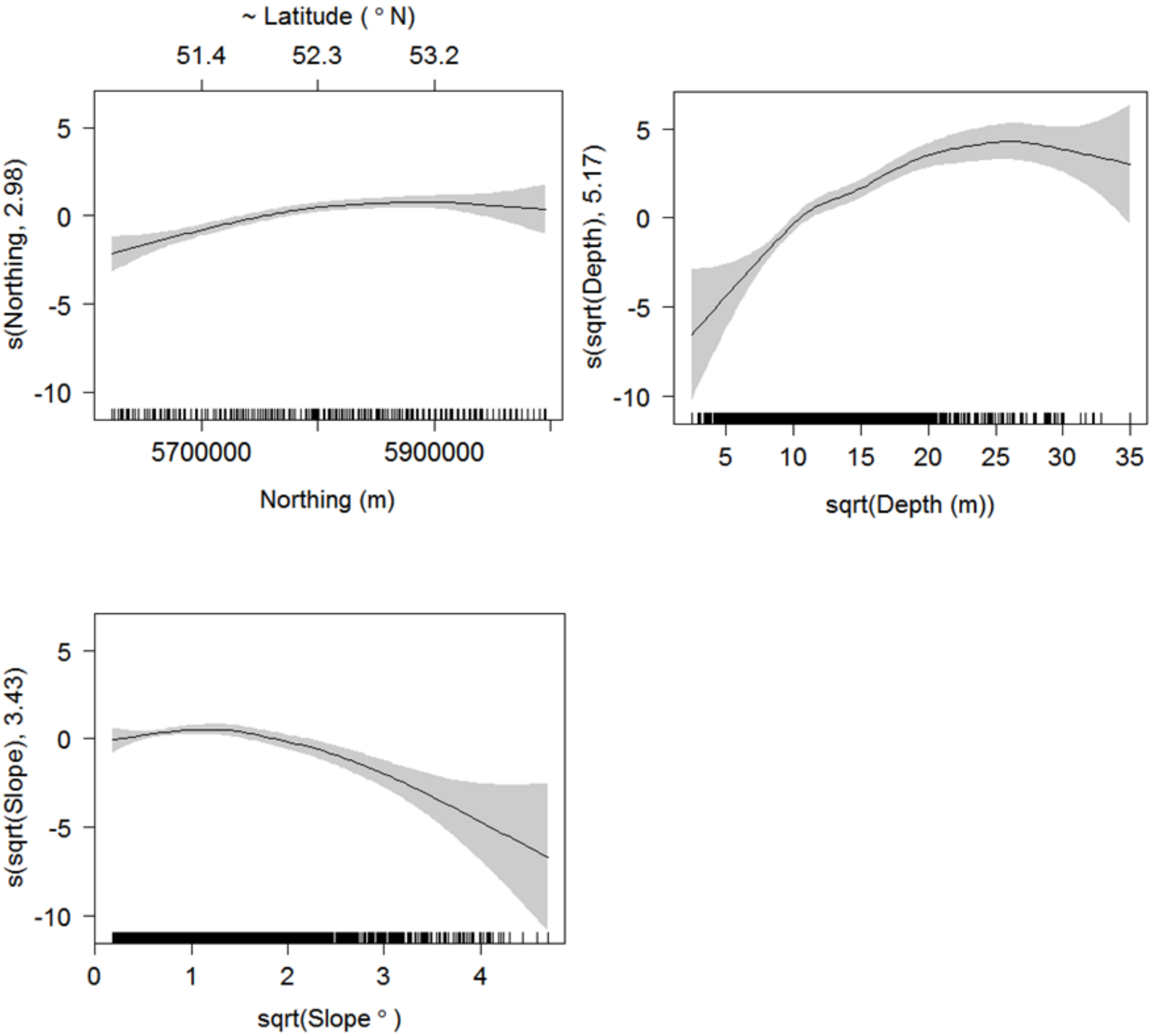

Figure 3: Smoothing functions (solid lines) with 95% confidence intervals (gray) for the explanatory variables, UTM Northing coordinate (corresponding to Latitude presented as well), square root of mean slope, and square root of mean depth of the top-ranked negative binomial GAM estimating Fin Whale densities per 25 km^2 grid cell . The y-axis labels display the fitted function with the estimated degrees of freedom in parentheses, while x-axis rug plots indicate distribution of sampled values within each explanatory variable.

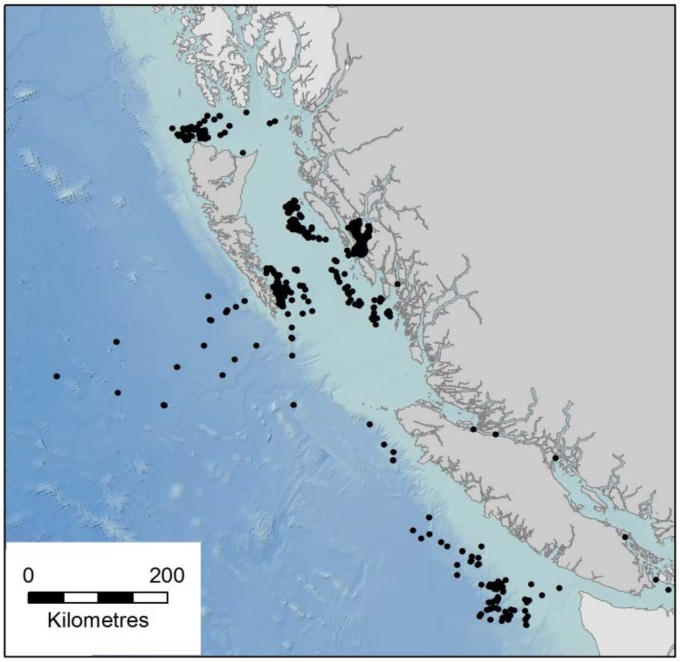

Figure 4: Distribution in Canadian Pacific waters of 1549 Fin Whale photo IDs (1995-2015).

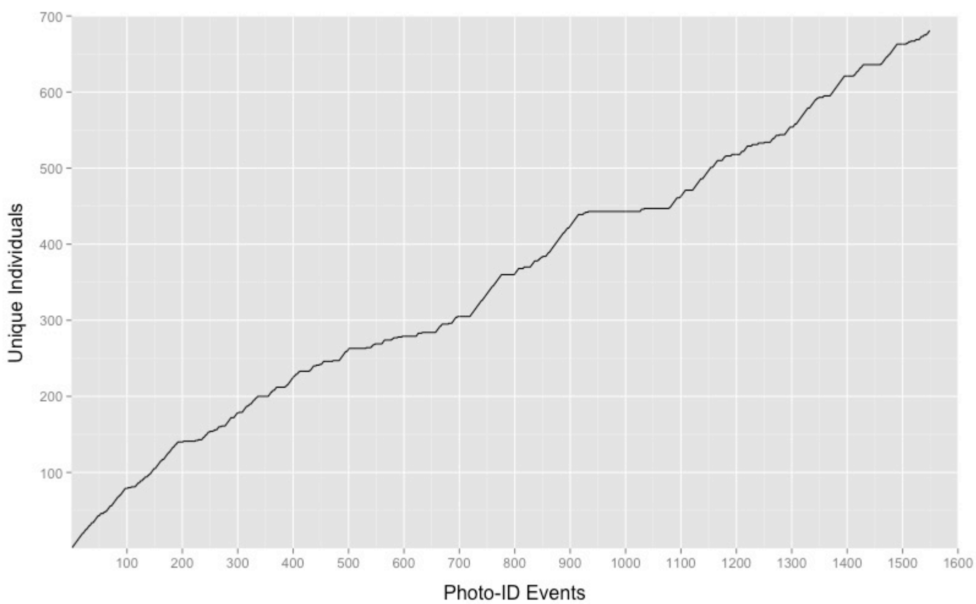

Figure 5: Discovery curve of unique individual Fin Whales (n=681) over the 1549 photo-ID events coast-wide (1995-2015).

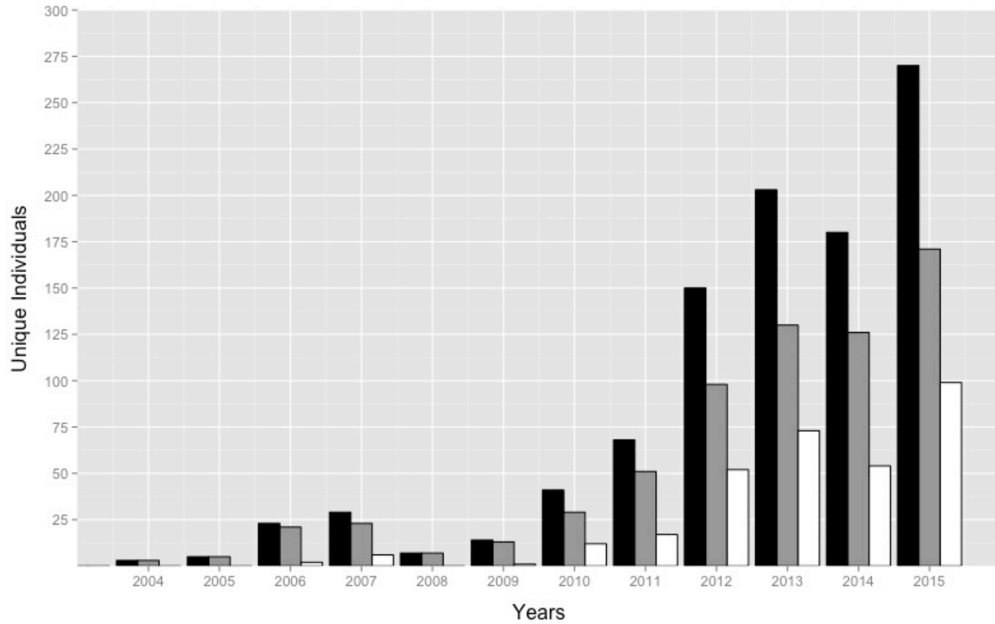

Figure 6: Coast-wide annual number of unique individual Fin Whales photographed (black), newly identified individuals (grey), and re-sighted individual (white) (2004-2015). Sightings prior to 2004 were omitted (n=4) due to sparse data.

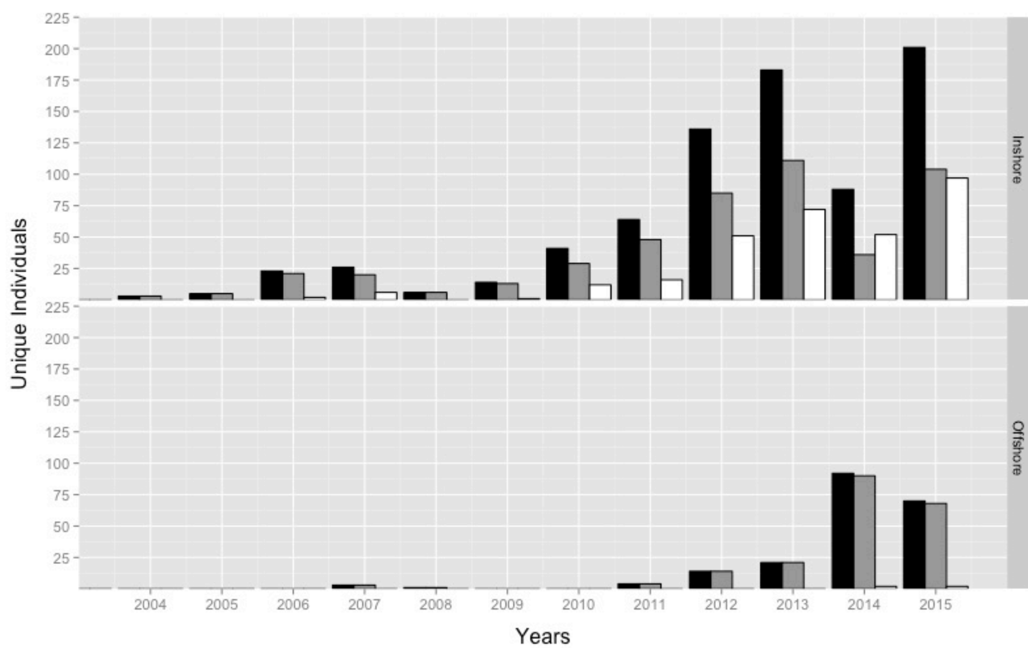

Figure 7: Inshore and offshore annual number of unique IDs, total individuals (black), newly identified individuals (grey), and re-sighted individual (white) (2004-2015).

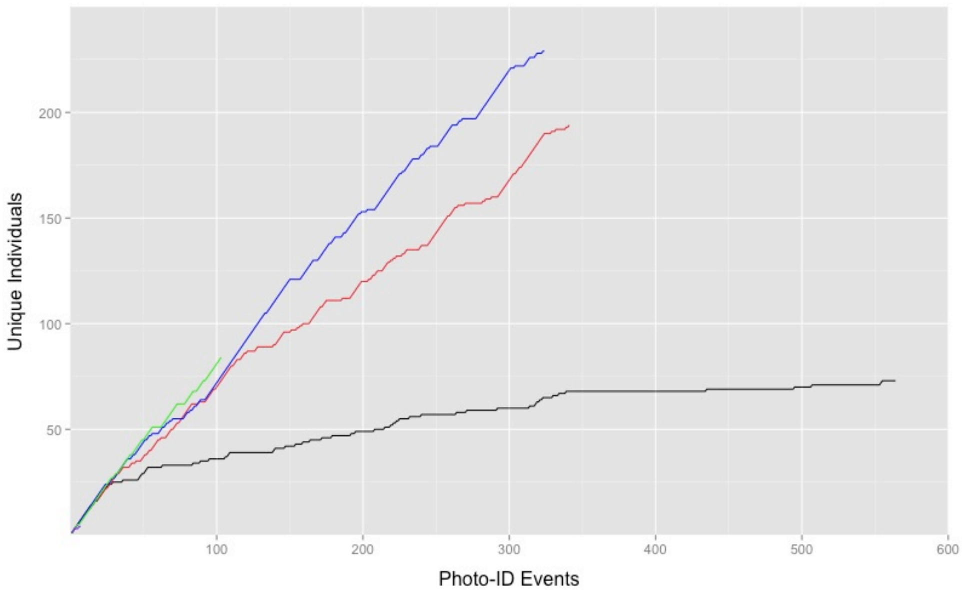

Figure 8: Discovery curves of unique Fin Whales by inshore sub-regions. Green – Dixon Entrance, Red – east Hecate Strait and Queen Charlotte Sound, Blue: west Hecate Strait and Queen Charlotte Sound, Black: Greater Caamaño Sound.

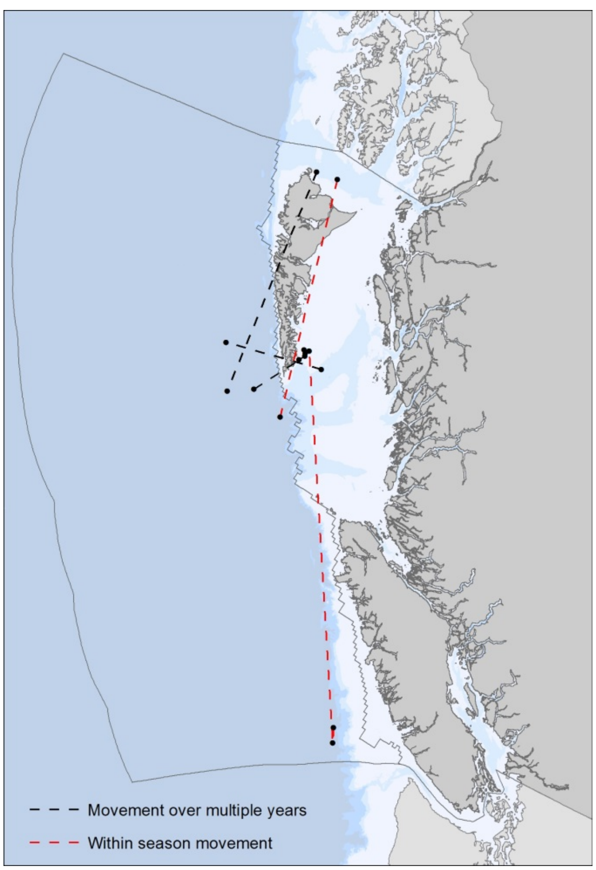

Figure 9: Individual Fin Whale inshore-offshore movements among years (black dashed line) and within years (red dashed line) (n=5 individuals).

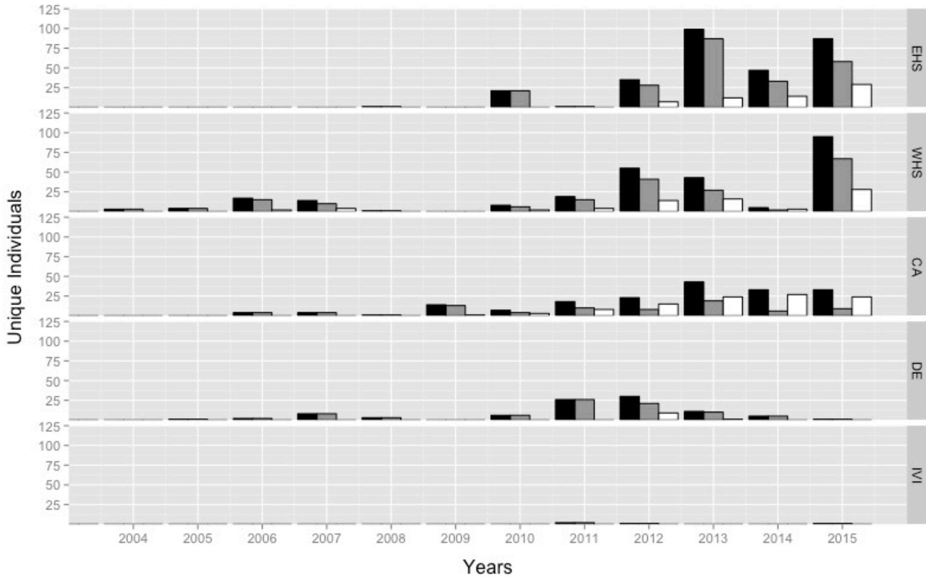

Figure 10: Inshore unique Fin Whales annually by sub-regions. Total individuals (black), newly identified individuals (grey), and re-sighted individual (white) (2014-2015). EHS = east Hecate Strait, WHS = west Hecate Strait, CA = Greater Caamaño Sound, DE = Dixon Entrance, IVI = coastal Vancouver Island

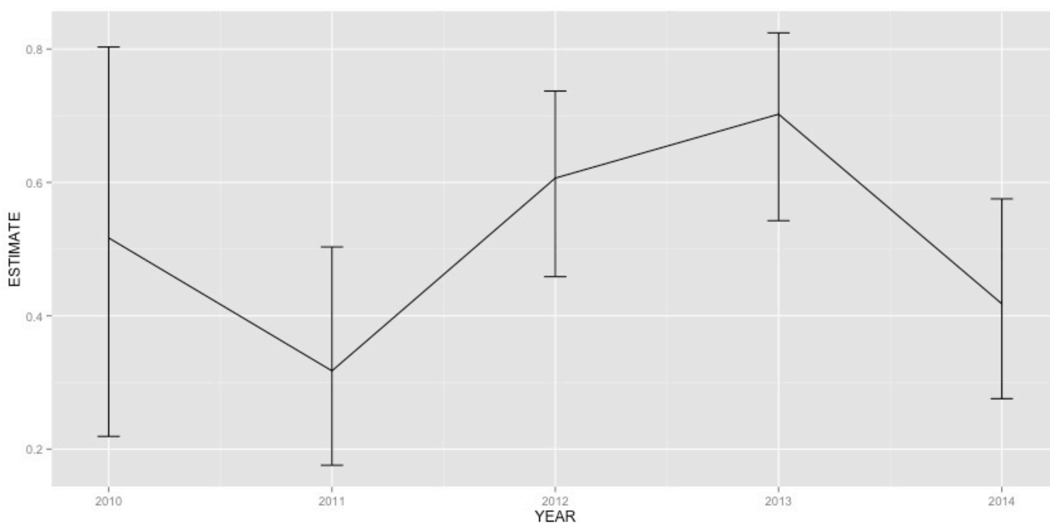

Figure 11: Annual recapture probabilities estimate from the Time-Since-Marking, Cormack-Jolly-Seber model to estimate apparent survival. Plot displays annual mean and 95% confidence intervals.

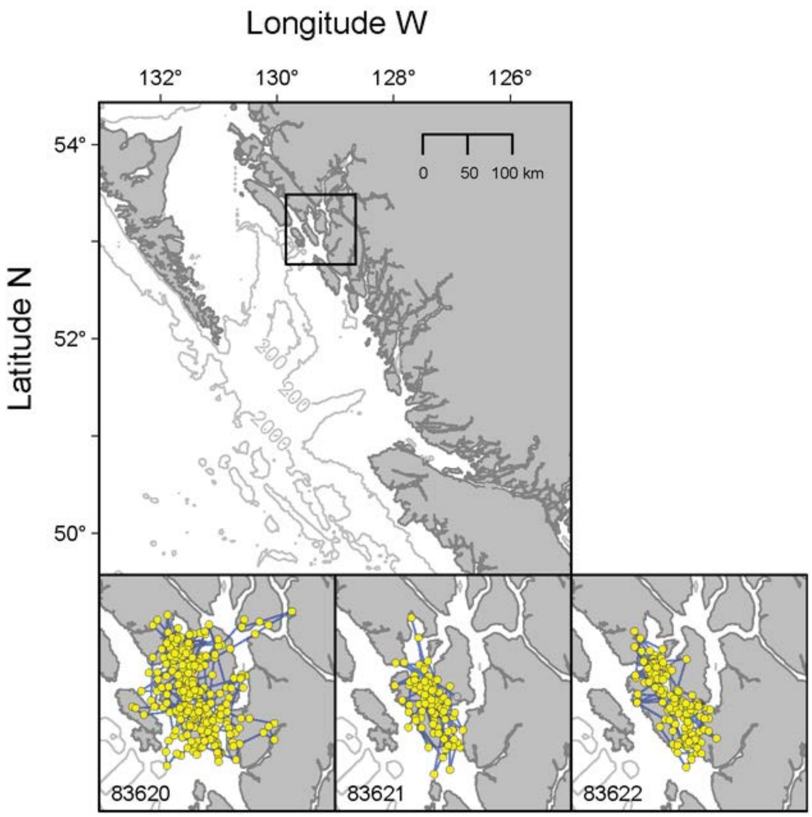

Figure 12: Fin whale tracks for 2011 deployments showing filtered locations with inferred behavioural modes (blue transiting, grey uncertain, and yellow ARS) from the hierarchical state-space model.

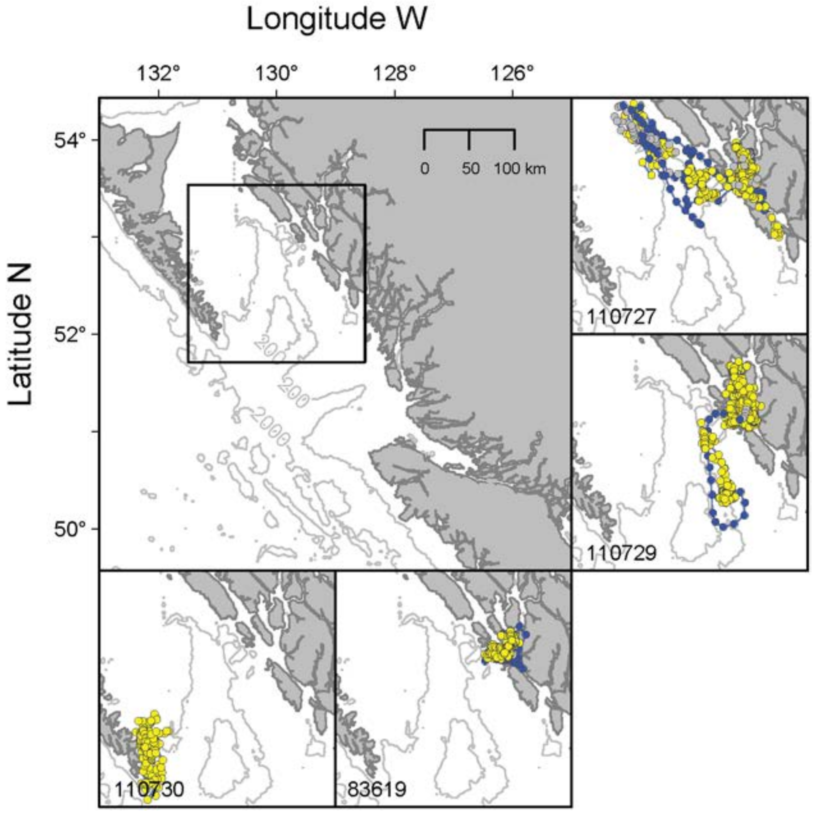

Figure 13: Fin whale tracks for 2012 deployments showing filtered locations with inferred behavioural modes (blue transiting, grey uncertain, and yellow ARS) from the hierarchical state-space model.

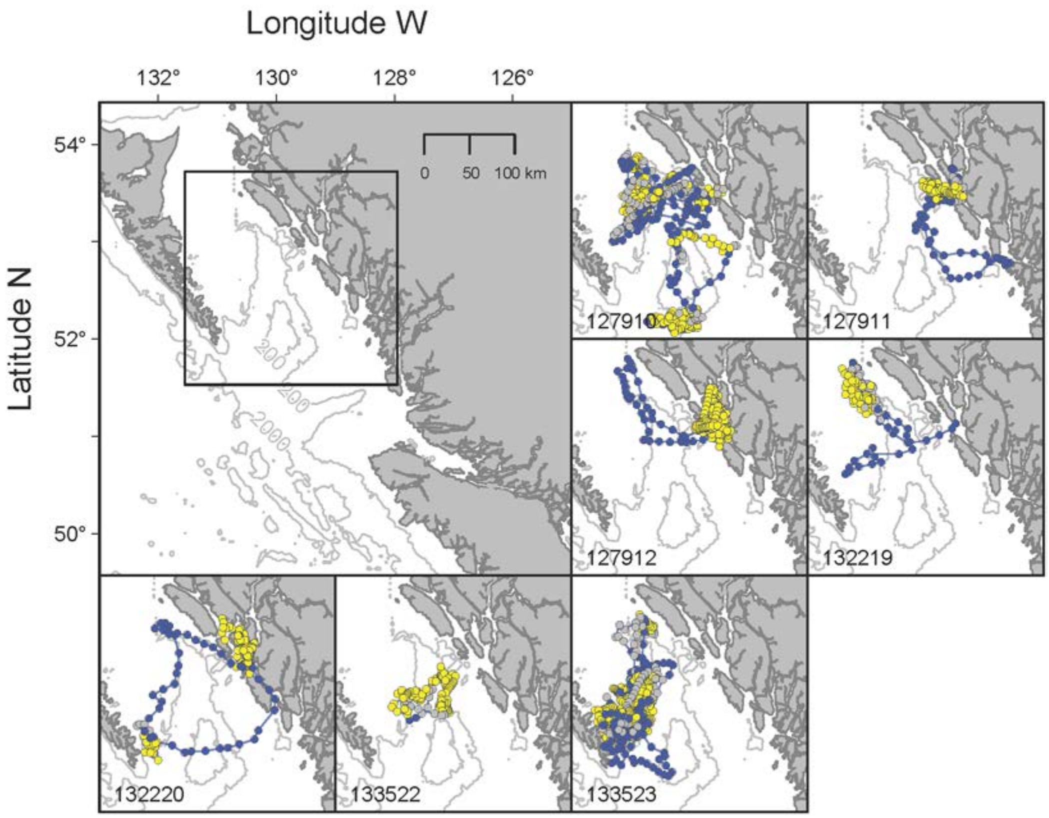

Figure 14: Fin whale tracks for 2013 deployments showing filtered locations with inferred behavioural modes (blue transiting, grey uncertain, and yellow ARS) from the hierarchical state-space model.

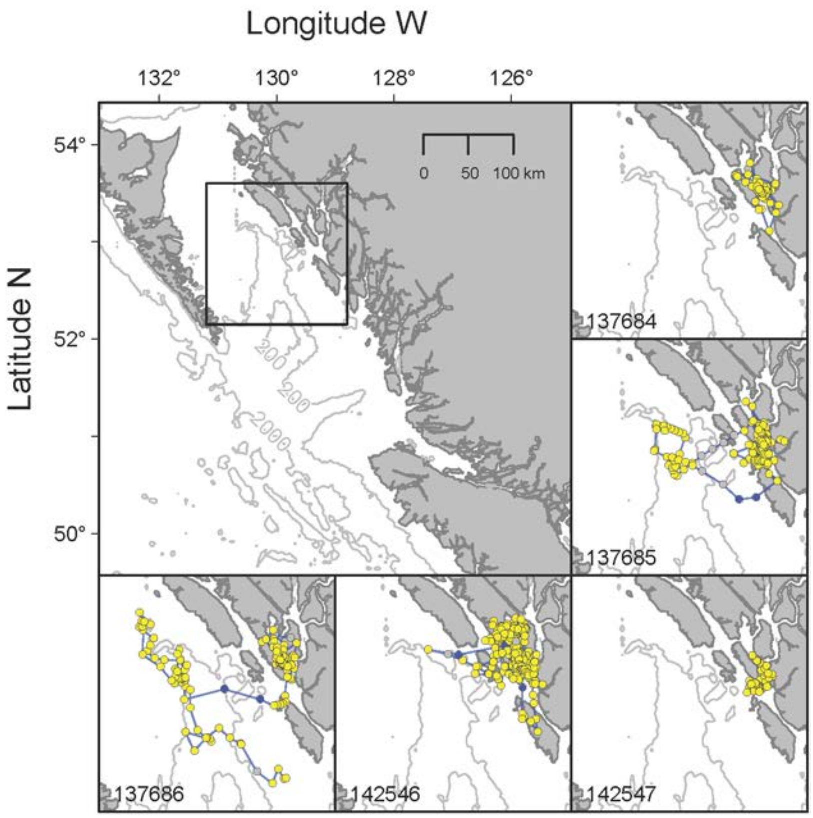

Figure 15: Fin whale tracks for 2014 deployments showing filtered locations with inferred behavioural modes (blue transiting, grey uncertain, and yellow ARS) from the hierarchical state-space model.

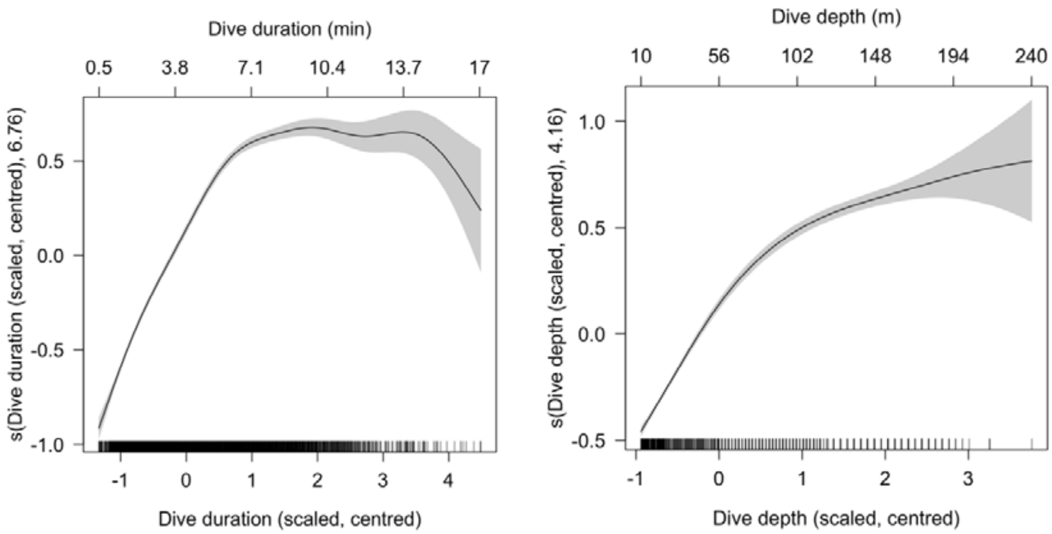

Figure 16: Top-ranked GAMM smoothers for dive duration (left) and dive depth (right). Both variables were centred and scaled prior to modelling (original scales are shown on top axes of plots). Shaded bands indicate roughly 95% confidence intervals and rug plots along each x-axis indicate the distribution of observations. Effective degrees of freedom (e.d.f.) of the smooth terms are displayed on the y-axes.

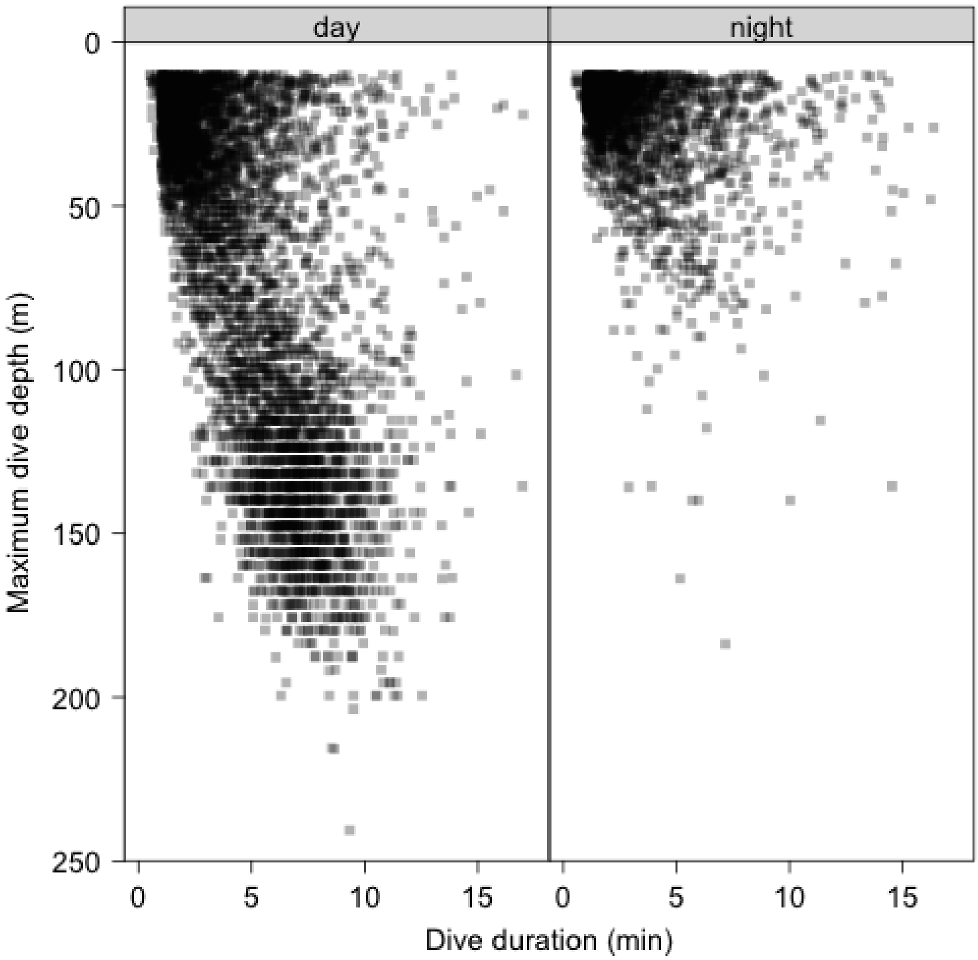

Figure 17: Maximum dive depth (m) as a function of dive duration (min) for dives conducted by 6 SPLASH10-tagged Fin Whales during area restricted search (ARS) behaviour (b > 1.75, presumed foraging), during the day (left, N = 5157) and night (right, N = 2332). Day and night periods were defined by times of nautical dawn (solar elevation < -12°) and dusk (solar elevation ≥ -12°) for each unique switching state-space model (SSSM) location estimate and its associated date. Note that points are semi-transparent to illustrate the density of the data, and that only dives reaching depths ≥10 m were recorded by the tags.

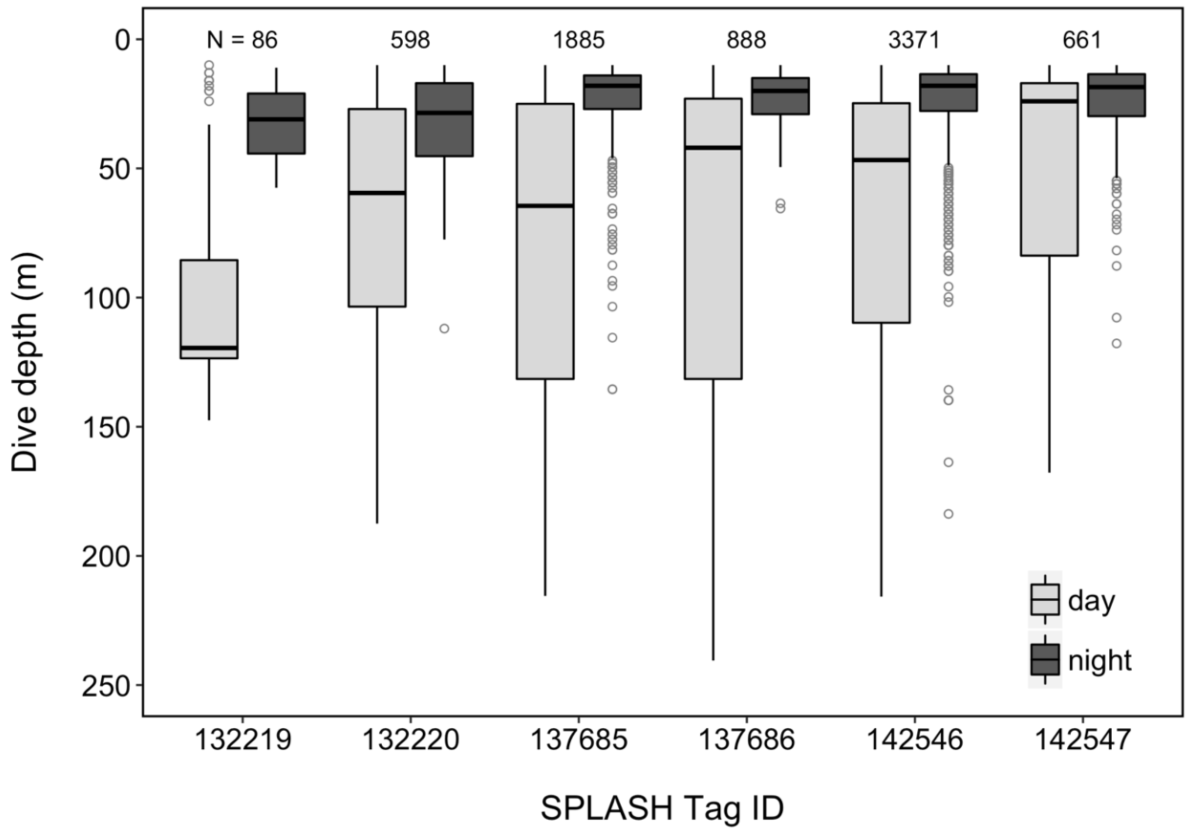

Figure 18: Maximum dive depths (m) recorded by SPLASH10 tags deployed on 6 individual Fin Whales conducting area restricted search (ARS) behaviour (presumed foraging, (b > 1.75), showing the difference in dive behaviour between day and night. Sample sizes (N, number of dives) recorded by each tag are displayed above the boxplots. Day and night periods were defined by times of nautical dawn (solar elevation < -12°) and dusk (solar elevation ≥ -12°) for each unique Switching State Space Model (SSSM) position and its associated date.

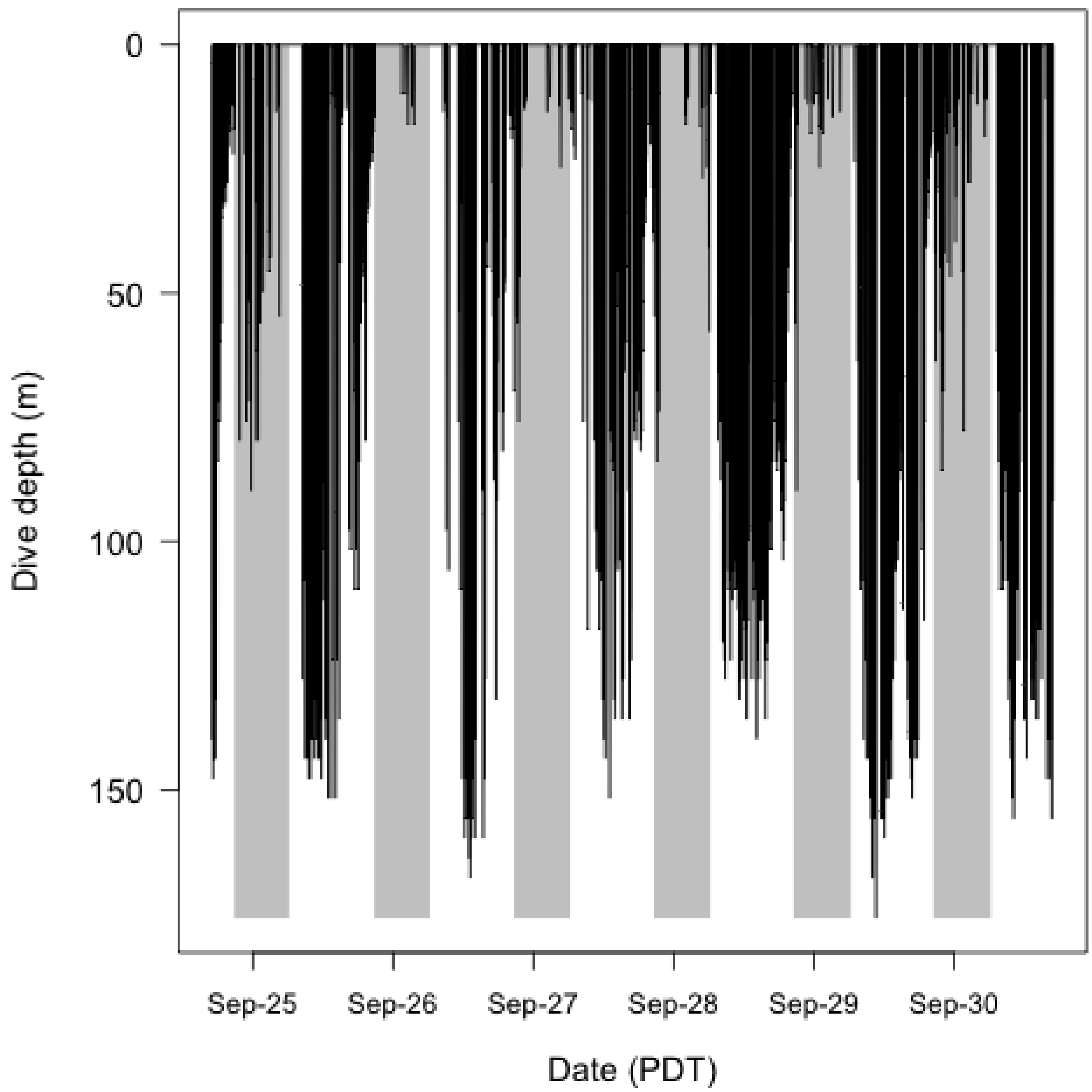

Figure 19: Time-depth profile showing maximum dive depths over the deployment of SPLASH tag 142546 (FW0162) from September 25-30, 2014 (Pacific Daylight Time). Grey shaded bands indicate periods of darkness bounded by nautical dusk and dawn (period during which the sun drops to ≥12° below the horizon).

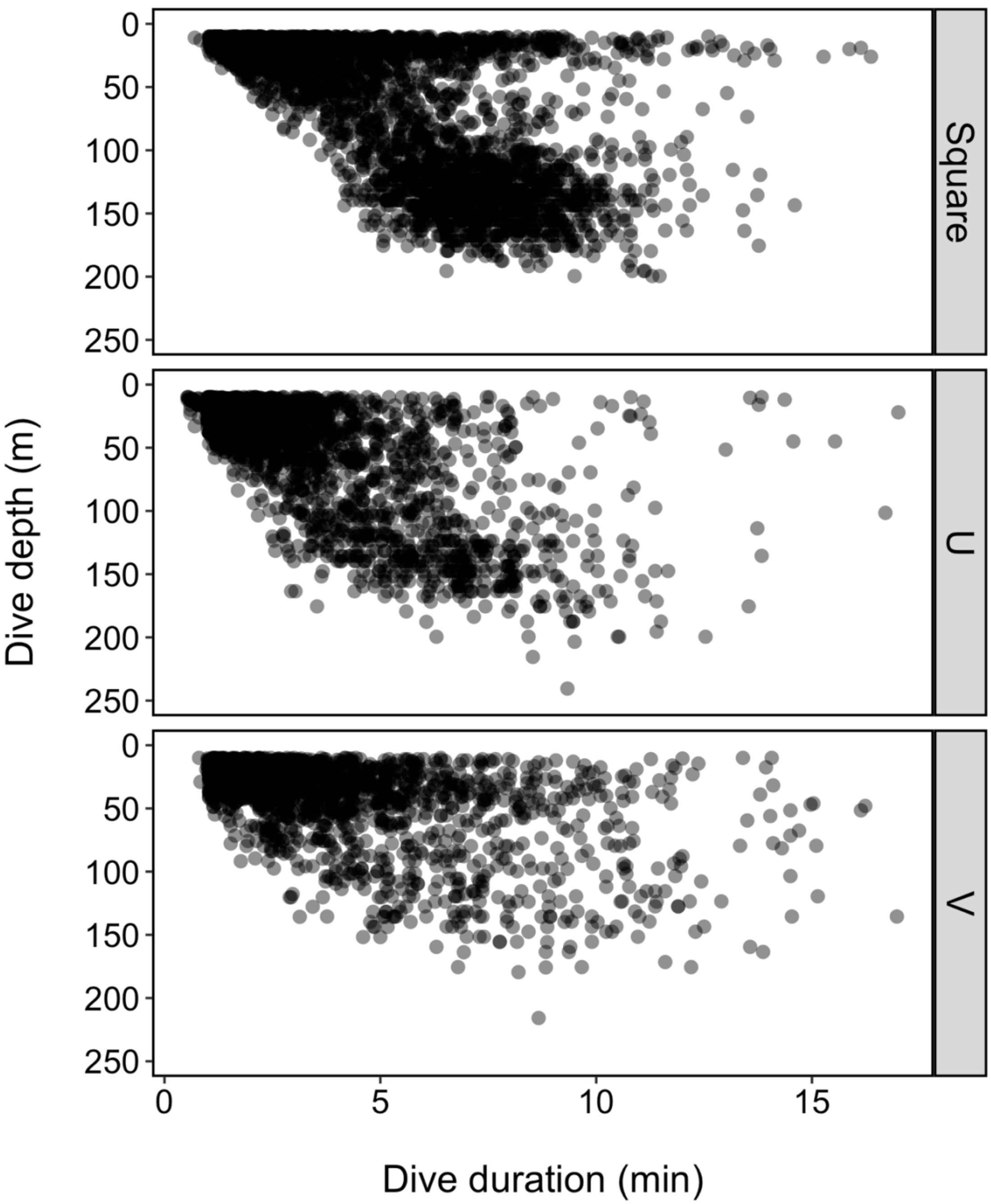

Figure 20: Maximum depths (m) of ARS-associated Fin Whale dives (N = 7489) as a function of dive duration (min) and binned by dive shape (Square, U, or V).

APPENDIX

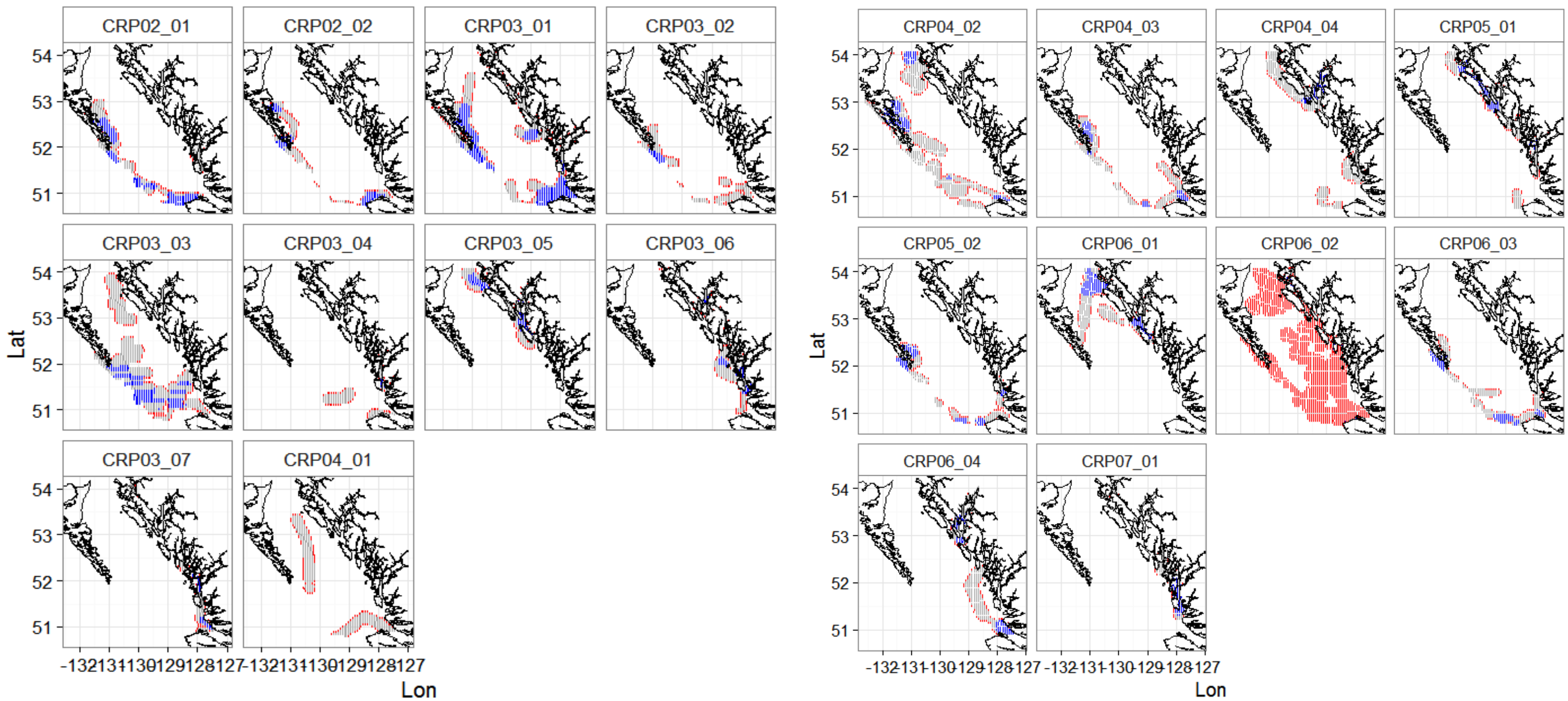

Figure A1. Maps depicting on-effort survey coverage in Hecate Strait and Queen Charlotte Sound from 2002 to 2014 led by the Cetacean Research Program (CRP). Surveys are identified by year and by survey number (eg. CRP02_01 is the first survey made in 2002). Maps depict survey effort on a 25 km2 gridded surface. Survey coverage is shaded as follows, <50% of a grid cell was surveyed (red), 50 to 100% of grid cell was surveyed (gray), >100% of a grid cell was surveyed (blue). Only effort in which ≥ 50% of a grid cell had been surveyed were included in the habitat model. Surveys CRP03_06, CRP03_07, CRP06_02, CRP07_01, CRP09_06 were excluded from the model dataset

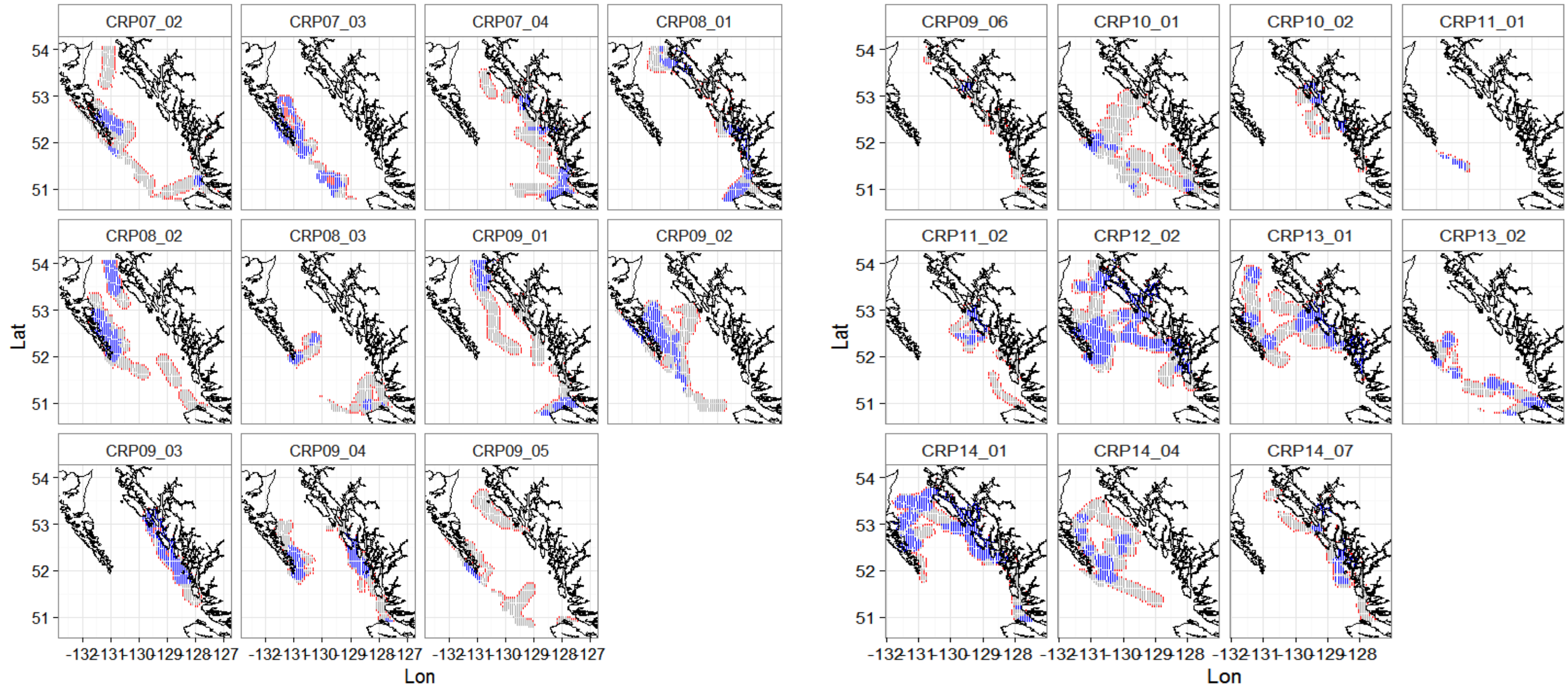

Figure A1. Continued.