Updated marine mammal distribution and abundance estimates in British Columbia

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ABSTRACT

Information relating to the distribution and abundance of species is critical for effective conservation and management. For many species, including cetacean species of conservation concern, abundance estimates are lacking, out of date and/or highly uncertain. Systematic, line-transect marine mammal surveys were conducted in British Columbia's (BC) coastal waters over multiple years and seasons (summer 2004, 2005, 2008, and spring/autumn 2007). In total, 10,057km of transects were surveyed in an 83,547km² study area. Abundance estimates were calculated using two different methods: Conventional Distance Sampling (CDS) and Density Surface Modelling (DSM). CDS generates a single density estimate for each stratum, whereas DSM explicitly models spatial variation and offers potential for greater precision by incorporating environmental predictors. Although DSM yields a more relevant product for the purposes of marine spatial planning, CDS has proven to be useful in cases where there are fewer observations available for seasonal and inter-annual comparison, particularly for the scarcely observed elephant seal. The summer abundance estimates (with lower and upper 95% confidence intervals; all DSM method unless otherwise stated), assuming certain trackline detection (underestimates true population size) were: harbour porpoise (*Phocoena phocoena*) 8,091 (4,885–13,401); Dall's porpoise (*Phocoenoides dalli*) 5,303 (4,638–6,064); Pacific white-sided dolphin (*Lagenorhynchus obliquidens*) 22,160 (16,522–29,721); humpback whale (*Megaptera novaeangliae*) 1,092 (993–1,200); fin whale (*Balaenoptera physalus*) 329 (274–395); killer whale (all ecotypes; *Orcinus orca*), 371 (222–621); common minke whale (*B. acutorostrata*) 522 (295–927); harbour seal (total; *Phoca vitulina*) 24,916 (19,666–31,569); Steller sea lion (total; *Eumetopias jubatus*) 4,037 (1,100–14,815); and northern elephant seal (CDS method; *Mirounga angustirostris*) 65 (35–121). Abundance estimates are provided on a stratum-specific basis with additional estimates provided for Steller sea lions and harbour seals that were 'hauled out' and 'in water'. This analysis updates previous estimates by including additional years of effort, providing greater spatial precision with the DSM method over CDS, novel reporting for spring and autumn seasons (rather than summer alone), and providing new abundance estimates for Steller sea lion and northern elephant seal. In addition to providing a baseline of marine mammal abundance and distribution, against which future changes can be compared, this information offers the opportunity to assess the risks posed to marine mammals by existing and emerging threats, such as fisheries bycatch, ship strikes, and increased oil spill and ocean noise issues associated with increases of container ship and oil tanker traffic in British Columbia's continental shelf waters.

KEYWORDS: SURVEY-VESSEL; ABUNDANCE ESTIMATE; DISTRIBUTION; CONSERVATION; BRITISH COLUMBIA; PACIFIC OCEAN; HUMPBACK WHALE; KILLER WHALE; COMMON MINKE WHALE; FIN WHALE; PACIFIC WHITE-SIDED DOLPHIN; STELLER SEA LION; ELEPHANT SEAL; HARBOUR SEAL; HARBOUR PORPOISE; DALL'S PORPOISE; NORTHERN HEMISPHERE

INTRODUCTION

Information relating to the distribution and abundance of species is critical for effective conservation and management approaches. Currently only a handful of marine mammal species in British Columbia's (BC) coastal waters are adequately monitored to gain information about their distribution, abundance, and/or population trends (e.g., resident killer whales, *Orcinus orca,* humpback whales, *Megaptera novaeangliae*, and sea otters, *Enhydra lutris*). For the remainder of species, including some that are listed under Canada's Species At Risk Act (SARA), there is a lack of quantitative abundance estimates. This problem is not unique to Canada; a recent global assessment showed that 75% of the world ocean has never been surveyed for cetaceans, and only 6% has been surveyed frequently enough to detect trends (Kaschner *et al.*, 2012).

In 2007, preliminary distribution and abundance estimates for eight marine mammal species were generated from the first systematic line-transect survey in BC's coastal (essentially continental shelf) waters during summer 2004

and 2005 (Williams and Thomas, 2007). As might be expected for the first survey of its kind, low sample sizes for many species resulted in abundance estimates with large confidence intervals. Large confidence intervals offer low power to detect trends, and available estimates apply only to summer waters. As the only estimates for some species in the region, they have been used in a management context. For example, the abundance estimates for harbour porpoise were used as conservation targets for Canada's Management Plan for the species in the Pacific Region (Fisheries and Oceans Canada, 2009). The estimates were used to calculate sustainable limits for small cetacean bycatch in fisheries (Williams *et al.*, 2008) and ship strikes of fin, humpback and killer whales (Williams and O'Hara, 2010), but these limits may have been overly precautionary because of the uncertainty around the abundance estimates, or insufficiently precautionary by not providing information on seasons other than summer.

With additional systematic surveys completed in 2006-08, the objective was to generate updated estimates. Here,

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updated abundance estimates for eight marine mammal species are given along with new estimates for elephant seals (*Mirounga angustirostris*) and Steller sea lions (*Eumetopias jubatus*). Estimates are directly compared with previous abundance estimates derived using a Conventional Distance Sampling (CDS) approach (Williams and Thomas, 2007) to gauge the effect of increased sample size on precision. New abundance estimates have been created for all 10 species using Density Surface Models (DSM), which uses statistical models to explain spatial heterogeneity in animal distribution using environmental covariates and therefore offers potential to improve precision (Hedley *et al.*, 1999; Marques and Buckland, 2003; Miller *et al.*, 2013). This DSM approach was essential to meeting the final objective of providing updated information on the distribution of marine mammals in BC's coastal waters for use in spatial planning and spatially explicit risk assessments.

Systematic, line-transect marine mammal surveys were conducted throughout the continental shelf waters of British Columbia during summer 2004, 2005, 2006, and 2008, and spring and autumn 2007. With the exception of 2004, surveys were concentrated in the Queen Charlotte Basin and mainland inlets of the North and Central Coasts. The summer 2004 survey encompassed a far larger area of BC's continental shelf waters, stretching from the BC-Alaska border south to the BC-Washington border.

Although more than 20 marine mammal species are found in BC's coastal waters, only 10 marine mammal species yielded a sufficient number of sightings for analysis: harbour porpoise (*Phocoena phocoena*); Dall's porpoise (*Phocoenoides dalli*); Pacific white-sided dolphin (*Lagenorhynchus obliquidens*); killer whale (resident, transient and offshore ecotypes); humpback whale (*Megaptera novaeangliae*); common minke whale (*Balaenoptera acutorostrata*); fin whale (*B. physalus*); harbour seal (*Phoca vitulina*); Steller sea lion; and elephant seal. Several of these species are of significant conservation concern at provincial, national and international levels (Table 1).

Sighting and density estimation of pinnipeds were further separated into 'haul-out' or 'in-water' categories, as both detectability on the trackline and the detection function are expected to differ widely.

Species information

Harbour porpoise

Harbour porpoises are listed as 'Least Concern' by the International Union for Conservation of Nature (IUCN) but as a species of 'Special Concern' within Canada's Pacific region (COSEWIC, 2003). Found predominantly in shallow waters less than 200m in the Northern Hemisphere, four subspecies have been genetically identified globally (Rice, 1998). Despite continuous distribution alongshore from Point Conception around the Pacific rim to the northern islands of Japan and as far north as Barrow, Alaska, many small populations appear genetically distinct, suggesting the need to consider small subpopulation management units (Chivers *et al.*, 2002). To date, no such stock structure analyses have been conducted in BC.

Dall's porpoise

Dall's porpoises are globally abundant with an estimated population of more than 1.2 million individuals. The species is listed as of 'Least Concern' by the IUCN (Hammond *et al.*, 2008) and 'Not At Risk' within Canada, but has not been assessed by Canada since 1989, when no abundance estimates were available. Dall's porpoise are distributed throughout the North Pacific Ocean, generally in deeper coastal waters, but no information is available on stock structure.

Pacific white-sided dolphin

Pacific white-sided dolphins are listed by the IUCN as a species of 'Least Concern' and 'Not At Risk' in Canadian waters, but the species has not been assessed by Canada since 1990, when no abundance estimates were available. They are distributed along the temperate coastal shelf waters and in some inland BC waterways of the North Pacific from approximately 35°N to 47°N (Heise, 1997; Stacey and Baird, 1991).

Humpback whale

Humpback whales were listed by the IUCN in 2008 as a species of 'Least Concern' and in Canada, were listed as of 'Special Concern' (COSEWIC, 2011) in 2014 by SARA. Studies indicate that the North Pacific population is

Table 1

Conservation status of marine mammals in British Columbia waters, including year assessed and designations for subpopulations and breeding status, where available. Note: COSEWIC lacked a 'Data Deficient' category in the 1980s and early 1990s, so older assessments in the 'Not At Risk' category should be interpreted with caution.

Common name	Provincial: British Columbia	National: COSEWIC	Global: IUCN
Harbour porpoise	Special Concern, 2006	Special Concern, 2003	Least Concern, 2008
Dall's porpoise	Apparently Secure/Secure, 2006	Not At Risk, 1989	Least Concern, 2008
Pacific white-sided dolphin	Apparently Secure/Secure, 2006	Not At Risk, 1990	Least Concern, 2008
Humpback whale	Special Concern, 2006	Special Concern, 2011	Least Concern, 2008
Fin whale	Imperilled (non-breeding), 2006	Threatened, 2005	Endangered, 2008
Killer whale	Special Concern, 2006		Data Deficient, 2008
Offshore	Imperilled, 2011	Threatened, 2008	
Transient	Imperilled, 2011	Threatened, 2008	
Southern resident	Critically Imperilled, 2011	Endangered, 2008	
Northern resident	Imperilled, 2011	Threatened, 2008	
Common minke whale	Apparently Secure (non-breeding), 2006	Not At Risk, 2006	Least Concern, 2008
Harbour seal	Secure, 2006	Not At Risk, 1999	Least Concern, 2008
Steller sea lion	Imperilled/Special Concern (breeding), 2006 Special Concern (non-breeding), 2006	Special Concern, 2003	Near Threatened, 2012
Northern elephant seal	Not Applicable, 2006	Not At Risk, 1986	Least Concern, 2008

recovering (e.g., Calambokidis *et al.*, 2008; Dahlheim *et al.*, 2009), following the substantial reduction of the population by commercial whaling (Baird, 2003). Within BC, adult survival is high (0.979, 95% CI: 0.914, 0.995), and a significant increase in abundance was observed between 2004 and 2011 in Ashe *et al.* (2013), although population growth and increased search effort were confounded in that study.

Fin whale
Fin whales are listed as 'Endangered' by the IUCN, 'Threatened' in Canada's Pacific region (COSEWIC, 2005) and 'Imperilled' in BC. Fin whales are found across the world's oceans, largely in offshore waters and less so in warm tropical regions (Reilly *et al.*, 2008a). Historical records reveal that fin whales were once one of the most abundant and heavily exploited marine mammals in the inshore waters of BC (Gregr *et al.*, 2000). Since the 1975 North Pacific estimate of roughly 17,000 animals, down from an estimated 44,000 that preceded intensive commercial whaling, survey data have been too insufficient to generate regional abundance estimates (Reilly *et al.*, 2008a). However, in the waters of western Alaska and the central Aleutian Islands, Zerbini *et al.* (2006) found a 4.8% annual rate of increase by comparing survey information from 1987 with 2001–03 surveys.

Killer whale
Found throughout the world's oceans, killer whales are listed by the IUCN as 'Data Deficient' (Taylor *et al.*, 2008). In BC, three ecotypes of killer whale have been identified (with 2006 population estimates based on photo-identification): (1) 261 Northern Residents (Ellis *et al.*, 2011) and 85 Southern Residents; (2) 243 West Coast Transient; and (3) Offshore (>288; COSEWIC, 2008). All of these populations are classified as 'Threatened' within Canadian waters, with the exception of the Southern Residents, which are listed as 'Endangered' (COSEWIC, 2008). In general, these populations feed on different prey, are reproductively isolated, and are genetically distinct (Ford *et al.*, 2009). Individuals are usually identified by dorsal fin morphology and relationships between individuals are often known, particularly with killer whales. The residents feed on fish (especially Chinook salmon), whereas transients prey on marine mammals. The more recently discovered and far less understood offshore ecotype feed on sharks (Ford *et al.*, 2011) and fish (Ford *et al.*, 2009).

Common minke whale
Common minke whales are found throughout the world's oceans and are listed by the IUCN as a species of 'Least Concern'. Population sizes for parts of the Northern Hemisphere are estimated at over 100,000 animals (Reilly *et al.*, 2008b). In Canada they are considered 'Not At Risk', but this assumes a potential rescue effect from whales in adjacent US or international waters. Without information on stock structure, it is conceivable that BC's common minke whales constitute a naturally small population.

Harbour seal
Harbour seals inhabit the temperate and polar coastal areas of the Northern Hemisphere with a global population estimated between 350,000 to 500,000 individuals (Thompson and Härkönen, 2008). The species is listed by the IUCN as 'Least Concern' and considered 'Not At Risk' in Canada. Following population reduction by commercial harvesting and subsequent predator control programmes, the British Columbia population of harbour seals appears to have recovered; the abundance of harbour seals in BC waters (including west coasts of Vancouver Island and Haida Gwaii, which are beyond our study area) is estimated at 105,000 animals (1966–2008; Olesiuk, 2010).

Steller sea lion
Steller sea lions inhabit the coastal waters of the North Pacific and are listed as 'Near Threatened' by the IUCN and as a species of 'Special Concern' in Canada. Recognised as 'Imperilled' and/or of 'Special Concern' in BC, the provincial breeding population is estimated to be 20,000–28,000 animals in 2006 (Fisheries and Oceans Canada, 2008), out of a total estimated Eastern Pacific population of between 46,000 and 58,000 animals (Fisheries and Oceans Canada, 2011). Although the population is increasing in BC, Steller sea lions breed at only four known locations in BC which makes them vulnerable to disturbances at these locations (e.g., oil spills), and unexplained population declines have occurred (e.g., 2002; Fisheries and Oceans Canada, 2011).

Northern elephant seal
Considered by the IUCN as a species of 'Least Concern', listed as 'Not at Risk' in Canada and as 'Not Applicable' within British Columbia, elephant seals have recovered from near extinction from historic hunting. Elephant seals are found throughout the northeastern Pacific and their population is estimated at around 171,000 (2005; Campagna, 2008). Their at-sea distribution and habitat preferences are very poorly described in BC.

METHODS
Survey design
Systematic surveys maximised coverage and minimised off-effort time over four strata (Fig. 1) for the purposes of design-based multi-species density estimation as seen in Thomas *et al.* (2007). Zigzag configurations were applied over the open strata (1) and (2), with sub-stratification for the more topographically complex strata (2). For the narrower strata (3) and (4), parallel lines oriented perpendicular to the long axis reduced edge effects. The four inlet strata were further subdivided into primary sampling units (PSUs) so that for a given season, a random sub-sample of PSUs was selected for surveying (Table 2). To estimate density, effort-weighted means were used for all strata, except stratum (4), which was derived from the un-weighted mean of the PSUs. Detailed survey design and strata are described in Thomas *et al.* (2007) and Williams and Thomas (2007).

Field methods
Field methods have been previously described in detail by Williams and Thomas (2007), but are summarized here. Two vessels were used to collect survey information. The 21m motorsailor *Achiever* was used in 2004, 2006, 2007, and
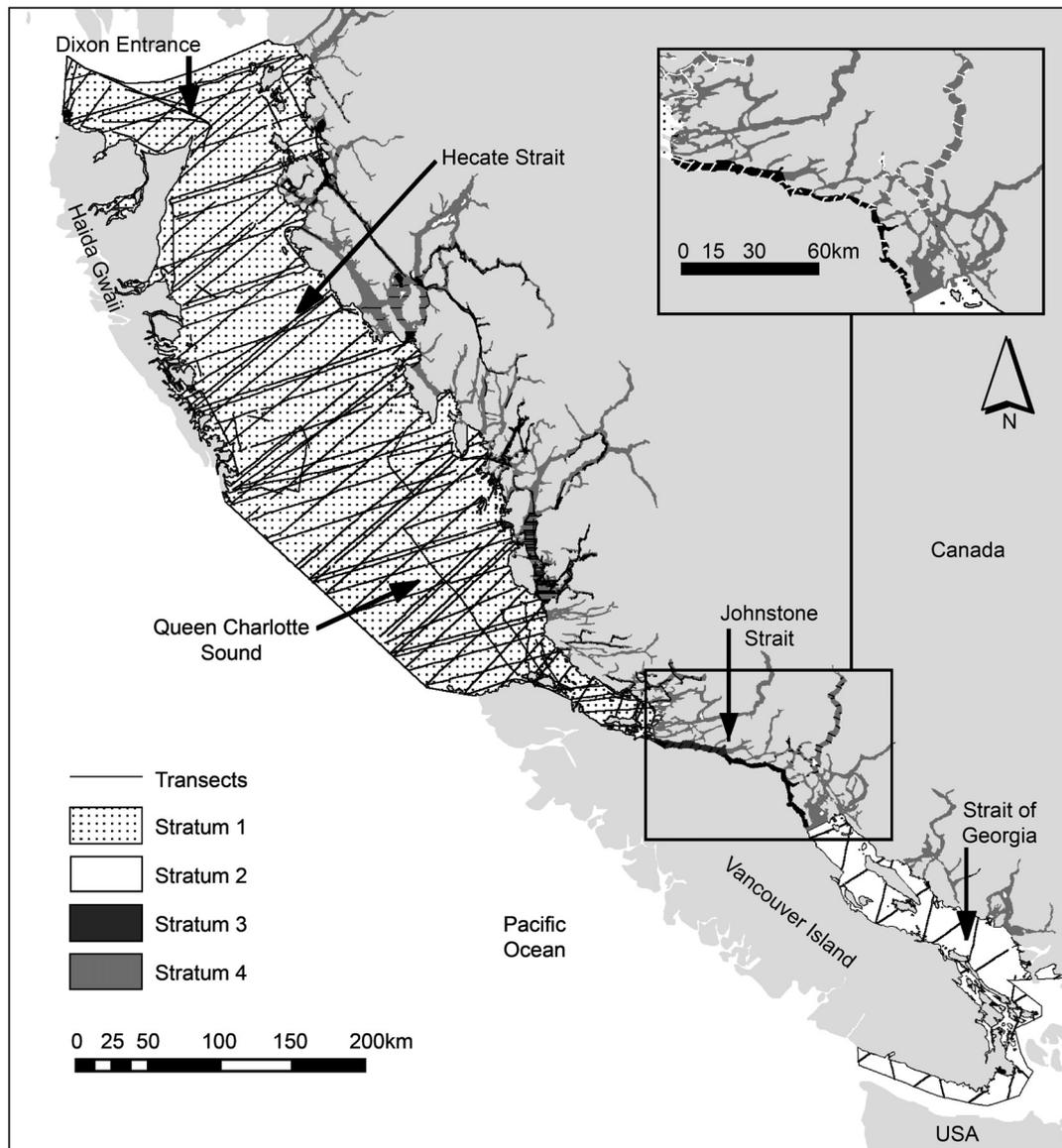
Fig. 1. Stratum identification and on-effort transects, including transit legs, between design-based transects (2004–2008) corresponding to Queen Charlotte Basin (Stratum 1), Straits of Georgia and Juan de Fuca (Stratum 2), Johnstone Strait (Stratum 3) and mainland inlets (Stratum 4) of coastal British Columbia.

2008 and the 20m powerboat, *Gwaii Haanas*, was used in 2005. Vessels actively surveyed at a relatively constant 15kmh^{-1}. On both survey vessels, observer eye height was approximately 5m. On *Achiever*, a platform was constructed over the boom and main cabin to allow for unobstructed sightings (with the exception of the mast, but observers were placed as far port and starboard to see past the mast).

A rotating group of six individuals primarily served as the observation team, although this number ranged from four to seven. A port and starboard observer searched the vessel's path, each person responsible for a sector that ranged from 30° on one side of the trackline to 90° on the other side but concentrating most of their effort on the trackline (0°). The use of two observers positioned at port and starboard also addressed any issues arising from the obstruction of sightings due to the mast. Observers used 8 × 50 and 7 × 50 binoculars to scan the area. A third team member was positioned between the observers; this individual recorded data when a sighting was made and assisted in identification and data collection. Sighting information was relayed by the data

collector to a fourth team member (the computer operator) located inside the vessel. The vessel's Global Positioning System (GPS) was connected to the survey computer that logged the vessel's position every 10 seconds, using *Logger 2000* software (developed by International Fund for Animal Welfare). In addition to sightings information and position, environmental conditions were recorded every 15min, or sooner if conditions were changeable. Environmental conditions recorded were: Beaufort sea state; cloud cover percentage; precipitation; and a ranking code based on overall sightability. The fifth team member functioned as deck hand, to assist as required and the sixth team member held a rest position. Positions rotated every hour and observer identity was recorded.

Sighting information was relayed by the data recorder to the computer operator via a two-way radio or by direct verbal communication. Two angle boards mounted to the port and starboard were used to measure the radial angle to the marine mammal school. Radial distance to the school was measured using: 7 × 50 reticle binoculars; a perpendicular sighting

Table 2

Realised survey effort by year and strata for line transect surveys of British Columbia's coastal waters. Note the sample unit for stratum 4 is based on primary sampling units (PSU), not number of transects.

Stratum/location	PSU	Year	Season	Length (km)	Number of transects	Area (km²)
1: Queen Charlotte Basin		2004	Summer	1,672	17	62,976
		2005	Summer	1,693	18	
		2006	Summer	605	9	
		2007	Spring	1,694	17	
			Autumn	897	13	
		2008	Summer	1,692	17	
2: Strait of Georgia		2004	Summer	479	24	8,186
3: Johnstone Strait		2005	Summer	74	29	420
4: Mainland inlets						11,965
	4	2004	Summer	24		
	10			84		
	17			47		
	21			98		
	29			79		
	17	2006	Summer	44		
	21			104		
	7	2007	Spring	49		
	13			39		
	17			32		
	21			119		
	23			13		
	7	2007	Autumn	51		
	13			39		
	17			33		
	21			123		
	23			13		
	8	2008	Summer	20		
	14			46		
	17			30		
	21			125		
	25			39		

gauge; a laser range finder; or by a visual estimate. For each school the following information was recorded: radial distance; radial angle; species; school size; behaviour (travel, forage, avoid, approach, breach, unknown and other); cue type (body, blow, seabird activity); and heading relative to the ship (profile, head-on, tail-on or uncertain). Off-transect data (e.g., when the vessel was re-positioning for another transect) were routinely collected while still actively observing (i.e., on-effort). This information was used to increase sighting number for detection functions but was not used in calculating encounter rate for the CDS density estimates. Density surface models were not constrained by the need to maximise coverage and did not limit detections to on-transect data, so off-transect on-effort data were used in modelling encounter rate (Miller *et al.*, 2013; Williams *et al.*, 2011b).

Data analysis and abundance estimation using conventional distance analysis

Data were analysed in the program *Distance* version 6 Beta 3 (Thomas *et al.*, 2010). CDS was used to generate marine mammal abundance estimates (Buckland *et al.*, 2001). This approach replicates the methods of Williams and Thomas (2007) for the entire 2004–08 survey to generate new and revised abundance estimates for 10 marine mammals inter-annually and for novel seasons. During the 2006 survey, observer effort within the inlet stratum 4 was not part of a designed survey and only included effort while on passage, so these data were excluded from the estimation of abundance estimates. Abundance was estimated as the density of animals

multiplied by the applicable study area or stratum. To estimate density ($\hat{D}$), the following formula was used:

$$\hat{D} = \frac{n\hat{s}}{L2w\hat{p}}$$

Where the encounter rate (n/L) or number of schools seen (n) over the length of the transect (L), is multiplied by twice the truncation distance (w) to obtain an area and the estimated school size ($\hat{s}$). In line transect surveys, the probability of detecting a school decreases with increase in distance. Accounting for this probability of detection ($\hat{p}$) helps to form the basis of CDS by fitting a detection function (Buckland *et al.*, 2001).

Detection functions were estimated using the software *Distance*, which can apply several key functions (uniform, half-normal or hazard rate) and series expansion terms (polynomial or cosine) to estimate the shape of the function. The observers recorded radial distance (d) and angle (θ) during the field surveys. These relative values are then converted to perpendicular distance from the trackline using simple geometry, $sin(\theta) \times d$. All on-effort sightings (i.e., periods when the observers were actively observing for animals), including off-transect observations, were used for detection model fitting. Models that minimise the Akaike Information Criterion (AIC) score were generally selected, which provides an explanation of deviance while penalising the addition of terms to achieve the most parsimonious model (Akaike, 1974). In addition, the Kolmogorov-Smirnov goodness-of-fit test was employed to provide a measure of agreement between the model and the data (Buckland *et al.*,

2004). If species exhibit an attraction to the survey vessel, then a spike is typically seen near the trackline, which can cause positive bias in the density estimates. Observations were truncated to within the perpendicular distance (w) used in Williams and Thomas (2007).

These detection functions all assume certain detection on the trackline, meaning $g(0) = 1$. A probability of availability is typically divided by the density to account for the fact that marine mammals are often below the water surface and not detected even when directly on the trackline of the vessel. Estimating this probability requires tracking of individuals to estimate proportion of time spent underwater (e.g., Laake *et al.*, 1997) or multiple platforms of simultaneous, independent observation. The research vessel was not large enough to offer two platforms for isolated observers, and $g(0)$ could therefore not be estimated. Due to this factor, the abundance estimates developed will underestimate the true population size, but the estimates should be consistent over the years the study took place, thereby allowing trends to be examined.

School size bias was estimated in *Distance* using the default CDS method. The natural logarithm of group size is regressed on the probability of detection and the value of *ln*() at zero distance is back-transformed to obtain the expected school size (E(s)).

Abundance estimates using\ density surface modelling (DSM)

Spatial patterns in animal density were modelled using a suite of geographic and environmental predictors (Density Surface Modelling (DSM); Miller *et al.*, 2013). This technique was performed using the software program *Distance* (Buckland *et al.*, 2004), which relies on a Generalised Additive Models (GAM) to associate environmental variables to the rate of encounter. This approach has the potential to improve precision of the final estimate (De Segura *et al.*, 2007) and can be used to identify areas of high animal density that may inform spatial management of natural resources. Because DSM methods do not require systematic or random sampling of the survey region (i.e. uniform coverage of the transects), they have the additional benefit of allowing inclusion of effort and sightings data when observers were on-effort but off-transect (i.e. 'transit-leg' segments).

Transects were segmented into one nautical mile (1,852m) in order to be at a scale relative to the underlying environmental data (Miller *et al.*, 2013). The response variable in this analysis is the estimated number of schools encountered per segment i, $\hat{N}_i$, given by the Horvitz-Thompson estimator (Horvitz and Thompson, 1952):

$$\hat{N}_i = \sum_{j=1}^{n_i} \frac{1}{\hat{p}_{ij}}, i = ,\ldots, v \ .$$

Here, the inverse of the detection probability ($\hat{p}$) for the jth detected school in the ith segment is summed across all detected schools n_i, per segment. Data was then merged to segments without sightings ($N = 0$), so a GAM was fitted using the quasi-Poisson distribution and a logarithmic link function to relate N to the environmental predictor variables:

$$\hat{N}_i = \exp\left[\alpha + \sum_{k=1}^{q} s_k(z_{ik}) + \log(a_i)\right] + e_i$$

Here, the predictor variables, z_{ik} are fitted by a smoothing function s_k, and subsequently summed with intercept α and an offset a_i, which represents the segment's area ($2wL_i$). The estimation of the smoothing function was performed by the R library MGCV (Wood, 2001).

Once the model was fitted to the observed environmental conditions, a prediction was made over the entire study area based on a single period of the input environmental data (z). So far the response $\hat{N}$ is the number of schools detected over the area, or the school density. To obtain an estimate of abundance ($\hat{A}$), we must then multiply by the estimated school size ($\hat{s}$).

Variance on the abundance estimate is calculated using the Delta method (Seber, 1982) to combine the variance of the school density ($CV(\hat{N})$) with the detection function ($CV(\hat{p})$) and the mean school size ($CV(\hat{s})$):

$$\hat{A} = \sum_{i=1}^{n} \hat{N}_i$$

$$CV(\hat{A}) = \sqrt{CV(\hat{p})^2 + CV(\hat{N})^2 + CV(\hat{s})^2}$$

To estimate variance of just $\hat{N}$ (e.g., $CV(\hat{N})$ term above), the *Distance* software historically used a moving block bootstrap resampling technique. Even for only 400 replicates, this technique can be very time consuming and frequently failed before reaching completion. As an alternative, the coefficients and variance from the fitted model were used to simulate predictions were generated using a multivariate normal sampler on the Bayesian posterior covariance matrix. From these simulated predictions confidence intervals were extracted. This method is described by Wood and Augustin (2002) and in the *R* documentation for the predict.gam function and has since been incorporated (in principle) into the latest density surface modelling variance estimation software under development[7].

The set of covariates used in the final model are selected to explain the greatest deviance while minimising unnecessary addition of parameters. Many criteria exist that weight these two factors against each other (e.g., AIC). For GAMs that have a dispersion term, as with the quasi-Poisson response dispersion used in these models, the lowest Generalised Cross-Validation (GCV) value is the preferred model selection tool (Wood *et al.*, 2008). The number of knots that govern the degree of smoothing, are further reduced in most of these models by using the non-default thin-plate spline with shrinkage (basis = 'ts') function, which adds a small penalty to additional knots, so that the whole term can be shrunk to zero, removing any contribution from the predictor. Term plots were inspected and any terms with confidence bounds spanning zero were removed to allow the process to test for a model with a lower GCV score. Models would sometimes fail to converge using this approach. In this situation, attempts were then made to limit the possible number of knots to five and to implement the default thin-plate spline (tp) without the shrinkage term. In addition to environmental covariates, the longitude-latitude bivariate term provided a spatial estimator, which can act as a proxy for unmeasured variables that influence hotspots not accounted for by the other predictors. Categorical variables

[7]*See: https://github.com/dill/dsm/blob/master/R/dsm.var.gam.R.*

such as season (summer, autumn, or spring) and inlet (in or out) were also tested using this approach.

Density surface model detection functions
The detection functions generated using CDS could not be reused for estimating $\hat{p}$ because the DSM module in the software program *Distance* is only compatible with the multiple covariate distance sampling (MCDS) function available through the mark recapture distance sampling (MRDS) R library, which at the time of the analysis only allowed for half-normal (hn) and hazard rate (hr) key functions. Based on the CDS analysis, the same truncation distances were used with the half-normal key function, unless a hazard rate model was used. The logic of this process is that as the school size increases, it should become easier to detect. This was accounted for by adding a covariate of size with detection function, which is possible with the MCDS function and not with CDS approach. When the use of size covariate was not possible, the detection function was chosen during our CDS model selection.

Environmental variables
The manipulation of spatial data was performed with ESRI ArcGIS 9.2 using the Spatial Analyst toolbox (ESRI 2009). Midpoints of the transect segments were used to extract the values of the environmental layers and then sampled for use in the GAM. To predict the seascape with the fitted model, a 5km prediction grid was generated using the NAD 83BC Environment Albers projection to correspond with the available environmental data. The raster grid was converted to a polygon vector layer and the cells were clipped to the coastline and strata areas. The areas were calculated per cell to be used as the offset value during prediction. The centroid location of each cell was used to extract values from the environmental layers.

Static environmental variables included bathymetric depth, slope, and distance to shore. Latitude and longitude were used as separate variables and as a co-varying term. Shoreline data were extracted from the Global Self-consistent, Hierarchical, High-resolution Shoreline (GSHHS) database (Wessel and Smith, 1996). Bathymetry data were extracted from the SRTM30 Plus 30-arc second resolution dataset (Becker *et al.*, 2009). Euclidean distance from shore and the local slope of the bathymetry surface were calculated in ArcGIS. The log of these predictors was tested in cases for which model convergence with a GAM was otherwise prohibitive.

The marine environment is highly dynamic, requiring the capture of this variability over the survey periods to build more temporally meaningful models. These models represent proxies for physiological or biological constraints (e.g., sea surface temperature) and prey patterns (e.g., primary productivity) associated with the species. However, attempts to incorporate dynamic variables, such as sea surface temperature (SST) and Chlorophyll *a* (Chl*a*), into the predictive model proved unsuccessful. Due to the continuous cloud cover experienced and the nearness to shore, sufficient satellite data matched to the specific observation periods of this analysis were not available for this study. After spatially interpolating these data with kriging and summarising inputs across seasons, it was still found that none of the DSM models with these dynamic data outperformed the environmentally static models that were to be chosen in the final model selection. Consequently, all subsequent analyses considered only the static variables described above as candidate covariates.

RESULTS

Survey effort
On-effort transects for the surveys (2004–08) occurred in the open waters of Queen Charlotte Basin (stratum 1), Strait of Georgia (stratum 2), Johnstone Strait (stratum 3) and mainland inlets (stratum 4; Fig. 1). Realised transect effort, in terms of kilometres covered, varied by stratum and year (Table 2). A number of complete transects in stratum 1 were cancelled in autumn 2007, due to extremely poor weather conditions and portions of transects that occurred in US waters in stratum 2 (2004) were cancelled due to transboundary permitting reasons. In addition, several small transect segments were excluded due to being non-navigable by the survey vessels and/or poor environmental conditions.

Sightings
Ten species were sighted with sufficient frequency for analysis (Fig. 2). The final detection models (Figs 3 and 4) and associated information for CDS and DSM were generated (Tables 3 and 4). School sighting information was also generated (Table 5). Species abundance and density estimates with 95% confidence intervals (CIs) and percentage coefficient of variation (%CV) were calculated across all surveys and strata using CDS (Fig. 5 and online supplement for detailed information).

Responsive movement can be a problem, in terms of both avoidance or attraction, but analyses to date suggest the field protocols generally allowed observers to search far enough ahead of the vessel to record distance and angle prior to responsive movement occurring. Using methods described by Palka and Hammond (2001), Williams and Thomas (2007) examined data on swimming direction of animals for evidence of responsive movement and found that only Pacific white-sided dolphins approached the boat before being detected by observers. A greater proportion of approaching behaviour for Dall's porpoise and prominent spike in the data warranted similar methods for coping with responsive movement in this study, namely not fitting the spike near zero. For all other species, no evidence for responsive movement was found, and was therefore ignored in the analysis.

Harbour porpoise
Combining all surveys, 128 harbour porpoise groups were sighted (Table 3). This species was distributed widely across the northern and southern extents of the study area, and were more common in nearshore and inlet waters (Fig. 2). Most (122/128 = 95%) exhibited travelling/foraging behaviour, with the remaining two feeding and two avoiding; no obvious response to the observer vessel is indicated with these data.

Restricting the observations to a truncation distance of 600m excluded 10 observations, or 8% of the sightings
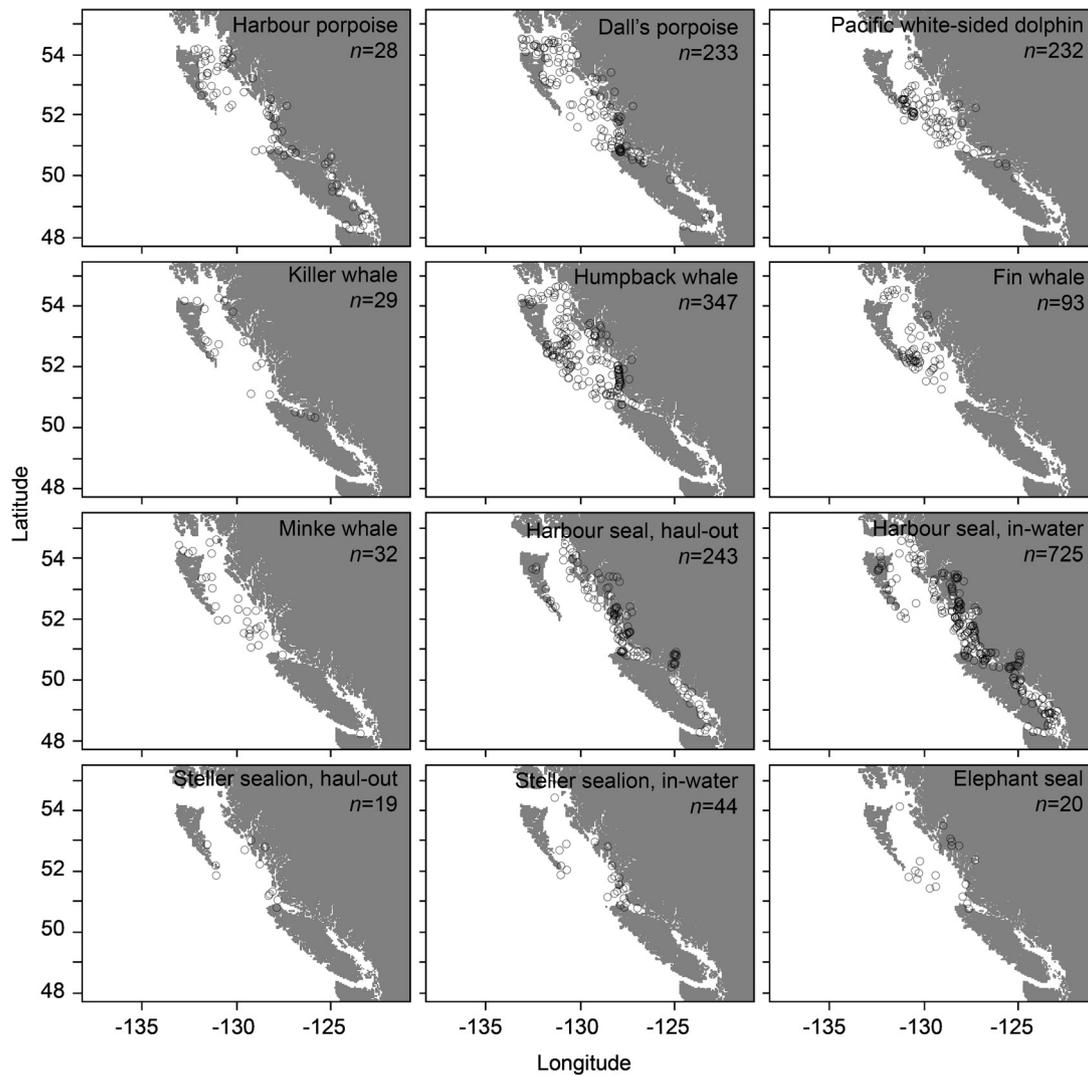
Fig. 2. Sightings of ten marine mammal species from surveys of British Columbia's coastal waters in summer 2004, 2005 and 2008 and spring and autumn 2007.

(Table 3). The preferred detection function was the hazard rate model with no adjustment terms (Table 3). The data show a spike near zero (Fig. 3). These spikes are typically linked with attractive movement, but none was noted in the field or in the data collected on behaviour or orientation relative to the ship, so alternate models that ignored the spike were not considered. The steeply declining detection function is likely to accurately reflect the cryptic nature of this species; that is, observers really did cover only a narrow strip for this species. All the other models tested with higher AIC values produced smoother fits than the data or the hazard rate model, which produced a higher $\hat{p}$ and lower abundance estimate. For example, the next lowest-AIC model (ΔAIC = 8.53), uniform with five cosine adjustments, produced a $\hat{p}$ 41% larger (0.284 vs. 0.201).

Dall's porpoise
Of the 239 Dall's porpoise school sightings (Table 3), most occurred in the offshore waters of the northern and southern portions of the Queen Charlotte Basin with relatively few schools within the inlets or the southern straits (Fig. 2). Whereas most observations (212/239 = 88.7%) were travelling/foraging, a small proportion (11/239 = 4.6%) were approaching and the same number feeding. Other behaviours

included socialising (2/239 = 0.8%), avoidance (1/239 = 0.4%), and unknown (2/239 = 0.8%).

A truncation distance of 700m excluded 18 observations, or 8% of the observations, from model fitting. The hazard rate function with one cosine adjustment fit the data best according to the AIC criteria, but exhibited a sharp spike near zero. Given that a small proportion of Dall's porpoise were recorded with attractive behaviour and are known to bow-ride (including our survey vessel), we believe that the spike near zero reflects responsive movement. Following Williams and Thomas (2007), we chose a half-normal model with two cosine adjustments having the next lowest AIC (ΔAIC = 7.02). Turnock and Quinn (1991) also found that a half-normal model corrected most for the attractive movement, using simulations and data from Dall's porpoises in Alaska. The half-normal model for Dall's porpoise detection was also chosen by Williams and Thomas (2007), except the approaching behaviours were less numerous (2/11 = 18% versus 11/239 = 4.6%) which presumably contributed to not having to override the AIC selected hazard rate model with the half-normal. To further quantify a correction factor, a secondary platform of observation is recommended but that could not be accomplished on our survey vessel.
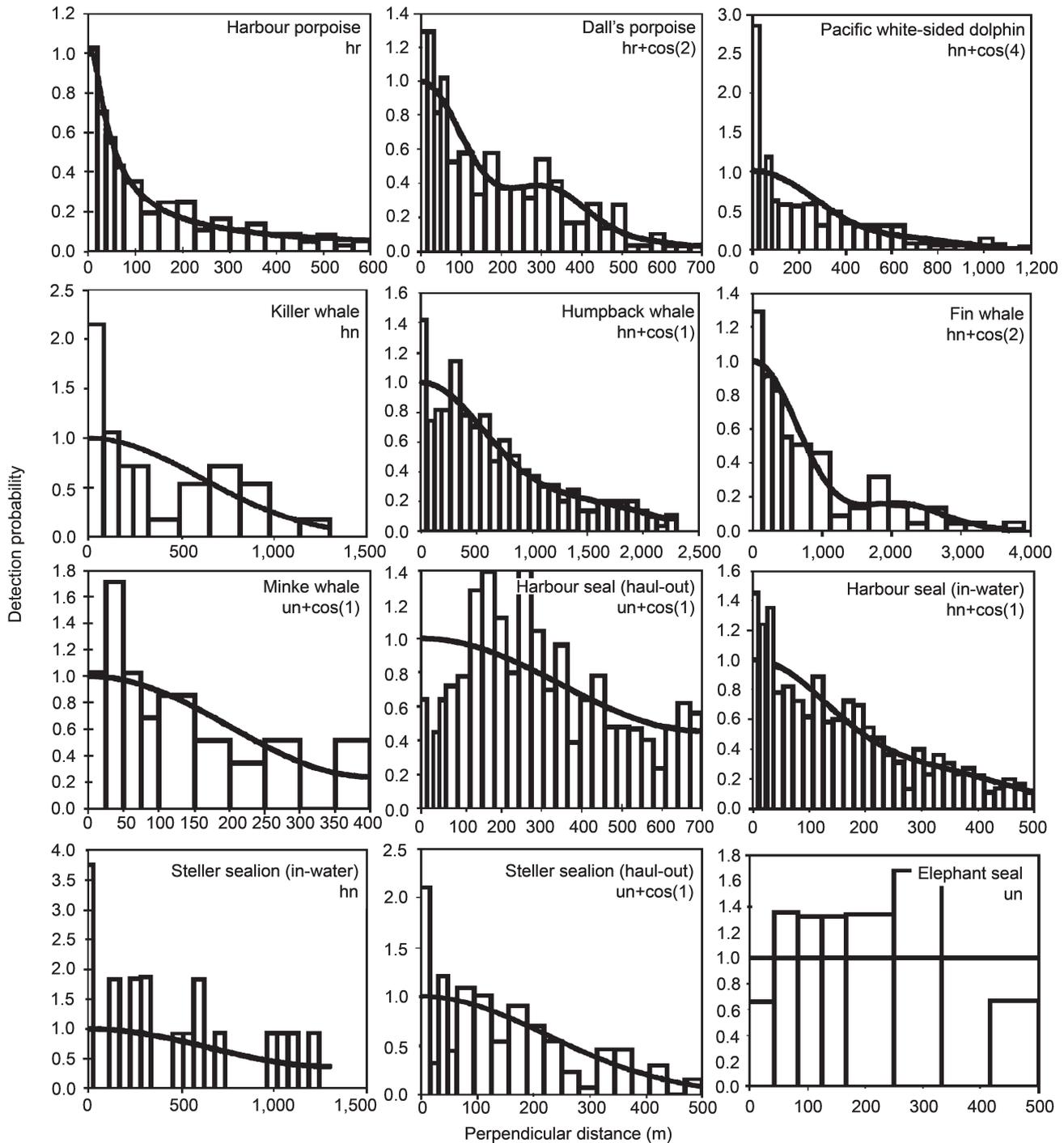
Fig. 3. Detection functions for marine mammal species generated using Conventional Distance Sampling (CDS) analysis for coastal British Columbia 2004–08 surveys.

Pacific white-sided dolphin

Of the 233 schools of Pacific white-sided dolphin, most were seen throughout the southern portion of the Queen Charlotte Basin, particularly near Haida Gwaii, with several additional sightings in the inlets and northern end of the southern straits (Fig. 2). This species exhibits the strongest approaching behaviour (47/233 = 20.2%). Other behaviours include: travelling/foraging (151/233 = 64.8%); feeding (18/233 = 7.7%); breaching (13/233 = 6%); socialising (1/233 = 0.4%); avoidance (1/233 = 0.4%); and uncertain (2/233 = 0.8%).

Using a truncation distance of 1,200m (Table 3), the lowest AIC values were achieved with a hazard rate model, which followed the spike of the data near zero distance. To minimise the bias of attractive movement, the model with the 2nd lowest AIC (ΔAIC = 23.89) was achieved with a half-normal model with four cosine adjustments to avoid fitting the spike (Fig. 3). This is a similar strategy for model selection as used with Dall's porpoise.

Humpback whale

The highest number of cetacean school sightings (*n* = 352) was attributed to humpback whale (Table 3). These sightings occurred exclusively in Queen Charlotte Sound and inlets, but not in the southern straits (Fig. 2). Most sightings were in deep water, with some preference towards the southern Haida Gwaii region and the southeastern portion of Queen
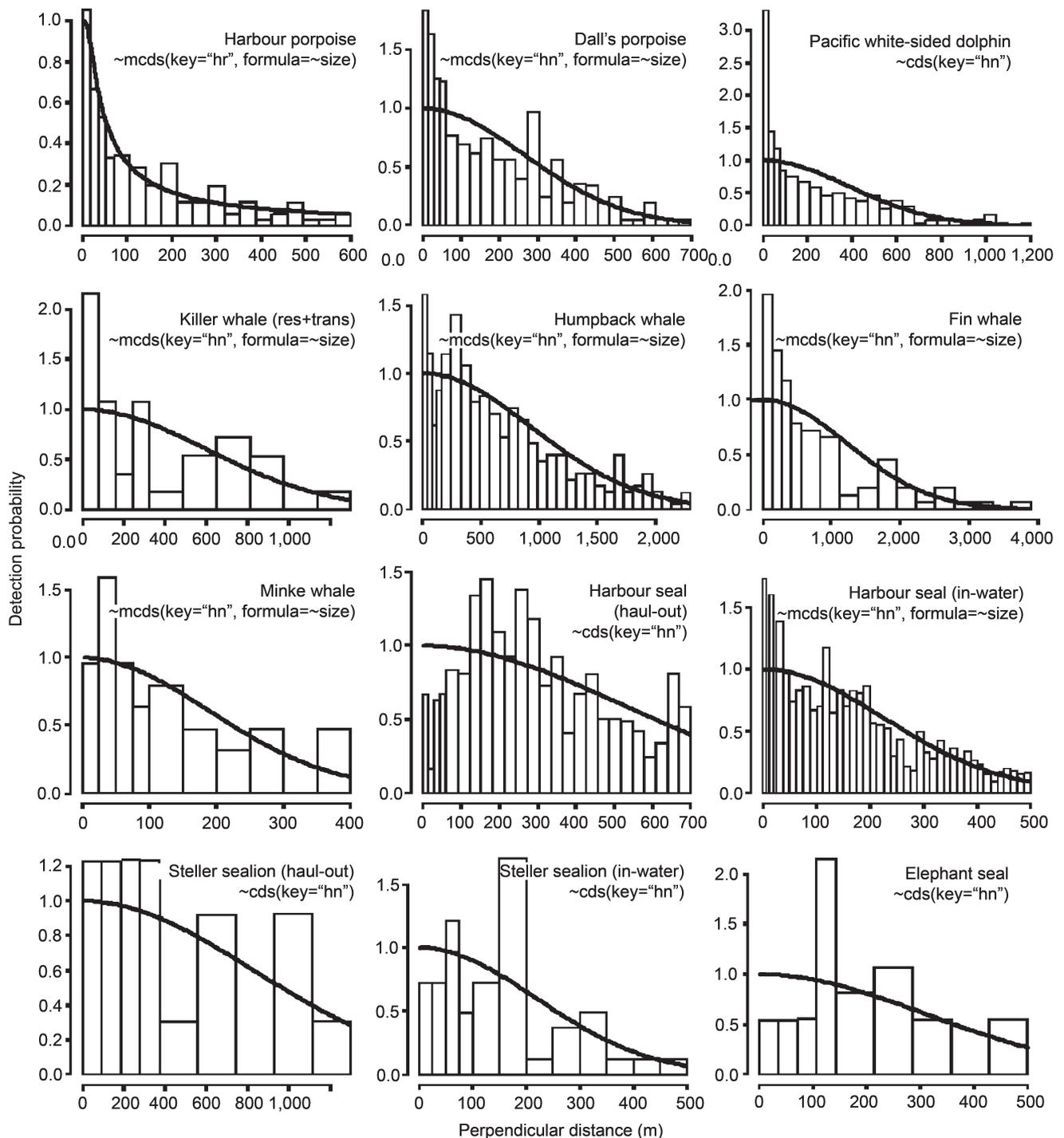
Fig. 4. Average detection probabilities for Density Surface Modeling (DSM) using the Multiple Covariates Distance Sampling (MCDS) engine with the covariate size where possible, otherwise using Conventional Distance Sampling (CDS) without a covariate. The detection function uses either a half-normal (hn) or hazard rate (hr) key functions. Marine mammal sighting information was obtained from line transect surveys in coastal British Columbia (2004–08).

Charlotte Sound. Only one observation was noted for approaching behaviour (1/352 = 0.2%) and the rest included: travelling/foraging (265/352 = 75.3%); feeding (41/352 = 11.6%); breaching (25/352 = 7.1%); socialising (3/352 = 8.5%); and unknown (5/352 = 1.4%). Using a 2,300m truncation distance, the lowest-AIC model selected used a half-normal model with one cosine adjustment term (Fig. 3).

Fin whale
All of the 91 school sightings of fin whale were found in the Queen Charlotte Basin, with the exception of two

observations in Grenville Channel, located on the North Coast of BC (Fig. 2). Most offshore sightings were located off southeastern Haida Gwaii, with another large cluster of sightings in the northern portion of the Sound (Fig. 2). The behaviours of sightings include: travelling/foraging (73/91 = 80.2%); feeding (3/91 = 3.3%); socialising (1/91 = 1.1%); and other/uncertain (4/91 = 4.4%). A 3,900m truncation distance was applied (Table 3). The hazard rate model obtained the lowest AIC, but exhibited a spike near zero, so a half-normal model with two cosine adjustment terms (ΔAIC = 1.4) was used instead (Fig. 3).
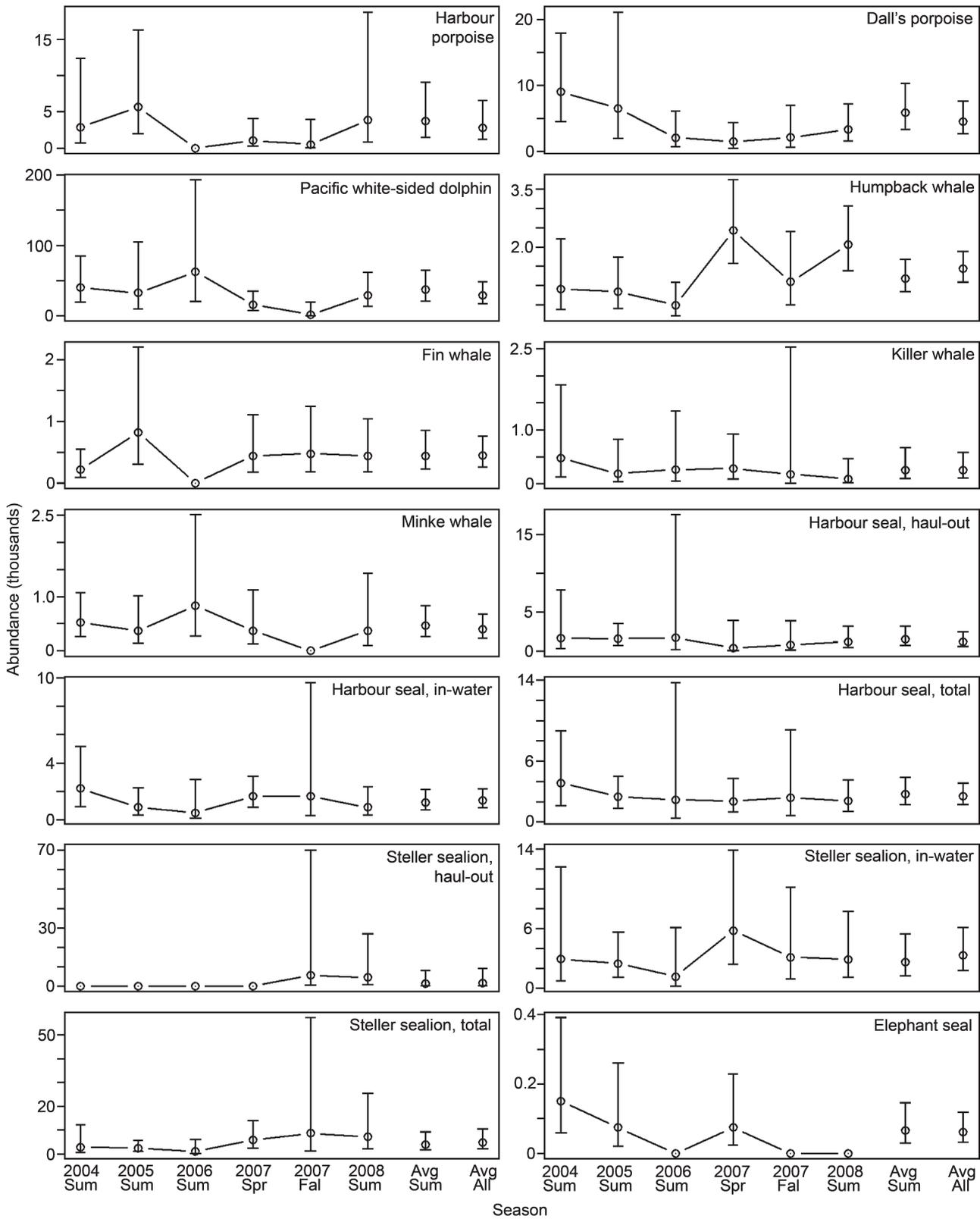
Fig. 5. Abundance estimates with 95% confidence intervals generated using Conventional Distance Sampling (CDS) over surveyed years and seasons in stratum 1 only, including the average of all seasons. Summer averages are included for seasonal comparison with 2007 autumn and spring in coastal British Columbia.

Killer whale
At 29 school sightings, the killer whale is the least frequently seen of the whale species analysed (Table 3). Most targeted killer whale studies differentially treat the ecotypes (Zerbini *et al.*, 2006), but data constraints forced the grouping of the resident, transient, and offshore types together for this analysis. Most sightings occurred in the Queen Charlotte

Basin and Johnstone Strait, most commonly in the nearshore (Fig. 2). Observed behaviours include: travelling/foraging (24/29 = 82.7%); feeding (2/29 = 6.7%); socialising (1/29 = 3.4%); and other (2/29 = 6.7%). A truncation distance of 1,300m was applied to provide a monotonically decreasing tail, while retaining as many observations as possible (25/29 = 86%). A hazard rate model best fit these data, but to offset

Table 3

Detection function summary statistics using Conventional Distance Sampling (CDS) for marine mammal species surveyed in coastal British Columbia (2004–08). Truncation distance (w) with number of sightings (n) before and after truncation. Model described by key function (hazard-rate (hr), half-normal (hn), or uniform (un)) with optional series expansion terms (polynomial (poly), or cosine (cos)). The p-value for the goodness-of-fit Kolmogorov-Smirnov (K-S), and the final probability of detection ($\hat{p}$) and its percent coefficient of variation (%CV ($\hat{p}$)).

Common name	w(m)	n before	n after	Model	K-S p	$\hat{p}$	%CV ($\hat{p}$)
Harbour porpoise	600	128	118 (–8%)	hr	0.899	0.201	24.29
Dall's porpoise	700	239	221 (–8%)	hn + cos(3)	0.190	0.344	9.86
Pacific white-sided dolphin	1,200	233	219 (–6%)	hn + cos(4)	0.001	0.253	8.63
Humpback whale	2,300	352	325 (–8%)	hn + cos(1)	0.951	0.421	6.43
Fin whale	3,900	91	82 (–10%)	hn + cos(2)	0.375	0.270	11.01
Killer whale	1,300	29	25 (–14%)	hn	0.302	0.558	16.71
Minke whale	400	32	29 (–9%)	un + cos(1)	0.641	0.620	13.81
Harbour seal (haul-out)	700	244	212 (–13%)	un + cos (1)	0.326	0.728	6.69
Harbour seal (in-water)	500	774	732 (–5%)	hn + cos (1)	0.030	0.477	4.74
Steller sea lion (haul-out)	1,300	20	17 (–15%)	un + cos (1)	0.639	0.686	21.57
Steller sea lion (in-water)	500	123	114 (–7%)	hn	0.047	0.548	7.71
Elephant seal	500	20	18 (–10%)	un	0.572	1.000	0.00

Table 4

Generalised Additive Model (GAM) formulation with truncation distances (w) and distance model type (Detection) for given stratum with generalized cross-validation score (GCV), deviance explained (DE) and GAM model terms for marine mammals surveyed in coastal British Columbia (2004–08). The Detection function is indicated by the key function of either hazard rate (hr) or half-normal (hn).

Common name	w	Detection	Strata	GCV	DE (%)	GAM model terms
Harbour porpoise	600	hr	1–4	0.486	25.6	lon,lat + depth + distcoast + slope + season + inlet
Dall's porpoise	700	hn	1–4	0.345	19.1	lon,lat + depth + distcoast + slope + season + inlet
Pacific white-sided dolphin	1,200	hn	1–4	0.377	33.4	lon,lat + depth + distcoast + slope + season + inlet
Humpback whale	2,300	hn	1	0.521	19.0	lon,lat + depth + distcoast + slope + season
			4	0.265	11.0	depth† + distcoast† + slope†
Fin whale	3,900	hn	1–4	0.145	41.8	lon,lat + depth + distcoast + slope
Killer whale (all ecotypes)	1,300	hn	1–4	0.040	39.5	lon,lat†
Minke whale	400	hn	1–4	0.045	32.5	lon,lat + depth + distcoast + slope
Harbour seal (haul-out)	700	hn	1–4	0.188	35.6	lon,lat + depth + distcoast + slope + season + inlet
Harbour seal (in-water)	500	hn	1	0.157	43.4	lon,lat + depth + distcoast + slope + season
			2–4	1.366	23.9	lon,lat + depth + distcoast + slope + inlet
Steller sea lion (haul-out)	1,300	hn	1–4	0.025	26.5	log(depth)* + distcoast* + log(slope)*
Steller sea lion (in-water)	500	hn	1–4	0.062	47.1	lon,lat + depth + distcoast + slope + inlet
Elephant seal	500	hn	1–4	0.018	51.8	lon,lat + depth + distcoast + slope + season

*Terms were limited to 5 knots. †Terms were used with a basis 'ts', which is the default thin-plate smooth but allowing for shrinkage to zero.

Table 5

Observed and estimated school sizes ($\hat{s}$) for marine mammal species from 2004–08 surveys in coastal British Columbia waters using Conventional Distance Sampling (CDS).

	Estimated school size		Observed school size		
Species	$\hat{s}$	%CV($\hat{s}$)	Mean	%CV	Maximum
Harbour porpoise	1.67	4.56	1.81	4.53	5
Dall's porpoise	2.41	4.54	2.43	5.55	15
Pacific white-sided dolphin	13.53	14.77	38.27	20.41	1,200
Humpback whale	1.51	2.79	1.57	3.75	8
Fin whale	1.78	6.86	1.99	12.73	20
Killer whale (all ecotypes)	3.67	18.26	3.80	15.27	28
Minke whale	0.99	2.36	1.03	3.33	2
Harbour seal (haul-out)	5.58	9.51	6.82	9.77	90
Harbour seal (in-water)	1.11	1.20	1.20	2.83	18
Steller sea lion (haul-out)	70.29	66.86	37.77	49.25	300
Steller sea lion (in-water)	6.11	20.31	14.41	26.89	370
Elephant seal	1	0	1	0	1

the spike near zero the half-normal model without adjustment terms ($\Delta AIC = 0.53$) was chosen.

Common minke whale

Only slightly more frequently seen ($n = 32$) than killer whales is the common minke whale (Table 3). Sightings were widely distributed within Queen Charlotte Basin, generally offshore (Fig. 2). All sightings were recorded as travelling/foraging behaviour, although minke whales are at surface less than other species so detailed behaviour is often difficult to determine. Of the 32 observations only three exceeded 400m in perpendicular distance from the transect

line (2,377m, 1,888m and 1,532m), so a truncation distance of 400m was used. The lowest-AIC model, a uniform model with one cosine adjustment term, was chosen in this case.

Harbour seal
The most commonly sighted of all marine mammals (*n* = 1,018; Table 3), harbour seals were typically sighted in nearshore waters throughout all strata (Fig. 2). They exhibited the following behaviours: travelling/foraging (701/1,018 = 68.9%); socialising (75/1,018 = 7.4%); feeding (13/1,018 = 1.3%); approaching (1/1,018 = 0.1%); and other/unknown (110/1,018 = 10.8%). Detectability is expected to vary as a function of whether the animal is in or out of water, hence the separation between in-water and haul-out observations for truncation distances and detection functions (Table 3). Roughly, one quarter of the sightings were haul-out versus three quarters in-water. For in-water observations, a truncation distance of 500m was used and the lowest-AIC model selected was a half-normal model with one cosine adjustment term (Fig. 3). For haul-out observations, a 700m truncation was used, indicative of greater visibility when out of water, and the lowest-AIC model selected was a uniform model with one cosine adjustment. The distance readings for haul-out observations exhibit a peak around 200m rather than monotonically increasing towards zero. Because most haul out sightings are to the side during along-shore transects, this off-zero peak was anticipated.

Steller sea lion
A total of 123 in-water sightings of Steller sea lions were recorded and an additional 20 on land (Table 3). All of these sightings were generally made in the nearshore and inlets of the southern Queen Charlotte Basin (Fig. 2). In-water animals appeared to exhibit slight responsiveness to the ship (avoidance: 30/123 = 24.4%; approach: 2/123 = 1.6%), otherwise found travelling/foraging (67/123 = 54.5%), socialising (10/123 = 8.1%), feeding (3/123 = 2.4%), or other/unknown (38/123 = 30.9%). For in-water observations, a 500m truncation distance was used and the lowest-AIC model selected was a half-normal model. For haul-out observations, a 1,300m truncation distance was used and the lowest-AIC model selected was a uniform model with one cosine adjustment.

Northern elephant seal
The least frequently sighted of all marine mammal species analysed (group sightings = 20; Table 3), the northern elephant seal was observed in the open waters of Queen Charlotte Basin as well as the southern and central coast inlets (Fig. 2). A 500m truncation distance was used, and the final model selected was a uniform model, which corresponds to a strip transect, i.e., density is assumed to not vary with distance from transect. In this case, there were too few observations to construct a robust distance detection function, as further evidenced by the unrealistic $\hat{p}$ value of 1 (Table 3).

Other species
Besides the marine mammals already mentioned, other species were observed during the survey, albeit too rarely

to estimate abundance or without sufficient taxonomic specificity. The number of sightings broken down to season, years and strata are listed in supplementary Table 7: gray whale (*Eschrichtius robustus*; *n* = 7), sei whale (*Balaenoptera borealis*; *n* = 1; reported previously in (Williams and Thomas, 2007)), sea otter (*Enhydra lutris*; *n* = 36), sunfish (*Mola mola*; *n* = 27) and sharks (*n* = 106). A high-density shark aggregation was described previously (Williams *et al.*, 2010). Sea otters were excluded from assessment because relatively few observations were made and their distribution is elsewhere better described by dedicated surveys conducted by Fisheries and Oceans Canada (Nichol *et al.*, 2009).

Comparison of estimates and uncertainty
Compared with previous abundance estimates by Williams and Thomas (2007), who relied on survey data from 2004 and 2005 alone, our analyses resulted in altered abundance estimates and tighter confidence intervals, often substantially so, for all mean abundance estimates over the study region (Fig. 6) and within stratum (see online supplement). For some species, mean abundance estimates for the entire study area (Fig. 6 and online supplement) are lower than earlier estimates (Williams and Thomas, 2007): harbour porpoise (6,631 and 34.9% CV vs. 9,120 and 40.5% CV); fin whale (446 and 26.4% CV vs. 496 and 45.8% CV); and harbour seal (in-water) (10,394 and 6.5% CV vs. 13,524 and 15.3% CV). The remainder of mean abundance estimates are higher, as with Dall's porpoise (6,232 and 20.0% CV vs. 4,913 and 29.2% CV), Pacific white-sided dolphin (32,637 and 24.6% CV vs. 25,906 and 35.3% CV), humpback whale (1,541 and 12.9% CV vs. 1,313 and 27.5% CV), killer whale (308 and 38.2% CV vs. 161 and 67.4% CV), minke whale (430 and 25.2% CV vs. 388 and 26.8% CV) and harbour seal (haul-out) (7,060 and 12.9% CV vs. 5,852 and 25.9% CV). Abundance estimates for Steller sea lions and elephant seals were available in this analysis and not in Williams and Thomas (2007) due to the limited sample size generated from 2004 and 2005 surveys.

Comparing 95% confidence intervals of abundance estimates between surveys for stratum 1, we see that with one exception, all of the estimates have overlapping confidence intervals (Fig. 5 and online supplement). This suggests no significant population changes occurred over the 2004–08 sampling period. The only clearly non-overlapping confidence interval was found for humpback whales, which have the lowest estimated abundances in summer 2006 (486 and 95% CI 219–1,081) and highest estimated abundances in the following spring survey in 2007 (2,431 and 95% CI 1,577–3,747). The second highest abundance estimate was in summer 2008 (2,057 and 95% CI 1,382–3,062). Notably, summer 2006 had the least amount of realised survey effort at 605km versus nearly 1,700km for all other summer surveys. In the case of humpback whales, a simple linear trend is non-significant, either by summer surveys (*p* = 0.276) or inclusive of 2007 autumn and spring (*p* = 0.204). Nonetheless, mean abundance estimates are appreciably higher in 2007–08 compared with the earlier period of 2004–06. Bayesian methods may suit a future study having more observational data to estimate trends in population abundance (Moore and Barlow, 2011; 2013).
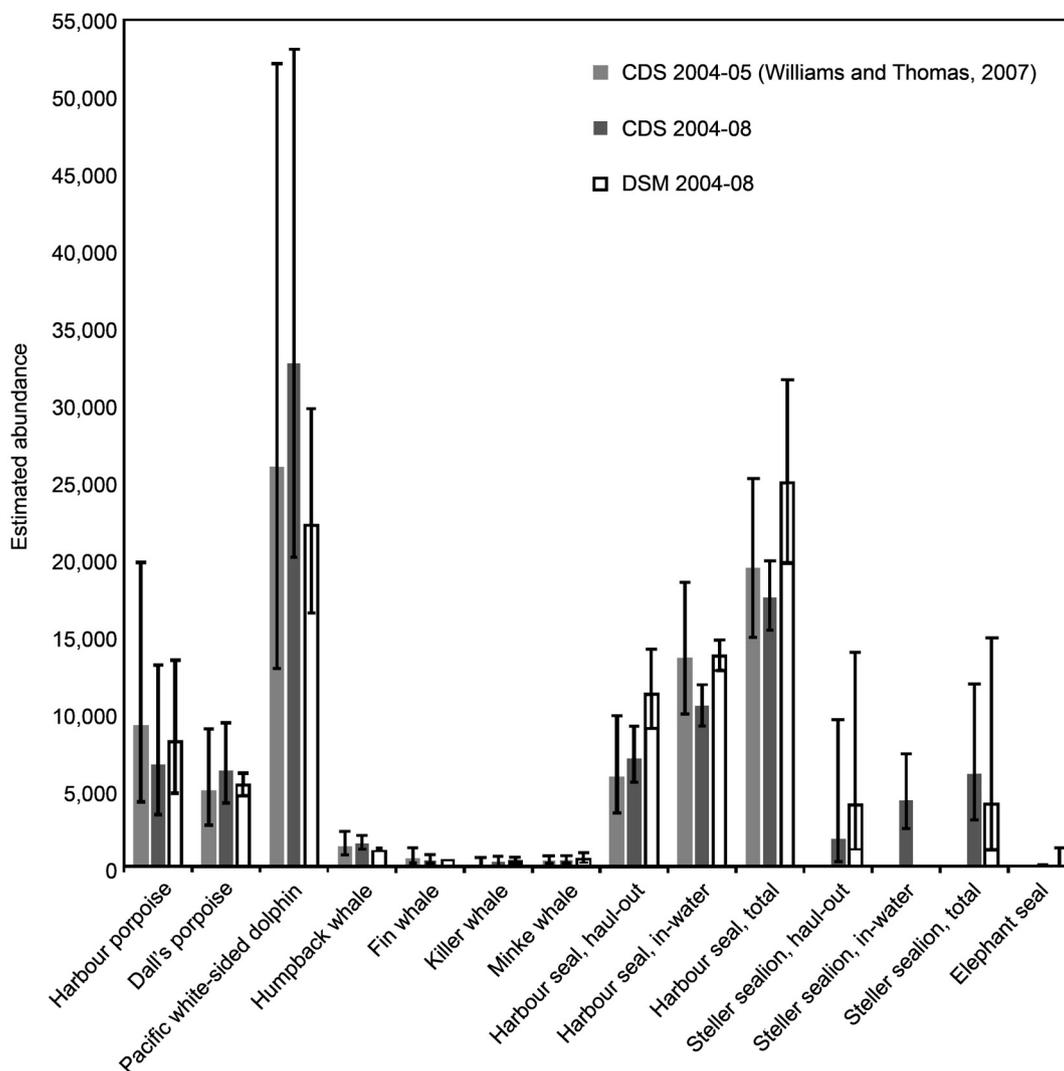
Fig. 6. Abundance estimate comparisons ±95% confidence intervals of the updated 2004–08 survey data pooled across all strata and seasons using Conventional distance Sampling (CDS) and Density Surface Models (DSM) and compared to Williams and Thomas (2007) estimates generated from the 2004–05 surveys in coastal British Columbia. Species abbreviations are for harbour porpoise, Dall's porpoise, Pacific white-sided dolphin, killer whale, humpback whale, common minke whale, fin whale, harbour seal, Steller sea lion, and elephant seal.

Density surface modelling abundance estimates
For harbour seals (in-water), separate models had to be fitted for stratum 1 and the other strata 2, 3 and 4. The humpback whale model had to be fitted with separate models for stratum 1 and stratum 4, excluding strata 2 and 3 where no observations were made. For Steller sea lion (haul-out), the log terms of depth and slope were used to obtain a fitted model (Table 4).

In general, differences between abundance estimates using our CDS and DSM approaches were minor, with significant differences for harbour seals (in water) only. When comparing the CVs between our CDS and DSM abundance estimates for the entire region (Fig. 6 and online supplement), the gain in precision is seen for almost all of the individual species: harbour porpoise (26.2% vs 34.95%); Dall's porpoise (6.8% vs 20.0%); Pacific white-sided dolphin (15.1% vs 24.6%); humpback whale (4.8% vs 12.9%); fin whale (9.3% vs 26.4%); killer whale (26.7% vs 38.2%); harbour seal haul-out (11.5% vs 12.9%); harbour seal in-water (3.7% vs 6.5%); Steller sea lion haul-out (70.3% vs 99.9%); and Steller sea lion in-water (24.2% vs 27.9%). Species where this was not the case were the minke whale

(29.9% vs 25.2%) and the elephant seal (2,452.4% vs 29.9%). The CV for the elephant seal is exceptionally high, mainly due to the high variance being divided by a very small mean value. Due to so few observations being made (*n* = 20) while so many more segments were zero, DSM is less reliable than estimates derived using CDS.

Spatial distributions
Density surface models are useful for identifying potential high-use areas or hotspots (see Fig. 7) where any conflicting human use should be avoided, highlighting low-use areas (blue in Fig. 7) where these activities may more safely be relocated. Comparing the observations (Fig. 2), we see general agreement with the distribution of the density surface models (Fig. 7). Much of the predictive power from the models is derived from the bivariate spatial location predictor (i.e., latitude, longitude).

Dall's porpoise is most highly concentrated in the northeastern section of the study region and the model is influenced most positively by medium range depths (Fig. 7a). Harbour porpoises are distributed heavily in the southern strata and some northern areas of Queen Charlotte Basin near
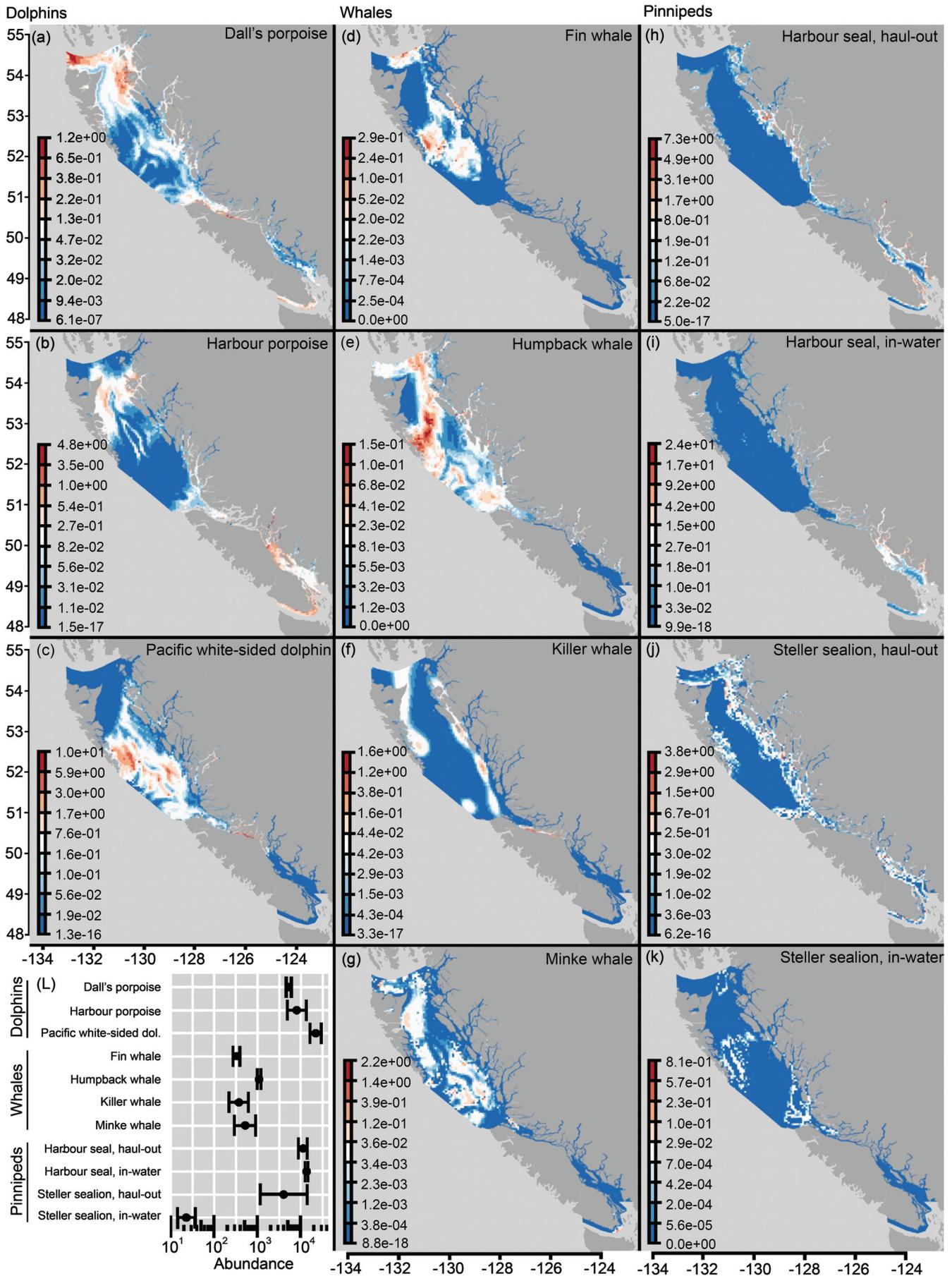
Fig. 7. Density surface models for marine mammals in coastal British Columbia reported as density (# animals/km²) for dolphins (a–c), whales (d–g) and pinnipeds (h–k), which are further differentiated between in water and hauled out populations. Colour breaks diverge above (red) and below (blue) the mean density (white) based on Jenk's natural breaks to maximise spatial differentiation. Note that the break intervals are unequal. Plotted in geographic coordinate space using cells generated in Albers BC. The whisker plot (L) of mean and 95% confidence interval of total abundance for the study area (Supplemental Tables 5 and 6) compares population sizes between species. Note the log 10 axis for abundance.

Prince Rupert (Fig. 7b). Because only encounter rate is spatially modelled, observations with larger groups are not heavily weighted for the density surface. The Pacific white-sided dolphin dominates the southern and central portion of the basin, with another 'hotspot' in Johnstone Strait (Fig. 7c). Distance from the coast is a dominant term positively influencing density, offset by the negative contribution of depth and slope.

Fin whales are clustered at the southern portion of Haida Gwaii and the northernmost section of the basin (Fig. 7d). Humpback whale distribution (Fig. 7e) is positively influenced by distance to coast and depth, with animals most prominently found off the southern portion of Haida Gwaii and along the tidally driven Hecate Strait Front, which is known to aggregate prey from spring to autumn (Clarke and Jamieson, 2006), and which corresponds with other humpback survey results (Dalla Rosa *et al.*, 2012). Killer whales are found in coastal pockets in the south and central basin (Fig. 7f). For this species, spatial location (latitude, longitude) was the only selected predictor. Common minke whales were spread throughout the basin at a low density with greater concentrations offshore (Fig. 7g).

Harbour seals hauled out (Fig. 7h) are found most in the south central portion of the nearshore basin and inlet waters. In-water harbour seals (Fig. 7i) are also distributed nearshore and in the southern strata. Steller sea lions haul-out (Fig. 7j) and in-water (Fig. 7k) are also found nearshore, but more widely throughout the basin. For all pinniped spatial models, distance to shore and depth were strong predictors in the model, reducing the in-water density of the hauled-out surfaces to negligible values. A single density surface per species is preferable for management. The in-water and hauled-out density surfaces could be summed with the hauled-out group truncated to nearshore cells. The full spatial surfaces, however, were retained separately to allow for later recombination given double platform estimates on the trackline $g(0)$ and to account for small islands and rocks present within the coarse 5km prediction grid.

The density surface map for elephant seals was omitted because of poor model performance due to few sightings and preference for the conventional distance sampling abundance results (supplemental Tables 2 and 4).

DISCUSSION

This study provides abundance estimates for 10 marine mammals that inhabit the coastal waters of British Columbia; two represent new abundance estimates for the region and eight represent improved and updated abundance estimates. With often substantial reductions in CIs, whether using conventional or model-based approaches, our revised abundance estimates offer greater precision and accuracy than previous estimates and provide new estimates for spring and fall seasons. A key finding is that humpback whale abundance was highest in spring, which suggests that our surveys sampled whales migrating through BC waters on their way to Alaska. This is particularly relevant because humpback whale abundance is often estimated using mark-recapture statistics from photo-identification. As a secondary objective, a larger, longer-term distributional dataset has also been generated, with relevance for future marine mammal habitat preference studies and further improvement of

abundance estimates using either CDS or DSM (Marques and Buckland, 2003). This study's density surface model-based abundance estimates, with the exception of elephant seals, should be viewed as the most reliable abundance estimates, mainly because this approach accounts for spatial heterogeneity over strata and can theoretically improve abundance estimates by narrowing confidence intervals relative to those generated by CDS methods (De Segura et al., 2007; Burt and Paxton, 2006; Hedley and Buckland, 2004).

The most significant and immediate uses of these improved marine mammal distribution and abundance estimates relate to conservation and management. In British Columbia's coastal waters and surrounding regions, marine mammals face numerous threats including: ship strikes (Williams and O'Hara, 2010); bycatch (Williams *et al.*, 2008); pollution and bio-accumulation of toxins (Ross, 2006; Ross *et al.*, 2004); exhaust emissions (Lachmuth *et al.*, 2011); marine noise (Morton and Symonds, 2002; Williams *et al.*, 2013); marine debris (Williams *et al.*, 2011a); competition with fisheries (Matthiopoulos *et al.*, 2008); climate change (Huntingdon and Moore, 2008); and habitat modification/destruction (Johannessen and Macdonald, 2009). These threats affect many populations that are experiencing reduced population sizes due to the long-term consequences of historical commercial whaling, predator control programs, and other factors. Information generated from a subset of these surveys has already contributed to spatial assessments of likely interaction between 11 marine mammal species and debris (Williams *et al.*, 2011a) and ship strike risk for fin, humpback, and killer whales (Williams and O'Hara, 2010). Although still uncertain, a proposal for an oil pipeline terminus and associated supertanker traffic on the north coast of BC represents an emergent and poorly understood threat to marine mammals and their habitat. The Northern Gateway Pipeline project is a proposal that joins a host of other energy developments which, in combination, signal increasing industrialisation of coastal BC. Lacking from most if not all of these projects is the quality baseline distribution and abundance information required to quantitatively assess risks to marine mammal species.

Given the number of threats faced by marine mammals and the relative paucity of baseline distribution and abundance information, these data provide opportunities for extensive future conservation, research management and decision-making. Further, baseline data represents a benchmark against which future population changes can be monitored, which is a crucial issue in the monitoring and management of marine mammals, particularly for those species that do not benefit from targeted census. As with any type of information regarding species assessment, the need to revise, improve, and subsequently apply updated information for more effective conservation and management strategies should be an ongoing priority. Our future research priorities are to, *inter alia*: expand spatial and seasonal coverage; use model averaging on the detection function to improve our estimates for rare species (Williams and Thomas, 2009); to integrate previously unpublished *in situ* data on temperature, salinity and zooplankton abundance and diversity; develop better methods for gauging distance to marine mammals at sea from small boats when the horizon

is not visible (Williams *et al.*, 2007); and explore potential to conduct surveys near land-based observation sites to conduct benign, non-invasive studies to assess the point at which cetaceans begin to avoid or approach our research vessel. Notwithstanding these limitations, the updated distribution and abundance estimates presented here are timely and important, given the backlog of SARA-listed species for which critical habitat has not been identified or fully protected (e.g., Taylor and Pinkus 2013, Favaro *et al.*, 2014).

REFERENCES

Akaike, H. 1974. A new look at the statistical model identification. *IEEE Transactions on Automatic Control* 19(6): 716–23.

Ashe, E., Wray, J., Picard, C.R. and Williams, R. 2013. Abundance and survival of Pacific humpback whales in a proposed critical habitat area. *PLoS ONE* 8(9): e75228. [Available at: *http://www.plosone.org/article/info%3Adoi%2F10.1371%2Fjournal.pone.0075228*].

Baird, R.W. 2003. Update COSEWIC status report on the humpback whale *Megaptera novaeangliae* in Canada. *In*: COSEWIC assessment and update status report on the humpback whale *Megaptera novaeangliae* in Canada. Committee on the Status of Endangered Wildlife in Canada, Ottawa, Canada. 25pp.

Becker, J.J., Sandwell, D.T., Smith, W.H.F., Braud, J., Binder, B., Depner, J., Fabre, D., Factor, J., Ingalls, S., Kim, S.-H., Ladner, R., Marks, K., Nelson, S., Pharaoh, A., Trimmer, R., Von Rosenberg, J., Wallace, G. and Weatherall, P. 2009. Global bathymetry and elevation data at 30 arc seconds resolution: SRTM30_PLUS. *Mar. Geod.* 32(4): 355–71.

Buckland, S.T., Anderson, D.R., Burnham, K.P., Laake, J.L., Borchers, D.L. and Thomas, L. 2001. *Introduction to Distance Sampling: Estimating Abundance of Biological Populations*. Oxford University Press, Oxford, UK. vi+xv+432pp.

Buckland, S.T., Anderson, D.R., Burnham, K.P., Laake, J.L., Borchers, D.L. and Thomas, L. 2004. *Advanced Distance Sampling: Estimating Abundance of Biological Populations*. Oxford University Press, Oxford, UK. 416pp.

Burt, M.L. and Paxton, C.G.M. 2006. Review of density surface modelling applied to JARPA survey data. Paper SC/D06/J4 presented to the JARPA Review Workshop, Tokyo, 4–8 December 2006 (unpublished). 5pp. [Paper available from the Office of this Journal].

Calambokidis, J., Falcone, E.A., Quinn, T.J., Burdin, A.M., Clapham, P.J., Ford, J.K.B., Gabriele, C.M., LeDuc, R., Mattila, D., Rojas-Bracho, L., Straley, J.M., Taylor, B.L., Urban R, J., Weller, D., Witteveen, B.H., Yamaguchi, M., Bendlin, A., Camacho, D., Flynn, K., Havron, A., Huggins, J. and Maloney, N. 2008. SPLASH: Structure of populations, levels of abundance and status of humpback whales in the North Pacific. Final report for Contract AB133F-03-RP-00078, US Department of Commerce Western Administrative Center, Seattle, Washington.

[Available at *http://www.cascadiaresearch.org/SPLASH/SPLASH-contract-report-May08.pdf*].

Campagna, C. 2008. *Mirounga angustirostris*. In: IUCN Red List of Threatened Species. Version 2009.2. [Available at: *http://www.iucnredlist.org*, downloaded on 25 November 2009].

Chivers, S.J., Dizon, A.E., Gearin, P.J. and Robertson, K.M. 2002. Small-scale population structure of eastern North Pacific harbour porpoises (*Phocoena phocoena*) indicated by molecular genetic analyses. *J. Cetacean Res. Manage.* 4(2): 111–22.

Clarke, C.L. and Jamieson, G. 2006. Identification of Ecologically and Biologically Significant Areas in the Pacific North Coast Integrated Management Area: Phase II – Final Report. *Can. Tech. Rep. Fish. Aquat. Sci.* 2686: v+25pp.

COSEWIC. 2003. COSEWIC assessment and update status report on the harbour porpoise *Phocoena phocoena* (Pacific Ocean population) in Canada. Committee on the Status of Endangered Wildlife in Canada, Ottawa, Canada. 22pp. [Available at: *http://www.sararegistry.gc.ca. status/status_e.cfm*.]

COSEWIC. 2005. COSEWIC assessment and update status report on the fin whale *Balaenoptera physalus* in Canada. Committee on the Status of Endangered Wildlife in Canada, Ottawa, Canada. 37pp. [Available at: *http://www.sararegistry.gc.ca.status/status_e.cfm*.]

COSEWIC. 2008. COSEWIC assessment and update status report on the killer whale *Orcinus orca*, Southern Resident population, Northern Resident population, West Coast Transient population, Offshore population and Northwest Atlantic / Eastern Arctic population, in Canada. Committee on the Status of Endangered Wildlife in Canada. Ottawa. viii+65pp [Available at: *http://www.sararegistry.gc.ca/status/status_e.cfm*].

COSEWIC. 2011. COSEWIC assessment and status report on the humpback whale *Megaptera novaeanglia*e in Canada. Committee on the Status of Endangered Wildlife in Canada. Ottawa, Canada. 32pp. [Available at: *http://publications.gc.ca/collections/collection_2012/ec/CW69-14-233-2011-eng.pdf*].

Dahlheim, M.E., White, P.A. and Waite, J.M. 2009. Cetaceans of Southeast Alaska: distribution and seasonal occurrence. *J. Biogeography* 36(3): 410–26.

Dalla Rosa, L., Ford, J.K.B. and Trites, A.W. 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.

De Segura, A.G., Hammond, P.S., Cañadas, A. and Raga, J.A. 2007. Comparing cetacean abundance estimates derived from spatial models and design-based line transect methods. *Mar. Ecol. Prog. Ser.* 329: 289–99.

Ellis, G.M., Towers, J.R. and Ford, J.K.B. 2011. Northern resident killer whales of British Columbia: Photo-identification catalogue and population status to 2010. *Can. Tech. Rep. Fish. Aquat. Sci.* 2942: vi+71.

Favaro, B., Claar, D.C., Fox, C.H., Freshwater, C., Holden, J.J., Roberts, A. and Uvic Research Derby. 2014. Trends in extinction risk for imperiled species in Canada. *PLoS ONE* 9(11): e113118. [Available at: *http://journals.plos.org/plosone/article?id=10.1371/journal.pone.0113118*]

Fisheries and Oceans Canada. 2008. Population assessment: Steller sea lion (*Eumetopias jubatus*). *Can. Sci. Advis. Sec. Sci. Advis. Rep.* 2008/047: 11pp. [Available at: *http://www.dfo-mpo.gc.ca/CSAS/Csas/Publications/SAR-AS/2008/SAR-AS2008_047_E.pdf*].

Fisheries and Oceans Canada. 2009. Management plan for the Pacific harbour porpoise (*Phocoena phocoena*) in Canada. Species at Risk Act Management Plan Series. Fisheries and Oceans Canada, Ottawa. 49pp. [Available at: *https://www.registrelep-sararegistry.gc.ca/document/doc1781f/ind_e.cfm*].

Fisheries and Oceans Canada. 2011. Management plan for the Steller sea lion (*Eumetopias jubatus*) in Canada. Species at Risk Act Management Plan Series. Fisheries and Oceans Canada, Ottawa. 69pp. [Available at: *http://publications.gc.ca/collections/collection_2011/mpo-dfo/En3-5-8-2011-eng.pdf*].

Ford, J.K.B., Ellis, G.M., Olesiuk, P.F. and Balcomb, K.C. 2009. Linking killer whale survival and prey abundance: food limitation in the oceans' apex predator? *Biology Letters* 6: 139–42. [Available at: *http://rsbl.royalsocietypublishing.org/content/early/2009/09/14/rsbl.2009.0468.full.pdf+html*].

Ford, J.K.B., Ellis, G.M., Matkin, C.O., Wetklo, M.H., Barrett-Lennard, L.G., Lance, G. and Withler, R.E. 2011. Shark predation and tooth wear in a population of northeastern Pacific killer whales. *Aquat. Biol.* 11(3): 213–24. [Available at: *http://www.int-res.com/articles/ab2010/11/b011p213.pdf*].

Gregr, E.J., Nichol, L., Ford, J.K.B., Ellis, G. and Trites, A. 2000. Migration and population structure of northeast Pacific whales of coastal British Columbia: an analysis of commercial whaling records from 1908–1967. *Mar. Mammal Sci.* 16(4): 699–727.

Hammond, P.S., Bearzi, G., Bjørge, A., Forney, K., Karczmarski, L., Kasuya, T., Perrin, W.F., Scott, M.D., Wang, J.Y., Wells, R.S. and Wilson, B. 2008.

Phocoenoides dalli. In: IUCN Red List of Threatened Species. Version 2009.2. [Available at: *http://www.iucnredlist.org*, downloaded on 13 November 2009].

Hedley, S., Buckland, S.T. and Borchers, D.L. 1999. Spatial modelling from line transect data. *J. Cetacean Res. Manage.* 1(3): 255–64.

Hedley, S. and Buckland, S.T. 2004. Spatial models for line transect sampling. *J. Agric. Bio. Env. Stat.* 9: 181–99.

Heise, K. 1997. Life history and population parameters of Pacific white-sided dolphins (*Lagenorhynchus obliquidens*). *Rep. int. Whal. Commn* 47: 817–25.

Horvitz, D.G. and Thompson, D.J. 1952. A generalization of sampling without replacement from a finite universe. *J. Am. Stat. Assoc.* 47(260): 663–85.

Huntingdon, H. and Moore, S. 2008. Arctic marine mammals and climate change. *Ecol. Appl.* 18(2): S157–S65.

Johannessen, S.C. and Macdonald, R.W. 2009. Effects of local and global change on an inland sea: the Strait of Georgia, British Columbia, Canada. *Climate Res.* 40(1): 1–21.

Kaschner, K., Quick, N.J., Jewell, R., Williams, R. and Harris, C.M. 2012. Global coverage of cetacean line-transect surveys: status quo, data gaps and future challenges. *PLoS ONE* 7(9): e44075. [Available at: *http://www.plosone.org/article/info%3Adoi%2F10.1371%2Fjournal.pone. 0044075#pone-0044075-g004*].

Laake, J.L., Calambokidis, J., Osmek, S.D. and Rugh, D.J. 1997. Probability of detecting harbour porpoise from aerial surveys: Estimating *g*(0). *J. Wildl. Manage.* 61(1): 63–75.

Lachmuth, C.L., Barrett-Lennard, L.G., Steyn, D.Q. and Milsom, W.K. 2011. Estimation of southern resident killer whale exposure to exhaust emissions from whale-watching vessels and potential adverse health effects and toxicity thresholds. *Mar. Poll. Bull.* 62(4): 792–805.

Marques, F.F.C. and Buckland, S.T. 2003. Incorporating covariates into standard line transect analyses. *Biometrics* 59: 924–35.

Matthiopoulos, J., Smout, S., Winship, A.J., Thompson, D., Boyd, I.L. and Harwood, J. 2008. Getting beneath the surface of marine mammal–fisheries competition. *Mammal Rev.* 38(2): 167–88.

Miller, D.L., Burt, M.L., Rexstad, E.A. and Thomas, L. 2013. Spatial models for distance sampling data: recent developments and future directions. *Methods in Ecology and Evolution* 4: 1,001–10.

Moore, J.E. and Barlow, J. 2011. Bayesian state-space model of fin whale abundance trends from a 1991–2008 time series of line-transect surveys in the California Current. *J. Appl. Ecol.* 48: 1,195–205.

Moore, J.E. and Barlow, J. 2013. Declining abundance of beaked whales (Family *Ziphiidae*) in the California Current Large Marine Ecosystem. *PLoS ONE* 8: e52770. [Available at: *http://journals.plos.org/plosone/ article?id=10.1371/journal.pone.0052770*].

Morton, A.B. and Symonds, H.K. 2002. Displacement of *Orcinus orca* (L.) by high amplitude sound in British Columbia, Canada. *ICES J. Mar. Sci.* 59: 71–80.

Nichol, L.M., Boogaards, M.D. and Abernethy, R. 2009. Recent trends in the abundance and distribution of sea otters (*Enhydra lutris*) in British Columbia. *DFO Can. Sci. Advis. Sec. Res. Doc.* 2009/016: iv + 16pp. [Available at: *http://www.dfo-mpo.gc.ca/csas-sccs/Publications/ResDocs-DocRech/2009/2009_016-eng.htm*].

Olesiuk, P.F. 2010. An assessment of population trends and abundance of harbour seals (*Phoca vitulina*) in British Columbia. *DFO Can. Sci. Advis. Sec. Res. Doc.* 2009/105. 157pp.

Palka, D.L. and Hammond, P.S. 2001. Accounting for responsive movement in line transect estimates of abundance. *Can. J. Fish. Aquat. Sci.* 58: 777–87.

Reilly, S.B., Bannister, J.L., Best, P.B., Brown, M., Brownell Jr, R.L., Butterworth, D.S., Clapham, P.J., Cooke, J., Donovan, G.P., Urbán, J. and Zerbini, A.N. 2008a. *Balaenoptera musculus*. In: IUCN Red List of Threatened Species. Version 2009.2. [Available at: *http://www.iucnredlist.org*, downloaded on 24 November 2009].

Reilly, S.B., Bannister, J.L., Best, P.B., Brown, M., Brownell Jr., R.L., Butterworth, D.S., Clapham, P.J., Cooke, J., Donovan, G.P., Urbán, J. and Zerbini, A.N. 2008b. *Balaenoptera acutorostrata*. In: IUCN Red List of Threatened Species. Version 2009.2. [Available at: *http://www. iucnredlist.org*, downloaded on 24 November 2009].

Rice, D.W. 1998. *Marine Mammals of the World: Systematics and Distribution, Special Publication Number 4, The Society for Marine Mammalogy*. Allen Press, USA. ix+231pp.

Ross, P.S., Jeffries, S.J., Yunker, M.B., Addison, R.F., Ikonomou, M.G. and Calambokidis, J.C. 2004. Harbour seals (*Phoca vitulina*) in British Columbia, Canada, and Washington State, USA, reveal a combination of local and global polychlorinated biphenyl, dioxin, and furan signals. *Toxicol. Chem.* 23(1): 157–65.

Ross, P.S. 2006. Fireproof killer whales (*Orcinus orca*): flame-retardant chemicals and the conservation imperative in the charismatic icon of British Columbia, Canada. *Can. J. Fish. Aquat. Sci.* 63(1): 224–34. [Available at: *http://www.nrcresearchpress.com/doi/pdf/10.1139/f05-244*].

Seber, G.A.F. 1982. *The Estimation of Animal Abundance and Related Parameters*. MacMillan Press, New York, New York, USA. 654pp.

Stacey, P.J. and Baird, R.W. 1991. Status of the Pacific white-sided dolphin, *Lagenorhynchus obliquidens*, in Canada. *Can. Field-Nat.* 105(2): 219–32.

Taylor, B.L., Baird, R., Barlow, J., Dawson, S.M., Ford, J., Mead, J.G., di Sciara, G.N., Wade, P. and Pitman, R.L. 2008. *Orcinus orca*. In: IUCN Red List of Threatened Species. Version 2009.2. [Available at: *http://www.iucnredlist.org*, downloaded on 24 November 2009].

Taylor, E. and Pinkus, S. 2013. The effects of lead agency, non-governmental organizations, and recovery team membership on the identification of critical habitat for species at risk: Insights from the Canadian experience. *Envir. Rev.* 21(2): 93–102.

Thomas, L., Williams, R. and Sandilands, D. 2007. Designing line transect surveys for complex survey regions. *J. Cetacean Res. Manage.* 9: 1–13.

Thomas, L., Buckland, S.T., Rexstad, E.A., Laake, J.L., Strindberg, S., Hedley, S.L., Bishop, J.R.B., Marques, T.A. and Burnham, K.P. 2010. Distance software design and analysis of distance sampling surveys for estimating population size. *J. Appl. Ecol.* 47: 5–14.

Thompson, D. and Härkönen, T. 2008. *Phoca vitulina*. In: IUCN Red List of Threatened Species. Version 2009.2. [Available at: *http://www.iucnredlist.org*, downloaded on 24 November 2009].

Turnock, B.J. and Quinn, T.J. 1991. The effect of responsive movement on abundance estimation using line transect sampling. *Biometrics* 47: 701–15.

Wessel, P. and Smith, W.H.F. 1996. A global, self-consistent, hierarchical, high-resolution shoreline database. *J. Geophys. Res.* 101(B4): 8,741–3.

Williams, R. and Thomas, L. 2007. Distribution and abundance of marine mammals in the coastal waters of British Columbia, Canada. *J. Cetacean Res. Manage.* 9(1): 15–28.

Williams, R., Leaper, R., Zerbini, A. and Hammond, P.S. 2007. Methods for investigating measurement error in cetacean line transect surveys. *J. of Mar. Biol. Assoc. of the UK* 87: 313–20.

Williams, R., Hall, A. and Winship, A. 2008. Potential limits to anthropogenic mortality of small cetaceans in coastal waters of British Columbia. *Can. J. Fish. Aquat. Sci.* 65: 1867–78.

Williams, R. and Thomas, L. 2009. Cost-effective abundance estimation of rare animals: testing performance of small-boat surveys for killer whales in British Columbia. *Biol. Cons.* 142: 1542–47.

Williams, R. and O'Hara, P. 2010. Modelling ship strike risk to fin, humpback and killer whales in British Columbia, Canada. *J. Cetacean Res. Manage.* 11(1): 1–8.

Williams, R., Okey, T.A., Wallace, S.S. and Gallucci, V.F. 2010. Shark aggregation in coastal waters of British Columbia. *Mar. Ecol. Prog. Ser.* 414: 249–56.

Williams, R., Ashe, E. and O'Hara, P.D. 2011a. Marine mammals and debris in coastal waters of British Columbia, Canada. *Mar. Poll. Bull.* 62(6): 1,303–16.

Williams, R., Hedley, S.L., Branch, T.A., Bravington, M.V., Zerbini, A.N. and Findlay, K.P. 2011b. Chilean blue whales as a case study to illustrate methods to estimate abundance and evaluate conservation status of rare species. *Conserv. Biol.* 25(3): 526–35.

Williams, R., Clark, C.W., Ponirakis, D. and Ashe, E. 2013. Acoustic quality of critical habitats for three threatened whale populations. *Anim. Conserv.* 17(2): 174–85. [Available at: *http://onlinelibrary.wiley.com/doi/10.1111/ acv.12076/abstract*].

Wood, S.N. 2001. mgcv: GAMs and generalized ridge regression for R. *R news.* 1(2): 20–25.

Wood, S.N. and Augustin, N.H. 2002. GAMs with integrated model selection using penalized regression splines and applications to environmental modelling. *Ecol. Modell.* 157(2–3): 157–77.

Wood, S.N., Bravington, M.V. and Hedley, S.L. 2008. Soap film smoothing. *J. Roy. Statist. Soc.* B70(5): 931–55.

Zerbini, A.N., Waite, J.M., Laake, J.L. and Wade, P.R. 2006. Abundance, trends and distribution of baleen whales off Western Alaska and the central Aleutian Islands. *Deep-Sea Res. I* 53: 1772–90.