SEASONAL ABUNDANCE AND DISTRIBUTION OF MARINE MAMMALS IN THE SOUTHERN STRAIT OF GEORGIA, BRITISH COLUMBIA

by

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ABSTRACT

The Strait of Georgia is a highly productive region and among the most important marine systems in British Columbia. It is at the mouth of the Fraser River, one of the most productive river systems in North America. Marine mammals are apex predators in this system, with at least ten species using the area during all or part of the year. Line transect surveys aboard B.C. Ferries vessels were conducted from May 1, 2000 to April 30, 2001 to determine the distribution and abundance of marine mammal species in the Strait of Georgia. A total of 2,879 individuals, representing nine species, were seen in 898 sightings. Harbour seals (n = 1,629), California sea lions (n = 415), Dall's porpoise (n = 397) and Steller sea lions (n = 205) were the most frequently observed, accounting for 92% of the sightings. Pacific white-sided dolphins (n = 110), harbour porpoise (n = 71), killer whales (n = 49), gray whales (n = 2), and a minke whale were also seen during the surveys. Abundance estimates were highest in spring and lowest in winter, with a second smaller peak in abundance in autumn. Pinnipeds were estimated to consume the most prey due to high population estimates for harbour seals and large body size of adult male sea lions. Peaks in marine mammal abundances appear to coincide with seasonal physical and biological factors in the Strait of Georgia and Fraser River system that may influence the availability of prey species.

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Most importantly, I would like to thank my family and friends. I would especially like to thank my husband and best friend, Jason Sandquist. Jason did not complain when I moved away to Vancouver to start grad school a week after we got married, and has been a wonderful source of support, encouragement, entertainment, humour, financial aid, love, inspiration, laughter, advice, a shoulder to cry on, distraction, amusement… I could go on and on. I could not have done this without him, and dedicate my thesis to him.

INTRODUCTION

The Strait of Georgia (Figure 1) is a highly productive area and one of the most important marine regions of British Columbia. It supports substantial populations of fish, birds and marine mammals. Large rivers can have significant impacts on coastal areas, primarily through the formation of large, nutrient-rich plumes (Meybeck 1982), and can have strong seasonal influences on the abundance and distribution of marine species.

The Fraser River is the fifth-largest river basin in Canada, and forms the biggest estuary on the Pacific coast (Thomson 1981, Northcote & Larkin 1989, Pomeroy 1995). It is also one of the most productive salmon rivers in the world, producing more salmon than any other river system in Canada (Northcote & Larkin 1989, Pomeroy 1995). A large plume created by the Fraser River over the southern and central Strait carries high concentrations of nutrients that fuel phytoplankton production at its boundaries (Harrison *et al.* 1983, Yin *et al.* 1997a). This in turn results in significantly higher biological productivity at higher trophic levels compared to other temperate estuaries due to nutrient entrainment (Stronach 1981, Harrison *et al.* 1983, Yin *et al.* 1997a, Yin *et al.* 1997b). The spring phytoplankton bloom that occurs during peak runoff from the Fraser River is essential for zooplankton production (Yin *et al.* 1996). Greater abundances of fish and zooplankton are found in the plume compared to surrounding waters (St. John *et al.* 1992, Beamish & Neville 1995). However, little is known about abundance and distribution patterns of several of the marine mammals species in this system.

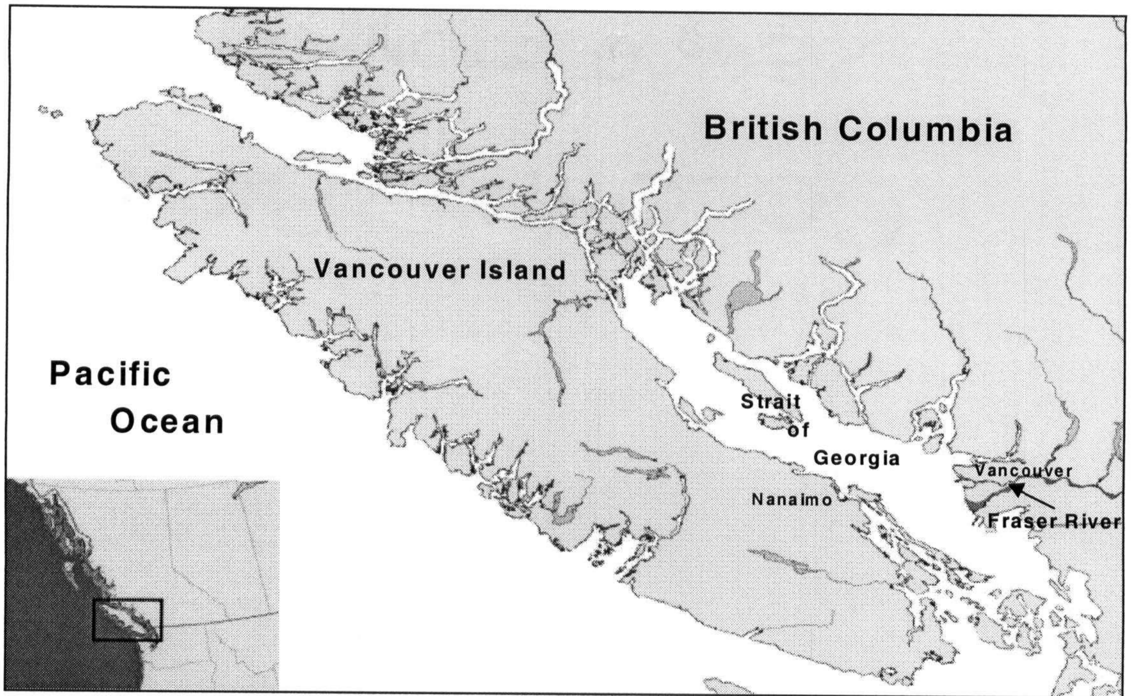

Figure 1 – Vancouver Island and the Strait of Georgia.

Several species of marine mammals are sighted regularly in the Strait of Georgia during all or part of the year. These include Dall's porpoise (*Phocoenoides dalli*), harbour porpoise (*Phocoena phocoena*) and killer whales (*Orcinus orca*), harbour seals (*Phoca vitulina*), and California and Steller sea lions (*Zalophus californianus* and *Eumetopias jubatus*). Dall's porpoise are believed to be the most abundant cetacean in inshore waters of British Columbia (Everitt *et al.* 1980, Leatherwood *et al.* 1982, Osborne *et al.* 1988, Jefferson 1990), followed by harbour porpoise (Stacey *et al.* 1997, Cowan 1988, Osborne *et al.* 1988). Resident and transient forms of killer whales are found frequently in the Strait of Georgia (Calambokidis & Baird 1994, Ford *et al.* 1994). Other cetacean species reported less commonly include Pacific white-sided dolphins (*Lagenorhynchus obliquidens*), gray whales (*Eschrichtius robustus*), minke whales (*Balaenoptera acutorostrata*) and humpback whales (*Megaptera novaeangliae*) (Everitt *et al.* 1980, Leatherwood *et al.* 1984, Osborne *et* *al.* 1988, Stacey & Baird 1991, Calambokidis & Baird 1994, Sheldon *et al.* 1999). Among the pinnipeds, harbour seals are the most abundant marine mammal and are found year-round in the Strait (Everitt *et al.* 1980, Osborne *et al.* 1988), unlike Steller and California sea lions that arrive in the fall and depart in spring (Everitt *et al.* 1980, Everitt *et al.* 1981, Steiger & Calambokidis 1986, Bigg 1988a, Bigg 1988b, Olesiuk 1990, Calambokidis & Baird 1994).

The ecological role of marine mammal species present in the Strait of Georgia is likely similar to predators that occupy top trophic positions in other systems (Riedman 1990). In general, marine mammals are thought to have a major influence on marine food webs because of their large body size, high metabolic rates, and large numbers (Estes 1979, Bowen 1997, Croll & Tershy 1998). One means of assessing their ecological role within marine ecosystems is with mathematical models that estimate abundance and consumption.

Conservation concerns are other reasons to determine the seasonal distribution and numbers of marine mammals using inshore and estuarine systems. Many large cities were built near river mouths (such as Vancouver) and draw significant numbers of commercial vessels. Determining regions with high concentrations of marine mammals may aid vessels in traveling through these areas, especially if there are concerns of collisions with animals present. Fisheries drawn to these productive areas may also want to avoid areas with high numbers of sightings to prevent incidental bycatch of marine mammals.

In the Strait of Georgia, there is anecdotal evidence that some species in this area are declining (e.g. Cowan 1988), and other populations are increasing after a period of exploitation (e.g. Olesiuk 1999). Estimates of population size are necessary for effective conservation and management programs. While several surveys for marine mammals have been undertaken in adjacent U.S. waters (e.g. Calambokidis & Baird 1994, Calambokidis *et al.* 1997b), few have been carried out in the Strait of Georgia.

The purpose of my study was to determine the seasonal changes in abundance and distribution of marine mammal species in the Strait of Georgia, British Columbia. I begin by describing the study area and the methods used to estimate marine mammal abundance from a commercial passenger ferry. Abundance estimates are presented by species and discussed in terms of seasonality and the influence of the Fraser River flow on the productivity of the Strait of Georgia. These data may form the basis for future monitoring programs in the Strait. Finally, I consider how much food is consumed by marine mammals by season and how marine mammals in general use large river estuarine systems.

METHODS

Study Area

The Strait of Georgia is located between southeastern Vancouver Island and the lower mainland of British Columbia. The Strait extends from 48°44'N to 50°N latitude, and is 222 kilometres long and 20 to 40 kilometres wide, covering an area of approximately 6,800 km^2 (Thomson 1981). Mean depth is 155 metres, with only 5% of the area deeper than 360 metres (Thomson 1981). It is connected to the Pacific Ocean by Johnstone Strait in the north and the Strait of Juan de Fuca in the south, and has a complex hydrology due to the relatively large tides, major freshwater input from the Fraser River and distinct seasonality in the prevailing winds (Thomson 1981, LeBlond 1983). Tides are strongly influenced by the Fraser River and are semi-diurnal, with two floods and two ebbs per day (Thomson 1981, LeBlond 1983). The central Strait of Georgia extends from the southern end of Texada Island to a line drawn from Point Roberts on the mainland to Sidney on Vancouver Island (Waldichuk 1957).

I conducted surveys from BC Ferries vessels *Queen of New Westminster* and *Queen of Alberni* along a fixed route from Duke Point on Vancouver Island (49°10.14N, 123°53.97W) to Tsawwassen on the mainland (49°00.26N, 123°08.14W). This route crosses the central Strait of Georgia and the Fraser River plume.

The study area for abundance estimates was between 49°16N and 48°50S, and followed the 30 metre isobath along the Gulf Islands to the west and Vancouver to the east (Figure 2). The northern boundary was a straight line from Point Grey on the mainland across to Vancouver Island, and the southern boundary was a straight line across the Strait from just south of the Tsawwassen ferry terminal to the Gulf Islands. This area was chosen for its homogenous currents and seafloor topography, and had an area of 2,114 km^2.

Survey Methods

Observations were made between May 1, 2000 to April 30, 2001 from the bridge of the ferries; observer height was 16.7 metres above the waterline on the *Queen of New Westminster*, and 16.5 metres on the *Queen of Alberni*. Surveys were conducted on the morning ferry runs departing at 0745 and 1015 hours, which typically offered better sightings conditions over later runs. Surveys were not undertaken in Beaufort sea states of >3, or when fog, glare, or other meteorological conditions obscured visibility. Beaufort sea state ≥3 have wind speeds which produce waves over three feet, with breaking crests forming scattered whitecaps (Griffiths 1971). Sea state is a significant factor affecting sighting rates for cetaceans (Barlow 1988, Turnock *et al.* 1995, Palka 1996, Calambokidis *et al.* 1992, Forney 2000). Clark (1982) found that *Phocoena* and *Phocoenoides* were unlikely to be observed in Beaufort sea states >2.

Date, time and tidal state were recorded at the beginning of each transect. Observations were made with the unaided eye and/or with Fujinon 7X50 reticle and compass binoculars from the front and left side of the bridge, and directly in front of the vessel to 60 degrees towards port. All animals seen during each scan were counted, including pinnipeds hauled out on land. Data collected for each sighting included time, species, group size, number of reticle marks or distance to sighting (depending on the method used), compass bearing to sighting and compass course of vessel travel, direction of animal travel, and objects within one kilometre of the sighting (e.g. boats, birds, debris). Groups in the water were defined as individuals within two body lengths of each other, or having nearly synchronous diving patterns. On land, groups of harbour seals, California sea lions and Steller sea lions were defined as distinct clusters of individuals. Environmental data were recorded every ten minutes, and included tidal state, Beaufort sea state, wind speed and visibility. A laptop computer with Nobeltec navigation software was interfaced with a Garmin 12-channel Global Positioning Satellite (GPS) receiver to record the vessel's position, speed and heading every minute.

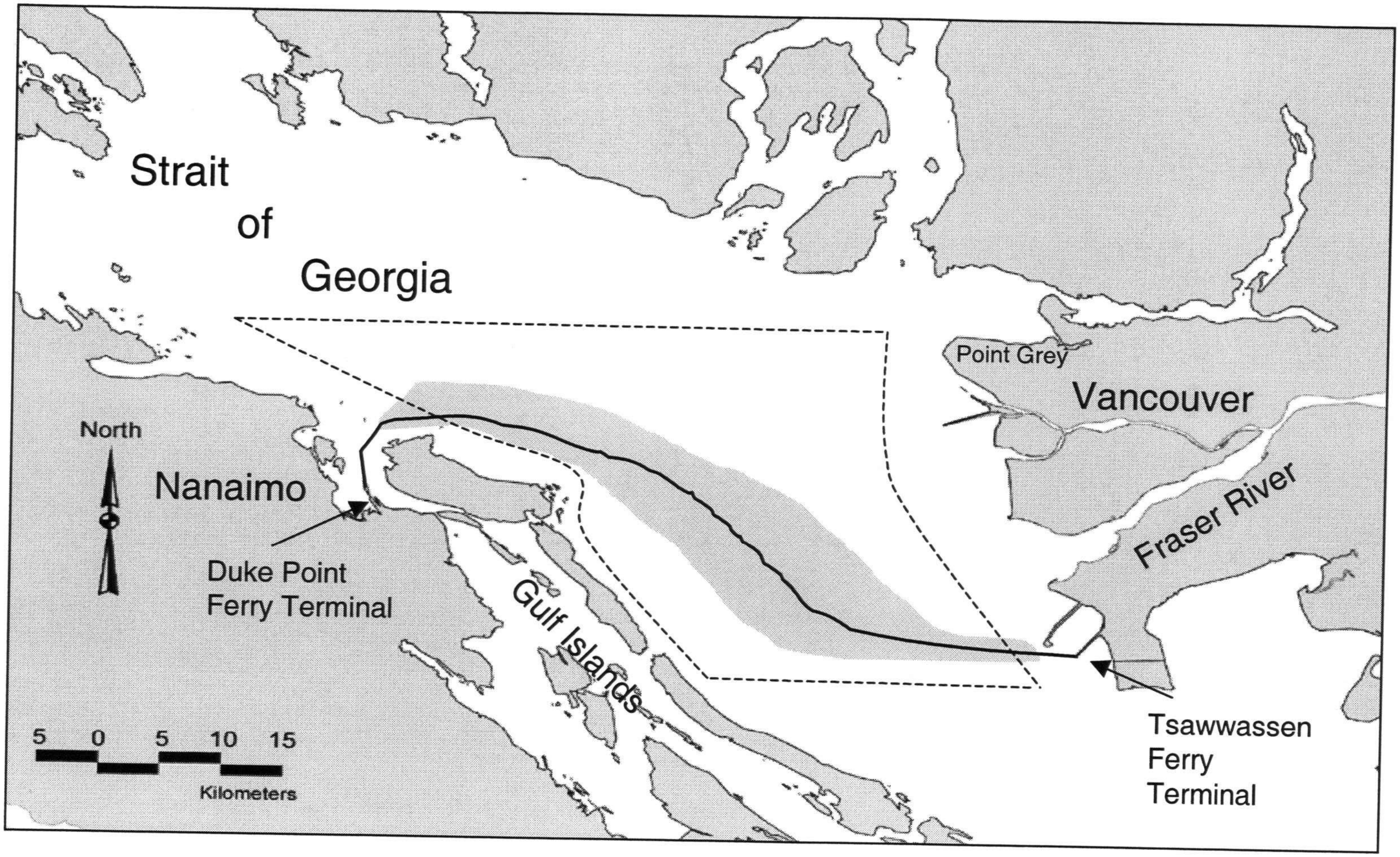

Figure 2 – Strait of Georgia, showing the study area for abundance estimates. The dotted lines are the study area boundaries. The solid line indicates the approximate route of one transect between the Duke Point and Tsawwassen ferry terminals. The grey area represents the width of the area covered by all the transects.

Data Analysis

Distances to sighted animals were determined using reticle marks in the binoculars (one reticle = 0.286 degrees), and the following formula:

$$D_r = \frac{H}{\tan(\alpha)} \qquad [1]$$

where D_r is the radial distance from the observer to the sighted animal, H is the height from the surface of the water to the observer's eye, and α is the vertical angle between the horizon and the sighting. Radial distance was also measured directly when a group of individuals was within 800 metres and large enough to obtain a reading using a Bushnell Yardage Pro 800 laser rangefinder. When the horizon was obscured by the shoreline, α was calculated using the shoreline as a reference according to Lerczak and Hobbs (1998).

Line transect sampling is used widely to estimate the density and abundance of cetacean populations. Reliable estimates can be calculated when the perpendicular distance between the transect line and the sighted animal is known (Burnham *et al.* 1980, Hiby & Hammond 1989, Buckland *et al.* 1993). Perpendicular distance from the trackline to the sighted animal was determined by:

$$D_x = D_r \cdot \sin(\theta) \qquad [2]$$

where θ is the angle from the sighting to the trackline (Figure 3).

Density and abundance estimates were calculated using DISTANCE computer software (Thomas *et al.* 1998) and the methodology outlined by Buckland *et al.* (1993). Abundance was calculated as:

$$N = \frac{A \cdot n \cdot f(0) \cdot s}{L \cdot g(0)} \qquad [3]$$

where A is the survey area, n is the number of sightings of a species, $f(0)$ is the probability density function of distances from the trackline evaluated at zero distance, s is the mean group size, L is the length of trackline, and $g(0)$ is the probability of detecting a group on the transect line. Confidence intervals in DISTANCE were converted to a log-normal distribution. Density was calculated as:

$$D = \frac{n \cdot f(0) \cdot s}{L \cdot g(0)} \qquad [4]$$

The probability detection function ($g(0)$) was assumed to be one (indicating all animals on the trackline were seen) as it was impossible to estimate bias. In all likelihood $g(0)$ was less than one and the density and abundance estimates were underestimated by an unknown amount because marine mammals could not be detected when submerged. However, $g(0)$ was probably close to one because of the height of the observation platform and surveys done in Beaufort sea state <3. Marine mammals also have several cues or behaviours, such as jumps, splashes or blows, that aid in their detection (Best 1982).

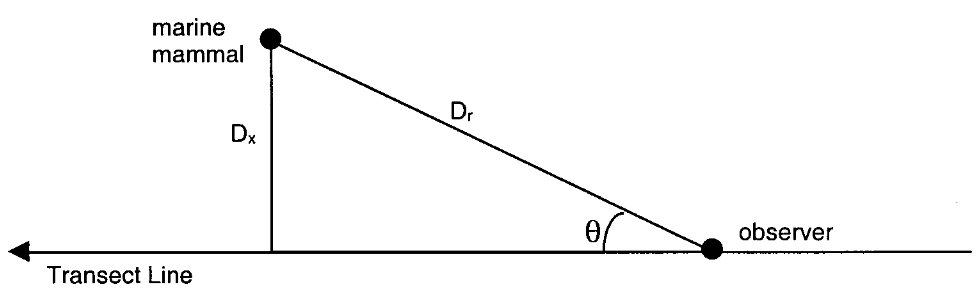

Figure 3 – Measurements of line-transect surveys. D_x is the perpendicular distance from the transect line to the marine mammal, D_r is the radial distance from the observer to the marine mammal (measured by the radial drop from the horizon to the marine mammal), and θ is the angle from the marine mammal to the transect line.

Effective half-strip width (ESW) is required to estimate abundance, and was calculated using DISTANCE according to:

$$\mu = \frac{1}{f(0)} \qquad [5]$$

DISTANCE was also used to select the best model to fit the perpendicular sighting distance distributions. The number of animals seen within the ESW was assumed to equal the number of animals that were not seen outside of it (Buckland *et al.* 1993).

DISTANCE software was also used to model the detection function $g(x)$, since the true detection function was not known. Several different models were considered to estimate $g(x)$, beginning with a key function followed by a series expansion to adjust the key function to improve the fit of the model (Buckland *et al.* 1993). Half-normal, hazard-rate, uniform and negative-exponential functions with either cosine or simple polynomial adjustments were used to model the perpendicular distances. Several different binning and truncating criteria were modeled to determine the best fit. Truncating 5-10% of sightings was recommended to eliminate outliers and help achieve a good fit of the detection function to the perpendicular sighting distance data (Buckland *et al.* 1993). As several detection functions may fit the perpendicular distance data, the best fit model was chosen based on the lowest Akaike Information Criterion (AIC). AIC identifies the model that both fits the data well and has a low number of parameters (Burnham & Anderson 1992, Buckland *et al.* 1993).

Sightings only from within the study area were used for the density and abundance calculations to avoid problems arising from truncation of sight lines due to shorelines or shallow water. The ferry route passed by Entrance Island, a major haulout for seals and sea lions. Pinnipeds hauled out on land were not used in any DISTANCE calculations because of differences in sightability between animals in the water and on land, and were treated separately.

Chi-squared analysis was used to determine if Dall's and harbour porpoise showed attraction or avoidance behaviour towards the survey vessel. Linear regression analysis was used to determine if group size was independent from the distance from the trackline. Analysis of variance was used to determine if group size changed over time, and Tukey multiple comparison tests were performed to examine the significant differences between abundance estimates. Mann-Whitney tests were used to determine if the number of sightings of each species was affected by tidal state. Arcview was used to plot the location of sightings within the study area.

Consumption Model

The amount of prey consumed per day was estimated using formulae from Innes *et al.* (1987) and Trites *et al.* (1997), where daily ration was:

$$R_s = 0.1 \cdot W_s^{0.8} \qquad [7]$$

and average daily consumption by a population was:

$$Q_s = \sum N_s \cdot R_s \qquad [6]$$

where N_s is the DISTANCE abundance estimate by sex s, W_s is the mean weight by sex, and R_s is the daily ration for an individual of weight W_s.

Mean weights over all age classes for Dall's porpoise, harbour porpoise and harbour seals were taken from Trites & Pauly (1998). An equal sex ratio was assumed for these species. Only sub-adult and adult male sea lions occur in the Strait of Georgia (Steiger & Calambokidis 1986, Bigg 1988a, Bigg 1988b). Mean weight of California sea lions was calculated for the age distribution of males that migrate north from California (Mate 1975) using a growth curve developed by Kastelein *et al.* (2000). The age of Steller sea lions in the Strait was assumed to range from 4 –10 years, since no large breeding males were seen. Weights at a given age were taken from Winship *et al.* (2001), and survival at a given age was taken from Trites & Larkin (1992).

RESULTS

A total of 143 transects were surveyed over 96 days between May 2000 and April 2001, for a total effort of 10,218 kilometres. Mean transect duration was 110 minutes (SE = 0.6, n = 143), with an average boat speed of 35.4 $km \cdot h^{-1}$ (SE = 0.07). Effort was similar across seasons: 41 transects (2,739 km) were surveyed in spring (March – May); 36 transects (2,405 km) were surveyed in summer (June – August); 37 transects (2,472 km) were surveyed in fall (September – November); and 29 transects (1,936 km) were surveyed in winter (December – February).

A total of 2,879 individual marine mammals, representing nine species, were seen in 898 sightings. Harbour seals (n = 1,629), California sea lions (n = 415) and Dall's porpoise (n = 397) were most frequently observed, accounting for 85% of the sightings. Steller sea lions (n = 205), Pacific white-sided dolphins (n = 110), harbour porpoise (n = 71), killer whales (n = 49), gray whales (n = 2), and a minke whale were also seen during the surveys. The highest number and diversity of sightings occurred in spring, when all species were seen (Figure 4). Diversity was also high during summer (with only minke whales not occurring; Figure 5), but low during winter (with no killer whales, Pacific white-sided dolphins, gray whales or minke whales observed; Figure 6). Number of sightings was lowest during winter, and somewhat higher during fall (Figure 7).

Sightings of all species were not affected by the distance from the trackline (Table 1). Similarly, numbers did not differ significantly during flood or ebb tides (Table 2); a total of 79 transects were surveyed during ebb tides and 55 during flood tides. Transects where tidal state changed during the survey were not used for this analysis.

Table 1. Group size of species vs. perpendicular sighting distances.

Species	df	R	P
Dall's porpoise	124	0.104	0.17
Harbour porpoise	21	0.179	0.22
Harbour seal	445	0.063	0.06
California sea lion	42	0.160	0.17
Steller sea lion	41	0.045	0.63

Table 2. Analysis of sightings during either flood or ebb tides.

Species	df	U	P
Dall's porpoise	79, 55	1.703	0.06
Harbour porpoise	79, 55	0.155	0.56
Harbour seal	79, 55	0.318	0.62
California sea lion	79, 55	0.273	0.61
Steller sea lion	79, 55	0.384	0.65

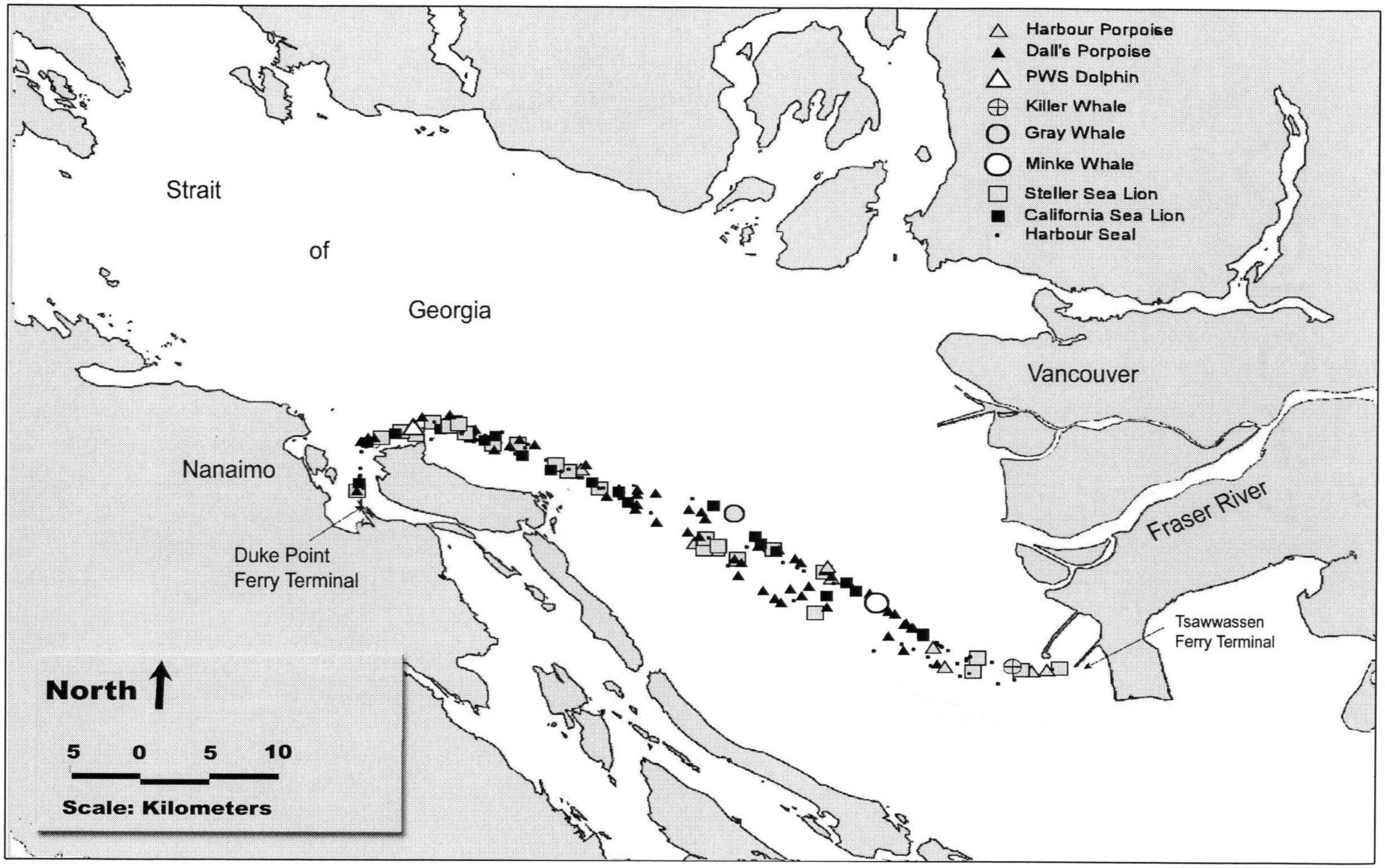

Figure 4 – Sightings made during Strait of Georgia surveys from May 1, 2000 to April 30, 2001 in spring.

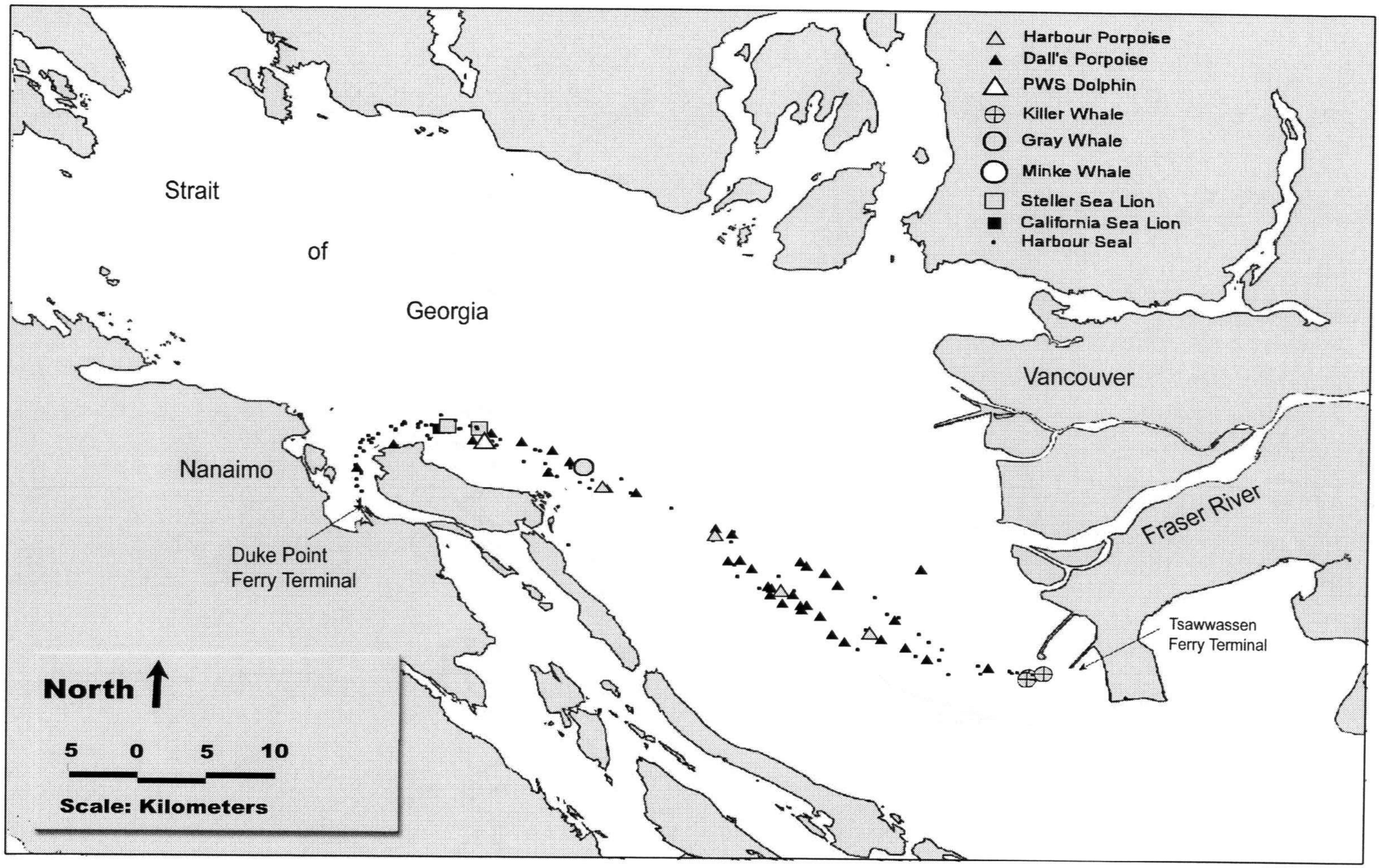

Figure 5 – Sightings made during Strait of Georgia surveys from May 1, 2000 to April 30, 2001 in summer.

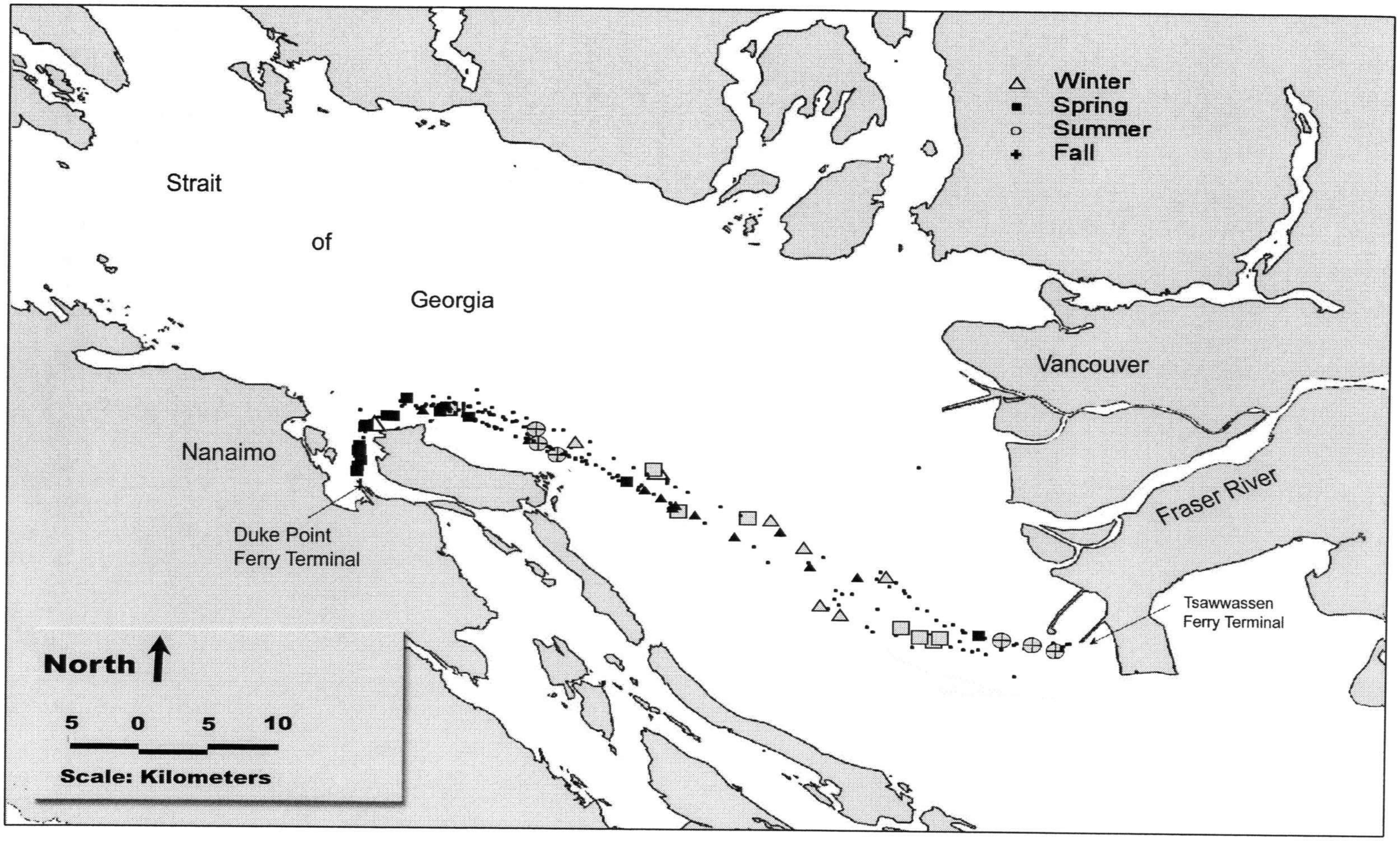

Figure 6 – Sightings made in fall during Strait of Georgia surveys.

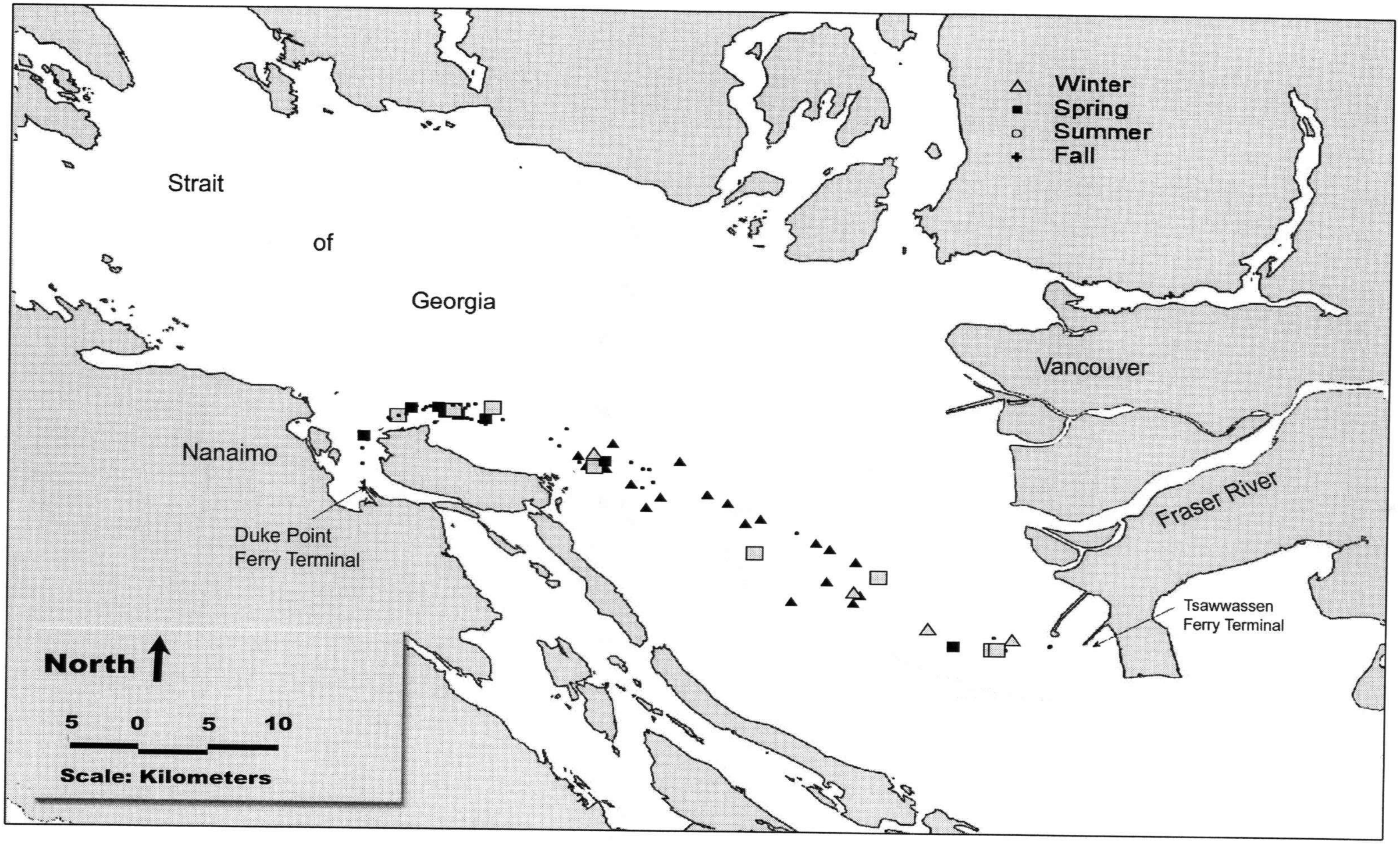

Figure 7 – Sightings made in winter during Strait of Georgia surveys.

Dall's Porpoise

Dall's porpoise were observed during 43% of the surveys and consisted of 397 individuals counted in 126 sightings. The half-normal/cosine model, truncated at 1,200 metres, best fit the distribution of perpendicular sighting distances from the trackline based on the lowest AIC score criteria (Figure 8).

Dall's porpoise were widely distributed over the route at all times of year, but were sighted most often in winter in the centre of the Strait (Figure 9). Abundance was estimated seasonally (Table 3). Abundance peaked in spring, with an estimated 370 individuals in the study area (95% CI = 234 – 584), and was lowest in fall, with an estimated 73 individuals (95% CI = 32 – 168; Figure 10). Abundance estimates differed significantly between seasons ($F_{3,139} = 3.38$, $p = 0.023$).

The probability density function, $f(0)$, was originally calculated by season, but an analysis of variance did not show any significant changes in detectability over time ($F_{3,139} = 0.001$, $p = 0.99$), so $f(0)$ was calculated by pooling data from all sightings to increase sample size (Buckland *et al.* 1993). The ESW was 370.48 metres (95% CI = 316.91 – 433.10), with an $f(0)$ of $0.0027 \cdot km^{-2}$ (95% CI = 0.00231 - 0.00316).

Dall's porpoise group size ranged from 1 to 16 (Figures 11 & 12) with mean group size differing by season ($F_{3,113} = 4.76$, $p = 0.004$; Figure 13). I observed Dall's porpoise swimming towards the vessel in only 39.5% of the observations, and analysis of swimming direction suggests they moved randomly with respect to the vessel ($\chi^2_1 = 3.46$, $p = 0.062$).

Running models with alternative binning and truncating criteria to assess the robustness of sightings data collected for Dall's porpoise yielded yearly abundance estimates ranging from 873 to 1,317 individuals (Table 4). The estimates did not vary substantially despite altering the detection function model, binning or truncation criteria (Figure 14).

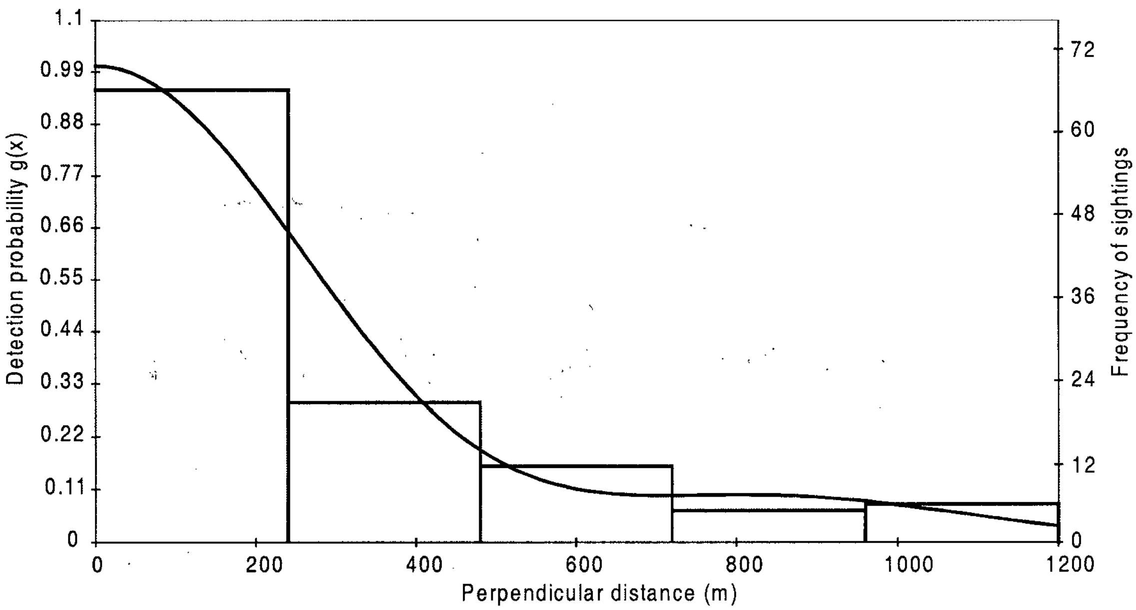

Figure 8. Probability detection distribution for perpendicular sighting distances of Dall's porpoise. Bars represent the frequency of sightings and the line represents the half-normal/cosine model of best fit, truncated at 1,200 m.

Table 3. Dall's porpoise abundance estimates and DISTANCE parameter values of the half-normal/cosine model, truncated at 1,200m, for the Strait of Georgia survey area, May 1, 2000 to April 30, 2001.

Parameter	Overall	Spring	Summer	Fall	Winter
Kilometres surveyed	10,218	2,739	2,405	2,472	1,936
Transect Lines	143	41	36	37	29
Truncation width (m)	1200.00				
ESW (m)	370.48				
SE of ESW	29.254				
95% CI of ESW	(316.91 – 433.10)				
% CV of ESW	7.90				
$f(0)\cdot km^{-2}$	0.0027				
SE of $f(0)$	0.00021				
95% CI of $f(0)$	(0.00231 – 0.00316)				
Groups sighted within truncated distance	117	55	31	11	20
Mean group size		2.6	2.2	2.4	4.3
SE of group size		0.19	0.25	0.41	0.83
Density (animals·km^{-2})		0.17	0.09	0.03	0.14
SE of density		0.041	0.030	0.150	0.046
95% CI of density		(0.11 – 0.28)	(0.05 – 0.18)	(0.02 – 0.08)	(0.08 – 0.27)
% CV of density		23.15	31.68	43.24	31.96
Abundance		370	200	73	306
SE of abundance		85.7	63.4	31.6	97.8
95% CI of abundance		(234 – 584)	(107 – 372)	(32 – 168)	(163 – 571)

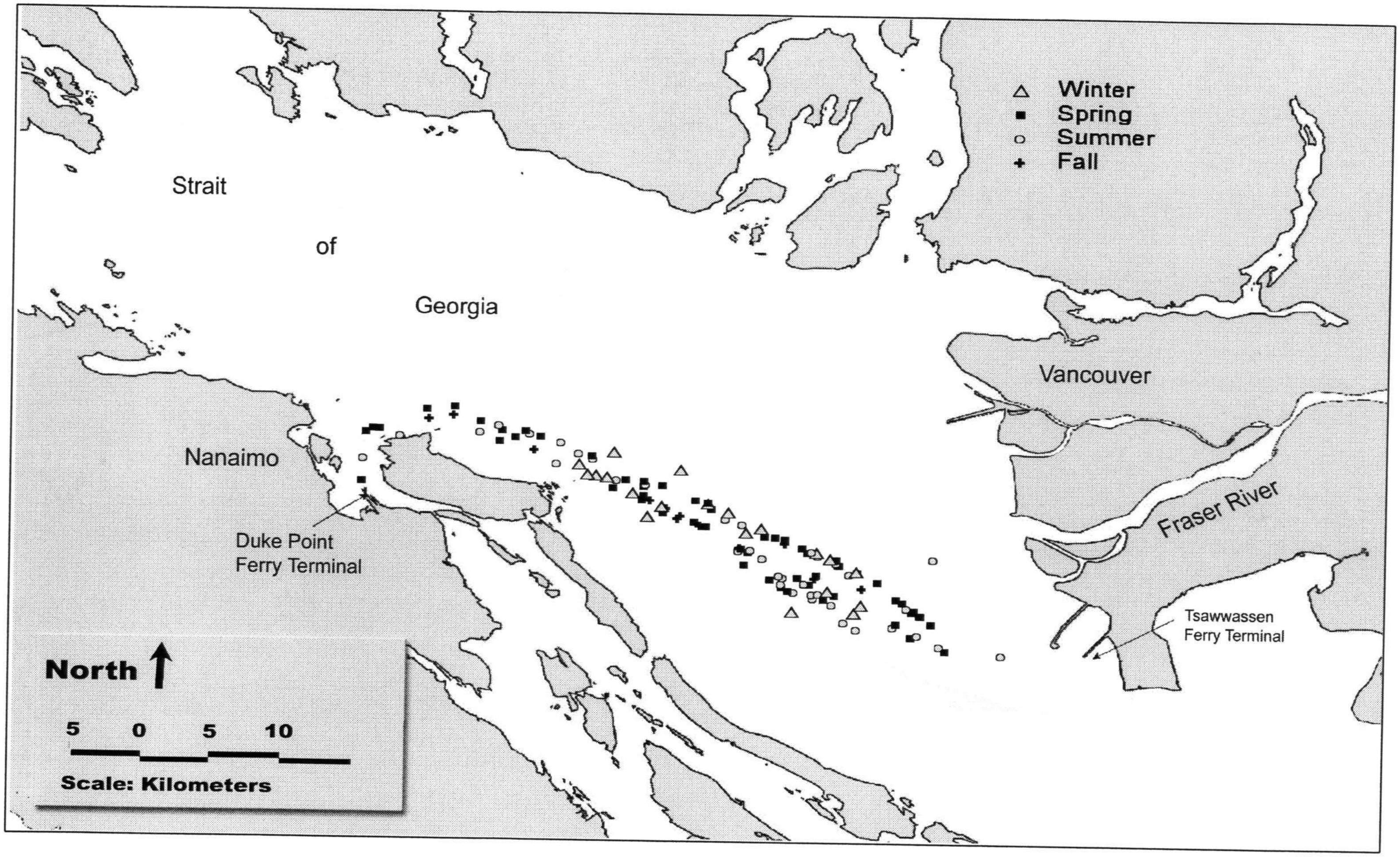

Figure 9 – Dall's porpoise sightings during Strait of Georgia surveys from May 1, 2000 to April 30, 2001.

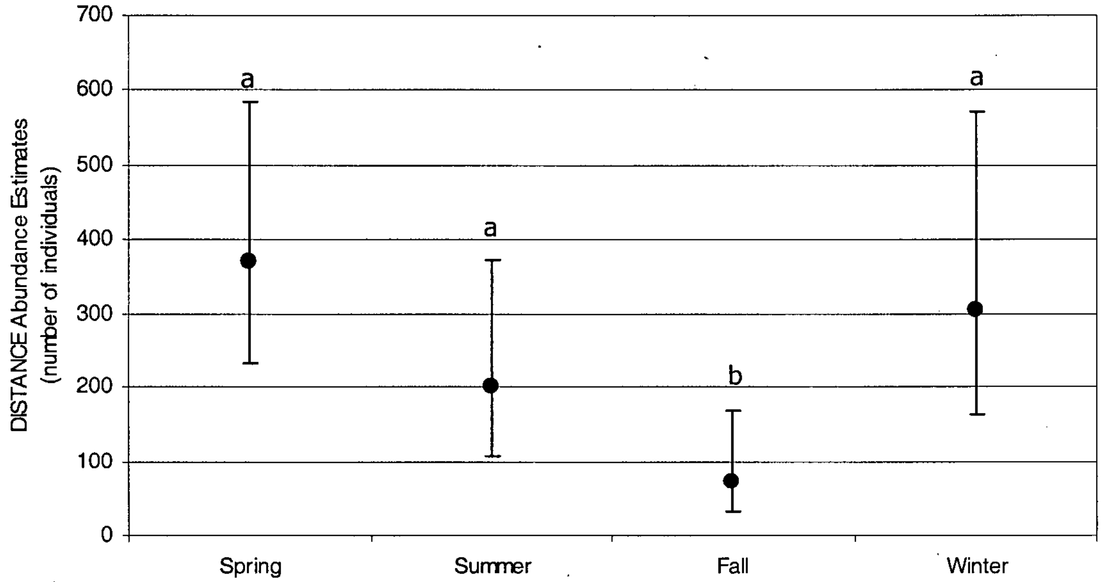

Figure 10. DISTANCE abundance estimates for Dall's porpoise in the Strait of Georgia study area from May 2000 – April 2001. Bars are log-normal 95% confidence intervals. Letters denote a significant difference.

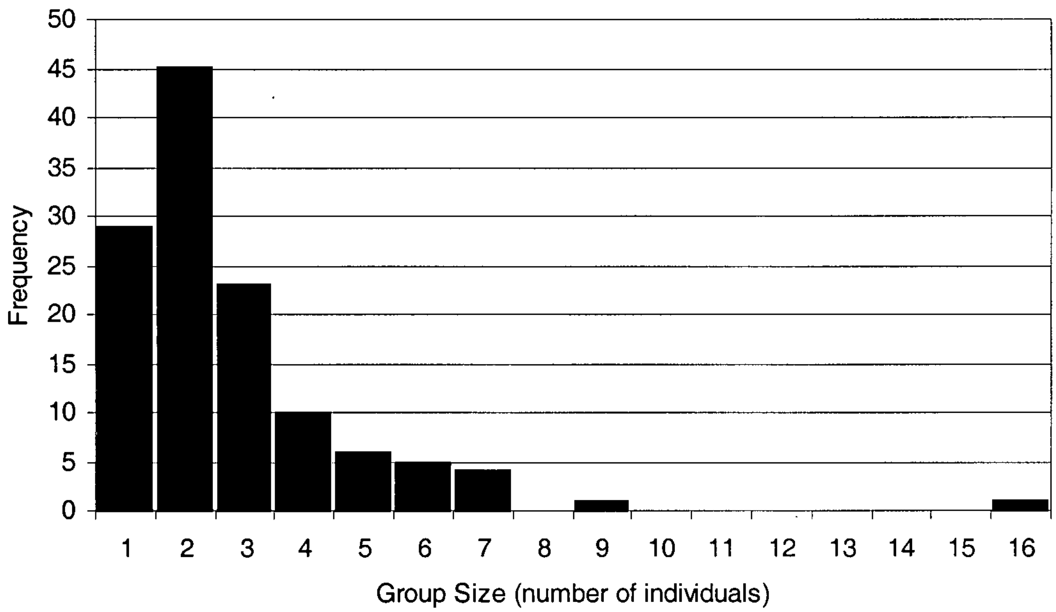

Figure 11. Frequency of Dall's porpoise group size observed during surveys in the Strait of Georgia, May 1, 2000 to April 30, 2001.

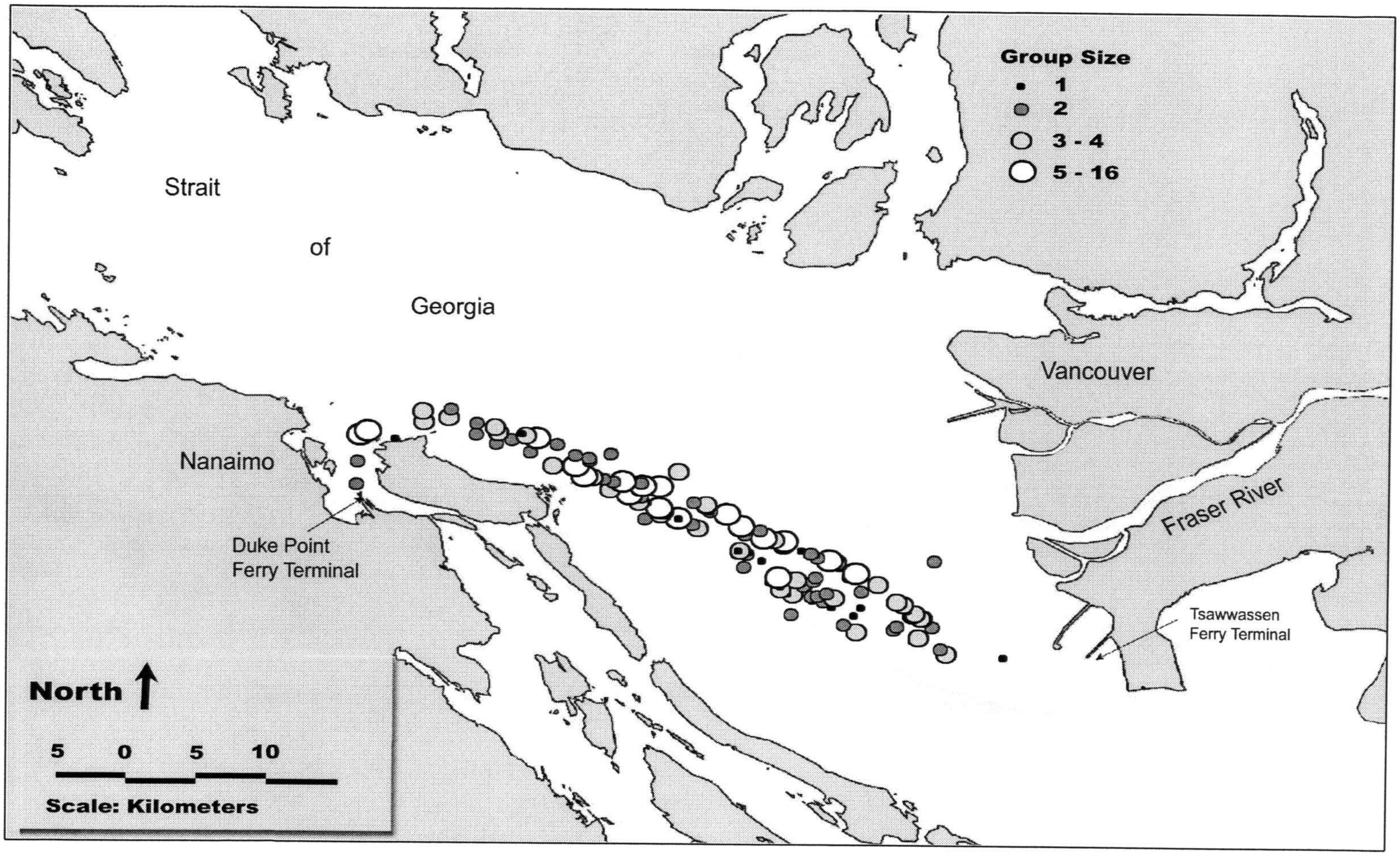

Figure 12 – Dall's porpoise sightings by group size.

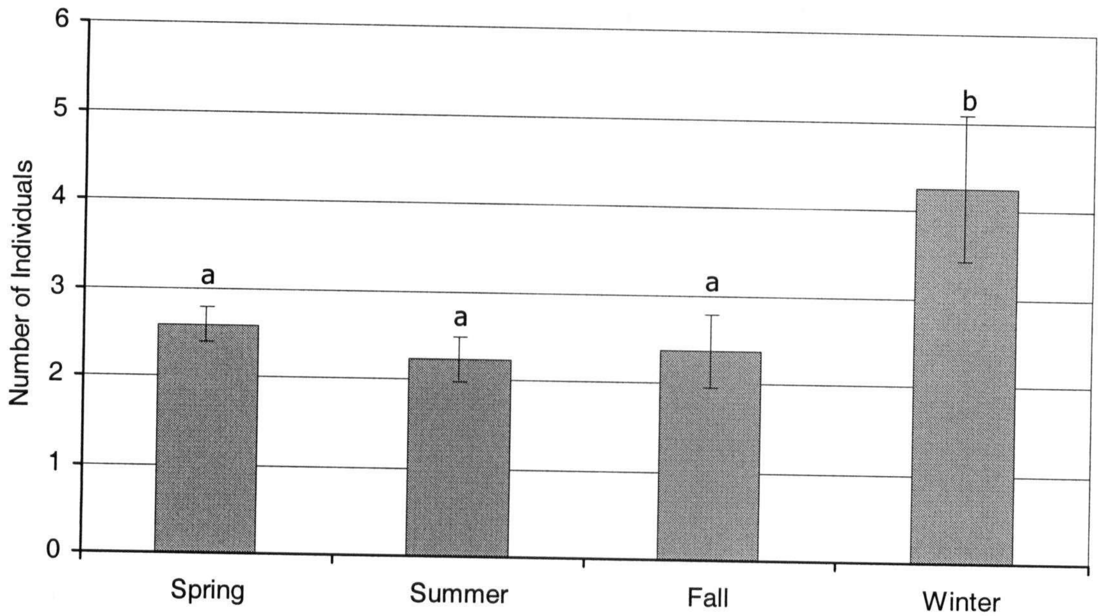

Figure 13. Mean group size of Dall's porpoise within the truncated distance, observed during Strait of Georgia surveys from May 1, 2000 to April 30, 2001. Bars are standard error. Letters denotes a significant difference.

Table 4. Yearly Dall's porpoise abundance estimates and confidence intervals from alternative models, binning and truncating criteria of the perpendicular sightings distances.

Case	Abundance estimate	Model	Binning Criteria	Truncation Point
Case 1	949	Half-normal/cosine	5 equal 240m intervals	1200m
Case 2	1317	Hazard-rate/cosine	7 equal 171m intervals	1200m
Case 3	918	Half-normal/cosine	7 equal 171m intervals	1200m
Case 4	1106	Half-normal/cosine	7 equal 121m intervals	850m
Case 5	978	Hazard-rate/cosine	5 equal 280m intervals	1400m
Case 6	873	Half-normal/cosine	5 equal 280m intervals	1400m
Case 7	932	Half-normal/cosine	5 unequal intervals	1200m
Case 8	1182	Half-normal/cosine	10 unequal intervals	1200m

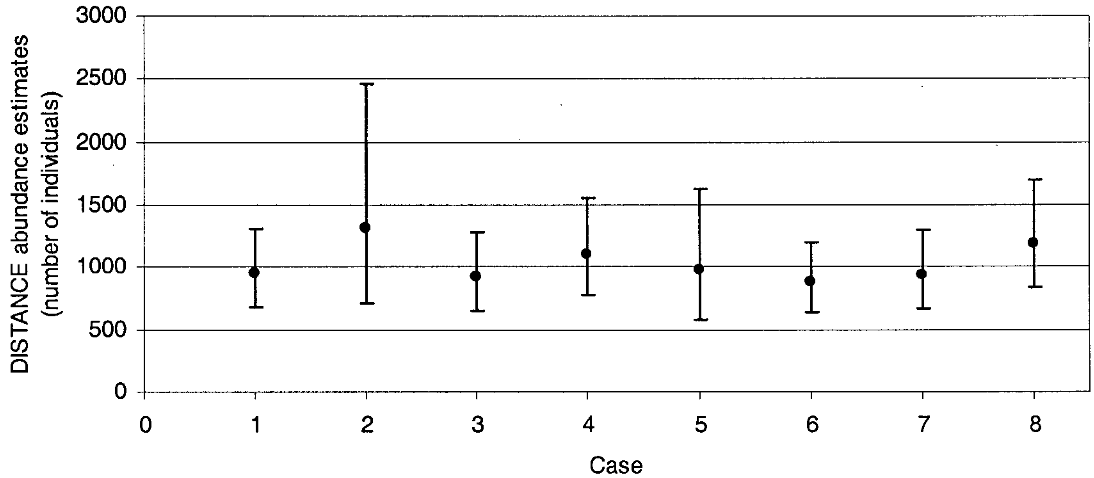

Figure 14. Dall's porpoise DISTANCE abundance estimates and log-normal 95% confidence intervals for the alternative cases modeled (see Table 4).

Harbour porpoise

Harbour porpoise were observed during 13% of the surveys (58 counted in 23 sightings). The distribution of perpendicular sighting distances was best fit by the hazard-rate/cosine model (truncated at 600 metres), based on the lowest AIC score criteria (Figure 15).

Abundance estimates by season were not statistically significant ($F_{3,139} = 0.23$, $p = 0.99$; Table 5, Figure 16). Harbour porpoise were most commonly sighted in the centre of the Strait, and were not observed north of the southern tip of Gabriola Island (Figure 17).

The low number of harbour porpoise observed led to pooling all sightings data to calculate $f(0)$. The ESW estimate was 418.4 metres (95% CI = 119.9 – 1,460.0), with an $f(0)$ of $0.0024 \cdot km^{-2}$ (95% CI = 0.00068 - 0.00834).

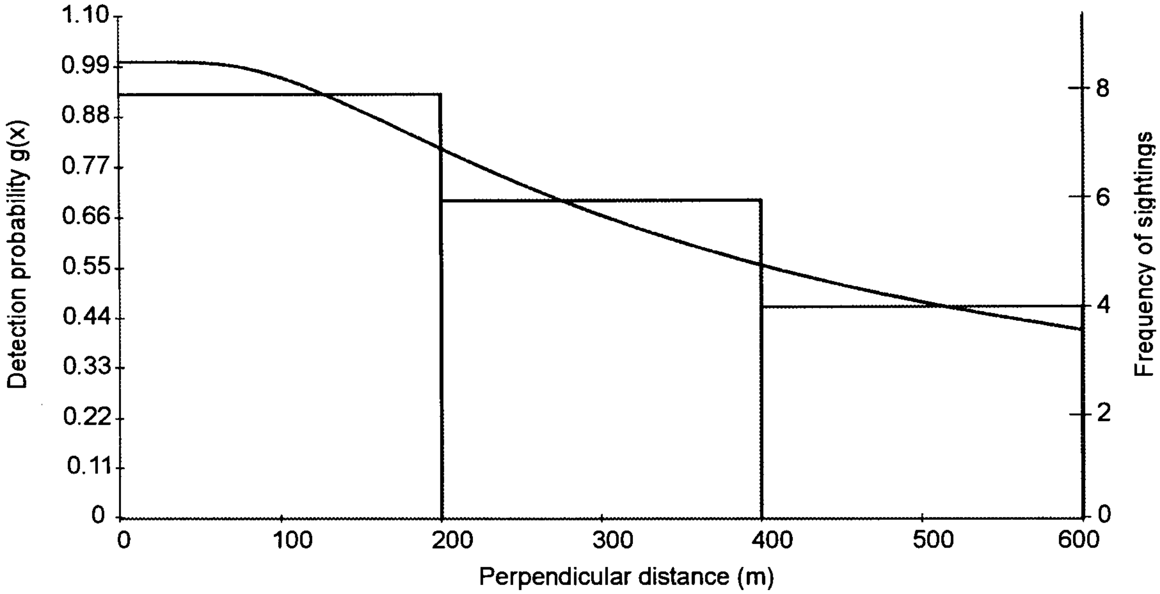

Figure 15. Probability detection distribution for perpendicular sighting distances of harbour porpoise. Bars represent the frequency of sightings and the line represents the hazard-rate/cosine model of best fit, truncated at 600m.

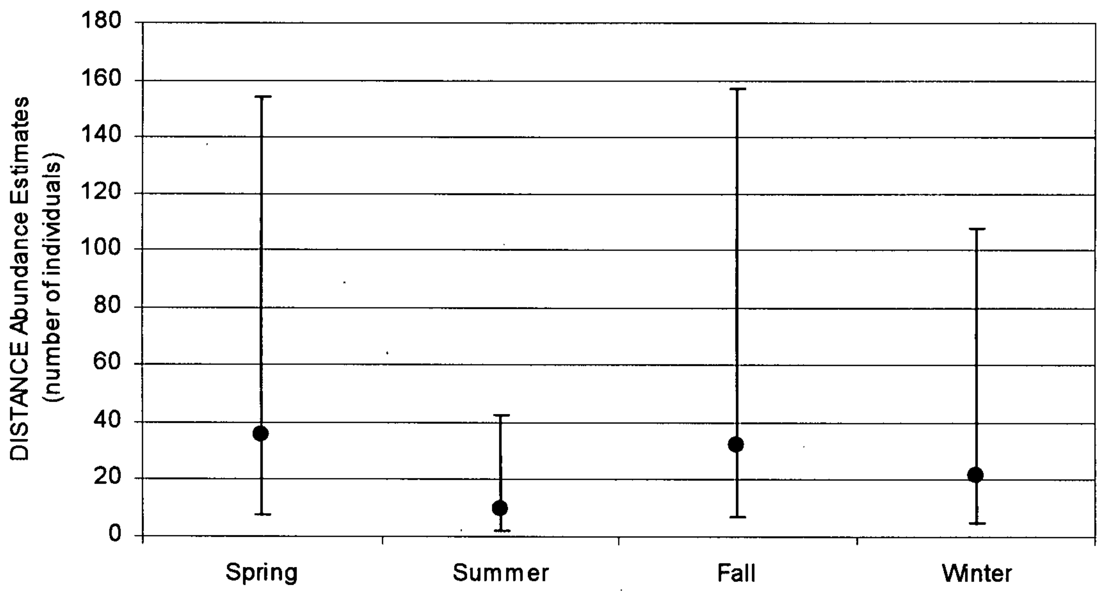

Figure 16. DISTANCE abundance estimates for harbour porpoise in the Strait of Georgia study area from May 2000 – April 2001. Bars are log-normal 95% confidence intervals.

Table 5. Harbour porpoise abundance estimates and DISTANCE parameter values of the hazard-rate/cosine model, truncated at 600 m, for the Strait of Georgia survey area, May 1, 2000 to April 30, 2001.

Parameter	Overall	Spring	Summer	Fall	Winter
Kilometres surveyed	10,218	2,739	2,405	2,472	1,936
Transect Lines	143	41	36	37	29
Truncation width (m)	600.0				
ESW (m)	418.39				
SE of ESW	269.73				
95% CI of ESW	(119.90 – 1460.00)				
% CV of ESW	64.47				
$f(0)\cdot km^{-2}$	0.0024				
SE of $f(0)$	0.00154				
95% CI of $f(0)$	(0.00685 – 0.00834)				
Groups sighted within truncated distance	18	6	4	4	4
Mean group size		2.7	1.0	3.3	1.8
SE of group size		0.61	0	0.85	0.48
Density ($animals\cdot km^{-2}$)		0.02	0.005	0.02	0.01
SE of density		0.014	0.004	0.014	0.010
95% CI of density		(0.004 – 0.07)	(0.001 – 0.02)	(0.003 – 0.07)	(0.002 – 0.05)
% CV of density		81.95	80.26	91.78	91.82
Abundance		36	10	32	22
SE of abundance		29.5	8.0	29.4	20.2
95% CI of abundance		(8 – 154)	(2 – 43)	(7 – 157)	(5 – 108)

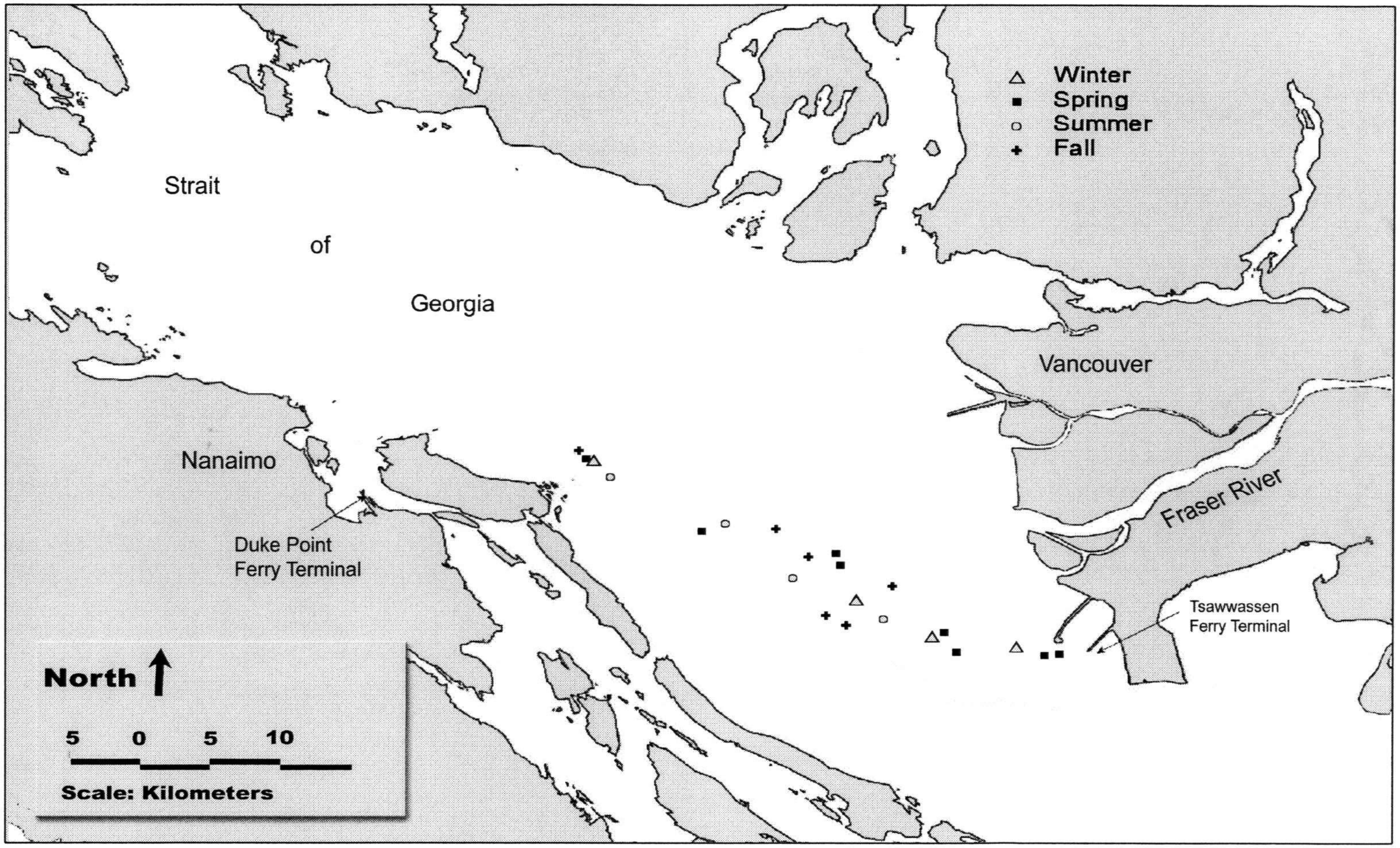

Figure 17 – Harbour porpoise sightings during Strait of Georgia surveys from May 1, 2000 to April 30, 2001.

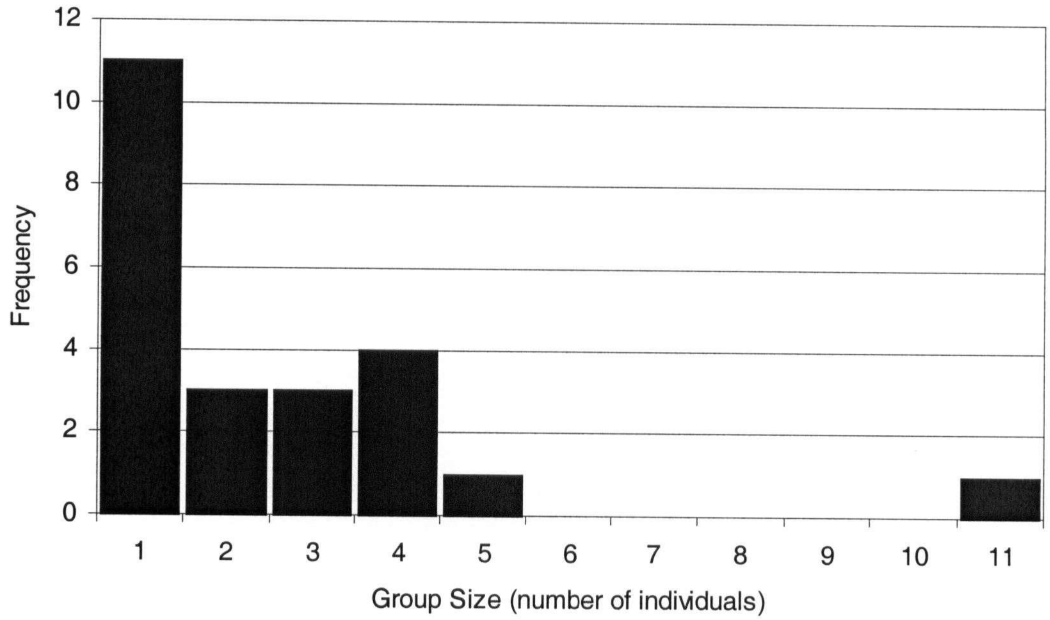

Figure 18. Frequency of harbour porpoise group size observed during surveys in the Strait of Georgia, May 1, 2000 to April 30, 2001.

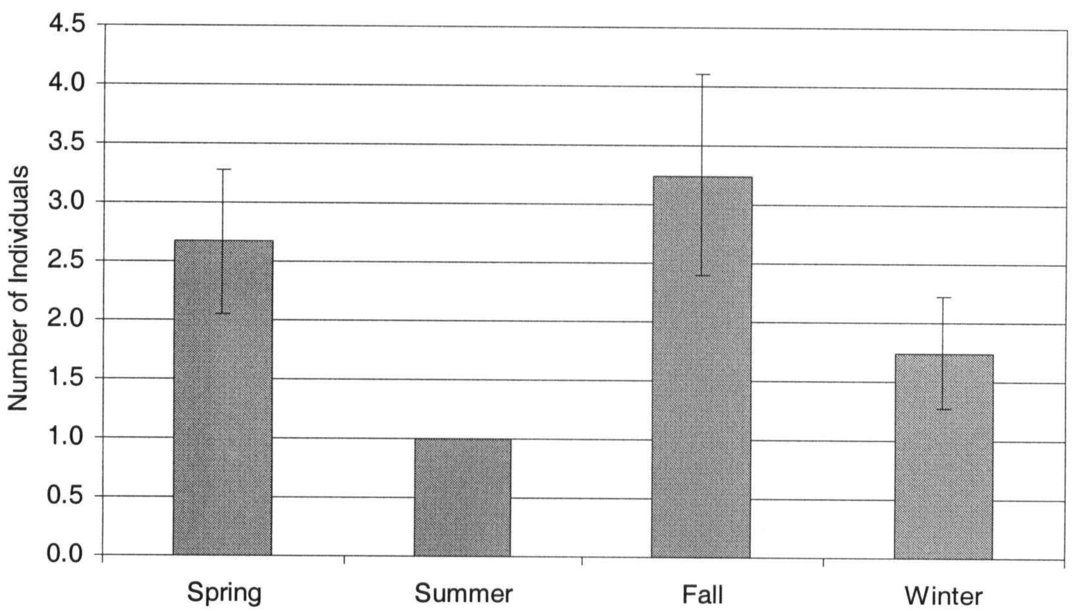

Figure 19. Mean group size of harbour porpoise within the truncated distance, observed during surveys in the Strait of Georgia, May 1, 2000 to April 30, 2001. Bars are standard error.

Group size ranged from 1 to 11 (Figure 18) and did not vary significantly by season ($F_{3,14} = 1.41$, $p = 0.30$; Figure 19).

Harbour porpoise moved away from the vessel during 48% of the observations, and showed random swimming direction with respect to the vessel ($\chi^2_1 = 0.034$, $p = 0.896$).

Harbour seals

Harbour seal sightings were common and occurred throughout the study area (Figure 20). A total of 1,629 individuals were counted over 499 sightings during 81% of the surveys. Of those, 914 were observed hauled out on land. The half-normal/cosine model, truncated at 915 metres (furthest 10% of sightings) best fit the perpendicular sighting distance distribution of animals in the water based on the lowest AIC score criteria (Figure 21).

Harbour seals occurred year-round in large numbers and differed significantly in abundance by season ($F_{3,139} = 6.73$, $p = 0.0005$; Table 6). DISTANCE abundance estimates peaked in fall, with 1,321 individuals in the study area (95% CI = 873 – 1,999), and were lowest in winter, with an estimated 280 individuals (95% CI = 144 – 545; Figure 22).

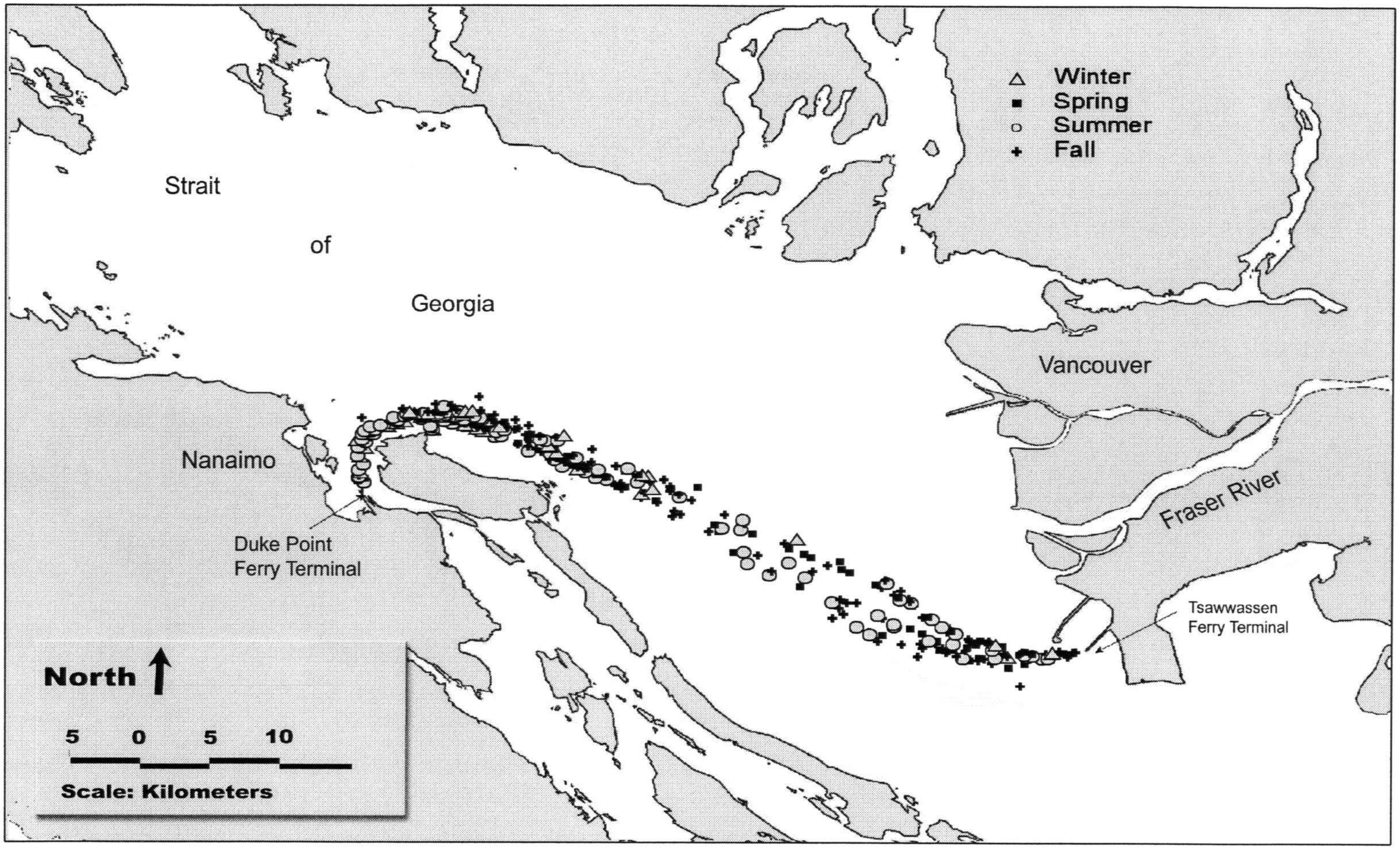

Figure 20 – Harbour seal sightings during Strait of Georgia surveys from May 1, 2000 to April 30, 2001.

Table 6. Harbour seal abundance estimates (excluding hauled out animals) and DISTANCE parameter values of the half-normal/cosine model, truncated at the furthest 10% of sighting distances, for the Strait of Georgia survey area, May 1, 2000 to April 30, 2001.

Parameter	Overall	Spring	Summer	Fall	Winter
Kilometres surveyed	10,218	2,739	2,405	2,472	1,936
Transect Lines	143	41	36	37	29
Truncation width (m)	915				
ESW (m)	204.62				
SE of ESW	11.051				
95% CI of ESW	(184.02 – 227.51)				
% CV of ESW	5.40				
$f(0)\cdot km^{-2}$	0.0049				
SE of $f(0)$	0.00026				
95% CI of $f(0)$	(0.00440 – 0.00543)				
Groups sighted within truncated distance	440	102	80	219	39
Mean group size (excluding haulouts)		1.2	1.2	1.2	1.1
SE of group size		0.08	0.09	0.10	0.06
Density ($animals\cdot km^{-2}$)		0.26	0.24	0.62	0.13
SE of density		0.054	0.059	0.131	0.044
95% CI of density		(0.17 – 0.39)	(0.14 – 0.39)	(0.41 – 0.95)	(0.07 – 0.26)
% CV of density		20.94	25.23	20.92	33.56
Abundance		543	498	1,321	280
SE of abundance		113.71	125.64	276.39	93.97
95% CI of abundance		(359 – 822)	(302 – 821)	(873 – 1999)	(144 – 545)

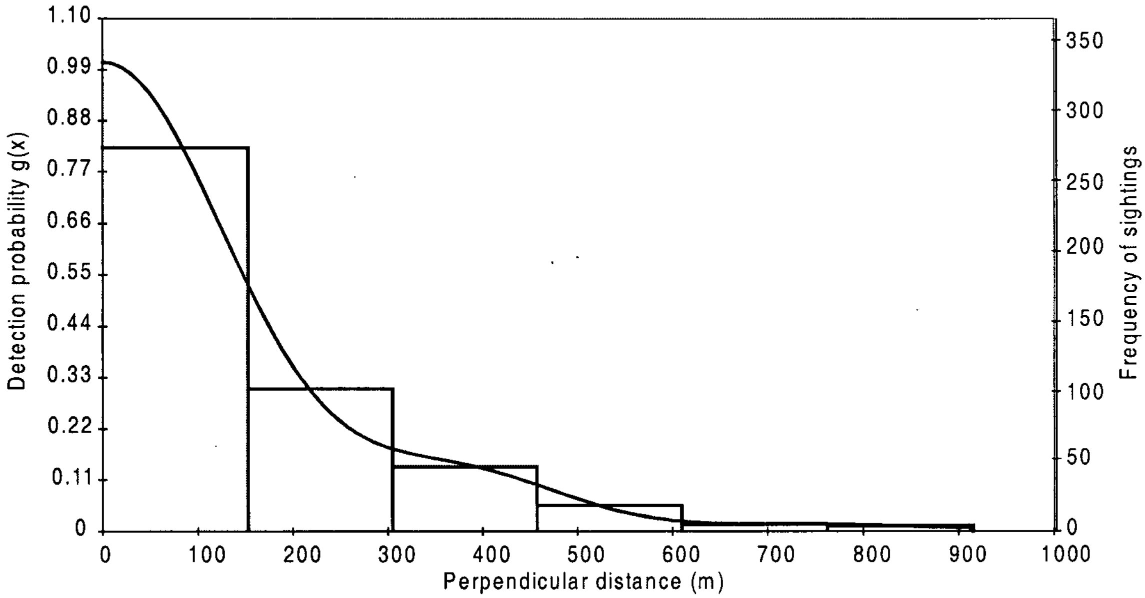

Figure 21. Probability detection distribution for perpendicular sighting distances of harbour seals. Bars represent the frequency of sightings and the line represents the half-normal/cosine model of best fit, truncated at 915 m.

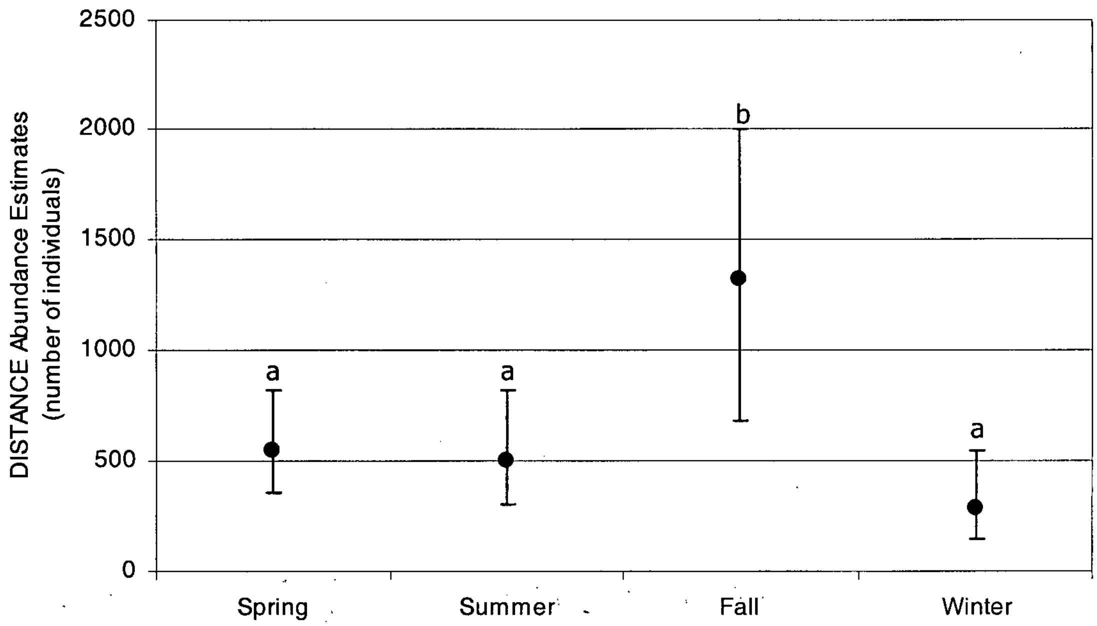

Figure 22. DISTANCE abundance estimates for harbour seals (excluding hauled out animals) in the Strait of Georgia study area from May 1, 2000 – April 30, 2001. Bars are log-normal 95% confidence intervals. Letters denotes a significant difference.

The probability density function, $f(0)$, was calculated for all data combined because analysis of variance showed no significant differences in detectability by season ($F_{3,139} = 0.99$, $p = 0.39$). Counts from haulout sites were excluded from this calculation. The ESW was 204.62 metres (95% CI = 184.02 – 227.51), with an $f(0)$ of $0.0049 \cdot km^{-2}$ (95% CI = 0.00440 - 0.00543).

Counts of harbour seals observed hauled out on land totaled 914 individuals (Figure 23). Although there appears to be distinct seasonality in haulout behaviour, seals were more often seen on land at low tide; tidal state when the ferry passed by the haulout site was related to season (Figure 24).

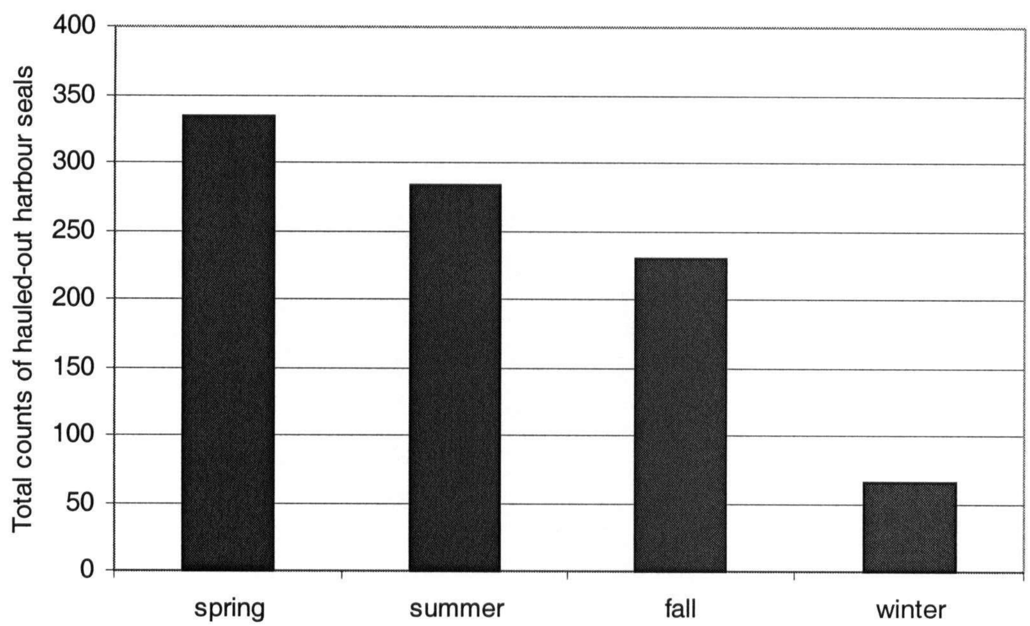

Figure 23. Number of harbour seals observed hauled out at Entrance Island during surveys in the Strait of Georgia, May 1, 2000 to April 30, 2001.

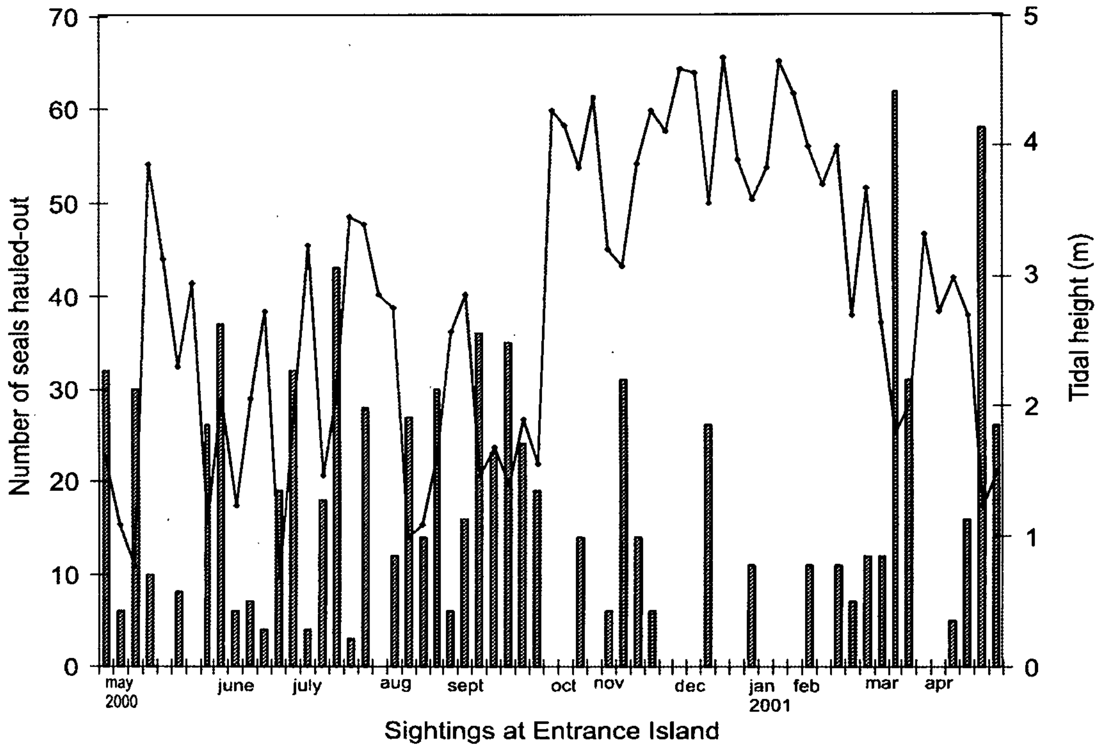

Figure 24. Number of harbour seals observed hauled out vs. tide height when passing the haulout site. Bars are total counts of seals on land, the line is the tide height (m) at Entrance Island at the time of the count.

Group sizes of harbour seals, excluding sightings from haulout sites such as Entrance Island, ranged from 1 to 22 (92% of the sightings were of single animals; Figure 25). Counts from haulout sites were not used to calculate average group size. Mean group size did not differ significantly over seasons ($F_{3,436} = 0.06$, $p = 0.73$; Figure 26). The largest group sighted was 62 individuals at a low-tide haulout site on Entrance Island.

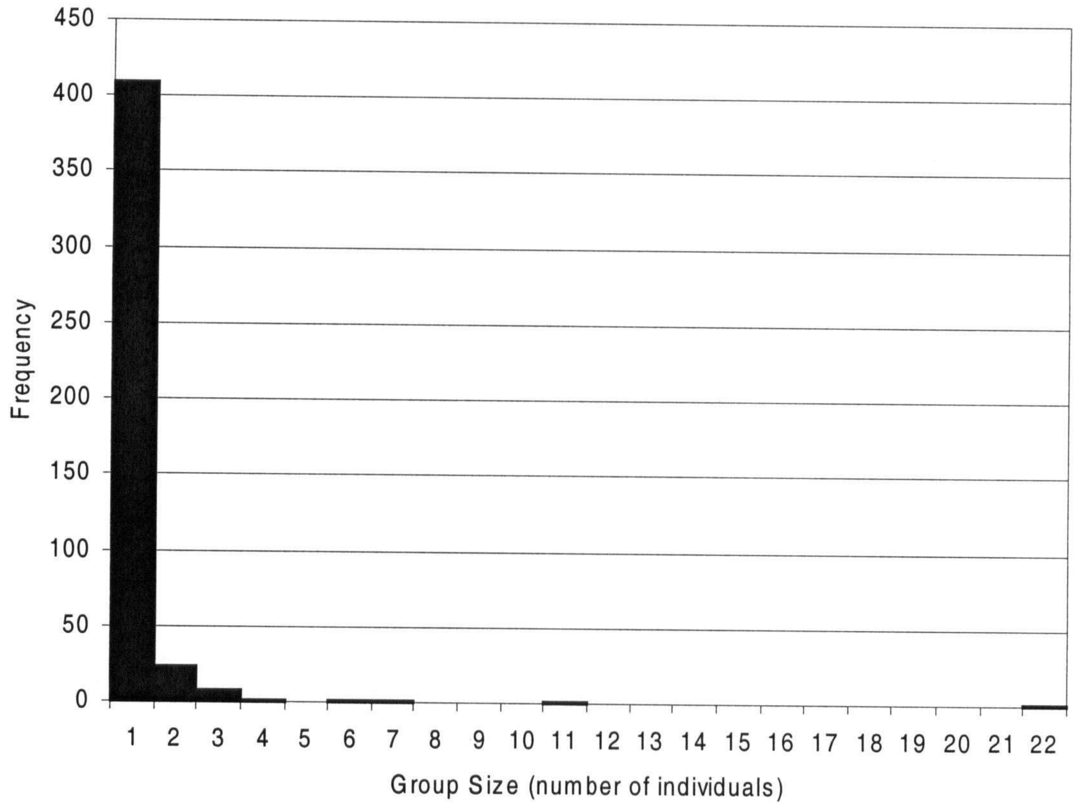

Figure 25. Frequency of harbour seal group size observed (excluding hauled-out animals) during surveys in the Strait of Georgia, May 1, 2000 to April 30, 2001.

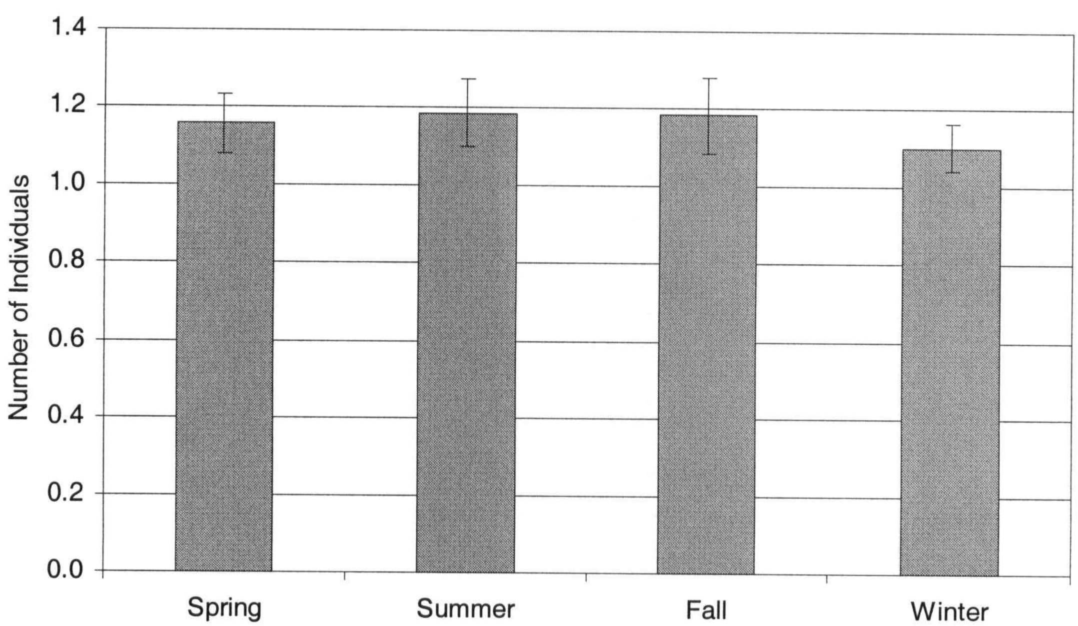

Figure 26. Mean group size of harbour seals (excluding hauled-out animals) within the truncated distance, observed during surveys in the Strait of Georgia, May 1, 2000 to April 30, 2001. Bars are standard error.

California sea lions

California sea lions were observed 63 times (29% of the surveys) for a total of 415 individuals, with 311 animals observed hauled out at Entrance Island. The half-normal/cosine model, truncated at 610m best fit the perpendicular sighting distances distribution based on the lowest AIC score (Figure 27).

California sea lions were seen in all seasons except summer (Figure 28), and were distributed over the entire survey route (but were most commonly observed around the northern end of Gabriola Island; Figure 29). Numbers did not differ significantly between fall, winter and spring ($F_{3,139} = 2.33$, $p = 0.047$; Table 7), although variability in mean numbers was greatest during the fall.

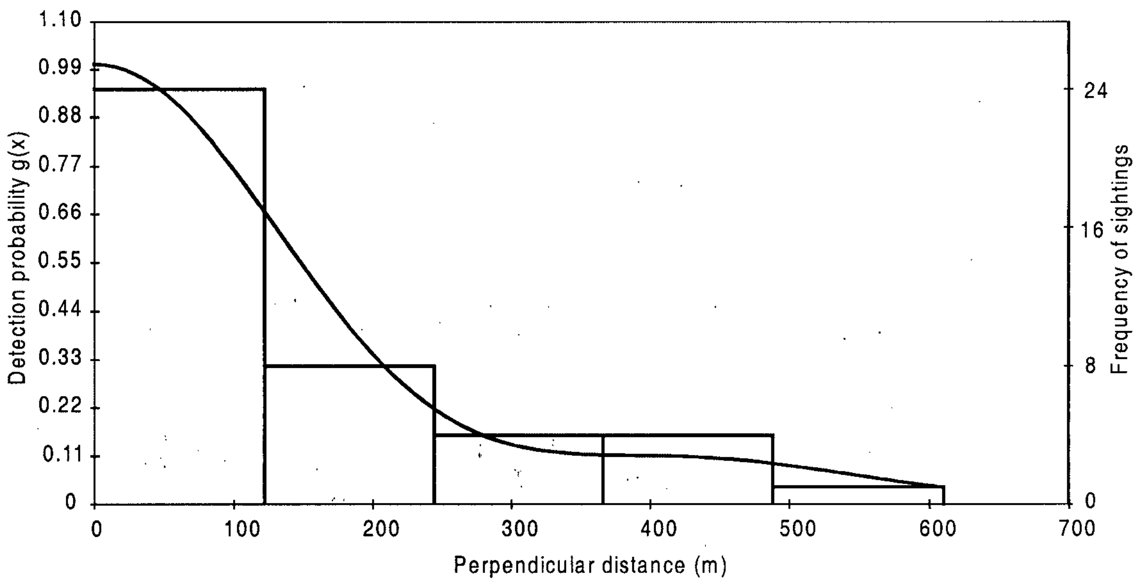

Figure 27. Probability detection distribution for perpendicular sighting distances of California sea lions. Bars represent the frequency of sightings and the line represents the negative-exponential/simple model of best fit, truncated at 610 m.

Table 7. California sea lion abundance estimates (excluding hauled out animals) and DISTANCE parameter values of the half-normal/cosine model, truncated at 610m, for the Strait of Georgia survey area, May 1, 2000 – April 30, 2001.

Parameter	Overall	Spring	Summer	Fall	Winter
Kilometres surveyed	10,218	2,739	2,405	2,472	1,936
Transect Lines	143	41	36	37	29
Truncation width (m)	610				
ESW (m)	196.37				
SE of ESW	27.756				
95% CI of ESW	(147.75 – 260.99)				
% CV of ESW	14.13				
$f(0)\cdot km^{-2}$	0.0051				
SE of $f(0)$	0.00072				
95% CI of $f(0)$	(0.00383 – 0.00677)				
Groups sighted within truncated distance	41	17	0	17	7
Mean group size (excluding haulouts)		1.1	0	2.2	2.0
SE of group size		0.06	0	0.54	0.85
Density ($animals\cdot km^{-2}$)		0.04	0	0.04	0.03
SE of density		0.015	0	0.041	0.027
95% CI of density		(0.02 – 0.08)	0	(0.04 – 0.21)	(0.01 – 0.14)
% CV of density		36.93	0	43.79	59.42
Abundance		86	0	197	95
SE of abundance		31.8	0	86.3	56.4
95% CI of abundance		(42 – 177)	0	(85 – 454)	(30 – 299)

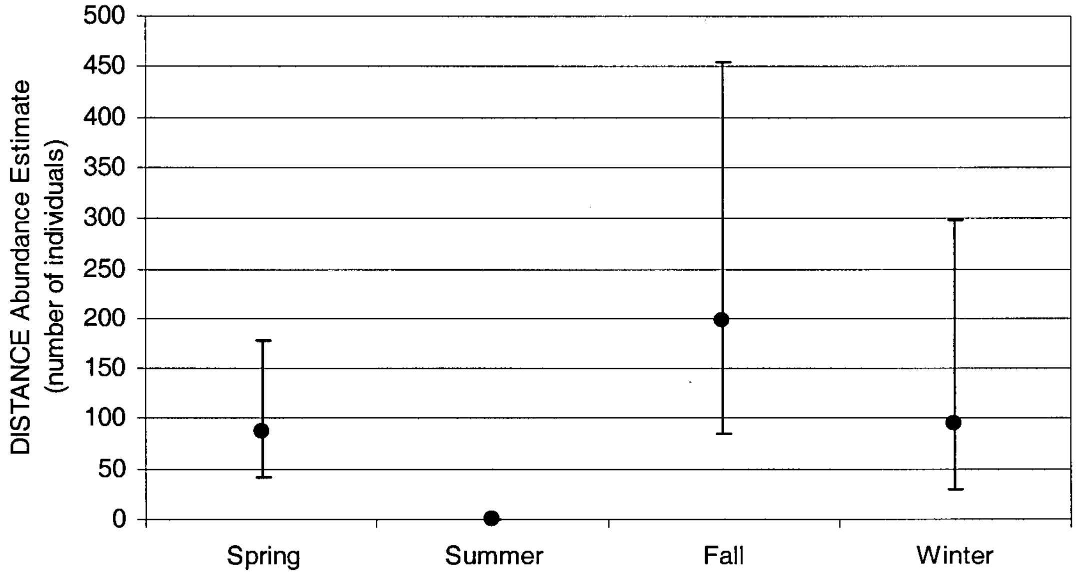

Figure 28. DISTANCE abundance estimates for California sea lions (excluding hauled out animals) in the Strait of Georgia study area from May 1, 2000 – April 30, 2001. Bars are log-normal 95% confidence intervals. The only observations of California sea lions in the summer were of animals hauled out on land.

Observations were pooled from all seasons to calculate the probability density function, $f(0)$, and counts from haulout sites were not included. The ESW was 196.37 metres (95% CI = 147.75 – 260.99) with an $f(0)$ of $0.0051 \cdot km^{-2}$ (95% CI = 0.00383 - 0.00679).

A total of 311 California sea lions were observed on land, the majority of which were counted during spring (Figure 30).

Group size of California sea lions (excluding data from haulout sites) ranged from one to seven individuals with 77% of sightings being of single animals (Figure 31). Mean group size by season (excluding hauled-out animals) did not differ significantly ($F_{3,37}$ = 1.29, p = 0.58; Figure 32). The largest groups occurred when the animals were hauled out, with the largest being 52 sighted at Entrance Island.

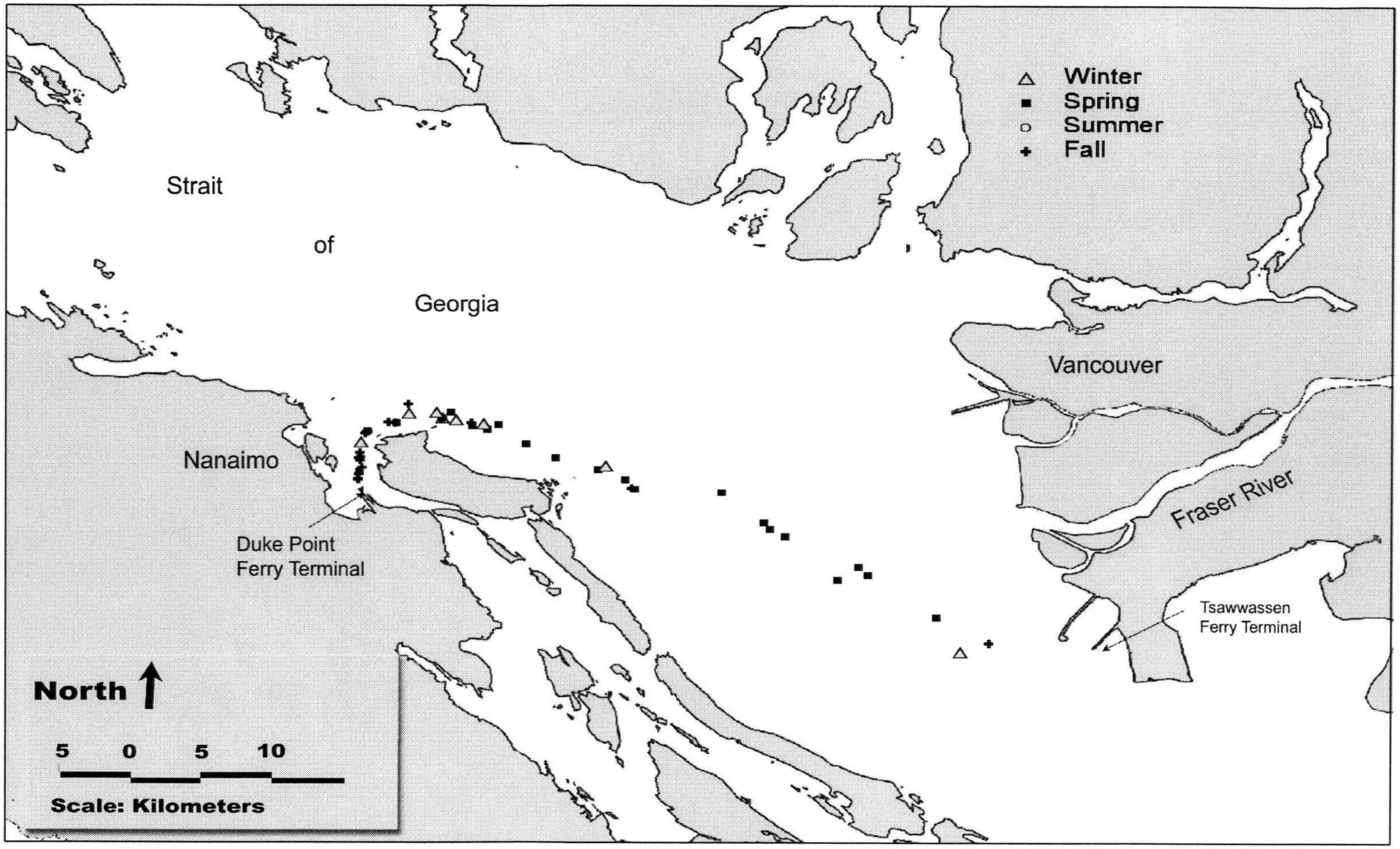

Figure 29 – California sea lion sightings during Strait of Georgia surveys from May 1, 2000 to April 30, 2001.

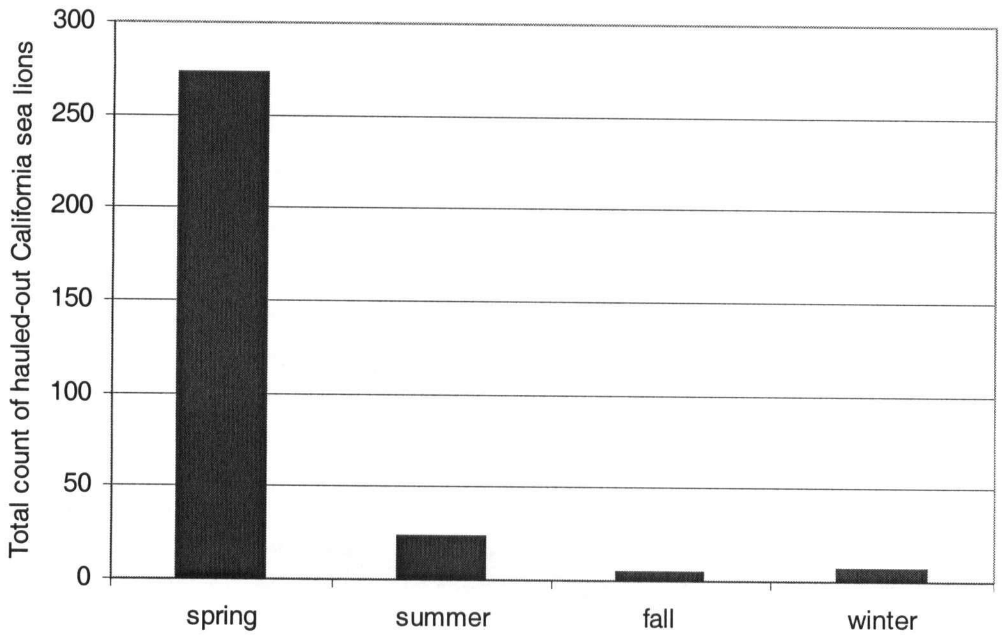

Figure 30. Number of California sea lions observed hauled out at Entrance Island during surveys in the Strait of Georgia, May 1, 2000 to April 30, 2001.

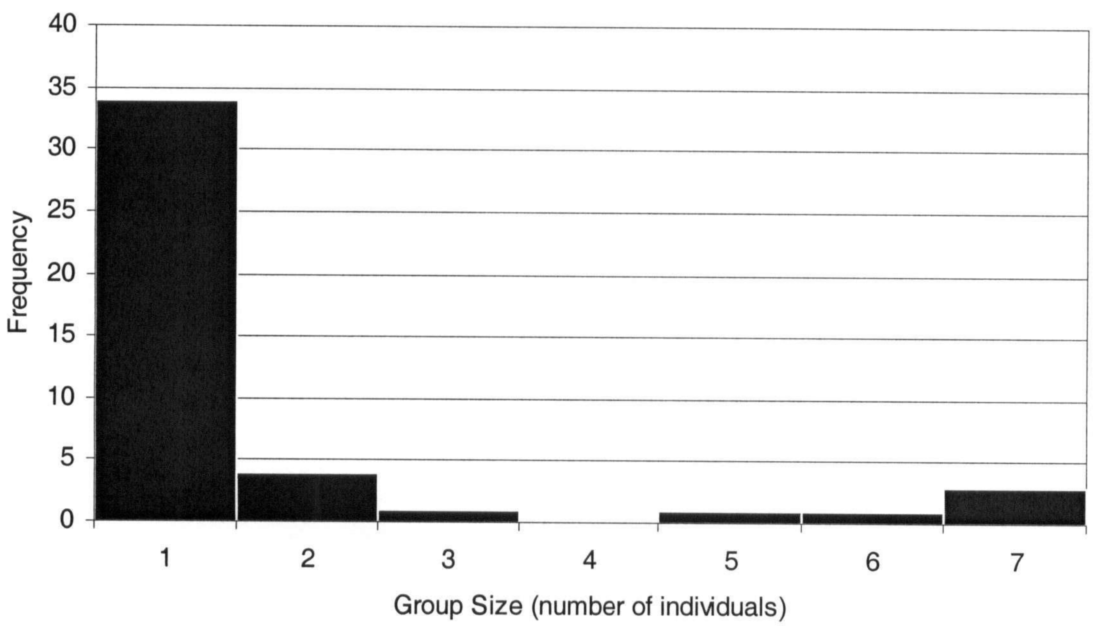

Figure 31. Frequency of California sea lion group size (excluding hauled-out animals) observed during surveys in the Strait of Georgia, May 1, 2000 to April 30, 2001.

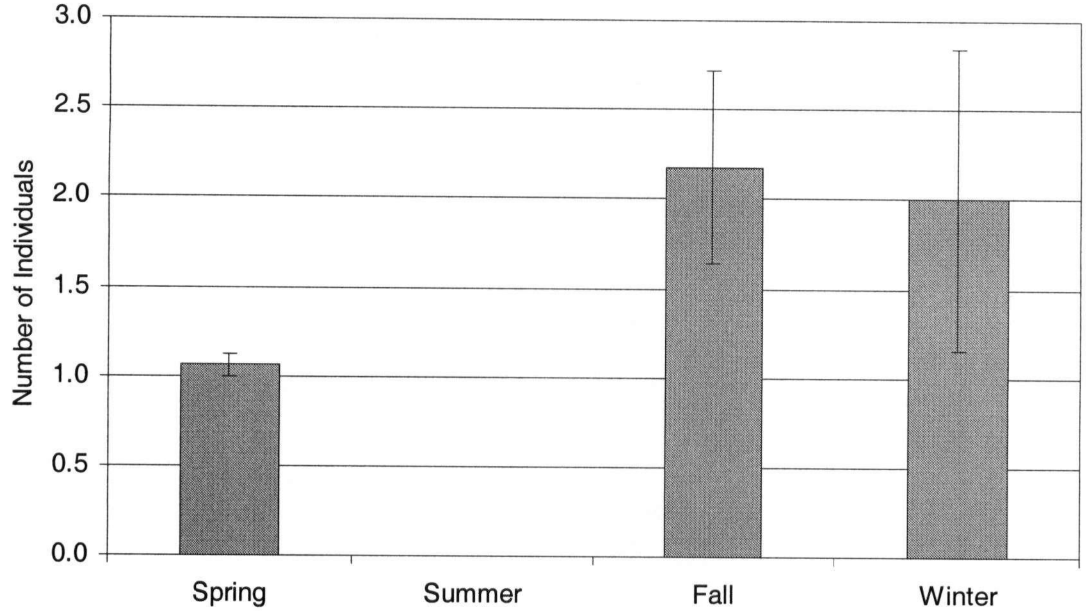

Figure 32. Mean group size (excluding hauled-out animals) of California sea lions within the truncated distance, observed during surveys in the Strait of Georgia, May 1, 2000 to April 30, 2001. Bars are standard error. The only observations of California sea lions in the summer were individuals hauled out at Entrance Island.

Steller sea lions

A total of 205 Steller sea lions were counted in 63 sightings (29% of the surveys), along with 142 individuals on land. The perpendicular sighting distances distribution of animals in the water was best fit by the half-normal/cosine model truncated at 770 metres based on the lowest AIC scores (Figure 33).

Abundance estimates of animals observed in the water differed significantly by season ($F_{3,139} = 2.74$, $p = 0.028$; Table 8), peaking at 87 individuals in spring (95% CI = 43 – 176; Figure 34), and bottoming out in summer with an estimated 4 individuals (95% CI = 1 - 21). Steller sea lions were observed over all parts of the survey route (Figure 35).

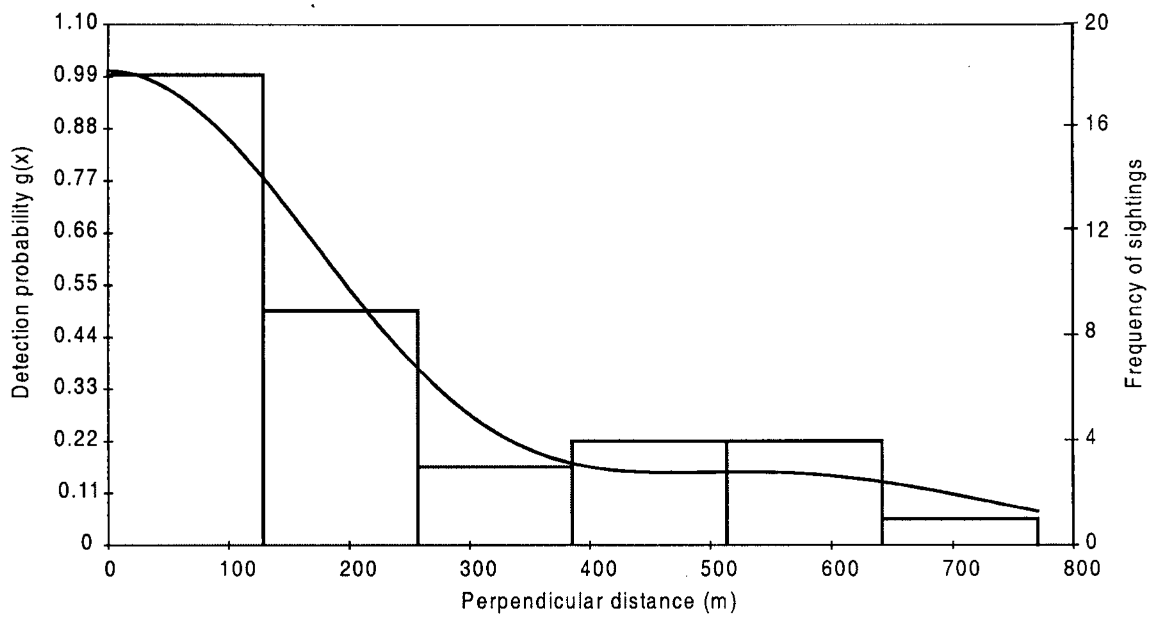

Figure 33. Probability detection distribution for perpendicular sighting distances of Steller sea lions. Bars represent the frequency of sightings and the line represents the half-normal/cosine model of best fit, truncated at 770 m.

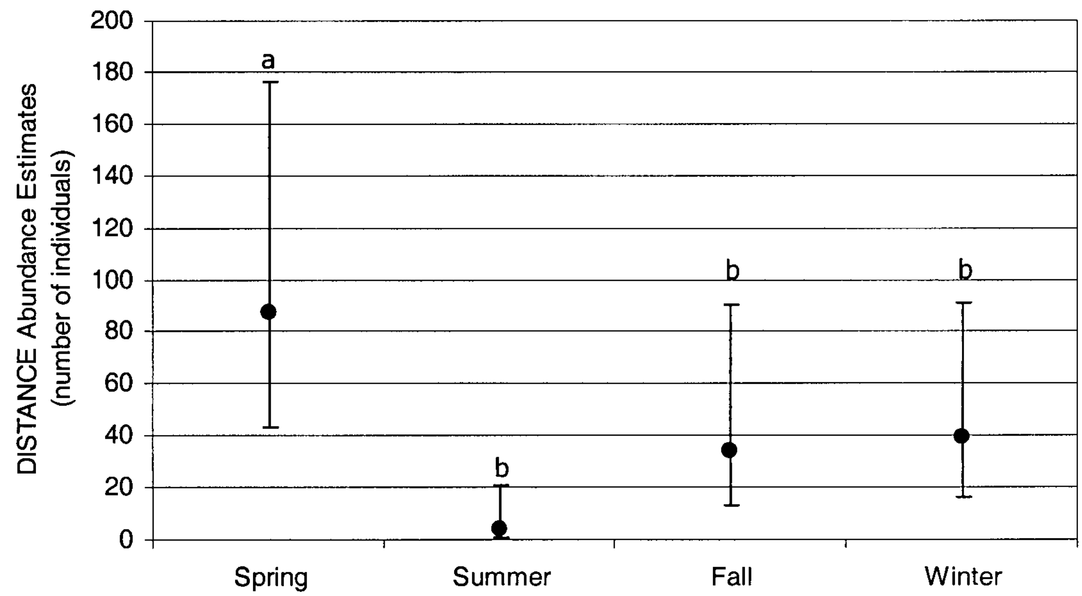

Figure 34. DISTANCE abundance estimates (excluding hauled out animals) for Steller sea lions in the Strait of Georgia study area from May 2000 – April 2001. Bars are log-normal 95% confidence intervals. Letters denote a significant difference.

Table 8. Steller sea lion abundance estimates (excluding hauled out animals) and DISTANCE parameter values of the half-normal/cosine model, truncated at 770m, for the Strait of Georgia survey area, May 1, 2000 – April 30, 2001.

Parameter	Overall	Spring	Summer	Fall	Winter
Kilometres surveyed	10,218	2,739	2,405	2,472	1,936
Transect Lines	143	41	36	37	29
Truncation width (m)	770				
ESW (m)	275.71				
SE of ESW	43.769				
95% CI of ESW	(200.27 – 379.56)				
% CV of ESW	15.88				
$f(0)\cdot km^{-2}$	0.0036				
SE of $f(0)$	0.00058				
95% CI of $f(0)$	(0.00263 – 0.00499)				
Groups sighted within truncated distance	39	22	1	9	7
Mean group size (excluding haulouts)		1.2	1.0	1.0	1.1
SE of group size		0.14	0	0	0.14
Density ($animals\cdot km^{-2}$)		0.04	0.002	0.008	0.02
SE of density		0.015	0.002	0.006	0.008
95% CI of density		(0.02 – 0.08)	(0.0003 – 0.01)	(0.006 – 0.04)	(0.008 – 0.04)
% CV of density		36.57	101.25	51.37	44.20
Abundance		87	4	34	39
SE of abundance		31.8	4.1	17.5	17.2
95% CI of abundance		(43 – 176)	(1 – 21)	(13 – 90)	(16 – 91)

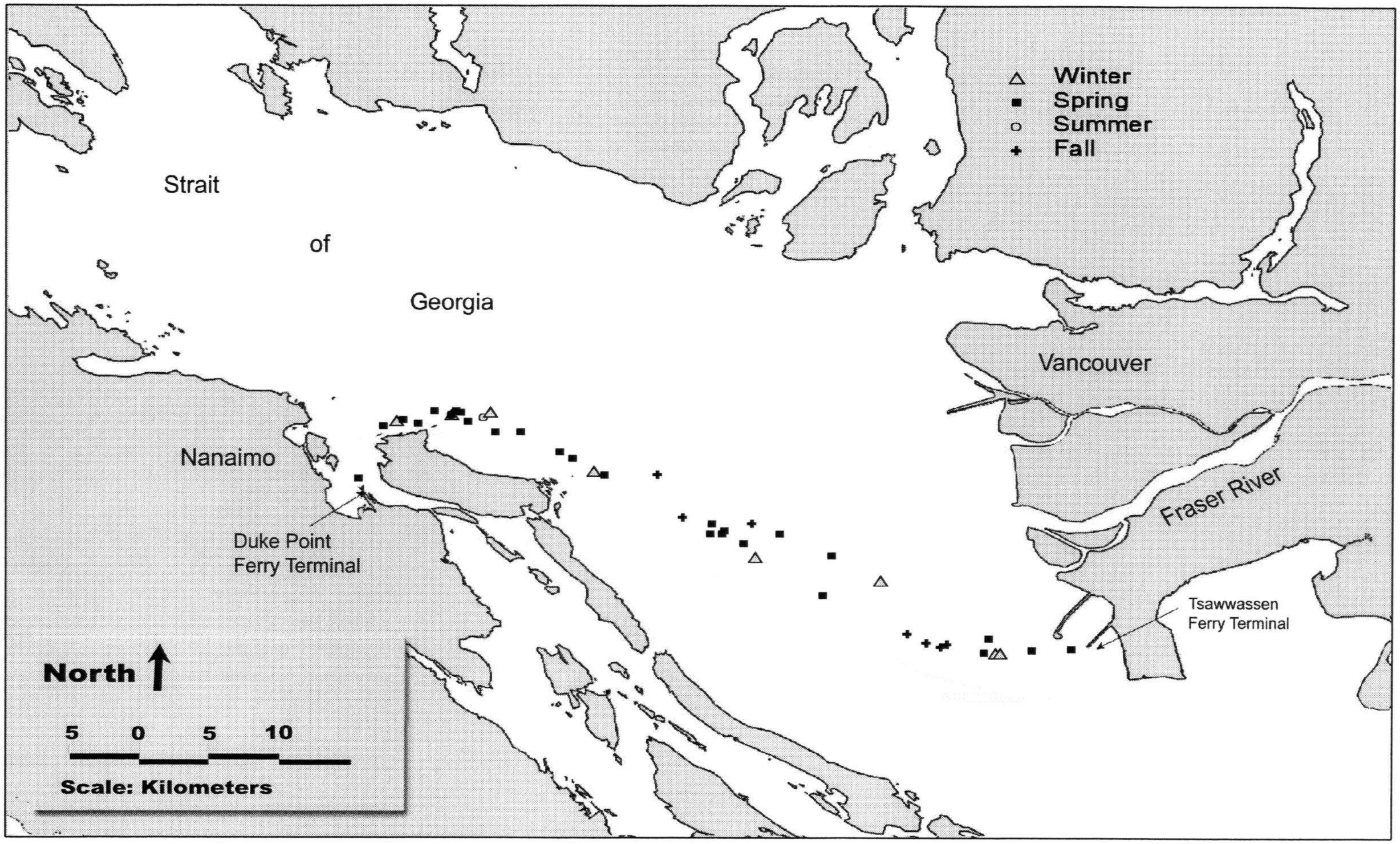

Figure 35 – Steller sea lion sightings during Strait of Georgia surveys from May 1, 2000 to April 30, 2001.

Sightings were combined from all seasons to calculate $f(0)$ because of the low number of observations of Steller sea lions from summer to winter. Sightings from haulout sites were excluded from this calculation. The ESW was 275.71 metres (95% CI = 200.27 – 379.56) with an $f(0)$ of $0.0036 \cdot km^{-2}$ (95% CI = 0.00263 - 0.00499).

Counts of Steller sea lions hauled out on land totaled 143 individuals and showed significant shifts from high abundance in spring to none in winter (Figure 36). Numbers of hauled out Steller sea lions significantly correlated with those of California sea lions during summer ($r = 0.927$, $p = 0.003$, $n = 7$), but not at other times of the year (spring: $r = 0.189$, $p = 0.39$, $n = 25$; fall: $r = 0.018$, $p = 0.99$, $n = 5$).

Groups of Steller sea lions observed in the water ranged from one to four individuals (93% of sightings were of single animals; Figure 37). Mean group size, excluding hauled-out animals, did not differ significantly over seasons ($F_{3,35} = 0.26$, $p = 0.57$; Figure 38). The largest group, 45 individuals, was hauled out at Entrance Island.

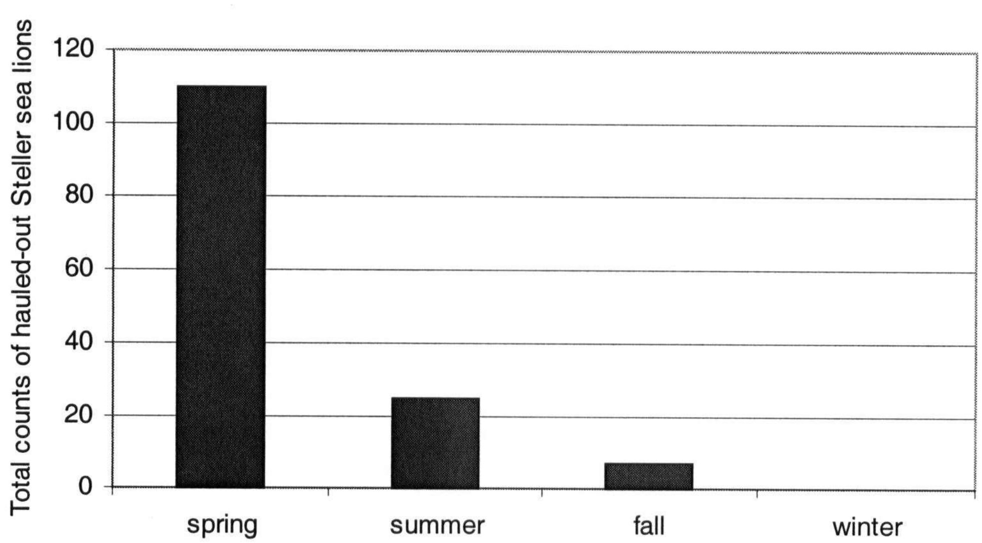

Figure 36. Number of Steller sea lions observed hauled out at Entrance Island during surveys in the Strait of Georgia, May 1, 2000 to April 30, 2001.

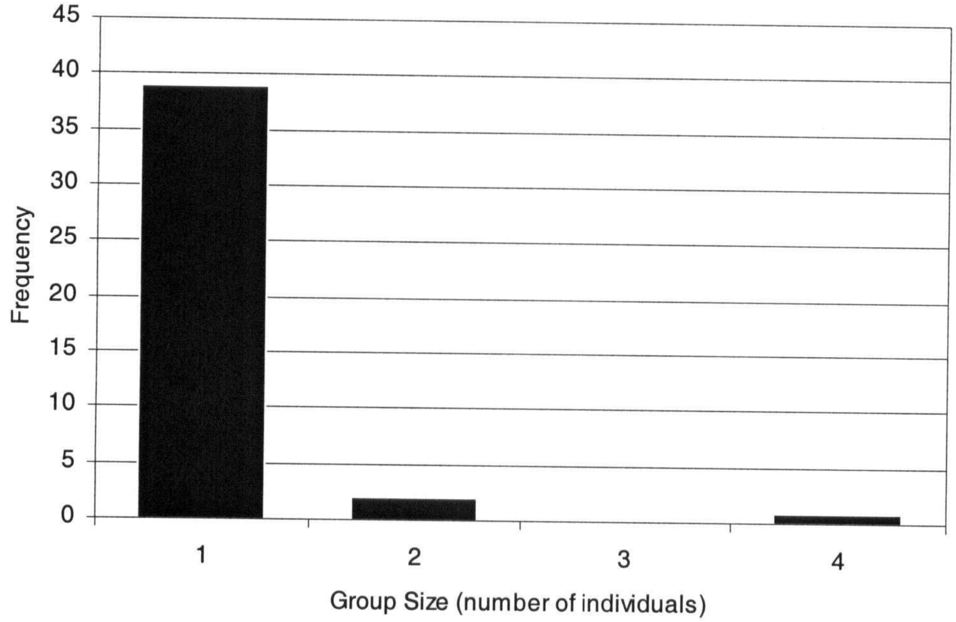

Figure 37. Frequency of Steller sea lion group size (excluding hauled-out animals) observed during surveys in the Strait of Georgia, May 1, 2000 to April 30, 2001.

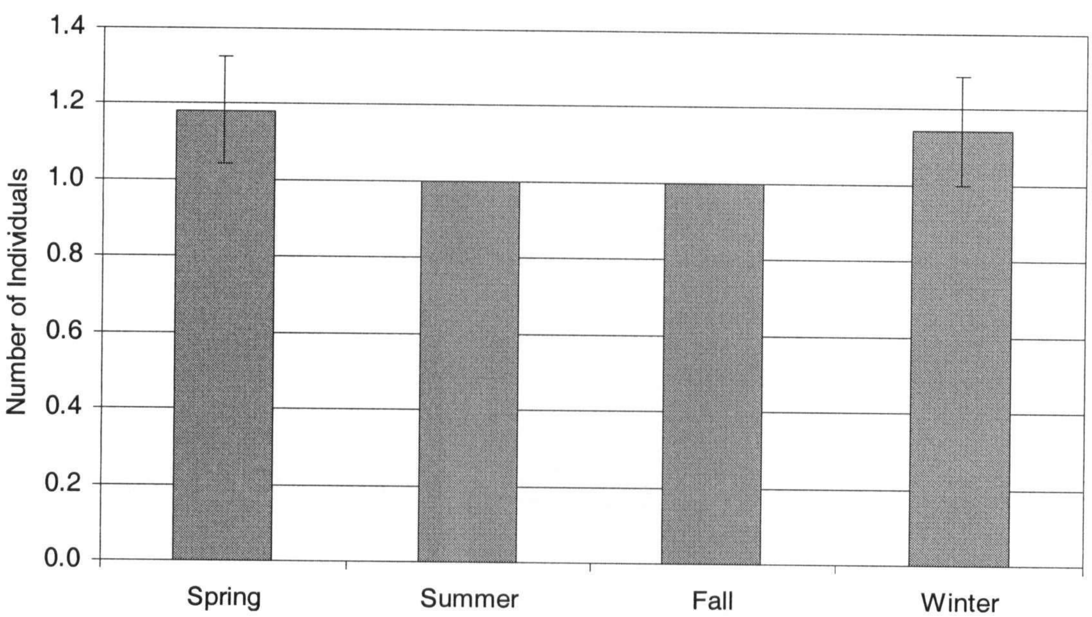

Figure 38. Mean group size of Steller sea lions (excluding hauled-out animals) within the truncated distance, observed during surveys in the Strait of Georgia, May 1, 2000 to April 30, 2001. Bars are standard error.

Other species

Pacific white-sided dolphins, killer whales, gray whales and a minke whale were also observed during the surveys (Table 9). Pacific white-sided dolphins were observed in spring, summer and fall, and all of the sightings were along the northern part of the survey route, primarily close to Gabriola Island (Figure 39). Killer whales were also sighted in all seasons except winter, and were mainly observed near the northern end of Gabriola Island or near the Tsawwassen terminal (Figure 40). Gray whales were observed twice during the surveys – once in spring in the centre of the Strait of Georgia, and once in summer off the northern tip of Gabriola Island (Figure 41). One minke whale was observed in the spring in the centre of the Strait (Figure 42).

Table 9. Other species sighted in the Strait of Georgia by month during the surveys conducted between May 2000 – April 2001.

Species		Spring	Summer	Fall	Winter	Total # sightings	Total # individuals
Killer whale	# sightings	1	3	12		16	
	# individuals	3	6	40			49
Pacific white-sided dolphin	# sightings	1	1	2		4	
	# individuals	7	16	87			110
Gray whale	# sightings	1	1			2	
	# individuals	1	1				2
Minke whale	# sightings	1				1	
	# individuals	1					1

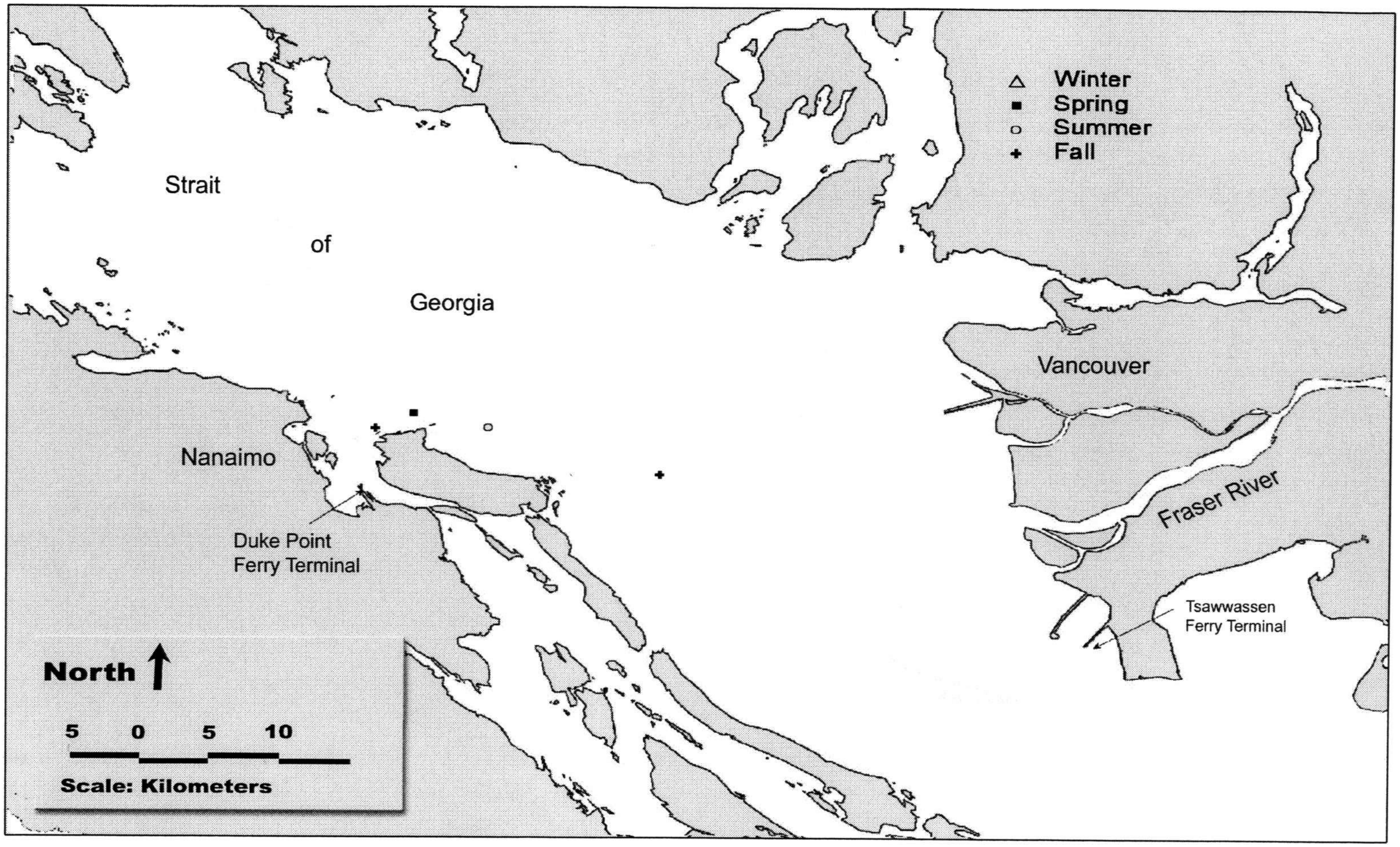

Figure 39 – Pacific white-sided dolphin sightings during Strait of Georgia surveys from May 1, 2000 to April 30, 2001.

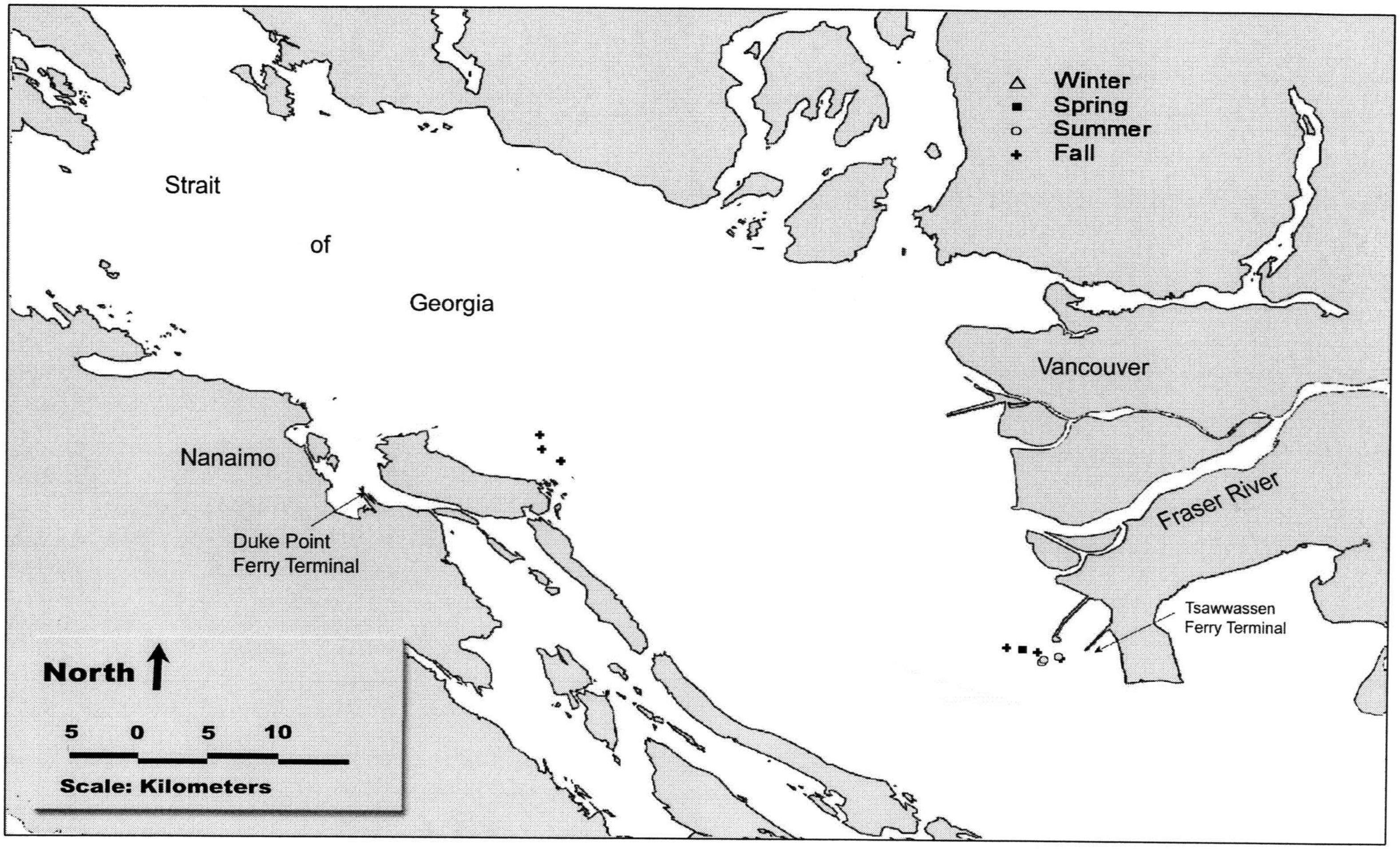

Figure 40 – Killer whale sightings during Strait of Georgia surveys from May 1, 2000 to April 30, 2001.

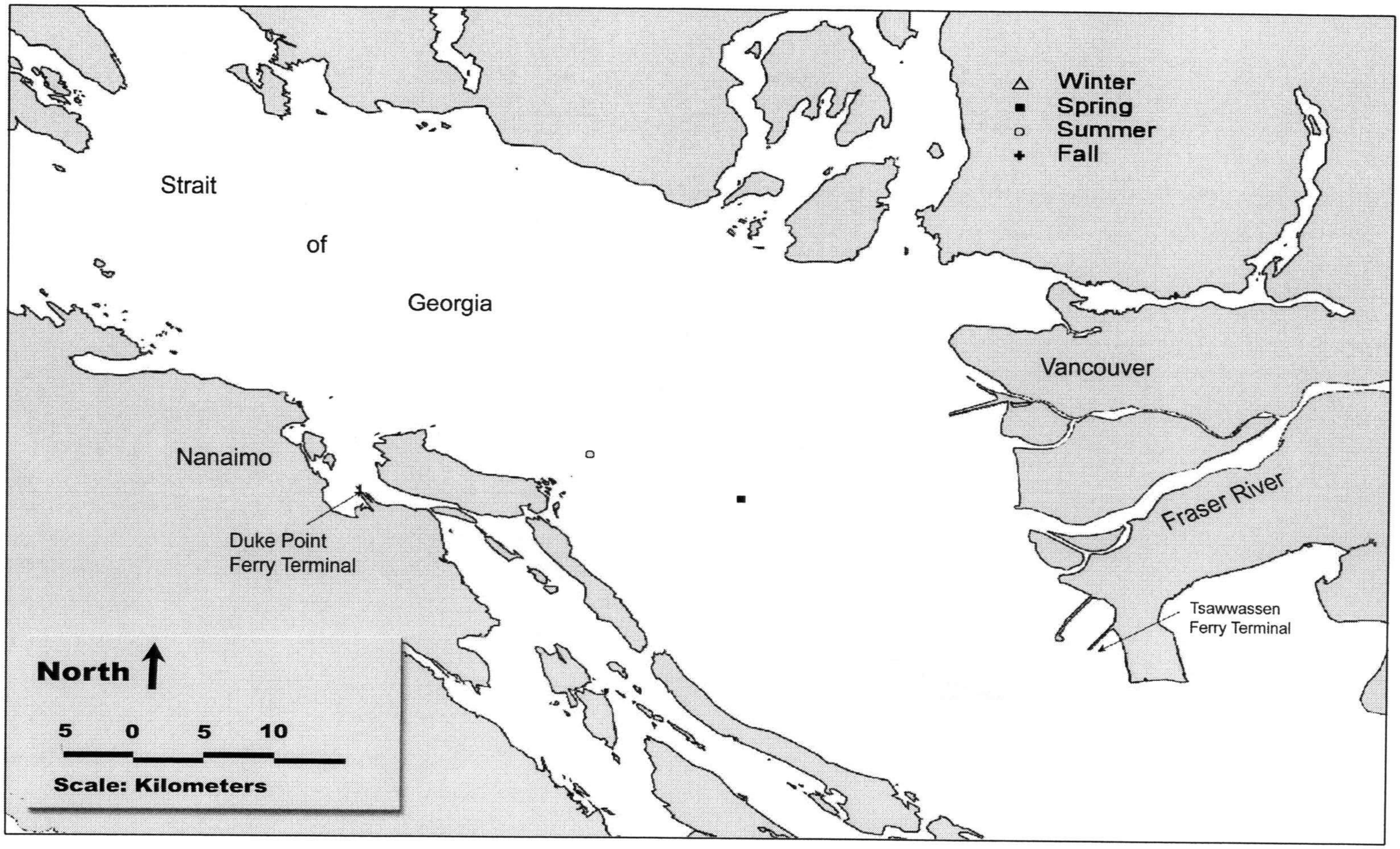

Figure 41 – Gray whale sightings during Strait of Georgia surveys from May 1, 2000 to April 30, 2001.

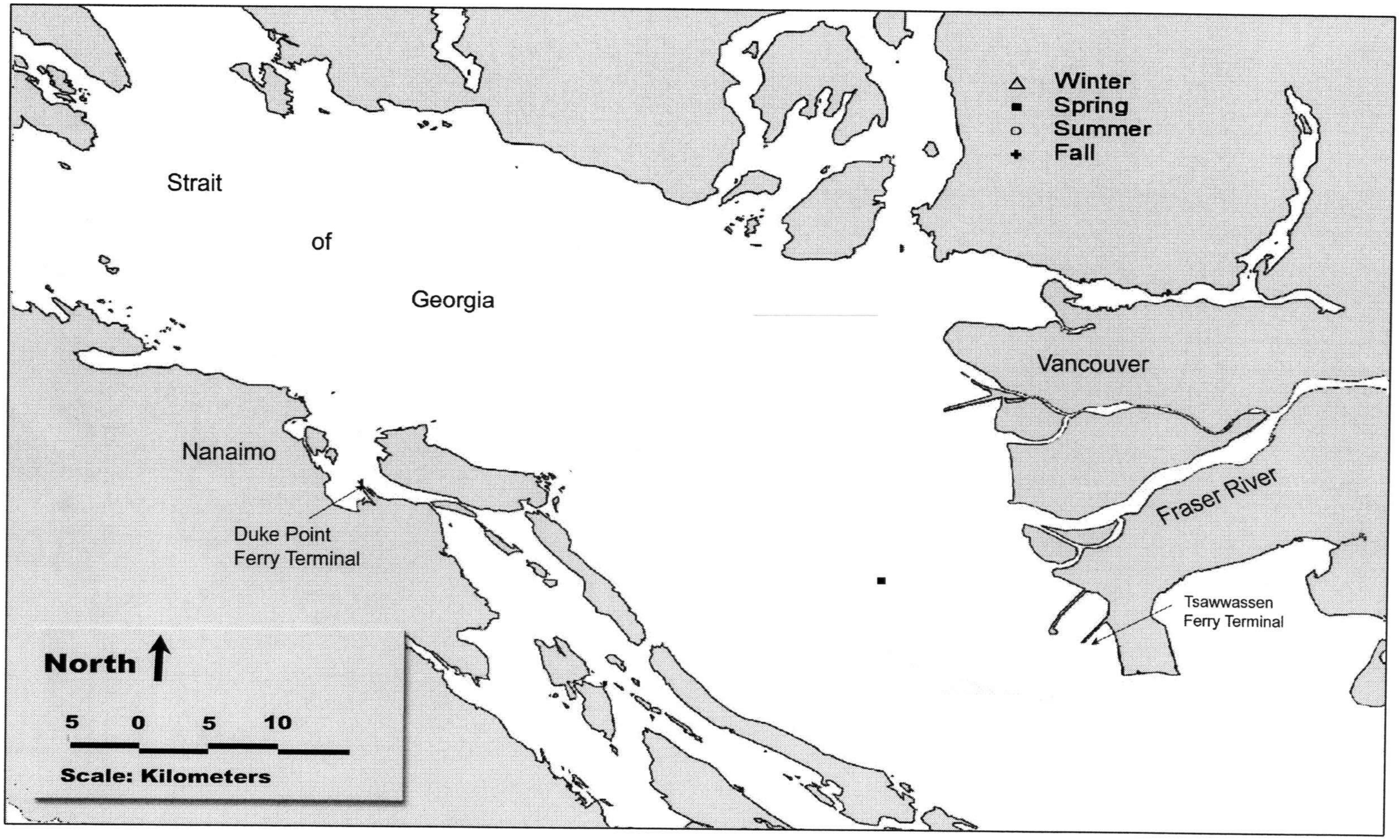

Figure 42 – Minke whale sighting during Strait of Georgia surveys from May 1, 2000 to April 30, 2001.

Consumption

Prey species of marine mammals present in the Strait of Georgia are listed in Table 10. Consumption by porpoises and pinnipeds in the water were calculated for the DISTANCE abundance estimates (Figure 43). Counts of hauled out animals were not used to calculate consumption estimates. Harbour seals consumed an estimated 668.2 $t \cdot y^{-1}$ (424.5 – 1,058.6 $t \cdot y^{-1}$ based on the 95% confidence intervals on the abundance estimates). This was more than for any other marine mammal. Sea lions (California and Steller) appear to have the next highest consumption in the Strait of Georgia study area, with California sea lions consuming an estimated 262.7 $t \cdot y^{-1}$ of prey (109.2 – 645.6 $t \cdot y^{-1}$), and Steller sea lions consuming an estimated 196.5 $t \cdot y^{-1}$ of prey (87.5 – 452.6 $t \cdot y^{-1}$). Dall's and harbour porpoise were estimated to consume 233.1 $t \cdot y^{-1}$ (131.8 – 416.2 $t \cdot y^{-1}$) and 14.2 $t \cdot y^{-1}$ (3.1 – 65.8 $t \cdot y^{-1}$), respectively.

A comparison of consumption estimates between seasons suggested that the estimated amount of prey consumed by combining the above five marine mammal species was highest in fall (Figure 44), with a second, smaller peak in spring. The model predicted that pinnipeds consumed more prey across all seasons compared to porpoises (Figure 45).

Table 10. Prey species present in the diet of marine mammal species in the Strait of Georgia. (Table compiled from data presented in Fiscus & Baines 1966, Everitt *et al.* 1981, Odell 1981, Stroud *et al.* 1981, Bigg 1988a, Bigg 1988b, Osborne *et al.* 1988, Hoezel *et al.* 1989, Gearin & Johnson 1990, Olesiuk 1990, Olesiuk *et al.* 1990, Gaskin *et al.* 1993, Olesiuk 1993, Heise 1997, Ford *et al.* 1998)

	Cetaceans					Pinnipeds		
Prey Species	Dall's porp.	Harbour porp.	Pacific white-sided dolphin	Resident killer whale	Minke whale	Harbour seal	Calif. sea lion	Steller sea lion
Herring	•	•	•	•	•	•	•	•
Salmon (adult)		•	•	•		•	•	
Salmon (juvenile)	•	•						
Pacific hake	•	•	•			•	•	•
Eulachon	•	•	•			•		•
Rockfish (*Sebastes* spp.)	•	•		•		•	•	•
Squid	•	•	•			•	•	•
Walleye pollock			•			•	•	•
Flatfish (Pleuronectidae)	•			•		•		•
Pacific cod (Gadidae)		•	•					•
Spiny dogfish						•	•	
Shrimp (Decapoda)		•	•					
Lingcod (*Ophiodon elongatus*)						•		
Sandlance					•			
Surfperch (Embiotocidae)						•		
Sculpins (Cottidae)						•		
Plainfin midshipman (*Porichthys notatus*)						•		

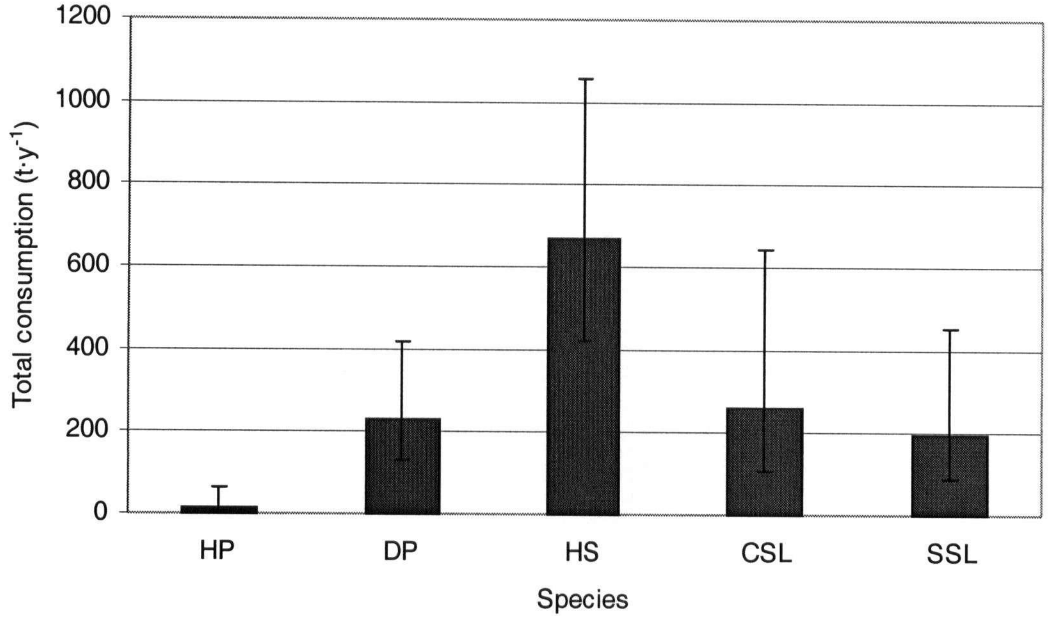

Figure 43. Estimated total consumption ($t \cdot y^{-1}$) by marine mammal species in the Strait of Georgia study area. DP = Dall's porpoise, HP = harbour porpoise, HS = harbour seals, CSL = California sea lions, SSL = Steller sea lions. Ranges are calculated based on the 95% confidence intervals obtained from DISTANCE abundance estimates.

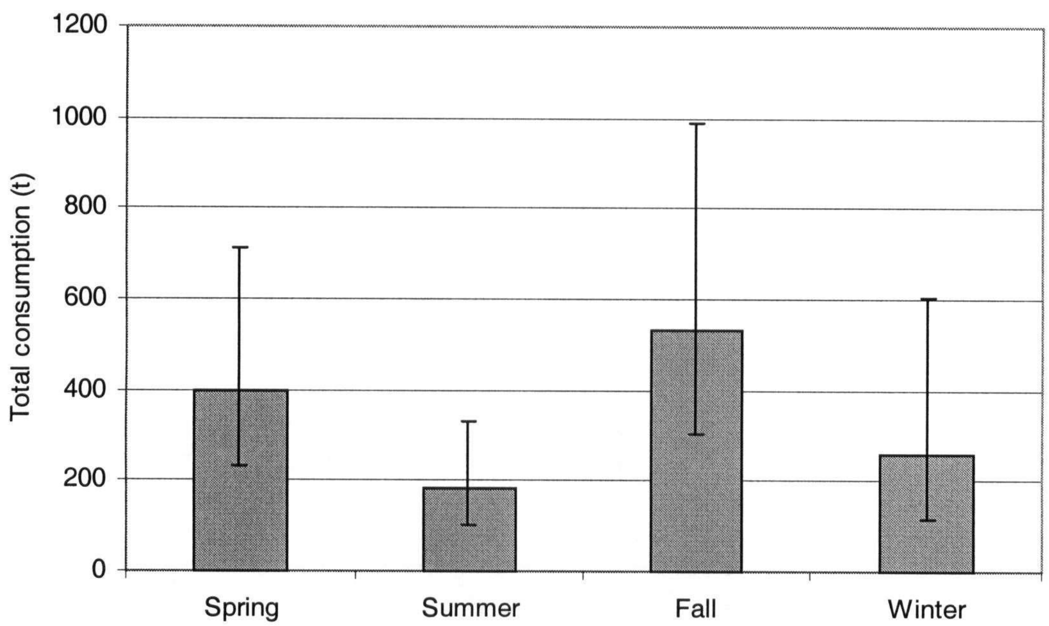

Figure 44. Seasonal estimate of total prey consumed (t) for all marine mammal species present in the Strait of Georgia study area, modeled from abundance estimates. Ranges are calculated based on the 95% confidence intervals obtained from DISTANCE abundance estimates.

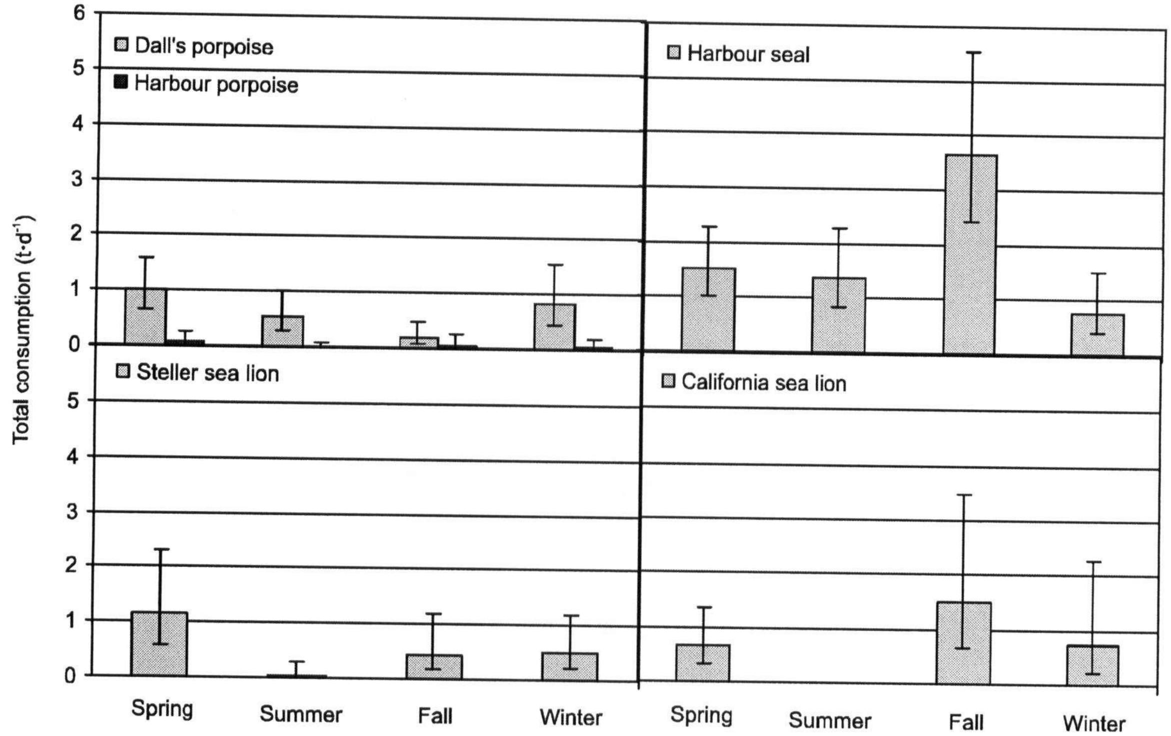

Figure 45. Comparison of estimated prey consumed by season ($t{\cdot}d^{-1}$) for marine mammal populations in the Strait of Georgia study area, modeled from abundance estimates. Ranges are calculated based on the 95% confidence intervals obtained from DISTANCE abundance estimates.

DISCUSSION

Line Transect Assumptions

The accuracy of the density and abundance estimates derived from distance sampling requires that a number of assumptions be met. One important assumption is that the study area be sampled randomly or that the animals be distributed randomly within the study area. In my case, it was impossible to place transects randomly because the B.C. Ferries' ships travelled along a fixed route. However, the reasonably homogenous seafloor topography and currents of the study area suggests that animals were likely distributed randomly.

A second assumption was that all animals on the transect line were detected (i.e. the probability of detection $g(0) = 1.0$). Unfortunately, marine mammals can be missed while diving and submerged (Best 1982, Jefferson 1996). It is likely, for example, that some harbour porpoise may have been missed given their mean dive times of 1.5 – 2.3 minutes (Taylor & Dawson 1984, Raum-Suryan 1995), and the average speed of the ferries during surveys of 35.4 $km \cdot hr^{-1}$ (589.6 $m \cdot min^{-1}$). Thus, the ferry would have traveled just over one kilometre in two minutes, during the time that a harbour porpoise might have been underwater.

I assumed that $g(0)$ equaled 1.0, as there was no way to estimate bias. Such an assumption would have underestimated density and abundance if $g(0)$ was actually less than one. The consistent sighting probability across surveys ensures that the population estimates derived from distance sampling are useful for temporal comparisons even if $g(0)$ was much lower than one (Thompson *et al.* 1998). In all likelihood, however, $g(0)$ was less than one, but was probably high due to the height of the observation platform, the use of binoculars, and surveying only under good sighting conditions.

The third assumption was that animals did not respond to the survey vessel prior to being seen. Density and abundance estimates will be over- or under-estimated, depending if animals react to the vessel by either moving towards or away from the transect line (Best 1982, Polachek & Thorpe 1990, Buckland *et al.* 1993). In my study, animals appeared to move randomly with respect to the survey vessel and were detected over a wide range of distances, due perhaps to the height of the survey platform and the use of binoculars. Unlike other studies that have shown Dall's porpoise are attracted to vessels (Turnock *et al.* 1995), I found they moved randomly with respect to the vessel. Similarly, I did not observe the avoidance behaviour reported for harbour porpoise (Barlow 1988, Polachek & Thorpe 1990) given that they also showed random swimming direction with respect to the vessel. Species present typically swam slower than the speed of the ferry (e.g. 5.1 $km \cdot h^{-1}$ for Dall's porpoise, Jefferson 1987; 3.2 $km \cdot h^{-1}$ for harbour porpoise, Otani *et al.* 2000) and should not have biased the population estimates (Burnham *et al.* 1980).

The fourth and final assumption concerns the distance and angle measurement error. I avoided heaping errors (measurements rounded to convenient values such as whole numbers) by not rounding angles and distances (Buckland *et al.* 1993, Jefferson 1996), and increased the accuracy of distance measurements due to the height of the survey platform from the water (16.7 metres above the waterline on the *Queen of New Westminster*, and 16.5 metres on the *Queen of Alberni*). High platforms should result in observing more animals than low platforms (Polachek & Smith 1989). I also standardized measurements by using a single observer, reticle and compass binoculars, and surveying only during optimal conditions (Beaufort sea states less than three, and in the absence of fog, glare, or other meteorological conditions that obscured visibility).

A question arising from this type of non-traditional survey design using a fixed-route platform is whether relative counts are preferable to distance sampling. In my case, I sampled the same transect line 143 times over one year, meaning that counts could be compared to each other using relative indices over time. The main disadvantage of distance sampling is through truncation of perpendicular sighting distances to fit a model, which results in some observations being effectively lost from the dataset. However, the advantage of distance sampling over relative counts is that density estimates can be compared not only over time, but also to other areas.

Tidal currents have been found to affect the distribution of marine mammals (Taylor & Dawson 1984, Gaskin & Watson 1985). However, in my study, tidal state did not affect the sightability of species present. Tidal amplitudes and currents in most of the Strait of Georgia are relatively weak, with currents usually not exceeding 1.0 m/s (LeBlond 1983).

Marine Mammal Density and Abundance

Abundance estimates for all species of marine mammals were generally highest in spring with a second, smaller peak in fall. These peaks in marine mammal abundance coincided with seasonal physical and biological factors in the Strait of Georgia and Fraser River system. Maximum flows from the Fraser River occur from April to June during peak snowmelt from interior mountain ranges, and in late fall due to storms and heavy precipitation along the coast (Thomson 1981, Northcote & Larkin 1989, Yin *et al.* 1997b). Nutrient entrainment and primary production parallel river flows (Stronach 1981, Harrison *et al.* 1983, Yin *et al.* 1997a, Yin *et al.* 1997b).

The plume boundaries are very productive, and phytoplankton at the edge of the plume receive a continual supply of nutrients due to entrainment (Harrison *et al.* 1991). The timing and duration of the spring phytoplankton bloom are determined by peak runoff from the Fraser River, tides, and strength and direction of the prevailing winds (Thomson 1994, Yin *et al.* 1997a). Response to increased primary production is manifested in the population biomass of higher trophic levels (Abrams 1993). In the Strait of Georgia, zooplankton production depends mainly on the timing of the spring bloom (Yin *et al.* 1996), which in turn has significant implications for food availability for juvenile fish and other higher trophic levels in the Strait (Yin *et al.* 1997c). Greater abundances of fish and zooplankton are found in the plume area compared to surrounding waters (St. John et al. 1992, Beamish & Neville 1995).

While it is difficult to characterize abundance patterns of marine mammals in the Strait of Georgia from only one year of data, my study is probably representative of a typical year in the Strait. Sea surface temperature (SST) and salinity in 2000 were near the long-term averages (DFO 2001), and SST in 2001 was also close to average (Entrance Island lighthouse data 2002). Phytoplankton blooms occurred in March (and at a lower level in September) in 2000 & 2001, and were near historical levels, following an unusually high bloom in 1999 (Dr. Jim Gower, pers. comm., April 4, 2002).

The abundance of zooplankton and some fish species may have been a bit higher compared to previous years. Euphausiid (*Euphausia pacifica*) size and biomass increased in 2000 (DFO 2001), and eulachon (*Thaleichthys pacificus*) were slightly more abundant but had later than normal spawning times (Hay & McCarter 2000). Coho (*Oncorhynchus kisutch*), chinook (*O. tshawytscha*) and chum (*O. keta*) salmon smolt abundance also increased in 2000 (DFO 2001), and the Strait of Georgia herring stock increased in both 2000 and 2001 and remained near historically high levels of abundance (DFO 2002).

Dall's porpoise

Dall's porpoise were present year-round in the Strait of Georgia. While there may be resident animals in this area, differences in seasonal abundances suggest that groups may be moving in and out of the Strait. In a photo-identification study of Dall's porpoise in Puget Sound, Miller (1989) continually identified new individuals over 13 months and had little consistent resighting, suggesting a transient population. Dall's porpoise have been reported to move inshore and southward in winter, and offshore and northward in summer (Pike & MacAskie 1969, Leatherwood *et al.* 1982). A radio-telemetry study of a single Dall's porpoise reported offshore movement in summer, and inshore into Haro Strait and the Strait of Georgia in winter and spring (Hanson & DeLong 2001). Animals in the Strait of Georgia may be present in higher numbers in spring and winter due to increased prey availability, and may migrate to other areas to the north or offshore in summer and fall.

Densities of Dall's porpoise ranged from 3.5 animals/100 km^2 during fall to 17.5 animals/100 km^2 in spring. Summer estimates (9.4 animals/100 km^2) were higher than those reported from aerial surveys flown in August 1996 by Calambokidis *et al.* (1997a) in U.S. and Canadian inshore waters (U.S. Juan de Fuca Strait: 6.3 animals/100 km^2; San Juan Islands: 3.5 animals/100 km^2; Canadian Juan de Fuca Strait: 4.7 animals/100 km^2; and Gulf Islands: 8.6 animals/100 km^2). No Dall's porpoise were observed during those surveys in the Strait of Georgia, suggesting either a temporary or general avoidance of Dall's porpoise to that region (Calambokidis *et al.* 1997a). Dall's porpoise have been reported as common in areas to the north (Johnstone Strait) and south (Puget Sound) of the Strait (Pike & MacAskie 1969, Everitt *et al.* 1980, Jefferson 1987, Osborne *et al.* 1988). Cowan (1944) and Pike & McAskie (1969) reported that Dall's porpoise rarely occur in the Strait of Georgia, however results from my study show that it is an important area for Dall's porpoise on both a seasonal and annual basis.

Group sizes ranged from 1 to 16 animals, and were similar to values reported by others. Mean group size varied seasonally, with the largest groups seen in winter (mean = 4.3 animals per group, SE = 0.83). Osborne *et al.* (1988) reported that Dall's porpoise in inshore waters form groups of between 2 to 15 individuals, while Jefferson (1988) stated that Dall's porpoise groups range from 1 to 12 individuals. Mean group size in Puget Sound was 3.9 animals (Miller 1989). Larger groups may represent a temporary association of several smaller groups.

The higher abundance of Dall's porpoise in spring coincides with peak flows from the Fraser River that results in a maximum plume size in late spring and early summer, and high primary productivity at the plume boundary (Harrison *et al.* 1991, Harrison & Yin 1998). Dall's porpoise feed opportunistically on small schooling fish and squid (Stroud *et al.* 1981, Jefferson 1988, Osborne *et al.* 1988). The plume acts as a dispersal mechanism for juvenile salmonids, and all five species of Pacific salmon (*Oncorhynchus* spp.) occur in high densities in late spring in the Strait of Georgia (Healey 1978, Healey 1980, Hay *et al.* 1989a, Haegele 1997). Large abundances of other fish species in the Strait of Georgia are also influenced by the runoff and plume of the Fraser River (St. John *et al.* 1992, Beamish & Neville 1995). Pacific herring (*Clupea harengus*) are the most abundant migratory fish in the Strait, with large numbers of adults congregating near spawning areas in March (Stoker *et al.* 1985, Hay & Kronlund 1987, Hay *et al.* 1989a, Hay *et al.* 1989b, Haegele 1997). Herring have been observed feeding on zooplankton in the Fraser River plume (St. John *et al.* 1992).

Dall's porpoise showed a second smaller peak in abundance in winter that coincided with the arrival of adult herring into the Strait of Georgia in late fall and early winter, where they form dense groups prior to spawning (Hourston & Haegele 1980, Ketchen *et al.* 1983, Haist & Stoker 1985, Hay *et al.* 1989a). I observed some marine mammal species, including Dall's porpoise, feeding on Pacific herring in the late fall.

Distribution of Dall's porpoise was similar across seasons, and showed a preference for deeper water. This was expected as Dall's porpoise are epi- and mesopelagic feeders (Stroud *et al.* 1981). Osmek *et al.* (1997) found that Dall's porpoise exhibit a preference for deeper waters in inshore areas of southern British Columbia and Washington. In winter, I found they were only present over deeper waters, which may reflect the seasonality of prey availability. However, in spring I sometimes observed Dall's porpoise in shallower water near the northern tip of Gabriola Island, which coincided with pink (*O. gorbuscha*) and chum (*O. keta*) salmon smolts congregating in nearshore areas prior to dispersing into deeper waters of the Strait (Hay *et al.* 1989a).

Harbour porpoise

Harbour porpoise were present year-round in low numbers in the Strait of Georgia. Abundance estimates did not show significant differences over time, due possibly to the low number of sightings and the corresponding high coefficient of variation. Harbour porpoise were once considered common in inshore waters of British Columbia and Washington (Scheffer & Slipp 1948), however populations may be decreasing in recent years (Everitt *et al.* 1980, Cowan 1988, Osborne *et al.* 1988, Calambokidis & Baird 1994). Harbour porpoise are considered vulnerable to human activities, especially pollution, entanglement in fishing gear, and heavy vessel traffic (Calambokidis & Baird 1994, Baird & Guenther 1995, Leatherwood *et al.* 1984). Harbour porpoise may also possibly avoid the Strait of Georgia due to vessel traffic. It is a major waterway for commercial, industrial and recreational boat traffic (Thomson 1981).

Estimates of harbour porpoise density were lower in my study than values reported elsewhere. Density estimates in the summer (0.48 animals/100 km^2) were lower than estimates from aerial surveys for harbour porpoise in August 1996 in the Strait of Georgia (4.2 animals/100 km^2) and surrounding regions (U.S. Juan de Fuca Strait: 18.6 animals/100 km^2; San Juan Islands: 22.1 animals/100 km^2; Canadian Juan de Fuca Strait: 23.6 animals/100 km^2; and Gulf Islands: 16.1 animals/100 km^2; Calambokidis *et al.* 1997a). My estimate was also substantially lower than that calculated by Raum-Suryan & Harvey (1998) in the San Juan Islands (126 animals/100 km^2), or by Barlow (1988) off the west coast of Washington (109 animals/100 km^2).

Group size was difficult to estimate because harbour porpoise are small, inconspicuous animals (Barlow 1988, Gaskin 1992), but appear to be similar to values reported in other studies. I observed harbour porpoise in groups of 1 to 11 individuals, which is similar to Leatherwood *et al.* (1984), who reported harbour porpoise in the north Pacific traveled in groups of up to 10 individuals. Mean group size in my study ranged from 1.0 – 3.3 individuals, similar to Flaherty & Stark (1982) who reported a mean group size of 3.1 – 3.9 individuals in inshore waters of Washington, and to Raum-Suryan & Harvey (1998) who found harbour porpoise traveled in mean group size of 1.9 individuals. Overall, group size was similar to areas of higher density even though the Strait of Georgia may have lower densities of harbour porpoise than surrounding areas.

Harbour porpoise feed on a variety of small schooling fish and squid. Stomach contents of animals incidentally caught in a salmon gillnet fishery on the west coast of Washington showed harbour porpoise fed on herring, squid (*Loligo opalescens*), smelt (Family Osmeridae) and cod (Family Gadidae), with salmon in smaller amounts (Gearin &

Johnson 1990). Eulachon is a small smelt that spawns in the lower reaches of the Fraser River from mid-March to May (Hay *et al.* 1989a), while herring are feeding on zooplankton in the river plume during peak flows (St. John *et al.* 1992). Harbour porpoise would likely take advantage of outgoing salmon smolts in the Strait of Georgia during the period of high flows from the Fraser River in the spring, as this coincides with peak harbour porpoise abundance estimates in the area. Harbour porpoise calves feed on euphausiids once weaned (Smith & Read 1992), which may in turn be dependent on increased zooplankton densities associated with the plume and high flows from the Fraser River (Healey 1980, St. John *et al.* 1992, Yin *et al.* 1997c).

Large-scale shifts in distribution have been reported for harbour porpoise on the east coast of North America (inshore and northern movements in the summer, and offshore and southern movements in winter; Neave & Wright 1968), but not on the west coast (Barlow 1988, Gaskin 1992). Local and seasonal movements of harbour porpoise on the east coast of Canada have been related to the availability of schools of herring, their primary prey species (Smith & Gaskin 1974, Gaskin 1992).

Harbour porpoise did not change their distribution by season, and were almost always observed over deep water (greater than 200 metres), with the exception of a few individuals sighted over depths of less than 100 metres near the Tsawwassen ferry terminal. Osmek *et al.* (1997) found harbour porpoise favoured deeper water in inshore areas of southern British Columbia and Washington. In the San Juan Islands, Raum-Suryan & Harvey (1998) found harbour porpoise occurred more frequently in depths greater than 125 metres as opposed to shallower water. Herring can be found at depth in high densities in the Fraser River plume during the day, especially in spring months when river flows are high (St. John *et al.* 1992). Euphausiids migrate vertically in the water column, residing in deep water during the day (Levy *et al.* 1996). Distribution of harbour porpoise may reflect the presence of prey species in deep water.

Harbour seals

The harbour seal population has recovered after past commercial kills and control programs, and has now stabilized (Olesiuk 1999). While density and abundance estimates showed seasonal changes, they were high year-round throughout the Strait of Georgia. Line-transect studies have not previously been conducted for harbour seals in this area. Osmek *et al.* (1997) found higher sighting rates of harbour seals in the San Juan and Gulf Islands compared to the Strait of Georgia and Juan de Fuca Strait.

Most of the seals observed in my study were hauled out because the ferry route passed by Entrance Island, a major haulout site for seals and sea lions. Harbour seals form large groups when hauled out, but disperse and become solitary in the water (Bigg 1969). Groups observed hauled out at Entrance Island ranged between 6 and 62 individuals. The vast majority (92%) of harbour seals observed in the water were solitary animals. One group of 22 animals was observed in late fall when large numbers of herring were present in the area.

Despite evidence for seasonal changes in abundance, the high numbers of harbour seals over all seasons reflects a non-migratory population. However, harbour seals do show local movements associated with food, reproduction and season (Bigg 1969, Olesiuk 1990). Studies of radio-tagged harbour seals showed movements primarily among haulout sites (Pitcher & McAllister 1981). Counts of seals hauled out on land differed by season, with reduced numbers sighted in fall and winter. Few or no seals were observed hauled out when the tide was high. Morning ferry trips in fall and winter passed Entrance Island at high tide, which may explain the apparent seasonality in haulout behaviour and abundance estimates. Olesiuk (1999) found that 61% of seals were hauled out at low tides, which suggests the abundance estimates could be 2.5 times larger than what I calculated. Abundance estimates and numbers of seals sighted hauled out were lowest in winter, suggesting that seals are moving to other areas in this season.

Harbour seals feed on a wide variety of prey species in the Strait of Georgia, such as Pacific hake (*Merluccius productus*) and herring (Olesiuk *et al.* 1990, Olesiuk 1993). Hake is the most abundant resident fish in the Strait (McFarlane & Beamish 1985, Hay *et al.* 1989a), and reside in deep water and spawn in spring in the south-central Strait near Halibut Bank (McFarlane & Beamish 1985). Hake are consumed by harbour seals largely from April to November, after spawners have dispersed to shallower nearshore water (Olesiuk *et al.* 1990). Herring are mainly consumed from December to March, which coincides with the presence of adult herring prior to spawning (Olesiuk *et al.* 1990). Large groups of harbour seals were observed in late fall during this study when herring was abundant in nearshore areas. Adult salmon comprise 4% of the diet of harbour seals in the Strait, but may be important seasonally as they return to their river spawning grounds (Olesiuk *et al.* 1990).

The distribution of harbour seals did not change over the year. Seals were distributed over all depths, but were mainly sighted in shallower water near shore. This likely reflects their connection to haulout sites, especially since harbour seal distribution was clumped around the northern tip of Gabriola Island, near several haulouts. Osmek *et* *al.* (1997) found significantly higher sighting rates of harbour seals in nearshore shallow waters as compared to deeper water. Harbour seal sighting rates were highest in areas with haulout sites nearby (Osmek *et al.* 1997).

California sea lions

After a long hiatus from B.C. waters due to overhunting, California sea lions were first resighted in 1969 at Race Rocks (Cowan 1988), and have been increasing off southeastern Vancouver Island since the 1970's (Bigg 1988a, Olesiuk 1990). Male California sea lions migrate from California, arriving in the fall and peaking in abundance by spring (Bigg 1988a, Olesiuk 1990).

I sighted California sea lions year-round in the Strait of Georgia. The abundance estimates did not peak in spring, nor did they show any significant differences between seasons. However, few were sighted in the Strait of Georgia during summer. Similarly, small numbers were present in Puget Sound year-round (NMFS 1994). Counts of California sea lions hauled out were very seasonal, and did not follow the same patterns as the abundance estimates of animals observed in the water. Hauled out animals were observed in high numbers during spring, with only small numbers counted hauled out over the rest of the year. The only California sea lions observed in the summer were hauled out at Entrance Island, and may have been sub-adult males that do not return to California to mate.

The majority of California sea lions that I saw were hauled out at Entrance Island with group size ranging from 2 to 52 individuals. California sea lions were often sighted with Steller sea lions, but were always observed in areas separate from harbour seals.

Group sizes of California sea lions in the water were smaller, ranging from one to seven, with 77% single animals.

The primary prey of California sea lions in the Strait of Georgia are hake, walleye pollock (*Theragra chalcogramma*), herring, dogfish (*Squalus acanthus*), and salmon (Bigg 1988a, Olesiuk 1990), all of which are abundant in the Strait (Hay *et al.* 1989a). The high abundance of herring in the spring (Haist & Stoker 1985, Hay *et al.* 1989a, Haegele 1997) coincided with the high numbers of California sea lions sighted at Entrance Island.

California sea lions were mainly distributed around the northern tip of Gabriola Island, close to haulout sites. They were also distributed in smaller numbers over the deeper waters of the Strait. Pacific hake and walleye pollock are deep-water species (Hay *et al.* 1989a), and California sea lions sighted over deeper water were most likely foraging individuals.

Steller sea lions

Steller sea lions seen in the Strait of Georgia peaked in the spring and likely migrated south from breeding colonies in northern British Columbia and southeast Alaska (Bigg 1985, Bigg 1988a, Cowan 1988). Bigg (1985) reported that the number of Steller sea lions seen in British Columbia was larger in the winter than in the summer, although in my study there were no significant differences between abundance estimates for summer and winter, and no animals were observed hauled out in the winter. Steller sea lions have not been observed in Puget Sound during August (Steiger & Calambokidis 1986).

Steller sea lions were most frequently observed hauled out with California sea lions at Entrance Island. Group size of hauled out individuals ranged from 1 to 45 individuals.

Steller sea lions observed in the water were primarily solitary (93%) or in small groups of up to 4 individuals.

Observations of Steller sea lions hauled out on land were highly seasonal, and like the abundance estimate of animals observed in the water, peaked in spring. The only Steller sea lions observed in winter were animals in the water. The small numbers of Steller sea lions sighted both in the water and hauled out in the summer may be sub-adult males not returning to northern rookeries to mate.

Steller sea lions feed primarily on gadoids, herring, eulachon, and squid (Fiscus & Baines 1966). Important prey species off southeastern Vancouver Island are herring and hake (McFarlane & Beamish 1985, Bigg 1988b). Steller sea lions have also been observed feeding on eulachon spawning at the mouth of the Fraser River in the spring (Bigg 1988b).

Steller sea lions were widely distributed over all depths and distances to shore, and were frequently observed over deep water in the central Strait. Hake and other deep water species likely affect the distribution of Steller sea lions. I observed sea lions actively foraging on several occasions, and often saw them consuming prey at the surface over deep water.

Other Species

Pacific white-sided dolphins are abundant in British Columbia offshore waters, and are seen regularly inshore (Leatherwood *et al.* 1984, Osborne *et al.* 1988). There are conflicting reports of seasonal trends in abundance, with Everitt *et al.* (1980) reporting Pacific white-sided dolphins more common inshore during winter, and Osborne *et al.* (1988) stating that they are more common inshore during summer and fall. In my study, I only saw Pacific white-sided dolphins on four occasions in the Strait of Georgia, none of which were during the winter.

Group sizes of Pacific white-sided dolphins in coastal waters commonly range from 5 to 15 individuals, with offshore groups occasionally comprising over 1,000 dolphins (Osborne *et al.* 1988, Stacey & Baird 1991). Group sizes in my study ranged from 7 - 52 individuals.

Pacific white-sided dolphins feed primarily on small schooling fish and squid in the epi- and mesopelagic zones. Important prey species in this area are herring, salmon, cod, shrimp (Order Decapoda) and capelin (*Mallotus villosus*; Heise 1997). Large numbers of herring and salmon in the Strait of Georgia may be responsible for the occasional visits by foraging groups.

I observed sixteen groups of killer whales from spring to fall, but none during winter. Group sizes of killer whales observed in my study ranged from 1 to 8. Ford *et al.* (1998) reported that killer whales occur during all months of the year in inshore waters. Southern residents are sighted mainly from May to October off southeastern Vancouver Island, and transients can be found sporadically in inshore waters year-round.

Both resident and transient killer whales occur in the Strait of Georgia (Ford *et al.* 1994). Resident groups in this area are J, K, and L pods; the range of J pod during summer and fall is confined to the Strait of Georgia and Puget Sound, while K and L travel throughout the area (Bigg 1982). Transient killer whales feed mainly on harbour seals (Ford *et al.* 1994). Visits by transient whales may reflect the abundant harbour seal population in the Strait. Resident killer whales are salmon specialists, with other species such as herring, rockfish (*Sebastes* spp.) and flatfish (Order Pleuronectiformes) taken in small amounts (Ford *et al.* 1998). Killer whales were most commonly observed in the summer and fall, coinciding with the return of migrating adult salmon to spawning rivers.

I observed two species of baleen whales – gray and minke whales. Two sightings were single gray whales, one in spring and one in summer. Gray whales migrate along the coast of British Columbia between their summer feeding grounds off Alaska and their winter breeding grounds off Mexico, with a small population residing on the west coast of Vancouver Island in the summer (Darling 1984). Gray whales have been reported to enter inshore waters in small numbers (Osborne *et al.* 1988). I observed one minke whale in the spring. Minke whales have been observed in inshore waters of British Columbia, and although they show peaks in abundance from July to September, they are present year-round (Everitt *et al.* 1980, Osborne *et al.* 1988). Minke whales feed primarily on herring and sandlance (*Ammodytes hexapterus*) in this area (Osborne *et al.* 1988, Hoelzel *et al.* 1989). My observation of a minke whale coincided with a peak in herring abundance and high flows from the Fraser River.

Consumption

The Strait of Georgia appears to be an important feeding area for marine mammals supporting both resident (e.g. harbour seals) and seasonal populations (e.g. sea lions). The large seasonal influx in marine mammals (particularly sea lions and Dall's porpoise) coincides with the return of spawning herring and eulachon in the spring. Resident populations of hake and cod appear to support marine mammals at other times of the year, while salmon are significant sources of energy in spring (smolts) and fall (adults).

The estimates of consumption by marine mammals within my study area are gross approximations derived from simple principles. Nevertheless, they provide a general sense of the overall importance of the Strait of Georgia in meeting the energy needs of marine mammals. The largest consumers of all the marine mammals I observed appear to be pinnipeds. However, the consumption estimates calculated from the abundance estimates for pinnipeds are a minimum because a proportion of their populations are hauled out at any given time. Actual numbers of harbour seals that feed in my study area could be as much as 2.5 times larger due to seals hauled out at low tide during the surveys (Olesiuk 1999). This may also hold true for sea lions, although haulout correction factors have not been determined for sea lions in this area – so again the consumption estimates should be viewed as minimums. The high consumption by harbour seals in the Strait can largely be attributed to their high numbers relative to other species. The high consumption by relatively low numbers of sea lions on the other hand reflects the fact that they are mostly mature males with large body size and associated energy needs.

The Strait of Georgia supports a high density of marine mammals compared to open ocean ecosystems (see Pauly *et al.* 1996). Marine mammals have likely adapted to take advantage of seasonally abundant prey, and are probably an integral part of this marine ecosystem and are major consumers at many trophic levels. Understanding when and how much food marine mammals require aids in evaluating their potential impact on prey populations and unraveling the complex ecological interactions that occur between predators and prey (Bowen 1997). Further effort is required to obtain detailed quantitative diet compositions of marine mammal species present in order to fully appreciate consumption patterns in the Strait of Georgia.

CONCLUSIONS

The Strait of Georgia is used by at least nine species of marine mammals. Most show some seasonal differences in abundance, with peak numbers primarily occurring in the spring and fall. The seasonal shifts in numbers appear to reflect seasonal changes in prey availability that are related to the return of spawning herring and eulachon in the spring, and spawning salmonids in the fall. These in turn are related to high primary productivity found in the Strait of Georgia. Estimates of consumption by marine mammals illustrate the importance of the Strait as a feeding area. Future studies detailing prey availability, as well as oceanographic variables, would assist in determining mechanisms affecting the seasonality of marine mammal abundance.

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PERSONAL COMMUNICATIONS

Dr. J. Gower. Institute of Ocean Sciences, Sidney, B.C., Canada. April 4, 2002.