Use of Multiple Methods to Estimate Walrus (*Odobenus rosmarus rosmarus*) Abundance in the Penny Strait–Lancaster Sound and West Jones Sound Stocks, Canada

Robert EA Stewart[1], Erik W Born[2], J Blair Dunn[1], William R Koski[3] and Anna K Ryan[1]

[1] *Department of Fisheries and Oceans, Freshwater Institute, 501 University Crescent, Winnipeg, Manitoba R3T 2N6, Canada*
[2] *Greenland Institute of Natural Resources, P.O. Box 570, DK-3900 Nuuk, Greenland*
[3] *LGL Limited, environmental research associates, 22 Fisher Street, King City, Ontario, L7A 1B6, Canada*

ABSTRACT

Surveys to estimate walrus abundance at terrestrial haulout sites in the Penny Strait–Lancaster Sound (PS-LS) and West Jones Sound (WJS) stocks were conducted in 1977 and 1998–2009. The Minimum Counted Population (MCP) was similar in 1977 (565) to recent years (557) for the PS-LS stock. The MCP for the WJS stock was higher in recent surveys (404) than in 1977 (290). Regression analysis of MCP and density (number of walrus divided by number of haulouts surveyed) showed no significant trends over time. We also calculated bounded count estimates for comparison. Finally, we used broad-scale behavioural data to estimate the proportion of the total stock that could be considered countable, to produce two adjusted estimates. We selected recent surveys with good coverage and ignored adjusted estimates that were lower than MCP. For the PS-LS stock, the adjusted MCP (with 95% CL) was 672 (575–768) and 727 (623–831) walrus in 2007 and 2009, respectively. For WJS, the best estimates were the adjusted MCP of 503 (473–534) in 2008 and the adjusted bounded count of 470 (297–1,732) in 2009. While both stocks appear to have remained stable over three decades, differences in survey coverage and possible differences in walrus distribution make precise population estimation difficult.

INTRODUCTION

Atlantic walrus (*Odobenus rosmarus rosmarus*) occur in Canada in a number of largely discrete stocks (Born et al. 1995, DFO 2002, COSEWIC 2006, Stewart 2008). In the Canadian Arctic Archipelago there are three recognized stocks (NAMMCO 2006, 2011, Stewart 2008): the Baffin Bay stock, the West Jones Sound stock and the Penny Strait–Lancaster Sound stock. Within the range of each stock, walrus are widely distributed in the open-water season when they are found at sea and on ice or land in numbers from 1 to over 1,000. This widely spread but clumped pattern is a challenge to quantitative survey design. However, censusing haulouts is a well-established technique (Buckland and York 2009) for estimating the population size of pinnipeds (e.g. harbour seals, *Phoca vitulina*: Olesiuk et al. 1990, Thompson et al. 1997, Jacobs and Terhune 2000, Boveng et al. 2003, Reder et al. 2003, Small et al. 2003, Gilbert et al. 2005, Cronin et al. 2007; northern elephant seals, *Mirounga angustirostris*: Lowry et al. 1996, Lowry 2002; and California sea lions, *Zalophus californianus*: Lowry 1999). It has also been used to survey sea otters (Enhydra lutris; Doroff et al. 2003) which occur in aquatic groups or 'rafts'.

Knowing the numbers of walrus in each stock is important for co-management of a species that sustains culturally and economically important harvests. Walrus are harvested by Inuit in Canada and Greenland, and by sports hunters in parts of Canada (Born et al. 1995, DFO 2002, Priest and Usher 2004). Herein, we report on surveys designed to exploit the clumped behaviour of walrus by counting walruses primarily at haul out sites. This approach is similar to the direct enumeration of populations to determine the minimum number alive, the sum of the number enumerated in one sample and those that must have been alive at the same time but were not included in the first sample (Krebs 1966). Krebs used marked animals to confirm that animals were not counted more than once. We did not have tagged animals, but we used this general approach to determine the Minimum Counted Population (MCP) of walruses in West Jones Sound and Penny Strait–Lancaster Sound areas. We compare data obtained from aerial and ground surveys from 1998–2009 to data from 1977 and use the number of haulout sites examined to generate an index to assess population trends. We also explore several methods to adjust counts for availability and detection bias to estimate absolute abundance.

METHODS

The survey area included the known ranges of the Penny Strait–Lancaster Sound (PS-LS) and West Jones Sound (WJS) stocks (NAMMCO 2006, Stewart 2008; Fig. 1). We identified former, current, and potential terrestrial haulout sites, where walrus traditionally come ashore to rest, using the scientific literature (e.g., Born et al. 1995), Inuit *qaujimaningit* or IQ (e.g., community consultations, Inuit participants) and other information (e.g., long-time Arctic researchers). Identified sites and intervening coastlines and ice edges were examined from aircraft multiple times each year during the open-water season (August) when maximum numbers were expected to occur based on IQ. Seasonal timing of surveys was adjusted according to previous surveys and subject to weather. The coastlines of the Arctic islands comprise an area of several tens of thousands of kilometres. Weather and logistics in the area are often challenging and sometimes unpredictable. When time and weather constrained surveys, emphasis was placed on examining previously known haulouts (Jacobs and Terhune 2000), even if there had been no walrus seen there for several seasons. New haulouts were added to the survey as they were discovered. Additionally, surveys were conducted from local boats in 1998, 1999 and 2001 along the north shore of Jones Sound, covering only small parts of the walruses actual range.

Data were collected without regard to stock boundaries but have been analyzed as separate stocks as the more precautionary approach (Taylor 1997, Taylor and Dizon 1999). Although Stewart (2008) considered movement of walrus west through Hell Gate and Cardigan Strait unlikely, we included Arthur Fjord among WJS sites.

1977 Surveys

The 1977 survey area included all coastlines and ice edges of Jones and Lancaster Sounds and adjacent waters, approximately bounded by 74–77° N and 87–101° W (Fig. 1). Surveys were conducted in April, June, July and August 1977. Only the August surveys, which had the highest counts (Davis et al. 1978), are presented here because they were conducted in the same month as the more recent surveys.

Aerial surveys were conducted using a Cessna 337 fixed-wing aircraft with one observer in the co-pilot position, facing the shoreline and the other behind the pilot. Most surveys were flown at 150 m above sea level (ASL) at approximately 280 kph. Survey track lines were automatically recorded onto a computer from an ONTRAC VLF navigation system. Haulouts were photographed opportunistically using a vertically-mounted camera in a camera port and a 70 mm Hasselblad camera with Ektachrome 200, colour slide film. Numbers of walrus in photographs were counted by one observer (WRK) from 20×25 cm custom prints overlaid with clear acetate. As each animal was counted, the acetate was marked with a dot to ensure all animals were counted only once.

1998–2009 Surveys

The survey area included the same coastline as in 1977, but extended farther east in both Jones and Lancaster Sounds (Fig. 1). The survey platform varied among years: a Bell 206L helicopter was used in 1998–2007, supplemented with a fixed-wing Twin Otter in 1999, and only the Twin Otter was used in 2008–2009. No surveys could be conducted in 2002 due to severe weather. Helicopter surveys were conducted with a target altitude of ~150 m ASL ~185 kph, but the aircraft slowed down to facilitate counting at haulouts. Surveys in the Twin Otter were flown at 200–250 m ASL and at a speed of ~210 kph, approximately 500 m from the shoreline. Observers sat in the left front and right rear seats in the helicopter. When present, a third observer occupied the left rear seat. In the Twin Otter, most surveys were flown with the data-logger/navigator in row 2/left and primary observers in row 6/right and row 7/left. These positions are least obstructed by the aircraft and engine exhaust which causes distortion in photographs. Additional observers sat in row 2/right. When approaching large numbers of walrus, one observer would move to the appropriate side to maximize the number of photos taken.

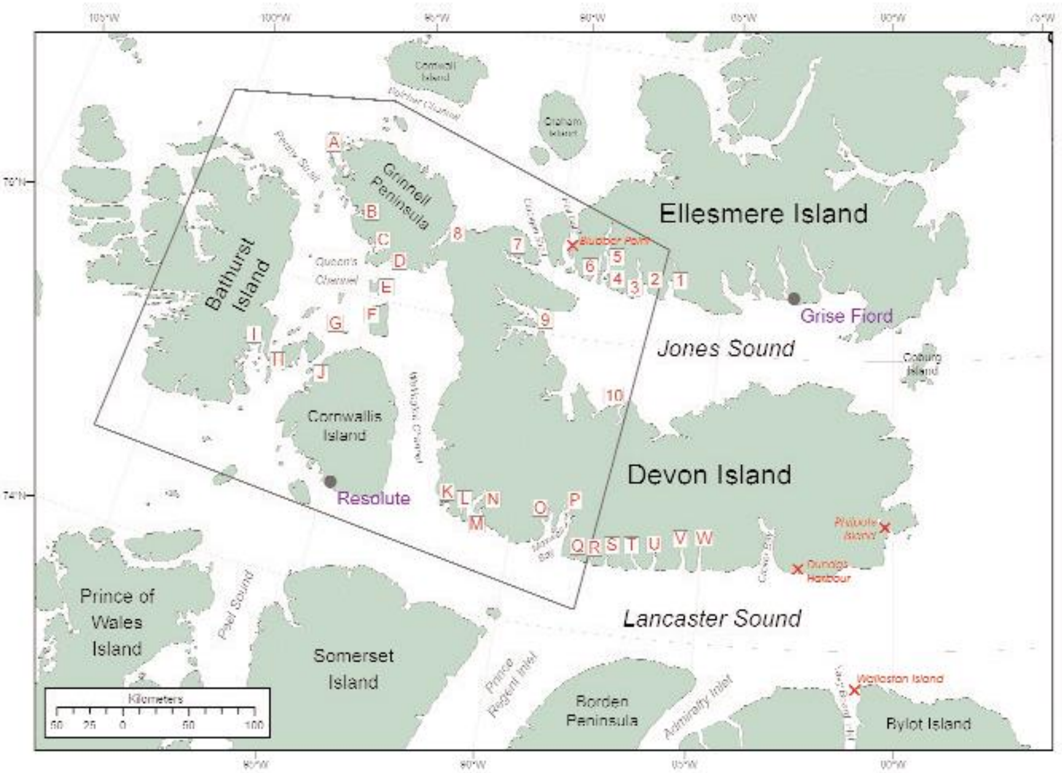

Fig 1. *Walrus survey area in 1977 (polygon) and haulout sites surveyed from 1998 to 2009 in the West Jones Sound area (numerals) and the Penny Strait–Lancaster Sound area (capital letters). See the Map Key in tables 3 and 4. X indicates a haulout that appears to have been abandoned (see text for details).*

In 1997, 1998 and 1999, a hand-held GPS was used in conjunction with topographical maps to record locations and sightings. Since 2000, a designated data-logger used a lap-top computer linked to a GPS to record the survey tracks and to enter sighting data; watches and digital cameras were synchronized to the GPS time. When walruses were seen, the numbers were estimated independently by each observer and oblique aerial photographs were taken whenever possible. Colour 35 mm slides (Nikon FM2 and Pentax SP cameras and zoom lenses, Ektachrome 200 film) were scanned to produce digital versions; digital photographs (Olympus E10 and Canon EOS-30D, EOS-40D, Rebel and S2 IS cameras, zoom lenses) were obtained as the technology became available. As back-up, in addition to relaying sighting information to the data-logger, all observers recorded their sightings in notebooks with accurate times.

Surveyors in helicopters often landed near the haulout and approached the walruses on foot. Each observer made an independent ground count and counts were compared at the site. When there was wide divergence in the estimates (>10%), each observer made a second count and observers again compared notes. If a single count diverged, it was deleted from the average. If there was high variation among all counts, all were retained and averaged to produce a final ground count. During boat surveys, visual estimates and photographs were obtained similar to during aerial surveys, including opportunistic sightings at sea.

Data analysis

Data included visual estimates from aircraft and surface-level observers, as well as aerial and surface-level photographs. Photographs from each encounter were examined in Adobe PhotoShop® CS2 and modified in size, contrast and brightness to produce the clearest image for counting. Coloured dots were super-imposed on each enumerated walrus and the image was re-examined for missed animals (Fig. 2).

Table 1. Maximum number of tagged walruses that were hauled out simultaneously used to estimate HO_{max}. Only studies with > 5 tags active concurrently were used. Variance is p(1-p)/n-1 (Zar 1999).

Location	Year	Season	Number of tags (dry/total)	Maximum Proportion Hauled out	Source
Alaska	1990	summer	5/6	0.833	Hills 1992
Svalbard	2003	August	6/9	0.667	Lydersen *et al.* 2008, C. Lydersen pers. Comm. 2011
	2004	August	9/11	0.818	
Alaska	2004	April	8/12	0.667	Udevitz *et al*. 2009 M. Udevitz pers. comm. 2011
	2006	April	17/24	0.708	
NE Greenland	2009	August	7/8	0.875	Born, unpublished
Overall Weighted average			52/70	0.743	
Variance				0.003	
Coefficient of Variation				0.07	

Fig. 2. *a) Original walrus survey oblique photo and b) cropped photo with contrast and bright- ness adjusted and counting marks over- lain. Green dots mark calves. (Photo credit: R. Stewart).*

Regression analysis (SigmaStat® v 3.11) was used to assess between-observer visual estimates, between-observer photographic counts and between-method counts (visual/photographic). Zero counts were excluded. Two pairs of visual observation data were available for aerial observers.

There were too few surface level observations to permit statistical comparisons. Two subsets of photographs were examined independently by three observers (REAS, EWB, AKR). We also conducted one within-observer (REAS) blind replicate on a subsample of photos. The original intention had been to collaboratively compare results when we had chosen different images or had very different counts from the same images, but congruence was sufficient (see Results) to use the counts from only one observer (REAS) who processed all the other images. Visual estimates were assessed against these photo-counts. These analyses indicated there was little variation among observers but photographic counts were superior to visual estimates. Although not statistically compared, aerial observations tended to be higher and had smaller discrepancies among observers than observations made from shore. Therefore, when data of more than one type were available for a site, the preferred data were (1) aerial photo-count (2) aerial estimate (3) surface photo-count (4) surface estimate in order of priority. Ultimately, sufficient data were available from aerial photos except for one haulout site where a ground photo was used in the final analysis.

The direct enumeration of populations assumes the greatest number enumerated in a survey of all locations is a minimum estimate of that population. In the current application, walruses at one haulout were counted and that number was subsequently augmented by animals at other sites when we were confident they had not been included in the previous counts, based on the time and distance separating counts.

We measured the minimum swimming distance between the haulouts using MapSource®, rounded to the nearest 5 km and used Stewart's (2008) estimate of relocation speed of 40 km/24 h to omit counts that could have included walruses counted pre- viously that season. For each year, there are therefore two summary counts. The maximum year- ly count is the sum of all observations, without considering redundancy, and the final yearly count omits potentially duplicate counts.

Survey effort, defined as the number of haulout sites observed in a year, varied greatly over the course of the study. We adjusted the maximum yearly counts for the number of haulouts observed to facilitate comparisons over time. Haulouts were included in the measure of effort even if they did not contribute to the final count. Similarly, walrus seen at sea were included in the final count. We refer to this adjusted number as total walrus density (D_{Σ} = MCP/Effort). We used linear regressions to examine changes in MCP and D_{Σ} over years, using the entire data set and 1998-2009 only.

Adjusting Counts

MCP methods attempt to maximize counts in an effort to most closely approximate true population size. Nonetheless, final counts are negatively biased estimators of population size because not all the walrus in the population are hauled out or visible at the sea surface at the time of the survey. Maximizing MCP estimates therefore approximates an estimate of the available component of the population (Gilbert 1999, Pollock et al. 2004).

The vast majority of our observations are derived from counts at terrestrial haulouts and included animals near the haulout (Udevitz 1999). The availability of animals in the water near the haulout was considered to be similar to that of the animals fully ashore and unlike animals at sea several kilometres away. To distinguish counts made at haulouts from counts that include walrus at sea, we denote the former as MCP_{HO}, the latter as MCP_{sea}, and the sum as MCP. No adjustment has been made for walrus at sea and diving below the visible detection depth because at-sea observations were incidental to the coastal survey.

We applied several approaches to adjust counts for walrus not hauled out during the surveys. First, we attempted to use data from 3 satellite-linked transmitters (SPOT4 tags, Wildlife Computers 2006) deployed on 24 and 25 August 2004 at two haulouts. The tagged walruses provided data into November (average 88.7± 6.6 (SD) days) and stayed in West Jones Sound throughout the sampling period (Stewart 2008). Although it is preferred to obtain tag data concurrent with the survey period (Thompson et al. 1997, Gilbert et al. 2005) and over the whole survey area (Huber et al. 2001, Sharples et al. 2009), there were no tag data for the years of maximum counts. Counts are samples with unequal probabilities and, to adjust for varying haulout behaviour recorded by the tags, we used the Horvitz-Thompson estimator (Cochran 1977, Udevitz et al. 2009), with a variance estimator to allow for variable sample size (Stehman and Overton 1994). Ultimately, we demonstrated that the Horvitz-Thompson estimator required more days of data from more tags to avoid spurious, negative variance estimators (C. Schwarz pers. comm.) and we abandoned the Horvitz-Thompson analysis.

Secondly, although not applicable to all years, we applied the bounded count method (Robson and Whitlock 1964) where the estimated population size $\hat{N}$ is a function of C_{max} and C_{max-1}, the largest and second largest counts obtained from a series of surveys:

$$\hat{N} = C_{max} + (C_{max} - C_{max-1}) = 2C_{max} - C_{max-1} \quad [1]$$

The lower confidence limit is C_{max} and the upper CL at α is:

$$C_{max} + (1-\alpha)(C_{max} - C_{max-1})/\alpha \quad [2]$$

From [1], the proportion of the population counted is

$$P_{it} = \overline{C}_{it} / (2C_{max} - C_{max-1}) \quad [3]$$

where $\bar{C}_{it}$ is the mean of all replicate counts (Olesiuk et al. 1990, Thompson et al. 1997, Walker et al. 2008). Only haulouts seen in both replicates were used to calculate bounded counts.

Both MCP_{HO} and bounded counts assume there is some non-zero probability, however slight, that 100% of the population might be counted at one time, that is $\max\{P_{it}\}=HO_{max}=1$. We used diverse published tagging studies to obtain an independent estimate of the maximum proportion of a walrus population, the available or countable component (Gilbert 1999, Pollock et al. 2004) that could be expected to be hauled out at any one time (Table 1). The notable congruence of these estimates suggests in the absence of site- and time- specific estimates, the most general estimate of HO_{max} could be a robust estimate. The weighted average and variance, calculated as pq/(n-1) (Zar 1999), were used for HO_{max} = 0.74 (variance 0.003) to account for animals at sea. Variances of the bounded counts [Eq. 2] and estimat- ed HO_{max} were combined following Thompson and Seber (1994) for an estimated constant detectability:

$$\text{var}(\tilde{N}) = \frac{\text{var}(\hat{N}_{HO})}{HO_{max}^2} + \hat{N}_{HO}\frac{1-HO_{max}}{HO_{max}} + \frac{\tilde{N}^2}{HO_{max}^2}\text{var}(HO_{max}) \quad [4]$$

where $\tilde{N}$ is the estimated total population with variance var($\tilde{N}$), $\tilde{N}_{HO}$ is the bounded count estimate with variance var($\tilde{N}_{HO}$) calculated from the upper confidence limit [Eq. 2], HO_{max} is the maximum expected proportion of the total population ever hauled out (= 0.74) with variance HO_{max}) = 0.003 (Table 1). MCP was similarly adjusted using 0.74 and variances combined although the first term in [Eq. 4] became zero because MCP does not have a variance.

RESULTS

Multiple counts

Neither between-observer regressions nor the within-observer regression differed significantly from 1:1 correspondence ($P > 0.05$, Table 2). However, visual estimates did significantly underestimate photographic counts ($P<0.001$, Table 2, Fig. 3). Divergence from 1:1 correspondence began at group sizes between 30 and 40 (Fig. 3).

Survey Coverage

Initial surveys were based on IQ and scientific knowledge available in 1977 and 1998. Subsequently, walrus were found at locations for which we had no previous reports. These may have been newly occupied sites, representing a shift in distribution, or sites which had been used routinely by walrus but were not previously observed by us or others working in the area. We used GPS track data and written accounts to determine, retrospectively, whether 'new' haulouts had been seen on previous surveys. We recorded zero walrus for those sites when we were confident they had been observed sufficiently (appropriate altitude and visibility) and walrus would have been

Table 2. Regression analysis comparing estimates and counts between observers and between methods. A-E are observers (B2 is the replicate count of B). Bold denotes significance at P < 0.05.

	n	Adjusted R^2	Intercept (±1 SE)	*P* (≠ 0)	Slope (±1 SE)	*P* (≠ 1)
Visual Estimates						
A = fn(B)	51	0.97	-0.02 (0.68)	0.97	1.04 (0.02)	0.13
C= fn(D)	23	0.92	1.35 (1.76)	0.45	0.98 (0.06)	0.73
Photo Estimates						
A = fn(B)	36	0.98	-0.44 (0.56)	0.44	0.97 (0.03)	0.32
E = fn(B)	76	0.97	0.01 (0.78)	0.99	0.97 (0.02)	0.19
B2 = fn(B)	33	1.00	-0.34 (0.19)	0.08	1.01 (0.01)	0.17
Visual vs photographic						
V_{1977} = fn(P_{1977})	7	0.83	11.30 (7.04)	0.17	0.71 (0.13)	0.06
$V_{98\text{-}09}$ = fn($P_{98\text{-}09}$)	77	0.83	8.05 (1.61)	**< .001**	0.57 (0.03)	**< 0.001**

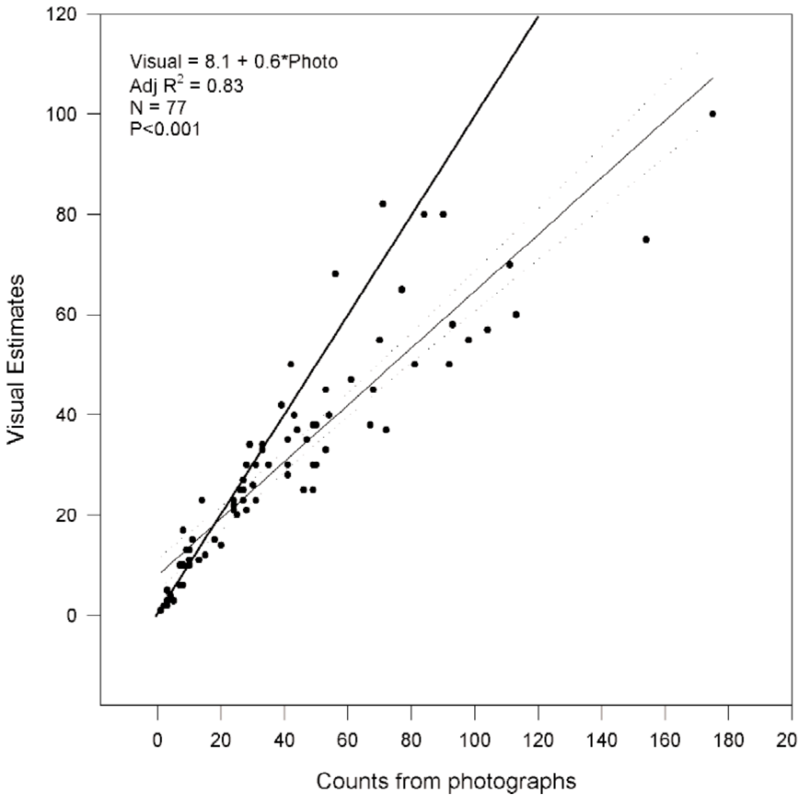

Fig. 3. *a) Visual estimates of the number of walruses present from counts during the aerial survey compared to the number counted in aerial photographs taken during the survey and counted later. The thin line is the fitted regression, the dashed line the 95% confidence interval and the heavy line denotes the theoretical 1:1 correspondence.*

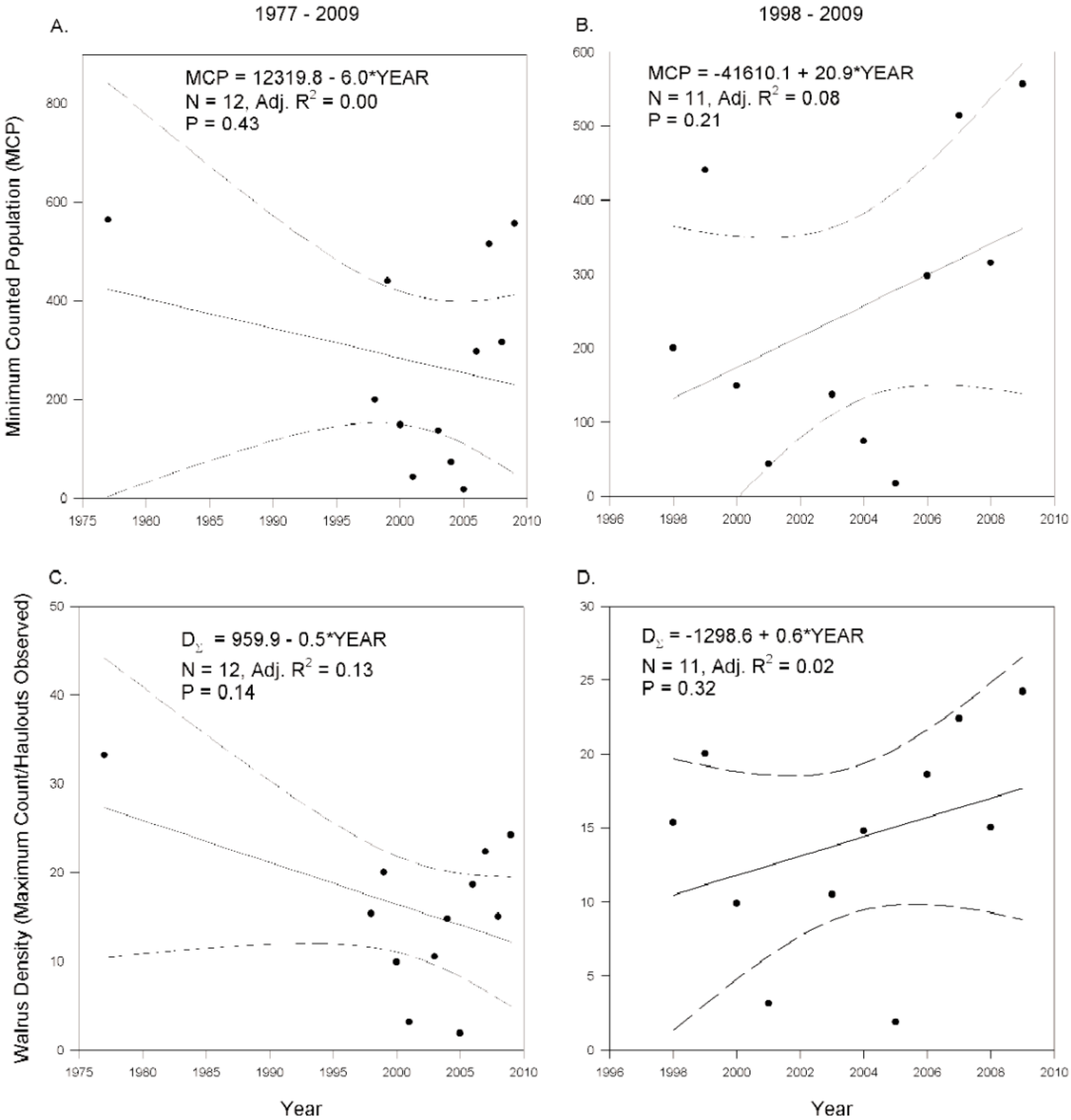

Fig 4. *Penny Strait-Lancaster Sound walrus abundance trends over time: fitted regression and 95% confidence interval (------). 1977–2009 (left); 1998–2009 (right). Minimum Counted Population (MCP) (upper) and density (lower).*

seen if they had been present. Minor shifts, such as from the east to the west side of Ryder Inlet were not considered to be new, additional haulouts. By 2009, 24 haulouts had been identified in PS-LS and 10 in WJS.

Minimum Counted Population

Yearly MCP estimates in the two areas (PS-LS and WJS) were independent (MCP_{WJS} = 119.1(±56.4) + 0.3(±0.2) * $MCP_{PS\text{-}LS}$, n=12, P = 0.17, Adj. R^2 = 0.10) (Regression coefficients are presented ±1 SE unless otherwise noted.). Thus, there was no evidence that walruses were moving between areas between years.

In 1977, 565 walruses were counted in the PS-LS area on 4 survey days from 11 to 23 August at 17 sites (Table 3). No counts at haulouts violated the distance criterion so the final minimum

Table 3. Penny Strait-Lancaster Sound - maximum yearly counts and the sites contributing to those maxima. Map Key is the designation of the haulout site shown in Figure 1.

	Map Key	1977	1998	1999	2000	2001	2003	2004	2005	2006	2007	2008	2009
Village Bay	A	86		53	0		10	34	0	0	0		111
Barrow Harbour	B	79	31	77	0		13	0	0	17	40	30	98
Inglis Bay	C	12		10	0		12	0		1	40	6	41
Cape Hornby	D	0		0		0				0			24
Margaret Island	E	32	30	41	9	0	0	2	0	89	81	49	43
Baillie Hamilton Island	F	0		2			41	0			63	46	50
Houston Stewart Island	G	0									86		39
Brooman Point	H	71	0	0	0	0					4	0	0
Markham Point	I	92	0	40	0	0					0	0	0
Markham West	I	45	0	54	0						103	61	27
Marshall Penn	J	44	0	0	0						4	1	
Union Bay	K	63	0	0		0	0		0	0	0	0	0
Gascoyne Inlet	L	0	11		0	0	0		0		1	0	0
Radstock Bay	M	0	0	0	0				0		3	0	0
Kearney Cove	N	72	0	59	0	0	41		17	0	16	1	14
Custance Inlet	O	0	13	33	0	0	0		0	0	0	0	0
Ryder Inlet	P	131	75	26	64	23	13		0	7	3	0	0
Graham Inlet	Q		0	0		0	0			3	0	0	0
No Name Bay[A]	R			0		0	0			25	10	0	10
Blanley Bay	S			0		0				8	20	50	27
Stratton Inlet	T			8	0	0	0			0	0	0	0
Burnett Inlet	U			0						47	0	95	24
Powell Inlet	V			28	0	12				60	53	0	113
Cuming Inlet	W			0						62	73	0	1
Total Walrus at haulouts		727	160	431	73	35	130	36	17	311	600	339	622
Haulouts (n)		17	13	22	15	14	13	5	9	16	23	21	23
Coverage		0.71	0.54	0.92	0.63	0.58	0.54	0.21	0.38	0.67	0.96	0.88	0.96
Final Count at Haulouts[B]		565	160	384	73	41	101	34	17	298	499	292	540
Haulouts in Final Count		10	13	21	11	10	12	5	7	10	21	22	22
Density (DHO)		56.5	12.3	18.3	6.6	4.1	8.4	6.8	2.4	29.8	23.8	13.3	24.5
At Sea		0	40	57	76	3	36	40	0	10	16	15	17
Minimum Counted Population		565	200	441	149	44	137	74	17	308	515	308	557
MCP/Effort (D∑)		33.2	15.4	20.0	9.93	3.14	10.5	14.8	1.89	19.3	22.4	14.6	24.2

[A] No Name Bay really has no name, according to both local Inuit (I. Kalluk, Chair, Resolute Bay HTA, pers. Comm.) and the Canadian Hydrographic Service (T. Janzen, Hydrographer, CHS).
[B] The Final Count at Haulouts excludes possible double counts of walrus that are included in the Total Walrus Sightings.

Dark green indicates the year in which walrus were first observed on a haulout.

Light green indicates an observed site and the maximum count for the year. Zeros that precede the dark green indicator were assumed retroactively (see text).

Table 4. West Jones Sound - maximum yearly counts and the sites contributing to those maxima. Map Key is the designation of the haulout sites shown in Figure 1.

	Map Key	1977	1998	1999	2000	2001	2003	2004	2005	2006	2007	2008	2009
Baad Fiord	1		0	0		34						12	15
Musk Ox Fiord - spit	2		75	10	8	16		0	0			3	2
Musk Ox Fiord – west	3		0	0		0		0	0			11	0
Clement Ugli	4	0	53	0	60	21	0	125	19	12	7	158	104
Borgen Mount	5	139	67	78	75	46	45	43	0	38	1	3	72
Walrus Fiord	6	0	68	0	79	0	0	12		0	24	90	54
Norfolk[A] Island	7	73	15	29	15	71	69	26		29	83	110	93
Arthur Fiord	8	65	0	0		0	0	20		0	0	0	0
West Fiord	9									44	0		17
Nookap/Saukuse Island	10			0		0		0				0	0
Total Walrus at Haulouts		277	278	117	237	188	114	206	19	123	115	387	357
Haulouts (n)		5	8	9	5	9	5	8	4	6	6	9	10
Coverage		0.50	0.80	0.90	0.50	0.90	0.50	0.80	0.40	0.60	0.60	0.90	1.00
Final Count at Haulouts[B]		**277**	**170**	**110**	**201**	**176**	**114**	**151**	**19**	**94**	**90**	**374**	**287**
Haulouts in Final Count		5	8	5	4	6	4	4	4	5	6	8	10

[A] Norfolk Island is an un-named island in Norfolk Inlet.
[B] Final Count at Haulout excludes possible double counts of walrus that are included in the Total Walrus Sightings.

Dark green indicates the year in which walrus were first observed on a haulout.

Light green indicates an observed site and the maximum count for the year. Zeros that precede the dark green indicator were assumed retroactively (see text).

Table 5. Bounded Count estimates and the proportion of countable walruses present at haulout sites during the survey. N is the number of haulouts providing replicates for the bounded count. The lower 95% confidence limit is C_{max} and the upper limit was calculated according to Eq. [2].

Area/Year	N haulouts	C_{max}	C_{max-1}	Mean	Bounded Count (upper 95% CL, cv)	P_{it}
PS-LS						
2006	6	201	65	133.0	337 (2785, 3.71)	0.39
2007	13	228	192	210.0	264 (912, 1.25)	0.80
2008	14	380	269	324.5	491 (2489, 2.08)	0.66
WJS						
2001	4	176	79	127.5	273 (2019, 3.26)	0.47
2003	4	114	6	60.0	222 (2166, 4.47)	0.27
2009	7	297	245	271.0	349 (1285, 1.37)	0.78

counted population (MCP) was also 565. From 1998 to 2009, this area was surveyed in 11 years, with 6 to 23 haulout sites observed. One of the two highest counts occurred in 2007 (~500 on 3 survey days 17 - 21 August) and the other in 2009 (~560 on 2 survey days 11 - 14 August). When potential duplicates were removed using the distance/time criterion, and walruses seen at sea far from haulouts added, MCP was 515 in 2007 and 557 in 2009 was 557.

Trends in MCP were not significant for 1977–2009 or 1998–2009 (Fig. 4). Seventeen haulouts were observed in 1977 with a walrus D_Σ of 33.2. Coverage was greater in 2007 and 2009 with D_Σ of 22.4 and 24.2 respectively. Regressions were not significant and explained little of the variation in the data.

In 1977, WJS was surveyed on 21 and 22 August; 277 walrus were counted at three haulouts in this area on 21 August (Table 4). Because the maximum count occurred on one day, there were no duplicates. A few walruses were recorded at sea so the MCP was 290. From 1998 to 2009, the area was surveyed in 11 years with 4 to 10 sites observed in individual years (Table 4). MCP was highest in 2008 (404, on 26 August) and in 2009 (388, on 14 August) based on 8 and 10 haulouts, respectively. MCP and D_Σ showed no trends over time, either from 1977 to 2009 or 1998 to 2009 (Fig. 5).

Adjusted Counts

Replicate counts in PS-LS in 2006, 2007 and 2008 were used to calculate bounded count estimates ranging from 264 to 491 with large confidence limits (Table 5). For WJS, bounded counts

Table 6. Four estimates of abundance for the Penny Strait-Lancaster Sound and West Jones Sound walrus stocks. MCP is Minimum Counted Population and includes animals at haulouts and at sea. Adjusted MCP is MCP at haulouts divided by the estimated maximum proportion of the population expected to be hauled out concurrently ($MCP_{HO}/0.74$). The 95% confidence interval and coefficient of variation are based on the variance of the tag data only (Table 1). Bounded Count is the estimate of the countable population at haulouts (Table 5) and Adjusted Bounded Count is BC/0.74 with variances combined according to Eq. [4]. Calculated estimates that were below MCP (in italics) were ignored. Estimates in bold were used in the final estimation of stock size (see text for details).

	MCP	$MCP_{HO}/0.74$ (95% CL, cv)	Bounded Count (95% CL[1],cv)	Bounded Count /0.74 (95% CL, cv)
PS-LS				
2006	308	401 (342–460, 0.08)	337 (201–2785, 3.71)	454 (201–3750, 3.71)
2007	**515**	**672 (575–768, 0.07)**	*264 (228–912, 1.25)*	*355 (228–1229, 1.25)*
2008	307	393 (335–451, 0.08)		
2009	**557**	**727 (623–831, 0.07)**	*491 (380–2489, 2.08)*	661 (380–3352, 2.08)
WJS				
2001	185	237 (201–273, 0.08)	273 (176–2019, 3.26)	368 (176–2718, 3.26)
2003	114	153 (129–178, 0.08)	222 (114–2166, 4.47)	299 (114–2916, 4.47)
2006	94	127 (106–142, 0.08)		
2007	101	121 (101–142, 0.09)		
2008	**404**	**503 (430–577, 0.07)**		
2009	**388**	*386 (329–446, 0.08)*	*349 (297–1285, 1.37)*	**470 (297–1732, 1.37)**

[1] Lower confidence limit= C_{max}

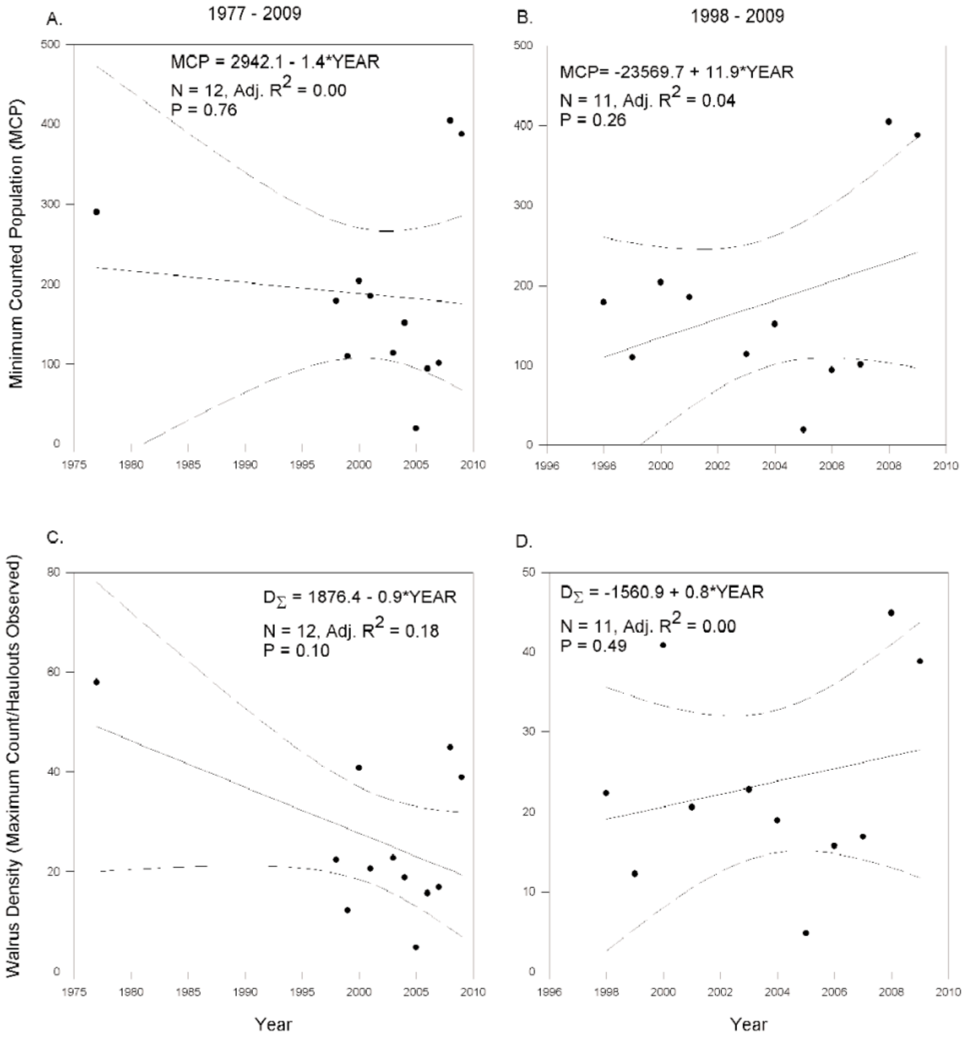

Fig 5. *West Jones Sound walrus abundance trends over time: fitted regression and 95% confidence interval (-----). 1977–2009 (left); 1998–2009 (right). Minimum Counted Population (MCP) (upper) and density (lower).*

for 2001, 2003 and 2009 ranged from 222 to 349 with similarly large confidence limits. In PS-LS, adjusted MCP_{HO} estimates ranged from 393 to 727, while adjusted bounded counts ranged from 355 to 661 (Table 6). In WJS, adjusted MCP_{HO} estimates ranged from 121 to 503 and adjusted bounded counts ranged 299 to 470.

The four methods of estimating walrus abundance produced some contradictory results (Table 6). The adjusted MCP_{HO} estimate for WJS in 2009 was smaller than the MCP estimate, due to the inclusion of 100 walrus counted at sea in the MCP that were not completely off-set by adjusting MCP. Three of six unadjusted bounded count estimates (PS-LS 2007, 2009; WJS 2009) and one adjusted bounded count (PS-LS 2007) were smaller than MCP. In PS-LS 2007 and 2009 estimates, substantially fewer haulouts contributed to bounded count estimates than MCP (13 and 13 vs 21 and 22, respectively). Some of the haulouts that did not have replicate counts provided large counts for MCP (Tables 3 and 4). The WJS 2009 bounded count differed due to the animals counted at sea.

For the PS-LS area, we used the 2007 and 2009 adjusted counts to represent the recent population estimate because coverage was high and MCP and adjusted MCP in both years, and adjusted bounded count in 2009, were in good agreement (Table 6). Using adjusted MCP, there were 672 (95% CI: 575–768) and 727 (623–831) walruses in PS-LS in 2007 and 2009, respectively. The 2009 adjusted bounded count of 661 falls within 95% confidence interval for the same year. The population is therefore at least 560 and more likely over 700 because surveys focused on the north side of Lancaster Sound and, although not common, some walrus do haulout on the south side and were likely missed.

For WJS, we used 2008 and 2009 as the most recent years with good coverage; these estimates were similar. The adjusted MCP was 503 (430–577) in 2008. As noted, adjusted MCP and the bounded count for 2009 were discounted because they were smaller than the number of walrus counted. The adjusted bounded count was 470 (297–1,732). The population is thus at least 400 and adjusted estimates suggest about 500 walruses are present. This is a small area and coverage was good.

DISCUSSION

Survey Design

Walruses are challenging to enumerate. In the winter, walrus distribution appears to be largely independent of ice cover and ice movement (Born et al. 2005, Freitas et al. 2009, Jay et al. 2010, Dietz et al. 2014). In summer, the variability in the numbers and proportions of the population at haulouts is high within and between years (Table 7) and there may be different drivers guiding haulout patterns for different age and sex classes. Haulout sites vary in spatial and temporal stability. There is some synchronicity apparent in walrus haulout patterns over large areas (Lydersen et al. 2008, Udevitz et al. 2009), often related to weather (Fay and Ray 1968, Salter 1979a, Born and Knutsen 1997, Udevitz et al. 2009, this study). Hauling out "in phase" (Lydersen et al. 2008) may occur after storms that cause most walrus to remain at sea (C. Jay, pers. comm. November 2009). In general, good surveying conditions and good hauling out conditions are similar in terms of weather.

Counting pinnipeds at locations where they concentrate ("colony counts") is a long-standing and widely accepted census technique (Eberhardt et al. 1979, Mathews and Pendelton 2006, Lydersen et al. 2008, Buckland and York 2009). In recent years, we flew repetitive flights, similar to the "trend routes" used in Alaskan harbour seal surveys (Small et al. 2003), giving lower priority to areas previously determined to be without haulouts (Jacobs and Terhune 2000). Adkison et al. (2003) investigated robust study designs for detecting trends in harbour seal populations using a similar survey design. Seals were counted at known haulouts multiple times within a year and over many years. They examined numerous covariates and found that, in general, corrected counts were superior to raw counts. They noted that in the detection of area-wide trends, differences between raw and corrected counts were much smaller than when comparing a single site over time. However, both methods were sensitive to the number of haulouts surveyed and more sensitive to the number of years in the trend analysis than the number of replicates within a year. Based on their modelling, they recommended at least 25 haulouts be examined each year, about 10% of the 244 haulouts in their survey area (Adkison et al. 2003). Our surveys included 21–96% (56.9±25.6%) of the known haulouts in PS-LS and 40–100% (70.0±20.5%) in WJS. Coverage in our final abundance estimates was 87.5% and 91.7% in PS-LS (2008 and 2009) and 80% and 100% in WJS (2008, 2009).

Table 7. Selected examples of within- and between-year variation in site occupancy. Not shown are counts that were similar on different dates in the same year. All dates in August.			
Site	Year	Count 1 (date)	Count 2 (date)
Borgen	1977	125 (21st)	35 (22nd)
	1998	67 (19th)	0 (21st)
	1999	35 (12th)	78 (19th)
	2003	45 (11th)	0 (15th)
	2009	49 (14th)	72 (15th)
Brooman	1977	55 (16th)	0 (23rd)
Clement	2000	30 (24th)	60 (30th)
	2004	125 (24th)	4 (25th)
	2009	71 (14th)	104 (15th)
Markham	1977	20 (10th)	85(23rd)
Markham	1977	0 (10th)	45 (23rd)
West Norfolk	2001	71 (20th)	0 (25th)
	2003	58 (11th)	0 (15th)
Village Bay	1977	25 (15th)	84 (22nd)

Fig. 6 *a) A mixed-composition herd of walruses on Ellesmere Island. Calves and adult males can be identified from the air. The presence of calves implies the presence of adult females. b) An all-male group of walruses on Houston Stewart Island. Identification of all-male groups from the air relied largely on the apparent absence of calves, which can be difficult to see in larger herds. The composition of this group was confirmed by several hours of ground-level observation. (Photo credits: a) R. Stewart b) B. Dunn)*

Adkison et al. (2003) commented on, but did not explore, the potential effects of movement among haulouts and abandonment/colonization of sites. We addressed the former by using a distance criterion to mitigate against double-counting due to movement among sites between surveys. The later was addressed by including all known sites whether or not they had been occupied recently and by retroactively including ‘new’ sites that had been previously observed.

Some colony counts are clearly focused on one segment of the population, such as the pup counts used in harp seal (*Phoca groenlandica*) assessments (Stenson et al. 2003, 2009, Haug et al. 2006). We observed walrus in both mixed herds (see also Salter 1979b) and in small groups of mature males (Fig. 6). We were unable to determine the proportion of age and sex classes in mixed groups, and when adult male groups were identified we could not determine their proportion of the population. Our surveys were, in that respect, most similar to harbour seal counts during moult (e.g. Cronin et al. 2007 and references). We made no adjustment for age/sex classes.

When a site was not observed, we made no adjustment to the count for the missed site (Olesiuk et al. 1990) because counts at haulouts were highly variable within years (Table 7). Many sites varied by over 100 animals in 24 h so interpolation was not appropriate. Instead, we adjusted the number of haulouts included in our estimate of effort.

Surface-level counts underestimated numbers present compared to counts from aerial surveys, as previously reported for harbour seal surveys (Mathews 1995). Similarly, visual estimates from aircraft (this study) or surface level counts (Udevitz et al. 2005) tend to diverge at larger group sizes. High resolution photographs produced precise and repeatable counts (Lydersen et al. 2008) but both aerial estimates and photographs can miss small animals within large, tightly spaced herds and it is sometimes possible to erroneously identify a body part as an uncounted small walrus.

Adjusting Counts

No adjustment was made to counts of walrus at sea. The survey path generally followed the shoreline and counts at sea were not comprehensive or systematic. At sea counts were only factored into MCP.

Walrus counts are vulnerable to both availability and detection biases (Pollock et al. 2004), but detection of individuals present is less of a concern than availability until the herd gets large. Calves especially may be overlooked in large groups. However, it is highly likely that not all the animals that use a particular haulout site are actually there during all surveys. In Johnson et al.'s (2007) terminology, if the Maximum Estimate equals the true population, then $\max\{P_{it}\} = 1$, (P_i = the combined availability-detection rate on the i^{th} survey), that is, in at least one survey all the animals were present and accounted for. This is unlikely in the case of walruses and a primary concern in using counts at haulouts is the proportion of the population that is at sea instead of on land at the time of enumeration (Eberhardt et al. 1979, Buckland and York 2009). Many attempts have been made to estimate the proportion of the population represented by counts at pinniped haulouts. Knowledge of how haulout behaviour varies with environmental factors has been used to plan harbour seal surveys around peak hauling out hours (e.g. Buckland and York 2009). The majority of haulout bouts in this species are less than 12 h and follow a tidal rhythm (Yochem et al. 1987, Cronin et al. 2009). However, individual walruses tend to haulout on land for longer periods, averaging from 20 to ~40 h (Born and Knutsen 1997, Gjertz et al. 2001, Lydersen et al. 2008), irrespective of the tidal cycle.

Monitoring tagged animals concomitant with the survey provides information that can be used to develop a real-time adjustment factor. Most simplistically, the proportion of tags dry at the time of the survey represents the proportion of the population available to be counted (Huber et al. 2001). Realistically, it is more complicated than this (e.g. Ries et al. 1998, Boveng et al. 2003). Udevitz et al. (2009) combined weather information and tagged animal behaviour in a sophisticated model for walruses hauling out on ice in the spring in Alaska. They showed high variation in the proportion hauled out among days (0 to 71%, mean 17%), which was related to weather. Ries et al. (1998) noted that tag deployments concomitant with a survey may be useful in generating an adjustment factor, but if wind direction or other abiotic factors influence haulouts differently, the area in which the adjustment factor is useful may be limited. Conversely, if biotic factors largely determine haulout patterns, tags must be deployed in proportion to age and sex class sizes (Reis et al. 1998, Härkönen and Harding 2001). The age/sex composition of the walrus herds surveyed in this study is unknown.

Walruses may prefer to haulout on ice (Born and Knutsen 1997), but during our surveys, when ice pans were near haulouts, we found walrus on land only, on ice only, and both on ice and land (Fig. 7, see also Salter 1979a). It is not clear whether presence of sea ice is a factor that greatly

Fig. 7. *Walruses on both a) ice and b) land in Norfolk Inlet. Both photos were taken at 1251 h on 11 August, 2003, looking about 45° apart (Photo credits: R. Stewart)*

influences haulout behaviour. However, the extent and distribution of ice in the survey area has changed immensely since 1977, and even since 1998. For example, surveys planned for 1978 and 1979 were cancelled because landfast ice surrounded many of the haulout sites while these same sites have been virtually ice-free in recent years (WRK and REAS, personal obs.). Many authors have commented on the potential impact of "lurking" covariates that change in a linear fashion over time (Thompson et al. 1997, Ries et al. 1998, Adkison et al. 2003, Sharples et al. 2009) and change in sea-ice over the course of the study period is a lurking covariate we were unable to assess.

Currently, we have no data on age and sex related haulout behaviour and how it might change through the survey period; nor do we know the size and degree of segregation among population components (Härkönen and Harding 2001). Our attempt to use tag data from 2004 was not successful, at least in part due to our small sample size which did not satisfy the Horvitz-Thompson requirements. Sharples et al. (2009) also reported that samples sizes of <10 may not be representative of the population's behaviour. In the future, it would be advantageous to have many tags, deployed in advance of the survey, but still operating during the survey, that are stratified with respect to age and sex, although calves may always be under-represented in actual counts due to their size.

As with many other survey methods (Williams et al. 2002), the bounded count method assumes the population is closed at each site (Johnson 2008). This assumption is reasonable for each year of walrus surveys because of the distance criterion we used for avoiding double-counting, which guards against immigration/emigration, and the birth season is well past. However, some mortality could occur during the survey period.

Bounded count estimates of the proportion of harbour seals hauled out during surveys were larger than proportions based generally on tag data (Olesiuk et al. 1990) or on concurrent tag data (Thompson et al. 1997). Olesiuk et al. (1990) attributed the discrepancy to the longer-term average represented by the tags in diverse weather conditions compared to the bounded counts which were derived from only good survey conditions. Thompson et al. (1997) countered that the bounded count estimate was still lower when surveys were conducted in a greater range of weather conditions. Olesiuk et al. (1990) applied the bounded count proportion to adjusted counts for areas, not just haulouts. Thompson et al. (1997) relied on data from tags affixed to the heads or backs of harbour seals (Thompson et al. 1989) and interpreted a continuous signal of 5 min in 1 h to indicate the seal was hauled out. This protocol might then assume a seal that was awash near a haulout for 6 min and immediately left was actually on the beach. The two estimates of P_{it} may not be directly comparable.

Udevitz et al. (2009) found that the percentage of walrus hauled out on ice in April averaged 17%, but ranged from 0 to 71% with no tagged walruses hauled out in 25% of the 322 intervals. Few if any tagged walruses hauled out on 4 and 26 April 2006 when there were blizzards in the area (Fig. 2 of Udevitz et al. 2009; DHS&EM 2006a,b). However, surveys are never flown in blizzard conditions; therefore, no walrus hauled out on those days is uninformative for the proportion hauled out during surveys. Lydersen et al. (2008) surveyed walrus at Svalbard during summer when there were short periods when no walrus were hauled out (their Fig. 3). During 2002–2004, 11 of the 13 days when no tagged walrus were ashore were rainy at Hopen Island, Svalbard (http://www.tutiempo.net/en/Climate/Hopen/10620.htm, accessed 4 April 2012). A similar pattern was present in 2005 but only 2 tags reported data relevant to their counts. Although less dramatic than blizzards in Alaska, there is some evidence from this study that reduced haulout activity and reduced survey effort are both related to inclement weather. It is also vital to note that both MCP and bounded counts are based on maximum counts and attempting to adjust them using average behaviour may be inappropriate.

Estimating population size of walrus using numbers at haulout sites has some parallels in avian biology. Population assessment of sage grouse (*Centrocercus urophasianus*) relies on counts made at specific locations (leks) several times a season, and the largest count, the Maximum Estimate, is the measure of the population size at that lek (Walsh et al. 2004, Johnson et al. 2007). The Maximum Estimate (Johnson et al. 2007) is equivalent to the Minimum Counted Population. In expanding MCP to an estimate of the total population, ornithologists also deal with detection (perception) bias, when birds present are not counted, and availability bias, when birds that use the lek are absent from it at the time of counting (Pollock et al. 2004, Johnson et al. 2007). The bounded count method has been closely scrutinized for this application.

The bounded count method was initially based on uniform distribution of the samples (Routledge 1982, Johnson et al. 2007) so the difference between the true population size and C_{max} would be the same as the difference between C_{max} and C_{max-1}. However, simulations (Johnson et al. 2007) indicated that bounded count estimates were more accurate, despite their higher variances, than the averages of MCP (when counts were uniformly distributed and when 50% of the counts were zeros).

Bounded counts have been thought to be severely negatively biased, to the extent that the confidence interval may not include the true population estimate, especially if detection probabilities are low (Routledge 1982, Williams et al. 2002, Walsh et al. 2004). Simulations that allowed the availability-detectability rates (P_{it}) and number of surveys to vary showed that when P_{it} was low (40%) the bounded count was less biased than MCP, although both were underestimates. When P_{it} was high (80%), both MCP and bounded counts were close to the true population size (Johnson et al. 2007). These authors also found that at low availability-detectability rates neither the bounded count nor the MCP correlated well with true population numbers but that at higher P_{it}, they were both acceptable. In our surveys, P_{it} varied from 0.27 to 0.80 and was reflected in the coefficients of variation (4.47 to 1.25 respectively, Table 5). The two highest P_{it} values (WJS 2009: 0.78 and PS-LS 2007: 0.80) were associated respectively with bounded counts that did not include a large number of walruses seen at sea or that included a limited number of haulouts and are therefore still under-estimates (Table 6).

We considered it unlikely that the maximum proportion of the population hauled out at one time could ever be 100% and estimated the maximum proportion, HO_{max}, from other studies to apply to our maximum counts. We considered theoretical max{P_{it}} = HO_{max} to be 74% of the total population. Using an estimate of HO_{max} is justified because our counts are maxima; all the biases in our survey and counting methods were positive in an attempt to gain the high- est count as the MCP. The estimated max{P_{it}} = 0.74 can be used to adjust both the haulout component of MCP (MCP_{HO}/0.74) (Johnson et al. 2007) and the bounded count estimate of the countable population. In general, MCP defines one limit of population estimates and can serve as an index for other studies. It maximized the number of haulouts contributing to the final estimate but high variation in counts at any haulout within and among years and low sur- vey coverage will produce highly variable results. MCP lacks an error estimate and will remain an enigmatic estimator of true population size until much more is understood about walrus haulout behaviour. Adjusted MCP_{HO} maintains all the benefits and caveats associated with MCP. It also makes generic assumptions about max{P_{it}}, and that assumption provides an error term. Adjusted MCP_{HO} is amenable to indexing but offers no benefit over unadjusted MCP_{HO} as an index. It can incorporate new and better data on general haulout behaviour. MCP and adjusted MCP_{HO} can be employed for any year because, unlike bounded counts, they do not rely on replicates.

Bounded counts were limited to the same haulouts counted on two different days, so they usually included only about 60% of the haulouts used in MCP estimates. They were also limited to years in which logistics permitted replicate counts. Although an error term is generated, the upper confidence limit is highly sensitive to the difference in the two highest counts [Eq. 2] and confidence intervals tend to be broad (Johnson et al. 2007). Adjusted bounded counts have the same logistic constraints as un-adjusted ones. The available data on HO_{max} provided a narrow range of estimates with a low variance, which had an insignificant effect on the combined variance compared to the variance in the bounded count, usually increasing the combined cv at the 4th decimal place.

When bounded counts and adjusted bounded counts relied on the same haulout counts as did MCP, they provided more information by including error estimates on both the count and the proportion of the population available for counting. But the logistics of walrus surveys preclude knowing in advance which site might be the 'correct' ones and often preclude surveying all sites during a short period. We conclude there is, as yet, no single best approach to estimating the total abundance of walrus in this area. We used estimates from recent years with good coverage and for which adjusted counts were equal to or larger than MCP.

Comparisons with Previous estimates

The Penny Strait–Lancaster Sound, the West Jones Sound and the Baffin Bay walrus stocks were previously known as the (single) Northwater stock (Born et al. 1995, Stewart 2008). Born et al.

(1995) collated reports spanning several decades to conclude these stocks numbered "1,700–2,000 and perhaps included as many as 3,000" animals (Born et al. 1995), indicating the uncertainty of the estimate.

Penny Strait–Lancaster Sound

By 2009, our surveys had identified 24 terrestrial haulout sites currently or historically used in the survey area (Fig. 1, Table 3). One historic site, Stratton Inlet (Born et al. 1995) was occupied only once (1999) and showed no signs (tracks, feces stains) of occupancy in any other survey. The locations of sites previously identified on the east side of Ryder Inlet and the north side of Marshall Peninsula were not occupied, but new sites <4 km away on the west and south sides, respectively, were occupied. A haulout on Houston-Stewart Island was first seen to be occupied in 2007. It may represent new walrus use or expanded survey effort. In 2009, walruses were hauled out on Cape Hornby, Devon Island. This cape was over-flown by four previous surveys in the area and represents a newly occupied haulout. None of the haulouts between Maxwell Bay and Croker Bay were reported by Born et al. (1995) and the sites they reported at Dundas Harbour and Philpots Island have not been used recently. The site at Wollaston Islands at the mouth of Navy Board Inlet (Brody 1976) was apparently abandoned after meat was left on the islands in the late 1940–50s (J. Alooloo 2010, pers. comm.).

The MCP for Penny Strait–Lancaster Sound region in 1977 was 565 compared to 515 (2007) and 557 (2009). Neither MCP nor walrus D_{Σ} in this region changed in a statistically significant way from 1977 to 2009 (Table 3, Fig. 4). The 1977 survey was conducted in a faster aircraft and at a lower altitude than later surveys and may therefore have had a lower detection function. Also, only about half the number of haulouts known by 2009 were observed in 1977. Coverage in 1977 extended only as far east as Ryder Inlet on the south side of Devon Island and additional animals may have been present east of this Inlet. Recent surveys extended approximately 100 km farther east and haulouts now exist where none had been documented previously, but it is unknown whether those haulouts were present in 1977. These factors suggest the 1977 MCP is negatively biased compared to later counts, although density did not change significantly over the interval in question. Conversely the heavier ice conditions may have concentrated walrus in the survey area resulting in the somewhat higher density estimates. It is unlikely that we will ever be able to fully assess changes in population size and redistribution that occurred since 1977.

Davis et al. (1978) reported approximately 700 walrus in the Penny Strait–Lancaster Sound area in August 1977 but did not adjust for possible duplicate counting. Born et al. (1995) includ- ed the Davis et al. (1978) data and suggested that 1,000 walrus from the Northwater stock occu- pied south Devon Island and Lancaster Sound in summer but noted the data supporting this conclusion were not robust. Koski (1980) estimated that there were 468 walruses in eastern Lancaster Sound before the ice break-up in 1979. On 7 June 1977, approximately 200 were counted in the region from Penny Straight to Queen's Channel (Fig 3. of Davis et al. 1978) with little potential for duplicate counting because there was extensive land-fast ice between this area and Lancaster Sound. The proportion of the population in eastern Lancaster Sound before break-up that moves into the PS-LS area in summer is unknown, although Davis et al. (1978) suggested approximately 150–200 walrus moved west for a projected summering population of ~400. If the entire estimated over-wintering population moved west, the summering popu- lation would have been about 670. Our estimates of 672–727 in 2007 and 2009 are consistent with previous estimates.

West Jones Sound

By 2009, 10 terrestrial haulout sites were used in the WJS stock area (Fig. 1, Table 4). Although Stewart (2008) thought it unlikely that walrus moved from West Jones Sound through Hell Gate to Arthur Fjord, Davis et al. (1978) presented information that suggest such movements do take place. They observed walrus in Arthur Fjord in the summer of 1977, many weeks after walruses that had over wintered north of Grinnell Peninsula had moved west. We included Arthur Fjord in the WJS stock, although only 20 walrus were counted there in 2004 and this count had no effect on the final conclusions.

The historic site(s) at Nookap and Saukuse Islands, identified by IQ were not occupied during any of the surveys in this study, nor has there been any signs of recent use, although it was occupied in the late 1970s. On 14 September 1979, Koski and Davis (1980) estimated ~150 walruses hauled out there and 19 walrus in the water near the haulout. In 2008 and 2009 we recorded a few walruses swimming within 5 km of these islands and this site is not yet considered abandoned. Haulouts in Baad, Musk Ox, and at Clement Ugli and Borgen Mount in Goose Fjords had been previously identified (IQ; Born et al. 1995). In Baad Fjord, the two sites are only about 4 km apart on the same shoreline and both places have not been occupied simultaneously. We consider these two sites as one site. In Musk Ox Fjord, the two sites are about 5 km apart, on opposite sides of the fiord and they have been both occupied at the same time. The western site was occupied by a few males in 1998 and a mixed herd in September 2001. Only males have been recorded at the eastern site. The two sites in Goose Fjord (Borgen and Clement) are approximately 20 km apart and are routinely occupied at the same time. In 2006, walrus were seen for the first time hauled out on a small island in West Fjord. This island is adjacent to usual survey flight patterns but was not closely scrutinized in a systematic manner until 2006. It may represent new walrus use or expanded survey effort. Sverdrup (1903) commented on walrus at Blubber Point (76° 39′ N/ 89° 50′ W) on western Ellesmere Island. This site was examined in 1999, 2003, 2006, and 2007 but no signs of walruses were detected.

The minimum counted population of walruses in the West Jones Sound area (Fig. 1) in 1977 was 290 compared to 404 in 2008 and 388 in 2009 (Table 4). Regressions of MCP and walrus D_{Σ} in WJS between 1977 and 2009 were not statistically significant but the two most recent counts are the highest on record. As in the PS-LS area, the distribution of ice has changed greatly in recent years and a redistribution of walrus from eastern Jones Sound is possible. People from Grise Fjord have reported groups of about 75 walrus in eastern Jones Sound immediately prior to our surveys in both 2008 and 2009. These groups were not obvious during our surveys and it is not known if they were included in the population estimate of PS-LS and Baffin Bay (Stewart et al. 2014).

Born et al. (1995) concluded there were 300–600 walrus in Jones Sound and on eastern Ellesmere Island, south of ~78°40′ N, relying largely on Davis et al. (1978) for the Jones Sound component. This estimate included 200-300 moving into Jones Sound, based on the 1977 survey included here. Walrus are known to overwinter in western Jones Sound (Sverdrup 1903, Riewe 1976) where 100 were seen in May 1972 (Kiliaan and Stirling 1978) and 102 were seen on 19 April 1977 (Davis et al. 1978). Our estimates of 400–500 for only western Jones Sound, west of South Cape are therefore higher than previously published estimates.

CONCLUSIONS

Abundance of both the PS-LS and WJS stocks appears to have remained stable over the period 1977–2009, although differences in survey coverage and possible changes in walrus distribution make a definitive answer problematic. Employing a standard survey track is a useful survey technique for other pinniped species and appears well suited for walruses as well. However, it should not preclude further exploration each year to search for new haulout sites. Changes in population abundance, ice patterns, and human activity may all lead to the formation of new haulout sites.

Ideally, future surveys should be frequent and strive to obtain within-year replicates but limited resources may require a choice between brief surveys conducted more often and comprehensive surveys conducted less often. The approach depends on whether the objective is to estimate population size or monitor trends. A "better" population size estimate can be obtained by multiple counts of haulouts within a year. Such surveys could be conducted every third year rather than every year. However, for trend data a single survey each year provides more data points for documenting changes in population trends but poorer information on population size and more variability in year-to-year estimates.

Adjusting counts for animals not at the haulouts remains an issue. Radio or satellite telemetry data collected during surveys has the potential to adjust counts but adequate sample size, proportional representation and changes in behaviour within a season are problematic. Moreover, walruses near a haulout site often "loaf" at the surface where they are counted while their wet tags would indicate they were "at sea"; location data are too imprecise to determine if they are at a haulout. Tag data should be filtered to represent survey days only. Bounded counts coupled with an independently informed estimate of the maximum proportion of the population that might be counted at once appear promising. By relying on maximum counts and maximum proportion hauled out, the bias of surveying only when maxima are likely to occur is largely negated. The method is vulnerable to the high variation in counts and is a poor estimator if a large count cannot be replicated due to logistics. Adjusted MCP appears more robust. There is considerable merit in comparing multiple methods for a single survey.

The MCP adjusted for effort provided useful indices of walrus abundance. The use of adjusted MCP and adjusted bounded counts allowed the first estimation of absolute abundance for these two stocks.

ACKNOWLEDGEMENTS

We thank the Hunters and Trappers Association of Grise Fjord and Resolute Bay for their support and participation. Valued observers were, H. Cleator, B. Danielson, A. Gardner, J. Hamilton, N. Idlout, J. Kigutaq, A. MacHutchon and E. Noah. Much appreciated logistic support was provided by Polar Continental Shelf Project, Resolute Bay. C. Swartz, Simon Fraser University as well as K. Hedges, G. Stenson and T. Doniol-Valcroze, all of DFO Science Branch, provided invaluable advice on statistics with indefatigable patience. Funding was provided by the Department of Fisheries and Oceans (DFO), Canada, DFO-Nunavut Implementation Funds, the DFO-Species At Risk Fund and Greenland Institute of Natural Resources. The 1977 surveys were funded by the Polar Gas Project and benefited from the guidance of L. Doran, J. Riddick and B. Ross. R.A. Davis and K. Finley assisted with the planning and performance of the surveys; W.J. Richardson, C. Holdsworth, W.E. Renaud, R.E. Salter, M. Foy and J. Freeman were observers or assisted with data analysis. NORCOR Engineering and Research Ltd. supplied the aircraft and automated data recording system. The manuscript benefitted from the thoughtful reviews by S. Ferguson, L. Lowry and L. Quakenbush. Sincere thanks to Jill Prewitt at NAMMCO for her editorial skills. Surveys were conducted under DFO Scientific permits S-07/08-1021-NU, S-08/09-1048-NU, and S-09/10-1034-NU.

REFERENCES

Adkison MD, Quinn II TJ and Small RJ (2003) Evaluation of the Alaska harbor seal (*Phoca vitulina*) population survey: a simulation study. *Mar. Mamm. Sci.* 19(4):764–790. doi: http://dx.doi.org/10.1111/j.1748-7692.2003.tb01129.x

Born EW, Gjertz I and Reeves RR (1995) Population assessment of Atlantic walrus (*Odobenus rosmarus rosmarus* L.). Norsk Polar Institute, Oslo, *Medd.* Nr. 138:1–100

Born EW and Knutsen LØ (1997) Haul-out and diving activity of male Atlantic walruses (*Odobenus rosmarus rosmarus*) in northeastern Greenland. *J. Zool. (Lond.)* 243(2):381–396. doi: http://dx.doi.org/10.1111/j.1469-7998.1997.tb02789.x

Born EW, Acquarone M, Knutsen LØ and Toudal L (2005) Homing behaviour in an Atlantic walrus (*Odobenus rosmarus rosmarus*). *Aquat. Mamm.* 31(1):23–33. doi: http://dx.doi.org/10.1578/AM.31.1.2005.23

Boveng P, Bengtson JL, Withrow DE, Cesarone JC, Simpkins MA, Frost K and Burns JJ (2003) The abundance of harbor seals in the Gulf of Alaska. *Mar. Mamm. Sci*. 19(1):111–127. doi: http://dx.doi.org/10.1111/j.1748-7692.2003.tb01096.x

Brody H (1976) Inuit land use in north Baffin Island and northern Foxe Basin. In: Freeman M (ed.) *Inuit Land Use and Occupancy Project*. Department of Indian and Northern Affairs, Ottawa, ON, 153–172

Buckland ST and York AE (2009) Abundance estimation. In: Perrin WF, Würsig B and Thewissen JGM (eds.) *Encyclopedia of Marine Mammals, Second Edition*. Academic Press, San Diego, 1–5.

Cochran WG (1977) *Sampling Techniques, third edition*. John Wiley & Sons, Toronto, 428 pp.

COSEWIC (2006) COSEWIC assessment and update status report on the Atlantic walrus *Odobenus rosmarus rosmarus* in Canada. Ottawa: Committee on the Status of Endangered Wildlife in Canada. http://publications.gc.ca/collections/Collection/CW69-14-461-2006E.pdf.

Cronin M, Duck C, Cadhla OÓ, Nairn R, Strong D and O'Keeffe C (2007) An assessment of population size and distribution of harbour seals in the Republic of Ireland during the moult season in August 2003. *J. Zool. (Lond.)*. 273(2):131–139. doi: http://dx.doi.org/10.1111/j.1469-7998.2007.00316.x

Cronin MA, Zuur AF, Rogan E and McConnell BJ (2009) Using mobile phone telemetry to investigate the haul-out behaviour of harbour seals *Phoca vitulina vitulina*. *Endang. Species Res*. 10:255–267. doi: http://dx.doi.org/10.3354/esr00170

Davis RA, Koski WR and Finley KJ (1978) Numbers and distribution of walruses in the central Canadian high Arctic. Rep. from LGL Ltd., Toronto, Ont., for Polar Gas Project, Toronto, Ontario, 50 pp.

DFO-Department of Fisheries and Oceans (2000) Atlantic walrus. DFO Science stock status report E5-21, 19 pp (available at Stock Assessment Regional Office, Central and Arctic

Region, 501 University Crescent, Winnipeg, MB, R3T 2N6 or www.dfo-mpo.gc.ca/csas.)

DHS&EM. 2006a. Situation Report 06-094 http://fc.ak-prepared.com/dailysitrep/FOV5-0000D6AC/FOV5-00017578/ (accessed 3 August 2010).

DHS&EM. 2006b. Situation Report 06-115 http://fc.ak-prepared.com/dailysitrep/FOV5-0000D6AC/FOV5-00017578/ (accessed 3 August 2010).

Dietz R, Born EW, Stewart REA, Heide-Jørgensen MP, Stern H, Rigét F, Toudal L, Lanthier C, Villum Jensen M and Teilmann J (2014) Movements of walruses (*Odobenus rosmarus*) between Central West Greenland and Southeast Baffin Island 2005-2008. *NAMMCO Sci. Publ.* 9:53–74. doi: http://dx.doi.org/10.7557/3.2605

Doroff AM, Estes JA, Tinker MT, Burn DM and Evans TJ (2003) Sea otter population declines in the Aleutian Archipelago. *J. Mammal.* 84(1):55–64. DOI: http://dx.doi.org/10.1644/1545-1542(2003)084<0055:SOPDIT>2.0.CO;2

Eberhardt LL, Chapman DC and Gilbert JR (1979) A review of marine mammal census methods. *Wildl. Monogr*. 63, 46 pp. URL: http://www.jstor.org/stable/3830620

Fay FH and Ray GC (1968) Influence of climate on the distribution of walruses, *Odobenus rosmarus* (Linnaeus). I. Evidence from thermoregulatory behavior. *Zoologica*. 53:1–14

Freitas C, Kovacs KM, Ims RA, Fedak MA and Lydersen C (2009) Deep into the ice: over-wintering and habitat selection in male Atlantic walruses. *Mar. Ecol. Progr. Ser*. 375:247–261. doi: http://dx.doi.org/10.3354/meps07725

Gilbert JR (1999) Review of previous Pacific walrus surveys to develop improved survey design. In: Garner GW, Amstrup SC, Laake JK, Manly BFJ, McDonald LL, and Robertson DG (eds.) *Marine Mammal Survey and Assessment Methods*. A.A. Balkema, Rotterdam, 75–84

Gilbert JR, Waring GT, Wynne KM and Guldager N (2005) Changes in abundance of harbour seals in Maine, 1981–2001. *Mar. Mamm. Sci.* 21(3):519–535. doi: http://dx.doi.org/10.1111/j.1748-7692.2005.tb01246.x

Gjertz I, Griffiths D, Krafft BA, Lydersen C and Wiig Ø (2001) Diving and haul-out patterns of walruses *Odobenus rosmarus* on Svalbard. *Polar Biol*. 24(5):314–319. doi: http://dx.doi.org/10.1007/s003000000211

Härkönen T and Harding KC (2001) Spatial structure of harbour seal population and the implications thereof. *Can. J. Zool*. 79(12):2115–2127. doi: http://dx.doi.org/10.1139/z01-172

Haug T, Stenson GB, Corkeron PJ and Nilssen KT (2006) Estimation of harp seal (*Pagophilus groenlandicus*) pup production in the North Atlantic completed: results from surveys in the Greenland Sea in 2002. *ICES J. Mar. Sci*. 63(1):95–104. doi: http://dx.doi.org/10.1016/j.icesjms.2005.07.005

Hills S (1992) The effect of spatial and temporal variability on population assessment of Pacific walruses. PhD-thesis, University of Maine, Orono, 120 pp.

Huber H, Jeffries SJ, Brown RF, Delong RI and Van Blaricom G (2001) Correcting aerial survey counts of harbor seals (*Phoca vitulina richardsi*) in Washington and Oregon. *Mar.*

Mamm. Sci. 17(2):276–293. doi: http://dx.doi.org/10.1111/j.1748-7692.2001.tb01271.x

Jacobs SR and Terhune JM (2000) Harbor seal (*Phoca vitulina*) numbers along the New Brunswick coast of the Bay of Fundy in autumn in relation to aquaculture. *Northeastern Nat*. 7(3):289–296. doi: http://dx.doi.org/10.1656/1092-6194(2000)007[0289:HSPVNA]2.0.CO;2

Jay CV, Udevitz MS, Kwok R, Fischbach AS and Douglas DC (2010) Divergent movements of walrus and sea ice in the northern Bering Sea. *Mar. Ecol. Prog. Ser*. 407:293–302. doi: http://dx.doi.org/10.3354/meps08575.

Johnson DH (2008) In defense of indices: the case of bird surveys. *J. Wildl. Manag*. 72:857–868. doi: http://dx.doi.org/10.2193/2007-294

Johnson DH, Braun CE and Schroeder MA (2007) The bounded-count method for analysis of lek counts. In: Reese KP and Bowyers RT (eds.) *Monitoring populations of sage-grouse, Proceedings of a symposium at Idaho State University*, Contribution 1015, Idaho Forest, Wildlife and Range Experiment Station, College of Natural Resources, University of Idaho, Moscow, ID 83844-1142, Station Bulletin 88, 25–30

Kiliaan HPL and Stirling I (1978) Observations on over wintering walruses in the Eastern Canadian high Arctic. *J. Mammal*. 59(1):197–200. URL: http://www.jstor.org/stable/1379895

Koski WR (1980) Distribution of marine mammals in the Canadian Central High Arctic, July–September 1979. Report by LGL Ltd., Toronto, Ontario, for Petro Canada Exploration, Calgary, Alberta, and Arctic Biological Station, Department of Fisheries and Oceans, Ste-Anne de Bellevue, Quebec. 107 pp.

Koski WR and Davis RA (1980) Studies of the late summer distribution and fall migration of marine mammals in NW Baffin Bay and E Lancaster Sound, 1979. Rep. by LGL Ltd., Toronto, Ontario, for Petro Canada Exploration Inc., Calgary, Alberta. 214 pp.

Krebs CJ (1966) Demographic changes in fluctuating populations of *Microtus californicus. Ecol. Monogr*. 36:239–273. doi: http://dx.doi.org/10.2307/1942418

Lowry MS (1999) Counts of California sea lion (*Zalophus californianus*) pups from aerial color photographs and from the ground: a comparison of two methods. *Mar. Mamm. Sci*. 15(1):143–158. doi: http://dx.doi.org/10.1111/j.1748-7692.1999.tb00786.x

Lowry MS (2002) Counts of northern elephant seals at rookeries in the Southern California Bight: 1981–2001. US Depar. Comm., NOAA Tech. Mem., NMFS, NOAA-TM-NMFS-SWFSC-345, 53 + 10 pp.

Lowry MS, Perryman WL, Lynn MS, Westlake RL and Julian F (1996) Counts of northern elephant seals, *Mirounga angustirostris*, from large-format aerial photographs taken at rookeries in Southern California during the breeding season. *Fish. Bull*. 94:176–185

Lydersen C, Aars J and Kovacs KM (2008) Estimating the number of walruses in Svalbard from aerial surveys and behavioural data from satellite telemetry. *Arctic* 61(2):119–128. Stable URL: http://www.jstor.org/stable/40513198

Mathews EA (1995) Long-term trends in abundance of harbour seals (*Phoca vitulina richardsi*) and development of monitoring methods. In: Engstrom DR (ed.) *Proc. Third Glacier*

Bay Science Symposium 1995, Nation Park Service, Anchorage AK, 254–263

Mathews EA and Pendelton GW (2006) Declines in harbor seal (*Phoca vitulina*) numbers in Glacier Bay National Park, Alaska, 1992-2002. *Mar. Mamm. Sci.* 22(1):167–189. doi: http://dx.doi.org/10.1111/j.1748-7692.2006.00011.x

NAMMCO (2006) North Atlantic Marine Mammal Commission Fifteenth Meeting of the Council 14-16 March 2006, Selfoss, Iceland NAMMCO /15/5, Scientific Committee Report of the Thirteenth Meeting Reine, Norway, 25–27 October 2005. http://www.nammco.no/webcronize/images/Nammco/766.pdf

NAMMCO (2011) Annual Report 2010. North Atlantic Marine Mammal Commission, Tromsø, Norway: 501 pp. http://www.nammco.no/webcronize/images/Nammco/955.pdf (accessed 5 April 2012)

Olesiuk PF, Bigg MA and Ellis GM (1990) Recent trends in the abundance of harbour seals, *Phoca vitulina*, in British Columbia. *Can. J. Fish. Aquat. Sci*. 47(5):992–1003. doi: http://dx.doi.org/10.1139/f90-114

Pollock KH, Marsh H, Bailey LL, Farnsworth GL, Simons TR and Alldredge MW (2004) Separating components of detection probability in abundance estimation: an overview with diverse examples. In: Thompson WL (ed.) *Sampling rare or elusive species. Concepts, designs and techniques for estimating population parameters*. Island Press, Washington, 43-58

Priest H and Usher P (2004) The Nunavut Wildlife Harvest Study August 2004, Final Report. Iqaluit: Published by the Nunavut Wildlife Management Board. 822 pp and CD

Reder S, Lydersen C, Arnold W and Kovacs KM (2003) Haulout behaviour of High Arctic harbour seals (*Phoca vitulina vitulina*) in Svalbard, Norway. *Polar Biol*. 27(1):6–16. doi: http://dx.doi.org/10.1007/s00300-003-0557-1

Ries EH, Hiby LR and Reijnders PJ (1998) Maximum likelihood population size estimation of harbour seals in the Dutch Wadden Sea based on a mark-recapture experiment. *J. Appl. Ecol*. 35(2):332–339. doi: http://dx.doi.org/10.1046/j.1365-2664.1998.00305.x

Riewe R (1976) Inuit land use in the high Canadian Arctic. In: Freeman M (ed.) *Inuit Land Use and Occupancy Project*. Department of Indian and Northern Affairs, Ottawa, ON, Vol. 1:173–184

Robson DS and Whitlock JH (1964) Estimation of a truncation point. *Biometrika* 51:33–39

Routledge RD (1982) The method of bounded counts: when does it work? *J. Wildl. Manage*. 46(3):757–761. URL: http://www.jstor.org/stable/3808569

Salter RE (1979a) Site utilization, activity budgets, and disturbance responses of Atlantic walruses during terrestrial haul-out. *Can. J. Zool*. 57(6):1169–1180. doi: http://dx.doi.org/10.1139/z79-149

Salter RE (1979b) Observations on social behaviour of Atlantic walruses (*Odobenus rosmarus* L.) during terrestrial haul-out. *Can. J. Zool*. 58(3):461–463. doi: http://dx.doi.org/10.1139/z80-061

Sharples RJ, Mackenzie ML and Hammond PS (2009) Estimating seasonal abundance of a central place forager using counts and telemetry data. *Mar. Ecol. Progr. Ser*. 378:289–298. doi: http://dx.doi.org/10.3354/meps07827

Small RJ, Pendleton GW and Pitcher KW (2003) Trends in abundance of Alaska harbour seals, 1983–2001. *Mar. Mamm. Sci.* 19(2):344–362. doi: http://dx.doi.org/10.1111/j.1748-7692.2003.tb01113.x

Stehman SV and Overton WS (1994) Comparison of variance estimators of the Horvitz-Thompson estimator for randomized variable probability systematic sampling. *J. Amer. Stats. Assoc*. 89(425):30–43. doi: http://dx.doi.org/10.1080/01621459.1994.10476443

Stenson GB, Rivest L-P, Hammill MO, Gosselin JF and Sjare B (2003) Estimating pup production of harp seals, *Pagophilus groenlandicus*, in the Northwest *Atlantic. Mar. Mamm. Sci*. 19(1):141–160. doi: http://dx.doi.org/10.1111/j.1748-7692.2003.tb01098.x

Stenson GB, Hammill MO, and Lawson JW (2009) Estimating pup production of Northwest Atlantic Harp Seals, *Pagophilus groenlandicus*: results of the 2008 surveys. *Canadian Science Advisory Secretariat Research Document* 2009/103.

Stewart REA (2008) Redefining walrus stocks in Canada. *Arctic* 61(3):292–398. URL: http://www.jstor.org/stable/40513028

Stewart REA, Born EW, Dietz R, Heide-Jørgensen MP, Villum Jensen M, Fossette S, Laidre K, Knutsen LØ, and Rigét FF (2014) Abundance of walrus (*Odobenus rosmarus rosmarus*) in Western Nares Strait, Baffin Bay stock, during summer. *NAMMCO Sci. Publ.* 9:123–140. doi: http://dx.doi.org/10.7557/3.2611

Sverdrup O (1903) (New Land: four years in the Arctic) H. Aschehoug & Co. (W. Nygaard). Kristiania Vol., I 505 p, Vol., II, 523 pp.

Taylor BI (1997) Defining "population" to meet management objectives for marine mammals. In: Dizon AE, Chivers SJ, and Perrin WF (eds.) *Molecular Genetics of Marine Mammals*. The Society for Marine Mammalogy Lawrence, Kansas, Special Publication 3, 49–65

Taylor BL and Dizon AE (1999) First policy then science: Why a management unit based solely on genetic criteria can't work. *Mol. Ecol*. 8:S11–S16. doi: http://dx.doi.org/10.1046/j.1365-294X.1999.00797.x

Thompson PM, Fedak MA, McConnell BJ and Nicholas KS (1989) Seasonal and sex-related variation in the activity patterns of common seals (*Phoca vitulina*). *J. Appl. Ecol.* 26(2):521–535. URL: http://www.jstor.org/stable/2404078

Thompson PM, Tollit DJ, Wood D, Corpe HM, Hammond PS and Mackay A (1997) Estimating harbour seal abundance and status in an estuarine habitat in north-east Scotland. *J. Appl. Ecol*. 34(1):43–52. URL: http://www.jstor.org/stable/2404846

Thompson SK and Seber GAF (1994) Detectability in conventional adaptive sampling. *Biometrics* 50(3):712–724. URL: http://www.jstor.org/stable/2532785

Udevitz MS (1999) Modeling variability in replicated surveys at aggregation sites. In: Garner GW, Amstrup SC, Laake JK, Manly BFJ, McDonald LL, and Robertson DG (eds.) *Marine Mammal Survey and Assessment Methods*. A.A. Balkema, Rotterdam, 167–177

Udevitz MS, Jay CV and Cody MB (2005) Observer variability in pinniped of walruses at haul-out sites counts: ground-based enumeration. *Mar. Mamm. Sci.* 21(1):108–120. doi: http://dx.doi.org/10.1111/j.1748-7692.2005.tb01211.x

Udevitz MS, Jay CV, Fischbach AS and Garlich-Miller JL (2009) Modeling haul-out behaviour of walruses in Bering Sea ice. *Can. J. Zool*. 87(12):1111–1128. doi: http://dx.doi.org/10.1139/Z09-098

Walker RS, Novara AJ and Perovic PG (2008) Comparison of two methods for estimation of abundance of mountain vizcachas (*Lagidium viscacia*) based on direct counts. *Mastazoologicia Neotrop*. 15:135–140

Walsh DP, White GC, Remington TE, and Bowden DC (2004) Evaluation of the lek-count index for the greater sage-grouse. *Wildl. Soc. Bull*. 32(1):56–68. doi: http://dx.doi.org/10.2193/0091-7648(2004)32[56:EOTLIF]2.0.CO;2

Wildlife Computers. 2006. SPOT4 user guide. http://www.wildlifecomputers.com/Downloads/Documentation/SPOT4%20Manual.pdf

Williams BK, Nichols JD and Conroy MJ (2002) *Analysis and management of animal populations*. Academic Press, San Diego, 817 pp.

Yochem PK, Stewart BS, Delong RL and DeMaster DP (1987) Diel haul-out patterns and site fideity of harbor seals (*Phoca vitulina richardsi*) on San Miguel Island, California, in autumn. *Mar. Mamm. Sci.* 3(4):323–332. doi: http://dx.doi.org/10.1111/j.1748-7692.1987.tb00319.x

Zar JH (1999) Biostatistical analysis. 4th edition, Prentice Hall, 929 pp.