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SOURCES OF VARIABILITY IN AERIAL SURVEY COUNTS OF HARBOUR SEALS ON HAUL-OUT SITES IN THE BAY OF FUNDY

by

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ABSTRACT

Multiple aerial censuses were conducted of a major harbour seal (*Phoca vitulina*) haul-out area off Grand Manan, New Brunswick, Canada, during the molting period to quantify sources of variability in aerial survey counts. Counts increased and decreased with local time, with peak counts between 1200-1600 EST. Low tide may have functioned as a delimiter to this relationship by degree of emergence of haul-out sites, assuming competition for space between seals, but the apparent effect could be an alias for cumulative survey disturbance or progression through the molt period. Hot days appeared to depress counts. Standard deviations of counts made between 1200-1600, computed independently for each day to negate tide or disturbance effects, ranged from 3.7 to 7.5% of the mean. We estimated the proportion of seals in the water during peak haul-out at 20% of the population. Photographic counts usually exceeded visual counts, but the difference extended to counts of small groups of animals unlikely to have been visually miscounted. The results (visual counts) of the aerial census study were used to derive correction factors for seals in the water and time of day. These correction factors were applied to earlier estimates of total Bay of Fundy area harbour seal abundance derived from aerial surveys in 1986 and 1992 (adjusted abundances of 2 362 and 4 218 harbour seals respectively). The earlier surveys were also used to adjust the 1995 study to provide a total abundance estimate for the Bay of Fundy (5 446 harbour seals). A growth curve fitted to the three point estimates for 1986, 1992 and 1995 suggested abundance increased at a rate of 9.3% per year.

Key words: harbour seal, *Phoca vitulina*, aerial survey, population census, haul-out behavior

RÉSUMÉ

On a procédé à de multiples recensements aériens dans une grande échouerie de phoques communs (*Phoca vitulina*) au large de Grand Manan, au Nouveau-Brunswick (Canada), durant la mue, en vue de quantifier les sources de variabilité dans les dénombrements aériens. Le nombre de phoques recensé augmentait ou diminuait selon l'heure locale et culminait entre 1200 h et 1600 h, HNE. La marée basse a pu jouer un rôle de délimiteur dans la relation par degré d'émergence des échoueries, si on tient pour acquis que les phoques se disputent l'espace, mais l'effet apparent pourrait être un reflet de la perturbation cumulée due au relevé ou de la progression dans la mue. Le nombre de phoques recensé semblait diminuer les journées chaudes. Les écarts-types dans le nombre de phoques recensé entre 1200 h et 1600 h, calculés indépendamment pour chaque jour afin d'éliminer les effets de la marée ou de la perturbation, se situaient entre 3.7 et 7.5 % de la moyenne. Nous avons estimé à 20 % de la population la proportion de phoques dans l'eau durant les périodes où le nombre de phoques présents sur l'échouerie était à son point culminant. Les dénombrements photographiques aboutissaient habituellement à des chiffres plus élevés que les dénombrements visuels, mais la différence se manifestait aussi dans le recensement des petits groupes d'animaux peu susceptibles d'avoir fait l'objet d'un compte erroné dans un dénombrement visuel. Les résultats (dénombrements

visuels) du recensement aérien ont servi à calculer des facteurs de correction pour tenir compte des phoques dans l'eau et du moment de la journée. Ces facteurs de correction ont été appliqués aux estimations antérieures de l'abondance totale de phoques communs dans la baie de Fundy qui provenaient de relevés aériens réalisés en 1986 et 1992 (abondance corrigée de 2 362 et 4 218 phoques commun, respectivement). On a également rajusté en fonction des relevés antérieurs l'étude de 1995 et obtenu une abondance totale de 5 446 phoques communs dans la baie de Fundy. Une courbe de croissance ajustée d'après les trois estimations ponctuelles de 1986, 1992 et 1995 semble indiquer que l'abondance a augmenté à un taux annuel de 9.3 %.

Mots-clés : phoque commun, *Phoca vitulina*, relevé aérien, recensement de la population, montée sur l'échouerie

INTRODUCTION

Aerial surveys have been used to estimate abundance of seal populations, such as the harbour seal *Phoca vitulina*, that remain dispersed throughout their life cycle. However, due to a lack of qualitative and quantitative knowledge about seal haul-out behavior and the precision of counting methods, most attempts to obtain estimates of harbour seal populations have been regarded only as relative abundance indices or minimum population estimates (e.g. Payne and Schneider 1984; Jeffries and Johnson 1990; Olesiuk et al. 1993; Stobo and Fowler 1994; Lesage et al. 1995). Many of the problems associated with counting dispersed seal populations have been explored, usually in studies conducted independently of actual surveys, or as post-census observations that were not resolved during surveys. From a review of the literature pertaining to harbour seal population estimates and aspects of seal censusing methodology, the major concerns appear to group into three categories – random error, counting error, and variations due to haulout behavior.

Random error represents occurrences, such as human disturbance (Schneider and Payne 1983; Stewart 1984; Harvey 1987; Stobo and Fowler 1994) or change in the weather (Schneider and Payne 1983; Olesiuk et al. 1990; Simpkins et al. 2003), that alter the consistency of haul-out tendencies during the period of a survey, or failure to account for all existing haul-out sites (Olesiuk et al. 1990; Stobo and Fowler 1994). Counting errors comprise observer (man or machine) inaccuracy (Eberhardt et al. 1979; Hiby et al. 1987; Thompson and Harwood 1990), and includes failure to discern species in mixed haul-out groups (Stobo and Fowler 1994; Lesage et al. 1995; Rugh et al. 1997). The third category, variation due to haul-out behavior, can be subdivided into three general sources of systematic error:

1. Differences between habitats.
2. Differences between seasons.
3. Changes within a census period.

Differences in haul-out behavior between habitats could be attributable to temperature (Schneider and Payne 1983; Watts 1992), relative levels of human activity (Harvey 1987), or haul-out site accessability (Schneider and Payne 1983; Stewart 1984; Calambokidis et al. 1987). Differences between seasons can reflect recruitment (Olesiuk et al. 1990; Thompson and Harwood 1990) and cyclic changes in haul-out motivation such as mating, pupping or molting (Jeffries and Johnson 1990; Thompson and Harwood 1990; Stobo and Fowler 1994). Variations within a census period may be related to diurnal haul-out patterns (Stewart 1984; Calambokidis et al. 1987; Pauli and Terhune 1987; Olesiuk et al. 1990; Thompson and Harwood 1990; Simpkins et al. 2003), the tidal cycle (Schneider and Payne 1983; Pauli and Terhune 1987; Thompson and Harwood 1990; Adkison et al. 2003; Simpkins et al. 2003; Hayward et al. 2005), or differences in human activities with day of the week (Harvey 1987).

Quantification of some of the sources of error in census counts has been used in the past to make adjustments to raw counts to derive total abundance estimates. Off the west coast of Canada, Olesiuk et al. (1990) adjusted several years of aerial census counts of *Phoca vitulina* for seasonal trends in recruitment (variation in timing of surveys relative to pupping season), sites missed in particular years, and the proportion of seals assumed to be still in the water during a census. Huber et al. (2001) used radio tagging information to estimate the proportion of seals on-shore during the pupping season and incorporated the derived correction factor into their estimates of abundance for harbour seals off Washington and Oregon of the western United States. Frost et al. (1999) used generalized linear modelling to determine the influence of time of day, date, and time relative to low tide, and used the results to adjust survey counts for their harbour seal population trend analysis in Prince William Sound, Alaska. In the vicinity of the Orkney Islands of the United Kingdom, Thompson and Harwood (1990) adjusted census counts for diurnal patterns in haulout behavior and proportions of seals in the water during peak haulout, separately by sex.

Simpkins et al. (2003) and Hayward et al. (2005), in developing models to account for factors influencing counts of molting Alaska and Washington harbour seals respectively, noted that different models would likely be required for different haul-out sites, as the relative importance of factors can vary between sites.

In 1995 we conducted an experiment to quantify potential sources of error in aerial census counts of harbour (and grey) seals hauled out in the Bay of Fundy on the east coast of Canada. This region is characterized by a much greater tidal amplitude than we have seen in any previous studies, averaging over 4m with a typical maximum of about 6m in the vicinity of our census counts, such that many haul-out sites favoured by harbour seals are emergent only at or near low tide. The 1995 study, in combination with five past aerial surveys (Stobo and Fowler 1994), provided information with which we could variously adjust or account for many of the potential sources of error described in other studies, as well as consider the ramifications of the tidal amplitude, in order to estimate total abundances of harbour seals in the Bay of Fundy. Our primary objective was to determine whether an abundance estimate for Bay of Fundy harbour seals, with an associated error distribution, was attainable using aerial survey methods. A secondary objective of our study was to determine if past aerial census counts might be upgraded to total abundance estimates.

METHODS

Based on five past aerial surveys of the Bay of Fundy and southwestern Nova Scotia (Stobo and Fowler 1994), we selected a region of consistently large numbers of hauled-out harbour seals off the east coast of Grand Manan, New Brunswick (Figure 1), in which to conduct repetitive enumerations of seals at known haul-out sites, and take photographs for later counting without time restrictions. The census methodology was similar to that which we have used in the past. We counted seals from a helicopter flying at a speed of approximately 70 knots and an altitude of 600-800 feet, within +/- 2.5 hours of a low spring tide between 1000 and 1800 hrs EST, during the molting season near the

end of summer (August 5-8). Differences between this methodology and our standard survey procedure involved the time period (2.0 hour window for standard surveys), the altitude (regular surveys commonly 400-600 ft, lower if species identification was in doubt), and no attempt was made to differentiate harbour and grey seals during the study. In regular surveys we would do a total count as described above, followed by a close approach to count the lesser species, usually disturbing the seals (often some, or all, would abandon the site). In the present study we needed the seals to remain undisturbed across counts, thus only total counts from non-intrusive distances were conducted. It was thought that the photography would provide resolution of species identification. Variability in speed was required to provide enough time for counts of large groups of seals without hovering (the change in pitch of a helicopter in transition from cruising flight to a hover will often cause seals to enter the water). The altitude was adjusted upwards if seals appeared to be agitated by the helicopter approach.

A count was made of seals hauled out at each site on approach to camera range, with the helicopter making its approach at constant speed, heading and altitude until the picture was taken. Local time to the nearest minute was recorded at the start of each count. The observer count was usually completed during the approach. For larger groups of seals (over about 50) counting sometimes continued after the picture was taken; in these cases the helicopter occasionally had to begin circling the haulout area to complete a count. A 35mm camera with an F1.8 50mm lens was used to take color photographs of the sites. Upon completion of the experiment the film negatives were examined for readability, developed into slides and digitized onto CDROMS. The slides were read using both dissecting and regular microscopes, and the digital images were read using Adobe Photoshop 3.

Out of twelve sites initially selected for the experiment, two were discarded (sites 3 and 8) due to an absence of seals. Site 4 was abandoned by the seals on day 3, possibly having been disturbed by a boat. Thus the counts from this site could not be used in all analyses. The census was repeated five times a day for four days, starting 2.5 hours before low tide and ending 2.5 after low tide (each flight taking 20-45 minutes to complete). The first two days (a weekend) were calm and overcast, the last two days sunny with a light breeze. Visibility was excellent throughout, the seals seemed generally indifferent to the overflights, and instances of disturbance by boat activity appeared limited. If we felt that the overflight or a nearby boat may have induced seals to abandon the haul-out site, the counts were discarded. Only a few instances of this nature occurred. In some analyses counts were discarded if the site was not perceived to be fully emerged (more seals in the water than the site could handle, or the site itself still underwater). For comparisons between censuses we relied on the visual flight counts. However in one instance a photographic slide count was included in this dataset to replace a null value – on the first flight of the first day we found ourselves on top of site 12 before discerning it; our position was suitable for a picture, but the animals were beginning to show signs of agitation so we departed without attempting a count.

Analysis of deviance, a form of generalized linear modelling using S-Plus 4.5, was applied to the harbour seal visual flight counts , combined across sites (giving a

dataset of 20 censuses), to test for possible effects of time of day (as one-hour blocks, modelled as a quadratic), time of low tide (linear sequence variate 1-4), and weather or day of the week (a two-level factor representing overcast versus sunny weather or weekend versus weekday counts, either variable an alias for the other). The order of entry of effects into the model was determined by comparing Akaike Information Criteria (AIC) for different models, which uses χ-square tests to determine the best fit from a set of possible models (Chambers and Hastie 1993). The relative ranking of a given factor, in terms of explanatory power, is estimated by inclusion and exclusion from iterative series of possible models, with calculation of AIC statistics, to achieve the most likely hierarchy of main effects for the model. Two-way interactions between main effects, whereby the nature of one main effect is modified nonadditively according to values of another main effect, were then sequenced according to the main effects ranking.

Results of the analysis of deviance were used to provide adjustments for time of day to past survey counts. The bounded-count method (Robson and Whitlock 1964) was applied to the combined optimal counts (day 1 counts made between 1200 and 1500 EST) of seals from two proximate sites (sites 9 and 12) to estimate the proportion of seals remaining in the water during the count. This approach, described by Olesiuk et al. (1990), uses the variance between replicates to estimate the proportion of animals missing from a sample as

1 - Mean Count/[Highest Count + (Highest Count – Second Highest Count)].

Sites 9 and 12 were chosen for the relatively large numbers of seals hauled out on them, to reduce the potential for small sample error (Olesiuk et al. 1990), and their distance from other haul-out sites. The next closest apparently suitable site was 5 km away, this distance assumed to be a deterrent to local migration over the four days. Observations from previous surveys of grey seal proportions in the special study area (Stobo and Fowler 1994) were used to adjust the 1995 counts for presence of grey seals; and then the proportion of the total census area that the special study area has represented of the Bay of Fundy survey (derived from Stobo and Fowler 1994), was used to adjust an optimal 1995 census to a full survey area abundance estimate. The above adjustments were used to derive total abundance estimates of harbour seals in the region for 1986, 1992 and 1995. Application of a growth curve, ${}_{e}(\beta_0 + \beta_1 * \tau)$, to these three data points was used to derive a population abundance trajectory, assuming a constant population growth rate.

RESULTS

COUNTING METHODS

Most of the photographs taken during the first two days of the study were devoid of problems (see below) that could affect the identification of individual seals. Unfortunately, very sunny conditions during the last two days created a glare problem that ruined several photographs. As well, the seals were more inclined to be restive upon

our approach during the last two days, obliging us to adjust our altitude upwards (first two days closer to 600 ft, last two days closer to 800 ft) so as not to agitate the animals.

All three methods for reading photographs (regular and dissecting microscopes, image analysis) were linearly correlated with the flight observer counts, all were very close to one another, and all tended to give higher numbers than the flight observer counts (Figure 2). The differences between photographic and flight observer counts were significant with respect to image analysis (paired t-test p=.0002)) and dissecting microscopes (p=.012), but not with respect to the regular microscope(p=.558). Both microscope counts showed slightly greater variability relative to the flight observer counts than the digital image counts. Rereading of the more discrepant scope-image-observed counts revealed that the greater variability of microscope counts compared to the digital image counts was due to 1) instances of small groups of seals being sufficiently distant from a centre of concentration of seals to be missed during microscope reading, and 2) confusion about site boundaries causing adjacent seals from other sites to be counted erroneously. For more detailed examinations of the differences between flight and slide counts we focused on the digital image counts.

Variation between flight and slide counts declined slightly with an increase in the number of seals. The greatest differences were mostly associated with smaller numbers of seals (under 25 animals). To investigate the possibility that the differences were due to counting inanimate objects as seals on photographs, we partitioned our counts according to whether the sky was sunny or overcast (the glare/focus concern) and whether the seals were wet or dry (first half versus second half of counts each day, indexed relative to the low tide midpoint time). The latter comparison was made because we observed that wet seals, being darker, are harder to distinguish from the rocky haul-out terrain than dry seals (and much harder to differentiate by species). The haul-out site itself offers less contrast if recently emerged (wet rocks). The most extreme differences (100% or more) were all applicable to wet seals/sites on sunny days (Figure 3). And almost all of the few instances of a flight count exceeding a slide count by any appreciable amount (10% or more difference) are associated with wet seals/sites.

Under conditions of least difference between visual and slide counts (post-low tide counts on overcast days), slide counts averaged 22% higher than visual counts in the visual 10-29 count range, and 16% higher in the visual 200-300 count range.

VARIABILITY IN OBSERVED COUNTS WITHIN AND BETWEEN SURVEY DAYS

Due to the problems encountered with our photographic counts, the visual flight counts (Table 1) were used to examine variations in numbers of seals hauled out over the course of a day, and across the four days. An initial look at these data considered the five legs (flights) summed across the four days for each site (Figure 4), and summed over sites (Figure 5, Table 2 raw data columns). These examinations presented a mixture of linear

and quadratic patterns by site, and two rough trends by day of increasing numbers (first two days) or decreasing numbers (last two days) over time. But a much clearer quadratic pattern could be discerned by plotting the counts by site against local time (Figure 6, Table 3 raw data columns). We defined our local time variable as a one-hour increment, giving 1 thru 8 one-hour periods for 1000-1100, 1100-1200,…,1700-1800. Depicting this pattern summed over sites as well as averaged over days (Figure 7) suggests that the seals were most inclined to be hauled out between 1200-1600, with the tidal cycle simply delimiting whether or not this could be achieved. Since the timing of low tide changed by about an hour a day (i.e. 1205, 1310, 1420, 1520) our flight legs 1 through 5 were temporally offset (staggered) relative to the haul-out pattern. Hence leg 1 of day 1 had no parallel representative in subsequent days, leg 5 of day 1 was equivalent to leg 2 of day 4, etc. The 1200-1600 hrs haul-out preference produced a gradual transition in the daily haul-out pattern. At the start of the study period the sites were already emerged when the seals wanted to haul out, but by day 3 the seals had to wait for several of the sites to emerge during 'prime time'.

Analysis of deviance of the 20 censuses produced a model in which significant effects explained 91% of the deviance (Table 4, Figure 8). The daily temporal pattern was the most important effect, accounting for 55% of the deviance. The preference for haul-out between 1200 and 1600 hrs local time was maintained over days – the peak time did not migrate along with the shift in timing of low tide. A linear decline in counts over the four days of the surveys (tide or disturbance effect) accounted for another 20%, while 16% was attributed to interaction between the daily temporal pattern and the weather/day of week effect. Sunny weekdays produced earlier haul-outs but steeper drops during the declining counts phase of the temporal cycle, while the overcast weekend produced a more gradual haul-out but pulled the declining counts phase of the temporal pattern back toward a plateau (see Figure 7).

We used the results of the generalized linear model as a guideline for extracting an 'optimal' dataset of survey counts, comprising 11 censuses started and completed between 1200 and 1600, for which all sites were fully emerged. Site 4, abandoned on day 3 as mentioned above, was removed from this dataset. Tables 2 and 3 present the census counts by flight and time periods for both the full and optimal datasets. Differences in paired counts between the full and optimal datasets represent removal of site 4, and optimal time period counts negated due to non-emergence of one or more sites have been asterisked. The mean survey counts in Table 2 provide a direct comparison of the variablity in counts between the two datasets. The full dataset counts show standard deviations ranging from 3 to 5 times those of their corresponding optimal datasets, and represent about 25% of the mean. The standard deviations for the 11 optimal censuses range from 15 to 40 for within-day counts, and 41 to 52 for between-day (within-time) counts. The between-day deviations are roughly 10% of their means, an appreciable reduction in variance relative to the full dataset. Further reduction in deviation to 4-8% of their means is achieved when considering only within-day count variations.

ADJUSTMENTS TO PAST SURVEYS

Taking the quadratic fit of our hourly mean counts (Table 3) to time as the bottom of each hour , gives:

Haul-Out Count = -2582.7 + 474.0 (Local Time) + (-18.1) (Local Time^2)

with an R^2 of .864. Using this formulation to standardize counts for peak haulout time provided rough adjustment factors for time of day (Table 5). To adjust 1986 and 1992 survey counts we did not require factors beyond the 1500-1600 block. The extrapolation to 0900 was necessary to resolve three 1986 counts for the New Brunswick side of the inner Bay of Fundy (total of 164 seals from Musquash Head up); one of these counts (28 seals), made at 0850 EST, was treated as 0900 EST.

The proportion of seals associated with sites 9 and 12 that were in the water at peak haul-out time on the first day of the study was estimated as:

P = 1 - Mean Count/[Highest Count + (Highest Count – Second Highest Count)]
= 1 - 290.3/[327+(327-292)]
= 0.20

The earlier survey totals were adjusted for time of day and seals in the water from 1 575 to 2 362 harbour seals in 1986, and from 3 534 to 4 218 harbour seals in 1992. Taking the 1995 special study counts for day 1, flight 4 (669), and considering those areas covered by the 1995 special study as 13% of the population (13-14% of the population based on 1986 and 1992 censuses), we adjusted the 1995 study count down by 10% for the approximate number of grey seals in the haul-out aggregations (13% and 7% of seals in 1986 and 1992 respectively). We then adjusted this result by +20% for seals in the water, to get an estimate of abundance for 1995 of 5 554 harbour seals. The three estimates for 1986, 1992 and 1995 give a growth curve against time ($e^{-177.651+.093*\tau}$) that suggests a rate of increase in abundance of 9.3% per year.

Based on the highest standard deviation for the 1995 optimal datasets (52), the likely error range associated with the 1986, 1992 and 1995 abundance estimates would be within roughly 10% of the adjusted values, provided all assumptions (reliability of flight counts, proportion of seals in water, 1995 grey seal and study area proportions) are valid. If between-day variation in the optimal count dataset of our study was due entirely to temperature and survey disturbance effects (no effect of low tide within this subset of the data), the error likelihood could reach as low as 4%.

DISCUSSION

COUNTING METHODS

The digital image of the photographs gave much greater flexibility for panning and zooming than reading slides with a microscope, such that seals on the fringe of a site were more likely to be perceived. Similarly, overlap between two proximate sites in a

single picture was easier to discern with a digital image. Other researchers have projected slides onto white surfaces (e.g. Frost et al. 1999) , which would provide another form of zooming to discern seals near the boundary of an image.

Based on our observations, our photographic census method overestimated the number of seals in general, but underestimated the number of wet seals. The extent of the difference may be confounded by distance and glare, as the photographs on the two sunny days were taken from a greater altitude. However differences between slide (if readable) and observer counts of dry seals/sites on sunny days are very similar to the differences for dry seals/sites on overcast days (same general distribution of data points in Figure 3). Thompson and Harwood (1990), comparing photographic to visual counting methods, reported that photographic counts exceeded visual counts, but attributed the difference to underestimation on the part of the visual counts. While we believe that much of the difference between results could be attributed to our lack of expertise with the photographic equipment, we feel the assumption of greater photographic count accuracy may be over-generalized. For example, Table 3 in Thompson and Harwood (1990) includes a visual count of 18 seals paired with a photographic count of 23 seals, a difference of 22% that parallels observations with our data in the 10-29 seals range. It is unlikely that difficulty would occur in counting 18-23 seals from a helicopter flying at 100 meters altitude, and we wonder if the Thompson and Harwood (1990) study may have had some of the same problems as our study. A tendency to under-estimate with visual counts is probably valid, but may be of lesser magnitude than the 11-22% difference in counts suggested. Nor did the difference between slide and visual counts increase with larger numbers in our study (the difference actually became less). We have no doubt that visual counts become less accurate as the numbers increase, but do not feel that the difference was a quantifiable bias in this study. More work on the relationship between visual and photographic counting methods for harbour seal surveys, along lines of research conducted for other species of seals, is necessary to address this issue. Unfortunately most of the existing comparisons of visual versus photographic counting methods for dispersed seal populations have focused on adults hauled out on ice (e.g. Lowry et al. 1996; Rugh et al. 1997), for which the contrast is markedly enhanced; or with respect to whitecoat pups (e.g. Oien and Oritsland 1993; Oritsland and Oien 1995), where the contrast is much worse relative to our study.

VARIABILITY IN OBSERVED COUNTS WITHIN AND BETWEEN SURVEY DAYS

The rise and fall in harbour seal haul-out numbers relative to time of day or low tide has been well-documented (Schneider and Payne 1983; Calambokidis et al. 1987; Pauli and Terhune 1987; Thompson and Harwood 1990; Adkison et al. 2003; Simpkins et al. 2003; Stewart 1984; Hayward et al. 2005). Within-day patterns (tide and local time effects) in haul-out numbers generally correspond among studies, the majority of seals being hauled out in mid-afternoon, but with regional differences in peak haul-out time. For example, haul-out numbers were observed to peak at 1300-1600 off California

(Stewart 1984), 1200-1400 in Glacier Bay, Alaska (Calambokidis et al. 1987), 1600 off the Orkney Islands (Thompson and Harwood 1990), and 1500 (Pauli and Terhune 1987) or 1200-1600 (this study) in the Bay of Fundy. Affiliation between peak haul-out and low tide was observed by Simpkins et al. (2003) with molting harbour seals off Alaska (peak at low tide for one site, 2 hours after low tide at another site), and with pupping harbour seals by Hayward et al. (2005) off Washington (peak midway between high and low tide, and varied with time of day).

The progressive decline in numbers of seals hauled out over the four days may reflect an increase in the susceptibility of seals to agitation over the course of the survey, or decline in haul-out motivation with progression through the molting period or as low tide occurred later in the day. Agitation could have been induced by a cumulative disturbance effect of the survey itself , or due to high air temperatures during the last two days (Watts 1992). Generally, observations of differences between weekend and weekday counts are considered to reflect differences in human activity levels (disturbance), such that lower counts tend to be associated with weekend observations (Harvey 1987). A reversal in this relationship (weekend counts higher than weekday counts) is apparent in our study, and we believe that the greater magnitude of the decline between days 2 and 3 is likely a temperature effect, while the linear component of the decline across all days reflects one or both of tide and survey disturbance effects. This would also fit with our subjective observations of little potential for human disturbance other than the survey itself. Increase and decrease in haul-out tendencies over the course of the molting period could influence numbers over the course of weeks, but we do not know that such an effect could be discerned on a daily basis (nor do we have a precise enough notion of the timing of the molt to know if our sampling period might be associated with a crucial stage in the molt). Competition for space could occur when haul-out sites emerge only during low tide periods, a common constraint in the Bay of Fundy due to the extreme tidal amplitude. When sites are already exposed prior to the preferred haul-out time, competition for a spot may be minimal, but when the sites do not emerge until the preferred haul-out time, it may be that dominant animals take the first spots. A dominance effect seems likely, given the observed milling of seals around emerging sites. Then, hypothetically, as the water recedes the more dominant animals shift down to remain close to the water, maintaining a barrier to subdominant animals. Should this conjecture prove correct, the 1992 abundance would be under-estimated by 4-10%, as low tide ranged from 1250 to 1445 EST over the course of the census. It would also make survey count adjustments (or survey scheduling) more problematic. Our data do not provide a means to differentiate potential contributions of tidal progression, molt period, or survey disturbance to the between-days decline in counts in our study. Resolution would require a similar study, but with at least expanded coverage of the tidal cycle and time of day.

ADJUSTMENTS TO PAST SURVEYS

As with the Thompson and Harwood (1990) adjustments for counts off the Orkney Islands, we have not corrected for potential tide effects. All surveys bracketed a spring tide**.** Our 1986 and 1995 estimates are based on counts that would not be adjusted for a potential tide effect in any case, as the timing corresponds to apparently optimal conditions. The 1992 estimate, as mentioned, could be too low by 4-10%, depending on whether the linear decline in counts over days is a reflection of low tide progression and/or survey disturbance. Our 1995 estimate could be 5% too high or too low according to the suitability of the adjustment for the probable number of grey seals in our counts, given that 1986 and 1992 varied by as much. Also, any systematic change over time in the relative representation of grey seals in our counts (change in population growth rate or rates of immigration/emigration of grey seals) would bias estimates proportionately. And all our estimates are subject to the accuracy of visual flight counts and the assumed proportion of seals in the water during surveys. Our determination of the proportion of seals in the water, at 20%, is higher than the 15% reported by Olesiuk et al. (1990), though it tends toward agreement with a later work (Olesiuk et al. 1993) based on radiotag studies of haulout behavior that suggests the proportion may be as high as 25%. A similar radio tagging study of harbour seals off Alaska during the molting period (Simpkins et al. 2003) produced an overall estimate for two distantly separated sites of 16.5% in the water, but with site-specific estimates at 14.3% and 18.7%. These two sites were mentioned earlier as also exhibiting different peaks relative to low tide.

Our estimate of a 9.3% annual abundance increase for Bay of Fundy harbour seals is close to the 8.7% growth rate estimated by Waring et al. (1997) for the Gulf of Maine between 1981 and 1993. Another long-term census study of harbour seals along the New Brunswick coast of the Bay of Fundy (Jacobs and Terhune 2000), focusing on the region of highest aquacultural activity between Saint John and Quoddy Head but excluding Grand Manan, found no change in abundance between 1984 and 1998. Our estimate would be highly influenced by Grand Manan numbers, as harbour seals in this small area alone typically account for over half of the entire population throughout the Bay of Fundy (see Stobo and Fowler 1994). Human activities along the mainland New Brunswick coast may be keeping local abundances in check relative to other parts of the Bay of Fundy via higher mortality or emigration rates. If the mainland coast portion of the New Brunswick population has been either not growing or consistently contributing its' recruitment elsewhere since 1986, our estimate of population growth would still be valid. However, if variations in emigration rates or destinations have occurred during this period, such that the proportionate representation of the population among areas has changed, our estimate would be confounded accordingly.

CONCLUSIONS

Past surveys of Bay of Fundy harbour seals (Stobo and Fowler 1994) have placed more emphasis on the timing of surveys relative to low tide than time of day, so long as it was daylight. The observation that the time of day at which low tide occurs is critical for these seals is very important. Future surveys in this area could either use the adjustments for time of day determined in this study, or narrow the survey window to 1200-1600 hrs local time and disregard the effect.

We don't know if the count decline over days is entirely or partially related to tide effects. The component involving simple non-emergence obviously is related to the tidal cycle, but we have no way to differentiate a natural disinclination to haul out from one induced by our survey. Nor can we quantify the role of partial site emergence, since we cannot say for sure whether a site is fully emerged - we don't know in detail what surfaced portions of a confirmed site are suitable as far as seals are concerned. Future surveys should be scheduled so that flights circumvent the issue of whether timing of low tide is an effect. The dynamic nature of the tidal cycle in the Bay of Fundy makes this feasable, as different portions of the survey area experience low tide at sufficiently different times that the minimum can be essentially 'chased' around the Bay with appropriate flight planning. Avoiding hot days would certainly be desirable, but the logistics of flight scheduling and delimitation of the survey period by the time/tide and molting period confluence will probably mitigate against such flexibility.

The still photography methods used in our study were unsuitable for conducting a census. We needed much greater magnification without loss of focus, possibly requiring image-motion compensation (Hiby et al. 1987). We are certain that greater proficiency in photography would have made a difference. It would also be worthwhile to investigate the use of video cameras for this type of survey. We believe that much of the visual discernment by human observers is related to movement by both viewer and object viewed. If this capability could be replicated photographically, concerns about missing or misidentifying seals, and the reliability of visual counts of large numbers, could be resolved. It would be important to continue to record visual counts even if a suitable photographic methodolgy was developed, to provide a backup and allow for refinement of historical estimates.

The standard deviations of the 'optimal conditions' counts range from 4-8% of the mean. Given that the error likelihood is possibly as large as any likely annual change in population abundance, aerial estimates probably couldn't be used to track population abundance on an annual basis. They should, however, be suitable for monitoring longer-term trends (any consistent increase or decrease in abundance of 5% or more should be apparent across periods of three or more years).

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Table 1. Harbour seal haul-out site counts.

APPROXIMATE LOCATION	SITE NUMBER	DATE	FLIGHT LEGS 1	2	3	4	5
Dutch Ledge	1	950805	13	46	67	50	28
		950806	40	44	66	48	55
		950807	75	77	48	0	0
		950808	56	17	33	23	11
Dutch Ledge	2	950805	21 .		9	3	0
		950806	0	0	11	11	6
		950807	0	1	24	0	0
		950808	0	20	17	3	0
Gull Island	4	950805	71	53	70	95	1
		950806	0	2	73	90	137
		950807	0	0	0	0	0
		950808	24	12	32	0	0
Andys Ledge	5	950805	24	28	50	60	85
		950806	25	28	47	48	48
		950807	53	57	58	67	68
		950808	0	8	0	0	0
Ox Head Island	6	950805	19	23	30	36	29
		950806	8	26	33	44	45
		950807	26	28	0	0	0
		950808	5	12	0	0	0
Ox Head Ledge	7	950805	20	16	14	17	18
		950806	23	20	18	21	0
		950807	2	2	30	45	3
		950808	0	2	19	0	0
Long Ledge	8	950805	3	3	2	2	2
		950806	0	0	0	0	0
		950807	0	0	0	0	0
		950808	0	0	0	0	0
Great Duck Island	9	950805	130	160	215	280	240
		950806	160	215	215	245	210
		950807	215	150	200	190	85
		950808	190	255	240	235	235
Duck Island	10	950805	50	20	16	19	29
		950806	0	0	6	22	32
		950807	10	12	20	26	0
		950808	0	4	1	5	0
Duck Island	11	950805	0	70	55	60	48
		950806	24	24	62	24	28
		950807	36	49	1	13	5
		950808	102	91	80	78	24
Great Duck Ledge	12	950805	22	25	37	47	52
		950806	60	64	44	46	47
		950807	90	110	105	100	95
		950808	68	2	0	0	0

Table 2. Seal census counts ordered by day and flight, with daily means and standard deviations for raw and optimized data.

Day	Flight	Raw	Daily Mean	Std Dev	Optimal	Daily Mean	Std Dev
1	1	373					
	2	444					
	3	565			493		
	4	669			572		
	5	532	517	114	529	531	40
2	1	340					
	2	423					
	3	575			502		
	4	599			509		
	5	608	509	121	471	494	20
3	1	507					
	2	486			486		
	3	486			486		
	4	441			441		
	5	256	435	103		471	26
4	1	445					
	2	423			411		
	3	422			390		
	4	344					
	5	270	381	73		401	15

Table 3. Seal census counts ordered by time of day, with hourly means and standard deviations for raw and optimized data.

Day	Time	Raw	Hourly Mean	Std Dev	Optimal	Hourly Mean	Std Dev
1	1000-1100	373	373	NA			
1	1100-1200	444					
2	1100-1200	340	392	74			
1	1200-1300	565			493		
2	1200-1300	423			***		
3	1200-1300	507	498	71	***	493	NA
1	1300-1400	669			572		
2	1300-1400	575			502		
3	1300-1400	486			486		
4	1300-1400	445	544	100	***	520	46
1	1400-1500	532			529		
2	1400-1500	599			509		
3	1400-1500	486			486		
4	1400-1500	423	510	74	411	484	52
2	1500-1600	608			471		
3	1500-1600	441			441		
4	1500-1600	422	490	102	390	434	41
3	1600-1700	256					
4	1600-1700	344	300	62			
4	1700-1800	270	270	NA			
	All counts		460	112		481	52

*** Optimal time period counts negated due to non-emergence of one or more sites.

Table 4. Generalized linear model of seal haul-out counts.

RESPONSE=NUMBER OF SEALS; 20 counts (4 days X 5 flights per day)
QUADRATIC TEMPORAL PREDICTOR= STANDARDIZED LOCAL TIME;hourly blocks of time 1 thru 8 (1000-1100,1100-1200,…,1700-1800)
CONFOUNDING LINEAR COVARIATE=STANDARDIZED TIME OF MAX LOW TIDE; increments 1-4
CONFOUNDING FACTOR=WEATHER; overcast or sunny OR DAY OF WEEK; weekend or weekday

Sequence of entry of main and interaction effects into model determined by iterative step function

Final Model Formula = poly(Time, 2) + Tide + Weather + interactions

Gaussian Model	Df	Null Deviance
none	19	236063

		Deviance Explained	Percent Explained	F Value	Significance
poly(Time, 2)	2	129699	55%	37.085	0.000
Tide	1	46699	20%	26.706	0.001
Weather	1	1832	1%	1.048	0.336
poly(Time, 2):Tide	2	1398	1%	0.400	0.683
poly(Time, 2):Weather	2	38189	16%	10.920	0.005
Tide:Weather	1	1850	1%	1.058	0.334
poly(Time, 2):Tide:Weather	2	2406	1%	0.688	0.530

Dispersion Parameter for Gaussian family taken to be 1748.679

Coefficients for Significant Effects

	Value	Std. Error	t value
(Intercept)	477.607	101.266	4.716
poly(Time,2)1	-920.479	597.687	-1.540
poly(Time,2)2	-913.135	508.483	-1.796
Tide	1.271	38.391	0.033
poly(Time,2)1:Tide	459.203	227.949	2.014
poly(Time,2)2:Tide	207.072	185.672	1.115

Table 5. Adjustment factors to standardize seal haul-out counts for local time.

Local Time	Adjustment Factor
0900-1000 (extrapolated)	2.4
1000-1100	1.5
1100-1200	1.2
1200-1300	1
1300-1400	1
1400-1500	1
1500-1600	1.1
1600-1700	1.4
1700-1800	2.1

Figure 1. Census study area and site locations of haul-out counts.

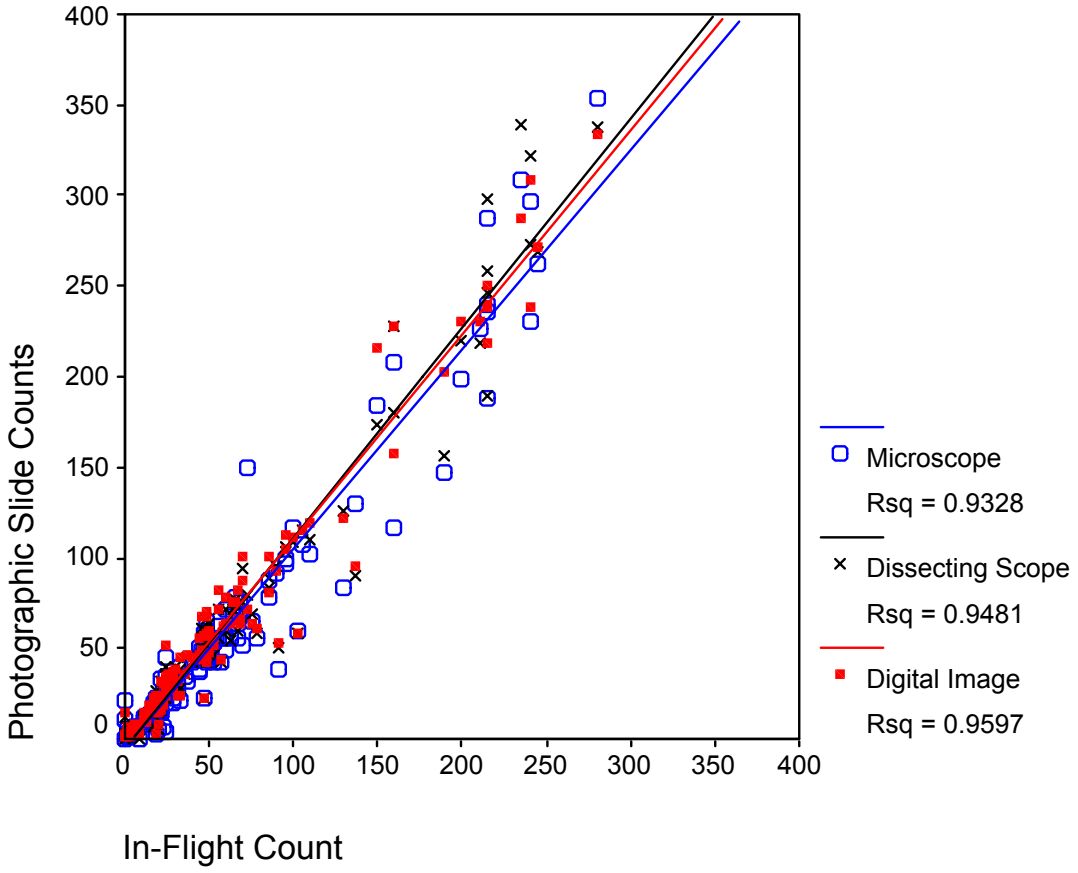

Figure 2. Comparison of in-flight observer counts to counts made later from photographic images.

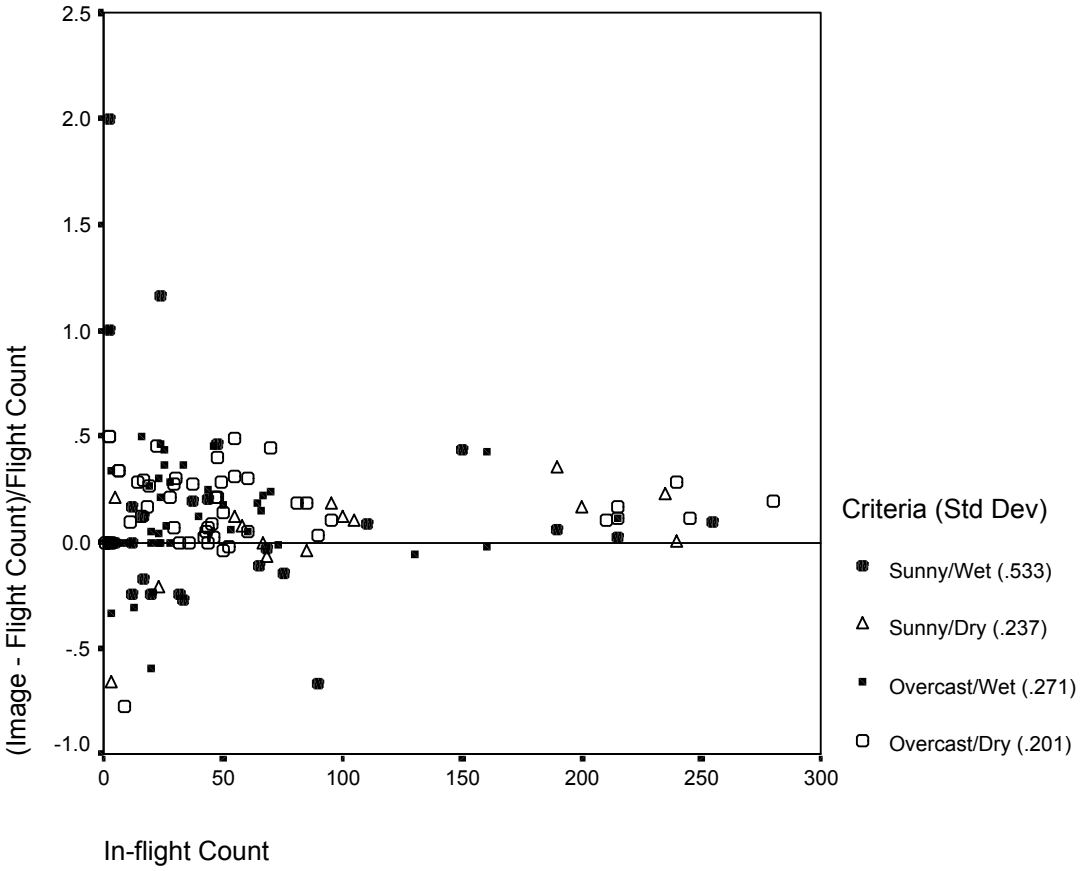

Figure 3. Differences between in-flight observer counts and post-survey counts of photographic images in relation to the magnitude of the in-flight count. Counts are categorized according to their association with potentially confounding aspects of weather and haul-out site dampness.

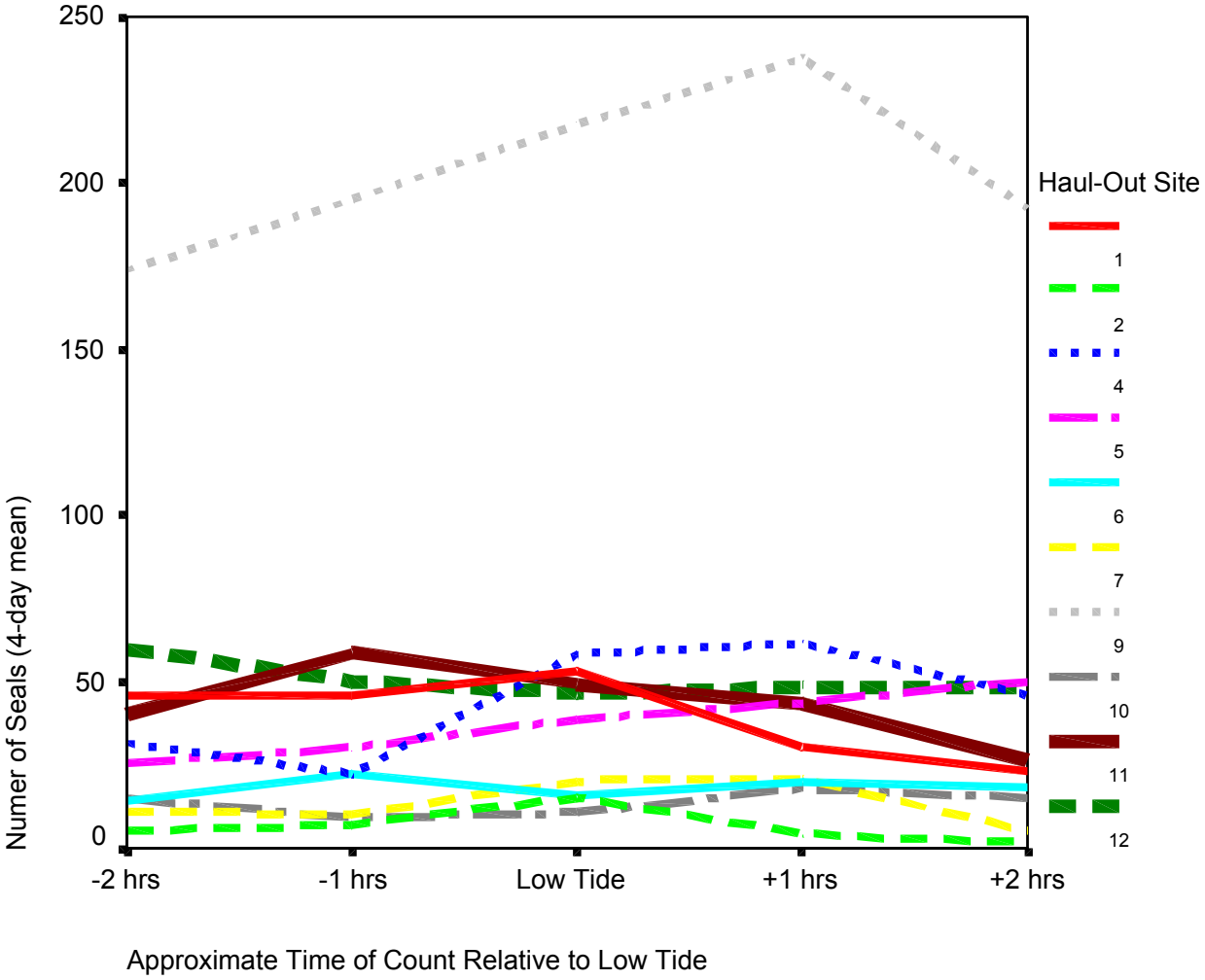

Figure 4. Mean counts of harbour seals on haul-out sites relative to time of lowest tide.

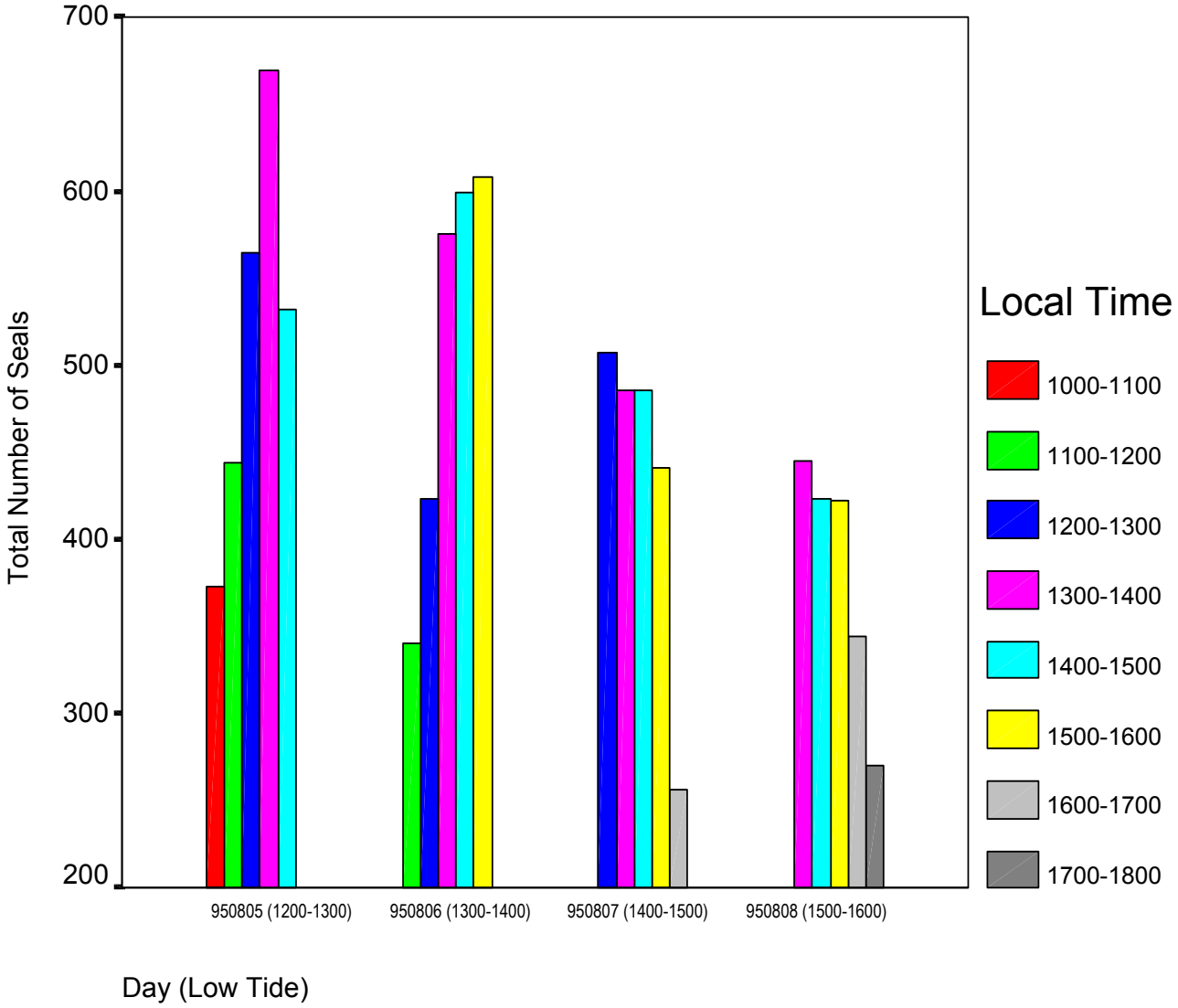

Figure 5. Total counts of seals during each local time period over the 4 days of the survey, as the timing of lowest tide gets later.

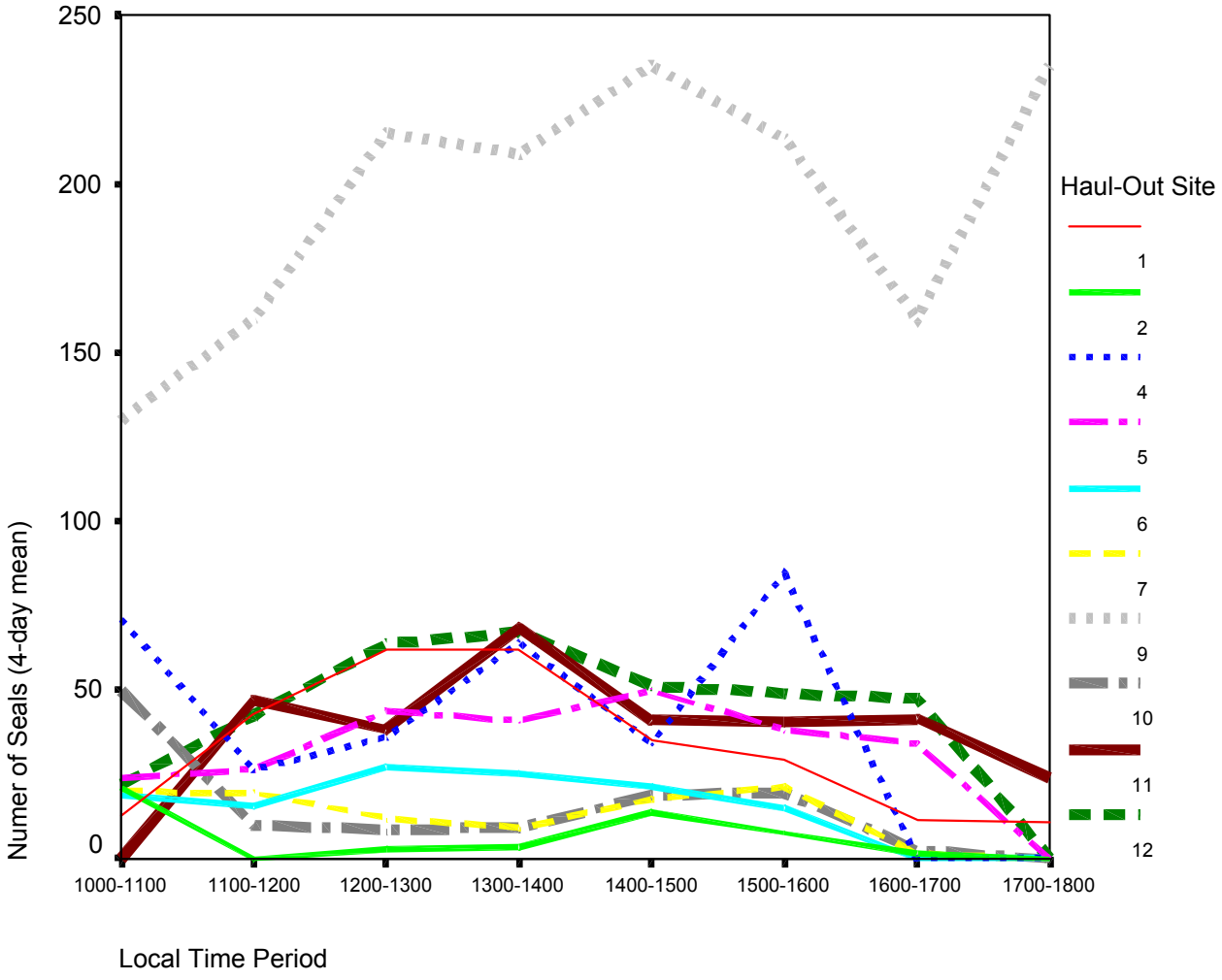

Figure 6. Mean counts of harbour seals at each site relative to local time.

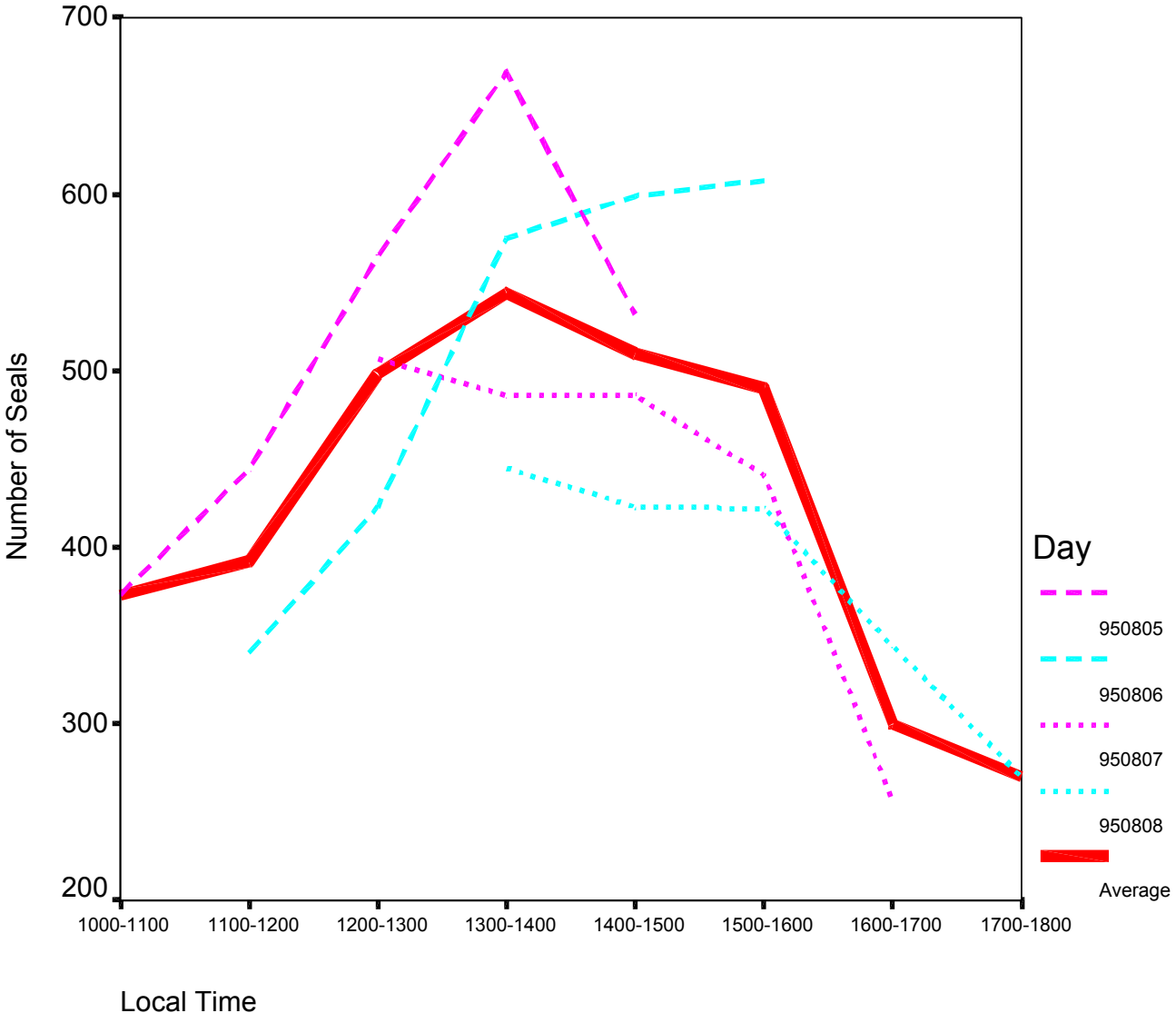

Figure 7. Counts of harbour seals relative to local time shown separately for each day of the survey (dashed lines), and with the average count across all days for each time period superimposed (solid line).

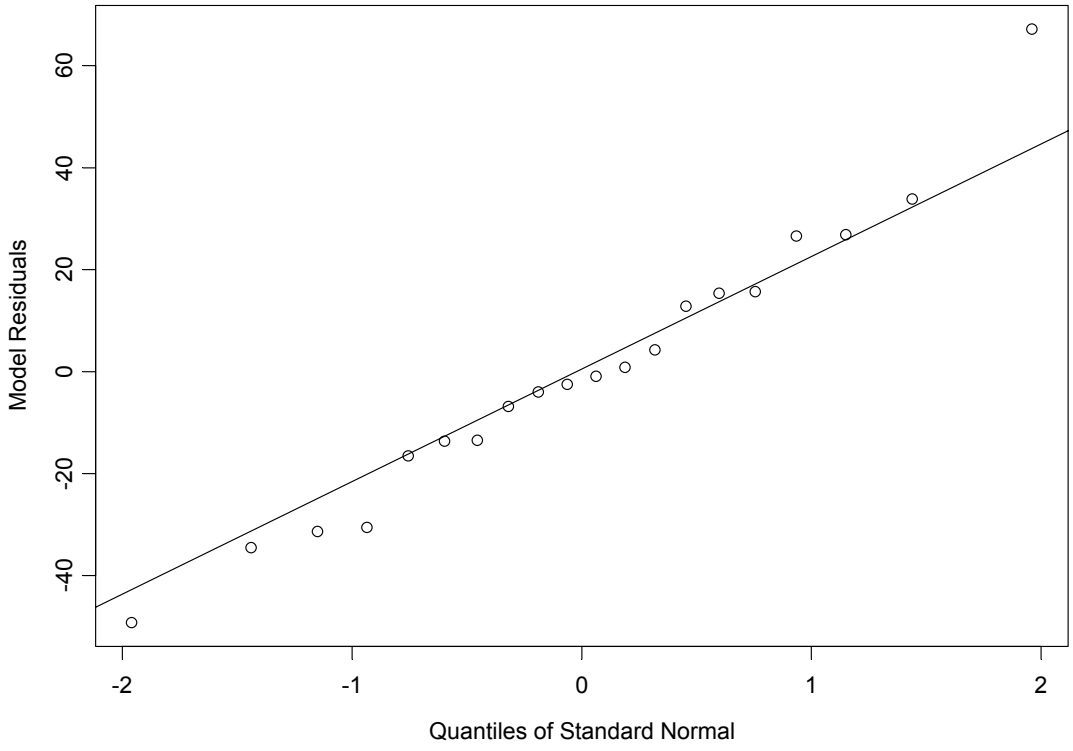

Figure 8. Quantile plot of the residuals from the generalized linear model of harbour seal haul-out counts. The straight line represents the perfect fit to a Gaussian model.