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An assessment of the status of harbour seals  
(*Phoca vitulina*) in British Columbia

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## ABSTRACT

Population trends and abundance of harbour seals in British Columbia are assessed based on aerial surveys conducted during 1966-98 (133 flights). The assessment is an update of an earlier report published in the *Canadian Journal of Fisheries and Aquatic Sciences* (Olesiuk et al. 1990a). Progress since the original assessment includes: 1) an analysis of more recent population trends based on census data collected during 1989-98 (an additional 58 flights); 2) expansion of survey coverage to include the central and northwest coast of Vancouver Island, the south and southwest Queen Charlotte Islands, northwestern Queen Charlotte Strait, and the Broughton Archipelago (an increase from 24 to 36% of the total British Columbia coastline); 3) an improved correction factor to account for animals not hauled out and hence missed during surveys based on an analysis of haulout patterns using time-depth recorders; and 4) a consideration of the statistical precision of the population growth rate and abundance estimates. It is estimated that abundance of harbour seals in the Strait of Georgia increased about ten-fold from 3,570 (95% confidence interval of 2,480 to 4,650) animals when the first standardized censuses were conducted in 1973 to about 37,300 (95% confidence interval of 28,200 to 46,300) by 1996-98. Populations grew at a rate of about 11.5% (95% confidence interval of 11.1 to 12.2%) per annum during the 1970s and 1980s, but the growth rate began to slow in the early 1990s and the population now appears to have stabilized. These trends appear to be indicative of harbour seal populations throughout British Columbia, and probably represent the recovery of populations that had been depleted by predator control programs and especially commercial harvests prior to the species being protected in 1970. Total abundance of seals in British Columbia in 1996-98 was estimated to be on the order of about 108,000 based on an extrapolation of the observed density of seals in surveyed areas to the entire province and on the relative distribution of historical bounty kills. This estimate is about 35% greater than our previous estimate of 75,000-88,000 in 1988 (Olesiuk et al. 1990a) due in part to the continued population growth, but also because time-depth recorders indicated that a greater proportion of animals were not hauled out and hence missed during surveys than was previously believed (39% as opposed to 12-20%). Recommendations are made for future aerial survey requirements to monitor population trends and to derive more reliable estimates of province-wide abundance.

## RESUME

Ce document présente une évaluation des tendances démographiques et de l'abondance du phoque commun en Colombie-Britannique qui est fondée sur des relevés aériens effectués de 1966 à 1998 (133 vols). Il s'agit d'une mise à jour d'une évaluation antérieurement publiée dans le Journal canadien des sciences halieutiques et aquatiques (Olesiuk et coll. 1990a). Les améliorations suivantes ont été apportées par rapport au relevé original : 1) une analyse des tendances démographiques récentes fondée sur les relevés effectués de 1989 à 1998 (58 vols supplémentaires); 2) l'élargissement de la couverture du relevé incluant le centre et le nord-ouest de la côte de l'île de Vancouver, le sud et le sud-ouest des Îles de la Reine-Charlotte, le nord-ouest du détroit de la Reine-Charlotte et l'archipel de Broughton (une augmentation de 24 % à 36 % du total de la côte de la Colombie-Britannique ; 3) un facteur de correction amélioré qui, grâce à une analyse des patrons de ramassage et à l'utilisation d'enregistreurs de durée-profondeur, permet de tenir compte des phoques non ramassés et non comptés lors des relevés ; et 4) la prise en compte de l'exactitude des valeurs estimées du taux de croissance démographique et de l'abondance. Selon les estimations, l'abondance du phoque commun dans le détroit de Georgia a décuplé, passant de 3 570 sujets (2 480 - 4 650, intervalle de confiance de 95 %) lors des premiers relevés standardisés effectués en 1973, à quelque 37 300 (28 200 - 46 300, intervalle de confiance de 95 %) en 1996-1998. Le taux de croissance de la population a augmenté à environ 11,5 % par an (11,1 - 12,2 %, intervalle de confiance de 95 %) au cours des décennies 1970 et 1980, mais a commencé à décliner au début des années 1990. La population paraît présentement s'être stabilisée. Ces tendances semblent refléter l'état des populations du phoque commun partout en Colombie-Britannique, et témoignent probablement d'un rétablissement des populations appauvries en raison du programme de contrôle des prédateurs et surtout de la chasse commerciale pratiquée avant la protection de l'espèce en 1970. En tout, le nombre de phoques communs en Colombie-Britannique en 1996-1998 était estimée à environ 108 000 individus. Cette valeur est fondée sur une extrapolation de la densité observée des phoques dans les zones de relevés à l'ensemble de la province ainsi que sur la distribution relative des résultats de la chasse contre primes antérieurement effectuée. Cette estimation est d'environ 35 % supérieure à la précédente, qui était de 75 000 à 88 000 individus en 1988 (Olesiuk et coll. 1990a), ce qui est attribuable à la poursuite de la croissance démographique et à l'utilisation d'enregistreurs de durée-profondeur qui a révélé que la proportion de phoques se trouvant dans l'eau, et n'étant donc pas comptés lors des relevés, était supérieure à ce que l'on avait cru jusque là (39 % plutôt que 12-20 %). Il est recommandé de procéder à d'autres relevés aériens afin d'effectuer un suivi des tendances démographiques et d'obtenir une estimation plus fiable de l'abondance à l'échelle de toute la province.

## INTRODUCTION

Harbour seals (*Phoca vitulina*) are widely distributed in temperate and subarctic waters throughout much of the Northern Hemisphere. Two subspecies occur in the Pacific: *P. v. stejnegeri* inhabits the western Pacific near Japan, and *P.v. richardsi* the eastern Pacific. The latter occurs in inshore waters from central Baja California northward as far as Bristol Bay and westward as far as the Aleutian and Pribilof Islands in Alaska (Shaughnessy and Fay 1977; Bigg 1981). The species is common in coastal areas, inlets and estuaries throughout British Columbia, and also occurs in some rivers and lakes (Fisher 1952; Spalding 1964; Bigg 1969a). Although animals may undertake local movements associated with feeding, breeding, and moulting (Scheffer and Slipp 1944; Fisher 1952; van Bemmell 1956; Vaughn 1971; Paulbitski and Maguire 1972; Brown and Mate 1983; Jeffries 1986; Thompson 1989), the species is considered to be non-migratory. Indeed, satellite and radio telemetry have shown that animals generally exhibit a high degree of site fidelity, with movements greater than several hundred kilometers being relatively uncommon (Pitcher and McAllister 1981; Harvey 1987; Huber et al. 1992; Olesiuk et al. 1995; Frost et al. 1996; Swain and Small 1997).

In recent years there has been much interest in the status of harbour seal populations in the northeastern Pacific. In the southern part of their range (California to southeast Alaska), harbour seal populations, as is the case for most pinniped populations, appear to be increasing (Barlow et al. 1995; Olesiuk et al. 1990a), and there is concern over their interactions with fishing activities and impact on fishery resources such as salmon (Mate 1980; Olesiuk 1993; Olesiuk et al. 1996). In the northern part of their range (Gulf of Alaska and Bering Sea), harbour seal populations, again as is the case for most pinniped populations, appear to be declining (Pitcher 1990; Hill et al. 1997), and the main focus has been on assessing the extent and ascertaining the causes of these declines (Small et al. 1997, 1998).

Knowledge of abundance and population trends is central to the management of wildlife, and considerable effort has recently been made to census harbour seal populations in the northeastern Pacific. Since the early 1980s, a series of systematic harbour seal surveys has been conducted annually along the California coast (Miller et al. 1983; Hanan 1996). During the 1970s and 1980s surveys were periodically conducted to monitor changes in relative abundance in Oregon and Washington State (Johnson and Jeffries 1977; Calambokidis et al. 1979; Brown and Mate 1983; Brown 1986; Jeffries 1986), and during 1991-93 an intensive 3-year project was undertaken to determine total abundance (Huber et al. 1992; Huber 1995; Brown 1997). In the early 1980s, several trend routes were established in Alaska to monitor harbour seal numbers at a fixed set of haulout sites, and the routes were monitored sporadically during the 1980s (Calkins and Pitcher 1984; Pitcher 1986; Pitcher 1989). In the 1990s the trend route surveys were expanded to other regions, and have since been monitored on a regular basis (Lewis et al. 1996; Mathews and Wamble 1997; Small et al. 1997, 1988). During 1990-94, a massive effort was undertaken to survey the entire state of Alaska (Loughlin 1992, 1993, 1994; Withrow and Loughlin 1995a), and the state-wide survey is now in the process of being repeated (Withrow and Loughlin 1996a, 1997a). In each case, small fixed-wing aircraft have been used to count seals hauled out on land during peak diurnal haulout periods (typically low tide) either during the

pupping season (California, Oregon, Washington and British Columbia) or the annual moult (Alaska).

It is widely recognized that not all harbour seals will be hauled out during surveys and because animals dispersed at sea are virtually impossible to count, some proportion of animals will always be missed. Along with the recent increase in survey effort, there have been several important developments in determining actual abundance from survey counts. During the late 1970s and through the 1980s, researchers began to use telemetry to establish what proportion of animals were hauled out on land at any given time and how this varied seasonally, diurnally, and with various environmental conditions (Pitcher and McAllister 1981; Stewart and Yochem 1983; Stewart 1984; Harvey 1987; Yochem et al. 1987), which provided the first basis for inferring what proportion of animals might have been seen during surveys (Harvey 1987; see also review by Boveng 1988). By the 1990s, researchers had begun to conduct surveys and telemetry studies concurrently, such that it was possible to calculate corrections that were more directly applicable to the census count. Hanan (1996) monitored radio-tagged animals at several haulout sites in California and was thus able to calculate correction factors based on the proportion of animals that came ashore each day during the survey period. Huber (1995) monitored radio-tagged seals during survey flights, and was thus able to calculate correction factors based on the proportion of animals hauled out while counts were actually being made. These techniques are currently being employed to investigate how correction factors may vary geographically, by substrate type, and with survey conditions (Withrow and Loughlin 1995b, 1996b, 1997b).

Significant developments have also been made in assessing population trends from survey data. Frost et al. (1997, 1999) noted that since harbour seal surveys cannot always be conducted under ideal or sometimes even similar conditions, underlying population trends tend to be masked by “noise” introduced by confounding factors that may affect the counts, such as date, time-of-day, and time relative to low tide. In order to minimize such noise, they developed generalized linear (Poisson regression) models to adjust survey counts to a standardized set of “optimal” conditions, and showed that such standardized counts were far more powerful and accurate at detecting underlying population trends (Frost et al. 1997, 1999). Analogous models have been refined to include variables on continuous scales and interactions among them, and are being routinely employed to assess harbour seal population trends in other regions (Lewis et al. 1996; Small et al. 1997, 1998).

In British Columbia, the first aerial harbour seal surveys were undertaken in the mid 1960s, and standardized aerial censuses have been conducted periodically since the early 1970s and routinely since the early 1980s. Olesiuk et al. (1990a) analyzed the census data collected up to 1988, and concluded that harbour seal populations throughout British Columbia had been increasing at a rate of about 12.5% per annum. Using a crude correction factor based on the variability of replicated surveys, they estimated that total abundance on the B.C. coast had increased from about 9,000-10,500 when the species was protected in 1970, to about 75,000-88,000 in 1988, which they attributed to recovery from predator control kills and especially commercial harvests conducted between the late 1800s and 1960s.

In this report, I present an updated and revised assessment of the status of harbour seals in British Columbia based on survey data collected and ancillary studies conducted since the

original assessment (Olesiuk et al. 1990a). Progress since the original assessment includes: 1) an analysis of more recent population trends based on surveys conducted during 1988-98 2) an examination of population trends in Queen Charlotte Strait and the Queen Charlotte Islands where there are now a time-series of census data; 3) an improved estimate of total abundance in British Columbia as survey coverage has now been expanded to include the central and northwest coast of Vancouver Island, northwestern Queen Charlotte Strait and the Broughton Archipelago, and the south and southwest coast of the Queen Charlotte Islands, which represents an increase from 24% to 36% of the total coastline; and 4) a consideration of the statistical precision of the abundance and population growth rate estimates. An improved correction factor to account for animals not hauled out and hence missed during surveys is also developed based on an analysis of haulout patterns as determined by deployment of time-depth recorders. My correction factor has features of both Frost et. al.'s (1997,1999) standardization and Huber's (1995) census correction factors. Like Frost et al., I adjust each count according to temporal and environmental factors at the precise time the count was made, such as time-of-day, height of the low tide, and most importantly the time relative to low tide. However, like Huber, my correction is based on the estimated proportion of animals actually hauled out under survey conditions, such that the adjusted counts represent estimates of absolute abundance.

## METHODS

### *Study Area and Duration*

Aerial harbour seal censuses (133 flights; Appendix I) were conducted in five regions of British Columbia: the Strait of Georgia including Jarvis Inlet, the west coast of Vancouver Island, Queen Charlotte Strait including the Broughton Archipelago, the Queen Charlotte Islands, and the lower Skeena River and surrounding area (Figure 1). In order to facilitate data analysis, the larger regions were partitioned into subareas. The Strait of Georgia was partitioned into seven subareas (*SGULF*, *BBAY*, *FRASERR*, *HOWESD*, *GULFISL*, *NEGULF*, *NWGULF*), the Queen Charlotte Islands into four subareas (*NEQCI*, *SEQCI*, *SQCI*, and *SWQCI*), the west coast of Vancouver Island into four subareas (*SWVANISL*, *BARKLYSD*, *MWVANISL*, *NWVANISL*), and Queen Charlotte Strait into three subareas (*SEQCSTR*, *NWQCSTR*, and *BROUGHT*). The subarea boundaries were delineated on the basis of areas which could be or had been surveyed within a single low-tide census window (see *Census Techniques*). Exceptions were *BBAY*, *FRASERR* and *HOWESD*, which could be surveyed together on one flight. The boundaries of the Strait of Georgia subareas were delineated in the early 1980s, but as a result of continued population growth surveys now take longer to conduct and several can no longer be surveyed during a single tidal window. The same boundaries used in the original assessment were nonetheless retained for consistency.

The primary study area was the Strait of Georgia (101 flights) which is herein defined as all Canadian waters from Race Rocks in the Strait of Juan de Fuca to the north end of Quadra Island (Figure 1). Traditional haulout sites in this area was first noted by the late Dr. Michael A.

Bigg in the early-1960s during field studies and conversations with seals hunters. Subareas *BBAY*, *FRASERR*, *GULFISL* and a portion of *SGULF* were first surveyed in 1966. All subareas were surveyed at least once and most twice during 1973-74 with the exception of the *NWGULF*, which was first surveyed in 1976. During 1982-87, three to seven (mean=4.3) of the subareas were surveyed annually. Duplicate censuses were conducted in *BBAY-FRASERR* in 1985 and 1986, and the *SGULF* in 1987. In 1988, the entire Strait of Georgia was surveyed once just prior to and again toward the end of the pupping season (14 flights), and a portion was surveyed a third time during the autumn moult (4 flights). Since 1990, the entire Strait of Georgia has been surveyed biennially (1990, 1992, 1994, 1996 and 1998). This extensive time-series provides the most powerful data for assessing population trends.

Two or more censuses have also been conducted off the southwest coast of Vancouver Island (4 flights), in Queen Charlotte Strait (5 flights), in a portion of the Queen Charlotte Islands (6 flights) (see Olesiuk et al. 1993), and in the lower Skeena River and surrounding area (9 flights). These time-series, albeit short and sporadic, provide additional information on trends in abundance, and were thus useful for determining whether the trends in the Strait of Georgia were indicative of those of other regions of the province.

In addition, Jervis Inlet was surveyed once in 1987 (one flight), the central and northwest coast of Vancouver Island was surveyed for the first time during 1993-96 as part of a *Nestucca Trust Fund* resource inventory (7 flights), the southern and southwest Queen Charlotte Islands were first surveyed in 1994 as part of *Parks Canada* resource mapping (3 flights), and the northwestern Queen Charlotte Strait and Broughton Archipelago were first surveyed in 1989 and 1996 respectively (4 flights). Although trends in abundance could not be assessed from these single surveys, they nevertheless provided additional information on the density of seals in other regions and thus facilitated improved estimates of total abundance on the British Columbia coast.

### ***Census Techniques***

Aerial censuses were conducted from small, fixed-wing aircraft, typically a *Cessna 172*, *180* or *185* or a *de Havilland Beaver*. The later model of aircraft was much preferred owing to its superior stalling characteristics, slower cruising speed, and because its window configuration was generally more suitable for photography. Aircraft were flown at an altitude of about 150-200 meters and an airspeed of 125 km·hr<sup>-1</sup>. Shorelines were followed and all islands circumnavigated at a distance of about 100-200 meters. All known haulout sites were specifically checked, and 1-3 observers scanned, usually with the aid of 8X40 or 7X35 binoculars, for new haulout sites and swimming animals. It is worth noting that we always conducted detailed searches of the entire survey area, even during replicate surveys, as opposed to the site-to-site type replicates that have been conducted by some other agencies. Visual counts were made of swimming animals and small groups (<10) of hauled out animals. Larger groups, unless widely scattered, were typically photographed with a hand held 35-mm SLR camera equipped with a motor drive and 135-200 mm lens using high speed Ektachrome (*ISO* 200-400) or Kodachrome (*ISO* 200) colour slide film, and subsequently counted from projected transparencies.

The above protocol had to be modified for two categories of haulout sites. In the smaller estuaries along the east side of Vancouver Island, animals typically hauled out on logbooms primarily during the high tides that occurred at night (see Figures 6b and 7b), and during the day animals not out foraging were usually found resting in groups on the ocean bottom in shallow water. In such cases it was difficult to photograph animals and we would therefore circle these restricted areas and obtain relatively good visual counts of animals in the water. During the June-August census period, these small estuaries account for only about 5% of the total Strait of Georgia population (Olesiuk et al 1990b). Some haulout sites, notably those in the northern Strait of Georgia, were comprised of numerous inter-tidal boulders scattered along beaches, and seals would haul out individually or in very small groups on each boulder. Some of these haulout sites were utilized by several hundred seals (the largest being Marina Reef with a maximum count of 594; Appendix II). Since these animals were usually too scattered to photograph, we would circle the area continuously, sometimes for up to 20 minutes, and make visual counts with the aid of binoculars until our estimates had stabilized.

Since 1973, censuses have been conducted under standardized conditions during which it was believed that maximum numbers of seals were hauled out (see *Results*; Olesiuk et al 1990a). Most importantly, censuses were timed to coincide with low tides that occurred between approximately 08:30 and 11:30 PDT. Summer tides in British Columbia are generally mixed semi-diurnal, such that there are generally two daily low tides that differ considerably in height, with a maximum scope of about 5 meters. Censuses usually began about 2.0-2.5 hours prior to the lower daily low tide, which typically ranged from about 0 to 1.5 meters above datum, and ended just before or within an hour after low tide. The precise point at which surveys were initiated and terminated was dictated by observations of seals made during the census flight (see *Discussion*). When possible, censuses in high traffic areas were conducted on weekdays so as to minimize disturbance by recreational boaters. Flights were canceled during inclement weather (i.e. rough seas, high winds or heavy precipitation) as seals appeared to be less inclined to haul out under such conditions and were difficult to count in the water. Censuses were generally conducted toward the end of the pupping season (see *Count Adjustments*). These preconditions limited censuses in a given region to usually two tidal cycles each year, each lasting 3-4 days. However, because pupping was earlier, census windows occurred about 1-1/2 months earlier on the northern coast than on the southern coast of the province.

### ***Count Adjustments***

Prior to trend analysis, survey counts were adjusted to account for: 1) known haulout sites that may have been missed during the survey flight; and 2) differences in the seasonal timing of the survey:

$$[1] C_{ADj_{it}} = C_{it} \cdot (1 - M_{it})^{-1} \cdot B_{it}$$

where  $C_{ADj_{it}}$  and  $C_{it}$  denote the adjusted and raw counts respectively for the  $i$ th subarea in the  $t$ th year respectively.

The first adjustment,  $(1-M_{it})^{-1}$ , was made to account for known haulout sites in the subarea that were known to have been missed. Because flight paths varied slightly between years, some known haulout sites in a subarea, particularly those near its periphery, were occasionally not surveyed. In a few instances counts were not attempted or were discarded when it was obvious the site had recently been disturbed (evidence of the disturbance was seen at the time of the census). In such cases the proportion of seals in the subarea that would have been on the missed sites,  $M_{it}$ , was estimated based on the proportion of the total number of animals in the subarea that occupied the missed sites during the closest preceding or proceeding complete census. This adjustment was usually very minor because surveys were not used in the analysis unless coverage was nearly complete (range 82.0 to 100%; mean = 99.4%).

The second adjustment,  $B_{it}$ , accounted for differences in the dates of censuses, which was important when censuses were conducted at different stages of the pupping season. Life tables for harbour seals in the Strait of Georgia indicated that pups comprised 20.4% of the total (including pups) post-pupping population (Bigg 1969a; Olesiuk 1993), which is similar to the composition of pups at the end of the pupping season reported for other areas: 18.6% in the Shetland Islands (Venables and Venables 1955); 19.9-23.8% in Atlantic Canada (Boulva and McLaren 1979); 20.8% in Ireland (Summers et al. 1980); 16.3-21.4% and 14.2-17.8% in Netarts and Tillamook Bays, Oregon (Brown and Mate 1983), and 16.7% in Puget Sound (Calambokodis et al. 1985). Thus, if its assumed pups constitute 20% of the post-pupping population, the population would increase by a factor of 1.25 during the relatively brief pupping season. As a result, a series of counts conducted progressively later in the pupping season would tend to exaggerate the true rate of increase and *vice versa* (Jeffries 1986).

The potential for the aforementioned bias was minimized by adjusting all counts to post-pupping levels. Biggs's (1969a) observations of neonates in the Strait of Georgia indicated that pupping was normally distributed over time (Shapiro and Wilke's [1965] small sample procedure;  $W=0.976$ ,  $n=39$ ,  $P=0.648$ ) with a mean pupping Julian date,  $\mu$ , of 208 (27 July) and standard deviation,  $\sigma$ , of 16.1 days (Figure 2). Accordingly, correction factors to account for births subsequent to censuses in the Strait of Georgia,  $B_{it}$ , were obtained from a cumulative normal function:

$$[2] B_{it} = 1.25 - \int_{-\infty}^{\frac{date-\mu}{\sigma}} \frac{1}{\sqrt{2\pi}} \cdot e^{-t^2/2} \cdot dt \cdot 0.25$$

which was solved using standard normal tables (Snedecor and Cochran 1980). Corrections ranged from 1.25 for censuses conducted prior to any births to 1.00 for censuses conducted after pupping was completed. Except as noted below, censuses in the Strait of Georgia were conducted toward the end of the pupping season (03 August - 09 September) so this adjustment was generally minor, ranging from 1.000 to 1.082. However, corrections for the 1973 censuses (11-15 June) and the earliest 1988 census (30 May - 16 June), which were conducted prior to most births, ranged from 1.249 to 1.250. Corrections for the 1996 censuses of *SGULF*, *BBAY*, *FRASERR* and *GULFISL* (27-28 July), which was about midway through the pupping season, ranged from 1.107 to 1.131.

Since the pupping season varies with latitude (Bigg 1969b; Temte et al. 1991), it was assumed that the timing of pupping in Jervis Inlet, off the west coast of Vancouver Island, and in Queen Charlotte Strait was similar to that in the Strait of Georgia, and equation [2] was thus used to adjust counts in those areas to post-pupping levels. Any violation of this assumption would have had a minimal effect because the censuses were conducted late (25 August - 20 September) in the pupping season such that the corrections were minor; 1.001 to 1.011.

Quantitative data on the timing of pupping in the Skeena River were not available, but it is known to occur earlier than in the Strait of Georgia (Bigg 1969b). Fisher (1952) reported that pupping in the Skeena River began in late May, peaked in early June, and was completed by late June. Assuming that the mean pupping date was on Julian day 161 (10 June) and that the duration of the pupping season was similar to that in the Strait of Georgia, an adjustment for the Skeena River counts was obtained by displacing the Strait of Georgia curve 47 days to the left (Figure 2). Because the Skeena River censuses were conducted toward the end of the pupping season and on virtually the same date most years, the correction factors were generally minimal, 1.006 to 1.106, and had a negligible effect on population trends.

The Skeena River pupping curve was also applied to counts for the Queen Charlotte Islands, since the two regions were at similar latitudes. The applicability of the Skeena River curve was substantiated by the recoveries of term fetuses by seal hunters in the Queen Charlotte Islands (B. and D. McNaughton, General Delivery, Sechelt, British Columbia, V0N 3A0, pers. comm.), which indicated that pupping peaked during late May or early June (Olesiuk, unpublished data). Since the Queen Charlotte censuses were conducted after essentially all pups had been born (22-24 July), the correction factors were negligible, 1.001.

The unadjusted counts for haulout sites, maps showing their location, the adjustment factors used for missed sites and unborn pups, and the adjusted counts are given Appendices II and III. The adjusted counts are intended to represent counts had the geographic coverage and timing (relative to the pupping season) of surveys had been identical in all years. They thus reflect all of the inherent variability due to the inaccuracy of visual counts or interpretation of photographs, imprecision and inaccuracies in the adjustment factors, inter-observer biases, immigration and emigration from the census area, variability in numbers hauled out during surveys due to different tidal and environmental conditions, etc.

### ***Absolute Abundance***

The adjusted counts undoubtedly underestimated actual abundance because some animals were not hauled out during the survey, and swimming animals were virtually impossible to count. Actual abundance in the  $i$ th subarea and  $t$ th year,  $N_{it}$ , was estimated from its corresponding adjusted counts,  $C_{ADJit}$ , as:

$$[3] N_{it} = C_{ADJit} \cdot p_{it}^{-1}$$

where  $p_{it}$  is the estimated proportion of animals hauled out during the survey, with its reciprocal  $1/p_{it}$  commonly referred to as the census correction factor (Huber 1995).

The proportion of seals hauled out during surveys was estimated based on haulout patterns as indicated by time-depth recorders (TDRs). That study will be reported in detail elsewhere, and the following brief overview is provided only to assist readers in understanding the census correction factors developed and utilized in this study. The analysis is based on TDRs deployed at 10 haulout sites (although many animals were subsequently observed utilizing haulouts other than where they were captured) in the Strait of Georgia during 1990-94 and subsequently recovered from 34 animals (Table 1). The instruments provided a continuous record (at 20-30 second intervals) of whether an animal was hauled out or in the water over deployment periods ranging from 12 to 154 days (mean=94.3 days), primarily between early May and the end of August (Figure 3). The entire TDR database was comprised of data for 3,209 seal'days<sup>-1</sup> (about 11.6 million data points), during which period the instruments recorded a total of 3,632 haulout bouts over the course of about 6,160 low tide cycles.

The proportion of time animals spent hauled out was fairly consistent and did not differ significantly among years (Figure 4a;  $F_{4,29}=1.08$ ;  $P=0.385$ ), between areas (Figure 4b;  $F_{3,30}=0.66$ ;  $P=0.584$ ), among age- and sex-classes (Figure 4c;  $F_{2,31}=0.46$ ;  $P=0.633$ ), or with body size (Figure 4d;  $r^2=0.0958$ ;  $F_{1,32}=3.39$ ;  $P=0.075$ ). Data for all years, areas and animals were thus pooled for subsequent analysis. There was, however, a significant seasonal trend, with animals spending significantly more time hauled out in August than earlier months (Figure 4e;  $F_{3,113}=10.16$ ;  $P<0.001$ ). The seasonal increase in time spent ashore was primarily attributable to and significant only for adult females (Figure 4f;  $F_{3,41}=21.73$ ;  $P<0.001$ ), and was not evident in any of the other sex- or age-classes ( $F_{3,30}=0.02$ ;  $F_{3,24}=2.43$ ;  $F_{3,1}=0.61$  for adult males and juvenile females and males;  $0.085<P<0.997$ ). The increase in time spent ashore for adult females appeared to be associated with a suite of behavioural changes that coincided with parturition (Figure 5a). Further analysis showed that while these presumably nursing females hauled out more frequently, most of the extra time spent ashore occurred at high tides and during the night (Figure 5b). In other words, although nursing females spent a greater amount of time ashore, the probability of them being hauled out and seen during surveys did not change appreciably because most of the extra time spent ashore occurred outside the survey window. Data were thus also pooled seasonally in estimating census correction factors.

The TDR records indicated that seals tended to initiate haulout bouts in mid-morning and terminate haulout bouts in late-afternoon (Figure 6a), such that the proportion of animals hauled out peaked just after mid-day (Figure 6b). Seals also tended to initiate haulout bouts several hours before low tide on ebbing tides, and terminate haulout bouts on several hours after low tide on flooding tides (Figure 7a), such that the proportion of animals hauled was greatest during low water levels (Figure 7b). Not unexpectedly, the two animals captured in Cowichan Bay, one of the small estuaries along the east side of Vancouver Island, exhibited a striking departure from this normal pattern, hauling out most often at night and on high tides (Figure 6b and 7b). A third animal, caught at Snake Island (a typical tidal haulout site) but subsequently observed to frequent the Nanaimo River estuary on a regular basis, also spent an inordinate amount of time hauled out at night and on high tides (Figures 6b and 7b).

The most dominant factors dictating the proportion of animals hauled out at a given time were time-of-day, height of the low tide, and most importantly the time relative to low tide. The latter was deemed the most important because, irrespective of the time or height of the low tide, the TDR data revealed a consistent (outside of estuaries) pattern in which the proportion of seals ashore increased during ebbing tides, peaked at low tide, and subsequently decreased during flooding tides. This consistent pattern is subsequently referred to as the *haulout response curve* (Figure 8). While consistent in its general shape, it varied in amplitude depending on the height and time of the low tide. In general, there was an inverse relationship between the height of the low tide and the peak proportion of seals hauled (Figure 8a). However, there was also a significant effect of time, particularly for higher low tides, such that a greater proportion of animals hauled out when the low tide occurred during daylight as opposed to night (Figure 8b).

In order to estimate the proportion of animals hauled out and presumably counted during aerial surveys, a haulout response curve was generated that approximated the tidal conditions during each survey flight. In doing so, first I excluded all time-depth records on days there was heavy precipitation, as it adversely affected haulout behaviour ( $F_{3,3101}=13.00$ ;  $P<0.001$ ) (Figure 9) and censuses were never conducted under such conditions (see *Census Techniques*). Because heavy rain was relatively uncommon during summer months, this resulted in the exclusion of only about 0.2% of all time-depth records. Second, since my objective was to derive a correction factor for typical tidal haulout sites<sup>1</sup>, I also excluded the time-depth records for the two Cowichan Bay animals as well as a third animal that frequented the Nanaimo River estuary on a regular basis. I then generated a haulout response curve for tidal conditions similar to the low tide that prevailed during the survey; similar tides being defined as those that occurred at approximately the same time of day ( $\pm 1.0$  hours) and were similar in height ( $\pm 0.5$  meters). Data for all similar tides were tabulated for each of the remaining 31 instrumented animals, and subsequently averaged to determine the mean proportion hauled out (and its standard error) as a function of time relative to low tide. It is worth noting that although much greater precision could have been obtained by simply averaging all similar tide cycles (because of the larger sample sizes and also because there was generally less intra-animal than inter-animal variation), I nevertheless averaged over animals as the objective was to estimate the mean proportion of *animals* hauled out at a given time (as opposed to the mean *proportion of time* that all instrumented animals had spent hauled out at a given time).

The haulout response curve was subsequently used to adjust each count during the survey flight based on the time it had been made relative to low tide. In other words, the correction depended not only on the height and time of the low tide on which the survey was conducted, but

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<sup>1</sup>A crude correction factor was also developed for small estuaries based on the two Cowichan Bay TDRs. It was assumed that animals were either actively foraging or were resting in the estuary, and since both hauled out and swimming animals were counted in estuaries, it was further assumed that all non-foraging animals would have been counted during surveys. From the TDR records, it was estimated that during the typical 08:00 to 12:00 PDT census period the two estuarine animals spent an average of 62% (range 51-72%) of their time actively diving (to depths greater than 10 meters (which is deeper than the shallows where animals were typically seen resting and could be counted) and the remaining 38% hauled out or milling in shallow water. It was therefore assumed that 38% of all estuary animals were counted during surveys, giving a correction factor of 2.6. This crude correction factor had little effect on the overall results since animals inhabiting the small estuaries accounted for only about 5% of the total Strait of Georgia population during the June-August census period (Olesiuk et al. 1990b).

also precisely when within the tide cycle the counts had been made. The overall weighted mean proportion of animals hauled out during the survey,  $p_{it}$ , was calculated as:

$$[4] \quad p_{it} = \frac{\sum_{j=1}^n [p_{ijt} \cdot C_{ADJijt}]}{\sum_{j=1}^n C_{ADJijt}}$$

where  $C_{ADJijt}$  represents the adjusted count for the  $j$ th of  $n$  haulout sites in the  $i$ th subarea in the  $t$ th year, and  $p_{ijt}$  the estimated proportion hauled out when the  $j$ th count had been made.

An example illustrating the derivation of the correction factor for the most recent survey flight (prior to the 1998 survey data being available) on 14-August-96 is shown in Figure 10. Figure 10a gives an overview of the survey day, which was a bit unusual in that it had only one low tide. This happens about once a month because the lunar tidal cycle is slightly longer than a solar day. Nevertheless, there was a low tide just before midnight and another just after midnight. As is typical of the spring tides (it being two days before new moon) on which the censuses were usually conducted, the lower low tide (1.09 meters at 11:23 PDT) was the only low tide that occurred during daylight and was considerably lower than the low tides that preceded and proceeded it (3.87 meters at 23:35 PDT and 3.03 meters at 00:10 PDT).

The three haulout response curves corresponding to similar low tides (in this case defined at tides of 3.37 to 4.37 meters between 22:35 and 00:35 PDT, 0.59 to 1.59 meters between 10:23 and 12:23 PDT, and 2.53 to 3.53 meters between 23:10 and 01:10 PDT respectively; of which 110, 520 and 629 such tides had been monitored by the time-depth recorders) indicated that seals clearly preferred to haul out on the lower low tide that occurred during daylight as opposed to the higher low tides that occurred at night. Indeed, a maximum of nearly 70% of animals would be expected to be ashore at the lower low tide. Incidentally, integration of the area beneath the three haulout response curves from midnight to midnight indicates that animals spent an average of about 25.0% of the day hauled out, which is slightly above the overall mean of 21.2% (Figure 4a).

Figure 10b shows the survey period in much greater detail. As indicated in the top panel, the first of the 38 haulout sites surveyed on the flight was counted at 09:24 (119 minutes before low tide), and the last counted at precisely noon (37 minutes after low tide). As indicated in the middle panel, the survey period generally coincided with the peak of the haulout response curve for similar tidal conditions. The estimated proportion of animals hauled out increased from 0.563 for the first count to a peak of 0.673 at 11:12 (11 minutes before low tide), and subsequently declined to 0.650 by the last count. The bottom panel shows the raw survey counts (solid bars) and the corresponding actual abundance estimates (vertical lines with SE bars) based on the proportion of animals hauled out at the time the count had been made (middle panel). Summing the abundance estimates for all sites, and dividing by the sum of the adjusted counts (equation [4]) gives a mean overall weighted estimate of 0.624 (SE=0.051), with a corresponding census correction factor of 1.60 for the 14-August-96 survey flight.

The variance of the correction factor was estimated, as per Mood et al (1974) cited in Huber (1995), using the delta method:

$$[5] \text{Var}(1/p_{it}) \approx \text{Var}(p_{it}) / p_{it}^4$$

where  $\text{Var}(p_{it})$  represents the square of the weighted standard error.

Assuming that the variances of the correction factor (derived from time-depth recorders) and of the adjusted counts (based on aerial survey counts and pupping curves) were independent of one another, the overall variance of the abundance estimate,  $\text{Var}(N_{it})$ , can be gotten by:

$$[6] \text{Var}(N_{it}) = 1/p_{it}^2 \cdot \text{Var}(N_{it}) + N_{it}^2 \cdot \text{Var}(1/p_{it}) - \text{Var}(1/p_{it}) \cdot \text{Var}(N_{it})$$

as per Goodman (1960; cited in Huber 1995). However, one might actually expect the two variances to be inversely related (see example in *Discussion*), the resulting confidence limits may be conservative (i.e. wider than necessary).

Since tidal regimes (mean sea level, scope of tides, general patterns) vary in other regions of the province, no attempt was made to extrapolate the haulout response curves beyond the Strait of Georgia. Nevertheless, because the basic haulout behaviour appears to be similar throughout the species range (see *Discussion*) and because the surveys in other regions were conducted under comparable conditions, abundance for other regions was estimated by applying the overall mean of the correction factors derived for the Strait of Georgia surveys.

### ***Trend Analysis***

Population growth rates for each of the  $i$ th subareas were estimated from log-linear regressions of abundance,  $N_{it}$ , over time,  $t$ . Mean annual finite growth rates,  $\alpha$ , were derived from the slopes of the regressions,  $b$ , by:

$$[7] \alpha = e^b - 1$$

In order to determine whether growth rates had been constant over the study period, I also fitted second-order polynomial regressions:

$$[8] \ln N_{it} = [a + bt] + [ct^2]$$

whereby the first-order term was forced into the regression and the improvement gained by adding the second-order term evaluated. This procedure is in essence a modification of DeMaster et al's (1982) Dynamic Response Assessment in that the first term of the equation describes a population increasing exponentially at a constant rate, whereas the second term allows for compensatory changes in the growth rate over time.

Where there was evidence of density dependence, population trajectories were described by a generalized logistic model:

$$[9] N_{t+1} = N_t + N_t \cdot R_{max} [1 - (N_t/K)^Z]$$

where  $R_{max}$  represents the maximum finite rate of increase that occurs in the absence of any density dependence,  $K$  the level at which the population stabilizes (carrying capacity), and  $Z$  a shape parameter that allows for non-linear density responses ( $Z=1$  represents the classic logistic model). The model was constrained such that  $N_t$  never exceeded  $K$  (i.e. any overshooting and subsequent oscillations around  $K$  were considered as noise), and was fitted by least squares criteria assuming that errors were proportional to counts (constant  $CV$ ) with a FORTRAN routine kindly made available by J. Laake (National Marine Mammal Laboratory, 7600 Sand Point Way N.E., Bldg. 4, Seattle, Washington, 98115, personal communication). The annual abundance estimates were weighted by the square root of number of replicate surveys conducted (for subareas) or proportion of animals surveyed for the entire Strait of Georgia (see below).

Abundance within the entire Strait of Georgia was estimated by summing the adjusted abundance estimates within each of its 7 subareas. Abundance for subareas not surveyed in a particular year was estimated by interpolating between the preceding and proceeding censuses on a logarithmic scale, which assumes that rate of population change was constant between surveys. Abundance for subareas prior to its first survey was extrapolated from the earliest survey by assuming that the proportion of the population within the subarea had remained constant relative to those subareas that had been surveyed. For example, the *NWGULF*, which comprised 12.5% of total abundance in the Strait of Georgia when first surveyed in 1976, was assumed to have also comprised 12.5% of total abundance in all years prior to 1976. In effect, this summation procedure merely re-scales the trends observed in surveyed subareas into terms of abundance in the entire Strait of Georgia.

The population growth rate for the entire Strait of Georgia was subsequently estimated from a log-linear regression of total abundance over time. However, in order to minimize the interdependence of the estimates arising from the between-census interpolations, each yearly estimate was weighted according to the square root of the proportion of the total population actually censused that year. Consequently, estimates that had been purely interpolated had no influence on the regression whereas estimates for years with extensive survey coverage exerted the greatest influence.

The same procedure of combining abundance estimates and fitting weighted log-linear regressions and generalized logistic models was used to examine overall population trends for all areas that had been surveyed outside the Strait of Georgia.

### ***Population Estimates***

Following Olesiuk et al. (1990a), total abundance of harbour seals on the British Columbia coast was estimated by extrapolating the abundance of seals observed in surveyed areas to those areas that have not yet been surveyed. I made two extrapolations, each with a differing set of underlying assumptions.

The first extrapolation was based on the assumption that the density of seals in the surveyed areas was representative of other regions. Density was calculated in terms of number of seals per kilometer of shoreline. Shoreline lengths were interpolated from 1:100,000 scale digitized maps (World Database II), which was previously shown to give good agreement with those manually traced from 1:525,000 scale nautical charts (Olesiuk et al. 1990a). Differences in the density of seals among subareas that had been surveyed was subsequently assessed with *ANOVA*, and the total number of seals in British Columbia estimated by extrapolating what was considered to be a representative density to the unsurveyed portion of the coast.

The second extrapolation was based on the assumption that seals had been hunted for bounty payments according to their relative abundance and that recovery rates were uniform throughout the province. The total number of seals in British Columbia was thus estimated by dividing the total abundance in all surveyed areas by the proportion of bounty kills taken from the same areas. Data on the distribution of bounty kills by DFO Statistical Area were available for the period 1927-28 to 1933-34 and again for 1957-58 to 1959-60. In situations where only a portion of a Statistical Area had been surveyed, it was assumed that the kills were uniformly distributed such that the proportion of bounty kills was directly proportional to the proportion of shoreline within the area that had been surveyed. Because at least some of the large number of bounty payments made in DFO Statistical Area 12 during 1927-34 were known to be fraudulent<sup>2</sup>, I also examined the effect of excluding them from the analysis.

## RESULTS

### *Absolute Abundance*

The aerial survey procedures utilized in this study were rigorously standardized. Either the author or the late Dr. Michael A. Bigg served as the primary observer for all but 4 of the 133 census flights (97%; PFO on 65% and MAB on 32% of the flights respectively), and during 1982-88 we flew most surveys together (Appendix I). Variation attributable to differences in techniques among observers was thus probably negligible.

The majority of counts (89%) were made within the prescribed census window of 2.5 hours before to 1 hour after low tide, and most (93%) were made between 08:00 and 12:00 PDT (Figure 11). However, several of the inaugural survey flights made in early 1970s, during which it would seem in retrospect that the census techniques were still being developed, began as much

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<sup>2</sup> Archival records indicated that an extraordinarily large numbers of the seal snouts received for bounty payment during this period had been submitted by a few individuals from one location. A subsequent investigation fortuitously led to a conversation with the son of one of those individuals, who revealed that it had been a common practice in that era to visit the nearby Steller sea lion rookery off Cape Scott, club young pups, and manipulate their snouts so as to appear they were harbour seals (Olesiuk, unpublished data).

as 5 hours before low tide (Figure 11) when water levels were still high and fewer animals would be expected to be hauled out (see Figure 8).

The majority of animals observed during surveys were subsequently counted from photographs. For the 1996 survey, as an example, 91.5% of animals were counted from slides. For the remaining 8.5%, about one-third were not photographed because they occurred in small groups that could be easily counted visually, or the photographs were of inadequate quality to count, and the remaining two-thirds of animals were counted in the water in small estuaries or on haulout sites comprised of boulder beaches where they were too scattered to photograph. As noted previously, in both cases we repetitively circled these sites until we were satisfied with their accuracy of our visual counts. With respect to the photographic counts, blind comparisons among different readers indicated that variability in interpretation of the photographic slides was negligible (Figure 12).

The adjusted aerial survey counts appeared to provide a reliable and reproducible index of abundance. The coefficient of variation (*CV*; defined as the standard error of the mean expressed as a proportion of the mean) for those surveys replicated ranged from 0.01 to 0.16 (mean=0.064) (Table 2). This was similar to the *CV*s ranging from 0.01 to 0.10 (mean=0.042) reported by Huber (1995) for replicated surveys in Washington State, which were conducted by very experienced primary observers using essentially identical census methodology, which suggests that *CV*s of this magnitude reflect the inherent variability of surveys of this nature (Eberhardt et al. 1979). The overall mean *CV* of 0.064 was therefore applied to all adjusted counts where replicates were unavailable. It should be noted that these *CV*s were calculated based on the variability of the total counts for the entire area, as opposed to the average variation among individual haulout sites within the area. Although the latter generally provides lower *CV*s, it requires independence of sites and hence implicitly assumes there are no movements of animals between haulout sites, which is known not to be the case in the study area (Olesiuk, unpublished data).

The estimated proportion of animals hauled out within subareas on survey flights ranged from 0.32 to 0.71 (mean=0.612), with corresponding correction factors thus ranging from 1.41 to 3.13 (mean=1.74) (Figure 13). The lowest proportions were associated with several flights made in the early 1970s that began very early in the tidal cycle while many animals had not yet hauled out (Figure 13). Several values in the mid 1980s were also atypically low, and represent surveys that were continued well beyond low tide when many animals had already begun vacating haulout sites. On an annual basis, the weighted mean proportions hauled out were less variable, ranging from 0.54 to 0.67 (mean=0.615). Corresponding annual correction values ranged from 1.49 to 1.85 (mean=1.63), with *CV*s ranging from 0.072 to 0.169 (mean=0.042). The proportion of animals hauled out during surveys tended to increase slightly over the course of the study ( $r^2=0.120$ ;  $F_{1,121}=10.6$ ;  $P<0.001$ ), with the regression indicating that the average proportion hauled out increased from about 0.58 when the first censuses with correction factors were conducted in 1973 to 0.65 by 1998. This can likely be attributed to refinements in census techniques, most of which appears to have occurred prior to the mid-1980s (Figure 13).

The calculations used to estimate actual abundance from survey counts are illustrated here for one of the most recent censuses of the Strait of Georgia conducted in 1996 (the example was

formulated before the 1998 data were available), since it shows the entire spectrum of adjustments and corrections (see Appendix II). A total of 22,663 animals were actually observed during the survey, of which 1,926 visually counted and 20,737 were subsequently counted from photographs. The survey covered most of the Strait of Georgia study area, except for 15 haulout sites, several of which were fairly substantial, in the northern reaches of the *NEGULF* and one minor site in *HOWESD* (denoted as *ns* for not surveyed; see Appendix II), where judging from the most recent preceding and proceeding surveys in 1994 and 1998, about 4.6% of the total Strait of Georgia population would have occurred (95.4% coverage during the 1996 survey was far below the overall average of 99.4%). The total, adjusted for missed sites, was therefore 23,752. The first series of flights was conducted atypically early on a tidal cycle that occurred during 27-31 July, which was just past the midpoint of the pupping season. Based on the chronology of pupping (Figure 2), an estimated 1,990 pups would have been born subsequent to the survey. The total adjusted count for the Strait of Georgia, adjusted to post-pupping levels, was therefore 25,742 animals. The *CV* of the adjusted count was assumed to be 0.064 based on the typical variability of replicates (Table 2).

Based on the haulout patterns for tides similar to those on each of the 7 survey flights (see example in Figure 10 for one of the flights), it was estimated that an average of 62.8% of animals were hauled out during the surveys, giving an overall correction factor of 1.59 ( $CV=0.064$ ). This correction factor was typical in magnitude but had a somewhat larger *CV* than normal<sup>3</sup>. Total abundance in the Strait of Georgia study area at the end of the pupping season in 1996 was thus estimated to be about 41,000 (95% confidence interval of 29,400 to 52,500).

Equation [6], which was used to derive the overall variance of the total abundance estimate, indicated that about 50% of the imprecision in the 1996 abundance estimate was attributable to the inherent variability of replicate counts, and the remaining 50% to uncertainty in the proportion of animals hauled out during the survey. More typically, based on the average *CVs* it is estimated that about 60% of the imprecision was attributable to the inherent variability in replicate counts and the remaining 40% to uncertainty in the proportion of animals hauled out. It should be noted that equation [6] implicitly assumes that these two sources of variation are independent, when in fact one might expect them to be inversely correlated. At least some, and perhaps most, of the inherent variability in the replicated counts may be attributable to variability in the proportion of animals hauled out during the survey, in which case the variability of the abundance estimates (which have been adjusted for differences in the estimated proportion of animals hauled out) would exhibit less variability (see example in Discussion; see also Frost et al. 1999). Unfortunately, I did not have sufficient numbers of replicates to evaluate the degree of covariance between these parameters, but as previously noted the resulting confidence limits may be too conservative.

The estimated abundance in the Strait of Georgia in 1996 was similar to and not significantly different from the estimates based on the preceding survey conducted in 1994 of 40,900 (95% confidence interval of 30,600 to 51,100) and the proceeding survey in 1998 of 32,300 (95% confidence interval of 24,800 to 39,900). In contrast to these recent estimates,

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<sup>3</sup> The lower precision seems to have resulted because the first half of the survey was conducted during a series of extremely low tides that occurred during 27-31 July. Since such low tides were quite uncommon, the TDR database contained fewer of them such that the Standard Errors were inflated.

analogous calculations indicate that the abundance of harbour seals in the Strait of Georgia when the first standardized surveys were conducted in 1973 was on the order of 3,570 (95% confidence interval of 2,480 to 4,650).

### *Trends in Abundance*

During the study period, abundance of seals increased in all seven of the Strait of Georgia subareas (Figure 14). The log-linear regressions were in all cases highly significant ( $P < 0.001$ ) (Table 3). During 1973-98, the mean annual finite rates of increase in subareas ranged from 4.1% to 15.4% per annum, but the rates were not constant over the course of the study. For example, abundance in *BBAY* and *FRASERR* increased at a rate of 13.4% and 11.6% per annum respectively during 1973-82 ( $r^2 = 0.961$ ;  $F_{1,2} = 49.5$ ;  $P = 0.002$  and  $r^2 = 0.991$ ;  $F_{1,2} = 228.8$ ;  $P = 0.004$ ), whereas during 1982-98 numbers in *BBAY* subsequently stabilized ( $r^2 = 0.009$ ;  $F_{1,12} = 0.09$ ;  $P = 0.766$ ) and growth in *FRASERR* slowed to an average of 6.2% per annum ( $r^2 = 0.550$ ;  $F_{1,14} = 15.9$ ;  $P = 0.766$ ). In contrast, the *NWGULF* and *NEGULF* sustained mean growth rates of 15.4% and 13.8% respectively over the entire study period ( $r^2 = 0.896$  and  $0.913$ ;  $F_{1,9} = 77.5$  and  $F_{1,9} = 84.1$ ;  $P < 0.001$ ; Table 3). However, the most recent surveys suggest that abundance is stabilizing in most or all subareas (Figure 14). In all cases, mean growth rates during 1973-98 were lower than those previously reported for 1973-88 (Table 3; Olesiuk et al. 1990a), which also implies declining growth rates in recent years.

As a result of the regional differences and temporal changes in growth rates, there was a pronounced redistribution of seals within the Strait of Georgia over the course of the study (Figure 15). The combined proportion of total abundance in the *NWGULF* and *NEGULF*, the two subareas exhibiting the highest growth rates, more than doubled from 19% in 1973 to 46% in 1998. In contrast, the once dominating seal herds found on the sandbars in *BBAY* and *FRASERR* dwindled in importance from 25% to 8% over the same period. There was also evidence of redistribution within some subareas. For instance, although the overall proportion in the *GULFISL* remained relatively constant over the study period (range 23-31%), there was a dramatic shift in distribution from the inside protected haulouts situated among the Gulf Islands toward more exposed sites along the outer coast; only 9% of animals occurred on the latter in 1973, but that number had increased to 47% by 1998.

Within the Strait of Georgia, there was an increase in both the mean size and total number of haulout sites (Table 4). Interestingly, however, there appears to have been a drop in the occupancy rate over the course of the study; 89% of all known haulout sites were occupied during the 1973-74, compared with only 84% during the 1988 survey and 62% during the 1998 survey. This suggests that even though the population has been growing and colonizing new haulout sites, some sites are also being abandoned (i.e. there is a turnover in haulout site utilization). This warrants closer analysis, since it could have implications for index surveys that are designed to monitor a fixed set of haulout sites (as opposed to searching an entire survey area).

During 1973-98 the overall Strait of Georgia population grew at a rate of 10.9% per annum, which was highly significant ( $r^2=0.950$ ;  $F_{1,15}=248.2$ ;  $P<0.001$ ). However, contrary to our original assessment (Olesiuk et al. 1990a), the fit of the population trajectory was significantly improved by adding a second-order term (adjusted  $r^2=0.973$ ;  $F_{1,14}=13.4$ ;  $P=0.003$ ), indicating that that growth was being affected by density dependent processes. The population trajectory was thus described by a generalized logistic equation:

$$[10] N_{t+1} = N_t + N_t \cdot 0.130 [1 - (N_t/37,980)^{7.18}] \quad (N_0=2,370 \text{ in } 1970)$$

(Figure 16a) which indicated that during the 1970s and into the late 1980s the population had been increasing exponentially at a rate of about 13.0% per annum, which presumably represents the maximum finite rate of increase ( $R_{max}$ ) that occurs in the absence of depensatory forces. However, the growth rate began slowing around 1990, and the population now appears to have stabilized at an average level of about 38,000, which presumably represents the current carrying capacity in the Strait of Georgia. The stabilization appears to have been rather abrupt, with maximum net productivity ( $MNPL$ ) of about 11.4% occurring at about 75% of carrying capacity, which for the Strait of Georgia equates to roughly 3,200 animals at a population level of 28,500. Fitting generalized logistic models individually to each of the 7 subareas (Figure 17) and summing their estimates gives a very similar result (never differing from equation [10] by more than 5%), with a mean annual growth rate of 13.1% during 1973-90, and a carrying capacity of 38,800.

As noted by Olesiuk et al. (1990a), the actual rate of population growth during the early part of the study may have been exaggerated due to the cumulative discovery of haulout sites that may have existed but been overlooked in the first surveys, but this bias was probably small. In our earlier assessment, the late Dr. Michael A. Bigg and I re-examined the flight paths of the earlier censuses and considered the location and visibility of haulout sites discovered in the late 1970s and early 1980s, and on that basis subjectively estimated that perhaps one-third of the new sites may have been missed in previous censuses (and the remaining two-thirds colonized as a result of population expansion and redistribution). Since I have no basis for refining that assessment, the same correction is applied to the Strait of Georgia trend for the period 1973-90, which suggests that the actual growth rate was about 11.5% per annum (95% confidence interval of 11.1-12.2%). I consider this to be a biologically more realistic estimate of  $R_{max}$ .

Surveys in other regions of the province indicated that the trends in the Strait of Georgia were generally indicative of population trends throughout British Columbia. Populations increased at rates ranging from 3.6% to 26.5% in all of the regions surveyed (Figure 14), but the paucity of the time-series precluded formal statistical analyses in most cases. The only exception was the Skeena River which has been surveyed on 9 occasions since 1977, indicating that populations increased at a mean finite rate of 4.9% per annum ( $r^2=0.620$ ;  $F_{1,5}=31.39$ ;  $P=0.012$ ). However, recent surveys indicate that population growth in the Skeena River has also slowed in recent years (Figure 14). A generalized logistic model indicated the growth rate was initially 12.7% per annum when the population was at low levels in the 1970s, but that abundance had stabilized at a level of about 1,950 animals by the late 1980s (Figure 17).

A log-linear regression fitted to a composite of all regions outside the Strait of Georgia combined indicated a mean rate of 9.5% during 1976-98 ( $r^2=0.880$ ;  $F_{1,10}=73.6$ ;  $P<0.001$ ), which was not significantly different from the mean rate for the Strait of Georgia ( $P>0.500$ ). As was the case in the Strait of Georgia and Skeena River, growth rates appeared to have slowed over the course of the study and the relationship could be significantly improved by incorporating a second-order term (adjusted  $r^2=0.991$ ;  $F_{1,9}=104.9$ ;  $P<0.001$ ). The population trajectory was thus described by a generalized logistic equation:

$$[11] N_{t+1} = N_t + N_t \cdot 0.1457[1-(N_t/5,842)^{4.93}] \quad (N_0=403 \text{ in } 1970)$$

(Figure 16b) which indicated that, similar to the Strait of Georgia, stabilization of populations in these other areas also appears to have been rather abrupt, with maximum net productivity (*MNPL*) of about 12.1% occurring at about 70% of carrying capacity. As was the case for the Strait of Georgia, the initial population growth rate of 14.6% during the first part of the study was probably slightly exaggerated as a result of the cumulative discovery of haulout sites that existed but were overlooked in the earliest surveys, but in this case I am not familiar enough with these areas to ascertain the likely degree of any such bias.

### ***Population Estimates***

Although harbour seals have never been surveyed along much of the British Columbia coastline, it is possible to make some reasonable inferences regarding total abundance.

The first estimate of total abundance is based on the observed density of seals along the coastline that has been surveyed. As noted by Olesiuk et al. (1990a), the Strait of Georgia appears to support an unusually high concentration of harbour seals compared with other regions of the province. There are now enough survey data from other regions to evaluate this observation using *ANOVA*, which indicated that the mean density in the Strait of Georgia of 11.57 seals·km<sup>-1</sup> was indeed significantly higher than densities in other regions ( $F_{1,18}=14.4$ ;  $P=0.001$ ), and also tends to be more variable (*CV* of 0.36 within versus 0.12 outside the Strait of Georgia). For some areas, such as the southern Strait and the Gulf Islands, densities are approximately an order of magnitude higher than those observed outside the Strait of Georgia (Table 5).

Densities in all other regions of the province were similar in magnitude and did not differ significantly ( $F_{3,8}=0.50$ ;  $P=0.690$ ), with an overall weighted mean of 2.66 seals·km<sup>-1</sup> (*CV*=0.115). Following Olesiuk et al. (1990a), it was assumed that this density was representative of those parts of the province that have yet to be surveyed, and total abundance outside the Strait of Georgia was thus estimated to be on the order of 63,800 (95% confidence interval of 48,600-78,800). Adding this to the estimated abundance in the Strait of Georgia (as well as their upper and lower confidence limits), total abundance in British Columbia was estimated to be on the order of 101,000 (95% confidence interval of 76,800 to 125,100). However, this estimate and particularly its confidence interval should be regarded as provisional, because the surveyed areas

on which the extrapolation is based were not selected randomly and hence may not be representative of those areas that have not yet been surveyed.

The second estimate of total abundance in British Columbia was based on the relative distribution of kills. Detailed data on the distribution is available during two periods: 1928-29 to 1933-34 and again during 1957-58 to 1959-60 (Table 6)<sup>4</sup>. During these periods, the proportion of bounty kills taken in surveyed regions was relatively constant at about 47.1% (range 41.9-51.1%;  $CV=0.026$ ; 95% confidence interval of 44.2- 49.9%). Total abundance in the Strait of Georgia was estimated to be 37,300 (95% confidence interval of 28,200 to 46,300), and the combined abundance in all other surveyed areas was estimated to be 17,300 (95% confidence interval of 13,000 to 21,500), giving a total of 54,500 (95% Confidence Interval of 41,300 to 67,900). Assuming that seals were killed in proportion to their relative abundance (i.e. the surveyed areas thus also constituted 47.1% of the total population), the province-wide population was estimated to be on the order of 115,700 (95% Confidence Interval of 81,400 to 155,800). However, this estimate and particularly its confidence interval should also be regarded as provisional since there may have been factors other than seal abundance, such as geographic variability in the accessibility of areas to hunters or in carcass recovery rates, that may have influenced the number of bounties claimed or pelts sold from a particular region.

Since the two abundance estimates were not significantly different and there was no impetus for favoring one over the other, I adopted their average. The total number of harbour seals on the British Columbia coast at the end of the pupping season during 1996-98 was thus estimated to be on the order of 108,000. The provisional confidence limits for the two estimates suggest that total abundance on the British Columbia coast is likely within the range 77,000 - 156,000. However, as noted above, the provisional confidence limits are subject to a number of biases, and cannot be validated until the entire coastline, or at least a randomized sample of representative regions, has been surveyed.

## DISCUSSION

This study reaffirms the finding in our original assessment that harbour seal populations in British Columbia had been increasing in recent years (Olesiuk et al. 1990a). Based on the more recent data and refined analysis presented in this report, it is estimated that populations in the Strait of Georgia were increasing at a rate of about 11.5% per annum during 1970s and 80s, but that growth rates subsequently slowed and have now stabilized. The revised rate of increase for the 1973-90 period is slightly lower than our original estimate of 12.5%, which can be attributed to slight improvements in census methodology made during the 1970s and early 1980s

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<sup>4</sup> In the original assessment, Olesiuk et al. (1990) also used data on the distribution of commercial seal harvests during 1963-66. While the locations of the commercial kills were precise enough for the southern part of the province to determine whether they had been taken off southern Vancouver Island (the region used in the original extrapolation), they were too imprecise in the northern part of the province to establish what proportion were taken within and outside of surveyed areas, and therefore could not be used in the revised analysis.

as revealed by the TDR-based correction factors (i.e. a greater proportion of animals were missed in the earlier censuses, and by not taking that into account the population growth rate was overestimated in the original assessment). These recent trends in the Strait of Georgia appear to be indicative of harbour seals in other regions of the province.

Harbour seal populations in neighbouring waters also appear to be increasing. In southeast Alaska, populations near Ketchikan increased at a rate of 9.3% during 1983-96 (Small et al. 1997) and populations near Sitka increased at a rate of 2.0% during 1983-97 respectively (Small et al. 1998). In the inland waters of Washington, populations increased at a rate of 6.1% during 1983-92; on the outer coast of Washington and Oregon at a rate of 11% during 1977-82 and 5.5% during 1983-92; and off California at a mean rate of 4.1% during 1982-94 (Barlow et al. 1995). This is in sharp contrast with some areas of the Gulf of Alaska and Bering Sea, where harbour seal numbers have experienced severe declines (Pitcher 1990; Lewis et al. 1996; Frost et al. 1997). The geographic differences in the status of harbour seal populations is also reflected in the status of other pinniped species, such as Steller sea lions (*Eumetopias jubatus*) and northern fur seals (*Callorhinus ursinus*), both of which are declining in the northern part of their range but generally flourishing in the southern part of their range (Barlow et al. 1995; Calkins et al. 1997; Hill et al. 1997; Olesiuk et al. 1993; Olesiuk, unpublished data).

Contrary to the original assessment, the present study found evidence of density dependence in the population growth rates both within and outside the Strait of Georgia. The generalized logistic model indicated that growth rates in both regions began to slow in the late 1980s or early 1990s and that populations had stabilized by the mid 1990s, which would explain why density dependence was not detected in the original assessment based on survey data collected up until 1988. There is also some evidence of slowing of growth rates and stabilization of harbour seal populations in Washington and Oregon (Brown 1997; Huber and Laake 1998). This is a relatively recent phenomena, and it is important that surveys be continued for at least several more years to confirm these trends and, perhaps more importantly, to establish the behaviour of population at their carrying capacity. For example, the high density of seals presumably increases the risk of massive die-offs, as recently experienced by European harbour seal populations (Dietz et al. 1989).

The detailed survey data available for subareas within the Strait of Georgia revealed geographic differences in population trajectories (see Figure 17). In some subareas, such as Boundary Bay (*BBAY*), populations appear to have stabilized by the early 1980s. Nevertheless, overall growth rates in the Strait of Georgia did not decline until the early 1990s, and it appears that the slowing in some areas was initially compensated by higher growth rates in other regions, such as the northeastern and northwestern reaches of the Strait of Georgia (*NEGULF* and *NWGULF*). Population growth rates sustained in the latter areas are too high to be biologically realistic, and populations in them are just now stabilizing. These patterns, as well as the resulting redistribution of animals that was observed over the course of the study (see Figure 15), suggest there was movement of animals among subareas, and implies that one of the earliest compensatory responses of animals was to immigrate from areas of higher density to areas supporting lower densities (as opposed to a decline in productivity levels).

In our previous assessment it was suggested that the recent increase in harbour seal abundance represented recovery from predator control kills and particularly commercial harvests that had depleted populations prior to the species being protected in 1970 (Olesiuk et al. 1990a). Reconstruction of population trends based on the reported number of seal kills, estimated recovery rates, and sustainable harvest levels suggest that the abundance had been drastically reduced during two periods of intense commercial harvesting, the first in the 1890s and early 1900s and the second in the 1960s. Peak historic population levels were estimated to have been on the order of 78,000 (range 59,000 to 120,000) just before the turn of the century (Olesiuk, in prep.). It would thus appear that harbour seal populations in British Columbia have now attained historic levels, which explains the recent stabilization.

One of the most significant improvements in this assessment has been the development of correction factors to account for animals at sea during surveys, based on haulout patterns as indicated by time-depth recorders. At the time of the original assessment, virtually no quantitative data were available on the haulout patterns of harbour seals in British Columbia. Instead, we derived a crude estimate of the proportion of animals missed based on the variability of replicated counts using the Bounded Count technique (Robson and Whitlock 1964). Although it was known the technique was subject to small-sample bias, the extent of the bias was unknown. Recently, however, mathematical simulations have shown that under certain circumstances the inherent biases in Bounded Count estimates can be substantial, and the direction of the bias may vary systematically with the size of the population (K. F. Abt, FTZ Westküste, Hafentörn, D-25761 Büsum, personal communication). The correction factors used in the original assessment are therefore no longer considered valid.

The new correction factors based on TDR records were similar in magnitude to those correction derived by Huber (1995) based on the proportion of radio-tagged seals that were hauled out during survey flights. Her correction factors, widely regarded as state-of-the-art for this species, ranged from 1.36 to 1.62 (mean=1.53) for various regions of the State of Washington. In comparison, my mean annual correction factors ranged from 1.49 to 1.85 (mean=1.63). Interestingly, Huber's (1995) study area included one of our subareas, *BBAY* in 1992, for which her correction factor was 1.51, which compares favorably with my correction factor of 1.49 for *BBAY* in the same year (Huber's 1992 mean count for *BBAY* of 787 animals also compares favourably with my adjusted count of 723 in *BBAY* in the same year; H. R. Huber, National Marine Mammal Laboratory, Seattle, Washington, 98115, personal communication). Huber (1995) found no significant geographic differences in correction factors between regions of Washington State, which included various substrate types on both the outer coast and inland waters. More recently, Withrow and Loughlin (1995b) used similar methods and reported a correction factor of 1.74 for rocky outcroppings in southeast Alaska under typical survey conditions, and Withrow and Loughlin (1997b) reported a correction factor of 1.90 for sandbars in Prince William Sound. Thus, correction factors appear to be quite consistent among areas and substrate types where haulout patterns are associated with low tide cycles. There will, however, be notable exceptions such as the small estuaries along the east side of Vancouver Island where seals haul out on logbooms (see Figure 6), and in fjords where seals haul out on glacial ice flows (D. E. Withrow, National Marine Mammal Laboratory, Seattle, Washington, 98115, personal communication).

My correction factors were considerably greater than the 1.2 (range 1.12 to 1.38) derived by Hanan (1996) for the coast of California based on the proportion of days that seals came ashore (range 72.5% to 89.2% for years; mean = 83.3%). The TDR records indicated that the proportion of days that seals came ashore in the Strait of Georgia was actually very similar (range 61.6-100% for individuals; mean=85.1%). However, the TDR records also indicated that even during optimal low tides some seals were terminating their haulout bouts before others were initiating theirs. Thus, the maximum proportion of animals hauled out at any given time will always be lower than the proportion that come ashore at some point on a given day (i.e. animals that come ashore on a given day are never all hauled out simultaneously), which accounts for my lower correction factors. Without a more detailed comparison of haulout patterns, it cannot be ascertained whether the differences in our correction factors were the result of haulout bouts being longer or more synchronized in California, or due to differences in the analytical methods used to derive them.

The haulout response curves on which my census correction factors are based encompass two of the three factors identified by Frost et al. (1997, 1999) as being most important when standardizing survey counts, namely time-of-day and time relative to low tide. This was not by design, but instead dictated by the nature of haulout patterns as revealed by the TDRs. Originally, I had intended on basing my correction factors on the proportion of animals hauled out as a function of time-of-day and *tide height*. The TDR records verified that time-of-day had an important effect on haulout behaviour (especially at intermediate low tides), with a greater proportion of animals hauling out on low tides that occurred near midday than on equivalent tides that occurred at other times (see Figure 8b). However, the TDR records also indicated that haulout patterns were not dictated so much by tide height *per se*, but instead more by changes in relative water levels (i.e. time relative to low tide). Regardless of how low a low tide was falling, animals normally initiated haulout bouts several hours before the low tide and terminated bouts within several hours after the low tide. As a result, seals were hauling out and entering the water at higher water levels on higher low tides than on lower low tides. Tide height itself played a relatively minor role, and when low tides occurred near midday the proportion of seals hauling out on them was almost independent of the height of the low tide (Figure 8c). Interestingly, this suggests that haulout bouts were not necessarily limited by the availability of the tidal substrates used as haulout sites.

Frost et al. (1997, 1999) also identified date as being an important factor in standardizing survey counts. In contrast, except for nursing females, the TDR records showed that the time animals spent ashore was quite constant over the period which surveys were conducted. Although nursing females spent more time ashore, most the extra time was during high tides and at night, such that the proportion of animals hauled out and presumably counted was quite insensitive to the date of the survey. Although I made minor adjustments to account for unborn pups based on the date of the survey, these would not have accounted for the seasonal effects reported by Frost et al. (1997, 1999). One plausible explanation for the apparent difference may be that surveys in British Columbia were conducted at the end to the pupping season, whereas those in Alaska were conducted during the annual moult. The proportion of moulting animals ashore and hence counted during surveys can vary appreciably over relatively short periods (Jemison et al. 1998). It is also possible the seasonal effects reported by Frost et al. (1997, 1999) were due to movements of animals during the survey period. In Alaska, large concentrations of

seals often occur in glacial fjords, and abundance in them and surrounding areas can fluctuate dramatically within a short time-frame (Mathews and Kelly 1996). Large reservoirs of seals whose movements could affect counts are not known to occur in British Columbia.

Frost et al. (1997, 1999) developed their standardization model primarily to enhance the statistical power for detecting trends from relatively short time-series of survey data. That was not my objective here. Given the long time-series of counts for the Strait of Georgia (1973-98) and continued population growth over much of that period, the resulting population trend (a ten-fold increase in abundance) greatly predominated any underlying variability due to slight differences in census conditions. Nevertheless, I would expect that application of the corrections derived from the haulout response curves would also enhance the power of detecting population trends were they not so overwhelming. This appeared to be evident for the two replicate censuses of the entire Strait of Georgia in 1988 conducted during 30 May -16 June, just prior to the pupping season, and again during 9-26 August, toward the end of the pupping season. The raw counts for the two surveys were 10,680 and 14,177 respectively, giving a CV of 0.141. Adjusted to post-pupping levels, the adjusted counts were 13,340.4 and 14,613.7, giving a CV of 0.046. Finally, when corrected for differences in the proportion of animals hauled out during the surveys, the estimated abundance was 23,431.7 and 23,125.7, giving a CV of 0.007. This implies that much of the variation in the adjusted counts was attributable to differences in the proportion of seals hauled out during surveys. Although this one example is tantalizing, I had too few replicates to evaluate how consistently and to what degree the TDR corrections might serve to standardize the survey counts.

One of the main drawbacks of my correction factors was that they were based on haulout patterns for similar tidal cycles, rather than the same tide cycles on which censuses were conducted. It would have been preferable to obtain correction factors during the actual survey, as did Huber (1995). However, it is not feasible to deploy and subsequently monitor sufficiently large numbers of transmitters or TDRs during every survey, such that it will be necessary to extrapolate correction factors beyond the surveys during which they were developed. In fact, in recent years, Huber's (1995) correction factor has been widely applied to harbour seal counts throughout the Pacific Northwest (Barlow et al 1995). One of the advantages of TDRs is that they provide very detailed records of haulout patterns over extended periods, which allow correction factors to be developed based on fairly large numbers of tidal cycles similar to those under which surveys are conducted. This allows correction factors to be calculated for the specific tidal conditions of each survey flight, and hence provides a basis for retrospectively correcting counts from earlier censuses that might have been done under different tidal conditions. TDRs also circumvent some of the more serious problems associated with haulout patterns ascertained by radio telemetry, such as emigration of animals from the study area and loss or failure of transmitters (Boveng 1988).

There is potential for introducing bias in the census correction factors when the sex- and age-structure of the sample of animals on which they are based is not representative of the population being censused. The TDR records in this study were obtained from a fairly balanced sample of males and females as well as of juveniles and adults, but owing to the bulk of the TDR packages pups and yearling were not represented. In developing her correction factors, Huber (1995) found that pups spent about as much time ashore as adult females in June, but

subsequently rarely hauled out in July, such that correction factors for pups can change quite markedly between months. Given the chronology of pupping in her study area, the seasonal changes she observed in pup behaviour were probably associated with weaning. Since most pups in the Strait of Georgia are born in late July and early August and typically nurse for about 5-6 weeks (Olesiuk 1993), few would have been weaned by August when most surveys were conducted.

It should be noted that the haulout response curves and corresponding census correction factors are only applicable to the period over which the TDR data were collected, in this case May through August. In the Strait of Georgia, this represents the period from about 6 weeks prior to the onset of the pupping season to the end of the pupping season. Unfortunately, since the TDRs were glued to the pelage and shed very early in the moult, it was not possible to evaluate how haulout patterns might have changed during the annual moult, the period during which most surveys have been conducted in Alaska. Several researchers have noted that the amount of time spent ashore declines dramatically during winter months when animals are not pupping or moulting (Harvey 1987; Swain et al. 1996). Withrow and Loughlin (1996b) also found that correction factors can vary quite markedly depending on the conditions under which surveys are flown. While I attempted to minimize these effects by excluding days with heavy precipitation, analysis of the TDR data could be further refined by accounting for other environmental factors<sup>5</sup>.

There was one unexpected and important discrepancy between the haulout patterns indicated by the TDRs and observations made by the author during the past 15 years of conducting aerial surveys. When surveys were attempted too far in advance of low tide, many animals were seen swimming or milling in the water adjacent to the haulout site, and animals on shore were still wet indicating they had just recently hauled out. In such cases we usually landed for 30-45 minutes before beginning the survey. In most instances, censuses were initiated 2 to 2-1/2 hours before low tide, and very few animals were generally seen in the water during the survey. Surveys were usually terminated just before or after low tide when I began to see an increase in the number of animals milling in the water adjacent to haulout sites. It was assumed this indicated animals were terminating haulout bouts and dispersing from haulout sites, and that counts would be too low if the survey was continued. Surprisingly, however, the haulout response curves indicate quite clearly that the proportion of animals hauled out is quite symmetric around the low tide, where I would have expected to see a rather sharp decline around the time of the low tide. One possible explanation is that seals were more susceptible to being disturbed once they had been hauled out for awhile, so that more animals were frightened into the water when counts were made beyond the peak of the haulout response curve. Indeed, in our original assessment we noted:

*...as censuses progressed, the pelage of seals dried which made seals more visible from the air. Few animals were observed in the water, except in small estuaries*

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<sup>5</sup> Mean or maximum daily wind speeds did not appear to affect the proportion of time animals spent hauled out. Surprisingly, however, wind direction seemed to have an effect, with seals spending significantly more time ashore during north and west winds, and less time ashore during south and east winds. The prevailing winds in the study area are from the northwest (generally associated with high pressure systems and clear skies), and from southeast (generally associated with low pressure systems and low overcast conditions with precipitation).

*where seals often gathered in groups and rested on the ocean floor and in deep inlets where there were few suitable haulout sites. Toward the end of censuses the pelages of seals became distinctly drier and lighter, which indicated we were approaching the end of the census window. Within an hour or so, seals were easily frightened into the water by the approach of our aircraft or were milling in the water near the haulout when we arrived, perhaps having been frightened before coming within sighting range. At the end of a census, it was not unusual to frighten 3-4 haulouts in succession whereas seals were rarely frightened earlier in the census.*

An alternative explanation is that seals may behave differently just prior to initiating a haulout bout than just after terminating a haulout bout. For example, one could imagine that seals arriving at a haulout site on an ebbing tide might haul out almost immediately, such that very few animals would be milling in the water prior to low tide. On the other hand, animals may linger adjacent to haulout sites after terminating bouts on flooding tides, such that an increasing number of animals would be milling adjacent to sites after a low tide. This is an important matter since the haulout response curves indicate that censuses could easily be extended another two hours or so, but one wants to be very cautious in modifying census protocol when it could jeopardize comparisons with all previous surveys.

The revised population estimate of 108,000 for 1996-98 is about 35% greater than our original estimate of 75,000-88,000 for 1988 (Olesiuk et al. 1990a). The apparent increase is partly attributable to continued population growth, but is mainly a result of the improved correction factors which have shown that appreciably more animals were not hauled out and hence missed during surveys than had previously been estimated (39% as opposed to 12-20%). Based on the provisional confidence limits for the total abundance estimates, roughly 40% of the overall imprecision was associated with uncertainty in the extrapolation of abundance from surveyed to unsurveyed areas, and of the remaining 60% about half was associated with the inherent variability of replicated counts and the other half with uncertainty in the estimated proportion of animals observed during surveys. In addition to this imprecision, the province-wide estimates are subject to bias as a result of violations of the assumptions underlying the extrapolations on which they are based. The potential for such bias could be explored with existing survey data by applying re-sampling techniques such as the jack-knife approach to determine how selection of specific survey areas can affect overall seal density estimates. However, it will not be possible to calculate valid confidence limits for the entire coast until a more representative sample of the coastline has been surveyed, particularly in the central and northern mainland regions which make up a significant part of the coast but for which few survey data presently exist.

The generalized logistic models indicated that the density dependent processes (at least those affecting overall productivity) were not expressed until the population was relatively close to carrying capacity, such that maximum productivity of about 11.5% (11.2% within and 11.9% outside the Strait of Georgia) occurred at about 70-75% of carrying capacity. For British Columbia, maximum productivity would be roughly 12,000 animals per annum. Although data are sparse, it would appear kills are presently far below that which could be sustained. Predator control permits have been issued to most of the 90 or so salmon farms in British Columbia, and

about 500-600 seals have been shot annually (Department of Fisheries and Oceans 1997; R. Ginetz, Department of Fisheries and Oceans, Aquaculture Division, 555 West Hastings Street, Vancouver, B.C., V6B 5G3, personal communication). During 1997-98, the Department of Fisheries and Oceans culled 52 seals in the Puntledge River for predator control (E. Lochbaum, Department of Fisheries and Oceans, South Coast Division, 3225 Stephenson Point Road, Nanaimo, B.C., V9T 1K3, personal communication), and during the last decade approximately 30 seals have been killed for research purposes (Addison et al. 1996; Olesiuk, unpublished data). Natives are permitted to harvest seals for subsistence use, and something on the order of several hundred are probably taken annually (D.M. Petrachenko, Department of Fisheries and Oceans, 555 West Hastings Street, Vancouver, B.C., V6B 5G3, personal communication). In addition to these authorized kills, there are undoubtedly animals taken incidentally in fishing gear and killed illegally. Although data on the magnitude of such kills are lacking, considering that populations have exhibited increases at rates close to the maximum intrinsic rate – even when populations were much smaller and sustainable kill levels would have been lower - in high traffic areas with intense fishing activity, such as the lower Skeena River and off the mouth of the Fraser River, it is likely that such kills are far below sustainable levels.

In comparison with the estimated 108,000 harbour seals on the British Columbia coast during 1996-98, abundance was estimated to be about 34,600 off California as of 1994, 29,900 off the outer coast of Oregon and Washington as of 1992, 13,800 in the inland waters of Washington as of 1992 (Barlow et al. 1995), 37,500 in southeast Alaska as of 1993, 30,300 in the Gulf of Alaska and Aluetian Islands as of 1994 and 1996 respectively, and 13,300 in the Bering Sea as of 1995 (Hill et al. 1997). Total range-wide abundance of *P. v. richardsi* is thus on the order of 267,000, of which about 40% occur in British Columbia. British Columbia, and in particular the Strait of Georgia, can thus be regarded as the center of distribution for this species in the northeastern Pacific. Indeed, the Strait of Georgia probably supports one of the largest concentrations of harbour seals in the world.

## RECOMMENDATIONS

1. Given the ten-fold increase in abundance over the last 25 years, and the recent slowing and the subsequent stabilization of populations at high levels, it is important that surveys be continued to confirm recent trends and to monitor the behaviour of populations near carrying capacity. It is unknown, for example, whether populations will remain stable or exhibit fluctuations, such as the 50% die-off recently experienced by harbour seals in Europe after an extended period of population growth (Dietz et al. 1989). It is therefore recommended that monitoring of population trends be continued in a number of index areas, which should be broadly distributed such that they are likely to be representative of the entire coast.
2. One of the last vast areas in British Columbia and indeed in the entire northeastern Pacific where harbour seal populations have not been surveyed is the central and northern mainland coasts, which represents about 60% of the province's coastline. Lack of knowledge of seal densities in this region contributes appreciably to the imprecision in the total abundance estimates for British Columbia, and there are emerging management concerns in this region, such as impacts on local salmon stocks, to which the Department is presently unprepared to respond due in large part to a lack of information on seal abundance and distribution. It is therefore recommended that an effort be launched to survey this area, and that a randomized or systematic sampling component be incorporated into the survey design so that density estimates and associated confidence limits can be calculated prior to obtaining complete coverage. Re-sampling techniques such as the jack-knife method should also be applied to existing survey data to explore the potential for bias and imprecision in extrapolating seal densities.
3. Since the abundance estimates are relatively sensitive to the correction factors applied to account for animals not hauled out during surveys, it is recommended that further work be conducted on this subject. This should include: a) write-up and publication of the time-depth recorder study in a peer-reviewed journal; b) additional deployments of time-depth recorders in other regions such as the Broughton Archipelago, Clayoquot Sound and central mainland coast so as to determine how correction factors vary geographically; and c) an examination of haulout patterns of younger animals, particularly pups and yearlings, using the newer miniaturized models of TDRs and remote release mechanisms now feasible.

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Table 1. Summary of the sex, body mass (kg) and maturity of animals instrumented with time-depth recorders and the dates and locations of deployments (for those instruments successfully recovered). Maturity status was inferred based on the mean body size at onset of maturation in each sex (48.6kg for females and 64.6kg for males; Olesiuk 1993).

Animal ID	Sex	Mass (kg)	Maturity	Deployment		Days of Data
				Date	Location	
01	F	68	A	01-Aug-90	Danger Reef	34
02	M	57	J	30-Jul-90	Danger Reef	16
03	F	43	J	03-Aug-90	NE Valdes Island	58
04	F	54	A	07-Aug-90	Miami Island	12
05	F	59	A	08-Aug-90	NE Valdes Island	30
06	F	73	A	10-May-91	Cowichan Bay	103
07	M	95	A	13-May-91	Cowichan Bay	105
08	M	95	A	30-May-91	Snake Island	81
09	M	64	J	30-May-91	Snake Island	82
10	M	43	J	12-Jun-91	Danger Reef	154
11	F	50	A	13-Jun-91	SE Orlebar Point	49
12	M	50	J	27-May-92	Ragged Island	94
13	M	64	J	19-May-92	Danger Reef	106
14	M	>91	A	28-May-92	Danger Reef	95
15	M	93	A	03-Jun-92	Danger Reef	106
16	M	57	J	29-Apr-92	Snake Island	95
17	F	41	J	02-May-92	Entrance Island	93
18	F	89	A	29-Apr-92	Snake Island	77
19	F	~95	A	03-May-92	NE Gabriola Island-B	137
20	F	75	A	01-May-92	Snake Island	105
21	M	61	J	28-Apr-93	Snake Island	98
22	M	57	J	28-Apr-93	Snake Island	106
23	M	93	A	30-Apr-93	Snake Island	121
24	M	84	A	22-Apr-93	Snake Island	125
25	M	68	A	23-Apr-93	Snake Island	124
26	M	98	A	29-Apr-94	NE Gabriola Island-C	110
27	F	96	A	05-May-94	NE Gabriola Island-C	101
28	F	55	A	03-May-94	NE Gabriola Island-C	108
29	F	45	A <sup>a</sup>	05-May-94	NE Gabriola Island-C	92
30	M	54	J	26-Apr-94	NE Gabriola Island-C	101
31	F	93	A	27-Apr-94	NE Gabriola Island-C	133
32	M	70	A	27-Apr-94	NE Gabriola Island-C	120
33	F	72	A	26-Apr-94	NE Gabriola Island-C	106
34	F	89	A	30-Apr-94	NE Gabriola Island-C	132

<sup>a</sup>classified as an under-sized adult on the basis that it was observed nursing a pup.

Table 2. Mean, standard error, and coefficient of variation of adjusted counts for replicated censuses (after Table 3 in Olesiuk et al. 1990a).

Subarea(s) Censused	Census period	Number replicates	Mean Count	Standard Error	Coefficient Variation
<i>Strait of Georgia</i>					
<i>BBAY – FRASERR</i>	Aug. 84	2	1,627.9	60.9	0.037
<i>BBAY – FRASERR</i>	Aug. 85	2	1,538.1	53.8	0.035
<i>SGULF</i>	Aug. 86	2	1,868.9	74.8	0.040
Complete	May-Aug. 88	2	13,977.1	636.7	0.046
Partial <sup>a</sup>	May-Sept 88	3	6,284.4	211.4	0.034
<i>Skeena River</i>					
Complete	Jun. 77	2	407.5	68.5	0.168
Complete	Jun. 83	2	712.0	63.6	0.089
Complete	Jun 87	2	1255.7	38.5	0.031
Complete	July 98	2	1093.4	101.1	0.092
Overall Mean					0.064

<sup>a</sup>Based on portion of region surveyed in September: *BBAY*, *FRASERR*, *HOWESD*, 46.3% of *SGULF*, 22.6% of *GULFISL*, and 47.6% of *NEGULF*.

Table 3. Mean annual finite population growth rates calculated from log-linear regressions fitted to June-August abundance estimates for the period 1973-98. For comparison, the mean finite rates of increase for the period 1973-88 are shown in parentheses (from Olesiuk et al. 1990a).

Region/ Subarea	Census period	Number of censuses	Correlation coefficient	Significance level	Finite rate of increase (%)	
<i>Strait of Georgia</i>						
<i>BBAY</i>	1973-98	18	0.496	<0.001	4.1	(8.6)
<i>FRASERR</i>	1973-98	18	0.747	<0.001	6.7	(9.4)
<i>HOWESD</i>	1973-98	15	0.751	<0.001	10.4	(16.2)
<i>SGULF</i>	1973-98	12	0.897	<0.001	8.3	(9.0)
<i>GULFISL</i>	1973-98	11	0.921	<0.001	11.1	(15.4)
<i>NWGULF</i>	1974-98	11	0.896	<0.001	15.4	(24.7)
<i>NEGULF</i>	1976-98	10	0.913	<0.001	13.8	(20.9)
Total <sup>a</sup>	1973-90	-	0.990	<0.001	12.9 <sup>b</sup>	(13.6)
	1990-98	-	0.990	0.002	7.2	-
<i>Lower Skeena River</i>						
Total	1977-98	7	0.620	0.011	4.9	(11.9)
<i>Southwest Vancouver Island</i>						
<i>SWVANISL</i>	1976-87	2	-	-	17.2	(17.2)
<i>BARKLYSD</i>	1976-87	2	-	-	26.5	(26.5)
Total	1976-87	2	-	-	20.9	(20.9)
<i>Queen Charlotte Islands</i>						
<i>SEQCI</i>	1986-92	2	-	-	9.2	-
<i>SEQCI</i>	1986-94	2	-	-	16.0	-
<i>Queen Charlotte Strait</i>						
<i>SWQCSTR</i>	1988-89	2	-	-	14.4	-
<i>BROUGHT</i>	1989-96	2	-	-	3.6	-
Combined <sup>a</sup>	1976-87	-	-	-	14.7 <sup>c</sup>	-
	1987-96	-	-	-	6.7	-

<sup>a</sup>Based on weighted piecewise regression.

<sup>b</sup>Estimate is probably biased upwards as a result of overlooking haulout sites in the earlier censuses. An adjustment for this bias (see text) gives a finite rate of increase of 11.9%.

<sup>c</sup>Estimate is probably also biased upwards as a result of overlooking haulout sites in the earlier censuses; but no adjustment for this potential bias could be determined.

Table 4. Observed changes in number and mean size of known haulout sites in the Strait of Georgia between 1973-74, 1988 and 1996 surveys. Numbers in brackets indicate the number of known haulout sites occupied during censuses (updated from Table 1 in Olesiuk et al. 1990a).

Subarea	1973-74 <sup>a</sup>		1988		1996	
	Number of haulouts	Mean size	Number of haulouts	Mean size	Number of haulouts	Mean Size
<i>BBAY</i>	8 (5)	66.3	10 (7)	125.7	11 (7)	127.0
<i>FRASERR</i> <sup>b</sup>	9 (7)	44.6	13 (7)	86.3	19 (8)	146.8
<i>HOWESD</i>	3 (3)	25.4	12 (8)	76.1	20 (13)	32.9
<i>SGULF</i>	34 (28)	28.6	63 (53)	62.3	81 (52)	96.6
<i>GULFISL</i>	46 (43)	12.4	91 (78)	46.6	131 (87)	67.2
<i>NEGULF</i>	19 (19)	18.6	64 (54)	59.8	114 (85)	67.7
<i>NWGULF</i>	8 (8)	9.3	32 (31)	57.1	37 (29)	122.5
Total	127 (113)	21.9	285 (238)	59.0	413 (281)	80.7

<sup>a</sup>1976 for the *NWGULF*

<sup>b</sup>May be some confusion over the exact location of animals and hence of the number of haulout sites in the earlier censuses.

Table 5. Estimated density of seals (seals·km<sup>-1</sup>) in all surveyed areas of British Columbia adjusted to 1996-98 levels, by which time populations had stabilized. Densities were estimated based on the average (weighted by coverage) observed on surveys conducted during 1996-98, or on the most recent surveys adjusted to 1996-98 levels based on recent population trajectories (see Figure 16; bottom line in Appendix II). The entire British Columbia shoreline measures 27,200 km at the scale used in the analysis (Olesiuk et al. 1990a).

Region / Subarea	Population size	Shoreline length (km)	Density of seals	Coefficient of Variation
<i>Strait of Georgia</i>				
<i>SGULF</i>	6,625	248	26.7	-
<i>BBAY</i>	1,513	50	30.3	-
<i>FRASERR</i>	1,631	124	13.2	-
<i>HOWESD</i>	885	221	4.0	-
<i>GULFISL</i>	9,635	354	27.2	-
<i>NEGULF</i>	10,319	968	10.7	-
<i>NWGULF</i>	5,864	779	7.5	-
Jervis Inlet	785	484	1.6	-
<b>Total (Strait of Georgia)</b>	<b>37,257</b>	<b>3221</b>	<b>11.6</b>	<b>0.32</b>
<i>West Coast Vancouver Island</i>				
<i>SWVANISL</i>	1,044	279	3.7	-
<i>BARKLYSD</i>	1,077	210	5.1	-
<i>MWVANISL</i>	1,228	813	1.5	-
<i>NWVANISL</i>	2,225	920	2.4	-
<b>Total (W.Vancouver Island)</b>	<b>5,574</b>	<b>2,222</b>	<b>2.5</b>	<b>0.27</b>
<i>Skeena River</i>				
<b>Total (Skeena River)</b>	<b>1,778</b>	<b>624</b>	<b>2.8</b>	<b>-</b>
<i>Queen Charlotte Strait</i>				
<i>NEQCSTR</i>	834	368	2.2	-
<i>SWQCSTR</i>	1,242	320	3.9	-
<i>BROUGHT</i>	764	234	3.3	-
<b>Total (Queen Charlotte Strait)</b>	<b>2,840</b>	<b>923</b>	<b>3.1</b>	<b>0.12</b>
<i>Queen Charlotte Islands</i>				
<i>NEQCI</i>	2,779	949	2.9	-
<i>SEQCI</i>	3,427	1,145	3.0	-
<i>SQCI</i>	542	255	2.1	-
<i>SWQCI</i>	320	358	0.9	-
<b>Total (Queen Charlotte Islands)</b>	<b>7,068</b>	<b>2,707</b>	<b>2.6</b>	<b>0.16</b>
<b>Overall (all regions)</b>	<b>54,517</b>	<b>9,697</b>	<b>5.6</b>	<b>0.36</b>
<b>Overall (excl. Strait of Georgia)</b>	<b>17,260</b>	<b>6,476</b>	<b>2.7</b>	<b>0.12</b>

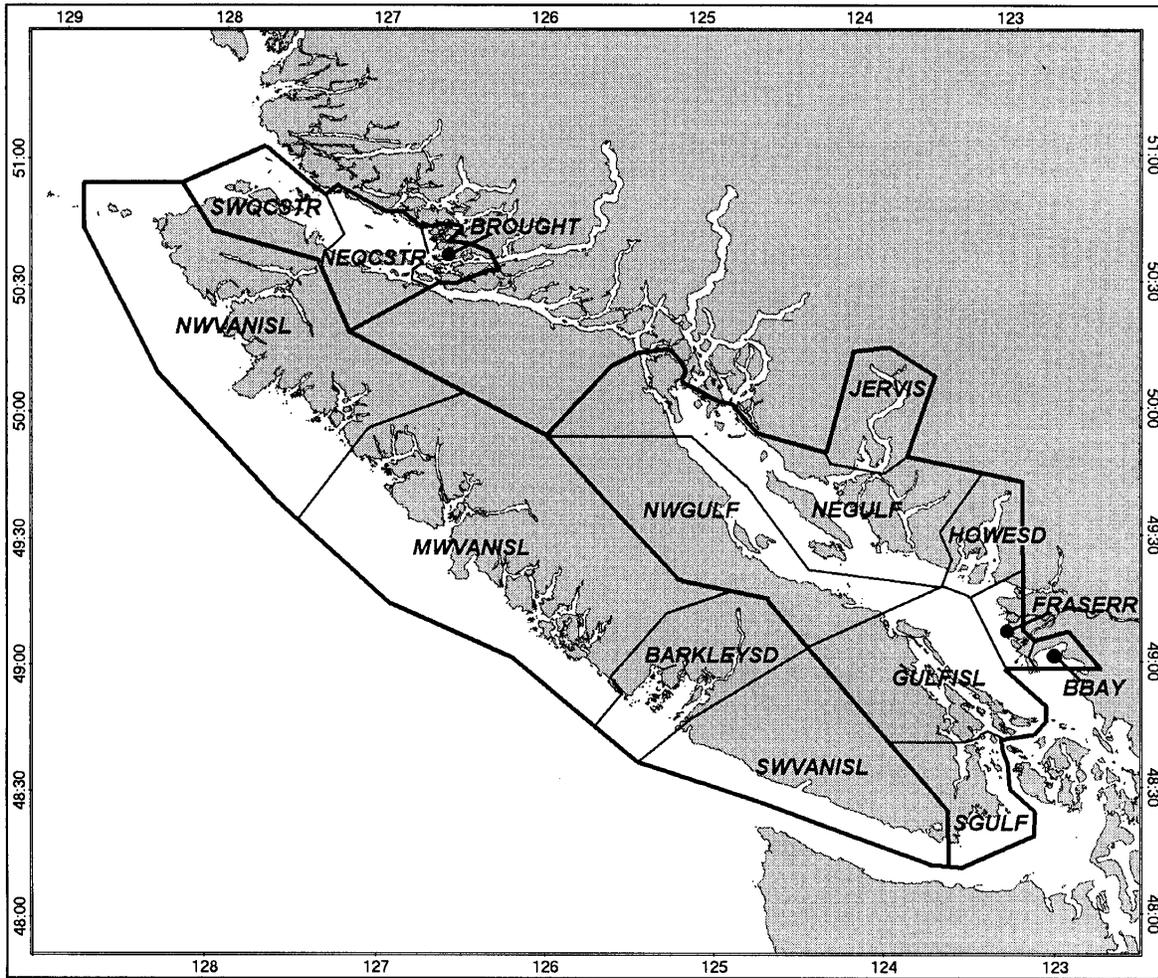
Table 6. Distribution of bounty kills during 1928-29 to 1933-34 and 1957-58 to 1959-60. Data were compiled from unpublished archival files. The estimated proportion of kills taken in surveyed areas was estimated by multiplying the proportion of the statistical area surveyed by the total number of kills in the statistical area. Because at least some of the large numbers of kills reported in DFO Statistical Area 12 during 1928-29 to 1933-34 were known to be fraudulent, a bias-corrected proportion was estimated by excluding all kills from this region for that period.

Statistical Area	Proportion surveyed	1928-29	1929-30	1930-31	1931-32	1932-33	1933-34	1957-58	1958-59	1959-60	Total
<i>Queen Charlotte Islands</i>											
01	0.72	17	165	58	133	147	0	549	310	206	1,585
02	0.66	643	831	916	1,098	523	27	1,017	1,002	223	6,280
<i>Lower Skeena River</i>											
03	0.52	489	577	550	881	372	10	66	85	557	3,587
04	0.01	103	199	235	404	272	13	47	153	67	1,493
<i>Queen Charlotte Strait</i>											
12	0.41	1,015	2,130	3,045	1,060	548	129	414	254	211	8,806
<i>Strait of Georgia</i>											
13	0.17	43	34	93	93	89	10	66	97	49	574
14	0.99	11	63	30	175	103	6	35	45	37	505
15	0.28	-	-	-	-	-	-	86	109	143	338
16	1.00	28	90	55	215	208	30	188	95	101	1,010
17	0.99	41	98	55	102	116	8	75	73	131	699
18	1.00	4	27	13	68	29	0	100	77	82	400
19	1.00	58	239	248	277	202	12	14	73	25	1,148
28	0.46	4	55	16	22	17	0	17	23	15	169
29	0.89	21	180	98	159	87	11	78	65	71	770

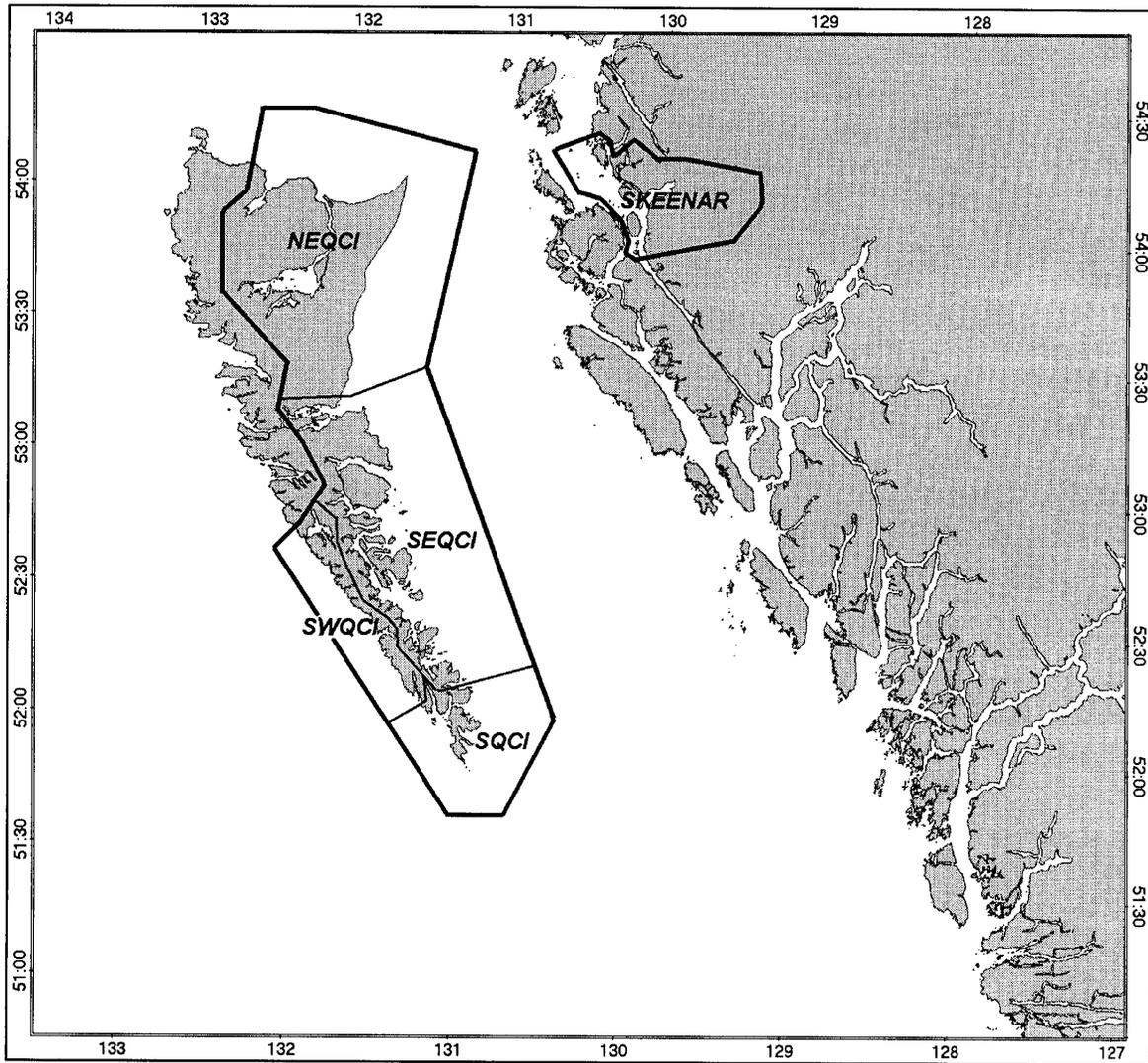
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Table 6. Continued from previous page.

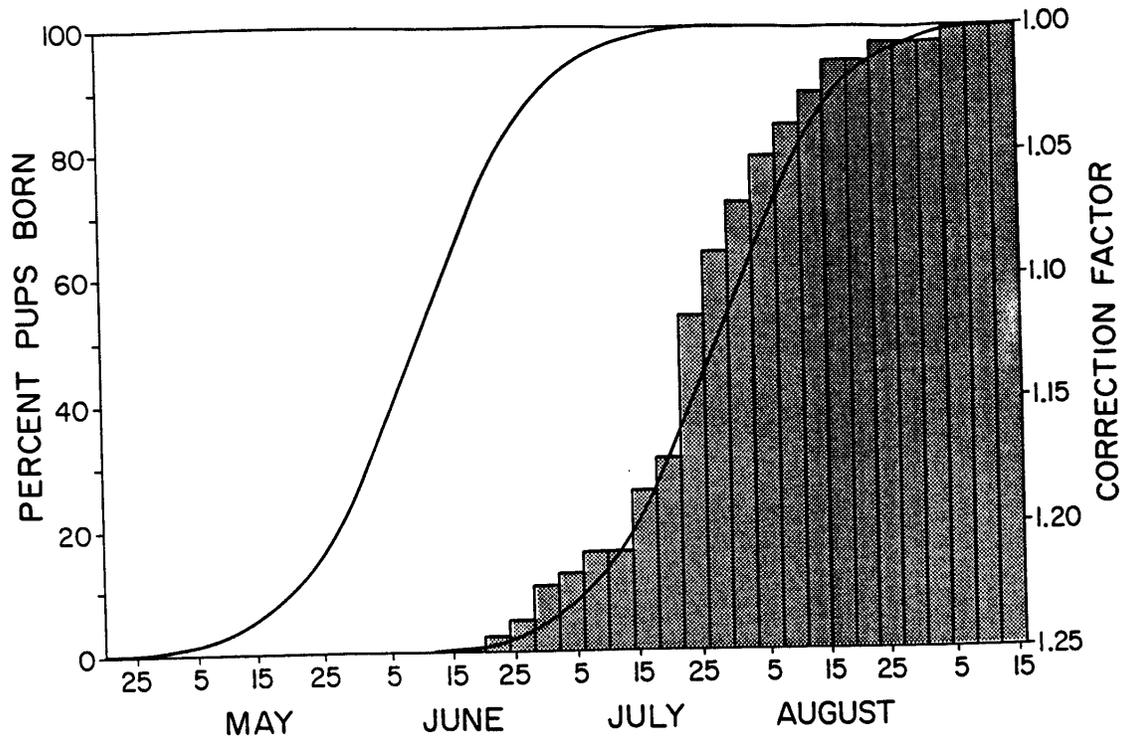
Statistical Area	Proportion surveyed	1928-29	1929-30	1930-31	1931-32	1932-33	1933-34	1957-58	1958-59	1959-60	Total
<i>West Vancouver Island</i>											
20	1.00	4	33	32	0	0	0	6	12	8	95
21	1.00	-	-	-	-	-	-	8	8	12	28
23	0.96	3	36	41	81	116	4	15	39	19	354
24	0.78	33	74	54	67	88	1	28	46	40	431
25	0.37	0	3	10	9	66	0	18	17	21	144
26	1.00	0	0	0	16	19	0	6	3	39	83
27	1.00	25	55	24	132	64	0	39	25	59	423
Number from surveyed areas		1,335	2,699	2,835	3,000	1,916	148	1,896	1,639	1,340	16,808
Total number of kills		3,209	5,944	6,308	6,084	4,300	400	3,825	3,612	3,058	36,740
Proportion surveyed area		0.416	0.454	0.449	0.493	0.445	0.370	0.496	0.454	0.438	0.457
Bias corrected proportion		0.419	0.479	0.486	0.511	0.451	0.351	-	-	-	0.471



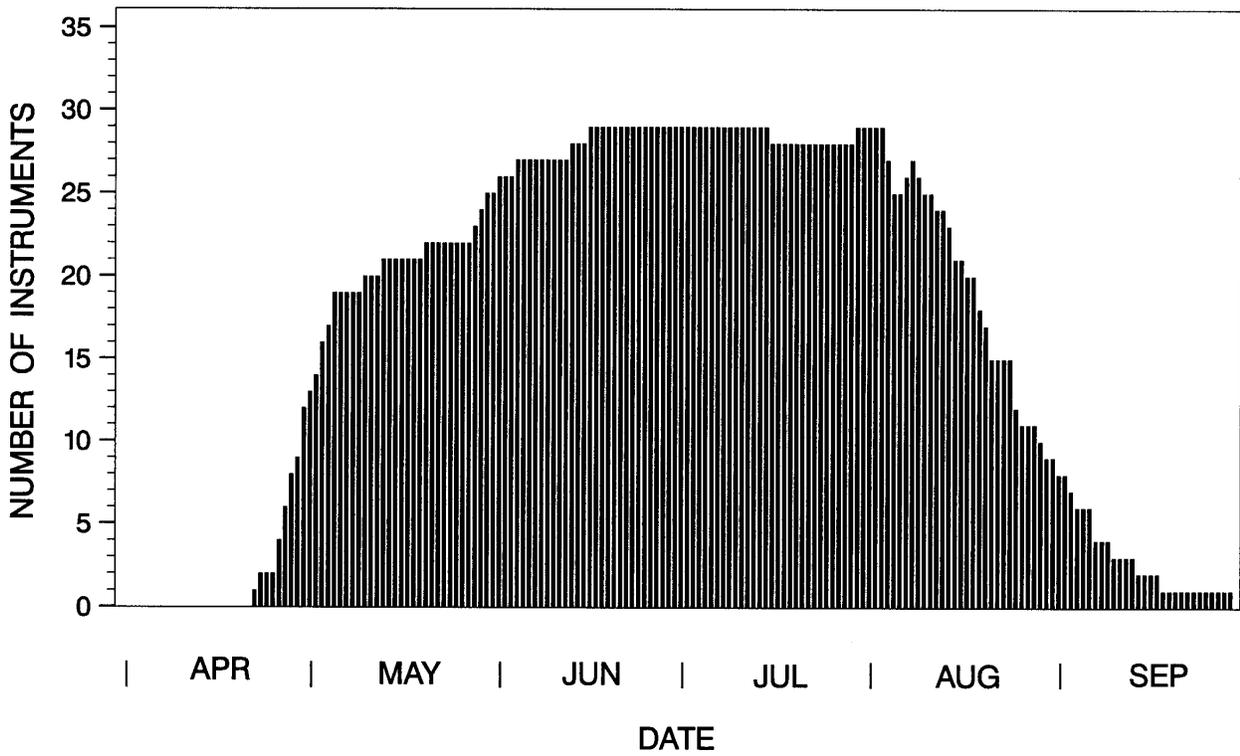
**Figure 1a.** Overview map showing coverage of harbour seal surveys in southern British Columbia. Thick lines denote study area boundaries and thin lines subarea boundaries. Detailed maps showing the location of haulout sites are given in Appendix III.



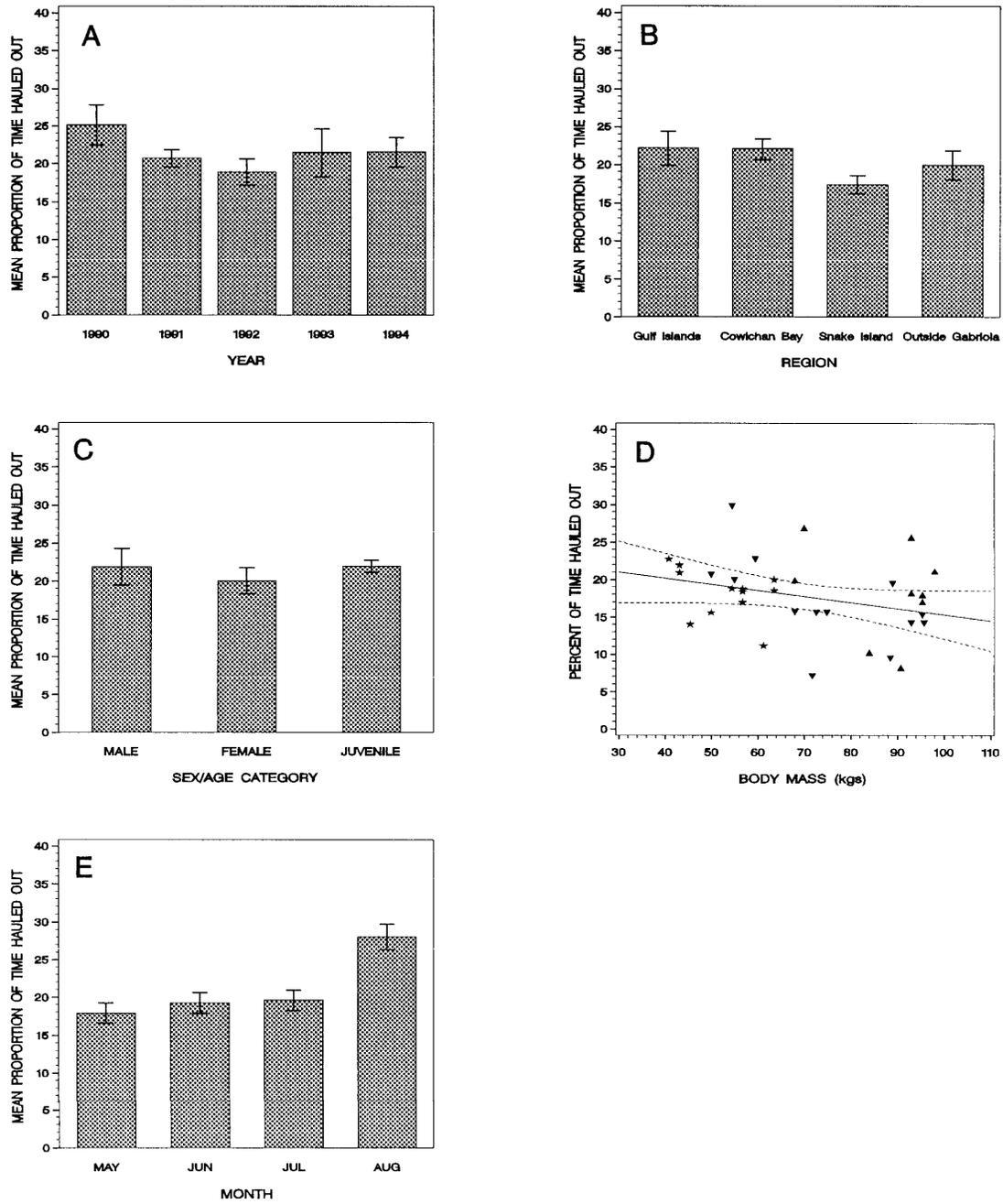
**Figure 1b.** Overview map showing coverage of harbour seal surveys in northern British Columbia. Thick lines denote study area boundaries and thin lines subarea boundaries. Detailed maps showing the location of haulout sites are given in Appendix III.



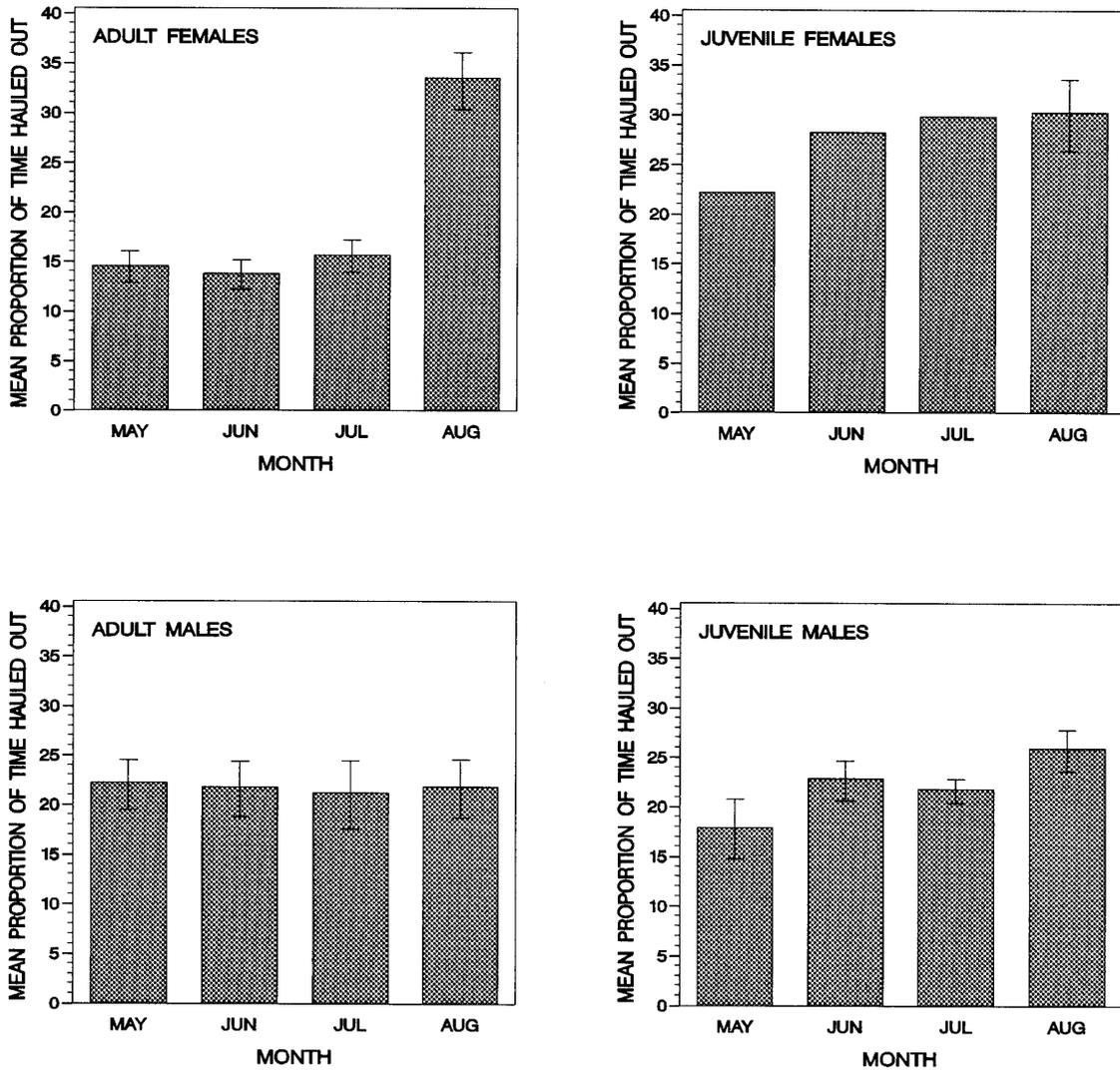
**Figure 2.** Popping curves for the Strait of Georgia and southern British Columbia (right) and for the Skeena River and northern British Columbia (left). The shaded histogram indicates the cumulative number of neonates observed in 4-day intervals in the Strait of Georgia (from Olesiuk et al. 1990a; data from Bigg 1969a).



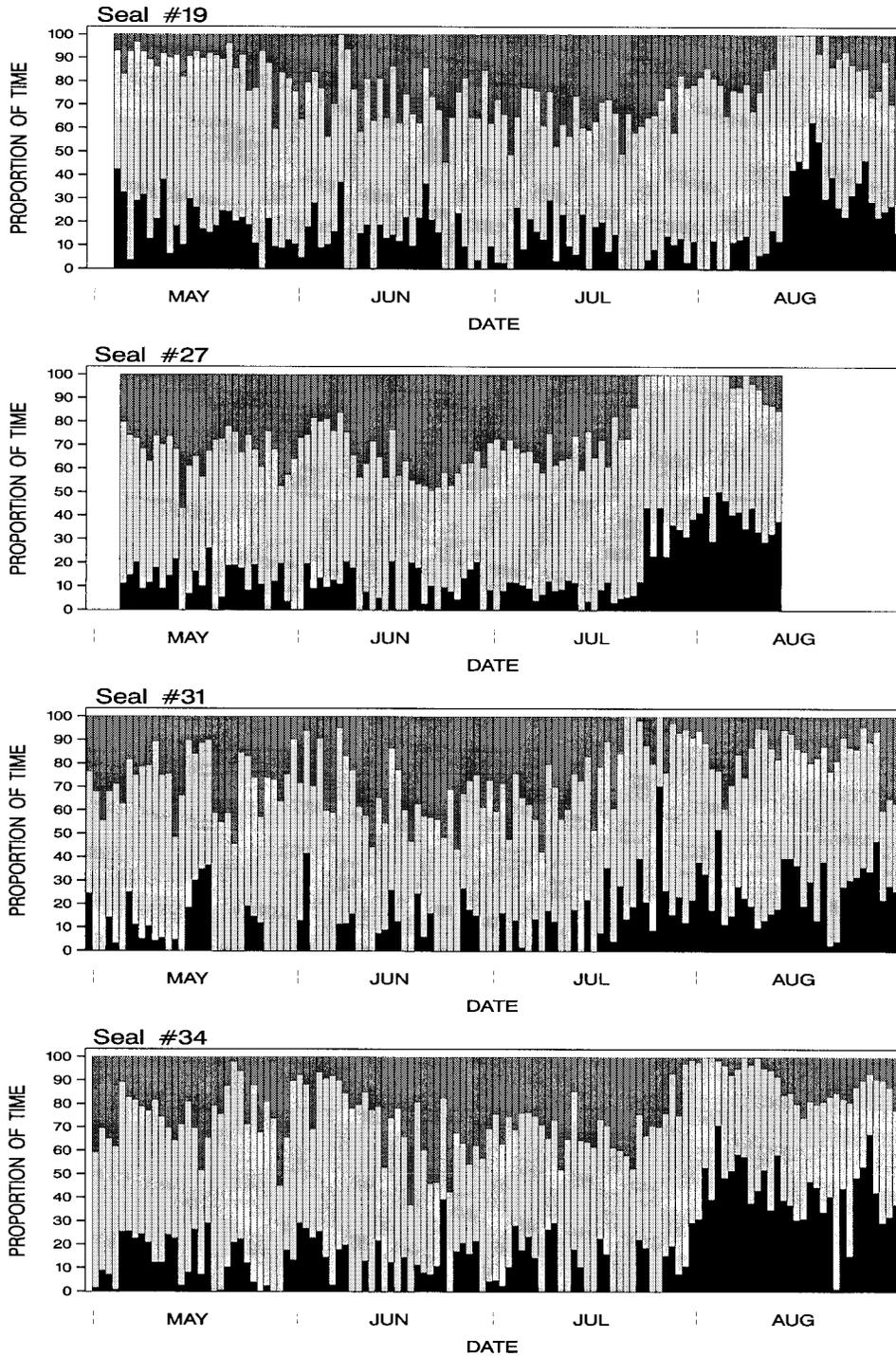
**Figure 3.** Seasonal distribution in time-depth recorder sampling effort. Bars show the number of instruments recovered that were actively recording by date.



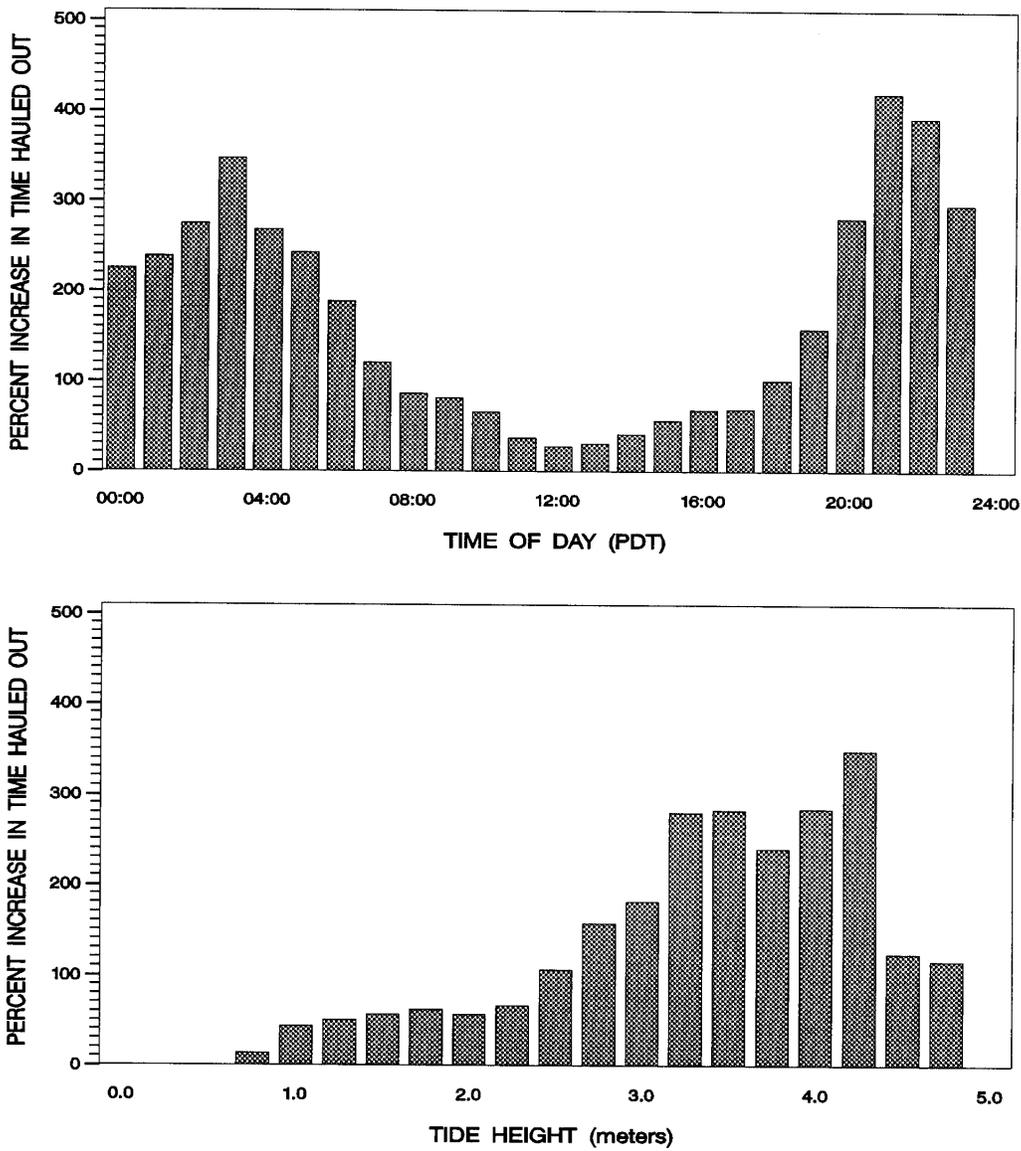
**Figure 4.** Mean proportion of time harbour seals spent hauled out as a function of: **a)** year; **b)** area; **c)** sex- and age-class; **d)** body mass; and **e)** month. Data were tabulated by animal and then averaged. Vertical bars denote standard errors of the animal means.



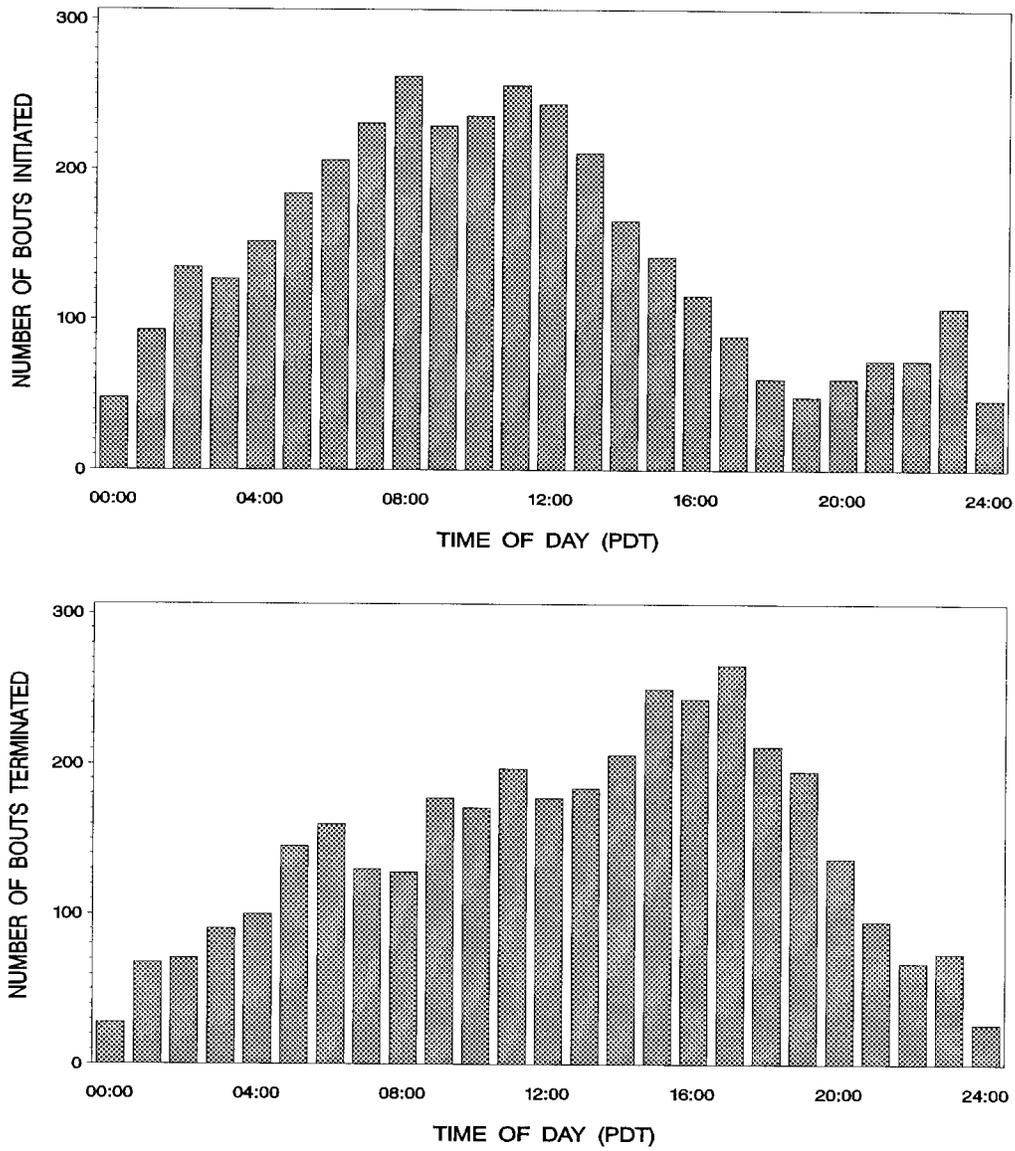
**Figure 4f.** Mean proportion of time harbour seals spent hauled out as a function of month for each sex- and age-class. Data were tabulated by animal and then averaged. Vertical bars denote standard errors of the animal means.



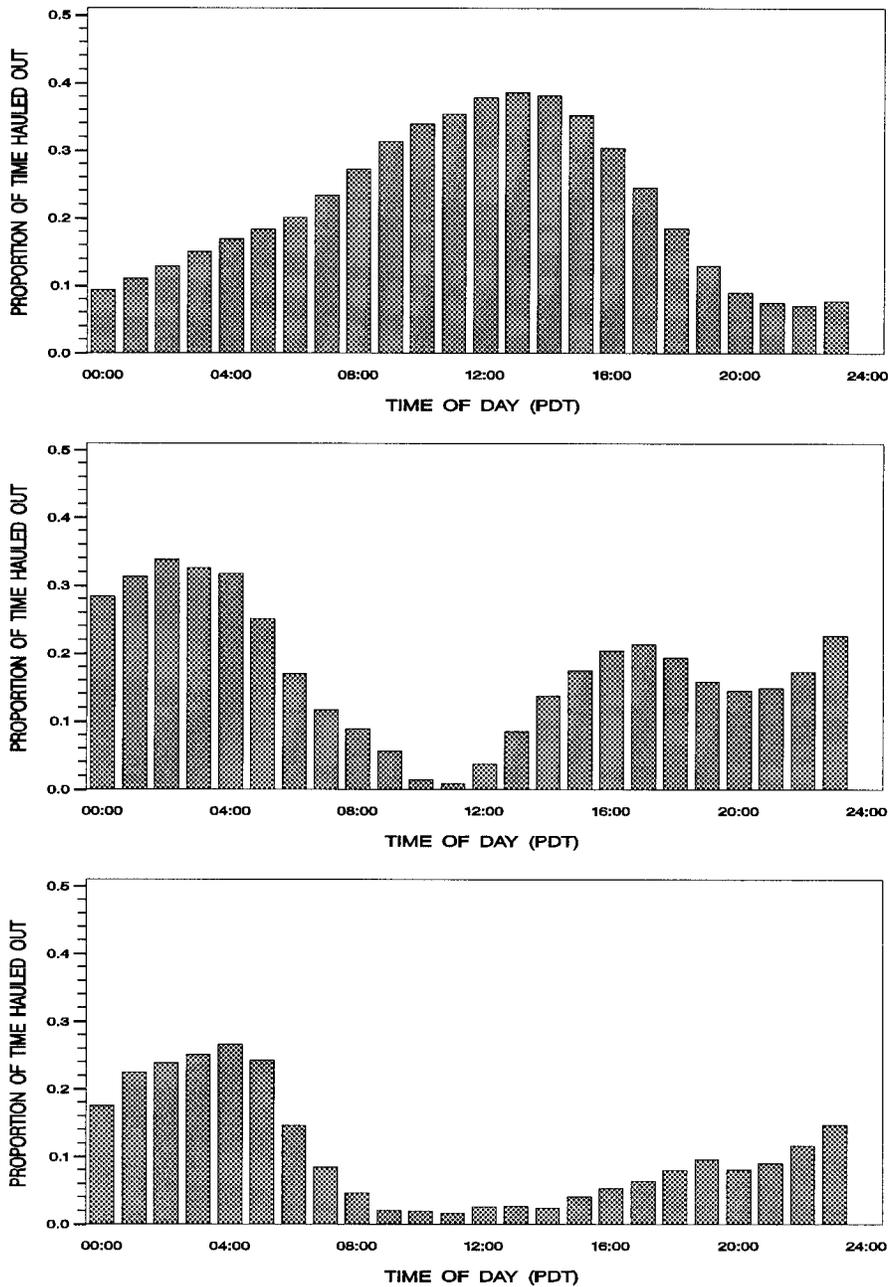
**Figure 5a.** Several examples showing seasonal changes in daily activity patterns for adult females that were seen nursing pups for which there was at least several weeks of data both preceding and proceeding the apparent date of parturition. The bars in each panel show, from bottom to top, the proportion of each day spent hauled out (black), in the water near the surface (<10 meters) (light grey) and diving (>10 meters) (dark grey). Each seal exhibited an abrupt change in behaviour sometime between mid-July and mid-August, which coincides with the pupping season (see Figure 2). These behavioural changes are characterized by: 1) hauling out every day rather than most days; 2) an increase in the proportion of time spent hauled out each day; and 3) a decline in the amount of time spent diving each day. The changes were most dramatic for Seal #27, but were also exhibited to varying degrees by the other nursing females.



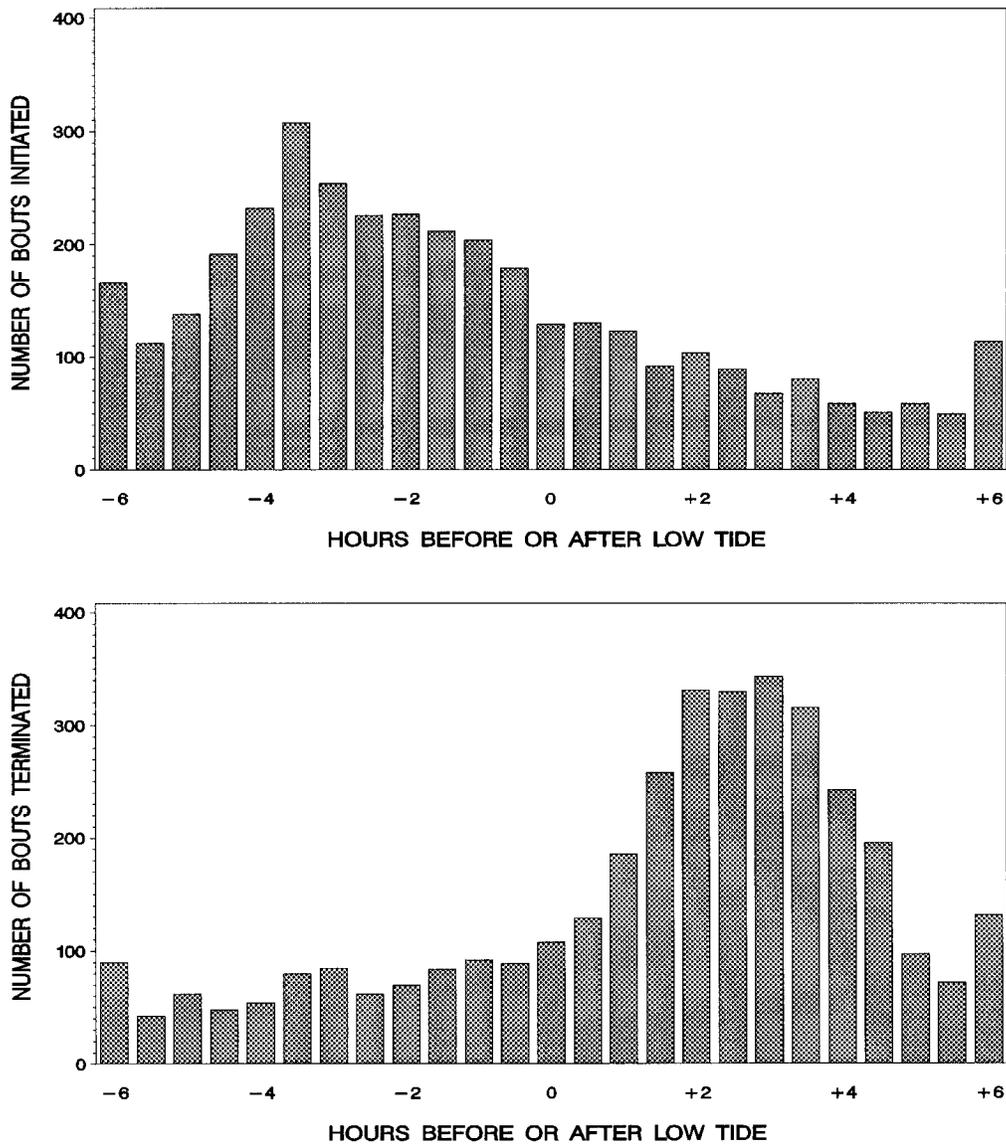
**Figure 5b.** Relative increase in amount of time spent ashore by adult females in August compared to May-July as a function of time of day (top panel) and tide height (bottom panel).



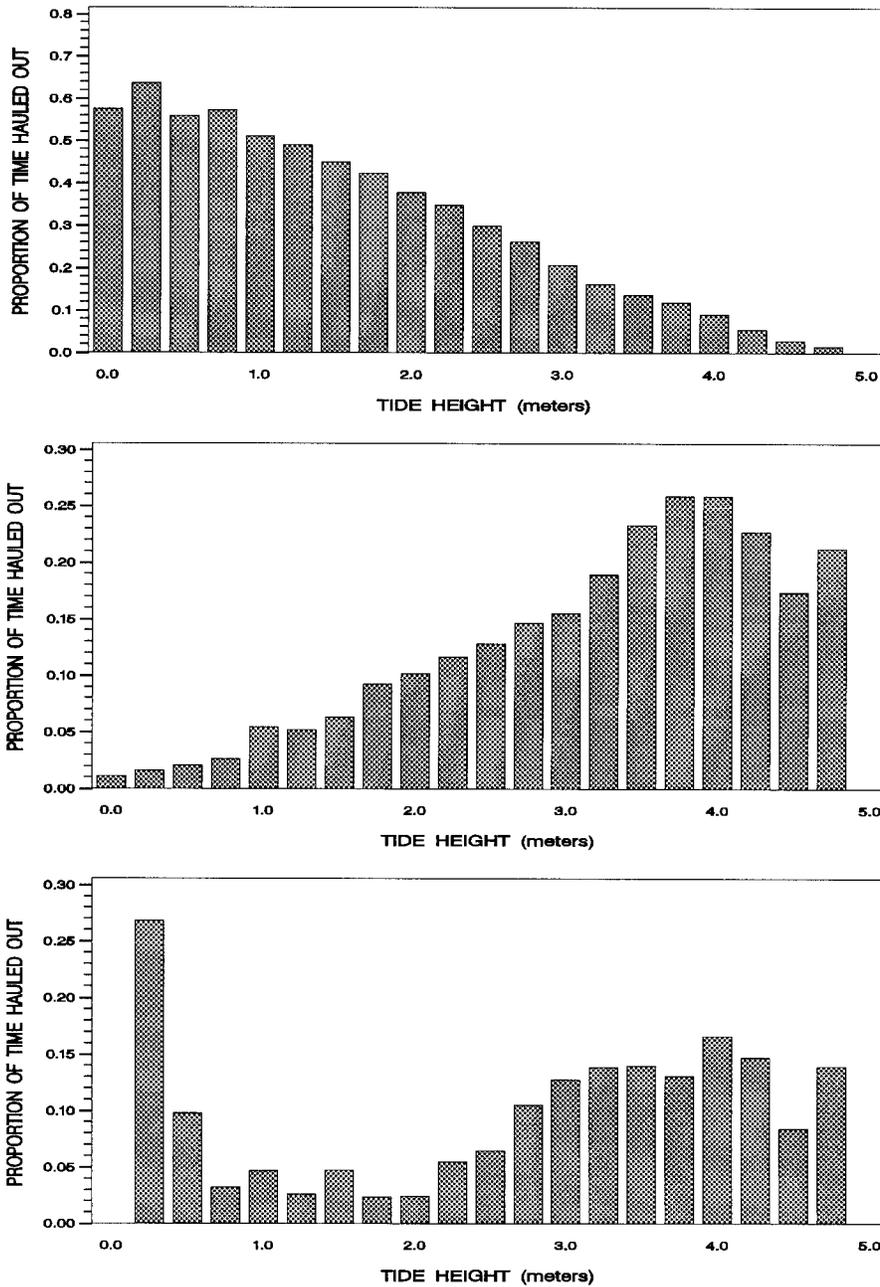
**Figure 6a.** Number of haulout bouts initiated (top panel) and terminated (bottom panel) as a function of time of day.



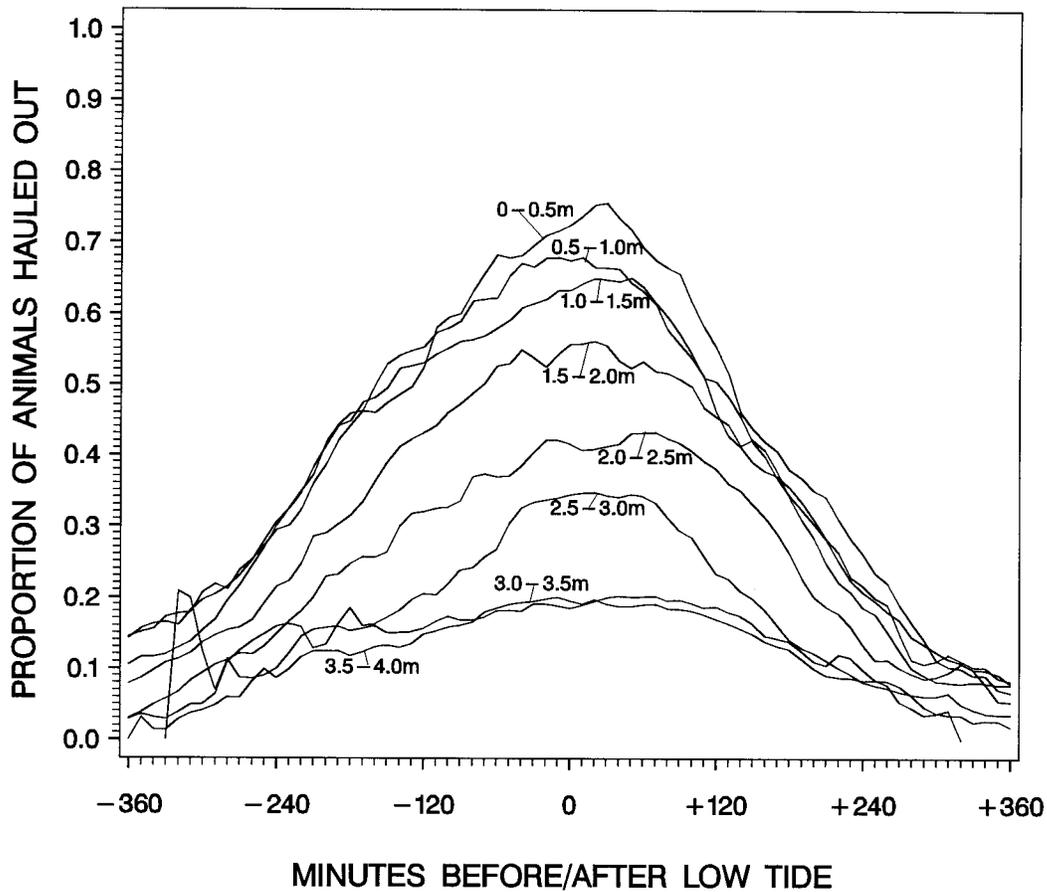
**Figure 6b.** Proportion of time spent hauled out as a function of time of day for the 31 time-depth records used to generate the haulout response curves on which the census correction factors are based (top panel), for the 2 time-depth records from instruments deployed in Cowichan Bay estuary (middle panel), and for the time-depth record of an animal captured at a tidal haulout but which frequented the Nanaimo River estuary on a regular basis (bottom panel).



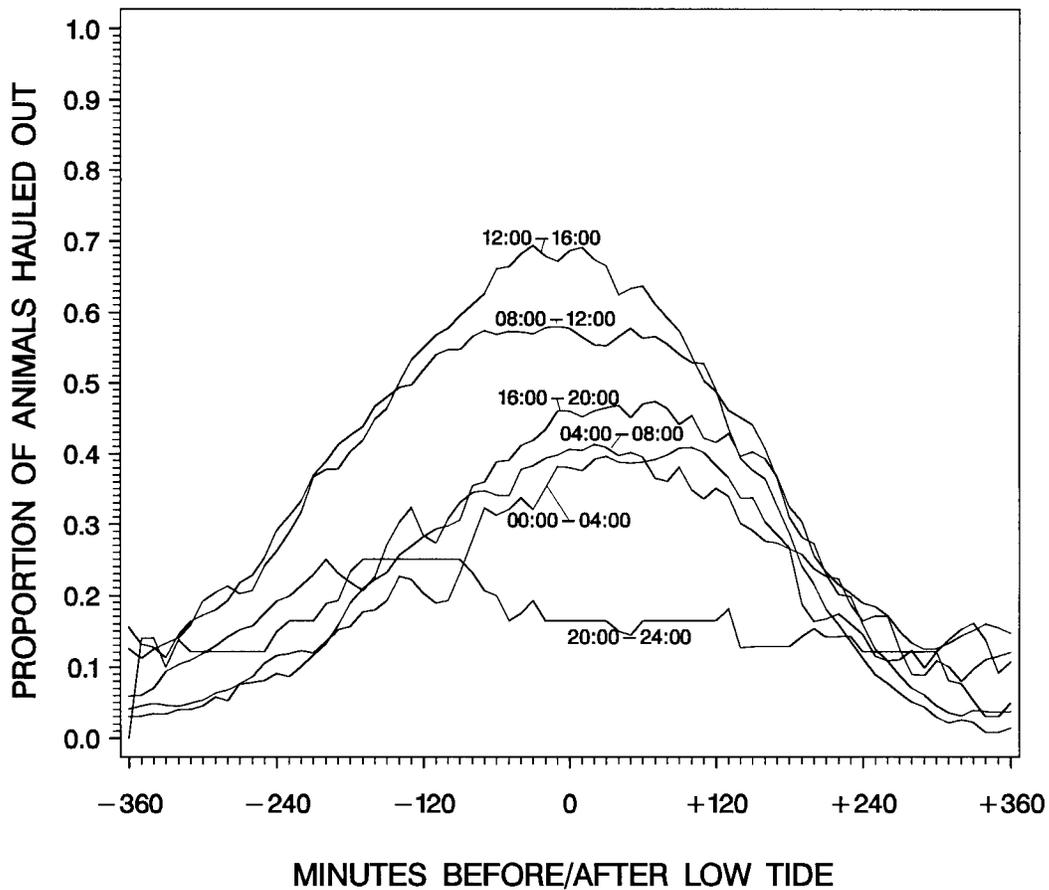
**Figure 7a.** Number of haulout bouts initiated (top panel) and terminated (bottom panel) as a function of time relative to low tide



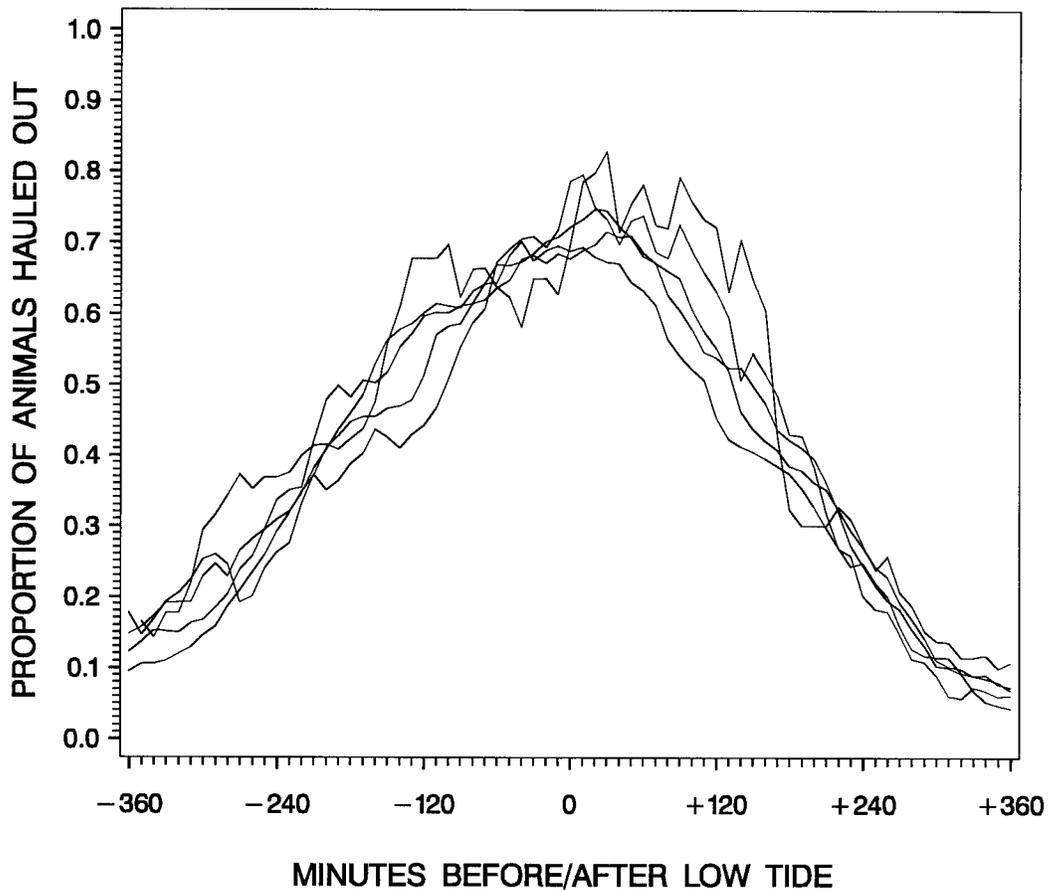
**Figure 7b.** Proportion of time spent hauled out as a function of time relative to low tide for the 31 time-depth records used to generate haulout response curves on which the census correction factors are based (top panel), for the 2 time-depth records from instruments deployed in Cowichan Bay estuary (middle panel), and for a time-depth record of an animal captured at a tidal haulout but which frequented the Nanaimo River estuary on a regular basis (bottom panel).



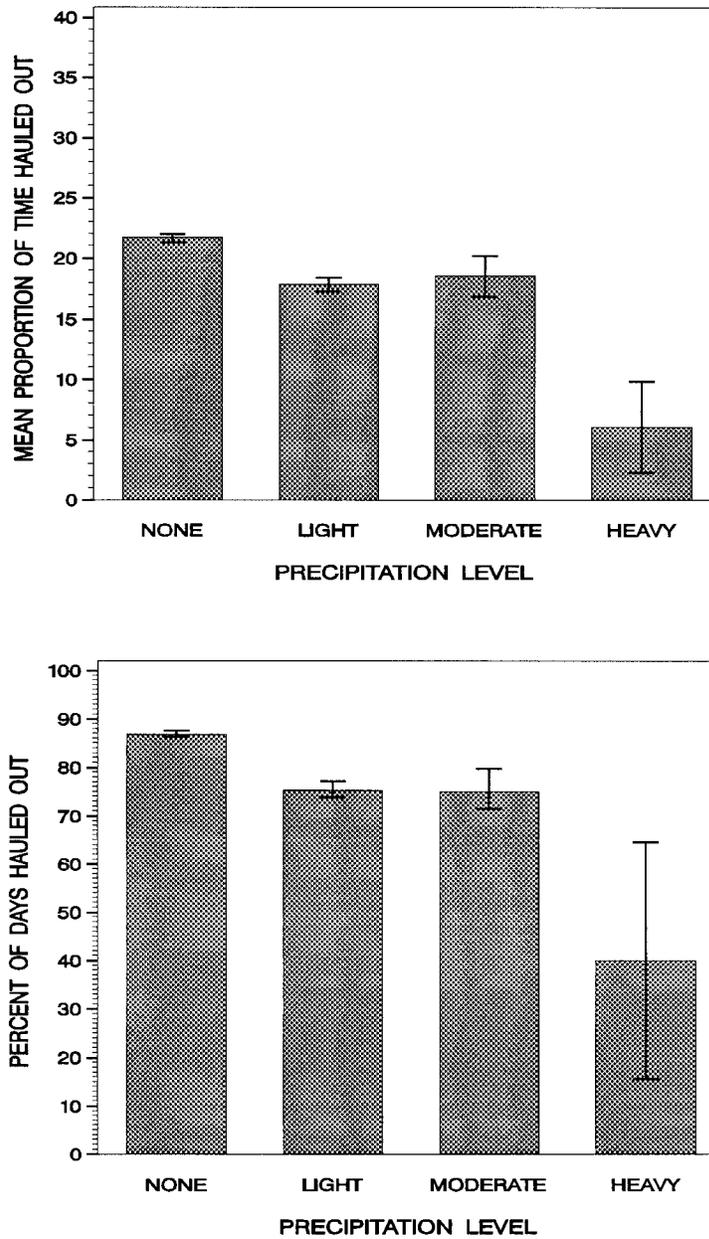
**Figure 8a.** Examples of haulout response curves showing the proportion of seals hauled out as a function of time relative to low tide for low tides of varying height irrespective of the time at which the low tide occurred, which shows that animals prefer to haul out on lower low tides. Note the consistent shape of the response curves irrespective of the time or height of the low tide.



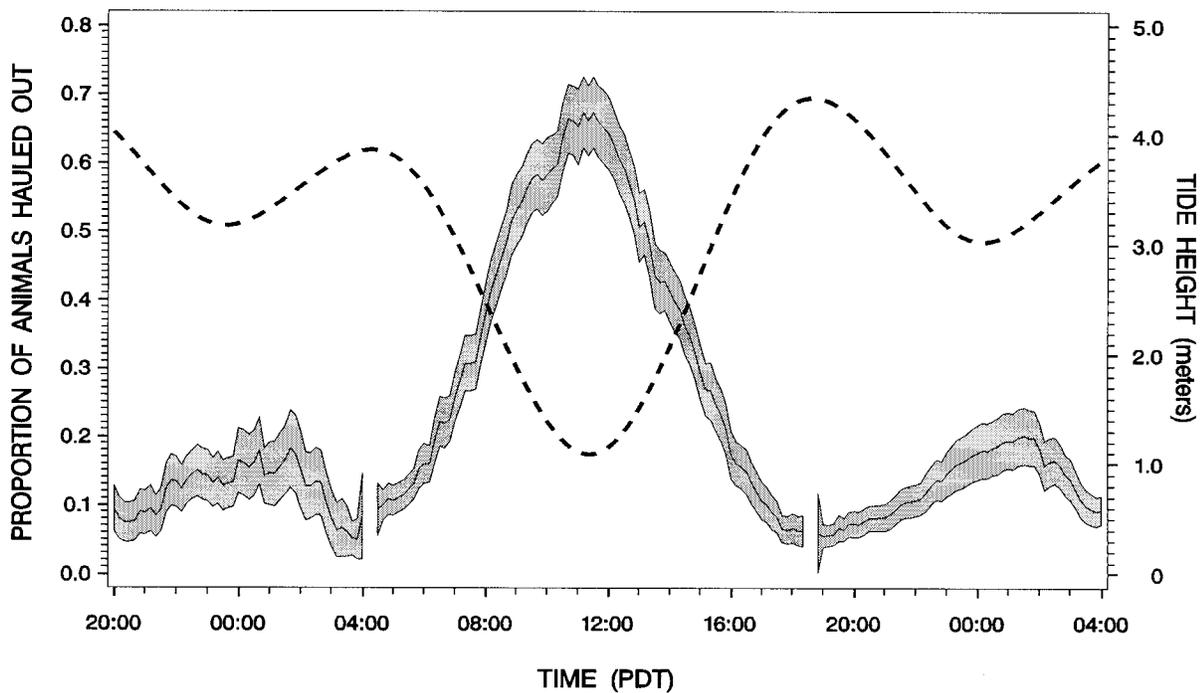
**Figure 8b.** Examples of haulout response curves showing the proportion of seals hauled out as a function of time relative to low tide for an intermediate low tide of 2.0-2.5 meters, which shows that for a tides of a fixed height animals prefer to haul out near mid-day as opposed to night-time. Note the consistent shape of the response curves irrespective of the time or height of the low tide.



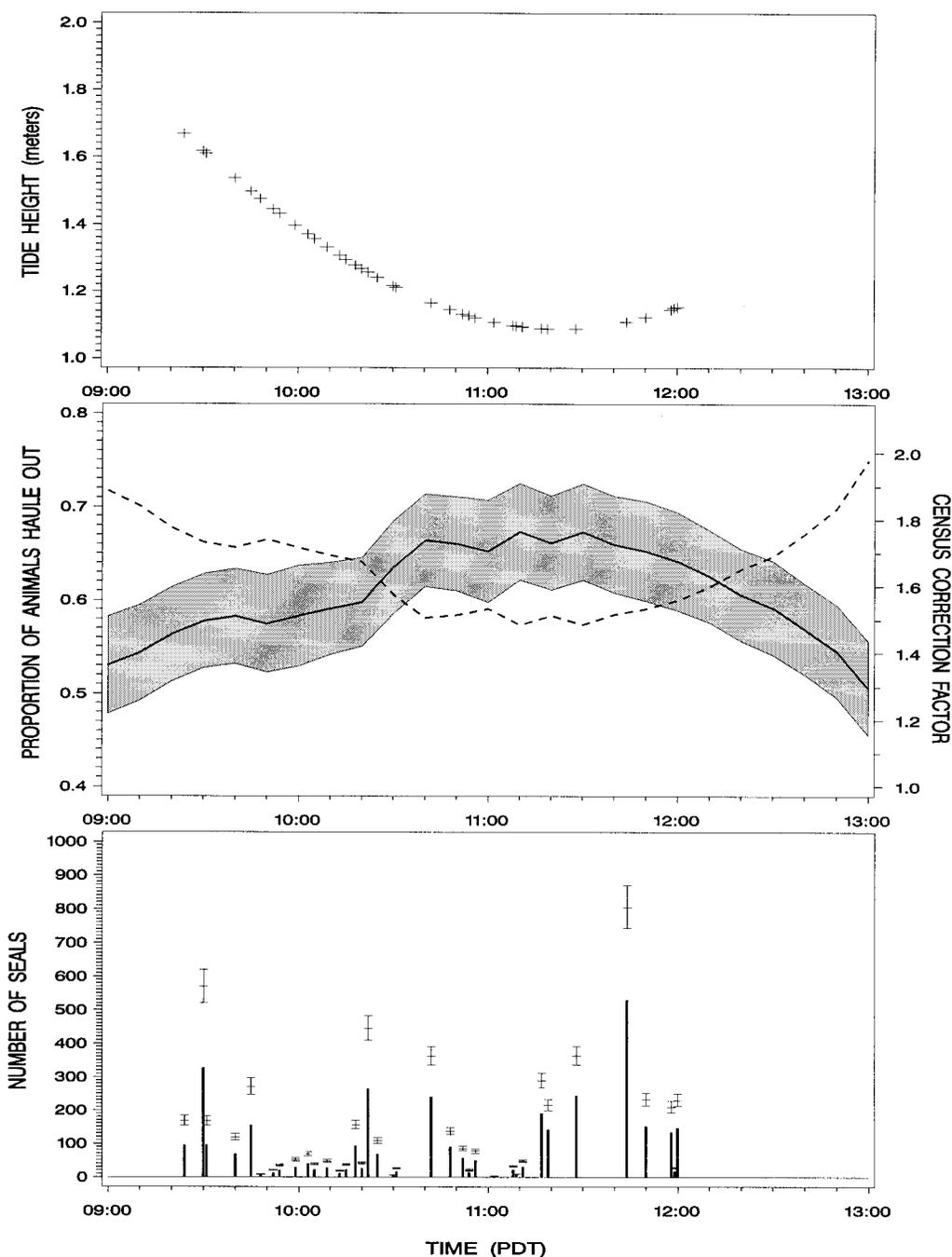
**Figure 8c.** Examples of haulout response curves showing the proportion of seals hauled out as a function of time relative to low tide for tides of varying heights that occur near mid-day (10:00-14:00), which shows that once the effects of time-of-day are removed, tide height has little effect on the proportion of animals hauled out (curves were too similar to label and represent tides of 0-0.5, 0.5-1.0, 1.0-1.5, 1.5-2.0, and 2.0-2.5m; low tides >2.5m never occur near mid-day during summer months).. Note the consistent shape of the response curves irrespective of the time or height of the low tide.



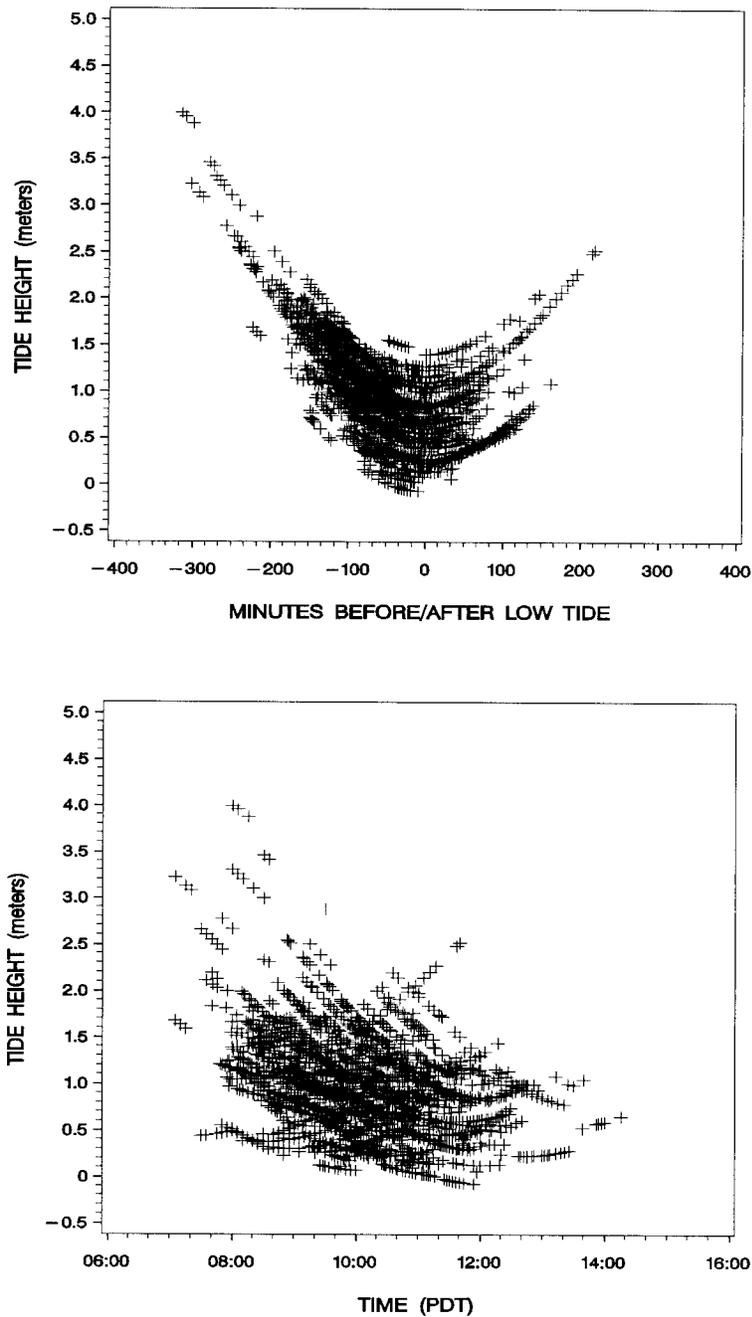
**Figure 9.** Effect of precipitation on the proportion of **a)** time spent hauled out; and **b)** days on which seals hauled out.. Light, moderate and heavy precipitation were defined days with 0-10mm, 10-20mm and >20mm of rain per day respectively as recorded at the Environment Canada station located on Gabriola Island near the centre of the study area. Data were tabulated by animal and then averaged. Vertical bars denote standard errors of the animal means.



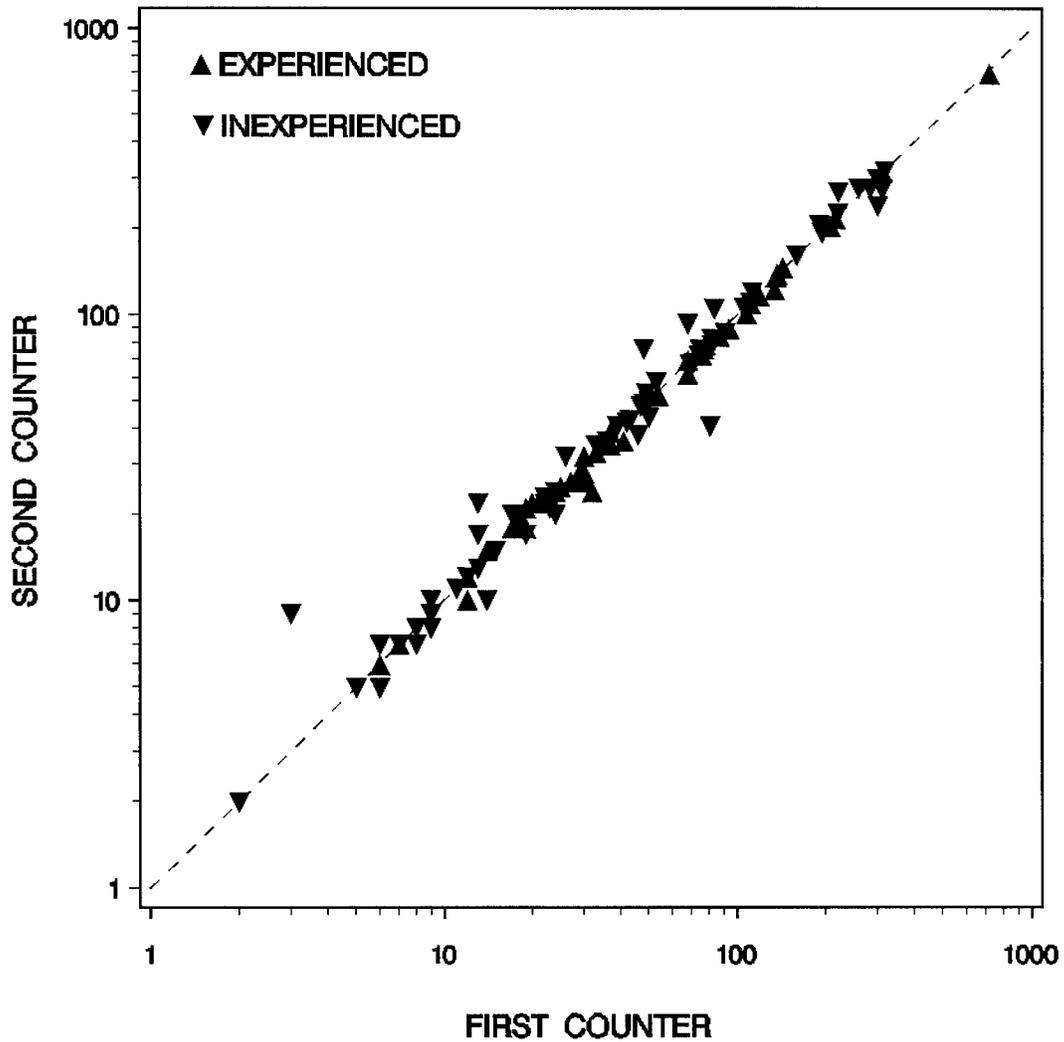
**Figure 10a.** Example illustrating calculation of correction factors for animals that were not hauled out and hence missed during surveys for one of the most recent flights (*NEGULF* on 14 August, 1996). This panel gives an overview of the day of the survey showing that the lower low tide of 1.09 meters occurred at 11:23 PDT and was preceded by a higher low tides of 3.87 meters that occurred at 23:35 PDT and proceeded by higher low of 3.03 meters that occurred at 00:10 PDT (dashed lines). The three haulout response curves (solid lines with  $\pm$ SE shaded) corresponding to similar tides (in this case defined at tides of 3.37 to 4.37 meters between 22:35 and 00:35 PDT, 0.59 to 1.59 meters between 10:23 and 12:23 PDT, and 2.53 to 3.53 meters between 23:10 and 01:10 PDT respectively; 110, 520 and 629 of which had been monitored by the time-depth recorders) indicated that animals clearly preferred to haul out on the lower low tide that occurred during daylight as opposed to the higher low tides that occurred at night.



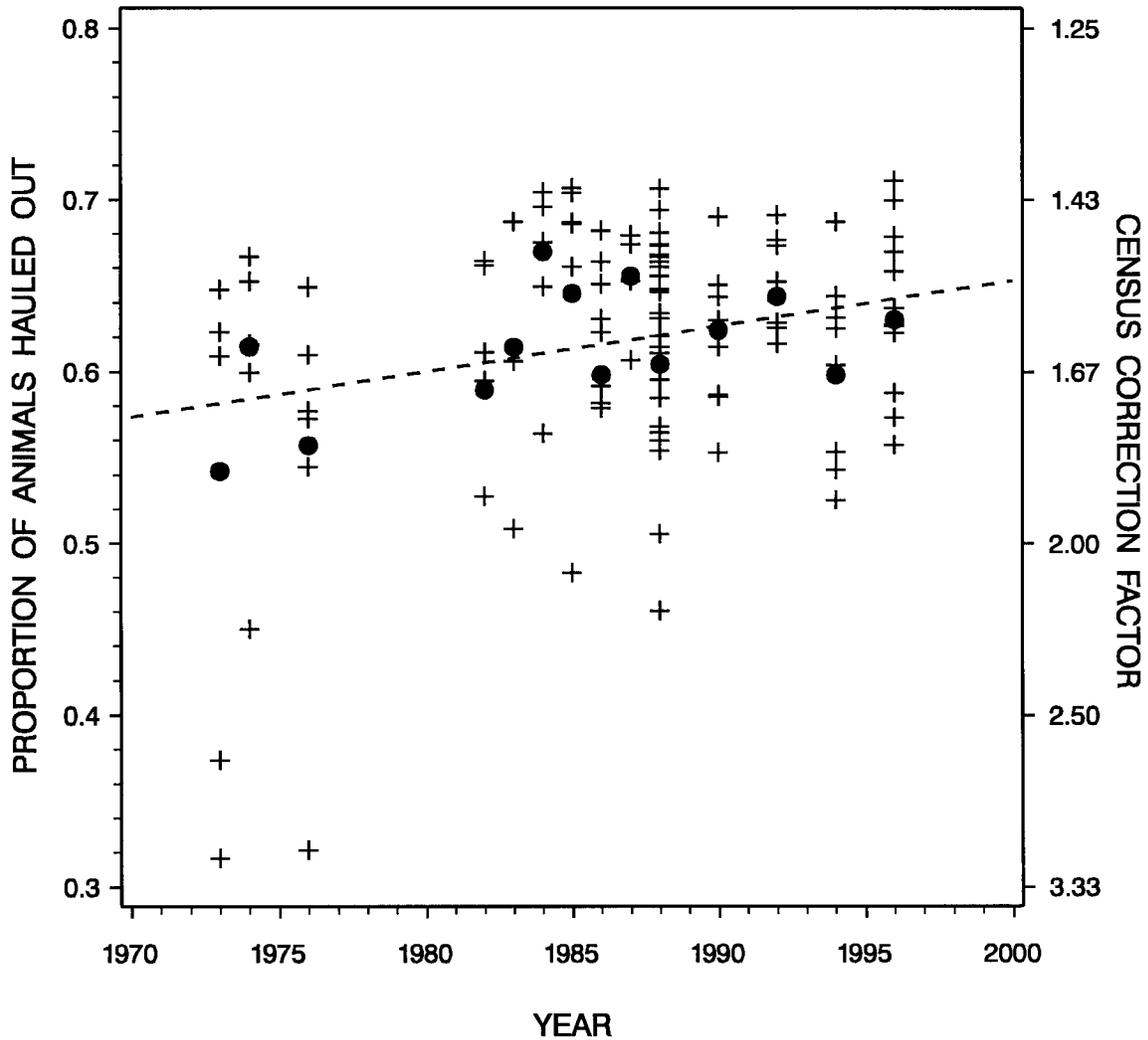
**Figure 10b.** Example illustrating calculation of correction factors for animals that were not hauled out and hence missed during surveys for one of the most recent flights (*NEGULF* on 14 August, 1996). The first count was made about 110 minutes prior to low tide and the final count about 22 minutes after low tide (top panel), which generally coincided with the peak haulout period (middle panel). Based on TDR records for similar tides, the proportion (solid line with  $\pm$ SE shaded / left scale) of animals hauled out increased from about 0.563 at the beginning of the survey, peaked at 0.673 about 11 minutes prior to low tide, and subsequently declined to 0.650 by the end of the survey, such that the corresponding census correction factors (dashed line / right scale) declined from 1.78 at the beginning to the census to a minimum of 1.49 about 11 minutes before low tide before increasing to 1.54 by the end of the survey. Bottom panel shows counts (solid bars) and estimated actual abundance (vertical lines with SE bars) for each haulout site based on the estimated proportion of animals hauled out when the site was surveyed. The overall weighted mean proportion of animals hauled out during the survey was 0.624 (SE=0.051), which corresponds with a census correction factor of 1.60.



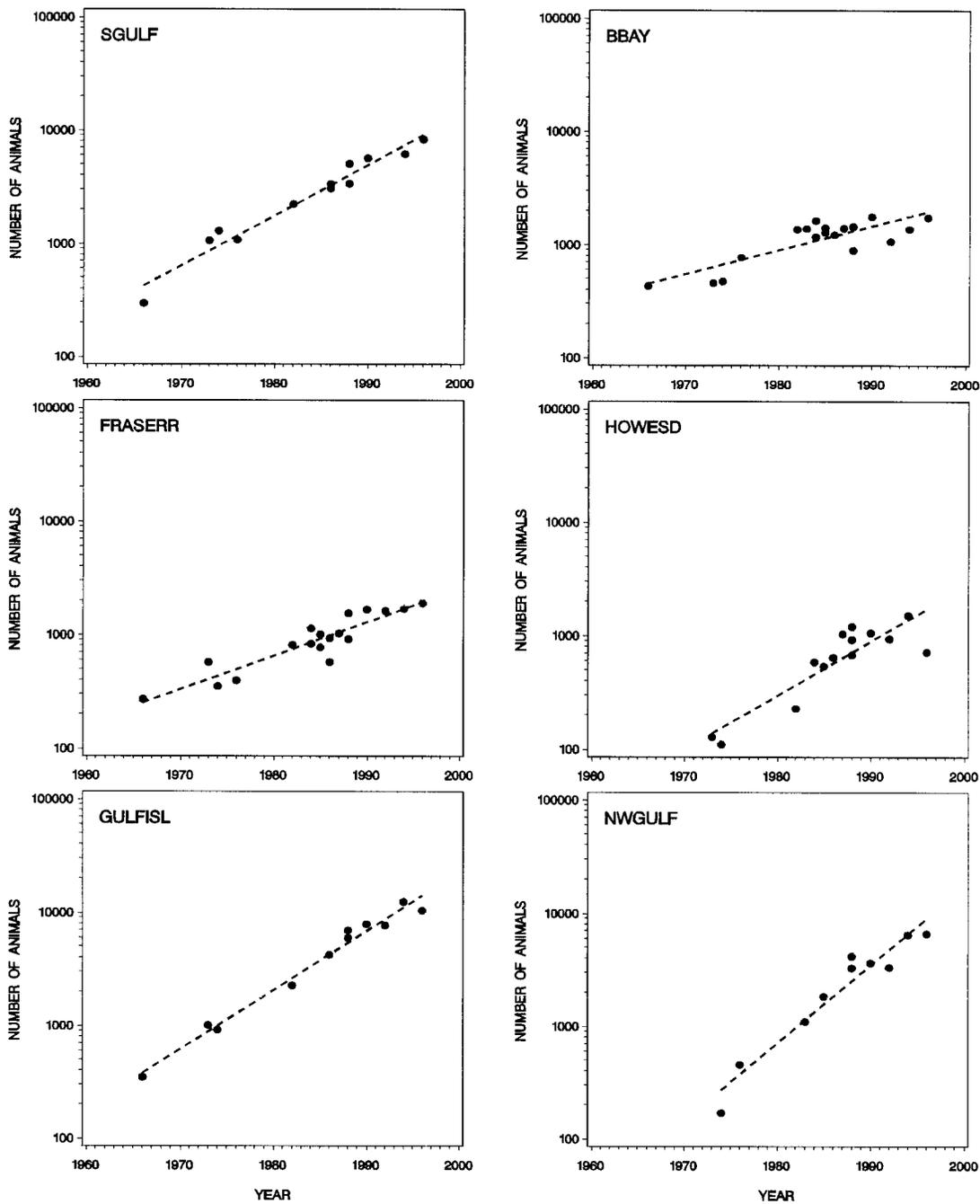
**Figure 11.** Scatterplots showing the time and tide height for all counts made in the Strait of Georgia during 1973-96 as a function of: **a)** time relative to low tide; and **b)** time of day. Each symbol represents one count, and the chains of symbols usually denote a sequence of counts made on the same survey flight. The outliers in the upper-left corner represent several survey flights in 1973 and 1974 that were initiated up to 5 hours before low tide while water levels were still high.



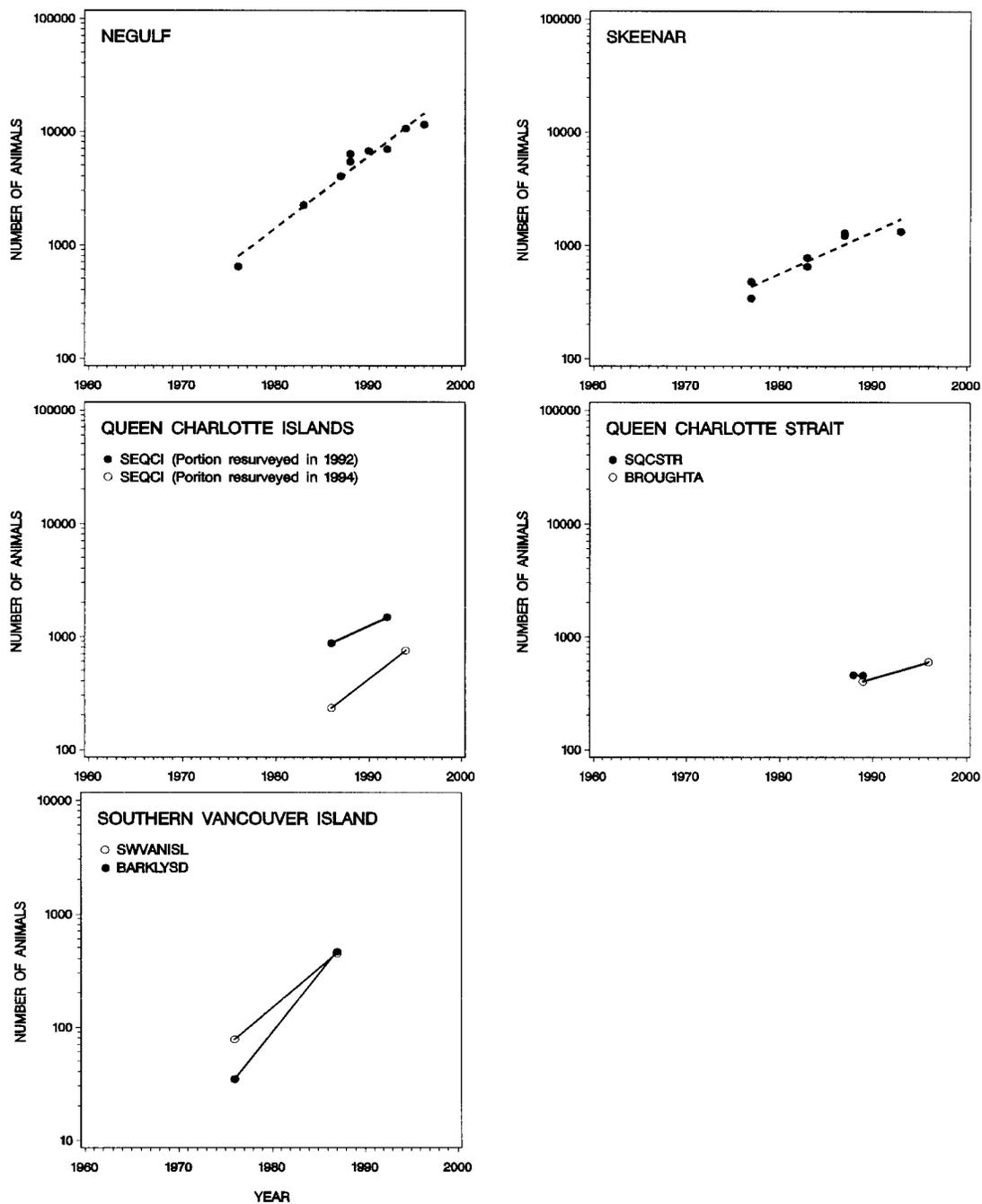
**Figure 12.** Blind comparisons of counts made from photographic slides by different readers. The dashed line denotes a 1:1 line indicating perfect agreement. The first counter in both cases was the author, who counted most slides from 1982-88 and about two-thirds of those from 1988-98. An experienced assistant counted most of the remaining one-third of slides from 1988-98. An inexperienced assistant also counted some of the more recent slides, but most were eventually recounted by either the author or the experienced assistant.



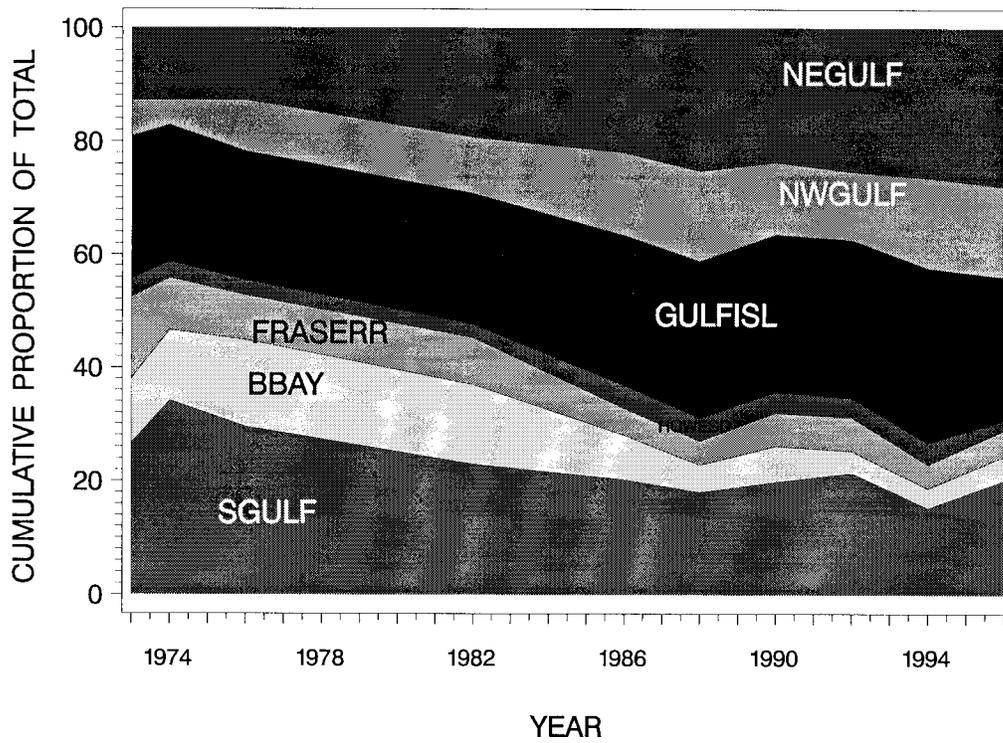
**Figure 13.** Census correction factors for the Strait of Georgia over the course of the study. Plus symbols denote correction factors for each subarea on each flight (i.e. there would be two symbols if the flight covered two subareas or if a subarea required two flights), circles represent the weighted annual means, and the dashed line a weighted least squares regression fitted to the annual means. The corresponding census correction factor is shown on the right-hand axis, but note that its scale is non-linear.



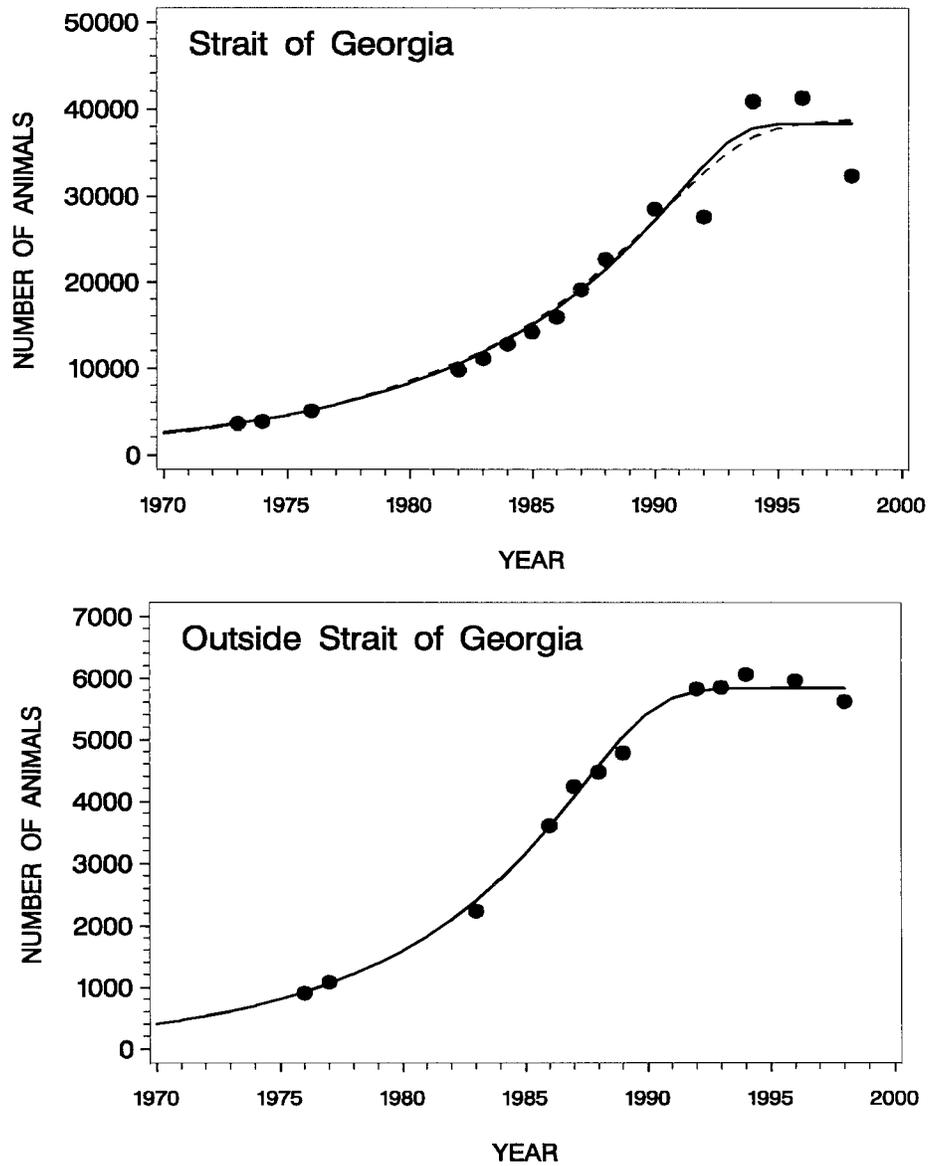
**Figure 14.** Trends in abundance observed in subareas surveyed more than once over the course of the study. Dashed lines represented weighted least squares log-linear regressions and solid lines join the point estimates where there were too few data to fit regressions.



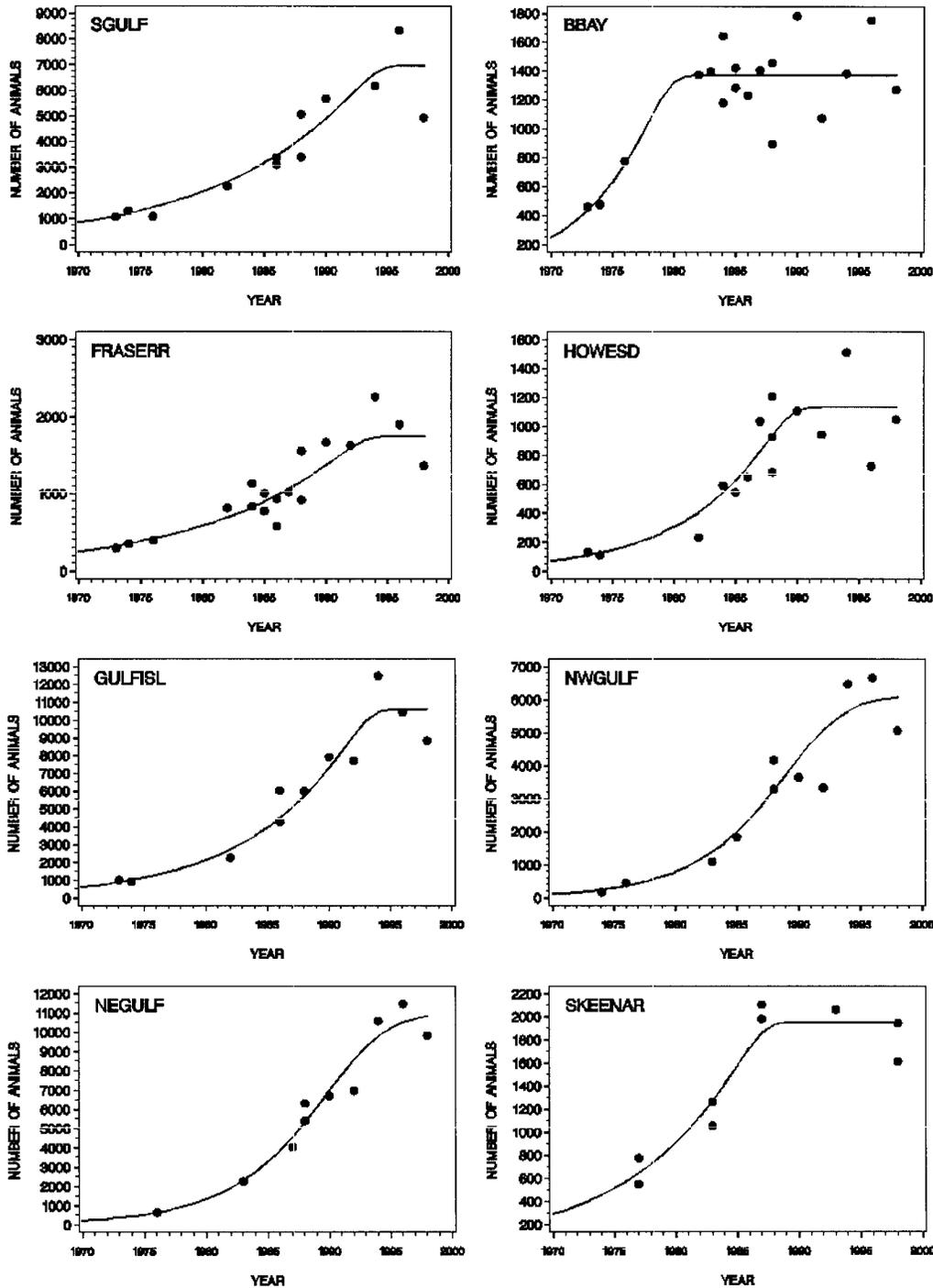
**Figure 14 continued.** Trends in abundance observed in subareas surveyed more than once over the course of the study. Dashed lines represented weighted least squares log-linear regressions and solid lines join the point estimates where there were too few data to fit regressions.



**Figure 15.** Shifts in the relative distribution of harbour seals among the Strait of Georgia subareas over the course of the study.



**Figure 16.** Population trends **a)** within the Strait of Georgia; and **b)** in a composite of all areas surveyed outside the Strait of Georgia. The solid line denotes a generalized logistic model fitted by least squares (weighted by the square root of the proportion of the region surveyed), and the dashed line in the first panel represents the sum of abundance estimates from generalized logistic models fitted individually to each of the seven subareas (see Figure 17).



**Figure 17.** Population trends within each of the seven Strait of Georgia subareas and the lower Skeena River. The solid lines denote generalized logistic model fitted by least squares (weighted by the square root on the number of replicate counts).