

Abstract.—A bioenergetic population model that integrated input on the abundance, distribution, sex- and age-structure, feeding rates, and diet of harbor seals was developed and used to estimate annual prey consumption in the Strait of Georgia during 1988. Owing to recruitment and mortality, the size of the Strait of Georgia population fluctuated seasonally from a minimum of 12,990 prior to the pupping season to a maximum of 15,810 following pupping. The study population represented a population that was increasing at an intrinsic rate of 12.5% per annum and was therefore skewed toward younger age-classes. Mean daily *per capita* gross energy requirements were estimated at 172 watts, of which 30% was lost in faeces, urine, and the heat increment associated with feeding, 42.3% was expended for basal metabolism, 23.4% for activity, 1.2% for body growth, and 3.2% for reproduction. Mean daily *per capita* food requirements were estimated to be 1.9 kg, or 4.3% of mean body mass. Diet composition varied seasonally: hake was dominant during April–November and herring during December–March. Combined, hake and herring accounted for 75% of the diet both in terms of energy and biomass. Total annual consumption was estimated at 9,892 (range 6,432–13,359) metric tons, which comprised 4,214 (2,215–6,664) t of hake, 3,206 (1,679–5,818) t of herring, 398 (171–846) tons of salmon, 335 (135–745) t of plainfin midshipman, 294 (137–556) t of lingcod, and the remaining 1,445 t of a wide variety of different prey. Gross and net population efficiency was estimated to be 3.9% and 2.2% in terms of energy, and 1.6% and 0.9% in terms of biomass.

Annual prey consumption by harbor seals (*Phoca vitulina*) in the Strait of Georgia, British Columbia

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The recovery of many formerly depleted pinniped populations and the rapid expansion of fisheries has prompted concern over potential pinniped-fishery conflicts (Mate¹; Beverton, 1982; Contos²; Melteff and Rosenberg, 1984; Beddington et al., 1985; Harwood and Croxall, 1988). The nature of these conflicts can be broadly categorized as operational (direct) or as ecological (indirect) interactions (e.g., Mate and Harvey, 1987). Operational interactions encompass those that occur when pinnipeds and fishing operations come in direct contact. For example, pinnipeds may be injured or killed in fishing gear, and fishing gear and catches may be damaged by pinnipeds (Beach et al.³; DeMaster et al., 1982; Mate and Harvey, 1987). Since these interactions can be observed, they are relatively straightforward, at least conceptually, to assess through observer programs, logbooks, or interview surveys.

Ecological interactions, in contrast, encompass the indirect effects of pinnipeds on fisheries and fisheries on pinnipeds. For example, sustainable harvest levels may be reduced as a result of pinniped predation on valuable prey species, and the carrying capacity of pinniped populations may be reduced by human exploitation of their prey. Because these interactions are temporally or spatially displaced, or both, they are conceptually more difficult to assess than operational interactions. In their comprehensive review, Lavigne et al. (1982) outlined how the prey requirements of pinnipeds could be addressed using a bioenergetics approach, and how the approach could be extended to the population level. However, such population assessments require detailed information on the abundance, distribution, sex- and age-structure, feeding rates, and diet of pinnipeds, as well as the interactions between these variables. For example, feeding rates (in biomass) are dependent upon the quality of the diet, and vary both with the sex and age of animals. The distribution and diet of pinnipeds may also be correlated if their seasonal movements are dictated by changes in the local and seasonal abundance of their prey.

In British Columbia, recent concern over potential pinniped—fishery conflicts has focused mainly on the harbor seal (*Phoca vitulina*) (Malouf, 1986). Historic and recent manage-

¹Mate, B. R. 1980. Workshop on marine mammal fisheries interactions. U.S. Dep. Commer. Rep. PBH80-175144, 48 p.

²Contos, S. M. 1982. Workshop on marine mammal-fisheries interactions. Final report for MMC contract MM2079341-0. NTIS PB82-189507, 64 p.

³Beach, R. J., A. C. Geiger, S. J. Jefferies, and S. D. Treacy. 1982. Marine mammal fisheries interactions in the Columbia River and adjacent waters. 2nd Annual Rep., Nov. 1, 1980–Nov. 1, 1981. Natl. Marine Mammal Lab., NWAFC Proc. Rep. 82–04, 186 p.

ment issues concerning harbor seals in British Columbia are similar to those facing pinnipeds in other regions. Earlier this century (1913–64), harbor seal populations throughout the province were maintained below historic levels by government-sponsored predator control hunts and bounty kills (Fisher, 1952; Bigg, 1969). During 1963–68, populations were further depleted by an intense commercial harvest for pelts⁴. However, in 1970 the species was protected and since then harbor seal populations throughout British Columbia have been increasing exponentially at an annual finite rate of about 12.5% (Olesiuk et al., 1990a). Abundance in British Columbia is estimated to have increased from 9,000–10,500 in 1970 to 75,000–88,000 by 1988 (Olesiuk et al., 1990a).

Investigations of harbor seals in British Columbia, particularly the Strait of Georgia, have provided much of the background information necessary to assess predator-prey interactions. Bigg (1969) described life history and population parameters, which were recently combined with information on the status of the population to construct life tables and a population model⁴. Aerial harbor seal censuses have been conducted in the Strait of Georgia periodically since 1966 and annually since 1982 to determine abundance and monitor population trends (Olesiuk et al., 1990a). Olesiuk et al. (1990b) recently described regional and seasonal variations in diet composition based on scat analyses. In addition to these local studies, the energetics of captive harbor seals and related phocids has been investigated in some detail by other researchers, and feeding rates of free-ranging harbor seals have been estimated from the volume of prey in stomachs collected on the east coast of Canada (Boulva and McLaren, 1979).

In this report, I synthesize these data into a bioenergetic population model and use the model to estimate annual prey consumption by harbor seals in the Strait of Georgia. The model serves several purposes. First, it provides improved estimates of the annual consumption by harbor seals of commercially and recreationally utilized species, which may be of particular interest to resource managers who must base real-time management decisions on the best information currently available. Second, the model identifies the relative sensitivity of the prey consumption estimates to, and the present level of certainty in, each of its parameters, and is therefore useful for directing future research. Third, the model provides a framework for examining interactions between its individual components. For example, Olesiuk⁴ employed the model

to predict the effects of demographic changes in harbor seal populations on mean *per capita* energy requirements. Finally, the basic model serves as a foundation upon which additional refinements can be added as more accurate and detailed information becomes available. For example, the basic model is a prerequisite for more elaborate models that incorporate the depensatory and compensatory responses of prey to their predators and predators to their prey (Beverton, 1985) or economic parameters (Clark, 1985).

Materials and methods

Study area

Annual prey consumption was estimated for harbor seals inhabiting the Strait of Georgia (Fig. 1) during the 1988 calendar year. The Strait of Georgia was selected for intensive study because the area is readily accessible and supports a higher concentration of harbor seals than other regions of British Columbia. Although the study area represents only 12% of the total British Columbia coastline, it supports 18–21% of the province's harbor seal population (Olesiuk et al., 1990a).

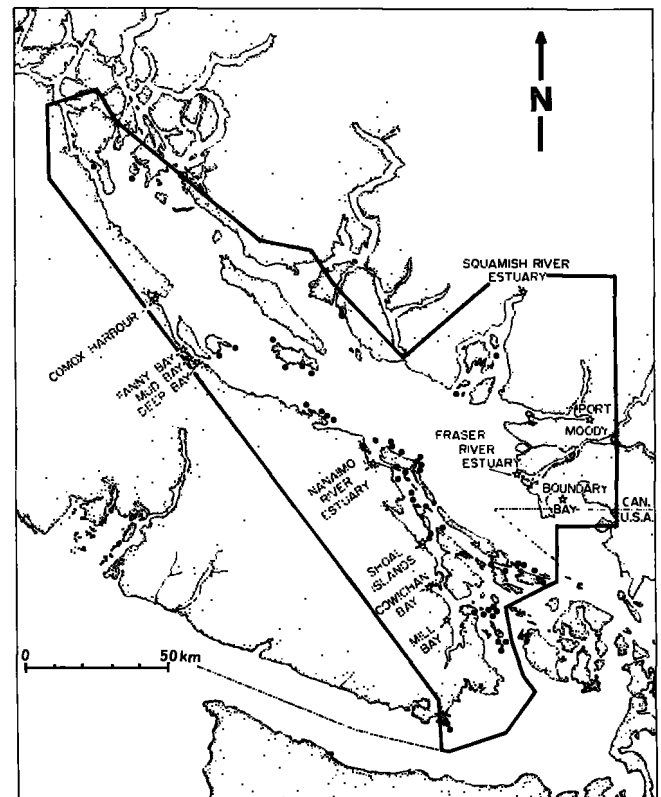


Figure 1

Map of southwestern British Columbia showing boundaries of the Strait of Georgia study area (solid line) and scat collection sites (☆ = estuaries; ● = non-estuaries).

⁴Olesiuk, P. F. Population dynamics of the harbor seal (*Phoca vitulina*) in British Columbia. Manuscr. in prep.

The Strait of Georgia also supports important commercial and sport fisheries. With respect to salmon, the most valuable fishery, the study area accounts for approximately 28% by number and 31% by weight of total escapement in British Columbia⁵. Ketchen et al. (1983) estimated that the Strait of Georgia accounted for 27% of the total non-salmonid commercial harvest by weight, 34% by landed value, and 26% by wholesale value. The Strait of Georgia also accounts for about 96% of all recreational angler-days expended in the tidal waters of British Columbia (Sinclair⁶), which represents about 600,000 boat-trips annually (Shardlow and Collicutt, 1989). Harbor seal-fishery conflicts in the Strait of Georgia would therefore be expected to be more intense than in other regions of the province.

Two distinct types of habitat were recognized within the study area: estuaries and non-estuaries. Estuaries were defined as the large, shallow, soft-bottomed areas that occurred at the mouths of some rivers. Twelve estuaries (Fig. 1) within the study area were inhabited by appreciable numbers (≥ 10) of seals. In estuaries, seals typically hauled out on logbooms or on tidal sandbars. Seals were widely distributed outside of estuaries and utilized 285 different haulout sites, most of which consisted of tidal boulders, reefs, islets, and ledges at the base of bluffs (Olesiuk et al., 1990a).

The model

Input parameters for the model consisted of information on harbor seal abundance, distribution, the sex- and age-structure of the population, diet composition, and daily energy and food requirements. The first four parameters were derived from local studies (Bigg, 1969; Olesiuk et al., 1990a; Olesiuk et al., 1990b; Olesiuk⁴), whereas the last parameter was deduced from the metabolic and feeding rates reported for phocids in the literature. The primary output from the model consisted of estimates of the annual consumption of each prey species.

The annual consumption of a particular prey was estimated as the product of the abundance of seals, feeding rates, and the proportion of that prey in their overall diet. Daily food requirements were estimated separately for each sex- and age-class in the population, and mean *per capita* requirements calculated from energetic life tables by weighting the individual estimates according to the sex- and age-structure of the population. Feeding rates were assumed to be the same within and outside of estuaries and constant with sea-

son. However, because the abundance and diet composition of seals differed between estuaries and non-estuaries and varied seasonally in both habitat types (Olesiuk et al., 1990b), the abundance and diet data were stratified by habitat type and integrated over time. The biomass of the k th prey species consumed annually, B_k , was thus estimated as

$$B_k = \overline{FR} \cdot \int_1^{365} N_{Et} \cdot P_{Ekt} \cdot dt + \overline{FR} \cdot \int_1^{365} N_{Ot} \cdot P_{Okt} \cdot dt \quad [1]$$

where \overline{FR} is the mean *per capita* daily food requirement, N_{Et} and N_{Ot} the number of seals within and outside of estuaries, respectively, on the t th date (1=January 1st; 365=December 31st), and P_{Ekt} and P_{Okt} the proportion of the diet within and outside estuaries comprised of the k th prey species on the t th date. The integrals were solved by calculating finite approximations using daily Δt increments.

Abundance and distribution

The abundance and distribution of harbor seals in the study area were determined by aerial censuses. In 1988, the entire study area was surveyed twice; once just prior to the pupping season (31 May–16 June) and again at the end of the pupping season (9–26 August). A third estimate of the population size in 1988 was obtained by projecting the population trends observed during censuses conducted between 1973 and 1988.

Aerial censuses were conducted under standardized conditions under which maximum numbers of seals were hauled out: 1) the lower of semi-diurnal low tides; 2) between 08:00–11:30 AM; 3) usually toward the end of the pupping season which extends from early July to mid August (Bigg, 1969); and 4) not during inclement weather such as rough seas or heavy precipitation. Under these conditions, the variability of replicate censuses indicated that counts represented, on average, 88.4% of the actual population (Olesiuk et al., 1990a).

The confounding effects of seasonal fluctuations in the size of the population due to recruitment during the protracted pupping season were removed by adjusting all census counts, C_t , to post-pupping levels by applying a correction, P_t , to account for pups born subsequent to the date, t , of the census. Since births are normally distributed over time with a mean julian birth date, μ , of 208 (27 July) and σ of 16.1 days (Bigg, 1969; Olesiuk et al., 1990a), P_t was calculated as

$$P_t = 1 + \beta - \int_{-\infty}^{\frac{t-\mu}{\sigma}} \frac{(t-\mu)^2}{2\sigma^2} \cdot 2\pi^{-0.5} \cdot e^{-\frac{(t-\mu)^2}{2\sigma^2}} \cdot dt \cdot \beta \quad [2]$$

⁵Estimated from data provided by G. Hudson, Pacific Biological Station, Nanaimo, B.C., pers. commun. 1989.

⁶Sinclair, W. F. 1972. The British Columbia sport fisherman. Can. Dep. Environ. Fish. Serv., Pac. Reg., 69 p.

where β denotes the finite annual *per capita* birth rate (see Population Parameters).

The actual size of the population at the end of the pupping season, N_p , was thus estimated by correcting the original census counts, C_t , for both the estimated number of pups born subsequent to censuses and the mean proportion of seals missed during censuses:

$$N_p = C_t \cdot P_t \cdot 0.884^{-1} \quad [3]$$

Seasonal fluctuations in the size of the population due to recruitment during the pupping season and mortality throughout the year could not be directly monitored because low tides suitable for censuses occurred only at night prior to May and after October. Seasonal fluctuations were thus modeled by adjusting the post-pupping population estimate, N_p , for births and deaths. The Strait of Georgia population was assumed to be closed to immigration and emigration, which was realistic considering that harbor seals are non-migratory (Bigg, 1981) and that the density of seals in neighbouring areas are much lower than in the study area (Olesiuk et al., 1990a). The size of the population, N_t , on the t th date was thus estimated by

$$N_t = (N_p/P_t) e^{-Z(t-p)} \quad [4]$$

where Z represents the instantaneous daily mortality rate. Assuming that mortality was uniformly distributed throughout the year, Z was obtained from the mean finite annual *per capita* mortality rate, ∂ (see Population Parameters):

$$Z = \{-\ln(1-\partial)\} \cdot 365^{-1} \quad [5]$$

Although it was not possible to monitor seasonal trends in abundance in the entire study area, seasonal trends in estuaries were monitored. Estuaries could be censused throughout the year because seals typically hauled out on logbooms that were exposed at all tides, and also because swimming seals could be counted in these shallow, confined areas. Between May 1988, and February 1989, a series of 5 aerial censuses of all estuaries, except Port Moody and the Squamish River estuary, were conducted at approximately 2-month intervals. The aerial counts were supplemented with periodic boat counts made during scat collections, and for Port Moody and the Squamish River estuary (which combined represented only 2–8% of the total number of seals in estuaries) with counts provided by knowledgeable volunteers. All counts for each estuary made in a particular month during 1988–89 were averaged and plotted at the mean date of the counts, and abundance linearly interpolated between consecutive

estimates. The total number of seals outside estuaries on the t th date, N_{ot} , was subsequently estimated by subtracting the total count for all estuaries, N_{Et} , from the estimated total size of the population, N_t .

Population parameters

Population parameters were derived from a sample of 324 specimens collected by Bigg (1969) from the Strait of Georgia and neighbouring waters during 1964–69. The sample was collected following a long period (1913–64) over which the size of the harbor seal population had been reduced and maintained below natural levels by control kills and commercial harvests (Olesiuk⁴). Since the control and commercial kills were likely non-selective by sex or age, except for pups which were probably more vulnerable than older animals (Olesiuk⁴), Bigg's (1969) post-pup sample was considered to be representative of a population below carrying capacity with a stable sex- and age-structure. Since the study population has been increasing exponentially since 1970 (Olesiuk et al., 1990a), it has also likely attained a stable sex- and age-structure indicative of a population below carrying capacity.

Age-specific maturation rates were calculated from the data given in Bigg's (1969) Tables 1 and 2. Owing to the small sample size available for males, maturation rates of males were smoothed by calculating 3-point running means. Age-specific fecundity rates (i.e., the proportion of all females in an age-class that give birth each year), $FEC_{(x)}$, were calculated as the product of the age-specific pregnancy rates for mature females (Bigg, 1969; Olesiuk⁴) and the estimated proportion of females in each age-class that were mature.

The stable sex- and age-structure of the study population was estimated from the sex- and age-composition of a subsample of 245 animals aged ≥ 6.0 months that were considered to have been collected in a random fashion (Bigg, 1969). Following Bigg (1969), specimens aged 0–5.9 months were excluded from the analysis because of potential sampling biases, specimens aged 6.0–17.9 months were tallied as 1-year-olds, specimens aged 18.0–29.9 months as 2-year-olds, etc. The exponential rate of decline, r , in the relative number of animals of each sex, S (f =female and m =male) in age-classes, $N_{s(x)}$, with age, X , was smoothed by regressing the logarithm of the estimated number of survivors in each age-class on age, such that

$$N_{s(x+t)} = N_{s(x)} e^{-rt}. \quad [6]$$

The residuals from the log-linear regressions indicated that the rates of decline differed between sexes and

were not constant with age (Bigg, 1969; Olesiuk⁴). The best fitting series of log-linear segments was therefore obtained iteratively by applying piecewise regressions with varying inflection points. Because pups aged <6 months were likely over-represented in Bigg's (1969) sample, their abundance, $N_{s(0)}$, relative to older age-classes, $N_{s(x)}$, was calculated as

$$N_{s(0)} = 0.5 \cdot \sum_{X=1}^{MA_f} (N_{f(x)} \cdot FEC_{(x)}), \quad [7]$$

which assumes that the sex ratio at birth was equal. The number of seals in each sex- and age-class at the end of the 1988 pupping was estimated by normalizing the relative $N_{s(x)}$ series to sum to N_p . Assuming that births occurred as a pulse at the beginning of the annual cycle and deaths throughout the year, the finite annual birth rate, β , was estimated as

$$\beta = (N_{f(0)} + N_{m(0)}) / (\sum_{X=1}^{MA_f} N_{f(x)} + \sum_{X=1}^{MA_m} N_{m(x)}), \quad [8]$$

and the mean annual finite death rate, δ , as

$$\delta = 1 - (\alpha / [1 + \beta]), \quad [9]$$

where α is the finite annual population multiplication rate (1.125; Olesiuk et al., 1990a) and MA_x denotes the maximum ages attained by each sex (see Results).

Rates of growth in body mass were calculated separately for each sex by fitting specialized von Bertalanffy curves (Zullinger et al., 1984) to the body mass at age data summarized in Bigg (1969). Ages were estimated to the nearest month by assuming that all animals were born in June. Owing to a small number of adult males in Bigg's (1969) sample, his data were supplemented with data for 10 males aged 10–25 years collected in the Gulf of Alaska (Bishop, 1967). Parameters of the specialized von Bertalanffy growth curves

$$M_{s(x)} = A \cdot [1 - 0.33 \cdot e^{K(I-X)}]^{3/4}, \quad [10]$$

where $M_{s(x)}$ represents the body mass of sex S at age X , and A , K , and I are the growth parameters, were estimated iteratively by a Quasi-Newton method (Fletcher⁷) using least squares criteria.

Energetics

Daily food requirements were estimated from two

sources of data: 1) energetic parameters reported in the literature for harbor seals and related phocids based on captive studies; and 2) volumes of undigested prey in the stomachs of harbor seals collected on the east coast of Canada (Boulva and McLaren, 1979). In both cases, daily food requirements were estimated separately for each sex- and age-class in the population based on their mean body masses, and mean *per capita* requirements calculated from energetic life tables by weighting the individual estimates according to the sex- and age-structure of the study population. Mean body masses of age-classes were obtained by taking the geometric mean of their estimated masses at the beginning and end of the age interval (Eqn. 10), which assumes that growth was uniform throughout the year. Energetic parameters were calculated according to the International System of Units (ASTM, 1982). Where necessary, non-conforming values in the literature were converted by assuming that 1 calorie = 4.184 joule (J), such that 1 kcal·day⁻¹ = 0.0484 J·sec⁻¹ or Watts (W). Where efficiency was not stated, net energy (NE) expenditures were transformed to gross energy (GE) requirements by assuming that overall efficiency was 70%; i.e. 13% of the GE in the diet, which usually consisted of herring, was not metabolizable (6% lost in feces and 7% in urine; Keiver et al., 1984) and 17% of GE was expended as the heat increment associated with feeding (Gallivan and Ronald, 1981).

The basal metabolic rates of adult pinnipeds (Lavigne et al., 1986), like those of other adult mammals, conform with Kleiber's (1975) relationship. The net basal metabolic rates of adults of aged X , $BMR_{s(x)}$, in watts, was therefore estimated as

$$BMR_{s(x)} = 3.4 \cdot M_{s(x)}^{0.75} \quad (\text{from Kleiber 1975}) \quad [11]$$

where $M_{s(x)}$ denotes the mean body mass (kg) of sex S at age X . Since other major components of the energetic budget also scale to $M^{0.75}$ (Lavigne, 1982), it is convenient to consider total energy requirements relative to BMR .

A large portion of the overall energy budget of seals is expended on maintenance, which encompasses the energy required for basal metabolism, activity and thermoregulation (Lavigne et al., 1982). Innes et al. (1987) provided one estimate of the gross maintenance requirements of non-growing, adult phocids based on the rates of energy ingestion in captivity, $MR1_{s(x)}$ in watts:

$$MR1_{s(x)} = 7.5 \cdot M_{s(x)}^{0.71} \quad (\text{Eqn. 7 in Innes et. al. 1987}) \quad [12]$$

The metabolic rates of juveniles, however, are usually elevated relative to those of adults of equivalent mass (Innes et al., 1987). For mammals, the magnitude by which juvenile metabolic rates are elevated generally declines from a peak at the onset of feeding

⁷Fletcher, R. 1972. FORTRAN subroutines for minimization by quasi-Newton methods. AERER 7125.

to adult levels by the onset of maturity (Kleiber, 1975; Brody, 1945). Data given in Worthy (1987a)'s Figure 4, together with his reported efficiency of 68%, indicates that the gross maintenance requirements of neonate harp and grey seals increases to about 1.8× the predicted adult $MR1$ (Eqn. 12) at the onset of feeding. In the absence of precise empirical data on the ontogeny of juvenile harbor seal metabolic rates, it was assumed that $MR1$ converged from a post-weaning maximum of 1.8× the predicted adult $MR1$ at the onset of feeding to adult $MR1$ levels at the onset of sexual maturity in an exponential fashion. A multiplier to account for elevated metabolic rates of juveniles at a given age, $JCF_{s(x)}$, was thus derived by calculating a series of 3- 4- 5- and 6-year exponential decays and weighting them according to the proportion of animals of each sex that matured at each of these ages. The correction for an age-class was calculated as the geometric mean of $JCF_{s(x)}$ at age X and age $X+1$, which assumes that the metabolic rate evolved at a constant rate throughout the year. The correction was used to correct both basal (Eqn. 11) and maintenance (Eqn. 12) requirements.

One of the potential shortcomings in directly extrapolating the maintenance requirements of captive seals, $MR1$, to free-ranging seals is that normal activity patterns may be disrupted in captivity. For example, Innes et al. (1987) noted that some of the phocids included in their analysis were quiescent, and would thus be expected to have lower energy requirements than seals in the wild which spend a portion of their time foraging. A second estimate of gross maintenance requirements, $MR2_{s(x)}$, was therefore derived by weighting the metabolic rates of swimming, $SMR_{s(x)}$, and resting, $RMR_{s(x)}$, harbor seals according to a crude activity budget for free-ranging harbor seals:

$$MR2_{s(x)} = (P_s \cdot SMR_{s(x)}) + (P_r \cdot RMR_{s(x)}) \quad [13]$$

where P_s and P_r denote the proportion of time seals spend swimming and resting. P_s and P_r were set at 0.6 and 0.4 respectively based on the mean estimated percentage of time free-ranging radio-tagged harbor seals spent hauled out on land: 44% (Sullivan, 1979), 35–60% (Pitcher and McAllister, 1981) and 37% (Yochem et al., 1987). Age-specific swimming metabolic rates, $SMR_{s(x)}$, were inferred (see Results) from the swimming metabolic rates of captive harbor seals (Davis et al., 1985; Williams, 1987). Resting metabolic rates, $RMR_{s(x)}$, were assumed to be equivalent to $BMR_{s(x)}$ (appropriately elevated for juveniles). Since the extreme air and sea temperatures in the study area were likely within the thermoneutral zone, thermoregulatory costs were assumed to be negligible (see Results and General Discussion).

In addition to maintenance requirements, growing animals require energy for body growth. Daily energy requirements for growth for each sex- and age-class, $DGR_{s(x)}$, were calculated as

$$DGR_{s(x)} = CG \cdot GI_{s(x)} \quad [14]$$

where CG is the apparent gross cost of growth, $201 \text{ W}(\text{kg} \cdot \text{d}^{-1})^{-1}$, as given in Innes et al. (1987), and $GI_{s(x)}$ the daily growth increment of each sex- and age-class (i.e. $[M_{s(x+1)} - M_{s(x)}]/365$).

Finally, mature seals may invest additional energy in reproduction. For females, the total costs of reproduction were partitioned into: 1) foetal development; and 2) nursing. The net energy invested in foetal development was estimated from the mass and energetic density of term fetuses and the placenta. The net energy invested in lactation was estimated indirectly from the amount of energy transferred to nursing pups as reflected by changes in the total mass and body composition of pups between birth and weaning and their maintenance requirements, MR , while nursing. The energy content of the placenta and the energetic densities of neonate carcasses and of the mass gained during nursing were extrapolated from those reported for harp seals (Worthy and Lavigne, 1983). The MR of nursing pups was assumed to be the same as that of adults of equivalent mass ($2.0 \times BMR$) and growth of pups was assumed to be linear while nursing. Gross reproductive costs were estimated from net costs by assuming that the net efficiency of mothers was 70% (see above) and that for lactation, 95% of the energy in milk transferred to pups was metabolizable (Ofstedal and Iverson, 1987). Since females deplete blubber reserves accumulated during the non-breeding season to meet these costs (Pitcher, 1986), age-specific daily reproductive requirements, $DRR_{s(x)}$, were estimated by amortizing the annual cost over the entire year and applying it to female age-classes based on their fecundity rates, $FEC_{s(x)}$. Since harbor seals are promiscuous and males are not known to fast or fiercely compete for breeding rights (Bigg, 1981), reproductive costs for males were assumed to be negligible and absorbed into their daily maintenance requirements.

Two estimates of daily food requirements, $FR_{s(x)}$ in kg, were derived. The first estimate, $FR1_{s(x)}$, was obtained by summing the components of the energetic budget ($MR_{s(x)}$, $DGR_{s(x)}$ and, for females, $DRR_{s(x)}$) to determine the total daily energy requirements, $DER_{s(x)}$. Estimates for each sex- and age-class were derived by taking the geometric mean of the parameters at age X and $X+1$, which assumes that the parameters changed at a constant rate throughout the year. $DER_{s(x)}$ was subsequently converted to units of biomass, $FR1_{s(x)}$ by dividing it by the mean weighted energetic density of

the diet. A second estimate, $FR2_{st(x)}$, was obtained directly from Boulva and McLaren's (1979) relationship between daily ingestion rates and body mass:

$$FR2_{st(x)} = 0.089 \cdot M_{st(x)}^{0.76} \quad (\text{from Fig. 2 in Boulva and McLaren, 1979}) [15]$$

based on the amount of undigested prey found in the stomachs of harbor seals collected on the east coast of Canada.

Diet composition

The diet of harbor seals in the study area was determined by scat analyses. During 1982–88, a total of 2,841 scats (216 collections) were collected from 58 sites (11 estuaries and 47 non-estuary sites) distributed throughout the Strait of Georgia (Fig. 1). Samples were collected in all months of the year (Fig. 2). Because most major haulout sites were sampled, the sampled sites accounted for about 45% of all seals ob-

served during censuses of the study area both in May–June and in August, 1988. The collections thus provided a representative sample from which regional and seasonal variations in diet composition could be assessed.

Undigested prey remnants were recovered from the scat samples with an elutriator (Bigg and Olesiuk, 1990). Elutriation recovery rates ranged between 90–100% ($\bar{X}=98.6\%$) for various fish structures and 70–100% ($\bar{X}=85.0\%$) for cephalopod beaks. In contrast to previous scat studies which have relied almost exclusively on otoliths to identify prey, harbor seal prey were identified by using a wide array of different structures including otoliths, teeth, scutes and scales, as well as numerous cranial, appendicular, axial and caudal elements (see Appendix I in Olesiuk et al., 1990b).

The relative importance of prey in the diet was measured by using a new index, termed split-sample frequency of occurrence, designed specifically for scat analyses (Olesiuk et al., 1990b). The index was predicated on two assumptions: 1) prey identified in scat samples represented all those consumed in the previous meal (i.e., 24-hour period); and 2) all prey species constituting a meal had been consumed in equal volumes. Thus, the proportion of the diet comprised of the k th prey species in the j th strata ($j=E$ for estuaries and $j=O$ for outside estuaries) in the m th month ($m=1$ for January, etc.), P_{jkm} , was estimated from the $i=1, \dots, n$ samples collected from that strata in that month by

$$P_{jkm} = \frac{\sum_{i=1}^n (O_{ijkm} / \sum_{k=1}^N O_{ijkm})}{n} \quad k=1, \dots, N \quad (N = \# \text{ different prey species}) [16]$$

where O_{ijkm} is a binary variate that indicates whether the k th prey species was absent or present (0=absent and 1=present) in the i th sample collected in the j th strata in the m th month, such that $\sum_{k=1}^N O_{ijkm}$ for $k=1, \dots, N$ represents the total number of prey species present in the i th sample. Therefore, if only one prey species occurred in a sample, its occurrence was scored as 1, if two prey species occurred each occurrence was scored as 0.5, and so forth. The split-sample index is considered an improvement over conventional frequency of occurrence indices in that prey species that comprised an entire meal, which had presumably been consumed in large quantities, weighted the split-sample index more than prey species consumed in a diverse meal comprising many species, each of which had presumably been consumed in smaller quantities. Estimates of the diet composition on the t th date, P_{Ekt} and P_{Okt} , were derived by linearly interpolating between the monthly estimates, P_{Ekm} and P_{Okm} , plotted at the midpoint of each month.

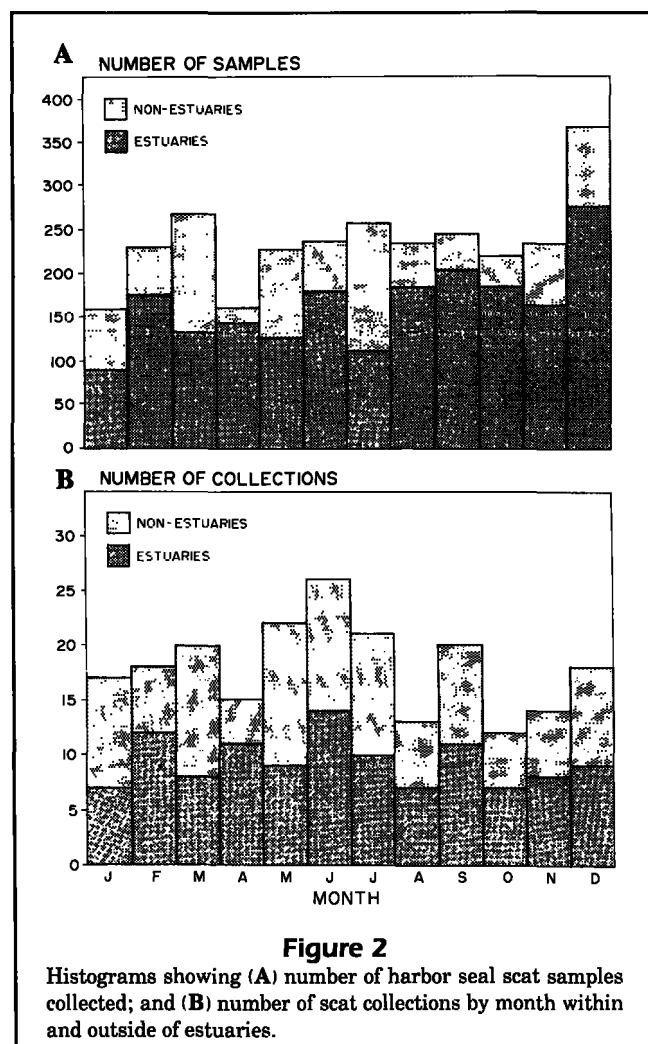


Figure 2

Histograms showing (A) number of harbor seal scat samples collected; and (B) number of scat collections by month within and outside of estuaries.

Although it was not possible to assess the assumption that all prey in a meal had been consumed in equal volumes (see Results), the maximum potential biases introduced by deviations from the assumption could be determined. An upper limit of the importance of a particular prey species in the overall diet was obtained by assuming that whenever the species occurred in a meal, it comprised the entire meal and that all other species in the same meal had been consumed in negligible quantities. Conversely, a lower limit was obtained by assuming that whenever a particular species was consumed in the same meal along with other species, it had been consumed in negligible quantities. Mathematically, the upper and lower limits for the l th of $k=1, \dots, N$ species were calculated from Equation 16 by

- 1) Setting $O_{ijkm}=1$ for $k=l$ and $O_{ijkm}=0$ for $k \neq l$;
- 2) Setting $O_{ijkm}=0$ for $k=l$ and $O_{ijkm}=1$ for $k \neq l$ when $N > 1$,

respectively.

Two corrections were applied to the split-sample index to account for suspected biases. First, very small scat samples, which undoubtedly represented only a small fraction of whole scats and probably contained only a portion of all the prey species actually consumed in meals, were weighted less than large scat samples. Second, the relative proportions of hake and herring, the two predominant prey species, in samples that contained both species were volumetrically weighted based on the mean relative number of elements of each species in the sample compared with the relative number in samples that were composed exclusively of each of these two species. Both corrections, each of which had a relatively minor influence on the results, are described in detail in Olesiuk et al. (1990b).

Results

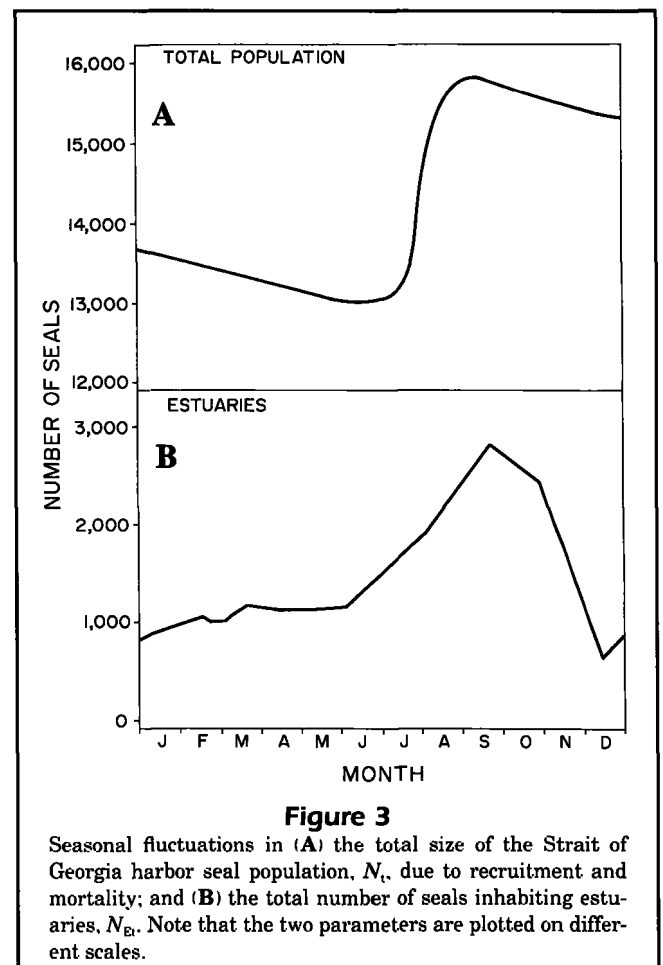
Abundance and distribution

The two complete censuses of the study area in 1988, when adjusted to post-pupping levels and corrected for missed seals (Eqn. 3), yielded population estimates of 16,531 and 15,091, respectively. Their mean, 15,810, was adopted in subsequent analyses. The mean was considered most appropriate because the proportion of the population counted during any single census may have been lower or greater than the mean estimate of 0.884. The validity of the 1988 census estimate was substantiated by a projected population estimate of 15,050 based on population trends during 1973–88, over which period the population had been steadily

increasing (log-linear $r^2=0.994$) at a rate of 12.5% per annum (Olesiuk et al., 1990a).

Seasonal fluctuations in the size of population as a result of mortality and recruitment are shown in Figure 3A. The total size of the population ranged from a low of 12,990 just prior to the pupping season (16 June) to a peak of 15,810 at the end of the pupping season (6 September). The mean size of the population was 14,270. Because the population was below carrying capacity and increasing at its intrinsic rate, it was 12.5% larger at the end than at the beginning of the year.

Seasonal changes in the distribution of harbor seals between estuaries and non-estuaries are shown in Figure 3B. The overall abundance within estuaries was lowest (4% of the total population) in December and remained low throughout the winter and into early spring. Numbers increased sharply during June–August, mainly due to large influxes into the two largest estuaries—Boundary Bay and lower Fraser River (Fig. 1). These influxes coincided with the pupping season (Bigg, 1969; Olesiuk et al., 1990a) which might indicate these two large estuaries were preferred whelping areas, as has been reported for other major es-



tuaries along the coast of Washington and Oregon (Jefferies⁸). Alternatively, these influxes also coincided with the earliest low tides of the year in which the sandbars utilized as haulouts were exposed during daylight hours and may therefore merely indicate that seals preferred to occupy areas where they could haulout during daylight.

Although numbers in Boundary Bay declined after August (i.e., the end of the pupping season), the overall proportion of the population in estuaries continued to increase and peaked at 18% in September. This was due largely to a migration of seals from Boundary Bay to the Fraser River and an influx of seals into many of the smaller estuaries, where peak abundance generally occurred in September–November coinciding with the return of spawning salmon to their natal rivers (Olesiuk et al., 1990b). Weighted seasonally, 10.3% of the total population inhabited estuaries.

Population parameters

As expected, the relative number of animals in age-classes decreased with age (Fig. 4). However, piecewise log-linear regressions indicated that the rate of decline for both sexes changed abruptly at 4 years of age, which roughly coincided with the onset of sexual maturity (see Tables 1 and 2). The regressions for females and males aged 1–4 years were not significantly

different ($t=0.18$; $P>0.50$), so juveniles of both sexes were pooled. For females, the rate of decline decreased beyond age 4 years, whereas for males the rate increased beyond age 4 years:

$$N_{s(x+t)} = N_{s(x)} e^{-0.2175 \cdot t} \quad \text{for both sexes aged 1–4 year [17]}$$

$$N_{f(x+t)} = N_{f(x)} e^{-0.1653 \cdot t} \quad \text{for females aged >4 years [18]}$$

$$N_{m(x+t)} = N_{m(x)} e^{-0.2878 \cdot t} \quad \text{for males aged >4 years [19]}$$

The $N_{s(x)}$ series were truncated at 29 years for females and 20 years for males. The truncation points, MA_f and MA_m , represent the oldest specimens collected by Bigg (1969) and also the ages by which the size of age-classes diminished to less than 0.5% the number of new recruits (see Tables 1 and 2). It should be noted that the rates of decline in the size of age-classes do not entirely reflect mortality because the population was non-stationary, such that the number of seals being recruited (i.e., the initial size of cohorts) had increased over time. When corrected for an intrinsic rate of increase of 12.5% per annum (Olesiuk et al., 1990a), the exponential decays represent finite annual mortality rates of 9.5% for juveniles aged 1–4 years, 4.6% for adult females aged >4 years and 15.6% for adult males aged >4 years (Olesiuk³). The finite *per capita* birth rate, β , was calculated to be 29.8%, which implied that mortality during the first year was 27.0%. The finite *per capita* mortality rate, δ , was subsequently estimated to be 13.3%.

The estimated number of seals in each sex- and age-class indicates that the population was markedly skewed toward younger age-classes (see Tables 1 and 2). The mean age was only 4.0 years (4.7 years for females and 3.2 years for males). A total of 74% of all individuals were aged ≤ 5 years and 91% were aged ≤ 10 years. As noted previously, this skewed age-structure was not due entirely to high mortality (mean life expectancy was 8.2 years—10.4 years for females and 6.0 years for males; Olesiuk⁴), but also because the population had been exponentially increasing since 1970 (Olesiuk et al., 1990a). Given a growth rate of 12.5%, the total population numbered only 8,770 in 1983 and 4,870 in 1978, such that the initial size of the 1983 cohort, represented by 5-year-olds in the population in 1988, was only 55% the initial size of the 1988 cohort, and the initial size of the 1978 cohort, represented by 10-year-olds in the population in 1988, only 31% the initial size of the 1988 cohort. In other words, the population in 1988 was skewed toward younger animals because most of its constituents had been recruited in recent years.

Bigg (1969) reported that mean body mass of pups increased from 10.2 kg at birth to 24.0 kg by the end of the 5–6 week nursing period, but there appeared to be little further increase in body mass during the

⁸Jefferies, S. J. 1986. Seasonal movements and population trends of harbor seals (*Phoca vitulina richardsi*) in the Columbia River and adjacent waters of Washington and Oregon. Final Rep. Mar. Mammal Comm., Contr. No. MM2079357-5, 41 p.

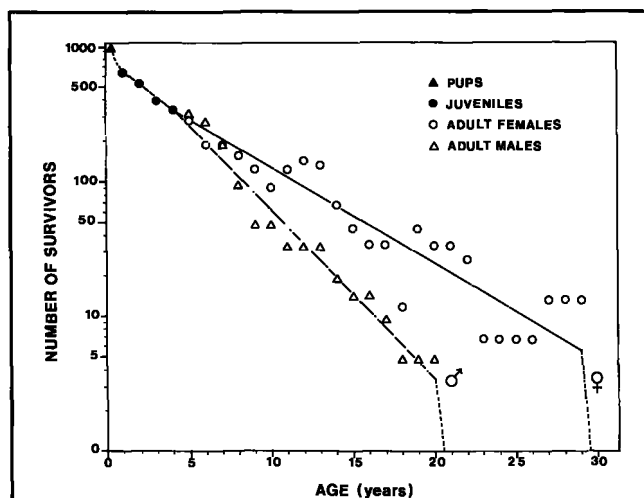


Figure 4

Exponential rates of decline in the size of age-classes of harbor seals as a function of age (Olesiuk⁴). The trend lines represent piecewise log-linear functional regressions fitted by least squares criteria and scaled to an initial cohort size of 1000.

Table 1

Energetic life table for males. Parameters are: N_{mix} number in age-class; M_{mix} mean body mass (kg); MAT_{mix} proportion of animals mature; JCF_{mix} multiplier to correct for elevated juvenile metabolic rates; BMR_{mix} basal metabolic rate; $MR1_{mix}$, $MR2_{mix}$ and \overline{MR}_{mix} gross maintenance requirements based on ingestion rates in captivity, daily activity budgets, and their average respectively; DGR_{mix} mean daily growth requirements; DER_{mix} mean daily total energy requirements; and $FR1_{mix}$, $FR2_{mix}$ and \overline{FR}_{mix} daily food requirements (kg) based on energetic life tables, volumes of stomach contents, and their average respectively. Parameters are given for the population of 15,810 at the end of the pupping season. All energetic parameters are in watts.

Age	N_{mix}	M_{mix}	MAT_{mix}	JCF_{mix}	BMR_{mix}	$MR1_{mix}$	$MR2_{mix}$	\overline{MR}_{mix}	DGR_{mix}	DER_{mix}	$FR1_{mix}$	$FR2_{mix}$	\overline{FR}_{mix}
0	1814	24.0	0.00	1.80	67.1	130.3	170.5	150.4	2.9	153.4	1.99	1.07	1.53
1	1178	29.3	0.00	1.60	71.4	137.3	181.4	159.4	5.3	164.6	2.14	1.29	1.71
2	948	38.9	0.00	1.42	76.9	146.3	195.3	170.8	5.5	176.3	2.29	1.57	1.93
3	762	48.9	0.06	1.26	79.5	150.2	202.0	176.1	4.7	180.8	2.35	1.82	2.08
4	613	57.5	0.29	1.13	80.4	151.1	204.3	177.7	3.9	181.6	2.36	2.02	2.19
5	460	64.5	0.53	1.05	81.5	152.5	207.0	179.7	3.1	182.9	2.38	2.18	2.28
6	345	70.2	1.00	1.00	84.1	156.8	213.5	185.2	2.5	187.6	2.44	2.31	2.37
7	259	74.6	1.00	1.00	87.5	162.9	222.3	192.6	1.9	194.5	2.53	2.40	2.46
8	194	78.1	1.00	1.00	90.1	167.5	228.9	198.2	1.5	199.7	2.59	2.47	2.53
9	145	80.8	1.00	1.00	92.1	171.0	234.0	202.5	1.1	203.6	2.65	2.53	2.59
10	109	82.8	1.00	1.00	93.7	173.7	237.9	205.8	0.9	206.6	2.68	2.57	2.63
11	82	84.4	1.00	1.00	94.8	175.7	240.8	208.3	0.6	208.9	2.71	2.60	2.66
12	61	85.5	1.00	1.00	95.7	177.2	243.0	210.1	0.5	210.6	2.74	2.63	2.68
13	46	86.4	1.00	1.00	96.3	178.4	244.7	211.5	0.4	211.9	2.75	2.65	2.70
14	34	87.1	1.00	1.00	96.8	179.2	245.9	212.6	0.3	212.9	2.77	2.66	2.71
15	26	87.6	1.00	1.00	97.2	179.9	246.9	213.4	0.2	213.6	2.77	2.67	2.72
16	19	88.0	1.00	1.00	97.5	180.4	247.6	214.0	0.2	214.1	2.78	2.68	2.73
17	15	88.3	1.00	1.00	97.7	180.7	248.1	214.4	0.1	214.5	2.79	2.68	2.74
18	11	88.5	1.00	1.00	97.8	181.0	248.5	214.7	0.1	214.8	2.79	2.69	2.74
19	8	88.7	1.00	1.00	97.9	181.2	248.8	215.0	0.1	215.1	2.79	2.69	2.74
20	6	88.8	1.00	1.00	98.0	181.3	248.9	215.1	0.1	215.2	2.80	2.69	2.74

Table 2

Energetic life table for females. Parameters are the same as described in Table 1 with the following additions: FEC_{fx} annual fecundity rate; and DRR_{fx} mean daily gross reproductive requirements. Parameters are given for the population of 15,810 at the end of the pupping season. All energetic parameters are in watts.

Age	N_{fx}	M_{fx}	MAT_{fx}	JCF_{fx}	BMR_{fx}	$MR1_{fx}$	$MR2_{fx}$	\overline{MR}_{fx}	DGR_{fx}	FEC_{fx}	DRR_{fx}	DER_{fx}	$FR1_{fx}$	$FR2_{fx}$	\overline{FR}_{fx}
0	1814	24.0	0.00	1.80	65.8	127.8	167.2	147.5	2.9	0.00	0.0	150.4	1.95	1.07	1.51
1	1178	29.3	0.00	1.54	65.4	125.9	166.0	146.0	3.7	0.00	0.0	149.6	1.94	1.25	1.60
2	948	36.0	0.00	1.31	64.9	124.1	164.9	144.5	4.3	0.00	0.0	148.8	1.93	1.46	1.70
3	762	43.9	0.36	1.12	64.8	123.0	164.7	143.8	3.4	0.29	9.6	156.9	2.04	1.66	1.85
4	613	50.0	0.83	1.02	66.5	125.6	168.9	147.2	2.5	0.66	22.1	171.9	2.23	1.80	2.02
5	520	54.5	1.00	1.00	69.5	131.0	176.5	153.8	1.8	0.79	26.5	182.1	2.37	1.90	2.13
6	441	57.9	1.00	1.00	72.2	135.7	183.3	159.5	1.3	0.91	30.7	191.6	2.49	1.97	2.23
7	374	60.2	1.00	1.00	74.0	139.0	188.1	163.5	0.9	0.91	30.7	195.2	2.54	2.03	2.28
8	317	62.0	1.00	1.00	75.4	141.4	191.4	166.4	0.7	0.91	30.7	197.8	2.57	2.06	2.32
9	268	63.2	1.00	1.00	76.3	143.0	193.8	168.4	0.5	0.91	30.7	199.6	2.59	2.09	2.34
10	227	64.0	1.00	1.00	76.9	144.2	195.4	169.8	0.3	0.91	30.7	200.9	2.61	2.11	2.36
11	193	64.6	1.00	1.00	77.4	145.0	196.6	170.8	0.2	0.91	30.7	201.7	2.62	2.12	2.37
12	163	65.0	1.00	1.00	77.7	145.5	197.4	171.5	0.2	0.91	30.7	202.4	2.63	2.13	2.38
13	139	65.3	1.00	1.00	77.9	145.9	197.9	171.9	0.1	0.91	30.7	202.8	2.63	2.13	2.38
14	117	65.5	1.00	1.00	78.1	146.2	198.3	172.3	0.1	0.91	30.7	203.1	2.64	2.14	2.39
15	100	65.6	1.00	1.00	78.2	146.4	198.6	172.5	0.1	0.91	30.7	203.3	2.64	2.14	2.39
16	84	65.7	1.00	1.00	78.3	146.5	198.8	172.6	0.0	0.91	30.7	203.4	2.64	2.14	2.39
17	72	65.8	1.00	1.00	78.3	146.6	198.9	172.8	0.0	0.91	30.7	203.5	2.64	2.15	2.39
18	61	65.9	1.00	1.00	78.3	146.7	199.0	172.8	0.0	0.91	30.7	203.6	2.65	2.15	2.40
19	51	65.9	1.00	1.00	78.4	146.7	199.1	172.9	0.0	0.91	30.7	203.7	2.65	2.15	2.40
20	44	65.9	1.00	1.00	78.4	146.8	199.1	172.9	0.0	0.91	30.7	203.7	2.65	2.15	2.40
21	37	65.9	1.00	1.00	78.4	146.8	199.1	173.0	0.0	0.91	30.7	203.7	2.65	2.15	2.40
22	31	65.9	1.00	1.00	78.4	146.8	199.2	173.0	0.0	0.91	30.7	203.7	2.65	2.15	2.40
23	27	66.0	1.00	1.00	78.4	146.8	199.2	173.0	0.0	0.91	30.7	203.7	2.65	2.15	2.40
24	22	66.0	1.00	1.00	78.4	146.8	199.2	173.0	0.0	0.91	30.7	203.7	2.65	2.15	2.40
25	19	66.0	1.00	1.00	78.4	146.8	199.2	173.0	0.0	0.91	30.7	203.7	2.65	2.15	2.40
26	16	66.0	1.00	1.00	78.4	146.8	199.2	173.0	0.0	0.91	30.7	203.8	2.65	2.15	2.40
27	14	66.0	1.00	1.00	78.4	146.8	199.2	173.0	0.0	0.91	30.7	203.8	2.65	2.15	2.40
28	12	66.0	1.00	1.00	78.4	146.8	199.2	173.0	0.0	0.91	30.7	203.8	2.65	2.15	2.40
29	10	66.0	1.00	1.00	78.4	146.8	199.2	173.0	0.0	0.91	30.7	203.8	2.65	2.15	2.40

remainder of the first year of life. The average body mass of 12 yearlings (7 females and 5 males) aged 1.0 years (± 2 months) was 29.3 kg (28.4 kg for females; 30.7 kg for males). Growth in subsequent years was asymptotic for both sexes and could be described by von Bertalanffy curves (Fig. 5). The equations indicated that females attained an asymptotic mass of 66.0 kg, 90% of which was attained by 7 years, and males an asymptotic mass of 89.2 kg, 90% of which was attained by 9 years. In accord with these predictions, the mean body mass of the 10 female specimens aged ≥ 7 years was 60.0 kg and the mean of the 8 male specimens aged ≥ 9 years was 86.6 kg (Fig. 5). The mean body mass of all ages, calculated at the end of the pupping season and weighted according to the stable age-structure, was 44.2 kg for females, 45.3 kg for males, and 44.7 kg overall.

Energetics

Energetic life tables are shown in Tables 1 and 2. The main advantage of the energetics approach over stomach volume analyses was that total energy requirements could be partitioned into energy required for basal metabolism, activity, growth and reproduction. This enabled an assessment of the relative magnitude and uncertainty associated with each component of the energy budget.

The estimated gross maintenance requirements of adult harbor seals, based on the rate of energy ingestion by captive phocids, $MR1_{s(x)}$, ranged from 1.85–1.94 \times ($\bar{X}=1.90\times$) the predicted adult BMR (Eq. 11).

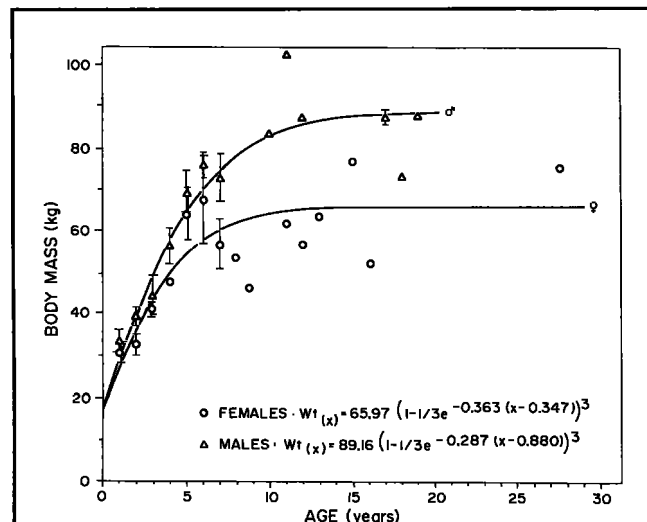


Figure 5

Mean body mass (\pm SE) as a function of age. Data are from Bigg (1969) supplemented with data from Bishop (1967). Growth curves represent specialized von Bertalanffy equations fitted to the data by least squares criteria.

Multipliers to account for the elevated metabolic rates of juveniles, $JCF_{s(x)}$ ranged from 1.8 at weaning to 1.0 at the onset of maturity. The corrected juvenile maintenance requirements, $MR1_{s(x)}$, thus declined from 3.5 \times the predicted adult BMR at weaning, to 3.1 \times the predicted adult BMR at age 1.0 years, to 2.6 \times the predicted adult BMR at age 2.0 years, and ultimately to 1.9 \times the predicted adult BMR at the onset of maturity. These predictions appear to be consistent with the metabolic rates of juveniles reported in the literature. Keiver et al. (1984) reported that the gross maintenance requirements of harp seals aged 5–24 months were 2.1–3.0 \times predicted adult BMR levels and data in Innes (1984) indicate that the gross maintenance requirements (assuming 70% net efficiency) of grey and harp seals aged 1–28 months were 2.9 \times predicted adult BMR levels. The unweighted mean correction for juveniles of all ages was 1.34, which was similar to the 1.4 derived by Innes et al. (1987) for juveniles of various ages pooled. Similarly, the average $MR1_{s(x)}$ for harbor seals aged 0–3 years was 2.9 \times the predicted adult BMR , which was similar to the 2.8 \times adult BMR estimated for captive harbor seals aged 0–3 years by Markussen et al. (1990) who, interestingly, found no evidence of age-specific changes in maintenance requirements between 0 and 3 years of age.

A second estimate of maintenance requirements, $MR2$, was obtained by weighting swimming and resting metabolic rates, SMR and RMR , according to an activity budget for free-ranging harbor seals. Davis et al. (1985) reported that the SMR of a 63-kg adult harbor seal swimming at 1.4 $m\cdot sec^{-1}$, its preferred swimming speed, was 2.3 \times its expected BMR (i.e., 2.2 \times its resting metabolic rate which was reported to be 1.1 \times BMR). Similarly, the net SMR of an 85-kg adult harbor seal swimming at the same speed was 210 watts (Williams, 1987), or 2.4 \times its predicted BMR . In contrast, a 33-kg yearling swimming at 1.4 $m\cdot sec^{-1}$ exhibited a relatively higher net swimming metabolic rate of 170 watts (Davis et al., 1985). Although this was 3.6 \times the predicted BMR for an adult of equivalent mass, it was only 2.3 \times the corrected BMR for a yearling (i.e., the juvenile SMR appeared to be elevated to the same extent as its total $MR1$). Age-specific $SMR_{s(x)}$'s were therefore assumed to be 2.3 \times $BMR_{s(x)}$ (appropriately elevated for juveniles) for all ages and both sexes. Assuming that seals spent 40% of their time resting on land and 60% swimming and that the $RMR_{s(x)}$'s were equivalent to $BMR_{s(x)}$ (again appropriately elevated for juveniles), the net $MR2_{s(x)}$ was estimated to be 1.8 \times the corrected $BMR_{s(x)}$, and the gross $MR2_{s(x)}$ to be 2.5 \times the corrected $BMR_{s(x)}$.

The second estimate of gross maintenance requirements, $MR2$, was approximately 34% (range 31–37%) greater than the first estimate, $MR1$, for all age-classes.

As noted earlier, $MR1$ probably tended to be an underestimate as it was derived from captive seals that were sometimes quiescent. On the other hand, $MR2$ may be an overestimate as it is unlikely that seals swim continuously while in the water, and also because the RMR of sleeping seals may actually fall below BMR (Ashwell-Erickson and Elsner, 1981; Worthy, 1987a). The mean of $MR1_{s(x)}$ and $MR2_{s(x)}$, denoted as $\overline{MR}_{s(x)}$, was therefore adopted for subsequent calculations.

Ambient sea and air temperatures in the study area were probably within the thermoneutral zone of free-ranging harbor seals. Oritsland and Ronald (1975) detected no change in the metabolic rate of an adult harp seal swimming in water temperatures ranging from 8.5–26°C and Gallivan (1977) no change in the metabolic rates of 3 adult harp seals in water temperatures ranging from 1.8 to 28.2°C. Hart and Irving (1959) reported that the lower critical temperature of harbor seals in air was 2°C and Matsuura and Whittow (1973) found that the metabolic rate of a resting harbor seal was constant in air temperatures up to 35°C. Mean monthly sea surface temperatures in the study area typically range between 6.2 and 17.0°C⁹ and minimum and maximum monthly air temperatures between -0.4 (January minimum) and 23.5°C (July maximum) (Canadian Hydrographic Service, 1990). Thermoregulatory costs were therefore assumed to be negligible (see also General Discussion).

The costs associated with growth were calculated based on actual growth rates rather than applying Innes' et al. (1987) empirical equations for growing phocids because there may be substantial differences between growth rates of captive and free-ranging seals. For instance, growth rates reported for recently weaned grey and harp seals in captivity (Worthy, 1987a) were about an order of magnitude greater than those estimated for harbor seals in the wild. The apparent gross cost of growth, 201 W(kg·d⁻¹)⁻¹ (Innes et al., 1987), represents, assuming net efficiency was 70%, a net cost of 141 W(kg·d⁻¹)⁻¹ or 12.2 MJ·kg⁻¹. Given the wet-weight energetic density of tissues (37.8 MJ·kg⁻¹ for blubber and 6.5 MJ·kg⁻¹ for proteinaceous tissue; Olesiuk and Bigg, unpubl. data), this implies that post-weaning body growth was composed of about 20% fat and 80% protein. Using these values to extrapolate the estimated body composition at weaning (see below), the adult body would be composed of approximately 30% blubber, which is consistent with the 27–30% reported for free-ranging harbor seals (Pitcher, 1986). Daily growth requirements, $DGR_{s(x)}$, were low for all age-classes, ranging from about 2.5–5.5 watts for juveniles to negligible values for adults.

In calculating the energy invested in foetal development, the energetic density of the fetus was assumed to be the same as the 7.2 MJ·kg⁻¹ reported for harp seal neonates (Worthy and Lavigne, 1983). This implies that neonates are essentially devoid of fat, which is probably true as neonate and near-term harbor seals have very thin blubber layers (Pitcher, 1986). In addition, neonates can tolerate little mass loss before dying (Boulva and McLaren, 1979). Applying this value to the mean mass at birth of 10.2 kg (Bigg, 1969), the total energy content of the term foetus is estimated to be about 73.4 MJ. If it is assumed that, as in harp seals (Worthy and Lavigne, 1983), the placenta contains an additional 5.9 MJ, the net foetal investment is estimated at 79.3 MJ, and the gross investment at 113 MJ. Additional energy would be required for the metabolism of the fetus. However, the foetal mass would represent only a negligible portion of a female's total mass through most of the pregnancy. Moreover, since the foetal masses were not subtracted from the total masses of pregnant females incorporated into the growth curves, it was assumed that the costs were absorbed into the maintenance requirements of adult females.

In calculating the costs invested in lactation, the energetic density of the mass gained by pups was assumed to be the same as the 33.1 MJ·kg⁻¹ reported for harp seal pups (Worthy and Lavigne, 1983), which implies that the mass gained was approximately 85% fat and 15% protein. In view of their rapid rate of growth, this value is probably also applicable to nursing harbor seal pups. When applied to the 13.8 kg increase between the mean birth and weaning mass (10.2 and 24.0 respectively; Bigg, 1969), the energy assimilated by nursing pups is estimated to be 456.8 MJ·pup⁻¹. In addition, each nursing pup would require about 172.4 MJ for maintenance during the 5-1/2 week nursing period (Bigg, 1969). Thus, the total net nursing investment was estimated to be 629.2 MJ, which represents a gross investment of 946 MJ. The total annual cost of foetal development and lactation was thus estimated to be about 1060 MJ for each reproductive female.

Estimates of the total daily energy requirements, $DER_{s(x)}$, were surprisingly constant with age, ranging from 150 W for yearlings of both sexes to 215 W for full-grown males (Tables 1 and 2). The range in $DER_{s(x)}$ was much narrower (1.4×) than the range in body mass (3.7×) because the major energy expenditures scaled to $M^{0.75}$, and also because juvenile metabolic rates were elevated relative to adults of equivalent mass. The mean *per capita* DER was estimated to be 172 W.

Most of the daily energy requirement, DER , was expended for maintenance and comparatively little for

⁹H. Freeland, Institute of Ocean Sciences, Pat Bay, B.C., pers. commun. 1989.

production. Daily growth requirements accounted for, on average, only 1.2% of the total gross *DER* (1.7% of NE), and only 2.1% (3.0% of NE) of the gross *DER* for seals aged 1–2 years which exhibited the highest growth costs. However, the estimates reflect only the direct costs associated with growth. A portion of the elevated metabolic rates of juveniles, which account for 8.4% of the overall population energy budget (12.0% of NE) but were incorporated into maintenance costs, may be indirectly associated with growth. Although the *DER* of lactating females were 2.8× those of non-lactating females of equivalent mass, and lactation accounted for 89% of the total costs of reproduction, lactation accounted for only 14.6% of the overall energy requirements of reproductive females when amortized over the entire year. Overall, net reproductive costs accounted for only 3.2% of the total population energy budget (4.5% of NE). Thus, growth and reproduction combined accounted for only 4.4% of the total population energy budget (6.2% of NE).

With respect to maintenance, basal metabolism accounted for 33.9% of the total population energy budget (48.4% of NE) when the corrections for elevated juvenile levels are excluded, or 42.3% (60.4% of NE) when the corrections are included. If it is assumed that 13% of gross maintenance requirements is lost in faeces and urine and 17% expended in the heat increment associated with feeding, and thermoregulatory costs were negligible, the remaining 23.4% of the total population energy budget (33.4% of NE) was expended on activity. However, there is considerable uncertainty in this estimate. Had total maintenance costs been directly extrapolated from captive animals using *MR1*, only 16.1% of the total budget (23.0% of NE) would have been available for activity. On the other hand, had total maintenance been estimated from the activity budget using *MR2*, 29.0% of the total budget (41.4% of NE) would have been available for activity. Averaging *MR1* and *MR2* thus introduced a potential error of about ±13% into the overall population energy budget.

Based on the energetic densities of 10 of the 15 most important prey species, which accounted for 86.1% of the overall diet, the mean weighted energetic density of the diet was estimated to be 6.65 MJ kg⁻¹ (see Table 3). The total daily energy requirements, *DER*_{st(x)}, therefore translated into daily food requirements, *FR1*_{st(x)}, ranging from 2.0 kg for yearlings of both sexes to 2.8 kg for full-grown males (Tables 1 and 2), which represented 8.2% and 3.1% of their mean body masses respectively. The mean daily *per capita* food requirement, weighted according to the sex- and age-structure of the population, was estimated to be 2.2 kg, or 5.0% of mean body mass.

Estimates of daily food requirements based on the volumes of stomach contents, *FR2*_{st(x)}, were consistently

lower than the estimates based on energetic life tables, *FR1*_{st(x)} (Fig. 6). The mean *per capita* food requirement estimate based on stomach volumes, *FR2*, was 1.6 kg, or 73% of the mean estimated of 2.2 kg based on energetic life tables, *FR1*. It is unlikely that much of the discrepancy between the two estimates can be attributed to differences in the energetic density of diets on the east and west coasts. A crude estimate of the mean energetic density of the east coast diet, obtained by applying energetic densities of similar species on the west coast to 10 of the 15 most important prey on the east coast, which combined accounted for 81.2% of the east coast diet, was 6.31 MJ kg⁻¹, or 95% of the diet in the study area.

The magnitude of the discrepancy between *FR1*_{st(x)} and *FR2*_{st(x)} declined with age (Fig. 6). There was fairly good agreement between the two methods for adults: 2.1 kg from stomachs versus 2.5 kg from energetic life tables. The former was almost within the ±13% potential error introduced in the latter owing to uncertainty in the costs associated with activity (see above). In contrast, juvenile estimates based on stomach volumes were substantially lower than corresponding estimates based on the energetic life tables (Fig. 6). The average *per capita* requirement for immature seals based on stomachs, 1.3 kg, was only 65% of the estimate based on energetic life tables, 2.1 kg. The estimate based on stomach volumes for yearlings, the age-class exhibiting the greatest discrepancy, was only 52% of the estimate based on energetic life tables. The reason for the larger discrepancy for immature age-classes was that the volumes of stomachs, when all ages were pooled, was scaled to $M^{0.76}$ (Eqn. 15), which was close to the $M^{0.75}$ expected for adults (Eqn. 11). In other words, there was no evidence that juveniles consumed greater quantities of prey than adults of equivalent mass, whereas significant corrections were applied in the energetic life tables to account for the elevated metabolic rates of juveniles.

One factor that might have contributed to this discrepancy may have been post-weaning changes in body composition. At weaning, about 50% of body mass of pups is composed of blubber which, as the animal ages, is used and displaced by proteinaceous tissue. Thus, although pups exhibited some post-weaning growth in body mass during the first year, they may actually have experienced negative growth in energetic terms. However, even if it is assumed that all of the post-weaning blubber reserves (37.8 MJ·kg⁻¹) were replaced with proteinaceous tissue (6.5 MJ·kg⁻¹) during the first year, the daily energy requirement of yearlings would decrease by only 0.15 kg day⁻¹, or 15% of the observed discrepancy.

The discrepancy between *FR1*_{st(x)} and *FR2*_{st(x)} for juveniles suggests that the metabolic rates of free-living

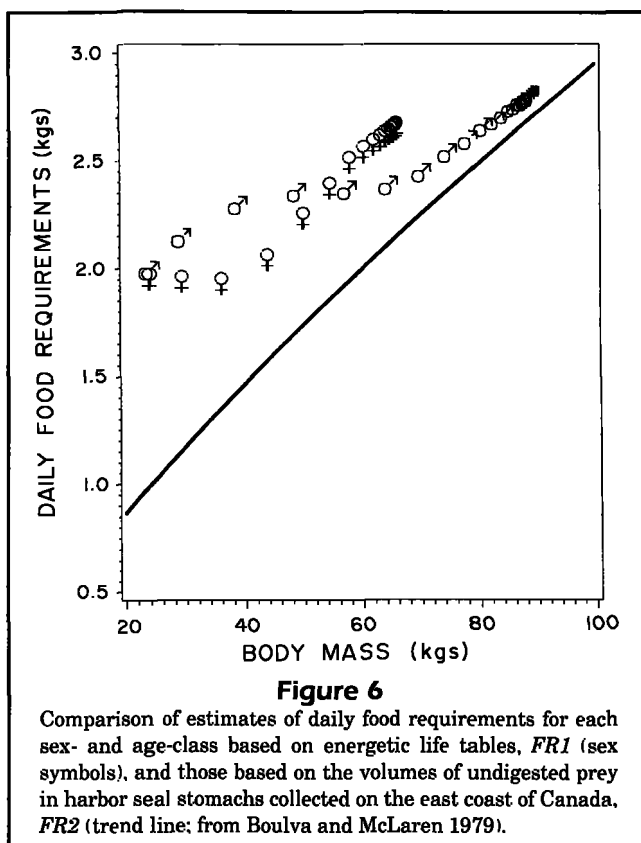
Table 3

Contribution to the overall diet (upper and lower limits), estimated annual consumption in metric tons (range), and energetic density ($\text{MJ}\cdot\text{kg}^{-1}$) of harbor seal prey in the Strait of Georgia. The range in annual consumption was calculated by assuming that daily food requirements were within $\pm 35\%$ of the point estimate and that realistic upper and lower limits of the importance of prey in the diet were half the width of the extreme limits (see Discussion). Energetic densities are from Perez and Bigg (1986) converted to joules assuming 1 calorie = 4.184 joules.

Prey species	Percentage of overall diet	Annual prey consumption (t)	Energetic density
Pacific hake (<i>Merluccius productus</i>)	42.6 (26.3–57.2)	4,214 (2,215–6,664)	4.90
Pacific herring (<i>Clupea pallasii</i>)	32.4 (19.8–54.7)	3,206 (1,679–5,818)	9.08
Pacific salmon (<i>Oncorhynchus</i> spp.)	4.0 (1.3– 8.6)	398 (171– 846)	8.41
Plainfin midshipman (<i>Porichthys notatus</i>)	3.4 (0.8– 7.8)	335 (135– 745)	—
Lingcod (<i>Ophiodon elongatus</i>)	3.0 (1.3– 5.4)	294 (137– 556)	—
Surfperches (Family Embiotocidae)	2.3 (0.5– 5.4)	230 (91– 520)	—
Cephalopods (Class Cephalopoda)	2.1 (0.0– 5.9)	208 (68– 535)	5.06
Flatfishes (Order Pleuronectiformes)	1.2 (0.5– 2.9)	123 (57– 284)	5.02
Sculpins (Family Cottidae)	1.2 (0.1– 3.1)	114 (40– 276)	—
Rockfishes (Family Scorpaenidae)	1.1 (0.4– 2.4)	112 (50– 241)	4.90
Pacific tomcod (<i>Microgadus proximus</i>)	1.0 (0.6– 1.4)	101 (53– 164)	—
Walleye pollock (<i>Theragra chalcogramma</i>)	1.0 (0.6– 1.3)	97 (50– 151)	5.90
Pacific sand lance (<i>Ammodytes hexapterus</i>)	0.8 (0.4– 2.1)	79 (39– 193)	5.10
Pacific cod (<i>Gadus macrocephalus</i>)	0.5 (0.3– 0.7)	54 (28– 87)	4.18
Smelts; mainly eulachon (Family Osmeridae)	0.4 (0.3– 1.8)	40 (23– 149)	5.90
Unidentified/other fishes	2.7 (1.0– 3.0)	267 (119– 380)	—
Other invertebrates	0.2 (0.0– 0.6)	20 (7– 54)	—
Total consumption / Weighted mean energetic density		9,892 (6,432–13,359)	6.65

¹Mean of values for market and gonatid squid.

²Value for eulachon, the dominant smelt in the diet.



juveniles may not be as elevated or may converge on adult rates more rapidly than those of captive juveniles. For example, the magnitude by which juvenile metabolic rates are elevated may be a function of their growth rates, which were generally much higher in captivity than in free-ranging harbor seals. Alternatively, the elevated metabolic rates of juveniles may have been obscured in Boulva and McLaren's (1979) analysis by the indiscriminate pooling of juveniles and adults, or the average meal sizes of juveniles underestimated due to seasonal biases. For instance, most of Boulva and McLaren's (1979) specimens were collected in summer and fall, which coincides with a post-weaning reduction in food intake in several other species of phocids (Worthy, 1987b).

In the absence of any compelling basis for favouring either $FR1_{s(x)}$ or $FR2_{s(x)}$, their mean, denoted as $\overline{FR}_{s(x)}$, was adopted in subsequent analyses. Since juvenile $FR1_{s(x)}$ and $FR2_{s(x)}$ differed by about $\pm 20\%$ of their mean, and juveniles accounted for 62% of the total population energy budget, this introduced a potential error of $\pm 12\%$ into the overall population energy budget. Estimated daily food requirements, $\overline{FR}_{s(x)}$, ranged from 1.5 kg for yearlings to 2.7 kg for full grown males, which represented 6.3% and 3.1% of their total body masses respectively. The mean *per capita* daily food requirement, \overline{FR} , was estimated to be 1.9 kg, or 4.3% of mean body mass.

Diet composition

Of the 2,841 scat samples collected in the Strait of Georgia, 2,765 (97.3%) contained identifiable prey. Samples typically contained one to three ($\bar{X}=1.91$) different prey species, but occasionally contained as many as seven. Marine and anadromous fishes, which accounted for 96.0% of all prey identified, were by far the most prevalent prey category. The diet included at least 48 species from 20 different families (Olesiuk et al., 1990b). The diet was dominated by gadoids and clupeids which were present in 62.0 and 59.2%, respectively of all samples containing identifiable prey. Other important families that occurred in at least 1% of samples were, in decreasing order of importance, salmonids, batrachoids, embiotocids, cottids, pleuronectids, hexagrammids, scorpaenids, ammodytids and osmerids.

The second most prevalent prey category was cephalopods, which occurred in 168 (6.1%) of all samples containing identifiable prey and represented 3.5% of all prey items identified. A superficial examination of their beaks indicated that the vast majority were squid (mainly *Loligo opalacens* with lesser amounts of *Gonatus* spp.), but at least one octopus was also consumed. The remaining prey categories, namely crustaceans, other molluscs, echinoderms, and birds, occurred in <1% of all samples containing identifiable prey and accounted for <0.5% of the total number of prey items identified.

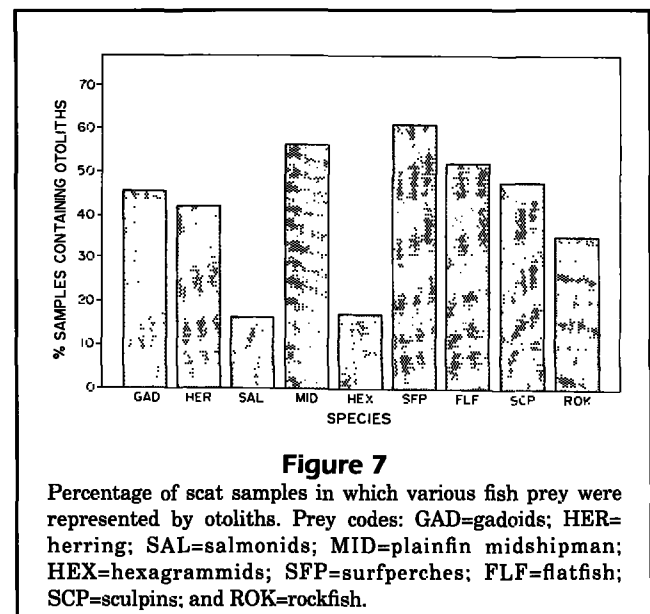
In assessing the relative importance of each prey (Eqn. 16), it was assumed that scats represented all prey consumed within a 24-hour period. Since pinniped gastrointestinal passage rates typically range from 5 to 30 hours (Pastukhov, 1975; Helm and Morejohn, 1979; Prime, 1979; Bigg and Fawcett, 1985; Prime and Hammond, 1987; Harvey, 1989), it is likely that most of the prey present in a scat sample had been consumed within the same 24-hour period. Although cephalopod beaks may be retained in stomachs over longer periods (Bigg and Fawcett, 1985), cephalopods constituted only a small part of the diet and beaks were usually accompanied by cephalopod eye lenses, which probably pass rapidly.

It is believed that essentially all species consumed in a meal were represented in scat samples, mainly because such a wide array of structures had been used to identify prey. Captive studies of otolith recovery rates have indicated that the fragile otoliths of small fishes, such as herring, may be completely digested and hence under-represented in scats (Hawes, 1983; Jobling and Breiby, 1986; Jobling, 1987; da Silva and Neilson, 1985; Dellinger and Trillmich, 1988; Harvey, 1989). Furthermore, based on a comparison between harbor seal stomach and intestinal contents, Pitcher (1980) concluded

that the otoliths of larger prey such as salmon would also tend to be under-represented in scats because their heads (i.e., otoliths) are sometimes discarded prior to being consumed. However, these studies merely demonstrate the inadequacy of relying exclusively on otoliths (see also Fig. 7), and are therefore not pertinent in the present study.

The improved resolution achieved by utilizing a wide array of structures can be illustrated by examining the prevalence of the above prey species in selected collections in which they constituted the dominant prey. For example, herring elements were identified in 86.4–100% of samples ($\bar{X}=96.1\%$; 150 of 156 samples) in 5 selected collections in which they were the dominant prey; and salmonids in 73.8–90.0% of samples ($\bar{X}=77.7\%$; 73 of 94 samples) in 5 selected collections in which they were the dominant prey. The slightly lower prevalence of salmonids was probably due to the fact they were not consumed by all seals as most of the samples without salmonids contained other prey species. Nevertheless, even if it were assumed that all seals had consumed these prey, the prevalence of herring in the diet would only have been underestimated by a factor of 1.04, and the prevalence of salmonids by a factor of 1.29. In contrast, in the same collections herring otoliths occurred in only 62.7% of the samples containing herring and salmonid otoliths in only 9.6% of the samples containing salmonids. Thus, the prevalence of herring would have been underestimated by a factor of 1.59 and salmonids by a factor of 10.42 had only otoliths been used to identify prey.

The assertion that scat samples provided an accurate representation of diets is further substantiated

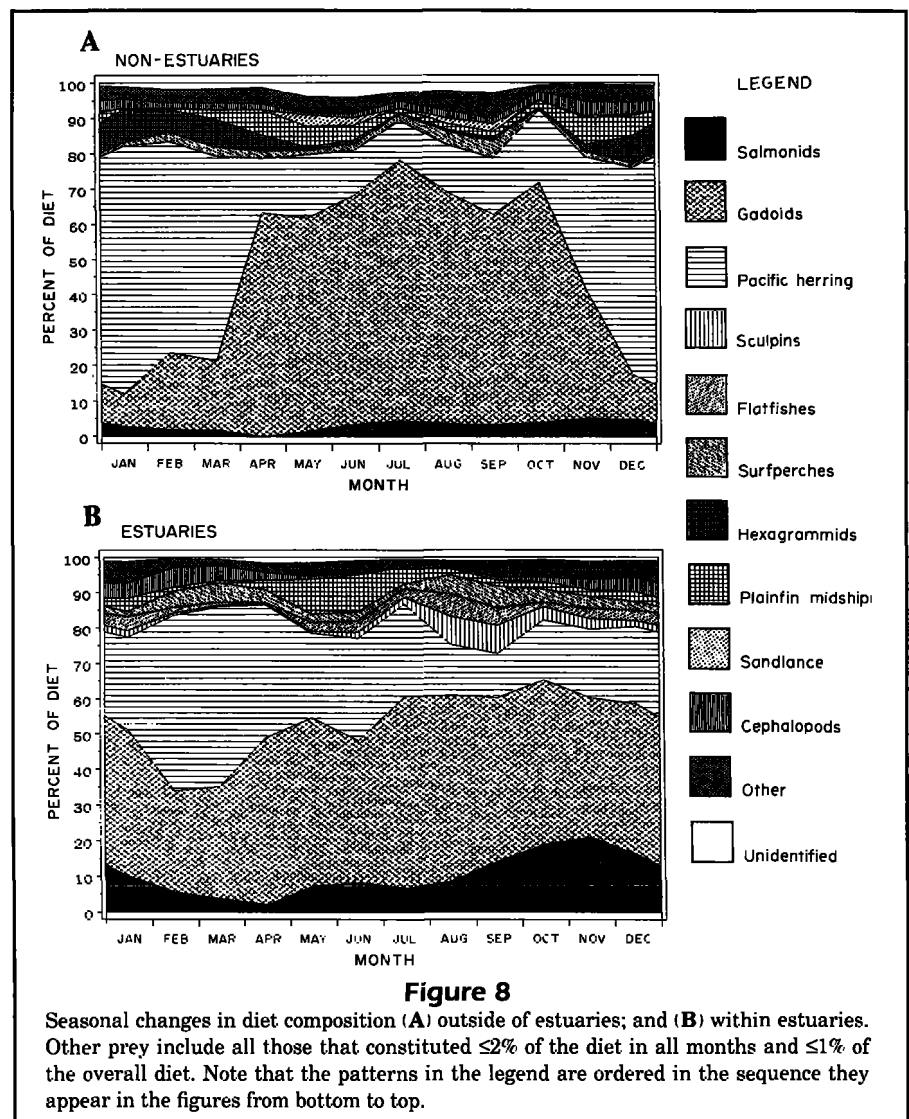


by the similarity of the prey identified in scat samples and those identified in stomachs collected within and adjacent to the study area. All but one of the 19 prey types identified in 69 stomachs collected throughout British Columbia (Fisher, 1952; Spalding, 1964) were represented in the scats, and all but 2 of the 22 prey types identified in 81 stomachs collected in Washington State (Scheffer and Sperry, 1931; Scheffer and Slipp, 1944). The exceptions were sablefish and ratfish, each of which occurred in one stomach, and burrowing crayfishes, which occurred in three stomachs. Furthermore, the mean number of prey species identified in the scat and stomach samples was also similar ($\bar{X}=1.91$ in scats versus 2.06 in stomachs).

Seasonal changes in diet composition outside of estuaries are shown in Figure 8A. Salmonids composed a relatively minor portion (0–5.2%; $\bar{X}=3.1\%$) of the diet in all months. The diet was dominated by gadoids ($\bar{X}=45.7\%$; 94.5% of which were hake) and herring ($\bar{X}=33.0\%$). There was a pronounced seasonal shift between these two prey, with gadoids dominating during April–October (54.3–73.7%) and herring during December–March (58.0–70.2%). Other important prey, defined as those constituting $\geq 1\%$ of the overall diet or $\geq 2\%$ of the diet in any month, were hexagrammids ($\bar{X}=3.4\%$; 95.8% of which were lingcod and 4.2% greenling), especially during December–April; plainfin midshipman ($\bar{X}=3.4\%$), especially during April–June and November–December; surfperches ($\bar{X}=2.2\%$; 81.3% of which were shiner perch and 18.7% pile perch); cephalopods (2.1%); and sandlance (0.9%). Incidental prey included, in decreasing order, rockfish, flatfishes, sculpins, smelts, skates, gunnels, lamprey, pricklebacks, crabs, sticklebacks, clingfishes, eelpouts and sea urchins. Unidentified prey accounted for a mean of 2.0% of the total non-estuary diet.

Seasonal changes in diet composition within estuaries are shown in Figure 8B. Salmonids were consumed in all months ($\bar{X}=10.3\%$), but were most preva-

lent during during September–January (14.5–21.2%). As was the case outside estuaries, the dominant prey in estuaries were gadoids ($\bar{X}=42.9\%$; 94.2% of which were hake) and, to a lesser extent, herring ($\bar{X}=27.3\%$). Gadoids dominate (39.2–53.9%) in all months except February–March, when herring were dominant (49.5–50.6%). However, the seasonal shift in the importance of these prey was not nearly as pronounced as it was outside estuaries. Other important prey included plainfin midshipman ($\bar{X}=3.6\%$) especially during May–June (9.7–10.5%); surfperches ($\bar{X}=3.6\%$; 91.9% of which were shiner perch), flatfishes ($\bar{X}=2.8\%$), sculpins ($\bar{X}=2.6\%$), all of which were most prevalent during August–September (5.4–6.1%, 5.0–6.3% and 7.8–7.9% respectively); and cephalopods ($\bar{X}=2.3\%$), especially during November–March (2.9–5.5%). Other incidental prey were, in decreasing order, rockfishes, sandlance, stick-



lebacks, hexagrammids, skates, northern anchovy, eelpouts, smelts, crabs, pricklebacks, gunnels, an unknown invertebrate, shrimp, lamprey, birds and mussels. Unidentified prey accounted for a mean of 1.0% of the overall diet within estuaries.

Estimates of the contribution of each prey to the total diet are shown in Figure 9, A–C. The estimates were obtained by integrating seasonal changes in distribution of seals (Fig. 3) with the seasonal changes in diet (Fig. 8), as per Equation 1. Although both the diet and abundance of seals varied regionally outside estuaries and among individual estuaries (see Olesiuk et al., 1990b for details), further stratification of the abundance and diet data by region and by individual estuary yielded estimates very similar to those shown in Figure 9, both in absolute terms ($r^2=0.996$ on an arithmetic scale) and in relative terms ($r^2=0.879$ on a log-log scale). The similarity can be explained by the fact that the scat samples were collected from all but one of 12 inhabited estuaries, from 47 widely distributed non-estuary sites and in all months of the year, and were thus representative of the entire population.

It was not possible to establish the absolute volumes of prey consumed from scats because the samples often represented only a portion of whole scats. Moreover, the relative volume of each prey consumed in a meal could not be reconstructed from the number and size of otoliths recovered and otolith length—fish weight keys (McConnell et al., 1984; Prime and Hammond, 1987; Harvey, 1989) because otolith recovery rates varied widely among species (Fig. 7) and intra-specifically depending on the size of prey (Olesiuk et al., 1990b). Furthermore, analogous analyses could not be applied to the other structures used to identify prey because their recovery rates also differed both among and within species (i.e., structures were recovered in proportions different from that in which they occur in whole prey). However, the lower and upper limits of the importance of prey in the diet, irrespective of the relative volumes of each prey consumed in meals, (see Table 3) indicate that estimates were fairly robust to violations of the equal-volume assumption. For example, the lower limits indicated that gadoids and herring combined accounted for no less than about half (47.8%) the overall diet. Indeed, subsequent calculations indicated that the two prey accounted for at least 63.2% of the total diet, because in many cases they were the only two prey species in a meal such that both could not have been consumed in negligible quantities. Upper limits for the remaining prey species indicated that none accounted for more than 10% of overall diet, and that only five families (salmonids, batrachoids, hexagrammids, embiotocids, and cephalopods) could have accounted for more than 5% of the overall diet.

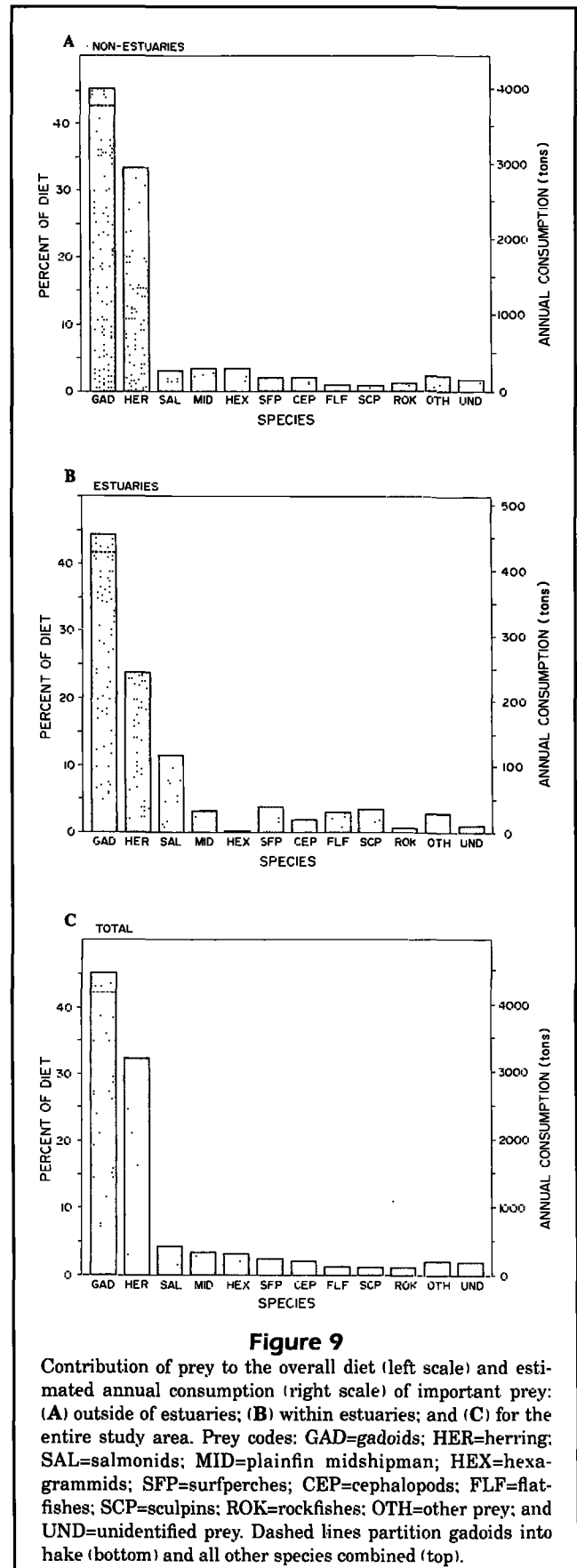


Figure 9

Contribution of prey to the overall diet (left scale) and estimated annual consumption (right scale) of important prey: (A) outside of estuaries; (B) within estuaries; and (C) for the entire study area. Prey codes: GAD=gadoids; HER=herring; SAL=salmonids; MID=plainfin midshipman; HEX=hexagrammids; SFP=surfperches; CEP=cephalopods; FLF=flatfishes; SCP=sculpins; ROK=rockfishes; OTH=other prey; and UND=unidentified prey. Dashed lines partition gadoids into hake (bottom) and all other species combined (top).

Prey consumption

Total annual prey consumption in the Strait of Georgia in 1988 was estimated at 9,892 metric tons (t) (range 6,432–13,359 t; Table 3), of which 1,023 t (range 665–1,381 t) was consumed within estuaries and 8,869 t (range 5,766–11,975 t) outside of estuaries. In energetic terms, this represented 65.8 TJ (6.8 TJ within estuaries and 59.0 TJ outside estuaries). The rate of energy consumption by the population was thus about 2.1 MW.

As noted earlier, most of the gross energy consumed was expended on maintenance and little on production. The ecological efficiency of the population was therefore low. Efficiency can be expressed either as the gross efficiency, which is the ratio of the gross energy consumed to energy added to the system through both mortality and surplus production (i.e., the 12.5% annual finite rate of increase), or as net efficiency, which includes only surplus production (i.e., net efficiency would be zero for a stationary population). In calculating energetic efficiency, the mean energetic density of carcasses was assumed to be $15.9 \text{ KJ}\cdot\text{kg}^{-1}$ based on a body composition of 30% blubber ($37.8 \text{ MJ}\cdot\text{kg}^{-1}$) and 70% proteinaceous tissue ($6.5 \text{ MJ}\cdot\text{kg}^{-1}$). In energetic terms, the gross population efficiency was estimated to be 3.9% and net efficiency to be 2.2%. The former estimate is consistent with the gross energetic efficiencies of 2.8% estimated for harbor seals in the Bering Sea (Ashwell-Erickson and Elsner, 1981), as well as the 3.8% and 3.9% for ringed and harp seals respectively (Parsons, 1977; Lavigne et al., 1982) and the 2–5% gross efficiency typical of mammals in general (Steele, 1974, cited in Lavigne et al., 1982). In terms of biomass, gross efficiency was estimated to be 1.6% and net efficiency 0.9%, which is also consistent with the gross estimate of 1.6% for harbor seals in eastern Canada (Boulva, 1973).

Gadoids (94% of which were hake both within and outside estuaries) accounted for the largest proportion of annual biomass consumed in the Strait of Georgia in 1988 (Table 3). Annual gadoid consumption was estimated at 4,467 t (454 t within and 4,013 outside of estuaries). Herring constituted the second largest proportion of the diet. Annual herring consumption was estimated at 3,206 t (244 t within and 2,962 t outside of estuaries). Salmonids ranked third in importance within estuaries and fifth outside of estuaries, and third overall. Annual salmonid consumption was estimated at 398 t (117 t within and 280 t outside of estuaries). Plainfin midshipman, which ranked sixth within estuaries and fourth outside estuaries, ranked fourth overall with an estimated 34 and 302 t consumed within and outside of estuaries respectively. Although hexagrammids constituted a negligible portion of the diet

within estuaries, they ranked third outside of estuaries and thus fifth overall. Annual hexagrammid consumption was estimated at 311 t, 308 t of which was consumed outside estuaries. Other prey consumed in appreciable quantities (i.e., >100 t) included surfperches (23 t), cephalopods (20 t), flatfish (123 t), sculpins (114 t) and rockfishes (112 t). Annual consumption of all other prey combined, none of which composed $\geq 1\%$ of the overall diet, was estimated at 208 t, and total consumption of unidentified prey at 181 t.

From the seal's perspective, approximately 44.2% (29.1 TJ) of the total annual energy requirements were obtained from herring and 33.3% (21.9 TJ) from hake. Thus, even though a larger biomass of hake than herring was consumed, hake were energetically less important than herring owing to their lower energetic density. Salmonids accounted for 3.3 TJ, which represented 5.1% of the total energy consumed compared to 4.0% of the biomass consumed. The precise energetic importance of other important prey could not be directly ascertained because their energetic densities were not known.

General discussion

Although formal statistical analyses are not possible with the available data, the model provides some insight into the likely accuracy of the annual prey consumption estimates. One potential source of bias in the consumption estimates are errors in the estimated daily energy requirements. Since the gross energy required for growth and reproduction constituted only a small portion of the overall population energy budget (1.7% and 4.5% respectively), uncertainties in these parameters, unless grossly underestimated, are unlikely to have an appreciable effect on the overall energy budget. Moreover, a large body of evidence indicates that the basal metabolic rates of adult phocids conform with Kleiber's (1975) equation (Lavigne et al., 1986). Thus, the two major potential sources of bias are the extent to which juvenile metabolic rates are elevated relative to adults, and the costs associated with activity. With respect to the former, the estimates of juvenile maintenance requirements based on captive seals and stomach contents of free-ranging seals differed by about $\pm 20\%$ of their mean. Because the study population was increasing at its intrinsic rate, it was markedly skewed toward juvenile age-classes which accounted for 62% of the total population energy budget. Hence, the discrepancy between the captive and stomach content estimates introduced a potential error of $\pm 12\%$ in the overall population energy budget. With respect to activity, the requirements of free-ranging seals probably fall somewhere between

those of captive seals and seals that swim continuously for 60% of the time. Since the latter two estimates differed from their mean by $\pm 13\%$ for all sex- and age-classes, the overall uncertainty in the estimated mean daily *per capita* energy daily requirements was probably on the order of $\pm 25\%$ of the point estimate.

Additional inaccuracies may be introduced in the conversion between units of energy and units of biomass due to seasonal, year-to-year, and age-related fluctuations in the energetic density of prey. For example, the energetic density of herring in the study area varies seasonally from 7.6 to 10.4 MJ·kg⁻¹ (Bigg and Olesiuk, unpubl. data), a range of $\pm 20\%$ of the mean. However, because the seasonal fluctuations in herring are probably more pronounced than other prey, and because median energetic values of prey were adopted in the analysis, the typical potential bias is more likely on the order of $\pm 10\%$. Since the potential biases in the energetic densities of prey and energy requirements are independent and additive, the total annual prey consumption estimate can be considered accurate to within about $\pm 35\%$ of the point estimate.

Further errors may be introduced in partitioning the total prey consumption among the different prey species. The main potential source of bias is the underlying assumption that all prey comprising a meal had been consumed in equal quantities. The lower and upper limits of the potential magnitude of this bias tended to be narrower for the two dominant prey (62–135% and 61–169% of the point estimates for hake and herring, respectively) than for other important prey, which averaged 35–211% of the point estimates. However, since it is very unlikely that a particular prey species was always consumed in negligible quantities or always comprised the entire meal when it was consumed along with other prey, these extreme limits undoubtedly overestimate the actual range of importance of prey. For example, when applied to the frequency of various fishes in 10,699 northern fur seal stomachs, the split-sample index actually gave results very similar to volumetric analyses ($r^2=0.929$ by region and $r^2=0.978$ overall with slopes and intercepts not significantly different from one and zero respectively) (Olesiuk et al., 1990b). If it is assumed that realistic lower and upper limits were half the width of the extreme limits, the total potential error in the estimates of annual consumption of hake and herring would be on the order of 50–170% of the point estimates, and 45–220% of the point estimates for other important prey species (see Table 3). It should be noted, however, that because the potential sources of bias in the consumption estimates are largely independent, the errors are just as likely to cancel as they are to compound.

The sex and age-structure of the population, which varies with the status of populations, had a surprisingly small effect on the mean *per capita* prey requirement. In the study population, which represented a population with a stable sex- and age-structure that was increasing at its intrinsic rate of 12.5% per annum, mean daily *per capita* food requirements were 1.9 kg, or 4.3% of mean body mass. If stationarity is induced by reducing fecundity rates, the parameter with the greatest influence on *per capita* requirements, the mean daily *per capita* requirement would increase to 2.1 kg, but decline to 3.9% of mean body mass. This is because the stationary population would be skewed more toward adults which not only have higher daily requirements, but also greater body masses. Thus, as also concluded by Lavigne et al. (1985) for harp seals in the northwest Atlantic, the population energy budget was relatively robust to direct changes in sex- and age-structure. In contrast, Hilby and Harwood (1985) found that energy requirements of grey seals were very sensitive to demographic changes. Their anomalous findings can be attributed to the fact that individual energetic requirements were scaled linearly to mass rather than mass^{0.75}, and also because the metabolic rates of juveniles were only marginally elevated (13%) relative to those of adults of equivalent mass. It should also be noted that populations may also experience density-dependent effects not directly related to demographic changes. For example, foraging costs may increase as prey become scarce, or seals may switch to alternate prey that would presumably have a lower energetic density or require greater energy expenditure to capture. These indirect effects were outside the scope of the basic model and could therefore not be evaluated.

Contrary to the assumption that thermoregulatory costs were negligible, some investigators have found that the metabolic rates of captive seals increased when immersed in colder water. Brodie and Pasche (1982) reported that resting metabolic rates of fasting grey seal pups increased in cold water as they depleted their blubber reserves, and on this basis suggested that *per capita* food requirements would increase in a population as prey became less abundant and the condition of animals declined. Hart and Irving (1959) found that the critical lower temperature of harbor seals in water was 20°C in summer and 13°C in winter, well above the ambient surface sea temperatures in the study area. However, because these experiments were conducted under artificial conditions, it is doubtful that the results can be validly extrapolated to free-ranging seals. For example, Figure 1 in Hart and Irving (1959) indicates that at 0°C, the resting metabolic rates of harbor seals were 1.4–1.8× greater than those within

the thermoneutral zone. However, the seals employed in their tests were restrained and probably post-absorptive. Even if it were assumed that basal requirements, which account for an average of 43% of the total energy requirements, were elevated to this extent for the 60% of the time seals spent in the water, thermoregulatory costs would only be on the order of 18–36 W. However, for a free-ranging seal, 17% of the GE ingested would be liberated as the heat increment associated with feeding and, since musculature is only about 25% efficient (Luecke et al., 1975), the remaining 75% of the 23% of GE expended for swimming would be liberated as heat. Since this “wasted” heat amounts to about 59 W for an average seal, it would appear that the thermoregulatory needs of free-ranging seals would be met indirectly through other energy expenditures.

One important assumption underlying the model was that daily ingestion rates were constant both with season and between regions. In contrast to other phocids such as harp and ringed seals (McLaren, 1958; Sergeant, 1973), Boulva and McLaren (1979) found no discernible seasonal pattern in the percentage of empty harbor seal stomachs, which implies that harbor seal feed throughout the year. As have previous models, the bioenergetics model assumed that feeding rates were constant in terms of biomass. Alternatively, it is possible that seals alter their foraging patterns in relation to the energetic density of prey. For example, greater quantities of poor-quality prey such as hake may be consumed when they are readily available compared to high-quality prey such as herring. Because any differences between the amount of energy ingested and required would be reflected by changes in energy reserves, the magnitude of potential biases introduced by these effects can be assessed from the seasonal changes in the condition of animals. Pitcher (1986) reported that the blubber composition of individual harbor seals ranged between extremes of 21% and 55% of body mass. Even if it assumed that the mean blubber content declined from 55% to 21% during a 6-month period of reduced food intake (or consumption of poorer quality prey) and increased from 21% to 55% during a second 6-month period of increased food intake (or consumption of higher quality prey), daily food requirements during the first and second 6-month periods would be only 125% and 75% of the annual mean respectively. Thus, gradual seasonal changes in food ingestion rates would not have a major effect on the prey consumption estimates.

Boulva and McLaren (1979) noted that the condition (i.e., girth:length ratio) of harbor seals of all ages and sexes combined was highest in winter and early spring, decreased during late spring, and was lowest

in summer and late autumn. Similarly, Pitcher (1986) found that the blubber layer of adult males and females harbor seals were thickest in winter, thinned during the summer, and that females had even thinner blubber layers by the autumn moult. These observations are consistent, at least qualitatively, with my bioenergetics model which predicts that animals would accumulate blubber during the winter while feeding mainly on energy-rich herring and deplete blubber during the summer while feeding mainly on energy-poor hake. The model also predicts that nursing females would utilize an additional 16.8 kg of blubber, or 22% of their total body mass, during the late July to early September nursing period (Bigg, 1969), and would therefore be in poorer condition than males by the autumn moult.

In an earlier assessment for harbor seals in the Bering Sea, Ashwell-Erickson and Elsner (1981) estimated the mean daily *per capita* gross energy requirements to be 216–238 watts, which is 26–38% greater than my estimate of 172 watts. The difference appears to be almost entirely attributable to geographic differences in body size. The mean body mass of harbor seals (both sexes were combined) in the Bering Sea was 67.7 kg, which is about 50% greater than the mean body mass of 44.7 kg in British Columbia. This difference translates into about a 37% difference in metabolic mass ($M^{0.75}$), to which energy expenditures were scaled in both our models.

After my model had been completed, Harkonen and Heide-Jorgensen (1991) published a very similar model for harbor seals in the Skagerrak. There is good agreement between our models on how the energy budget is partitioned among various components. Harkonen and Heide-Jorgensen (1991) estimated that, for an increasing population, 73.1% of metabolizable energy (NE and the heat increment) is expended on maintenance, 19.0% on activity, 2.0% on growth, 4.5% on reproduction, and 1.5% on the annual moult. According to my model, 68.1% is expended on maintenance (including the heat increment), 26.9% on activity, 1.4% on growth, 3.7% on reproduction, and I made no allowance for any costs associated with the annual moult. However, there is a considerable discrepancy between our estimates of the mean daily *per capita* gross energy requirements, even though the mean body mass of seals in the Skagerrak and British Columbia are very similar (41.8 and 44.7 kg respectively). Harkonen and Heide-Jorgensen's (1991) estimate of 227 watts is 32% greater than my estimate of 172 watts. This discrepancy is due primarily to differences in the way energetic requirements were scaled to body mass. Harkonen and Heide-Jorgensen (1991) first estimated the requirements of juveniles and then extrapolated these estimates to adults by assuming

that energy expenditures were linearly related to body mass (their correction of 1.4 to account for non-mass related differences between juveniles and adults was almost identical to mine). In contrast, energy expenditures in my model were scaled according to metabolic mass ($M^{0.75}$), which increases less rapidly with age than body mass. According to my growth curves, the increase in body mass between weaning and adulthood would be 29% greater than the increase in metabolic mass over the same period for females, and 39% greater for males.

Despite the aforementioned limitations, my bioenergetics model provides some insight into the foraging patterns of harbor seals in the Strait of Georgia. Hake and herring, the two most abundant fishes in the study area (Shaw et al., 1990; Hay et al., 1989), are clearly also the two most important prey of harbor seals. Combined, they account for an estimated 75% (at minimum 63%) of the total consumption both in terms of biomass and energy. One would therefore expect hake and herring stocks to play an important role in regulating the size of the harbor seal population, if in fact carrying capacity is food-limited. The annual consumption of these prey by harbor seal population in 1988, which is thought to be near or perhaps slightly above historic levels (Olesiuk⁴), represents approximately 3.2% of the total hake biomass in the study area (Shaw et al., 1990) and 3.5% of the total herring biomass (Haist et al. 1988; Hay¹⁰).

Interestingly, both hake and herring appear to be only seasonally available in the Strait of Georgia, but in a reciprocal manner to one another. The Strait of Georgia of herring stock is largely migratory. Adult herring normally reside off the west coast of Vancouver Island, but emigrate into the Strait of Georgia during December–March to spawn (Taylor, 1964; Hay et al., 1987; Hay et al., 1989). Although the Strait of Georgia hake stock is resident, hake are scarce throughout much of the Strait during December, and by March have congregated in deep (150–300 m) spawning aggregations in offshore waters. Following spawning, the spawning aggregations disperse and during April–November hake occur in shallower waters (50–100 m) throughout much of the Strait of Georgia (McFarlane and Beamish, 1985), which coincides with the period herring are unavailable. Thus, hake and herring provide an abundant year-round source of food, as reflected by the seasonal shift in the predominance of these prey in the diet (Fig. 8A). The year-round availability of these two abundant prey may account for the much higher density of seals in the study area

compared to other regions of British Columbia (Olesiuk et al., 1990a).

Seasonal fluctuations in the overall importance of hake and herring were much less pronounced in estuaries (Fig. 8B). In some estuaries the seasonal shift between these two prey were similar to those outside estuaries, whereas in other estuaries hake dominated the diet in all months (see Olesiuk et al., 1990b for details). Seals in the latter estuaries were probably feeding on small, localized stocks that are non-migratory and are known to reside nearby¹¹, or on juvenile hake which move inshore and inhabit shallow waters (McFarlane and Beamish, 1985).

Although hake and herring represented the major food items, a wide array of other species were consumed in small quantities. Predation on these prey appeared to be largely limited to the particular areas and periods each was most available or vulnerable. For example, adult salmon were consumed primarily as they concentrated en route to spawning rivers, and especially within estuaries. Numbers of seals in most estuaries also increased during September–December coinciding with the return of spawning salmon to adjacent rivers (Olesiuk et al., 1990b). Plainfin midshipman and lingcod were also preyed upon primarily during their spawning seasons when males defend nests, and trout in a few localities as they were released in large quantities from hatcheries or returning to spawn in natal rivers (Olesiuk et al., 1990b). Since these prey comprised a minor component of the overall diet, they probably play little role in regulating harbor seal abundance.

This study indicates that the harbor seal is an opportunistic predator in that it is capable of adjusting its foraging patterns to take advantage of seasonally and locally abundant or vulnerable prey. Although the low efficiency of the population may be construed as reinforcing the premise that seals are “inefficient converters of fish flesh” (Sergeant, 1973), the ecological efficiency of harbor seals is actually comparable to that of many terrestrial mammals (see review in Lavigne et al., 1982) and slightly above the theoretical upper limit of 2–3% expected for homeotherms (Turner, 1970). In order to acquire a more complete understanding of the role of harbor seals in the ecosystem, it will be necessary to extend the bioenergetics model to the community level (Lavigne et al., 1982). The population model raises several complex questions that can only be answered by community models. For example, to what extent is the sex- and age-structure and productivity of herring stocks affected by harbor seal

¹⁰D. Hay, Pacific Biological Station, Nanaimo, B.C., pers. commun. 1989.

¹¹G. McFarlane, Pacific Biological Station, Nanaimo, B. C., pers. commun. 1989.

predation; or to what degree are the overall predatory pressures on herring affected indirectly by seal predation on other herring predators such as hake, salmon, and lingcod? Such a bioenergetics community model will need to incorporate not only data on the size of prey consumed, which can be obtained from a more detailed analysis of scat contents (e.g., Bailey and Ainley, 1982; Antonelis et al., 1983), but also the dynamics and compensatory and depensatory mechanisms of population regulation of prey populations.

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