

Diet, Activity Budgets, and Movement Patterns
of Harbour Seals (*Phoca vitulina*) in Cowichan Bay and
Adjacent Areas

by



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DIET, ACTIVITY BUDGETS, AND MOVEMENT PATTERNS OF HARBOUR
SEALS (*PHOCA VITULINA*) IN COWICHAN BAY AND ADJACENT AREAS.

ABSTRACT

The diet, activity budgets, and movements of harbour seals are important for understanding the species interactions with fisheries, but they are poorly documented and have been studied separately from one another. Harbour seals are considered opportunistic predators that consume solitary and schooling fishes and cephalopods of most sizes and species. However, this view is based upon isolated studies on diet and movement studies that have strong biases due to the methods employed.

This project investigated harbour seals using Cowichan Bay and adjacent areas, and the interaction of seasonal changes in diet with movement patterns, population fluctuations, and activity budgets. Seasonal and diel variation in prey distribution, abundance, and behaviour also were examined in relation to harbour seal diet, movement patterns, and diel haul-out and swimming patterns.



Captive harbour seal feeding studies were conducted to evaluate and improve techniques for prey identification. Teleost otoliths in faeces have been used to characterize pinniped diet. I evaluated the potential of using hard parts other than otoliths for identifying prey. Four harbour seals were fed five fish species during experiments. Otoliths represented only 17% of >22,000 hard parts identified, while vertebrae represented 66% (excluding scales). Incorporating all prey hard parts into prey identification decreased the likelihood of not identifying prey or incorrectly identifying prey.

A total of 471 prey occurrences ($\bar{x}=1.5$ per scat) representing 19 species in 16 families were identified. Teleost fish represented 93% of all prey identified. Prey diversity was greatest during September and October. Seasonal variation in the diet was pronounced for most prey species. This variation appeared to be a result of annual changes in prey abundance, distribution, or behaviour.



Nineteen harbour seals were captured and fitted with radio-tags. Seals were monitored every 3-5 minutes for 20 seconds from May 1991 to June 1992 from a remote monitoring station located in Cowichan Bay. The diel and seasonal haul-out and swimming patterns of radio-tagged seals were determined. In addition, the movement patterns and foraging areas of radio-tagged seals outside the study area were located by finding animals from land or boat with a hand held radio-receiver.

Harbour seal haul-out patterns on log-booms were closely correlated with tidal height and, to a lesser extent, time of day. Sixteen of 18 seals had significant, positive linear relationships of time hauled out to tidal height. The proportion of time that seals spent hauled out was low at dawn and dusk during the summer and at dusk during the winter. The two main prey items of harbour seals in this area were herring and hake (>65%), which are diel vertical migrators. Crepuscular movements of these prey types closer to the surface combined with changes in their schooling behaviour may increase harbour seal foraging success. Seals spent more time hauled out in August to February than the rest of the year. This corresponds to the moulting period and growth of new pelage of harbour seals in the area.


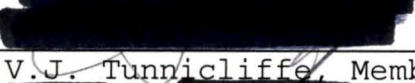
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1. GENERAL INTRODUCTION

1.1 Harbour Seal Diet

Harbour seals are the most widely distributed pinniped, inhabiting inshore waters throughout their range. The abundance of harbour seals combined with their easy accessibility make harbour seals the most well studied pinniped. However, the relationship of harbour seal diet to prey abundance, distribution, or behaviour is poorly understood.

Traditionally, pinniped diet studies have relied on the examination of food remains in stomachs (e.g. Scheffer and Slipp 1944; Fisher 1952; Spalding 1964; Rae 1973; Pitcher 1980a; Murie and Lavigne 1991). However, it is difficult to collect large numbers of samples from one area at regular intervals. Furthermore, the use of stomachs for dietary studies poses ethical problems, as well as conservation problems for some species.

Alternative methods of diet estimation such as faecal analysis have become increasingly important. However, recent studies have found the ingestion, digestion, passage, and ultimate recovery of teleost otoliths and cephalopod beaks lead to biases in the estimation of the relative importance of different prey species in the diet (e.g. Prime 1979; da Silva and Neilson 1985; Murie and Lavigne 1986;

Jobling 1987; Dellinger and Trillmich 1988; Harvey 1987; Harvey and Antonelis 1994). Captive pinniped feeding studies examining the use and recovery of other taxa specific prey hard parts have not been conducted. Improvements in the reliability and accuracy of prey identification techniques will enable researchers to better estimate dietary composition.

Many studies have examined harbour seal diet (e.g. Scheffer and Slipp 1944; Fisher 1952; Spalding 1964; Boulva and McLaren 1979; Pitcher 1980a; Harkonen 1987; Pierce et al. 1991). However, it is often difficult to differentiate seasonal changes from regional differences. Also, differences in methods of collecting (e.g. stomachs, faeces or visual observation), processing (e.g. sieves, elutriator), identifying (e.g. whole fish, otoliths, all prey hard parts), and analyzing (e.g. volume, index of relative importance, count, frequency of occurrence, split-sample-index) seal prey make comparisons among studies difficult (Bigg and Perez 1985; Murie 1987; Bigg and Olesiuk 1990). Most studies have found harbour seals are opportunistic predators utilizing demersal, pelagic, schooling, and solitary inshore fish and cephalopods of most sizes and species.

1.2 Activity Budgets

The biological significance of hauling out in harbour seals has not been closely investigated. The reasons for hauling out include, but are not limited to; thermo-regulatory benefits, skin and pelage growth, giving birth, suckling, resting, avoidance of aquatic predators and sleeping. Further complicating the reasons why seals haul-out are the many factors influencing when seals haul-out which vary among areas and haul-out substrate (e.g. Boulva and McLaren 1979; Sullivan 1980; Hoover 1983; Allen et al. 1984; Calambokidis et al. 1987). Most studies have attempted to correlate circadian cycle, tidal height, or weather with diel haul-out behaviour. Diel changes in prey availability or presence of predators (e.g. killer whales) may also influence swimming and haul-out patterns. The many factors influencing harbour seal haul-out behaviour makes the prediction of diel and seasonal patterns difficult.

1.3 Thesis Overview

The body of my thesis consists of three parts; Chapter 2 explores seal prey identification techniques and the potential biases affecting diet estimation methods. This work addresses potential shortcomings from using only single prey structures and identifies other species specific

structures that can be used in prey identification. This study provides the ground work for Chapter 3.

Chapter 3 examines harbour seal diet, and biases from secondary prey. I also examine seasonal changes in prey abundance, distribution, or behaviour, and the relationship these have with seasonal variation in harbour seal diet and abundance.

Chapter 4 relates diet, movement patterns, activity budgets, and population fluctuations of harbour seals with diel and seasonal tidal and circadian cycle.

Finally, a note on format. Each chapter was designed to be more or less self-contained. Although all chapters report upon different aspects of the same basic research, the reader should be able to read any chapter independently of the others. This entails some necessary redundancy in the various introductions.

2. IDENTIFYING HARBOUR SEAL PREY FROM HARD PARTS IN FAECES.

2.1 INTRODUCTION

The relationship of pinniped diet to inshore commercial fisheries is poorly understood (Fiscus 1979; Harwood and Croxall 1988). Improved methods for estimating fish and seal abundance and distribution patterns, combined with improved techniques for determining diet, are needed for pinniped conservation and management. Knowledge of seasonal changes in diet is necessary to assess when food resources may be limiting, and when impacts on commercial fisheries occur. Many concurrent diet samples from different regions throughout the year are needed to characterize regional and seasonal trends in diet. Techniques to study the diet of pinnipeds without disturbing or destroying individuals will become increasingly important in future studies, especially for depleted pinniped species. Examining the reliability of these techniques is necessary for determining the limitations of diet-estimation methods.

Studies of pinniped diet traditionally have relied on examination of food remains in stomachs of animals killed incidentally during commercial fishing, or by intentional collecting (e.g. Scheffer and Slipp 1944; Fisher 1952; Spalding 1964; Rae 1973; Pitcher 1980a; Perez and Bigg 1986; Murie and Lavigne 1991). Diet estimates obtained in these ways have been unrepresentative of the population or biased

towards species of commercial interest. Other problems with the analysis of stomach contents are the difficulty and expense of collecting animals, and the high incidence of empty stomachs. Furthermore, use of stomachs for dietary studies poses ethical problems, as well as conservation problems for some species (e.g. Steller sea lion, *Eumetopias jubatus*; Hawaiian monk seal, *Monachus schauinslandi*).

Alternative methods for studying pinniped diet have been developed: e.g. northern elephant seals (*Mirounga angustirostris*) can be captured and have their stomachs lavaged (Antonelis et al. 1987). However, this method is labour-intensive, which combined with the high incidence of empty stomachs makes it difficult to collect many samples. Diet can be estimated by directly observing feeding pinnipeds in some areas like estuaries (Brown and Mate 1983; Roffe and Mate 1984; Gearin et al. 1988; Bigg et al. 1990; Olesiuk et al. in prep.). However, only large prey that are brought to the surface can be identified, and observations are restricted to daylight hours (Spalding 1964). Another method for estimating diet is the examination and identification of cephalopod beaks and sagittal otoliths of teleosts that occur in faeces (e.g. Pitcher 1980b; Roffe and Mate 1984; Prime and Hammond 1987). The advantage of this method is that many samples can be collected from different geographical locations with little disturbance, effort, or expense.

Recent evidence suggests that otoliths may provide a biased representation of diet (Jobling 1987; Olesiuk et al. 1990b; Harvey and Antonelis 1994). Prey species that lack otoliths or whose otoliths are not ingested are not represented in digestive tracts or faeces. In addition, otoliths can be lost or damaged during ingestion (see Methods), and the heads of large prey often are not consumed (Scheffer and Slipp 1944; Spalding 1964; Rae 1968; Boulva and McLaren 1979; Pitcher 1980b; Roffe 1981; Roffe and Mate 1984). Cartilaginous fishes have tiny diffuse otoliths that are unsuitable for identification (Pitcher 1980b). Similarly, the small fragile otoliths of some fish species (e.g. herring, *Clupea harengus*) often are partially or totally digested during passage through the digestive tract, making identification difficult or impossible (Prime 1979; da Silva and Neilson 1985; Murie and Lavigne 1986; Murie 1987; Dellinger and Trillmich 1988). Thus, some investigators have questioned the reliability of quantitative diet estimates based on otoliths and their usefulness for prey identification (Jobling and Breiby 1986; Jobling 1987).

Hard parts other than otoliths have been documented as remains in many studies of pinniped diet (see Fitch and Brownell 1968; Pitcher 1980b; Bigg and Fawcett 1985; Prime and Hammond 1990; Croxall 1993). However, they have been

used to identify prey species only recently. For example, Roffe and Mate (1984) identified Pacific lamprey (*Lampetra tridentata*) using infraoral and supraoral structures found in harbour seal (*Phoca vitulina*) and California sea lion (*Zalophus californianus*) digestive tracts. In their study on harbour seal faeces, Olesiuk et al. (1990b) identified 58% of fish prey using hard parts other than otoliths. Pierce et al. (1991) found that bones improved the frequency of detection of prey taxa in seal digestive tracts and faecal samples.

The greater the accuracy in the number, size, and type of prey identified from pinniped faeces, the better researchers will be able to interpret diet composition. Several studies on captive pinnipeds have estimated recovery rates of otoliths (da Silva and Neilson 1985; Murie and Lavigne 1985; Dellinger and Trillmich 1988; Harvey 1989; Harvey and Antonelis 1994). However, this approach has not been extended to other fish structures, nor has cross-validation between otoliths and other hard parts been carried out.

The present study was designed to meet some of these shortcomings. The main objectives of this project were to: (1) determine which taxon-specific fish hard parts pass through the harbour seal digestive tract; (2) identify which

taxon-specific structures are useful for qualitative and quantitative estimates of fish consumed; and (3) compare the accuracy of identifying prey using otoliths and other hard parts.

2.2 METHODS

2.2.1 Recovery of Fish Hard Parts

Four captive harbour seals (two males and two females) were housed individually in continuously flowing saltwater tanks (5x2x2 m) at the Vancouver Aquarium (Table 2.1). Daily water temperature and salinity averaged 9.1°C and 27.6‰ respectively. The animals had access to a 1x2 m haul-out platform and were fed twice per day. They consumed 5-8% of their body weight each day in 5-15 day experiments from January to June 1993. Five species of fish were used: Pacific herring (*Clupea harengus pallasii*), walleye pollock (*Theragra chalcogramma*), Pacific hake (*Merluccius productus*), surf smelt (*Hypomesus pretiosus*), and juvenile chinook salmon (*Oncorhynchus tshawytscha*). These prey species will be referred to by their abbreviated common names for the remainder of the chapter (herring, pollock, hake, smelt, salmon).

The seals were fed fish fillets (i.e. no bones) 48 h

before each experimental trial, to allow the passage of structures¹ from previous meals. In other studies, seals have had food withheld for 18-48 h before trials (e.g. Bigg and Fawcett 1985; Murie 1987; Markussen 1993) which may affect passage rate and recovery of fish structures. At the end of each trial, seals again were fed fish fillets for 48 h to facilitate continuing passage of structures still in the gut. Fish hard parts should pass through the digestive tract or be digested completely within 30 h (Pastukhov 1975; Helm 1979; Prime 1979; Prime and Hammond 1987).

Table 2.1 Harbour seals used in feeding trials.

Seal	Sex	Age (yr)	Weight*(kg)
1 (Aretha)	F	>12	93
2 (Dolly)	F	10	80
3 (Benny)	M	5	85
4 (Morgan)	M	3	65

* Mean weight during trials.

Standard lengths and weights of all fish were recorded to 5 mm and 0.1 g respectively (Table 2.2). Initial feeding

¹ *Structure* indicates the hard part type, while *element* refers to their frequency; e.g. 3 gill rakers plus 2 otoliths equals 2 structures but 5 elements.

trials indicated that the seals tore the heads off those fish that were too large to be swallowed whole. Otoliths of these large fish were found 1 h after the seals were fed, when the tank was cleaned. No other structures from these prey items were recovered after 1 h. The minimum published passage rate of food in pinnipeds is 6 h (Prime 1979). Thus the otoliths of the large food items were assumed to have fallen out of the cranial cavity during ingestion. Subsequently, only fish that could be swallowed whole were fed to seals for this experiment.

Tanks were drained and cleaned daily by filtering their contents through 0.495 mm nylon mesh fitted to the outflow. Faecal material was dried and stored in petri dishes for examination.

Table 2.2 Mean size (\pm S.D.) and number of fish fed to harbour seals.

Species	Length (mm)		Weight (g)		N
Herring	183	\pm 16.6	121	\pm 17.7	1978
Hake	331	\pm 18.3	344	\pm 56.9	145
Pollock	293	\pm 32.1	372	\pm 118.2	119
Salmon	143	\pm 8.3	51	\pm 10.2	1174
Smelt	167	\pm 11.7	49	\pm 14.5	1530

2.2.2 Identification of Prey Hard Parts

Fish hard parts recovered from the scats were compared with a reference collection held at the Department of Anthropology, University of Victoria. Fish scales were identified by staff at the Pacific Biological Station (Nanaimo, B.C.). Prey hard parts were identified to the lowest possible taxon using a dissecting microscope (8-24X). Naming of fish hard parts follows Casteel (1976) and Cannon (1987). The proportion of fish structures recovered was computed as the greatest number of left or right elements divided by the total number of fish fed to the seal during the experimental trial. In some cases the estimate was based on the total number of elements recovered divided by two, when erosion or fragmentation made determining right or left side impossible. Structures useful for determining the presence or absence of a prey type, but not suitable for quantifying the number of prey consumed were simply counted (e.g. vertebrae).

2.2.3 Fish Structure Recovery Test

The ability to successfully recover fish hard parts was tested by scattering 20-25 elements of certain fish structures marked with waterproof ink into the tank (Table 2.3). Seals were present during these trials as part of the

ongoing feeding experiments. All marked elements were recovered during the next tank cleaning. Thus I assumed that all fish hard parts passed in faeces during each trial were recovered (i.e. within 24 h).

Table 2.3 Fish structures used in element recovery test to assess the ability to retrieve structures during tank cleaning.

Species	Structure	No. Elements	No. Recovered
Herring	Vertebra	25	25
Herring	Otolith	25	25
Pollock	Otolith	20	20
Pollock	Postcleithrum	25	25
Salmon	Vertebra	25	25
Salmon	Otolith	25	25

Some structures recovered from the faecal remains were not morphologically distinct enough to be of use in identifying prey. Structures diagnostic of taxa were chosen for statistical analysis and separated into three categories:

I. *Identify both type and number of prey.* These are structures that could be used to estimate the number of prey consumed, and that represented >10% of the prey species fed (e.g. otolith, atlas/axis and postcleithrum). Structures that accounted for <10% of the fish consumed would be of

little use for quantitative estimates.

II. *Identify only type of prey.* Structures that represented <10% of the total fish eaten or were not suitable for estimating the number of a particular species consumed (i.e. structures that have numerous elements which often vary within taxa) but could be used to determine the presence or absence of a prey taxon (e.g. scale, tooth, and vertebrae other than atlas or axis).

III. *Identify only number of prey.* Structure that could not be used to identify prey but whose frequency could be used to estimate the number of fish consumed (e.g. lens).

Recovery rates (as proportions) of Category I structures were arcsin-transformed for statistical analysis (Zar 1984). Analysis of variance (ANOVA) was used to test whether differences in recovery rates of fish structures among seals were statistically significant.

2.3 RESULTS

Over 50,000 elements were recovered from 4,946 fish consumed during the 6-month experiment period. Of these elements, 22,383 (21 structures) were diagnostic of taxa (Categories I and II, excluding scales). In addition, 7,963

lenses were recovered (Category III).

Differences in recovery rates of 8 of the 9 structures of various fish hard parts did not differ significantly among the four seals (Table 2.4), but there was a significant difference in the recovery rate of salmon otoliths. A Tukey test [$F=7.93$, $P=0.05$] revealed that seal No. 4 (the youngest animal) had an unusually low recovery rate. In general it appears that differences in structure recovery rates among seals was not significantly different. Thus, I pooled the results of individual feeding trials.

Table 2.4 Results of ANOVAS on recovery rates (in percent) of fish structures for different seals (*=significantly different).

Species	Structure(s)	df	F	P
Herring	Otolith	3,8	2.96	$P>0.05$
Herring	Prootic/Synotic	3,8	3.54	$P>0.05$
Herring	Atlas/Axis	3,8	1.17	$P>0.05$
Hake	Otolith	2,4	0.66	$P>0.05$
Pollock	Otolith	2,6	0.92	$P>0.05$
Pollock	Postcleithrum	2,6	1.00	$P>0.05$
Pollock	Interopercle	2,6	0.60	$P>0.05$
Salmon	Otolith	3,8	16.00	$P<0.05^*$
Smelt	Otolith	2,7	0.63	$P>0.05$

Otoliths of all five prey species were recovered in sufficient quantities to estimate the total number of fish consumed. In fact, otoliths were the only useful structure

for estimating the number of fish consumed for all species. Overall, 23-77% (\bar{x} =54%) of otoliths were recovered, but recovery rates differed significantly among fish species [$F_{4,39}$ =5.39, $P<0.05$]. Otoliths were the only structure recovered that were useful for estimating the numbers of smelt and salmon consumed. However, additional structures were recovered from herring (atlas/axis, prootic/synotic), pollock (postcleithrum, interopercle, dentary) and hake (dentary) for quantitative estimates (Table 2.5). Herring atlas and axis, and prootic and synotic, were combined because the erosion of distinguishing characteristics within both groups made separate structure identifications unreliable.

Previous captive feeding studies did not record or quantify any fish hard parts except otoliths. Yet otoliths represented only 17% of all taxon specific structures identified (excluding scales; Table 2.6). Other types of fish hard parts can be used to estimate the type and number of fish consumed. For example, 35% of atlas/axis of herring were recovered, compared with 30% of otoliths. Similarly, herring prootic/synotic bones were recovered more often than otoliths (32%). In other prey species, otoliths had the highest recovery rates of any structure, though other structures were recovered frequently (e.g. 56% for postcleithrum of pollock).

Table 2.5 Recovery rates for fish structures that could be used to detect incidence or presence (+) of prey species. For category I structures, table entries indicate percent recovery (see text).

Structure (s)	Herring	Hake	Pollock	Salmon	Smelt
Vertebra	+	+	+	+	+
Otolith	29.8	72.8	76.5	64.7	23.1
Prootic/Synotic	32.5	-	-	-	-
Atlas/Axis*	35.3	-	-	+	-
Dentary	+	35.5	35.3	+	-
Gill Raker	-	+	+	+	-
Tooth	-	+	-	+	-
Ultimate Vertebra	+	-	-	-	-
Postcleithrum	-	-	55.9	-	-
Ceratohyal	+	-	-	-	-
Epihyal	+	+	-	-	-
Interopercle	-	-	28.7	-	-
Pharyngobranchial	-	+	+	+	-
Angular	-	+	+	-	-
Quadrate	+	-	-	-	-
Hypobranchial	-	+	+	-	-
Epibranchial	-	-	+	-	-
Basioccipital	+	-	-	-	-
Hyomandibular	+	-	-	-	-
Scale	+	-	-	+	-

*Identifications of herring include atlas and axis, otherwise only atlas.

Table 2.6 Numbers of fish fed to harbour seals and numbers of structures recovered from seal faeces. Structures that were not taxon specific or digested beyond recognition were classified as unknowns.

Structure(s)	Herring	Hake	Pollock	Salmon	Smelt	Unknown	Totals
Fish Fed	1978	145	119	1174	1530		4946
-----	-----	-----	-----	-----	-----	-----	-----
Scales*	6	--	--	6	--	>20000	>20000
Vertebra**	5574	145	35	6629	799	509	13691
Eye Lens	--	--	--	--	--	7963	7963
Otolith	1179	211	182	1519	707	310	4108
Prootic/synotic	2572	--	--	--	--	154	2726
Atlas/axis***	1398	--	--	135	--	46	1579
Dentary	10	103	84	52	--	--	249
Gill Raker	--	114	8	81	--	8	211
Tooth	--	52	--	89	--	6	147
Ultimate Vert.	138	--	--	--	--	--	138
Postcleithrum	--	--	133	--	--	--	133
Ceratohyal	104	--	--	--	--	--	104
Epihyal	83	14	--	--	--	--	97
Interopercle	--	--	82	--	--	--	82
Pharyngobranch.	--	15	11	20	--	--	46
Angular	--	22	15	--	--	--	37
Quadrate	21	--	--	--	--	--	21
Hypobranchial	--	10	10	--	--	--	20
Epibranchial	--	--	13	--	--	--	13
Basioccipital	9	--	--	--	--	--	9
Hyomandibular	5	--	--	--	--	--	5
Totals	11099	686	573	8531	1506	>28996	>51379

*Thirty scales analyzed for taxa and age

**Excluding atlas, axis, and ultimate vertebrae.

***Identifications of herring include atlas and axis, otherwise only atlas.

The most abundant skeletal structure was the vertebra (14,853; includes axis/axis and ultimate vertebrae that were taxon specific). Some fish taxa have distinctive vertebrae that are diagnostic to species (e.g. herring, hake). Other vertebrae can be identified to genus (e.g. salmon, smelt) or family (e.g. pollock). The diagnostic properties of structures varied among taxa (Table 2.5). Many other fish hard parts were also present and potentially diagnostic of taxa. However, the huge effort to sort, enumerate, and catalogue the small number of elements recovered from the remaining structures would have contributed little to overall prey identification. Nevertheless, as techniques to identify fish hard parts improve, some of these additional structures may prove useful for prey identification. Table 2.6 is a summary of the different taxon-specific hard parts and the numbers of them recovered.

The most numerous hard part recovered was scales (>20,000). In a small sample, 23 of 30 scales (77%) were identified to species, genus, or family (Table 2.7). In addition age could be estimated from 12 of the scales (40%).

Table 2.7 Results of 30 scales analyzed.

Determination	Herring	Salmon	Gadid
Age	5	2	5
Species	6	3	0
Genus	-	6	0
Family	-	-	8

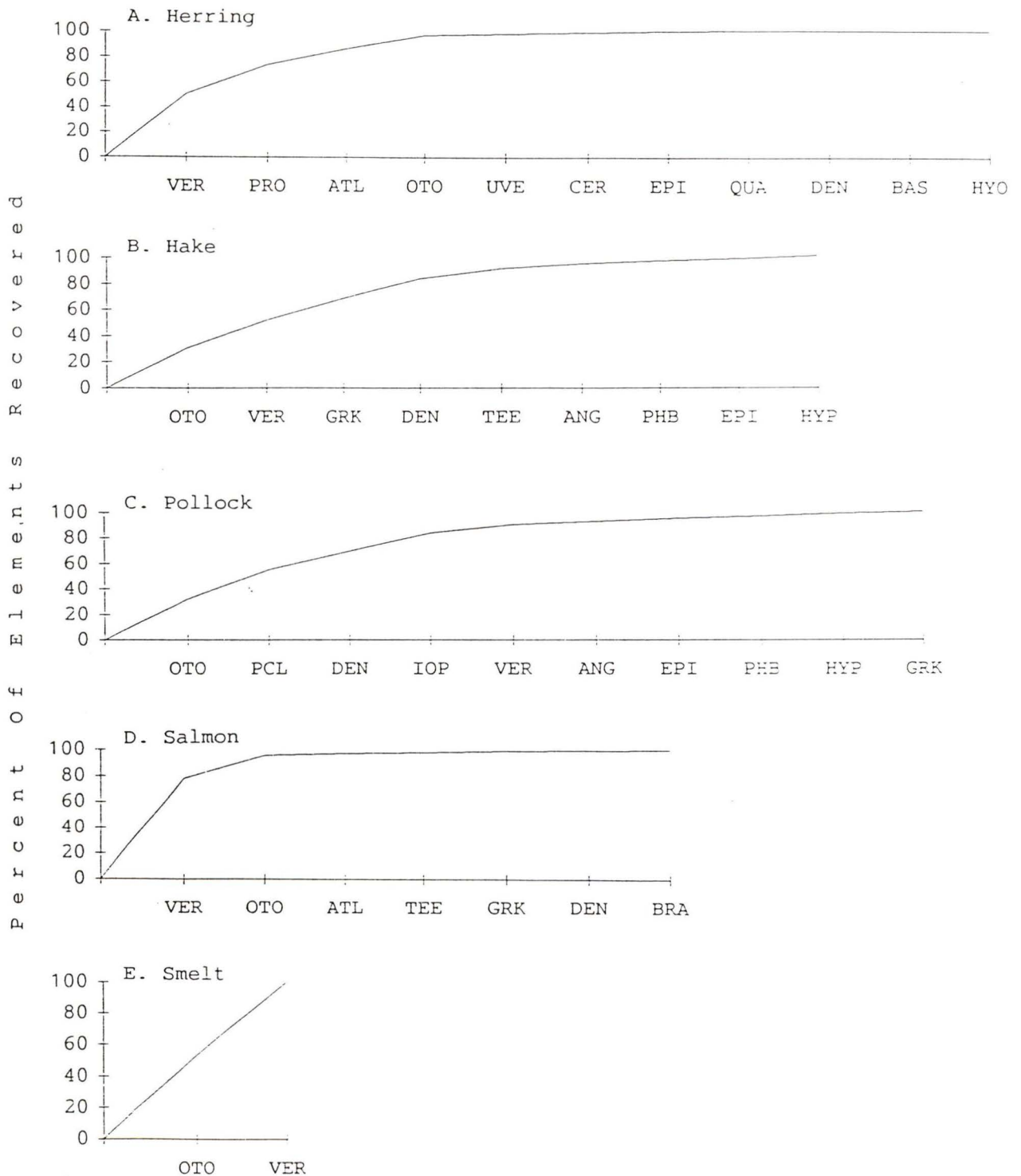
I found that 2-5 structures per fish taxa represented >90% of all elements recovered (Fig. 2.1). The average number of structures recovered per fish (excluding scales) varied among species from 0.98 to 4.28; numbers of elements varied from 1.08 to 7.27 (Table 2.8).

Table 2.8 Mean number of structures and elements recovered per fish (\pm S.D.) consumed.

Species	No. Fed	Structures/Fish	Elements/Fish
Herring	1978	3.49 \pm 0.93	5.61 \pm 1.63
Hake	145	4.28 \pm 0.65	4.73 \pm 2.16
Pollock	119	4.17 \pm 0.58	4.82 \pm 1.66
Salmon	1174	2.33 \pm 0.23	7.27 \pm 1.84
Smelt	1530	0.98 \pm 0.21	0.98 \pm 0.35

Numbers of eye lenses recovered was the best estimate of numbers of fish consumed. In all, 7,963 eye lenses were recovered representing 80.5% of the fish consumed. Unfortunately at present it is not possible to identify prey species from eye lenses.

Fig. 2.1 Cumulative percent of elements recovered by structure. Structures are ranked from highest to lowest incidence (left to right). In general 5 or fewer structures accounted for >90% of the elements recovered (VER=vertebrae, PRO=prootic/synotic, ATL=atlas/axis, OTO=otolith, UVE=ultimate vertebrae, CER=ceratohyal, EPI=epihyal, QUA=quadrate, DEN=dentary, BAS=basioccipital, HYO=hyomandibular, GRK=gill raker, TEE=teeth, PHB=pharyngobranchial, HYP=hypobranchial, PCL=postcleithrum, IOP=interopercle, and ANG=angular).



2.4 DISCUSSION

Feeding studies on captive seals are the only way to evaluate the accuracy of estimating pinniped diets from prey hard parts in scats. Only through captive studies can the biases associated with consumption, digestion, and passage of prey be understood, thereby permitting estimates of the composition and size of prey consumed (Prime and Hammond 1987; Dellinger and Trillmich 1988; Harvey 1989).

As shown here and in previous feeding studies, pinnipeds can completely digest otoliths of many fish species (Prime 1979; da Silva and Neilson 1985; Murie and Lavigne 1985; Dellinger and Trillmich 1988; Harvey 1989; Prime and Hammond 1990). The presence of hard parts in scats depends upon the pinniped species and the type and size of prey ingested. Using South American fur seals (*Arctocephalus australis*) and California sea lions held in dry enclosures, Dellinger and Trillmich (1988) recovered 49% and 34% of herring otoliths, respectively. However, even within a pinniped species, recovery rates of otoliths can vary widely. For example, da Silva and Neilson (1985) recovered only 4% of herring otoliths fed to one adult harbour seal, compared with 33% recovered from 6 seals by Harvey (1989), and 30% recovered from 4 seals in this study. Prime (1979) recovered 86% of the gadid otoliths fed to one

harbour seal, compared with 73% reported by Harvey (1989) and 74% (i.e. pollock and hake) in this study. For juvenile salmon, Harvey recovered 62%, while I recovered 65%.

Differences in recovery rates probably reflect several factors, including activity levels, enclosure characteristics, access to water (swimming), and feeding methods. High activity is associated with increased movement of digesta such that fish do not remain in the stomach and are not exposed to digestive acids as long as in inactive seals (Helm 1979; Dellinger and Trillmich 1988). In previous studies, otoliths were inserted into other prey (e.g. Prime 1979; Bigg and Fawcett 1985) or numerous heads were inserted into the abdominal cavity of one fish (Dellinger and Trillmich 1988). I employed similar methods to Harvey (1989) and had similar recovery rates of otoliths. His study animals (harbour seals) had continuous access to water and unlimited movement.

Fewer otoliths were recovered from harbour seals that were fed small (<30 cm in length) herring compared with larger ones (>30 cm) (da Silva and Neilson 1985). However, no previous captive studies have examined recovery rates of prey too large to be swallowed whole. Pinniped stomach remains and field observations indicate that when seals eat fish too large to be swallowed whole, only portions of the

fish's body are ingested, (Spalding 1964; Pitcher 1980b; Bigg et al. 1990) and the heads are often not consumed (Cottrell in prep.a). Furthermore, Bigg et al. (1990) and Olesiuk et al. (in prep.) observed that individual salmon were often torn apart and consumed by more than one seal. Future pinniped feeding studies need to examine hard part recovery rates of large prey to determine if tearing apart fish during consumption affects which hard parts are recovered, and also what effect multiple seals feeding on the same prey item have on prey structure recovery.

Vertebrae were the most numerous skeletal structure recovered during experiment trials (66% of all taxon specific structures, excluding scales), and were the most important structure for determining the presence or absence of herring, smelt, and salmon. The value of vertebrae in archaeological studies for identifying fish has long been recognized (Casteel 1976). However their value in mammal diet studies has not been examined in detail. Fish vertebrae recovered from otter (*Lutra lutra*) and mink (*Mustela vison*) scats provide reliable information on the presence of various fish prey as well as estimates of prey size (Wise 1980). Herring atlases and axes recovered during this study provided reliable length and weight estimates (Trites and Cottrell unpubl. data). In addition, atlases and axes provided estimates of the number of prey

consumed.

The abundance of scales in pinniped faeces, and their value for identification and age estimates, suggest great potential for pinniped diet studies. Bigg et al. (1990) collected scales from salmon kills by harbour seals and sea lions using a dipnet. They found scales provided accurate age and species identifications. My study is the first to examine the diagnostic distinctiveness of scales that have passed through the digestive tract. The small sample size examined suggests scales are useful in identifying some types of pinniped prey. Age-length and age-weight regression relationships from scale identifications may help to improve quantitative estimates for some prey species. Additional studies on the diagnostic properties and aging of fish scales that have passed through pinniped digestive tracts need to be done to confirm this work and examine other prey taxa.

Gill rakers, teeth, and other hard parts were important in confirming prey identifications based on otoliths, vertebrae and scales. These structures also are often present in scats without otoliths (Olesiuk et al. 1990b; see Chapter 2). I found that 2-5 structures per fish species represented greater than 90% of all elements recovered. This may allow researchers to concentrate identification

efforts for certain prey to specific structures. It must be noted that hard-part recovery rates of fish structures during this study are only representative of the prey size class and species used. The size and ontogeny of certain types of fishes are known to affect hard-part recovery (da Silva and Neilson 1985; Jobling 1987). For example, adult salmonids and gadids have better developed teeth and branchial structures than do juveniles (B. Wigen² pers. comm.). Therefore structures diagnostic to taxa on adult fish may not be morphologically distinct or developed in juvenile fish.

I found that the mean number of identifiable structures and associated elements varies among fish species. Fish that have low numbers of identifiable structures have a greater chance of not being detected in faecal remains. This bias becomes greater for large fish that are consumed in small numbers during a feeding bout. Further captive pinniped studies are needed to examine the potential extent of this bias among and within fish species.

Probably the main reason for skeletal elements rarely being used in prey identification is the misconception that fish hard parts cannot be used to identify prey. Other

² B. Wigen, Pacific Identifications, Victoria, B.C., pers. commun. 1992.

reasons include the time, effort, and money required to set up a reference fish bone collection and the years of training necessary to identify digested fish structures contained in scats. Fish hard-part identification keys are currently limited to a narrow range of species and structures (Fitch and Brownell 1968; Casteel 1976; Harkonen 1986; Cannon 1987; Hansel et al. 1988).

Accurately identifying the size and type of prey consumed by harbour seals is necessary for evaluating intra- and interspecific competition for food resources (Fiscus 1979; Lowry and Frost 1985; Gearin et al. 1988; Harwood and Croxall 1988; Bigg et al. 1990). Previous faecal studies estimating the quantitative composition of prey have relied on otolith identification (Prime and Hammond 1987; Pierce et al. 1991). However, using only otoliths or any other single prey hard part provides an incomplete understanding of diet. Seals tearing up large prey during consumption, multiple seals feeding on the same prey, and digestive processes all affect prey hard-part recovery. Using several prey structures will minimize the likelihood of failing to identify a prey type in scat remains and reduce the subjectivity in prey identifications.

3. HARBOUR SEAL DIET IN COWICHAN BAY ESTUARY AND ADJACENT
AREAS.

3.1 INTRODUCTION

The harbour seal, *Phoca vitulina*, is a widely distributed pinniped in the North Atlantic and Pacific Oceans. On the Pacific coast of North America, harbour seals inhabit inshore waters from the Gulf of California to Alaska. They are considered to be non-migratory, but often travel short distances in association with feeding, breeding, and moulting (Fisher 1952; Brown and Mate 1983; Thompson et al. 1989).

The harbour seal is an opportunistic predator throughout its range consuming solitary and schooling fishes of most species and sizes (Boulva and McLaren 1979; Harkonen 1987; Harkonen and Heide-Jorgensen 1991; Pierce et al. 1991). In the northeast Pacific, diet studies have been conducted in California (Shaffer 1989), Oregon (Fiscus 1980; Graybill 1981, Brown and Mate 1983; Roffe and Mate 1984; Harvey 1987), Washington (Scheffer and Slipp 1944), British Columbia (Fisher 1952; Spalding 1964; Bigg 1969; Bigg et al. 1990; Olesiuk 1993), and Alaska (Pitcher 1980a). Differences in methods of collecting (e.g. stomachs, faeces or visual observation), processing (e.g. sieves, elutriator), identifying (e.g. whole fish, otoliths, all prey hard parts) and analyzing (e.g. volume, index of relative importance, count, frequency of occurrence, split-

sample-index) seal prey make comparisons among studies difficult (Bigg and Perez 1985; Murie 1987; Bigg and Olesiuk 1990). However, regional differences in diet are obvious and appear to be related to local prey abundance.

In southeastern Alaska, British Columbia, Washington and Oregon, harbour seal populations have remained stable or have increased since the early 1970s (Jefferies 1986; Harvey 1987; Boveng 1988; Olesiuk et al. 1990a; Loughlin 1993). This has been due in part to amendments in the Canada Fisheries Act in 1970 and introduction of the U.S. Marine Mammal Protection Act in 1972 that protects harbour seals. Increases may also be attributed to but not limited to decreases in predators and increases in food fish.

Increased harbour seal numbers combined with the decline of some inshore commercial fisheries yields have created conflicts. Traditionally studies describing pinniped diet have been conducted in areas where commercially important species aggregate during spawning (Fisher 1952; Spalding 1964; Jameson and Kenyon 1977; Roffe 1981). Prespawning salmon and steelhead predation by pinnipeds in some estuaries have reduced returns by >45% (Gearin et al. 1988; Bigg et al. 1990).

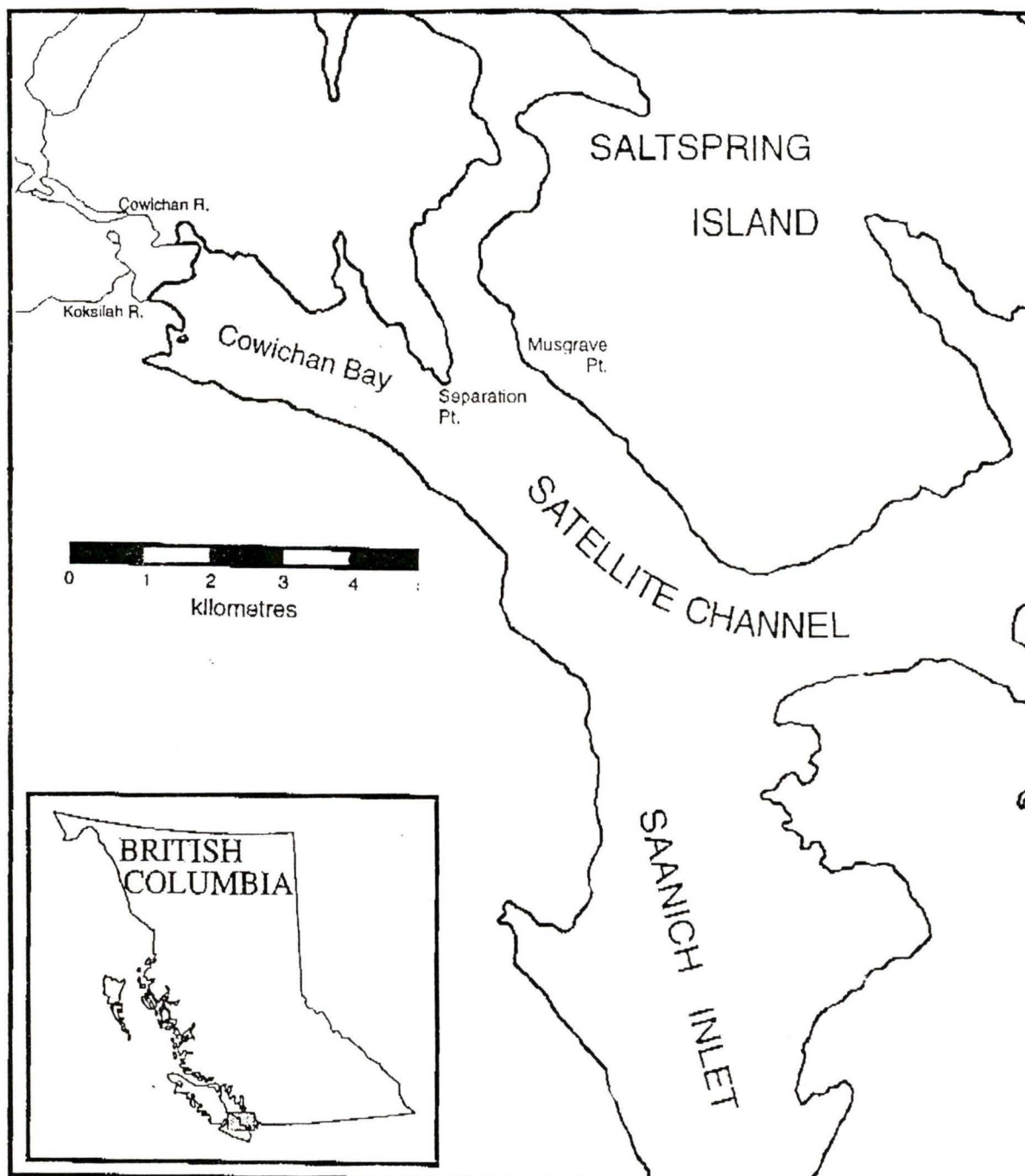
This study examines prey species consumed by harbour seals in the waters of Cowichan Bay and the factors affecting seasonal changes in diet. I examine the distribution, behaviour, and spawning patterns of prey species and discuss the ecological role these factors play in harbour seal foraging.

3.2 STUDY SITE

The Cowichan and Koksila rivers empty into the Cowichan Bay Estuary (48°45'N, 123°37'W). The estuary is approximately 1 km long and 1 km wide, dropping off to >10 meters at the seaward edge (Fig. 3.1). As with many medium to large estuaries along the coast of British Columbia, this estuary is used to store logbooms, on which harbour seals often haul-out. Seals defecate on the logbooms, and unlike intertidal haul-out sites, which are wave washed, faeces accumulate daily.

Harbour seals are found in the estuary year round whereas California (*Zalophus californianus*) and Steller (*Eumetopias jubatus*) sea lions are present from September to December but do not haul-out.

Fig. 3.1 Map of Cowichan Bay ($48^{\circ}45'N$, $123^{\circ}37'W$) and adjacent areas.



3.3 METHODS

3.3.1 Collection of Faecal Samples

Faecal samples were collected biweekly from logbooms from May 1991 to April 1992. Samples were collected from the same booms or new booms during successive sampling trips to ensure that only recently deposited scats were taken. Each sample was put in a labelled 600 ml polystyrene jar.

3.3.2 Processing of Faecal Samples

Scats were processed at the Pacific Biological Station (Nanaimo, B.C.) using an elutriator (Bigg and Olesiuk 1990). The elutriation process separated more dense particles (prey hard parts) from flocculent organic material. The prey hard parts were dried and stored until examination.

3.3.3 Identification of Prey

Prey remains were identified by comparing fish hard parts (e.g. teeth, gill rakers, scales, otoliths) with a reference collection at the University of Victoria, Department of Anthropology. Prey hard parts were identified to the lowest taxonomic level possible. All identifiable

structures³ were counted. Nomenclature for fish follows Hart (1973).

3.3.4 Analyses

The relative importance of each food type was calculated by two methods. The traditional frequency of occurrence diet estimation method was used to enable comparison with previous diet studies. The other method is the recently proposed split-sample frequency index (Olesiuk et al. 1990b). A correction factor for secondary prey was developed and incorporated into both diet estimation methods. "Secondary prey" refers to fish or invertebrate prey consumed by fish which in turn are consumed by seals.

Frequency of Occurrence (P_k)

The proportional frequency of occurrence of a prey type is the total number of scats containing that taxon divided by the total number of prey occurrences, for example the occurrence of salmon in five of ten scat samples that contain a total of twenty prey occurrences has a sample proportion of 0.25 salmon (i.e. 5/20) . This method estimates the proportion of the diet a particular food type

³ Hereafter "structure" refers to the type of hard part while "element" refers to specific occurrences (e.g. 20 teeth, are equivalent to 20 elements of the structure tooth).

represents, independent of the volume (or mass) and number of prey. This method assumes that all prey types are consumed in equal quantities regardless of the number of prey types present in a scat. The proportional occurrence of a prey type (P_K) in N faecal samples equals the number of occurrences of a prey type (P_{Ki}) divided by the sum of all prey occurrences (P_{KTi}).

$$[1] \quad P_K = \frac{\sum_{i=1}^N P_{Ki}}{\sum_{K=1}^n P_{KTi}}$$

$k=1, \dots, n$ (Where n is the number of different prey species)

Split-Sample Frequency Index (P_K^*)

Split-sample frequency of occurrence is a modified form of the frequency of occurrence method. This method accounts for the presence of more than one prey type per scat (see Olesiuk et al. 1990b). Where O is a binary variate that indicated whether the K prey species was absent or present in a faecal sample ($O=$ absent and $1=$ present):

$$[2] \quad P_K^* = \frac{\sum_{i=1}^N \frac{O_{Ki}}{\sum_{K=1}^n O_{Ki}}}{\sum_{K=1}^n P_{KTi}}$$

Secondary Prey

Prey eaten by fish prior to being consumed by seals are

a potential bias in pinniped diet studies (McConnell et al. 1984; Prime and Hammond 1987). I examined the number of hard parts of four herring structures (vertebra, prootic, synotic and otolith) in scat samples that contained only herring, herring and other prey, or herring and a potential predator (e.g. hake or salmon). A median test was used to test for differences in the number of herring elements recovered among the different situations. Herring is a major prey item of hake and salmon, representing >30% of their diet during certain months (Hart 1973; McFarlane and Beamish 1985; Healy 1991; Sandercock 1991; Tanasichuk et al. 1991).

Diversity of Prey

Harbour seal diet diversity was estimated by the Shannon-Weaver index (Zar 1984). Prey families that represented >3% of the annual diet totalled five categories, with the remaining families and unknowns pooled for sixth and seventh categories, respectively. Diet diversity, D was plotted monthly to examine seasonal variation. Here, k is the number of categories and P_i is the proportion of observations found in category i .

$$[3] \quad D = - \sum_{i=1}^K P_i \log P_i$$

3.4 RESULTS

3.4.1 Recovery of Fish Hard Parts

A total of 313 scats was analyzed for prey hard parts; all but five (1.6%) contained identifiable prey remains. Faecal samples were collected in all months (\bar{x} =26 per month, range 16-39). Faeces without prey hard parts were excluded from further analysis. Such scats were small in volume (\bar{x} =15 ml versus 74 ml overall), suggesting that they represented only portions of original scats.

Prey remains exhibited different levels of erosion; some structures were too eroded to permit identification. The number of taxon specific structures and elements recovered per scat ranged from 1-11 (\bar{x} =5.3) and 2-713 (\bar{x} =65), respectively. The type, number, and diagnostic characteristics of structures recovered varied among fish taxa (Table 3.1).

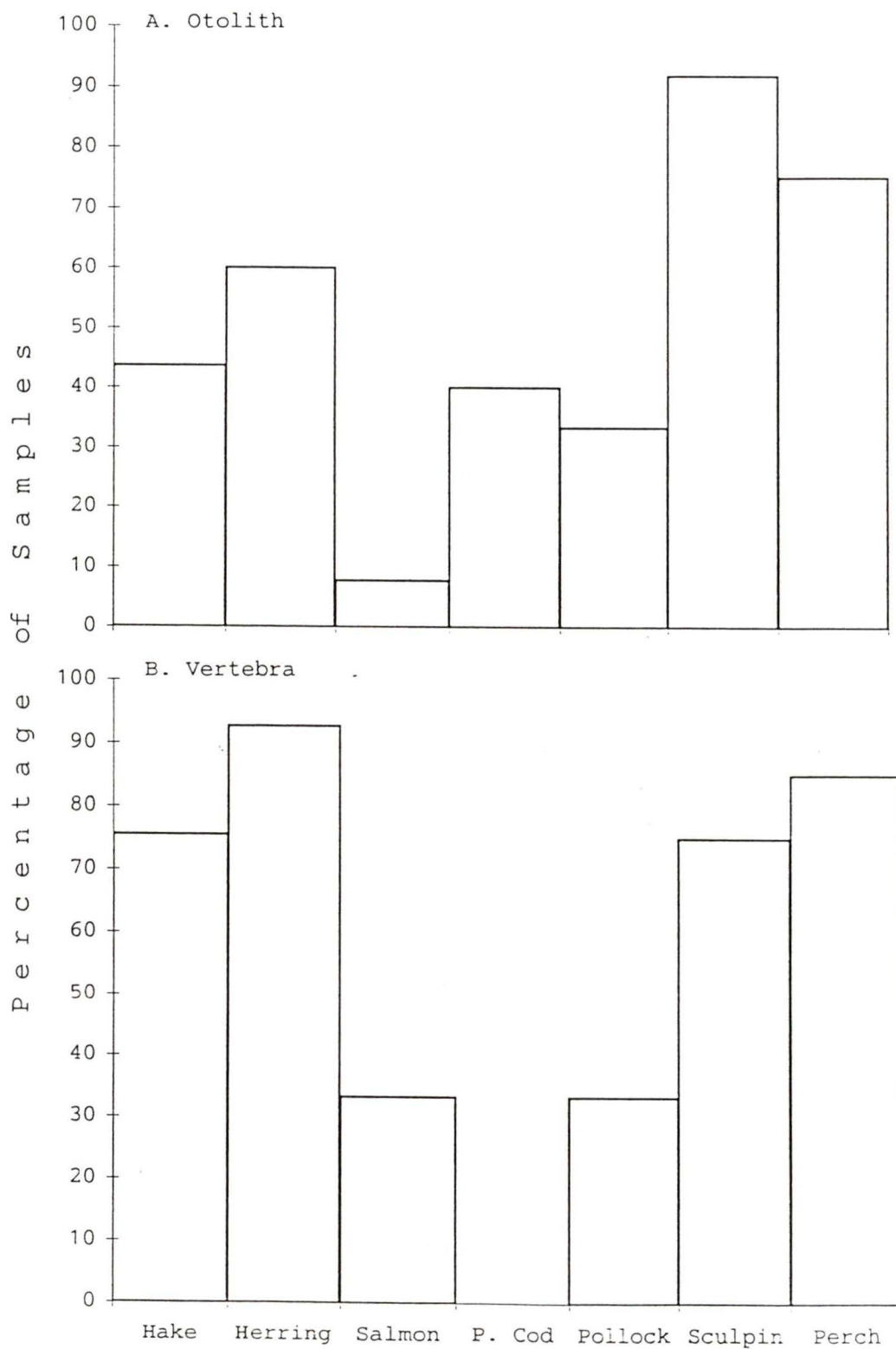
3.4.2 Otoliths Versus Other Prey Hard Parts

Fifty-five percent of all prey occurrences were identified from structures other than otoliths. Otoliths were present in 45% of all prey identifications and vertebrae were present in 68%. The occurrence of otoliths and vertebrae in scat samples varied across taxa (Fig. 3.2).

Table 3.1 The relative importance (in percent) of the numbers of identifiable structures recovered from prey taxa that represented >3% of the harbour seal diet (N=number of hard parts).

Taxon	Structure	Percent	Taxon	Structure	Percent	
Pacific Hake (N=3035)	Vertebra	68	Salmon (N=5921)	Vertebra	35	
	Gillraker	13		Tooth	31	
	Tooth	7		Gillraker	31	
	Otolith	6		Pharyngobranch.	2	
	Angular	3		Otolith	1	
	Pharyngobranch.	1		Atlas	<1	
	Epihyal	<1				
	Hypobranchial	<1				
Pacific Cod (N=162)	Vertebra	70	Shiner Perch (N=2167)	Vertebra	43	
		Angular		10	Otolith	33
		Otolith		10	Inferior pharyn. plate	9
		Gillraker		8	Superior pharyn. plate	8
		Hypohyal		<1	Tooth	3
		Hypobranchial		<1	Vomer	2
		Pharyngobranch.		<1	Inferior pharyn.	<1
					Premaxilla	<1
Walleye Pollock (N=140)	Vertebra	45	Sculpin (N=1189)	Vertebra	39	
		Dentary		16	Otolith	30
		Postcleithrum		11	Preopercle	12
		Otolith		9	Quadrate	4
		Interopercle		7	Basioccipital	3
		Angular		6	Premaxilla	3
		Gillraker		3	Superior pharyn. plate	2
		Hypobranchial		1	Inferior pharyn. plate	2
Pharyngobranch.	<1	Vomer	2			
Epihyal	<1	Post-temporal	<1			
Herring (N=11,456)	Vertebra	55		Pharyngobranch.	<1	
		Prootic/Synotic		24		
		Atlas/Axis		11		
		Otolith		7		
		Ultimate Vert.		1		
		Ceratohyal		<1		
		Epihyal		<1		
		Quadrate		<1		
		Dentary		<1		
		Basioccipital		<1		
		Hyomandibular		<1		

Fig. 3.2 Percentage of scats that contained otoliths or vertebrae for various prey taxa.



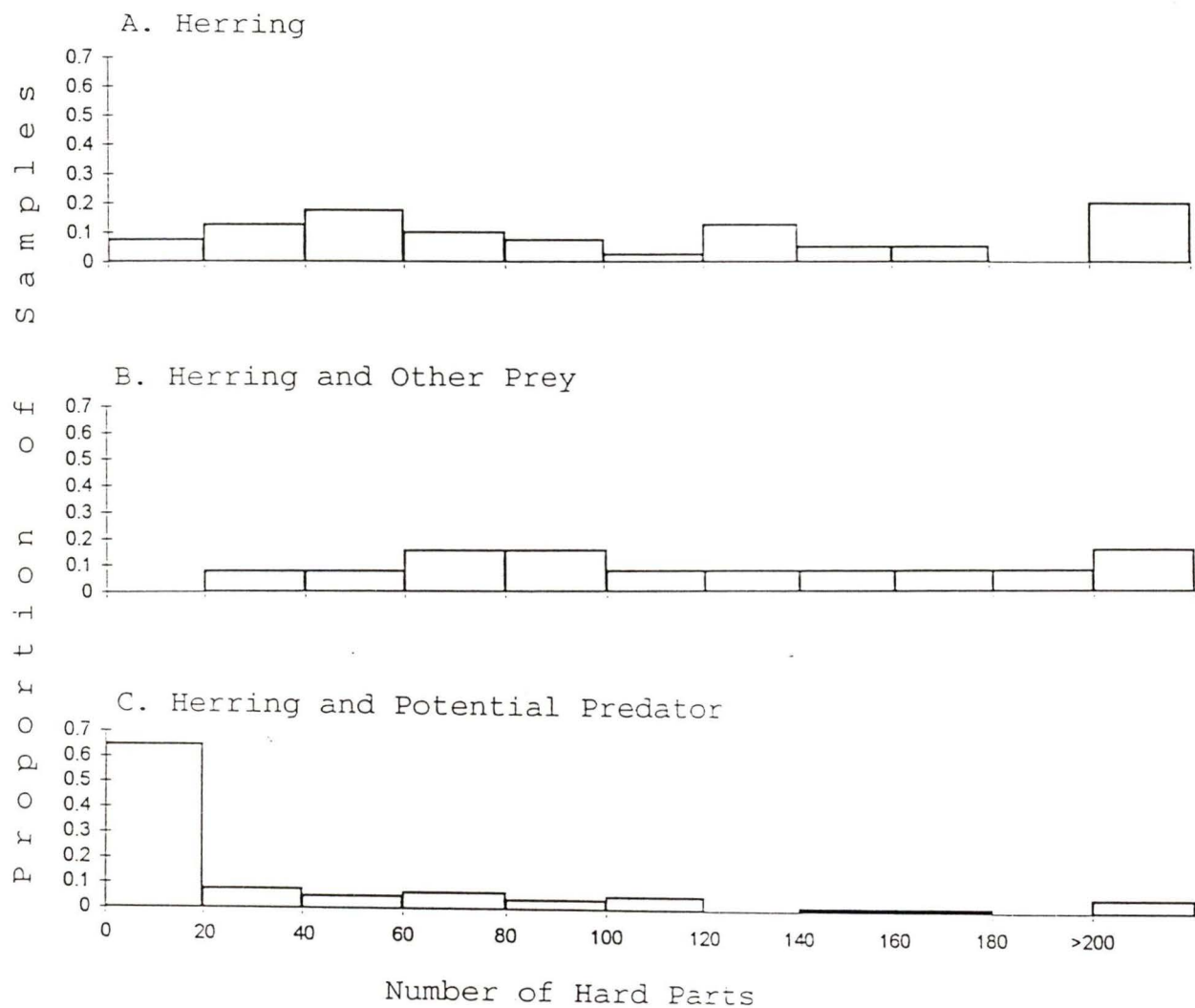
3.4.3 Secondary Prey

The number of herring hard parts recovered per scat was significantly greater for scats containing only herring [$X^2=16.4$, $P<.01$] or herring and other prey [$X^2=13.0$, $P<.01$], than for scats containing herring and a potential predator (Table 3.2). There was no difference in recovery of herring hard parts between samples with just herring and herring plus other prey [$X^2=3.71$, $P>.01$]. Figure 3.3 shows the distribution of prey hard parts in samples that have potential fish predators of herring. Herring were considered to be secondary prey in faecal samples that contained <5 herring elements and a herring predator. Captive studies indicated that 5.61 elements per herring consumed are identifiable in faecal remains (see Chapter 1). Therefore, samples that contained the remains of <1 herring (5 herring elements) when a potential predator was present were considered to be secondary prey. A total of 94 scats contained potential secondary prey; of these, 30 (31.9%) contained herring as secondary prey. Hake or salmon were judged to have consumed herring in 27 and 3 samples, respectively.

Table 3.2 The recovery rate of herring hard parts from scats when herring was present alone, with other prey, or with a potential predator. The volume of organic material from each faecal sample collected was measured to ± 5 ml.

Herring Present With:	No. Scats	Herring			
		Structures Per Scat	Elements Per Scat	Structures/ml	Elements/ml
Nothing	59	4.23	101	0.08	1.99
Other Prey	13	4.58	150	0.08	2.73
Potential Predator	94	2.61	36	0.04	0.53

Fig. 3.3 Number of herring hard parts in faecal samples when (A) herring was present alone, (B) with other prey, or (C) with a potential fish predator.



3.4.4 Diet Composition

The 308 faecal samples contained 471 prey occurrences (\bar{x} =1.5 per scat). Nineteen species in 16 families were identified (Table 3.3). Teleost fishes represented 93% of prey species identified. A total of 406 (86%) bony fish identifications were to species. Six families accounted for >97% of bony fishes identified, including Gadidae 160 (36.5%), Clupeidae 137 (31.3%), Salmonidae 78 (17.8%), Embiotocidae 28 (6.4%), Cottidae 20 (4.6%) and Batrachoididae 5 (1.1%). Each of the remaining five families represented <1% of the diet.

Cephalopods, the second most prevalent category, occurred in 14 (3%) of the samples. Each cephalopod occurrence was associated with at least one other prey type, suggesting that cephalopods were probably consumed opportunistically while feeding on other prey types. Furthermore cephalopods, when eaten, were consumed in low numbers \bar{x} =1.5 (range 1-5).

The third prey category, cartilaginous fish, occurred in <1% (4) of the samples. Interestingly, I found two incidences of spiny dogfish (*Squalus acanthias*), the first record of harbour seals consuming dogfish. Both occurrences were small fish. One rat fish (*Hydrolagus colliei*) and skate (Rajidae) were also identified.

Table 3.3 Prey identified from 308 harbour seal scats collected in Cowichan Bay, with incidence statistics (FO= frequency of occurrence; SSI= split sample index).

Taxon (N)	FO	FO*	SSI	SSI*
Osteichthyes (438)				
Gadidae (160)	31.9	34.0	30.8	34.5
<i>Merluccius productus</i> (107)				
<i>Gadus macrocephalus</i> (28)				
<i>Theragra chalcogramma</i> (22)				
<i>Microgadus proximus</i> (3)				
Clupeidae (137)	33.3	29.1	37.0	31.3
<i>Clupea harengus</i> (137)				
Salmonidae (78)	15.6	16.6	19.3	19.7
<i>Oncorhynchus</i> spp. (78)				
Embiotocidae (28)	5.6	5.7	4.4	4.4
<i>Cymatogaster aggregata</i> (20)				
<i>Rhacochilus vacca</i> (2)				
Cottidae (20)	4.0	4.2	3.1	3.1
<i>Leptocottus armatus</i> (12)				
<i>Enophrys bison</i> (2)				
Batrachoididae (5)	1.0	1.1	1.2	1.2
<i>Porichthys notatus</i> (5)				
Pleuronectidae (4)	<1.0	<1.0	<1.0	<1.0
<i>Microstomus pacificus</i> (1)				
<i>Platichthys stellatus</i> (1)				
Ammodytidae (2)	<1.0	<1.0	<1.0	<1.0
<i>Ammodytes hexapterus</i> (2)				
Scorpaenidae (2)	<1.0	<1.0	<1.0	<1.0
Hexagrammidae (1)	<1.0	<1.0	<1.0	<1.0
<i>Ophiodon elongatus</i> (1)				
Stichaeidae (1)	<1.0	<1.0	<1.0	<1.0
<i>Lumpenus sagitta</i> (1)				
Chondrichthyes 4				
Squalidae (2)	<1.0	<1.0	<1.0	<1.0
<i>Squalus acanthias</i> (2)				
Chimaeridae (1)	<1.0	<1.0	<1.0	<1.0
<i>Hydrolagus colliei</i> (1)				
Rajidae (1)	<1.0	<1.0	<1.0	<1.0
Agnatha 1				
Petromyzonidae (1)	<1.0	<1.0	<1.0	<1.0
<i>Lampetra tridentatus</i> (1)				
Cephalopoda 14				
Loliginidae (14)	2.8	3.0	1.6	1.7
<i>Loligo opalacens</i> (8)				
Other Invertebrates 3	<1.0	<1.0	<1.0	<1.0
Unidentified 11	2.2	2.3	1.5	1.7

* Corrected for secondary prey.

The fourth prey category, other invertebrates, included shrimp, crab, and one unidentified form. These prey were assumed to have been consumed incidentally. Each prey occurred only once and were represented by only one animal. There were also four occurrences of polychaetes, identified from mouth parts. Each occurrence was associated with shiner perch (*Cymatogaster aggregata*). Shiner perch are known to feed extensively on polychaete worms (J. Marliave⁴, pers. comm.). Polychaete were thus considered to be secondary prey and were not included in dietary estimates. Unidentified fish (i.e. hard parts that could not have come from any of the species identified in a sample) represented 11 (2.2%) of the total occurrences.

3.4.5 Seasonal Variation in Diet

The relative importance of each prey taxon varied throughout the study period. Prey diversity was greatest during September and October (Fig. 3.4). During May and June a combination of herring and gadids were the primary prey, whereas in July and August the primary prey was gadid. In September and October a high diversity of prey types, contributed <25% to the total diet (Figs. 3.5a-h). During November and December salmon were the primary dietary component. The diet from January to April was mainly herring.

⁴ J. Marliave, Vancouver Public Aquarium, Vancouver, B.C., pers. commun. 1994.

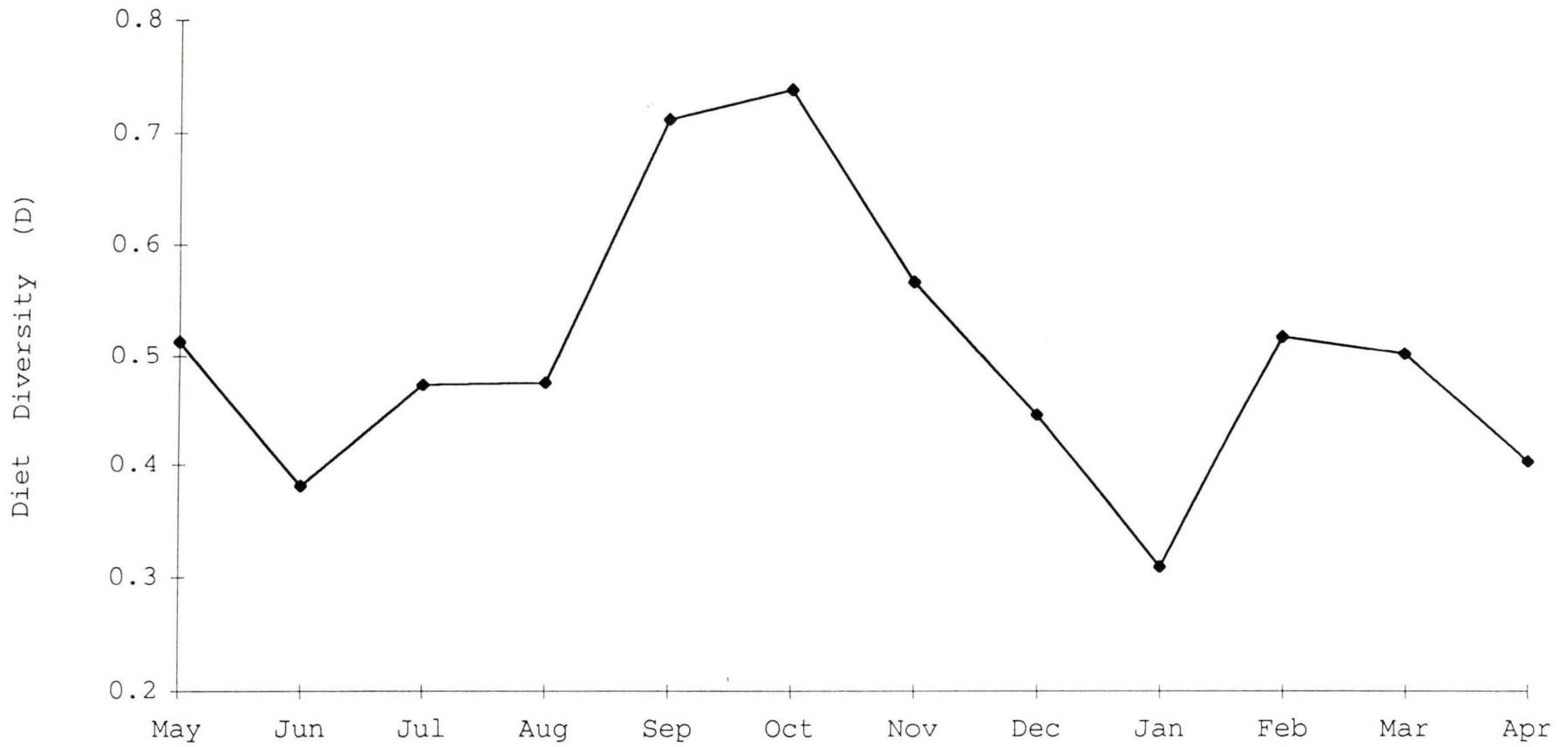


Fig. 3.4 Seasonal trends in diet diversity (D), as estimated by the Shannon-Weaver index.

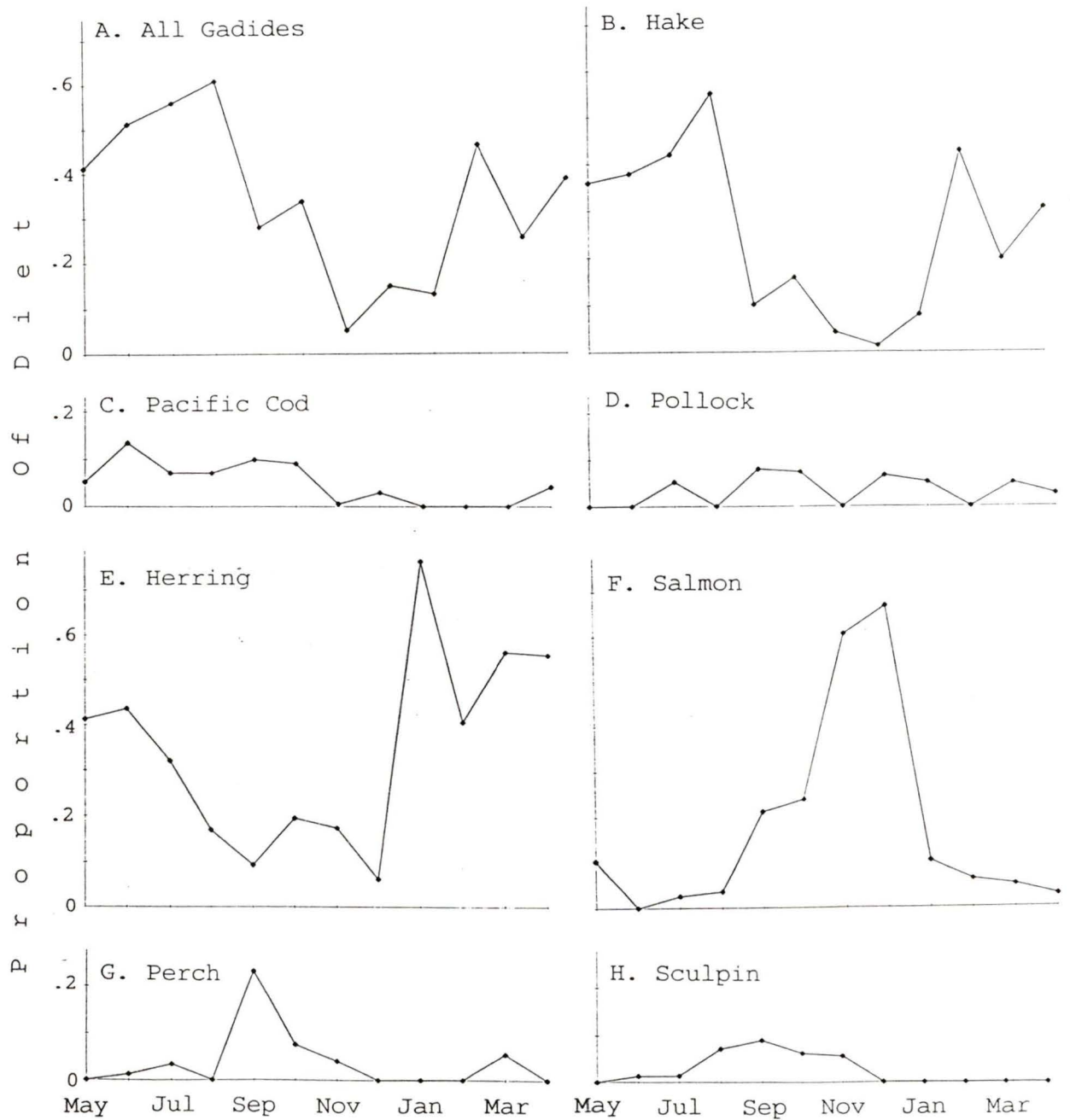
Gadidae

Gadids made up most of the diet and were consumed year round (Fig. 3.5a). A total of 83% of the occurrences were identified to species. The remaining 17% were identified as either gadids or gadids but not hake (GNH). These occurrences were apportioned to the identified species based on level of identification (e.g. GNH were divided among Pacific cod, pollock, and tom cod) according to the proportion of diet each species represented. The proportion of hake in the diet varied seasonally: May to August and February to April 20-43% (\bar{x} =31%); and September to January 1-16% (\bar{x} =8%) (Fig. 3.5b). The occurrence of Pacific cod also varied throughout the study period, representing >5% from May to October, and <1% from November to March (Fig. 3.5c). The proportion of pollock in the diet was distributed evenly throughout the year (Fig. 3.5d).

Clupeidae

All clupeids were identified as herring. It showed strong seasonal variation, representing >40% of the diet during May and June, and decreasing over the summer to a low of 9% in September. Herring represented <20% of the diet from October to December with a sharp increase to 76% in January (Fig. 3.5e).

Fig. 3.5 Seasonal trend in the diet of harbour seals at Cowichan Bay (prey species that represented >3% of total diet).



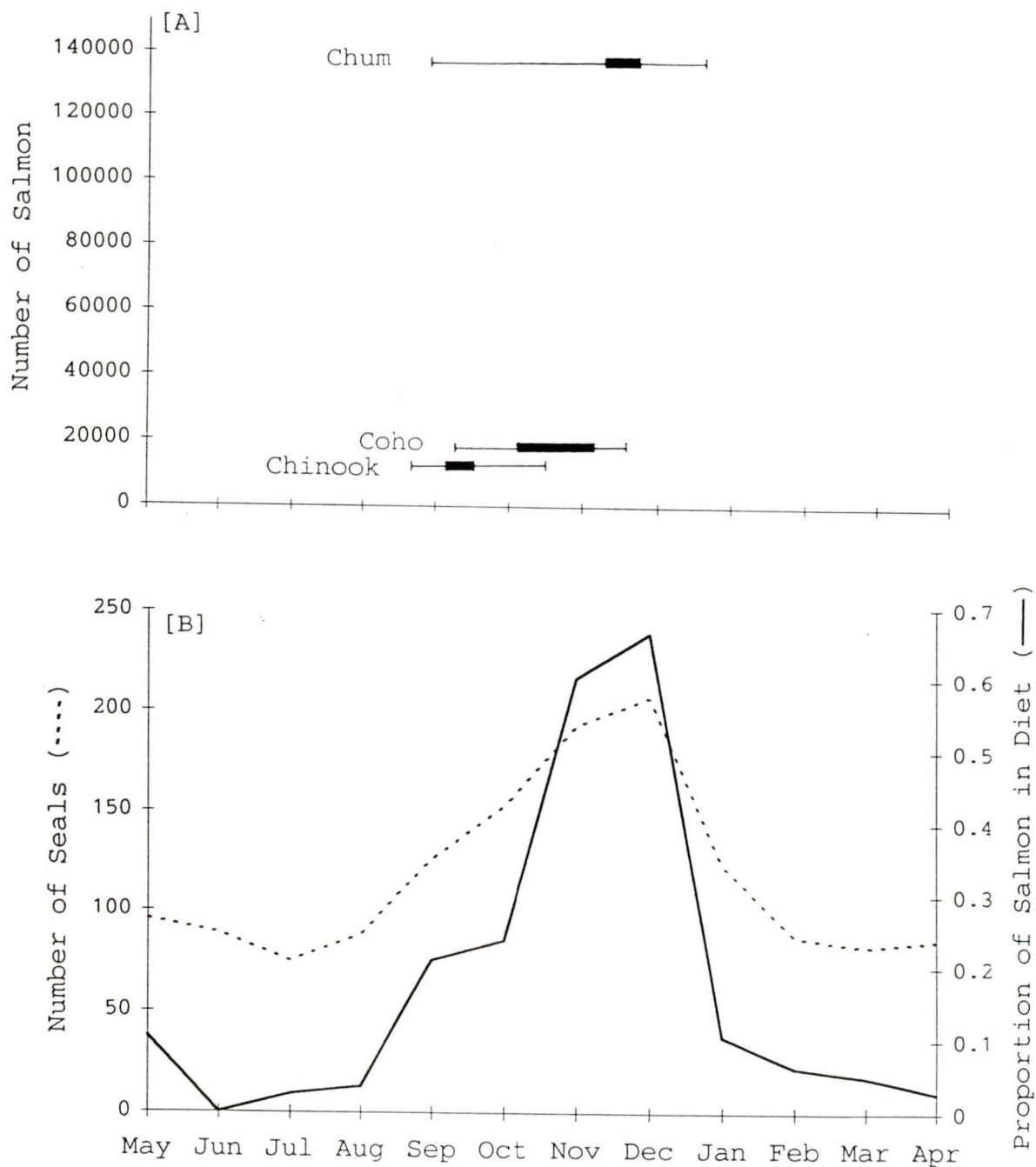
Salmonidae

Salmonids occurred 78 times (19.7% of total diet); unfortunately salmon could only be identified to genus. The seasonal increase in salmon abundance due to movement into the area to migrate up the Cowichan and Koksila rivers to spawn was reflected in the high proportion of salmon in the diet (Fig. 3.5f). Cowichan Bay prespawning salmon arrival time and total numbers differ among species (B. Hurst⁵ pers. comm.). Figure 3.6 illustrates the peak in proportion of salmon in the diet during November and December, coinciding with the greatest number of salmon returning. Chum salmon (*Oncorhynchus keta*) represents the greatest number of salmon in the estuary at this time, which is at the end of the coho (*Oncorhynchus kisutch*) run. Interestingly, salmon in the May diet coincides with salmon smolts released from the Cowichan River Hatchery. Size estimates of these salmon occurrences (\bar{x} =10 g, based on vertebra width measurements) are within the size range of smolts released from the hatchery (D. Mallard⁶ pers. comm.).

⁵ B. Hurst, Pacific Biological Station (South Coast), Nanaimo, B.C., pers. commun. 1994.

⁶ D. Mallard, Cowichan River Hatchery, Cowichan, B.C., pers. commun. 1994.

Fig. 3.6 The estimated arrival time and number of salmon returning to the Cowichan River [A] (thick horizontal lines indicate main spawning times, thin horizontal lines indicate typical seasonal range); and seasonal trends in harbour seal abundance and proportion of salmon in diet [B].



Embiotocidae

Shiner perch represented >70% of all perch. Perch represented >20% of the diet during September but decreased to 0% in December to February (Fig. 3.5g). They increased to 6% of the diet in March, which coincides with annual perch parturition (Hart 1973). Very little is known about perch distribution and movement patterns.

Cottidae

Sculpins were consumed seasonally, occurring in the diet from June to November (June to July <1%; August to November >10%) (Fig. 3.5h). Staghorn sculpin (*Leptocottus armatus*) represented 86% of sculpins identified. Predation was confined almost exclusively to August to November, coinciding with movement of staghorn sculpins into shallow estuarine habitat for spawning (Jones 1962).

3.5 DISCUSSION

3.5.1 Recovery of Fish Hard Parts

Hard parts of prey recovered from pinniped faecal remains have many biases affecting identification and estimation of diet (Hawes 1983; da Silva and Neilson 1985; Jobling and Breiby 1986; Jobling 1987; Dellinger and Trillmich 1988; Harvey 1989; Harvey and Antonelis 1994). Morphological distinctiveness, diagnostic properties, and susceptibility to digestion of hard parts vary among fish taxa, resulting in different rates of recovery and identifiability among species. Recovery of fish hard parts also varies according to fish size and ontogeny (da Silva and Neilson 1985; Jobling 1987; Cottrell in prep.a). Structures from small prey tend to be totally digested while those of large prey may be uneaten (e.g. heads) or damaged during ingestion and digestion (Spalding 1964; Boulva and McLaren 1979; Cottrell in prep.a; see Chapter 1). Analysis of faecal material provides no information on sex, age, or physical condition of the individual pinniped, yet such factors also may affect digestion rate of prey hard parts.

The biases mentioned above appear to make absolute quantitative estimates of pinniped diet from faecal samples unfeasible, given current methods of identification and

understanding of digestive processes. However, this study found, that improved estimates of the number and occurrence of fish consumed were achieved by considering all taxon specific hard parts (Chapter 1). Furthermore, captive feeding studies may determine other prey hard parts useful in detecting and estimating prey number and size. During this study qualitative estimates of harbour seal dietary composition using percent frequency of occurrence and split-sample frequency index were considered to be the most suitable methods to represent dietary information obtained from faeces. Numerous other pinniped faecal studies have examined diet using one of these methods or slightly modified versions (e.g. Pitcher 1980a; Green et al. 1990; Pierce et al. 1990; Olesiuk 1993).

3.5.2 Secondary Prey

Secondary prey were a strong bias, and caused herring to be over-represented in diet estimates. Herring is an important prey item of hake and salmon in British Columbian waters year round, representing up to 30% of the diet in certain months (McFarlane and Beamish 1985; Healy 1991; Sandercock 1991; Ware and McFarlane in press). In faecal samples containing potential secondary prey, the predator (hake or salmon) had a greater proportion of hard parts present in most samples. Olesiuk et al. (1990b) found that

most harbour seal scats containing herring and hake had a greater number of hake hard parts. Likewise Prime and Hammond (1987) found Grey seal (*Halichoerus grypus*) scats contained few sandeel (*Ammodytes* spp.) hard parts when gadids were present. They speculated that gadids had eaten sandeels when few sandeel hard parts were present in scats containing gadid structures. When sandeels are consumed by Grey seals they are consumed in large numbers and are represented by numerous elements in scat remains (Prime and Hammond 1987).

Samples containing only herring had large numbers of hard parts. However, samples containing herring and other prey, or herring and a potential predator, also often contained large numbers of herring hard parts, suggesting that herring can not be assumed to be secondary prey just because they were present with a fish predator. More samples contained fewer herring hard parts when present with a predator, suggesting that harbour seals often consume fish that have consumed herring. Based on this observation, scat samples should be analyzed on an individual basis to determine if secondary prey are present.

Cottrell (in prep.b) fed herring to coho salmon 4 h before the salmon were fed to harbour seals. The harbour seal faeces contained identifiable herring hard parts among

salmon remains. The biases of secondary prey need to be examined in other pinniped species. The extent of secondary prey occurrences in other fish predator-prey relationships also needs to be examined in future pinniped diet studies.

3.5.3 Diet Composition

Harbour seals are considered to be opportunistic foragers feeding on seasonally abundant, schooling, and inshore prey (Bigg 1981). Harbour seal diet varies according to season and region (Pierce et al. 1990; Harkonen and Heide-Jorgensen 1991; Pierce et al. 1991; Olesiuk 1993). It is often difficult to distinguish seasonal changes from regional differences. Intense dietary studies carried out over long periods in several regions, and with large sample sizes at each collection period, are necessary. In previous studies of harbour seal diet, faecal samples often were collected in different years and were pooled to increase sample size or samples were collected for only part of a year (Harkonen and Heide-Jorgensen 1991; Pierce et al. 1991; Olesiuk 1993). Prey abundance and distribution often vary annually, so data pooling either over years or within years will not show distinct seasonal diet variation. In this study, consistent numbers of faecal samples were collected weekly for an entire year at one location. Thus I was able to examine the marked seasonal variation of diet in

association with annual prey abundance and distribution changes. Distribution patterns and foraging areas were also established from 19 radio-tagged animals (see Chapter 3).

Changes in the relative importance of gadids, herring, salmon, and sculpins were examined in light of known patterns of fish movements in the waters surrounding Cowichan Bay. These prey groups represented >85% of identified occurrences. Unfortunately, prey species that are not of commercial importance have been studied infrequently, so little information is available on their distribution or seasonal abundance.

Hake are the most abundant resident fish in the Strait of Georgia (Shaw et al. 1990). Saanich Inlet (8 km south of the study area) contains a year-round population of hake and pollock (S. McFarland⁷ pers. comm.). Trawls conducted in Saanich Inlet indicate that juvenile and adult hake (3-12 y old) inhabit depths from 50-300 m (S. McFarland unpubl. data). Radio-tagged harbour seals were observed swimming or hauled out in Saanich Inlet on 65 occasions (>80% of all resightings outside study area; see Chapter 3). Hake, although present year round show seasonal changes in distribution. During spawning, from March to May, hake

⁷ S. McFarland, Pacific Biological Station, Nanaimo, B.C., pers. commun. 1994.

stratify by depth in two distinct midwater layers; a shallow layer of discrete schools between 50-120 m, and a deeper layer representing the main body of fish between 150-320 m (Cass et al. 1977; Thompson and McFarlane 1982). Post-spawning fish aggregate in shallow water (50-100 m) and are found in association with a dense plankton layer. By the fall hake appear to disperse (McFarlane and Beamish 1985). The proportion of hake in the harbour seal diet is greatest from February to August coinciding with when hake occur in dense schools. The proportion of hake in harbour seal diet drops precipitously in September when schools disperse, suggesting that harbour seals are more successful at finding or foraging on schooling hake. Alternatively, increases in the abundance of other species (e.g. salmon) may be preferred as prey at this time. However, prey diversity was greatest during September and October, suggesting that no single prey species in this area was available in large numbers. Interestingly trawls recovered a ratio of 6:1 and 8:1 of hake to pollock in Georgia Strait (Shaw et al. 1990), a similar ratio (6:1) was found in the harbour seal diet.

There are two separate groups of herring in Georgia Strait. One of them travels to the west coast of Vancouver Island when 1-3 y old, returning to Georgia Strait to spawn. This group makes up most of herring biomass. The second population of herring spawns and resides in Georgia Strait

year round (D. Hay⁸ pers. comm.). Juvenile (<1 y old) and yearling herring (<2 y old) of both groups appear to spend most of their time in Georgia Strait (D. Hay pers. comm.). The sharp peak in occurrence of herring in the January diet coincides with the movement of prespawning herring into Georgia Strait from the west coast of Vancouver Island. Herring were consumed in all months; however, from May to August and January to April herring was particularly prevalent (>40%).

Salmon occur throughout Georgia Strait and along the west coast of Vancouver Island year round. During the late summer, prespawning salmon begin to migrate to the mouth of natal streams (Hart 1973). In Cowichan Bay, salmon begin arriving in September, with peak abundance occurring in late November. Salmon occurred in the diet almost exclusively from September to December. Most salmon in the diet (>75%) was consumed in November and early December, coinciding with the peak number of salmon arriving into the estuary. Previous studies have also described harbour seal predation of prespawning salmon in estuaries and the lower reaches of rivers (Fisher 1952; Spalding 1964; Roffe and Mate 1984; Olesiuk et al. 1990b). Bigg et al. (1990) found that harbour seal salmon kills per hour increased as the

⁸ D. Hay, Pacific Biological Station, Nanaimo, B.C., pers. commun. 1994.

number of prespawning salmon increased (salmon identified visually and from scales retrieved during fish kills).

Sculpins were consumed seasonally, coinciding with movements of sculpins from deep water (>30 m) into shallow estuarine water for breeding and spawning (Jones 1962). Staghorn sculpins move into the upper reaches of estuaries in late May and peak in September. They remain in shallow water until early December (Jones 1962). The increased vulnerability of sculpins to seal predation while in shallow water may be a combination of easier detection and the increased amount of time the seals are able to spend pursuing and locating prey. Alternatively, behavioural changes of sculpins defending nests or aggregating during spawning and breeding may increase their vulnerability to predation. Olesiuk et al. (1990b) found that the occurrence of lingcod (*Ophiodon elongatus*) in the harbour seal diet occurred almost exclusively from November to April, when males were defending nests.

Movement of radio-tagged harbour seals in Cowichan Bay and surrounding areas suggest that most seals do not move great distances to follow migrating prey (see Chapter 3). Colbourne and Terhune (1991) found that harbour seals did not follow herring movements in the Bay of Fundy. However, in Cowichan Bay harbour seal numbers increased by >200%

during November and December, which coincided with salmon moving into the estuary (see Chapter 3), which suggests that harbour seals move short distances to exploit locally abundant seasonal prey. For example, one seal swam >50 km to the Fraser River in late April, which coincided with the aggregation of spawning eulachon (*Thaleichthys pacificus*) there (Hart 1973). California sea lions also aggregate off the mouth of the Fraser River at this time (P. Olesiuk⁹ pers. comm.).

My study complements previous work describing harbour seals as opportunistic foragers utilizing demersal, pelagic, schooling and solitary inshore prey species (Fisher 1952; Spalding 1964; Pierce et al. 1990; Harkonen and Heide-Jorgensen 1991; Pierce et al. 1991; Olesiuk 1993). However, I also found that prey which is abundant year round (e.g. hake) may vary seasonally in the diet. Fluctuations in diet may be due to distributional changes in prey, such as dispersal of dense schools or movement into deep water, making fish more difficult to locate or capture. Alternatively this may be due to the movement of other prey types into the area. More work is needed on the diet selectivity and foraging techniques of harbour seals, and on fish abundance estimates and distribution patterns, to

⁹ P. Olesiuk, Pacific Biological Station, Nanaimo, B.C., pers. commun. 1994.

better understand harbour seal foraging strategy.

4. HARBOUR SEAL DISTRIBUTION, ABUNDANCE, AND ACTIVITY
BUDGETS IN COWICHAN BAY AND ADJACENT AREAS.

4.1 INTRODUCTION

All pinnipeds rest, breed, give birth, or suckle their young on land or ice. The terrestrial component of pinniped life cycles differs in its frequency and duration both spatially and temporally among and within species. Animal age, sex, breeding system, type and time of moulting, and sleeping patterns affect haul-out cycles (Ridgway et al. 1975; Boulva and McLaren 1979; Bonner 1981; Schneider and Payne 1983; Stewart 1984; Thompson 1989). Extrinsic variables such as location of feeding areas, incidence of terrestrial and aquatic predators, and weather also influence haul-out patterns (Boulva and McLaren 1979; Brown and Mate 1983; Thompson D. et al. 1991; Thompson P. et al. 1991; Watts 1991). The synergistic effect of variables on pinniped haul-out behaviour, combined with environmental and density-dependent factors that affect the availability of haul-out sites, make the prediction of diel and seasonal patterns difficult.

Some species are almost entirely pelagic coming ashore only to reproduce or moult. Examples are the northern fur seal (*Callorhinus ursinus*), harp seal (*Phoca groenlandica*) and northern elephant seal (*Mirounga angustirostris*). Other species haul-out throughout the year: Steller sea lions (*Eumetopias jubatus*), grey seals (*Halichoerus grypus*) and

harbour seals (*Phoca vitulina*) are examples.

Harbour seals haul-out on natural and human-altered substrate including sand bars, reefs, pebble beaches, mud flats, jetties, floating ice, piers and logbooms (Sullivan 1980; Bigg 1981; Pitcher 1984; Yochem et al. 1987; Hoover 1988). The seasonal and diel availability of haul-outs differ among substrate. Tidal influences are greatest on gently sloping substrate. Intertidal haul-outs are restricted in area by tidal height. The presence of pack ice and fast ice are affected by temperature, wind, and current (Bishop 1967). Logbooms and wharfs are often anchored inter-tidally, limiting access to higher tides. The use of logbooms as haul-outs has been mentioned only anecdotally (Hoover 1988; Olesiuk et al. 1990a). Logbooms are found in most medium to large estuaries along the northeast Pacific coast.

Seasonal and diel patterns of harbour seals hauling out are poorly understood. Often studies have relied on visual observation of groups of seals at haul-outs (e.g. Sullivan 1980; Terhune and Almon 1983; Stewart 1981; Allen et al. 1984; Calambokidis et al. 1987; Watts 1991). Visual observations are usually restricted to daylight hours and animal activity upon leaving the haul-out is unknown. Radio-tagging studies of harbour seals indicate animals

haul-out at more than one site (Pitcher and McAllister 1981; Yochem et al. 1987; Thompson 1989; Thompson et al. 1989).

Most studies have attempted to correlate circadian cycle, tidal height, or weather with haul-out behaviour. These variables are not mutually exclusive during certain times of the year (e.g. during the summer in British Columbia the lowest low tides occur during the day, whereas in the winter they occur during the night). Therefore, studies examining haul-out behaviour for only part of the year or at discrete intervals throughout the year fail to observe entire seasonal cycles. Mathews and Kelly (in press) found that a three week difference in the timing of a population survey of harbour seals hauled out in John Hopkins Inlet, Glacier Bay, resulted in a ten-fold change in population estimates.

Temperatures $< -15^{\circ}\text{C}$ (corrected for wind chill) were found to significantly decrease the number of seals hauled out on Sable Island (Boulva and McLaren 1979). However, most times of the year and throughout most of the harbour seals' range, haul-out site temperatures are well within their thermo-neutral zone (Matsuura and Whittow 1973).

The effects of circadian cycle and tidal height on harbour seal haul-out patterns differ markedly between

studies and areas. In areas where haul-out substrates are available at all tidal heights or regions that have small tidal ranges, circadian cycle appears to be important (Boulva and McLaren 1979; Stewart 1981; Hoover 1983; Calambokidis et al. 1987). Studies conducted at haul-outs with large tidal ranges that affect the area of substrate available for hauling out have strong negative correlations between tide and seal numbers (Fisher 1952; Allen et al. 1984; Sullivan 1980). In areas of high human activity frequent disturbance of seals alters haul-out patterns (Allen et al. 1984).

Studies examining haul-out patterns of many individuals (i.e. representative of the population) in specific areas for the entire year are needed to determine factors influencing hauling out. Counting groups of animals at haul-outs over time provides information on general trends. However, monitoring a seal's behaviours continuously for long periods enables examination of the independent effects of weather, tidal height, and time of day on hauling out.

This study was designed to examine continuous animal behaviour within a specific area. This included examination of diel and seasonal changes in the duration, periodicity, and timing of hauling out and swimming. In addition, I observed the location and activity of radio-tagged seals

outside of the study area. Estimates of the number of animals in the study area were conducted to determine the rate of immigration and emigration. Activity patterns, movements, and abundance of harbour seals are discussed in association with dietary information to explore the ecological processes affecting their interaction with the environment and each other (see Chapter 2).

The main objectives of this project were to: (1) determine the site fidelity of harbour seals hauling out on logbooms; (2) identify diel and seasonal patterns of swimming and hauling out within a estuary; and (3) determine the range of movements and population fluctuations of harbour seals utilizing Cowichan Bay.

4.2 METHODS

4.2.1 Capture and Instrument Attachment

Seals were captured using a seal net. The animals were weighed, sexed, and immobilized on a restraining board (Fig. 4.1). Nineteen animals were fitted with radio tags (RTs) and two of these with time depth recorders (TDRs) (Table 4.1). The instruments were attached to the top of the head (RT) or middle back region (TDR) using quick setting epoxy glue (Fedak et al. 1983, Ellis and Trites 1992). The

instruments were colour-coded so as to enable the correlation of visual identification with radio signal (see Fig. 4.1). These devices fall off during moulting. Transmitters were deployed at pre-moult (May 1991) and post-moult (November 1991), ten and nine transmitters respectively.

Table 4.1 Harbour seals radio-tagged at Cowichan Bay Estuary; (a) May 1991, (b) November 1991.

SEAL	RADIO (MHz) FREQUENCY	DATE ATTACHED	SEX	WEIGHT (KG)	LAST DAY RESIGHTED (NUMBER OF DAYS)
(a)					
1	159.020	30-APR-91	F	93	16-SEP-91 (140)
2	159.500	30-APR-91	F	39	08-AUG-91 (100)
3	159.760	30-APR-91	M	59	25-AUG-91 (117)
4	160.000	01-MAY-91	M	32	16-AUG-91 (107)
5	160.320	01-MAY-91	F	50	09-AUG-91 (100)
6*	159.820	10-MAY-91	F	73	26-AUG-91 (108)
7*	159.948	13-MAY-91	M	95	29-AUG-91 (108)
8	160.560	13-MAY-91	F	41	23-AUG-91 (102)
9	161.150	13-MAY-91	F	43	19-JUL-91 (67)
10	161.250	21-MAY-91	F	32	08-AUG-91 (79)

(b)					
11	159.020	05-NOV-91	F	39	04-JUN-92 (214)
12	159.500	12-NOV-91	F	68	28-JUN-92 (230)
13	159.540	12-NOV-91	M	41	11-JUN-92 (213)
14	159.760	12-NOV-91	F	34	22-JUN-92 (224)
15	159.820	15-NOV-91	M	57	23-MAY-92 (191)
16	159.950	15-NOV-91	M	47	18-MAY-92 (186)
17	159.998	22-NOV-91	M	68	26-APR-92 (157)
18	161.149	22-NOV-91	M	45	12-MAY-92 (173)
19	161.250	28-NOV-91	M	61	10-APR-92 (135)

*Denotes animals with radio-tags and time depth recorders.

Fig. 4.1 Harbour seal immobilized on restraining board with a colour-coded radio-tag attached. The restraining board was built by the author adapted from M. Bigg's original design.



4.2.2 Data Collection

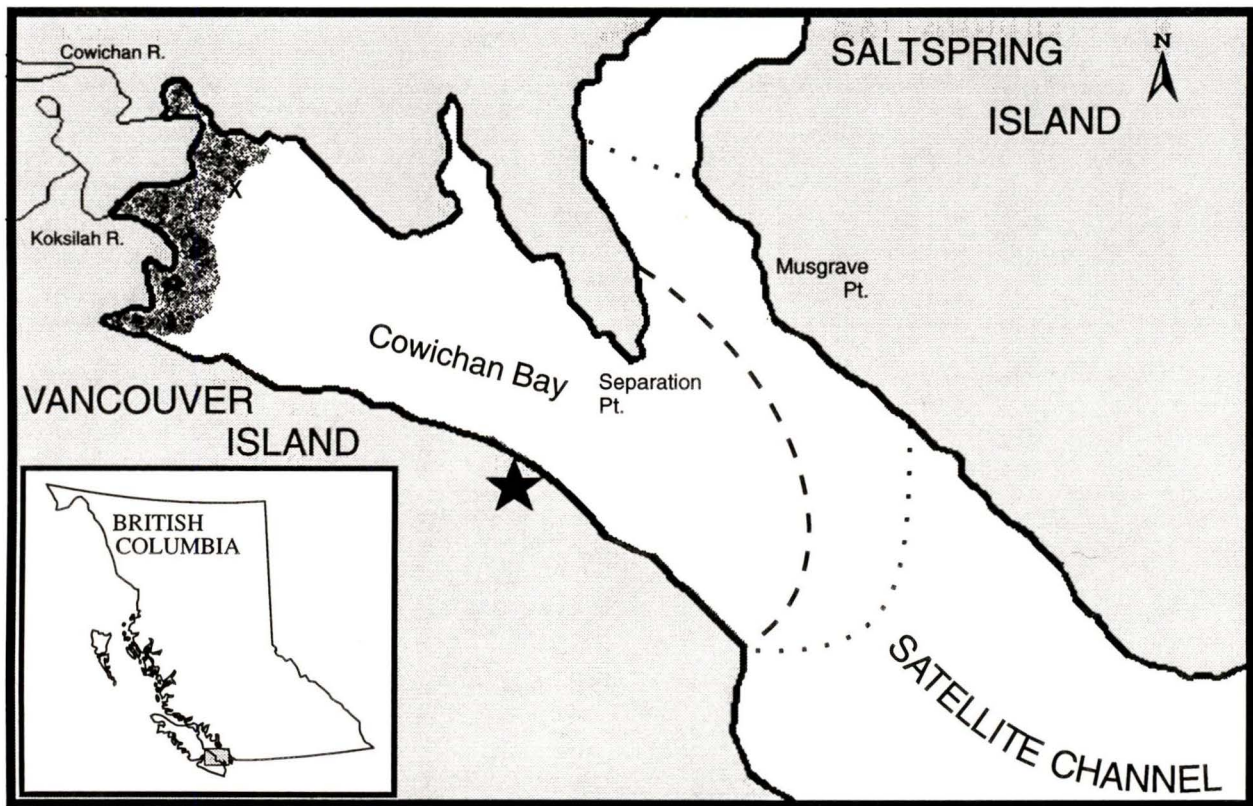
i) Telemetry

The Advanced Telemetry Systems (ATS) very high frequency (VHF) transmitters (model 5B) pulse at a constant rate of 70-72 pulses per minute at predetermined frequencies ranging from 159.00-162.25 MHz. Thirty frequencies (channels) were monitored over a three week period prior to radio-tag attachment to identify 10 channels that had little or no interference. Signals from the head-mounted transmitters were received while the animal was at the surface or hauled out (particles in salt water attenuate the signal).

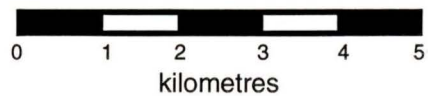
Remote Station

A data logger (ATS, model DCC II), two four-element Yagi antennae, receiver (ATS, R2100) and a 12 volt power source were located within Cowichan Bay (Fig. 4.2). The receiver was programmed to continuously scan frequencies in series for 20 seconds, 12 and 9 frequencies respectively for May and November 1991 deployments. The data logger stored the date, time, and number of pulses received from each frequency. The data were down-loaded into a Toshiba T1000 laptop computer every 7-14 days before replacing the remote station power supply.

Fig. 4.2 Study site and range of radio-signal reception; (---) indicates range of total reception, (- - -) indicates area of partial reception.



- ★ Remote station
- X Log boom anchorage



Range Test

The range of signal reception was tested on three occasions, April 30, 1991, November 18, 1991 and October 2, 1992. One to six transmitters were taken varying distances from the remote station for 15-30 minute periods. Figure 4.2 shows the zone of total signal reception (- - -) and partial reception (. . .).

Boat and Land Monitoring

Individual animals were located with a hand held receiver (ATS, model R2000) attached to a Yagi antenna and head phones. A minimum of 2 days per week were spent determining the location and activity of individual animals. An inflatable (Zodiac mark III) or aluminum (Kellahan) 3 m boat with 20 or 40 horsepower engines respectively were used for locating animals within the estuary. A 5 m fiberglass boat with a 160 horsepower engine was used to locate animals outside of the estuary (available November 1991 to June 1992). Animals were also located from land using triangulation. Individual animals were directionally located from three separate locations, the intersect of the plots on a map provided an estimate of animal location.

ii) Time Depth Recorders (TDRs)

Two harbour seals with radio transmitters were also fitted

with TDRs (Wildlife Computers, model Mark III+), that were programmed to record water depth and conductivity (i.e. dive depth and whether the animal was swimming or hauled out) every 30 seconds for 3-4 months. The TDR's store data internally that was down-loaded by computer once the units were recovered.

iii) Tidal Height

Tidal heights were obtained from the Institute of Ocean Sciences in Sidney. The heights were actual measurements from a tidal station in Patricia Bay. Because the study area was within 8 km of Patricia Bay and the accuracy of predicted tidal heights of Cowichan Bay was $\pm 2\%$ (D. Sinnott¹⁰, pers. comm.), actual Patricia Bay tidal heights were used.

iv) Estimates of Harbour Seal Numbers

The number of harbour seals using Cowichan Bay was estimated using three methods:

1) Absolute Counts (minimum estimates)

Hauled out and swimming animals were counted biweekly between 13:00-17:00 h at >2.0 m tides. Counts were conducted from a boat or on land with binoculars.

¹⁰ D. Sinnott, Institute of Ocean Sciences, Sidney, B.C., pers. commun. 1993.

2) Corrected Counts

The number of radio-tagged animals included in the count was divided by the actual number of radio-tagged animals within the study area (obtained from remote station). This provided an estimate of the proportion of animals present in the study area that were included in the count. Counts were corrected for the proportion of radio-tagged seals that were present but not included in counts.

3) Number of Seals Using the Study Area

The corrected absolute counts were divided by the mean proportion of time that animals spent in the study area (between 13:00-17:00 and >2.0 m tides) the week the count was conducted (i.e. three days before and after the day of the count, animals absent for all days were excluded). This accounted for animals that use the study area but were not present during counts.

4.2.3 Analyses

A) Remote Station (Telemetry Data)

Swimming and haul-out behaviour patterns were apparent from graphed data (Fig. 4.3). Interpretation of data was required when signal reception was interrupted due to radio interference or animals dipping their heads into the water while hauled out, although such occurrences were rare (see verification tests). The graphed telemetry data were digitized using the program Sigmascan. The type and

duration of each behaviour were recorded with the corresponding time of day into an ASCII file. The harbour seal data were divided into five categories; hauled out (H), swimming (S), partial reception (PR), leave (L), and quit (Q).

Hauled Out (H)

A animal was considered hauled out if the data logger recorded 20 or more pulses per scan of its frequency for >20 minutes. This prevented incorrectly identifying an animal hauled out while swimming at the surface. Separate haul-out bouts were defined as >20 minutes swimming between haul-out periods.

Swimming (S)

Animals swimming within the study area had a unique pattern of signal reception by the receiver. Graphing of these data showed intermittent reception of large numbers of pulses (at the surface for majority of scan), few pulses (at the surface for only part of scan), and no pulses (beneath the surface for entire scan) (see Fig 4.3).

Partial Reception (PR)

Range studies of radio-tags indicated that beyond a certain distance, reception of radio-signals was reduced (i.e. the number of pulses recorded by the data logger were

decreased). This zone of partial reception (PR) is defined as signal reception of <20 pulses per scan for >5 h period, where reception of pulses must be >5 at least once every 5 h period. No haul-outs were within the PR area, therefore, all incidences of PR were considered to be swimming.

Leave (L)

Leave was defined as <5 pulses each scan for >5 h period. Although radio-interference was infrequent, discarding scans of <5 pulses reduced the possibility of incorrectly identifying an animal in the study area due to radio-interference.

Quit (Q)

Category Q represents times when the remote station was not operating due to the replacement or failure of the power source. Replacing the battery took <30 minutes. Failure of the power source occurred May 28, 1991 (3 days) and April 14, 1992 (3 days). Also the data logger was improperly initialized after battery replacement, July 28, 1991 (11 days).

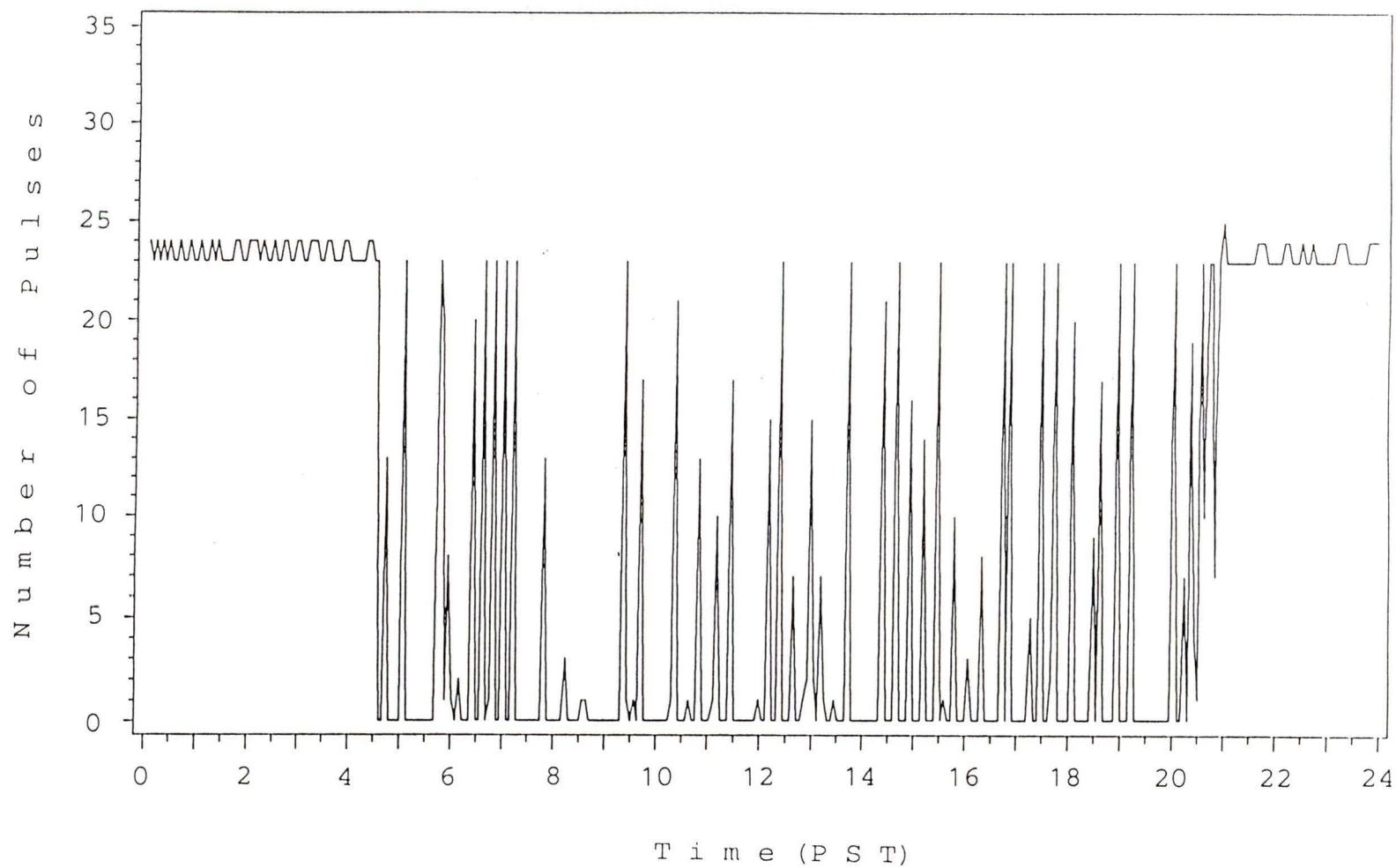


Fig. 4.3 Twenty-four hour sample of seal activity pattern from remote monitoring station (00:00-04:29 hauled out, 04:30-20:40 swimming, 20:41-24:00 hauled out).

B) Verification of Remote Station Data

Boat and Land Observations

The location and behaviour (i.e. swimming or hauled out) of radio-tagged harbour seals discovered visually or with a hand held receiver were recorded. The presence or absence (i.e. within study area) and activity were compared with remote station data for accuracy.

Time Depth Recorders

Two animals with RTs were also fitted with TDRs. Both devices provided the same behavioural data (i.e. swimming or hauled out). The similarity of swimming and haul-out behaviour duration between the two types of data collection methods (while animal within study area) were examined to determine the accuracy of remote station data.

C) Activity Budgets

Four activity budget categories, hauling out (H), swimming (S), partial reception (PR), and leave (L) were examined to determine the amount of time seals spent hauled out or swimming while within the study area. Activity budgets (as proportions) of specified categories were arcsin-transformed for statistical analysis (Zar 1984).

The proportion of time hauled out (H_p) was calculated

as the mean of: (a) the proportion of time spent hauled out while within absolute range; and (b) the proportion of time hauled out while within the absolute and partial reception zone. This provided a minimum and maximum value of the proportion of time spent ashore.

$$[1] \quad H_p = \frac{\left(\frac{H}{H+S+PR}\right) + \left(\frac{H}{H+S}\right)}{2}$$

The proportion of time swimming (S_p) was calculated as the mean of: (a) the proportion of time swimming when within absolute range; and (b) the proportion of time swimming when within absolute and partial range.

$$[2] \quad S_p = \frac{\left(\frac{S}{S+H}\right) + \left(\frac{S+PR}{S+H+PR}\right)}{2}$$

The proportion of time spent in category L (L_p) represents the mean of: (a) the proportion of time spent outside of the study area; and (b) the proportion of time spent outside of the study area and within partial range.

$$[3] \quad L_p = 1 - (H_p + S_p)$$

$$[4] \text{ Proportion of time in estuary} = (H_p + S_p) - L_p$$

The effects of tidal height and time of day on activity patterns were examined in four-week and total radio-tag attachment periods. When correlating tidal height to haul-out behaviour numerous studies have used the number of hours before or after low tide (Terhune and Almon 1983; Thompson 1989; Thompson et al. 1989). Tidal height follows a seasonal diurnal cycle (Canadian Tide and Current Tables Vol. 5, 1991). Tide fluctuates in minimum and maximum height, the period of time at various tidal heights, and with circadian cycle. High tides are frequently lower than low tides the next day. Therefore, to eliminate the differences in relative tidal cycles, I used absolute tidal height in 0.25 m intervals when correlating tidal height to haul-out behaviour. The relationship of tidal height and haul-out behaviour was examined using simple linear regression.

Preliminary examination of data indicated a large drop in the percentage of animals hauled out at tides >3.25 m in the summer and >3.75 m in the winter. Upon talking with tug operators that move booms within the estuary, I learned that movement of booms occurred at the highest weekly tides (A. Fault¹¹ pers. comm.). Since tug disturbance (movement of booms) often affected seal haul-out behaviour at highest

¹¹ A. Fault, Fault Towing, Cowichan Bay, B.C., pers. commun. 1994.

tides (i.e. >3.25 m and >3.75 m in summer and winter respectively), these data were not included in further analysis. This was <6% of all tidal heights.

The proportion of time hauled out at various times of the day (1h intervals) was examined for individual and combined diel patterns. May 1991 radio-tagged animals were also compared to the November 1992 radio-tagged animals for any significant differences in the proportion of time spent within the study area (Mann-Whitney *U*-test).

4.3 RESULTS

4.3.1 Duration of Instrument Attachment

Two methods were used to determine the duration of attachment; either the last visual sighting or the last radio-signal received, whichever was greatest. These estimates were considered conservative because some animals (e.g. seals No.8 and No.15) spent most of their time outside of the estuary and were resighted infrequently. Animals had radio-tags attached for 67-230 days (\bar{x} =145) (Table 4.1). The different mean dates for moulting of transmitters for May and November attachments, August 18 and May 25 respectively, were assumed to be the result of hair growth after newly moulted animals were tagged in November (i.e.

hair breaking as the pelage became longer and worn). In addition, November 1991 tagged animals spent less time within the study area, therefore the lack of resightings may have biased radio-tag loss to an earlier date.

4.3.2 Verification of Remote Station

All 270 visual and hand-held radio-receiver identifications of animal location and behaviours (i.e. swimming, hauled out, or not present in study area) agreed with data collected from the remote station (Table 4.2).

Table 4.2 Summary of seal resightings and corresponding remote station behavioural data (H= hauled out, S= swimming); a) May 1991 attachment (May-September 1991), b) November 1991 attachment (November 1991-June 1992).

	Seal Resightings		Remote Station		
	H	S	H	S	L
a)					
In Estuary	21	33	21	33	-
Outside Estuary		(no sightings)			
b)					
In Estuary	41	94	41	94	-
Outside Estuary	5	76	-	-	81

4.3.3 Distribution of Radio-Tag Resightings

The remote station telemetry and TDR behavioural data (i.e. swimming and hauling out duration and corresponding time of day while within study area) of animals No.6 and No.7 had high agreement: 98.2% and 99.5%, respectively. The small differences were assumed to be the result of different parts of the animal (i.e. back or head region) partially submerged while hauled out.

Animals were located visually or with a hand-held receiver 270 times, 189 times within the estuary and 81 times outside the estuary. Figure 4.4 shows the distribution of seal resightings outside the study area (i.e. within 25 km). The resighting effort in areas was not spread evenly between months, therefore, the data were not separated temporally. Animals tagged in May 1991 were not sighted outside of the study area. However, animals tagged in November 1991 were regularly sighted outside of the study area. One animal (No.15) spent >95% of the time outside of the study area. This animal was resighted in the same area four times, 35 km North of the study site. Another animal (No.17) spent 48% of the time within the study area until April 8. This animal was not resighted in the southern Gulf Islands. On April 26 the seal was resighted in the Fraser River Estuary, 50 km East of the study area. Most of the resightings outside the study area (>80%) were in Saanich Inlet (see Fig. 4.4).

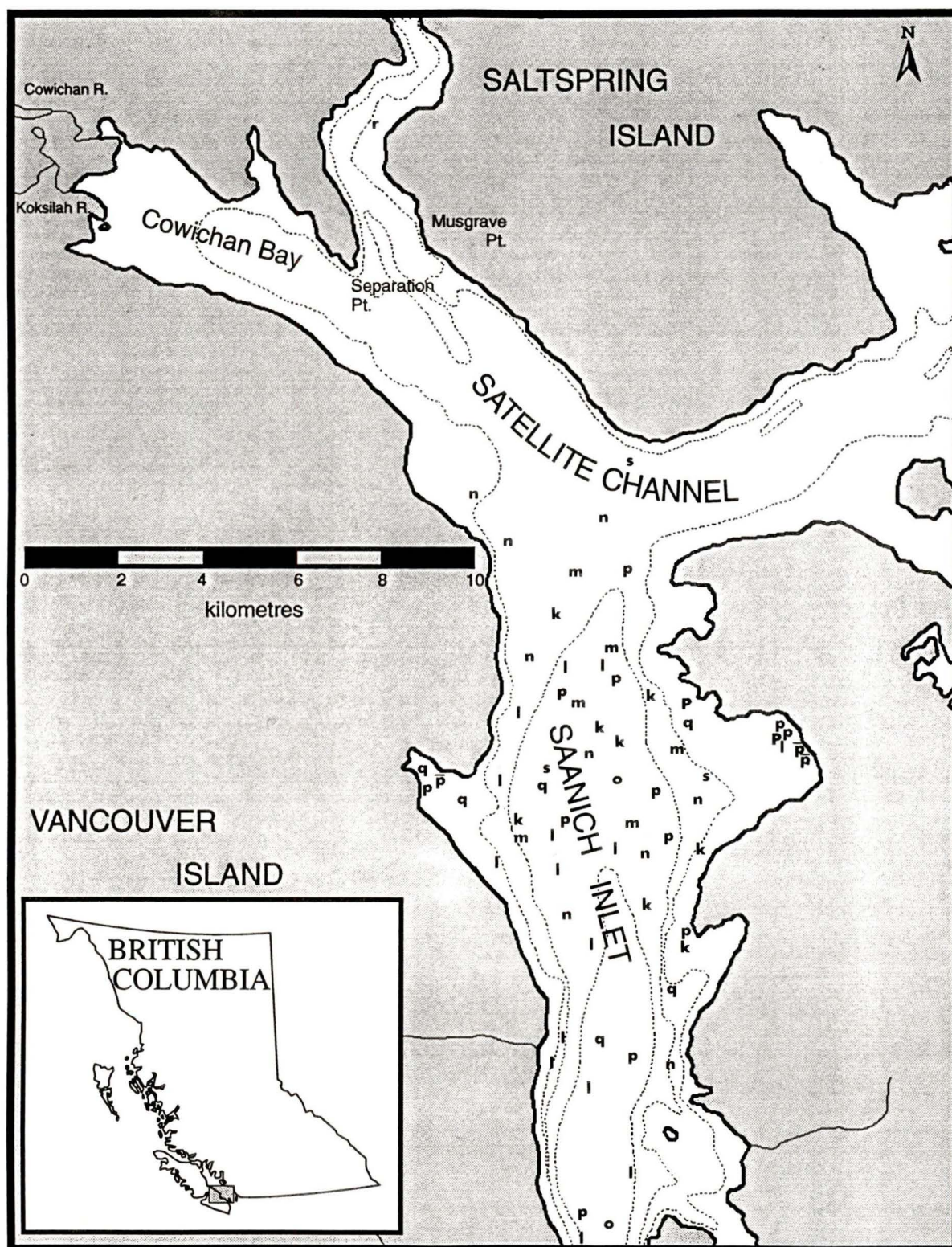


Fig. 4.4 Distribution of seal resightings outside the range of the remote monitoring station that were within 25 km of the study area (seal 1=a, 2=b, ..., 19=t). Plain letter indicates swimming, letters with over-bar represent seal hauled out.

4.3.4 Use of Study Area

Harbour seals tagged in May 1991 spent significantly more time within the study area than animals tagged in November 1991 [$t_{0.05(2),17}=3.17$ $0.01>P>.005$] (Table 4.3). Population estimates indicated that <100 (<120 corrected) harbour seals inhabit Cowichan Bay during the periods May to September and February to April (Fig. 4.5). Seal numbers increased to 256 (308 corrected) at their peak in early December, decreasing abruptly in late December and early January. The increase corresponded with salmon migration into the estuary and the decline coincided with the end of salmon spawning (see Chapter 2).

Seals radio-tagged in the estuary during May tended to be more *resident*, occupying the study area for >60% of the time except for one animal (No.8=34%). All seals, however, made trips outside the study area. Animals tagged during November 1991 coincided with the influx of animals from surrounding areas. Therefore, many of the radio-tagged animals were considered to be *migrants* (i.e. animals in estuary utilizing the seasonally available salmon). This would account for the lower proportion of time spent in the study area. A comparison of the proportion of time May and November 1991 tagged animals spent in the study area during May and June indicated seals tagged in November 1991 spent

significantly less [Mann-Whitney, U -test, $U=67$, $P=.02$].

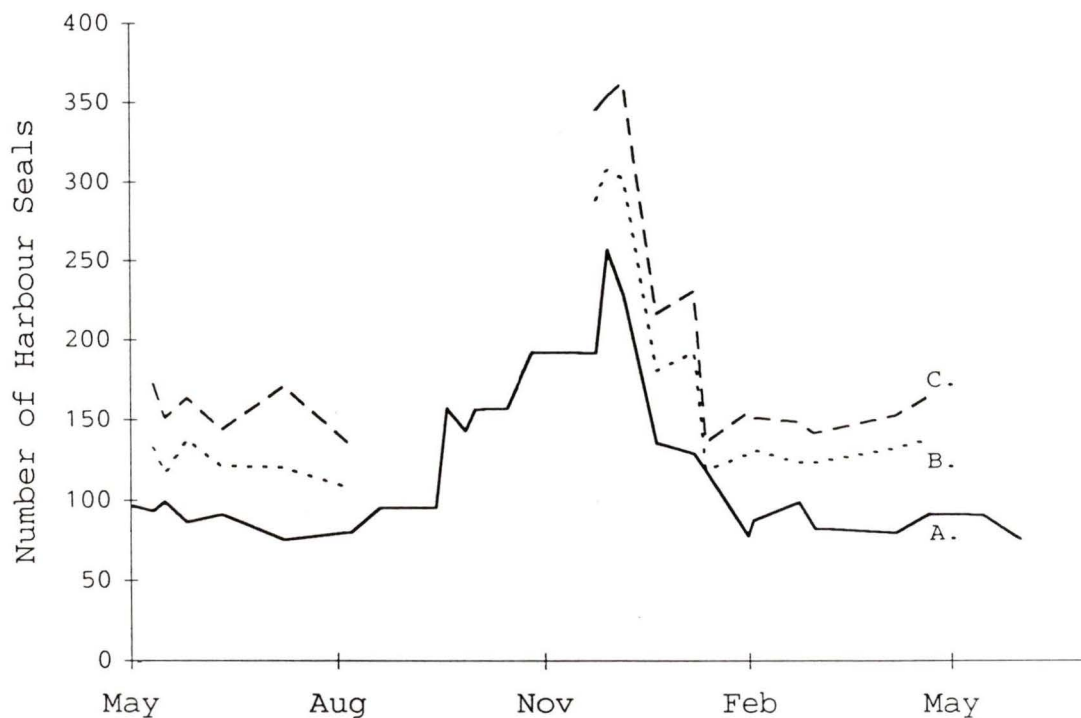
Table 4.3 Proportion of time each radio-tagged harbour seal spent within the study area and the proportion of time spent hauled out; (a) May 1991 radio-tagged animals, (b) November 1991 radio-tagged animals.

Seal Number	Proportion of Time in Study Area	Proportion of Time Hauled Out	Proportion of Time Swimming
(a)			
1	.64	.16	.84
2	.84	.21	.79
3	.96	.15	.85
4	.77	.20	.80
5	.67	.12	.88
6	.76	.25	.75
7	.93	.18	.82
8	.34	.23	.77
9	.89	.14	.86
10	.64	.16	.84

(b)			
11	.74	.18	.82
12	.47	.19	.81
13	.51	.21	.79
14	.48	.20	.80
15	.04	.02	.98
16	.24	.22	.78
17	.43	.24	.76
18	.69	.07	.93
19	.48	.23	.77

Although the amount of time May and November tagged animals spent within the estuary varied significantly, the proportion of time animals spent hauled out or swimming while within the study area did not [$t_{0.05(2),17} = .47$ $P>0.50$].

Fig. 4.5 Estimates of the number of seals in the study area: A, visual count; B, corrected for seals in the study area not counted (i.e. proportion of radio-tagged seals not counted that were within the study area); C, corrected as in B, and for animals that use the study area (i.e. the week the count was conducted) but were not present during counts.



Haul-Out Behaviour

The average time (all seals) spent hauled out varied seasonally ranging from 9-29% ($\bar{x}=19\%$) (Fig. 4.7). Animals spent significantly more time hauled out August to February (excluding September and October when no data were collected). This coincides with moulting times of harbour seals and the growth of new pelage (Bigg 1981). There was no significant difference between the total proportion of time males and females hauled out ($t_{0.05(2),16} = -.05$, excluding seal No. 15 who spent <5% in the study area). However, there was high variability among animals.

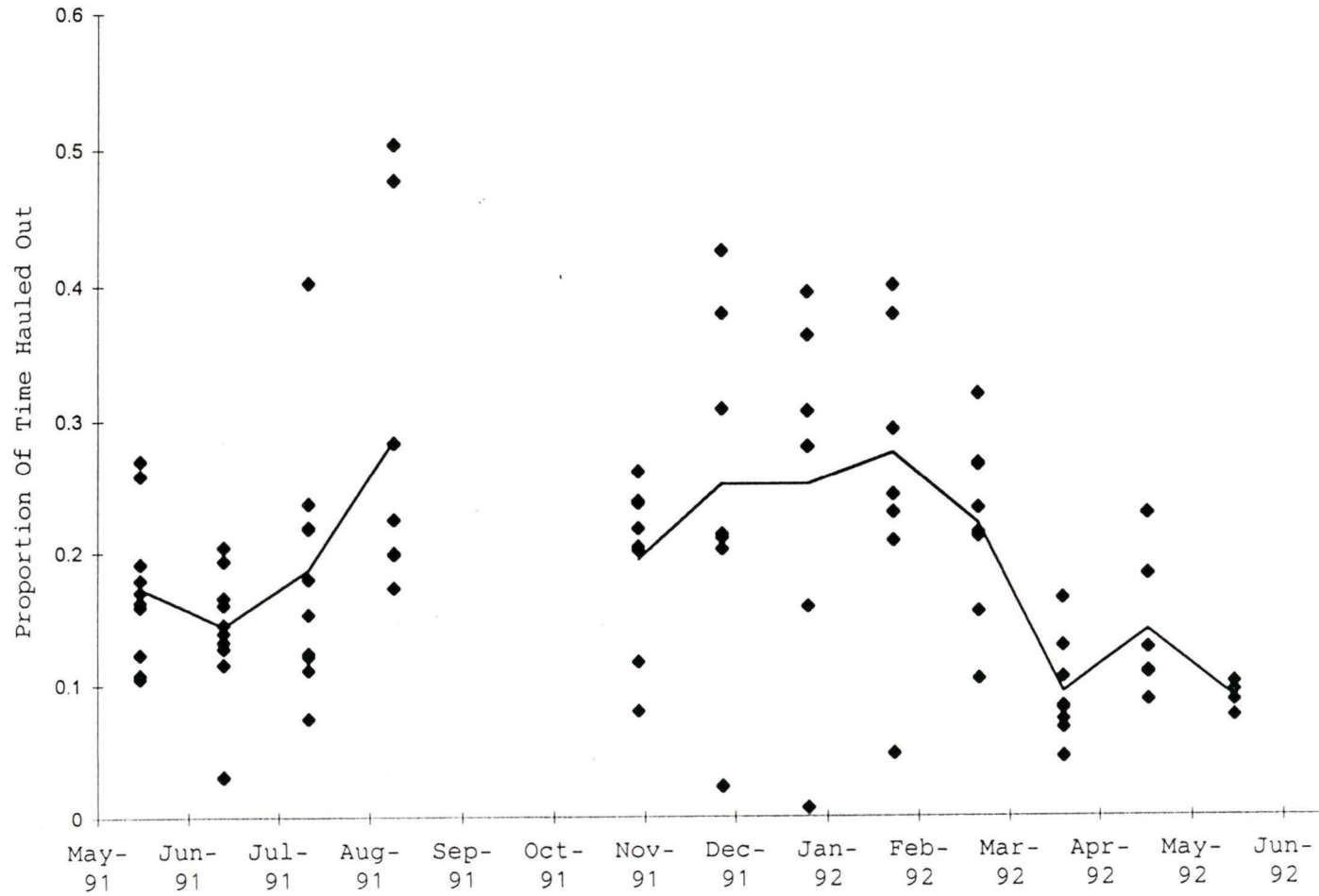


Fig. 4.6 Seasonal change in the proportion of time seals hauled out: the horizontal line joins the mean of all seals for each month.

Table 4.4 Relationship between haul-out behaviour and tidal height for radio-tagged seals (see Table 4.1 for animal codes), H=percentage of sample points when hauled out, T=tide height (.25 m intervals), N=number of tidal cycles used to calculate H; (a) May 1991 radio-tagged seals, (b) November 1991 radio-tagged seals.

Seal	Sex	Regression	r^2	P	N
(a)					
1	F	$H=0.09T+0.02$	0.76	<0.005	456
2	F	$H=0.18T-0.07$	0.78	<0.005	296
3	M	$H=0.11T-0.01$	0.84	<0.005	364
4	M	$H=0.10T+0.10$	0.46	<0.01	328
5	F	$H=0.08T+0.01$	0.75	<0.005	300
6	F	$H=0.18T-0.01$	0.81	<0.005	368
7	M	$H=0.09T+0.08$	0.81	<0.005	376
8	F	$H=0.08T+0.17$	0.34	<0.025	352
9	F	$H=0.10T-0.01$	0.80	<0.005	256
10	F	$H=0.09T+0.02$	0.68	<0.005	260

(b)					
11	F	$H=0.06T+0.02$	0.76	<0.005	840
12	F	$H=0.02T+0.16$	0.09	<0.25*	908
13	M	$H=0.06T+0.07$	0.69	<0.005	840
14	F	$H=0.09T-0.01$	0.92	<0.005	884
15	M	Not Enough Time Spent In Study Area			
16	M	$H=0.09T+0.02$	0.88	<0.005	732
17	M	$H=0.11T-0.01$	0.82	<0.005	616
18	M	$H=-0.003T+0.07$	0.01	<0.5*	680
19	M	$H=0.11T-0.02$	0.91	<0.005	528

*Not significant

Haul-out behaviour of most seals was positively correlated with tidal height (Table 4.4). The hourly diel swimming and haul-out patterns of May 1991 (May to August) and November 1991 (November to June) radio-tagged seals indicated that animals hauled out at higher mean tides (Fig. 4.7a,b). Animals also preferred to haul-out in the afternoons (14:00-17:00) in summer (May 1991 attachment),

which appeared to be independent of tide. The least amount of time spent hauled out was between 7:00-12:00 and 18:00-21:00 during the summer and 17:00-21:00 during the winter (Fig. 4.7a,b). There was considerable variation among individuals (Fig. 4.8).

4.4 DISCUSSION

Harbour seals inhabit inshore waters. As the human population increases in coastal areas, seal habitats often become altered and the incidence of human interactions with harbour seals increase (Allen et al. 1984). I found that harbour seals appear to have habituated to the presence of logbooms in estuaries and often haul-out on them. Movement of haul-out substrate (logbooms) occurred at the highest tides. Seals hauled out on booms moved by tugs returned to the water. The haul-out patterns of harbour seals were negatively affected when booms were moved (i.e. tidal heights >3.25 m summer, >3.75 m winter). However, seals scared into the water often rehailed within five minutes and animals regularly used booms that were rarely moved. The affect of disturbance on overall diel and seasonal haul-out patterns was considered negligible. Human disturbance (movement of logbooms) at most tides throughout the year was low.

Fig. 4.7 Scatter plot of diel pattern of the proportion of time harbour seals hauled out, (a) May to August 1991, (b) November 1991 to June 1992; (—) is the mean of all seals and (- -) is the mean tidal height.

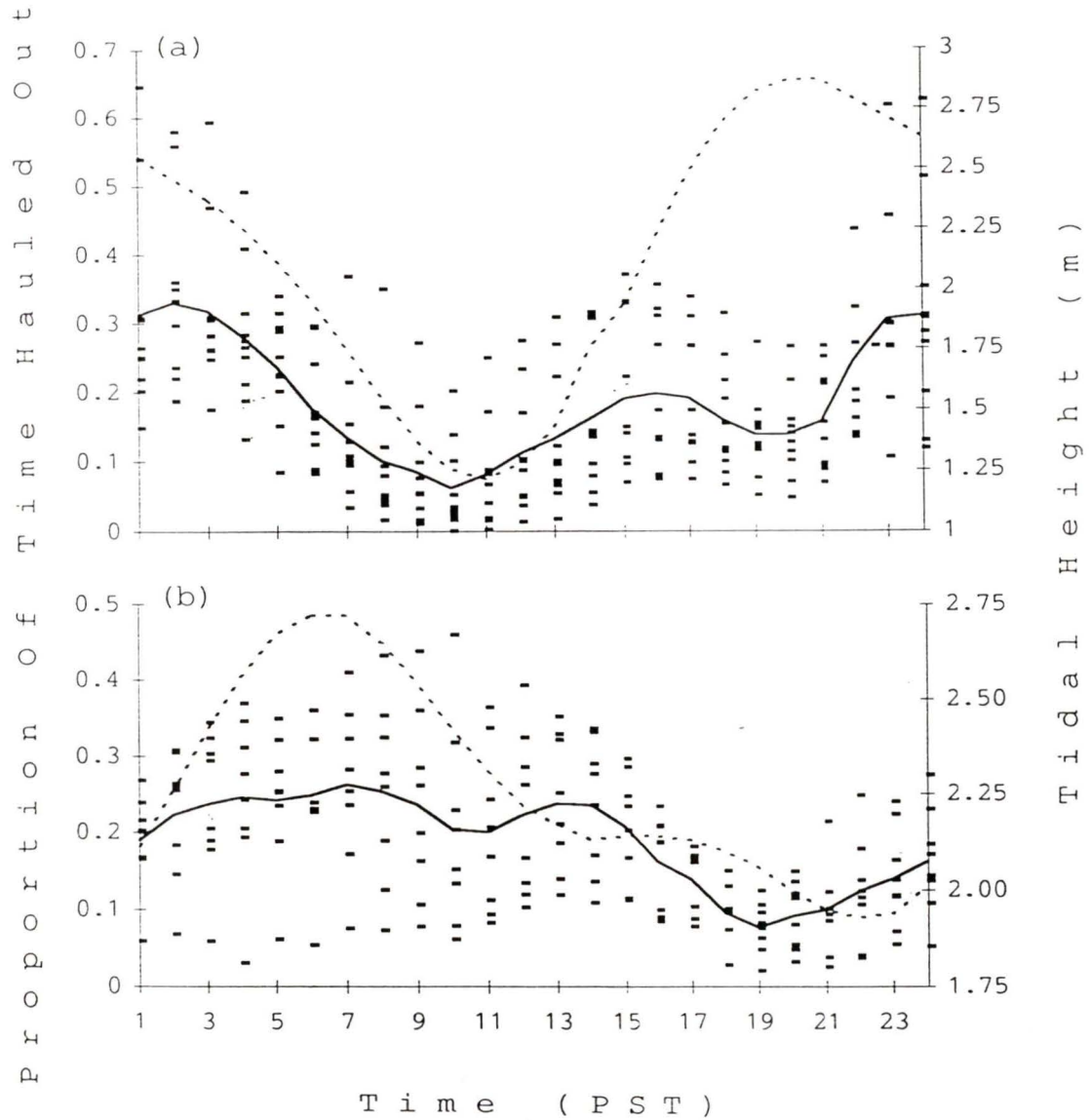
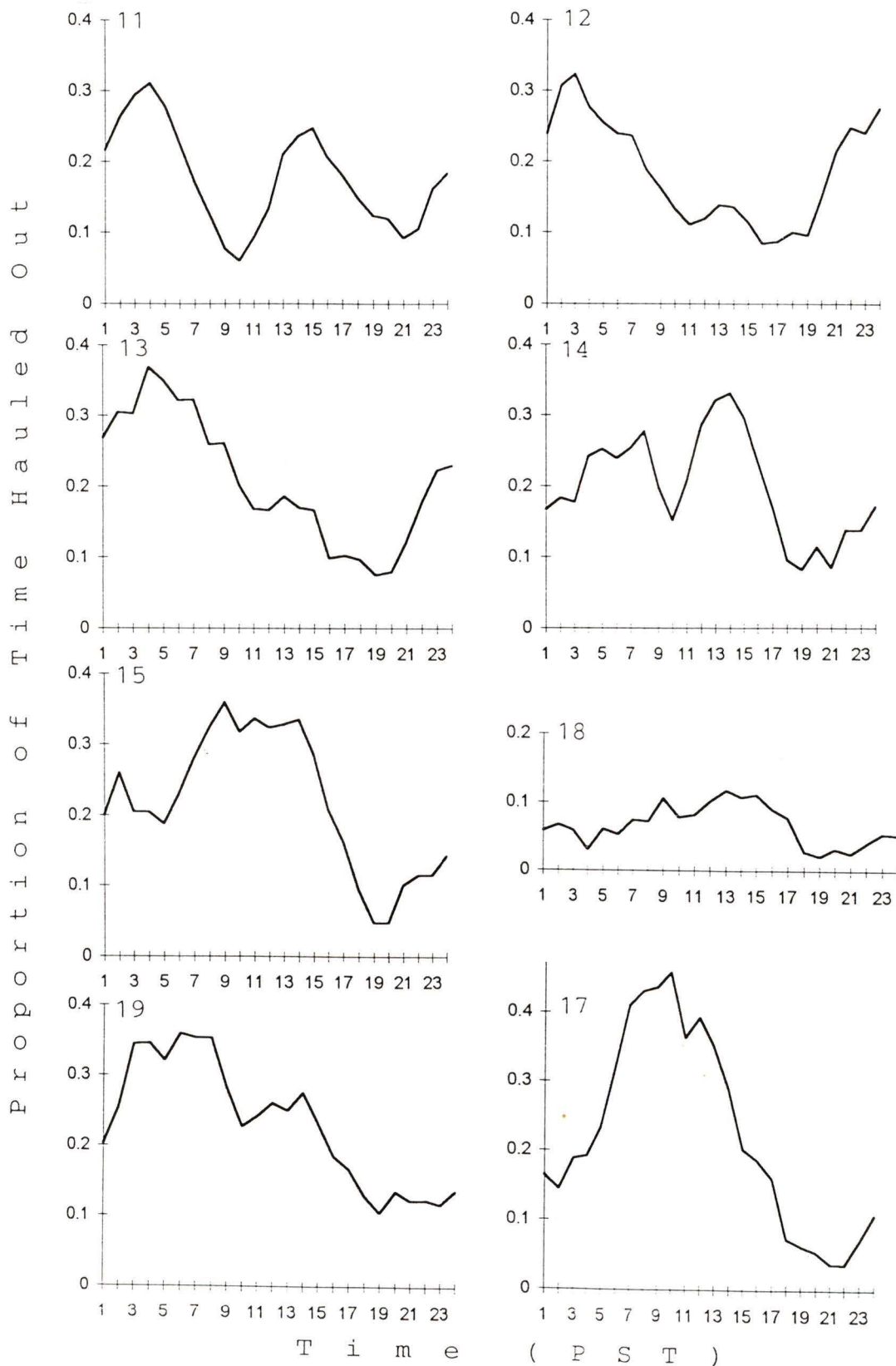


Fig. 4.8 Diel haul-out patterns of harbour seals tagged November 1991. Seal No. 16 did not spend enough time in the study area to enable determination of diel pattern. See Table 4.1 for seal identification codes.



4.4.1 Seasonal Distribution

Little is known about seasonal changes in harbour seal movement patterns and activity budgets (Yochem et al. 1987; Thompson et al. 1989). I found that the number of seals and the time seals spent in the study area changed seasonally. Population fluctuations during the year indicated that animals regularly moved into and out of the study area. Radio-tagging animals while the population in the study area was low (May 1991) and while numbers were high (November 1991) provided insights into seasonal and localized movement patterns. Two groups of seals used the study area. Animals that spent most of their time within the estuary (90% of animals tagged April to May 1991, 33% of animals tagged in November 1991) and seals that spent the majority of their time in surrounding areas (10% of the animals tagged May 1991; 67% of animals tagged in November 1991). Pitcher and McAllister (1981) found that of 35 radio-tagged harbour seals at Tugidak Island 75% were full time residents while others used it in addition to other haul-outs 24-194 km away.

Greater harbour seal numbers in the estuary during the autumn were the result of seals that periodically use the estuary during the year, increasing the proportion of time present. This increase in the time animals spent in the

study area during November and December coincided with prespawning salmon moving into the estuary. Previous studies have found increased numbers of seals in estuaries coinciding with the presence of prespawning salmon (Brown and Mate 1983; Bigg et al. 1990).

Most *migrant* seals appeared to be from nearby haul-outs as most animals continued to visit the estuary (study area) for the remainder of the year. Tagging studies have shown high site fidelity as well as long distance movements between haul-outs (Pitcher and Calkins 1979; Brown and Mate 1983; Beach et al. 1985). Brown and Mate (1983) observed 5 of 11 radio-tagged seals (45%) to make at least one move between two bays 25 km apart and Beach et al. (1985) observed 75% of the 58 seals radio-tagged in the Columbia River on haul-out sites 30-55 km away. It appears that harbour seals have a "home range" where they spend most of their time; however, they often make localized trips to surrounding areas and less often longer range movements (i.e. >50 km).

4.4.2 Haul-Out Patterns

During August to February (excluding September and October, no animals radio-tagged) harbour seals spent a greater proportion of their time hauled out. Harbour seals

in this area moult from August to November (Bigg 1981). Hauling out has been shown to increase skin temperature and cell division, facilitating hair growth and moulting [harbour seal skin cells cannot metabolize properly at temperatures below 17°C (Felz and Fay 1966)]. Thompson et al. (1989) found that radio-tagged male harbour seals hauled out more during the day while moulting than at other times of the year.

Haul-out patterns on logbooms were closely correlated with the seasonal variation in tidal cycle and to a lesser extent time of day. Radio-tagged harbour seals spent the greatest amount of time hauled out at higher tides. In contrast, many harbour seal studies at rock, mud, and sand intertidal haul-out sites showed a strong negative relationship between hauling activity and tidal height (Sullivan 1980; Graybill 1981; Schneider and Payne 1983; Allen et al. 1984; Harvey 1987; Pauli and Terhune 1987; Thompson 1989). Haul-out substrate availability appears to limit hauling out to certain conditions which are substrate specific. For example, logbooms often are anchored intertidally, limiting hauling out to higher tides, while, intertidal sand bars, reefs, and beaches have a greater area available for hauling out at lower tides.

4.4.3 Swimming

Diel patterns indicated that, in the summer, harbour seals spent most of their time swimming during dawn (7:00-12:00) and dusk (18:00-21:00), while animals tagged in November (winter) spent most of their time swimming at dusk (17:00-20:00). Crepuscular changes in vertical distribution or schooling behaviour of prey may increase the foraging success of harbour seals. Studies examining harbour seal stomach contents indicate that most animals collected during the day have empty stomachs while a much higher proportion of animals collected at dawn or dusk contain food (Spalding 1964; Boulva and McLaren 1979).

Herring and hake which make up >65% of the diet of harbour seals in this area (see Chapter 2) are diel vertical migrators. Schooling herring rise to the surface during dusk, dispersing throughout the night, regrouping at dawn, before retreating into deeper water (Blaxter 1985). Hake also migrate closer to the surface at dusk, remaining until dawn (McFarlane and Beamish 1985).

Harbour seals are capable of dives >250 m in depth, therefore their prey is accessible at all times of the day (maximum TDR reading seal No. 7). However, deep dives during the day would be far more energetically expensive than shallow dives at dawn and dusk.

Daytime dives also may give foraging seals a visual disadvantage. It takes about 30 minutes for the eyes of harp seals (*Phoca groenlandica*) to become fully dark-adapted (Lavigne et al. 1977). It is reasonable to assume that similar constraints exist for harbour seals.

Annual harbour seal distribution, abundance, and activity patterns and the relationship with prey distribution, abundance, and behaviour requires long term studies of large numbers of seals. This study provides insights into seasonal harbour seal behavioural patterns in estuaries. Additional studies are required to examine non-estuary habitats and inter-annual variation within estuaries.

5. GENERAL DISCUSSION

Studying pinnipeds is difficult because most of their lives are spent in the water, much of this below the surface. As a result, until recently most pinniped research has focused on terrestrial behaviour. Recent advances in technology have reduced the size of transmitters (satellite, very high frequency, ultrasonic) and sensors (heart rate, light intensity, velocity, water depth, etc.), allowing researchers to attach data-recording and transmitting devices to individual seals. The continuous monitoring of activities has increased our knowledge of terrestrial behaviour of pinnipeds and has yielded new insights into aquatic behaviour and ecology over great spans of time and space. Technological advances also have enabled some problems to be addressed that were formerly intractable, such as, feeding and feeding ecology, the subject of my research.

Previous studies of harbour seals have examined diet, abundance, or movements in isolation from one another. This study is the first to collectively examine these subjects simultaneously in one area over an entire year. This integrated approach permitted a more comprehensive and ecologically realistic appraisal of harbour seal feeding ecology.

Diet analysis traditionally has relied upon analysis of stomach contents or faeces, and has used hard parts that resist digestion (e.g. cephalopod beaks, teleost otoliths). Little attention has been given to biases that result from so few markers. This study considered a range of hard parts, particularly postcranial structures. In addition, I evaluated biases due to digestive processes by exhaustively collecting and analyzing all faeces from captive seals provided with known diets.

Qualitative and quantitative estimates of harbour seal diet were improved by incorporating all taxon specific hard parts into prey identification. I found that 2-5 taxon specific hard parts per species represented >90% of identifiable elements. I believe that these results should be applied to future diet studies so that more comprehensive diet estimates can be made in other species and other ecological circumstances. Identifying scales in stomach contents or faecal remains needs to be considered for additional prey types and with other pinniped species. Vertebrae were the most numerous skeletal structure recovered from harbour seal faeces in both captive and field studies (Chapters 2 and Chapter 3). Vertebrae were present in 68% of prey identifications, the highest incidence of any taxon specific structure. Further improvements in quantitative and qualitative estimates of diet will rely

upon a better understanding of seal handling, ingestion, and digestion of prey, and how those processes affect success in prey hard part type and size determination. Another significant finding from this study concerned the age of ingested prey: age estimates from scales were possible for some prey species.

My observations on captive and wild seals suggest other biases in diet estimation resulting from natural feeding behaviour. For example, harbour seals must tear apart prey that are too large to swallow whole. Furthermore, several seals often tear apart and consume different pieces of a single large fish (Bigg et al. 1990; Olesiuk et al. in prep.). Use of taxon specific hard parts that are numerous throughout most of the length of a fish (scales, vertebrae) increases the likelihood of detecting prey that are consumed in pieces. Otoliths and other cranial hard parts often are damaged during ingestion of large prey items or are not consumed at all. Therefore, relying on otoliths or any other single prey structure decreases detection success. Using several hard part types reduces the likelihood of overlooking a prey species.

Individual differences in feeding strategies or prey preference may be substantial, but no information exists on this important topic. Also, the incidence of several seals

feeding upon a single prey item, and the dynamics of capture for large prey in general, are virtually unknown. Finally, diel variation in prey ingestion is poorly understood, but probably varies according to prey type, size, abundance, location, and behaviour.

This study revealed that the diet of harbour seals in Cowichan Bay and surrounding areas varied seasonally for most prey species, which was related to prey abundance, distribution, and behaviour. Diversity of harbour seal diet was low for most of the year (November to August), when one or two prey species comprised >75% of the diet. However, in September and October, diet diversity was high with no single prey type representing >25%, suggesting that no single prey species was available in abundance. Prey resources may be limiting at this time of the year in the southern Gulf Islands; alternatively many different prey types may be available. Estimates of prey type and abundance in this area suggest that the latter is not the case.

Hake and herring have the largest fish biomasses in the Strait of Georgia, and are the two most important prey species (>65% of the annual diet) for harbour seals. Hake represented >20% of the diet each month from February to August, then dropped abruptly in September to <10%. The

decrease of hake in harbour seal diet coincided with the dispersion of hake schools in September. The increased dispersion of hake may have reduced their vulnerability to seal predation. In contrast, the abrupt increase of herring in the harbour seal diet in January coincided with great increases of prespawning herring into Georgia Strait from the west coast of Vancouver Island.

Increased predation on salmonids by harbour seals corresponded with increased salmonid abundance and movement into the shallow estuarine habitat. Shallow estuaries and the slow-moving lower reaches of rivers probably increase the vulnerability of salmon to predation. Staghorn sculpins also became prevalent in the diet when the fish moved into shallow estuarine habitat for spawning from deeper areas of Cowichan Bay. Behavioural changes associated with spawning such as territorial defense may further increase the susceptibility of staghorn sculpins to predation.

Many prey attributes affect the overall benefit (energetic, nutritional) gained from feeding such as: prey abundance, distribution, water depth, schooling behaviour, swimming speed, size, behaviour, and caloric value, and seasonal changes in and interactions between these factors. These subjects merit attention in future research on pinniped feeding.

Diel foraging patterns in harbour seals appear to be related to changes in prey distribution and movement. Hake and herring have crepuscular changes in vertical distribution and schooling behaviour (Blaxter 1985; McFarlane and Beamish 1985). I found that radio-tagged harbour seals spent the greatest proportion of their time swimming at dawn or dusk. Hake schools in the Strait of Georgia remain below 200 m during the day. Hake migrate towards the surface at dusk, and remain within 100 m of the surface until dawn (McFarlane and Beamish 1985). Herring migrate closer to the surface at dusk, concentrating into relatively tight schools, and move to deeper water after sunrise (Blaxter 1985). Herring in dense schools near the surface may be more vulnerable to predation by harbour seals. Such conditions likely enable seals to consume many herring in one dive, whereas more widely dispersed herring at greater depths during the day would require seals to spend more energy on separate dives to locate and consume them.

Another advantage to crepuscular foraging may lie in the low light conditions during twilight, presenting a visual advantage for locating prey. Such an advantage could work in two ways. First, twilight illumination levels reduce the time and decrease the effects of eye adaptation to the low light conditions at depth. Bright surface

illumination during the day does not allow harbour seal eyes to accommodate to the low light intensity at greater depth. In the harp seal, the eye becomes fully dark-adapted in about 30 minutes (Lavigne et al. 1977). Second, at dawn and dusk the surface enhances the visual contrast of any object seen from below (Lythgoe 1979). Seals pursuing prey from beneath at twilight may have high success rates of capture.

This study documented some interesting and ecologically significant movement patterns of harbour seals. In addition to the resident population of harbour seals in Cowichan Bay (<120 seals), other seals moved into the estuary from surrounding areas throughout the year. During the fall, when many salmonids moved into Cowichan Bay, seals from surrounding areas spent more time there. At this time salmon was prevalent in harbour seal diet. Following the spawning of salmon, harbour seal numbers in Cowichan Bay decreased. Seals from surrounding areas spent less time in Cowichan Bay. It appears that there is much movement of harbour seals into and out of Cowichan Bay throughout the year, with more animals using the area when prey (salmonids) were abundant. The small number of long-range movements by harbour seals (>50 km) suggest that they are uncommon. The lack of information on juvenile harbour seal movement patterns during this study (no juveniles radio-tagged) may have biased movement patterns to shorter distances, however.

Haul-out patterns of harbour seals are affected by many factors, which include but are not limited to: human disturbance; access to haul-out substrates; air and water temperature; presence of predators; and diel availability of prey. Seasonal changes in these factors and interactions between them, combined with intrinsic variables concerned with breeding, moulting, or parturition, and the intrinsic variability among seals, make it difficult to distinguish the importance of each factor at this time.

Human disturbance of harbour seal haul-out behaviour at Cowichan Bay was infrequent during most of the year and at most tidal heights. At very high tides, tugboat activity (movement of booms) often caused seals to return to the water. Seals in this area appear to have habituated to the presence of boats, and often hauled out again within minutes of being disturbed. As human populations in coastal areas of British Columbia and seal populations increase, the effects of human disturbance are likely to change in many areas.

Air and water temperature likely had little effect on haul-out behaviour in this study as annual temperatures were well within harbour seal thermoneutral zones (Matsuura and Whittow 1974). Watts (1991) found that on calm, very hot days, harbour seals hauled out only for brief periods.

During moulting and the growth of new pelage (August to February) harbour seals spent more time hauled out. Moulting is facilitated by high peripheral temperatures, as skin temperatures above 17°C increase the rate of cell division.

No effects of terrestrial predators (excluding humans) on harbour seal haul-out behaviour were documented in this study (no interactions were observed). In other areas of the Pacific Northwest, wolves, bears, and eagles disrupt haul-out behaviour (King 1983). Killer whales eat harbour seals, but none was observed in Cowichan Bay during the study. Killer whales in British Columbia waters primarily have been observed near rocky haul-outs, which provide ready access to deep water (G. Ellis¹⁰ pers. comm.). The shallow waters of Cowichan Bay probably are not suitable for killer whales feeding on harbour seals.

The diel availability of prey appears to affect haul-out behaviour. The least amount of time spent hauled out was at dawn and dusk, which is when hake and herring, (crepuscular migrators) move toward the surface. At those times this time harbour seal foraging success may be high, making it preferred for foraging.

¹⁰G. Ellis, Pacific Biological Station, Nanaimo, B.C., Pers. comm. 1995.

There was no significant difference in haul-out behaviour between males and females. Sex differences in haul-out behaviour presumably were masked during lactation because lactating harbour seals, unlike other phocids, forage (Boness et al. 1994).

Documenting diel and seasonal haul-out patterns and relationships among intrinsic and extrinsic variables is important for conservation and management of harbour seals. The best time to census harbour seals is when most animals are hauled out (Olesiuk et al. 1990a). This study provides valuable seasonal, diel, and tidal information regarding when it is best to census harbour seals hauled out on logbooms in estuaries. In addition, the complex diel and seasonal relationships among harbour seal diet, abundance, distribution, and activity budgets examined during this study improve our understanding of harbour seal behaviour patterns in estuaries.

6. LITERATURE CITED

- Allen, S.G., Ainley, D.G., Page, G.W., and Ribic C.A. 1984. The effect of disturbance on harbor seal haul-out patterns at Bolinas Lagoon. California Fishery Bulletin **82**: 493-500.
- Antonelis, G.A., Lowry, M.S., DeMaster, D.P., and Fiscus, C.H. 1987. Assessing northern elephant seal feeding habits by stomach lavage. Mar. Mamm. Sci. **3**: 308-322.
- Beach, R.J., Geiger, A., Jefferies, S.J., Treacy, S., and Troutman, B.L. 1985. Marine mammals and their interactions with fisheries of the Columbia River and adjacent waters, 1980-1982. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Seattle, Wash.
- Bigg, M.A. 1969. The harbour seal in British Columbia. J. Fish. Res. Board Can. No. 172.
- Bigg, M.A. 1981. Harbour seal, *Phoca vitulina* Linnaeus, 1758 and *Phoca larga* Pallas, 1811. In Handbook of marine mammals. Edited by Ridgway, S.H. and R.J. Harrison. Vol. 2. Seals. Academic Press, London. pp. 1-27.
- Bigg, M.A., and Fawcett, I. 1985. Two biases in diet determination of northern fur seals (*Callorhinus ursinus*). In Marine mammals and fisheries. Edited by J.R. Beddington, R.J.H. Beverton, and D.M. Lavigne. George Allen & Unwin Publishing, London, U.K. pp. 285-291.
- Bigg, M.A., and Perez, M.A. 1985. Modified volume: a frequency-volume method to assess marine mammal food habits. In Marine mammals and fisheries. Edited by Beddington J.R., Beverton R.J.H., and D.M. Lavigne. George Allen & Unwin Publishing, London, U.K. pp. 277-283.
- Bigg, M.A., and Olesiuk, P.F. 1990. An elutriator for processing marine mammal scat. Mar. Mamm. Sci. **6**: 350-355.
- Bigg, M.A., Ellis, G.M., Cottrell, P., and Milette, L. 1990. Predation by harbour seals and sea lions on adult salmon in Comox Harbour and Cowichan Bay, British Columbia. Can. Tech. Rep. Fish. Aquat. Sci. No. 1769

- Bishop, R.H. 1967. Reproduction, age determination, and behavior of the harbour seal, *Phoca vitulina*, in the Gulf of Alaska. M.Sc. thesis, Univ. of Alaska, Fairbanks.
- Blaxter, J.H.S. 1985. The herring: a successful species? *Can. J. Aquat. Sci.* **42**: 21-30.
- Boness, D.J., Bowen, W.D., and Oftedal, O.T. 1994. Evidence of a maternal foraging cycle resembling that of otariid seals in a small phocid, the harbor seal. *Behav. Ecol. Sociobiol.* **34**: 95-104.
- Bonner, W.N. 1981. Grey seal, *Halichoerus grypus*. In *Handbook of marine mammals. Edited by S.H. Ridgway, and R.J. Harrison. Vol. 2. Seals. Academic Press, London. pp. 111-144.*
- Boulva, J., and McLaren, I.A. 1979. Biology of the harbour seal, *Phoca vitulina*, in eastern Canada. *J. Fish. Res. Board Can.* No. 200.
- Boveng, P. 1988. Status of Pacific harbor seal population on the U.S. west coast. Southwest Fish. Center Rep. 88-06.
- Brown, R.F., and Mate, B.R. 1983. Abundance, movements, and feeding habits of harbor seals, *Phoca vitulina*, at Netarts and Tillamook Bays, Oregon. *Fish. Bull.* **81**: 291-301.
- Calambokidis, J., Taylor, B.L., Carter, S.D., Steiger, G.H., Dawson, P.K., and Antruim, L.D. 1987. Distribution and haul-out behaviour of harbour seals in Glacier Bay, Alaska. *Can. J. Zool.* **65**: 1391-1396.
- Canadian Hydrographic Service. 1991, 1992. Canadian tide and current tables. Vol. 5. Fisheries and Oceans, Canada.
- Cannon, D.Y. 1987. Marine fish osteology. A manual for archaeologists. Dept. Anthropology, Simon Fraser Univ. Publ. No. 18.
- Cass, A.J., Beamish, R.J., Smith, M.S, and Scarsbook J.R. 1977. Hake and pollock study, Strait of Georgia cruise G.B. Reed, March 17-24, 1975. *Fish. Mar. Serv. Data Rep.* **50**: 1-66.
- Casteel, R.W. 1976. Fish remains in archaeology and paleo-environmental studies. Academic Press, London, U.K.

- Clements, E.T., Stevens, G.E., and Southworth, M. 1975. Sites of organic acid production and pattern of digesta movements in the gastrointestinal tract of swine. *J. Nutr.* **105**: 759-768.
- Colbourne, P.L., and Terhune, J.M. 1991. Harbour seals (*Phoca vitulina*) do not follow herring movements in the Bay of Fundy, Canada. *Ophelia* **33**: 105-112.
- Cottrell, P.E. (a). The lengths, widths and girths at which three harbour seal prey species must be torn apart to be consumed (in prep.).
- Cottrell, P.E. (b). Captive harbour seal feeding experiment examining the biases of secondary prey (in prep.).
- Croxall, J.P. 1993. Diet. *In Antarctic seals: research methods and techniques. Edited by R.M. Laws. Cambridge University Press, Cambridge, U.K. pp. 268-290.*
- da Silva, J., and Neilson, J.D. 1985. Limitations of using otoliths recovered in scats to estimate prey consumption in seals. *Can. J. Fish. Aquat. Sci.* **42**: 1439-1442.
- Dellinger, T., and Trillmich, F. 1988. Estimating diet composition from scat analysis of otariid seals (Otariidae): is it reliable? *Can. J. Fish. Aquat. Sci.* **42**: 1865-1870.
- Doutt, J.K. 1942. A review of the genus *Phoca*. *Annals of the Carnegie Museum* **29**: 61-125.
- Ellis, G.M., and Trites, A.W. 1992. The RAM-packs came back: a method for attaching and recovering pinniped data recorders. *J. Aquat. Mamm.* **18**: 61-64.
- Fedak, M.A., Anderson, S.S., and Curry, M.G. 1983. Attachment of a radio tag to the fur of seals. *J. Zool., Lond.* **200**: 298-300.
- Feltz, E.T., and Fay, F.H. 1966. Thermal requirements in vitro of epidermal cells from seals. *Cryobiol.* **3**: 261-264
- Fiscus, C.H. 1979. Interactions of marine mammals and Pacific hake. *U.S. Natl. Mar. Fish. Serv., Mar. Fish. Rev.* **41**: 1-9.

- Fiscus, C.H. 1980. Marine mammal-salmonid interactions: a review. In salmonid ecosystems of the North Pacific. Edited by McNeil, W.J., and D.C., Himsworth. Oregon State University Press, Corvallis.
- Fisher, H.D. 1952. The status of the harbour seal in British Columbia, with particular reference to the Skeena River. J. Fish. Res. Board Can. No. 93.
- Fitch, J.E., and Brownell, R.L. 1968. Fish otoliths in cetacean stomachs and their importance in interpreting feeding habits. J. Fish. Res. Board Can. **25**: 2561-2574.
- Gearin, P.J., Pfeifer, R., Jefferies, S.J., DeLong, R.L., and Johnson, M.A. 1988. Results of the 1986-1987 California sea lion - steelhead trout predation control program at the Hiram M. Chittenden Locks. Northwest and Alaska Fisheries Center Rep. 88-30.
- Graybill, M.R. 1981. Haul out patterns and diet of harbour seals, *Phoca vitulina*, in Coos County, Oregon. M.S. thesis, Univ. of Oregon, Eugene.
- Green, K., Williams, R., Handasyde, K.A., Burton, H.R., and Shaughnessy, P.D. 1990. Interspecific and intraspecific differences in the diets of Fur seals, *Arctocephalus* species (Pinnipedia: Otariidae) at Macquarie Island. Austral. Mammal. **13**: 193-200.
- Hansel, H.C., Duke, S.D., Lofty, P.T., and Gray, J.A. 1988. Use of diagnostic bones to identify and estimate original lengths of ingested prey fishes. Trans. Amer. Fish. Soc. **117**: 55-62.
- Harkonen, T.J. 1986. Guide to the otoliths of the bony fishes of the northeast Atlantic. Hellerup, Denmark: Danbiu.
- Harkonen, T.J. 1987. Seasonal and regional variations in the feeding habits of the harbour seal, *Phoca vitulina*, in the Skagerrak and the Kattegat. J. Zool., Lond. **219**: 101-111.
- Harkonen, T.J., and Heide-Jorgensen, M.P. 1990. Comparative life histories of East Atlantic and other harbour seal populations. Ophelia **32**: 211-235.
- Harkonen, T.J., and Heide-Jorgensen, M.P. 1991. The harbour seal *Phoca vitulina* as a predator in the Skagerrak. Ophelia **34**: 191-207.

- Hart, J.L. 1973. Pacific fishes of Canada. Fish. J. Res. Board Can. No. 180.
- Harvey, J.T. 1987. Population dynamics, annual food consumption, dive behaviors, and movements of harbor seals, *Phoca vitulina richardsii*, in Oregon. Ph.D. dissert., Oregon State Univ., Corvallis.
- Harvey, J.T. 1989. Assessment of errors associated with harbour seal (*Phoca vitulina*) faecal sampling. J. Zool., Lond. **219**: 101-111.
- Harvey, J.T., and Antonelis, G.A. 1994. Biases associated with non-lethal methods of determining the diet of northern elephant seals. Mar. Mamm. Sci. **10**: 178-187.
- Harwood, J., and Croxall, J.P. 1988. The assessment of competition between seals and commercial fisheries in the North Sea and the Antarctic. Mar. Mamm. Sci. **4**: 13-33.
- Hawes, S.D. 1983. An evaluation of California sea lion scat samples as indicators of prey importance. M.A. thesis, San Francisco State Univ., San Francisco.
- Helm, R.C. 1979. Initial defecation time and intestinal length of three species of pinnipeds: *Phoca vitulina*, *Zalophus californianus*, and *Mirounga angustirostris*. M.A. thesis, California State University, California.
- Healy, M.C. 1991. Life history of chinook salmon (*Oncorhynchus tshawytscha*). In Pacific salmon life histories. Edited by Groot C. and L. Margolis. U.B.C. Press, Vancouver. pp. 313-393.
- Hoover, A.A. 1983. Behavior and ecology of harbor seals *Phoca vitulina richardsi* inhabiting glacial ice in Aialik Bay, Alaska. M.S. thesis, Univ. of Alaska, Fairbanks.
- Hoover, A.A. 1988. Harbour seal. In Selected marine mammals of Alaska: Species accounts with research and management recommendations. Edited by J.W. Lentfer. Mar. Mammal. Comm. Rep., Washington, D.C. pp 125-157.
- Jameson, R.J., and Kenyon, K.W. 1977. Prey of sea lions in the Rogue River, Oregon. J. Mammal. **58**: 672.
- Jefferies, S.J. 1986. Seasonal movements and population trends of harbor seals in the Columbia River and adjacent waters of Washinton and Oregon: 1976-82. Unpubl. ms.

- Jobling, M. 1987. Marine mammal faeces samples as indicators of prey importance: a source of error in bioenergetics studies. *Sarsia* **71**: 255-260.
- Jobling, M., and Breiby, A. 1986. The use and abuse of fish otoliths in studies of feeding habits of marine piscivores. *Sarsia* **71**: 265-274.
- Jones, A.C. 1962. The biology of the euryhaline fish *Leptocottus armatus armatus* (Girard). Univ. Calif. Publ. Zool. **67**: 321-367
- Lavigne, D.M., Bernholz, C.D., and Ronald, K. 1977. Functional aspects of pinniped vision. In Functional anatomy of marine mammals. Edited by R.J. Harrison, Academic Press.
- Loughlin, T.R. 1993. Abundance and distribution of harbor seals (*Phoca vitulina richardsi*) in southeastern Alaska during 1993. Unpubl. ms., NMFS, NMML, Seattle Wash.
- Lowry, L.F., and Frost, K.J. 1985. Biological interactions between marine mammals and commercial fisheries in the Bering Sea. In Marine mammals and fisheries. Edited by J.R. Beddington, R.J.H. Beverton, and D.M. Lavigne. George Allen & Unwin Publishing, London, U.K. pp. 41-61.
- Lythgoe, J.N. 1979. The ecology of vision. Clarendon Press, Oxford.
- Mansfield, A.W. 1967. Distribution of the harbour seal, *Phoca vitulina* Linnaeus, in Canadian arctic waters. *J. Mammal.* **48**: 249-257.
- Markussen, N.H. 1993. Transit time of digesta in captive harbour seals (*Phoca vitulina*). *Can. J. Zool.* **71**: 1071-1073.
- Mathews and Kelly 1994. Extreme temporal variation in harbor seal (*Phoca vitulina richardsi*) numbers in Glacier Bay, a glacial fjord in southeast Alaska (in prep.).
- Matsuura, D.T., and Whittow, G.C. 1973. Oxygen uptake of the California sea lion and harbor seal during exposure to heat. *Am. J. Physiol.* **225**: 711-715.

- McConnell, B.J., Prime, J.H., Hilby, A.H, and Harwood, J. 1984. Grey seal diet. In Interactions between grey seals and UK fisheries. Natural Environ. Research Council, Sea Mammal Research Unit, Cambridge. pp. 148-183
- McFarlane, G.A., and Beamish, R.J. 1985. Biology and fishery of Pacific whiting, *Merluccius productus*, in the Strait of Georgia. Mar. Fish. Rev. **47**: 23-34.
- McLaren, I.A. 1966. Taxonomy of harbour seals of the western North Pacific and evolution of certain other hair seals. J. Mammal. **47**: 466-473.
- Murie, D.J. 1987. Experimental approaches to stomach content analysis of piscivorous marine mammals. In Approaches to marine mammal energetics. Edited by A.C. Huntly, D.P. Costa, G.A.J. Worthy, and M.A. Castellini. Soc. Mar. Mamm., Spec. Publ. No. 1. pp. 147-163.
- Murie, D.J., and Lavigne, D.M. 1985. Digestion and retention of Atlantic herring otoliths in the stomachs of grey seals. In Marine mammals and fisheries. Edited by J.R. Beddington, R.J.H. Beverton, and D.M. Lavigne. George Allen & Unwin, Publishing, London, U.K. pp. 292-299.
- Murie, D.J., and Lavigne, D.M. 1986. Interpretation of otoliths in stomach content analyses of phocid seals: quantifying fish consumption. Can. J. Zool. **64**: 1152-1157.
- Murie, D.J., and Lavigne, D.M. 1991. Food consumption of wintering harp seals, *Phoca groenlandica*, in the St. Lawrence estuary, Canada. Can. J. Zool. **69**: 1289-1296.
- Naito, Y., and Nishiwaki, M. 1973. Kuril harbour seal (*Phoca kurilensis*). In Seals. IUCN Publ. New Ser., Suppl. Paper No. 39. pp. 44-49.
- Olesiuk, P.F., Bigg, M.A., and Ellis, G.M. 1990a. Recent trends in the abundance of harbour seals, (*Phoca vitulina*) in British Columbia. Can. J. Fish Aquat. Sci. **47**: 992-1003.
- Olesiuk, P.F., Bigg, M.A., Ellis, G.M., Crockford, S.J, and Wigen, R.J. 1990b. An assessment of the feeding Habits of harbour seals (*Phoca vitulina*) in the Strait of Georgia, British Columbia, based on scat analysis. Can. Tech. Rep. Fish. Aquat. Sci. No. 1730.

- Olesiuk, P.F. 1993. Annual prey consumption by harbour seals (*Phoca vitulina*) in the Strait of Georgia, British Columbia. Fish. Bull. **91**: 491-515.
- Olesiuk, P.F., Cottrell, P.E., and Neville, C.E. Foraging patterns of harbour seals (*Phoca vitulina*) on prespawning salmon in Comox Harbour and lower Puntledge River (in prep.).
- Pastukhov, V.D. 1975. Some observations on the Baikal seal under experimental conditions. Morskije mlekopitaiushchie 1:105-110. Translated by the Canadian Fish and Marine Service (No. 3544).
- Pauli, B.D., and Terhune, J.M. 1987. Tidal and temporal interaction on harbour seal haul-out patterns. J. Aquat. Mamm. **13**: 93-95.
- Perez, M.A., and Bigg, M.A. 1986. Diet of northern fur seals, *Callorhinus ursinus*, off western North America. Fish. Bull. **84**: 957-971.
- Pierce, G.J., Boyle, P.R., and Thompson, P.M. 1990. Diet selection by seals. In Trophic relationships in the marine environment, 1990. Edited by Barnes M., and Gibson R.N. Aberdeen University Press, Aberdeen, Scotland. pp. 222-238.
- Pierce, G.J., Thompson, P.M., Miller, A., Diack, S.W., Miller, D, and Boyle, P.R. 1991. Seasonal variation in the diet of common seals (*Phoca vitulina*) in the Moray Firth area of Scotland. J. Zool., Lond. **223**: 641-652.
- Pierce, G.J., Boyle, P.R., and Diack, S.W. 1991. Identification of fish otoliths and bones in faeces and digestive tracts of seals. J. Zool., Lond. **224**: 320-328
- Pitcher, K.W., and Calkins, D. 1979. Biology of the harbor seal, (*Phoca vitulina richardsi*), in the gulf of Alaska. U.S. Dep. Commer., NOAA, OCSEAP Final Rep. **19**: 231-310.
- Pitcher, K.W. 1980a. Food of the harbour seal, *Phoca vitulina*, in the Gulf of Alaska. Fish. Bull. **78**: 544-549.
- Pitcher, K.W. 1980b. Stomach contents and feces as indicators of harbour seal, *Phoca vitulina*, foods in the Gulf of Alaska. Fish. Bull. **78**: 797-798.

- Pitcher, K.W., and McAllister, D.C. 1981. Movements and haulout behaviour of radio-tagged harbor seals, *Phoca vitulina*. *Can. Field. Nat.* **95**: 292-297.
- Pitcher, K.W. 1984. The harbour seal (*Phoca vitulina richardsi*). In *Marine mammal species accounts*. Edited by Burns J.J., K.J. Frost, and L.L. Lowry. Alaska Dep. Fish and Game Bull. **7**: 65-70.
- Prime, J.H. 1979. Observations on the digestion of some gadoid fish otoliths by a young common seal. *Int. Counc. Explor. Sea C.M.* 1979/N No. 14.
- Prime, J.H., and Hammond, P.S. 1987. Quantitative assessment of grey seal diet from faecal analysis. In *Approaches to marine mammal energetics*. Edited by A.C. Huntly, D.P. Costa, G.A.J. Worthy, and M.A. Castellini. *Soc. Marine Mammal., Spec. Publ. No. 1.* pp. 165-181.
- Prime, J.H., and Hammond, P.S. 1990. The diet of grey seals from the south-western North Sea assessed from analyses of hard parts found in faeces. *J. Appl. Ecol.* **27**: 435-447.
- Rae, B.B. 1968. The food of seals in Scottish waters. *Marine research* 1968. No. 2.
- Rae, B.B. 1973. Further observations on the food of seals. *J. Zool., Lond.* **169**: 287-297.
- Reijnders, P.J.H., Brasseur, S., van der Toorn, J., van der Wolf, P., Boyd, I., Harwood, J., Lavigne, D.M., Lowry, L., and Stuart, S. 1993. Seals, fur seals, sea lions and walruses: status of pinnipeds and conservation action plan. IUCN, Gland, Switzerland.
- Ridgway, S.H., Harrison, R.J., and Joyce, P.L. 1975. Sleep and cardiac rhythm in the grey seal. *Science*, **187**: 553-555.
- Roffe, T.J. 1981. Population, food habits, and behavior of pinnipeds in the Rogue River and their relation to salmonid runs. Ph.D. dissert., Oregon State Univ., Corvallis.
- Roffe, T.J., and Mate, B.R. 1984. Abundances and feeding habits of pinnipeds in the Rogue River, Oregon. *J. Wildl. Manage.* **48**: 1262-1274.

- Sandercock, F.K. 1991. Life histories of coho salmon (*Onchorhynchus kisutch*). In Pacific salmon life histories. Edited by C. Groot and L. Margolis. U.B.C. Press, Vancouver. pp. 397-464.
- Scheffer, V.B., and Slipp, J.W. 1944. The harbour seal in Washington State. Amer. Midl. Nat. **32**: 373-416.
- Schneider, D.C., and Payne, P.M. 1983. Factors affecting haul-out of harbor seals at a site in southeastern Massachusetts. J. Mamm. **64**: 518-520.
- Shaffer, K. 1989. Seasonal and site variations in the diet of harbor seals, *Phoca vitulina richardsi*, in northern California. M.S. thesis, California State Univ., Humboldt, California.
- Shaughnessy, P.D., and Fay, F.H. 1977. A review of the taxonomy and nomenclature of North Pacific harbour seals. J. Zool., Lond. **182**: 385-419.
- Shaw, W., McFarlane, G.A, and Kieser, R. 1990. Distribution and abundance of the Pacific hake (*Merluccius productus*) spawning stocks in the Strait of Georgia, British Columbia, based on trawl and acoustic surveys in 1981 and 1988. Proceedings of the symposium on application of stock assessment techniques to gadids. Vancouver, Canada. International North Pacific Fisheries Commission Bull. **50**: 121-134.
- Spalding, D. 1964. Comparative feeding habits of the fur seal, sea lion and harbour seal on the British Columbia coast. Can Tech. Rep. Fish. Aquat. Sci. No. 146.
- Stewart, B.S. 1981. Seasonal abundance, distribution, and ecology of the harbour seal (*Phoca vitulina richardsi*) on San Miguel Island, California. M.S. thesis, San Diego State Univ., San Diego.
- Stewart, B.S. 1984. Diurnal hauling patterns of harbor seals at San Miguel Island, California. J. Wild. Manag. **48**: 1459-1461.
- Sullivan, R.M. 1980. Seasonal occurrence and haul-out use in pinnipeds along Humboldt County, California. J. Mamm. **61**: 754-760.

- Tanasichuk, R.W., Ware, D.M., Shaw, W., and McFarlane, G.A. 1991. Variations in the diet, daily ration, and feeding periodicity of Pacific hake (*Merluccius productus*) and spiny dogfish (*Squalus acanthias*) off the west coast of Vancouver Island. *Can. J. Fish. Aquat. Sci.* **48**: 2118-2128.
- Terhune, J.M., and Almon, M. 1983. Variability of harbour seal numbers on haul-out sites. *J. Aquat. Mamm.* **10**: 71-78.
- Thompson, J.M., and McFarlane, G.A. 1982. Distribution and abundance of Pacific hake and walleye pollock in the Strait of Georgia, March 24 - May 2, 1981. *Can. Tech. Rep. Fish. Aquat. Sci. No.* 1661.
- Thompson, P.M. 1989. Seasonal changes in the distribution and composition of common seal *Phoca vitulina* haul-out groups. *J. Zool., Lond.* **212**: 597-603.
- Thompson, P.M., Fedak, M.A., McConnell, B.J., and Nicholas, K.J. 1989. Seasonal and sex related variation in the activity patterns of common seals (*Phoca vitulina*). *J. Appl. Ecol.* **26**: 521-535.
- Thompson, P.M., and Harwood, J. 1990. Methods for estimating population size of common seal (*Phoca vitulina*). *J. Appl. Ecol.* **27**: 924-938.
- Ware, D.M., and McFarlane, G.A. 1994. Climate-induced changes in Pacific hake (*Merluccius productus*) abundance and pelagic community interactions in the Vancouver Island Upwelling System. *Can. Spec. Publ. Fish. Aquat. Sci.* (in press).
- Watts, P. 1991. Hauling out behaviour of harbour seals (*Phoca vitulina richardsi*), with particular attention to thermal constraints. Ph.D. dissert., Univ. of British Columbia, Vancouver.
- Wise, M.H. 1980. The use of fish vertebrae in scats for estimating prey size of otters and mink. *J. Zool., Lond.* **192**: 25-31.
- Yochem, P.K., Stewart, B.S., DeLong, R.L., and DeMaster, D.P. 1987. Diel haul-out patterns and site-fidelity of harbour seals (*Phoca vitulina richardsi*) on San Miguel Island, California in autumn. *Mar. Mamm. Sci.* **3**: 323-332.
- Zar, J.H. 1984. *Biostatistical analysis*. Prentice-Hall, New Jersey.

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Cottrell, P.E. The lengths, widths, and girths at which
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Cottrell, P.E. Captive harbour seal feeding experiments
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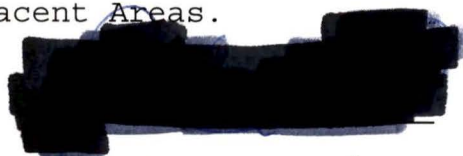
Olesiuk, P.F., Cottrell, P.E., and Neville, C.E. Foraging
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Title of Thesis: Diet, Activity Budgets, and Movement Patterns of Harbour Seals (*Phoca vitulina*) in Cowichan Bay and Adjacent Areas.

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April 19/95

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