

LIFE HISTORY PARAMETERS OF THE PACIFIC WHITE-SIDED DOLPHIN
(*Lagenorhynchus obliquidens*)
AND ITS DIET AND OCCURRENCE
IN THE COASTAL WATERS OF BRITISH COLUMBIA

by

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ABSTRACT

Throughout most of their range, Pacific white-side dolphins (*Lagenorhynchus obliquidens*) inhabit pelagic waters, or the continental shelf and slope. In recent years, however, their abundance has increased markedly in the nearshore waters of British Columbia, and the species is likely the most numerous cetacean in the region. In this study I examined the timing of this increase, and ecological and population factors that may have contributed to it.

No systematic population censuses of Pacific white-sided dolphins have been conducted in British Columbia. However, because the species is gregarious, active at the surface, and interacts with vessels, many mariners take note of it. I surveyed mariners on the timing and locations of their sightings, and received 165 written responses. They reported relatively few sightings between 1978 and 1984, and frequent sightings after 1985.

I estimated life-history parameters for Pacific white-sided dolphins using data taken from animals that were killed accidentally or deliberately during fisheries, or for scientific reasons, or recovered as stranded carcasses. The average age at first reproduction was 8.5 years for females, gestation was 12.0-12.2 months, and the calving interval was 4.67 years ($S.E.=1.81$). The rate of population increase was estimated to be between 0.94-1.02/yr, reflecting a stationary population. This suggests that the increase in abundance in British Columbia cannot be explained by population growth alone, and must have resulted, at least partly, from a movement of dolphins from other areas.

To examine the potential role of prey in the movement of dolphins, I examined their diet in inshore waters, using prey fragment sampling ($n=64$) and stomach content analyses ($n=11$). Prey consisted mostly of herring (*Clupea harengus*), salmon (*Oncorhynchus* spp.), cod (Family Gadidae), and shrimp (Order Decapoda). Previous studies found that in offshore areas, dolphins feed on mesopelagic fish and squid, thus dolphins moving inshore may be exploiting new food resources. The inshore movement of dolphins appears to coincide with a 'regime shift', characterised by a change in water temperatures. It is suggested that this may have caused changes in the relative abundance of the prey of Pacific white-sided dolphins.

TABLE OF CONTENTS

ABSTRACT	Page ii
LIST OF TABLES	vii
LIST OF FIGURES	viii
PREFACE	x
ACKNOWLEDGEMENTS	xi
CHAPTER ONE General Introduction	1
REFERENCES	4
CHAPTER TWO Changes in the Abundance of Pacific White-sided Dolphins in the Coastal Waters of British Columbia	5
ABSTRACT	5
INTRODUCTION	5
METHODS	7
RESULTS	8
DISCUSSION	11
REFERENCES	17
CHAPTER THREE Life History and Population Parameters of Pacific White-sided Dolphins (<i>Lagenorhynchus obliquidens</i>)	27
ABSTRACT	27
INTRODUCTION	28
LIFE HISTORY TRAITS OF PACIFIC WHITE-SIDED DOLPHINS	30
Growth	30

TABLE OF CONTENTS (Continued)

	Page
CHAPTER THREE (Continued)	
Sources of Data	30
Length, Weight and Age of Animals Sampled	30
Relationship of Weight to Length	32
Age at Length Estimates: Comparing Growth Models	32
Reproduction	33
Age at Sexual Maturity and Age at First	
Pregnancy	33
Annual Pregnancy Rate	35
Gestation Period	35
Calving Period	36
Lactation Period	37
Resting Period	38
Calving Interval	38
Survival	39
Age Specific Survival	39
 POPULATION PARAMETERS FOR PACIFIC WHITE-SIDED DOLPHINS	 41
Population Growth	41
Impact of Driftnet Fishing	42
Population Estimates for the North Pacific	42
REFERENCES	45
 CHAPTER FOUR Diet and Feeding Behaviour of Pacific White-sided Dolphins Based on Prey Fragment and Stomach Content Analyses	 55
ABSTRACT	55
INTRODUCTION	56
METHODS	57
Sampling Prey Fragments	58
Stomach Contents	59
RESULTS	60
Group Size and Dive Durations	60
Sampling Prey Fragments	60
Stomach Contents	61
DISCUSSION	63
Prey Consumed by Pacific White-sided Dolphins	63
The Collection of Prey Fragments to Confirm Diet	65

TABLE OF CONTENTS (Continued)

	Page
CHAPTER FOUR (Continued)	
Foraging Behaviour	66
Comparison With Other Schooling Delphinids	68
Daily Consumption Estimates	70
Total Population Consumption	71
REFERENCES	72
 CHAPTER FIVE	
Conclusions and Recommendations for Further Research	79
Recommendations for further research	80
REFERENCES	83
 APPENDIX ONE	
Questionnaire distributed to mariners	86
 APPENDIX TWO	
Prey recorded in the diet of Pacific white-sided dolphins in the North Pacific	91

LIST OF TABLES

	Page
Table 1. Mariner's responses to the question "Has the abundance of Pacific white-sided dolphins increased, decreased or remained the same since you first saw them?". Experienced mariners were those with more than 10 years of experience.	10
Table 2. Distribution of first sightings of Pacific white-sided dolphins in inshore waters by all respondents. Number of observers are those who were on the water during each 5 year interval.	10
Table 3. Summary statistics for adult Pacific white-sided dolphins based on data sources listed in the text. Number of animals examined is included in parentheses.	31
Table 4. Growth models for male and female Pacific white-sided dolphins.	33
Table 5. Parameter estimates for Barlow and Boveng's (1991) age-specific mortality model for female Pacific white-sided dolphins, northern fur seals, old world monkeys and human females.	41
Table 6. The number of encounters and dates surveyed for each of the three study areas.	59
Table 7. Prey of Pacific white-sided dolphins in the inshore waters of British Columbia, based on the collection of fragments following foraging bouts. Scientific names are listed in Appendix 2.	62
Table 8. Stomach contents of 11 Pacific white-sided dolphins recovered in British Columbia between 1990 and 1996.	62
Table 9. Percent occurrence of the principal prey of Pacific white-sided dolphins based on published stomach content analyses.	67

LIST OF FIGURES

	Page
Figure 1. Distribution of sighting effort per month by all observers. Sighting effort was the product of the number of hours per day and the number of days per month each observer was on the water.	24
Figure 2. The coastal waters of British Columbia and Alaska, showing geographic areas mentioned in the text.	25
Figure 3. Distribution of observer months in each coastal area.	26
Figure 4. The number of observers per year and the proportion of those observers who saw dolphins for the first time.	26
Figure 5. Age-frequency distribution of 186 females and 229 male Pacific white-sided dolphins (based on data sources cited in the text). The solid bars indicate females and the clear bars are the number of males in each age group.	51
Figure 6. The median ages of dolphins sampled by the collection of stranded animals ($n=183$), and by the drive ($n=88$) and driftnet ($n=180$) fisheries. Boxes are notched and return to full width at the 95% confidence limits.	51
Figure 7. Weight (kg) vs. lengths (cm) for 35 male and 54 female Pacific white-sided dolphins. Males and females are shown as hollow and closed circles respectively.	52
Figure 8. Length at age measurements for 206 female (hollow circles) and 250 male (solid circles) fitted with the Bertalanffy growth curve from Table 4, where $Length(t)=191.41(1-e^{-0.461(t+1.75)})$, and t is age in years.	52

LIST OF FIGURES (Continued)

	Page
Figure 9. Number of corpora by age for female Pacific white-sided dolphins (from data in Walker <i>et al.</i> 1986). Regression of the line is $ASM = -5.53 + 0.861X$, where ASM is the age of sexual maturity, and X is the number of corpora ($r^2_{corrected} = 0.83$).	53
Figure 10. Survivorship curves for humans, old world monkeys, northern fur seals, and Pacific white-sided dolphins. All but the dolphin parameter values are from Barlow and Boveng (1991) and were scaled to the lifespan of Pacific white-sided dolphins.	53
Figure 11. Range of Pacific white-sided dolphins in the Pacific Ocean. The outer lines indicate the known range for the species. The black shading indicates areas where animals were sighted during observer programs in the late 1980's and early 1990's, based on sighting data from Buckland <i>et al.</i> (1993), Hobbs and Jones (1993) and Miyashita 1993).	54
Figure 12. Net used to collect fragments of prey. Fish scales can be seen in the centre of the net.	77
Figure 13. Foraging leaps by Pacific white-sided dolphins	77
Figure 14. The distribution of encounter hours and the number of prey fragments recovered during those encounter hours as indicated by cross hatches, for the 1995 field season.	78

PREFACE

Earlier versions of Chapters 3 and 4 of this thesis were presented at the 48th International Whaling Commission meeting in Aberdeen, Scotland in June, 1996. Chapter 3 was presented as SC/48/SM45 (Diet and feeding behaviour of Pacific white-sided dolphins as revealed through the collection of prey fragments and stomach content analyses). Chapter 4 was presented as SC/48/SM46 (Life history and population parameters of Pacific white-sided dolphins (*Lagenorhynchus obliquidens*)). Modified versions of these chapters are forthcoming in the 1997 *Report of the International Whaling Commission* Volume 47.

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Much of the work that has gone into this thesis was conducted in the coastal waters of British Columbia, where I was helped by many people. Special thanks go to my volunteer assistants Lance Barrett-Lennard, David Fernandez, Rachel Holt and Linda Kalban for going above and beyond the call of duty, enduring 20 hour days with me and all my equipment on a 6m boat, tolerating my homebrew and always maintaining good humour. I also thank the fishermen and other mariners who shared their observations and experience openly and called me on the VHF regularly to report sightings of dolphins. There is a wealth of knowledge in the experiences of those who spend so much time travelling along our coast. I would like to particularly thank those who took the time to complete my survey.

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CHAPTER ONE: General Introduction

From 1981 to 1988 I worked as a lighthouse keeper at remote locations along the coast of British Columbia. Despite the fact that I spent hours per day scanning the water from shore or travelling in small boats, it was not until 1986 that I first saw Pacific white-sided dolphins (*Lagenorhynchus obliquidens*). Over the next few years, I sighted them more frequently, especially in the spring and fall. Many other mariners observed the species for the first time during this period as well. Unlike populations of harbour seals and California sea lions that have been increasing in British Columbia since the 1970's due to a release from hunting pressure (Olesiuk and Bigg, 1988), the increase in dolphin sightings could not be explained by a cessation of harvesting. Pacific white-sided dolphins have not been hunted in the eastern North Pacific this century, and the only significant known sources of anthropogenic mortality were due to bycatch associated with the high-seas flying-squid driftnet fishery between 1978 and 1991 (Tanaka, 1993), and to drive fisheries off Japan (Kasuya, 1995).

Pacific white-sided dolphins are now almost certainly the most abundant cetacean in the nearshore waters of British Columbia, yet little is known of their absolute numbers or ecology, particularly in inshore waters. If there was a terrestrial equivalent roaming the prairies, it would no doubt have been the subject of numerous investigations. The paucity of studies on this and other common cetacean species reflects the challenges inherent in studying marine animals that are not harvested.

Pacific white-sided dolphins are not the only cetacean to show an apparent change in distribution or abundance. On the coast of British Columbia there are three forms of killer whale: *resident* fish-eating killer whales, *transient* mammal-eating killer whales and *offshore* killer whales (Ford *et al.* 1994). The offshore form of killer whale was first encountered by researchers off the west coast of Vancouver Island in 1989. This group of killer whales is not well understood but it is thought that they spend the majority of time foraging on the continental shelf. From 1977 to 1992 there were no sightings of these whales in Johnstone Strait, despite intensive research effort on residents and transients in the area. Since 1993, offshore whales are known to have visited Johnstone Strait and adjacent areas eight times (G. Ellis, Dept. of Fisheries, pers. comm.). It will likely be many years before we can move beyond speculation about the life history of these animals and their apparent change in distribution, since sightings of offshore killer whales in all areas are relatively rare. By comparison, Pacific white-sided dolphins are sighted frequently and are, therefore, more easily studied.

The results presented in this thesis focus on three main questions: (i) Has the abundance or distribution of Pacific white-sided dolphins in inshore waters changed? (ii) What are the population dynamics of the species and could population growth explain the increase in sightings inshore? (iii) What do Pacific white-sided dolphins feed on in coastal areas and how may this have contributed to a change in distribution?

Chapter 2 reports on the results of a survey of mariners designed to quantify the common perception that dolphins were increasing in abundance inshore, as there were no sources of data

to corroborate or refute these accounts. I asked mariners when and where they first saw dolphins, and whether they believed the population to be growing or declining. I focused on the responses of those with more than 10 years of experience, and I invited all observers to include any other observations that they felt might be relevant.

Second, I estimated basic population and life history parameters for Pacific white-sided dolphins, in order to determine whether the increase in dolphin sightings could be explained by population growth. To estimate growth rates, I compiled published records of demographic and life history data from the driftnet and drive fisheries in the North Pacific, as well as stranded and scientifically harvested animals. Although a reasonable amount of raw data had been collected on this species, it had not been analyzed. I discuss my results, as well as the limitations of these sources of data, in Chapter 3.

Third, it was important to understand what the dolphins were feeding on in inshore waters, to determine whether their presence inshore might have been due to a change in the distribution of their prey offshore. In offshore waters, Pacific white-sided dolphins feed on mesopelagic fish and squid (Walker and Jones, 1993). In Chapter 4, I report the results obtained from a study of the feeding habits of dolphins in nearshore areas, using both stomach content analyses and prey-fragment sampling methods, and compare these results with those of studies of Pacific white-sided dolphins from other locations. I conclude (Chapter 5) by summarizing the results of these three endeavours, and by making recommendations for further research.

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CHAPTER TWO: Changes in the Abundance of Pacific White-sided Dolphins in the Coastal Waters of British Columbia

ABSTRACT

Pacific white-sided dolphins (*Lagenorhynchus obliquidens*) are frequently seen in the coastal waters of British Columbia, but have never been systematically surveyed in that area. Because anecdotal reports indicated that the species was formerly rare near the coast, I surveyed mariners for recent and past sighting information. Of 165 respondents, 109 had seen Pacific white-sided dolphins and had more than 10 years of experience on the British Columbian coast. Few respondents reported sightings between 1978 and 1984, but sighting frequencies began to increase in 1985. Over 65% of the respondents believed that the abundance of dolphins had increased since they first saw them, and 22% believed that the population had remained the same. This apparent increase in abundance is discussed in the context of data on climate change, fluctuations in the abundance of forage fish species, and the recoveries of dolphin remains from aboriginal midden sites.

INTRODUCTION

Concern over the effects of climate change, global warming and the impacts of over-fishing have led to questions about whether changes in the abundance of certain species have natural or anthropogenic causes (see papers in Keller, 1993; Beamish, 1995). Within the last two decades, there has been a significant decline of Steller sea lion (*Eumetopias jubatus*), Red-legged Kittiwake (*Rissa brevirostris*), and northern fur seal (*Callorhinus ursinus*) populations in the

North Pacific (Merrick et al. 1987; Springer, 1993; Trites, 1992), yet pink and sockeye salmon (*Oncorhynchus gorbuscha* and *O. nerka*) populations have doubled in productivity since the 1950's (Hare and Francis, 1995; Brodeur and Ware, 1995). Anecdotal accounts suggest that Pacific white-sided dolphins (*Lagenorhynchus obliquidens*) have increased markedly in abundance along certain areas of the British Columbia coast since the mid-1980's. These gregarious dolphins travel in large groups, sometimes exceeding 1,000 animals in size, and are known for the wide variety of surface behaviours they display (Leatherwood and Reeves, 1983). However, their distribution is primarily in temperate waters along the continental shelf and slope, and further offshore (Leatherwood et al. 1984).

C.M. Scammon, a 19th century whaling captain, suggested that *L. obliquidens* "has the widest range, congregates in the largest numbers and exhibits more activity than any other of the Dolphin family" (Scammon, 1874). Buckland et al. (1993) estimate the total North Pacific population to be 931,000 dolphins (95%CI=204,000-4,216,000). This estimate, based on ship surveys, may be biased upwards significantly, because most sightings of dolphins were within 100m of the trackline, indicating that the dolphins were strongly attracted to the research vessels. This source of bias was quantified by Turnock and Quinn (1991) for Dall's porpoises (*Phocoenoides dalli*), which are also strongly attracted to boats. Pacific white-sided dolphins are even more attracted to boats than Dall's porpoises (unpubl. data). If Turnock and Quinn's (1991) vessel attraction correction factor is applied to white-sided dolphins, then the population in the North Pacific is more like 223,000 animals (95%CI=49,440-1,011,840). Unfortunately, no population censuses of these dolphins have been conducted in the coastal waters of British

Columbia. In the light of anecdotal reports of an increase in the numbers of dolphins in nearshore areas, I conducted a survey of mariners to obtain information regarding the species' occurrence and abundance.

Questionnaires distributed to lay people have been used in previous studies to obtain post-hoc estimates of animal abundance and/or distribution when no data were available from other sources. For example, Chitty (1950a,b) used this method to determine the onset and duration of cycles in snowshoe hare, lemming, mouse, snowy owl and Arctic fox populations. More recently, a survey of mariners was used to estimate the abundance of killer whales in British Columbia. The accuracy of this survey was later confirmed by population estimates based on photo-identification studies of all individual killer whales (Bigg *et al.* 1987). Here I report the results of a survey which asked mariners where and when they first saw dolphins, and whether they perceived dolphin populations to be increasing, decreasing or remaining the same. Although mariners' recollections were often imprecise, collectively they clearly indicate an increase in dolphin abundance in inshore waters. I discuss the results of this survey in the context of changes in the abundance of other species, as well as in relation to ecosystem-level changes presently taking place in the North Pacific Ocean.

METHODS

During the spring of 1996 I distributed a four page survey to over 500 mariners in British Columbia and Alaska. The survey consisted of a one-page explanatory letter, an information sheet on the differences between Dall's porpoises, harbour porpoises (*Phocoena phocoena*) and

Pacific white-sided dolphins, and a two page questionnaire (Appendix 1). The results of these surveys were compiled to produce an account of the experience and primary activities of the observers, the geographical areas in which they worked, when and where they first saw dolphins, and their perceptions on whether the distribution and abundance of dolphins had changed or remained the same.

RESULTS

I did not analyze any survey responses in which the species identification was uncertain. The use of the information sheet explaining the difference between white-sided dolphins and the two species of porpoises was helpful in this process, and only four completed questionnaires were rejected. One hundred and sixty-five of the approximately 500 mariners (33%) provided usable responses to the survey. They came from a wide variety of backgrounds and included commercial fishermen (35), tourboat operators (28), Department of Fisheries, and Ministry of Transport (Coast Guard) ship staff (22), recreational boaters (22), lighthouse keepers (22), researchers (16), tugboat operators (10) and British Columbia Ferry staff (10). All were mariners from either British Columbia, Alaska, or both, and 46 had 25 or more years of experience on the water. The product of the number of observer days per month and the number of observer hours per day was used as an index of monthly sighting effort, which was highest during the month of July (Fig. 1).

Over 80% ($n=136$) of respondents had seen Pacific white-sided dolphins, and of those who provided comment ($n=85$), 60% felt that the population had increased (Table 1). When this was

adjusted to include only the responses of the 109 mariners who had spent 10 or more years on the water, and who provided comment ($n=69$) this increased to 66%. The experience of observers dated back to 1936, but both 'first sightings' of Pacific white-sided dolphins inshore were in 1952 from the central coast area (Table 2). Figure 2 shows the coast of British Columbia and southeast Alaska and the geographic areas used to describe the locations of dolphin sightings. The number of months that observers spent in each area on the coast grew with time (Fig.3). Many mariners travelled in more than one area, and some reported travelling throughout the entire coast.

Although the number of observers in all areas increased steadily over the years, the number of people who had seen dolphins did not follow the same pattern (Figure 4, KS test $D_{0.05,61}=0.46$, $p<0.005$). There was a plateau in new sightings of dolphins between the years 1978 and 1984, despite growth in the number of observers during that period. These observations were further corroborated by those involved with an intense research effort in Johnstone Strait beginning in 1978, in which killer whales were photo-identified and hydrophones were permanently installed to facilitate the detection of killer whales. Hydrophones detect the underwater vocalizations of both killer whales and Pacific white-sided dolphins. None of the researchers or local tourboat operators reported seeing or hearing any dolphins during this period. The first acoustic detection of Pacific white-sided dolphins was reportedly made during December 1984, and between 1984 and 1989 the number of sightings and acoustic detections of dolphins increased steadily.

Table 1. Mariner's responses to the question "Has the abundance of Pacific white-sided dolphins increased, decreased or remained the same since you first saw them?". Experienced mariners were those with more than 10 years of experience.

	No. Mariners	No. Seen Dolphins (%)	Up (%)	Down (%)	Same (%)	Mean. No. Years Experience
All Mariners	165	136 (82)	51 (60)	10 (12)	24 (28)	19.35
Experienced Mariners	131	109 (83)	45 (66)	10 (14)	14 (20)	23.5

Table 2. Distribution of first sightings of Pacific white-sided dolphins in inshore waters by all respondents. Number of observers are those who were on the water during each 5 year interval.

AREA	YEAR (19--)												TOTAL
	35- 40	41- 45	46- 50	51- 55	56- 60	61- 65	66- 70	71- 75	76- 80	81- 85	86- 90	91- 96	
South-east Alaska											2	5	7
Queen Charlotte Islands									1	2	2	3	9
North Coast										3		3	6
Central Coast				2	1		2	3	8	6	11	9	42
Queen Charlotte & Johnstone Strait						4	4	2		7	11	9	37
Strait of Georgia											3	4	7
Juan de Fuca Strait					1	1					3	1	3
Vancouver Island West Coast							1	1				1	6
No. Sightings Inshore	0	0	0	2	2	5	8	6	9	18	32	35	117
No. Observers	1	4	7	15	20	31	46	62	102	128	156	162	

DISCUSSION

Several clear trends emerged from the responses to the survey and from additional information provided by respondents. First, prior to the late 1970's, the majority of sightings of Pacific white-sided dolphins along the mainland coast were between northern Johnstone Strait and the central coast. Second, dolphins were less commonly sighted on the coast between the late 1970's and the mid-1980's than they were prior to this period. Third, since the mid-1980's, dolphins have been regularly sighted in the Queen Charlotte Islands, Johnstone Strait, Queen Charlotte Strait, and the central and northern mainland coast of British Columbia. Finally, since 1992, dolphins have been regularly sighted in the inshore waters of southeast Alaska, and sightings of dolphins in the inshore waters of Georgia Strait are becoming more common.

There are several references to the occurrence of Pacific white-sided dolphins in the coastal waters of British Columbia. The oldest recorded sighting in Hecate Strait in 1900 (Osgood, 1901) is somewhat questionable because only one dolphin was seen. Pacific white-sided dolphins are usually found in groups of 40 to over 1,000 animals (Leatherwood and Reeves, 1983; Stacey and Baird, 1991; Heise, 1997a forthcoming), and sightings of solitary individuals are rare. A pregnant female was harpooned off Race Rocks in Victoria in 1936 (Scheffer and Slipp, 1948). It is not clear from this account whether the presence of dolphins in the area was an unusual event. G. Pike, a biologist with the Canadian Dept. of Fisheries from the late 1940's onwards (Webb, 1988) reported seeing Pacific white-sided dolphins for the first time in 1959, when he sighted a school of over 1000 animals 25 miles northwest of the Queen Charlotte Islands (Pike, 1969). McTaggart-Cowan and Guiget (1956) report in their field guide *The Mammals of British*

Columbia that Pacific white-sided dolphins are found in open ocean in summer and off the north and south ends of Vancouver Island in winter. However, Calambokidis and Baird (1994) do not list Pacific white-sided dolphins in their status report on marine mammals in Georgia Strait, and the waters off southern Vancouver Island. Whether this reflects a change in distribution of the species is unclear, because I do not know how reliably the field guide reflected the true distribution of dolphins. However, the responses of mariners in this survey support the suggestion that these dolphins have not been common in southern B.C. waters during the past 30 years.

Stacey and Baird (1991) compiled 156 records from Canadian waters dating back to 1936, including those in Pike and MacAskie (1969), and found that the majority of Pacific white-sided dolphin sightings took place more than 16km offshore ($n=94$) and 48 (77%) of the remaining sightings were in the central coast or Johnstone Strait/Queen Charlotte Strait area. There were no sightings of dolphins in these or any inside waters during July. These observations are supported by Guiget (1953) who spent May through August, 1948, in the vicinity of Goose Island on the central coast, and did not see any white-sided dolphins, despite intensive searching for marine mammals. This is in marked contrast to the numerous sightings I and others have made in the area during summer months for at least the last 5 years (unpubl. data).

A movement of dolphins into inshore waters also appears to have taken place in southeast Alaska, but not until 1992. Several mariners who responded to this survey reported that prior to 1992 dolphins were occasionally seen in small groups in the Gulf of Alaska, and in the outer

entrances to inshore passages, even as far north as Prince William Sound, but rarely inshore. A recent field guide to the wildlife of southeast Alaska (O'Clair *et al.* 1992) does not mention the species. Beginning in 1992 dolphins were also sighted inshore, at times in large groups of hundreds to thousands of animals. This is supported by information reported from marine mammal survey cruises summarized in Dahlheim and Towell (1994). Dolphins were particularly abundant in inshore waters of southeast Alaska during April and May of both 1992 and 1993. Several mariners also reported seeing dolphins for the first time in the inshore waters of Prince William Sound in 1996, despite extensive previous experience in the area. Pike and MacAskie (1969) reported no sightings of white-sided dolphins from research vessels operating in the Gulf of Alaska prior to 1965. Brueggeman *et al.* (1987) did not see the species during their surveys of the northwestern Gulf of Alaska or the Bering Sea, and Hall and Tillman (1977) and Hall (1979) reported sighting dolphins only once, at the entrance to Prince William Sound.

Several questions arise out of the results of this survey. Is this movement of Pacific white-sided dolphins into the coastal waters of British Columbia a new phenomenon, or were dolphins generally common along the coast apart from the period 1978-1984? If the latter is true then why did they leave for seven years? Although I can only speculate about the answers to these questions, similar shifts in the distribution of species have been reported in other areas. Based on aerial and boat surveys off the coast of California during the winter and spring of 1991 and 1992, common dolphins (*Delphinus delphis*) were much more abundant than they had been during the period 1975-1983, but short-finned pilot whales (*Globicephala macrorhynchus*) were much less abundant (Forney *et al.* 1995). These results are consistent with the observation that

in recent years, common dolphins have declined in abundance in more southern waters (Anganuzzi and Buckland, 1994). These combined observations support a northward shift in distribution of common dolphins, rather than an increase in their abundance off California.

The evidence suggests that Pacific white-sided dolphins have changed their distribution. The simplest explanation for this may be that their numbers are increasing and that their range is extending. However, demographic data suggest that the population of Pacific white-sided dolphins in the North Pacific appears to be stationary (Heise, 1997b forthcoming), so this explanation seems unlikely. Alternatively, increased sightings could have resulted from the movement of dolphins inshore in response to disturbance offshore associated with high-seas flying-squid driftnets. This fishery killed an estimated 49,000 to 89,000 Pacific white-sided dolphins between 1978 and 1990 (Tanaka, 1993) before it ended in 1992. As the dolphins have remained inshore since this fishery was discontinued, this explanation does not seem sufficient.

Many mariners attributed the apparent shift of dolphins inshore to the El Niño event of 1982-83. Herring and salmon, both prey of Pacific white-sided dolphins (Stroud *et al.* 1981, Heise, 1996a) are affected by warm water conditions. Herring production appears to increase as a consequence of El Niño events (Mysack, 1986), possibly due to increased zooplankton biomass that is brought on by increased storm activity in winter (Brodeur and Ware, 1992). The migration routes of sockeye salmon change in response to warming events, as well as to changes in salinity (Mysack, 1986). Strong El Niño events have been taking place every 12 years on average since at least

1726, and moderate to strong events even more frequently (Quinn *et al.* 1978). Presumably these warming periods have been having effects on fish populations for many years. Another El Niño Southern Oscillation event (ENSO) began in 1990 (Trenberth and Hoar, 1996), yet dolphins were consistently sighted in coastal waters prior to the onset of this warming period. The 1990 ENSO continued through 1995, an unusually long period, during which dolphins have continued to be sighted inshore. Therefore, the presence of dolphins in coastal waters does not appear to be strongly associated with ENSO events.

Archaeological records provide further support for the suggestion that Pacific white-sided dolphins have been found in coastal waters in the past. The recovery of dolphin teeth from aboriginal midden sites from Queen Charlotte Strait (Mitchell, 1988, further analyzed by R. Wigen, Pacific Identifications), Denman Island (R. Wigen, S. Crockford, pers. comm.) and Valdez Island (Matson and Mclay, 1996), indicate that dolphins have been in the area during the last 2,000 years. Porpoise bones were more prevalent than dolphin bones in the middens, but the extent to which native peoples utilized dolphins for food is unknown, so the relative abundance of porpoise remains compared to dolphins is difficult to interpret. Coastal midden sites also show a shift from mammals to salmon within the last 2000 years (Mitchell, 1988). If fish populations change significantly, it is possible that dolphins move in response to these changes. Changes in species composition can be inferred from the presence of bluefin tuna (*Thunnus thynnus*) in coastal middens from the central coast. Although not abundant in the eastern North Pacific at present (Polovina, 1996), bluefin tuna were regularly consumed by native people from the central coast over a 5,000 year history and were the target of a coastal fishery

in the 1880's (Crockford, 1997, forthcoming).

Sediment samples from the Santa Barbara Basin in California provide additional evidence that there have been consistent fluctuations in the abundance of several species of fish over the past 2,000 years (Soutar and Issacs, 1969, 1974; Baumgartner *et al.* 1992). These sediments show annual depositions of fish scales that can be identified to species. Sardine (*Sardinops sardine*) and anchovy (*Engraulis mordax*), both prey species of Pacific white-sided dolphins off California (Walker *et al.* 1986, Black, 1994), fluctuate at intervals of 60 to 100 years (Baumgartner *et al.* 1992). Soutar and Issacs (1974) report that hake (*Merluccius productus*) were abundant before 1925, declined until 1965, and are now increasing in abundance, based on evidence in the sediment record. During the 1940's when sardine and anchovy numbers were low, saury (*Colalabis sp.*) and Pacific mackerel (*Scomber japonicus*) became more abundant. These fish species are all known prey items of Pacific white-sided dolphins, and the fluctuations in prey abundance probably affect dolphin movements and distribution. Off the British Columbia coast, sardines were abundant until the mid 1940's, particularly off the west coast of Vancouver Island (Hart, 1973). Sardine populations from California are now recovering (Barnes *et al.* 1992), and may eventually extend once again into British Columbia. Whether the dolphins will change their distribution in response to this increasing prey population remains to be seen.

Studies on the fluctuations of marine species such as zooplankton (Brodeur and Ware, 1992), seabirds (Springer, 1993), herring (Hallowed and Wooster, 1995), salmon (Brodeur and Ware, 1995) and other forage fish species (Brodeur and Ware, 1995; Hallowed and Wooster, 1995;

Anderson *et al.* 1996) have pointed to the existence of a 'regime shift' in the North Pacific that began in 1976-77 (Beamish and Bouillon, 1993; Hare and Francis, 1995). This coincides with a shift from cool to warm ocean conditions, and was preceded by a shift from warm to cool temperatures that took place during the winter of 1946-47 (Hare and Francis, 1995). There is, however, insufficient historical evidence of dolphin abundance to link the earlier regime shift with changes in dolphin distribution.

In conclusion, the results of this survey suggest that the abundance and/or distribution of Pacific white-sided dolphins has changed significantly in the last 30 years, and increased markedly in certain areas in the past 10 years. Evidence from coastal midden sites indicates that the species has been found in nearshore waters in the past. There are three possible reasons for their recent appearance inshore. These are (i) a population increase, (ii) avoidance of open ocean due to disturbance associated with high-seas fishing and (iii) recent changes in the distribution and abundance of forage fish and other marine species associated with the 'regime shift' and climate change. I suggest that the effects of these climatic events on marine species may provide the most plausible explanation for this recent movement of dolphins into the coastal waters of British Columbia.

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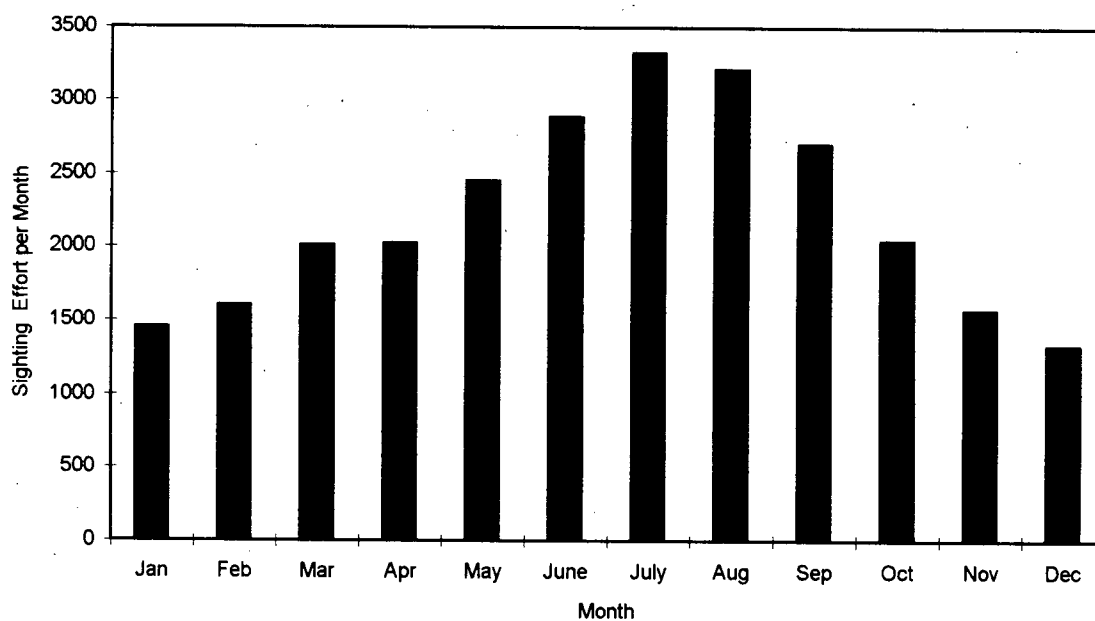


Figure 1. Distribution of sighting effort per month by all observers. Sighting effort was the product of the number of hours per day and the number of days per month each observer was on the water.

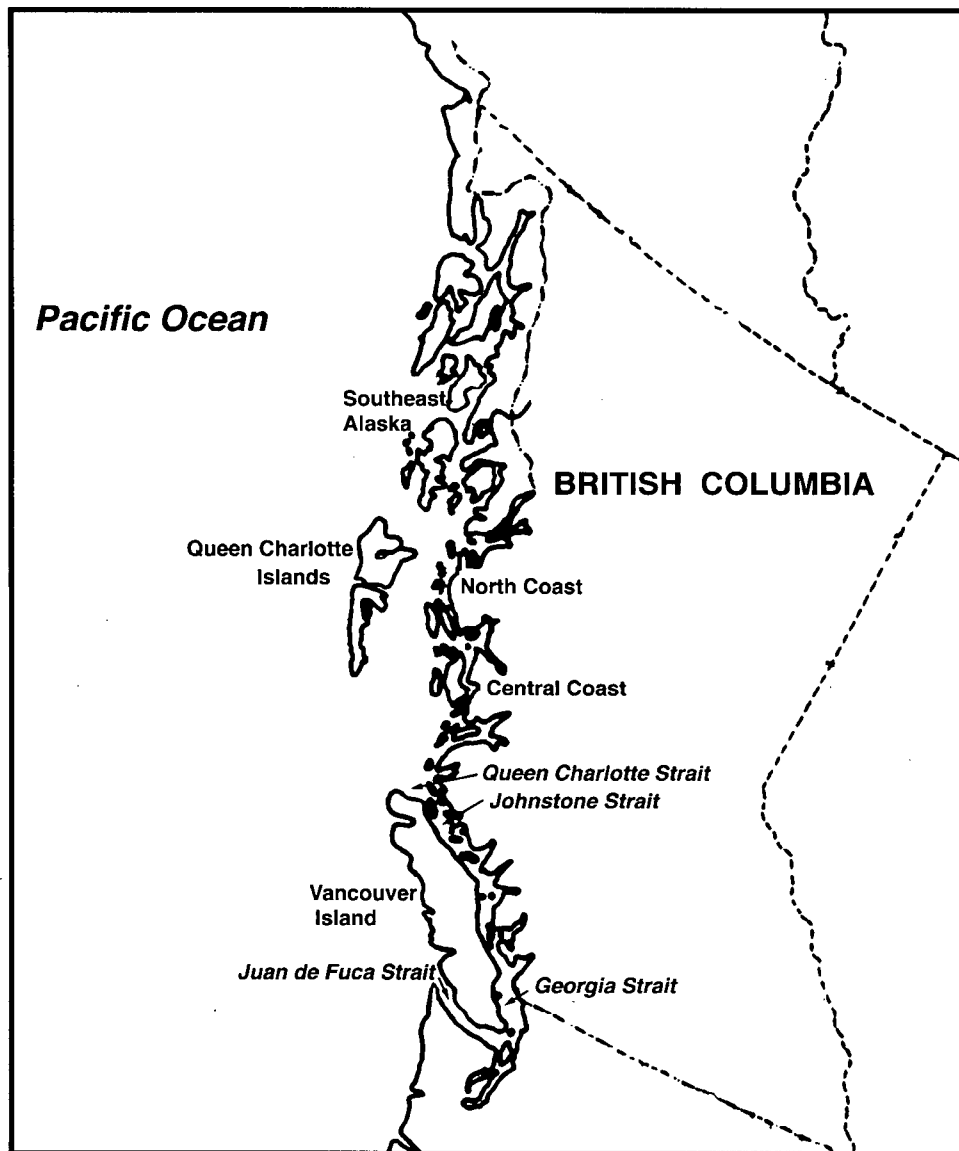


Figure 2. The coastal waters of British Columbia and Alaska showing geographic areas mentioned in the text.

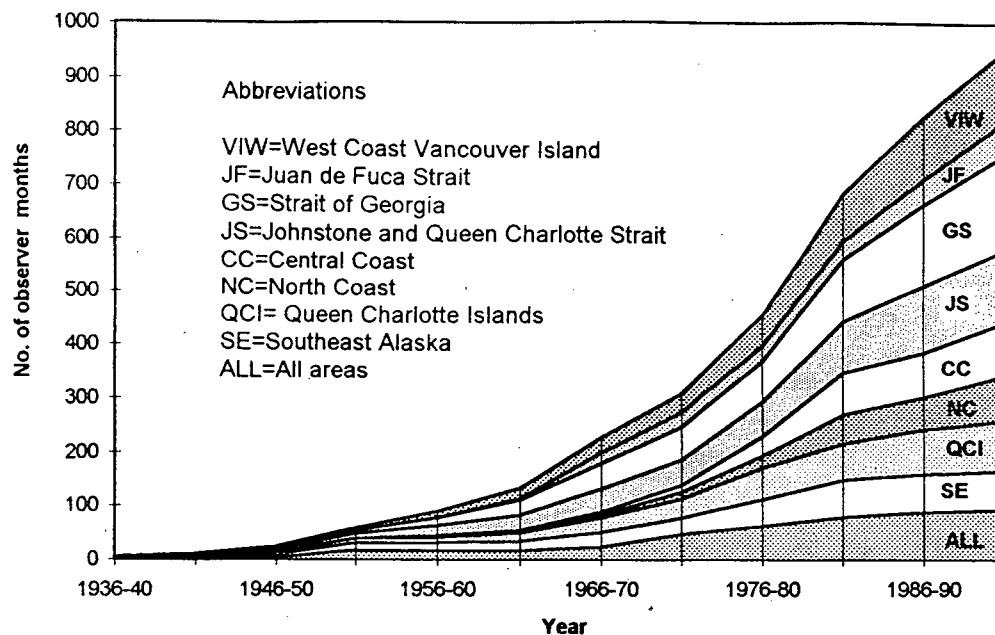


Figure 3. Distribution of observer months in each coastal area.

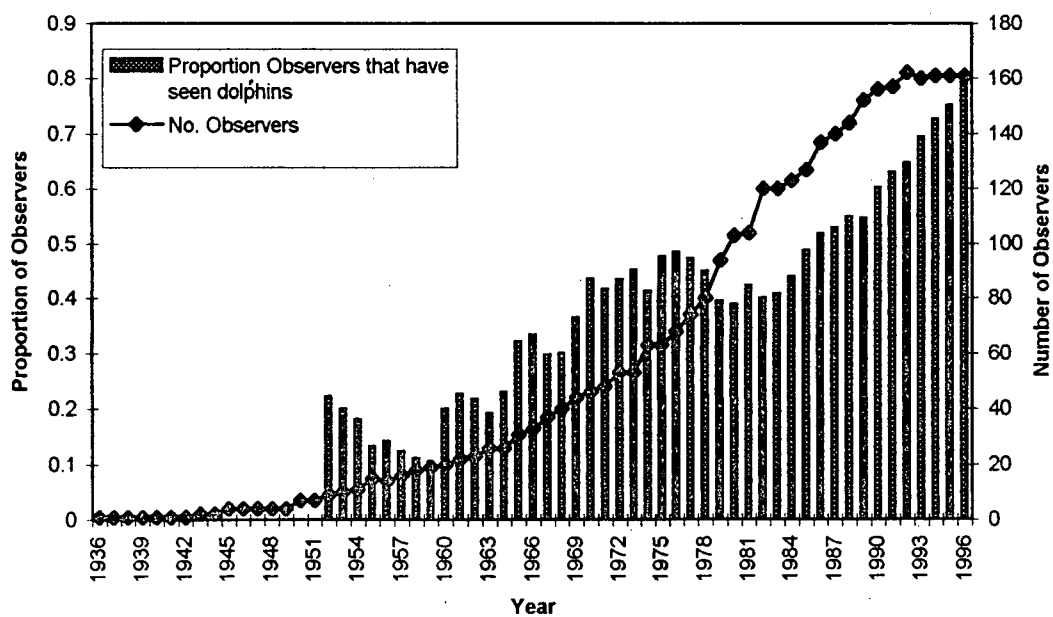


Figure 4. The number of observers per year and the proportion of observers who saw dolphins for the first time.

CHAPTER THREE: Life History and Population Parameters
of Pacific White-Sided Dolphins (*Lagenorhynchus obliquidens*)

ABSTRACT

Life-history and population parameters for Pacific white-sided dolphins (*Lagenorhynchus obliquidens*) were estimated from published records of animals caught in driftnet and drive fisheries in the North Pacific, and from stranded and scientifically harvested animals. Males and females did not differ significantly in mean age, length or weight ($p>0.05$), and the sex ratio was approximately equal when all data sources were combined. Five growth models were fitted to the data. Although the Bertalanffy model provided the best fit, the differences between models were not statistically significant. Age at sexual maturity was estimated to be 7.5-7.6yrs, and the annual pregnancy rate 21.4% ($S.E. = 2.5$). Calving peaked in June through August. Estimated gestation and lactation periods were 12.0-12.2 months, and 8.1-10.0 months respectively, with an average calving interval of 4.67yrs ($S.E.=1.81$). Survivorship, calculated using Barlow and Boveng's (1991) model for age-specific mortality, was an exponential decay function of age, with no indication of increased mortality due to senescence in old animals. The finite population growth rate was between 0.94 and 1.02/yr, assuming constant fecundity over the lifespan of females, suggesting that the population is stationary. Thus population growth is unlikely to explain the recent increase in dolphin sightings in the coastal waters of British Columbia.

INTRODUCTION

Opportunities to analyze large life-history data sets on cetaceans occur relatively infrequently. Some of the most comprehensive analyses come from the drive fisheries of pilot whales (summarized in Donovan *et al.* 1993) and from the study of individually recognizable cetaceans such as killer whales in British Columbia (Bigg *et al.* 1990, Olesiuk *et al.* 1990). These studies yield insights into important population characteristics, such as rate of increase and average mortality, which are needed to understand the capacity of populations to sustain harvests and environmental changes. These studies have also revealed life-history traits that were not anticipated by studies of terrestrial mammals, such as female reproductive senescence in both killer whales and pilot whales (Bigg *et al.* 1990; Marsh and Kasuya, 1986), and the non-dispersing nature of resident killer whale social groups (Bigg *et al.* 1990). As well as being of theoretical interest, these traits affect the capacity of populations to respond to perturbations.

Pacific white-sided dolphins were the focus of a comprehensive review by Walker *et al.* (1986) which summarized records of stranded and scientifically harvested animals off Baja California, California, Oregon and Washington. Since 1986, additional information on the species has been collected from sources such as the dolphin bycatch from high seas flying-squid driftnet fisheries (Iwasaki 1991, Ferrero *et al.* 1993), and Japanese drive fisheries (Kasuya 1995). In this paper I have used much of the data in these recent sources, in combination with that presented by Walker *et al.* (1984; 1986), to develop estimates of life history and population parameters for the species. I also compare my estimates with previously published values, and discuss the differences.

It is likely that several different stocks of Pacific white-sided dolphins exist throughout the North Pacific Ocean. In the eastern Pacific, Walker *et al.* (1984; 1986) identified at least two stocks based on morphology. Dolphins south of 33°N tended to be larger than northern animals, but the ranges of these putative populations overlapped, and the stocks could not be differentiated for the purposes of abundance and/or length-weight estimates. The northern limit of sampled animals was 48°30'N. Preliminary genetic analyses by Lux *et al.* (1996) has suggested that there may be three stocks of Pacific white-sided dolphins in the eastern North Pacific: one in Baja California; one in California/Washington/Oregon and a third Canadian/Alaskan stock. They found no evidence of genetic differences between dolphins from coastal and offshore areas. Sample sizes were small for the Canadian/Alaskan analysis. In the western North Pacific, Sleptsov (1955) differentiated between *L. obliquidens* and *L. ognevi*, but this new species was rejected by Tomilin (1957), and the differences may be indicative of variation between stocks. Miyazaki and Shikano (1989) suggested that there were two forms of *L. obliquidens* in Japanese waters, but these forms also could not be defined by geographic boundaries. Because all of these putative populations overlap in distribution, data segregated by geographic location would not reveal potential inter-stock differences. For the analyses presented here, I pooled all sources of data, assuming that the errors arising from population level differences are less than those that would occur as a result of separately analyzing small samples with biased age-distributions. Pooling these data may also have created biased parameter estimates, or masked changes in parameters over time. Acknowledging these possible limitations, the results presented here are useful for gaining insight into a species for which there has been very limited information.

LIFE HISTORY TRAITS OF PACIFIC WHITE-SIDED DOLPHINS

Growth

Sources of Data

I obtained length, weight and age data for 245 male and 206 female Pacific white-sided dolphins from the following sources: (1) stranded and scientifically harvested animals from Scheffer and Slipp (1948), Wilke *et al.* (1953), Sleptsov (1955) and Walker *et al.* (1984; 1986) ($n=183$); (2) animals accidentally killed in the driftnet fishery (Iwasaki, 1991; Ferrero *et al.*, 1993) ($n=180$), and (3) from the Japanese drive-fishery ($n=88$) (Kasuya, 1995). Animals collected in the driftnet fishery were caught between 34° and 46°N and 170°E and 145°W. Records compiled by Walker *et al.* (1986) came from a variety of sources, including animals processed by the U.S National Museum, by the National Marine Mammal Lab, by private individuals, and by aquaria staff. Where appropriate, I have included additional sources of information, including some from my own behavioural observations of Pacific white-sided dolphins in British Columbia.

Length, Weight and Age of Animals sampled

Table 3 reports the maximum and mean age, lengths and weights for 451 Pacific white-sided dolphins based on data from all sources (Wilke *et al.* 1953, Sleptsov 1955, Walker *et al.* 1984, 1986, Iwasaki, 1991, Ferrero *et al.* 1993, Kasuya, 1995). Stranded and scientifically harvested animals as well as those collected from the driftnet bycatch suggest a 50:50 male:female sex ratio ($n=363$). The drive fishery was strongly biased towards males (85:15, $n=88$), suggesting that animals may travel in sexually segregated groups, at least during juvenile stages. The mean ages,

Table 3. Summary statistics for adult Pacific white-sided dolphins based on data sources listed in the text. Number of animals examined is included in parentheses.

	Females	Males	All animals
Maximum age (yrs)	46 (n=186)	42 (n=229)	46 (n=415)
Mean +/- S.E.	10.01 +/-0.70	11.13 +/-0.63	10.63 +/-0.47
Maximum Length (cm)	236 (n=206)	250 (n=245)	250 (n=451)
Mean +/- S.E.	172.05 +/-1.98	177.01 +/-1.94	174.75 +/-1.39
Maximum Weight (kg)	145 (n=54)	198 (n=35)	198 (n=89)
Mean +/- S.E.	81.78 +/-2.38	83.71 +/-5.80	82.5 +/-2.68

lengths and weights for males and females were not statistically different (two-tailed *t*-test, $p>0.05$). Figure 5 shows the age-distribution of all animals. Although juveniles were under-represented in the samples recorded by Walker *et al.* (1986), the distribution improved when this was combined with data from animals killed during the driftnet and drive fisheries (Iwasaki, 1991; Ferrero *et al.* 1993). The drive and driftnet data were biased towards juveniles (Fig. 6). For example, of 42 females reported in Ferrero *et al.* (1993), only 6 were sexually mature. Bias may also have arisen if large numbers of individuals were captured from a single school, as schools may have been segregated by age or sex. Although northern right whale dolphins (*Lissodelphis borealis*) were caught individually by driftnets (Ferrero and Walker 1993), it was not clear from Iwasaki (1991) or Ferrero *et al.* (1993) whether the same was true for Pacific white-sided dolphins, or whether entire schools were entangled at once.

Relationship of Weight to Length

The length-weight relationship for post-natal animals was estimated from data in Wilke *et al.* (1953), Sleptsov (1955) and Walker *et al.* (1984). The following relationship was derived for both male and female Pacific white-sided dolphins ($r^2_{\text{raw}}=0.977$, $r^2_{\text{corrected}}=0.725$)

$$W = .000035 * L^{2.82},$$

where W is the mean body weight in kg and L is mean length in cm. This regression and the weight at length data are shown in Figure 7.

Age at Length Estimates: Comparing Five Growth Models

Several growth curves have been applied to cetaceans including the Bertalanffy model (von Bertalanffy, 1938 in Lockyer, 1981; Bloch *et al.* 1993), the Laird/Gompertz model (Laird, 1969 in Bloch *et al.* 1993) and the Laird model (Laird, 1969 in Ferrero and Walker, 1993). I fitted each of these models, as well as the Gompertz and Richard's growth models (from Zach *et al.* 1984) to the length at age data to determine which provided the best fit, using the NONLIN least squares loss function and the simplex algorithm in SYSTAT (1992). Each model, its parameter estimates and the raw and corrected r^2 values are listed in Table 4. Examination of the corrected r^2 values and the residuals indicated that the models were not significantly different. Thus, the Bertalanffy model was used for subsequent length-at-age estimates (see the section on lactation period below), and is shown in Figure 8. Both the Laird and the Laird-Gompertz model are two parameter models, but rely on the availability of an estimate of length at birth, and so may be

less useful for species for which this information is not available. Bloch *et al.* (1993) suggest that these models are better at approximating more sigmoid growth patterns, but in Pacific white-sided dolphins the data indicate that the period of fastest growth is at $t=0$. The Richard's model, a four parameter growth curve model, did not provide any additional predictive power, and I suggest judicious use of Ockham's razor.

Table 4. Growth models for male and female Pacific white-sided dolphins.

Growth Model* (Reference)	Model with parameter estimates (model)	Raw r^2	Corrected r^2
Bertalanffy (Hilborn and Walters, 1992)	$Length(t) = 191.41(1 - e^{-0.461(t+1.75)})$ $L(t) = A(1 - e^{-k(t-t_0)})$	0.991	0.701
Gompertz (Zach <i>et al.</i> 1984)	$Length(t) = 190.68e^{-0.612e(-0.528t)}$ $L(t) = Ae^{-ce^{(-kt)}}$	0.991	0.698
Laird/Gompertz (Bloch <i>et al.</i> 1993)	$Length(t) = 99e^{0.375/0.575(1 - e^{(-0.575t)})}$ $L(t) = L_0e^{A_0/\infty(1 - e^{(-\infty t)})}$	0.991	0.697
Laird (Ferrero and Walker 1993)	$Length(t) = 99e^{0.653(1 - e^{(-.475t)})}$ $L(t) = L_0e^{A_0(1 - e^{(-\infty t)})}$	0.991	0.697
Richard's (Zach <i>et al.</i> 1984)	$Length(t) = 190.65(1 \pm e^{-3.336-0.534t})^{-1/0.571}$ $L(t) = A(1 \pm e^{-c-kt})^{-1/n}$	0.991	0.698

* For all estimations, initial values were $A=200$, $k=0.5$, $c=1$, $n=5$. In the Laird-Gompertz and Laird models, the estimated length at birth (L_0) was 99cm, and A_0 and ∞ were estimated from Bloch *et al.* 1993 (0.12 and 0.13 respectively).

Reproduction

Age at Sexual Maturity and Age at First Pregnancy

Walker *et al.* (1986) listed the age and number of corpora for 35 females, from which I estimated the average age at sexual maturity (ASM) by regressing the number of corpora albicantia (CA) on age (following the method of DeMaster, 1984). The regression

$$ASM = -5.533 + 0.8661X$$

was fit to the data, where X is the number of CA's ($r^2_{raw}=0.83$, $r^2_{corrected}=0.83$, Fig. 9), and the resulting age at sexual maturity was estimated to be 7.5yrs. DeMaster also suggested using the formula

$$ASM = AgeIMM_{all} + SUM\%IMM,$$

where $AgeIMM_{all}$ is the age when 100% of all animals sampled are immature, which yielded a similar estimate of female sexual maturity (7.6yrs).

Walker *et al.* (1986), Iwasaki, (1991) and Ferrero *et al.* (1993) used the presence of at least one corpus luteum or corpus albicans on an ovary to classify an animal as sexually mature. Walker *et al.* (1986) report that of 28 females with at least 1 CA, 6 were pregnant including 3 at age 7.2, 8.6 and 8.7yrs respectively. Iwasaki (1991) suggests sexual maturity begins at about 7-9, based on a sample of females caught incidentally during the Japanese flying-squid driftnet fishery. However, his sample of females of known reproductive status did not include any animals between the ages of 6.5 and 16.5yrs. Interestingly, he did report a female aged 16.5 that was sexually immature. Based on additional samples of females caught in the driftnet fishery, Ferrero *et al.* (1993) reported that the youngest lactating female was 11yrs, and the oldest immature female was 10. They suggested that sexual maturity is reached at 10-11. The disparity in the estimates of age at maturity may be due to the fact that a high proportion (74%) of the 42 females Ferrero *et al.* (1993) sampled were less than 7yrs of age.

Insufficient data were available to reliably determine the mean age at first pregnancy. However, because 3 of the 6 pregnant females that Walker *et al.* (1986) reported were less than 9yrs of age, I assume that female Pacific white-sided dolphins can become pregnant at or shortly after their first ovulation.

Annual Pregnancy Rate

The annual pregnancy rate (APR) for animals sampled by Walker *et al.* (1986) was 21.4% ($n = 6$ of 28, $S.E. = 2.5\%$), for females 7yrs and older. Variance in APR was estimated by

$$var(APR) = APR(1-APR)/n,$$

where n is the number of reproductive females in the sample (Perrin and Reilly, 1984). If this same rate was applied to data in Ferrero *et al.* (1993), one would expect at least 2 pregnant females in the sample of 11 females age 7 and over, which is what they did find.

Gestation Period

Iwasaki (1991) and Ferrero *et al.* (1993) estimated length at birth to be 100 and 98cm, respectively. Using the mean length at birth presented in these sources, the gestation period can be predicted by

$$\log(T_G) = 0.4586\log(L_o) + 0.1659,$$

where T_G is the gestation period in months, and L_o is the length at birth in cm (from Perrin and

Reilly, 1984, Fig. 3). Depending on whether the estimate of birth length is 98 or 100cm, the gestation period is 12.0 or 12.2 months respectively. Perrin and Reilly (1984) suggest that gestation period is one of the least variable vital parameters in cetaceans, as in most mammals.

Calving Period

Pacific white-sided dolphins may be spontaneous ovulators (Harrison *et al.* 1972) without a clear mode in calving. In British Columbia, newborn calves have been reported as early as April (A. MacDonald, pers. comm.), but most sightings have occurred in June through August (unpubl. data). Of 7 pregnant wild animals that Walker *et al.* (1984) reported, one recovered in April contained a 'full term fetus', and two animals recovered in May of different years contained fetuses in excess of 80cm. Brown and Norris (1956) reported sighting calves in June 1954 off California, and Norris and Prescott (1961) reported sightings in June through September, as did Black (1994). Ferrero *et al.* (1993) found that a large proportion of dolphins entangled in driftnets were newborn calves (33% of males and 45% of females), particularly in June and July. This may reflect age segregation of groups, although in British Columbia, my own observations suggest that newborn calves rarely exceed 5% of a group of dolphins. The high proportion of calves caught in driftnets may reflect their increased vulnerability to nets. Only two pregnant females were sampled from June through November 1990 in driftnets. This could be because there were relatively few sexually mature females in the sample, or because most females had given birth prior to the start of the fishery.

Lactation Period

Walker and Jones (1993) examined 32 animals less than 150cm for the presence of milk in their stomachs. Milk was found only in animals less than 125cm. Unfortunately there were no animals between 125 and 130cm in their sample, so I assume that the length at weaning is 125cm. This may be an underestimate, as animals may continue to suckle at lengths between 126 and 130cm, although they were also obviously eating solid food. Scheffer and Slipp (1948) reported a 124cm dolphin with milk in its stomach and Walker and Jones (1993) describe a 120cm 0.5yr male that had both solid food and milk in its stomach. Using the 95% confidence interval parameter estimates for the Bertalanffy growth curve to estimate age, the lactation period for Pacific white-sided dolphins ranges from 8.1 to 10.0 months.

Lactation period (T_L) may also be estimated by the following formula (Perrin and Reilly 1984)

$$T_L = T_G * L / P,$$

where T_G = length of gestation period, L = proportion of females lactating and P = proportion of sample pregnant. Six of the 28 sexually mature females described by Walker *et al.* (1986) were pregnant, and three were lactating, suggesting a pregnancy and lactation rate of 21.4% and 10.7% respectively. Assuming a minimum of 12.0 months gestation, then the lactation period is at least 6 months.

Resting Period

Following lactation, female Pacific white-sided dolphins appear to go through a reproductive resting period, defined by Perrin and Donovan (1984) as a time when females are neither pregnant or lactating. No females were simultaneously lactating and pregnant (Walker *et al.* 1986, Iwasaki 1991, Ferrero *et al.* 1993). The resting rate, based on the number of females not lactating or pregnant, was 67.9%. Using Perrin and Reilly's (1984) formula for the length of the resting period

$$T_R = T_G * R/P,$$

where T_G = gestation time, R = proportion resting and P = proportion pregnant, a resting period T_R of 38.0 months is obtained.

Calving Interval

Perrin and Reilly (1984 Table 6) suggest that the calving interval for delphinids for which there are no data could be assumed to be between 2 and 4yrs. However, if the pregnancy rate is known, then the calving interval (CI) and variance can be estimated by the following

$$CI = 1/APR, \quad var(CI) = (APR^{-4})var(APR).$$

For Pacific white-sided dolphins, this yields an estimate of 4.67yrs ($S.E.=1.81$, $n=28$). Using the minimum estimates for gestation (12.0 months), lactation (6.0 months) and resting (38.0 months), the calving interval is also estimated to be 4.67yrs (56 months). If maximum estimates based

on the available data are used, (gestation = 12.2 months; lactation = 10.0 months; resting = 38.7 months) then the calving interval is 5.1yrs (60.9 months). This is considerably higher than the estimates suggested for animals for which there are few data, and merits further investigation. It is possible that pregnant and/or lactating animals were under-recorded or missed in the necropsies. Olesiuk *et al.* (1990) estimated the calving interval for killer whales to be between 5.0 and 5.9yrs, based on the number of viable calves born to individually recognizable killer whales. However, barren females were excluded in their estimates, unlike the case here. More observations such as those of Black (1994), who reported the sighting of one dolphin with a newborn calf in early August of one year, and resighted the same adult with the same calf almost a year and a half later, may help to shed more light on calving intervals.

Reproductive senescence has been shown in killer whales (Bigg *et al.* 1990) and in pilot whales (Marsh and Kasuya 1986). Insufficient numbers of older females were examined to determine whether it occurs in Pacific white-sided dolphins, as only about 5% of sampled females were over 30yrs of age. Iwasaki (1991) found one 27.5yr old female lactating, and the oldest recorded pregnant female was 29.2 (Walker *et al.* 1986).

Survival

Age Specific Survival

Age-specific survival was estimated using Barlow and Boveng's (1991) 5 parameter model, where total mortality at age x , $l(x)$, is a function of exponentially decreasing risk due to juvenile mortality ($l_j(x)$), a constant risk of mortality for all age classes ($l_c(x)$) and an exponentially

increasing risk due to senescent mortality ($l_s(x)$). Originally derived from Siler (1979), the model does not assume a stable age distribution and is based on minimal information: an estimate of longevity for the species and a model life table. The probability of survivorship is expressed as

$$l(x) = l_j(x) * l_c(x) * l_s(x) ,$$

where

$$l_j(x) = \exp[(-a_1/b_1) * \{1 - \exp(-b_1 * x/\Omega)\}]$$

$$l_c(x) = \exp(-a_2 * x/\Omega)$$

$$l_s(x) = \exp[(a_3/b_3) * \{1 - \exp(b_3 * x/\Omega)\}].$$

Longevity, Ω , defined by Barlow and Boveng (1991) as the 99th percentile of the age distribution of a sample, was 37yrs for female Pacific white-sided dolphins based on all data sources. Barlow and Boveng's model was fitted using maximum-likelihood methods. The resulting parameter estimates are shown in Table 5, along with those for fur seals, old world monkeys and humans. The parameter values of these species were estimated by Barlow and Boveng because of the similarity in their life history traits to those of cetaceans. The resulting survival curves for all four species are shown in Figure 10, rescaled to dolphin longevity. The lack of an inflexion point in the curve suggests that unlike other mammals, Pacific white-sided dolphins do not experience increases in mortality due to senescence. Whether this is an artifact of the data, or a consequence of accumulating social status or survival skills with age, merits further investigation.

Table 5. Parameter estimates for Barlow and Boveng's (1991) age-specific mortality model for female Pacific white-sided dolphins, northern fur seals, old world monkeys and humans.

	a_1	a_2	Parameters a_3	b_1	b_3
Dolphin	5.276	0.0000	0.1084	2.0298	3.7685
Fur seal	14.343	0.1710	0.0121	10.259	6.6878
Monkey	30.430	0.0000	0.7276	206.720	2.3188
Human	40.409	0.4772	0.0047	310.360	8.0290

POPULATION PARAMETERS FOR PACIFIC WHITE-SIDED DOLPHINS

Population Growth

I estimated the finite rate of increase in Pacific white-sided dolphins using a life-table and incorporating the age-specific survival estimates for females from Barlow and Boveng's model determined previously. The age of first reproduction was assumed to be 8.5yrs, based on an ASM of 7.5yrs, and a gestation period of 12 months. The birth rate was assumed to be 21.4%/yr, for females ages 8.5 to 45yrs. I assumed that females experienced constant fecundity but did not give birth beyond age 45, to allow for a minimum of 10 months to nurse any offspring. The resulting rate of increase was 0.94/yr. If the age of first reproduction was lowered by one year, the population growth rate increased to 1.02/yr. It thus appears that the population was growing slowly, or was stationary.

Impact of Driftnet Fishing

Tanaka (1993) estimated that from 1978 to 1990, 49,000 to 89,000 Pacific white-sided dolphins were killed in the Japanese, Korean and Taiwanese squid driftnet fisheries as well as the Taiwanese large-mesh driftnet fishery. Since the United Nations resolution on large-scale pelagic driftnet fishing in 1992, these fisheries have been discontinued. Had they not ended, Tanaka estimated that Pacific white-sided dolphin populations would have been seriously depleted within 10yrs.

Population Estimates for the North Pacific

The most recent abundance estimates for Pacific white-sided dolphins are based on line-transect surveys in California, Washington and Oregon (Green *et al.* 1992; Barlow, 1995; Forney and Barlow 1995 and Forney *et al.* 1995), and from marine mammal observer programs operated during the course of the driftnet fishery (Buckland *et al.* 1993; Miyashita 1993). Buckland *et al.* (1993) and Miyashita (1993) estimated total North Pacific populations of 931,000 (95% *CI* = 206,000-4,216,000) and 988,033 (95% *CI* = 163,000-6,890,000) dolphins respectively. Although the mean populations of these two estimates are similar, the confidence intervals are large. Precision is generally lacking in most population abundance estimates; all of the above listed studies have high coefficients of variation (*C.V.* range 0.466-0.9).

A source of bias that has yet to be quantified in boat surveys is the attraction that Pacific white-sided dolphins have to vessels. Buckland *et al.* (1993) found most of their sightings occurred within 100m of the vessel trackline. Green *et al.* (1992) also reported that perpendicular sighting

distances were strongly skewed towards the vessel track. Turnock and Quinn (1991) estimated that Dall's porpoise population estimates were biased upwards due to porpoise' attraction to vessels, and proposed a 0.24 (CV= 0.34) correction factor for abundance estimates. The correction factor for Pacific white-sided dolphins has not yet been estimated, but is likely even smaller (unpubl. data). Therefore, population estimates based on ship surveys may be biased upwards, possibly by five-fold or more. If Turnock and Quinn's (1991) correction factor for the attraction Dall's porpoises have to vessels was applied to Buckland *et al.*'s, (1990) population estimate, then the revised mean is 223,400 dolphins (95% *CI* = 49,440-1,011,840).

Bias due to vessel attraction (or avoidance) likely occurred to a lesser extent in the results reported by Miyashita (1993), because the observers in that study used binoculars to sight animals and therefore were more likely to see animals before they responded to the vessel. However, unlike Buckland *et al.* (1993), Miyashita (1993) did not allow for bias due to group size in his analyses. Since large schools are more likely to be seen than smaller schools, this effect also biases the population estimate upwards.

Hobbs and Jones (1993) used an alternative method of estimating population size, which was based on bycatch data from the high seas flying-squid driftnet fishery. They scaled the amount of bycatch to the amount of fishing effort during two years of the driftnet fishery, and then extrapolated backwards to estimate what the minimum sustainable population size was prior to the start of the fishery. Assuming that 2% of all dolphins were being caught in driftnets, they estimated that the minimum sustainable population size was 330,000. If 4% of the population

was being killed, then the sustainable population size was 165,000 animals.

Scammon (1874) suggested that *L. obliquidens* "has the widest range, congregates in the largest numbers and exhibits more activity than any other of the Dolphin family". Figure 11 shows the distribution of Pacific white-sided dolphins in the North Pacific. Areas of concentration are indicated with black shading, based on sighting records from marine mammal observer programs operated by the National Marine Fisheries Service (NMFS), and from bycatch data from the squid driftnet fishery (Leatherwood and Walker 1982, Walker and Jones 1993, Green *et al.* 1992, Miyashita 1993, Buckland *et al.* 1993). Leatherwood and Walker (1982) suggested that sightings decline west of 135°W and south of 45°N, but this may reflect observer effort. However, in pelagic waters between 20°N and 30°N where there was considerable effort, relatively few sightings were made. Yatsu *et al.* (1993) suggested that Pacific white-sided dolphins concentrate in the transition and subarctic domains of the North Pacific. Although the species' range extends into the Gulf of Alaska and Prince William Sound, aerial surveys by Brueggeman *et al.* (1987) in the northwestern Gulf of Alaska and southeastern Bering Sea did not locate any schools of Pacific white-sided dolphins. Questionnaires distributed to mariners from Prince William Sound revealed infrequent sightings of dolphins in the area, and the sightings that were reported were of small groups (Chapter 2).

Based on the results of a survey of mariners reported in Chapter 2, there appears to have been an increase in the abundance of Pacific white-sided dolphins in inshore waters of British Columbia since 1984, and in southeast Alaska since 1992. Dahlheim and Towell (1994) reported

that there may have been an unusually high number of dolphins in inside waters of southeast Alaska in May 1992 and May 1993 compared to previous years. They suggested this may have been related to elevated sea surface temperatures, or to changes in the presence of prey species. These inshore movements coincided with changes in the distribution of many fish species in the North Pacific (discussed in Beamish, 1995), and further research is needed to determine the mechanisms for these changes. Given that (i) Pacific white-sided dolphins reproduce slowly, and that the population appears to be stationary, (ii) the population could be significantly overestimated, due to bias in sightings resulting from the attraction dolphins have to boats, and (iii) from 49,000 to 89,000 white-sided dolphins were killed in the driftnet fishery from 1978 to 1990, it seems unlikely that the increase in sightings inshore is due to an increase in the population.

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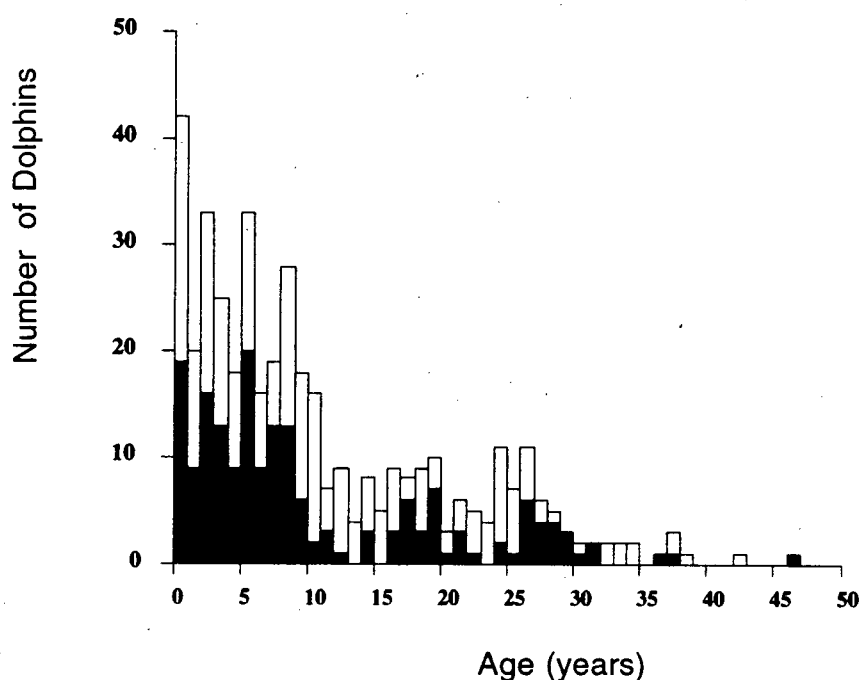


Figure 5. Age frequency distribution of 186 female and 229 male Pacific white-sided dolphins (based on data sources listed in the text). The solid bars indicate females, and the clear bars are the number of males in each age group.

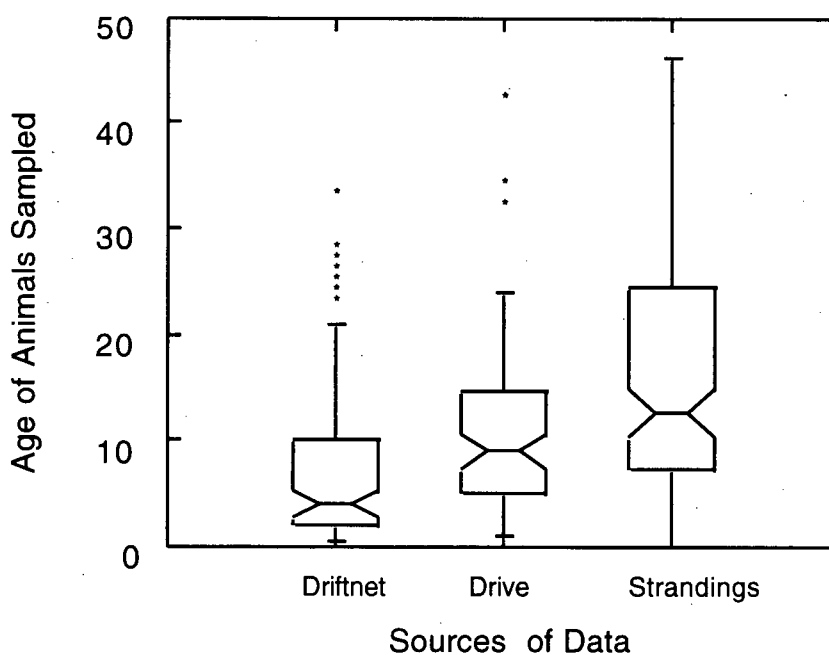


Figure 6. The median ages of dolphins sampled by the collection of stranded and scientifically harvested animals ($n=183$), and by the drive ($n=88$) and driftnet ($n=180$) fisheries. Boxes are notched and return to full width at the 95% confidence limits.

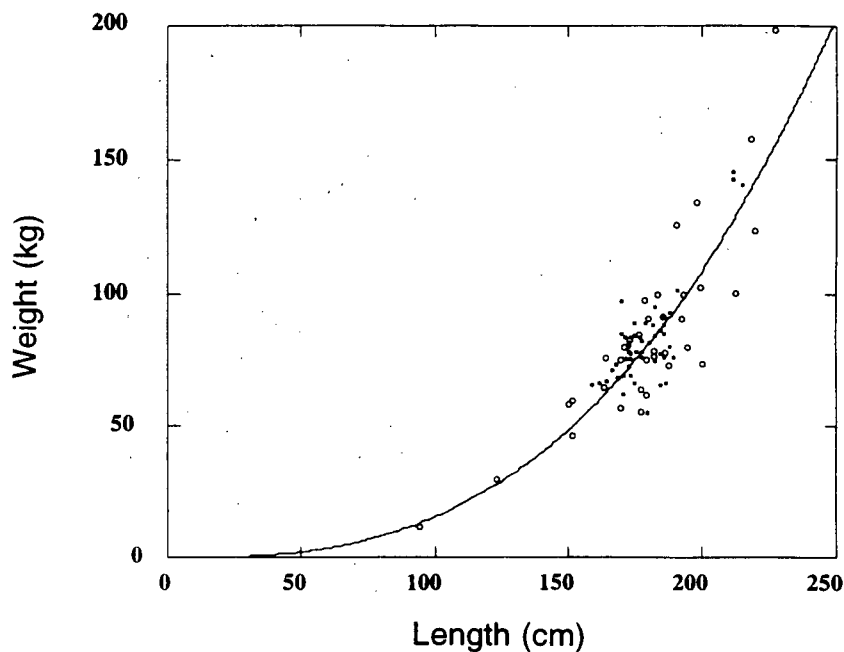


Fig. 7. Weight vs lengths for 35 male and 54 female Pacific white-sided dolphins. Males and females are shown as hollow and closed circles respectively (data from Walker *et al.* 1984). The equation of the line is $Weight = 0.000035 * Length^{2.82}$ ($r^2_{corrected} = 0.725$).

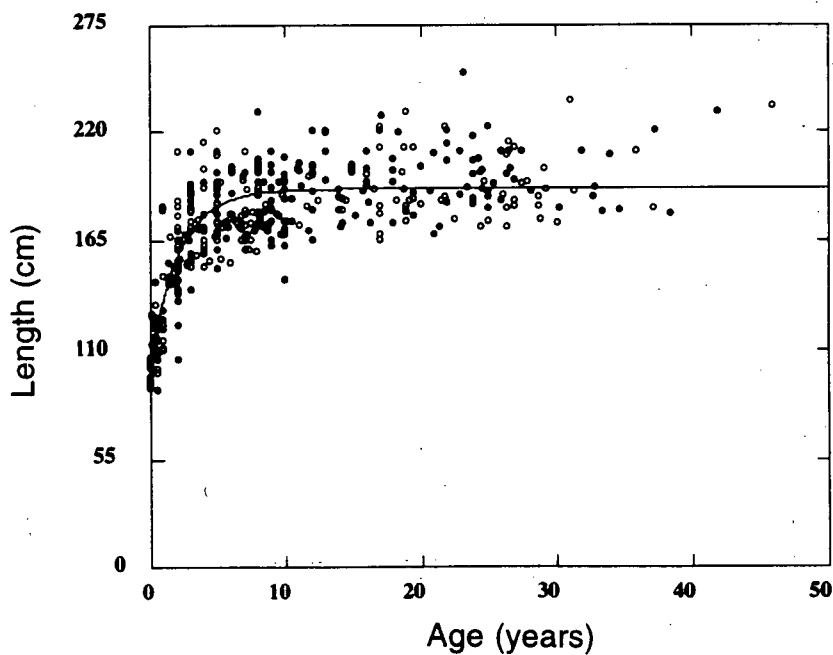


Fig. 8. Length at age measurements for 206 female (hollow circles) and 250 male Pacific white-sided dolphins (solid circles) fitted with the Bertalanffy growth curve from Table 4, where $Length(t) = 191.41(1 - e^{-0.461(t+1.75)})$, and t is the age in years.

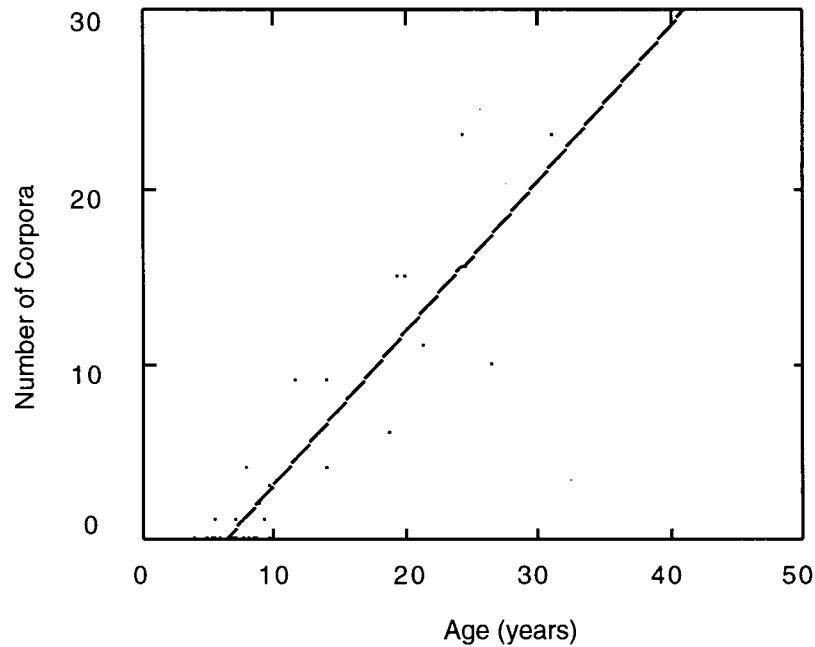


Figure 9. Number of corpora by age for female Pacific white-sided dolphins (from data in Walker *et al.* (1986). Regression of the line is $ASM = -5.533 + 0.8661X$ where ASM is the age of sexual maturity in years and X is the number of corpora ($r^2_{corrected} = 0.83$).

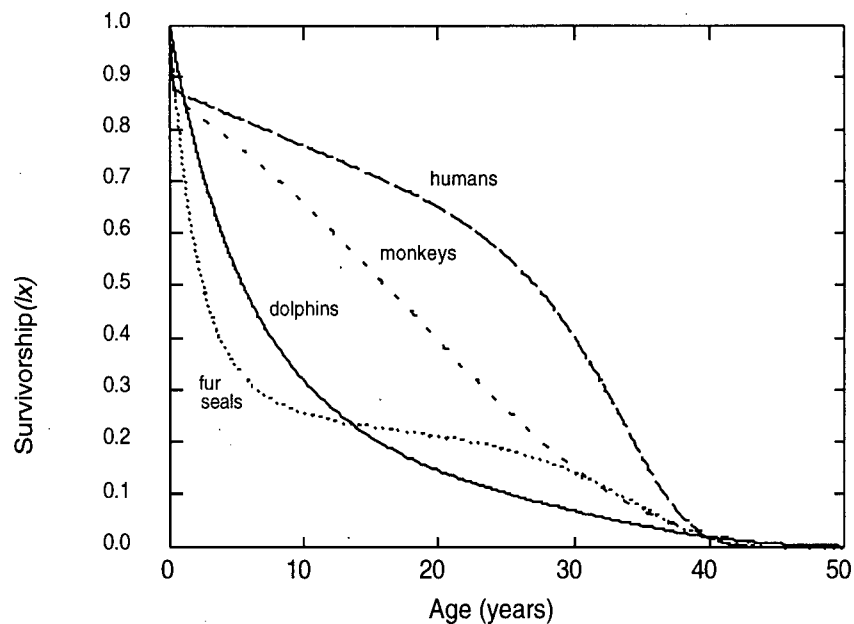


Figure 10. Survivorship curves for female humans, old world monkeys, northern fur seals and Pacific white-sided dolphins. All but the dolphins parameter values were taken from Barlow and Boveng (1991) and were scaled to the lifespan of dolphins.

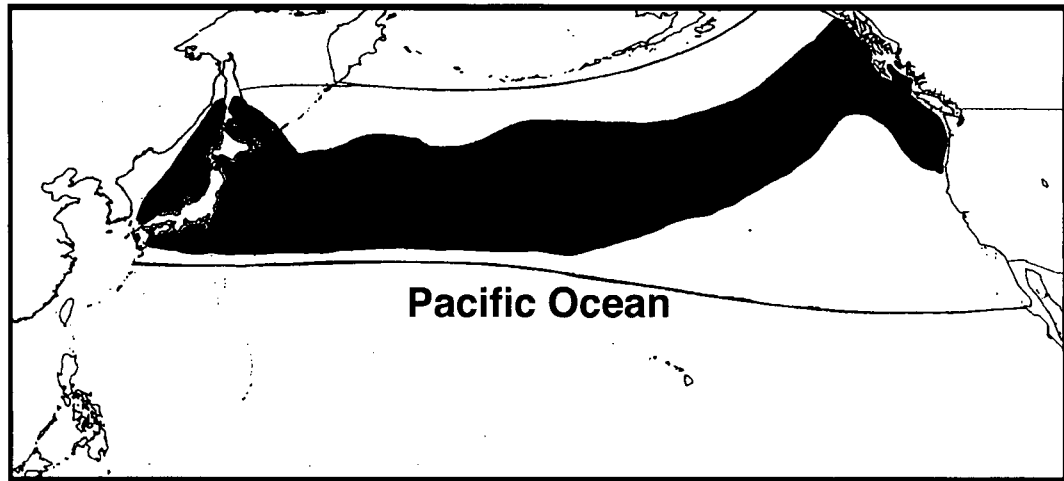


Figure 11. Range of Pacific white-sided dolphins in the Pacific Ocean. Outer black lines indicate the known range for the species. The black shading indicates areas where dolphins were sighted during observer programs in the late 1980's and early 1990's, based on sighting data from Buckland *et al.* (1993), Hobbs and Jones (1993) and Miyashita (1993).

CHAPTER FOUR: Diet and Feeding Behaviour of Pacific White-Sided

Dolphins (*Lagenorhynchus obliquidens*) Based on

Prey Fragment and Stomach Content Analyses.

ABSTRACT

The Pacific white-sided dolphin (*Lagenorhynchus obliquidens*) is likely the most abundant cetacean in the coastal waters of British Columbia. Data collected in pelagic regions suggest that it is a generalist feeder, but little is known of its diet in inshore areas. Here I describe a non-invasive method of obtaining diet information by identifying prey fragments and scales collected near actively foraging dolphins, and the results obtained from 92 encounters with dolphins. Prey species were identified from both fragments and scales, and counts of scale annuli were used to estimate the age and size of fish prey. In 1994 and 1995, herring (*Clupea harengus*) was the most commonly occurring prey species (59%), followed by salmon (*Oncorhynchus* spp.; 30%), cod (Family Gadidae; 6%), shrimp (Order Decapoda; 3%) and capelin (*Mallotus villosus*; 1%). Fish prey ranged from 15 to 60cm. Foraging was observed during all daylight hours, in water depths ranging from 10 to 600m, and 70% of all foraging dives were 15sec or less. Most foraging occurred in groups of two or more dolphins, although individuals sometimes took herring or small salmon. In all cases, large fish were captured by groups of dolphins. Prey species determined from fragment sampling were similar to those obtained from the stomach contents of 11 dolphins that stranded on the British Columbia coast since 1990.

INTRODUCTION

Pacific white-sided dolphins (*Lagenorhynchus obliquidens*), one of six species of *Lagenorhynchus*, are found from 20°N to 61°N in the eastern Pacific, and in the west along the coast of Japan to the Kurile and Commander Islands (Leatherwood *et al.* 1982). Although the diet of Pacific white-sided dolphins has been reported from a variety of locations throughout their range, there are no published reports of their diet in the nearshore waters of British Columbia. As reported in Chapter 2, the distribution of this species has shifted markedly, and today it is likely the most abundant cetacean in the coastal waters of British Columbia. Consequently their role in the marine food web and as potential competitors with commercial fisheries merits further investigation.

The majority of information on the diet of Pacific white-sided dolphins comes from stomach contents recovered from stranded animals and those that were accidentally killed during the high-seas driftnet fishery or deliberately killed for research purposes prior to 1972. A non-invasive method to determine the diet of pinnipeds is scat analysis (Olesiuk *et al.* 1990; Cottrell *et al.* 1996), however, this method is not practical for cetaceans. Stomach contents from stranded animals yield useful information, but strandings occur infrequently. There are also biases inherent in the data obtained from stomach content and scat analyses due to differential rates of prey digestion. For example, in a feeding study on harbour seals, 72% of hake otoliths were recovered, whereas only 30% of herring otoliths were recovered (Cottrell *et al.* 1996).

In this chapter I describe a simple and non-invasive diet sampling method initially developed by the late Dr. Michael Bigg and Graeme Ellis (Dept. of Fisheries and Oceans, Pacific Biological Station, Nanaimo, BC). The method relies on identifying prey type or species from fragments of prey collected following foraging bouts, and I used it to sample the diet of Pacific white-sided dolphins in the inshore waters of British Columbia. I compare these results with those obtained from the analysis of stomach contents of stranded animals, as well as from published records of stomach contents of dolphins from California and pelagic waters. I briefly describe Pacific white-sided dolphin foraging behaviours, and compare them with those of other delphinids. I conclude by estimating the total food consumption of these dolphins and compare it with estimates for the harvest taken by commercial fisheries in the North Pacific.

METHODS

I collected data on the feeding ecology of Pacific white-sided dolphins in three principal study areas along the coast of British Columbia (Fig. 2, Chapter 2): the east coast of the Queen Charlotte Islands; the central mainland coast, and Queen Charlotte Strait/Johnstone Strait. A 6m aluminum vessel powered by a 115hp outboard was used throughout this study. During 141 survey days from April to November 1994 and from June to September 1995, I observed Pacific white-sided dolphins during 92 *encounters* (Table 6). Although dolphins were also sighted on other occasions, during each encounter I collected behavioural and/or acoustic data. Behaviours were recorded using a Hi-8 video recorder with 10:1 zoom magnification. Dive times were recorded by following uniquely marked individuals during foraging bouts.

Sampling Prey Fragments

Surfacing dolphins leave smooth oil-like patches (surface prints) on the water that can persist for up to a minute under light sea conditions. When foraging was observed, I waited for the dolphin(s) to leave, and then proceeded to the surface print at slow speed, so as not to disturb either the dolphins or the surface of the water. By manoeuvring the research vessel carefully and by scanning the surface of the water visually, fragments of prey could be observed to depths of 3m, depending on water clarity, light and sea state conditions. I collected scales and/ or other fragments using a fine-mesh net mounted on a 4m pole (Fig. 12). The net was cleaned thoroughly after each collection of prey. Opportunities to collect scale samples were generally made while observing dolphins within 100m of the research vessel, to minimize travelling time to the area where foraging occurred.

I developed a reference collection of scales from known local fish species, and from the literature (eg. Bilton *et al.* 1964). Species identifications and age estimates based on scales were confirmed by the scale-aging laboratory at the Pacific Biological Station, Dept. of Fisheries and Oceans, Nanaimo, British Columbia. When the age of the fish was uncertain, the youngest age estimate was reported. To test for the possibility that scales remain suspended in near-surface waters, and thus could not be reliably attributed to dolphin foraging activity, I frequently scanned the water's surface on calm days in areas where no foraging dolphins or seabirds were observed. Randomly floating scales were never found. Further, when scales were observed after foraging bouts, they typically sank below reach of the sampling net within one to two minutes.

Table 6. The number of encounters and dates surveyed for each of the three study areas.

Location	Water Depths	Dates	Number of Encounters
Eastern Queen Charlotte Islands	20-100m	April-May 1994	8
Central Mainland Coast	50-500m	June-Sept 1994 July 1995	46
Queen Charlotte and Johnstone Straits	20-600m	Oct-Nov 1994 Aug-Sept 1995	38

Stomach Contents

The collection of stomach content samples was opportunistic, based on the discovery of stranded dead dolphins. Animals were in varying states of decomposition when recovered. In cases in which the entire animal was available, measurements were recorded, a necropsy was conducted and tissue samples were collected. Subsamples of the tissue are archived with the Marine Mammal Research Group (Box 6244, Victoria, BC, V8P 5L5). Stomachs were washed and either processed through an elutriator (Bigg and Olesiuk, 1990), or passed through a series of strainers. Fleshy prey remains were frozen or preserved in alcohol. All bones were washed and dried and compared with a reference collection.

RESULTS

Group Sizes and Dive Durations

The mean total group size for all encounters was about 100 dolphins (mean=102.6, *S.E.*=13.4, *n*=92), however the dolphins often split into smaller groups (subgroups) when foraging. When prey fragments were recovered from subgroups, the minimum estimate of the number of dolphins involved ranged from 2 to 10 animals. It was not possible to determine the maximum number of dolphins involved in each foraging bout, because it was rare that more than four animals surfaced simultaneously.

The most consistent behaviour that occurred prior to the collection of prey was that one or more dolphins circled repeatedly in an area. Fish were often seen flipping at the surface, presumably being chased or herded by dolphins beneath the water, but this did not occur consistently. Dolphins often leapt out of the water while foraging (Fig. 13) but this was also not consistent across foraging bouts. On two occasions fish greater than 30cm long were observed lying at the surface of the water just prior to being captured from below by dolphins. The duration of foraging dives by dolphins ranged from 1 to 153sec (mean = 14.9sec, *S.E.*=1.05sec, *n*=331 dives by 41 individuals), and 70% of all foraging dives were 15sec or less in duration.

Sampling Prey Fragments

Ninety-two encounters with dolphins led to the recovery of 64 samples of prey, including 59 scale samples. Figure 14 shows the distribution of encounter time by hour of the day and the number of scales recovered. Effort and the number of scales recovered were highly correlated

(Spearman pairwise coefficient=0.72). Table 7 shows the species and age class of prey, where known. In all but two cases, prey chasing and herding involved two or more dolphins. In the two observed instances of dolphins foraging alone, the prey were herring (*Clupea harengus*, less than 1 year old) and pink salmon (*Oncorhynchus gorbuscha*, age 1 year). The most frequently occurring prey was herring (59%), then salmon (30%), cod (Family Gadidae 6%), shrimp (Order Decapoda 3%), and capelin (*Mallotus villosus*, 1%).

Debilitated and wounded capelin and Pacific cod (*Gadus macrocephalus*, Family Gadidae) found at surface prints were measured. Lengths of herring were estimated from Ricker (1975). Lengths of pink, sockeye, and coho salmon were estimated from Takagi *et al.* (1981), Burgner (1991) and Sandercock (1991) respectively. Fish ranged from 15 to 60cm in length (Table 7).

Stomach Contents

Table 8 lists the date, location, and stomach contents of 11 dolphins found stranded on the BC coast since 1990. Three dolphins reported from Kent Inlet were part of a group of 8 carcasses that were found by sea urchin fishermen and Dept. of Fisheries and Oceans personnel during January 1996. At least some of the dolphins had been trapped in the inlet for several days and possibly up to two weeks prior to death (Karen Hansen, *Fisheries Patrol Vessel Bluefin II*, pers. comm.). A complete list of all prey species recorded from the stomachs of Pacific white-sided dolphins can be found in Appendix 2.

Table 7. Prey of Pacific white-sided dolphins in the inshore waters of British Columbia based on the collection of fragments following foraging bouts. Scientific names are listed in Appendix 2.

Species	Age	Number	Estimated Prey Length (cm)
Herring	All	38	
	0	12	15.4
	1	16	16.4
	2	5	18.6
	3	1	19.6
	4	1	20.8
	5	1	21.6
	8	2	23.3
Salmon	All	19	
Unidentified	?	1	
Pink salmon	0	2	1 fish at 19cm, 1 at 22.5cm
	1	11	4 fish at 54cm, 7 fish at 58cm
Sockeye salmon	1	1	37
	3	2	50
	4	1	60
Coho salmon	1	1	18
Gadidae	3	4	one <i>Gadus macrocephalus</i> at 42 cm, others unknown
Shrimp		2	not available
Capelin		1	capelin found near surface print measured at 12.5cm

Table 8. Stomach contents of 11 Pacific white-sided dolphins recovered in British Columbia between 1990 and 1996.

DATE	LOCATION	CONTENTS
October 1990	Johnstone Strait	2 chum salmon*
June 1991	Goose Island	Herring, other unidentified small fish
August 1991	Round Is. Pt Hardy	Pollock, sablefish, salmon, 2 squid beaks, feather
June 1992	Queen Charlotte Is.	Pollock, salmon, herring, unidentified small fish
Sept. 1992	Waddington Island	Pollock, salmon, herring, smelt, shrimp, squid
August 1995	Johnstone Strait	Empty
August 1995	Gordon Channel	Salmon
January 1996	Kent Inlet	Empty
January 1996	Kent Inlet	Empty
January 1996	Kent Inlet	Shrimp fragments
Feb. 1996	Johnstone Strait	Shrimp fragments, fish bone**

* Based on scales in the stomach, these fish were 54 and 59cm long

** Otolith embedded in surface of lung, possibly Gadidae

DISCUSSION

Prey Consumed by Pacific White-sided Dolphins

Based on prey fragment sampling, dolphins appear to be taking larger prey in British Columbia than they do in the open Pacific or off California. This may be because prey fragment sampling is a less biased method for collecting information on the size of prey consumed than more traditional methods. Black (1994) found that off California, fish prey recovered in dolphin stomachs ranged between 3 and 42cm in length, and in the open Pacific, Pacific white-sided dolphins preyed predominantly on Myctophids (Walker and Jones 1993) which rarely exceed 18cm (Hart 1973). The absence of large prey in the diet of dolphins from other areas may be due to the abundance of smaller schooling prey, or it may be a bias resulting from the use of otoliths found in stomach contents to determine prey age and size. For example, if dolphins feed on fish too large to swallow whole, the head may be discarded when the fish is broken up. If this takes place, the otolith is lost and the large prey item will not be represented in the analyses.

Pacific white-sided dolphins are clearly opportunistic predators, feeding on over 60 species of fish and 20 species of cephalopods throughout their range (Appendix 2). In British Columbia, they feed on at least 13 different prey species. Analyses of stomach contents and prey fragment samples indicate that salmon are an important component in the diet of dolphins, ranging from 30 to 60% of their diet depending on the sampling method used (Tables 7,8, 11). Salmon were taken from June through November, and many of the kills were of small fish less than 25cm, although fish more than 50cm in length were taken on at least 12 occasions. Dolphins collected off the Columbia River, Washington over a two day period in February 1968 also ate salmon

(Stroud *et al.* 1981), but all fish were between 26 and 34cm long, considerably smaller than the salmon consumed by dolphins in this study.

Table 9 summarizes the principal prey species and their frequency of occurrence in the stomachs of Pacific white-sided dolphins from California, Washington, the central North Pacific Ocean, Japan, and British Columbia. Herring was an important prey item in British Columbia, yet was absent from the 101 animals sampled off California, despite the existence of a large commercial herring fishery there (Oliphant *et al.* 1990). Similarly it is surprising that squid did not occur with greater frequency in the stomachs of dolphins in British Columbia since they are an important prey in other locations. The abundance and distribution of squid has not been well quantified in inshore waters, but its general absence in the diet of dolphins suggests that it is not common in British Columbia. By contrast, in California there has long been a commercial squid fishery for *Loligo opalescens* in areas where dolphins have been found (Fiscus 1982). Myctophids are uncommon along the nearshore waters of British Columbia (Taylor 1967) and thus it is not surprising that they were absent in the stomach contents of dolphins.

Walker and Jones (1993) analyzed the stomach contents of dolphins killed during the high seas flying-squid driftnet fishery in 1990. The animals were caught between 145°W and 170°E in the North Pacific Transition Zone during summer. The diet of dolphins in the area may be very different in winter. *Onychoteuthis borealijaponica* was the predominant squid species consumed by dolphins, and not *Ommastrephes bartrami*, the target species of the driftnet fishery (Walker and Jones 1993). The diet of animals from Japan sampled by Wilke *et al.* (1953) was similar

to that of the dolphins sampled from the driftnet fishery. Walker and Jones (1993) suggested that squid and Myctophids were predominant in the diet of Japanese dolphins because they were sampled in an area where the continental shelf is narrow, and water depth is typically in excess of 1000m. Dolphins captured in shallower areas by Sleptsov (1955) and Hotta *et al.* (1969) were foraging primarily on squid, anchovy (*Engraulis* sp.), saury (*Cololabis* sp.) and jack mackerel (*Trachurus japonicus*).

The discovery of jellyfish in the stomach of a dolphin by Scheffer (1953) was intriguing. Jellyfish are reported as prey of coho salmon when foraging offshore (Sandercock 1991). Jellyfish are high in protein on a per weight basis, but deteriorate beyond recognition within 20 to 30 minutes of consumption (Mary Arie, University of Alberta, pers. comm.). If present in the stomach of a dolphin, it is very likely that jellyfish would be missed during the course of most necropsies. Perhaps more concentrated effort to look for active foraging on jellyfish when sampling for prey fragments may provide insight into whether or not they are typical prey in the diet of Pacific white-sided dolphins.

The Collection of Prey Fragments to Confirm Diet

The sampling of prey fragments during foraging bouts provides the potential to collect diet information relatively quickly and non-invasively. During the course of this two year field study, 64 prey fragment samples were collected compared to only two stomachs. The collection of fragments helps to confirm behavioural observations that dolphins are indeed foraging. This can be important in behavioural studies, as Pacific white-sided dolphins display a wide variety of

aerial behaviours, only some of which are associated with foraging (unpubl. data). As discussed above, the use of scale samples rather than otoliths to estimate prey age and length may reduce bias in estimating the size of prey. As prey species identification and size estimates are traditionally based on length regressions on otolith size, these larger prey would be missed when stomach contents are examined.

Prey fragment sampling does have some biases. Observations are based only on foraging behaviours that take place at or near the surface during daylight hours. The observers must be reasonably familiar with the behaviour of the study species to recognize that foraging is taking place. Only prey that are damaged or broken apart during the foraging bout will be sampled. Some fish such as hake have deciduous scales and therefore cannot be aged reliably (Hart 1973). It is possible that some fish, such as Gadids (including hake) are under-represented in the diet of Pacific white-sided dolphins when sampled by collecting prey fragments, because they rise to the surface at night (Lamb and Edgell 1986), a time when it is not practical to collect prey fragments of foraging dolphins. The method also depends on the use of a manouverable boat and good sighting conditions to collect fragments successfully.

Foraging Behaviour

In this study foraging was observed during all daylight hours. Peaks in the collections of prey fragments generally reflect varying observer effort (Fig. 14), and not increased foraging behaviour of the dolphins. These results differ from observations made in other areas. Many of the dolphin stomachs reported from California and the open Pacific contained prey that are

Table 9. Percent occurrence of the principal prey of Pacific white-sided dolphins based on stomach content analyses. Empty stomachs were not included in the calculations.

Prey	CALIFORNIA					OPEN PACIFIC	JAPAN	WASHINGTON	B.C.
	Stroud <i>et al.</i> * 1981	Walker <i>et al.</i> 1986	Black 1994	Morejohn <i>et al.</i> 1978	Jones 1981	Walker and Jones 1993	Wilke <i>et al.</i> 1953	Stroud <i>et al.</i> 1981	This study
Anchovy (<i>Engraulis mordax</i>)	57.6	78.3	56.3	p	p	0	10	0	0
Hake (<i>Merluccius productus</i>)	30.3	60.9	68.8	p	p	0	0	0	0
Squid (Cephalopods)	70.0	60.9	68.8	p	43	100	90	100	12.5
Saury (<i>Cololabis saira</i>)	27.3	0	0	u	0	15.1	0	0	0
Salmon (<i>Oncorhynchus spp.</i>)	0	0	0	u	0	0	0	91	62.5
Myctophids (Myctophidae)	3	8.7	0	u	0	78.8	70	0	0
Midshipmen (<i>Porichthys notatus</i>)	0	13	50	u	p	0	0	0	0
Herring (<i>Clupea harengus</i>)	0	0	0	0	0	0	0	0	37.5
Pollock (<i>Theragera sp.</i>)	0	0	0	0	0	0	0	0	37.5
Shrimp	0	0	0	0	0	0	0	0	37.5
Decapoda	0	0	0	0	0	0	0	0	12.5
Sablefish (<i>Anoplopoma sp.</i>)	0	0	0	0	0	0	0	0	12.5
Smelt Osmeridae	0	0	0	0	0	0	0	0	12.5
Number of stomachs with prey/ number stomachs examined	?/33	20/23	16/18	5/10	7/10	33/62	10/13	?/11	8/11
Percent stomachs containing prey	75	87.0	88.9	50.0	70.0	53.2	76.9	75.0	72.7
Method acquired	shot	mostly stranded	strand	strand	strand	bycatch	harpoon	strand	strand

* = Results reported are identical to those reported in Kajimura *et al.* (1980), therefore only Stroud *et al.* is cited here

p = Present but could not determine frequency from data presented

u = Not stated

? = In the original reference, the number of stomachs containing prey were pooled for both California and Washington.

benthic or inhabit deep water by day, and rise to the surface by night (mesopelagics, midshipmen, hake). Walker *et al.* (1986) summarize several small studies that suggest feeding occurs from dusk through dawn. Behavioural observations by Black (1994) recorded between 0800 and 1400 suggest that foraging occurred more often in the morning than in the afternoon, in water 200-1000m deep off of Monterey Bay California. Stroud *et al.* (1981) suggested that because the largest stomach volumes were recorded from animals harvested before 10am, most feeding occurs at night or in the morning.

The locations where animals were sampled by Stroud *et al.* (1981) and observations of dolphins by Black (1994) suggest that dolphins are frequently found in deeper water off California than in British Columbia. Black (1994) found the bottom depth in areas where dolphins were most commonly found was 200 to over 1000m. In the study area in British Columbia, water depth rarely exceeded 600m. Many of the foraging bouts observed were in waters less than 100m (unpubl. data). Although dolphins were found in deeper water in California, their mean dive times based on radio-tagged dolphins appeared to be similar to those of feeding dolphins observed in this study. Black (1994) found that 70% of all recorded dives were less than 20sec in duration. In this study, 70% of foraging dives were 15sec or less. This suggests that most foraging occurs at relatively shallow depths, regardless of location. When dolphins forage on deepwater prey, they appear to wait for the prey to rise to the surface, rather than diving deeply to capture it.

Comparison with Other Schooling Delphinids

Pacific white-sided dolphins are very similar to dusky dolphins (*Lagenorhynchus obscurus*), ecologically and taxonomically. After comparing the cranial morphology of specimens of both species, Webber (1986) questioned whether it was justifiable to separate the two. Both inhabit temperate waters and display a variety of aerial behaviours. They are found in groups from a few to over a thousand animals, and feed on a diversity of prey (Leatherwood and Reeves 1983). Fish herding behaviour of dusky dolphins (Wursig 1986) is similar to that observed in Pacific white-sided dolphins foraging in British Columbia during this study, and to foraging in Atlantic spotted dolphins (*Stenella frontalis*, Fertl and Wursig, 1995). Groups of dolphins moved in a co-ordinated manner to maintain fish in a tight school. Although dolphins often surfaced in the middle of the school of fish, they also frequently swam along the periphery of the school and appeared to pick off individual fish.

Pacific white-sided dolphins were frequently observed herding schools of fish. Fish in the middle of a school may experience reduced oxygen concentration, as suggested by McFarland and Moss (1967). Moss and McFarland (1970) found that schools of anchovy increased their swimming speed and that schools changed shape more frequently when oxygen concentrations were reduced. They hypothesized that this was part of a behavioural response by fish to avoid spending time in the centre of the school. When being corralled by dolphins, it is possible that fish within the school cannot alter their behaviours to avoid the anoxic environment in the centre of the school, and so become oxygen stressed and vulnerable to predation. I frequently observed dolphins and seabirds capturing debilitated small fish at the surface, without active pursuit of the fish. This

foraging strategy may be quite efficient for groups of dolphins, and allow them to catch individual fish without expending large amounts of energy in pursuit. Thus the co-ordinated movements of the dolphins may serve to hold the school of prey in place, and increase the foraging efficiency of the individuals within the group.

Like Pacific white-sided dolphins, dusky dolphins from different areas also vary in their diets. Wursig *et al.* (1989) and Cipriano (1992) found that dolphins fed predominantly on squid and myctophids off the southern tip of New Zealand, an area where the continental shelf is relatively narrow and depths of over 2,000m can be found within 2 km of shore. Groups of dolphins generally were large and tightly grouped. By comparison, dusky dolphins travel in widely dispersed groups in Argentina, and feed predominantly on small schooling fish (anchovy) (Wursig and Wursig, 1980). The water depth is typically less than 200 m in this area. This more closely resembles the situation in British Columbia, whereas the situation off New Zealand is more typical of animals in the central North Pacific (Walker and Jones, 1993) and off southern Japan (Wilke *et al.* 1953).

Daily Consumption Estimates

In aquaria, Pacific white-sided dolphins receive about 8 to 9 kg of food per day (Clint Wright, Vancouver Aquarium, BC, pers. comm.). A typical diet is 5 kg of herring and 3 kg of squid. Herring has a caloric value ranging from 2.05 kcal/g in spring to 2.29 kcal/g in winter, and squid has an average caloric value of 1.14 kcal/g (Perez 1990). This suggests a minimum caloric requirement of 13,670-17,160 kcal/day/dolphin. Animals in the wild likely consume more. If

a dolphin fed exclusively on squid, then an average animal could be expected to consume 12kg to 15.1kg of squid per day. Lanternfish, an important prey of dolphins offshore, are estimated to have an energy value of 1.63kcal/g (Perez 1990), thus a dolphin might consume between 8.4kg to 10.5kg of lanternfish per day to meet its minimum daily requirements.

Innes *et al.* (1987) calculated daily consumption (R) for marine mammals using

$$R_s = 0.123W_s^{0.8},$$

where W_s is mean weight of sex s . This estimate yields a daily consumption of 4.5 kg for an average male dolphin (weighing 90 kg), which is significantly less than that reported for animals in captivity. Sergeant (1969) suggested that cetaceans in captivity consume approximately 4-13 % of their body weight per day depending on age. Thus a 90 kg dolphin in captivity might consume between 3.6 and 11.7kg/day. Based on the volume and nutritional quality of material recovered during stomach content analyses, Cipriano (1992) conservatively estimated that 14,750 kcal/day were required for a 77kg wild dusky dolphin (*Lagenorhynchus obscurus*), a species similar in morphology and behaviour to the Pacific white sided dolphin. This translates to a daily consumption of 9.2% of its body weight per day, if the dolphin consumed herring.

Total Population Consumption

If we assume that dolphins in the wild eat 9% of their body weight per day, then it is possible to estimate the total food consumption of Pacific white-sided dolphins in the North Pacific. The

mean weight of an individual is about 82.5 kg (Heise 1997, Chapter 3 of this thesis). Assuming that there are approximately 931,000 animals (range 206,000-4,216,000) in the population (Buckland *et al.* 1993), which is an overestimate (see Chapter 3), then the total food consumption of Pacific white-sided dolphins in the North Pacific is about 6,900tonnes/day (range 680-45,000tonnes/day), or 2,518,000tonnes/year (range 248,200-16,425,000tonnes/year). By comparison, commercial fisheries in the entire North Pacific in 1992 took 36,399,000tonnes (FAO,1995). The diet of dolphins varies by location, and may be a function of both the abundance and the distribution of prey species. As factors such as climate change influence the distribution of prey (Beamish 1995), we may see a shift either in the diet or the distribution of dolphins. In fact, this may already be occurring. In British Columbia, the distribution and/ or abundance of Pacific white-sided dolphins in inshore waters has increased markedly over the past 12 years (Chapter 2).

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Figure 12. Net used to collect fragments of prey. Fish scales can be seen in the centre of the net.



Figure 13. Foraging leaps by Pacific white-sided dolphins.

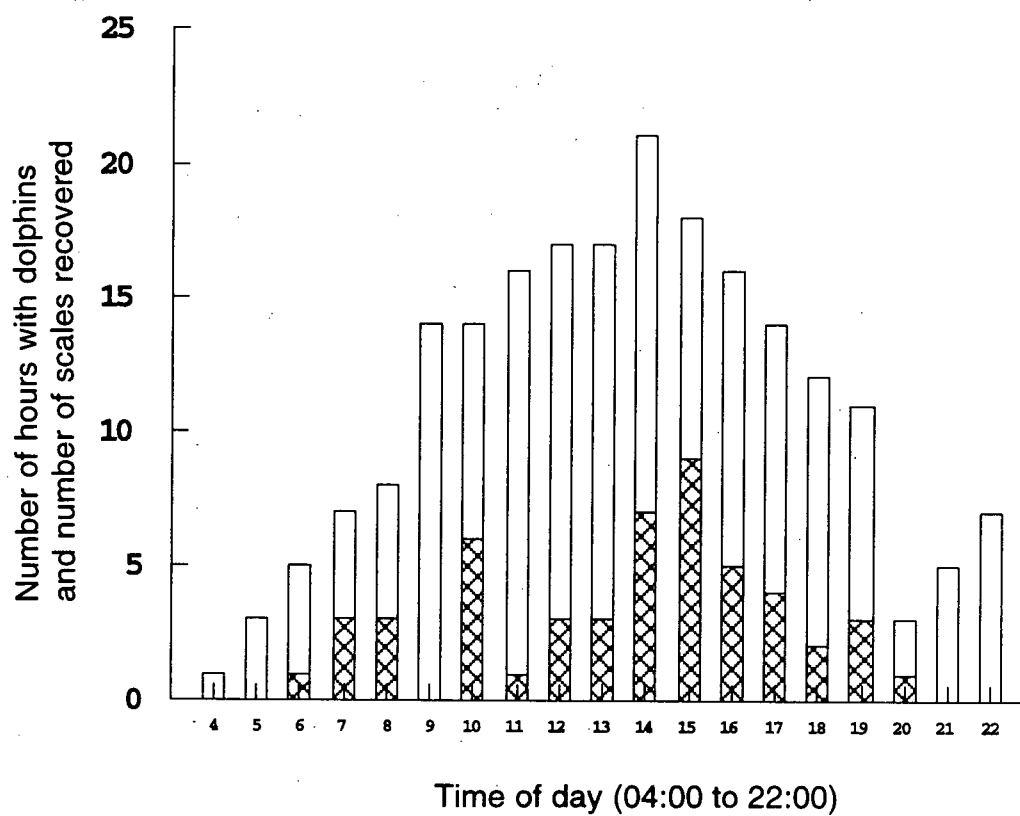


Figure 14. The distribution of encounter hours and the number of prey fragments recovered during those encounter hours, as indicated by cross-hatches, for the 1995 field season.

CHAPTER FIVE: Conclusions and Recommendations for Further Research

I could not begin this study, which examines potential reasons for the increase in Pacific white-sided dolphins in the coastal waters of British Columbia, without first verifying that the population had indeed increased. This was challenging, as there were no population estimates for dolphins in inshore waters, so I surveyed mariners who had spent significant time on or near the water for their opinions. As reported in Chapter 2, responses to the surveys indicated a shared belief that there has been a marked increase in sightings of these dolphins inshore after 1984. Between 1978 and 1984 there were relatively few sightings of these animals. This period coincides with a 'regime shift' from relatively cool to warm water in the North Pacific (Beamish 1995), and there may be a correlation between the two events. Changes in the distribution and abundance of other species were noted during the same period (Beamish and Bouillion, 1993; Hare and Francis, 1995). However, the appearance of dolphins in coastal waters is not unprecedented, based on the recovery of Pacific white-sided dolphin teeth from aboriginal midden sites (Mitchell 1988). It remains unclear whether dolphins were relatively abundant prior to 1978, or if they were occasional visitors to coastal waters.

In Chapter 3, I examined whether population growth could explain the increase in abundance of dolphins in coastal waters. Based on previously published data collected from the drive and high-seas driftnet fisheries, as well as from records of stranded and scientifically harvested animals, I estimated the finite rate of population growth of Pacific white-sided dolphins to be approximately 0.94 to 1.02/yr, suggesting that the population is close to stationary. The increase

in sightings of dolphins inshore coincided with a period of high mortality offshore due to the high seas flying-squid driftnet fishery (Tanaka 1993). Even if dolphins were producing calves at the maximum rate for the species, it seems unlikely that population growth could provide a sufficient explanation for the increase in sightings of dolphins in inshore waters after 1984.

The role of diet in the increase in abundance of Pacific white-sided dolphins is less clear. The movement of dolphins inshore may have been related to changes in the distribution of their prey. An alternative explanation may be that dolphins were responding to a decline in food resources in other locations. Although I do not have any evidence to support or refute the latter hypothesis, Chapter 4 shows that Pacific white-sided dolphins were feeding on different prey species in other areas. In the nearshore waters of British Columbia, herring, salmon, cod and shrimp were important prey. In offshore waters, dolphins feed primarily on mesopelagic fish and squid (Walker and Jones, 1993), and off California squid, anchovy and hake are predominant in the diet (Stroud *et al.* 1981; Walker *et al.* 1986; Black, 1994). Thus, the inshore shift of dolphins cannot be simply a response to a change in the distribution of their prey. However, the regime shift has affected the abundance of herring, salmon and other forage fish species (Brodeur and Ware, 1995; Hallowed and Wooster, 1995; Anderson *et al.* 1996) which may result in changes in the distribution of dolphins. Further research on this is needed.

Recommendations for Future Research

The most obvious 'next step' is to develop a more quantitative estimate of dolphin abundance in coastal waters. A population census is long overdue. At present, there could be anywhere

from 3,000 to 30,000 or more dolphins in the inshore waters of British Columbia. In the open Pacific, Buckland *et al.* (1993) encountered schools of dolphins at rates varying from 0.0003 to 0.007 groups per km during line transect surveys. In transect surveys in southeast Alaska, Dahlheim and Towell (1994) found between 0 and 0.015 groups per km. Many mariners suggested that dolphins were most abundant in spring when they were foraging on spawning herring, and this might be the logical time to conduct a census.

The range movements of Pacific white-sided dolphins are not well understood, and could influence the accuracy of a population census in British Columbia. The extent to which dolphins travel between British Columbia and California or between nearshore and offshore waters is unknown. Preliminary genetic analysis suggests that dolphins may move between coastal and pelagic regions. Lux *et al.* (1996) found no haplotype differences between animals sampled from inshore and offshore areas, based on the analysis of mitochondrial DNA. However, they did find haplotype differences in dolphin samples from Baja California, California/Washington/Oregon, and British Columbia/Alaska, suggesting that in the eastern North Pacific there may be three stocks (management units). This population structure is considered preliminary, since only 11 of the 69 samples analyzed were from the northern region. For many years researchers off the coasts of California and Washington have photographed anomalously pigmented dolphins (e.g. Walker *et al.* 1986; Black, 1994). The absence of these light-coloured dolphins in the coastal waters of British Columbia (unpubl. data) further supports the suggestion that dolphins from California are from a different population. A greater emphasis on photo-identification of individuals would help to define the home ranges of Pacific white-sided dolphins. Alternatively,

radio-tags or satellite tags could be used to record the range of dolphin movements.

Five to 10 years have passed since Buckland *et al.* (1993) and Miyashita (1993) conducted ship surveys to estimate Pacific white-sided dolphin abundance in the North Pacific. If additional surveys are made in future, it may be possible to determine whether dolphin populations are growing or remaining stationary, relative to estimates made in the 1980's. Any future effort should also quantify the bias in population estimates due to the attraction that white-sided dolphins have to boats, as per Turnock and Quinn (1991).

It would also be worthwhile to conduct a study of dolphin diet by conducting prey-fragment sampling year-round. While the results reported in Chapter 3 suggest that the diet of dolphins in the inshore waters of British Columbia is quite different from that of animals further offshore and off California, a different situation may exist in winter months. As well, by combining more realistic population estimates of Pacific white-sided dolphins with a better understanding of their diet, it would be quite feasible to model the effect of dolphins on forage fish populations.

In this thesis I have discussed the possibility that large scale oceanographic processes may be influencing the distribution of dolphins. These changes may be normal fluctuations, such as those seen over 2,000 years in pelagic fish populations in the California basin (Soutar and Issacs, 1969; 1974), or they may have anthropogenic causes. Trenberth and Hoar (1996) have expressed concern that the recent El Niño event lasted longer than any other in the previous 113 years, and may be a signal of global warming. I would like to close this thesis by speculating that if the

warming trend of the North Pacific continues, Pacific white-sided dolphins will continue to be found regularly in inshore waters. I predict that the abundance of dolphins will decline in inshore waters when and if water temperatures begin to decline.

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APPENDIX 1: Questionnaire distributed to mariners.

PACIFIC WHITE-SIDED DOLPHIN*(Lagenorhynchus obliquidens)*

- can be very animated, often leaping clear of the water, either alone or in small groups
- will ride on the bow and in the wake of boats
- group sizes range from 2 to over 1,000 animals, and average 40-100 in inshore waters
- produce sounds underwater at frequencies that humans can hear (if they have a hydrophone)
- colouration is a mix of gray, white and black
- dorsal fin is usually larger and more curved than Dall's or harbour porpoises, and is typically black at the front and pale gray at the rear
- 5 to 7.5 feet long (1.5-2.5 m)
- 220-330 pounds (100-200 kg)
- teeth are cone-shaped

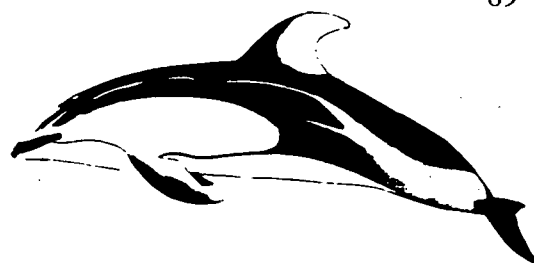
**DALL'S PORPOISE***(Phocoenoides dalli)*

- do NOT leap clear of the water, although they often produce a rooster-tail of spray when travelling quickly
- group sizes range from 2 to 20 animals, rarely larger
- will bowride boats on occasion
- colouration is mostly black, with white patches on the chest/belly area and the tips of the tail
- dorsal fin is small, almost triangular in shape and ranges in colour from all black to nearly all white
- produce sounds underwater at frequencies that are too high for humans to hear
- 4 to 6.5 feet long (1.2 - 2.2 m)
- 220 to 480 pounds (100-220 kg)
- teeth are spade-shaped

**HARBOUR PORPOISE***(Phocoena phocoena)*

- do NOT leap clear of the water
- usually seen alone or in small groups of 2 to 10 animals
- do not bowride
- colouration is variable, mostly dark brown or gray above, slightly lighter on the undersides, but with no distinct markings
- dorsal fin is small and the same colouration as the body
- underwater sounds are at frequencies too high for human hearing
- 4 to 6 feet long (1.2-2 m)
- 100 to 155 pounds (45-75 kg)
- teeth are spade-shaped





Your Name:

Address:

Phone:

1. What is your principal activity on the water (e.g. commercial fishing, commercial towing, lighthouse keeper, recreational boating, research etc.)?
2. In which areas have you spent the majority of time (e.g. Juan de Fuca Strait, Johnstone Strait, Queen Charlotte Islands, Southeast Alaska, etc.)?
3. Please list the years that you have spent significant time on or by the ocean (for example: (1982-1995 inclusive), or (1989, 1992 and 1994)).
4. In a typical year, how many days per month do you spend on the water?

January	_____	July	_____
February	_____	August	_____
March	_____	September	_____
April	_____	October	_____
May	_____	November	_____
June	_____	December	_____
5. On average, how many hours per day do you spend on or in view of the water?
 _____ hours/day
6. a) Have you ever seen Pacific white-sided dolphins?
 YES NO
- b) When did you first see them? (Approximate month/year is OK)
- c) Where did you first see them and how many did you see there?
- d) Do you know if Pacific white-sided dolphins are found there on a regular basis?

Please Turn Over

APPENDIX 2. Prey recorded in the diet of Pacific white-sided dolphins in the North Pacific.

APPENDIX 2. Prey recorded in the diet of Pacific white-sided dolphins in the North Pacific.

FISH

Family	Scientific Name	Common Name	Reference
Anoplopomatidae			
	<i>Anoplopoma fimbria</i>	Sablefish	2,11
Argentinidae			
	<i>Argentina</i> sp.	Argentines	1
	<i>Nansenia candida</i>	Bluethroat argentine	1
Bathylagidae			
	<i>Leuroglossus schmidtii</i>	Smooth tongues	1
	<i>Leuroglossus stilbius</i>		2
	<i>Bathylagus</i> spp. (3)	Black smelts	1
	Unidentifiable		1
Batrachoididae			
	<i>Porichthys myriaster</i>		2
	<i>Porichthys notatus</i>	Plainfin midshipmen	2, 3
Bothidae			
	<i>Citharichthys sordidus</i>	Pacific sandab	3, 4
Carangidae			
	<i>Trachurus japonicus</i>	Jack mackerel (Japan)	10
	<i>Trachurus symmetricus</i>	Jack mackerel (N. America)	2, 3, 4
Centrolophidae			
	<i>Icihthys lockingtoni</i>	Medusafish	1, 4
Clupeidae			
	<i>Sardinops sardine</i>	Pacific sardine	2, 3
	<i>Clupea harengus</i>	Pacific herring	11
Cynoglossidae			
	<i>Symphurus atricauda</i>		2
Engraulidae			
	<i>Engraulis mordax</i>	Northern anchovy	2, 3, 4, 6
	<i>Engraulis japonica</i>		9, 10
Gadidae			
	<i>Merluccius productus</i>	Hake/ Pacific whiting	2, 3, 4, 6
	<i>Gadus macrocephalus</i>	Pacific cod	11
	<i>Theragra chalcogramma</i>	Walleye pollock	11
	Unidentifiable		11
Gempylidae			
	<i>Gempylus serpens</i>		1
Gonostomatidae			
	<i>Ichthyococcus</i> sp.		1
	Unidentifiable		1
Melanostomiidae			
	Unidentifiable		1
Myctophidae			
	<i>Ceratoscopelas</i> sp.		1
	<i>Diaphus gigas</i>		1
	<i>Diaphus</i> sp.		1
	<i>Diaphus theta</i>		1, 2

FISH cont.

Family	Scientific Name	Common Name	Reference
Myctophidae (cont.)			
	<i>Hygophum</i> sp.		1
	<i>Lampadena urophaos</i>		1
	<i>Lampanyctus jordani</i>		1
	<i>Lampanyctus regalis</i>		1
	<i>Lampanyctus</i> sp. A		1
	<i>Myctophum asperum</i>		1
	<i>Myctophum nitidulum</i>		1
	<i>Notoscopelas resplendens</i>		1
	<i>Protomyctophum</i> spp.		1
	<i>Stenobrachicus</i> spp.		1
	<i>Symbolophorus</i> sp.		1
	<i>Symbolophorus californiensis</i>		4
	<i>Tarletonbeania</i> sp.		1
	<i>Triphoturus mexicanus</i>		2
	Unidentifiable		1, 9
Ophidiidae			
	<i>Chilara taylori</i>		2
Osmeridae			
	<i>Mallotus villosus</i>	Capelin	11
	<i>Thaleichthys pacificus</i>	Eulachon	11
Paralepididae			
	<i>Lestidiops ringens</i>		1
	<i>Paralepsis atlantica</i>		1
Pentacerotidae			
	<i>Pentaceros richardsoni</i>	Armorheads	1
Pleuronectidae			
	<i>Hypsosetta guttata</i>		2
Salmonidae			
	<i>Oncorhynchus</i> sp.	Salmon	4, 11
	<i>Oncorhynchus gorbuscha</i>	Pink salmon	11
	<i>Oncorhynchus keta</i>	Chum salmon	4, 11
	<i>Oncorhynchus kisutch</i>	Coho	4, 11
	<i>Oncorhynchus nerka</i>	Sockeye	11
	<i>Oncorhynchus tshawytscha</i>	Chinook	No records
Sciaenidae			
	<i>Genyonemus lineatus</i>	Drums	2, 3
	<i>Seriphus politus</i>		2, 8
	Unidentified		4
Scomberosocidae			
	<i>Colalabis</i> sp.		10
	<i>Colalabis saira</i>	Pacific saury	1
Scombridae			
	<i>Scomber japonicus</i>	Pacific (Chub) mackerel	2
Scopelarchidae			
	<i>Benthalbella dentata</i>		1
Scopelosauridae			
	<i>Scopelosaurus harryi</i>		1
Scorpaenidae			
	<i>Sebastes</i> sp.	Rockfish	3, 4, 6

FISH cont.

Family	Scientific Name	Common Name	Reference
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Stromateidae

Peprilus simillus

2

Tetragonuridae

Tetragonurus cuvieri

1

Trachipteridae

Trachipterus altivelis

King of the salmon

1, 4

Order Petromyzoniformes

Lampetra tridentatus

Pacific Lamprey

4

CEPHALOPODS

Family	Scientific Name	Common Name	Reference
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Unidentified

7, 11

Chiroteuthidae

Chiroteuthis sp.

1, 3, 4

Cranchiidae

Galiteuthis sp.

3, 4

Galiteuthis phyllura

1

Enoploteuthidae

Enoploteuthis chuni

1

Abraliopsis felis

1

Abraliopsis sp.

1, 3, 4, 5

Gonatidae

Gonatus spp. (3 species)

1, 2, 3, 4, 5

Gonatopsis borealis

1, 3, 4

Gonatopsis berryi

3

Gonatopsis-Berryteuthis type

1

Berryteuthis anonychus

1

Histoteuthidae

Histoteuthis heteropsis

3

Loliginidae

Loligo opalescens

2, 3, 4, 5, 6

Mastigoteuthidae

Mastigoteuthis sp.

1

Octopoteuthidae

Octopoteuthis deletron

1, 3

Octopoteuthis sp.

2, 5

Octopodidae

Octopus sp.

2

Octopus rubescens

3

Ocythoidae

Ocythoe tuberculata

3, 4

Ommastrephidae

Ommastrephes bartrami

1

Onychoteuthidae

Onychoteuthis borealijaponica

1, 3, 4

Onychoteuthis sp.

2, 5

Sepiolidae

Rossoa pacifica

3

OTHER

Family	Scientific Name	Common Name	Reference
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Crustaceans

	Unidentified		11
	<i>Pandalus sp.</i>		10

Jellyfish

	Unidentified	?	7
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SOURCES

1. Walker and Jones, 1993 2. Walker *et al.* 1986 3. Black, 1994 4. Stroud *et al.* 1981
 5. Jones, 1981 6. Morejohn *et. al.*, 1978 7. Schefffer, 1953 8. Fitch and Brownell, 1968
 9. Wilke *et al.* 1953 10. Sleptsov, 1955 11. This study.