

Diet and Feeding Behaviour of Pacific White-Sided Dolphins (*Lagenorhynchus obliquidens*) as Revealed Through the Collection of Prey Fragments and Stomach Content Analyses

Kathy Heise

Dept. of Zoology, University of British Columbia, 6270 University Blvd., Vancouver, BC, Canada V6T 1Z4

ABSTRACT

The Pacific white-sided dolphin (*Lagenorhynchus obliquidens*) is probably the most abundant cetacean in the coastal waters of British Columbia, Canada. Data collected in pelagic regions suggest that it is a generalist feeder, but little is known of its diet in inshore areas. This paper describes a non-invasive method of obtaining diet information by identifying prey fragments and scales collected near actively foraging animals, and the results obtained from 92 encounters with dolphins are presented. 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 lasted 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 have stranded on the coast of British Columbia since 1990. In the North Pacific, Pacific white-sided dolphins consume about 2.5 million tonnes of fish per year, which is approximately 7% of the total commercial harvest for the area.

KEYWORDS: DIET; FEEDING; PACIFIC WHITE-SIDED DOLPHINS; NORTH PACIFIC

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. The distribution of this species has shifted markedly since the mid-1980s (Heise, 1996) and it is now probably the most abundant cetacean in the coastal waters of British Columbia. Consequently its role in the marine food web and as a potential competitor with commercial fisheries merits further investigation.

The primary source 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. Stomach contents from stranded animals may sometimes yield useful information, but strandings occur infrequently. 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. There are also biases inherent in the data obtained from both 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).

This paper describes a simple and non-invasive diet sampling method initially developed by the late Dr. M. Bigg and G. 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 it is used here to

sample the diet of Pacific white-sided dolphins in the inshore waters of British Columbia. These results were compared 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. The foraging behaviour of Pacific white-sided dolphins are briefly described and are compared with those of other delphinids. An estimate of the total food consumption of these dolphins and a comparison with estimates for the harvest taken by commercial fisheries in the North Pacific is made.

METHODS

Data on the feeding ecology of Pacific white-sided dolphins were collected in three principal study areas along the coast of British Columbia (Fig. 1): the east coast of the Queen Charlotte Islands; the central mainland coast, and Queen Charlotte Strait/Johnstone Strait. A 6m aluminium vessel powered by a 115hp outboard was used throughout the study. During 141 survey days from April to November 1994 and from June to September 1995, I observed Pacific white-sided dolphins in 92 encounters (Table 1). Although dolphins were also sighted on other occasions, during each encounter behavioural and/or acoustic data were collected. Behaviour was 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 dolphins left the immediate vicinity after foraging, I approached the surface print at slow speed, to avoid disturbing either the dolphins or the surface of the water. With careful manoeuvring and searching,

fragments of prey could be observed to depths of about 3m, depending on water clarity, light and sea state conditions. Scales and/or other fragments were collected using a fine-mesh net mounted on a 4m pole (Fig. 2). The net was cleaned thoroughly after each use. Opportunities to collect scale samples were generally made while observing dolphins within 100m of the research vessel, to minimise travelling time to the area where foraging occurred.

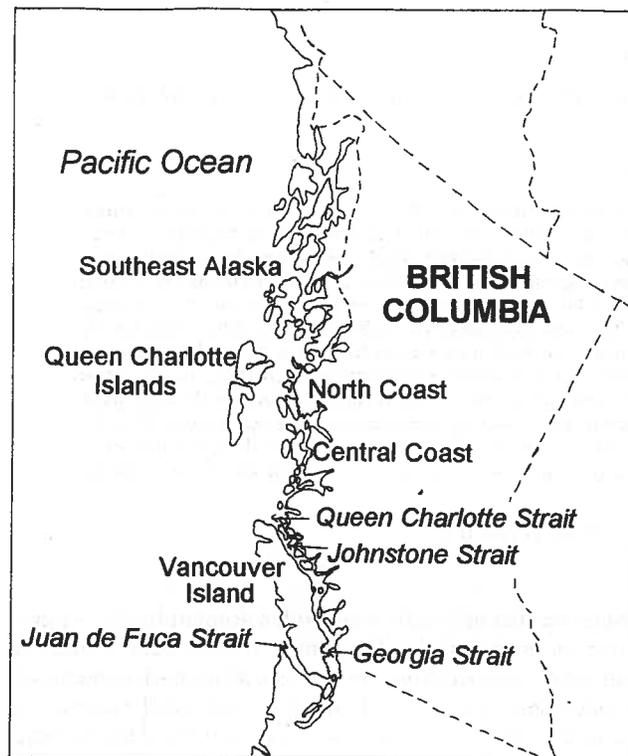
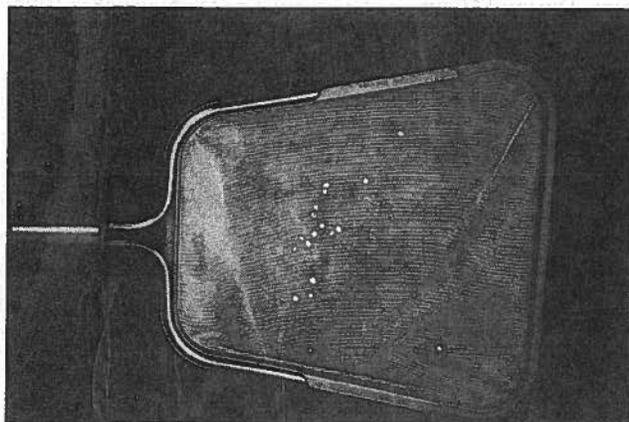


Fig. 1. The coastal waters of British Columbia showing the three principal study areas.

Table 1
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	Apr.-May 1994	8
Central Mainland Coast	50-500m	Jun.-Sep. 1994 Jul. 1995	46
Queen Charlotte and Johnstone Straits	20-600m	Oct.-Nov. 1994 Aug.-Sep. 1995	38



A reference collection of scales from known local fish species and from the literature (e.g. Bilton *et al.*, 1964) was developed. Species identifications and age estimates based on scales were confirmed by the scale-ageing laboratory at the Pacific Biological Station, Department of Fisheries and Oceans, Nanaimo, British Columbia. When the age of the fish was uncertain, the youngest age estimate was reported. Lengths of herring based on age 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. To test for the possibility that scales remain suspended in near-surface waters, and thus could not be reliably attributed to dolphin foraging activity, the water's surface was frequently scanned 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.

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. Stomachs were washed and either processed through an elutriator (Bigg and Olesiuk, 1990), or passed through a series of strainers. Fleishy prey remains were frozen or preserved in alcohol. All bones were washed and dried and compared with a reference collection. The problems of interpreting data obtained from stranded animals are well-known (e.g. IWC, 1986).

RESULTS

Group sizes and dive durations

The mean total group size for all encounters was about 100 dolphins (mean = 102.6, SE = 13.4, $n = 92$). However, the dolphins often divided 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. 3) 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., SE = 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. Fig. 4 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's $r = 0.92$).

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*) < 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*) found at surface prints were measured. Based on age-length regressions, the sizes of fish prey ranged from 15 to 60cm in length (Table 2).



Fig. 3. Foraging leaps by Pacific white-sided dolphins.

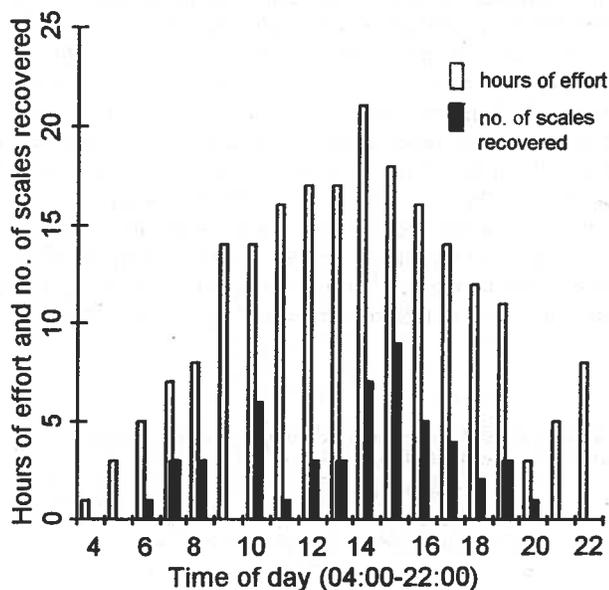


Fig. 4. The distribution of encounter hours and the number of prey fragments recovered during those encounter hours, for the 1995 field season.

Stomach contents

Table 3 lists the date, location and stomach contents of 11 dolphins found stranded along the British Columbian coast since 1990. Three dolphins reported from Kent Inlet were part of a group of eight carcasses that were found by sea urchin fishermen and Department 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 (K. Hansen, *FPV 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 1.

Table 2

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 1.

Species	Age	No.	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 at 58cm
	Sockeye salmon	1	1	37
		3	2	50
		4	1	60
	Coho salmon	1	1	18
	Gadidae	3	4	1 <i>Gadus macrocephalus</i> at 42cm, others unknown
Shrimp		2	Not available	
Capelin		1	Capelin found near surface print measured at 12.5cm	

Table 3

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

Date	Location	Contents
Oct. 1990	Johnstone Strait	2 chum salmon ¹
Jun. 1991	Goose Island	Herring, other unidentified small fish
Aug. 1991	Round Is. Pt Hardy	Pollock, sablefish, salmon, 2 squid beaks, feather
Jun. 1992	Queen Charlotte Is.	Pollock, salmon, herring, unidentified small fish
Sep. 1992	Waddington Island	Pollock, salmon, herring, smelt, shrimp, squid
Aug. 1995	Johnstone Strait	Empty
Aug. 1995	Gordon Channel	Salmon
Jan. 1996	Kent Inlet	Empty
Jan. 1996	Kent Inlet	Empty
Jan. 1996	Kent Inlet	Shrimp fragments
Feb. 1996	Johnstone Strait	Shrimp fragments, fish bone ²

¹ Based on scales in the stomach, these fish were 54 and 59cm long.

² Otolith embedded in the surface of a 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 from dolphin stomachs ranged between 3-42cm 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 1). 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 these dolphins, ranging from 30-60% of their diet depending on the sampling method used (Tables 2, 3 and 4). Salmon were taken from June through November and many of the kills were of small fish < 25cm, although fish > 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 26-34cm long, considerably smaller than the salmon consumed by dolphins in this study.

Table 4 summarises 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) analysed 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 1,000m. Dolphins captured in shallower areas by Slepsov (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 (M. Arai, pers. comm.). If present in the stomach of a dolphin, it is very probable that jellyfish would decompose before the stomach would be examined during the course of most necropsies. A more concentrated effort to look for active foraging on jellyfish when sampling for prey fragments may provide an 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 (own 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

Table 4

Percent occurrence of the principal prey of Pacific white-sided dolphins based on stomach content analyses. Empty stomachs were not included in the calculations. W. = Washington, B.C. = British Columbia.

Prey	California					Open Pacific	Japan	W.	B.C.
	Stroud <i>et al.</i> , 1981 ¹	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/Octopus (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</i> spp.)	0	0	0	u	0	0	0	91	62.5
Myctophids (<i>Myctophidae</i>)	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</i> sp.)	0	0	0	0	0	0	0	0	37.5
Shrimp, Decapoda	0	0	0	0	0	0	0	0	37.5
Sablefish, (<i>Anoplopoma</i> sp.)	0	0	0	0	0	0	0	0	12.5
Smelt, Osmeridae	0	0	0	0	0	0	0	0	12.5
No. of stomachs with prey/no. of stomachs examined	?/33	20/23	16/18	5/10	7/10	33/62	10/13	?/11	8/11
Percent of 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	stranded	stranded	stranded	bycatch	harpoon	stranded	stranded

¹Results reported are identical to those reported in Kajimura *et al.* (1980), therefore only Stroud *et al.* (1981) is cited here. p = present but could not determine frequency from data presented; u = not stated; ? = in the original reference. the number of stomachs

Prey species composition and size estimates are traditionally based on otoliths and on regressions of fish length on otolith size, these larger prey would be missed when stomach contents are examined, if the heads of large fish were discarded during feeding.

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 recognise that foraging is taking place. Only prey that are damaged or broken apart during the foraging bout will be sampled, and not all damaged prey may be consumed. 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. Other prey such as cephalopods may be consumed whole, and fragments, if any, would be difficult to recognise. The method also depends on the use of a manoeuvrable 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. 4) and not increased foraging behaviour by 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 benthic or inhabit deep water by day and rise to the surface by night (mesopelagics, midshipmen and hake). Walker *et al.* (1986) summarise 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 200-1,000m deep off 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 1,000m. In the study area in British Columbia, water depth rarely exceeded 600m. Many of the foraging bouts I 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 deep water prey, they appear to wait for the prey to rise to the surface, rather than diving deeply to capture it.

Pacific white-sided dolphins are similar to dusky dolphins (*Lagenorhynchus obscurus*), ecologically and taxonomically. After comparing the cranial morphology of specimens of both species, Webber (1987) 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 they feed on a diversity of prey (Leatherwood and Reeves, 1983). The fish herding behaviour of dusky dolphins (Würsig, 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 Würsig, 1995). Groups of dolphins moved in a coordinated 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 hypothesised 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. During the present study, dolphins and seabirds were often observed 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 coordinated movements of the dolphins may serve to hold the school of prey in place and increase the foraging efficiency of individuals within the group.

Like Pacific white-sided dolphins, dusky dolphins from different areas also vary in their diets. Würsig *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 2km 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) (Würsig and Würsig, 1980). The water depth is typically less than 200m 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 8-9kg of food per day (C. Wright, Vancouver Aquarium, BC, pers. comm.). A typical diet is 5kg of herring and 3kg of squid. Herring has a caloric value ranging from 2.05kcal/g in spring to 2.29kcal/g in winter, and squid has an average caloric value of 1.14kcal/g (Perez, 1990). This suggests a minimum caloric requirement of 13,670-17,160kcal/day/dolphin. Animals in the wild are likely to consume more. If a dolphin is fed exclusively on squid, then an average animal could be expected to consume 12-15.1kg 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 - 10.5kg of lanternfish per day to meet its minimum daily requirements.

Innes *et al.* (1987) calculated the daily consumption (R_s) 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 4.5kg for an average male dolphin (weighing 90kg), 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 90kg dolphin in captivity might consume between 3.6-11.7kg/day. Based on the volume and nutritional quality of material recovered during stomach content analyses, Cipriano (1992) conservatively estimated that 14,750kcal/day were required for a 77kg wild dusky dolphin, 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 82.5kg (Heise, 1997). Assuming that there are approximately 931,000 animals (range 206,000-4,216,000) in the population (Buckland *et al.*, 1993), then the total food consumption of Pacific white-sided dolphins in the North Pacific is about 6,900 tonnes/day (range 680-45,000 tonnes/day), or 2,518,000 tonnes/year (range 248,200-16,425,000 tonnes/year). By comparison, commercial fisheries in the entire North Pacific in 1992 took 36,399,000 tonnes (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 (Heise, 1996) and a similar increase has been reported in the nearshore waters of Southeast Alaska (Dahlheim and Towell, 1994).

CONCLUSIONS

The use of prey fragment sampling is a relatively new method which has provided information on the diet of healthy Pacific white-sided dolphins non-invasively, the results of which were supported by the data from stomach content analyses. For field researchers, the method is useful for confirming observations of feeding behaviour, and it is a fast and inexpensive way to collect data on diet opportunistically during the course of other activities. Prey fragment sampling can be used to acquire diet information on any marine mammal or seabird which feeds on or brings its prey near to the surface.

ACKNOWLEDGEMENTS

I owe a great deal of thanks to the many people who have assisted me throughout this project: my field assistants, particularly L. Kalban and D. Fernandez; B. Lamont and R. West of Clam Cove, J. Borrowman and Stubbs Island Charters of Telegraph Cove and the staff of Namu Resorts for providing me with a base to conduct my research; S. McFarland and the staff of the scale ageing laboratory at the

Pacific Biological Station in Nanaimo and P. Cotrell at UBC for helping me to identify prey fragments; the Marine Mammal Research Group for supplying me with unpublished data; G. Ellis for field support; J. Ford for field and academic support, and L. Barrett-Lennard for his support in all ways. I thank L. Barrett-Lennard, J. Ford, A.R.E. Sinclair, J. Smith and two anonymous reviewers for their comments on earlier versions of this manuscript. I am also grateful to the Vancouver Aquarium, Laskeek Bay Conservation Society, BC Challenge Grant and BC Parks for both financial and logistic support throughout this project.

REFERENCES

- Beamish, R.J. 1995. The need to understand the relationship between climate and the dynamics of fish populations. *Can. Spec. Publ. Fish. Aquat. Sci.* 121:1-2.
- Bigg, M.A. and Olesiuk, P.F. 1990. An enclosed elutriator for processing marine mammal scats. *Mar. Mammal Sci.* 6(4):350-5.
- Bilton, H.T., Jenkinson, D.W. and Shepard, M.P. 1964. A key to five species of Pacific Salmon (Genus *Oncorhynchus*) based on scale characters. *J. Fish. Res. Board Can.* 21:1267-88.
- Black, N. 1994. Behavior and ecology of Pacific white-sided dolphins (*Lagenorhynchus obliquidens*) in Monterey Bay, California. MSc Thesis, San Francisco State University. 133pp.
- Buckland, S.T., Cattanach, K.L. and Hobbs, R.C. 1993. Abundance estimates of Pacific white-sided dolphin, northern right whale dolphin, Dall's porpoise and northern fur seal in the North Pacific, 1987-1990. *Int. N. Pac. Fish. Comm. Bull.* 53(111):387-407.
- Burgner, R.L. 1991. Life history of sockeye salmon (*Oncorhynchus nerka*), pp. 1-118. In: C. Groot and L. Margolis (eds.) *Pacific Salmon Life Histories*. UBC Press, Vancouver, BC. 564pp.
- Cipriano, F. 1992. Behavior and occurrence patterns, feeding ecology, and life history of dusky dolphins (*Lagenorhynchus obliquidens*) off Kaikoura, New Zealand. Doctoral Thesis, University of Arizona. 216pp.
- Cotrell, P., Trites, A.W. and Miller, E.H. 1996. Assessing the use of hard parts on faeces to identify harbour seal prey: results of captive feeding trials. *Can. J. Zool.* 74(5):875-80.
- Dahlheim, M.E. and Towell, R.G. 1994. Occurrence and distribution of Pacific white-sided dolphins (*Lagenorhynchus obliquidens*) in southeastern Alaska, with notes on an attack by killer whales (*Orcinus orca*). *Mar. Mammal Sci.* 10(4):458-64.
- FAO. 1995. The state of world fisheries and aquaculture. FAO Rome. 57pp.
- Fertl, D. and Wursig, B. 1995. Coordinated feeding by Atlantic spotted dolphins (*Stenella frontalis*) in the Gulf of Mexico. *Aquat. Mamm.* 21(1):3-5.
- Fiscus, C.H. 1982. Predation by marine mammals on squids of the eastern North Pacific Ocean and the Bering Sea. *Mar. Fish. Rev.* 44(2):1-10.
- Fitch, J.E. and Brownell, R.L. 1968. Fish otoliths in cetaceans stomachs and their importance in interpreting feeding habits. *J. Fish. Res. Board Can.* 25(12):2561-74.
- Hart, J.L. 1973. Pacific Fishes of Canada. *Fish. Res. Bd Can., Arctic Biol. Stn Circ.* 180:740.
- Heise, K.A. 1996. Life history parameters of the Pacific white-sided dolphin (*Lagenorhynchus obliquidens*) and its diet and occurrence in the coastal waters of British Columbia. MSc Thesis, University of British Columbia. 95pp.
- Heise, K. 1997. Life history and population parameters of Pacific white-sided dolphins (*Lagenorhynchus obliquidens*). (Published in this volume.)
- Hotta, H., Mako, H., Okada, K. and Yamada, U. 1969. On the stomach contents of dolphins and porpoises off Kyushu. *Bull. Seikak Reg. Fish Res. Lab.* 37:71-85.
- Innes, S., Lavigne, D.M., Earle, W.M. and Kovacs, K.M. 1987. Feeding rates of seals and whales. *J. Anim. Ecol.* 56(1):115-30.
- International Whaling Commission. 1986. Report of the Scientific Committee, Annex K. Report of the working group on ways of maximising information from strandings. *Rep. int. Whal. Commn* 36:119-32.
- Jones, R.E. 1981. Food habits of smaller marine mammals from northern California. *Proc. Calif. Acad. Sci.* 42(16):409-33.
- Kajimura, H., Fiscus, C.H. and Stroud, R.K. 1980. Food of the Pacific white-sided dolphin, *Lagenorhynchus obliquidens*, Dall's porpoise,

- Phocoenoides dalli*, and northern fur seal, *Callorhinus ursinus* off California and Washington, with appendices on size and food of Dall's porpoise from Alaskan waters. U.S. Dep. Commer., NOAA Tech. Memo. NMFS F/NWC-2. 30pp.
- Lamb, A. and Edgell, P. 1986. *Coastal Fishes of the Pacific Northwest*. Harbour Publ., Madeira Park, BC. 224pp.
- Leatherwood, S. and Reeves, R.R. 1983. *The Sierra Club Handbook of Whales and Dolphins*. Sierra Club Books, San Francisco. xviii+302pp.
- Leatherwood, S., Reeves, R.R., Perrin, W.F. and Evans, W.E. 1982. Whales, dolphins and porpoises of the eastern North Pacific and adjacent waters: a guide to their identification. NOAA Technical Report, NMFS Circular 444. 245pp.
- McFarland, W.N. and Moss, S.A. 1967. Internal behaviour in fish schools. *Science* 156:260-2.
- Morejohn, G.V., Harvey, J.T. and Krasnow, L.T. 1978. The importance of *Loligo opalescens* in the food web of marine vertebrates in Monterey Bay, California. *California Fish and Game (Fish. Bull.)* 169:67-98.
- Moss, S.A. and McFarland, W.N. 1970. The influence of dissolved oxygen and carbon dioxide on fish schooling behaviour. *Mar. Biol.* 5:100-7.
- Olesiuk, P.F., Bigg, M.A., Ellis, G.M., Crockford, S.J. and Wigen, R.J. 1990. An assessment of the feeding habits of harbour seals (*Phoca vitulina*) in the Strait of Georgia, British Columbia, based on scat analysis. *Can. Tech. Rep. Fish. Aquat. Sci.* 1730:135.
- Oliphant, M.S., Gregory, P.A., Ingle, B.J. and Madrid, R. 1990. California marine fish landings for 1977-1986. *California Fish and Game (Fish. Bull.)* 173:52.
- Perez, M.A. 1990. Review of marine mammal population and prey information for Bering Sea ecosystem studies. NOAA Technical Memorandum NMFS F/NWC-186, 81pp.
- Ricker, W.E. 1975. Computation and interpretation of biological statistics of fish populations. *Bull. Fish. Res. Board Can.* 191:382.
- Sandercock, F.K. 1991. Life history of coho salmon (*Oncorhynchus kisutch*). pp. 395-446. In: C. Groot and L. Margolis (eds.) *Pacific Salmon Life Histories*. UBC Press, Vancouver, BC. 564pp.
- Scheffer, V.B. 1953. Measurements and stomach contents of eleven Delphinids from the Northeast Pacific. *Murrelet* 34(2):27-30.
- Sergeant, D.E. 1969. Feeding rates of Cetacea. *Fiskeridir. Skr. Ser. Havunders.* 15:246-58.
- Sleptsov, M.M. 1955. A new species of porpoise. *Fish. Res. Board Can. Transl. Series* 1670(1971):16.
- Stroud, R.K., Fiscus, C.H. and Kajimura, H.K. 1981. Food of the Pacific white-sided dolphin, *Lagenorhynchus obliquidens*, Dall's porpoise, *Phocoenoides dalli*, and northern fur seal, *Callorhinus ursinus*, off California and Washington. *Fish. Bull., US* 78:951-9.
- Takagi, K., Aro, K.V., Hartt, A.C. and Dell, M.B. 1981. Distribution and origin of pink salmon (*Oncorhynchus gorbuscha*). *Int. N. Pac. Fish. Comm. Bull.* 40:195.
- Taylor, F.H.C. 1967. Unusual fishes taken by midwater trawl off the Queen Charlotte Islands, British Columbia. *J. Fish. Res. Board Can.* 24(10):2101-15.
- Walker, W.A. and Jones, L.L. 1993. Food habitats of northern right whale dolphin, Pacific white-sided dolphin and northern fur seal caught in the high seas driftnet fisheries of the North Pacific Ocean, 1990. *Int. N. Pac. Fish. Comm. Bull.* 53(II):285-95.
- Walker, W.A., Leatherwood, S., Goodrich, K.R., Perrin, W.F. and Stroud, R.K. 1986. Geographical variation and biology of the Pacific white-sided dolphin, *Lagenorhynchus obliquidens*, in the north-eastern Pacific. pp. 441-65. In: M.M. Bryden and R. Harrison (eds.) *Research on Dolphins*. Oxford University Press, Oxford. xiv+478pp.
- Webber, M.A. 1987. A comparison of dusky and Pacific white-sided dolphins Genus *lagenorhynchus*: morphology and distribution. Ms Thesis, San Francisco State University. 102pp.
- Wilke, F., Taniwaki, T. and Kuroda, N. 1953. *Phocoenoides* and *Lagenorhynchus* in Japan with notes on hunting. *J. Mammal.* 34(4):488-97.
- Würsig, B. 1986. Delphinid foraging strategies. pp. 347-59. In: R.J. Schusterman, J.A. Thomas and F.G. Wood (eds.) *Dolphin Cognition and Behavior: A Comparative Approach*. Lawrence Erlbaum Associates, Hillsdale, New Jersey. 393pp.
- Würsig, B. and Würsig, M. 1980. Behavior and ecology of the dusky dolphin, *Lagenorhynchus obscurus*, in the South Atlantic. *Fish. Bull., US* 77(4):871-90.
- Würsig, B., Würsig, M. and Cipriano, F. 1989. Dolphins in different worlds. *Oceanus* 32(1):71-5.

Appendix 1

Prey recorded in the diet of Pacific white-sided dolphins in the North Pacific. 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. Scheffer, 1953; 8. Fitch and Brownell, 1968; 9. Wilke *et al.* 1953; 10. Sleptsov, 1955; 11. This study.

Family	Scientific name	Common name	Reference	Family	Scientific name	Common name	Reference
FISH				Batrachoididae			
Order Petromyzoniformes					<i>Porichthys myriaster</i>		2
	<i>Lampetra tridentatus</i>	Pacific lamprey	4		<i>Porichthys notatus</i>	Plainfin midshipmen	2, 3
Clupeidae	<i>Sardinops sagax</i>	Pacific sardine	2, 3		<i>Theragra chalcogramma</i>	Walleye pollock	11
	<i>Clupea harengus</i>	Pacific herring	11		Unidentifiable		11
Engraulidae	<i>Engraulis mordax</i>	Northern anchovy	2, 3, 4, 6	Ophidiidae	<i>Chilara taylori</i>		2
	<i>Engraulis japonica</i>		9, 10	Scomberosocidae	<i>Colalabis</i> sp.		10
Salmonidae	<i>Oncorhynchus</i> sp.	Salmon	4, 11		<i>Colalabis saira</i>	Pacific saury	1
	<i>Oncorhynchus gorbuscha</i>	Pink salmon	11	Trachipteridae	<i>Trachipterus altivelis</i>	King of the salmon	1, 4
	<i>Oncorhynchus keta</i>	Chum salmon	4, 11	Carangidae	<i>Trachurus japonicus</i>	Jack mackerel (Japan)	10
	<i>Oncorhynchus kisutch</i>	Coho	4, 11		<i>Trachurus symmetricus</i>	Jack mackerel (N. America)	2, 3, 4
	<i>Oncorhynchus nerka</i>	Sockeye	11	Sciaenidae	<i>Genyonemus lineatus</i>	Drums	2, 3
	<i>Oncorhynchus tshawytscha</i>	Chinook	No records		<i>Seriplus politus</i>		2, 8
Osmeridae	<i>Mallotus villosus</i>	Capelin	11		Unidentified		4
	<i>Thaleichthys pacificus</i>	Eulachon	11	Pentacerothidae	<i>Pentaceros richardsoni</i>	Armorheads	1
Argentinidae	<i>Argentina</i> sp.	Argentines	1	Gempylidae	<i>Gempylus serpens</i>		
	<i>Nansenia candida</i>	Bluethroat argentine	1	Scombridae	<i>Scomber japonicus</i>	Pacific (Chub) mackerel	2
Bathylagidae	<i>Leuroglossus schmidti</i>	Smooth tongues	1	Centrolophidae	<i>Icithys lockingtoni</i>	Medusafish	1, 4
	<i>Leuroglossus stilbius</i>		2	Stromateidae	<i>Peprius simillimus</i>	Pacific pompano	2
	<i>Bathylagus</i> spp. (3)	Black smelts	1	Tetragonuridae	<i>Tetragonurus cuvieri</i>	Smalleye squaretail	1
	Unidentifiable		1	Scorpaenidae	<i>Sebastes</i> sp.	Rockfish	3, 4, 6
Gonostomatidae	<i>Ichthyococcus</i> sp.		1	Anoplopomatidae	<i>Anoplopoma fimbria</i>	Sablefish	2, 11
	Unidentifiable		1	Bothidae	<i>Citharichthys sordidus</i>	Pacific sandab	3, 4
Melanostomiidae	Unidentifiable		1	Pleuronectidae	<i>Hypsosetta guttata</i>		2
Scopelarchidae	<i>Benthalbella dentata</i>		1	Cynoglossidae	<i>Symphurus atricauda</i>		2
Paralepididae	<i>Lestidiops ringens</i>	Barracudina	1	CEPHALOPODS			
	<i>Paralepis atlantica</i>		1	Unidentified			7, 11
Scopelosauridae	<i>Scopelosaurus harryi</i>		1	Sepiolidae	<i>Rossia pacifica</i>		3
Myctophidae	<i>Ceratoscopelas</i> sp.		1	Loliginidae	<i>Loligo opalescens</i>		2, 3, 4, 5, 6
	<i>Diaphus gigas</i>		1	Enoploteuthidae	<i>Enoploteuthis chuni</i>		1
	<i>Diaphus</i> sp.		1		<i>Abraliopsis felis</i>		1
	<i>Diaphus theta</i>		1, 2		<i>Abraliopsis</i> sp.		1, 3, 4, 5
	<i>Hygophum</i> sp.		1	Octopoteuthidae	<i>Octopoteuthis deletron</i>		1, 3
	<i>Lampadena urophaos</i>		1		<i>Octopoteuthis</i> sp.		2, 5
	<i>Lampanyctus jordani</i>		1	Onychoteuthidae	<i>Onychoteuthis borealijaponica</i>		1, 3, 4
	<i>Lampanyctus regalis</i>		1		<i>Onychoteuthis</i> sp.		2, 5
	<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>Stenobranchicus</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				

cont...

Appendix 1 cont.

Family	Scientific name	Common name	Reference	Family	Scientific name	Common name	Reference
Gonatidae	<i>Gonatus</i> spp. (3 species)		1, 2, 3, 4, 5	Cranchiidae	<i>Galiteuthis</i> sp.		3, 4
	<i>Gonatopsis borealis</i>		1, 3, 4		<i>Galiteuthis phyllura</i>		1
	<i>Gonatopsis berryi</i>		3	Octopodidae	<i>Octopus</i> sp.		2
	Gonatopsis-Berryteuthis type		1		<i>Octopus rubescens</i>		3
	<i>Berryteuthis anonychus</i>		1	Ocythoidae	<i>Ocythoe tuberculata</i>		3, 4
Histioteuthidae	<i>Histioteuthis heteropsis</i>		3	OTHER			
Ommatstrephidae	<i>Ommastrephes bartrami</i>		1	Crustaceans	Unidentified		11
Chiroteuthidae	<i>Chiroteuthis</i> sp.		1, 3, 4		<i>Pandalus</i> sp.		10
Mastigoteuthidae	<i>Mastigoteuthis</i> sp.		1	Jellyfish	Unidentified		7