

Factors influencing the diving behaviour of fish-eating killer whales: sex differences and diel and interannual variation in diving rates

Robin W. Baird, M. Bradley Hanson, and Lawrence M. Dill

Abstract: Diving behaviour of air-breathing vertebrates may be influenced by a variety of factors including age, body size, and changes in prey behaviour and (or) abundance over both short and long timescales. We studied the diving behaviour of a highly sexually dimorphic odontocete cetacean, the killer whale, *Orcinus orca* (L., 1758), using suction-cup-attached time-depth recorders (TDRs). We tested the hypotheses that dive rates (no. of dives/h greater than or equal to specific depths) of fish-eating killer whales varied between males and females, with age, between day and night, and among pods and years. Data were used from 34 TDR deployments between 1993 and 2002 in the inshore waters of southern British Columbia, Canada, and Washington, USA. Dive rates did not change with age or differ among pods or between males and females, although analyses restricted to adults showed that adult males dove deep significantly more frequently than adult females during the day. For all whales, dive rates and swim speeds were greater during the day than at night, suggesting decreased activity levels at night. Dive rates to deeper depths during the day decreased over the study, suggesting a long-term change in prey behaviour or abundance, though uncertainty regarding the diet of this population precludes determination of the cause of such changes.

Résumé : Une multitude de facteurs, tels que l'âge et la taille, ainsi que des modifications des comportements et (ou) de l'abondance des prédateurs sur des échelles temporelles courtes et longues peuvent affecter le comportement de plongée des vertébrés à respiration aérienne. Nous avons étudié le comportement de plongée chez un odontocète à fort dimorphisme sexuel, l'épaulard, *Orcinus orca* (L., 1758), au moyen d'enregistreurs de la profondeur en fonction du temps (TDR) fixés à l'aide de ventouses. Nous avons testé l'hypothèse selon laquelle les taux de plongée (nombre de plongées/h supérieures ou égales à profondeurs déterminées) chez les épaulards piscivores varient en fonction du sexe, de l'âge, du jour et de la nuit, des groupes et des années. Les données ont été générées par l'utilisation de TDR à 34 reprises de 1993 à 2002 dans les eaux côtières du sud de la Colombie Britannique (Canada) et du Washington (É.-U.). Les taux de plongée ne varient en fonction ni de l'âge, ni du groupe, ni du sexe, bien que des analyses des adultes seuls montrent que les mâles adultes plongent en profondeur durant la journée significativement plus souvent que les femelles adultes. Chez l'ensemble des épaulards, les taux de plongée et la vitesse de nage sont plus importants le jour que la nuit, ce qui semble indiquer une activité réduite la nuit. Les taux de plongée vers les eaux plus profondes le jour ont diminué au cours de l'étude, ce qui laisse croire à des changements à long terme dans le comportement ou l'abondance des proies; des incertitudes concernant le régime alimentaire de cette population nous empêchent cependant de déterminer les causes de ces variations.

[Traduit par la Rédaction]

Introduction

For aquatic air-breathing vertebrates, diving behaviour should reflect a species' ecology: how they use the water column should be a function of where their prey are, with the constraint of always having to return to the water's surface to breathe. For any particular species, or perhaps for

any population of a particular species (since ecological conditions may vary among the ranges of different populations), diving behaviour is likely to be influenced by a variety of factors. For sexually dimorphic species, body size differences between adult males and adult females should influence how deep they can dive, since mass-specific metabolic rates (Kleiber 1961) result in greater diving capabilities for

Received 11 August 2004. Accepted 12 January 2005. Published on the NRC Research Press Web site at <http://cjz.nrc.ca> on 20 April 2005.

R.W. Baird.¹ Cascadia Research Collective, 218½ West 4th Avenue, Olympia, WA 98501, USA, and Biology Department, Dalhousie University, Halifax, NS B3H 4J1, Canada.

M.B. Hanson. National Marine Fisheries Service, Northwest Fisheries Science Center, 2725 Montlake Boulevard East, Seattle, WA 98112, USA.

L.M. Dill. Behavioural Ecology Research Group, Department of Biological Sciences, Simon Fraser University, Burnaby, BC V5A 1S6, Canada.

¹Corresponding author (e-mail: rwbaird@dal.ca or rwbaird@cascadiaresearch.org).

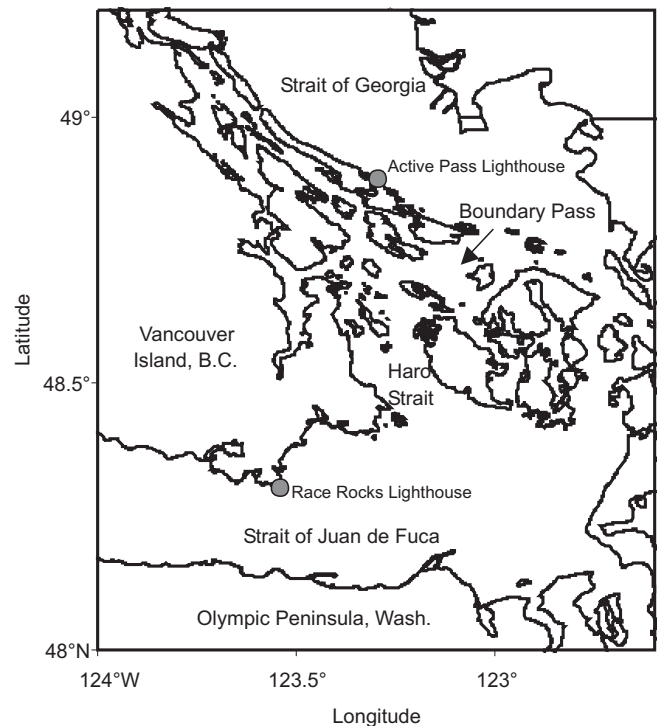
larger animals (Schreer and Kovacs 1997). Diving capabilities should also increase with age, owing to increases in body mass and increases in haemoglobin and myoglobin concentrations and thus oxygen storage capacity in the blood and muscle (Ponganis et al. 1999; Noren et al. 2001, 2002). The abundance or distribution of prey within the water column may also vary with time, on both short (e.g., diel) and long (e.g., interannual) timescales, and such differences should influence how divers utilize the water column (see, for example, Boyd et al. 1994; Baird et al. 2001, 2002).

Among marine mammals, detailed information on diving behaviour has been collected for many species of pinnipeds through long-term deployment of recoverable data-logging time-depth recorders (TDRs) glued onto the pelage of animals captured at haulout sites. Studies of cetacean diving behaviour have been much more limited, primarily because of issues associated with deployment and recovery of instruments (Hooker and Baird 2001). Studies of cetacean diving have used remotely deployable tags that implant in the blubber; surgically attached tags with animals that have been captured and temporarily restrained; or short-term, remotely deployable, suction-cup-attached tags. Because of the difficulty in recovering tags from animals that do not return to a haulout site, implantable and surgically attached tags typically transmit low-resolution data to a satellite; in contrast, high-resolution data can be collected from data-logging tags. For killer whales, *Orcinus orca* (L., 1758), currently available implantable tags do not have dive logging capabilities, and capture operations for surgical attachments are difficult and expensive; thus relatively few studies of diving behaviour have been undertaken (see Baird 2000).

In the inshore waters between southern Vancouver Island, British Columbia, Canada, and the San Juan Islands, Washington, USA, fish-eating killer whales are regularly encountered between May and November each year. Long-term research on this population has resulted in detailed information on the age, sex, and maternal relatedness of every whale in the population (Center for Whale Research 1999–2002). This population (colloquially termed the “southern residents”) numbers fewer than 100 individuals (Baird 2001; Center for Whale Research 1993–2002), and information on diet suggests they feed primarily on salmon (*Oncorhynchus* spp.) and at least occasionally on bottom fish (Ford et al. 1998). Based on association patterns, whales within the population have been grouped into distinct “pods”, defined as groupings of whales that spend more than 50% of their time together over a period of years; each pod is a collection of matrilineal units, with no dispersal of either sex from the matrilineal unit (Bigg et al. 1990). Each pod’s use of the area varies both spatially and temporally (Osborne 1999), suggesting there may be some habitat partitioning or targeting of different runs or species of salmon (see Nichol and Shackleton 1996).

Between 1993 and 2002 we studied the diving behaviour of this population of fish-eating killer whales using remotely deployed suction-cup-attached tags containing a data logger. Here we test the hypothesis that diving rates to different depths increase with whale age (and thus size). Furthermore, because killer whales are strongly sexually dimorphic in body size, with fully grown adult males characteristically 1 m longer than adult females and weighing 45% more than an adult

Fig. 1. Map of killer whale (*Orcinus orca*) study area showing place names noted in text.



female of the same length (Dahlheim and Heyning 1999), we test the hypothesis that diving rates to deeper depths are greater for males than females. We also test the hypotheses that dive rates vary among pods and years and between day and night because of differences in species of fish targeted or temporal variation in fish numbers or behaviour.

Methods

Fieldwork was undertaken in US and Canadian waters of the Strait of Juan de Fuca, Haro Strait, Boundary Pass, and the southern Strait of Georgia (Fig. 1). Tags were deployed in 1993, 1996, 1997, 1998, and 2002. In all years except 1993, tagging was undertaken during one or two short (1–3 weeks) field periods. Vessels used for tagging included a 4.7-m rigid-hulled inflatable (1993, 1996, 1997) and an 8-m aluminum monohull (1998, 2002).

Tags contained two main components, a TDR and a VHF radio transmitter. These components were housed in a syntactic foam body (for flotation) that was coated with yellow Plasti Dip® (to increase visibility for recovery). An 8 cm diameter suction cup was affixed to the tag body with flexible plastic tubing, allowing the tag to be oriented into the current flow when deployed. Tags weighed between 250 and 450 g (approximately 0.01%–0.02% of the body mass of a killer whale), depending on the type of TDR used (see below). Tags were labeled with a phone number and notice of a reward to encourage a return if found by a member of the public.

Three different types of TDRs (all manufactured by Wildlife Computers, Redmond, Washington) were used in this study: Mk5, Mk6, and Mk8 TDRs. For all instruments, depth was sampled at 1-s intervals. Depth resolution and

range varied among and within TDR types. Mk6 and Mk8 TDRs contained a swim-speed sensor (a paddle wheel), though differences in available memory influenced sampling intervals for swim speed (either 1-s or 5-s intervals). In 1993, Mk5 units were deployed, which recorded at 1-m depth increments (± 1 m). In 1996–1998, Mk6 TDRs were used. Because of memory limitations, there was a trade-off between maximum depth range and depth resolution. Depth resolution for most of the Mk6 TDRs was 1 m (± 1 m), though two units had depth sensors that recorded at 4-m depth increments (± 4 m). Maximum depth range for Mk5 and Mk6 units was either ~ 230 m (for those that recorded at 1-m increments) or ~ 1000 m (for those that recorded at 4-m increments). In 2002, both Mk6 TDRs (with 1-m resolution) and Mk8 TDRs were used. Depth resolution of Mk8 TDRs was 0.5 m (± 0.5 m) and depth range was 1000 m. Overall sampling differences between TDRs influenced the available sample size for some analyses.

Whales were tagged opportunistically, with no preference for a particular age, sex, or pod, though groups or individuals away from other vessels were preferentially approached for tagging. Whales were approached slowly, and the research vessel attempted to match the whales' speed and direction of travel. Tagging was attempted at distances of approximately 3–7 m from the target whale. Tags were deployed by crossbow (RX-150, Barnett International, Inc., Odessa, Florida), using a modified bolt with extra-wide flights to improve stability. Immediate reactions of whales to tagging were recorded and classified after Weinrich et al. (1991; see also Hooker et al. 2001) as follows: (i) no reaction; (ii) low reaction (slight modification of behaviour); (iii) moderate reaction (more forceful reaction though no prolonged evidence of disturbance); or (iv) strong reaction (succession of forceful activities). Tagged whales were photographed and information on individual identity (including age, sex, and pod membership) was obtained by comparing photographs to existing catalogs (Bigg et al. 1987; Center for Whale Research 1993–2002). Although traditionally there have been three pods recognized in this population (J, K, and L), some consider L-pod to have split into two or more pods in recent years; we follow Hoelzel (1993) in splitting L-pod into two pods for pod-specific comparisons of diving behaviour.

During 1993, suction cups contained a galvanic release mechanism to limit attachment duration; after 1993, tag release was uncontrolled (i.e., tags detached owing to a simple failure of suction). When released from a whale, tags floated upright with the antenna clear of the water and were recovered using VHF radio signals. In 1997, 1998, and 2002, tags were sometimes deployed on multiple whales within 1–2 h of each other.

After tags were recovered, data were downloaded to a computer in a hexadecimal format. Downloaded files were processed with several programs provided by the TDR manufacturer (Wildlife Computers), depending on TDR type. To produce raw ASCII files with all data values for examination of swim speed, Mk6 files were processed with Minimum-Maximum-Mean (Version 1.22), and Mk8 files were processed with Hexdecode (Version 2.02). To correct for

temperature-related drift in the surface values (see Hooker and Baird 2001), Mk5 and Mk6 files were processed with Zero-Offset Correction (Version 1.30), and Mk8 files with Instrument Helper (Beta version). To calculate statistics for each dive (dive duration, maximum depth), the resulting Mk5 and Mk6 files were processed with Dive Analysis (Version 4.08), and Mk8 files were further processed with Instrument Helper. The outputs of these programs were ASCII files, which were then imported into Microsoft Excel (Version 2000) or SYSTAT® (Version 10.0) for statistical analysis and graphing.

Discriminating between the typically short-duration and shallow dives, which function primarily for gas exchange, and longer (and potentially deeper) dives, which may be important for foraging, is problematic (Hooker and Baird 2001), in part because of individual variability in diving behaviour. Therefore, for comparisons of diving behaviour between different groupings (age, sex, pod, day or night, year), we used a variety of measures including both depth (i.e., dives ≥ 5 m, 10 m, 20 m, 30 m, 50 m, 100 m, and 150 m) and duration (dives ≥ 1 min). Dive rates were calculated as the number of dives/h greater than or equal to these criteria; i.e., these were not depth bins (e.g., ≥ 20 m also included dives ≥ 30 m, ≥ 50 m, etc.). Mean dive duration for each individual tag deployment was also calculated for all dives ≥ 1 min. Dive rates and durations were calculated separately for day and night, using the times of sunrise and sunset for delineation. For individual tag deployments where data were collected from more than one day or night period, data from both day or night periods were pooled to produce single dive rates or durations for day or night. These dive rates were used in pairwise comparisons of daytime and nighttime behaviour. Because swim-speed readings vary with tag orientation, position of the tag on the body, and body size (Baird 1998), swim speed is presented in uncalibrated units. When swim-speed data for both day and night were available for a particular tag deployment, the mean speed was calculated separately for all daytime and nighttime data. Comparisons of daytime and nighttime swim speeds used these two mean values. All pairwise comparisons were done using Wilcoxon paired-sample tests. The relationships between dive rates and pod, year, whale age, whale sex, and day or night period were explored using Generalized Linear Interactive Models (GLIMs). All combinations of interactive terms were also included. GLIMs were run on each dive rate measure (e.g., no. of dives/h ≥ 1 min, 10 m, 20 m, etc.) and on dive durations (≥ 1 min) in a forward stepwise manner, incorporating terms with significant p -values ($p < 0.05$). For examination of sex differences in diving rates that might be due to body size differences, we also compared daytime dive rates and dive durations of adults (>15 years of age) only, collected in 1997, 1998, and 2002 (no data were available for adult males during 1993 and 1996), using Mann–Whitney U tests.

Because sea surface temperature (SST) could influence the depth at which salmon travel (e.g., Tanaka et al. 2000), and thus could influence killer whale diving behaviour, we examined SST data collected from the Active Pass and Race Rocks Lighthouse sampling stations,² which span a large proportion of our study area (Fig. 1). For each month that

²Sea surface temperature data obtained from <http://www-sci.pac.dfo-mpo.gc.ca/osap/data/lighthouse/bcsop.htm>.

Table 1. Details on "southern resident" killer whales, *Orcinus orca*, tagged for ≥ 2 h.

Whale ID	Pod	Age	Sex	Date tagged	TDR data collection			Max. dive depth (m)	TDR type
					No. of hours (day)	No. of hours (night)	Tag duration (h)		
L58	L8	13	M	24 June 1993	8.40	0	8.40	147	Mk5
L9	L8	60	F	19 July 1993	4.00	0	4.00	142	Mk5
L74	L8	7	M	23 Sept. 1993	5.47	0	5.47	233	Mk5
L62	L8	13	M	11 Oct. 1993	1.17	1.30	2.47	49	Mk5
L32	L10	42	F	22 Sept. 1996	10.67	11.83	22.50	200	Mk6
L79	L10	8	M	6 June 1997	2.47	0	2.47	120	Mk6
L44	L10	23	M	14 June 1997	3.74	6.35	10.09	128	Mk6
J26	J1	7	M	18 June 1997	2.93	3.82	6.75	47	Mk6
L26	L8	41	F	21 June 1997	3.45	7.34	10.79	77	Mk6
K1	K1	42	M	20 Sept. 1997	3.40	2.11	5.51	225	Mk6
L88	L8	4	M	23 Sept. 1997	12.60	11.89	24.49	133	Mk6
K22	K1	10	F	27 Sept. 1997	13.40	16.84	30.24	264	Mk6 (4 m)
K14	K1	20	F	27 Sept. 1997	13.86	17.19	31.05	225	Mk6
K21	K1	11	M	28 Sept. 1997	2.10	0	2.10	199	Mk6
K1	K1	42	M	3 Oct. 1997	2.17	0.31	2.48	116	Mk6
K28	K1	3	F	6 Oct. 1997	3.25	8.72	11.97	135	Mk6
K16	K1	12	F	6 Oct. 1997	6.99	12.65	19.64	167	Mk6
J26	J1	8	M	28 May 1998	14.63	8.27	22.90	127	Mk6
L38	L10	33	M	29 May 1998	5.99	2.98	8.97	192	Mk6 (4 m)
L3	L8	52	F	8 July 1998	3.35	0	3.35	160	Mk6
L92	L8	3	M	8 July 1998	11.61	8.08	19.69	148	Mk6
L67	L8	13	F	9 July 1998	5.30	0	5.30	68	Mk6
L39	L8	23	M	9 July 1998	12.59	8.12	20.71	192	Mk6
K13	K1	26	F	11 July 1998	2.69	5.33	8.02	79	Mk6
J26	J1	8	M	11 July 1998	4.21	8.15	12.36	42	Mk6
L27	L8	33	F	16 July 1998	2.71	8.14	10.85	66	Mk6
L91	L8	3	Unknown	16 July 1998	11.1	8.32	19.56	118	Mk6
L54	L8 ^a	25	F	2 July 2002	0.72	1.33	2.05	194	Mk8
K12	K1	31	F	2 July 2002	7.26	7.97	15.23	24	Mk6
K21	K1	16	M	2 July 2002	7.02	7.97	14.99	152	Mk6
L87	L10	10	M	7 July 2002	6.75	8.07	14.82	228	Mk6
L41	L10	25	M	7 July 2002	1.1	4.10	5.20	146	Mk8
L92	L8	7	M	9 July 2002	9.61	4.73	14.33	87	Mk6
L91	L8	7	Unknown	9 July 2002	12.42	0	12.42	158	Mk8

^aL54 was included in L8-pod because of associations in recent years (D. Ellifrit, personal communication).

tags were deployed we used the mean SST, and for each year that tags were deployed in more than 1 month we calculated a simple average (e.g., for 1997 we calculated a mean from the average temperatures for the months of June, September, and October).

Results

Forty tags were deployed between 1993 and 2002, and all were recovered. A total of 419.5 h of TDR data were recorded. Animals either had no reaction to tagging (24% of taggings in US waters from 1997 to 2002) or had low or moderate reactions consisting of a fast dive and a flinch or tail flick (76% of taggings in US waters from 1997 to 2002). No strong reactions were observed. No changes were observed in general behavioural state (e.g., travel, foraging) immediately following tagging. The tagged whales were easy to approach, always remained within their social groups, and performed surface behaviours similar to those of

other whales in the group. Acoustic monitoring at the time of one tagging documented no change in sound production associated with the tagging event (D. Bain, personal communication). For all of these reasons, we believe the tag attachment did not influence the tagged animals' behaviour.

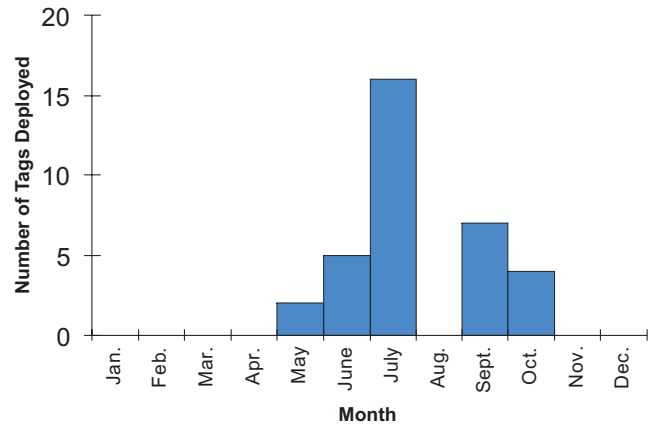
Attachment duration ranged from 15 min to 30 h 52 min (mean duration = 10.48 h, median = 8.70 h). It is probable that extremely short-duration attachments do not accurately represent the full range of killer whale diving behaviours; therefore, maximum depth recorded was compared against attachment duration. There was a significant positive relationship ($r^2 = 0.20$, $p = 0.004$) using all 40 deployments. If attachments <2 h in duration were excluded, this relationship was no longer significant ($r^2 = 0.074$, $p = 0.12$). All further analyses were therefore restricted to attachments ≥ 2 h ($n = 34$, Table 1). These deployments averaged 12.09 h in duration (median = 10.8 h; total data 411 h). Using data from either daytime or nighttime hours from these taggings, we found no significant relationship between any dive rate mea-

sure and attachment duration. Tags were deployed during 5 different months over the 6 months of summer and early fall (Fig. 2), though there was insufficient spread in tag deployment dates to examine potential seasonal trends. Whales were tagged in the Strait of Juan de Fuca (9 taggings), Haro Strait (20 taggings), Boundary Pass (2 taggings), and the southern Strait of Georgia (3 taggings), though tagged whales often moved between these areas. Age of tagged whales ranged from 3 to 60 years (median = 13 years, mean = 20.03 years; Fig. 3).

Twenty-eight individuals were tagged; 5 of these were tagged on more than one occasion (4 twice and 1 three times). Of the 28 individuals, 1 was from J-pod (3 taggings), 8 were from K-pod (10 taggings), 12 were from L8-pod (15 taggings), and 7 were from L10-pod (6 taggings). Time intervals between repeated taggings of the 5 individuals averaged 27 months (SD = 26 months). Since there is a possibility that data from repeated taggings are not independent, statistical tests were undertaken on both the complete data set and a reduced data set using only one tagging from each individual (*p*-values and means or medians are shown only for the complete data set unless repeated testing changed results of significance testing). Thirteen of the deployments were on females, 19 were on males, and 2 were on individuals of unknown sex. Only one of the adult females tagged had an offspring ≤ 2 years of age. The age of weaning has been suggested to be 1.5–2 years (Haenel 1986).

Using time of sunset and sunrise to delineate periods of day and night, we collected approximately 53% of the data during the day (219.1 h) and 47% of the data during the night (191.9 h). With the complete data set, depth and swim-speed data during both day and night were available for 26 and 25 individual deployments, respectively. With the reduced data set (only one deployment per individual), depth and swim-speed data during both day and night were available for 22 and 21 individual deployments, respectively. Average dive durations (for dives ≥ 1 min) were similar ($p = 0.174$) between day (mean = 2.4 min, SD = 0.6 min, $n = 26$) and night (mean = 2.3 min, SD = 0.4 min, $n = 26$) using either the complete or the reduced data set. Swim speed during the night (mean = 1.12, SD = 0.59, $n = 25$) was significantly lower ($p < 0.001$) than swim speed during the day (mean = 1.45, SD = 0.58, $n = 25$) using either data set. Because many of the tags were deployed late in the evening and remained attached throughout the night and into the next day, nighttime swim-speed data were collected both at the end (12 of 25) and during the middle or close to the start of (13 of 25) deployments. Thus potential tag movements on the body during deployments were not likely to influence swim-speed data in any consistent way. A variety of dive rate measures (no. of dives/h \geq specific depths, see Table 2, all $n = 26$) were significantly greater during the day than at night using the complete data set: ≥ 10 m ($p = 0.035$); ≥ 20 m ($p = 0.001$); ≥ 30 m ($p = 0.003$); ≥ 50 m ($p = 0.007$); ≥ 100 m ($p = 0.035$); and ≥ 150 m ($p = 0.050$). With the reduced data set ($n = 22$), several of these dive rate measures were no longer significantly different (≥ 10 m ($p = 0.058$); ≥ 100 m ($p = 0.063$); and ≥ 150 m ($p = 0.074$)), though trends remained the same, with dive rates during the day being greater than dive rates at night. Some measures were not significantly different (≥ 5 m ($p = 0.829$) and ≥ 1 min ($p = 0.269$)) using either

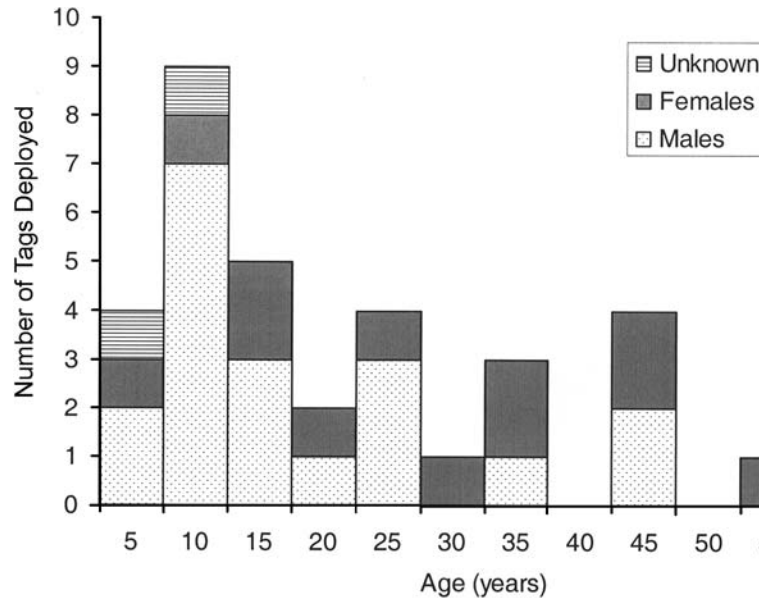
Fig. 2. Seasonal distribution of tag deployments ($n = 34$).



data set. As dive rate measures increase in depth, the proportion of individuals with zero values (i.e., no dives greater than the limit) increases, thus *p*-values generally increase as depth limits increase.

Results of the GLIM using the complete data set indicated that dive rates were significantly related to year, day or night, and the interaction between year and day or night (Table 3; Fig. 4). There were no significant relationships between dive rate and whale age, sex, or pod, nor interactions between these terms, for any of the dive rate measures. The trend for deep dives to decrease in frequency over the 10-year range of the study exists only during the day (Fig. 4). There was no significant relationship between dive duration and any of the variables tested. Using the reduced data set, GLIM results were similar for five of the seven dive rate measures examined, though for dives ≥ 10 m and ≥ 30 m only a single term was significant (year in the former and day or night in the latter).

Maximum recorded dive depths averaged 140.8 m (SD = 61.8 m, $n = 34$; Table 1). Maximum dive depths recorded for the youngest whales tagged in our study (3 years old, $n = 3$) averaged 133.7 m (SD = 15.0 m). Comparisons of daytime dive rates between tag deployments on adult males and adult females between 1997 and 2002 were undertaken with the complete data set ($n = 7$ deployments on adult males and $n = 7$ deployments on adult females), as well as a reduced data set containing only a single value for each individual ($n = 6$ adult males, $n = 7$ adult females). There were significant differences in dive rates (no. of dives/h) using either data set for dives ≥ 30 m (male mean = 3.46, SD = 3.02; female mean = 0.74, SD = 0.90; $p = 0.025$; Fig. 5). Using the complete data set, we also found significant differences for dives ≥ 10 m (male mean = 9.08, SD = 1.94; female mean = 7.46, SD = 4.43; $p = 0.035$), ≥ 20 m (male mean = 4.68, SD = 3.83; female mean = 1.44, SD = 1.37; $p = 0.034$), and ≥ 50 m (male mean = 1.37, SD = 1.09; female mean = 0.52, SD = 0.69; $p = 0.047$). Such differences were not due to interannual differences in diving patterns; relatively equal numbers of adult males and adult females were tagged in each of the 3 years (Table 1), and within each year dive rates for adult males were higher, on average, than for adult females (data not shown). Differences for dive rates ≥ 100 m were not significant ($p = 0.058$), though the adult males dove below 100 m more than twice as often as adult females

Fig. 3. Age distribution of tagged whales ($n = 34$).

(adult male mean = 0.78, SD = 0.67; adult female mean = 0.31, SD = 0.53). Daytime dive durations (for dives ≥ 1 min) were also significantly longer ($p = 0.041$) for adult males (mean = 2.79 min, SD = 0.46, $n = 7$) than for adult females (mean = 2.09 min, SD = 0.61, $n = 7$), using the complete data set. When one of the two repeated deployments was excluded, this relationship was not significant ($p = 0.054$), regardless of which one was excluded. Depending on which deployment is excluded for the individual sampled twice, the mean dive duration for adult males, using the reduced data set, may be either longer (mean = 2.81 min, SD = 0.51, $n = 6$) or shorter (mean = 2.76 min, SD = 0.50, $n = 6$) than that for the complete data set, suggesting that the result is not significant because of the reduced sample size.

Average SST data (using only months when tags were deployed) indicated no consistent trend between 1993 and 2002, although at both sites SST was higher in 2002 than in 1993 (Race Rocks: 1993, 10.7 °C; 2002, 11.2 °C; Active Pass: 1993, 15.1 °C; 2002, 17.1 °C).

Discussion

We obtained dive data from approximately one third of the total population of fish-eating killer whales within the summer core of their home range. Both sexes were well represented and we covered a wide range of ages (Fig. 3) and a large enough temporal scale (both in years and through the summer season; Fig. 2) to broadly characterize the diving behaviour of this population, at least during the summer months in the core part of their home range. Of the five factors we examined (pod, age, sex, day or night, year), three (sex, day or night, year) were significantly related to killer whale diving behaviour, though the relationships were not easily discernable owing to complex interactions between them. Despite documented differences in the geographic and seasonal use of the area among pods (Osborne 1999), we found no effect of pod on diving behaviour. This suggests that the pods search for prey at similar depths in the water

Table 2. Information on diving rates (no. of dives/h) from individuals ($n = 26$) for which both day- and night-time data were available.

Dive rate measure (no. of dives/h)	Mean no. of dives/hour (SD)	
	Day	Night
≥ 1 min	10.29 (2.67)	10.37 (3.17)
≥ 5 m	27.96 (25.10)	24.25 (11.59)
≥ 10 m	8.32 (2.97)	7.09 (3.37)
≥ 20 m	3.45 (2.79)	1.24 (0.78)
≥ 30 m	2.12 (2.11)	0.66 (0.55)
≥ 50 m	1.04 (1.03)	0.40 (0.46)
≥ 100 m	0.50 (0.67)	0.22 (0.32)
≥ 150 m	0.20 (0.39)	0.07 (0.17)

column. Also, this implies that although our sample for J-pod included only a single individual (tagged on three occasions), it is likely that our results from the other pods may be applicable to the diving behaviour of J-pod whales.

The relationship between diving activity and age and sex of fish-eating killer whales is complex. Results of a GLIM indicated no effects of age or sex on any of the diving rate measures. It is not surprising that some of the shallower rate measures (dives ≥ 10 m or 20 m) do not change with age. If larger body size played an important role in increased diving capabilities in this species, such effects would be more likely to be seen for deeper dive rate measures, as similar-sized species of delphinids regularly dive to much greater depths (Baird et al. 2002; Heide-Jorgensen et al. 2002). The lack of an effect does not mean that the diving capabilities for this species do not increase with age, but may reflect both the maximum depths available to the animals and, more importantly, where their prey concentrate in the water column. The maximum depth of the study area is approximately 330 m, with the majority being <250 m in depth. These whales do dive below 150 m on a regular basis (on

Table 3. Results of GLIMs of dive rates in relation to age, sex, pod, day or night, and year, using the complete data set.

Dive rate measure (no. of dives/h)	No. of significant terms	r ² value	Significant terms
≥1 min	1	0.087	Year
≥10 m	2	0.174	Year, Day/Night × Year
≥20 m	2	0.393	Day/Night, Year
≥30 m	2	0.326	Day/Night, Year
≥50 m	1	0.233	Day/Night
≥100 m	1	0.083	Day/Night
≥150 m	1	0.174	Year

Note: GLIM results using the reduced data set were similar for all dive rate measures except ≥10 m and ≥30 m (see text).

Fig. 4. Box plots showing variation in dive rate (no. of dives/h) by year, for dives >20 m, during the day (top) and at night (bottom). Boxes showing overall values use only a single (mean) value for each year. GLIM results for dives >20 m indicate that dive rates are related to both year and day or night periods, though the year effect appears to occur only during the day. Upper and lower box lines represent first and third quartiles, and the middle line represents the median value.

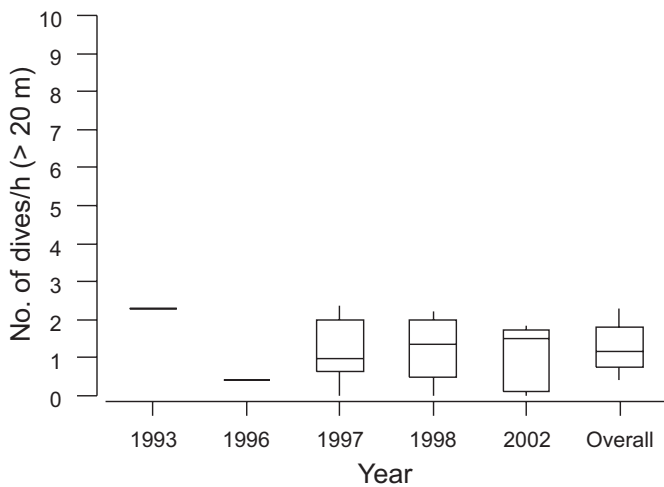
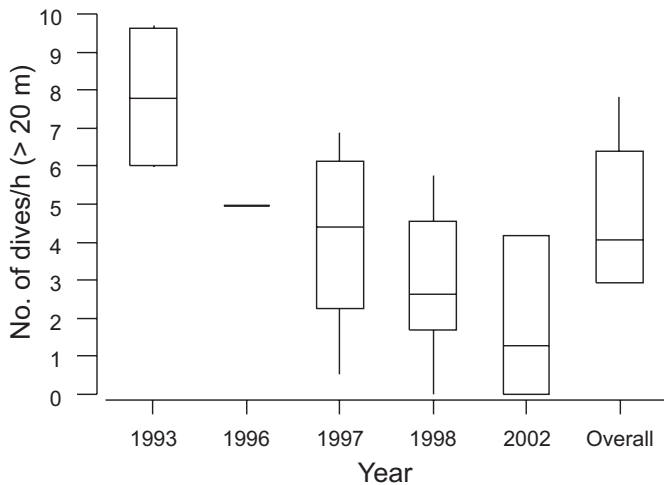
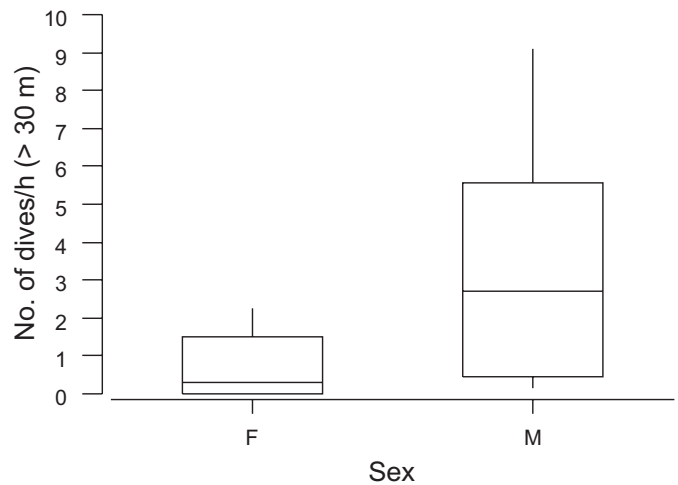


Fig. 5. Box plot showing difference in daytime dive rate (no. of dives/h ≥30 m) between adult females (F) and adult males (M), using data collected between 1997 and 2002. Upper and lower box lines represent first and third quartiles, and the middle line represents the median value.



average, once every 5 h during the day; Table 2), with the maximum dive depth recorded for a killer whale in this study being 264 m. Despite some deep dives, this population, in general, appears to use primarily near-surface waters, presumably because prey availability in near-surface waters is high enough to meet energetic needs (see below). The lack of an age effect on diving behaviour may be due to individuals generally foraging in near-surface waters (i.e., no strong need to dive deep), the development of diving capabilities in the first few years of life, and the age distribution of our sample. The youngest whales tagged in our study were 3 years old, and maximum dive depths recorded for these individuals were similar to the overall average. Although killer whales do not stop growing until after 10 or more years of age (males continue to grow until at least 15 years of age; Duffield and Miller 1988), by 3 years they are likely to have developed sufficient body oxygen storage capacity to reach even the deepest portions of the study area (see Noren et al. 2001, 2002). The age distribution may also influence these analyses; almost half (16) of our tagged animals were fully grown adults, with no age-related change in body size over a 44-year age range.

We did find sex differences in diving behaviour, though only when restricting the analyses to adults. Analyses restricted to years when data were available for adults of both sexes (1997–2002) indicate that adult males do dive deeper more frequently than adult females (see, for example, Fig. 5). Bain (1989) has suggested that observations of adult male fish-eating killer whales foraging in peripheral positions in a group, or over deeper water than females, reflect differences in diving behaviour due to body size differences, and our evidence supports his suggestion. Adult males and adult females within a pod may spatially segregate to some degree when foraging, both horizontally and vertically, to minimize competition for food.

Differences in vocal activity and behaviour between day and night have been documented for captive killer whales (Bain 1986; Ray et al. 1986). Diel changes in serum cortisol concentrations have also been reported from captive killer whales, similar to changes exhibited by diurnal terrestrial mammals (Suzuki et al. 2003), though whether such differences are artifacts of the captive environment is unclear. There are several possible explanations for the differences in diving patterns between day and night and among years for our study population. However, understanding the potential role of diel or interannual shifts of prey within the water column is complicated by uncertainty in our knowledge of the diet of this population, and the potential geographic and interannual variability in the behaviour of prey species. There are large-scale correlations between killer whale presence in the area and runs of salmon (Heimlich-Boran 1986; Osborne 1999), and limited fish-scale samples collected opportunistically behind foraging whales have indicated that chinook salmon (*Oncorhynchus tshawytscha* (Walbaum in Artedi, 1792)), the largest salmon species, appears to be taken more frequently than other species (Ford et al. 1998). However, biases in the scale-sampling technique towards larger species of fish, which have potentially longer handling times and a greater likelihood of being broken up prior to consumption, render precise conclusions regarding diet composition impossible. In addition, predicting the depth distributions of potential prey species in our study area is complicated by known geographic and interannual variability in depth distributions of at least some species of salmon (e.g., Quinn et al. 1989). None of the studies of salmon depth distribution were undertaken in our study area or in the same years in which we collected killer whale dive data.

Differences in day–night patterns (i.e., fewer deep dives and slower swim speed at night) could presumably reflect either a shift into near-surface waters at night owing to diel vertical movements of prey or an overall reduction in foraging activity at night. Information on diel vertical movements of salmon is limited. Two species, chum (*Oncorhynchus keta* (Walbaum in Artedi, 1792)) and sockeye (*Oncorhynchus nerka* (Walbaum in Artedi, 1792)) salmon, are known to spend more time near the surface at night than during the day (Quinn et al. 1989; Friedland et al. 2001; Ishida et al. 2001), while a third, chinook salmon, dives deeper at night (Candy and Quinn 1999). If foraging were occurring as often at night as during the day, but simply closer to the surface, we would expect swim speeds to be similar during these periods. Average swim speed at night is only approximately 75% of that during the day, suggesting that there may

be less foraging at night. Less foraging at night could result if prey were less accessible or more costly to obtain, or if light levels strongly influenced foraging. Prey could shift deeper in the water column during the night and thus be less accessible. However, the differences in mean swimming depth for chinook salmon during the day (25–64 m) and at night (49–78 m) are small (Candy and Quinn 1999) and not likely to add a significant cost to foraging. Alternatively, since salmon may exhibit a variety of escape behaviours in the presence of predators (Yano et al. 1984), vision could be critically important for prey capture, and lower light levels could make foraging less profitable. It is well known that echolocation is used in detecting prey (Barrett-Lennard et al. 1996; Au et al. 2004), but how important vision is in the final instants of prey capture is unknown.

As noted above, the trend for deep dives to decrease in frequency over the years of the study exists only during the day; no evidence of such a trend exists for diving at night (Fig. 4), even between 1997 and 2002 when samples sizes at night were adequate. Such a trend does not appear to be due to any sampling issues regarding age, sex, or pod; in fact, in the year when deep dive rates were highest (1993), no adult males, which have higher rates of deep dives than adult females, were tagged. Interannual variation in dive depths is not surprising in itself (see, for example, Boyd et al. 1994). Chum salmon spend their time at more shallow depths in the water column as SSTs decrease (Tanaka et al. 2000); therefore, annual fluctuations in SST could lead to different foraging depths for killer whales. If SST were influencing salmon depths (and thus killer whale dive depths), we would expect to see a reduction in SST between 1993 and 2002. While our analyses of SST were very coarse, the lighthouse SST data show a slightly opposite trend, suggesting that it is unlikely that reductions in SST were responsible for shallower daytime dives in recent years. The changes could also be due to a shift in the prey species consumed, since there are differences in where in the water column different species of salmon tend to spend their time (Quinn et al. 1989; Ruggerone et al. 1990; Candy and Quinn 1999). Unfortunately, no information is available on interannual variation in diet.

It is also possible that the day–night or interannual differences we report could be a response to vessel traffic. Trends in vessel traffic within the habitat of the whales are complex when the different types of vessels are taken into account (e.g., commercial fishing vessels, shipping traffic, and dedicated whale-watching boats). Shipping and commercial fishing traffic have remained stable or have declined in recent years, respectively (Osborne 1999). Commercial whale watching first began in the late 1970s, although it was not a regular occurrence in the area until the mid- to late 1980s. The numbers of commercial and recreational whale-watching vessels operating in the area, and the number of boats following whales, more than doubled between 1993 and 1997, then more or less leveled off between 1998 and 2002 (Osborne 1999; Foote et al. 2004). By 1993, the average number of vessels following whales was already relatively high (Foote et al. 2004), so effects of boats may have already existed prior to the initiation of our study. The number of shipping and commercial fishing vessels transiting through the area is not likely to vary dramatically between

day and night, whereas whale-directed vessel traffic occurs only during daylight hours. Vessel traffic in close proximity to whales may result in changes in behaviour (Williams et al. 2002; Foote et al. 2004), and it is possible that foraging could be influenced by high underwater sound levels (e.g., Erbe 2002; but see Au et al. 2004). If foraging were negatively affected by vessel noise, and whales were able to forage at night (i.e., vision was not critically important for prey capture), increased activity levels would be expected at night. Alternatively, vessel traffic could interfere more with resting activity (see Constantine et al. 2004), which could shift to nighttime hours when whale-directed vessel traffic is absent. There is some suggestion that daytime resting behaviour for this population declined between the 1970s to early 1980s, when whale-directed vessel traffic was rare, and the 1990s, when vessel traffic had increased (R. Osborne, personal communication). If such a shift continued during the period of this study (between 1993, when vessel traffic was relatively low, and 1997–2002, when vessel traffic was comparably high), we would expect lower dive rates during the day in 1993 compared with 1997–2002, since more resting would occur during daytime hours in 1993. Such is clearly not the case (Fig. 4), though this does not preclude an effect of vessel traffic occurring prior to the start of our study.

We have documented that the diving behaviour of fish-eating killer whales varies on both short (day versus night periods) and long (interannual) time scales. Such variation is most likely related to the foraging ecology of this population but, at least for diel effects, could also be influenced by the high levels of whale-directed vessel traffic that have existed since before the start of our study. Understanding the causes of such variation is confounded by uncertainties regarding the diet of this population, by a lack of information on the three-dimensional spatial distribution of potential prey species within the study area, and by uncertainty regarding the importance of vision and light levels in prey capture. Information on depth distributions of some species of salmon is available from studies elsewhere, though documented geographic and interannual variability in depth distributions makes it difficult to assess whether such information can be appropriately applied to the years and area of our study. How various species of prey respond to environmental influences such as water temperature may also be important. Our data suggest that the studied population of fish-eating killer whales is less active at night, although whether this is due to changes in prey behaviour or prey species, a critical role of vision in prey capture, or a large-scale shift in activity patterns due to vessel traffic, is unknown. Similarly, the causes of the interannual changes in dive depths are also unclear. The decrease in daytime dive depths of fish-eating killer whales over the 10-year span of our study does suggest that future research on the diving behaviour of this population is warranted, particularly research incorporating methods to simultaneously monitor the abundance and behaviour of potential prey species and collect information on the actual diet of the whales. In addition to helping understand the interannual and diel variation in diving behaviour, further research could also address seasonal and geographic variability in diving patterns for this population, since whales are known to spend substantial parts of the year outside of our study area.

Acknowledgements

The first year of the study was undertaken as part of R.W.B.'s Ph.D. research at Simon Fraser University. Funding or support for field activities was provided by a Natural Sciences and Engineering Research Council of Canada (NSERC) grant to L.M. Dill (1993), an NSERC Postdoctoral Fellowship to R.W.B. (1996–1998), the Free Willy Keiko Foundation (1997–1998), and the National Marine Fisheries Service, National Marine Mammal Laboratory (1997–2002). Funding for data analyses was provided by the National Marine Fisheries Service, Northwest Fisheries Science Center. Loans of equipment by Marilyn Dahlheim and David Duffus were crucial to the initiation of this research. Steve Wischniowski and Jeff Goodyear also loaned equipment in the first year of field research, and Jeff Goodyear designed the first tags used in this research. A number of individuals helped in the field, including Erin Ashe, Tamara Guenther, Louise Hahn, Allan Ligon, Jennifer Marsh, Nicole Phillips, Jodi Smith, Daniel Webster, Pam Willis, and Steve Wischniowski. Analyses of diving behaviour in relation to age, sex, and pod would not have been possible without the long-term work of Ken Balcomb and the Center for Whale Research. Ken Balcomb, David Ellifrit, and Astrid van Ginniken of the Center for Whale Research confirmed identifications and provided information on age, sex, and association patterns of tagged whales. Erin Falcone, Autumn Miller, and Erin Ashe assisted with data processing. Logistical support was provided by Friday Harbor Laboratories from 1997 to 2002. The sea surface temperature data were available because of the long-term efforts of Fisheries and Oceans Canada. Research in US waters was undertaken under National Marine Fisheries Service Scientific Research Permit Nos. 926 and 731-1509. We thank Solange Brault, John Calambokidis, and Rob Williams for helpful discussions. We also thank David Bain, Linda Jones, Dawn Noren, and two anonymous reviewers for comments on the manuscript.

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