The diving behaviour of mammal-eating killer whales (*Orcinus orca* L., 1758): variations with ecological not physiological factors

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ABSTRACT

Mammal-eating killer whales (*Orcinus orca* L., 1758) are a rare example of a social predator where sexually dimorphic adults and juveniles with diverse physiological diving capacities.hunt together in groups Day-night ecological differences should also affect diving as their prey show diel variation in activity and mammal-eating killer whales do not rely on echolocation for prey detection. Our objective was to explore the extent to which physiological aerobic capacities versus ecological factors shape the diving behaviour of this cooperatively feeding breath-hold diver. We used suction-cup attached depth recorders (Dtags) to record diving behaviour of 11 animals in Southeast Alaska over 7,608 dives that

1   showed a strong bout structure in both dive depth and duration. Day-night comparisons

2   revealed reduced rates of deep dives, longer shallow dives and shallower long-duration dives

3   at night. In contrast, dive variables did not differ by age-sex class. Estimates of the aerobic

4   dive limit (cADL) suggest that juveniles exceeded their cADL during up to 15% of long

5   dives, whereas adult males and females never exceeded their cADL. Lack of variation

6   among age-sex classes indicates that mammal-eating killer whales in this area employ a

7   strategy of physiological compromise, with smaller group members diving nearer their

8   physiological limits and large-bodied males scaling down their physiological performance.

9

12   **INTRODUCTION**

13   In this study, we examine how physiological versus ecological factors shape the diving

14   patterns of a sexually-dimorphic marine mammal, the killer whale (*Orcinus orca* L., 1758).

15   Studies in the North Pacific have documented distinct forms, or ecotypes, of killer whales

16   that specialize on different prey (Ford et al. 1998; Saulitis et al. 2000, Morin et al. 2010).

17   Similar dietary specialization appears to apply to other populations of killer whales as well

18   (Berzin and Vladimirov 1983; Pitman and Ensor 2003). Within the inshore waters of the

19   Eastern North Pacific, members of the 'resident' ecotype feed only on fish, especially on

20   Pacific salmon (*Oncorhynchus* spp.). 'Transient' killer whales, however, exclusively hunt

21   warm-blooded marine mammals and birds. Their primary food source in the summer months

22   is harbour seals (*Phoca vitulina* L., 1758, Ford et al. 1998), though transients also attack

23   Steller (*Eumetopias jubatus* Schreber, 1776) and California (*Zalophus californianus* Lesson,

24   1828) sea lions, harbour porpoises (*Phocoena phocoena* L., 1758), Dall's porpoises

25   (*Phocoenoides dalli* True, 1885), and Pacific white-sided dolphins (*Lagenorhynchus*

1   *obliquidens* Gill, 1865). Transients also occasionally take minke (*Balaenoptera acutorostrata*

2   Lacépède, 1804, Ford et al. 2005) and grey whales (*Eschrichtius robustus* Lilljeborg, 1861,

3   Baldridge 1972; Goley and Straley 1994), as well as seabirds (Ford et al. 1998).

4   Typical body lengths of adult male killer whales exceed adult female body length by

5   20% and adult males weigh roughly 75% more than adult females (Clark and Odell 1999;

6   Sato et al. 2006).   The factors driving adult sexual dimorphism in killer whales are not

7   understood, but two alternative hypotheses propose that male body size evolved under either

8   sexual selection, or natural selection for greater diving capabilities.   With a 75% greater body

9   mass than adult females, adult male killer whales should have roughly a 15% longer aerobic

10 dive limit, based on a mass$^{0.75}$ scaling of diving metabolic rate (Kleiber 1975). Despite

11 pronounced sexual dimorphism, mammal-eating killer whales in the north-eastern Pacific are

12 social predators that typically hunt in groups of mixed age and sex.

13   Killer whales have an extended period of maternal care.   Offspring often travel with

14 their mothers beyond the onset of sexual maturity around 15 years of age (Olesiuk et al.

15 1990).   Dependent offspring typically travel in close associations with their mothers, possibly

16 benefiting energetically from swimming in echelon formation (Noren 2008).   In eastern

17 North Pacific transients, social groups typically consist of one or more adult females and their

18 offspring (Ellis et al. 2008).   Adult males travel in long-term stable associations with an adult

19 female (presumed to be their mothers) or roam between groups, and occasionally travel by

20 themselves (Baird and Whitehead 2000). Hunting in these animals typically involves prey

21 sharing and a high degree of coordination among all group members (Jefferson et al. 1991;

22 Ford et al. 1998; Ford et al. 2005).

23   Since adult males and females with dependent offspring typically hunt in communal

24 groups, group members face the challenge of reconciling their different physiological

25 constraints dictated by their different body sizes into a common hunting strategy. This could

1   be done in one of two ways: either the larger animals in the group could scale down their

2   physiological performance to accommodate the lower physiological limits of smaller group

3   members (physiological compromise), or the animals could take different roles in the

4   foraging process to capitalize on a greater range of physiological capacities (division of

5   labour). A strategy of physiological compromise suggests that all group members employ a

6   common strategy geared to the limitations of the most constrained individual. A strategy of

7   division of labour implies that the less constrained animals use their greater physiological

8   capacities to maximise prey capture rates for the group, potentially exploiting a wider range

9   of prey niches.

10   All marine mammals must dive underwater without breathing in order to forage.

11   Performing energetic underwater movements without intake of oxygen represents a clear

12   physiological challenge (Kooyman and Ponganis 1997; Acevedo-Gutiérrez et al. 2002).

13   Many studies have focused on the ability of marine mammals to remain underwater without

14   utilizing significant anaerobic metabolism (aerobic dive limit) as a critical factor in their

15   diving behaviour (e.g. Weise and Costa 2007). However, the actual diving behaviour

16   undertaken by a marine mammal should be influenced by physiological, ecological and social

17   factors, with the ultimate goal of foraging being to consume and process sufficient prey to

18   meet energetic requirements (Rosen et al. 2007). Consuming prey requires accessing the

19   prey underwater, and is thereby constrained by the diving ability and budget of the predator,

20   and critically by the location, behaviour, and detectability of prey in the water column.

21   One particularly strong ecological factor that influences depth use and behaviour in a

22   wide range of marine species is the presence of light (Hays 2003). The presence or absence of

23   light alters the sensory basis by which predators can detect prey. As a consequence, prey

24   may be adapted to reduce their risk of being captured during daytime by shoaling (i.e. Ryer

25   and Olla 1998; Brehmer et al. 2007) or moving to depths with less light (Stich and Lampert

1 1981). Vertical diel migrations of marine organisms are well documented, including for

2 zooplankton (Hays 2003) and fishes (Bozzano et al. 2005). The diel diving patterns of many

3 marine mammal species are thought to be shaped by the diel activities of their primary prey

4 (i.e., crab-eater seals, *Lobodon carcinophagus* Hombron and Jacquinot, 1842, Burns et al.

5 2008, sperm whales, *Physeter macrocephalus* L., 1758, Aoki et al. 2007, long-finned pilot

6 whales, *Globicephala melas* Traill, 1758, Baird et al. 2002). Several species eaten by

7 mammal-eating killer whales in the eastern Pacific show pronounced diel variation in their

8 activity patterns. Harbour seals off Alaska do most of their foraging during the hours of

9 darkness (Frost et al. 2001; Hastings et al. 2004) and Steller sea lions are also reported to

10 forage extensively at night (Thomas and Thorne 2001).

11 In addition to indications that their prey are more active during nighttime, the vast

12 difference in sensory ecology of nighttime versus daytime may be particularly marked for

13 mammal-eating killer whales. Marine mammal-eating killer whales echolocate much less

14 than fish-eating killer whales, likely because most of their prey have good hearing in the

15 frequency range of killer whale echolocation clicks (Barrett-Lennard et al 1996). Although

16 the methods of prey detection of mammal-eating killer whales remain poorly understood,

17 vision and passive acoustic detection are therefore thought to be the primary sensory

18 modalities available to detect their prey, and this would be influenced by day-night

19 differences in ambient light. Any changes in predation between day and night would have

20 especially important ecological implications in high latitudes where daylight is limited

21 throughout a large part the year.

22 To date, most of the limited research on the diving behaviour of free-ranging killer

23 whales has been conducted on fish-eating populations. Baird et al. (2005) investigated the

24 diving behaviour of 34 southern resident killer whales in the inshore waters of southern

25 British Columbia, Canada and Washington State, USA. Diving rates did not vary

1 significantly between social groups or between males and females of all age classes.

2 However, adult males made deep dives significantly more frequently during the day than

3 adult females. Both sexes swam significantly faster and dove significantly deeper during the

4 day compared to nighttime, suggesting decreased levels of activity during the night.

5 However, diving performance and behaviour could vary greatly between killer whale

6 ecotypes given the differences in prey type. For mammal-eating killer whales, Baird (1994)

7 presents a single dive record that also suggests reduced nighttime activity of the tagged

8 individual. Erickson (1978) used VHF telemetry to track a pair of mammal-eating killer

9 whales for 10 consecutive days in the inshore waters of British Columbia and Washington

10 State and noted a decrease in dive duration in the afternoon and evening, which they

11 interpreted as an increase in foraging activity during this time.

12 In this study, we analysed the diving behaviour of 13 mammal-eating killer whales

13 recorded using Dtags containing high-resolution depth loggers (Johnson and Tyack 2003).

14 We examined how diving behaviour was influenced by ecological and physiological factors

15 by testing whether diving behaviour differed across body-size class and day-vs-night. To

16 determine how changes in ambient light might have affected the diving behaviour of

17 mammal-eating killer whales, we compared diving behaviour between daytime and nighttime

18 for tagged individuals. Day-night differences would suggest a direct consequence of the

19 difference in ambient light on the ability of marine-mammal eating killer whales to detect

20 their prey, or an indirect consequence of changes in depth usage or behaviour of their prey. If

21 foraging success depended primarily upon diving capabilities and the group members

22 exhibited role specialization, then we would have expected each member of a foraging group

23 to maximize its diving performance. In that case, adult males should have taken advantage of

24 their greater oxygen stores by diving longer or spending more time at depth than adult

25 females or juvenile animals. Thus, comparing the dive performance of different age and sex

1   classes allowed us to evaluate how the diving and hunting behaviours of these social

2   predators have evolved in light of different physiological capacities of group members. By

3   analysing day-night differences and body-size factors together, we assessed whether they

4   varied independently or interacted somehow. Body-size differences in diving behaviour

5   should have been most apparent in the context of maximal diving effort, which was most

6   likely limited by physiological constraints.

7

8   **METHODS**

9   Groups of transient killer whales in the eastern North Pacific that belonged to the West

10 Coast Transient population (Ellis et al. 2008) were studied in the inshore waters of Southeast

11 Alaska in summer 2006 and 2007. We used digital archival tags (Dtags: Johnson and Tyack

12 2003) to record diving behaviour of individual animals. Upon encountering a group, all

13 individuals were photographed from a skiff for identification using the method of Bigg

14 (1982). Tags were deployed on animals using a 7m hand pole and attached non-invasively

15 with suction cups. The tagged individual was re-photographed to confirm its identity. The

16 tag samples pressure at 50 Hz, later down-sampled to 10Hz. Pressure data were converted to

17 depth in meters using calibration constants derived in the laboratory. The tag also records

18 sound using two hydrophones at 96 kHz and 3-axis magnetic and acceleration vectors at 50

19 Hz. After deployment, the tagged individual was tracked from an 18m fishing vessel using a

20 VHF beacon and visual observations. Whales were followed at a distance of 1-2km to

21 minimize potential influences of the vessel on their behaviour.

22   Each surfacing of each whale was identified using the depth record. Initially, this was

23 done automatically based on a threshold of whale dive depth. All of the automatically-

24 detected surfacings were carefully checked by eye and by listening to the acoustic record.

25 Several corrections were necessary, likely because the minimum depth of the tag during a

1 surfacing event depended on where the tag was placed on each whale's body and on how

2 much of the tagged whale's body came out of the water when it surfaced. In a few cases,

3 surfacing events could be clearly identified using the acoustic record even though the tag did

4 not break the surface of the water. This was observed in the field when the whale surfaced

5 without a VHF signal received from the tag. However, in those cases, the surfacing by the

6 tagged whale was still audible as splashing and/or blow sounds heard in the tag recording.

7 The most common surfacing behaviour of killer whales is to surface and then dive

8 again immediately, with one breath taken during the surfacing. Killer whales are occasionally

9 observed to drift, or log, at the surface (Martinez 1978). We inspected this in the tag records

10 as the duration between a surfacing and start of the subsequent dive. In our records, no

11 interval exceeded 16s total, and 99.3% of the durations between the end of a dive and the

12 start of a subsequent dive were <5s. Field observations indicated a whale would breathe once

13 during such an interval. Because the whales in our tag records were not observed to log at

14 the surface, respiration events of the whales were identified as surfacings (Fig. 1). The half-

15 way point between the end of the previous dive and the start of the subsequent dive was

16 considered the time of the respiration event. Although the exact time of the respiration may

17 have varied slightly, it should be accurate to within ±2.5s.

18 Time of day, duration and maximum depth associated with all dives were tabulated.

19 Visual inspection of the depth records indicated that whales often conducted numerous short

20 and shallow dives that were occasionally followed by a longer, deeper dive. This suggests

21 that diving is conducted in bouts, which can be separated either by duration or depth. To test

22 the possibility that the diving behaviour could be broken into bouts to obtain dive bout

23 criteria (Sibly et al. 1990), we conducted a log-frequency analysis of dive duration and

24 maximum dive depth separately. Using these criteria, dives were separated into long and

1   short dives for analyses of dive depth, and shallow and deep dives for analyses of dive

2   duration.

3   To contrast the roles of physiological constraints and ecology on the diving behaviour

4   of transient killer whales, we tested for differences both by age-sex class and day-night for

5   three dive variables: dive rate for deep and shallow dives, dive duration for deep and shallow

6   dives, and dive depth for long and short dives. Here, deep and long dives referred to dives

7   deeper than and longer than the bout criterion interval, respectively. The effects of age-sex

8   and time of day were assessed in separate analyses rather than a single 2-way model as 4

9   records did not include both day- and nighttime data. For the age-sex class comparison, we

10 calculated the mean value for each individual and tested for differences using a non-

11 parametric Kruskal-Wallis test. All recorded dives were classified as day or night dives using

12 civil twilight (Seidelmann 1992) to define the start and end of nighttime. We computed

13 differences in diving behaviour during day versus nighttime and tested the differences using

14 paired *t*-tests.

15   We conducted three additional analyses to explore whether physiological limitations

16 might have influenced diving and breathing performance. We expected that if physiological

17 limitations primarily shaped the behaviour of these whales, large-bodied males should have

18 had a lower overall breathing rate, the capacity to spend more time at greater dive depths, and

19 required fewer breaths to prepare for, and recover from, a long-duration dive. First, for each

20 whale, we tabulated the maximum dive depth, maximum dive duration, and the overall blow

21 rate (equivalent to the dive rate since only one breath was taken per surfacing) of the tag

22 record. Next, the proportion of time spent at depth was calculated for each whale. Finally,

23 we analysed the effect of dive duration on the number of breaths taken before and after each

24 long dive: we averaged the number of breaths before and after each long dive to consider

25 both preparation and recovery aspects of diving limitations. We plotted duration of dives

1 greater than the bout criterion interval against the number of breaths. Limitations in

2 behaviour due to physiological constraints would be revealed by a lack of data points

3 representing a small number of breaths before or after long duration dives, whereas there are

4 no limits to more breaths being taken after any duration of dive. We used quantile regression

5 to evaluate the slope of a line anchored at (0,0) above which 95% of the data would fit, with

6 only 5% below the line. This slope was then compared across age-sex classes.

7

8 **RESULTS**

9   A total of 12 tags were deployed on 11 transient killer whales, with a total recording

10 time of 123 hours. Two other tag records of less than one hour duration were not included in

11 the analysis. One individual killer whale, adult female T91, was tagged on two subsequent

12 days. All of the dive data for that individual were pooled, leaving a total of 11 individual

13 whales for analysis: 3 adult males, 4 adult females, and 4 juveniles, comprising a total of

14 7,608 dives. Data from 7 individuals (1 adult male, 2 adult females, and 4 juveniles) included

15 more than one hour of nighttime data, and were used in the day-night comparison (Table 1).

16   Log-frequency analysis demonstrated that diving behaviour of transient killer whales

17 was strongly characterized by bouts of dive duration and maximum depth (Fig 2). A two-

18 process exponential model provided a significantly better fit for dive duration ($F_{2,45}$ = 74.3,

19 $P<0.001$) and maximum dive depth ($F_{2,45}$ = 14.2, $P<0.001$) than a single-process exponential

20 model (Sibly et al. 1990). Using the formula to minimize the number of events misclassified

21 (Slater and Lester 1982), we calculated bout criteria of 57.77s (0.96 min) for dive duration

22 and 12.73m for dive depth.

23   There were some clear differences between daytime and nighttime diving behaviour for

24 the seven animals tagged both during the day and at night (Fig. 3). The rate of deep diving

1 was higher during the daytime than during the night ($t_6 = 3.46$, $P = 0.014$), but the rate of

2 shallow diving did not differ ($t_6 = 1.12$, $P = 0.31$). The duration of deep dives did not differ

3 significantly between day- and nighttime ($t_6 = -1.33$, $P = 0.23$), but shallow dive duration

4 tended to be longer during the night ($t_6 = -2.80$, $P = 0.031$). Dividing the dives by duration

5 showed that depths of short duration dives did not differ for day versus night ($t_6 = 0.258$, $P =$

6 0.81), but that maximum dive depths of long duration dives were shallower during the night

7 than during the day ($t_6 = 2.87$, $P = 0.029$). Blow rates differed only slightly, with a mean of

8 68.8 blows/hr during the daytime, and 62.9 blows/hr during the night, a non-significant

9 difference ($t_6 = 1.43$, $P = 0.20$). Interestingly, the rate of occurrence of long duration dives

10 was almost equivalent during the day (10.7/hr) and night (10.6/hr).

11   For the same parameters, none differed significantly among age and sex classes (Fig.

12 4). Juveniles did have a somewhat higher rate of deep diving than adult females and adult

13 males, but that difference was not statistically significant ($H_2 = 2.96$, P $= 0.23$), nor were

14 differences in the rate of shallow diving ($H_2 = 0.58$, $P = 0.75$). The only difference that had

15 borderline statistical significance involved large males tending to dive deeper during the short

16 dives between breaths ($H_2 = 5.60$, $P = 0.06$), a difference likely due to biomechanical factors

17 (e.g., the greater height of the male dorsal fin).

18   Because deep dives were more common during the day, we retested the same

19 parameters using only the daytime data recorded from all 11 individuals. Doing so did not

20 result in any substantial changes in the observed age-sex patterns and no significant

21 differences were found across age-sex classes using only the daytime dives.

22   Further testing of dive performance by age-sex class did not reveal any strong

23 differences. Diving performance did not differ significantly by age-sex class for overall

24 blow-rate ($H_2 = 0.60$, $P = 0.74$), duration of the single longest dive recorded ($H_2 = 1.69$, $P =$

25 0.74), or depth of deepest dive recorded ($H_2 = 1.30$, $P = 0.52$). The proportion of time spent

1   at depth by each whale and the proportion of time spent below a given depth showed

2   considerable variability from whale to whale (Fig. 5, left panel), likely shaped by the

3   particular behavioural states which dominated during the tag deployment or individual

4   variation. Inspection of cumulative depth use revealed no consistent differences in depth use

5   by age-sex class (Fig. 5, right panel).

6   Finally, analysis of the number of blows following and preceding dives versus duration

7   of dives which exceeded 57.77s (the bout criterion) did reveal a clear tendency for there to be

8   few data points in the lower-right corner of the plot (Fig. 6). This pattern is consistent with

9   whales needing to breathe more before or after a longer dive. However, there was no clear

10 pattern of differences by age-sex class and no significant differences by age-sex class ($H_2 =$

11 0.39, $P = 0.82$).

12

13 **DISCUSSION**

14   Our results indicate consistent differences in diving behaviour of mammal-eating killer

15 whales in the daytime versus the nighttime. Though our statistical analyses were limited to a

16 sample of 7 whales, we found a consistent and statistically significant increase in the rate of

17 deep (>12.74m) diving during the day compared to the nighttime (Fig. 3). While the duration

18 of deep dives did not differ from day to night, the duration of shallow dives was significantly

19 longer during the night than during the day. Consistently, long duration (>57.77s) dives were

20 shallower during the night than during the day, while short-duration dives did not differ from

21 day versus night. The rate of long-duration dives was almost equivalent during the day

22 (10.7/hr) and night (10.6/hr).

23   Taken together, these results indicate a tendency for whales to dive deep less often and

24 to make shallower long dives during the night than during the day. Blow rates were ~9%

1 lower overall during the night than the daytime, but we cannot conclude that mammal-eating

2 killer whales were simply less active during the nighttime because that difference was not

3 consistent across individuals in our sample and therefore not statistically significant. Instead,

4 the differences in diving behaviour were likely also related to day-night differences in the

5 diving behaviour of their prey and/or to differences in ambient light. High levels of

6 downwelling light during the day could enable a strategy of foraging using visual cues at

7 greater depths than would be possible during the night. More detailed information on the

8 diving behaviour of killer whale prey and the sensory ecology of mammal-eating killer

9 whales is needed to assess these possible explanations for day-night differences in the diving

10 behaviour of mammal-eating killer whales.

11   In contrast to consistent day-night differences in diving behaviour, we found no clear

12 differences between age-sex classes for overall blow rate, depth of the deepest recorded dive,

13 or duration of the longest recorded dive. The rate and duration of deep and shallow dives and

14 the depth of long and short dives did not differ across the 11 animals in our sample – even

15 though these parameters did show day-night differences (Figs. 3 and 4). We also tested these

16 parameters using only the daytime intervals, as day-night comparison indicated that deep

17 dives were more common during the day than the night, but again no significant differences

18 were found across age sex-classes. Further tests indicated no differences by age-sex class in

19 depth use or the number of breaths taken before or after a long dive.

20   Because of the substantial differences in body size, we would predict differences in the

21 aerobic dive limit capacity among juvenile, adult female, and adult male killer whales.

22 Though the aerobic dive limit has not been experimentally measured in killer whales, we can

23 calculate an estimated aerobic dive limit (cADL) by scaling up measurements taken from

24 other cetaceans for which the ADL has been measured (see Watwood et al. 2006, Tyack et al.

25 2008). The lean mass (M) specific basal metabolic rate of mammals scales as $M^{-0.25}$ (Kleiber

1   1975), while oxygen stores scale in a linear fashion. Consequently, larger animals can dive

2   longer aerobically than smaller animals (Castellini et al. 1992). Assuming diving metabolic

3   rate scales with lean body mass in a manner similar to the basal metabolic rate, and that killer

4   whales contain similar mass-specific oxygen stores as bottlenose dolphins (Noren et al.

5   2002), the cADL of killer whales can be estimated from the 5.4 minute aerobic dive limit of a

6   187 kg bottlenose dolphin (Noren et al. 2002). With this approach ($cADL_{killer}=ADL_{bottlenose}$*

7   $(M_{killer}/M_{bottlenose})^{-0.25}$), we estimate that killer whale cADLs should range from 10.2 and 11.8

8   min for mean mass estimates of 2418kg for captive adult females and 4249 kg for captive

9   adult males, respectively (Clark et al. 2000; Sato et al. 2006). The body mass of the tagged

10 juveniles can be estimated using age-mass regression curves derived from captive juveniles

11 (Clark et al. 2000). The exact birth date of free-ranging killer whales is not known, but the

12 birth year is known (Ellis et al. 2008; Table 1). Assuming the birth date of a calf is ½ year

13 before the summer it was first sighted, we can calculate the mass of 1, 2, and 8 year juveniles

14 to be 673kg, 865kg, and 2008kg, respectively. These mass estimates correspond to cADLs of

15 7.4, 7.9, and 9.8 min, which is probably an over-estimate of cADL as 0-2 year old bottlenose

16 dolphins have been shown to have substantially lower oxygen stores than adults (Noren et al.

17 2002).

18   Using these estimates for cADL, no dives of adult males (N = 1256 dives) or adult

19 females (N = 3004 dives) exceeded their cADL. From a total of 3348 dives from the 4

20 tagged juvenile animals, 23 exceeded their cADL. These dives represented 0.3%, 0.1%, and

21 2.7% of all dives made by 1-2 yr old juveniles T073A1, T002C2, and T068B2, respectively.

22 The 8-year old juvenile T124E did not conduct any dives longer than its cADL of 9.8 min.

23 This suggests that the dives of adult killer whales were almost entirely aerobic, and their

24 foraging behaviour did not substantially challenge their aerobic capacity. Interestingly, the

25 youngest juveniles made some dives that exceeded their cADL. Although dives exceeding

1   cADL were only a small proportion of the total dives, they represent 1.6%, 0.8%, and 15.2%

2   of the long-duration dives defined using the bout criterion interval of 57.77s. Juveniles also

3   had a non-significant tendency to breathe more (i.e., higher dive rate) and make shorter

4   duration dives for both deep and shallow dives (Fig. 4). These observations indicate that

5   smaller animals in killer whale groups are more aerobically challenged than larger animals.

6   Our results argue against a pronounced division of labour among body-size classes

7   while diving to search for and attack prey, which would predict males to dive longer and

8   deeper and breathe less often than female or juvenile killer whales. Instead, the behaviour

9   indicates a strategy of physiological compromise with individuals of different age-sex classes

10   diving similarly. This strategy pushes the smaller animals closer to their aerobic dive limits

11   and in the case of young juveniles sometimes even beyond it, while leaving adult males with

12   the largest unutilized aerobic diving capacity.

13   Physiological limitations influence the behaviour of both predators and prey in an

14   encounter (Ydenberg and Dill 1986). A solid understanding of the physiology of both players

15   is therefore crucial when examining these dynamics. In predator-prey interactions involving

16   breathhold divers that forage in the water column, the ability of both the predator and the

17   prey to remain submerged and dive to depth typically exerts one of the primary physiological

18   constraints that impact foraging decisions (e.g., Frid et al. 2007). The large body size of the

19   killer whale may enable them to exceed the aerobic diving capacities of their prey. An

20   important characteristic of mammal-eating killer whales is that their prey types are

21   constrained to come to the surface to obtain oxygen. This may enable mammal-eating killer

22   whales to remain close to the surface, waiting for their prey to return. Such a strategy might

23   reduce the need for extended dives beyond aerobic capacities. Coordinated foraging by the

24   group may allow individuals to take turns diving to prevent marine mammal prey from

25   coming to the surface (Jefferson et al. 1991), which would reduce the need for individuals to

1 exceed their aerobic capacities. Thus, our conclusion that physiological factors do not appear

2 to influence the diving patterns of mammal-eating killer whales may reflect the fact that their

3 ecology does not put heavy demands on aerobic diving capability.

4 We should stress that our results should not be extrapolated to killer whales feeding on

5 other prey types. For example, specialized diving roles that take advantage of the greater

6 aerobic capacity of males may be advantageous for killer whale that feed on deep-sea squid

7 or deeper diving mammals such as sperm whales (Pitman et al. 2001) or ziphiids

8 (Notobartolo-di-Sciara 1987). For deep-diving prey, one avenue of escape may be to dive

9 away from the killer whale predator. In such a case, the greater aerobic capacity of the adult

10 male may allow it to pursue such prey more effectively than smaller bodied females or

11 juvenile animals. Observations of mammal-eating killer whales foraging on diverse prey

12 types will help to unravel more fully how ecological factors influence role specialization and

13 coordination of feeding in sexually-dimorphic predators.

14

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1 Table 1. Details of whales tagged with Dtags for this study. Whale ID and date of birth
2 information is based on Ellis et al. 2008. An '*' in the Hrs tagged column indicates
3 individuals for which nighttime data was recorded.

Tag ID	Whale ID	Age-sex	Date of birth*	Date tagged	Hrs tagged	Location	Blow rate (blows/hr)	Longest dive duration (min)	Deepest dive depth (m)
oo06_180a	T068A	Male	≤1984	29/06/2006	1.4	Frederick Sound	56.8	7.2	127
oo06_181a	T065B	Female	1993	30/06/2006	12.7*	Stephens Passage	77.1	8.3	112
oo06_182a	T073A1	Juvenile	2005	01/07/2006	4.8*	Seymour Canal, Stephens Passage, Frederick Sound	71.6	8.9	51
oo06_183a	T002C2	Juvenile	2005	02/07/2006	12.3*	Frederick Sound, Chatham Strait	75.8	7.5	123
oo06_186a	T068B2	Juvenile	2004	05/07/2006	16.3*	Endicott Arm	46.9	11.2	122
oo06_188b/ oo06_189a	T091	Female	≤1974	07/07/2006, 08/07/2006	18.1*	Snettisham Inlet, Stephens Passage, Tracy Arm	57.9	9.4	80
oo06_188c	T092	Male	≤1969	07/07/2006	4.0	Endicott Arm	60.5	5.8	42
oo06_190a	T077	Female	1981	09/07/2006	10.3	Tracy Arm, Endicott Arm	56.4	7.9	65
oo06_190b	T103	Male	≤1968	09/07/2006	16.0*	Stephens Passage, Frederick Sound, Chatham Strait	58.7	9.3	143
oo06_191a	T018	Female	<1974	10/07/2006	8.0	Chatham Strait	49.3	8.3	53
oo07_199a	T124E	Juvenile	1999	18/07/2007	18.4*	Stephens Passage, Endicott Arm	71.1	8.5	254

4

5

1   FIGURE LEGENDS:

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3   Figure 1. A typical dive and surfacing sequence with respiration events marked in green.

4

5   Figure 2. Log-frequency analysis of dives by duration (top) and depth (bottom). The arrow

6   indicates the bout criteria interval used in this study to split dives into long vs short dives

7   (top) and deep vs shallow dives (bottom).

8

9   Figure 3. Diving behaviour of individual transient killer whales during day- and nighttime.

10   Each whale is given a symbol to identify its age-sex class.   There were consistent and

11   statistically-significant day-night differences (indicated within each panel) in: the rate of deep

12   diving, the duration of shallow dives, and the depth of long dives.

13

14   Figure 4. Diving behaviour of transient killer whales divided by age-sex class. AM – adult

15   male, AF – adult female, J - juvenile. Boxes show median with upper and lower quartile

16   values.   Errorbars show the total extent of the data.   None of the parameters differed

17   significantly.

18

19   Fig. 5. Left: proportion of time spent at depth for each of the 11 tagged whales separated by

20   age-sex class. Right: cumulative proportion of time spent below a given

21   depth separated by age-sex class. Overall, the whales spent 50% of their time 8m or

22   shallower, and 90% of their time 40m or shallower. There was no consistent difference in

1   depth use by age-sex class with the possible trend that males had more variable depth use

2   than females or juveniles.

3   Fig. 6. Duration of each long dive (>57.77s) versus the averaged number of blows before and

4   after each dive for a representative example from each age-sex class. The green line shows

5   the slope of the 5% quantile regression fits, which did not differ significantly across age-sex
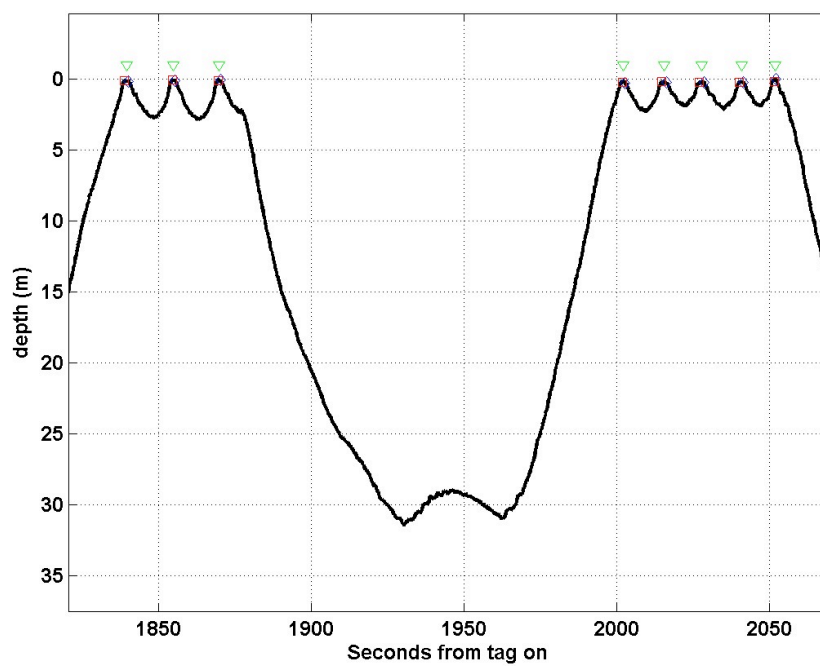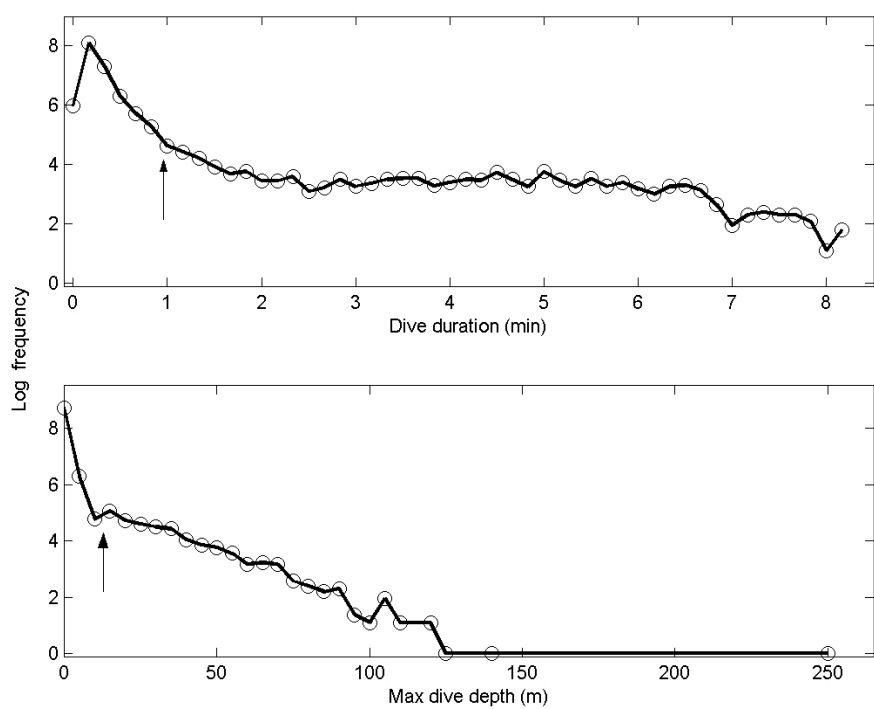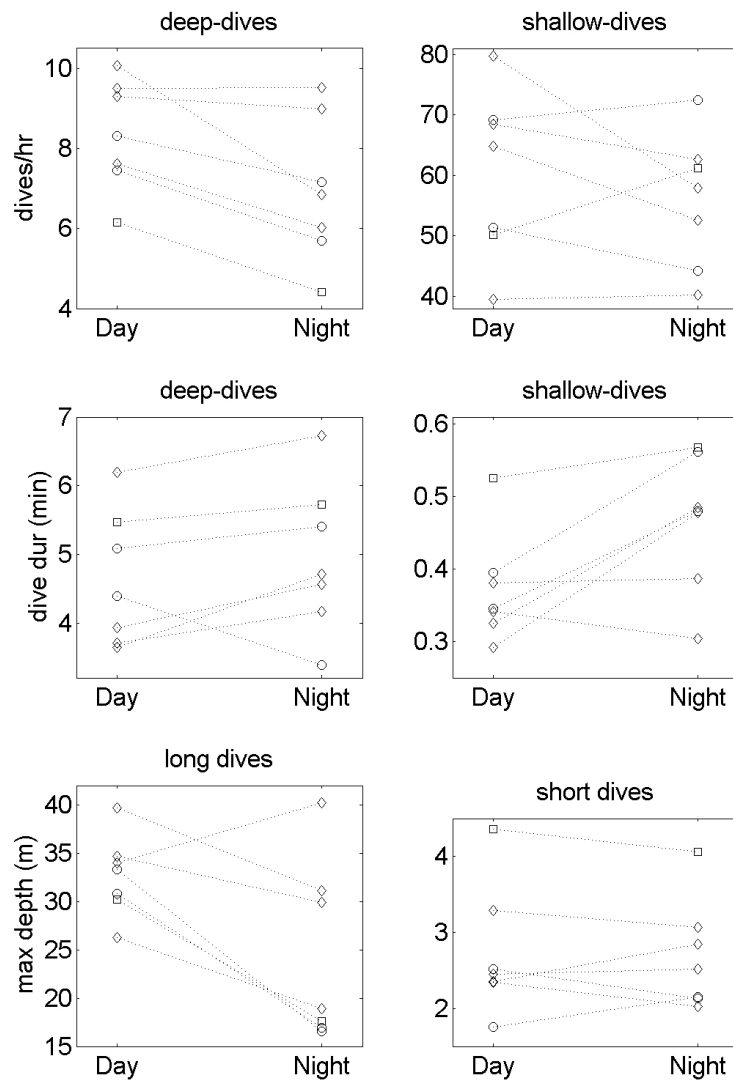
6   class.

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2   Figure 1

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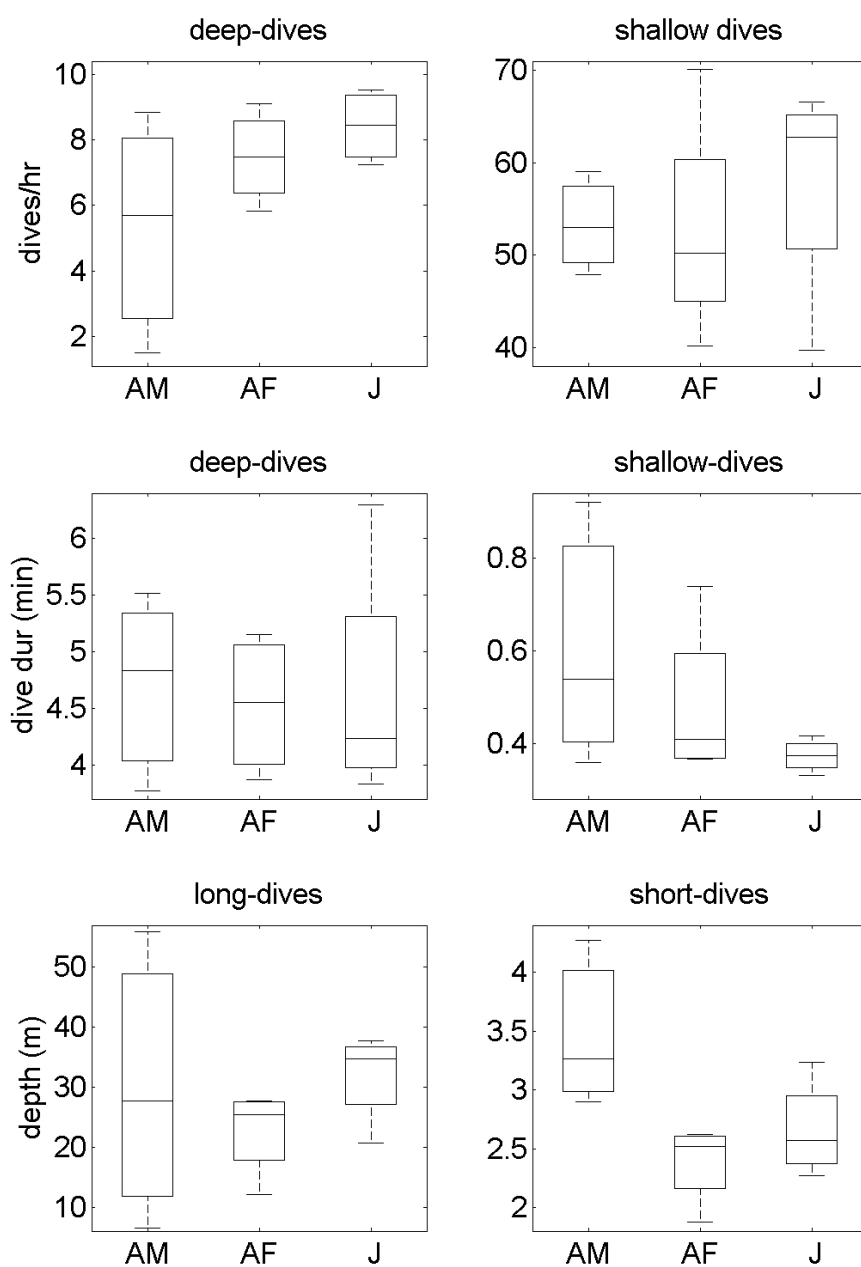

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1   Figure 3

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