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# 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 showed a strong bout structure in both dive depth and duration. Day-night comparisons revealed reduced rates of deep dives, longer shallow dives and shallower long-duration dives at night. In contrast, dive variables did not differ by age-sex class. Estimates of the aerobic dive limit (cADL) suggest that juveniles exceeded their cADL during up to 15% of long dives, whereas adult males and females never exceeded their cADL. Lack of variation among age-sex classes indicates that mammal-eating killer whales in this area employ a strategy of physiological compromise, with smaller group members diving nearer their physiological limits and large-bodied males scaling down their physiological performance.

Key-words: cetacean, diving, group-hunting, sexual dimorphism, diel variation, aerobic dive limit

## INTRODUCTION

In this study, we examine how physiological versus ecological factors shape the diving patterns of a sexually-dimorphic marine mammal, the killer whale (*Orcinus orca* L., 1758). Studies in the North Pacific have documented distinct forms, or ecotypes, of killer whales that specialize on different prey (Ford et al. 1998; Saulitis et al. 2000, Morin et al. 2010). Similar dietary specialization appears to apply to other populations of killer whales as well (Berzin and Vladimirov 1983; Pitman and Ensor 2003). Within the inshore waters of the Eastern North Pacific, members of the ‘resident’ ecotype feed only on fish, especially on Pacific salmon (*Oncorhynchus* spp.). ‘Transient’ killer whales, however, exclusively hunt warm-blooded marine mammals and birds. Their primary food source in the summer months is harbour seals (*Phoca vitulina* L., 1758, Ford et al. 1998), though transients also attack Steller (*Eumetopias jubatus* Schreber, 1776) and California (*Zalophus californianus* Lesson, 1828) sea lions, harbour porpoises (*Phocoena phocoena* L., 1758), Dall's porpoises (*Phocoenoides dalli* True, 1885), and Pacific white-sided dolphins (*Lagenorhynchus* *obliquidens* Gill, 1865). Transients also occasionally take minke (*Balaenoptera acutorostrata* Lacépède, 1804, Ford et al. 2005) and grey whales (*Eschrichtius robustus* Lilljeborg, 1861, Baldridge 1972; Goley and Straley 1994), as well as seabirds (Ford et al. 1998).

Typical body lengths of adult male killer whales exceed adult female body length by 20% and adult males weigh roughly 75% more than adult females (Clark and Odell 1999; Sato et al. 2006). The factors driving adult sexual dimorphism in killer whales are not understood, but two alternative hypotheses propose that male body size evolved under either sexual selection, or natural selection for greater diving capabilities. With a 75% greater body mass than adult females, adult male killer whales should have roughly a 15% longer aerobic dive limit, based on a mass$^{0.75}$ scaling of diving metabolic rate (Kleiber 1975). Despite pronounced sexual dimorphism, mammal-eating killer whales in the north-eastern Pacific are social predators that typically hunt in groups of mixed age and sex.

Killer whales have an extended period of maternal care. Offspring often travel with their mothers beyond the onset of sexual maturity around 15 years of age (Olesiuk et al. 1990). Dependent offspring typically travel in close associations with their mothers, possibly benefiting energetically from swimming in echelon formation (Noren 2008). In eastern North Pacific transients, social groups typically consist of one or more adult females and their offspring (Ellis et al. 2008). Adult males travel in long-term stable associations with an adult female (presumed to be their mothers) or roam between groups, and occasionally travel by themselves (Baird and Whitehead 2000). Hunting in these animals typically involves prey sharing and a high degree of coordination among all group members (Jefferson et al. 1991; Ford et al. 1998; Ford et al. 2005).

Since adult males and females with dependent offspring typically hunt in communal groups, group members face the challenge of reconciling their different physiological constraints dictated by their different body sizes into a common hunting strategy. This could be done in one of two ways: either the larger animals in the group could scale down their physiological performance to accommodate the lower physiological limits of smaller group members (physiological compromise), or the animals could take different roles in the foraging process to capitalize on a greater range of physiological capacities (division of labour). A strategy of physiological compromise suggests that all group members employ a common strategy geared to the limitations of the most constrained individual. A strategy of division of labour implies that the less constrained animals use their greater physiological capacities to maximise prey capture rates for the group, potentially exploiting a wider range of prey niches.

All marine mammals must dive underwater without breathing in order to forage. Performing energetic underwater movements without intake of oxygen represents a clear physiological challenge (Kooyman and Ponganis 1997; Acevedo-Gutiérrez et al. 2002). Many studies have focused on the ability of marine mammals to remain underwater without utilizing significant anaerobic metabolism (aerobic dive limit) as a critical factor in their diving behaviour (e.g. Weise and Costa 2007). However, the actual diving behaviour undertaken by a marine mammal should be influenced by physiological, ecological and social factors, with the ultimate goal of foraging being to consume and process sufficient prey to meet energetic requirements (Rosen et al. 2007). Consuming prey requires accessing the prey underwater, and is thereby constrained by the diving ability and budget of the predator, and critically by the location, behaviour, and detectability of prey in the water column.

One particularly strong ecological factor that influences depth use and behaviour in a wide range of marine species is the presence of light (Hays 2003). The presence or absence of light alters the sensory basis by which predators can detect prey. As a consequence, prey may be adapted to reduce their risk of being captured during daytime by shoaling (i.e. Ryer and Olla 1998; Brehmer et al. 2007) or moving to depths with less light (Stich and Lampert

1981). Vertical diel migrations of marine organisms are well documented, including for zooplankton (Hays 2003) and fishes (Bozzano et al. 2005). The diel diving patterns of many marine mammal species are thought to be shaped by the diel activities of their primary prey (i.e., crab-eater seals, *Lobodon carcinophagus* Hombron and Jacquinot, 1842, Burns et al. 2008, sperm whales, *Physeter macrocephalus* L., 1758, Aoki et al. 2007, long-finned pilot whales, *Globicephala melas* Traill, 1758, Baird et al. 2002). Several species eaten by mammal-eating killer whales in the eastern Pacific show pronounced diel variation in their activity patterns. Harbour seals off Alaska do most of their foraging during the hours of darkness (Frost et al. 2001; Hastings et al. 2004) and Steller sea lions are also reported to forage extensively at night (Thomas and Thorne 2001).

In addition to indications that their prey are more active during nighttime, the vast difference in sensory ecology of nighttime versus daytime may be particularly marked for mammal-eating killer whales. Marine mammal-eating killer whales echolocate much less than fish-eating killer whales, likely because most of their prey have good hearing in the frequency range of killer whale echolocation clicks (Barrett-Lennard et al 1996). Although the methods of prey detection of mammal-eating killer whales remain poorly understood, vision and passive acoustic detection are therefore thought to be the primary sensory modalities available to detect their prey, and this would be influenced by day-night differences in ambient light. Any changes in predation between day and night would have especially important ecological implications in high latitudes where daylight is limited throughout a large part the year.

To date, most of the limited research on the diving behaviour of free-ranging killer whales has been conducted on fish-eating populations. Baird et al. (2005) investigated the diving behaviour of 34 southern resident killer whales in the inshore waters of southern British Columbia, Canada and Washington State, USA. Diving rates did not vary significantly between social groups or between males and females of all age classes. However, adult males made deep dives significantly more frequently during the day than adult females. Both sexes swam significantly faster and dove significantly deeper during the day compared to nighttime, suggesting decreased levels of activity during the night. However, diving performance and behaviour could vary greatly between killer whale ecotypes given the differences in prey type. For mammal-eating killer whales, Baird (1994) presents a single dive record that also suggests reduced nighttime activity of the tagged individual. Erickson (1978) used VHF telemetry to track a pair of mammal-eating killer whales for 10 consecutive days in the inshore waters of British Columbia and Washington State and noted a decrease in dive duration in the afternoon and evening, which they interpreted as an increase in foraging activity during this time.

In this study, we analysed the diving behaviour of 13 mammal-eating killer whales recorded using Dtags containing high-resolution depth loggers (Johnson and Tyack 2003). We examined how diving behaviour was influenced by ecological and physiological factors by testing whether diving behaviour differed across body-size class and day-vs-night. To determine how changes in ambient light might have affected the diving behaviour of mammal-eating killer whales, we compared diving behaviour between daytime and nighttime for tagged individuals. Day-night differences would suggest a direct consequence of the difference in ambient light on the ability of marine-mammal eating killer whales to detect their prey, or an indirect consequence of changes in depth usage or behaviour of their prey. If foraging success depended primarily upon diving capabilities and the group members exhibited role specialization, then we would have expected each member of a foraging group to maximize its diving performance. In that case, adult males should have taken advantage of their greater oxygen stores by diving longer or spending more time at depth than adult females or juvenile animals. Thus, comparing the dive performance of different age and sex classes allowed us to evaluate how the diving and hunting behaviours of these social predators have evolved in light of different physiological capacities of group members. By analysing day-night differences and body-size factors together, we assessed whether they varied independently or interacted somehow. Body-size differences in diving behaviour should have been most apparent in the context of maximal diving effort, which was most likely limited by physiological constraints.

## METHODS

Groups of transient killer whales in the eastern North Pacific that belonged to the West Coast Transient population (Ellis et al. 2008) were studied in the inshore waters of Southeast Alaska in summer 2006 and 2007. We used digital archival tags (Dtags: Johnson and Tyack 2003) to record diving behaviour of individual animals. Upon encountering a group, all individuals were photographed from a skiff for identification using the method of Bigg (1982). Tags were deployed on animals using a 7m hand pole and attached non-invasively with suction cups. The tagged individual was re-photographed to confirm its identity. The tag samples pressure at 50 Hz, later down-sampled to 10Hz. Pressure data were converted to depth in meters using calibration constants derived in the laboratory. The tag also records sound using two hydrophones at 96 kHz and 3-axis magnetic and acceleration vectors at 50 Hz. After deployment, the tagged individual was tracked from an 18m fishing vessel using a VHF beacon and visual observations. Whales were followed at a distance of 1-2km to minimize potential influences of the vessel on their behaviour.

Each surfacing of each whale was identified using the depth record. Initially, this was done automatically based on a threshold of whale dive depth. All of the automatically-detected surfacings were carefully checked by eye and by listening to the acoustic record. Several corrections were necessary, likely because the minimum depth of the tag during a surfacing event depended on where the tag was placed on each whale's body and on how much of the tagged whale's body came out of the water when it surfaced. In a few cases, surfacing events could be clearly identified using the acoustic record even though the tag did not break the surface of the water. This was observed in the field when the whale surfaced without a VHF signal received from the tag. However, in those cases, the surfacing by the tagged whale was still audible as splashing and/or blow sounds heard in the tag recording.

The most common surfacing behaviour of killer whales is to surface and then dive again immediately, with one breath taken during the surfacing. Killer whales are occasionally observed to drift, or log, at the surface (Martinez 1978). We inspected this in the tag records as the duration between a surfacing and start of the subsequent dive. In our records, no interval exceeded 16s total, and 99.3% of the durations between the end of a dive and the start of a subsequent dive were <5s. Field observations indicated a whale would breathe once during such an interval. Because the whales in our tag records were not observed to log at the surface, respiration events of the whales were identified as surfacings (Fig. 1). The half-way point between the end of the previous dive and the start of the subsequent dive was considered the time of the respiration event. Although the exact time of the respiration may have varied slightly, it should be accurate to within ±2.5s.

Time of day, duration and maximum depth associated with all dives were tabulated. Visual inspection of the depth records indicated that whales often conducted numerous short and shallow dives that were occasionally followed by a longer, deeper dive. This suggests that diving is conducted in bouts, which can be separated either by duration or depth. To test the possibility that the diving behaviour could be broken into bouts to obtain dive bout criteria (Sibly et al. 1990), we conducted a log-frequency analysis of dive duration and maximum dive depth separately. Using these criteria, dives were separated into long and short dives for analyses of dive depth, and shallow and deep dives for analyses of dive duration.

To contrast the roles of physiological constraints and ecology on the diving behaviour of transient killer whales, we tested for differences both by age-sex class and day-night for three dive variables: dive rate for deep and shallow dives, dive duration for deep and shallow dives, and dive depth for long and short dives. Here, deep and long dives referred to dives deeper than and longer than the bout criterion interval, respectively. The effects of age-sex and time of day were assessed in separate analyses rather than a single 2-way model as 4 records did not include both day- and nighttime data. For the age-sex class comparison, we calculated the mean value for each individual and tested for differences using a non-parametric Kruskal-Wallis test. All recorded dives were classified as day or night dives using civil twilight (Seidelmann 1992) to define the start and end of nighttime. We computed differences in diving behaviour during day versus nighttime and tested the differences using paired *t*-tests.

We conducted three additional analyses to explore whether physiological limitations might have influenced diving and breathing performance. We expected that if physiological limitations primarily shaped the behaviour of these whales, large-bodied males should have had a lower overall breathing rate, the capacity to spend more time at greater dive depths, and required fewer breaths to prepare for, and recover from, a long-duration dive. First, for each whale, we tabulated the maximum dive depth, maximum dive duration, and the overall blow rate (equivalent to the dive rate since only one breath was taken per surfacing) of the tag record. Next, the proportion of time spent at depth was calculated for each whale. Finally, we analysed the effect of dive duration on the number of breaths taken before and after each long dive: we averaged the number of breaths before and after each long dive to consider both preparation and recovery aspects of diving limitations. We plotted duration of dives greater than the bout criterion interval against the number of breaths. Limitations in behaviour due to physiological constraints would be revealed by a lack of data points representing a small number of breaths before or after long duration dives, whereas there are no limits to more breaths being taken after any duration of dive. We used quantile regression to evaluate the slope of a line anchored at (0,0) above which 95% of the data would fit, with only 5% below the line. This slope was then compared across age-sex classes.

## RESULTS

A total of 12 tags were deployed on 11 transient killer whales, with a total recording time of 123 hours. Two other tag records of less than one hour duration were not included in the analysis. One individual killer whale, adult female T91, was tagged on two subsequent days. All of the dive data for that individual were pooled, leaving a total of 11 individual whales for analysis: 3 adult males, 4 adult females, and 4 juveniles, comprising a total of 7,608 dives. Data from 7 individuals (1 adult male, 2 adult females, and 4 juveniles) included more than one hour of nighttime data, and were used in the day-night comparison (Table 1).

Log-frequency analysis demonstrated that diving behaviour of transient killer whales was strongly characterized by bouts of dive duration and maximum depth (Fig 2). A two-process exponential model provided a significantly better fit for dive duration ($F_{2,45} = 74.3$, $P<0.001$) and maximum dive depth ($F_{2,45} = 14.2$, $P<0.001$) than a single-process exponential model (Sibly et al. 1990). Using the formula to minimize the number of events misclassified (Slater and Lester 1982), we calculated bout criteria of 57.77s (0.96 min) for dive duration and 12.73m for dive depth.

There were some clear differences between daytime and nighttime diving behaviour for the seven animals tagged both during the day and at night (Fig. 3). The rate of deep diving was higher during the daytime than during the night ($t_6 = 3.46$, $P = 0.014$), but the rate of shallow diving did not differ ($t_6 = 1.12$ , $P = 0.31$). The duration of deep dives did not differ significantly between day- and nighttime ($t_6 = -1.33$, $P = 0.23$), but shallow dive duration tended to be longer during the night ($t_6 = -2.80$ , $P = 0.031$). Dividing the dives by duration showed that depths of short duration dives did not differ for day versus night ($t_6 = 0.258$, $P = 0.81$), but that maximum dive depths of long duration dives were shallower during the night than during the day ($t_6 = 2.87$, $P = 0.029$). Blow rates differed only slightly, with a mean of 68.8 blows/hr during the daytime, and 62.9 blows/hr during the night, a non-significant difference ($t_6 = 1.43$, $P = 0.20$). Interestingly, the rate of occurrence of long duration dives was almost equivalent during the day (10.7/hr) and night (10.6/hr).

For the same parameters, none differed significantly among age and sex classes (Fig. 4). Juveniles did have a somewhat higher rate of deep diving than adult females and adult males, but that difference was not statistically significant ($H_2 = 2.96$, P = 0.23), nor were differences in the rate of shallow diving ($H_2 = 0.58$, $P = 0.75$). The only difference that had borderline statistical significance involved large males tending to dive deeper during the short dives between breaths ($H_2 = 5.60$, $P = 0.06$), a difference likely due to biomechanical factors (e.g., the greater height of the male dorsal fin).

Because deep dives were more common during the day, we retested the same parameters using only the daytime data recorded from all 11 individuals. Doing so did not result in any substantial changes in the observed age-sex patterns and no significant differences were found across age-sex classes using only the daytime dives.

Further testing of dive performance by age-sex class did not reveal any strong differences. Diving performance did not differ significantly by age-sex class for overall blow-rate ($H_2 = 0.60$, $P = 0.74$), duration of the single longest dive recorded ($H_2 = 1.69$, $P = 0.74$), or depth of deepest dive recorded ($H_2 = 1.30$, $P = 0.52$). The proportion of time spent at depth by each whale and the proportion of time spent below a given depth showed considerable variability from whale to whale (Fig. 5, left panel), likely shaped by the particular behavioural states which dominated during the tag deployment or individual variation. Inspection of cumulative depth use revealed no consistent differences in depth use by age-sex class (Fig. 5, right panel).

Finally, analysis of the number of blows following and preceding dives versus duration of dives which exceeded 57.77s (the bout criterion) did reveal a clear tendency for there to be few data points in the lower-right corner of the plot (Fig. 6). This pattern is consistent with whales needing to breathe more before or after a longer dive. However, there was no clear pattern of differences by age-sex class and no significant differences by age-sex class ($H_2$ = 0.39, $P$ = 0.82).

## DISCUSSION

Our results indicate consistent differences in diving behaviour of mammal-eating killer whales in the daytime versus the nighttime. Though our statistical analyses were limited to a sample of 7 whales, we found a consistent and statistically significant increase in the rate of deep (>12.74m) diving during the day compared to the nighttime (Fig. 3). While the duration of deep dives did not differ from day to night, the duration of shallow dives was significantly longer during the night than during the day. Consistently, long duration (>57.77s) dives were shallower during the night than during the day, while short-duration dives did not differ from day versus night. The rate of long-duration dives was almost equivalent during the day (10.7/hr) and night (10.6/hr).

Taken together, these results indicate a tendency for whales to dive deep less often and to make shallower long dives during the night than during the day. Blow rates were ~9%

lower overall during the night than the daytime, but we cannot conclude that mammal-eating killer whales were simply less active during the nighttime because that difference was not consistent across individuals in our sample and therefore not statistically significant. Instead, the differences in diving behaviour were likely also related to day-night differences in the diving behaviour of their prey and/or to differences in ambient light. High levels of downwelling light during the day could enable a strategy of foraging using visual cues at greater depths than would be possible during the night. More detailed information on the diving behaviour of killer whale prey and the sensory ecology of mammal-eating killer whales is needed to assess these possible explanations for day-night differences in the diving behaviour of mammal-eating killer whales.

In contrast to consistent day-night differences in diving behaviour, we found no clear differences between age-sex classes for overall blow rate, depth of the deepest recorded dive, or duration of the longest recorded dive. The rate and duration of deep and shallow dives and the depth of long and short dives did not differ across the 11 animals in our sample – even though these parameters did show day-night differences (Figs. 3 and 4). We also tested these parameters using only the daytime intervals, as day-night comparison indicated that deep dives were more common during the day than the night, but again no significant differences were found across age sex-classes. Further tests indicated no differences by age-sex class in depth use or the number of breaths taken before or after a long dive.

Because of the substantial differences in body size, we would predict differences in the aerobic dive limit capacity among juvenile, adult female, and adult male killer whales. Though the aerobic dive limit has not been experimentally measured in killer whales, we can calculate an estimated aerobic dive limit (cADL) by scaling up measurements taken from other cetaceans for which the ADL has been measured (see Watwood et al. 2006, Tyack et al. 2008). The lean mass (M) specific basal metabolic rate of mammals scales as $M^{-0.25}$ (Kleiber

1975), while oxygen stores scale in a linear fashion. Consequently, larger animals can dive longer aerobically than smaller animals (Castellini et al. 1992). Assuming diving metabolic rate scales with lean body mass in a manner similar to the basal metabolic rate, and that killer whales contain similar mass-specific oxygen stores as bottlenose dolphins (Noren et al. 2002), the cADL of killer whales can be estimated from the 5.4 minute aerobic dive limit of a 187 kg bottlenose dolphin (Noren et al. 2002). With this approach ($cADL_{killer}=ADL_{bottlenose}*(M_{killer}/M_{bottlenose})^{-0.25}$), we estimate that killer whale cADLs should range from 10.2 and 11.8 min for mean mass estimates of 2418kg for captive adult females and 4249 kg for captive adult males, respectively (Clark et al. 2000; Sato et al. 2006). The body mass of the tagged juveniles can be estimated using age-mass regression curves derived from captive juveniles (Clark et al. 2000). The exact birth date of free-ranging killer whales is not known, but the birth year is known (Ellis et al. 2008; Table 1). Assuming the birth date of a calf is ½ year before the summer it was first sighted, we can calculate the mass of 1, 2, and 8 year juveniles to be 673kg, 865kg, and 2008kg, respectively. These mass estimates correspond to cADLs of 7.4, 7.9, and 9.8 min, which is probably an over-estimate of cADL as 0-2 year old bottlenose dolphins have been shown to have substantially lower oxygen stores than adults (Noren et al. 2002).

Using these estimates for cADL, no dives of adult males (N = 1256 dives) or adult females (N = 3004 dives) exceeded their cADL. From a total of 3348 dives from the 4 tagged juvenile animals, 23 exceeded their cADL. These dives represented 0.3%, 0.1%, and 2.7% of all dives made by 1-2 yr old juveniles T073A1, T002C2, and T068B2, respectively. The 8-year old juvenile T124E did not conduct any dives longer than its cADL of 9.8 min. This suggests that the dives of adult killer whales were almost entirely aerobic, and their foraging behaviour did not substantially challenge their aerobic capacity. Interestingly, the youngest juveniles made some dives that exceeded their cADL. Although dives exceeding cADL were only a small proportion of the total dives, they represent 1.6%, 0.8%, and 15.2% of the long-duration dives defined using the bout criterion interval of 57.77s. Juveniles also had a non-significant tendency to breathe more (i.e., higher dive rate) and make shorter duration dives for both deep and shallow dives (Fig. 4). These observations indicate that smaller animals in killer whale groups are more aerobically challenged than larger animals.

Our results argue against a pronounced division of labour among body-size classes while diving to search for and attack prey, which would predict males to dive longer and deeper and breathe less often than female or juvenile killer whales. Instead, the behaviour indicates a strategy of physiological compromise with individuals of different age-sex classes diving similarly. This strategy pushes the smaller animals closer to their aerobic dive limits and in the case of young juveniles sometimes even beyond it, while leaving adult males with the largest unutilized aerobic diving capacity.

Physiological limitations influence the behaviour of both predators and prey in an encounter (Ydenberg and Dill 1986). A solid understanding of the physiology of both players is therefore crucial when examining these dynamics. In predator-prey interactions involving breathhold divers that forage in the water column, the ability of both the predator and the prey to remain submerged and dive to depth typically exerts one of the primary physiological constraints that impact foraging decisions (e.g., Frid et al. 2007). The large body size of the killer whale may enable them to exceed the aerobic diving capacities of their prey. An important characteristic of mammal-eating killer whales is that their prey types are constrained to come to the surface to obtain oxygen. This may enable mammal-eating killer whales to remain close to the surface, waiting for their prey to return. Such a strategy might reduce the need for extended dives beyond aerobic capacities. Coordinated foraging by the group may allow individuals to take turns diving to prevent marine mammal prey from coming to the surface (Jefferson et al. 1991), which would reduce the need for individuals to exceed their aerobic capacities. Thus, our conclusion that physiological factors do not appear to influence the diving patterns of mammal-eating killer whales may reflect the fact that their ecology does not put heavy demands on aerobic diving capability.

We should stress that our results should not be extrapolated to killer whales feeding on other prey types. For example, specialized diving roles that take advantage of the greater aerobic capacity of males may be advantageous for killer whale that feed on deep-sea squid or deeper diving mammals such as sperm whales (Pitman et al. 2001) or ziphiids (Notobartolo-di-Sciara 1987). For deep-diving prey, one avenue of escape may be to dive away from the killer whale predator. In such a case, the greater aerobic capacity of the adult male may allow it to pursue such prey more effectively than smaller bodied females or juvenile animals. Observations of mammal-eating killer whales foraging on diverse prey types will help to unravel more fully how ecological factors influence role specialization and coordination of feeding in sexually-dimorphic predators.

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Table 1. Details of whales tagged with Dtags for this study. Whale ID and date of birth information is based on Ellis et al. 2008. An '*' in the Hrs tagged column indicates 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/<br>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 |

FIGURE LEGENDS:

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

Figure 2. Log-frequency analysis of dives by duration (top) and depth (bottom). The arrow indicates the bout criteria interval used in this study to split dives into long vs short dives (top) and deep vs shallow dives (bottom).

Figure 3. Diving behaviour of individual transient killer whales during day- and nighttime. Each whale is given a symbol to identify its age-sex class. There were consistent and statistically-significant day-night differences (indicated within each panel) in: the rate of deep diving, the duration of shallow dives, and the depth of long dives.

Figure 4. Diving behaviour of transient killer whales divided by age-sex class. AM – adult male, AF – adult female, J - juvenile. Boxes show median with upper and lower quartile values. Errorbars show the total extent of the data. None of the parameters differed significantly.

Fig. 5. Left: proportion of time spent at depth for each of the 11 tagged whales separated by age-sex class (coloured lines). Right: cumulative proportion of time spent below a given depth separated by age-sex class. Overall, the whales spent 50% of their time 8m or shallower, and 90% of their time 40m or shallower. There was no consistent difference in

depth use by age-sex class with the possible trend that males had more variable depth use than females or juveniles.

Fig. 6. Duration of each long dive (>57.77s) versus the averaged number of blows before and after each dive for a representative example from each age-sex class. The green line shows the slope of the 5% quantile regression fits, which did not differ significantly across age-sex class.

Figure 1

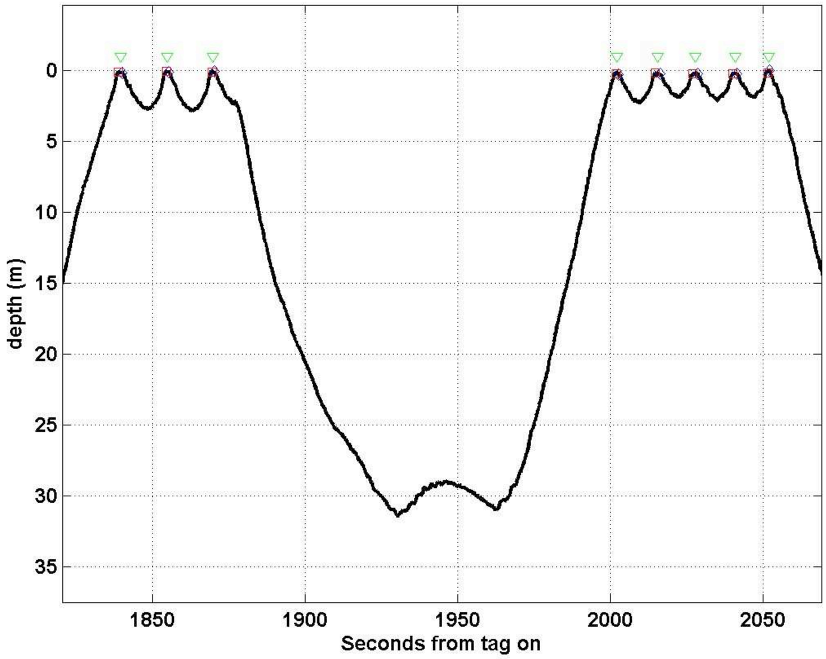

0
5
10
15
20
25
30
35
depth (m)
1850
1900
1950
2000
2050
Seconds from tag on

Figure 2

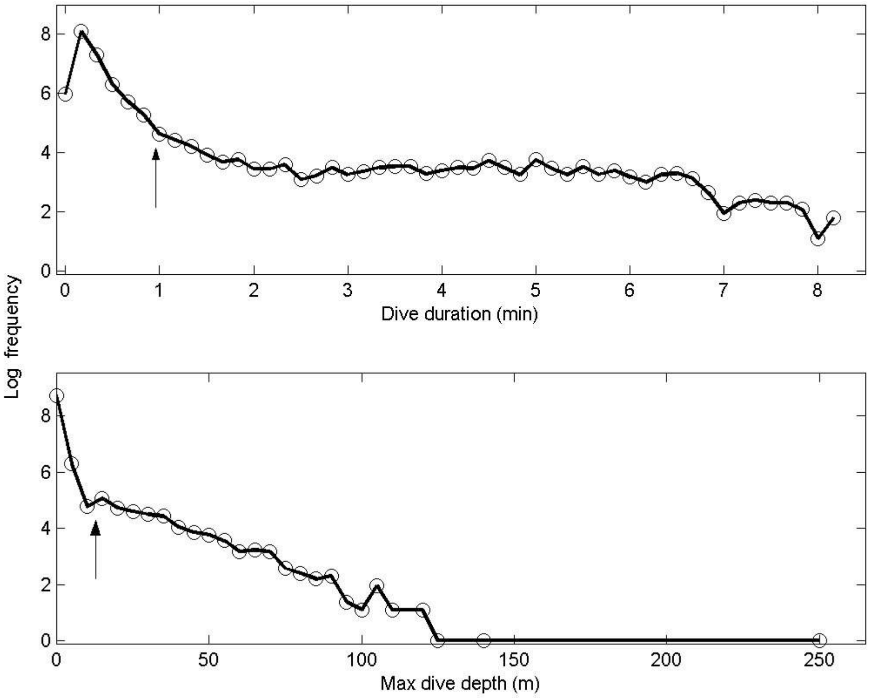

Log frequency
8
6
4
2
0
0
1
2
3
4
5
6
7
8
Dive duration (min)
8
6
4
2
0
0
50
100
150
200
250
Max dive depth (m)

Figure 3

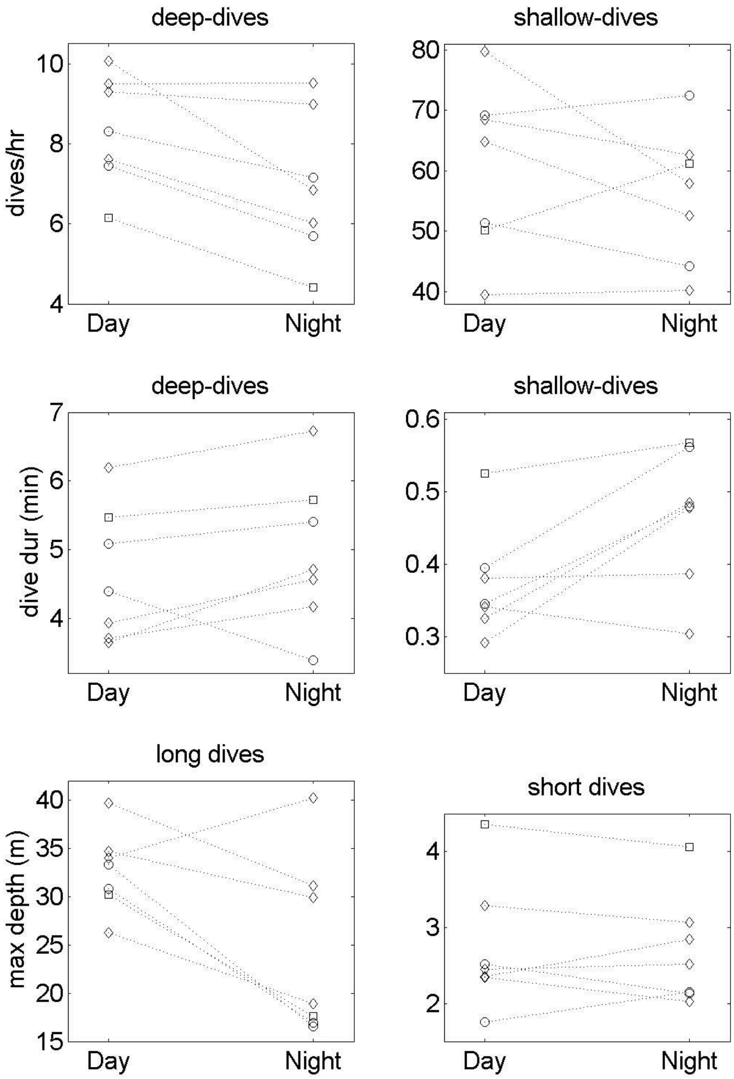

deep-dives
dives/hr
10
8
6
4
Day
Night
shallow-dives
80
70
60
50
40
Day
Night
deep-dives
dive dur (min)
7
6
5
4
Day
Night
shallow-dives
0.6
0.5
0.4
0.3
Day
Night
long dives
max depth (m)
40
35
30
25
20
15
Day
Night
short dives
4
3
2
Day
Night

Figure 4

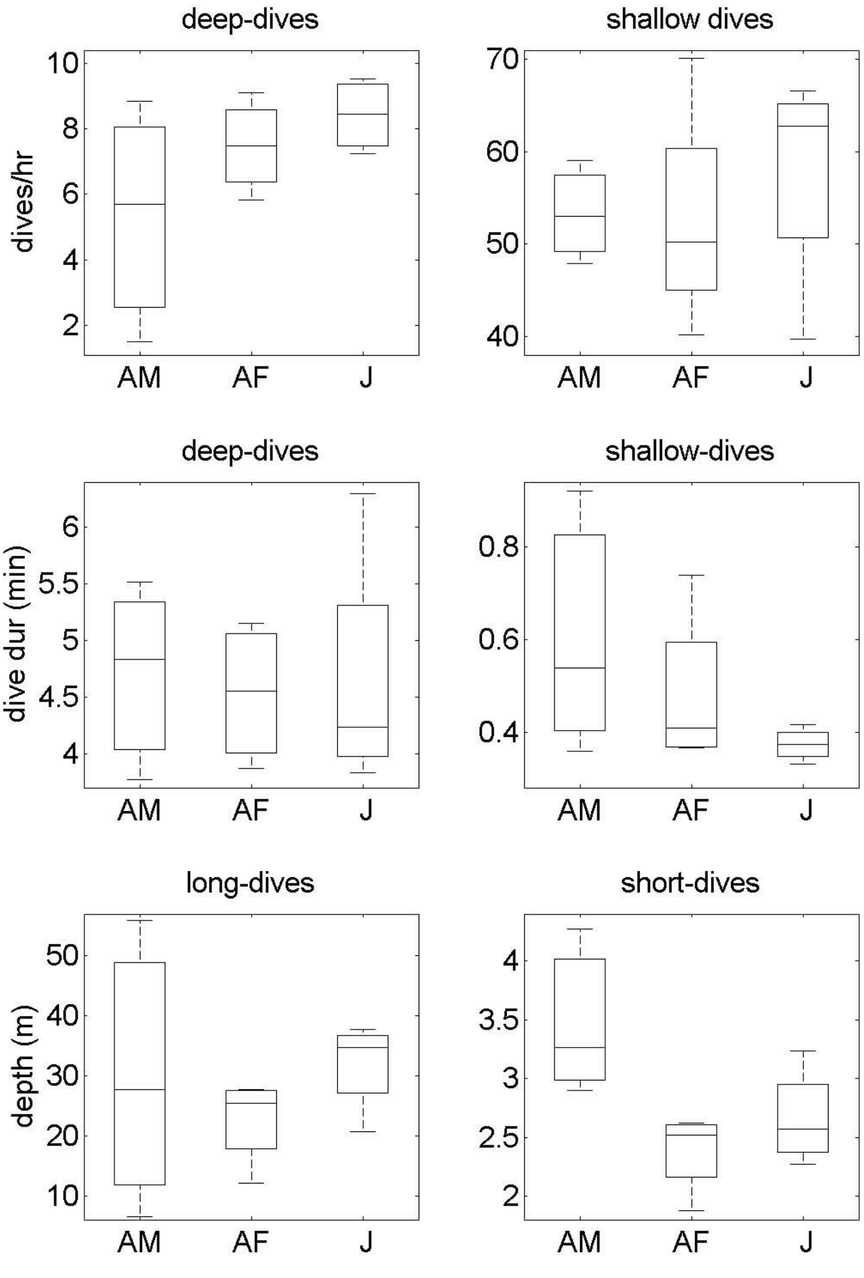

deep-dives
dives/hr
10
8
6
4
2
AM
AF
J
shallow dives
70
60
50
40
AM
AF
J
deep-dives
dive dur (min)
6
5.5
5
4.5
4
AM
AF
J
shallow-dives
0.8
0.6
0.4
AM
AF
J
long-dives
depth (m)
50
40
30
20
10
AM
AF
J
short-dives
4
3.5
3
2.5
2
AM
AF
J

Figure 5

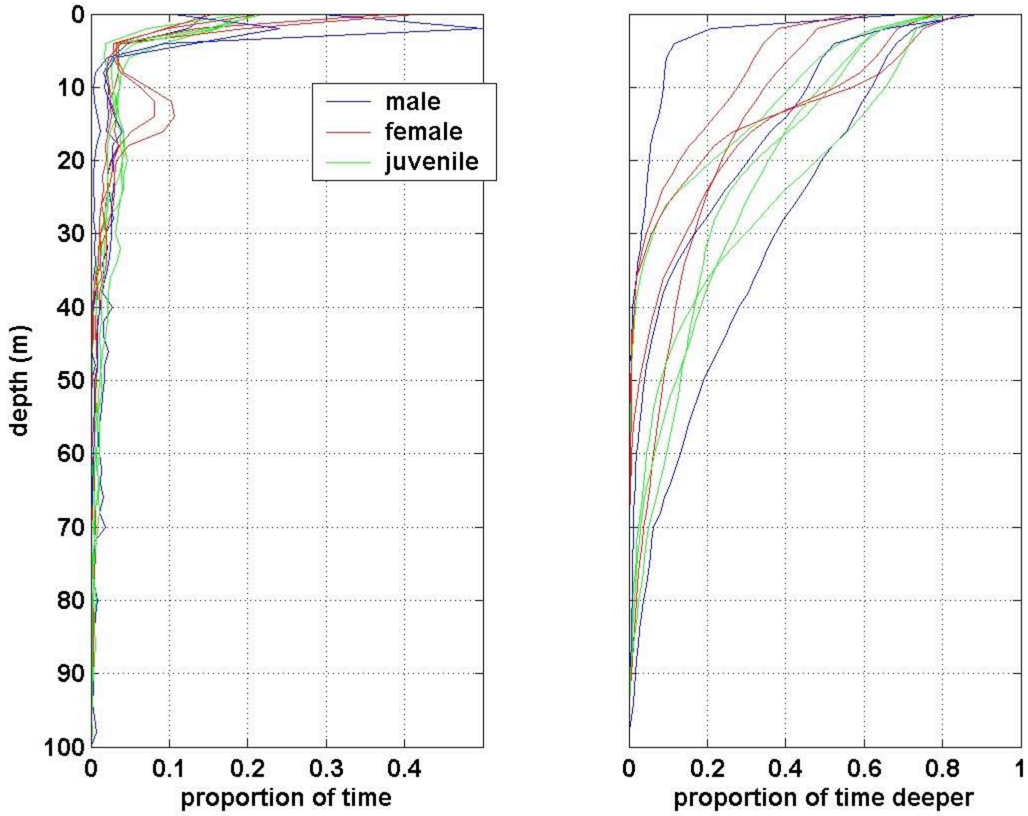
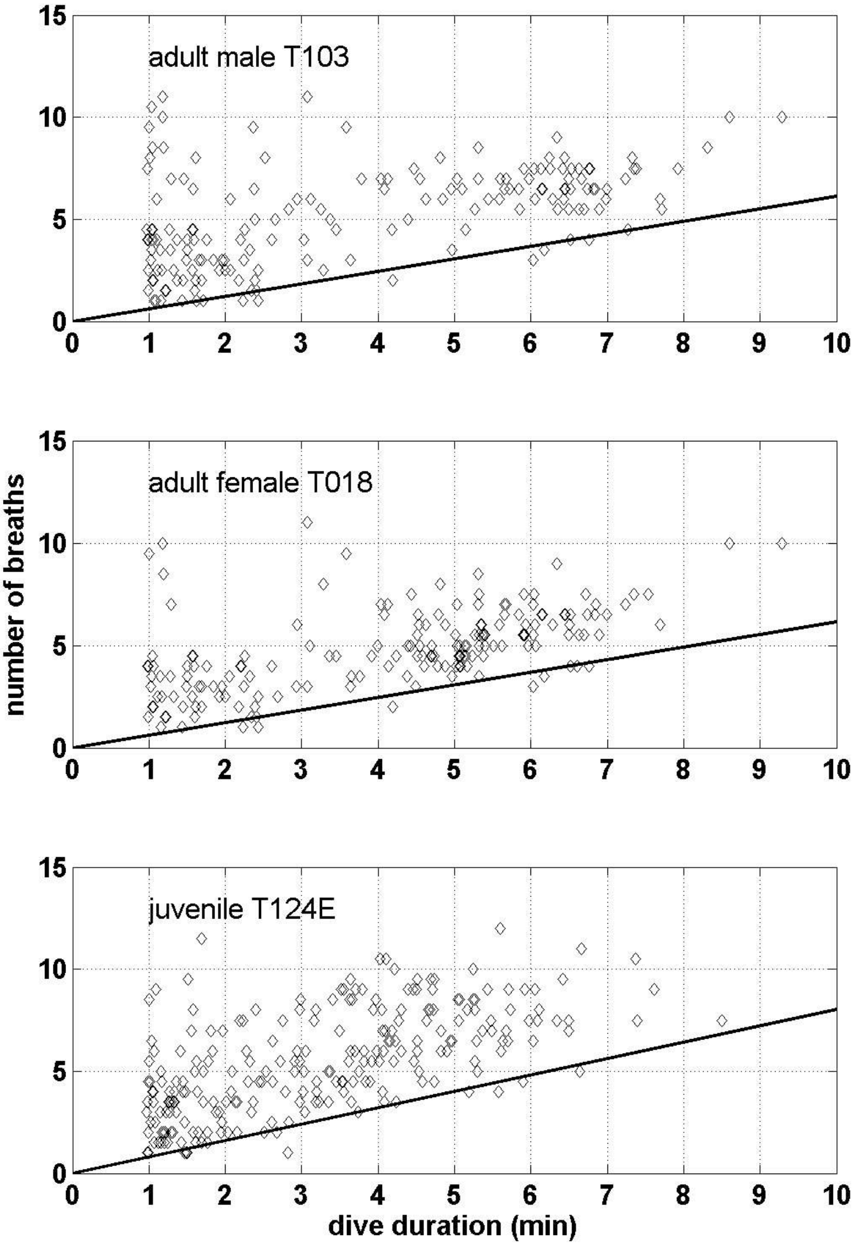

male
female
juvenile
depth (m)
0
10
20
30
40
50
60
70
80
90
100
0
0.1
0.2
0.3
0.4
proportion of time
0
0.2
0.4
0.6
0.8
1
proportion of time deeper

Figure 6


adult male T103
adult female T018
juvenile T124E
number of breaths
dive duration (min)
0
5
10
15
0
1
2
3
4
5
6
7
8
9
10