# Developmental changes in the resting strategies of killer whale mothers and their calves in managed care from birth to 36 months

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## Abstract

The development of cetacean sleep has not been explored fully. Questions such as whether cetacean mothers regulate their offspring's resting behaviour and do resting behaviours change over the course of cetacean development remain unanswered. To address these questions, an investigation of the resting strategies and activity levels for four killer whale (*Orcinus orca*) calves and their mothers in managed care during free-swim conditions was conducted during the first three years of life. A series of interrelated hypotheses were assessed using three independent sets of archived data (24 h behaviour records, video recordings, and instantaneous sampling) collected from two facilities. Together, the results indicated that mothers adjusted their activity levels based on their calves' current level of development. Floating, often a preferred resting behaviour, was rarely observed during the first post-parturition month for any of the mother–calf pairs. Rather, the mother–calf pairs tended to display fast-moving mother–calf swims with frequent trajectory changes as the calf gained swimming proficiency. Although floating occurred more frequently over time for all pairs, all four killer whale mother–calf pairs displayed a preference for a slower-paced pattern swim (i.e., swim-rest). Calves preferred to rest with their mothers over resting with others or independently. The similarities in resting strategies displayed by the killer whale mother–calf pairs housed in independent facilities without temporal overlap emphasizes the conserved nature and development of these strategies in a precocial cetacean species with extended maternal care.

## 1. Introduction

### 1.1. *Characteristics and development of mother–calf resting strategies*

Early studies of cetaceans, including mother–calf pairs, found that cetaceans in both human care and their natural habitat display several forms of resting behaviours, including quiescent hanging either at the bottom, in middle of the water column, or at the surface (also called floating or logging) and slow, pattern swimming (i.e., swim-rest) (McBride & Kritzler, 1951; McCormick, 1969; Flanigan, 1974; Mukhametov, 1984; Norris et al., 1994; Goley, 1999; Gnone et al., 2001, 2006; Ford, 2002; Ridgway, 2002; Sekiguchi & Kohshima, 2003; Lyamin et al., 2005; Sekiguchi et al., 2006). Some studies used the different forms of stationary floating or periods of immobility as the primary indicator of rest (e.g., McBride & Krtizler, 1951; Norris et al., 1994; Ford, 2002; Sekiguchi & Kohshima, 2003; Lyamin et al., 2005, 2007). Other studies, examining resting behaviours by adult bottlenose dolphins (*Tursiops* sp.) and dolphin mother–calf pairs, highlighted the necessity to include slow, pattern swims (i.e., swim-rest) as an alternative means by which dolphins may rest (Goley, 1999; Sekiguchi & Kohshima, 2003; Gnone et al., 2006; Hill et al., 2008; Sekiguchi et al., 2006). Both major categories of rest behaviour exhibited by odontocetes have been corroborated with electrophysiological evidence for unihemispheric slow-wave sleep (USWS, reviewed by Lyamin et al., 2008).

Although precocial at birth, cetacean calves are biologically constrained by their size, body composition, thermoregulation mechanisms, and immature muscle development (Noren et al., 2006; reviewed by Lyamin et al., 2008). These constraints likely influence the swim speeds and activities of mother–calf pairs by inhibiting the ability of neonates to float alongside their mothers frequently and for long periods. For example, on the rare occasions when bottlenose dolphin and killer whale (*Orcinus orca*) mothers were observed floating shortly after parturition, neonates and very young calves (1–2 months) displayed continuous active movements around their stationary mothers (McBride & Kritzler, 1951; Lyamin et al., 2007). The tendency for adults to move continuously is correlated with the presence of calves, particularly young calves (Lyamin et al., 2005, 2007; Hill et al.,

2008). When all forms of resting behaviour are considered, the nature of continuous swims of mothers and their neonates shift from fast-moving swims with changing trajectories to slower, pattern swims within several days of birth (a single bottlenose dolphin mother–calf pair, Gnone et al., 2006) and through the first month, post-parturition (Sekiguchi et al., 2006; Hill et al., 2008). These behavioural changes in swim patterns have been observed across several groups of bottlenose dolphins in managed care (Sekiguchi & Kohshima, 2003; Gnone et al., 2006; Sekiguchi et al., 2006; Hill et al., 2008). Parental investment theory proposes that caregiving strategies, facilitating offspring survival, will be selected based on the offspring needs and resources available to the caregivers (Trivers, 1974). For example, most terrestrial mammalian offspring need to sleep more than adults because without sufficient rest or sleep, physical and cognitive development is negatively affected (Siegel, 2005). For aquatic mammals, the ability to select a swim pattern that accommodates the current physical limitations of a calf (e.g., precocial species with poor motor control and limited blubber for thermoregulation) would promote offspring survival and reflect parental investment. Parental investment theory would predict that marine mammal mothers may have different resting strategies based on their calf's age and developmental state, such that resting strategies are based on mother–calf swim patterns early in development while floating-based strategies emerge later.

To date, these predictions have only been assessed with a small number of bottlenose dolphin mother–calf pairs in managed care for differing lengths of time during the first year of life (Lyamin et al., 2005, Gnone et al., 2006; Sekiguchi et al., 2006; Lyamin et al., 2007; Hill et al., 2008). Even less research exists on the resting behaviours of killer whale calves and their mothers. The results of one study, conducted in a controlled environment, indicated that two killer whale mothers swam continuously with a fast-paced activity level with their calves immediately after birth up through one month (Lyamin et al., 2005). However, several researchers noted that this study did not measure the continuously moving, slow pattern swim strategy as an alternative resting option (Gnone et al., 2006; Sekiguchi et al., 2006; Hill et al., 2008). Given that killer whales are delphinids and show similar maternal care as smaller delphinids like bottlenose dolphins (Asper et al., 1988; Baird, 2000), it seems likely that killer whales should also utilize this resting strategy.

## 1.2. *Role of the mother in the calf's developmental changes*

As precocial calves that are highly dependent on maternal care for extended periods of time (i.e., 2–5 years, depending on the species), much of the first year of life for many odontocetes is governed by the mother. Overall, odontocete mothers display similar offspring care patterns despite differences between individual mothers in the degree to which they exhibit specific maternal care behaviours, such as retrievals, pair swims, discipline and separations (Mann & Smuts, 1998; Krasnova et al., 2006, 2009; Hill et al., 2007, 2013; Hill, 2009). Most of the first year of life for cetacean calves is characterized by frequent and synchronized pair swims with their mothers (belugas, *Delphinapterus leucas*: Krasnova et al., 2006, 2009; Hill, 2009; Hill et al., 2013; dolphins: McBride & Kritzler, 1951; Cockcroft & Ross, 1990; Reid et al., 1995; Gubbins et al., 1999; Mann & Smuts, 1999; Hill et al., 2007; killer whales: Asper et al., 1988; Baird, 2000; Olesiuk et al., 2005; Guarino et al., 2016). Maintenance of proximity between mothers and calves is regulated initially by the mother during the first six months of life after which the calves become responsible (Asper et al., 1988; Mann & Smuts, 1999; Hill et al., 2007). Corresponding to these developmental changes in proximity maintenance, calves increasingly engage in independent activities and social interactions with similar-aged peers and adults other than their mothers as they mature (Mann & Smuts, 1999; Baird, 2000; Hill et al., 2007; Greene et al., 2011; Guarino et al., 2016). Finally, of the available studies investigating odontocete mother–calf behaviour beyond the first year of life, mother–calf pair swims and synchronized behaviours decrease as the calf matures (Baird, 2000; Miles & Herzing, 2003; Gibson & Mann, 2008; Hill & Campbell, 2014).

## 1.3. *Purpose of the study*

The primary purpose of the present study was to investigate the resting strategies exhibited by killer whale mothers upon parturition through three years of life. Utilizing three sets of archived data collected from two different facilities with different procedures (i.e., 24-h instantaneous point sampling from archived records, intermittent continuous video recordings, and instantaneous point sampling from real-time observations), a number of developmentally-oriented hypotheses regarding swim behaviour at various levels of activity (e.g., slow, moderate, fast) were examined for four unique

killer whale mother–calf pairs from birth through three years of age. The different data sets allowed us to address hypotheses regarding pregnant killer whale activity levels and resting behaviours across a 24-h period one month pre-parturition and up to three months post-parturition, questions regarding mother–calf swim activities and partner preferences, and finally similarities across mothers housed at two different facilities (Table 1).

## 1.4. Hypotheses

While individual cetaceans show variations in resting preferences (e.g., slow, pattern swim versus floating; Sekiguchi & Kohshima, 2003; Lyamin et al., 2005; Gnone et al., 2006; Sekiguchi et al., 2006; Hill et al., 2008), few studies have measured the pre-parturition resting behaviour of pregnant odontocetes. Noren et al. (2006) reported slower swim speeds and less efficiency in pregnant bottlenose dolphins while Hill et al. (2008) found that five bottlenose dolphins engaged in significantly higher levels of floating pre-parturition compared to their individual activity levels and behaviours post-parturition. Based on these findings and the resting patterns reported by Lyamin et al. (2005) in killer whales, we expected (a) stationary floating to be exhibited more often as a resting strategy than other forms of rest (i.e., swim-rest) pre-parturition than post-parturition. Given that the females were expected to significantly reduce their resting behaviour, as measured by stationary floating, following parturition, we expected (b) a reciprocal increase in time spent in active, alert swims with frequent swim trajectory changes through the first month post-parturition (Lyamin et al., 2005, 2007; Gnone et al., 2006; Sekiguchi et al., 2006; Hill et al., 2008). For a bottlenose dolphin mother–calf pair measured continuously over time, slow, pattern swims emerged two days after birth and continued to increase until it stabilized, comprising almost 50% of the night-time observations and almost none of the day-time observations by the end of the first year of life (Gnone et al., 2006). A similar pattern emerged in a group of five bottlenose dolphin pairs within the first four weeks post-parturition (Hill et al., 2008). Based on these observations, we expected (c) killer whale mothers to exhibit different resting strategies by modifying their swims and speeds over the first month of life (i.e., weeks) based on the developmental state of their calf (Gnone et al., 2006; Hill et al., 2008; Noren et al., 2011) and that (d) more resting behaviour should be observed during night hours than during day hours.

These developmental trends were predicted to continue beyond the first month of life and through the first few years. Thus, (e) mothers were ex-

**Table 1.**
Summary of hypotheses and data sets utilized.

|  |  | Facility A | Facility B |
|---|---|---|---|
| Subjects | Studied companions | 1 mother–calf pair | 3 mother–calf pairs |
|  |  | 3 adult males, 1 adult female | Up to 2 adult females, 1 adult male, 1 juvenile male |
| Behavioural observations | Observation period | 1 month pre- to 2 months post-parturition (24 h/day) | 1–36 months post-parturition* (0700–1100) |
|  | Sampling method | Instantaneous sampling at beginning of record | 1-min sample point |
|  | Behaviours recorded | Activity level swims (see Table 2) | Activity level swims (see Table 2) |
|  | Related hypotheses | a) More frequent floating pre- vs. post-parturition | c) Decrease in mother floating and increase in active swim 1-month post-parturition |
|  |  | b) More frequent floating during nighttime vs. daytime | d) Calf developmental changes in active swim |
|  |  |  | e) Increase in mother–calf slow pattern swim |
|  |  |  | f) Maturational increase in calf floating |
|  |  |  | g) Occurrence of calf independent swims at higher vs. lower levels |
|  |  |  | h) More mother–calf vs. other-calf or independent calf resting |
| 24-h video recordings – daytime hours | Observation period | 1 month post-parturition (24 h/day) | N/A |
|  | Sampling method | Instantaneous sampling at beginning of 5-min segments, randomly selected from 3-h blocks | N/A |
|  | Behaviours recorded | Activity level and swims (see Table 2) | N/A |
|  | Related hypotheses | a) More frequent floating pre- vs. post-parturition |  |

**Table 1.**
(Continued.)

|  |  | Facility A | Facility B |
| --- | --- | --- | --- |
| Daytime video recordings | Observation period | 6–36 months post-parturition (0700–1900) at 6-month intervals | N/A |
|  | Sampling method | 5–15 min continuous recording | N/A |
|  | Behaviours recorded | Activity level of mother–calf, independent calf, and other–calf swims | N/A |
|  | Related hypotheses | c) Decrease in mother floating, and increase in active swim 1 month post-parturition | |
|  |  | d) Calf developmental changes in active swim | |
|  |  | e) Increase in mother–calf slow pattern swim | |
|  |  | f) Maturational increase in calf floating | |
|  |  | g) Occurrence of calf independent swims at higher vs. lower levels | |
|  |  | h) More mother–calf vs. other-calf or independent calf resting | N/A |

* Data were collected up to 75 months post-parturition at Facility B, but only 1 to 36 months post-parturition data were analyzed to match the video recorded data from Facility A.

pected to continue to display slow, pattern swims as their primary resting strategy as their calves aged although (f) floating by both mothers and calves would likely increase as the calves matured, if not to pre-parturition levels (Lyamin et al., 2005; Gnone et al., 2006; Sekiguchi et al., 2006; Hill et al., 2008). Finally, we predicted that (g) despite an increase in independence by the maturing calves, calves would engage in resting behaviours more often with their mothers than when alone or with other conspecifics (Cockcroft & Ross, 1990; Mann & Smuts, 1999; Hill et al., 2007; Gibson & Mann, 2008; Guarino et al., 2016).

## 2. Methods

### 2.1. Subjects

A total of four killer whale mother–calf pairs were examined for this study. One killer whale mother–calf pair was located at a facility in the southern United States (Facility A). The calf was born in January 2010 to her 19-year-old mother. They were housed with up to four other unrelated adult killer whales, three males and one female. Based on the daily training plan, different social groupings were created after the calf was one month old. The adult female was integrated with the mother–calf pair at three weeks post-parturition. Three additional mother–calf pairs were housed at a facility located in Canada (Facility B). Calf 1 was born in 1998 and monitored for more than 75 months with access to an adult male killer whale and an unrelated adult female killer whale. Calf 2 was born to the same mother in 2004 and housed with one to three killer whales depending on social groupings. This calf was monitored for up to 18 months. Calf 3 was born in 1999 to a different mother and was monitored from 2 months until 32 months. This mother–calf pair shared the facility with the adult male and killer whale mother–calf pair 1. All adults were wild-born.

### 2.2. Measures

The data gathered at Facility B were collected independently and prior to the data collected at Facility A. Both facilities independently developed and utilized two different coding schemes to record the overall level of activity (i.e., swim speed, SS, SS1–SS4; Table 2) for the following types of swims: (1) mother–calf swims in which the mother and her offspring move synchronously and/or in a coordinated direction within one-two adult body lengths of each other, (2) calf swim with other in which the calf moves synchronously and/or in a coordinated direction with a conspecific) and (3) independent calf swims in which calf moves in its own trajectory regardless of other animals. As summarized in Table 2, the coding scheme used to code the data for the current study for Facility A initially utilized five categories of activity level (Speeds 1–4) dependent upon speed of the activity and pattern of swimming. The coding scheme at Facility B also utilized five categories of activity level that were based upon speed and activities of the animals (Speeds 0–4; Table 2).

**Table 2.**
Operational definitions of activity levels.

| Activity level* | Facility A | Activity level | Facility B |
|---|---|---|---|
| SS1 | Floating at the surface or at the bottom of the pool remaining still with no orienting behaviours. | 0 | Stationary position, floating at the surface, within the water column, including the bottom of the pool (0–2 km/h; 0–1 mph). |
| SS2 | Slow, pattern swim with no directional changes and possible repetitive behaviour, such as switching from dorsal to ventral swim in the same area of the pool. | 1 | Drifting or very slow forward movement (2–5 km/h; 1–3 mph). |
| SS2.5 | Moderate, alert swim with possible directional changes and dorsal to ventral rotations, but no social interaction involved. | | |
| SS3 | Active swim involving directional changes, social interaction and play behaviours. | 2 | Normal swim movements with forward progression (6–10 km/h; 4–6 mph). |
| SS4 | High intensity swim involving chasing other animals and aerial behaviours, such as jumps and bows. | 3–4 | Faster, high intensity swims and motor movements in which white water and substantial wave action was observed (11+ km/h; 7+ mph). |

* Activity level = swim speed (SS). The coding scheme used at Facility A differentiated the type of swims based on speed and behaviours. The pace of the swim increased from levels SS1 to SS4; only SS1 and SS2 are used as indicators of resting behaviours. SS3 and SS4 categories were combined for analysis purposes. The coding scheme used at Facility B differentiated activity level using speed designation that were identified by observable changes in body position, revolutions around the pool, and water action. Speed designations are estimates based on calculations made by Dr. F. Fish for Facility A.

## 2.3. Data sets and procedure

### 2.3.1. Archived 24 h behavioural observations.
Thirty-min continuous behavioural observations were conducted by the training personnel of Facility A almost every hour for 24 h from one month

pre-parturition to three months post-parturition. As the calf aged, the continuous behavioural observations were not collected every hour and the 24-h per day sampling decreased to more limited sampling (e.g., one every other hour or every couple of hours, producing some days with less than 24 continuous behavioural observations). Trainers recorded a number of behavioural events that were dependent upon the female's parturition state, including swim speed, respirations, feeding, social interactions, vocalizations, and nursing.

We used a randomly selected sub-set of data for the final analyses, which included 120 behavioural observation records (of 660) collected the month before parturition and 120 behavioural observation records per month (of 1000) collected post-parturition (Table 1). After these records were selected, the variables of interest (i.e., type of swim and activity level) were coded using instantaneous sampling per hour of observation. Some 24-h observation periods produced 24 behavioural observation records, which were instantaneously sampled based on the beginning of the record at each hour (i.e., 24 instantaneous sample points for the 24-h period). Other 24-h observation periods accumulated only seven behavioural observation records, which when instantaneously sampled, produced seven instantaneous sample points in the 24-h period. We analysed the data from one month pre-parturition to two months post-parturition. Most of the analyses utilized the data from one month pre- and post-parturition. A time-of-day comparison (day: 0700–1900 versus night: 2000–0600) was possible for this time frame. We utilized the second month of post-parturition data for a week-by-week developmental analysis.

Activity level was initially determined by interpreting the training records that utilized the standardized coding scheme developed by Facility A. These activity levels were transformed into the coding scheme used for this study (Table 2) with the assistance of written comments. The frequency of each activity level swim category was recorded and then aggregated over predetermined periods of time (e.g., day, week, month) to produce percentages, the summed frequencies for the total number of swims in each activity level category were divided by the total number of swim events.

### 2.3.2. Daytime video recordings

Beginning with the birth of the calf at Facility A, more than 500 independent video recordings (4000+ min) were collected in conjunction with the behavioural records. Video recordings were collected at six-month intervals for a 30-day period from 1 to 36 months, post-parturition (Table 1). Data

collected during the first month of life were recorded continuously 24-h per day. These 24 h video recordings were recorded by an overhead camera that was operated by Facility A personnel. To facilitate the coding of these data, the 24-h day was divided into three-hour blocks, and one hour within these blocks was randomly selected for coding (e.g., 0600–0900 was the block and 0700 was the hour randomly selected). The selected hour was then sampled for a 5-min segment. The behaviours exhibited by the mother–calf pair at the beginning of the 5-min segment was coded for this study using instantaneous point sampling.

For the remaining 6-month intervals, during the 30-day recording period, observations were collected three to seven days per week, and within an observation day, two to six video recordings were made for 5–15 min each during the daytime hours (0700–1900). Observations were conducted at times when human influence was minimized so that less than 5% of the observations were made with humans present (trainers or guests) and were subject to weather and schedules.

A different number of available video recordings for each month: Month 1, a total of 174 video recordings with 144 collected during the day; Month 6, 53 video recordings; Month 12, 36 observations; Month 18, 57 video recordings; Month 24, 38 observations; Month 30, 130 observations; and Month 36, 33 video recordings. For the current study, 30 recordings were randomly selected for each six-month interval to control for the different number of video recordings available at each month. These 30 recordings comprise the sample for the study.

Each video recording collected at Facility A was coded for the type of swim (mother–calf swims, calf swim with other animal, and independent calf swims), its frequency, its duration, the activity level, and the duration of the swim at each activity level. If activity level changed in the course of a swim, the time spent at that new level was recorded. The frequencies and durations of individual swim events were aggregated across each activity level identified for each recording. The total duration of each type of swim at a specific activity level was converted into a percentage, dividing the total time the behaviour occurred by the length of the video-recording. To evaluate resting strategies, the frequencies for the mother–calf swims and independent calf swims at swim speeds 1 or 2 were summed per speed for each month (i.e., total number of SS1 or SS2 mother–calf swims, SS1 or SS2 independent calf swims). These aggregated values were converted into rates

by dividing the total frequency of this swim speed category by the length of the video-recording. The same aggregation procedure was used for SS2.5 swim category and the combined category of SS3 and SS4.

### 2.3.3. Instantaneous sampling with ethogram daytime observations

Using a team of independent observers who were positioned at the surface or below water at underwater viewing windows, real-time observations were conducted for each mother–calf pair between 0700 and 1100, 3–5 days a week, each month, for up to 75 months post-parturition at Facility B. Each rater coded the activity level for the calf or the mother independently every minute using an instantaneous recording rule (i.e., a snapshot of the animal's behaviour). This recording method produced a maximum of nine sample points for a 9-min sample frame (i.e., the length of the observation session). Due to variability, a different number of observations were made for each calf, which affected the total sample points available for each calf.

To accommodate this variability, the number of sample points observed for each type of swim at a particular activity level (e.g., mother–calf swim at SS1, Table 2) were summed and then divided by the observation day's total sample points, producing a proportion with which each activity was observed in a given day. Activity levels 3 and 4 were combined due to low observation occurrences. Mother–calf pairs were observed a different number of days within a month. Data from the individual days were summed for the month for each pair and then divided by the total number of observation days for the pair in that month. To facilitate comparisons between the two facilities, the data were collapsed per month for the first 12 months and then at 6 month intervals until 36 months to correspond with the data from Facility A.

### 2.4. Statistical analyses

Repeated measures one-way ANOVAs were performed for each month to determine if the percent of each activity level within a type of swim category differed from one another. All dependent variables were within statistical standards for normal distributions. A Huynh–Feldt correction was used if the assumption for homogeneity of variance was not met. Significant effects were examined using a Fisher's Least Significant Difference (LSD) as a post hoc test. Additionally, repeated measures one-way ANOVAs were conducted across months at each speed to determine if any developmental changes in activity level occurred over the three-year period. Bonferroni corrections were made to the overall alpha as multiple tests were performed on each

variable ($\alpha = 0.007$ for the activity level tested at each month and 0.01 for the change over time for each speed).

## 3. Results

### 3.1. Monthly changes in activity level: pre- and post-parturition

Using the archived 24-h behavioural observation records, the pregnant killer whale at Facility A exhibited a significant effect across activity levels, $F_{2.45,70.93} = 7.33$, $p < 0.001$, $\eta_p^2 = 0.20$. Significantly more SS1 independent, stationary floating (M = 35.20%, SD = 15.37) was displayed by the female compared to any other activity at any other level (SS2: M = 22.88%, SD = 16.79; SS2.5: M = 16.57%, SD = 8.79; LSD post hoc, $p < 0.05$) the month before parturition. The pregnant female spent the majority of her time across a 24-h period in a resting state (58%, SS1 and SS2 combined, Figure 1) and only about 25% (SD = 11.85%) of her time actively engaged and swimming about her environment (SS3/4, Figure 1). When comparing daytime and nighttime observations, the mother spent 70% of her time in a resting state at night versus 46% of her time during the day (Figure 2(a)).

A significant effect was also found for activity levels of the mother–calf pair at Facility A one month after birth, $F_{2.44,70.70} = 103.42$, $p < 0.001$, $\eta_p^2 = 0.78$. During this first month, the calf and her mother engaged in significantly more SS3/4 swims (M = 63.57%, SD = 15.34) than swims with each other at any other activity level (SS2.5: M = 14.84%, SD = 12.62; SS2: M = 18.14%, SD = 14.28; LSD post hoc, $p < 0.05$, Figure 1). In contrast to pre-parturition activity levels, post-parturition SS1 or floating reduced significantly to 3.46% (SD = 6.23), dependent $t$-test, $t_{28} = 9.79$, $p < 0.001$, and SS3/4 swims increased significantly, dependent $t$-test, $t_{28} = -13.31$, $p < 0.001$. The very active state was consistent even when data were examined for time of day effects. Daytime observations indicated that the mother–calf pair engaged in active swimming 62% of the time versus 55% of the time during nighttime observations (Figure 2(b)).

### 3.2. Weekly changes in activity level: two months post-parturition

As expected, the repeated measures ANOVAs using the archived 24-h behavioural observation records indicated significant effects for each of the first seven weeks (Table 3). Only one day of observation was available for the eighth week, which resulted in its removal from analyses. LSD post hoc
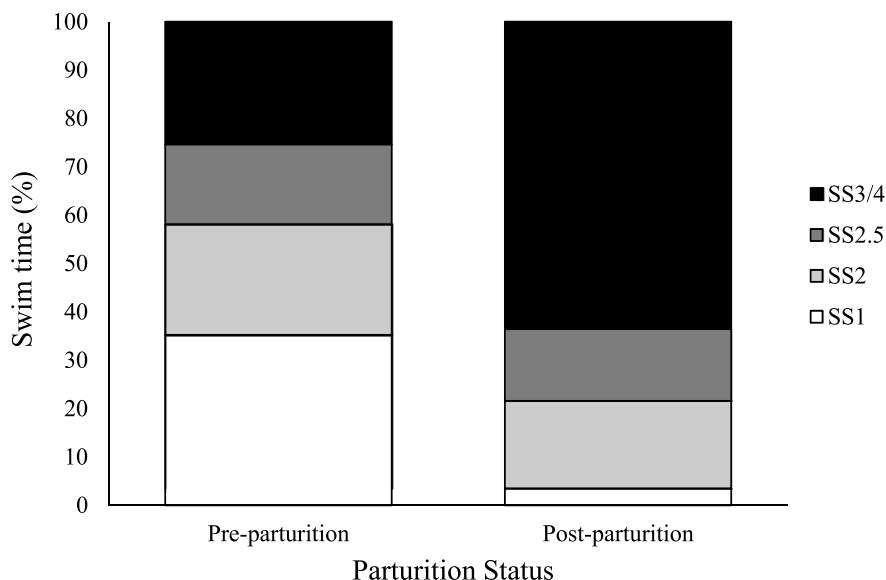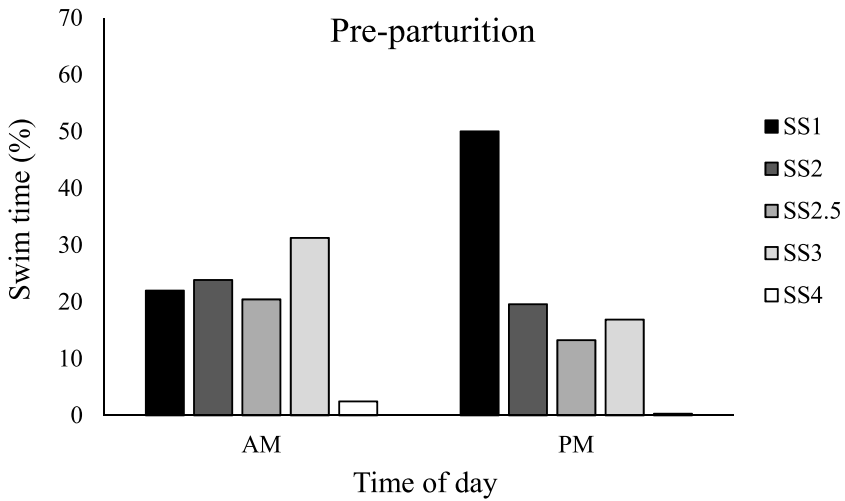
**Figure 1.** Changes in activity level swims from 1 month pre-parturition to 1 month post-parturition using 24 h behavioural observation instantaneous sampling data from Facility A. The graph represents the estimated mean percent of time the killer whale mother spent at each activity level 1 month before birth as compared to the estimated mean percent of time the killer whale mother–calf pair spent at each activity level during the first month after the birth of the calf.

tests indicated that significantly more active swims (SS3/4) occurred during weeks 1, 2, 3 and 4 as compared to the other activity levels (SS1, SS2, or SS 2.5; Table 3). During the fifth week after birth, there was no significant difference between the percentage of slow pattern swims (SS2) and the percentage of active swims (SS3/4) displayed by the mother–calf pair (Table 3). When resting strategies were combined (SS1 and SS2), the amount of time the mother–calf pair engaged in resting together was approximately the same as the amount of time they swam together in active swim (Figure 3). By weeks 6 and 7, the amount of time the mother–calf pair swam more actively (SS3/4) gradually reduced, and seemed to be replaced by more time at slower speeds (i.e., SS1 and SS2 combined, Figure 3).

Floating behaviours (SS1) remained below 11%, post-parturition, and never returned to the mother's pre-parturition level (Table 3). Changes in resting strategies occurred at week 3 when the slow circular swims (SS2) were significantly more frequent than floating behaviours (SS1) (Figure 3).
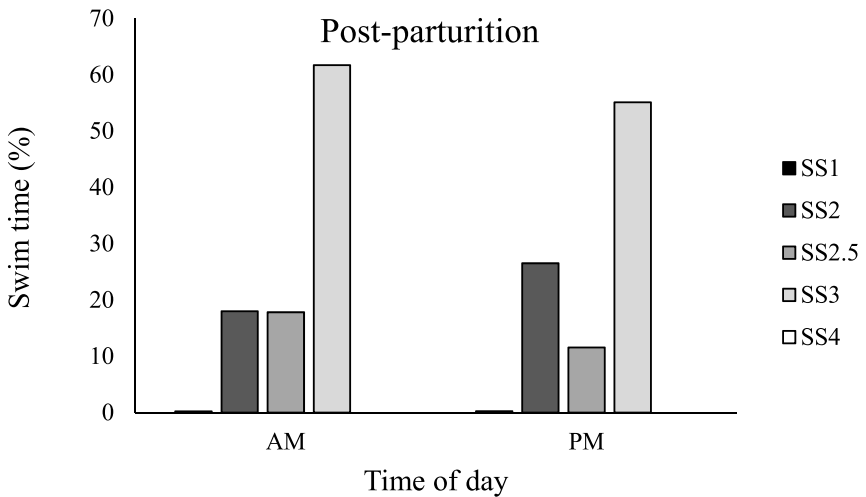
(a)



(b)



**Figure 2.** Changes in activity level swims according to time of day (AM vs PM) for the pregnant female killer whale 1 month pre-parturition (a) and for the killer whale mother–calf pair 1 month post-parturition (b) at Facility A. The *y*-axis indicates the mean percent of time the mother (a) or the mother–calf pair (b) spent swimming at each activity level.

**Table 3.**
Changes in mother–calf swims across the seven-week period post-parturition at Facility A.

| Age (weeks) | SS1 (mean ± SD) | SS2 (mean ± SD) | SS2.5 (mean ± SD) | SS3/4 (mean ± SD) | N | F | df | p | $\eta_p^2$ |
|---|---|---|---|---|---|---|---|---|---|
| 1 | 3.79 ± 9.28 | 14.09 ± 12.72 | 1.50 ± 3.67 | 80.64 ± 12.35* | 6 | 61.13 | 3, 15 | <0.001 | 0.92 |
| 2 | 0.00 ± 0.00 | 10.12 ± 14.41 | 19.05 ± 14.60 | 70.83 ± 14.03* | 7 | 33.81 | 2.99, 17.93 | <0.001 | 0.85 |
| 3 | 4.17 ± 5.89 | 16.07 ± 7.77 | 23.21 ± 9.27 | 56.55 ± 10.45* | 7 | 36.47 | 3, 18 | <0.001 | 0.86 |
| 4 | 5.18 ± 6.41 | 27.62 ± 11.66 | 14.05 ± 10.87 | 53.13 ± 8.68* | 10 | 35.42 | 3, 27 | <0.001 | 0.80 |
| 5 | 7.82 ± 8.60 | 35.09 ± 13.99 | 10.06 ± 9.68 | 47.02 ± 14.76 | 7 | 13.31 | 2.88, 17.27 | <0.001 | 0.69 |
| 6 | 10.83 ± 11.56 | 25.96 ± 17.51 | 21.43 ± 12.52 | 41.78 ± 11.06 | 7 | 4.83 | 2.29, 13.74 | 0.02 | 0.45 |
| 7 | 8.33 ± 9.21 | 48.49 ± 16.62 | 13.09 ± 10.48 | 30.07 ± 10.19 | 7 | 12.14 | 2.66, 15.96 | <0.001 | 0.67 |

* SS3/4 means that were significantly different from all other swim speeds per LSD post hocs.
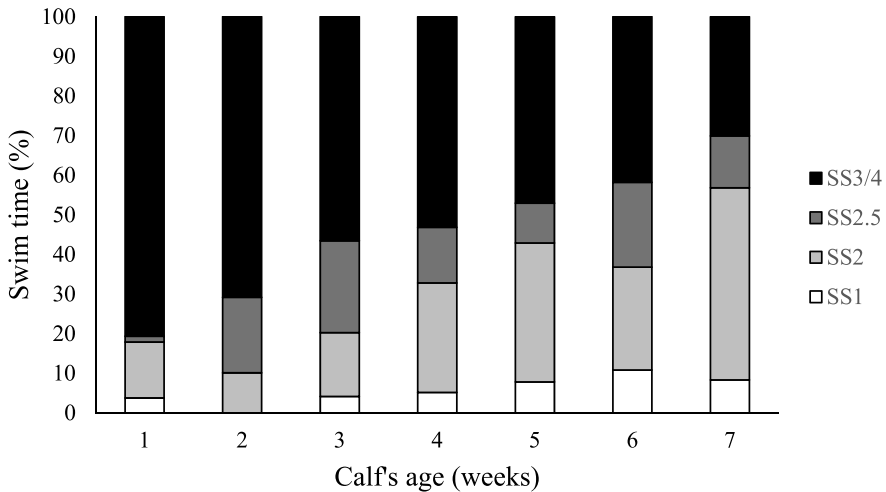
**Figure 3.** Mean percent of time the killer whale mother–calf pair at Facility A spent swimming at each activity level over the first 7 weeks post-parturition.

The mother–calf pair steadily increased the percentage of SS2 swims across the first two months of life, with the exception of a decrease during week 6 (Figure 3).

Additional follow-up descriptive analyses indicated that when the two clear resting strategies were combined together (SS1 and SS2 activity level swims), the mother–calf pair steadily increased the time spent resting each week (Figure 3). At week 1, the mother–calf pair spent about 17% of their time floating or slow swimming together. By 7 weeks, the mother–calf pair displayed resting behaviours (SS1 and SS2) about 52% of their time.

### 3.3. Six-month interval developmental changes in activity level: mother–calf swims

#### 3.3.1. Facility A

Using the daytime video recordings, the activity levels of mother–calf swims differed significantly across the three-year period of the calf's life. In partial support of the proposed hypothesis, the calf was most likely to engage in moderate, alert swims (SS2.5) with her mother immediately after birth, $F_{6,174} = 7.10$, $p < 0.001$, $\eta_p^2 = 0.197$, with these swims occurring most often during the first month than at any other month (LSD post hocs, $p < 0.05$), except 18 months ($p = 0.06$, Table 4). A Pearson correlation between age and SS2.5 supported the decreasing trend in active swims over

time, $r_{208} = -0.318$, $p < 0.05$ (Figure 4(a)). As expected, a significant effect was found for mother–calf very fast, vigilant swims (SS3/4), $F_{6,174} = 7.45$, $p < 0.001$, $\eta_p^2 = 0.204$, which accounted for a greater percent of time during the first month post-parturition than at any other observed month, except for six months (LSD post hocs, $p < 0.05$, Table 4). A Pearson correlation between age and SS3/4 also supported the expected decrease in active swim over time, $r_{208} = -0.258$, $p < 0.05$ (Figure 4(a)). Mother–calf swims at activity level SS2.5 and activity levels SS3/4 decreased by the end of the first year and remained steady for the following six-month intervals (Figure 4(a)).

Mother–calf swims at slower swim speed and resting categories (SS1 and SS2) changed over time with an initial increase in time spent swimming at a slow, SS2 pace, $F_{6,174} = 5.05$, $p < 0.001$, $\eta_p^2 = 0.148$ (Figure 4(a)). Significantly more mother–calf SS2 swims were present when the calf was 12 months old than any other six-month interval (LSD post hocs, $p \leqslant 0.05$, Table 4). At 18 months SS2 dropped and stabilized for the rest of the observation period (Table 4). Even though no observation of SS1 swim type during the first month of life was captured in the sampled recordings, no changes over time were detected for stationary floating (Figure 4(a)).

### 3.3.2. Facility B

Using the archived data from the instantaneous sampling with ethogram observations, no difference in the average percentage of very active swims displayed by the three mother–calf pairs across the 6-month intervals was observed (Table 5). However, a follow-up Pearson correlation suggested that the percentage of active fast swims significantly decreased with age, $r_{46} = -0.389$, $p = 0.005$, which was expected (Figure 5). While very active-paced swims comprised about 15% of the mother–calf pairs' activity budget during the first month, these three pairs exhibited normal-paced active swims most of the time with non-significant fluctuations across the 6-month intervals (Figure 5).

As with the two speeds of active swimming, no significant effects were found for age on either stationary floating or slow swimming for the calves at Facility B (Table 5). Stationary floating remained consistently low from the first month of life through the three-year period examined and slow swimming increased as the calves matured (Figure 5). When monthly activity levels were compared, there was no significant difference between activity levels at 1 month, but there were differences at 6, 12 and 18 months (Table 5). Stationary floats occurred significantly less often than slow swims

**Table 4.**

Changes in mother–calf & independent calf swims per month across a three-year period at Facility A.

| Age (months) | N | SS1 | | SS2 | | SS2.5 | | SS3/4 | |
|---|---|---|---|---|---|---|---|---|---|
| | | MC (mean ± SD) | Solo (mean ± SD) | MC (mean ± SD) | Solo (mean ± SD) | MC (mean ± SD) | Solo (mean ± SD) | MC (mean ± SD) | Solo (mean ± SD) |
| 1 | 144 | 0.00 ± 0.00 | 0.00 ± 0.00 | 13.60 ± 33.52 | 0.00 ± 0.00 | 50.00 ± 51.00* | 0.00 ± 0.00 | 34.03 ± 47.60* | 2.50 ± 11.03 |
| 6 | 53 | 9.00 ± 22.00 | 0.00 ± 0.00 | 9.03 ± 21.07 | 0.00 ± 0.00 | 23.20 ± 31.00 | 3.11 ± 10.24 | 15.40 ± 28.00* | 11.20 ± 28.14 |
| 12 | 36 | 11.02 ± 29.83 | 0.06 ± 0.30 | 34.00 ± 39.61* | 0.30 ± 1.40 | 12.00 ± 25.43 | 11.70 ± 25.45 | 2.00 ± 11.00 | 3.40 ± 18.25 |
| 18 | 57 | 17.50 ± 31.15 | 1.28 ± 4.45 | 5.00 ± 13.60 | 0.50 ± 1.90 | 29.00 ± 34.13 | 10.00 ± 22.20 | 1.00 ± 4.00 | 1.00 ± 4.00 |
| 24 | 38 | 5.00 ± 10.00 | 2.50 ± 5.10* | 5.33 ± 19.07 | 0.00 ± 0.00 | 11.00 ± 14.30 | 6.21 ± 8.10 | 2.02 ± 4.90 | 6.00 ± 9.14 |
| 30 | 103 | 14.32 ± 28.08 | 1.00 ± 3.00 | 6.70 ± 18.82 | 0.12 ± 1.00 | 10.24 ± 20.00 | 9.00 ± 19.36 | 4.34 ± 12.00 | 3.00 ± 6.04 |
| 36 | 33 | 10.00 ± 22.70 | 1.60 ± 4.00* | 7.50 ± 23.16 | 0.00 ± 0.00 | 9.31 ± 21.40 | 9.00 ± 20.20 | 9.50 ± 25.05 | 12.30 ± 24.30 |

* Means that are significantly different per LSD post hoc tests.
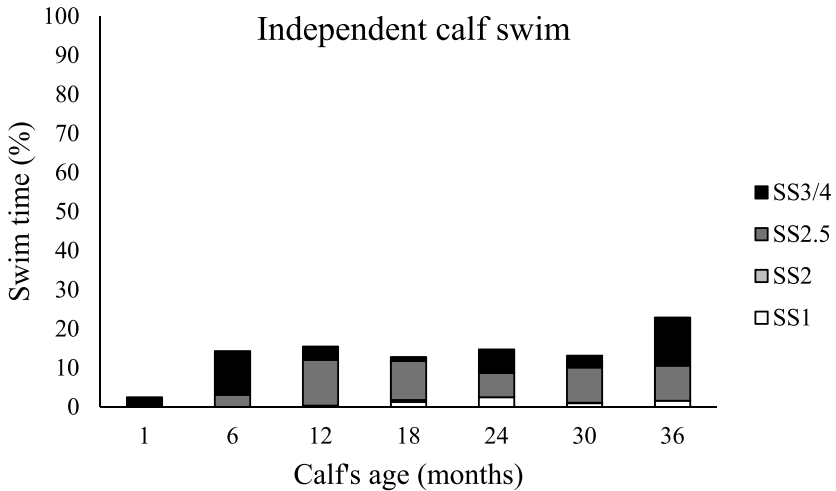
(a)
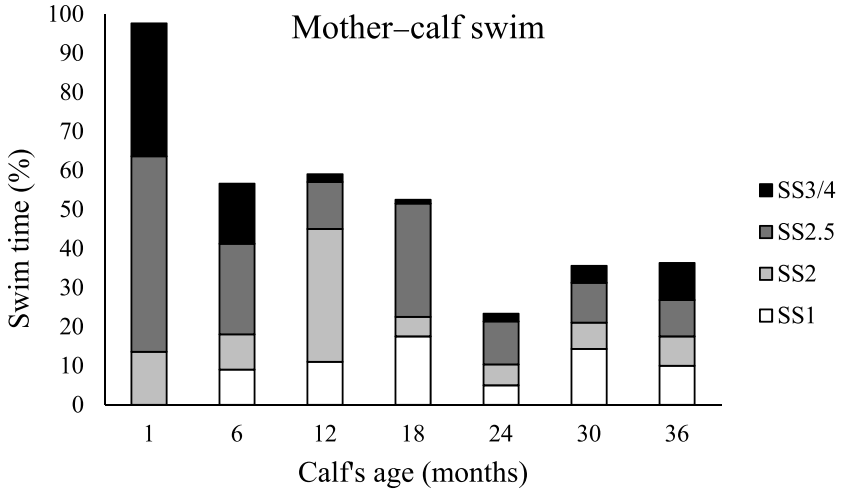


(b)



**Figure 4.** Developmental changes for mother–calf and independent calf swims at Facility A at 6 month intervals from 1 month until 36 months post-parturition. (a) Mean percent of time the calf spent swimming with her mother at each activity level. (b) Mean percent of time the calf spent swimming independently at each activity level.

**Table 5.**
Changes in activity level in mother–calf swims per month across a three-year period for 3 calves at Facility B.

| Age (months) | Available calves | Stationary floats (mean ± SD) | Slow swims (mean ± SD) | Normal active swims (mean ± SD) | Fast active swims (mean ± SD) | $F$ | df | $p$ | $\eta_p^2$ |
|---|---|---|---|---|---|---|---|---|---|
| 1 | 2 | 0.07 ± 0.12 | 6.13 ± 9.03 | 45.10 ± 48.66 | 15.36 ± 25.36 | – | – | ns | – |
| 6 | 3 | 5.39 ± 8.92 | 39.58 ± 9.10 | 47.60 ± 12.11 | 7.43 ± 8.45 | 11.17 | 3,6 | 0.007 | 0.85 |
| 12 | 3 | 4.17 ± 7.22 | 19.41 ± 8.68 | 67.86 ± 13.50 | 8.09 ± 9.86 | 19.09 | 3,6 | 0.002 | 0.91 |
| 18 | 3 | 1.42 ± 1.23 | 32.64 ± 4.34 | 61.60 ± 4.39 | 3.62 ± 2.10 | 164.78 | 3,6 | 0.001 | 0.99 |
| 24 | 2 | 1.92 ± 3.14 | 24.00 ± 21.41 | 39.51 ± 35.17 | 0.48 ± 0.84 | – | – | ns | – |
| 30 | 2 | 0.74 ± 1.28 | 26.45 ± 23.24 | 34.70 ± 30.08 | 2.46 ± 2.26 | – | – | ns | – |
| 36 | 1 | 0.14 ± 0.24 | 17.36 ± 30.06 | 15.11 ± 26.17 | 0.07 ± 0.13 | – | – | ns | – |

The three calves were observed for different time frames. The number of calves constituting the data are indicated in the table. At 6 months, normal active swim > float and fast active swim; slow swim > float (LSD: $p = 0.07$). At 12 months, normal active swim > float and fast active swim (LSD: $p < 0.05$). At 18 months, normal active swim > fast active swim and slow swim; slow swim > fast active swim and float ($p < 0.05$).
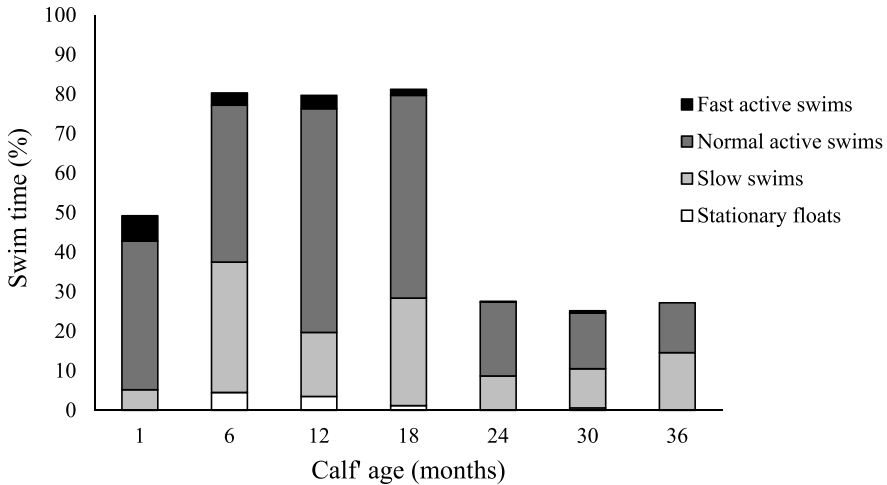
**Figure 5.** Developmental changes in estimated mean percent of time 3 killer whale calves at Facility B spent swimming at each activity level at 6 month intervals from 1 month until 36 months post-parturition.

($p = 0.003$) and/or normal active swims ($p = 0.001$) at these three months of life (Figure 5). The results supported the expectation that killer whale mothers would slow down their activity level as the calves aged and perhaps replace the adult preferred resting strategy of stationary floating with slower swimming. This preference appeared by the end of the first month, increased during the first year of life, after which it stabilized (Figure 5).

### 3.3.3. Monthly developmental changes in activity level of mother–calf swims

The continuous monthly observations collected at Facility B for the three mother–calf pairs enabled a more detailed examination of the developmental changes in activity level for the calves and their mothers for the first year of life (Figure 6). While the coding schemes of the two facilities differed slightly in their operational definitions, it is clear that stationary floating was extremely rare in the first month of life for all calves and continued to remain low across calves at each facility (A: Figures 3 and 4; B: Figure 6). Secondly, fast active swims peaked for the Facility B calves measured during the first month of life although some individual variation occurred. Finally, the calves at Facility B consistently swam at normal swim activity level with some fluctuation across the first year of life (Figure 6).
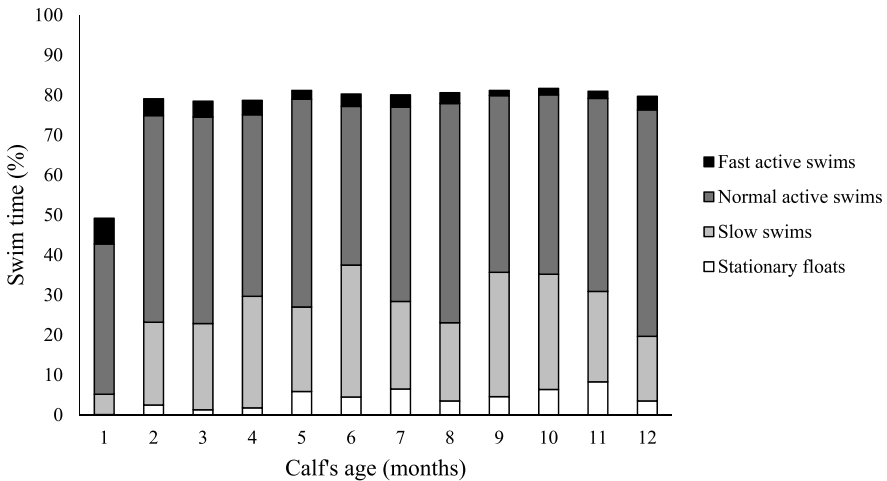
**Figure 6.** Estimated mean percent of time 3 killer whale calves at Facility B spent swimming at each activity level every month for the first year of life.

### 3.4. Six-month interval developmental changes in activity level: independent calf swims

The percent of time the Facility A calf spent swimming independently remained relatively stable across the three-year period using the data from daytime video recordings. A significant effect for SS1 was detected across time, $F_{6,174} = 2.74$, $p = 0.014$, $\eta_p^2 = 0.086$ (Figure 4(b)). As expected, independent swims by the calf at activity levels SS1 and SS2 were never observed until 18 months of age. At 24 months, the calf displayed significantly higher percentages of stationary floating behaviours than all other months but 18 months, $p < 0.05$. A significantly higher percentage of SS1 independent swim was also found at 36 months, when floating behaviours differed from all but 18 and 24 months, $p < 0.05$ (Table 4). A Pearson correlation supported the increase in behaviour over time, $r_{208} = 0.200$, $p < 0.05$ (Figure 4(b)). No other significant effects were found for SS2, SS2.5, or SS3/4 (Table 4), although the calf displayed higher percentages of very active swim when alone periodically (e.g., 6 and 36 months, Figure 4(b)).

### 3.5. Calf's preferred partner during rest

Using the daytime video recording data, dependent $t$-tests were conducted at each month for the percentage of time and rate at each level of mother–calf and independent calf swims for Facility A. Swimming with another whale

**Table 6.**
Comparison percentages independent calf and mother–calf swims (SS1 and SS2) at Facility A.

| Swim speed (SS) | Age (months) | $t_{29}$ | $p$ | Independent calf swim (mean $\pm$ SD) | Mother–calf swim (mean $\pm$ SD) |
|---|---|---|---|---|---|
| SS1 | 1 | | | $0.00 \pm 0.00$ | $0.00 \pm 0.00$ |
| | 6 | −2.23 | 0.03 | $0.00 \pm 0.00$ | $8.86 \pm 21.73$ |
| | 12 | −2.01 | 0.05 | $0.06 \pm 0.30$ | $11.02 \pm 29.83$ |
| | 18 | −2.83 | 0.008 | $1.28 \pm 4.45$ | $17.46 \pm 31.15$ |
| | 24 | −1.05 | ns | $2.50 \pm 5.09$ | $4.78 \pm 9.63$ |
| | 30 | −2.66 | 0.013 | $0.88 \pm 2.98$ | $14.32 \pm 28.07$ |
| | 36 | −1.83 | ns | $1.57 \pm 3.64$ | $9.45 \pm 22.70$ |
| SS2 | 1 | −2.22 | 0.04 | $0.00 \pm 0.00$ | $13.58 \pm 33.52$ |
| | 6 | −2.35 | 0.03 | $0.00 \pm 0.00$ | $9.03 \pm 21.07$ |
| | 12 | −4.62 | 0.000 | $0.25 \pm 1.37$ | $33.85 \pm 39.61$ |
| | 18 | −1.74 | ns | $0.48 \pm 1.87$ | $4.89 \pm 13.57$ |
| | 24 | −1.53 | ns | $0.00 \pm 0.00$ | $5.33 \pm 19.07$ |
| | 30 | −1.91 | ns | $0.12 \pm 0.63$ | $6.69 \pm 18.82$ |
| | 36 | −1.77 | ns | $0.00 \pm 0.00$ | $7.48 \pm 23.16$ |

during the day occurred so infrequently across the study period, we did not include swim with other in the current analyses. SS1 and SS2 activity levels occurred most frequently during swims with mother as compared to independent SS1 swims. At all examined months, the dependent $t$-test analyses demonstrated that calf spent more time stationary floating (SS1) with her mother than alone, except at 24 and 36 months (Table 6, Figure 4).

Similarly, the percentage of time the calf swam in slow pattern swims (SS2) with her mother as compared to when alone was significantly higher during the first year (i.e., 1, 6 and 12 months) but not during the second and third years (i.e., 18, 24, 30 and 36 months) (Table 6, Figure 4). The rates ($f$/sec) at which mother–calf and independent calf swims occurred over the three-year period were also assessed at each activity level. Significantly higher rates of mother–calf swims occurred at SS1 (M = 0.06, SD = 0.15) and SS2 (M = 0.08, SD = 0.17) levels when compared to independent calf swims (SS1: M = 0.02, SD = 0.06, SS2: M = 0.00, SD = 0.02), SS1: $t_{209} = 4.04$, $p < 0.001$ and SS2: $t_{209} = 6.29$, $p < 0.001$. The rates of these swims indicate that mother–calf swims occurred three times more frequently at the SS1 level and eight times more frequently at the SS2 level as compared

to independent calf swims, providing additional support for our expected hypotheses.

## 4. Discussion

Previous research quantified the frequency with which different resting behaviours occurred in killer whales and other cetaceans in managed care (Gnone et al., 2001, 2006; Sekiguchi & Kohshima, 2003; Lyamin et al., 2005, 2007; Sekiguchi et al., 2006; Hill et al., 2008). While research with dolphins included both stationary floating and slow pattern swimming (i.e., swim rest), the original study of two killer whale mother–calf pairs only considered stationary floating as an opportunity to rest (Lyamin et al., 2005). The current study expanded on this research with four more killer whale mother–calf pairs in managed care from birth through 36 months and considered the possibility of mothers choosing between floating or swim rest based upon their calf's current developmental state and the resting needs of the calf and the mother herself (i.e., resting strategies). The use of differential resting strategies based on the current state of offspring development would be predicted by parental investment theory (Trivers, 1974) as cetaceans, like killer whales, invest greatly in their offspring with long periods of gestation and dependent care (Asper et al., 1988; Baird, 2000).

### 4.1. Changes in resting strategies pre-parturition to post-parturition

#### 4.1.1. Pre-parturition
Asper et al. (1988) reported on the pre-parturition behaviour of a pregnant female but emphasized the characteristics that were indicative of parturition such as respirations, discharge, and contractions. Overall activity level and types of swim of the pregnant female were not reported (1988). As the first study to investigate the swim behaviour of a pregnant killer whale empirically, the results of the current study indicated that the female at Facility A spent 35% of her time floating and another 23% slow swimming, for a total of almost 60% of her time involved in resting behaviours averaged across a day. This trend was even stronger at night when the pregnant female exhibited more floating at night than during the day. These patterns of rest for the pregnant female were similar to the resting behaviours of an adult female without a calf reported by Lyamin et al. (2005), suggesting that while the last month of pregnancy for delphinids is associated with slower speeds

and less swimming efficiency (Noren et al., 2011), pregnancy alone may not significantly alter a female's preferred resting strategy. Rather, resting preferences (e.g., to float or swim slowly) are likely subject to individual differences in overall activity level, an explanation that is tentatively supported by the pre-parturition behaviour of five individual bottlenose dolphins (Hill et al., 2008), but additional research would be helpful in understanding the influence of individual differences (Highfill & Kuczaj, 2007).

*4.1.2. Post-parturition*

Upon birth, immediate increases in speed were observed for the four mothers when swimming with their neonates, corroborating previous observations (e.g., Asper et al., 1988; Gnone et al., 2001, 2006; Sekiguchi & Kohshima, 2003; Lyamin et al., 2005, 2007; Sekiguchi et al., 2006; Hill et al., 2008). The mother–calf pair at Facility A spent about 80% of their time at fast speeds and active pattern swims (greater than 6 km/h (4 mph)) immediately after birth (Figures 1, 3 and 4(a)). Similarly, the three killer whale mother–calf pairs at Facility B spent about 60% of their time engaged in mother–calf swims at fast speeds and active pattern swims immediately after birth (Figures 5 and 6). About 10–20% of the time, the mother–calf pairs at both facilities exhibited patterned, mother–calf swims at slower swim speeds (2–5 km/h (1–3 mph)), which were likely the periods of swim in which both the mother and calf had opportunities to rest. A more detailed analysis of the weekly changes indicated that the pair at Facility A began to exhibit these slower swim speeds during the first week of life (i.e., SS2 and SS1 activity levels) much like Gnone et al. (2006) reported for a bottlenose dolphin mother–calf pair. These resting opportunities increased steadily across the following weeks (Figure 3). A month-by-month analysis of the three pairs of killer whales at Facility B corroborated the fluctuating, but increasing, opportunities to rest (Figure 6), despite individual differences between the calves. The similarity in behavioural patterns between four different killer whale mother–calf pairs observed at different times with different social groupings and housing suggests that these resting strategies are conserved across the species and captive environments. These results from a controlled environment are supported by anecdotal observations that free-ranging killer whale mothers with neonates swim continuously and rarely float (Baird, 2000). However, until a similar empirical study is conducted with killer whales in their natural habitat the current results must be interpreted with caution when generalizing to free-ranging killer whales.

## 4.2. Developmental changes in calf behaviours and activity level

Overall, the four killer whale calves spent very little time engaged in swims less than 6 km/h (4 mph) across the three-year period, unless they were with their mothers. Developmentally, all four calves displayed slow pattern swimming with their mothers more often than stationary floating at the water surface or in the water column for the first year and a half as indicated in daytime observations. Brief episodes of mother–calf floating were observed soon after birth for all four mother–calf pairs, which increased slightly with age. However, none of the pairs ever exhibited floating at the same levels as the pregnant female did prior to parturition during her daytime observations. By the third year of life, the killer whale calves from both facilities spent less time with their mothers and exhibited independent activities at higher levels of activity and alertness, especially for daytime observations.

A variety of researchers have speculated that the absence of floating by neonate cetaceans may be related to developmental limitations of the neonate. In particular, the need of the calf to thermoregulate may elicit the continuous movement of the mother–calf pair (reviewed by Lyamin et al., 2008). Similarly, the size of the calf (Lyamin et al., 2008) or immature motor control and muscle development of the calves (Weihs, 2004; Noren, 2008; Noren & Edwards, 2011) may preclude their ability to float for long periods of time. Echelon and infant swims seem to facilitate the physical (e.g., increased blubber layer or size) and motor development (e.g., swimming efficiency) of calves as they mature (Gubbins et al., 1999; Weihs, 2004; Noren, 2008; Noren & Edwards, 20114). The results of the current study clearly support the role of these developmental limitations as a clear relationship existed between the age of the calf and the resting strategies exhibited by the mothers when swimming with their calves. When calves likely needed assistance to thermoregulate or to swim more efficiently (i.e., first month, post-parturition), the killer whale mothers swam with their calves most frequently in continuous, moderately active or fast-paced swims. The appearance of a steadily increasing trend to engage in slower, patterned mother–calf swims and a significant reduction in floating by the end of the first month, suggested that the mothers may have adopted a resting strategy that favoured the current level of calf development.

## 4.3. Preferred resting partner

While it was clear that the calves spent the majority of their time with their mothers, the calves did become more independent and social over time.

When away from her mother, the calf at Facility A (Figure 4(a)–(b)) spent most of her time engaged in alert swims, social interactions, and play activities (at higher levels of activity including SS2.5 and SS3/4). This calf rarely displayed independent resting behaviours (SS1 and SS2) and almost never rested with adult killer whales other than her mother. Unfortunately, the data collected from Facility B did not describe calf behaviours when independent of their mothers, thus caution must be applied when interpreting the results of a single calf. For all four calves, it was clear that the mother initiated the type of swim and speed at which it was displayed, particularly during the first year of life. This first year of life is a critical period in the lives of cetacean calves as the calves are often at their greatest vulnerability (e.g., Mann & Smuts, 1999; Mann et al., 2000; Mann & Watson-Capps, 2005). As explained earlier, parental investment theory (Trivers, 1974) would predict the presence of maternal-initiated regulation of rest and general activities of cetacean calves as long-lived animals with extended periods of dependence (e.g., Mann et al., 2000; Mann & Watson-Capps, 2005). Killer whales may invest even more energy compared to other cetaceans based on recent research that found the post-reproductive period of females to be related to higher rates of survival for their adult male offspring (e.g., Foster et al., 2012). As would be expected from previous research on mother–calf interactions in a number of odontocetes (e.g., Reid et al., 1995; Mann & Smuts, 1999; Baird, 2000; Hill et al., 2007, 2013; Hill, 2009), the regulator of resting opportunities likely becomes more ambiguous as the calf matures. When away from the mother, the calf may have initiated her own resting opportunities by terminating independent or social activities to return to swim or float with her mother. It is also possible that the mother could have initiated the termination of the calf's independent or social activities to elicit the calf's return for rest (Kuczaj et al., 2015). Once together, it was unclear if the selected resting strategy was initiated by the calf, the mother, or both. Additional observations and mother–calf pairs are needed to better understand the function of these resting opportunities and how they might elucidate the role of calf physical and social development, individual differences, and maternal styles.

## 4.4. Conclusions

Although these conclusions are based on the activities of four killer whales in managed care, the current study demonstrated that killer whale neonates typically swim in active or fast-paced swims with their mothers during the first

month of life, corroborating previous research of two killer whale mother–calf pairs (Lyamin et al., 2005) and multiple bottlenose dolphin pairs (Gnone et al., 2001, 2006; Sekiguchi & Kohshima, 2003; Lyamin et al., 2005, 2007; Sekiguchi et al., 2006; Hill et al., 2008). By the end of the first month of life and during the first year of life, mothers were able to rest using the slow swim, USWS strategy while facilitating calf rest as the calves drafted from their mothers during these swim patterns (Weihs, 2004; Noren, 2008; Noren & Edwards, 2011). Although the current study did not specifically measure the amount of time the calves spent in echelon or infant swim positions, the calves were usually in one of those two positions during the slow, pattern swims.

Together, the results of this study suggest that while mothers with neonates may have limited opportunities to rest during the first month post-parturition, the mothers appear to regulate the speed and position with which they swim with their calves. As calves become more efficient swimmers and develop thicker blubber layers that not only aid in thermoregulation but in buoyancy, mothers can then adapt a resting strategy (e.g., floating or slow swimming) that best corresponds to the calf's current developmental state. Additional research with other mother–calf killer whales in managed care as well as in their natural habitat is necessary to better understand the role of calf physical development in the resting strategies selected by the mothers. Moreover, additional observations regarding the initiator and regulator of resting opportunities would provide information about the nature of the mother–calf bond in the context of regulating the proximate behaviour of sleep, which has been shown to be instrumental in the development of many other mammals (e.g., Siegel, 2005).

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