Zoo Biology 14:417–430 (1995)

Killer Whale (*Orcinus orca*) Reproduction at Sea World

Deborah A. Duffield, Daniel K. Odell, James F. McBain, and Brad Andrews

Department of Biology, Portland State University, Portland, Oregon (D.A.D.); Sea World Inc., Orlando, Florida (D.K.O., B.A.), and San Diego, California (J.F.M.)

Sea World has maintained killer whales (*Orcinus orca*) since 1965. The total killer whale inventory (1965–1993) has included 39 whales (25 females, 14 males); 28 were wild-caught and 11 captive-born, including one second-generation calf. As of September, 1993, there were 19 whales in the breeding program. Ten of these whales (53%) were captive-born, either at Sea World or other facilities in North America. The live wild-caught whales ranged in estimated age from 12–27 years ($\bar{x} \pm$ sd = 17.6 ± 4.2 years). The captive-born whales ranged in age from <1 to 8 years. In the Sea World breeding program (through September, 1993), there have been nine live births and one stillbirth, with eight calves part of the current inventory. Births occurred from July to February. Calving intervals ranged from 32–58 months. Female age at birth of first calves ranged from 8 years to an estimated 17 years ($\bar{x} \pm$ sd = 12.7 ± 3.0 years). Gestation, based on conception estimates from serum progesterone analysis, averaged 17 months ($\bar{x} \pm$ sd = 517 ± 20 days), but successful pregnancies with viable calves occurred from 15–18 months (468–539 days). Females, in the presence and absence of males, were polyestrus with periods of cycling interspersed with individually variable noncycling (presumed anestrous) periods ranging from 3–16 months. Mean serum progesterone levels (±se) were as follows: noncycling periods = 121 ± 20 pg/ml; peak elevations during nonconceptive ovulatory (estrous) cycles = 3,962 ± 2,280 pg/ml; first pregnancies = 14,592 ± 3,854 pg/ml; second pregnancies = 8,389 ± 395 pg/ml; and third pregnancy = 8,180 ± 4,556.

Key words: *Orcinus orca,* reproduction, serum progesterone

INTRODUCTION

Killer whales (*Orcinus orca*) were first brought into captivity in the United States and Canada in 1965 [Duffield and Miller, 1988]. Sea World has maintained

Received for publication January 10, 1994; revision accepted December 18, 1994.

Address reprint requests to Deborah Duffield, Department of Biology, Portland State University, P.O. Box 751, Portland, OR 97207-0751.

killer whales since that time and, with the construction of a large multipool breeding facility at Sea World of Florida in 1984, followed by construction of similar facilities at Sea World of California and Sea World of Texas, established a substantive captive breeding program for killer whales in the United States. The first calf was born 26 September 1985 [Asper et al., 1988]. Captive propagation of marine mammal species, in general, has been increasingly successful in zoological facilities in the US and Canada [Asper et al., 1990]. During the last marine mammal census, 1983–1990, births were reported in 17 different species, with dramatic increases in numbers of births per year for a number of cetacean and pinniped species. Prior to 1985, the only captive births of killer whales were those to a single breeding pair which had been maintained together since 1969 [Duffield and Miller, 1988]. The female had her first calf at an estimated age of 11 years, and the male was estimated to be 16 years at the time of first conception. The pair had a total of six calves (four live born, two stillborn) in 9 years, none surviving longer than 42 days. However, by September, 1993, 18 additional killer whale births had occurred in facilities in North America, with 11 of the young surviving [Asper et al., 1990; Marine Mammal Census Database: Duffield and Shell, unpublished data]. Ten of these births were in the Sea World breeding program.

The ability to maintain and breed killer whales in controlled environments has provided an invaluable opportunity to contribute to the understanding of killer whale biology in ways not possible with free-ranging populations. Comparative data have been gathered on demographic, behavioral, acoustic, reproductive, and physiological characteristics in captive killer whales. These data are useful for refining models of killer whale biology developed from the study of wild populations [for examples, see collections of papers in Kirkevold and Lockard, 1986; Sigurjonsson and Leatherwood, 1988; Hammond et al., 1990]. The existence of a long-term breeding program for killer whales has, in particular, made possible the collection of reproductive hormone data for characterization of estrus, pregnancy, and reproductive behavior [Walker et al., 1988; Robeck et al., 1993]. This report adds to the reproductive biology database by presenting the reproductive histories of the killer whales maintained by Sea World and the accumulated data from 10 years of twice-monthly to monthly serum progesterone analysis.

MATERIALS AND METHODS

Animals

As of September, 1993, 39 killer whales have been maintained at Sea World (Table 1). Twenty-eight (18 females, 10 males) were wild-caught. Thirteen of these came from North Pacific collection sites and 15 from North Atlantic sites off the coast of Iceland. Nine of the wild-caught whales (seven females, two males) are in the current breeding program. Eleven of the whales in the inventory were captive-born; ten of these (six females, four males) are in the current breeding program. Eight of these were born in the Sea World breeding program; one was a second-generation birth. Two were born in other facilities in North America.

The whales were maintained in behaviorally compatible social groups which included adult females and their current calves, captive-born juveniles, and adult males.

Ages at capture for the wild-caught whales (Table 1) were estimated from body

TABLE 1. Sea World killer whale inventory, 1965–1993

ID	Date into Sea World	Date collected	Birth date[a]	Site of collection/birth	Death date	Length at capture (cm)	Estimated age at capture (years)
Females							
51	12/25/65	10/65	1961	Carr Inlet, WA	08/27/71	410	4
94	12/17/69	02/67	1965	Yukon Harbor, WA	06/16/71	312	2
8727	01/21/87	12/69	1966	Pender Harbour	Alive	366	3
8628	04/27/86	03/70	1965	Pedder Bay, B.C.	03/13/90	430	5
15	09/10/71	08/71	1969	Penn Cove, WA	06/15/75	323	2
16	09/16/71	08/71	1967	Penn Cove, WA	09/28/77	434	5
7602	06/09/77	10/76	1974	Iceland	08/06/91	300	2
8702	11/17/87	10/76	1974	Iceland	Alive		2
7701	12/12/77	10/77	1973	Iceland	10/15/87	351	4
7706	12/12/77	10/77	1971	Iceland	08/21/89	370	6
9101	10/26/91	10/77	1976	Iceland	Alive		1
7802	10/26/78	10/78	1976	Iceland	09/03/79	295	2
7803	10/26/78	10/78	1976	Iceland	05/14/91	312	2
7804	10/26/78	10/78	1976	Iceland	Alive	292	2
7806	06/20/79	10/78	1974	Iceland	Alive	350	4
8951	05/03/89	1982	1980	Iceland	03/14/92		2
9301	01/08/93	10/82	1980	Iceland	Alive	290	2
9376	01/08/93	10/82	1976	Iceland	Alive	380	6
8501	09/26/85		09/26/85	Sea World	Alive		
8626	01/05/86		01/05/86	Sea World	01/16/86		
8826	09/23/88		09/23/88	Sea World	Alive		
8801	11/04/88		11/04/88	Sea World	Alive		
8876	11/26/88		11/26/88	Sea World	Alive		
8901	07/11/89		07/11/89	Sea World	Alive		
9126	07/09/91		07/09/91	Sea World	Alive		
Males							
72	03/11/67	08/66	1965	Yukon Harbor, WA	09/23/78	290	1
13	03/11/67	02/67	1963	Yukon Harbor, WA	01/12/82	406	4
8726	01/21/87	05/68	1959	Pender Harbour, B.C.	09/26/88	510	9
7601	10/17/76	08/70	1966	Penn Cove, WA	04/28/86	406	4
27	03/12/72	02/72	1971	Carr Inlet, WA	11/30/74	290	1
302	10/25/73	07/73	1962	Pedder Bay, B.C.	01/29/74	594	11+
8701	01/09/87	08/75	1970	Pedder Bay, B.C.	09/20/90	427	5
7705	12/12/77	10/77	1974	Iceland	08/02/81	335	3
7801	10/26/78	10/78	1977	Iceland	Alive	280	1
9201	01/07/92	11/84	1980	Iceland	Alive	351	4
9226	04/17/92		08/15/89	Marineland, CAN	Alive		
9377	01/08/93		12/24/91	Sealand, CAN	Alive		
9378	02/02/93		02/02/93	Sea World	Alive		
9302	09/09/93		09/09/93	Sea World	Alive		

[a]Birth year for the wild-caught whales was estimated from length-growth curves [Duffield & Miller, 1988].

length recorded at capture, compared with subsequent length-growth curves [following Duffield and Miller, 1988].

Facilities

Multipool facilities housed killer whales at four Sea World parks in Florida, California, Texas, and Ohio. They were designed, as described in Asper et al. [1988, 1992], to offer a variety of pool environments and flexibility in handling the whales, individually and in groups. Depth in the pools varied from 2.4–4 m in medical pool areas to 10.7 m in performance pool areas. All pools were connected by gated channels allowing the whales to be maintained separately or together, as social interactions dictated. When channels were open, the whales were provided with a diverse environment in which they could choose to be in groups or alone and in pools of differing size and depth.

General Husbandry

The general aspects of diet, food intake, and water quality standards were described previously [Asper et al., 1988]. Monthly health exams were routine on all whales and included clinical evaluation of hematology, serum chemistry, urinalysis, and blowhole cultures. Whales were trained to present their flukes for venipuncture and to station themselves for physical measurements and collection of voluntary urine samples.

Serum Progesterone

Blood samples were taken for serum progesterone analysis on a twice-monthly to monthly basis from all females, starting in 1983. Blood was drawn and placed in serum stat-chem tubes containing 2 NIH units of thrombin. Serum was separated within an hour of collection, stored at −20°C, and sent to an independent reference laboratory (American Clinical Laboratory, San Diego, CA) for serum progesterone analysis. The analyses were performed using a no-extraction, solid-phase ^{125}I radioimmunoassay kit designed to measure progesterone in serum or plasma (Coat-A-Count Progesterone®; Diagnostic Products Corporation, Los Angeles, CA). Urinary progesterone metabolites were measured as described by Robeck et al. [1993].

Pregnancy

Diagnosis of pregnancy was made by serum progesterone analysis, urine progesterone metabolite analysis [Robeck et al., 1993], ultrasound, and daily observation of social interactions and copulatory behavior. Levels of serum progesterone continued to be monitored twice-monthly to monthly throughout pregnancy. Fetal viability was confirmed during physical exams with real-time ultrasonography or electrocardiography.

Data Analysis

Mean ± standard deviation (sd) or standard error (se) were generated using a SPSS/PC+ stat package. Serum progesterone values for first vs. second pregnancies in individual females were compared using a Mann-Whitney U–Wilcoxon Rank Sum W test to look for a shift in distribution ($\alpha = 0.05$). Seasonality in onset of estrus and anestrus was tested by chi square analysis ($\alpha = 0.05$), random distribution being the null hypothesis.

RESULTS

Demographics

Survivorship is illustrated in Figure 1. As of September, 1993, 19 killer whales (49% of the total inventory) were alive. Ten of these, 53% of the current inventory,

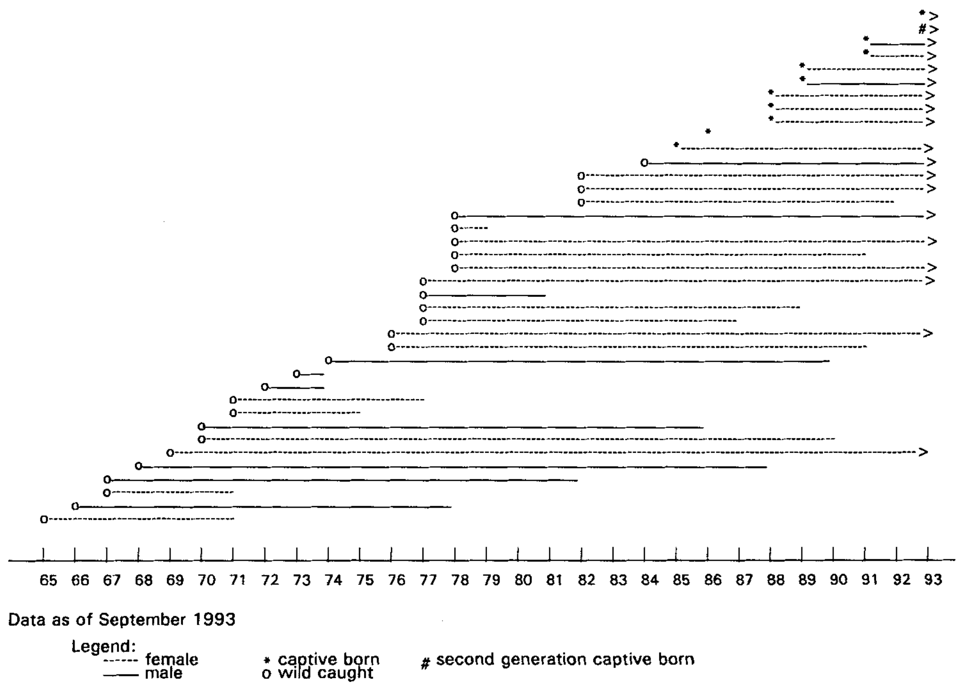

Fig. 1. Survivorship of killer whales at Sea World. Arrows indicate animals alive at inventory, September, 1993.

were captive-born. The age distribution of the inventory (Fig. 2) was bimodal, with the captive-born whales representing the younger age categories and the wild-caught whales representing the older age categories. Estimated mean age (±sd) of the wild-caught whales (September, 1993) was 17.6 ± 4.2 years (range: 12–27 years); ages of the captive-born whales ranged from under 1 year to 8 years.

The mean estimated age (±sd) at death for wild-caught whales was 13.7 ± 7.1 years, ranging from 3 to >29 years (Fig. 3). Of the nine captive-born whales which were live-born in the Sea World breeding program, one calf (8626) had congenital failure of the foramen ovale to close. At birth, the calf was vigorous but, despite nursing, grew progressively weaker and died 11 days after birth.

Reproduction

As of September, 1993, six females had borne calves, sired by five different wild-caught males (Table 2). One female had three calves; two others had two calves. The oldest captive-born female (8501) had her first calf in February, 1993. A total of ten calves have been born. All but one of the births were tail-first, but both tail-first and head-first presentations resulted in live births.

Estimated age of wild-caught females at first parturition ranged from 11–15 years ($\bar{x}$ ± sd = 12.7 ± 3.0 years; Table 2). The captive-born female (8501) was 8 years old at first parturition. Calving intervals ranged from 32–58 months. These intervals were influenced by access to males and lactation.

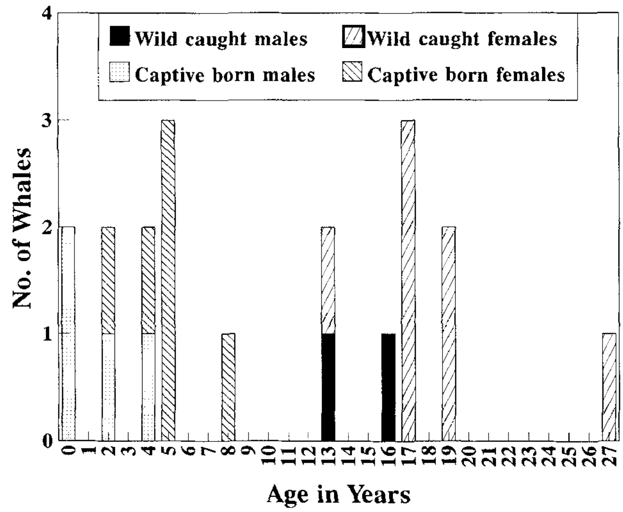

Fig. 2. Age distribution of the current population (September, 1993) of killer whales on display at Sea World. Ages for the wild-caught animals were estimated as described in the text.

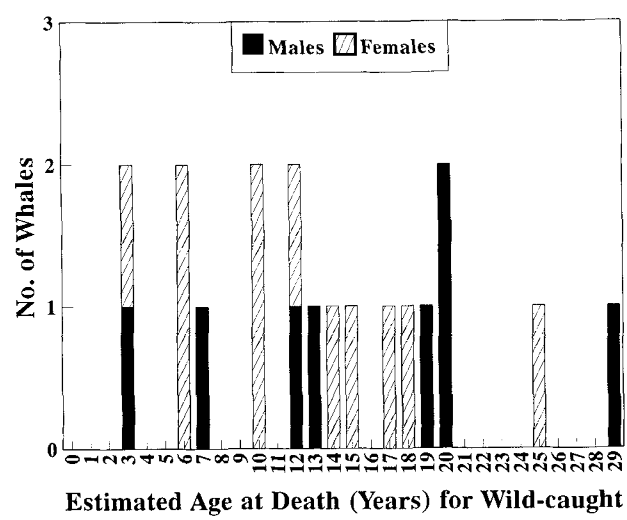

Fig. 3. Estimated ages at death for killer whales in the Sea World collection.

Serum Progesterone

Conceptive and nonconceptive ovarian cycles of these killer whales were investigated by Walker et al. [1988] and Robeck et al. [1993], using urine concentrations of ovarian steroid hormone metabolites and direct or indirect (bioactive) concentrations of urinary gonadotropins. In nonconceptive estrous cycles, an estrogen surge was followed by an increase in progesterone, which peaked at about 2 weeks after the initial rise and returned to baseline at 4 weeks. Based on this pattern of change in reproductive hormones during the estrous cycle, twice-monthly to monthly

TABLE 2. Gestation and calving intervals in the captive population at Sea World

Female ID	Age[a] at primiparity (in years)	Calf ID: Date of birth (sex)	Status	Gestation (in days)	Calving intervals (in months)	Sire ID
7806	11	8501: 09/26/85 (F)	Alive	512		7601
		8801: 11/04/88 (F)	Alive	522	38	8701
		9302: 09/09/93 (M)	Alive	519	58	9201
7602	12	8626: 01/05/86 (F)	Dead	523		7601
		8876: 11/26/88 (F)	Alive	530	35	8726
7706	15	8627: 01/31/86 (F)	Stillbirth	504		7601
		8826: 09/23/88 (F)	Alive	468	32	8726
8702	15	8901: 07/11/89 (F)	Alive	519		8701
7804	15	9126: 07/09/91 (F)	Alive	535		7801
8501	8	9378: 02/02/93 (M)	Alive	539		7801
$\bar{x} \pm$ sd:	12.7 ± 3 years of age			517 ± 20 days		

[a]Ages at primiparity (first parturition) for three other females currently part of the Sea World breeding programs but whose first calves were born at other facilities were 11 years of age (8727), 13 years (9301), and 17 years (9376). The dam of 9226 was 12 years of age at primiparity.

serum progesterone sampling was used to monitor female reproductive condition. This sampling has continued for 10 years, and the cumulative data are summarized for individual whales in Table 3. Overall mean serum progesterone values (±se) were as follows: periods of noncycling, 121 ± 20 pg/ml (N = 11; range: <100–420 pg/ml); peak elevation during nonconceptive ovulatory cycles, 3,962 ± 2,280 pg/ml (N = 10; range: 1,000–13,740 pg/ml); first pregnancy, 14,592 ± 3,854 pg/ml (N = 6; range: 1,500–68,670 pg/ml); second pregnancy, 8,389 ± 395 pg/ml (N = 3; range: 900–22,370 pg/ml); and third pregnancy, 8,180 ± 4,556 pg/ml (N = 1).

The length of gestation was estimated by taking, as a starting date, the midpoint between the last low serum progesterone value and the first elevated value of the pregnancy and, as an ending date, the birth of the calf. Mean gestation (±sd) for ten pregnancies was 517 ± 20 days (17 months; range: 468–539 days; Table 2). Serum progesterone profiles are shown for three females (Fig. 4). A general pattern of an initial rapid elevation in progesterone levels, followed by an overall decrease in levels, a second period of elevation, and a gradual decline throughout the remainder of the pregnancy, was seen in all pregnancies. Progesterone levels during first pregnancies were higher than those of second or third pregnancies (Wilcoxon Rank Sum W test: U = 2398.5, df1 = 111, df2 = 106, $P < 0.0001$).

Females exhibited periods (data not shown) of multiple estrous cycling (polyestrus) interspersed with periods of noncycling (presumed anestrus). The mean interval (±sd) between estrous cycles during polyestrus, measured from one serum progesterone peak elevation to the next, was 43.8 ± 2.9 days (N = 50; range: 18–91 days). On average, there were four estrous cycles per polyestrous period, but duration of polyestrus was highly variable, both over time for a given whale and between whales. The number of cycles per period varied from one to 12, the latter polyestrous period spanning 20 months. The length of intervening noncycling periods was also highly variable, lasting on average 7–8 months but ranging from 3–16 months. No synchrony to the timing of polyestrous cycling and noncycling periods among females was observed. Long sustained periods of anestrus were observed in three females in

TABLE 3. Mean serum progesterone values for adult female killer whales for anestrous periods, peak progesterone values during ovulatory cycles, and first through third pregnancies

Female	Total number of values	Anestrous pg/ml ± se (range)	Ovulation peak pg/ml ± se (range)	First pregnancy pg/ml ± se (range)	Second pregnancy pg/ml ± se (range)	Third pregnancy pg/ml ± se
7806	222	121 ± 07	4,368 ± 586	12,749 ± 1,072	7,675 ± 521	8,180 ± 4,556
		(<100–340)	(1,850–8,960)	(1,500–38,400)	(3,300–13,680)	
7602	75	109 ± 03	5,441 ± 1,149	17,556 ± 2,123	9,342 ± 798	
		(<100–170)	(1,830–7,420)	(4,750–68,670)	(1,030–22,370)	
7706	52	108 ± 08	3,744 ± 732	20,503 ± 1,805	8,044 ± 635	
		(<100–150)	(1,300–7,900)	(2,880–56,200)	(900–18,470)	
8702	50	171 ± 36	2,738 ± 293	11,282 ± 1,493		
		(<100–420)	(1,290–5,330)	(2,030–37,020)		
7804	117	132 ± 06	3,323 ± 368	14,883 ± 1,459		
		(<100–290)	(1,290–5,950)	(6,050–38,430)		
8501	53	122 ± 08		10,577 ± 573		
		(<100–280)		(1,490–22,840)		
7701	33	116 ± 06	4,819 ± 487			
		(<100–190)	(1,330–7,760)			
7803	85	124 ± 05	3,529 ± 605			
		(<100–230)	(1,000–13,740)			
8628	29	108 ± 06	4,268 ± 242			
		(<100–250)	(3,840–5,050)			
8727	69	100 ± 04	2,527 ± 59			
		(<100–320)	(2,410–2,600)			
8951	8		5,761 ± 945			
			(1,060–9,180)			
9101	32	122 ± 07				
		(<100–260)				
Mean ± se		121 ± 20	3,962 ± 2,280	14,592 ± 3,854	8,389 ± 395	8,180 ± 4,556

their 20s, possibly indicating that they were in postestrous condition. The oldest female of the current inventory (>27 years) has exhibited continuous anestrus for the past 6 years. This female previously had six term pregnancies [Duffield and Miller, 1988], prior to coming to Sea World in January, 1987, and cycled at Sea World until mid-1987.

Monthly distribution of onset of polyestrous cycling, onset of noncycling periods, and births are compared in Figure 5. Onset of polyestrous periods occurred throughout the year, with no statistical evidence of seasonality ($\chi^2 = 7.21$, df = 11, $P > 0.5$). Onset of noncycling periods occurred from June to February but did not show statistical evidence of seasonality ($\chi^2 = 16.0$, df = 11, $P > 0.1$). Similarily, births occurred from July to February, with no statistical evidence of seasonality ($\chi^2 = 17.66$, df = 11, $P > 0.05$).

DISCUSSION

The breeding of killer whales in captivity makes it possible to examine physiological and behavioral aspects of their reproductive biology that are difficult or impossible to observe in the wild. These include age of sexual maturity and first parturition (primiparity), length of gestation, calving intervals, reproductive hormone

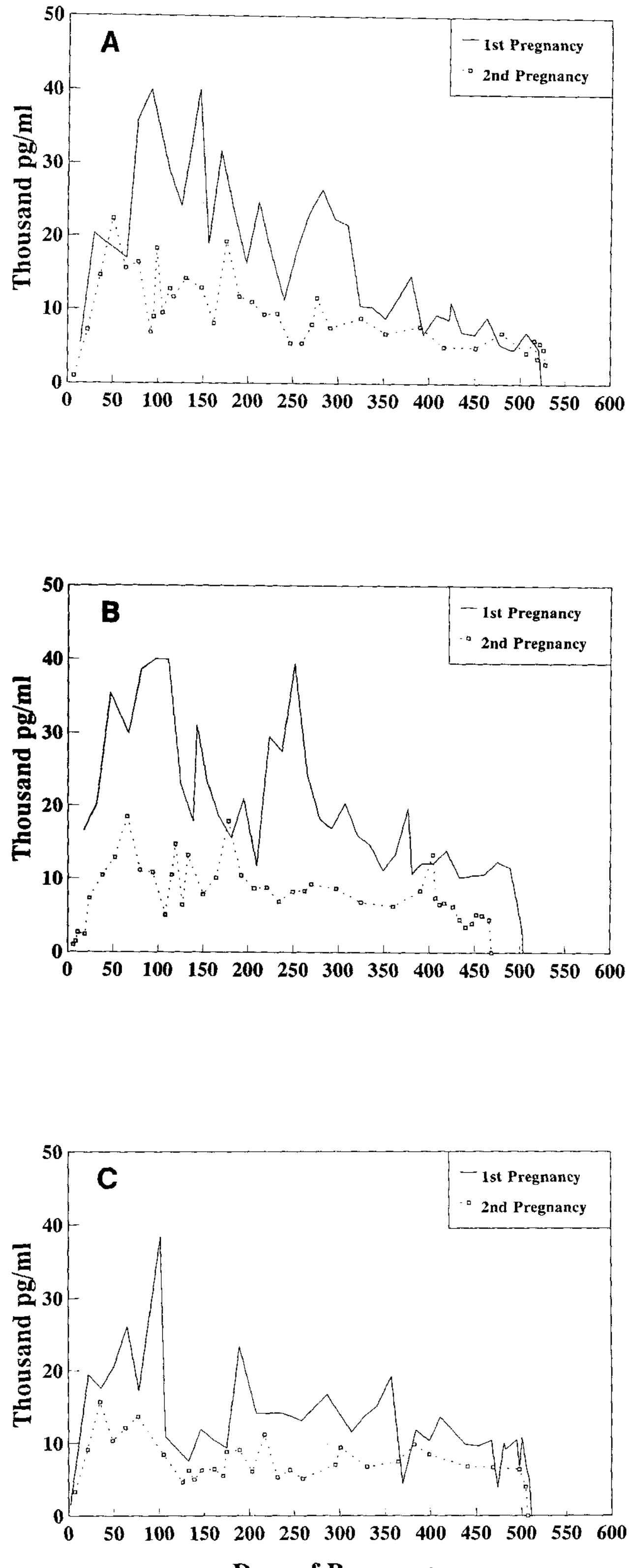

Fig. 4. Serum progesterone profiles for first and second pregnancies in three females. **A** = 7602, **B** = 7706, **C** = 7806. The third pregnancy for female 7806 was similar in values to her second pregnancy.

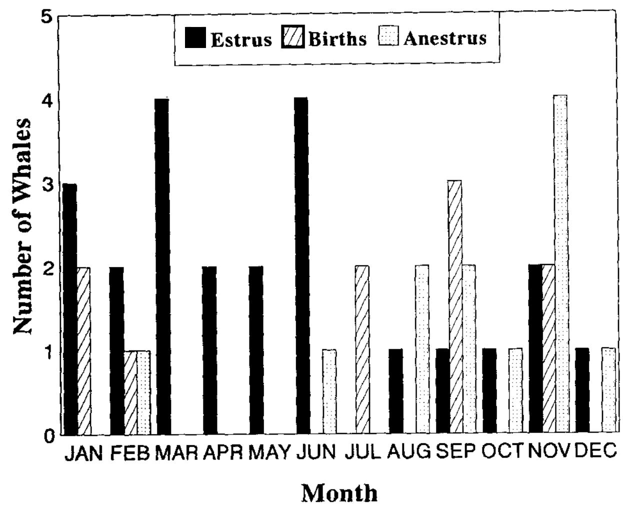

Fig. 5. Distribution of onset of estrus cycles, onset of anestrus period, and birth events by month of occurrence.

cycles, and male and female reproductive behavior as well as the events of parturition and calf development.

The ages of primiparity for killer whales in British Columbia and Washington State coastal waters are reported to be approximately 12–16 years, suggesting, by extrapolation from gestation of 17 months, first conception and, therefore, sexual maturity between 10.6 and 14.6 years of age [Bigg et al., 1990; Olesiuk et al., 1990]. Primiparity, in these field studies, was based on first observed viable calf and probably biases the suggested age of sexual maturity upwards, as neonatal mortality (defined as occurring between birth and 0.5 years of age) was estimated to be approximately 43%. To this mortality estimate is added the possibility that, as seen in reproductive data on bottlenose dolphins (*Tursiops truncatus*) in captivity, the stillbirth and failure to thrive rate is substantially higher for first-time mothers than subsequent births [Marine Mammal Census Data; Duffield and Shell, manuscript in preparation]. Christensen [1982, 1984] suggested that for killer whales off Norway, pregnancy could occur as early as 6–8 years. Estimated age at first pregnancy for whales in captivity was 9 years for a North Pacific female [Duffield and Miller, 1988], 9–13 years for Icelandic females in the Sea World breeding program, and 6 years for a captive-born female (8501). The captive-born female became pregnant on her first or second estrous cycle. Mean estimated age at which six wild-caught Icelandic females at Sea world first exhibited luteal activity was 8.3 ± 0.21 years, with a range of 8–9 years [Robeck et al., 1993]. These data fit with the Norwegian observations but suggest that the estimate of age at sexual maturity for coastal eastern Pacific females is high. Field observations of first viable calf to known-aged females of 12–16 years of age more likely reflects their first successful contribution to recruitment.

Neonatal mortality in the wild of approximately 43% [Olesiuk et al., 1990] was estimated from stranding and survival rates of observed newborn calves and corrected for an assumed stillbirth rate. Neonatal mortality (including stillbirth) in the Sea World breeding colony was 20%. There was one stillbirth and one postnatal death, presumably due to a congenital heart defect.

Calving intervals have been estimated to range from 3.0–8.3 years for North Atlantic and 7.3 years for Antarctic killer whale stocks [Perrin and Reilly, 1984] and from 2–12 years for resident killer whale pods in the coastal waters of British Columbia and Washington State [Olesiuk et al., 1990]. Calving intervals in captivity ranged from 32–38 months (with an average of 3 years) between first and second calves to 58 months (>4 years) for a third calf. These intervals may be biased upward by periods when males were not present.

Walker et al. [1988] and Robeck et al. [1993] looked at the production of urinary reproductive steroid metabolites and gonadotropins to investigate estrous cycling and pregnancy in females of the Sea World breeding colony. These studies reported a 6–7 week ovarian cycle [Walker et al., 1988], which was further characterized as a mean nonconceptive ovarian cycle of 41.6 ± 6.7 days [Robeck et al., 1993]; described the luteal and follicular phases of the estrous cycle; and determined that females were spontaneous ovulators and variably polyestrous. In conjunction with these studies, the serum progesterone analyses, taken on a twice-weekly to monthly basis, provided a 10 year overview of polyestrous and anestrous periods and pregnancies.

The length of gestation for seven of the ten pregnancies in the Sea World breeding program were closer to the mean of 17 months ± 20 days. However, successful live births occurred from gestations of 15–18 months. The reproductive hormone data do not support earlier estimates of killer whale gestation of 12 months [Jonsgård and Lyshoel, 1970; Perrin and Reilly, 1984] and extend the higher estimates of 15–16 months [Perrin and Reilly, 1984] to 15–18 months, with the average being 17 months. Further investigation is needed to establish whether there are geographic differences in killer whale gestation. For example, gestation of 15 months has been suggested for Antarctic killer whales, based on bimodality of fetal length data from Antarctic whaling data [Perrin, 1982].

In many small whale and dolphin species, although births can occur throughout the year, there characteristically are peaks in birth activity that are bimodal or spread over several months [for examples, see Perrin et al., 1984], and there can be extensive geographical differences in these distributions [Barlow, 1984]. Regional differences in reproductive timing have been observed for killer whales [Matkin and Leatherwood, 1986]. Calving in killer whale communities of British Columbia and Washington State waters has been reported to be diffusely seasonal, with most births occurring from October to March [Olesiuk et al., 1990] but with some births recorded from all months except August. Calf sightings in British and Irish Atlantic waters were concentrated from November through February [Evans, 1988]. Births occurred at Sea World from July to February (Fig. 4). Observations that estrous cycle activity, in these females, was individually variable and occurred throughout the year [Robeck et al., 1993; and serum progesterone data summarized here] suggest the potential for year-round births.

Periods of polyestrous cycling in the females were initiated in the presence and absence of males. Mating behavior by males was not sufficient to cause noncycling females to enter estrus. Based on daily behavior logs, males demonstrated concentrated courting activity towards a particular female for 5–10 days during what has been shown by examination of urinary reproductive steroid metabolites and gonadotropins to be the time of presumptive ovulation [Robeck et al., 1993]. However, males were observed to copulate not only with females in estrus, but with noncycling (presumed anestrous) and pregnant females as well. Mating and sexual behavior has been noted in a wide variety of social, nonreproductive contexts in dolphins [Norris and Dohl, 1980; Wells, 1984; Ostman, 1991]. Copulation during nonovulatory periods has been well documented in other species, such as chimpanzees [Goodall, 1986]. This has cautionary implications for interpretation of observations of mating behavior (and seasonality based on mating behavior) in the wild [for example see, Jacobsen, 1986; Matkin and Leatherwood, 1986; Osborne, 1986].

In the majority of the pregnancies, particularly the first pregnancies (Fig. 4), a decrease in serum progesterone levels was observed around the end of the first trimester of pregnancy. The actual timing of this decrease varied with individual whales, occurring from 5 to as late as 8 months of gestation. This time of decrease and second elevation in serum progesterone levels may be indicative of a switch from corpus luteum to placental production of progesterone as noted in other mammals [Edqvist and Stabenfeldt, 1980]. A similar pattern of change in serum progesterone levels during pregnancy was observed in the bottlenose dolphin [Cornell et al., 1987]. Both at Sea World and at other facilities with breeding killer whales, females with sustained elevated progesterone levels have exhibited apparent pregnancy terminations, either as spontaneous abortions or presumed false pregnancies, at this interface. The females, typically, entered estrous cycling immediately and became pregnant again. Observations of prolonged luteal phase elevation of progesterone, possibly indicating false pregnancy, have also been reported for bottlenose dolphins [Schroeder and Keller, 1990; Yoshioka et al., 1986]. A transition period when progesterone levels are dropping may signal an important time to monitor during the pregnancy in order to evaluate whether progesterone levels are too low to sustain pregnancy [Schroeder, 1990]. These observations suggest an area for further study. Matching the timing of change in progesterone levels with the progesterone profile of whales in other breeding facilities whose conception dates were not known has allowed assessment of the stage of the pregnancy when detected and accurate prediction of parturition date.

CONCLUSIONS

1. Through September, 1993, Sea World has maintained 39 killer whales, including wild-caught and captive-born animals. Nineteen whales are in the current breeding program: 53% of these (10 of the 19 whales) were captive-born. One second-generation birth had occurred.

2. Average gestation, based on estimates of conception from twice-monthly to monthly serum progesterone analysis, was 17 months ($\bar{x} \pm sd = 517 \pm 20$ days). However, normal full-term calves were born after gestations of 15 and 18 months.

3. Polyestrus was variable and interspersed with anestrous periods lasting from 3–16 months. Alternating periods of polyestrus and noncycling (anestrus) varied from female to female and were not synchronous.

4. Females experienced estrus whether or not males were present. The estrous cycle ($\bar{x} \pm sd$) was 43.8 ± 2.9 days. Males were observed to copulate with females during estrus, anestrus, and pregnancy.

5. Serum progesterone levels were higher for first than for second or third pregnancies, and there was a common pattern of progesterone level change during pregnancy, characterized by an initial rise, fall, and second rise, followed by a gradual decline throughout the rest of gestation.

ACKNOWLEDGMENTS

We thank the animal care, veterinary, laboratory, training, and curatorial staffs at all the Sea World Parks for their care of these killer whales and for their thorough and painstaking data collection. This is Sea World technical contribution 9212-F.

REFERENCES

Asper, E.D.; Young, W.G.; Walsh, M.T. Observations on the birth and development of a captive-born killer whale. INTERNATIONAL ZOO YEARBOOK 27:295–304, 1988.

Asper, E.D.; Duffield, D.A.; Dimeo-Ediger, N.; Shell, D. Marine mammals in zoos, aquaria and marine zoological parks in North America: 1990 census report. INTERNATIONAL ZOO YEARBOOK 29:179–187, 1990.

Asper, E.D.; Andrews, B.F.; Antrim, J.E.; Young, W.G. Establishing and maintaining successful breeding programs for whales and dolphins in a zoological environment. IBI REPORTS, INTERNATIONAL MARINE BIOLOGY RESEARCH INSTITUTE Kamogawa, Japan, 3:71–78, 1992.

Barlow, J. Reproductive seasonality in pelagic dolphins (*Stenella* spp.): Implications for measuring rates. REPORT, INTERNATIONAL WHALING COMMISSION (special issue) 6:191–198, 1984.

Bigg, M.A.; Olesiuk, P.F.; Ellis, G.M.: Ford, J.K.B.; Balcomb III, K.C. Social organization and genealogy of resident killer whales (*Orcinus orca*) in the coastal waters of British Columbia and Washington State. REPORT, INTERNATIONAL WHALING COMMISSION (special issue) 12:383–405, 1990.

Christensen, I. Killer whales in Norwegian coastal waters. REPORT, INTERNATIONAL WHALING COMMISSION 32:633–641, 1982.

Christensen, I. Growth and reproduction of killer whales, *Orcinus orca,* in Norwegian coastal waters. REPORT, INTERNATIONAL WHALING COMMISSION (special issue) 6:253–258, 1984.

Cornell, L.H.; Asper, E.D.; Antrim, J.E.; Searles, S.S.; Young, W.G.; Goff, T. Progress report: Results of a long range captive breeding program for the bottlenose dolphin, *Tursiops truncatus* and *Tursiops truncatus gilli.* ZOO BIOLOGY 6:41–53, 1987.

Duffield, D.A.; Miller, K.W. Demographic features of killer whales in oceanaria in the United States and Canada, 1965–1987. RIT FISKIDEILDAR 11:297–306, 1988.

Edqvist, L.; Stabenfeldt, G.H. Reproductive hormones. Pp. 513–544 in CLINICAL BIOCHEMISTRY OF DOMESTIC ANIMALS, 3rd ed. J.J. Kaneko, ed. New York, Academic Press, 1980.

Evans, P.G.H. Killer whales (*Orcinus orca*) in British and Irish waters. RIT FISKIDEILDAR 11:42–54, 1988.

Goodall, J. Sexual behavior. Pp. 443–485 in THE CHIMPANZEES OF GOMBE: PATTERNS OF BEHAVIOR. Cambridge, MA, Belknap Press, 1986.

Hammond, P.S.; Mizroch, S.A.; Donovan, G.P., eds. INDIVIDUAL RECOGNITION OF CETACEANS: USE OF PHOTO-IDENTIFICATION AND OTHER TECHNIQUES TO ESTIMATE POPULATION PARAMETERS. Special Issue 12. Cambridge, International Whaling Commission, 1990.

Jacobsen, J.K. The behavior of *Orcinus orca* in the Johnstone Strait, British Columbia. Pp. 135–185 in BEHAVIORAL BIOLOGY OF KILLER WHALES. B.C. Kirkevold; J.S. Lockard, eds. New York, Alan R. Liss, 1986.

Jonsgård, A.; Lyshoel, P.B. A contribution to the knowledge of the biology of the killer whale *Orcinus orca* (L.). NORWAY JOURNAL OF ZOOLOGY 18:41–48, 1970.

Kirkevold, B.C.; Lockard, J.S., eds. BEHAVIORAL BIOLOGY OF KILLER WHALES. New York, Alan R. Liss, 1986.

Matkin, C.O.; Leatherwood, S. General biology of the killer whale, *Orcinus orca:* A synopsis of knowledge. Pp. 35–68 in BEHAVIORAL BIOLOGY OF KILLER WHALES. B.C. Kirkevold; J.S. Lockard, eds. New York, Alan R. Liss, 1986.

Norris, K.S.; Dohl, T.P. Behavior of the Hawaiian spinner dolphin, *Stenella longirostris.* FISHERIES BULLETIN, U.S. 77:821–849, 1980.

Olesiuk, P.F.; Bigg, M.A.; Ellis, G.M. Life history and population dynamics of resident killer whales (*Orcinus orca*) in the coastal waters of British Columbia and Washington state. REPORT, INTERNATIONAL WHALING COMMISSION (special issue) 12:209–243, 1990.

Osborne, R.W. A behavioral budget of Puget

Sound killer whales. Pp. 211–249 in BEHAVIORAL BIOLOGY OF KILLER WHALES. B.C. Kirkevold; J.S. Lockard, eds. New York, Alan R. Liss, 1986.

Ostman, J. Changes in aggressive and sexual behavior between two male bottlenose dolphins (*Tursiops truncatus*) in a captive colony. Pp. 305–317 in DOLPHIN SOCIEITES. K. Pryor; K.S. Norris, eds. Berkeley, University of California Press, 1991.

Perrin, W.F. Report of the workshop on identity, structure and vital rates of killer whale populations. REPORT, INTERNATIONAL WHALING COMMISSION 32:617–631, 1982.

Perrin, W.F.; Reilly, S.B. Reproductive parameters of dolphins and small whales of the Family Delphinidae. REPORT, INTERNATIONAL WHALING COMMISSION (special issue) 6:97–133, 1984.

Perrin, W.F.; Brownell, R.L., Jr.; DeMaster, D.P., eds. REPRODUCTION IN WHALES, DOLPHINS AND PROPOISES. Special Issue 6. Cambridge, International Whaling Commission, 1984.

Robeck, T.R.; Schneyer, A.L.; McBain, J.F.; Dalton, L.M.; Walsh, M.T.; Czekala, N.M.; Kraemer, D.C. Analysis of urinary immunoreactive steroid metabolites and gonadotropins for characterization of the estrous cycle, breeding period, and seasonal estrous activity of captive killer whales (*Orcinus orca*). ZOO BIOLOGY 12: 173–187, 1993.

Schroeder, J.P. Breeding bottlenose dolphins in captivity. Pp. 435–446 in THE BOTTLENOSE DOLPHIN. S. Leatherwood; R.R. Reeves, eds. San Diego, Academic Press, 1990.

Schroeder, J.P.; Keller, K.V. Artificial insemination of bottlenose dolphins. Pp. 447–460 in THE BOTTLENOSE DOLPHIN. S. Leatherwood; R.R. Reeves, eds. San Diego, Academic Press, 1990.

Sigurjonsson, J.; Leatherwood, S., eds. NORTH ATLANTIC KILLER WHALES. Reykjavik, Rit Fiskideildar XI, 1988.

Walker, L.A.; Cornell, L.; Dahl, K.D.; Czekala, N.M.; Dargen, C.M.; Joseph, B.; Hsueh, A.J.W.; Lasley, B.L. Urinary concentrations of ovarian steroid hormone metabolites and bioactive follicle-stimulating hormone in killer whales (*Orcinus orca*) during ovarian cycles and pregnancy. BIOLOGY OF REPRODUCTION 39: 1013–1020, 1988.

Wells, R.S. Reproductive behavior and hormonal correlates in Hawaiian spinner dolphins, *Stenella longirostris*. REPORT, INTERNATIONAL WHALING COMMISSION (special issue) 6: 465–472, 1984.

Yoshioka, M.; Mohri, E.; Tobayama, T.; Aida, K.; Hanyu, I. Annual changes in serum reproductive hormone levels in the captive female bottle-nosed dolphins. BULLETIN, JAPANESE SOCIETY OF SCIENTIFIC FISHERIES 52: 1939–1946, 1986.