Animal Reproduction Science 124 (2011) 184–193

Contents lists available at ScienceDirect

Animal Reproduction Science

journal homepage: www.elsevier.com/locate/anireprosci

# Reproductive cycles of marine mammals☆

P. Pomeroy

*NERC Sea Mammal Research Unit, University of St Andrews, St Andrews KY16 8LB, UK*

ARTICLE INFO

*Article history:*
Available online 24 September 2010

*Keywords:*
Marine mammal
Seals
Whales
Dolphins
Reproductive cycles

ABSTRACT

Marine mammals conform to the general mammalian reproductive system centered on the hypothalamic–pituitary–gonadal axis. Most marine mammals are long-lived and of large body size with lesser reproductive rates than many other animals, a consequence of their interaction with the marine environment where the demands of acquiring resources from the ocean must be balanced with the need for bearing offspring in a suitable place for survival. The degree of spatial and temporal separation of these life history phases in many species is a key feature of their ecology. The reproductive physiology of pinnipeds, cetaceans, sirenians, sea otters and polar bears has been more thoroughly characterized for the more accessible species.



## 1. Introduction

Current knowledge of the reproductive cycles of marine mammals has been acquired necessarily from relatively few species, sometimes from few individuals and consequently descriptive generalizations are the norm. However, there are important differences in comparative anatomy and physiology even in quite closely related species. The group conforms to the general mammalian reproductive system of the hypothalamic–pituitary–gonadal axis. A reproductive cycle is defined as the normal time for a female to reproduce, i.e. to complete the processes associated with a fertile oestrus, ovulation, conception, gestation, birth and lactation. Environmental, nutritional or social influences may affect the timing of this cycle, such that the consequences of one breeding episode may be apparent subsequently (Arnbom et al., 1997; Boyd et al., 1999; Pomeroy et al., 1999; Reijnders et al., 2010).

It is impossible to separate a reproductive cycle from its context, therefore, the issues of when, where and how much breeding occurs is as much a function of phylogeny as of ecological imperatives. This review includes a complex and varied group of species (Table 1). Thus while an obvious difference among the subjects under consideration is whether they are totally or partially aquatic, reproductive similarities between the pinnipeds, polar bears and sea otters betray their carnivore origin, while the major life history differences between the toothed and baleen whales reflect at least to some extent whether or not reproduction is tied intimately to seasonal or annual migrations. Similarly, reproductive differences between manatees and dugongs are partially explained by the ways in which they interact with their environments. The fact that most marine mammals are long-lived and of large body size with lesser reproductive rates than many other species is also linked to the need to balance the demands of acquiring resources from the ocean with the need for bearing offspring in a suitable place for survival. The degree of spatial and temporal separation of these life history phases in many species is a key feature of their ecology (Table 1).

## 2. Pinniped reproductive cycles

Pinniped female reproductive cycles are characterised by a period of delayed implantation, during which development of the blastocyst is either very slow or negligible. In pinnipeds, as in ursids and mustelids, delayed implanta-

☆ This paper is part of the special issue entitled: Reproductive Cycles of Animals, Guest Edited by Michael G Diskin and Alexander Evans.

*E-mail address:* pp6@st-andrews.ac.uk

0378-4320/$ – see front matter. Crown Copyright © 2010 Published by Elsevier B.V. All rights reserved.
doi:10.1016/j.anireprosci.2010.08.021

**Table 1**
Classification and examples of marine mammals.

| Order | Family | Examples |
|---|---|---|
| Carnivora | | |
| Pinnipedia | Phocidae | Earless seals, e.g. elephant, hooded, grey, harbour seals |
| | Otariidae | Eared seals, e.g. northern fur seals, Steller sea lions |
| | Odobenidae | Walrus |
| | Ursidae | Polar bear |
| | Mustelidae | Sea otter |
| Cetacea | | |
| Mysticeti | Balaenopteridae | Blue, fin, minke |
| | Eschrichtiidae | Gray whale |
| | Balaenidae | Southern right whale |
| | Neobalaenidae | Pygmy right whale |
| Odontoceti | Delphinidae | Orca, beluga |
| | Phocoenidae | Porpoises |
| | Monodontidae | Narwhal, beluga |
| | Pontoporidae | Franciscana |
| | Liptotidae | Baiji |
| | Iniidae | Boto |
| | Plantanistidae | Indian river dolphin |
| | Ziphidae | Beaked whales |
| | Kogiidae | Pygmy sperm whale |
| | Physeteridae | Sperm whale |
| Sirenia | | |
| Trichechidae | Manatees | |
| Dugongidae | Dugongs | |

tion appears to be obligate. It has been suggested that the period of delayed implantation confers flexibility of timing of parturition on females and is most closely controlled by photoperiod. Neurological transduction of stimuli in the brain appears to be centered in the hypothalamus, but the physiology of delayed implantation is less clear (for further details see Boyd et al., 1999).

Most species are thought to implant during a decreasing photoperiod. Photoperiodic response may be controlled by periods of receptivity when exposure to light or dark may define endocrine response. Pinnipeds are thought to be particularly receptive to blastocyst reactivation when they are exposed to a particular day length, during decreasing day length (Temte, 1991). Harbour seals showed a decreased pituitary sensitivity to LH during winter and spring, consistent with photoperiod control (Gardiner et al., 1999). Nutritional state is also an important factor which may impact reproductive patterns (Boyd et al., 1999).

### 2.1. Oestrus

Oestrus is the state of receptivity to mating that a female enters during the reproductive cycle. It has physiological and behavioural components. The following description is based on pinnipeds for which most information is available (Table 2), obvious contrasts with other groups are highlighted. Greater maternal plasma concentrations of oestrogens at parturition (>30 pg/mL in northern fur seals) decrease rapidly and then increase rapidly, as cells in the ovary secrete oestrogens, which together with decreasing concentrations of progesterone are likely the stimulus for hypothalamic GnRH secretion, LH and FSH production, allowing an ovarian follicle to mature. While phocids such as grey seals begin follicular recruitment from the pool of immature ovarian follicles around parturition, taking around 14 days to mature, northern fur seals *Callorhinus ursinus* may take 5 months for a similar process to occur. This difference is probably directly related to the relative functional activity of phocid and otariid corpora lutea. Rapid follicular growth ends with follicle maturation and ovulation as the epithelium of the ovary thins and ruptures. The process of follicular maturation and the secretion of large quantities of oestrogen by the theca interna surrounding the mature follicle marks the onset of oestrous behaviour in the female. The ovum is released and collected by the fimbria into the oviduct where fertilization normally occurs. A conceptus migrates around the uterine horn before implantation and placentation occurs, but once implanted, active gestation begins. The follicle that produced the ovum released at ovulation continues to develop into a corpus luteum. The lining of granulosa cells in the matured follicle secretes steroid precursors of the hormones produced by the corpus luteum. The empty vacuole of the ruptured follicle is quickly filled by expanding luteal cells. Progesterone produced by the corpus luteum, which may eventually occupy a large portion of the ovary, is necessary in controlling pregnancy along with placental and pituitary hormones (but see below). Hilar rete glands have been observed in grey and ringed seal ovaries and although most abundant during delayed implantation, their function is not known (Boyd, 1984).

Ovulation tends to occur in pinnipeds from alternate ovaries at successive oestrous episodes. Follicular growth in the ovary from which ovulation does not occur may be inhibited by local or paracrine activity from the adjacent uterine horn containing the current pregnancy. Thus ovulation and implantation tend to occur contralaterally, although this is not always the case. In contrast, in most odontocetes ovulations occur more frequently from the left ovary until later in life when ovulation from the right ovary predominates (Slijper, 1949).

Most pinnipeds that have been studied are functionally monoestrus. Oestrus occurs postpartum either during

**Table 2**
Reproductive Characteristics of three species of Pinnipeds.

| Reproductive characteristics | Harbor seal (*Phoca vitulina*) | California sea lion (*Zalophus californianus*) | Walrus (*Odobenus rosmarus*) |
|---|---|---|---|
| Pupping period | Early May | Late may, early June | Mid-April to mid-June, peak May |
| Timing of ovulation | End of lactation | Approx. 28 days postpartum | Mid-lactation |
| Conception | June | Late June, early July | January–March (peak February) |
| Duration of lactation | 21–42 days | 6–12 months | 24+ months |
| Delayed implantation period | July–August | July–September | March–July |
| Delayed implantation | 1.5–3 months | 3 months | 4–5 months |
| Postimplantation gestation | September–May | October–May | August–May |
| Total gestation interval | 11 months | 11 Months | 15 months |