Reproductive biology of seals

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The reproductive biology of seals is fascinating in many aspects. As in most mammals, the time of onset of puberty in seals is variable. Once sexually mature, most but not all seals are seasonally mono-oestrous, with highly synchronized breeding seasons. They have evolved as either terrestrial or aquatic copulators, although a few species mate in a variety of habitats. Their mating strategies are diverse, ranging from serial monogamy to extreme polygyny. Gestation in seals is characterized by an embryonic diapause, which is obligate in most species. Reactivation of the blastocyst is followed by a placental gestation. All species of seal require a terrestrial (including ice floes) habitat for parturition. Lactation differs between the two seal families: phocid seals have an intense period of maternal investment, during which the mothers fast; otariid seals have a prolonged lactation during which intense bouts of suckling are interspersed by days of separation from their pups while the mother forages at sea. Although the anatomy and functional morphology of seals has been well described, less is known of the endocrinology of reproduction. This is due mainly to the logistical difficulties that researchers experience in collecting serial samples from a species that is relatively difficult to handle. This article reviews the basic anatomy and physiology, and our current understanding of the comparative aspects of reproduction in seals. Reproductive behaviours as well as the influences of environmental factors, such as photoperiod, nutrition and xenobiotics, are also discussed.

The suborder Pinnipedia consists of three families: the true seals (Phocidae), the sea lions and fur seals (Otariidae), and walruses (Odobenidae). The most pronounced physical difference between the two families of seal is that the otariid seals have more functional and articulate appendages than do phocid seals; in addition, otariids have external ears, or pinnae, whereas phocids do not. The two families of seal also differ in their reproductive strategies.

This review will focus our current understanding of the reproductive anatomy and functional morphology, endocrinology, and behaviour of phocid and otariid seals during the major reproductive events. These reproductive events include puberty, oestrous cycles and mating, gestation and lactation. This discussion is followed by a review of environmental influences on reproduction, including photoperiod, nutrition and xenobiotics.

Age of sexual maturity

Historically, when seals were hunted for skins and blubber, or during routine management culls, scientists and naturalists studied the ovaries to determine the age of sexual maturity (by the presence of corpora lutea) of a given species (Craig, 1964; Yoshida *et al.*, 1977; Born, 1982; Bester, 1990). Puberty, or the age of sexual maturity, in seals is not fixed but occurs over a range of years that is similar among female phocid and otariid seals (Tables 1 and 2). The age of sexual maturity is important because it is used as an index of the reproductive potential of a given species and can be assessed using a number of techniques (DeMaster, 1981).Various researchers have used slightly different definitions for the age at which sexual maturity is reached in seals. For female seals, this definition is either the age of first ovulation (considered puberty for this review), or the age of reproductive maturity, when the first embryonic attachment (implantation) takes place (Craig, 1964; Yoshida, 1982; Bester, 1995).

The age of sexual maturity is much more variable with male seals. This is due in part to the need for males to gain a necessary amount of behavioural experience after they have undergone physiological puberty. In many cases, spermatozoa may be present in the testes and epididymides of male seals from 3 to 6 years of age; however, these seals would not become prime breeders until they were 9–15 years of age (Boness and James, 1979; Bester, 1990; Bartsh *et al.*, 1992; Tables 3 and 4). The discrepancy between the ages is the necessary period for physiological maturity and social maturity to become coordinated. This coordination should ensure that the males can successfully sustain the energetic costs of reproduction.

Reproductive anatomy and morphology

The reproductive anatomy of female seals is remarkably similar to that of terrestrial mammals with the exception of a genital lock system in the lower vagina of seals (Fig. 1). This genital lock is composed of a fold of fibrous tissue, called hymeneal folds, which are located 4–6 cm from the entrance of the vagina (S. Atkinson, unpublished; Fig. 1). The hymeneal folds contain muscular cells that appear to constrict the entrance to the vagina. Presumably, the purpose of this genital lock is to contract the vaginal canal after intromission by the male, thereby excluding sea water, sand, pebbles and debris during copulation, or to prevent the entry of seawater during diving.

The uterus of seals is bicornuate, composed of a uterine body and two uterine horns (Fig. 1). The length of the uterine

Table 1. Reproductive characteristics for female phocid seals

Common name / *Scientific name*	Age of sexual maturity (years)	Duration of gestation (months)	Embryonic diapause (months)	Timing of post-partum oestrus (days post partum)	Duration of lactation (weeks)	Reproductive rates	Good sources of information
Caribbean monk seal / *Monachus tropicalis*	Unknown	Unknown	Unknown	Unknown	Unknown	Unknown	King, 1956
Mediterranean monk seal / *Monachus monachus*	4–5	9–11	Unknown	Unknown	6–20	Unknown	Sergeant et al., 1978; Marchessaux and Pergent-Martini, 1991
Hawaiian monk seal / *Monachus schauinslandi*	4–7	9–11?	Unknown	Unknown	5–6	0.16–0.75	Atkinson et al., 1994; Johanos et al., 1994; Iwasa and Atkinson, 1996
Northern elephant seal / *Mirounga angustirostris*	2–8	11	None?	22–24	3–4	0.8–0.92	Le Boeuf, 1972; Huber, 1987; Le Boeuf and Laws, 1994
Southern elephant seal / *Mirounga leonina*	2–6	11	3–4.5	14–19	3	0.66	Laws, 1956a; Griffiths, 1984; Crawley, 1990
Harbour seal / *Phoca vitulina*	3–6	9–11	1.5–3.5	Few days after weaning	4–6	0.2, 4 year old 0.5, 6 year old 0.9, >8 year old	Bigg and Fisher, 1974; Hayama et al., 1986; Bjorge, 1992
Spotted seal / *Phoca largha*	3–5	5–10	1.5–4	Immediately after weaning	2–4	?	Beier and Wartzok, 1979; Naito and Konno, 1979
Caspian seal / *Phoca caspica*	2–5	10	Unknown	Unknown	4–5	0.3–0.36	Krylov, 1990; Reeves et al., 1992
Ringed seal / *Phoca hispida*	4–6	11	3–4	Near end of lactation	5–7	0.73–0.85	McLaren, 1958; Fedoseev, 1975
Baikal seal / *Phoca sibirica*	3–6	9–11	3.5	Near end of lactation	8–10	0.37–0.9	Thomas et al., 1982; Reeves et al., 1992
Ribbon seal / *Phoca fasciata*	3–5	11	2–2.5	Near end of lactation	3–4	0.9	Burns 1970; Naito and Konno, 1979
Harp seal / *Phoca groenlandica*	4–6	11	2–3	10–14	12 days	0.69–0.8	Nazarenko, 1975; Ouellette and Ronald, 1985
Grey seal / *Halichoerus grypus*	3–5	11	3.5	12–17	17–21 days	0.18, 4 year old 0.86, 5 year old 0.88, >6 year old	Boness and James, 1979; Hammill and Gosselin, 1995
Bearded seal / *Erignathus barbatus*	3–7	11	1.5–3.5	End of lactation	2–3	0.45–0.85	McLaren, 1958; Potelov, 1975
Hooded seal / *Cystophora cristata*	3–4	12	3–5	5–14	4 days	0.9	Oritsland, 1975; Born, 1982; Kovacs, 1990
Weddell seal / *Leptonychotes weddellii*	2–6	10	1–2	Near end of lactation	6–8	0.8	Testa et al., 1990; Bartsh et al., 1992
Crabeater seal / *Lobodon carcinophagus*	1–3	9–10	1–2	28–35	2–5	0.8	Siniff et al., 1979; Bengtson and Siniff, 1981
Leopard seal / *Hydrurga leptonyx*	2–6	10–12	None–1?	Unknown	8	0.47–0.61	Kooyman, 1981; Reeves et al., 1992
Ross seal / *Ommatophoca rossi*	2–7	Unknown	2–3	After weaning	3–5	Unknown	Skinner and Westlin-van Aarde, 1989

Table 2. Reproductive characteristics for female otarid seals

Common name / Scientific name	Age of sexual maturity (years)	Duration of gestation (months)	Embryonic diapause (months)	Timing of post-partum oestrus (days post partum)	Duration of lactation (months)	Reproductive rates	Good sources of information
California sea lion / *Zalophus californianus*	5–9	11–12	Yes	21–28	4–8 (up to 12)	0.71	Peterson and Bartholomew, 1967; Odell, 1975
Stellar sea lion / *Eumetopias jubatus*	4–6	11.5	3.5	11–14	3–12 (up to 36)	0.87	Pitcher and Calkins, 1981
Southern sea lion / *Otaria byronia*	3–4	11	Yes	6	5–12	Unknown	Campagna, 1985; Campagna and Le Boeuf, 1988
Australian sea lion / *Neophoca cinerea*	3	17.5 / 14–15*	4–5	7–10	12–24 / 17–18	Unknown	Tedman, 1991; Gales et al., 1992
Hooker's sea lion / *Phocarctos hookeri*	3	11–12	Unknown	6–10	8–12	Unknown	Marlow, 1975; Crawley, 1990; Reeves et al., 1992
Northern fur seal / *Callorhinus ursinus*	3–5	12	3–5	3–10	3–4	0.57–0.65, 5 year old; 0.3, 4 year old	Craig, 1964; Yoshida, 1982; Temte, 1985
South American fur seal / *Arctocephalus australis*	3–5	11–12	Unknown	5–8	7–36	0.82	Reeves et al., 1992
Galapagos fur seal / *Arctocephalus galapoensis*	Unknown	Unknown	Unknown	8	24	Unknown	Bonner, 1984; Reeves et al., 1992
Subantarctic fur seal / *Arctocephalus tropicalis*	4–6	12	4–5	7	10	0.79–0.84	Bester, 1990; Bester 1995
Antarctic fur seal / *Arctocephalus gazella*	3–4	11–12	Unknown	4–12	4	0.57, 4 year old 0.90, 6 year old	McCann, 1980; Boyd, 1991b
South African fur seal / *Arctocephalus pusillus*	1–4	11–12	3–5	4–6	6–12	0.70	Rand, 1955; Reeves et al., 1992
New Zealand fur seal / *Arctocephalus forsteri*	4–6	11–12	Unknown	9	9–12	Unknown	Stirling, 1971; Miller, 1975; Crawley, 1990
Guadalupe fur seal / *Arctocephalus townsendi*	Unknown	Unknown	Unknown	7–10	9	Unknown	Reeves et al., 1992
Juan Fernandez fur seal / *Arctocephalus philippii*	Unknown	11–12	Unknown	4–12	7–10	Unknown	Torres et al., 1985; Reeves et al., 1992

*Captive births

Table 3. Reproductive characteristics of male phocid seals

Common name *Scientific name*	Age of sexual maturity (years)	Mating habitat	Breeding season	Mating strategy	Sexual dimorphism	Comments
Caribbean monk seal *Monachus tropicalis*	Unknown	Probably aquatic	Unknown	Unknown	No	Presumed extinct
Mediterranean monk seal *Monachus monachus*	5–6	Aquatic	Apr–Dec	Polygynous?	No	Highly endangered
Hawaiian monk seal *Monachus schauinslandi*	Unknown	Aquatic	Mar–Jul	Promiscuous	No	Endangered
Northern elephant seal *Mirounga angustirostris*	6–8	Terrestrial	Jan–Feb	Polygynous	Yes: males larger	9–12 years old before breeding; extremely gregarious
Southern elephant seal *Mirounga leonina*	3–6	Terrestrial	Sept–Nov	Polygynous	Yes: males larger	9–14 years old before breeding; extremely gregarious
Harbour seal *Phoca vitulina*	3–7	Aquatic	May–Jun Sep–Oct	Promiscuous	No	Pupping season varies with latitude and location
Spotted seal *Phoca largha*	4–5	Aquatic	Apr–May Jun–Jul	Annually monogamous	No	
Caspian seal *Phoca caspica*	6–7	Probably aquatic	Feb–Mar	Unknown	Slight: males larger	Freshwater
Ringed seal *Phoca hispida*	5–8	Aquatic	Apr–May Aug	Promiscuous	No	
Baikal seal *Phoca sibirica*	7–10	Aquatic	Feb–Mar	Unknown	No	Freshwater
Ribbon seal *Phoca fasciata*	3–5	Pack ice	Apr–May	Unknown	Slight: males larger	
Harp seal *Phoca groenlandica*	7–8	Aquatic or terrestrial (pack ice)	Jan–Apr	Promiscuous	Slight: males larger	
Grey seal *Halichoerus grypus*	4–8	Aquatic, terrestrial or fast ice	Sep–Mar	Polygynous to monogamous	Yes: males larger	10 years old before breeding; pupping season varies with location
Bearded seal *Erignathus barbatus*	4–8	Aquatic	Mar–May	Male territories	Slight: females larger	Solitary
Hooded seal *Cystophora cristata*	4–6	Aquatic	Feb–Apr	Promiscuous or serially monogamous	Yes	Solitary
Weddell seal *Leptonychotes weddellii*	3–6	Sea ice or aquatic, under ice	Oct–Dec	Polygynous	Slight: females larger	6–8 years old before breeding
Crabeater seal *Lobodon carcinophagus*	2–6	Terrestrial	Nov–Dec	Monogamous	Slight: females larger	Solitary
Leopard seal *Hydrurga leptonyx*	4	Aquatic	Jan–Mar	Male territories	Slight: females larger	Solitary
Ross seal *Ommatophoca rossi*	3–6	Aquatic	Dec–Jan	Unknown	Slight: females larger	Solitary

Table 4. Reproductive characteristics of male otariid seals

Common name *Scientific name*	Age of sexual maturity (years)	Mating habitat	Breeding season	Mating strategy	Sexual dimorphism	Comments
California sea lion *Zalophus californianus*	5	At waters edge; terrestrial	May–Jul	Polygynous; promiscuous	Yes	
Stellar sea lion *Eumetopias jubatus*	3–7	Terrestrial	May–Jun	Polygynous	Yes	10 years old before breeding
Southern sea lion *Otaria byronia*	5–6	Terrestrial	Dec–Jan	Polygynous	Yes	
Australian sea lion *Neophoca cinerea*	Unknown	Terrestrial	Oct–Dec	Polygynous	Yes	
Hooker's sea lion *Phocarctos hookeri*	5	At waters edge; terrestrial	Nov–Jan	Polygynous	Yes	8 years old before breeding
Northern fur seal *Callorhinus ursinus*	4–5	Terrestrial	Jun–Jul	Polygynous	Yes	8–9 years old before breeding
South American fur seal *Arctocephalus australis*	Unknown	Terrestrial	Nov–Dec	Polygynous	Yes	
Galapagos fur seal *Arctocephalus galapoensis*	Unknown	Terrestrial	Sep–Oct	Polygynous	Yes	
Subantarctic fur seal *Arctocephalus tropicalis*	4–8	Terrestrial	Nov–Dec	Polygynous	Yes	8 years old before breeding
Antarctic fur seal *Arctocephalus gazella*	3–4	Terrestrial	Nov–Dec	Polygynous	Yes	7 years old before breeding
South African fur seal *Arctocephalus pusillus*	2–4	Terrestrial	Nov–Dec	Polygynous	Yes	3–13 years old before breeding
New Zealand fur seal *Arctocephalus forsteri*	8–9	Terrestrial	Nov–Dec	Polygynous	Yes	10 years old before breeding
Guadalupe fur seal *Arctocephalus townsendi*	Unknown	Terrestrial	Jun–Jul	Polygynous	Yes	
Juan Fernandez fur seal *Arctocephalus philippii*	Unknown	Terrestrial	Nov–Jan	Polygynous	Yes	

body and horns is significantly longer in parous females compared with nulliparous seals (Atkinson *et al.*, 1994). The uterine mucosa consists of an epithelial cell layer and a connective tissue stroma, throughout which mucus-producing glands are located (Boshier, 1981; Atkinson *et al.*, 1994). In prepubertal animals these glands are undeveloped.

The ovaries of seals are spherical to ovoid, 2–4 cm in length and 2–3 cm in width. In prepubertal females, the bursa covers the ovaries completely and is partially released around the time of puberty, allowing the ovary to become exposed to the peritoneal cavity. The prepubertal ovary is characterized by the lack of corpora lutea or dominant follicles (6–14 mm diameter), although antral follicles may be present.

The reproductive tract of male phocid and otariid seals differs in that the testes of the otariids are held in a scrotal sac, while the testes in phocid seals are ascrotal and lie below the blubber layer, adjacent to the abdominal musculature (Fig. 2). Puberty in males seals is considered to be the time when the testes are capable of spermatogenesis. Morphological changes in postpubertal seals include increased testis size and mass, increased mass and length of the baculum (penis bone), as well as the development of secondary sexual characteristics such as the growth of the sagittal crest, a calloused chest shield, more or less elongated guard hairs on the neck and shoulders, an elongated proboscis or hood, and the development of pungent odours (McLaren, 1958; Noonan, 1989; Bjorge, 1992; Fig. 2).

The baculum, also known as the penis bone, *os priapi* or *os penis*, develops with age and is thought to act as a simple stiffening rod (Morejohn, 1975; Fig. 2). In some species, the length of the baculum is a linear function of age (for example, up to 8–10 years of age in Northern fur seals and Subantarctic fur seals, respectively); however, in other species (for example, California sea lion), the baculum does most of its growing by three years of age and grows to its final length by five years (Morejohn, 1975; Bester, 1990). The bacula of mature breeding bulls are more massive but not longer than those of younger bulls. After the final length is attained, the baculum proceeds to develop osseous knobs, mainly at the apex. These knobs are the major morphological difference between bacula of different genera (Morejohn, 1975).

Endocrinology

The endocrinology of prepubertal seals is characterized by low or undetectable concentrations of sex steroids, including progesterone and various forms of oestrogen, that fluctuate
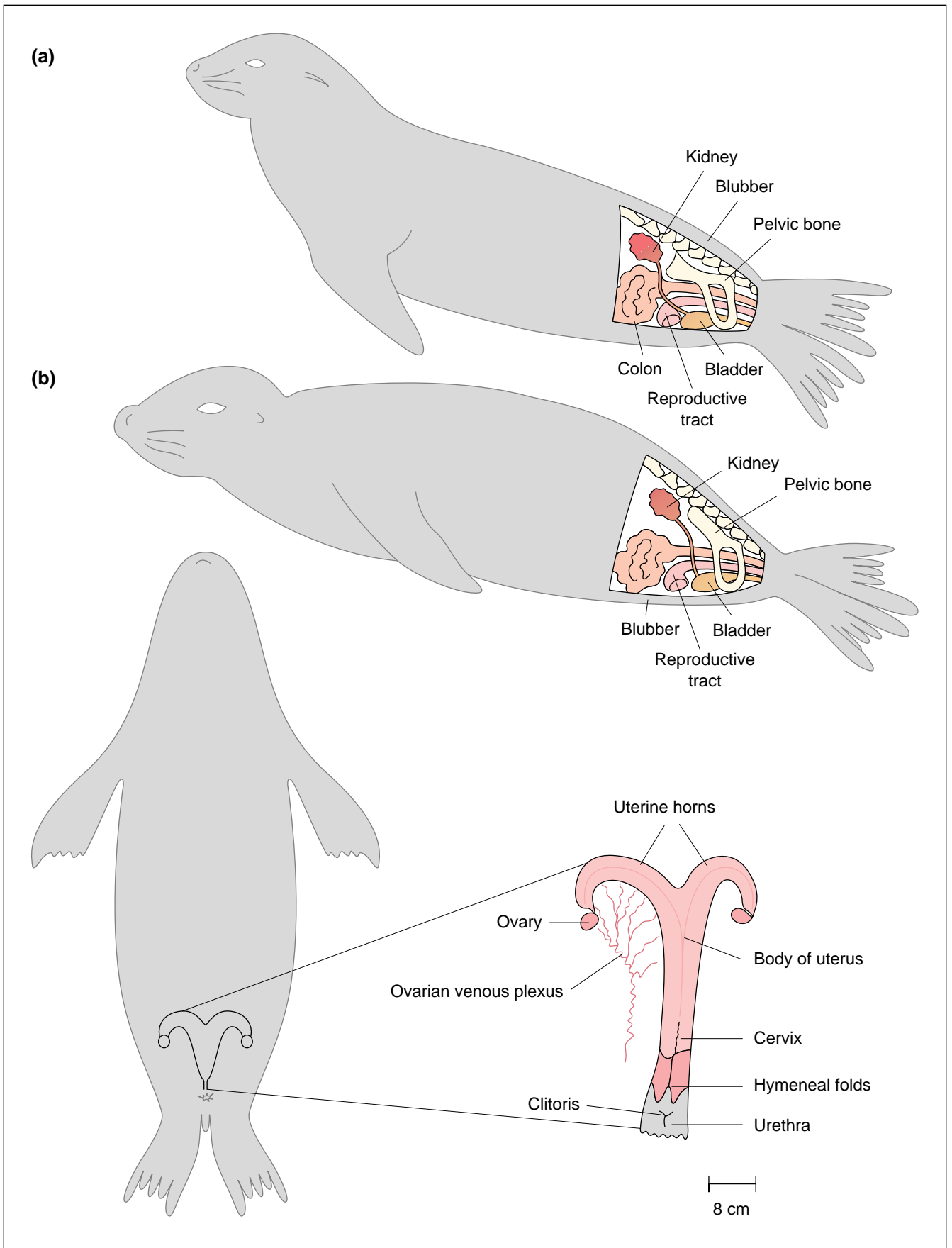
Fig. 1. Anatomy of the reproductive tract of female (a) otariid and (b) phocid seals. Redrawn from Rommel (unpublished).
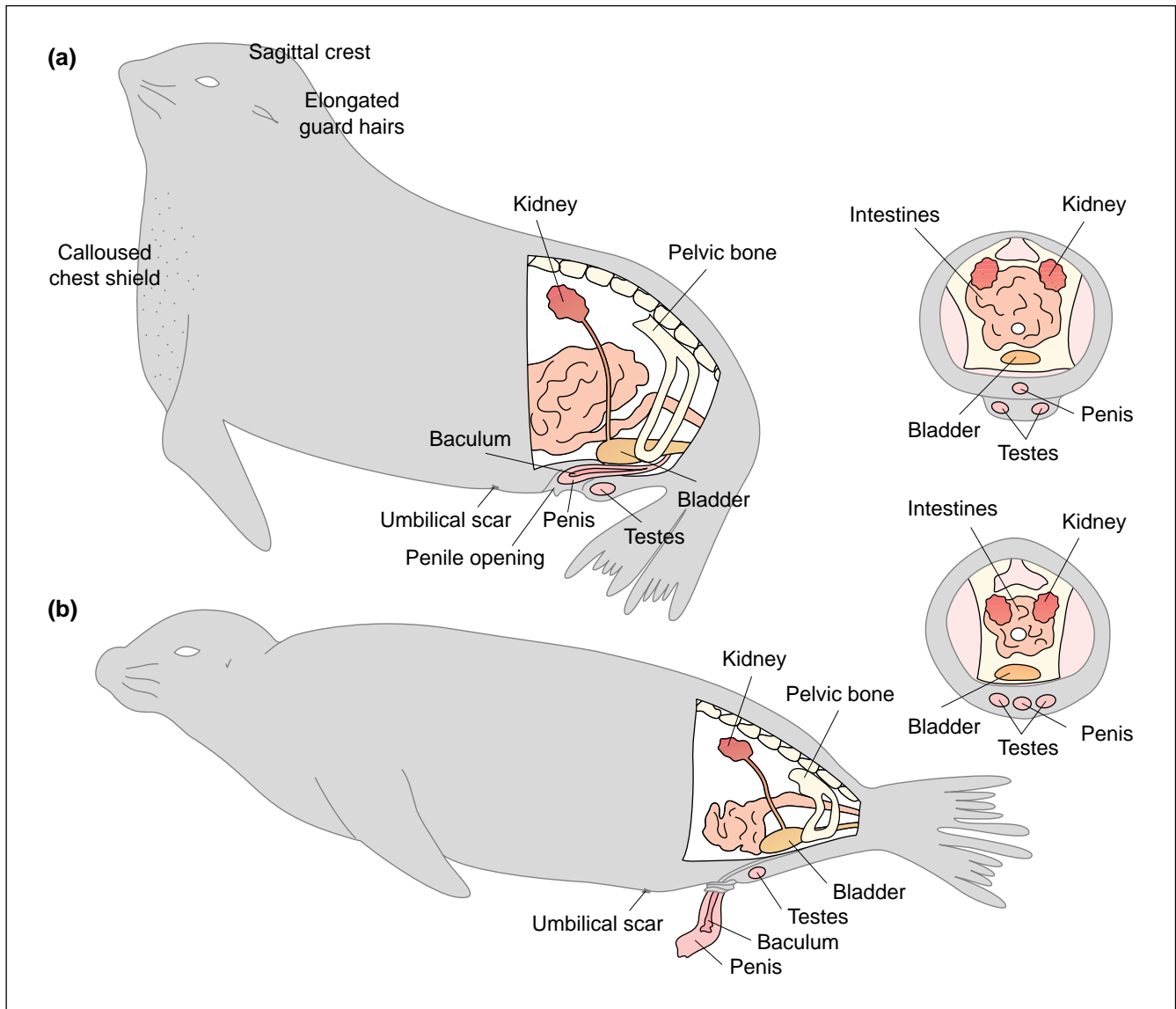
Fig. 2. Anatomy of the reproductive tract of male (a) otariid and (b) phocid seals. The penis of the phocid seal is drawn with an erection. Secondary sexual characteristics include the sagittal crest , the calloused chest shield, and elongation of the guard hairs, and are more prevalent in sexually dimorphic species, including all otariid seals, but only a few phocid seals. Redrawn from Rommel (unpublished).

very little (Fig. 3). Testosterone concentrations are generally lower than 1 ng ml^{-1} in prepubertal male seals, and progesterone and oestrone sulfate concentrations are each less than 0.5 ng ml^{-1} in prepubertal female seals (Noonan, 1989; Pietraszek, 1992; Gardiner, 1994). Assessment of changes in plasma concentrations of sex steroids provides a non-lethal method of determining sexual maturity (Noonan, 1989; Bartsh *et al.*, 1992; Gardiner *et al.*, 1996). Despite the inactivity of the sex steroids, the pituitary–gonadal axis appears to function in prepubertal seals. Injection of 10 μg GnRH into the extradural vein can induce the predicted response of increased concentrations of LH, FSH, progesterone or testosterone (Gardiner, 1994). The LH response after GnRH administration is immediate and repeatable at 90 min intervals, while there is a latent period of at least

20 min in the testosterone response in grey seals (Gardiner, 1994). The concentrations of male or female sex steroids have not been reported for neonatal seals.

Behaviour

Some prepubertal seals are the targets of sociosexual advances by male seals during the breeding season (Atkinson *et al.*, 1993). This strategy is generally unsuccessful and may be hormone driven, or may be part of the social learning that occurs while physiological development becomes coordinated with social maturity (Atkinson *et al.*, 1994). Prepubertal seals generally do not play a major role in the population dynamics of the annual reproductive cycle. They are described as being
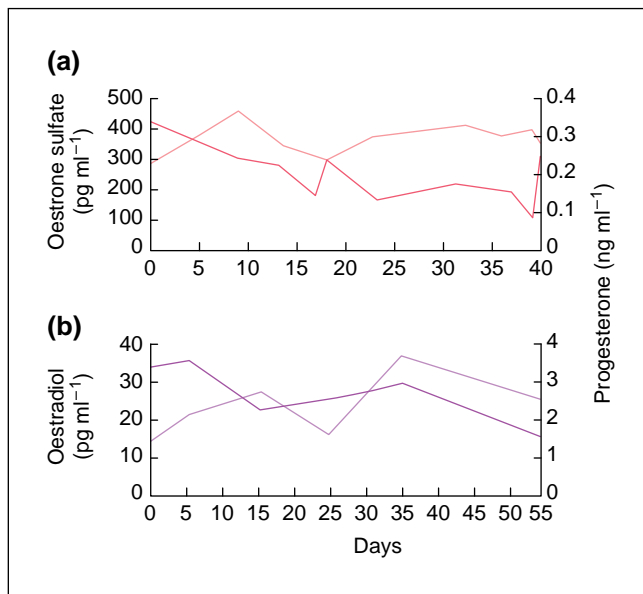
Fig. 3. Hormone profiles from prepubertal female seals. (a) Salivary oestrone sulfate (—) and progesterone (—) concentrations in Hawaiian monk seals (redrawn from Pietraszek, 1992). (b) Oestradiol (—) and progesterone (—) concentrations in harbour seals (redrawn from Reijnders, 1990).

'inconspicuous and hard to identify among the other animals' (Rand, 1955).

Oestrous cycles and mating

With the exception of one species, all seals are annual seasonal breeders, and their oestrous cycles are synchronized by parturition (Tables 1 and 2). The exception is the Australian sea lion, which exhibits an 18 month aseasonal, breeding cycle (Ling and Walker, 1978; Tedman, 1991; Gales *et al.*, 1992). This unusual cycle will be discussed in the sections on gestation and environmental influences on reproduction. Although the timing of oestrus is synchronized to parturition in all seal species, it differs between the two families of seal (Fig. 4). Otariid seals enter oestrus soon (the majority approximately 1 week) after parturition, whereas phocid seals enter oestrus close to the end of lactation (Tables 1 and 2). In the case of the hooded seal, a phocid seal, this timing also is within a week of parturition. The breeding season for male seals extends from before parturition through oestrus and mating (Tables 3 and 4). The breeding season in male seals can be identified by the presence of spermatozoa in the epididymis; however, the seasonal development of pungent odours in some species (for example, ringed seals and hooded seals) as well as agonistic behaviours, mounting and mating activity, and intense male–male competition, are good indicators of adult male seals in the breeding season.

Reproductive anatomy and morphology

In many species, there are no obvious external signs of oestrus. However, a swollen and flushed appearance of external genitalia has been reported in female Northern fur seals, spotted seals and hooded seals (Beier and Wartzok, 1979; Noonan, 1989). In most species, oestrus is inferred from male–female behaviour. Female seals are spontaneous ovulators and will ovulate in the absence of male seals.

Most seals are seasonally mono-oestrous, with ovulation and mating occurring once around the same time each year. A second ovulation occurs if the first ovulation does not result in conception; however, these second ovulations may not occur in all females of these species (Laws, 1956a; McLaren, 1958; Tedman, 1991). Iwasa and Atkinson (1996) examined the ovaries of the endangered Hawaiian monk seal, which is poly-oestrous in contrast to most seals. In many seal species, ovulation occurs on each ovary in alternate years (Rand, 1955; Craig, 1964; Bigg and Fisher, 1974; Boyd, 1983; Tedman, 1991; Bester, 1995), although this is not the case in some other species (McLaren, 1958; Skinner and Westlin-van Aarde, 1989; Atkinson *et al.*, 1994). Iwasa and Atkinson (1996) found four of five corpora haemorrhagica and one of two dominant follicles in Hawaiian monk seals were attached to regressing corpora lutea. In a study of Ross seals, Skinner and Westlin-van Aarde (1989) found more antral follicles in the ovaries that contained the active corpus luteum than in the contralateral ovary, and ovulation also did not appear to alternate between ovaries. These findings contrast with studies indicating that the corpus luteum inhibited follicular growth in the ipsilateral ovary (Bigg and Fisher, 1974; Boyd, 1983). In Hawaiian monk seals, ringed seals and Ross seals, one ovary is more active than the other, as shown by a difference in ovarian mass owing to the respective numbers of corpora lutea or corpora albicantia (Skinner and Westlin-van Aarde, 1989; Atkinson *et al.*, 1994; Iwasa and Atkinson, 1996). This does not represent true asymmetry as the active ovary in these species does not always occur on the same side.

Numerous primordial follicles are present throughout the ovarian cortex, with subsequent wave(s) of follicular development during the breeding season. Either a single wave or two waves of follicular development have been reported for various seal species (Pearson and Enders, 1951; Rand, 1955; Boyd, 1983). Throughout the prolonged breeding season of Hawaiian monk seals, a few small antral follicles (> 0.5 mm diameter) can be found together with one or two medium-sized follicles (2–4 mm diameter). Antral follicles possess the characteristic granulosa cells adjacent to the thecal cell layer, which form the cumulus oophorus adjacent to the oocyte (Iwasa *et al.*, 1977; Yoshida *et al.*, 1997). Dominant follicles are characterized by a thin cell membrane on the exterior surface, and an abundance of follicular fluid. Dominant follicles (6–14 mm diameter) appear 24–48 h before ovulation. In grey and harbour seals, an abundance of follicles (3–6 mm diameter) are present on the ovary contralateral to the corpus luteum at the beginning of lactation, which is considered the start of the cycle in seasonally mono-oestrous species (Boyd, 1983, 1991a), and there is a lower frequency of antral follicles in the ipsilateral ovary (Bigg and Fisher, 1974; Boyd, 1983). Female grey seals have an average of just over one follicle > 12 mm throughout the final third of lactation, approaching the time of weaning, oestrus and mating (Boness and James, 1979; Boyd, 1983). As the nonbreeding season equates to the period of gestation in many female seals, there are no large or preovulatory follicles, possibly due to the action of a functional corpus luteum in females that have
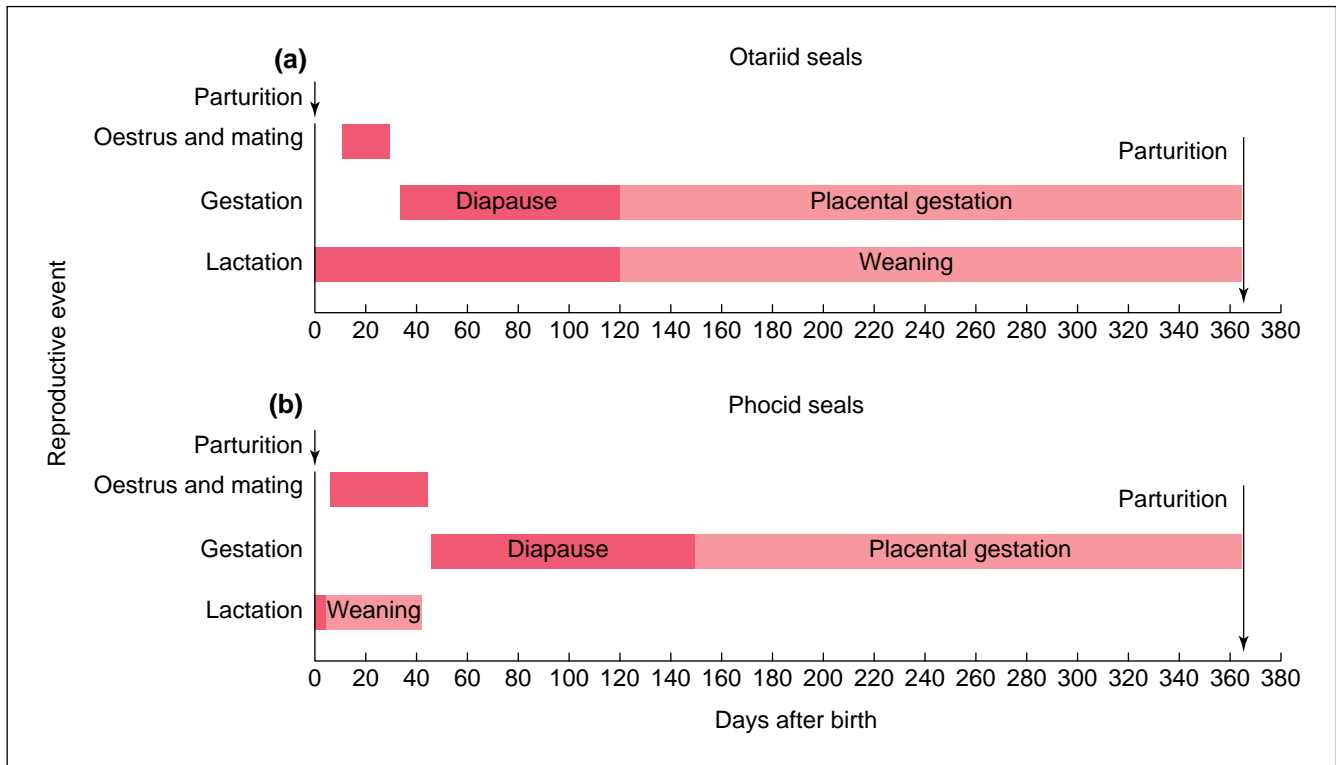
Fig. 4. Temporal relationship of the annual reproductive events of otariid and phocid seals. Oestrus and mating are synchronized by the timing of parturition, and may begin as early as 4 days postpartum in hooded seals and many fur seals. Oestrus and mating for otariid seals usually occurs before 2 weeks postpartum. Postpartum oestrus in phocid seals occurs near the end of lactation, which is under 6 weeks for all phocid seals except Mediterranean monk seals, in which it is greater than 2 months. Gestation comprises an embryonic diapause and a placental gestation. The embryonic diapause is obligate in most species. Lactation in otariid seals is prolonged compared with that in phocid seals. All otariid species lactate for at least 3–4 months, and weaning for the majority of otariid species occurs between 4 months and 12 months, although a few otariid species may lactate for 1–3 years.

conceived (Yoshida *et al.*, 1977). The diameter of the corpus luteum ranges from 0.5 to 1.5 cm.

During the periovulatory period, the uterine mucosal glands open to the endometrial mucosal surface. If conception does not occur, or during the period of embryonic diapause, the uterine glands regress and no longer open to the uterine lumen. The change of glandular tissue appears to be consistent between species (harbour seals, Bigg and Fisher, 1974; crabeater and Weddell seals, Boshier, 1981; grey and harp seals, Ouellette and Ronald, 1985; Hawaiian monk seals, Atkinson *et al.,* 1994). Histological changes in the vaginal epithelium are marked by the apparent increase in cornification of cells, which reflects increased plasma and salivary oestrone sulfate concentrations (Pietraszek and Atkinson, 1994).

The size of the testes increases during the breeding season. The increased size and mass are due to increased diameter of the seminiferous tubules and the epididymis (Griffiths, 1984; Bester, 1990). Thermoregulation of the testes has been questioned particularly in phocid seals because of their inability to contract or relax the position of the testes, which are extraabdominal yet surrounded by thermogenic muscle and insulating blubber (Bryden, 1967; Rommel *et al.*, 1995). Bryden (1967) first proposed a vascular heat exchange mechanism for maintaining the testes of Southern elephant seals 6–7°C below the rectal and body cavity temperature. Rommel *et al.* (1995) identified anastomoses between the veins of the distal hind flippers and the pelvis of harbour, grey, harp, hooded and ringed seals. These venous anastomoses allow large volumes of cool blood to return from the skin to the inguinal region, preventing hyperthermic insult to the testes (Rommel *et al.*, 1995). The testes of otariid seals are contained in a scrotal sac that is under the control of the cremaster and dartos muscles. This muscular control of the scrotum may serve to keep the testes at an optimal temperature for spermatogensis, and also to protect the scrotum when the animals are moving on land (Crawley, 1990). Some otariid seals are reported to be seasonally scrotal; their testes descend into the scrotum only during the breeding season (S. A. Rommel, unpublished).

The copulatory success of males in polygynous species is postulated to be related to dominance rank, which is a function of body size (Haley *et al.*, 1994). In most polygynous species, sexual dimorphism is demonstrated by the large body size of the male, where sexual selection appears to favour large males (Haley *et al.,* 1994). Large males are at an advantage in intrasexual competition for dominance status and territory acquisition (Stirling, 1983). There is a functional relationship between size of the testes
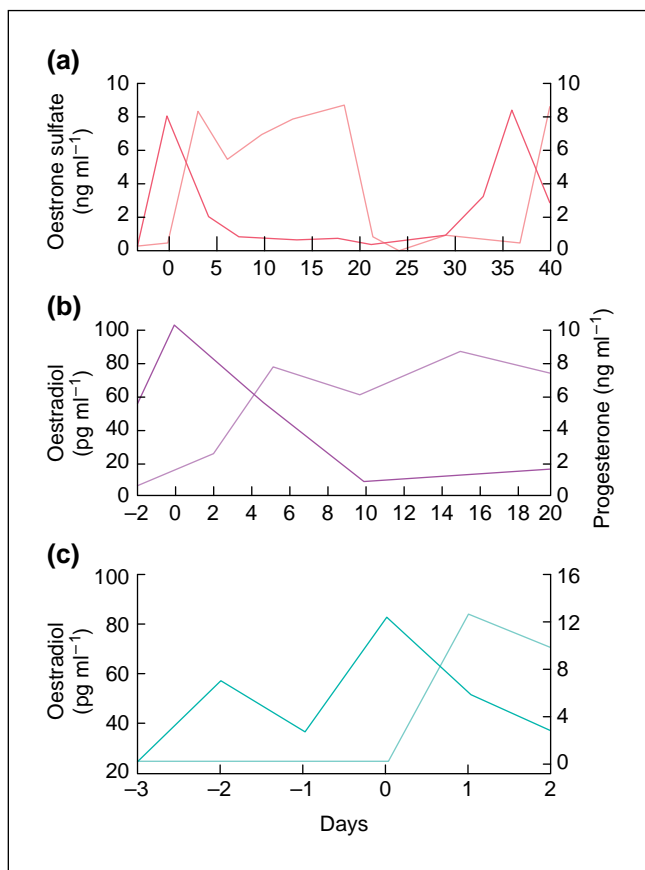
Fig. 5. Hormone profiles from female seals during oestrus, where day 0 is the estimated day of ovulation. (a) Plasma oestrone sulfate (—) and progesterone (—) concentrations from Hawaiian monk seals (redrawn from Pietraszek and Atkinson, 1994). The peri-ovulatory phase is from day –3 to day 2 and from day 32 to day 37, the luteal phase is from day 1 to day 17 and the follicular phase is from day 17 to day 35. (b) Serum oestradiol (—) and progesterone (—) in harbour seals (redrawn from Reijnders, 1990). The follicular phase is the 15 days before ovulation. The luteal phase may last 4–5 months after ovulation. (c) Plasma oestradiol (—) and progesterone (—) concentrations from Antarctic fur seals (redrawn from Boyd, 1991b). The follicular phase is the period from parturition to postpartum oestrus, about 4–12 days.

and mating system in many mammals; testes are relatively large in polygynous and promiscuous mating systems, and relatively small in monogamous systems (Kenagy and Trombulak, 1986). Northern fur seals correspond well to the mammalian positive allometric relationship between body mass and testes mass; however, no other pinniped species have been tested.

Endocrinology

Steroid hormone patterns of peaks in circulating oestrogen concentrations followed 1–2 days later by peaks in circulating progesterone concentrations have been characterized in several species of seal (grey seals, Boyd, 1984a; hooded seals, Noonan, 1989; harbour seals, Reijnders, 1990; Antarctic fur seals, Boyd, 1991b; and Hawaiian monk seals, Pietraszek and Atkinson,

1994). This pattern reflects preovulatory follicular maturation and corpus luteum formation (Fig. 5). The ovulatory process was temporally shifted later for previously pregnant versus non-pregnant harbour seals (Reijnders, 1990). In Hawaiian monk seals, a subtropical polyoestrous phocid, less invasive methods of monitoring the oestrous cycle have been adopted. The correlation coefficients between plasma and salivary concentrations of progesterone and oestrone sulfate have been recorded as 0.868 and 0.982, respectively (Pietraszek and Atkinson, 1994). Consecutive oestrous cycles are typified by increases in salivary and circulating oestrone sulfate, a primary metabolite of oestradiol, followed by increases in progesterone (Pietraszek and Atkinson, 1994; Fig. 5). The duration of the follicular phase in this species is 15–18 days, with the period of oestrus of approximately 2–6 days duration (Atkinson *et al.*, 1994; Pietraszek and Atkinson, 1994; Fig. 5). Reijnders (1990) has estimated the follicular phase of the harbour seal at approximately 15 days (Fig. 5).

Although the process of ovulation and corpus luteum formation occurs across seal species, the functional life of corpora lutea seems to vary between species. In Hawaiian monk seals, salivary and circulating progesterone concentrations decrease precipitously 17–20 days after ovulation, with the next ovulation occurring 15–18 days after the progesterone decrease (Pietraszek and Atkinson, 1994; Fig. 5). This hormonal pattern reflects a distinct period of luteolysis and a subsequent follicular phase (Pietraszek and Atkinson, 1994), whereas in harbour seals (Reijnders, 1990) and hooded seals (Noonan, 1989), circulating progesterone concentrations remain high for 4–5 months. This prolonged luteal phase is characteristic of pseudo-pregnancy and will be discussed in the gestation section of this review.

Male seals exhibit seasonal fluctuations in circulating concentrations of testosterone. In species with a short, tightly synchronized pupping and breeding season, testosterone concentrations are increased for 1–3 months at the start of the breeding season, but decrease to baseline concentrations before breeding behaviour ends (Griffiths, 1984; Noonan *et al.*, 1991; Bartsh *et al.*, 1992; Fig. 6). In grey seals, testosterone concentrations are 10–20 times higher during the breeding season than during the nonbreeding season (Sangalang and Freeman, 1976). Similarly, testosterone concentrations are below limits of detection during the nonbreeding season in harbour seals and Northern elephant seals, but high concentrations are found during the breeding season (P. Yochem, B. Stewart and S. Atkinson, unpublished). The increase in concentrations of circulating testosterone at the start of the breeding season is followed by a surge in cortisol concentrations in male Weddell seals (Bartsh *et al.*, 1992). This suggests that competition for breeding territory suppresses concentrations of circulating testosterone and that this may function through cortisol, which hastens the decline in testosterone. Testosterone has also been measured in the subtropical Hawaiian monk seals, in which the pattern of testosterone has been found to be seasonal, although not as pronounced as in the more temperate or polar species of seal (Atkinson and Gilmartin, 1992; Theodorou and Atkinson, in press; Fig. 6).

Mean salivary testosterone concentrations have been related to dominance rank in male Hawaiian monk seals, a species with no sexual dimorphism and a poorly understood mating strategy (J. Theodorou and S. Atkinson, unpublished). Testosterone

concentrations are not linearly related to dominance rank, although the dominant male in that study did have the highest salivary testosterone concentration (J. Theodorou and S. Atkinson, unpublished). Salivary testosterone concentrations did parallel the frequency of agonistic behaviours, which increased during the spring months and declined during the summer months as the breeding season ended (Atkinson and Gilmartin, 1992; J. Theodorou and S. Atkinson, unpublished). Body size has been correlated positively with testosterone concentrations in Weddell seals (Bartsh *et al.*, 1992).

Behaviour

Seals are either aquatic or terrestrial breeders (Tables 3 and 4). The otariid seals are relatively uniform in the habitat used for mating; most otariids are either strictly terrestrial breeders, or they mate at the water's edge. Mating at the water's edge has been hypothesized as being advantageous in reducing hyperthermia of the male seal during copulation. Phocid seals are either terrestrial or aquatic copulators. Understandably, the reproductive biology of terrestrial breeders has been better studied since these seals are more accessible to researchers.

Male–female behavioural dynamics in the breeding season are the most obvious indicators of oestrus. While these behaviours vary with the mating strategy, some behaviours are fairly consistent among species. Reproductive behaviours of male seals include approaching, nudging and chasing of females, vocalizations, and agonistic threats to neighbouring males. In hooded seals, male reproductive behaviours also include hood inflation and display of the nasal septum (Noonan, 1989). Behaviours of oestrous females include aggressive open-mouth threats, growling and drumming vocalizations, and nosing and biting interactions during the period leading up to oestrus (Beier and Wartzok, 1979; Noonan, 1989).

Gestation

Definitive aspects of gestation in seals are the embryonic diapause that is obligate in many species, the occurrence of pseudopregnancy in some species, and the obligatory requirement of a terrestrial habitat for parturition in all species. Otariid seals differ from most phocid seals in their ability to conceive 1–2 weeks post partum (Fig. 4). The ovulation and subsequent conceptus are contralateral to the postpartum side of the reproductive tract (Enders *et al.*, 1946; Tedman, 1991). Thus, postpartum uterine involution occurs unilaterally while fertilization and formation of the blastocyst are in progress.

The exception to the annual reproductive cycle of seals is the Australian sea lion, which experiences a 17–18 month breeding cycle across its natural range (Ling and Walker, 1978; Gales *et al.*, 1992). The postpartum oestrus follows the pattern of other otariid seals (approximately 1 week post partum), and the embryonic diapause is at least 7 weeks (Tedman, 1991) and probably 4–5 months (Gales *et al.*, in press). The placental portion of gestation can be up to 14 months, the longest for any seal. Factors responsible for this prolonged gestation in Australian sea lions are unknown; however, Gales (1995) presents a compelling argument that it has evolved as an adaptation to a marine environment characterized by low concentrations of nutrients and patchy and low prey abundance. This argument
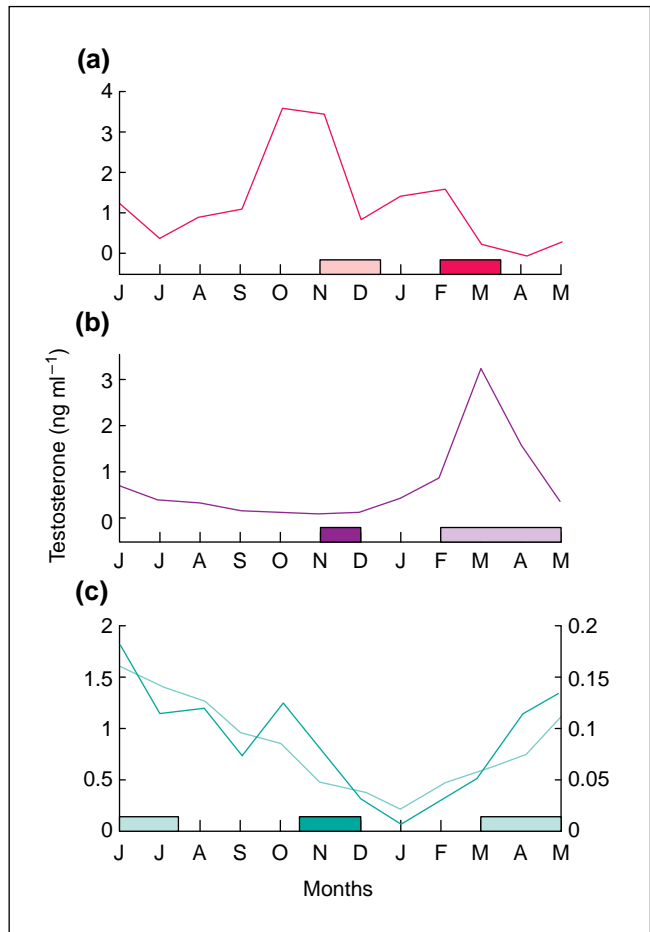

Fig. 6. Testosterone profiles of male seals throughout the year. (a) Plasma concentrations from Subantarctic fur seals (redrawn from Bester, 1990). ■, period of moult; ■, mating season. (b) Plasma concentrations from hooded seals (redrawn from Noonan *et al.*, 1991). ■, period of moult; ■, mating season. (c) Plasma (— ; left *y* axis) and salivary (— ; right *y* axis) concentrations from Hawaiian monk seals ■, period of moult; ■, mating season. (Redrawn from Atkinson and Gilmartin, 1992 and Theodorou and Atkinson, in press, respectively).

is supported by a shortened gestation in captive Australian sea lions (Table 2).

Reproductive anatomy and morphology

The corpus luteum of all seals appears to persist throughout pregnancy, but regresses shortly after parturition (Yoshida *et al.*, 1977; Boyd, 1983; Bester, 1995; Iwasa and Atkinson, 1996). There is no substantial difference between the regressed corpora lutea of pregnancy and regressed corpora lutea that did not result in pregnancy in Hawaiian monk seals (Iwasa and Atkinson, 1996; Iwasa *et al.*, 1997). Several researchers have tried unsuccessfully to detect the number of offspring, age of sexual maturation, or rates of reproduction in seals retrospectively, using the number of corpora lutea in the ovaries of seals. These attempts were modelled after studies in dolphins and whales which reported
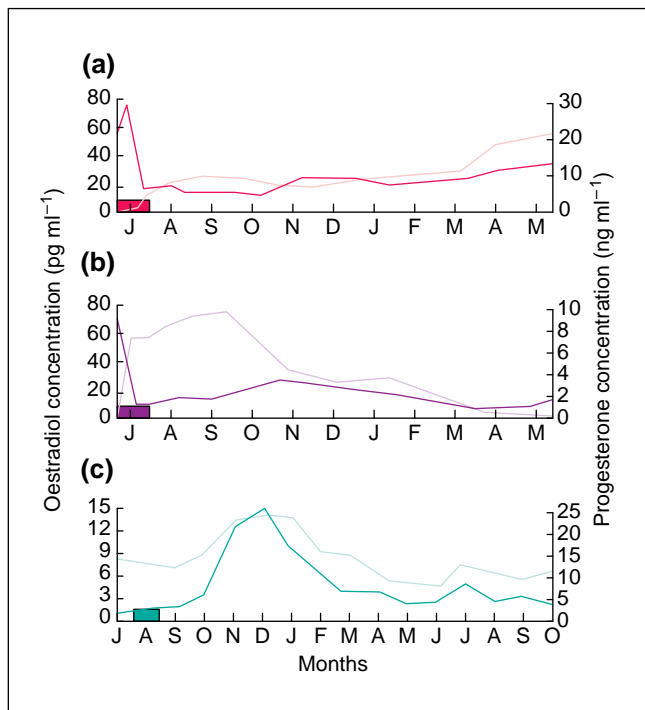
Fig. 7. Hormone profiles from female seals during gestation and pseudopregnancy. (a) Serum oestradiol (—) and progesterone (—) concentrations from pregnant harbour seals (redrawn from Reijnders, 1990). ■, period of mating. (b) Serum oestradiol (—) and progesterone (—) concentrations from nonpregnant harbour seals (redrawn from Reijnders, 1990). ■, period of mating. (c) Plasma oestradiol (—) and progesterone (—) concentrations from Australian sea lions, which have an aseasonal 18 month breeding cycle (redrawn from Gales et al., in press). ■, period of mating. The embryonic diapause in harbour seals is 3–3.5 months and ends between September and October, as does the period of pseudopregnancy. Embryonic diapause is 4–5 months in Australian sea lions and is characterized by an increase in both oestradiol and progesterone during November and December. The remaining period of gestation in both species is placental.

that the corpora albicantia persist throughout life and are assumed to reflect the reproductive history of the animal (Kirby, 1990). However, these attempts in phocid and otariid seals were unsuccessful because corpora lutea in seals regress completely, usually within a few years (Sergeant, 1973; Yoshida et al., 1977; Iwasa and Atkinson, 1996). In many species, the corpus luteum will develop after ovulation but then become quiescent until immediately before the reactivation of the blastocyst (Bigg and Fisher, 1974; Boshier, 1981). During this quiescent phase, the number and size of antral follicles increase, although not to the point of ovulation (Rand, 1955; Bigg and Fisher, 1974; Skinner and Westlin-van Aarde, 1989). Just before the embryonic reactivation, the size of the corpus luteum increases (Daniel, 1975).

The uterine horns are the site of attachment of the blastocyst, occurring in alternate oviducts each year in many species (Bigg and Fisher, 1974; Boshier, 1981). Enders et al. (1946) were the first to report embryonic diapause, or delayed implantation,

in Northern fur seals, and later the same phenomenon was reported in harbour seals (Fisher, 1954). Since that time, embryonic diapause has been reported in many seal species (Boshier, 1981; Renfree, 1993). During embryonic diapause, the embryo is arrested during the blastocyst stage of development and requires a physiological trigger to release it from the diapause and synchronize its development with the uterus (Renfree, 1993). The blastocyst experiences retarded growth during the diapause. The delay is variable between and within species, ranging from 1 to 5 months (Tables 1 and 2). The stimulus to end the diapause is unknown; however, reactivation of the blastocyst does not seem to be linked to physiological changes associated with weaning (Boyd, 1991b) or the sex of the embryo (Boyd, 1984a). Blastocyst reactivation may be determined by the ovary, although the exact cue remains elusive (Daniel, 1981; Renfree, 1993).

The uterine glands also acquiesce during the embryonic diapause and no longer open to the lumen (Boshier, 1981; Ouellette and Ronald, 1985; Skinner and Westlin-van Aarde, 1989). Once the blastocyst is reactivated and implantation occurs, the uterine glands hypertrophy and reopen to the uterine lumen (Laws, 1956a; Bigg and Fisher, 1974; Boshier, 1981). In many seal species, the period of delay has been calculated retrospectively using a least squares regression between fetal length (from hunted or culled specimens) and the date of collection. Subtracting this date from the period of mating gives the approximate duration of the diapause (Hayama et al., 1986). It is the variable duration of the embryonic diapause that gives such similar gestation periods for the various seal species (Daniel, 1981; Tables 1 and 2).

The fetus develops with a diffuse placental attachment. During placentation, the fetal membranes do not extend into the opposite oviduct, and so only the gravid uterine horn enlarges (Bigg and Fisher, 1974; Ouellette and Ronald, 1985). The trophoblast penetrates into the maternal endometrium and a placental labyrinth is formed. This labyrinth thickens over the course of gestation (Ouellette and Ronald, 1985) and maternal blood vessels extend into it to supply the necessary nutrients via oxygenated blood.

Endocrinology

Several studies have demonstrated increased concentrations of progesterone after ovulation (Reijnders, 1990; Gardiner, 1994; Pietraszek and Atkinson, 1994). In pregnant phocid seals, these continue to increase throughout the duration of gestation to a high concentration in the last 2 months (Boyd, 1983; Reijnders, 1990; Fig. 7). Circulating concentration of progesterone is an accurate indicator of pregnancy in harbour seals, when combined with standard body length and month of capture (Gardiner et al., 1996). Salivary progesterone and oestrone sulfate concentrations have also been used successfully to detect pregnancy in a captive California sea lion (S. Atkinson and M. Breese, unpublished).

In otariid seals, progesterone concentrations remain low during the embryonic diapause and increase just before reactivation of the blastocyst (Daniel, 1975; Boyd, 1991b; Gales et al., in press; Fig. 7). FSH concentrations, measured using an ovine FSH assay validated for pinniped plasma, are high during the embryonic diapause (Gardiner, 1994). Follicular activity is also

increased during embryonic diapause (Bigg and Fisher, 1974; Boshier, 1981; Skinner and Westlin-van Aarde, 1989). Most studies report a prominent surge of oestrogen just before embryonic reactivation in both phocid and otariid seals (Daniel, 1974; Reijnders, 1990; Gales *et al.*, in press; Fig. 7). These findings suggest that steroids may play a significant role in the reactivation of the blastocyst. Single intramuscular injections of oestradiol (0.5 mg), progesterone (50 mg) or both of these steroids in corn oil carriers did not induce reactivation (Daniel, 1981); however, this experimental approach of a single injection may not have been as effective as continuous delivery of the steroids or other hormones over a longer period. Prolactin is luteotrophic and may function in embryonic reactivation, although the concentrations of prolactin, measured using a double antibody enzymeimmunoassay validated for seal plasma, gradually declined throughout the diapause in Antarctic fur seals (Boyd, 1991b). This decline in prolactin is not known to be associated with other seasonal or photoperiodic changes and is assumed to be related to reproductive events or processes.

The duration of the embryonic diapause has been well studied in marsupials and other terrestrial mammals and differs markedly among species (Mead, 1993; Renfree, 1993). In marsupials, suckling has an inhibitory influence on the reactivation of the blastocyst, and the corpus luteum, by producing progesterone, will induce blastocyst reactivation (Renfree, 1993). In contrast, progesterone does not stimulate reactivation of the blastocyst in carnivores (Mead, 1993). Prolactin secretion prevents embryonic attachment in wallabies, but hastens renewed development in mink and spotted skunks (Mead, 1993). The hormonal role in controlling the duration of the embryonic diapause in seals will remain unclear until more intensive studies can be conducted.

In nonpregnant seals, the functional life of the corpus luteum is variable. At least one species experiences luteolysis and subsequent oestrous cycles (Hawaiian monk seals, Pietraszek and Atkinson, 1994; Fig. 5), while others experience pseudopregnancy (harbour seals, Bigg and Fisher, 1974; Reijnders, 1990; hooded seals, Noonan, 1989; Boyd, 1991a; harp seals, Renouf *et al.*, 1994; Fig. 7). Pseudopregnancy is defined as the prolonged period of high concentrations of plasma progesterone in animals that are not carrying a fetus. During pseudopregnancy, progesterone concentrations remain high for at least the duration of the embryonic diapause (Yoshida *et al.*, 1977; Reijnders, 1990; Renouf et al, 1994; Fig. 7) and possibly longer (Noonan, 1989). Noonan (1989) reported high concentrations of progesterone for 210 days in hooded seals. Fetal development from implantation to birth is approximately 240–250 days in hooded seals; therefore, the corpus luteum remains active during most of gestation in nonpregnant animals (Noonan, 1989). It is not known whether pseudopregnancy can be distinguished hormonally from early embryonic mortality.

Hormone changes around the time of parturition include a steady decrease in total concentrations of oestrone over the last month of gestation (Raeside and Ronald, 1981). Total concentrations of corticosteroids reach peak values 1–2 weeks before parturition and then reach a peak again, doubling in concentration shortly after birth (Raeside and Ronald, 1981). The placentae of seals produce substantial amounts of progesterone, which increase as gestation progresses (Craig, 1964; Hobson

and Boyd, 1984), declining rapidly in the circulation just before parturition (Raeside and Ronald, 1981; Boyd, 1983, 1984a; Reijnders, 1990). As the corpus luteum remains active throughout gestation and the placenta also produces progesterone, it is unclear which of these endocrine glands contributes most to the circulating concentrations of progesterone (Hobson and Boyd, 1984). In addition, it is not known whether gestation can be maintained in the absence of ovaries in seals.

Behaviour

There is little information on the behaviour of either male or female seals during the period of gestation. In phocid seals, most males and females are foraging intensively because they generally do not feed during oestrus and mating. In otariid seals, the females alternate foraging bouts with periods on shore caring for their young. There is much less interaction between males and females than during the breeding season.

Parturition is highly synchronized in most species, with polar and temperate seals having shorter birthing seasons than tropical dwelling seals (Stirling, 1983; Atkinson and Gilmartin, 1992). A few species exhibit substantial irritability before parturition, becoming restless, removing themselves from the main herd, chasing away seals that are too close, and flipping sand on themselves to keep cool (Rand, 1955; Crawley, 1990). Expulsion of the pup during parturition is fast and may involve little obvious behavioural display. Most seals expel their pups head first, although breech presentations have been recorded in several species (Frank *et al.*, 1985; Crawley, 1990). Female seals give birth a few days after arriving on shore (Peterson and Bartholomew, 1967; Le Boeuf, 1972; Bigg, 1984). There is some evidence that parturition can be delayed voluntarily during foul weather (Trites and Antonelis, 1994). The process of hauling out of the water to the obligatory terrestrial environment (including ice floes), as well as social cues may induce parturition (Bigg, 1984). The mechanisms for these cues have not been identified.

Lactation

The duration of lactation is the most noticeable difference in the reproductive biology of phocid and otariid seals (Fig. 4). The period of lactation is prolonged (4–36 months) in otariid seals and intensive suckling bouts are interspersed with foraging trips away from the pup (Crawley, 1990; Table 2). The period of lactation in phocid seals is short (4–120 days) and characterized by a rapid transfer of high fat milk from mother to pup (Oftedal, 1993; Table 1). Phocid seals generally fast during lactation and may lose up to 40% of their initial body mass (Oftedal, 1993). This loss of body mass is in the form of blubber and lean muscle mass, from which lipid and amino acid substrates can be mobilized.

The milk composition of all seals tends to be low in carbohydrate, protein and water and high in milk fat (Van Horn and Baker, 1971; Peaker and Goode, 1978; Oftedal, 1984, 1993). The milk composition of both phocid and otariid seals in early lactation is < 66% water, < 3% sugars, 5–18% protein and 20–60% milk fat (Van Horn and Baker, 1971; Peaker and Goode, 1978; Oftedal, 1993). As lactation progresses, the water content of milk declines to < 35%, with 5–10% protein, while fat content

of the milk increases to 50–65% (Oftedal, 1993). The milk composition of seals provides a striking contrast to that of terrestrial mammals which contain 70–90% water, 4–8% milk fat, 7–40% protein, and 5–60% sugars (Oftedal, 1984). In both families of seal, the offspring deposit large amounts of body fat in preparation for weaning. Weaning in phocid seals is abrupt and results in a postweaning fast of the young, until they learn how to forage on their own. This fast may last up to 2 months. Weaning in otariid seals is more gradual as these seals slowly learn to forage on their own towards the end of lactation.

Reproductive anatomy and morphology

The size and number of ovarian follicles increases during lactation in phocid seals as the commencement of lactation coincides with the follicular phase of the oestrous cycle in these seals (Bigg and Fisher, 1974; Ouellette and Ronald, 1985). In otariid seals, the ovary of the nonpregnant uterine horn experiences follicular development, resulting in ovulation a few days to 2 weeks after parturition (Table 2). The corpus luteum degenerates rapidly after parturition but remains visible as a corpus albicans on the surface of the ovary throughout lactation in most species (Bigg and Fisher, 1974; Yoshida *et al.*, 1977; Ouellette and Ronald, 1985; Iwasa and Atkinson, 1996).

The uterus of phocid seals undergoes rapid involution during the first part of lactation (Bigg and Fisher, 1974; Ouellette and Ronald, 1985). Hyperplasia and hypertrophy characterize the uterus and oviducts during the second half of lactation in preparation for oestrus, which occurs around the end of lactation in most phocid seals (Table 1).

Endocrinology

The endocrinology of oestrus and conception occurring simultaneously with postpartum uterine involution is curious and not fully understood. Prolactin concentrations are high before birth and reach a peak 0–3 days after birth, declining to undetectable amounts before the end of lactation. The prepartum increase in prolactin concentrations suggests that prolactin plays a role in development of the mammary glands in anticipation of lactation. Prolactin is important in maintaining early lactation and is typically under inhibitory dopaminergic control in mammals. Presumably, oxytocin and prolactin are produced in response to suckling; however, prolactin does not decline precipitously when lactation is stopped abruptly, and so is probably not the only hormone involved in controlling lactation cycles (Boyd, 1991b). Intramuscular injections of bromocriptine (0.2–0.4 mg kg^{-1}) were administered from day 2 to day 4 post partum to Antarctic fur seals that had their pups present (Boyd, 1991b). Bromocriptine reduced the circulating concentrations of prolactin within 1 day after the bromocriptine treatment was stopped, although this effect was not observed after a further 5 days (Boyd, 1991b). Nevertheless, lactation was terminated in the seals treated with bromocriptine, and these females did not experience the loss of body mass that is normal for lactating seals. Bromocriptine also suppressed the postovulatory rise in progesterone concentrations, indicating that prolactin may control ovulation and luteal development in seals (Boyd, 1991b).

Progesterone fluctuations are dictated primarily by ovarian and uterine events, and pituitary activity; the influence of lactation appears to be minimal. Progesterone concentrations remain low during lactation until the time of ovulation in both phocid and otariid seals (Daniel, 1975; Boyd, 1983, 1991b). Thereafter, progesterone concentrations increase relative to postpartum concentrations, and follow the pattern described for gestation.

Behaviour

Lactation in phocid seals is characterized by a short period of intense maternal investment. With these seals, the mother will tend not to forage from just before birth until weaning. This period ranges from 4 days for hooded seals to 4 months for Mediterranean monk seals (Table 1). In otariid seals, there is an intense period of maternal investment for 1–2 weeks, or until mating occurs. After this time, the female will leave her pup for foraging trips that may last from a couple of days to a couple of weeks. The duration of these foraging trips is gradually increased until weaning, usually 6–12 months after birth (Table 2). When a mother is on shore, the pups feed strongly and opportunistically. A prolonged period of maternal investment is necessary, even though the pup may spend substantial time on its own and may be foraging to some degree. An example of the necessity of this maternal investment is in South African fur seals that perish after losing their mothers at 6–8 months of age, when some these offspring are naturally weaning (Rand, 1955; Table 2).

Maternal–offspring recognition is facilitated by auditory and olfactory cues. These are generally more important in otariid seals than in phocid seals because of the separation of mother and pup for periodic foraging trips. Fostering behaviour, defined as one mother adopting a nonfilial pup and raising it as her own, is more prevalent in phocid seals (McCann, 1982; Reidman and Le Boeuf, 1982; Boness, 1990) than in otariid seals (Stirling, 1975, Lunn, 1992). The evolution of this behaviour is unclear, although Lunn (1992) proposed that the lack of maternal experience and nutritional stress contributed to the increased fostering behaviour in Antarctic fur seals. Other possible causes are human disturbance and high density of animals.

Environmental influences on reproduction

Many factors in the environment influence reproductive events and processes. Some of these factors may simply cue normal physiological events, while others act as major disrupters to the system (Fig. 8). The physiological mechanisms involved are generally unclear; however, our knowledge of their causes and effects is increasing.

Photoperiod and local climate

Reproduction in most seal species is characterized by tight synchrony of births, which ensures that pups are born at the optimal time of year for weather, prey abundance, and general availability of necessary resources. With few exceptions, seals breed during periods of increasing daily photoperiod, and the end of the embryonic diapause occurs during decreasing daily photoperiod. Although most species have narrowly defined breeding seasons, a few species that have broad habitat ranges have asynchronous or variable breeding seasons
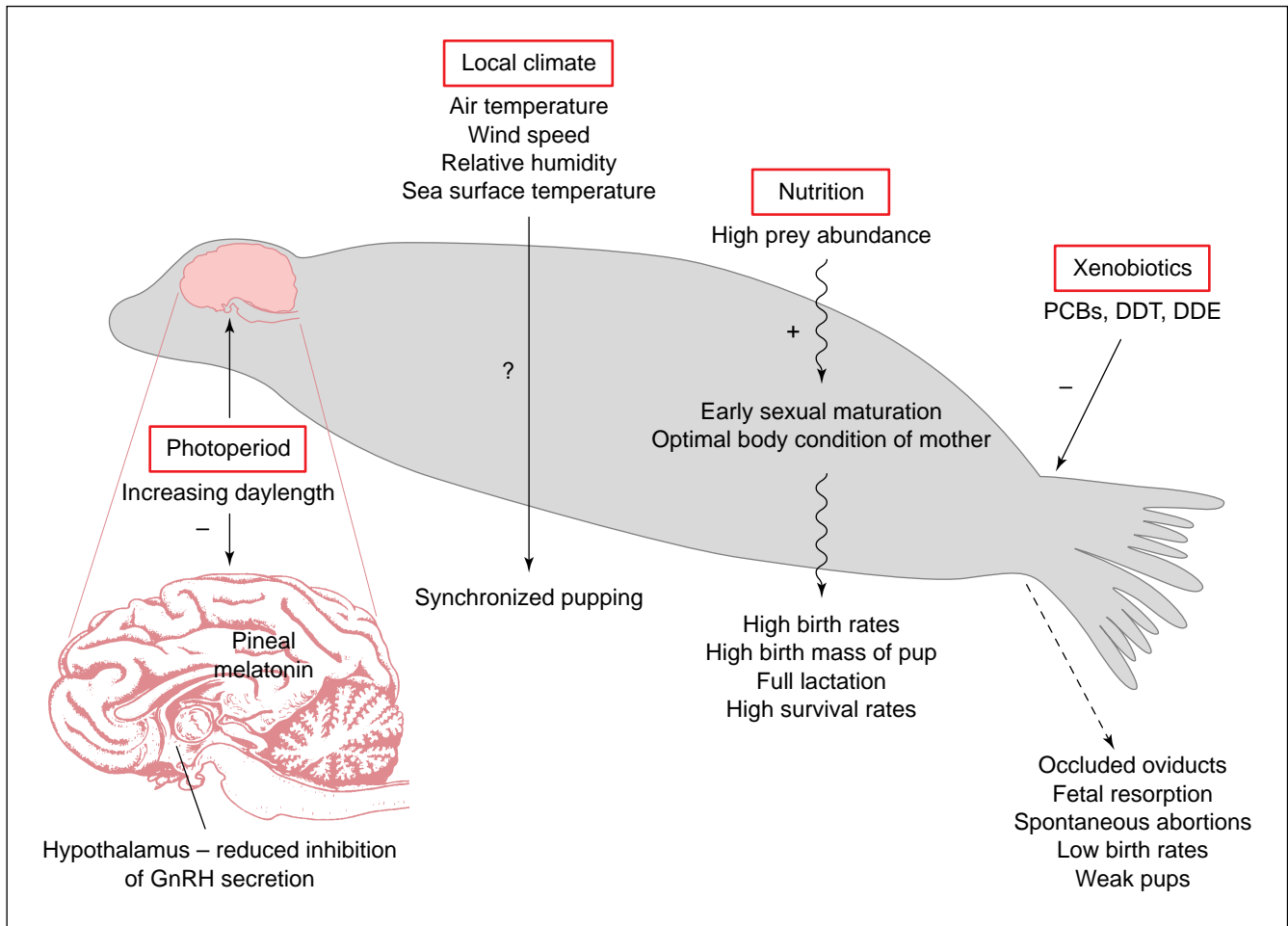
Fig. 8. Environmental influences on reproduction in seals. The major environmental influences identified to date include photoperiod and local climate, nutrition and xenobiotics. Photoperiodic effects work through the pineal gland to decrease the secretion of melatonin during increasing daylength. Melatonin probably acts in the mediobasal hypothalamus to relay photoperiodic cues through dopaminergic receptors that inhibit GnRH secretion. Local climate patterns, including wind speed, air temperature, sea temperature, and relative humidity, are reported to alter the timing of parturition and the subsequent breeding season. A high plane of nutrition, in the form of optimal prey availability, leads to good body condition of the mother, high birth rates, high birth mass of the pup, high survival rates, and early sexual maturation. Xenobiotics, specifically polychlorinated biphenyls (PCBs), dichlorodiphenyl trichloroethane (DDT), and dichlorodiphenyl dichloroethane (DDE), are reported to cause occluded oviducts, possibly as a result of fetal resorption, spontaneous abortions, low birth rates and weak pups. The mechanisms of action for all of the environmental influences are unknown or not well tested in seals.

(Tables 3 and 4). The variable embryonic diapause appears to synchronize birth both within a population and across the natural habitat.

Photoperiod is the most commonly cited environmental cue for synchronizing physiological reproductive processes in both male and female seals (Elden *et al.*, 1971; Temte, 1985; Boyd, 1991a; Fig. 8). The end of the embryonic diapause is hypothesized to be under the control of photoperiod (Temte, 1985). Elden *et al.* (1971) suggested that the pineal gland was responsible for the marked photoperiodic nature of the life cycle of seals. The pineal gland in newborn elephant seals is very large and active for the first 1–2 weeks of postnatal life (Bryden, 1994). The precisely timed reproductive events in Northern fur seals are the result of photoperiodic regulation mediated by the pineal neuroendocrine system, specifically hydoxy-indole (melatonin)

concentrations (Keyes *et al.*, 1971). Melatonin secretion ceases in Weddell seals under continuous natural daylight, a response similar to that observed in terrestrial mammals (Barrell and Montgomery, 1989). In terrestrial mammals, melatonin acts in the mediobasal hypothalamus to relay photoperiodic cues through dopaminergic receptors that inhibit GnRH secretion (Tortonese and Lincoln, 1994, 1995).

There is now a wealth of information on photoperiodic synchronization of reproduction (for review see Boyd, 1991a). One model dictates the duration of the photoperiod on a critical day near the end of the embryonic diapause as the primary determinant for the prediction of birthing time in captive California sea lions (Temte and Temte, 1993). Although the correlation between predicted and actual birthing periods are good (Temte and Temte, 1993) and experimental alteration of photoperiod

was successful in altering the timing of oestrus (Bigg and Fisher, 1975), altering photoperiod was not successful in changing the time of blastocyst reactivation (Daniel, 1981). These results indicate that other environmental or endocrine factors contribute to the reproductive synchrony of seals.

Climatic seasonality, including air temperature, wind speed, and relative humidity, during the breeding season, may be the ultimate determinant of the tight synchrony of the timing of birth (Trites and Antonelis, 1994; Fig. 8). Coulson (1981) suggested that sea surface temperature is a cue for synchronizing the pupping of grey seals, although as a single environmental cue, sea-surface temperature is probably too variable to account for the observed synchrony of birthing. Grey seals and harbour seals are the exceptions to the tight synchrony of birth timing across habitat ranges (Bigg and Fisher, 1975; Boyd, 1991a; Table 3), and may have evolved responses to different critical environmental cues to dictate the birthing period depending on the local climate around the time of parturition. In this regard, local climates probably do serve to fine tune the synchrony of birthing.

The Australian sea lion, with its nonannual, aseasonal reproductive cycle, provides evidence that no single environmental cue is universal for synchronized birthing in all species of seal. Despite the differences reported for the various seal species in various habitats, photoperiod is clearly a strong environmental cue that entrains an endogenous neuroendocrine cycle. While the mechanisms controlling photoperiodic effects on reproduction have been popular areas of study for terrestrial mammals, such studies involving marine mammals are hampered by a lack of sophisticated facilities to manipulate photoperiod, relatively long gestation periods, and difficulty in collecting serial samples to monitor changes in hormone concentrations. A few researchers have used the nearly continuous photoperiod of Antarctica and Macquarie Island to demonstrate the lack of melatonin secretion in seals during the austral summer (Griffiths et al., 1979; Barrell and Montgomery, 1989). This approach eliminates the need for complex photoperiod facilities; however, it can be used only for polar species.

Nutrition

Nutritional effects on the reproductive biology of seals is an emerging field of study. Rapid increases in seal populations are facilitated by high birth rates, high survival rates of both adult female seals and their offspring, as well as early sexual maturation (Fig. 8). All of these events can be influenced by the plane of nutrition of the seals during key reproductive events. Sexual maturity is attained when seals have reached about 87% of their final body size (Laws, 1956b), and can be attained at an earlier age when the growth rate is increased (Sergeant, 1973). Therefore, it is possible to use the age of sexual maturity as an indicator of the abundance or quality of food supply for a given population (Bengtson and Siniff, 1981; Boyd, 1991a): that is, puberty occurs earlier when food is available and later when food is limited. Rapid rises in the population of Antarctic fur seals may be accelerated by increased food availability, owing to the decline of interspecific food competitors (Laws, 1973). Similarly, poor body condition of female Antarctic fur seals in 1990, resulting in smaller pups and shorter perinatal periods, was probably due to decreased prey abundance or availability (Lunn and Boyd, 1993). The prolonged gestation reported in the Australian sea lion may be a result of poor nutrition (Gales, 1995).

Female body mass and blubber thickness decline during lactation in grey seals (Boyd, 1984b), and increase during the period of embryonic attachment. Nonpregnant females and females whose embryonic attachment was not complete have a lower blubber depth than females whose embryonic attachment was advanced (Boyd, 1984b). Boyd (1984b) postulated that either early embryonic attachment was dependent on an early or rapid increase in body condition during the spring, or that endocrine changes associated with embryonic attachment induced metabolic changes that resulted in fat deposition. In Antarctic fur seals, embryonic attachment occurred later than usual when the females were in poor body condition (Lunn and Boyd, 1993). This scenario was exacerbated for younger females (< 6 years), which weighed less, were in poorer body condition than older females, and also gave birth later in the season (Lunn and Boyd, 1993). While most of these studies are correlative, as opposed to causative, they indicate a functional relationship between nutrition and reproduction.

Bowen et al. (1994) demonstrated that birth mass is significantly correlated with maternal mass, and that birth mass increases with maternal age. High prepartum maternal body mass is an indication of the presence of large stores of fat and protein that can be mobilized during lactation. Milk production may require the export of up to 33% of maternal body fat and 15% of body protein in species that fast during lactation (Oftedal, 1993). This export of maternal resources requires the mobilization of substrates from maternal tissues, without which milk production will decline (Oftedal, 1993).

Changes in prey abundance are normally associated with interspecific competition (for example, human fisheries or rapid changes in the natural balance of top predators) or normal oceanographic processes. The El Niño–southern oscillation (ENSO) is a climatological and oceanographic phenomenon that occurs irregularly. The El Niño part of the ENSO nomenclature describes the changes in the circulation of the tropical Pacific Ocean that result in decreased abundance of marine life in the eastern tropical Pacific (Philander, 1990). When the atmospheric pressure is high in the Pacific Ocean, it tends to be low in the Indian Ocean, resulting in pressure fluctuations termed southern oscillations (Philander, 1990). Severe ENSO events disrupt the ecological system, resulting in lower prey abundance and diminished growth, body condition, reproduction and survival in numerous species. For example, during the 1982–1983 ENSO, seals on the west coasts of North and South America produced fewer pups, lactation periods were shorter, pup mortality was high (up to 100%), growth rates of pups decreased, periods of foraging trips by lactating otariid seals were shorter, age of first reproduction was higher, breeding seasons were missed, and adult female mortality was higher (Trillmich et al., 1991). ENSO events are a distinct time of food shortage and their intensity is not usually as great as the 1982–1983 event. The changes in body condition and reduced reproductive success in Antarctic fur seals reported by Lunn and Boyd (1993) were probably also the result of a less intense ENSO event. The ENSO-induced changes in the abundance of food for seals create a natural experimental setting that will undoubtedly be intensively studied in the future.

Although the functional or mechanistic nature of the nutrition–reproduction relationship remains unclear, it is intuitive to conclude that a high plane of nutrition will provide a female that with greater energy stores, facilitating a pregnancy that results in the birth of a large, healthy pup. Good nutrition also enhances lactation. Both the measurement of body condition and its effect on various reproductive events and processes during natural environmental perturbations will continue to be important areas of seal research.

Xenobiotics

Xenobiotics are defined as chemical compounds that are foreign and toxic to biological systems. The relationship between xenobiotics and reproduction has not been well studied in seals. The best known xenobiotics that may interfere with reproductive processes are organochlorines, and possibly heavy metals. Polychlorinated biphenyls (PCB), dichlorodiphenyl trichloroethane (DDT), and the degradation product of DDT, dichlorodiphenyl dichloroethane (DDE), as well as lead (Pb), zinc (Zn), mercury and numerous other metals, are common in waters polluted by heavy industry and contribute to the reproductive problems of seals (Helle *et al.*, 1976; Reijnders, 1986; Hutchinson and Simmonds, 1994; Fig. 8). Lead and zinc have been implicated in the high rates of female infertility in Caspian seals (Krylov, 1990; Kliks *et al.*, 1997; Table 1), although the causal mechanism has yet to be defined.

Although the metabolism and individual effects of PCB, DDT and DDE compounds have not been elucidated in seals, the effects of PCB compounds are thought to have a greater impact on reproductive failure than those of DDT or DDE (Helle *et al.*, 1976). Male seals continue to accumulate organochlorines throughout their lives, while females tend to lose some of their accumulated toxins to their offspring via transplacental transfer and lactation (for review see Hutchinson and Simmonds, 1994).

From 1968 to 1976, 20% of California sea lions were born prematurely (DeLong *et al.*, 1973; Gilmartin *et al.*, 1976), and 47% of week-old pups were found dead (Le Boeuf and Bonnell, 1971) in rookeries off the Californian and Mexican coasts. DDT residues in this species were higher than in all other marine mammals (Le Boeuf and Bonnell, 1971), and DDT and PCB concentrations were higher in affected mother and pups than in seals giving birth to full term pups (DeLong *et al.*, 1973). Low reproductive rates of ringed seals from the Baltic Sea were also the result of serious DDT and PCB pollution (Helle *et al.*, 1976). Concentrations of DDT and PCB compounds were significantly higher in the tissues of nonpregnant seals compared with those of pregnant seals; the pregnant seals only comprised 32% of the adult females collected for the study (Helle *et al.*, 1976). In addition, the oviducts of 64% of the nonpregnant females were restricted or occluded, preventing fertilization (Helle *et al.*, 1976). The occlusions may have been the result of fetal resorption by the mother (Hutchinson and Simmonds, 1994). More than 50% of the female grey and harbour seals found in nearby areas also had the same pathological changes (Helle *et al.*, 1976).

Reijnders (1986) conducted a landmark experiment, feeding harbour seals with fish from the polluted waters of the Dutch Wadden Sea versus fish from the Northeast Atlantic. He demonstrated that seals consuming the fish diet high in PCB and DDE had fewer pups than those consuming the control diet. The reproductive failure appeared to occur at the time of embryonic attachment and may have been due to hormone disturbance or a direct lethal effect of the toxicants on the embryo (Reijnders, 1986).

Uterine blockages, spontaneous abortions, weak pups and low birth rates are the most common problems associated with organochlorine contaminants (Hutchinson and Simmonds, 1994; Fig. 8). The causal mechanism for these reproductive problems has not been identified for seals (Hutchinson and Simmonds, 1994). The combined effects of organochlorines and epizootic viruses are probably the most devastating to seal populations; it was proposed that this combination was the cause of the 1988 epizootic to harbour seals in Europe (Olsson *et al.*, 1994). The interrelationship between disease agents, environmental contaminants and reproductive processes of seal populations that inhabit industrial coastlines will continue to be the subject of research.

Conclusion

The reproductive biology of seals is typically mammalian with several unique features. The hymeneal folds of the female reproductive tract allow aquatic breeding, and the embryonic diapause allows for synchrony of births to ensure maximal survival of offspring. The obligate requirement for a terrestrial habitat for birthing is the main factor keeping these mammals from being completely aquatic. Lactation and mating strategies have evolved to ensure that adult females can make an optimal maternal investment in their offspring while maintaining the ability to reproduce annually. This explains how many seal populations have increased so rapidly after centuries of decimation. Knowledge of the endocrinology of these physiological achievements needs to be improved and applied to the few seals species (for example, Mediterranean and Hawaiian monk seals, and Stellar sea lions) whose populations continue to decline despite increased political protection. Understanding the physiology of environmental influences on reproductive events and processes will enable us to manage this unique group of mammals, which sits at the top of an aquatic food chain, thereby helping to maintain global biodiversity.

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