# Reproduction in the Porpoises (Phocoenidae): Implications for Management

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ABSTRACT

The population biology of most phocoenid species is still rather poorly understood. It is important that we improve our knowledge in view of concerns which have been expressed in recent years about the status and long-term viability of some populations. A survey of the literature suggests that it would be unwise to assume that an unknown life-cycle parameter of a phocoenid species would necessarily be similar to that of another species, simply on the basis of taxonomic relationship. Each population and species has experienced a unique evolutionary history in a different ecological regime, and selective influences will have moulded life cycle parameters accordingly.

Most quantitative published data relate to *Neophocaena phocaenoides* (coastal waters of eastern Asia), *Phocoenoides dalli* (boreal – temperate North Pacific), and *Phocoena phocoena* (boreal – temperate N. Pacific and N. Atlantic, and Black Sea). *Phocoena dioptrica* (southern South America and the New Zealand subantarctic), *P. sinus* (Gulf of California), and *P. spinipinnis* (temperate – subtropical waters of South America) are not well known yet. Body-size variation within the family is relatively limited: 65–192 cm (*N. phocaenoides*); 100–225 cm (*P. dalli*); 67–190 cm (*P. phocoena*); and gestation periods are very similar in these three species: 11 months (*P. phocoena* and *N. phocaenoides*) and 11.4 months in *P. dalli*. Far greater differences are apparent in estimates of the age at sexual maturity, the life span, the duration of weaning, and the mean calving interval. It is important to determine if such differences result from misinterpretations or if they relate to radically different evolutionary adaptations (among animals of about the same body size) which have arisen in response to different environmental histories and ecological constraints.

The age at which sexual maturity is attained in *N. phocaenoides* is not yet known. The maturation process seems to be complete between 4–5 and 5–6 years of age in the western North Atlantic and North Sea populations of *P. phocoena*, respectively, and at about 7 years in *P. dalli*. The mean calving intervals appear to be 2 years in *N. phocaenoides*, 3 years in *P. dalli*, and variable in *P. phocoena* from 1–3 years, depending perhaps on nutritional levels. The duration of weaning is not well known in *N. phocaenoides* (estimated between 6–15 months). It could be as short as a few months (6–8) in *P. phocoena* and as long as 2 years in *P. dalli*. As with other odontocetes, controversies exist concerning the accuracy of age determination, but all direct evidence points to *P. phocoena* being relatively short-lived, to a maximum of about 12–13 years. On the basis of age determined from dentinal or cementum layers, *P. dalli* and *N. phocaenoides* have longer life spans than this; at least 16–17 years and 23 years respectively. Attempts to correlate numbers of corpora albicantia with body length have generally not been very successful.

## INTRODUCTION

Three genera are recognized in the family Phocoenidae:[1] *Neophocaena* with a single species *N. phocaenoides* (G. Cuvier, 1829); *Phocoenoides* with a single species *P. dalli* (True, 1885) (having two colour morphs 'dalli' and 'truei' Andrews, 1911); and *Phocoena* with four species, *P. phocoena* (Linnaeus, 1758); *P. dioptrica* Lahille, 1912; *P. sinus* Norris and McFarland, 1958; and *P. spinipinnis* Burmeister, 1865. All species have distributions which are essentially coastal in nature except *P. dalli*, which ranges widely across the pelagic North Pacific. While phocoenids are relatively familiar animals to coastal observers in the temperate zones of Europe, North and South America, their biology is not that well known, and probably about 90% of published literature relates to *P. phocoena*. The population biology of *P. dioptrica*, *P. sinus*, and *P. spinipinnis* is best described as virtually unknown.

Concern has been expressed for the long-term viability of some populations of *P. phocoena* (Wołk, 1969; Andersen, 1972; 1974; IWC, 1977), and the single population of *P. sinus* may be in immediate danger (Brownell, 1983). Like other shallow-water small cetaceans, phocoenids are particularly vulnerable to incidental capture in gill nets and other set fishing gear. Directed fisheries exist for several species in various parts of the world (Mitchell, 1975), but at present the incidental net

[1] Some workers prefer use of a subfamily Phocoeninae.

captures probably represent not only the major threat to several phocoenid species, but may also prove to be the most frustrating and intractable obstacle to any successful management programs for these animals.

## MATERIALS AND SOURCES

### *Neophocaena phocaenoides*:

Published data by Chi Ping (1926), Mizue, Yoshida and Masaki (1965), Harrison and McBrearty (1973–74) and Kasuya and Kureha (1979).

### *Phocoenoides dalli*:

Published data by Okada and Hayashi (1951), Wilkie, Taniwaki and Kuroda (1953), Mizue and Yoshida (1965), Mizue, Yoshida and Takemura (1966), Koga (1969), Kuzin and Perlov (1975), Houck (1976), Kasuya (1976a; 1978) and Morejohn (1979).

### *Phocoena phocoena*:

One hundred and eighty-one specimens obtained directly or indirectly by the authors from the western North Atlantic between 1969 and 1981; published data by Fraser (1934; 1953; 1974), Møhl-Hansen (1954), Ropelewski (1957), Wołk (1969), Fisher and Harrison (1970), Harrison (1970), Andersen (1972, 1974), Nielsen (1972), van Bree (1973), Gaskin, Arnold and Blair (1974), Gaskin and Blair (1977), Smith and Gaskin (1974), Watson

(1976), Yurick (1977), van Utrecht (1978) and Yasui (1980).

## *Phocoena dioptrica*:

Published data by Lahille (1912), Bruch (1916), Hamilton (1941), Praderi (1971), Praderi and Palerm (1971), Brownell (1975) and Baker (1977).

## *Phocoena sinus*:

Published data by Norris and McFarland (1958), Noble and Fraser (1971) and Brownell (1983).

## *Phocoena spinipinnis*:

Published data by Allen (1925), Pilleri and Gihr (1972), Aguayo (1975), Würsig, Würsig and Mermoz (1977), and Brownell and Praderi (1982).

## REPRODUCTIVE SYSTEMS OF PHOCOENIDS

The urinogenital systems of both sexes are quite typical for odontocetes, perhaps with the exception of the very large proportional size of the testes in the sexually active male (see General Discussion). The right ovary is usually permanently submature in appearance, and non-functional. Descriptions of all or part of male systems of phocoenids can be found in Hepburn and Waterston (1904), Braun (1907), Meek (1918), Chi Ping (1926), Fisher and Harrison (1970) and Harrison (1970); and of the female systems in Klaatsch (1886), Daudt (1898), Wislocki (1933), Harrison (*loc. cit.*), and Fisher and Harrison (*loc. cit*). The most recent and comprehensive descriptions specifically relating to morphology and histology of ovary and testis have been given by Fisher and Harrison for *P. phocoena*.

## LIFE HISTORY PARAMETERS

### Age

*The status of age determination in phocoenids*

Kasuya (1978) estimated age in *P. dalli* from dentinal layers using decalcified sections stained with haematoxylin. A layer of enamel persists in the teeth of this species after the decalcification treatment. Growth layers were found to be irregular and unclear in postnatal dentine after the first layer, with a pulp cavity rapidly narrowing with age. Teeth in this species are proportionately smaller than in *P. phocoena*. Layering in dentine in older specimens was indistinguishable, or had ceased. In some cases, no distinct layers could be recognized at all. Cementum layers were present and useful to some extent, but the thickness was greatly variable from one individual to another, and accessory layers were often present. Independent counts on the same teeth produced discrepancies of up to 20%. Precise determination of age in this species is not yet possible (Kasuya, 1978).

Age, based on analysis of dentinal growth layers, has been estimated in *P. phocoena* by Nielsen (1972), Gaskin and Blair (1977) and van Utrecht (1978). Nielsen worked with decalcified, hematoxylin-stained transverse and longitudinal sections, the other authors with untreated, unstained longitudinal axial sections. All concurred in the conclusion that two laminations, one opaque and one translucent (with respect to transmitted light), were deposited to form a single growth layer each year. Nielsen reported that she was unable to distinguish growth layers in the osteodentine of older animals, but van Utrecht made no mention of such a problem, and Gaskin and Blair suggested that Nielsen's chance of recording animals older than about 8 years was limited by the small sample size at her disposal.

Studies of age determination in *N. phocaenoides* are still in progress (Kasuya and Kureha, 1979); the problem has yet to be addressed in the case of *P. dioptrica, P. sinus* and *P. spinipinnis*.

### Age at sexual maturity

The mean regressions of body length on age in the two species for which sufficient data are available (*P. dalli* and *P. phocoena*) are presented in Fig. 1.

Kasuya (1978) concluded that the maturing process occurred rapidly in both sexes of *P. dalli*. He estimated that 50% of the males of *P. dalli* were mature by about 7.7 years of age, and 50% of the females by 7.0 years. By using his data and applying the method of DeMaster (1981), we calculated a value of about 7.3 for the average age at which first birth occurs (Table 1). Given the difficulty of interpreting the status of maturing testis tissue however, the two methods obviously yield a similar result. The data base available for *P. phocoena* is not really large enough to apply Kasuya's method to that species.

Van Utrecht (1978) and Yurick (1977) drew attention to differences in growth curves for both sexes of *P. phocoena* in the eastern and western North Atlantic; data for the Bay of Fundy and southern North Sea populations of *P. phocoena* are plotted separately in the figure. The degree of overlap between the individual points (not shown) is considerable, however, and the differences can only be shown statistically, not as absolutes which separate any two individuals from these populations at a given age. The unbroken section of each curve indicates those age classes in which significantly more than 50% of specimens sampled have clearly attained sexual maturity. The curve published by Nielsen (1972) for *P. phocoena* is included for comparison, but since she plotted males and females together, and lacked samples from reproductive organs, the age at sexual maturity of animals in the Baltic population cannot be indicated.

Both males and females of *P. phocoena* appear to reach maturity earlier in the western North Atlantic than in the North Sea. Males and females are mature in the Bay of Fundy population at three to four years of age (Gaskin and Blair, 1977); in the North Sea however, van Utrecht (1978) found males maturing at age five and females at six. Previous suggestions that *P. phocoena* might mature at about 14 or 15 months of age (Møhl-Hansen, 1954; Slijper, 1962) have already been discounted by Fisher and Harrison (1970), and we are in full agreement with this conclusion.

Much less information is available for the other phocoenid species. Kasuya and Kureha (1979) found a male of *N. phocaenoides* 141 cm in length to have testes still in the 'early pubertal stage', while other specimens of 148 cm and upwards were sexually mature. Two females of *P. dioptrica* 186 and 191 cm long were pregnant; two males 200 and 204 cm long were physically
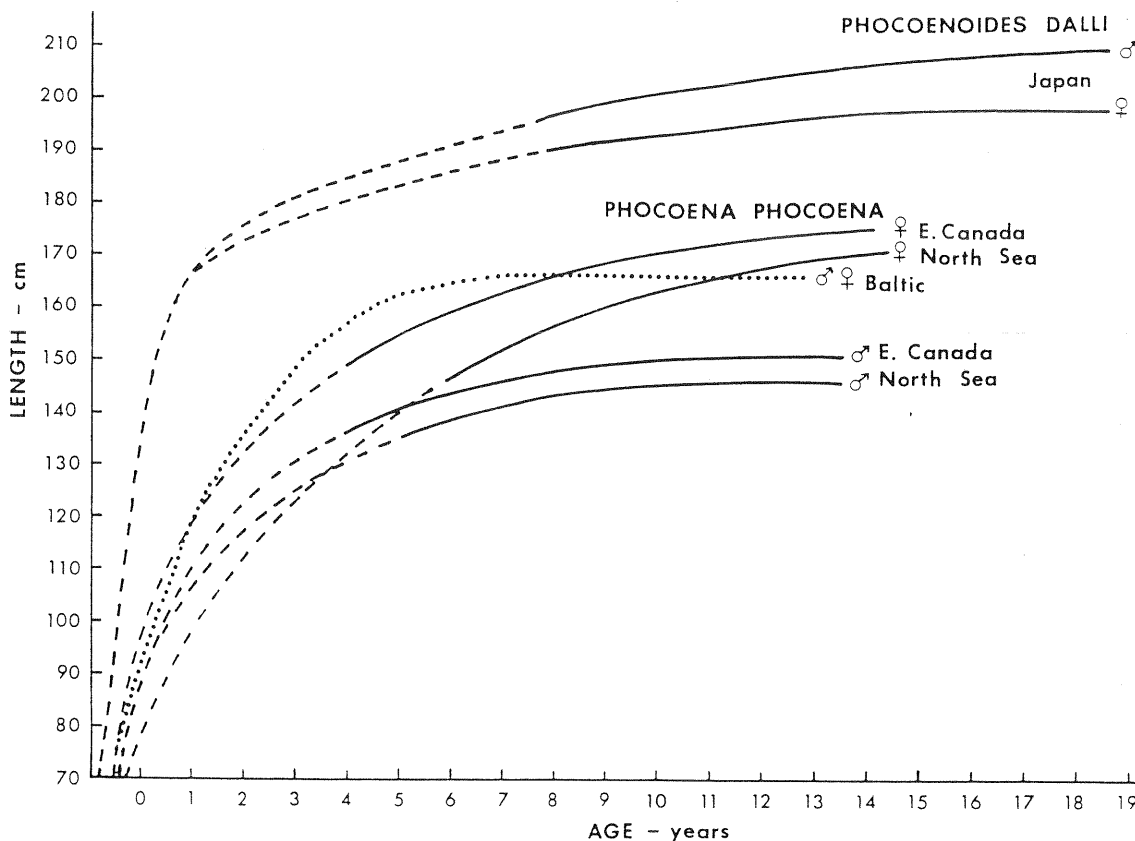
Fig. 1. Relationship between body length and age in years (based on dentinal layers), of specimens of *Phocoenoides dalli* from the vicinity of Japan, and males and females of three populations of *Phocoena phocoena* (Baltic data from Nielsen (1972), North Sea data from van Utrecht (1978) and eastern Canadian data from Gaskin and Blair (1977)).

Table 1

Calculation of the average age of first birth of *Phocoenoides dalli* (data from Kasuya, 1978) using the method of DeMaster (1981)

| Age in years (x) | No. females observed n(x) | No. females pregnant t(x) | Proportion of reproductive ♀ z(x) | P (give birth at or before age x) r(x) | P (1st birth at P age x) xr(x) | |
|---|---|---|---|---|---|---|
| 2 | 23 | 0 | 0 | 0 | 0 | 0 |
| 3 | 17 | 0 | 0 | 0 | 0 | 0 |
| 4 | 26 | 1 | 0.038 | 0.038 | 0.038 | 0.152 |
| 5 | 24 | 2 | 0.083 | 0.118 | 0.080 | 0.400 |
| 6 | 22 | 4 | 0.182 | 0.279 | 0.161 | 0.966 |
| 7 | 27 | 16 | 0.593 | 0.707 | 0.428 | 2.996 |
| 8 | 13 | 3 | 0.231 | 0.775 | 0.068 | 0.544 |
| 9 | 9 | 5 | 0.556 | 0.900 | 0.125 | 1.125 |
| 10 | 9 | 4 | 0.444 | 0.944 | 0.044 | 0.440 |
| 11 | 4 | 1 | 0.250 | 0.958 | 0.014 | 0.154 |
| 12 | 3 | 1 | 0.333 | 0.972 | 0.014 | 0.168 |
| 13 | 1 | 1 | 1.000 | 1.000 | 0.024 | 0.312 |
| 14 | 1 | 1 | 1.000 | 1.000 | 0 | 0 |
| 15 | 1 | 1 | 1.000 | 1.000 | 0 | 0 |
| 16 | 0 | 0 | 0 | 0 | 0 | 0 |
| 17 | 1 | 1 | 1.000 | 1.000 | 0 | 0 |
| | | | | | | 7.257[a] |

[a] Average age of 1st birth in this sample = 7.257 years.

mature (Brownell, 1975). Only two female specimens of *P. sinus* 139 and 150 cm long have been reported; both appeared to be physically mature (Brownell, 1983). A male of *P. spinipinnis* 180 cm long had active testes according to Brownell and Praderi (1982).

## Life span

Accurate estimation of life span, both maximum and average, remains a contentious and difficult problem in phocoenid biology, and obviously any simulations of long-term population production are suspect until this issue is resolved. Kasuya and Kureha (1979) reported
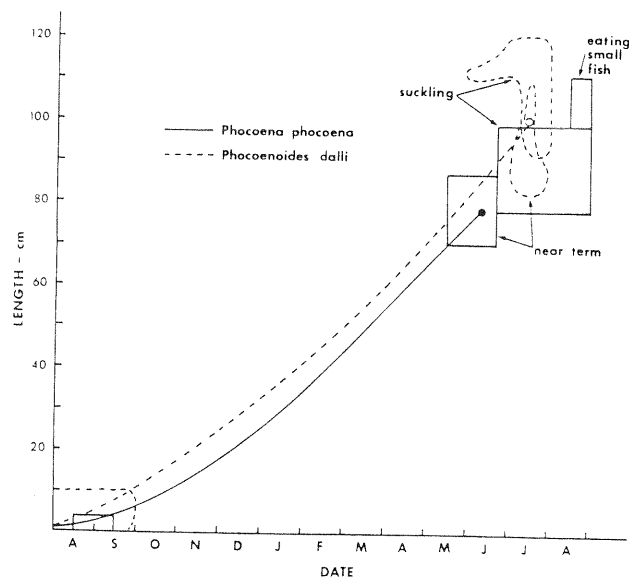
Fig. 2. Foetal development, time of birth, and neonatal development in *P. dalli* (broken lines and areas) and *P. phocoena* (solid lines and boxes). The circles at the end of each line represent best estimate of mean size at birth from Kasuya (1978) and Mizue *et al.* (1966) for *P. dalli*, and from our data, and data in Fisher and Harrison (1970), Harmer (1927). Møhl-Hansen (1954) for *P. phocoena*. Time of recognition and size range of early embryos, near-term foetuses and sucklings in *P. dalli* are drawn from Okada and Hayashi (1951), Mizue *et al.* (1966) and Kasuya (1978). The same stages in *P. phocoena* are from sources in our own data, Fisher and Harrison (1970), and Baltic and Norwegian data summarized by Møhl-Hansen (1954).
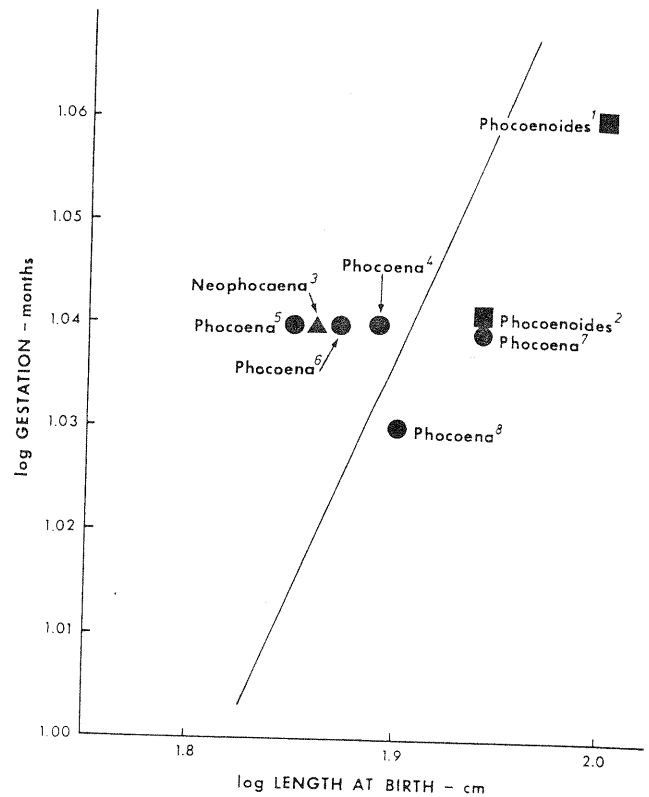


Fig. 3. The relationship in phocoenids of log gestation (in months) with log size at birth (cm), after the diagram of Perrin *et al.* (1977). Data drawn from: 1. Kasuya (1978); 2. Mizue *et al.* (1966); 3. Kasuya and Kureha (1979); 4. Data of present authors; 5. Harmer (1927); 6. Møhl-Hansen (1954); 7. Fisher and Harrison (1970); 8. Van Utrecht (1978, replotted). See note in text concerning data for *P. dalli* of Okada and Hayashi (1951).

specimens of *N. phocaenoides* with up to 23 dentinal growth layers in their samples from coastal Japan; as in most other odontocetes, one growth layer appeared to be deposited each year. Kasuya (1978) had a very few males and females of *P. dalli* in his samples between the ages of 14–18 and 14–16 years respectively, but based on (debatable) assumptions about the magnitude of bias in the fishery for animals of different age groups, he extrapolated regression lines from the right-hand peak of the catch curve (from the Sanriku coast harpoon fishery) that suggested that males and females of *P. dalli* could attain maximum ages of approximately 40 and 35 years, respectively, i.e. somewhat less than, but comparable to, the life span of *Stenella coeruleoalba* as estimated by Kasuya (1976b; 1978, Fig. 25).

Gaskin and Blair (1977) and van Utrecht (1978) reported several specimens of *P. phocoena* with 10–13 annual layers in the dentine. The former workers suggested that catch curves of animals shot more or less at random at sea (sex ratio nearly 1:1 and all size classes well represented) pointed to the maximum life span of this species in western North Atlantic waters being from 12–13 years, somewhat less than the maximum of 15 years suggested by Slijper (1962). However, Yurick (1977) reported that the results of his study, and the studies of Gaskin and Blair (1977) and Nielsen (1972) indicated that few harbour porpoise live beyond 7–8 years of age. There is no published information on the possible life span of *P. dioptrica*, *P. sinus*, or *P. spinipinnis*.

## Growth

### Foetal growth rates

Foetal growth rates have been described by Kasuya (1978) for *P. dalli* and for the Baltic, eastern North Atlantic and North Sea populations of *P. phocoena* by Møhl-Hansen (1954), who re-plotted data gathered by earlier authors, and van Utrecht (1978). With few exceptions, only foetuses at a very early stage were available to Fisher and Harrison (1970), Gaskin *et al.* (1974) and Gaskin and Blair (1977) during studies of the western North Atlantic population. We have summarized information for this species and *P. dalli* in Fig. 2, in the form of a pair of mean foetal growth curves extrapolated to the times of year at which near-term foetuses and the smallest sucklings have been recorded.

Perrin, Holts and Miller (1977) explored the relationship between length at birth ($\log x$) and duration of the gestation period ($\log y$) in delphinids. Van Utrecht (1978) redrew this figure and added *P. phocoena* based on data drawn from the southern North Sea population. Unfortunately, as a result of an arithmetical or plotting error ($\log 10.66$ is 1.028, not 1.04), *P. phocoena* appears to fall right on the theoretical line in his figure. This is not the case. In Fig. 3, we have replotted his value, together with estimates drawn from our own data and those of other authors, and compared these with equivalent values for *P. dalli* given by Okada and Hayashi (1951). Based on their data the point for that species lies

Reproductive parameters of Phocoenidae

| Species | Locality | Mating season | Gestation period | Size at birth | Parturition season | Duration of lactation | Comments |
|---|---|---|---|---|---|---|---|
| *Neophocaena phocaenoides* | Inland Sea of Japan | Late August–early September[1]* | 11 months[2] | 65–85+ cm[2, 3] | March–June,[2] with peak in April–May[2] | Poorly known, 6–15 months[2] ($\bar{x} < 12$) | * Considered to be erroneous estimate[2] |
| *Phocoenoides dalli* | Coastal waters of Japan | Mid-August–late October[7] with peak in September | 11.4 months[7] | 99.7 cm[7] | August–September[7]* | 0.5 to 3.5 years[7] ($\bar{x} = 2.07$ years) | * Peak in late August[7] |
| | Sea of Okhotsk and Sea of Japan | Late June–early July[4]*, mid-August–October[7] | 7–9 months[4]* | — | April–May[4]* | About 2 years | * Considered by Kasuya (1978)[7] to be in error; he believed peak of pairing to be in September in all N.W. Pacific–Bering Sea regions. |
| | Bering Sea and N. Pacific | July and August[5, 6] | 11 months[6] | 100 cm[6] | Peak in late August[6, 8] | About 2 years[7] | — |
| | Coastal waters of western United States | All year round[9] | — | — | All year round[9] | — | Morejohn (1979)[9] presents data to challenge the concept of a unimodel birth peak in the N. Pacific, and believed that the Japanese conclusions resulted from using samples taken during limited seasonal fisheries. |
| *Phocoena sinus* | Gulf of California | Not known[10] | Not known[10] | 74 cm[10] | April[10] | Not known[10] | |
| *Phocoena dioptrica* | Coastal waters of southern South America, and N.Z. subantarctic | August–?[11]* | Not known | 48.4+ cm[12] | Not known | Not known[11] | * Apparent near-term foetuses recorded in July and August[11] |
| *Phocoena spinipinnis* | Southern South America | Not known[13] | Not known[13] | 44+ cm[13] | Austral fall?[13] | Not known[13] | — |
| *Phocoena phocoena* | Northern European waters | August–September[14]* | — | — | June–July[14] | — | * Considered to be in error, and inconsistent with same author's comments on sizes of foetuses in August[19] |
| | Norwegian waters | — | 8–10 months[15, 16] | 70–85 cm[17] | March–July[15, 16] | 8 months[16] | — |
| | Norwegian waters | — | c. 10 months[18] | 80–86 cm[18] | May–July[18] | — | — |
| | West Baltic Sea | July–August[19] | 11 months[19] | $\bar{x} = 75$ cm[19] | June–July[19] | 8 months[19] | — |
| | United Kingdom waters | June–August[20] | 10+ months[20] (11 months)[23, 24] | $\bar{x} = 71$ cm[20] (76.2–99.1 cm)[25–27] | June onwards[20] (June–July)[23, 24] | — | — |
| | Netherlands waters | June–August[22]* (–October)[17] | 10.66 months[22] | 67–80 cm[22] (70 cm)[17] | June–early July[22] (July)[22] | — | * Judged by birth data given by this author[22] |
| | North Atlantic in general | June–August[23] | 11 months[23] | 80–90 cm[23] | June–July[23, 24] | — | — |
| | Bay of Fundy region, Canada | June–August[28] | 11 months[28, 30] | $\bar{x} = 78$ cm[29] | June–early August[23, 29, 30, 31] | 8 months* | * Estimated from age-length data in [30] and lengths at which solid food starts to be recorded[29] |
| | Northwest coast of U.S.A. | July–August[32] | c. 10 months[32] | 80–86 cm[32] | May–July[32] | — | |

References: [1] Mizue *et al.* (1965); [2] Kasuya and Kureha (1979); [3] Harrison and McBrearty (1973–74); [4] Okada and Hayashi (1951); [5] Mizue and Yoshida (1965); [6] Mizue *et al.* (1966); [7] Kasuya (1978); [8] Koga (1969); [9] Morejohn (1969); [10] Brownell (1983); [11] (1975); [12] Bruch (1916); [13] Brownell and Praderi (1982); [14] Collett (1912); [15] Grieg (1891); [16] Slijper (1962); [17] Grieg (1898); [18] Guldberg and Nansen (1894); [19] Møhl-Hansen (1954); [20] Harmer (1927); [21] Van Diense (1946); [22] Van Utrecht (1978); [23] Fisher and Harrison (1970); [24] Harrison (1974); [25] Fraser (1970); [26] (1946); [27] (1953); [28] Gaskin *et al.* (1974); [29] Smith and Gaskin (1974); [30] Gaskin and Blair (1977); [31] Gilpin (1875); [32] Scheffer and Slipp (1948).

very far below the regression line, somewhere between 0.84 and 0.95 on the *x* axis. Like Kasuya (1978), we consider their estimate to be wrong. As can be seen from the figure, the spread among the three species is not great, even allowing for variation and some uncertainty about the exactitude of mean values for gestation period and size at birth, inevitable at this stage of our knowledge of these animals.

### Size at birth in phocoenids

Probably no phocoenid is less than about 60 cm long at birth, judging from the body size of adults. Statements by Bruch (1916) that a 48.4 cm foetus in a specimen of *P. dioptrica* was 'near-term' should be treated with considerable caution. Even the value of 60 cm for a 'near-term' foetus of *N. phocaenoides* seems to be on the low side. For this species, *P. phocoena* and *P. dalli*, the size spectrum appears to lie between about 67–100 cm, with the average in *Phocoena* and *Neophocaena* perhaps not far from 75 cm. The estimates for each species in the literature are summarized in Table 2.

### Postnatal growth

Sexual dimorphism is a characteristic of phocoenids, although few data are available for some species. The largest known male and female specimens of *N. phocaenoides* were 192 and 175 cm, respectively (Kataoka, Furuta and Kitamura, 1974; Kataoka, Kitamura, Yamamoto, Manabe and Sekida, 1969). Similarly in *P. dalli*, males are larger than females, with the largest male and female reported by Kasuya (1978) to be 219 cm (*n* = 485) and 209 cm (*n* = 399), respectively. In harbour porpoises, however, it is the female which is larger. Data on growth in body length in the latter two species are summarized in Fig. 1. Almost no data exist on total length differences between sexes for *P. dioptrica*, *P. sinus* and *P. spinipinnis*.

Yurick (1977) found that sexual dimorphism is present in *P. phocoena* from birth, with neonatal skull length greater in females than in males. This dimorphism is maintained throughout life, being present at the onset of sexual maturity (Fisher and Harrison, 1970), upon reaching physical maturity (Gaskin and Blair, 1977; Møhl-Hansen, 1954), and in the annual growth increment estimated for female and male harbour porpoises

stranded on the California coast, 95 and 55 mm/year respectively, by Stuart and Morejohn (1980). The maximum body length reached by both sexes in different parts of the range are presented in Table 3. The 178-cm male from the Bay of Fundy was exceptional in our extensive experience with this population. No other male in the Fundy sample (*n* = 66) was longer than 150 cm; several females however, were greater than 160 cm in length. Further details are not available to us for the 191-cm male from the English Channel, but it is no doubt the largest harbour porpoise ever recorded. Despite these two apparently unusual males, Yurick (1977), using data from 473 specimens, found that female *P. phocoena* were larger on average than males throughout the range of this species.

Population differences have been recognized in *P. phocoena*; growth curves for both sexes from eastern Canada and the North Sea are presented separately in Fig. 1. Differences between the males at any age are minimal, and the length/age relationship also converges in the females of the two populations with increasing age. Van Utrecht (1978) claimed that linear regression of length and weight also revealed some differences in growth rates between the North Sea and Baltic Sea populations as he had indicated in an earlier paper (van Utrecht, 1960). The differences, however, are quite small, and possibly not significant when the standard errors about the two regressions are compared (without the raw data, we were unable to do this). Yurick (1977) also suggested that the Baltic population might be morphometrically distinct, but did not carry out a detailed comparison because of numerous statistical objections and different sample sizes.

## Reproductive cycles in phocoenids

### Mating seasons

Mating seasons of cetacean species can be inferred (assuming a discrete season actually exists) from direct observations of mating behaviour, from the distribution of the annual peak of births and from studies of the state of the testes of adult males. Even reasonably good data from such sources may not necessarily permit us to define a mating season with great precision, often because sampling is limited to a particular time of the year.

Table 3

Maximum body length attained by male and female harbour porpoises

| Location | Females | Males | Source |
|---|---|---|---|
| N.E. Pacific | 176 (27)[a] | 161 (22) | Stuart and Morejohn (1980) |
| | 179 (16) | 163 (5) | Yurick (1977) |
| Bay of Fundy | 175 (50) | 178 (66) | Yurick (1977) |
| Baltic | 180 (164) | 164 (225) | Møhl-Hansen (1954) |
| | 180–189 (357) | 160–169 (296) | Van Bree (1973) |
| | 173 (10) | 152 (17) | Yurick (1977) |
| Irish coast | 178 (22) | 178 (14) | Yurick (1977) |
| North Sea (English coast) | 168 (32) | 168 (29) | Yurick (1977) |
| English Channel | 183 (17) | 191 (27) | Yurick (1977) |
| North Sea (Dutch coast) | 186 (62) | 151 (43) | Van Utrecht (1978) |
| | 164 (21) | 149 (12) | Yurick (1977) |

[a] Length in cm followed, in parentheses, by sample size.

Published data on the timing and duration of mating season of phocoenid species are summarized in Table 2, by species and locality. In virtually all cases the season occurs in the high summer months in boreal-temperate species and appears to have a duration of about two months on average, although sexual behaviour in *P. phocoena* has been noted by us between May and September (but sometimes between small (apparently immature) animals). From published accounts of *P. phocoena* (Table 2), mating seems to take place later in Baltic and Scandinavian waters than in those off the United Kingdom and the Netherlands. It is noteworthy that the observations published by Morejohn (1979) are in direct contradiction to Japanese reports about mating and calving periods in *P. dalli* (see General Discussion).

### Gestation period

The duration of gestation is known with reasonable accuracy in three species of phocoenid: *N. phocaenoides*, *P. dalli*, and *P. phocoena* (Table 2; Figs 2 and 3). In each case, it appears to be close to 11 months.

### Parturition season

This is relatively well known for the same three species listed above; earlier in *N. phocaenoides* than in *P. dalli* or *P. phocoena* in the Northern Hemisphere, yet also earlier in *P. phocoena* in Norwegian than in western European waters (Table 2). Mother–calf pairs of *P. phocoena* begin to arrive in Bay of Fundy coastal waters in June, or rarely in late May. They have the calves with them when they arrive, so we assume (Watson, 1976) that birth takes place away from the near-shore region. Very small sucklings can still be observed in the beginning of August, and a 78-cm specimen was taken in early August in 1971 off southern New Brunswick. Morejohn (1979) argued that calving in the population of *P. dalli* off the west coast of the United States could occur at any time of the year.

### Duration of lactation and mean age at weaning

The duration of lactation is perhaps the least known of this group of life-cycle parameters. Kasuya and Kureha (1979) considered the mean duration in *N. phocaenoides* to be about 12 months, but the error around the mean was large, with estimates ranging from six to 15 months. A similar problem was encountered by Kasuya (1978) when studying the Japanese coastal population of *P. dalli*; the mean period was long, as in larger odontocetes, about 2.07 years, with the low estimate at 0.5 years and the high of 3.5 years.

There is general agreement among workers on both sides of the North Atlantic that lactation in *P. phocoena* appears to last for no more than 8 months. Females taken by our group in the Bay of Fundy in early mid-summer (July) which were accompanied by small animals (but not the size of calves) usually showed some residual fluid production in the mammary gland, but not milk. Watson (1976) observed the progress of a nursing mother of this species, recognizable by a large scar across her back, from mid-July to early September, a period of about 8–9 weeks. In July, and through to the first week of August, the calf stayed very close to the caudal peduncle of the mother, hardly ever leaving this position. By the last two weeks of August and into September, growing independence was observed in the behaviour of this calf; by the end of the observation period, it was frequently 'foraging' 5–10 m away from the female, sometimes diving with her, sometime moving away independently, and sometimes being temporarily left at the surface as she dived, presumably to feed.

We found milk in the stomachs of 10 calves of *P. phocoena* (82–99 cm in length) taken between 8 July and 20 August in the Bay of Fundy, and to these can be added another five (90–110.5 cm) collected by Fisher in the same area between 2 August and 28 September. A small (104 cm) animal examined by us in mid-August had the remains of small fish in its stomach (Smith and Gaskin, 1974), indicating that solid food can be taken as early as about eight weeks after birth. Møhl-Hansen (1954) found fish in stomachs of juveniles in the Baltic in November, and, based on the state of tooth eruption and the presence of parasites, concluded that they were taking much solid food by five months of age. There seems little doubt (Fisher and Harrison, 1970; Nielsen, 1972; Gaskin and Blair, 1977) that calves of *P. phocoena* attain body lengths of 100–110 cm by the end of their first summer of life, and there is little or no evidence to support the idea of an extended lactation period in this species. It seems unlikely that intensive lactation lasts much more than five to six months, and it is probably complete within eight months. There is some evidence, however, that young may stay with the mother until the birth of the next calf and perhaps for a month or so after that, judging by the number of mother + calf + juvenile combinations sighted in July–August in the Bay of Fundy. Kasuya and Brownell (1979) have recently reported a lactation period of similar duration in another very small cetacean, *Pontoporia blainvillei* (Gervais and d'Orbigny, 1844), off the coast of Uruguay.

### Changes in the testes

Little published information is available on testis size and weight in *N. phocaenoides*. Harrison and McBrearty (1973–74) reported that two males 130 and 150 cm long had single testis weights (including the epididymis) of 78.3 and 603 g respectively. The latter specimen was believed to be mature and was captured (December) during the breeding season. Mean testis weights in *P. dalli* increase with age (Kasuya, 1978, Fig. 11) and also with body length (Kasuya, 1978, Fig. 14). Kasuya also examined the relationship between the mean diameter of seminiferous tubules and testis weight in that species, and correlated testis weight and tubule diameter with the ratios of immature and mature animals determined from histological samples.

Fisher and Harrison (1970) examined testes of 26 male specimens of *P. phocoena*, some with incomplete data. Their histological material was very limited, but they collected some useful volumes and weights. The present authors collected another 66 specimens; paired weights for mature animals in the combined sample ranged from 971–3,740 g in May and June ($\bar{x} = 1,971$ g) and from 165–538 g in August ($\bar{x} = 403$ g). The series of 66 specimens taken by us were examined histologically; 26 were immature and 40 mature. The immature males were all 3 years of age or less and had seminiferous tubules ranging in diameter from 37.0 to 63.9 $\mu$m (mean: 48.0 $\mu$m; Table 4). A significant increase in tubule diameter was found with increasing body length,

Table 4

Comparison, by age and body length, of seminiferous tubule diameters, percentage of tubules containing sperm, and single testis volumes from a sample of 74 harbour porpoises, *P. phocoena*, collected in coastal waters of eastern Canada (9 July–2 September)

| Age | Sample size | Body length cm | Tubule diameter μm | % tubules with sperm | Single testis volume, cc |
|---|---|---|---|---|---|
| 0 | 9 | 86.0–103.5 (94.8) | 37.0–56.3 (42.9, 8)* | — | 7.8 |
| 1 | 15 | 109.0–124.5 (116.9) | 37.0–62.6 (49.4, 14) | — | 8.8–26.2 (15.8, 7) |
| 2 | 4 | 116.5–134.0 (126.9) | 52.2–63.9 (58.1, 3) | — | 18.3–40.3 (29.3, 2) |
| 3 | 3 | 126.0†–142.0 (132.0) | 54.0†–156.4 (101.9, 3) | 0–100 (60) | 96.3–538.2 (317.3, 2) |
| 4 | 6 | 137.0–155.0 (145.9) | 100.4–140.6 (118.6, 5) | 10–100 (77) | 99.5–651.2 (239.3, 5) |
| 5 | 20 | 134.0–158.0 (142.2) | 96.8–176.3 (128.4, 17) | 0–100 (66) | 92.3–539.1 (254.0, 14) |
| 6 | 5 | 125.0–145.5 (138.0) | 100.7–163.5 (119.3, 5) | 0–80 (33) | 118.8–415.1 (216.9, 5) |
| 7 | 6 | 132.0–178.0 (148.1) | 91.0–150.2 (110.0, 5) | 0–95 (64) | 114.9–412.7 (226.2, 3) |
| 8 | 4 | 137.0–150.0 (144.9) | 107.7–141.8 (129.7, 4) | 0–100 (64) | 104.1–175.8 (138.6, 3) |
| 10 | 1 | 141.5 | 105.4 | 55 | — |
| 13 | 1 | 137.0 | 168.6 | 95 | — |

\* Mean, followed by number of animals examined.
† This animal immature.



expressed by $y = 0.34x + 10.4$ (d.f. = 24, and $0.01 < P < 0.001$). This relationship is indicative of normal growth and development of the testes relative to increase in body size. The mature males were 3 to 13 years old and had tubules 91.0 to 176.3 μm in diameter (mean: 124.2 μm; Table 4). No correlation was found between tubule diameter and age, nor between percentage of tubules with sperm and age. Both of these parameters, however, were correlated significantly with date of capture (Figs 4 and 5). The decreasing percentage of seminiferous tubules containing sperm during the summer months (Fig. 4) could be described by $y = -9.72x + 120.9$ (d.f. = 39, and $P < 0.001$); and the decreasing diameter of seminiferous tubules over time (Fig. 5) by $y = -7.95 + 170.3$ (with d.f. = 38, and $P < 0.001$).

The statistically significant relationship of declining tubule diameter and the percentage of tubules containing sperm with date of capture seems indicative of a seasonal cycle of spermatogenesis and agrees with data presented by Fisher and Harrison (1970), who concluded that testicular activity in North Atlantic harbour porpoises increased from May onwards (reaching a peak in the latter half of July) and then decreased dramatically by mid-August.

The possibility that declining activity could also be reflected by decreasing testicular volume was investigated by plotting bi-monthly mean volumes for mature males from the Bay of Fundy (Fig. 6). Mean volume during the first half of September was nearly 50% less than that calculated for the latter half of July. In conjunction with the aspermatogenic state of some of the samples in late August and early September, this is further evidence of
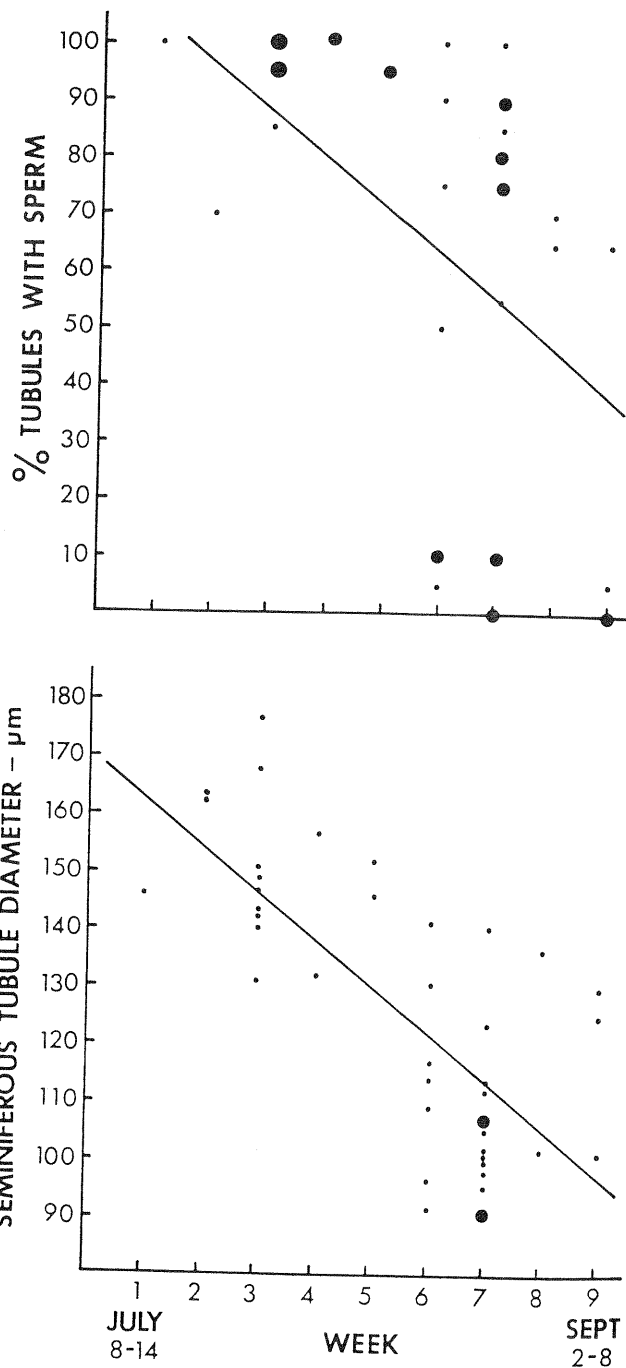
Figs 4, 5. Evidence of an annual sexual cycle in male harbour porpoises indicated by declining testicular activity during a 9 week period in summer. Decreasing percentage of seminiferous tubules containing sperm (Fig. 4) is described by the equation $y = -9.27x + 120.9$, where $y$ is the percentage of tubules containing sperm and $x$ is the date in sequential weeks (week 1 = 8–14 July). Decreasing diameter of the seminiferous tubules (Fig. 5) is described by the equation $y = -7.95x + 170.3$, where $y$ is the diameter in μm and $x$ is the date in sequential weeks (as above). Levels of significance and d.f. values given in text. The three sizes of circles represent one, two and three observations.

the existence of an annual reproductive cycle in the male harbour porpoise. We also found that immature and mature males of *P. phocoena* may be easily differentiated during the summer months on the basis of single testis volume: 7.8–40.3 cc, mean 17.7 cc, $n = 10$; compared to 92.3–651.2 cc, mean 236.4 cc, $n = 32$, respectively.
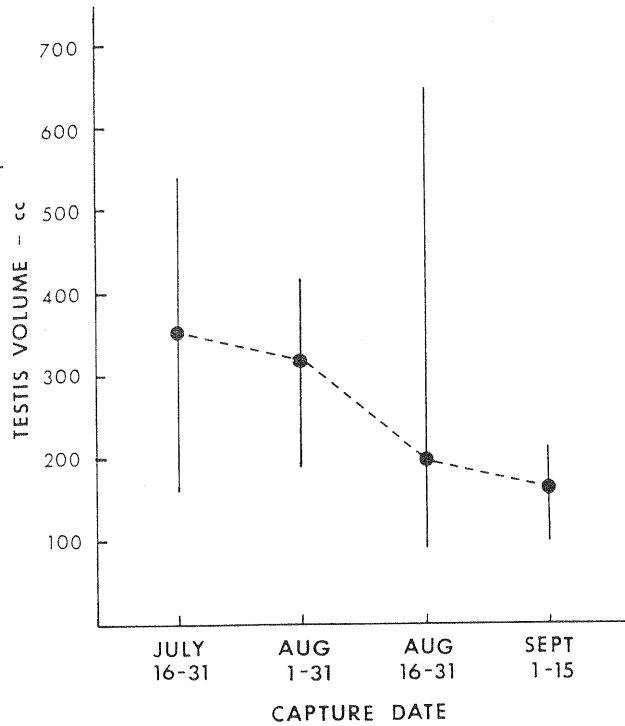
Fig. 6. The single testis volumes (calculated as ellipsoids) for 32 mature harbour porpoises collected in eastern North American waters. The closed circles represent the mean volume for each 2 week period and the ranges are defined by the vertical lines.
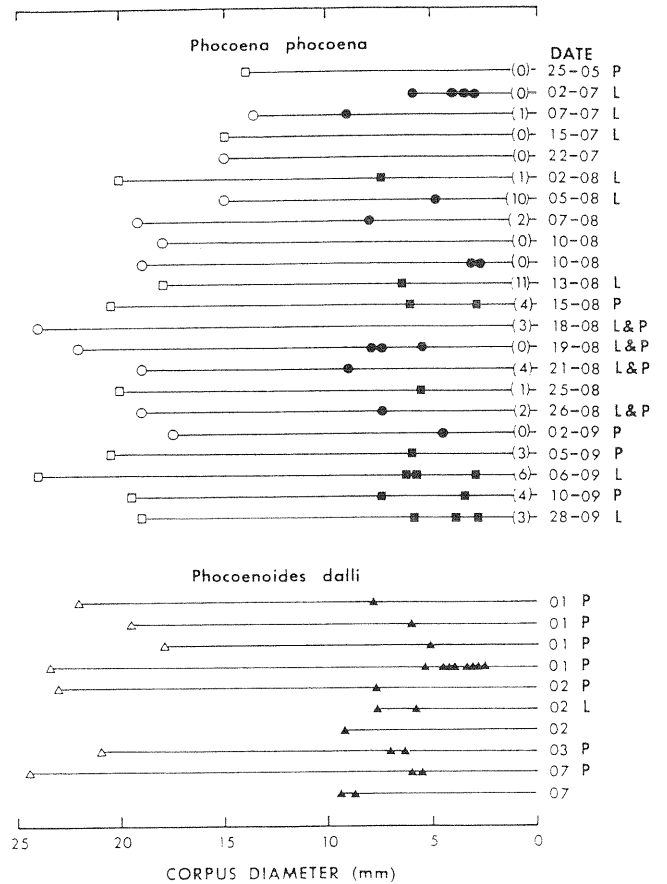


Fig. 7. Relationship between size of corpora lutea (open symbols) and corpora albicantia of Type I (i.e. containing much acellular material) of Fisher and Harrison (1970) (closed symbols) and time of year, fo *P. phocoena* (above), and *P. dalli* (below). Circles are data of th present authors, squares represent data drawn from Fisher and Harrison (1970), and triangles from Kasuya (1978). The numbers of Type II corpora albicantia noted in parentheses. P = pregnant; L = lactating; blanks = resting or not examined; date = day-month (*P. phocoena*), month (*P. dalli*).

*Changes in the ovary*

In this section, we have restricted ourselves to terminology used by Harrison, Boice and Brownell (1969) and Perry (1971) to describe ovarian features; we adopt the terms Type I and Type II for two kinds of corpora albicantia described in delphinids by Harrison *et al.* (*loc. cit.*) and Fisher and Harrison (1970).

*Follicular development and ovulation.* Kasuya (1978) presented little information on follicles in *P. dalli*, nor has follicular growth been well-studied in *P. phocoena*, in both cases primarily because of the lack of material from all months of the year. Ovarian activity is almost exclusively sinistral, although Fisher and Harrison (1970) reported one specimen with a corpus albicans in the right ovary. In our series of summer-caught specimens of *P. phocoena*, we found both primary and secondary follicles ranging in size from one to six mm. The largest follicle was found in the ovary of a female taken in early July. Fisher and Harrison (*loc. cit.*) reported follicles from 1.0–4.5 mm in diameter in specimens from the same area; Graafian follicles were not found in either species. The timing of ovulation is not really understood in phocoenids, nor has the question of possible/probable multiple ovulations been satisfactorily resolved. Fisher and Harrison found up to 9 corpora albicantia in several of their smaller females and speculated that ovarian activity had become established out of phase with, or in the absence of, males. In our material, we counted up to 15 corpora albicantia in females 4 and 5 years of age, suggesting that multiple ovulations without fertilization occur regularly in younger females of *P. phocoena* before they are fully incorporated into the breeding population.

Kasuya *et al.* (1974) established that a polyoestrus cycle of one month occurred in *Stenella attenuata*, and that the largest follicles were found in resting or lactating females.

*Corpora lutea.* We have no confidence that corpora lutea of pregnancy and corpora lutea of ovulation can be satisfactorily distinguished in phocoenids. Kasuya, Miyazaki and Dawbin (1974) tentatively suggested that in *Stenella attenuata* those less than about 15–16 mm in diameter might be from ovulation, while those about 19 mm in diameter might be corpora lutea of pregnancy (see end of this section with respect to *P. phocoena*). They did not point out, however, that five of the females in the former sample were lactating. In *P. dalli*, Kasuya (1978) noted that the diameters of 20 corpora lutea of pregnancy ranged from 17.2–24.6 mm with a mean of 21 mm, with no accessory corpora lutea being observed. We have compared the size range of corpora lutea (and corpora albicantia) in *P. dalli* and *P. phocoena* against time of year in Fig. 7.

Since material of *P. phocoena* was collected by Fishe and Harrison and ourselves during the summer month. in the Bay of Fundy, one would expect to find corpora of both ovulation and pregnancy. In our series of mature

animals, three females with corpora lutea were pregnant, three were lactating, and five were in neither condition. The corpora lutea in the latter must surely be the result of unfertilized ovulation. We are in agreement with Fisher and Harrison (1970) that the corpus luteum in lactating females always shows some signs of regression (see those authors for a histological description). An ANOVA test of this Bay of Fundy material revealed no statistically significant differences between the mean diameters of the corpora lutea of pregnant, lactating, simultaneously pregnant and lactating, and resting female harbour porpoises.

*Corpora albicantia.* As pointed out by Harrison *et al.* (1969) and Fisher and Harrison (1970), two kinds of corpora albicantia can be differentiated histologically in delphinids and phocoenids. The first (which we designate Type I) is typically 5–10 mm in diameter and consists of a firm mass of connective tissue with sparsely distributed cellular elements and large obliterated blood vessels around the periphery. Narrow radiating septa of fibrous connective tissue are present. The second (Type II) is smaller, only 3–5 mm in diameter, contains numerous closely-packed obliterated and degenerate arteries, and characteristically lacks the acellular material found in quantity in Type I.

Fisher and Harrison (*loc. cit.*) suggested that Type I bodies were derived from corpora lutea of pregnancy, while Type II bodies might result from corpora lutea of ovulation, or even represent the remains of large lutealized follicles (corpora atretica). They speculated that the largest Type I corpora found in animals taken in August were associated with pregnancies that had come to term about 13 months previously. In this respect their argument for the above associations of the two types was logically developed, especially considering the larger size of Type I bodies. Unfortunately, we found in our series of *P. phocoena* two females that provide some contradictory evidence which must be considered. The first was the youngest pregnant animal recorded by us, 133 cm in length, with only two dentinal growth layers. This animal not only had a corpus luteum in the left ovary, but also a single Type I corpus albicans and six Type II albicantia. Three alternative explanations can be considered: (i) this specimen was more than two years of age, or (ii) was reproductively abnormal and had had a previous pregnancy in its first year of life, or (iii) Type I corpora are not invariably associated with pregnancy. Several members of our group aged this animal independently and arrived at the same conclusion about its age; the layers are distinct and in no way unusual, and the body length is normal for that age class. Nor was there any indication of obvious abnormality other than the relatively small size of the animal at maturity. Option iii, therefore, provides the most parsimonious explanation. Further support for this hypothesis was provided by another animal in our series, a 153.5-cm four-year-old pregnant female with a corpus luteum and no less than three Type I corpora albicantia. We can only conclude that neither type of corpus albicans can be specifically related to pregnancy or ovulation in *P. phocoena*.

The regression and ultimate fate of corpora albicantia in general is not well understood in phocoenids. We attempted to plot the regression of numbers of corpora
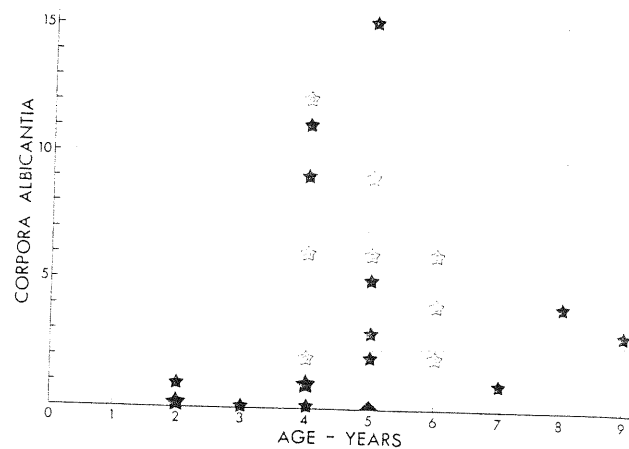


Fig. 8. Relationship between number of corpora albicantia of both types and age in years (based on dentinal growth layer groups – GLGs) in *P. phocoena* from the Bay of Fundy. Closed stars are data of the present authors; open stars are data from Fisher and Harrison (1970) with number of GLGs estimated from the relationship:

$$d = \left[ \frac{b}{(-0.84b + 156.15)} \right] - 1$$

where *d* is the number of GLGs and *b* is body length in cm (Gaskin and Blair, 1977). The large closed stars represent two specimens and the triangle includes four specimens examined by the present authors and one by Fisher and Harrison.

albicantia on age in Bay of Fundy female *P. phocoena* (Fig. 8); no relationship was found – the same negative result obtained by Gaskin and Blair (1977) with a smaller sample. A similar plot for *P. dalli* was also considered to be inconclusive (Kasuya, 1978, Fig. 23). Fisher and Harrison (1970) offered no explanation for the fate of Type I bodies, but suggested that they might eventually become totally indistinguishable. We agree with this postulation; in our series of animals the greatest numbers of both types of corpora were found in four- and five-year-old females. In two females estimated to be eight and nine years old, four Type I albicantia only (with no corpus luteum) were present in the former (pregnant) specimen, but only three Type II in the latter animal, which was simultaneously lactating and pregnant. Although the evidence is by no means conclusive, both types appear to be resorbed.

Some guide as to what occurs during the ovarian cycle in these animals might be obtained from the studies on *Stenella attenuata* by Kasuya *et al.* (1974) and *S. coeruleoalba* by Miyazaki (1977), with the caution that the former is a largely tropical species and the latter subtropical, in contrast to the boreal-temperate distributions of *P. phocoena* and *P. dalli*. Kasuya *et al.* recorded corpora albicantia as small as 1 mm, and speculated that they might persist throughout life in *S. attenuata*. Their size appeared to decrease significantly after parturition, reaching a 'mean final diameter' perhaps some 70 months after that event. Miyazaki (1977) produced a clear and interesting figure (1977, Fig. 11) based on examination of 206 pregnant females of *S. coeruleoalba*. He demonstrated a steady reduction in the size of the corpus luteum prior to parturition, from about 27 mm some five months before parturition to about 23.5 mm immediately prior to the event. He was also able to plot a curve to show actual decrease in size of the mean modal sizes of the largest

corpora albicantia from about 12 mm after parturition to barely 5 mm 27–28 months after parturition. Neither Miyazaki nor Kasuya *et al.* concerned themselves with histological differences among corpora albicantia, other than the latter (p. 202) indicating that they did not include in their counts 'corpora atretica' considered to result from atretic lutealized follicles as described in ovaries of *Tursiops truncatus* by Harrison and Ridgway (1971). The latter authors reported that *all* corpora lutea in *T. truncatus* related to pregnancy events, and not to infertile ovulations. They considered that ovulation was induced, not cyclic.

*Post-partum and post-lactum oestrus.* Post-partum oestrus is characterized (Perry, 1971) by regression of the corpus luteum of pregnancy immediately before parturition, and the maturation of one or more follicles, which 'ripen' and rupture within 24 h of parturition. Kasuya (1978) was able to present little information on this aspect of reproduction in *P. dalli.* Fisher and Harrison (1970) found no females in their sample of *P. phocoena* from the Bay of Fundy that were simultaneously pregnant and lactating; they concluded that harbour porpoises did not necessarily become pregnant every year, even though Møhl-Hansen (1954) had presented some evidence for post-partum pregnancy in the Baltic population of that species. In a sample of 36 Bay of Fundy mature females, we found 3 were pregnant, 5 were simultaneously pregnant and lactating, and 7 were lactating. These catch data suggest that the percentage of animals experiencing post-partum pregnancy is 14% of all mature females, and 62.5% of all pregnant females. It is also worth noting that three recognisable marked females studied by Watson (1976) in the Fish Harbour region of New Brunswick not only returned several years in succession (3 years, 2 years and 2 years), but in each year had newborn calves with them. At the beginning of at least four of these seasons they were also accompanied for a time by a larger juvenile assumed to be the offspring from the previous season. We are therefore left to wonder if Fisher and Harrison (1970) missed some very small embryos in some of their lactating specimens (easy to do, since the earliest embryos are almost impossible to find by routine gross inspection, and we suspect we missed some in our own series during field examination). The size of corpora lutea quoted by them in one or two animals might support this suspicion (Fig. 7).

## GENERAL DISCUSSION AND CONSIDERATIONS

While it may be useful to draw parallels between phocoenids and other small cetaceans, especially delphinid species for which much more reproductive material has been examined, this should be tempered by the realization that phocoenids may perhaps be quite different mammals in many respects.

Although it is dangerous to assume that taxonomic affinity necessarily implies similarity in life cycles, the body size, life zone and behaviour of *P. dalli* are such that we would nevertheless formulate any first hypothesis on the basis that its life cycle parameters probably would be more similar to those of *P. phocoena* than to those of tropical *Stenella* species.

As in other cetaceans, the problem of accurate age determination, so critically important for population analysis, remains vexing. Most workers seem to be agreed that one growth layer is laid down in a single year in those phocoenids so far examined, but evidence relating to their average life span – and hence lifetime calf production by females – is far from satisfactory. We have, for example, produced data here and elsewhere to support our contention that *P. phocoena* is relatively short-lived for its body size, and this seems to be borne out by the recent paper by van Utrecht (1978) on the North Sea population. A short life span, with no more than about three or four calves produced on average by each mature female, is certainly not out of the question, especially if this species, as a small cold-water cetacean, has an elevated metabolic rate (Kanwisher and Sundnes, 1965). Such a reproductive pattern renders the species highly vulnerable to excessive additional mortality through exploitation.

Kasuya (1978) went to great length to estimate possible fishing bias in the harpoon fishery for *P. dalli* in the western North Pacific. That some level of bias exists in the fishery is not disputed, nor is the possibility of segregation of some social categories (such as lactating females) to other areas, thus preventing their full representation in the catch. What does worry us is that while Kasuya develops a sophisticated argument to support the hypothesis that this animal can live to much greater ages than indicated by dentinal or cemental layers, the basic fact of the matter remains that no animal in his samples could be *confirmed* as being more than 16–18 years of age. He considered a whole series of hypotheses, and adopted a compact mathematical method (1978, p. 51) to estimate mortality fractions in the population, and another series of hypotheses to examine catch bias and measure its impact (p. 45). We believe that one should also examine such situations from the most conservative viewpoint. This would involve re-examining four possibilities: (i) That mortality rates in this phocoenid population remain rather steep, and that the life span of the average *P. dalli* is in fact not much greater than the values suggested by tooth sections and, furthermore, that many assumptions related to the age composition of *Stenella attenuata* are valid only if Kasuya's (1976b) re-evaluation of the life span of that species is valid. (ii) That scarcity of individuals over seven years of age results not just from catch selection or inability to age the material accurately, but simply because there are not that many animals beyond age seven in the population. (For example, he did not find older animals in any quantity in the salmon gill net fishery either, yet we have taken some of our oldest specimens of *P. phocoena* from nets.) (iii) That the possibility of a male sexual cycle in phocoenids, coupled with the limited season of capture, may have led to misinterpretation of the real percentage of mature males from age 4 onwards, since 'maturing' testis is so difficult to assess in these animals. The mean age at maturity could then be significantly lower than he suggested. (iv) Contagious distribution of animals on the hunting grounds (which would include areas where nets were being set for fish, because the porpoises would also be concentrating for prey) could disguise a significant decline in population size until it was far advanced. While Kasuya may well have provided a reasonably accurate,

Table 5

Estimation of gross annual reproductive rate (GARR) of *P. phocoena* from three life history studies

| | Baltic (Møhl-Hansen, 1954) | Bay of Fundy | |
| --- | --- | --- | --- |
| | | (Fisher and Harrison, 1970) | (This study) |
| Proportion female | 0.38[c] | 0.50 | 0.50 |
| Proportion of females reproductive | 0.47 | 0.42 | 0.52 |
| Proportion of reproductive females pregnant | 0.84 | 0.45 | 0.22[d] |
| Duration of pregnancy (years) | 0.92 | 0.92 | 0.92 |
| Annual pregnancy rate[a] | 0.91 | 0.49 | 0.24 |
| GARR[b] | 0.16 | 0.10 | 0.06 |

[a] Annual pregnancy rate calculated by dividing the proportion pregnant by the duration of pregnancy (0.92 yr).
[b] GARR = (proportion female) × (proportion reproductive) × (annual pregnancy rate); method of Perrin *et al.* (1977).
[c] Preponderance of males attributed to catch bias; if equal numbers of each sex is true for this population, GARR would be 0.21.
[d] See text for explanation of low proportion pregnant.

optimistic picture of the status of the western North Pacific population of *P. dalli*, it seems to us that his conclusions rest on a series of rather fragile assumptions.

The argument put forward by Morejohn (1979) to support the possibility of *P. dalli* having diffuse mating and calving seasons (at least in the coastal waters of the western United States) merits attention, since it is completely at variance with the findings of the Japanese workers. He noted that large testes could be present in both winter and summer, but the case for continuous activity is weakened by the statement that the largest testes observed were rather flaccid and in a non-reproductive state. We can see no reason to assume, as he did, that 114.9-cm and 118-cm juveniles taken in July and February respectively were necessarily born months apart; although Mizue *et al.* (1965) noted growth rates of about 5 cm/month, these are only averages, with wide variance. The stronger points of his case are certainly (i) a record of a stranded animal with a near-term foetus in November (although one could ask how near term was it, cf. Bruch's (1916) record for a 48.4-cm foetus in *P. dioptrica* as 'near-term'), and (ii) an 87.6-cm foetus found in April. There is suspicion, therefore, that Dall's porpoise on this coast are not necessarily breeding in synchrony with their western Pacific counterparts.

The possibility that a male sexual cycle exists in phocoenids is interesting and would seem to be at odds with the situation in larger odontocetes. Best (1969) and Gambell (1968; 1972) considered that there was little real evidence for a seasonal change in the male testis of the sperm whale. Best noted that 'There is no enlargement of the testes of mature males during the female breeding season, no increase in the diameter of the seminiferous tubules, and no increase in the incidence or number of spermatozoa per tubule. These facts fail to demonstrate the presence of a seasonal cycle of spermatogenic activity, but the enlargement of Leydig cells during the female breeding season could be indicative of an increase in testis androgen production, which might produce significant changes in the social and sexual behaviour of mature males at this time of year.'

Why then might such a cycle exist in *P. phocoena* (and the evidence is not totally conclusive) but not in other species? The answer may be related to the large proportional size of the active testes in phocoenids *P. phocoena*, according to the data of Fisher and Ha son (1970) and the present authors, peak paired te weights of adults can range up to 3.5% of total b weight. In the sperm whale, assuming an animal of ah 30,000 kg and combined testes weights of about 3 kg equivalent percentage is only about 0.01%. The differ is very great, and since the harbour porpoise is relati small, it seems to make sense in energetic terms selection to have occurred leading to minimization of surplus tissue during the non-productive part of the yc

Like Kasuya (1978) working with *P. dalli*, we w unable to derive any workable estimates of ovulai rates or true pregnancy rates for *P. phocoena* from limited samples. It is, therefore, nearly impossible at time to arrive at accurate estimates for birth rates e in the Bay of Fundy population. Based on sighting d for the period 1970–78 collected in the western Bay Fundy, the average proportion of calves in population is 10.3%. This value is supported by proportion of animals of year class 0 in the sam collected for age determination by Gaskin and Bl (1977), which comes to almost exactly 10%. It is possi that fluctuations can be detected in the extensive sight data, but these data are still under investigation Yurick.

For a randomly collected sample ($n = 95$) and subsample of 36 mature females (see Section 3.6.4), estimated the gross annual reproductive rate (GARR) this population using the method of Perrin *et al.* (197 and compared it to GARR values calculated A. J. Read (personal communication) from the data Møhl-Hansen (1954) for the Baltic population and for Bay of Fundy population in the 1950s (Fisher a Harrison (1970)) (Table 5). The GARR of 0.06 for t recent Bay of Fundy population is lower than that in t 1950s and much lower than that calculated for the Ball population. It is also less than estimates for *Stenella* sp (0.08–0.14), *Delphinis delphis* (0.14), *Globicephala melaen* (0.10–0.13) and *Delphinapterus leucas* (0.12) calculated Perrin *et al.* (op. cit.). We suspect (as noted in sectio 3.6.4) that we underestimated the proportion of adul females that were pregnant by failing to find a few ver tiny embryos during routine autopsies in the field. Unlil

Møhl-Hansen's specimens which were collected from November to February when he found foetuses 14 cm to 45 cm long, the females we examined were mostly captured in the period June to September; embryos discovered ranged from 0.8 cm to 1.0 cm in length. It is quite possible that additional embryos of microscopic size were overlooked. If in the sample of 36 females we had found five more that were pregnant, the GARR would be 0.10, perhaps a more realistic value in light of the observed proportion of calves (10.0–10.3%). Alternatively, a decline in reproductive rate may have taken place in the Bay of Fundy population of *P. phocoena* between 1950–55 and 1970–80.

It is difficult to provide any discussion of approaches to management of phocoenids at this stage, given the impoverished state of our knowledge about life-cycle parameters of even the commercially exploited species. Initiation of scientific collecting in all months of the year in specific areas is easy to recommend, but would not necessarily produce the desired results. For example, because of the nature of its migration and behaviour, *P. phocoena* is only readily available for systematic biological sampling in the western North Atlantic during the summer, from May to September.

In the case of this species, however, we do believe that we are dealing with a short-lived animal that may already be maximizing its productivity, and the reproductive flexibility of *P. phocoena* is, therefore, likely to be limited, especially if more than half of the breeding females already appear to be producing calves in successive seasons.

The obvious recommendations that must be made, however, are for strict control or reduction of the directed catches of phocoenids until we have better knowledge of population sizes and production, and for all efforts to be made to reduce the magnitude of incidental catches in all kinds of fishing gear to which the porpoises are vulnerable.

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# Review of Reproduction in Platanistid Dolphins

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## ABSTRACT

Length at birth is about 75–80 cm in *Pontoporia*, about 80 cm or greater in *Inia* and *Platanista*, and 95 cm or greater in *Lipotes*. Gestation is 10.5 months and the lactation period is eight to nine months in *Pontoporia*; both are unknown in the other genera. The calving interval is two years in *Pontoporia* and assumed to be the same or greater in the other genera. Some *Inia* and *Pontoporia* females are known to be lactating and pregnant at the same time. Males and females of *Pontoporia* attain sexual maturity on the average at lengths of about 131 and 140 cm, respectively. The smallest known sexually mature females of *Pontoporia*, *Inia*, *Platanista* and *Lipotes* are 137, 183, 200 and 202 cm long, respectively. The smallest known sexually mature males of *Pontoporia*, *Platanista*, *Lipotes* and *Inia* are 121, 199, 206 and 209 cm, respectively. The age at the attainment of sexual maturity is two to three years for both sexes in *Pontoporia*. It is unknown in the other genera but is probably two to three times greater than in *Pontoporia*. The total number of corpora albicantia accumulated in the ovaries in all five species is small. The corpora albicantia appear to persist in all the platanistids, as in other cetaceans, and are found in both ovaries.

   Females are clearly larger than males in *Pontoporia*, *Platanista* and *Lipotes*, but the reverse is the case in *Inia*. Available data indicate that the life span of *Pontoporia* may be only 15 to 20 years. This may explain why *Pontoporia* has a lower corpora count than *Platanista* and *Lipotes*. Few data are available for the other genera but one male specimen of *Inia* has lived in captivity for over 18 years. One male specimen of *Platanista* and one female specimen of *Inia* had 28 dentinal growth-layer groups.

## INTRODUCTION

Little was known about reproduction in the platanistid dolphins until the early 1970s. Recent data on the ovaries, testes, and reproduction in the franciscana (*Pontoporia blainvillei*) were reported by Harrison, Brownell and Boice (1972); Brownell (1975); Kasuya and Brownell (1979); and Harrison, Bryden, McBrearty and Brownell (1981). Data on the gonads of the boutu (*Inia geoffrensis*) were published by Harrison and Brownell (1971). Harrison (1972), Kasuya (1972) and Harrison *et al.* (1972) reported on new reproductive materials and summarized what is known about the Ganges and Indus susus, *Platanista gangetica* and *P. minor*. Brownell and Herald (1972) reviewed knowledge on the beiji (*Lipotes vexillifer*). Other more recent information on reproduction in *Lipotes* can be found in Chen and Chen (1975); Zhou, Qian and Li (1977); and Chen, Liu and Lin (1982). In addition, reproduction in *Lipotes* is reviewed by Chen, Liu and Lin (1984), and in *Inia* by Best and da Silva (1984).

## MATERIALS AND METHODS

Between 1964 and 1970, specimens of *I. geoffrensis* were obtained from rivers near Iquitos, Peru; Leticia, Columbia; Manaus, Brazil; and from San Fernando de Apure, Venezuela. Specimens of *P. blainvillei* were collected offshore between Punta del Diablo and Playa La Coronilla, Uruguay between 1969 and 1973. Three specimens of the Indus susu, *P. minor*, were collected in November 1968 near Sukkur, Pakistan. Specimens of *I. geoffrensis* and *P. minor* were caught for display at various aquariums in the United States. Some of the boutus died on capture or during transport; others survived in captivity for periods of only a few days to over 18 years (as of November 1983). The three susus only lived 24 to 44 days. All the franciscanas were taken dead in shark gillnets (Table 1). Additional data for all

Table 1

Samples of postnatal specimens of *Pontoporia blainvillei* by month between 1969 and 1973

| Month | Females | Males | Total |
|---|---|---|---|
| January | 63 | 87 | 150 |
| February | 20 | 10 | 30 |
| March | 15 | 15 | 30 |
| April | 0 | 0 | 0 |
| May | 1 | 4 | 5 |
| June | 5 | 10 | 15 |
| July | 25 | 22 | 47 |
| August | 17 | 16 | 33 |
| September | 15 | 11 | 26 |
| October | 15 | 6 | 21 |
| November | 6 | 2 | 8 |
| December | 45 | 37 | 82 |
| Total | 227 | 220 | 447 |

three genera and *Lipotes* were taken from the literature.

The total length (straight line from the tip of the rostrum to the notch between the flukes) of each dolphin was measured. Reproductive tracts were examined and foetal sizes recorded. Mammary glands were visually examined for evidence of lactation. The gonads were removed from the carcasses and fixed in 10% formalin. They were subsequently photographed, weighed and sectioned by hand to count corpora lutea and corpora albicantia. The presence of one or more corpora in one or both ovaries was used as the criterion of female sexual maturity and probable ovulation.

Slices of selected ovaries and testes were embedded in paraffin, sectioned and stained with haematoxylin and eosin (H and E). The determination of sexual maturity in male franciscanas was based on the examination of all the available seminiferous tubules in a slide, usually a cross section of the entire testis. An individual was classified as mature if all the tubules contained spermatids