

# Report of the Workshop

Edited by  
W. F. PERRIN AND G. P. DONOVAN



*Sperm Whales*

## CONTENTS

I	INTRODUCTION	2
II	QUESTIONS OF MORPHOLOGY AND PHYSIOLOGY	3
	(A) Interpreting ovarian scars.	3
	(1) <i>Do corpora albicantia persist indefinitely?</i>	3
	(2) <i>Are corpora albicantia of simple ovulation distinguishable from those of pregnancy?</i>	3
	(B) Variation in ovulation rate.	3
	(1) <i>Variation among species.</i>	3
	(2) <i>Variation within species.</i>	4
	(3) <i>Accessory corpora lutea.</i>	4
	(C) Biases in estimating the reproductive interval.	4
	(D) Definition of 'sexual maturity'.	5
	(E) Male seasonality.	5
	(F) Pathology and anomalies.	5
	(1) <i>Reproductive senescence.</i>	5
	(2) <i>Cystic follicles and ovarian cysts.</i>	6
	(3) <i>Parasites.</i>	6
	(4) <i>Abortion.</i>	6
	(5) <i>Multiplets.</i>	6
	(6) <i>Vaginal calculi.</i>	7
	(7) <i>Other pathology.</i>	7
III	MODELLING REPRODUCTION	7
	(A) Terminology and assumptions.	7
	(1) <i>Density dependence.</i>	8
	(2) <i>Pregnancy rate.</i>	8
	(3) <i>Age at first parturition.</i>	8
	(4) <i>Specifying intervals.</i>	8
	(5) <i>Specifying assumptions underlying terminology.</i>	8
	(B) Current models.	8
	(1) <i>The sperm whale model.</i>	8
	(2) <i>The ETP dolphin model.</i>	9
	(3) <i>The North Pacific baleen whale model.</i>	9
	(C) Density dependence.	10
	(1) <i>Pregnancy rate or calving interval.</i>	10
	(2) <i>Age at attainment of sexual maturity in females.</i>	10
	(3) <i>Percentage simultaneously lactating and pregnant.</i>	11
	(4) <i>Mean age in the population.</i>	11
	(5) <i>Population growth in depleted populations.</i>	11
	(6) <i>Additional comments.</i>	11
	(a) <i>The problem of 'noise'.</i>	11
	(b) <i>The dangers of extrapolation.</i>	11
IV	DATA AND SPECIMEN NEEDS FOR STOCK ASSESSMENT AND MANAGEMENT	11
	(A) Information needs.	11
	(1) <i>General comments.</i>	11
	(2) <i>Some specific needs.</i>	12
	(a) <i>Age composition of the catch.</i>	12
	(b) <i>Sex composition of the catch.</i>	12
	(c) <i>Calf counts.</i>	12
	(B) Data sources and sampling problems.	12
	(1) <i>Samples from commercial catches.</i>	12
	(a) <i>Large whales.</i>	13
	(b) <i>Directed small cetacean fisheries.</i>	13
	(i) <i>Japan.</i>	13
	(ii) <i>Canada.</i>	13
	(iii) <i>Greenland.</i>	13
	(c) <i>Incidental takes.</i>	13
	(i) <i>ETP tuna fishery.</i>	13
	(ii) <i>Other incidental catches.</i>	13
	(2) <i>Direct counts from surveys.</i>	13
	(3) <i>Strandings.</i>	14
	(4) <i>Individual-animal studies.</i>	14
V	LITERATURE CITED	15
	(A) <i>Papers/Abstracts published in this volume</i>	15
	(B) <i>Others</i>	15
VI	APPENDICES	18
	(A) <i>Agenda.</i>	18
	(B) <i>Terminology of female reproductive morphology and physiology.</i>	18
	(C) <i>Specimen collection, preservation, storage and preparation.</i>	22

## I. INTRODUCTION

The main charges to the workshop were to examine the interpretation of ovarian corpora, to review the reproductive components of quantitative models currently used in assessment and management, and to explore how research in the field and laboratory on the one hand and quantitative modelling on the other, can be better integrated. The agenda (Appendix A) was structured to alternate group discussions and laboratory sessions. Discussion leaders and rapporteurs prepared draft reports that formed the basis for this report. The organization

and content of the report do not correspond entirely to the workshop agenda, but rather reflect the course of the discussions. Participants in the workshop are indicated in the list of conference participants at the beginning of this volume.

The following participants acted as discussion leaders and/or rapporteurs during the workshop sessions: Barlow, Benirschke, Braham, Brownell, DeMaster, Donovan, Goodman, Hester, Kirkwood, Lockyer, Marsh, Mead, Mizroch, Odell, Perrin, Reilly and Wells. Marsh and Benirschke prepared the meeting draft and subsequent revisions of Appendix B.

## II. QUESTIONS OF MORPHOLOGY AND PHYSIOLOGY

### (A) Interpreting ovarian scars

Implicit in the use of ovulation rate as a vital parameter in modelling reproduction of cetaceans (see Section B) is the assumption that corpora albicantia (CA) persist through life and thus reflect the actual number of ovulation events. Some workers have also assumed that corpora of simple ovulation can be distinguished from those of pregnancy, yielding an accurate history of calf-bearing.

#### (1) *Do corpora albicantia persist indefinitely?*

The consensus opinion is that CAs do persist indefinitely in the ovaries of at least some cetaceans, e.g. sei whales and fin whales (Gambell, 1968; Laws, 1961). It is likely, however, that not every ovulation results in a corpus luteum (CL). This can be investigated only by steroid monitoring coupled with ovarian histology. The implication of this possibility is that we cannot necessarily assume that ovulation rate is measurable by counting corpora.

For the short-finned pilot whale, *Globicephala macrorhynchus*, no major gaps in the size distribution of CAs indicative of CA disappearance were noted and they are thought to persist indefinitely (Marsh and Kasuya, this volume). The smallest were about 3 mm in diameter. Ohsumi reported that the same is true for the sperm whale, *Physeter macrocephalus*, although final size is greater (about 8 mm in diameter, Gambell, 1972). CAs may also persist indefinitely in *Stenella* spp. (Perrin and Reilly, this volume); however, it was noted that some apparently 'old' females have shrunken ovaries with relatively few CAs. Two explanations were suggested: as a result of ovarian shrinkage many CAs were still present but no longer detectable by gross observation; or some types of CAs may disappear while others persist. The group recommends that the shrunken ovaries be re-examined, using histological techniques, to determine if very small CAs have been missed.

Regarding rate of CA regression, data from *Globicephala* spp., *Stenella* spp., *Delphinus delphis* and other species indicate that CLs regress very quickly initially (first few days or weeks), then slowly thereafter. Regression in the sei whale is rapid immediately after calving, from about 84 mm to about 36 mm in diameter in the first month, then slowing during the balance of the lactation period. Minimal size is reached after perhaps years or decades (Gambell, 1968).

A distinction has been made in some studies between corpora atretica and CAs. In *G. macrorhynchus*, for example, the size distribution of corpora atretica is very different to that of CAs. Corpora atretica shrink to a smaller size (< 1 mm) and may ultimately disappear (Marsh and Kasuya, this volume). Kasuya, Miyazaki and Dawbin (1974) were able to distinguish these two types of corpora for *Stenella* spp. in the western Pacific, but this is not true for the eastern Pacific populations of the same species (Perrin, Coe and Zweifel, 1976). Consequently, corpora counts and size distributions for these two areas for similar species may not be strictly comparable.

Marsh noted much variation in the number of corpora atretica in mature *G. macrorhynchus*, ranging from 0 to

34 per pair of ovaries (usually less than ten). Some of the whales with very high numbers of corpora atretica were found to have low CA counts for their age, but not all with high corpus atreticum counts had low CA counts.

#### (2) *Are corpora albicantia of simple ovulation distinguishable from those of pregnancy?*

The group concluded that a difference cannot be discerned with currently used methods. Marsh, Ohsumi and Benirschke reported no discernable difference for odontocetes, either macroscopically or histologically. It has been reported by Laws (1961) that no difference exists for fin whales. However, Zimushko (1970) reported that he could distinguish the two types of CAs in gray whales. Other Soviet researchers report similar findings (Ivashin, this volume). Ivashin mentioned his (1958) study in which this was also done for humpback whales, based on the size of the CA, under the assumption that a CL of pregnancy regresses more slowly than a CL of ovulation only. He also reported finding morphological differences between CLs of pregnancy and of ovulation. It was pointed out, however, that lactation can affect the rate of regression, and it was agreed that size of the CA alone, (even when adjusted for age) cannot be considered an indicator of the original nature of the event giving rise to it. Marsh noted that in *G. macrorhynchus* large CAs do not appear to regress further during pregnancy and suggested that in this species the rate of regression of a CA may be affected by hormonal status. In contrast, Larsen reported that he found significant regression of corpora during pregnancy in minke whales.

The group discussed possible new techniques to distinguish between CLs of pregnancy and ovulation. Erickson noted that the compound relaxin appears in a CL of pregnancy but not in a CL of ovulation, and it is only necessary to freeze specimens very soon after death to test tissues for presence of this substance. The substance disappears rapidly during regression of the CL. However, it is necessary to fix ovaries properly and immediately following death in order to examine structure at this level, and this may be impractical under field conditions. Miyazaki suggested that since organochlorines (PCBs and DDT) are flushed from a female during lactation (Tanabe, Tanaka and Tatsukawa, 1981), perhaps differential presence of these residues may be used to distinguish between CLs of the two types; work on this is in progress in Japan. Ohsumi noted that it should be possible to determine whether a female with one CA has been pregnant by histological examination of the mammary glands. This may offer a method of identifying reference CAs of the two types so that they can be compared histologically.

### (B) Variation in ovulation rate

#### (1) *Variation among species*

It is clear that there is great variability among species. Evidence for varying ovulation rates exists in the literature for both mysticetes and odontocetes. For example, in Southern Hemisphere fin whales, the ovulation rate is one corpus per 1.4 years (Lockyer, 1972; Gambell, 1973) whereas in minke whales the rate is approximately one corpus per year (Masaki, 1979). For the sperm whale, Gambell (1973) has calculated a mean

ovulation rate of 1 corpus per 2.33 years. For the gray whale, a rate of one ovulation per 1.93 years has been calculated (Reilly, this volume).<sup>1</sup>

### (2) Variation within species<sup>2</sup>

Mizroch (1981) has found evidence of age-specific ovulation in southern fin whales, the rate decreasing in old animals. Evidence by Best (1967; 1980) and Gambell (1972) for sperm whales and Marsh and Kasuya (this volume) for pilot whales suggests a fall-off in rate with older age. Sergeant (1962) reported that in *G. melaena* there is evidence of multiple ovulations per pregnancy in young females. Similar findings have been reported for *Lagenorhynchus obliquidens* (Harrison, Brownell and Boice, 1972).

There are indications that frequency of ovulation as recorded in CAs (disregarding the question as to whether every ovulation results in a CA) decreases in older individuals in some populations, while *per-capita* pregnancy rate does not. This was reported by Mizroch for Southern Hemisphere fin whales (although other factors, such as the difficulty of accurate age determination, may be involved) and by Kasuya for western Pacific striped dolphins, *Stenella coeruleoalba*. The implication is that decline in frequency of CAs with age does not necessarily indicate a decline in pregnancy rate.

Gambell (1968; 1972) has used regression rates of corpus size to estimate age-independent ovulation rates from sei and sperm whales in catches. Lockyer, Gambell and Brown (1977) also used this technique to determine ovulation rates for fin whales taken in the Icelandic catch. However, Collet and Harrison (1981) found that in *Delphinus delphis* the rate of regression of a corpus is not constant but seems to follow a complex pattern. Perrin reported data from *Stenella longirostris* in the eastern Pacific for two stocks, one heavily exploited and the other lightly exploited (Perrin and Henderson, this volume). His data on size frequency of CAs indicate that young females in the more-exploited stock have a lower number of ovulations per unit of age.

Recent studies of reproductive physiology have determined that captive dolphins may have highly variable ovulation rates. Kirby and Ridgway (this volume) reported multiple ovulations per year for *Tursiops* and *Delphinus*, and Wells (this volume) reported similar findings for *Stenella*. Kirby also found that a female that is anoestrous one year may cycle the next. Based on ovarian morphology, Collet and Harrison (1981) observed multiple successive ovulations in *D. delphis* and possible variation in ovulation rate related to age and social hierarchy.

Benirschke noted that similar variation in ovulation rates occurs in other mammals. Some human females

<sup>1</sup> Editors' note. Other published ovulation rates (years per corpus) include: Bryde's whales - Best (1977), 0.4 (S. African inshore), 2.4 (offshore); sei whales - Lockyer and Martin (1983) 1.7 (N. Atlantic), Gambell (1968) 1.4 (S. Hemisphere); fin whales - Lockyer and Brown (1979) 1.6 (N. Atlantic); minke whales - Kato (1982) 1.1-1.2 (S. Hemisphere); humpback whales - Chittleborough (1965) 0.9 (S. Hemisphere); sperm whales - Best (1974) 1.7-3.0 (review of various estimates).

<sup>2</sup> Editors' note. Best (1977) reported an interesting variation in ovulation rates for Bryde's whales found in Southern African waters: the average number of ovulations per reproductive cycle was found to be 3.75 for whales of the 'inshore' form but only 1.00 for whales of the 'offshore' form.

ovulate only once per year. There is also evidence in the literature of 'sterile ovulations', or Graafian follicles without eggs in humans. It can be assumed that these become corpora atretica. Males also exhibit sterile ovulations in which a CL-like body forms and the follicle becomes atretic.

### (3) Accessory corpora lutea

Accessory CLs, defined as occurring when there is more than one CL per foetus in a pair of ovaries, are found in some species. After a brief discussion on the differentiation between the main CL and the accessory corpora, a consensus was reached that in most cases one cannot differentiate between the two, and further that one cannot distinguish between a CA formed from the regression of an accessory CL and one formed from the regression of a primary or single CL. This led to the question of the interpretation of ovulation rates in species that are known to have accessory corpora. It was agreed that for species in which accessory corpora are likely to occur and the rate of occurrence is known, the estimated ovulation rate should be adjusted, as, for example had been done for *Delphinapterus leucas* by Sergeant (1973).

The group agreed that nothing is known of the origin or function of accessory CLs. They seem to be most common in the odontocete genera *Delphinapterus* and *Monodon*, where they have been reported as occurring in about 12% of pregnant females (Brodie, 1972; K. Hay, pers. comm.). Members of the group reported them as being very rare in all *Balaenoptera* species, *Megaptera*, *Eschrichtius*, *G. macrorhynchus*, *Delphinus delphis*, *Stenella longirostris*, *S. attenuata* and *S. coeruleoalba*. Mitchell reported an occurrence of 0.45% in fin whales taken in the former hunt in the maritime provinces of Canada. Laws (1961) reported a rate of 3.5% and Gambell (1968) a rate of 2.0% in fin and sei whales respectively in the Southern Ocean.

### (C) Biases in estimating the reproductive interval

It was noted that calf mortality may shorten the average reproductive interval of a female if that female is capable of becoming pregnant shortly after a calf's death. Several factors were identified that might influence the time between calf loss and re-impregnation: (i) the age of the calf at death; (ii) the degree and timing of reproductive seasonality; (iii) Kirby & Ridgway (this volume) presented evidence that *Tursiops* females in captivity tend to ovulate seasonally and need not be synchronous within a group. This may also influence the length of time between calf death and the next ovulation.

Calf death would, in effect, shorten the average lactation time in a population. Depending on how the reproductive interval is estimated, calf death can introduce a bias. For instance, 'method 2' of Perrin *et al.* (1976), which is based on the maximum length of calves assumed to accompany lactating females, estimates reproductive interval from something that is closer to the maximum lactation time rather than the average. Calf death would thus increase the bias that is inherent in this method. However, 'method 1' in the same paper, which is based only on proportion of adult females lactating, would not be biased in its estimate of reproductive interval by calf death. It should be remembered when

using this method that the calving intervals calculated are averages that include some cycles for which fetal or neonatal death may have decreased the time to re-impregnation.

#### (D) Definition of 'sexual maturity'

The group discussed the question of whether the usual definition of the attainment of sexual maturity in females as being the first ovulation is adequate for modelling purposes. Pubescent females may ovulate more than once before conceiving. It was concluded that three criteria of maturity are useful: first ovulation, first conception and first lactation. The first can be ascertained from examination of ovaries. With regard to ascertaining conception, Benirschke noted that the gross aspect of the uterus in terms of development of stretch marks along the uterine body, marked increase in diameter of the uterine horns and the increase in vascular supply to the uterus, are all indications that the female has borne a large foetus. In addition, the myometrium may show changes in its histology in terms of thickening and vascularity which persist after a pregnancy. These all indicate that the female has born a foetus of substantial size but will occur regardless of whether the foetus is aborted or borne until term. Benirschke also reported that there are irreversible changes in the mammary gland that reflect lactation. These indicate whether a female has borne her calf until at least full term but not whether she has successfully maintained it until weaning.

Histological examination of the endometrium from both cornua may be helpful in identifying whether or not pregnancy existed at the time of capture in situations which are known to have a high risk of causing foetus loss, either through mode of operation of a fishery resulting in spontaneous abortion and/or during work-up of the carcass.<sup>3</sup>

It was noted that in newly-mature fin and sei whales, the apparent pregnancy rate is similar to that for older ages (Laws, 1961; Gambell, 1968) and hence in these and other baleen whales, age at first ovulation is perhaps still the best definition of age at attainment of sexual maturity.

#### (E) Male seasonality

The group discussed the question of seasonal aspermatogenesis in cetaceans. Several examples were noted of reduced activity evidenced by decrease in testis weight, but histological evidence for aspermatogenesis was cited for only 3 odontocetes: *Delphinus delphis* (Collet and St. Girons, this volume), *Phocoenoides dalli* (by Kasuya) and *Monodon monoceros* (K. Hay, pers. comm.), and two mysticetes: fin whales (Laws, 1961) and humpback whales (Chittleborough, 1955). Gambell (1968) did not find histological evidence of seasonality in *B. borealis*. Collet reported that while she found aspermatogenesis in most adult males in the eastern north Atlantic population of *D. delphis*, during the apparent breeding season (February to November), at least some individuals were spermatogenic throughout that period. This suggests that in this area, while there is an overall pattern of seasonality in breeding, male seasonality may be individual rather than populational. Some of the

<sup>3</sup> Editors' note. E.g. see Martin (1982).

participants were of the opinion that the activity of a single male should not make any difference as long as there are enough sexually active males to service all of the sexually active females, but some other participants thought that the seemingly complex social structure in odontocetes could make the status of individual males more important, e.g. as in the polygynous mating system of sperm whales.

Kasuya noted that in *G. macrorhynchus* in Japan, the pubertal animals produce small amounts of sperm in the breeding season but no sperm in the nonbreeding season.

Perrin described seasonal change in testes weight in two populations of *Stenella longirostris* in the eastern tropical Pacific with different histories of exploitation by the tuna purse-seine fishery (Perrin and Henderson, this volume). Males that have combined testis-epididymis weight of more than 700 g are fully 'potent', that is, have copious sperm in the epididymes. In the less exploited population (northern whitebelly spinners) a large proportion (about 50%) of adult males attain such testis weights seasonally (in February and in July-August), with maximum weights of more than 2 kg. In the more exploited population (eastern spinners), testis weights increase seasonally, but only a very small number of adult males (less than 5%) reach testis weights of 700 g or more, and maximum recorded testis/epididymis weight is less than one kg. This is correlated with lower pregnancy rates in young, but not old, females in this population. It is possible that some aspect of the exploitation has resulted in reproductive difficulties in the more heavily exploited population. The group agreed that this phenomenon should have high priority for further investigation, as it runs counter to the conventional wisdom that lower density (due to exploitation) leads to higher reproductive rates.

It was agreed that from the point of view of assessing male sexual maturity, in addition to recording testis weights, both the routine examination of the epididymis for sperm and the histological examination of smears of the testis tissue from the periphery and centre are essential to differentiate between immature, pubertal, active and resting mature animals. This is especially important because of the fact that an inactive older male can have testes larger than those of a younger but active male (as found for *D. delphis* by Collet and St. Girons, this volume).

Indications of seasonal testicular activity for dolphins are also available from studies of reproductive physiology. Wells (this volume) found an apparent annual cycle in testosterone production in male *Stenella longirostris*, and Kirby and Ridgway (this volume) reported seasonal variation in testosterone concentrations for *Tursiops*.

#### (F) Pathology and Anomalies

##### (1) Reproductive senescence

Senescent ovaries apparently exist in some odontocete cetaceans, but they have not been found in mysticetes. Marsh reported that in *G. macrorhynchus* from Japan, such ovaries are characterized macroscopically by a lack of follicles, CLs and young or partially regressed CAs. Histological samples indicate a lack of primordial and Graafian follicles, with much of the tissue being fibrotic and sclerotic. While there is no evidence of follicular

activity, numerous, generally easily counted CAs may be evident both macroscopically and microscopically. In the 50-year-old pilot whale presented in the laboratory session as an example, there were 13 CAs present. Sergeant (1962) reported up to 14 corpora in ovaries of apparently senescent *G. melaena* females.

Female *G. macrorhynchus* exhibit a high incidence of reproductive senescence. Marsh and Kasuya (this volume) found that although females live up to about 63 years, the oldest pregnant female was 34.5 years, the oldest with a CL of ovulation was 37.5 years; and the oldest with a young CA was 38.5 years. Sixty-one (26%) of the 235 mature females sampled were older than 35 years, and ten of these, including the 50-year-old example given above, were lactating. The old lactating females did not show any greater ovarian activity than other old females.

Perrin reported that reproductive senescence in *Stenella* spp. is probably indicated by the presence of 'withered' ovaries (Perrin *et al.*, 1976; Perrin, Holts and Miller, 1977). This condition first appears when there are ten or more corpora present in the ovaries. The frequency of 'withered' ovaries in *Stenella* appears to be very low, on the order of 0.1%, but this figure should be considered approximate as it is not known if these females may be more vulnerable to capture. A comparison of the *Globicephala* spp. with the *Stenella* spp. suggests that the frequency of reproductive senescence may be quite variable from species to species within the odontocetes.

Changes in ovulation rates (discussed above) may be indications of reproductive senescence, but the available evidence is inconclusive.

Reproductive senescence has not been reported for baleen whales. Withered ovaries have not been found, nor have any whales lacking follicular activity been seen in several hundred ovaries examined by Lockyer and colleagues. Female whales over 70 years old have been examined and still exhibit folliculate activity; as many as 50 corpora have been found in some ovaries (although no accessory CLs have been reported).

In summary, reproductive senescence apparently exists in some cetaceans, although it has not yet been identified for baleen whales, and may be of a highly variable frequency from species to species in the odontocetes. The question remains of why it should exist at all; the answer probably cannot be obtained except through sociobiological research.<sup>4</sup>

### (2) Cystic follicles and ovarian cysts

Cystic follicles can apparently only be distinguished from mature follicles on the basis of histology. During a given ovarian cycle, follicle stimulating hormone (FSH) induces many follicles to develop, and the granulosa cells begin to multiply. When an egg is released from one follicle and pregnancy occurs, the others become atretic i.e. cystic with some thecal luteinisation. During atresia, the granulosa cells are the first to die. The loss of or change in the granulosa cells provides the distinction between cystic follicles and mature follicles, but the distinction cannot be made grossly. The group recommends that identification of such bodies be made through

<sup>4</sup> Editors' note. There will be some discussion of this in *Rep. int. Whal. Commn* (special issue 8): Behaviour of Whales in Relation to Management, which will be published in late 1984 or early 1985.

histological examination. Information on occurrence and histology of cystic follicles and other 'ovarian cysts' in baleen whales is contained in Laws (1961) and Gambell (1968).

### (3) Parasites

In dolphins, parasites are frequently found in the lungs or in the hilus of the reproductive tract but generally are not on the surfaces where they can interfere with reproduction. Tapeworm cysts (*Monorygma* sp.) have been seen in the ovarian hilus of *Stenella* spp., forming flimsy adhesions to the ovarian surface. Usually there is fibrosis around the cysts, and histologically some granuloma formation; the granuloma are an indication of the animal's mobilization against the foreign organism. It is believed that these parasites do not interfere with the reproductive function of the ovary.

Parasites have been found to lower reproductive success in at least two cases, however. Geraci, Dailey and St. Aubin (1978) found that parasites in the mammary glands can interfere with successful calf-rearing in *Lagenorhynchus acutus* (through necrosis of mammary tissue), and Walker reported a similar situation in *Phocoenoides dalli*. The rate of infection and its consequences as reported for *L. acutus* suggest that parasitism can significantly affect reproduction in a population.

### (4) Abortion

Abortions occur in cetaceans, but determining if an abortion has occurred when there is no foetus in the vagina is difficult. In the absence of an obvious foetus, neither macroscopic nor histologic examination can confirm abortion, but certain criteria can be used to provide the impetus to look more closely for a possible aborted foetus. The presence of a recent CA, asymmetry of the uterine horns and histologic differences between the horns suggest abortions. Differences in the uteri include a thickened endometrium with evidence of chronic inflammation and remnants of secretions and placental tissue in the larger horn. Abortions of pre-implantation embryos will show only minimal changes in the uterus, and will therefore be even more difficult to detect.

Ichihara (1962) reported on 13 incidences of prenatal death of the foetus in fin whales taken in the Antarctic. The great majority of these incidences occurred in older mothers with 10 or more corpora. Ichihara estimated a minimal prenatal death rate of 0.14% for animals actually observed. Prenatal death in early pregnancy had resulted in rapid foetal disintegration and reabsorption whilst that in late pregnancy resulted in mummification and retention for long periods; lack of a CL and partial decomposition of the foetus had commenced. Prenatal death was observed most frequently for multizygotic foetuses yet one dead and one live foetus were discovered simultaneously in one uterus. A few of the foetuses were deformed.

### (5) Multiplets

Multiplets have been found *in utero* in cetaceans, but there is no evidence of mature delivery of these young. About 1% of fin whale foetuses are twins (Laws, 1961; Gambell, 1968) and Mizroch reported that this proportion

had not changed from 1931–1974. About 25 of 95,000 (0.003%) pregnant fin whales reported to the International Bureau of Whaling Statistics had triplets in their uteri. Jonsgård (1953) reported a fin whale with 6 foetuses, of varying sizes. All of these multiple foetuses have been smaller than term. Kimura (1957) reported multiplet frequencies of 0.57% for humpback whales to 2.28% for sei whales. Kato (1982) reported 0.56% twins and 0.03% triplets for Southern Hemisphere minke whales. The largest fin whale twin was reported to be about 20 ft long, but most were 12 ft or less in length. Two sets of sei whale twins, including one conjoined pair, were about 6 ft long. Multiple calves accompanying their presumed mothers have not been seen in long-term field observations of *Tursiops* or *Stenella* populations by Scott or Wells, nor have they been reported for baleen whales except for a drawing of a humpback whale with two calves published by Scammon (1874).

Benirschke noted that the frequency of *in utero* twins for fin whales is similar to that reported for humans. Humans have an average twinning frequency of 1–2%, but this is highly variable between races. For example, some African tribes have a frequency of 5%, while in Japan the rate may be 0.5 to 0.7%.

The rate of twinning may increase with age in cetaceans, e.g. 0.1% (at 1–5 corpora) to 6.25% (at 30–35 corpora) in Southern Hemisphere fin whales, (Kimura, 1957).

Both monozygotic and dizygotic twins have been reported for the Cetacea. The presence of conjoined or incompletely-split foetuses indicates the existence of monozygotic or identical twins. The presence of two foetuses with a single CL was reported for fin whales by Ohsumi (Kimura, 1957) and for sei whales by Gambell (1968), but the presence of a single CL does not necessarily indicate identical twins (e.g. Gambell found a foetus of each sex in a sei whale with one CL). Collet has found a single Graafian follicle with two eggs in *Delphinus*. This is relatively common in cats, humans and other mammals. Dizygotic twins have been identified by the presence of two CLs or because the foetuses were of different sexes.

An observation of twinning in a bottlenose dolphin in captivity suggested that the CL in dolphins is under local rather than systemic control. Gray and Conklin (1974) reported that a female bottlenose dolphin died one week after aborting one twin. Upon examination it was found that the CL for the aborted foetus had regressed, while that for the foetus *in utero* was still active. This is one of the few available observations on the regression rates for CLs.

In summary, it is believed that the mature delivery of twins is unlikely, as it is as yet unrecorded, and that typically either the calves are aborted or the female dies.

#### (6) Vaginal calculi

Vaginal calculi have been reported for a variety of cetacean genera, including *Stenella*, *Delphinus*, and *Lagenorhynchus*. In one *S. attenuata*, 13 vaginal calculi of calcium phosphate were reported, but their origin is unknown (Sawyer and Walker, 1977). Collet reported that she found calculi in 3 of approximately 30 stranded specimens in France. Sawyer and Walker summarized other calculi data. In some cases the calculi may be

calcified semen or vaginal mucus, but in at least three cases calculi have been shown to contain bones from embryos (Benirschke, Henderson and Sweeney, this volume). The incompletely expelled foetus was located in the false cervix between the vagina and cervix in each case. The fate of this kind of calculus is unknown. It may be resorbed eventually, or it may remain in the false cervix for a long time. It is not known if the false cervix opens except during copulation. Walker reported a large calculus in a *Delphinus* with a large foetus. It is believed that the unusual structure of the dolphin reproductive system, especially the false cervix, contributes most significantly to the presence of these calculi, which in at least some cases may interfere with reproduction.

#### (7) Other pathology

Benirschke noted that cetaceans are remarkable in their lack of pathology in the reproductive system. The incidence of pathology is much less than that seen for humans or other terrestrial mammals. In addition to the granulomas from worms described above, two other pathologies were noted in the material available to the workshop:

(1) A granulosa cell tumour previously undescribed for cetaceans that was found by Marsh in a 34.5-year old *G. macrorhynchus*. The tumour did not have the infoldings of cavity remnants found in a typical corpus luteum, and showed a great proliferation of granulosa cells. This type of tumour is found in humans and can be induced in rats.

(2) Uncharacteristic calcifications were found in the ovaries of two *G. macrorhynchus* aged 44.5 years and 62.5 years. These abnormal calcifications may have resulted from old bleeding.

In addition, Collet reported finding 3 cases of hydramnios in 5 stranded females of *Delphinus delphis* and another in a stranded pygmy sperm whale, *Kogia breviceps*, and felt that this may have been the cause of death.

Differences in the incidence of pathology exist between genera, but it is unclear if the total occurrence of pathology within a population can be used as an index of the status of the population. Kasuya reported less pathology in *Stenella* spp. than in *G. macrorhynchus*, but there were apparently no differences between *S. attenuata* and *S. coeruleoalba*. It was suggested that the difference between genera may at least in part be explained by the difference in life spans. In humans and other terrestrial mammals, cancers, fractures and congenital abnormalities are seen more frequently than in animals with shorter life spans.

Pathologies in cetacean reproductive systems are apparently so unusual that any specimens are noteworthy and should be examined in detail. Part of the reason for the low rate of occurrence may be related to examiner acuity and experience. Greater attention to pathologies should be paid in the future.

### III. MODELLING REPRODUCTION

#### (A) Terminology and assumptions

The group considered a draft glossary of terms used in modelling reproduction. After considerable discussion, it was concluded that there really is no accepted 'standard'

terminology; many terms, for example, have been used differently in IWC assessment and management of whales than in terrestrial game management. Given this lack of consensus, the group decided that it would be impractical to try to develop a comprehensive glossary during the workshop. The problem of terminology remains, and the workshop recommends strongly that terms which might be interpreted in more than one way are fully defined whenever used. Some particular points brought out in the discussion are summarised below.

(1) *Density dependence*

It was agreed that 'density dependence' should be thought of as a general term relating to *some* specific resource, which is not necessarily area. The limiting factor could be, for example, abundance of food or of predators.

(2) *Pregnancy rate*

Frequently models assume pregnancy is synonymous with birth. Although this is not true, it is usually unimportant in practice, as the assumed juvenile mortality rate incorporates pre-natal mortality.

(3) *Age at first parturition*

The value of the mean age at first birth, used as a parameter in most models, is often estimated as the mean age at maturity plus the gestation period. This is appropriate, however, only if the first ovulation results in a birth. If it does not, the age of first birth should be increased.

(4) *Specifying intervals*

With the discrete-time models used for real populations, it is necessary in light of both the discrete intervals of our sampling and the tendency for seasonality in population dynamics, to specify when, with respect to the interval(s), the censuses which describe the population trajectory (or the vital rates which define the *per capita* dynamics) are to refer. Commonly, the census refers to the beginning of the interval, age class  $x$  refers to the sum of individuals aged  $x-1$  to  $x$  at that time, survival rates refer to proportion surviving from one census to the next, and fecundities refer to the number of offspring censused (alive) at time  $t+1$  per mature female in the appropriate age class censused at time  $t$ . Other sets of definitions are possible, but it is important to note that it is not necessarily innocuous to mix them.

(5) *Specifying assumptions underlying terminology*

It is unfortunately only very rarely that the elementary parameters for a population dynamics model can be estimated directly from feasible experiments or field programmes; what can be measured are certain population parameters, such as relative frequencies of individuals in different age classes or reproductive states. Various assumptions are then made (usually concerning age distributions and mortality rates in between censuses) depending on the particular instance, to enable one to compute the desired parameters from the available measures. Since the opportunities both for errors and inappropriate data manipulations are fairly extensive at this stage, all models should thoroughly describe how the dynamical parameters they employ were calculated from

observed biological quantities, so that this process may be scrutinized. This is important because although the underlying mathematical theory of the computations may be standard, the improvisation carried out in each particular model may require some unravelling, and the reasonableness of the assumptions must be evaluated case by case.

**(B) Current models**

The participants in the workshop expressed a desire to examine a sample of the models currently being used in cetacean population assessment and management. Three approaches to modelling cetacean populations were reviewed, with emphasis placed on the role of reproductive rates as inputs to these models. The models presented were (1) the current [1981] sperm-whale management model used by the IWC (presented by Kirkwood), (2) the NMFS model for managing dolphins involved in the tuna fishery (presented by Smith), and (3) the IWC management model for North Pacific baleen whales (presented by Horwood).

(1) *The sperm whale model*

The IWC model for sperm whale dynamics (Allen, 1973) belongs to a large class of population models known collectively as age-structured models. With such models, a strict accounting is kept of the numbers of individuals estimated to be within each age class; in this case, age classes are given in one-year intervals. In addition, in the sperm whale model the numbers of males and females are both significant to population growth rates and are examined separately. At the core of this model is the simple updating relationship; the number of individuals in a given age class in a year is equal to the number of individuals in the previous age class one year earlier minus the catch from the previous age class during that year, all multiplied by the survival rate of that age class. The number of individuals entering the first age class is given by the number of mature females in the previous year times the birth rate of mature females.

The assumptions of this approach have to do with the functional form given to the age-specific survivorship and birth-rate parameters. Females are classified as either juveniles (0-2 years), sexually immature (3-9 years), or sexually mature (10+ years). Males are classified as either juveniles (0-2 years), sexually immature (3 to ~20 years), sexually mature (~20 to 24), or socially mature (25+ years). The first assumption used is that survival rates for all non-juvenile males and females are constant with age and through time. These rates are estimated from age samples from the catches. The second assumption is that the juvenile mortality rate is the same for males and females and is constant through time. This rate is estimated from a balance equation by assuming that, at unexploited equilibrium, the number of adult females dying in any year will equal the number of females being recruited into the adult population. Because pregnancy rates are used rather than birth rates, the estimates of juvenile mortality by this method will be biased; this will not, however, affect the results of the model.

All aspects of density dependence are incorporated into the assumptions about the functional form of the



pregnancy rate.<sup>5</sup> Pregnancy rates are assumed to be equal for all mature females. These rates are assumed to be related to the ratio of the number of mature females in the population to the number of mature females in the unexploited population by a non-linear function. The maximum pregnancy rate is taken to be 0.25 and the minimum is taken as 0.20 (corresponding respectively to 4- and 5-year calving cycles). The degree of non-linearity was chosen so as to obtain a single-sex maximum sustainable yield level (MSYL) of 60% of equilibrium density. The pregnancy rates are also dependent on the number of socially mature males in the population. Once the number of socially mature males falls below some threshold, pregnancy rates are assumed to be linearly related to the abundance of such males. The number of males can thus strongly influence pregnancy rates if they fall below this threshold (IWC, 1981a, pp. 100-1).

It was emphasized that actual evidence for density-dependence in the pregnancy rate of sperm whales is insufficient to empirically determine relationships such as those assumed here. For most stocks, the estimates of population sizes are not sensitive to the form of the pregnancy model. However, estimates of replacement yields and MSY levels are very sensitive to the pregnancy model.

#### (2) *The ETP dolphin model*

The second example of a management model is that used by the United States National Marine Fisheries Service (NMFS) to determine the status of the dolphins which are involved in the tuna purse-seine fishery in the Eastern Tropical Pacific (ETP). Reproductive rates enter into two rather distinct models, which are both inputs to the management decision process. The first model involves the estimation of the ratio of current abundance to historical (assumed equilibrium) abundance of the populations. The second model involves the estimation of the MSYL of these populations. As currently mandated by US law, the classification of populations of marine mammals as 'depleted' is defined by population levels falling below MSYL (maximum net productivity level, or MNPL in NMFS' terms), hence both elements are required for management decisions.

The ratio of current to historical abundance is estimated by back calculating the abundance of dolphins in 1959 (the beginning of incidental dolphin mortality) from the abundance of dolphins estimated in the last aerial survey (1979). The back calculation can be thought of as a simple accounting exercise. The number of dolphins in a given year is calculated from the number in the next year minus the net recruitment into the population plus the mortality due to fishing in that year. Although reproductive rates do enter into this calculation as an element of the net reproductive rate, the model is quite insensitive to the actual functional form of this net reproduction relationship. It is relatively insensitive to the value chosen for the maximum net reproductive rate over the range of values (0-4%) considered in a recent stock assessment exercise (Smith, 1979). An example can be

given for the offshore spotted dolphin: if the MSYL is assumed to be 0.65, the ratio of current to historic abundance would only change from 0.45 to 0.52 if the net reproductive rate were doubled from 0.02 to 0.04.

The net reproductive rate was assumed to be density dependent, and the specific functional form of this density dependence is of prime importance in determining the second element of the management decision processes, the estimation of MSYL for the species involved. The net reproduction function used in the above model is given by

$$\rho(N) = \rho_0 \left( 1 - \left( \frac{N}{N_{1959}} \right)^\zeta \right) \quad (1)$$

The parameter  $\rho_0$  in this equation is what can be referred to as a phenomenological parameter. Simply stated, this means that this parameter is a composite of many processes which for convenience have been lumped into a single term. As is usually the case, these processes were lumped because they could not be measured separately. Roughly,  $\rho_0$  can be thought of as the difference between the gross annual birth rate and the gross annual death rate in a population that is growing at its maximum rate. The parameter  $\zeta$  affects the shape of the density dependence. Values of this parameter can be chosen so as to obtain MSYs from any desired fraction of the equilibrium population levels (Smith, 1979). The assumption here that is of concern to the workshop is that reproductive rates and/or survival rates are density dependent. Currently there is no solid evidence that either of these life history parameters of ETP dolphin are density dependent.

#### (3) *The North Pacific baleen whale model*

The third management model presented was that used for the North Pacific large whale populations and for the Southern Ocean species before the interspecific relationships were recognized. Unlike the sperm and to a lesser extent the current BALEEN (Allen and Kirkwood, 1979) models, but similar to the above dolphin model, this model does not involve detailing age structure. The number of whales in the component of the population recruited to the fishery is given by those surviving from the previous year plus the incoming recruitment (Breiwick, 1978).

The natural survival rates are assumed to be constant for all population densities. Recruitment rates are assumed to be density dependent and the functional form of this is modelled in a similar way to the net reproductive rate in the dolphin model.

$$N_{t+1} = N_t(1 - M) + \left( r_0 \left( 1 - \left[ \frac{N_t}{N_0} \right]^s \right) + M \right) N_t$$

Where  $N_t$  is the recruited population size at time  $t$ ,  $M$  is the proportional mortality and  $(r_0 + M)$  is the maximum gross recruitment rate. Often  $M$  is estimated from the age composition of a catch taken in the early years of the fishery and  $r_0$  and  $s$  are given by assuming that MSY is 4% of the population size at 50-60% of the initial population size. If exploitation has existed for a shorter time than the age of recruitment then exploitation will have no effect on current levels of recruitment (similar to that described for sperm whales). In this case a modified DeLury estimation technique can be used (Chapman, 1974; Tillman and Grenfell, 1980).

<sup>5</sup> Editors' note. There has been considerable discussion in recent years over the appropriateness of this aspect of the model, e.g. see IWC, 1980, pp. 67-9, 111-12; IWC, 1982a, p. 73; IWC, 1983, pp. 687-8.

### (C) Density dependence

As evident from the examples discussed above, reproductive rates in cetaceans are often assumed to be density dependent in management models. In none of these examples do sufficient data exist to actually estimate the functional response of birth rates to changes in population density. In some cases, there is no direct evidence at all for density dependence in reproductive rates. A question was therefore directed to the participants in the workshop: 'What direct evidence is there for density-dependent responses in reproductive parameters for Cetacea?'

#### (1) *Pregnancy rate or calving interval*

The evidence for density dependence in reproductive rates of Southern Hemisphere fin whales was examined in two papers presented in the Symposium (Beddington and Grenfell, this volume; Mizroch and York, this volume). Although these reports were not in agreement, both included important points for consideration which should be kept in mind when reviewing the evidence for density dependence that follows. First, apparent pregnancy rates may be correlated with other factors such as the area, season and methods of sampling; hence, care should be taken to properly stratify samples. Second, by considering only the mean pregnancy rates, significant patterns in the residuals can be missed. Third, analyses of density dependence should not be limited to correlations between vital parameters and absolute abundance; the response of prey species may also be important, as well as competition and other factors. Finally, since pregnancy rates can be dependent on the age of females, care should be taken to ensure that changes in length frequencies do not confound attempts to examine density dependence.

Evidence for density dependence in eastern Pacific dolphins was discussed in two symposium papers (Hester, this volume; Smith, this volume). Hester showed an extremely rapid decrease in apparent pregnancy rates of spotted dolphins which occurred during a period of decreasing incidental mortality. Possible implications of this are that the population was increasing very rapidly during this time, or that sampling bias changed during this time, or both. There are, however, no data on changes in population size during this period. Smith (this volume) showed evidence of a higher gross annual reproductive rate in those populations of spinner dolphin that had been subject to greater reductions in population size as a consequence of tuna net mortality. Possible problems with these results are, again, sampling bias and the differences in the habitat of the three populations. Another problem is the number of fitted parameters involved in the analysis.

Positive evidence of density dependence in pregnancy rates was cited at the workshop for two other odontocetes. Best (1980) presented data for sperm whales. Kasuya (this volume) showed that the apparent pregnancy rate of striped dolphins changed through time in an exploited stock, however, the area fished expanded during this time period.

Two cases were pointed out for which evidence for density dependence might have been expected. Sergeant

reported the case of long-finned pilot whales in the western North Atlantic, where approximately 50% of a local stock was removed and no change was seen in apparent pregnancy rates. The time period of this study was, however, very short. Reilly mentioned that although the California gray whale stock is apparently growing, insufficient data exist for determining any consequential change in pregnancy rates.

Mitchell cited one case of apparent inverse density dependence in pregnancy rates, in Atlantic fin whales (Mitchell, 1974). Apparent pregnancy rates were lower in one stock (heavily fished over a long period, from Dildo and Williamsport, Newfoundland) than in another, less-heavily exploited stock (fished from Blandford).

#### (2) *Age at attainment of sexual maturity in females*

Perhaps the strongest evidence for density dependence in reproductive rates is a decrease in the age at sexual maturity of females as population size decreases. It was noted that in several cases (Lockyer, this volume), although the average age at sexual maturity did decrease with population density, the average length at sexual maturity did not change, implying changes in growth rates.

The only evidence cited for odontocetes of a reduction in the age of sexual maturity was for striped dolphins. Kasuya (this volume) documented that the age at which 50% were mature in an exploited population of this species decreased from 9.7 to 7.4 years during the period 1955-1970. Sexual maturity was inferred from ovarian activity.

Two sources of data were used to show a reduction in the mean age at sexual maturity in Southern Hemisphere fin and sei whales (Lockyer, 1972; 1974; 1977a; 1979). First, age at sexual maturity was inferred from ovarian activity and number of earplug laminae. Second, the onset of ovarian activity was found to be correlated with a reduction in the thickness of the annual layers in the earplugs of these whales (Lockyer, 1972; 1974). The first method was used to calculate the age at sexual maturity for both recent harvests and those in the 1950s. Earplugs were not, however, collected during the earlier history phase of fin and sei whale exploitation. The second method used therefore was to back-calculate the age at sexual maturity of females that had matured many years prior to the time when earplugs were first collected. Three possible problems were identified with this approach. The average age of sexual maturity for the most recent years will tend to be biased downward because those females that would mature late have not yet come of age. Second, early-maturing animals may be under-represented in the earlier cohorts if their mortality rates are higher. This would also lead to a downward bias. Third, an early age of sexual maturity would not result in increased birth rates if younger-maturing animals had a lower survival rate. The order of decline in age at first maturity is from about 10 years to about 6-7 years in fin whales and from about 11 years to about 8 years in sei whales.

There is one case where the age at sexual maturity has shown resource dependence. Although the Southern Hemisphere minke whale has only recently been exploited, its food supply might be expected to have increased as a result of the depletion of the great whales.

Indeed the age at sexual maturity has apparently decreased in this species (Lockyer, this volume).<sup>1</sup>

(3) *Percentage simultaneously lactating and pregnant*

The length of the calving interval in cetaceans could be reduced if they were capable of ovulating and becoming pregnant while still lactating. A change in the proportion of pregnant and simultaneously lactating females may therefore indicate a density-dependent response. At least since the establishment of the IWC in 1946, protection has been granted to animals accompanied by calves, which effectively means that for all large whale species, lactating females are protected – hence detecting any change would be difficult. Mitchell (1974) showed that for fin whales in a previously heavily exploited population, 6% were both pregnant and lactating, as opposed to 0–2% in a stock only recently fished. No other evidence was cited for density dependence in this parameter. Kasuya noted that the pregnant and lactating category was limited to those spotted dolphins less than 20 years of age and striped dolphins of less than 35 years in populations off Japan. Perrin stated that this category was uncommon in dolphins of the ETP. No evidence for density dependence was cited for any of these dolphin species.

(4) *Mean age in the population*

If the rate of population growth is density-dependent, the equilibrium age structure of a population will typically vary with density. For example, if calf survival is the only density-dependent factor, then as a population increases, the mean age in that population will also increase. If only adult survival were density-dependent, the mean age would decrease. For cetaceans, no evidence was cited for a change in age structure associated with a change in density. This kind of change would be difficult to detect in exploited species since most harvests show age specificity.

It was pointed out that in the case of small odontocetes, difficulty in ageing old animals has sharply limited the use of age-structure data in modelling population dynamics.

(5) *Population growth in depleted populations*

These are essentially two approaches to determining density-dependent response of populations. The above discussions have dealt only with the deductive approach: what effect does density have on the life-history attributes of a population? An alternative approach would be to ignore the details and look for the gross effect of density dependence: a change in the growth rate of a population. At equilibrium, net growth rates are zero. If growth rates increase in an exploited population, this is evidence for density dependence. The choice of approaches will depend on the types of information that can be gathered and the precision of each.

Evidence for positive growth rates in depleted stocks was cited for two species of baleen whale: gray whales from shore counts (Reilly, this volume) and right whales from shore and aerial counts (Mermoz, 1980; Best, 1970; 1981; Best and Roscoe, 1974).

<sup>1</sup> Editors' note. A recent workshop (IWC, 1984b) discussed the available evidence for a decline in age at sexual maturity in the Southern Hemisphere minke whale but was unable to conclude whether or not such a decline had taken place. The discussion was also relevant to other species.

(6) *Additional comments*

(a) *The problem of 'noise'*. Any population which persists must, as a mathematical certainty, exhibit some density dependence in its population dynamics. This mathematically necessary property does not establish what time lags the density dependence operates on, which components of the life history display the density dependence, or the functional form of the density dependence. The biological problem lies in discovering the mechanism by which the density-dependence occurs, and the associated statistical difficulty lies in demonstrating this from a limited and noisy data base. It will often be the case that density dependence cannot be 'demonstrated' nor can statistically defensible values be estimated for the parameters of the governing dynamics of the population, even though it is certain, on other grounds, that the dynamics are indeed density dependent. For similar reasons, it may only be possible to justify parameterization of a linear model for density dependence, but this is more in the way of a conventional linear approximation than an assertion that the response really is linear.

(b) *The dangers of extrapolation*. The estimation of parameters for a density dependent model of population growth is an empirical exercise in curve fitting. Thus some data will be available concerning population growth rates at a set of densities and parameterization of the model will consist in fitting some function to the observed growth-density relationship. Once the parameters of the function have been fitted, it becomes possible to compute a predicted population growth rate at any density, but the security of these predictions will, of course, deteriorate as the densities to which they refer depart from those densities bracketed by the data which were used in the actual curve fitting. For example, it is possible to compute the theoretical density at which the fitted growth curve yields a zero value (and call this the 'carrying capacity'), or to compute the percentage growth rate associated with a zero density (and call this the 'maximum reproductive rate'), but these values should not be taken seriously if the data were remote from these particular external densities. The temptation to be seduced by extrapolations is greater when the parameters of the equation used are conventionally given names such as 'k' or 'intrinsic rate of increase' which seem to denote some biological reality that in fact does not exist.

#### IV. DATA AND SPECIMEN NEEDS FOR STOCK ASSESSMENT AND MANAGEMENT

##### (A) Information needs

###### (1) General comments

The ultimate use of sampling data is in the fitting of bio-mathematical models to aid us in understanding what is happening to the particular stock. Simple models usually do not use all the types of data that are or should be collected, and more complex models are needed to incorporate behavioural and physiological data and information on life history in terms of ecological interactions.

In stock assessment models it is important to estimate

all the demographic characteristics of the population under study, but in most instances knowledge of many of these is limited. Often the effect of the characteristics is multiplicative e.g. pre-natal mortality and juvenile mortality; thus if only one is known; the outcome, as the product of the two, is also unknown. In many instances therefore, the accurate estimation of a particular parameter may not help in the short term, at least in terms of stock assessment. However when additional problems are resolved, our knowledge of the population demography will be greatly enhanced. Therefore, it is essential to maintain long term basic research, for only this will ultimately provide the knowledge to develop correct population models.

In conclusion, it is important to collect as much biological data as possible, even if the information provided may not be 'necessary' direct input for the population model currently being used; such data may, for example, provide a check on the internal consistency of these models as well as serve to develop a realistic model of a species' demography in the long run.

(2) *Some specific needs*

In addition to the obvious need for data on age-specific pregnancy and maturity already discussed earlier in this report, other, less obvious needs can be identified.

(a) *Age composition of the catch.* Cohort-analysis techniques are available which can give good estimates of past population size (although not for very recent years) and an estimate of recruitment rates independent of information on pregnancy and juvenile mortality rates. For these techniques it is important to have accurate information on the age structure in the catch over a number of years. Various authors (e.g. Cooke and Beddington, 1982; Cooke and de la Mare, 1983; Shirakihara, Tanaka and Nakano, 1983) have recently described population estimation techniques for sperm whales which utilize the age and length distribution in the catch.<sup>7</sup> The exploitation history of most sperm whale stocks has been such that the estimates of population sizes from the start of exploitation to the present are little affected by recent possible changes in reproductive performance. Consequently, independent comparisons of observed and predicted pregnancy rates may be possible.<sup>8</sup>

(b) *Sex composition of the catch.* In certain fisheries the sex ratio in the catch varies significantly from 1:1. In some of the minke whale fisheries, for example off Norway, there is a preponderance of females in the catch in certain areas and at certain times (Christensen, 1975; 1979). In other fisheries, notably for sperm whales, where the males are considerably larger than the females, a preponderance of males is caught. The effect of these removals on reproduction may depend on the degree of reduction of mature whales (see description of the sperm whale model above). Further information on the social behaviour of individual species is essential if the effect of the distortion of the sex ratio is to be fully understood.

(c) *Calf counts.* In several sighting surveys, the proportion of calves to adults has been much lower than might be

<sup>7</sup> Editors' note. For a discussion of these see IWC, 1983.

<sup>8</sup> Editors' note. Some attempts to do this have been made e.g. see IWC, 1981a, pp. 79-80; IWC, 1983, p. 691.

expected from current population models (IWC, 1981 b). It is important that further work is undertaken to determine if these proportions are truly representative of the population or if they are the result of survey problems (e.g. segregation of cow/calf pairs, or differential sightability of adults and calves).<sup>9</sup> Payne (1984) reported that for right whales in Argentina, three separate breeding populations use the Peninsula Valdes area in separate years. This needs to be taken into account in right whale surveys in other areas.

**(B) Data Sources and Sampling Problems**

Discussions on data sources and sampling problems in the estimation of cetacean reproductive parameters focused on the relationship between what is actually measured in field samples and the corresponding population values needed for stock assessment and management. Several distinct sampling methods were identified, each possessing its own set of sampling problems.

(1) *Samples from commercial catches*

(a) *Large whales.* By far the greatest source of information on cetacean reproductive parameters lies in catches taken from stocks that are exploited in a directed or incidental fishery.

Since 1946 the following data have been routinely collected from each whale caught in accordance with The International Convention for the Regulation of Whaling: species, length, sex, position and date of capture, presence or absence of foetus, length and sex of foetus if possible, and whether lactating. More recently the requirements have been expanded to include the collection, wherever possible, of material for ageing (either earplugs or teeth), of ovaries and of testes weight or at least a sample of testis tissue, although much of this was already collected under national programmes. In addition, data on school size and on sightings of all species (including those protected) are included in the effort forms which each catcher boat must complete.

While very large samples have been taken from commercial catches, there are a number of problems in converting sample estimates of reproductive parameters to the population estimates. Most of them relate to the degree in which the samples are representative of the whole population. For large whales, IWC regulations prohibit the taking of animals accompanied by calves, with the result that the 'lactating' segment of the mature female population is largely missing from samples. Consequently, apparent sample pregnancy rates overestimate true pregnancy rates. Allowance for the under-representation of lactating females has been addressed by Horwood, Donovan and Gambell (1980) and Martin (1982).

Even if no specific segment of the population is absent from catch samples, several reasons can be identified for the possible failure of catches to be representative even of the segment of the population in the area from which samples were taken. By their nature, most fishing methods are selective. In the large cetacean fisheries, it was noted that deliberate selection of large animals could lead to bias in the samples.

A problem common to all catch samples is that due to

<sup>9</sup> Editors' note. This problem is discussed in IWC, 1984a.

changes in whaling/fishing grounds with time, samples are taken from different segments of the population at different times. Such problems have been noted for Antarctic fin whales by Mizroch and York (this volume). Time series of apparent pregnancy rates for North Pacific sperm whales have been partially confounded by changes in whaling grounds over time (e.g. see IWC, 1981b, p. 689).

It is apparent from the above discussion that while very large samples are available from commercial catches, there are a number of difficulties in using these data in stock assessment. Clearly, nothing can be done about the historical data. In discussing possible means for minimizing the bias in future samples from catches, several members suggested that it may be possible to increase the representativeness of the catch samples by requiring allowable catches to be taken over a wide area. Changes in methods of handling carcasses may reduce the incidence of lost foetuses. It was recognized that such suggestions may have a significant impact on profitability of the industry. Lockyer reported that new methods were being investigated in Iceland for determining whether captured mature females were pregnant in cases where the foetus had been lost. The methods involve histological study of the endometrium and assay of hormone levels in blood and urine (see Sigurjónsson and Kjeld, 1982).

(b) *Directed small cetacean fisheries*: Mitchell (1975) and subsequent reports of the IWC Sub-Committee on Small Cetaceans (IWC, 1976–1982) reviewed the known small cetacean fisheries of the world. The following additional information on data collection in certain fisheries was available to the workshop.

(i) *Japan*. Ohsumi reported that in certain prefectures a licence from the local government is required for small cetacean hunting, and catch statistics are systematically collected. In other prefectures, no licence is required, but statistics are collected. National research programs have been initiated on the populations of dolphins and other small cetaceans taken at Iki Island and in other directed fisheries. Kasuya and Marsh (this volume) have reported on the drive fishery for short-finned pilot whales and Kasuya (this volume) has reported on the exploitation of striped and spotted dolphins in Japanese coastal waters. Problems of representativeness exist here also. Miyazaki reported that in the striped dolphin fishery there were differences in apparent pregnancy rates between samples drawn from the harpoon fishery and the 'driving' fishery.

In fisheries for small cetaceans that segregate by age and sex (even when there may be no specific bias in catch samples), samples taken from individual schools show greater variability between than within schools. For example, Miyazaki and Nishiwaki (1978) found that apparent pregnancy rates in schools of striped dolphins varied from 0 to 94.4%. In such circumstances it is necessary to take samples from as many schools as possible.

(ii) *Canada*. Sergeant reported that there are no data collection requirements for the white whale and narwhal fisheries other than species and number caught, but some data on sinking-loss rate have been collected by (government and non-government) scientists.

(iii) *Greenland*. Larsen reported that no data beyond

species and numbers caught are collected from the small cetaceans taken in Greenland.

(c) *Incidental takes*. Incidental takes of cetaceans have been reviewed extensively in recent IWC Reports (IWC, 1976–82). Additional information made available at the workshop follows.

(i) *ETP tunafishery*. Hammond reported that although there are no obligatory requirements under IATTC (Inter-American Tropical Tuna Commission) regulations, the following data are routinely collected from incidentally killed dolphins by IATTC and NMFS scientific observers (on board US vessels): species, sex, length, reproductive tract of females, testis sample (including epididymis), sex and length of foetus (small foetuses are brought back in formalin), teeth. IATTC observers on non-US vessels, however, do not currently collect specimen material. Although the percentage varies considerably by year, this programme covers about 25% of the estimated total kill on observed cruises. It is noted that younger animals and lactating females are more frequently killed in 'sets' on tuna and dolphin schools that result in lower total mortality than in those that result in high mortality.

(ii) *Other incidental catches*.

*People's Republic of China* – Chen reported that although it is against Chinese law to catch river dolphins, they are sometimes killed accidentally during fishing operations. Chen reported about 10 specimens of *Lipotes vexillifer* and more than 20 of *Neophocaena phocaenoides* have been examined and the reproductive organs analysed by the Institute of Hydrobiology of the Academia Sinica (Chen, Liu and Lin, this volume).

*Brazil* – *Inia geoffrensis* and *Sotalia fluviatilis* are caught incidentally in fisheries in the Central Amazon, and where possible reproductive tracts (Best and da Silva, this volume) stomach contents, parasites, etc. are collected. Tucuxis (*Sotalia*) are occasionally taken near the coast and used for fish bait, and the increasing use of drifting gillnets may result in an increase in the incidental kill in the Amazon. Franciscanas, *Pontoporia blainvillei*, are also captured in the coastal waters of Rio Grande do Sul in fishing nets; over 200 have been collected and are under study.

*Japan* – Ohsumi reported that Dall's porpoise, *Phocoenoides dalli*, are taken incidentally in the Japanese gillnet fishery in American waters of the North Pacific. As part of the research programme, scientists on board certain vessels collect reproductive organs, stomach contents, whole animals and other specimens. There appears to be bias towards pregnant females (over 90% in the samples) and an over-representation of younger males.

*Denmark* – Harbour porpoises, *Phocoena phocaena*, caught incidentally in fisheries in Danish waters are sampled for studies of reproduction, parasite infection, etc. by the Institute for Physiology of the University of Odense.

(2) *Direct counts from surveys*

An alternative method to sampling from commercial catches for estimating the proportion of calves in the population is the use of direct counting techniques through aerial or ship-based surveys or coastal censuses. Where it is possible to cover most, if not all, of the range

of a stock, or if the entire stock migrates past a single point, survey techniques may provide much more representative data than those available from catch samples. Cliff-top or aerial surveys aimed at least in part at obtaining calf counts have been carried out for right, humpback, gray and bowhead whales. Several participants commented that for humpback and bowhead whales, much lower calf/adult ratios had been observed in these surveys than might have been expected. Much higher ratios had been observed for southern right whales off South Africa (Best, 1981; IWC, 1981b). Other participants, citing Payne's (1984) suggestion that there may be 3 separate groups of calf-bearing females off Peninsula Valdes, queried whether the estimates obtained by Best for the waters of southern Africa may be too high (Best, 1970; 1981; Best and Roscoe, 1974).

It was recognized that it is often difficult to obtain full counts of calves from shore-based observations. For example, for Alaskan bowheads Braham reported that the gross recruitment rates estimated from ice camp surveys (1-3%) were generally lower than estimated from aerial surveys (2-5%) (Marquette, Braham, Nerini and Miller, 1982; Cabbage and Rugh, 1982).<sup>10</sup> In this context, much interest was expressed in the application of aerial photogrammetric techniques described by Perryman, Scott and Hammond (this volume) for obtaining calf percentages and length distribution. They have developed a technique for measuring small cetaceans from vertical aerial photographs. Preliminary analyses of some of the data have revealed that modal length distributions can be seen which may correspond to 6-months age groups up to an age of 1½-2 years (i.e. during the linear phase of the growth curve) and may therefore enable estimates of first-year mortality to be obtained. Such techniques may be particularly useful for coastal species.

It was noted that use of aerial survey techniques has been restricted largely to coastal cetacean species, because of the high cost of farther-ranging surveys, such as that carried out in the eastern tropical Pacific (Smith, 1979). It was pointed out that in view of the diving synchrony of sperm whales, aerial photographic surveys may be particularly valuable under appropriate circumstances.

### (3) Strandings

The group agreed that stranded animals are a special and probably unrepresentative segment of a population, particularly single stranded animals. The causes for strandings are still unknown. A common observation in mass strandings is an apparent over-representation of very young and much older animals, as well as unbalanced sex ratios, although it was reported by Sergeant that stranded groups of *Globicephala* spp. and *Pseudorca* appear to resemble schools driven ashore in fisheries in age and sex composition. It was agreed that in most cases it is difficult to use estimates of reproductive parameters obtained from stranded animals for stock assessments. A possible exception noted is mass strandings of whole schools of predominantly sperm whale cows and calves. However, when a species is not taken in any directed or incidental fishery, stranded animals represent the sole source of samples from which

reproductive data can be obtained. Many participants commented on the difficulty in obtaining biological samples from mass strandings in isolated areas, and noted that it took many years for adequate sample sizes to be accumulated. In view of this, it is important that standard procedures be adopted in collecting biological data from mass strandings of cetaceans. 'Strandings networks' such as have been established in the US, the UK, Canada, France and Australia have proved extremely valuable in this regard. It was urged that tooth or earplug samples for ageing be taken from stranded animals.

### (4) Individual-animal studies

The final category of samples that may provide information on cetacean reproductive parameters is that of studies on individual animals. These fall into two types: captive-animal studies and long-term studies of population of identifiable individuals in the wild.

Captive-animal studies have included monitoring of births for individual females, measurement of reproductive hormone levels and observations of social behaviour coupled with measurements of reproductive-hormone concentrations in dolphin colonies dedicated to such research. The information from records of captive births is of value in determining reproductive seasonality or, in some cases, age of first reproduction, but complete records of the female's tankmates are necessary to obtain data on other parameters. Concentrations of reproductive hormones in either serum or plasma have been measured for a number of delphinid species in attempts to determine reproductive condition. The most extensive measurements have been made for *Tursiops truncatus* (Harrison and Ridgway, 1971; Judd and Ridgway, 1977; Kirby and Ridgway, this volume; Richkind, 1977; Sawyer-Steffan and Kirby, 1980; Sawyer-Steffan, Kirby and Gilmartin, 1983) *Stenella longirostris* (Wells, this volume) and *Delphinus delphis* (Kirby and Ridgway, this volume). Kirby reported that hormone information is also available from studies of single live specimens of *Globicephala macrorhynchus* and *Orcinus orca* and from occasional measurements from a few specimens of *Lagenorhynchus obliquidens* and *Delphinapterus leucas*. Measurements of concentrations of progesterone and oestrogens in female delphinids have generally shown that multiple ovulations within a given season are possible, as are seasons without ovulations, and spontaneous ovulations occur in at least some delphinids. Hormonal monitoring is also yielding information on gestation length for several of these species. Seasonal changes in testosterone production in male delphinids have also been recorded.

Detailed behavioural observations in conjunction with regular blood sampling have been made for three species of delphinids in captive colonies. Kirby has closely observed 1 male-2 female *Tursiops* combinations while monitoring steroid concentrations. Kirby and Ridgway observed captive female *Delphinus delphis* over a period of two years while regularly measuring progesterone and oestrogen. Wells observed a captive colony of *Stenella longirostris* and noted changes in association and interaction patterns of individuals correlated with changes in reproductive hormone concentrations.

Captive animals whose entire reproductive histories are known may eventually also contribute greatly in

<sup>10</sup> Editors' note. The most recent discussion of this problem is included in IWC, 1984a.

- Best, P. B. 1974. The biology of the sperm whale as it relates to management. pp. 257-93. In: W. E. Schevill (ed.) *The Whale Problem. A status report*. Harvard University Press, Cambridge, Mass. 419 pp.
- Best, P. B. 1977. Two allopatric forms of Bryde's whale off South Africa. *Rep. int. Whal. Commn* (special issue 1): 10-38.
- Best, P. B. 1980. Pregnancy rates in sperm whales off Durban. *Rep. int. Whal. Commn* (special issue 2): 93-7.
- Best, P. B. 1981. The status of right whales (*Eubalaena glacialis*) off South Africa, 1969-79. *Investl Rep. Div. Sea Fish. S. Afr.* 123: 1-44.
- Best, P. B. and Roscoe, M. J. 1974. Survey of right whales off South Africa, 1972, with observations from Tristan da Cunha, 1971-72. *Rep. int. Whal. Commn* 24: 136-41.
- Breiwick, J. M. 1978. Reanalysis of Antarctic sei whale stocks. *Rep. int. Whal. Commn* 28: 179-82.
- Brodie, P. 1972. Significance of accessory corpora lutea in odontocetes with reference to *Delphinapterus leucas*. *J. Mammal.* 53(3): 614-16.
- Byskov, A. G. 1979. Atresia. pp. 41-58. In: A. R. Midgley and W. A. Sadler (eds). *Ovarian Follicular Development and Function*. Raven Press, New York, 414 pp.
- Chapman, D. G. 1974. Estimation of population size and sustainable yield of sei whales in the Antarctic. *Rep. int. Whal. Commn* 24: 82-90.
- Chittleborough, R. G. 1954. Studies on the ovaries of the humpback whale, *Megaptera nodosa* (Bonnaterre), on the western Australian coast. *Aust. J. Mar. Freshw. Res.* 5(1): 35-63.
- Chittleborough, R. G. 1955. Aspects of reproduction in the male humpback whale, *Megaptera nodosa* (Bonnaterre). *Aust. J. Mar. Freshw. Res.* 6: 1-28.
- Chittleborough, R. G. 1965. Dynamics of two populations of the humpback whale, *Megaptera novaeangliae* (Borowski). *Aust. J. Mar. Freshw. Res.* 16: 33-128.
- Christensen, I. 1975. Preliminary report on the Norwegian fishery for small whales: expansion of Norwegian whaling to Arctic and Northwest Atlantic waters, and Norwegian investigations of the biology of small whales. *J. Fish. Res. Bd Can.* 32: 1083-94.
- Christensen, I. 1979. Norwegian minke whales fishery in 1976 and 1977. *Rep. int. Whal. Commn* 29: 467-72.
- Chuzhakina, E. S. 1963. [The process of follicle maturation and atresia in the sperm whale]. pp. 48-9. In: *Vtorye Vsesoyuzhnoye Soveshchaniya po Izucheniю Morskikh Mlekopitayushchikh*; Nauk, USSR.
- Collet, A. and Harrison, R. J. 1981. Ovarian characteristics, corpora lutea and corpora albicantia in *Delphinus delphis* stranded on the Atlantic coast of France. *Aquat. Mamm.* 8: 69-76.
- Cooke, J. G. and Beddington, J. R. 1982. Further development of an assessment technique for male sperm whales based on length data from the catches. *Rep. int. Whal. Commn* 32: 239-41.
- Cooke, J. G. and de la Mare, W. K. 1983. Description of and simulation studies on the length-specific sperm whale assessment technique. *Rep. int. Whal. Commn* 33: 741-5.
- Cubbage, J. and Rugh, D. 1982. Bowhead whale length estimates and calf counts in the eastern Beaufort Sea. *Rep. int. Whal. Commn* 32: 371-3.
- Curtis, F. 1905. Nos méthodes de coloration élective du tissu conjunctif. *Archs Med. exp. Anat. path.* 17: 603-36.
- Fisher, H. E. and Harrison, R. J. 1970. Reproduction in the common porpoise (*Phocoena phocoena*) of the North Atlantic. *J. Zool., Lond.* 161: 471-86.
- Gambell, R. 1968. Seasonal cycles and reproduction in sei whales of the Southern Hemisphere. *Discovery Rep.* 35: 31-134.
- Gambell, R. 1972. Sperm whales off Durban. *Discovery Rep.* 35: 199-358.
- Gambell, R. 1973. Some effects of exploitation on reproduction in whales. *J. Reprod. Fert. Suppl.* 19: 531-51.
- Geraci, J. R., Dailey, M. D. and St. Aubin, D. J. 1978. Parasitic mastitis in the Atlantic white-sided dolphin, with implications of its role in reproductive success. *J. Fish. Res. Bd Can.* 35: 1350-5.
- Gray, K. N. and Conklin, R. H. 1974. Multiple births and cardiac anomalies in the bottlenosed dolphin. *J. Wildl. Dis.* 10: 155-7.
- Harrison, R. J. 1949. Observations on the female reproductive organs of the ca'ing whale *Globicephala melaena* Traill. *J. Anat.* 83: 238-53.
- Harrison, R. J. 1969. Reproduction and reproductive organs. pp. 253-348. In: H. T. Anderson (ed.). *The Biology of Marine Mammals*. Academic Press, NY and London, 511 pp.
- Harrison, R. J. 1972. Reproduction and reproductive organs in *Planista indi* and *Platanista gangetica*. *Invest. on Cetacea* 4: 71-82.
- Harrison, R. J., Boice, R. C. and Brownell, R. L. Jr. 1969. Reproduction in wild and captive dolphins. *Nature, Lond.* 222: 1143-7.
- Harrison, R. J. and Brownell, R. L. Jr. 1971. The gonads of the South American dolphins, *Inia geoffrensis*, *Pontoporia blainvillei* and *Sotalia fluviatilis*. *J. Mammal.* 52: 413-19.
- Harrison, R. J., Brownell, R. L. Jr and Boice, R. C. 1972. Reproduction and gonadal appearances in some odontocetes. pp. 361-429. In: R. J. Harrison (ed.). *Functional Anatomy of Marine Mammals*, Vol. 1, Academic Press, London and New York, 451 pp.
- Harrison, R. J., Bryden, M. M., McBrearty, D. A. and Brownell, R. L. Jr. 1981. The ovaries and reproduction in *Pontoporia blainvillei* (Cetacea, Platanistidae). *J. Zool., Lond.* 193: 563-80.
- Harrison, R. J. and McBrearty, D. A. 1973-74. Reproduction and gonads of the black finless porpoise, *Neophocaena phocaenoides*. *Invest. on Cetacea* 5: 225-30.
- Harrison, R. J. and Ridgway, S. H. 1971. Gonadal activity in some bottlenosed dolphins, *Tursiops truncatus*. *J. Zool., Lond.* 165: 355-66.
- Harrison, R. J. and Weir, B. J. 1977. Structure of the mammalian ovary. pp. 113-218. In: S. Zuckerman and B. J. Weir (eds). *The Ovary*, Vol. 1. Academic Press, New York, 512 pp.
- Hirose, K., Kasuya, T., Kazihara, T. and Nishiwaki, M. 1970. Biological study of the corpus luteum and the corpus albicans of blue white dolphin (*Stenella coeruleoalba*). *J. Mamm. Soc. Japan* 5: 33-40.
- Horwood, J. W., Donovan, G. P. and Gambell, R. 1980. Pregnancy rates of the Southern Hemisphere sei whales (*Balaenoptera borealis*). *Rep. int. Whal. Commn* 30: 531-5.
- Ichihara, T. 1962. Prenatal dead fetuses of baleen whales. *Sci. Rep. Whales Res. Inst., Tokyo* 16: 47-60.
- International Whaling Commission. 1976-82. [Annual] Report of the sub-committee on small cetaceans. *Rep. int. Whal. Commn* 26-32.
- International Whaling Commission. 1980. Sperm whales: special issue. *Rep. int. Whal. Commn* (special issue 2): 275 pp.
- International Whaling Commission. 1981a. Report of the sub-committee on sperm whales. *Rep. int. Whal. Commn* 31: 78-102.
- International Whaling Commission. 1981b. Report of the sub-committee on other protected species and aboriginal whaling. *Rep. int. Whal. Commn* 31: 133-9.
- International Whaling Commission. 1981c. Report of the Sperm Whale Workshop. *Rep. int. Whal. Commn* 31: 687-705.
- International Whaling Commission. 1982a. Report of the sub-committee on sperm whales. *Rep. int. Whal. Commn* 32: 68-86.
- International Whaling Commission. 1982b. Report of the Workshop on Identity, Structure and Vital Rates of Killer Whale Populations. Cambridge, England, 23-25 June 1981. *Rep. int. Whal. Commn* 32: 617-31.
- International Whaling Commission. 1983. Report of the Special Meeting on Western North Pacific Sperm Whale Assessments. Cambridge, 1982. *Rep. int. Whal. Commn* 33: 685-721.
- International Whaling Commission. 1984a. Report of the sub-committee on other protected species and aboriginal whaling. *Rep. int. Whal. Commn* 34.
- International Whaling Commission. 1984b. Report of the Minke Whale Ageing Workshop. *Rep. Int. Whal. Commn* 34.
- Irvine, A. B., Scott, M. D., Wells, R. S. and Kaufmann, J. H. 1981. Movements and activities of the Atlantic bottlenose dolphin, *Tursiops truncatus*, near Sarasota, Florida. *Fish. Bull. U.S.*, 79: 671-88.
- Ivashin, M. V. 1958. Metodika opredeleniya sledov zhelytkh tel beremennosti i ovulyachii u gorbatogo kita. [A method for determining the corpora lutea traces of pregnancy and ovulation in humpback whales]. *Tr. VNIRO* 33: 161-72.
- Jonggård, Å. 1953. Fin whale with six foetuses. *Norsk Hvalfangsttid.* 42: 685-6.
- Judd, H. L. and Ridgway, S. H. 1977. Twenty-four hour patterns of circulating androgens and cortisol in male dolphins. pp. 269-77. In: S. H. Ridgway and K. Benirschke (eds), *Breeding dolphins: present status, suggestions for the future*. PB-273 673, National Technical Information Service, Springfield, VA., 308 pp.
- Kasuya, T. 1972. Growth and reproduction of *Stenella coeruleoalba* based on the age determination by means of dental growth layers. *Sci. Rep. Whales Res. Inst., Tokyo* 24: 57-79.
- Kasuya, T., Miyazaki, N. and Dawbin, W. H. 1974. Growth and reproduction of *Stenella attenuata* in the Pacific coast of Japan. *Sci. Rep. Whales Res. Inst., Tokyo* 26: 157-226.
- Kato, H. 1982. Some biological parameters for the Antarctic minke whale. *Rep. int. Whal. Commn* 32: 935-45.
- Kimura (Ohsumi), S. 1957. The twinning in southern fin whales. *Sci. Rep. Whales Res. Inst., Tokyo* 12: 103-25.
- Laurie, A. H. 1937. The age of female blue whales and the effect of whaling of the stock. *Discovery Rep.* 15: 223-84.

interpretation of the reproductive history via examination of ovaries after death.

In recent years, declining catch limits set by the IWC for large cetaceans and increasing national controls over small cetacean fisheries have resulted in samples from commercial catches becoming increasingly difficult to obtain. Thus greater emphasis must be placed on gathering data on population reproductive rates and parameters from free-ranging animals. Longterm studies of populations in which individuals have been reliably identified on a repeated basis have been carried out for coastal populations of both baleen and toothed whales. Observations of recognizable individuals over several years can provide information on calving cycles, recruitment and loss from the population, and the relative position of individuals in the social/breeding structure of the population. Payne has identified over 500 right whales, *Eubalaena australis*, off Patagonia over the last ten years and has constructed reproductive histories for his identifiable females. Glockner-Ferrari (this volume) and others have been able to identify several hundred humpback whales from colour patterns, 'facial' grooves, and scars, and have been able to follow a number of identifiable females through several breeding seasons on their wintering grounds. Bigg, Balcomb, and others have been monitoring populations of killer whales, *Orcinus orca*, in the northeast Pacific over the last ten years. They have been able to identify nearly every individual in the populations, and have determined the sex of most of the population members (IWC, 1982). Wells reported that Norris and Dohl began identifying individuals from a population of *Stenella longirostris* off Kona, Hawaii over ten years ago. Norris, B. Würsig, M. Würsig, Wells, and others have continued the observations of this population since 1979, and at present can identify nearly 200 individuals, including females with calves. Irvine, Wells, and Scott have been working with a marked population of *Tursiops truncatus* off the west coast of Florida since 1970 (Irvine, Wells, Scott and Kaufmann, 1981). They tagged approximately half of the resident population, thereby obtaining information on the approximate age and sex of those identifiable individuals, and identified much of the rest of the population from natural marks, allowing the construction of reproductive histories for identifiable females over the last eleven years in some cases. As techniques for individual recognition from natural markings become better developed and more widely applied, much of the requisite information for assessment of populations that were previously inaccessible should become available. However, it must be recognized that the application of such techniques to oceanic populations may be extremely difficult if not impossible. In addition, capture/tagging/sampling/release programmes such as those of Irvine *et al.* (1981) can (a) provide much information on the age/sex structure of a population (particularly for a sexually non-dimorphic species), (b) produce physiological and reproductive profiles for recognizable individuals on a long term basis, (c) identify population differences, and (d) potentially identify the relative contribution of particular males to calf production within populations through analysis of genetic characteristics as has been attempted by Duffield, Odell, Asper, Searles, Evans, Finley and Fraker (this volume).

## V. LITERATURE CITED

### (A) Papers/Abstracts published in this volume

- Benirschke, K., Henderson, J. R. and Sweeney, J. C. A vaginal mass, containing fetal bones, in a common dolphin, *Delphinus delphis*. pp. 457-8.
- Beddington, J. R. and Grenfell, B. Baleen whales and their food supply in the Southern Ocean: the effect on reproduction. [Abstract.] p. 476.
- Best, R. C. and da Silva, V. M. F. Preliminary analysis of reproductive parameters of the boto, *Inia geoffrensis*, and the tucuxi, *Sotalia fluviatilis*, in the Amazon River system. pp. 361-9.
- Chen, P., Liu, R. and Lin, K. Reproduction and the reproductive system in the beiji, *Lipotes vexillifer*. pp. 445-50.
- Collet, A. and Saint Girons, H. Preliminary study of the male reproductive cycle in common dolphins, *Delphinus delphis*, in the eastern North Atlantic. pp. 355-60.
- Duffield, D. A., Odell, D. K., Asper, E. D., Searles, S., Evans, W. E., Finley, K. J. and Fraker, M. A. Biochemical variability in *Tursiops* and *Delphinapterus*, application to evaluation of population dynamics. [Abstract.] p. 477.
- Glockner-Ferrari, D. A. and Ferrari, M. J. Reproduction in humpback whales, *Megaptera novaeangliae*, occurring in Hawaiian waters. pp. 237-42.
- Hester, F. J. Possible biases in estimates of reproductive rates of the spotted dolphin, *Stenella attenuata*, in the eastern Pacific. pp. 337-41.
- Ivashin, M. V. Characteristics of ovarian corpora in dolphins and whales as described by Soviet scientists. pp. 433-44.
- Kasuya, T. Effect of exploitation on the reproductive parameters of two species of *Stenella* off the Pacific coast of Japan. [Abstract.] p. 478.
- Kasuya, T. and Marsh, H. Life history and reproductive biology of the short-finned pilot whale, *Globicephala macrorhynchus*, off the Pacific coast of Japan. pp. 259-310.
- Kirby, V. L. and Ridgway, S. H. Hormonal evidence of spontaneous ovulation in captive dolphins, *Tursiops truncatus* and *Delphinus delphis*. pp. 459-64.
- Larsen, F. Reproductive parameters of the minke whale, *Balaenoptera acutorostrata*, off West Greenland. pp. 233-6.
- Lockyer, C. Review of baleen whale (Mysticeti) reproduction and implications for management. pp. 27-50.
- Marsh, H. and Kasuya, T. Changes in the ovaries of the short-finned pilot whale, *Globicephala macrorhynchus*, with age and reproductive activity. pp. 311-35.
- Mizroch, S. A. and York, A. E. Have pregnancy rates of Southern Hemisphere fin whales, *Balaenoptera physalus*, increased? pp. 401-10.
- Payne, R. Reproductive rates and breeding area occupancy in the southern right whale, *Eubalaena australis*. [Abstract.] p. 482.
- Perrin, W. F. and Henderson, J. R. Growth and reproductive rates in two populations of spinner dolphins, *Stenella longirostris*, with different histories of exploitation. pp. 417-30.
- Perrin, W. F. and Reilly, S. B. Reproductive parameters of dolphins and small whales of the family Delphinidae. pp. 97-133.
- Perryman, W. L., Scott, M. D. and Hammond, P. A technique for estimating reproductive parameters for small cetaceans from vertical aerial photographs. [Abstract.] p. 482.
- Reilly, S. B. Observed and maximum rates of increase in gray whales, *Eschrichtius robustus*. pp. 389-99.
- Smith, T. D. Estimating the dolphin population size yielding maximum production. pp. 187-90.
- Wells, R. S. Reproductive behavior and hormonal correlates in Hawaiian spinner dolphins, *Stenella longirostris*. pp. 465-72.

### (B) Others

- Allen, K. R. 1973. The computerized sperm whale population model. *Rep. int. Whal. Commn* 23: 70-4.
- Allen, K. R. and Kirkwood, G. P. 1979. Program to estimate baleen whale population sizes (BALEEN). *Rep. int. Whal. Commn* 29: 367-8.
- Benirschke, J., Johnson, M. L. and Benirschke, R. J. 1980. Is ovulation in dolphins, *Stenella longirostris* and *Stenella attenuata*, always copulation induced? *Fish. Bull., U.S.* 78: 507-28.
- Best, P. B. 1967. The sperm whale (*Physeter catodon*) off the west coast of South Africa. I. Ovarian changes and their significance. *Invest Rep. Div. Sea Fish. S. Afr.* 61: 1-27.
- Best, P. B. 1970. Exploitation and recovery of right whales *Eubalaena australis* off the Cape Province. *Invest Rep. Div. Sea Fish. S. Afr.* 80: 1-20.



- Laws, R. M. 1958. Recent investigations of fin whale ovaries. *Norsk Hvalfangsttid.* 47(5): 225-54.
- Laws, R. M. 1961. Reproduction, growth and age of southern fin whales. *Discovery Rep.* 31: 327-486, pl. 4-7.
- Lennepe, E. W. van. 1950. Histology of the corpora lutea in blue and fin whale ovaries. *Proc. K. ned. Akad. Wet.* 53(4): 593-9.
- Lockyer, C. 1972. The age at sexual maturity of the southern fin whale (*Balaenoptera physalus*) using annual layer counts in the ear plug. *J. Cons. int. Explor. Mer.* 34: 276-94.
- Lockyer, C. 1974. Investigation of the ear plug of the southern sei whale, *Balaenoptera borealis*, as a valid means of determining age. *J. Cons. int. Explor. Mer.* 36: 71-81.
- Lockyer, C. 1977. A preliminary study of variations in age at sexual maturity of the fin whale with year class, in six Areas of the Southern Hemisphere. *Rep. int. Whal. Commn* 27: 141-7.
- Lockyer, C. 1979. Changes in a growth parameter associated with exploitation of southern fin and sei whales. *Rep. int. Whal. Commn* 29: 191-6.
- Lockyer, C. and Brown, S. G. 1979. A review of recent biological data for the fin whale off Iceland. *Rep. int. Whal. Commn* 29: 185-9.
- Lockyer, C. and Martin, A. R. 1983. The sei whale off Western Iceland. II. Age, growth and reproduction. *Rep. int. Whal. Commn* 33: 465-76.
- Lockyer, C., Gambell, R. and Brown, S. G. 1977. Notes on age data of fin whales taken off Iceland, 1967-74. *Rep. int. Whal. Commn* 27: 427-50.
- Mackintosh, N. A. and Wheeler, J. F. G. 1929. Southern blue and fin whales. *Discovery Rep.* 1: 257-540.
- Mackintosh, N. A. 1942. The southern stocks of whalebone whales. *Discovery Rep.* 22: 197-300.
- Marquette, W., Braham, H., Nerini, M. and Miller, R. V. 1982. Bowhead whale studies, autumn 1980 to spring 1981: harvest, biology and distribution. *Rep. int. Whal. Commn* 32: 357-70.
- Martin, A. R. 1982. Pregnancy rates of fin whales in the Icelandic catch. *Rep. int. Whal. Commn* 32: 325-9.
- Masaki, Y. 1979. Yearly change of the biological parameters for the Antarctic minke whale. *Rep. int. Whal. Commn* 29: 375-95.
- Mermoz, J. F. 1980. Preliminary report on the southern right whale in the southwestern Atlantic. *Rep. int. Whal. Commn* 30: 183-6.
- Miller, R. J. and Campbell, R. S. F. 1978. Anatomy and pathology of the bovine ovary and oviduct. *Vet. Bull.* 48(9): 737-53.
- Mitchell, E. D. 1974. Present status of northwest Atlantic fin and other whale stocks. pp. 108-69. In: W. E. Schevill, (ed.), *The Whale Problem. A status report.* Harvard University Press, Cambridge, Mass., 419 pp.
- Mitchell, E. D. (ed.). 1975. Review of biology and fisheries for small cetaceans. *J. Fish. Res. Bd Can.* 32: 875-1240.
- Miyazaki, N. and Nishiwaki, M. 1978. School structure of the striped dolphin off the Pacific coast of Japan. *Sci. Rep. Whales Res. Inst., Tokyo* 30: 65-115.
- Mizroch, S. A. 1981. Analysis of some biological parameters of the Antarctic fin whale (*Balaenoptera physalus*). *Rep. int. Whal. Commn* 31: 421-34.
- Mossman, H. W. and Duke, K. L. 1973. *Comparative Morphology of the Mammalian Ovary.* University of Wisconsin Press, Wisconsin, 461 pp.
- Ohsumi, S. 1965. Reproduction of the sperm whale in the north-west Pacific. *Sci. Rep. Whales Res. Inst., Tokyo* 19: 1-35.
- Perrin, W. F., Coe, J. M. and Zweifel, J. R. 1976. Growth and reproduction of the spotted porpoise, *Stenella attenuata*, in the offshore eastern tropical Pacific. *Fish. Bull., U.S.* 74: 229-69.
- Perrin, W. F., Holts, D. B. and Miller, R. B. 1977. Growth and reproduction of the eastern spinner dolphin, a geographical form of *Stenella longirostris* in the eastern tropical Pacific. *Fish. Bull., U.S.* 75: 725-50.
- Peters, H. and McNalty, K. P. 1980. *The Ovary. A Correlation of Structure and Function in Mammals.* Granada, London, 174 pp.
- Peters, N. 1939. Über Grosse, Wachstum und Alter des Blauwhales (*Balaenoptera musculus* (L.)) und Finnwhales (*Balaenoptera physalus* (L.)). *Zool. Anz.* 127: 193-204.
- Richkind, M. 1977. Steroid hormone studies in pregnant and non-pregnant bottlenosed dolphins, *Tursiops truncatus*. pp. 261-8. In: S. H. Ridgway and K. Benirschke (eds), *Breeding Dolphins: Present Status, Suggestions for the Future.* PB 273 673, National Technical Information Service, Springfield, VA., 308 pp.
- Robins, J. P. 1954. Ovulation and pregnancy corpora lutea in the ovaries of the humpback whale. *Nature, Lond.* 173: 201-3.
- Sawyer, J. E. and Walker, W. A. 1977. Vaginal calculi in the dolphin. *J. Wildl. Dis.* 13: 346-8.
- Sawyer-Steffan, J. E. and Kirby, V. L. 1980. A study of serum steroid hormone levels in captive female bottlenose dolphins, their correlation with reproductive status, and their application to ovulation induction in captivity. PB 80-177 199 National Technical Information Service, Springfield, VA., 21 pp.
- Sawyer-Steffan, J. E., Kirby, V. L. and Gilmartin, W. G. 1983. Progesterone and estrogens in the pregnant and non-pregnant dolphin, *Tursiops truncatus*, and the effect of induced ovulation. *Biol. Reproduct.* 28: 897-901.
- Scammon, C. M. 1874. *The Marine Mammals of the North-western Coast of North America.* Carmany, San Francisco, 319 pp+v.
- Sergeant, D. E. 1972. The biology of the pilot or pothead whale, *Globicephala melanea* [Traill] in Newfoundland waters. *Bull. Fish. Res. Bd Can.* 132: 1-84.
- Sergeant, D. E. 1973. Biology of white whales (*Delphinapterus leucas*) in western Hudson Bay. *J. Fish. Res. Bd Can.* 30: 1065-90.
- Shirakihara, K., Tanaka, S. and Nakano, T. 1983. The revised age-specific model for population assessment of the western North Pacific sperm whales. *Rep. int. Whal. Commn* 33: 757-9.
- Sigurjónsson, J. and Kjeld, J. 1982. Progress report on research on hormonal levels in fin and sei whales caught off Iceland. Paper SC/34/Ba 14 presented to the IWC Scientific Committee, June 1982 (unpublished).
- Sleptsov, M. M. 1940. O biologii razmnozheniya chernomorskogo del'fina *Delphinus delphis*. [On the biology of reproduction of the Black Sea dolphin, *Delphinus delphis*]. *Zool. Zh.* 20: 632-53.
- Smith, T. D. (ed.). 1979. Report of the Status of Porpoise Stocks Workshop (27-31 August 1979, La Jolla, California). Southwest Fisheries Center, La Jolla, California Admin. Rep. LJ-79-41, 120 pp.
- Tanabe, S., Tanaka, H. and Tatsukawa, R. 1981. Ecology and bioaccumulation of *Stenella coeruleoalba*. Considerations on the several factors related to the variation of DDT residue levels with age. pp. 123-32. In: T. Fujiyama, (ed.), *Studies on the Levels of Organochlorine Compounds and Heavy Metals in the Marine Organisms.* Univ. Ryukyus, Okinawa, 132 pp.
- Tillman, M. F. and Grenfell, B. 1980. Estimates of abundance for the western North Pacific stock of Bryde's whales. *Rep. int. Whal. Commn* 30: 369-77.
- Weir, B. J. and Rowlands, I. W. 1977. Ovulation and atresia. pp. 265-302. In: S. Zuckerman and B. J. Weir (eds), *The Ovary*, Vol. 1. Academic Press, New York, 512 pp.
- Zemsky, V. A. 1956. [Methods of establishing traces of corpora lutea in the ovaries of the gray whale - *Eschrichtius robustus* (Cetacea, Eschrichtiidae)]. *Zool. Zh.* 69: 1073-80.
- Zimshuk, V. V. 1970. Opredelenie sledov zheltikh tel na yaichnikakh u serogo kita - *Eschrichtius gibbosus* (Cetacea, Eschrichtiidae). [Materials on the determination of corpora lutea traces in the ovaries of the gray whale - *Eschrichtius gibbosus* (Cetacea, Eschrichtiidae)]. *Zool. Zh.* 49: 1073-80. [translated by S. Pearson, Nat. Mar. Mammal Lab., nat. Mar. Fish. Ser. Sand Point NAS, Seattle Wash., 11 pp].

## VI. APPENDICES

## Appendix A

## AGENDA

1. Opening business.
  - (a) Introduction
  - (b) Adoption of agenda
  - (c) Adoption of schedule
  - (d) Confirmation of appointments
    - (i) Discussion leaders
    - (ii) Rapporteurs
    - (iii) Laboratory-demonstration coordinators
  - (e) Review of conference documents
2. Terminology of reproductive morphology and physiology.
  - (a) Group discussion
  - (b) Laboratory demonstrations
3. Interpreting ovarian scars.
  - (a) Group discussion
  - (b) Laboratory demonstrations
4. Current models of reproduction.
  - (a) Terminology and concepts – group discussion
  - (b) Testing hypotheses inherent in current models and management
5. Sampling problems – group discussion.
6. Comparative morphology of reproductive system.
  - (a) Laboratory demonstrations
  - (b) Group discussion
7. Data and specimen needs for stock assessment and management – group discussion.
8. Pathology of the reproductive system.
  - (a) Laboratory demonstrations
  - (b) Group discussion
9. Collection, storage and preparation of reproductive materials – group discussion.
10. Discussion of additional topics.
11. Write and review report of the workshop.

## Appendix B\*

## TERMINOLOGY OF FEMALE REPRODUCTIVE MORPHOLOGY AND PHYSIOLOGY

**(1) Morphology of the cetacean ovary**

The external appearance of the ovaries of various cetaceans have been described and/or figured. Harrison (1969) and Harrison, Brownell and Boice (1972) summarize the relevant literature. Subsequent papers include those of Brodie (1972), Harrison (1972), Harrison and Weir (1977), Harrison and McBrearty (1973–74, 1977), Harrison, Bryden, McBrearty and Brownell (1981), Collet and Harrison (1981) and Marsh and Kasuya (this volume).

The ovary, like several other visceral organs, is basically composed of a cortex and medulla. The larger cortex contains most of the active cell types and tissues, the most important of which are the follicles with their oocytes, the corpora lutea, corpora albicantia and corpora atretica (each of which is considered separately below), the interstitial cells supported by stromal connective tissue, nerves, and lymph and blood vessels. Surrounding the cortex is a dense connective-tissue capsule or tunica albuginea, which is itself positioned under the covering 'germinal' epithelium.

The medulla consists mainly of dense connective tissue and larger blood vessels, although interstitial cells, hilar cells and structures of the rete ovarii are also found. Fisher and Harrison (1970), Harrison (1949; 1972), Harrison *et al.* (1972), Harrison and McBrearty (1973–74) have briefly described the rete ovarii of various odontocetes.

**(2) Follicular development (Fig. 1)**

'The follicle consists of the oocyte and its envelope which is composed of cells and an outer membrane. During follicular development the morphology changes as the

\* Cited references are included in the Literature Cited section of the main body of the report above.

oocyte and the surrounding cells differentiate' (Peters and McNalty, 1980).

The primordial follicle consists of a small oocyte, a single layer of granulosa cells and a basement membrane. Its appearance and size change little with advancing age. The primordial follicles represent the pool from which all follicles emerge.

The preantral (secondary) follicle is characterized by an oocyte that is in the growth phase with one or more layers of granulosa cells surrounding it. The wall of the follicle differentiates into two layers, the theca interna and theca externa. The transition from a preantral to an antral (tertiary, vesicular, Graafian) follicle is gradual and continuous. As the granulosa cells multiply, there is concomitant increase in the production and accumulation of fluid leading to the development of a follicular cavity or antrum.

As ovulation approaches, the (primary) oocyte resumes meiosis. After a reduction division, one set of homologous chromosomes remains in the cell, which is now called a secondary oocyte. A marked expansion of the whole follicle occurs shortly before ovulation and it bulges from the ovarian surface. In order to allow the secondary oocyte to exit, a localized part of the wall of the ovary and that of the follicle has to disintegrate. At ovulation, the secondary oocyte is released from the follicle and enters the oviduct. In cetaceans, ovulation is usually recognizable by the presence of a stigma, a scar on the surface of the ovary resulting from damage to the tunica albuginea and 'germinal' epithelium at ovulation.

**(3) Follicular atresia and the development of corpora atretica**

Coupled with the normal follicular development cycle is the concurrent normal phenomenon of follicular atresia,

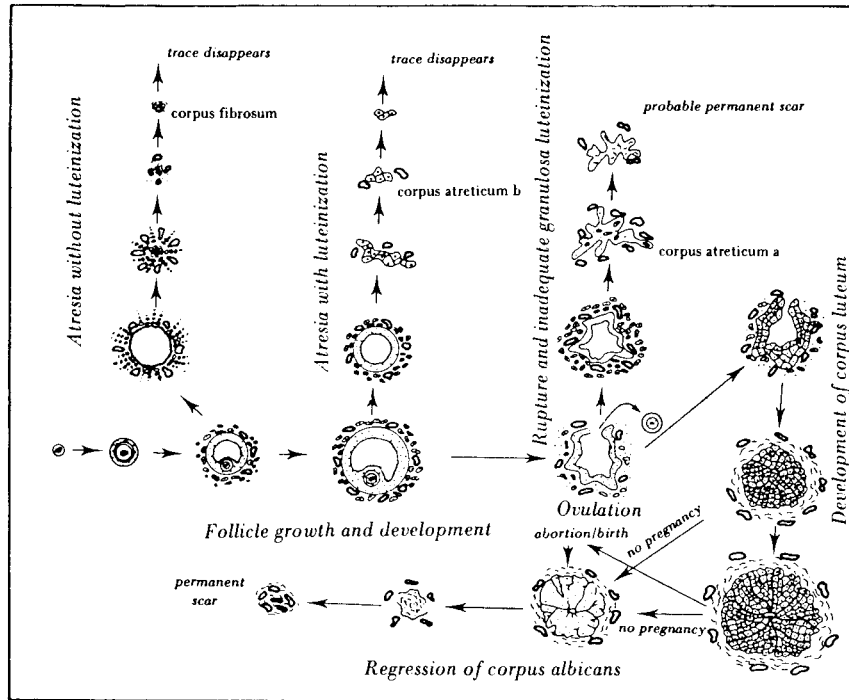


Fig. 1. A schematic representation in the form of a flowchart of the follicular changes occurring in a cycling cetacean ovary. It is also possible for a follicle to form an 'accessory' corpus luteum without releasing the egg. Some large antral follicles may also persist as cystic follicles. In this case macroscopically-detectable luteal tissue does not develop.

which is not necessarily simply a degenerative process. This metamorphosis of the follicle wall into a different kind of probably functional tissue occurs without ovulation as a normal and essential event in the ovarian cycle (Weir and Rowlands, 1977). Atresia gives rise to secondary interstitial tissue (usually considered difficult to find in cetaceans (Harrison and Weir, 1977), an exception being *Pontoporia blainvillei* (Harrison *et al.*, 1981)), or to accessory corpora lutea, both of which may be hormonally active (Weir and Rowlands, 1977). Relatively few Graafian follicles ovulate, many more become atretic.

Follicles may become atretic at any stage of their development (Byskov, 1979). Little is known about the atresia of small follicles, as this may not modify the macroscopic or microscopic structure of the ovary. However, the atresia of medium and large follicles is conspicuous and presents a variety of appearances depending on the stage of the follicle at the time it begins. In medium-sized follicles, atresia usually occurs without luteinization, i.e. without accumulation of lipids in the granulosa or theca cells. Small corpora fibrosa (Marsh and Kasuya, this volume) are derived from the basement membrane of atretic medium-sized follicles. These fibrous bodies are probably slowly resorbed; otherwise they would accumulate in far greater numbers than are seen in the ovaries.

Atresia of Graafian follicles of various sizes often progresses via different stages of luteinization. Lipid accumulation usually starts in the granulosa cells close to the basement membrane and in the cells of the theca

interna. As atresia continues, the granulosa cell numbers become reduced by lysis and phagocytosis with concomitant collapse of the follicle (Byskov, 1979). During the atretic differentiation few thecal cells become necrotic. Rather they hypertrophy and accumulate lipid droplets, undergoing a type of 'fatty' degeneration. The resulting lipid is usually pale yellow at first and readily soluble in fat solvents but gradually oxidizes, becoming darker and more insoluble. The resulting structures persist for some time but usually not indefinitely (Marsh and Kasuya, this volume).

Lutealized (luteinized) follicles have been described in the ovaries of several cetaceans. Different terms have been used by various authors to describe different stages in the development and regression of these bodies as follows: corpora lutea atretica (Best, 1967); atretic follicles (Zimushko, 1970); unruptured lutealizing follicles (Harrison and McBrearty, 1973-74); luteinized follicles (Sergeant, 1962; 1973); atretic lutealized follicles (Harrison and Ridgway, 1971; Harrison, 1972; Harrison *et al.*, 1972); atretic corpora (Zimushko, 1970); yellow bodies (Laurie, 1937), corpora atretica (Laws, 1961; Kasuya, Miyazaki and Dawbin, 1974; Collet and Harrison, 1981; corpora atretica *b* (Best, 1967; Marsh and Kasuya, this volume), or corpora albicantia type 5 (Perrin, Coe and Zweifel, 1976). Most authors have not included them in counts of corpora albicantia; an exception being Perrin *et al.* (1976). We suggest that in future they should be called corpora atretica *b*. (Corpora atretica *a* are discussed below).

Another form of atresia occurs when a follicle behaves

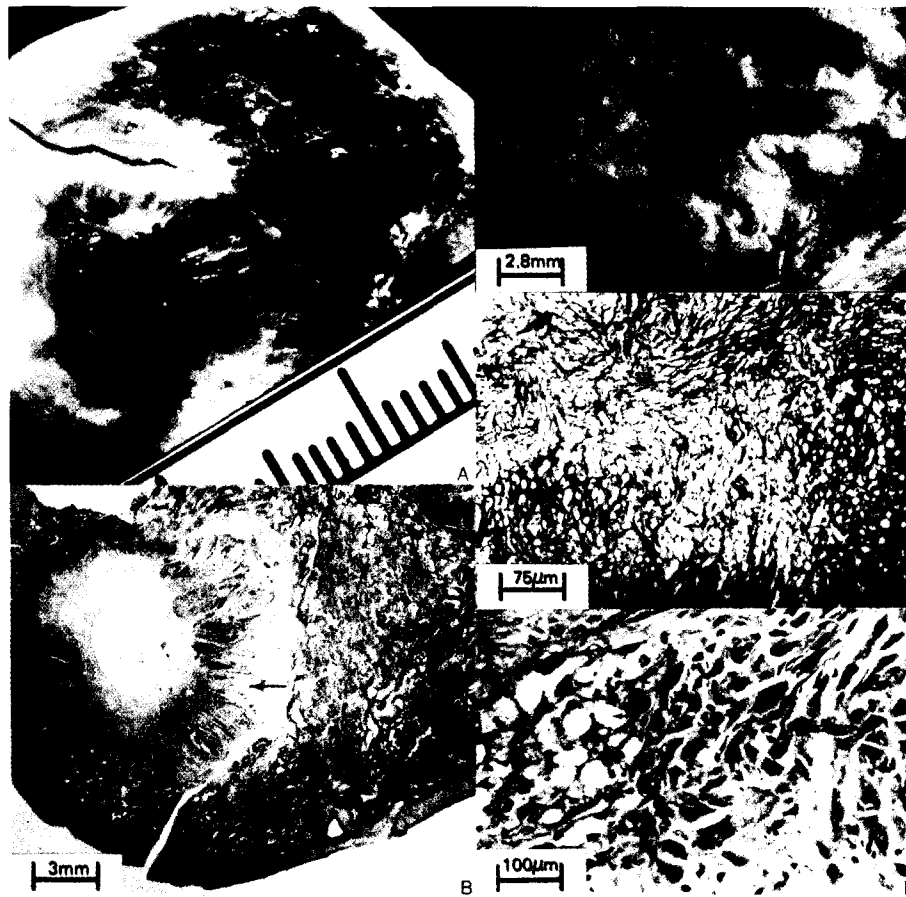


Fig. 2. Structures observed in the ovaries from minke whales, *Balaenoptera bonaerensis*, brought to the workshop by C. Lockyer. The scale is in mm.

- A. Macrophotograph of a young corpus atreticum *a* (lower left) and a corpus albicans (upper right). The young corpus atreticum *a* had a fibrin-filled centre and a prominent stigma on the ovary surface.
- B. Histological section of the structures in A. The granulosa layer of the corpus atreticum *a* (left side) has been replaced by fibrous tissue. The theca layer has luteinized. Some of the theca luteal cells (L) are still active; others (arrowed) are undergoing fatty degeneration. The corpus albicans is on the right. Stained with van Gieson's stain (Curtis, 1905) and celestin blue haemalum.
- C. Macro-photo of an older corpus atreticum *a*.
- D. Histology of part of the corpus atreticum *a* in C. Some theca cells, all of which have undergone fatty degeneration, are still present (examples arrowed) but there has been extensive fibrous replacement. Stained with van Gieson and celestin blue.
- E. Higher-power photograph of the theca layer in B showing the theca lutein cells before (L) and during (arrowed) fatty degeneration. Stained with van Gieson and celestin blue.

as it would have done had ovulation occurred, but the egg is not released, thus forming an accessory corpus luteum (see multiple corpora, below).

Laws (1961) described 'yellow', 'buff-cellular' and 'yellow and white' corpora aberrantia in fin whale ovaries, which he included in counts of corpora albicantia. Gambell (1968; 1972) also recorded corpora aberrantia in sei and sperm whales respectively and included them in corpora counts. Similar structures were also observed in sperm whale ovaries by Chuzhakina (1963). Best (1967) described similar bodies, also in the sperm whale, which he called corpora atretica *a*, excluding them from his counts of corpora albicantia. Marsh and Kasuya (this volume), observed these

structures in *Globicephala macrorhynchus* ovaries, followed Best's terminology and did not include them in corpus counts.

These structures can be derived from ruptured follicles in which corpus luteum development has not proceeded normally (Best, 1967). As these bodies seem to result from mainly thecal luteinization (like the smaller corpora atretica *b* described above), Best (1967) suggested that these structures should be called corpora atretica *a*.

The term 'corpora aberrantia' should be avoided, as it has a different and precise meaning in the general ovarian literature (see Harrison and Weir, 1977).

Fig. 2A shows the general morphology of a young corpus atreticum *a*. The granulosa layer has been

replaced by fibrous tissue. Extensive thecal luteinization has occurred on one side of this body. Some of the thecal lutein cells still appear active, others are undergoing fatty degeneration (Figs 2B, E). A fibrin clot fills the centre. Even though a conspicuous stigma was visible on its surface, this corpus atreticum *a* is macroscopically and histologically quite different from a normal corpus albicans (Figs 2A, B).

Figs 2C, D shows an older corpus atreticum *a* which also appeared to have developed from a ruptured follicle. In this case, a central fibrous clot probably did not develop. The number of lipid-rich luteal cells has been greatly reduced and the fibrous replacement is much more extensive. This structure (Figs 2C, D) is also macroscopically and histologically quite distinct from a corpus albicans. However, it is possible that an old corpus atreticum *a* in which fibrous replacement has been extensive could not be distinguished from a regressing corpus albicans (Laws, 1961; Best, 1967).

Miller and Campbell (1978) discussed cystic corpora lutea in cattle. Such cysts are considered non-pathological and perhaps normal if less than 10 mm in diameter. Like corpora atretica *a* these cysts are formed after ovulation and result from rapid infiltration by fibroblasts through the granulosa layer of the ruptured follicle. Factors which may predispose to this condition include explosive rupture of the follicle, premature closure of the ovulation point and an over-ripe follicle with the membrane propria degenerating at the time of ovulation. Cetacean corpora atretica *a* may have a similar etiology.

As outlined above, the inclusion or exclusion of corpora atretica *a* in counts of normal corpora albicantia is variable with author and results in differences in the interpretation of the ovulation rate and the record of possible past pregnancies. It is proposed that, whenever possible, workers distinguish between the different types of corpora (which may be difficult without histological evidence) bearing in mind that ovulation which is not followed by normal corpus luteum development almost certainly does not give rise to pregnancy.

#### (4) Corpus luteum

The corpus luteum is the endocrine gland which normally develops from the cellular components of the ovarian follicle after ovulation (Harrison and Weir, 1977). When a foetus is found in the uterus, the corpus luteum is generally referred to as a corpus luteum of pregnancy or a corpus gravidatum. A corpus luteum which persists for a short time without a subsequent pregnancy is termed a corpus luteum of ovulation or a corpus luteum of the cycle.

On morphological grounds cetacean corpora lutea have been classified as everted, cavitate, meandrine, vesicular and non-vesicular (see Laws, 1961). Despite the earlier claims (e.g. Robins, 1954) and the fact that in at least several species most presumed corpora lutea of ovulation are smaller than those accompanying a definite pregnancy (Mackintosh and Wheeler, 1929; van Lennep, 1950; Robins, 1954; Laws, 1961; Sergeant, 1962; Best, 1967; Marsh and Kasuya, this volume), it seems unlikely that the corpus luteum of early pregnancy can be distinguished with certainty from one from a non-pregnant animal (Benirschke, Johnson and Benirschke, 1980).

Several workers including Harrison (1949), van Lennep (1950), Best (1967), Hirose, Kasuya, Kazihara and Nishiwaki (1970), Mossman and Duke (1973), Harrison *et al.* (1981) and Marsh and Kasuya (this volume), have observed two distinct types of gland cells in the corpora lutea of various cetaceans. These have sometimes been referred to as theca and granulosa lutein cells but, as Harrison (1949) pointed out, this classification cannot be verified without following the development of corpora lutea through several stages.

The corpus luteum persists throughout pregnancy in all cetaceans studied. There is also histological evidence that the activity of the corpus luteum changes during pregnancy, in at least some species (e.g. blue and fin whales (Mackintosh and Wheeler, 1929); sperm whales (Chuzhakina, 1963); *Phocena phocena* (Fisher and Harrison, 1970); *Stenella graffmani* [= *S. attenuata*] (Harrison *et al.*, 1972); *Globicephala macrorhynchus* (Marsh and Kasuya, this volume).

#### (5) Multiple corpora lutea

Pregnant cetaceans have been described with more than one active corpus luteum but only one foetus. This phenomenon is very rare in most species (Chittleborough, 1954; Laws, 1961; Sergeant, 1962; Ohsumi, 1965; Best, 1967; Gambell, 1968, 1972; Perrin *et al.*, 1976; Harrison *et al.*, 1981; Marsh and Kasuya, this volume), exceptions being the white whale (Brodie, 1972; Sergeant, 1973) and the narwhal (K. Hay, pers. comm., 1981). The relative functions of members of a set of multiple corpora lutea have not been studied. If they differ in size, all but the largest are called accessory corpora lutea. Strictly speaking, the term accessory corpus luteum should not be so limited. In the general mammalian literature, it is applied to any unruptured follicle which forms a corpus luteum irrespective of whether the female is pregnant, (Harrison and Weir, 1977). (See also Laws, 1961; Best, 1967; Marsh and Kasuya, this volume.)

#### (6) Corpus albicans

Regressing and regressed corpora lutea are now almost always referred to as corpora albicantia whether they are pigmented or not. Even though regression is essentially a continuous process, various cetologists have divided corpora albicantia into several categories to analyse the course of regression (e.g. Laws, 1958, 1961; Sergeant, 1962; Best, 1967; Gambell, 1968, 1972; Perrin *et al.*, 1976; Harrison *et al.*, 1981; Larsen, this volume; Marsh and Kasuya, this volume).

Several workers have separated the corpora albicantia observed in various cetaceans into two types (usually on histological grounds) and have suggested that one type might have developed from corpora lutea of ovulation, the other from corpora lutea of pregnancy (e.g. Peters, 1939; Sleptsov, 1940; van Lennep, 1950; Robins, 1954; Zemskiy, 1956; Ivashin, 1958; Hirose *et al.*, 1970; Fisher and Harrison, 1970; Zimushko, 1970; Harrison and Brownell, 1971; Harrison, Boice and Brownell, 1969; Harrison *et al.*, 1972; Collet and Harrison, 1981). The essential distinguishing feature of the two types is usually the amount of amorphous, relatively acellular, hyaline material present. The validity of this distinction has never been confirmed. Most workers who have studied the corpora albicantia from a large series of conspecifics (e.g.

Laws, 1961; Sergeant, 1962; Best, 1967; Gambell, 1968, 1972; Kasuya, 1972; Kasuya *et al.*, 1974; Perrin *et al.*, 1976; Harrison *et al.*, 1981; Marsh and Kasuya, this volume), have not managed to separate corpora albicantia of pregnancy from those of ovulation.

#### (7) Terms used to describe female reproductive status

(a) *Immature*: The female has no corpora lutea or corpora albicantia on her ovaries.

(b) *Pregnant*: The female has a live embryo/foetus in her uterus.

(c) *Lactating*: The female has active mammary glands producing milk. Some simultaneously pregnant and lactating females have been observed in most cetaceans for which a large series has been studied. These animals should be considered as pregnant in estimating the average length of the reproductive cycle.

(d) *Resting*: The (mature) female is neither pregnant nor lactating. As pointed out by Perrin *et al.*, 1977, this is a catch-all phrase which includes females truly resting, i.e. not ovulating because of being between cycles, those which have just ovulated but did not get pregnant, some with extremely small embryos missed in dissections, those which have recently aborted, and those which have prematurely terminated lactation due to the death of the suckling calf.

(e) *Post-reproductive/senescent*: The female either

cannot conceive or cannot sustain a pregnancy successfully because of age-related changes to her reproductive system. Marsh and Kasuya (this volume) present evidence for a post-reproductive or senescent phase in the ovaries of *Globicephala macrorhynchus* in which there appears to be no evidence of ovulation after age 40, when females have a life expectancy of 13 years. However, post-reproductive *G. macrorhynchus* are not infrequently lactating. Sergeant (1962) also observed a small percentage of such females in *G. melaena* as did Perrin *et al.* (1976) in *Stenella attenuata* and Perrin *et al.* (1977) in *S. longirostris*. As discussed by Marsh and Kasuya (this volume), it is difficult to be certain that an individual female is post-reproductive.

(f) *Post-partum and post-lactation oestrus*: Problems arise in the precise definition of such terms. The shortest times a female can recycle after parturition, cessation of lactation or indeed after unsuccessful oestrus and ovulation are not known for most cetaceans and are likely to be highly variable with individuals both in and between species. The incidence of such events is likely to be more significant in some species than others. It is proposed therefore that these terms be avoided unless specific evidence of timing can be referred to, such as in closely-observed captive animals, or animals where past reproductive history is clear from examination of the entire reproductive tract.

### Appendix C

#### SPECIMEN COLLECTION, PRESERVATION, STORAGE AND PREPARATION

The collection and subsequent examination of cetacean reproductive material is an essential part of the documentation of the species' life history parameters which, in turn, are an essential component of population models. Collection of reproductive material must be accompanied by the collection of earplugs, bullae or teeth for age estimation. The nature and extent of specimen collection will vary greatly with the conditions under which the work is done (e.g. single specimens, mass strandings, drive fisheries, factory ships or incidental kills in other fisheries), personnel available, facilities, etc. The following section is intended to serve as a guide and not as a final determination as to how the work should be done. Each investigator must select the protocol most appropriate for the specific needs of the research project. In addition, new and better techniques will become available from time to time.

##### (1) Collection

The size of the animal and its components will have a great effect on the material collected.

(a) *Females*. For small odontocetes, wherever possible, the entire reproductive tract should be collected and should include the complete vagina (this is obviously impractical for large whales). This technique preserves tissue orientation and lessens the chance of mis-labelling ovaries and the loss of small embryos and vaginal mucous plugs. The flat width of each uterine horn should be taken at the mid-point of each horn. If the animal is obviously pregnant the foetus can be removed and the horn subsequently measured. The ovaries and foetus may be weighed fresh, and it is important that this be noted for

subsequent analyses. A detailed comparison of fresh versus preserved weights has not been made. A section of each uterine horn (and vagina) should be taken if the entire tract is not collected.

The mammary glands should be examined and a tissue sample taken. Length, width and thickness of the glands can be measured, but this is often impractical. If thickness is measured, it should be at the thickest part of the gland or a fixed distance from a topographical landmark. The colour of the freshly cut gland should be noted, using a consistent scale (e.g. pink, pink-brown, brown). A milk sample should be collected when possible for nutritional, pollutant and parasitic examination. Ideally, the milk should be taken directly from the teat to avoid contamination. Alternatively it can be taken from the incised reservoir. The colour of the uncontaminated milk should be noted.

Vaginal smears may be taken from fresh animals. Results may vary with the location within the vagina from which the smear is taken. Collections should be from a consistent location or the specific location noted.<sup>11</sup>

(b) *Males*. The testes should be weighed and measured (length, width, and thickness when laying flat). In some smaller cetaceans, the testes can be taken intact, while in most cases only samples can be taken. It is important to note whether the testes were measured or weighed fresh or preserved, and with or without the epididymis. If only one testis is taken, it should be so noted and taken consistently from the left or right side.

<sup>11</sup> Editors' note. In captive bottlenose dolphins, contents of vaginal smears were not correlated with ovulation, but copulation could be confirmed by presence of sperm (V. L. Kirby, pers. comm.).

Samples of the testes should be taken at mid-length and include the core from small whales and both core and peripheral samples from large whales, to account for differential maturation. Epididymis samples can be taken at mid-length, but more sperm are likely to be encountered in the cauda (posterior) epididymis. The testes of most species have not been sampled to determine if there are areas of differential maturation. In any event, sampling sites should be noted and consistent. Smears can be taken from both the cut surfaces of the testes and the epididymis.

The activity of a testis can be determined most accurately through histology, but in general there also appears to be a good correlation between sperm production and the weight of the testis. Histologically, an active or recrudescing testis is characterized by the presence of meiosis and mitosis. This can be easily determined through a 'touch preparation,' in which a few tubules are teased out and touched to a slide. The specimen is then fixed in ether alcohol, stained with haematoxylin and eosin and examined for very dark cells indicative of meiosis. When a testis is actively producing sperm, the cellular associations characteristic of spermiogenesis (spermatogonia through spermatozoa) can be observed in histological sections and sperm can be seen in smears or teased preparations.

In some terrestrial mammals (e.g. lemurs) testis size can change dramatically with season, but some spermatozoa may be present even when the testes are considered inactive; sperm can remain in the tubules for a long time after initial production, but generally they are not of the same quality as more recently produced sperm.

## (2) Preservation

(a) *Fixatives.* The most widely used fixative is 10% neutral buffered formalin (NBF) or 10% sea-water formalin. Bouin's solution is the traditional fixative for embryological material and may be used for other specimens. Problems arise, however, in the identification of gross structures because of yellow staining by the fixative. A further problem with Bouin's solution is its relatively low power of penetration of tissues. Material fixed in formalin can be refixed in Bouin's (or other fixative) at a later time. Electron microscope (EM) material usually requires fixation in glutaraldehyde, but this is not usually practical when large numbers of animals are being processed. Specimens should be fixed within minutes of death for the best EM results.

Tissue samples should be on the order of one cubic centimetre, to permit rapid permeation of the specimen. Tissue-to-fixative volumes should be on the order of 1:10. Smaller volumes can be used if the fixative can be changed one or more times and the samples agitated. Tissue samples can be individually placed in perforated plastic tissue containers and remain there through most histological processing. Perforated plastic bags can be used to store all samples from one individual. Samples from several animals can be placed in a large container of fixative.

Gross specimens (e.g. large whale ovaries and whole testes) should be slit once longitudinally to ensure fixative penetration. Uterine horns can be injected with 10% NBF.

Containers holding several specimens should be

agitated to ensure the samples are not packed together and thus retarding fixation.

Alternative preservation methods include freezing and packing in dry-salt, although these will usually not yield adequate histological preparations.

Milk samples should be preserved by freezing. Formalin can be used if nutritional analyses are not done.

Smears can be adequately preserved by air drying. Specific spray fixatives are available.

(b) *Storage.* Formalin-preserved material can be stored indefinitely in tightly sealed containers kept in the dark, although storage for years may affect the quality of histological preparations due to hardening of the tissue. Some routine curation is necessary to prevent samples from being damaged from fluid loss. Addition of 59% (by vol.) glycerine can temporarily prevent specimen damage if fluid is lost.

Smears can be stored in slide boxes, without further attention until stained.

Five-percent (5%) formalin is adequate for the storage of thoroughly fixed material. Likewise, the tissue-to-fluid volume ratio can be reduced to about 1:5. Recent concern has been expressed, however, over the health and safety aspects of the use of formalin, which may be banned from usage in certain laboratories. Concensus was that once fixed in 10% NB formalin, specimens may be transferred to other less noxious preservatives for personnel safety. Alcohol was considered a possible alternative for some tissues, although tissue shrinkage might be a problem.

The use of heat-sealed plastic bags appears to be a superior method for long-term storage. A bag is constructed by heat-sealing one end of a piece of 'Lay flat' plastic tubing; the specimen, preservative and label are inserted, and the bag sealed. A second label can be sealed dry in an adjacent compartment. It is important that nonpermeable (polyester) plastic tubing be used.

Frozen samples can, of course, be stored in the frozen state. Containers should be tightly sealed to prevent oxidation ('freezer burn') and drying.

Samples for EM work must be removed from the fixative after about 24 hours and then stored in a buffer solution until further processing.

## (3) Preparation

Samples for histological examination are usually embedded in paraffin and stained with hematoxylin and eosin (H & E) after sectioning. Other stains (trichromes) are a matter of individual preference. H & E is the choice of pathologists, as it allows for structure identification in poorly preserved or autolyzed samples. Smears can be stained appropriately and a cover-slip mounting medium applied.

Prior to cutting an intact specimen (especially ovaries), it should be photographed in more than one plane. The resulting working prints may then be used to document the location(s) of any part sliced and subsequently removed for histological examination. Further photographs of cut surfaces, particularly of ovaries, prior to the dehydration and embedding process are also useful; it is often the case that an impression gained macroscopically is different from the final histological picture. Photos should include a scale and relevant identification numbers.

Ovaries have been sliced (in order to count corpora) at varying thicknesses. Certainly thinner slices are necessary for small cetacean ovaries than for large cetaceans, where 2–5-mm is adequate, given the relative sizes of the structures. Sections should be left attached along one side of the ovary where possible, to preserve sequence and orientation. If sections are cut too thin, they will not lay

flat during embedding if a complete histological section is subsequently required.

It is important to save ovaries and any other material that may require re-examination and/or reinterpretation. It is impossible to corroborate an interpretation if the material has been discarded.