Reproductive Parameters of Dolphins and Small Whales of the Family Delphinidae

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ABSTRACT

The purposes of this review are to describe and critique methods used to estimate reproductive parameters, to summarize estimates in the literature and to examine patterns in the estimates and their implications. Reviewed are gestation period, fetal growth rate, size at birth, size and age at attainment of sexual maturity, average size and age of adults, maximum size, asymptotic length, ovulation rate, pregnancy rate, calving interval, length of lactation, weaning age, length of "resting" period, age and sex structure, and birth rates. Also discussed are the effects on the estimates of seasonality, schooling segregation, geographical variation and exploitation and the relationships between parameters.

INTRODUCTION

Many populations of dolphins and small whales are exploited directly or incidentally (IWC, 1976–83) and must be assessed and managed. Most of the approximately 32 species (Mitchell, 1975) are poorly known, and the published information on them is scattered in a diverse and often obscure literature. For some species the literature contains widely varying estimates of parameters, a matter of some concern when scientists are asked to provide advice for management (e.g. see Smith, 1983).

The purposes of this review are several: to describe and critique methods used to estimate reproductive parameters, to summarize estimates in the literature and to examine patterns in the estimates and their implications.

It is not the purpose of this paper to review reproductive morphology, physiology, behavior or pathology, except to the extent that they are immediately relevant to estimation of parameters used in stock assessment and management. Broad reviews of reproductive morphology and function have been presented by Harrison (1969), Harrison, Brownell and Boice (1972) and others. Other relevant papers are contained in this volume.

METHODS

In assembling parameter estimates we surveyed as much of the literature as was possible under the time constraints for publication of this volume. We do not believe that we have missed any major references and, while some length data may have been missed, the ranges of values presented here should be definitive of the present state of knowledge of the delphinids. We did not include data from the popular or semi-popular literature unless an obviously measured value was specified and the source of the information could be determined. We did not include lengths identified as estimates, but undoubtedly some of the supposed measurements are in fact estimates. We took considerable pains to avoid inclusion of the same data more than once but there likely is some duplication. We have taken into account information in other papers in this volume. However, because of considerations of timing this was not possible in all cases.

Body length can be measured in several ways: from the tip of the upper jaw to the notch in the flukes, or to the posteriormost extension of the flukes; in a straight line, or over the curvature of the body. We've tried to include only linear beak-tip-to-notch lengths, but some of the included lengths were probably taken in other ways, possibly contributing artificially to the range of length.

For derived estimates, such as average length of adults, we have included published estimates or have calculated the estimates ourselves where only raw data were published or for samples pooled across sources. We calculated standard deviations where sample size was adequate ($\geqslant 25$).

Where specific identification was equivocal, we have omitted the data. It is possible that some early strandings of pilot whales in the eastern North Atlantic referred to *Globicephala melaena* were actually of *G. macrorhynchus* (see Duguy, 1968). Although two species of spotted dolphin (*Stenella* spp.) probably exist in the Atlantic (Perrin, Mitchell and van Bree, 1978), we included data only for specimens referred to *S. plagiodon*, because of the uncertain identity of animals referred to other nominal species (*S. frontalis* and *S. attenuata*).

PARAMETERS

Gestation Period and Fetal Growth Rate

Background and estimation methods

Gestation period is one of the least variable reproductive parameters on a within-species basis in delphinids and in mammals in general (Kiltie, 1982). Estimation of the gestation period is important to stock assessment and management because it comprises one segment of the calving interval. Fetal growth rates are important in determining the age of fetuses and in estimation of the length of gestation.

Estimates of gestation period, of some type, exist for 13 of the 32 delphinid species. Data of varying amounts and quality have been available for producing these estimates. Fetal growth rate has been estimated in only some of these cases. At least seven different methods have been employed. We group them here into three major categories: (*a*) direct observational estimates, (*b*) statistical

Table 1

Outline of the methods used to estimate gestation period for small cetaceans, with species for which the methods have been used

	DIRECT	
I.	Live captive	
	Tursiops truncatus	*T. aduncus*
II.	Embryology	
	Orcinus orca	*Lagenorhynchus actus*
	STATISTICAL	
III.	Huggett and Widdas/Laws	
	a. Within-population	
	Stenella attenuata	*Globicephala melaena*
	Sotalia fluviatilis	
	b. Comparative	
	Pseudorca crassidens	*Berardius bairdii*
	Pontoporia blainvillei	
IV.	Sacher and Staffeldt	
	Stenella longirostris	*T. truncatus*
V.	Comparative G vs L_n	
	a. Other delphinids	*S. longirostris*
	b. Human growth curve	*G. melaena*
	OTHER	
VI.	Visual inspection of data	
	L. acutus	*O. orca*
	Delphinus delphis	*S. coeruleoalba*
VII.	Not reported	
	O. orca	*S. attenuata*
	G. melaena	*D. delphis*
	G. macrorhynchus	*L. acutus*
	P. crassidens	*L. obliquidens*
	T. truncatus	

estimates from series of specimens, and (*c*) 'other,' mostly non-rigorous methods (Table 1).

A. Direct observation

Captive animals. Estimates of this type are available for *Tursiops truncatus* only. The dates of conception and birth were observed for tank-held individuals. There are actually only a very few cases where conception date was known, with a larger series of observed births. Similar data may exist for other delphinids, but we did not find them.

Embryology. Guldberg and Nansen (1894) estimated gestation periods for *Orcinus orca* and *Lagenorhynchus acutus.* They gave detailed descriptions of the state of development of 'representative'-sized fetuses with collection dates and then inferred gestation periods qualitatively. This may have been an accurate technique, but Guldberg and Nansen's estimates have not to date been verified by direct observation or by statistical estimates based on data series.

B. Statistical estimates

All estimates in this category utilize standard regression techniques. Most require discrimination between modes in the distribution of fetal sizes by collection dates.

Method of Hugget and Widdas (1951)/Laws (1959). This the most commonly used technique for mammals in general, including delphinids. It utilizes the empirical concept that fetal growth in length (L) or cube root of weight ($W^{\frac{1}{3}}$) is directly related to time, and that two observable phases occur: a linear phase for most of the period, preceeded by a briefer nonlinear phase (Fig. 1).

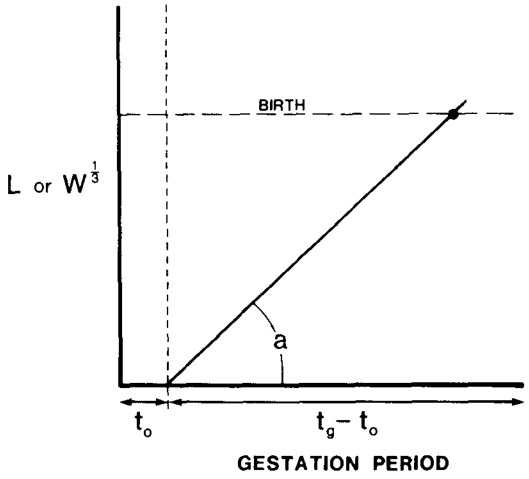

Fig. 1. Estimation of gestation period (t_g) and fetal growth rate (a) by the method of Hugget and Widdas (1951). L is total length, W is body weight, t_0 is the early 'nonlinear' phase of growth.

In estimating the total gestation period the gestation time is divided into two phases. One phase (t_g–t_0) extends to birth from the point where a straight line fitted to the data intersects the time axis. The other phase (t_0) is from conception to the intersection. The linear phase is usually defined by a least-squares fit of time to modal points in L or $W^{\frac{1}{3}}$. The slope of the linear phase a is termed the fetal growth velocity. There is some indication that it is species-characteristic and varies with other measurable characters. The variables a and t_0 are not the same for L and $W^{\frac{1}{3}}$, and the conversion from one set of units to the other is poorly defined. Work by Frazer and Hugget (1973) indicates that, at least for a, the relationship is *not* simply linear (i.e. not convertible by a common 'factor').

Estimation of (t_g–t_0) requires a dependable estimate of length at birth. This in turn requires a series of specimens in sizes bracketing the true birth size. Length at birth can be estimated by interpolation as shown for *Stenella attenuata* by Perrin, Coe and Zweifel (1976) (also see below). In some cases a mean is calculated, in others the median is used. Both should be adequate if the real distribution of points is symmetrical. This method also requires an accurate separation of modes in size in a large data series. When modes are not distinct, this is undoubtedly a poor method. In some cases individuals are plotted rather than modes. This should be valid if breeding is distinctly seasonal.

Estimation of the early phase t_0 is not straightforward or well defined. All applications refer back to Hugget and Widdas' (1951) simple breakdown of the proportion of gestation time in t_0 by length of (t_g–t_0). For example, for (t_g–t_0) > 400 days, they said that t_0 should be approximately $0.1 \times t_g$. Laws (1959) defined the relationship for length as being about 90% of that for weight. Both rules of thumb are arbitrary. Hugget and Widdas proposed the original scheme based on data from only seven species of terrestrial mammals. They extrapolated outside the limits of their data for the extreme values (t_g > 400). Gestation periods for many delphinids lie outside the data range used by Hugget and Widdas.

A more precise definition of t_0 is needed. As

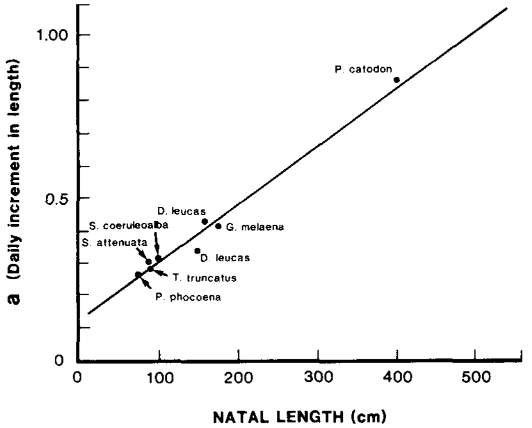

Fig. 2. Interspecific relationship between fetal growth rate (a) and natal length, from Kasuya (1977).

mentioned above there appears to be a reasonably consistent relationship between *a*, (the slope of the linear phase) and size at birth. As shown in Fig. 2 (from Kasuya, 1977), the relationship appears to be linear, although the sample size employed is not large.

This relationship has been employed to estimate *a* for *Pseudorca crassidens* (Purves and Pilleri, 1978) and the non-delphinids *Pontoporia blainvillei* (Kasuya and Brownell, 1979) and *Berardius bairdii* (Kasuya, 1977). With this comparative slope estimate and an estimate of length at birth, the Hugget and Widdas procedure can be carried out. Unfortunately the large data series required for direct estimation of *a* is also generally required for a good estimate of natal length, so this relationship is of limited use.

Method of Sacher and Staffeldt (1974). The second type of statistical estimation is based on an empirically defined relationship between the duration of gestation and brain weight at birth, the ratio of birth to adult brain weight, and litter size. Sacher and Staffeldt examined a data series on 91 species of eutherian mammals. Variables included in the multiple-regression analysis were the above, plus (1) body weight at birth and (2) ratio of birth weight to adult body weight. The body-weight variables were not significantly related to gestation period. In applying this method one simply uses natal brain weight and litter size in the multiple-regression model. Our reservations about this procedure include the following:

1. Only two cetacean species were included in the 91 species from which the model was derived (*Tursiops truncatus* and *Phocoena phocoena*).
2. The use of data across many orders is useful in defining general patterns but probably does not provide good prediction within a particular order.
3. Use of ratios which include another predictor variable in the model is of questionable validity as a statistical technique.
4. Variables included in the original study were limited in scope; but R^2 was high (> 0.9).

Comparative G vs L_n. The third statistical approach utilizes the apparent relationship between duration of gestation (G) and size at birth (L_n) for other species within the Delphinidae (Fig. 3). Perrin, Miller and Sloan (1977) utilized this for *S. longirostris*. There was a fairly good fit by a straight line, but as with the other comparative relationship, the sample size available was not large.

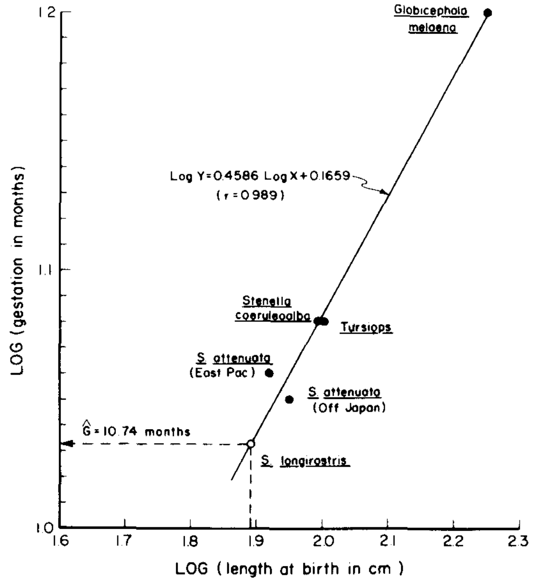

Fig. 3. Interspecific relationship between duration of gestation and size at birth, in four delphinid cetaceans, with extrapolation to predict length of gestation in the eastern spinner dolphin (from Perrin *et al.* 1977).

C. Other methods

These are generally visual fits to apparent modes in length frequencies or in frequencies of parturition or conception, e.g. *L. acutus* (Sergeant, St Aubin and Geraci, 1980) and *D. delphis* (Kleinenberg, 1956). This type of method may be a good first approximation for small data series but should be replaced by more quantitative, repeatable methods where possible.

Lastly, for nine species, estimates of gestation period were published with no accompanying information on data methods or sources.

Available estimates

The published estimates of gestation period range from about 10 months to over 16 months (Table 2). As discussed above, there appears to be a relationship between length of gestation, fetal growth rate and birth size or brain weight at birth, such that larger delphinids (e.g. *Orcinus* and *Globicephala*) have longer gestation periods than do the smaller forms (*Stenella* or *Lagenorhynchus*).

There is an apparent contradiction between the results of Sacher and Staffeldt (1974) and those of the other statistical studies discussed here. They found no significant relationship between body size and gestation period. It would be of interest to pursue this disparity further, since the majority of comparative estimates (not just for delphinids) appear to utilize the body size/gestation relationship in some way.

Table 2

Gestation periods reported for delphinid cetaceans. Method types are defined in Table 1

Species	Estimate (months)	Method type	Source	Estimate (months)	Method type	Source	Estimate (months)	Method type	Source
Sotalia fluviatilis	10.0–10.3	III	Best and da Silva, 1984						
Tursiops truncatus	12	I	Essapian, 1963	12	I	McBride and Kritzler, 1951	12	I	Tavolga and Essapian, 1957
	13	IV	Perrin *et al.*, 1977						
('*aduncus*')	11.5–12	I	Ross, 1977						
Globicephala melaena	15.2	III	Sergeant, 1962	16.2	V	Sergeant, 1962	15.7	III	Frazer and Hugget, 1973
	15–16	VII	Harrison, 1969						
G. macrorhynchus	12	VII	Lowry, 1974						
Stenella attenuata	11.5	III	Perrin *et al.*, 1976	11.2	III	Kasuya *et al.*, 1974	9–10	VII	Harrison, 1969
S. longirostris	10.7	Va	Perrin *et al.*, 1977	9.5, 10.5	IV	Perrin *et al.*, 1977			
S. coeruleoalba	12	VI	Kasuya, 1972						
Delphinus delphis	10–11	VI	Kleinenberg, 1956	10	VII	Tomilin, 1957	11	VII	Harrison, 1969
	10	VII	Mal'm, 1932						
Pseudorca crassidens	15.5	III	Purves and Pilleri, 1978	11–12	VII	Harrison, 1969			
Orcinus orca	12–16	VI	Nishiwaki and Handa, 1953	12	II	Guldberg and Nansen, 1894	12	VII	Fraser, 1937
	12	VII	Grieg, 1889	11–12	VII	Harrison, 1969	12	VII	Christensen, 1984
'best'	15	I, VII	Perrin (ed.), 1982						
Lagenorhynchus acutus	10	II	Guldberg and Nansen, 1894	10	VII	Fraser, 1937	11	VI	Sergeant *et al.*, 1980
	11–12	VII	Geraci and St. Aubin, 1977						
L. obliquidens	10	VII	Harrison, 1969						
			(Comparative estimates for other odontocetes)						
Phocoena phocoena	11	III	Laws, 1959	9	VII	Harrison, 1969			
Pontoporia blainvillei	11	III	Kasuya and Brownell, 1979	10.5–12	Va	Kasuya and Brownell, 1979			
Berardius bairdii	17	V	Kasuya, 1977	10	VII	Harrison, 1969			
Delphinapterus leucas	12	VII	Vladykov, 1944	14	III	Laws, 1959			
Physeter macrocephalus	16	III	Laws, 1959	16–17	VII	Harrison, 1969			

Size at Birth

Estimates of size at birth are used in estimating the length of gestation and the time of birth. They are also the starting point for growth curves and ultimately contribute to estimates of the reproductive capacity of a population.

There are two basic categories of methods used to estimate length at birth. One quantitative method which has been employed for delphinids is termed '50% interpolation' in Table 3. In this method, the percentage of specimens which are postnatal is plotted for length categories or for length modes. The point on the length axis which corresponds to 50% postnatal from a linear regression is defined as the estimate of length at birth. The basic assumptions of the method are that (1) pregnant females (i.e. fetuses) and calves are equally available to the sampling procedure used, (2) both suffer natural mortality at the same rate, (3) naturally born calves are accurately distinguished from aborted, near-term fetuses, and (4) the sample size is adequate.

A second quantitative method used to determine size at birth is calculation of the mean length in a sample of apparently newborn calves. This method assumes that newborn calves are easily distinguishable from slightly older individuals. It will usually overestimate size at birth, especially if the calving season is protracted.

The other category of methods can be roughly termed 'qualitative' in that they don't use statistical techniques. One common method is to examine a relatively small series of fetuses and newborn calves, note the lengths and qualitatively infer a likely intermediate value for length at birth. Another is to use the length of the smallest postnatal specimen. (See Appendix 1 for smallest calf and largest fetal lengths reported.) For a number of other populations the methods used to arrive at the reported birth length were not reported. There is a total of 28 estimates available for 14 of 32 delphinid species (Table 3).

Of the methods discussed, the 50%-interpolation method is preferable. The assumptions of the method should be closely examined for each situation, however. Hohn and Hammond (1983) have discussed the basic methods for estimating length at birth in detail.

Size and Age at Attainment of Sexual Maturity

Age at attainment of sexual maturity is an important parameter in stock assessment because it is thought to vary with exploitation, as part of the density-dependent response that theoretically yields a net reproductive rate greater than zero (Smith, 1983). Such change has not been observed but it has been inferred to have occurred in some

Table 3

Body lengths at birth reported for delphinids

Species and region	Length at birth (cm)	Method	Source
Sotalia fluviatilis	75	Qualitative interpolation	Best and da Silva, 1984
Stenella coeruleoalba			
(Japan)	99.8	50% interpolation	Kasuya, 1972
(Japan)	100	50% interpolation	Miyazaki, 1977
S. attenuata			
(Japan)	89	Mean length of 'newborns' in drive fishery	Kasuya *et al.*, 1974
(E. trop. Pacific)	82.5	50% interpolation	Perrin *et al.*, 1977
S. longirostris			
(E. trop. Pacific)	77	50% interpolation	Perrin *et al.*, 1977
Delphinus delphis			
(E. trop. Pacific)	81.3	50% interpolation	Hui, 1977
(E.N. Pacific)	79.0	50% interpolation	Hui, 1977
(Black Sea)	80–90	Not reported	Tomilin, 1957
(All)	105	Not reported	Scott, 1949
Globicephala melaena			
(W.N. Atlantic)	177	50% interpolation	Sergeant, 1962
G. macrorhynchus			
(W. Pacific)	135–146	Range in size of 'newborns'	Yonekura *et al.*, 1980
(S. Africa)	140	Qualitative inference from small sample	Ross, 1979
Lagenorhynchus acutus			
(W. Atlantic)	110	Method not reported	Sergeant *et al.*, 1980
L. albirostris			
(E.N. Atlantic)	125	Method not reported	Tomilin, 1957
Orcinus orca			
(Japan)	276	Smallest postnatal specimen	Nishiwaki and Handa, 1958
(N. Atlantic)	210	Qualitative inference from fetal and calf lengths	Jonsgård and Lyshoel, 1970
(NE. Pacific)	246	Direct observations of five stranded newborn	Bigg, 1982
(N. Atlantic)	208–220	Qualitative extrapolation from fetal development	Guldberg and Nansen, 1894
(All?)	210–250	Not reported	Tomilin, 1957
Pseudorca crassidens			
(All?)	193	Mean length youngest calves	Purves and Pilleri, 1978
(S. Africa)	160	Qualitative inference from few specimens	Ross, 1979
Tursiops truncatus			
(W.N. Atlantic)	100	Not reported	Sergeant *et al.*, 1973
(W.N. Atlantic)	115	Average length of 'true neonates'	Hohn, 1980
(All)	980–1260	Range of reports	Harrison, 1969
(?)	130	Not reported	Scott, 1949
(S. Africa '*aduncus*')	838–1120	Range of eight specimens	Ross, 1977
Sousa chinensis			
(S. Africa)	100	Qualitative inference from specimen series	Ross, 1979
Grampus griseus			
(All?)	150	Not reported	Tomilin, 1957
(Japan)	110–120	Qualitative inference from specimen series	Mizue and Yoshida, 1962

instances, based on comparison of populations of one species (*Stenella longirostris* – Perrin and Henderson, 1984) or populations of two species (*S. coeruleoalba* and *S. attenuata* – Kasuya, 1976) with different histories of exploitation.

Knowledge of size at maturation is useful because it allows estimation of maturity status of animals for which only length data are available.

Definition and criteria of sexual maturity

For females, the most accepted definition of sexual maturity is that the animal has ovulated at least once, as evidenced by presence of at least one corpus luteum or corpus albicans in the ovaries. The assumption is made that scars of ovulation (whether or not followed by pregnancy) remain visible in the ovaries indefinitely (see Perrin and Donovan, 1984). An additional assumption commonly made is that presence of any scar or body in the ovaries means that ovulation has occurred (e.g. Perrin *et al.* 1976). This is not a valid assumption, because some scars may denote non-ovulatory events, e.g. lutealization of unerupted Graafian follicles (Perrin and Donovan, 1984).

For males the question of what constitutes sexual maturity is more complex. Several criteria have been used in population studies. Presence of spermatozoa in the center of the testis was employed by Kasuya, Miyazaki and Dawbin (1974). Miyazaki (1977) defined immature, pubertal and mature males as those having, respectively, no spermatozoa, both spermatogonia and spermatocytes, and spermatozoa in the center of the testis. Perrin *et al.* (1976) defined puberty and maturity based on presence of spermatogenesis in the center of the testis, rapid change in diameter of seminiferous tubules, and presence of spermatozoa in the epididymis. Perrin *et al.* (1977) and Perrin and Henderson (1984) defined several levels of sexual 'maturity' based on presence of spermatogenesis and amount of sperm in the epididymis. Sergeant (1962) defined the onset of 'functional' maturity as the point at which gross examination of the epididymis shows presence of seminal fluid, which occurs at testis weights somewhat greater than those at which spermatogenesis can be detected histologically. Other workers have used various combinations of these criteria; this, as well as the use of various estimation procedures - described below - must be kept in mind when making comparisons of estimates of size or age at attainment of maturity across species or across studies.

An assumption made in the use of presence of sperm in the epididymis as a criterion of sexual maturity is that adult males produce sperm on a constant basis. This assumption is not valid, as it has been shown in at least some species that males may enter a resting phase, during which testis size decreases and sperm are absent from the epididymis (Hirose and Nishiwaki, 1971; Perrin and Henderson, 1984; Collet and St Girons, 1984).

Estimation methods

Length and age at attainment of maturity in females have been estimated in various ways:

(*a*) *The mean length or age when 50% are mature*, by inspection of data tabulated by length or age interval (Mayarova and Danilevskiy, 1934; Sergeant, 1962) or by estimation of the 50%-mature length (or age) from a line fitted to a plot of % mature on length or age intervals (Kasuya, 1972; Perrin *et al.*, 1976; Perrin *et al.*, 1977). Perrin *et al.* (1976) noted that an estimate obtained in this way is an overestimate, because some of the smaller mature animals are those that have stopped growing at a shorter-than-average length, yielding an asymmetrical (left-skewed) maturity-length curve.

(*b*) *The length or age at which the number of smaller or younger mature females equals the number of larger or older immature females.* Kasuya *et al.* (1974) pointed out that an estimate by this method is biased downward, because it does not take into account the effect of natural mortality in reducing the relative number of longer or older animals.

(*c*) *The length or age corresponding to the age or length at which 50% are mature*, taken from an age-length key or growth curve (Kasuya *et al.*, 1974; Perrin *et al.*, 1976).

(*d*) *The average greatest length at which females have not yet ovulated*, estimated by back-extrapolation to the origin of a body-length/corpus-count curve (Perrin *et al.*, 1976). Average age at maturity can then be estimated from a length/age curve.

(*e*) *The length at first conception*, estimated in gravid females with only one ovarian corpus (a corpus luteum). A length increment (taken from a length/age curve) corresponding to the estimated time since conception as estimated from the length of the fetus (taken from a fetal length/age curve) is subtracted from body length (Perrin *et al.*, 1976). Average age at maturity can then be taken from a length/age curve. This is a probable underestimate, because it is based only on females that become pregnant at the first ovulation.

DeMaster (1984) has examined the properties of these estimates in more detail.

Average length and testis weight at age at attainment of sexual maturity in males have been estimated by some of the same methods used for females (*a*, *b* and *c* above). In more recent studies, e.g. Perrin *et al.* (1977) and Perrin and Henderson (1984), values have been estimated for several indices of 'maturity' (described above), with the caution that not enough is known about the breeding systems of these animals at any particular length, age, testis size, etc., to say that they are 'socially mature' in the sense of Best (1969a).

Available estimates

Estimates of age at attainment of sexual maturity are available for 11 of the roughly 32 species of delphinids (Table 4). They range from 3 (*Delphinus delphis*) to 16 years (*Orcinus orca*). (The former is almost certainly an underestimate, due to the effects of schooling segregation – see discussion below.) In many cases only a fairly broad range of estimates is available (e.g. 8–14 years for *Pseudorca crassidens*), which highlights the rudimentary state of knowledge of the life histories of most of the delphinids. Additional data on testis weight (of smallest 'adult' testis and of largest testis) and on body length (largest sexually immature and smallest mature animals) are included in Appendices 2 and 1, respectively. It should be noted that many species vary in these parameters from region to region (discussed below).

Average Size and Age of Adults

Average adult size and age are other parameters that may change under exploitation, with changes in age structure of the population caused by selective harvest or by increased reproductive rates. Average size and age are also useful parameters in cross-species comparisons and deductive modeling (discussion below). Available estimates of average adult length and age are given in Appendices 3 and 4, respectively.

Maximum Size and Age and Asymptotic Length

These parameters are useful in deductive modeling of life history. Asymptotic length is important in any model of growth. Values of maximum size based on adequate samples ($n \geqslant 25$) are available in the literature for about half the delphinid species (Appendix 1). The wide geographical variation apparent in some species is discussed below. Maximum ages based on large samples are available for only a handful of species (Appendix 4) and in many cases are expressed in terms of dentinal or cemental growth-layer groups (GLGs, terminology of

Table 4

Estimates of average length and age at attainment of sexual maturity and ages of oldest immature and youngest immature for delphinids. Sample sizes in parentheses; values rounded off to nearest year (y) or GLG – terminology of Perrin and Myrick 1980 – (G)

Species and region (stock in parentheses)	Average length at attainment of sexual maturity		Average age at attainment of sexual maturity		Oldest immature animal		Youngest mature animal		Source
	Male	Female	Male	Female	Male	Female	Male	Female	
Steno bredanensis									
W. North Pacific	—	—	—	—	—	—	14G (9)	17G (9)	Miyazaki, 1980
Peponocephala electra									
W. South Pacific	—	—	—	—	3G (1)	4G (2)	7G (3)	12G (1)	Bryden *et al.*, 1977
Pseudorca crassidens									
E. North Atlantic	396–457	366–427	8–14y	8–14y	—	—	—	—	Purves and Pilleri, 1978
W. North Pacific	—	380–399	—	—	—	—	—	—	Kasuya and Izumisawa, 1981
Orcinus orca									
E. North Atlantic	~ 579	457–488	~ 16y	~ 10y	—	—	—	—	Christensen, 1982; Jonsgård and Lyshoel, 1970
Globicephala melaena									
W. North Atlantic	490	365	12y	6–7y	15y (13)	6y (5)	11y (19)	5y (12)	Sergeant, 1962
G. macrorhynchus	—	380–390	—	—	—	14G (2)	12G (2)	11G (1)	Ross, 1979
Lagenorhynchus obliquidens									
E. North Pacific	170–180	—	—	—	—	—	—	—	Harrison *et al.*, 1972
L. obscurus									
E. South Atlantic	—	—	—	—	—	—	—	18y	Best, 1976
L. actus									
W. North Atlantic	230–240	201–222	—	—	—	12y (6)	—	6y (26)	Sergeant *et al.*, 1980
Tursiops truncatus									
Both coasts of Florida	245–260	220–235	~ 11y[1]	~ 12y[1]	20y (10)	14y (11)	12y (6)	9y (17)	Harrison *et al.*, 1972; Leatherwood *et al.*, 1978; Sergeant *et al.*, 1973
S.W. Indian Ocean ('*aduncus*')	210–240	213–230	9–11G	—	4G (7)	4G (6)	9G (11)	10G (6)	Ross, 1979
Grampus griseus									
S.W. Indian Ocean	—	—	—	—	3G (4)	5G (4)	—	> 9G (1)	Ross, 1979
Stenella longirostris									
Gulf of Mexico	~ 190	~ 188	—	7–10G	> 8G (3)	> 11G (7)	> 9g (8)	> 8G (4)	Mead *et al.*, 1980
E. trop. Pac. (eastern)	160–170	164	6–9y	4–5y	8–9y (106)	6–9y (94)	5–7y (106)	3–5y (153)	Perrin *et al.*, 1977
E. trop. Pac. (n. whitebelly)	165–170	167	6–8y	4–6y	11–16y (48)	7–11y (37)	4–5y (52)	3–4y (150)	Perrin and Henderson, 1984
S. coeruleoalba									
E. trop. Pacific	195–200	—	—	—	—	—	—	—	Gurevich and Stewart, 1979
W. North Pacific	219	216	9y	9y	12y (70)	13y (126)	7y (222)	5y (541)	Miyazaki, 1977
S.W. Indian Ocean	210–220	—	—	—	13+G (5)	3G (1)	12+G (2)	7G (2)	Ross, 1979
S. attenuata									
E. trop. Pac. (offshore)	~ 195	181	11G	8G	13G (55)	11G (100)	7G (42)	7G (209)	Perrin *et al.*, 1976
W. North Pacific	194	182	12y	9y	16y (81)	12y (69)	8y (49)	8y (124)	Kasuya, 1976; Kasuya *et al.*, 1974
Delphinus delphis									
Black Sea	170–180	150–170	3y	(a) 4y (b) 2y	—	—	—	—	Kleinenberg, 1956; Kleinenberg and Klevezal', 1962; Mayarova and Danilevskiy, 1934; Sleptsov, 1941
E. North Atlantic	200	190	5–7G	6–7G	—	—	—	—	Collet, 1981
E. trop. Pac. (cent. trop.)	200	—	6–7G	—	—	—	—	—	Gurevich and Stewart, 1978; Oliver, 1973
E. North Pacific	—	—	7–12y	—	12y (21)	14y (9)	9y (10)	8y (19)	Hui, 1977
S.W. Indian Ocean	—	—	—	—	12G (3)	8G (6)	11+G (2)	10G (1)	Ross, 1979

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[1] From N.E. Florida.

Perrin and Myrick, 1980) that have not yet been calibrated to real time. The greatest ages reported in terms of years are for *Stenella attenuata* (40 years for males and 46 years for females) and in GLGs for *Peponocephala electra* (47 GLGs for males).

Adequate estimates of asymptotic length are available for even fewer species (Appendix 3). In most cases it has been estimated simply as the average length of physically mature specimens (those in which the vertebral epiphyses are fused to the centra and which are presumed to have stopped growing in length). In cases where the authors presented length data for physical maturity but did not estimate asymptotic length, we carried out the calculation and included the value in Appendix 3.

Perrin *et al.* (1976) estimated asymptotic length in *Stenella attenuata* as the average length of specimens in which the pulp cavity of the tooth was occluded. They used this estimate in fitting a Gompertz model of growth to their data. In similar development of a growth model, Perrin *et al.* (1977) estimated asymptotic length for *S. longirostris* (eastern form) as the average length of animals with 13 or more dentinal GLGs. Kasuya (1976) estimated asymptotic length in *S. attenuata* and *S. coeruleoalba* (later revised upward by Miyazaki, 1977) as the length at which growth rate levels off, based on growth curves fitted to length/age data by eye. Perrin and Henderson (1984) estimated asymptotic length for the northern whitebelly form of *S. longirostris* with iterative fits of Gompertz models to age/length data. This last method involves the fewest assumptions and is probably the most appropriate of those discussed here, providing that the sample includes adequate numbers of older animals.

Ovulation Rate

Background and estimation methods

The ovaries of cetaceans are unusual in that scars (corpora albicantia, or CAs) resulting from ovarian events persist for years and probably indefinitely in at least some species. Early on, it was thought by some workers (e.g. Sleptsov, 1941) that CAs persist indefinitely in all delphinids, that they result only from regression of corpora lutea (CLs) of pregnancy, and that there is never more than one CL per pregnancy. This supposedly resulted in a permanent record of the number of pregnancies experienced by a particular female. The potential value of such a record, coupled with accurate age determination, in modeling population dynamics for stock assessment and management is obvious, but more recent research has shown that the genesis and significance of ovarian scars are more complex than earlier thought (see sections II A and B and Appendix B of Perrin and Donovan, 1984). CAs do apparently persist indefinitely in at least some species, e.g. *Globicephala macrorhynchus* (Marsh and Kasuya, 1984) and perhaps *G. melaena* (Sergeant, 1962). In *Tursiops truncatus*, CAs resulting from several successive infertile ovulations in females just entering sexual maturity may be resorbed (Harrison *et al.*, 1972). In *Stenella* spp. (*S. attenuata, S. longirostris* and *S. coeruleoalba*) the data are equivocal. Some apparently senescent females have withered ovaries containing fewer CAs than do the ovaries of some other younger females still reproductively active, indicating that some CAs may eventually be resorbed, or at least not detected with the methods used to examine the ovaries in most studies (Perrin *et al.*, 1976; 1977; Kasuya, 1976; Perrin and Donovan, 1984). CAs of infertile ovulation may be more likely to be resorbed than those of pregnancy (Harrison *et al.*, 1972). In any case, for most delphinids there is no assurance that the CAs represent a complete history of ovarian activity.

All CAs do not represent pregnancies; some are the result of regression of CLs of infertile ovulation (Harrison *et al.*, 1972; Benirschke, Johnson and Benirschke, 1980). Although CAs of pregnancy may be more likely to persist indefinitely than those of simple ovulation, there is the problem of distinguishing between the two types of CAs. Some workers (e.g. Ivashin, 1984) maintain that this can be done based on histological criteria, but the balance of scientific opinion holds that CAs of pregnancy cannot be distinguished from those of infertile ovulation with present knowledge (Perrin and Donovan, 1984).

There may be more than one CL per pregnancy. Multiple CLs are common in some odontocetes (e.g. monodontids, Brodie, 1972) but rare in delphinids (loc. cit.).

Although ovarian scars do not provide a reliable record of fecundity, they are, at least for younger animals, a relative index of ovarian activity, i.e. estrus and ovulation, and thus potentially are still valuable in characterizing the structures, breeding systems and dynamics of populations. The somewhat controversial question of spontaneous vs induced ovulation is relevant to interpretation of CAs and estimation of ovulation rate. Harrison (1969) and Harrison *et al.* (1972) concluded that some delphinids (e.g. *Globicephala melaena*, *Pseudorca crassidens*, and perhaps *Stenella* spp. and *Lagenorhynchus obliquidens*) are probably spontaneous ovulators, but that others, in particular *Tursiops truncatus*, are reflex ovulators, i.e. require copulation and/or presence of a mature male to trigger ovulation. This and similar conclusions by Saayman and Taylor (1977) and Ross (1977) are based mainly on data for captive animals, i.e. observations that the ovaries of some captive females that have not been kept with adult males contain very few or no CAs despite having been of adult size and age for several years. In view of more recent work, however, it seems likely that these low rates or absence of ovarian activity may be related to other aspects of captivity. Longitudinal monitoring and experimentation have now shown clearly that both *Delphinus delphis* and *Tursiops truncatus* in captivity are spontaneous, albeit sporadic, ovulators (Kirby and Ridgway, 1984), and results of analyses of ovaries of *Stenella attenuata* and *S. longirostris* suggest that these dolphins ovulate spontaneously in the wild (Benirschke *et al.*, 1980), perhaps with more regularity than observed for other species in captivity. This endogenicity and regularity makes corpus-count data from wild populations potentially more valuable in modeling than would otherwise be the case.

Another important consideration in estimating ovulation rate from corpus-count data is that of variation with age. Models of ovulation rate that employ a linear fit to corpus-count/age data (e.g. Kasuya, 1972, for *Stenella coeruleoalba*; Kasuya, 1976, for *S. coeruleoalba* and *S. attenuata*) assume no change in ovulation rate with age, but these linear fits are not good; inspection of the data shows systematic underestimation of rates in very young females and overestimation for old females. Curvelinear models (Perrin *et al.*, 1976; Perrin *et al.*, 1977; Perrin and Henderson, 1984) fit the data better and are consonant with data for captive animals, which indicate that young females may ovulate two or more times in relatively quick succession when entering sexual maturity (Harrison *et al.*, 1972). Data for old females indicate that some are reproductively senescent (Perrin *et al.*, 1976; Marsh and Kasuya, 1984). A typical pattern is that in *S. attenuata* (Perrin *et al.*, 1976) of 4 ovulations in the first year of sexual maturity, 2 in the second, and about 1 per year thereafter, until some time beyond about 13 years of reproductive age, when some individuals become senescent. In some other populations (e.g. *Stenella longirostris* – Perrin *et al.*, 1976) the rates for very young females are only slightly higher than for older females. As pointed out by Perrin *et al.* (1976) and Kasuya *et al.* (1974), estimates for ages beyond about 12 years have been unreliable because of underestimation of age caused by difficulty in interpreting very thin and convoluted dentinal GLGs in older animals.

Another source of error in corpus count/age data is the inclusion of corpora atretica and other scars of non-ovulatory events in the corpus-count (e.g. Perrin *et al.*, 1976 and 1977; Perrin and Henderson, 1984). The count should include only CLs and CAs (Perrin and Donovan, 1984).

In fitting models to corpus-count/age data to estimate ovulation rates, individual variation in age at attainment of sexual maturity must be taken into consideration. If the relationship of % mature to age is a symmetrical S-shaped curve and the curvilinear fit to corpus-count/age data is unweighted, this factor does not affect the analysis. In some instances, however, e.g. in the 'eastern' population of *Stenella longirostris* in the eastern Pacific (Perrin and Henderson, 1984), the maturation curve is quite skewed, and in such cases allowance for individual variation in age at maturation should be incorporated in the model. Perrin *et al.* (1976 and 1977) and Perrin and Henderson (1984) estimated average reproductive age $\bar{A}$ for an age interval p as

$$\bar{A} = \left(\sum_{i-1}^{p} a_i b_i \right) \div c$$

where $a_i = \%$ maturing in ith interval (% mature in i minus % mature in $i-1$); $b_i =$ average reproductive age in interval p of females mature in i; and $c = \%$ mature in interval p. Average reproductive age in the ith interval of females maturing in i was set at 0.50.

Another method of estimating ovulation rate is based on estimated ages of CAs as indicated by size and other indices of degree of regression of the CL (Sergeant, 1962; Kasuya, 1972; Kasuya *et al.*, 1974). As pointed out by Kasuya (1976) and Miyazaki (1977), this method is not satisfactory for the delphinids because size of a CA is not a reliable index of its age, beyond the very early stages of regression of the CL.

Any use of estimates of ovulation rate in modeling (e.g. application to a corpus-count frequency distribution to obtain an age-frequency distribution) should only be done keeping in mind the very great individual variation in ovulation rate and resulting relatively low precision of the estimator. As can be seen in any scatterplot of corpus-count on age for a wild population (Kasuya, 1972; Kasuya *et al.*, 1974; Perrin *et al.*, 1976 and 1977; Sergeant *et al.*, 1980), variation can be sixfold or greater even among fully-mature females. Rates for adult captive animals of the same species kept under the same conditions can range from none to several ovulations per year (Wells, 1984; Kirby and Ridgway, 1984). Thus, corpus count is not a reliable predictor of age for individual animals, and any population index based on it will have an extremely large variance.

Available estimates

The available estimates of ovulation rates (Table 5) vary broadly among the delphinids. They also vary considerably within a species, depending on region and on the model employed. The curvilinear models are more consonant with the estimates based on direct observations than are the linear models. The difference between the estimates for the two stocks of *Stenella longirostris* is discussed below in the section on effects of exploitation.

Pregnancy Rate and Calving Interval

Estimation methods

Annual pregnancy rate (APR) is usually estimated as the percentage of mature females pregnant (including those that are simultaneously pregnant and lactating) divided by the length of gestation (expressed in years). Several assumptions are implicit in this simple model:

(a) There is no sampling bias caused by selectivity, i.e. the distribution of reproductive conditions in the sample is the same as in the population sampled. Factors that can invalidate this assumption include differential vulnerability (e.g. pregnant females easier to catch) and school or areal segregation by age or reproductive condition (e.g. more 'breeding' schools sampled than other types of schools). The latter factor is discussed below.

(b) There is no sampling bias caused by seasonality of calving (also discussed below).

(c) All pregnancies are detected. A very small embryo can be overlooked, especially in the field. If presence of a corpus luteum (CL) is used as a criterion of pregnancy, the estimate of APR is biased upward, because not all CLs derive from pregnancies and some pregnancies result in more than one CL (Perrin and Donovan, 1984).

APR can also be estimated as the reciprocal of calving interval (CI) calculated as the sum of independent estimates of the lengths of the component phases of the reproductive cycle: gestation, lactation (discussed below) and 'resting' (time spent neither pregnant nor lactating). The estimate of the length of the cycle obtained this way must be adjusted downward to take into account any overlap of lactation and pregnancy, by a factor equal to

Table 5

Ovulation rates in delphinids

Species and region (stock in parentheses)	Rate (ovulations/year or GLG)	Model/method	Source
Pseudorca crassidens			
E. North Atlantic	Possibly several/y	—	Comrie and Adams, 1938
E. North Atlantic	About one/y	—	Purves and Pilleri, 1978
Globicephala melaena			
W. North Atlantic	2.4–2.5/y	—	Sergeant, 1962
Lagenorhynchus obliquidens			
E. North Pacific	High compared to other delphinids	—	Harrison *et al.*, 1972
L. acutus			
W. North Atlantic	> 1/y	—	Sergeant *et al.*, 1980
Tursiops truncatus			
W. North Atlantic	~ 1/GLG after ~ 15 GLGs	—	Sergeant *et al.*, 1973
Not given (captive)	None to several/y	Direct observations	Kirby and Ridgway, 1984
Stenella longirostris			
E. trop. Pacific (eastern)	~ 1/GLG, declining slightly with age	$Y = 1.39X^{0.79}$	Perrin *et al.*, 1977
E. trop. Pacific (eastern)	Same	$Y = 13.68(i-e^{-0.099x})$	Perrin and Henderson, 1984
E. trop. Pacific (n. whitebelly)	~ 3/first GLG, 2/second, falling off rapidly to < 1/GLG.	$Y = 6.80(i-e^{-0.654x})$	Perrin and Henderson, 1984
Central Pacific (captive)	Several/y	Direct observations	Wells, 1984
S. coeruleoalba			
W. North Pacific	0.69/y (0.25 to 1.6)	$Y = 0.69X-5.16$	Kasuya, 1972
W. North Pacific	0.59/y, between 10 and 15y	$Y = 0.590X-4.875$	Kasuya and Miyazaki, 1975
W. North Pacific	0.41/y, between 5 and 25y	$Y = 0.414X-2.40$	Kasuya, 1976
	0.12/y, between 26–43y	$Y = 0.115X-6.55$	Kasuya, 1976
W. North Pacific	~ 3/y (1.5 to 12)	Ovary diagram	Miyazaki, 1977
S. attenuata			
W. North Pacific	0.43, increasing slightly with age	$Y_t = 0.00327X_t+0.4286$	Kasuya *et al.*, 1974
W. North Pacific	0.41/y	$Y = 0.412X-1.97$	Kasuya *et al.*, 1974
E. trop. Pacific (offshore)	~ 4/first GLG, 2/second, falling off to ~ 1/GLG	$Y = 4.06X^{0.51}$	Perrin *et al.*, 1976
Delphinus delphis			
E. North Pacific (captive)	None to several/y	Direct observations	Kirby and Ridgway, 1984

the percentage of lactating females also pregnant (Perrin *et al.*, 1977).

An approximate variance of the APR has been estimated (e.g. Perrin *et al.*, 1977) as

$$\mathrm{var}(\mathrm{APR}) = \mathrm{APR}(1-\mathrm{APR})/n$$

which is the variance of a simple proportion. Since the basic APR estimate includes adjustment of the proportion pregnant (P) by the gestation period in years (T_G), the above method will generally underestimate var (APR). A better approximation of var (APR), using the delta method (Seber, 1973), is

$$\mathrm{var}(\mathrm{APR}) = (-P/T_G^2)^2\,\mathrm{var}(T_G)+(1/T_G^2)\,P(1-P)/n_p,$$

where n_p is the sample size used to estimate P. This assumes that P and T_G are independently estimated, i.e. $\mathrm{cov}(P, T_G) = 0$ and, on a more practical level, that an estimate of the variance of T_G exists. While gestation period is one of the least variable vital parameters, estimation of T_G is usually not straightforward and variances have not been estimated in most cases (see 'Gestation period and fetal growth rate,' above).

The above does not hold for APR estimated as the reciprocal of the sum of the component phases of the reproduction cycle. This estimate of APR and its variance are more complex and dependent upon unbiased estimates of not only the proportion pregnant, but those lactating and in gestation. Also, pregnancy rate estimated by this second method is systematically negatively biased (L. L. Eberhardt, personal communication to WFP, 2/13/80).

The variance of the calving interval estimate can also be derived using the delta method. With CI = 1/APR, the approximate variance is

$$\mathrm{var}(\mathrm{CI}) = (\mathrm{APR}^{-4})\,\mathrm{var}(\mathrm{APR}).$$

Available estimates

Estimates of APR are available for only a few species (Table 6). They range from 12% (from the data of Jonsgård and Lyshoel, 1970, for *Orcinus orca* in the North Atlantic) to about 75% (*Tursiops truncatus* and *Delphinus delphis* in the Black Sea). In some cases where two or more estimates are available for the same population, they vary by a factor of about two or more (*Orcinus orca*, *Stenella coeruleoalba* and *Delphinus delphis*). At least some of this variation must be due to violation of the above-listed assumptions. In the case of the Black Sea (*Tursiops truncatus* and *Delphinus delphis*), Kleinenberg (1956) pointed out that calving females apparently leave the area of the fishery and remain apart during early lactation, thus causing a downward bias in the estimated length of lactation and an upward bias in APR. The estimate of APR for the Black Sea population

Table 6

Estimates of annual pregnancy rate (APR) and calving interval (CI) for delphinids. Criterion of pregnancy noted as fetus present (F) or corpus luteum present (CL). Method for estimating APR noted as percentage of mature female pregnant P divided by gestation period G expressed in years (P/G); as reciprocal of sum of separately estimated reproductive phases (S); or as inferred from several lines of evidence (I). Estimates of calving interval CI noted as reciprocal of APR or of sum of phases S

Species and Region (stock or years in parentheses)	Mature females (no.)	Percent pregnant P (and criterion) (%)	Annual pregnancy rate APR (and method) (%)	Calving interval CI (and method) (years)	Source of estimates or data
Pseudorca crassidens					
E. North Atlantic	(59)	14.0 (F)	— —	— —	Purves and Pilleri, 1978
W. North Pacific	(38)	21.1 (F)	— —	— —	Kasuya and Izumisawa, 1981
Orcinus orca					
E. North Atlantic	(430)	13.7 (F)	12.0 (P/G of 15 months)	8.3 (1/APR)	IWC, 1982 (Jonsgård and Lyshoel, 1970)
E. North Atlantic	(161)	34.9 (F)	28.9 (P/G of 15 months)	3.5 (1/APR)	IWC, 1982 (Christensen, 1981)
E. North Atlantic	(51)	39.2 (CL)	32.8 (P/G of 15 months)	3.0 (1/APR)	IWC, 1982 (Christensen, 1982)
Antarctic	(91)	27.5 (F)	13.7 (P/G, adj. for season)	7.3 (1/APR)	IWC, 1982 (Mikhalev *et al.*, 1981)
Globicephala melaena					
W. North Atlantic	(500)[1]	39.8 (F)	30.0 (1/S)	3.3 (S)	Sergeant, 1962
E. North Atlantic	(30)	40.0 (F)	— —	— —	Purves and Pilleri, 1978
Tursiops truncatus					
Black Sea	(24)	63.0 (—)	63.0 (P/G of 12 months)	1.3–1.5 (1/APR)	Danilevskiy and Tyutyunnikov, 1968
W. North Pacific	(140)	43.6 (F)	43.6 (P/G of 12 months)	— —	Kasuya and Izumisawa, 1981
Grampus griseus					
W. North Pacific	(13)	30.8 (F)	— —	— —	Kasuya and Izumisawa, 1981
Stenella longirostris					
E. trop. Pacific (eastern, 1973–81)	(569)[2]	30.8 (F)	34.9 (P/G of 10.6 months)	2.9 (1/APR)	Henderson *et al.*, 1980; Oliver *et al.*, 1983
E. trop. Pacific (n. whitebelly, 1973–81)	(435)[2]	29.0 (F)	32.8 (P/G of 10.6 months)	3.0 (1/APR)	
E. trop. Pacific (s. whitebelly, 1973–81)	(132)[2]	26.5 (F)	30.0 (P/G of 10.6 months)	3.3 (1/APR)	Perrin and Oliver, 1982
S. coeruleoalba					
E. trop. Pacific (all stocks)	(23)	30.4 (F)	30.4 (P/G of 12 months)	3.3 (1/APR)	Perrin and Oliver, 1982
W. North Pacific (1968–71)	(361)	29.9[4] (F)	29.9 (P/G of 12 months)	~ 3 (S)	Kasuya, 1972
W. North Pacific (1952–58)	(321)	40.5[4] (CL)	40.5 (P/G of 12 months)	4.2 (est. initial) to 1.8 (1973) (1/APR)	Kasuya and Miyazaki, 1975
W. North Pacific (1961–68)	(301)	33.6[4] (CL)	33.6 (P/G of 12 months)		
W. North Pacific (1970–73)	(950)	55.6[4] (CL)	55.6 (P/G of 12 months)		
W. North Pacific (1971–75)	(165)	70.9[4] (—)	70.9 (P/G of 12 months)	1.4 (1/APR)	Kasuya, 1976
S. attenuata					
E. trop. Pacific (n. offshore, 1973–78)[3]	(522)[2]	36.0 (F)	37.6 (P/G of 11.5 months)	2.7 (1/APR)	Henderson *et al.*, 1980; Oliver *et al.*, 1983; Perrin and Oliver, 1982
E. trop. Pacific (n. offshore, 1979–81)	(493)[2]	28.4 (F)	29.6 (P/G of 11.5 months)	3.4 (1/APR)	
E. trop. Pacific (s. offshore, 1973–80)	(277)[2]	39.4 (F)	40.0 (P/G of 11.5 months)	2.5 (1/APR)	Perrin and Oliver, 1982
W. North Pacific (1970–73)	(250)	26.8[4] (—)	28.7 (P/G of 11.2 months)	3.5 (1/APR)	Kasuya *et al.*, 1974
W. North Pacific (1970–76)	—	— (—)	25.4[5] —	3.9 (1/APR)	Kasuya, 1976
Delphinus delphis					
Black Sea (1936–39)	(1179)	— —	75.0 (I of preg. in 3 out of	1.3 (1/APR)	Sleptsov, 1941
Black Sea (1946)	(934)	80.4 (—)	75.0 4 years)	1.3 (1/APR)	Kleinenberg, 1956
Black Sea (1949)	(231)	40.7 (—)	46.4 (P/G of 11.5 months)	2.2–2.3 (1/APR)	Sokolov, 1962
E. trop. Pacific (all stocks)	(365)	36.2 (F)	37.8 (P/G of 11.5 months)	2.6 (1/APR)	Henderson *et al.*, 1980; Oliver *et al.*, 1983; Perrin and Oliver, 1982

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[1] Excludes 29 'anoestrous or infertile'.

[2] Excludes senescent.

[3] Includes only specimens from sets in which 40 or more killed.

[4] Values differ from those in sources because all PL (simultaneously pregnant and lactating) included here, rather than only ½.

[5] ½ PL included.

of *Delphinus delphis* of 75% reflects a conclusion by Sleptsov (1941) that adult females become pregnant 3 years running and skip the fourth year. The inference was also based on modal progression of fetal and calf length and on regression of ovarian corpora, but mainly on the proportion of pregnant females in the catch. For *Stenella coeruleoalba* in the western North Pacific, Miyazaki and Nishiwaki (1978) have posited similar segregation by reproductive condition and pointed out that the various types of schools have not been equally sampled, causing an overestimate of APR in some studies (e.g. Kasuya and Miyazaki, 1975, and Kasuya, 1976).

For some species, e.g. *S. attenuata* and *S. longirostris*, the range of estimates is fairly small. Where sample size allowed, Henderson, Perrin and Miller (1980) adjusted for bias caused by differential capture vulnerability with age in *S. attenuata* by including data only from purse-seine sets in which 40 or more dolphins were killed; these samples are thought to be more accurately representative of the population than are small-kill samples. The effect is to adjust APR upward. Perrin and Oliver (1982) discussed other biases in the data. The estimates for *S. attenuata* (n. offshore, 1973–78) by the two methods described above (37.6% and 32.3%) are not statistically different from each other (at $\alpha = 0.05$) nor are the estimates of APR for three populations of *S. longirostris* in the eastern tropical Pacific. The 'Method-2' estimates of APR of Perrin *et al.* (1977), Perrin and Henderson (1979) and Henderson *et al.* (1980) are invalid for reasons discussed below in the section on lactation.

The estimate of 13.7% for *Orcinus orca* in the Antarctic (IWC, 1982, from data in Mikhalev, Ivashin, Zavusin and Zelemaya, 1981) is based on division of fetuses into yearly cohorts based on length. This correction is necessary because gestation lasts more than a year and possible because breeding is sharply seasonal.

Length of Lactation and Age at Weaning

The lactation period is the most variable component of the calving cycle. As such, it is important in any model or hypothesis of change in reproductive rate in a population. It can change in two ways: through change in average age at weaning, or through change in differential calf mortality (mortality of nursing calves minus mortality of lactating females). In the former case, the average lactation time per weaned calf decreases with decreased lactation time, but in the latter case it increases (because the lactation time spent on calves that die before weaning must be added to that spent on calves that survive to weaning age).

Estimation methods

(*a*) *Ratio of lactating to pregnant.* The most common method of estimating length of lactation is based on the assumption that the proportion of a sample of mature females that is in a particular reproductive condition is directly proportional to the relative length of time spent in that condition. Thus, if an estimate of length of gestation is available, length of lactation can be estimated as

$$T_L = T_G \cdot L/P$$

where T_G = length of gestation; L = proportion of sample lactating; P = proportion of sample pregnant (including animals both lactating and pregnant). This estimation is based on the same assumptions and subject to the same potential biases as discussed above for the estimation of pregnancy rate.

(*b*) *Cow-calf method.* This method estimates age at weaning. Age at weaning is not equivalent to length of lactation, because it does not take into account differential calf mortality. However, it has often been used as an estimate of lactation time. The cow-calf method assumes that for each lactating cow in a sample there should be also a suckling calf present. The age of the longest calf thus assumed suckling is an estimate of maximum age at weaning. The method assumes that at least some calves reach weaning age. It contains both a downward bias because the longest suckling calf could be expected to continue suckling for some unknown length of time, and an upward bias because it does not consider individual variation in length with age. The method is very sensitive to random error because dispersion of length in the longer calves assumed to be suckling is relatively great and growth at these lengths is relatively slow, meaning that a small difference in length yields a relatively large difference in age estimated from a growth curve.

The cow–calf estimate has been used inappropriately as an estimate of average age at weaning ('Method 2' calculation in Perrin *et al.* (1977) Perrin and Henderson, 1979 and Henderson *et al.* (1980)); the overestimation of lactation time is in addition to that caused by the differential calf mortality (discussed below) that is known to exist in the dolphin population involved in the tuna purse-seine fishery in the eastern tropical Pacific (Perrin and Oliver, 1982). Miyazaki (1977) modified the cow–calf method in an attempt to estimate average weaning age. After assigning calves to suckling or non-suckling categories in each of 19 samples (based on length of the assumed oldest suckling calf in that sample), he used the age at which 50% of all the calves in the pooled sample were estimated to be still suckling as an estimate of average age at weaning. This procedure may improve the accuracy of maximum weaning age as an estimate of length of lactation, but it does not address the problem of differential calf mortality.

In the simplest situation, that of no differential calf mortality (Fig. 4), the accuracy of maximum age at weaning ($w_{\max}$ in Fig. 4a) as an estimate of length of lactation depends on the total length of suckling and on the variance of average weaning age ($\bar{w}$). With the addition of differential calf mortality (in Fig. 4b), lactation can cease in two ways (because of weaning or because of death of the calf with survival of the mother), and weaning age ($w_{\max}$) becomes still more of an overestimate of length of lactation (l). Sensitivity to amount of differential mortality is high (B and C in Fig. 4). A countervailing factor causing underestimation of maximum weaning age (by $w_{\max}$ in Fig. 4b) from tuna-fishery data is the fact that too many suckling calves are present in the sample in relation to the number of lactating cows (calves are more vulnerable to capture), causing the length of the longest suckling calf to be underestimated. In the extreme case of complete differential mortality, i.e. no survival to weaning age (D in Fig. 4), the estimate of weaning age by the cow–calf method becomes actually an estimate of maximum length of lactation corresponding to maximum age to which

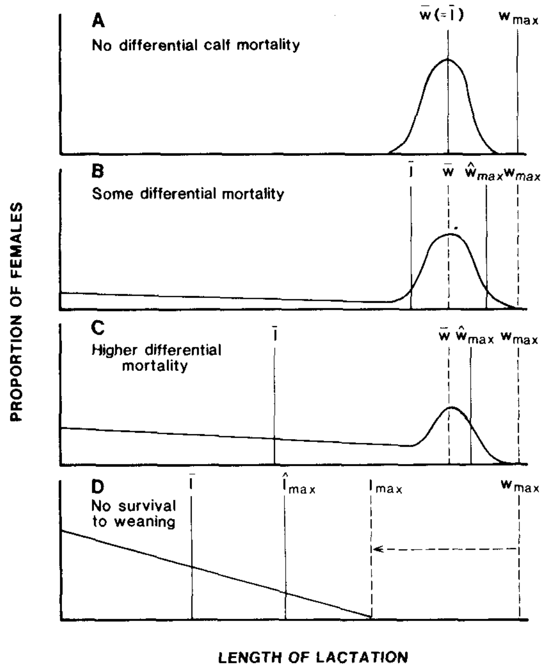

Fig. 4. Conceptual model of relationships between length of lactation (*l*), age at weaning (*w*) and differential calf mortality.

calves survive (l_{max}). The complete relationships between estimates of weaning, estimates of length of lactation and differential calf mortality have not been quantitatively modeled, so the usefulness of the cow–calf method at this point is problematical.

(*c*) *Stomach contents*. Although the examination of stomach contents allows direct determination of a shift from milk to solid food plus milk, (e.g. Perrin *et al*., 1976) estimation of age at weaning by this method is open to question because of the difficulty of detecting small quantities of milk mixed with solid food. Odontocetes may continue to suckle for long periods, in some cases years after a major shift to solid food. The extended duration of cow–calf bonding may serve some non-nutritional function (Brodie, 1969). P. B. Best (personal communication to WFP) has employed a chemical test for lactose in his examination of sperm-whale stomachs. The color reagent used can detect sperm-whale milk at a 30-fold dilution. Without data on suckling rates and milk volume consumed during the latter stages of nursing lasting for years and data on the rate of digestion of milk, it is not possible to know whether this test is sufficiently sensitive to allow estimation of weaning age from stomach contents.

If mortality rates for weaned and unweaned calves are different, an estimate of average age at weaning based on a 50%-weaned criterion for a sample of animals would be biased. For example, if weaned calves have higher mortality, the estimate of average weaning age would be biased upward.

(*d*) *Behavioral observations*. Individual nursing calves can be observed in captivity or in the wild. This method has resulted in a general concensus that *Tursiops truncatus* calves usually nurse about 18 months, with a lot of variation. For other species that are rare in captivity or difficult to observe in the wild, a sample-size problem is soon encountered. There is also the question of the effect of captivity. A bottlenose dolphin in an oceanarium in South Africa developed a habit of squirting milk at the glass at an observation post to startle visitors. This animal suckled for 38 months, possibly because of the learned behavior (Ross, 1979).

Available estimates

The available estimates of length of lactation (Table 7) range from 8 months (*Stenella coeruleoalba* off Japan during the period 1970–73) to 27 months (*S. attenuata* off Japan, 1970–76). The modal value appears to be 18–20 months (8 of the 21 estimates in Table 7). The relatively low values for *S. coeruleoalba* off Japan (8–20 months) and *Delphinus delphis* in the Black Sea (14–19 months) reflect the segregation of calving females discussed above for both cases. The possible effects of exploitation on length of lactation (thought to have operated, for example in the western Pacific population of *S. coeruleoalba* and the eastern Pacific populations of *S. longirostris*) are discussed below in the section on the topic.

The range of estimates of age at weaning is greater (5 months to 34 months) than for length of lactation. The lowest value of 5–6 months for *D. delphis* in the Black Sea again reflects segregation of lactating females. The estimates of weaning age for the three populations of *S. longirostris* (11, 19 and 34 months) are inversely correlated with the three estimates of length of lactation (19, 18 and 15 months); this inconsistency is discussed below in the section on effects of exploitation.

Solid food is taken in the first year of life in delphinids; the six estimates range from 3–6 months to 4–11 months with the mean at about 6 months. Maximum length of suckling is at least 2 years; the six estimates range from 24 months to 48–60 months.

Length of 'Resting Period'

In estimating reproductive rates, mature females are usually classified into four categories: pregnant only (*P*), pregnant and lactating (*PL*), lactating only (*L*) and 'resting' (*R*) (all those neither pregnant nor lactating). In some analyses, e.g. Perrin *et al*. (1976), Perrin *et al*. (1977) and Henderson *et al*. (1980), senescent females (those neither pregnant nor lactating and with small withered ovaries containing no recent corpora) were not included in the resting category. In most studies, the category is a catchall and includes females in estrus, those between ovulation cycles, senescent females, those that have recently aborted and those pregnant with very small embryos missed in dissection. The length of the 'resting' period is calculated in the same manner and is subject to the same potential biases as the estimates of length of lactation or length of gestation:

$$T_R = T_G \cdot R/P$$

where T_G = gestation time, R = proportion resting and P = proportion pregnant.

In alternative estimates of annual pregnancy rates based on independent estimates of gestation and weaning age (the 'Method 2' estimates of Perrin *et al*. (1977)

Table 7

Estimates of length of lactation, age at weaning and length of 'resting period' in delphinids. Methods noted: observed in wild, observed in captivity, determined from stomach contents, determined from eruption of teeth, estimated by cow–calf method (C–C), estimated from ratio of lactating to pregnant (L/P) and estimated from ratio of 'resting' to pregnant

	LACTATION		WEANING							
Species and region (stock or year in parentheses)	Mature females (*no.*)	Length (by L/P) (*months*)	Age at first solid food (*months*)	(Method)	Oldest nursing (*months*)	(Method)	Average age at weaning (*months*)	(Method)	'Resting' (by R/L) (months)	Source of estimate or data
Pseudorca crassidens										
W. North Pacific	(38)	18[1]	—	—	—	—	—	—	—	Kasuya and Izumisawa, 1981
Orcinus orca										
E. North Pacific	—	—	—	—	—	—	⩾ 12	(ob. wild)	—	IWC, 1982
Globicephala melaena										
E. North Atlantic	(485)	22	6–9	(stom.)	—	—	—	—	8	Sergeant, 1962
Lagenorhynchus acutus										
E. North Atlantic	(32)	18[2]	—	—	—	—	—	—	—	Sergeant *et al.*, 1980
Tursiops truncatus										
All regions	(31)	19[3]	4–11	(ob. cap.)	38	(ob. cap. and wild)	18–20	(ob. cap. and wild)	5	Kasuya and Izumisawa, 1981; Leatherwood *et al.*, 1978; McBride and Kritzler, 1951; Prescott, 1977; Ridgway and Benirschke, 1977; Ross, 1977, 1979, Saayman and Taylor, 1977; Sergeant, 1962
Stenella longirostris										
E. trop. Pacific (eastern, 1973–81)	(569)	19	—	—	—	—	11[4]	(C–C)	6	Henderson *et al.*, 1980; Oliver *et al.*, 1983; Perrin and Oliver, 1982
E. trop. Pacific (n. whitebelly, 1973–81)	(435)	18	—	—	—	—	19[4]	(C–C)	9	
E. trop. Pacific (s. whitebelly, 1973–81)	(132)	15	—	—	—	—	34[4]	(C–C)	15	
S. coeruleoalba										
E. trop. Pacific (all stocks)	(28)	14[3]	—	—	—	—	—	—	10	Perrin and Oliver, 1982
W. North Pacific (1968–71)	(361)	12[3]	~ 6	(erupt. teeth)	24	(—)	⩾ 15	(C–C)	5	Kasuya, 1972
W. North Pacific (1952–58)	(321)	17[3]	—	—	—	—	—	—	4	Kasuya and Miyazaki, 1975
W. North Pacific (1961–68)	(301)	20[3]	—	—	—	—	—	—	5	Kasuya and Miyazaki, 1975
W. North Pacific (1970–73)	(950)	8[3]	—	—	—	—	—	—	2	Kasuya and Miyazaki, 1975
W. North Pacific (1971–75)	(—)	13[3]	—	—	~ 36	(—)	—	—	4	Kasuya, 1976
W. North Pacific (1972–73)	—	—	3–6	(stom.)	36	(C–C)	18	(C–C)[5]	—	Miyazaki, 1977
S. attenuata										
E. trop. Pacific (n. offshore, 1973–78)	(522)[6]	17	5–7	(stom.)	33	(C–C)	20	(C–C)	5	Henderson *et al.*, 1980; Oliver *et al.*, 1983; Perrin *et al.*, 1976; Perrin and Oliver, 1982
E. trop. Pacific (n. offshore, 1979–81)	(493)	26	—	—	—	—	—	—	6	
E. trop. Pacific (s. offshore, 1973–80)	(277)	13	—	—	—	—	—	—	5	
W. North Pacific (1970–73)	(250)	26	3–6	(stom.)	48–60	(C–C)	—	—	7	Kasuya *et al.*, 1974
W. North Pacific (1970–76)	(—)	27	—	—	—	—	—	—	9	Kasuya, 1976
Delphinus delphis										
Black Sea (1931–33)	(~ 800)	14[7]	—	—	—	—	—	—	—	Mayarova and Danilevskiy, 1934
Black Sea (1936–39)	—	—	—	—	—	—	5–6[8]	(—)	—	Sleptsov, 1941
Black Sea (1946)	(934)	—	—	—	—	—	6[8]	(—)	—	Kleinenberg, 1956
Black Sea (1949)	(231)	19[7]	—	—	—	—	—	—	4	Sokolov, 1962
E. trop. Pacific (all stocks)	(365)	19[7]	—	—	—	—	—	—	4	Henderson *et al.*, 1980; Oliver *et al.*, 1983; Perrin and Oliver, 1982

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[1] Assumed gestation of 16 months.

[2] Assumed gestation of 11 months.

[3] Assumed gestation of 12 months.

[4] For 1973–78 only (n = 521, 366 and 123).

[5] Modified as described in text.

[6] Includes only specimens from net hauls in which 40 or more were killed (see text, under *Pregnancy rate*).

[7] Assumed gestation of 11.5 months.

[8] But see text.

and Henderson *et al.* (1980)), *R/P* estimates of length of the 'resting' portion of the calving cycle were used.

The available estimates (Table 7) range from 2 months (for the reportedly depleted population of *S. coeruleoalba* off Japan) to 15 months (for the southern whitebelly population of *S. longirostris* in the eastern tropical Pacific). The modal value is 4–5 months (9 of the 18 estimates).

Age and Sex Structure

Background and methods

Sex ratios and age structure are usually estimated from series of specimens captured in fisheries or collected from strandings. Rather than follow a single age class throughout its life (which has not been possible for delphinids) to determine sex ratios, age structures and mortality/survival rates, the usual method is to estimate these parameters using a sample from one time period. These techniques are adapted from human demography and fisheries and wildlife sciences (e.g. Keyfitz, 1968; Ricker, 1975; Caughley, 1977).

Assumptions involved in making sex- and age-structure inferences from specimen series include (1) age and sex are accurately determined; (2) the sample is representative of the population; and (3) the population is stationary in structure. The difficulty of testing these assumptions increases in the order in which they are listed.

Sex is more easily determined than age for dead specimens, and estimates of sex ratio are therefore generally more reliable than those of age structure. Both sex and age are often very difficult to determine for live specimens in studies that do not involve capture. Species with marked sexual dimorphism (e.g. *O. orca*) are exceptions to this, at least for sex ratio of adults.

Recent developments in age determination are reviewed in Perrin and Myrick (1980). In some cases, ovarian-corpora frequencies have been used to represent age in adult females on the assumption that ovulation is a regular event. Since this assumption is probably not valid (see discussion above), age estimates from corpus frequencies are not reliable.

While it is probably not possible to determine with a great deal of certainty that an observed age series is representative of the population, some simple methods can identify strongly biased samples. For example, there should in general be fewer individuals in older age classes. Distributions which have peak frequencies at ages over 0–1 indicate under-representation of juveniles. This type of age distribution has been observed for many delphinid populations (see below).

To date, stationarity has not been demonstrated for any delphinid population. Again, this would in fact be very difficult to do. Any information suggesting recent changes in overall population size would invalidate this assumption.

Common methods used to estimate adult mortality rates in fisheries and wildlife sciences include log-linear regression (e.g. Ricker, 1975) and the Chapman–Robson (1960) method. Regression methods were used by Kasuya *et al.* (1974) and Kasuya (1976) for *S. attenuata*, and by Sergeant (1962) for *G. melaena*. In some instances it is possible to factor out influences from population growth and mortality via exploitation from the total mortality represented by an observed age structure (e.g. see Ohsumi, 1979).

Available estimates

In every case for which data exist on sex and age structure of a delphinid population, two patterns have surfaced. First, the ratio of males to females appears to decline with age (Table 8). Second, a certain segment of the population, roughly 'juvenile' in age, appears to be under-represented in the samples. This second observation suggests that any reproductive parameter estimated from relative frequencies of age classes (mortality rate, ages at sexual maturity and first birth, relative pregnancy by age) may be biased. In some cases there are also sex differences in the under-representation of juveniles, e.g. in *Stenella attenuata* of the eastern tropical Pacific (J. Barlow, A. Hohn and A. Myrick, pers. comm. to SBR), *Globicephala melaena* near Newfoundland (Sergeant, 1962), and *Stenella coeruleoalba*, near Japan (Miyazaki and Nishiwaki, 1978).

A wide range in sex ratios for entire populations has been reported (Table 8): from 5.5:1 for *Lagenorhynchus acutus* in Norway down to 0.5:1 for *Tursiops truncatus* off North Carolina (Townsend, 1914). Within the Black-Sea *Delphinus* data alone, the range is from 0.64:1 to 2.85:1, depending upon the month during which the nearshore schools were captured. This variation is most likely due in great part to age/sex segregation, which has been shown to be seasonal in the Black Sea (Kleinenberg, 1956; Tomilin, 1957; Mayarova and Danilevskiy, 1934). The same is true for *Tursiops truncatus* off the eastern US (True, 1891). Segregation by sex and/or age has been observed both within and between groups in studies of free-ranging *Tursiops truncatus* (Lear and Bryden, 1980; Wells, Irvine and Scott 1980; Würsig, 1978), *Stenella longirostris* (Norris and Dohl, 1980a; Pryor and Kang, 1980), *Stenella attenuata* (Pryor and Kang, 1980), *Sousa* sp. (Saayman and Tayler, 1979), *Lagenorhynchus obliquidens* (Norris and Prescott, 1961), *L. obscurus* (Würsig and Würsig, 1980) and *Orcinus orca* (Bigg, 1982; Balcomb, Boran and Heimlich, 1982; Condy, van Arde and Bester, 1978). Age/sex segregation has been reported from studies of captured schools for *Stenella attenuata* (Kasuya, 1976; Kasuya *et al.*, 1974) *S. coeruleoalba* (Kasuya, 1972, 1976; Miyazaki and Nishiwaki, 1979), *Delphinus delphis* (Mayarova and Danilevskiy, 1934; Kleinenberg, 1956; Tomilin, 1957; Hui, 1973), *Tursiops truncatus* (True, 1891; Mead, 1975b), *Lagenorhynchus acutus* (St Aubin and Geraci, 1979) and *Globicephala melaena* (Sergeant, 1962). The implications of age and asexual segregation on estimating delphinid population parameters are profound. As discussed above, unbiased estimation of many vital rates requires representative age-structure samples. Since age and/or sex segregation may be the rule rather than the exception for delphinids, data should be scrutinized closely before calculation of vital-rate statistics.

Estimates of natural mortality have been made for only three delphinid cetaceans: *G. melaena* (0.115: Sergeant, 1962), *S. coeruleoalba* (0.137: Kasuya, 1976) and *S. attenuata* (0.161: Kasuya, 1976), as reviewed and evaluated by Ohsumi (1979). In each case the original authors made more than one estimate. Values reported

(continued on p. 114)

Table 8

Sex ratios reported for delphinids, listed here as ♂:♀, with female values scaled to 1.0. Data from studies which selected by sex are not listed here

Species and region	Data type	Age class and sample size	♂:♀ ratio	Age class and sample	♂:♀ ratio	Age	♂:♀ ratio	Source
Orcinus orca								
(Pacific N.W., U.S.)	Live observation	Adult (43)	0.48:1	—	—	—	—	Balcomb *et al.*, 1982
(Pacific N.W., U.S.)	Live observation	Adult (132)	0.83:1	—	—	—	—	Bigg, 1982
(Marion Island)	Live observation	Adult (478)	1.34:1	—	—	—	—	Condy *et al.*, 1978
Globicephala macrorhynchus								
(Florida)	Mass stranding	All (135)	0.53:1	—	—	—	—	Irvine *et al.*, 1979
(California)	Mass stranding	All (27)	0.28:1	—	—	—	—	Hall *et al.*, 1971
G. melaena								
(Nova Scotia)	Mass standing	All (99)	1.91:1	—	—	—	—	Geraci and St. Aubin, 1977
(Newfoundland)	Drive fishery	Newborn (250)	1.43:1	6–10 years (87)	0.85:1	8–22 years (213)	0.32:1	Sergeant, 1962
Pseudorca crassidens								
(Scotland)	Mass stranding	All (72)	0.85:1	—	—	—	—	Purves and Pilleri, 1978
(Scotland)	Mass stranding	All (62)	0.82:1	—	—	—	—	Peacock *et al.*, 1936
Feresa attenuata								
(Japan)		All (14)	1:1	—	—	—	—	Nishiwaki *et al.*, 1956
Steno bredanensis								
(Florida)	Mass stranding	All (10)	1.5:1	—	—	—	—	Layne, 1965
Lagenorhynchus acutus								
(New England)	Mass stranding	'Young' (16)	1.67:1	'Intermed.' (30)	1.72:1	'Adult' (56)	0.22:1	Sergeant *et al.*, 1980
(Norway)		All (22)	5.5:1	—	—	—	—	Guldberg and Nansen, 1894
Tursiops truncatus								
(N. Carolina)	Drive fishery	All (157)	1.14:1	—	—	—	—	True, 1890
(Florida)	Live capture	All (61)	1:1	—	—	—	—	Sergeant *et al.*, 1973
(Florida)	Live capture	All (47)	0.96:1	—	—	—	—	Irvine *et al.*, 1981
(N. Carolina)	Drive fishery	All (51)	0.5:1	—	—	—	—	Townsend, 1914
(Black Sea)	Drive fishery	All (53)	1:1	—	—	—	—	Danileyskiy and Tyutyunnikov, 1968
Stenella longirostris								
(Florida)	Mass stranding	All (25)	0.85:1	—	—	—	—	Mead *et al.*, 1980
(ETP: 1973–75)	Tuna seine	— (294)	1.1:1	1.3–1.6 m (631)	0.99:1	Adult (1,330)	0.94:1	Perrin *et al.*, 1976
(ETP: 1979–80)	Tuna seine	All (734)	0.98:1	—	—	—	—	Perrin and Oliver, 1982
(ETP: 1981)	Tuna seine	All (305)	1.15:1	—	—	—	—	Oliver *et al.*, 1983
S. attenuata								
(ETP)	Tuna seine	Neonate (412)	1:1	'2-tone' (1,367)	0.95:1	'Speckled' (1,275)	0.91:1	Perrin *et al.*, 1976
		Mottled (1,298)	0.73:1	'Fused' (5,019)	0.75:1	—	—	Perrin *et al.*, 1976
(ETP: 1976)	Tuna seine	All (6,225)	0.8:1	—	—	—	—	Perrin *et al.*, 1977
(ETP: 1979–80)	Tuna seine	All (2,246)	0.75:1	—	—	—	—	Perrin and Oliver, 1982
(ETP: 1981)	Tuna seine	All (830)	0.73:1	—	—	—	—	Oliver *et al.*, 1983
(Japan)	Drive and harpoon fishery	Juv. (149)	1.16:1	'Puberal' (167)	2.21:1	'Mature' (422)	0.38:1	Kasuya *et al.*, 1974

Table 8 (*continued*)

S. coeruleoalba								
(Japan)	Drive and harpoon	Juv. school (276)	3.07:1	Mixed school (653)	1.06:1	Adult school (1,638)	0.78:1	Miyazaki and Nishiwaki, 1978
(Japan)	Drive and harpoon	Fetus (661)	1.13:1	'Suckling' (744)	1.07:1	Others (7,967)	1.19:1	Kasuya and Miyazaki, 1975
(Japan)	Drive and harpoon	0–1.5 year (251) 14.5+year (747)	1.09:1 0.77:1	2.5–8.5 years (1,438)	1.55:1	9.5–13.5 years (847)	0.93:1	Miyazaki, 1977
(Japan)	Drive and harpoon	'Prenatal' (115)	1:1	'Postnatal' (1,048)	0.73:1	—	—	Miyazaki, 1977
Delphinus delphis								
(ETP: 1973–78)	Tuna seine	All (140)	0.95:1	—	—	—	—	Henderson *et al.*, 1980
(ETP: 1979–80)	Tuna seine	All (363)	0.85:1	—	—	—	—	Perrin and Oliver, 1982
(ETP: 1981)	Tuna seine	All (117)	1.05:1	—	—	—	—	Oliver *et al.*, 1983
(Black Sea: 1930s)	Drive fishery	All (82, 843)	1.12:1	—	—	—	—	Tomilin, 1957
(ETP: north)	Tuna seine	All (286)	0.87:1	—	—	—	—	Hui, 1977
(ETP: south)	Tuna seine	All (799)	0.85:1	—	—	—	—	Hui, 1977
(Black Sea: 1931)	Drive-or-gun fishery	All (395)	1.5:1	—	—	—	—	Danilevskiy and Tyutyunnikov, 1968
(Black Sea: 1931, Jan.)	Drive-or-gun fishery	All (212)	0.64:1	—	—	—	—	Mayarova and Danilevskiy, 1934
(Black Sea: 1931, Feb.)	Drive-or-gun fishery	All (176)	2.85:1	—	—	—	—	Mayarova and Danilevskiy, 1934
(Black Sea: 1931, Mar.)	Drive-or-gun fishery	All (589)	1.44:1	—	—	—	—	Mayarova and Danilevskiy, 1934
(Black Sea: 1931, Apr.)	Drive-or-gun fishery	All (687)	1.56:1	—	—	—	—	Mayarova and Danilevskiy, 1934
(Black Sea: 1931, May)	Drive-or-gun fishery	All (277)	2.12:1	—	—	—	—	Mayarova and Danilevskiy, 1934
(Black Sea: 1931, Jul.)	Drive-or-gun fishery	All (384)	1.56:1	—	—	—	—	Mayarova and Danilevskiy, 1934
(Black Sea: 1931, Aug.)	Drive-or-gun fishery	All (440)	1.17:1	—	—	—	—	Mayarova and Danilevskiy, 1934
(Black Sea: 1931, Sept.)	Drive-or-gun fishery	All (135)	0.69:1	—	—	—	—	Mayarova and Danilevskiy, 1934
(So. Calif: 1971)	Tuna seine	0–4 (68)	—	5–10 (28)	0.70:1	11+(19)	0.9:1	Hui, 1973
(ETP: 1977)	Tuna seine			—	—	—	—	Gurevich and Stewart, 1978

Table 9

Annual birth rates reported for populations of delphinids

Species and region/stock	b or GARR	Notes	Source
Sousa chinensis			
Indian Ocean	0.10(b)	Visual obs. % calves in population	Saayman and Tayler, 1979
Orcinus orca			
Puget Sound, WA.	0.04–0.05	Visually obs. preg. rate × % female adult	Dahlheim, 1980
Vancouver Is., B.C.	0.046(b)	No. calves/no. all others ('cropped' population)	IWC, 1982
Vancouver Is., B.C.	0.032	'Uncropped' state	IWC, 1982
Puget Sound, WA.	0.026(b)	Obs. no. calves/no. all others	IWC, 1982
Globicephala melaena			
Newfoundland	0.132	% female × % mature female preg. divided by gestation (exploited)	Sergeant, 1962 Harrison, 1969
Tursiops truncatus			
Florida	0.082(b)	% calves visually counted (non-exploited)	Irvine *et al.*, 1981
N. Gulf of Mexico	0.077(b)	% calves visually counted (exploited)	Leatherwood, 1977
Argentina, S. Atlantic	0.096(b)	% calves visually counted (non-exploited)	Würsig, 1978
E. Australia	0.012(b)	% calves visually counted (non-exploited)	Lear and Bryden, 1980
Black Sea	0.30?	% female × % female mature × % preg. (biased sampling suspected) (exploited)	Danilevskiy and Tyutyunnikov, 1968
Stenella longirostris			
Eastern stock, ETP	0.08	% female × % female mature × % preg. (exploited)	Perrin *et al.*, 1977
	0.075	% female × % female mature × % preg. (exploited)	Perrin and Henderson, 1984
Northern whitebelly stock, ETP	0.094	% female × % female mature × % preg. (exploited)	Perrin and Henderson, 1984
Southern whitebelly stock, ETP	0.067	% female × % female mature × % preg. (exploited)	Henderson *et al.*, 1980
Stenella coeruleoalba			
All stocks, ETP	0.109	% female × % female mature × % preg. (exploited)	Henderson *et al.*, 1980
Japan	0.11	% female × % mature × % preg. (exploited) (calculation from data given)	Kasuya, 1972
Japan	0.103	% female × % mature × % preg. (exploited) (calculation from data given)	Kasuya, 1976
Stenella attenuata			
Japan	0.103	% female × % mature × % preg. (exploited) (calculated from data in both papers)	Kasuya, 1976 and Kasuya *et al.*, 1974
Northern offshore stock, ETP	0.117	% female × % mature × % preg. (exploited) (calculated from data in both papers); 1973–1978 data	Henderson *et al.*, 1980
Northern offshore stock, ETP	0.109	% female × % mature × % preg. (exploited); 1973–1975 data	Perrin *et al.*, 1977
Southern offshore stock, ETP	(0.195)	(M1)	Henderson *et al.*, 1980
Delphinus delphis			
ETP	0.096	(Exploited) (M1)	Henderson *et al.*, 1980
Northern stock, E. Pac.	0.087	No. preg./total population	Hui, 1977
Southern stock, ETP	0.066	No. preg./total population	Hui, 1977
Black Sea	0.106[1]	% all female preg. × % female (exploited)	Danilevskiy and Tyutyunnikov, 1968

[1] Adjusted for 10-month gestation = (12/10) × (22/35) × 0.35 × 0.4 = 0.106. Unadjusted = 0.22 × 0.4 = 0.088.

here are those which Ohsumi (1979) concluded to be the most appropriate. All of these estimates are tentative, incorporating unresolved problems in age determination and possibly sampling biases. Direct observations of *O. orca* in Puget Sound indicated a relatively low adult natural mortality rate of $M = 0.01$ (Balcomb *et al.*, 1982).

Ohsumi (1979) and Ralls, Brownell and Ballou (1980) have reviewed the available data on mortality rates for delphinid cetaceans (among other taxa). Ralls *et al.* found that the degree to which males have higher mortality increases with the degree of sexual dimorphism. Ohsumi (1979) investigated the relationships between M, life span and asymptotic body size. He found that, in general, larger, longer-lived taxa have lower natural mortality rates. Since his data included mysticete as well as odontocete species, it is not clear how accurate his predictions of M would be for species not included in the original analysis.

Reproductive Rates

There are two types of population reproductive rates of interest in stock assessment and management. These can be generally categorized as gross and net rates, differing roughly by annual natural mortality. Each category encompasses a number of specific types of estimates and each has been addressed in more than one way. These are summary parameters, usually estimated from combina-

Table 10

Net annual reproductive rates reported for delphinids

Species and region	Net repro. rate	Notes	Source
Orcinus orca			
Vancouver Is., B.C.	0.031	Observed net pod change 'cropped' state	IWC, 1982
Vancouver Is., B.C.	0.017	Observed net pod change 'uncropped' state	IWC, 1982
Puget Sound, WA	0.023	Observed net pod change 'cropped' state	IWC, 1982
Stenella coeruleoalba			
Japan	0.031–0.032	Computed in complex manner, observed F, assumed M, est. N, CI, sex ratio	Kasuya and Miyazaki, 1975
Japan	0.023–0.024	Above data re-evaluated from new age determinations and catch data	Kasuya, 1976
Japan	0.044	'Intrinsic' rate, extrapolated from series of r_t, N_t	Kasuya, 1976

tions of other, directly measured (or assumed) statistics. It is generally assumed that one or both categories vary in a density-dependent manner such that net reproduction increases as density decreases from the so-called carrying capacity level. Such a change in net reproduction was estimated to have occurred for *Stenella coeruleoalba* near Japan (Kasuya, 1976).

The general category of 'gross' rates (Table 9) includes estimates of crude birth rates (b) (Keyfitz, 1977) and gross annual reproductive rates (GARR) (Perrin *et al.*, 1976; Smith, 1983). Ideally the crude birth rate is estimated as $b = \int_{x=0}^{\infty} c_x m_x dx$, where m_x is the probability that a female aged x will give birth during each time period, and c_x is the proportion of the population composed of mature females aged x (Keyfitz, 1977). In practice the crude birth rate has been calculated as the estimated number of newborn calves divided by the estimated total population (e.g. Saayman and Taylor, 1977; Leatherwood, 1977, Würsig, 1978). This is usually a biased estimate since (1) it doesn't consider calf mortality from birth to the census time; (2) calving is usually diffusely seasonal and some births may take place after the census; and (3) cow mortality is not considered. The degree of inaccuracy is related to the degree of calving seasonality, the timing of the census in relation to the calving pulse, and the differentials in mortality between newborn calves, reproductive females and the rest of the population. The most accurate estimate of this type would be made from a census taken just following the completion of a very sharply-defined annual calving period. Even then it would be an overestimate, not considering cow mortality during the previous time period. (Such mortality is implicitly considered in the 'ideal' formulation given above).

The other type of gross rate, 'GARR', is usually estimated as the product of the proportion of the population that is female, the proportion of females sexually mature and the annual pregnancy rate (APR). GARR has been shown to be very sensitive to the method of estimation of APR (Perrin and Henderson, 1984; Henderson *et al.*, 1980). Estimation of GARR by the product method also requires the assumption of unbiased estimates of sex ratio and the proportion of females which are sexually mature; it is therefore sensitive to problems in estimating these parameters (as discussed above). However, GARR can also (more simply) be estimated as the proportion of pregnant females in the total population, with adjustment for length of gestation. While subject to some of the same assumptions this method is more straightforward than the product method.

The 'Method-2' estimates of GARR of Perrin *et al.* (1977) are invalid for reasons discussed above in the section on lactation.

GARR and the crude birth rate differ in that the latter includes integration of mortality of cows while GARR does not. Both statistics can be useful indices of relative population status. Especially with GARR, within-population comparisons over time are more informative than between-population comparisons. Polacheck (1982) has shown that age-structure effects alone can confound between-population comparisons of GARR estimates, obscuring any looked-for trend in GARR with population level (e.g. see Perrin and Henderson, 1984).

Net reproductive rates represent reproduction in excess of mortality for a population as a whole. They are extremely difficult to obtain for cetaceans, as demonstrated by the paucity of points in Table 10. In the strict context of human demography, the term 'net reproduction' refers to R_0, which is the number of female offspring expected to be born to a female given existing rates of age-specific survival and reproduction (Keyfitz, 1977). In practice, for delphinids, the more general definition given above is usually the one used. One method of estimating net reproduction which has been considered is the subtraction of population natural mortality from GARR (Smith, 1983). This is incorrect, as the natural mortality should be subtracted from crude birth rate to estimate net increase. Unfortunately, natural mortality is also very difficult to measure and (in the case of *Stenella* spp.) must be assumed from comparison with other populations. In this case, the GARR of an assumedly unexploited stock has been taken as equivalent to natural mortality for that stock. This second GARR has then been subtracted from that for the exploited population. This systematically overestimates net recruitment for the exploited population (personal communication to SBR from D. Goodman).

The most accurate way to measure net reproduction is to observe net changes in total population size in the absence of (or concomitant with a known level of) removals by humans. So far this has been feasible only for small groups of killer whales in the Pacific Northwest in which nearly all individuals are identifiable (Table 10).

Another method which has been employed to estimate net reproduction of a delphinid population is that utilized by Kasuya (1976) and Kasuya and Miyazaki (1975) for *Stenella coeruleoalba* off Japan. Theirs is a fairly complex series of computations which is based upon observed fishing mortality, estimated sex ratio, age structure, population size and an assumed natural mortality rate (i.e. a version of GARR – M, which doesn't explicitly compute GARR enroute).

No variances are listed for gross or net rates in Tables 9 or 10. This is because they were usually not reported in the source literature. It would be possible to derive and compute them in most cases. The ranges reported (0.026–0.144 gross and 0.017–0.032 net) reflect different estimation methods and different amounts and quality of data and represent populations in a variety of states: heavily, lightly or not exploited. Consequently it is not appropriate to draw any general inferences from the ranges except perhaps as indications of reasonable limits for these parameters.

DISCUSSION

Effects of Seasonality

Seasonality of mating and calving has been demonstrated for all delphinids that have been studied in any depth, although the degree of seasonality (intensity of breeding peaks) varies greatly. The impact of seasonality on estimating parameters depends on the degree of seasonality (Fig. 5) and also on the length of gestation and lactation. For example, if pregnancy and lactation each last about a year and breeding peaks are moderately diffuse (as in *S. attenuata* in the eastern Pacific – Perrin *et al.*, 1976), seasonality can be expected to have negligible effect on estimates of reproductive parameters. On the other hand, if pregnancy lasts about a year and a third (as in the pilot whales and the killer whale – Table 2), even moderate seasonality can lead to considerable bias in estimates. Barlow (1984) discusses the nature and impact of seasonal bias.

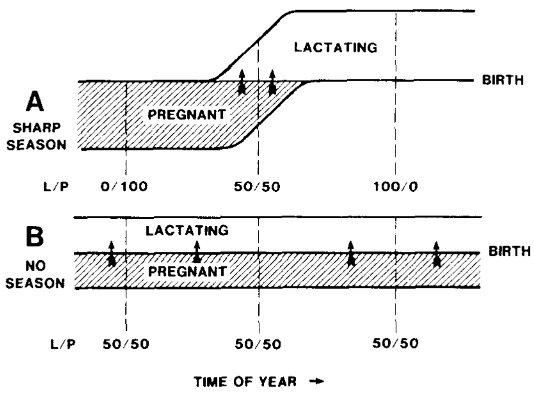

Fig. 5. Effect of sharp breeding seasonality on estimates of pregnancy and lactation. A hypothetical extreme case in which pregnancy and lactation each last six months.

Effects of Schooling Segregation

Estimates of reproductive parameters based on samples from a catch assume that the samples accurately represent the population at large in terms of age, sex and reproductive condition, and initial population studies of several delphinids relied on this assumption (*Delphinus delphis* – Mayarova and Danilevskiy, 1934; Sleptsov, 1941; *Stenella coeruleoalba* – Kasuya, 1972; *S. attenuata* and *S. longirostris* – Perrin *et al.*, 1976 and 1977, Perrin and Henderson, 1984; Henderson *et al.*, 1980). More recent work, however, has indicated that schooling segregation of one sort or another may be a general feature of delphinid life history and must be taken into account in estimating reproductive parameters (Norris and Dohl, 1980a and b; Würsig and Würsig, 1980; Miyazaki and Nishiwaki, 1978). As discussed above, Kleinenberg (1956) discovered that female common dolphins, *D. delphis*, in the Black Sea to some extent school separately during calving and early lactation in an offshore area not usually involved in the dolphin fishery, leading to erroneously high estimates of pregnancy rate and low estimates of length of lactation based on samples of the catch. The estimate of the length of the calving cycle is now about twice the earlier estimates, about 2 years rather than about 1 year (Sokolov, 1962), a difference obviously of great import to assessment and management. The most recent parameter estimates for *S. coeruleoalba* off Japan (Miyazaki, 1984; Kasuya, 1984) take into account the now-well-documented existence of several kinds of schools that are sampled differentially by the fishery (Miyazaki and Nishiwaki, 1978). The most recent information on age structure of the northern offshore population of *S. attenuata* in the eastern Pacific (personal communication, A. A. Hohn, A. C. Myrick, Jr. and J. Barlow) indicates that a substantial portion of females just at or below the average age at attainment of sexual maturity are not represented in the samples of dolphins killed incidentally in the tuna fishery and probably school separately in schools that for some reason are not associated with tuna, throwing all the published estimates of reproductive parameters in the population (cited above) into question.

Clearly schooling segregation is possibly a general phenomenon in delphinids, and it should not be assumed to not exist or not be of importance in any population. In some cases, the sampling problems caused by it may be insoluble but they cannot be denied.

Effects of Geographical Variation

As can be seen in the various tables and in the appendices to this report, estimates of life-history parameters often vary sharply between populations of the same species. Several reasons for this are possible:

1. Sample sizes were inadequate, and the differences are ascribable to statistical error.
2. The samples were biased in one case or the other and were not accurately representative of the population(s).
3. Different analytical methods were used to arrive at the estimates.
4. The differences reflect real differences in the status

of the populations, e.g. change in carrying capacity or density (discussed in next section).

(5) The differences are real and inherent, i.e. genetically determined geographical variation.

For dynamic parameters such as age at attainment of sexual maturity, pregnancy rate and length of lactation, it is difficult or impossible to determine whether reasons 2, 4, or 5 are responsible for differences in estimates. For example, the differences between estimates for *Stenella attenuata* in the eastern Pacific and the western Pacific (Tables 4, 6 and 7) could be due to differential bias known to exist (but not measured – Perrin and Oliver, 1982; Miyazaki, 1977) in the two kinds of fisheries involved, to the differential status *vis-a-vis* exploitation (Smith, 1983) or, at least partially, to inherent differences in basic life-history features. It is interesting to note, however, that where problems of sampling bias are thought to be uniform and analytical methodologies are the same for two or more populations of the same species, e.g. *S. attenuata* and *S. longirostris* in the eastern Pacific, differences in most or all estimates of dynamic parameters are statistically insignificant.

Some parameters, such as maximum size and average size of adults, vary geographically independent of dynamic factors. *Tursiops truncatus* is a notable example. The range of variation in adult length (Appendix 1) is enormous, from 202 cm for the smallest female to 381 cm for the largest male, nearly a two-fold difference. The sample sizes for adult female bottlenose dolphins from two regions, Florida and the western North Pacific (Appendix 3), are sufficiently large to allow determination that the difference in average length (239 cm vs 288 cm) is real ($P < 0.001$). The differences in maximum size, length of largest immature and length of smallest mature animals (Appendix 1) between samples from several other regions suggest that there are probably real differences among them as well (eastern North Atlantic, Black Sea, western North Atlantic, Gulf of Mexico, eastern North Pacific, and Indian Ocean – the '*aduncus*' form). This pattern of wide geographical variation in the best-known delphinids and similar patterns in other species for which large volumes of data have been available for two or more regions (e.g. *Stenella longirostris*, and *Delphinus delphis*, Appendices 1 and 3) suggest that considerable geographical variation in size is to be expected in any broadly distributed small cetacean and should be taken into account in any deductive modeling of relationships among parameters (discussed below).

Effects of Exploitation

Population and management models that incorporate the concept of net production (sustainable yield available for harvest, or population growth increment) are based on the assumption that reproductive rates and/or natural mortality rates change with population density (Perrin and Donovan, 1984; Smith, 1983). The reproductive parameter estimates tabulated here can be examined for correlation with population status (present size/pre-exploitation size). The species for which large amounts of data exist for one population through time (or for more than one population of the same species for which the analytical methods are the same) and any sampling biases can be expected to be the same, are *Stenella longirostris* (in the eastern tropical Pacific) and *S. coeruleoalba* (in the western North Pacific). In a simple comparison of trends in reproductive parameters with population status (Table 11), the estimates do not behave entirely as would be predicted by the assumption of density-dependent response. For *S. longirostris*, age at attainment of sexual maturity is greater in the less exploited southern whitebelly population, as expected, and the ranking in pregnancy rate parallels status in the expected way, but length of lactation shows a trend the reverse of what would be expected, i.e. it is longest in the most-exploited population and shortest in the least-exploited population (due to the same trend in length of the 'resting period' Table 7). Perrin and Henderson (1984) found that estimated gross reproductive rate is not different (at $\alpha = 0.05$) in the eastern and northern whitebelly populations, although the former is probably at less than 25% of its original size and the latter at more than 75% of original (Smith, 1983).

For the heavily exploited population of *S. coeruleoalba* off Japan, Kasuya and Miyazaki (1975) estimated that pregnancy rate has increased and length of lactation decreased over the period 1952 to present but the lowest estimate of pregnancy rate and highest estimate of

Table 11

Comparison of trends in reproductive-parameter estimates to trends in status of populations in two delphinids. Rankings are of estimates from Tables 4, 6 and 7

	Percent of pre-exploitation size (rank: 1 is largest)	Age at attainment of sexual maturity (rank: 1 is highest)	Annual pregnancy rate (rank: 1 is lowest)	Length of lactation (rank: 1 is longest)
Stenella longirostris				
E. trop. Pacific				
S. whitebelly	1	—	1	3
N. whitebelly	2	1	2	2
Eastern	3	2	3	1
S. coeruleoalba				
W. Pacific				
1952–1958	1	—	2	2
1961–1968	2	—	1	1
1970–1973	3	—	3	3

length of lactation are for an intermediate period, 1961–68.

These simple comparisons suggest that reproductive parameters may behave in unexpected ways in a population under exploitation (see also section above on net reproductive rate).

Relationships Between Parameters

Ohsumi (1979) has extensively reviewed the topic of deductive modelling to estimate reproductive parameters. In the context of the present review, two cautionary points suggest themselves.

In any comparison across species or populations, care should be taken to use similarly derived estimates. For example, in modeling a relationship between size and other parameters (mortality rate, maximum net reproductive rate, etc.), the possible choices of measures of size include length at attainment of sexual maturity in males or females, average size of adult males or females, asymptotic length and other indices. Whatever the index used, it should be of the same parameter and calculated in the same way throughout. Further, and perhaps more difficult to ensure, any morphological or quantitative criteria used in estimating, e.g. the histological criteria of sexual maturity in males, should be comparable.

Another important point is that geographical variation should be taken into account in any analysis based on specimens that come from more than one location, or that come from only one population when considerable geographical variation is known to exist. Thus the results of an analysis relating mortality rate to body size across several species might be different (and probably more useful) if the component estimates included estimates for two or more populations of *Tursiops truncatus* than if they included only a pooled *Tursiops* estimate or an estimate for only one population. In a deductive analysis involving several parameters, it is, of course, essential that the estimates of input parameters for a species come from the same or similar populations of the species.

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[*Appendices 1–4 are on the following 8 pages*]

Appendix 1

Length data for delphinids. Sources listed for tabulated values; other sources consulted (which contributed to sample sizes) are included in Literature Cited

Species and region (stock in parentheses)	Largest fetus		Smallest individual		Largest immature animal				Smallest mature animal				Largest individual				Source
					Male		Female		Male		Female		Male		Female		
	cm	(*n*)	cm	(*n*)	cm	(*n*)	cm	(*n*)	cm	(*n*)	cm	(*n*)	cm	(*n*)	cm	(*n*)	
Steno bredanensis																	
All regions	87	(4)	—	—	—	—	—	—	216	(28)	212	(14)	265	(68)	255	(65)	Cadenat, 1949; Layne, 1965; Lütken, 1889; Perrin and E. Walker, 1975
Sotalia fluviatilis																	
Coastal	59	(1)	92	(> 13)	157	(3)	170	(4)	167	(4)	162	(4)	187	(7)	182	(8)	Best and da Silva, 1984; Carvalho, 1963; Harrison and Brownell, 1971; van Utrecht, 1981
Riverine	71	(3)	83	(> 28)	138	(> 9)	132	(> 4)	140	(> 6)	139	(> 7)	152	(> 17)	149	(> 11)	
Sousa chinensis																	
All regions	—	—	97	(9)	—	—	—	—	—	—	—	—	320	(6)	244	(> 5)	Blanford, 1888–91; Ross, 1979
Sousa teuszii																	
E. trop. Atlantic	—	—	—	—	—	—	—	—	—	—	—	—	248	(3)	235	(3)	Cadenat and Paraiso, 1957; Cadenat, 1959
Peponocephala electra																	
All regions	65	(1)	112	(8)	212	(2)	229	(3)	264	(3)	257	(1)	273	(9)	257	(8)	Bryden *et al.*, 1977; Perrin, 1976
Feresa attenuata																	
All regions	53	(2)	82	(16)	—	—	—	—	216	(2)	221	(2)	264	(14)	243	(12)	Best, 1970; Nishiwaki *et al.*, 1965; Perrin and Hubbs, 1969; Pryor *et al.*, 1965; Ross, 1979
Pseudorca crassidens																	
All regions	183	(> 10)	157	(> 429)	366	(12)	364	(> 10)	372	(28)	349	(> 54)	596	(> 119)	506	(> 253)	Mizue and Yoshida, 1961; Purves and Pilleri, 1978; Ross, 1979; Scott and Green, 1975; Tomilin, 1957
Orcinus orca																	
All regions	274	(272)	183	(> 2,741)	617	(> 4)	488	(> 16)	520	(> 6)	457	(> 215)	975	(> 2,306)	853	(1,744)	Allen, 1977; Anon. 1982b; Best and Ross, 1977; Carl, 1945; Christensen, 1982; Condy, van Aarde and Bester, 1978; Fiscus and Niggol, 1965; Ivashin, 1981; Jonsgård and Lyshoel, 1970; Mikhalev *et al.*, 1981; Nishiwaki and Handa, 1958; Pike and MacAskie, 1969; Ridgway, 1979; Scheffer, 1967; Tomilin 1957
North Atlantic	255	(239)	183	(693)	559	(—)	488	(10)	660	(—)	457	(111)	975	(1,239)	853	(822)	
North Pacific	193	(1)	228	(134)	520	(2)	—	—	760	(1)	560	(1)	829	(> 56)	698	(52)	
South Pacific	140	(1)	200	(12)	—	—	—	—	—	—	—	—	805	(5)	670	(6)	
Indian Ocean	—	—	381	(37)	—	—	—	—	—	—	—	—	884	(25)	792	(12)	
Antarctic	250	(16)	320	(1,229)	—	—	370	(1)	—	—	540	(91)	910	(652)	762	(577)	
Globicephala melaena																	
All regions	195	(308)	137	(3,629)	472	(65)	386	(> 471)	48	(> 5)	351	(89)	762	(> 1,398)	570	(2,086)	Anon., 1981a and 1982a; Budker, 1968; Duguy 1973–82; Duguy and Budker, 1972; Fraser, 1974; Gray, 1846; Guiler, 1978; Paulus, 1960; Sergeant, 1962
E. North Atlantic	195	(2)	137	(206)	—	—	238	(> 5)	—	—	375	(5)	762	(88)	570	(56)	
W. North Atlantic	190	(306)	165	(3,399)	472	(65)	386	(466)	48	(> 5)	351	(84)	617	(> 1,378)	511	(2,020)	
New Zealand	—	—	177	(14)	—	—	—	—	—	—	—	—	600	(7)	500	(5)	
Tasmania	—	—	187	(95)	—	—	—	—	—	—	—	—	620	(40)	555	(55)	
G. macrorhynchus																	
All regions	140	(25)	135	(661)	437	(16)	396	(17)	508	(3)	335	(6)	610	(> 231)	525–550	(> 344)	Alagarswami *et al.*, 1973; Hall *et al.*, 1971; Harrison *et al.*, 1972; Layne, 1965; Lowery, 1974; Perrin and Myrick, 1980; Ross, 1979; SEAN, 1977; van Bree *et al.*, 1978; Walker, 1975; Yonekura *et al.*, 1980
W. North Atlantic	—	—	162	(369)	383	(1)	334	(3)	—	—	335	(2)	535	(> 95)	478	(> 146)	
E. North Pacific	104	(2)	135	(64)	352	(2)	336	(8)	—	—	396	(3)	590	(23)	480	(32)	
W. North Pacific	140	(17)	182	(153)	—	—	—	—	—	—	—	—	491	(51)	392	(102)	
Indian Ocean	—	—	168	(95)	437	(1)	396	(2)	508	(3)	405	(1)	610	(> 49)	525–550	(35)	

Appendix I (*continued*)

Lagenorhynchus obliquidens																	
North Pacific	102	(7)	124	(269)	198	(13)	216	(28)	170	(8)	170	(> 13)	230–234	(> 162)	236	(> 115)	Fiscus and Niggol, 1965; Harrison *et al.*, 1972; Harrison and McBrearty, 1977; Kasuya and Izumisawa, 1981; Scheffer and Slipp, 1948
L. acutus																	
North Atlantic	114	(> 59)	108	(233)	210	(16)	222	(6)	244	(4)	194	(51)	275	(> 99)	243	(> 83)	Sergeant *et al.*, 1980; Tomilin, 1957; van Utrecht, 1959
L. obscurus																	
Southern Hemisphere	—	—	92	(37)	—	—	130	(1)	—	—	170	(3)	211	(10)	193	(21)	Allen, 1977; Anon., 1978; Best, 1976; Brownell, 1974
L. cruciger																	
Southern Hemisphere	—	—	110	(3)	—	—	—	—	—	—	—	—	—	—	*183*	(2)	Brownell, *in press*; Fraser, 1966; Liouville, 1913; Nichols, 1908
L. albirostris																	
North Atlantic	125	(> 6)	119	(> 152)	257	(2)	249	(5)	251	(2)	250	(9)	315	(> 36)	305	(> 53)	Duguy, 1982; Fraser, 1974; Tomilin, 1957; van Utrecht, 1981; Weber, 1887
L. australis																	
E. South Pacific	—	—	—	—	—	—	—	—	—	—	—	—	216	(1)	—	—	Kellogg, 1941
Lagenodelphis hosei																	
All regions	45	(3)	95	(23)	184	(3)	231	(2)	264	(1)	226	(> 4)	264	(6)	264	(12)	Miyazaki and Wada, 1978; Perrin *et al.*,1973; Perrin and Leatherwood, in press; Ross, 1979;
Tursiops truncatus																	
All regions	122	(78)	84	(> 3,338)	314	(91)	295	(72)	202	(51)	190	(194)	381	(~ 1,400)	367	(~ 1,400)	Allen, 1977; Cadenat, 1959; Cornell, 1977; *van Deinse, 1946*; Duguy, 1974, 1976, 1980; Fraser, 1934, 1953; Gunter, 1942; Harmer, 1927; Harrison *et al.*, 1972; Harrison and Fanning, 1973; Harrison and McBrearty, 1977; Kasuya, 1973; Kasuya and Izumisawa, 1981; Kleinenberg, 1956; Leatherwood *et al.*, 1972; Norris and Prescott, 1961; Ross, 1977, 1979; SEAN, 1976, 1977, 1979; 1981; Sergeant *et al.*, 1973; Tomlin, 1957; True, 1889; Walker, 1981; Zeiller, 1977
E. North Atlantic	91	(2)	116	(235)	314	(1)	295	(1)	—	—	312	(3)	381	(> 74)	350	(50)	
Mediterranean	—	—	140	(25)	160	(1)	—	—	—	—	300	*(1)*	*330*	*(14)*	*320*	*(6)*	
Black Sea	—	—	122	(> 1,450)	—	—	—	—	—	—	226	(> 4)	310	(~ 700)	234	(4)	
W. North Atlantic[1]	117	(6)	92	(305)	210	(3)	—	—	—	—	232	(6)	310	(121)	339	(132)	
Florida coasts	112	(8)	95	(284)	277	(32)	238	(22)	242	(10)	225	(38)	290	(127)	276	(143)	
Gulf of Mexico[1]	122	(7)	91	(123)	—	—	239	(1)	218	(3)	229	(13)	380	(43)	367	(46)	
E. North Pacific (all forms)	—	—	110	(50)	269	(3)	264	(1)	263	(7)	276	(6)	340	(20)	330	(27)	
E. North Pacific (onshore)	—	—	—	—	269	(1)	255	(4)	297	(4)	—	—	333	(8)	307	(9)	
E. North Pacific (offshore)	—	—	114	(14)	234	(2)	264	(5)	263	(3)	276	(3)	310	(5)	290	(9)	
E. tropical Pacific	88	(2)	—	—	236	(5)	242	(7)	244	(7)	243	(2)	266	(12)	256	(9)	
W. North Pacific	120–129	(60)	—	—	*292*	*(18)*	*280–289*	*(8)*	288	(12)	250–259	(107)	335	(194)	320–329	(258)	
Indian Ocean (all forms)	60	(2)	84	(84)	278	(18)	280	(15)	202	(13)	190	(12)	327	(56)	280	(33)	
Indian Ocean ('*aduncus*')	60	(2)	84	(89)	235	(16)	220	(14)	202	(13)	190	(12)	254	(44)	252	(41)	
Indian Ocean ('*truncatus*')	—	—	270	(7)	278	(3)	280	(1)	—	—	—	—	327	(5)	280	(2)	
E. tropical Atlantic	—	—	—	—	—	—	—	—	—	—	—	—	368	(11)	350	(7)	
Grampus griseus																	
All regions	166	(10)	135	(> 243)	297	(15)	280–284	(14)	262	(10)	260–264	(22)	383	(> 81)	366	(69)	Duguy, 1974, 1979, 1981; Fraser, 1934, 1974; Kasuya and Izumisawa, 1981; Murie, 1870; Pilleri and Gihr, 1969b; Ross, 1979; SEAN, 1976, 1980; Tomilin, 1957; True, 1889
Mediterranean	—	—	135	(62)	—	—	—	—	—	—	298	(1)	360	(11)	310	(10)	
E. North Atlantic	166	(4)	173	(78)	244	(1)	—	—	—	—	320	(3)	383	(29)	366	(27)	
W. North Atlantic	—	—	158	(25)	—	—	—	—	—	—	305	(5)	340	(9)	318	(12)	
W. North Pacific	90–94	(4)	180–184	(43)	297	(11)	280–284	(10)	262	(9)	260–264	(13)	307	(20)	285–289	(23)	
S.W. Indian Ocean	84	(2)	163	(19)	243	(2)	257	(4)	—	—	291	(1)	325	(9)	277	(6)	
Stenella longirostris																	
All regions	84	(331)	70	(5,001)	192	(9,249)	190	(1,067)	160	(766)	152	(1,054)	235	(2,340)	204	(2,621)	Layne, 1965; Mead *et al.*, 1980; Oliver, Walker and Miller, 1982; Perrin, 1975a; Perrin *et al.*, 1977, 1979, 1981; Perrin and Henderson, 1984; Perrin and Oliver, 1982; Schmidly and Shane, 1978
Tropical Atlantic	81	(2)	90	(41)	158	(1)	190	(7)	173	(17)	177	(17)	208	(18)	204	(22)	
E. tropical Pacific (Costa Rican)	—	—	—	—	—	—	—	—	181	(2)	193	(3)	216	(2)	203	(3)	
E. tropical Pacific (eastern)	84	(169)	70	(2,566)	192	(594)	182	(608)	160	(356)	152	(536)	195	(1,102)	187	(1,297)	
E. tropical Pacific (n. whitebelly)	82	(159)	72	(2,218)	191	(330)	188	(433)	160	(319)	157	(425)	203	(1,063)	195–199	(1,155)	
E. tropical Pacific (s. whitebelly)	—	—	85–89	(123)	—	—	—	—	167	(69)	162	(63)	235	(142)	190–194	(119)	

Appendix 1 (*continued*)

Species and region (stock in parentheses)	Largest fetus		Smallest individual		Largest immature animal				Smallest mature animal				Largest individual				Source
					Male		Female		Male		Female		Male		Female		
	cm	(*n*)	cm	(*n*)	cm	(*n*)	cm	(*n*)	cm	(*n*)	cm	(*n*)	cm	(*n*)	cm	(*n*)	
S. clymene																	
Atlantic	—	—	—	—	—	—	188	(1)	184	(2)	—	—	196	(7)	188	(2)	Perrin *et al.*, 1981
S. plagiodon																	
Atlantic	—	—	120	(40)	—	—	—	—	—	—	—	—	223	(15)	226	(22)	Caldwell and Caldwell, 1966; SEAN, 1975, 1981
Stenella coeruleoalba																	
All regions	108	(114)	80	(6,236)	—	—	—	—	—	—	—	—	256	(> 2,272)	240–250	(> 2,239)	Duguy, 1980; Duguy *et al.*, 1978; Gurevich and Stewart, 1979; Kasuya, 1972; Miyazaki, 1977; Perrin and Oliver, 1982; Ross, 1979; SEAN, 1979
Mediterranean	—	—	80	(232)	—	—	—	—	—	—	—	—	220	(97)	215–220	(96)	
North Atlantic	—	—	116	(72)	—	—	—	—	—	—	194	(1)	248	(41)	244	(22)	
E. trop. Pacific	80	(13)	90	(202)	—	—	—	—	—	—	—	—	225–229	(103)	220	(99)	
W. North Pacific	108	(99)	95	(5,493)	240–250	(~ 127)	230–240	(~ 231)	200–210	(222)	200–210	(545)	256	(> 2,003)	240–250	(> 2,006)	
S.W. Indian Ocean	—	—	—	—	244	(5)	206	(1)	218	(5)	200	(5)	250	(16)	228	(10)	
S. attenuata																	
All regions	106	(562)	75–79	(6,347)	202	(> 259)	209	(440)	162	(> 820)	167	(> 1,462)	257	(> 3,566)	240–244	(> 3,235)	Allen, 1977; Best, 1969; Kasuya *et al.*, 1974; Nishiwaki *et al.*, 1965; Perrin, 1975a; Perrin *et al.*, 1976; Perrin and Oliver, 1982; Ross 1979
E. tropical Pacific (coastal)	—	—	90–94	(128)	—	—	—	—	203	(37)	184	(76)	257	(43)	240–244	(85)	
E. tropical Pacific (n. and s. offshore)	90	(468)	75–79	(5,348)	201	(> 150)	193	(307)	179	(> 724)	167	(> 1,127)	225–229	(> 3,141)	220–224	(> 2,792)	
Central Pacific	—	—	—	—	180	(1)	160	(1)	182	(6)	189	(3)	202	(8)	203	(4)	
W. North Pacific	—	—	89	(959)	202	(103)	209	(132)	162	(44)	173	(253)	234	(> 300)	220	(> 344)	
S.W. Indian Ocean	—	—	89	(9)	198	(3)	—	—	216	(2)	215	(1)	220	(5)	215	(5)	
Delphinus delphis																	
All regions	108	(> 446)	70	(> 45,650)	206	(33)	222	(> 1,973)	171	(> 5,090)	141–150	(> 8,583)	260	(> 27,211)	230	(> 26,368)	Allen, 1977; Aloncle, 1964; Anon., 1981a; Cadenat, 1957; 1959; Casinos and Vericad, 1976; Collet, 1981; Danilevskiy and Tyutyunnikov, 1968; Duguy, 1973, 1980; Evans, 1975; Fischer, 1881; Fraser, 1934, 1946, 1953, 1974; Guiler, 1978; Gurevich and Stewart, 1978; Hui, 1977; Kleinenberg, 1956; Legendre, 1926; Mercer, 1973; Mitchell, 1970; Ross, 1979; Scammon, 1874; SEAN, 1975; Sleptsov, 1941; Slijper, 1936; Tomilin, 1957; van Deinse, 1946; van Utrecht, 1981
Black Sea	95	(> 287)	70	(> 43,000)	171–180	(—)	161–170	(> 1,928)	171	(> 5,000)	141–150	(> 8,500)	219	(> 25,000)	196–200	(> 25,000)	
Mediterranean	—	—	120	(60)	—	—	—	—	—	—	—	—	222	(33)	208	(24)	
E. North Atlantic	108	(39)	84	(420)	206	(12)	194	(14)	206	(16)	174	(18)	258	(126)	230	(272)	
W. North Atlantic	—	—	—	—	—	—	—	—	—	—	212	(1)	236	(8)	212	(15)	
E. N. Pacific (Baja neritic)	—	—	—	—	—	—	—	—	—	—	—	—	240–244	(~ 16)	206	(2)	
E. N. Pacific (n. temp. offshore)	80–84	(40)	80–84	(> 109)	—	—	—	—	—	—	—	—	179	(5)	195	(8)	
E. tropical Pacific (n. trop.)[2]	> 80–89	(25)	75–79	(453)	—	—	—	—	—	—	—	—	240–244	(216)	220–224	(236)	
E. tropical Pacific (cent. trop.)	80–89	(81)	65–69	(1,468)	—	—	—	—	176–180	(40)	176–180	(48)	235–239	(741)	205–210	(625)	
W. South Pacific	84	(1)	91	(31)	199	(5)	174	(5)	203	(5)	198	(3)	260	(> 19)	209	(16)	
W. North Pacific	—	—	128	(22)	—	—	—	—	—	—	—	—	197	(7)	187	(13)	
S.W. Indian Ocean	85	(3)	90	(26)	186	(6)	222	(8)	236	(4)	212	(1)	254	(13)	222	(12)	
E. tropical Atlantic	76	(7)	123	(72)	—	—	197	(1)	189	(9)	198	(5)	235	(34)	222	(31)	
Lissodelphis borealis																	
North Pacific	—	—	114	(49)	212	(4)	200	(2)	220	(7)	201	(9)	307	(23)	229	(22)	Leatherwood and Walker, 1979; Sullivan and Houck, 1979
L. peronii																	
S. Hemisphere	—	—	184	(10)	—	—	—	—	—	—	—	—	~ 210	(5)	~ 230	(5)	Baker, 1981; True, 1889
Cephalorhynchus hectori																	
New Zealand	48	(1)	85	(18)	—	—	—	—	—	—	153	(1)	137	(10)	153	(4)	Abel *et al.*, 1971; Anon., 1981a and 1982a; Baker, 1978; Mörzer-Bruyns and Baker, 1973
C. eutropia																	
No data	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
C. heavisidii																	
No data	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
C. commersonii																	
W. South Atlantic	—	—	92	(37)	—	—	144	(2)	136	(1)	—	—	137	(15)	146	(10)	Harmer, 1922; Lockyer *et al.*, 1981; Spotte *et al.*, 1979

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[1] Exclusive of Florida.

[2] May include some 'Baja neritic' (on the average larger).

Appendix 2

Testis data for delphinids

Species and region (stock in parentheses)	Minimum weight of 'adult' testis		Maximum weight of testis		Source
	g	(*n*)	g	(*n*)	
Steno bredanensis					
W. North Pacific	175	(9)	1,150	(9)	Miyazaki, 1980
Sotalia fluviatilis					
Amazon basin	27	(7)	1,060	(10)	Best and da Silva, 1984; Harrison and Brownell, 1971
Peponocephala electra					
W. trop. Pacific	674	(3)	685	(3)	Bryden *et al.*, 1977
Central trop. Atlantic	~ 1,100[1]	(1)	~ 1,100[1]	(1)	Goodwin, 1945
Feresa attenuata					
Central trop. Pacific	321	(1)	377	(1)	Pryor *et al.*, 1965
Pseudorca crassidens					
W. North Pacific	~ 1,700[1]	(21)	~ 7,400[1]	(31)	Kasuya and Izumisawa, 1981
Orcinus orca					
All regions	—	—	23,100	(64)	Ross, 1979; Allen, 1977; Mikhalev *et al.*, 1981; Harrison *et al.*, 1972
Antarctic	—	—	23,100	(57)	Mikhalev *et al.*, 1981
Globicephala melaena					
E. North Atlantic	575	(12)	7,200	110)	Sergeant, 1962
G. macrorhynchus					
S.W. Indian Ocean	770	(4)	3,540	(4)	Ross, 1979
E. trop. Pacific	264[2]	(7)	548[2]	(10)	Walker, 1981
W. North Pacific	~ 50[1]	(12)	~ 700[1]	(29)	Kasuya and Izumisawa, 1981
W. South Pacific	505	(1)	572	(8)	Ross, 1979
S.W. Indian Ocean ('*aduncus*')	318	(5)	800	(5)	Ross, 1979
Grampus griseus					
E. North Pacific	3,130	(3)	6,360	(3)	Orr, 1966; Harrison *et al.*, 1972
W. North Pacific	~ 350[1]	(9)	~ 5,300[1]	(20)	Kasuya and Izumisawa, 1981
Lagenorhynchus obliquidens					
E. North Pacific	548	(16)	559	(16)	Harrison *et al.*, 1972
W. North Pacific	~ 170[1]	(25)	~ 390[1]	(87)	Kasuya and Izumisawa, 1981
L. obscurus					
E. South Atlantic	—	—	800	(—)	Best, 1976
L. acutus					
W. North Atlantic	180	(5)	370	(21)	Sergeant *et al.*, 1980
Lagenodelphis hosei					
W. North Pacific	990	(1)	990	(1)	Tobayama *et al.*, 1973
S.W. Indian Ocean	1,280	(1)	1,280	(2)	Ross, 1979
Tursiops truncatus					
All regions	~ 50[1]	(45)	983	(98)	Below, and Harrison and Fanning, 1974, Allen, 1977 and Leatherwood, 1978

[1] Estimated as ½ combined testis weight.

[2] Includes epididymis.

Appendix 2 (*continued*)

Species and region (stock in parentheses)	Minimum weight of 'adult' testis		Maximum weight of testis		Source
	g	(*n*)	g	(*n*)	
Florida and Gulf of Mexico	280	(6)	532	(19)	Harrison *et al.*, 1972; Sergeant *et al.*, 1973; Harrison and Ridgway, 1971;
E. North Pacific (onshore)	536	(4)	983	(5)	Walker, 1981
E. North Pacific (offshore)	248	(3)	530	(5)	Walker, 1981
S. attenuata					
E. trop. Pacific (offshore)	100[2]	(> 207)	~ 1,200[1,2]	(> 415)	Harrison, 1969; Harrison *et al.*, 1972; Perrin *et al.*, 1976
W.N. Pacific	66	(142)	~ 650[1]	(> 138)	Kasuya *et al.*, 1974; Kasuya, 1976
S.W. Indian Ocean	—	—	121	(5)	Ross, 1979
Stenella longirostris					
Gulf of Mexico	320	(9)	980	(12)	Mead *et al.*, 1980; Layne, 1965
E. trop. Pacific (eastern)	20–30[2]	(50)	800–900	(826)	Perrin *et al.*, 1977; Perrin and Henderson, 1984
E. trop. Pacific (n. whitebelly)	60–80[2]	(92)	1,354[2]	(695)	Perrin and Henderson, 1984
Centr. trop. Pacific	—	—	330	(8)	Harrison *et al.*, 1972; Allen, 1977;
E. trop. Atlantic	—	—	925	(2)	Cadenat and Doutre, 1959
S. coeruleoalba					
E. trop. Pacific	—	—	~ 157[1,2]	(38)	Gurevich and Stewart, 1979
W. North Pacific	8	(> 222)	~ 250[1]	(> 437)	Kasuya, 1976; Miyazaki, 1977; Hirose and Nishiwaki, 1971
S.W. Indian Ocean	94	(2)	136	(2)	Ross, 1979
Delphinus delphis					
Black Sea	300	(—)	1,000	(2,138)	Sleptsov, 1941
E. North Atlantic	100	(9)	800	(20)	Collet and St. Girons, 1984
E. North Pacific (offshore)	465	(12)	1,672	(31)	Harrison, 1969; Harrison *et al.*, 1972; Ridgway and Green, 1967
E. trop. Pacific (centr. trop.)	129	(12)	853	(42)	Oliver, 1973
S.W. Indian Ocean	1,815	(3)	4,085	(3)	Ross, 1979
E. trop. Atlantic	—	—	883	(7)	Cadenat, 1959
Lissodelphis borealis					
E. North Pacific	705	(2)	705	(3)	Harrison *et al.*, 1972; Sullivan and Houck, 1979
Cephalorhynchus hectori					
W. South Pacific	—	—	465	(1)	Baker, 1978

[1] Estimated as ½ combined testis weight.

[2] Includes epididymis.

Appendix 3

Average length of adults and asymptotic length in delphinids. Minimum sample size for inclusion is at least 2 for at least one column. Standard deviation given for sample size of 25 or more, where possible

Species and region (stock in parentheses)	Average length of sexually mature animals						Asymptotic length				Source
	Males			Females			Males		Females		
	cm	(*n*)	SD	cm	(*n*)	SD	cm	(*n*)	cm	(*n*)	
Steno bredanensis											
W. North Pacific	232	(24)	—	231	(11)	—	—	—	—	—	Miyazaki, 1980
E. trop. Atlantic	227	(3)	—	234	(1)	—	—	—	—	—	Cadenat, 1959
Sotalia fluviatilis											
Coastal	177	(4)	—	176	(4)	—	—	—	—	—	van Utrecht, 1981
Riverine	146	(6)	—	145	(7)	—	—	—	—	—	Best and da Silva, 1984; Carvalho, 1963
Sousa teuszii											
E. trop. Atlantic	200	(3)	—	—	—	—	—	—	—	—	Allen, 1977
Peponocephala electra											
E. South Pacific	268	(3)	—	—	—	—	—	—	—	—	Bryden *et al.*, 1977
Pseudorca crassidens											
E. North Atlantic	532	(4)	—	447	(14)	—	541	(3)	452	(10)	Peacock *et al.*, 1936; Purves and Pilleri, 1978
W. North Atlantic	520	(1)	—	458	(2)	—	—	—	—	—	Odell *et al.*, 1980
W. North Pacific	—	—	—	430	(92)	27.1	—	—	—	—	Kasuya and Izumisawa, 1981; Mizue and Yoshida, 1961
W. South Pacific	—	—	—	400	(18)	—	—	—	—	—	Scott and Green, 1975
Orcinus orca											
E. North Atlantic	945	(1)	—	566	(110)	65.5	—	—	—	—	Christensen, 1982; Gray, 1846; Jonsgård and Lyshoel, 1970
Antarctic	—	—	—	645	(91)	56.6	—	—	—	—	Mikhalev *et al.*, 1981
Globicephala melaena											
W. North Atlantic	545	(12)	—	381	(85)	11.5	~ 550	(> 4)	~ 460	(> 19)	Sergeant, 1962
G. macrorhynchus											
W. North Atlantic	—	—	—	345	(2)	—	~ 470	(—)	~ 360	(—)	Harrison *et al.*, 1972; Irvine *et al.*, 1979
E. North Pacific	—	—	—	466	(2)	—	—	—	—	—	Harrison *et al.*, 1972
W. North Pacific	453	(13)	—	358	(72)	14.2	—	—	330–360	—	Yonekura *et al.*, 1980
Lagenorhynchus obliquidens											
E. North Pacific	190	(8)	—	192	(12)	—	—	—	—	—	Fitch and Brownell, 1968; Harrison *et al.*, 1972; Ridgway and Green, 1967
L. acutus											
W. North Atlantic	250	(4)	—	224	(30)	6.0	—	—	—	—	Sergeant *et al.*, 1980
L. obscurus											
E. South Atlantic	188	(2)	—	191	(1)	—	—	—	—	—	Best, 1976
L. albirostris											
E. North Atlantic	260	(2)	—	259	(9)	—	—	—	—	—	Duguy, 1982; van Bree and Husson, 1964; van Utrecht, 1981
Lagenodelphis hosei											
All regions (4)	236	(3)	—	235	(7)	—	234	(7)	241	(4)	Perrin *et al.*, 1973; Ross, 1979; SEAN, 1978; Tobayama *et al.*, 1973
Tursiops truncatus											
Black Sea	275	(—)	—	233	(—)	—	—	—	—	—	Kleinenberg, 1956
W. North Atlantic[1]	—	—	—	252	(6)	—	—	—	—	—	Leatherwood *et al.*, 1972
Florida (both coasts)	258	(13)	—	239	(45)	8.7	270	(7)	250	(13)	Cornell, 1977; Harrison *et al.*, 1972; Harrison and McBrearty, 1977; Sergeant *et al.*, 1973; Zeiller, 1977
Gulf of Mexico[1]	241	(4)	—	251	(12)	—	—	—	259	(1)	Gunter, 1942; Harrison *et al.*, 1972; Harrison and McBrearty, 1977, Schmidly, 1978
E. N. Pacific (onshore)	—	—	—	312	(4)	—	—	—	—	—	Walker, 1981
E. N. Pacific (offshore)	283	(3)	—	282	(3)	—	—	—	—	—	Walker, 1981
E. trop. Pacific	256	(7)	—	250	(2)	—	—	—	—	—	Walker, 1981
W. North Pacific	—	—	—	288	(138)	13.4	—	—	—	—	Kasuya and Izumisawa, 1981
Indian Ocean ('*aduncus*')	239	(15)	—	237	(26)	—	239	(5)	241	(14)	Allen, 1977; Harrison and Fanning, 1973; Harrison and McBrearty, 1977; Ross, 1979

Appendix 3 (*continued*)

Species and region (stock in parentheses)	Average length of sexually mature animals: Males cm	Males (*n*)	Males SD	Females cm	Females (*n*)	Females SD	Asymptotic length: Males cm	Males (*n*)	Females cm	Females (*n*)	Source
Grampus griseus											
E. North Atlantic	—	—	—	332	(5)	—	370	(1)	342	(1)	Flower, 1872; Fraser, 1934, 1946; Harmer, 1927; Murie, 1870; Tomilin, 1957
W. North Pacific	288	(9)	—	276	(13)	—	—	—	—	—	Kasuya and Izumisawa, 1981
Stenella longirostris											
Gulf of Mexico	192	(15)	—	189	(17)	—	201	(1)	201	(1)	Mead *et al.*, 1980; Layne, 1965
E. trop. Pacific (Costa Rican)	192	(2)	—	—	—	—	—	—	—	—	Perrin, 1975a
E. trop. Pacific (eastern)	176	(594)	6.0	171	(560)	6.1	180	(12)	171	(60)	Perrin *et al.*, 1977, 1979; Perrin and Oliver, 1982
E. trop. Pacific (n. whitebelly)	179	(319)	7.0	176	(425)	6.8	180	(21)	175	(28)	Perrin and Henderson, 1984
E. trop. Pacific (s. whitebelly)	181	(69)	6.6	178	(63)	7.3	—	—	—	—	Perrin *et al.*, 1979; Perrin and Oliver, 1982
S. clymene											
Atlantic	185	(3)	—	—	—	—	—	—	—	—	Perrin *et al.*, 1981
S. coeruleoalba											
E. trop. Pacific	—	—	—	—	—	—	205	(3)	200	(2)	Gurevich and Stewart, 1979
W. North Pacific	227	(157)	—	220	(151)	—	238	(214)²	225	(584)²	Miyazaki, 1977
S.W. Indian Ocean	235	(5)	—	218	(5)	—	244	(1)	217	(2)	Ross, 1979
S. attenuata											
E. trop. Pacific (coastal)	228	(32)	10.7	209	(70)	9.0	—	—	—	—	Perrin, 1975a; Perrin and Oliver, 1982
E. trop. Pacific (n. and s. offshore)	201	(730)	8.5	187	(1,123)	7.0	200	(—)	190	(—)	Harrison *et al.*, 1972; Perrin *et al.*, 1979; Perrin and Oliver, 1982
W. North Pacific	204–207	(80)	—	192–195	(251)	—	207	(—)	194	(135)²	Harrison *et al.*, 1972; Kasuya, 1976; Kasuya *et al.*, 1974; Nishiwaki *et al.*, 1974
S.W. Indian Ocean	217	(3)	—	215	(2)	—	—	—	215	(1)	Best, 1969; Ross, 1979
Delphinus delphis											
Black Sea	178	(890)	—	(a) 170 (b) 175	(1,809) (25)	— 9.4	—	—	—	—	Mal'm and Trotskaya, 1932; Mayarova and Danilevskiy, 1934; Slepstov, 1941; Sokolov, 1962
E. North Atlantic	219	(17)	—	193	(23)	—	243	(1)	211	(3)	Collet, 1981; Fischer, 1881; Fraser, 1934; Slijper, 1936; van Utrecht and Husson, 1968
W. North Atlantic	—	—	—	211	(2)	—	—	—	—	—	Mercer, 1973; Ulmer, 1981
E. trop. Pacific (centr. trop.)	208	(40)	—	196	(48)	—	—	—	—	—	Evans, 1975
W. South Pacific	219	(5)	—	201	(3)	—	—	—	—	—	Allen, 1977; van Utrecht, 1981
S.W. Indian Ocean	242	(4)	—	212	(1)	—	—	—	212	(1)	Ross, 1979
E. trop. Atlantic	210	(9)	—	208	(5)	—	—	—	—	—	Cadenat, 1959
Lissodelphis borealis											
E. North Pacific	263	(7)	—	217	(9)	—	—	—	—	—	Leatherwood and Walker, 1979; SEAN, 1981; Sullivan and Houck, 1979
Cephalorhynchus commersonii											
W. South Atlantic	136	(1)	—	—	—	—	130	(6)	139	(2)	Lockyer *et al.*, 1981; Spotte *et al.*, 1979

[1] Exclusive of Florida.
[2] Total in analysis, mature and immature.

Appendix 4

Average age and maximum age of sexually mature delphinids, in years (y) or GLGs – terminology of Perrin and Myrick 1980 – (G)

Species and region (stock in parentheses)	Average age of sexually mature				Maximum age of sexually mature				Source
	Males		Females		Males		Females		
	y or G	(*n*)	y or G	(*n*)	y or G	(*n*)	y or G	(*n*)	
Steno bredanensis									
W. North Pacific	20y	(24)	21y	(10)	32y	(24)	30y	(11)	Miyazaki, 1980
Peponocephala electra									
W. South Pacific	27G	(2)	12G	(1)	47G	(2)	12G	(1)	Bryden *et al.*, 1977
Feresa attenuata									
S.W. Indian Ocean	14G	(2)	—	—	14G	(2)	—	—	Ross, 1979
Pseudorca crassidens									
E. North Atlantic	16y	(3)	17y	(3)	20y	(33)	22y	(40)	Purves and Pilleri, 1978
Orcinus orca									
All regions	—	—	—	—	35G	(56)	34G	(68)	Christensen, 1980; Mitchell, 1980; Ross, 1979
Globicephala melaena									
W. North Atlantic	> 11y	(58)	> 13y	(203)	26G, 14y	(165)	> 19G, > 20y	(296)	Perrin and Myrick, 1980; Ross, 1970; Sergeant, 1962
G. macrorhynchus									
W. North Atlantic	—	—	—	—	21G	(6)	49G	(11)	Perrin and Myrick, 1980; Ross, 1979
W. North Pacific	—	—	—	—	30G	(7)	> 29G	(3)	
S.W. Indian Ocean	13G	(2)	14G	(1)	15G	(2)	14G	(1)	
Lagenorhynchus obscurus									
E. South Atlantic	—	—	—	—	7y	(1)	21y	(2)	Best, 1976
L. acutus									
W. North Atlantic	—	—	12G	(26)	22G	(14)	27G	(38)	Sergeant *et al.*, 1980
Tursiops truncatus									
All regions	19y, > 12G	(17)	> 26y, > 11G	(26)	25y, 25G	(158)	> 30y, 27G	(166)	Hohn, 1980; Ross, 1977, 1979; Sergeant *et al.*, 1973
W. North Atlantic	19y	(6)	> 19y	(17)	25y, 25G	(90)	> 30y, 27G	(98)	
S.W. Indian Ocean ('*aduncus*')	> 12G	(11)	> 11G	(6)	> 17G	(11)	13G	(6)	
Grampus griseus									
S.W. Indian Ocean	—	—	> 13G	(2)	> 13G	(2)	> 17G	(2)	Ross, 1979
Stenella longirostris									
Gulf of Mexico	9G	(2)	12G	(2)	10G	(3)	12G	(4)	Mead *et al.*, 1980; Perrin *et al.*, 1977; Perrin and Henderson, 1984
E. trop. Pacific (eastern)	7–10y	(39)	—	—	12–15y	(182)	15–21y	(250)	
E. trop. Pacific (n. whitebelly)	8–12y	(57)	—	—	13–19y	(170)	16–23y	(270)	
S. coeruleoalba									
E. trop. Pacific	—	—	—	—	16G	(38)	15G	(48)	Gurevich and Stewart, 1979; Miyazaki, 1977
W. North Pacific	14y	(222)	14y	(541)	29y	(222)	28y	(541)	
S. attenuata									
E. trop. Pacific (n. offshore)	> 11G	(42)	—	—	> 17G	(42)	> 17G	(209)	Kasuya, 1976; Perrin *et al.*, 1976
W. North Atlantic	—	—	—	—	40y	(158)	46y	(200)	
Delphinus delphis									
Black Sea	—	—	15y	(17)	22y	(—)	20y	(17)	Kleinenberg and Klevezal', 1962
E. North Atlantic	—	—	—	—	> 12G	(5)	> 9G	(4)	Collet and St. Girons, 1984
Cephalorhynchus commersonii									
W. South Atlantic	—	—	—	—	15G	(13)	11G	(7)	Lockyer *et al.*, 1981