Harbour porpoises (*Phocoena phocoena*) in the North Atlantic: Biological parameters

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ABSTRACT

Biological parameters for harbour porpoises are reviewed throughout their range in the North Atlantic. Most information is based on studies of a combination of directed catches, bycatches and strandings. All these sources are valuable for providing biological information, but each carries some bias when it comes to interpretation of parameters, especially those involving age structure.

Information on age-related parameters, reproduction and growth is presented and assessed by region and/or population, of which there may be 14 throughout the North Atlantic. Among age-related parameters, maximum longevity recorded is 24 years; maximal rate of population growth is probably 9.4% but in the range 5-10%; mortality is highest in year 1, and <5% of the population live beyond 12 years; an estimate of 0.867 with a maximum age of 23 years has been given for survival. Among reproductive parameters, age at sexual maturation falls between 3-4 years for both sexes; age at first parturition is probably 4-5 years; age at first ovulation is >3 years; ovulation rates fall in the range 0.64 - 0.988 corpus per year, and reproductive interval is 1.01-1.57 years; pregnancy rates are generally in the range 0.74 - 0.986 per year, meaning that not all females produce a calf every year; there is seasonal breeding/mating in the period June–August; gestation lasts 10-11 months; parturition generally occurs between mid-May to mid-July; duration of lactation is uncertain, but is probably at least 8 months; size at birth is usually in the range 65-75 cm with a maximum size of about 80 cm. Sex ratio is biased to males throughout life: 1.1-1.2 males : 1.0 females in the foetal stage, and 1.1-1.7 males : 1.0 females post-natal. Growth parameters indicate an asymptotic length and weight that varies with population, but usually falls in the range 153-163 cm and 55-65 kg for females and 141-149 cm and 46-51 kg for males. Growth models used for length and weight are typically based on von Bertalanffy and Gompertz models. Length at sexual maturity also varies with population, but is usually in the range 138-147 cm for females and 127-135 cm for males. There is no information based on vertebral epiphyseal fusion to indicate age at physical maturity. Foetal growth appears normal, but there is uncertainty about the existence of embryonic diapause. Size/age at weaning are uncertain, but size may be <115 cm and at an age >8 months; however, entirely independent feeding may not occur until about 10 months.

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INTRODUCTION

The North Atlantic includes several populations or subpopulations of the harbour porpoise (Andersen 2003, Donovan and Bjørge 1996). They are present from the equator to Arctic regions, the most southerly records coming from Florida and Senegal. Their distribution includes coastal areas of eastern Canada and USA, Greenland, Iceland, Faroe Islands, British Isles (including Ireland), France, Norway (including Svalbard), North Sea-bordering countries of Germany, Netherlands, Belgium, Sweden, Denmark, all Baltic Sea-bordering countries, and eastern Atlantic-bordering countries Spain, Portugal, Morocco and Mauritania,and for completeness, the Mediterranean and Black seas (see Fig. 1, Andersen (2003) (this volume)). Some areas have been more studied than others, some we know almost nothing about, and certain areas have a generally low abundance so that very little is known at all.

The harbour porpoise is generally regarded as predominantly a coastal dwelling species, so that most studies reflect information gathered from a combination of directed catches, bycatches and strandings. All these sources are valuable for providing biological information, but each carries some bias when it comes to interpretation of parameters. For example, strandings often tend to represent predominantly the very young and very old members of the population, while bycatches are often biased towards younger juveniles, and directed catches may often focus on the older and larger members with a bias in sex ratio (Lockyer and Kinze 2003). Some supplementary information, especially regarding reproduction, is available from live sightings and behavioural observations, and very recently from captive porpoises.

Another bias that can affect the assessment of biological parameters is trend over time. Fluctuating external factors such as food supply, exploitation, and disease can change the profile of a population, so that in dealing with biological parameters, long term monitoring is advisable.

The aim of this paper is to present as comprehensive review as feasible on actual reported parameters, and provide information on the data sources, methods of parameter derivation and degree of uncertainty in parameters when known, in the hopes that they can be used appropriately in various population evaluations.

AGE

Data and materials

The usual source of age determination is the Growth Layer Groups (GLGs) in teeth of harbour porpoises, although research on the use of layering in mandibular sections and tympanic bullae has been carried out (Perrin and Myrick 1980). The usual problems encountered in the latter are associated with tissue and mineral resorption in bone in older animals.

Use of GLGs in teeth has been accepted as the most reliable method for age determination (Bjørge *et al.* 1995). Methods of collection, storage, preparation and reading and interpretation are presented by Bjørge *et al.* (1995), Lockyer (1995a) and Kvam (1995). Earlier reports and methodologies are also worth examining (Nielsen 1972, Gaskin and Blair 1977, Perrin and Myrick 1980, Kremer 1990 1989, Kull and Berggren MS 1993). Currently, deposition rate in dentine and cementum is accepted as one GLG per year (Bjørge *et al.* 1995).

Methods

The most usual preparation method is decalcification and thin sectioning of teeth on a freezing microtome (about 25 µ) followed by staining with haematoxylin stain (Ehrlich's acid, Mayer's) or Toluidine Blue stain. Typical methods are described by Lockyer (1995a), Kvam (1995) and Read and Hohn (1995). The teeth are normally examined under plain transmitted light using a low-power binocular microscope. Both dentinal and cemental GLGs are counted whenever possible. A regime for reading teeth has been described by Bjørge *et al.* (1995).

Results

Longevity

Longevity is always a trade off between potential and actual maximum age achievable. In wild populations it is frequently difficult to ascertain

TABLE 1. Age-related biological parameters for harbour porpoise from different regions and populations.

Population / region	Sex	Longevity, (yr)	Age at Sexual Maturity (yr)	Reference source
1 Eastern Canada:				
Bay of Fundy 1969-73	F	9	3.97	Read and Gaskin (1990)
	M	10	>3.0	
1985-88	F	10	3.44 / 3.15±0.20	Read (1990b); Read and Gaskin (1990)
	M	10	?	
1 Eastern Canada/USA:				
Bay of Fundy + Gulf of Maine	F	17	3.36±0.13 / 3.27±0.20	Read and Hohn (1995)
1990-93	M	15	>3.0	
3 Eastern Canada:				
Newfoundland and Labrador	F	9	3.1±0.07	Richardson (1992)
	M	12	3.0	
4 West Greenland	F	14	2.2 – 3.6	Lockyer *et al.* (2002a); *Lockyer et al.* (2001)
	M	17	2.0 – 2.45	
5 Iceland	F	20	2.81±1.03 / 3.20 / 2.15	Ólafsdóttir *et al.* (2002)
	M	16	2.64±0.10 / 1.94	
7, 8, 9 Norway:				
North Norway, North Sea,	F	>8+ (precise age >8 GLGs	3.9±0.4 / 2.8±1.3	Karstad (1993)
Skagerrak and Kattegat	M	>8+ not counted)	2.0 – 3.0	
8 British Isles, mainly	F	22	3.0 – 4.0	Lockyer (1995b, c)
North Sea	M	24	3.0	
Southern North Sea	F	-	5.0	Addink *et al.* (1995)
8, 9 Danish waters + North Sea	F	22 (24 personal data)	3.3	Lockyer and Kinze (2002)
	M	21	3.0 – 4.0	
9, 10 Sweden:				
Skagerrak, Kattegat	F	15	4.3+0.5 / 3.8±2.4	Karstad (1993); Berggren (1995); Kull and
and western Baltic	M	15		Berggren (MS 1993)

longevity because of sampling biases. Extrapolating from age frequency distributions to predict potential longevity often underestimates because samples originate from directed catches, bycatches or strandings where age distributions are not representative of the population. Strandings may sometimes provide a natural source of older animals and thus permit an estimation of maximum age. In survivorship models, longevity has been set as 10 years (Barlow and Boveng 1991) and 12 years and also 15 years (Woodley and Read 1991). Longevity appears generally not to differ significantly between the sexes, but may be very variable according to the geographic area and population being studied. The age of the oldest animal so far recorded was 24 years. Examples of animals more than 20 years of age have been recorded from widely differing areas as Scotland, Inner Danish waters and further afield in the north-eastern Pacific ocean off California (Hohn and Brownell MS 1990) (Table 1). Longevity, as indicated above, may be artificially reduced in populations where exploitation exists in one form or another, *e.g.* Bay of Fundy/Gulf of Maine, West Greenland. However, one cannot safely assume this because it is clear that the North Sea population suffers a high bycatch rate (Vinther 1996), yet longevity both in the Danish and British North Sea remains highest anywhere (Table 1). The Danish age sample also exceeds 700 cases.

Recruitment

Very little has been published on recruitment and maximal population growth rate of harbour porpoises. More recently estimates of population growth rate allowing for estimates of age at sexual maturity, age-specific fertility and age-specific survival have been presented for Gulf of Maine harbour porpoise (Caswell *et al.* 1998), with a likely range of 5-10%. Woodley and Read (1991) calculated that intrinsic rate of increase, r, of a population would approximate 0 *i.e.* no population growth, with calf mortality of .41 and .42 with a maximum age of 12 years and 15 years respectively and no incidental take. Barlow and Hannan (1995) examined the status of the porpoise population off California, and concluded that a maximal rate of population growth was 9.4% allowing for inherent aspects of the species biology and life history (*e.g.* minimum calving interval of one year, youngest age at first birth of 4 years, 99% longevity of 10 years – see Barlow and Boveng 1991) and using 3 different survivorship models only one of which (human model) was considered applicable. However, this rate of population growth appears unreasonably high relative to other cetaceans and is only theoretical. Analyses of models of population growth rate for east coast Canada and US porpoises considered a theoretical maximum of 10% (NOAA 1994). All authors agree that models indicate that population growth is very vulnerable to any form of removals, and will quickly assume a negative r value (population decline).

Mortality and survival

Estimates of mortality can sometimes be obtained from age frequency distributions. However, the assumptions that recruitment and year class strength are stable must be valid. The main difficulty with analysing data from strandings, bycatches and catches is that biases are introduced primarily because of the origin of the sample. Thus conventional methods for estimating natural mortality and survival (*e.g.* Chapman and Robson 1960, Heincke 1913, Robson and Chapman 1961) are not always strictly valid, although the Chapman and Robson method appears robust to potential inaccuracies in age estimations so long as all age classes are included in the analyses. Imprecision in age estimation by even a year can produce biased life history parameters but these can be corrected (Barlow 1984). A general discussion of mortality patterns in mammals and the methods of investigating life tables and fecundity is given by Caughley (1966). Estimates of survival have been presented by Kinze (MS 1990a) where he produced a life-table assuming longevity to 23 years and a calving interval of 1-3 years, resulting in an annual survival rate of 0.867. Lockyer (1995b) presented survival estimates for porpoises in British waters, using Heincke's (1913) method, and gave estimates of .816 (females) and .800 (males) excluding the first year animals. The maximum age observed was 24 years in males and 23 years in females. However, the sample was a mixture of primarily strandings and bycatches. There are many reports of a high apparent mortality of males between birth and the end of the first year of life (Lockyer 1995b, Lockyer *et al.* 2003a, Lockyer *et al.* 2001, Lockyer and Kinze 2003), with mortality of males returning to near-parity with that of females in the second year of life.

REPRODUCTION

Data and materials

Information on reproductive parameters depends heavily on collection and examination of carcasses, from catches, bycatches and strandings. Observations in the field of mother-calf pairs and breeding activity are also valuable, but are more difficult to obtain and cannot give as precise information for most parameters. Normally the samples investigated include all reproductive tracts and examination of mammary glands in females. In males, testis size and weight (most combined testes weights >200g are reckoned as mature – Lockyer 1995b, c), epidydimal smears for sperm presence, formalin-fixed testis tissue for histological investigation of spermatogenesis (Karakosta *et al.* 1999, Read and Hohn 1995, Neimanis *et al.* 2000), and if feasible, blood for hormone levels (testosterone, if blood is really fresh) (Desportes *et al.* 2003) are used to determine sexual maturity. Usually, because of practical constraints, only the testis weights are collected, and occasionally histology is performed. In females, the uterus should always be thoroughly searched for any implanted embryo and foetus which should be retained if found. The endometrium can be collected for histological investigation (Lockyer and Smellie 1985) but this is less usual, and most frequently the ovaries are retained for examination of follicular activity and *corpora lutea* and *albicantia* presence and size (Read 1990a, Read and Hohn 1995). The latter will also provide a guide as to how many pregnancies have been experienced. A good overview of cetacean reproduction, sampling and methodology is given by Perrin *et al.* (1984) and also Boyd, Lockyer and Marsh (1999).

Methods

Age at sexual maturity and parturition

A variety of methods have been employed to obtain mean age at sexual maturation. These include the method of DeMaster (1978) which uses the fraction immature animals at age, and of Hohn (1989) which uses a modified version of this algorithm. Another method for females uses the age at first ovulation derived from backward extrapolation of the relationship between ovarian *corpora* number and age (see examples in Read 1990b, Lockyer and Kinze 2003). However this is unreliable because the slope of the line and where it intersects the axis are greatly influenced by outliers where perhaps multiple ovulation has occurred. Other methods fit a sigmoid curve (maturity ogives – see Read and Gaskin 1990) to the proportion immature/mature at age and estimate the age at which 50% are mature. The reliability of this depends much on fitting the curves on some mathematical basis rather than fitting by eye. These methods are, however, usually easier to apply to females because maturity is more readily recognisable from the presence of at least one ovulation. In males, pubertal and seasonal changes can mask or confound maturity determination. Age at first parturition can also be calculated according to the method of DeMaster (1981). This is often regarded as being a more important parameter than age at sexual maturity because first ovulations may be unsuccessful in either conception or delivering a term foetus. In general, assuming post-ovulatory conception, age at first birth may be calculated by adding approximately 10 months (gestation) to the age at sexual maturity in harbour porpoise.

Length / weight at sexual maturity

The methods employed for estimating age at sexual maturity (see above) can also be applied for determining mean length (size) at sexual maturity. In general, maturation is greatly influenced by attainment of a minimum size (Brody 1968), particularly body weight which may be about 70-75% or more of average physically mature adult weight in cetaceans (Lockyer 1981), and perhaps about 90% of adult body length (Lockyer 1981). This is certainly a reflection, not only of the need to be a minimum size in order to accommodate the foetus in the female, but also of the functional developmental rates of organs and tissues and the accumulation of fat and energy reserves required for reproduction.

Seasonal mating / parturition

Methods for determining these parameters are primarily based on observations of ovarian follicular activity and spermatogenesis in the testes of dissected animals (Read 1990a, Sørensen and Kinze 1994). However, visual records of live calves and neonates at certain times of year (Kinze 1990b) – and dead ones especially from strandings, and embryo and foetal presence in the uterus as well as engorged post-parturitive uterine changes visible in dissections can help determine these factors. In the case of captive animals, blood hormone levels may be monitored (Desportes *et al.* 2003, Kristensen *et al.* 2000) as well as reproductive activity evidenced from the presence of male semen ejaculate in vaginal swabs.

Ovulation / pregnancy rates and reproductive interval

Methods for determining these parameters have been detailed in Read (1990b) and Read and Hohn (1995). The overriding problem is that, most frequently, the sample used in the investigation does not encompass the entire year, so that there are large gaps in time when reproductive status remains unknown. However, methods include calculating the proportion of mature females pregnant at any one time (when pregnancy might be anticipated from the seasonal cycle), and attempts to improve these estimates by discounting lactating and other females of immature status. Ovulation rates have most commonly been investigated by simply correlating ovarian *corpora* counts with age. The reproductive interval is the period between one pregnancy and the next. This interval usually corresponds with the interval between ovulations, but not always. Reproductive interval can be calculated in monitored living individuals where the presence of a calf/calves can be observed. However, the death of a calf or an abortion may go unnoticed. Such methods have been used in bottlenose dolphins (*Tursiops truncatus*) off Sarasota, Gulf of Mexico (Wells and Scott 1999) where animals are known individually and have been monitored for many years, but have not been used with harbour porpoise and may not be feasible.

Gestation

Methods of calculating gestation period are intimately linked to those for estimating foetal growth (*e.g.* Huggett and Widdas 1951, Frazer and Huggett 1974). From a practical viewpoint, data are needed on the presence and size of embryos and foetuses, and again the limitation is often the absence of material for critical periods during the year. Investigations in which overlapping data from consecutive years are analysed are useful (Read 1990a; Martin and Rothery 1993). This is especially useful where, even if the peak mating and birth periods are known, they are protracted. Circumstantial information on timing of appearance of calves and lactating females is also valuable.

Foetal sex ratio

The sex and size of the foetus is normally recorded when found. In very small foetuses and embryos, the sex may not be easily discernible without DNA analysis. An in-depth investigation of foetal sex ratio has been undertaken on long-finned pilot whales (Desportes *et al.* 1994) and been found to alter throughout the duration of pregnancy, with a predominance of females that increased throughout gestation. They also found that females >25 years old bore more female foetuses than younger mothers. Such an investigation could also be applied to harbour porpoises and could be valuable in the light of the foetal sex ratio imbalance in favour of male porpoises reported from Danish waters (Lockyer and Kinze 2003) and Iceland (Ólafsdóttir *et al.* 2003) – see below.

Post-natal sex ratio

Post-natal sex ratio was also investigated in pilot whales by Desportes *et al.* (1994) and the mortality of females was discovered to be higher than that in males in the first 3 years of life, resulting in a return to parity in the sex ratio. Essentially this is another way of examining relative age-specific survival by sex throughout life. The problems likely to confound studies of this type include possible geographic or temporal segregation of the sexes. However, in all such investigations, the age structure of the samples investigated would be necessary.

Neonatal size

A common method for investigating this parameter is by comparing maximum size of foetuses and minimum sizes of neonates during the usual months of birth (see Read and Hohn 1995, as an example). Other methods depend on the examination of stranded neonates and recording the presence or absence of a healed umbilicus. Webb (1997) reported that amongst marine mammals, relative to maternal mass, the greatest neonatal mass was evident in cetaceans. A theoretical approach to estimation of neonatal size relative to the size of the mother implies a logarithmic weight relationship between the two (Webb 1997), and this would indicate a birth size of 6 to 9 kg in porpoises, depending on maternal size.

Length of lactation

The duration of lactation may possibly be determined from dissection of dead porpoises throughout the year. Presence of milk, quantity, quality, size of mammaries, relative size and appearance of the uterus and ovarian structures may all provide clues as to the stage of lactation. However, investigation depends on access to material from all months of the year. Another approach is to examine the stomach contents of small calves and juveniles for the presence of milk and determine their relative age in months according to body length. However, this becomes complicated once the calf commences taking some fish and other prey as well as milk. Chemical analyses may be required to detect the presence of milk in such circumstances. Recent techniques, such as those described by Møller (MS 1999), using lipid tracers in blubber may be very useful in determining this parameter in the future. Techniques utilising stable isotope levels of nitrogen (15N/14N) in muscle tissues of the calf may also help in calculating whether or not an animal is still suckling (Särnblad Hansson *et al.* MS 1999).

Results

Age at sexual maturity and parturition

Estimates of mean age at sexual maturity are presented in Table 1 for several populations and regions. Generally the age falls within the range 3-4 years for both sexes, but may be 2 years or even 5 years. In the North Atlantic, porpoises from West Greenlandic waters appear to mature earliest. In contrast, the mean age of maturity of porpoises from Californian waters in the North Pacific, which are not included in Table 1, exceeds 4.5 years (Hohn and Brownell MS 1990). There have been reports of porpoises maturing at ages of 5 years and more (van Utrecht 1978) in the southern North Sea (Dutch waters), but these are currently being verified. It is clear that there is a pronounced seasonal breeding cycle (see below) so that one might assume that for most practical purposes, such as investigating population dynamics, maturity must come in the first summer after attainment of age 3 or perhaps 4 years with parturition the following year in the majority of individuals. Read and Gaskin (1990) reported temporal changes in the age at maturation in Bay of Fundy waters (Table 1), and correlated these changes with exploitation in the form of bycatches and a resultant increase in prey availability that would allow a faster growth rate.

Length/weight at sexual maturity

Size at sexual maturity in terms of length is given in Table 2. Lengths in the North Atlantic populations range from 138 - 152 cm in females and 127 - *ca* 135 cm in males. For comparison, Californian male porpoise size may be 140 cm at first maturation while females mature at 142 cm (Hohn and Brownell MS 1990). West Greenlandic porpoises appear to mature at the smallest lengths. These sizes, excluding only the outlying Norwegian data as they are based on small samples, lie between 88-94% asymptotic length (Table 3), and are as predicted for large cetaceans (Lockyer 1981). Few data have been published on weight at sexual maturation, although records for females and males respectively, are >45 kg and >41 kg in British waters (Lockyer 1995d), about 47 kg and 40 kg in Danish waters (Lockyer and Kinze 2003), and 46 kg and >36 kg in West Greenlandic waters (Lockyer *et al.* 2001, 2003a). These weights are approximately 70-82% of asymptotic weight. The high percentages in British waters and also for females in Danish waters where the values are 80-82% may be influenced both by the presence of stranded and consequently lean old animals which would result in a lower than normal asymptotic weight, and year-round sampling. The West Greenland animals were all hunted animals, and in good nutritive condition, and only taken in a short late summer period. In retrospect, weight may be influenced by seasonal changes in blubber thickness and also by reproductive status in females, so that weight at sexual maturity would be unlikely to remain a fixed percentage of asymptotic weight which

TABLE 2. Reproductive parameters, excluding age at sexual maturity (see Table 1), for harbour porpoise from different regions and populations.

Population /region	Sex	Length at Sexual Maturity, cm	Mating season	Birth season	Neonatal length, cm	Lactation period, mo	Gestation period, mo	Pregnancy rate	Ovulation rate, per yr / interval, yr	Reference source
1 Eastern Canada: meeting); Bay of Fundy										
1969-73	F	147	-	-	-	-	-	-	0.89	Read and Gaskin (1990)
	M	134								
1985-88	F	143	June- July	Mid- May	-	8-12	10.6	0.86 / 0.74	0.66 / 1.515	Read (1990a) (two methods)
	M	?								
1 Eastern Canada/USA: Bay of Fundy + Gulf of Maine										
1990-93	F	?	June- July	Mid- May	-	-	<11	0.95	0.68 / 1.47	Read and Hohn (1995); Neimanis *et al.* (2000)
	M	?								
3 Eastern Canada: Newfoundland and Labrador	F	146.4	July	June or earlier	-	-	-	0.76	-	Richardson (1992)
	M	135.1								
4 West Greenland	F	138 – 142	August	Summer	70 ?	?	?	-	0.73 / 1.37	Lockyer *et al.* (2003a) Lockyer *et al.* (2001)
	M	127								
5 Iceland	F	147.6±7.15 / 146	Summer	June- July	75-80	7-8+	ca 10	0.986	0.988 / 1.01	Ólafsdóttir *et al.* (2003); Halldórsson and Víkingsson (2003)
	M	135								
7, 8, 9 Norway: N. Norway, North Sea, Skagerrak and Kattegat	F	152.4±5.5	July- August	Mid-May Mid-July	ca 77-78	?	10 - 11		-	Karstad (1993)
	M	>130								
8 British Isles, mainly North Sea	F	140 – 145	June- August	June May-	65 – 70 (ca 5 kg)	?	<12	-	-	Lockyer (1995b, c, d); Karakosta *et al.* (1999)
	M	130 – 135								
Southern North Sea	F	-	?	August	74.3	?	?	-	-	Addink *et al.* (1995)
8, 9 Danish waters + North Sea	F	143	August	June	60 - 75 (ca 3.5 kg)	>8?	ca 10 / 11	-0.64 / 1.57		Sørensen and Kinze (1994); Møhl-Hansen (1954); Lockyer and Kinze (2003)
	M	135								
9, 10 Sweden:	F	145.3±2.2	-	March- August	-	-	10 -11	-	0.66 – 0.71	Berggren (1995); Karstad (1993)
Skagerrak, Kattegat and western Baltic	M									
10 Baltic Sea	F	-	-	-	75	8	11	-	-	Møhl-Hansen (1954)
	M	-								

TABLE 3. Growth parameters for harbour porpoise from different regions and populations.

Population /region	Sex	Maximum Length, cm	Asymptotic Length, cm	Asymptotic Weight, kg	Length at weaning, cm	Age at weaning, mo	Reference source
1 Eastern Canada: Bay of Fundy							
1969-73	F	175	163±8.4	-	-	-	Read and Gaskin (1990);
	M	178	146±4.1	-			Gaskin *et al.* (1984); Yurick (1977)
1985-88	F	-	155±3.5	-	-	-	Read (1990b); Read and Gaskin
	M	-	144±3.5		-		(1990)
1 Eastern Canada/USA:							
Bay of Fundy + Gulf of Maine							
1990-93	F	-	-	-	-	-	Read and Hohn (1995)
	M	-	-		-		
1985-93	F	-	158±1.56	65±1.87	-	-	Read and Tolley (1997)
	M	-	143±1.25	50±1.053			
3 Eastern Canada:							
Newfoundland and	F	-	156.3±2.9	61.6±3.0	-	-	Richardson et al. (2003)
Labrador	M	-	142.9±1.2	49.1±1.3			
4 West Greenland	F	166	154.0±2.6	64.4±2.	?	<12 ?	Lockyer *et al.* (2003a)
	M	158	142.8±1.7	51.2±1.8			Lockyer *et al.* (2001)
5 Iceland	F	174	160.6	-	-	>7-8	Ólafsdóttir *et al.* (2003)
	M	165	148.8	-			
7, 8, 9 Norway:	F	-	153.4±2.3	-	-	-	Karstad *et al.* (1994)
N. Norway, North Sea,	M	-	140.1±1.2	-	-	-	
Skagerrak and Kattegat							
8 British Isles, mainly	F	189	160	55	-	-	Lockyer (1995b, c)
North Sea	M	163	145	50			
8, 9 Danish waters +	F	189	160	65	<115	<10	Lockyer and Kinze (2003);
North Sea	M	167	145	50			Lockyer *et al.* (2003b)
9, 10 Sweden:	F	167	153	60	-	-	Kull and Berggren (MS 1995);
Skagerrak, Kattegat	M	154	141.5	46.4			Berggren (1995)
and western Baltic							
10 Baltic Sea	F	180/189	-	-	-	-	Møhl-Hansen (1954);
	M	164 (160 – 169)	-	-			van Bree (1973)

itself could vary. However, the values are again as expected for cetaceans (Lockyer 1981), and exceed 70%.

Seasonal mating / parturition

The time of breeding and peak births appears highly seasonal. Mating likely occurs mainly in June-July in Canadian waters (or at least testicular activity is at a peak during this period – Neimanis *et al.* 2000), and July through August in other areas including the eastern North Atlantic and Greenland (Table 2). The reported breeding season for Californian porpoises is July-August (Hohn and Brownell MS 1990). The peak birth period for most populations (including California) is May-June (Table 2). Addink *et al.* (1995) reported a very protracted birth period from May through August in porpoises from the southern North Sea off the Dutch coast, although most births were in July. They also reported spermatogenic activity and sperm in March and the presence of sperm in November. The birth season also appears protracted in Swedish waters (Table 2).

Ovulation / pregnancy rates and reproductive interval

Read (1990b) has reported some change in fecundity with age in Bay of Fundy porpoises with lower success in first-time pregnancies (many young mature females ovulate frequently before first conception). Older mature females ovulated less frequently, generally annually, but were more successful in becoming pregnant. Therefore the assumption of a simple linear relationship between fecundity as measured by ovulation and age may be incorrect. Read observed no evidence of reproductive senility. Ovulation rates presented in Table 2 range between 0.64 and 0.988 with an interpolated reproductive interval of 1.01-1.57 years. Apparent pregnancy rates have been estimated at 0.74 - 0.986 (Table 2), but are generally based on information from a limited period of the year. Because of the marked seasonal nature of the reproductive cycle (Sørensen and Kinze MS 1990, 1994), we might anticipate that, although in theory ovulation and pregnancy may be feasible yearly, the likelihood is that the true reproductive interval may vary from 1 to 2 years (see Lockyer and Kinze (2003) for a discussion of this point). Lockyer and Kinze (2003) estimate that even if females have a longevity of 20 years, the maximum expected number of young produced in a lifetime might only be 11 to 12 calves, and for most females, longevity does not exceed 10 years, so that only 5 young might be produced of which not all may be viable.

Gestation

Estimates of gestation all concur on a period of less than a year, with the majority suggesting 10-11 months (Table 2). Sørensen and Kinze (1994) have provided detailed information about the proposed reproductive cycle of harbour porpoise in Danish waters, based on a sample of 59 females and 60 males. They observed follicular activity in the ovaries in July and active *corpora lutea* in August, and peak testicular development in July-August. Births peak in June-July, so this would be consistent with a gestational period of 10-11 months. Read (1990a) proposed delayed implantation (embryonic diapause) in Bay of Fundy porpoises with implantation in early August but conception (mating) in June and birth in the following May. Delayed implantation beyond the normal few days of free-living blastocyst stage has not been reported elsewhere for porpoises, nor for any other cetacean, so this proposal clearly requires further investigation. Delayed implantation may permit the mother to recover energetically from a previous pregnancy before proceeding with a new one (Read 1990a), and would certainly facilitate an annual pregnancy cycle. Lockyer (1995d) and Read (1990c) have reported on the implied energy demands of pregnancy and subsequent lactation in terms of both relative fatness of pregnant females and leanness of lactating females.

Foetal sex ratio

Lockyer and Kinze (2003) reported a bias to males in the foetal phase, 1.1:1.0 (males:females). Ólafsdóttir *et al.* (2003) also reported a bias to males with a ratio of 1.2:1.0 in foetuses.

Post-natal sex ratio

The imbalance of sex ratio appears to persist in those porpoise populations where it has been investigated, with a preponderence of males in British (Lockyer 1995b, c), West Greenlandic (Lockyer *et al.* 2003a, Lockyer *et al.* 2001), Icelandic (Ólafsdóttir *et al.* 2003) and Danish waters (Lockyer and Kinze 2003), where generally the ratio exceeds 1.1 males:1.0 females. Lockyer and Kinze (2003) reported a bias to males in all post-natal animals with an overall ratio of 1.3:1.0. This bias to males was particularly pronounced in the neonatal phase with 1.4 males:1.0 females during the first year of life. In the bycatches in Danish waters, the ratio of males is 1.2:1.0; in the historic directed catches, 1.5:1.0, and in the strandings, 1.1:1.0 (Lockyer and Kinze 2003). In the bycatches and directed take, the predominance of males may be because of geographical segregation or some other artefact. Lockyer (1995b) also reported a similarly heavy bias to males in the first year of life for porpoises in British waters - and an overall post-natal bias of 1.1:1.0 (Lockyer 1995c). Ólafsdóttir *et al.* (2003) reported a bias to males with a ratio of 1.7:1.0 in post-natal animals. However, they observed that the bias to males increased with age in post-natal animals, unlike the findings in Danish waters. The above ratios were not reported as significantly different from parity. However, there is an overall consistency in the male bias, regardless of sample origin, that suggests either selective mortality and/or segregation, and it would seem that in general males outnumber females in the population.

Neonatal size

Published records have indicated a neonate size from 60 – 85 cm (see also Table 2), and perhaps as high as 90 cm (Gaskin *et al.* 1984). However Lockyer and Kinze (2003) consider it unlikely that neonates are normally larger than 80 cm. They base this conclusion on two observations: 1) the reported incidence of a ruptured uterus in a stranded female in inner Danish waters during parturition, resulting in deaths of both calf (89 cm length and weighing nearly 10 kg) and mother (173.5 cm in length and weighing 80 kg, of age 13 years) because of birth difficulties; and 2) that a length of 80 cm is a more likely maximum size, based on the lack of occurrence of fetuses larger than this in the Danish sample (apart from the 89 cm foetal death noted above). Most neonates were within the size range 65-75 cm, based on the examination of unhealed umbilicus and absence of neonatal line in the tooth dentine. Lockyer (1995c, d) noted that females appeared to have a higher birth size than males, with extra blubber mass, and the foetal growth curves presented by Lockyer and Kinze (2003) also suggest a higher weight for length in females. This may favour the survival of females after birth because of additional intrinsic energy reserves. In the North Pacific, Hohn and Brownell (MS 1990) reported a birth size of 75 – 80 cm. For harbour porpoises in general, it has been noted that size at birth corresponds to about 45% maternal length and 8% maternal body weight (Read and Tolley, 1997).

Length of lactation

Møhl-Hansen (1954), Gaskin *et al.* (1984), Ólafsdóttir *et al.* (2003), Read (1990a), and Sørensen and Kinze (1994) provide evidence on the likely duration of lactation. The duration of the suckling phase is not actually known but is considered to be at least 8 months (Table 2). A rescued bycaught female porpoise of 115 cm length in late April 1999 from inner Danish waters (Lockyer *et al.* 2003b) readily consumed fish. Since peak births occur in June-July in this region, a likely age of about 10 months is indicated. Of course she may also have taken some milk, but when trapped in the net, she was alone.

GROWTH

Data and Materials

Normally total body length, measured in a direct line parallel to the body from snout tip to notch in the tail flukes is recorded both in the pre- and post-natal phases, but total body weight has also often been collected. Age, sex and date are also essential information for constructing growth curves.

Methods

Growth of the individual is usually described from a composite picture based on size at age for many individuals from a population, especially one being exploited, when samples are often readily available. Thus the “growth” curve represents no one individual but the “average” individual in that population. Monitoring of a specific individual is not normally possible, although recent studies on captive porpoises in Denmark (Lockyer *et al.* 2003b) have been able to do exactly this type of individual monitoring. Methods of fitting growth curves to such data are reviewed by Kaufmann (1981), and the most frequently used models include von Bertalanffy (1960) and Gompertz (1825) – see also Zullinger *et al.* (1984). Both models express growth exponentially and provide an asymptotic size. In some cetacean species the growth model is complicated by a secondary growth spurt around the time of sexual maturation, in which case the Gompertz model often provides a better fit.

Foetal growth has been described by Huggett and Widdas (1951) and Frazer and Huggett (1974). Their growth model also permits a theoretical determination of the conception age and gestation period. One of the obvious flaws in estimating growth curves from collective data is that individuals are conceived and born at different times, and thus estimating foetal growth is particularly difficult if the breeding season is even slightly spread.

Physical maturity, the point in time when further increase in length is no longer possible and asymptotic length is attained, is ideally determined by examination of the epiphyseal fusion along the vertebral column. In practice, this has rarely been performed, and asymptotic size has been generally determined by extrapolation or calculation from growth curves.

Results

Growth rates/formulae

Several studies have examined growth in the harbour porpoise. von Bertalanffy and/or Gompertz models have been applied to Canadian populations at Bay of Fundy (Read and Gaskin 1990) and Newfoundland/Labrador (Richardson 1992) and West Greenland (Lockyer *et al.* 2003a, Lockyer *et al.* 2001). It appears that individuals in most populations have reached near-asymptotic size by 8 years of age. In their first year of life harbour porpoises grow rapidly from about 70 cm to 115 cm, with >50% increase in length, and a weight increase from about 5 kg to 31 kg. Lockyer *et al.* (2003b) record massive cyclical seasonal weight gains of up to 8 kg for porpoises from Danish waters in late autumn and subsequent losses in late spring, so that growth in weight reflects energetic needs and is not a reliable record of actual growth. Hohn and Brownell (MS 1990) could not find any easy fit of standard growth models. They proposed a secondary growth spurt with a complex two-phase growth curve for California porpoises. They found an asymptotic length of >170 cm in females and >150 cm in males – higher than for North Atlantic porpoises, although maximum lengths recorded of 184 cm in females and 160 cm in males were similar to North Atlantic animals. Such a secondary spurt has not been described for porpoises elsewhere.

Asymptotic length/weight

These have been calculated most usually employing the growth formulae mentioned above (von Bertalanffy and Gompertz for length and weight) and findings are given in Table 3. However, in some cases a mean adult size has been interpolated from small data sets. In the North Atlantic, lengths in females vary between 153.4 – 163 cm, and in males between 141.1 – 148.8 cm. It is thus clear that females attain larger body size than males. West Greenland porpoises appear to be amongst the smallest in length yet heaviest for length of all populations investigated. The maximum lengths in Table 3 merely reflect the potential attainment of size by some individuals. There is a documented record of a female porpoise attaining a length of almost 2 m in Scottish waters, and the data and skull of this animal are held at the Royal Museum of Scotland in Edinburgh. I have seen the skull and can verify that it is abnormally large with teeth that are about twice the normal anticipated size for the species. Weights given in Table 3 do not reflect possible seasonal trends or allowances for weight gains in pregnancy. Some females may attain weights of up to 89 kg (Lockyer and Kinze 2003) and 81 kg (Lockyer 1995b).

Physical maturity – age

There is a complete lack of any reliable direct data on this aspect of life history. Most studies of age at physical maturity are based on growth models fitted to length at age data. Read and Tolley (1997) calculated age when asymptotic length was attained as 7 years for females and 5 years for males in the Bay of Fundy region. Probably all animals may be assumed to be physically mature by 8 years of age judging from the published growth models fitted to data cited in Table 3. Males complete their growth earlier than females. However, a study of vertebral epiphyses is required to confirm this directly. In view of the generally short life span for the majority of porpoises, probably most never attain physical maturity. Several authors have noted that the majority of porpoises do not live longer than about 12 years. In fact, even in the longest-living populations (North Sea areas), <5% exceed 12 years of age (Lockyer and Kinze 2003).

Foetal growth

Information on foetal growth has been provided by Lockyer and Kinze (2003), Read and Hohn (1995), Sørensen and Kinze (1994) and Møhl-Hansen (1954). The possibility of embryonic diapause remains (Read 1990a). Until this matter is resolved, it is not known if conventional growth models may be applied.

Size/age at weaning

There is little information available on this topic. It is worth noting that Nuka, a captive porpoise from inner Danish waters, fed readily immediately after rescue from a pound net, suggesting that weaning occurs before length 115 cm and age of 10 months in females (Lockyer *et al.* 2003b,). This animal was not accompanied by an adult when found. Although fish were readily taken and eaten, Nuka displayed some uncertainty in holding the fish in the mouth and manipulating it in order to swallow, suggesting that solid food had not been taken for very long. Weaning is a gradual process, and spans a period during which the calf will continue to take milk but increasingly eat fish. The most likely scenario for age at weaning is >8 months but <10 months. However, Smith and Read (1992) observed shrimp (*Meganyctiphanes norvegica*) consumption in calves of only 4 months of age in the Bay of Fundy, and Särnborn Hansson *et al.* (MS 1999) suggested that calves may start to consume fish earlier than 6 months from investigations employing stable nitrogen isotopes in muscle tissue. These observations would still not preclude continued simultaneous milk consumption, and weaning would not be complete until the calf could exist without access to milk.

CONCLUDING REMARKS

One may conclude that biological parameters generally fall within a close range of values in all geographical regions, notwithstanding certain size differences between populations. It is recognised that there may be differences in parameters between populations, which may be explained by either intrinsic (*e.g.* in mating and parturition seasons or asymptotic size), or brought about by external factors such as food abundance and exploitation pressure (*e.g.* in age at sexual maturity, growth rate, longevity (Read and Gaskin 1990), or survival/mortality).

This review indicates that while overall quite a lot is known about biological parameters for harbour porpoises, there remain several aspects of life history that are uncertain: for example, duration of pregnancy, age at weaning and lactation. There are also several areas and populations for which almost nothing is yet reported: for example, the Gulf of St Lawrence and the Faroe Islands. Information on porpoises off North Africa, Spain and Portugal, the Mediterranean and Black seas is similarly lacking, and although effort is and has been directed to the Baltic, the low abundance of porpoises makes any study very difficult and results inconclusive.

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