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Natural regulation of population size in large mammals by means of two new delayed density-dependent fertility mechanisms

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It is generally assumed that population size of all wild animal species is regulated through density-dependent mechanisms, but the mechanisms responsible have been difficult to identify for elephants and large whales. We have used information on physiological reproductive mechanisms in humans in a stochastic computer simulation study to explore how known density-dependent fertility mechanisms in humans could regulate population size in a hypothetical large mammal species, assuming no deliberate interference with sexual or reproductive processes. Two physiological reproductive mechanisms in women are dependent on nutrition in utero or early life: age at menarche and post-partum amenorrhea during lactation and were included in the model. If large female mammals in general have physiological reproductive mechanisms similar to human females, strong density-dependence mechanisms will be the result, but with a substantial delay, 20 to 50 years. The model results are discussed in relation to what is known about populations of the Eastern North Pacific gray whales (*Eschrichtius robustus*), Antarctic minke whales (*Balaenoptera bonaerensis*) and elephants (*Loxodonta africana*) in Amboseli National Park, Kenya.

Keywords Delayed density-dependence, Fertility mechanisms, Elephants, Large whales, Stochastic simulation model

Many populations of wild animals show fluctuations, sometimes large, in population size, and these fluctuations are often correlated with stochastic changes in the environment. The biological mechanisms that are sometimes able to keep population size approximately constant and at other times cause fluctuations correlated with changes in environment are likely to be density-dependent[1].

Sinclair[2] summarized the theoretical basis for population regulation and reviewed the empirical evidence for density dependence in a number of populations. For large mammals, species with long life spans, low reproductive rates and high parental investment in offspring, there seems to be agreement in the literature that density-dependent mechanisms are strongest for high population levels, near the carrying capacity for the habitat[2–4]. There is only a limited number of potential density-dependent mechanisms in large mammal populations.

What about the possibility of density-dependent changes in fertility in large mammals[5–7]? The type of model for density-dependent population regulation that many have explored for whales without clear results is to assume that poor nutrition one or two years reduces the fertility of the adult females or increases the mortality of the young animals one or two years later[8–10]. Other authors have not found evidence of such density-dependent regulation in elephants[11].

The limited amount of information on reproduction in wildlife populations makes it difficult to test our hypotheses on regulation of population size by reproductive mechanisms directly in a specific species. However, by using a hypothetical human-like species as a proxy species we can gain an understanding of how these mechanisms work, which could help us understand how they could affect other species.

Modern humans are the only large terrestrial species for which substantial amounts of information are available on fertility. The main difficulty in using information on fertility from human populations is the influence of cultural variables, especially how fecundity early in life is influenced by traditions and rules for adolescent sexual activity, and also later in life how pregnancies can be prevented by conscious decisions. As a

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way of avoiding these difficulties, we here discuss the available human information in relation to a hypothetical human species, which has physiological reproductive mechanisms similar to those of modern humans, but no conscious interference with sexual or reproductive processes. Two physiological reproductive mechanisms that in women are dependent on nutrition in utero or early life: age at menarche and post-partum amenorrhea during lactation. This hypothetical human-like species could perhaps be thought of as a very early *Homo* species, although we do not argue that such a species has ever existed.

Our main objective in this article is to explore how effectively these density-dependent physiological fertility mechanisms could regulate populations of large mammals like whales and elephants if they operated alone, and how delayed the population response would be after a step change in available resources. We have assumed constant age-dependent mortality and the existence of reproductive mechanisms observed in modern Western human populations from the nineteenth century and in hunting and gathering people in South Africa[12], South America[13,14] and New Guinea[15–17] in the 1950s and 60 s. The investigation was carried out by computer simulation of relevant hypothetical populations.

Methods

The hypothetical humanlike population was studied by stochastic simulation of the total reproductive life history of a large number of women, using a continuous time model. Each important event in the life histories of the women was recorded and could be subject to statistical analysis. Simulations were run using the CLASS SIMULATION in the computer language SIMULA[18].

Simulated population

Each simulation run starts at time zero, when a number of newborn women are created with properties drawn from the relevant distribution of environmental resources. These women are treated individually, and each of them is given a personal number. In the starting phase, 20 women are generated each year until 500 women are generated. This takes 25 years. After birth, the women enter their reproductive life history with age at menarche, birth of children and death drawn from the relevant distributions (these are discussed below). The probability that the child is a girl and is assigned a personal number is 0.5. Each simulation run lasts for 2000 years. The first 300–400 years must be regarded as the 'running in' period needed for the female population to achieve an approximately constant age distribution. The simulation results for the first 400 years of each run are therefore not plotted in the figures. During the rest of the 2000-year period, the availability of environmental resources (≈food) is changed three times, after 500 years, 1000 years and 1500 years. In most simulation runs, these changes are abrupt, to better show the effect of the assumed regulatory mechanisms, but we have also explored gradual changes in resources.

The important reproductive events throughout each woman's life are simulated, with all timings determined at birth. The waiting times to the events are drawn from the relevant probability distributions (see below).

Males are also simulated and are assigned birth dates and death dates drawn from the same distributions as the females. Since no density-dependent mechanisms operate on the male segment of the population, they only appear in the results in plots of intervals between births and distributions of number of children.

Fertility mechanisms in human females dependent on nutrition early in life

Two physiological reproductive mechanisms in females have been shown to be dependent on nutrition in utero or early in life: age at menarche (= first menstruation, the first ovulation follows somewhat later, see below)[19] and post-partum amenorrhea (= period without menstruation (ovulation) following childbirth) during lactation[20]. The first ovulation occurs some months after the first menstruation, see later for details. The age at menarche is approximately normally distributed both in Dobe ¡Kung[12] and in modern female populations[21]. In the simulations, we assumed that the mean of the distributions could vary between 10 and 21 years with a coefficient of variation of 0.1. These distributions approximate to what has been observed in hunting and gathering peoples and in modern populations under varying nutritional levels. For post-partum amenorrhea, we used observations from our own investigations[20]. A logistic relationship between post-partum amenorrhea and age at menarche, based on observations in working class women in Christiania (Oslo) in 1840–1900[20], was used in the model.

The resources in the environment were modelled as a term n between 0 and 10, 10 representing the most abundant resources and 0 the most limited resources.

The mean age at menarche μ is a linear function of two terms, n and p, where p is the size of the female population.

$$\mu = 148.9 * \mathrm{n} \ + \ \mathrm{p} \ - 1979$$

The slope 148.9 and the constant 1979 have been chosen to fit the observations by[20]. The mean age at menarche has a lower limit of 10 years and an upper limit of 21 years, corresponding to what has been observed in modern human populations under extreme living conditions.

It was assumed that menstruation never resumes during the first two months after birth. The additional duration of post-partum amenorrhea during lactation was modelled as an Erlang distribution of order 3 with coefficient of variation of 0.75[20].

The mean duration of postpartum amenorrhea was modelled as a cumulative logistic distribution with mean 19 months for age at menarche of 16 years and slope 3.25 months/year in the middle section. Asymptotes at 9 and 29 months.

In most simulation runs, both these density-dependent mechanisms were active. However, we also included simulation runs where one of these two variables was kept at its mean value (either mean age at menarche = 17 years or postpartum amenorrhea = 19 months) to explore the effect of each mechanism alone.

Adolescent sexual activity

In the simulation model, we assumed that adolescent girls start sexual activity as soon as they are sexually mature. Physiologically, there is a varying delay between the first menstruation and the first ovulation[15]. This is modelled as a constant equal to 2.5 years, plus a varying waiting time until conception similar to the waiting time after post-partum amenorrhea (see below).

Mortality

In the model, we assumed constant age-dependent mortality. This was divided into two phases, infant mortality of about 40%, similar to what has been found in many aboriginal human populations and mortality for older children and adults. Infant mortality, which occurs during the breastfeeding period, was modelled as a negative exponential distribution with half time 15 months.

For children who survived until weaned, the duration of additional life was drawn from a uniform distribution between 0 and 80[22]. Other distributions were also tested, but without any marked changes in the results.

Breastfeeding

The duration of breastfeeding was modelled as a normal distribution with mean 3 years and standard deviation 1 year, which is similar to what has been observed in Dobe Kung[12] and many other human populations[23–25] and in the gorilla[26]. When breastfeeding is terminated, either because the infant dies or because it is weaned, menstruation resumes after two months.

Interval between births

The interval between succeeding births is the sum of three terms: duration of post-partum amenorrhea, waiting time until conception and 9 months pregnancy. This interval was about 4 years in Dobe ¡Kung and similar in many other aboriginal populations. Again, a third order Erlang distribution with mean 16 months for the waiting time until conception gives the right distribution of intervals between births.

Duration of a woman's fertile period

We modelled the end of a woman's fertile period in two different ways. The simplest was to use the observed age at last birth in Dobe ¡Kung, which is approximately a normal distribution with mean 35 years and SD = 3 years[12]. The alternative was to use normally distributed age at menopause with mean 47 years and standard deviation 1 year, and a 10% probability of permanent sterility after each birth. The two models gave similar results for population development. In the results we present here, the simplest method was used.

Results

The results for total female population size during one simulation run of 2000 years are shown in Fig. 1a. The 'environment resources' term starts at 1 (very limited resources available), changes abruptly to 8 at 500 years (abundant resources available), changes back to more limited resources at 1000 years (resource level 3) and finally back to 6 at 1500 years (Fig. 1d).

The time development of mean age at menarche and mean duration of post-partum amenorrhea are shown in Figs. 1b and c. The development of the female population size during the years 500 to 1000 is shown at higher time resolution in Fig. 2a.

Much of the first 500 years should be regarded as a running-in period for the simulation model, and the results for this period should therefore be ignored. The figures clearly show a transitional period of approximately 200 years after each abrupt change in living conditions. After the transitional periods, the female population size shows only small fluctuations. Both age at menarche and duration of post-partum amenorrhea are approximately constant and the same in all three periods (Fig. 1b and c). Figure 2a clearly shows that the female population increases more than 20-fold during the first 200 years after an abrupt change in living conditions (≈available food), but also that the increase is slow to appear. It takes more than 50 years for the population to double.

The effects of the two fertility mechanisms were studied separately by keeping either the mean age at menarche or the mean duration of post-partum amenorrhea constant at the long-term values shown in Figs. 1b and c. The corresponding changes in female population size following two abrupt changes in natural resources are shown in Fig. 2a and b.

The effect of changing the resources term gradually instead of abruptly is shown in Fig. 2c. The figure shows the age at menarche when the availability of resources term is allowed to decrease linearly over a period of 100 years. The changes in age at menarche are roughly delayed one hundred years but are largely the same as following a step decrease.

Figures 1 and 2 show the mean values of the relevant variables. The figures show an overshoot in the population response after year 500 resulting in a damped oscillation. Since the simulation is stochastic, each variable has a distribution. Figure 3a–c show three typical distributions.

Figure 4a shows the distribution of time intervals between births for women born in a stable period. Figure 4b shows the mean number of children plotted for the year of birth of the women.

Figure 5 shows two distributions of the number of children, one from a stable period, and one from a period with a growing population.

Discussion

The population effects of two density-dependent physiological fertility mechanisms were explored by stochastic simulation. One of the mechanisms assumes that age at sexual maturity is dependent on nutrition early in life. We have evidence for this mechanism both from the investigations by McCance and Widdowson[27] and by Liestøl[18]. In

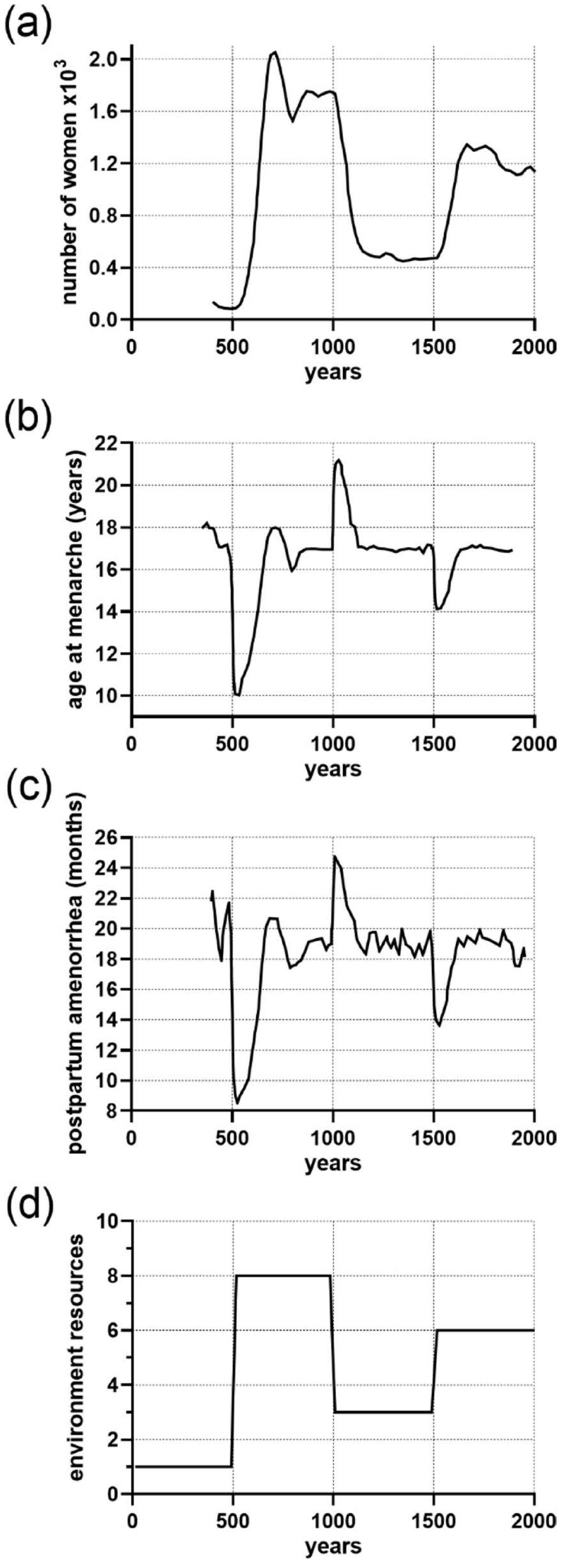

Fig. 1. The total female population size as a function of time over a 2000-year period (**a**). Mean age at menarche (**b**) and mean duration of post-partum amenorrhea (**c**) over this period. In (**b**) and (**c**), the mean values are plotted for the year of birth of the women. Figure (**d**) shows an index of the environment resources. The first 300–400 years should be regarded as a running-in period, and the simulation results are not plotted. The environment resources term in the model changes abruptly from 1 to 8 at 500 years, from 8 to 3 at 1000 years, and from 3 to 6 at 1500 years.

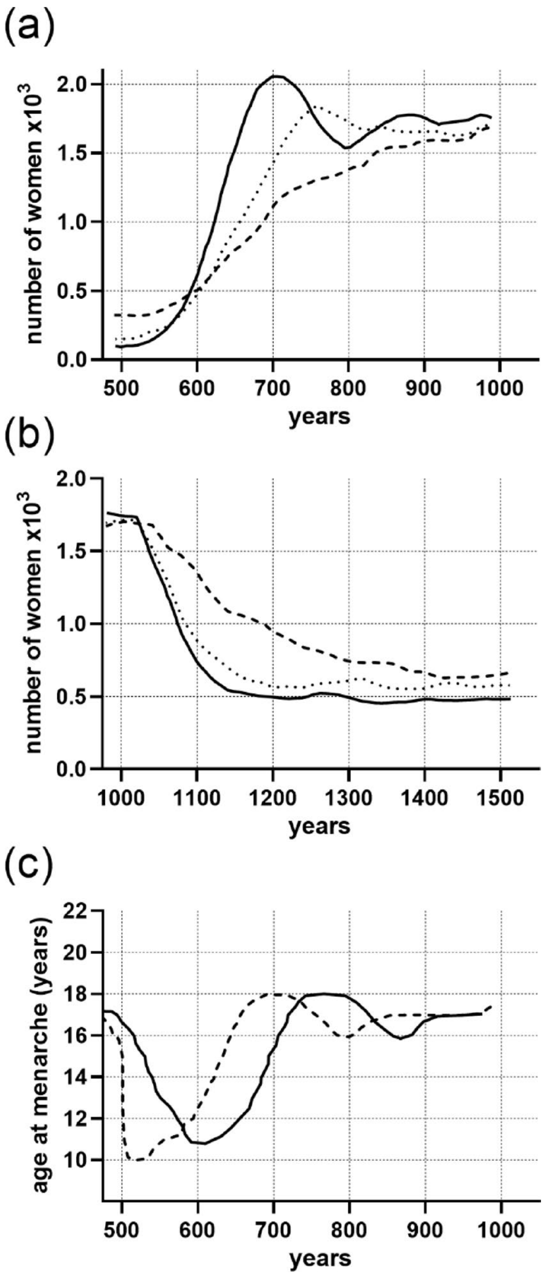

Fig. 2. Female population size from year 500 to year 1000 (**a**) and from year 1000 to year 1500 (**b**), in a model where density-dependent mechanisms operate only on the duration of post-partum amenorrhea, while age at menarche is kept constant at 17 years (broken line), in a model where density-dependent mechanisms operate only on the age at menarche, while the mean age of post-partum amenorrhea is kept constant at 19 months (dotted line), and in a model in which both mechanisms are operating (unbroken line). (**c**) Time development of the mean age at menarche in a model where the environment resources term increases abruptly from 1 to 8 at 500 years (broken line), or linearly from 1 to 8 from year 500 to year 600 (unbroken line).

addition, other biological and medical conditions in humans have been shown to be dependent on conditions in utero or in early life (fetal programming, physiological imprinting, the Baker hypothesis)[28,29].

The mean duration of post-partum amenorrhea has been shown to be dependent on age at menarche but has not been shown to be directly related to living conditions near the time of a woman's birth. We have assumed that this linear relationship can also be extended back through the age at menarche to the period near a woman's birth. Using only two density-dependent fertility mechanisms known from observations on human females result in strong regulation of population size in our simulated populations. Either of the two mechanisms could regulate the population on its own, without the help of the other (Fig. 2).

All the situations displayed in Fig. 2 show a much-delayed response. It is not until 50 years after the running-in period that a small response can be seen, and only after nearly one hundred years that the population increase

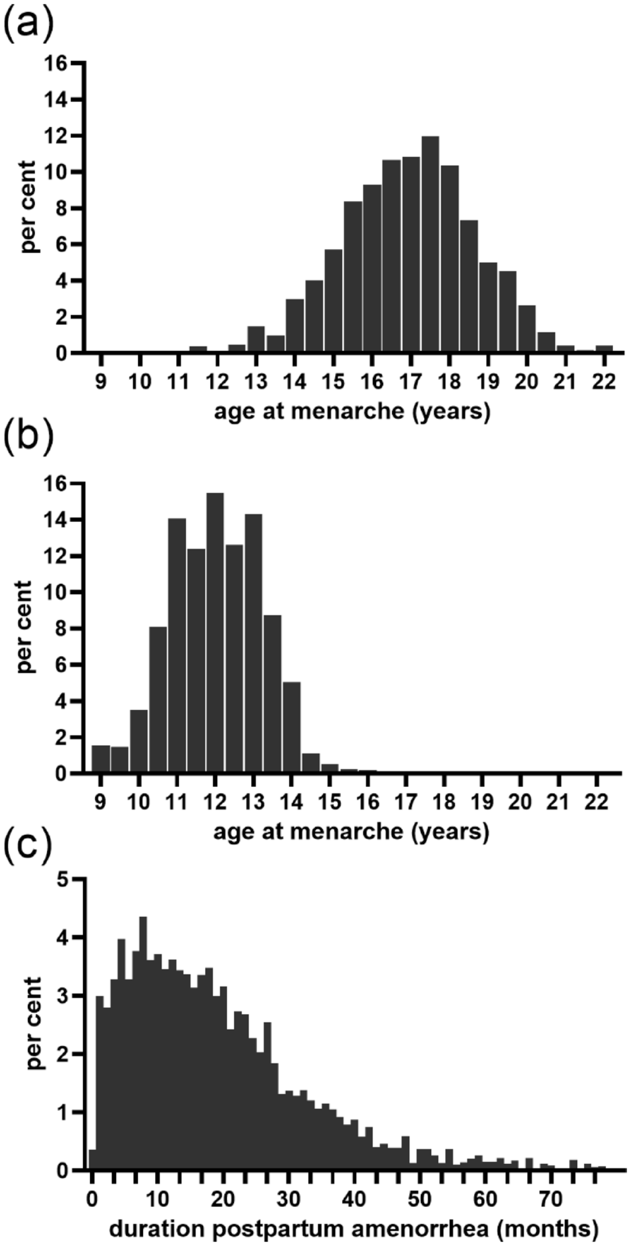

Fig. 3. Examples of distribution of age at menarche ((**a**) and (**b**)), and distribution of duration of post-partum amenorrhea (**c**). (**a**) During a stable period, years 1300–1400, mean age 17.0 years, N = 1129, (**b**) during linear increase of the environment resources term, year 600–700, mean age 12.0 years, N = 410, and (**c**) during a stable period, years 1300–1400, mean duration 19.1 months, N = 3770.

reaches its maximal rate. The rate of increase in the female component of the population between years 600 and 700 is then 6.0 women/year for the model where age at menarche was kept constant, 9.6 women/year for the model where the mean duration of post-partum amenorrhea was kept constant, and 17.5 women/year where both were allowed to vary. The population response was found to be much faster when the environment was abruptly changed to harsher in the year 1000, but the response was still considerably delayed.

As regards the growth of real *Homo* populations, it is possible that an increase in fertility has been important during periods of expansion into new and possibly richer habitats in human prehistory. One likely example is the rapid population growth indicated by archaeological evidence following the first arrival of a maximum of a few hundred *Homo sapiens* (including about 70 women) in New Zealand around 1280 AD[30,31].

To our knowledge, there is no aboriginal human population today in which the two main assumptions of our model are approximately fulfilled. In all known populations, there are cultural restrictions on early sexual activity. The situation in populations of non-human large mammals is different. There is some, but only weak, evidence of density-dependent fertility regulation of populations of whales[6,32–34] and elephants[5,35,36]. Witting discussed the population dynamics of eastern Pacific gray whales over the last 150 years[9] and found, like others

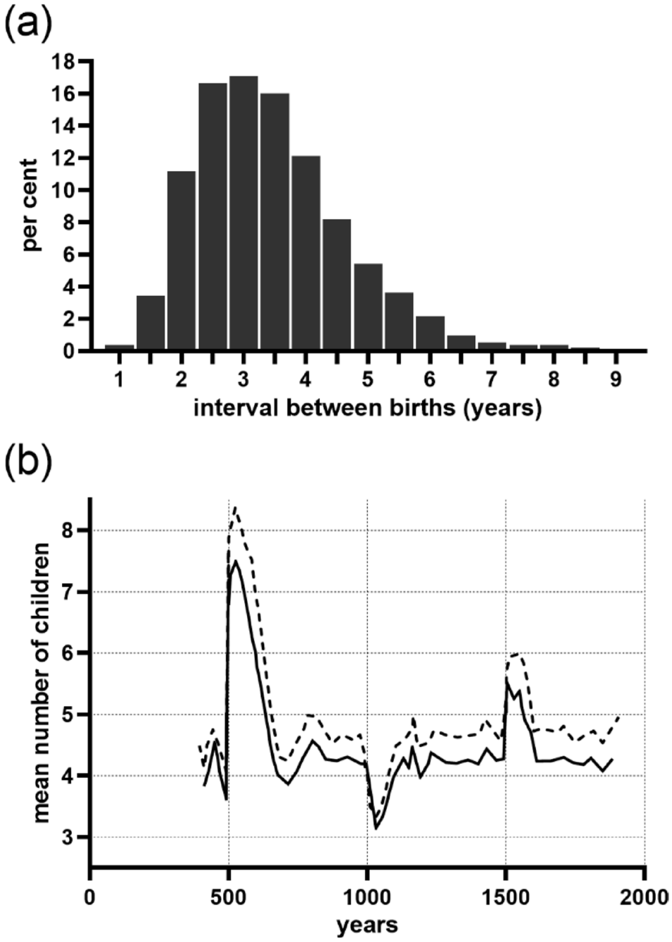

Fig. 4. Distribution of time distances between births for women born in a stable period, years 1300–1400, mean distance 3.5 years, N = 2880 (**a**), and mean number of children (girls and boys) in the population plotted for the year of birth of the women (**b**). All women: unbroken line, women who have survived the menopause: broken line.

before him[38], that a "hypothesis of density-regulated growth does not reconcile the known historical catches with the recent trajectory in abundance estimates". This is different for population growth models with delayed density regulation. Witting[9] explored population growth in 'inertial age-structured models' and obtained a reasonable fit to observations of abundance and catches during the last 150 years. However, he did not have any reasonable biological explanation for his assumptions of a delayed response in the fertility rate or of a delayed age at sexual maturity in female gray whales. We believe that the delayed fertility mechanisms known from human females, which we have explored in this paper, may be the biological mechanisms Witting would have needed in his model. However, including these mechanisms in his model would probably result in different predictions from those made by Witting from his original mathematical model.

Many different biological mechanisms could in theory be responsible for delayed density regulation in whales, but the two mechanisms explored in the present paper are obvious candidates. The most likely candidate is age at sexual maturity. For gray whales, age at sexual maturity has been determined to be between 6 and 12 years, and females give birth every one to three years. Neither of the two variables has been related to stock size during the last 50 years, mainly because of a lack of relevant observations. However, relevant observations have been obtained for other whale species, especially the Antarctic minke whale[38]. Individual minke whales are a little smaller than gray whales, but the life history variables are similar. For Antarctic minke whales, age at sexual maturity decreased from 13 to 7 years during the period 1920 to 1960 when the large baleen whales (blue whales, humpback whales and later fin whales) were hunted down to very low population levels in the Southern Ocean. All these whale species competed with minke whales for krill. As numbers of the other whale species were reduced, more krill became available for the minke whales – "The krill surplus hypothesis"[33]. The other fertility mechanism explored for humans, the duration of post-partum amenorrhea, is perhaps not so likely to be important in animals with estrus restricted to specific times of year. However, even in gray whales the time between births vary between one and three years and possibly even longer.

The model's assumption of constant age-dependent mortality is not realistic in real-world situations when available natural resources decrease rapidly (e.g. in model year 1000). In such situations, mortality is likely

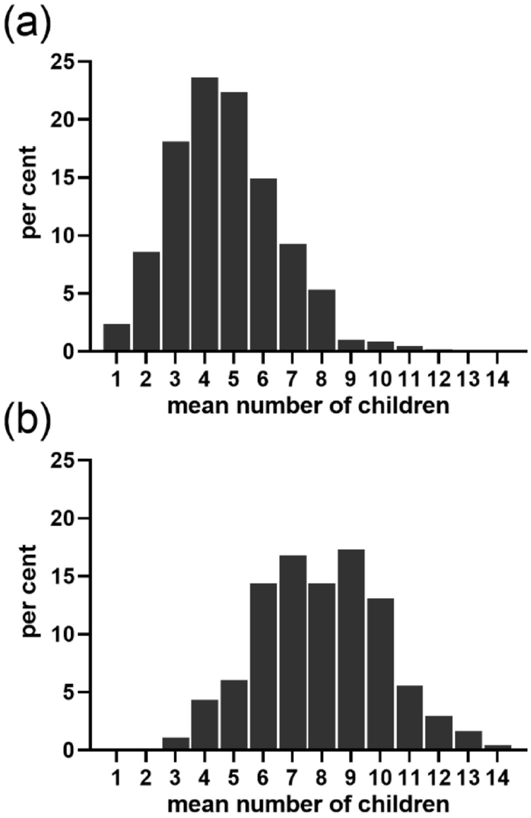

Fig. 5. Distribution of number of children in a stable period (year 1300–1400) for women surviving menopause, mean size 4.6 children/woman, N = 662, (**a**), and for women born in the period 500 to 550, and surviving menopause, mean size = 8.0 children/woman, N = 118 (**b**).

to increase. The simulation results show that even without an increase in mortality, the fertility mechanisms investigated would result in a rapid reduction in population size, but only starting after a delay of about 20 years.

It is not easy to investigate whether the assumptions of our model simulations based on observations from human populations are fulfilled for populations of other large mammal species. Based on our limited knowledge, only two populations have been studied over a sufficiently long period and in enough detail to be potentially interesting: the eastern North Pacific stock of gray whales[9,10] and the elephant population in Amboseli National park, Kenya[36,37,39]. For both populations, the critical factor is the level of detail in the available information about age at sexual maturity. Some of the published observations on the elephants indicate that our model could be relevant: "Early reproducers(< 12.5 years) had higher age-specific fertility rates than did females who commenced reproduction late (15 + years) with no difference in survival between these groups."[37].

Age at sexual maturity is not known to be a function of living conditions or nutrition near the time of birth either in elephants or in gray whales. However, for both species a large range of values has been published for age at sexual maturity for different areas and/or time periods. Observation from minke whales indicate a functional relationship similar to that we have found for humans. Assuming that this relationship also applies to elephants and gray whales, the results shown in our graphs should be approximately valid for these two species as well and should be able to explain delayed density-dependent fertility mechanisms in these species. The most surprising result is perhaps how large the delay may be. In this case, it was more than 50 years before an effect could be seen on the population size after an abrupt improvement in living conditions. For elephants, the delay would be expected to be of this order of magnitude, for gray whales perhaps somewhat smaller, since they reach sexual maturity at a somewhat younger age than humans do.

The population response is faster when the environment changes from abundant to more harsh conditions, but even then, more than 20 years before a significant fall in population size can be seen (Fig. 2b). Under such circumstances, our model assumption about constant mortality is in addition unrealistic, and we would expect an immediate density-dependent increase in mortality. This can explain Fowler and Sinclair's observation[2,3] that density-dependent mechanisms in large mammals operate near the carrying capacity of the environment.

The delayed density-dependent fertility mechanisms we are proposing for large mammals could also be relevant to the current discussion and the model investigations related to the regrowth of baleen whale populations (blue, fin and humpback whales) in the Antarctic Ocean after commercial whaling was stopped, and their competition with minke whales, seals and penguins for the krill resources[33,40].

Data availability

The simulation program is written in the old SIMULA language. Interested readers can contact the corresponding author to obtain a printout of the program.

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Author contributions

S-M H B wrote the SIMULA program and ran the simulations as part of her master thesis in informatics, instructed about the biological model and supervised by L W, who also wrote the manuscript.

Competing interests

The authors declare no competing interests.

Additional information

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