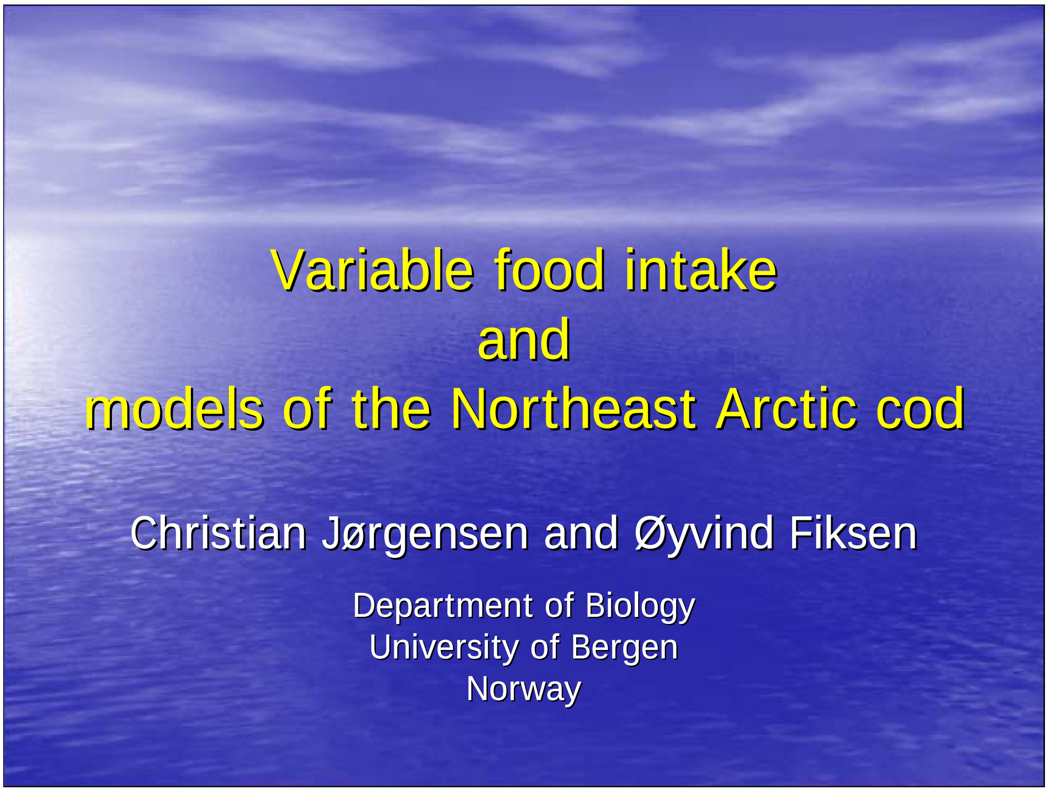



I am going to talk today about Variable food intake and models of the Northeast Arctic cod. This work has been done in collaboration with Øyvind Fiksen at the University here in town.

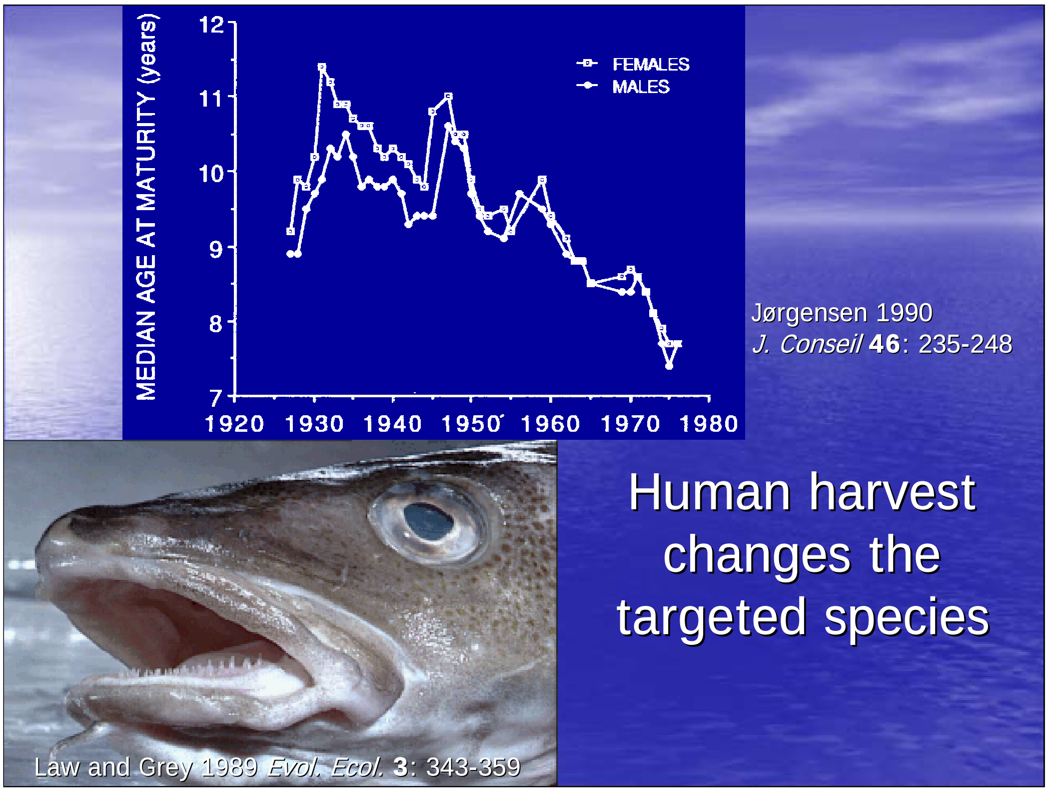
I'll start by asking: what kind of models do we need to address the biological implications of climate change.


Can you see what is wrong with this elephant? Ivory has a high value on the illegal market. Pouching is put forward as the reason that the number of tuskless elephants has been steadily increasing the last decades.

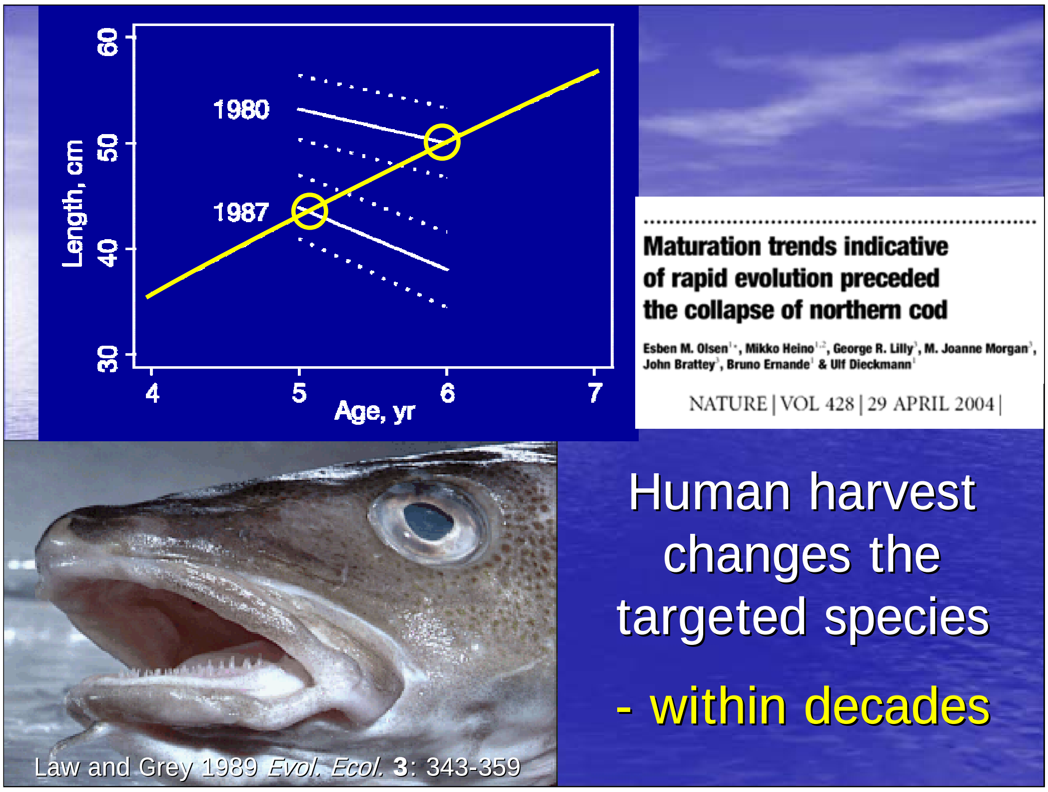
** Trophy hunting for the bighorn ram has selectively targeted the largest males with the biggest horns. Traditionally these males also had the highest fitness, but as a consequence of trophy hunting mean buck size and mean horn size is decreasing in this species.

** The trawler fishery for Northeast Arctic cod in the Barents Sea dramatically increased the juvenile mortality for this species. In response, the age and size at sexual maturity has steadily decreased throughout last century. Common for these three examples is that…

** …human harvest changes the targeted species.




** This graph shows the decrease in the median age at maturation in Northeast Arctic cod from 1925 until 1975, and the trend is continuing.

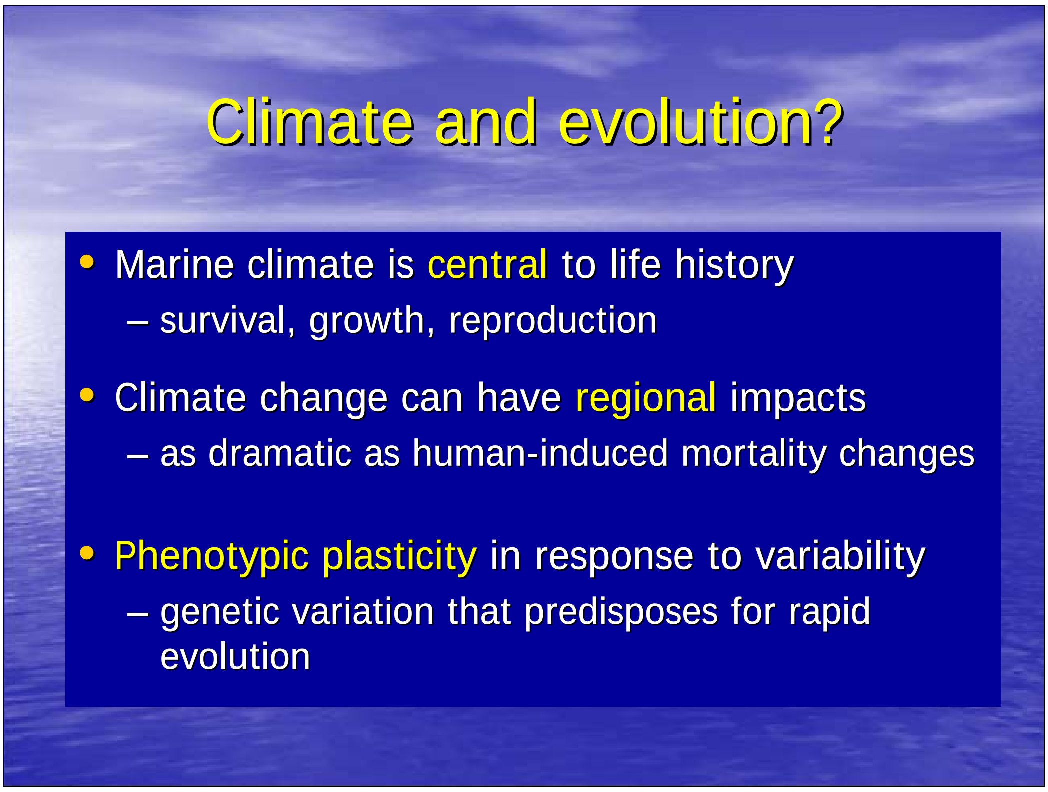



Two weeks ago we could also read in Nature a study on sexual maturation of the northern cod outside Canada during the collapse years in the late 1980s.

** This graph show the length at age for which there was a 50% probability of maturing, and how it changed between the 1980 and the 1987 cohort. If we overlay the average growth trajectory for this stock…

** …we can se that the maturation reaction norm intersects the growth trajectory one year earlier for the 1987 cohort. This approach strips away the environmental influence, and the change visualized here is assumed to be entirely genetic. For cod, human-induced changes in the mortality regime cause an evolutionary response in key life history characteristics. It is a common misunderstanding that evolution only takes place on the geological time-scale. These examples show that substantial evolutionary change can happen…

** …within decades. The question is then: will climate change be a strong enough selective force to trigger evolutionary responses?




Climate is central to life history in that it directly or indirectly affects the three main components identified in life history theory.

** **Survival** is linked to the distribution of predator species, which may change with changes in temperature or ocean currents, and energy expenditure may be temperature-dependent. **Growth** and metabolic processes rely on temperature, as well as the distribution of potential prey species. For **reproduction**, many marine species target areas or seasons with a favourable marine climate for eggs and larvae in the vulnerable first period of development and growth.

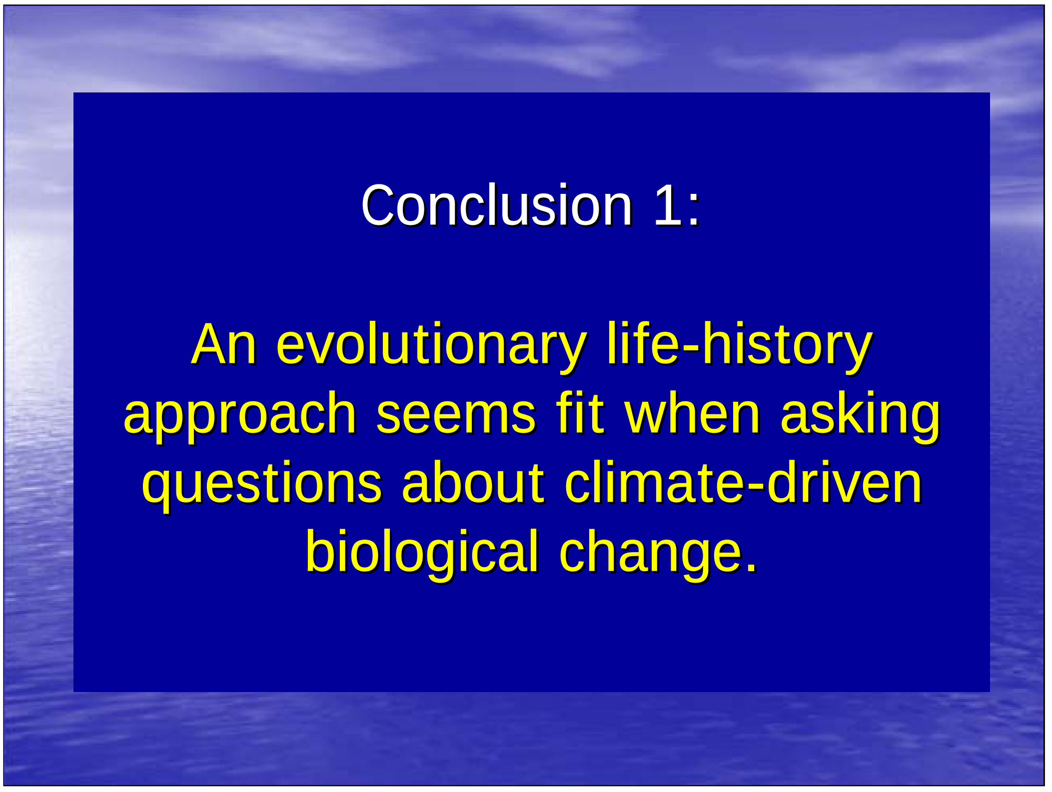
** Climate change can have a regional impact, and within regions it is our view…

** …that the changes can be just as dramatic as the human-induced mortality changes.

** Most marine organisms show phenotypic plasticity in response to a variable marine climate.

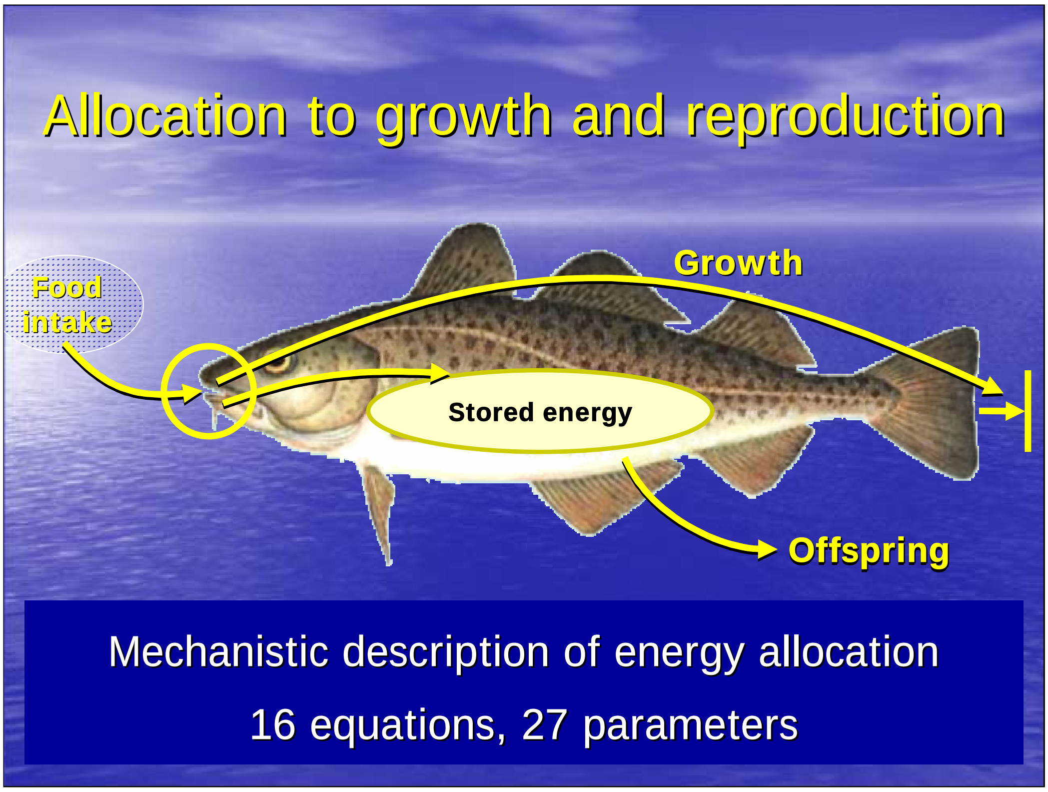
** Thus, life history traits are already plastic, meaning that the genetic variation is already there for evolution to act upon.

From these considerations we argue that climate change can be a strong evolutionary force comparable to the human-induced mortality changes already discussed.




Our first conclusion is therefore that an evolutionary life-history approach seems fit when asking questions about climate-driven biological change.

As an example of evolutionary modeling we will show a life-history model for the Northeast Arctic cod.




The model is based on bioenergetics and whether ingested energy should be diverted to growth or reproduction. The time resolution of the model is months.

** Every month, the cod receives a variable food intake.

** The energy can be allocated to storage in the muscles and in the liver.

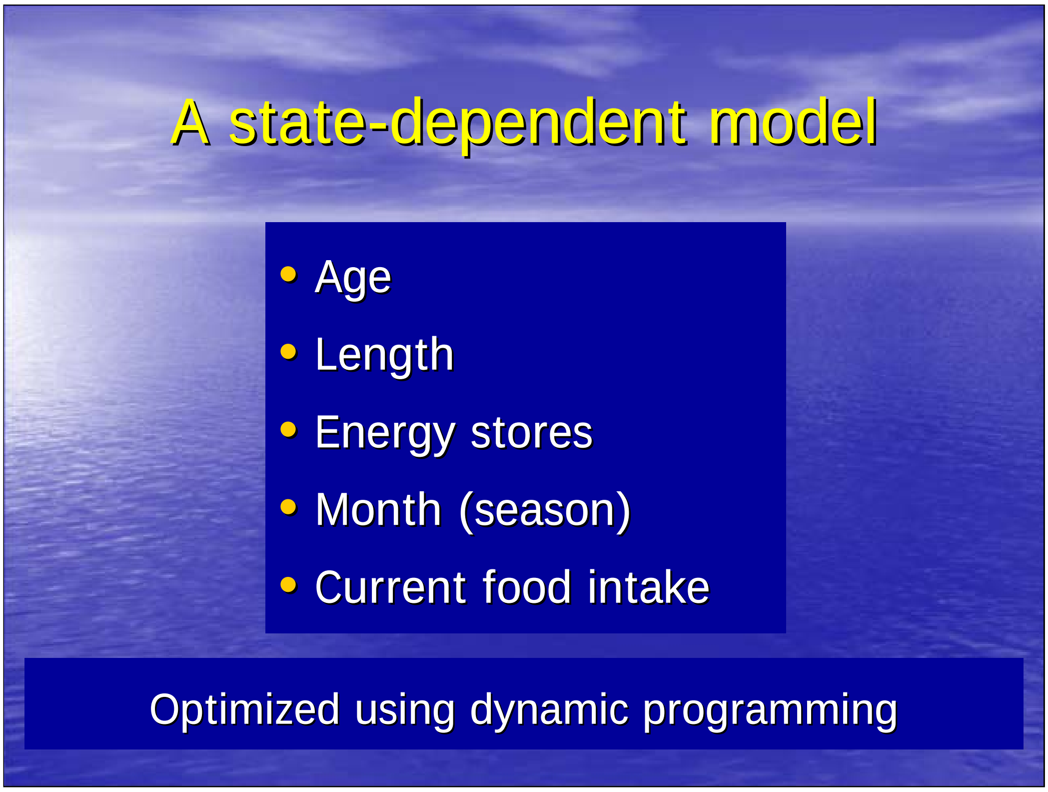
** This stored energy is used to produce offspring during the spawning season.

** Or, energy can be used to grow to a larger size. Larger size has many benefits, amongst others a higher fecundity, lower predation rates, and more economic swimming.

** The model is based on a physiological description of energy allocation, and a large body of experimental and field studies is used to parameterize the model.

** The model is rather complex. In total, it has 16 equations and 27 parameters, all with sound biological meaning.

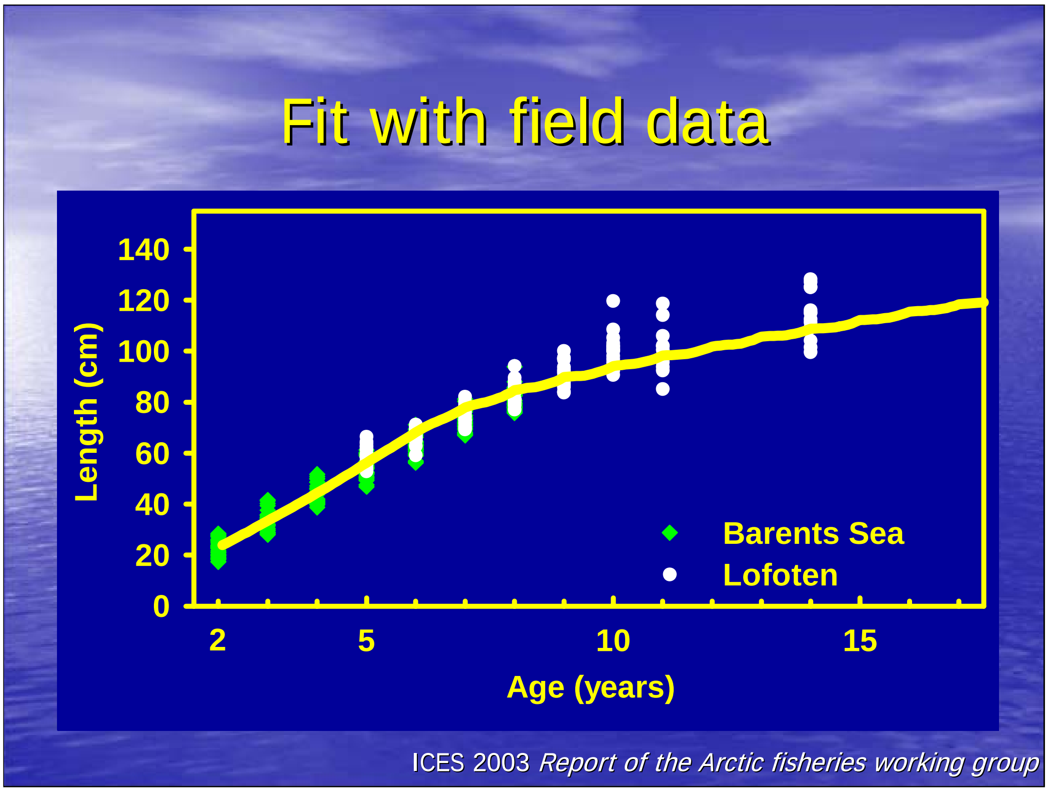
** The model focuses totally on the allocation decision. In all situations the model asks: what is the best thing to do with the energy that is available.



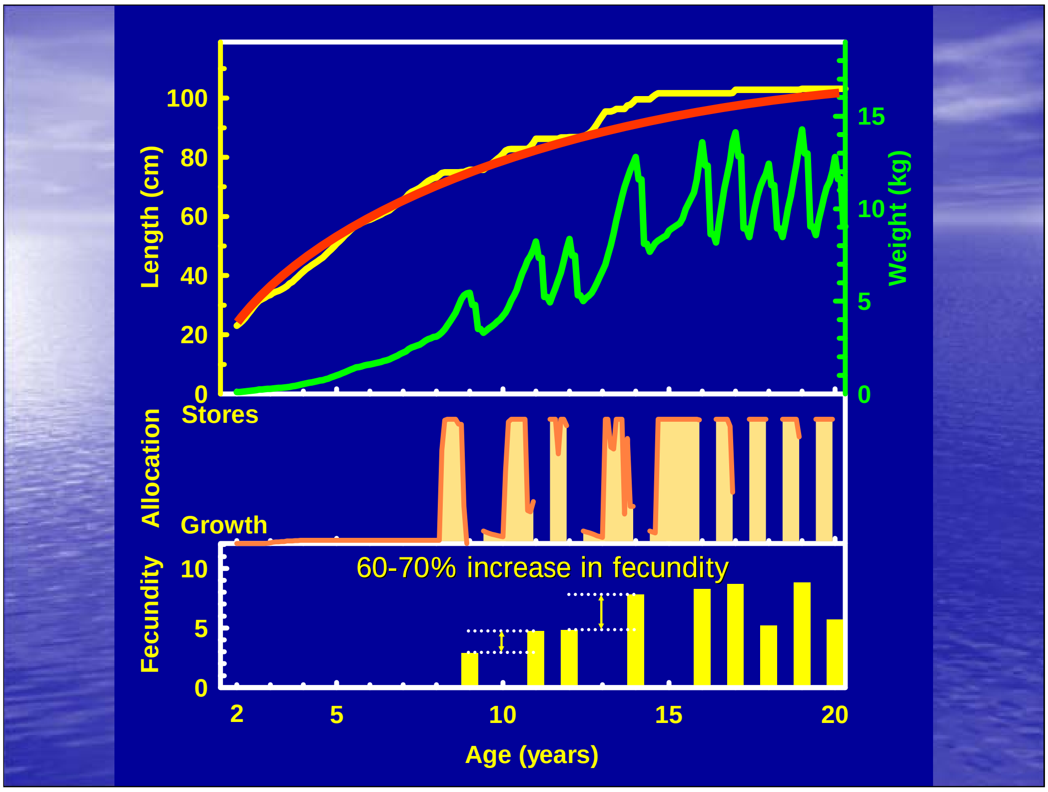

The model is state-dependent, meaning that the allocation decision relies on the situation the individual is in.

** The states used are Age, Length, Size of energy stores, Month of the year, and the current food intake.

** For the technically inclined: the model is optimized using dynamic programming.




This graph shows growth in the model and how it fits with field data. Age is on the x-axis, and length in centimeters on the y-axis. The white and green points are length at age for cod from the Barents Sea and Lofoten between 1978 and 2000. The yellow line is growth as it is predicted by the model when representative parameters are used.




This graph shows the life history of one example individual. Age is on the x-axis. In the top panel, the yellow line is length and the green line is weight. The allocation decision is shown in the middle panel. A low value means that energy is allocated to growth, while a high value indicates allocation to stores. In the lower panel is the egg production in the years that this cod spawns.

** This cod starts out with allocating all its resources to growth.

** As a result, length growth is almost linear with time.

** Approximately one year before this cod spawns for the first time, it start allocating energy to stores.

** At the same time, length growth levels out…

** ...and weight increases rapidly.

** The stored energy is spawned. There are two important life-history phenomena that this model produces that optimization models have had a very hard time predicting. The first is that in the next year…

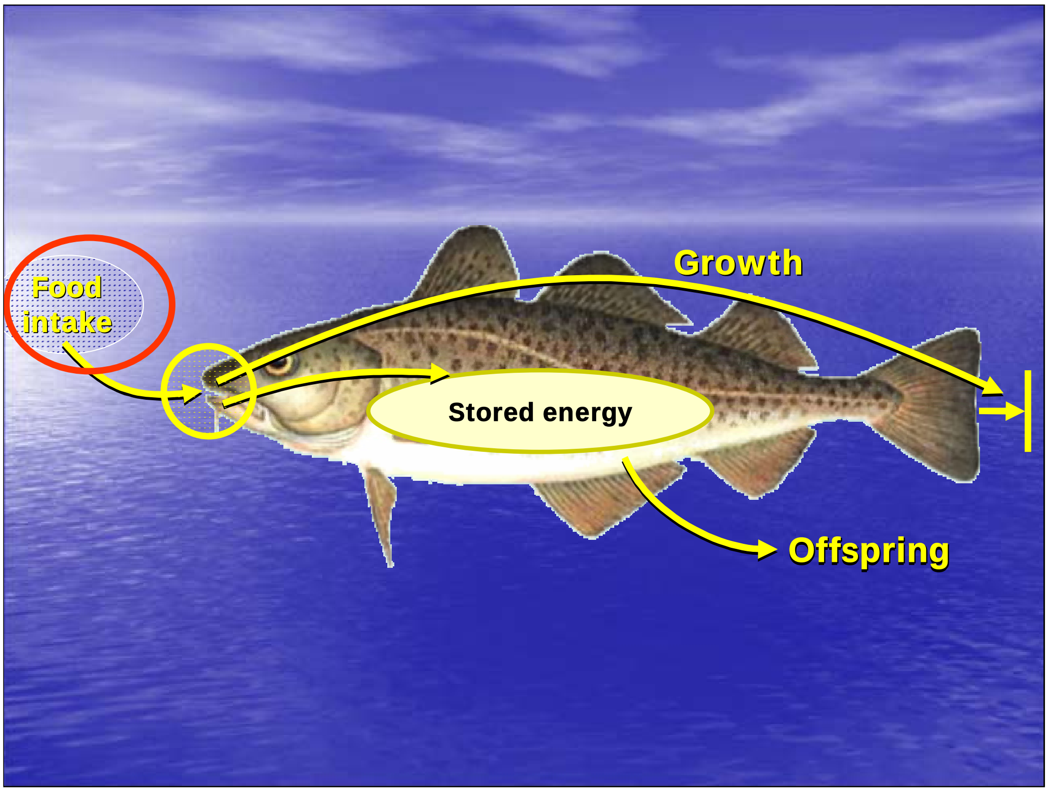
** …this cod starts allocating everything to growth again.

** As a result, length once again increases and…

** …the cod skips spawning.

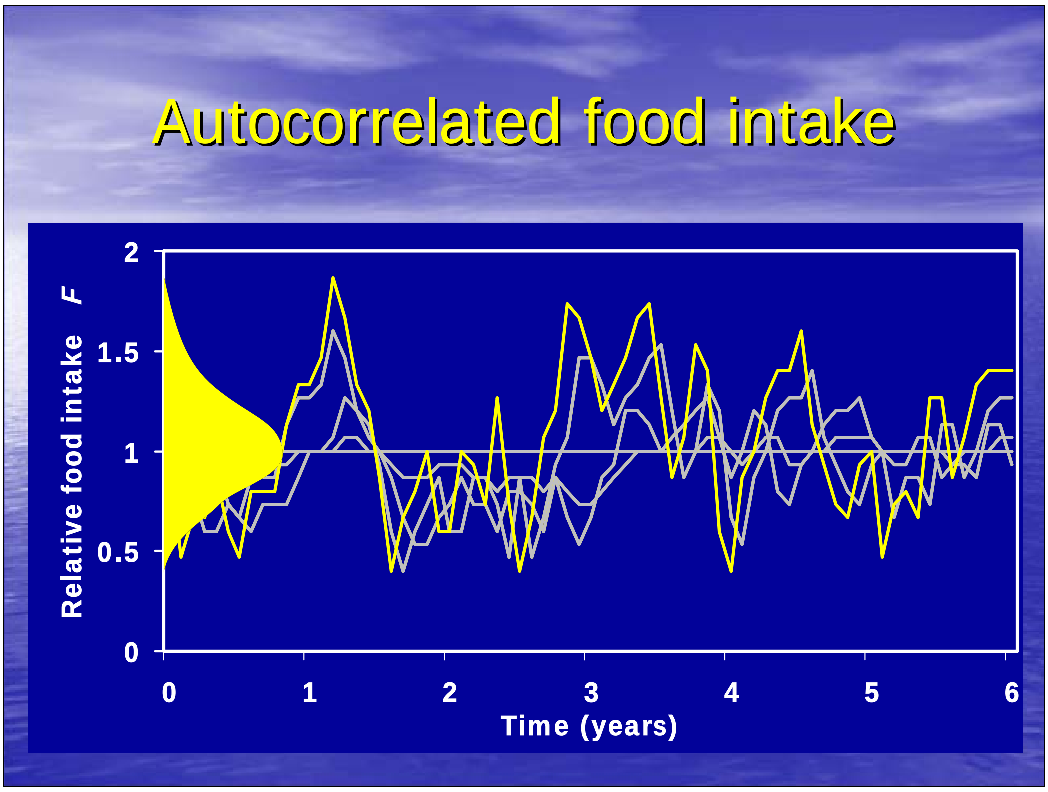
** Such skipped reproduction is more common in nature than is often believed. I will later in this talk show that environmental variability is a prerequisite if models are to predict this phenomenon. The second phenomenon I want to draw your attention to is indeterminate growth.

** This model shows the gradual transition from growth only to reproduction only that is common in nature but only rarely emerges in models. Thus, such a complex evolutionary model describes with amazing realism how life histories should be optimally designed.




Climate change can have many ecosystem effects. It can change the geographical distribution of prey or predator species, or alterations in temperature can affect physiological processes. The focus of this talk will be on the food intake.

** Again, many processes linked to feeding can change in response to future climate. I will present some results that analyze the effects of variability in the food intake. While the effects of a higher or lower mean food intake can be easily envisaged, the effects that variability has on models is often less intuitive.

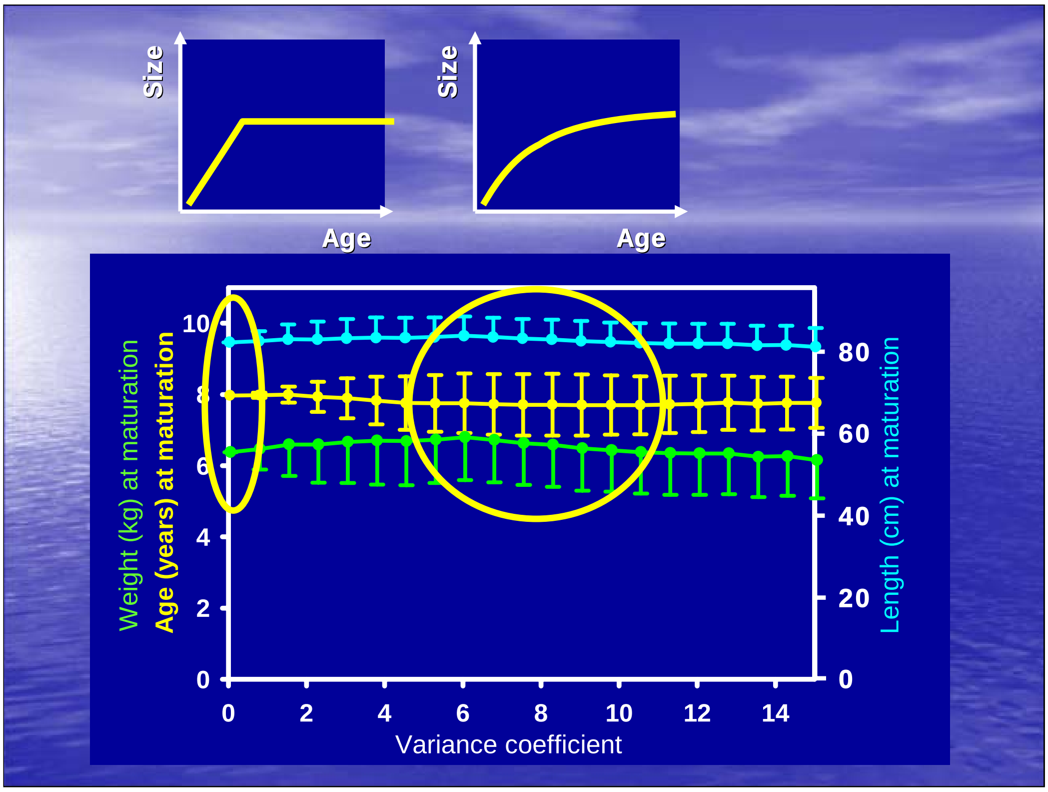



We constructed a set of auto-correlated time-series of food intake. The autocorrelation parameters are chosen so that good and bad feeding periods will persist for around one to three years. On the x-axis is time in years, and on the y-axis a relative index of food intake.

** We started from absolutely no variance, where the average food intake was received every month.

** We then increased the variance and ran the model for each scenario.

** If the different values are summed up, the result is a normal distribution around the mean.




Let us now see how increasing the variability will affect the maturation dynamics in this modeled fish stock. On the x-axis is increasing variance in the food intake…

** …exemplified by these plots on top that show normal distributions with increasing variance towards the right.

** First we plot age at maturation. Since the mean food intake is constant, mean age at maturation does not increase or decrease. If we look at the variation around the mean, however, it increases with environmental variability up to a certain point, where it reaches a plateau.

** The same also goes for weight at maturation and…

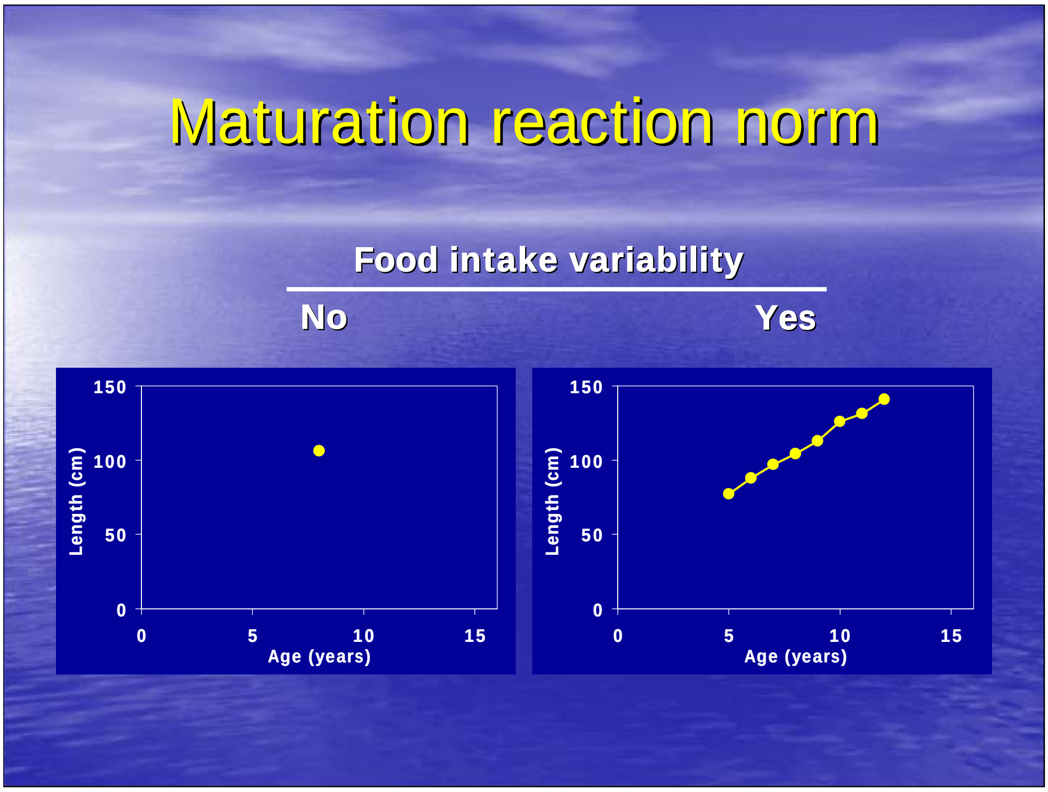
** …length at maturation.

** If we first consider the situation with no variability on the food intake, we see here that there is also no variation in age and size at maturation. In this case…

** …growth is determinate. This is often called a bang-bang strategy, meaning that all resources are diverted to growth early in life, until sexual maturation after which everything is diverted to reproduction.

** Let us now turn to situations with a certain level of variability. Here, age, length, and weight at maturation vary in response to the variable feeding conditions…

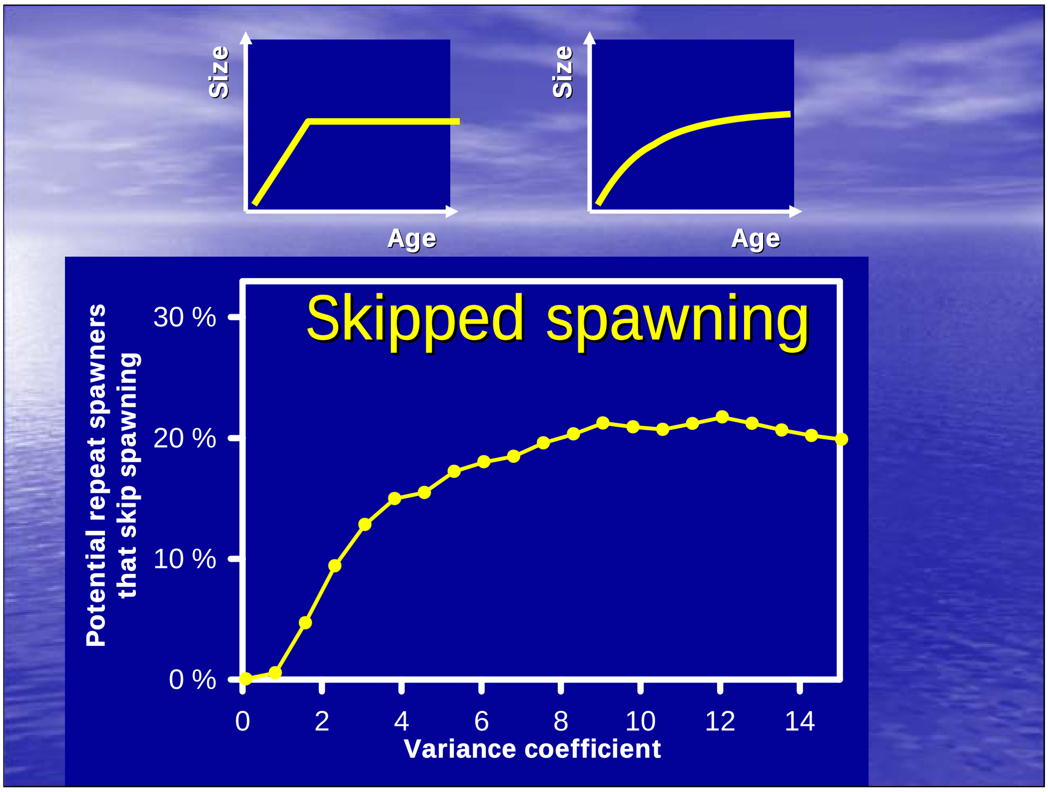
** …and the model now predicts indeterminate growth.




We can also plot the maturation reaction norms. The maturation reaction norm is the combination of size and age at which there is a 50% probability of maturing. We see that in the case of no environmental variability, to the left, …

** … the reaction norm is a singular point.

** When there is environmental variability, there may be inter-annual differences in maturation, and cohorts may also mature over several years depending on the growth conditions experienced by the individual fish.

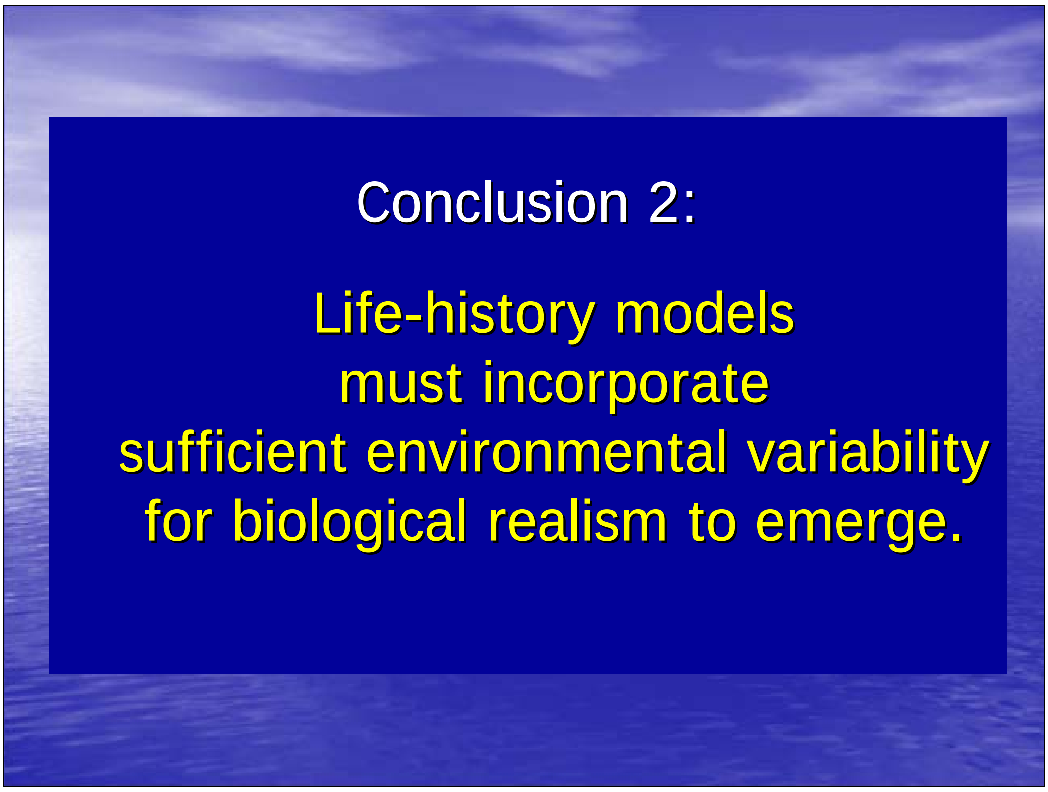



We now turn again to skipped spawning. Skipped reproduction means that a reproductive event is omitted after sexual maturation has occurred. This graph again shows increasing environmental variability on the x-axis, and on the y-axis is the proportion of the potential repeat spawners that skip reproduction.

** We see that spawning is never skipped when there is no environmental variability. Skipped spawning becomes more common when variability in the food intake is increased, and stabilizes at a level where approximately 20% of the repeat spawners skip spawning.

** This is part of the explanation for determinate growth versus indeterminate growth at the individual level, where skipped spawning seasons gives opportunity for further growth.

**To summarize**: There are examples of rapid human-induced evolution in harvested species. We argue that climate change can have similar impacts, and that an evolutionary life-history approach is suitable when one would like to model biological implications of climate change. We then investigated the effects that a variable food intake has on a life-history model of Northeast Arctic cod. We found that variability was necessary to predict indeterminate growth, realistic dynamics in age and size at maturation, and skipped spawning. From this we draw our second conclusion,




…namely that life-history models must incorporate sufficient environmental variability for biological realism to emerge. A consequence is that forecasts of biological implications of climate change require that we further understand the nature and future prospect for environmental variability.

Thank you for your attention!