Fisheries-Induced Evolution: Overview

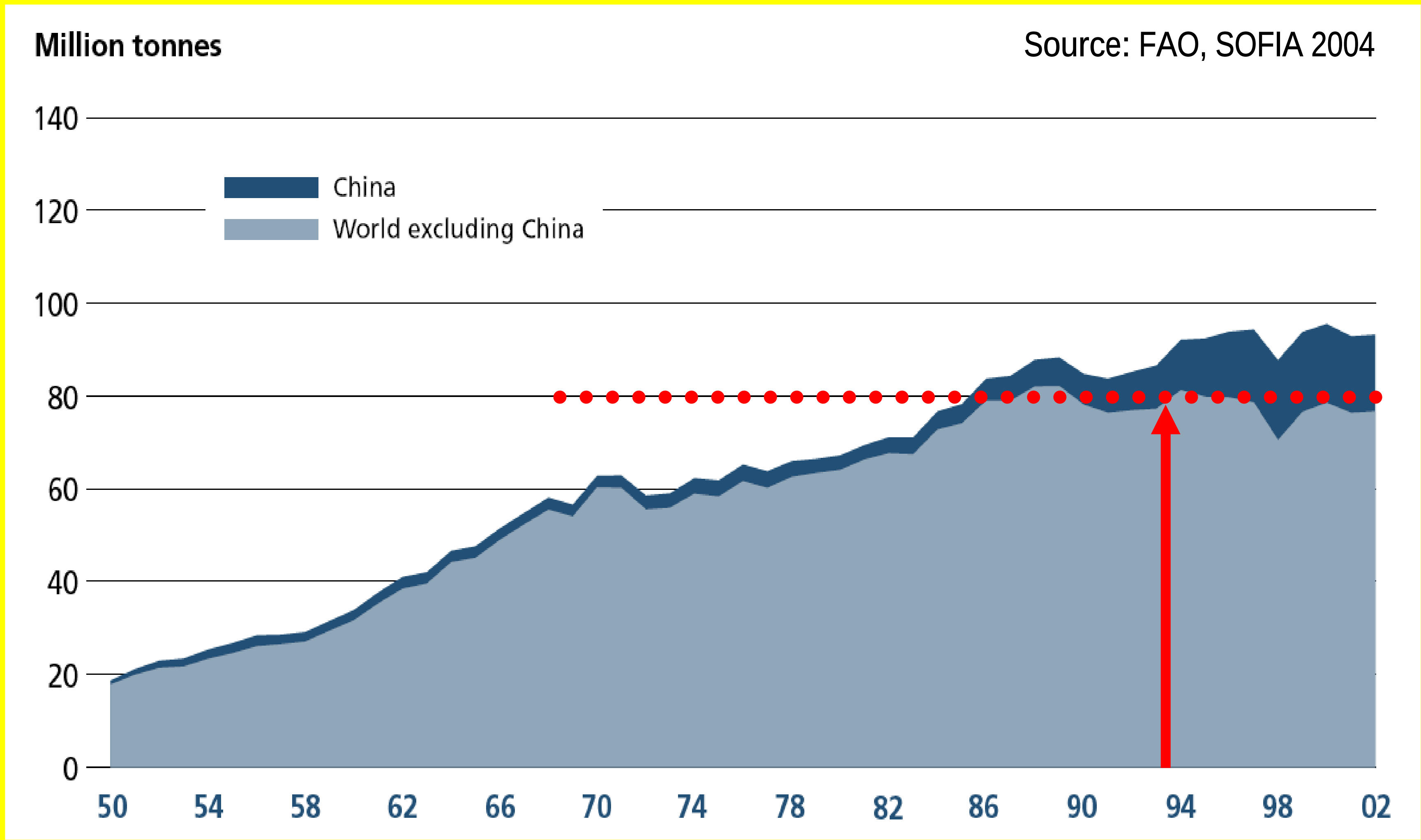
Ulf Dieckmann

Adaptive Dynamics Network, International Institute for Applied Systems Analysis, Laxenburg, Austria

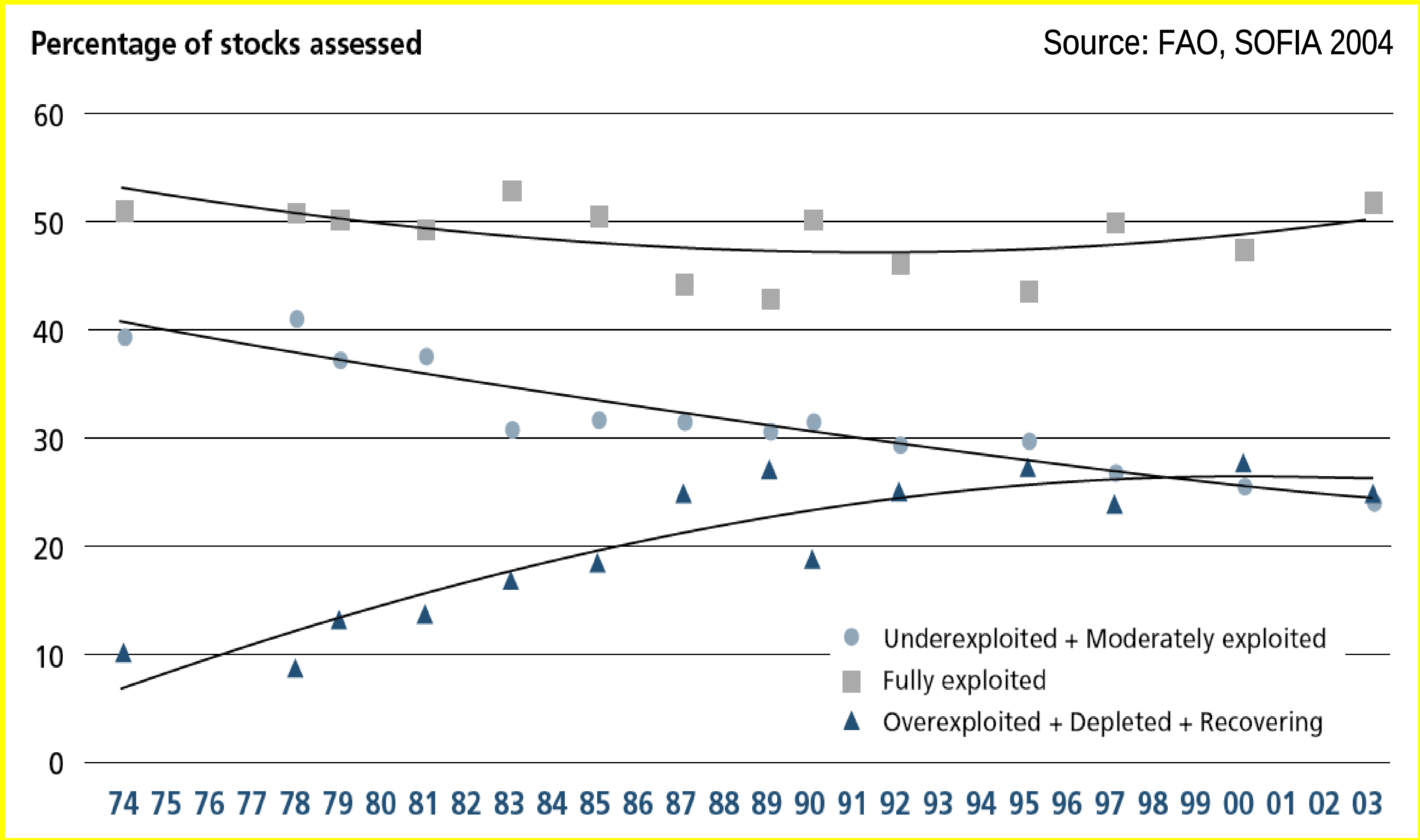
Mikko Heino

Institute of Marine Research, Bergen, Norway

World Fisheries Have Reached a Ceiling



75% of Stocks Are Maximally Exploited



The Overlooked Evolutionary Dimension

- Modern fishing results in such substantial changes of mortality patterns that evolutionary responses of stocks are inevitable.
- Such changes are not as slow as is widely believed: Significant evolution can occur within 10 or 20 years.
- Evolutionary changes are not necessarily beneficial, neither to the stock nor to the exploiting agents.
- Once evolutionary changes have occurred, they may be very difficult to reverse.
- In short: Fishing does not only change the numbers, but also the traits of exploited fish.

Fisheries-induced Evolution: A Caricature

A Personal Experience, by Richard Law

- "Outside a small band of enthusiasts, I think it is true to say that scepticism about evolution under exploitation remained the rule through to the mid 1990s, despite the ideas being available to a wide audience. The response to a talk I gave to an influential group of fisheries scientists at the Lowestoft Laboratory in the late 1980s epitomised the reaction. At the end there was a statement from the floor that the heritabilities of traits under selection would not be significantly different from zero so that, in effect, any pattern of fishing could continue indefinitely without ever causing genetic change to fish stocks. Coming from a geneticist at the Laboratory, this statement was bound to be taken seriously, and I could almost hear the sound of closing doors."

The Precautionary Approach

- Rio Declaration on Environment and Development (UN, 1992)

  "In order to protect the environment, the precautionary approach shall be widely applied by States according to their capabilities. Where there are threats of serious or irreversible damage, lack of full scientific certainty shall not be used as a reason for postponing cost-effective measures to prevent environmental degradation."

- Other conventions endorsing the precautionary approach

1992	Convention on Climate Change (UN)
1992	Convention for the Protection of the Marine Environment of the North-East Atlantic (OSPAR)
1993	Convention on Biological Diversity (UNEP)
1993	Guidelines for Preventing the Introduction of Unwanted Aquatic Organisms and Pathogens from Ships' Ballast Water and Sediment Discharges (IMO)
1994	Code of Practice on the Introduction and Transfer of Marine Organisms (ICES)
1995	Agreement on Fish Stocks (UN)
1995	Guidelines on the Precautionary Approach to Capture Fisheries and Species Introduction (FAO)

Fisheries-induced Evolution in the Lab

REPORTS

Science

July 2002

Sustaining Fisheries Yields Over Evolutionary Time Scales

David O. Conover* and Stephan B. Munch

Fishery management plans ignore the potential for evolutionary change in harvestable biomass. We subjected populations of an exploited fish (*Menidia menidia*) to large, small, or random size-selective harvest of adults over four generations. Harvested biomass evolved rapidly in directions counter to the size-dependent force of fishing mortality. Large-harvested populations initially produced the highest catch but quickly evolved a lower yield than controls. Small-harvested populations did the reverse. These shifts were caused by selection of genotypes with slower or faster rates of growth. Management tools that preserve natural genetic variation are necessary for long-term sustainable yield.

Hunting-induced Evolution in the Wild

Undesirable evolutionary consequences of trophy hunting

David W. Coltman[1], Paul O'Donoghue[1], Jon T. Jorgenson[2], John T. Hogg[3], Curtis Strobeck[4] & Marco Festa-Bianchet[5]

[1]*Department of Animal and Plant Sciences, University of Sheffield, Sheffield S10 2TN, UK*
[2]*Alberta Department of Sustainable Development, Fish and Wildlife Division, Box 1059, Canmore, Alberta T0L 0M0, Canada*
[3]*Montana Conservation Science Institute, Missoula, Montana 59803, USA*
[4]*Department of Biological Sciences, University of Alberta, Edmonton, Alberta T6G 2E9, Canada*
[5]*Département de biologie, Université de Sherbrooke, Sherbrooke, Québec J1K 2R1, Canada*

nature

December 2003

Phenotype-based selective harvests, including trophy hunting, can have important implications for sustainable wildlife management if they target heritable traits[1–3]. Here we show that in an evolutionary response to sport hunting of bighorn trophy rams (*Ovis canadensis*) body weight and horn size have declined significantly over time. We used quantitative genetic analyses, based on a partly genetically reconstructed pedigree from a 30-year study of a wild population in which trophy hunting targeted rams with rapidly growing horns[4], to explore the evolutionary response to hunter selection on ram weight and horn size. Both traits were highly heritable, and trophy-harvested rams were of significantly higher genetic 'breeding value' for weight and horn size than rams that were not harvested. Rams of high breeding value were also shot at an early age, and thus did not achieve high reproductive success[5]. Declines in mean breeding values for weight and horn size therefore occurred in response to unrestricted trophy hunting, resulting in the production of smaller-horned, lighter rams, and fewer trophies.

Fisheries-induced Evolution in the Wild

nature

April 2004

Maturation trends indicative of rapid evolution preceded the collapse of northern cod

Esben M. Olsen[1*], **Mikko Heino**[1,2], **George R. Lilly**[3], **M. Joanne Morgan**[3], **John Brattey**[3], **Bruno Ernande**[1] & **Ulf Dieckmann**[1]

[1] *Adaptive Dynamics Network, International Institute for Applied Systems Analysis, A-2361 Laxenburg, Austria*
[2] *Institute of Marine Research, P.O. Box 1870 Nordnes, N-5817 Bergen, Norway*
[3] *Northwest Atlantic Fisheries Centre, Department of Fisheries and Oceans, P.O. Box 5667, St John's, Newfoundland, Canada A1C 5X1*

* Present address: Division of Marine Biology and Limnology, Department of Biology, University of Oslo, P.O. Box 1064, Blindern, N-0316 Oslo, Norway

Northern cod, comprising populations of Atlantic cod (*Gadus morhua*) off southern Labrador and eastern Newfoundland, supported major fisheries for hundreds of years[1]. But in the late 1980s and early 1990s, northern cod underwent one of the worst collapses in the history of fisheries[2–4]. The Canadian government closed the directed fishing for northern cod in July 1992, but even after a decade-long offshore moratorium, population sizes remain historically low[4]. Here we show that, up until the moratorium, the life history of northern cod continually shifted towards maturation at earlier ages and smaller sizes.

Because confounding effects of mortality changes and growth-mediated phenotypic plasticity are accounted for in our analyses, this finding strongly suggests fisheries-induced evolution of maturation patterns in the direction predicted by theory[5,6]. We propose that fisheries managers could use the method described here as a tool to provide warning signals about changes in life history before more overt evidence of population decline becomes manifest.

Which Traits Are at Risk?

- Age and size at maturation:
  Reproducing late may not be a viable option.
- Reproductive effort:
  Saving for future reproduction may be futile.
- Growth rate:
  Staying below mesh size pays.
- Behavior:
  Reducing exposure to fishing is selected.

Focus of my talk

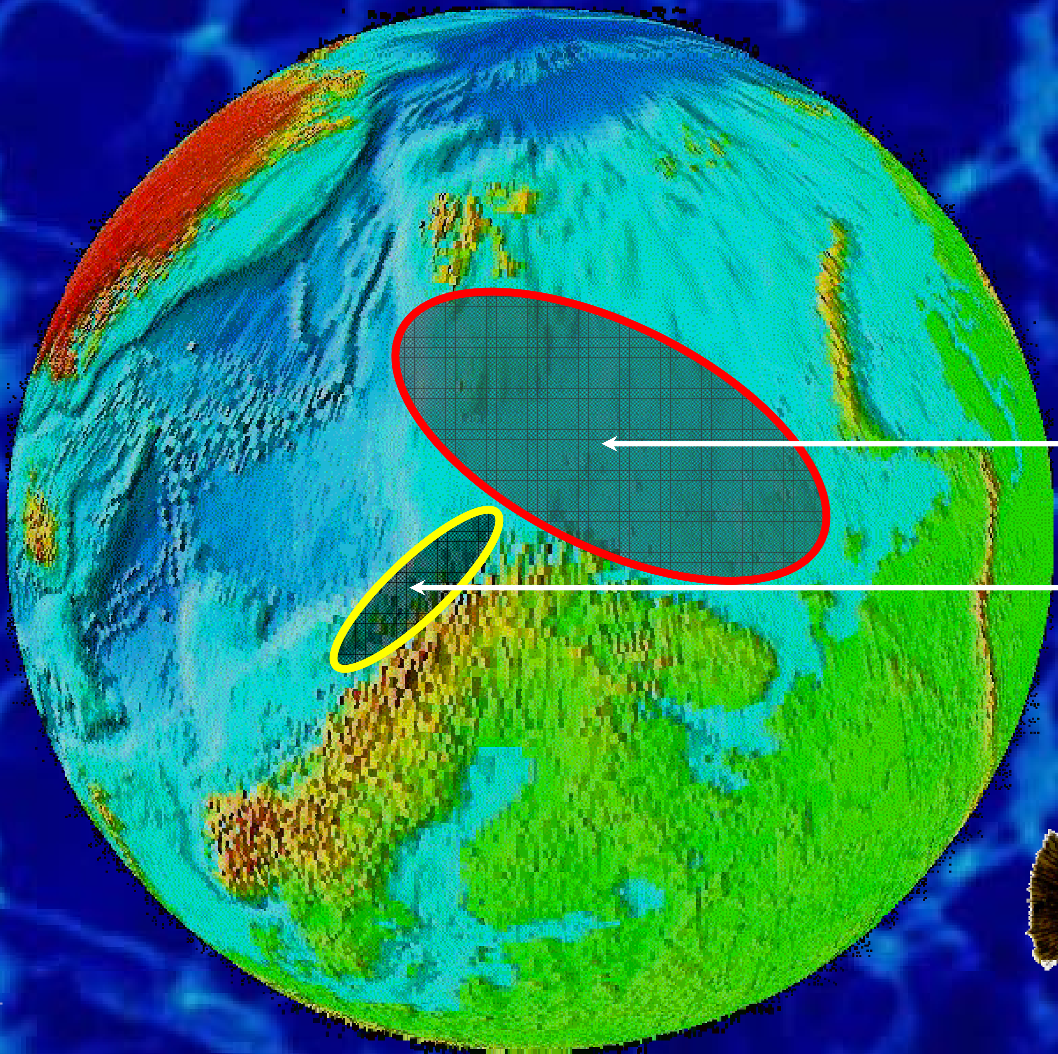
Two Parts to Come

1. Estimating Evolutionary Change

2. Modeling Evolutionary Change

1 Estimating Evolutionary Change

Northeast Arctic Cod: Stock Structure



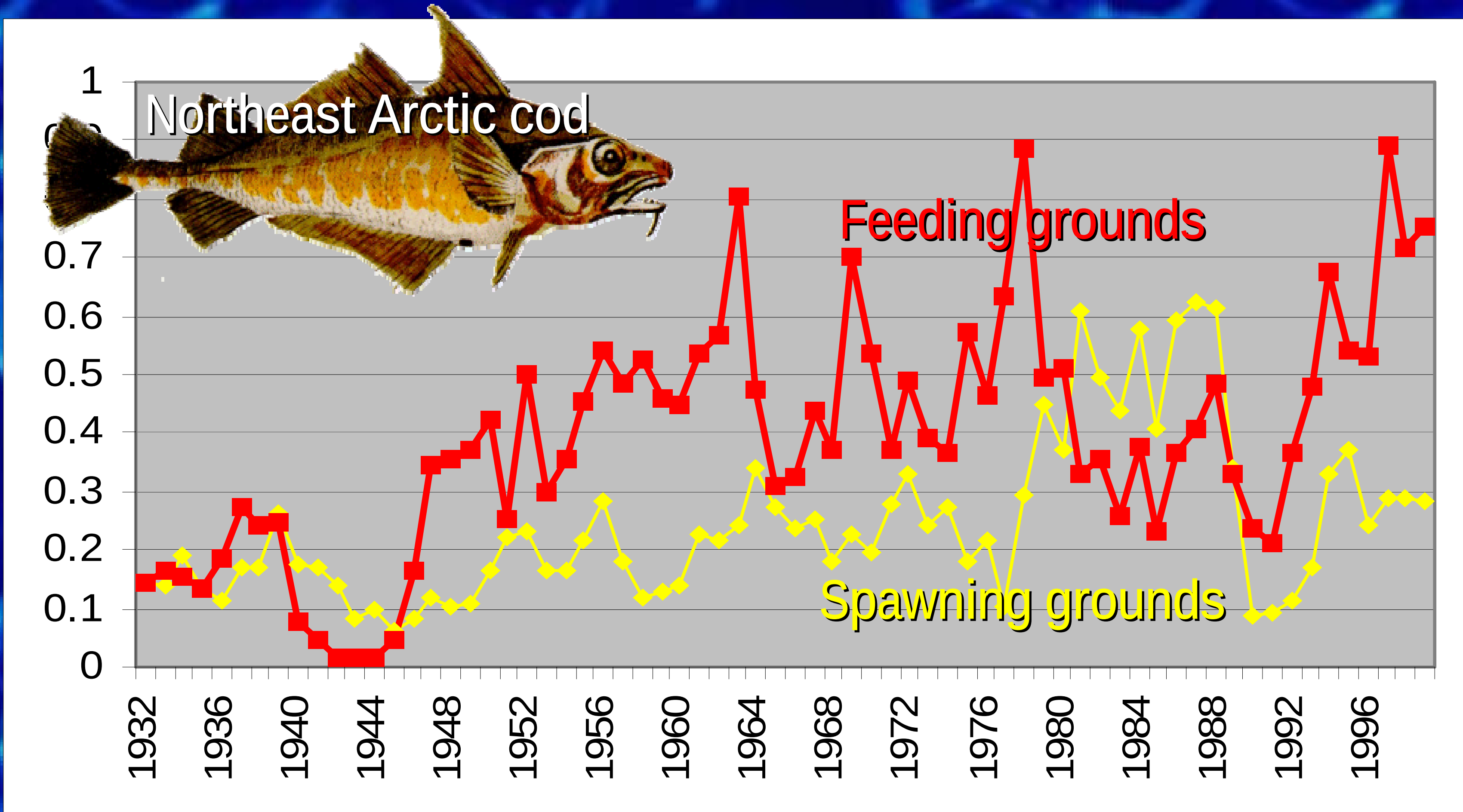
With a catch of 400,000 tons per year, Northeast Arctic cod is one of the most important gadoid stocks worldwide.

Feeding grounds
(mature & juvenile fish)

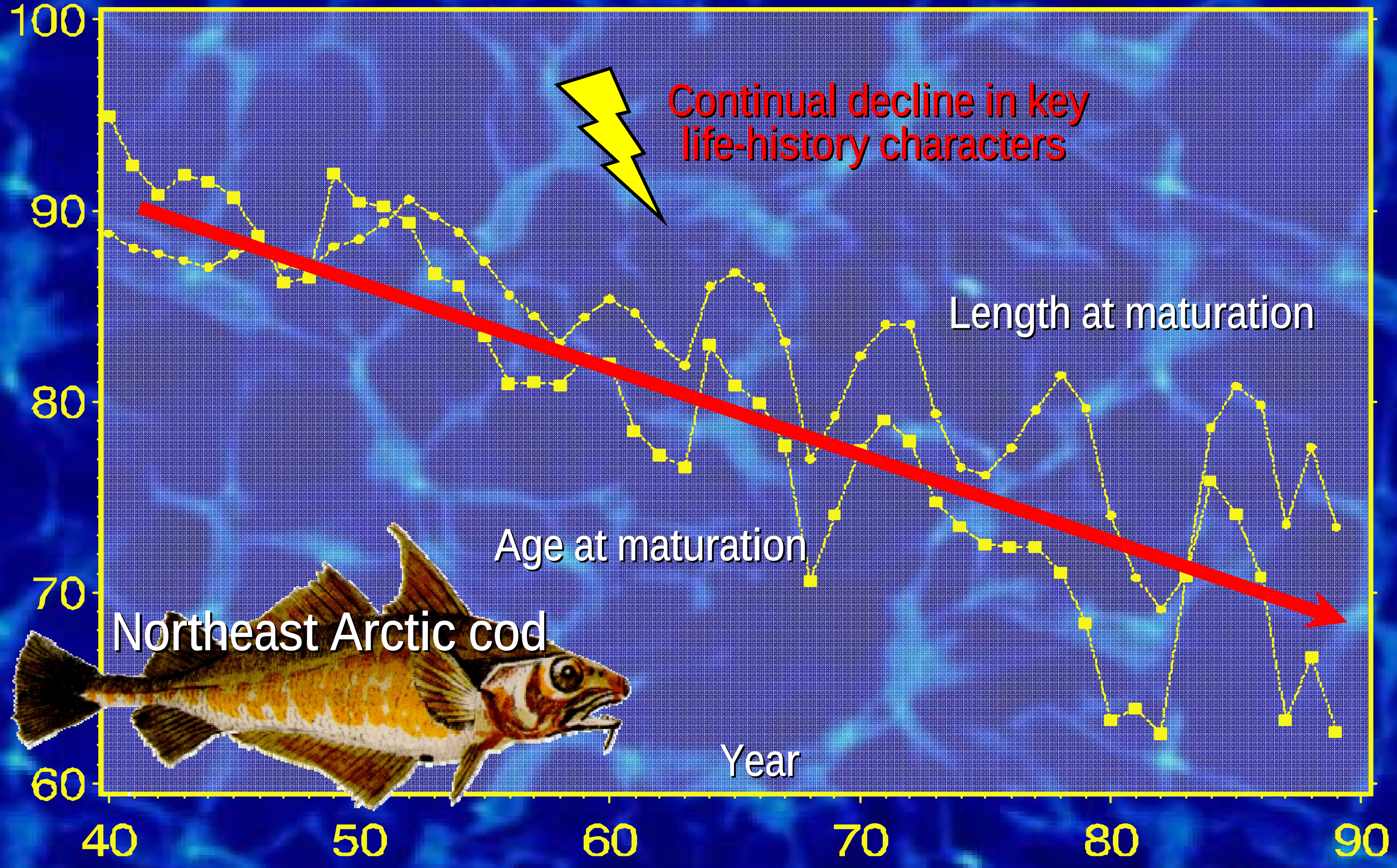
Spawning grounds
(only mature fish)

Northeast Arctic cod

Northeast Arctic Cod: Fishing History



Northeast Arctic Cod: Stock Response



Two Hypotheses for Explaining the Trend

- Compensatory response (plastic change):

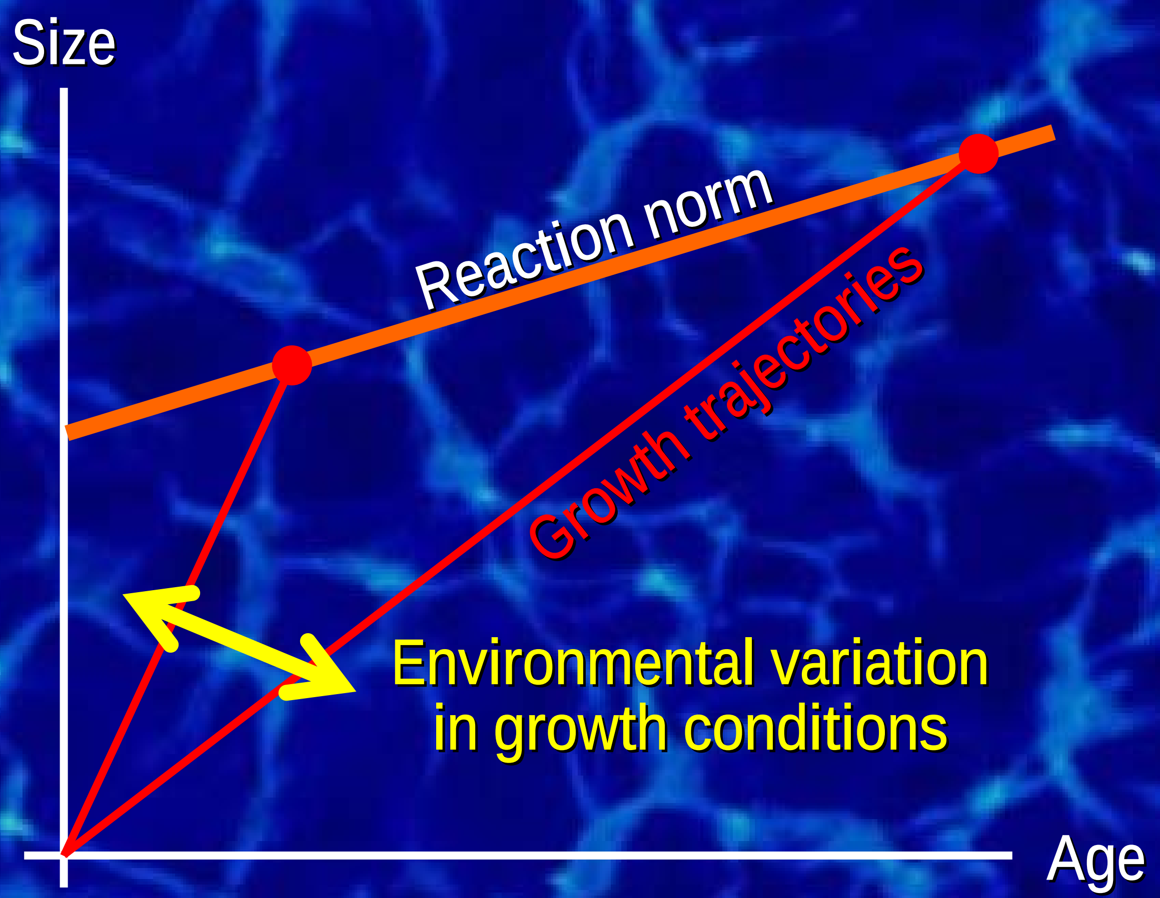
  Decreased biomass > Increased growth > Earlier maturation

and/or

- Reaction norm evolution (genetic change):

  Shift in maturation reaction norm > Earlier maturation at smaller size

Deterministic Maturation Reaction Norms



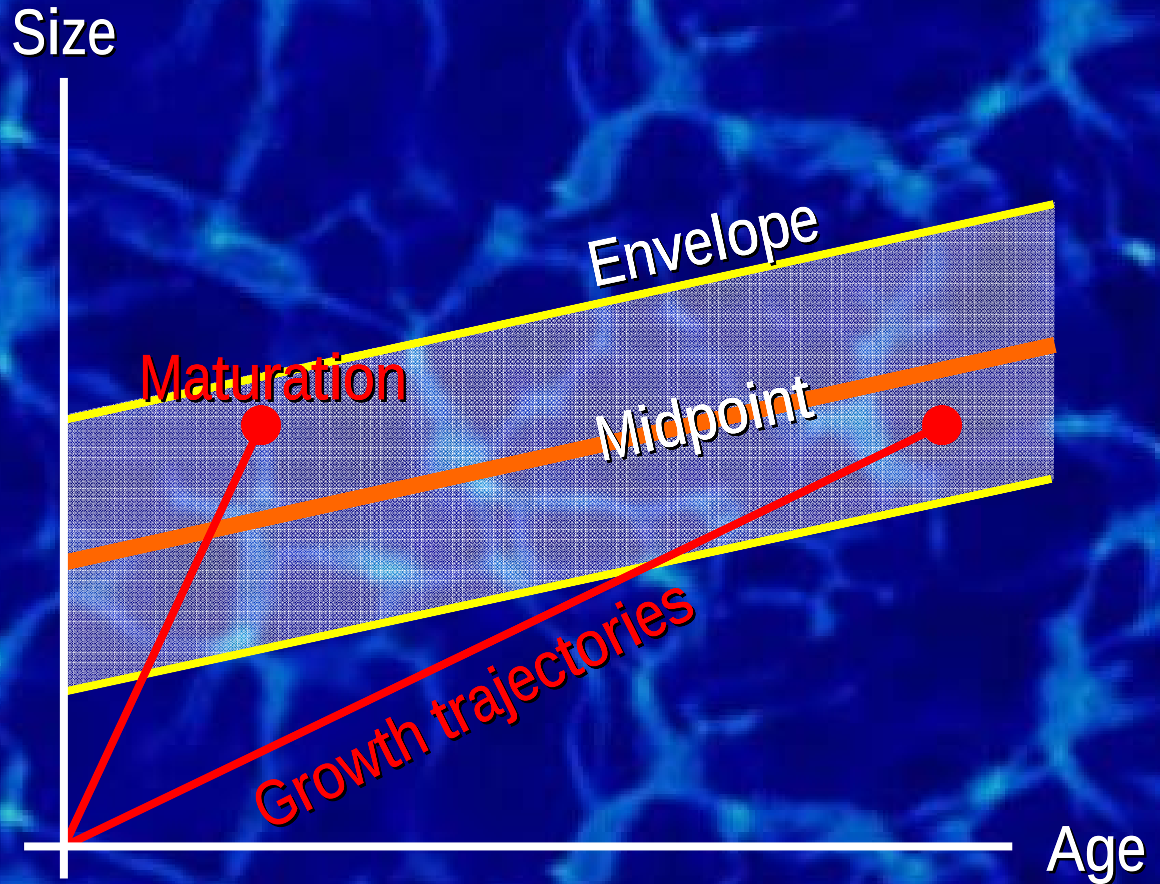
Mature

Maturing

Immature

Growth trajectories and reaction norms can also be curved.

Probabilistic Maturation Reaction Norms



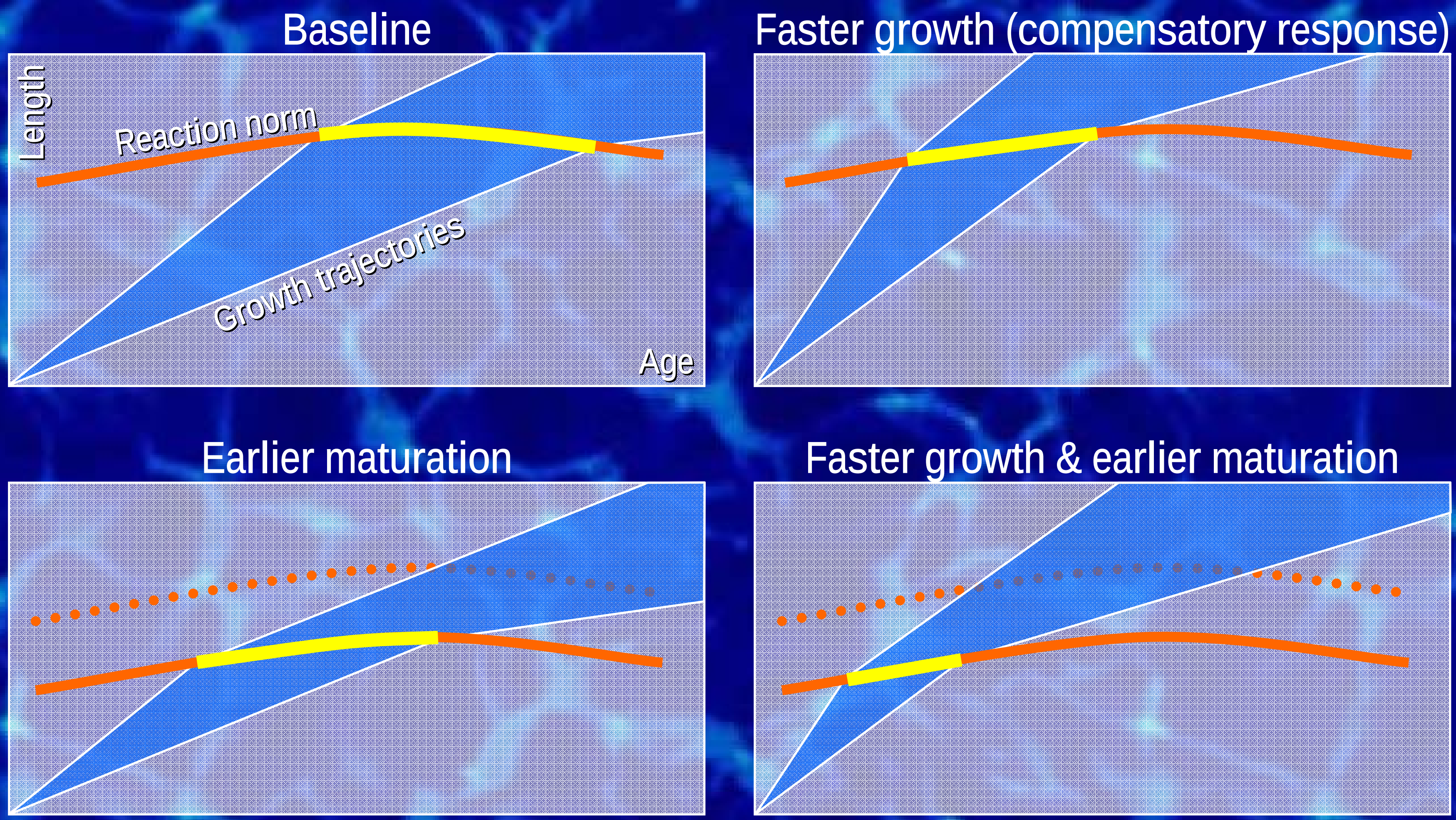
75% maturing

50% maturing

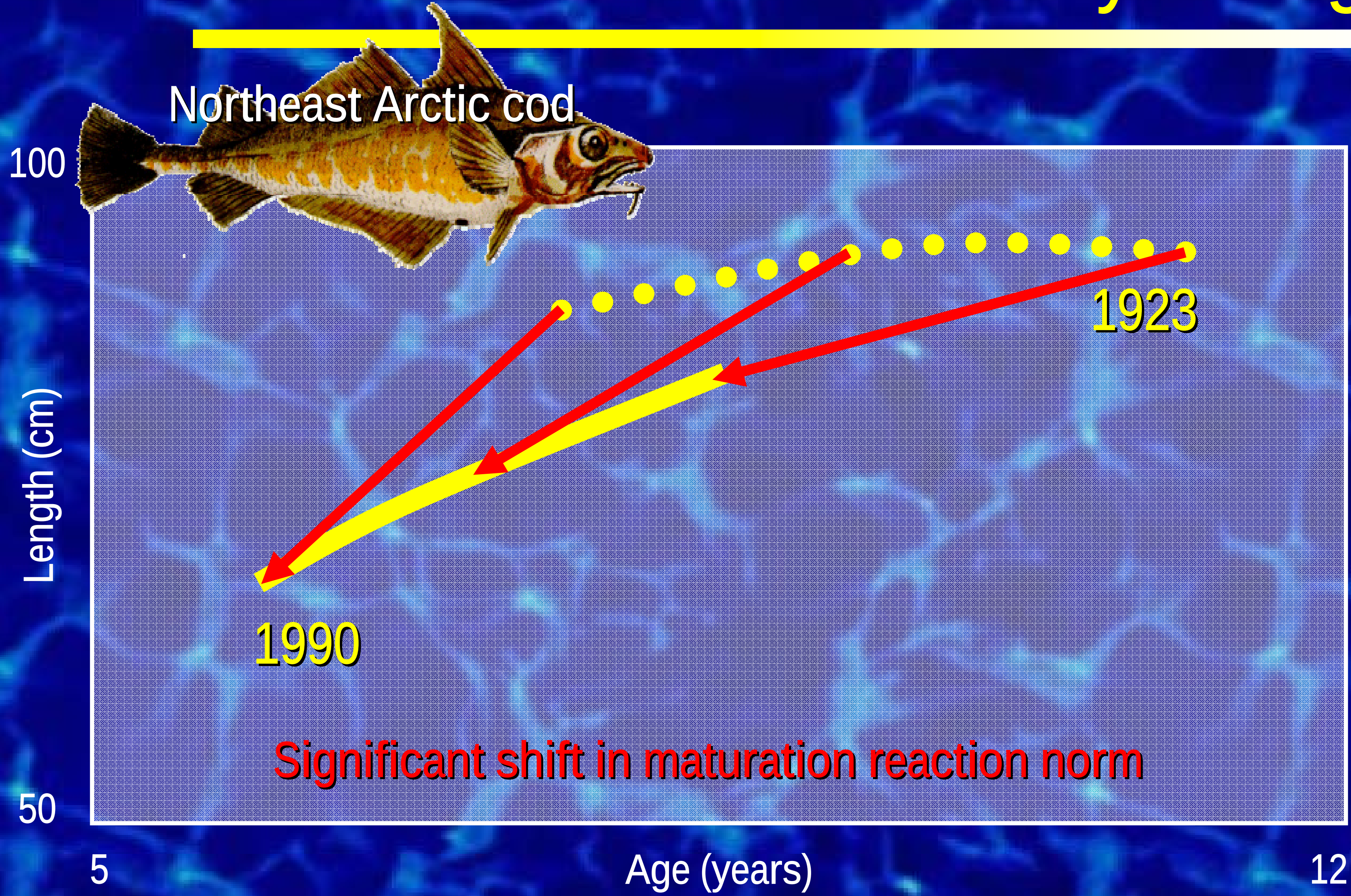
25% maturing

Growth trajectories and reaction norms can also be curved.

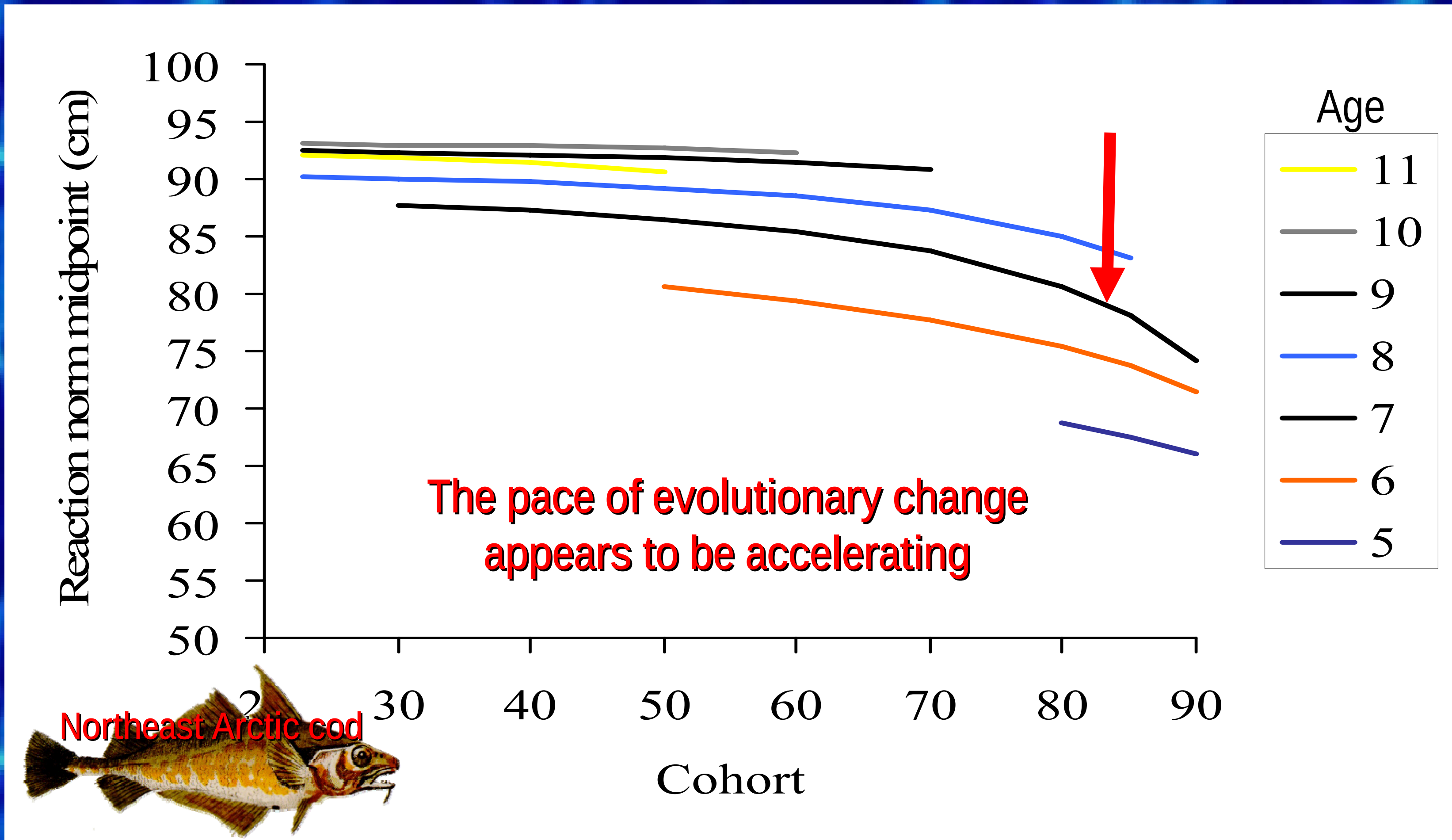
Reaction Norm Analysis



Northeast Arctic Cod: Evolutionary Change

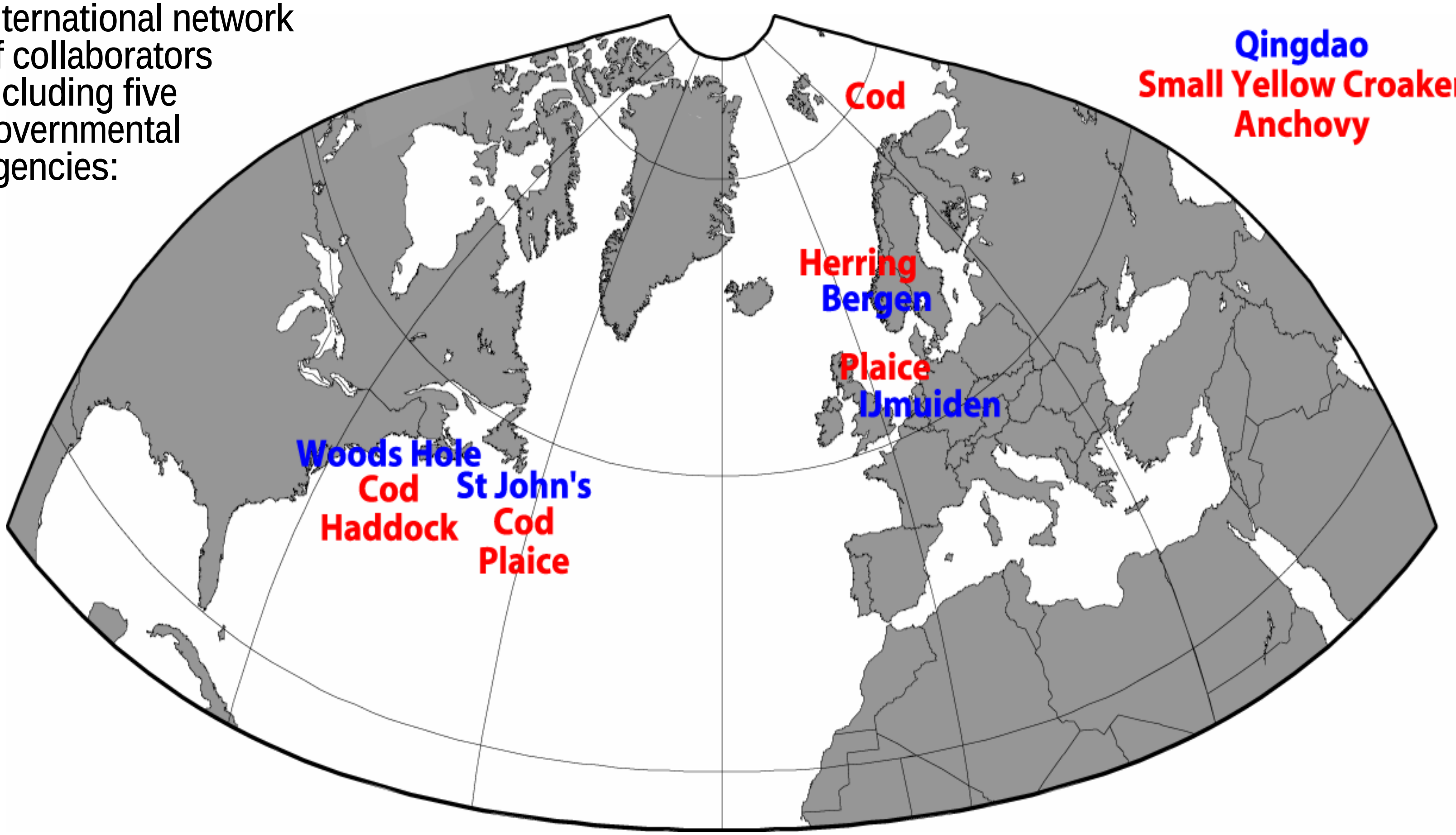


Northeast Arctic Cod: Evolutionary Change

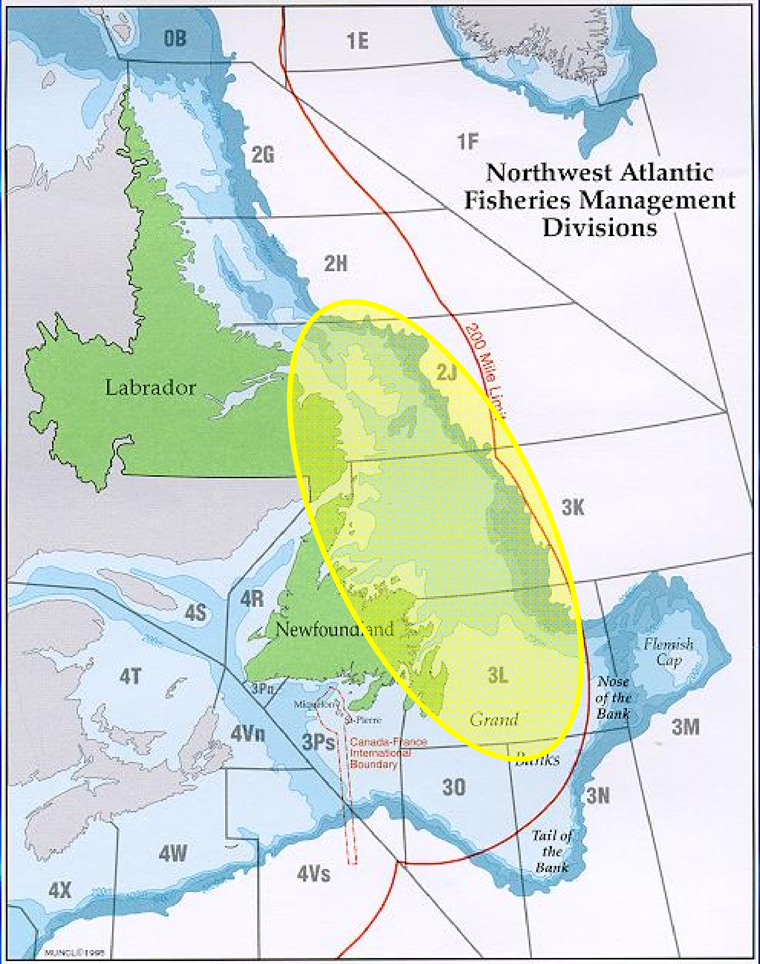


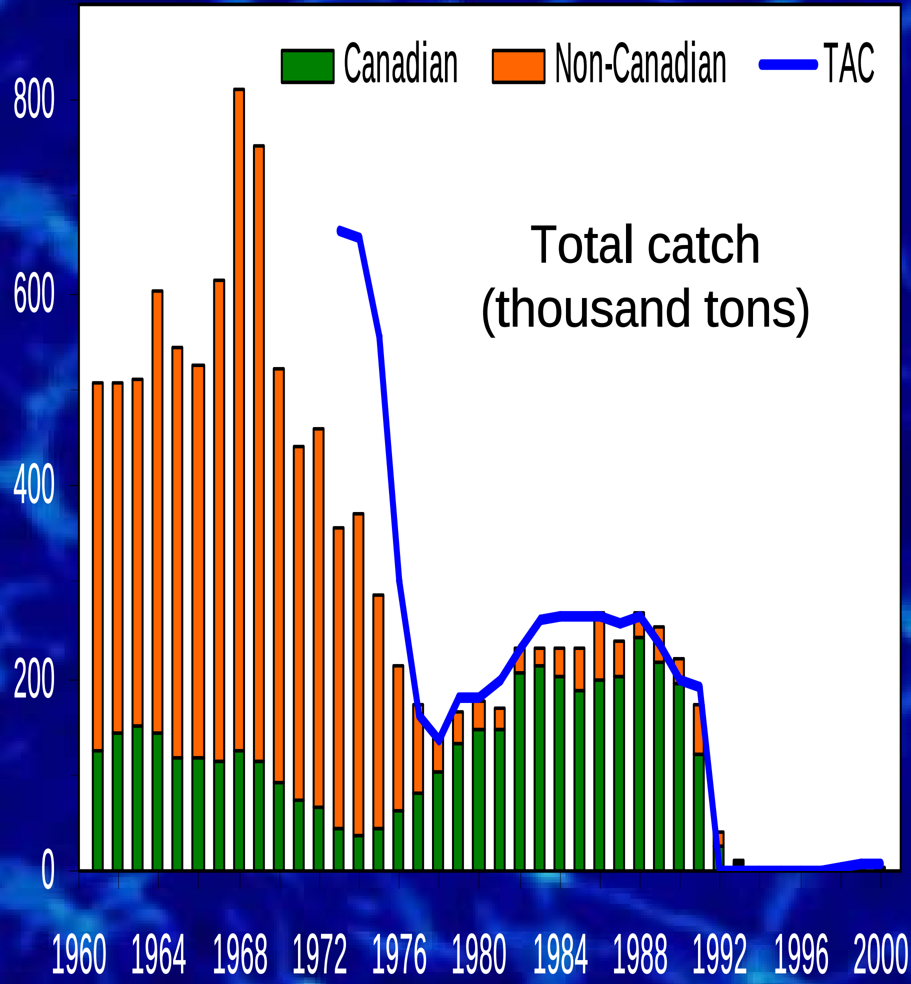
Other Case Studies: Overview

International network of collaborators including five governmental agencies:

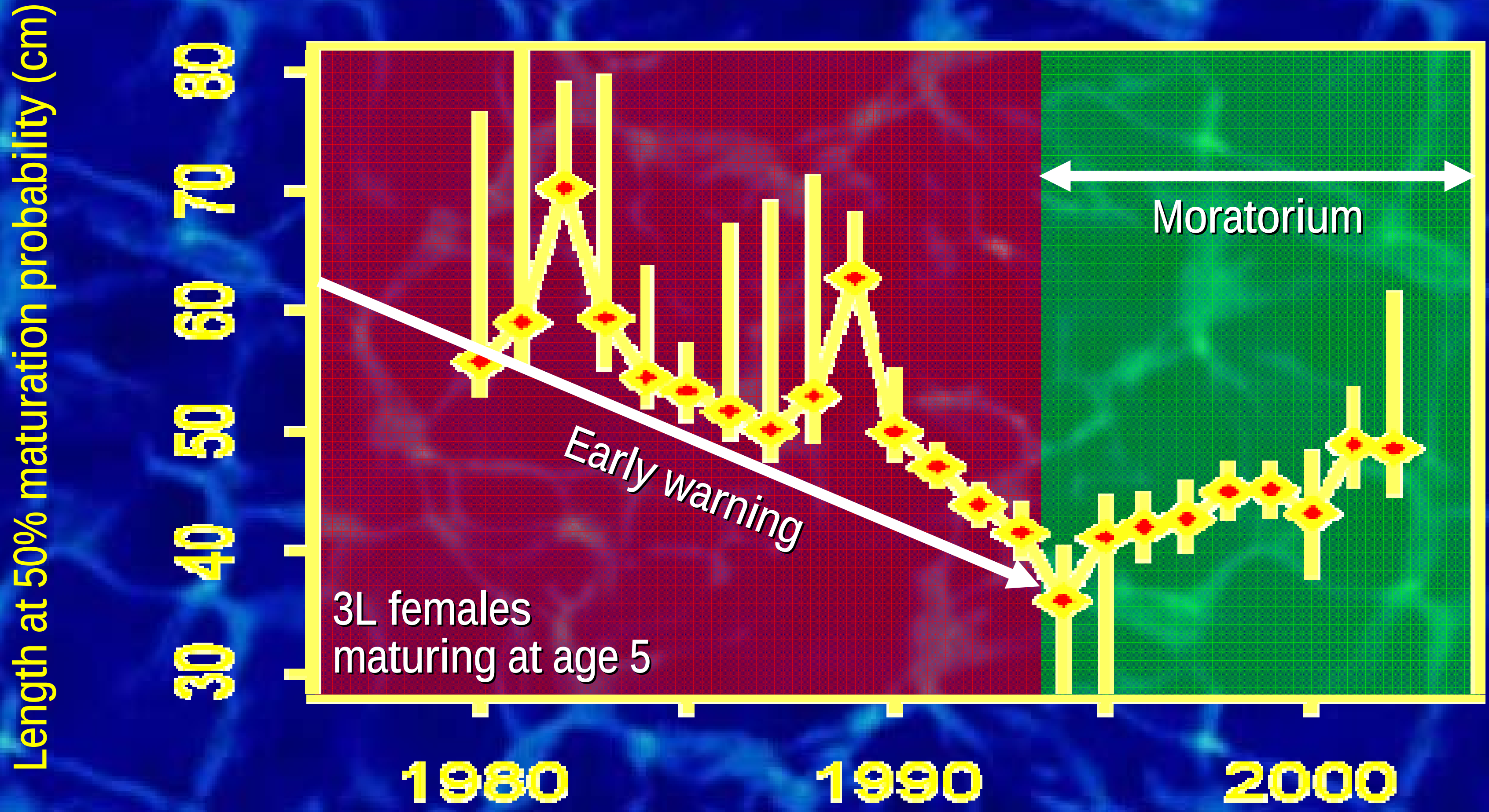


Northern Cod: Fishing History

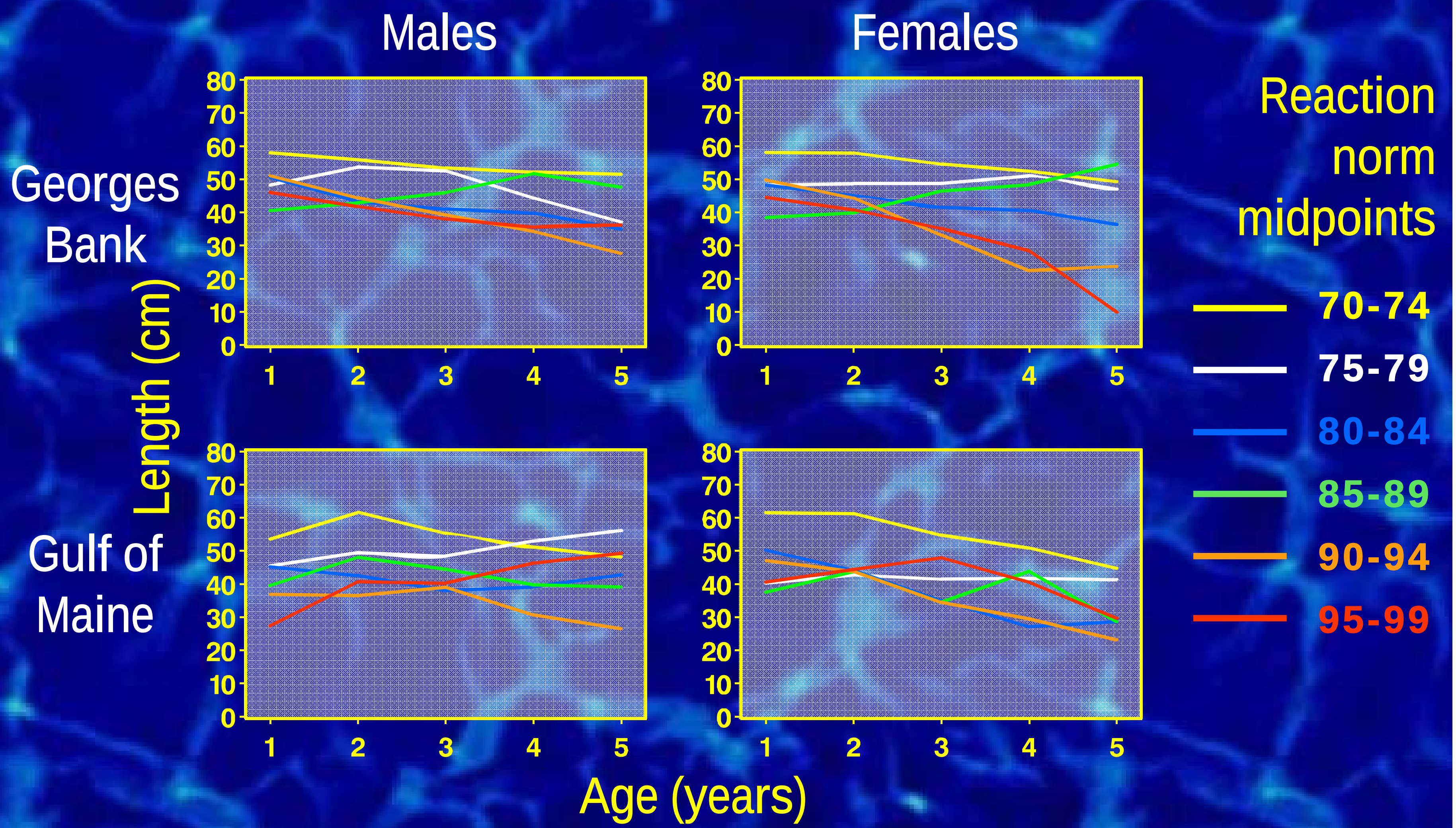




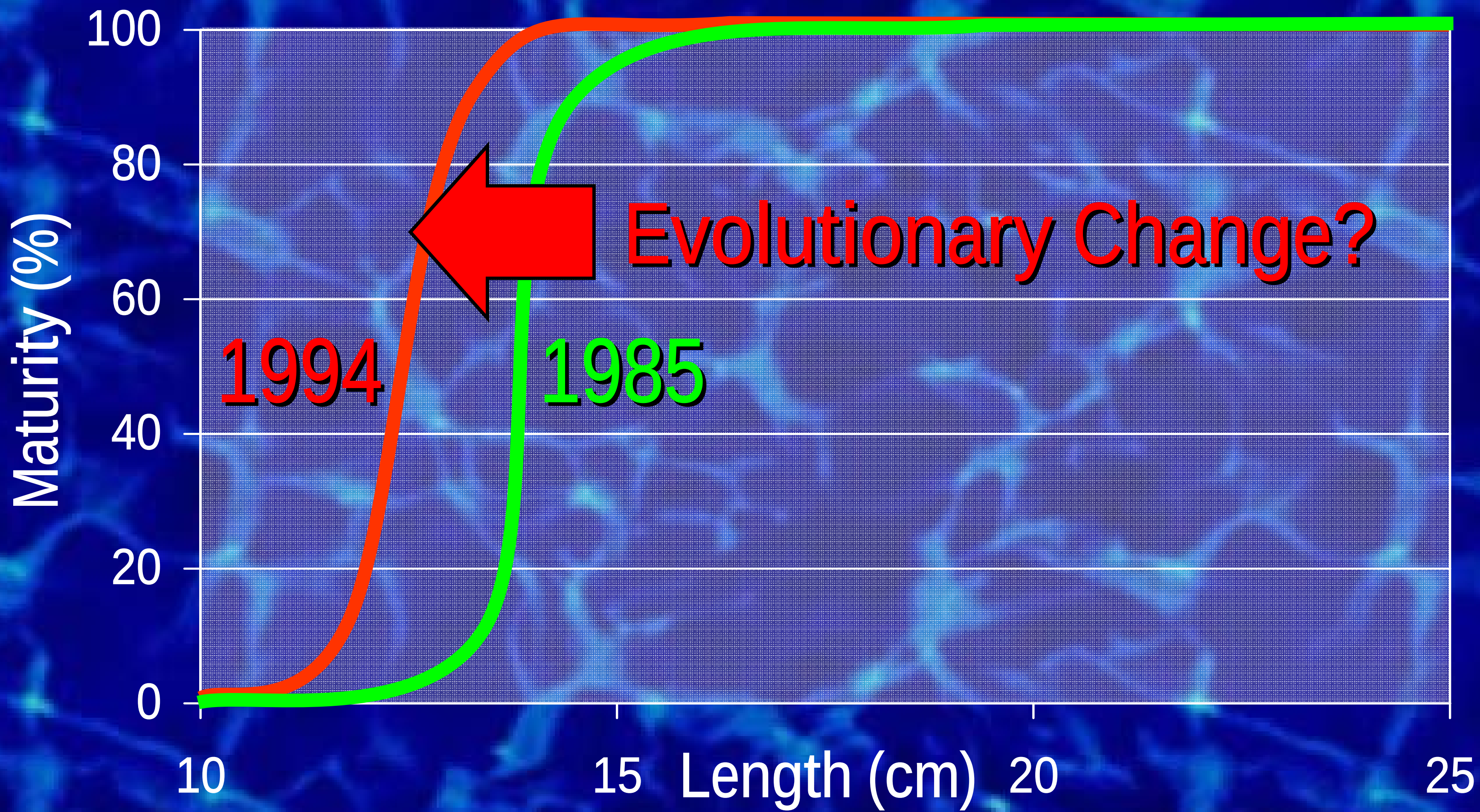
Northern Cod: Evolutionary Change



Georges Bank and Gulf of Maine Cod

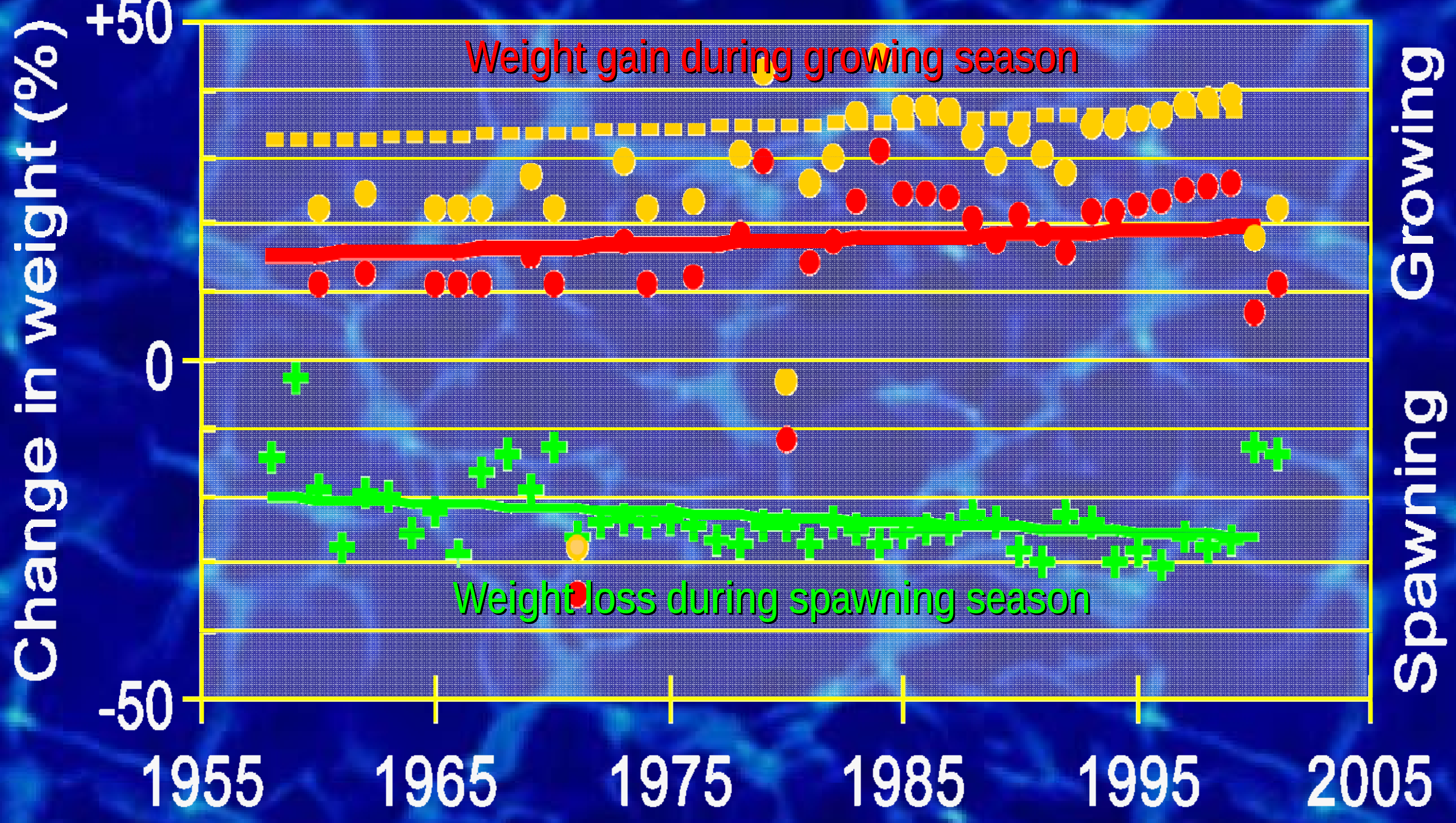


Small Yellow Croaker in the Yellow Sea



North Sea Plaice

Grift & Rijnsdorp



Case Studies: Summary of Results

Species	Population or stock	Period with data	Trend towards earlier maturation?	Reference
Atlantic cod *Gadus morhua*	Northeast Arctic	1932–1998	Yes	Heino et al. 2002c
	Georges Bank	1970–1998	Yes	Barot et al. 2004b
	Gulf of Maine	1970–1998	Yes	
	Northern (2J3KL)	(1977–)1981–2002	Yes	Olsen et al. 2004
	Southern Grand Bank (3NO)	1971–2002	Yes	Olsen et al. 2005
	St. Pierre Bank (3Ps)	1972–2002	Yes	
Plaice *Pleuronectes platessa*	North Sea	1957–2001	Yes	Grift et al. 2003
American plaice *Hippoglossoides platessoides*	Labrador–NE Newfoundland (2J3K)	1973–1999	Yes	Barot et al. 2004c
	Grand Bank (3LNO)	1969–2000	Yes	
	St. Pierre Bank (3Ps)	1972–1999	Yes	
Atlantic herring *Clupea harengus*	Norwegian spring-spawning	1935–2000	Yes, weak	Engelhard & Heino 2004
Small yellow croaker *Pseudosciaena polyactis*	Yellow Sea	1959–2002 (ca. 8 years)	Yes (?)	Heino, Yin & Dieckmann, in prep.
Grayling *Thymallus thymallus*	Lake Lesjaskogsvatnet, Norway	1903–2000 (ca. 15 years)	Yes	Haugen et al., in prep.
Small-mouth bass *Micropterus dolomieu*	Opeongo Lake, Ontario, Canada	1936–2002	No	Dunlop et al. 2005

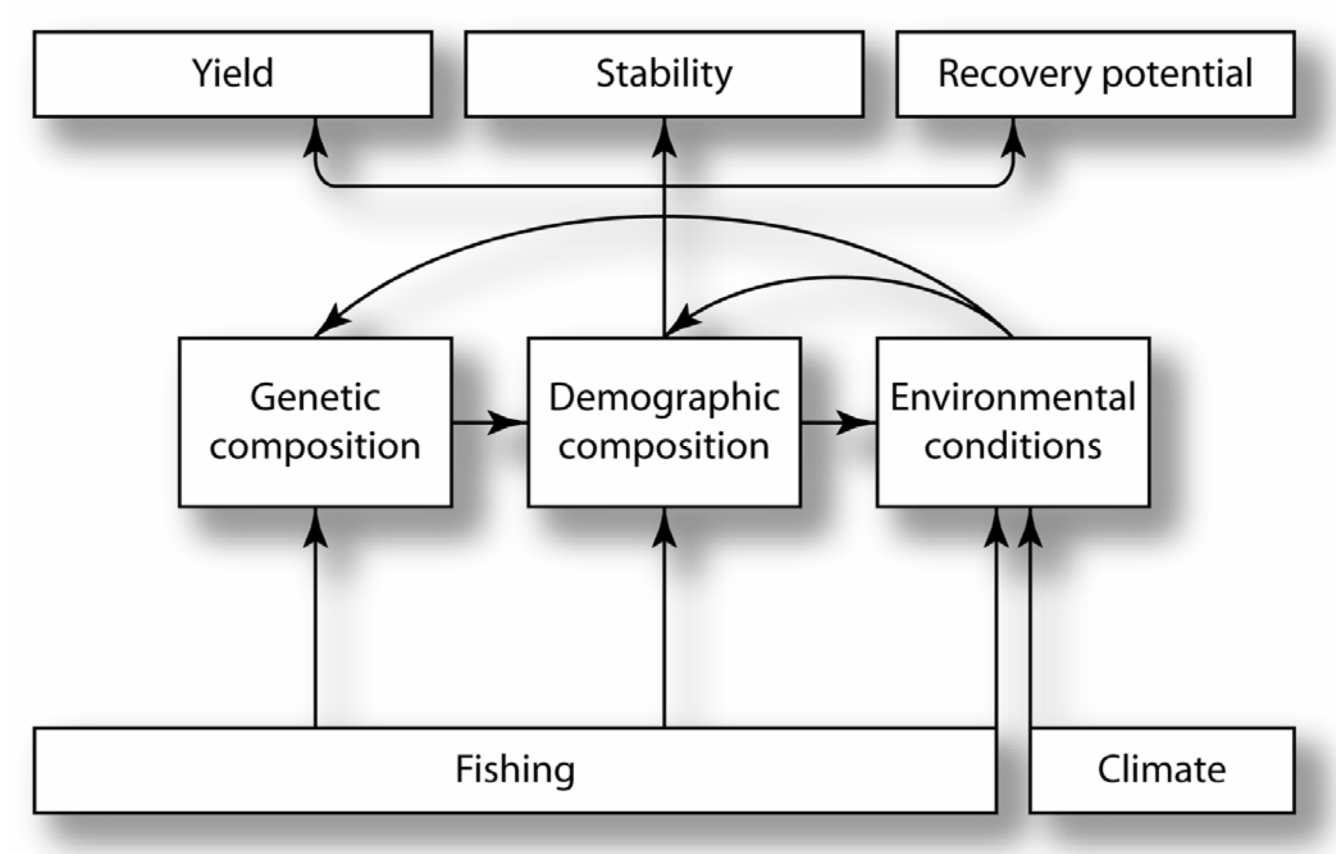
2 Modeling Evolutionary Change

Two Salient Questions

A Given the mounting empirical evidence for fisheries-induced adaptive change, are the observed rates of selection compatible with heritability estimates?

B How can we predict the future course of fisheries-induced adaptive change and evaluate the impact of potential management measures?

The Context for Modeling



Complicating Factors for Modeling

- Selection differentials and demographic processes greatly vary across structured populations, causing them to depend on age, size, and maturation status.
- Population dynamics are subject to substantial phenotypic plasticity.
- Ecological feedback through frequency and density dependence can greatly alter selection pressures.
- Selection responses crucially depend on available genetic variation.

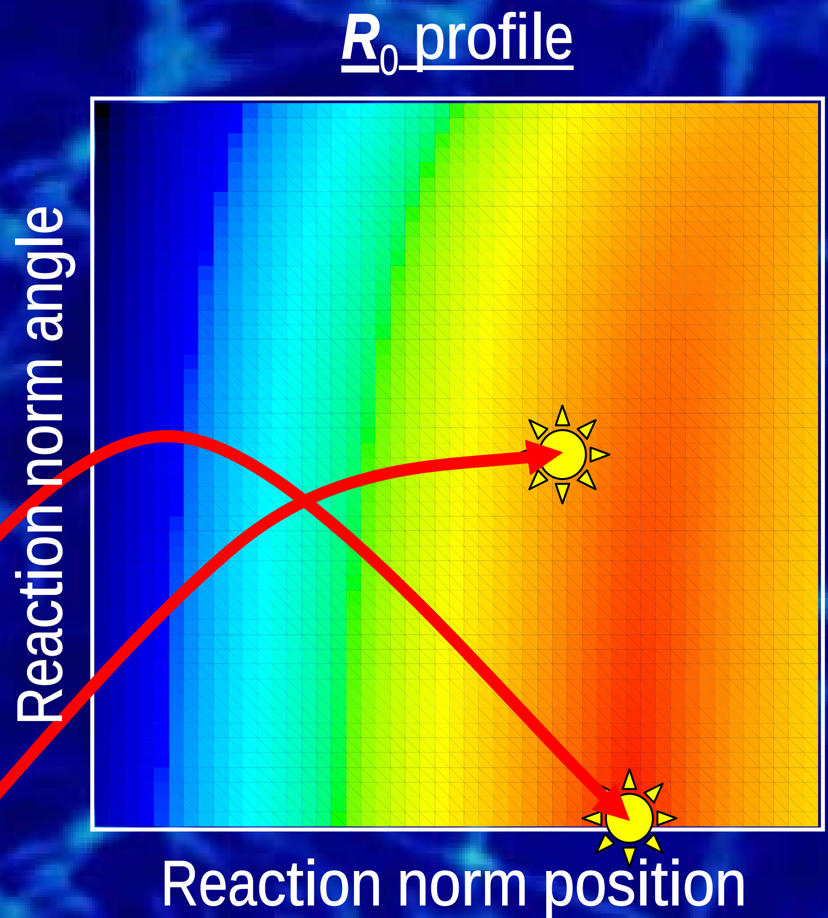
Alternative Modeling Frameworks

	(1)	(2)	(3)
Optimization models	Simple	No	No
Breeder's equation models	Simple	No	Yes
Adaptive dynamics models	Flexible	Yes	No
Eco-genetic models	Flexible	Yes	Yes

(1) Simplicity versus flexibility
(2) Incorporates frequency- and density-dependent selection
(3) Allows predicting the speed of evolution

Optimization Models

- In the presence of frequency-dependent selection, predictions of evolutionary outcomes based on maximizing the basic reproduction ratio R_0 are misleading:



Prediction from R_0 profile

Actual evolutionary outcome

Breeder's Equation Models

- Scalar traits, discrete time

$$\Delta x_R = h^2 \Delta x_S \quad \text{with heritability} \quad h^2 = V_G / V_P$$

- Scalar traits, continuous time

$$\tfrac{d}{dt} x = h^2 g_x \quad \text{with selection gradient} \quad g_x = \tfrac{d}{dx} f(x)$$

- Function-valued traits, continuous time

$$\tfrac{d}{dt} x(a) = \int h^2(a', a) g_x(a')\, da'$$

Weakness: The fitness function ***f*** is usually assumed, rather than being derived from the underlying ecology.

Adaptive Dynamics Models

- Canonical equation of function-valued adaptive dynamics

$$\frac{d}{dt}x(a) = \frac{1}{2}\mu_x n_x \int \sigma_x^2(a', a) g_x(a')\, da'$$

Weakness: The speed of short-term evolution cannot be predicted, since short-term evolution is usually not mutation-limited.

General Insights: Maturation Evolution

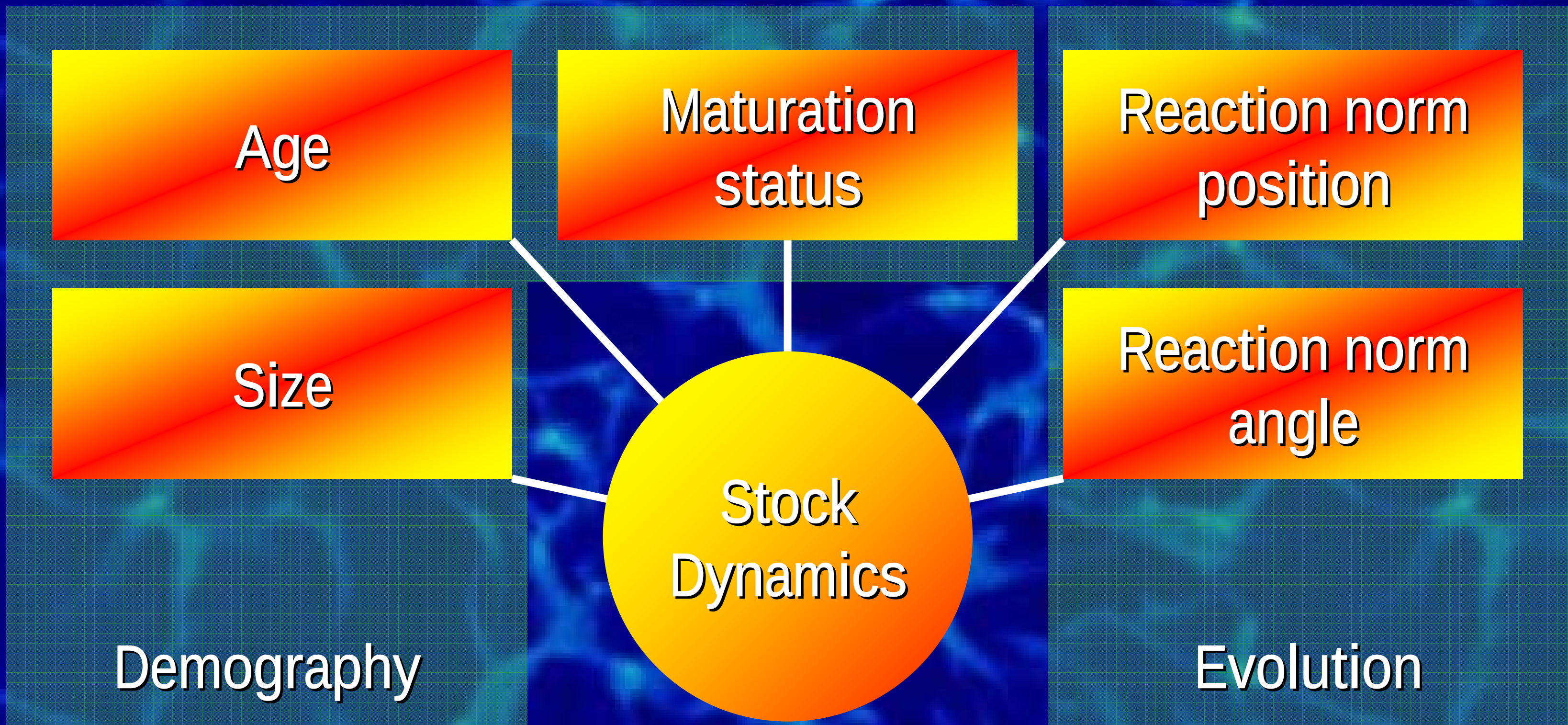
Type of mortality	Increased mortality among small/young/immature	Increased mortality among large/old/mature
Unspecific	↓	↓
Size-specific	↑, ↓, or ↕	↓
Age-specific	↓ or ↕	↓
State-specific	↓	↑

↓ Selection for earlier maturation ↑ Selection for later maturation ↕ Evolutionary bistability

Results by Anna Gårdmark, National Board of Fisheries, Öregrund, Sweden

Structure of an Eco-genetic Model

- Five characteristics of individuals are tracked through time:



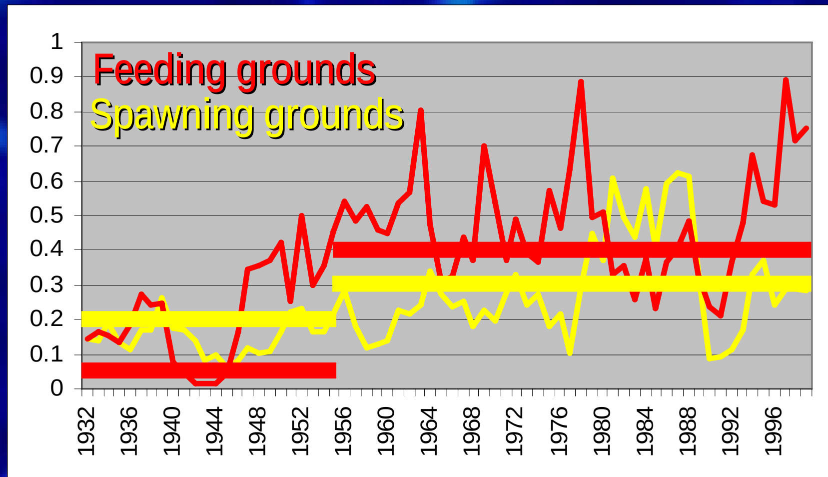
Modeling Northeast Arctic Cod

Demography

- Linear growth before maturation
- Growth increments of mature individuals dependent on size and gonadosomatic index
- Growth increments negatively correlate with stock biomass
- Growth increments vary between individuals
- Natural mortality (0.2)
- Density-dependent newborn mortality
- Density-dependent cannibalism on age classes 1 and 2
- Linear maturation reaction norm of constant width
- Fecundity allometrically dependent on size

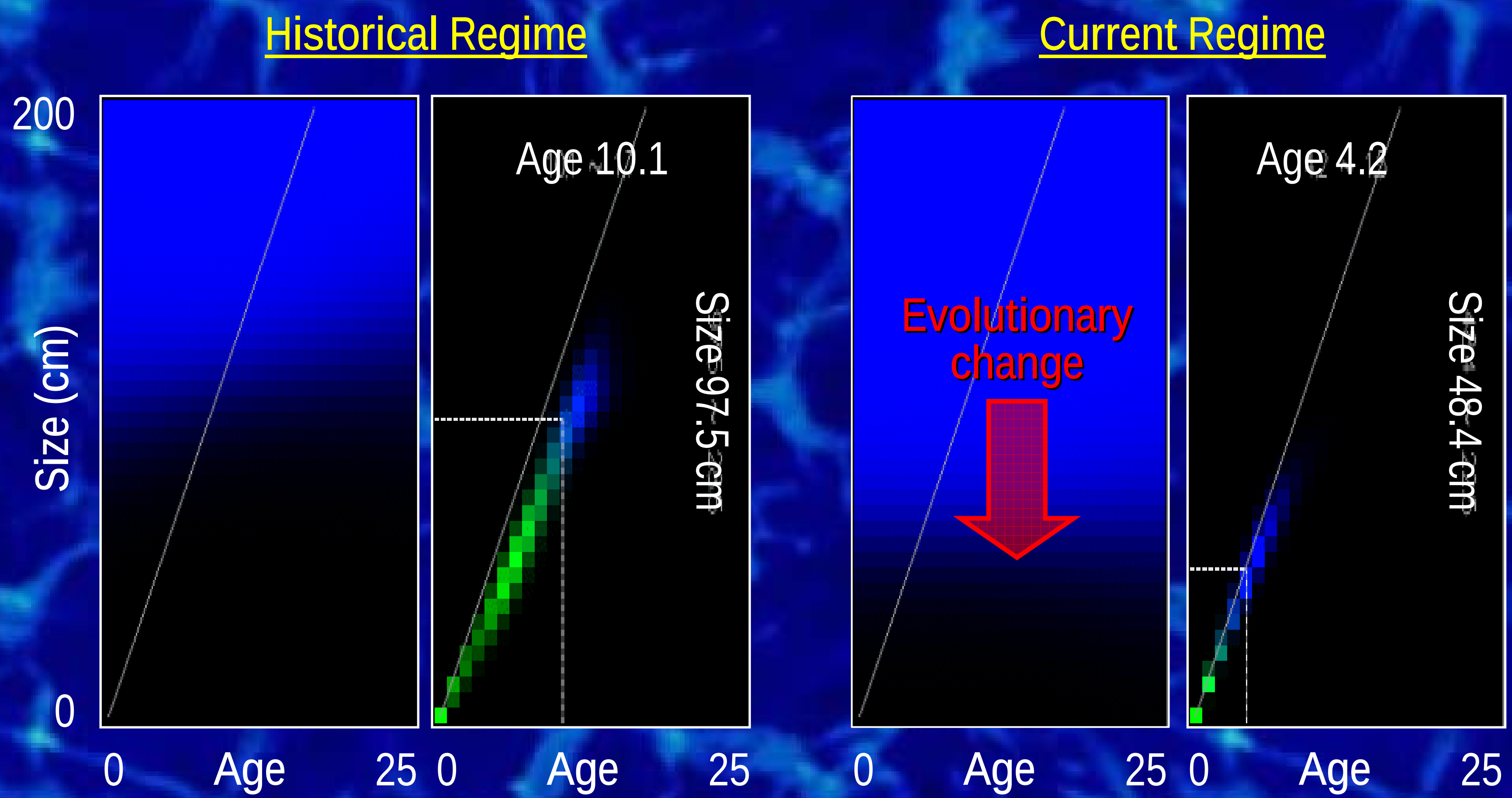
Fishing Mortality

- Historical regime:
  $F_{feeding} = 0.05$ and $F_{spawning} = 0.2$
- Current regime:
  $F_{feeding} = 0.4$ and $F_{spawning} = 0.3$

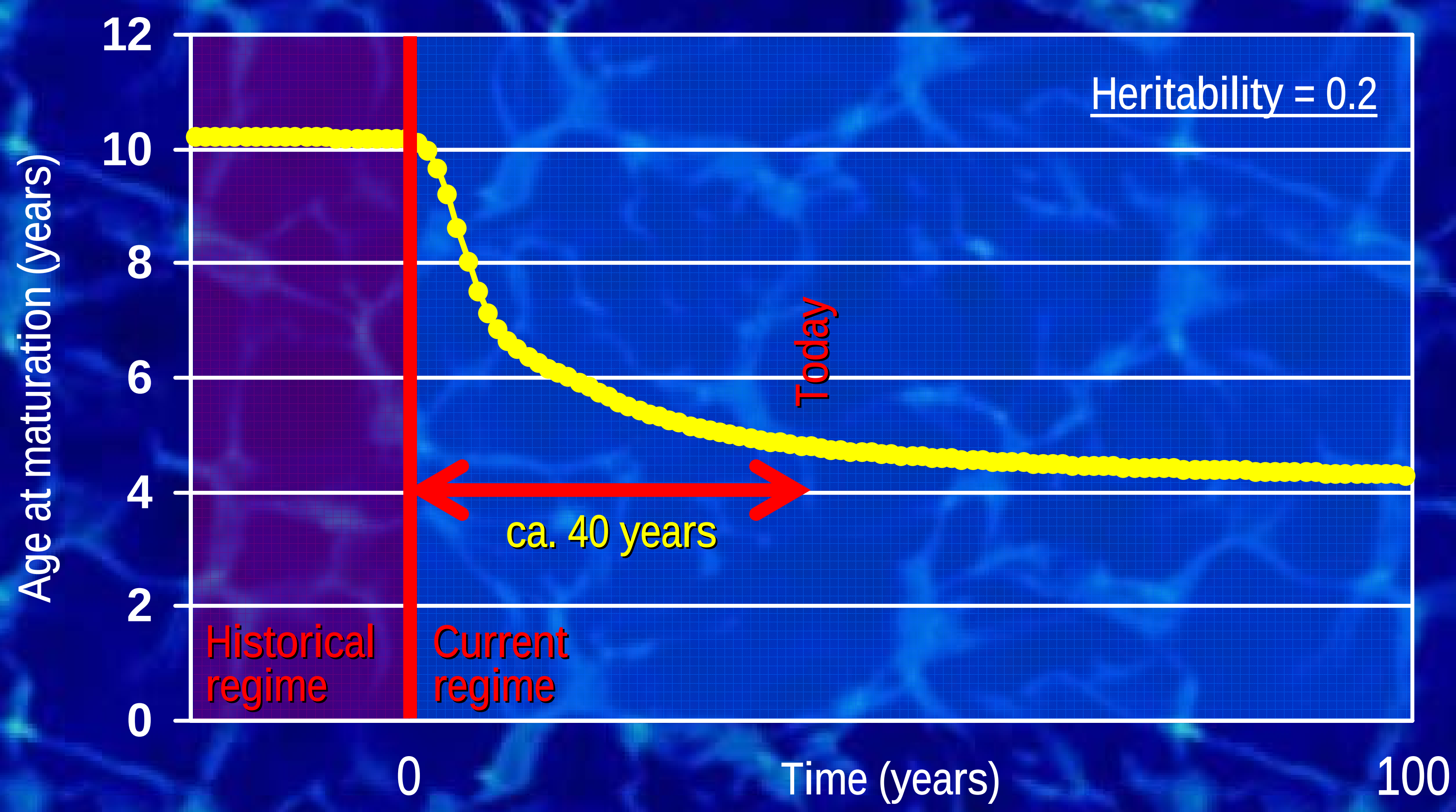


- Estimated size selectivity of fishing gear taken into account

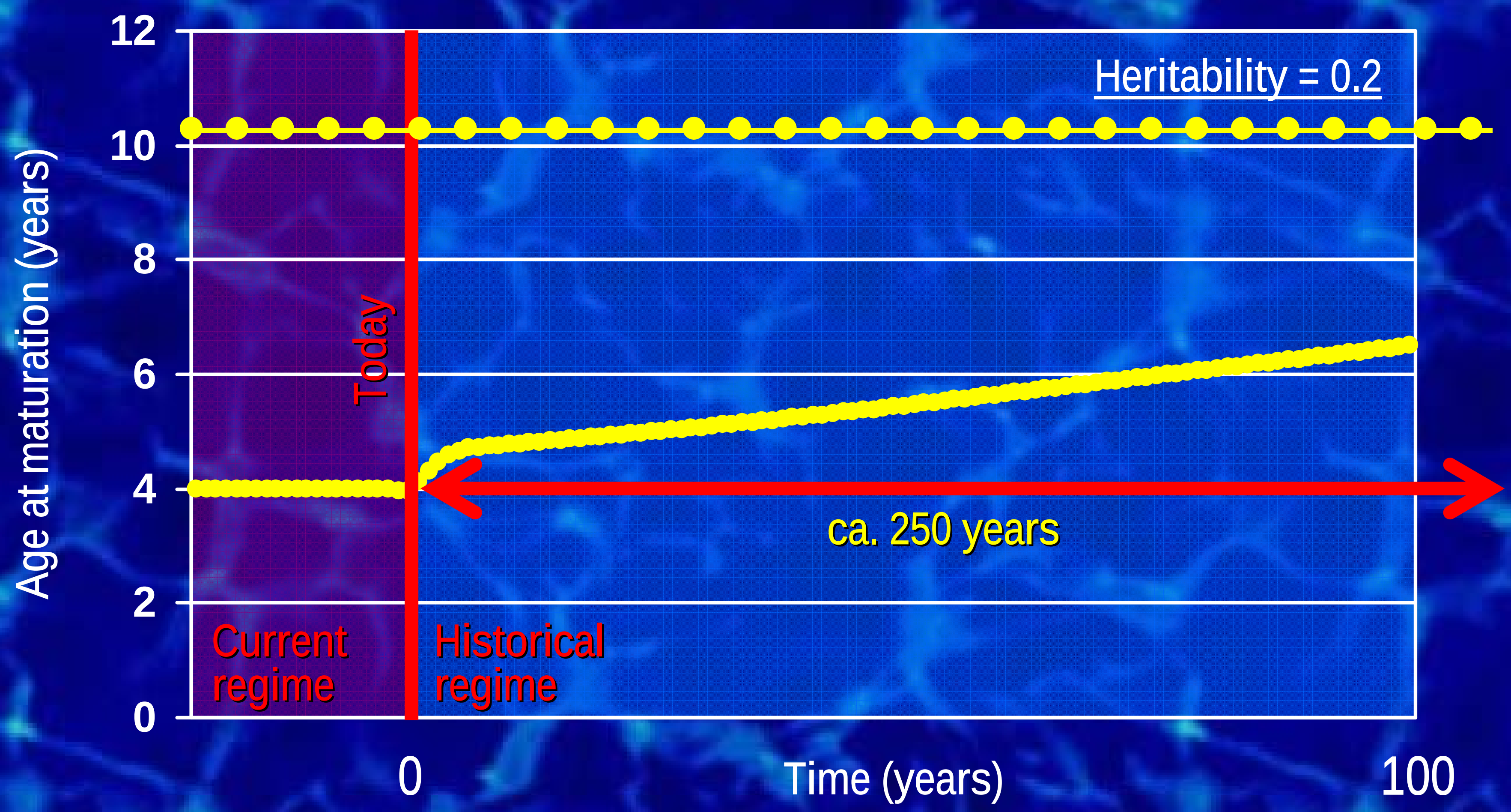
Resultant Life Histories



Speed of Fisheries-induced Evolution



Speed of Evolutionary Recovery



Conclusions

- Fisheries-induced evolution has been with us for several decades without having been properly recognized.
- The speed of such evolution is much faster than previously believed .
- Fisheries-induced evolution affects yield, stock stability, and recovery potential.
- Models suggest that each year during which current exploitation continues may require several years of evolutionary recovery:

  A "Darwinian debt" to be paid by future generations.