

Fisheries-induced Evolution in the Wild

Mikko Heino^{1,2} & Ulf Dieckmann²

¹Institute of Marine Research, Bergen, Norway

²International Institute for Applied Systems Analysis, Laxenburg, Austria

Fishing as an evolutionary force?

NATURAL HISTORY OF THE QUINNAT SALMON.

A REPORT OF INVESTIGATIONS IN THE SACRAMENTO
RIVER, 1896-1901.

By CLOUDSLEY RUTTER,

Naturalist, United States Fish Commission Steamer Albatross.


F. C. B. 1902-5

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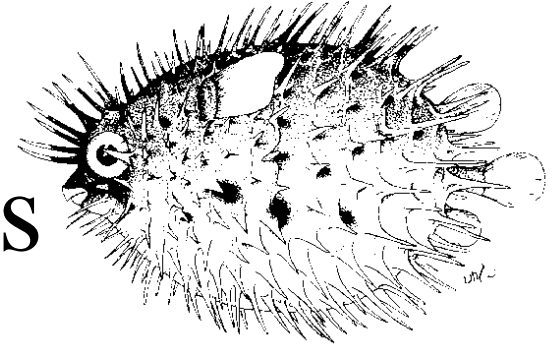
“...a stock-raiser would never think of selling his fine cattle and keeping only the runts to breed from.”

“The salmon would certainly deteriorate in size ... if only the smaller ... [are] allowed to breed.”

Fishing as an evolutionary force?

- Most fish stocks are heavily impacted – fishing mortality $>$ natural mortality
- Survival is a very hard currency in evolution
- Relevant traits have heritable variability
-  Adaptation is inevitable
- ...but is it of significance for fisheries management in short/medium term?

Possible responses



- *Life history traits*: age and size at maturation, growth rate, reproductive effort
- *Behavioural traits*: gear avoidance behaviour, risk proneness
- *Morphological traits*: body shape
- *Physiological traits*: metabolic rate, growth efficiency

Age & size at maturation

Theory:

- Increased mortality mostly favours earlier maturation

Observation:

- Earlier maturation is ubiquitous in exploited fish stocks (e.g., Trippel 1995 *BioScience*)

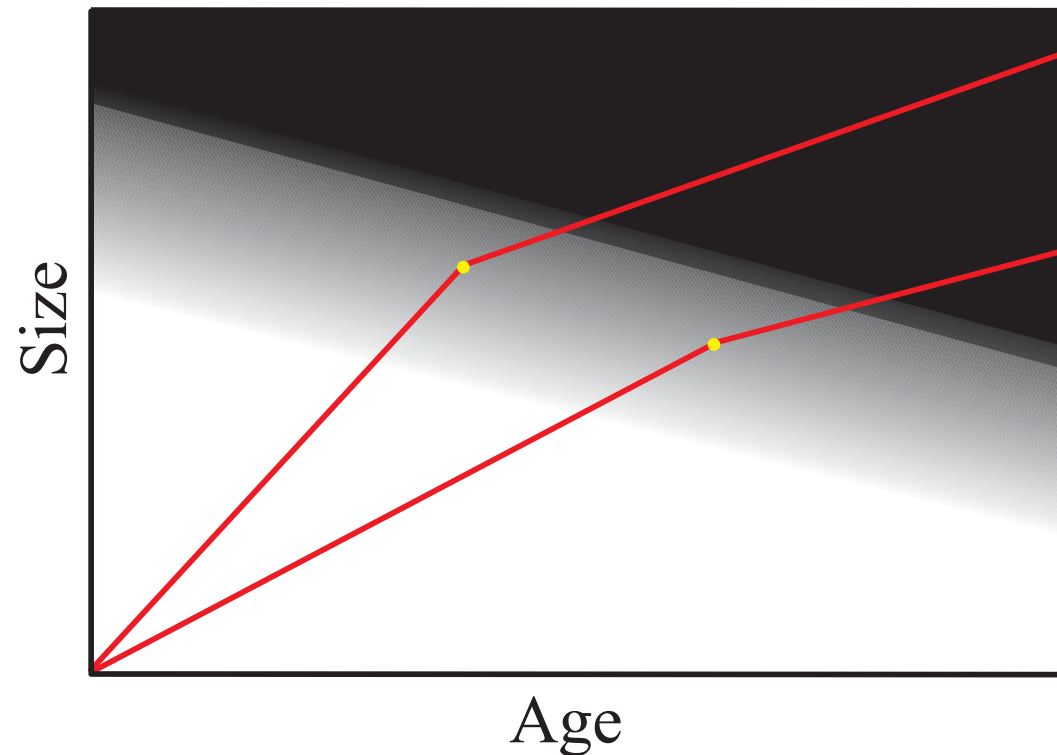
Competing explanations

1. Evolutionary response
2. Phenotypic plasticity ('compensatory response')
3. Direct demographic response

Until recently it has been difficult to disentangle these *non-exclusive* explanations

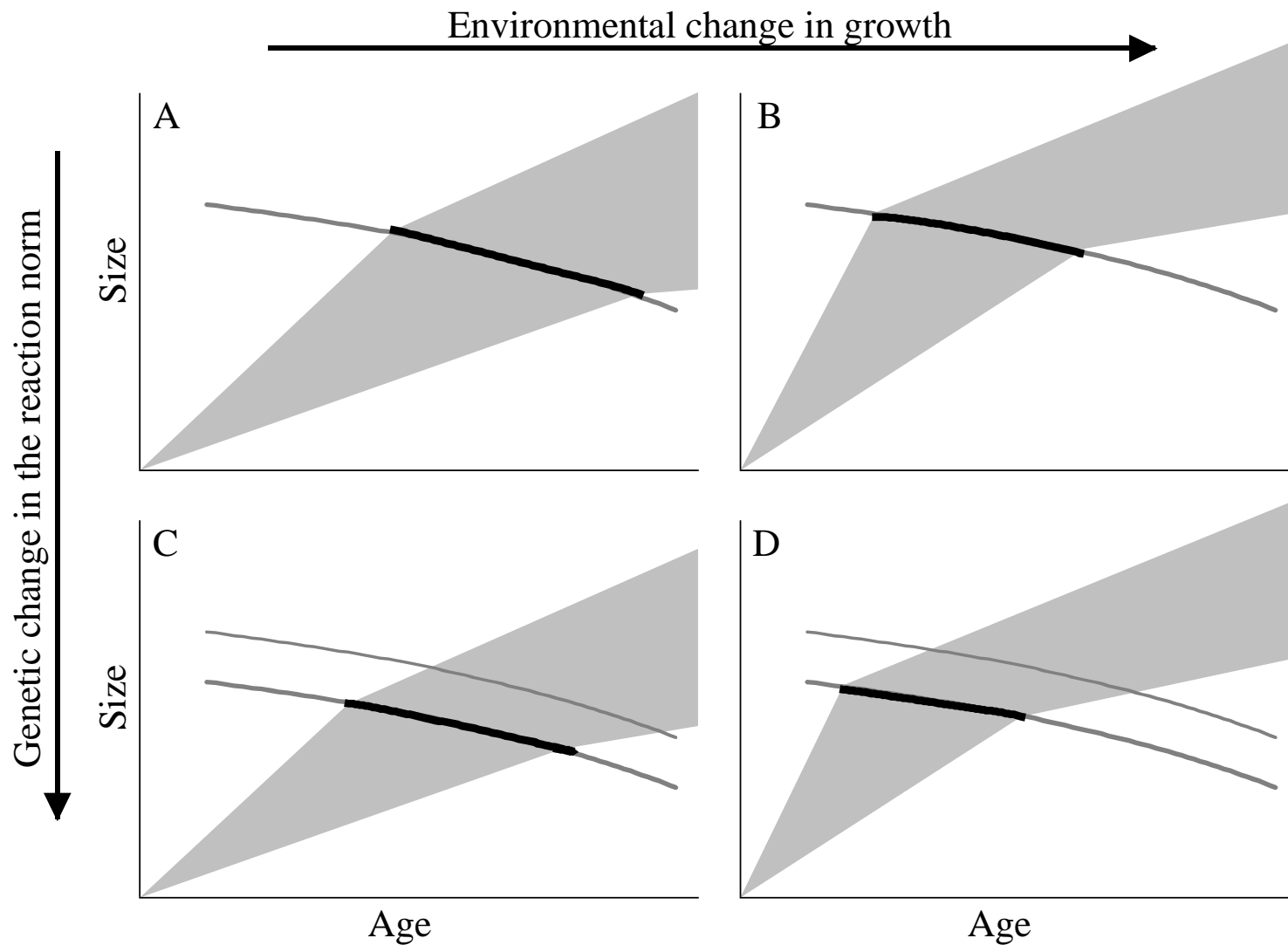
Probabilistic maturation reaction norms

- Probability that an immature individual, depending on its age and size, matures during a given time interval



Size-at-age ~ growth ~ environment

Maturation reaction norm analysis



Maturation reaction norm analysis

Process-oriented description:

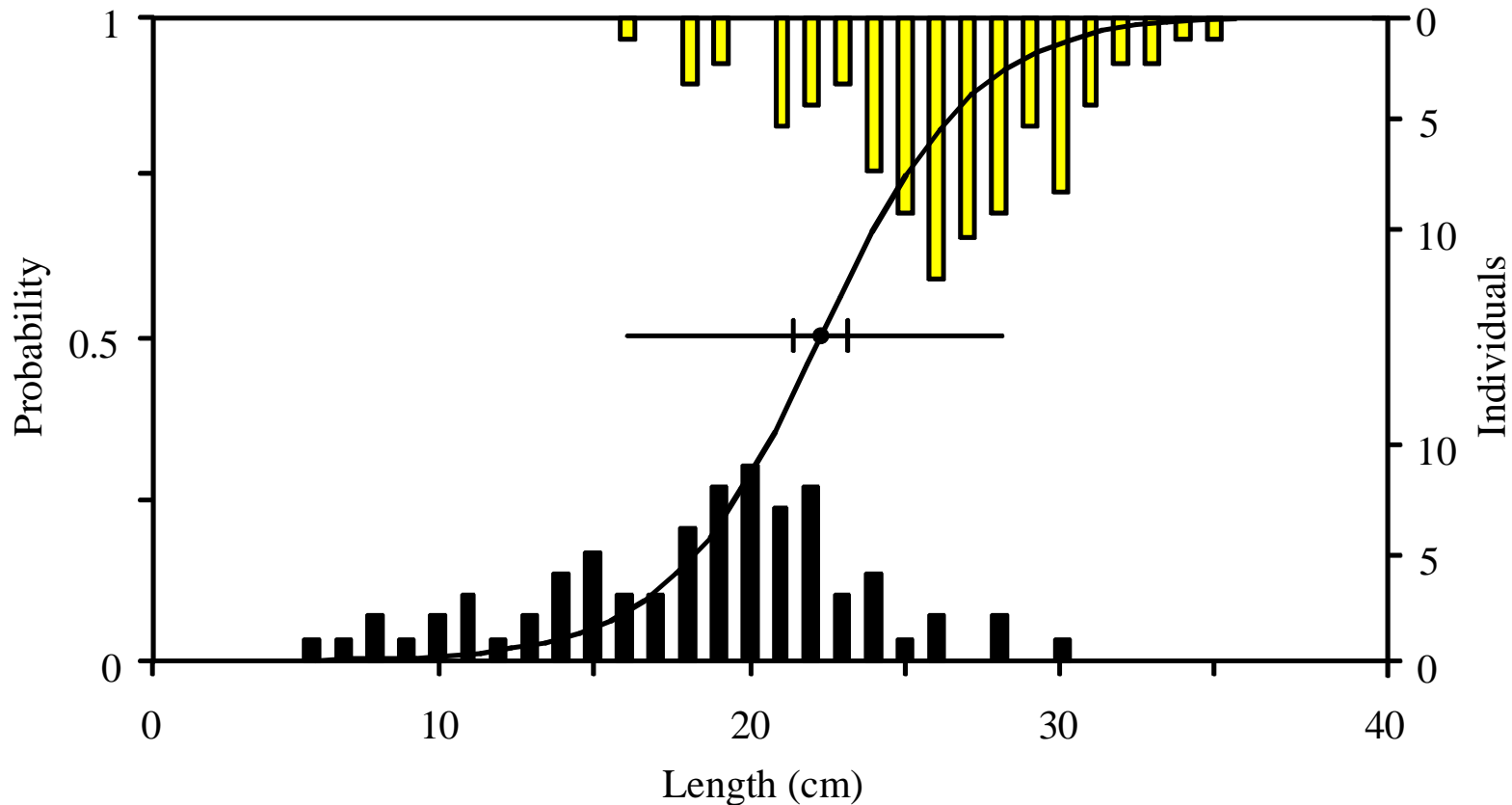
- Reaction norm describes the tendency to mature, given age and size
 - Variations in demography and growth determine the parts of the reaction norm 'sampled' by the population, but leave the reaction norm itself unaffected
- ⇒ A trend in the reaction norm suggests evolution

Caveats

- The method tackles with a major source of plastic variation in maturation, but residual environmental effects are bound to remain
- Inferring a cause-effect relationship from observational data always is ambiguous

How to estimate the probabilistic reaction norm? — Method #1

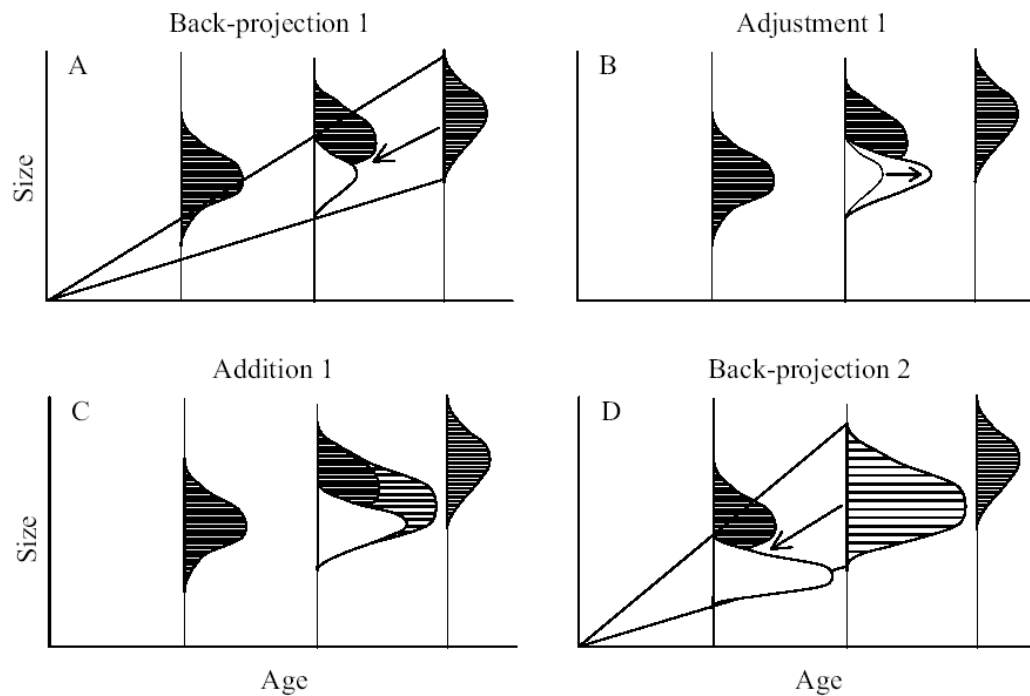
Logistic regression fitted to a representative sample of immature and newly-matured individuals, sized and aged



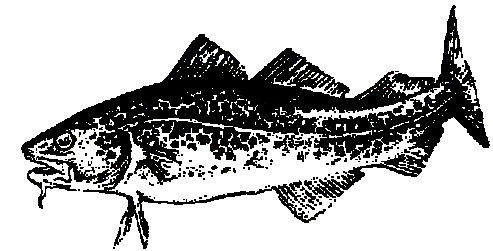
Incomplete data

✳ Representative data only on mature individuals -
data on immature individuals missing

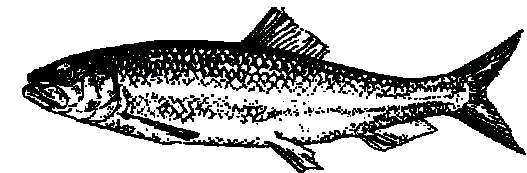
Solution: reconstruct missing data



✓ Barents Sea cod



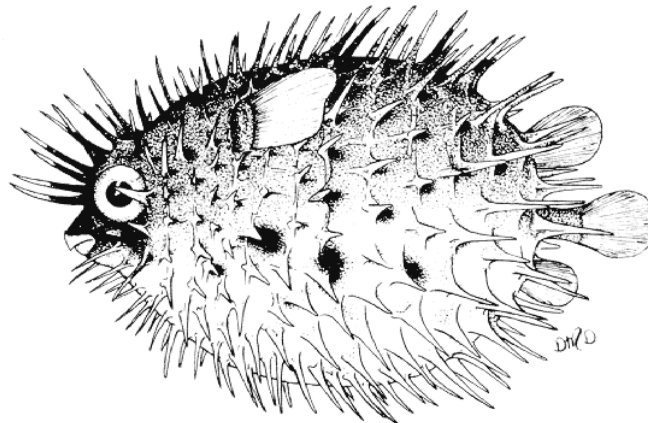
✓ Norwegian herring



How to estimate the probabilistic reaction norm? — Method #2

✱ Representative data on immature and mature individuals, but *newly-matured individuals cannot be identified*

✓ Almost all fish



Estimation based on age- and size-based maturity ogives

Ordinary age-based maturity ogive:

$$\begin{aligned} o(a) &= o(a-1) + (1 - o(a-1)) m(a) \\ \Leftrightarrow m(a) &= \frac{o(a) - o(a-1)}{1 - o(a-1)} \end{aligned}$$

where $o(a)$ is ogive (proportion of mature at age), a is age, s is size, and $m(a)$ is probability of maturing

[simplifying assumptions]

The formula can be extended to account for age **and** size:

$$m(a, s) = \frac{o(a, s) - o(a - 1, s - \delta s)}{1 - o(a - 1, s - \delta s)}$$

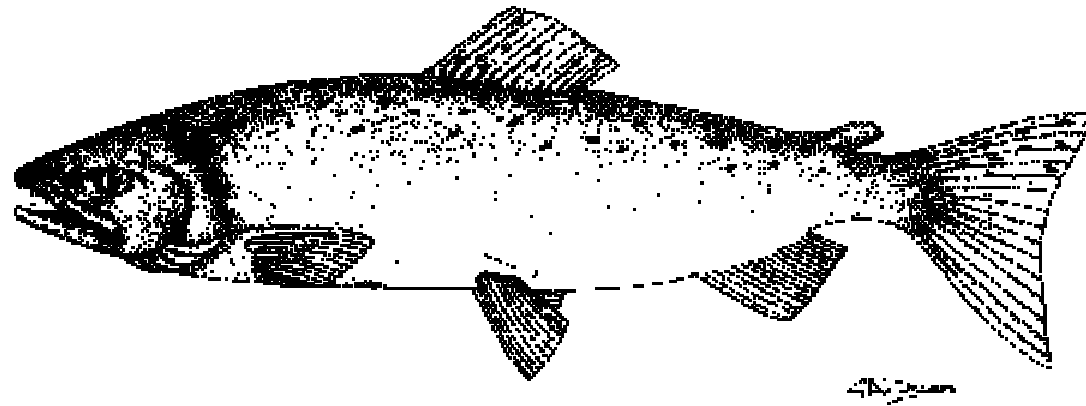
where δs is annual growth increment, and
 $m(a, s)$ is the reaction norm!

[more simplifying assumptions]

How to estimate the probabilistic reaction norm? — Method #3

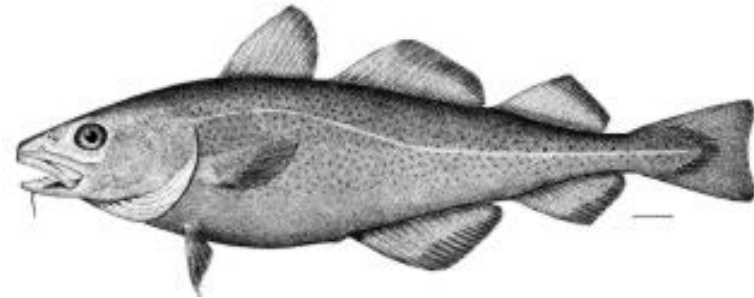
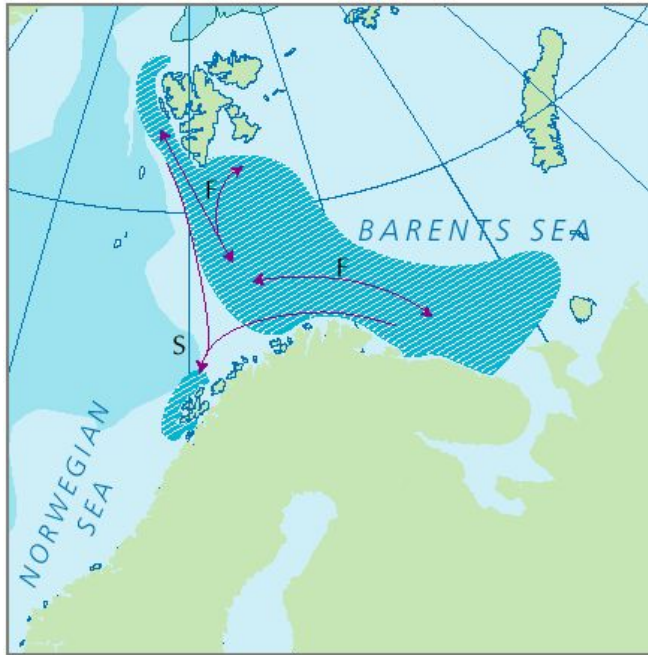
✳ Repeated observations on single individuals

✓ Practical with e.g. salmonids, experiments

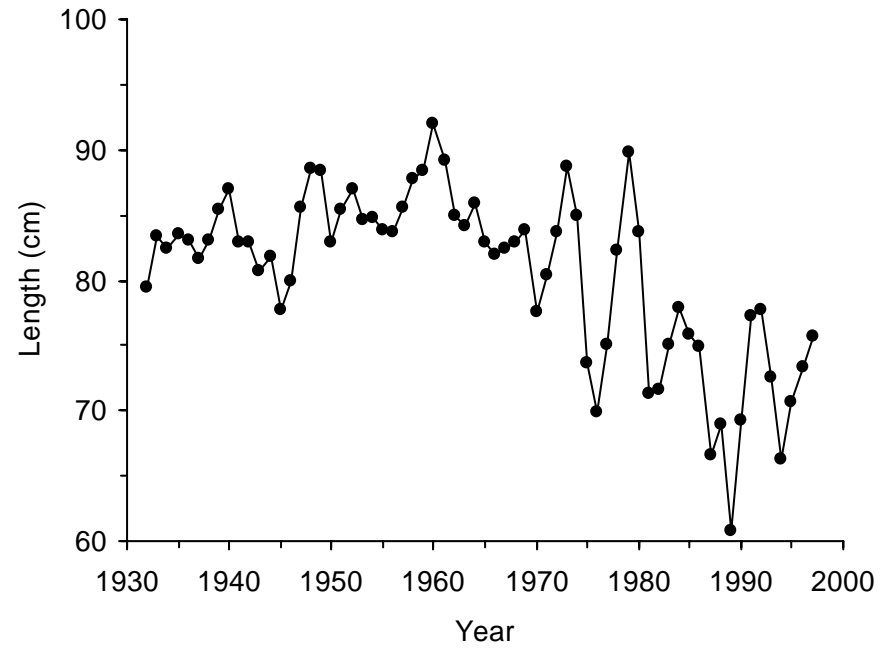
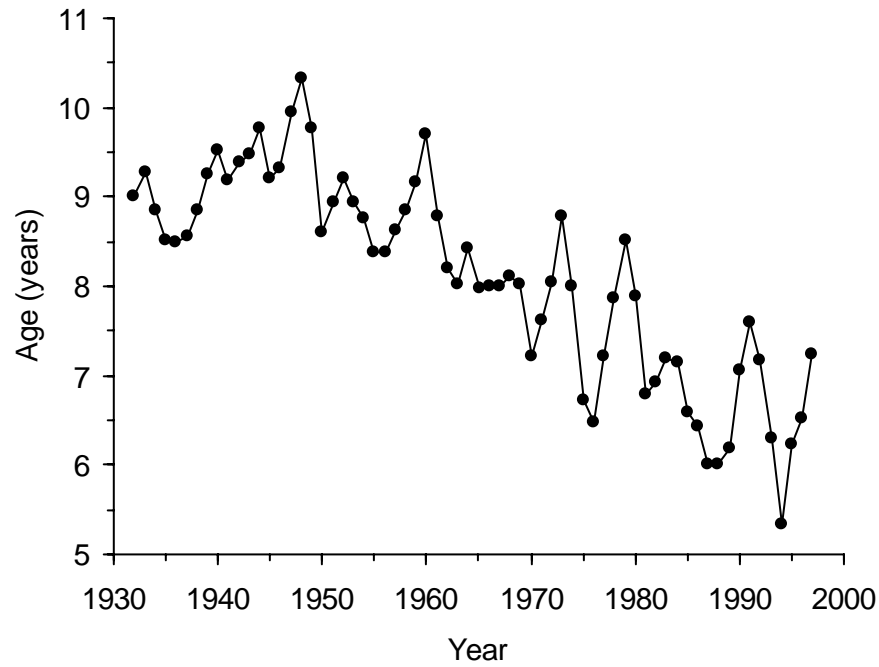


Species	Population or stock	Period with data	Trend towards earlier maturation	Reference
Atlantic cod	Northeast Arctic	1932–1998	Yes	Heino et al. 2002c
	Georges Bank	1970–1998	Yes	Barot et al. 2004b
	Gulf of Maine	1970–1998	Yes	
	Northern (2J3KL)	(1977–) 1981–2002	Yes	Olsen et al. 2004
	Southern Grand Bank (3NO)	1971–2002	Yes	Olsen et al. 2005
	St. Pierre Bank (3Ps)	1972–2002	Yes	
Plaice	North Sea	1957–2001	Yes	Grift et al. 2003
American plaice	Labrador–NE Newfoundland (2J3K)	1973–1999	Yes	Barot et al. 2005
	Grand Bank (3LNO)	1969–2000	Yes	
	St. Pierre Bank (3Ps)	1972–1999	Yes	
Atlantic herring	Norwegian spring-spawning	1935–2000	Yes, but weak	Engelhard & Heino 2004
Grayling	Lake Lesjaskogsvatnet, Norway	1903–2000 (ca. 15 years)	Yes	Haugen & Vøllestad, in press

Northeast Arctic cod

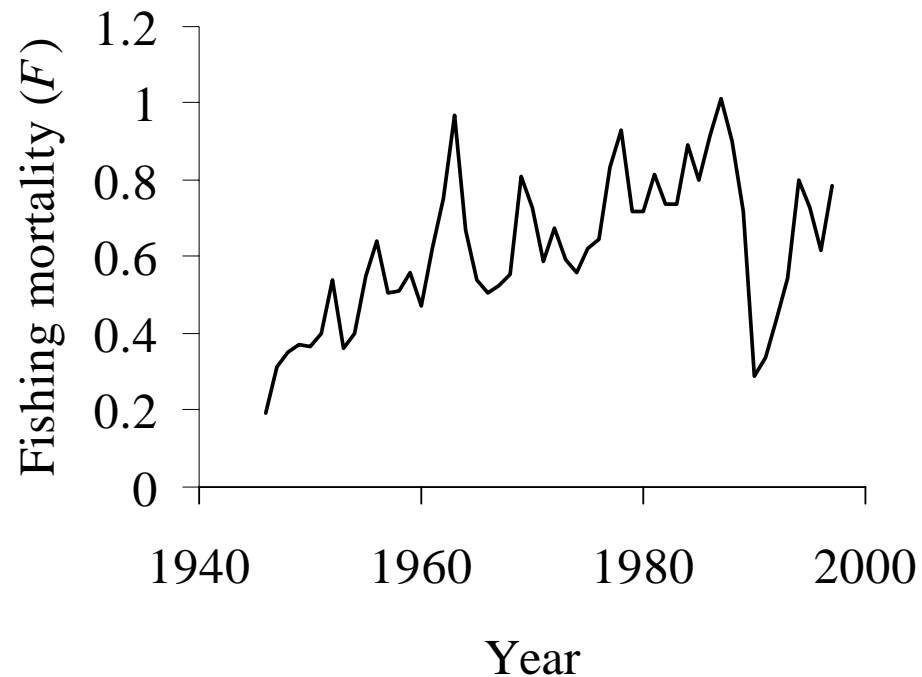


Major decline in age & size at maturation



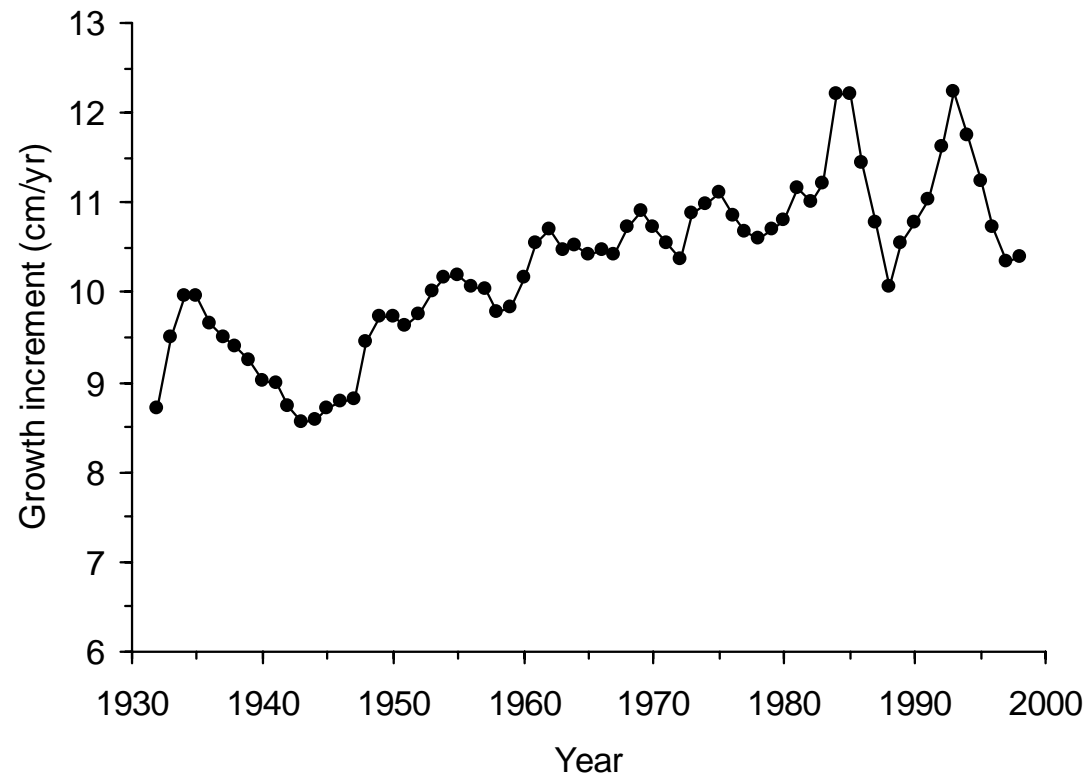
Demographic change?

- 1) Total mortality has increased
- 2) Population dominated by younger cod
⇒ Lower average age at maturation



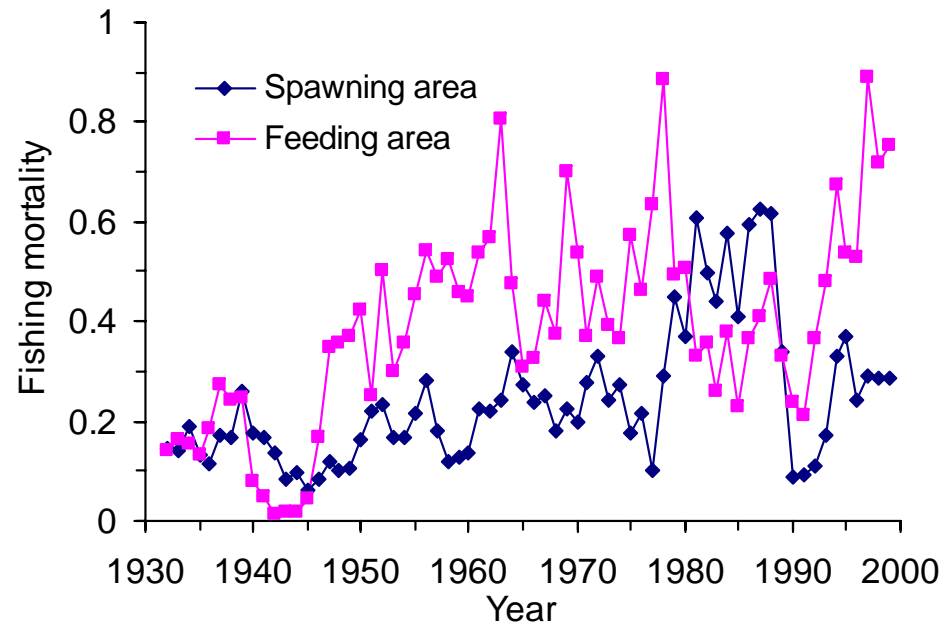
Phenotypic plasticity?

- 1) Growth has accelerated ("compensatory growth")
- 2) Fast-growing cod mature earlier
- 1) + 2) \implies Earlier maturation



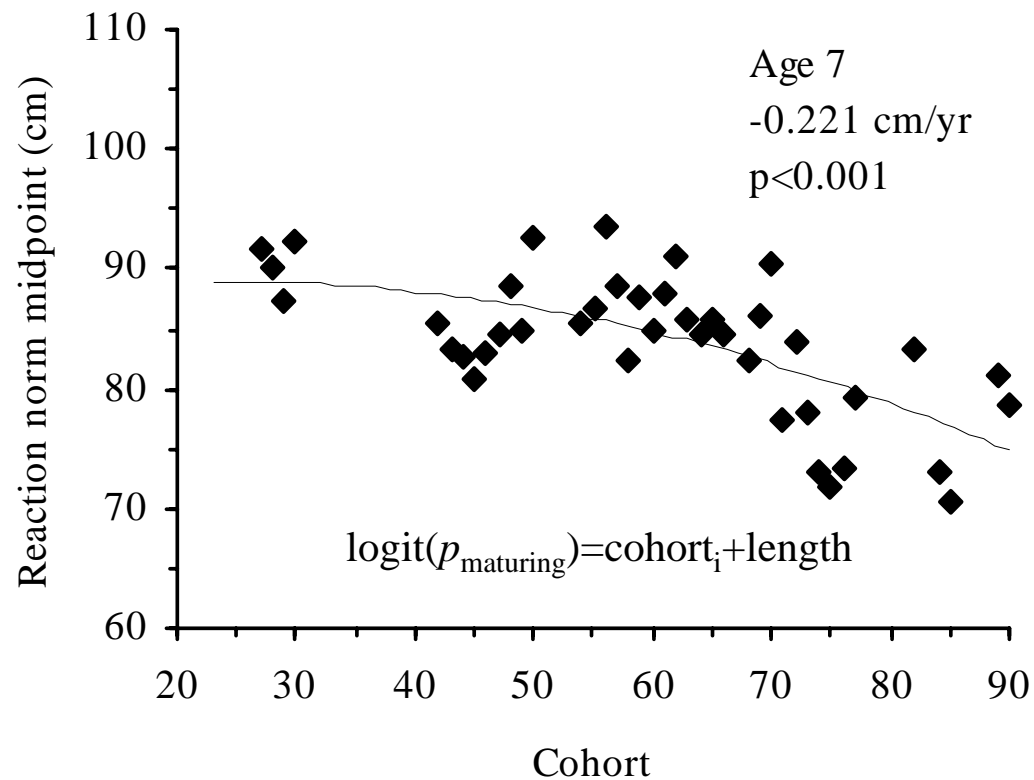
Genetic change?

- 1) Historic harvest regime targeting mostly mature cod
⇒ Genetic selection for delayed maturation
- 2) Modern harvest only size-selective
⇒ Genetic selection for earlier maturation



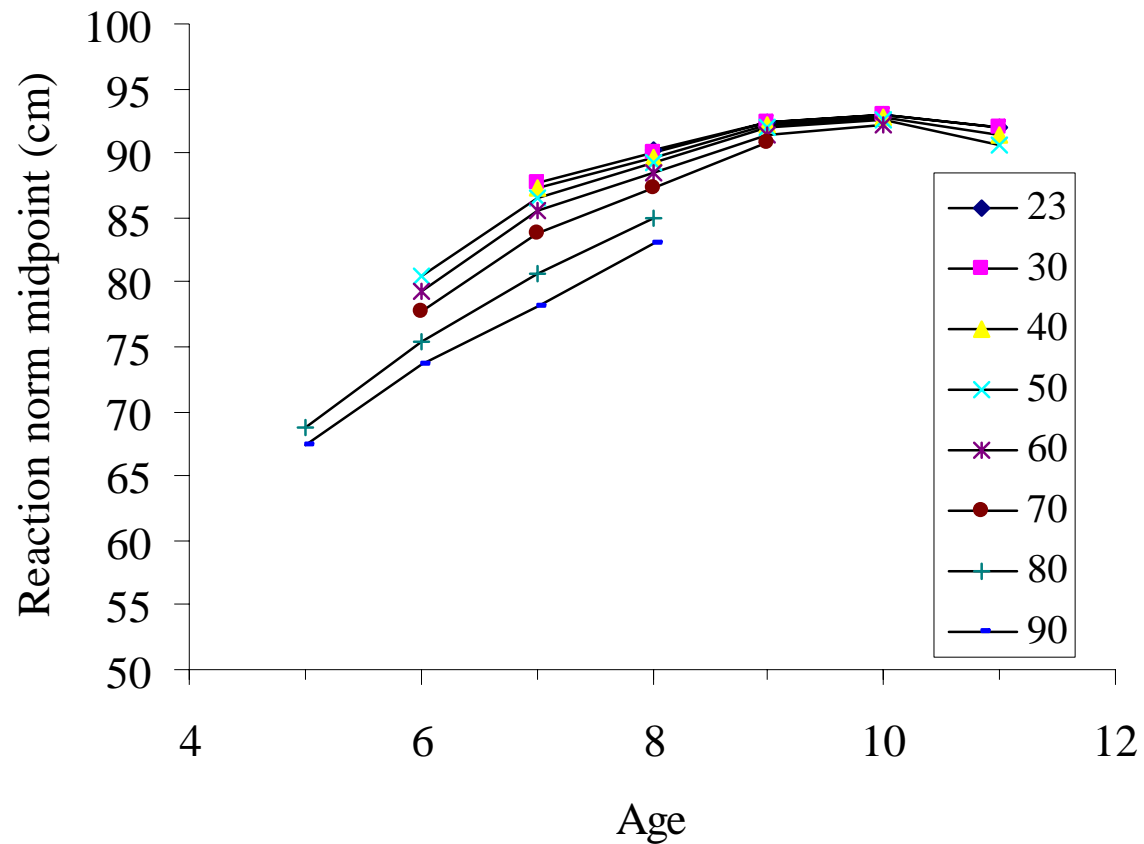
Northeast Arctic cod

Change in length at which probability of maturing is 50% (“midpoint”) at age 7



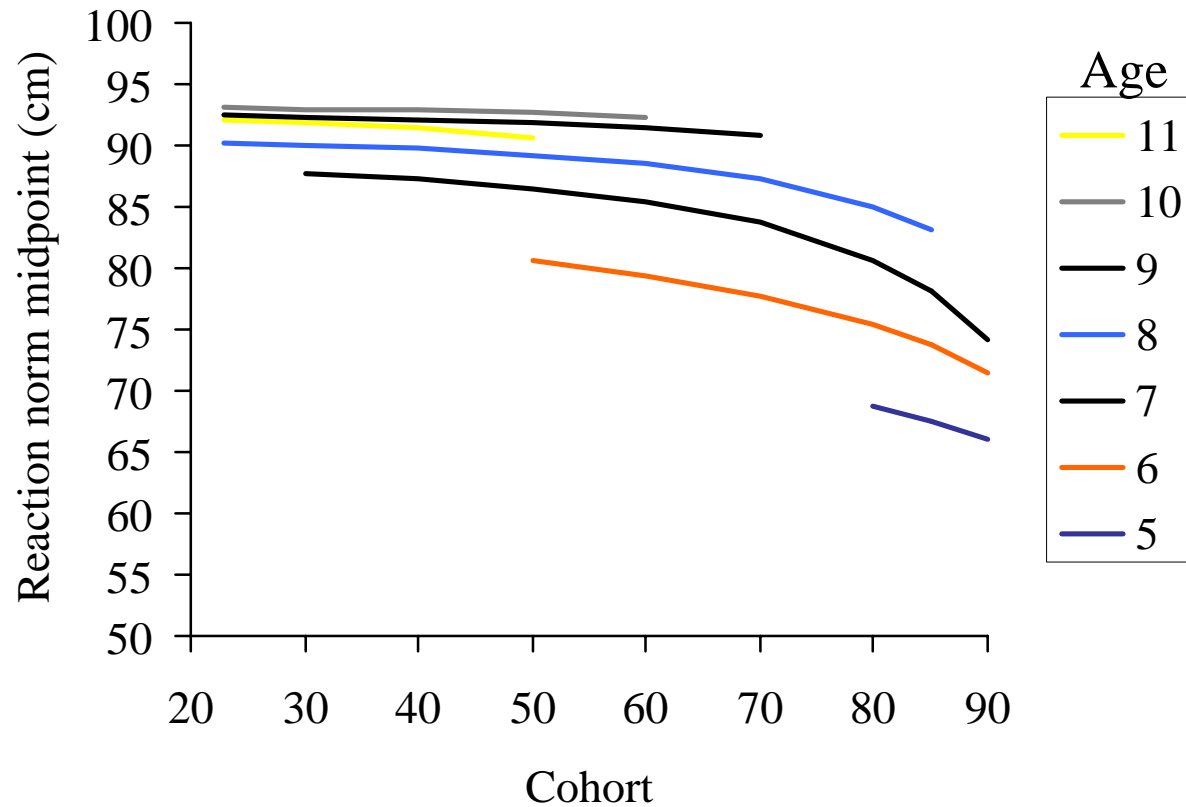
Northeast Arctic cod

Predicted reaction norm midpoints for cohorts 1923-90:

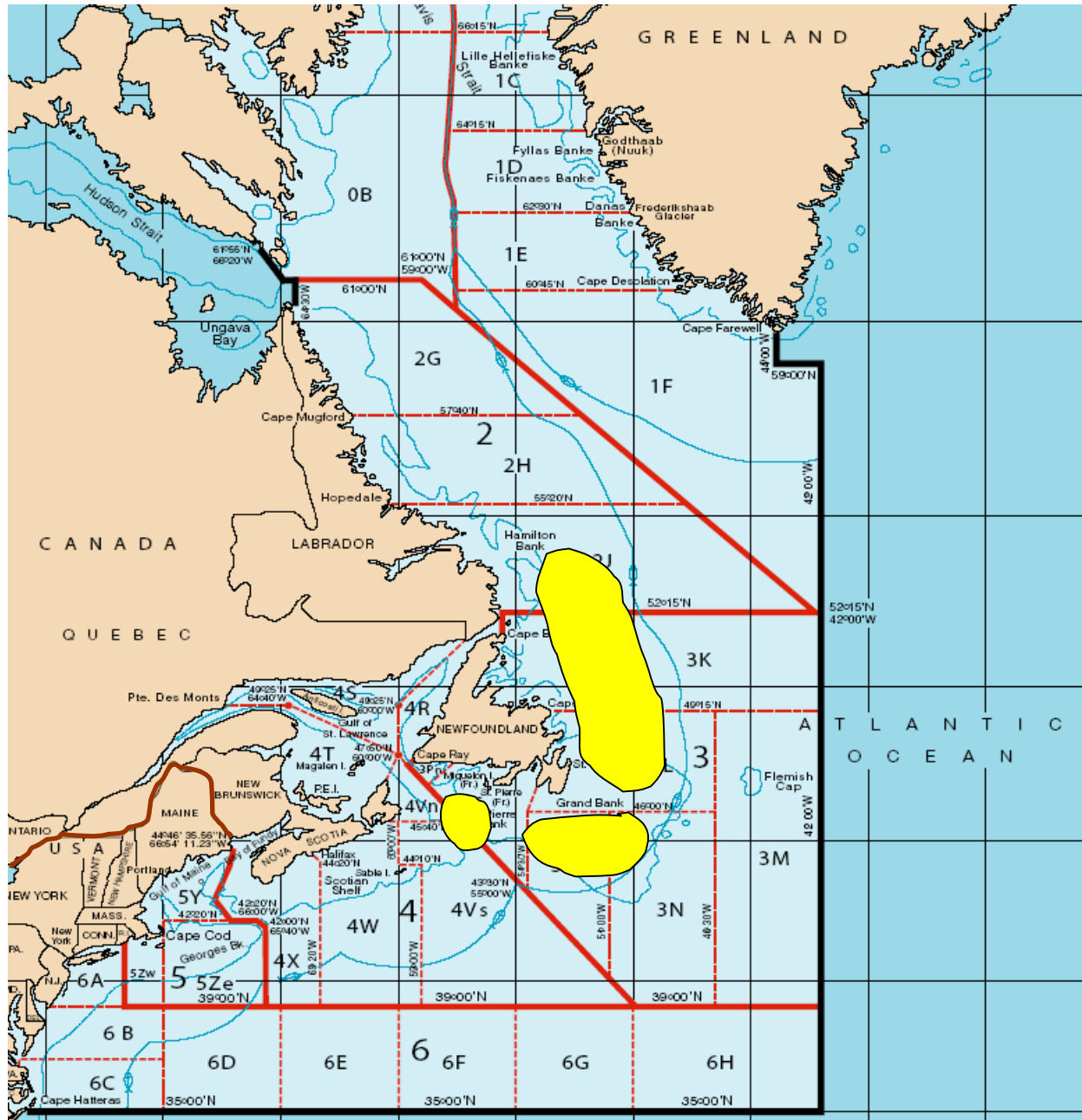


Northeast Arctic cod

Change in the reaction norm midpoints:

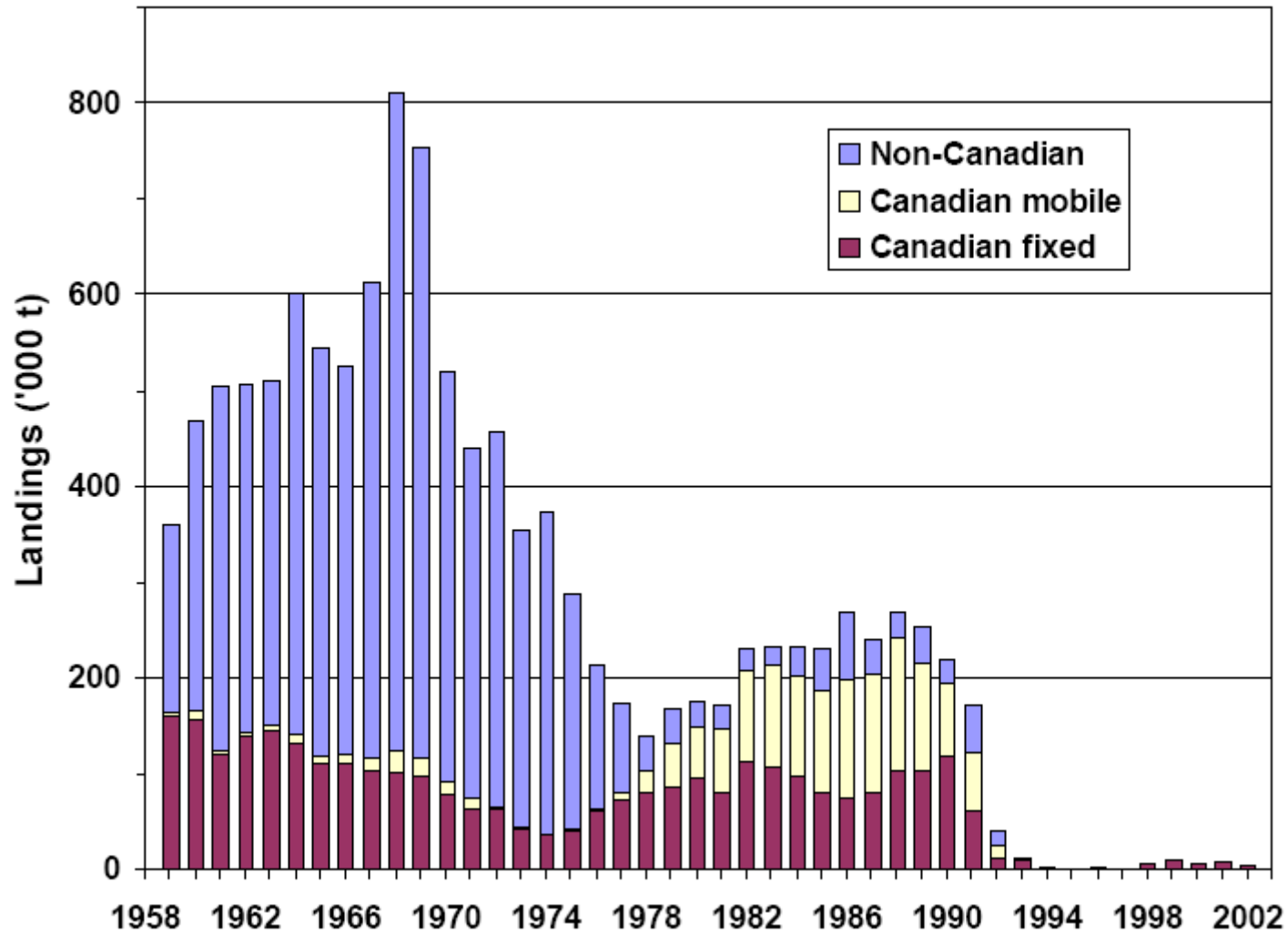


Atlantic cod in Canada



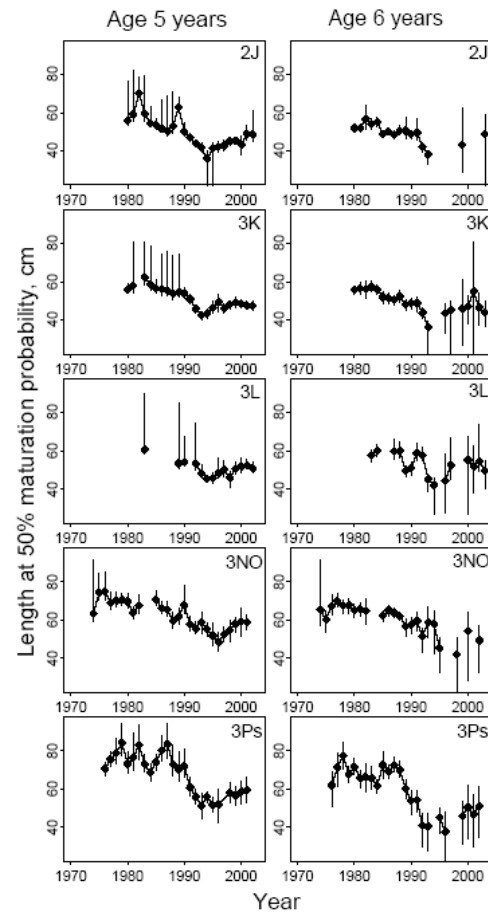
Thomas W (c) 2000-2003

Northern cod

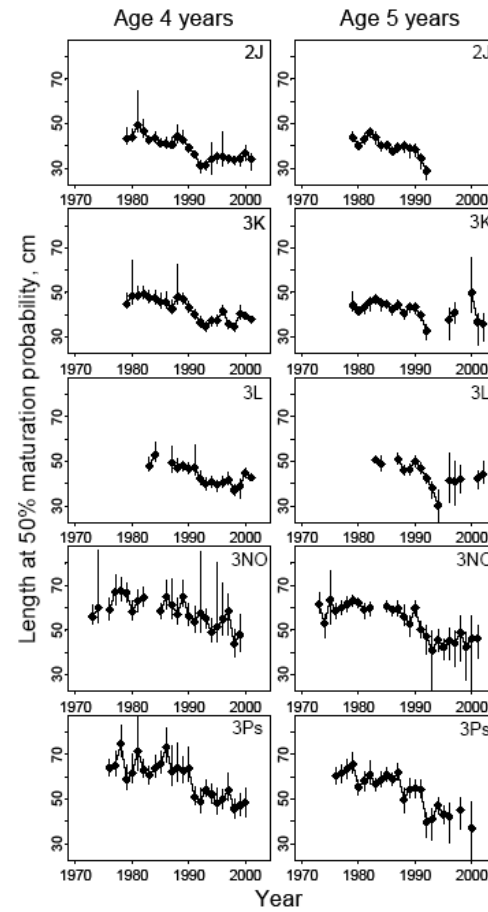


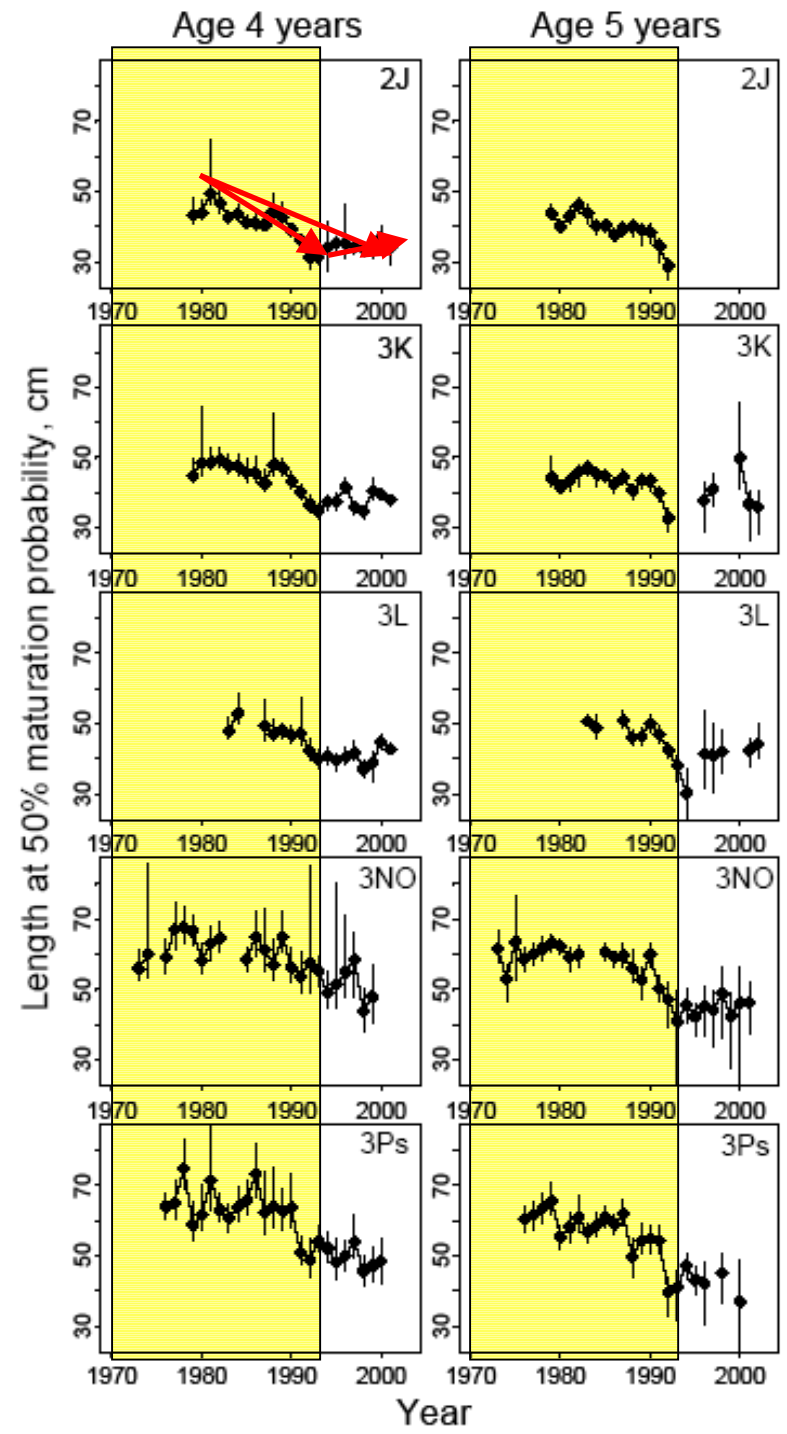
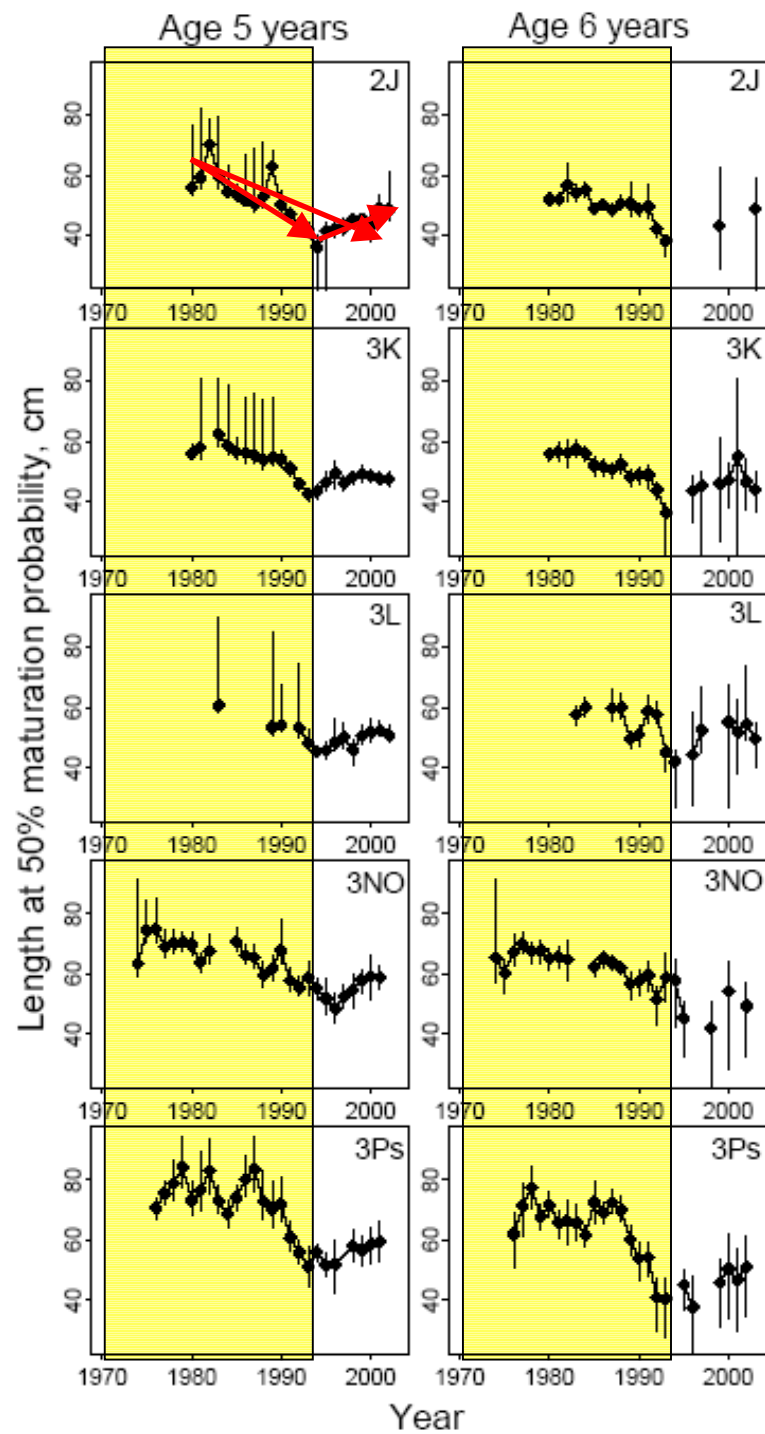
Atlantic cod off Newfoundland–Labrador

Females



Males

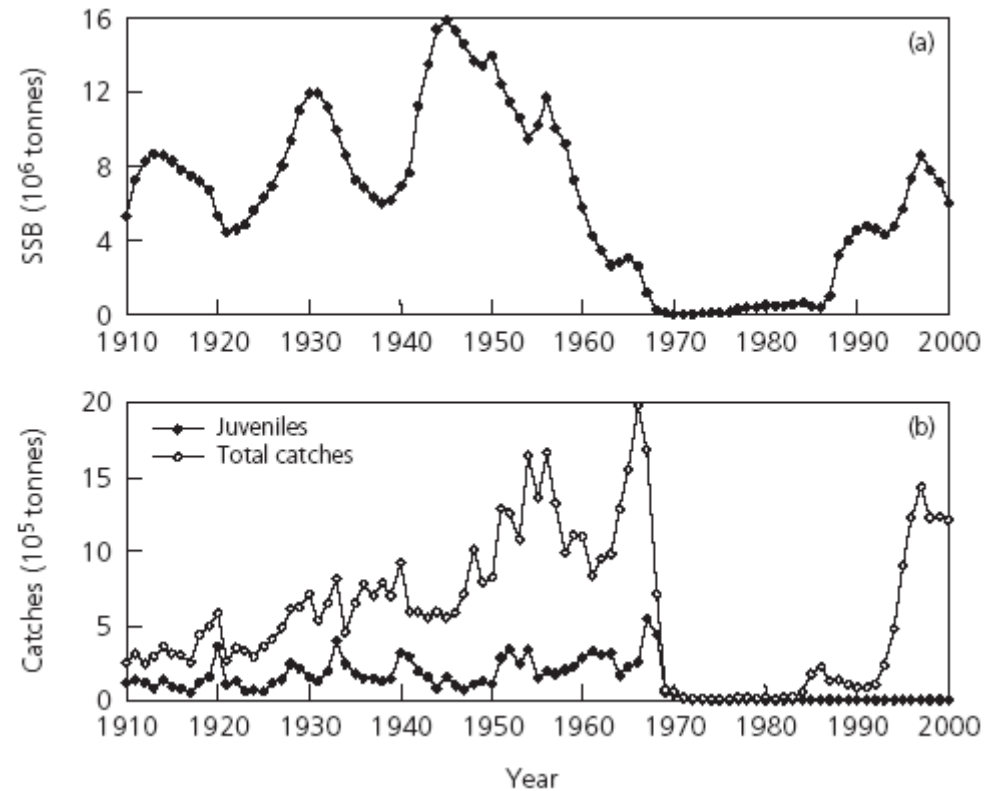


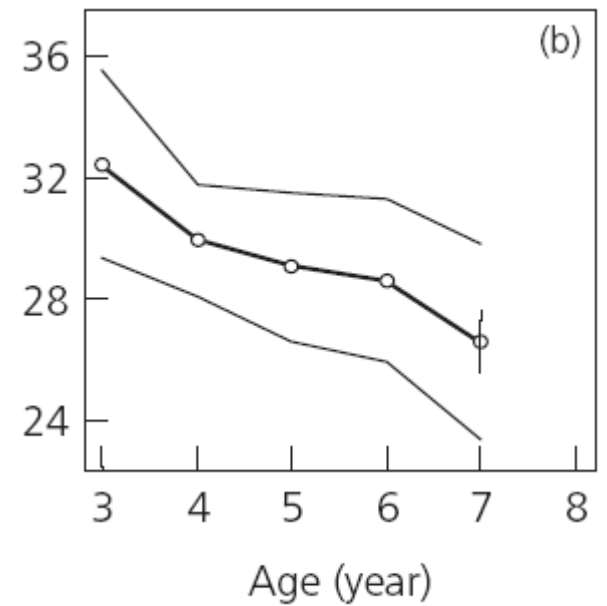
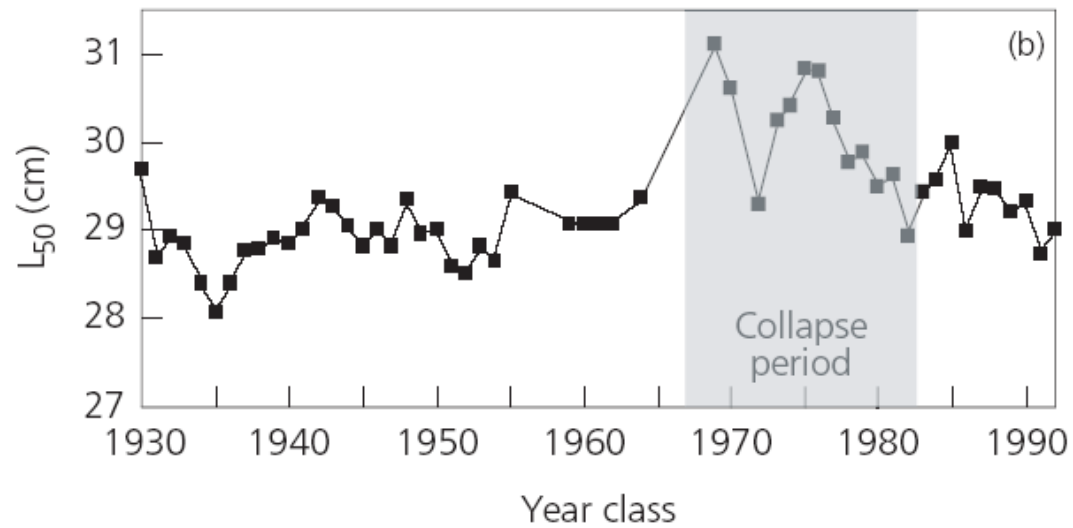
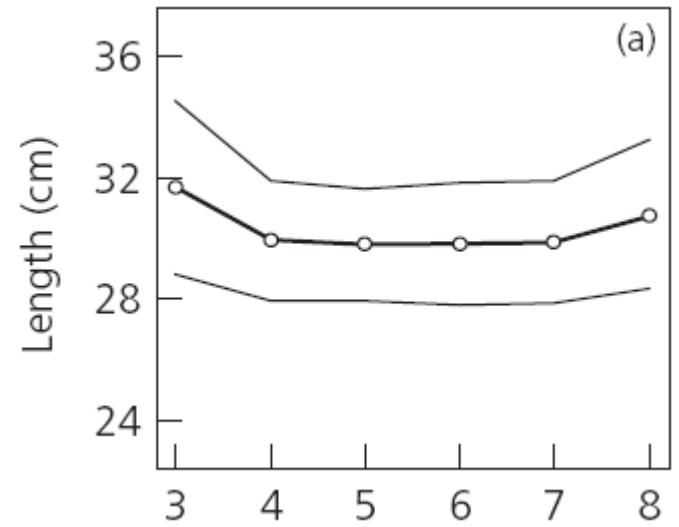
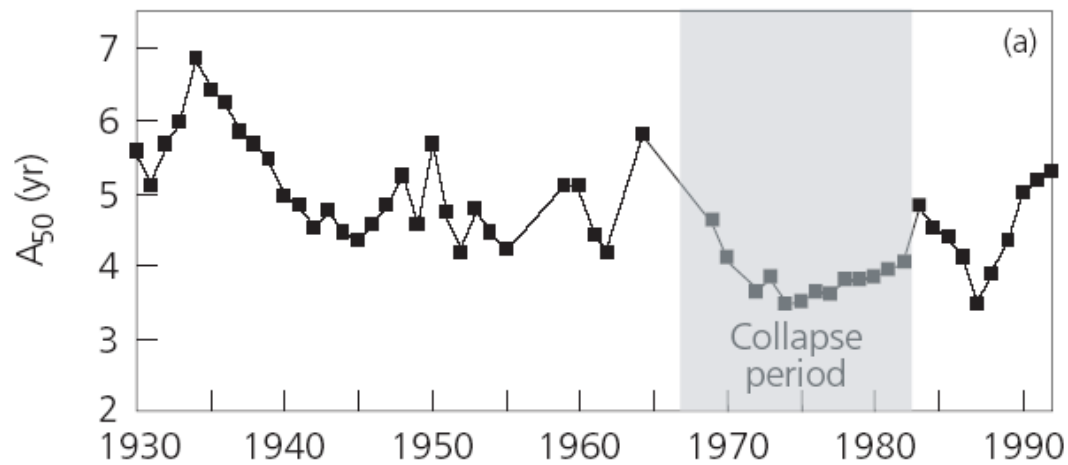


Atlantic cod off Newfoundland–Labrador

- The stocks have not recovered, despite 10+ years of severe fishing restrictions
- Is the change in maturation hampering recovery?
- ✓ Large females are superior spawners
- ✓ Possibly faster “recovery” of female than male reaction norms suggests that natural selection for maturation at large size is stronger in females

Norwegian spring-spawning herring “the” fisheries collapse of the 60’s





Why is herring an outlier?

- Spawner fishery very important – both historically and at present
- Before the collapse also an intensive fishery on juveniles, but before potential maturation age
- Uncertainty on fishing mortality on late immature herring confounds expectations



Do evolutionary changes matter?



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Do we have the right to radically modify wild species?

1920's



© Norsk Folkemuseum, Oslo, Norway

now



© Esben Moland Olsen, Univ. Oslo, Norway

Do evolutionary changes matter?

- Reduced sustainable fisheries yield
 - Smaller body size of fish in the catch
 - Small females produce *relatively fewer eggs of lower quality* and have a *shorter spawning period*
 - ✓ Disproportionate loss of reproductive capacity
 - ✓ Greater vulnerability to unfavourable conditions
- ➡ Should be a concern to managers

Can fisheries-induced evolution be managed?

Generic tool that always works:

- Other things being equal,
lowering fishing mortality will slow down, and
eventually stop, fisheries-induced evolution

Can fisheries-induced evolution be managed?

Specific tools:

- Exclusively harvesting mature fish favours delayed maturation
- Shifting exploitation from large to small individuals favours fast growth and may favour maturation at large sizes
- ✓ Management tools would need to be evaluated with the help of eco-genetic models!



Conclusions

Thomas W (c) 2000-2003

Fisheries-induced evolution...

- can be measured
- occurs at contemporary time scales
- is commonplace
- will often reduce the value of fish stocks as renewable resources, and hence needs to be managed

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Thrond Haugen, University of Oslo, Norway

1 Presently at IRD-LEST, France

2 Presently at IFREMER-MFL, France

3 Presently at University of Oslo, Norway

4 Presently at CEFAS, UK

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