INSTITUTE OF MARINE RESEARCH

Modelling fisheries-induced evolution: probabilistic maturation reaction norm methodology

Nordic Marine Academy course on *Modelling marine populations from physics to evolution*
10-16.10.2005 Espegrend, Norway

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*)

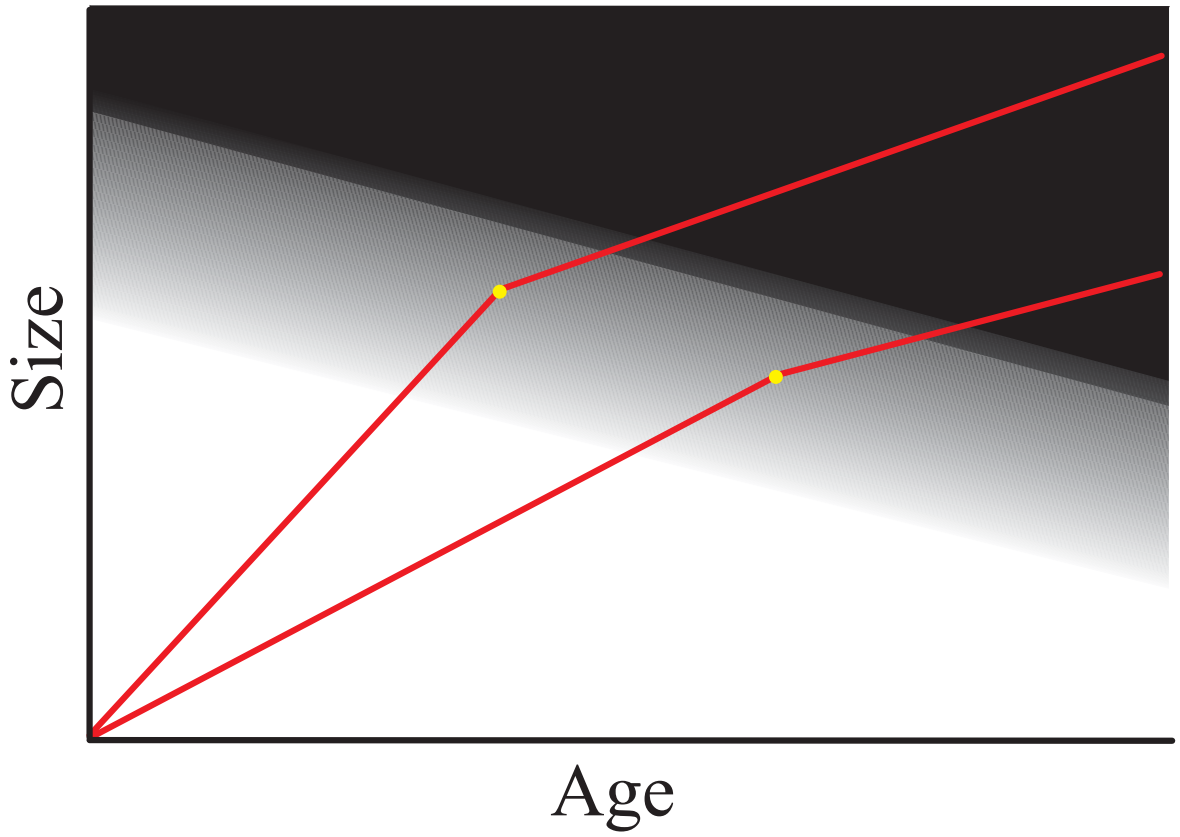
Competing explanations

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

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

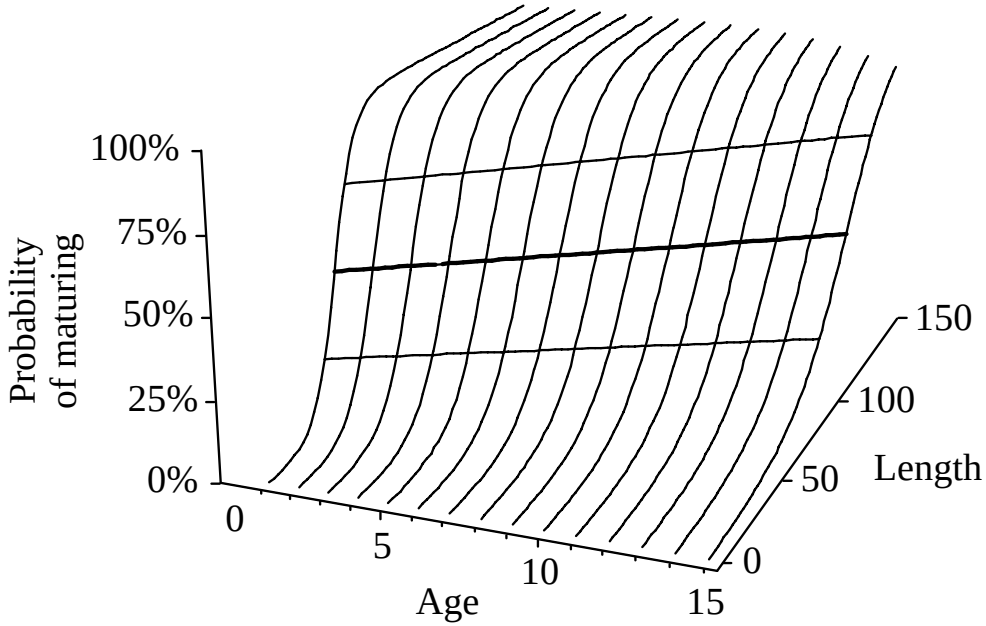
Probabilistic maturation reaction norms

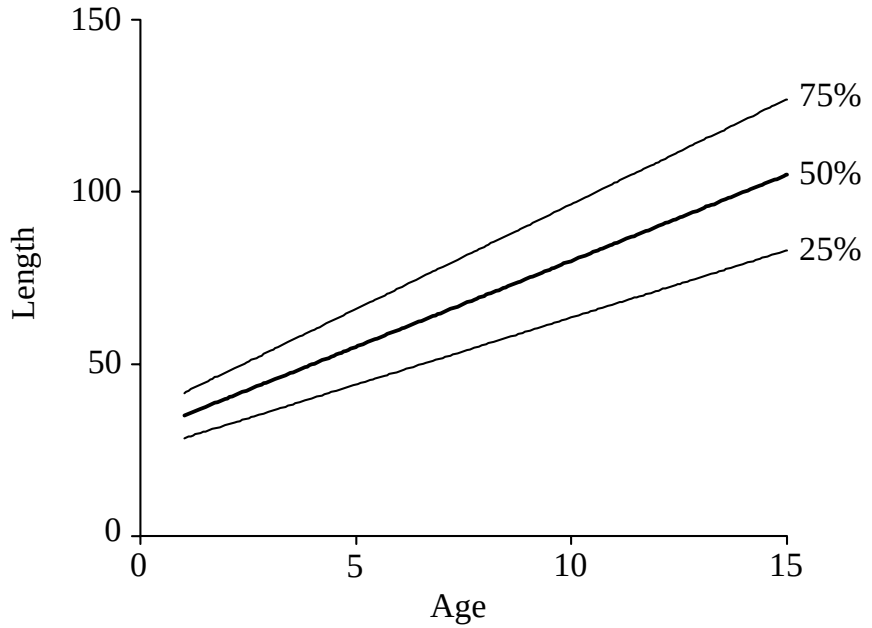
- Probability that an immature individual, depending on its age and size, matures during a given time interval

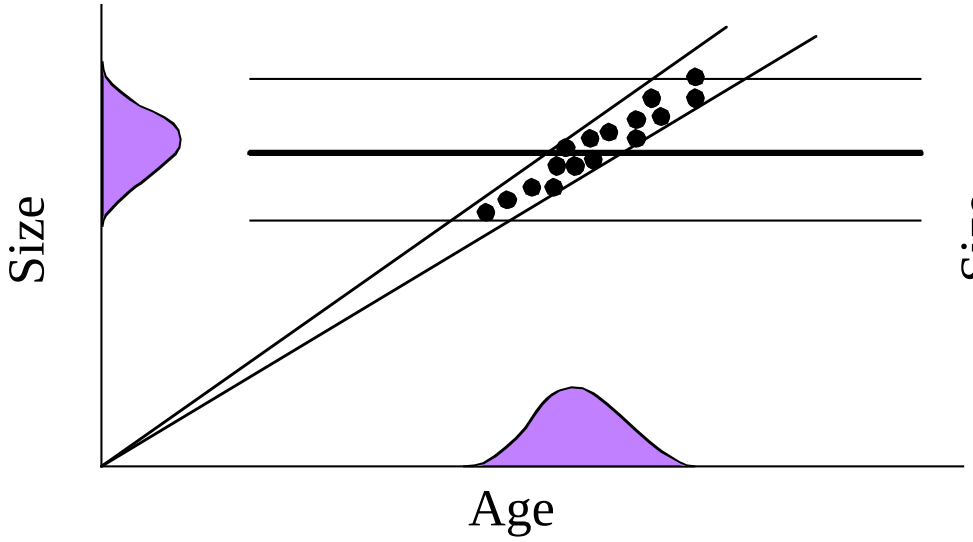


Size-at-age ~ growth ~ environment

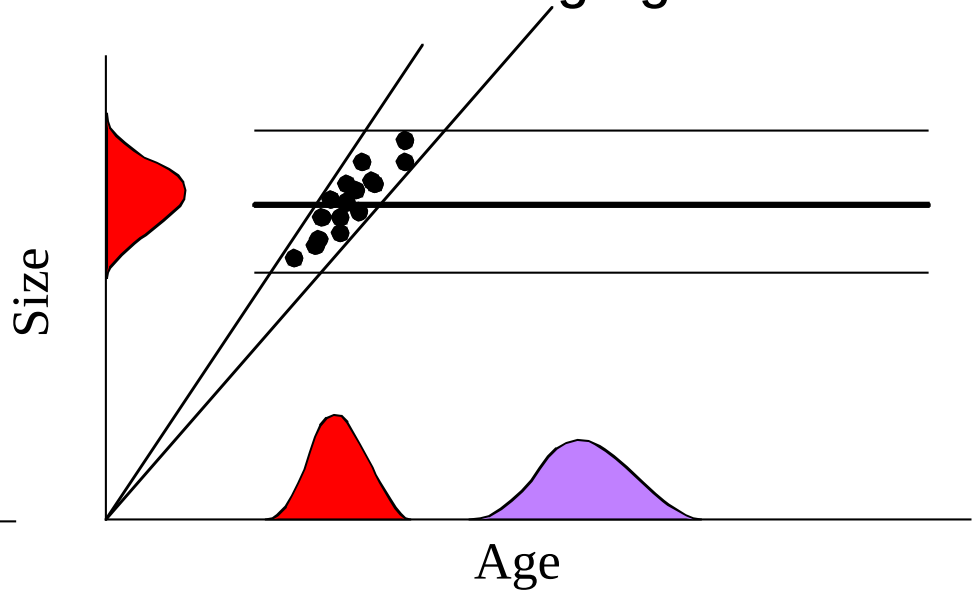
Probabilistic maturation reaction norms



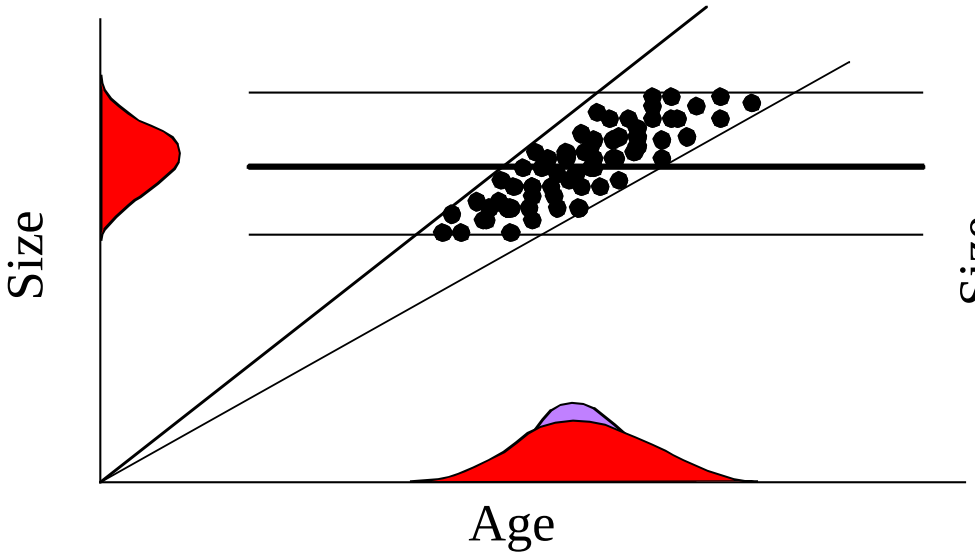




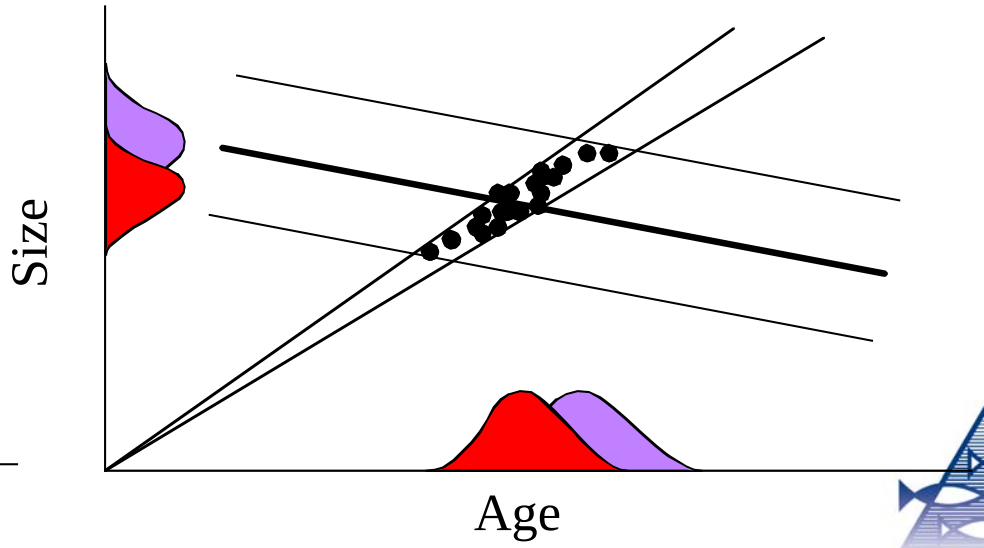
Increase in average growth



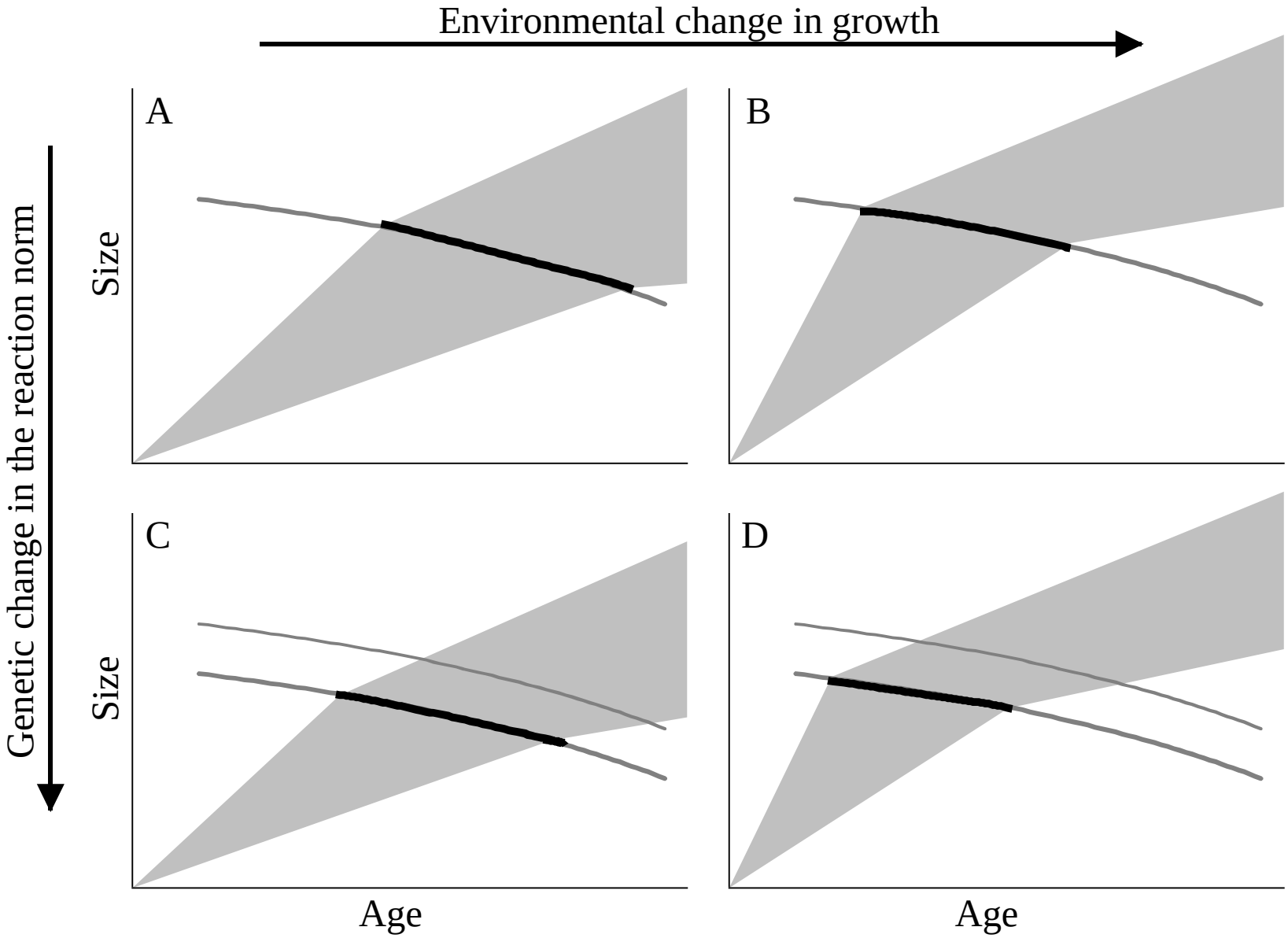
Increase in variance in growth



Change in the reaction norm



Disentangling plasticity and genetics



Maturation reaction norm analysis

Process-oriented description:

- Reaction norm describes the tendency to mature, given age and size
- Variations in demography and growth determine how the reaction norm is ‘sampled’ by a population, but leave the reaction norm itself unaffected

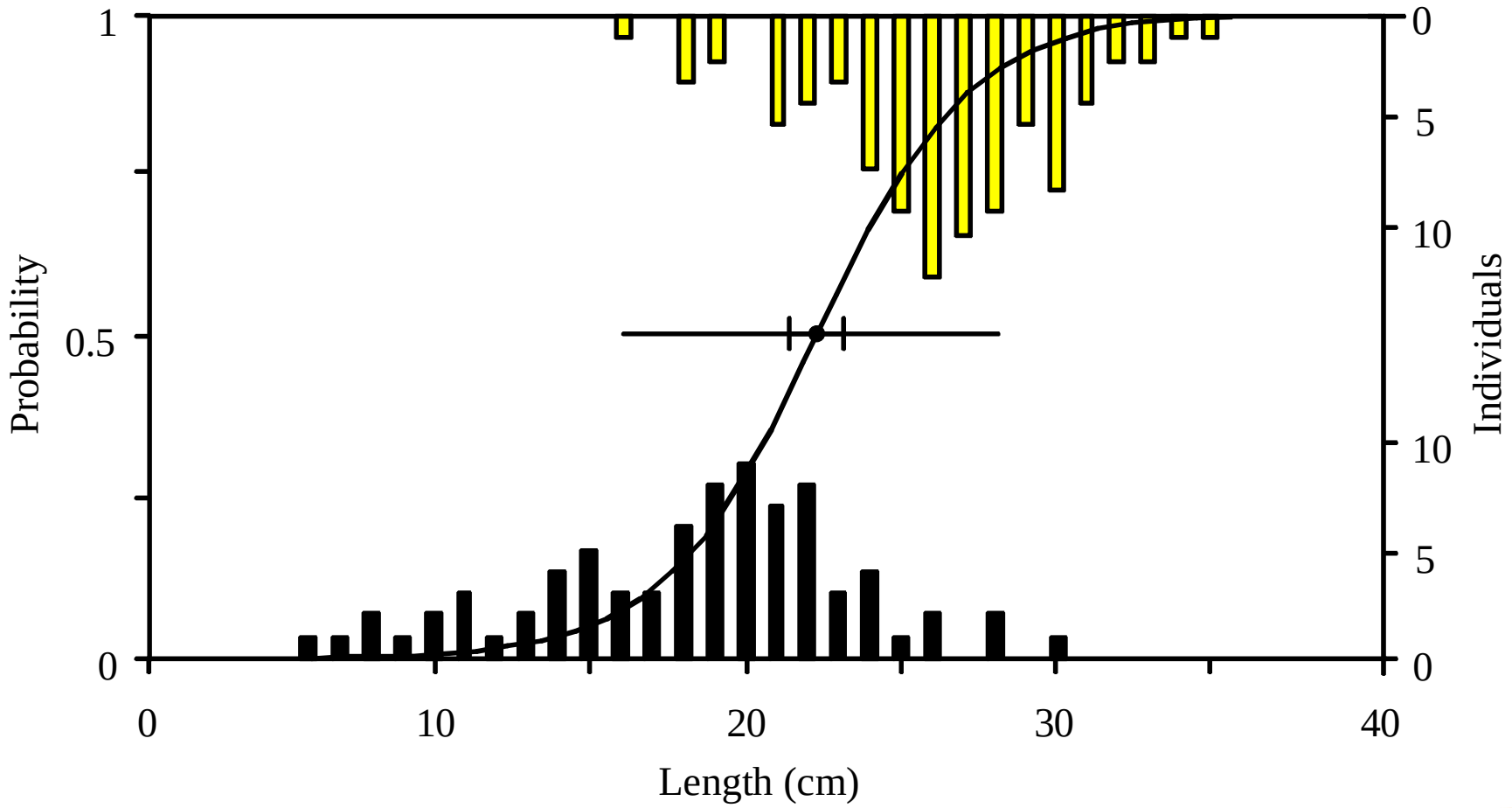
⇨ A trend in the reaction norm suggests evolution

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 ambiguous

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

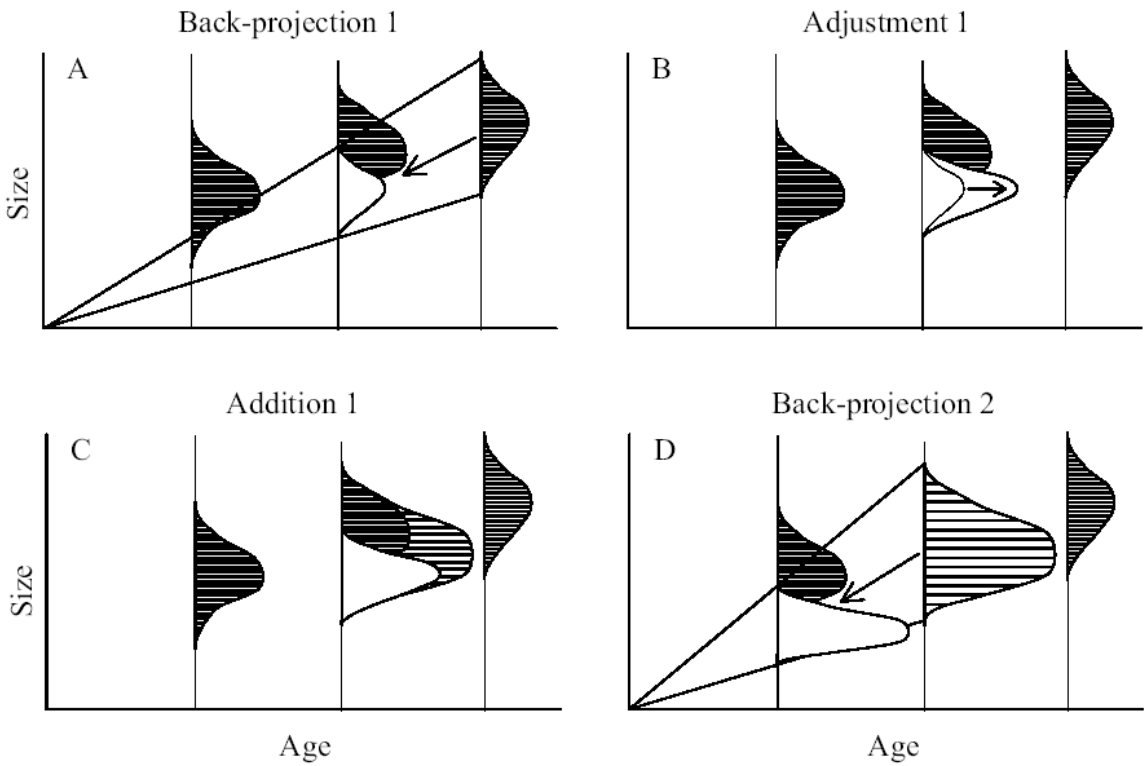
Logistic regression fitted to a representative sample of immature and newly-matured individuals, sized and aged



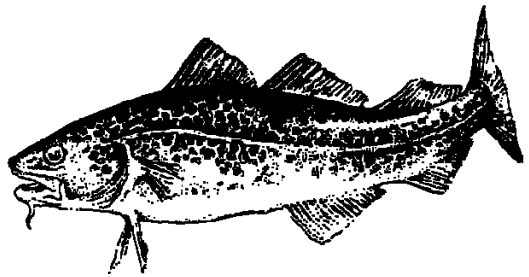
Incomplete data

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

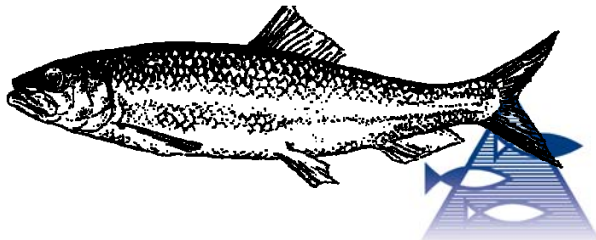
Solution: reconstruct missing data



✓Barents Sea cod



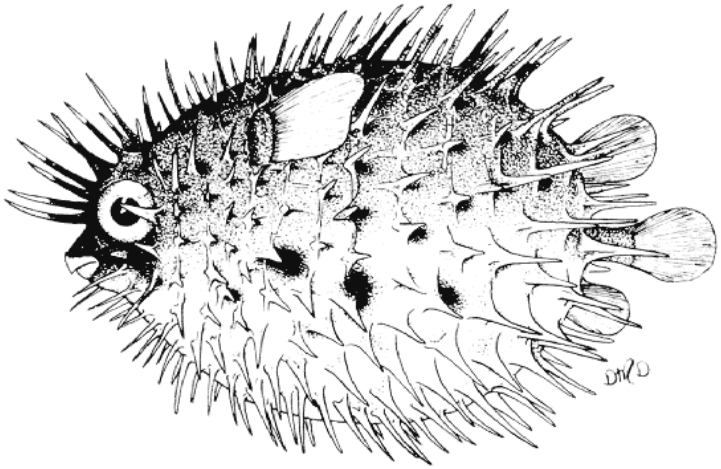
✓Norwegian herring



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:

$$o(a) = o(a-1) + (1 - o(a-1))\, m(a)$$

$$\Leftrightarrow m(a) = \frac{o(a) - o(a-1)}{1 - o(a-1)}$$

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

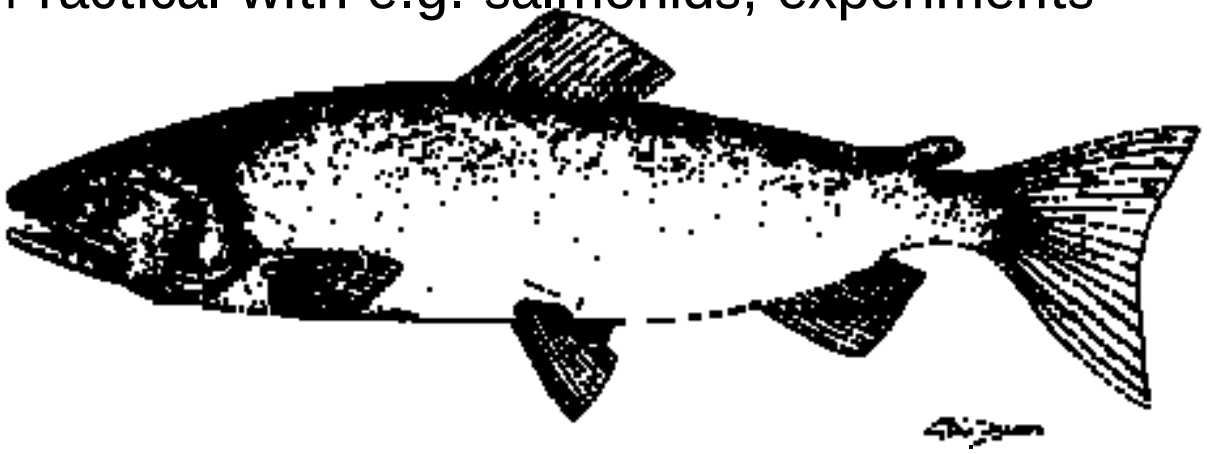
***m*(*a*,*s*) is the reaction norm!**

[more simplifying assumptions]

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

- Repeated observations on single individuals
  - Van Dooren, T. J. M., Tully, T. & Ferrière, R. 2005. The analysis of reaction norms for age and size at maturity using maturation rate models. *Evolution* 59:500-506.

✓Practical with e.g. salmonids, experiments



INSTITUTE OF MARINE RESEARCH

Modelling fisheries-induced evolution: case studies

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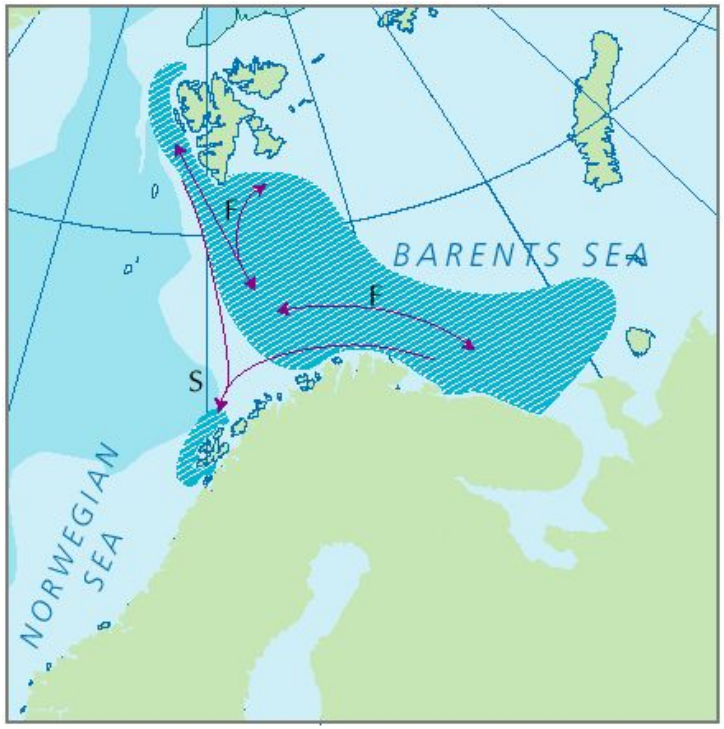
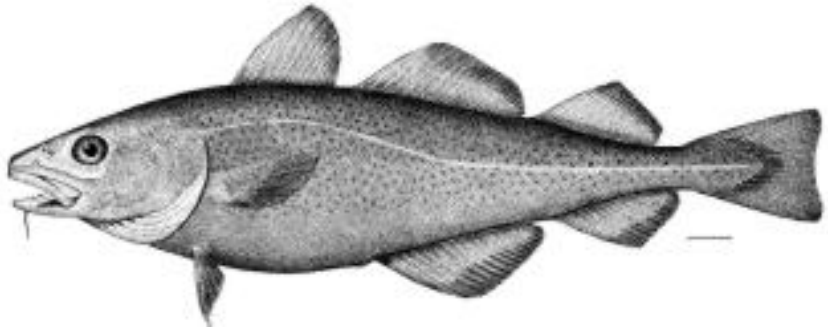
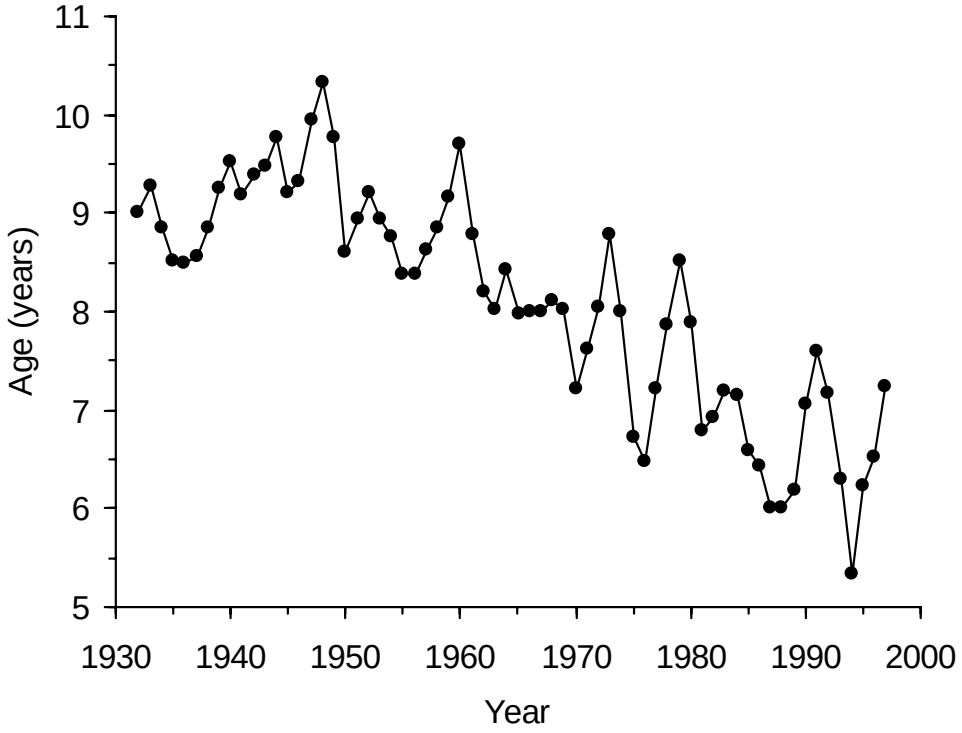
Species	Population or stock	Period with data	Trend towards earlier maturation?	Reference
Atlantic cod *Gadus morhua*	Northeast Arctic	1932–1998	Yes	Heino et al. 2002c
	Georges Bank	1970–1998	Yes	Barot et al. 2004b
	Gulf of Maine	1970–1998	Yes	
	Northern (2J3KL)	(1977–)1981–2002	Yes	Olsen et al. 2004
	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

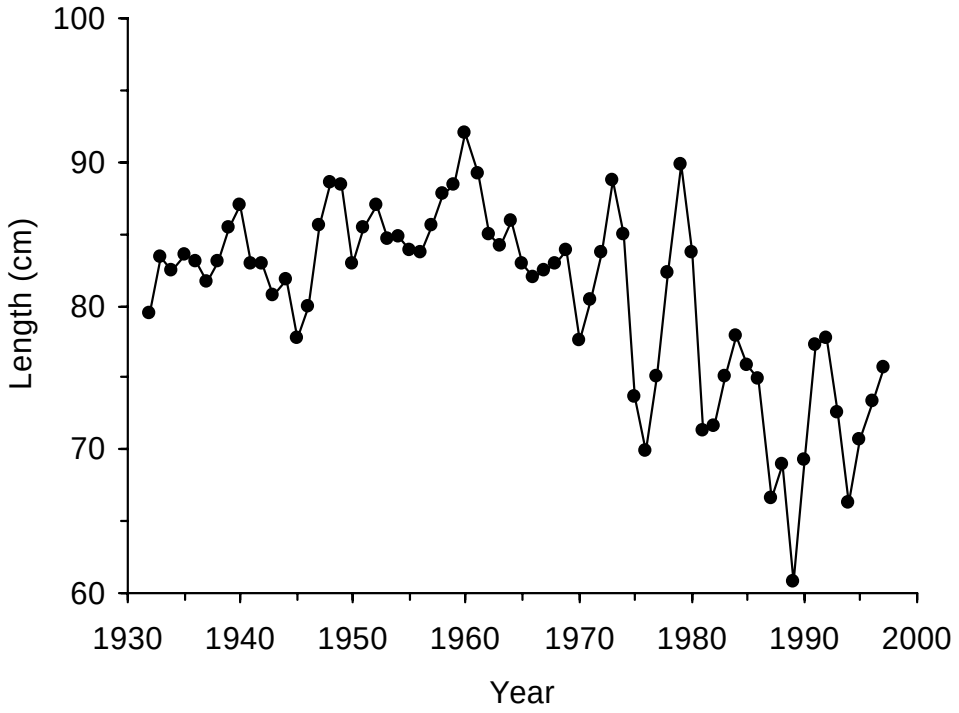
Northeast Arctic cod





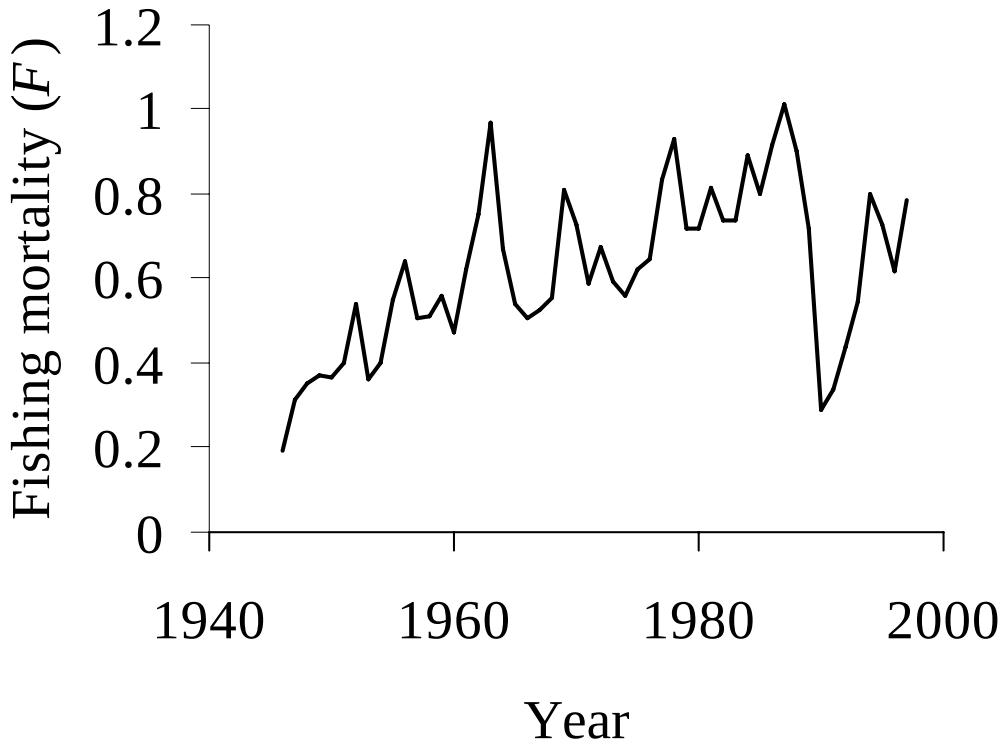
Major decline in age & size at maturation





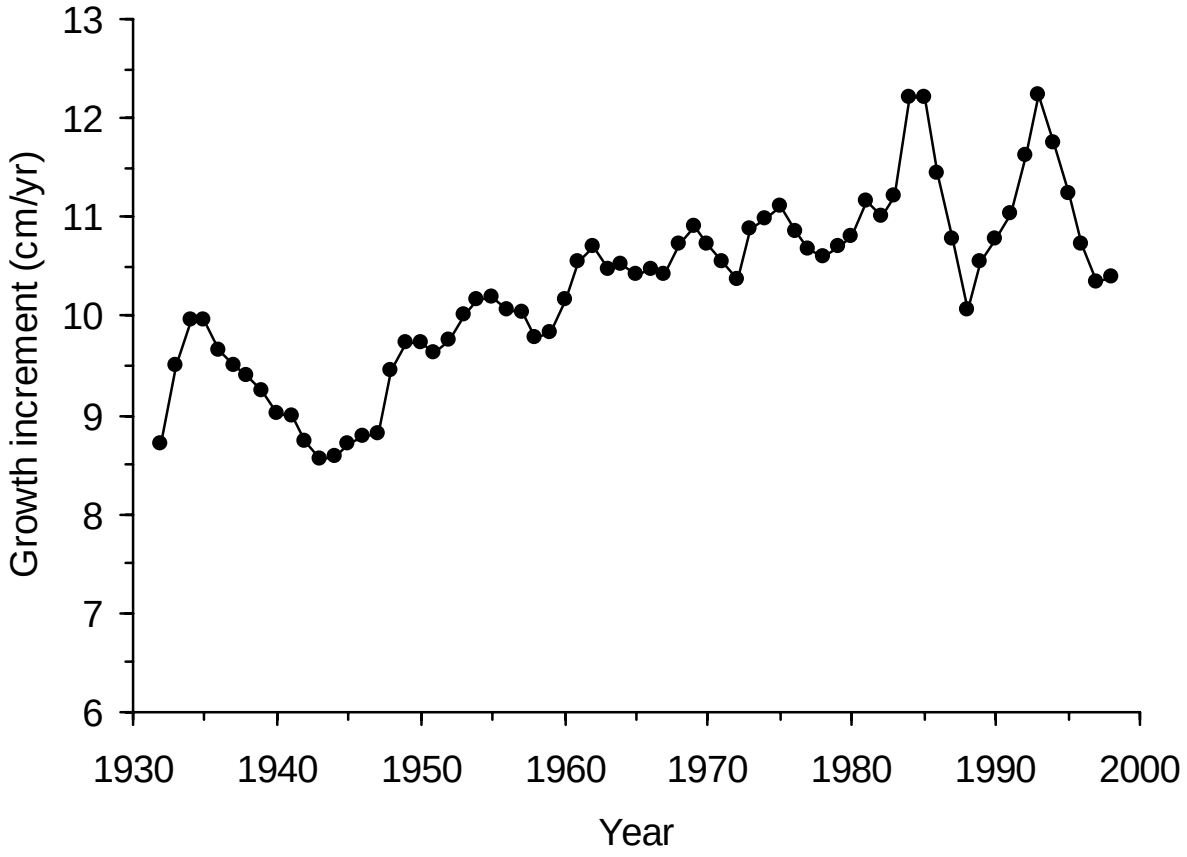
Demographic change?

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



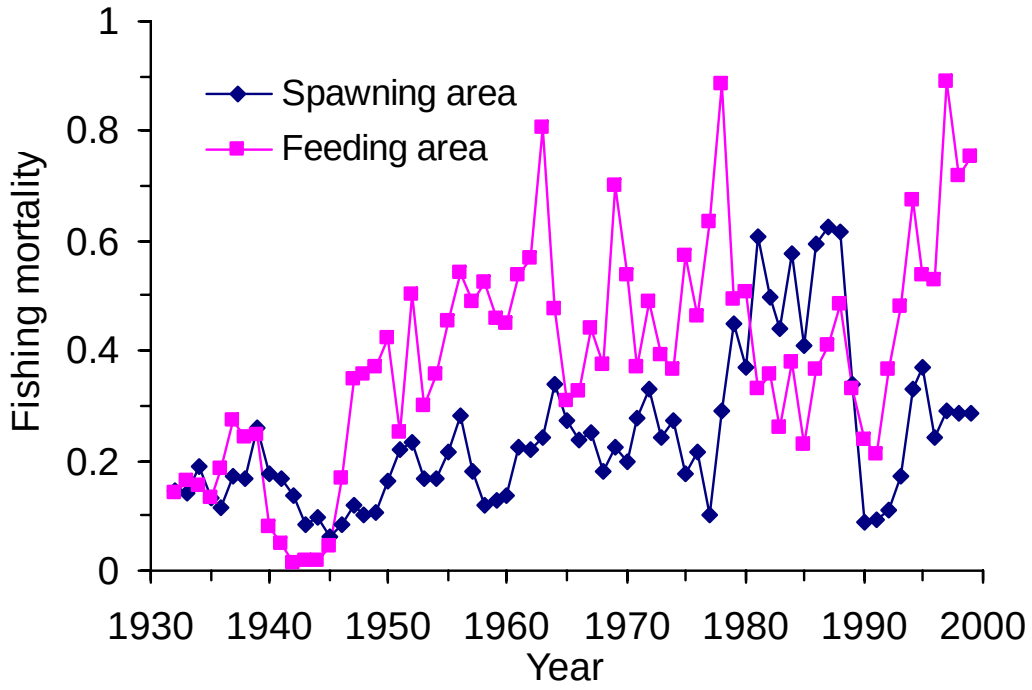
Phenotypic plasticity?

1) Growth has accelerated (”compensatory growth”)
2) Fast-growing cod mature earlier
1) + 2) -> Earlier maturation



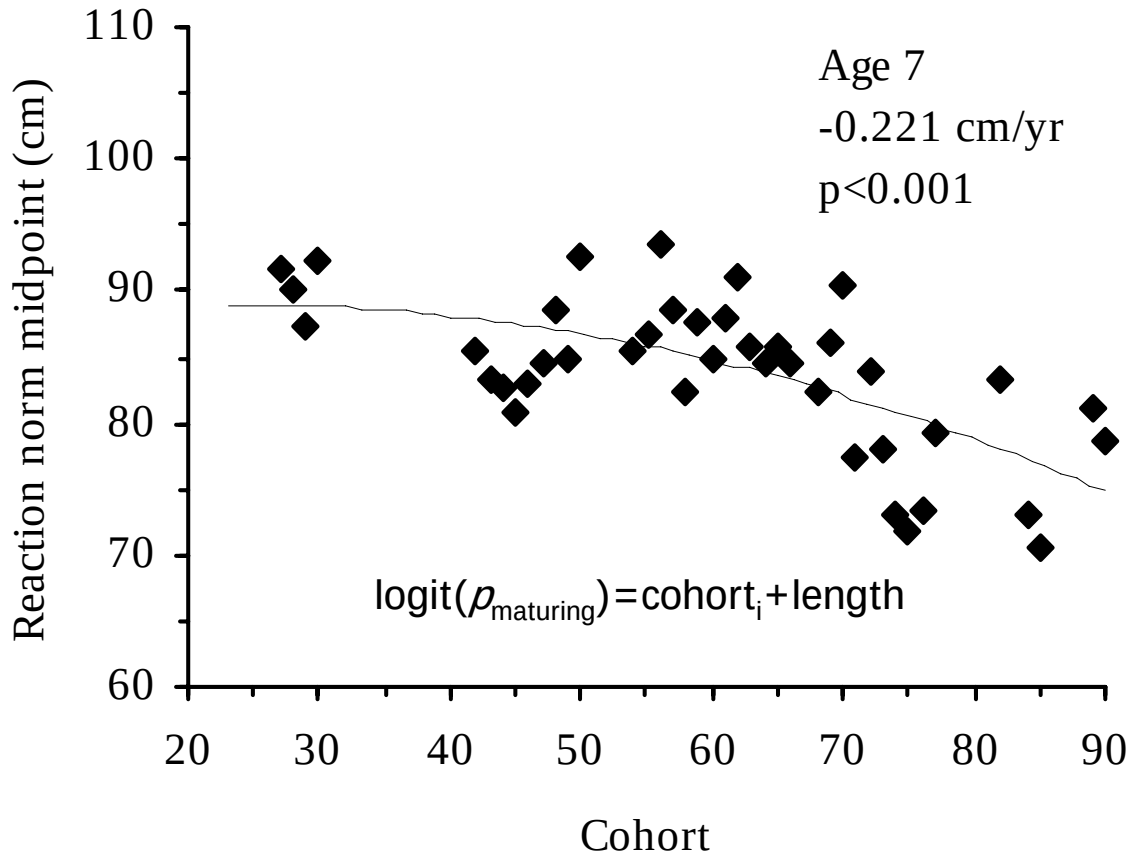
Genetic change?

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



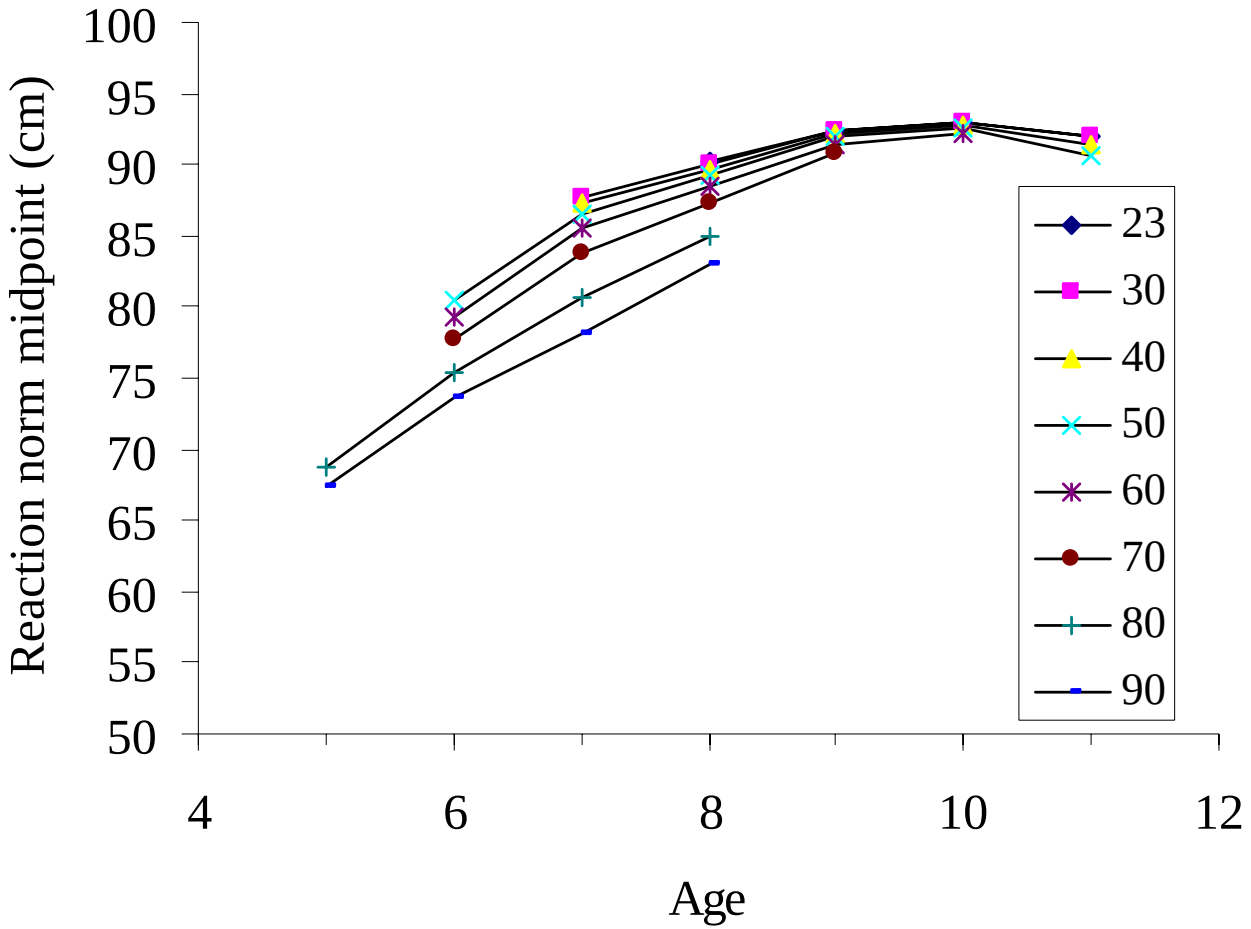
Northeast Arctic cod

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



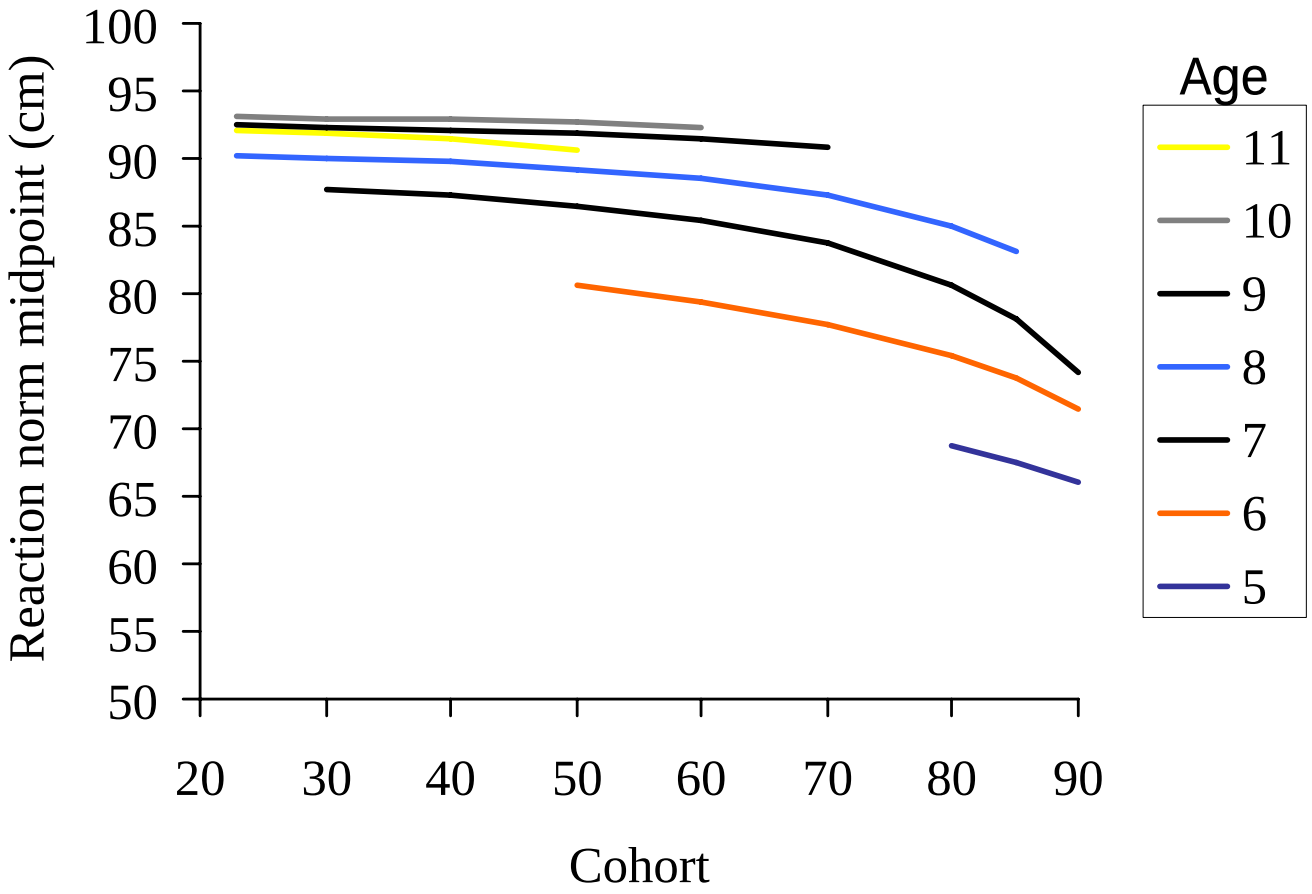
Northeast Arctic cod

Predicted reaction norm midpoints for cohorts 1923-90:



Northeast Arctic cod

Change in the reaction norm midpoints:

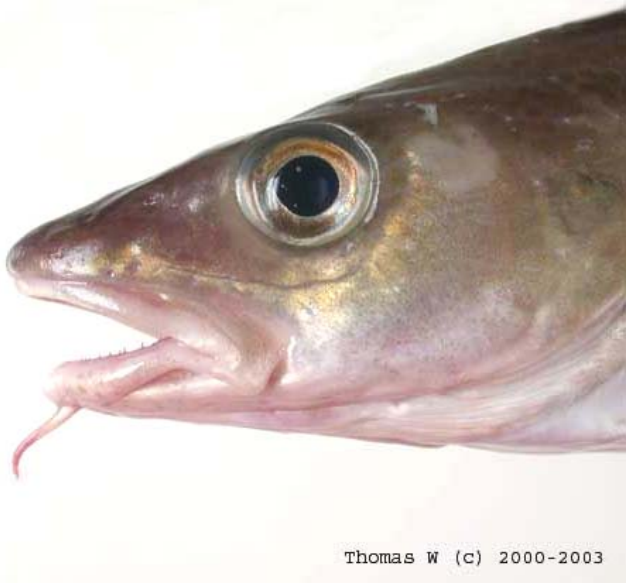


Northeast Arctic cod

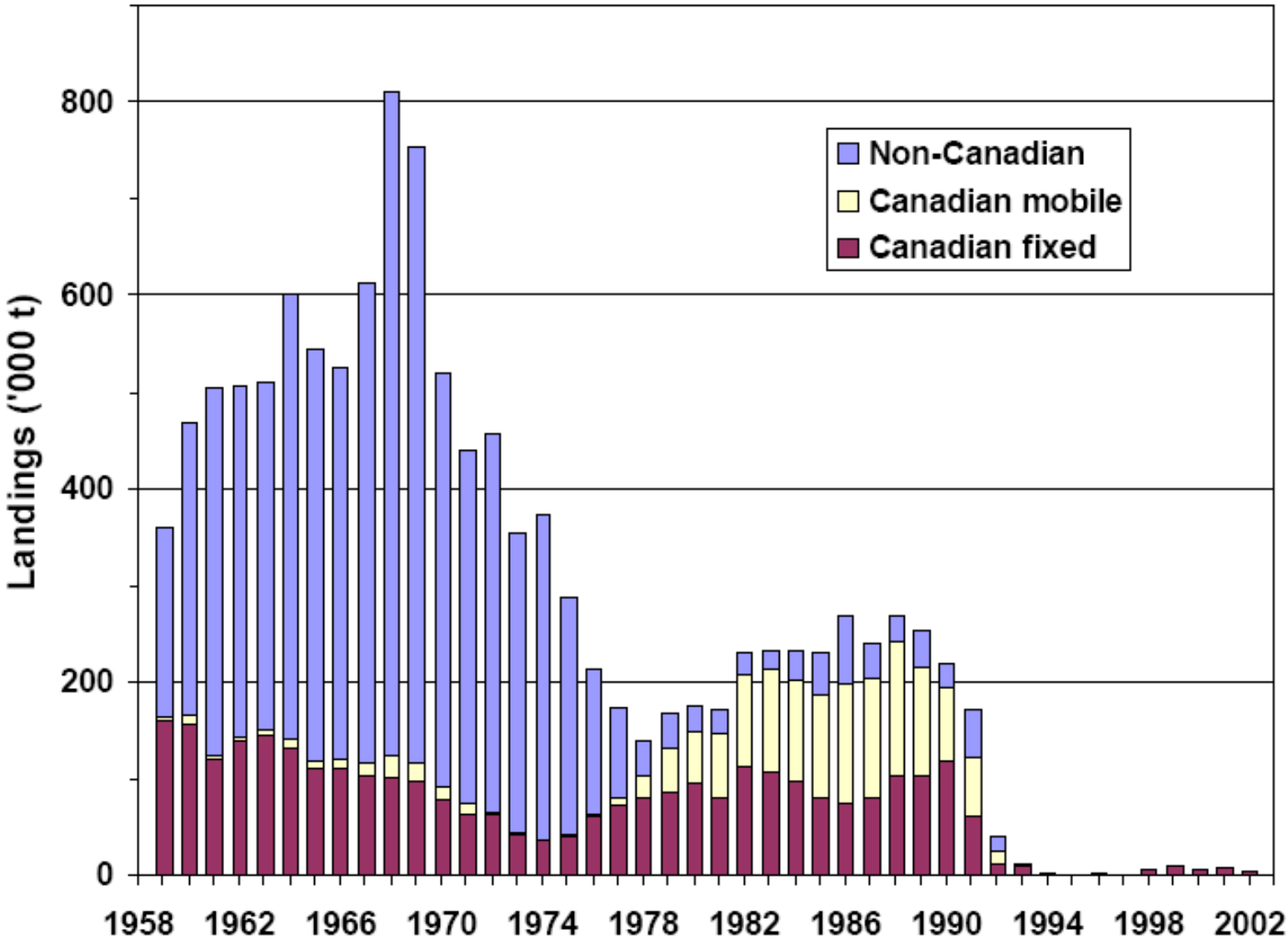
- How much genetics contribute to the change in maturation compared to plasticity?

	Age at maturation	Length at maturation
Change in growth	35 %	-20 %
Change in PMRN	80 %	130 %
Interaction	-15 %	-10 %

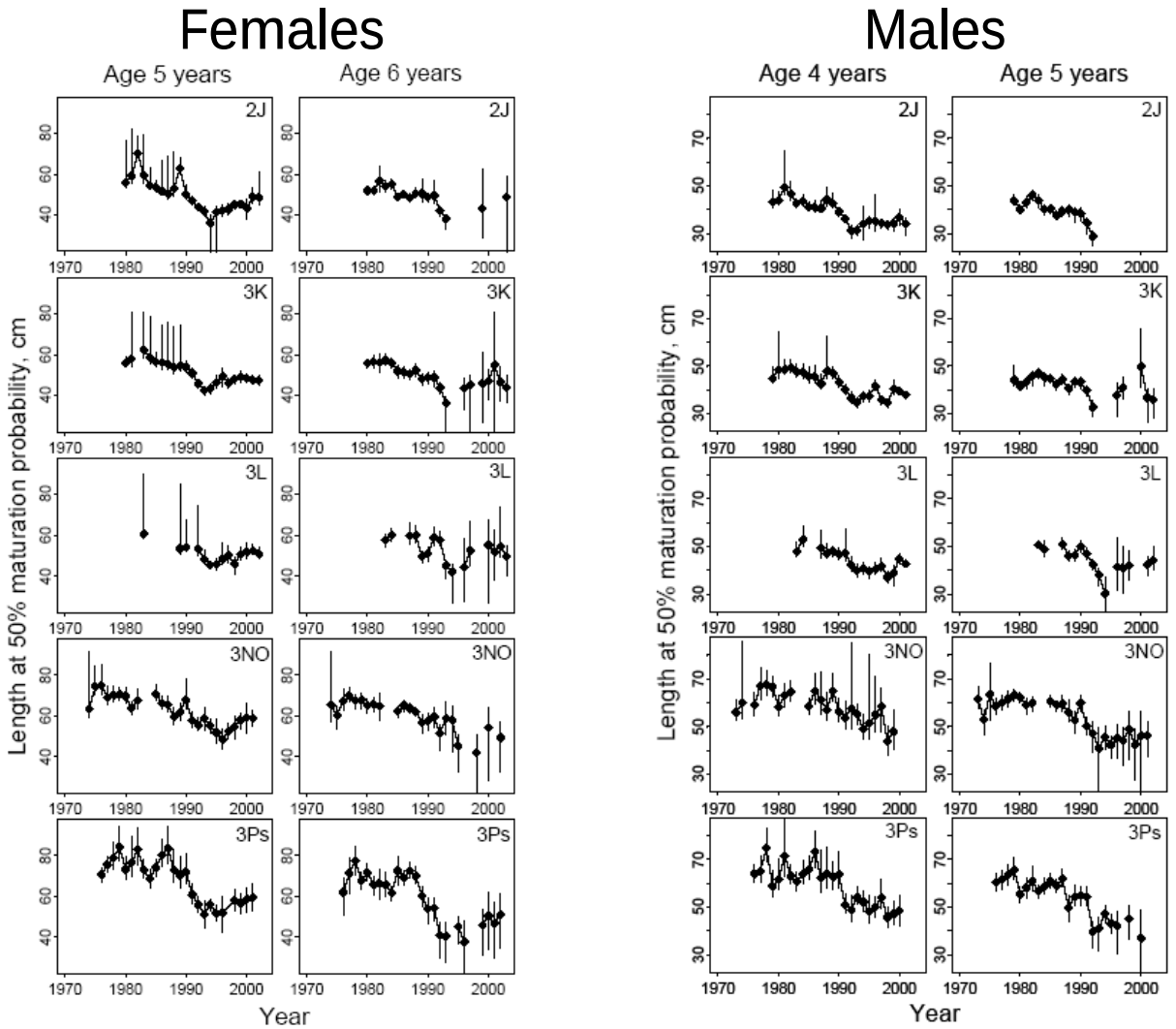
Atlantic cod in Canada

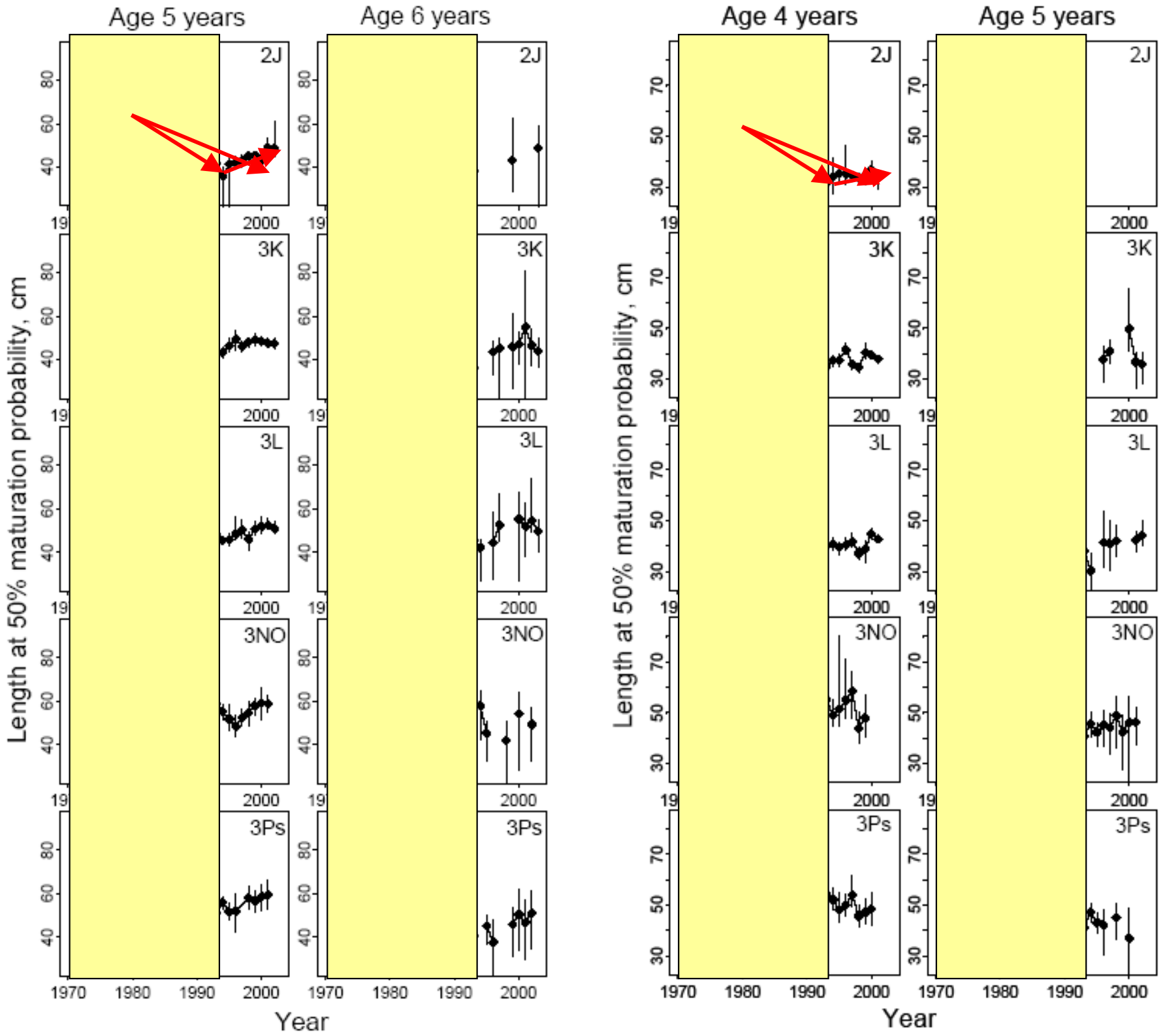


Northern cod



Atlantic cod off Newfoundland–Labrador



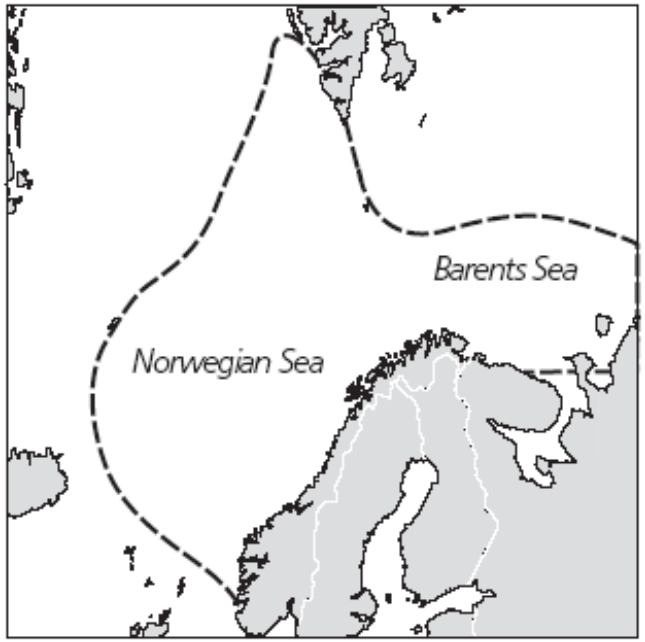

Age 5 years
Age 6 years
Age 4 years
Age 5 years
2J
3K
3L
3NO
3Ps
Length at 50% maturation probability, cm
Year
1970
1980
1990
2000

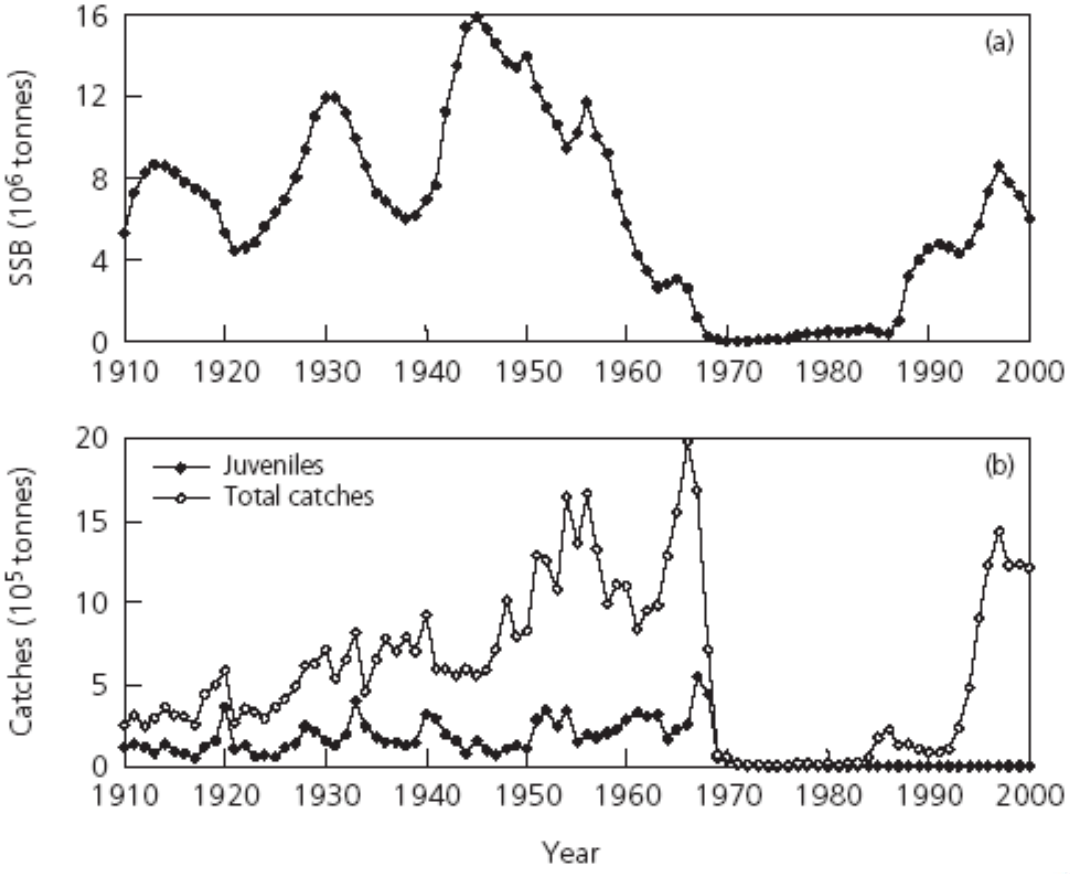
Atlantic cod off Newfoundland–Labrador

- ❑ The stocks have not recovered, despite 10+ years of severe fishing restrictions
- ❑ Is earlier maturation hampering recovery?
- ✓ Hutchings (2005): 25-30% decrease in *r*
- ✓ Large females are superior spawners
- ✓ Possibly faster “recovery” of female compared to male reaction norms – natural selection for maturation at large size is stronger in females?

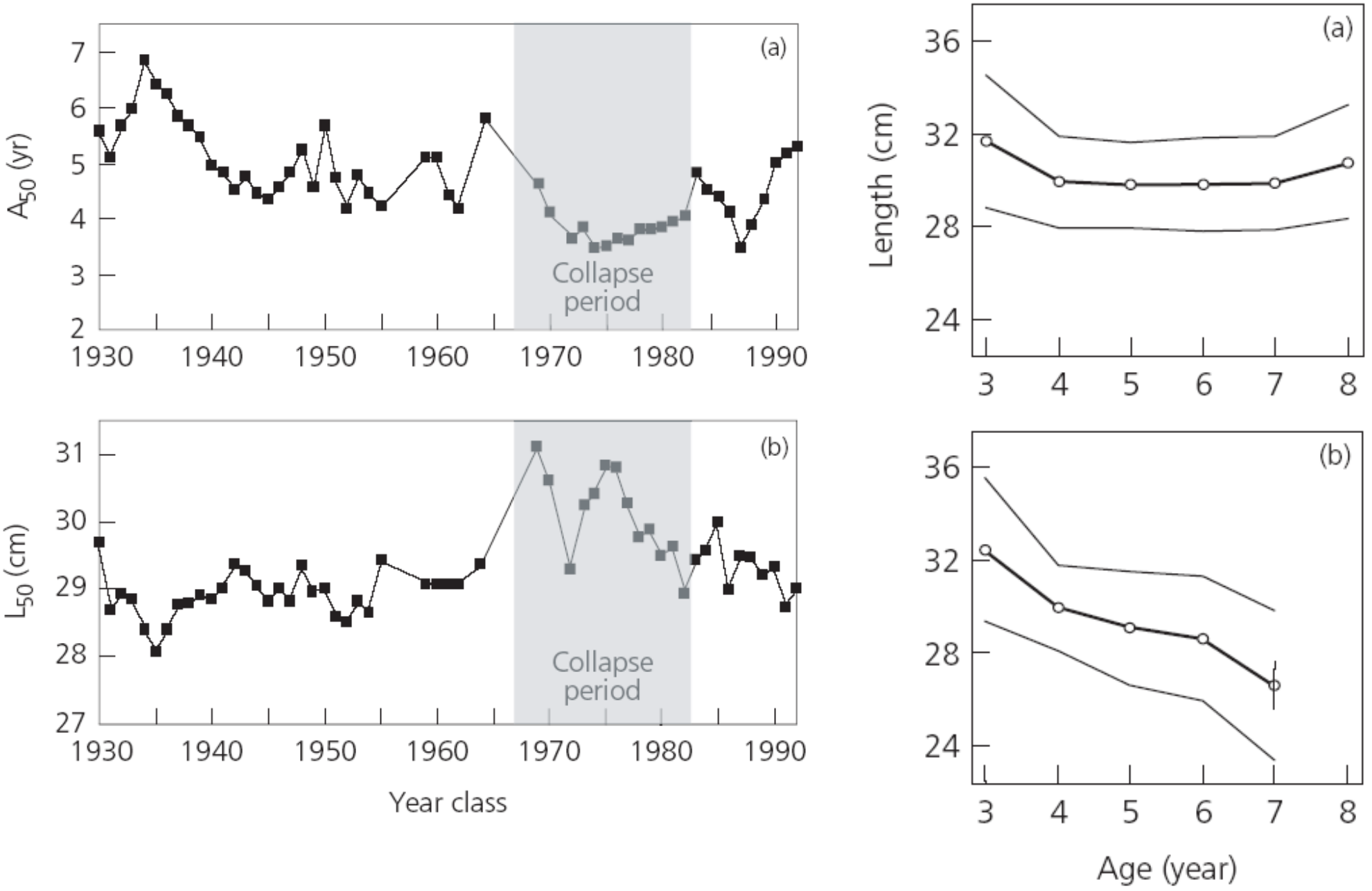
Norwegian spring-spawning herring

“the” fisheries collapse of the 60’s





Thomas W (c) 2000-2003


(a)
A_{50} (yr)
7
6
5
4
3
2
Collapse period
1930
1940
1950
1960
1970
1980
1990
(b)
L_{50} (cm)
31
30
29
28
27
Collapse period
Year class
(a)
Length (cm)
36
32
28
24
3
4
5
6
7
8
(b)
Age (year)

Why herring is an outlier?

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