



INSTITUTE OF MARINE RESEARCH



General life-history theory

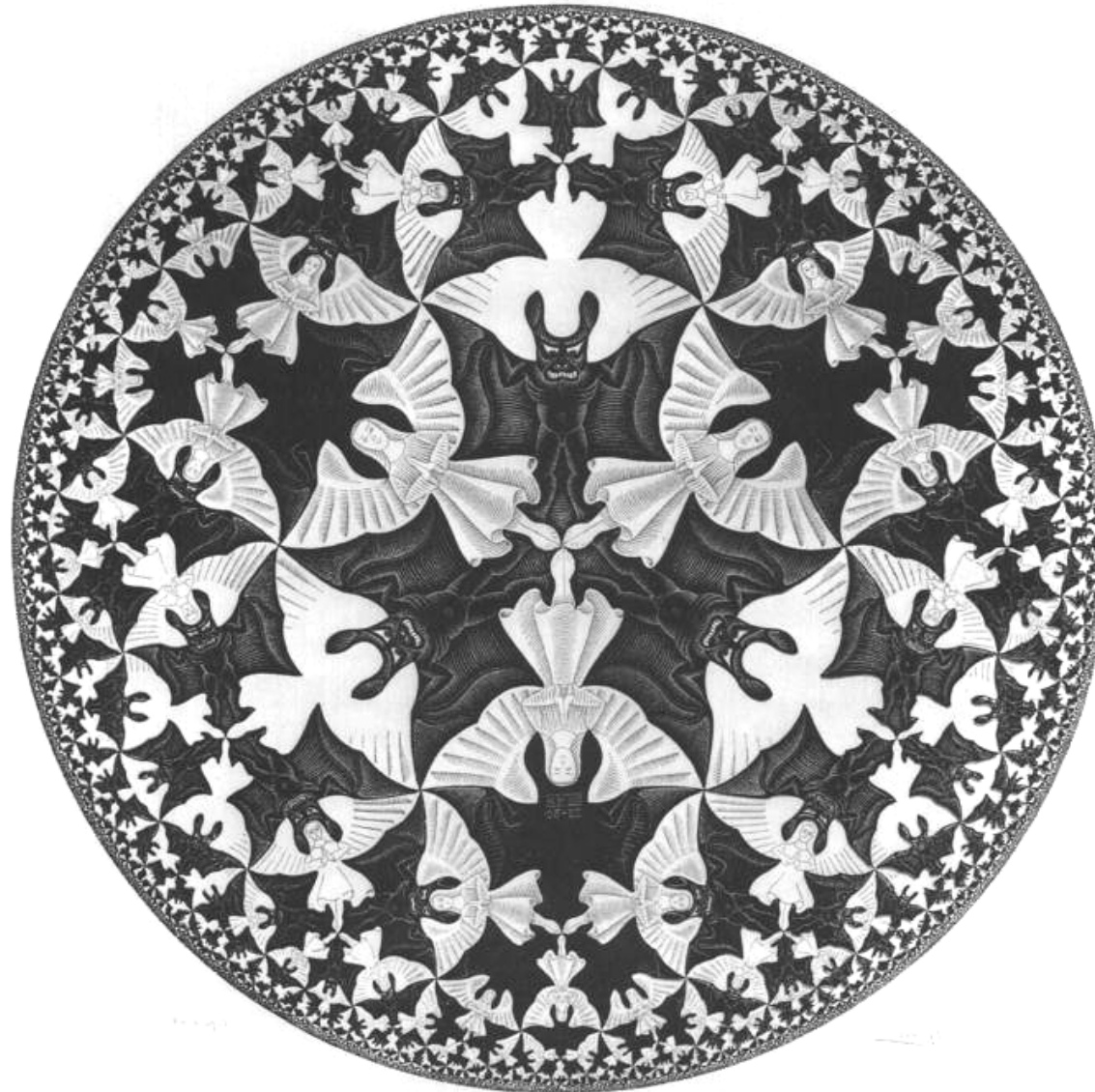
Nordic Marine Academy course on *Modelling marine populations from physics to evolution*
10-16.10.2005 Espesrend, Norway

Outline

- ❑ Definition and the classic setting
- ❑ The classic questions
- ❑ Applications of life history theory in marine context (or lack of)
- ❑ Fisheries-induced life-history evolution



Part I - Basics



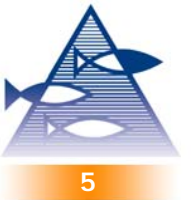
Life history theory

- ❑ ... tries to explain how evolution designs organisms to achieve reproductive success (Stearns 2000)
- ❑ Life history evolution: ... the major features of a life cycle, principally age distribution of birth and death rates, growth rates, and the size of offspring (Stearns 1992)
- ❑ Understanding origin and maintenance of life history diversity (Roff 1992)
- ❑ *Understanding*, not mere description – the field has always been very much influenced by modelling & theory!



Life history theory

- Life-history traits
 - Age and size at maturation, reproductive effort, offspring size, growth, ...
 - Mostly single traits, occasionally vector/function-valued traits (reaction norms)
- It is assumed that evolution “optimises” life histories, respecting trade-offs and constraints that determine what is feasible
- Evolutionary optimality used to refer to trait maximising a fitness measure – nowadays optimality mostly refers to unbeatability



Euler-Lotka equation

- Original, continuous time

$$\int_{\alpha}^{\omega} l_x m_x e^{-rx} dx = 1 \quad \left[\text{or } \int_{\alpha}^{\omega} l_x m_x \lambda^{-x} dx = 1 \right]$$

- Discrete time equivalent

$$\sum_{\alpha}^{\omega} l_x m_x e^{-rx} = 1 \quad \left[\text{or } \sum_{\alpha}^{\omega} l_x m_x \lambda^{-x} = 1 \right]$$

- l_x = survival to age x , m_x = fecundity at age x ,
 r = intrinsic rate of increase



Euler-Lotka equation

- ❑ Intrinsic rate of increase r gives population's instantaneous growth rate, once it has reached stable age distribution
- ❑ Thus, for viable populations necessarily $r \geq 0$
- ❑ Classic thinking ("optimisation paradigm"): population (type) that has the highest r will eventually outnumber its competitors $\rightarrow r$ as a fitness measure



Cole's paradox (1954)

- ❑ A semelparous annual plant produces b offspring that survive until next season and dies
- ❑ An immortal iteroparous plant produces b^* offspring that survive until next season
- ❑ Which one takes over?



	Annual		Perennial	
x	l_x	m_x	l_x	m_x
1	1	b	1	b^*
2	0		1	b^*
		

$$\sum_{x=1}^{\omega} l_x m_x e^{-rx} = b e^{-r} = 1$$

$$\Rightarrow r = \ln(b)$$

$$\sum_{x=1}^{\omega} l_x m_x e^{-rx} = b^* e^{-r} + b^* e^{-2r} + b^* e^{-3r} + \dots = 1$$

$$\Leftrightarrow b^* e^{-r} (1 + e^{-r} + e^{-2r} + \dots) = 1$$

$$\Leftrightarrow b^* e^{-r} \frac{1}{1 - e^{-r}} = 1$$

$$\Rightarrow r = \ln(b^* + 1)$$



Why do perennials exist?

$$r_{annual} > r_{perennial} \text{ if } b > b^* + 1$$

- ❑ Thus, annuals are at advantage if they can produce just one more offspring
- ❑ As annuals avoid investment to survival after maturity, this should be easily achieved
- ❑ How come there are perennials?



	Annual		Perennial	
x	l_x	m_x	l_x	m_x
1	p_0	b	p_0	b^*
2	0		$p_0 p_1$	b^*
			$p_0 p_1^2$...

- ❑ Gadgil & Bossert (1970): newborn survival $p_0 < 1$ favours perennials
- ❑ Charnov & Schaffer (1973):
annuals favoured if $b > b^* + p_1/p_0$
- ❑ What about density dependence?

A simpler alternative?

Reproductive ratio

- A.k.a. basic reproductive number, expected lifetime reproductive success
- Continuous time

$$R_0 = \int_{\alpha}^{\omega} l_x m_x dx$$

- Discrete time equivalent

$$R_0 = \sum_{\alpha}^{\omega} l_x m_x$$



A simpler alternative?

Reproductive ratio

- R_0 gives population's growth *ratio* on generation basis
- Thus, for viable populations necessarily $R_0 \geq 1$
- An alternative fitness measure?
- While $r = 0 \Leftrightarrow R_0 = 1$ $r_1 > r_2$ does not necessarily mean $R_{0,1} > R_{0,2}$



	Annual			Perennial	
x	l_x	m_x		l_x	m_x
1	p_0	b		p_0	b^*
2	0			p_0p_1	b^*
				$p_0p_1^2$...

$$R_0 = \sum_{\alpha}^{\omega} l_x m_x = p_0 b$$

$$R_0 = \sum_{\alpha}^{\omega} l_x m_x = p_0 b^* + p_0 p_1 b^* + p_0 p_1^2 b^* + \dots$$

$$\Leftrightarrow R_0 = p_0 b^* (1 + p_1 + p_1^2 + \dots)$$

$$\Rightarrow R_0 = p_0 b^* \frac{1}{1 - p_1}$$

A new paradox?

- ❑ Assuming that R_0 is the proper fitness measure, annuals favoured if $b > b^* / (1 - p_1)$
- ❑ Assuming that r is the proper fitness measure, annuals favoured if $b > b^* + p_1 / p_0$
- ❑ Both results cannot be true!
- ❑ Conventional wisdom: use r in increasing and R_0 in stationary populations



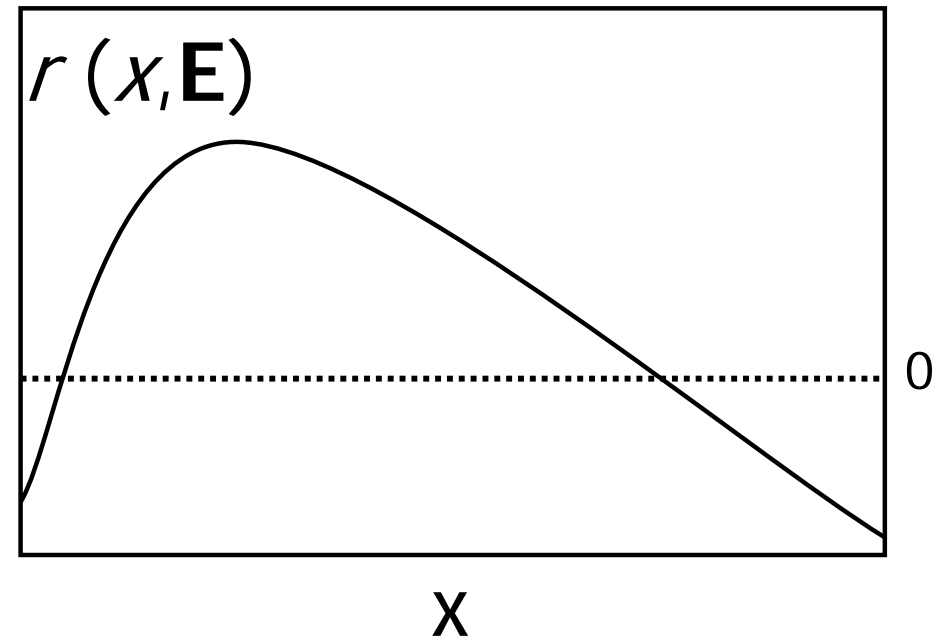
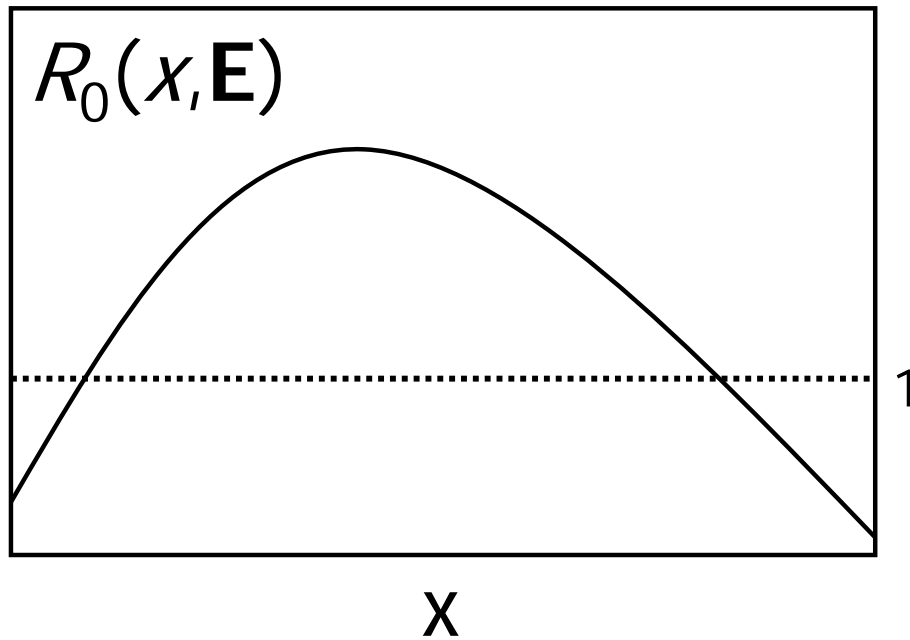
Another paradox?

- ❑ In the long run, viable populations cannot be neither growing nor decreasing, on average: $r = 0$ and $R_0 = 1$
- ❑ What to optimise when the fitness measures are so constrained?

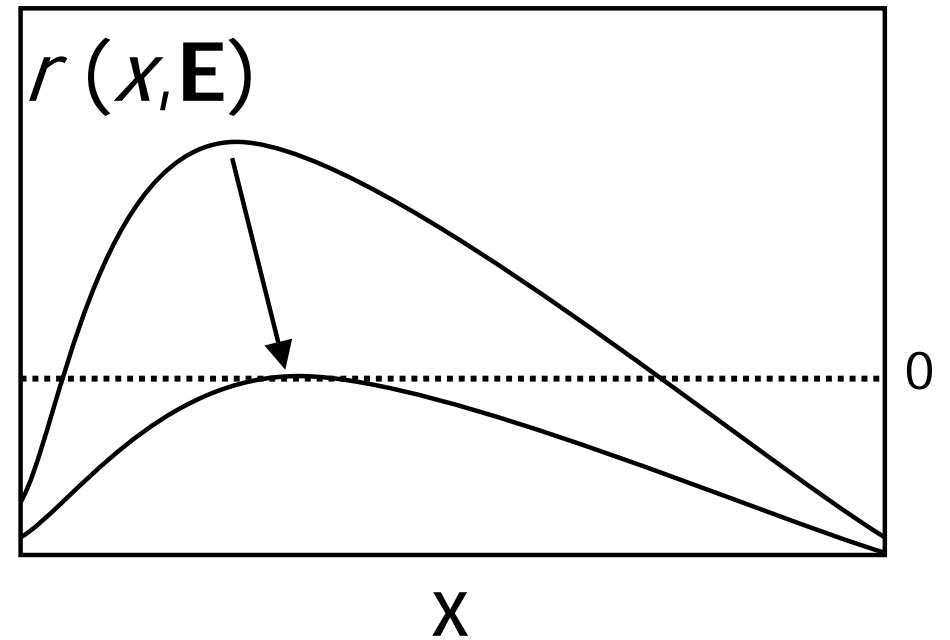
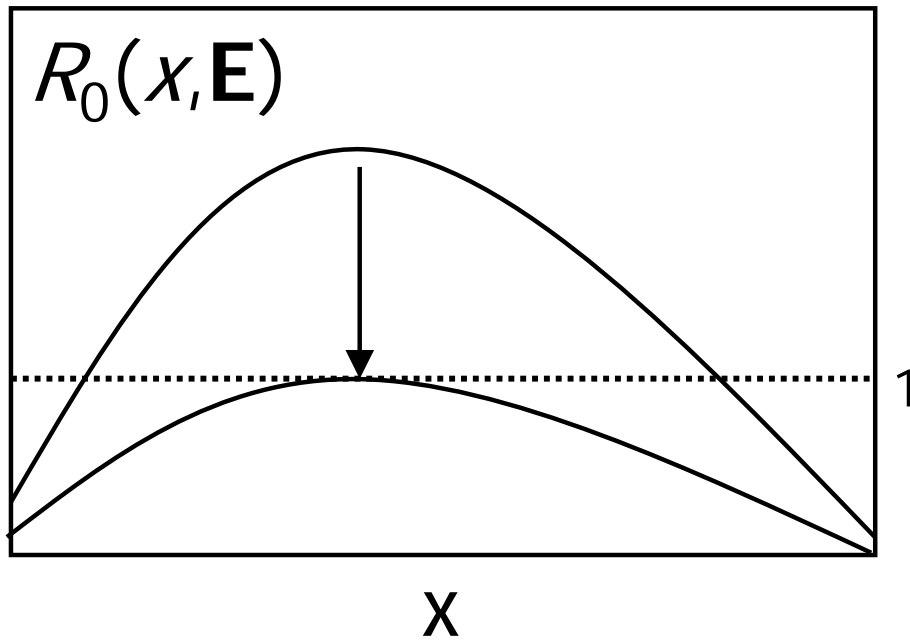
Solution

- ❑ Source of problems: population feedbacks ignored
- ❑ Tool: ESS/invasion analysis (=adaptive dynamics)
- ❑ Solution: it all depends on how feedback work [Mylius & Diekmann, 1995]

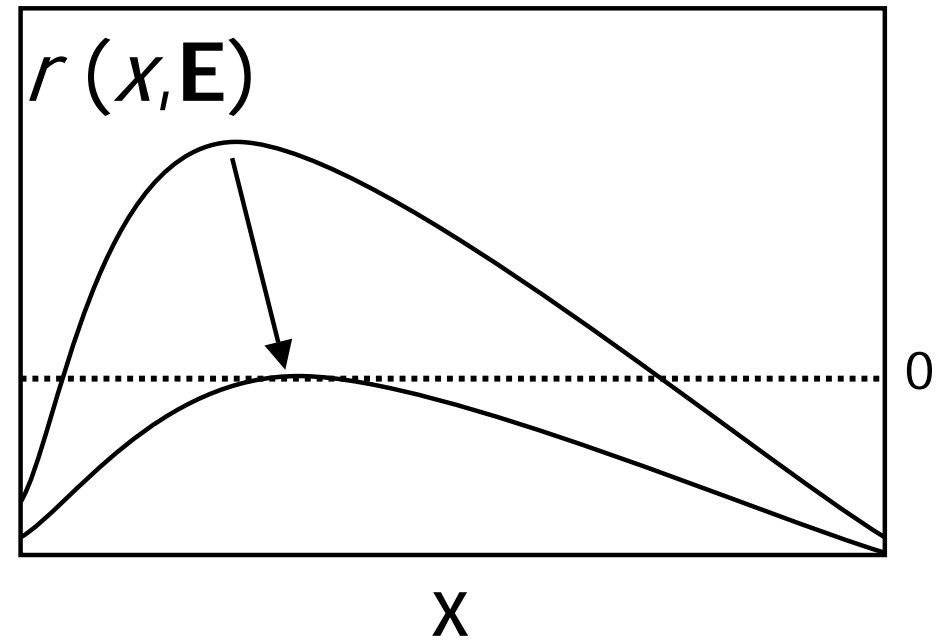
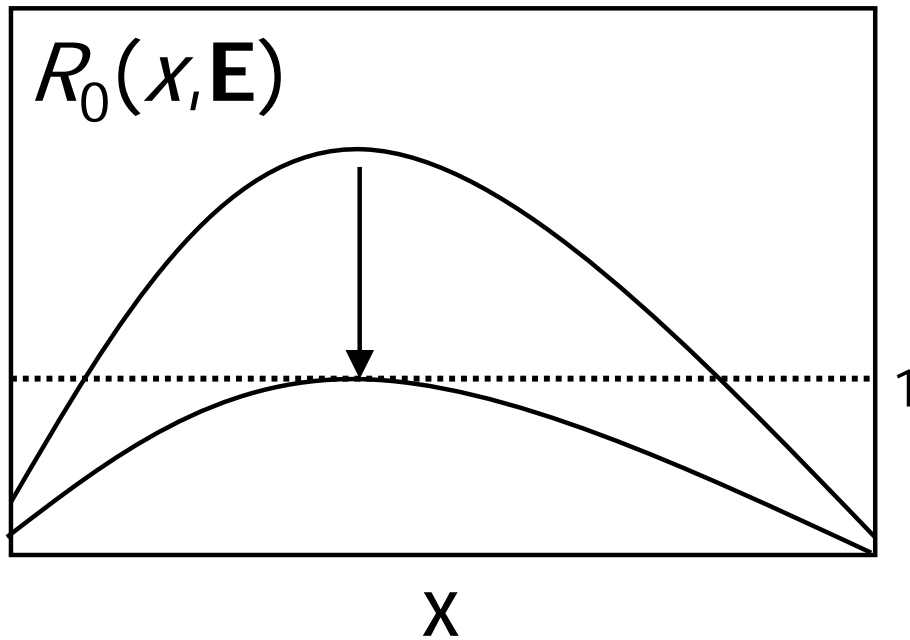




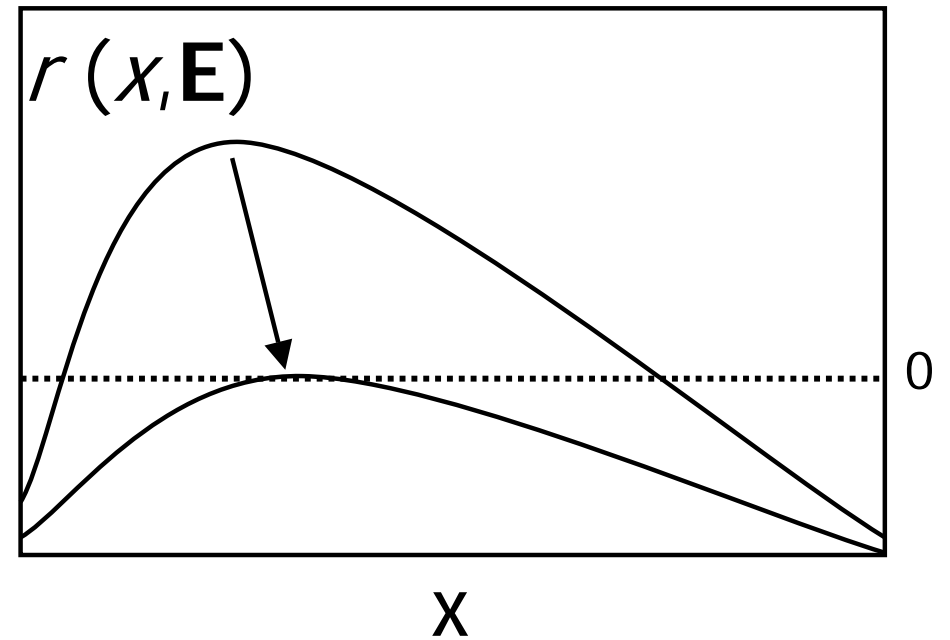
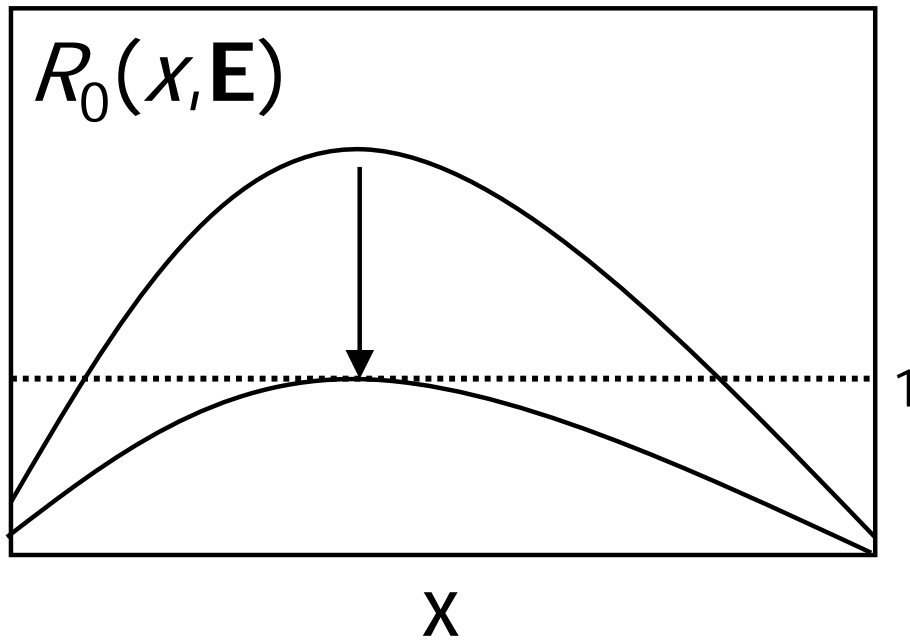
- ❑ Think that we evaluate a fitness measure in a specific environment \mathbf{E}_v as functions of the evolving trait x , e.g., $r(x, \mathbf{E}_v)$ or $R_0(x, \mathbf{E}_v)$
- ❑ The optimisation paradigm suggests that this gives you the evolutionarily optimal trait (but does not tell you which fitness measure to use)



- The effect of density-dependence is to reduce r and R_0 until the maximum value is exactly $r = 0$ and $R_0 = 1$ – the ecological equilibrium
- Then the maxima of these fitness measures correspond to exactly the same trait value – this never happens otherwise

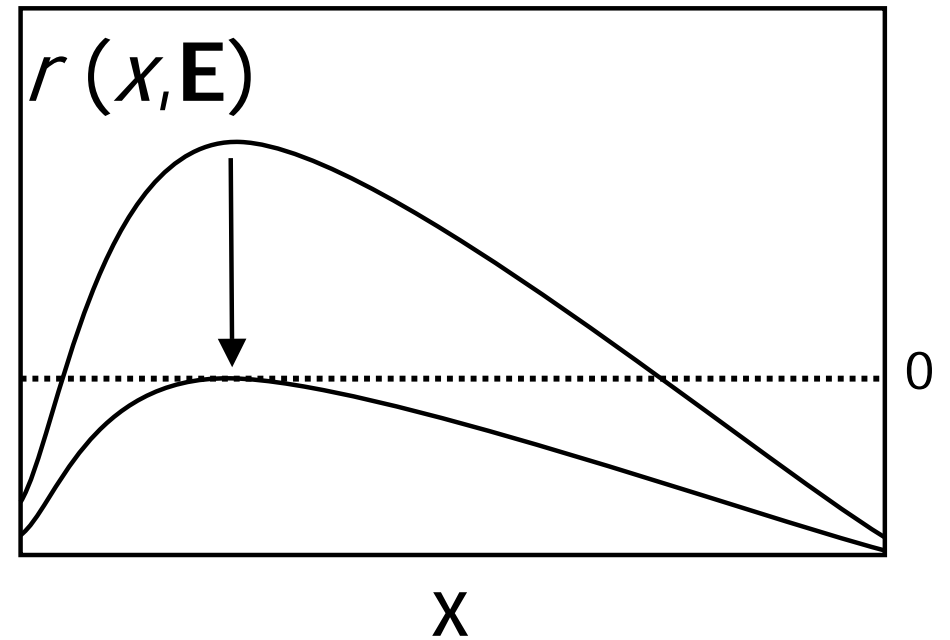
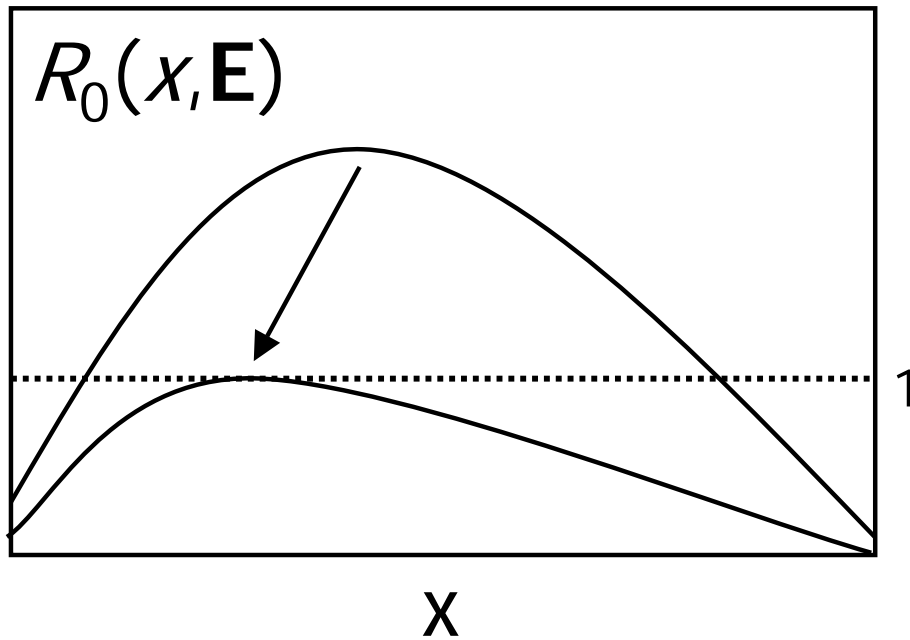


- ❑ Generally, the effect of density dependence is to change both the shape and level of the fitness curve
- ❑ Therefore, “optimal” trait in one specific environment will usually not correspond to the optimum in the ecological equilibrium
- ❑ Thus, optimisation paradigm is generally not expected to work



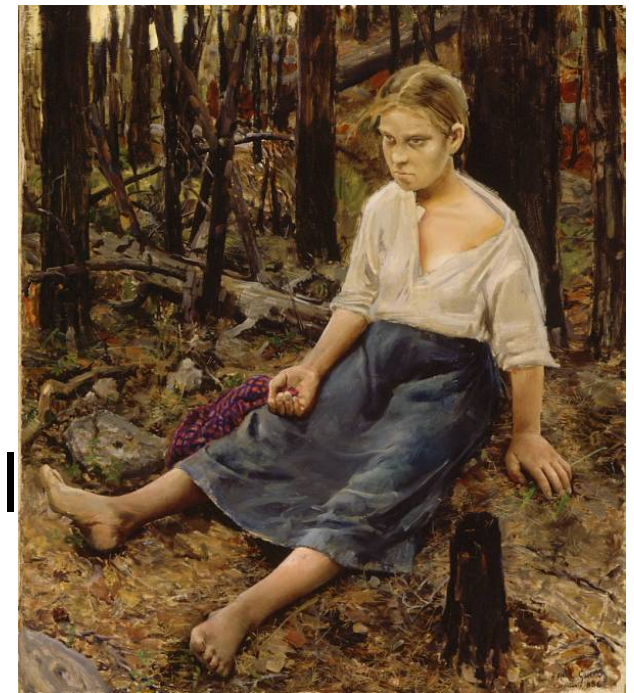
- ❑ However, there are notable exceptions!
- ❑ If density dependence acts such as to affect reproductive success multiplicatively ($R_0(x, \mathbf{E}) = f(\mathbf{E}) R_0(x, \mathbf{E}_v)$), the shape of $R_0(x, \mathbf{E})$ is independent of \mathbf{E}
- ❑ In this case, optimising $R_0(x, \mathbf{E})$ in just any specific \mathbf{E} will give the evolutionary optimum.
- ❑ In this case, optimising $r(x, \mathbf{E})$ will not work



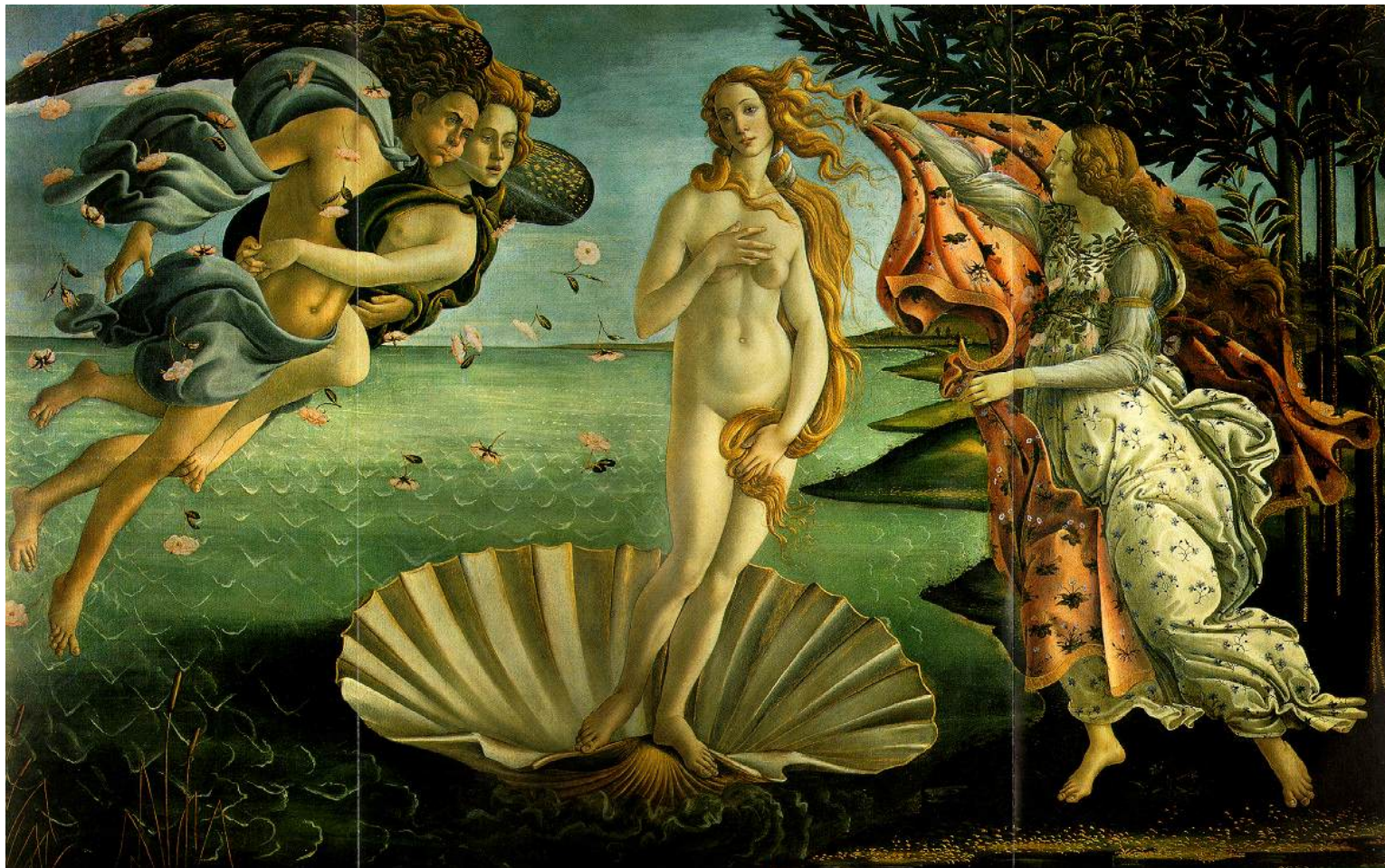


- If density dependence acts such as to affect mortality rate uniformly across all ages, the shape of $r(x, \mathbf{E})$ is independent of \mathbf{E}
- In this case, optimising $r(x, \mathbf{E})$ in just any specific \mathbf{E} will give the evolutionary optimum.
- In this case, optimising $R_0(x, \mathbf{E})$ will not work

- ❑ Optimising r or R_0 in a specific environment is valid, but implies specific assumptions on density dependence
- ❑ Theory guarantees that for 1-dimensional environmental feedback (...), there always exists a valid fitness measure, optimising which in just any environment gives you the evolutionary optimum
- ❑ Theory also guarantees that for 1-dimensional environmental feedback, no robust polymorphisms are possible
- ❑ For >1 -dimensional environmental feedback, simple optimisation will not work

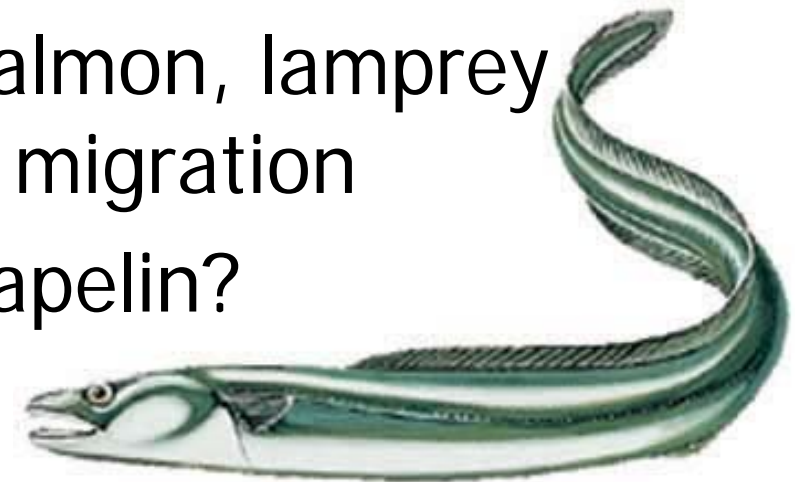


Classic questions

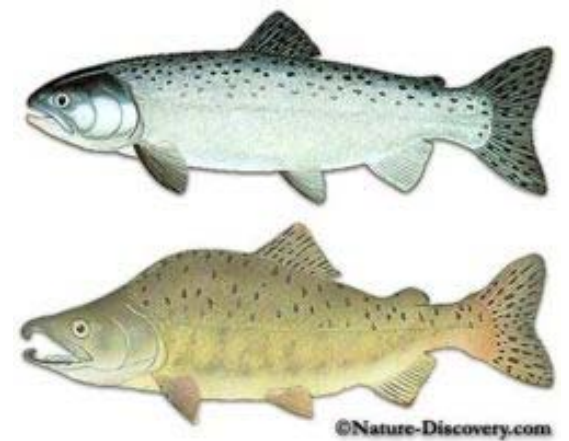


Semelparity vs. iteroparity

- ❑ Cole's paradox
- ❑ Annuals win if $b > b^* / (1 - p_1)$ [max of R_0]
- ❑ Iteroparity – don't put all eggs in one basket
- ❑ Fish examples: eels, Pacific salmon, lamprey
= species with long spawning migration
- ❑ Atlantic silverside (annual), capelin?

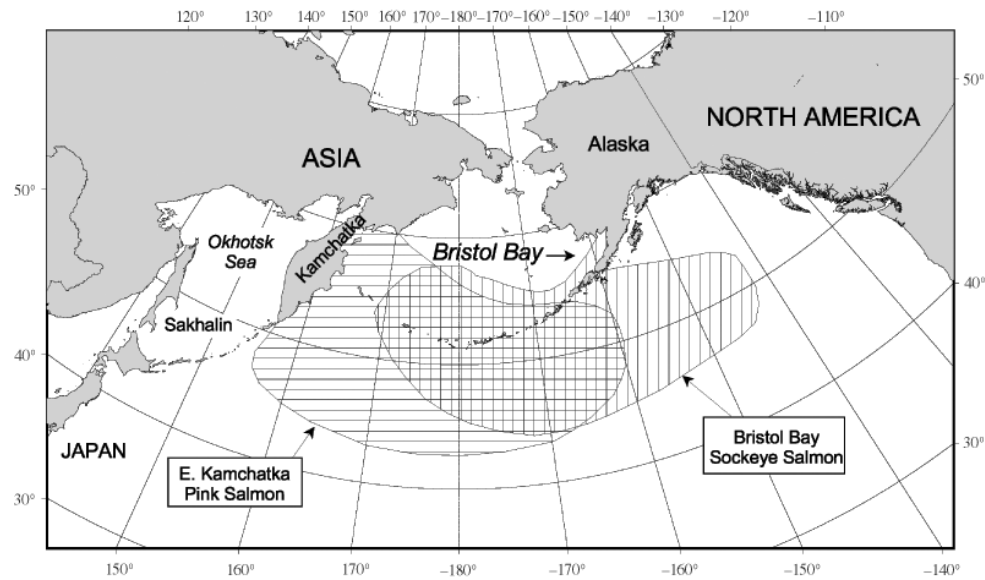


Pink salmon

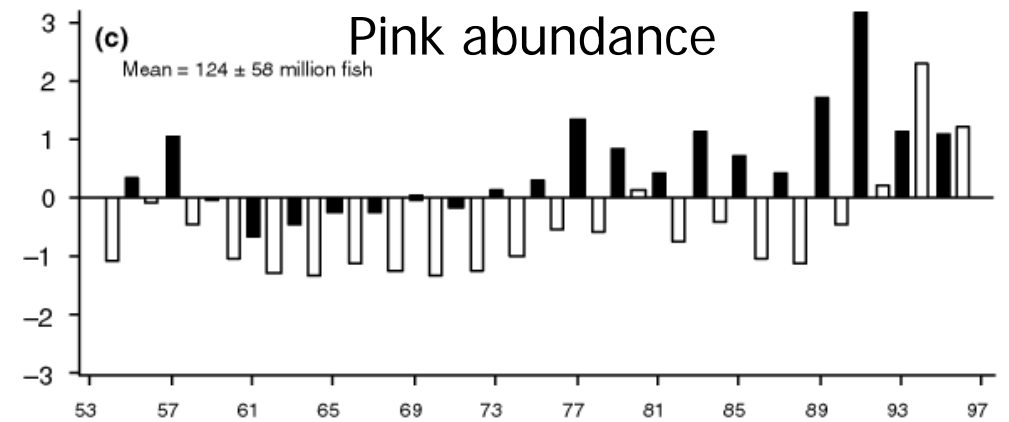
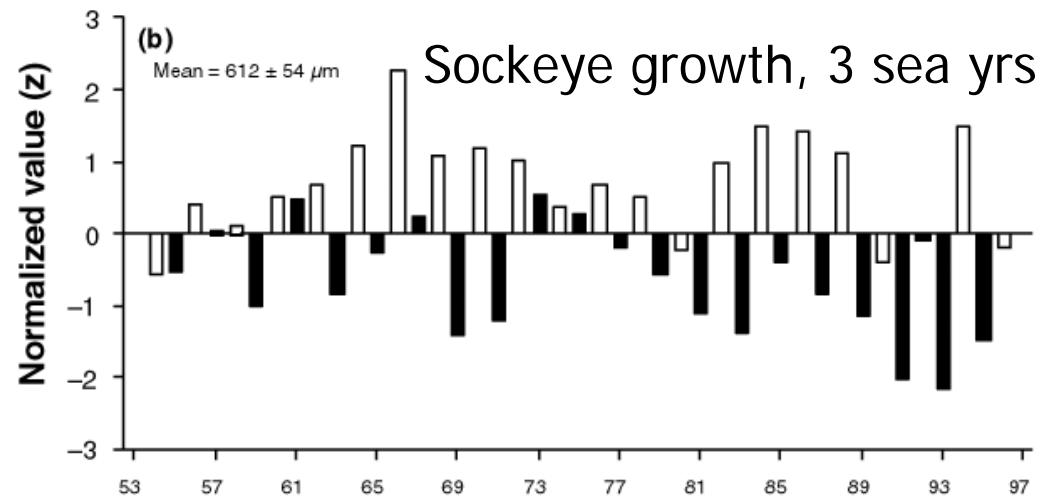
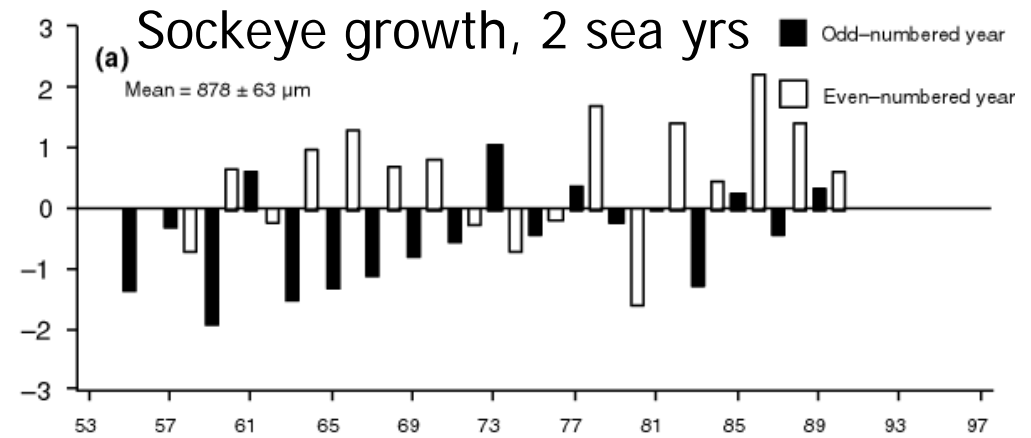


- Semelparous, maturing always at age 2 years
- Isolated odd and even year populations spawning in the same river, often with different abundance
- Large-scale synchrony
- Straying as a risk spreading strategy?



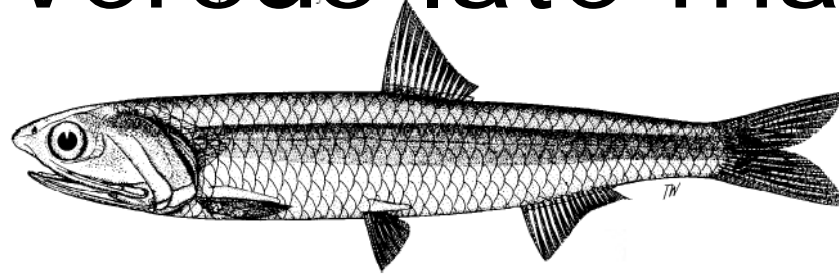


□ Abundance of Asian pink salmon affects life history of Alaskan sockeye salmon



Year at sea

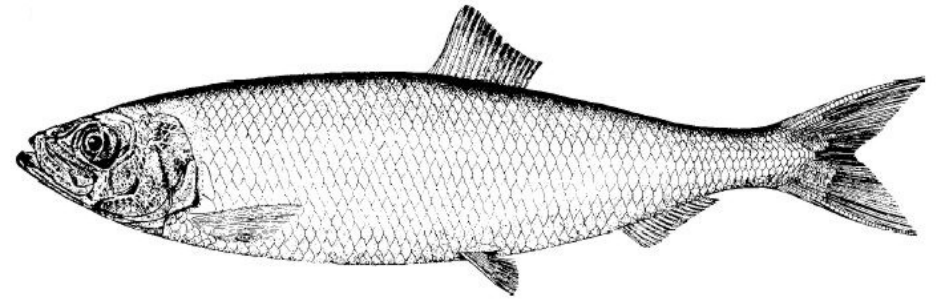
Early versus late maturation



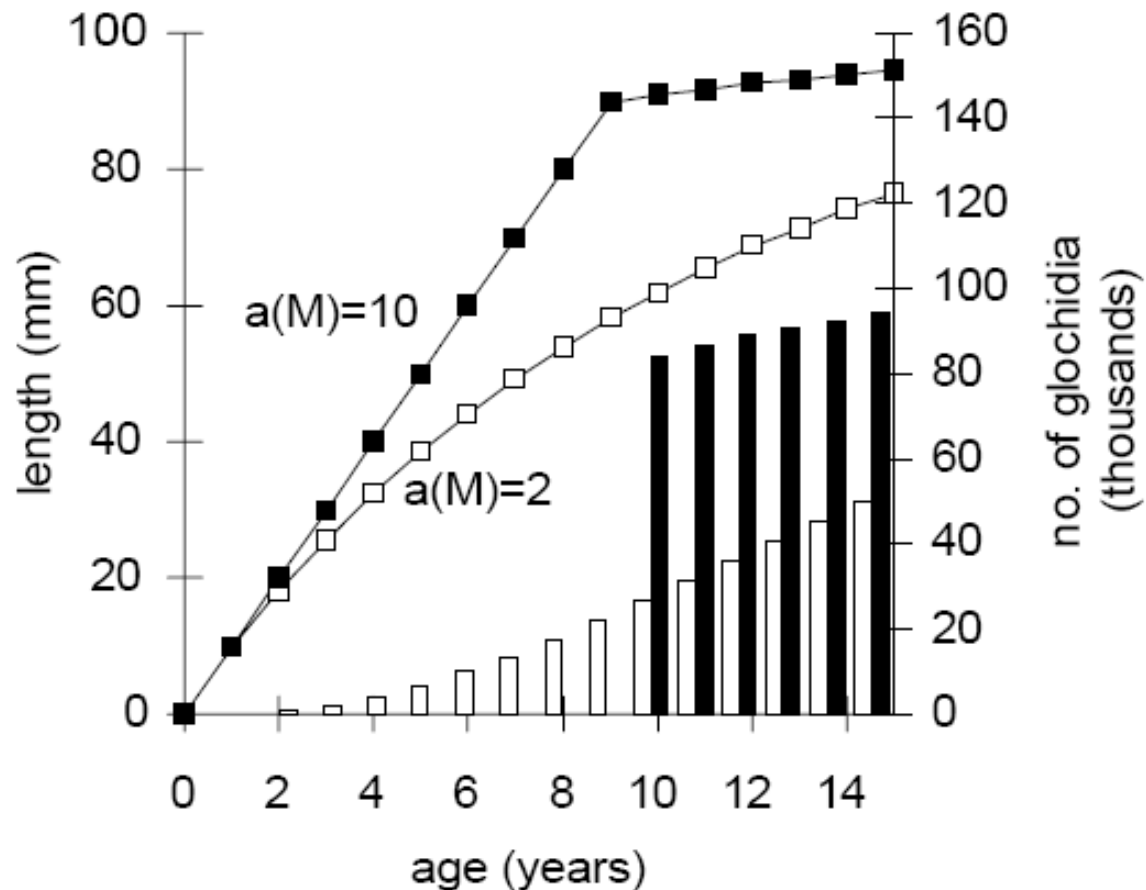
Anchovy: 1 year

Herring: 3-8 years

Orange roughy: 20 years (?)



Early versus late maturation



- ❑ For fish-like life history, age at maturation has major impact on later demography

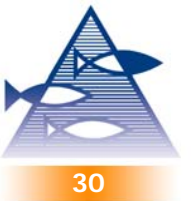
Early versus late maturation

□ Benefits of early maturation

- Higher chance of reaching maturation

□ Benefits of late maturation

- Larger size at a given age (access to a larger range of prey; growing over vulnerable size range)
- Larger size gives higher fecundity, once mature



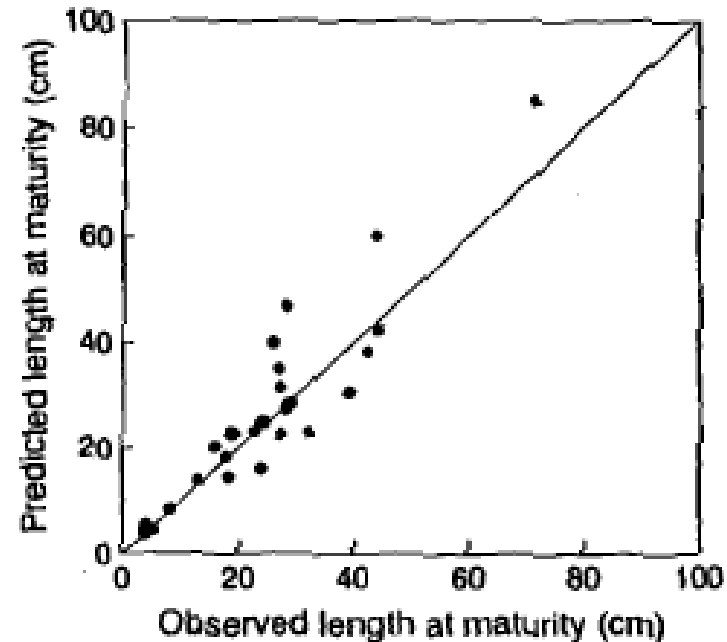
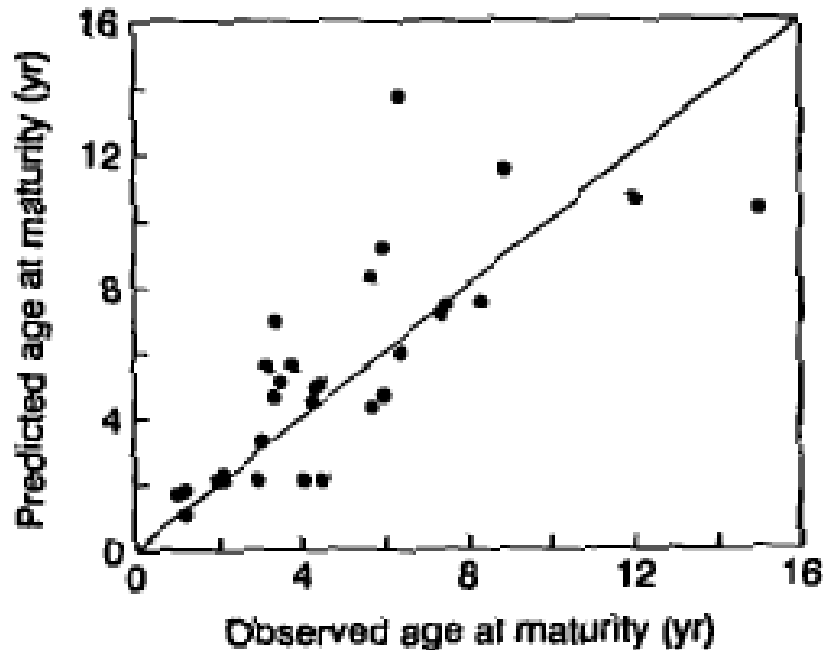
Details matter: age-, size- vs. state-dependent mortality

Type of mortality	Mortality among	
	small/young/immature	large/old/mature
unstructured	↓	↓
size-dependent	↑, ↓, or ⇕	↓
age-dependent	↓ or ⇕	↓
maturation	↓	↑

Courtesy Anna Gårdmark & Ulf Dieckmann, unpubl.



... but not all details

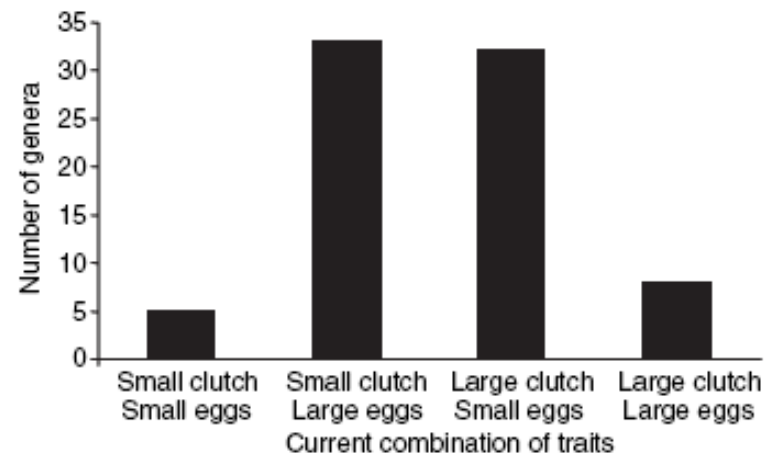


- ❑ Data from 30 species of fish (k , M , a_{mat})
- ❑ Simple model assuming determinate growth and maximisation of R_0
- ❑ Results probably driven by mortality



Size versus number of offspring

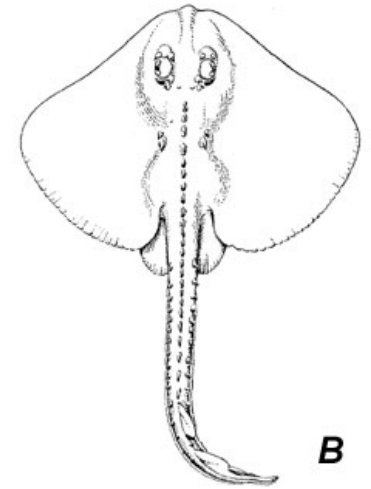
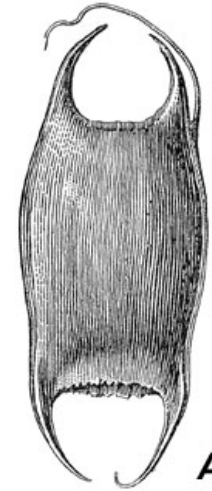
- Simple energetic trade-off: many small or few large offspring



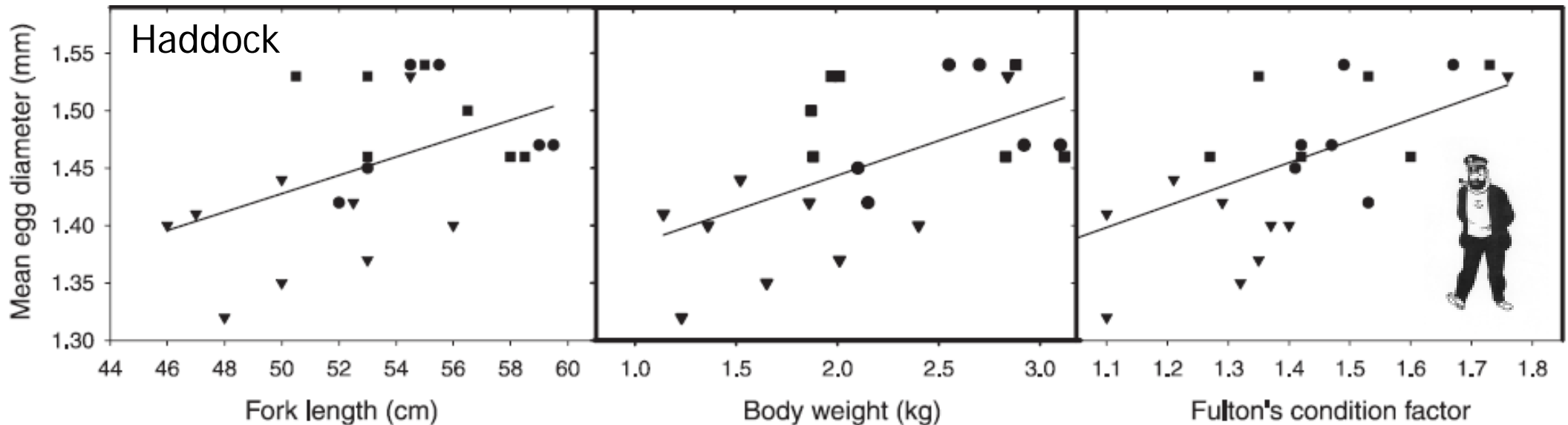
Clutch and egg size in cichlids

Size versus number of offspring

- ❑ Whales: 1
- ❑ Elasmobranchs: few-
some tens
- ❑ Many fish and bivalves:
~10-100 thousand
- ❑ Ocean sunfish: 300
million



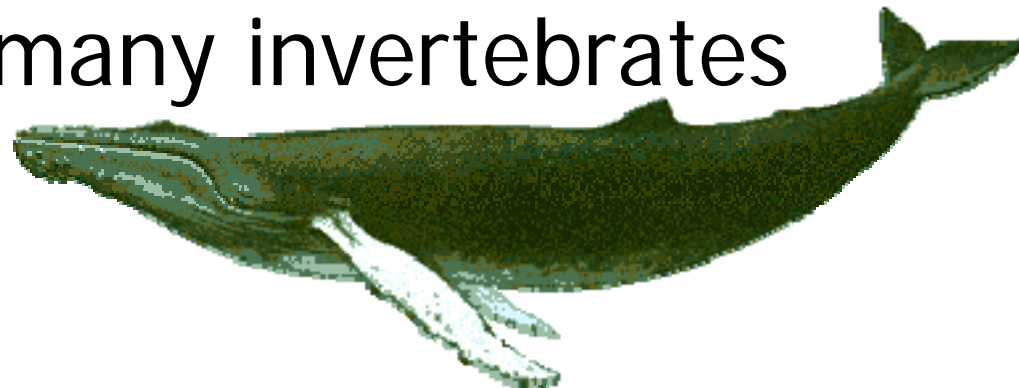
Within-species variation



- In fish, egg size ~ larval fitness
- In fish, egg size often shows adaptive (?) plasticity

Determinate vs. indeterminate growth

- ❑ Indeterminate growth: growth continuing past maturation
- ❑ Indeterminate growth: cold-blooded vertebrates, many invertebrates (e.g., molluscs, crustaceans)
- ❑ Determinate growth: warm-blooded vertebrates, many invertebrates



Indeterminate growth is paradoxical in view of simple models

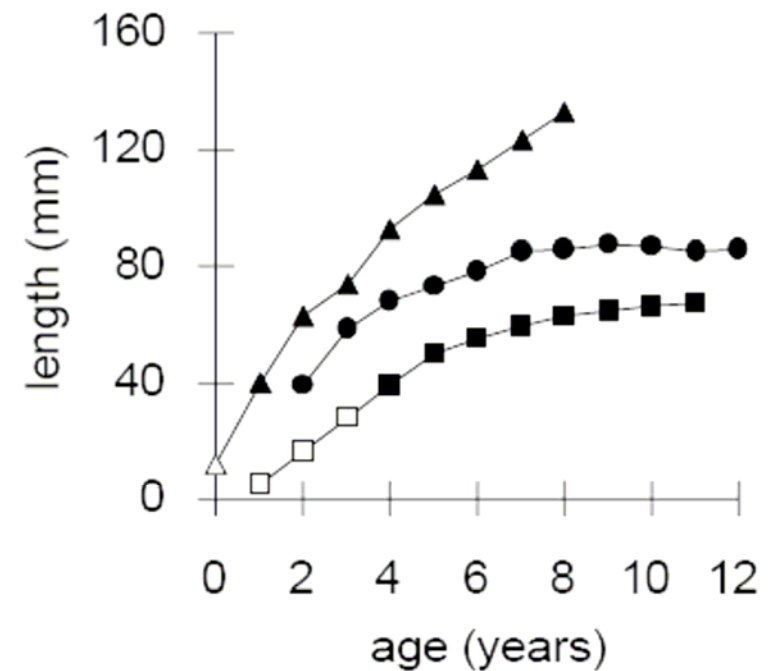
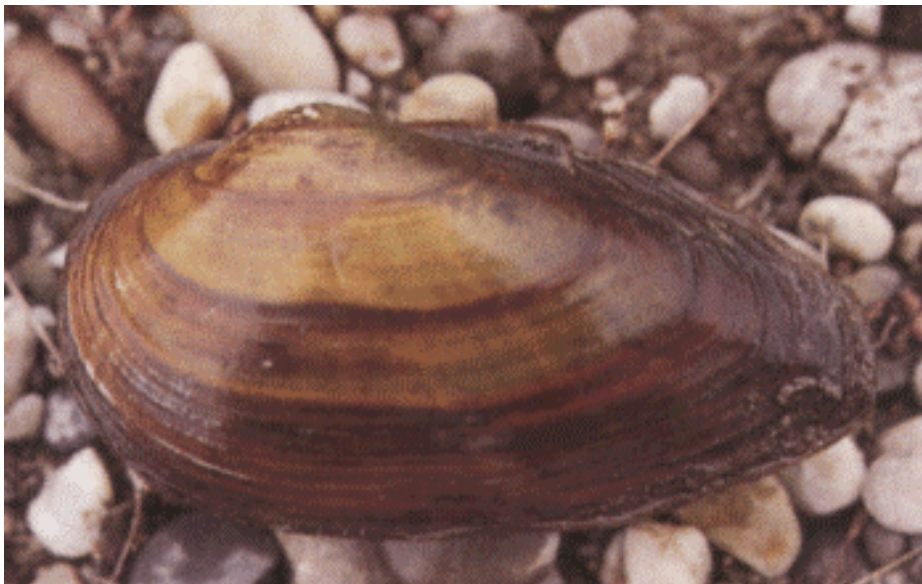
- ❑ Related to the general life history problem: allocation of resources between growth and reproductive effort (and maintenance)
- ❑ Simple models suggest that determinate growth is evolutionarily optimal – growth to “optimal” adult size



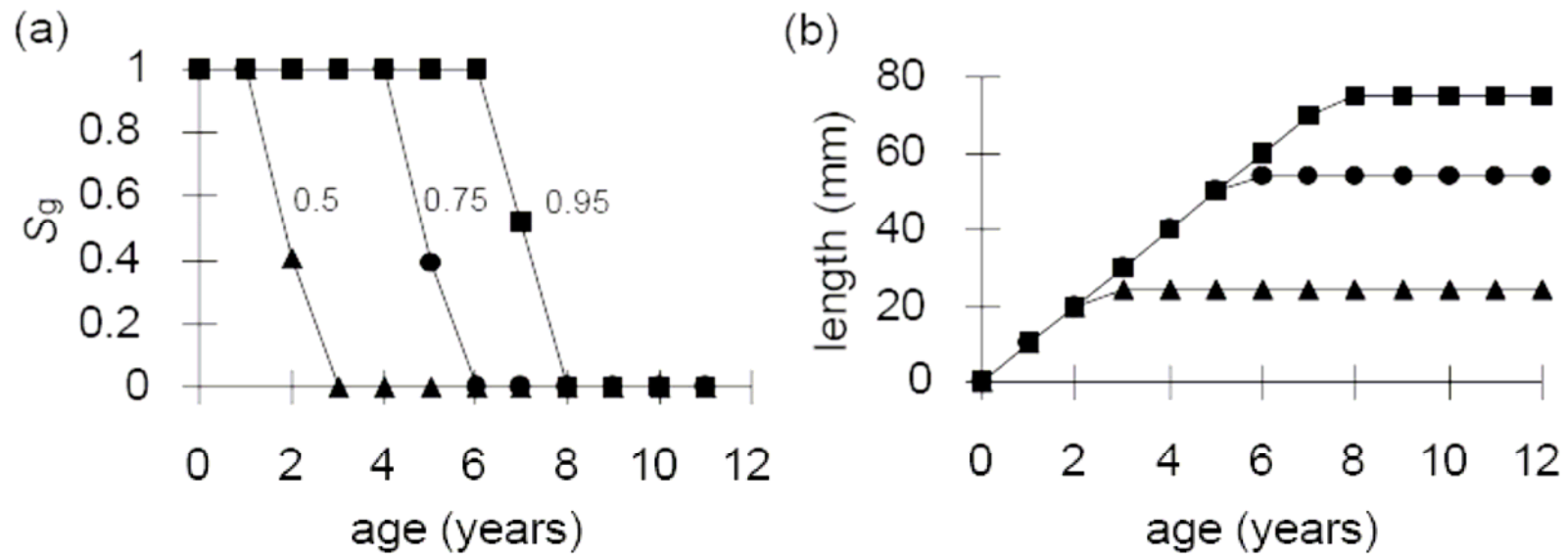
Factors favouring indeterminate growth

- ❑ Seasonality
- ❑ Diminishing return from reproductive investment
- ❑ [production and survival rates that both increase/decrease with size]

Why do freshwater clams grow indeterminately?

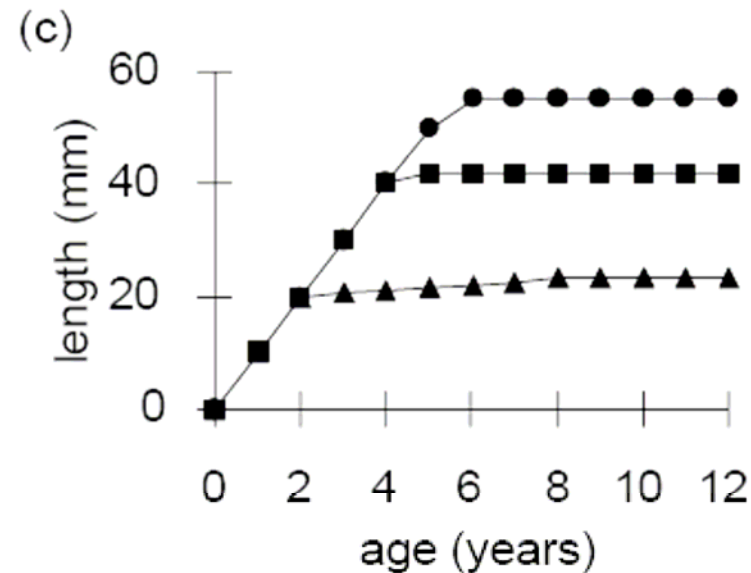
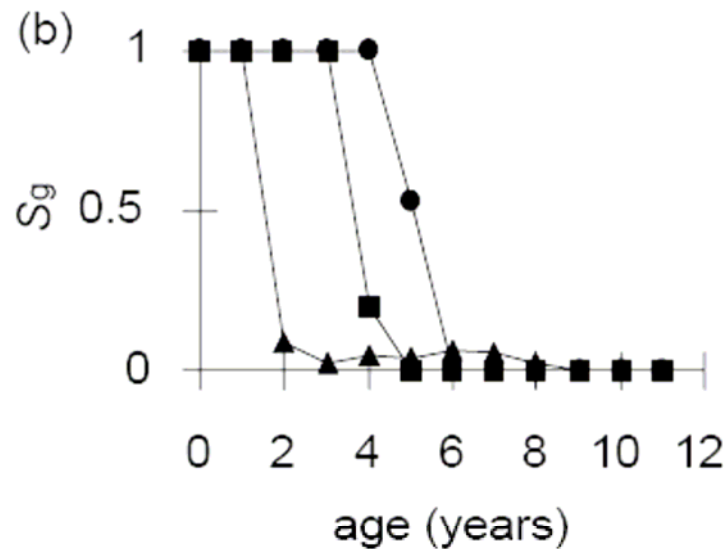


Why do freshwater clams grow indeterminately?



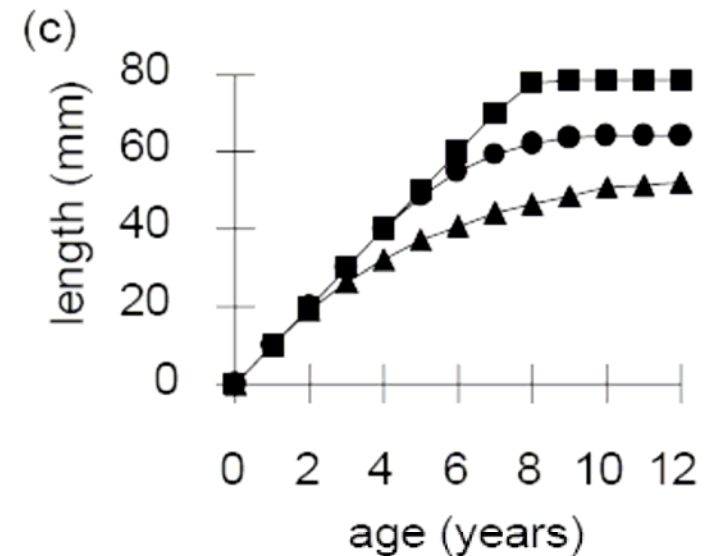
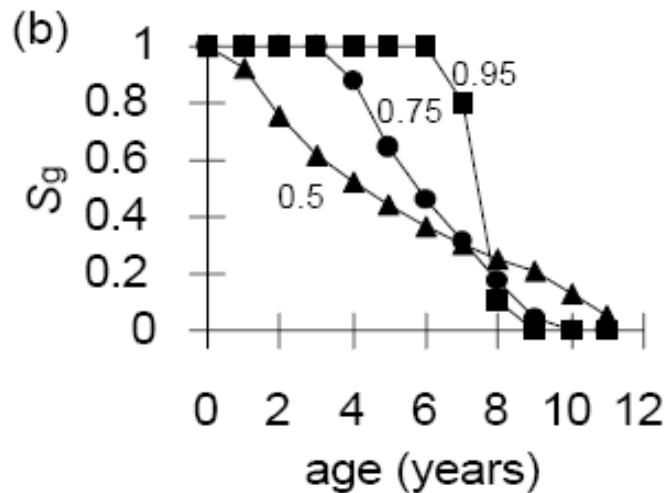
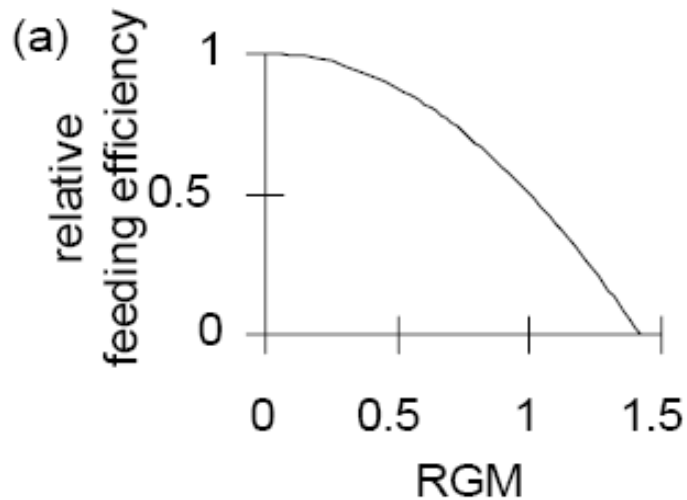
□ Simple optimisation model shows very little growth after maturation

Why do freshwater clams grow indeterminately?



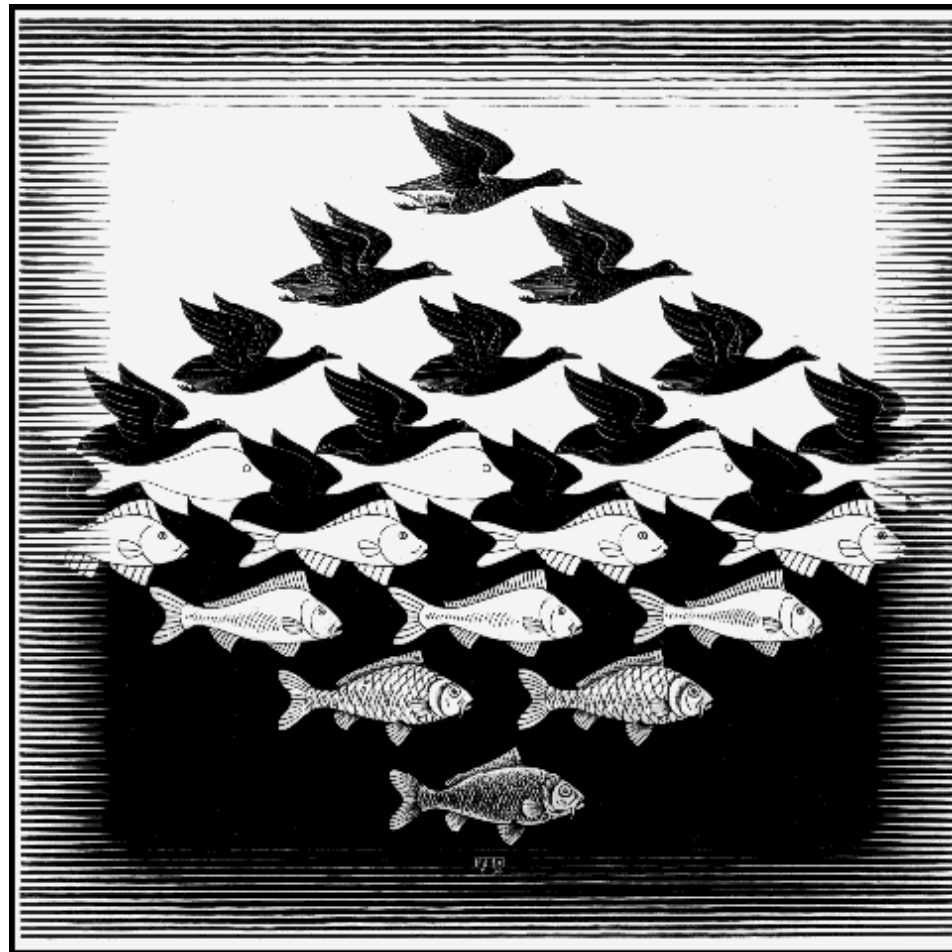
- ❑ Size-specific survival and production rates do not yield observed levels of growth after maturation

Why do freshwater clams grow indeterminately?



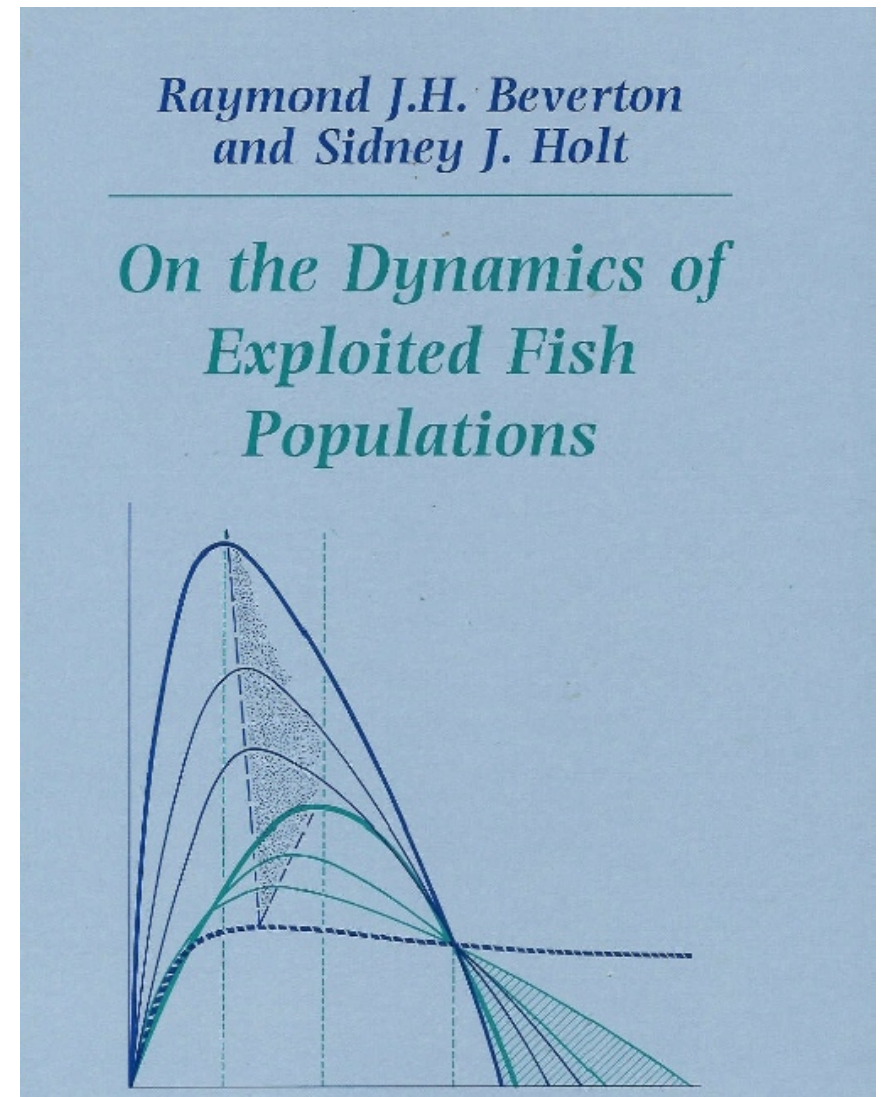
- ❑ Costs of reproduction can yield plenty of growth after maturation
- ❑ Seasonality was not considered

Part II – applications of life history theory in the marine context



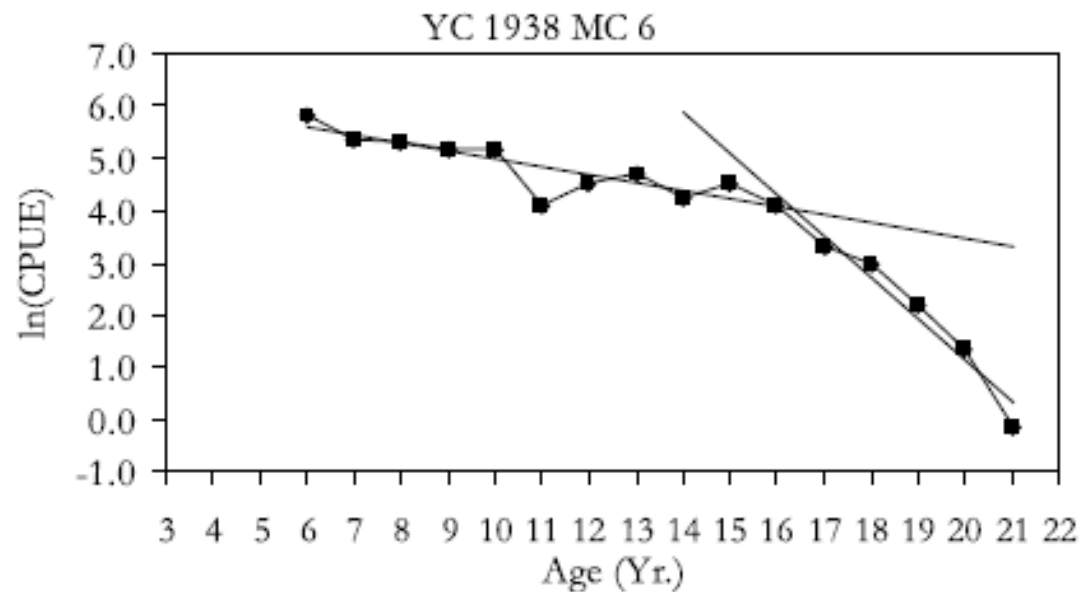
Beverton's legacy

- Building on Beverton's legacy: life history variation and fisheries management (2003 AFS meeting, Quebec)
 - Life history dynamics
 - Life history statics



Beverton's legacy

□ Longevity

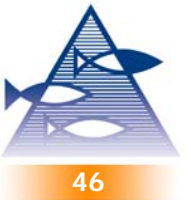


- Increasing natural mortality in Norwegian spring-spawning herring after ~10 spawning seasons [Beverton et al. 2004]

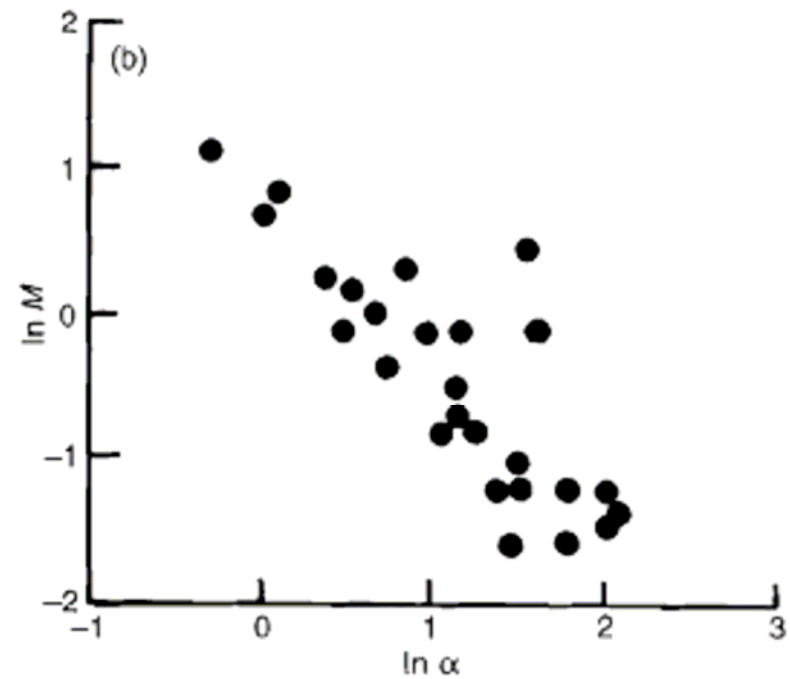
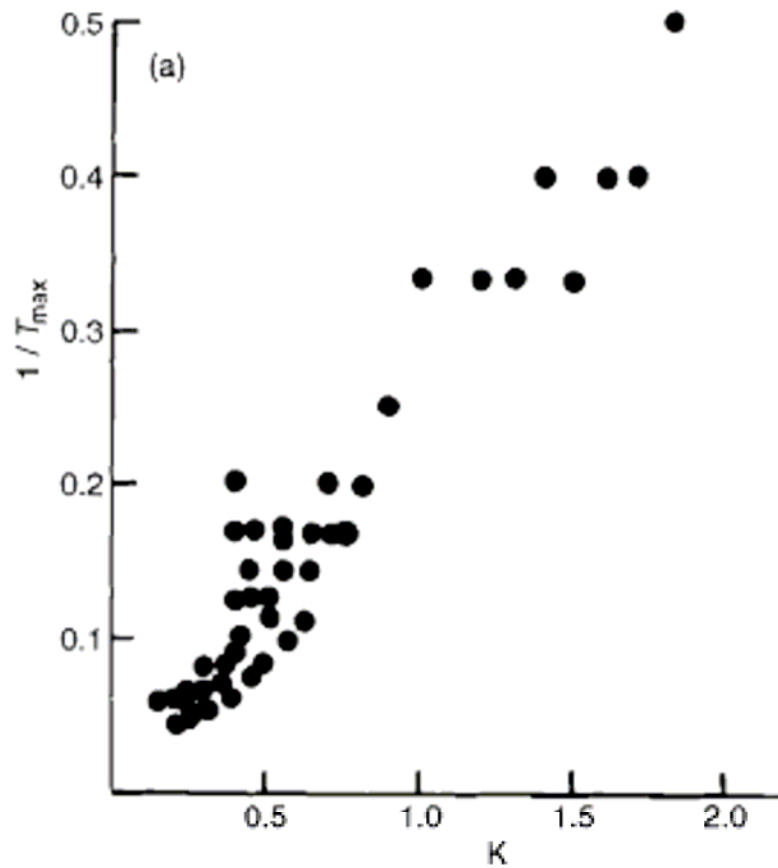
Beverton's legacy

□ Life-history statics (invariants)

- Close relations among life history parameters
→ dimensionless numbers
- From across populations within species to higher taxonomic levels (?)
 - Instantaneous natural mortality rate \times age at maturation \sim constant [1.5-3.3]
 - Instantaneous natural mortality rate / von Bertalanffy growth coefficient \sim constant [1.5]
 - Length at maturation / asymptotic maximum length \sim constant [0.4-0.8]

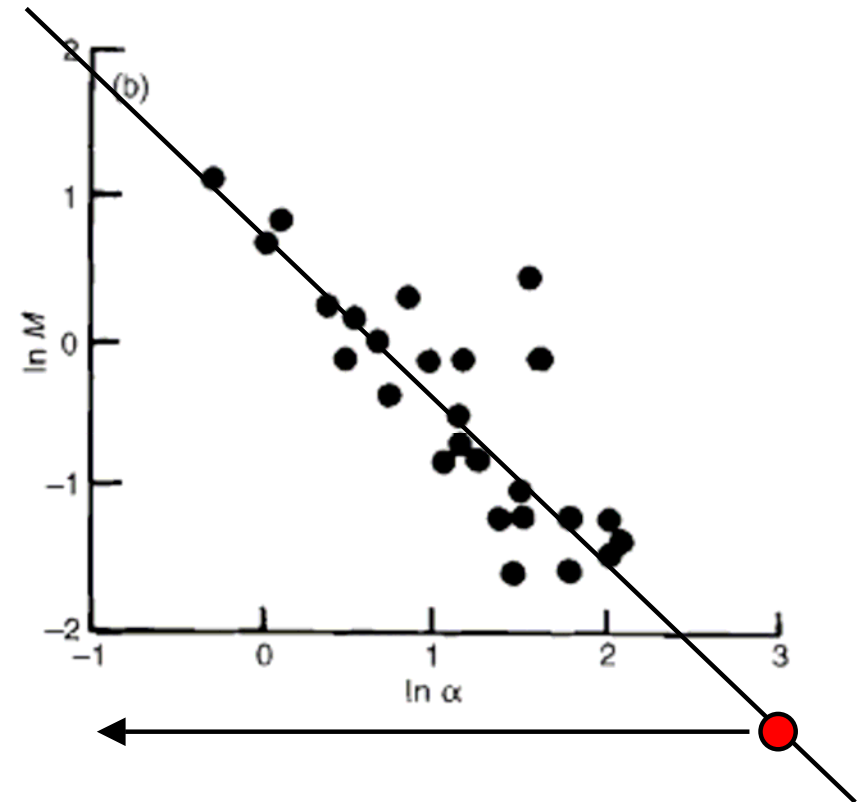


Life-history invariants



Life-history invariants

- Let's play orange roughly!
 - Maturation at age 20 year $\rightarrow \ln(\alpha) \sim 3$
 - $\rightarrow \ln(M) \sim -2.6$
 - $\rightarrow M \sim 0.075^{-1}$ or $s \sim 0.93$

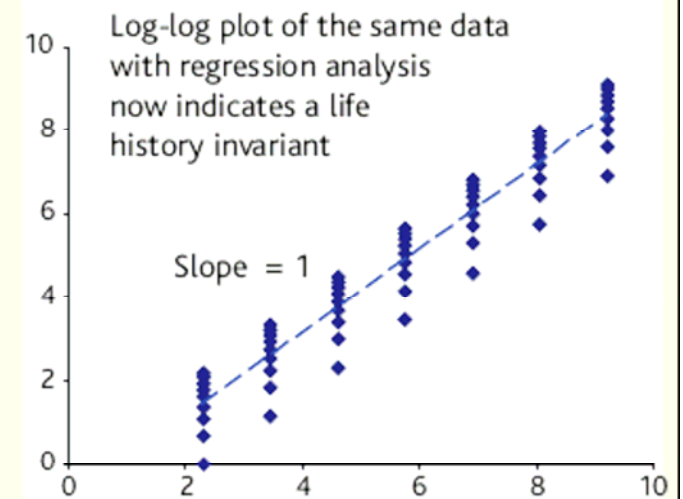
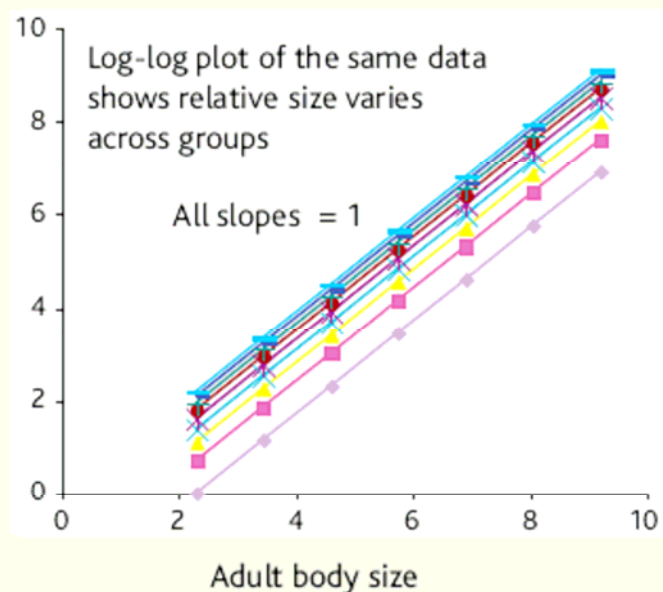
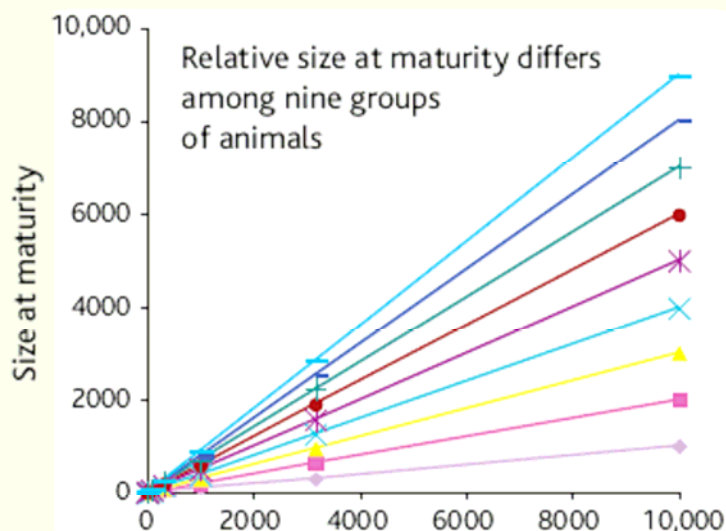


Life-history invariants

- ❑ Simple models can predict invariants that are not too far from the observed (Charnov, Jensen, ...)
- ❑ There is some tendency to regard life-history invariants as fundamental biological laws, rather than descriptive, empirical laws

Life-history invariants

- ❑ A warning note – strong invariance may be spurious



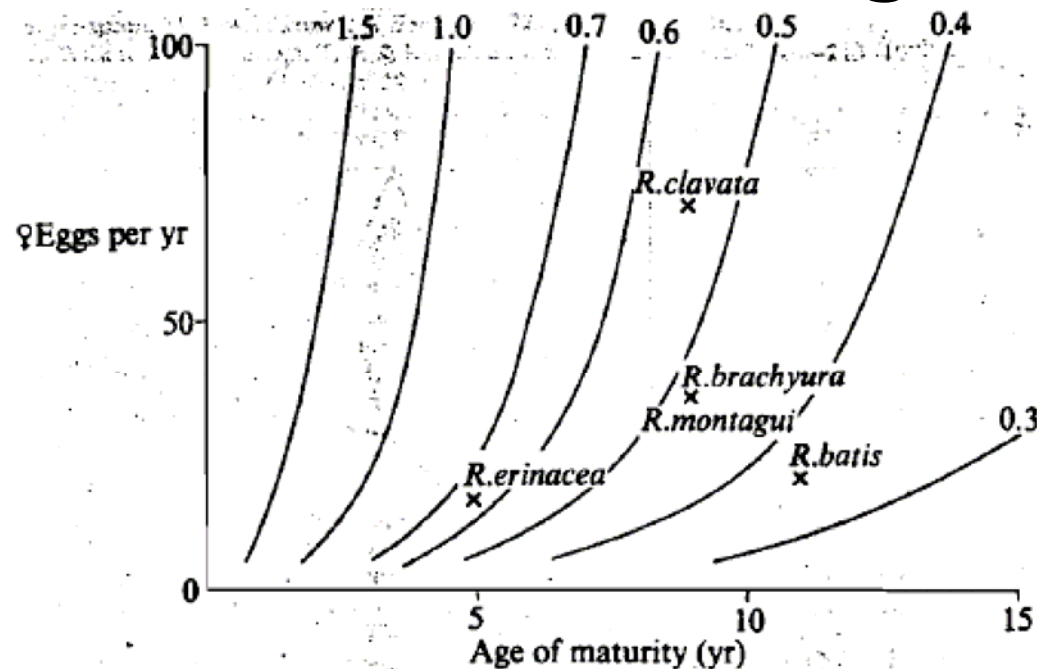
- ❑ Nee et al. Science 2005, with a Perspective by de Jong



How to use life history data to support managing marine ecosystems?



Simple demographics can suggest vulnerability to overfishing

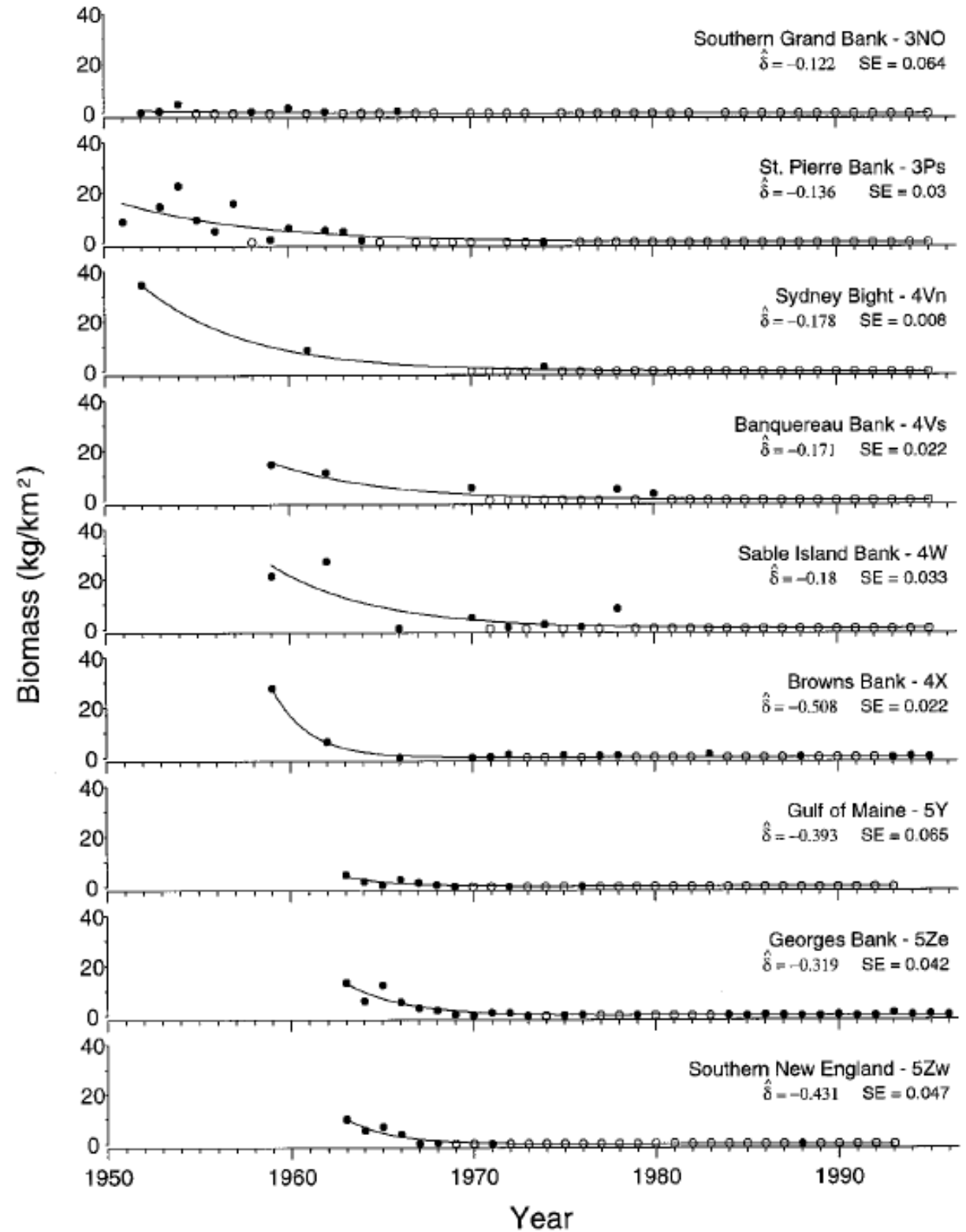


Brander, K. 1981.
Disappearance of
Common Skate *Raia*
batis from Irish Sea.
Nature

- Simple model with only fecundity, age at maturation and total mortality as inputs

□ Barndoor skate

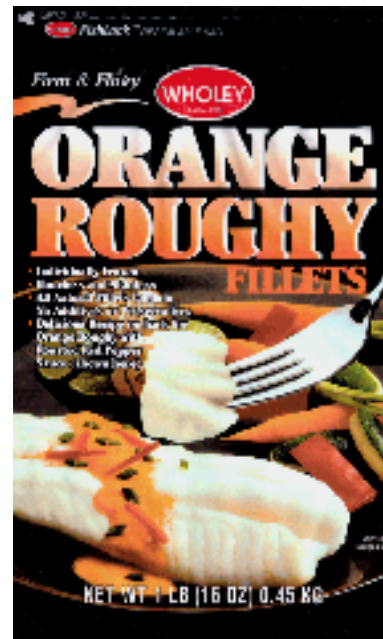
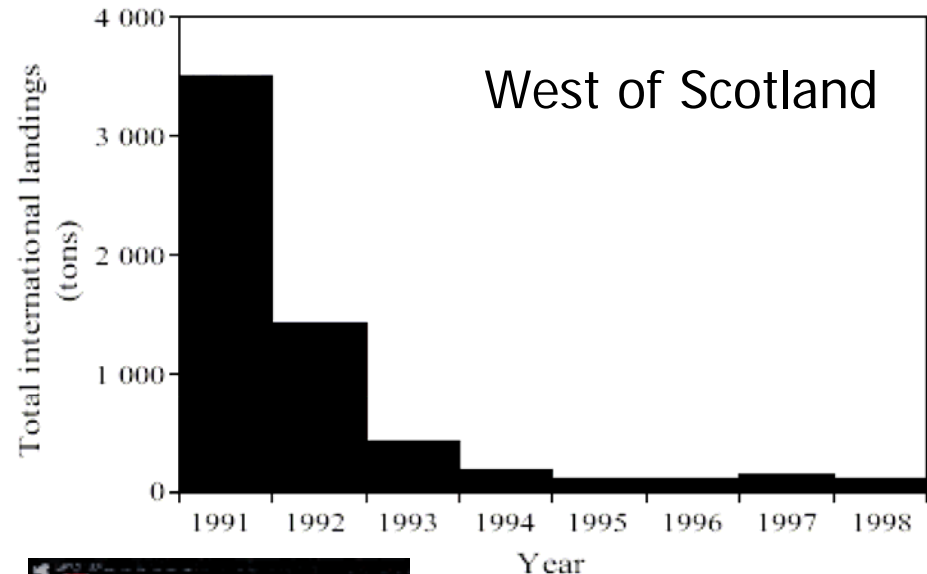
- Casey & Myers 1998. Near extinction of a large, widely distributed fish. Science



Orange roughy again

❑ Recipe for a fisheries collapse?

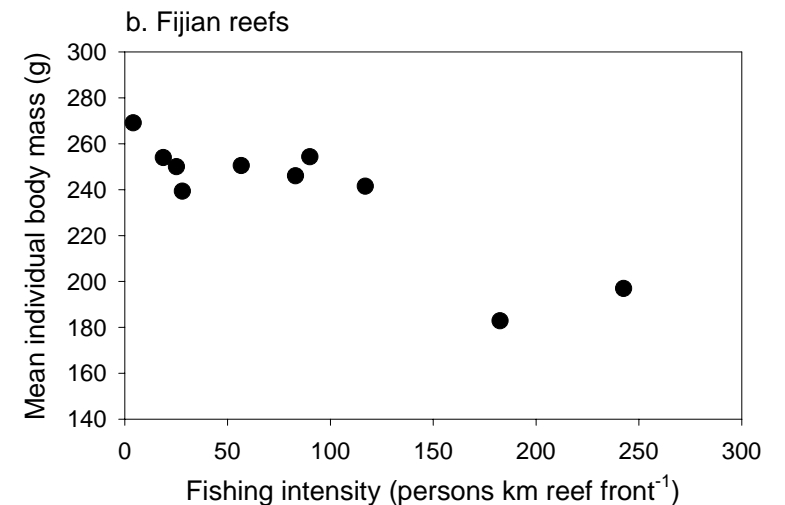
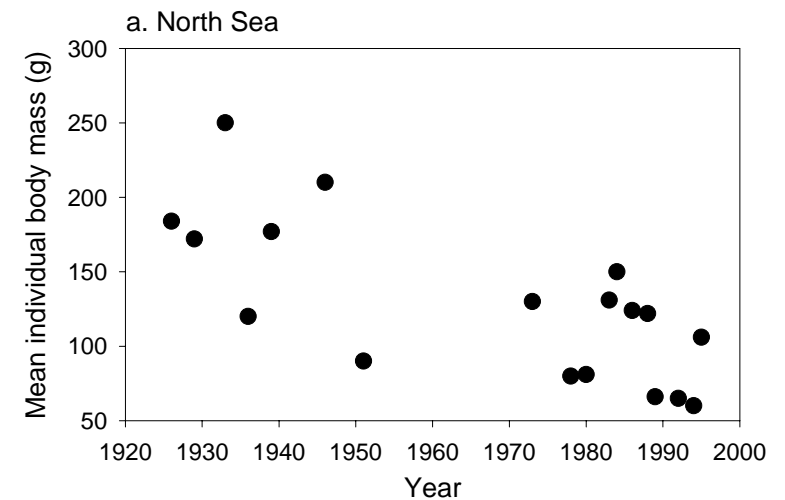
- Maturation at age ~20 years (life span >100 years?)
- Natural mortality rate ~0.05 yr⁻¹
- Sustainable exploitation level (gu) estimated to be 5-10% of virgin biomass



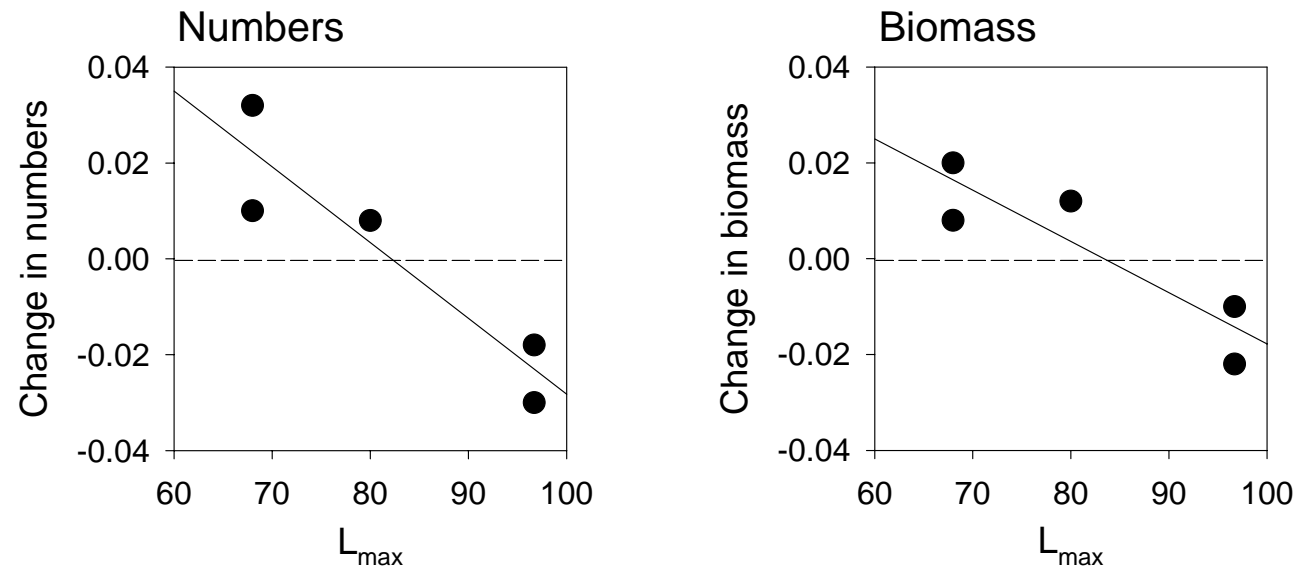
Demographic correlates to responses to exploitation

- ❑ Simple demographic response
- ❑ Not all species are equally affected

Dulvy, Greenstreet, Jennings, Reynolds, ...



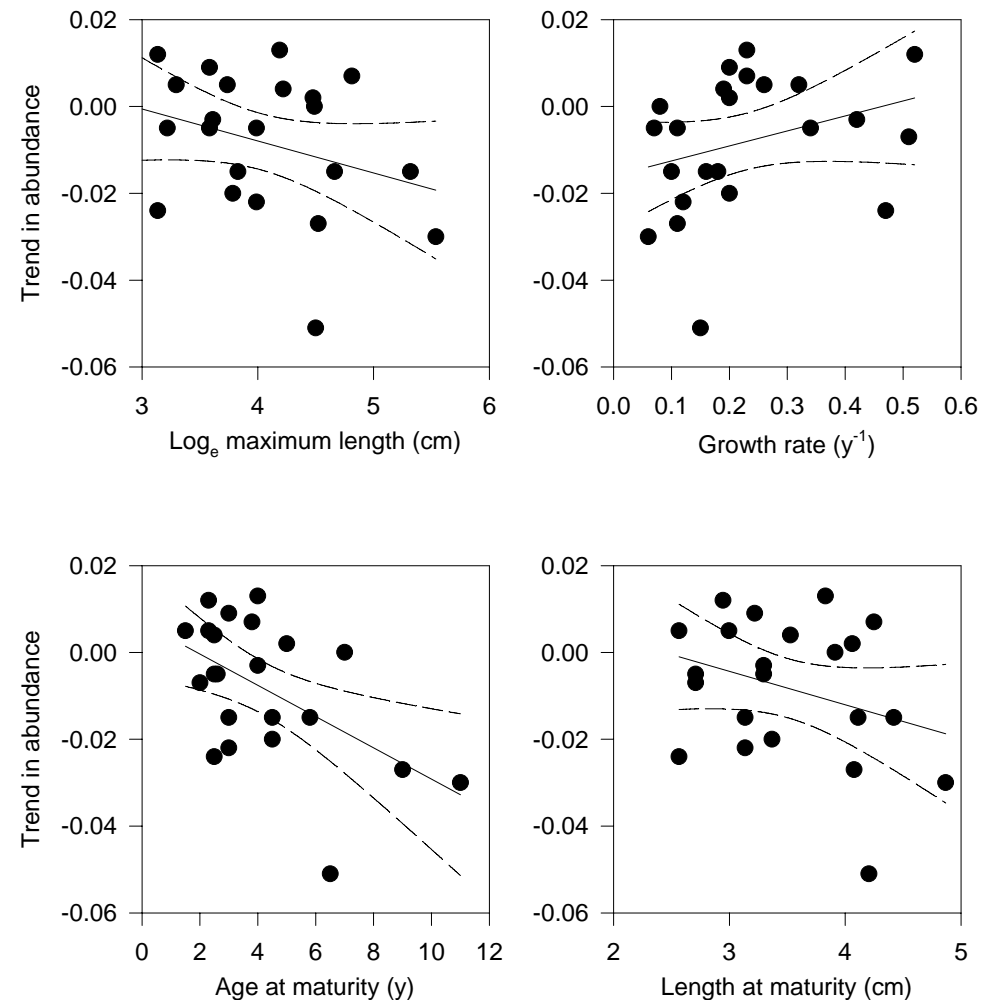
Demographic correlates to responses to exploitation



- Large species of rays in the Irish Sea tend to decline most

Demographic correlates to responses to exploitation

- Trend in abundance in the North Sea correlated with life-history traits



Use of life-history information on routine fisheries stock assessments

- ❑ Life-history information is mostly not used
- ❑ The goal is to estimate abundance cohort-wise, without attention to other attributes than age
- ❑ Most assessment models are thus age-structured, but not length- nor maturity-structured.

Use of life-history information on routine fisheries stock assessments

- ❑ Size-at-age & maturity-at-age is used to estimate spawning stock biomass
- ❑ Maturity data often rather fictional
- ❑ Spawning stock biomass → recruitment
- ❑ Usually, SSB-R relationship is so noisy that it is of no use in estimating recruitment.
Therefore closed life cycle models cannot be used.



“Fleksibest” model for northeast Arctic cod

- ❑ Process-oriented, closed life-cycle
- ❑ Age-, length-, and maturity-structured
- ❑ Maturation reaction norm parameters as input
- ❑ Growth parameters estimated/input



Fisheries-induced evolution

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

65

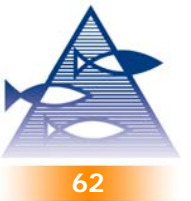
"...a stock-raiser would never think of selling his fine cattle and keeping only the runts to breed from."

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



Fisheries-induced evolution

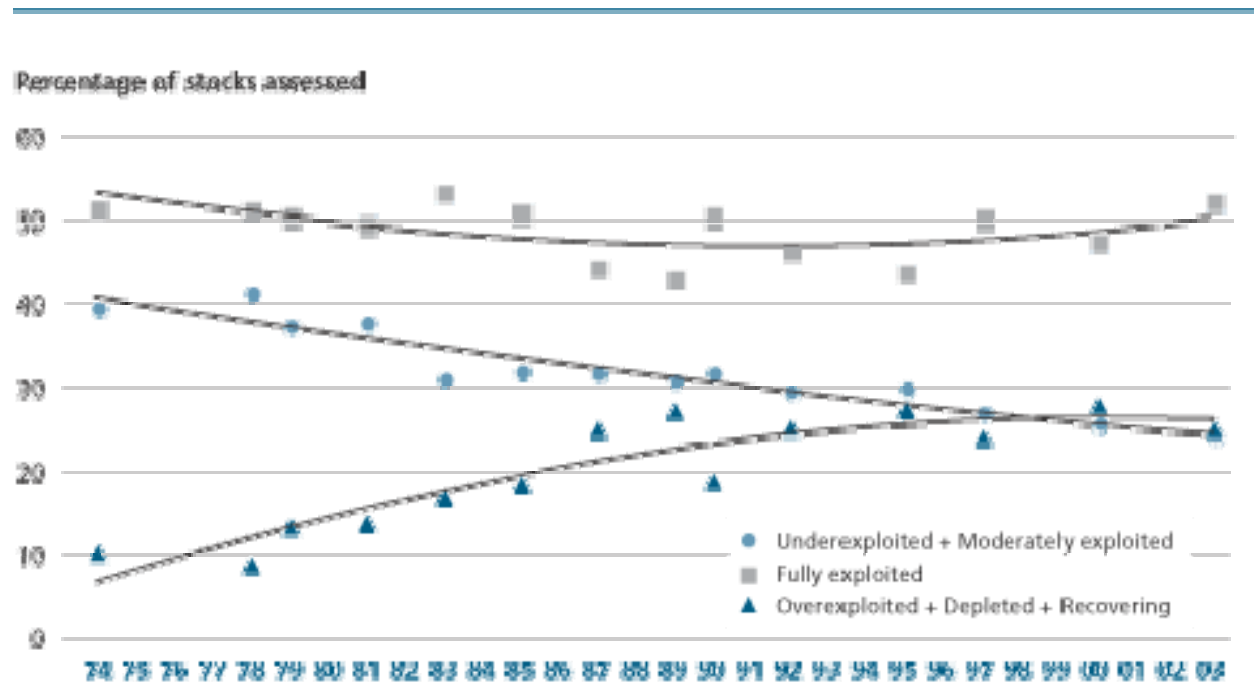
- ❑ Lesson from animal breeding: strong selection causes rapid genetic changes
- ❑ Additional insight from life-history theory: *selectivity* not necessary – just any change in mortality causes life-history evolution
- ❑ Fishing=mortality
 - Overall increase in mortality (often $F > M$)
 - Selective



Trends in world fisheries

Figure 19

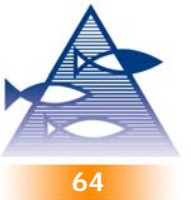
Global trends in the state of world marine stocks since 1974



The State of World Fisheries and Aquaculture 2004, FAO 2004

Fisheries-induced evolution

- ❑ 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...



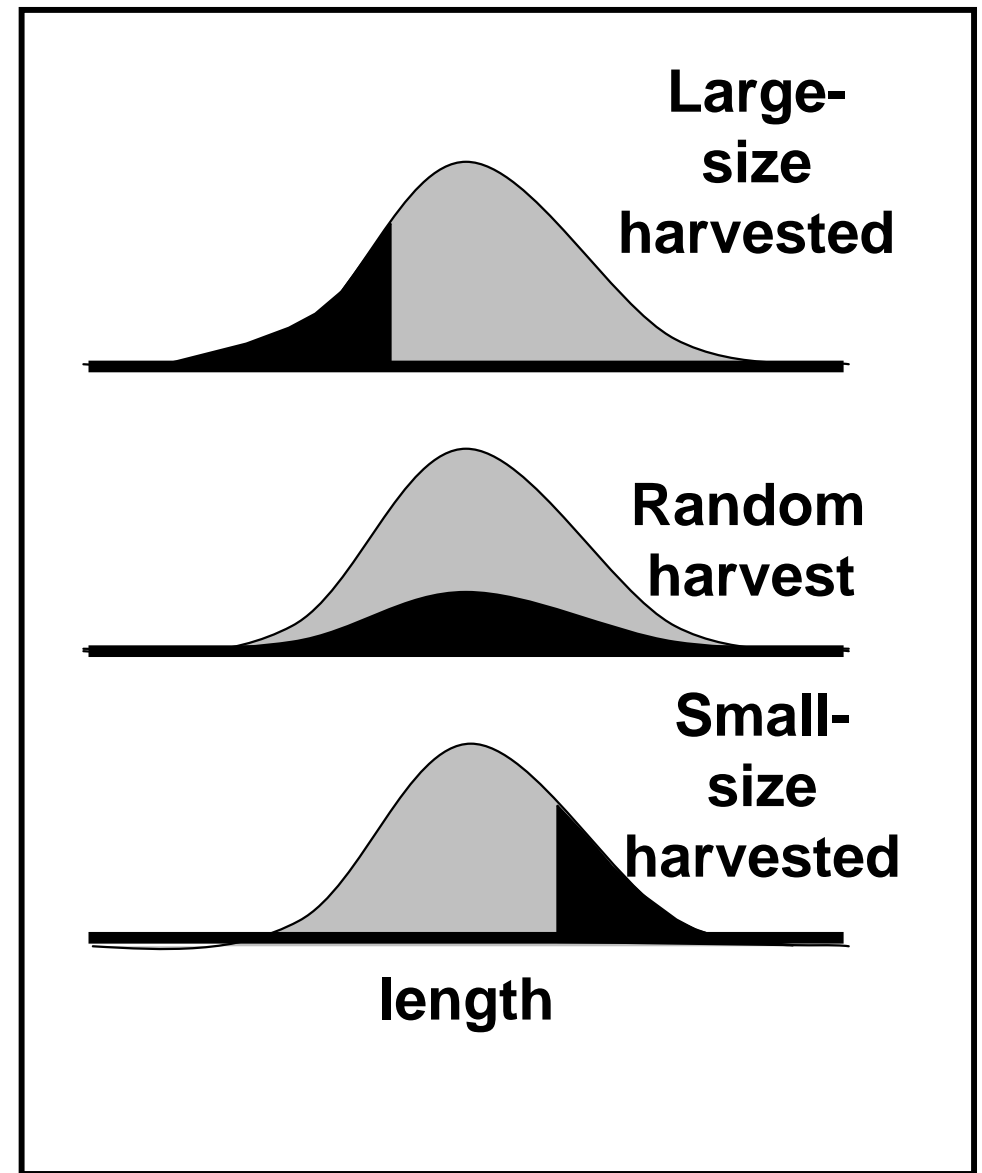
Fisheries-induced evolution in the lab

- ❑ Edley & Law 1988: Size-selective harvest of *Daphnia*
- ❑ David Conover & colleagues: Size-selective harvest of Atlantic silverside [Conover & Munch, Science 2002]

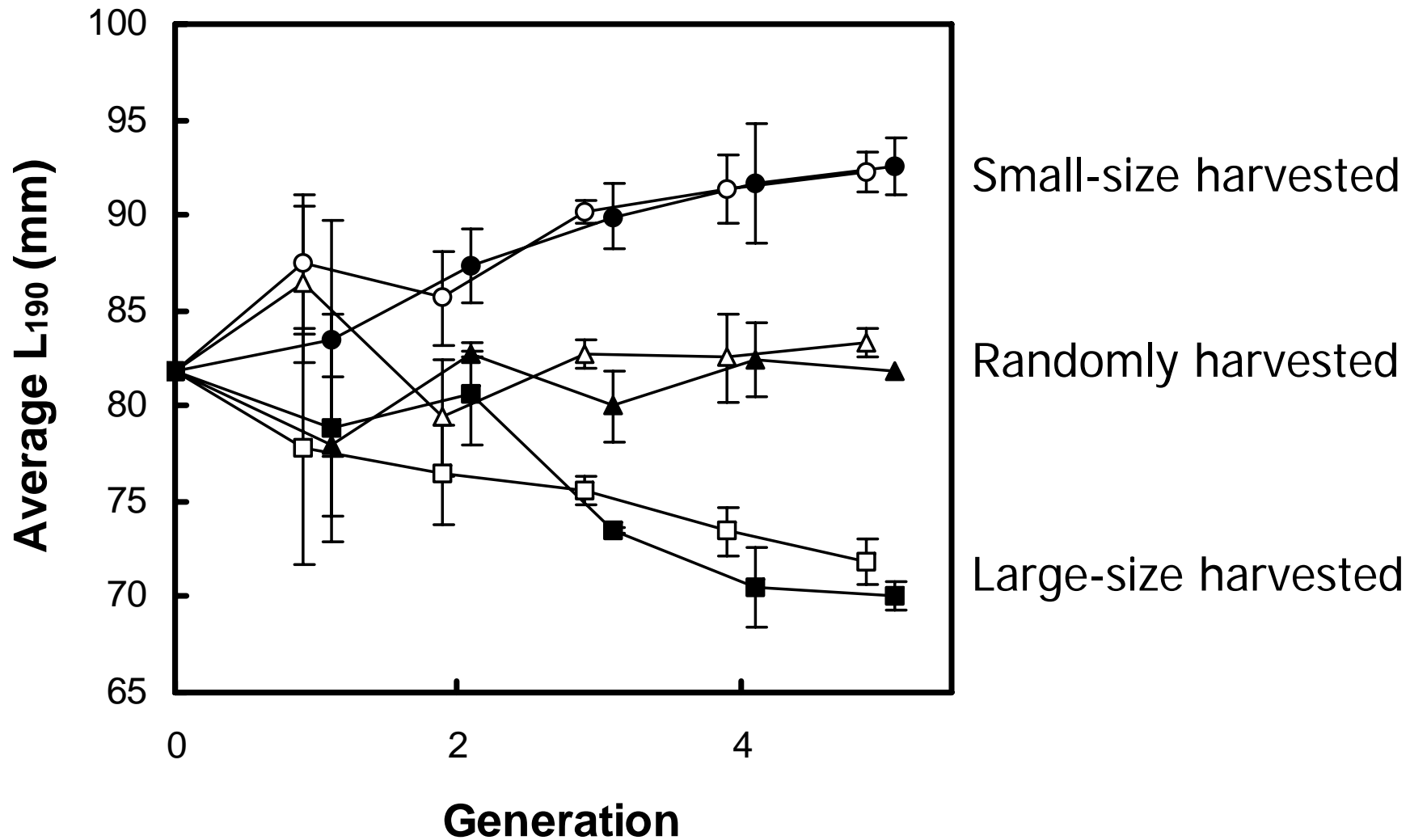


Design of fishing experiment

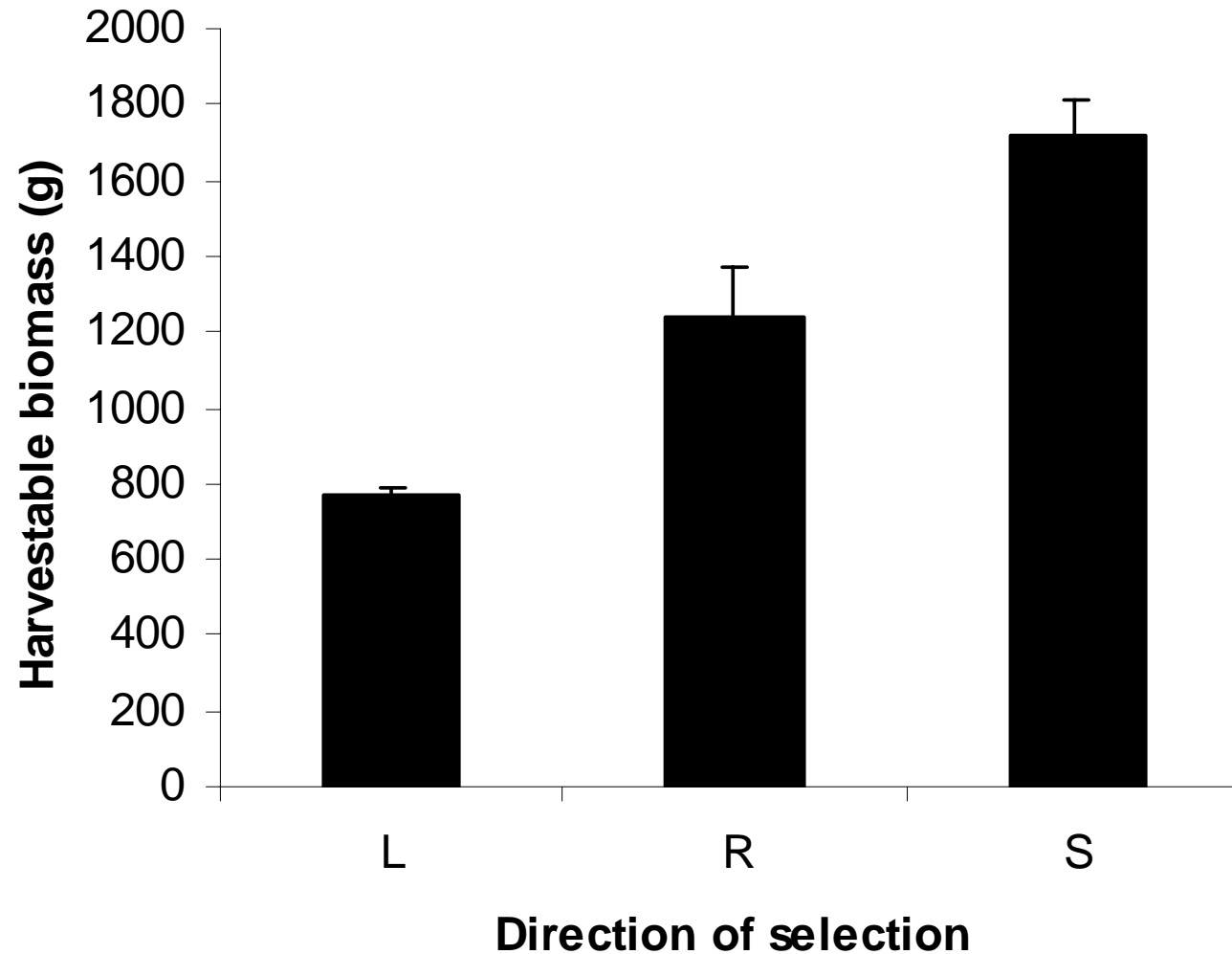
- ❑ Six populations founded from NY fish
- ❑ 90% harvest applied on day 190
- ❑ Prediction: body size, growth rate and harvested biomass will evolve in opposition to the size bias of the harvest regime



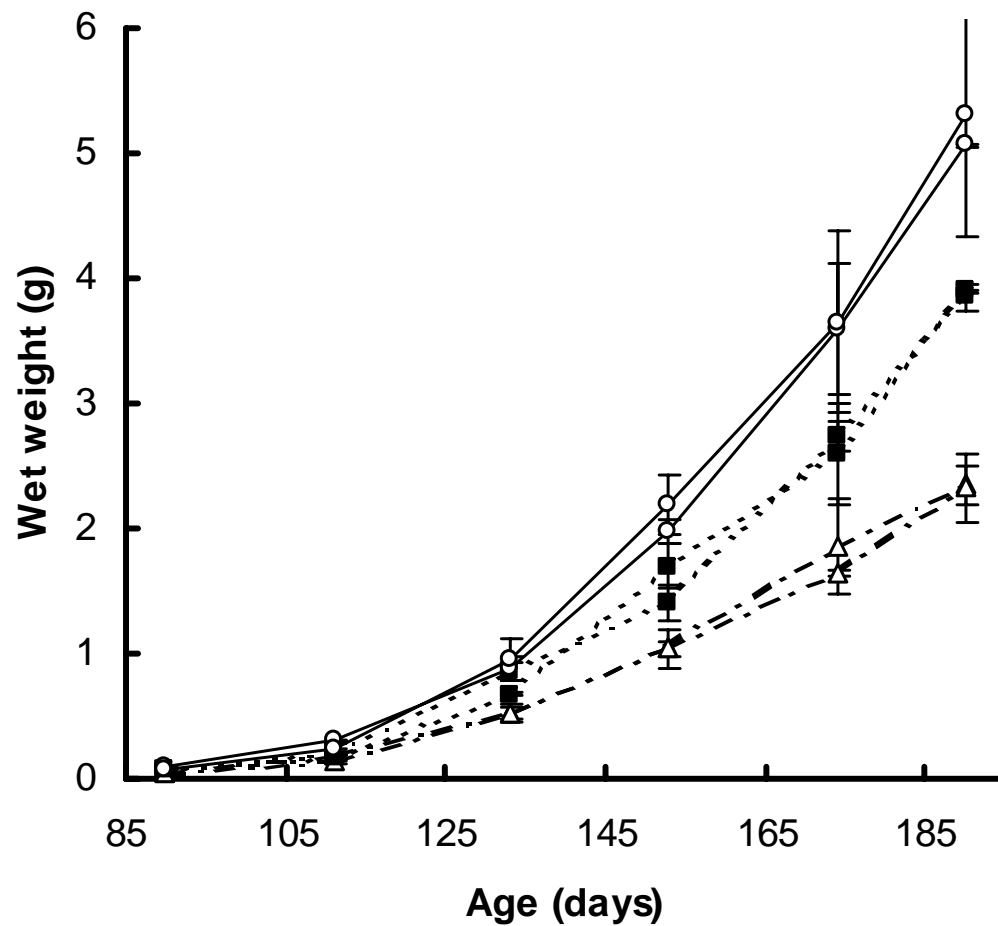
Selection response



Selection response

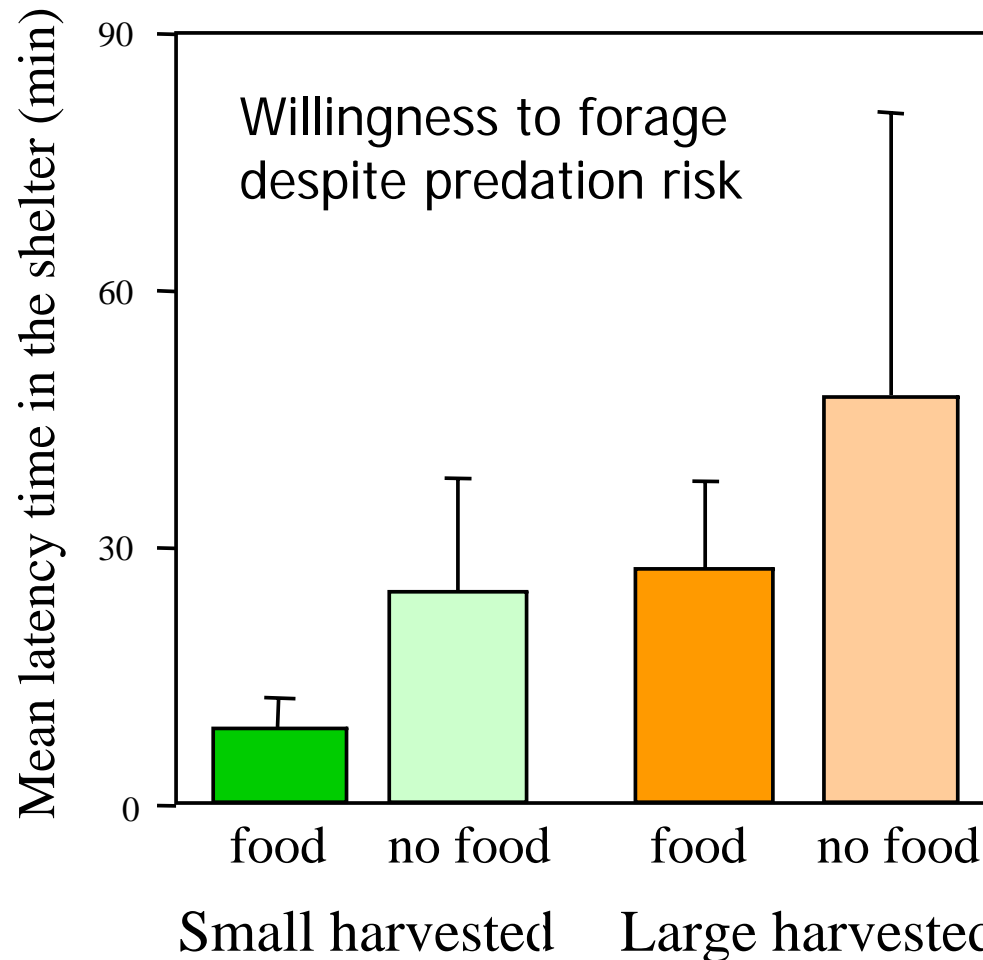


Selection response



Beyond the direct selection response

- Response = slower somatic growth rate
- Mechanisms?



Correlated changes in other traits

Reproductive traits

Egg size	18% higher vol. in small-size harvested stocks
Length at hatch	7% longer in small-size harvested stocks
Larval survival	3-fold higher in small-size harvested lines
Larval growth rate	20% higher in small-size harvested lines
Fecundity	2-fold higher in small-size harvested stocks

Growth physiology

Food consumption rate	44% higher in small-size harvested stocks
Growth efficiency	54% higher in small-size harvested stocks

Behavior

Foraging	Small-size harvested fish are more risky foragers
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Morphology

Vertebrae number	Higher in small-size harvested stocks
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