Hjort's critical period hypothesis; When does density-dependent and stochastic mortality occur?

Models, Analysis and Meta-Analysis

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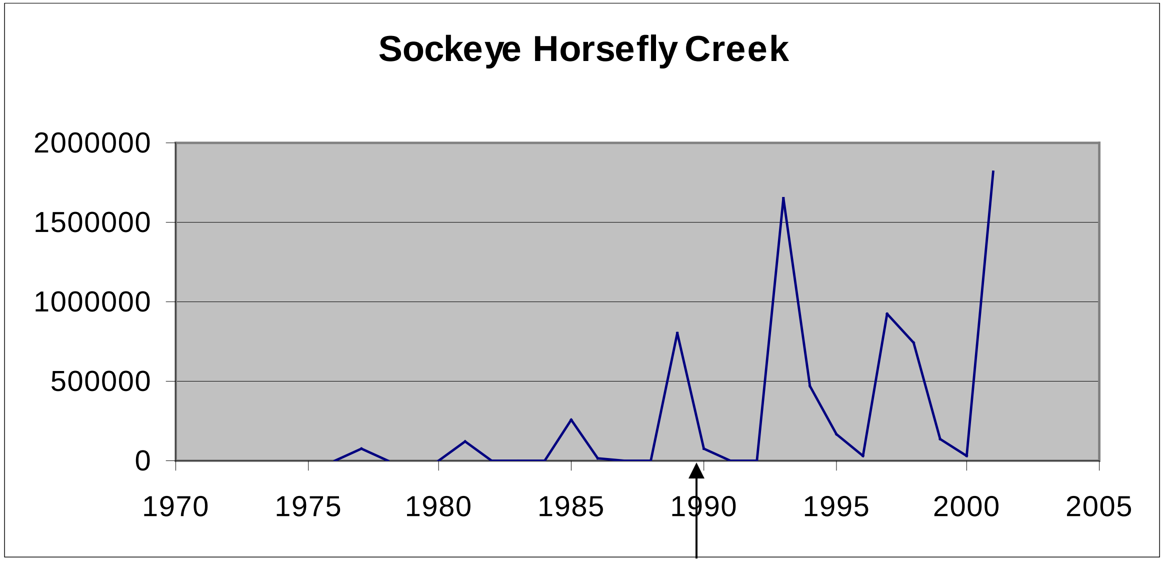
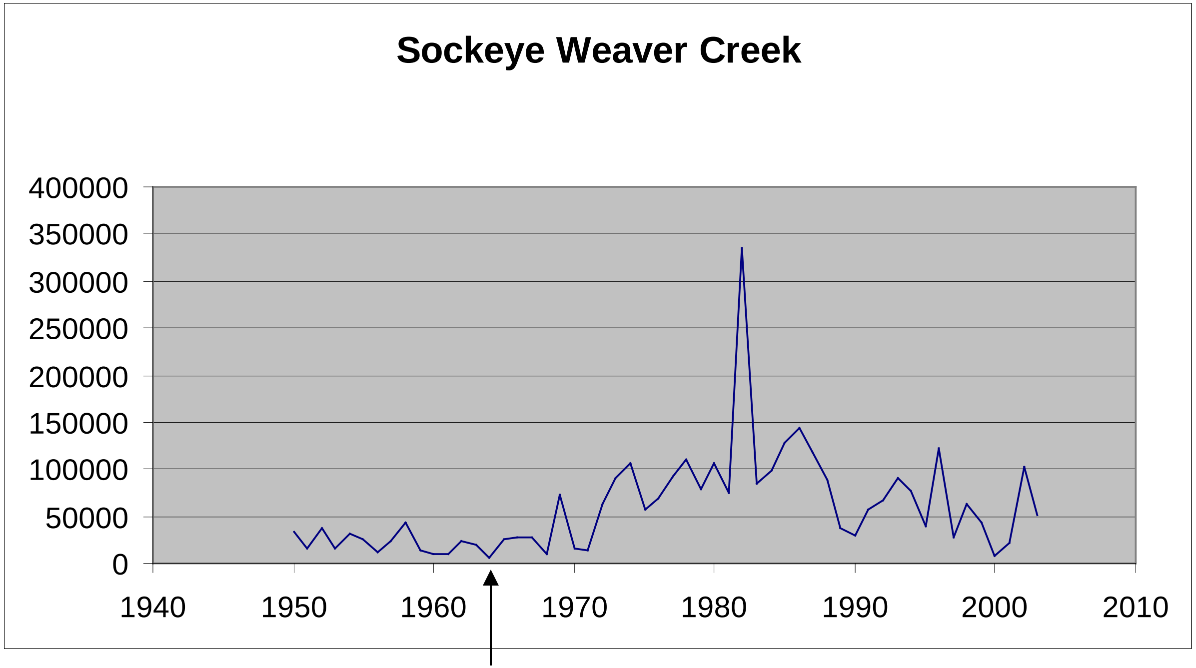
Hjort's (1914) critical period hypothesis

- ‘the numerical value of a year class is apparently stated at a very early age, and continues in approximately the same relation to that of other year classes throughout the life of the individuals”
- This is the fundamental issue in population regulation and ecology of fish.



Spawning channel



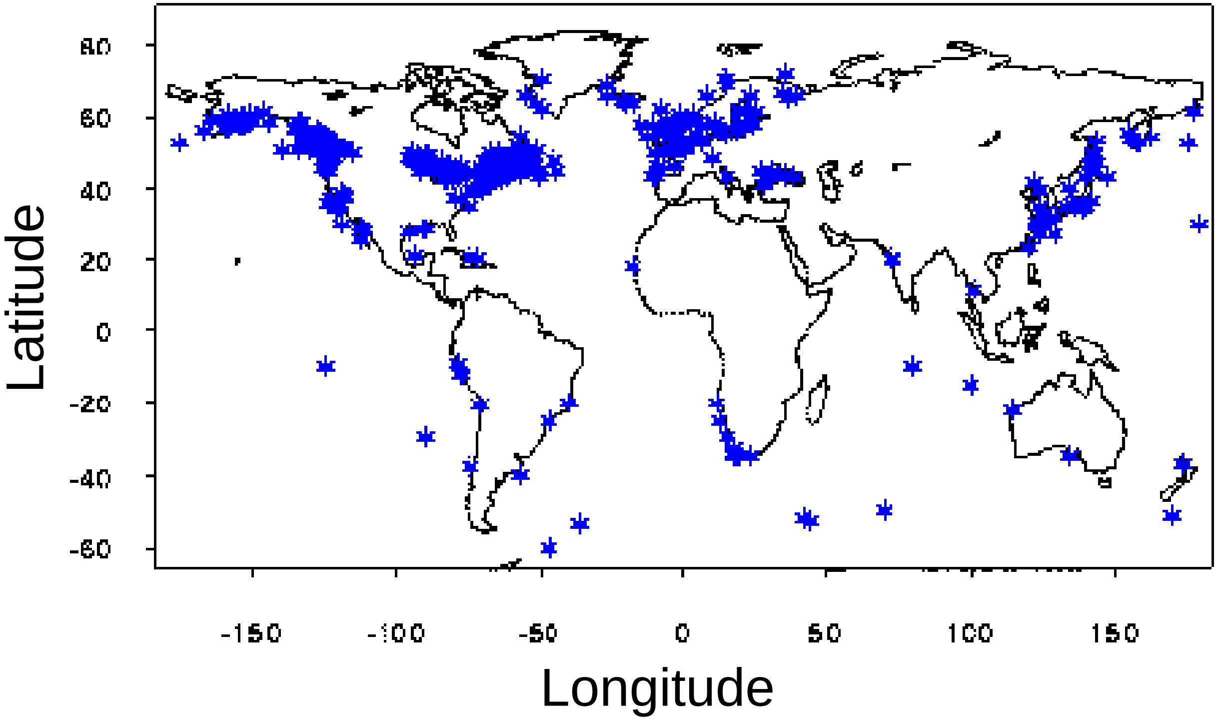
Spawning channel

Approach

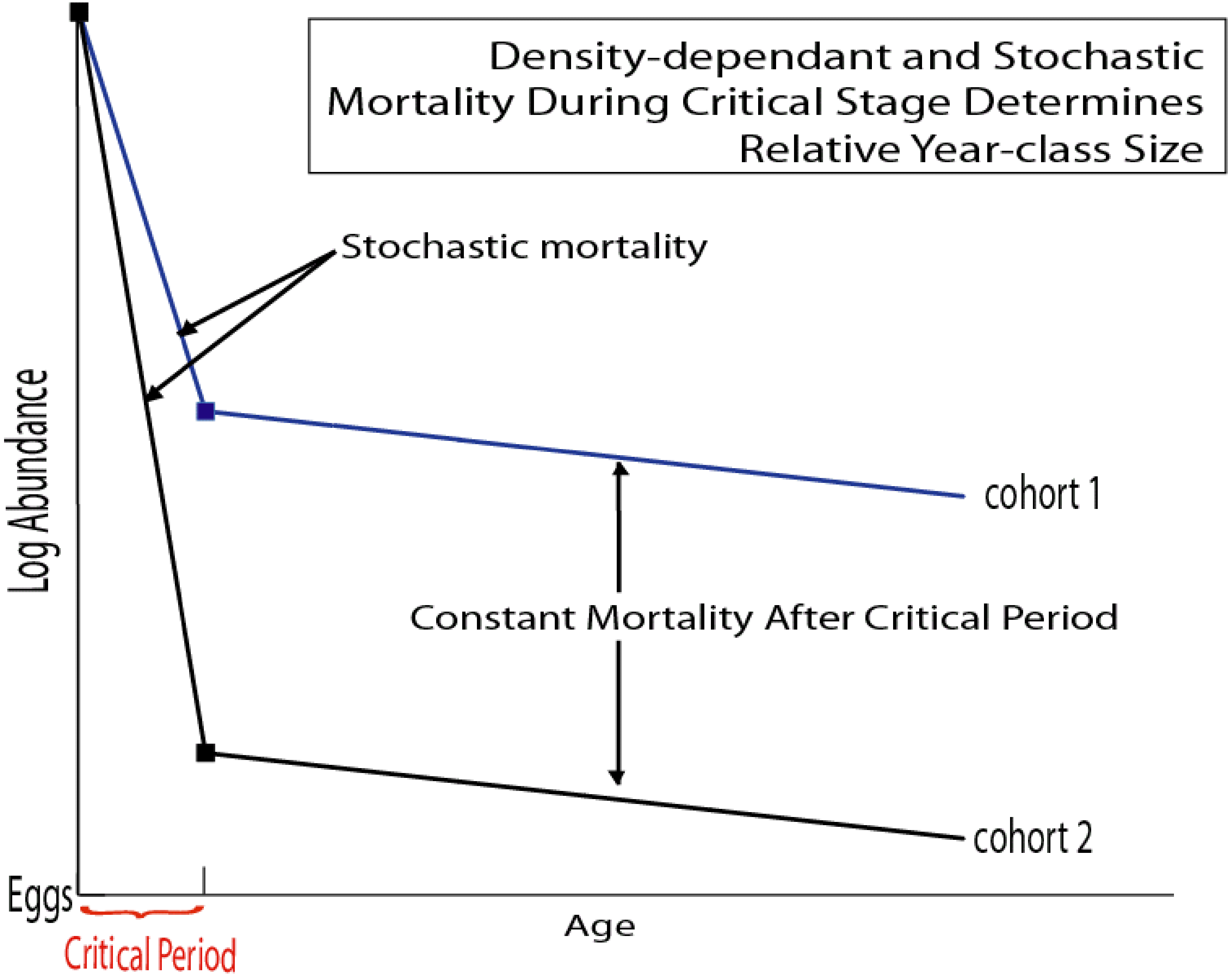
- Develop Mathematical Models
- Develop Statistical Methods
- Collect all the data in the world
- Solve Problem

Testing for general patterns

http://www.fish.dal.ca/welcome.html



Hjort's Hypothesis: Strong Version

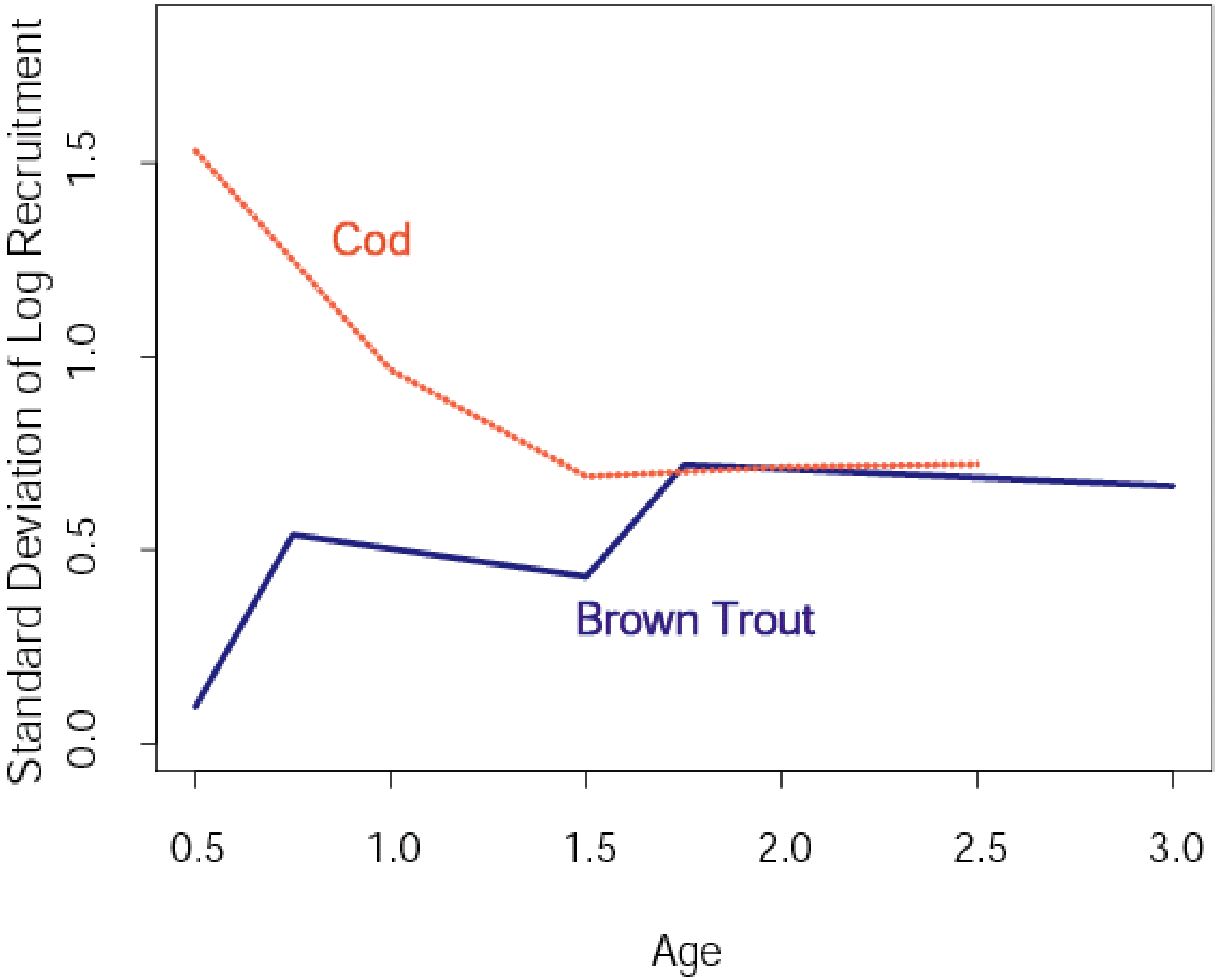


Density-dependant and Stochastic Mortality During Critical Stage Determines Relative Year-class Size

Critical period hypothesis: strong version

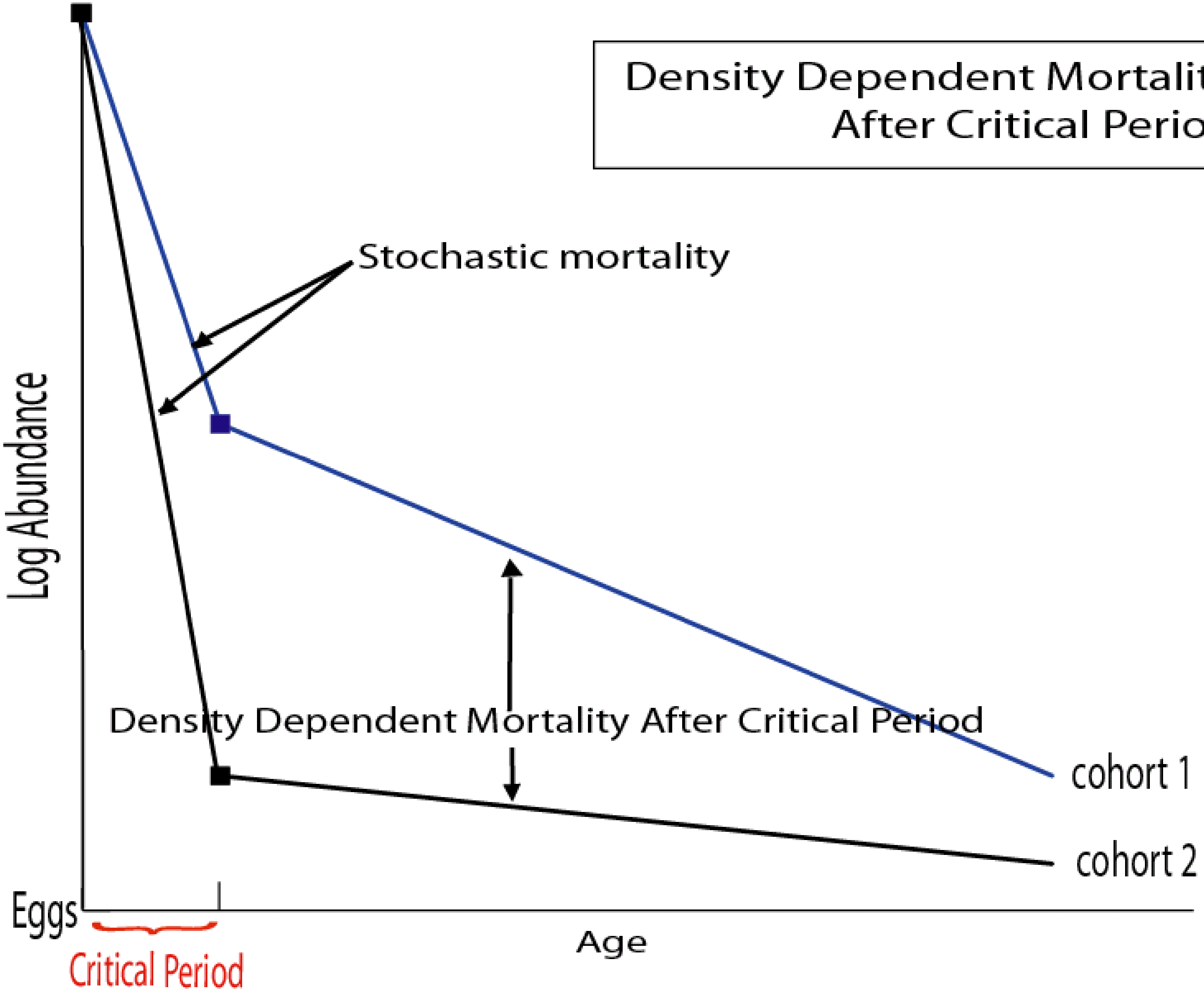
- $\mathrm{Var}(\mathrm{mortality}_{\mathrm{age<critical}}) \gg \mathrm{Var}(\mathrm{mortality}_{\mathrm{age>critical}})$
- Density dependent mortality ≈ 0 for age > critical age
- We know of no cases where this is even approximately true.

Variability in recruitment increase with age for cod and decreases for trout.



Hjort's Hypothesis: Weak Version

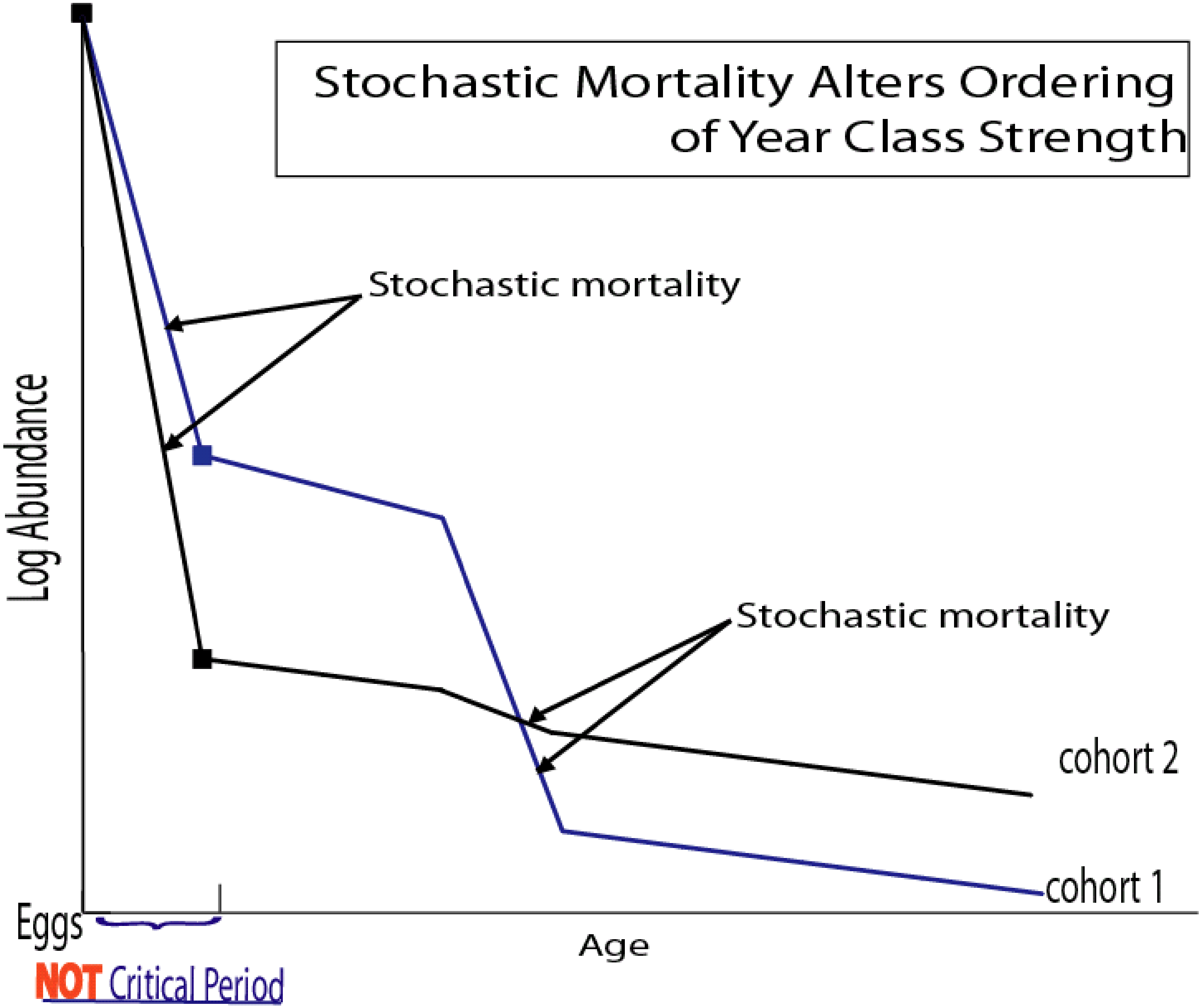
Density Dependent Mortality
After Critical Period



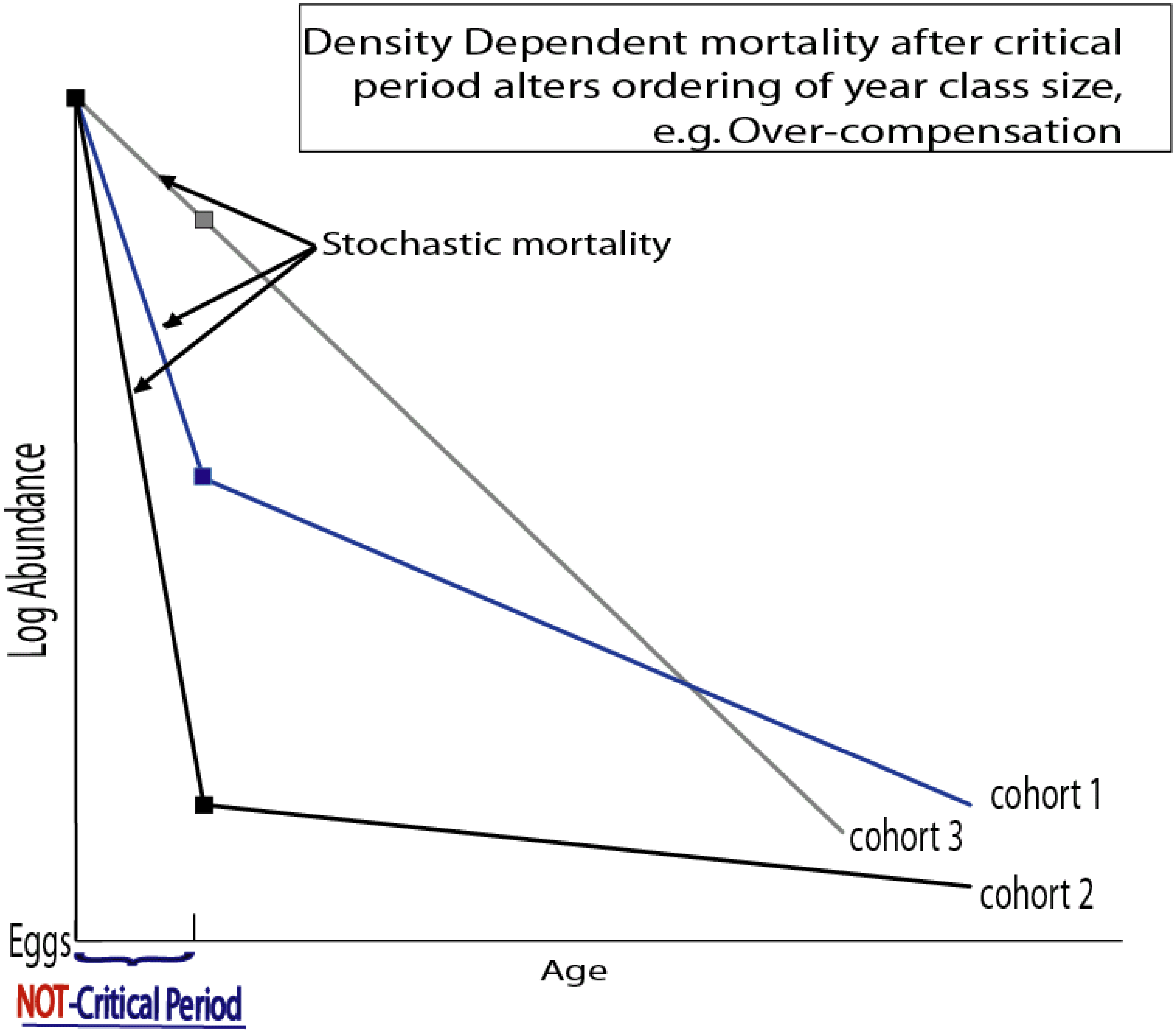
Critical period hypothesis: weak version

- $\mathrm{Var}(\mathrm{mortality}_{\mathrm{age}<\mathrm{critical}}) \gg \mathrm{Var}(\mathrm{mortality}_{\mathrm{age}>\mathrm{critical}})$ Density-dependent mortality after the critical period does not alter ordering of year-class size.

Hjort's Hypothesis: NOT Stochastic Mortality



Hjort's Hypothesis: NOT



To test Hjort’s hypothesis we need a model which:

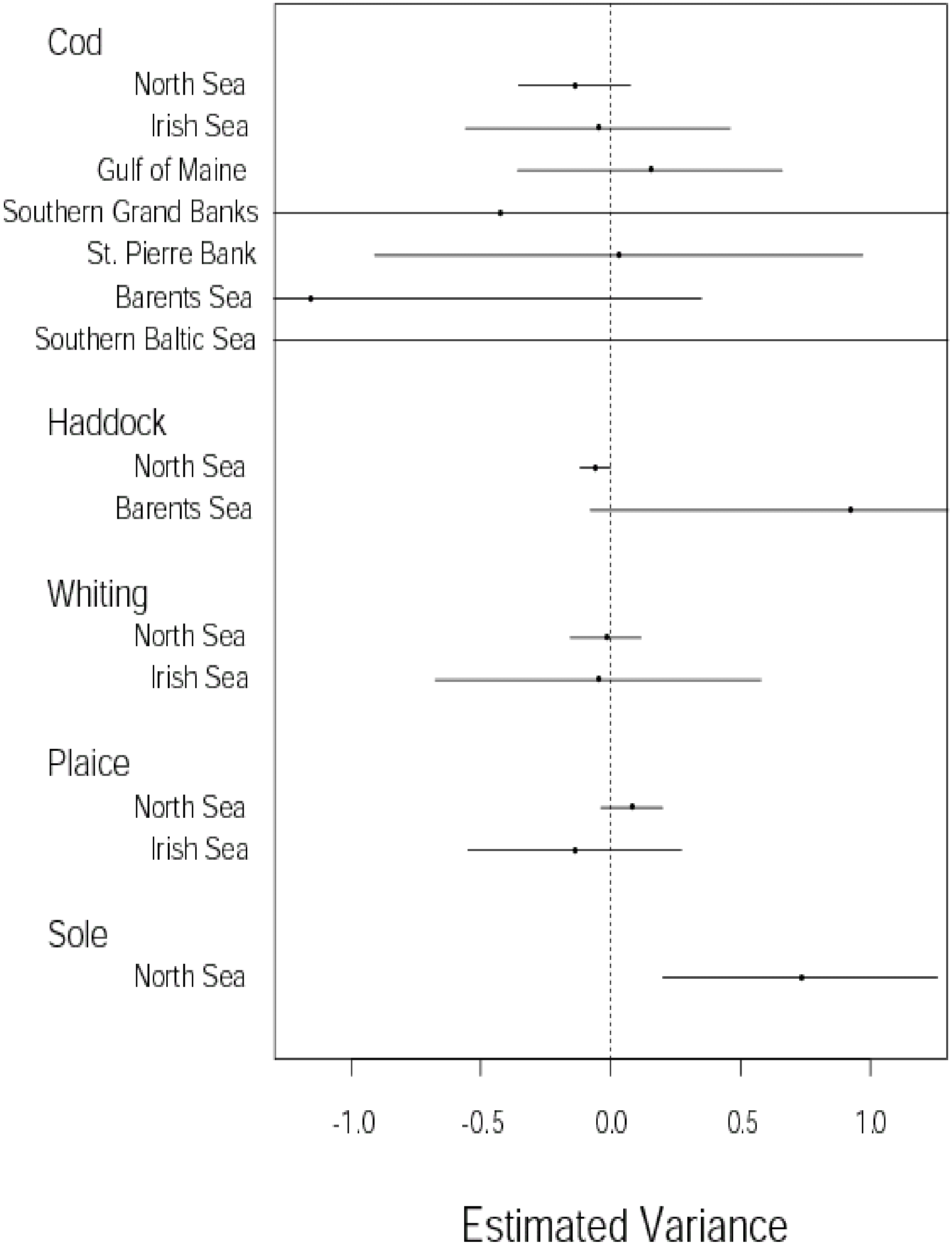
- Use research surveys which estimate abundance at different ages of the same cohort.
- Estimate the variance in mortality.
- Estimate density-dependent mortality.

- Treat cohorts as random effects.
- Include measurement error.
- Obtain estimates that can be combined across populations.

The state of the art until now:

- Myers and Cadigan (1993a and b) developed method to estimate density-dependent mortality and the variance in mortality in the presence of measurement error.
- Results could be combined across populations using meta-analysis.
- Can. J. Fish Aquat. Sci. 50: 1576—1590.
- Can. J. Fish Aquat. Sci. 50: 1591 – 1598.

Variance in mortality after critical period low for gadoids and flatfish.



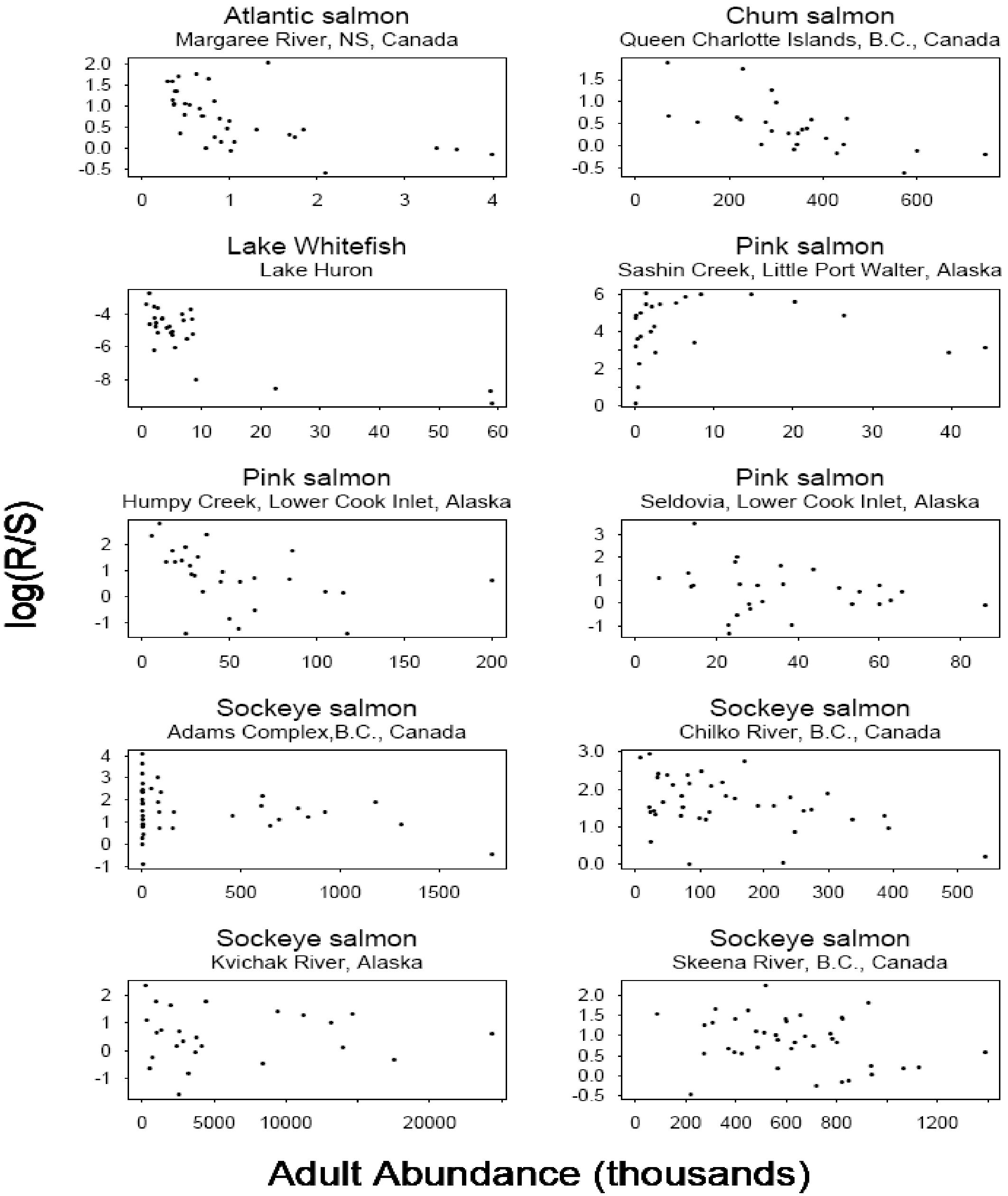
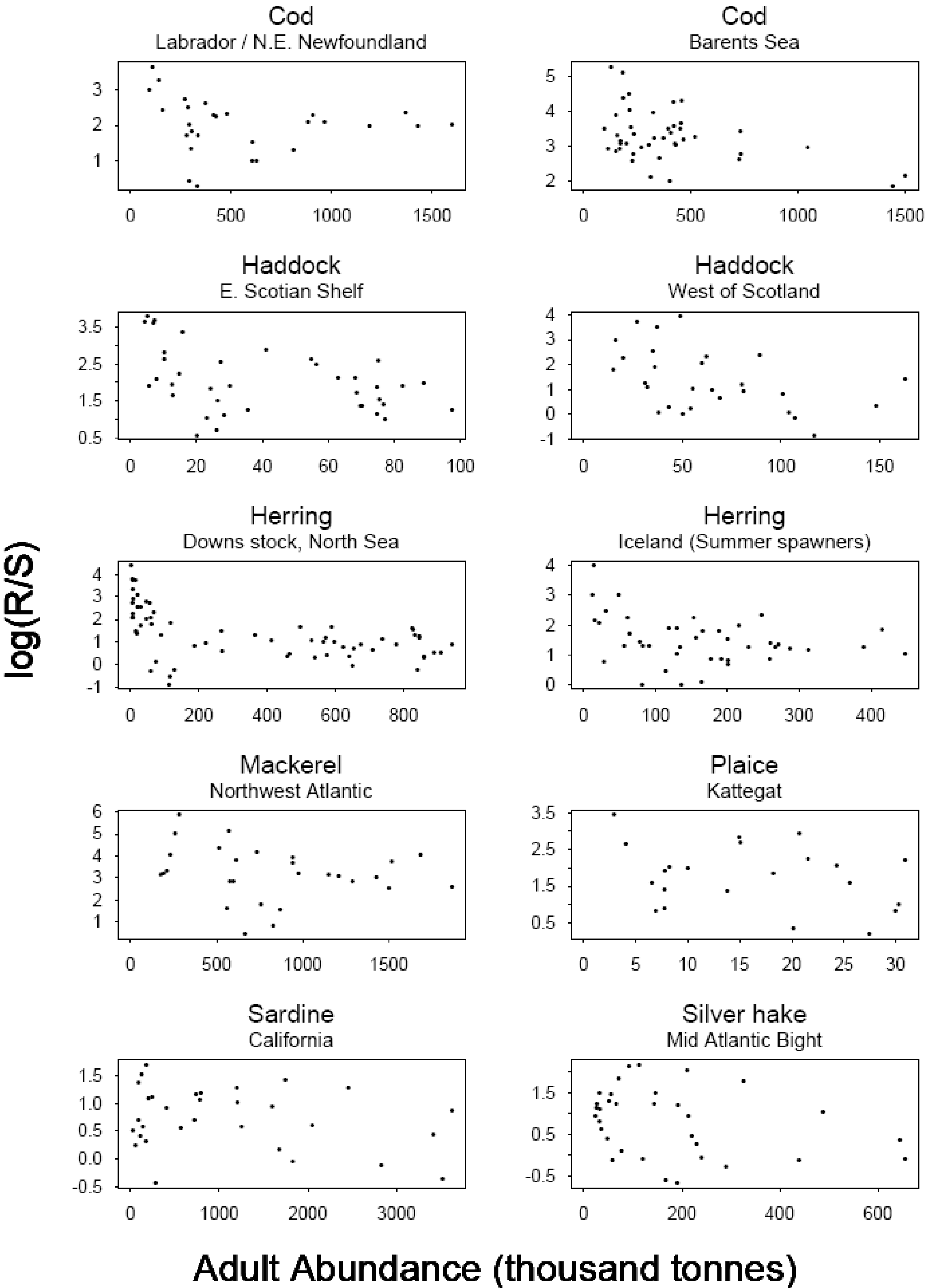


Figure 1: Adult abundance (thousands) versus the log survival rate for some representative salmonid populations. (Note: for lake whitefish (Lake Huron population) and pink salmon (Sashin Creek, Little Port Walter, Alaska population) the recruitment units are relative year-class strength and number of fry, respectively and the abundance units are numbers of eggs and number of females, respectively.)


Cod
Labrador / N.E. Newfoundland
3
2
1
0
500
1000
1500
Cod
Barents Sea
5
4
3
2
0
500
1000
1500
Haddock
E. Scotian Shelf
3.5
2.5
1.5
0.5
0
20
40
60
80
100
Haddock
West of Scotland
4
3
2
1
0
-1
0
50
100
150
Herring
Downs stock, North Sea
4
3
2
1
0
-1
0
200
400
600
800
Herring
Iceland (Summer spawners)
4
3
2
1
0
0
100
200
300
400
Mackerel
Northwest Atlantic
6
5
4
3
2
1
0
500
1000
1500
Plaice
Kattegat
3.5
2.5
1.5
0.5
0
5
10
15
20
25
30
Sardine
California
1.5
1.0
0.5
0.0
-0.5
0
1000
2000
3000
Silver hake
Mid Atlantic Bight
1.5
0.5
-0.5
0
200
400
600
log(R/S)
Adult Abundance (thousand tonnes)

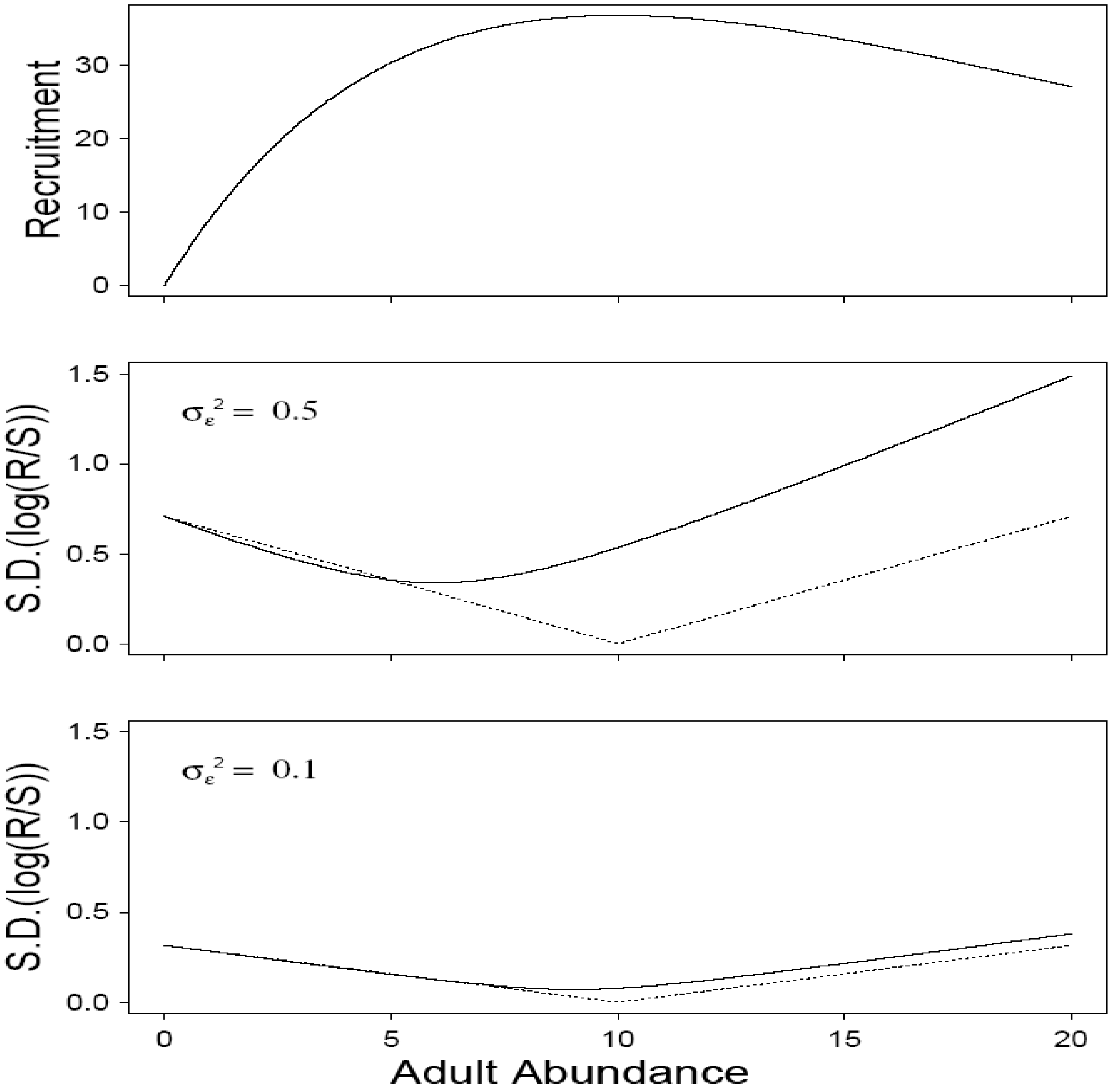


Figure 3: The relationship between recruitment (top panel) and the standard deviation of survival at median ($\sigma_\varepsilon^2 = 0.5$, middle panel) and low ($\sigma_\varepsilon^2 = 0.1$, lower panel) pre-density dependent variable mortality levels. The solid line is the exact solution and the dotted line in the approximation. The recruitment is from the equation $R = 3Se^{-\frac{1}{10}S}$.

Stock	n	P	$\text{Median}\left(\frac{\hat{\sigma}_B^2}{\hat{\sigma}_A^2}\right)$	$\text{Median}\left(\frac{\mu_{R_B}}{\mu_{R_A}}\right)$
CLUPEIFORMES	27	1.02×10^{-10}	2.32	0.84
Clupeidae	26	1.11×10^{-10}	2.38	0.87
Alewife (*Alosa pseudoharengus*)	1	0.01	12.2	0.53
Atlantic Menhaden (*Brevoortia tyrannus*)	1	0.37	1.71	0.89
Gulf Menhaden (*Brevoortia patronus*)	1	0.15	2.60	0.64
Herring (*Clupea harengus*)	19	2.36×10^{-10}	2.45	0.89
Sardine (*Sardinops sagax*)	2	0.52	1.16	0.65
Sprat (*Sprattus sprattus*)	2	0.10	3.06	0.88
Engraulidae	1	0.18	2.18	0.68
Peruvian anchoveta (*Engraulis ringens*)	1	0.18	2.18	0.68
GADIFORMES	24	3.29×10^{-8}	2.11	0.63
Gadidae	24	3.29×10^{-8}	2.11	0.63
Cod (*Gadus morhua*)	10	5.52×10^{-7}	3.38	0.62
Haddock (*Melanogrammus aeglefinus*)	6	0.04	1.64	0.61
Hake (*Merluccius merluccius*)	1	0.10	5.00	0.60
Pollock or saithe (*Pollachius virens*)	2	0.26	1.52	0.77
Red hake (*Urophysics chuss*)	1	0.48	1.05	0.38
S.A. Hake (*Merluccius capensis*)	1	0.24	1.73	0.89
Silver hake (*Merluccius bilinearis*)	2	0.01	3.37	0.32
Walleye pollock (*Theragra chalcogramma*)	1	0.11	2.09	1.21
PERCIFORMES	3	0.02	2.39	0.69
Percidae	1	0.66	0.74	1.32
Eurasian perch (*Perca fluviatilis*)	1	0.66	0.74	1.32
Scombridae	2	7.61×10^{-3}	4.92	0.58
Chub mackerel (*Scomber japonicus*)	1	0.17	2.39	0.47
Mackerel (*Scomber scombrus*)	1	5.72×10^{-3}	7.45	0.69
PLEURONECTIFORMES	6	0.62	0.86	0.85
Pleuronectidae	4	0.37	1.74	0.50
Petrale sole (*Eopsetta jordani*)	1	0.13	3.27	0.46
Plaice (*Pleuronectes platessa*)	1	0.64	0.80	0.52
Yellowtail flounder (*Limanda ferruginae*)	2	0.45	1.54	2.16
Soleidae	2	0.87	0.80	2.36
Sole (*Solea vulgaris*)	2	0.87	0.80	2.36
SALMONIFORMES	51	4.20×10^{-3}	1.43	0.58
Esociadae	1	0.26	1.43	0.81
Pike (*Esox lucius*)	1	0.26	1.43	0.81
Salmonidae	50	4.41×10^{-3}	1.37	0.57
Atlantic salmon (*Salmo salar*)	3	0.12	3.89	0.58
Chum salmon (*Oncorhynchus keta*)	3	0.13	2.09	0.94
Lake Whitefish (*Coregonus clupeaformis*)	1	0.32	5.79	6.26
Pink salmon (*Oncorhynchus gorbuscha*)	15	6.04×10^{-3}	1.56	0.56
Sockeye salmon (*Oncorhynchus nerka*)	27	0.37	1.04	0.56
Whitefish (*Coregonus lavaretus*)	1	0.01	6.01	0.34
ALL SPECIES	111	3.3×10^{-16}	1.82	0.64

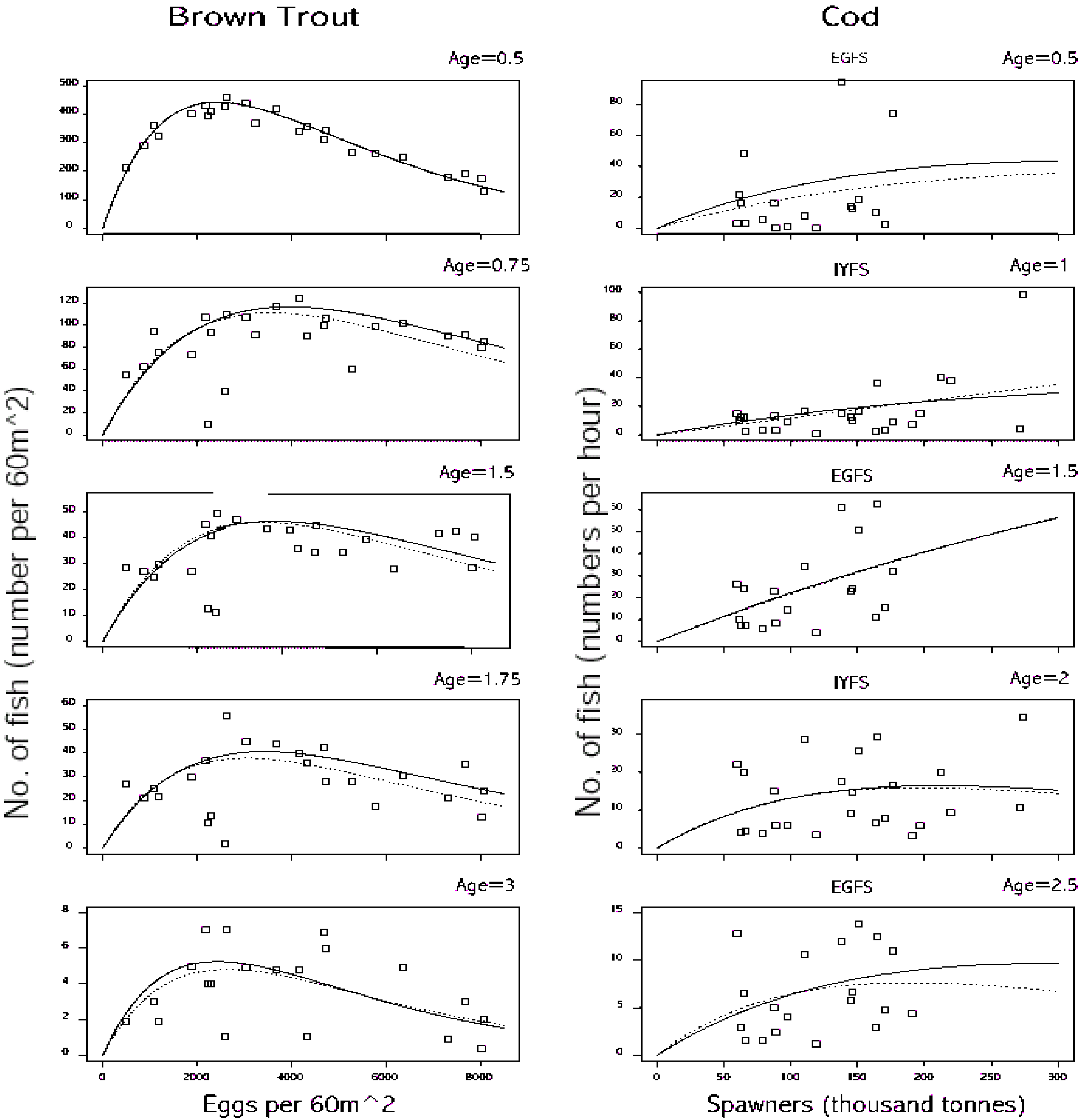

Brown Trout
Cod
Age=0.5
EGFS
Age=0.5
Age=0.75
IYFS
Age=1
Age=1.5
EGFS
Age=1.5
Age=1.75
IYFS
Age=2
Age=3
EGFS
Age=2.5
No. of fish (number per 60m^2)
No. of fish (numbers per hour)
0
2000
4000
6000
8000
Eggs per 60m^2
0
50
100
150
200
250
300
Spawners (thousand tonnes)

TABLE 1. Numbers of populations (n), results of Fisher's method to combine the probability (P) levels from one-sided significance tests to test if the variance in log survival below the midpoint of the observed adult abundance, $\hat{\sigma}_B^2$ is greater than the variance above the midpoint, $\hat{\sigma}_A^2$, the median values of the ratio of the two variances (Median$\frac{\sigma_B^2}{\sigma_A^2}$), and the median values of the ratio of the mean recruitment for SSB below the midpoint to the mean recruitment for SSB above the midpoint of the observed adult abundance.

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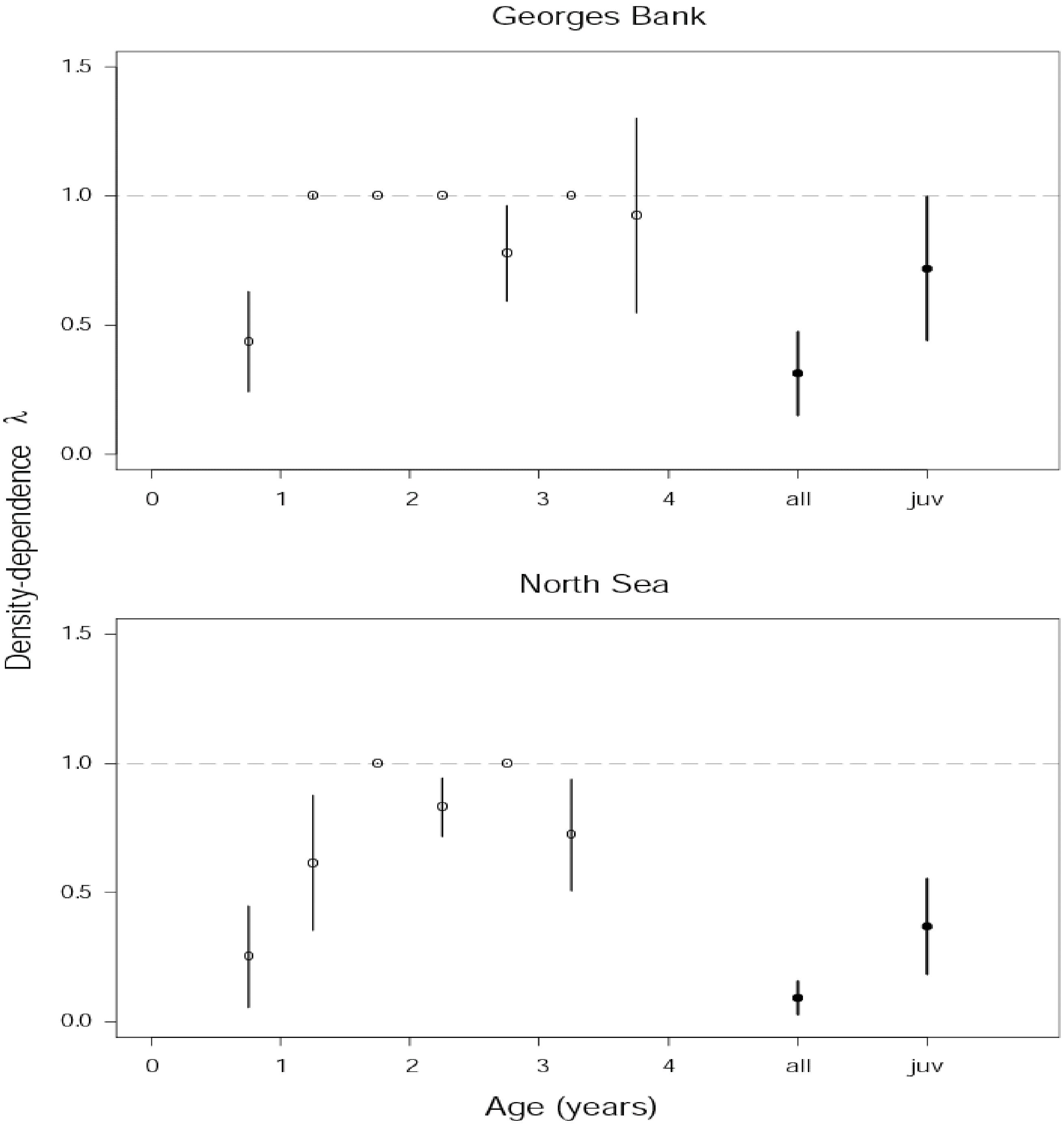
Nonlinear key factor analysis with measurement error.

- Myers and Cadigan analysis limited to one form of density-dependent mortality – mortality proportional to log abundance, other cases VERY hard.
- We have recently developed solutions for nonlinear random effects models with measurement error for the general problem that can estimate ANY nonlinear function and ANY distribution for mortality and estimation errors.
- These methods use simulated maximum likelihood methods to in a random effects nonlinear state space model using auto-differential software.


Georges Bank
North Sea
Density-dependence λ
Age (years)
1.5
1.0
0.5
0.0
0
1
2
3
4
all
juv

Predictions and Preliminary Results:

- Hjort’s strong hypothesis: never true.
- Hjort’s weak hypothesis: approximately true for gadoids, flatfish, and freshwater percids.
- Hjort is wrong for salmonids
- Small pelagics – At low abundance Hjort’s weak hypothesis true, but not true for high abundance.
- Species interactions more important.

Conclusion

- We can test Hjort's hypothesis, we now have the methods and data.