A Meta-analysis of all the spawner recruit data in the world

  

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FMAP (Future of Marine Animal Populations)
part of the Sloan Census of Life http://www.fmap.ca

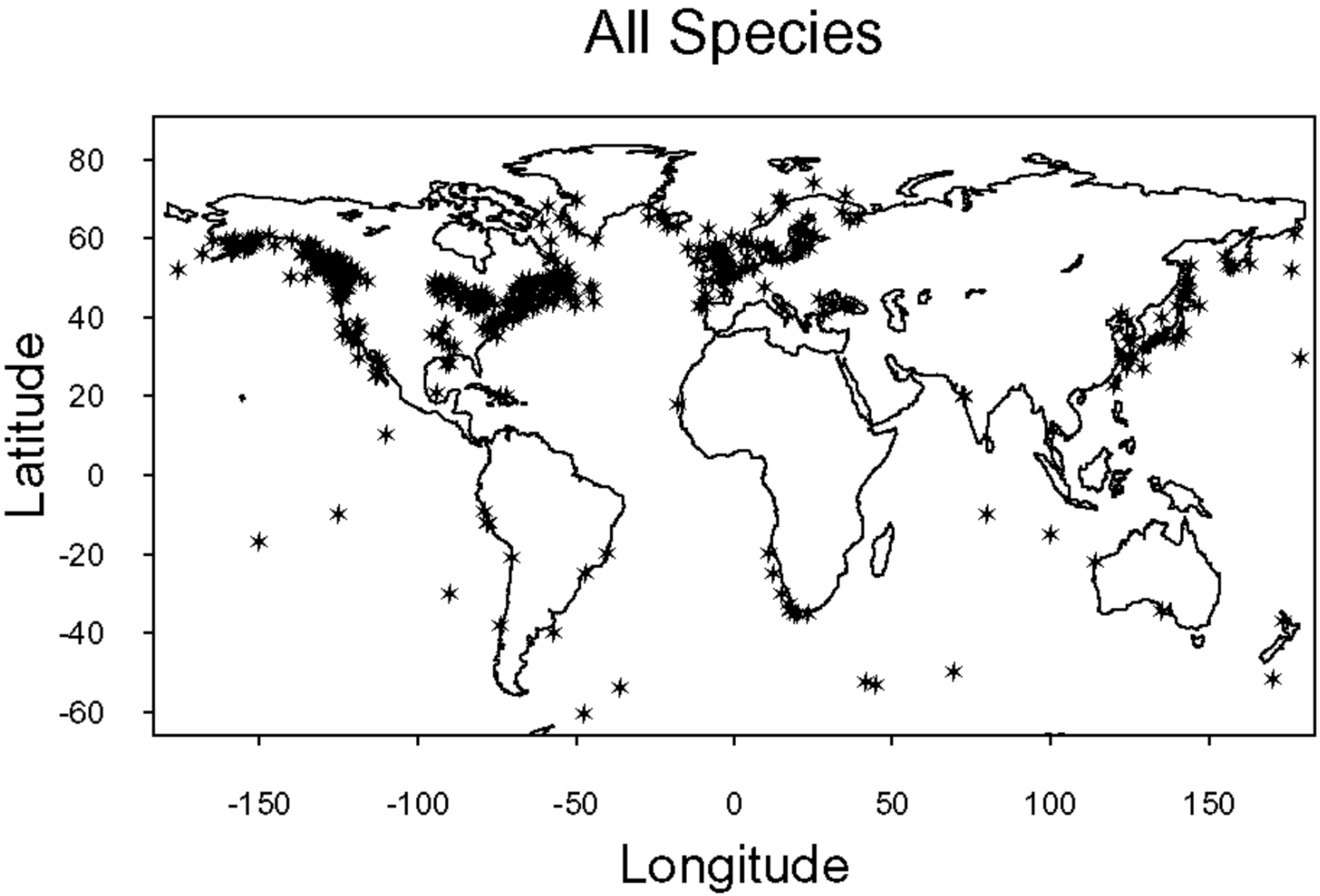
Why is estimating a Spawner-Recruit relationship so hard?

- Large estimation error
- Autocorrelated error
- Complex nonlinear process
- The issue is primarily one about creation and elimination of variability, it is simply not possible to think about these processes without models

Solutions

- Collect all the data in the world
- Analyze it in the right way using meta-analytic methods

Meta-analysis has fundamentally altered the practice of medicine.



http://fish.dal.ca

General result 1:

- More Egg => More Fish

Three simple questions

1. Does the largest recruitment occur when the spawner abundance is high?

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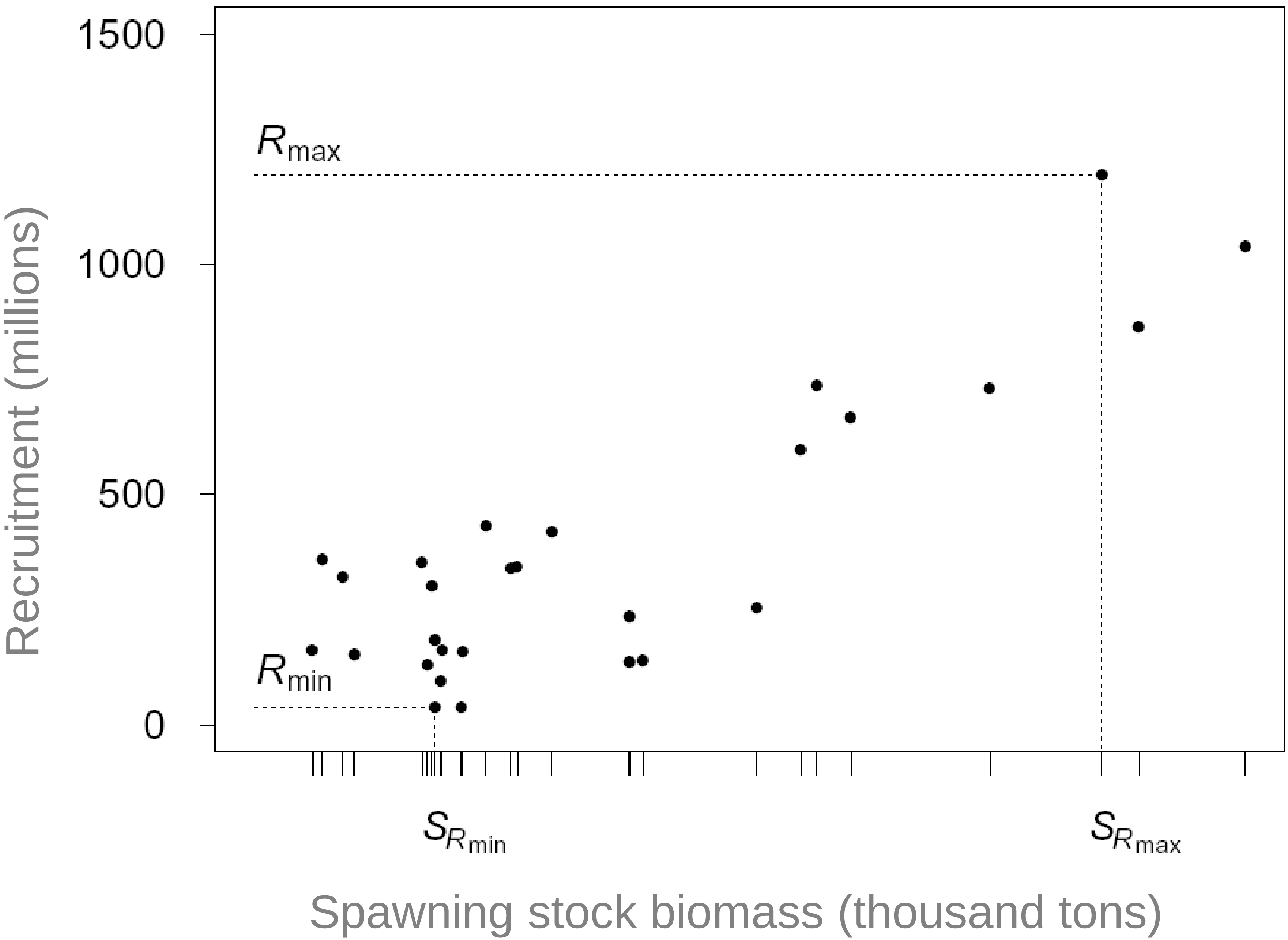
2. Does the smallest recruitment occur when spawner abundance is low?

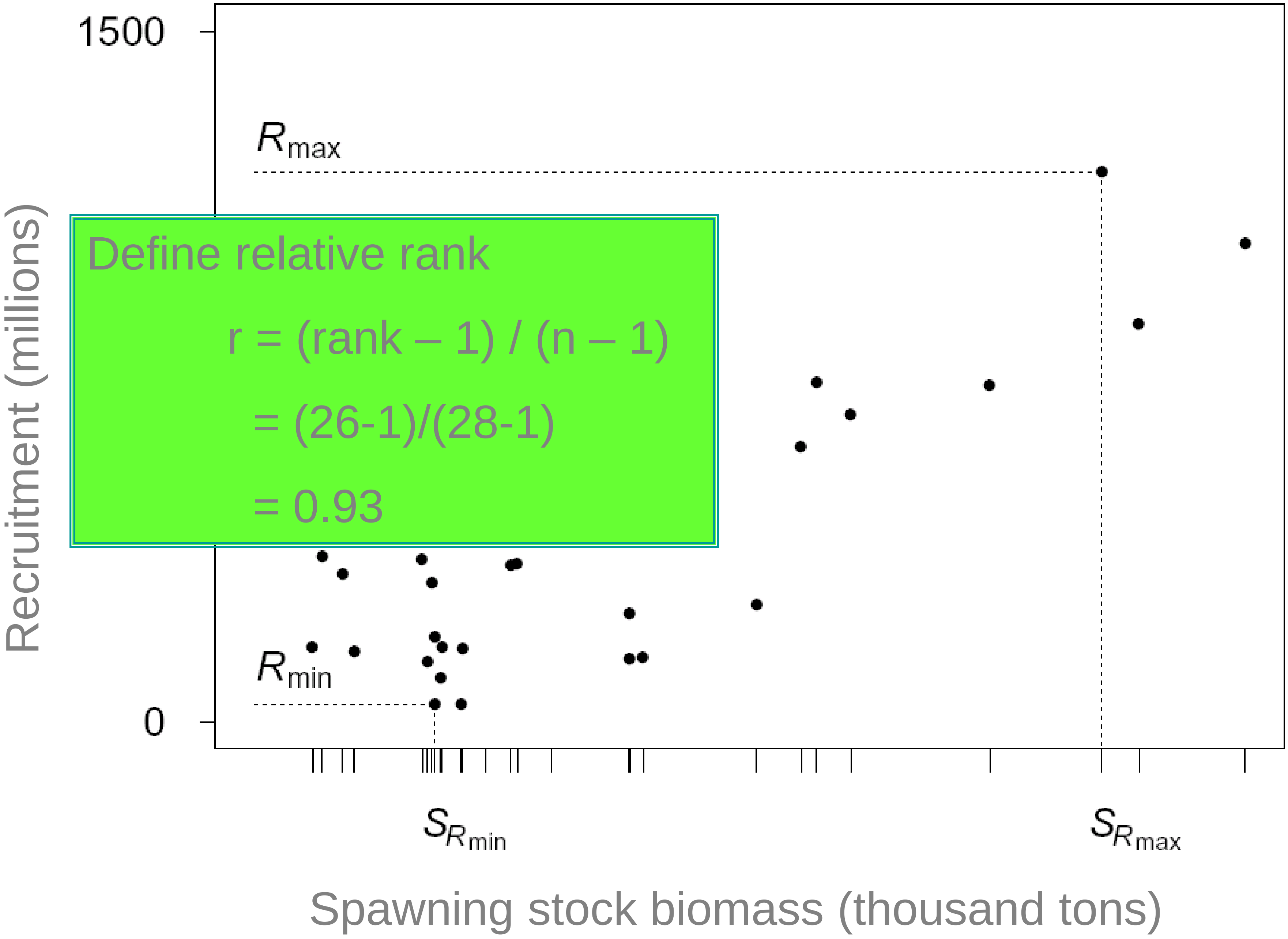
Three simple questions

1. Does the largest recruitment occur when the spawner abundance is high?
2. Does the smallest recruitment occur when spawner abundance is low?
3. Is the mean recruitment higher if the spawner abundance is above rather than below the median?

Myers RA, Barrowman NJ (1996)



Myers RA, Barrowman NJ (1996)



Define relative rank

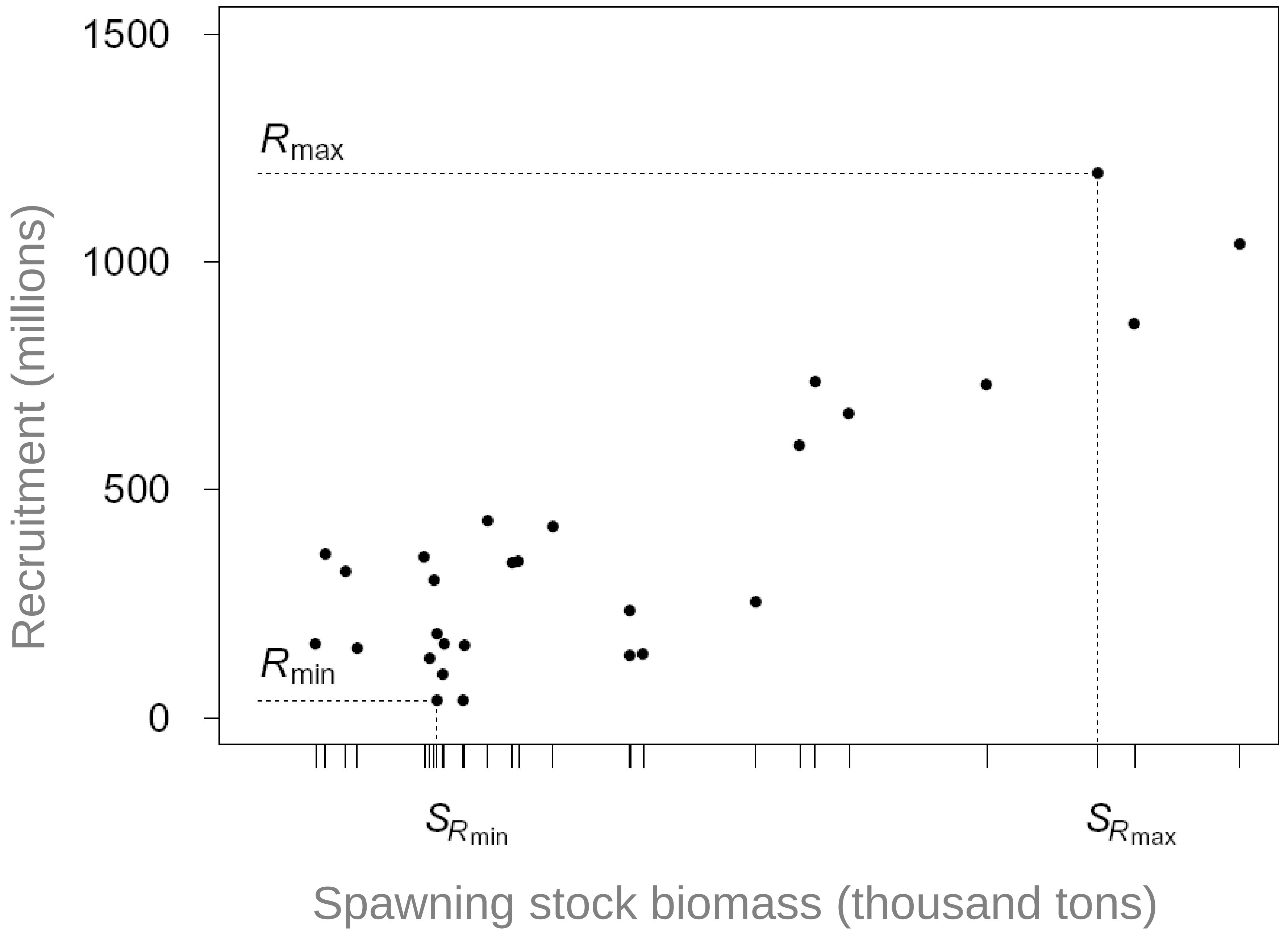
$$r = (\text{rank} - 1) / (n - 1)$$
$$= (26-1)/(28-1)$$
$$= 0.93$$

Summarizing information from more than one population

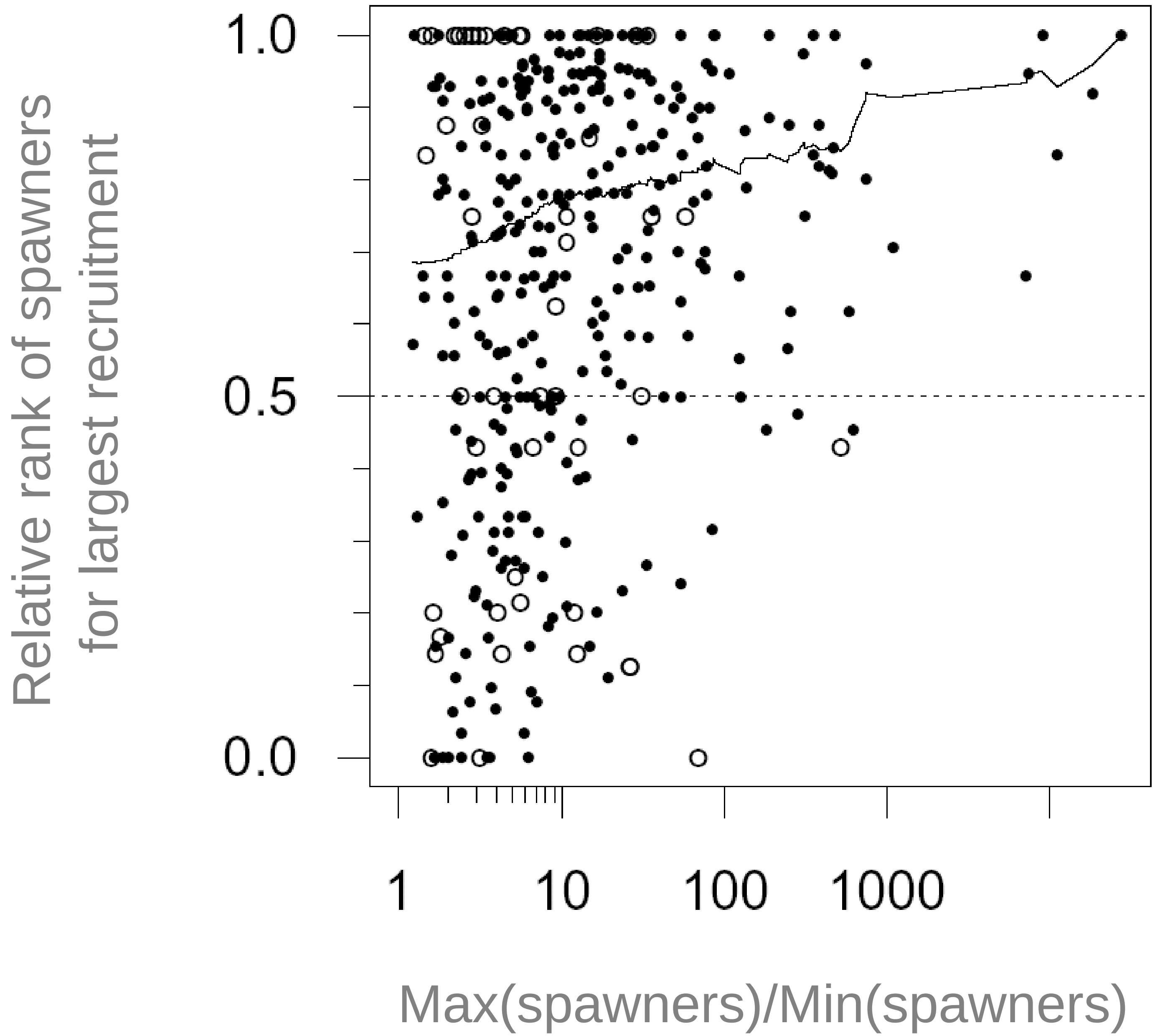
- Weighted mean of relative ranks

$$\frac{\sum_{i=1}^{k} n_i r_{\max,i}}{\sum_{i=1}^{k} n_i}$$

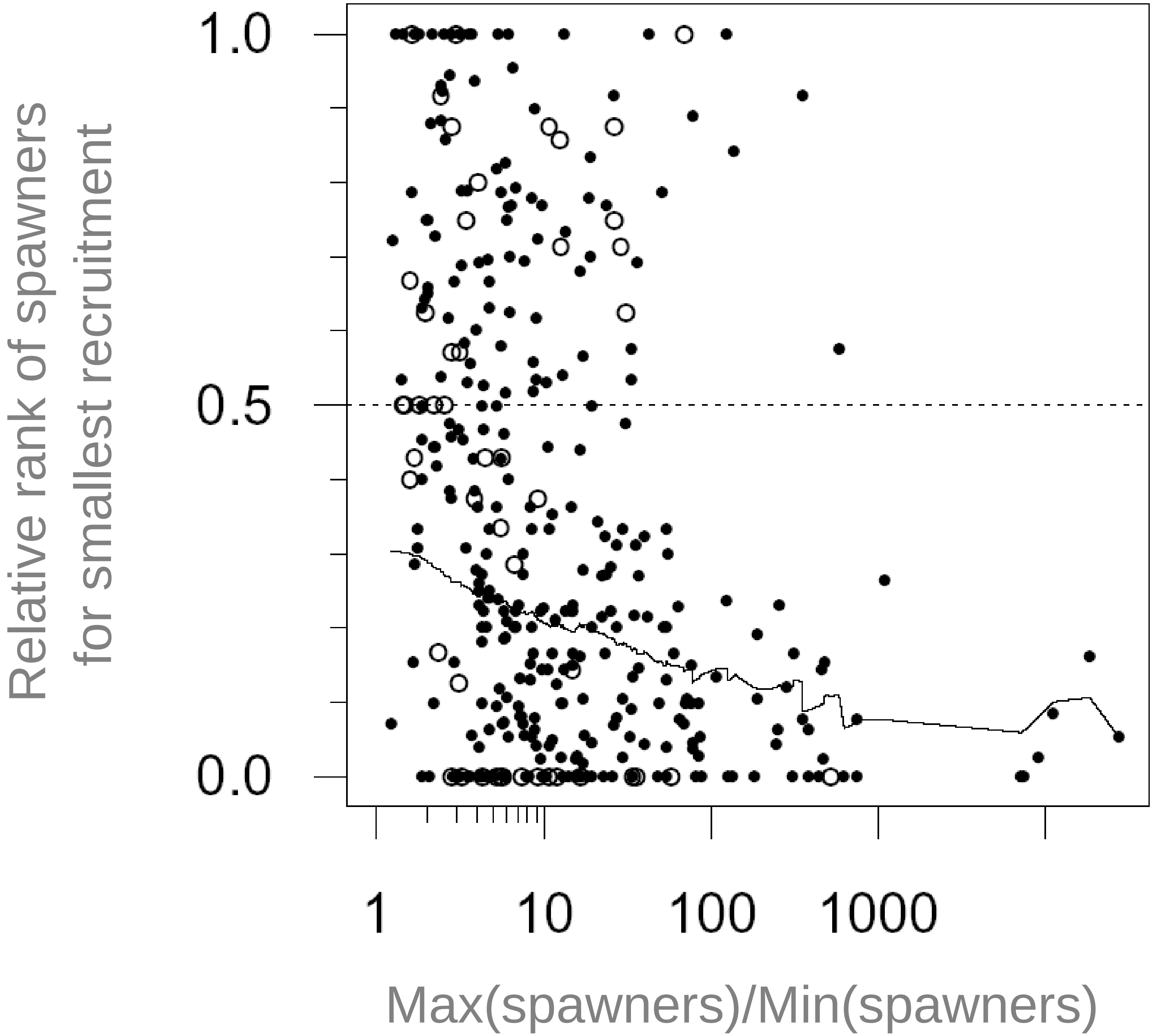
- If spawner abundance and recruitment were independent, the expected value of $r_{\max,i}$ would be 0.5



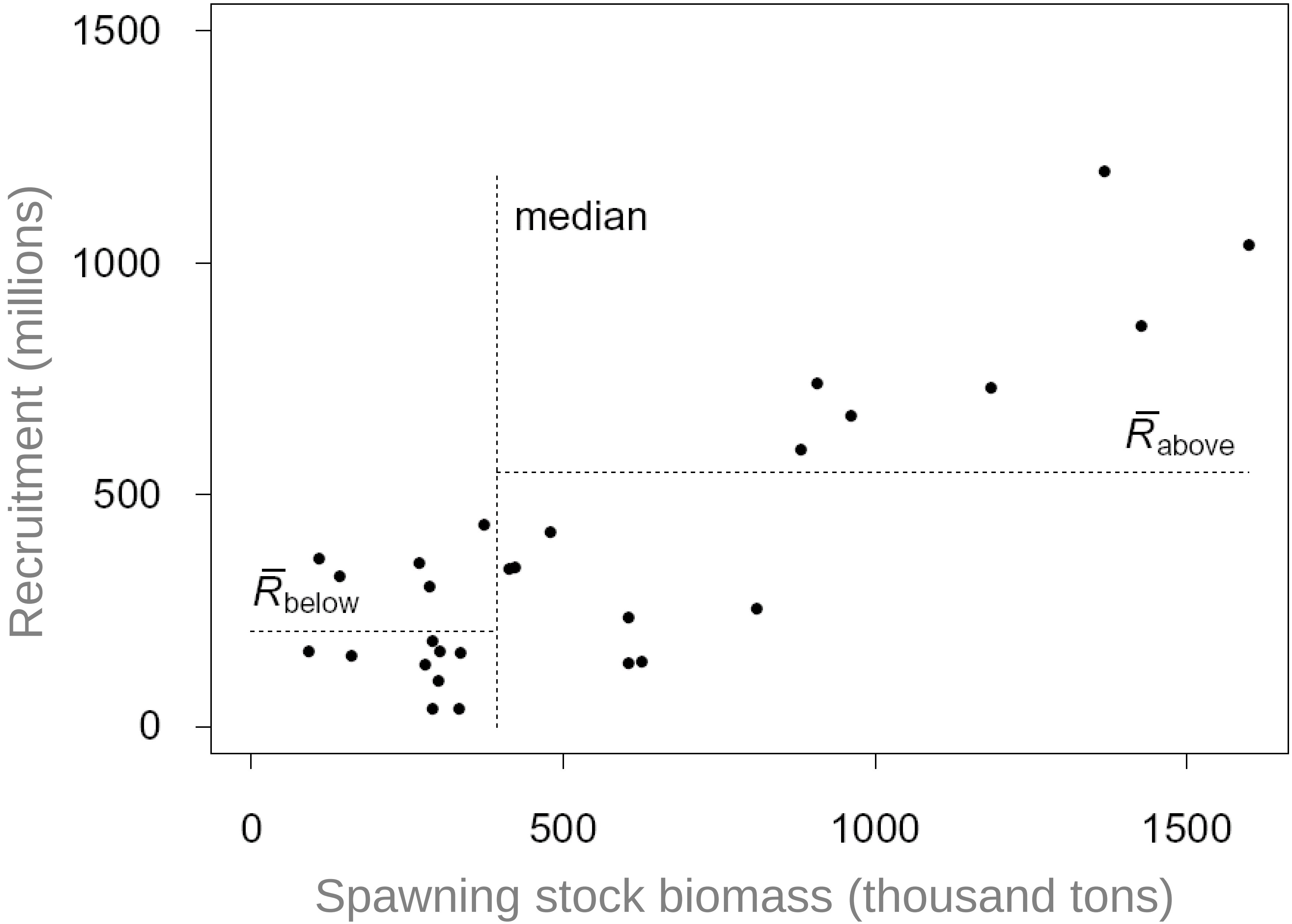
1500
1000
500
0
Recruitment (millions)
R max
R min
S R min
S R max
Spawning stock biomass (thousand tons)



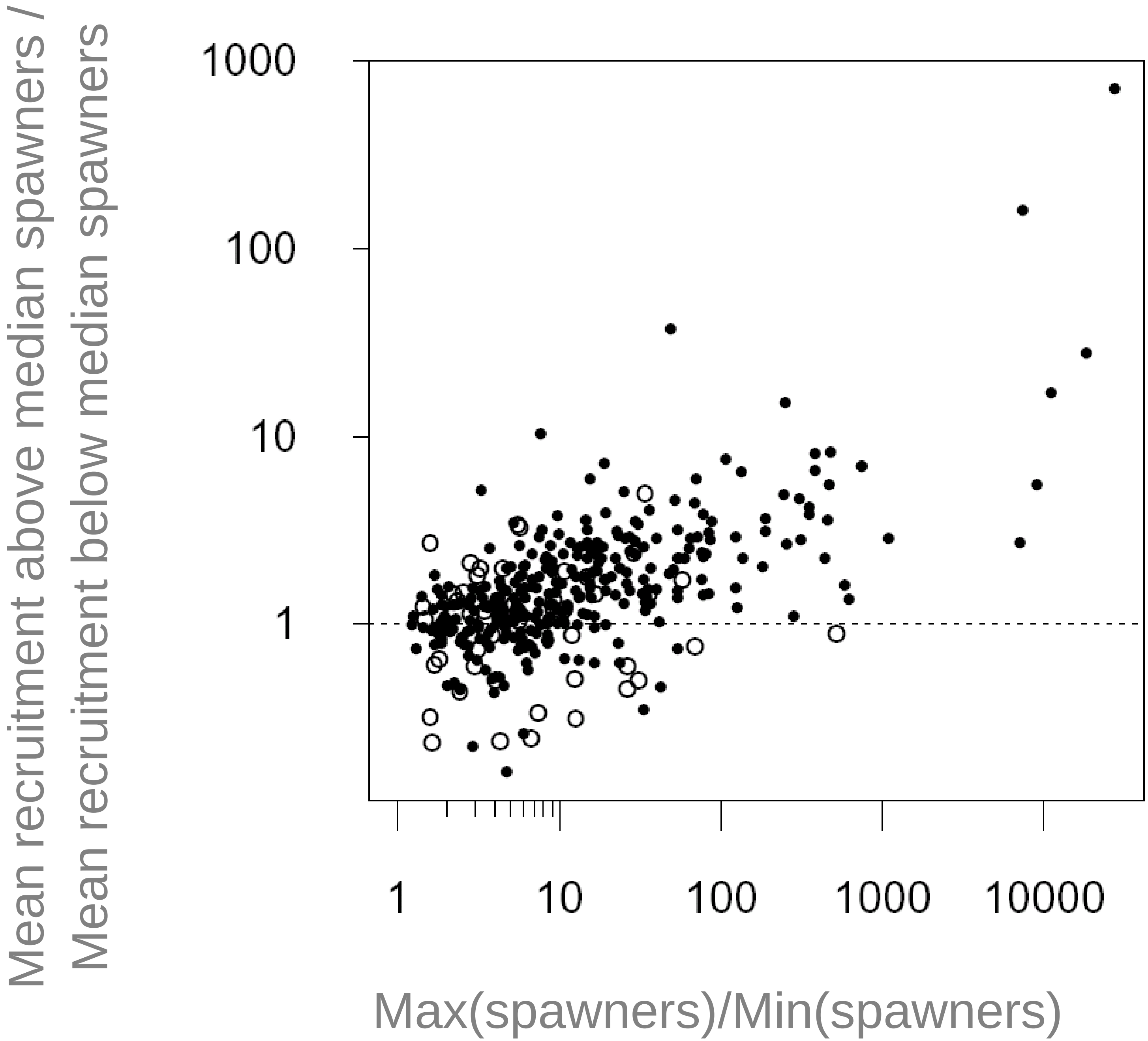
Myers RA, Barrowman NJ (1996)



Myers RA, Barrowman NJ (1996)



1500
1000
500
0
Recruitment (millions)
median
$\bar{R}_{above}$
$\bar{R}_{below}$
0
500
1000
1500
Spawning stock biomass (thousand tons)



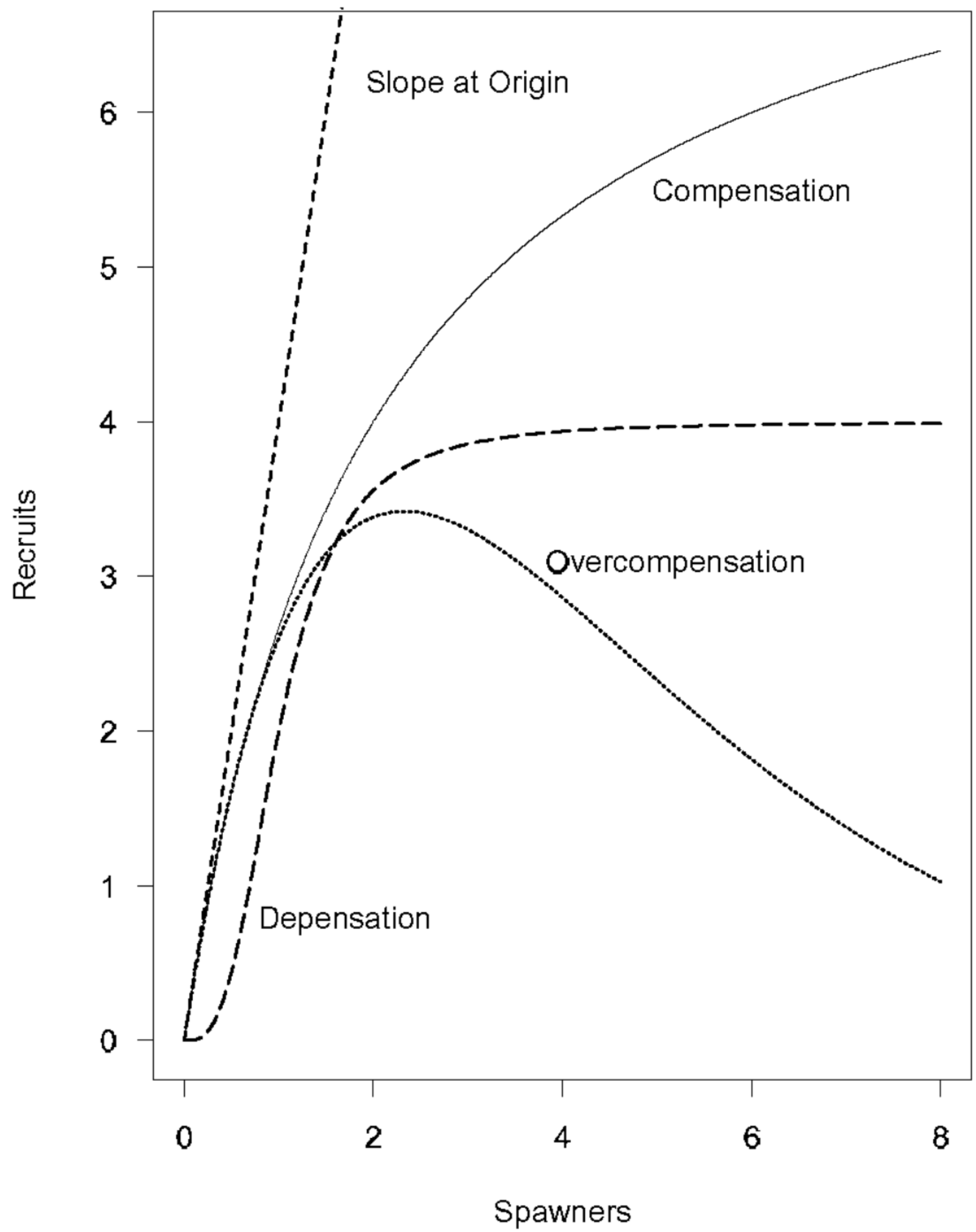
Myers RA, Barrowman NJ (1996)

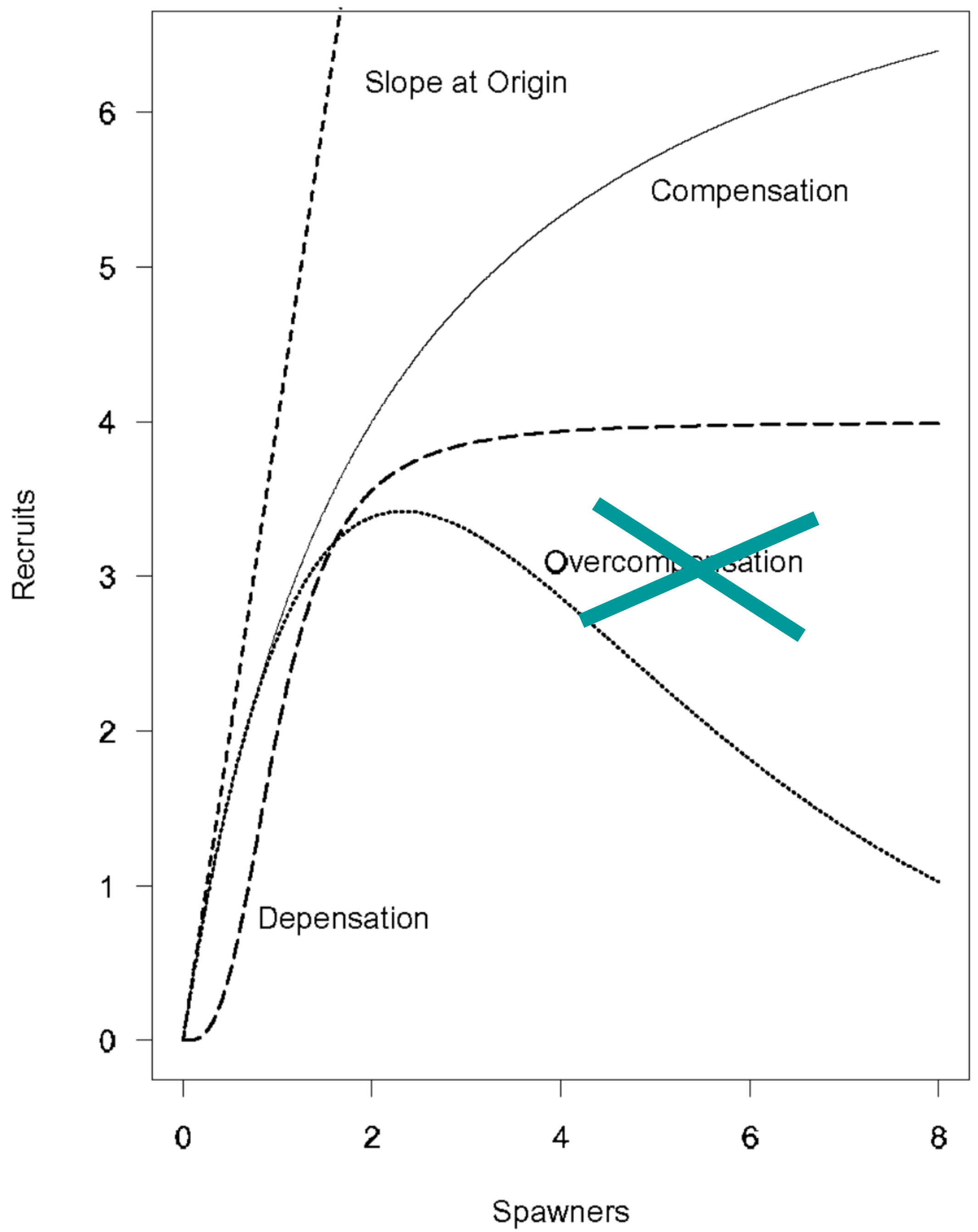
What does this imply 1:

- Compensation (the ability of a population to compensate for reduction in spawner numbers) is not infinite.

What does this imply 2:

Ricker type recruitment is very rare, at least in the range of spawner abundances usually observed in exploited populations (it is not good for the fish to kill a lot of them).

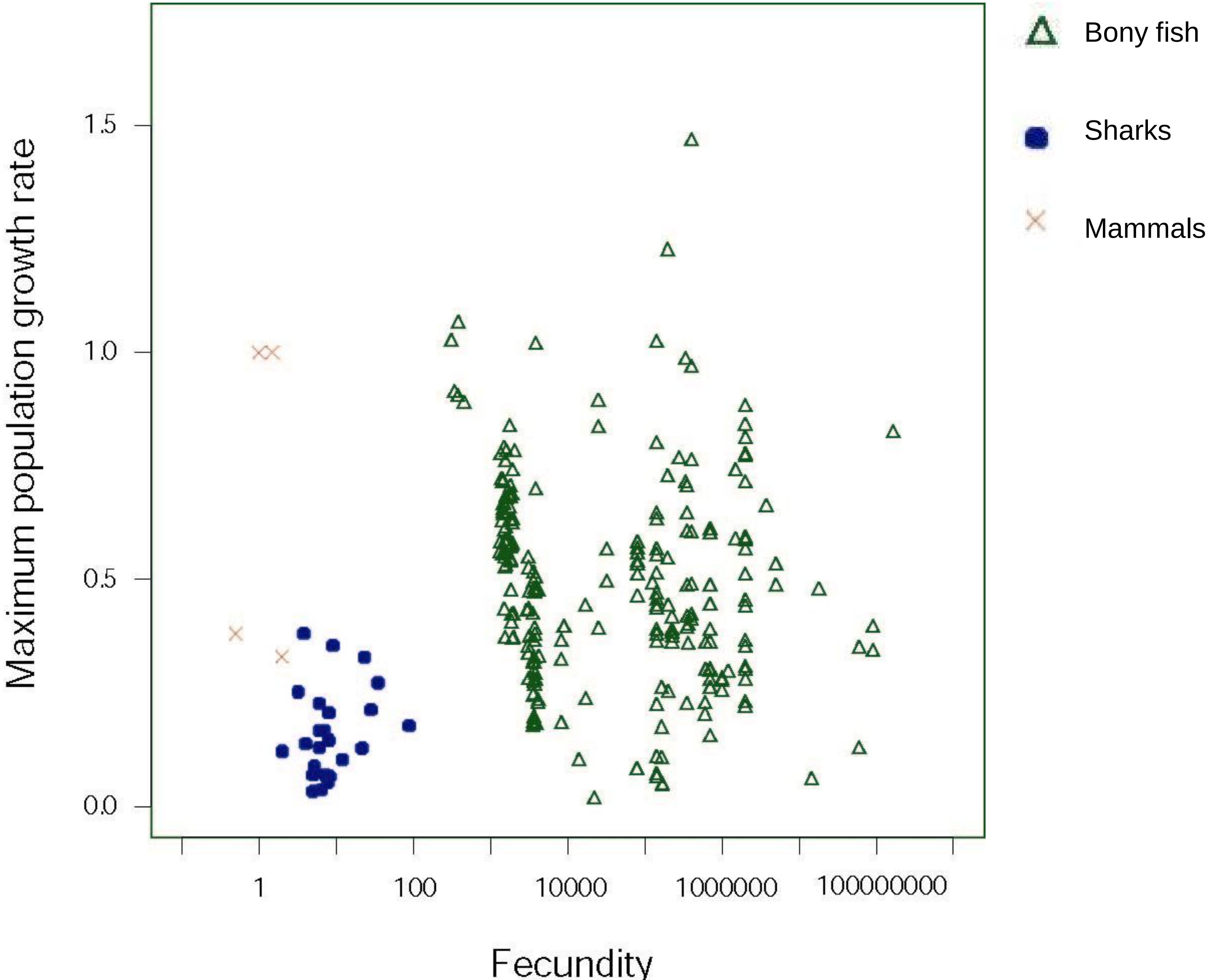

Slope at Origin
Compensation
Overcompensation
Depensation
Recruits
Spawners
0
1
2
3
4
5
6
0
2
4
6
8

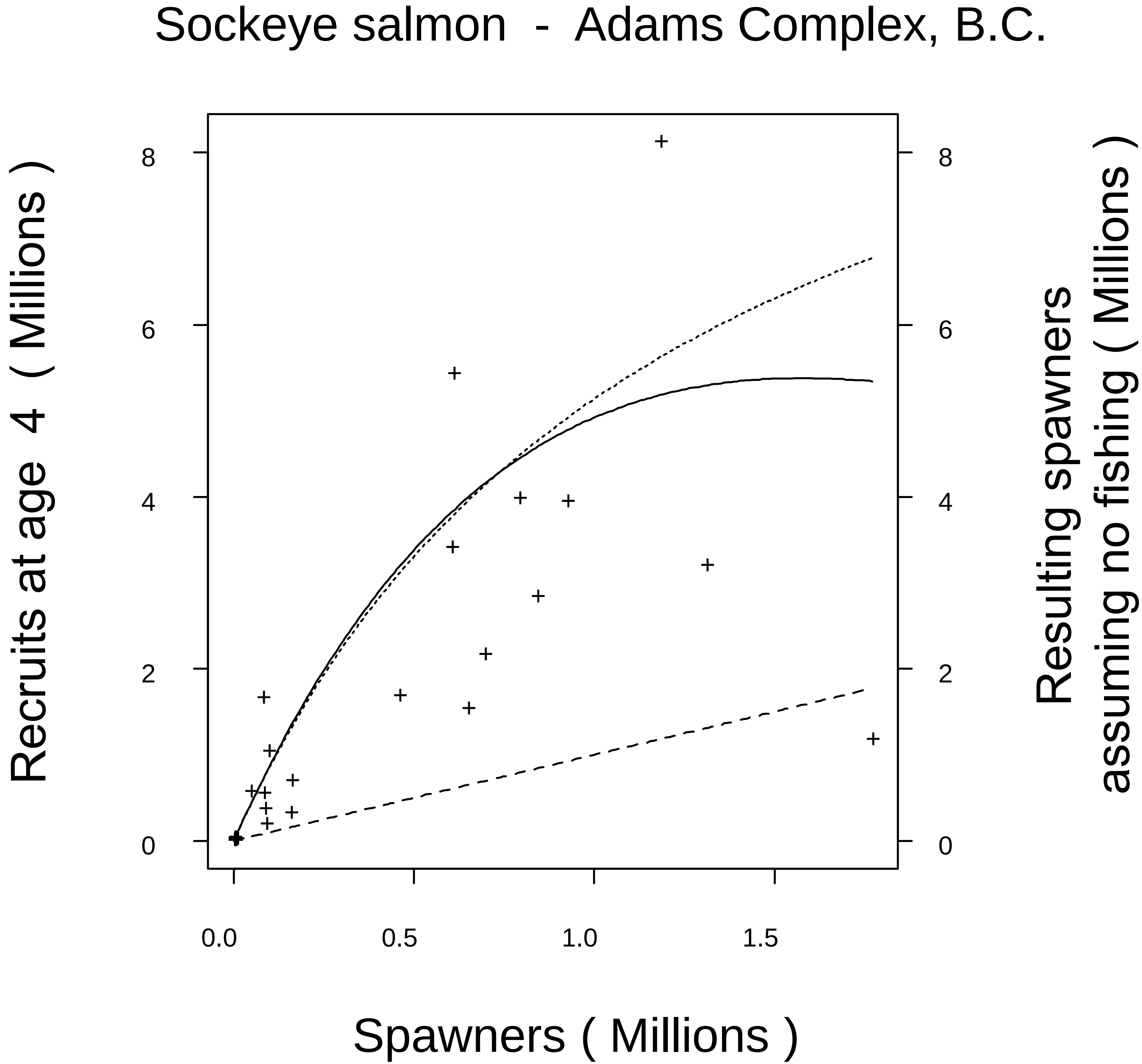

Slope at Origin
Compensation
Overcompensation
Depensation
Recruits
Spawners
0
1
2
3
4
5
6
0
2
4
6
8

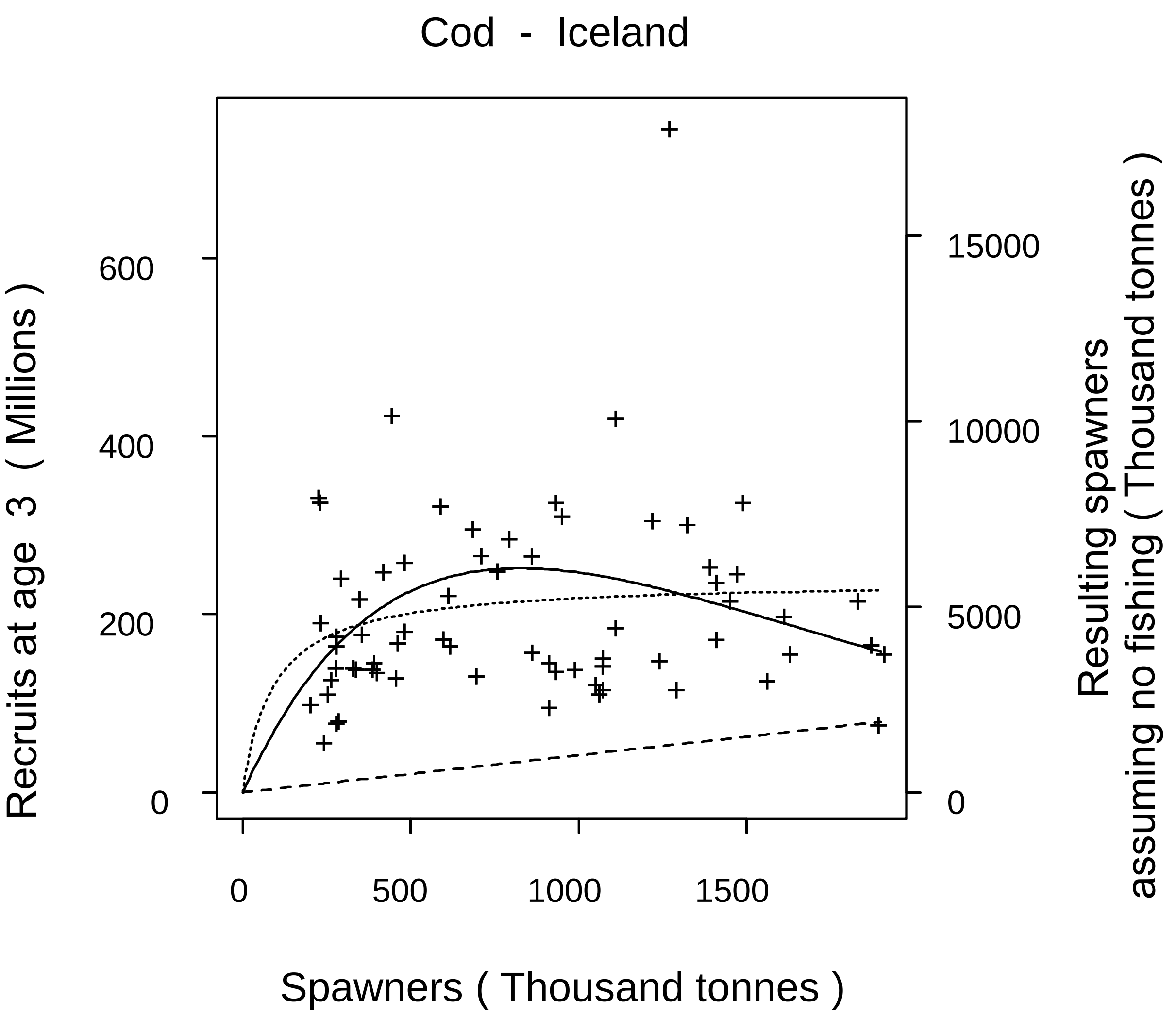
General Result 2:

- The level of compensation (the scope for the reduction in density-dependent mortality to allow a population increase) is relative constant among almost all fish species

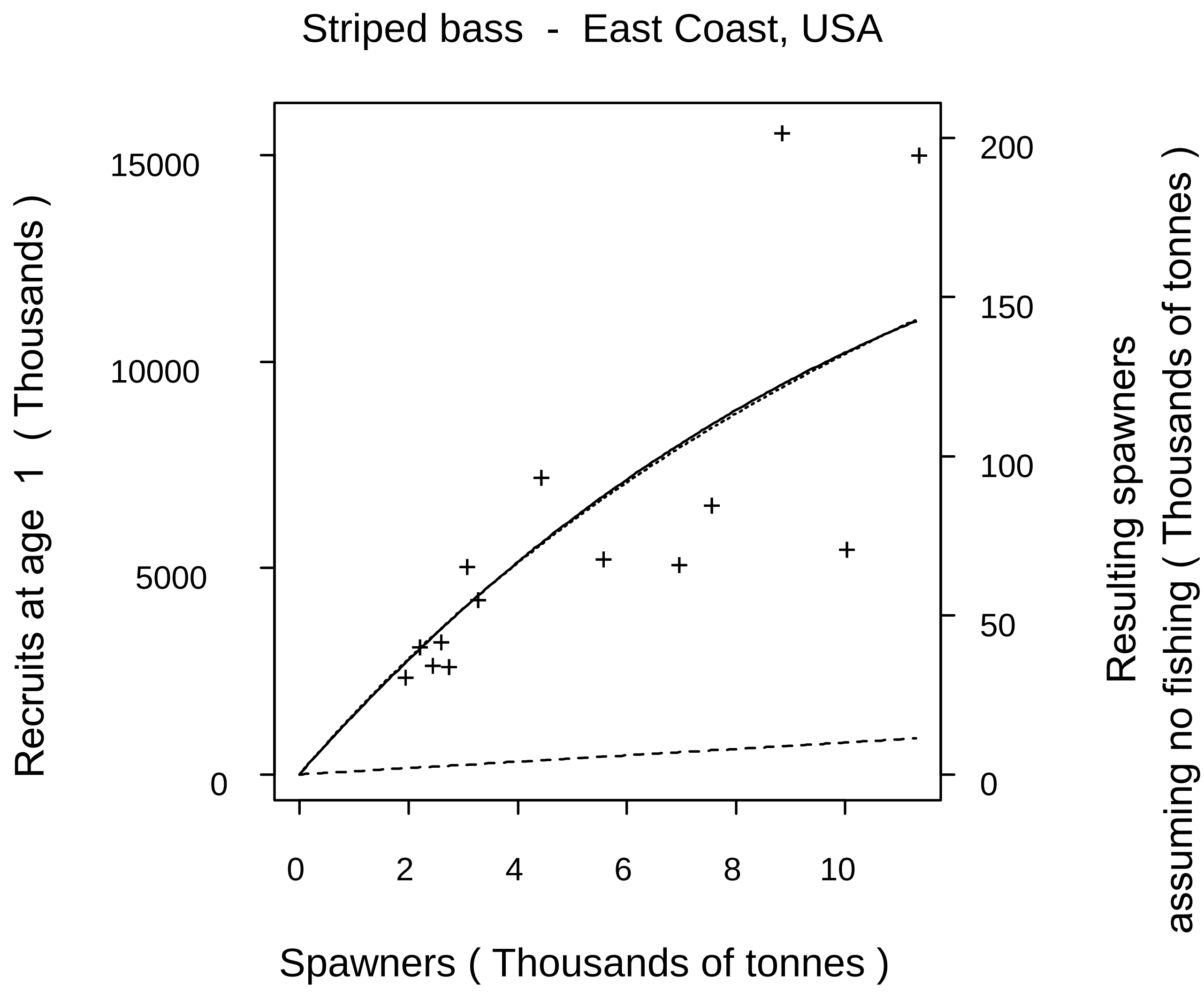
What is the maximum interest rate (on average) you can obtain by investing in Icelandic cod futures?

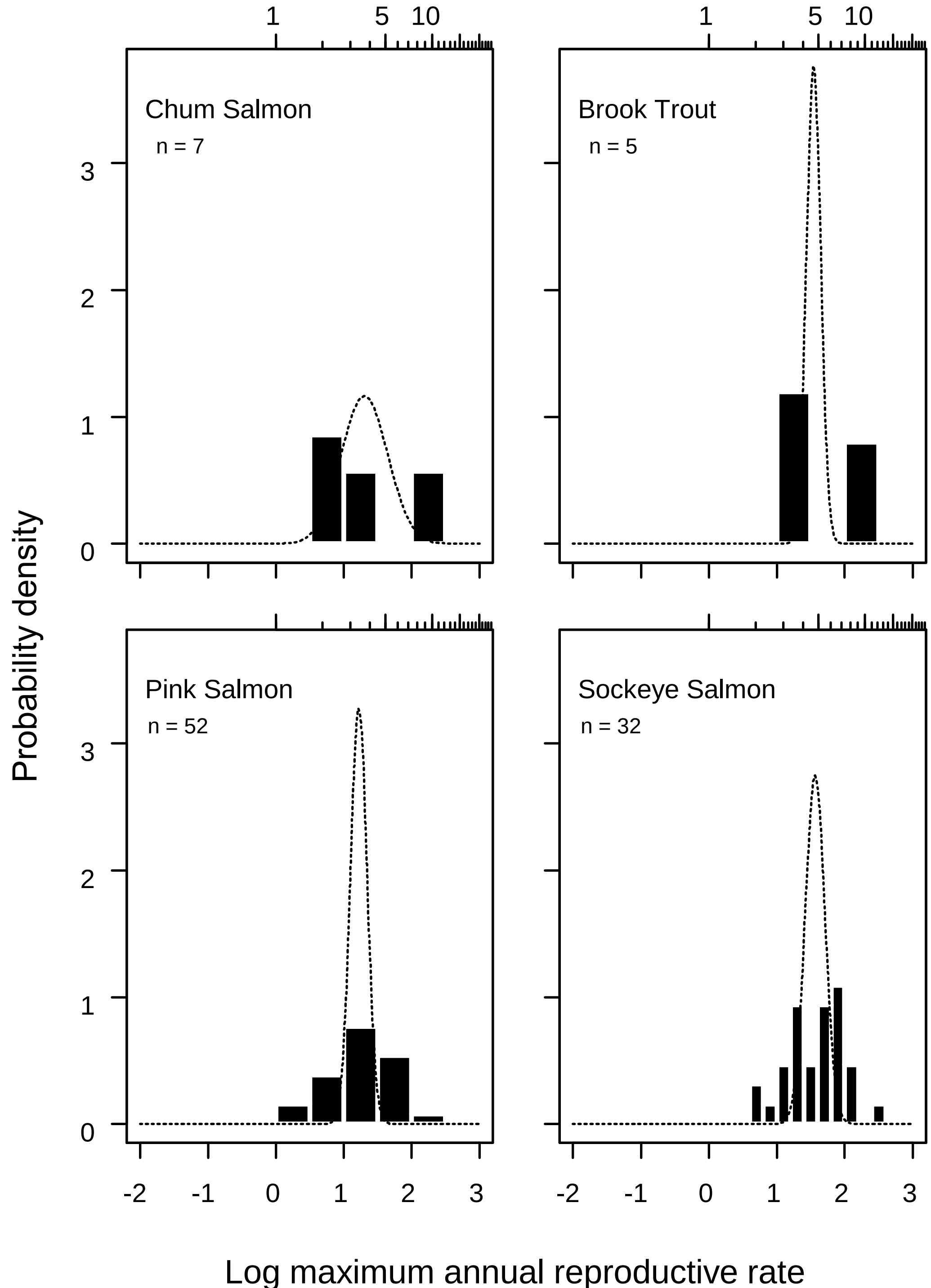



Sockeye salmon - Adams Complex, B.C.
Recruits at age 4 (Millions)
Resulting spawners
assuming no fishing (Millions)
Spawners (Millions)
0
2
4
6
8
0.0
0.5
1.0
1.5

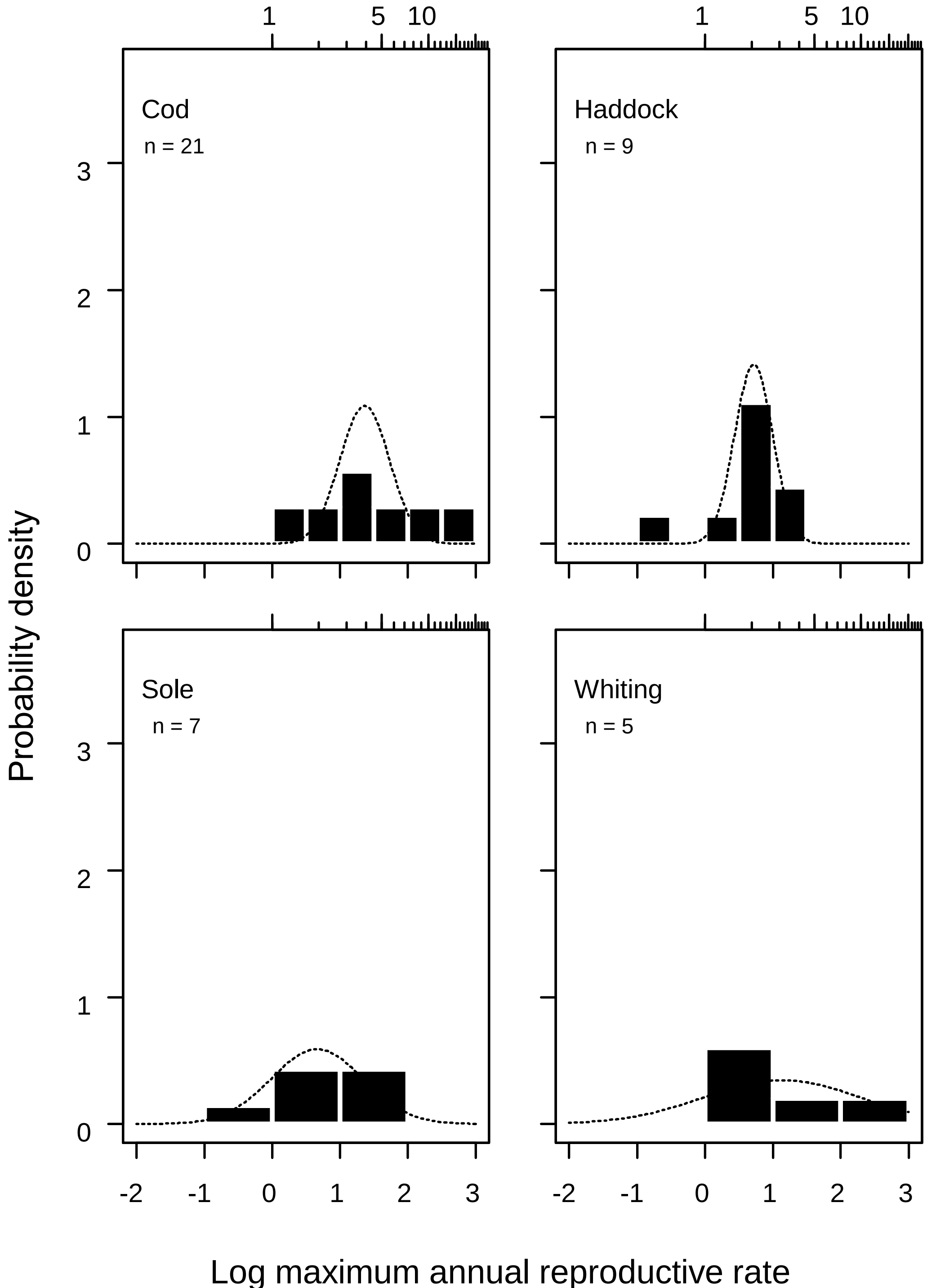


Cod - Iceland
Recruits at age 3 (Millions)
0
200
400
600
Resulting spawners
assuming no fishing (Thousand tonnes)
0
5000
10000
15000
0
500
1000
1500
Spawners (Thousand tonnes)


Striped bass - East Coast, USA
Recruits at age 1 (Thousands)
0
5000
10000
15000
Spawners (Thousands of tonnes)
0
2
4
6
8
10
Resulting spawners
assuming no fishing (Thousands of tonnes)
0
50
100
150
200

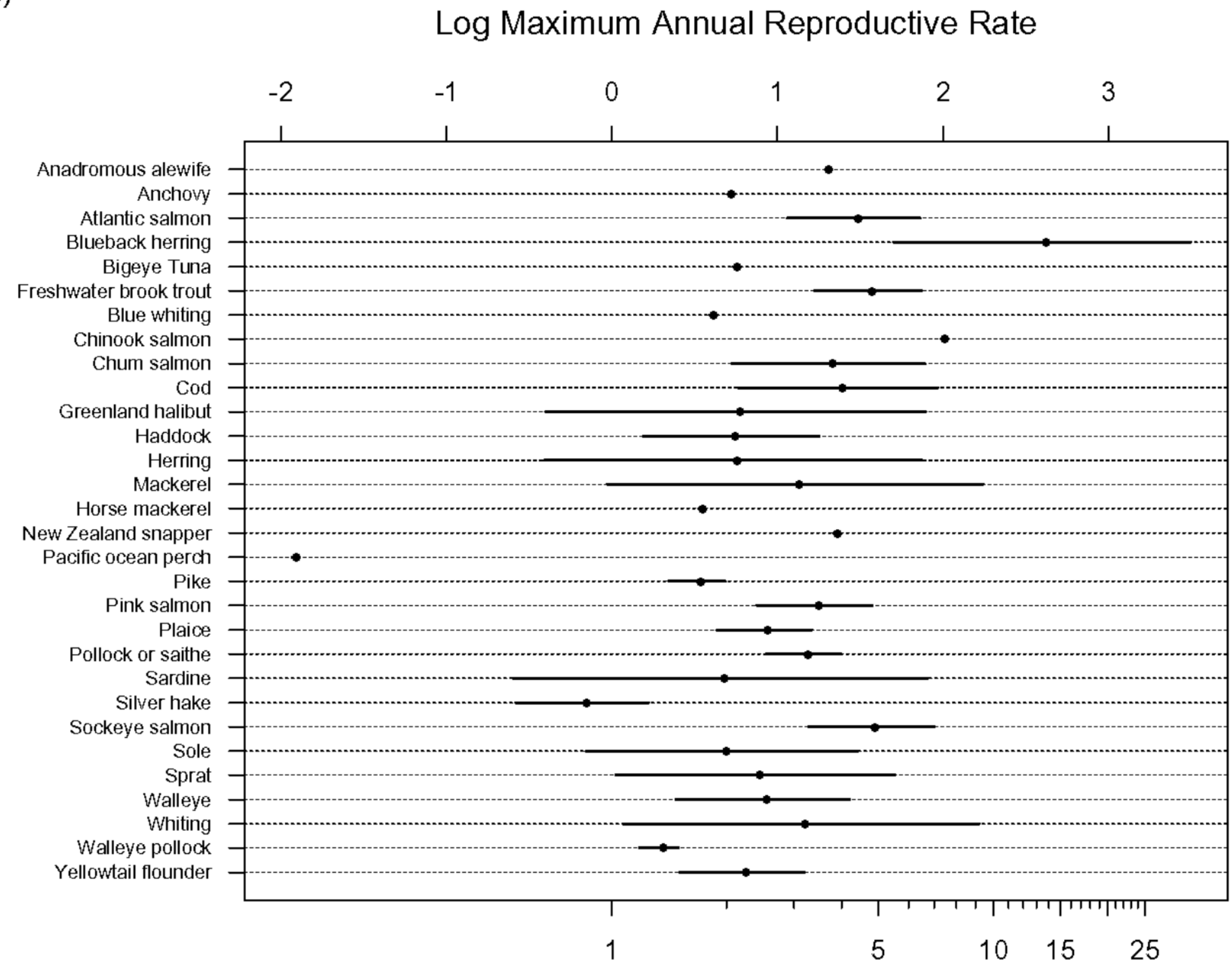


Myers, Bowen, Barrowman 1999

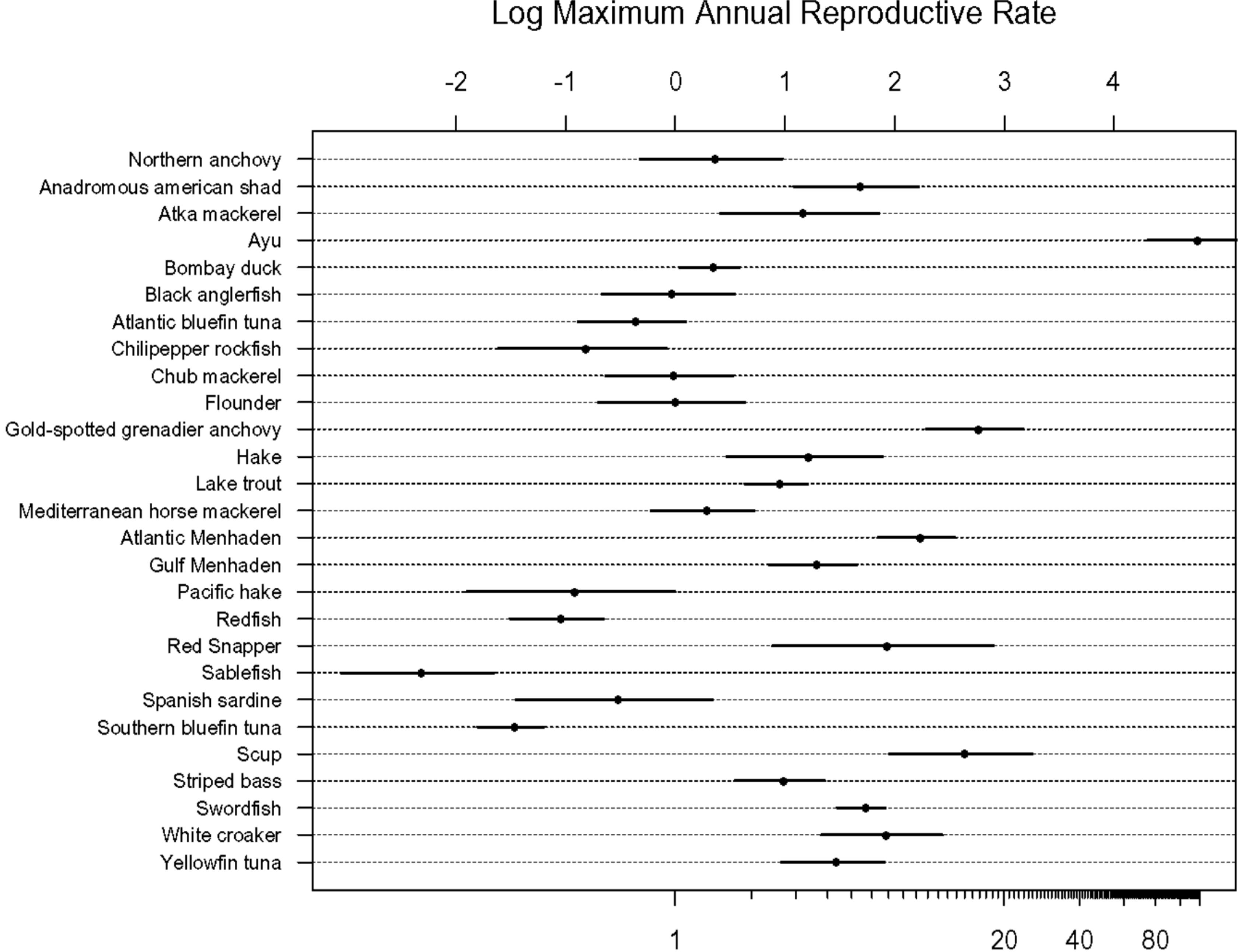


Myers, Bowen, Barrowman 1999

a)

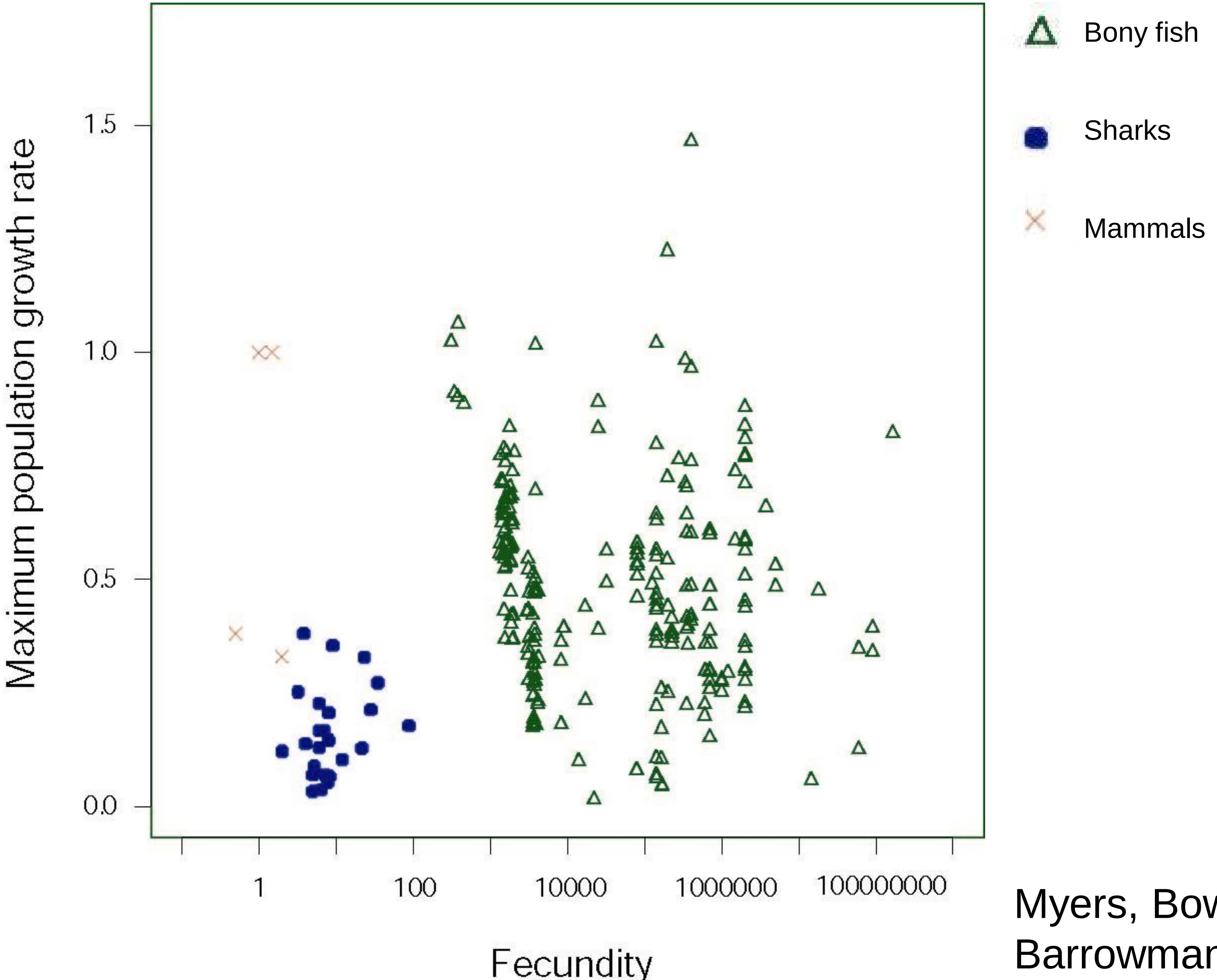


Maximum average rate that spawners can produce replacement spawners per year



Maximum average rate that spawners can produce replacement spawners per year

Are fish different from mammals?

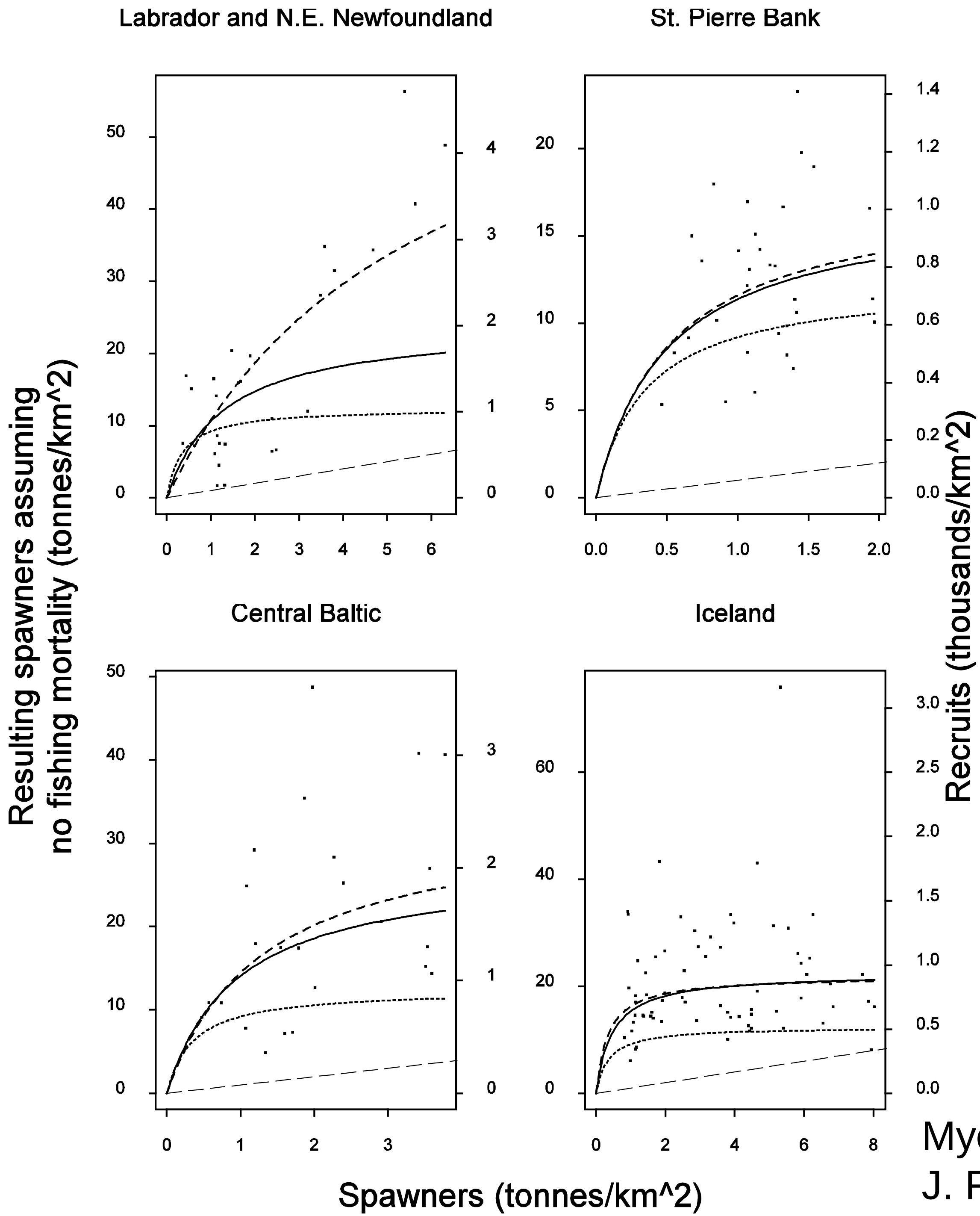


Myers, Bowen, Barrowman 1999

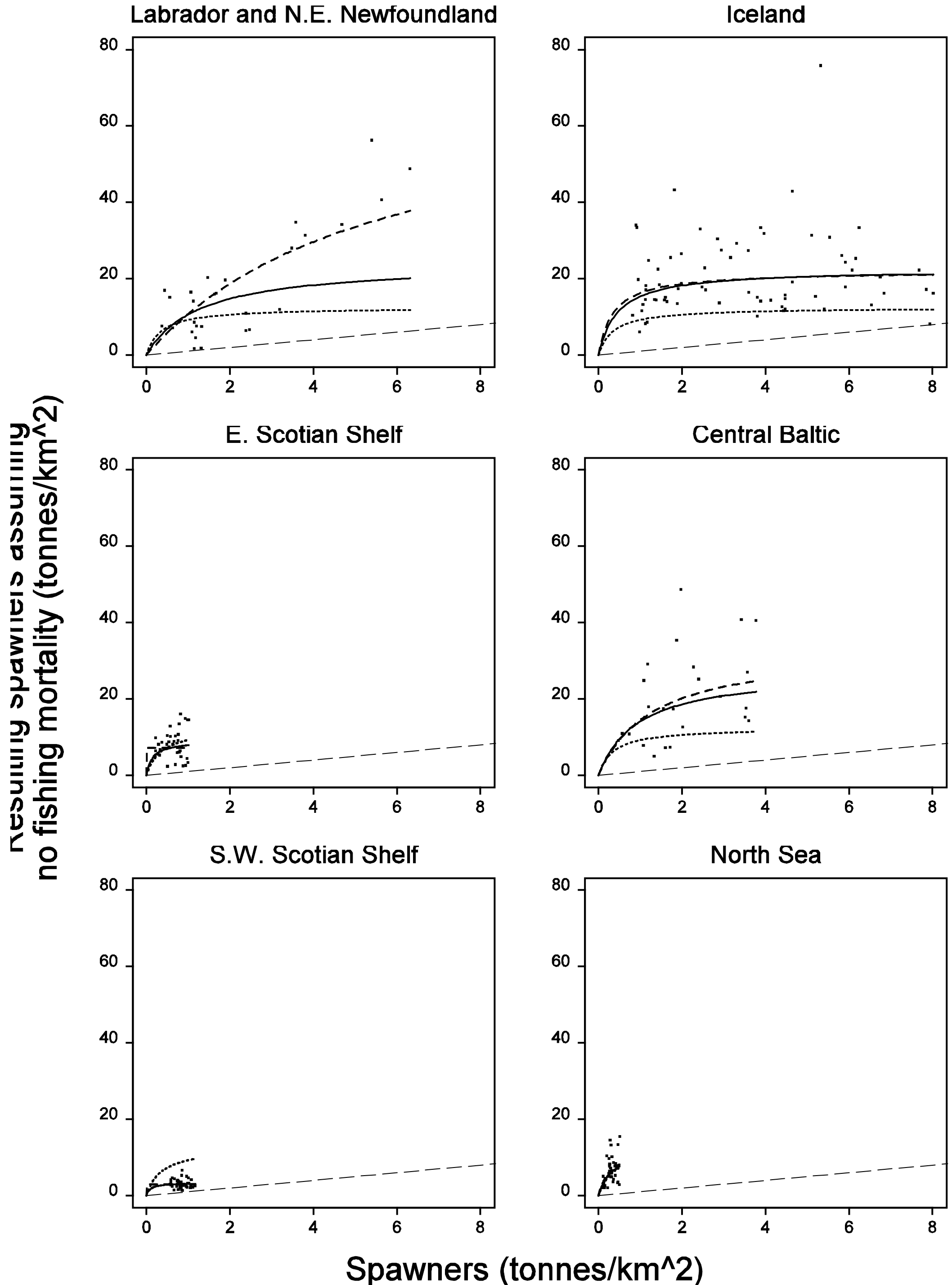
What is the carrying capacity of the world's cod stocks?

- I will use nonlinear mixed effects models to combine all the data on the worlds cod stocks.
- Production will be standardized by shelf area.

Myers et al. Can. J. Fish. Aq. Sci. 1999

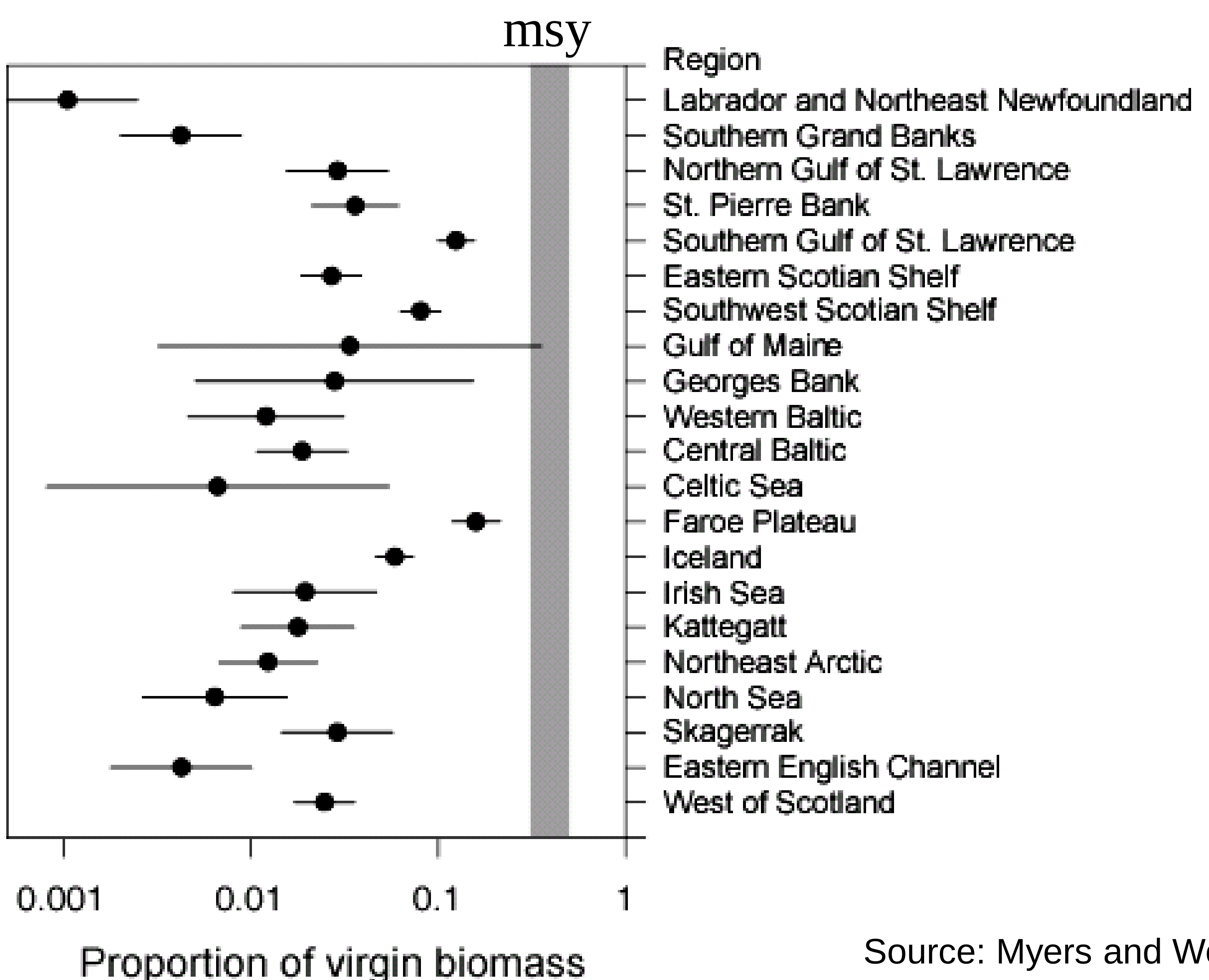


Myers et al. Can. J. Fish. Aq. Sci. 1999

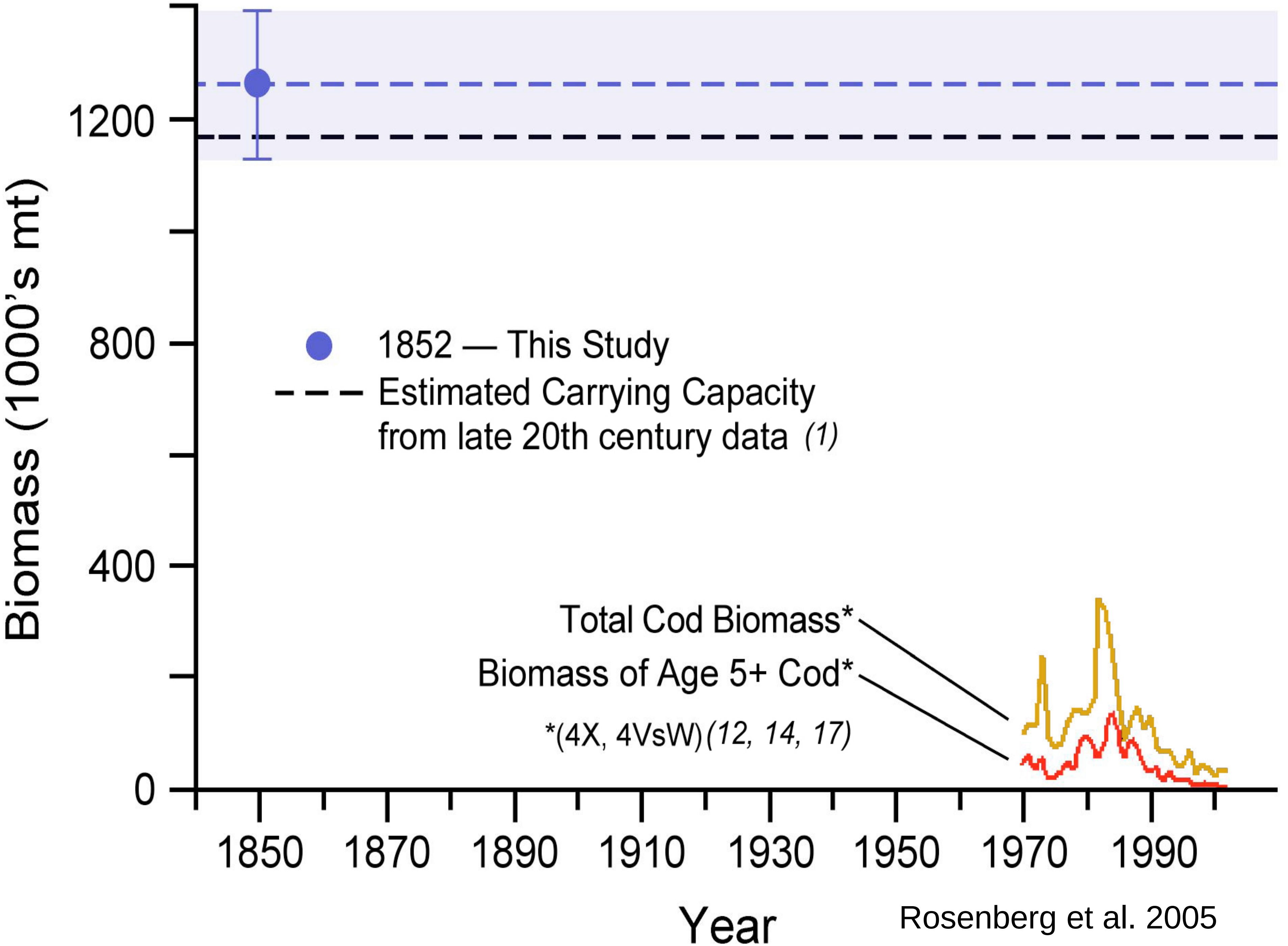


Myers et al. Can. J. Fish. Aq. Sci. 1999

There is much less than 10% of cod left -



Source: Myers and Worm 2005.
Proc. R. Soc. Lond. B



Rosenberg et al. 2005

Two Ways to Look at Spawner Recruit Data

- Use Virtual Population Analysis to obtain an estimate of scope of compensation (we just did this)
- Use Meta-analytic nonlinear, non-Gaussian state space models, where age specific survey data is used.

1-Compensation

Abundance

Dynamical Equation: $$N_{t,1} = N_{t,0}\, e^{-m - (1-\lambda) \log N_{t,0} + \varepsilon_t}$$

Cohort Age

Log Abundance

Log Transformation: $$L_{t,a} = \log N_{t,a}$$

Abundance

Background Mean Mortality Stochastic Mortality

Dynamical Equation for Log Abundance: $$L_{t,1} = -m + \lambda L_{t,0} + \varepsilon_t$$

Myers and Cadigan 1993a,b 1993

Model the research survey data

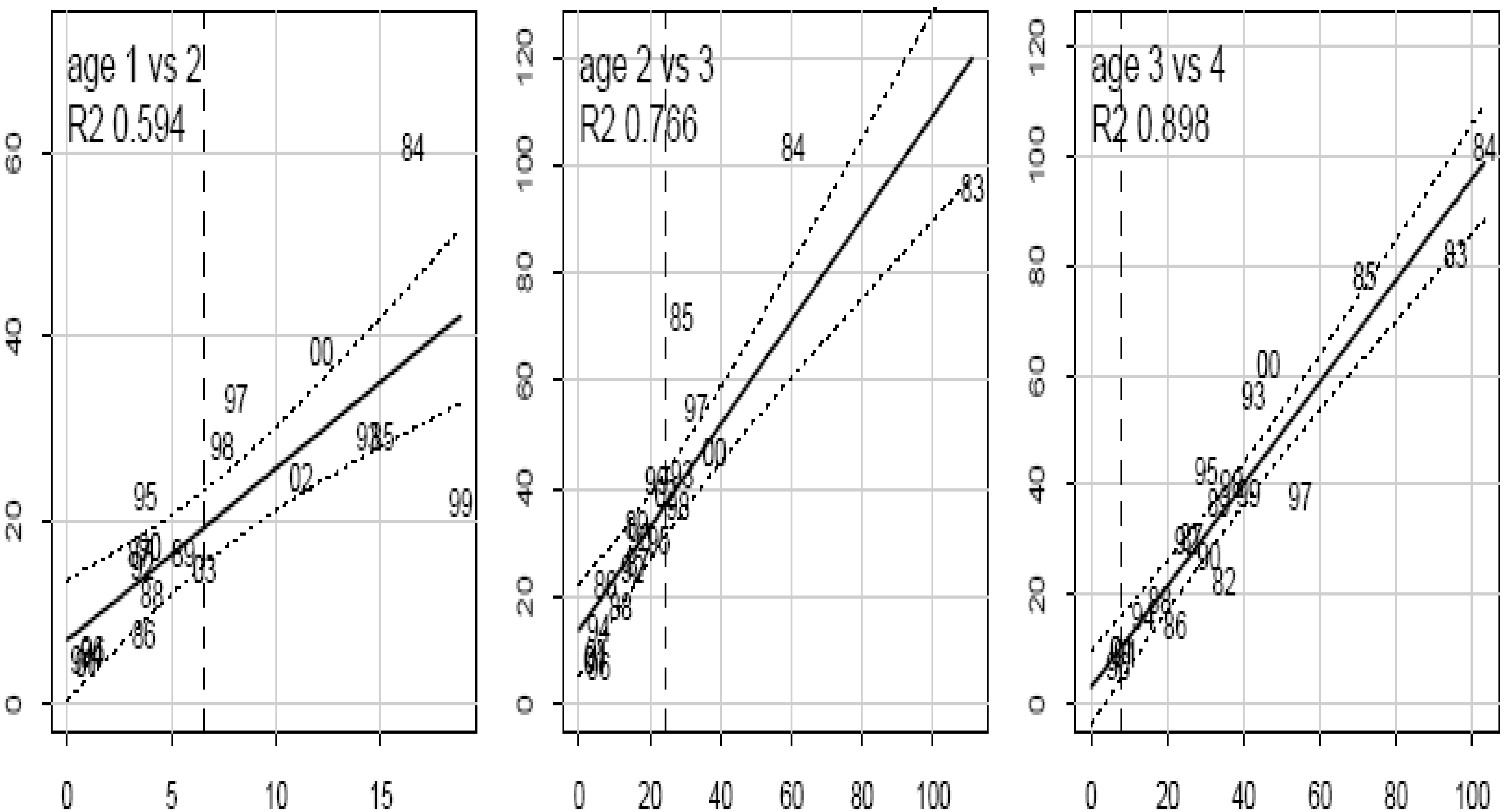


TABLE 1. Data for the North Sea cod stock from VPA in millions of fish, IYFS innumbers per hour fished, and EGFS in numbers per hour fished.

Year class	VPA 1-yr-olds	IYFS 1-yr-olds	IYFS 2-yr-olds	EGFS 0-yr-olds	EGFS 1-yr-olds	EGFS 2-yr-olds
1970	847	98.30	34.50			
1971	159	4.10	10.60			
1972	289	38.00	9.50			
1973	232	14.70	6.20			
1974	426	40.30	19.90			
1975	196	7.90	3.20			4.50
1976	726	36.70	29.30		62.70	12.50
1977	426	12.90	9.30	13.90	22.80	5.80
1978	449	9.90	14.80	12.60	24.20	6.70
1979	800	16.90	25.50	18.60	50.80	13.90
1980	271	2.90	6.70	10.20	11.40	2.90
1981	557	9.20	16.60	74.20	32.40	11.00
1982	269	3.90	8.00	2.50	15.40	4.70
1983	534	15.20	17.60	95.10	61.20	11.90
1984	108	0.90	3.60	0.40	4.30	1.20
1985	581	17.00	28.80	8.30	34.40	10.70
1986	257	8.80	6.10	1.20	14.20	4.10
1987	201	3.60	6.30	0.40	8.40	2.50
1988	324	13.10	15.20	16.80	22.80	5.10
1989		3.30		6.0	6.10	
1990				3.90		

Myers and Cadigan 1993a,b 1993

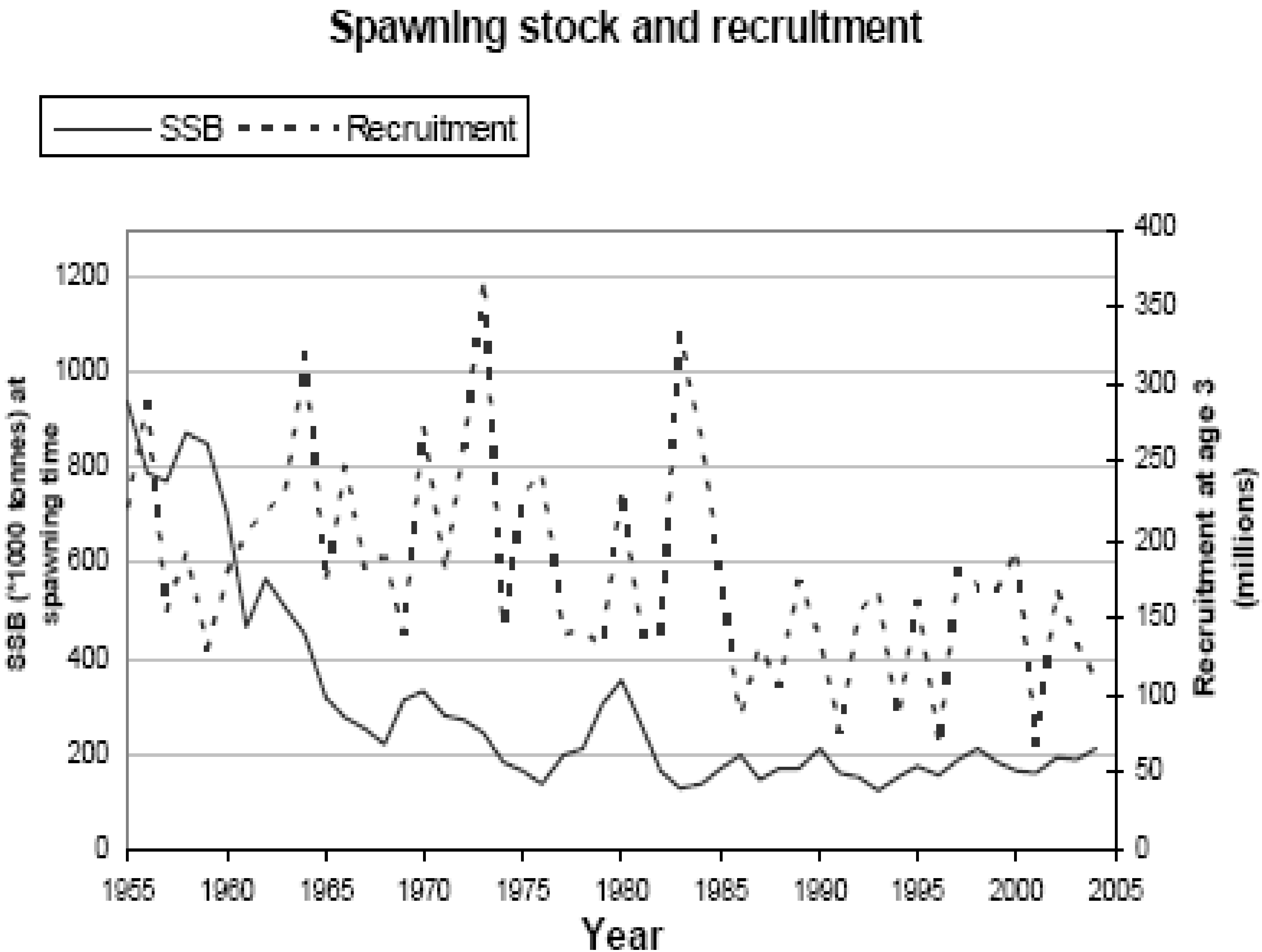
Conclusion from examination of research surveys

- Strong density-dependence at the juvenile stage.
- More eggs => more recruits

Myers and Cadigan 1993a,b 1993, and updated analysis

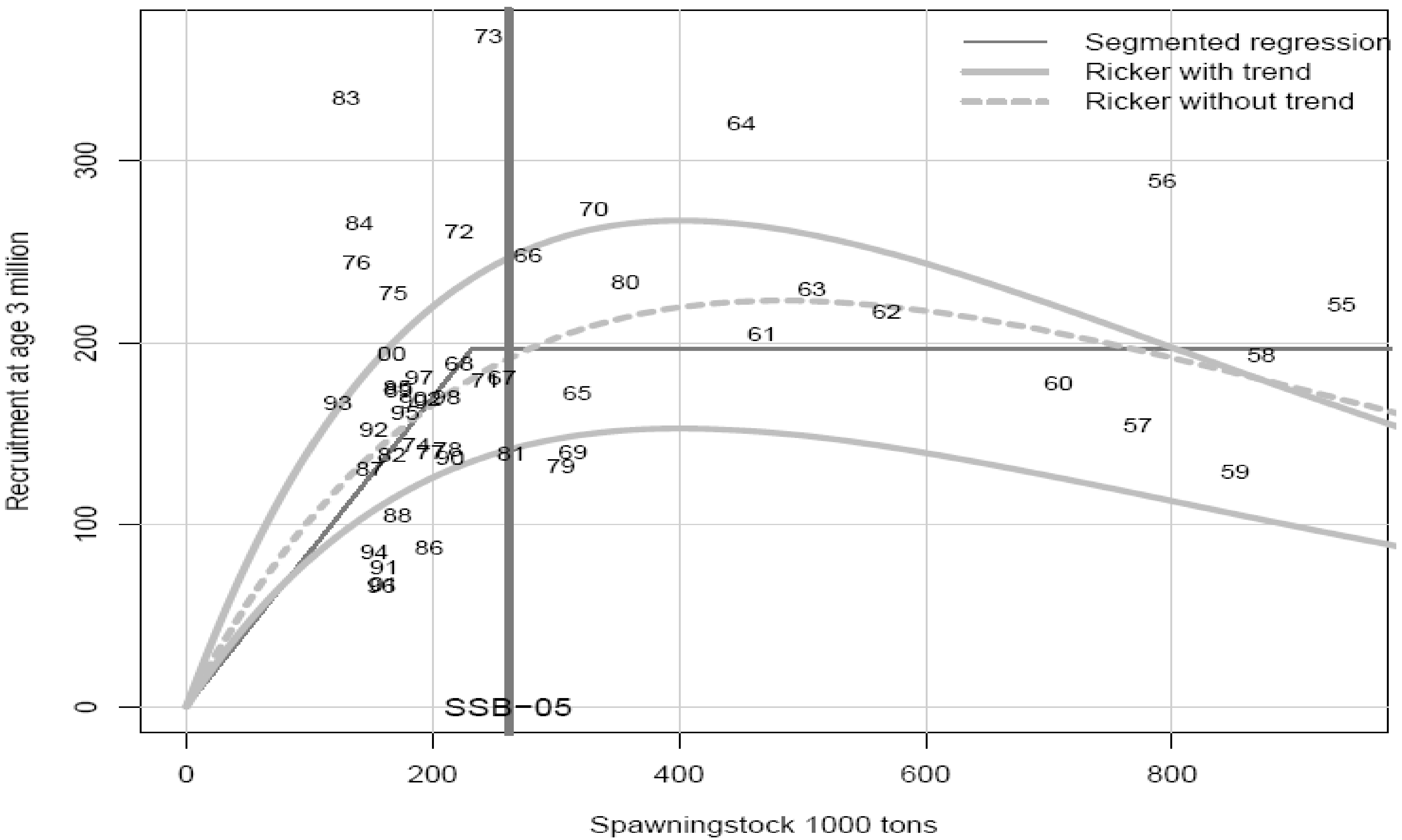
What is the most important challenge in managing the worlds cod stock?

- Decline in recruits per spawner over time.



Spawning stock and recruitment
SSB
Recruitment
SSB ('1000 tonnes) at spawning time
Recruitment at age 3 (millions)
Year
0
200
400
600
800
1000
1200
0
50
100
150
200
250
300
350
400
1955
1960
1965
1970
1975
1980
1985
1990
1995
2000
2005

What is going on with the Iceland Cod, and why it is so important?



Why is there a loss of productivity in Iceland cod?

- Chance – long-term changes in physical environment
- Long-term changes in species interactions
- Loss of BOFF's (Big Old Fat Females)
- Loss of suppopulations
- Genetic changes within a population
- Depensation (higher mortality at lower spawner abundance).

Long-term changes in physical environment

- The marine environment varies over the long term, e.g. survival may be relatively high for 10 years and then relatively low for 10 years, this type of environmental variability makes it difficult to distinguish other important causes of survival variability from noise.

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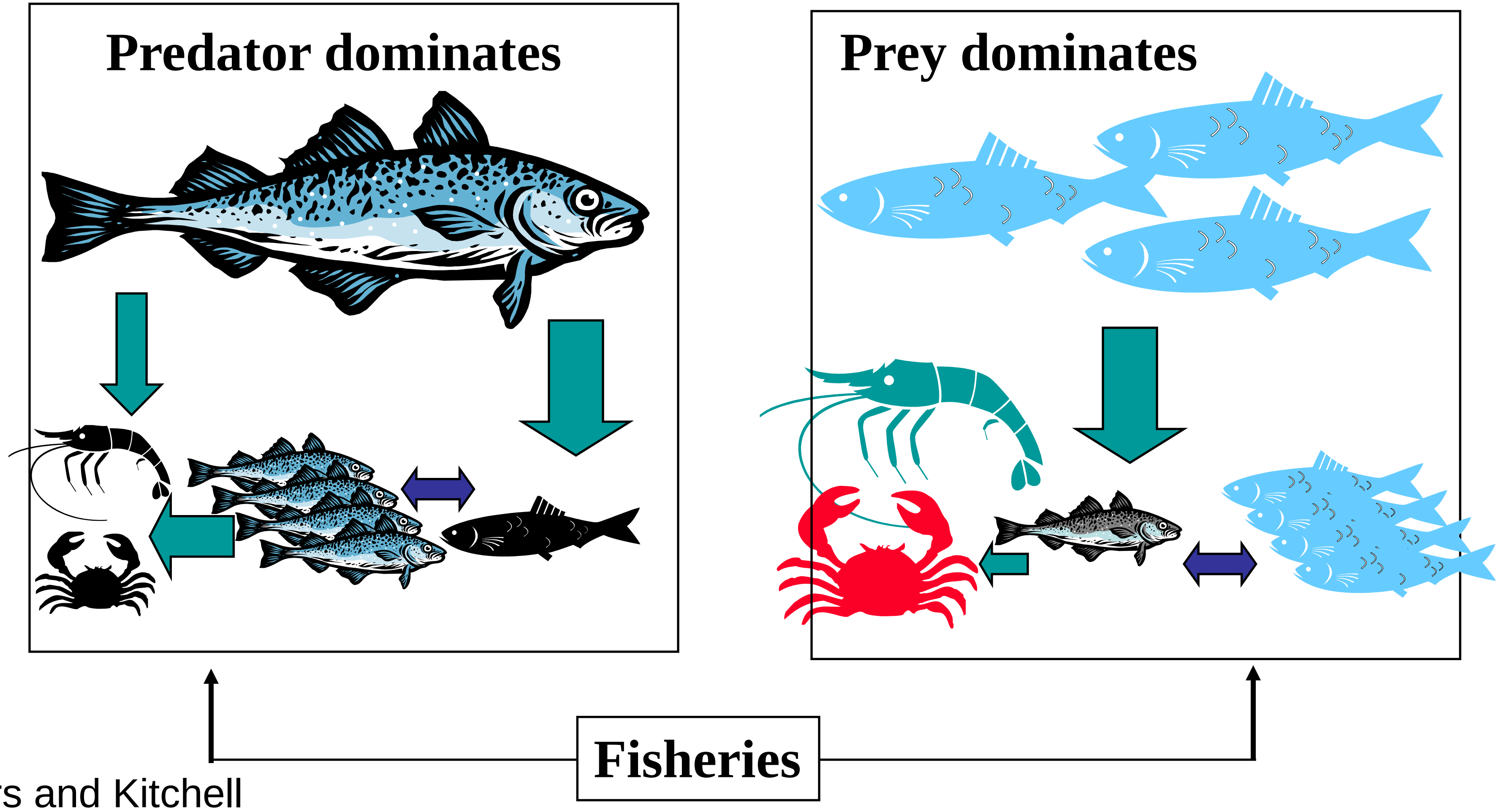
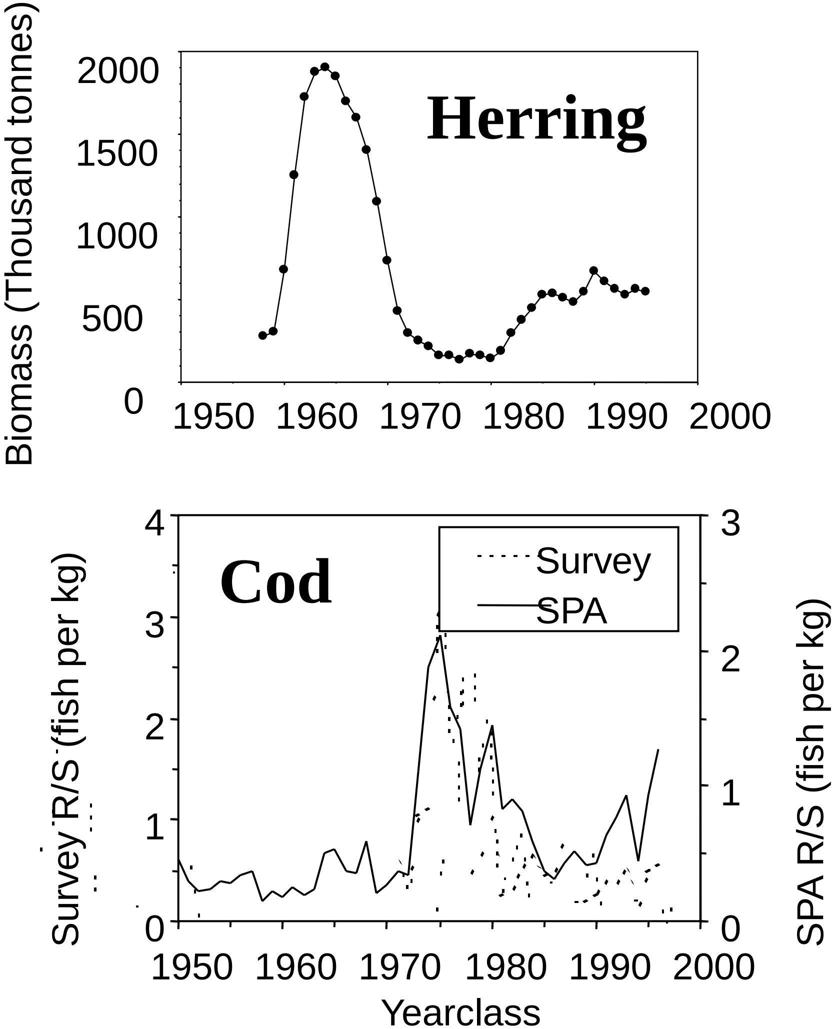
Multiple stable states in ocean food webs: a hypothesis



Walters and Kitchell
Can. J. Fish. Aq. Sci.

Swain DP, Sinclair AF (2000)

Herring-cod interaction in the Gulf of St. Lawrence



Source: Swain & Sinclair 2000

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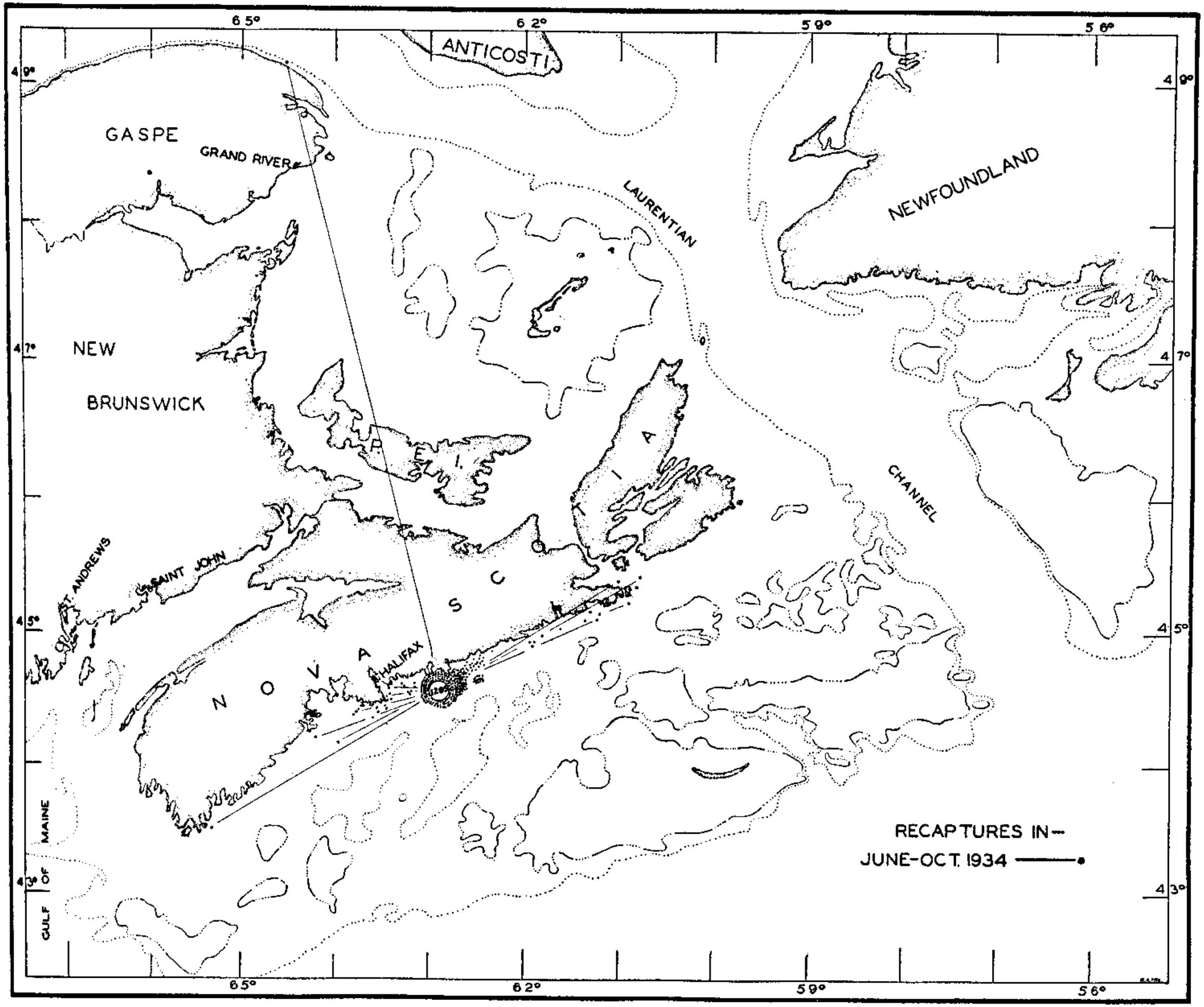

FIG. 21.—Recaptures to October, 1934, of cod tagged in the Jeddore Rock to Egg Island area, N.S., in May, 1934.

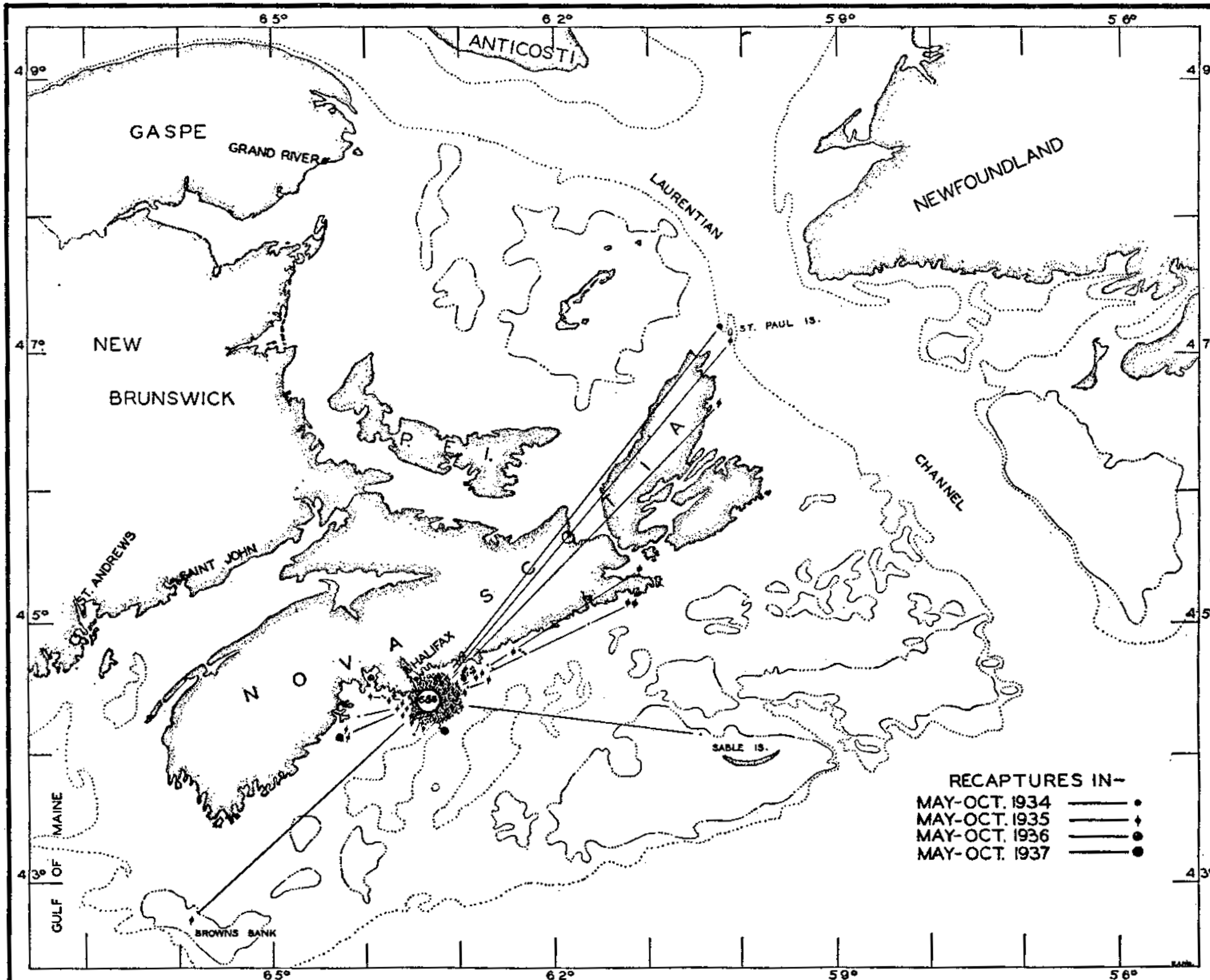

FIG. 18.—Recaptures in May to October, 1934, 1935, 1936 and 1937, of cod tagged near Halifax in June, 1934.

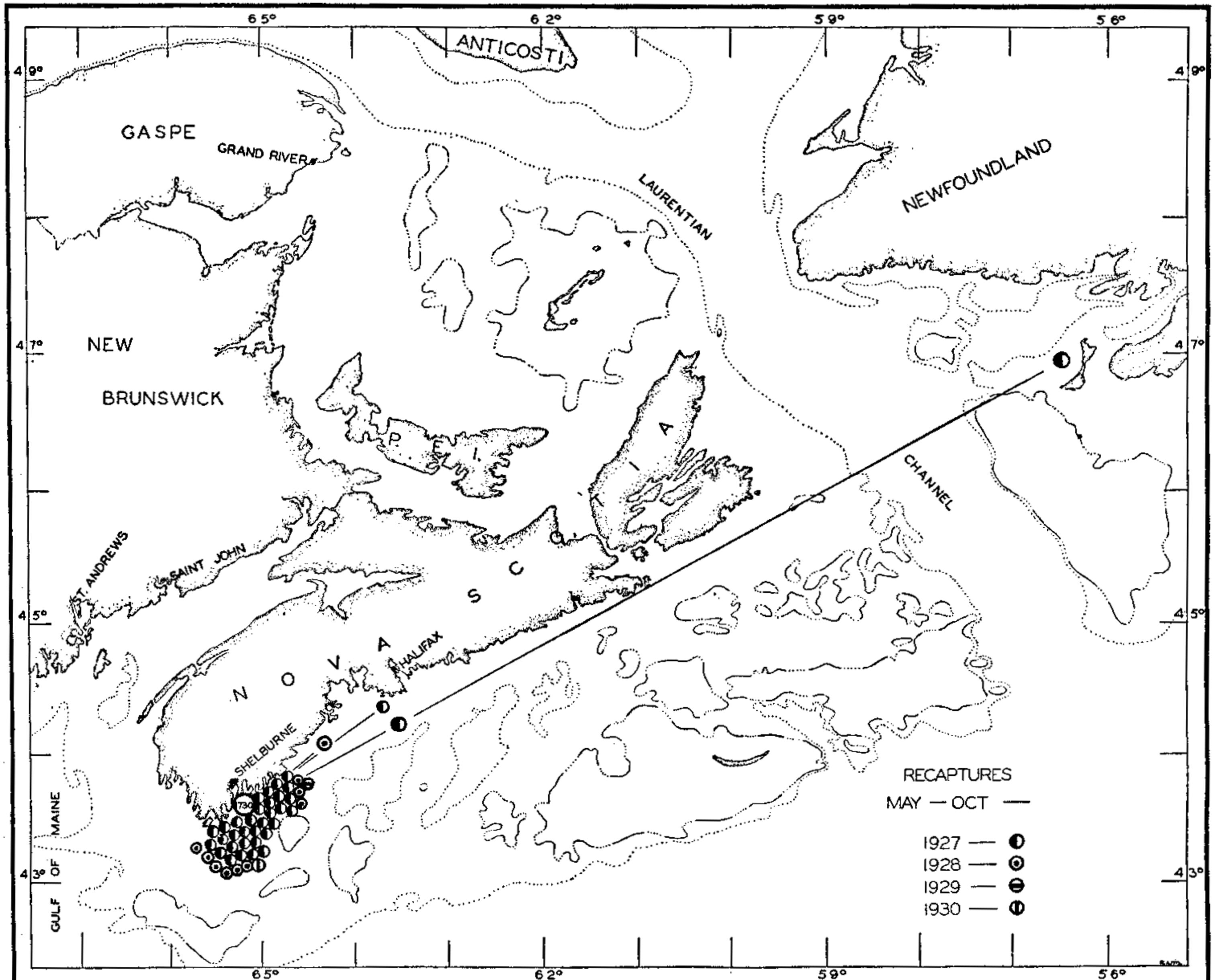

FIG. 15.—Recaptures during "summers" of 1927, 1928, 1929 and 1930 of cod tagged off Shelburne, N.S., during September and the first day of October, 1926.

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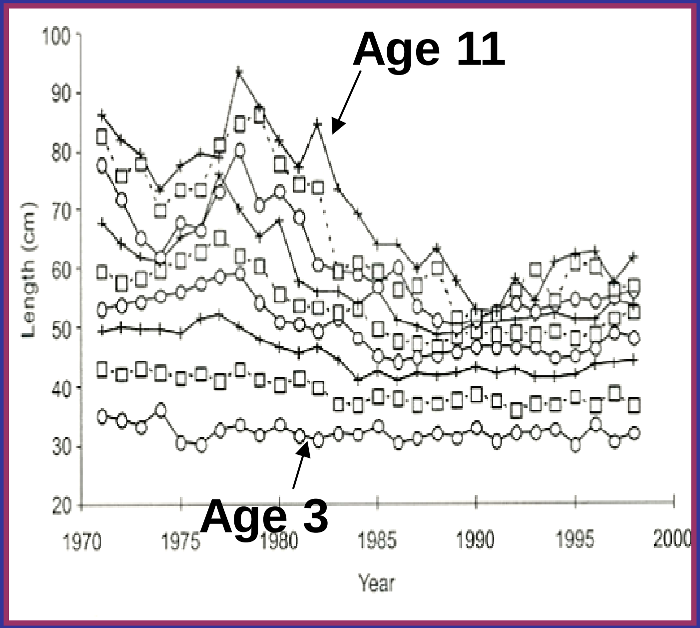
Should we expect evolutionary changes in wild harvested fish?

- Fishing mortality rates are often 2-3x natural mortality
- Strongly size-selective
- Declines in size at age and age at maturity have frequently been observed in wild harvested fish
- Life history evolution occurs rapidly in the wild
  - Guppies (Reznick et al. 1990)
  - Salmon (Quinn et al. 2001; Hendry 2001)
  - Grayling (Haugen and Vollestad 2001)

Cod length at age, 1971-1998



from Sinclair et al. 2002

Conover, and . Munch. 2002

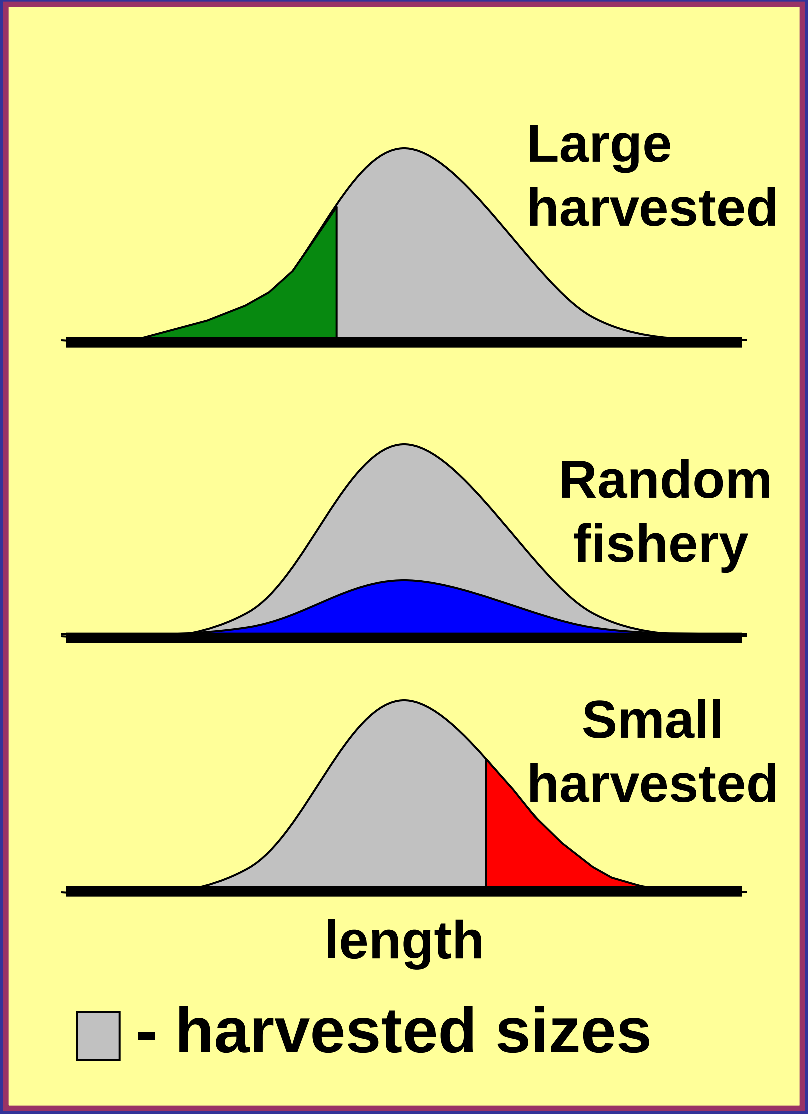
Ecology of *Menidia menidia*

- Distributed from PEI, Canada to Florida
- Typical marine life history traits
- Annual life cycle

Conover, and . Munch. 2002

Design of fishing experiment

- Six populations founded from large gene pool of NY fish
- Fed *ad libitum* throughout life
- “Recruitment” standardized to 1,100 fish at juvenile stage
- 3 Harvest regimes applied on day 190 ~one month before maturity
  - a typical fishery (largest 90%)
  - harvested randomly (random 90%)
  - counter to the typical fishery (smallest 90%)



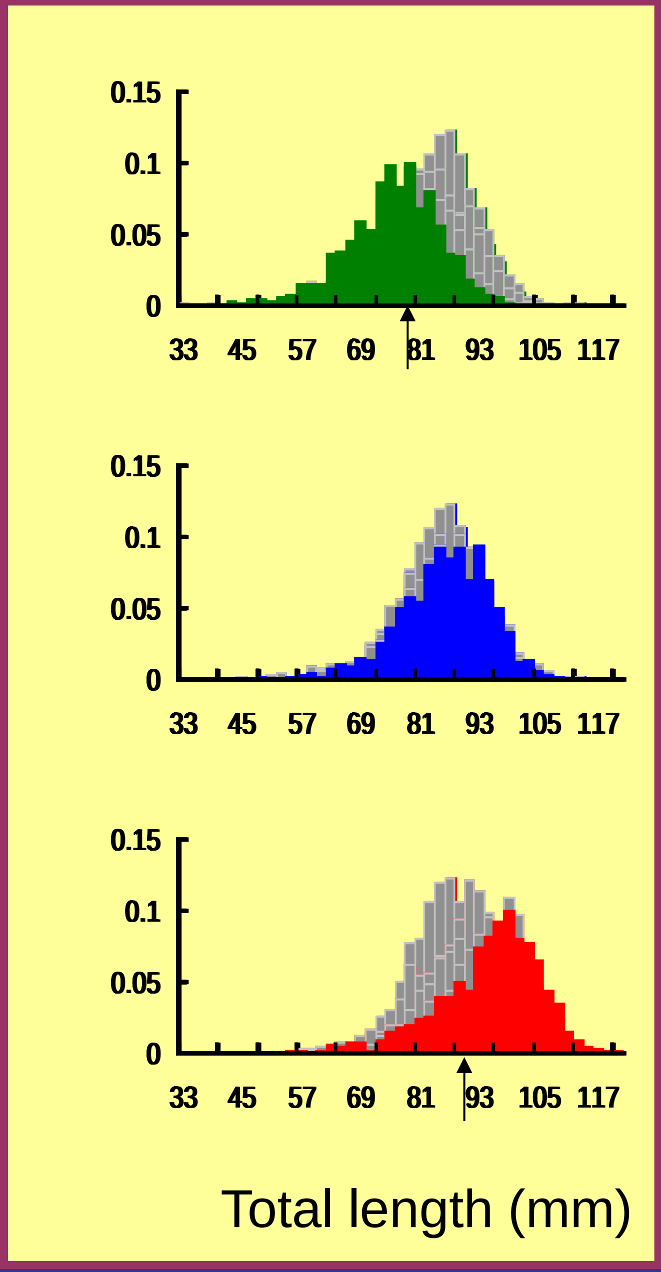
Conover, and . Munch. 2002

Size frequency distributions

▲ typical fishery - large fish harvested

■ random fishery

● small fish harvested



Generation 4 ↓

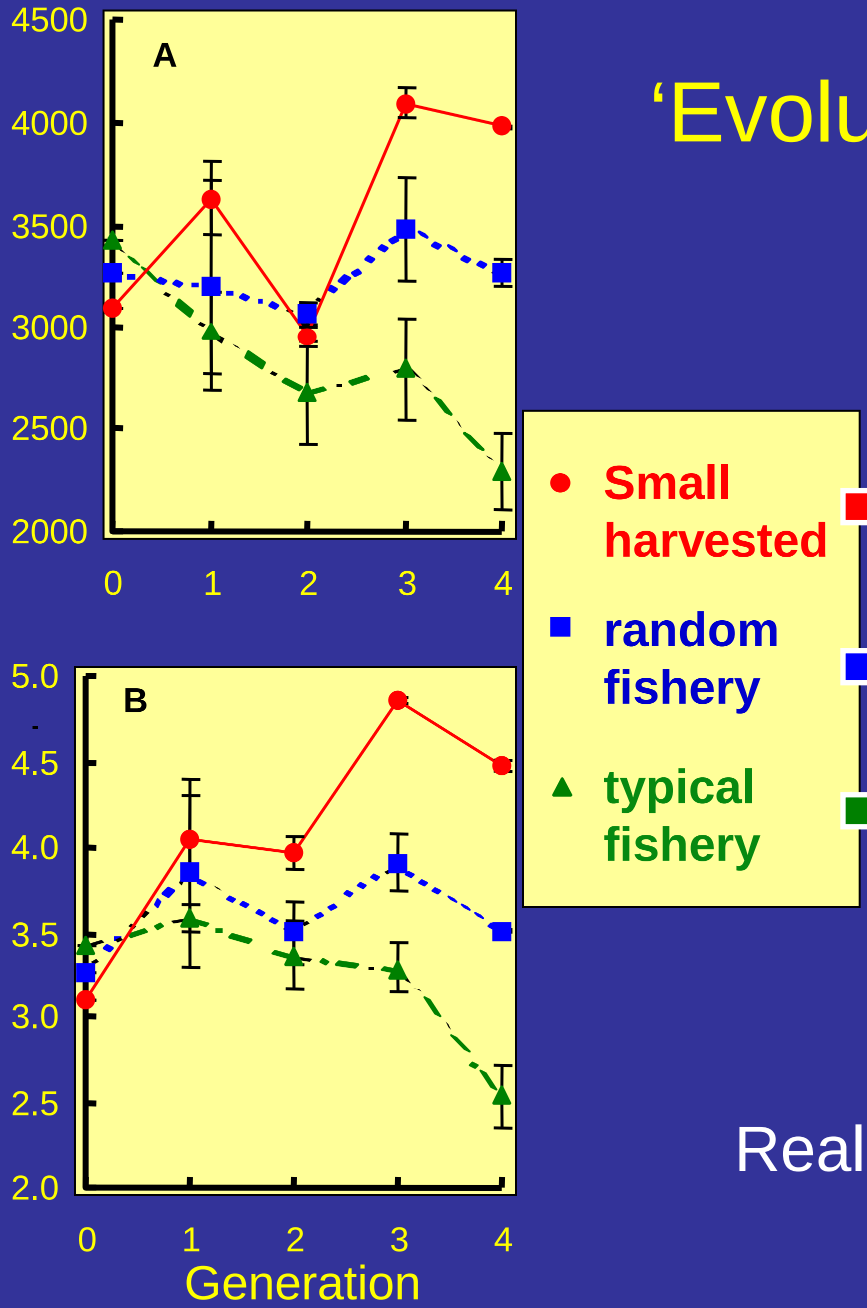
Harvest 4

Conover, and . Munch. 2002

‘Evolution’ of yield

Yield (g)

Yield per recruit (g)

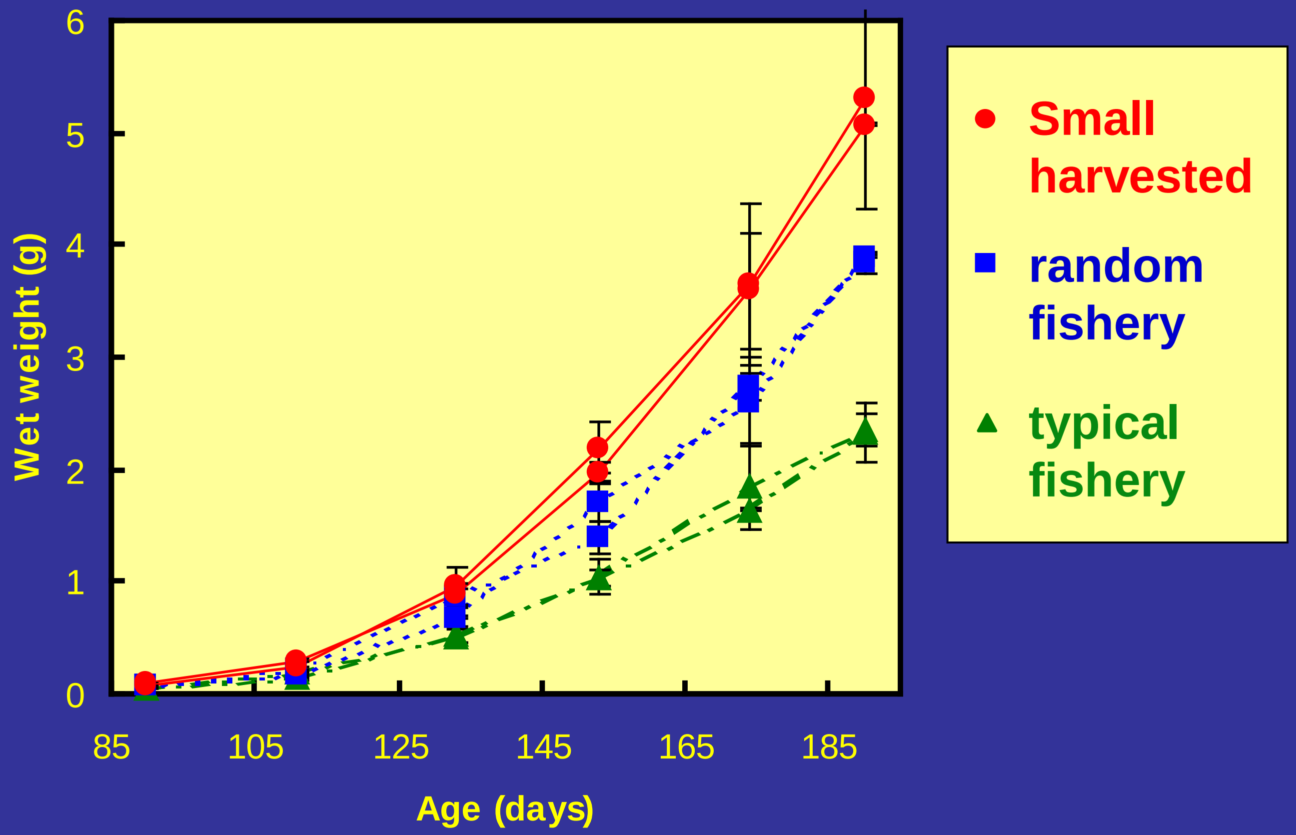


Spawners at generation 4

Realized heritability = 0.2

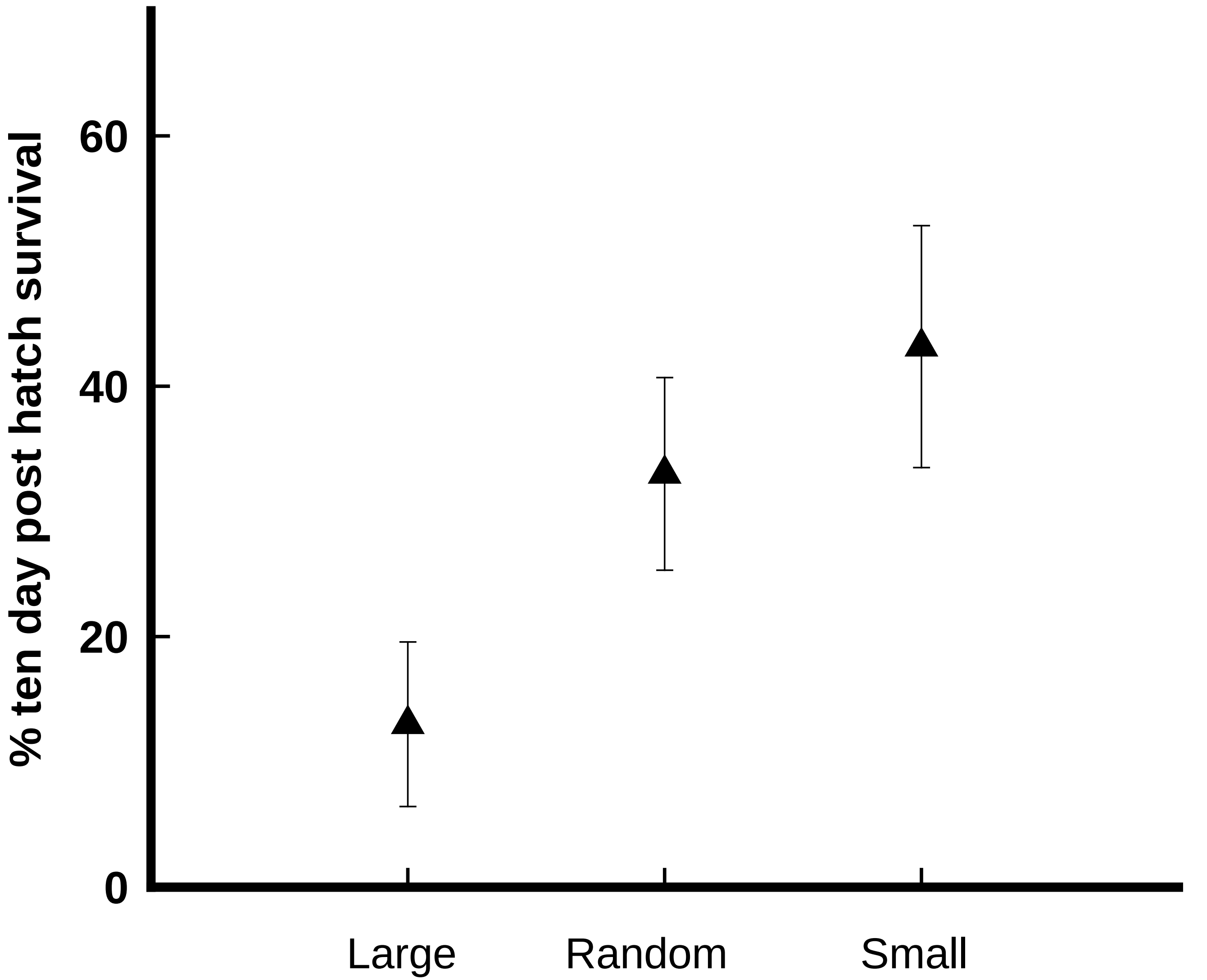
Conover, and . Munch. 2002

Size trajectories after 4 generations of selection



Conover, and . Munch. 2002

Possible consequences of overfishing:lower larval survival



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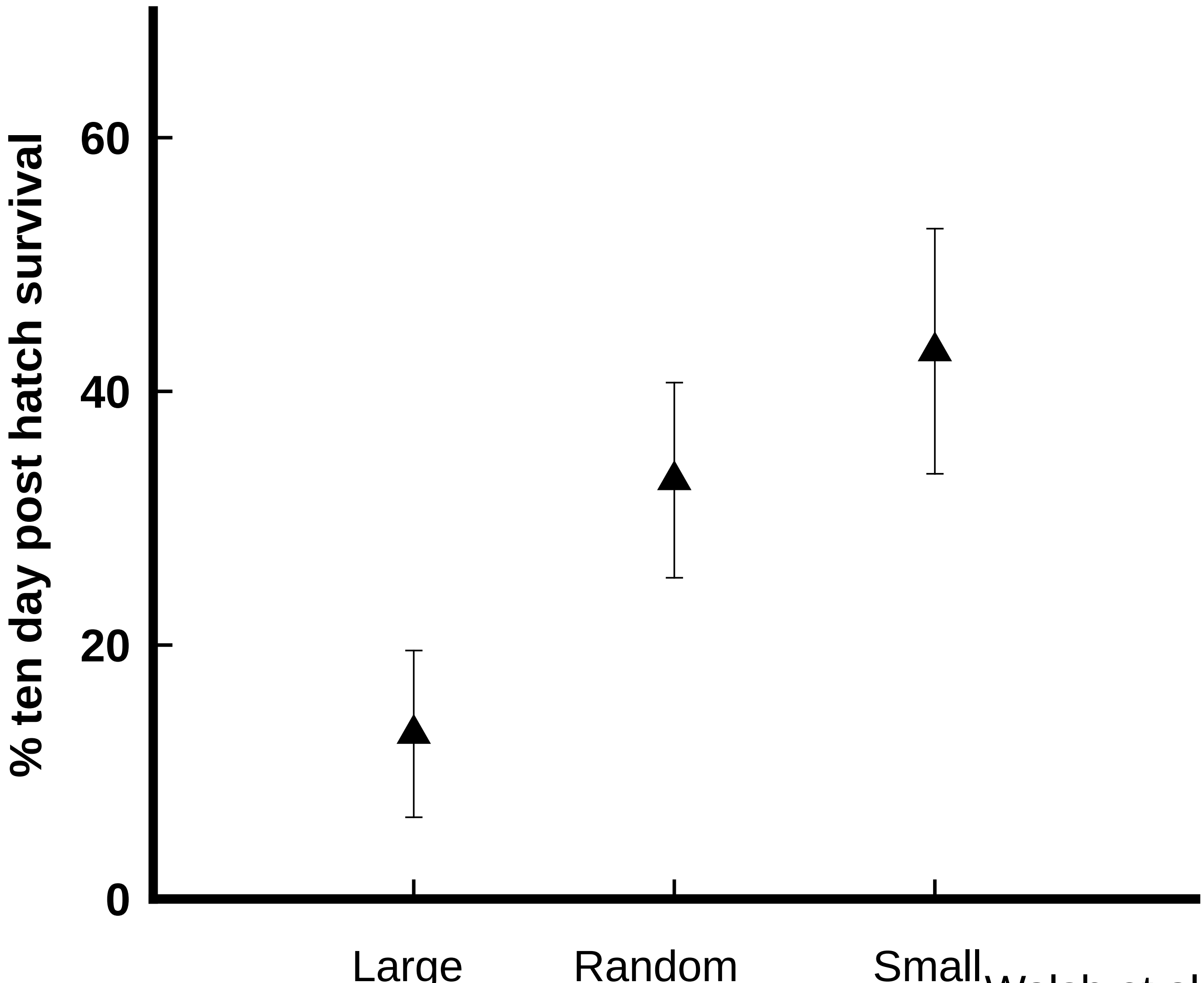
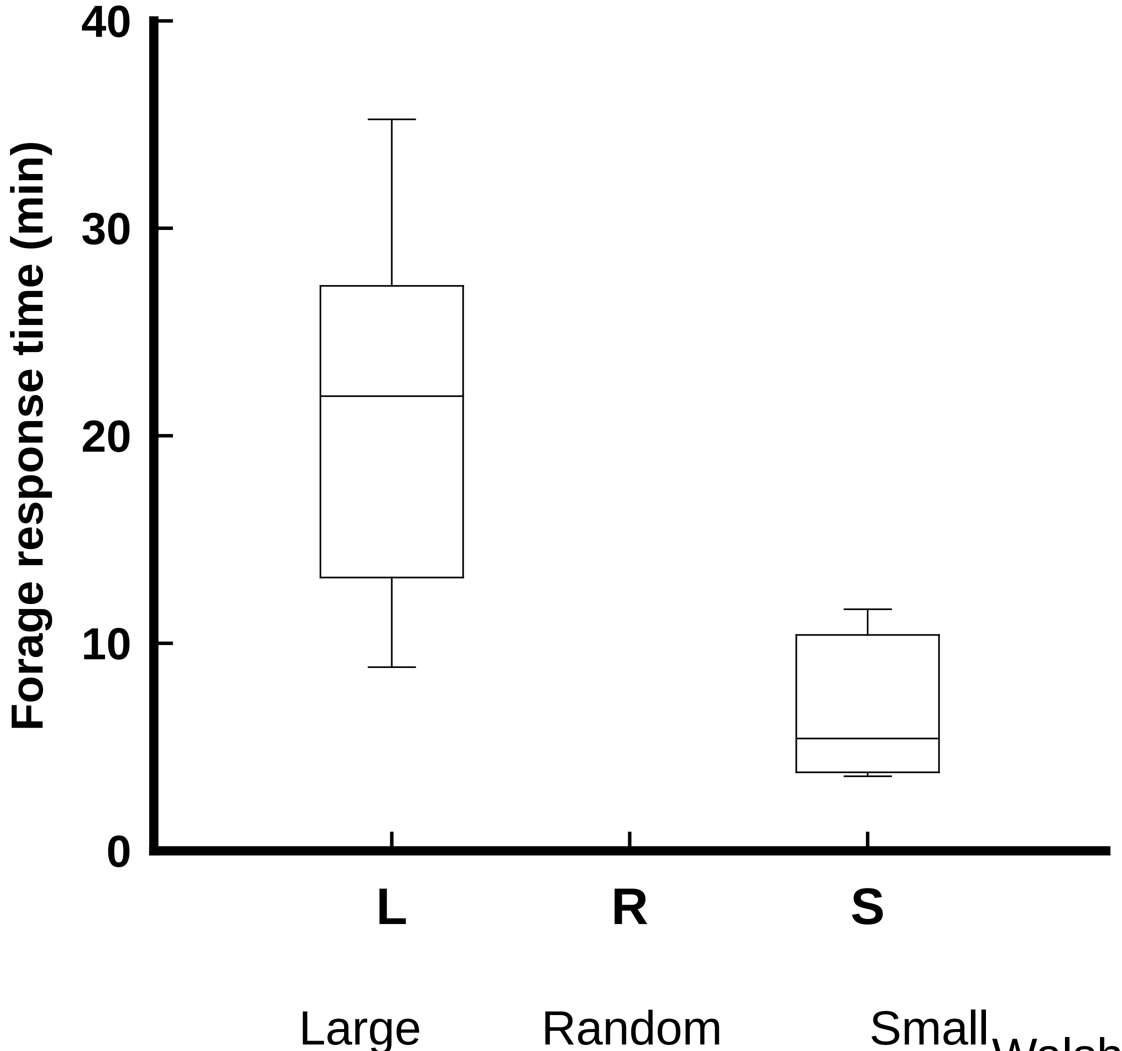


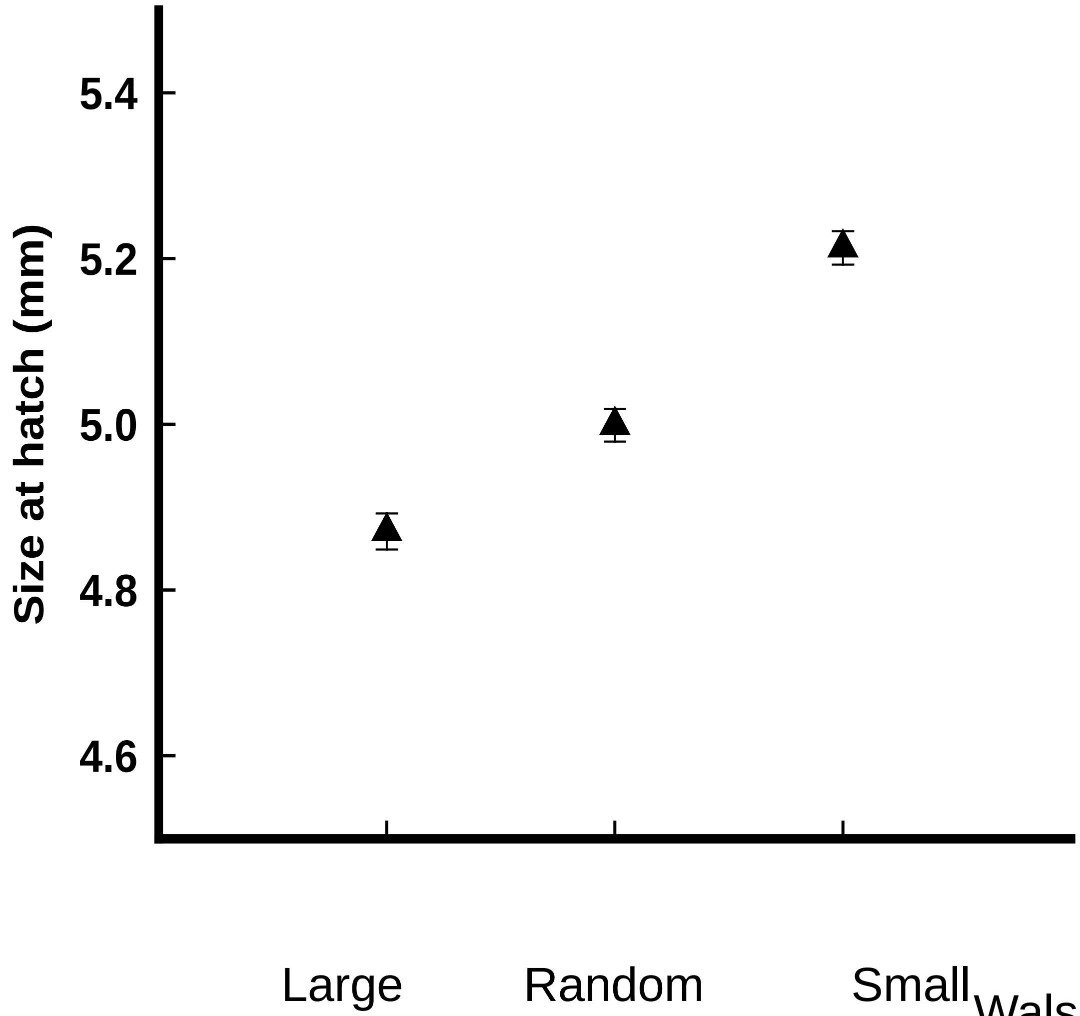
Walsh et al.in press

Possible consequences of overfishing: poorer foraging



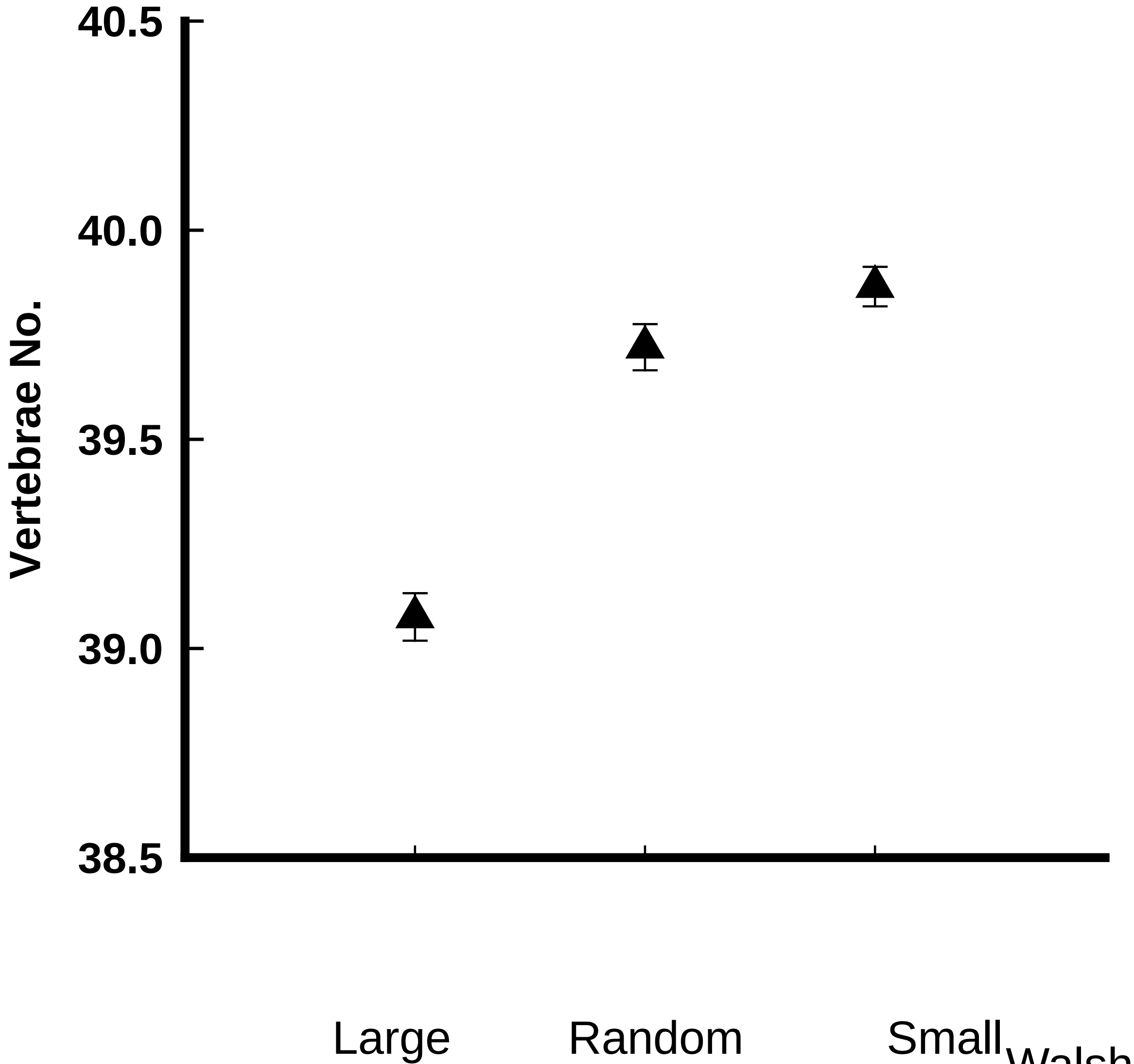
Walsh et al.in press

Possible consequences of overfishing: decreased larval size



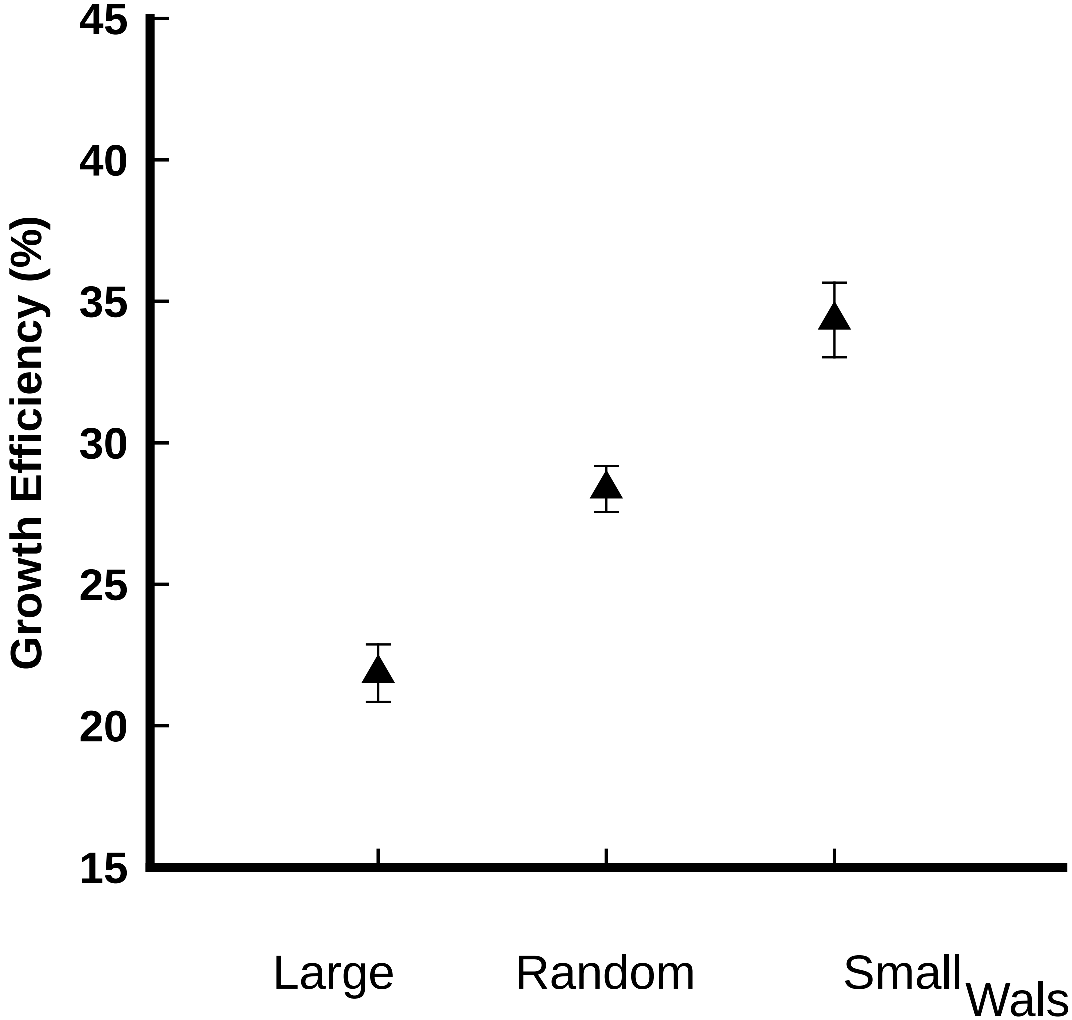
Walsh et al.in press

Possible consequences of overfishing: changed fish shape



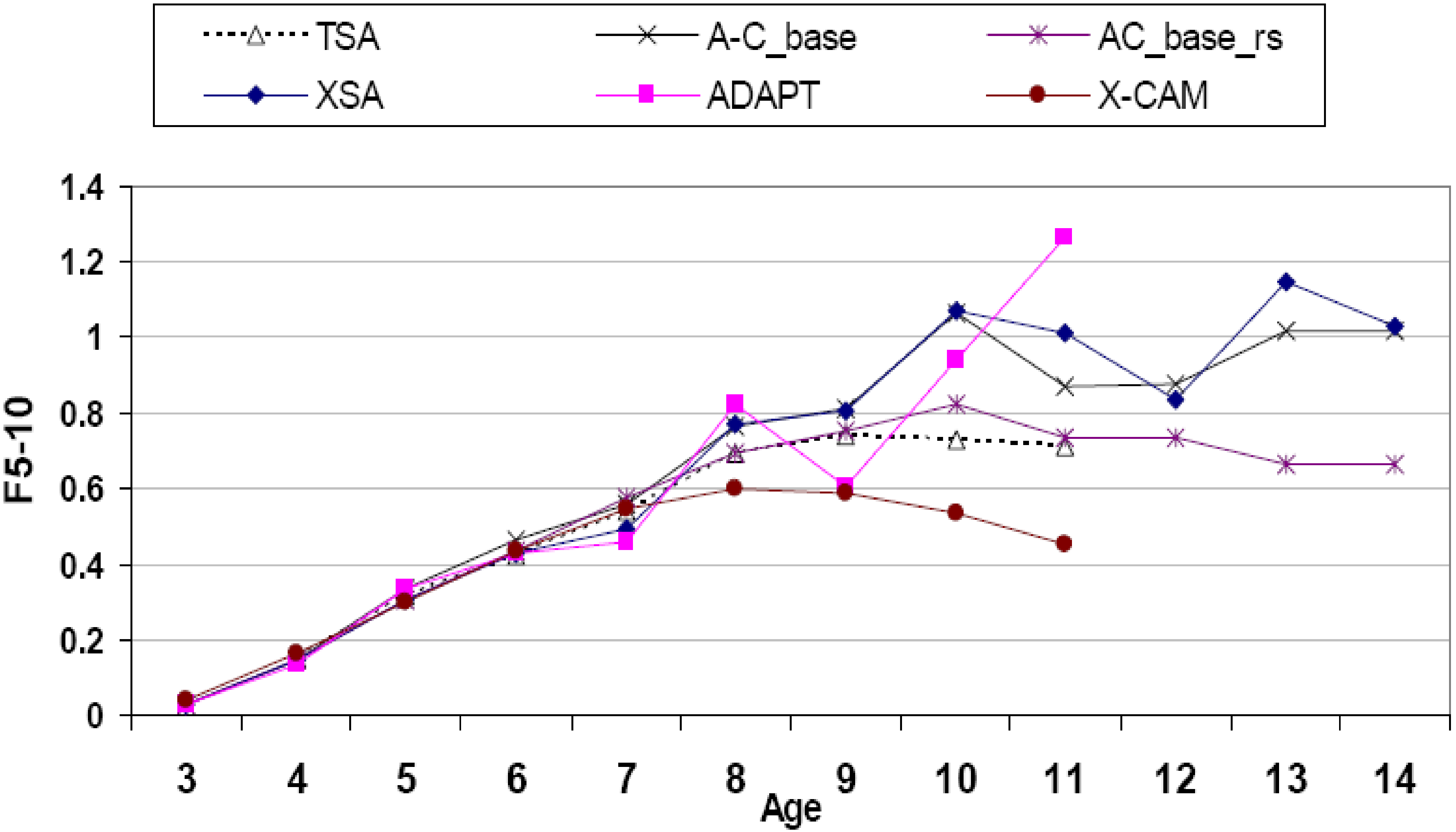
Walsh et al.in press

Possible consequences of overfishing: lower growth



Walsh et al.in press

Selection of Icelandic cod fishery may be bad in the long-term.



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- Depensation or the Allee effect (higher mortality at lower spawner abundance).

Depensation or the Allee effect

- Single species depensation or the Allee effect does not appear to be a strong explanation for the observations because of the strong time trends in survival.
- It may be important for sup-populations, that have been reduced to very low levels.

The need for meta-analysis

- We need a meta-analysis of all the data in the North Atlantic. The loss of fitness for Iceland cod is an incredibly important issue.
- I could give you a progress next summer, we will hold an international meeting of the Future of Marine Animal Populations here.

Conclusion

- Recruitment will decline in the short term if overfishing of the spawners occurs.
- There are bad long-term consequences of reduction in spawners, e.g. loss of sup-populations, genetic changes, and loss of Big Old Fat Females.

Refrences

- Barot, S., M. Heino, L. O'Brien, and U Dieckmann. 2004. Long-term trend in the maturation reaction norm of two cod stocks. *Ecol. Appl.* 14: 1257-1271.
- Conover, D.O. and S.B. Munch. 2002. Sustaining fisheries yields over evolutionary time scales. *Science* 297: 94-96.
- Frank, K.T. and D. Brickman. 2000. Allee effects and compensatory population dynamics within a stock complex. *Can. J. Fish. Aquat. Sci.* 57: 513-517.
- Hutchings, J.A. 2000. Collapse and recovery of marine fishes. *Nature* 406: 882-885.
- ------. 2004. Evolutionary biology: The cod that got away. *Nature* 428: 899-900.
- Hutchings, J.A. and J.K. Baum. 2005. Measuring marine fish biodiversity: temporal changes in abundance, life history, and demography. *Philos. T. Roy. Soc. B.* 360: 315-338.
- Hutchings, J.A. and R.A. Myers. 1994. What can be learned from the collapse of a renewable resource? Atlantic cod, *Gadus morhua*, of Newfoundland and Labrador. *Can. J. Fish. Aquat. Sci.* 51: 2126-2146.
- Hutchings, J.A. and J.D. Reynolds. 2004. Marine fish population collapses: consequences for recovery and extinction risk. *Bioscience* 54: 297.
- Hutchinson, W.F., C. van Oosterhout, S.I. Rogers, and G.R. Carvalho. 2003. Temporal analysis of archived samples indicates marked genetic changes in declining North Sea cod (*Gadus morhua*). *Proc. R. Soc. Lond. B* 270: 2125-2132.

- Jennings, S. and J.L. Blanchard. 2004. Fish abundance with no fishing: predictions based on macroecological theory. *J. Anim. Ecol.* 73: 632-642.
- Law, R. 2000. Fishing, selection, and phenotypic evolution. *ICES J. Mar. Sci.* 57: 659-668.
- Liermann, M. and R. Hilborn. 1997. Depensation in fish stocks: a hierarchic Bayesian meta-analysis. *Can. J. Fish. Aquat. Sci.* 54: 1976-1984.
- Myers, R.A. (2001). Stock and recruitment: generalizations about maximum reproductive rates, density dependence, and variability using meta-analytic approaches.ICES *J. Mar. Res.* 58: 937-951.
- Myers RA (2002) Recruitment: understanding density-dependence in fish populations. In: Hart PJB, Reynolds JD (eds) Handbook of fish biology and fisheries, Vol. 1. Fish biology. Blackwell Science, Oxford, p 123–148
- Myers RA, Barrowman NJ (1996) Is fish recruitment related to spawner abundance? Fish Bull 94:707–724
- Myers RA, Bowen KG, Barrowman NJ (1999) Maximum reproductive rate of fish at low population sizes. Can J Fish Aquat Sci 56:2404–2419
- Myers RA, MacKenzie BR, Bowen KG, Barrowman NJ (2001) What is the carrying capacity of fish in the ocean? A metaanalysis of population dynamics data from the North Atlantic. Can J Fish Aquat Sci 58:1464–1476
- Myers, R.A., N.J. Barrowman, J.A. Hutchings, and A.A. Rosenberg. 1995. Population dynamics of exploited fish stocks at low population levels. *Science* 269: 1106-1108.
- Myers RA, Cadigan NG (1993) Density-dependent juvenile mortality in marine demersal fish. Can J Fish Aquat Sci 50(8):1576–1590
- Myers RA, Mertz G (1998) Reducing uncertainty in the biological basis of fisheries management by meta-analysis of data from many populations: a synthesis. Fish Res 37:
- 51–60
- Myers, R.A., J.A. Hutchings, and N.J. Barrowman. 1997. Why do fish stocks collapse? The example of cod in Atlantic Canada. *Ecol. Appl.* 7: 91-106.
- Myers, R.A. and K. Stokes. 1989. Density dependent habitat utilization of groundfish and the improvement of research surveys. *ICES CM 1989/D* 15, 11pp.
- Myers, R.A. and B. Worm. 2003. Rapid worldwide depletion of predatory fish communities. *Nature* 423: 280-283.
- ------. 2005. Extinction, survival or recovery of large predatory fishes. *Proc. R. Soc. Lond. B* 360: 13-20.
- Olsen, E.M., M. Heino, G.R. Lilly, M.J. Morgan, J. Brattey, B. Ernande, and U. Dieckmann. 2004. Maturation trends indicative of rapid evolution preceded the collapse of northern cod. *Nature* 428: 932-935.
- Palumbi, S.R. 2001. Humans as the world's greatest evolutionary force. *Science* 293: 1786-1790.

- Ricker, W.E. 1958. Maximum sustained yields from fluctuating environments and mixed stocks. *J. Fish. Res. Board Can.* 15.
- Ruzzante, D.E., C.T. Taggart, R.W. Doyle, and D. Cook. 2001. Stability in the historical pattern of genetic structure of Newfoundland cod (*Gadus morhua*) despite the catastrophic decline in population size from 1964 to 1994. *Conserv. Genet.* 2: 257-269.
- Swain DP, Sinclair AF (2000) Pelagic fishes and the cod recruitment dilemma in the northwest Atlantic. Can J Fish Aquat Sci 57:1321–1325
- Thompson, J.N. 1998. Rapid evolution as an ecological process. *Trends. Ecol. Evol.* 13: 329-332.
- UNEP (United Nations Environmental Programme). 2004. Provisional global indicators for assessing progress towards the 2010 biodiversity target., pp. 26pp. Nairobi, Kenya: CBD COP Document UNEP/CBD/COP/7/INF/33.
- Walsh, M.R., S.B. Munch, S. Chiba, and D.O. Conover. In press. Why stocks don't rebound: maladaptive changes caused by fishing. *Ecol. Lett.* In press.
- Walters, C. & Kitchell, J. F. 2001 Cultivation/depensation effects on juvenile survival and recruitment: implications for the theory of fishing. *Can. J. Fish. Aquat. Sci.* **58**, 1-12..
- Worm, B., M. Sandow, A. Oschlies, H. K. Lotze, and R. A. Myers. 2005b. Global patterns of predator diversity in the open oceans. *Science* 309: 1365-1369.
- Worm, B. and R.A. Myers. 2003. Meta-analysis of cod-shrimp interactions reveals top-down control in oceanic food webs. *Ecology* 84: 162-173.