Introduction
To
Mathematical Biology II

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Mathematical Biology

- Ecology and Evolution
- Cell Biology
- Infectious Diseases
- Genomics and Computational Biology
- Neuroscience
- Physiology
- Developmental Biology (Morphogenesis, Cell Growth and Cellular Differentiation)
- etc

Global Challenges: Complex, Multi-disciplinary Questions

- Human population is swelling toward 10 billion. All these people need adequate food, clean water, housing, good health, a secure and pleasant environment. To stay within the planet's carrying capacity, we are going to have to be extraordinarily clever about how we use the Earth's resources.
- What are the impacts of our actions on the environment we depend on?
- How does the natural world function?
- How do we plan for the inevitable changes to come?

Human Well-being and the Natural Environment

- A basic but challenging need is the ability to quantify how well the ecosystems we depend on are doing, so that we can determine whether they're getting better or worse.
- When we (mathematicians) examine ecosystem health, how do we define it?

Ecosystem Health and Bio-diversity

- An ecosystem that is more diverse, is more robust and healthier – and the people who depend on it are less vulnerable.

Examples:

1. Potato blight of Ireland in 1840s (**Irish Potato Famine**). A third of the population depend on 2 species of potato and both were susceptible to the disease. A million people starved.
2. Rice grassy stunt virus of Asia in 1970s. 6,000 species of rice and only one withstood the virus. By hybridizing that type of rice, rice cultivation could be saved.

Questions

- What do we mean by biodiversity?
- How do we measure it? A first attempt is to simply use the number of species. More species imply greater diversity.
- How do you effectively count the number of species, particularly when comparing different ecosystems in which species may be easier or harder to find?
- How does the length of time you explore an ecosystem affect the number of species discovered?
- How does the number of species discovered in a day decrease or increase over time?

Mathematical challenges in area of human-well-being and natural environment

- We need clear, mathematically precise criteria to measure biodiversity that are robust even given the difficulties of gathering data in sometimes harsh environments.
- We need models of animal migration that take climate change and other human disruptions into account. Network theory and others might offer an opportunity for developing richer models than existing ones.
- We need mathematical models that will describe how agriculture both affects and is affected by the availability and quality of fresh water.
- We need improved monitoring methods using statistics, machine learning and remote sensing to allow us to detect changes in the environment much more quickly.

Managing Human-Environment Systems

Example: Fish don't stop at international boundaries. They swim where they will. This willfulness has created nasty problems for fishery managers (disputes between nations, broken agreements and collapse of fisheries). Some of these problems can be solved by mathematicians.

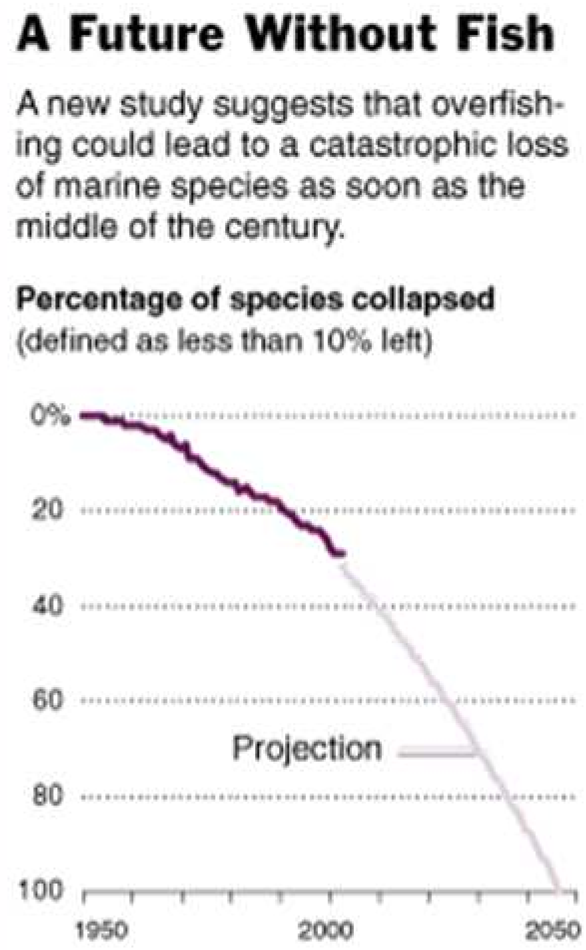
Mathematical challenges in the area of managing human-environmental systems

- Management problems often involve finding the optimal solution to a set of mathematical equations. For example, we want to know how many fish we can catch per year to get maximum harvest over the long run, or how we minimize the spread of invasive species.
- Methods for finding the optimal solutions in systems with large variability are essential to solving these management problems.

World's Fish Supply Running Out, Researchers Warn

(Journal of Science) by Juliet Eilperin Washington Post Writer, November 3, 2006

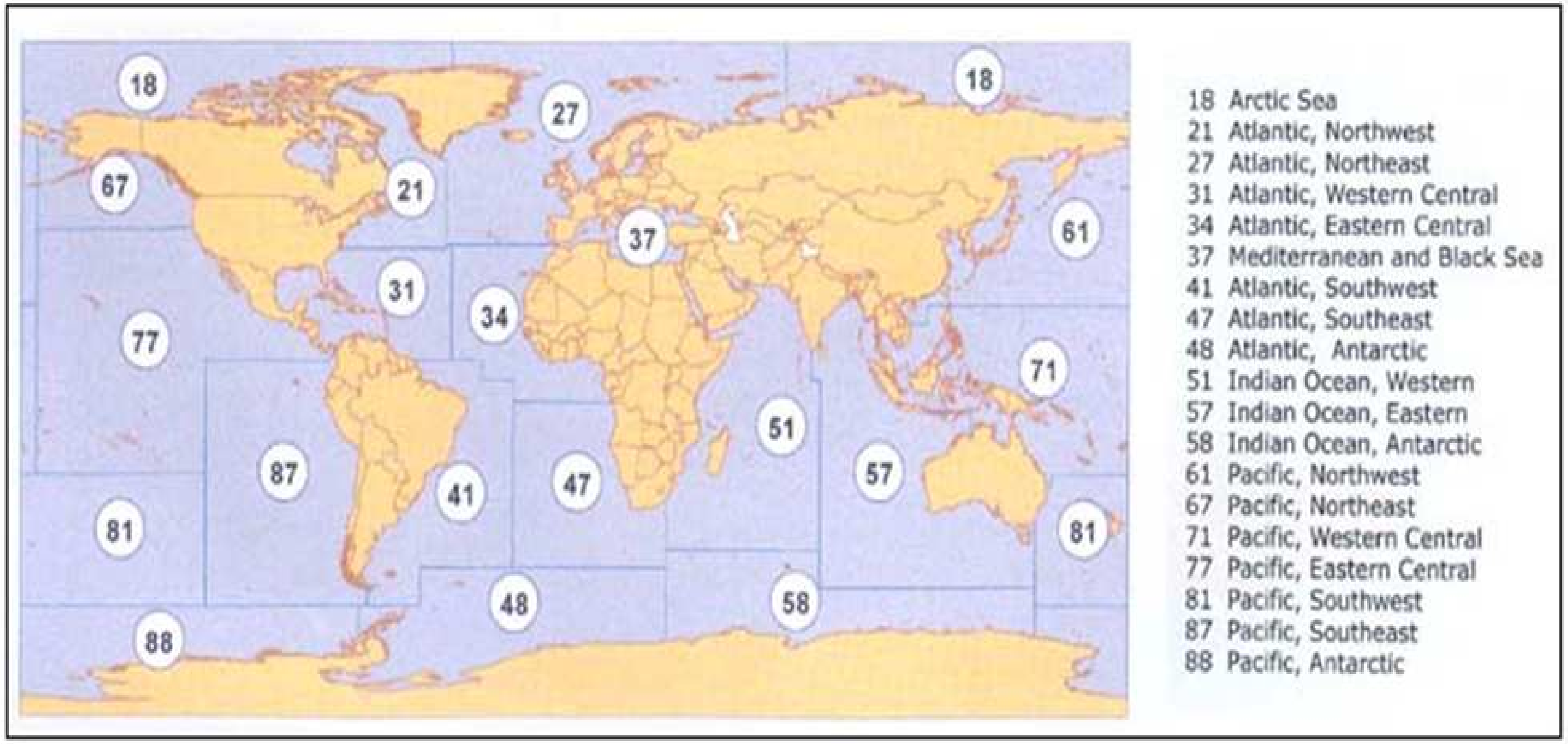
- Economists' and ecologists' warning: No more seafood as of 2048
- Based on 4-year study of
  - Catch data
  - Effects of fisheries collapses
- Causes
  - Overfishing
  - Pollution
  - Other Environmental Causes
- Loss of Species affects oceans' ability
  - Produce seafood
  - Filter nutrients
  - Resist the spread of disease
  - Store CO_2



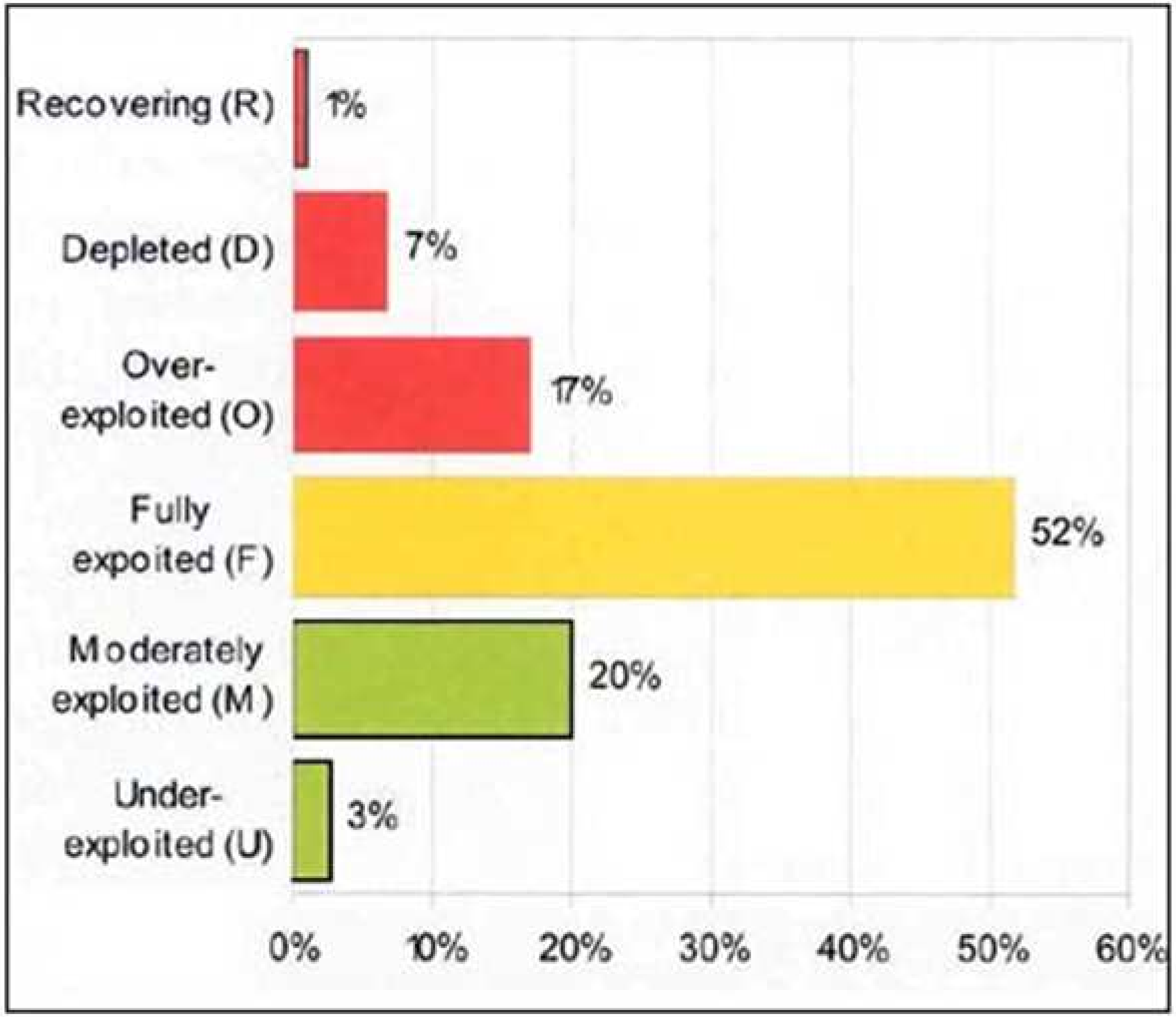
Overfishing Threatens Food Security

- Fish: A vital source of protein for billions
- Fish provide roughly 40 per cent of the protein consumed by nearly two-thirds of the world's population.
- For example, over a billion people throughout Asia depend on fish and seafood as their major source of animal protein. But, fish have moved into the luxury-style, high-priced food class.
- The United Nations Educational, Scientific and Cultural Organization (UNESCO) warns that fish, long regarded as the "poor man's protein", is diminishing globally as a result of increasing market demand and overfishing.

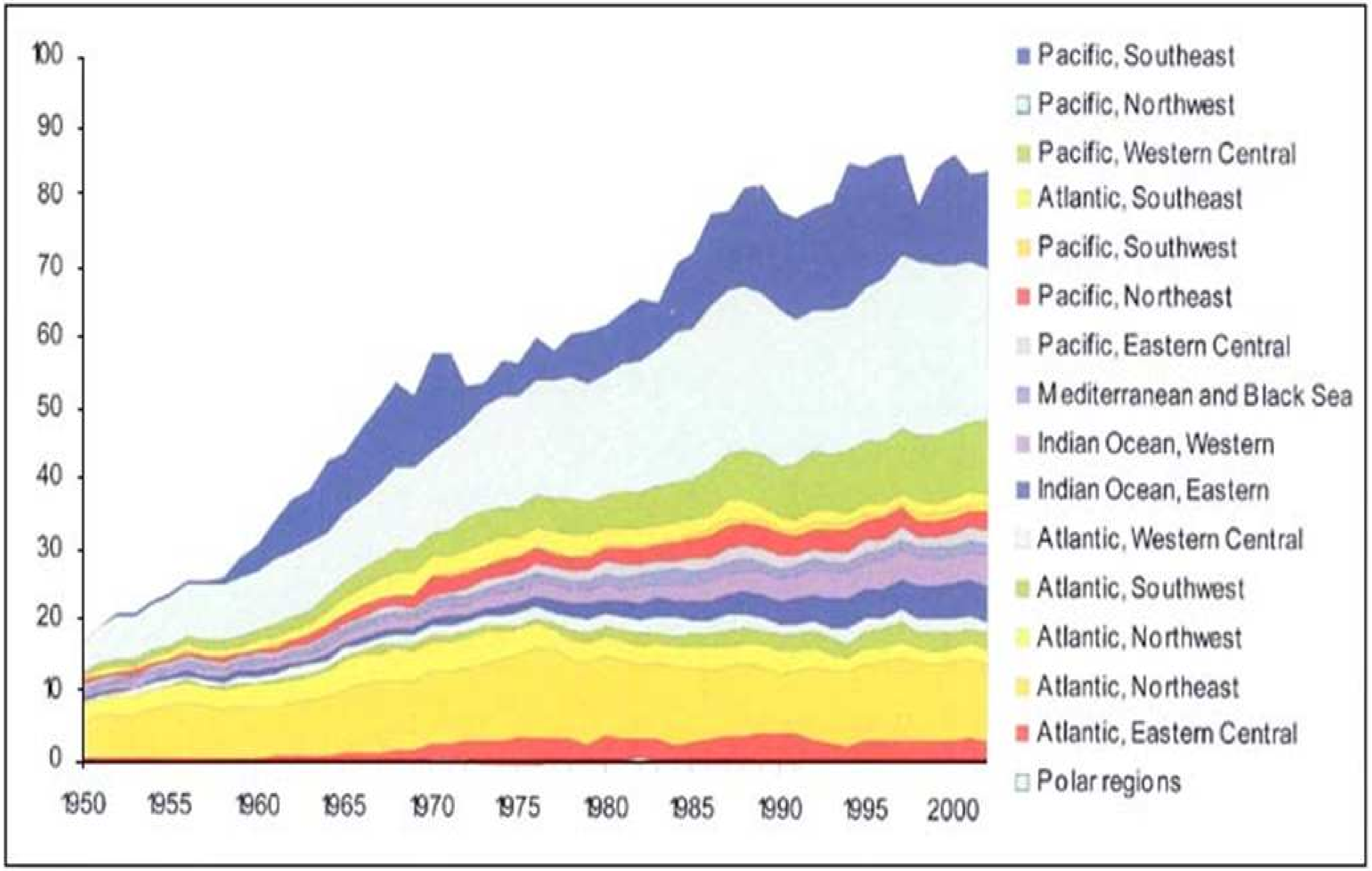
World Major Marine Fishing Areas



GLOBAL TRENDS IN THE STATE OF MARINE FISHERIES RESOURCES 1974–2004



World marine catch (million tonnes) by major marine fisheries areas



Rebuilding Depleted Fish Stocks (challenging necessity)

- Seven of the top ten marine fish species -- which together account for about 30 percent of all capture fisheries production -- are fully exploited or overexploited. This means that major increases in catches cannot be expected from them, and serious biological and economic drawbacks are likely if fishing capacity for these stocks is further increased.
- Regions with fish stocks in greatest need of recovery include the **Northeast Atlantic**, the **Mediterranean Sea** and the **Black Sea**, followed by the **Northwest Atlantic**, the **Southeast Atlantic**, the **Southeast Pacific** and the **Southern Ocean**.

Emerging Ocean Diseases

Disease is increasing among most marine organisms (Ward and Lafferty, 2004).

Examples: Recent epizootics (epidemics in animals) of Atlantic Ocean bottlenose dolphins and endangered Florida manatees.

Contributing Factors include

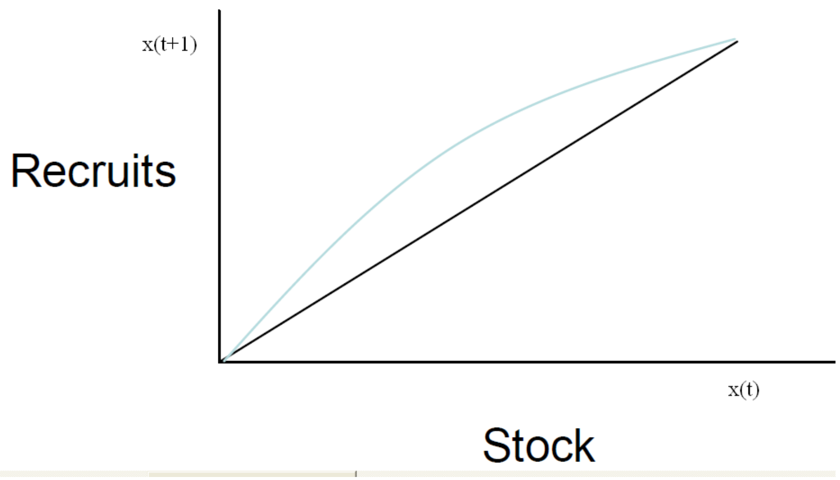
- global warming
- habitat destruction
- human overfishing
- etc

Overfishing Implicated in Sea Urchin Epidemics

- Sea urchin epidemics have risen over the last 30 years, and diseases have decimated urchin populations in many parts of the world.
- In the early 1980s, an epidemic killed more than 95 percent of the long-spined sea urchins (*Diadema antillarum*) in the Caribbean. After the urchins died, prevalence of seaweeds increased dramatically; today, many coral reefs there are dead.
- Biologists have suggested that overfishing urchin predators such as toadfish (*Opsanus sp.*) and queen triggerfish (*Balistes vetula*) may have played a role in this epidemic.

Fish Population Models

- Stock-recruit relations have been used in fisheries modeling and management since the 1950's.
- At generation t,
- x(t) = Parents or spawner stock
- x(t+1) = Offspring or recruits.

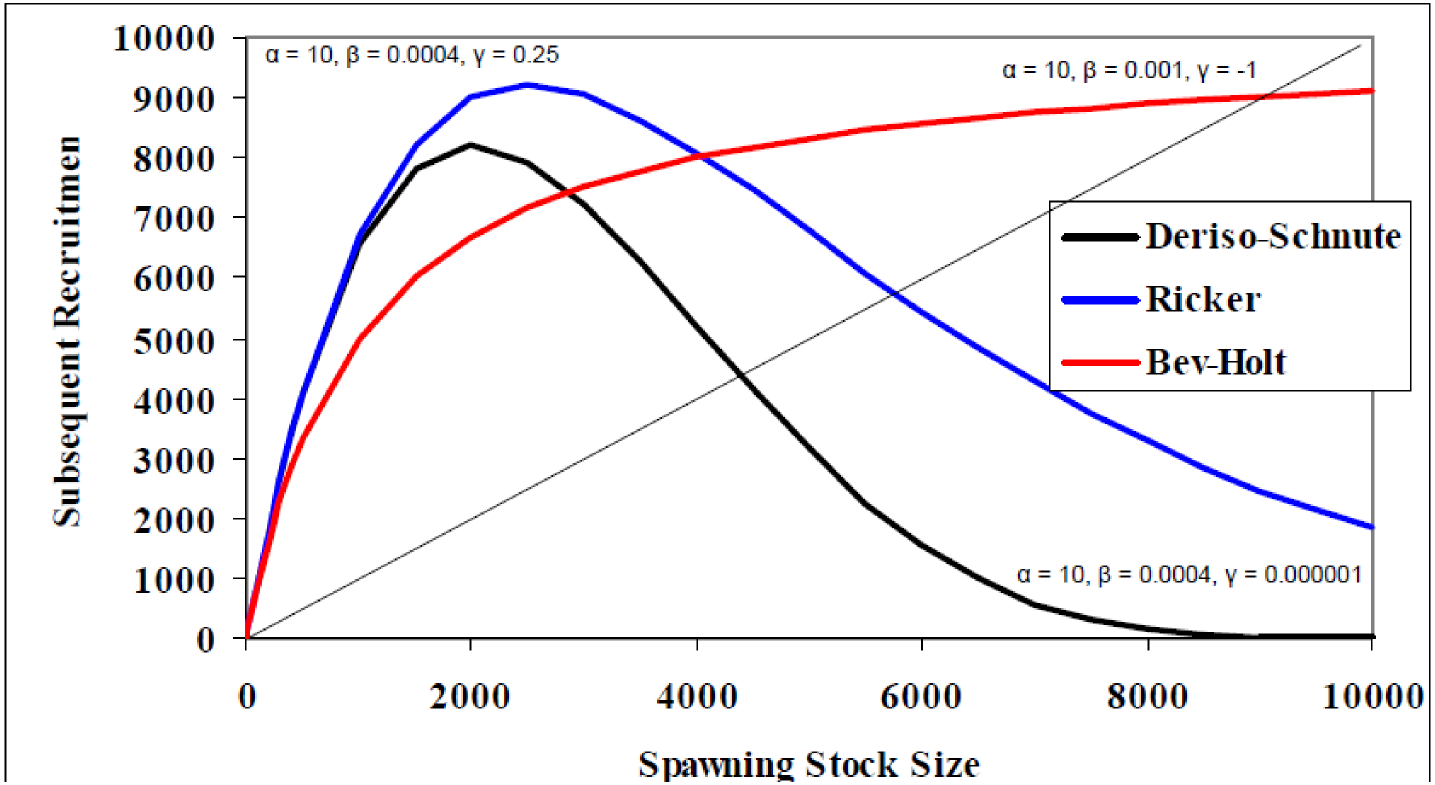


Parametric Models

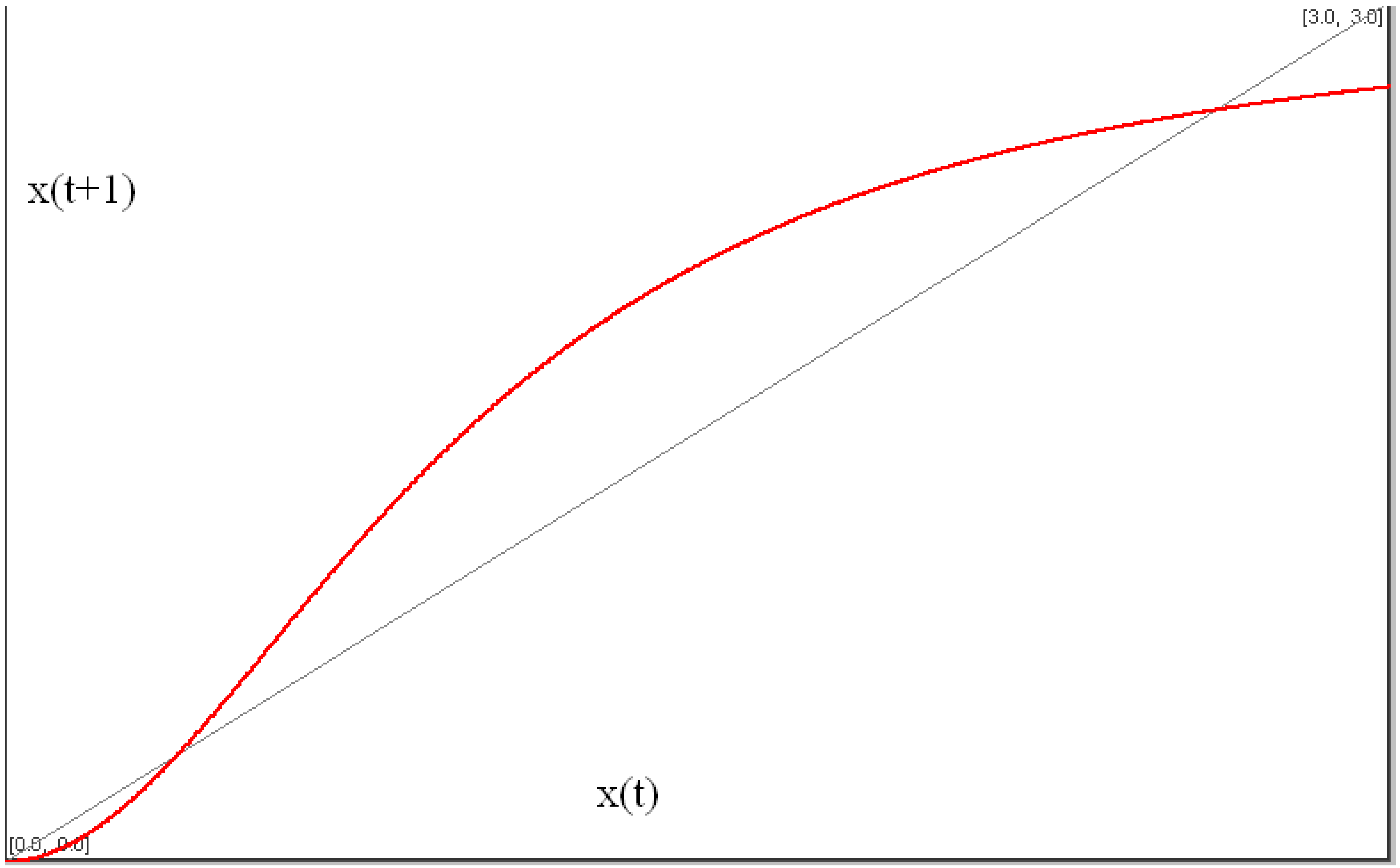
Stock-Recruit Relationships

3. Deriso's Generalized Model $R = \alpha S(1-\beta\gamma S)^{1/\gamma}$

R = recruitment
S = spawner stock
α,β,γ = parameters



Modified Beverton-Holt Model



Total Allowable Catch (TAC)

- Many fisheries are regulated using TAC.
- A TAC within a system of individual transferable quotas (ITQs) is currently used to manage the Alaskan halibut fishery.
- The Alaskan halibut is one of the few success stories in the book on US fisheries management. The TAC did a reasonable good job of preventing overfishing, but created another set of problems.
- Regulated open access: If TAC is imposed on a fishery where access to the resource is free or of minimal cost, fishers have an incentive to “race for the fish,” trying to capture as large a share of the TAC for themselves before the cumulative harvest reaches the TAC and the season is ended.
- Regulated open access may result in a severely compressed fishing season where vast amounts of “fishing effort” are expended in a few day (halibut derby…Prior to 1995…one or two day season).

  - fishers sit idle or re-gear and cause overfishing in other fisheries.

Periodic Proportion Policy (PPP)

At start of year t:

$\boldsymbol{x}(\boldsymbol{t}) =$ estimated fish stock (biomass)

$y(t) =$ total allowable catch (TAC)

$y(t) = \boldsymbol{a}(\boldsymbol{t})\boldsymbol{x}(\boldsymbol{t})$ (PPP)

$a(t) = \boldsymbol{G}(\boldsymbol{F}(\boldsymbol{t}), \boldsymbol{m})$

$F(t) =$ fishing mortality

$m =$ natural mortality

Under Periodic (rotation) Fishing:

Fishing mortality is periodic and $F(t+p) = F(t)$.

Therefore:

$a(t+p) = a(t)$.

Periodic Proportion Policy

- Under PPP, fishing mortality in a given area is varied periodically. Typically, the area is closed for a period of time, then fished, and then closed again. The openings of the different areas are timed so that at least one area is open to fishing each year.
- PPP is actually being used in the management of the Atlantic sea scallops, corals, sea urchins, etc.

Pulse Rotation

The area is closed for (p-1) years, then the area is pulse fished for one year, then closed again for additional (p-1) years, then pulse fished again for one year, etc.

Symmetric Rotation

The area is closed for p/2 years (p even) and then fished at a constant rate for the next p/2 years.

Constant Proportion Policy (CPP)

- y(t) = a x(t)
- a =G(F, m), where F is constant.
- CPP is transparent, easy to implement and acceptable to fishers.

Harvested Fish Stock Model

- Escapement

$$S(t) = x(t) - y(t) = (1 - a(t))x(t)$$

- Model

$$\boldsymbol{x}(\boldsymbol{t}+1) = \boldsymbol{f}(\boldsymbol{S}(\boldsymbol{t})) = (1-\boldsymbol{m})\boldsymbol{S}(\boldsymbol{t}) + \boldsymbol{S}(\boldsymbol{t})\boldsymbol{g}(\boldsymbol{S}(\boldsymbol{t}))$$

or

$$\boldsymbol{x}(\boldsymbol{t}+1) = (1-\boldsymbol{a}(\boldsymbol{t}))\boldsymbol{x}(\boldsymbol{t})((1-\boldsymbol{m}) + \boldsymbol{g}((1-\boldsymbol{a}(\boldsymbol{t}))\boldsymbol{x}(\boldsymbol{t})))$$

CPP and Asymptotically Constant Population Dynamics

$$\boldsymbol{f}(\boldsymbol{x}) = (1-\boldsymbol{a})\boldsymbol{x}((1-\boldsymbol{m}) + \boldsymbol{g}((1-\boldsymbol{a})\boldsymbol{x})),$$

where

$$\boldsymbol{g} : [0,\infty) \to [0,\infty)$$

is a strictly decreasing smooth function,

and

$$\boldsymbol{a} = \boldsymbol{G}(\boldsymbol{F}, \boldsymbol{m}).$$

CPP & Stock Steady State

If $a > \dfrac{g(0) - m}{1 + g(0) - m}$,

then the stock size approaches zero for any initial stock level.

If $a < \dfrac{g(0) - m}{1 + g(0) - m}$ and the dynamics is compensatory,

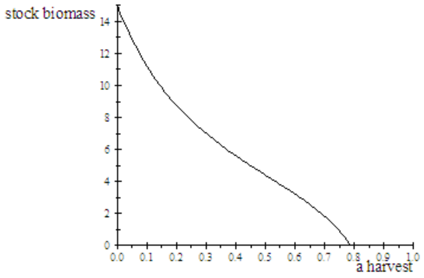
then the steady state biomass is the fixed point

$$x^{\infty} = x^{\infty}(a) = \frac{1}{(1\text{-a})} g^{-1}\left(\frac{1}{\left(1\text{-a}\right)} - (1\text{-m}) \right).$$

CPP & Beverton-Holt Model

$$f(x) = (1-a)x\left((1-m) + \frac{\alpha}{1+\beta(1-a)x}\right),$$

where $1-m+\alpha > 1.$



The stock is depleted when $a > \dfrac{\alpha - m}{1-m+\alpha}.$

The stock persists on a globally attracting fixed point at

$$x^{\infty} = \frac{(1-a)(\alpha+1-m)-1}{\beta(1-a)\left(1-(1-a)(1-m)\right)}$$

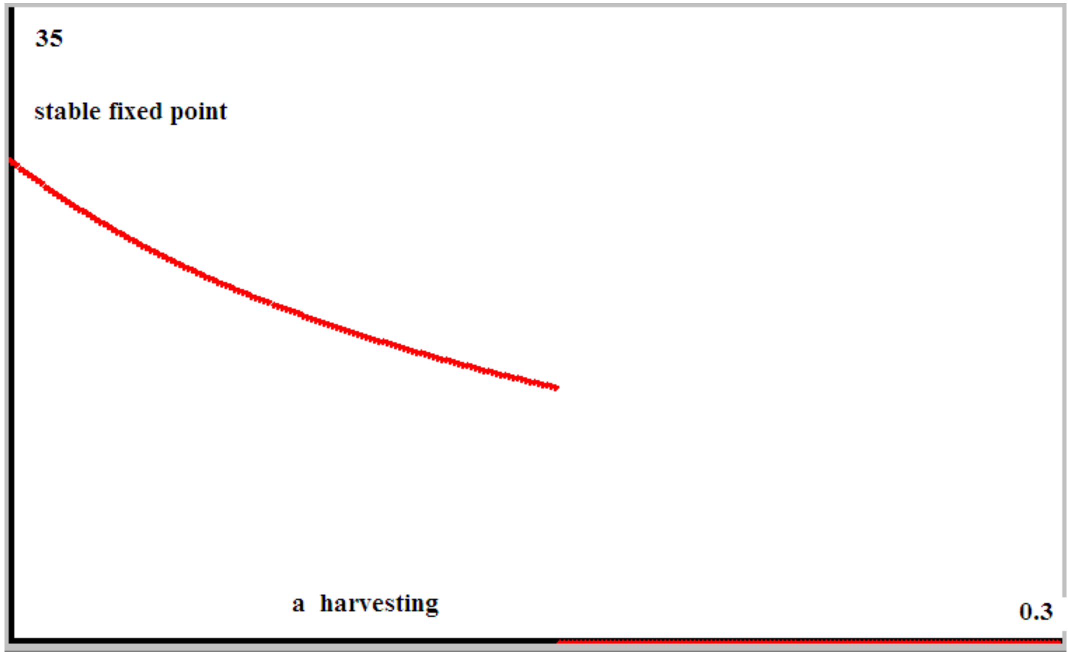
whenever $a < \dfrac{\alpha - m}{1-m+\alpha}.$

Alaskan Halibut $\mathrm{m} = 0.15$

CPP & Modified Beverton-Holt Model

T :

$$f(a,x) = (1-a)x\left((1-m) + \frac{\alpha(1-a)x}{1+\beta((1-a)x)^2} \right) \quad \textit{exhibits the fold bifurcation.}$$



A. –A. Yakubu, M. Li, J. Conrad and M. L. Zeeman, Mathematical Biosciences, 2011.

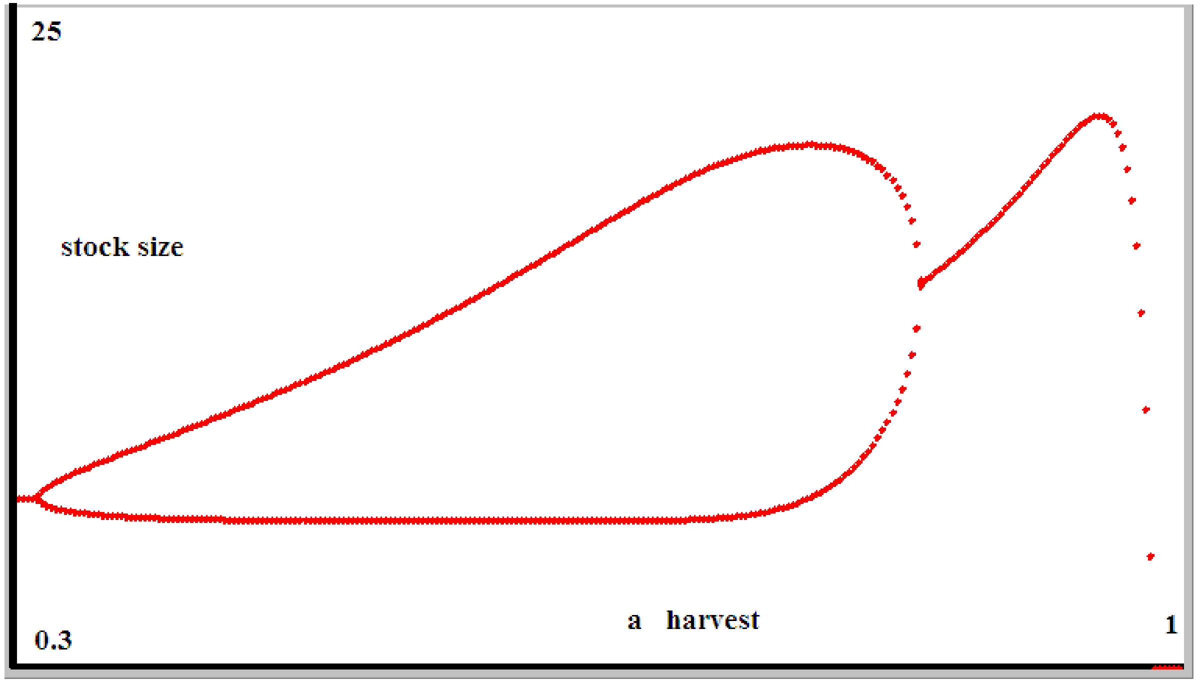
CPP & Ricker Model

- Ricker Model:

$$x(t+1) = (1-a)x(t)\left(1 - m + e^{r-(1-a)x(t)}\right),$$

$$m = 0.2 \text{ (salmon)}$$

CPP & Ricker Model



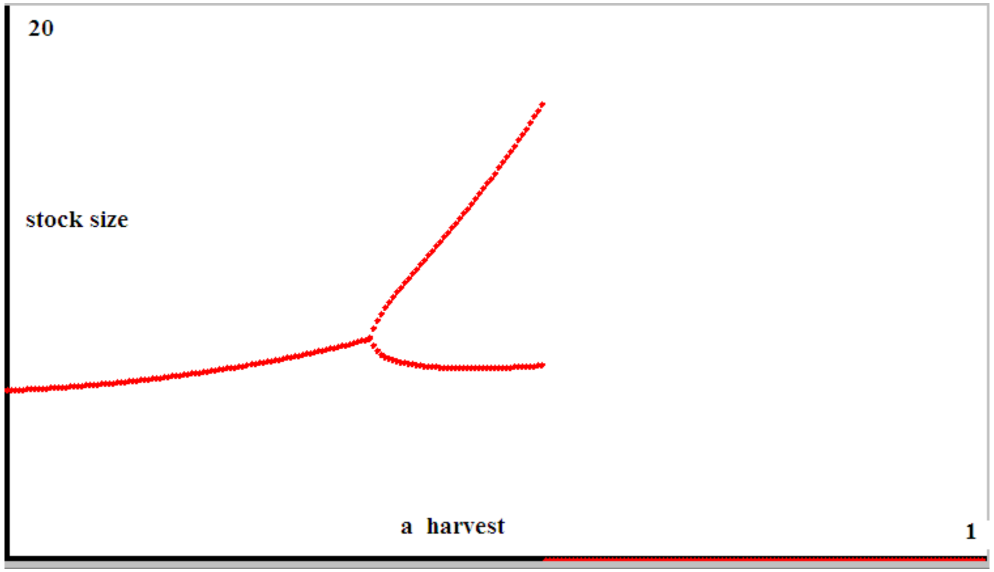
Under Ricker stock recruitment and CPP, the stock size decreases smoothly to zero with increasing levels of harvesting.

Period-doubling reversals L. Stone, Nature 1993.

CPP & Modified Ricker Model

T :

$$f(a,x) = (1-a)x\left(1-m+(1-a)xe^{r-(1-a)x}\right)$$ *exhibits the fold bifurcation.*



A. –A. Yakubu, M. Li, J. Conrad and M. L. Zeeman, Mathematical Biosciences, 2011.

Periodic Proportion Policy (PPP)

We assume a $k-$*periodic fishing mortality* $(F(t+k)=F(t))$,

so that

$$f(t,x)=(1-a(t))x\big((1-m)+g((1-a(t)x)\big),$$

where

$$a(t+k)=a(t).$$

PPP & Asymptotically Constant Dynamics

T :

For each $j \in \{0,1,2,\ldots,k\text{-}1\}$, *let* $f_j(x) = (1 - a(j))x\big((1-m) + g((1-a(j))x\big))$

be an increasing *concave down map under compensatory dynamics in* $(0,\infty)$,

where $a(j+k) = a(j)$.

Then the stock population under period-k harvesting exhibits a globally asymptotically stable r-cycle, where r divides k.

Proof :*Use the general result of Elaydi-Sac*ker *(JDEA'*05*),*

*a period-k extension of the result of Cushing-Henson (JDEA'*01*).*

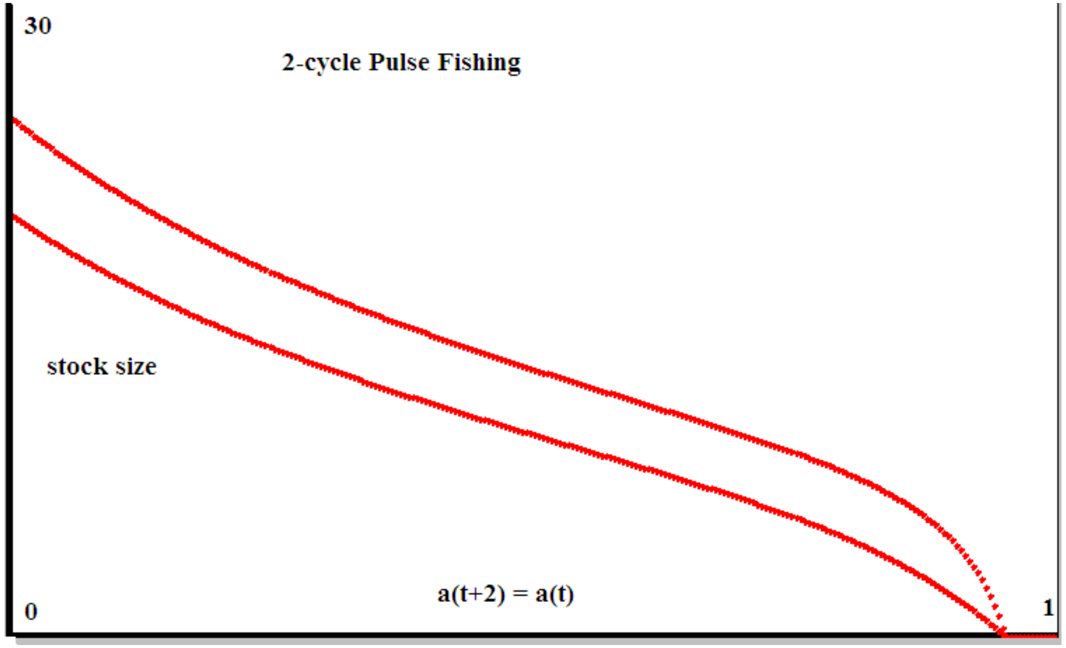
PPP & Beverton-Holt Model

C :

For each $j \in \{0,1,2,\ldots k-1\}$, *let* $f_j(x) = (1-a(j))x\left((1-m) + \dfrac{\alpha}{1+\beta(1-a(j))x}\right)$,

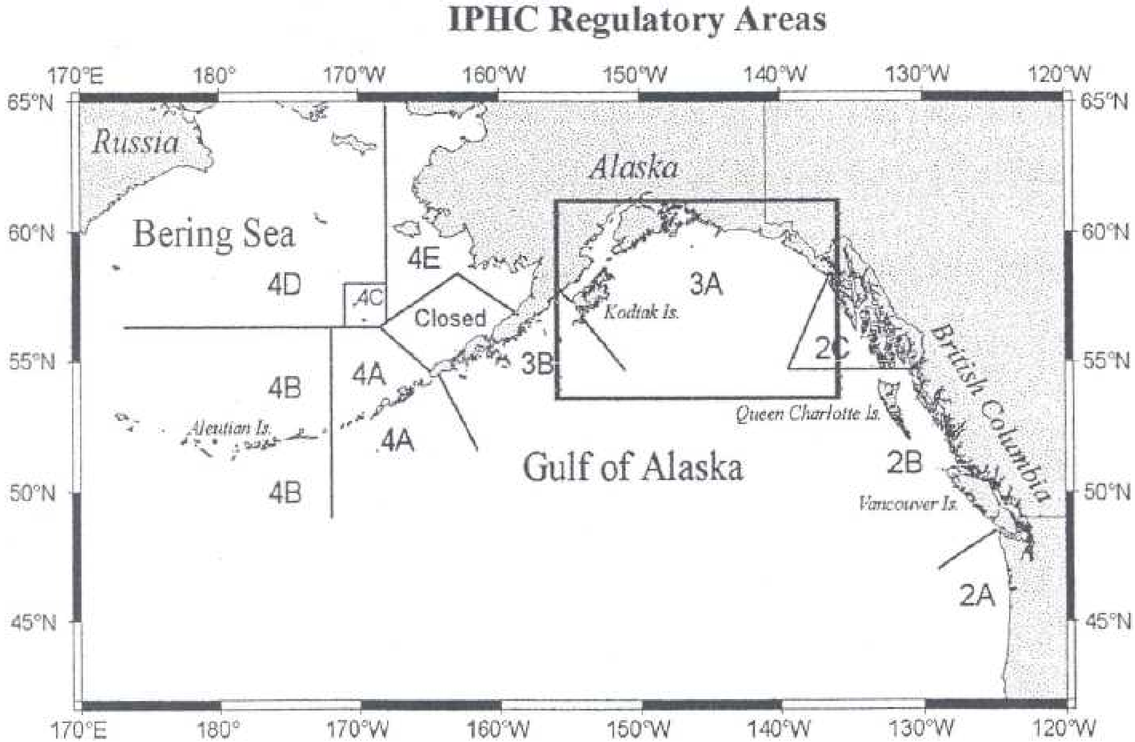
where $(1-a(j))(1-m+\alpha) > 1, \beta > 0$ *and* $a(j+k) = a(j)$.

Then, the stock population under period-k harvesting exhibits a globally asymptotically stable k-cycle.



PPP & Modified Ricker Model

Alaskan Halibut

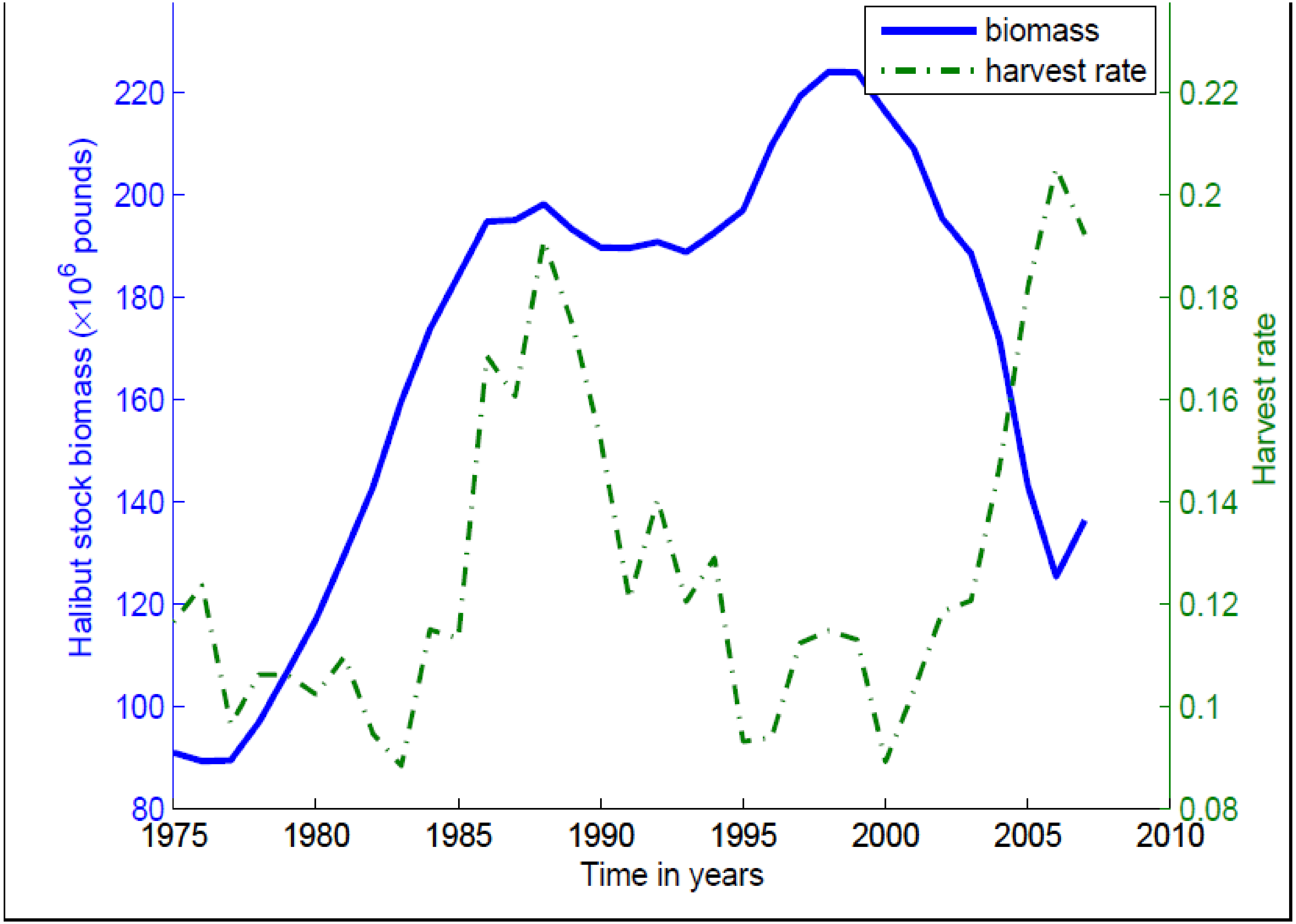


Halibut Data

Year	X_t	Y_t	E_t	Year	X_t	Y_t	E_t
1975	90.989	10.6	192	1992	190.776	26.782	69.093
1976	89.339	11.044	154.848	1993	188.782	22.738	58.728
1977	89.484	8.641	141.639	1994	192.548	24.844	72.776
1978	96.987	10.295	132.051	1995	196.91	18.342	44.375
1979	106.831	11.335	131.86	1996	209.634	19.696	42.008
1980	116.954	11.966	101.441	1997	219.196	24.628	53.93
1981	129.693	14.225	100.211	1998	223.962	25.703	57.317
1982	142.881	13.53	79.529	1999	223.847	25.292	58.192
1983	159.637	14.112	58.629	2000	216.138	19.288	43.634
1984	173.717	19.971	37.729	2001	208.928	21.541	46.055
1985	184.207	20.852	40.54	2002	195.243	23.131	45.897
1986	194.695	32.79	66.398	2003	188.546	22.748	46.858
1987	194.991	31.316	65.258	2004	171.794	25.168	52.041
1988	198.127	37.862	78.25	2005	143.105	26.033	58.543
1989	193.12	33.734	77.341	2006	125.32	25.714	63.921
1990	189.684	28.848	84.873	2007	136.344	26.2	64.024
1991	189.582	22.926	75.455	2008	-	-	-

TABLE Pacific Halibut Biomass ($\times 10^6$ pounds) and Harvest ($\times 10^6$ pounds) in Gulf of Alaska.

Pacific Halibut

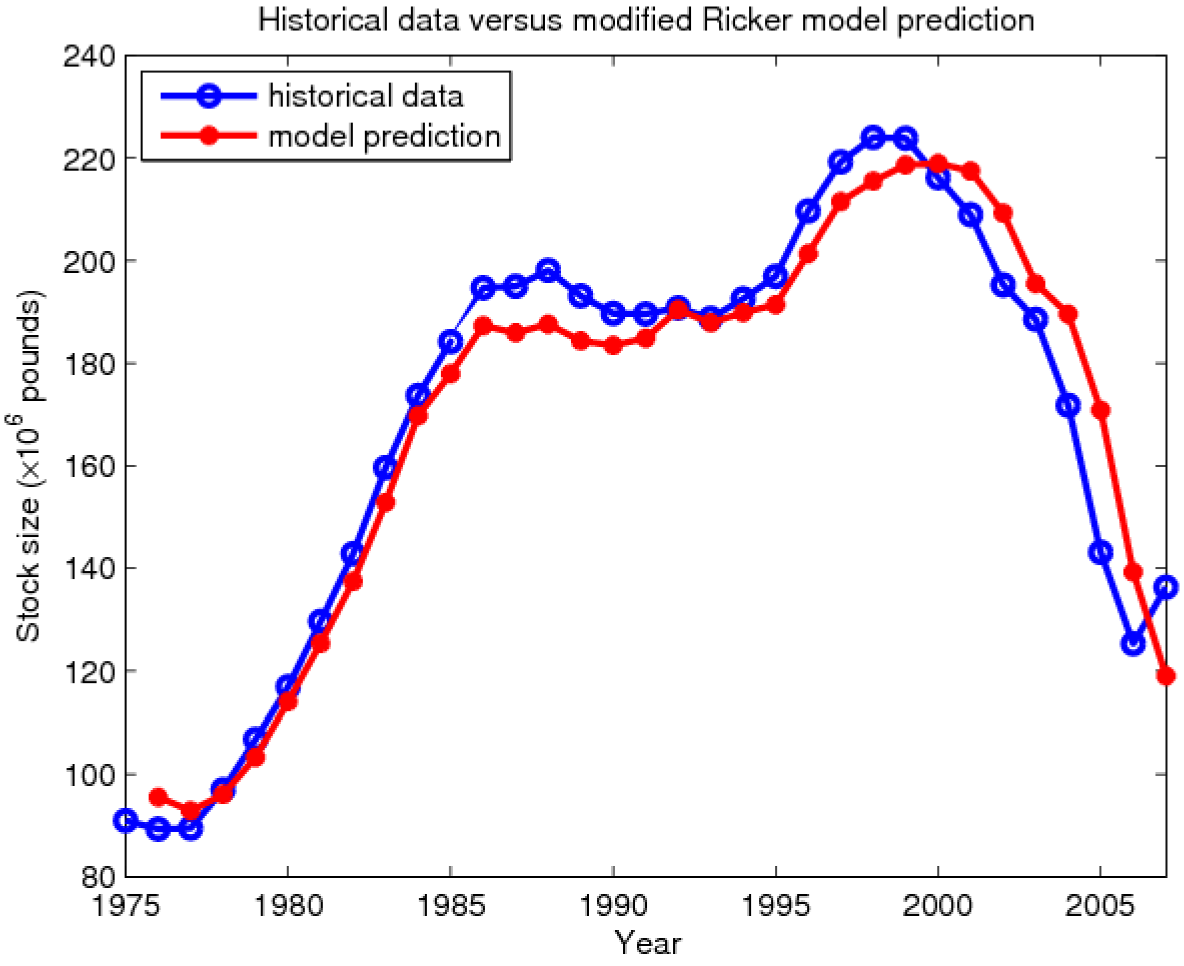


Parameter Estimation

Model	g(s)	Parameters	$c^2\chi^2$
1. Beverton-Holt	$\frac{\alpha}{1+\beta s}$	$\alpha = 0.4455,\ \beta = 3.240 \times 10^{-3}$	0.1203
2. Ricker	$\alpha e^{-\beta s}$	$\alpha = 0.4273,\ \beta = 2.343 \times 10^{-3}$	0.1197
3. Modified Beverton-Holt	$\frac{\alpha s}{1+\beta s^2}$	$\alpha = 7.474 \times 10^{-3},\ \beta = 1.180 \times 10^{-4}$	0.1158
4. Modified Ricker	$\alpha s e^{-\beta s}$	$\alpha = 9.504 \times 10^{-3},\ \beta = 1.013 \times 10^{-2}$	0.1152
5. Logistic	$r(1 - \frac{s}{K})$	$r = 0.4145,\ K = 551.6$	0.1191

TABLE Parameter estimates for the Logistic, Beverton-Holt and Ricker models fit to stock (x) and harvest rate (a) data for the Alaskan halibut Using AIC.

"Fitted" Modified Ricker Model Vrs Halibut Data



Halibut's Future & Fishing Pressure

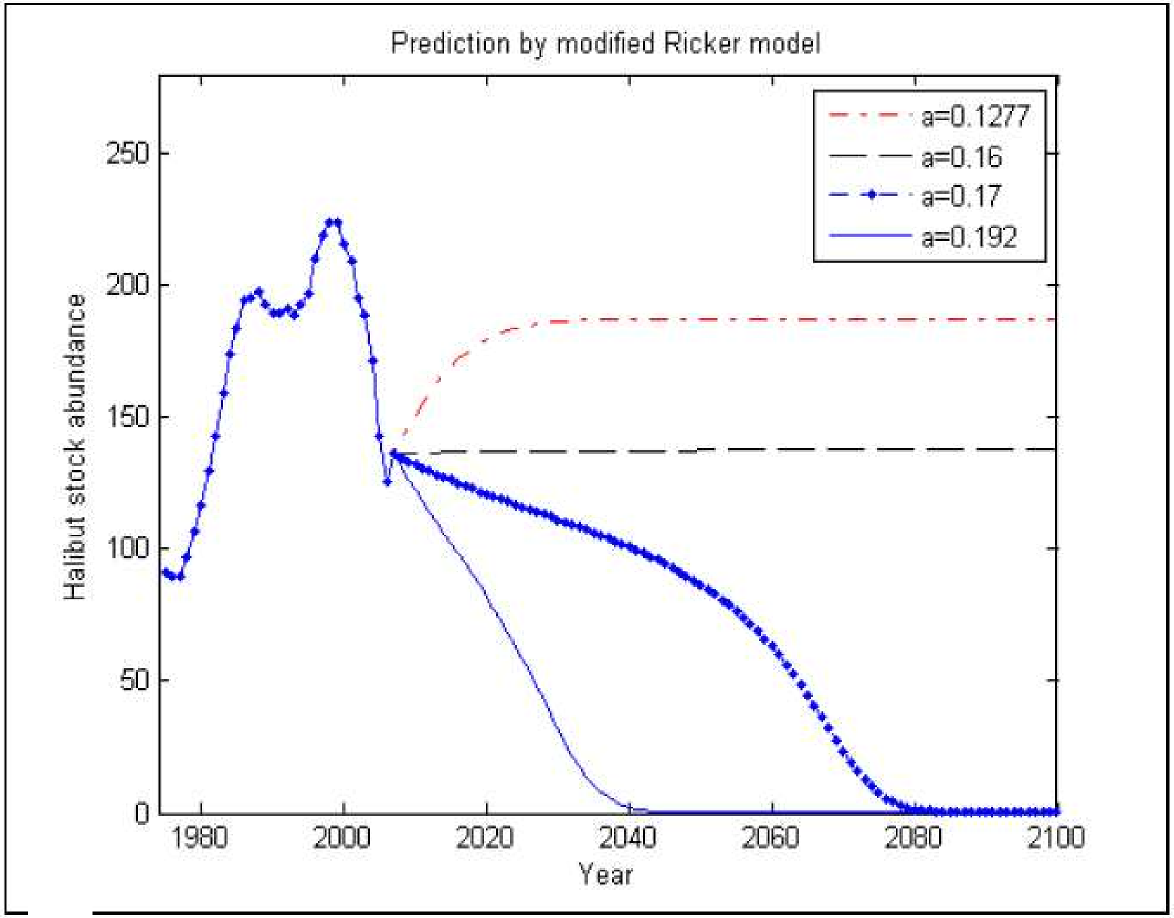


FIGURE 11: Modified Ricker model predictions of halibut stock size (in millions of pounds) after 2007 at the constant harvest values $a = 0.1277$, 0.16, 0.17 and $a(t) = 0.192$, where $\alpha = 0.0102$ and $\beta = 0.0104$ and intial population size $x(0) \equiv x(2007)$.

Stochastic Model
(Random Environment and Fisheries)

Let $\zeta(t) \sim U(1-\sigma, 1+\sigma)$ be a "mean – preserving spread" uniformly distributed random variable.

Stochastic Model:

$$x(t+1) = (1-a(t))x(t)\big((1-m) + \zeta(t)g((1-a(t))x(t))\big)$$

Unstructured Populations in Random Environments

$$x(t+1) = x(t)G(\zeta(t), x(t))$$

where

$$G(\zeta(t), x(t)) = (1-a(t))(1-m+\zeta(t))g((1-a(t))x(t)))$$

* Lewinton and Cohen (1969)

* Birkhoff Ergodic Theorem

* Chesson (1982), Ellner (1984), Hardin *et al* (1988) etc

Let $\gamma = \text{Expected}\{\ln G(\zeta(1),0)\}.$

If $\gamma < 0$ the population goes extinct with probability 1.

If $\gamma > 0$ the population has a low probability of reaching low abundances in the long-term.

Stochastic Halibut Extinctions

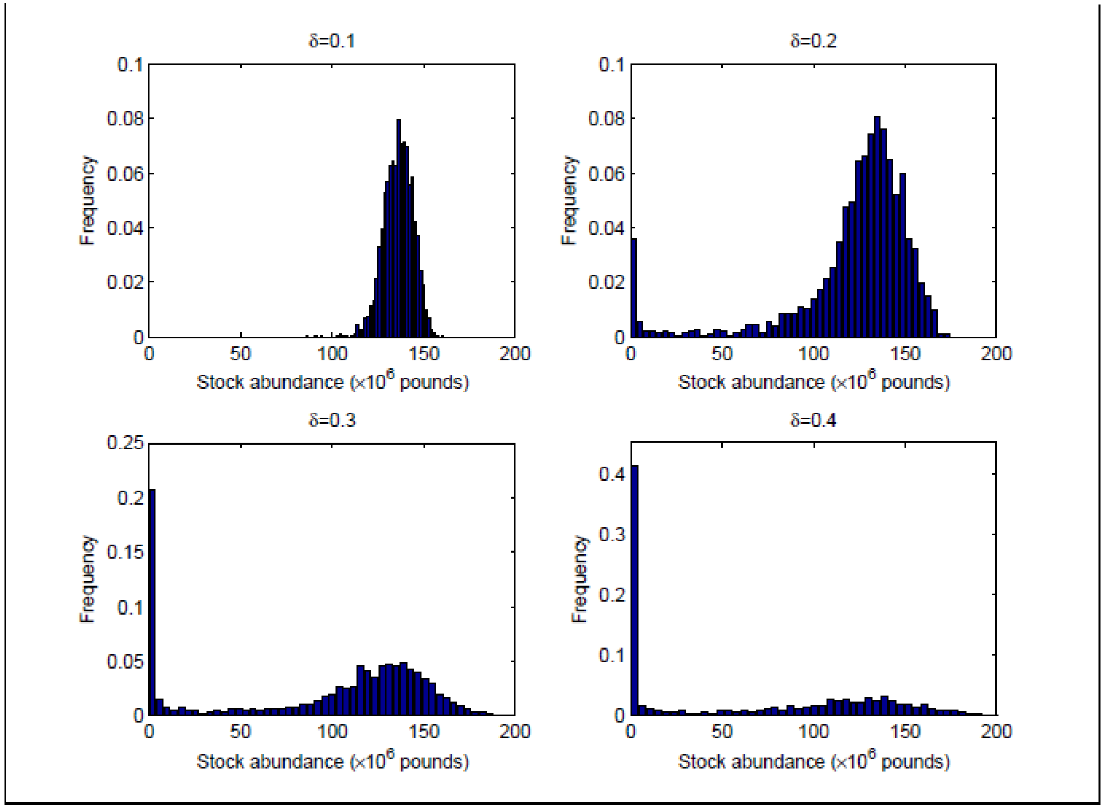
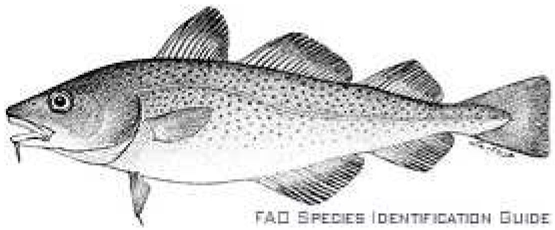


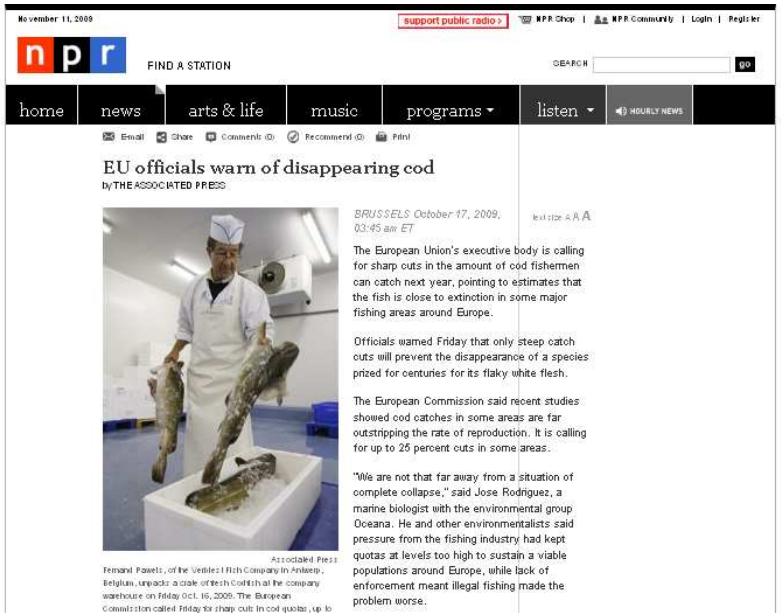
FIGURE 12: Stochastic modified Ricker model predictions of halibut stock size (in millions of pounds) in 2100 at the constant harvest value $a = 0.16$, for $\delta \in \{0.1, 0.2, 0.3, 0.4\}$ where $\alpha = 9.504 \times 10^{-3}$ and $\beta = 1.013 \times 10^{-2}$.

Cod Fishery



The Atlantic cod has, for many centuries, sustained major fisheries on both sides of the Atlantic.

However, the North American fisheries have now largely collapsed.



November 11, 2009

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EU officials warn of disappearing cod

by THE ASSOCIATED PRESS

BRUSSELS October 17, 2009, 03:45 am ET

The European Union's executive body is calling for sharp cuts in the amount of cod fishermen can catch next year, pointing to estimates that the fish is close to extinction in some major fishing areas around Europe.

Officials warned Friday that only steep catch cuts will prevent the disappearance of a species prized for centuries for its flaky white flesh.

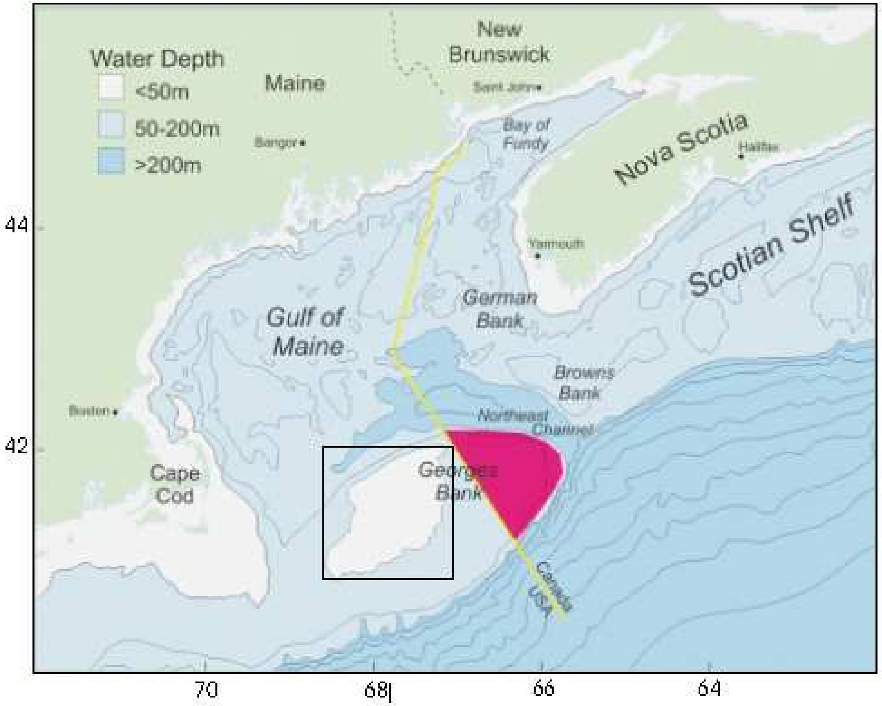
The European Commission said recent studies showed cod catches in some areas are far outstripping the rate of reproduction. It is calling for up to 25 percent cuts in some areas.

"We are not that far away from a situation of complete collapse," said Jose Rodriguez, a marine biologist with the environmental group Oceana. He and other environmentalists said pressure from the fishing industry had kept quotas at levels too high to sustain a viable populations around Europe, while lack of enforcement meant illegal fishing made the problem worse.

Associated Press

Fernand Pawels, of the Verbiest Fish Company in Antwerp, Belgium, unpacks a crate of fresh Codfish at the company warehouse on Friday Oct. 16, 2009. The European Commission called Friday for sharp cuts in cod quotas, up to

Georges Bank Atlantic Cod



Cod Data From Georges Bank

Year	X_t	h_t	Year	X_t	h_t
1978	72148	0.18847	1994	21980	0.282701
1979	73793	0.149741	1995	17463	0.199275
1980	74082	0.219209	1996	18057	0.18781
1981	92912	0.176781	1997	22681	0.193574
1982	82323	0.282033	1998	20196	0.189526
1983	59073	0.34528	1999	25776	0.170108
1984	59920	0.206545	2000	23796	0.156601
1985	48789	0.338185	2001	19240	0.281787
1986	70638	0.147236	2002	16495	0.252869
1987	67462	0.19757	2003	12167	0.255417
1988	68702	0.231541	2004	21104	0.081034
1989	61191	0.208597	2005	18871	0.0873972
1990	49599	0.335648	2006	21241	0.0819517
1991	46266	0.295344	2007	22962	0.105181
1992	34877	0.331848	2008	21848	unknown
1993	28827	0.350394	2009	-	-

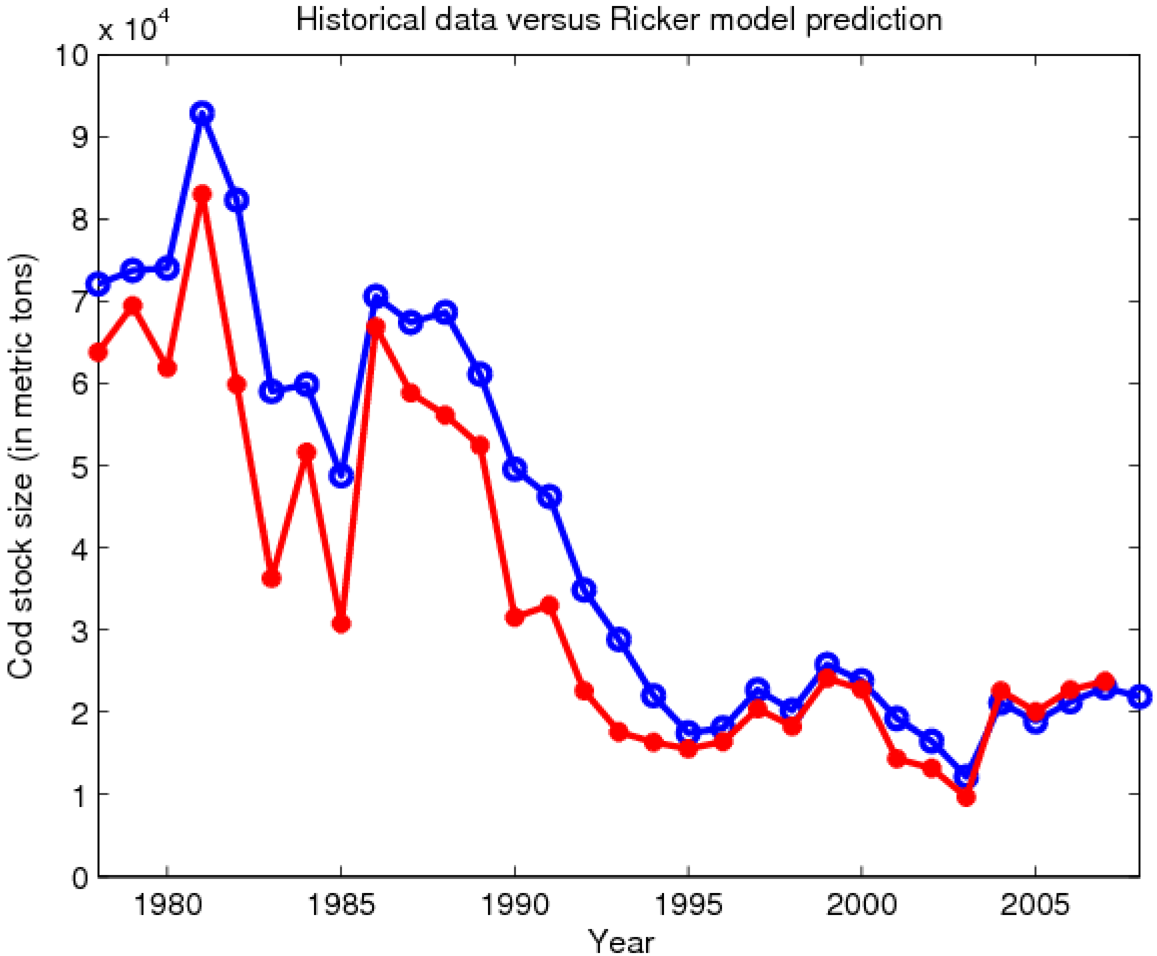
TABLE A3: ıntic cod biomass (in metric tons) and harvest rate in Georges Bank.

Parameter Estimation

Model	g(s)	Parameters	$c^2\chi^2$
1. Beverton-Holt	$\frac{\alpha}{1+\beta s}$	$\alpha = 0.3949$ and $\beta = 2.179 \times 10^{-6}$	1.00362
2. Ricker	$\alpha e^{-\beta s}$	$\alpha = 0.3940$ and $\beta = 2.014 \times 10^{-6}$	1.00360
3. Modified Beverton-Holt	$\frac{\alpha s}{1+\beta s^2}$	$\alpha = 2.860 \times 10^{-5}$ and $\beta = 1.141 \times 10^{-6}$	1.06790
4. Modified Ricker	$\alpha s e^{-\beta s}$	$\alpha = 3.597 \times 10^{-5}$ and $\beta = 3.096 \times 10^{-6}$	1.0594
5. Logistic	$r(1 - \frac{s}{K})$	$r = 0.5999$ and $K = 170014$	1.00356

TABLE Parameter estimates for the Logistics, Beverton-Holt and Ricker models fit to stock (x) and harvest rate (a) data for Georges Bank Cod.

“Fitted” Ricker Model Vrs Cod Data



Cod's Future & Fishing Pressure

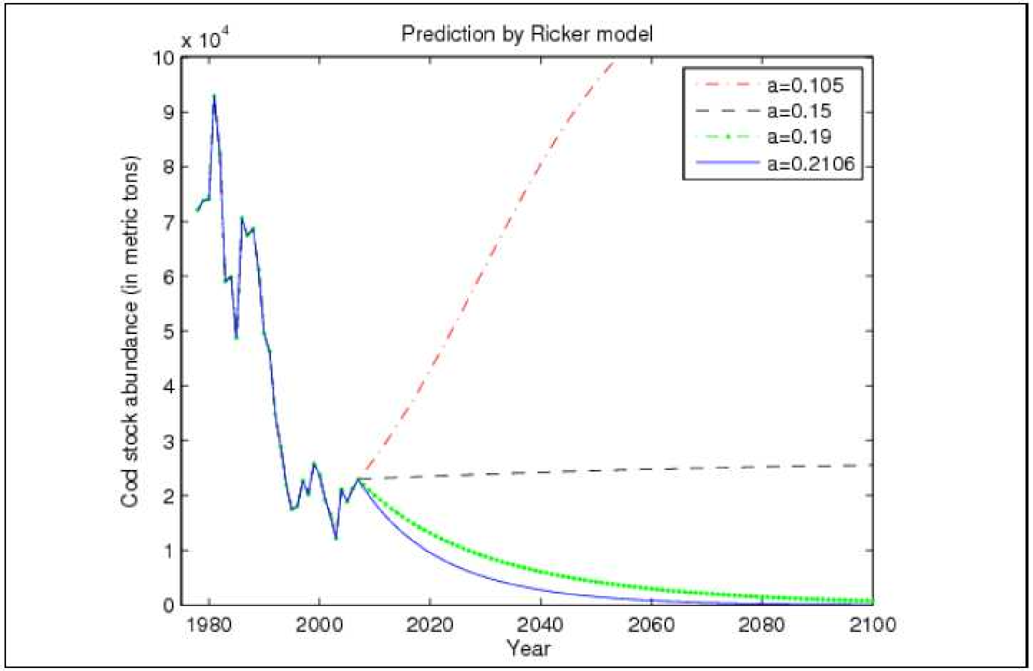


FIGURE [illegible]. The Ricker model predictions of cod stock size (in metric tons) after 2007 at the harvest values $a \in \{0.105, 0.15, 0.19, 0.2106\}$, where $\alpha = 3.94 \times 10^{-1}$ and $\beta = 2.014 \times 10^{-6}$ and initial population size $x(0) \equiv x(2008)$.

Stochastic Cod Extinctions

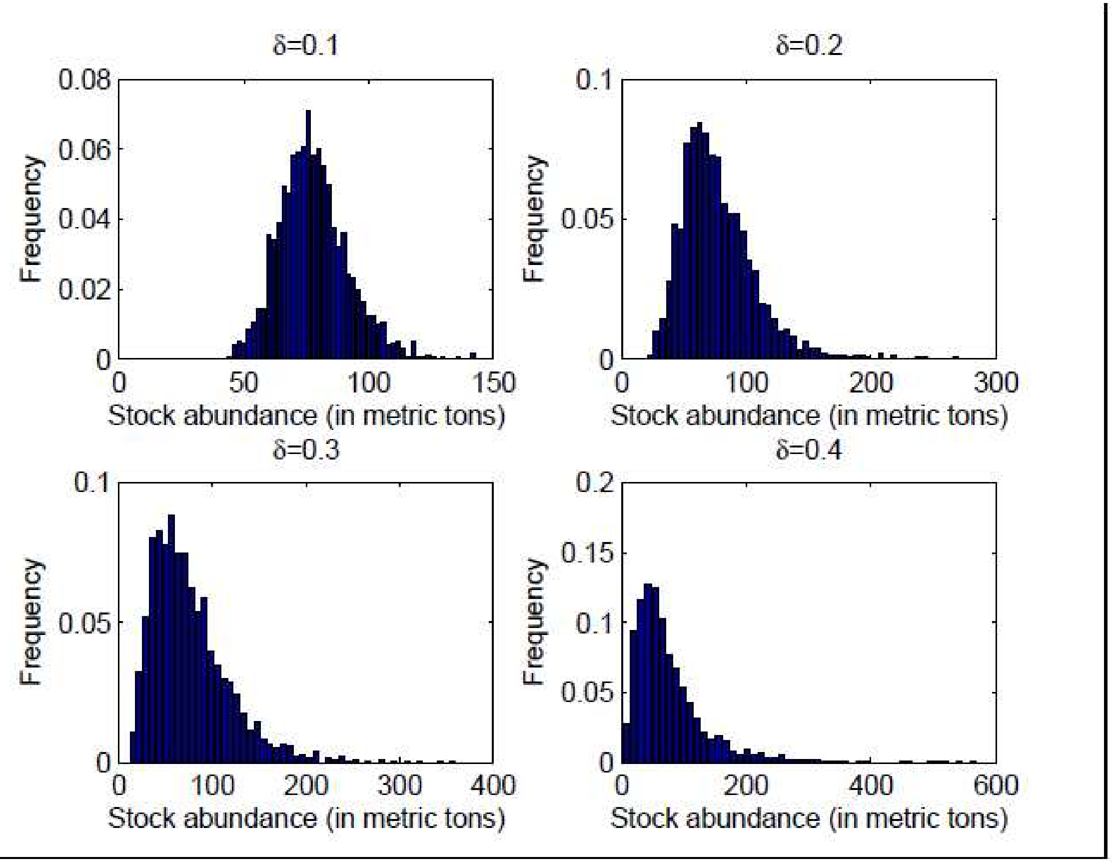


FIGURE Stochastic Ricker model predictions of cod stock size (in metric tons) in 2100 at the constant harvest value $a = 0.2106$, for $\delta \in \{0.1, 0.2, 0.3, 0.4\}$ where $\alpha = 3.94 \times 10^{-1}$ and $\beta = 2.014 \times 10^{-6}$.

Halibut and Cod Sustainability

- Under high fishing mortality, halibut is vulnerable to sudden population collapse while cod is vulnerable to a steady decline to zero.
- Under harvesting levels from the last 30 years, CPP did a reasonable job of preventing collapse of halibut, but left Atlantic cod at risk of collapse.
- Under increased uncertainty, such as more severe weather extremes as predicted by models of climate change, fisheries managed by CPP may be more susceptible to collapse.

Per Capita Growth Rate

(Negative and Positive Density-Dependent Factors)

- Negative density-dependent factors
  - Resource depletion due to competition
  - Environment modification
  - Mutual interference
  - Cannibalism, etc
- Positive density-dependent factors
  - Predator saturation
  - Cooperative predation
  - Increased availability of mates
  - Conspecific enhancement of reproduction, etc

Allee Effect

- An Allee effect occurs when the per-capita growth rate increases at low stock size.
- A strong Allee effect occurs when there is a positive equilibrium stock size A, the Allee threshold, such that the per-capita growth rate is less than one for lower densities (that is, $g(z)<1$ for $z<A$) and is greater than one for some densities greater than A.

Allee Effect In Harvested Fish Stock Model

$$x(t+1) = f(S(t)) = (1-m)S(t) + S(t)g(S(t))I(S(t))$$

or

$$x(t+1) = (1-a(t))x(t)((1-m) + g((1-a(t))x(t))I((1-a(t))x(t))$$

S. J. Schreiber, Theor. Pop. Biol. 2003

Predator Saturation Induced Allee Effect

- The Allee effect is known to occur in populations that are subject to predation by a generalist predator with a saturating functional response.
- Many fish populations prey on cod larva and juvenile, but cod adults are so large that they have few predators; typically sharks only.
- Unlike cod, halibut is close to the top of the food chain of most marine ecosystems. In the northern Pacific, its known predators are the orca whale, sea lion and salmon shark.

Let

$$I(z) = e^{-\frac{\eta}{1+\mu z}}$$

be the probability of escaping predation due to a predator with a saturating functional response, where the positive constant η represents predation intensity and $\mu > 0$ is the proportionality constant to the handling time.

Mate Limitation Induced Allee Effect

- Another mechanism that can force an Allee effect to occur in populations is mating limitations.
- A field experiment of Levin et al. reported that 0% of a small dispersed group of sea urchins *Strongylocentrotus franciscanus* were fertilized, while a fertilization rate of 82.2% was found in the center of a large aggregated group of sea urchins.

Let

$$I(z) = \frac{\lambda z}{1 + \lambda z}$$

be the probability of finding a mate, where the positive constant λ is the searching efficiency of each fish.

Double Allee Effects

- Two or more Allee effects are known to occur in fish populations. For example, in cod *Gadus Morhua* stock populations, indivduals in small-sized populations experience both reduced fertilization efficiency and reduced juvenile survival due to a cultivation effect.

L. Berec, E. Angulo and F. Courchamp, Trends in Ecology and Evolution, 2006

Parameter Estimation

Table 1: Parameter estimates for the Beverton-Holt and Ricker models with and without the induced Allee effects fit to stock (x) and harvest rate (a) data for the Alaskan halibut Using AIC.

Model	AIC_{χ^2}	Parameters
Beverton-Holt	5.337	$\alpha = 0.4455,\ \beta = 0.0032$
Beverton-Holt - P	9.3370	$\alpha = 0.465,\ \beta = 0.0033,\ \eta = 0.0031,\ \mu = 0.0005$
Beverton-Holt - M	7.3149	$\alpha = 1.397,\ \beta = 0.014,\ \lambda = 0.014$
Beverton-Holt - M & P	11.3149	$\alpha = 1.397,\ \beta = 0.0144,\ \lambda = 0.0143,\ \eta \approx 0,\ \mu = 0.0148$
Ricker	5.330	$\alpha = 0.4274,\ \beta = 0.0023$
Ricker - P	9.3300	$\alpha = 0.4273,\ \beta = 0.0023,\ \eta = 0.00087,\ \mu = 0.0101$
Ricker - M	7.2804	$\alpha = 6.81,\ \beta = 0.0089,\ \lambda = 0.014$
Ricker - M & P	11.2813	$\alpha = 2.28,\ \beta = 0.0073,\ \lambda = 0.0045,\ \eta = 0.0053,\ \mu = 0.092$

Fitted Ricker Model Vrs Data

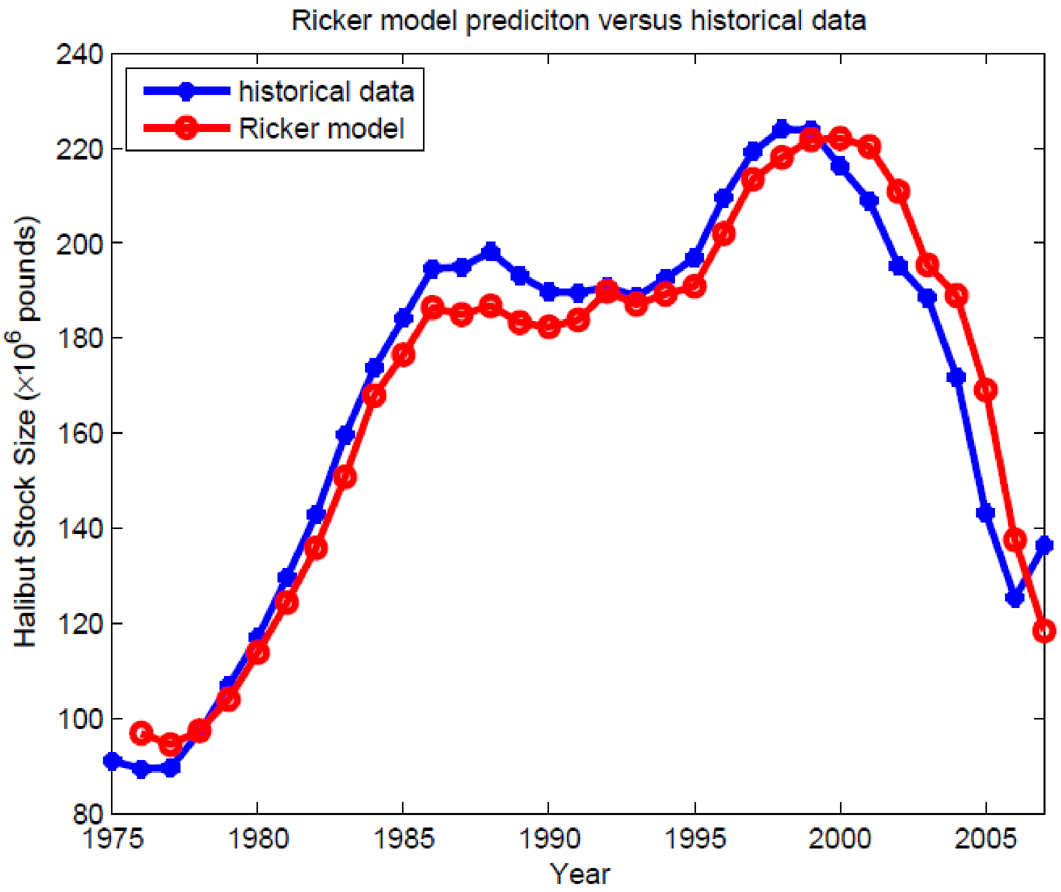
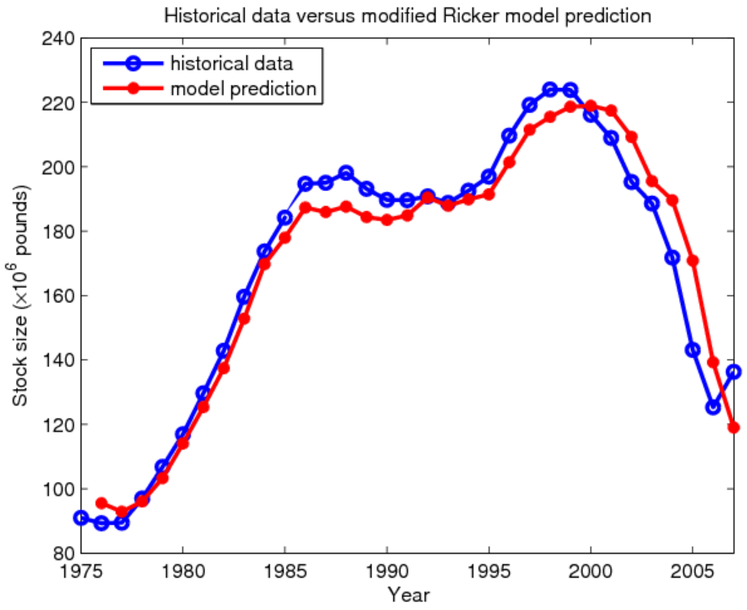
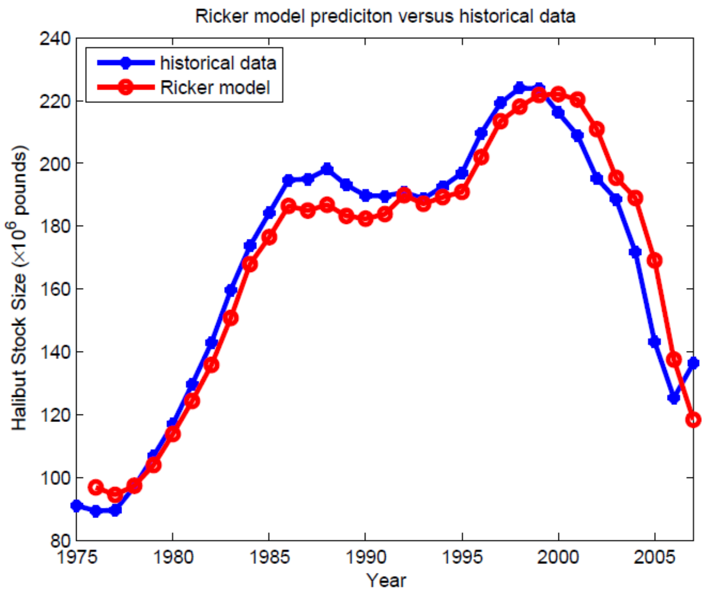


FIGURE Best "fit" Ricker Model versus Pacific halibut data.

Ricker Vrs Modified Ricker





Fitted Ricker Model Predictions

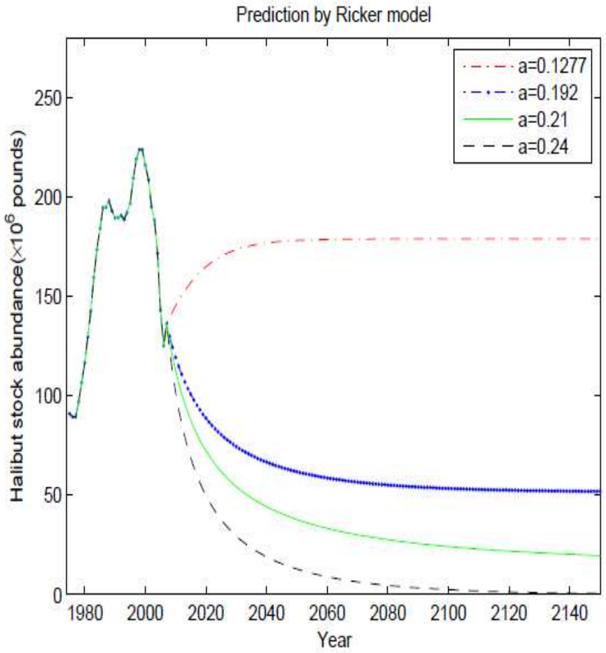


Figure : Ricker model predictions of halibut stock size (in millions of pounds) after 2007 at the constant harvest values $a = 0.1277$, 0.192, 0.21 and 0.24, where $\alpha = 0.4274$ and $\beta = 0.0023$ and intial population size $x(0) \equiv x(2007)$.

Table : Estimates of Lyapunov Exponents for $a = 0.21$ and $a = 0.24$.

δ	$\gamma(\delta)$ when a = 0.21	$\gamma(\delta)$ when a = 0.24
0.1	0.00895	−0.0298
0.2	0.00883	−0.0303
0.3	0.00727	−0.0312
0.4	0.00715	−0.0324

Sea Scallop

- The Atlantic sea scallop resource is healthy and is harvested at sustainable levels.
- Fishing effort has been reduced in order to keep the sea scallop fishery sustainable.
- Areas where scallops can be harvested are rotated to maximize scallop yields and protect beds of young scallops as they grow.
- Scallops are a good low-fat source of protein and are high in selenium and B vitamins (USDA).
- The U.S. sea scallop fishery is extremely important to our economy and is the largest wild scallop fishery in the world.
- In 2009, U.S. fishermen harvested 58 million pounds of sea scallop meats worth over $382 million.
- Massachusetts and New Jersey are responsible for the majority of the U.S. harvest

Georges Bank & Mid-Atlantic Scallop

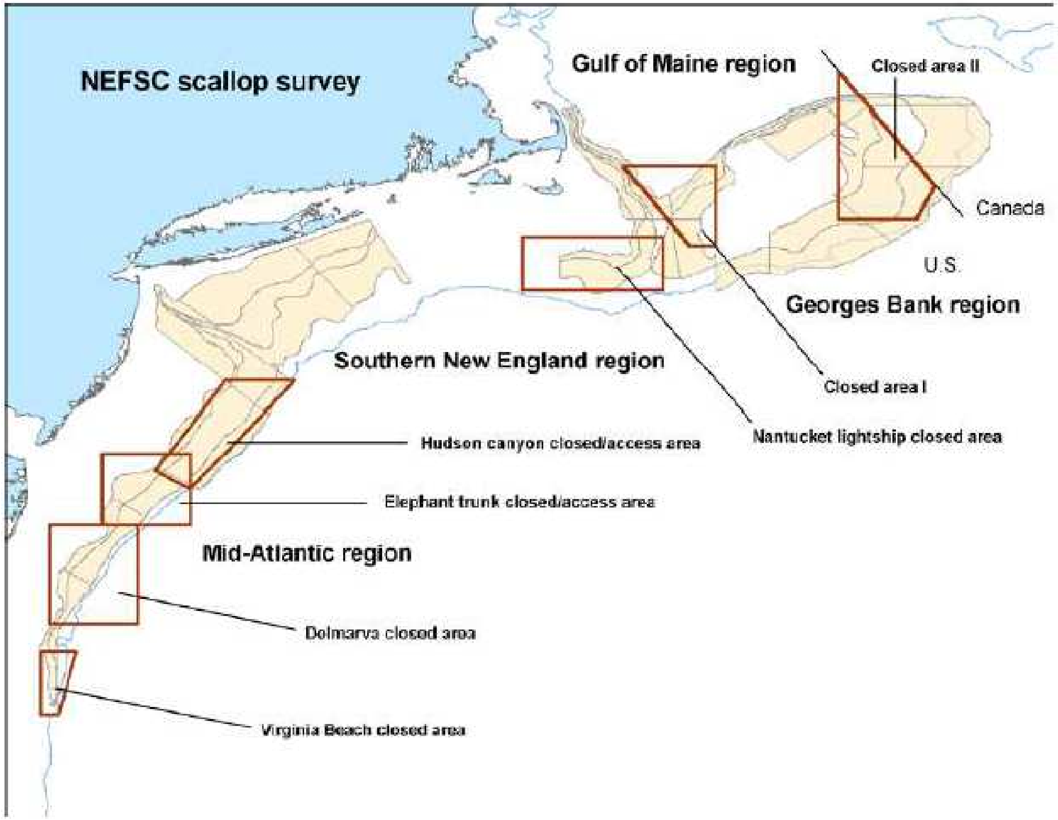


Figure 5: Map of NEFSC sea scallop survey areas (yellow, with stratum boundaries shown) and the closed or rotational access areas (bounded by dark red lines).

Sea Scallop Data

	Georges Bank						MidAtlantic						Total			
Year	Full_F	SE	Abundance (millions)	SE	Biomass (mt meats)	SE	Full_F	SE	Abundance (millions)	SE	Biomass (mt meats)	SE	Full_F	SE	Abundance (millions)	SE
1975	0.11	0.02	1148	56	20780	1038	0.59	0.09	591	34	6503	386	0.21	0.09	1739	66
1976	0.20	0.04	1419	60	24705	1112	1.00	0.16	787	33	7931	491	0.38	0.16	2205	69
1977	0.33	0.05	1115	52	24522	1056	0.53	0.07	772	30	9933	487	0.39	0.23	1886	60
1978	0.39	0.06	1260	51	21973	920	1.05	0.15	567	21	9690	443	0.57	0.3	1827	55
1979	0.53	0.08	878	40	17822	762	1.07	0.20	364	15	7678	364	0.63	0.44	1242	43
1980	0.47	0.08	1060	43	14970	628	0.35	0.05	343	16	6365	347	0.44	0.34	1403	45
1981	0.62	0.09	747	34	12579	533	0.13	0.03	403	18	6754	364	0.48	0.44	1151	38
1982	0.83	0.13	808	35	9505	425	0.25	0.04	442	21	7401	386	0.58	0.46	1250	41
1983	0.71	0.11	573	30	7680	393	0.53	0.07	497	25	6987	417	0.64	0.41	1070	39
1984	0.42	0.08	565	34	7364	442	0.80	0.12	536	31	6062	459	0.58	0.25	1101	46
1985	0.51	0.10	610	42	7840	528	0.75	0.13	744	40	6346	506	0.61	0.3	1354	58
1986	0.88	0.21	984	60	8481	542	0.57	0.09	977	47	8704	556	0.72	0.41	1962	76
1987	0.76	0.16	1096	66	9988	596	1.20	0.17	1171	49	9340	585	0.96	0.43	2267	82
1988	0.83	0.18	1251	77	11321	686	0.90	0.12	[illegible]	49	10365	558	0.86	0.44	2399	91
1989	0.64	0.13	1415	81	13453	736	1.14	0.15	1147	42	9852	534	0.85	0.39	2562	91
1990	1.11	0.21	1369	74	12791	678	0.96	0.11	1018	36	9747	418	1.05	0.63	2387	82
1991	1.53	0.28	1486	68	10725	475	1.07	0.10	705	26	8026	327	1.32	0.8	2191	73
1992	1.72	0.25	783	36	7056	303	1.10	0.12	468	24	5426	298	1.47	1.01	1251	43
1993	1.19	0.21	553	32	4868	279	0.86	0.14	894	38	5634	319	1.05	0.66	1448	49
1994	0.31	0.07	531	36	5719	394	1.37	0.18	1137	40	8027	360	0.87	0.18	1668	53
1995	0.16	0.03	1003	48	9878	553	1.08	0.11	965	34	8785	361	0.62	0.1	1968	59
1996	0.33	0.07	1201	53	15406	727	0.74	0.08	647	31	8167	411	0.53	0.18	1849	62
1997	0.28	0.07	1305	62	20141	885	0.47	0.06	690	44	7850	528	0.35	0.18	1995	76
1998	0.22	0.06	1924	82	27276	1022	0.53	0.10	1695	82	11858	716	0.31	0.16	3619	116
1999	0.54	0.13	2008	87	33163	1211	0.49	0.09	2872	106	23689	1043	0.51	0.23	4881	137
2000	0.48	0.12	3129	99	41066	1410	0.48	0.08	3523	112	37324	1326	0.48	0.14	6652	149
2001	0.26	0.05	3294	95	53064	1704	0.54	0.07	3766	107	45795	1433	0.43	0.11	7061	143
2002	0.23	0.05	2819	88	62370	1994	0.61	0.08	3427	100	48798	1449	0.41	0.12	6246	133
2003	0.17	0.04	2945	96	69416	2294	0.68	0.08	4174	115	48756	1397	0.42	0.1	7119	150
2004	0.10	0.02	2708	96	74629	2603	0.87	0.09	3703	112	50029	1468	0.38	0.07	6411	147
2005	0.18	0.03	2571	103	73828	2862	0.84	0.14	3609	131	49027	1728	0.37	0.13	6180	167
2006	0.38	0.06	2128	108	62768	3090	0.35	0.06	3805	166	56405	2377	0.37	0.23	5933	198
2007	0.25	0.05	2364	151	53650	3472	0.55	0.09	3853	209	61784	3260	0.40	0.14	6217	258
2008	0.19	0.04	2769	204	55508	4234	0.54	0.10	4509	313	63983	4518	0.37	0.11	7278	374
2009	0.18	0.05	3453	294	62470	5341	0.60	0.13	3993	352	67233	6460	0.38	0.11	7446	458

Figure CASA model estimates and standard errors for fully recruited sea scallop fishing mortality, July 1 abundance 40+mm SH, and July 1 biomass 40+ mm SH.

Parameter Estimation

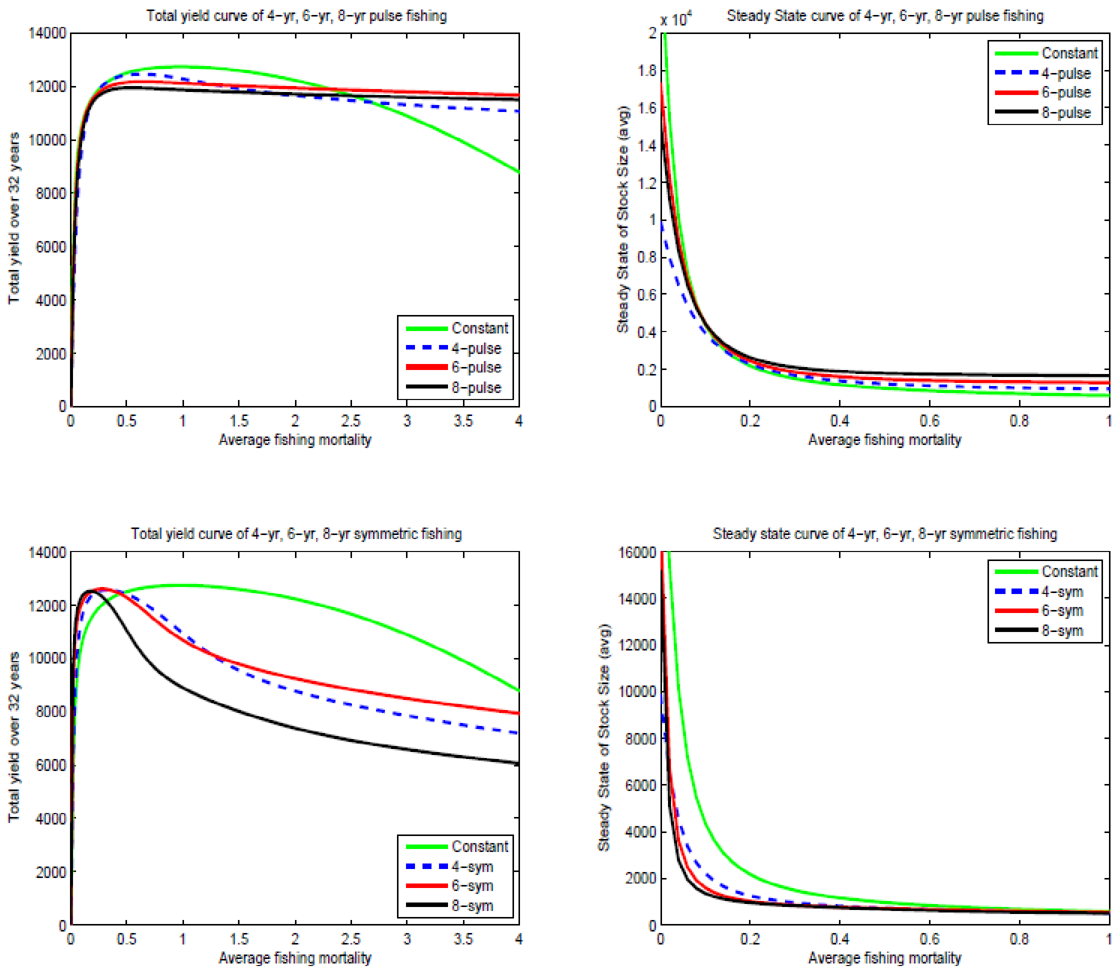
Table Parameter estimates Geroges Bank sea scallop with 4-patch model.

Model	$c^2\chi^2$	AIC	Parameters
Beverton-Holt	1.9026	769.7	$\alpha = 5.64, \beta = 0.0425$
Beverton-Holt -M	1.9026	771.7	$\alpha = 5.64,\ \beta = 0.0425,\ \lambda = 1.34 \times 10^{10}$
Beverton-Holt -P	1.8643	758.3	$\alpha = 326.3,\ \beta = 0.318,\ \eta = 2.39,\ \mu = 0.00052$
Beverton-Holt P&M	1.8721	763.4	$\alpha = 37.6,\ \beta = 0.115,\ \lambda = 1.37,\ \eta = 1.16,\ \mu = 0.00095$
Ricker	2.2032	890.7	$\alpha = 1.56, \beta = 0.00409$
Ricker -M	2.2032	892.7	$\alpha = 1.56,\ \beta = 0.00409,\ \lambda = 1.28 \times 10^8$
Ricker -P	2.2032	894.7	$\alpha = 1.56,\ \beta = 0.00409,\ \eta = 0.00015,\ \mu = 0.00109$
Ricker P&M	2.2040	897.0	$\alpha = 5.5,\ \beta = 0.0041,\ \lambda = 1.26,\ \eta = 5.93 \times 10^{-6},\ \mu = 10.97$

Table Parameter estimates Geroges Bank sea scallop with 6-patch model.

Model	$c^2\chi^2$	AIC	Parameters
Beverton-Holt	1.9026	769.7	$\alpha = 5.64, \beta = 0.0638$
Beverton-Holt -M	1.9026	769.7	$\alpha = 5.64,\ \beta = 0.064,\ \lambda = 3.34 \times 10^9$
Beverton-Holt -P	1.8635	758.0	$\alpha = 2415,\ \beta = 1.011,\ \eta = 3.659,\ \mu = 0.000495$
Beverton-Holt P&M	1.873	761.0	$\alpha = 174.3,\ \beta = 1.339,\ \lambda = 13.94,\ \eta = 0.826,\ \mu = 0.0004795$
Ricker	2.2032	890.7	$\alpha = 1.56, \beta = 0.00613$
Ricker -M	2.2032	892.7	$\alpha = 1.56,\ \beta = 0.00613,\ \lambda = 1.28 \times 10^8$
Ricker -P	2.2032	894.7	$\alpha = 1.56,\ \beta = 0.00613,\ \eta = 0.000096,\ \mu = 0.00077$
Ricker P&M	–	–	$\alpha = -,\ \beta = -,\ \lambda = -,\ \eta = -,\ \mu = -$

Pulse Versus Symmetric Rotations



Conclusion

- Under harvesting levels from the last 30 years, the CPP did a reasonable job of preventing the collapse of the halibut, but left the Atlantic cod at risk of collapse. Using Lyapunov exponents, we obtain that under increased uncertainty, such as more severe weather extremes as predicted by models of global climate change, fisheries managed using CPP may be more susceptible to collapse.

- At high fishing mortalities, pulse PPP leads to both highest sea scallop yield and sea scallop steady state biomass.

- At low fishing mortalities, CPP can lead to highest scallop yield with lowest steady state biomass.

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- Michael Fogarty, NEFSC, Woods Hole
- NSF Funded Project on Computational Sustainability

Thank You!

Data

Table 1. Important species landed or raised in the Northeast, their landings, L (thousand mt), ex-vessel revenue, R ($, millions), and prices,P ($ per lb), 1995-1999

Year	L	R	P	L	R	P	L	R	P	L	R	P	L	R	P
	American lobster			Sea scallops			Blue crab			Atlantic salmon2			Goosefish		
1995	31.8	215	3.06	8	91.1	5.16	56.7	101	0.81	10	56.7	2.56	25.1	36.1	0.65
1996	32.5	243	3.39	7.9	98.2	5.64	37.7	64.3	0.77	10	46.2	2.1	25.3	32.3	0.58
1997	37.5	272	3.29	6.3	90.5	6.56	45.3	82.7	0.83	12.2	49.5	1.84	28.3	35.2	0.56
1998	36.3	255	3.19	5.6	76	6.19	39.1	90.1	1.05	13.1	60.4	2.09	26.7	33.9	0.58
1999	39.7	323	3.69	10.1	123	5.5	39	80.6	0.94	12.2	58.2	2.16	25.2	47	0.85
	Hard Clam			Surf clam			Menhadin			Squid Loligo			Cod		
1995	4.2	42.1	4.5	30.1	47.1	0.71	345	45.7	0.06	18.5	23.8	0.58	13.7	28.6	0.95
1996	3.2	35.1	4.94	28.8	42.6	0.67	283	37.9	0.06	12.5	18.6	0.68	14.3	26.7	0.85
1997	4.4	44.5	4.62	26.3	38.9	0.67	247	33.8	0.06	16.2	26.5	0.74	13	24.6	0.86
1998	3.6	41.2	5.2	24.5	33	0.61	249	44.4	0.08	19.2	32.7	0.77	11.1	25.5	1.04
1999	3.5	40.7	5.25	26.7	34.1	0.58	189	33.2	0.08	18.8	32.2	0.78	9.7	23.9	1.11