Dynamic macroecology on ecological time scales

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- Outline:
- Some major challenges
- Temporal dynamics of macroecological patterns
  - Examples
    - I. Abundance-distribution relationships
    - II. Latitudinal gradients in fish diversity
    - III. Trophic dynamics
      - Model development
      - Model validation
- Summary

•use of rich data bases from fisheries surveys
•focus on NW Atlantic)

Collaborators: J. Fisher, B. Petrie, N. Shackell, W.C. Leggett

Major challenges for macroecology

- Identifying and isolating mechanisms underlying patterns
  - Patterns revealed by large-scale, comparative, non-experimental studies
  - Most data obtained from secondary sources rather than primary ones
  - Heavy focus on determining shapes of relationships with ensuing debates

- Determining whether revealed patterns are real
  - Relationships based on snapshots of different systems
    - Single survey
    - Time averaged
    - Cumulative data

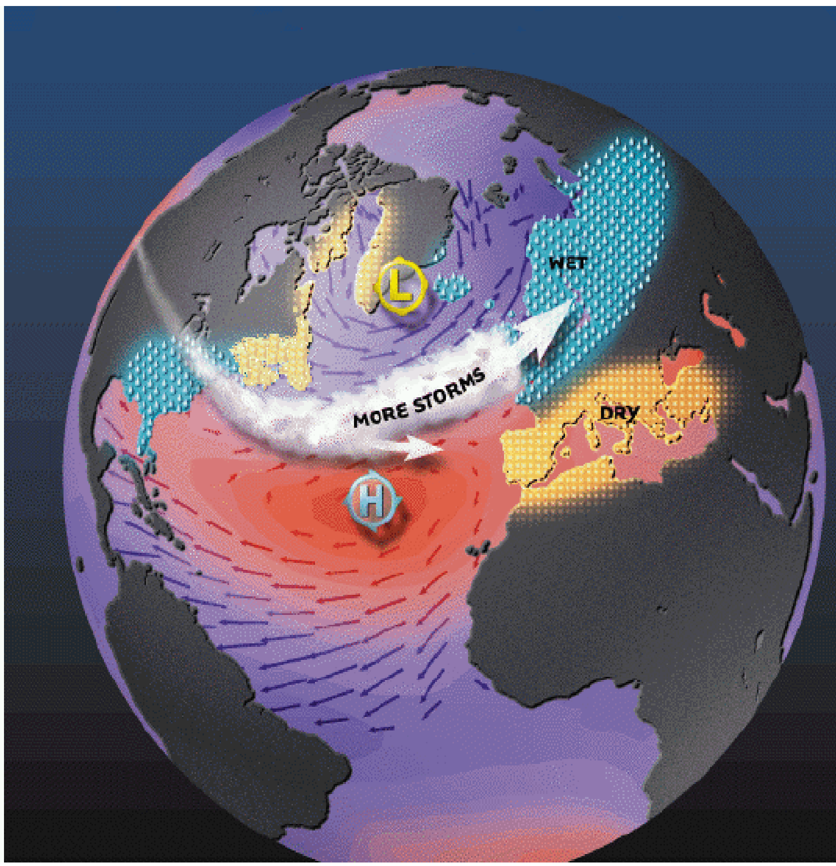
    } Often non-contemporaneous

  - Reliance on such data could obscure patterns and conceal identity of processes

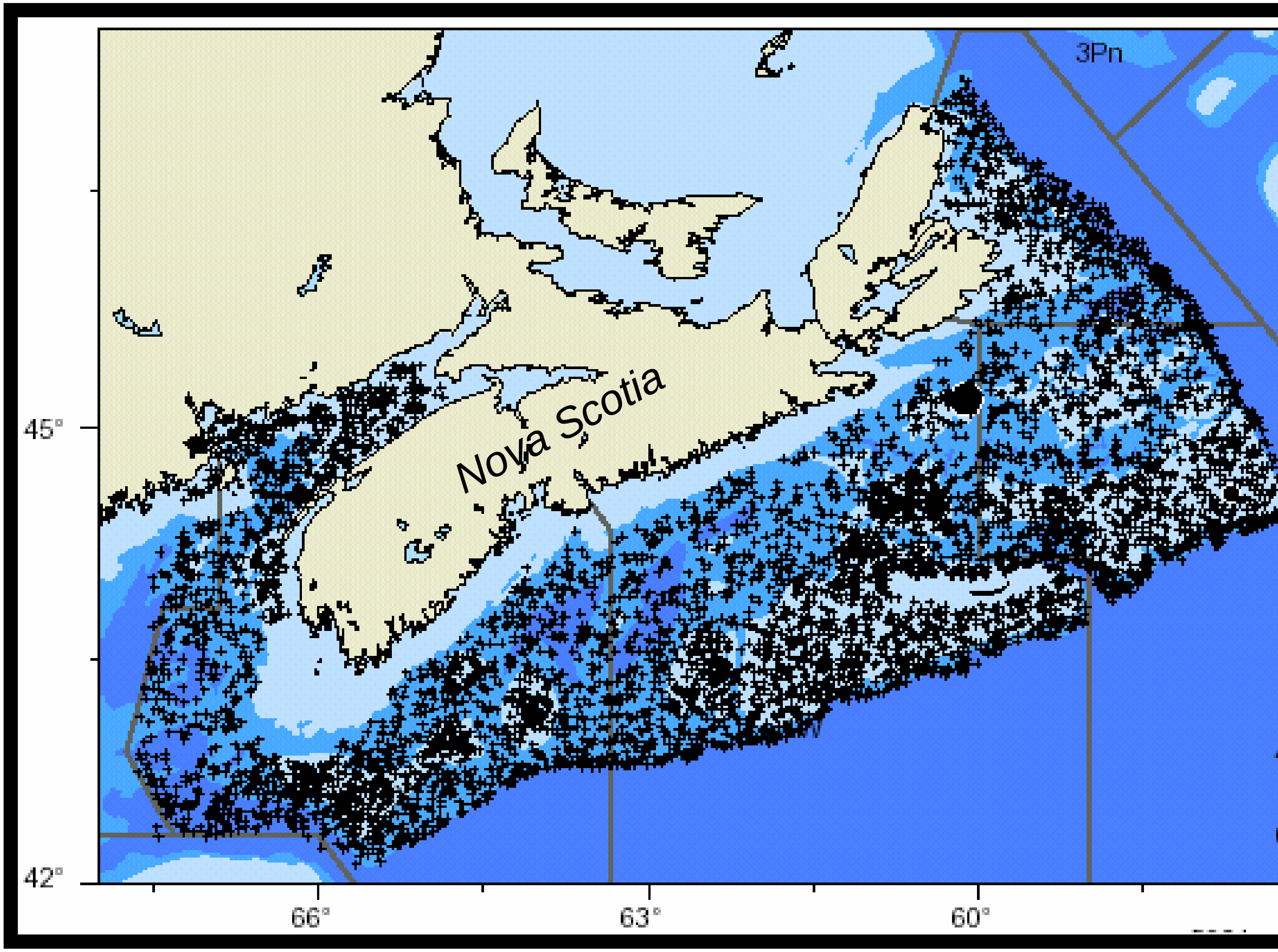
- Using relationships to make predictions (future or historical states, other areas)
    - If derived from cross-system comparisons cannot be used to infer time dependent processes
    - Models cannot predict anything that was not built into them from the start
  - Need for temporal analyses

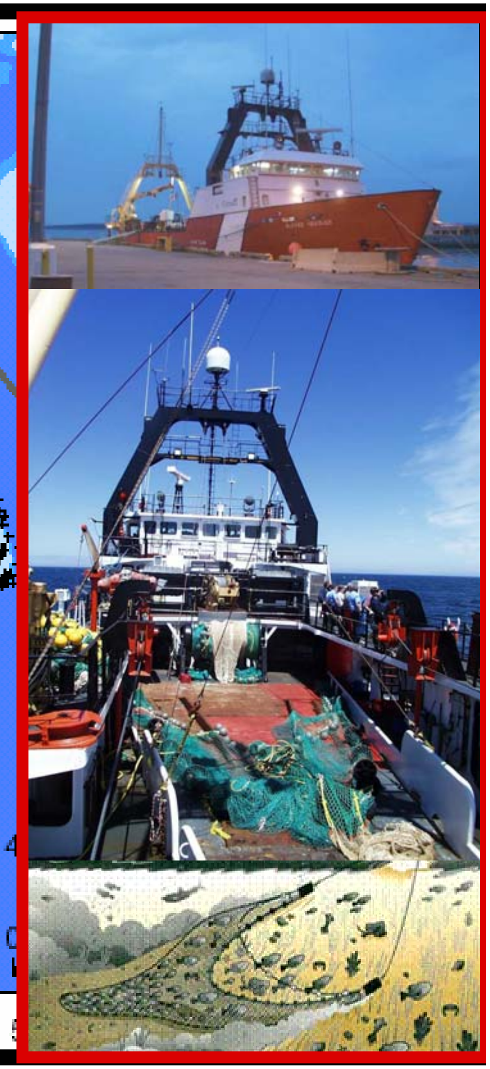
Temporal analyses

– Increasing documentation of human influences and climate change/variability as modifiers of macroecological patterns



Annual groundfish surveys on Scotian Shelf , 1970-present





Groundfish species and small pelagics; macro-invertebrates (crab, shrimp, starfish, . . .

Data derived independently from commercial fishery

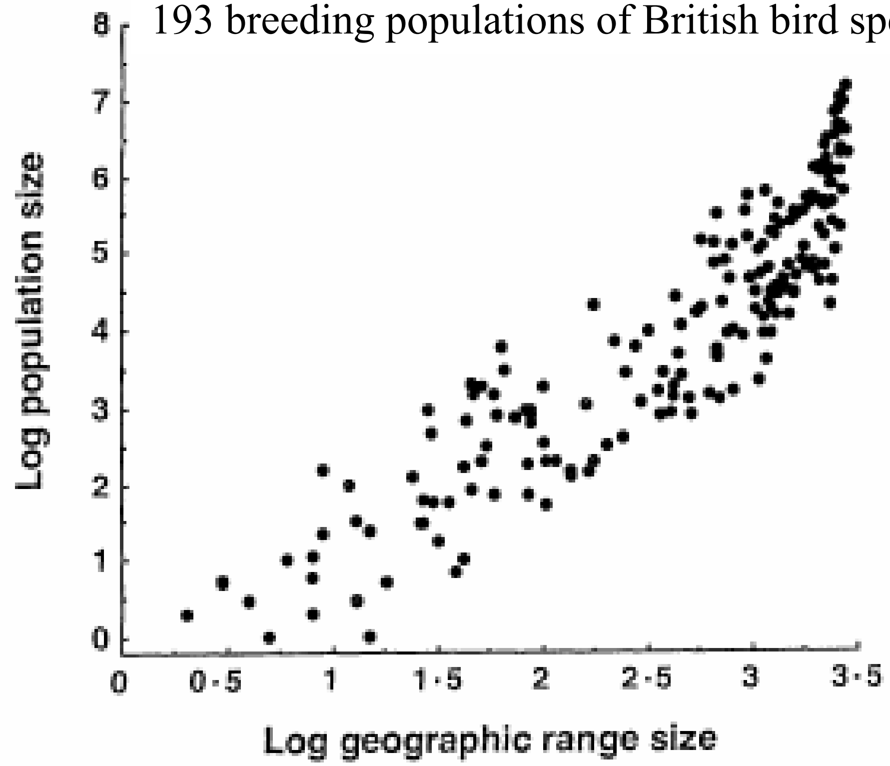
Dynamic macroecology

- Studies involving temporal dynamics of macroecological patterns increasing
  - Abundance-distribution relationships
  - Latitudinal gradients in fish diversity
  - Trophic dynamics

I. One of the most common macroecological relationships: abundance-occupancy

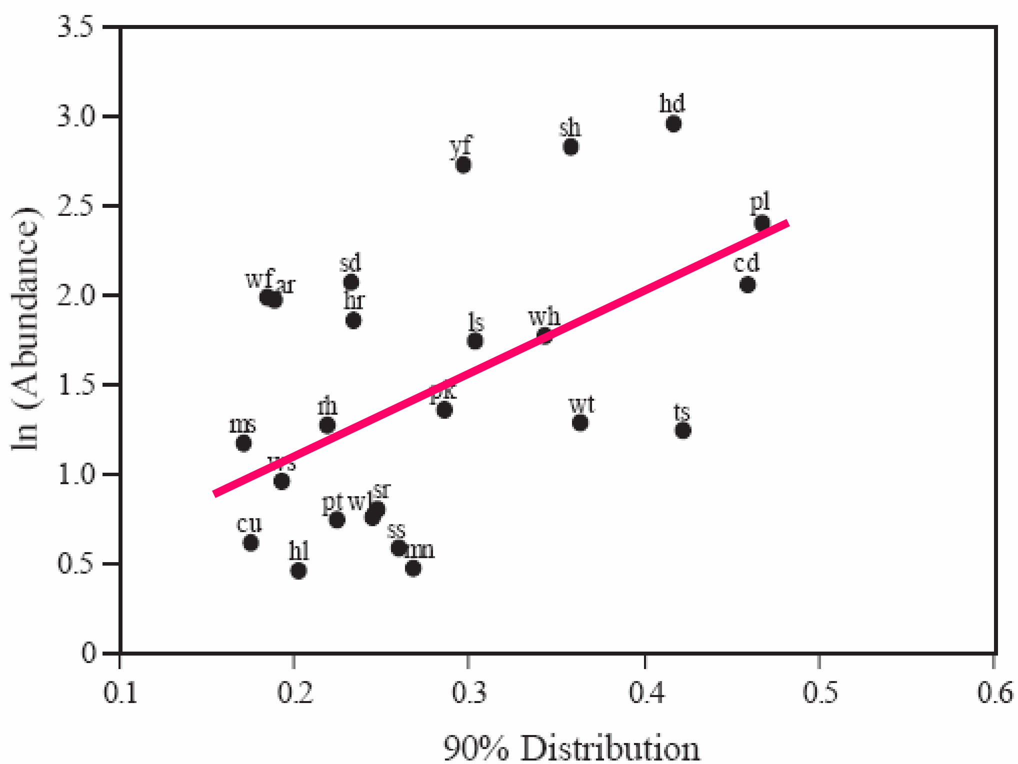
- Documented for wide variety of taxa
  – Plants
  – Butterflies
  – Frogs
  – Mammals
  – Spiders
  – Fish
  – Birds

193 breeding populations of British bird species



On average, widespread species locally abundant; narrowly distributed species rare

Similar analysis conducted for 24 dominant marine fish species on the Scotian Shelf



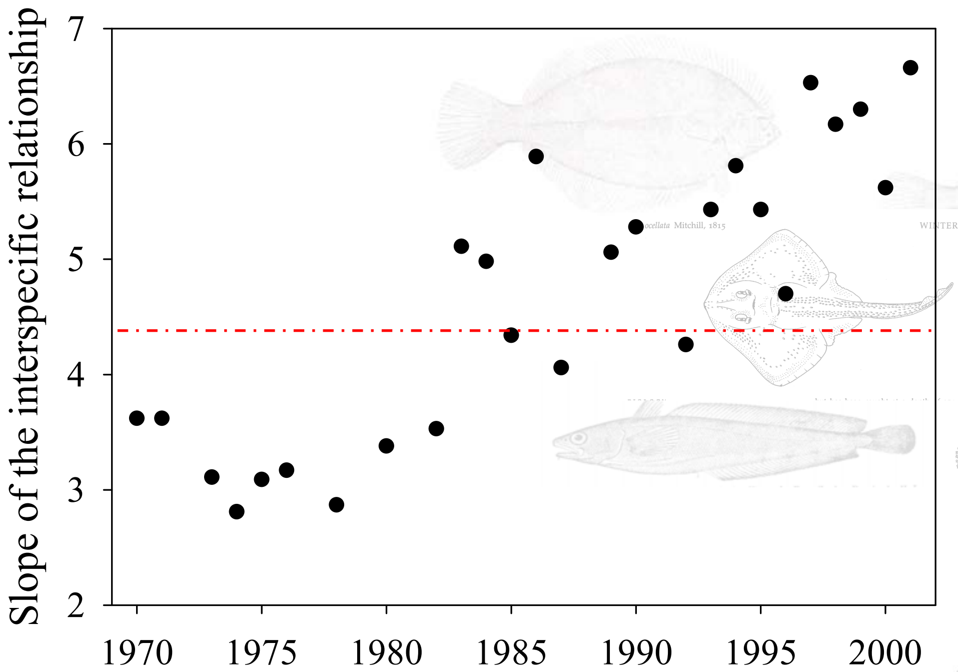
Average abundance and distribution calculated for each of 24 species over 32 y

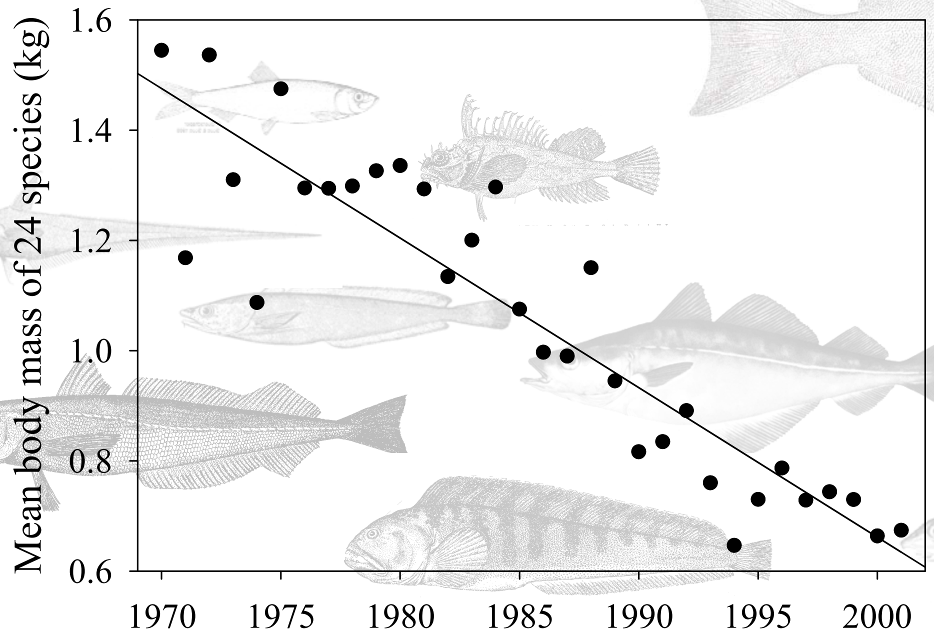
Widespread/abundant: haddock, plaice, cod; local/ rare: cusk, mailed sculpin

Represents typical, time-averaged pattern (supports British bird survey results)

Do annual patterns differ? If estimate slope each year from distribution and abundance data will it remain unchanged?

Fisher and Frank 2004 MEPS

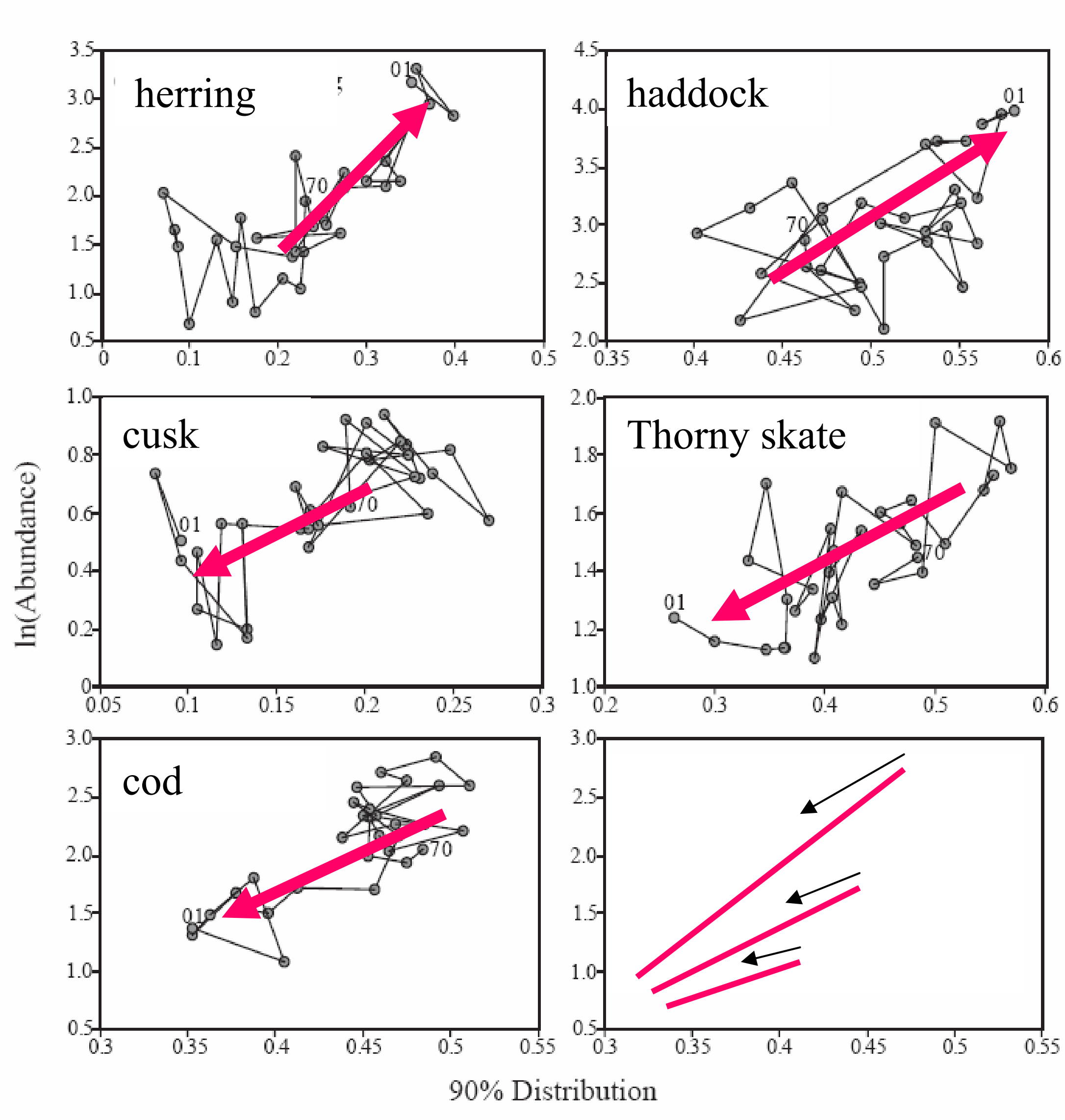




- When examined annually, slope of abundance-distribution relationship increased; nearly doubled through time
- Why?
- 55% decline in average body size
- Can pack in more individuals in the same space
- Macroecological patterns in exploited assemblages can change rapidly

Intra-specific, temporal series also shows positive relationship

Annual surveys from 1970-2001 on Scotian Shelf



Changes in habitat quality or system productivity could change slope (Gaston 1994 – trajectories to extinction)

Fisher and Frank 2004

- Changes in individual species distribution and abundance through time alter form of the inter-specific relationship
  - Fishing or climate effects can change ranks of species in inter-specific space
- If body size changes are one of the main drivers of changing inter-specific relationship then expect slope to decrease if exploitation removed
- Recent evidence of changes in the inter-specific slope for British birds (Webb et al. 2007)

II.

Where sufficient data exists –

Near universal pattern of latitudinal trends in species richness

Decrease in species richness from tropics to the poles

Mammal species richness

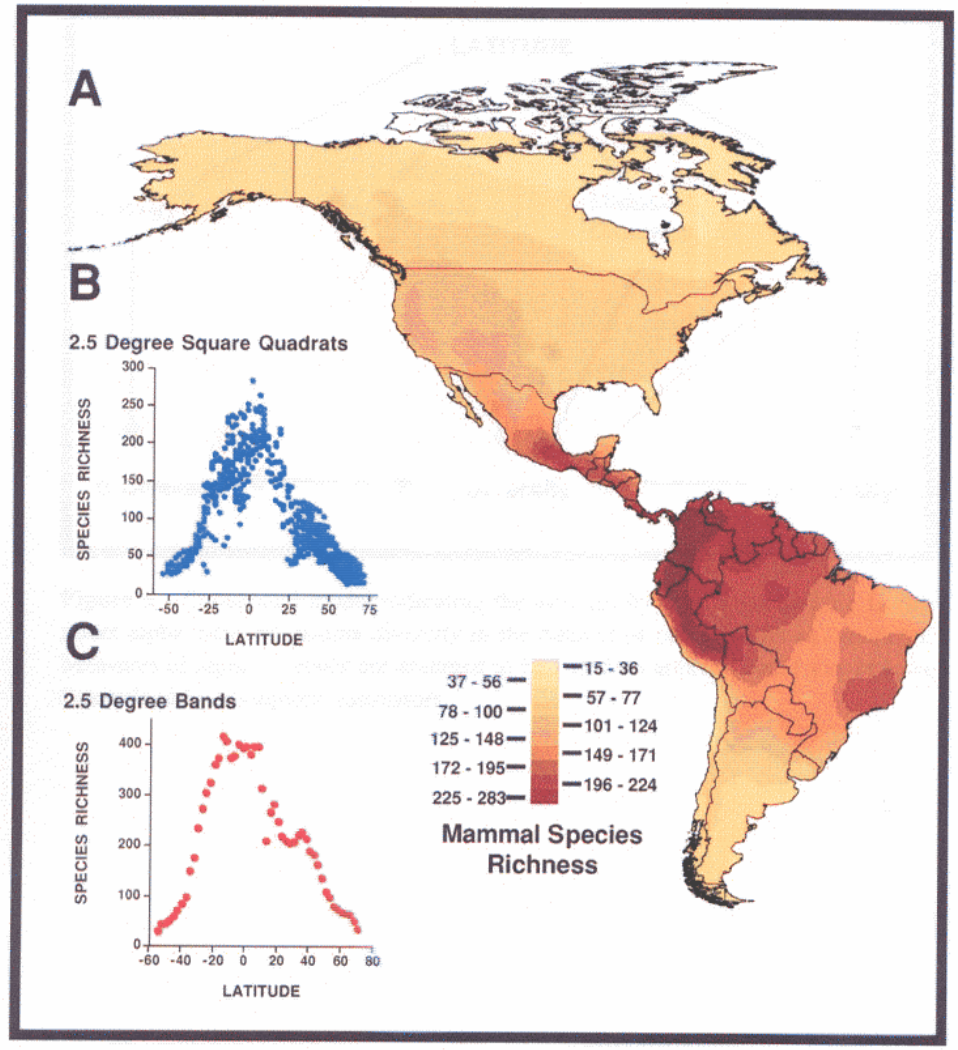
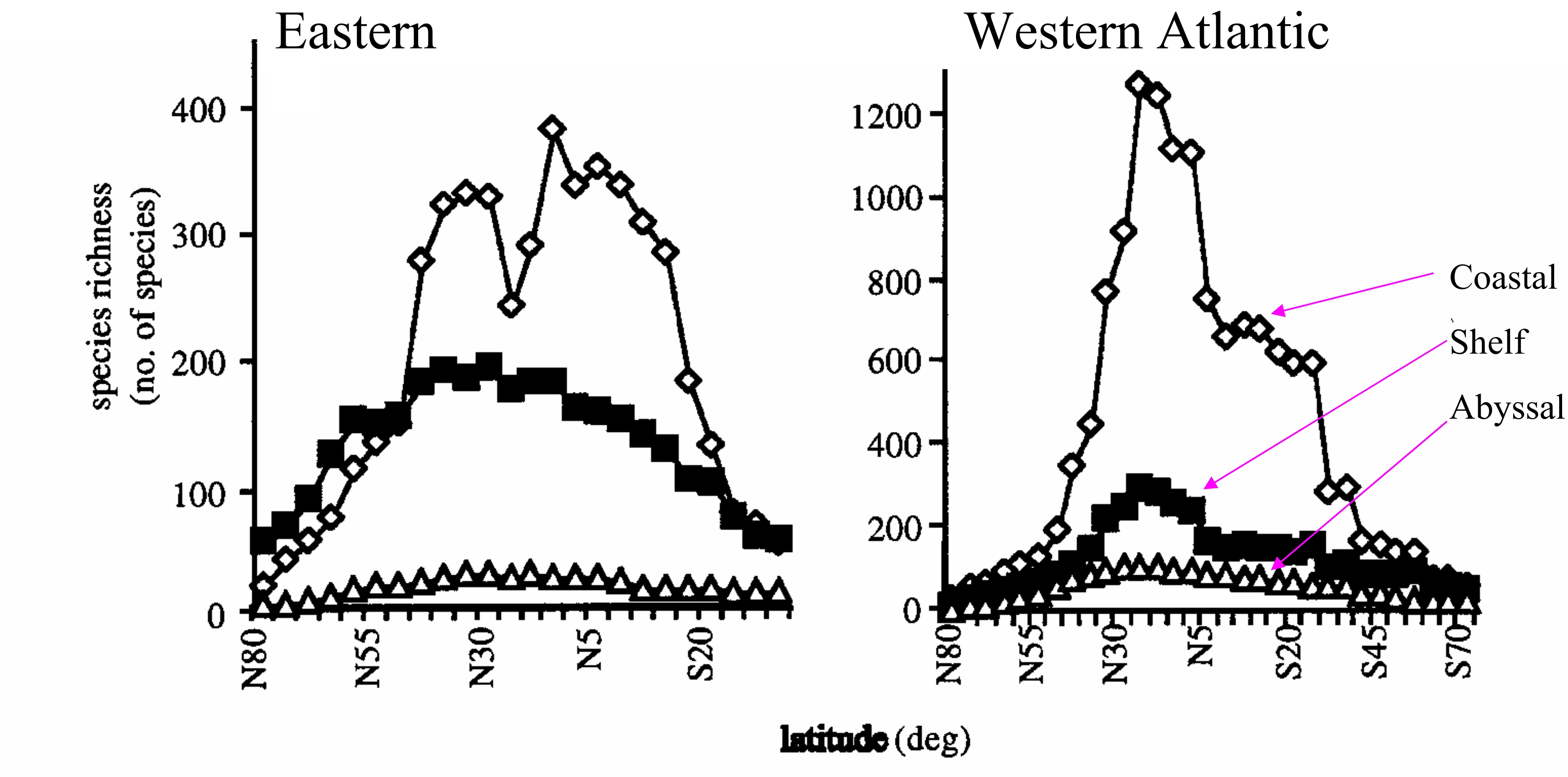


Figure 4 Spatial gradient of mammalian species richness in the continental New World for cells defined by 2.5° parallels and meridians. (*A*). Interpolated richness values in the map were created using the tension spline function in the Spatial Analyst extension to ArcGIS 8.2. Graphic representation of the latitudinal gradient in species richness for those same data (negative values for latitude indicate southern parallels), based on 2.5° cells (*B*) and 2.5° latitudinal bands (*C*). Data from Kaufman & Willig (1998).

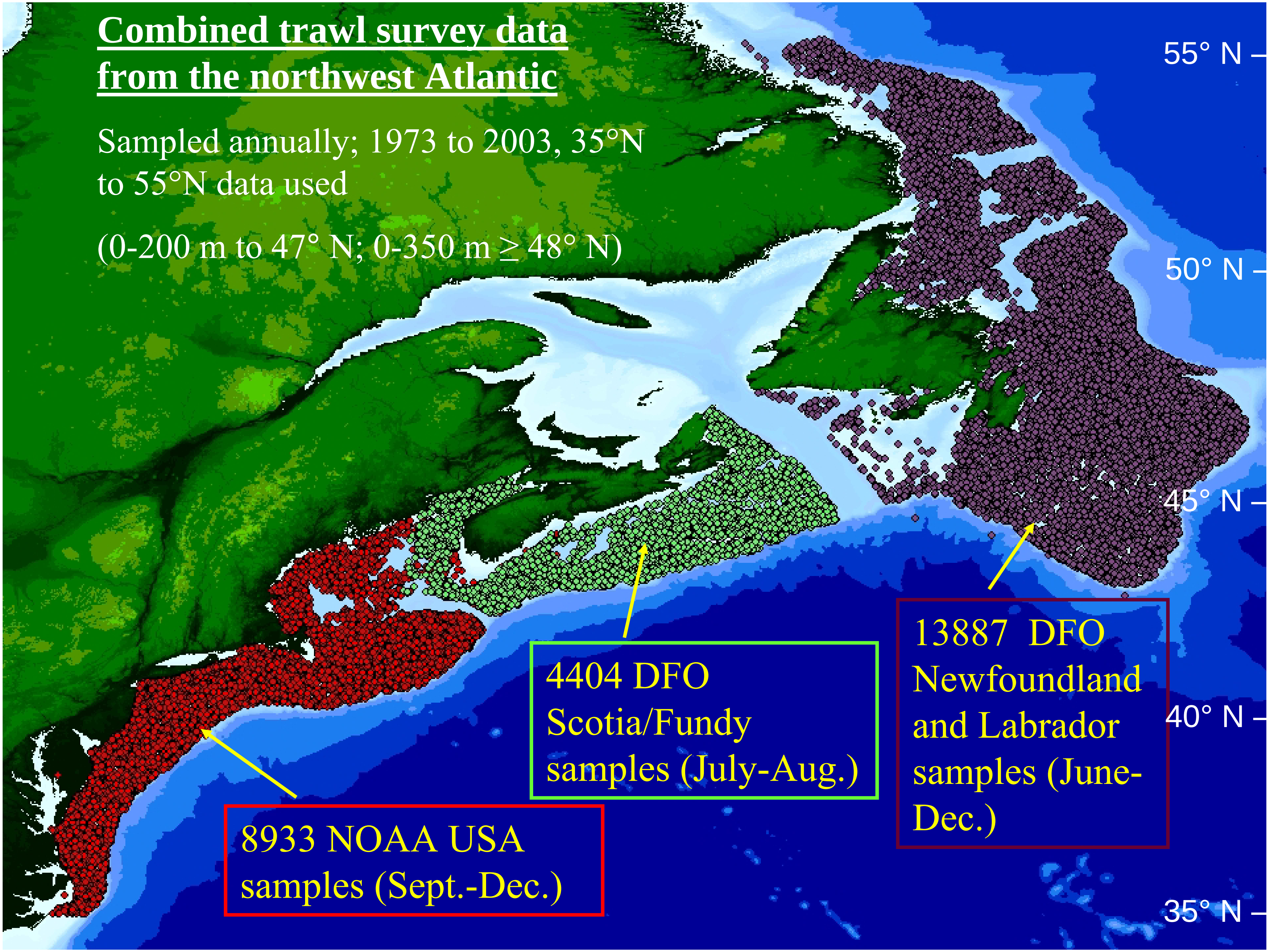
Macpherson 2002

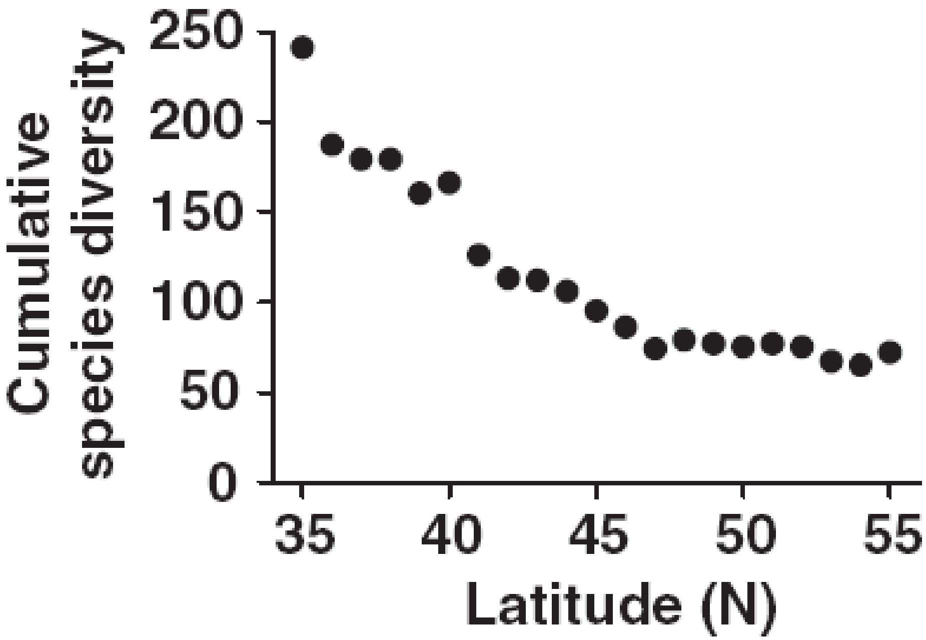
Pisces

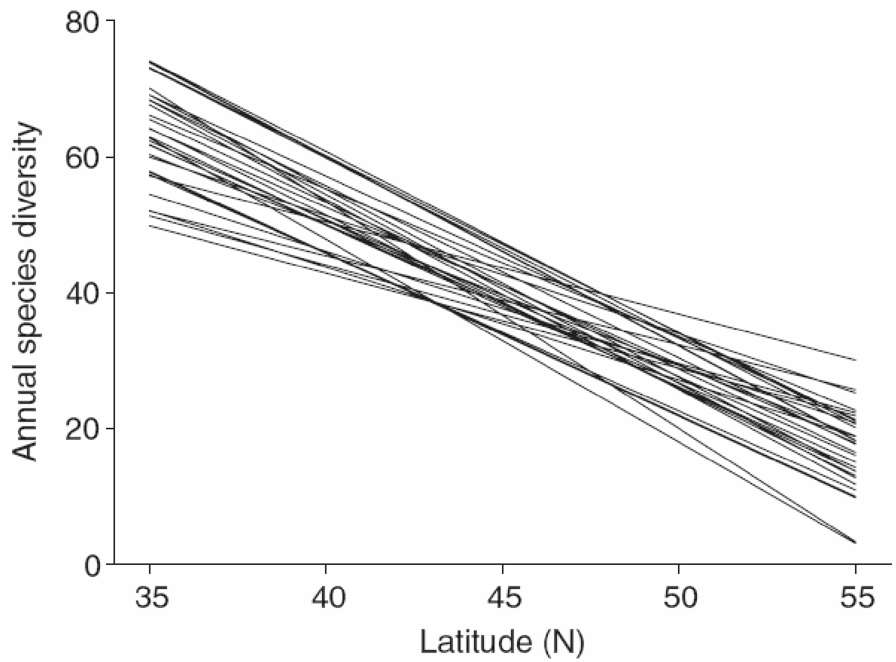


Main data sources: Fishes of the western Atlantic (Bohlke 1989),Check-list of the fishes of the eastern tropical Atlantic (Quero et al. 1990), Caribbean reef fishes (Randall 1983), Fishes of the northeastern Atlantic and the Mediterranean (Whitehead et al. 1986), Manual de peixes marinhos do sudeste do Brasil. V. Teleostei (Menezes&Figueiredo 1985)

- All such relationships based on cumulative data
- Gradients assumed static
- Much attention paid to shape of relationship
- Fisheries data allow evaluation of temporal variation (*Fisher et al. 2008 Ecol. Lett.*)


Combined trawl survey data from the northwest Atlantic
Sampled annually; 1973 to 2003, 35°N to 55°N data used
(0-200 m to 47° N; 0-350 m ≥ 48° N)
55° N
50° N
45° N
40° N
35° N
4404 DFO Scotia/Fundy samples (July-Aug.)
13887 DFO Newfoundland and Labrador samples (June-Dec.)
8933 NOAA USA samples (Sept.-Dec.)

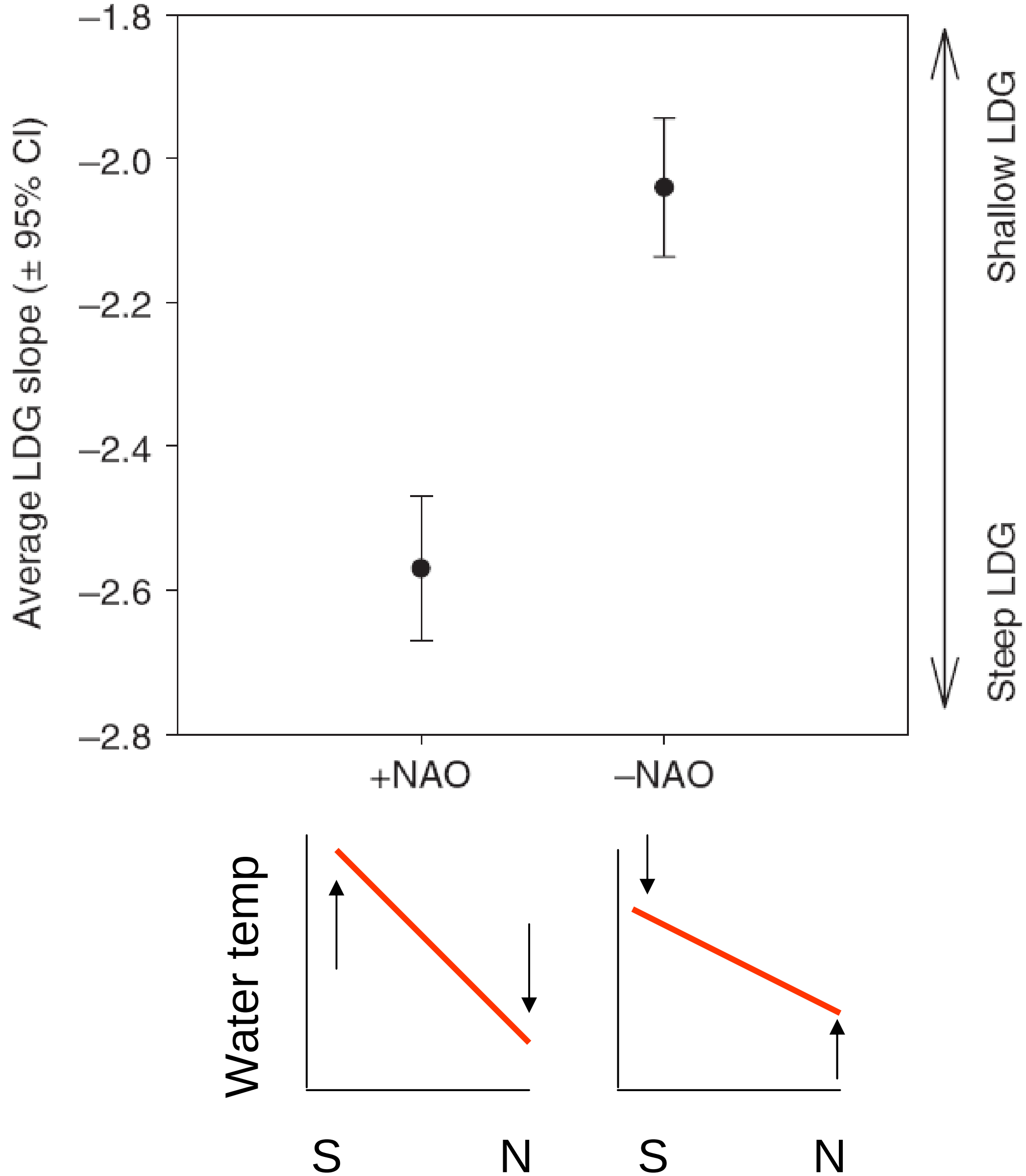


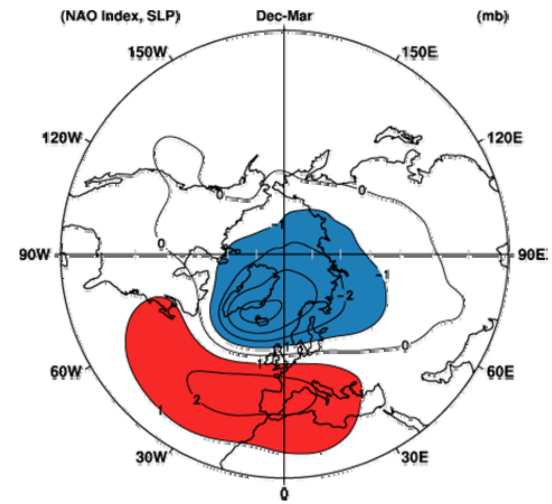


Annual gradients show 2.6 × variation in slopes (-1.31 to -3.34)

All 31 annual diversity gradients are linear (average R2 = 0.78)

Cumulative pattern conceals important interannual variations

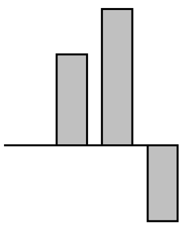


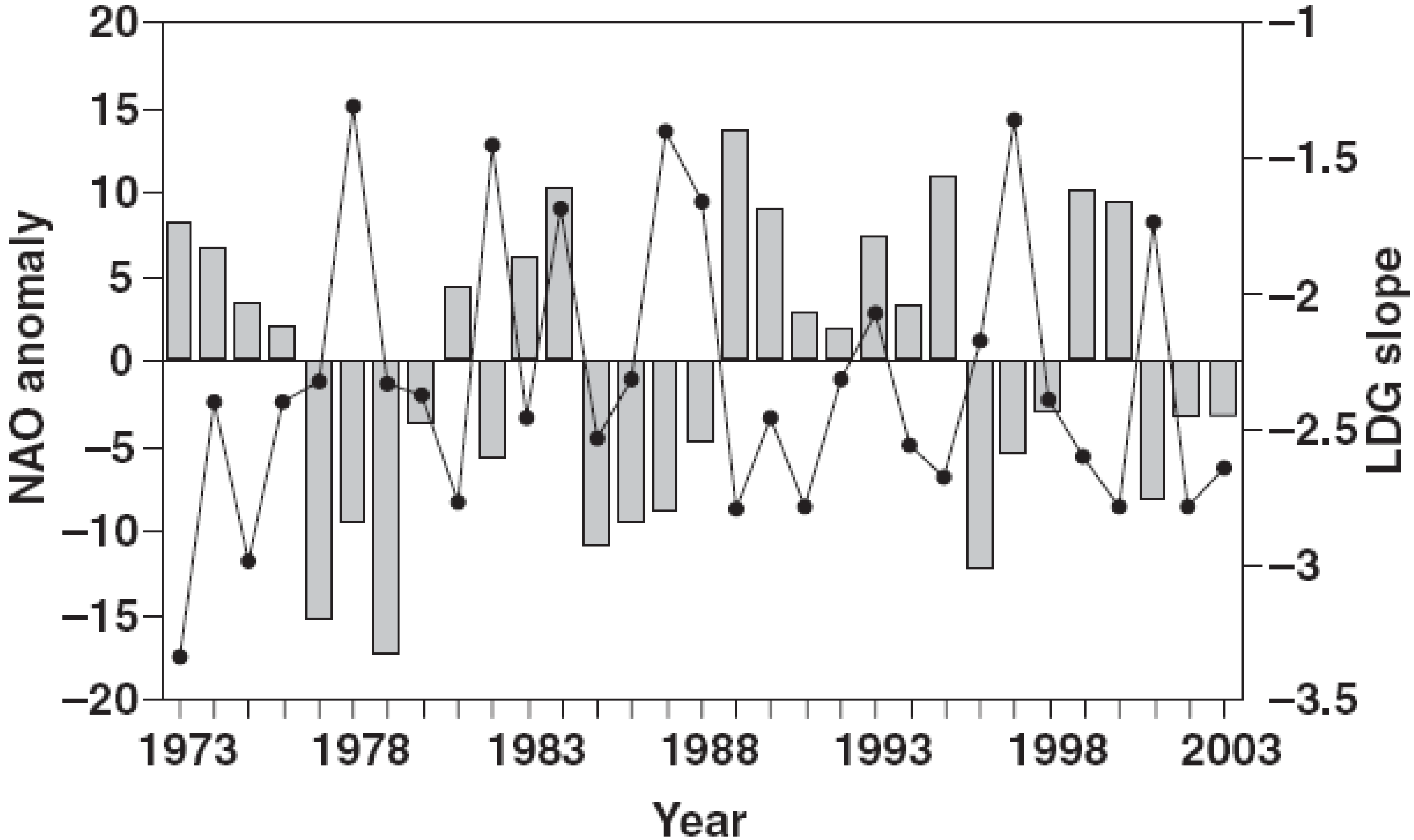


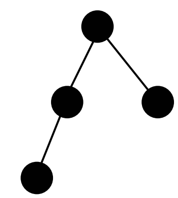
Grouping of years into + and – NAO anomalies revealed clear differences in strength of gradient

NAO influences large scale temperature field

Variability in slope of LDG due to NAO forcing operates on annual times scales







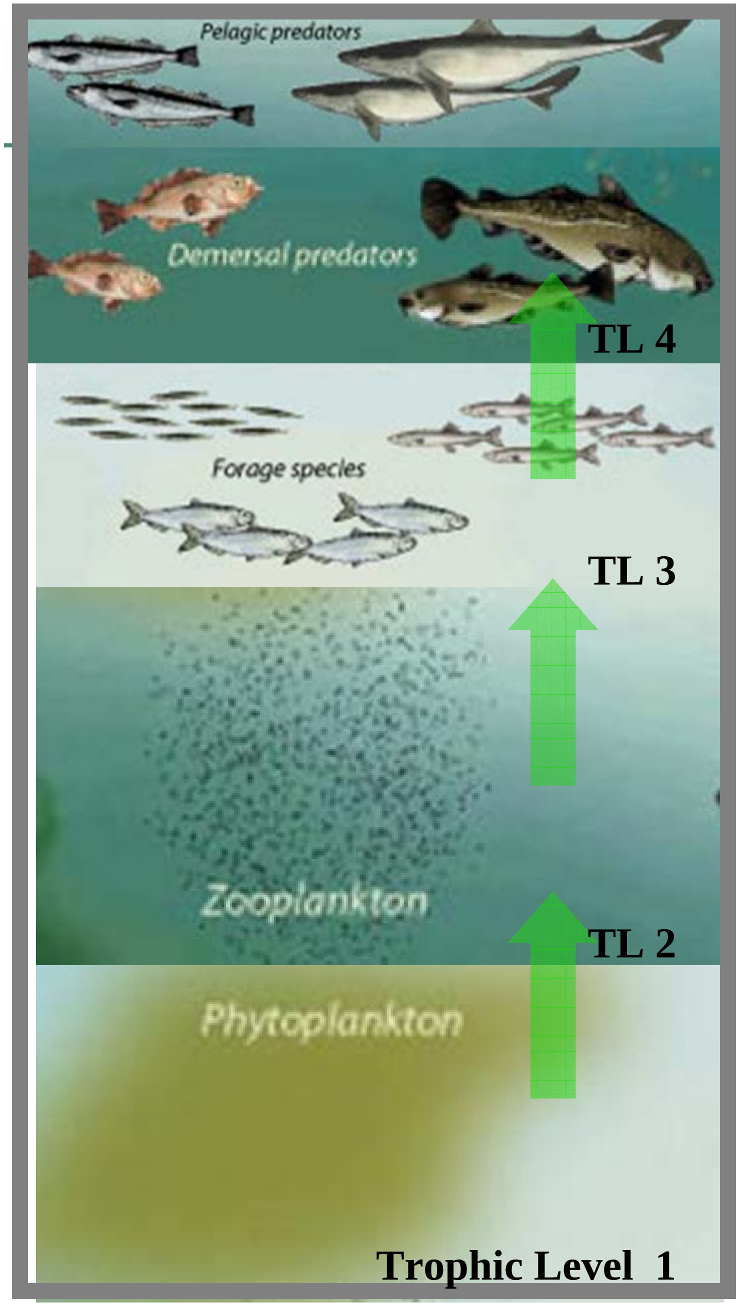
NAO is a wintertime atmospheric phenomenon influencing conditions later in the year when fish community surveyed

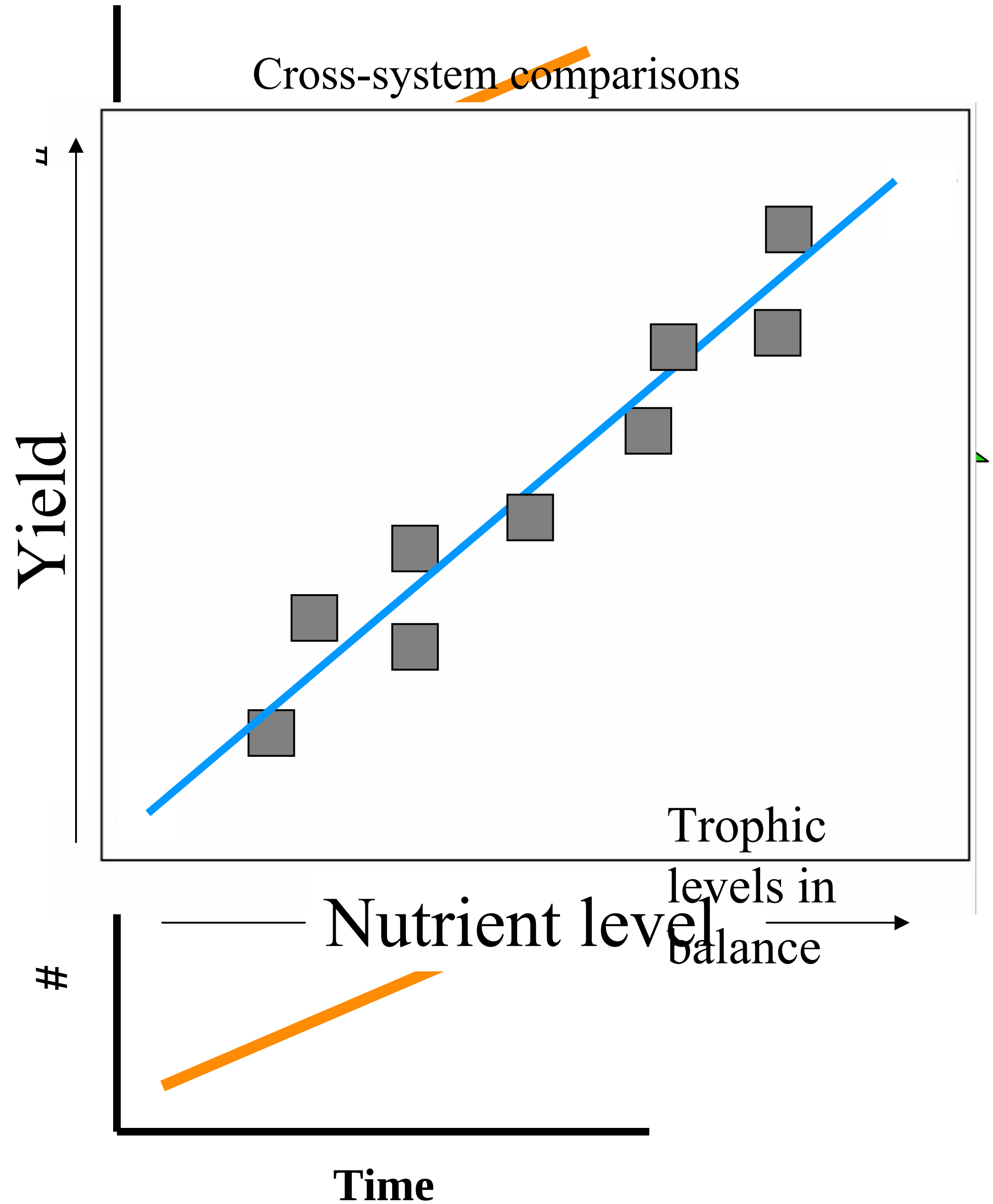
- High frequency, temporal dynamics exists within one of the oldest macroecological patterns previously assumed static
- The relationships between LDG variability, changing geographic distributions and the NAO provides mechanistic link via spatially variable changes in ocean temperature
- Suggests spatially complex responses of temperate marine assemblages to future climate change

III. Trophic dynamics

- Higher trophic level production is proportional to primary production via “bottom up control”

Marine food chains normally operate this way – bottom-up



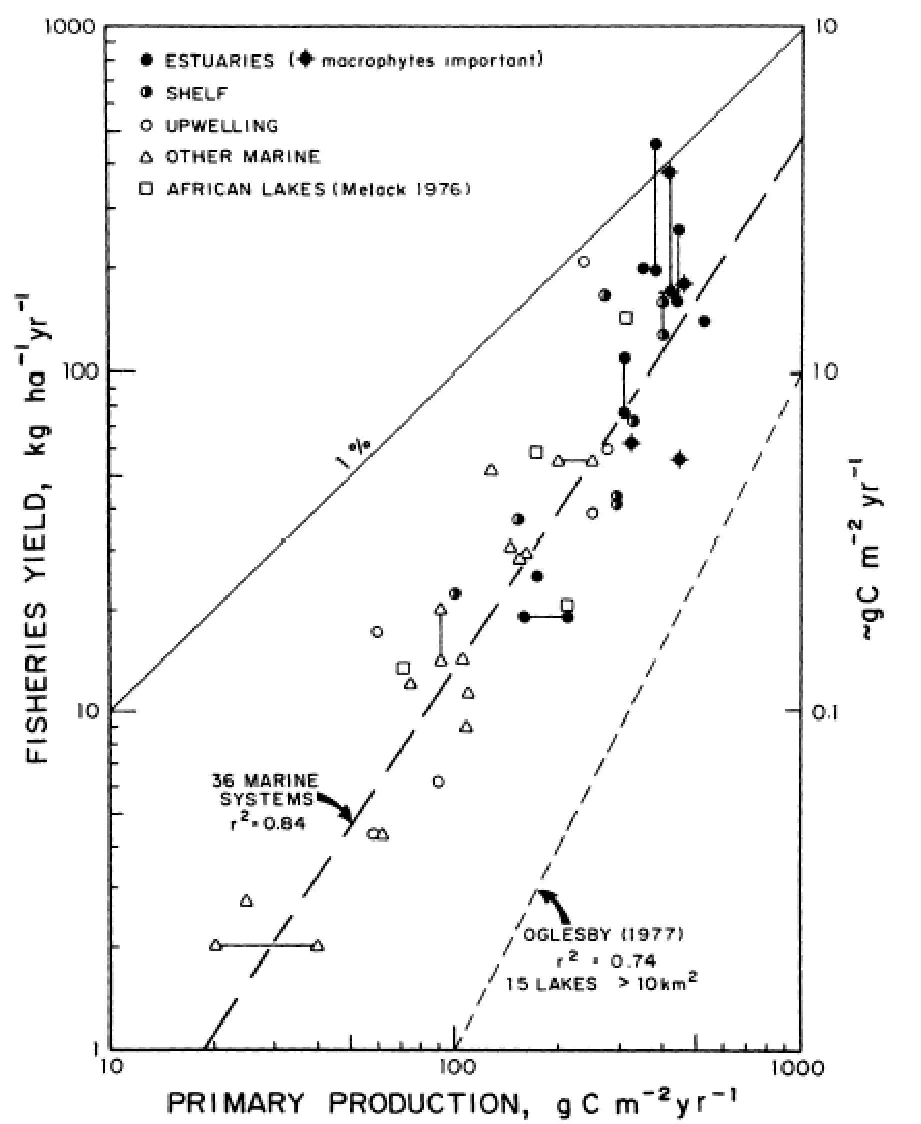


Nixon 1988 – Physical energy inputs and the comparative ecology of lake and marine ecosystems

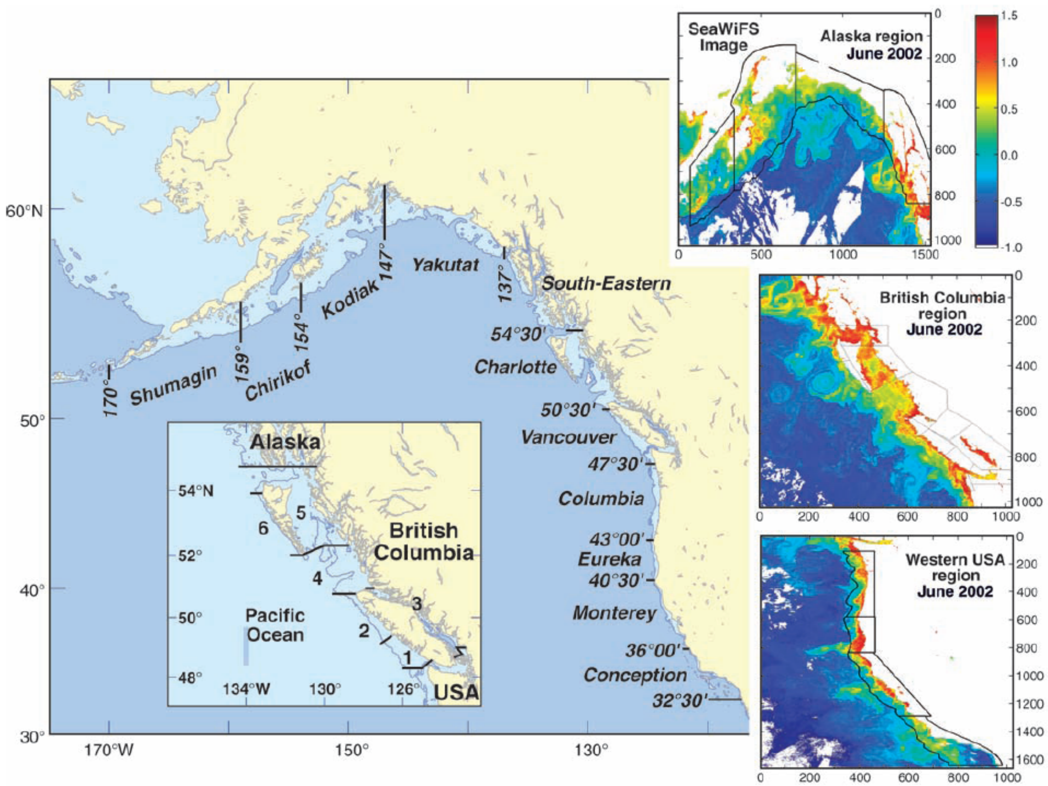
- One of the earliest quantitative relationships developed through cross-system comparisons

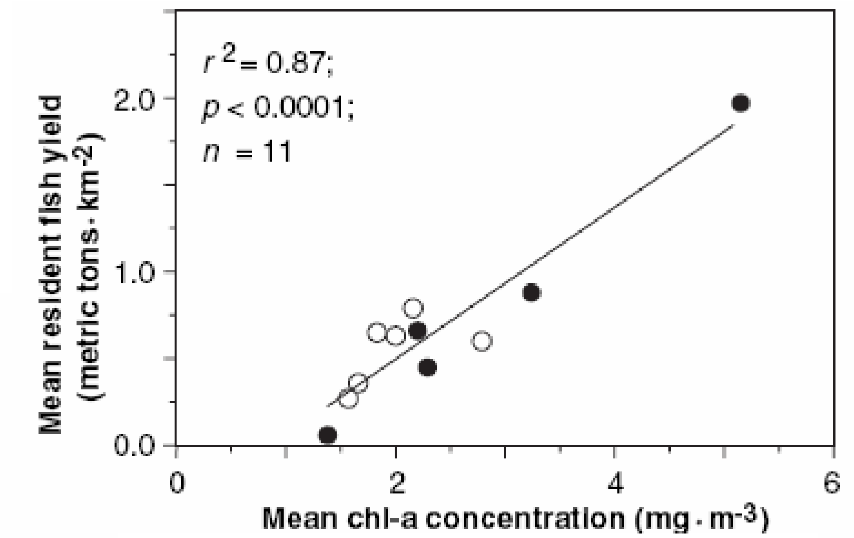
- Based on mean states

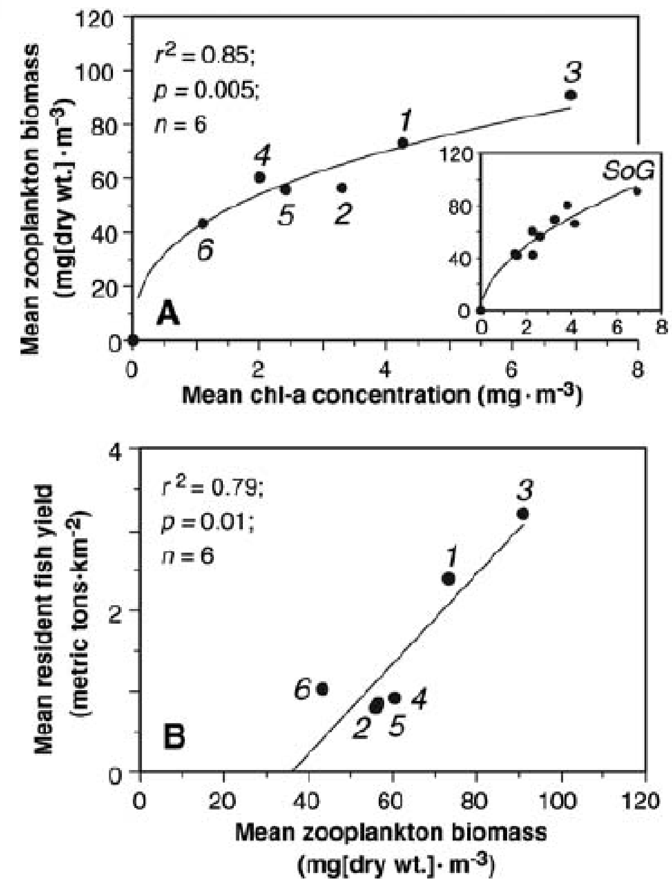
ln FY = 1.55 ln PP - 4.49



Ware and Thompson 2005. *Science* *308:* 1280-1284

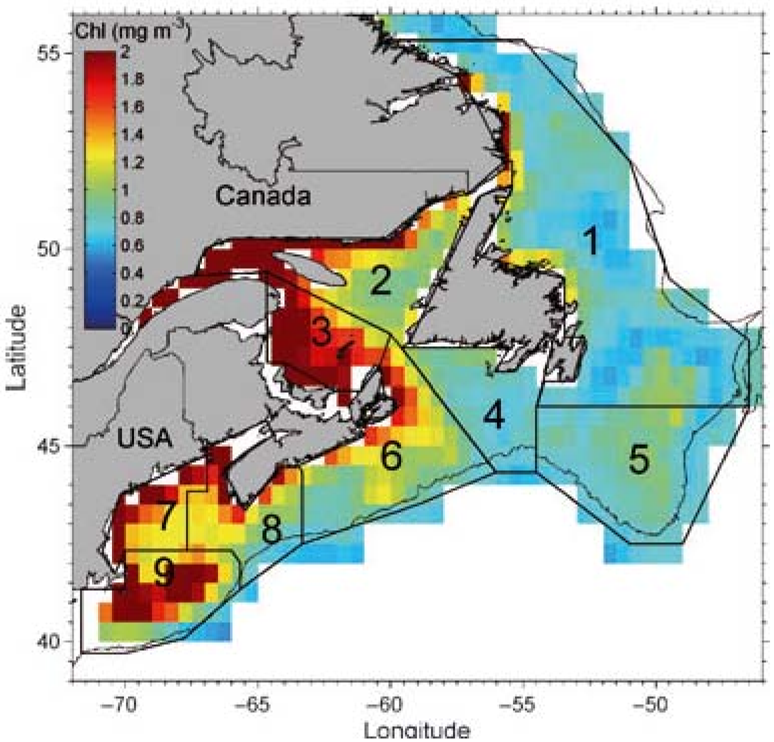


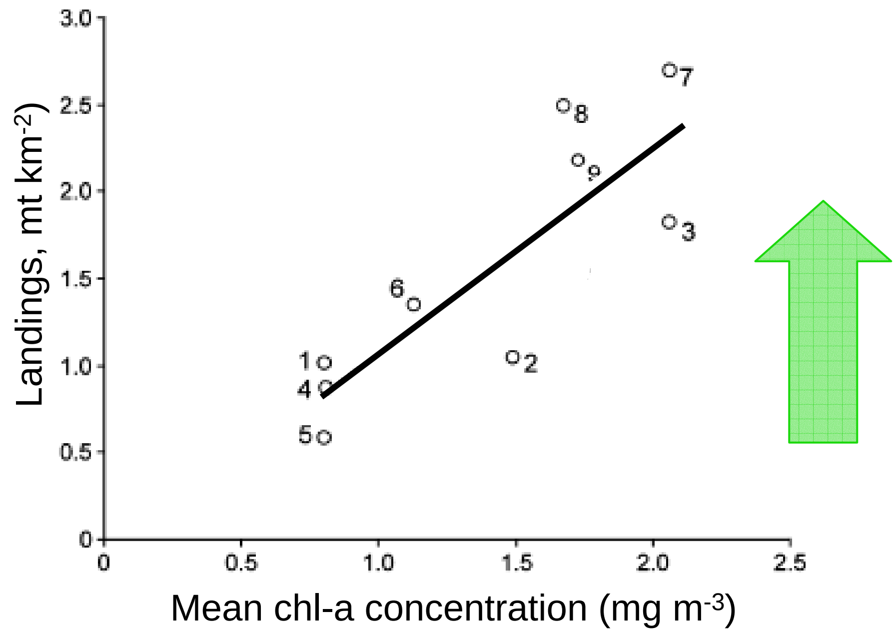




Relationship between SeaWiFS – chlorophyll a and fish yield from 11 areas

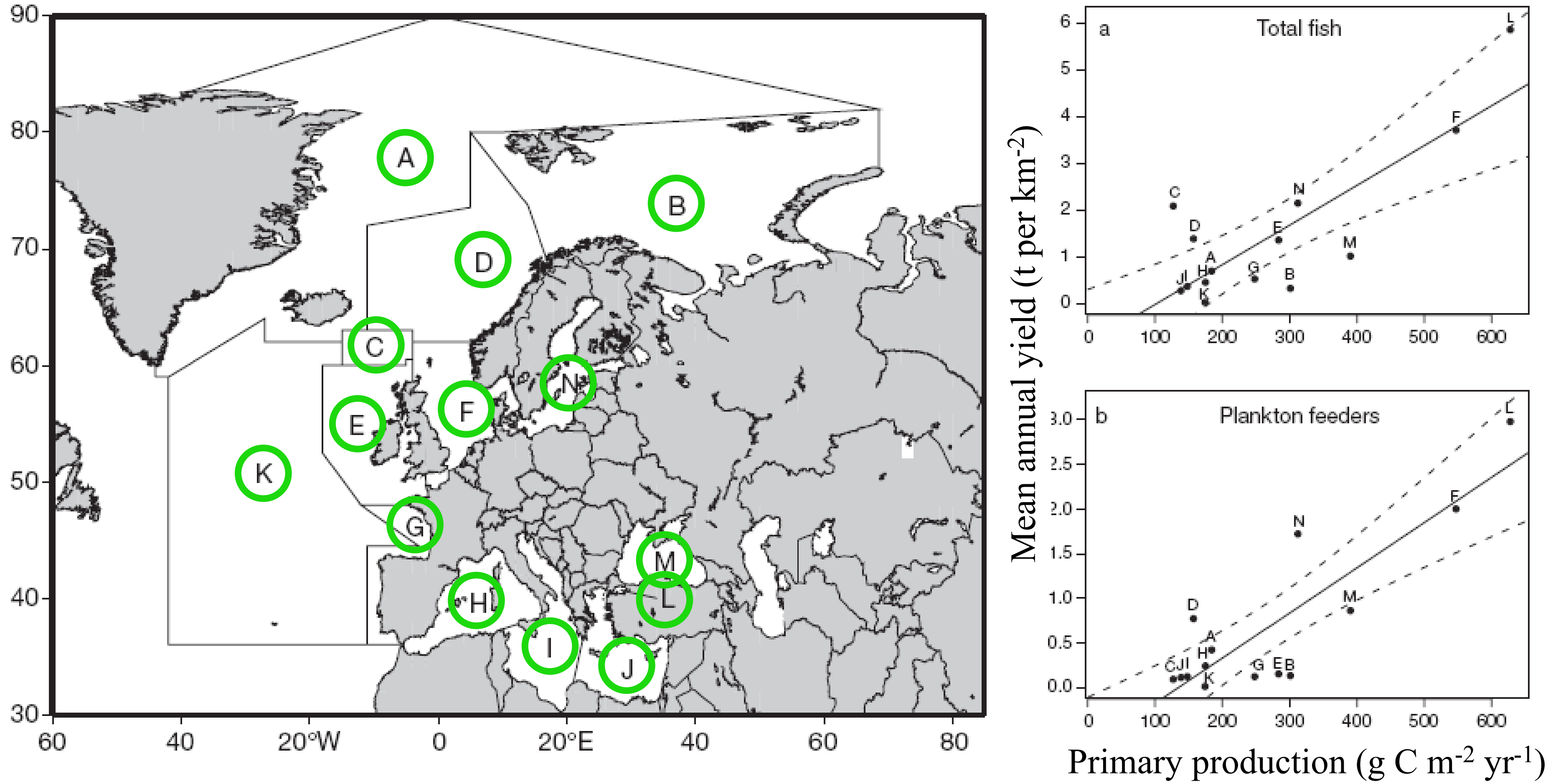
Frank et al. 2006. *Ecol. Lett*. 9: 1096-1105





9 areas in NW Atlantic, outlined in black polygons, showing the annual mean SeaWiFS chl a (mg m^3)

European Seas



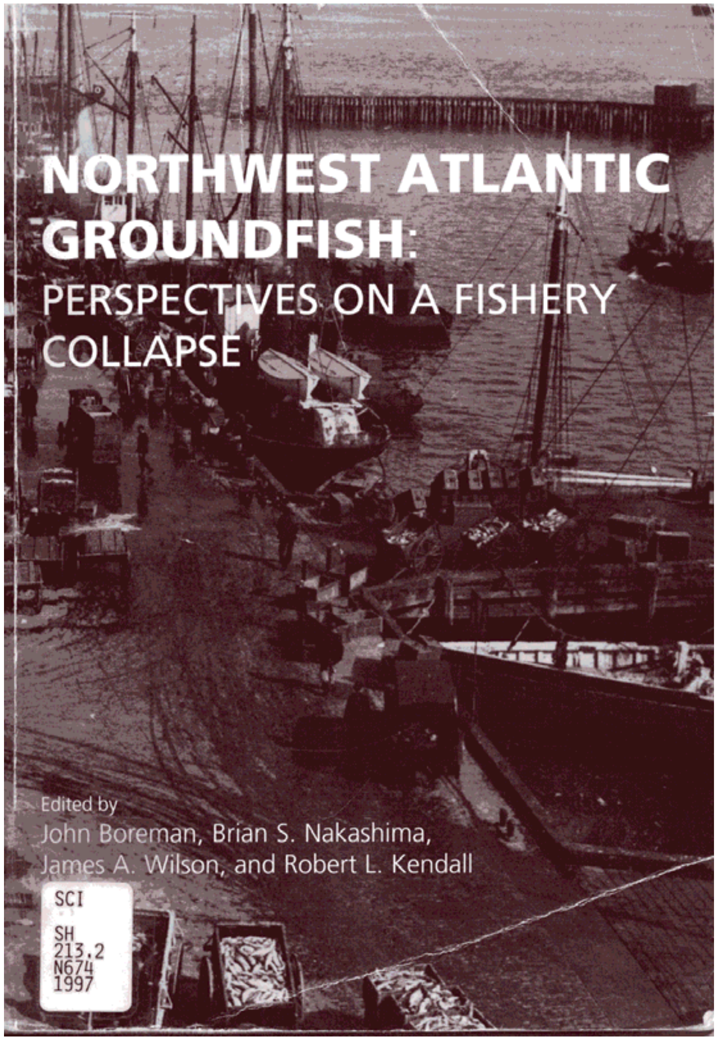
Conclusion: primary production regulates fisheries production

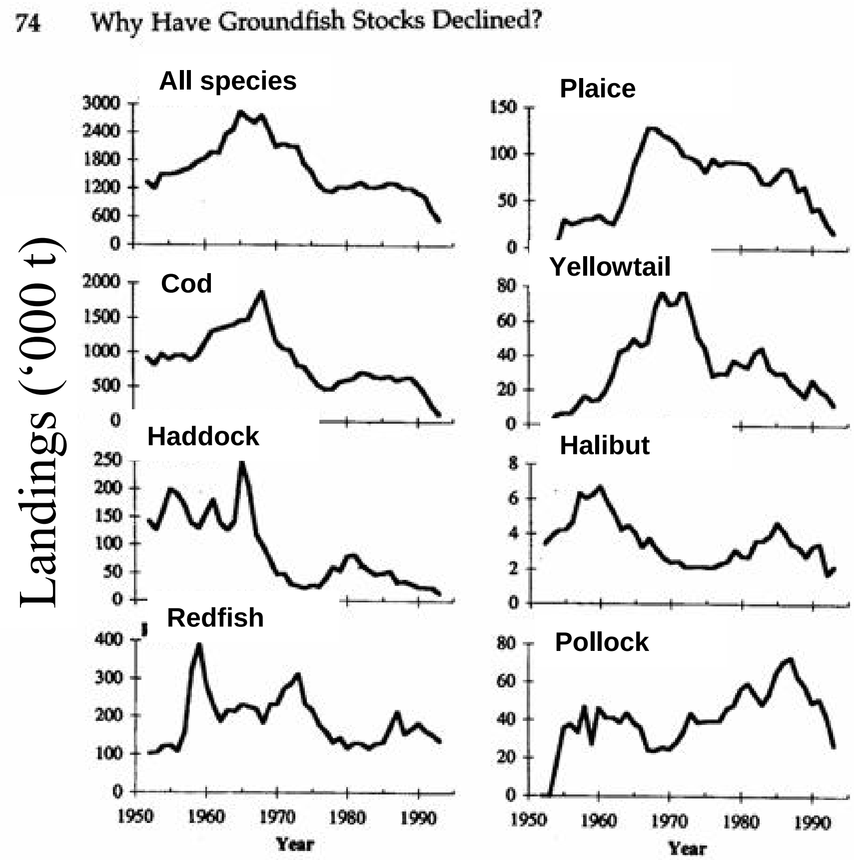
Chassot et al. 2007 *MEPS* 343: 45

Assumptions

- Relationship between primary productivity and trophic biomass is stable within sites through time
- Conclusions drawn from comparisons across ecosystems can be generalized to individual ecosystems
- Many marine ecosystems perturbed by over-fishing, particularly NW Atlantic

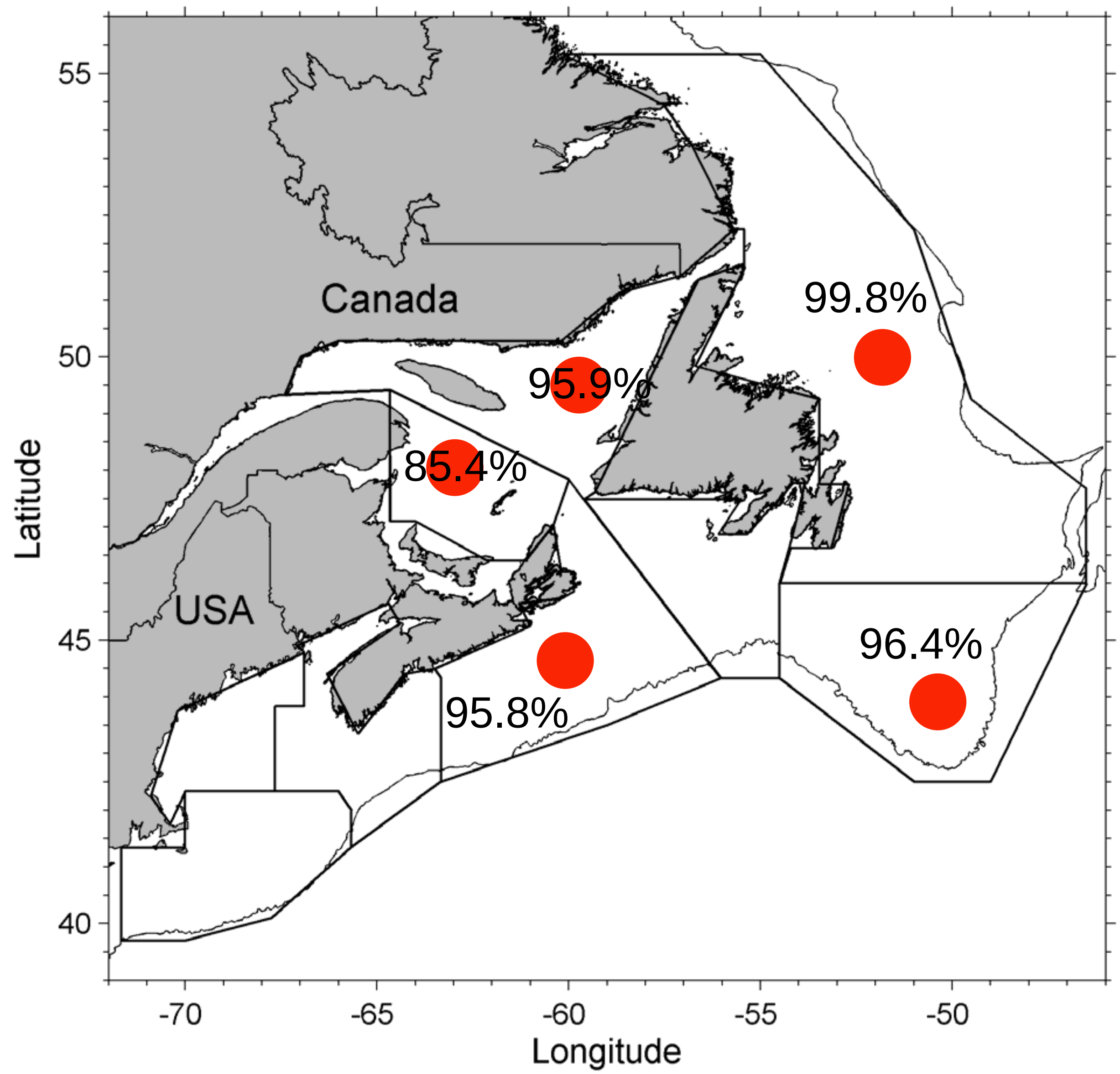
Structure and stability shaken by over-fishing of top predators



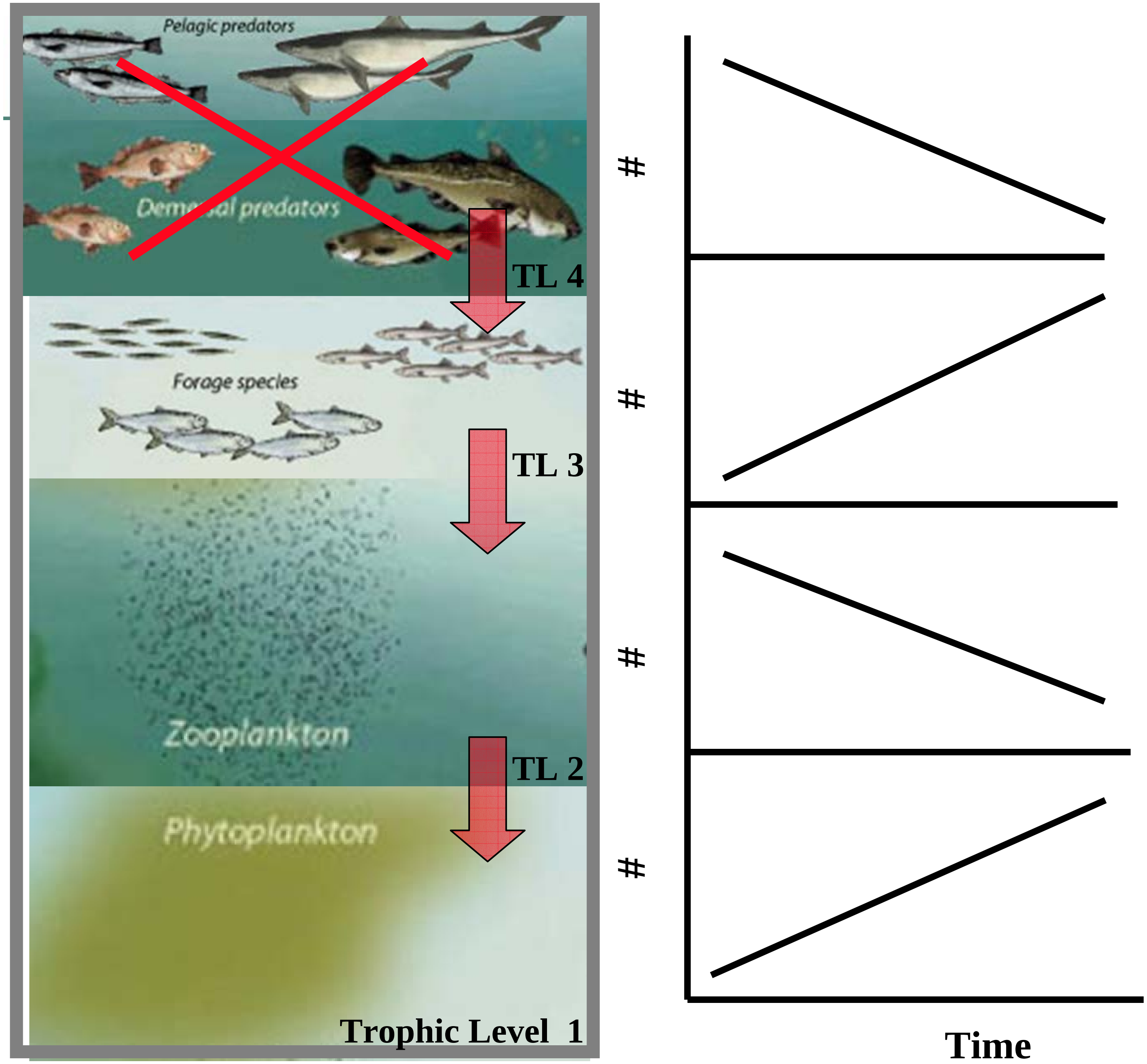


Groundfish landings from 1952 to 1993

NW Atlantic Cod stocks collapsed in 1990s



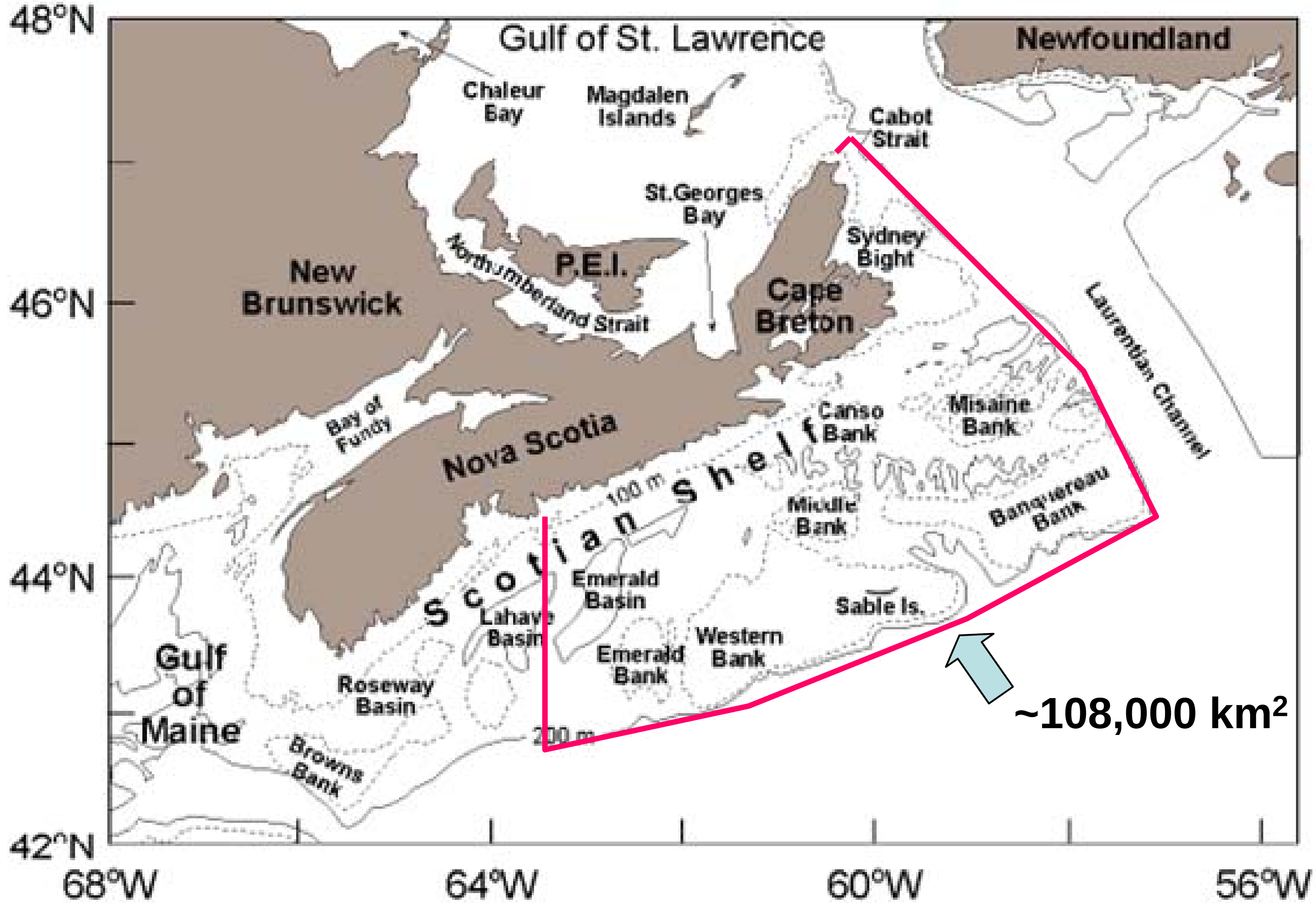
If top predators depleted then marine food chains may become altered



Negative correlation between adjacent trophic levels in food chain

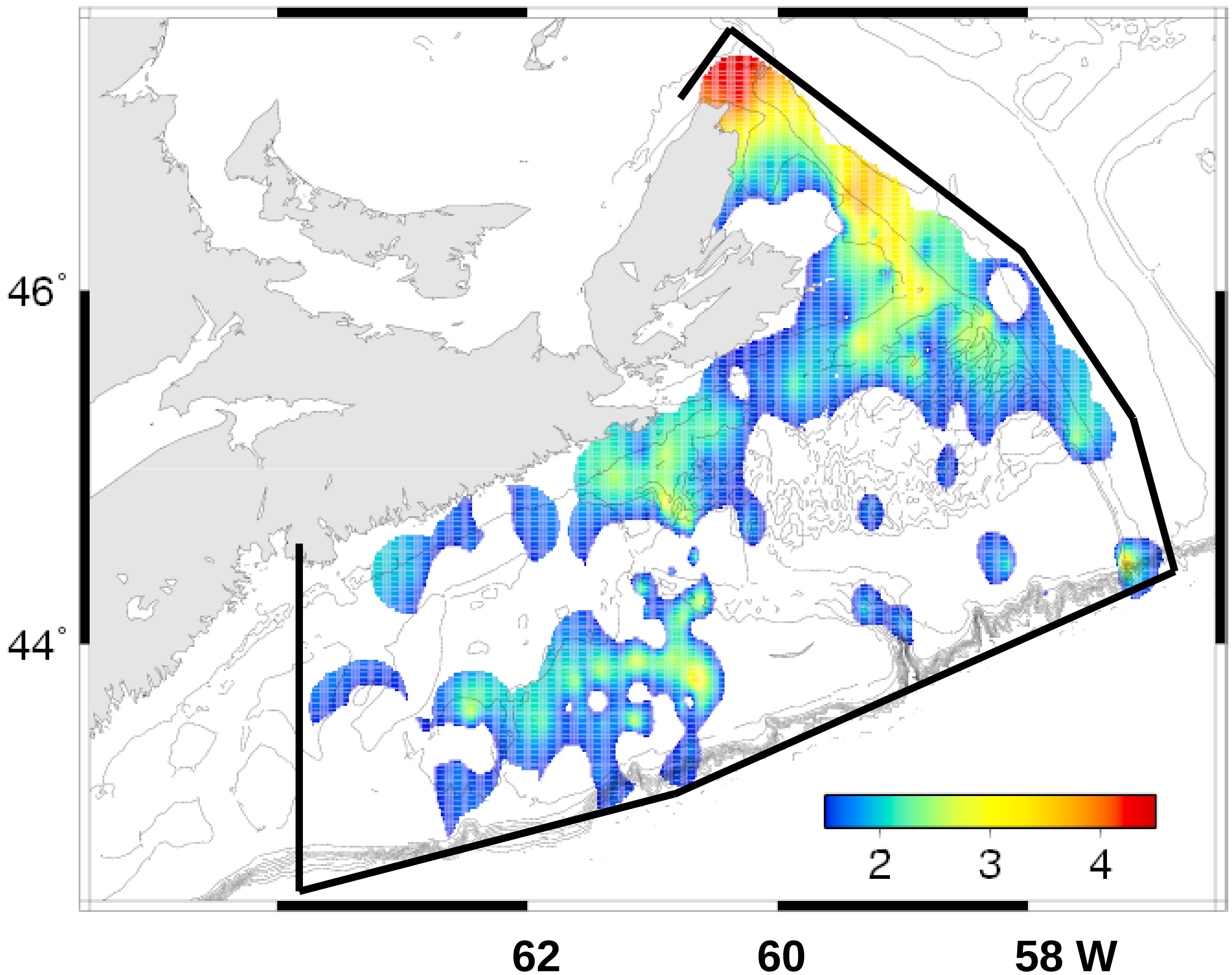
Could lead to trophic cascades/ indirect effects

Trophic levels unbalanced



Data rich area: long-term (30+ yr), standardized, annual monitoring programs representative of major trophic levels (RV surveys, CPR, nutrients, etc.)

Over-exploitation of cod and other top predators on the eastern half of Scotian Shelf



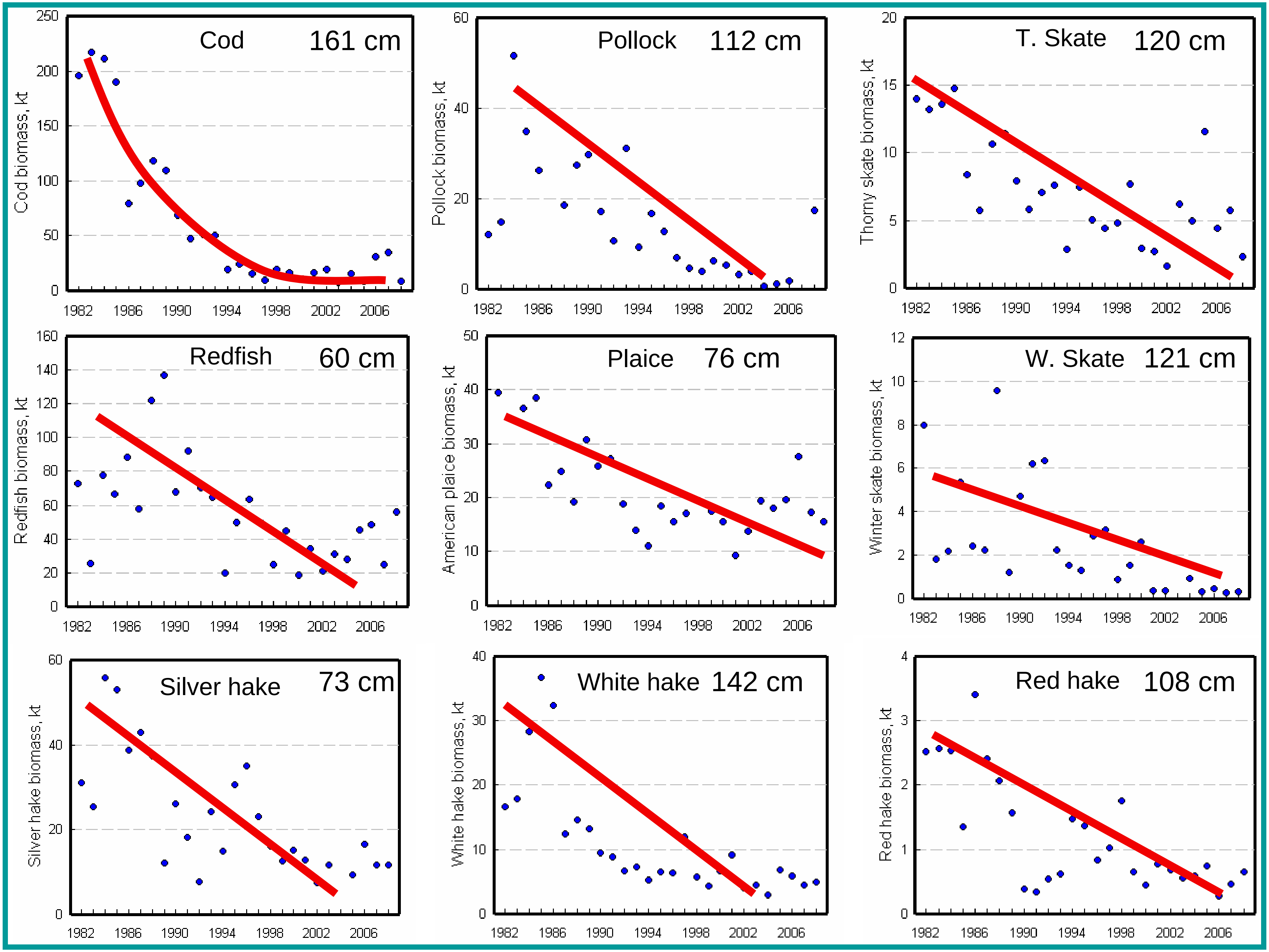
1970s

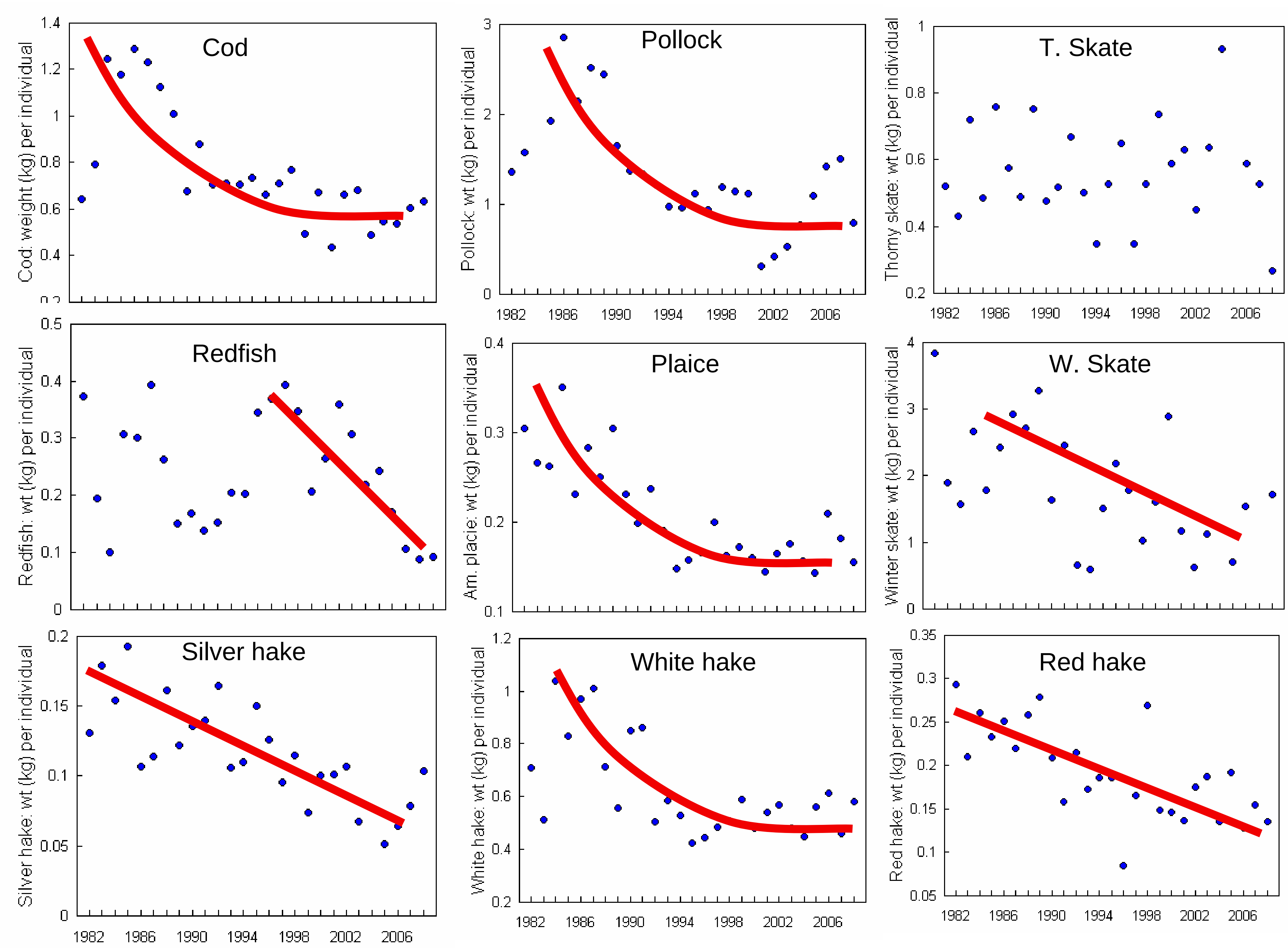
1980s

1990s

2000s

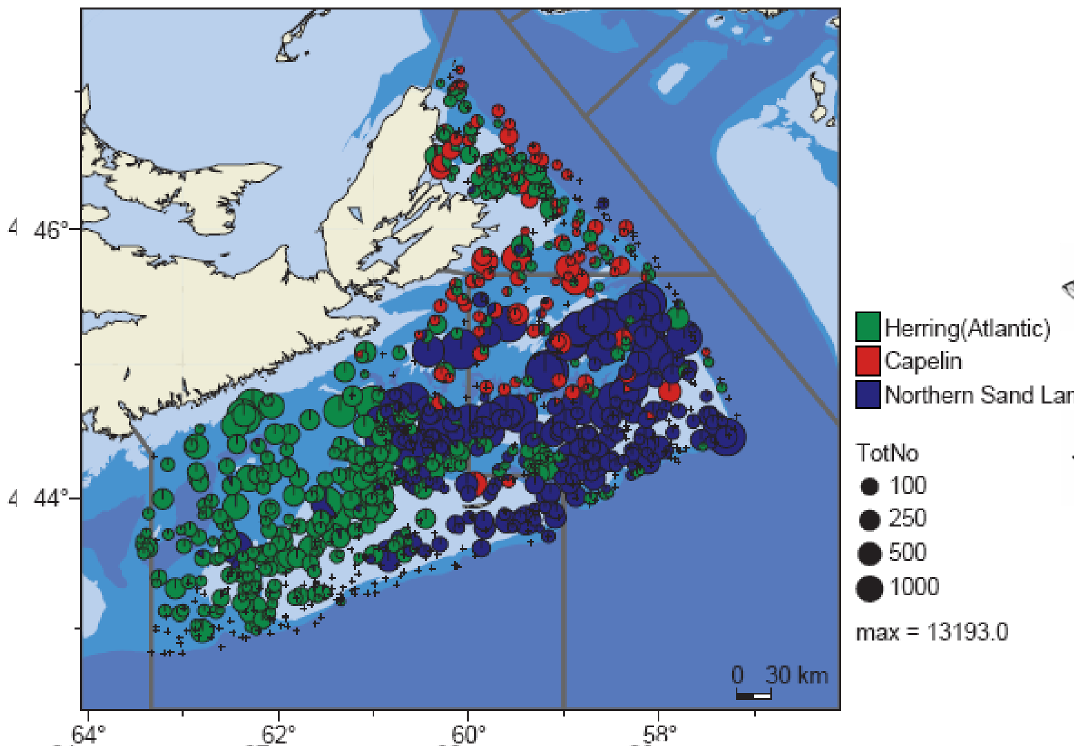
Cod biomass: $\log_{10}$(kg per km^2)

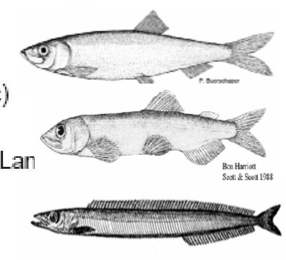

Cod 161 cm
Cod biomass, kt
Pollock 112 cm
Pollock biomass, kt
T. Skate 120 cm
Thorny skate biomass, kt
Redfish 60 cm
Redfish biomass, kt
Plaice 76 cm
American plaice biomass, kt
W. Skate 121 cm
Winter skate biomass, kt
Silver hake 73 cm
Silver hake biomass, kt
White hake 142 cm
White hake biomass, kt
Red hake 108 cm
Red hake biomass, kt
1982
1986
1990
1994
1998
2002
2006


Cod
Cod: weight (kg) per individual
Pollock
Pollock: wt (kg) per individual
T. Skate
Thorny skate: wt (kg) per individual
Redfish
Redfish: wt (kg) per individual
Plaice
Am. placie: wt (kg) per individual
W. Skate
Winter skate: wt (kg) per individual
Silver hake
Silver hake: wt (kg) per individual
White hake
White hake: wt (kg) per individual
Red hake
Red hake: wt (kg) per individual
1982
1986
1990
1994
1998
2002
2006

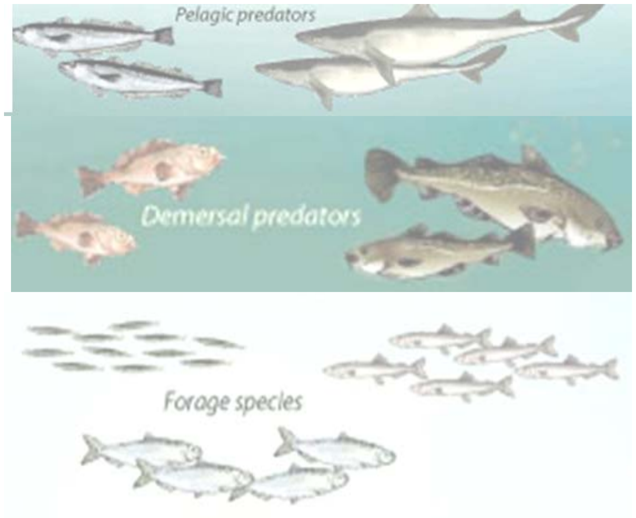
Response of major forage fish species (planktivores)

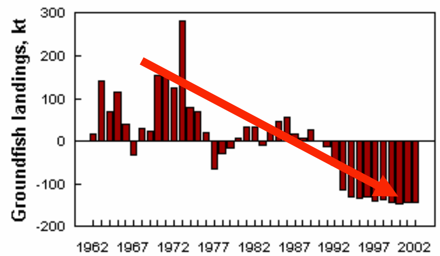
2000s

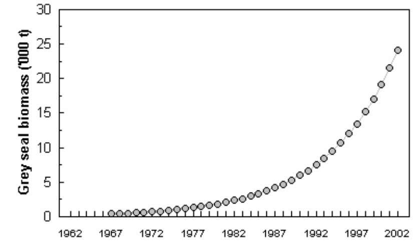


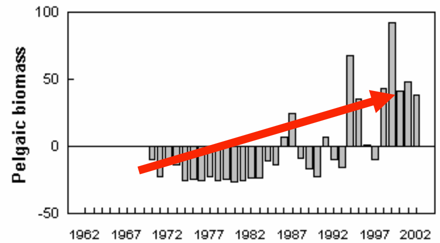


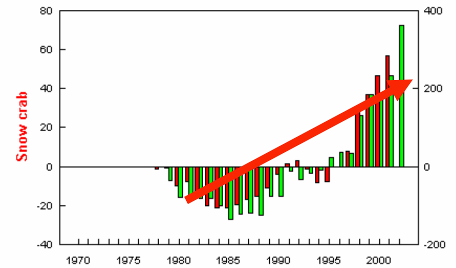
Explosive increase/unnaturally abundant
Precipitated chain of events extending to base of food chain

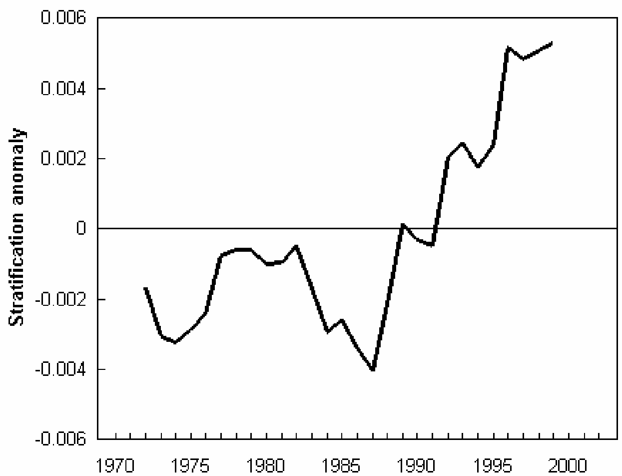


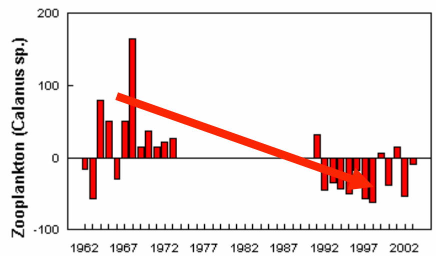








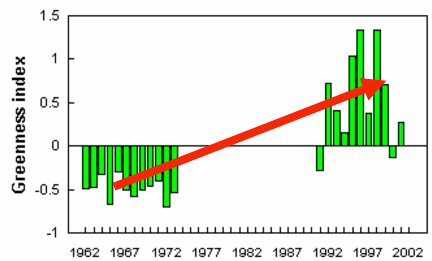




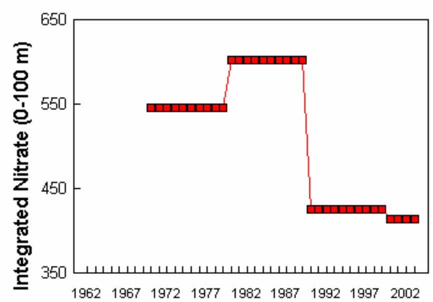
Trophic Cascades in a Formerly Cod-Dominated Ecosystem

Kenneth T. Frank,[1]* Brian Petrie,[1] Jae S. Choi,[1,2] William C. Leggett[2]

Removal of top predators from ecosystems can result in cascading effects through the trophic levels below, completely restructuring the food web. Cascades have been observed in small-scale or simple food webs, but not in large, complex, open-ocean ecosystems. Using data spanning many decades from a once cod-dominated northwest Atlantic ecosystem, we demonstrate a trophic cascade in a large marine ecosystem. Several cod stocks in other geographic areas have also collapsed without recovery, suggesting the existence of trophic cascades in these systems.

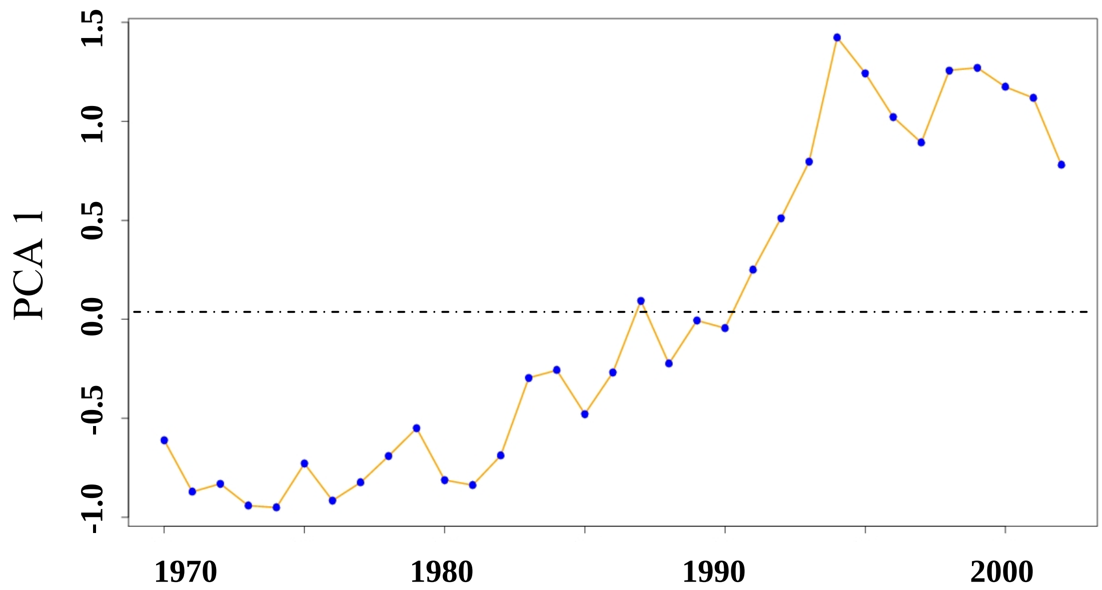


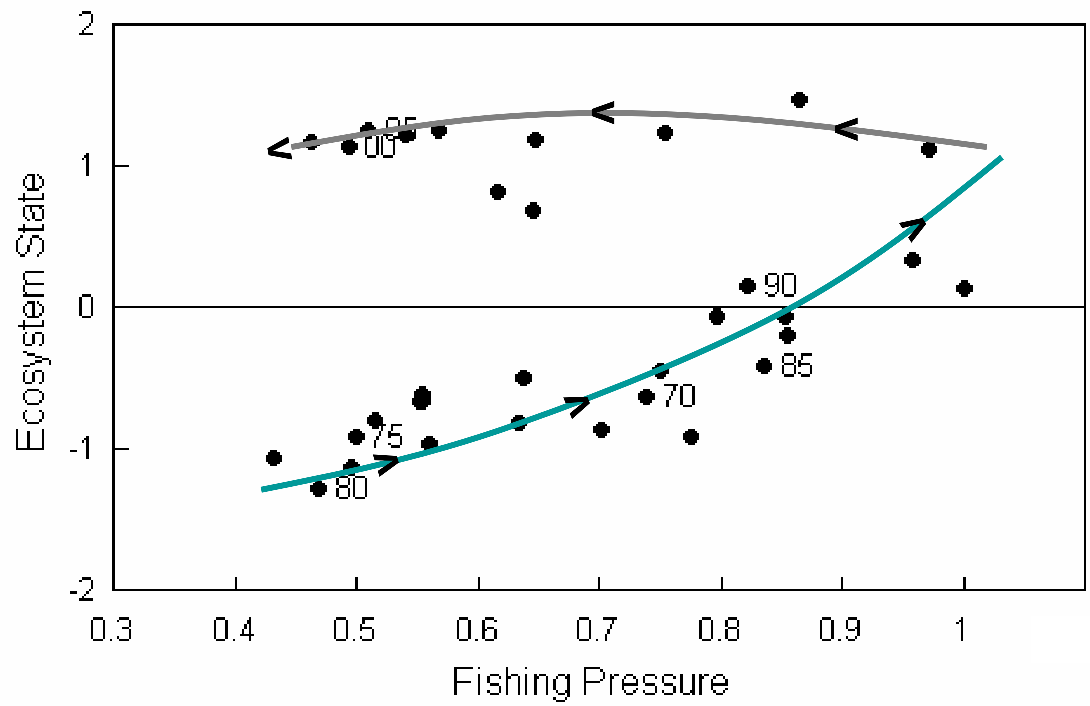
www.sciencemag.org SCIENCE VOL 308 10 JUNE 2005



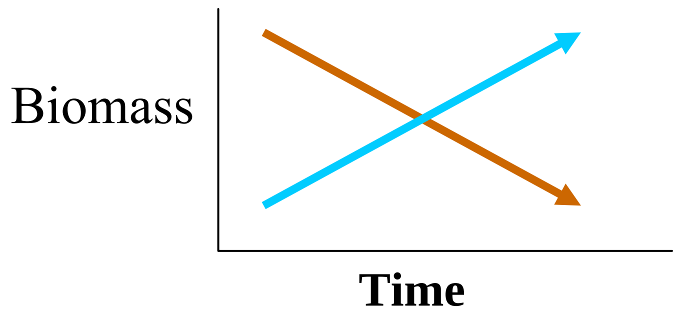
- Top-down effects of fishing can lead to alternate states

- Such systems do not respond well to conventional management approaches
  - Despite cessation of fishing (15+ y) – little or **no recovery**





- Many ideas put forward to explain lack of recovery
  - Role reversal – **predators** become **prey**



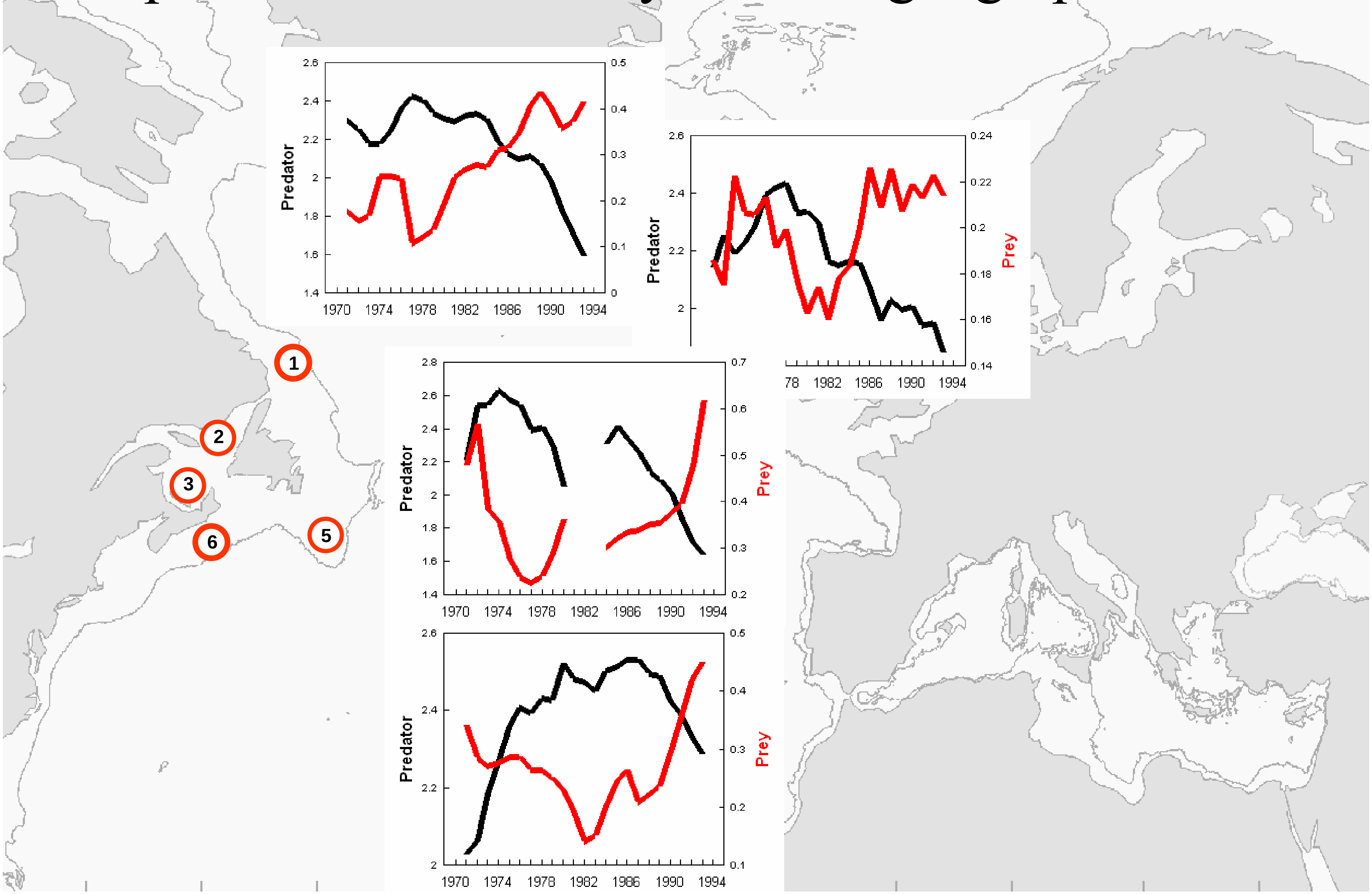
- By-catch in other groundfish fisheries (Shelton et al. 2006; illegal fishing (King and Sutinen 2009)

- Seal predation (increasing M)

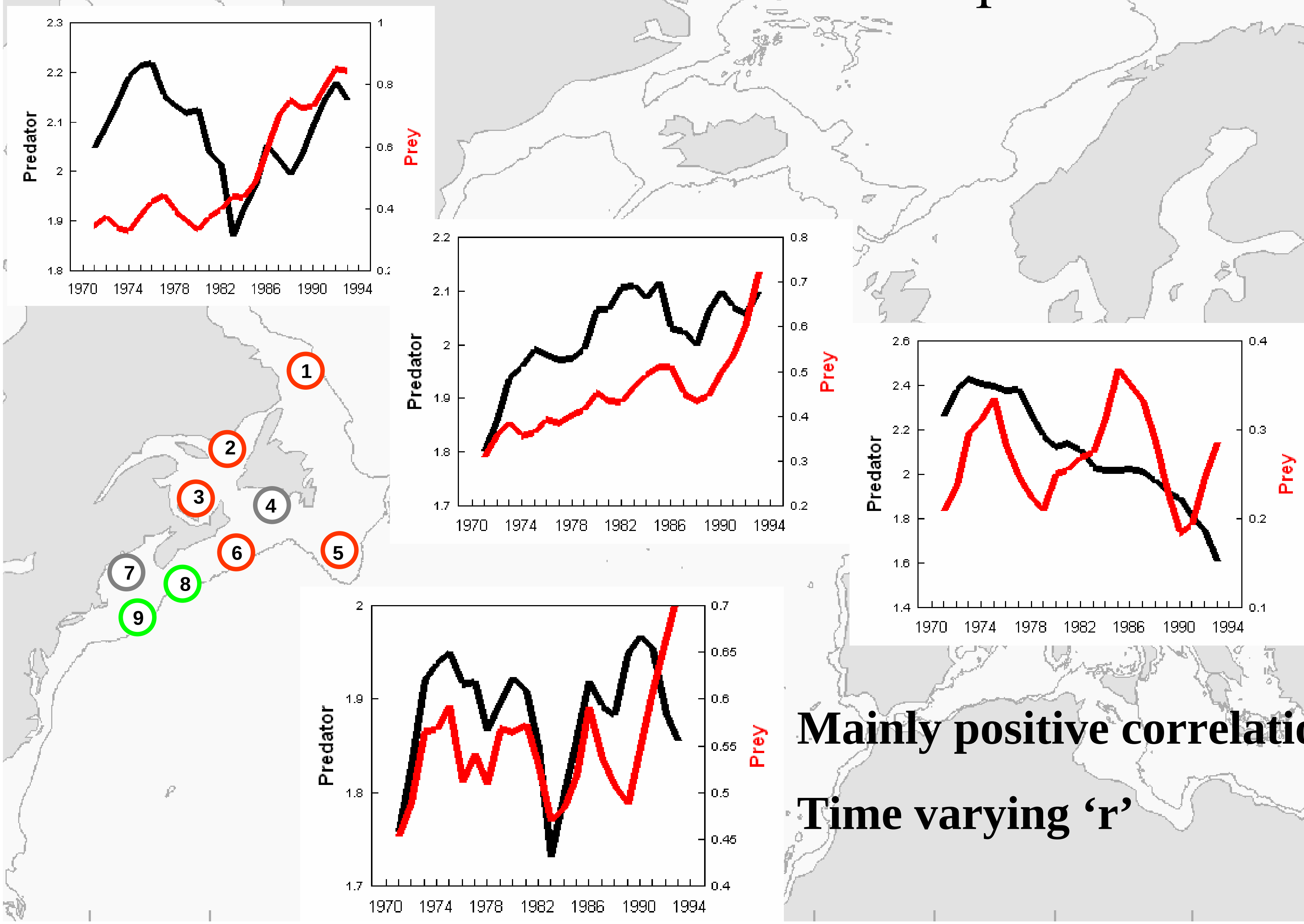
- Allee effects (increasing M)

- decreased body growth/reduced recruitment

Functional groups of predator (TL4) and prey (TL3) responded the same way in other geographic areas

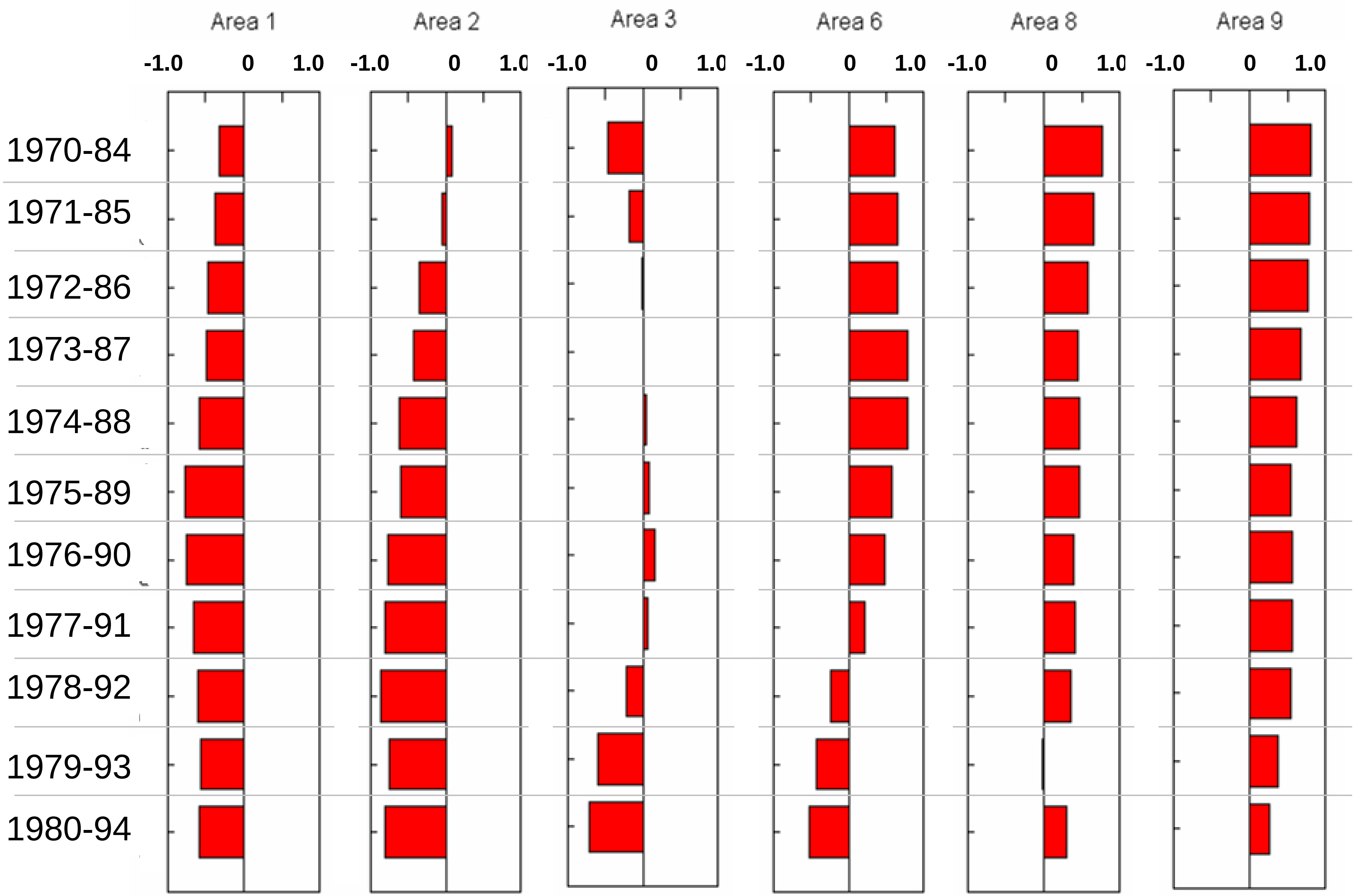


Other geographic areas more stable and did not collapse



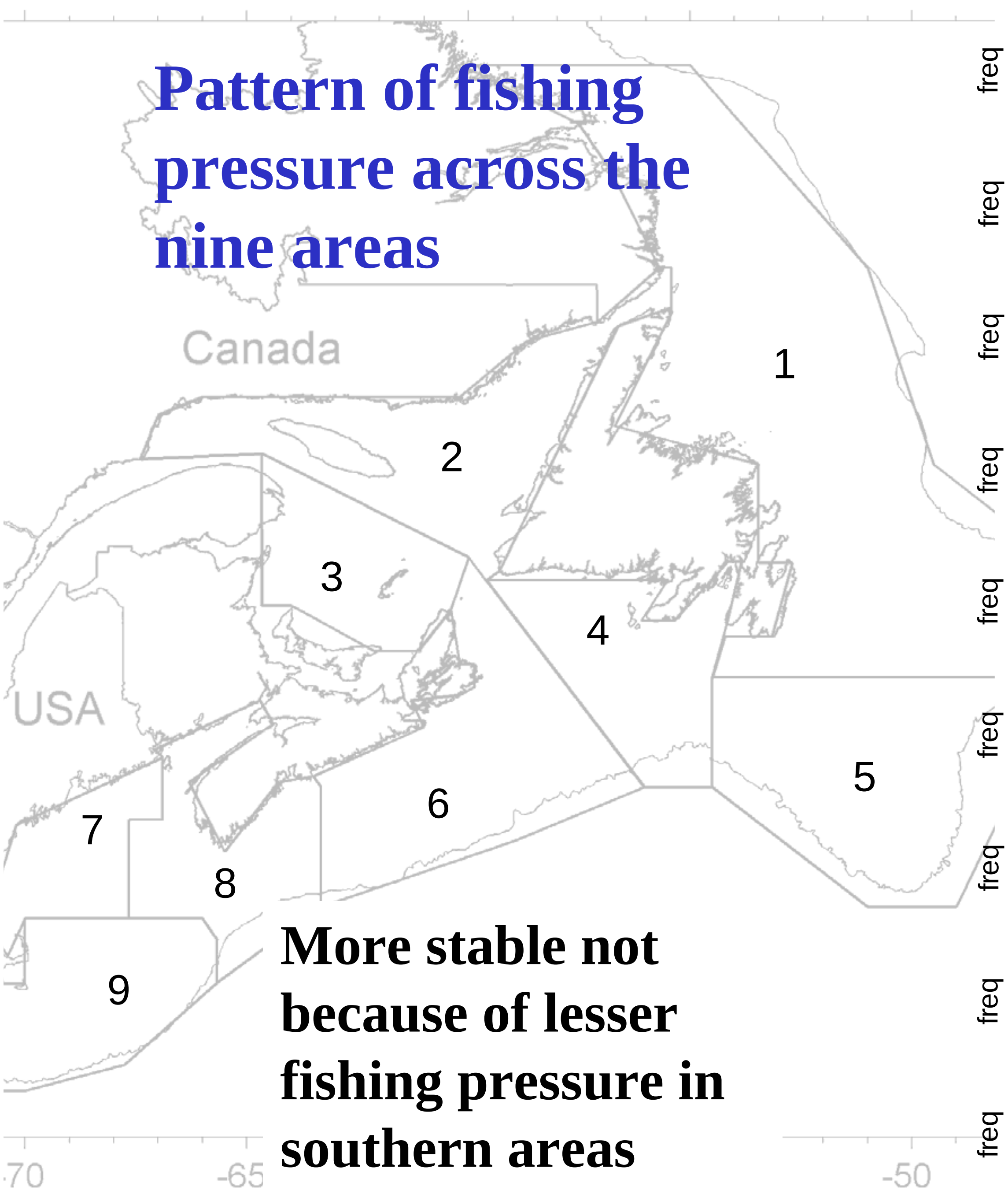
Mainly positive correlations

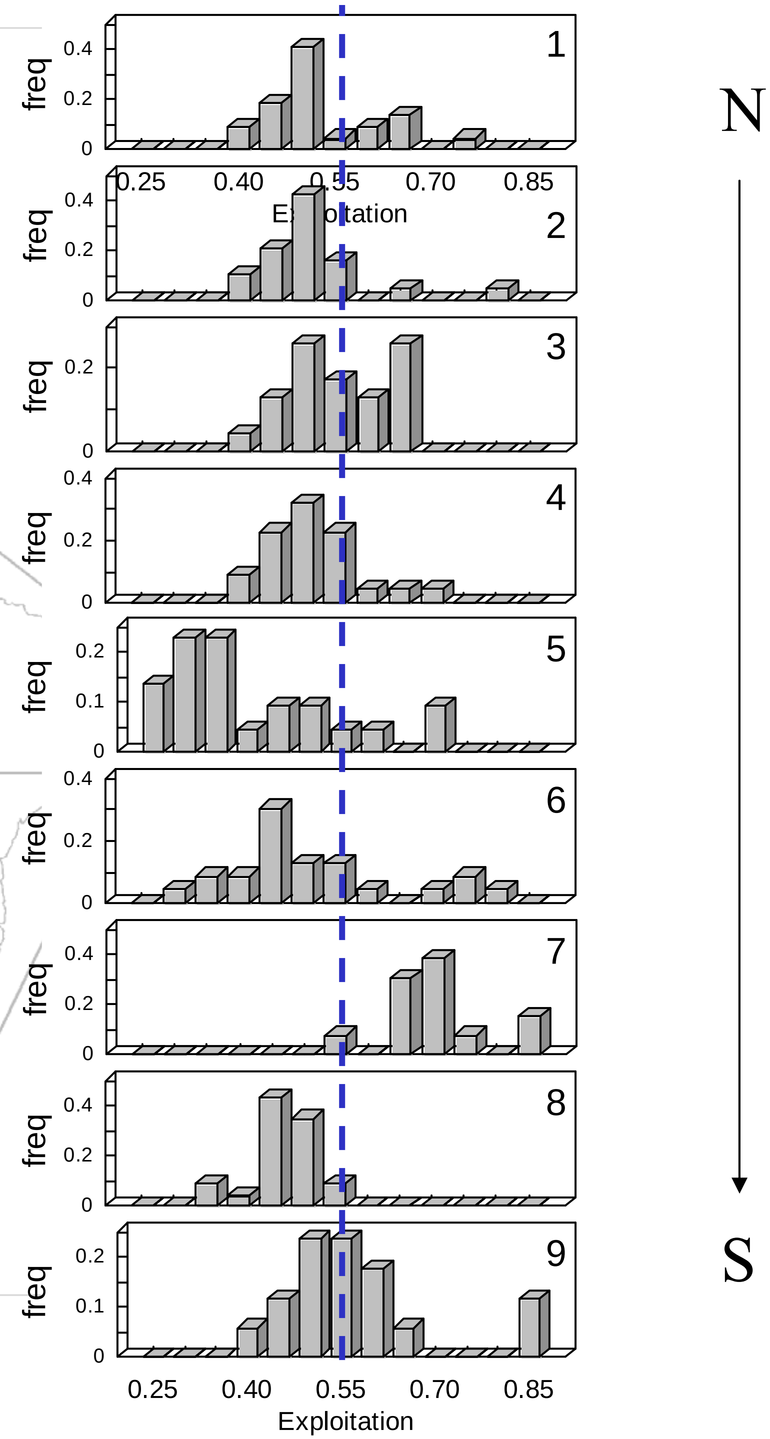
Time varying ‘r’



Fishing effects lower in south?

Pattern of fishing pressure across the nine areas

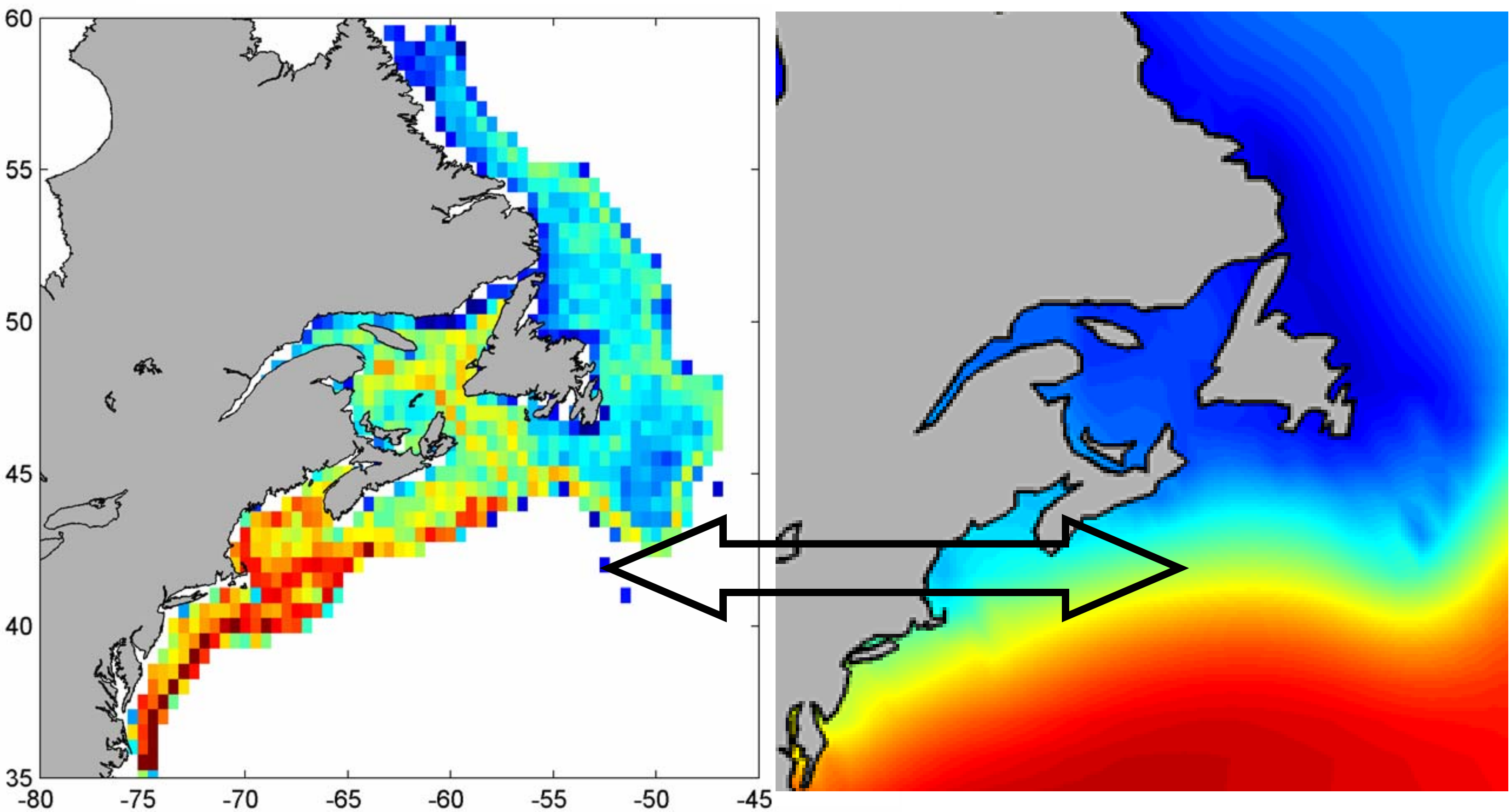




More stable not because of lesser fishing pressure in southern areas

Instead …

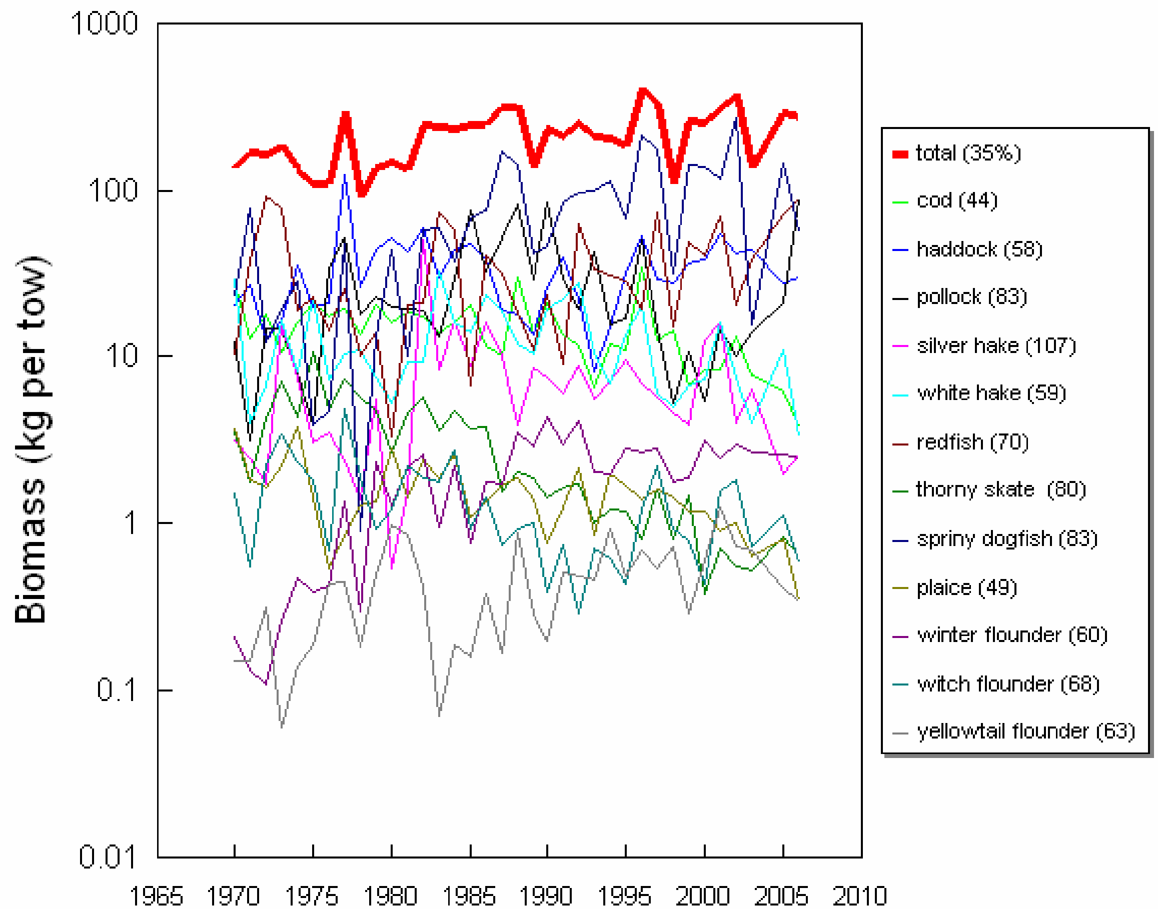
Fish species richness   Water temperature



Strongly correlated

Greater potential for compensation in species rich areas (e.g. Area 8 -- western Scotian Shelf)

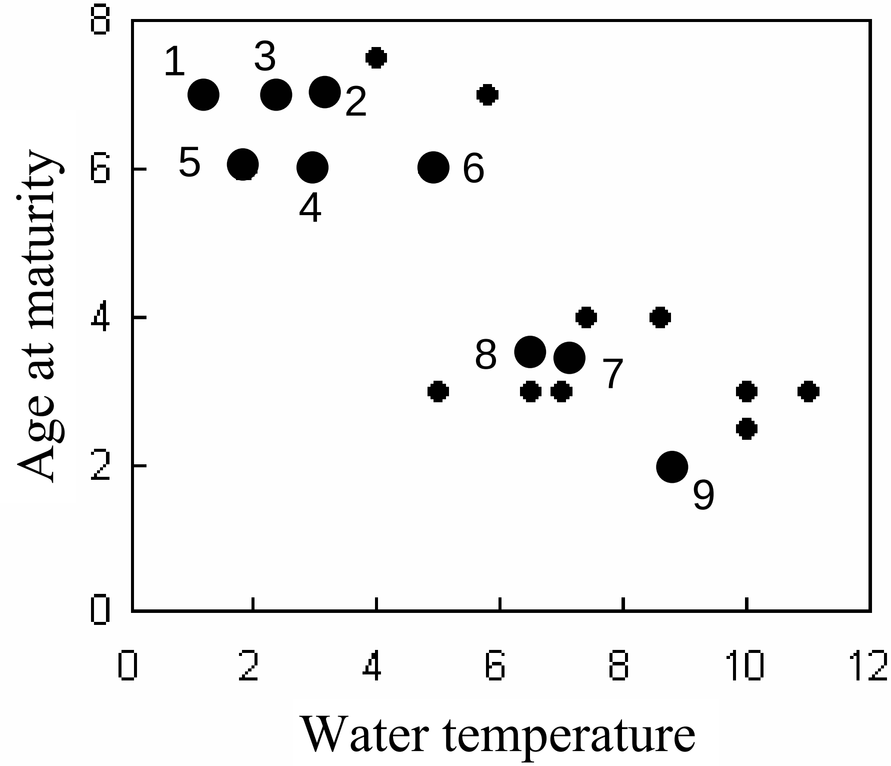
Functional substitutes keep forage fishes in check



Warmer waters accelerate growth

and maturation rates

20 cod populations in N. Atlantic



Target species able to sustain higher exploitation

Myers et al. 1997

Fundamental challenge: How much can apex predators be depleted before a fish community becomes unbalanced?
Goals:

- Develop a 1st Order model relating **pred-prey functional group*** correlations to Total Annual Depletion (**X1**; natural+fishing mortality), Temperature (**X2**), Species Richness
- Define exploitation thresholds to avoid undesirable states
- Test with independent data from other regions

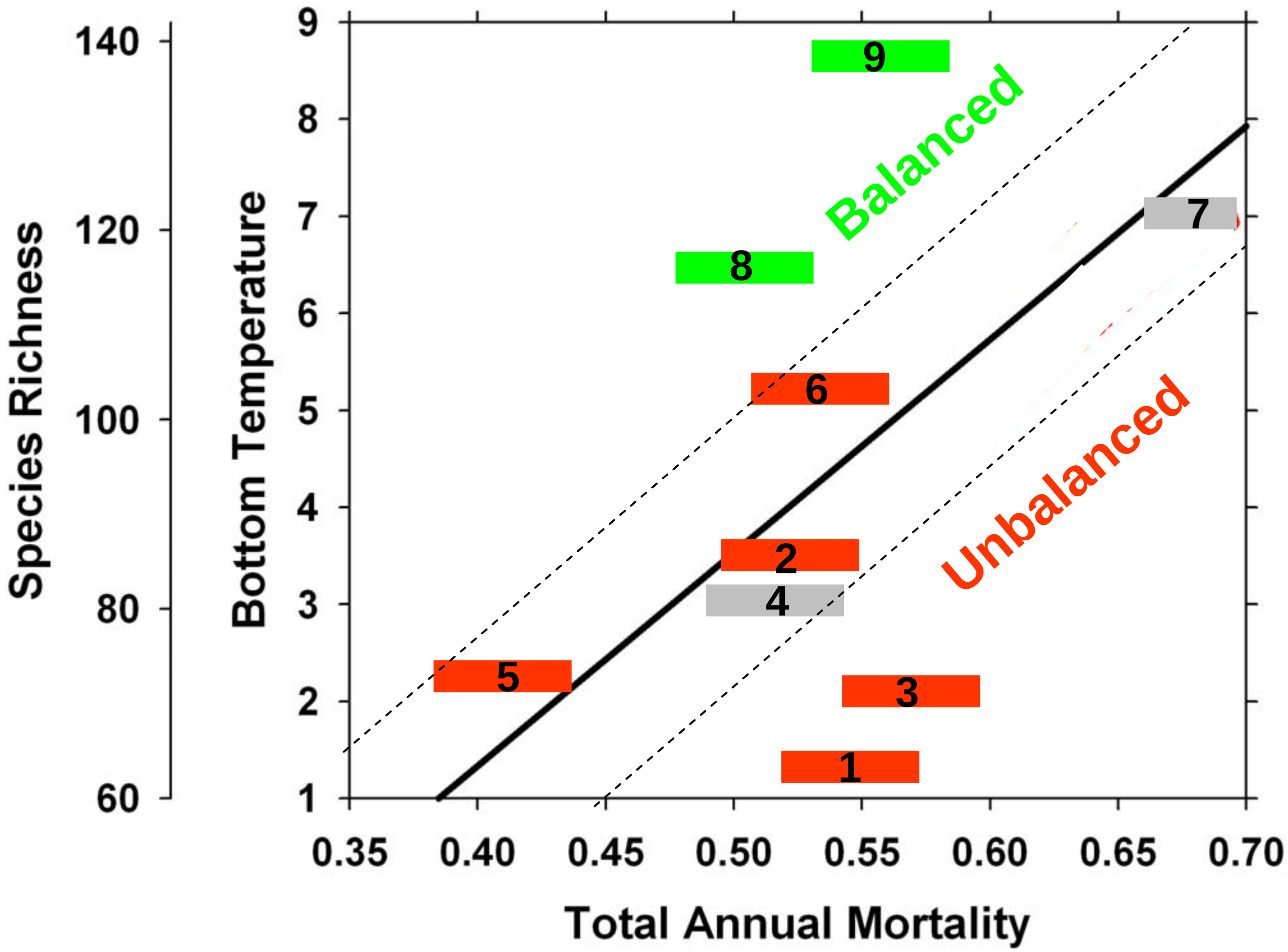
$$Y = 1.1 + 0.14 * X2 - 3.2 * X1$$

RMS difference = 0.29

Explained variance = 0.58

*Functional group: 15 predator species; 8 prey species

Mapping Correlation on Annual Depletion & T (or Species Richness)

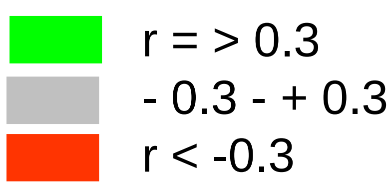


Warmer, species rich areas retain positive correlation with exploitation high as 55-60%

Colder areas sustain positive correlation status at < 35%

Exploitation & Temp terms -- equal contribution to explained variance

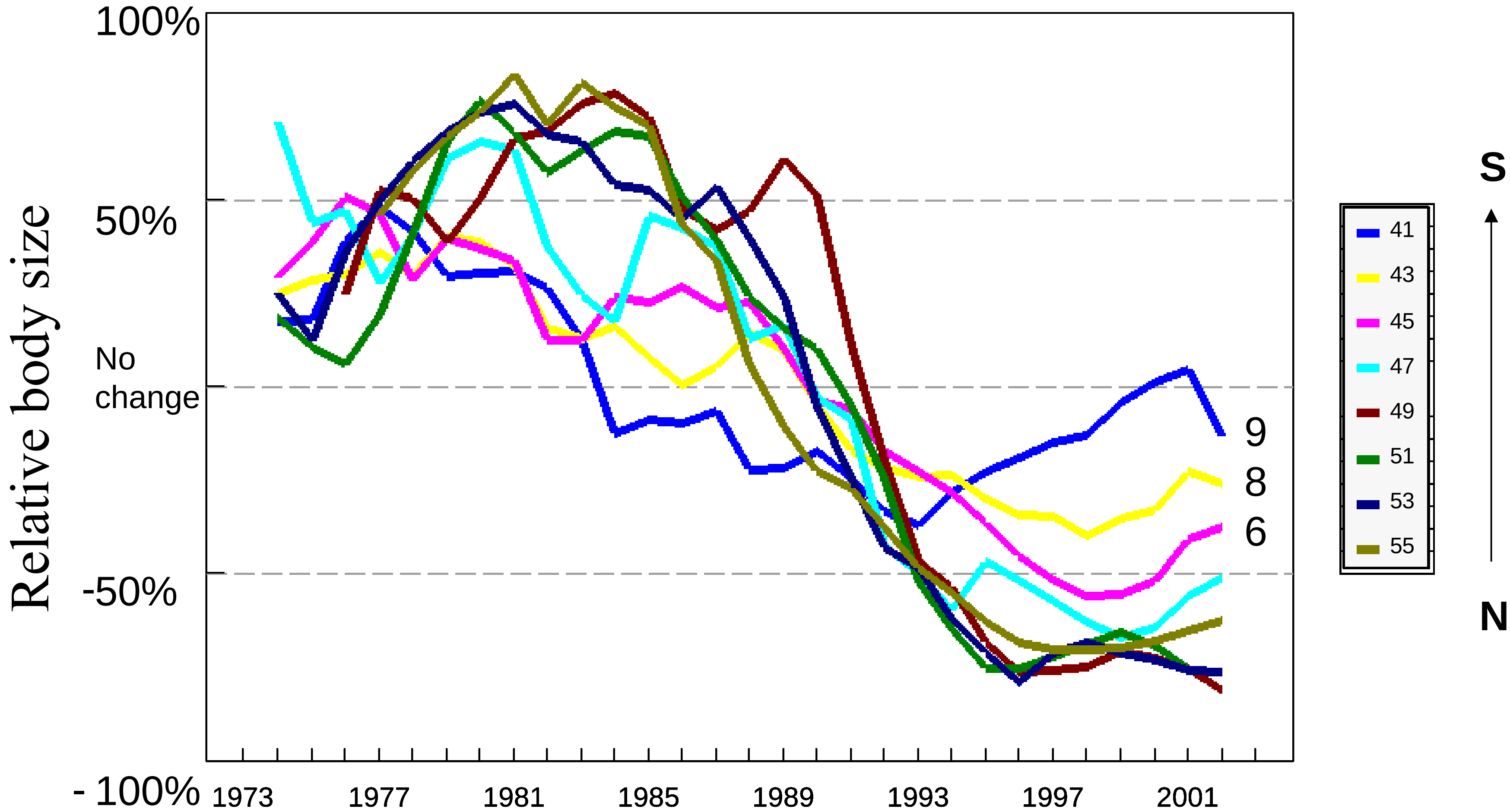
Predator-prey correlation



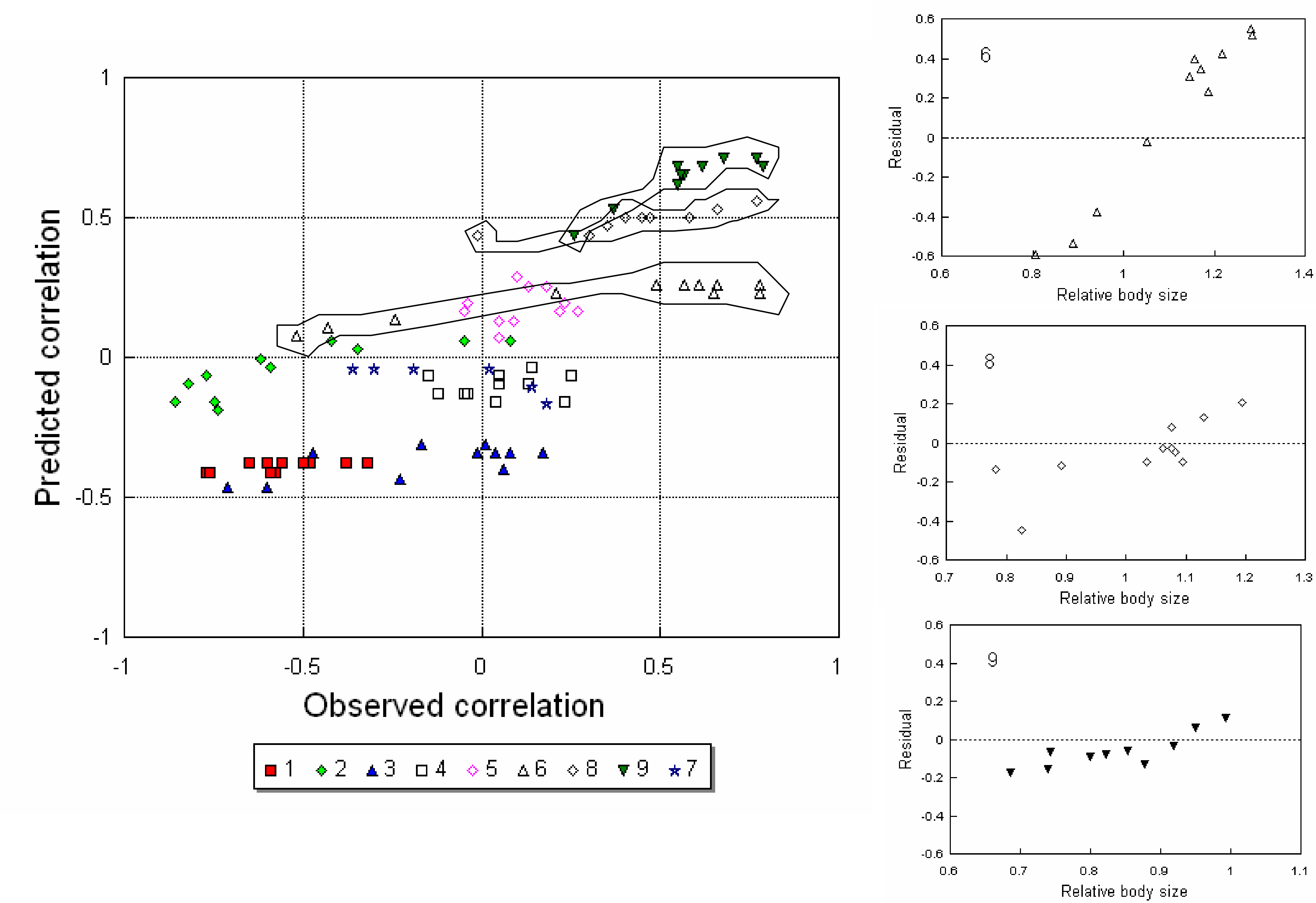
Petrie et al 2009 Fish. Oceanogr.

- Residual variation appears to be explained by changes in average body size

Changes in body size of predator complex



Additional variation explained by body size changes of predator complex



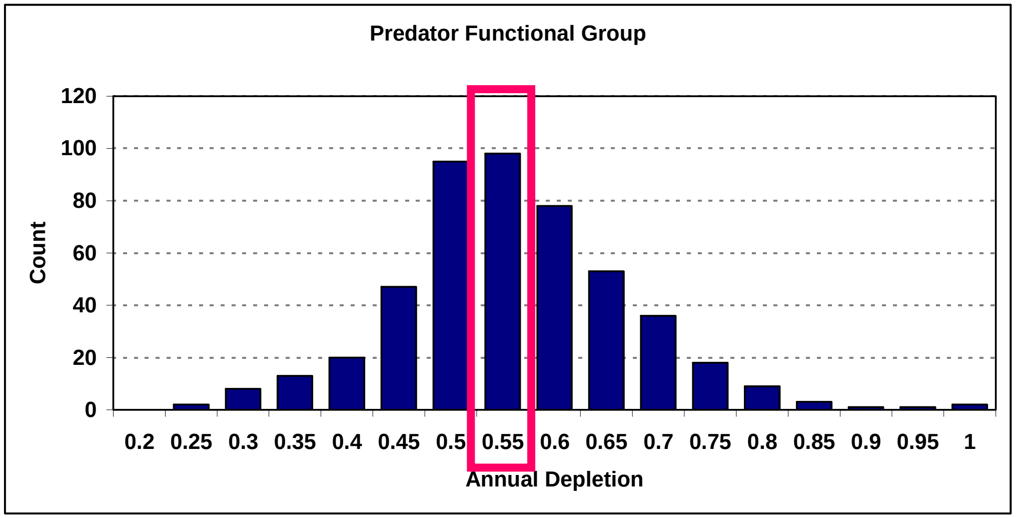
- Large complex systems not immune to indirect effects of fishing top predators
- Conclusions drawn from comparisons across ecosystems cannot be generalized to individual ecosystems (context dependent)
- Next steps in modeling will involve incorporation of body size data, but first let’s look at performance of existing model

- Testing model against data from independent areas

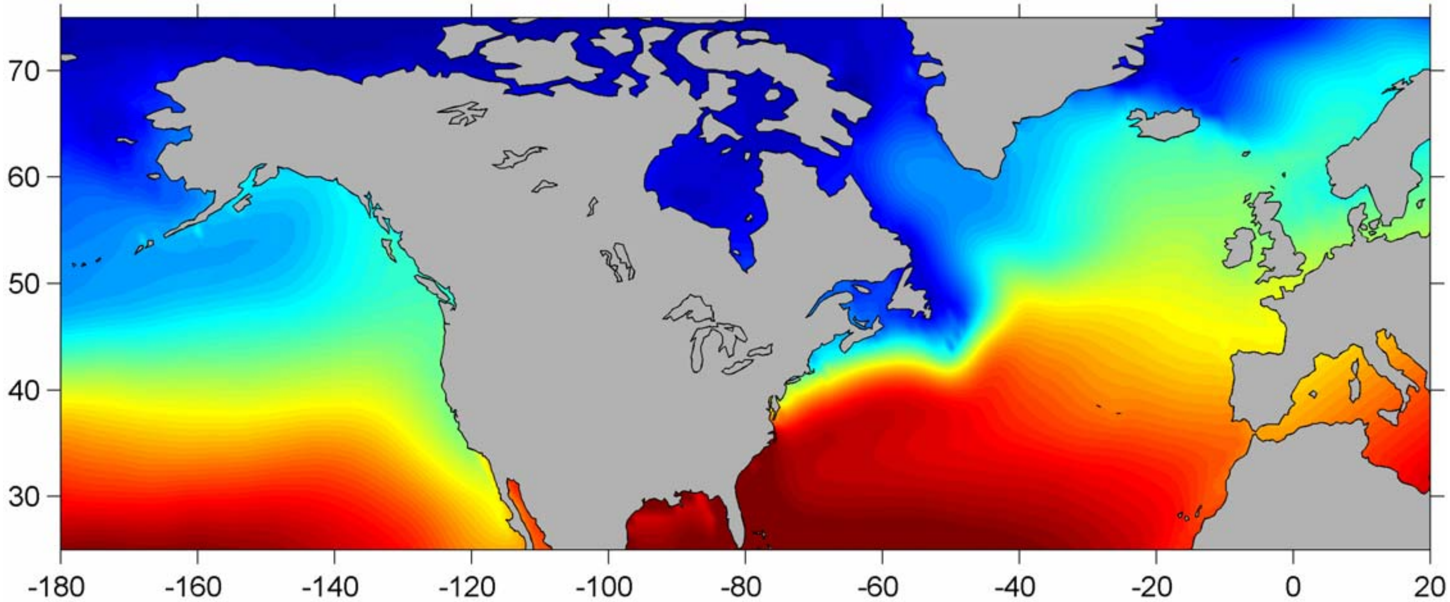
Using representative level of annual exploitation

Annual Depletion Statistics

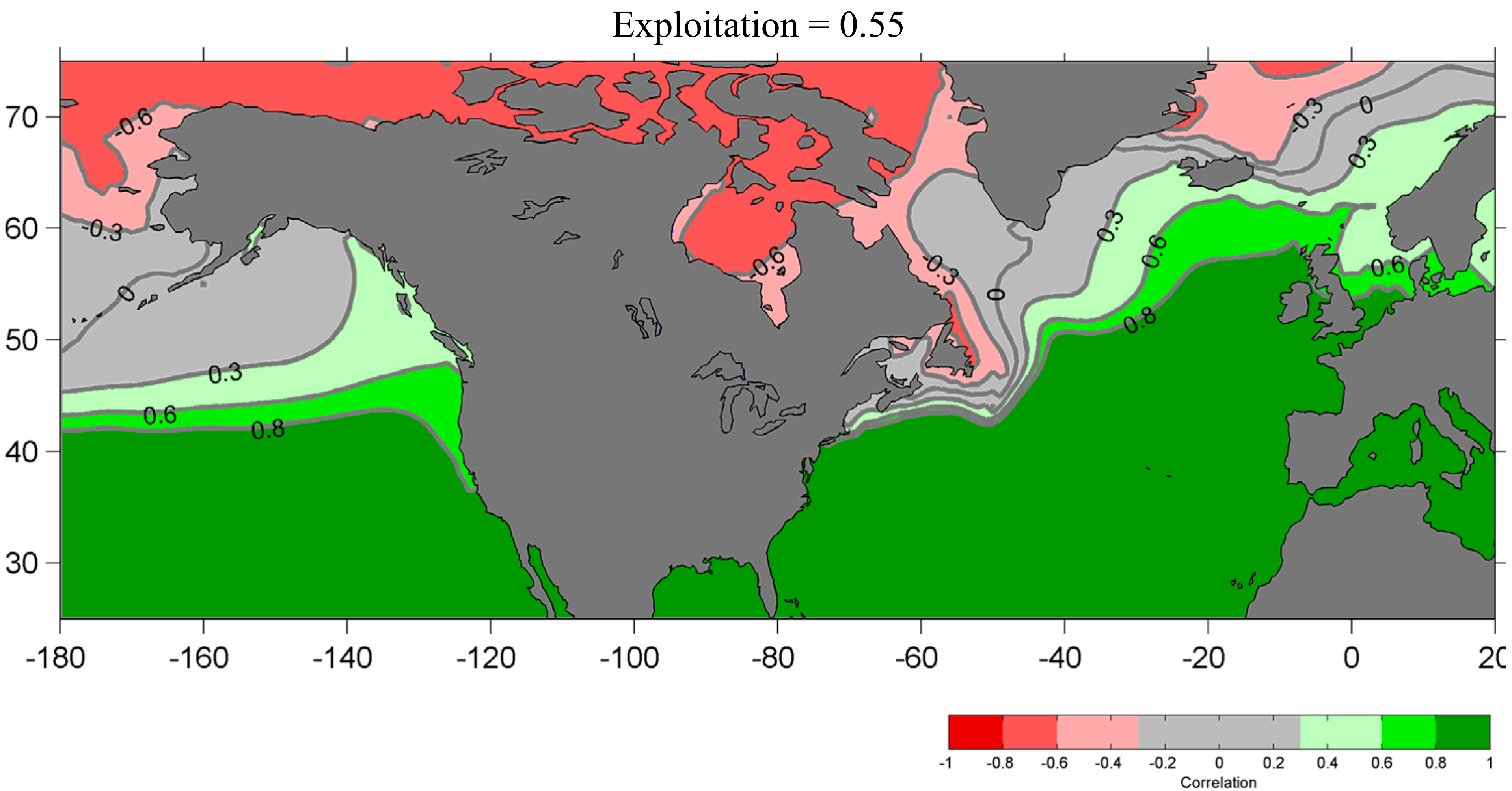
Bin	*Frequency*
0.2	0
0.25	2
0.3	8
0.35	13
0.4	20
0.45	47
0.5	95
0.55	98
0.6	78
0.65	53
0.7	36
0.75	18
0.8	9
0.85	3
0.9	1
0.95	1
1	2



and spatially intensive temperature data

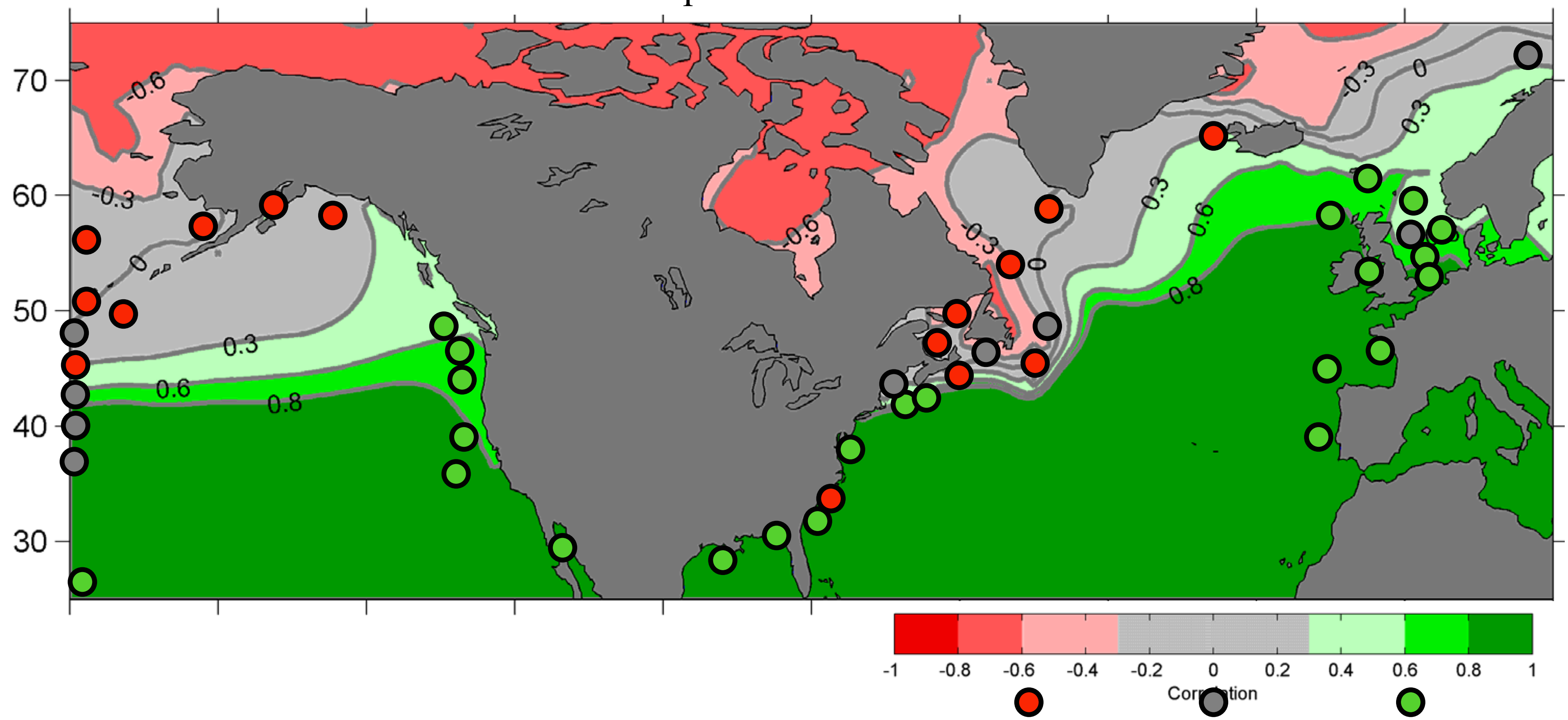


can generate maps of trophic forcing metric



And conduct independent testing of model with data/available literature

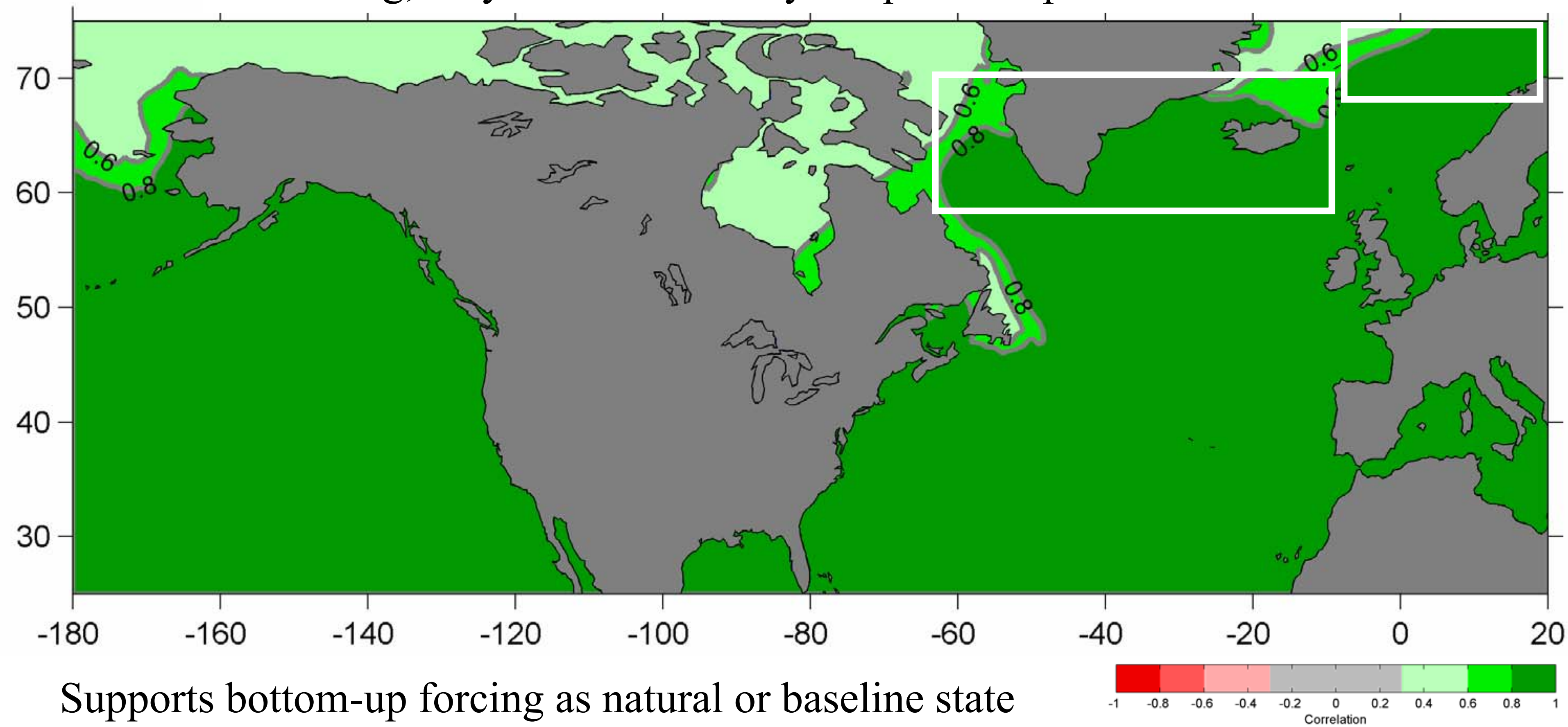
Exploitation = 0.55



	TL1	TL2	TL3
TL 1			
TL2	5		
TL3	3	1	
TL4	3	8	8

Published studies based on single species or aggregates of species considered representative of trophic levels

No fishing, only natural mortality ~ equal to exploitation of 0.20

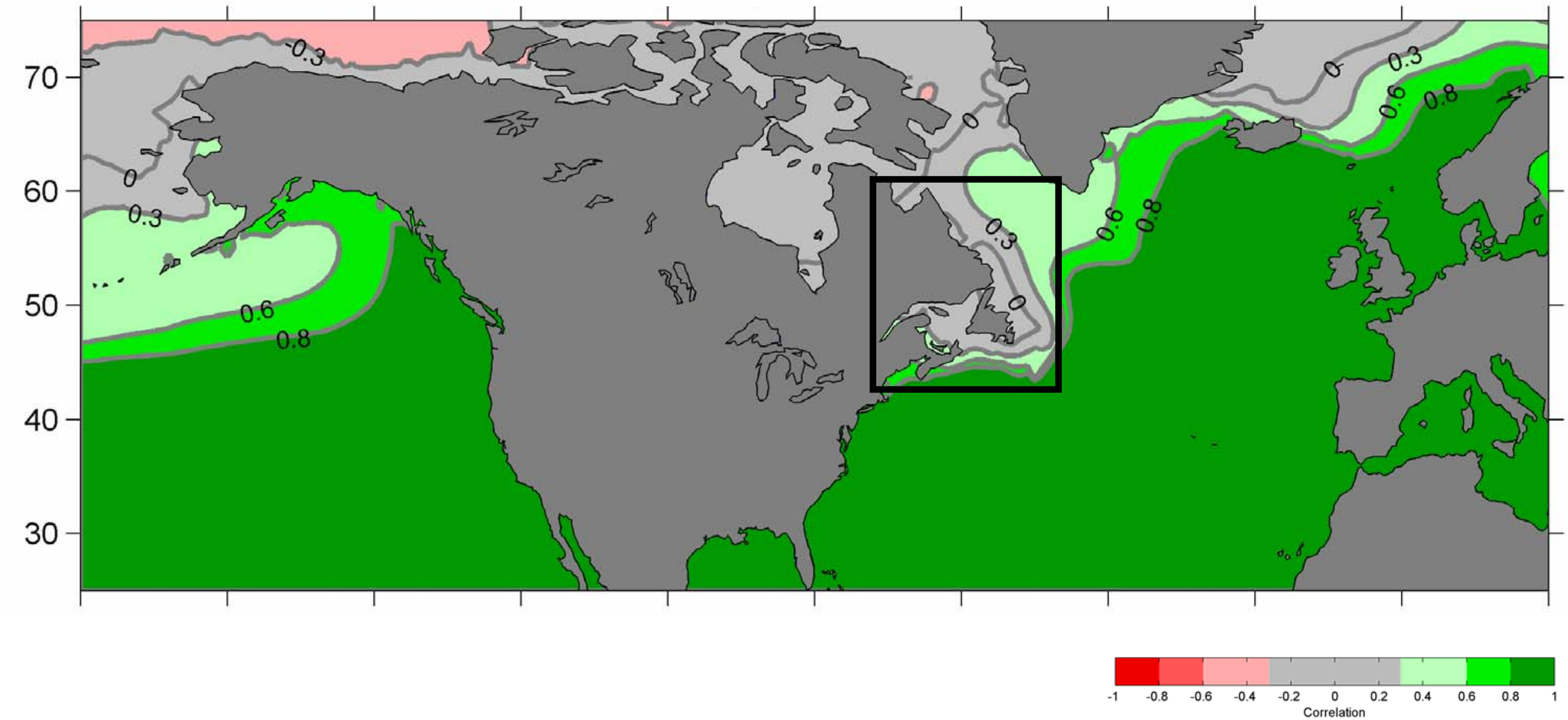


Supports bottom-up forcing as natural or baseline state

Nordic Seas typified by high biomass of cod, herring, phytoplankton and zooplankton production in 1920s/30s(Drinkwater, K.F. 2006.Prog. Oceanogr. 68: 134)

Steele and Schumacher (2000) argued that ecosystem structure before fishing was bottom-up (+ correlations among trophic levels)

Exploitation = 0.4



At even the most conservative level of fishing – 2X assumed level of natural mortality – NW Atlantic in transition zone and easily pushed into alternate state

Model - powerful 1st approximation of an ecosystem based approach to resource management but …

- Built on correlation among variables
- Time series are 25y but few df
- Exploitation estimates involve assumptions not met in other areas (use of fishing pressure on dominant species)
- No accounting for exploitation of prey species (common in eastern Atlantic and elsewhere)
  - Influences sign and magnitude of trophic forcing metric
- Testing requires time series of functional group predator and prey abundances

Summary

- Outlook for Macroecology
  - acknowledge limitations associated with poor controls, unassessed factors, surrogate variables, and heterogeneous data
  - recognize that many explanations can be advanced for any set of observations and resist over-enthusiasm for any particular explanation (Peters et al. 1991)
  - progress in discipline requires moving from pattern to mechanism, therefore accurate description of pattern is essential first step
  - Stress the compensating advantages of macroecological analyses: breadth, generality, economy and timeliness