HARMFUL ALGAL BLOOMS
GLOBAL SPREADING OR GLOBAL SYNCHRONY?

Ted Smayda

PICES

“Do links exist between the apparent increase in the duration, distribution and impact of HABs, and environmental factors associated with human activities, including urban and agricultural runoff, climatic change and mariculture? “

HABs - FIVE MAJOR UNCONTROLLED EXPERIMENTS COMPROMISE THE SEARCH FOR EXPLANATIONS

- ***CLIMATE CHANGE***
- ***EUTROPHICATION***
- ***INCREASED HARVESTING OF FISH AND SHELLFISH***
- ***ALTERED FRESHWATER RUNOFF***
- ***REDISTRIBUTION AND DISPERSAL OF SPECIES IN BALLAST WATER***

INADEQUATE TIME SERIES DATA = ABSENCE OF A CONTROL

PATTERNS IN THE GLOBAL HAB SYNDROME

- ***GLOBAL SPREADING OF HAB SPECIES***
  Pyrodinium bahamense var. compressum
  Gymnodinium catenatum; Alexandrium catenella

- ***NOVEL OCCURRENCES***
  Chrysochromulina polylepis

- ***CHANGE IN BLOOM FREQUENCY***
  - ***a. Increase in Bloom Frequency***
    ***Cochlodinium polykrikoides* (regionally)**
  - ***b. Progressive Increase in Annual Blooms***
    ***Cochlodinium polykrikoides* (within system)**
  - ***c. Progressive Decrease in Annual Blooms***
    Heterosigma akashiwo, Chattonella spp.

PATTERNS IN THE GLOBAL HAB SYNDROME *(cont.)*

- ***CHANGES IN BLOOM FREQUENCY***

  d. Progressive Increase in Dominance

  Karenia mikimotoi, Prorocentrum* cf. *cordatum

  e. Range Extensions of HAB Species

  ? (problem of "hidden" vs. "alien" species)

  f. Increased Blooms within Distributional Range

  Prorocentrum minimum & many others

  g. Increase in Novel Species' Blooms

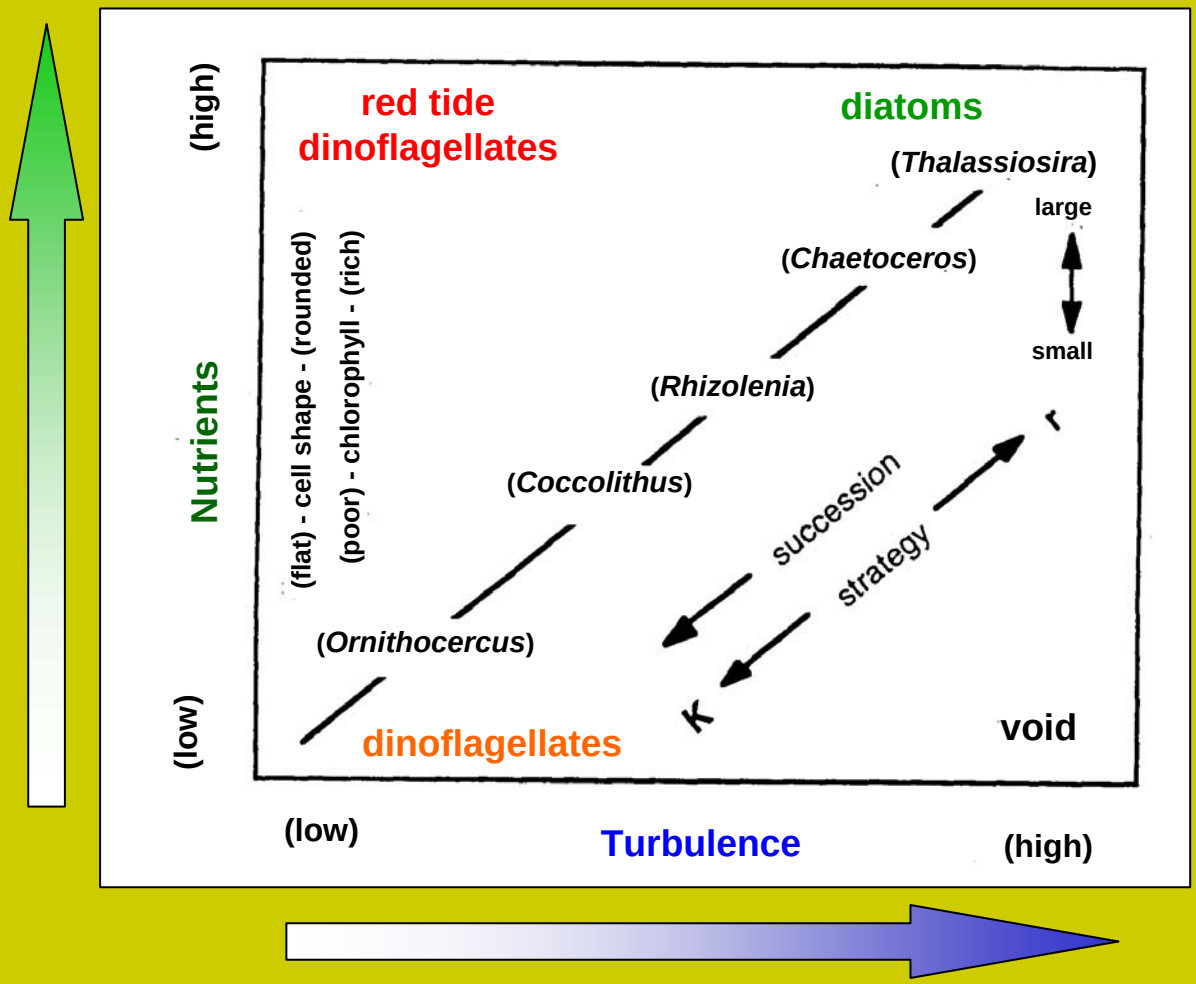
  Aureococcus anophagefferens, Heterocapsa circularisquama

- ***GLOBAL EXPANSION IN SHELLFISH TOXICITY***

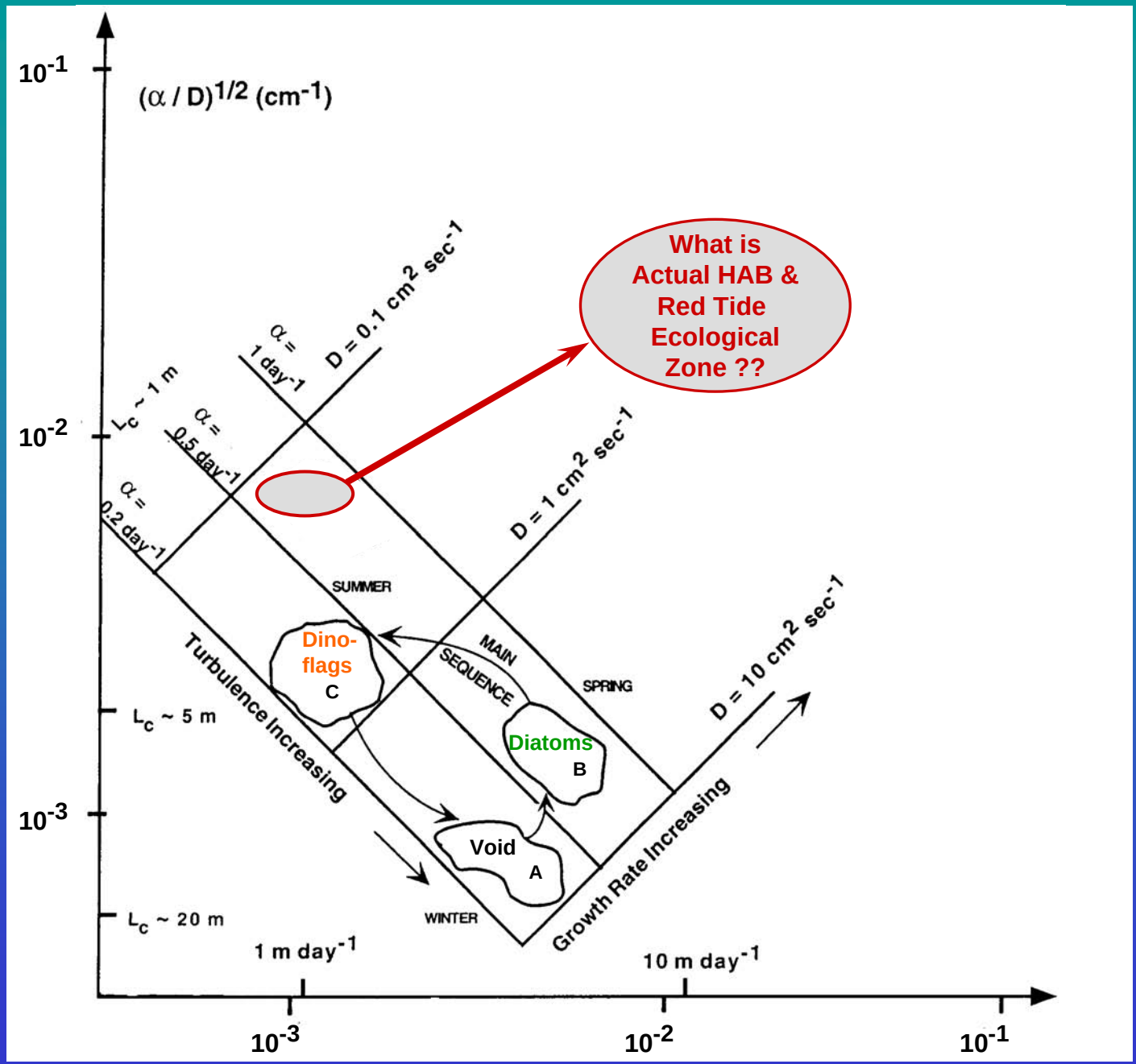
  Increased Occurrences; New Diseases

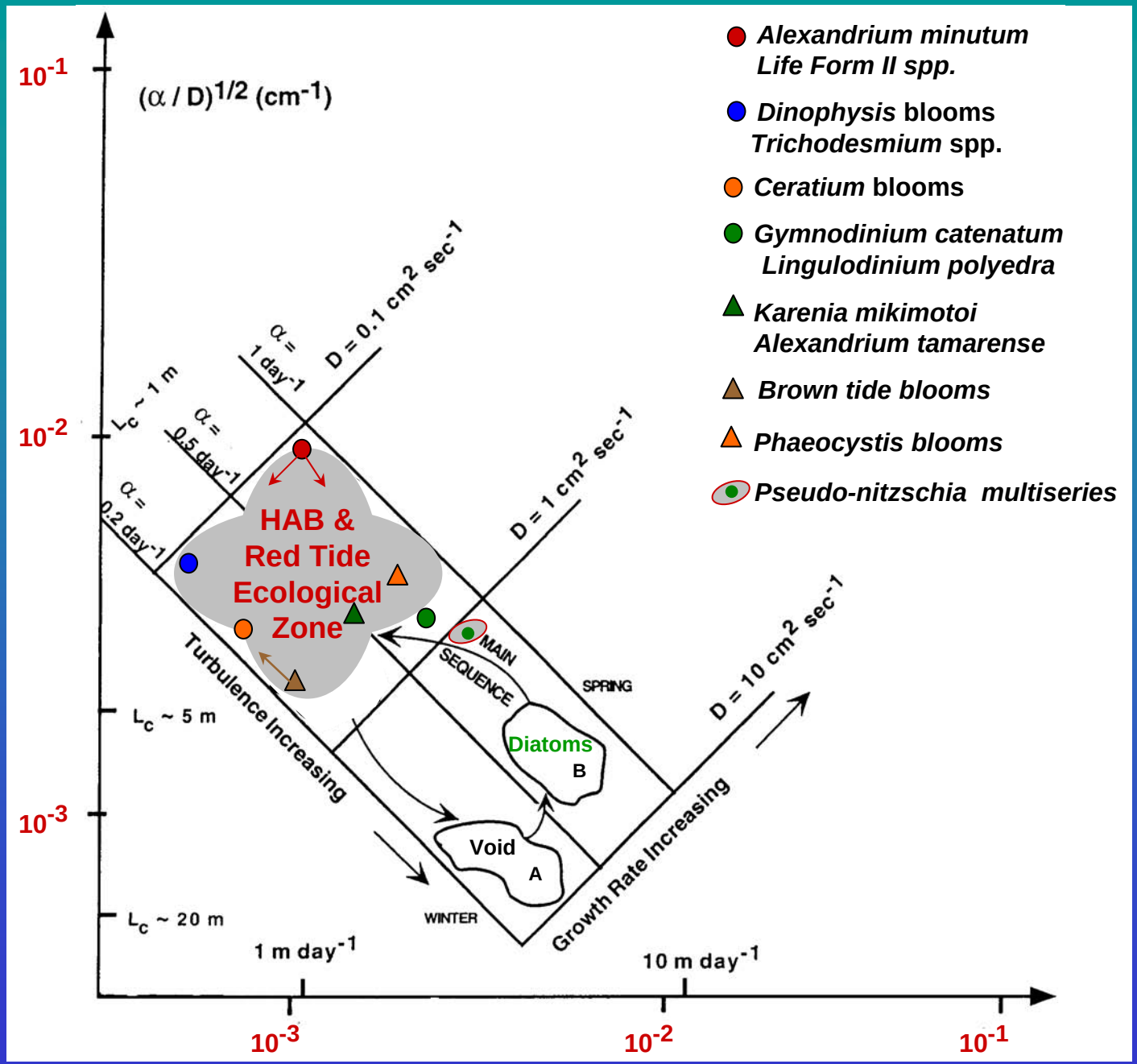
- ***APPARENT AQUACULTURAL STIMULATION OF HARMFUL BLOOMS***

  Heterosigma akashiwo



Modified from Cullen & MacIntyre (1998)


10^{-1}
$(\alpha / D)^{1/2}$ (cm^{-1})
What is Actual HAB & Red Tide Ecological Zone ??
α = 1 day^{-1}
D = 0.1 cm^2 sec^{-1}
L_c ~ 1 m
α = 0.5 day^{-1}
10^{-2}
α = 0.2 day^{-1}
D = 1 cm^2 sec^{-1}
SUMMER
Dino-flags
C
MAIN SEQUENCE
SPRING
D = 10 cm^2 sec^{-1}
Turbulence Increasing
L_c ~ 5 m
Diatoms
B
10^{-3}
Void
A
L_c ~ 20 m
WINTER
Growth Rate Increasing
1 m day^{-1}
10 m day^{-1}
10^{-3}
10^{-2}
10^{-1}
CRITICAL SIZE INCREASING
FASTER SPREADING; SINKING
$(\alpha\ D)^{1/2}$ (cm sec^{-1})


10^{-1}
10^{-2}
10^{-3}
$(\alpha / D)^{1/2}$ (cm^{-1})
L_c ~ 1 m
L_c ~ 5 m
L_c ~ 20 m
α = 1 day^{-1}
α = 0.5 day^{-1}
α = 0.2 day^{-1}
D = 0.1 cm^2 sec^{-1}
D = 1 cm^2 sec^{-1}
D = 10 cm^2 sec^{-1}
HAB & Red Tide Ecological Zone
Turbulence Increasing
Growth Rate Increasing
MAIN SEQUENCE
SPRING
Diatoms
B
Void
A
WINTER
1 m day^{-1}
10 m day^{-1}
10^{-3}
10^{-2}
10^{-1}
Alexandrium minutum
Life Form II spp.
Dinophysis blooms
Trichodesmium spp.
Ceratium blooms
Gymnodinium catenatum
Lingulodinium polyedra
Karenia mikimotoi
Alexandrium tamarense
Brown tide blooms
Phaeocystis blooms
Pseudo-nitzschia multiseries
CRITICAL SIZE INCREASING
FASTER SPREADING; SINKING
$(\alpha\ D)^{1/2}$ (cm sec^{-1})

Periodic Table of the Elements

H 1																He 2
Li 3	Be 4										B 5	C 6	N 7	O 8	F 9	Ne 10
Na 11	Mg 12										Al 13	Si 14	P 15	S 16	Cl 17	Ar 18
K 19	Ca 20	Sc 21	Ti 22	V 23	Cr 24	Mn 25	Fe 26	Co 27	Ni 28	Cu 29	Zn 30	Ga 31	Ge 32	As 33	Se 34	Br 35	Kr 36
Rb 37	Sr 38	Y 39	Zr 40	Nb 41	Mo 42	Tc 43	Ru 44	Rh 45	Pd 46	Ag 47	Cd 48	In 49	Sn 50	Sb 51	Te 52	I 53	Xe 54
Cs 55	Ba 56	Lu 71	Hf 72	Ta 73	W 74	Re 75	Os 76	Ir 77	Pt 78	Au 79	Hg 80	Tl 81	Pb 82	Bi 83	Po 84	At 85	Rn 86
Fr 87	Ra 88	Lr 103	Db 104	Jl 105	Rf 106	Bh 107	Hn 108	Mt 109	110	111	112	113	114	115	116	117	118

La 57	Ce 58	Pr 59	Nd 60	Pm 61	Sm 62	Eu 63	Gd 64	Tb 65	Dy 66	Ho 67	Er 68	Tm 69	Yb 70
Ac 89	Th 90	Pa 91	U 92	Np 93	Pu 94	Am 95	Cm 96	Bk 97	Cf 98	Es 99	Fm 100	Md 101	No 102

HAB CAUSATION HYPOTHESES

A. EMIGRATION HYPOTHESIS

1. Ballast Water Vectoring of HAB Species
2. Shellfish Transplant Vectoring

i.e.: geographical range expansion, with bioinvasion

B. CHANGING ENVIRONMENT HYPOTHESES

1. Eutrophication (chemical)
2. Climate Change (physical)
3. Top-Down, Bottom-Up Modification (biological)

I.e.: habitat has changed, or is being modified

C. NATURAL VARIATION HYPOTHESES

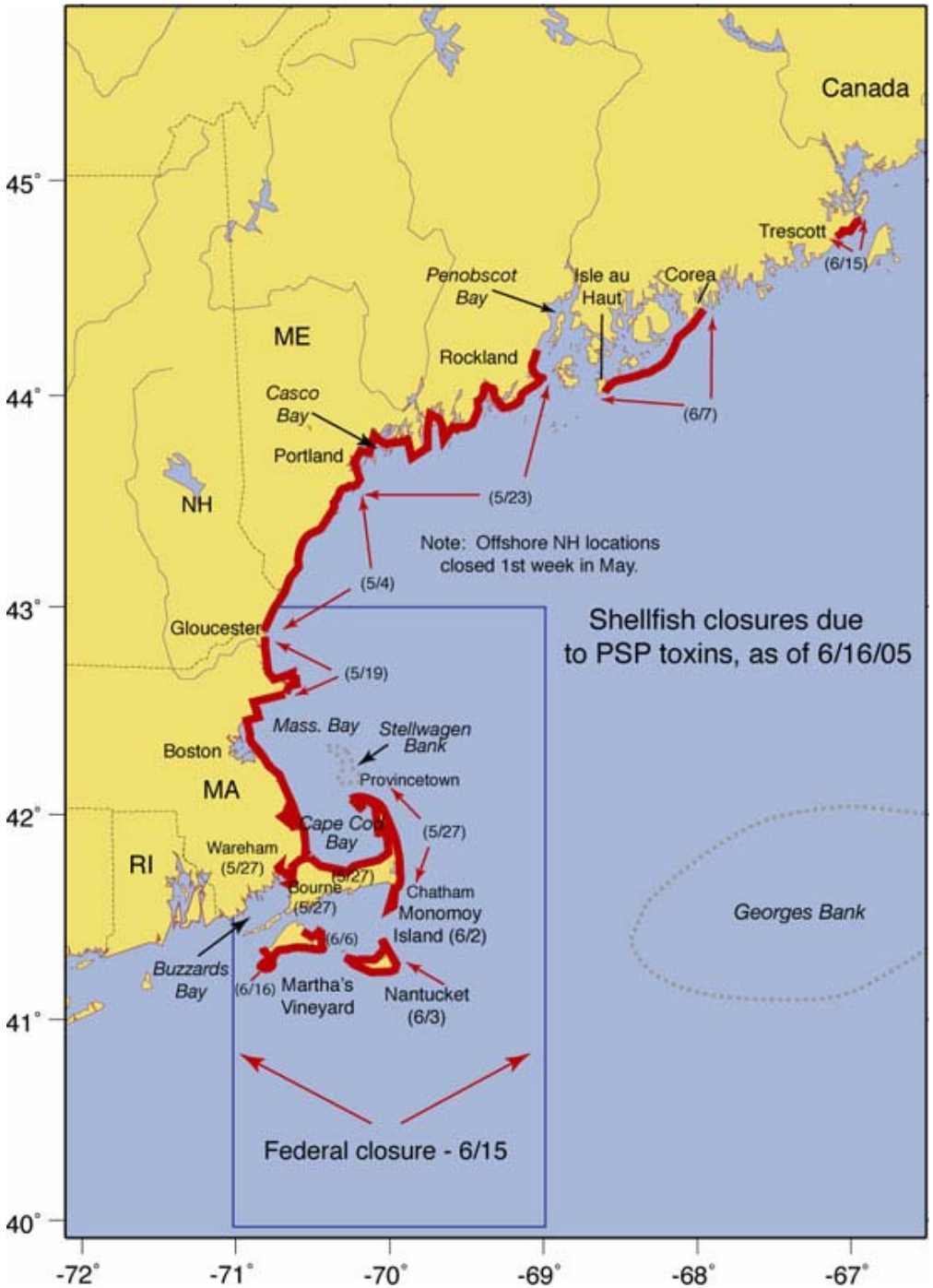
1. Climate-driven (NAO, ENSO) Oscillations
2. Intrinsic Rhythmicity

EXPATRIATION LEADING TO BLOOMS

1. NATURAL EXPATRIATION

a). Alexandrium tamarense/fundyense/catenella
Chrysochromulina polylepis
Karenia brevis
Pyrodinium bahamense var. compressum

b). Latitudinal vs. longitudinal emigration corridors



At the height of the potent 2005 bloom of *Alexandrium fundyense,* coastal resource managers closed shellfish beds from Maine to Martha's Vineyard. This map was compiled from information provided by the Massachusetts Division of Marine Fisheries, the New Hampshire Department of Environmental Services, and the Maine Department of Marine Resources. Individuals should consult local shellfish wardens regarding up-to-date closures. (Don Anderson Laboratory, WHOI). Oceanus, 15 July 2005

EXPATRIATION LEADING TO BLOOMS

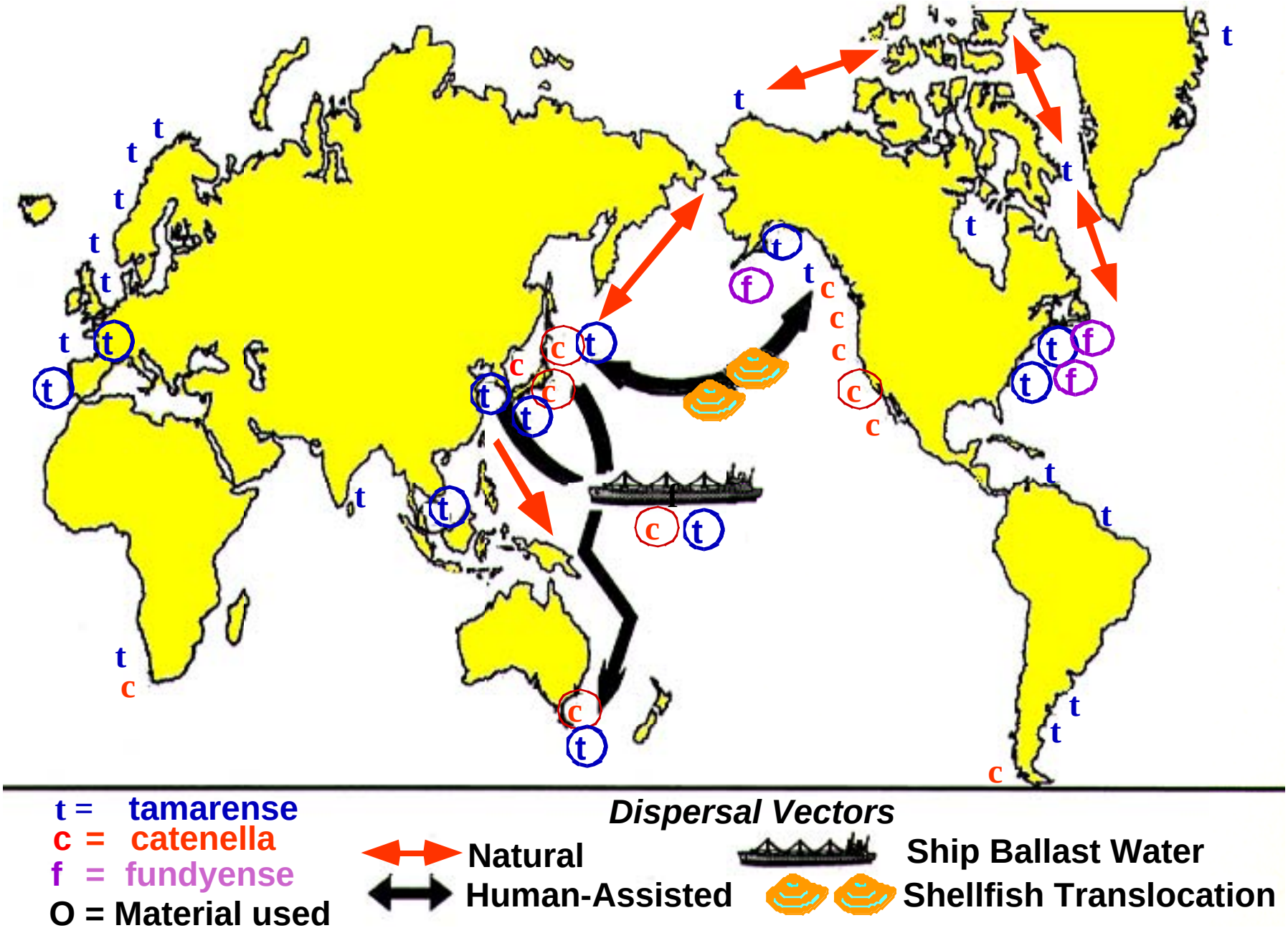
1. NATURAL EXPATRIATION

a). *Alexandrium tamarense/fundyense/catenella*
Chrysochromulina polylepis
Karenia brevis
Pyrodinium bahamense var. compressum

b). *Latitudinal vs. longitudinal emigration corridors*

2. HUMAN ASSISTED EXPATRIATION

a). Ballast water delivery
b). Shellfish transplantation



Miami

Modified from Scholin et al.

EXPATRIATION LEADING TO BLOOMS

1. NATURAL EXPATRIATION

a). *Alexandrium tamarense/fundyense/catenella*
Chrysochromulina polylepis
Karenia brevis
Pyrodinium bahamense var. compressum

b). Latitudinal vs. longitudinal emigration corridors

2. HUMAN ASSISTED EXPATRIATION

a). Ballast water delivery
b). Shellfish transplantation

3. THREE COLONIZATION STAGES

a). Stage I = Colonizing Pioneers
b). Stage II = Persistence
c). Stage III = Community Entry

COLONIZATION STAGE I: COLONIZING PIONEERS

REQUIREMENTS AND HURDLES

- *A 'founder population' must be established*
- *Success dependent on degree of habitat resistance*
- *Habitat resistance = Time to extinction:*

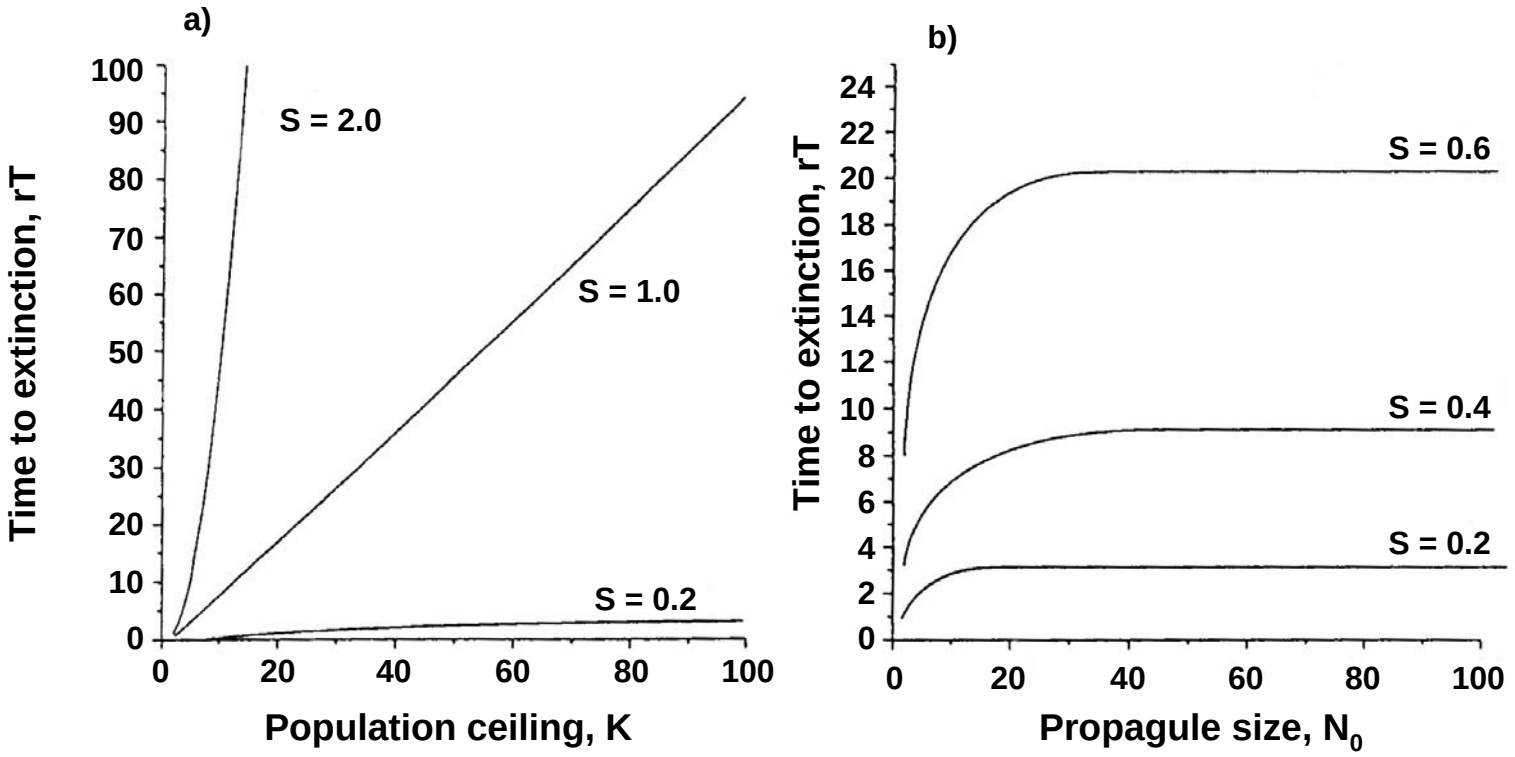
$$T_e = K^S / Sr$$

where K = habitat carrying capacity for colonizing species, and S = ratio (r/v) of the population growth rate (r) to its variance (v), and is a measure of environmental stochasticity

- ***When S large:*** *- habitat stochasticity weak*
  - ratio of growth to variance high
  - population growth promoted
  - T_e increases

- ***When S small:*** *- population growth impeded*
  - T_e decreases

- ***T_e increases:*** *w/ - seed population (inoculum) size (No)*
  - carrying capacity (K)
  - population produced (N)



Relationships between time to metapopulation extinction and population ceiling (a), and between time to extinction and propagule size (b), based on eqn 2.2. In (a) the propagule size (N_0) equals the ceiling (K), in (b) K = 100.

Hanski (1999)

COLONIZATION STAGE II: PERSISTENCE

Stage I colonization achieved:

only when propagules complete species life cycle, and their resting stages, deposited in the local seed bank, germinate to continue colonization. For holoplanktonic species, pelagic survival required; e.g. auto-recruitment vs. repeated seedings.

Stage II problem:

FOUNDER POPULATION MUST ACHIEVE PERSISTENCE

- ***ratio of colonization (c) to extinction rate (e) fundamental***
- ***difference in c - e = rate of population increase***
- ***when e/c ≥ 1, the population becomes extinct***
- ***emigrant population must grow towards stable equilibrium point (P^*) allowing persistence***
- ***Stage II colonization may take years to achieve***
- ***initial and subsequent year-class success no guarantee of successful colonization***
- ***to achieve persistence, niche level barriers must be overcome by colonist***
- ***niche success required if species is to bloom and not remain in its persistence phase***

COLONIZATION STAGE III: COMMUNITY ENTRY

1. INVADER SPECIES MUST INTERACT WITH RESIDENT SPECIES

2. INVASION SUCCESS INFLUENCED BY NICHE SPACE (SIZE) OF RESIDENT SPECIES BEING "ATTACKED"

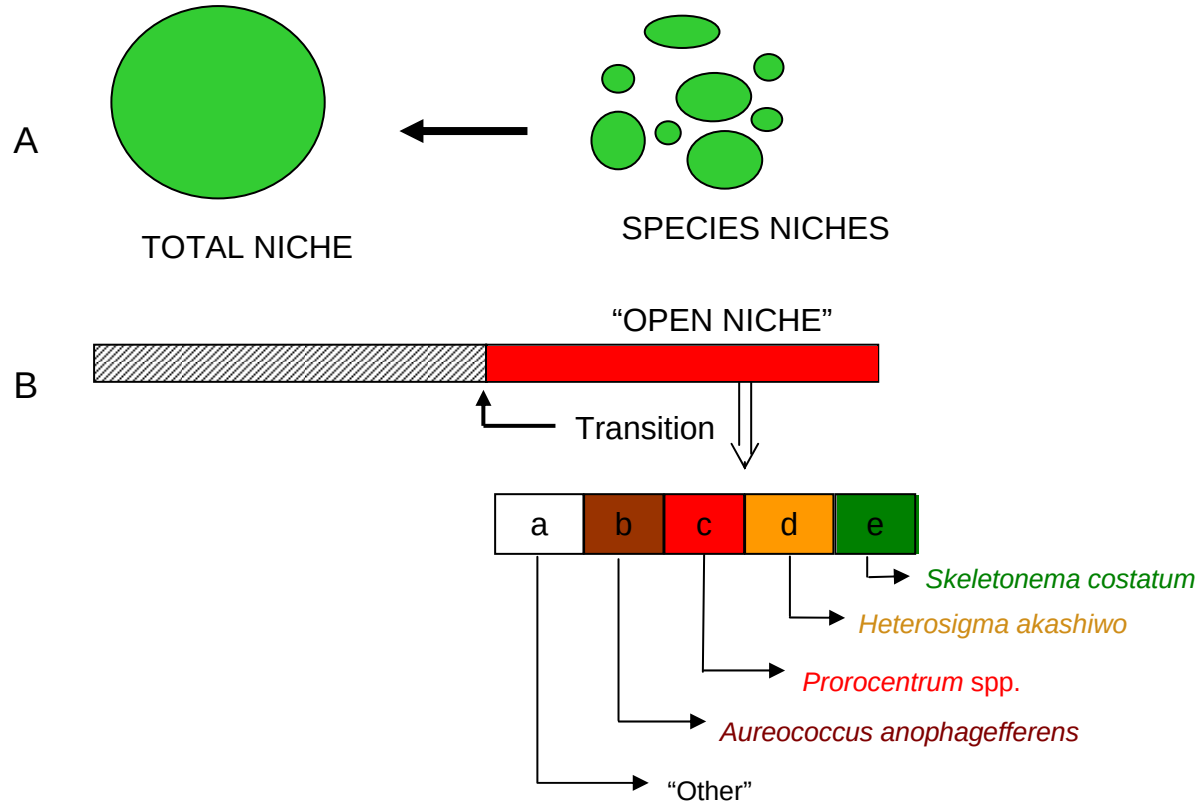
- ***a). Rare species niches***
- ***b). Abundant species niches***
- ***c). Niche preemption***
- ***d). Niche fragmentation***
- ***e). Unused niche space***

3. ATTACKING THE DOMINANT SPECIES

- ***a). Dominance decay***
- ***b). Transition from K- behavior $\Rightarrow$ r- behavior***

4. THE ECOLOGICAL DEMAND

- ***a). To persist: competitive maintenance needed***
- ***b). To bloom: competitive dominance required***



Smayda (unpublished)

PICES

BALLAST WATER AND HABs

1. ***THE CONCEPT***

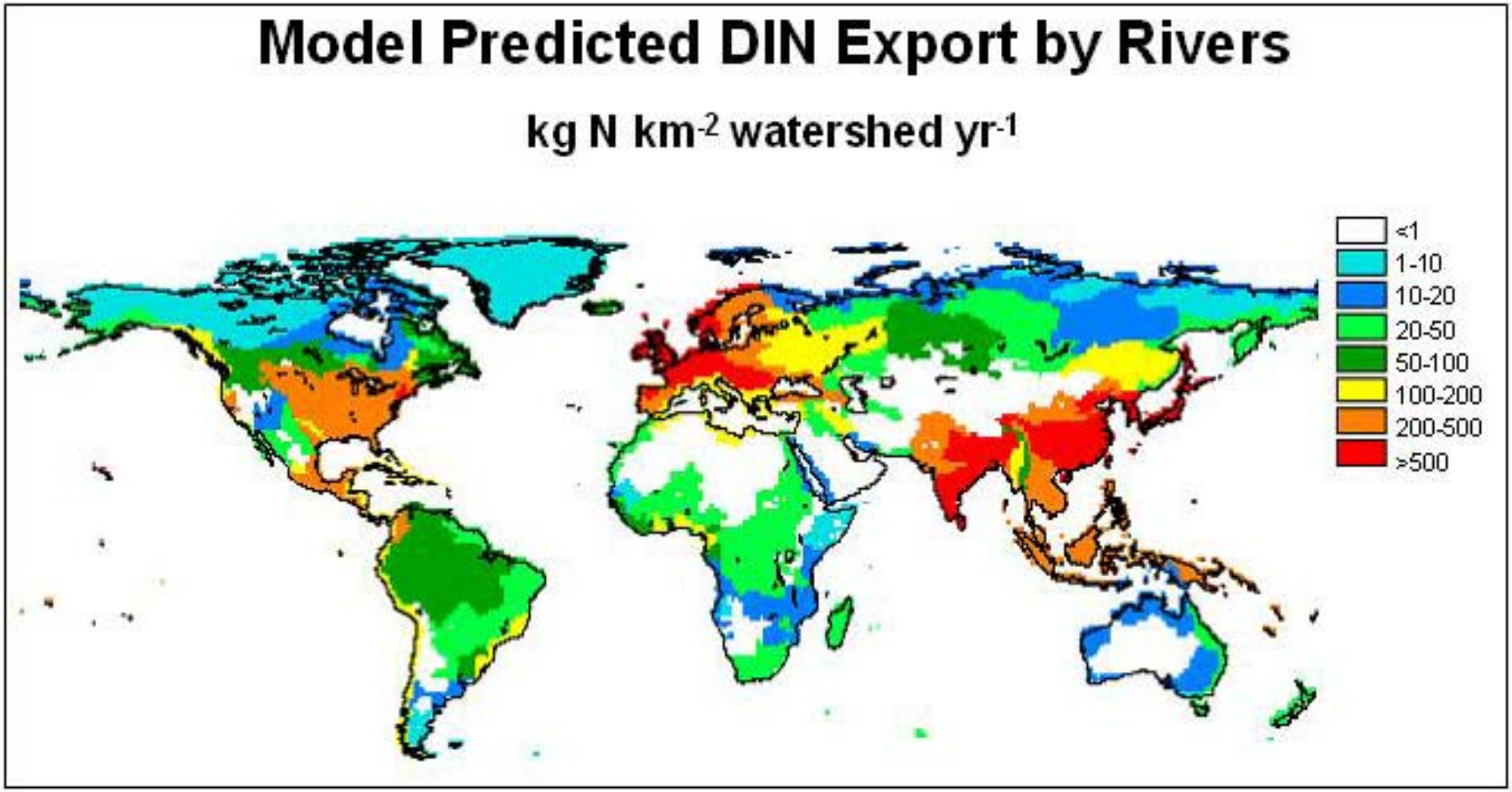
2. ***THE EVIDENCE***

   a). Species
   b). Disjunct geographic distribution
   (metapopulations)
   c). Molecular
   d). Toxin profiles

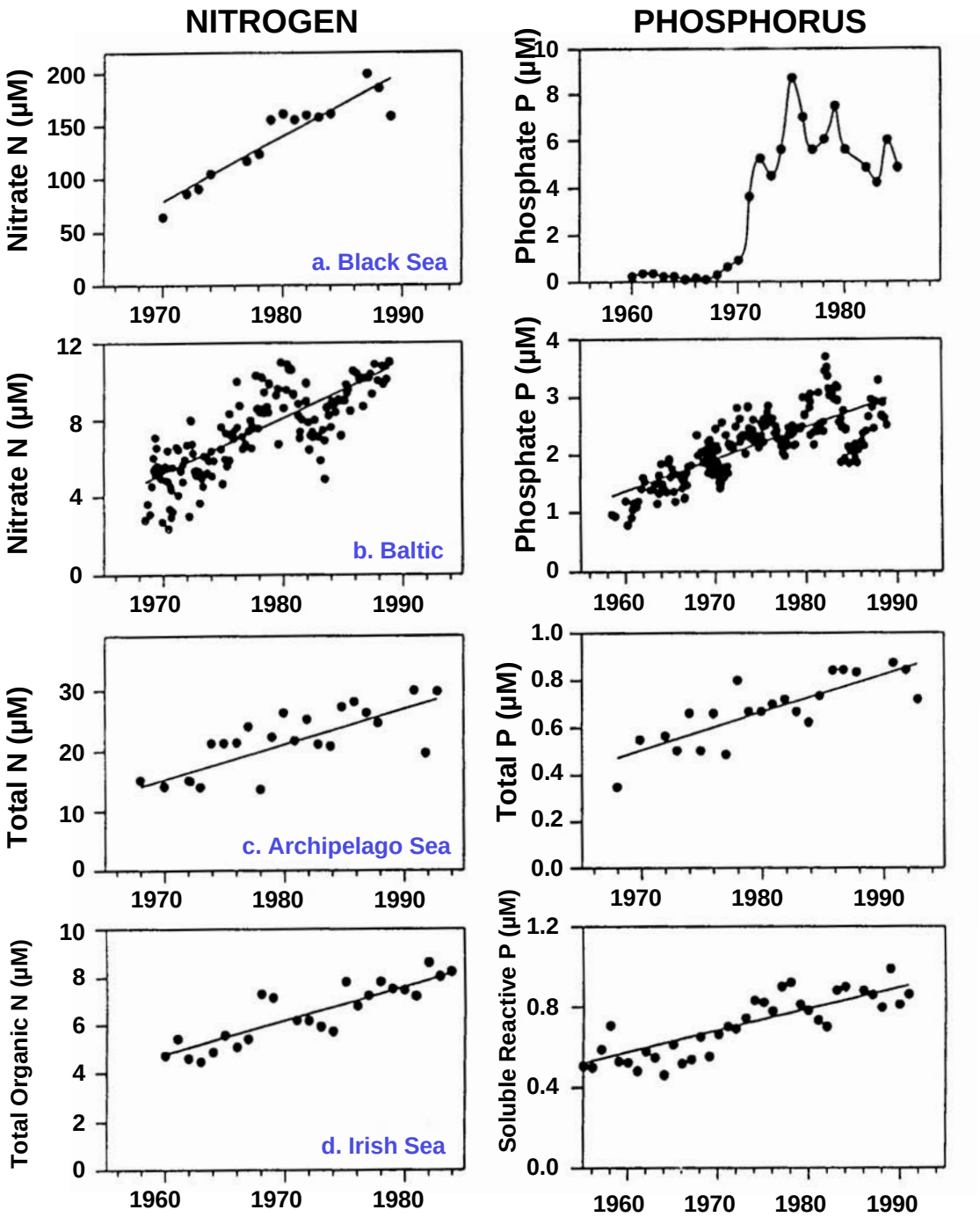
3. ***SOME PROBLEMS***

   a). Hybridization with indigenous population
   b). New taxa discovery vs. evoulutionary rates
   Heterocapsa circularisquama
   Aureococcus anophagefferens
   Aureoumbra lagunensis
   c). Paucity of examples
   d). Cosmopolitanism among species?
   e). Species richness
   "everything is everywhere" **(Finlay, 2002)**

4. ***SUCCESSFUL COLONIZATION ALONE INSUFFICIENT; HABITAT DISTURBANCE MUST OCCUR AT SOME POINT***



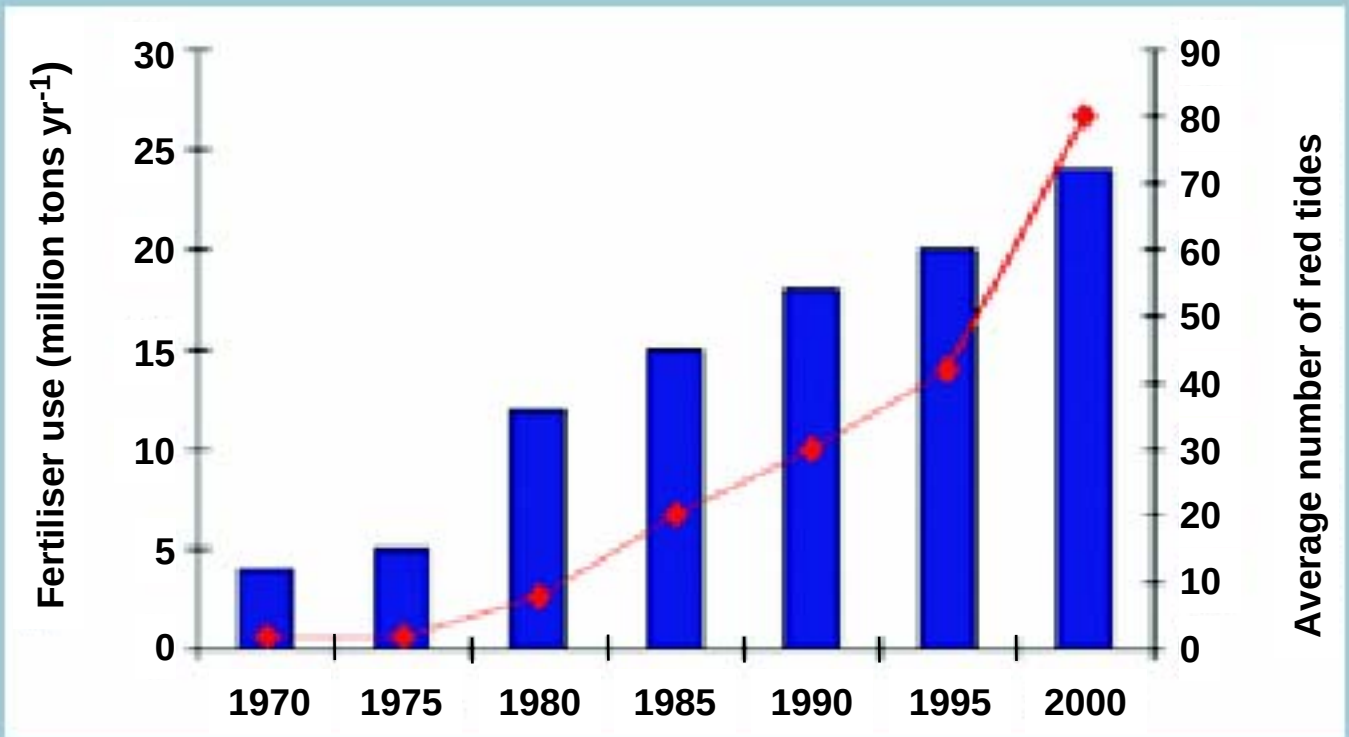
Model-predicted export of dissolved inorganic nitrogen from watersheds to coastal systems (kg N km^{-2} $watershed^{-1}$ $year^{-1}$. (Seitzinger and Kroze, 1998).



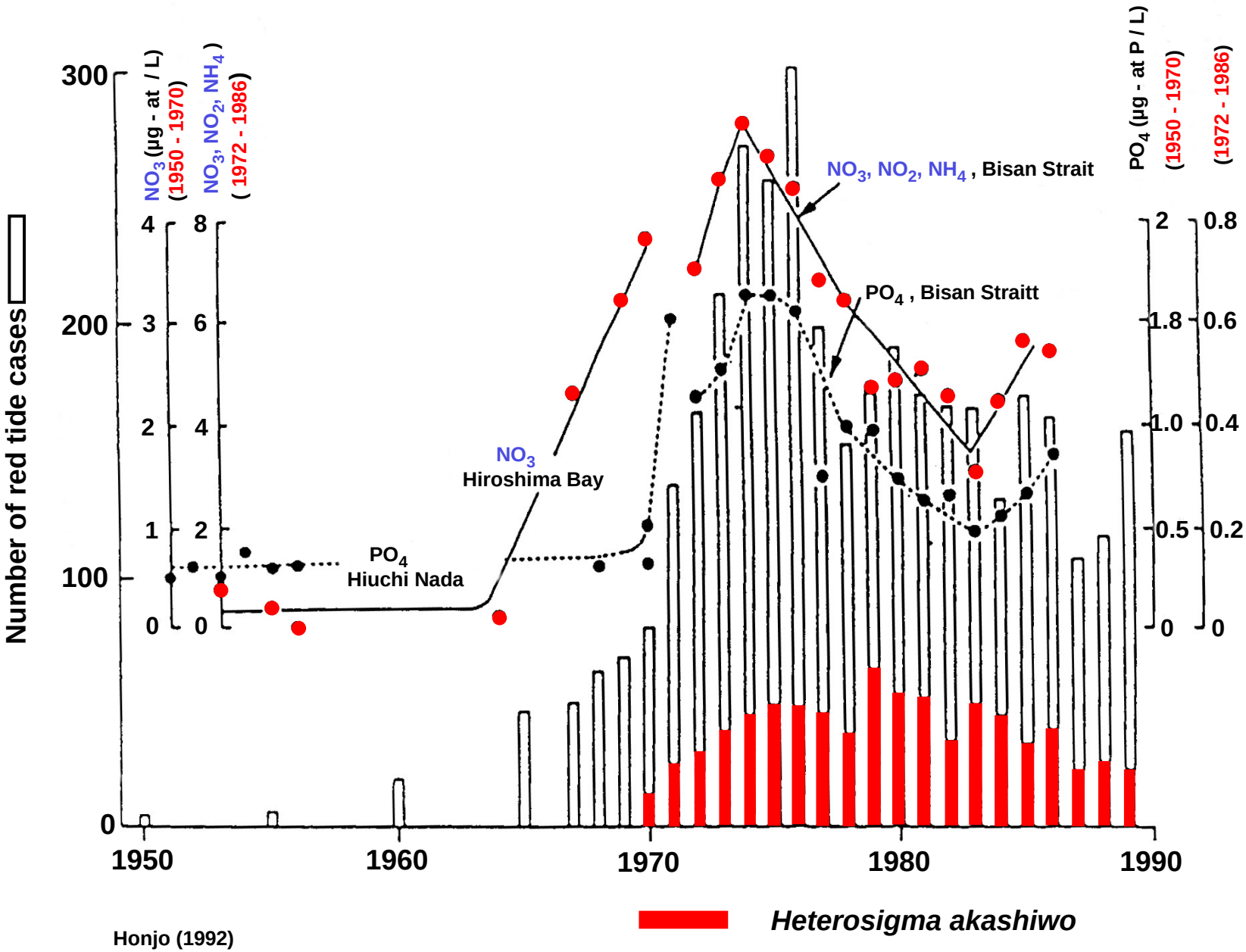
Cloern (2001)

PICES

The average number of harmful blooms (red line), in addition to their areal extent and duration along the east coast of China have escalated in the past two decades coincident with the increasing use of synthetic fertiliser (blue bars).



Redrawn from Anderson et al. 2002 and Zhou 2005.


Number of red tide cases
300
200
100
0
1950
1960
1970
1980
1990
NO3 (μg - at / L)
(1950 - 1970)
NO3, NO2, NH4
(1972 - 1986)
PO4 (μg - at P / L)
(1950 - 1970)
(1972 - 1986)
NO3, NO2, NH4 , Bisan Strait
PO4 , Bisan Straitt
NO3
Hiroshima Bay
PO4
Hiuchi Nada
Heterosigma akashiwo
Honjo (1992)

THE NUTRIENT – HAB PROBLEM

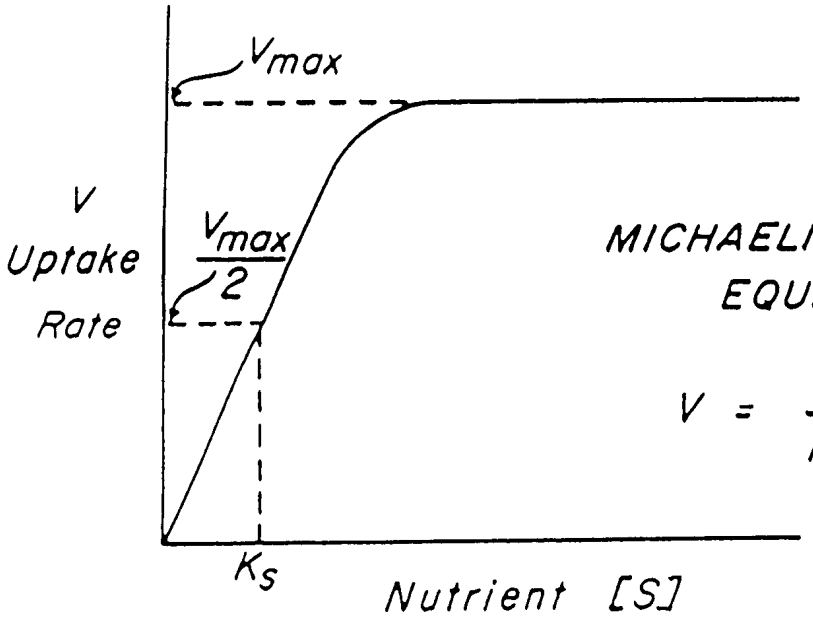
- ***Classical View***

  Dinoflagellates presumed to have low nutrient uptake (K_s) coefficients to allow efficient uptake of nutrients for growth in warm, stratified, nutrient-poor seasons and regions when/where they tend to predominate and often bloom

- ***Experimental Evidence***

  Paradoxically, dinoflagellates and other HAB flagellates lack the expected high affinity for nutrient uptake thought to be essential for their frequent bloom occurrences in nutrient-depleted waters

NUTRIENT UPTAKE KINETICS



MICHAELIS-MENTON EQUATION

$$V = \frac{V_{max}\, S}{K_s + S}$$

Half-saturation Coefficients (K_s) for Nutrient Uptake Reported for Dinoflagellates and Diatoms

Ks	<1.0 *µM*	≥ 1.0 *µM*	≥ 2.0 *µM*	≥ 5.0 *µM*
Dinoflagellates (n = 22)	4 (18%)	18 (82%)	15 (68%)	7 (32%)
Diatoms (n = 28)	12 (43%)	16 (57%)	6 (18%)	2 (7%)

Maximum K_s Coefficients (*µM*):	NH_4	NO_3	PO_4
Dinoflagellates	27	29	6.3
Diatoms	5.5	5.1	1.7

Smayda (1997)

ENIGMA: MANY WATER-DISCOLORING BLOOMS OCCUR DURING PERIODS OF STRIKINGLY LOW NUTRIENTS

- **Exs: *Karenia brevis* (Gulf of Mexico)**

  ***Trichodesmium erythraeum* (tropical coastal; oceanic)**

- **Physical accumulation can be the bloom formation mechanism, operating alone, or together with**
  rapid nutrient recycling rates along with growth at depth
  (in thin layers or as migratory populations),
  followed by displacement to near-surface
  during local or far-field transport, or
  vertical migration and bloom display:

  a. *Prorocentrum minimum* (Chesapeake Bay)

  b. *Karenia mikimotoi* (North Sea)

- **Blooms in oligotrophic waters can also result from slow growth, repressed grazing, or reduced inter-specific competition operative over an extended period:**

  a. *Aureococcus anophagefferens* (= brown tide)

- **MAXIM: BLOOMS ARE BLOOMS !**

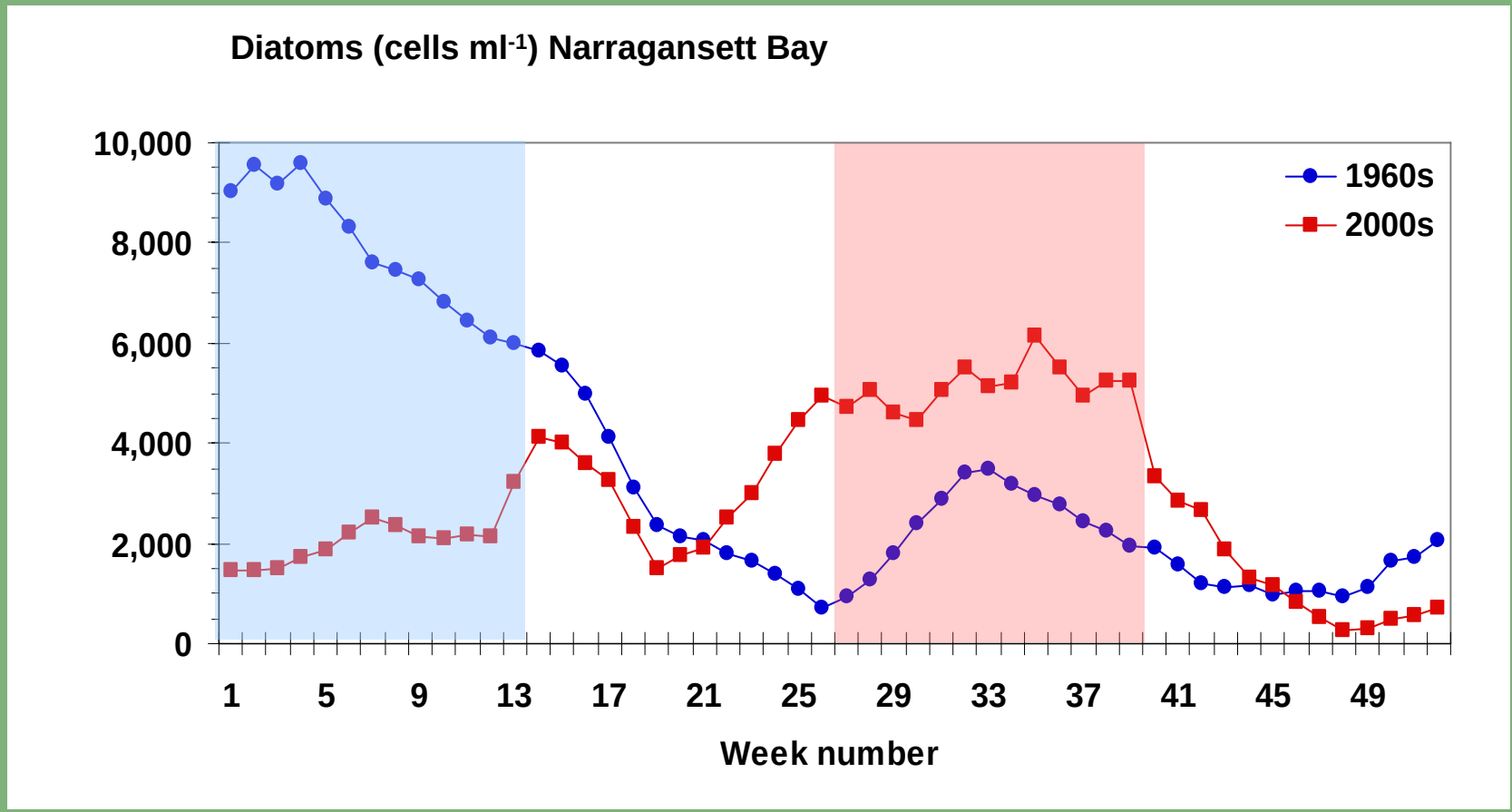
  they need nutrients to occur;

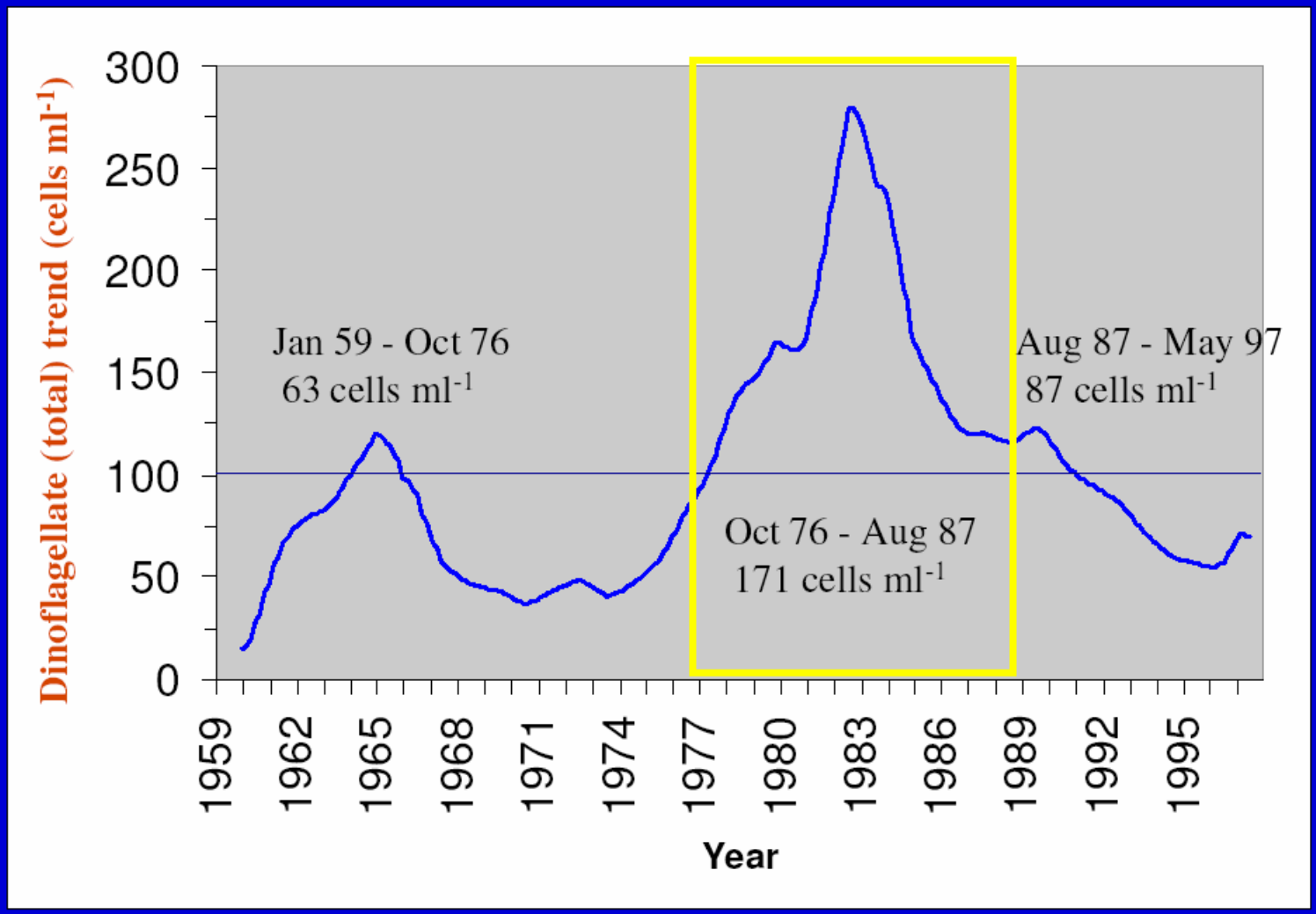
  where concentrated by physical mechanisms,

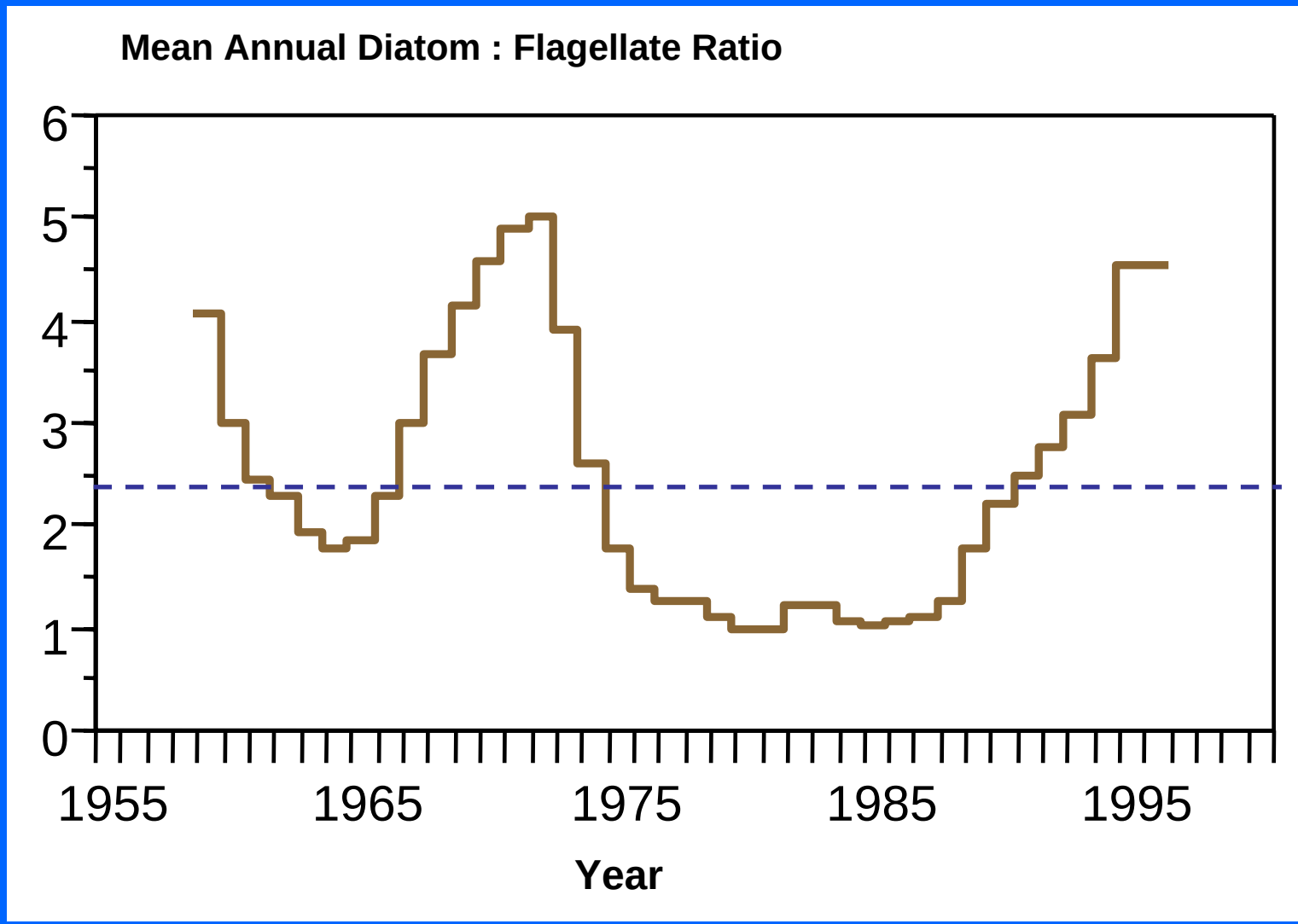
  their aggregation exaggerates their growth rate

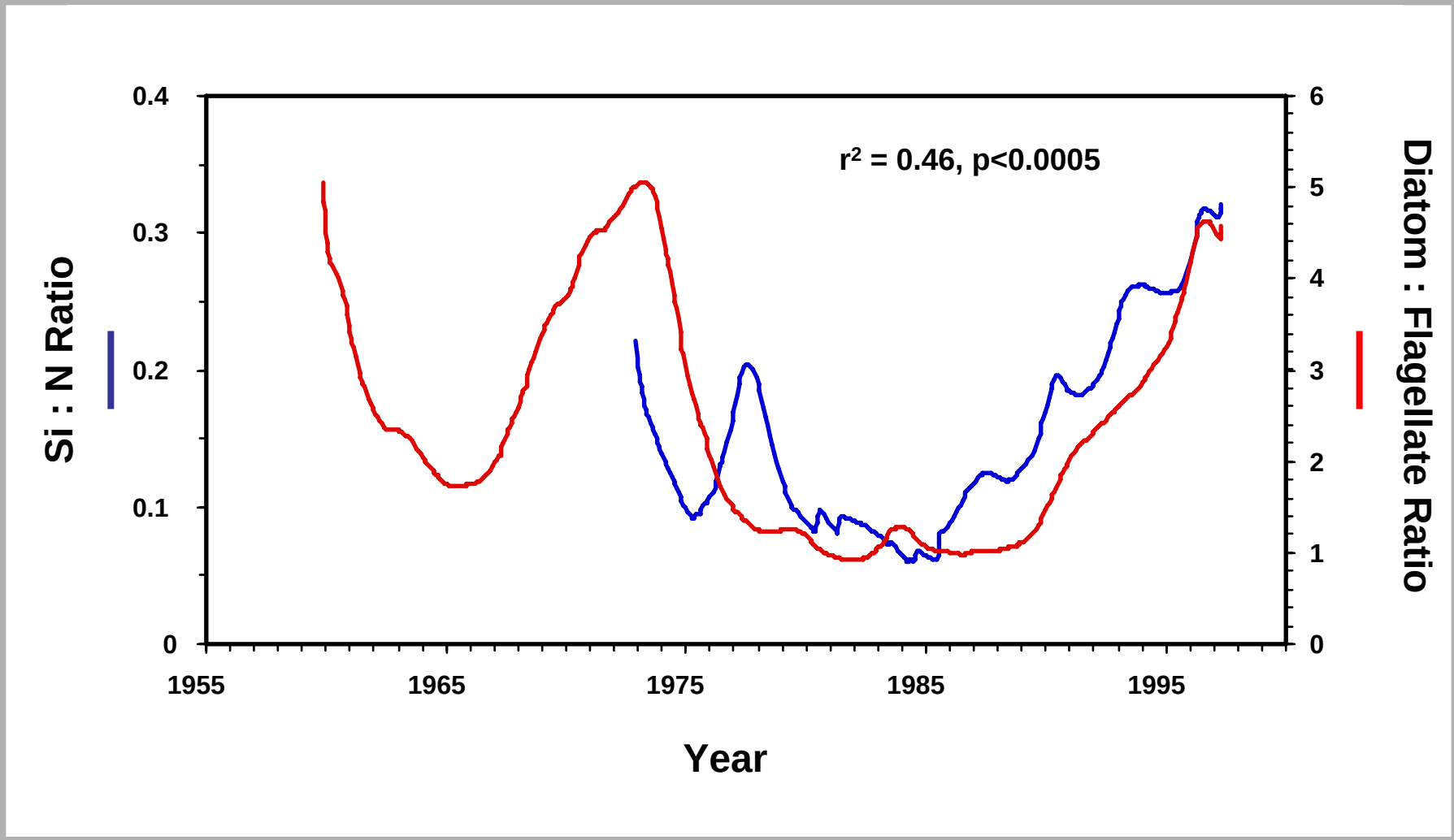
  and

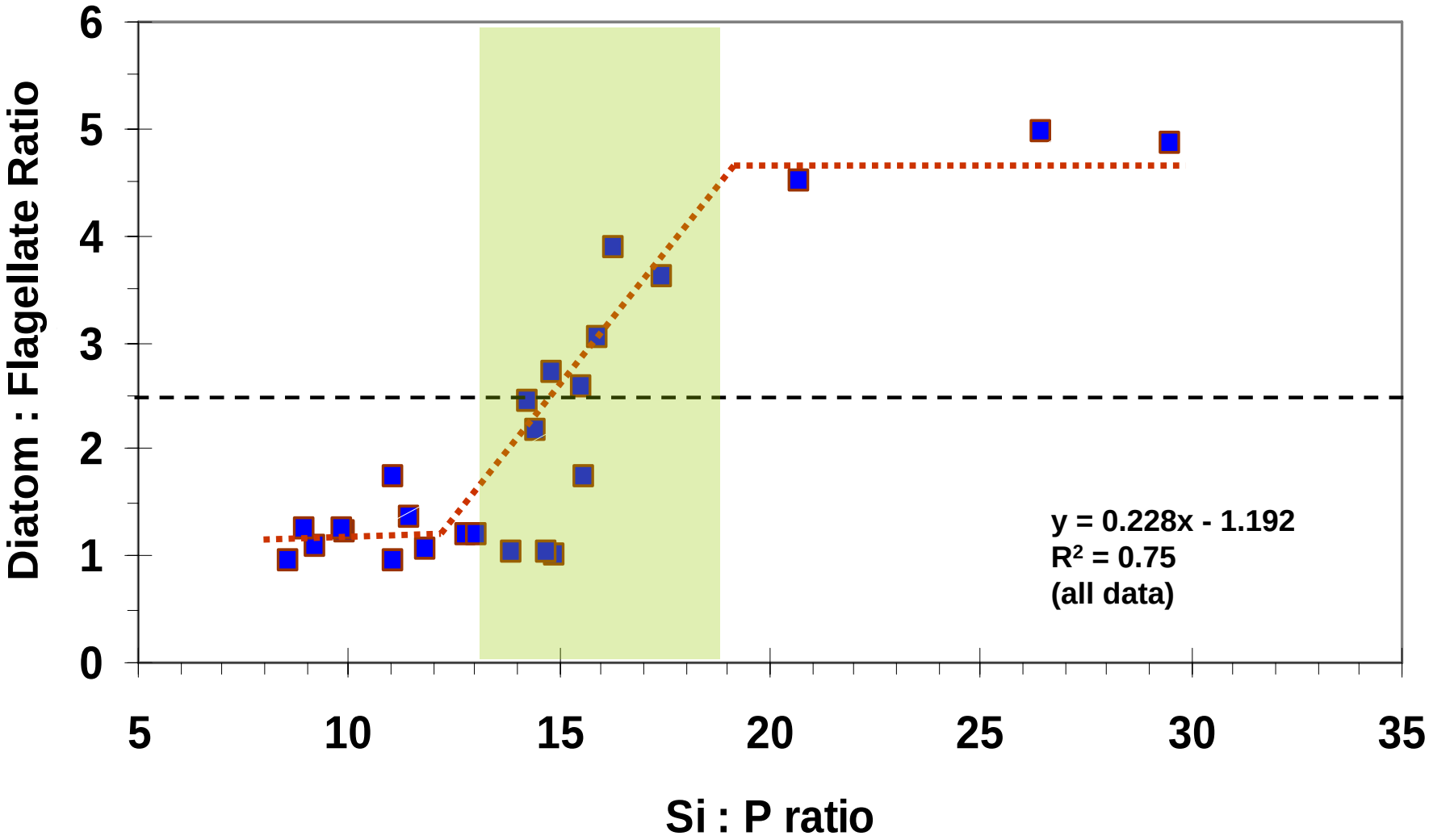
  masks the nutrient-growth-bloom relationship


Diatoms (cells ml-1) Narragansett Bay
10,000
8,000
6,000
4,000
2,000
0
1
5
9
13
17
21
25
29
33
37
41
45
49
Week number
1960s
2000s

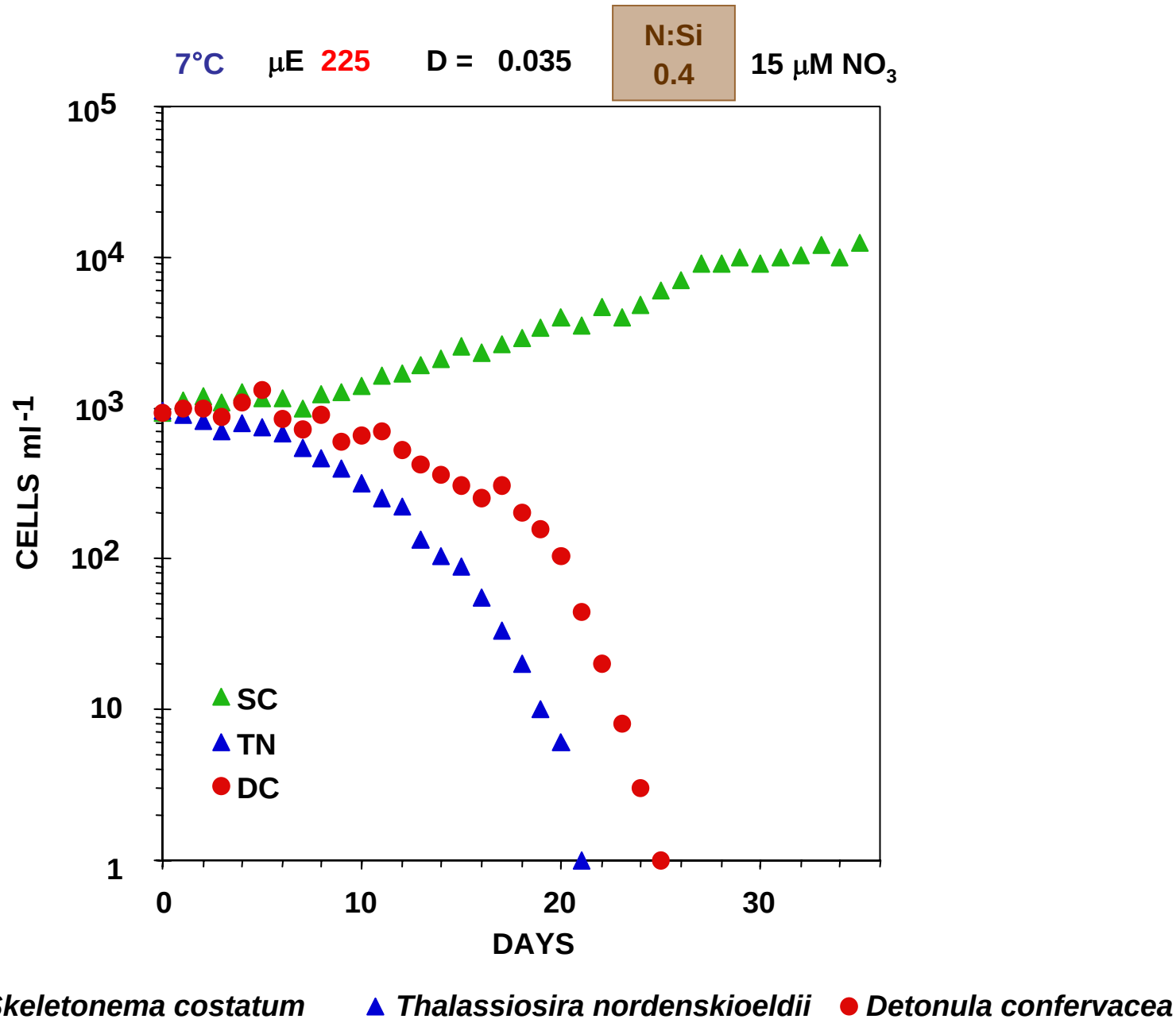

Dinoflagellate (total) trend (cells ml-1)
300
250
200
150
100
50
0
Jan 59 - Oct 76
63 cells ml-1
Oct 76 - Aug 87
171 cells ml-1
Aug 87 - May 97
87 cells ml-1
1959
1962
1965
1968
1971
1974
1977
1980
1983
1986
1989
1992
1995
Year


Mean Annual Diatom : Flagellate Ratio
6
5
4
3
2
1
0
1955
1965
1975
1985
1995
Year

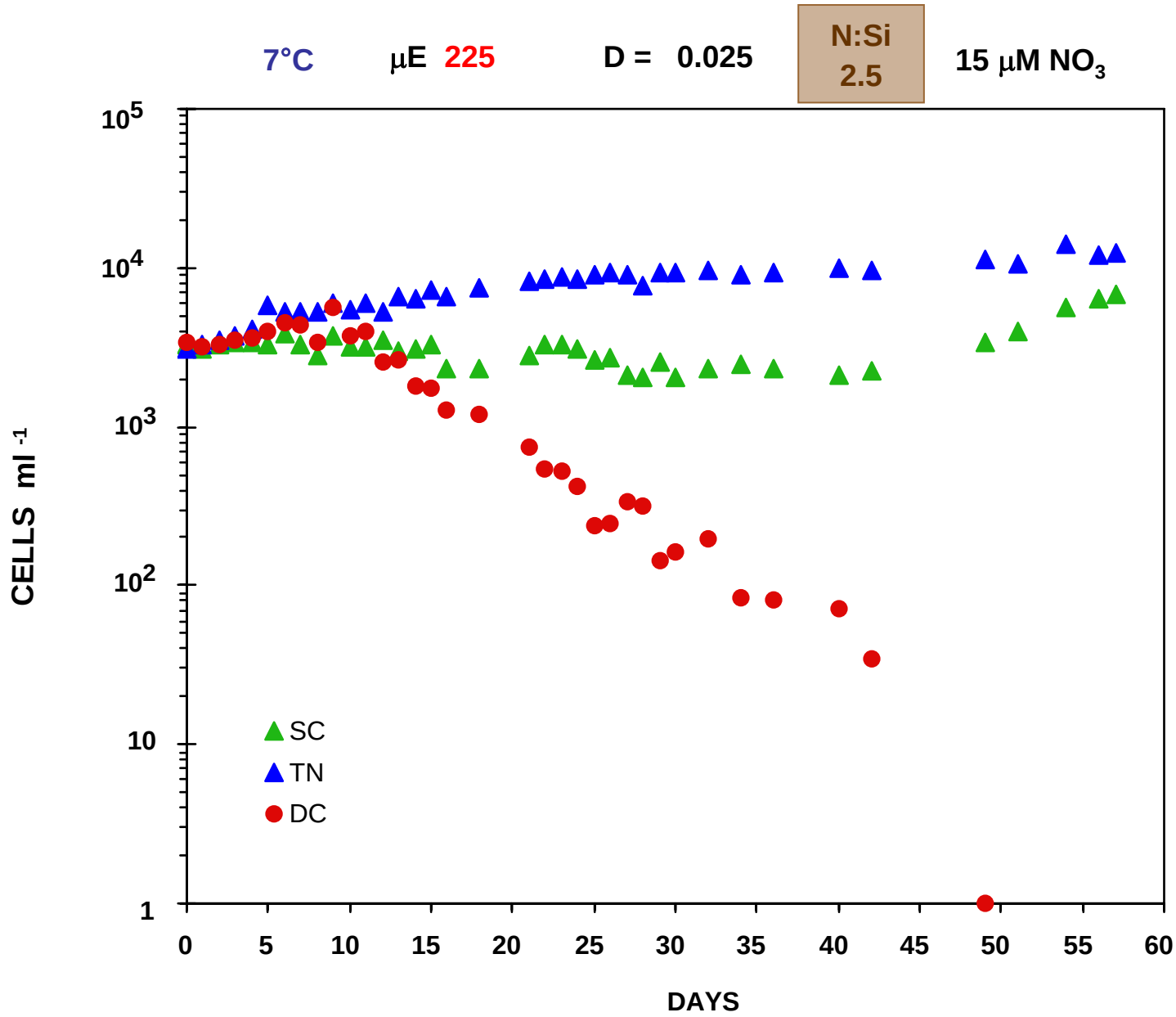

0.4
0.3
0.2
0.1
0
6
5
4
3
2
1
0
1955
1965
1975
1985
1995
Year
Si : N Ratio
Diatom : Flagellate Ratio
r² = 0.46, p<0.0005



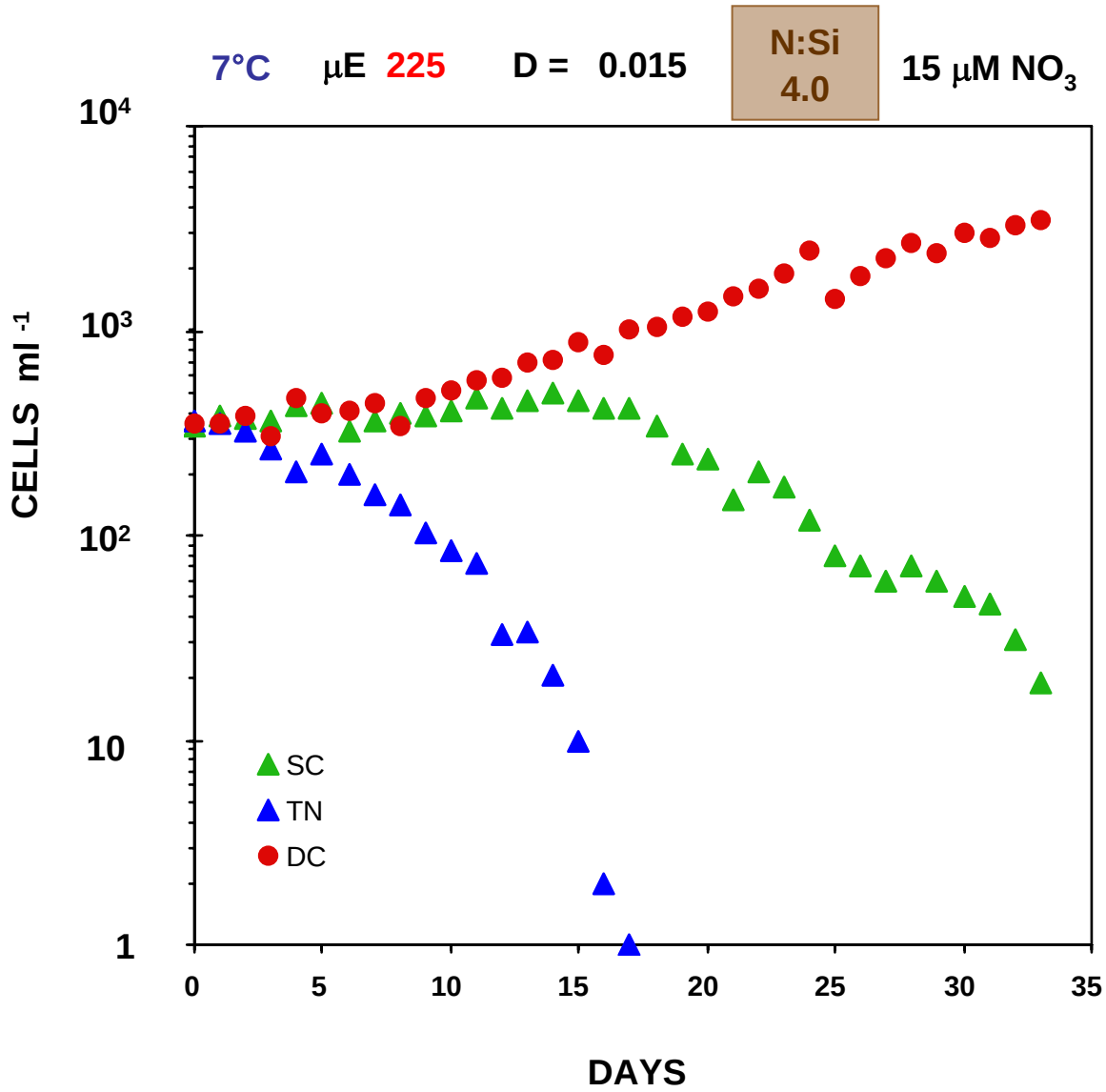
Station II, Narragansett Bay


7°C
µE 225
D = 0.035
N:Si
0.4
15 µM NO3
CELLS ml-1
10^5
10^4
10^3
10^2
10
1
0
10
20
30
DAYS
SC
TN
DC
▲ Skeletonema costatum
▲ Thalassiosira nordenskioeldii
● Detonula confervacea

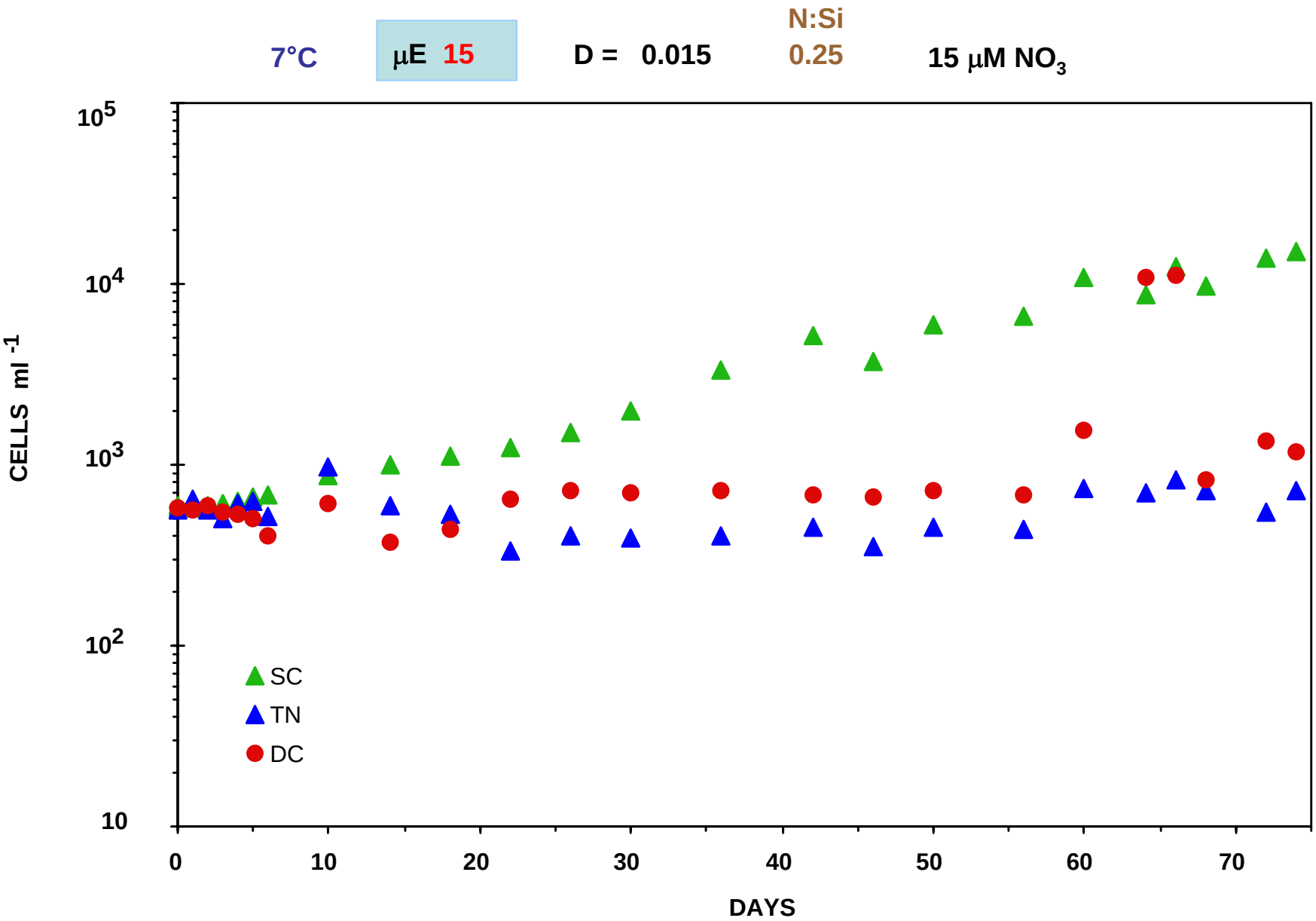
Miami


7°C
μE 225
D = 0.025
N:Si
2.5
15 μM NO3
CELLS ml -1
10^5
10^4
10^3
10^2
10
1
0
5
10
15
20
25
30
35
40
45
50
55
60
DAYS
SC
TN
DC

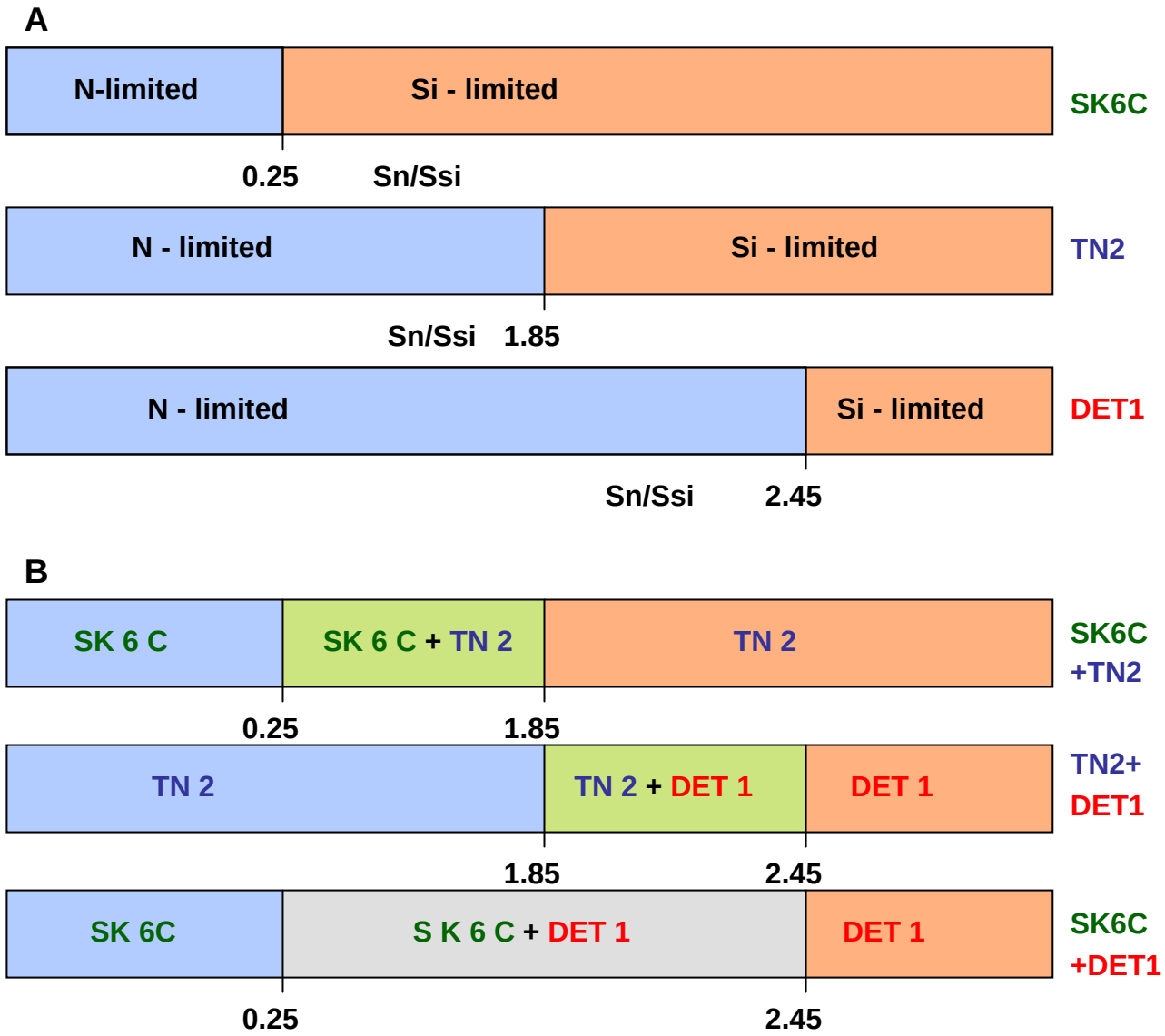
Miami


7°C
µE 225
D = 0.015
N:Si
4.0
15 µM NO3
CELLS ml -1
10⁴
10³
10²
10
1
0
5
10
15
20
25
30
35
DAYS
SC
TN
DC

Miami


7°C
µE 15
D = 0.015
N:Si
0.25
15 µM NO3
CELLS ml -1
10^5
10^4
10^3
10^2
10
SC
TN
DC
0
10
20
30
40
50
60
70
DAYS

Miami


A
N-limited
Si - limited
SK6C
0.25
Sn/Ssi
N - limited
Si - limited
TN2
Sn/Ssi
1.85
N - limited
Si - limited
DET1
Sn/Ssi
2.45
B
SK 6 C
SK 6 C + TN 2
TN 2
SK6C
+TN2
0.25
1.85
TN 2
TN 2 + DET 1
DET 1
TN2+
DET1
1.85
2.45
SK 6C
S K 6 C + DET 1
DET 1
SK6C
+DET1
0.25
2.45

HABs, RED TIDES and NUTRIENT RATIOS
Conceptual, Field, Experimental Issues

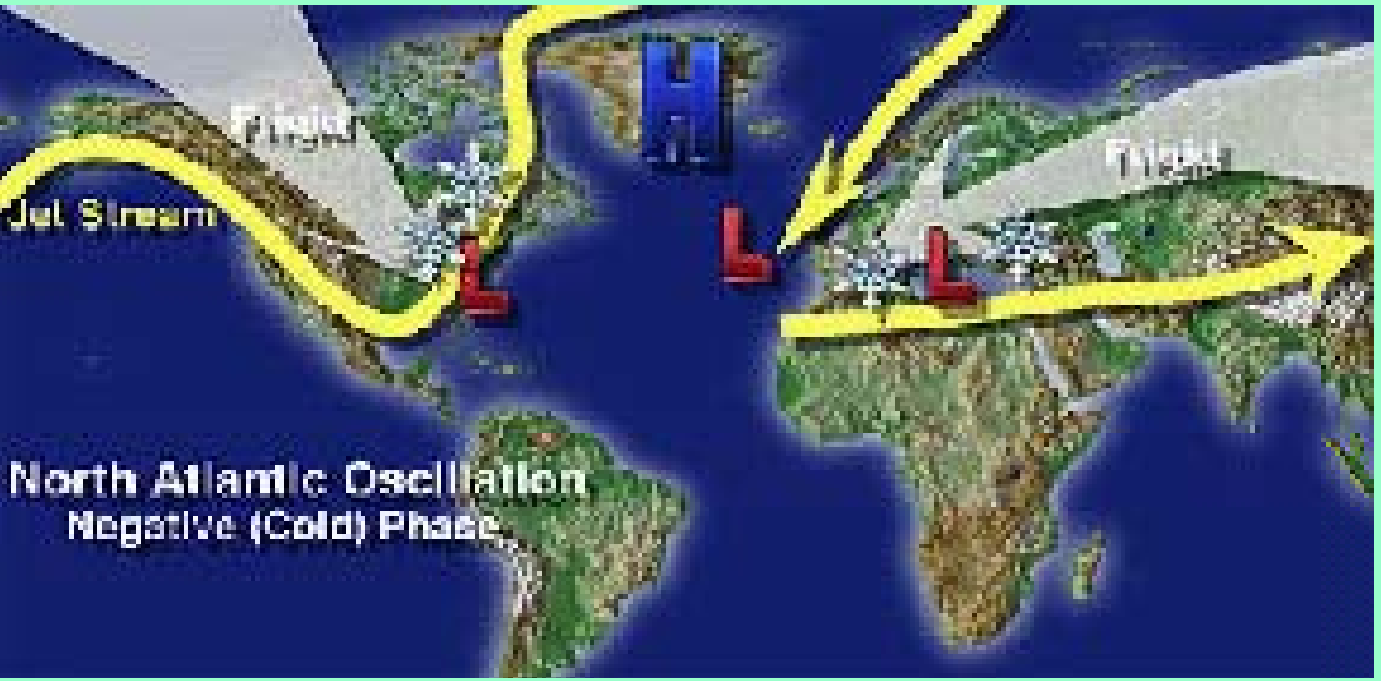
- ***Nutrient ratios are community structuring elements, not the cause of blooms; it is the concentrations of nutrients, not their proportions that determine a species' abundance***
- ***The primary influence of nutrient ratios is on functional group selection, not bloom stimulation of individual species within that functional group***
- ***The response to nutrients and their ratios is a whole system process***

HABs, RED TIDES and NUTRIENT RATIOS
Conceptual, Field, Experimental Issues

- ***Long-term time series data are essential to establish whether locally observed flagellate bloom patterns are nutrient-related events rather than displays of the intrinsic variability and stochasticity of their blooms, or attributable to other (physical, biotic) factors***

- ***Laboratory, field and modeling approaches must be ecologically relevant, of appropriate methodology and experimental design, and apply sound ecological theory to evaluate the nutrient ratio hypothesis***

North Atlantic Oscillation (NAO)

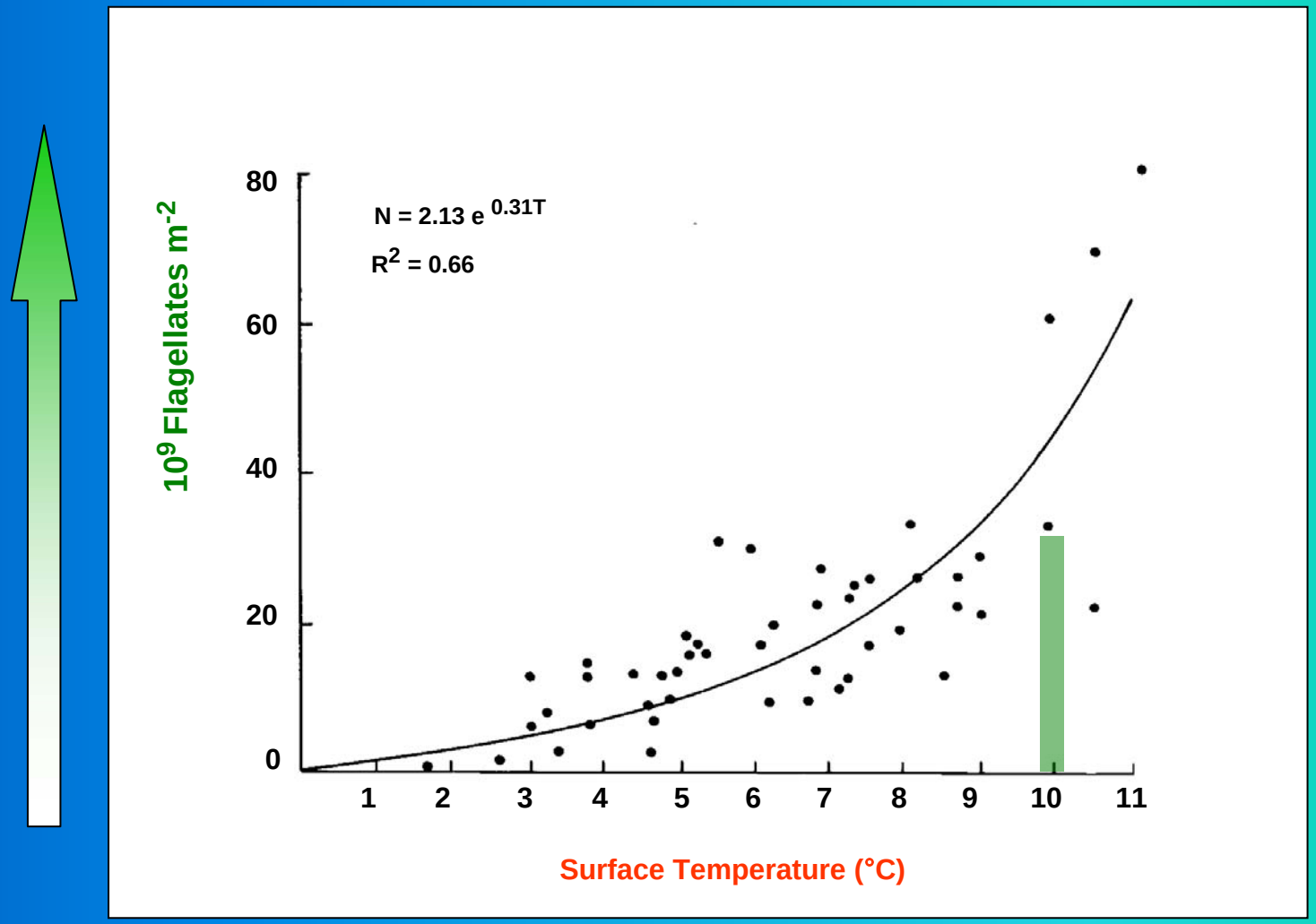


An index of 500mb (ca. 18,000 feet altitude) height and surface pressure over the North Atlantic.

Positive (warm) phase = low pressure Greenland, high pressure Azores
NBay = Warm Winter

Negative (cold) phase = high pressure Greenland, low pressure Azores
NBay = Cold Winter

Image credit: J. D'Aleo



Modified from Levasseur et al. (1984)

TENTATIVE CONCLUSION 1

- *"COOL WATER" HAB FLAGELLATES, i.e. THOSE THAT TOLERATE AND CAN GROW AT ca. 5° TO 15°C PREDOMINATE IN LIFE FORM TYPES I TO III.*
- *THESE LIFE FORMS GENERALLY HAVE MUTED OR NO TOXIC EFFECTS.*
- *WHEN TOXIC, THEY TEND TO BE ICHTHYOTOXIC.*
- *EXAMPLES:*
  Karlodinium veneficum
  Prymnesium parvum

TENTATIVE CONCLUSION 2

- *THE MIXING - DRIFT DINOFLAGELLATE SPECIES, i.e. LIFE FORMS IV, V, VI, GENERALLY EXHIBIT POOR OR NO GROWTH BELOW 15°C, AND ARE HARMFUL.*
- *EXAMPLES:*
  Pyrodinium bahamense var. compressum
  Gymnodinium catenatum
  Lingulodinium polyedrum
  Karenia mikimotoi
  Karenia brevis

CONCLUSION

- ***ALEXANDRIUM*** **SPECIES GENERALLY HAVE OPTIMAL GROWTH TEMPERATURES > 15°C,**
- **THEY GROW POORLY OR ARE INTOLERANT OF TEMPERATURES BELOW 15°C.**
- **EXAMPLES:**

  Alexandrium affine

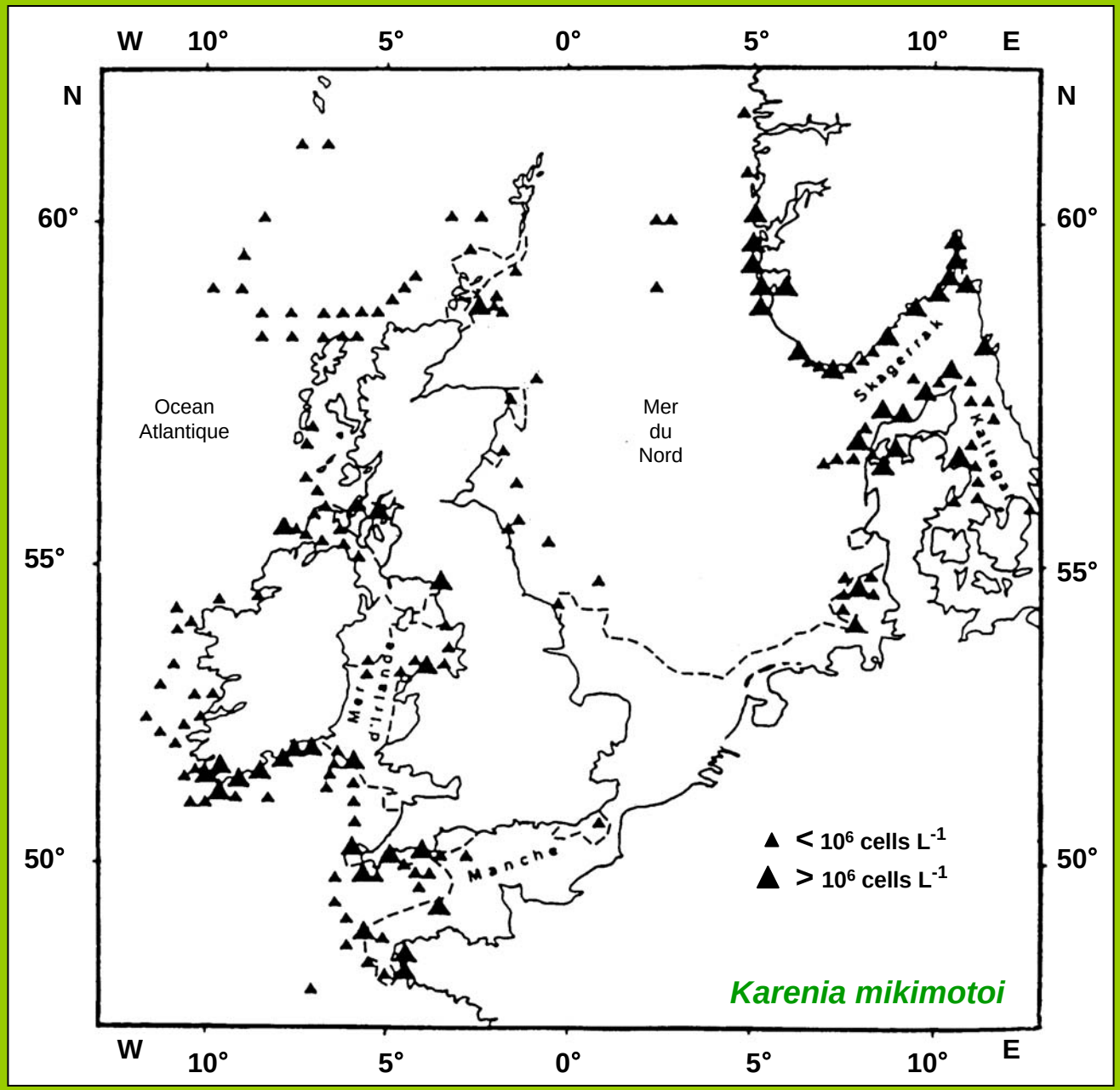
  Alexandrium minutum

  Alexandrium monilatum

  Alexandrium ostenfeldii

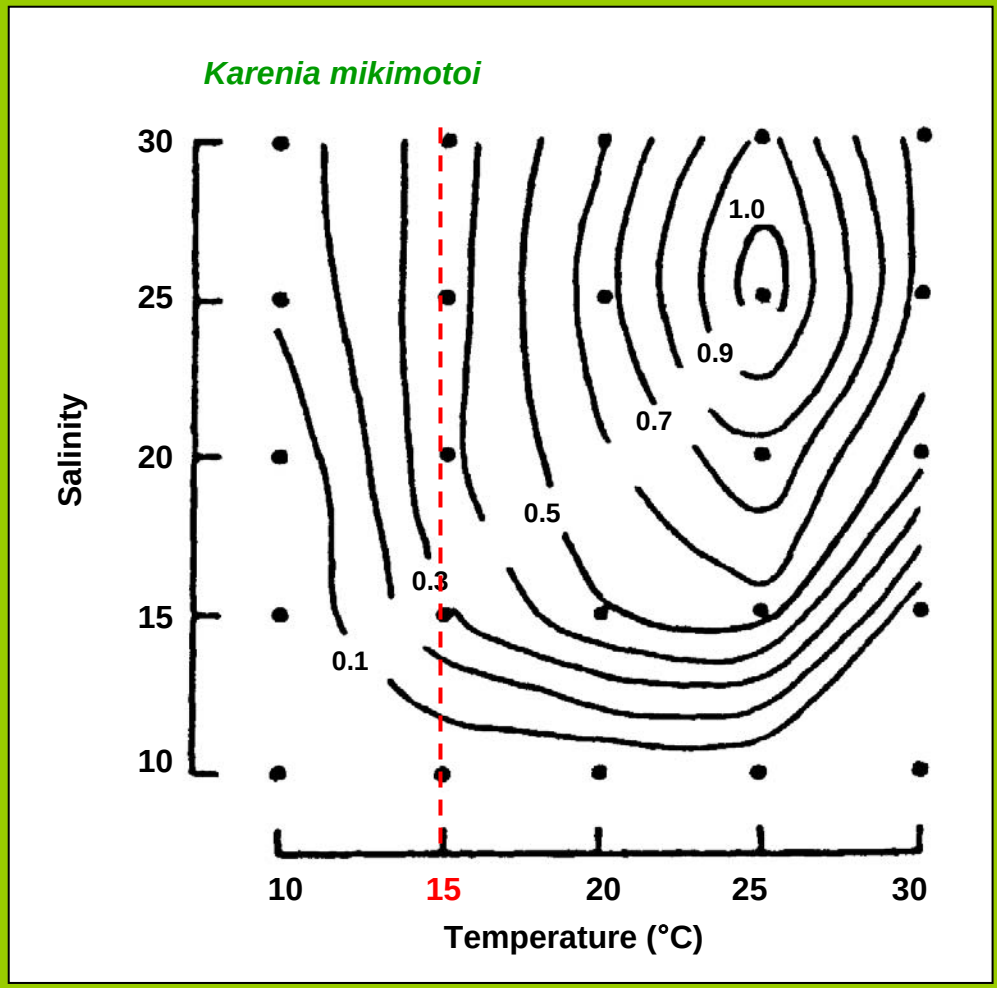
  Alexandrium tamiyavanichii

- ***Alexandrium tamarense*** **IS AN EXCEPTION TO THIS GENERALIZATION. IT BRIDGES THE HABITAT BEHAVIOR AND TEMPERATURE RESPONSES OF LIFE FORMS II AND IV**



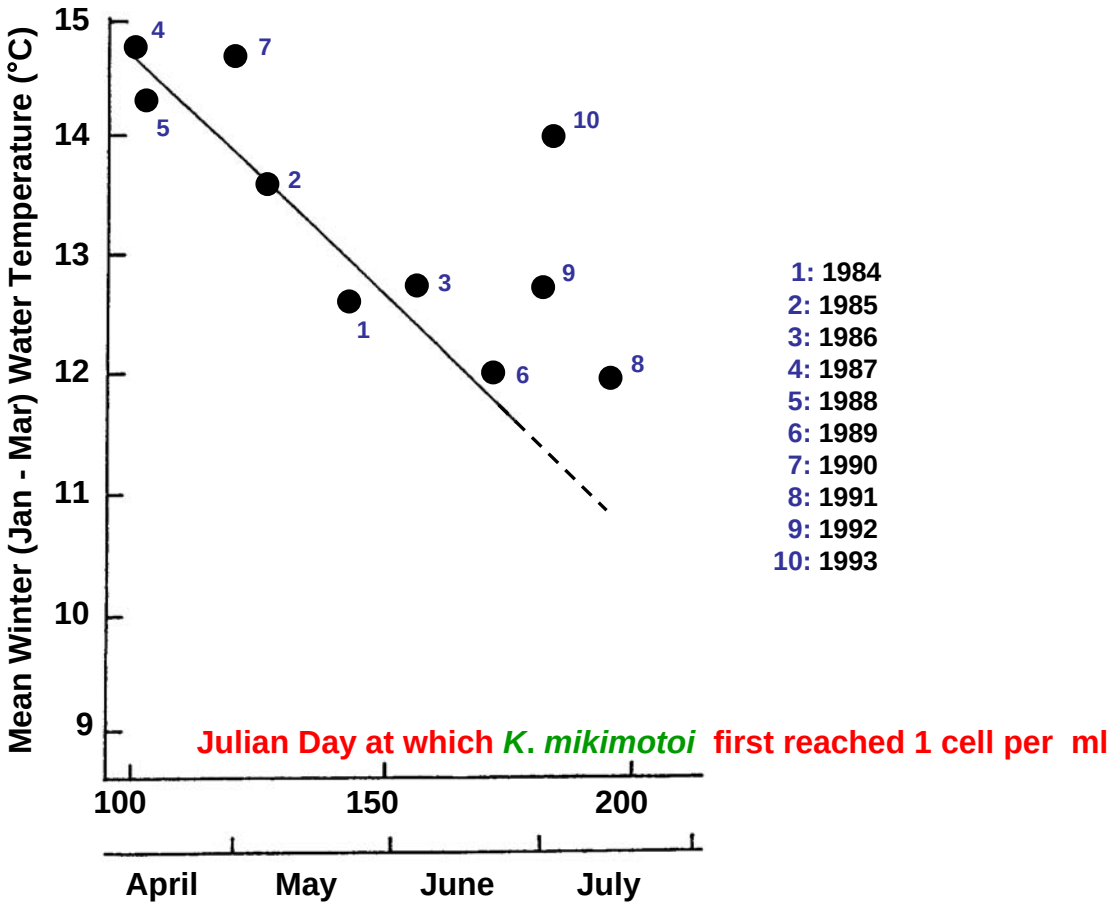
Tireté : Position moyenne des fronts de marée selon Pingree & Griffiths (1978)

Partensky & Sournia (1986)

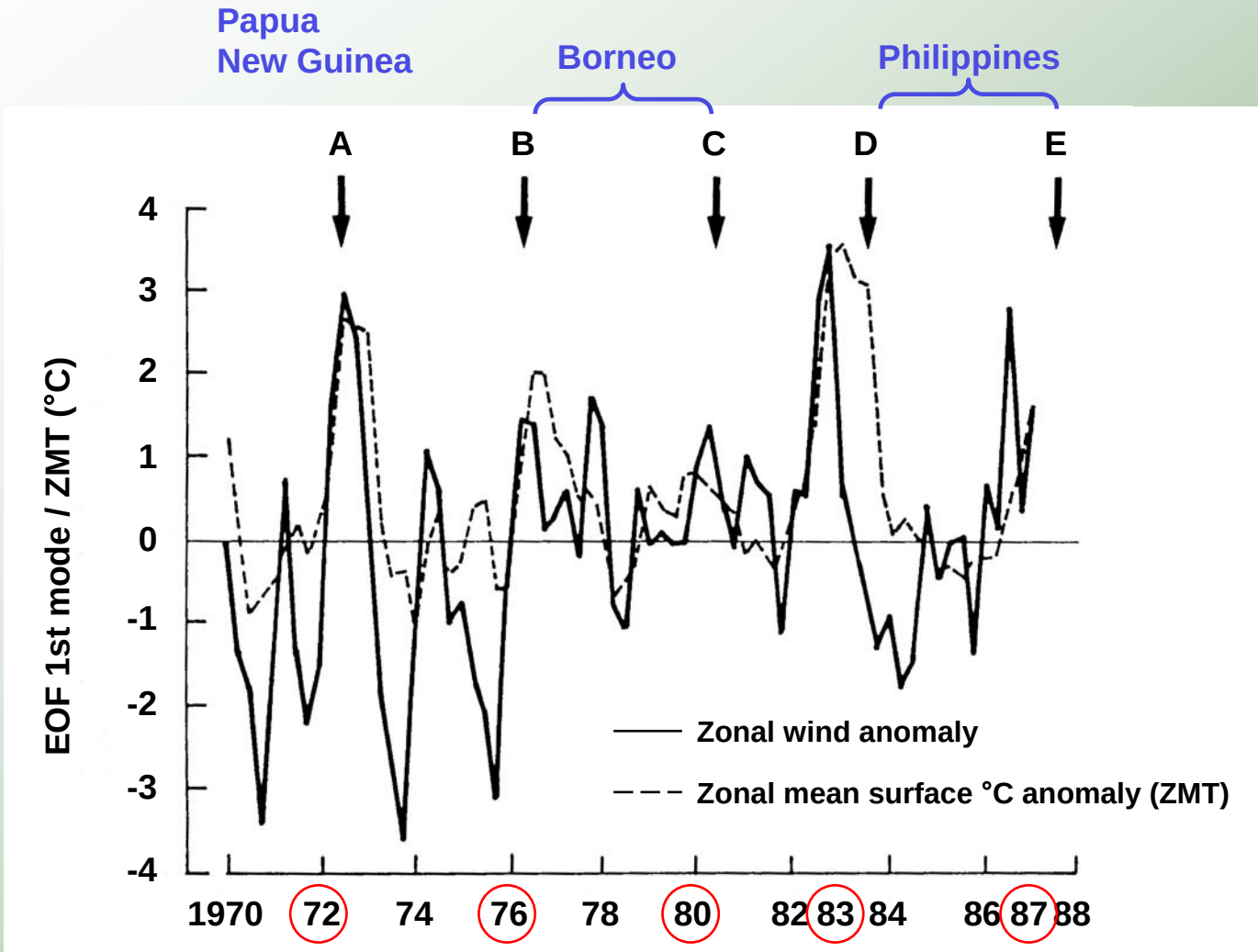


Yamaguchi & Honjo (1989)

Karenia mikimotoi



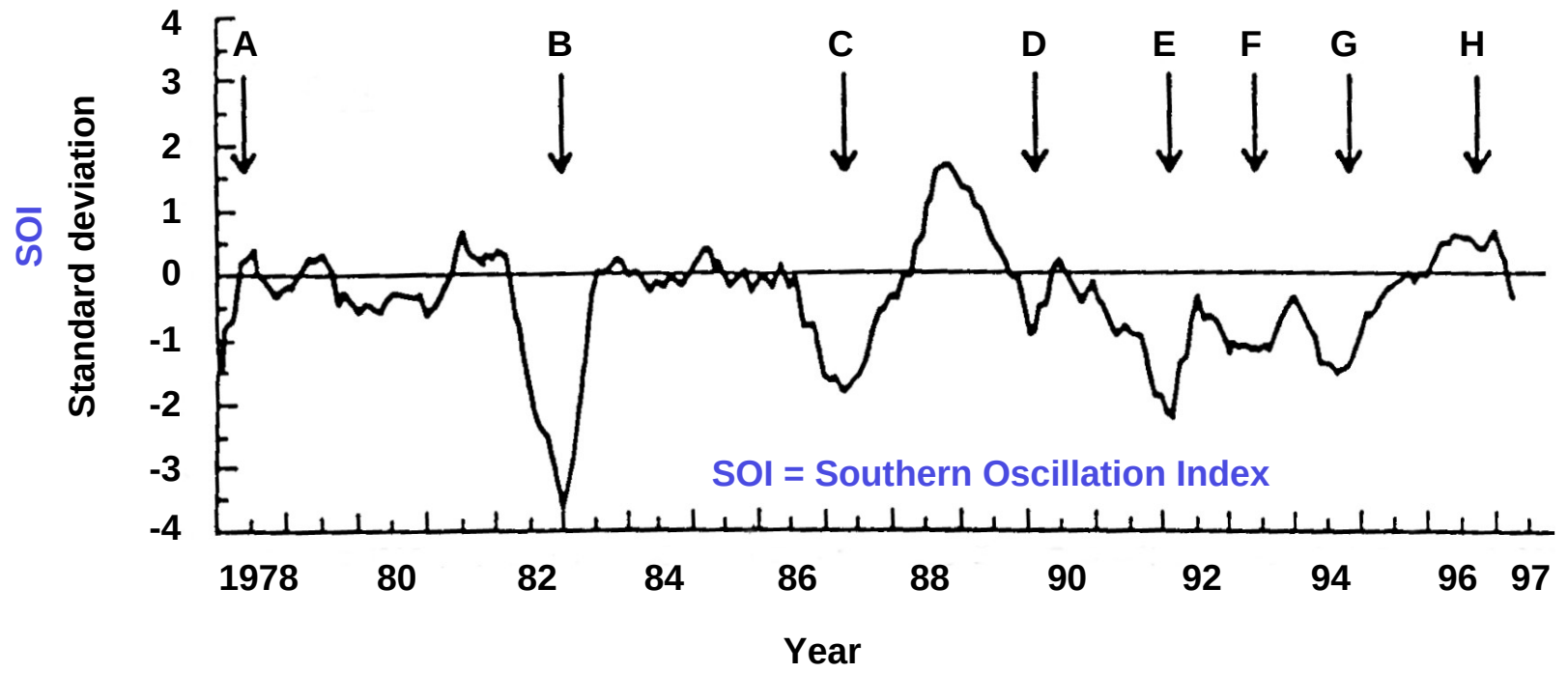
Uchida et al. (2001)



"strong positive anomalies indicative of ENSO events seemingly correlated with *Pyrodinium bahamense* var. *compressum* red tide events"

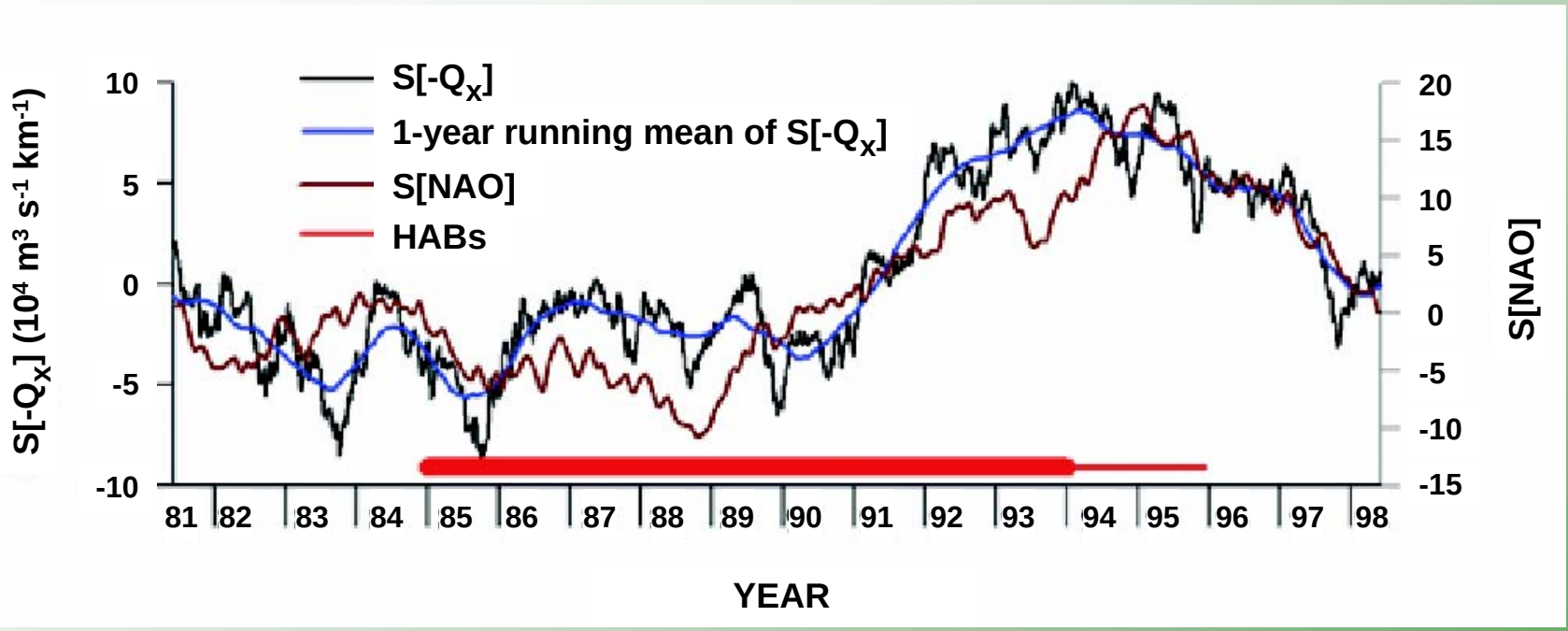
Maclean (1989)

ENSO events and major *Pyrodinium bahamense* var. *compressum* blooms in Philippines and Malaysia, 1978 - 1997.



Usup et al. (1998)

Possible long-term relationship between climate variability and PSP events caused by *Gymnodinium catenatum* in the Galician Ria Baixas (NW Iberian peninsula).



S[- Q_X] and S[NAO] are de-seasonalised cumulative sums of offshore Ekman transport (-Q_X) and the North Atlantic Oscillation Index (NAO) over the period 1981 - 1998.

Straight red line: years when *G. catenatum* was detected in association with PSP toxins in shellfish (▬), or was absent (—).

A positive trend in S[NAO] indicates transition to upwelling favourable periods. A negative trend indicates transition to downwelling-favourable periods.

PSP outbreaks caused by *G. catenatum* were more frequent and intense during the transition period (1980s - 1990s) from downwelling- to upwelling-favourable conditions.

(Alvarez-Salgado et al. 2003).

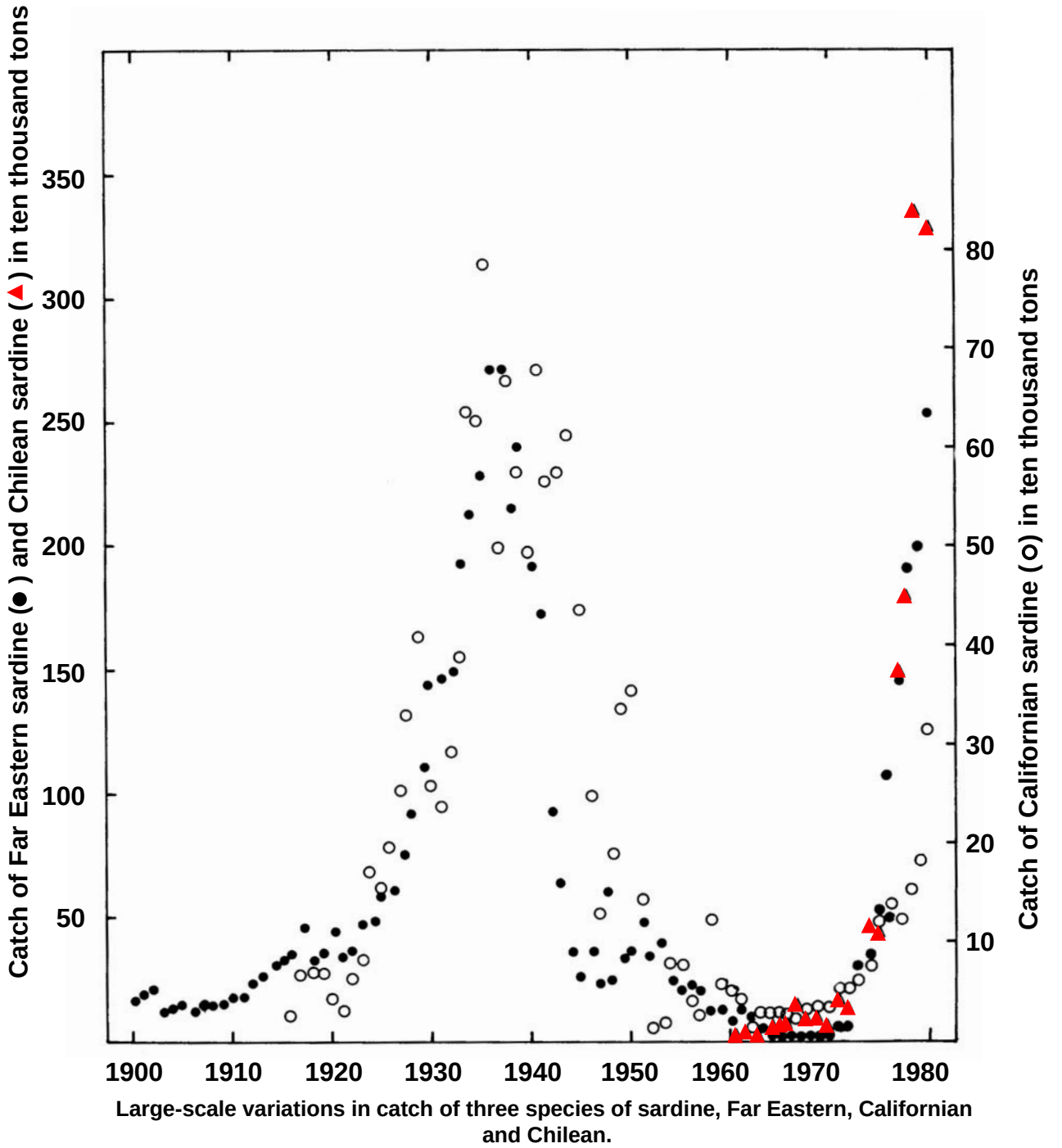
THE ENIGMA

GLOBAL CHANGE ?

GLOBAL INCREASE ?

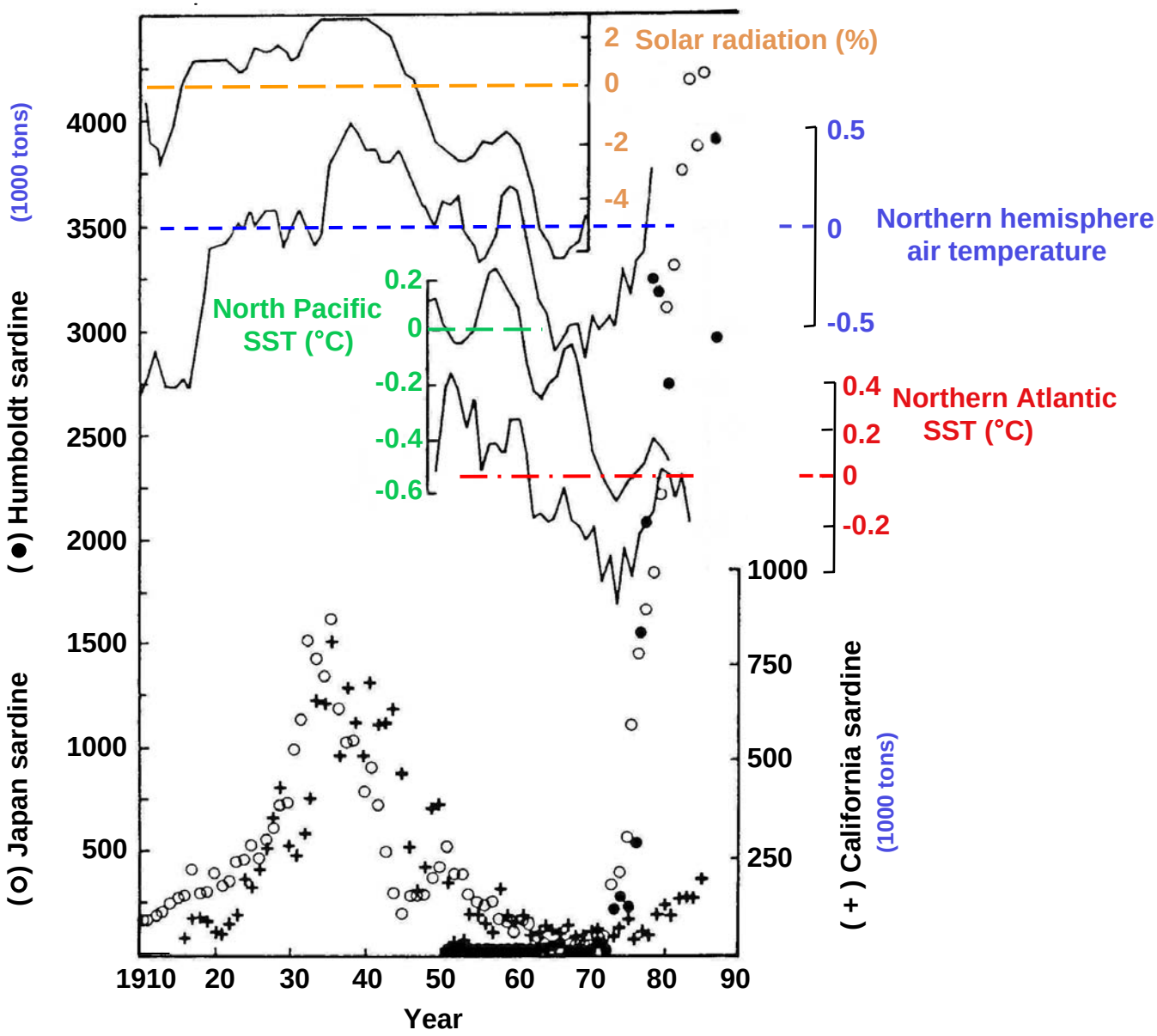
GLOBAL SPREADING ?

GLOBAL SYNCHRONY ?



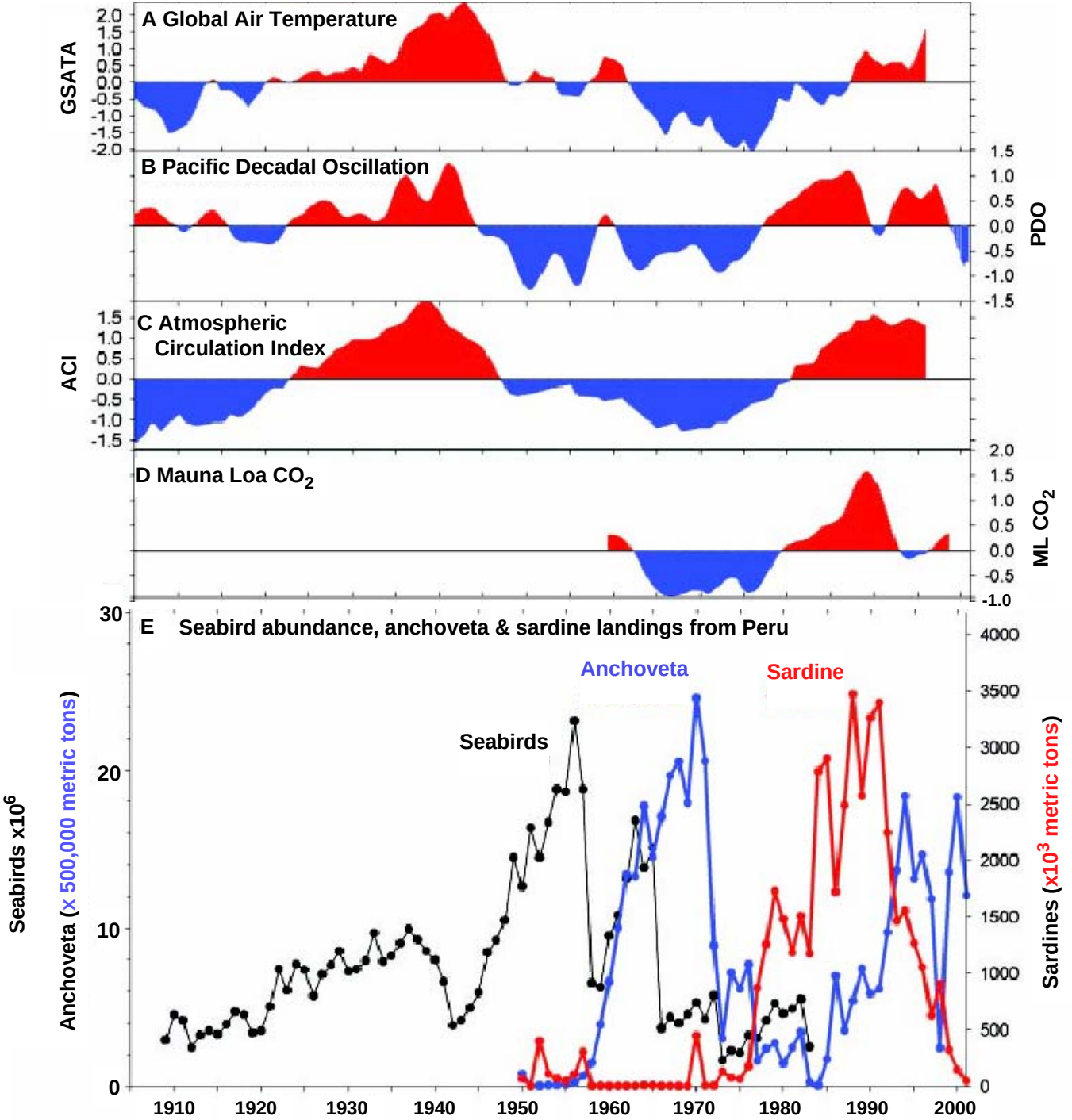
Large-scale variations in catch of three species of sardine, Far Eastern, Californian and Chilean.

Kawasaki (1983)



Lluch-Belda et al. (1989)

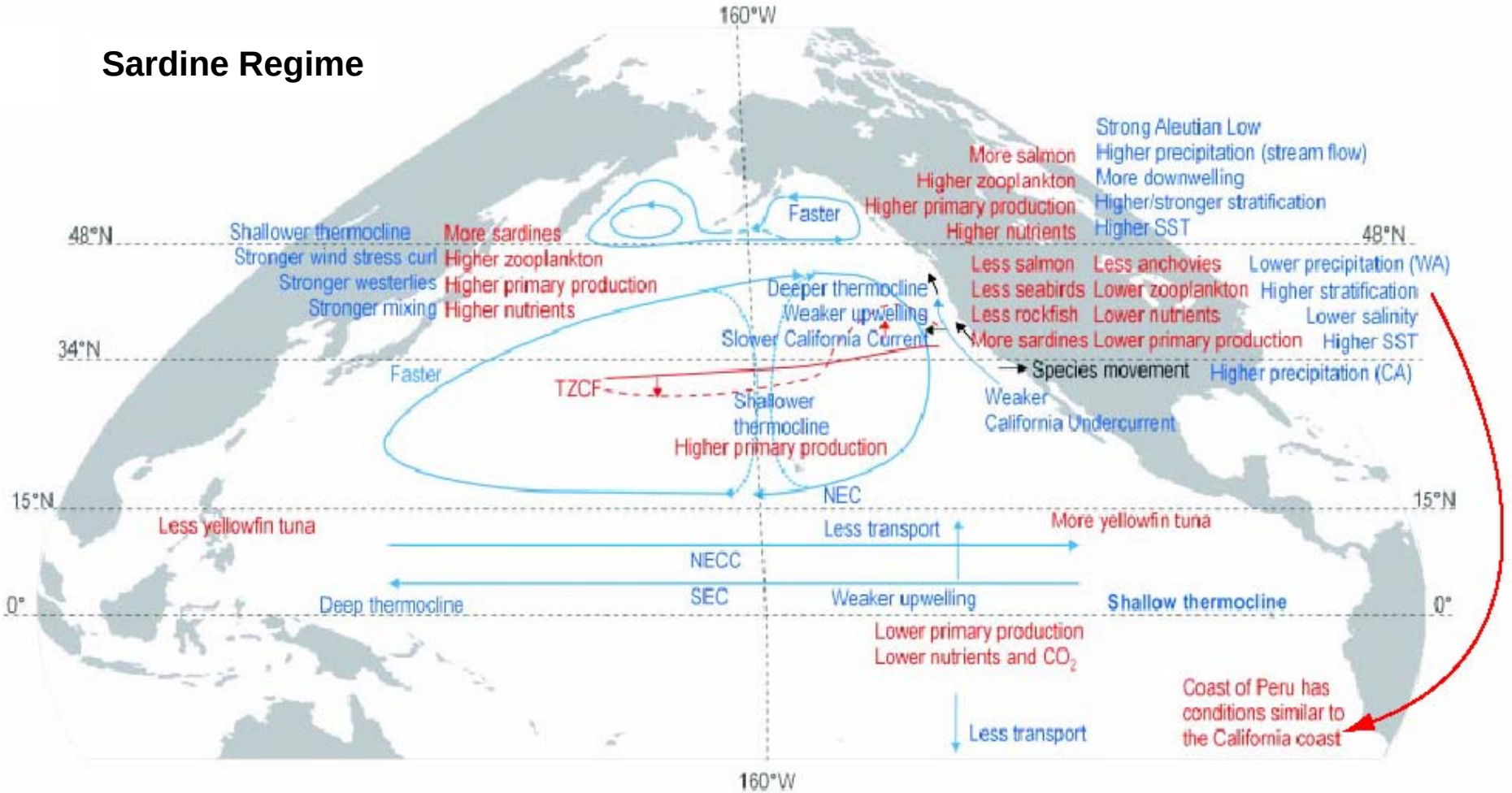
PICES



Revised from Chavez et al. (2003)

PICES

Sardine Regime

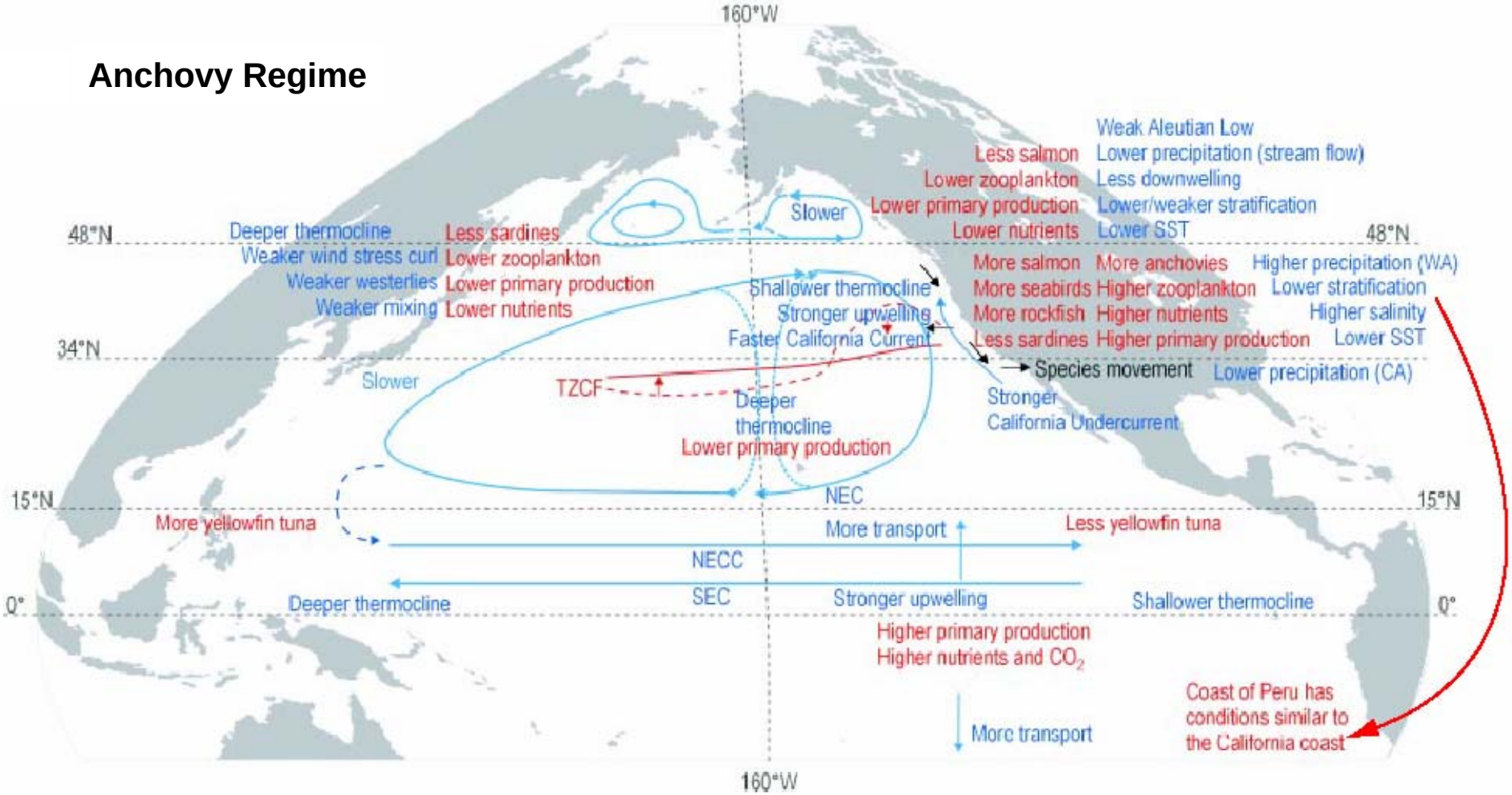


Synthesis of Pacific conditions during the sardine regime. Physical changes in blue; biological and chemical changes in red.

Modified from Chavez et al. (2003)

PICES

Anchovy Regime



Synthesis of Pacific conditions during the anchovy regime. Physical changes in blue; biological and chemical changes in red.

Modified from Chavez et al. (2003)

PICES

HYPOTHESIS

A GLOBAL SYNCHRONY IN HABS IS OCCURRING INDEPENDENT OF, BUT ENHANCED BY LOCAL AND REGIONALLY VARIABLE ANTHROPOGENIC FACTORS:

- ***Nutrient enrichment***
- ***Warming, altered winds and physics***
- ***Metapopulation hybridization (ballast vectoring)***
- ***Food web modification (harvesting)***
- ***Aquaculture***

HYPOTHESIS (cont.)

THERE IS NO UNIFORM EXPLANATION FOR THE HAB SYNDROME; i.e. THERE IS NEITHER A SINGLE, NOR A COMMON ANTHROPOGENIC CAUSE

ANTHROPOGENIC EFFECTS ARE EMBEDDED WITHIN THE GLOBAL HAB RHYTHM

ANTHROPOGENIC ENHANCEMENTS OF HABS ARE SECONDARY STIMULI TO THE GLOBAL SYNCHRONY DRIVER

END