



An assessment of the functional variability of coastal ecosystems in the context of environmental changes.

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Rationale and Objectives of this presentation:

- Holistic approach to ecosystem behavior
- Can we detect changes/variability at the systems level of the same ecosystem over time due to a changing environment?
- Can we assess the impact of a “singular” environmental parameter on the functioning of coastal ecosystems?

Objectives:

- (a) to examine the food web dynamics of several coastal ecosystems over temporal scales (i.e. the same system over time) which have changed due to a change in some environmental parameter, and use the output results from ENA to illustrate functional changes at the ecosystem level, and
- (b) to illustrate the impact of fresh water input into estuaries on ecosystem function over spatial scales.

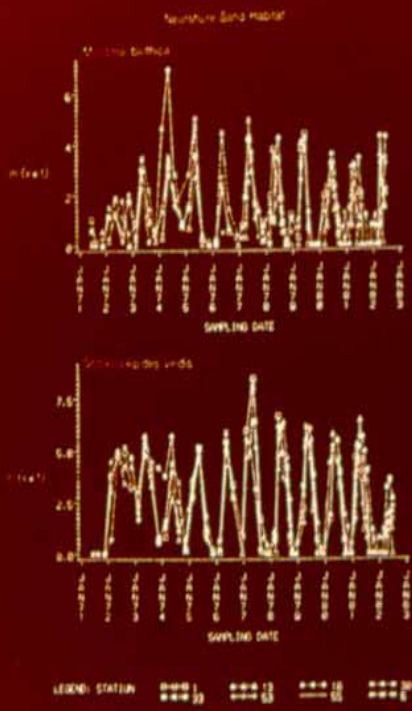


Fig. 3. Mean abundance $[\ln(x + 1)]$ for *Macoma balthica* and *Scolecolepides viridis* in the nearshore sand habitat.

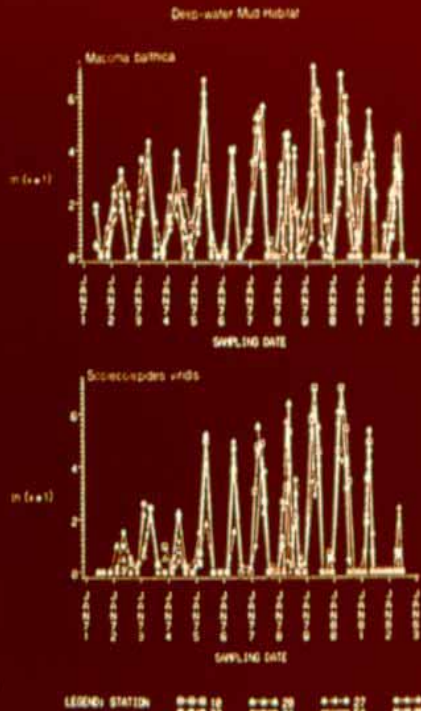


Fig. 4. Mean abundance $[\ln(x + 1)]$ for *Macoma balthica* and *Scolecolepides viridis* in the deep-water mud habitat.

Seasonal fluctuations of mollusk specie abundance in Chesapeake Bay

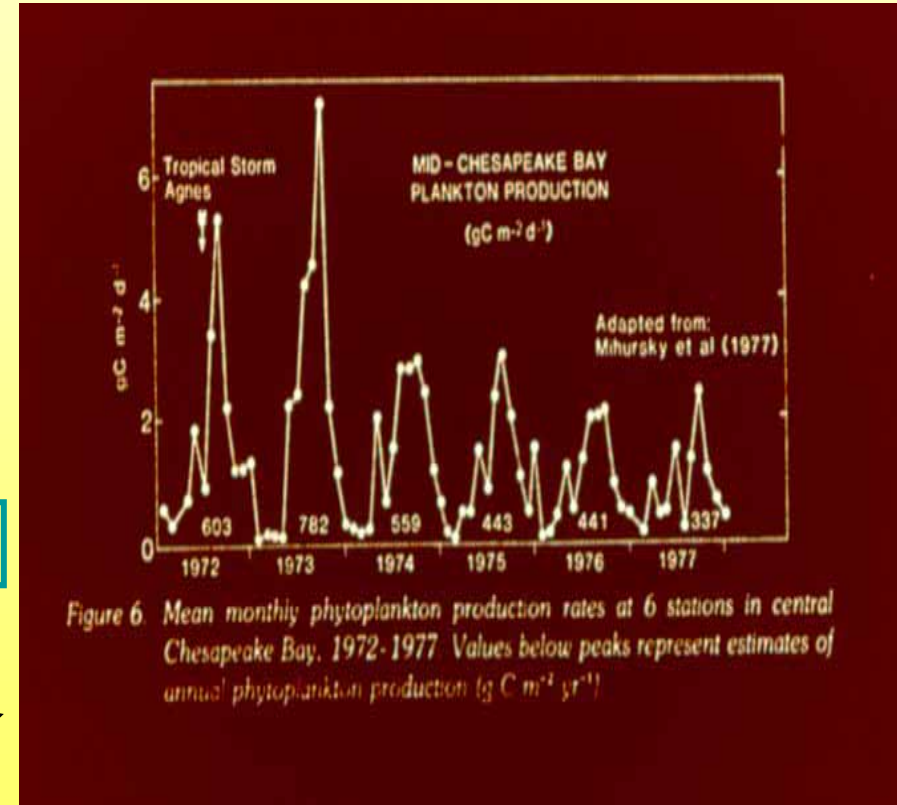
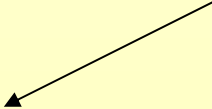
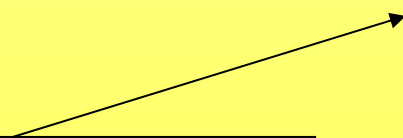


Figure 6. Mean monthly phytoplankton production rates at 6 stations in central Chesapeake Bay, 1972-1977. Values below peaks represent estimates of annual phytoplankton production ($gC m^{-2} yr^{-1}$)

Natural variability of species and communities

Monthly variability in phytoplankton production in Chesapeake Bay



Concept of variability in natural ecosystems universally accepted.

- Variability in coastal ecosystems:
 - natural, anthropogenic, climate change.

- Rate and magnitude of variability not constant, nor predictable.

- Temporal fluctuations of **components** of coastal ecosystems well studied....**systems over time not.....very few examples.**

- Behavior of ecosystems not well understood...why not???

- If we could, then we can predict and assess how climate change will affect biodiversity, energy flow pathways, nutrient cycling, etc. and how this will impact on ocean and coastal ecosystem function..... the Biodiversity-Ecosystem Function [BEF] debate.

Why difficult to understand how ecosystems work?

- Ecosystems possess properties which do not emerge by summing the properties of the component parts.

- **Inherent variability of biological parameters and processes**. Confidence limits of prediction of biological outcomes in the order of 25%. When process models with inherent variability is coupled the confidence limits on outputs are wide.

- **Hierarchical nature of ecosystems**

- Hierarchical nature of ecosystems

Various levels of the hierarchy of an ecosystem are characterized by different time scales [lower levels smaller and more rapid scales of fluctuations; individual phytoplankton species populations show greater fluctuations in numbers and productivity than the total phytoplankton community];

“...the variability of the whole is less than the sum of the variability of the parts...”. I.e. the behavior of the total system cannot be inferred solely from the behavior of the parts;

An ecosystem an entity with at least two dimensions: one, it is structured according to constraints related to species interactions; in another to constraints related to fluxes and mass balances. Contemporary simulation models unable to accommodate these two hierarchies.

- Ecosystems have the capacity for self-organization

Concept of self-organization of in ecosystems has its roots in the thermodynamic theory of dissipative structures [Prigogine 1945, 1947], and in Bronowski's [1973] concept of stratified stability.

A dissipative structure maintains its structure by the dissipation of energy supplied from outside itself, maintaining a high state of internal organization [minimum entropy production] by the flow of energy derived from the sun [plants] or from food [animals].

Ecosystems evolve from interacting dissipative structures to form new and complex combinations within the framework of the total system, which thus seems to be undergoing self-organization.

Sudden change of state that can occur in populations and ecosystems leads to the parallel ideas of bifurcations and multiple stable states. Thus sudden changes of state are manifestations of an ecosystem's ability to create new forms of internal organization [in response to perturbations, natural or [perhaps] human induced].

Approaches to Ecosystem studies

- Graphs and networks

Stocks and flows

Network Analysis and
ECOPATH

Material and
elemental fluxes

- Thermodynamic approach

- Dissipative structures exist as a consequence of building energy into structure;

- Changes in energy: high quality, low entropy, heat;

- Calculation of state components in dynamic flux.

Resulted in different sub-directions:

- maximum entropy formation [Aoki 1987];

- minimum dissipation [Johnson 1995]

- maximum energy storage [Jorgensen & Meyer 1992]

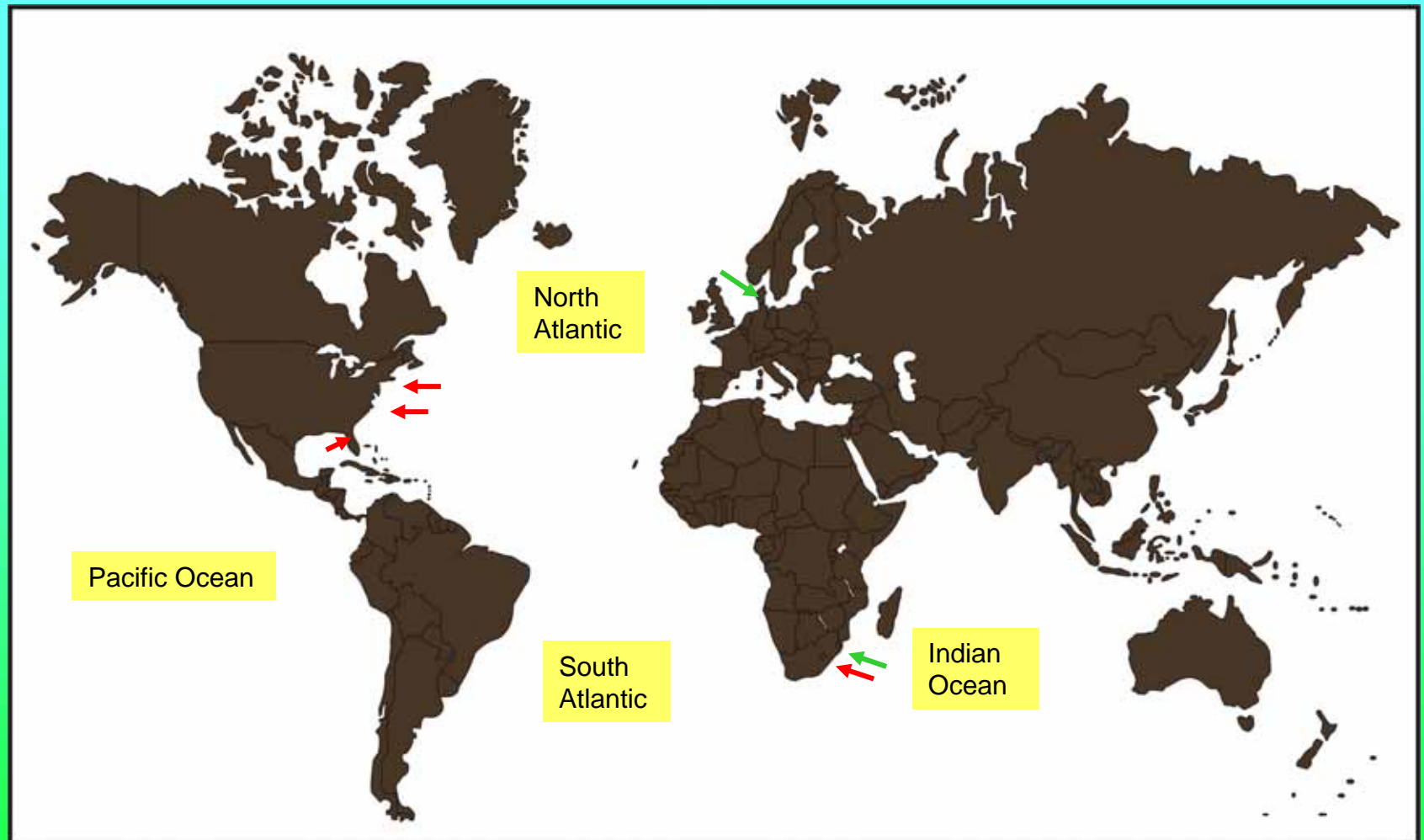
- maximum energy degradation [Kay & Schneider '92, '93]

Approaches not mutually exclusive

Based on the 1st and 2nd Laws of the Thermodynamics:

+ conservation of energy [in biomass]: + dissipation of energy [flows & heat]

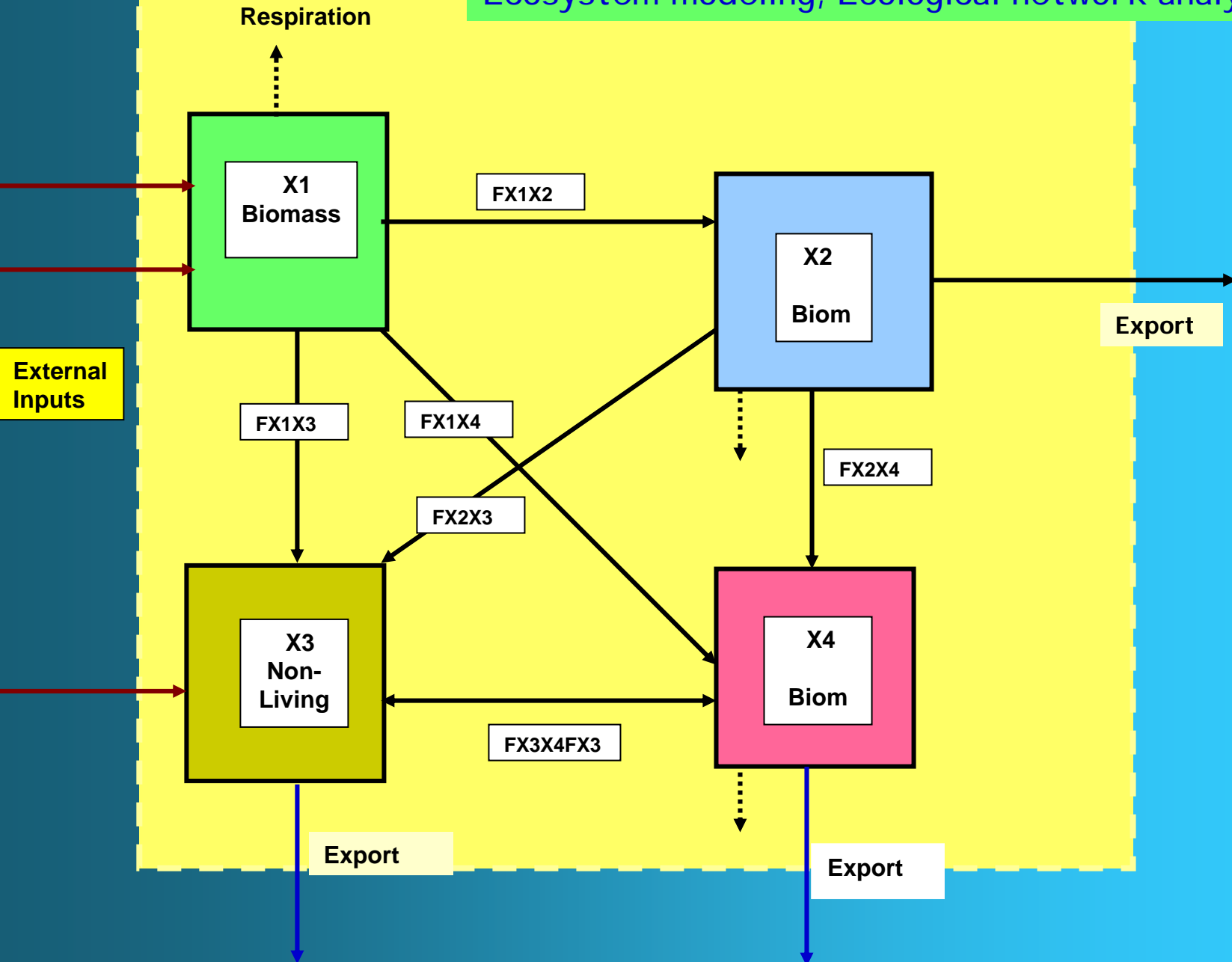
Which systems and where?



**Temporal
Comparisons**

**Spatial
Comparisons**

Ecosystem modeling, Ecological network analysis



Network composition

- Flow networks for each system comprised of living and non-living balanced compartments

- Systems assumed to be in equilibrium.

• Living compartments

- ✓ Phytoplankton
- ✓ Benthic microalgae
- ✓ Submerged macrophytes
- ✓ Salt marsh plants
- ✓ Epiphytes
- ✓ Free living water column bacteria
- ✓ Attached water column bacteria
- ✓ Sediment bacteria
- ✓ Microzooplankton
- ✓ Mesozooplankton
- Meiofauna
- ✓ Benthic invertebrate macrozoobenthos [carnivores, deposit feeders, grazers, suspension feeders]

- ✓ Ichthyonekton [fish larvae, zooplanktivores, piscivores, herbivores, benthic feeders]
- ✓ Birds

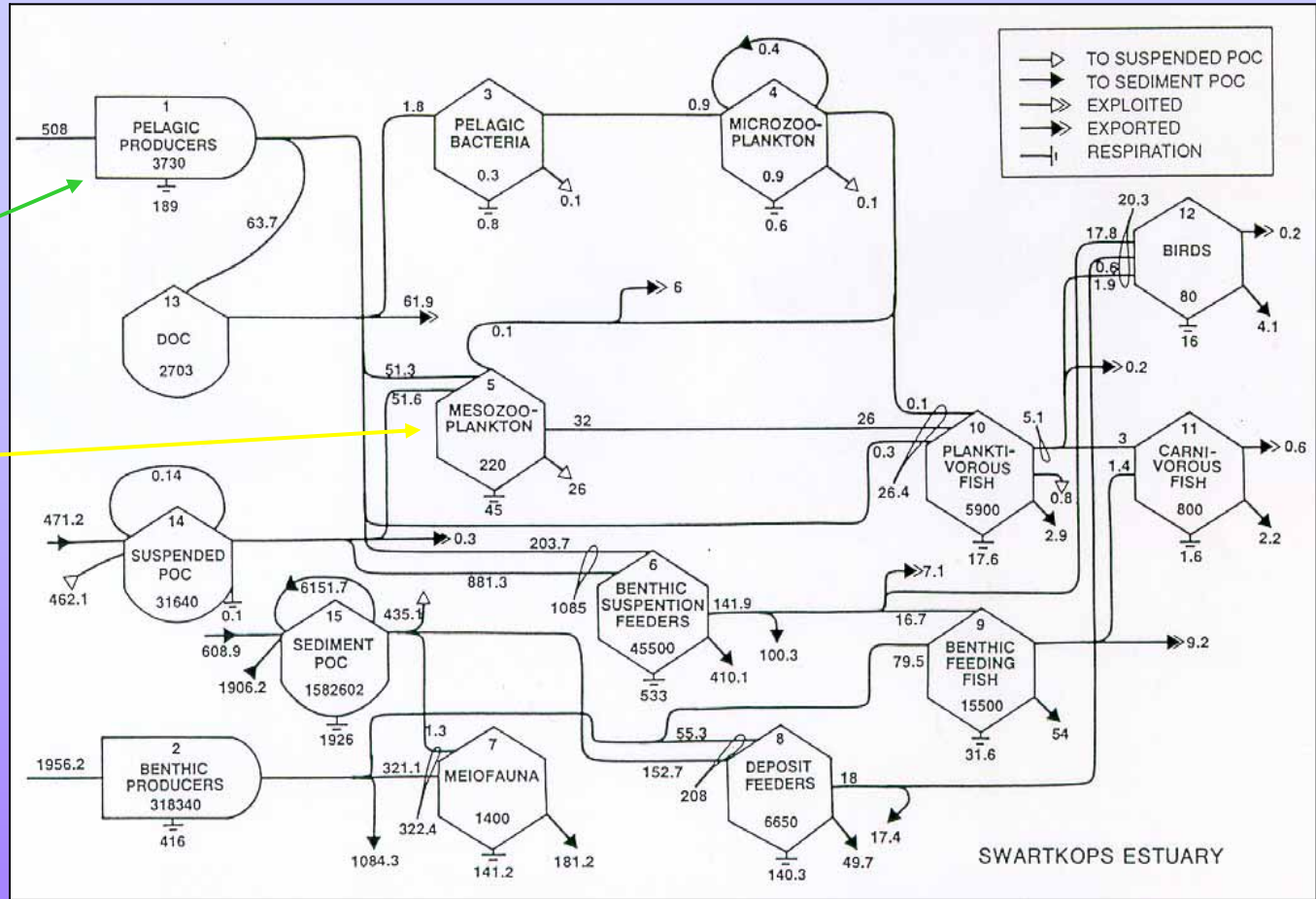
• Non-living compartments

- ✓ DOC
- ✓ Suspended POC
- ✓ Sediment POC



Primary producers: $GPP = NPP + \text{Respiration}$

Animals: $C = P + R + E$



Simplified network of stocks and flows

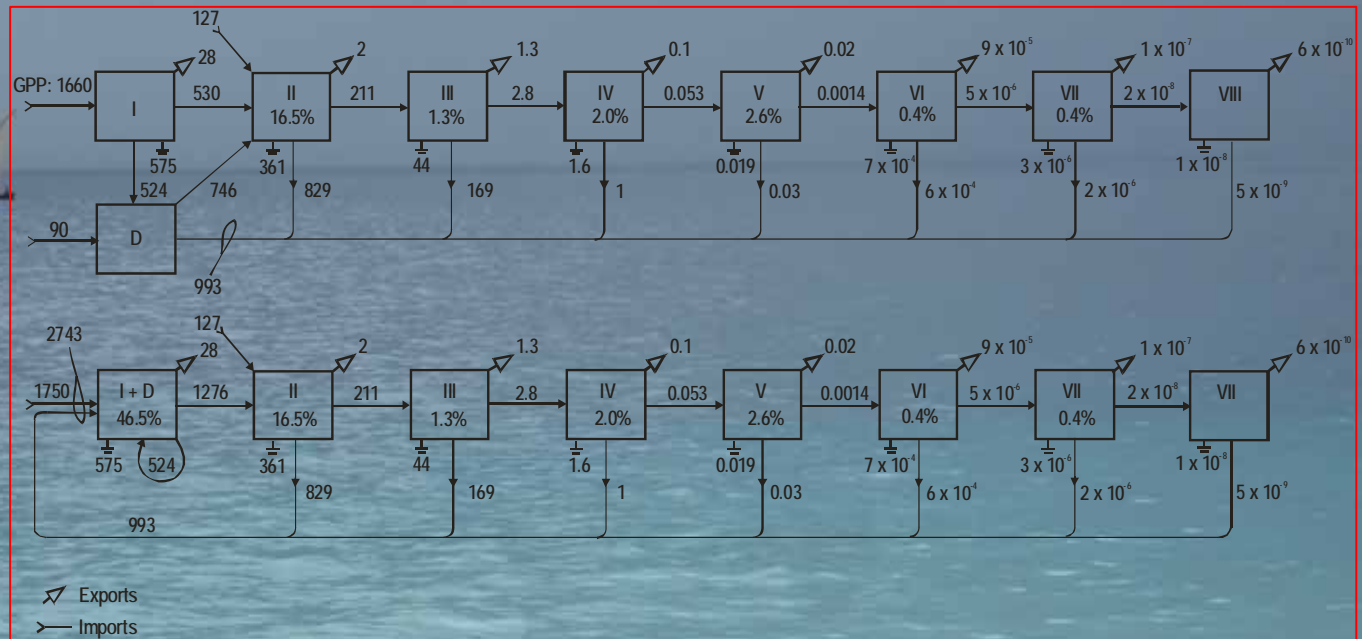
- Data requirements
- Biomass
 - Population energetics
 - Diet composition

What data are required to analyze ecosystem functionality by ENA?

Outputs from Ecological Network Analysis

- **Input – Output analysis:** i.e. how any particular species/trophic guild is directly and indirectly affected by any other species/compartments in the food web
- **Lindeman Trophic Analysis:** e.g. how efficient an ecosystem is in processing energy [or any other currency]
- **Biogeochemical Cycle Analysis:** i.e. the structure of recycle pathways and the magnitude of recycled material relative to the system's activity...e.g. the Finn Cycling Index [FCI]
- **Global Ecosystem Properties:** i.e. indices derived from thermodynamics and information theory [...such as Development Capacity, Ascendancy, Redundancy, Overheads, Average Mutual Information, Flow Diversity, Connectance Indices, etc.]

Example of Lindeman Trophic Analysis: Lindeman Spine allocate individual species/communities to Integer trophic levels. Spine shows the transfer of energy/material from one trophic level to a higher one, and the efficiency by which it was transferred. The geometric mean of the % efficiency of all levels gives the trophic efficiency of the whole system.....an ecosystem attribute.



Total Systems Throughput [TST]: the extent of the total activity of the system; calculated as the sum of all the flows through all compartments.

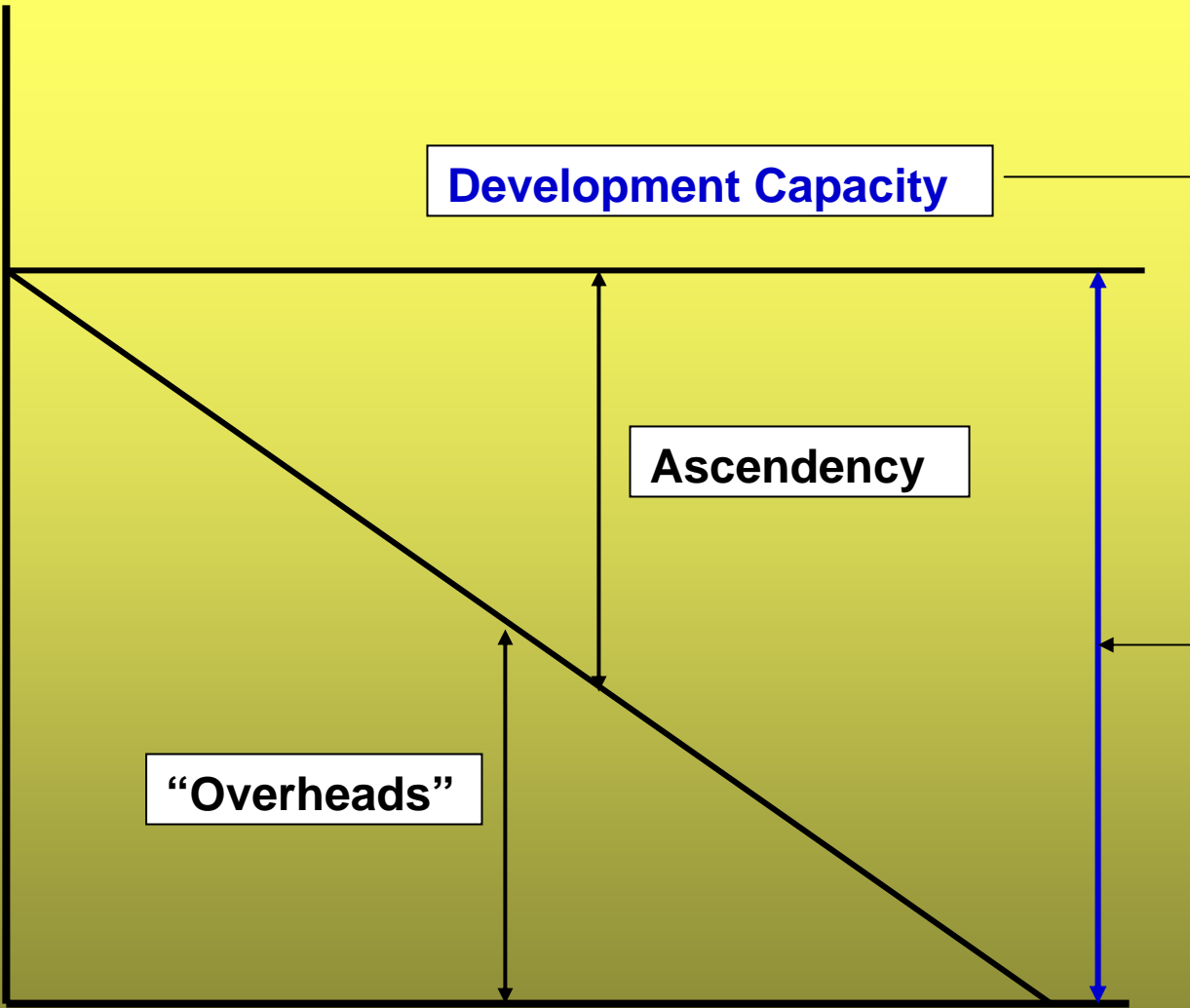
System Ascendency [A]: a single measure of the magnitude and diversity of flows between compartments and reflects on functional attributes of the system. It incorporates both size and organization of flows in a single index, and is expressed as the product of TST and the Average Mutual Information [AMI] inherent in the flow network.

Development Capacity [DC]: =product of TST and flow diversity. It measures the potential of a system to develop and is the natural upper limit of A.

Overheads: On Imports, Exports, Dissipation, and Redundancy
[R = measure of uncertainty associated with the presence of multiple parallel pathways among the components of the network].

Finn Cycling Index [FCI]: fraction of TST that is devoted to cycling [T_c/TST].

no i t a m r o n i



Development Capacity

Ascendency

“Overheads”



Organization & Specialization



Resilience

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Objectives:

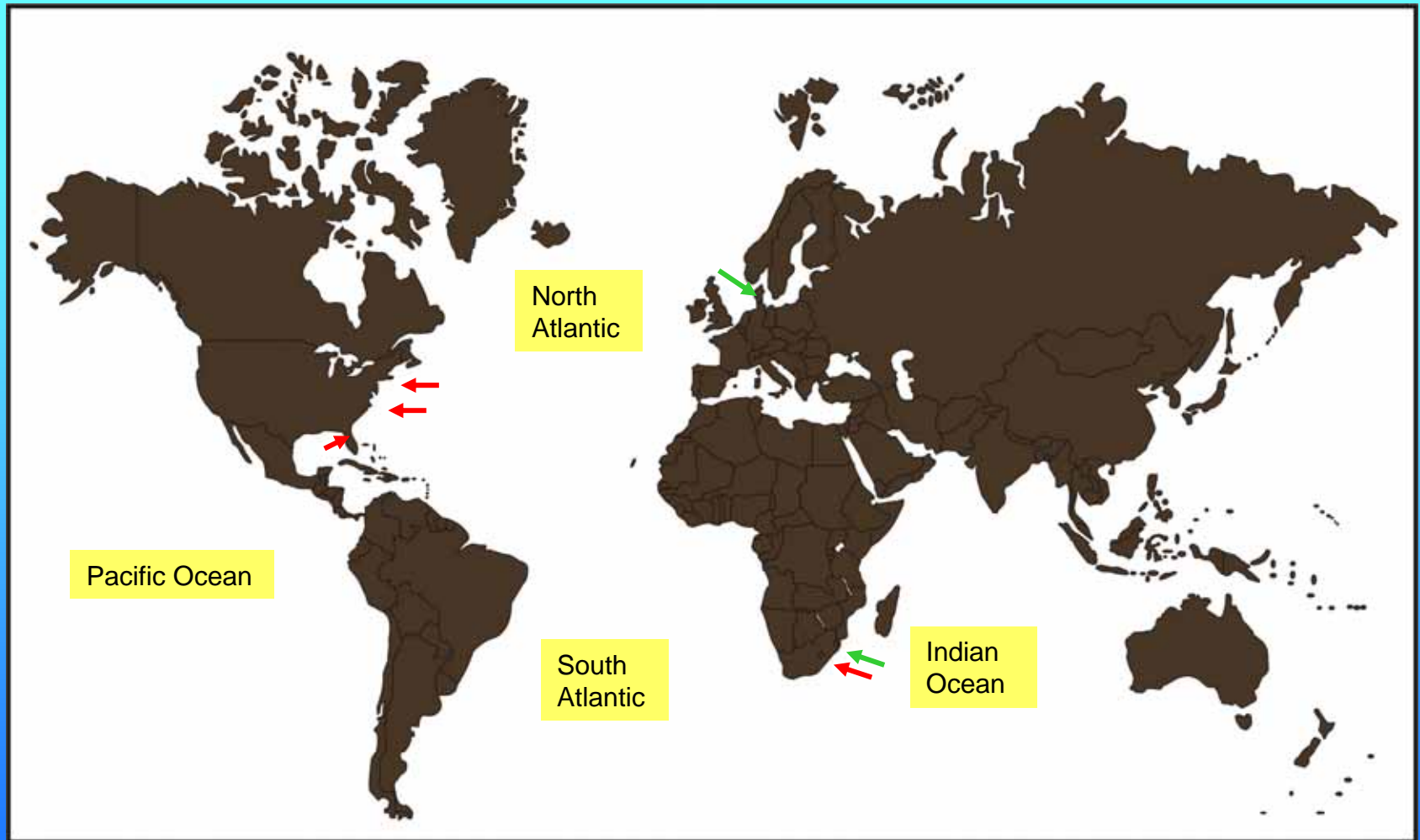
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An aerial photograph of a coastal estuarine ecosystem. In the foreground, blue ocean waves with white foam break onto a sandy beach. A wide, winding river or estuary flows from the background towards the beach, with various channels and sandbars. The surrounding land is green with vegetation and has some small buildings or houses scattered across it. In the far background, a range of blue mountains stretches across the horizon under a clear sky.

Comparison of the same estuarine ecosystem over time:

- How has the environment change [e.g. temperature, oxygen concentration, salinity]?
- How was the impact of these environmental changes reflected in system attributes and function?

Which systems and where?



**Temporal
Comparisons**

**Spatial
Comparisons**

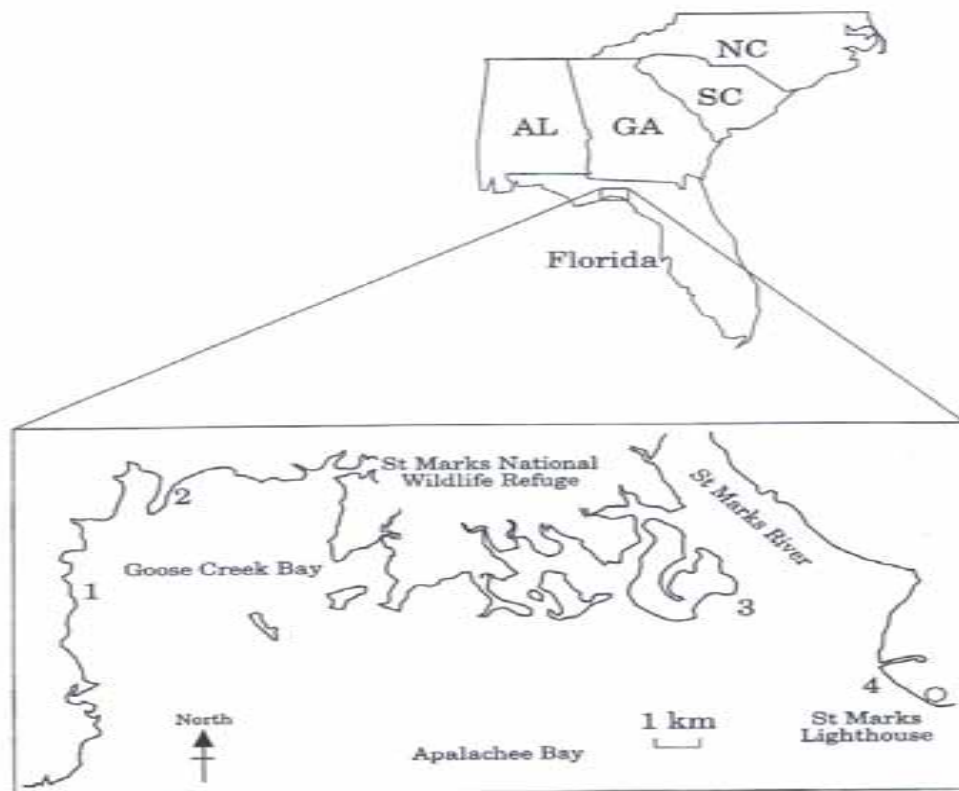


FIGURE 1. Map of the of the St Marks National Wildlife Refuge seagrass ecosystem, Apalachee Bay, Florida, and sample locations shown by numbers.

**St. Marks
Wildlife Refuge
Goose Creek
Bay**



**EPA Seagrass
1: 24,000
Color photograph
Dec 1992**



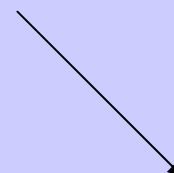
System attributes during January and February of the St Marks Wildlife National Refuge, Apalachee Bay, Florida [28 compartment models].

Main environmental change: an increase in water temperature of 5°C from January to February

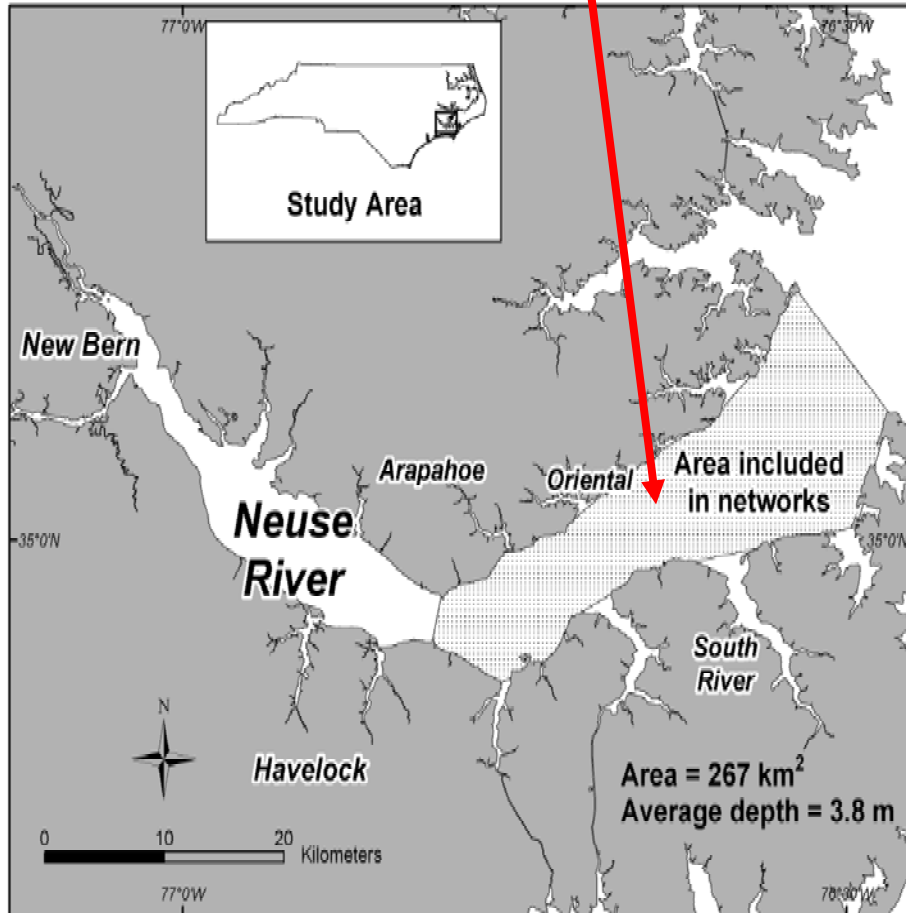
System Attribute	January	February	% increase + % decrease -
Temperature [°C]	12	17	41.7
Spp Diversity [H']	0.742	1.174	58.2
Total Biomass [mgCm ⁻²]	11601	11641	0.3
System Production [mgCm ⁻² day ⁻¹]	431	482	11.8
P/B day	0.037	0.041	10.8
System Trophic Efficiency [%]	4.91	3.33	-32.2
No of cycles	608	1006	65.5
Finn Cycling Index [%]	15.53	20	28.8
TST [mgCm ⁻² day ⁻¹]	1877	2321	23.7
Ascendency	3392	4210	24.1
A/C [%]	35.6	32.2	-9.6
Ai/Ci	39.1	37.1	-5.1
AMI [A/TST]	1.81	1.81	0.4
Redundancy	2767	4078	47.4
Food Web Connectance	3.6	3.4	-5.6
Flow Diversity	5.1	5.6	9.8

Increase in several system indices

Nevertheless, decrease in some functional indices



Oxygen depletion from early to late summer



System attributes during early and late summer in the Neuse River Estuary, North Carolina.

Main environmental change:		Development of hypoxic conditions		
		from early to late summer		
System Attribute	Early Summer	Late Summer	% increase + % decrease -	
Temperature (°C)				
O ₂ Concentration [mg l ⁻¹]	> 6	< 2	-66.7	
Algal Biomass [mgCm ⁻²]	1988	2180	9.7	
Heterotrophic Biomass [mgCm ⁻²]	18149	11185	-38.4	
System Production [mgCm ⁻² day ⁻¹]	3810	4260	11.8	
System Trophic Efficiency [%]	4.12	4.82	17.0	
No of cycles	135	641	374.8	
Finn Cycling Index [%]	14.8	15.3	3.4	
TST [mgCm ⁻² day ⁻¹]	18404	19175	4.2	
Ascendency	37723	37141	-1.5	
A/C [%]	47.1	46.6	-1.1	
AMI [A/TST]	2.05	1.94	-5.5	
Normalized Redundancy [R/TST]	0.96	0.8	-16.7	
Food Web Connectance	1.35	1.36	0.7	
Flow Diversity [D/TST]	4.35	4.16	-4.4	

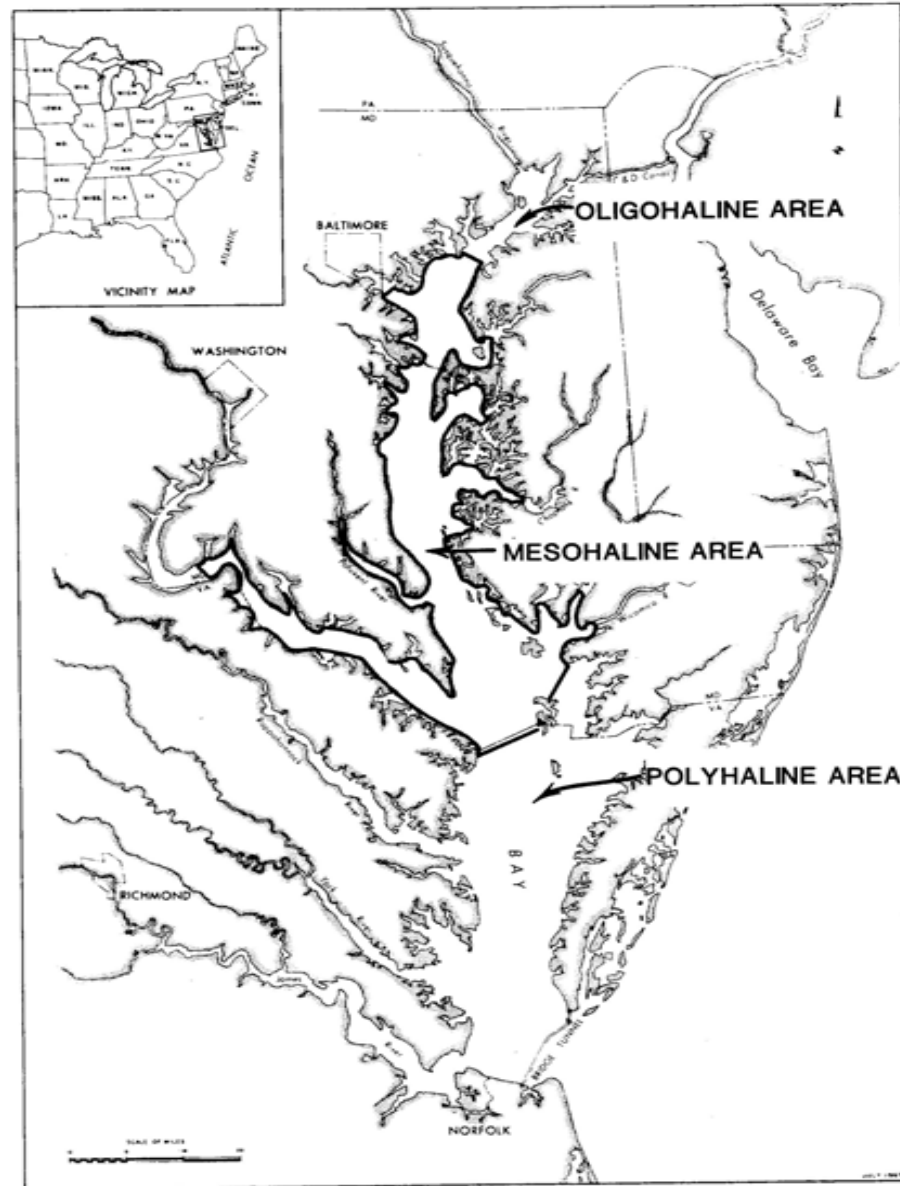
Mortality due to hypoxia

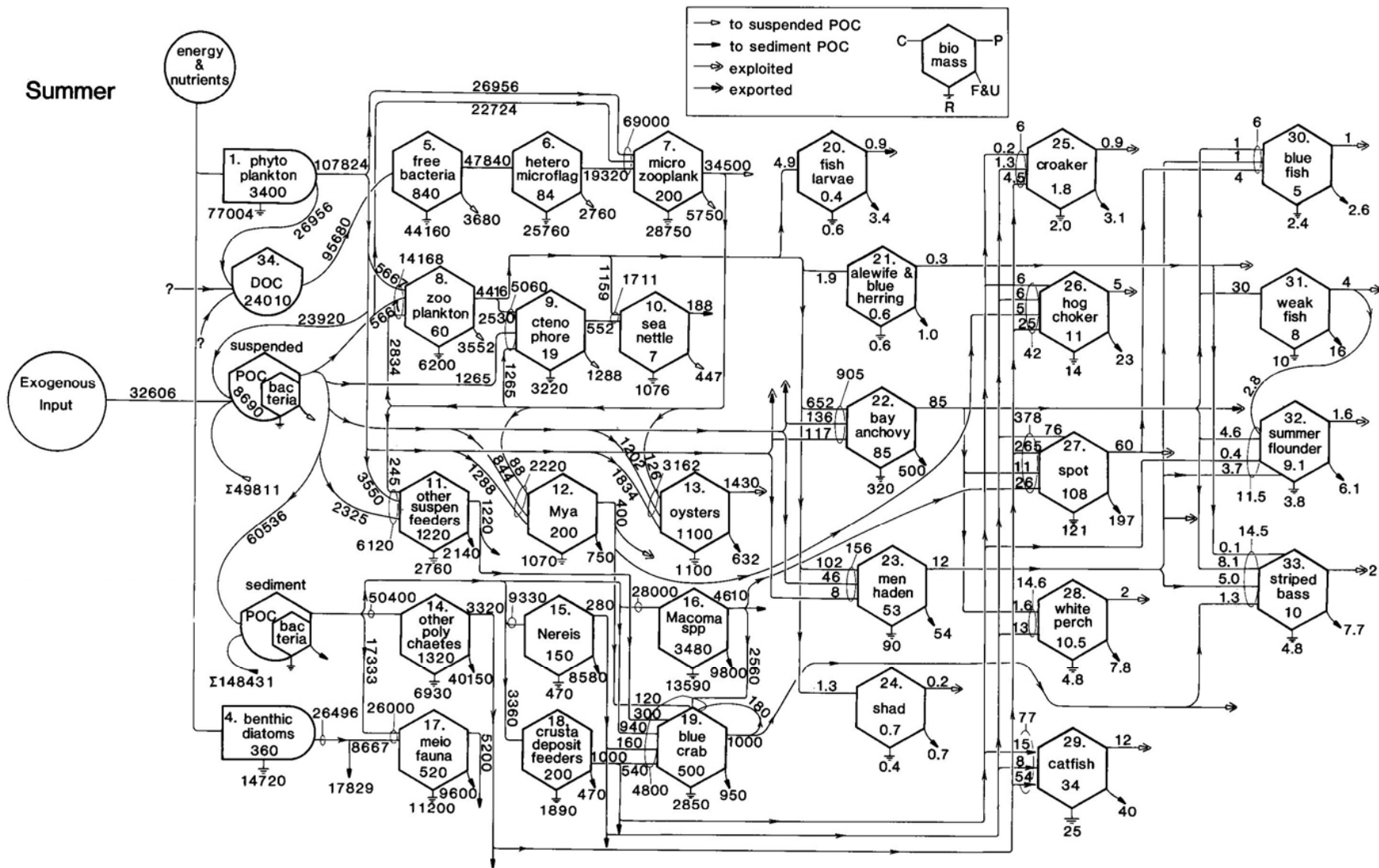
Increase due to increased microbial activity

Decrease in most system functional indices show decline in system organization and function.

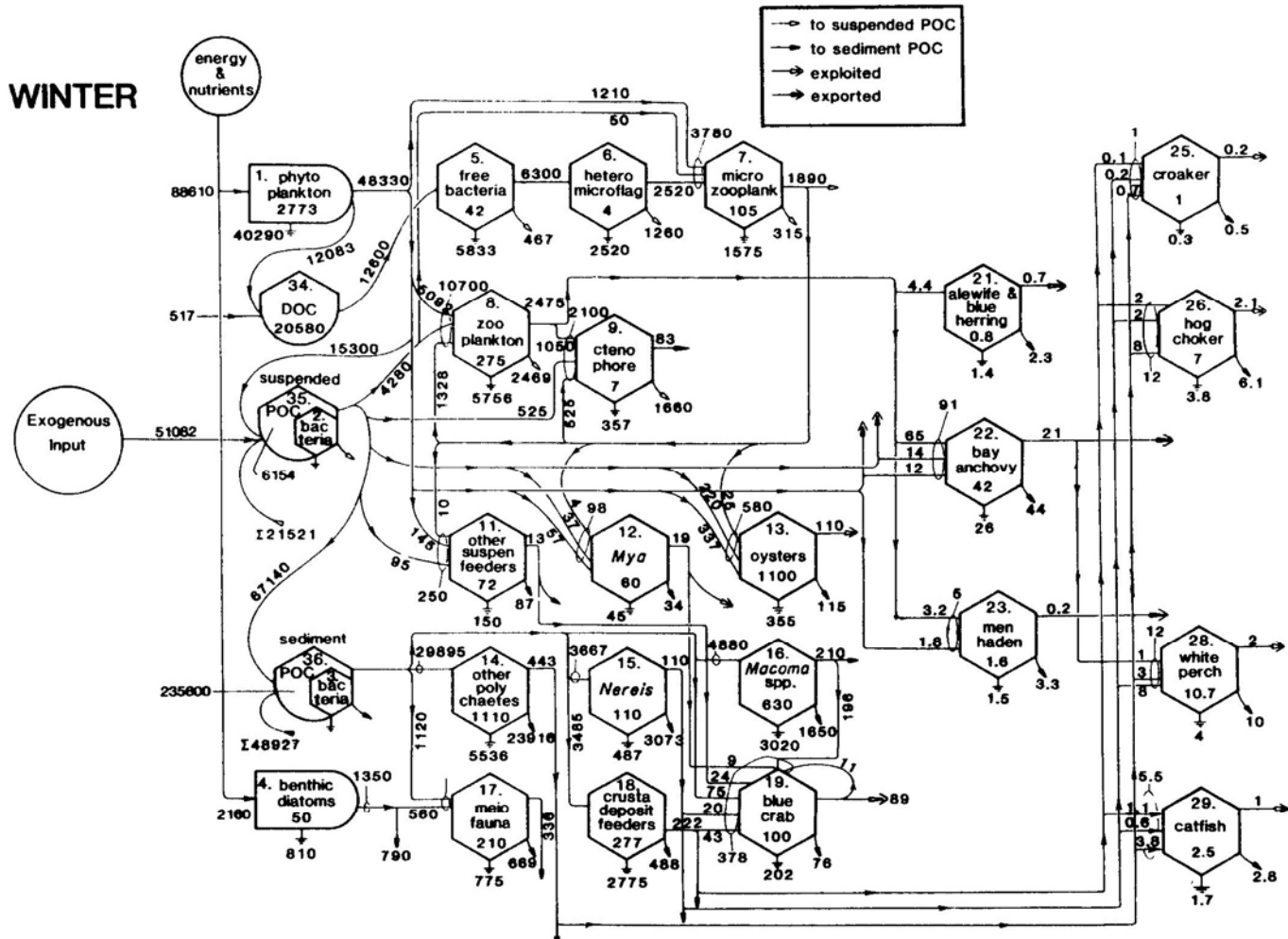
Chesapeake Bay

Seasonal dynamics of energy flow [33 compartments]



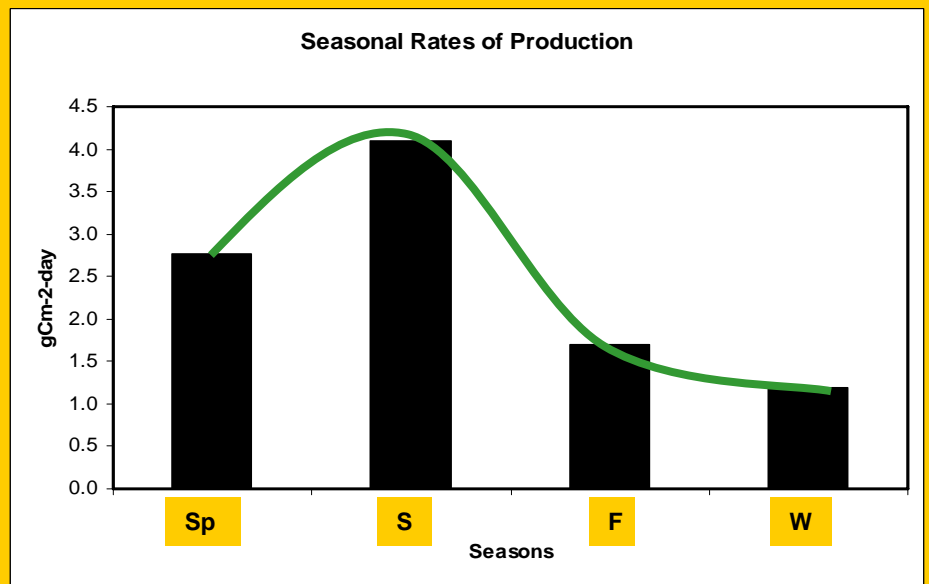
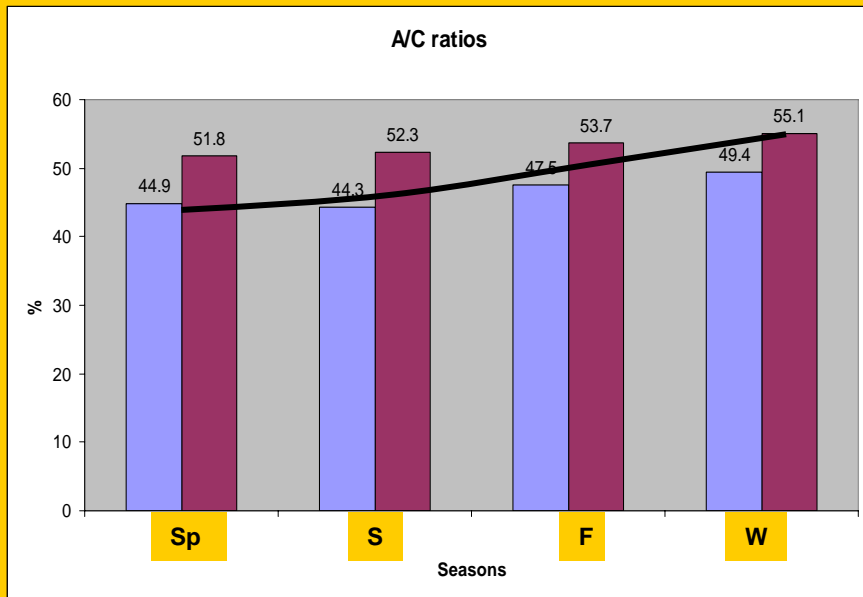
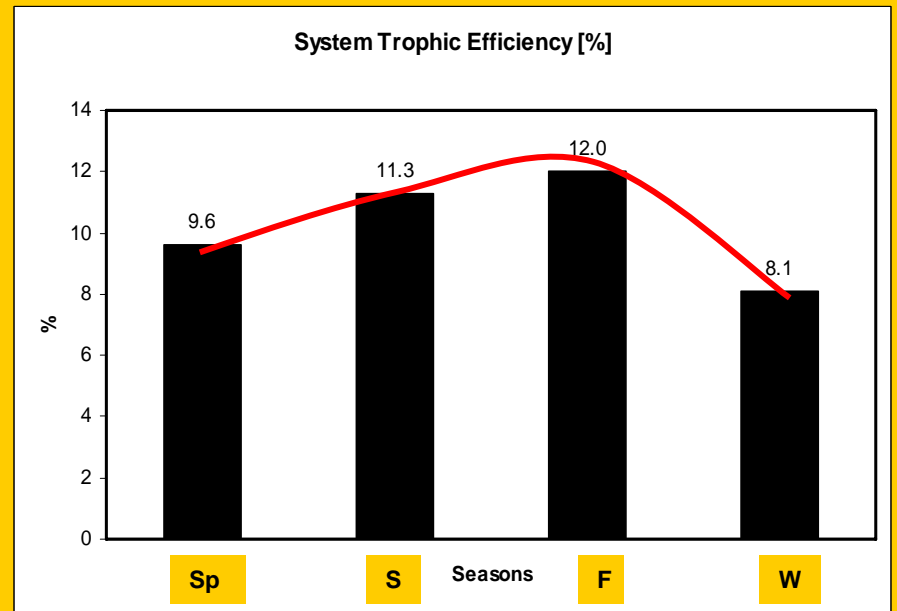
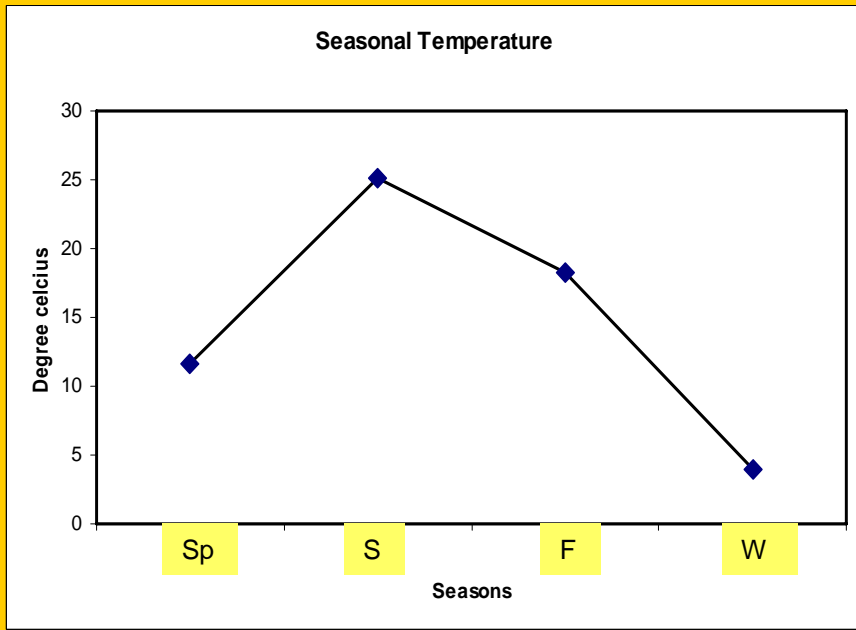


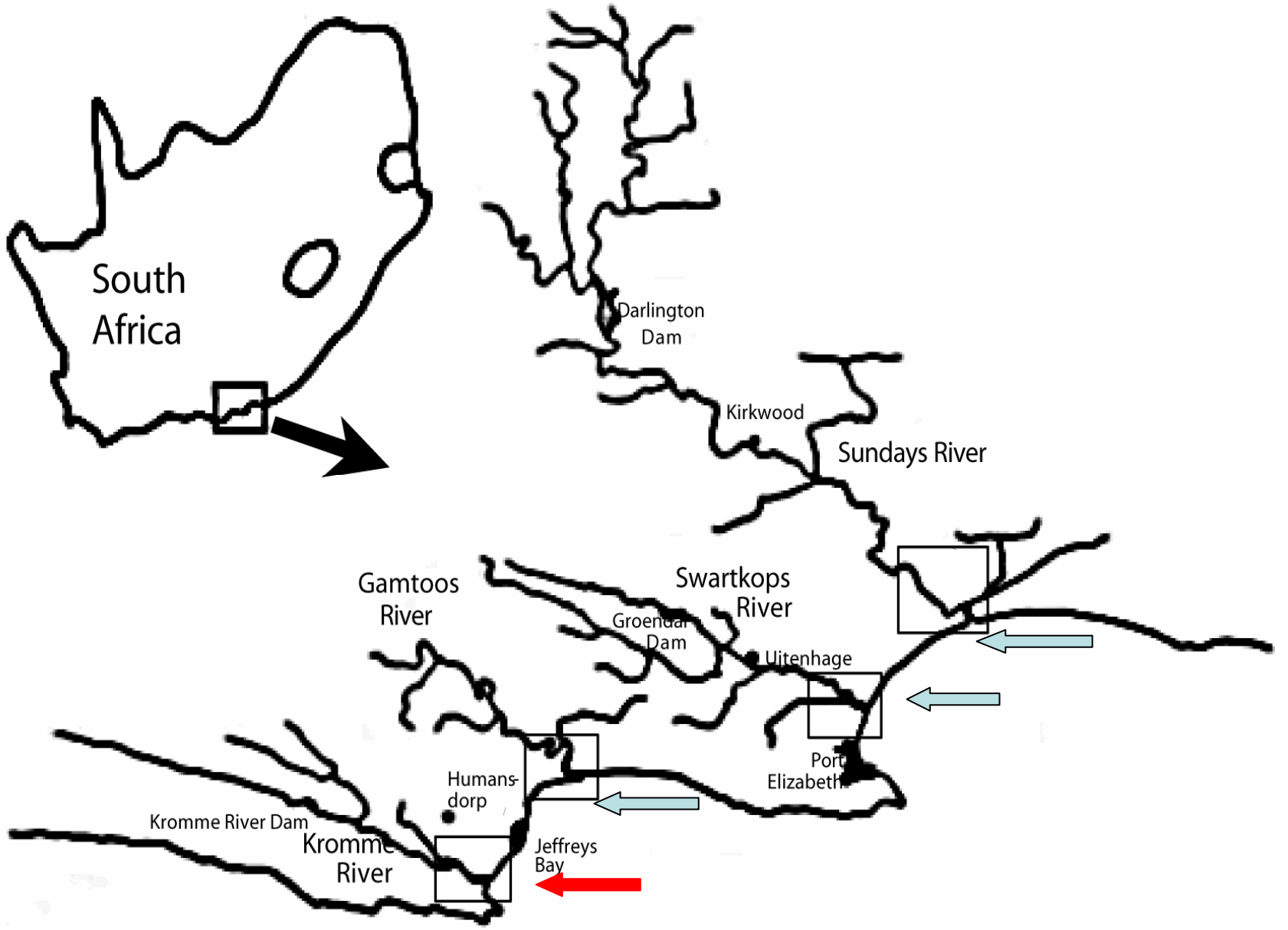
Energy flow network of the Chesapeake Bay during summer [Standing stocks in mgCm⁻², flows in mgCm⁻² season⁻¹]. [From Baird & Ulanowicz 1989, Ecological



Energy flow during winter in Chesapeake Bay

Chesapeake Bay.....seasonal differences in temperature and system attributes.

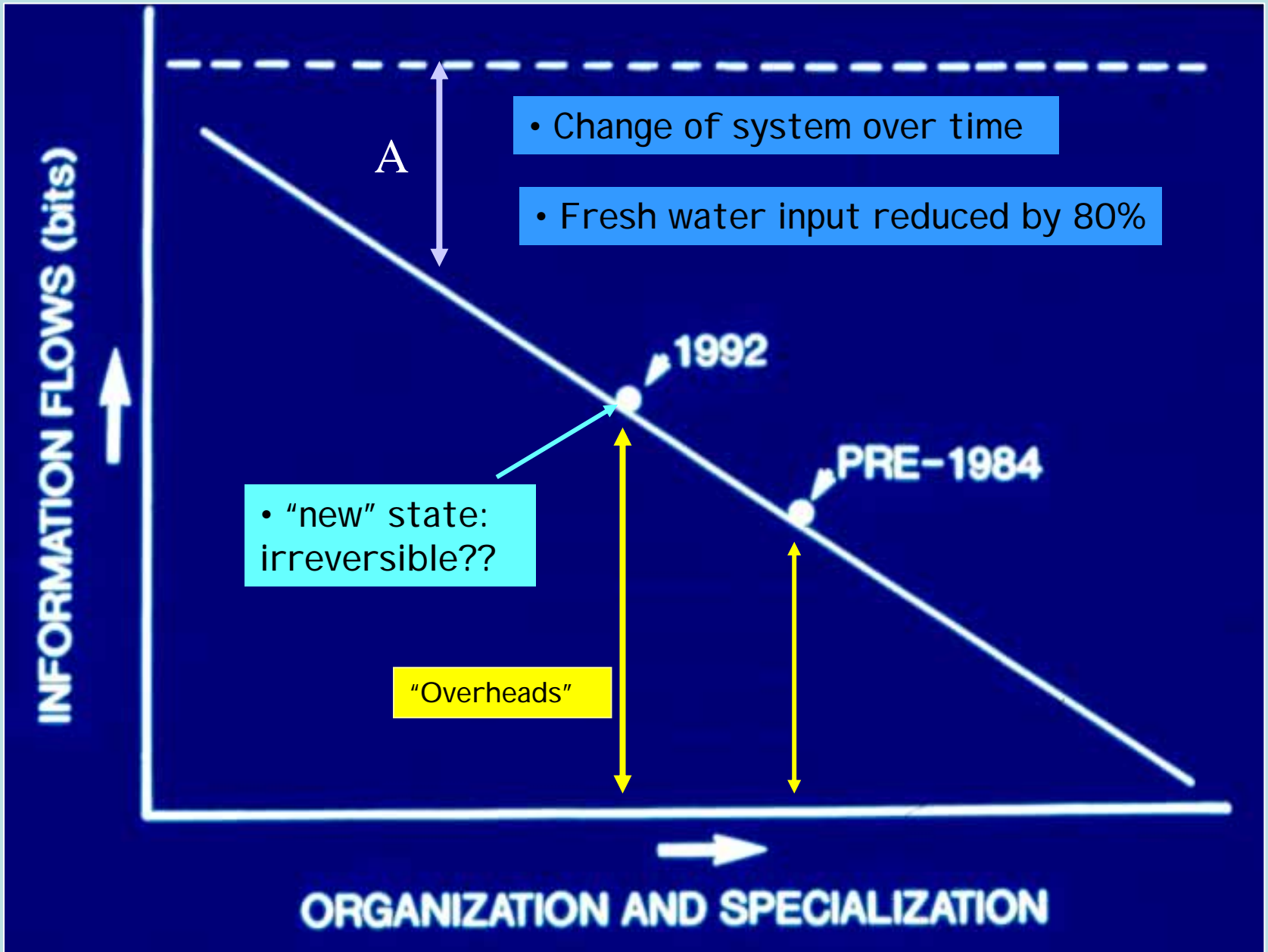




System attributes during years of high and low freshwater inflows in the Kromme River estuary, South Africa.

Main environmental change: Reduction in Freshwater supply

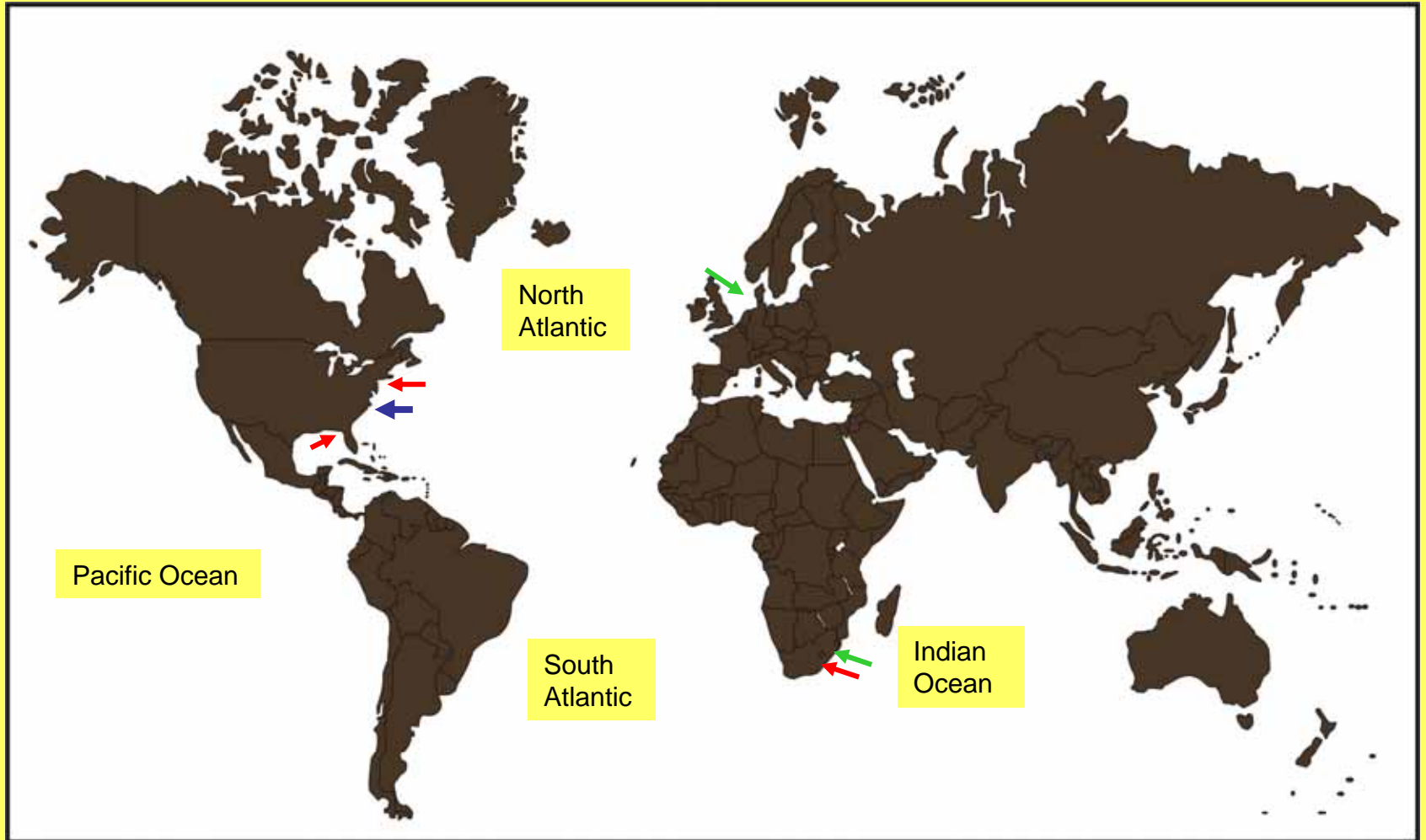
System Attribute	Pre- 1984 [1978 - 84]	Post-1984 [1992 -95]	% increase + % decrease -
Mean annual inflow [$\times 10^6\text{m}^3$]	116.8	1.3	-99%
Annual Temperature range [$^{\circ}\text{C}$]	12.2 - 27.8	12.0 - 28	no change
Annual mean salinity range	16 - 35	33 - 35	33% increase in mean salinity range
Total Biomass [mgCm^{-2}]	562600	648400	15.3
Production [$\text{mgCm}^{-2}\text{day}^{-1}$]	6870	6750	-1.7
P/B day	0.037	0.041	10.8
System Trophic Efficiency [%]	4.5	2.8	-37.8
No of cycles	100	90	-10.0
Finn Cycling Index [%]	11	10.8	-1.8
TST [$\text{mgCm}^{-2}\text{day}^{-1}$]	42831	45784	6.9
Ascendency	68587	74367	8.4
A/C [%]	48.3	46.2	-4.3
Ai/Ci	40.2	38.4	-4.5
Food Web Connectance	2.1	1.77	-15.7



Comparison of ecosystems on spatial scales



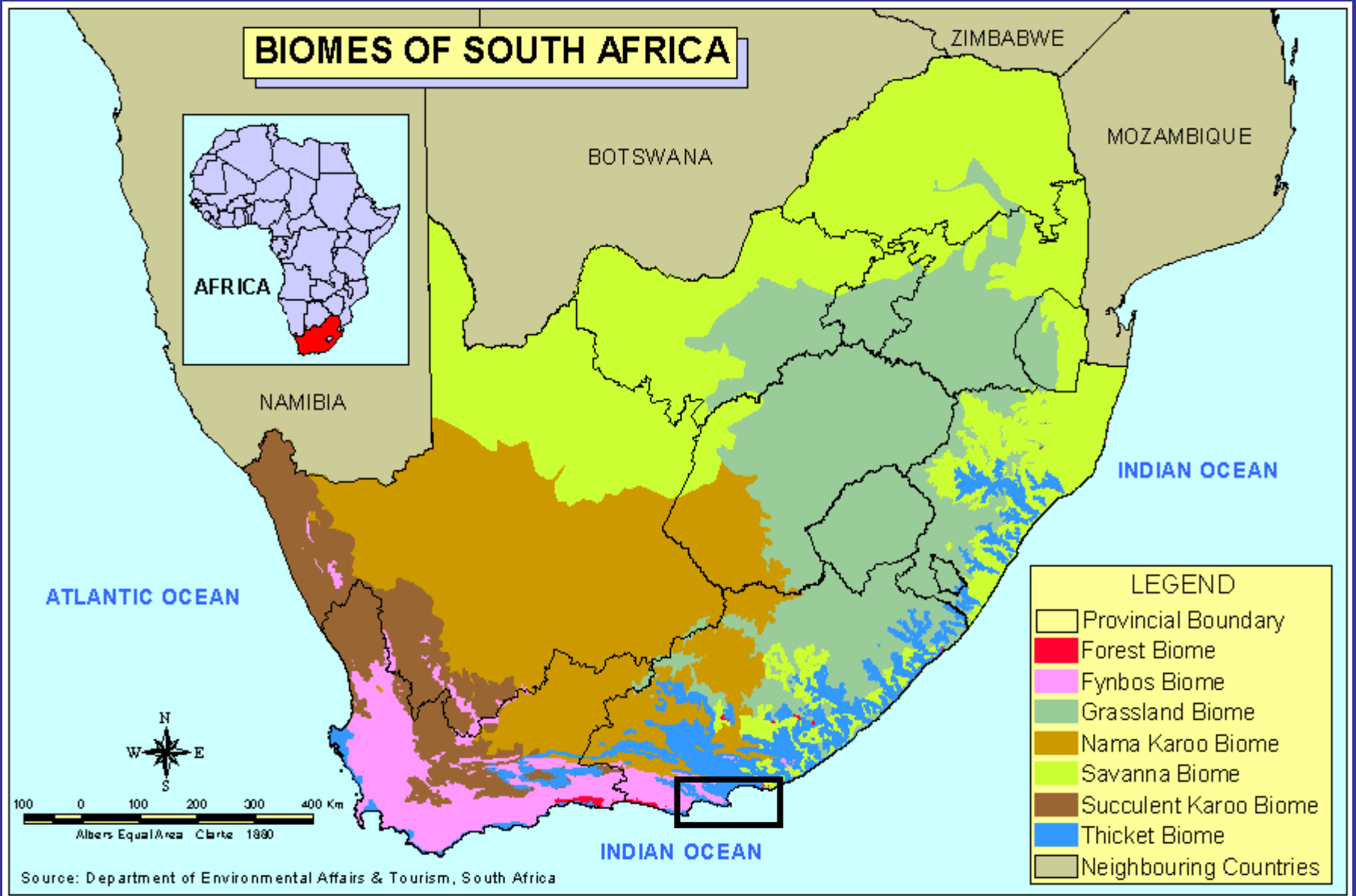
Which systems and where?



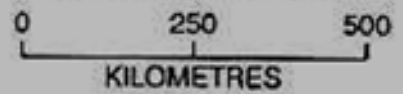
**Temporal
Comparisons**

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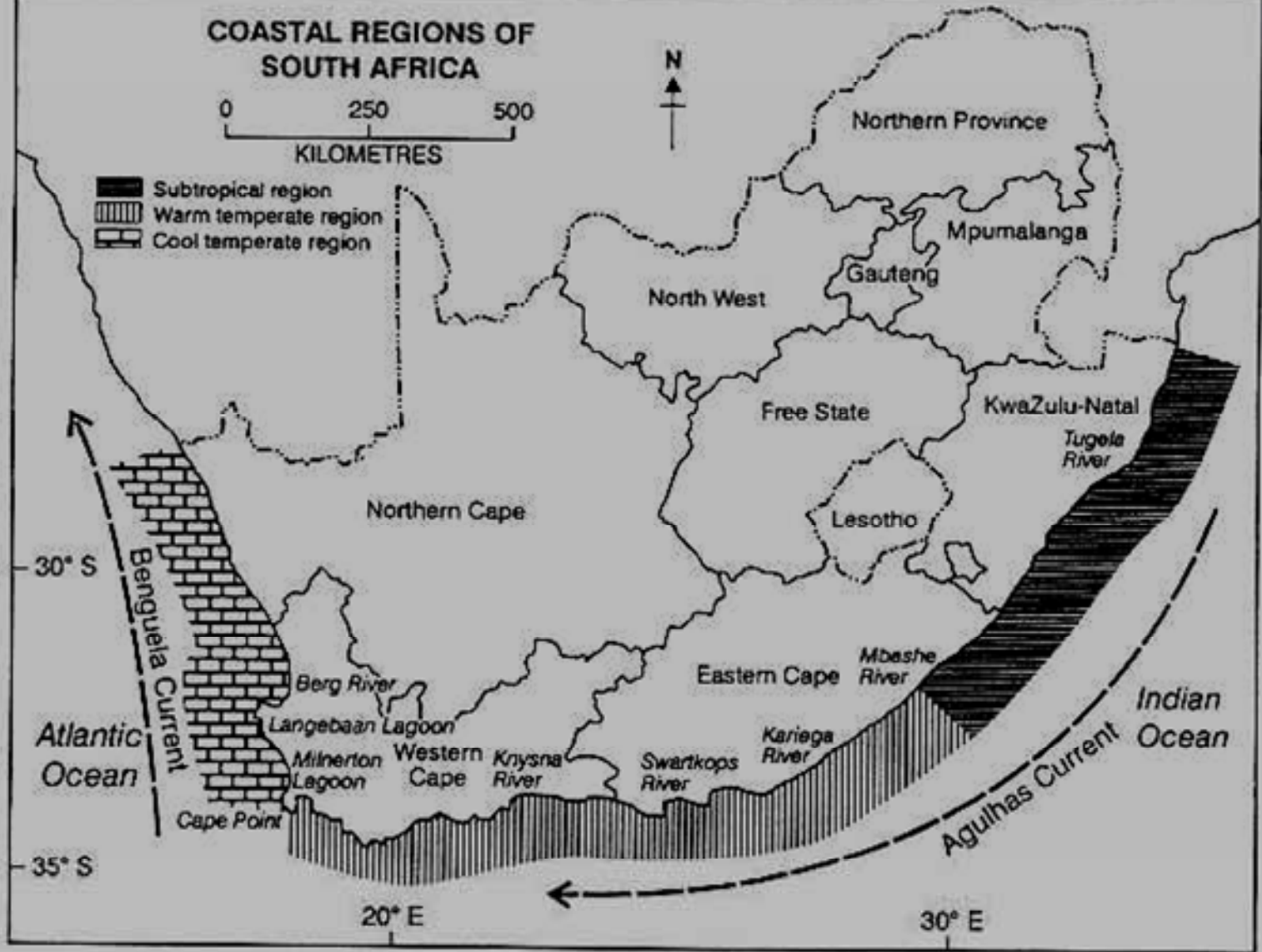
BIOMES OF SOUTH AFRICA

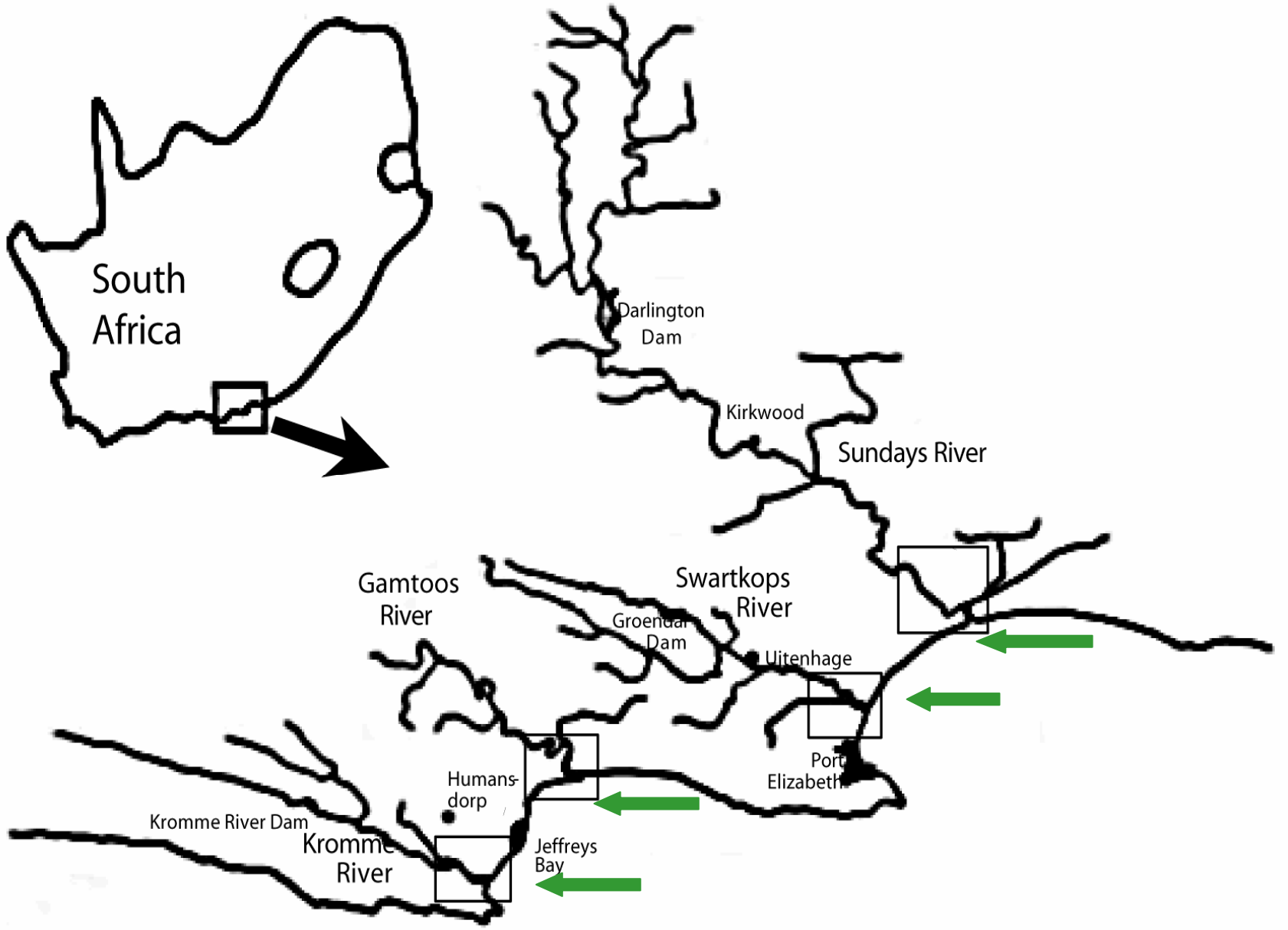


COASTAL REGIONS OF SOUTH AFRICA



- Subtropical region
- Warm temperate region
- Cool temperate region







Kromme River estuary



Gamtoos River estuary



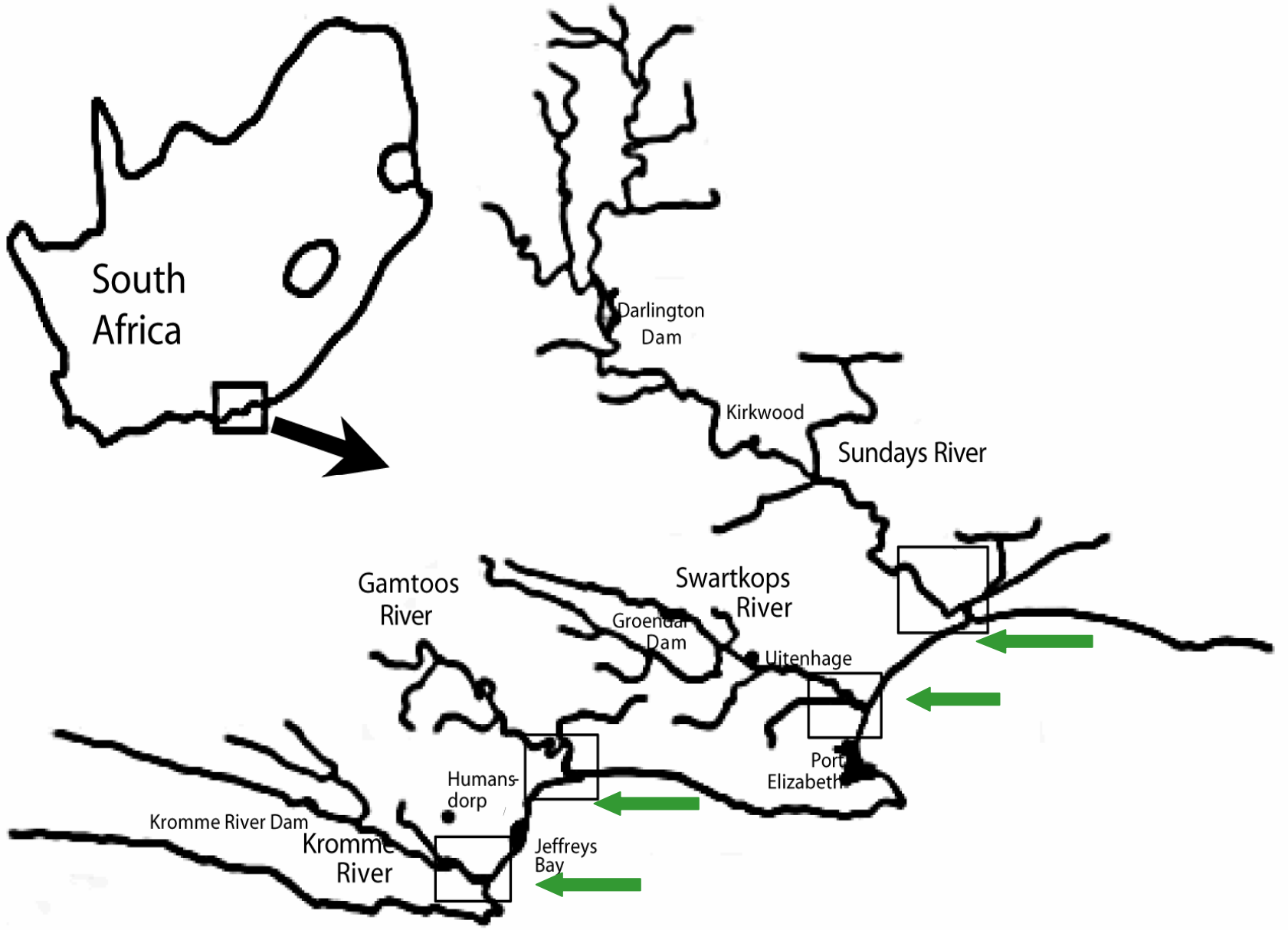
Swartkops River estuary



Swartkops River estuary

Sundays River estuary





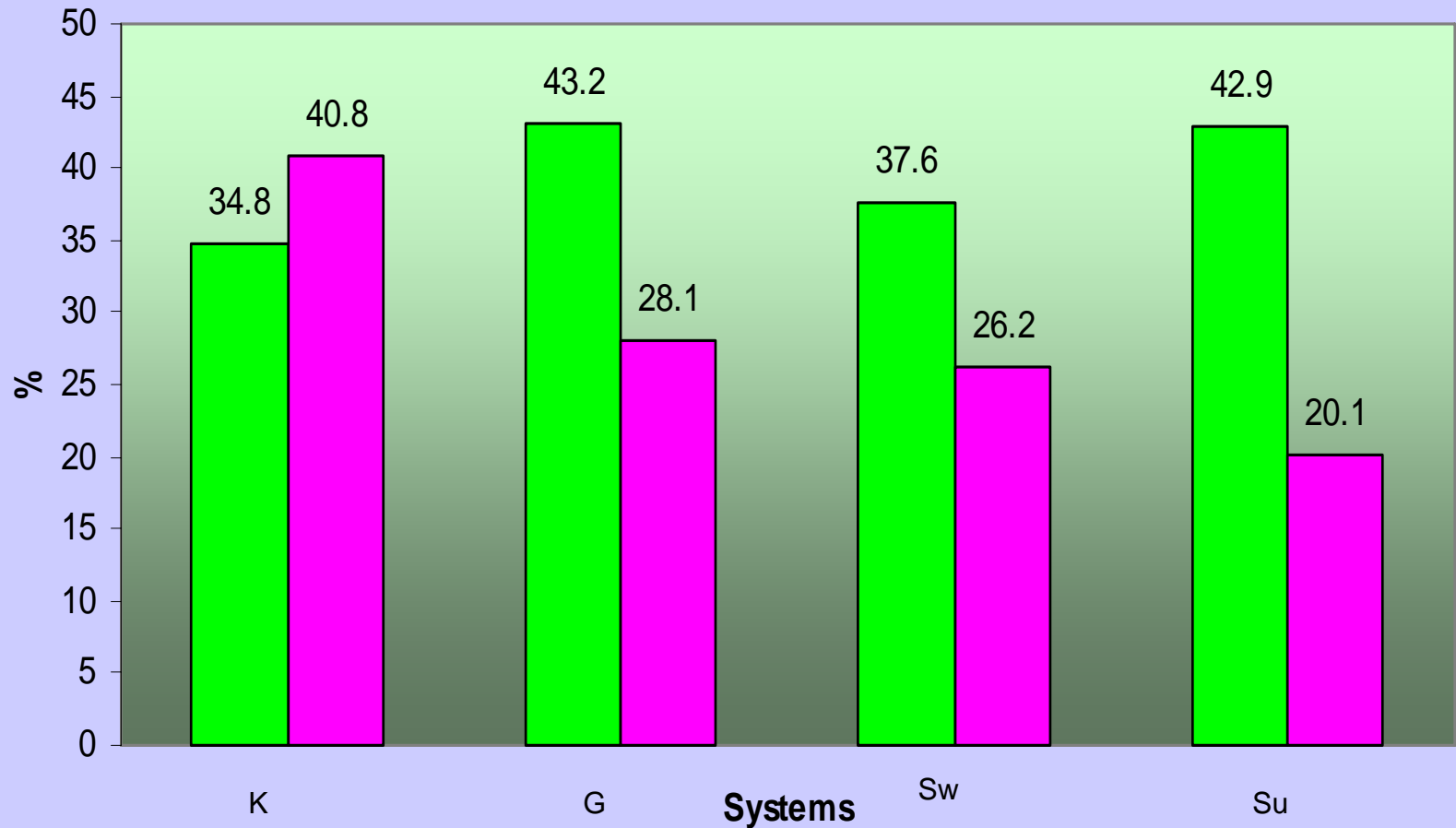
River Characteristics

System	Catchment [km ²]	MAR [10 ⁶ m ³]	Water Exchange Time [days, LOICZ]	Fresh water Inflow [m ³ sec ⁻¹]	
Kromme	936	105.2	87	0.07	SD=0.14, n=42
Gamtoos	34500	485	26	1.02	SD=0.85, n=36
Swartkops	1360	84.2	34	0.82	SD=0.86, n=26
Sundays	20792	186.0	42	2.74	SD=1.03, n=30

System attributes of four eastern Cape estuaries, South Africa.

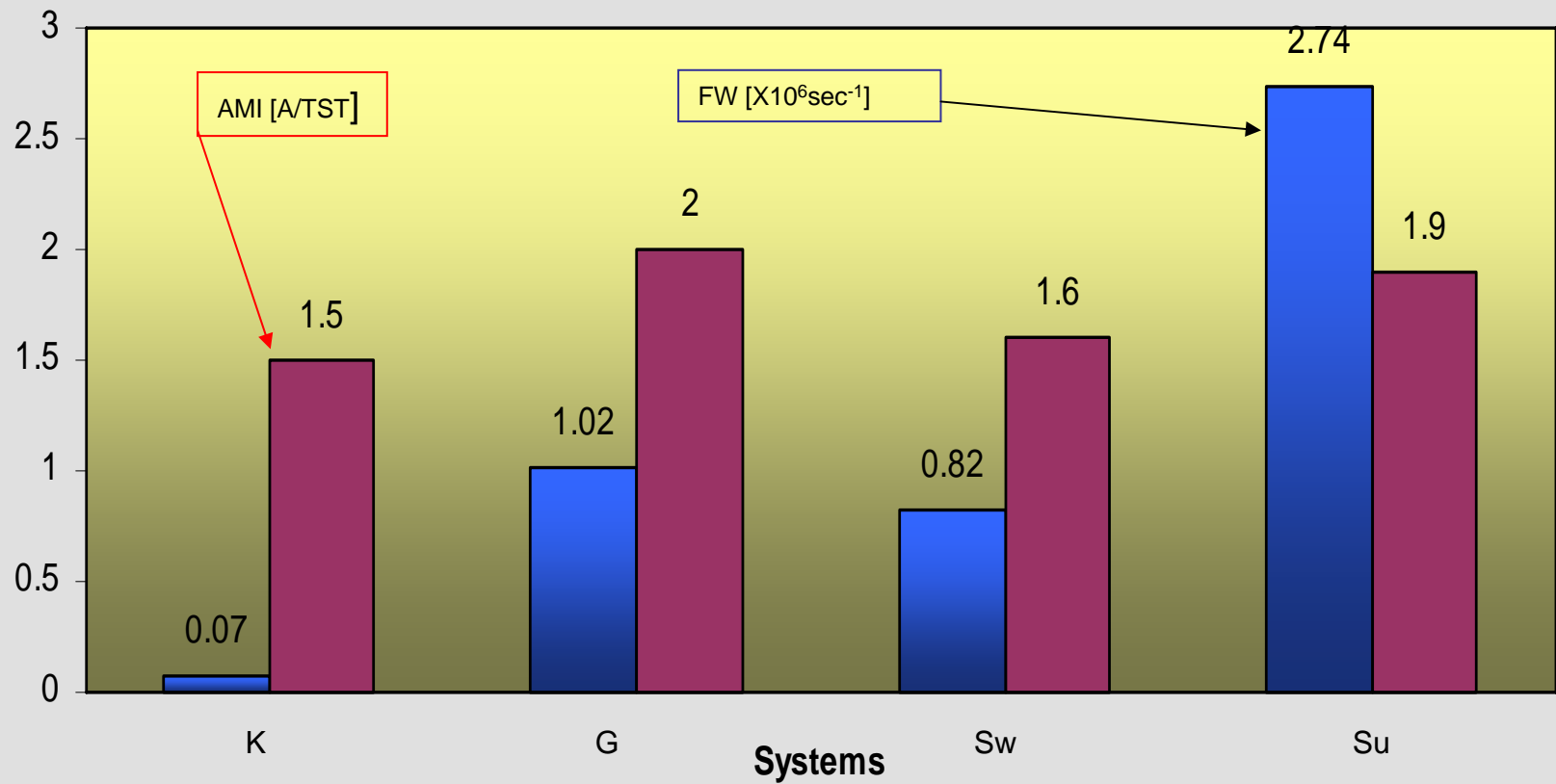
Attributes	Kromme	Gamtoos	Swartkops	Sundays
Air temperature range all seasons [°C]	14 - 32			
Water temperature [winter min - summer max; °C]	17 - 27	17 -27	14 -28	17 - 25
Mean annual fresh water inflow [m³sec⁻¹]	0.07 [SD=1.4, n=36]	1.02 SD=0.85, n=36]	0.82 [SD=0.9, n=48]	2.74 [SD=1.03, n=36]
Salinity range [head to mouth]	32 -35	12 - 35	10 - 35	3.5 - 35
Catchment [km ²]	936	34500	1360	20792
Water exchange time [days]	87	26	34	42
Total Dissolved Inorganic N [µM]	5.03	13.42	6.39	11.81
Total Dissolved Inorganic P [µM]	0.58	0.33	2.43	0.52
System Production [mgCm ⁻² day ⁻¹]	1571.4	4474.5	1761.8	3030.3
Number of model compartments	25	25	25	25
TST [mgCm ⁻² d ⁻¹]	13641	23640	11809	16385
Development Capacity [DC, mgCm ⁻² d ⁻¹ bits]	58883	106680	50205	72692
Ascendency [A, mgCm ⁻² d ⁻¹ bits]	20491	46034	18893	31161
Average Mutual Information [AMI, A/TST]	1.5	1.95	1.6	1.9
Relative Ascendency [A/DC, %]	34.8	43.2	37.6	42.9
Relative Redundancy [R/DC, %]	39.2	31	31	27.1
Relative Internal Ascendency [Ai/DCi, %]	33.4	43.2	38.1	44.1
Number of Cycles	895	1117	917	1209
Fin Cycling Index [%]	40.8	28.1	26.2	20.1
Trophic Efficiency [log mean]	1.8	3.2	1.33	2.56
Flow Diversity [DC/TST]	4.32	4.5	4.25	4.44
Food web connectance	1.77	1.99	1.83	2.33
Overall Connectance	2.33	2.03	2.03	1.91

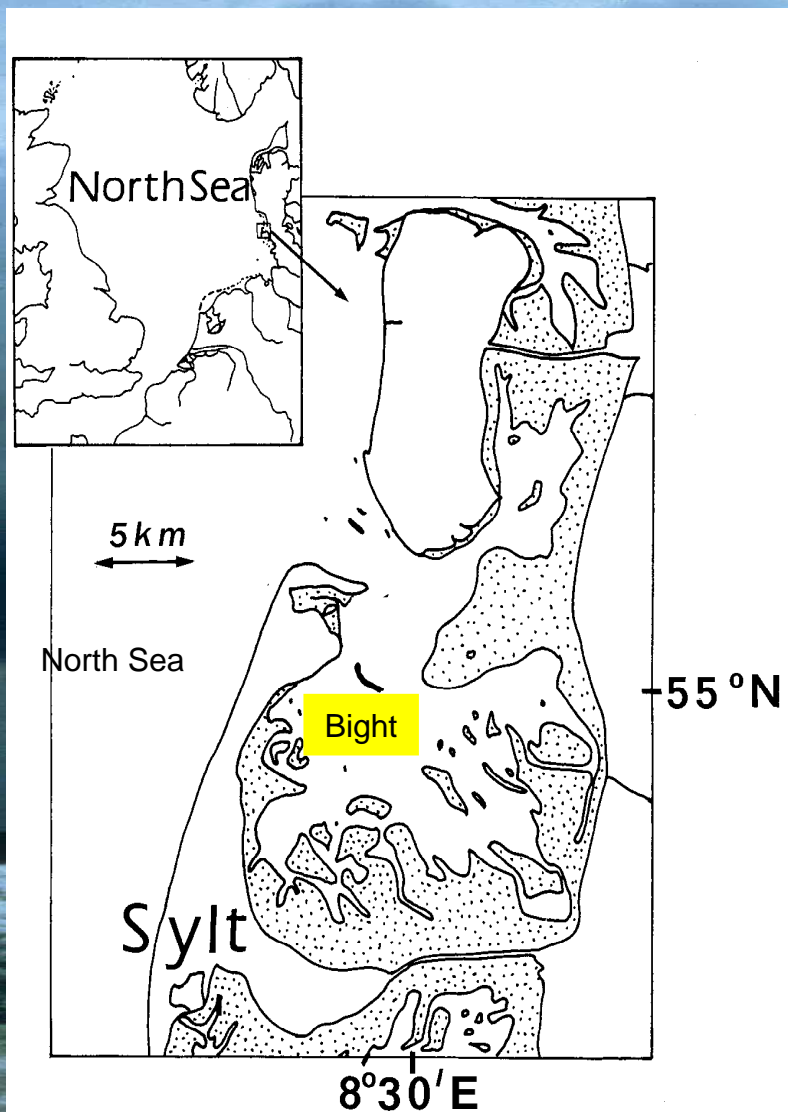
Finn Cycling Index [Tc/TST] and Relative Ascendency [A/DC]



- Inverse relationship between FCI and A/C ratio. High degrees of cycling not necessarily indicate high levels of organization.
- System properties not viewed individually.

Freshwater inflow rate and Average Mutual Information





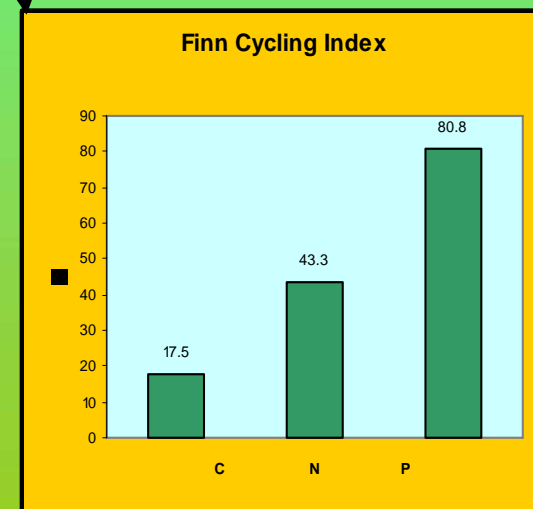
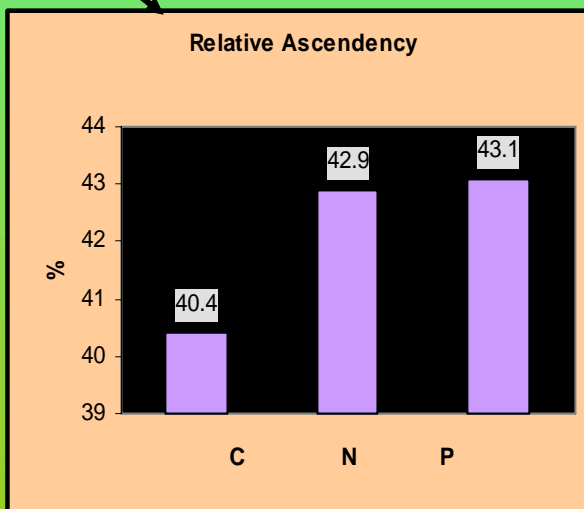
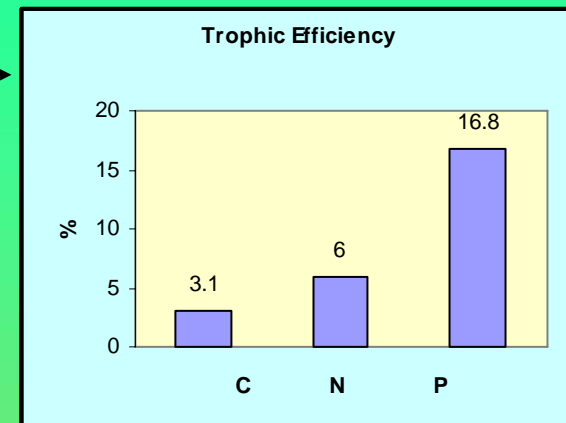
Nutrient dynamics in coastal ecosystems of great importance of system function. Functioning of C, N & P from systems point of view not well studied or understood. Using ENA on networks of C, N & P flows between producers and consumers, inputs, internal generation, recycling, demand, and exports give us some idea of behavior of these macro elements.

Few studies on simultaneous dynamics of C, N & P in ecosystems [exceptions: Chesapeake Bay, Sylt-Rømø Bight [German Wadden Sea].



Selected global system attributes derived from ENA for Carbon, Nitrogen and Phosphorous in the Sylt-Rømø Bight [54 compartment models].

System Attributes	Carbon	Nitrogen	Phosphorous
Trophic efficiency (logarithmic mean, %)	3.1	6	16.8
Number of cycles	1 185	414 744	538 800
Finn Cycling Index (%)	17.5	43.3	80.8
Average Path Length (APL=TST-Z/Z)	2.8	3.65	9.81
Average Residence Time (ART; days)	33	29	201
Relative Ascendancy (A/DC, %)	40.4	42.9	43.1
Average Mutual Information (A/TST) (normalized A)	1.95	1.89	2.03
Overall connectance	2.242	2.474	2.657



• How will climate change affects nutrient dynamics?

• Higher water temperatures, less oxygen, nitrification rates down, denitrification rates up?

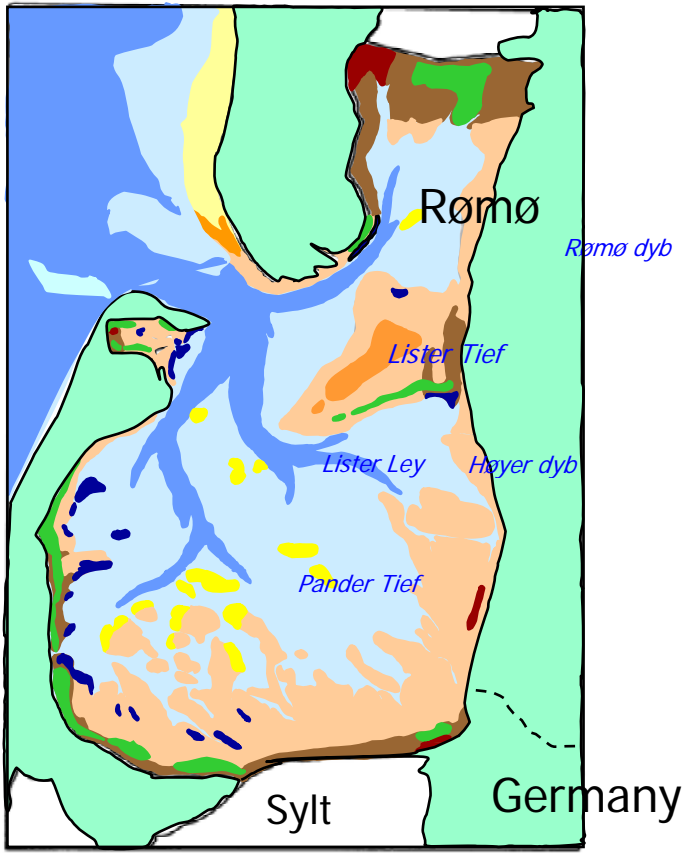
• Warmer environment, increased energy dissipation, faster C cycling?

Concluding Remarks

- Ecosystems respond to variable environmental conditions: natural or anthropogenic induced;
- ENA of food web models show changes in system attributes over time associated with changes in the environment;
- Climate change will exacerbate natural variability, and the dynamics of ecosystems will respond to a far greater extent as components disappear, by the invasion of new ones, altered growth and mortality rates, changing energy flow patterns, etc.
- Analyses of quantitative flow models by ENA allow insights of changes and responses at **ecosystem level** which cannot be inferred from the variability of individual components, or at a single trophic level;
- Climate change affects most, if not all, of the species/communities in an ecosystem; results presented here indicate we can assess changes in system function and contribute to our understanding of the relationship between climate change and ecosystem function.

An aerial photograph of a coastal landscape. In the foreground, a wide, sandy beach meets the ocean with white-capped waves. A river flows from the left, forming a delta that surrounds a small town with colorful buildings. The middle ground shows rolling green hills and fields. In the background, a range of blue mountains stretches across the horizon under a clear sky.

Thanks



Denmark

- Why difficult to understand how ecosystems work?
- Why not predict or simulate how an ecosystem will behave? [engineering models predict behavior of engineering systems; outcome of chemical reactions can be predicted, simulated and repeated]

- Ecosystems possess properties which do not emerge by summing the properties of the component parts.

- Inherent variability of biological parameters and processes.

Variability a fundamental property of organisms in population, populations in a community;

Confidence limits of prediction of biological outcomes in the order of 25%;

When process models with inherent variability are coupled, the confidence limits on the output are very wide.