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TITLE: "PARAMETERS FOR PREDICTING RED TIDES OF BIOLUMINESCENT
DINOFLLAGELLATES: METEROLOGICAL EVENTS AND FRONTAL WATER
CIRCULATION PATTERNS"

SHORT TITLE: "RED TIDES AND FRONTAL WATER CIRCULATION PATTERNS"

INTRODUCTION

The goals for the second year of this research remain the same.

1. Analysis and correlation of timings and magnitudes of abiotic parameters with dinoflagellate "red tides" in order to predict red tide occurrences.

2. Verification of predictive capability of the correlational analysis with field observations using "platforms of opportunity".

Emphasis has been placed, as suggested by the Program Manager, on bioluminescent species of red tide dinoflagellates.

PROGRESS REPORT FOR FIRST YEAR

During the past months major emphasis has been placed on the following aspects:

- 1. Concepts

I have developed a set of meteorological, hydrographical and physiological interaction descriptors of events and processes that are common to red tide formation in estuarine,

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coastal and oceanographic environments. The premise is simple. Abiotic processes are the essential driving forces in any ecotope. Environmental selection occurs for those phytoplankton species whose physiological responses to the (changing) photic, nutrient and physical hydrographic regimes permit them to (temporarily) outproduce their competitors. In order to begin this analysis it has been necessary to define more precisely the terms "blooms" and "red tides", both associated with phytoplankton assemblages.

For example, ice melting and rainfall events during early spring and the consequent runoff of nutrient-containing waters into estuaries and coastal waters produce "spring blooms". Likewise persistent winds alongshore produce coastal upwelling and "island effects" in the oceans, resulting in phytoplankton "upwelling blooms". The term "bloom" should be defined as "a significant increase in the standing crop of phytoplankton in any specified geographical region, resulting from an increase in primary production due to a change in the nutrient concentrations in the surface waters". Blooms may include species from different phytoplankton classes; diatoms, cyanobacteria, dinoflagellates. The chlorophyll concentrations in bloom waters may become so high that the waters become "discolored". Regions of such "discolored" waters have been referred to in the literature as "red tides".

The term "red tide" should be reserved for a subclass of bloom phenomena in which phytoplankton species, "are transported and mixed into the euphotic zone of shallow offshore waters by reverse flow below the pycnocline of a surface plume and/or have accumulated dynamically, by virtue of their positive phototaxis, along frontal interfaces". Of the hundreds of potential candidate phytoplankton species present in any ecotope (as can be determined empirically by extensive net tows), a dinoflagellate red tide usually consists of one (or a small number of) "dominant" (or co-dominant) species.

Once red tides are thus defined, temporal and spatial factors can be separated from the overall mechanisms, leaving PROCESSES and SEQUENCES OF PROCESSES, common to red tides in all types of geographical areas. This conceptual framework makes it possible to predict occurrences of red tides. By identifying common sequences of processes characteristic of observed red tides in any region it becomes evident that certain specific sequence of abiotic events must have occurred. This refines the choices for time sequences of climatic events and for physical hydrographic circulation patterns specific to the production of the red tide. The corollary is that in any specific geographic (bathymetric) area, once the temporal and spatial patterns and the functional relationships among the prior abiotic events have been correlated with previous red tide appearances, it should be possible to identify a minimum number of physical parameters that can be monitored as functions of time, from which the temporal and spatial distributions of bioluminescent red tides might be predicted.

The first attempt to elucidate the processes common to red tides is contained in the enclosed preprint of the paper:

H.H. SELIGER, "RED TIDE MECHANISMS: SPATIAL AND TEMPORAL SCALES"
in: Proc. 5th Internat. Conf. Toxic Marine Phytoplankton, Eds.
T.J. Smayda and Y. Shimizu, Pergamon Press N.Y. 1992.

Subsequently two sequential process diagrams, shown in Figures 1 and 2, one for coastal upwelling and the other for estuarine regions, were devised. These incorporate the complete sequences of red tide mechanisms for each ecosystem in terms of the common processes listed in the paper above, and are included with this annual report.

2. Data Accumulation

An extensive literature search revealed a significantly larger anecdotal red tide database than was submitted with the original proposal. Most of these were additional reports of red tides in specific areas. Despite the large number of additional reports there was still a paucity of pertinent climatological or physical hydrographic data. However, there is a positive side. The increase in the number of reported red tide locations and frequencies of occurrence increases the range of the study and increases the probability that abiotic factors can be found that correlate with sequences shown in Figures 1 and 2.

The hardware and software for accumulating, referencing and correlating the meteorological, hydrographical and biological data are purchased and set up so as to be compatible with NOAA and a number of other oceanographic databases. I have switched over to MSDOS (operating system) - WINDOWS-PROGRAMMING and this has required an accelerated learning process.

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RED TIDE MECHANISMS: SPATIAL AND TEMPORAL SCALES

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ABSTRACT

Climatic events and bio-physical sequences involved in red tide formation have been characterized by mnemonic symbols and applied to geographical regions with spatial scales from meters to hundreds of kilometers and temporal scales ranging from daily to annual. Red tides may represent selections for optimization for sexual mating and for delivery of sexual or overwintering benthic cysts to "seed bed" areas. A frontal convergence zone at the seaward edge of upwelling regions can exist and be a source of dinoflagellates transported into nearshore waters below a pycnocline. The physical hydrographic integrity of red tide surface patches enhances transport within geostrophic surface current jets with minimal dilution losses. Stepwise emigration and colonization are fortuitous consequences of red tide formation. Anthropogenic hypereutrophication along coastlines may have enhanced the efficiencies of stepwise emigrations, permitting colonization of areas not previously accessible.

INTRODUCTION

"Red tides" of dinoflagellates, many bioluminescent and/or containing Paralytic Shellfish Poisoning, PSP, toxins have recently "spread" into new areas and red tides and PSP events have increased in frequency and magnitude in areas where they have occurred only sporadically [1]. In this paper dinoflagellate red tides in geographical areas and ecosystems as diverse as tropical bioluminescent bays, temperate estuaries and coastal waters along continental land masses, with spatial scales from meters to hundreds of kilometers and with time scales ranging from diurnal to annual, are linked by common mechanisms, having as their basis the interaction of species-specific physiological responses of organisms with physical hydrographic circulation dynamics driven by specific sequences of meteorological events. These mechanisms are given mnemonic symbols that are used to describe the common sequences leading to red tides.

PHYSIOLOGICAL FEATURES AND PHYSICAL HYDROGRAPHIC MECHANISMS.

A. Observations of Red Tides.

In calm sunny waters phototactic accumulation of dinoflagellates can produce strong vertical concentration gradients of organisms within the upper few meters, with concentrations 10x the mean concentration within the mixed layer. Continued phototactic accumulation within convergence zones of

surface fronts can produce patches or streaks with concentrations (10^6 - 10^7 cells L^{-1}) up to 500x the concentrations in adjacent, contiguous waters [2,3]. Color discontinuities become visible in sunlight from the deck of a ship or an airplane when chlorophyll a concentrations in a convergence zone reach $> 50 \mu g L^{-1}$, depending on water turbidity. If the dinoflagellates are bioluminescent it is possible to see the wakes of ships at night at concentrations $\geq 10^3 L^{-1}$, and to measure even lower concentrations with towable bioluminescence photometers.

B. Physical Hydrographic Features and Processes.

1. Coastal Upwelling Fronts, The Largest Time and Distance Scales.

Coastal upwelling processes involve continental land masses and are driven by large scale annual climatic variations that occur at certain seasons [4-6]. In specific geographical areas the temporal and spatial parameters are mesoscale, \approx days to weeks and \approx tens to hundreds of km.

Sequence I:

Ideally we begin with a previously thermally STRATified nearSHORE system, **STRATSHORE**, produced by INSOLation, **INSOL**.

INSOL ----> **STRATSHORE** **Ia**

Under conditions of increased, sustained alongshore WINDs, **WIND⁺⁺**, where the superscript, **++**, indicates strong effects, higher salinity, colder, nutrient-rich, bottom waters from depths of 100-300 m will be UPWelled, **UPW**, into the surface in the nearshore region, as a reaction to the wind-induced EKman transport, **EK**, of surface waters away from the coast.

STRATSHORE + WIND⁺⁺ ----> **EK** ----> **UPW** **Ib**

All of this takes time (\approx days). If the wind is persistent the higher density, recently upwelled waters will in turn be subject to wind-driven surface Ekman transport. An instability will then develop because the Ekman layer is now the recently upwelled water and is denser than the warmer, less saline waters seaward of the upwelling region. As the denser Ekman layer sinks below these less dense waters, an intermediate-density layer forms, resulting in a shallow density gradient between adjacent upwelling, nutrient-rich bottom waters on one side and the less dense surface waters at the frontal interface. As a consequence there is nutrient mixing into the frontal interface. The net effect is that with continued wind, upwelled, nutrient-rich waters are mixed, not only into the nearshore upwelling region (region of vertical turbulence and diatom dominance), but are moved seaward by the Ekman transport, forming a shallow, density STRATified layer SEAWard of the upwelling region, **STRATSEA**, (region of stratification and potential dinoflagellate dominance).

UPW + WIND⁺⁺ ----> **EK** ----> **UPW** ----> **STRATSEA** **Ic**

The Ekman surface transport also contains an alongshore component of the water motion. The suggestion that the stratified

region seaward of the upwelling region is also fed by the upwelling waters and therefore can support dinoflagellate populations may explain observations of dinoflagellate populations at the edges of upwelling regions.

Sequence II:

When the wind and its ensuing upwelling subside, insolation re-establishes stratification in the nearshore region. This results in a surface density-layer flow, extending seaward, effectively a lower density SURface PLume, **SURPL**. The higher density, colder, stratified layer sinks below the advancing thermal layer, resulting in a REverse FLOW of dinoflagellate-containing waters below the Pycnocline, **REFLOP**. Sequence **IIa** may be only marginally effective in continuing the process of red tide formation.

INSOL-->STRATSHORE-->SURPL-->REFLOP **IIa**

However runoff from RAIN events, **RAIN**, in the watersheds will produce well defined surface runoff plumes, **SURPL++**, resulting in enhanced reverse flow below the pycnocline, **REFLOP++**. This will result in enhanced sub-surface transport of dinoflagellates into nearshore waters where they will be mixed throughout the shallow water column in the photic zone. In the vicinity of estuaries the reverse momentum will also be sufficient to deliver the dinoflagellates into estuary embayments and into the estuaries where, again by bottom frictional turbulence, they will be mixed into surface waters. In addition runoff waters will contain high nutrient concentrations, providing maximal GROWth conditions for the delivered dinoflagellates, **GROW**.

INSOL+ RAIN-->SURPL++-->REFLOP++--> GROW **IIb**

Sequence III:

In calm waters in bright sunlight dinoflagellates, having grown to high concentrations, will ACCUMulate vertically, by phototaxis, **ACCUM**, and form surface patches, the beginning of RED Tides, **RET**. In the convergence zones of ESTuarine fronts, **EST**, TIDal fronts, **TID**, and minor surface runoff plumes, **SURPL**, the already high surface concentrations of dinoflagellates are now subject to further concentration by horizontal advection, and can be enhanced by an additional order of magnitude. Red tides formed in estuaries or embayments may also drift, on ebb tidal excursions, into coastal waters.

GROW ---> ACCUM ---> RET **IIIa**

ACCUM + EST ---> RET++ **IIIb**

ACCUM + TID ---> RET++ **IIIc**

ACCUM + SURPL---> RET++ **IIId**

2. ALONGshore Transport, **ALONG**, and INOCulation, **INOC**.

Sequence IV:

The alongshore, wind-driven geostrophic current deviates only slightly from the wind direction. The speed of the coastal surface JET, **JET**, decreases rapidly (and is rotated slightly) with depth. At the surface the maximum current speed is 2-3% of

the wind speed and at 5 m it is reduced to 5% of the surface speed. The high density of organisms in red tides serves to absorb most of the incident solar radiation, heating up the patch so that it becomes 1-1.5° higher than the contiguous waters, resulting in a hydrographically distinct lens, with vertical dimensions within the effective depth of the alongshore jet. The density discontinuity inhibits mixing with the contiguous waters and thus serves to retain the dinoflagellate populations within the lens. This lens density discontinuity may also be retained at night during seasons when air temperatures are higher than water temperatures.

RET⁺⁺ + WIND ---> JET ---> ALONG IVa

As the coastal jet transports the surface lenses alongshore there results an elongation of the lenses into streaks. Even under these conditions positive phototaxis will continue to replenish the streaks and net transport will continue. The combination of the timing of the meteorological conditions for red tide formation, alongshore transport and inoculation, **INOC**, into a density front seaward of a second upwelling region may be a common mechanism for stepwise emigration of red tide dinoflagellates.

ALONG+WIND⁺⁺ --> EK--> UPW + INOC/STRATSEA IVb

followed by Sequence **III** as the wind subsides. Sequence **IVb** is consistent with the suggestion of Hartwell [7] for a long range transport of dinoflagellates from the northern Gulf of Maine to upwelling regions in the southern gulf.

As the jet proceeds, rain events downwind, producing runoff and **SURPL⁺⁺**, will continue to deliver portions of the alongshore red tide streaks to inshore areas and into estuaries by **REFLOP⁺⁺**, spreading the incidences of red tide events along shore areas far outside of the original locus. In these case the red tide streaks within the jet are already close to inshore areas so that even moderate surface plumes can also effect significant inoculation.

ALONG+RAIN--> SURPL⁺⁺ --> REFLOP⁺⁺--> INOC IVc

Sequence **IVc**, taking place stepwise, may be essential to successful long range alongshore transport [8]. Red tides formed in any nearshore regions can independently be re-transported alongshore by Sequence **IV** to inoculate additional downwind shorelines and embayments. With time, during alongshore transport, the continued (mixing) exchange and dilution of red tide streaks with contiguous waters and the continuing assimilation of nutrients within the streaks will eventually dissipate the red tide. Therefore, it is likely that nutrient concentrations in runoff waters prior to anthropogenic increases may not have permitted growth sufficient to form red tides via Sequence **IIB**. The stepwise emigration and inoculation sequence depends on the timings of storm events as well as the nutrient concentrations carried in runoff waters. It is at this stage that anthropogenic increases in nutrients in runoff can significantly enhance the success of stepwise emigration of red

tides and the introduction of possibly toxic species into new areas or increase the frequency of their success.

a. *Ceratium*, *Dinophysis* and *Peridinium*, Gulf of Guinea, Africa. The climatic events [9] are consistent with sequences **Ia**, **Ib**, **II** and **III**.

b. *Protogonyaulax affina* and *Gymnodinium catenatum* (NW Coast of Spain). The Ria de Vigo (42.2° N 8.7° W) is one of a group of four oceanic bays on the NW coast of Spain which support a major raft-suspension blue mussel *Mytilus edulis* aquaculture industry [10]. Climatic events are consistent with sequence **Ib**, and in Ria de Ares y Betanzos, on the north coast, with **IIIb**.

c. *Pyrodinium bahamense* var. *compressum* (NW Borneo). The general sequence of meteorological events in this region [8], the progression of events leading to red tides, is completely consistent with sequences **I** through **IV**.

2. Bioluminescent Bays. Smallest Time and Distance Scales.

Sequence V:

In Oyster Bay, Jamaica, West Indies, a partially enclosed, kidney-shaped ($\approx 1 \text{ km} \times 0.5 \text{ km}$), hyposaline (32.5 ppt), shallow tropical embayment, open on its western end to coastal waters, a single bioluminescent, non-toxic dinoflagellate species, *Pyrodinium bahamense* Plate, (recently re-named *P. bahamense* var. *bahamense* to differentiate it from the bioluminescent, toxic Indo-Pacific species *P. bahamense* var. *compressum*), is dominant [11]. Red tides with surface concentrations $> 10^7$ cells L^{-1} are produced by reverse flow below a pycnocline and by phototactic accumulation almost every day of the year. A daily, easterly-wind-driven (westerly) current produces the same effect as the density-driven **SURPL⁺⁺** in **Ib**. The events can be represented as

(morning) INSOL --> ACCUM⁺⁺ (below pycnocline)	Va
WIND⁺⁺ --> SURPL⁺⁺ --> REFLOP⁺⁺ --> INOC⁺⁺ (Eastern end)	Vb
INOC⁺⁺ + INSOL --> ACCUM⁺⁺ --> RET⁺⁺	Vc

3. Estuaries. Intermediate Time and Distance Scales.

In the Chesapeake Bay identical mechanisms, involving **SURPL⁺⁺** and **REFLOP⁺⁺** and the physiological response of inhibition of phototactic migration across a sharp salinity discontinuity, operate for the dinoflagellate *Prorocentrum minimum*, over vertical and horizontal scales of tens of meters and tens and hundreds of kilometers respectively [3]. Processes **Ib**, and **IIIb**, **IIIc** and **IIId** operate along the main axis of the bay and in the major tributary estuaries. In addition inoculation of *P. minimum* into the major tributaries proceeds via **IVc**, except that the surface currents for the **ALONG** mechanism are driven by density flow. The phenomenon of cyst formation and delivery to seed bed areas by Sequence **Ib** has been

studied in detail for another dinoflagellate species, *Gymnodinium pseudopalustre*.

CONCLUSIONS

1. This paper proposes that sequences **II**, **III**, and **IV** or **V**, the latter a modification of **II**, are common to all red tides. Sequence **I** applies to upwelling regions.

2. Red tides may have functional significance. Photosynthetic marine dinoflagellates undergo sexual as well as vegetative reproduction. The probability of (+) free-swimming gametes finding (-) partners is proportional to the product of the concentrations of (+) and (-) gametes respectively. If the instantaneous dinoflagellate concentration within a red tide is N , the probability for successful mating and cyst formation is proportional to N^2 and to the time of persistence of the red tide. Since dinoflagellate red tides are formed within the convergence zones of estuarine or tidal shear or plume fronts, the sexual cysts subsequently formed will be transported by reverse flow in the bottom salt wedge, to sediments in "seed bed" areas, below the pycnoclines of the same frontal systems that produced the red tides. When favorable environmental conditions return, the sexual or overwintering benthic cysts will be turbulently re-suspended, along with nutrients, into the water column and triggered to germinate by exposure to high light intensities.

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PROPAGATION OF RED TIDES

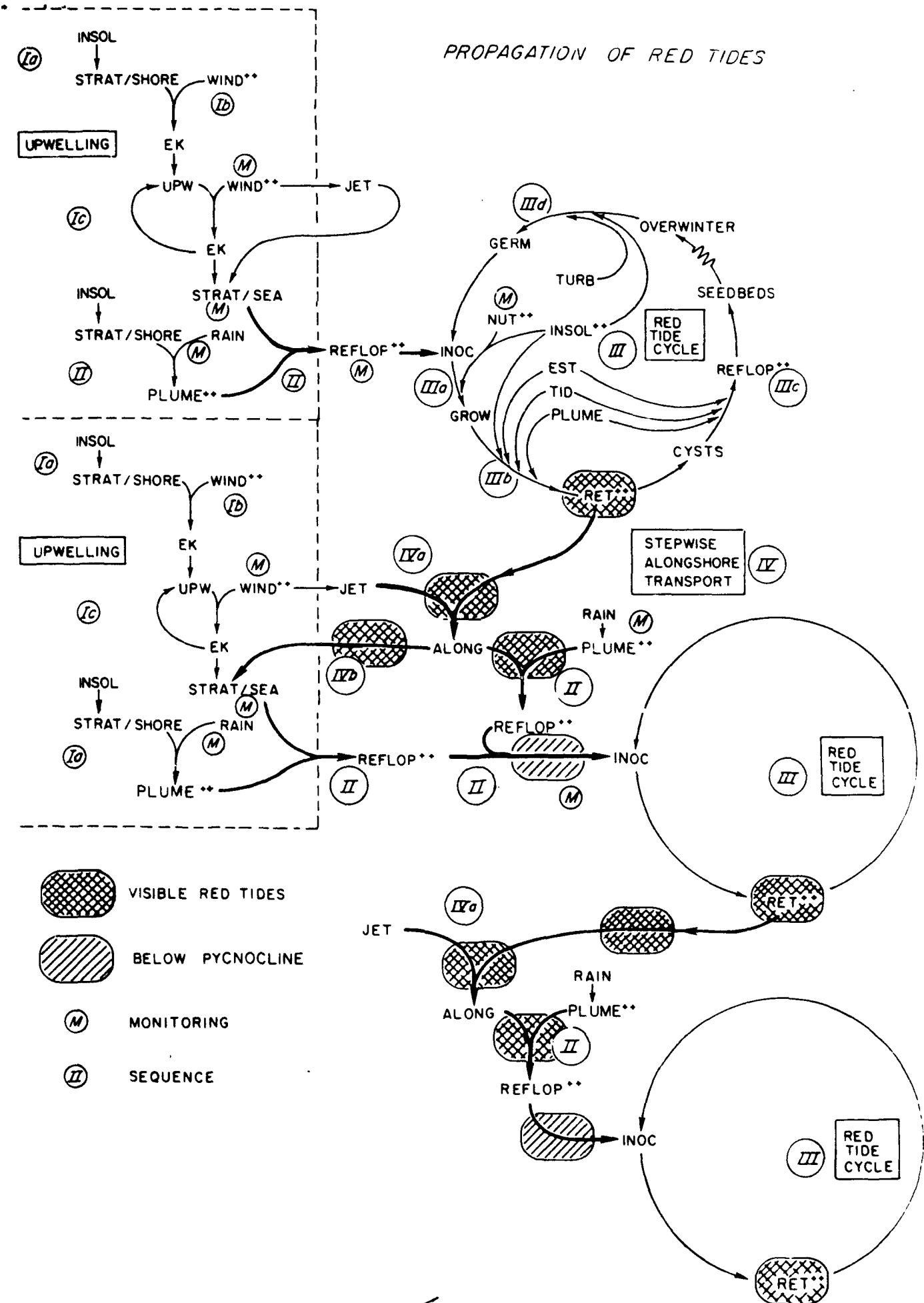


FIG 1

RED TIDES
IN ESTUARIES

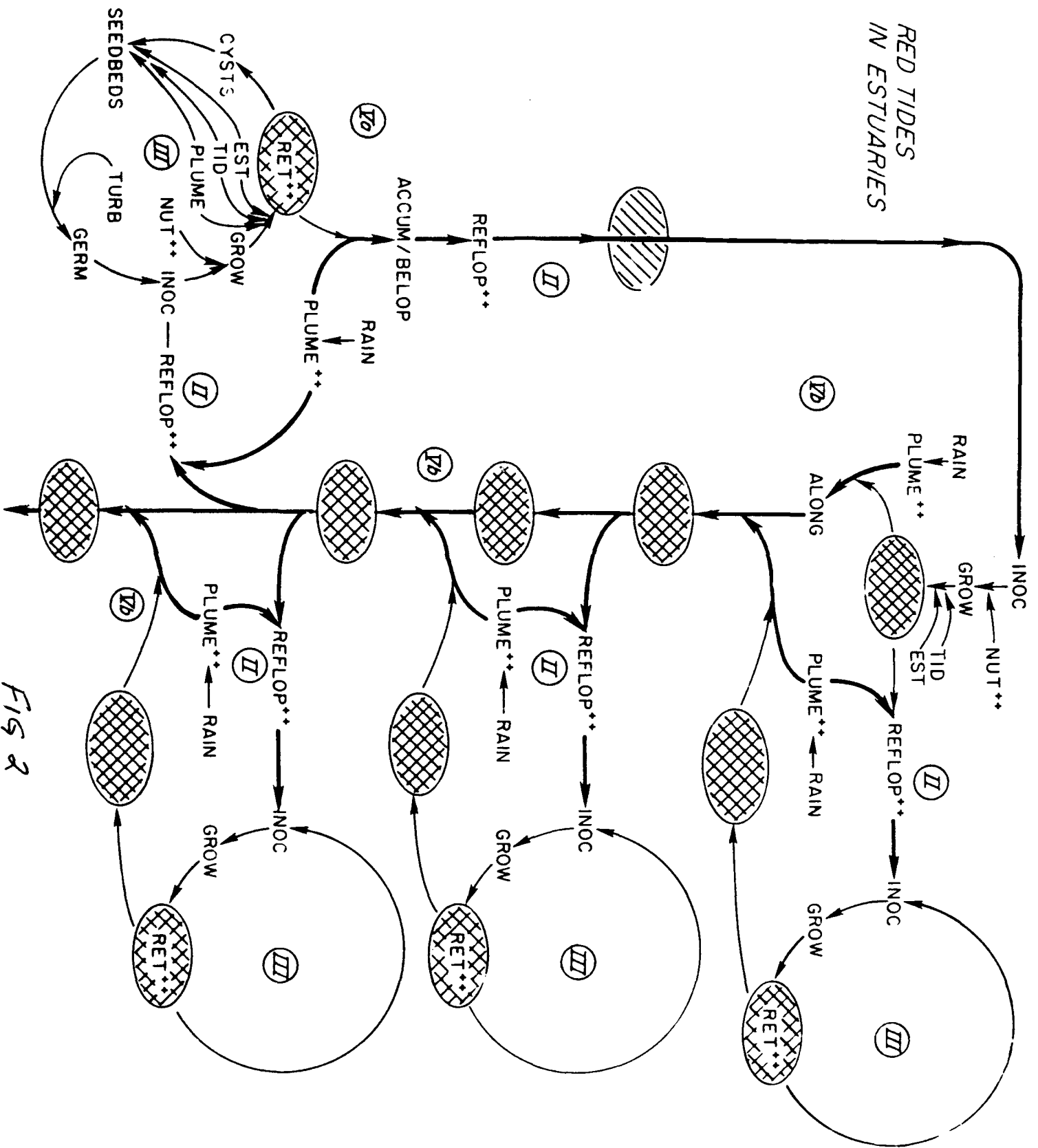


FIG 2