A Conceptual Ecosystem Model of the Corpus Christi Bay National Estuary Program Study Area

A CONCEPTUAL ECOSYSTEM MODEL OF THE CORPUS CHRISTI BAY NATIONAL ESTUARY PROGRAM STUDY AREA

Paul A. Montagna, Ph.D.
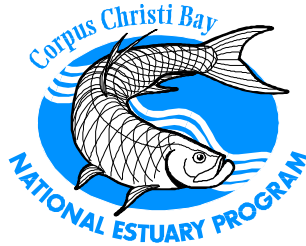Principal Investigator

Contributors
Jian Li, Ph.D.
Gregory T. Street, B.A.

Marine Science Institute
The University of Texas at Austin
P.O. Box 1267
Port Aransas, Texas 78373
512/749-6779
512/749-6777 fax

Policy Committee

Commissioner John Baker
Policy Committee Chair
Texas Natural Resource
Conservation Commission

Ms. Jane Saginaw
Policy Committee Vice-Chair
Regional Administrator, EPA Region 6

Mr. Ray Allen
Coastal Citizen

Commissioner John Clymer
Texas Parks and Wildlife Department

The Honorable Vilma Luna
Texas Representative

Commissioner Garry Mauro
Texas General Land Office

The Honorable Josephine Miller
County Judge, San Patricio County

Mr. Bernard Paulson
Coastal Citizen

The Honorable Mary Rhodes
Mayor, City of Corpus Christi

The Honorable Carlos Truan
Texas Senator

Management Committee
Mr. Dean Robbins, Co-Chair   Mr. William H. Hathaway, Co-Chair

Local Governments Advisory Committee
Mr. James Dodson, Chair   Commissioner Gordon Porter, Vice-Chair

Scientific/Technical Advisory Committee
Dr. Terry Whitledge, Chair   Dr. Wes Tunnell, Vice-Chair

Citizens Advisory Committee
Mr. William Goldston, Co-Chair   Mr. John Hendricks, Co-Chair

Financial Planning Advisory Committee
Dr. Joe Moseley, Chair

Program Director
Mr. Richard Volk

TAMU-CC Campus Box 290 • 6300 Ocean Drive • Corpus Christi, TX 78412
512/985-6767 • FAX 512/985-6301 • CCBNEP home page: //www.sci.tamucc.edu/ccbnep

TNRCC

Barry R. McBee, *Chairman*
R. B. Ralph Marquez, *Commissioner*
John M. Baker, *Commissioner*

Dan Pearson, *Executive Director*

Authorization for use or reproduction of any original material contained in this publication, i.e., not obtained from other sources, is freely granted. The Commission would appreciate acknowledgment.

Published and distributed
by the
Texas Natural Resource Conservation Commission
Post Office Box 13087
Austin, Texas 78711-3087

CORPUS CHRISTI BAY NATIONAL ESTUARY PROGRAM

The Corpus Christi Bay National Estuary Program (CCBNEP) is a four-year, community based effort to identify the problems facing the bays and estuaries of the Coastal Bend, and to develop a long-range, Comprehensive Conservation and Management Plan. The Program's fundamental purpose is to protect, restore, or enhance the quality of water, sediments, and living resources found within the 600 square mile estuarine portion of the study area.

The Coastal Bend bay system is one of 28 estuaries that have been designated as an **Estuary of National Significance** under a program established by the United States Congress through the Water Quality Act of 1987. This bay system was so designated in 1992 because of its benefits to Texas and the nation. For example:

- Corpus Christi Bay is the gateway to the nation's sixth largest port, and home to the third largest refinery and petrochemical complex. The Port generates over $1 billion of revenue for related businesses, more than $60 million in state and local taxes, and more than 31,000 jobs for Coastal Bend residents.
- The bays and estuaries are famous for their recreational and commercial fisheries production. A study by Texas Agricultural Experiment Station in 1987 found that these industries, along with other recreational activities, contributed nearly $760 million to the local economy, with a statewide impact of $1.3 billion, that year.
- Of the approximately 100 estuaries around the nation, the Coastal Bend ranks fourth in agricultural acreage. Row crops -- cotton, sorghum, and corn -- and livestock generated $480 million in 1994 with a statewide economic impact of $1.6 billion.
- There are over 2600 documented species of plants and animals in the Coastal Bend, including several species that are classified as endangered or threatened. Over 400 bird species live in or pass through the region every year, making the Coastal Bend one of the premier bird watching spots in the world.

The CCBNEP is gathering new and historical data to understand environmental status and trends in the bay ecosystem, determine sources of pollution, causes of habitat declines and risks to human health, and to identify specific management actions to be implemented over the course of several years. The 'priority issues' under investigation include:

- altered freshwater inflow
- declines in living resources
- loss of wetlands and other habitats
- bay debris
- degradation of water quality
- altered estuarine circulation
- selected public health issues

The **COASTAL BEND BAYS PLAN** that will result from these efforts will be the beginning of a well-coordinated and goal-directed future for this regional resource.

STUDY AREA DESCRIPTION

The CCBNEP study area includes three of the seven major estuary systems of the Texas Gulf Coast. These estuaries, the Aransas, Corpus Christi, and Upper Laguna Madre are shallow and biologically productive. Although connected, the estuaries are biogeographically distinct and increase in salinity from north to south. The Laguna Madre is unusual in being only one of three hypersaline lagoon systems in the world. The study area is bounded on its eastern edge by a series of barrier islands, including the world's longest -- Padre Island.

Recognizing that successful management of coastal waters requires an ecosystems approach and careful consideration of all sources of pollutants, the CCBNEP study area includes the 12 counties of the Coastal Bend: Refugio, Aransas, Nueces, San Patricio, Kleberg, Kenedy, Bee, Live Oak, McMullen, Duval, Jim Wells, and Brooks.

This region is part of the Gulf Coast and South Texas Plain, which are characterized by gently sloping plains. Soils are generally clay to sandy loams. There are three major rivers (Aransas, Mission, and Nueces), few natural lakes, and two reservoirs (Lake Corpus Christi and Choke Canyon Reservoir) in the region. The natural vegetation is a mixture of coastal prairie and mesquite chaparral savanna. Land use is largely devoted to rangeland (61%), with cropland and pastureland (27%) and other mixed uses (12%).

The region is semi-arid with a subtropical climate (average annual rainfall varies from 25 to 38 inches, and is highly variable from year to year). Summers are hot and humid, while winters are generally mild with occasional freezes. Hurricanes and tropical storms periodically affect the region.

On the following page is a regional map showing the three bay systems that comprise the CCBNEP study area.
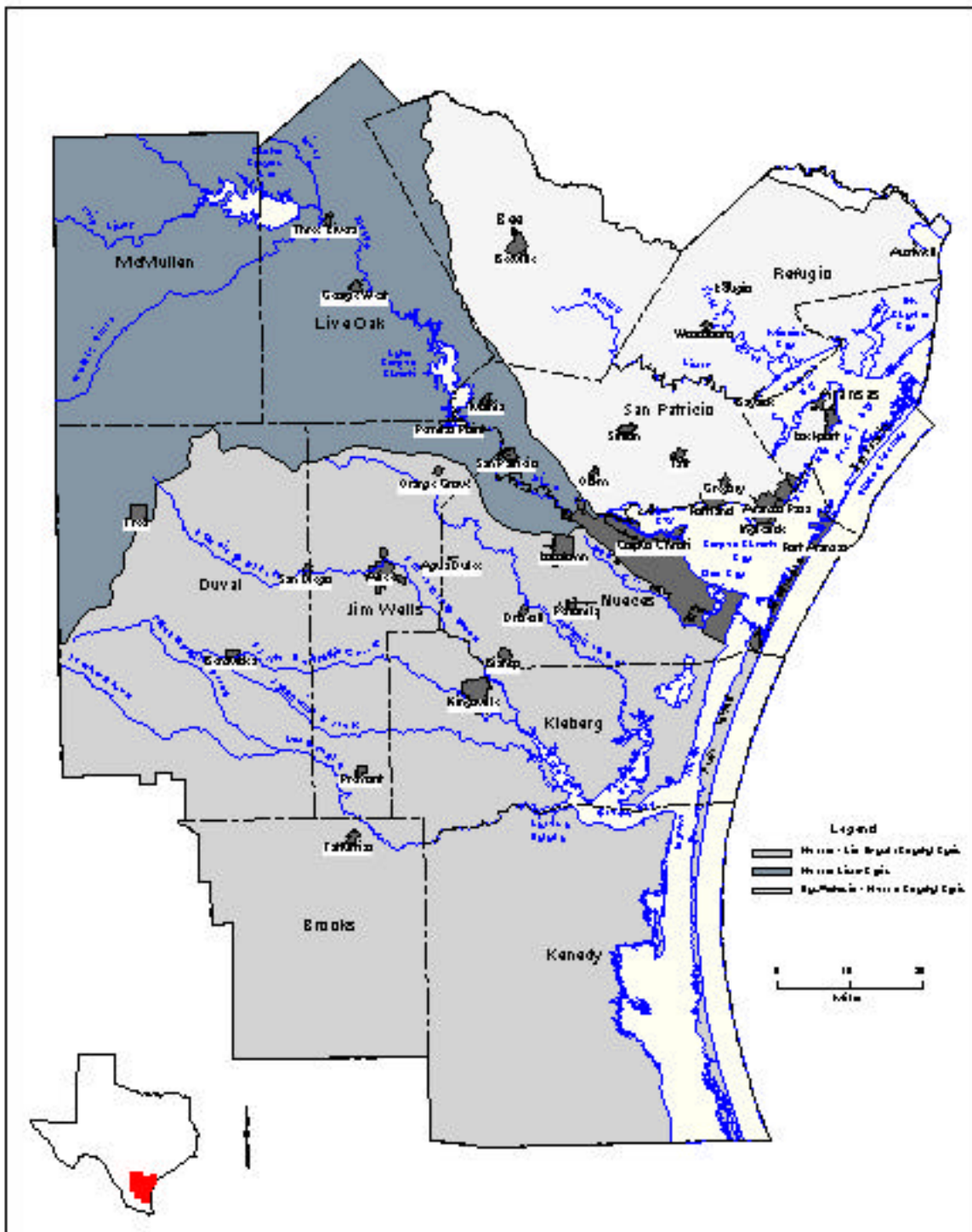
Corpus Christi Bay National Estuary Program Study Area

**A CONCEPTUAL ECOSYSTEM MODEL OF THE CORPUS CHRISTI BAY
NATIONAL ESTUARY PROGRAM STUDY AREA**

TABLE OF CONTENTS

A CONCEPTUAL ECOSYSTEM MODEL OF THE CORPUS CHRISTI BAY NATIONAL ESTUARY PROGRAM STUDY AREA

by

Paul A. Montagna, Jian Li, and Gregory T. Street

EXECUTIVE SUMMARY

The purpose of this project is to develop a conceptual model to describe mechanistic relationships among biotic, abiotic, and anthropogenic components of the estuarine ecosystems contained within the Corpus Christi Bay National Estuary Program (CCBNEP) area. A conceptual model is a presentation of the ecosystem components and linkages among components in a schematic format. The model also includes components for socioeconomic and management policy mechanisms. Therefore, the conceptual model will be useful to environmental managers in the resolution of CCBNEP priority problems.

The conceptual model was developed using a hierarchical structure. The CCBNEP area can be viewed as a single unit with components; the components are composed of subcomponents, and so on. If all the details of an ecosystem are presented in one large model, then it is nearly impossible to identify relationships among components. The hierarchical view allows us to begin focusing on the broadest picture of the CCBNEP area first, then zoom into details of specific subcomponents of interest. Another advantage of the hierarchical nature of the model is that a reader can continue to focus down to finer details depending on the reader's expertise and interest.

The conceptual model is presented in both a technical and public format. The two different formats are tailored to audiences of different levels of technical expertise, i.e., resource managers, scientists and engineers versus the general public. The technical format presents the model using energy circuit language, which is a standard format for presenting ecosystem diagrams. The public format presents the same information that is in the technical format, but it is in "cartoon form". Therefore, words, names, or relationships that may not be familiar to the lay person are not an obstacle to understanding the underlying concepts being presented.

The model encompasses the three major ecosystems of the CCBNEP study area. These three systems are the Baffin Bay-upper Laguna Madre Estuary, the Nueces Estuary, and the Mission-Aransas Estuary. The generic processes that occur in the CCBNEP study area are included in the model as all these processes occur in each system. The relative importance of some of the processes changes among the ecosystems based on the environmental characteristics that may differ among the three ecosystems. These differing characteristics are primarily freshwater inflow, oceanic exchange with the Gulf of Mexico (both of which are greater in the Nueces and Mission-Aransas Estuaries than in Laguna Madre) and areal extent of specific habitat types within the three estuaries.

A CONCEPTUAL ECOSYSTEM MODEL OF THE CORPUS CHRISTI BAY NATIONAL ESTUARY PROGRAM STUDY AREA

Paul A. Montagna, Jian Li, and Gregory T. Street

I. INTRODUCTION

The Corpus Christi Bay National Estuary Program (CCBNEP) is currently in a Characterization Phase. The Characterization Phase will increase the understanding of estuarine problems, probable causes, and recognize management implications. One way to understand and present the complex processes that occur in estuaries is to have a conceptual model of the ecosystems. The goal of this project is to compile existing information regarding conceptual modeling for estuaries, and develop a conceptual (qualitative) model, both pictorial and narrative, of the CCBNEP study area. A conceptual model demonstrates ecosystem linkages at all trophic levels and all habitat types, and provides a conceptual framework that can be used to assess environmental impacts (both episodic and cumulative) associated with external influences.

The conceptual model encompasses the entire CCBNEP area to enable comparison of the region's three major ecosystems. The study area covers about 125 kilometers of the southeast Texas coast and includes all marine and estuarine waters behind the surf-line from the eastern edge of Mesquite Bay to the Land Cut of Laguna Madre, and the 12 associated counties of the Coastal Bend Council of Governments. This includes three distinct ecosystems (Fig. I.1): the Baffin Bay-upper Laguna Madre Estuary, the Nueces Estuary, and the Mission-Aransas Estuary. The Nueces Estuary includes Nueces, Corpus Christi and Redfish Bays. The Mission-Aransas Estuary includes Mesquite, Copano, and Aransas Bays. The models developed apply to all bays and estuarine ecosystems.

The goal in developing the conceptual model is to describe biotic, abiotic, and anthropogenic components of the CCBNEP estuarine ecosystems, and the functional relationships among the components. Such a model would provide the conceptual framework to incorporate socioeconomic issues into environmental management policy. This is necessary to enable resolution of CCBNEP priority problems. Therefore, the conceptual model is didactic, that is, it teaches as well as demonstrates, ecosystem components
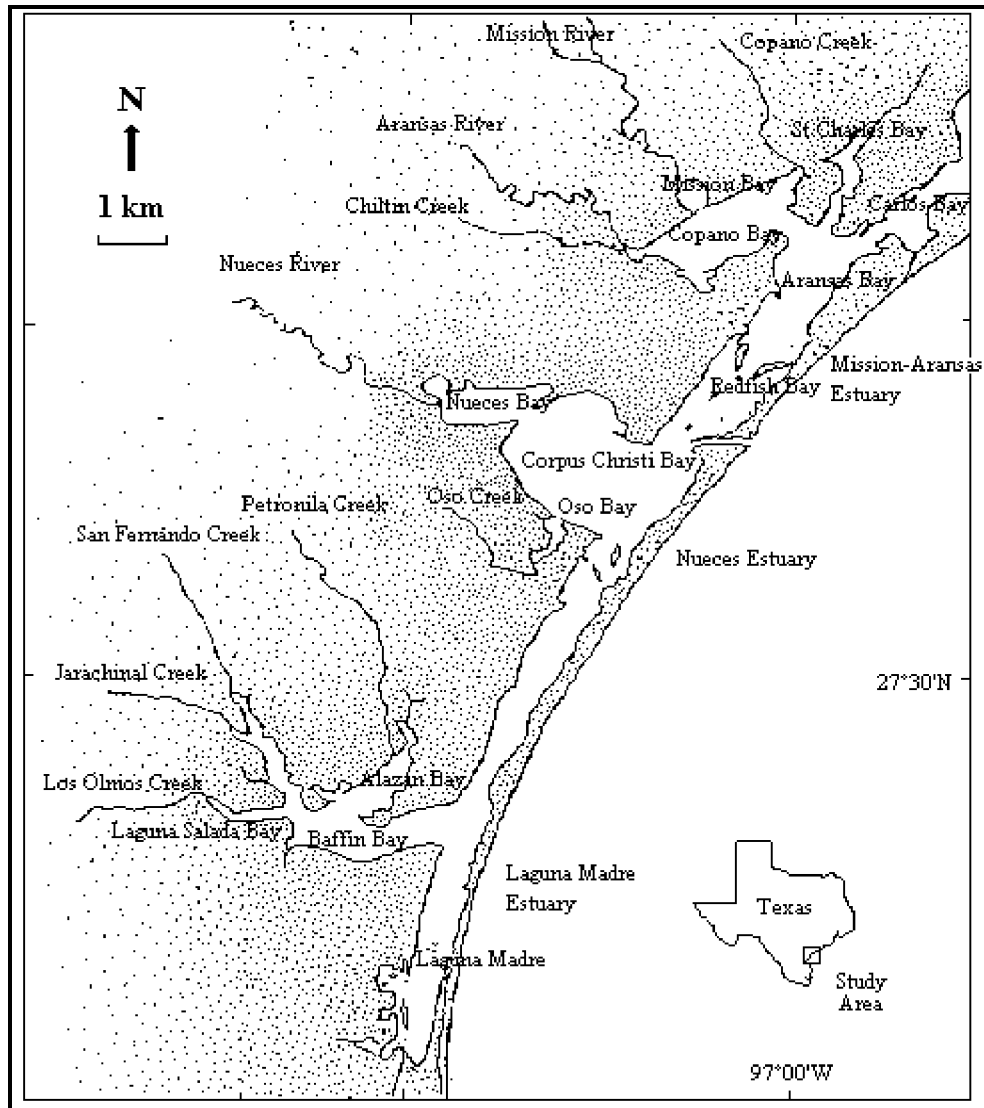
Fig. I.1. Map of study area including three estuaries, Mission-Aransas, Nueces and Laguna Madre Estuaries, and their primary bays, secondary bays, rivers, and creeks.

4

and linkages. The conceptual model should be understandable to a broad audience including the lay public, as well as environmental experts.

There were five objectives that were accomplished by this project:

(1) To develop a systems model to describe the mechanistic relationships among abiotic, biotic, and anthropogenic components of the estuarine ecosystems contained within the CCBNEP area.

(2) To incorporate socioeconomic and management policy mechanisms, where possible, to enable resolution of the CCBNEP priority problems.

(3) To provide a conceptual characterization of the CCBNEP area.

(4) To develop a two-layered model tailored to audiences of different levels of technical expertise.

(5) To compare ecological differences between the three distinct ecosystems within the two ecotones of the CCBNEP study area.

II. METHODS

Many conceptual and quantitative modeling studies of estuaries have been completed during the last 30 years. The first task of the current project was to review this information to assure that all ecosystem components found in other models were incorporated, where appropriate, into the CCBNEP conceptual model. However, we did not simply "cut and paste" existing literature. Rather, we tried to be creative, and develop a different, but accurate view of the estuaries in South Texas.

All models developed for estuarine ecosystems describe components of the ecosystem and the interrelationships among the components. Many go beyond the qualitative state and also provide mathematical relationships for the flow of material among the compartments or for changes in the standing stocks (or amounts) contained in the compartments. Although the current project was limited to developing the qualitative relationships, we provide most of the basic mathematical equations necessary to model most ecological processes. The equations will enhance the presentation of the conceptual model to the technically trained reader.

The presentation of models occurs in a variety of different schematic formats. The most common format, and the only one that comes close to being a standard format, is based on energy circuit language and was developed and refined by H.T. Odum (1972). The conceptual models in this report are drawn using this format. Models consist of a series of diagrams and figures showing the biotic and abiotic components of the ecosystems and the functional linkages present (i.e., the flow of materials between the components).

One innovation presented here is to present the CCBNEP model as a series of hierarchical, conceptual models. The conceptual models presented here include three hierarchical levels: the estuarine trophic component, food web subsystem components, and processes for each component (Fig. II.1). The conceptual model also includes habitat components. Essentially, we started at the highest level, and focused down to detailed levels. This approach was adopted so that we would not produce one figure with an indecipherable amount of information on it. Models are like examining specimens from the macroscopic to microscopic levels. For example, imagine viewing the ecosystem from an airplane, then a boat, then a microscope. This hierarchical view is the technique we used to develop the conceptual submodels.
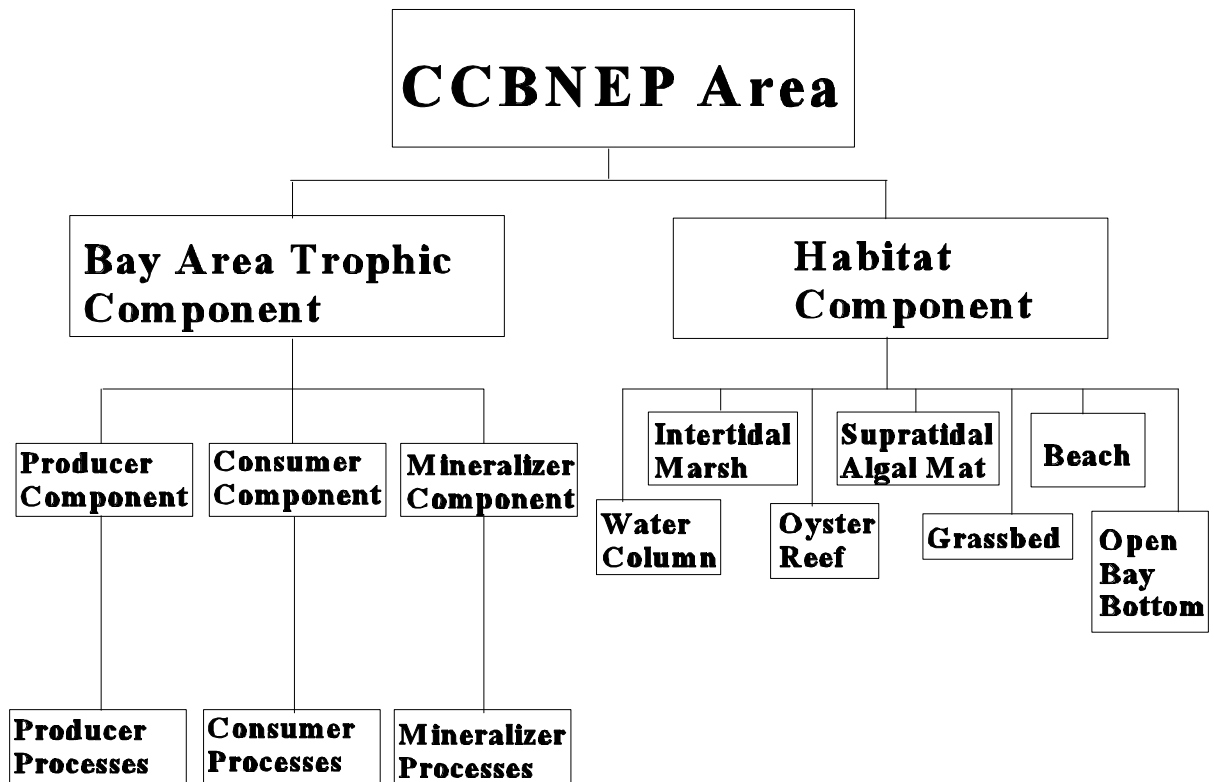
Fig. II.1. The conceptual models described in this study.

The three estuaries of the CCBNEP area share many similarities, but differ in some significant ways. It would be redundant to simply repeat each model three times. The way the models change for each system, is in the quantitative aspects of the sizes of the compartments and flows among the compartments. This is largely controlled by the sizes of two variables: the freshwater inflow balance, and the area of specific habitats or geological features. Therefore, one common view suffices for all three ecosystems. However, specific differences are discussed in section V.

Including biotic and abiotic components into conceptual models is a relatively simple task. However, humans are also an important component in the CCBNEP ecosystems. Incorporating human activities is more complex, and rarely performed. There are a variety of anthropogenic influences that are important, such as effects on water quality and supply, resource utilization (e.g., fishing and hunting), and habitat alteration (e.g., channelization, altering circulation, or habitat destruction). Some activities "act like a switch." For example, fishing yield is translated into dollars, but for some fisheries (e.g. shrimp), the season is either open or closed, which is analogous to turning on or off a switch. Other management strategies "act like a dial," to increase or decrease flows. In this case, there are variable settings and not just "on or off." For example, pressure on a recreational finfishery can be increased or deceased by a range values by changing the size and bag limits on the species. Human impacts and management policies have been incorporated into our models through the switches and dials that alter flows between compartments.

Conceptual models presented using energy circuit language are easily understood by people with a high degree of technical and quantitative skills. The language, because it is technical jargon, contains many shorthand notations that convey detailed information about the system being described. However, the jargon used in these technical models may be an obstacle to the lay public or to members of the Management Conference without specific training in ecosystem science. Therefore, all models have also been presented in a second, pictorial format, which should be relatively easy for people from any background to understand. In some cases, important relationships are emphasized, and the less important relationships are deleted. The pictoral formats are described in lay terms in "summaries" that follow the sections describing each energy circuit model. Energy circuit language and scientific models demonstrate the principles of the interactions within ecosystems. Additional figures or "cartoon" views of the models will ensure that the final product will be useful to scientists, engineers, managers, and the general public. The lay person who has no interest in the technicl details is encourage to skip directly to the sections labled "Summary" and figures with a "B" as a suffix.

The remainder of this report has six sections. The first of these sections describes the ecological processes that occur within estuaries of the CCBNEP area. The description of ecological processes is a typical format for conceptual models. Many of the processes are modified or have unique pathways in different habitats. Therefore, we have also identified the major habitats and unique pathways in these habitats in the next section. The third section describes the relative differences in the ecological processes among the three estuaries within the CCBNEP study area. The next section describes the anthropogenic influences upon ecological processes within the estuaries. The next section describes the "Priority Problems" identified by the CCBNEP as potential problems worthy of further scientific investigation. The final task was to identify data and information needs, and this is the subject of the last section of the current report. There will be gaps in the understanding of these ecosystems. The conceptual model identifies the compartments that exist and the arrows identify the existing linkages. Other CCBNEP characterization reports can be used to determine which compartments are well known, and for which information is lacking.

III. ESTUARINE PROCESSES

Background

Communities of organisms, considered together with their physical settings or habitats, are known as ecosystems. The flow of energy through an ecosystem is very complex, involving many different types of energy sources, interactions and sinks. A convenient way to represent energy flow through an ecosystem is by using energy circuit diagrams. Models based on energy circuit diagrams, developed by Odum (1971, 1972 and 1983), symbolically represent the thermodynamic constraints, feedback mechanisms and energy flows in ecosystems. An energy circuit diagram is used to divide an ecosystem into its component parts and illustrate the relationships and connections among those parts. The symbols used in energy circuit diagrams include paths, sources, storage tanks, interactions, heat sinks, switches, transactions and subsystems (e.g., producers, mineralizers and consumers) (Fig. III.1). Paths, represented by arrows, show the direction of energy flow through an ecosystem. Sources, represented by open circles, are energy inputs from outside the ecosystem, such as sunlight.

There are two, basic, trophic processes: production and consumption. Producers are represented with a bullet. Consumers are represented with a hexagon. These two process symbols are shorthand notation for the processes that occur within the symbol, e.g., storage, interactions and energy flow. Storage tanks, represented by shields, are temporary depositories for energy. Living things can be considered storage tanks, because of the energy tied up in living tissue. Interactions, represented by arrow boxes, occur between two or more types of energy flow. For example, temperature has an interaction with the biological process of respiration. Energy sinks, represented by shrinking parallel lines are the energy losses in an ecosystem. Uneaten food that becomes buried, and therefore inaccessible, is a common energy sink. Switches, illustrated by concave boxes, reflect some management control on the flow of energy from outside the ecosystem. Transactions, represented by a rhombus, occur when there is feedback from an energy path to an energy source. Subsystems are smaller units within the main ecosystem. For example, the general category of "producers" can be broken down into specific types of producers, such as plankton and seagrass.

There are different ways in which an ecosystem may be represented by using an energy circuit diagram. One approach is to model different trophic levels, such as the producer
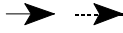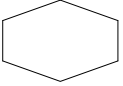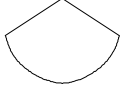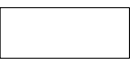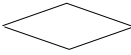
→➤ ⋯➤	Paths of energy flow
◯	Energy source
⬭	Producer
⬡	Consumer
⬭	Storage
⬠	Interaction
⏚	Heat sink symbol
▭	A system or subsystem
⬙	Switch
◇	Transaction

Fig. III.1. The symbols used for parts of an ecosystem.

subsystem, consumer subsystem, or mineralizer subsystem. Ecosystems can also be portrayed as different habitat subsystems, such as beaches, intertidal and shallow subtidal flats, deeper areas, and deltas. Biotic habitats include salt marshes, oyster reefs, mussel beds or seagrass beds. In this report, we present models using both approaches to cover both general and specific information.

Bay System

Like all ecosystems, the CCBNEP bay ecosystem consists of the system itself and its input sources and output targets (Fig. III.2A). The bay area ecosystem receives energy from external sources. The primary source of energy for the bay is the sun. Energy also comes from rivers, groundwater and terrestrial runoff, which provide nutrients for primary producers and detritus for consumers and mineralizers. Energy is exchanged between the coastal ocean and bay as current, wind and tide movements of nutrients and detritus, and the migration of some consumers, such as fish and shrimp. Energy leaves the bay ecosystem through a heat sink, returns to land through human fishing and hunting or else is transferred to the coastal ocean (Fig. III.2B).

The main structure of the bay system includes six energy sources, seven storage tanks and three subsystems (Fig. III.3A). Sun, wind, tide, river, runoff and ocean are the energy sources. The storage tanks are salinity, temperature, carbon dioxide (CO_2), water (H_2O), nutrients, kinetic energy, oxygen and detritus. Three main subsystems (ecological processes) are: producers, consumers, and mineralizers. All processes require input from sources that are modified by storage systems.

Sources

Irradiance from the sun increases the temperature of the whole ecosystem (Fig. III.3A), which, in turn, affects the physiology of every producer, consumer and mineralizer. Sunlight provides the energy for photosynthesis, the biochemical pathway used by almost all producers to increase their biomass, and indirectly gain energy (Parsons et al. 1984).

Heat from the sun also creates wind. Warm air is less dense and tends to rise upward in the atmosphere. Cool air is more dense and sinks through the atmosphere. The movements of these parcels of air are known as air currents, or on a more local scale, wind. In the bay
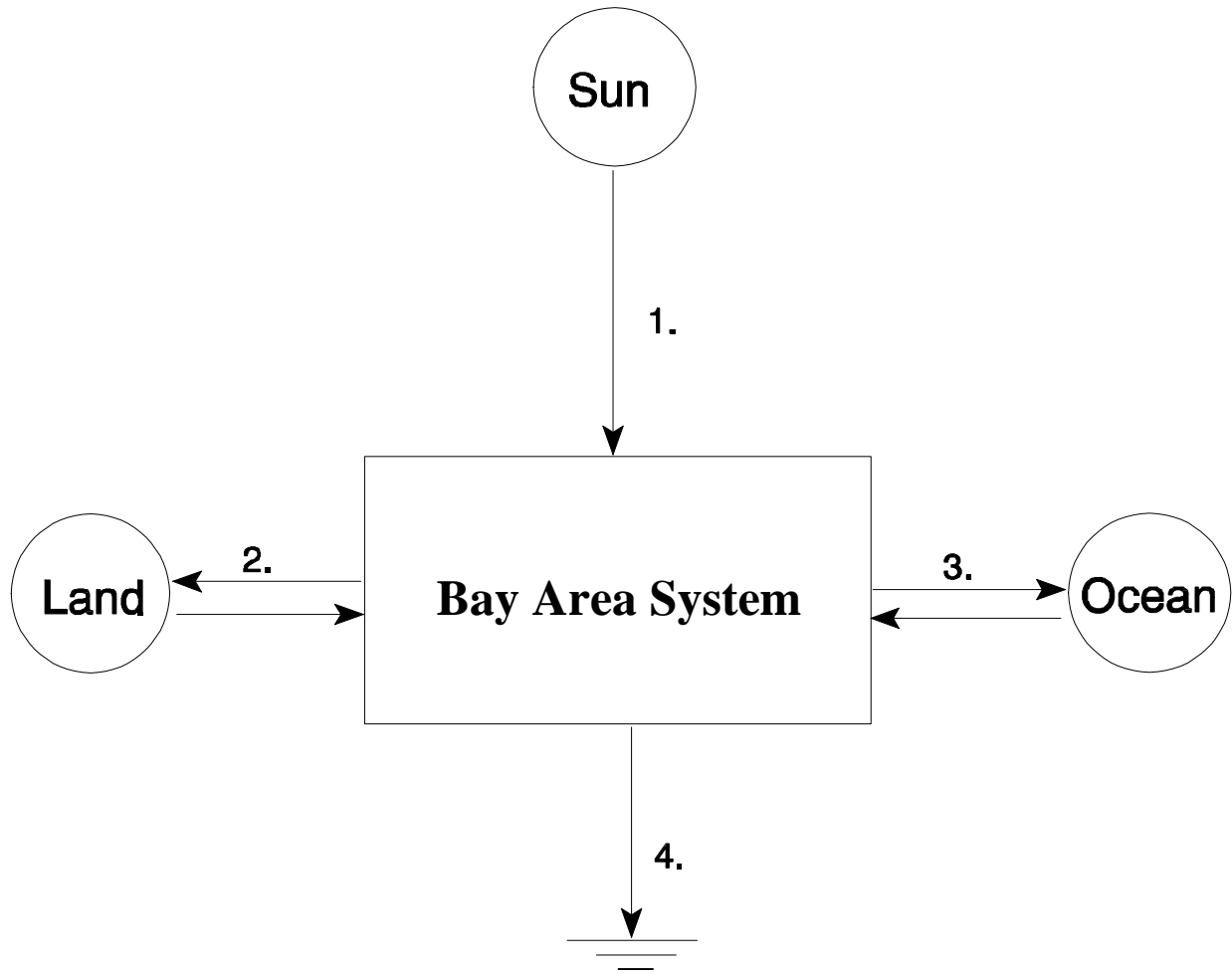
Fig. III.2A. The landscape and seascape of the Corpus Christi Bay National Estuary Program study area in terms of input and output from the Bay Area System. 1. Energy for primary producers from sun. 2. Energy input from land through rivers, groundwater and runoff, which provide nutrients for primary producers, organic matter for consumers and mineralizers, and output to people through human fishing or hunting. 3. Energy input and output through coupling with the coastal ocean including currents, wind and tide carrying out nutrients and organic matter, and migration of macrofauna. 4. Energy sink in the form of heat to produce CO_2 and H_2O.
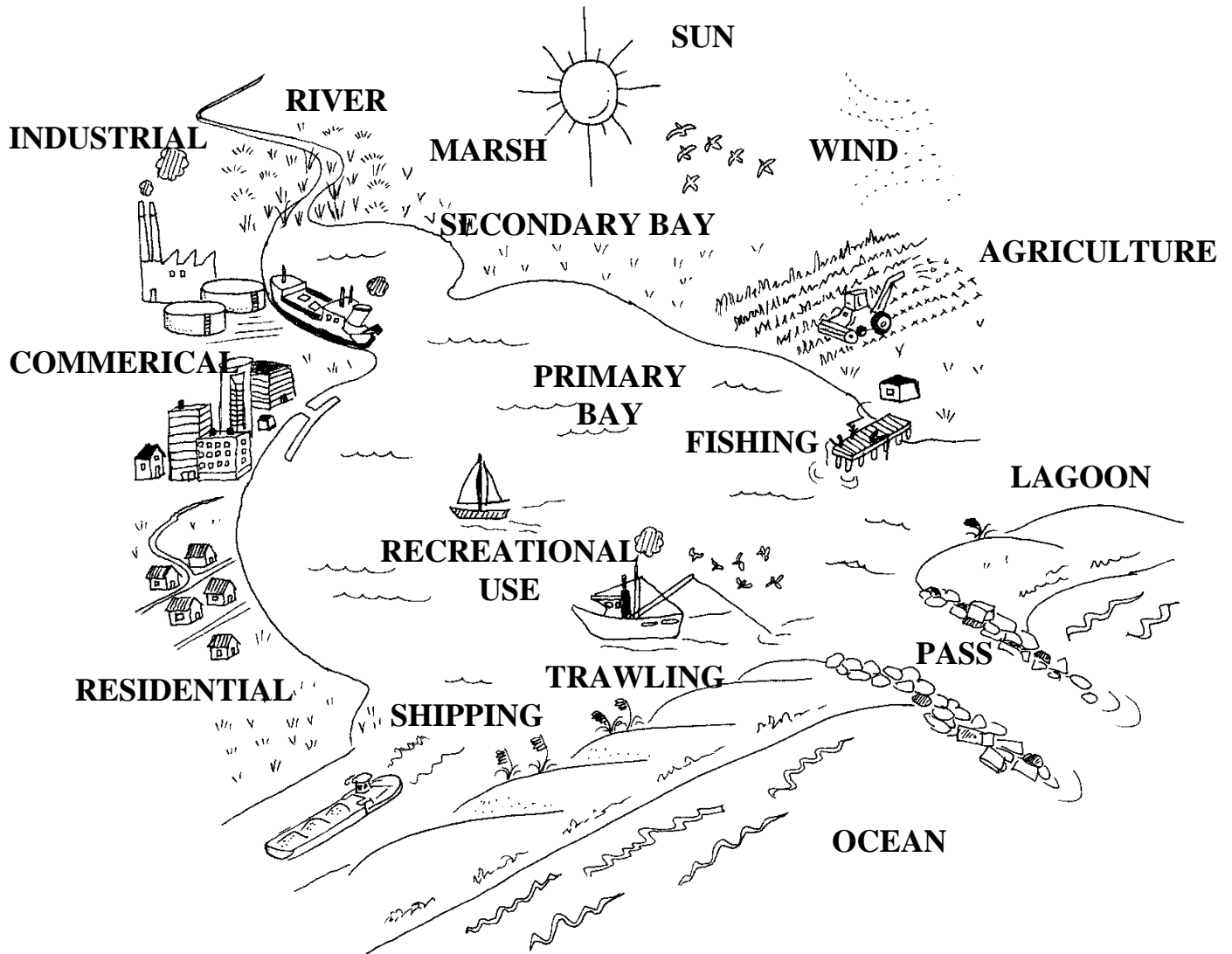
Fig.III.2B Summary of the Corpus Christi Bay National Estuary Program (CCBNEP) Bay Area System. The Bay Area includes rivers, marshes, primary and secondary bays, lagoons, and the coastal ocean. The natural processes in the Bay Area are driven by sun and exchange with the land and ocean. Humans use the Bay Area for a variety of uses, including many shown here. However, many of these activities also have the potential to negatively impact the Bay Area.

ecosystem, wind transfers kinetic energy and oxygen pressure from the air into water. Energy leaves the bay system through sedimentation and subsidence of organic matter as well. Tides originate from the gravitational forces of the sun and moon. Depending upon many factors, including latitude, weather, and local geography, different places on the planet have different tidal zones (ranging from a few centimeters to tens of meters) and a different number of tides in a day (usually 1 or 2). Tides behave much like large, slow waves; they can transfer kinetic energy and transport nutrients and detritus between the ocean and bay systems.

Rivers are indirectly a product of the sun and gravity. River water is the product of precipitation. Precipitation results from atmospheric water vapor that is itself the product of evaporation from the ocean. Rivers provide kinetic energy and transport nutrients and detritus from land to the bay ecosystem.

Runoff is fresh water that originates from sources other than rivers. Typically, this is drainage from the land directly into the bay. However, we also include non-river sources, such as return flow from a city sewer system, and direct rainfall onto the bay surface. Runoff can transport nutrients and detritus from land to the bay ecosystem.

Finally, the ocean provides energy for the bay ecosystem. Upwelling currents can bring up nutrients and detritus from the sea bottom. Water currents, waves, and tides act to transfer energy between the ocean and bay. Migrating consumers can also transport energy into the bay ecosystem. Typically, the net effect of migrating consumers is to transport energy and nutrients out of the estuary.

Storage

The bay ecosystem has seven main storage tanks (Fig. III.3A). Storage tanks in an ecosystem are nonliving things that stand for an energy storage level, or can be transferred into an energy storage level in an ecosystem. The storage tank is passively accumulated or lost due to the effects of energy sources or a living component's processes in the system. Inside a living component, the biomass can be defined as a storage tank accumulated or lost due to biological processes (see the following section: Representative Producer).
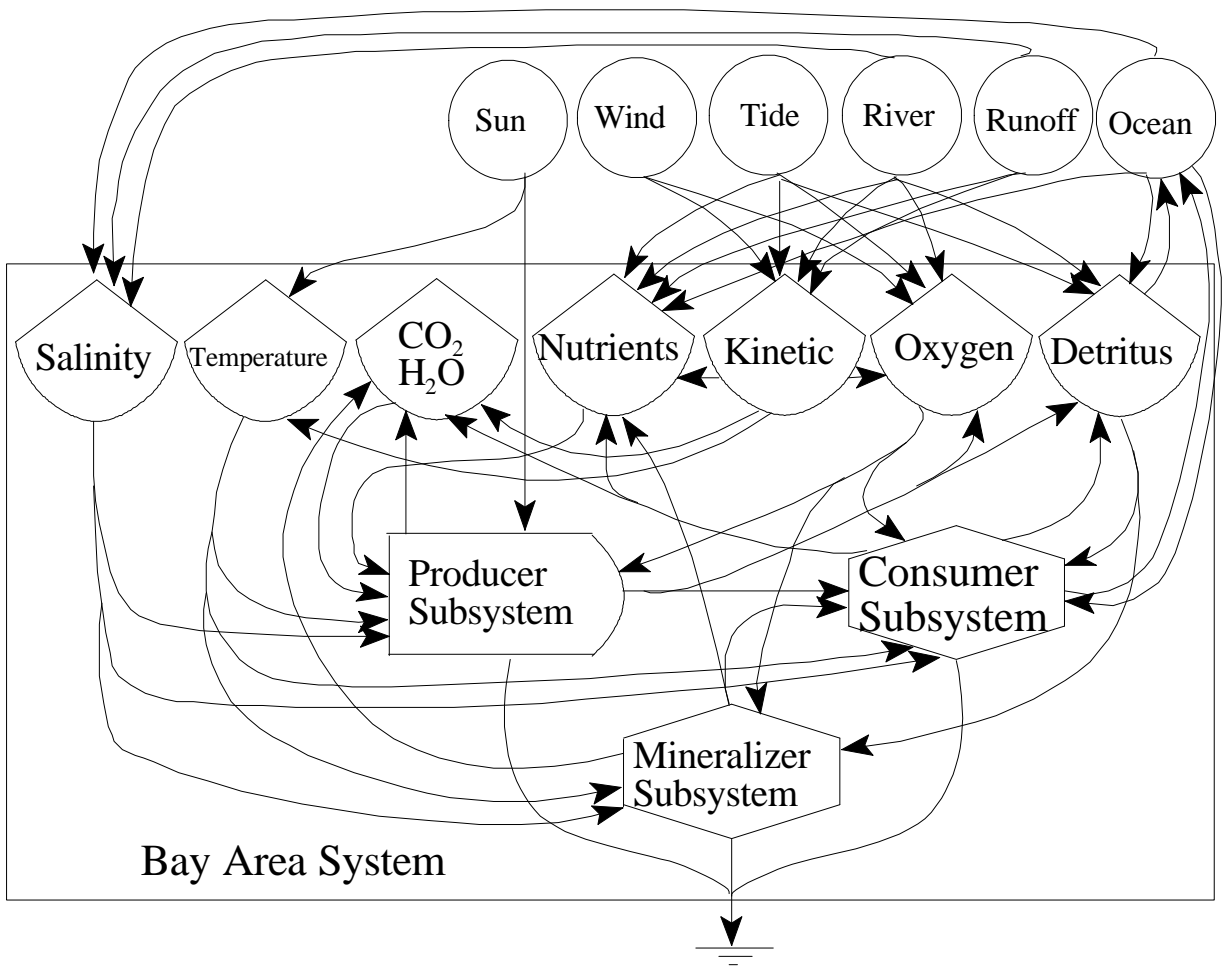
Fig. III.3A. The Bay Area System Components. The diagram represents the energy flow and transformation inside the Bay Area System.

SUNLIGHT

RIVER   RUNOFF

WIND

TIDE

NUTRIENTS

PRODUCERS CARBON DIOXIDE CONSUMERS

OXYGEN   OXYGEN

CARBON DIOXIDE

EXCHANGE

BACTERIA

BAY

OCEAN

DECOMPOSING MATTER
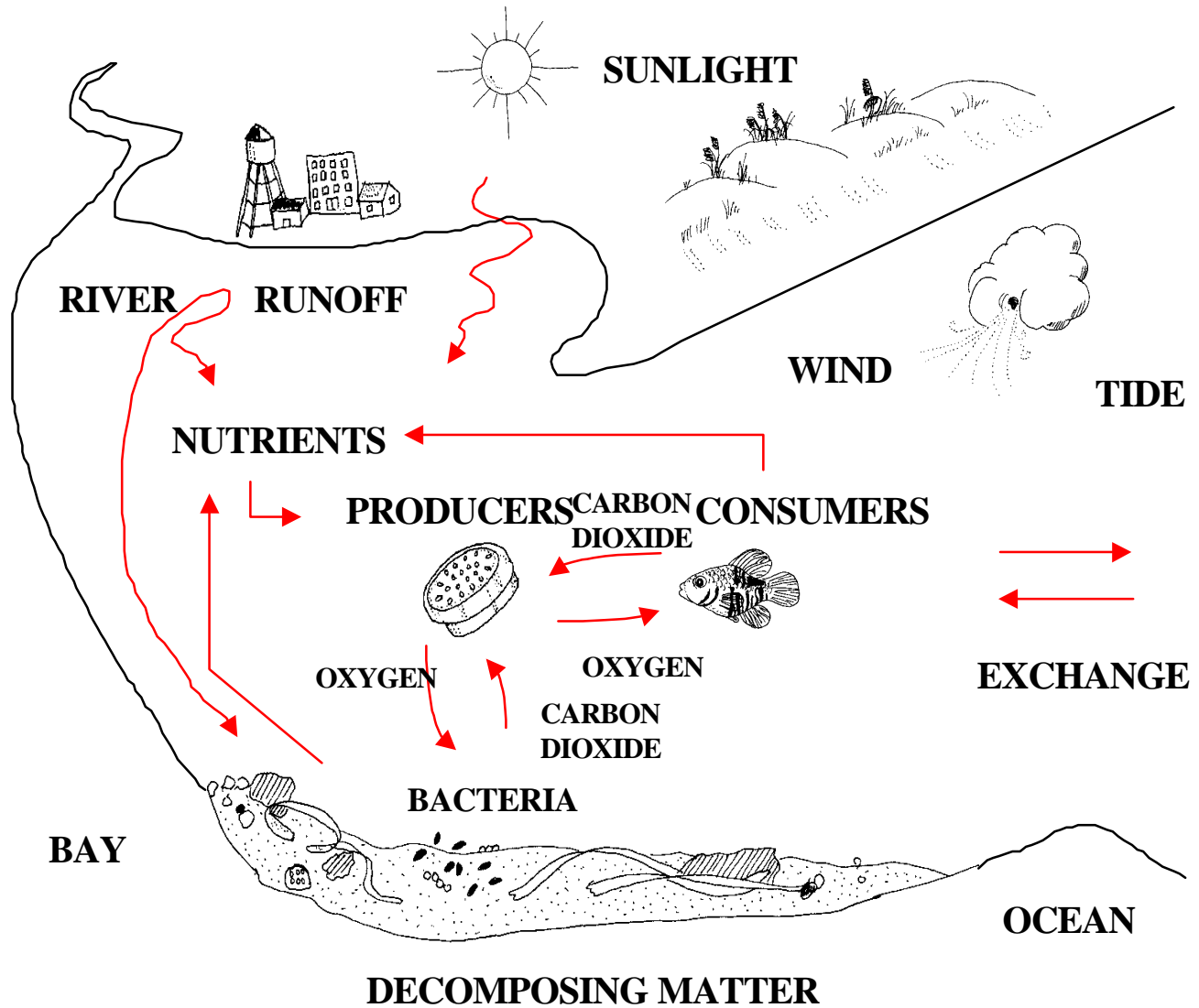
Fig. III.3B. Summary of the CCBNEP Bay Area System components. The arrows illustrate a simplified flow of energy within the Bay Area. Producers, such as this diatom, require sunlight and nutrients to grow. Consumers, such as this fish, survive by eating producers. Dead plants and consumers and their waste products sink to the bottom, where they are decomposed by other consumers and bacteria. Decomposition also results in recycling of nutrients that can be re-used by producers. New nutrients can enter the bay from rivers and terrestrial runoff. Because a bay is directly connected to the ocean, everything from nutrients to consumers can be exchanged between the two bodies of water.

Temperature storage is a product of solar radiation. Heat is lost through sea water evaporation to air or conduction to the deep sediment layer. Water loss by evaporation has a cooling effect on any moist surface (585 calories lost g^{-1} of water evaporated at 20 °C) (Prosser, 1991). Temperature increase may increase physiological processes, such as photosynthesis, energy intake, respiration, excretion, natural death, migration and reproduction. The relationship between temperature and physiology is usually represented by the term Q_{10}. Q_{10} is the factor by which reaction velocity is increased by a rise of 10 °C:

$$Q_{10} = (\frac{k_1}{k_2})^{\frac{10}{t_1 - t_2}}$$

Where k_1 and k_2 are velocity constants corresponding to temperatures t_1 and t_2.

Salinity is determined by the influences of freshwater from rivers and runoff (0 ppt) and the influence of seawater from the ocean (36 ppt). Salinity is also determined by evaporation. Salinity in bays is usually between about 5 and 25 ppt, but can become much lower in times of flooding, or much higher, even saltier than the ocean, in areas or periods of low rainfall. Salinity limits some physiological processes, such as photosynthesis, natural death, respiration, reproduction, excretion, and migration.

Carbon dioxide (CO_2) and water (H_2O) are needed for photosynthesis or chemosynthesis, and are produced by respiration. Photosynthesis and chemosynthesis are biological processes that convert inorganic carbon into organic carbon (C) and produce oxygen (O_2). Respiration, on the other hand, consumes oxygen, converts organic carbon into inorganic carbon, and releases energy for cellular functions. By definition, consumers can only respire, but producers both respire and synthesize. Autotrophic production occurs by photosynthesis or chemosynthesis.

Nutrients, such as, nitrogen (N) and phosphorous (P), are also needed by producers. Ammonia (NH_4^+), nitrates ($NO_3^=$), and nitrites (NO_2^-) are sources of N, which is needed to construct some organic molecules, particularly proteins and fatty acids. Phosphorus, which comes from phosphates (PO_4), is important for cell membranes making nucleic acids and in molecules that transfer energy through the tissues, such as adenosine triphosphate (ATP). Mineralizers and consumers break down tissue and release nutrients back into the ecosystem, a process called recycling.

Kinetic energy originates from wind, river, tide, runoff and ocean currents. Kinetic energy refers to the movement of water in the bay. The higher the kinetic energy of water, the more oxygen and nutrients it is able to contain.

O_2 is necessary for respiration. O_2 is used to help break down organic carbon bonds to release the energy for use by tissues. The oxygen-carbon molecules that are released as a by-product of respiration are in the form of CO_2. Consumers cannot generate their own O_2, and must rely on the O_2 generated from producers. Producers generate O_2 through photosynthesis by removing the carbon from CO_2. The carbon is used to form organic molecules such as carbohydrates, proteins and lipids, while the remaining O_2 is released. The amount of O_2 in the water is affected by physical factors, such as, wind, tide, rivers, and kinetic energy. O_2 solubility in water is also affected by salinity, temperature and pressure.

Detritus is nonliving, decomposing organic material, including fresh leaves sloughed from seagrass or marsh grass, fecal matter from animals, and dead animal and plant tissue. Particulate material from the water column, such as dead phytoplankton or zooplankton, also forms detritus. Detritus is classified as autochthonous, detritus that originates from within the ecosystem, or allochthonous, detritus that is transported into the ecosystem. Because of gravity, detritus usually sinks to the sediment, where it is either decomposed or becomes buried. Detritus is decomposed by bacteria that convert the detritus into nutrients and energy through a process called mineralization. In addition to bacteria, other animals, including meiofauna and macrofauna invertebrates, can affect the amount of detritus in the sediment. For example, an abundance of nematodes can increase the decomposition of salt marsh leaves (Alkemade et al., 1993). Because of their small size, nematode defecation cannot significantly affect detritus levels (Li, et al., in press). However, defecation from larger animals may have greater affects on the amount of detritus in an ecosystem.

Subsystems

There are three main trophic subsystems within the bay ecosystem: producers, consumers and mineralizers (Fig.III.3A). Producers can generate biomass and energy from sunlight and atmospheric carbon, and are commonly known as plants or autotrophs. Consumers, including animals and most bacteria, are incapable of generating their own energy or biomass, and must eat producers or other consumers; these organisms are called heterotrophs. Consumers also require O_2 for respiration. Mineralizers are a specific kind of consumer. Mineralizers include

microscopic bacteria that respire by decomposing detritus. They liberate CO_2 from the organic matter in the process, hence the name mineralizer. There are two main categories of mineralizers. Aerobes use O_2 as terminal electron acceptors that are essential to the oxidation of organic matter as an energy source. Anaerobes use compounds other than O_2, such as, sulfate $(SO_4^=)$.

Summary

Life in the bay is dependent upon the sun (Fig. III.3B). Producers, such as, phytoplankton, require sunlight, carbon dioxide and nutrients to grow and produce energy. Consumers, such as, fish, receive the carbon by eating producers, and the oxygen they need from water. Non-living organic matter is produced from producers and consumers, and "rains down" upon the bottom of the bay. In the sediment, bacteria use oxygen to break down the organic matter to receive energy. Like consumers, these bacteria produce carbon dioxide. Bacteria also release nutrients back into the water. The three living subsystems in the bay, producers, consumers and mineralizers, are dependent upon a variety of non-living factors that operate on the bay. For example, new nutrients enter the bay from rivers or as runoff from cities, farms, and other adjacent landscapes. Another factor that affects the bay ecosystem is the ocean. Energy, nutrients, oxygen and living organisms are all exchanged between the bay and ocean. The rate of exchange is determined by the number and size of passes and by the intensity of the wind and tide.

Producers

Producers in the bay ecosystem can be classified as photoautotrophs (salt marsh, mangrove, seagrass, phytoplankton, benthic macroalgae and microbenthos) or chemoautotrophs (bacteria) (Fig. III.4A). Photoautotrophs receive energy from sunlight, and include familiar plants such as, salt marsh cord grass (*Spartina alterniflora*), mangroves (*Avicennia germinans*), seagrasses (*Halodule wrightii, Halophila englemannii* and *Thalassia testudinum*), phytoplankton, benthic macroalgae, and microphytobenthos. Chemoautotrophs are groups of bacteria, such as, sulfur, hydrogen, or methane bacteria. These organisms can satisfy their primary energy requirement by using simple inorganic compounds. In the bay, chemoautotrophs live primarily in the sediment, especially at the oxic-anoxic interface. All benthic autotrophs are food sources for deposit feeding benthos.

20
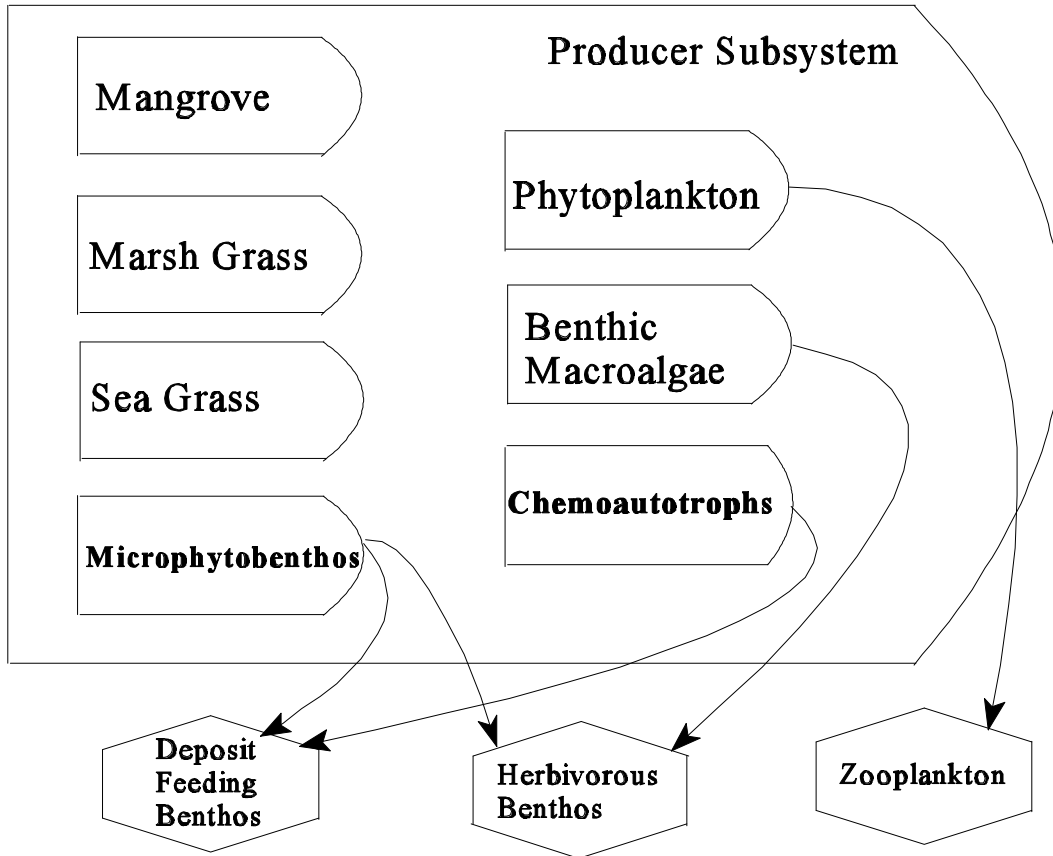
Fig. III.4A. The Producer Subsystem. The energy flows from producers to consumers.
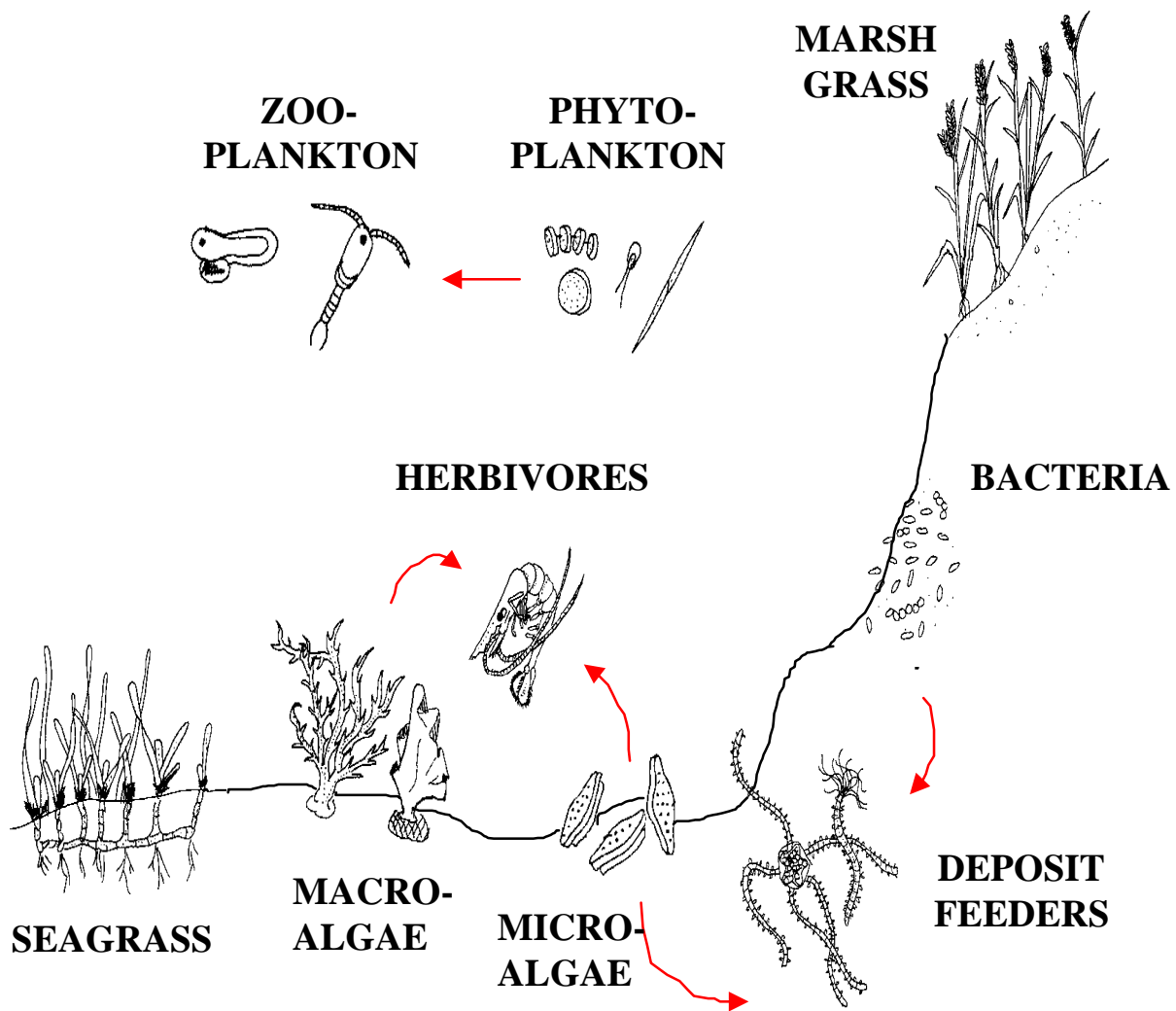
Fig. III.4B. There are six different types of producers in the CCBNEP Bay Area. Phytoplankton are microscopic, one-celled algae that live in the water. Marsh grasses live at the margin between the shore and the bay. Some types of bacteria are capable of photosynthesis. There are also one-celled algae that grow on sediment called microalgae or microphytobenthos. Larger producers include seagrasses and macroalgae, also known as "seaweed." Consumers eat most types of producers, except for seagrasses and marsh grasses. However, seagrasses and marsh grasses are important sources of organic matter and as habitats for many animal species.

Salt marshes develop adjacent to the water margin. They are beds of intertidal, rooted vegetation, particularly grasses, that are alternately inundated and drained by tides. Because they have adapted to a life of sun, salt, and wind, these plants are tough, difficult to digest, and generally are poor food sources for consumers. However, salt marsh plants can be an important input of detritus sources to the bay ecosystem. Mangroves are typically adapted to loose, wet soils, a dominantly saline habitat, and periodic, submerged tides (Davis, 1940). Because they are also difficult to digest, generally only the woody parts of mangroves are consumed by a few boring isopods such as the root-boring *Sphaeroma tenebrans* or the wood-boring *Limnoria lignoria*. The boring isopods increase the carbon flow from mangrove to decomposing materials. Mangrove detritus can be important to the ecosystem in situtations where these isopods are found. Mangroves are not a dominant plant in the CCBNEP area but are found in isolated areas, particularly after several years of mild winters.

Seagrasses exist in habitats similar to salt marshes, but exist entirely underwater, growing in shallow estuarine sediments. The contribution of seagrass production to estuarine carbon budgets can range from negligible to almost 50% of the total production within an estuary (Day et al. 1989). Like salt marsh plants, seagrasses contribute carbon to the detritus pool, and are not usually consumed by herbivores except for a few exceptions, such as diving ducks. Seagrasses are extremely important habitats for a variety of invertebrates and fish.

Phytoplankton are tiny, single-celled algae, such as flagellates, dinoflagellates, diatoms and nannoplankton (summarized by Parsons et al., 1984). Plankton have limited movement capabilities, and are usually carried about with the motion of the water. Phytoplankton are very productive, and can support a high abundance and diversity of their main consumer, zooplankton (see next section, "Consumer"). Small phytoplankton are the dominant producers in the open ocean.

Benthic macroalgae, such as brown algae and other seaweed, grow in sea water in the shallow water or subtidal area. Because they have no root system, many macroalgae need a hard substrate for attatchment. For this reason, macroalgae are not a dominant producer in the CCBENP study area. Unlike sea grasses and mangroves, macroalgae are easily digestible, and are eaten by some herbivorous benthos or fish.

Microphytobenthos include single-celled algae, particularly diatoms, that live on the sediment surface. Microphytobenthos are very productive in shallow water, and are food sources for

herbivorous and deposit-feeding benthos, such as some gastropods, most harpacticoid copepods, and many polychaetes and free-living nematodes.

Summary

There are five main components of the producer subsystem (Fig. III.4B). Marsh grasses grow on the edge of the bay. They are not directly eaten, but may contribute substantially to the pool of decomposing matter. Seagrasses are a dominant feature in shallow water in the bay. Like marsh grasses, seagrasses are very productive but difficult to eat, due to tough, fibrous tissue. Macroalgae, including the large brown, red and green "seaweeds," are eaten by benthic herbivores, such as grass shrimp and amphipods. Microalgae, particularly small diatoms, are very productive, and live on the sediment surface. Microalgae are eaten by grazing herbivores, such as shrimp, but are also eaten by deposit feeding animals, such as polychaete worms and brittle stars. The same deposit feeders also eat chemoautotrophs, small, sediment-dwelling bacteria. In the water column are other small plants, the phytoplankton. These organisms are eaten primarily by zooplankton, small animals that include tiny crustaceans and the larvae of larger shrimp, crabs and fish. All producers are important contributors to the pool of decomposing matter.

Representative Producer

The biomass of a single producer is balanced by several physiological processes (Fig. III.5A). Producers increase in biomass, either by growth or reproduction, i.e., synthesis of new biomass. Biomass is lost from the producer compartment through respiration, natural death and consumption by herbivores.

Synthesis

Both photoautotrophs and chemoautotrophs synthesize inorganic carbon (C), CO_2, into organic carbon, $n(CH_2O)$, and produce O_2 as a by-product through the reaction:

$$nCO_2 + 2nH_2O \Rightarrow n(CH_2O) + nO_2 + nH_2O$$
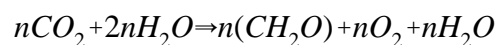
Photosynthesis includes: (1) production of ATP and molecular O_2 from adenosine diphosphate

(ADP) through the cytochrome system, and reduction of nicotinamide adenine dinucleotide (NAD); and (2) fixation of CO_2 using ATP and production of NAD. The difference between photosynthesis and chemosynthesis depends upon the source of the energy to produce ATP and reduce NAD. Photosynthesis uses light energy for this purpose; whereas, chemosynthesis uses chemical reducing power produced through dehydrogenization (Gundersen, 1968). Dehydrogenization occurs through the reaction:

$$nAH_2 + nH_2O \Rightarrow nAO + 4n[H^+ + e^-]$$
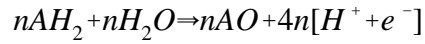
Where AH_2 represents simple inorganic compounds, such as NH_4^+, methane (CH_4), or NO_2, or elements, such as ferrous iron, hydrogen gas, or water-insoluble amorphous sulfur. AO is the oxidized end-product. The reducing power ($[H^+ + e^-]$) is utilized for producing ATP and reducing NAD.

The effects of light intensity on photosynthesis can be represented by the light limitation (*Light-L*) equation:

$$Light-L = \frac{I_m}{I_{opt}} \exp(1 - \frac{I_m}{I_{opt}}) - r(1+r)$$

Where I_m is mean light in the water column, calculated from:

$$I_m = \frac{I_s(1 - e^{-Cz})}{Cz}$$

Where I_s is average visible light at the surface that may be taken directly from field measurements or obtained by multiplying an estimate of total incident light, by 0.45 to eliminate long-wave radiation. C is the diffuse attenuation coefficient (or extinction coefficient), per meter. z is thickness of the water layer. I_{opt} is light intensity at which phytoplankton growth is maximum. r is a correction factor allowing for a negative change in biomass at very low light levels ($I_m < 0.01 \, I_{opt}$) (Carrada et al. 1983).

Temperature effects on photosynthesis (Aruga, 1965) can be represented by the temperature limitation (*Temperature-L*) equation (Li, et al., in press):

$$Temperature\text{-}L = Q_{10}^{\frac{(T-MAT)}{10}}$$

where Q_{10} comes from the temperature effects on physiology (see p.18, above). T is temperature, and MAT is the maximal action temperature, at which the lives have their maximal physiological action.

In addition to light and temperature, production in producers can be limited by concentrations of nitrogen, phosphorus, and silicate in the water and sediment. The uptake of carbon, nitrogen, silicate and phosphorus by weight, generally occurs according to the ratio of 106:16:15:1, respectively (Redfield, 1934; Parsons et al. 1961). A different nutrient may be limiting at a different time of the year, such as, is the case for phosphorous in the spring and nitrogen in the summer for Delaware Bay (Pennock and Sharp, 1994). The limitation of production by a nutrient (*Nutrient-L*) can be represented by the equation:

$$Nutrient\text{-}L = Minimum(\frac{[NH_4+NO_3]}{PKN+[NH_4+NO_3]}, \frac{[PO_4]}{PKP+[PO_4]}, \frac{[Si(OH)_4]}{PKSi+[Si(OH)_4]})$$

where *PKN*, *PKP* and *PKSi* represent the half maximum production rates for concentrations of nitrogen ($NH_4 + NO_3$), phosphorus (PO_4) and silicate ($Si(OH)_4$), respectively (Carrada et al. 1983). The values of PKN, PKP and PKSi are different for different producers since the required ratio for nutrients are different, e.g., diatoms and flagellates have different Si:N requirement ratios (Sommer, 1994).

Synthesis by a producer can be estimated by the formula:

$$Production = B \cdot R_M \cdot (Light\text{-}L) \cdot (Temperature\text{-}L) \cdot (Nutrient\text{-}L)$$

where B is biomass, R_M is the maximal synthesis rate. This equation includes feedback from biomass to photosynthesis, because biomass is involved in producing more biomass (Fig. III.5A). Nutrient limitation may also come from competition between producers. For instance, the uptake of inorganic carbon by seagrass can be reduced significantly by microalgal growth on leaf surfaces (Sand-Jensen, 1977).
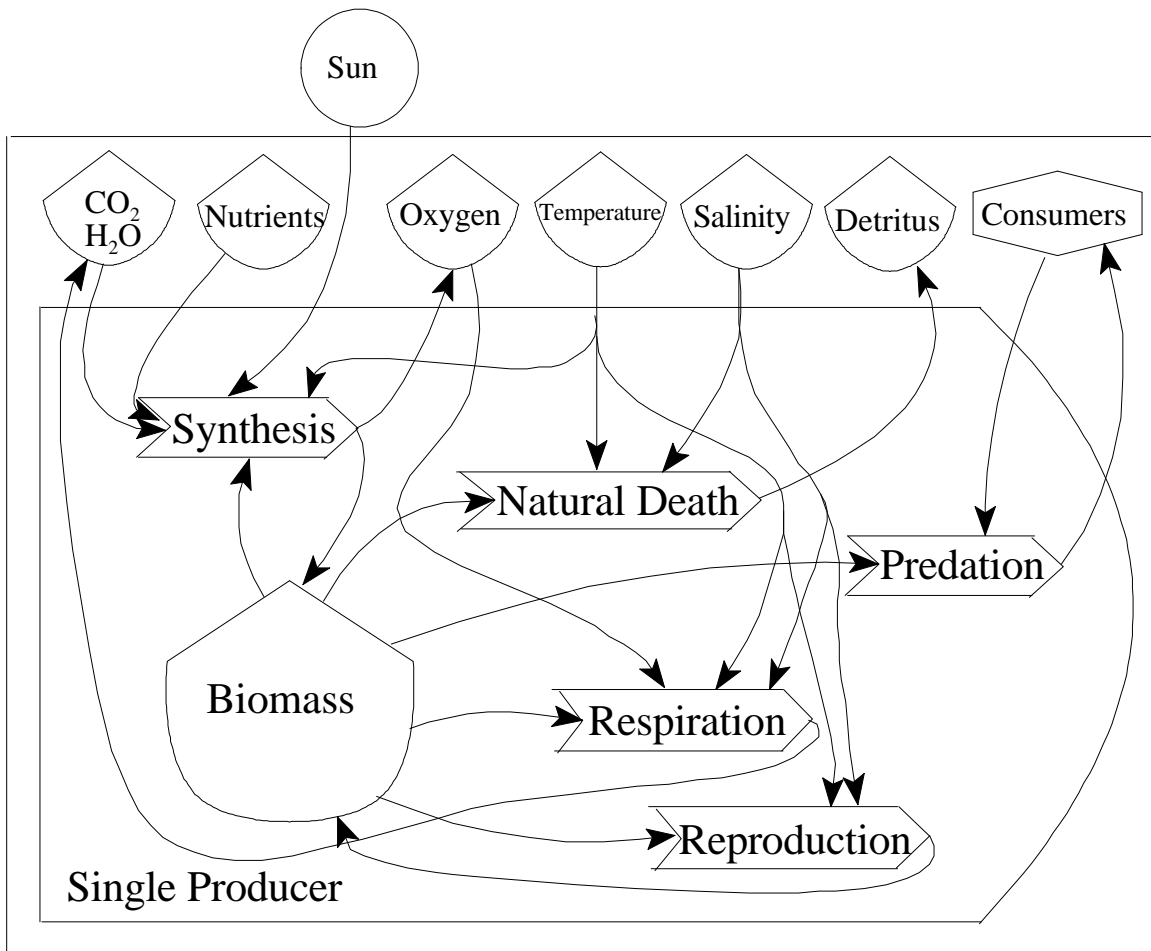
Fig. III.5A. Representative producer subsystem. The Energy flows and controlling processes inside a single producer subsystem. The input is through synthesis by either photoautotrophs or chemoautotrophs, and the output includes predation, respiration and natural death.

OXYGEN

PHOTOSYNTHESIS

RESPIRATION

CARBON DIOXIDE

NUTRIENTS

REPRODUCTION

HERBIVORY

DEATH

TEMPERATURE + SALINITY
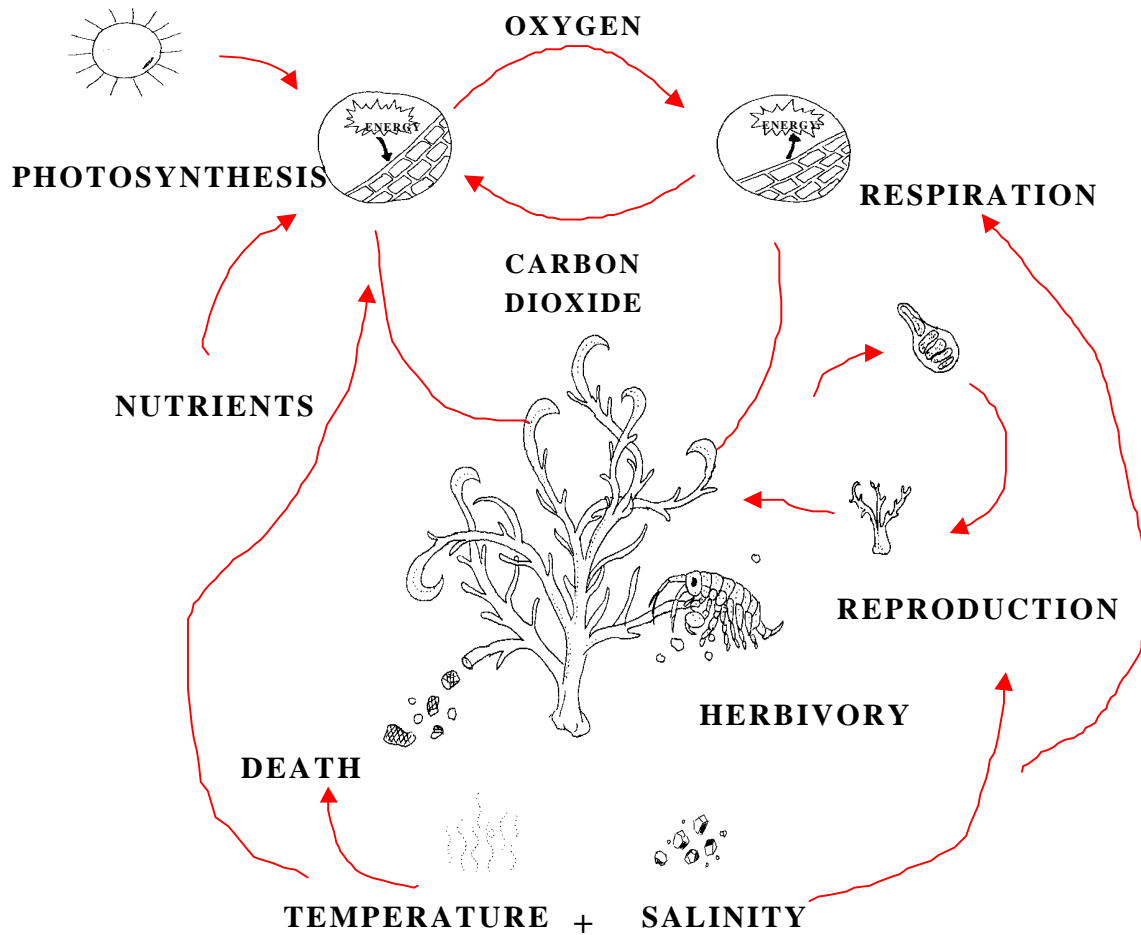
Fig. III.5B. Summary of a representative producer, a red algae. The alga gains energy and biomass from light and nutrients and loses biomass through natural death or by being eaten by consumers. The algae are also affected by the temperature and salinity of the surrounding water.

Respiration

Producers gain biomass by synthesizing new organic matter using energy and simple carbon molecules. Stored energy from photosynthesis is released by respiration. Respiration involves breaking down carbon bonds (nCH_2O) to produce energy. Respiration requires O_2, and produces CO_2 and H_2O:

$$nCH_2O + nO_2 \rightarrow nCO_2 + nH_2O + energy$$

The rate of the respiration process is increased as temperature increases up to a point, because the rate at which catalytic enzymes work is increased. Respiration can also be affected by environmental conditions, such as an unfavorable salinity or the presence of toxic chemicals. Stressed organisms must respire faster to keep cells functioning properly.

Reproduction

In addition to increasing their own biomass, producers can also produce offspring. Like all organisms, producers reproduce through the process of cell division. Reproductive and early life stages of most organisms are often very sensitive periods. Therefore, reproduction may be greatly affected by stressful environmental conditions, such as the presence of toxins or unsuitable temperature or salinity.

Predation / Grazing

Producers lose biomass to consumers. When a consumer eats a producer, it is usually called herbivory, grazing, or foraging. Zooplankton graze on phytoplankton. Herbivores graze on microphytobenthos and benthic macroalgae. Deposit-feeding benthos consume microphytobenthos and sediment bacteria by incidental ingestion of sediment or by the selection of specific particles. The grazing action of consumers is affected by environmental conditions, such as temperature and kinetic energy (see following section Consumers).

Natural death

Whereas smaller producers, such as phytoplankton, usually die only through grazing, larger organisms may die "naturally". Seagrass blades become senescent and fall off during the late

summer and early fall. Environmental changes, such as salinity change or high turbidity may also kill or stress producers.

Summary

Producers, such as macroalgae, are dependent upon sunlight for photosynthesis (Fig. III.5B). Photosynthesis is the process by which a producer may create biomass from sunlight, carbon dioxide and nutrients, releasing oxygen in the process. To utilize the energy that is stored during photosynthesis, producers use oxygen and produce carbon dioxide in the process called respiration. Some of the biomass produced by an organism may be used to repair damage or increase the plant's own size. Additional biomass and energy are used to reproduce. Producers lose biomass either through respiration, natural death or by being partially or totally eaten by an herbivore. Many of the biochemical reactions that occur in a producer's cells are affected by the temperature and salinity of the surrounding water.

<div align="center">Consumers</div>

The consumer subsystem of the CCBNEP area includes zooplankton, herbivorous benthos, deposit-feeding benthos and predators (Fig. III.6A). Different consumers in the bay system have different energy inputs, that is, they live off different resources.

The zooplankton community is composed of tiny animals that live in the water column. There are two types of zooplankton: holoplankton spend their entire lives in the water column, meroplankton spend only their larval forms in the water column. Examples of holoplankton include calanoid copepods and small jellyfish. Examples of meroplankton include larval shrimp, crabs, worms or fish. Almost all zooplankton derive their energy from grazing on phytoplankton or other zooplankton.

Herbivorous benthos include those animals that graze on phytoplankton, macroalgae, epiphytic algae, or microphytobenthos. Some herbivorous benthos are filter feeders, such as oysters, whereas others graze the sediment surface, as do some mudflat-dwelling snails. Animals such as amphipods and other rock-dwelling snails graze on macroalgae, while small harpacticoid copepods and nematodes graze on benthic microalgae. Most herbivores are invertebrates that live in association with the bottom, either epifaunally or infaunally, and are either motile or sessile. There are, however, also some herbivorous fishes.
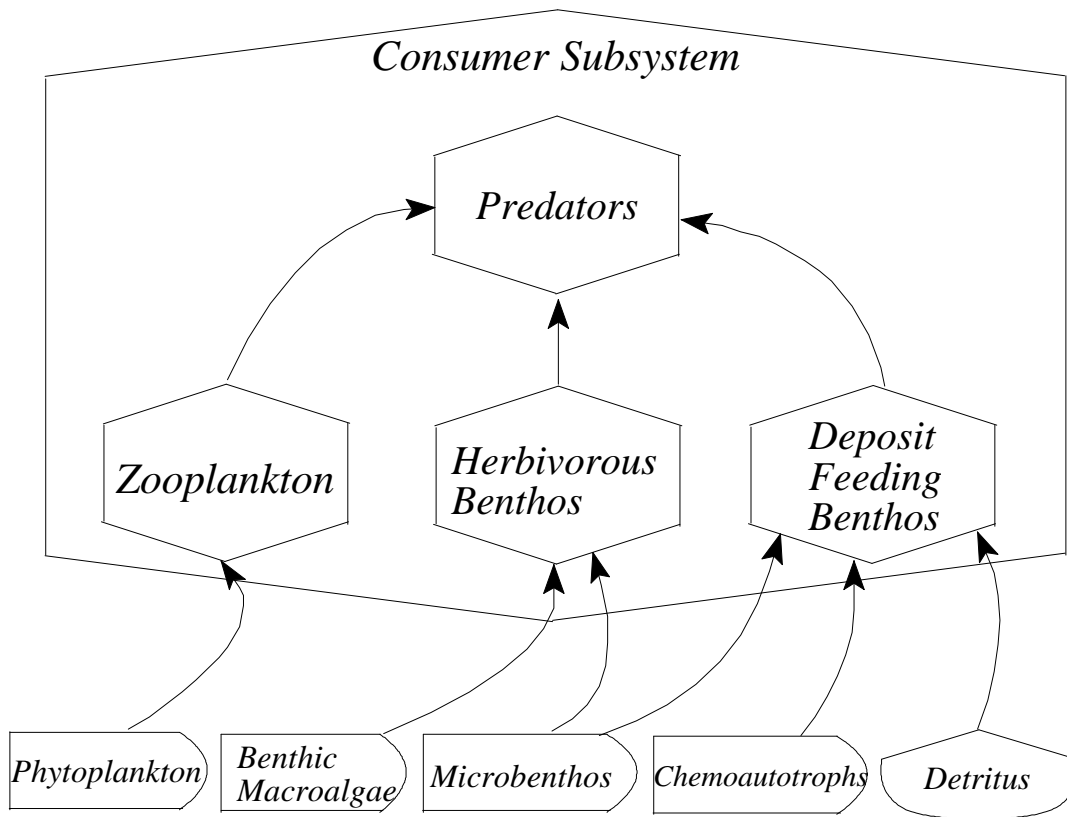
Fig. III.6A. The Consumer Subsystem. The energy flows from food sources to consumers.

TERTIARY
CONSUMERS

SECONDARY
CONSUMERS

ZOO-
PLANKTON

PHYTO-
PLANKTON

BACTERIA

HERBIVORES

MACRO-
ALGAE

MICRO-
ALGAE

DEPOSIT
FEEDERS

DECOMPOSING
MATTER
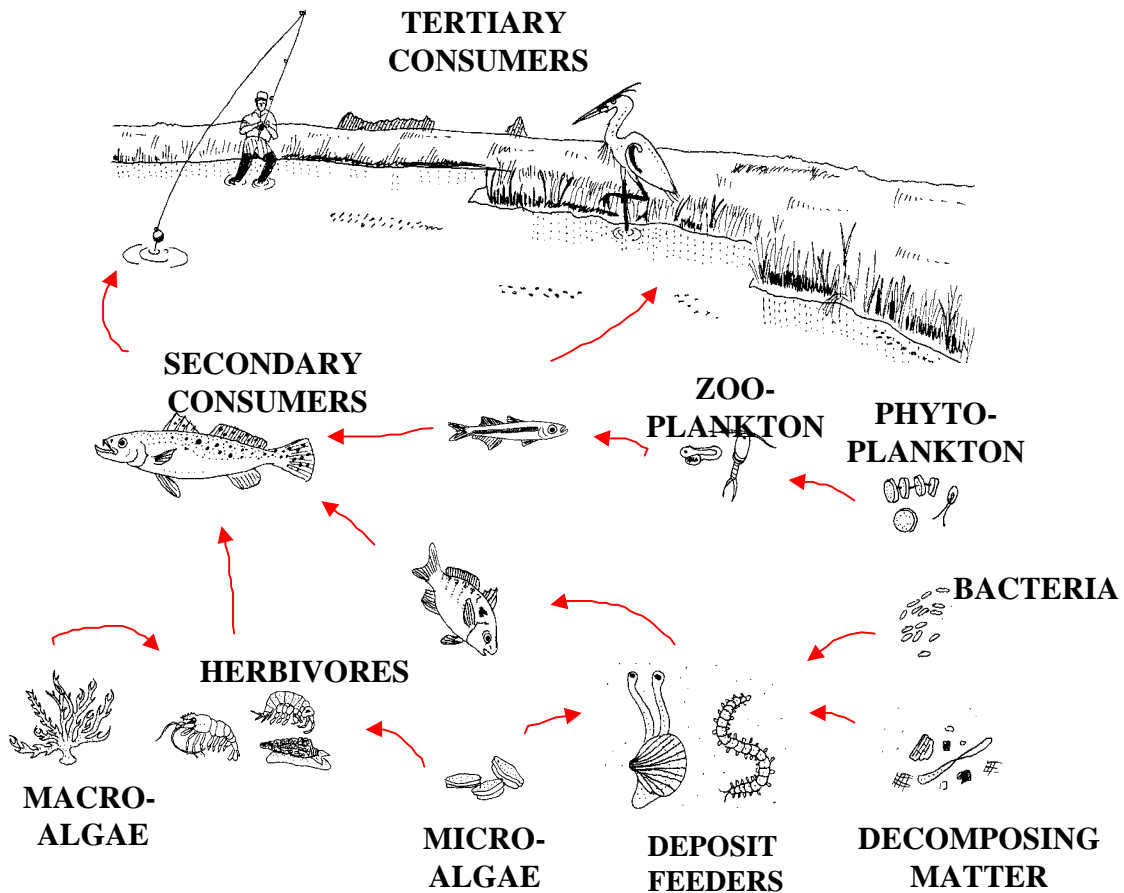
Fig. III.6B. There are several different kinds of consumers in the CCBNEP Bay Area. Zooplankton, small crustaceans and the larvae of larger animals, eat mainly phytoplankton. Deposit feeders, such as polychaete worms and some clams, eat decomposing matter (also called detritus). Benthic herbivores, such as shrimp and amphipods, eat a variety of plants. Secondary consumers, such as many fish, are predators that eat other consumers. Tertiary consumers, such as large fish, humans and birds, eat secondary consumers.

Deposit-feeding benthos, such as most polychaete worms, include those animals that derive their food sources from organic matter in sediment. Organic matter that is processed by these animals can include detrital material, bacteria, or microbenthos, such as ciliates and flagellates. Some deposit feeders process all the sediment they encounter and are called "non selective deposit feeders". Others seek out organic matter specifically, and are called "selective deposit feeders." At the top of the food chain are predators. Predators, such as crabs, feed on benthic organisms, while some fish, such as, red drum and black drum, feed on crabs. Some fish prey on zooplankton. There are also predators that eat other predators, such as, the largest fish, as well as birds and humans.

Summary

Consumers are animals that cannot synthesize inorganic matter into organic matter (Fig. III.6B). Those consumers that eat plants, including algae and microphytes, are called herbivores, and include grass shrimp. Those consumers that feed on bacteria or organic matter in the sediment are called deposit feeders, and include many types of polychaete worms. Small consumers that live in the water column and feed on phytoplankton are called zooplankton. There are also consumers that eat other consumers. A small fish that feeds on zooplankton may itself become prey to larger fish, such as seatrout or red drum. These large fish may, in turn, be eaten by a terrestrial predator, such as a human or bird of prey.

Representative Consumer

Biomass that is stored by a consumer is balanced by several physiological processes (Fig. III.7A). Processes that contribute to increases in biomass storage include assimilation and reproduction. The processes that contribute to a loss of biomass include respiration, excretion, predation, and natural death. The loss of biomass also includes the thermodynamic heat loss due to biological processes like searching for food, ingesting food, assimilation, respiration, excretion and escaping from predators. Some consumers gain or lose biomass from their populations due to migration of individuals between the bay and ocean.
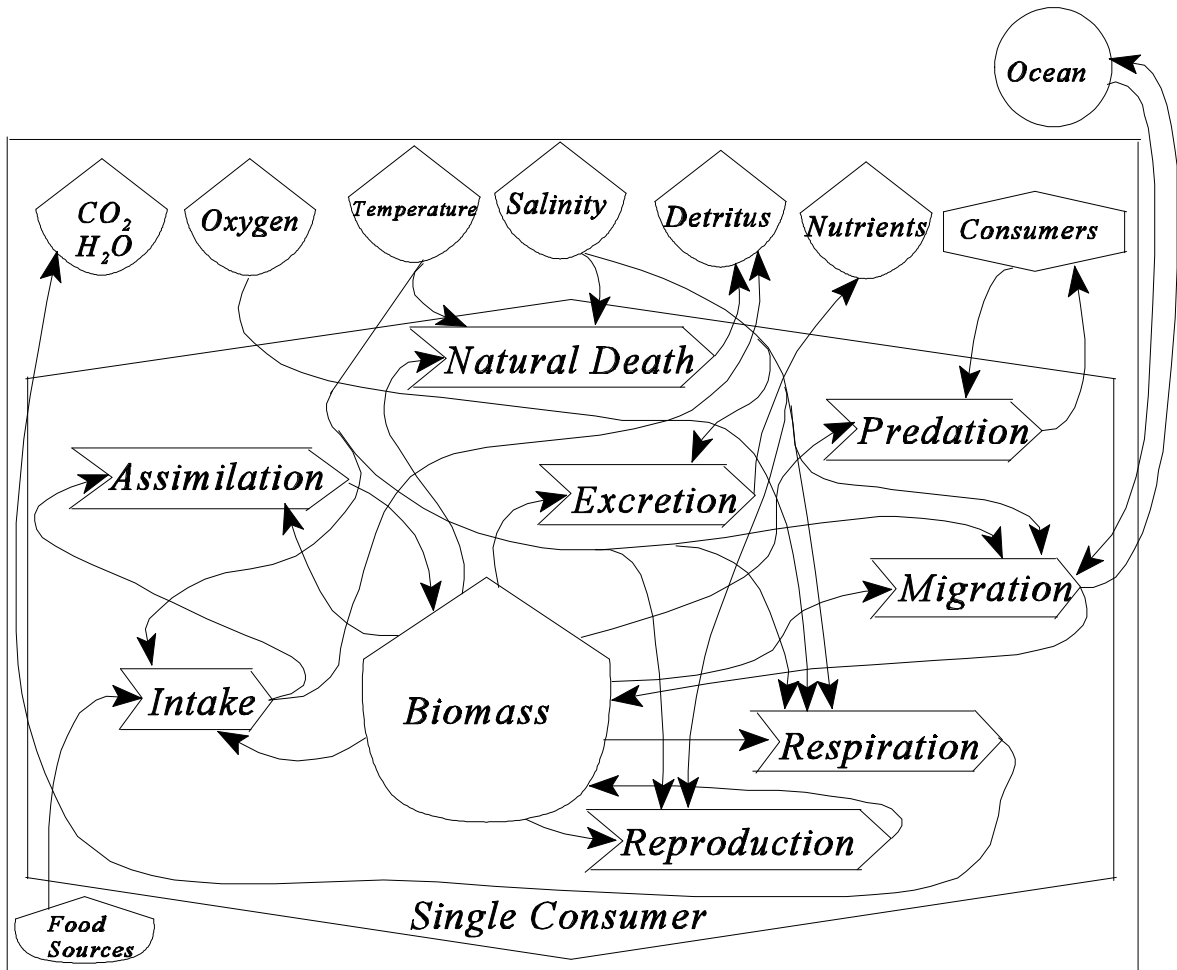
Fig. III.7A. Representative Consumer Subsystem. The energy flows and controlling processes inside a single consumer system. The food sources and consumers are different for different consumers as shown in Fig. III.6A. Migration occurs only for some consumer groups.

34

ASSIMILATION

RESPIRATION

OXYGEN

CARBON DIOXIDE

PREY

MIGRATION

NUTRIENTS

PREDATION

DEATH
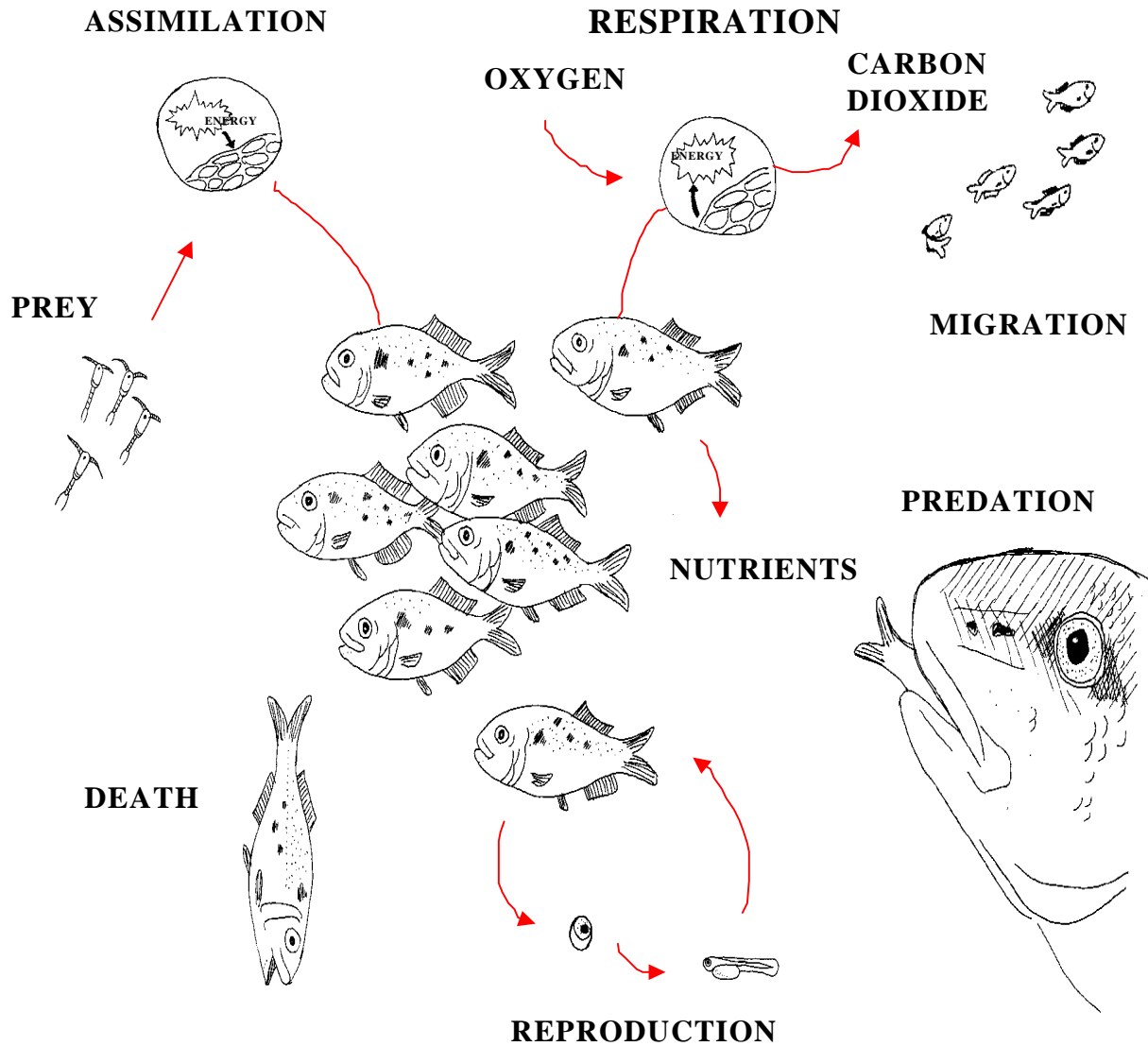
REPRODUCTION

Fig. III.7B. Summary of a representative consumer, the menhaden. The fish gain energy by eating prey, in this case, calanoid copepods. This energy can be used for growth or for reproduction. The menhaden lose energy by natural death or by being eaten by a predator, such as a redfish. Menhaden can move from the bay to the ocean or back by migration. Like most organisms, these fish are affected by the temperature and salinity of the surrounding water. Furthermore, because they cannot synthesize, all consumers need oxygen.

Intake

In order to gain energy, a consumer must encounter and assimilate prey. The chance that a consumer will meet a food unit per unit time and the ingestion speed of the consumer are key factors that affect intake. Some consumers may actively search for food. For these consumers, such as most fish, movement and ingestion speeds are more important factors than food concentration. For sessile animals that do not actively search for food items, such as oysters, food concentration and kinetic energy in the water will be more important. The intake process is, therefore, not only controlled by the food concentration and consumer density, but also by the current speed and the consumer's own physiology. Water temperature may increase a consumer's physiological actions, such as rate of ingestion and swimming speed, therefore increasing the chances of successfully assimilating food. The intake rate (*IR*) can be expressed by the Michaelis-Menten equation (Carrada et al. 1983):

$$IR = \frac{MR \cdot FC}{FC + HMRFC}$$

Where *MR* is the maximal intake rate per unit time, which depends upon ingestion speed and stomach capacity, the *FC* is the food concentration, which may be a function of current speed for passively feeding consumers, and *HMRFC* is the one-half maximum food concentration that a consumer can process. The total intake is also dependent on the consumer population level, which is a feedback from the biomass to the intake interaction:

$$Intake = D \cdot IR$$

where *D* is the density or the biomass of a consumer dependent on the unit of *IR*.

Assimilation

Once food is ingested, it is assimilated into the cells through a series of biochemical reactions with digestive enzymes, through which the consumer transforms the energy from a food source into its body (Prosser, 1991). Many consumers only assimilate part of a food source. The unassimilated part is excreted and becomes detritus. Assimilation rates are controlled by food quality. Consumers have different requirements, leading to differences in assimilation rates. For instance, nematodes feeding on diatoms have higher assimilation rates than those feeding on

particlulate organic matter (POC), because the nutritional quality of diatoms is higher than that of POC (Li et al., in press).

Many aquatic invertebrates extract organic molecules directly from solution (Allendorf, 1981), without the use of a capturing or ingesting process. For instance, the parasitic animals in a rich environment of host tissue do not require special digestive structures. Their body surfaces resemble intestinal epithelia in surface area and transport mechanisms (Prosser, 1991). Many free living cnidarians, molluscs, echinoderms, annelids, and arthropods also extract some organic substances directly from solution. The result is that these animals excrete less organic matter, which means that their assimilation rates are higher than other animals.

Respiration

The respiration rate of a consumer is dependent upon its physiological activity. Fast swimming fish, including many predators, may require high quality foods, rather than POC. These animals would have much higher respiration rates per unit time than slowly moving animals, like many snails, or nonmotile animals, such as sponges. Respiration per unit time is normally described in a power relation to its body size (Zeuthen, 1970; Banse, 1982):

$$Respiration = aV^b$$

where the respiration rate is reported in units of the consumption of oxygen (nl O_2 h^{-1} ind.$^{-1}$), V is body volume (nl ind.$^{-1}$), proportional to the mean individual biomass, a is a parameter indicating the metabolic intensity (Schiemer and Duncan 1974) or reflecting the internal metabolism of the organism (Zeuthen, 1970) due to different feeding habits. b is a parameter that approximates the body volume to body weight. It is different for different species, for example, differences among tropical, temperate, and boreal species (Ikeda, 1970). Usually, b is less than one. For example, a meiobenthic nematode with a dry weight of 0.3 µg and a respiration rate of 0.6 nl O_2 h^{-1} ind.$^{-1}$ has a weight-specific respiration of 2 nl O_2 h^{-1} µg^{-1} while b is about 0.75 (Heip et al., 1985). It is clear that the smallest animals have the highest metabolic rate (since the b is less than one and the respiration rate $R/V = aV^{b-1}$). The transformation of oxygen consumption to energy usage may be estimated using the conversion factors: 1 ml O_2 = 20.2 J (Schiemer, 1982) and 1 mg C = 48.26 J (Sikora et al., 1977). The respiration rate of an animal is highly variable due to variations in temperature (Comida, 1968), food availability (Ivlev, 1945), and biological activity (Heyraud, 1979; Vidal, 1980).

Excretion

Excretion maintains the body's internal constancy (homeostasis) by the elimination of excess substances (or their metabolic byproducts) that enter the body. Such substances may be water, salts, and by-products of cellular activity, especially nitrogenous wastes (Ruppert & Barnes, 1993). This is because animals cannot store excess amino acids, unlike carbohydrates and lipids, which can be stored as glycogen and triglycerides (Krebs, 1972). For instance, nematodes have high C:N ratios (8:1 to 12:1) in comparison with their food, such as bacteria, (3:1 to 4:1) and thus must release N as a waste product (Anderson et al. 1983). Nitrogen excretion is dependent on body size and costs energy (Wright and Newall, 1980). The representation by a mathematical formula can be similar to the one for respiration. A nematode of 1 μg wet wt. would excrete 1.92 μmol N h^{-1} g^{-1}; in mammals, 1 g of nitrogen excreted corresponds to 5.94 l O_2 respired. Mammals and other large animals, such as echinoderms, molluscs, and some crustaceans, have excretory systems, such as metanephridial organs that help to maintain a body less salty than the surrounding sea water. Animals can also excrete salt through a metanephridial system that depends on the salinity of the environment, which in a high saline environment can increase the speed of nitrogen excretion.

Reproduction

Reproduction for a consumer is similar to that for a producer. Reproduction is affected by the physical factors, such as temperature and salinity. Some consumers, like fish, produce a large number of eggs, but have high egg mortality or predation loss rates. Other consumers, such as dolphins and other mammals, are viviparus. Although they produce very few young, those that are produced have a lower mortality, because there is a high investment of parental care. Having young that develop internally is not limited to mammals. For instance, eggs of the nematode, *Anoplostoma viviparum*, characteristically contain developing larvae (Platt and Warwick, 1983).

Predation

Some consumers are eaten by other consumers. For example, zooplankton and herbivorous benthos (e.g., copepods) are consumed by fish; deposit feeding meiobenthos (e.g., nematodes) are eaten by deposit-feeding macrobenthos (e.g., polychaetes); small fish are eaten by large fish, and large fish are eaten by ducks, humans and other mammals. Many consumers are both

predators and prey. A pinfish may eat small shrimp, but is itself preyed upon by red drum.

The predation rate of a predator or predation mortality of prey is dependent on the chance of the interaction between the predator and the prey, and the predator's ingestion speed and the stomach capacity. The chance of the interaction is affected by the density of both predator and prey, mobility of predator and prey, and the type of spatial distribution in the habitat, (e.g., a contagious or random distribution, Elliot, 1971). A linear relationship between the prey survival rate and the predator abundance is the well known "Lotka-Volterra Model" (Lotka, 1925). It can be applied to those non-moble or infrequently moving predators, such as filter feeding of plankton by bivalves:

$$f(N_t, P_t) = 1 - a \cdot P_t$$

Where $f(N_t, P_t)$ is the prey survival rate (*predation mortality*=1 - *survival rate*) at time t, a is the predation rate of the predator, N_t is the prey's abundance at the time t and P_t is the predator's abundance at the time t. A non-linear relation between the prey survival rate and the predator's abundance, e.g., "Nicholson-Bailey Model" (Nicholson and Bailey, 1935), can be used for moving predators who actively search for food sources (i.e., fish feeding on grass shrimp):

$$f(N_t, P_t) = e^{-a \cdot P_t}$$

For prey that aggregate, such as nematodes, Li et al. (in press) suggested using an exponential relationship between prey abundance to their predation mortality:

$$N_r = P_r \cdot P_t \cdot e^{-\frac{k}{N_t}}$$

Where N_r is the prey's predation mortality due to all P_t, and P_r is the prey's predation mortality due to each single predator and k is a parameter. The exponential term, $e^{(-k/Nt)}$, is the effect that is due to the aggregate distribution of prey, which exponentially decreases predatory mortality when its abundance is low.

In the field, the relationship between prey and predator is not always this simple. Many predators share more than one prey population. Most prey populations have more than one predator (Kerfoot, 1987). Obviously, predation is not quite as simple as it is represented by

these equations.

Natural death

In this context, "natural death" refers to causes of death other than predation. In general, the life-span of animals corresponds to body size. The rate of aging, i.e., death per unit time, for a population is dependent on the total biomass. The representation by a mathematical formula is similar to that for respiration. Some small animals, such as most meiofauna, have a short life-span of a few days to a few months. Larger animals, such as most macrofauna and fish, have longer life-spans of a few months to a few years. An unfavorable environment, such as unsuitable temperature or salinity may prevent an animal from reaching its maximum possible life-span.

Migration

Migration between the bays and the ocean occurs in many large, swimming animals, such as red drum (*Sciaenops ocellatus*) and blue crabs (*Callinectes sapidus*). Animals may migrate to reproduce, find better food sources, or escape unfavorable environmental conditions. Therefore, environmental parameters such as temperature, salinity and the behavioral ecology of the species can all affect migration. For example, some species require specific environments for reproduction and nurseries for developing larvae, e.g., the migration of red drum larvae or shrimp larvae back into the bays.

Summary

Consumers must ingest prey items in order to increase their own biomass and reproduce (Fig. III.7B). A consumer must first assimilate a prey item, and then respire to gain energy from the ingested tissue. Both assimilation and respiration are dependent on the temperature and salinity of the environment. An increase in temperature speeds up enzymatic activity. An increase in salinity will divert energy reserves as the animal is forced to adjust water concentrations to compensate for a change in salt concentrations. Consumers can lose biomass and energy when they excrete organic material, die, or are eaten by larger consumers. Biomass can be transferred from one ecosystem to another if the consumers migrate from bay to ocean or back.

Mineralizers

The process of mineralization is important in transforming organic matter in an ecosystem, because mineralizers decompose and reduce the organic matter back into nutrients. Mineralizers are microscopic bacteria and fungi that gain their energy from detritus (Fig. III.8A). The degradation of organic matter is a function of the rate of exoenzymatic hydrolysis which is proportional to the biomass of bacteria (Billen and Lancelot, 1988). Mineralizing bacteria can be classified as aerobes and anaerobes based on how organic matter is reduced (Parsons et al., 1984). Aerobes use oxygen as an electron acceptor to reduce detritus. They reduce O_2 to CO_2 and H_2O. Anaerobes include nitrate reducers, sulphate reducers and methanogens. Anaerobes use other compounds, such as $NO_3^=$ and NO_2^-, sulphate ($SO_4^=$), and CO_2 as electron acceptors to reduce detritus. The nutrients that are produced by anaerobes include ammonia (NH_4^+), nitrous oxide (N_2O) and nitrogen (N_2), reduced sulfide (H_2S and $S^=$), and methane (CH_4), respectively. The breakdown of organic matter provides a pathway for buried energy to be recycled into the bay ecosystem.

The compounds that can be used by respiring organisms form a vertical sequence in their main activity within sediments. The respiratory compounds are electron acceptors that carry the detrital energy. The distribution of these compounds follows the following sequence with respect to depth in sediments: oxygen, nitrate, sulphate, and carbon dioxide. The distribution is determined by a combination of factors, such as: differences in requirements for specific redox levels, differences in energy yield of the respiration types, competition for electron donors, and differences in the concentration and distribution patterns of the electron acceptors (Jørgensen, 1989). The energy yield from respiration of this sequence of compounds decreases from oxygen to nitrate to sulphate to carbon dioxide as the electrons acceptors become less oxidizing. Concordant with this decrease in energy, the organisms become increasingly restricted in the range of energy substrates that they can utilize (Jørgensen, 1980). The aerobes and denitrifiers are very versatile with respect or organic energy sources, but the sulphate reducers and methanogens are dependent on substrates that are the products of fermentation processes in the reducing sediments (Jørgensen, 1980).

Aerobic respiration

Aerobes require oxygen and undergo the familiar process of aerobic respiration. The respiration of substrates, e.g., carbohydrates is represented by the formula:

$$C_6H_{12}O_6 + 6\ O_2 \rightarrow 6\ CO_2 + 6\ H_2O$$
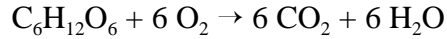
Aerobic respiration requires oxygen and is only possible in oxic waters and sediments. Typically this can occur at deeper depths in sandy than muddy sediments. However, it is restricted to the top few mm in mud and top few cm in sand. The change in oxidation level using oxygen as an electron acceptor is -4.

Anaerobic respiration

Anaerobic respiration occurs in anoxic environments and is also called fermentation. Anaerobes require compounds other than oxygen as electron acceptors to decompose organic matter. Therefore, energy flow is decoupled from carbon flow in anaerobic environments. Energy flow can be traced through the nitrogen and sulphur cycles in anaerobic sediments.

The changing chemistry of sediments is reflected in changes in "redox potential" and pH (Malcolm and Stanley, 1982). The redox potential (Eh) generally decreases (i.e., becomes more negative) in sediments as organic matter is destroyed. Eh measurements generally indicate the extent of organic matter decomposition in anaerobic sediments. There are primarily three respiratory processes, denitrification, sulfate reduction, and methanogenesis.

Denitrification is the respiration of substrates, e.g., carbohydrates, using nitrate in anoxic environments. Typically this can occur below the top few cm of sediment. The change in oxidation level using nitrate as an electron acceptor is -5, and is represented by the formula:

$$5\ C_6H_{12}O_6 + 24\ NO_3^- + 24\ H^+ \rightarrow 30\ CO_2 + 12\ N_2 + 42\ H_2O$$
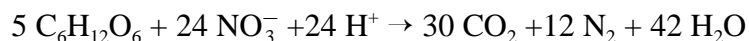
Sulphate reduction is the respiration of substrates, e.g., carbohydrates, using sulfate in highly reduced sediments. Sulfide production via this process is responsible for the familiar "rotten eggs" smell common in many organically enriched marine environments, such as salt marshes. Typically sulphate reduction occurs well below the top few cm of sediment. The change in oxidation level using sulphate as an electron acceptor is -8, and is represented by the formula:

$$C_6H_{12}O_6 + 3\ SO_4^- + 6\ H^+ \rightarrow 6\ CO_2 + 3H_2S + 6\ H_2O$$
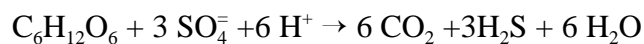
Carbonate reduction, or methanogenesis is a form of respiration in the deepest sediments.
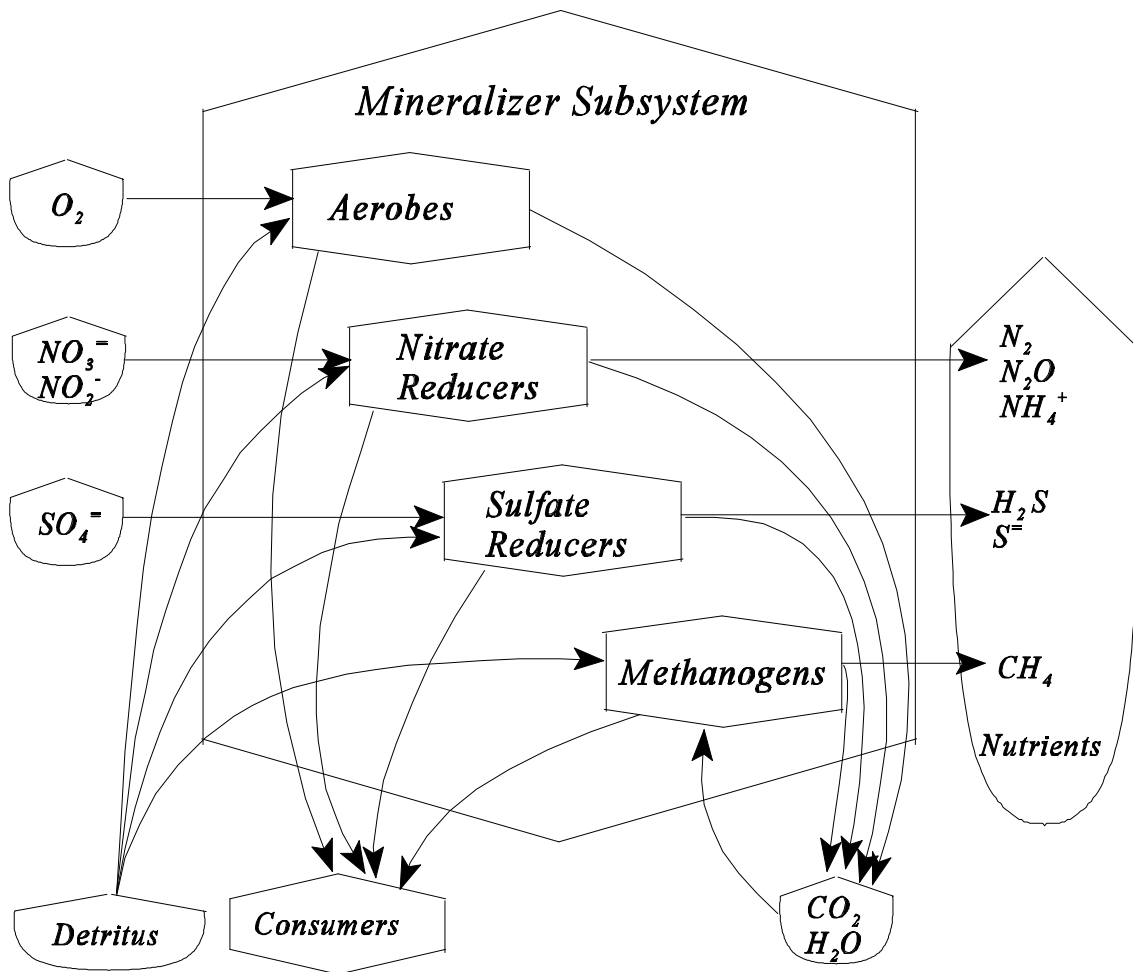
Fig. III.8A. The Mineralizer subsystem. The energy flows through mineralizers via aerobic or anaerobic respiration.

CONSUMERS

OXYGEN

O X Y G E N

D E C O M P O S I N G

M A T T E R

NITRATES → **AMMONIA**

CARBON DIOXIDE AND NUTRIENTS

SULFATE → **SULFIDE**

METHANE

S E D I M E N T **W I T H O U T** **O X Y G E N**

BURIAL
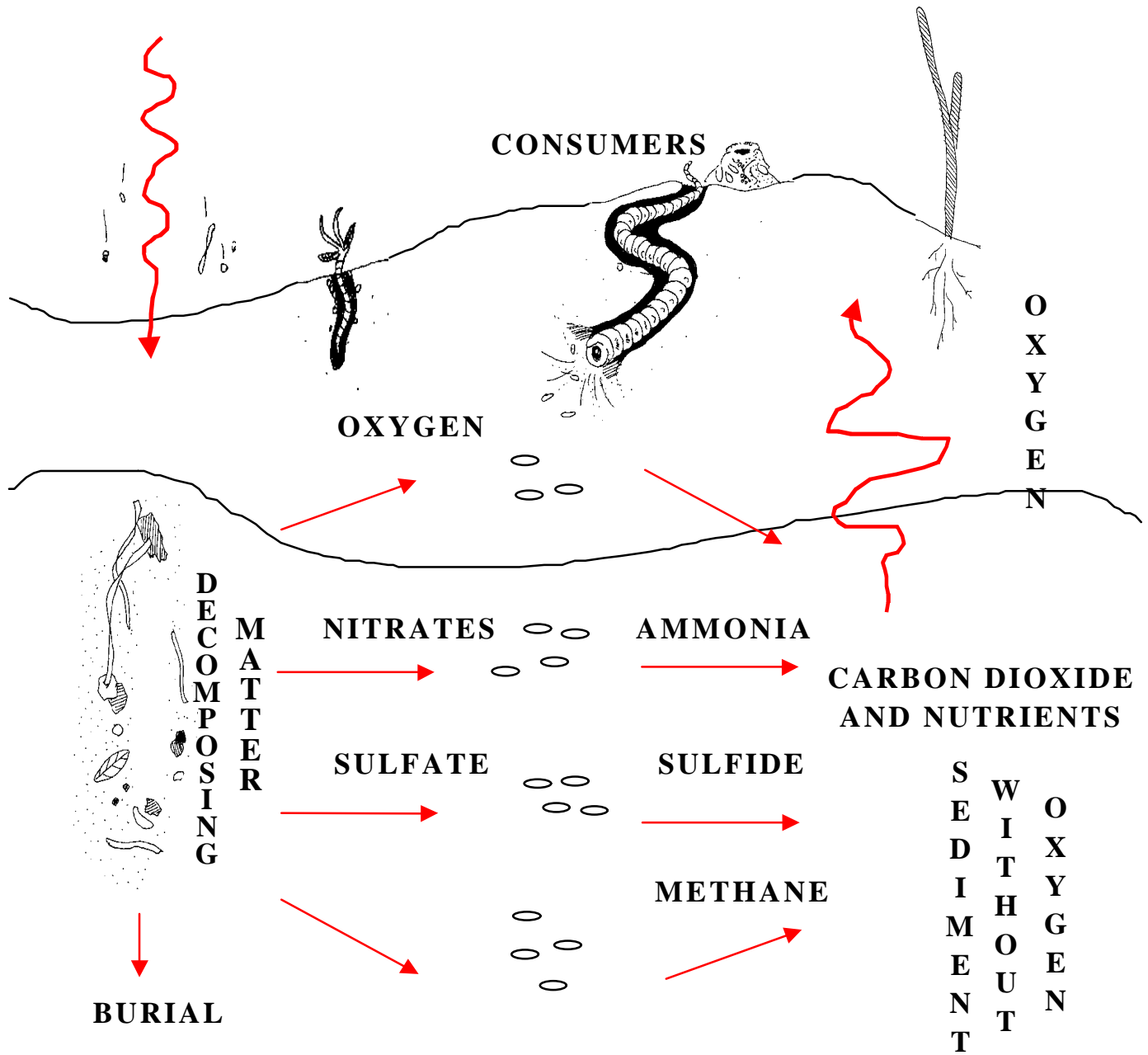
Fig. III.8B. Some bacteria live in sediment and decompose organic material. Some of these bacteria use oxygen for their decomposition. However, if oxygen is depleted from the sediment, other compounds can be used for this purpose, including sulfate and nitrate. These bacteria are very important to the bay ecosystem because they return many of these nutrients to the water, where they can be used by producers.

Methanogenesis typically occurs below the top m or so of sediment. The change in oxidation level using carbonate as an electron acceptor is -8, and is represented by the formula:

$$CO_2 + 4\ H_2 \rightarrow CH_4 + 2\ H_2O$$
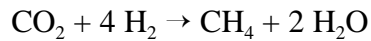
Summary

Mineralizers are bacteria that convert decomposing matter into energy using different biochemical respiration pathways (Fig. III.8B). Mineralizers that use oxygen to decompose detritus are called aerobes. When the oxygen is depleted from the sediment, a second group of bacteria takes over. These bacteria reduce nitrogen, converting nitrate and nitrite to ammonium. When nitrogen is depleted, another group of bacteria reduces sulfate to sulfide. A final group simply decomposes the organic carbon in detritus into methane. All of the mineralizers produce carbon dioxide as a by-product of their activities as well as certain nutrients, such as ammonium, that can be recycled back into the bay system. These bacteria are essential to an ecosystem because they process organic matter and regenerate nutrients.

<div align="center">Representative Mineralizer</div>

Increasing biomass

The biomass storage tank of a mineralizer increases through the decomposition of detritus. Like other organisms, mineralizers can reproduce, creating new bacterial cells. Processes such as natural death, respiration, and predation decrease the biomass storage tank of a mineralizer (Fig. III.9A).

Decomposition

Mineralizing bacteria get their energy through decomposition of organic matter in the detritus pool. The turbulence of water or sediment by kinetic energy may accelerate the decomposition process. The high defecation rate of nematodes, or other invertebrates, may also accelerate this process. For example, the maximum mineralization rate can be doubled by adding only ten nematodes per 10 cm^2 (Findlay & Tenore 1982). A high temperature can also increase the physiological activity of bacteria, increasing their uptake action. For example, there can be a significant difference in the rate of degradation of plant detritus in deep-sea sediments between

spring and summer (Poremba 1994).

Other factors

Factors affecting the respiration rate of a mineralizer are similar to those affecting a consumer. Respiration is limited by oxygen for aerobes, and other potential electron acceptors for anaerobes. Reproduction of mineralizing bacteria is limited to an oxic environment for aerobes and anoxic environment for anaerobes. Thus, disruption of the sediment may affect mineralizers when turbulence removes or resuspends a specific sediment layer. The predation of mineralizing bacteria is predominantly due to grazing of sediment by deposit-feeding fauna, such as nematodes or polychaetes. The life-span of mineralizing bacteria is probably much shorter than small invertebrates, such as meiofauna. Because of the small size of bacteria, and the difficulty of culturing all species of bacteria in the lab, there is not a lot of information available about the lifespan of individial cells.

Summary

Like consumers, mineralizing bacteria are limited by sources of energy, and by death and predation (Fig. III.9B) . However, for bacteria, the food source is sediment detritus and predation is by deposit-feeding animals. Furthermore, not all bacteria require oxygen. Sulfate reducing bacteria utilize sulfate, and release hydrogen sulfide into the environment. The "rotten egg" smell that occurs in some parts of Corpus Christi Bay during the summer is caused by sulfide released by these bacteria. However, without these organisms, important nutrients, such as nitrogen, phosphorous, and sulfur would be buried in the sediment and lost from the ecosystem.
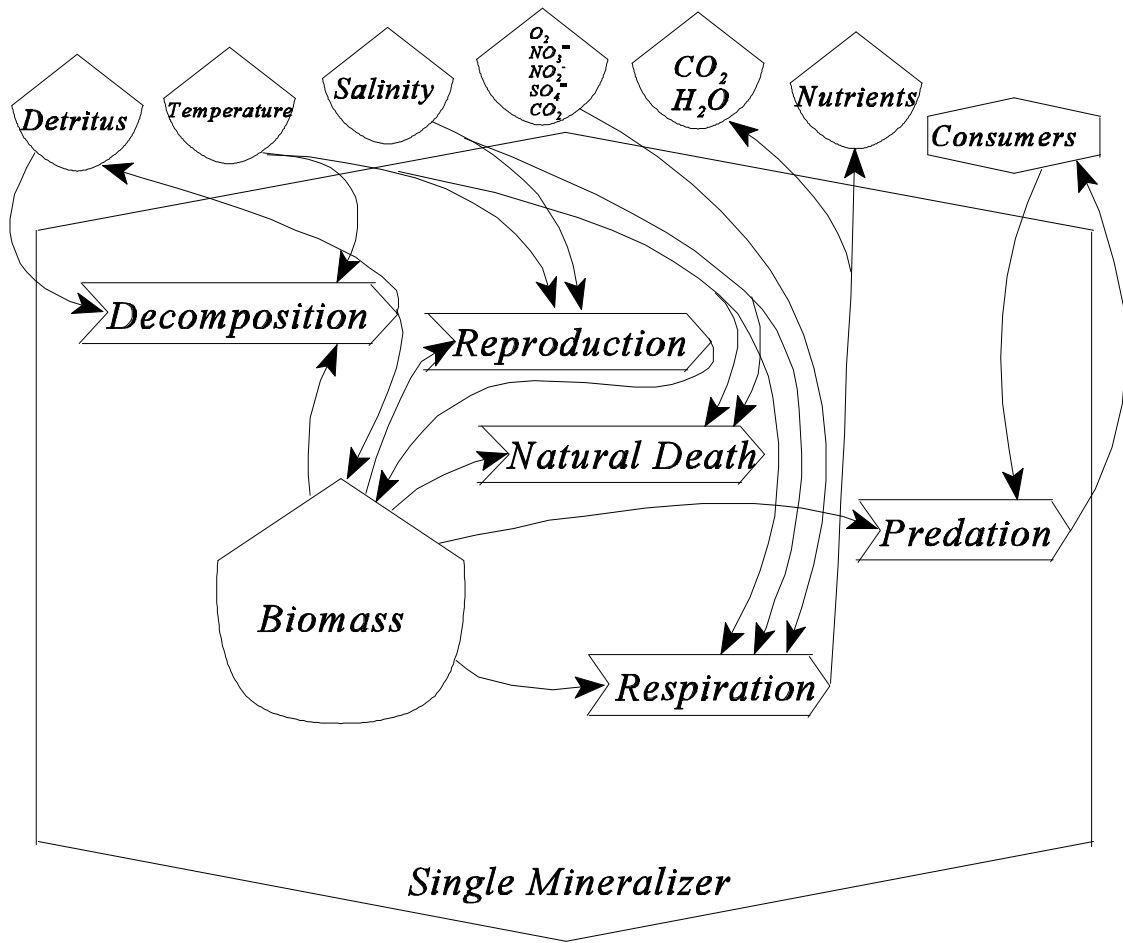
Fig. III.9A. The Mineralizer Subsystem. The energy flows and controlling processes inside a representative mineralizer.

OXYGEN

NUTRIENTS

HYDROGEN SULFIDE

DECOMPOSING MATTER

ENERGY

RESPIRATION

SULFATE

SEDIMENT WITHOUT OXYGEN

DEATH

PREDATION

REPRODUCTION

TEMPERATURE + SALINITY
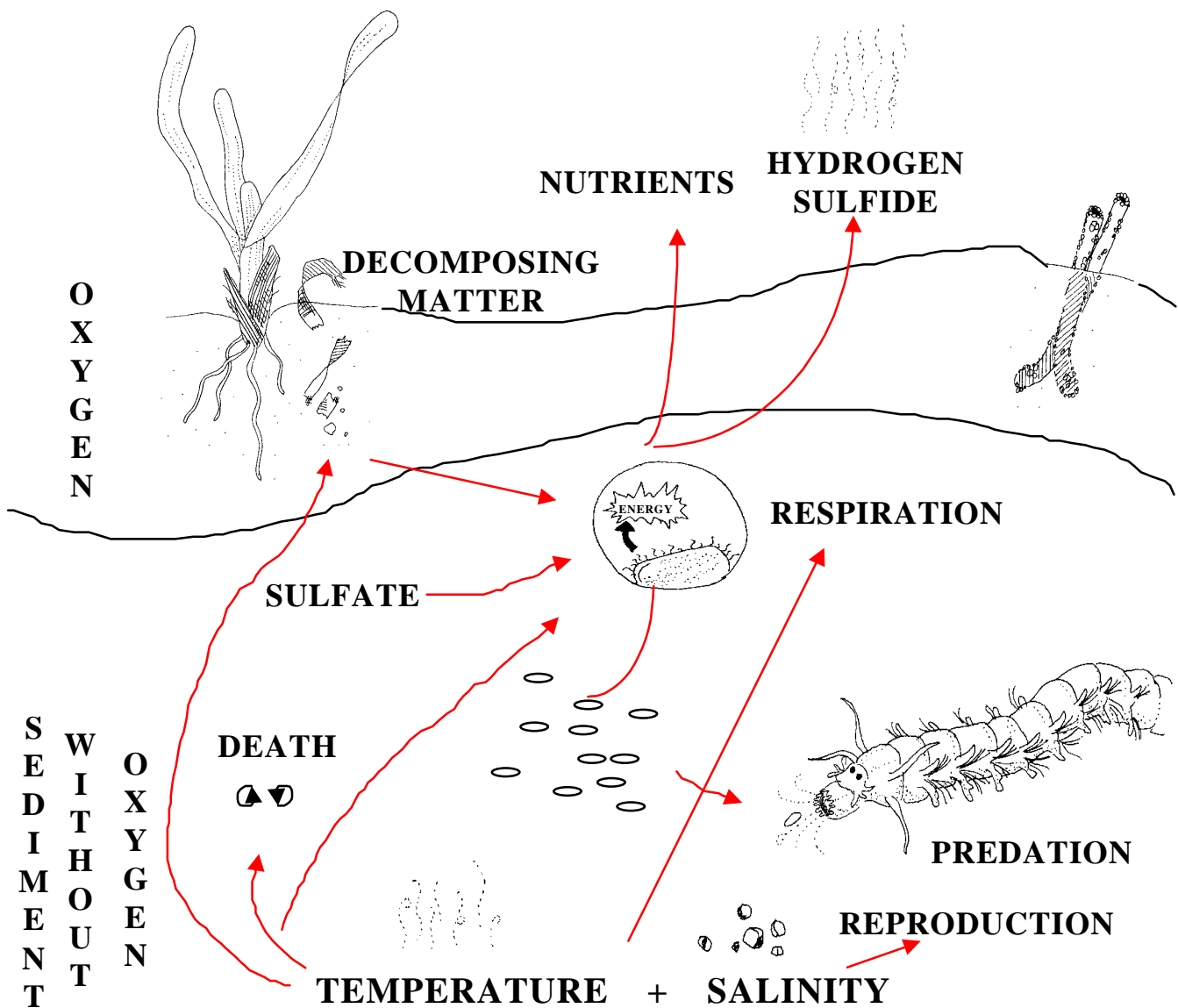
Fig. III.9B. Summary of a representative bacteria, a colony of sulfate reducing bacteria. These bacteria utilize sulfates, which are abundant in the sediments, to decompose organic material, such as this seagrass. The bacteria gain energy from the organic matter, and the sulfate is converted into hydrogen sulfide (which is easy to smell on hot, summer days). Like producers and consumers, bacteria are affected by temperature and salinity. Bacteria also have their own predators, particularly polychaete and nematode worms.

IV. HABITATS

Another way to characterize ecosystems, in addition to considering energy flow for each trophic level, is to consider each habitat within an ecosystem. Habitats are the elements of an environment that sustain an organism or a specific community of organisms. The populations of different species of organisms living in a habitat is called a community. In a Texas bay ecosystem, typical habitats include riverine, salt marsh, algal mat, seagrass bed, water column, open bay bottom, oyster reef, beach and oceanic habitats (Fig. IV.1A - IV.1B) (Day et al. 1989). Energy can be transferred among habitats by physical movement of the water, or by movement of the organisms between habitats. The interaction among habitats is partly responsible for the high productivity that is characteristic of estuaries.

Like other Texas estuaries, the CCBNEP estuaries have a common structure. Ocean water exchange with the Gulf of Mexico occurs through a break in the barrier island called a pass. Beach habitat faces the ocean or barrier island. There is only one continously open inlet, Aransas Pass, that connects Corpus Christi and Aransas Bays to the Gulf of Mexico. Corpus Christi and Copano Bays have a bottom that is predominantly a muddy habitat. However, there are patchy areas of sandy bottom or oyster reefs. Oyster reef habitats occur mostly in secondary bays, such as Nueces or Copano Bays, because oysters depend upon freshwater brought by rivers. The rivers empty into the secondary bays; sometimes there are tertiary bays or lakes associated with the river, e.g., Mission Lake, which empties into Copano Bay. Marshes line the river sources of tertiary and secondary bays. Lagoons run parallel to the barrier islands, and perpendicular to primary bays. Primary bays are connected by the lagoons; therefore, lagoons are important for transport of materials and recruitment between systems. Lagoons are long and narrow, with a short fetch. Furthermore, lagoons are in the lee of the barrier island. Therefore, the water in a lagoon is calm and clear, relative to the primary bays. Seagrass beds develop well in this habitat. Algal mats develop on broad, supratidal tidal flats.

Within the CCBNEP Bay Area System, all different habitat types can be found in all three estuaries. However, the area of each habitat varies within each estuary. The muddy bottom is typical of the bays, but there are regions with a sandy bottom, particularly near shore. The oyster reef and salt marsh habitats are common in the Mission-Aransas Estuary. The oysters in this estuary are an important commercial harvest. The algal mat, and grass bed habitats are common in Laguna Madre. The Laguna is well known for its populations of fish, due, in part to the nursery habitat provided by the extensive seagrass beds. The Nueces

49
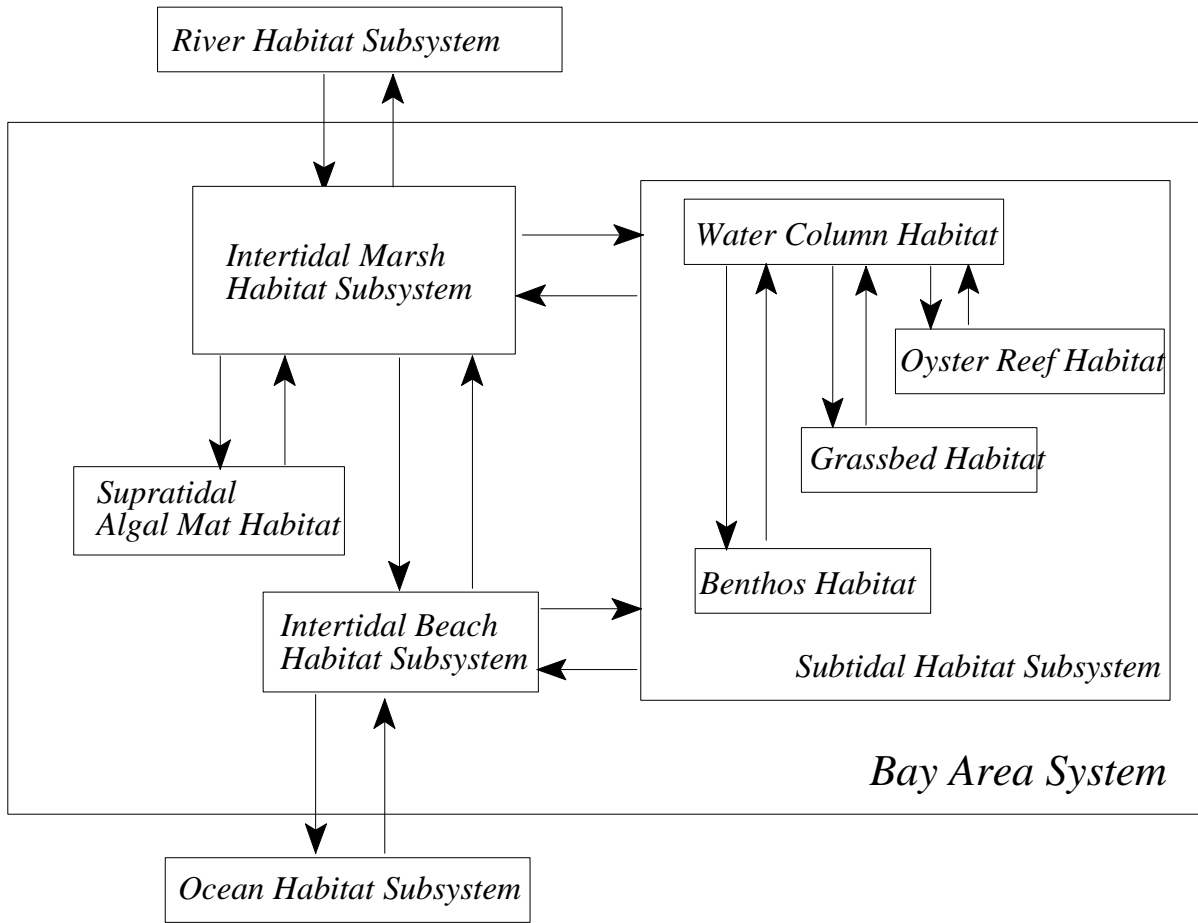
Fig. IV.1A. Habitat subsystems of the CCBNEP area ecosystem.
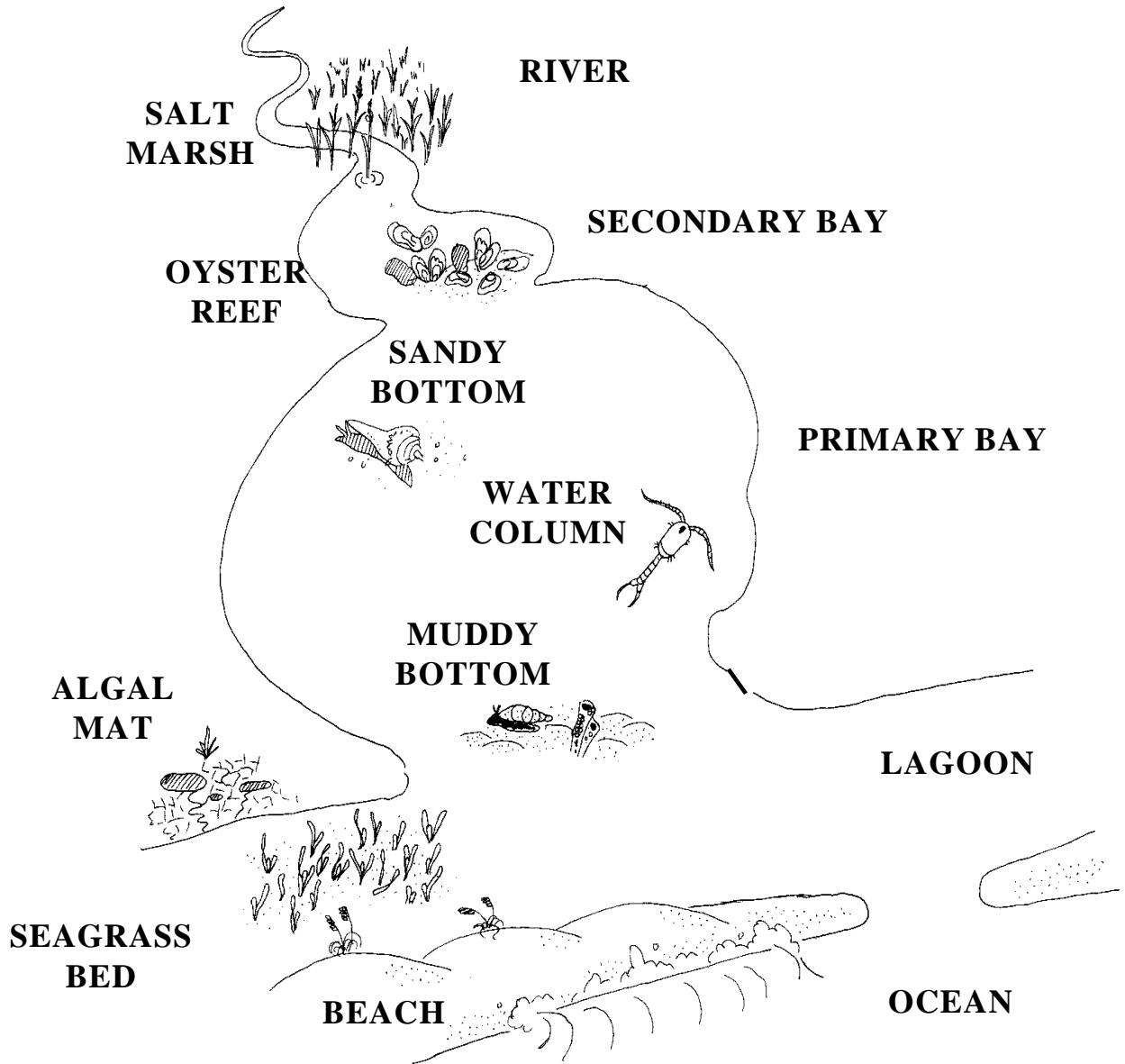
Fig. IV.1B. Habitat subsystems of the CCBNEP Bay area System. Water column refers to water that fills the three estuaries. While there is a lot of surface area for this habitat, it is not very deep, and is less productive than the vegetated benthic habitats. The most common benthic habitats are muddy bottoms in Nueces Estuary and Mission-Aransas Estuary, and seagrass beds in Laguna Madre. Sandy bottoms occur in patches in all three estuaries, particularly near shorelines. Oyster reefs are common in Copano Bay and Nueces Bay. Salt marshes occur alon much of the shoreline of the CCBNEP Bay Area, but are particularly abundant in the Nueces Delta. Algal mats are a unique supratidal habitat that occurs in patches around the Bay Area, particularly along Baffin Bay. Beaches occur along the ocean side of the barrier islands of all three estuaries.

Estuary is intermediate between the other two estuaries, because the extent of algal mat, grassbed, beach, oyster reef and salt marsh habitats are intermediate in size. The open bay bottom, therefore, is a large habitat in the Nueces Estuary. The Nueces Estuary has a gradient from muddy to sandy bottom from Nueces to Corpus Christi Bay. The nutrient storage in Nueces Bay is much higher than in Corpus Christi Bay because the Nueces River and marsh provide Nueces Bay with intermittent fresh water (Whitledge, 1989). Although there are more nutrients in Nueces Bay, chlorophyll *a* per unit area is higher in Corpus Christi Bay (Stockwell, 1989). Correspondingly, a higher zooplankton abundance is also found in Corpus Christi Bay (Buskey, 1989). The sandier Corpus Christi Bay has higher abundance and species diversity of benthic mollusks than the muddier Nueces Bay. However, the Corpus Christi mollusks tend to be smaller than those in Nueces Bay (Montagna and Kalke, 1995).

Seagrass Bed Habitat

Much of the Laguna Madre, and shallow, fringing areas of Nueces Bay, Redfish Bay and Copano Bay are covered with beds of seagrasses (Fig. IV.2A - IV.2B). There is also a large seagrass bed in Corpus Christi Bay (i.e., East Flats). There are five species of seagrasses, but the thin-bladed shoal grass, *Halodule wrightii,* and the thick-bladed turtle grass, *Thalassia testudinum,* are the most common. *Halodule* grows rapidly in disturbed areas, but is usually out-competed by *Thalassia* over time. The areas in which seagrasses grow are characterized by strong currents and a shallow bottom. The sediments range from sandy to fine, and are usually reducing just below the surface due to high oxygen consumption rates of decomposers.

Seagrass beds support a very diverse and productive foodweb by providing a source of carbon for the food web, and a place for fish and invertebrates to hide from predators. The high amount of biomass from these plants leads to high rates of gross primary productivity and net community productivity. Seagrass is difficult to digest, because of structural compounds. However, seagrass is an important contributor to the detrital foodweb. Seagrass is also a substrate for epiphytic algae (e.g., microalgae that grow on seagrass blades) and animals (e.g., crustaceans and polychaete worms). Seagrass beds serve an important role as nursery grounds for larval fish and invertebrates. They also serve as buffers against storms and can help filter contaminants from the water.
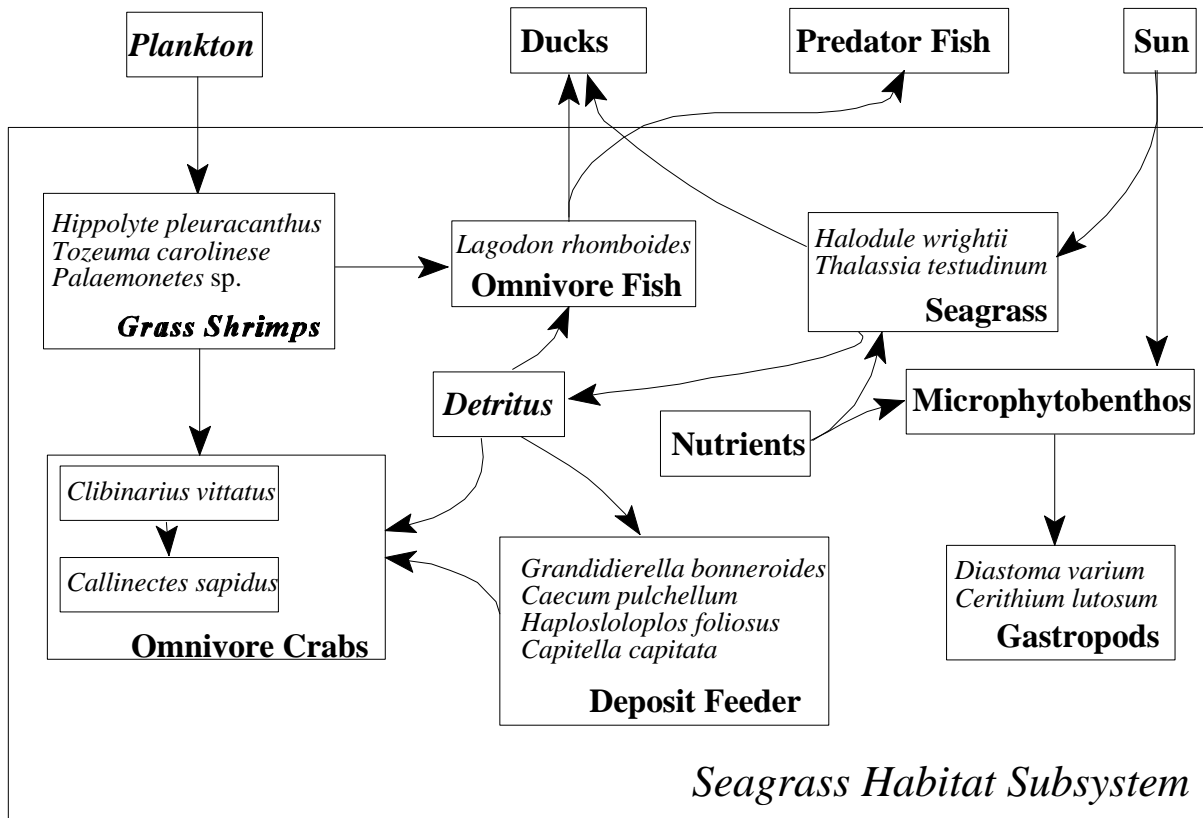
Fig. IV.2A. The components of the Seagrass Habitat Subsystem.

PLANKTON AND ORGANIC MATTER

14

13

1

4

5

3 **2**

6

EPIPHYTES

12

7

DECOMPOSING MATTER

8

10 **9**

11
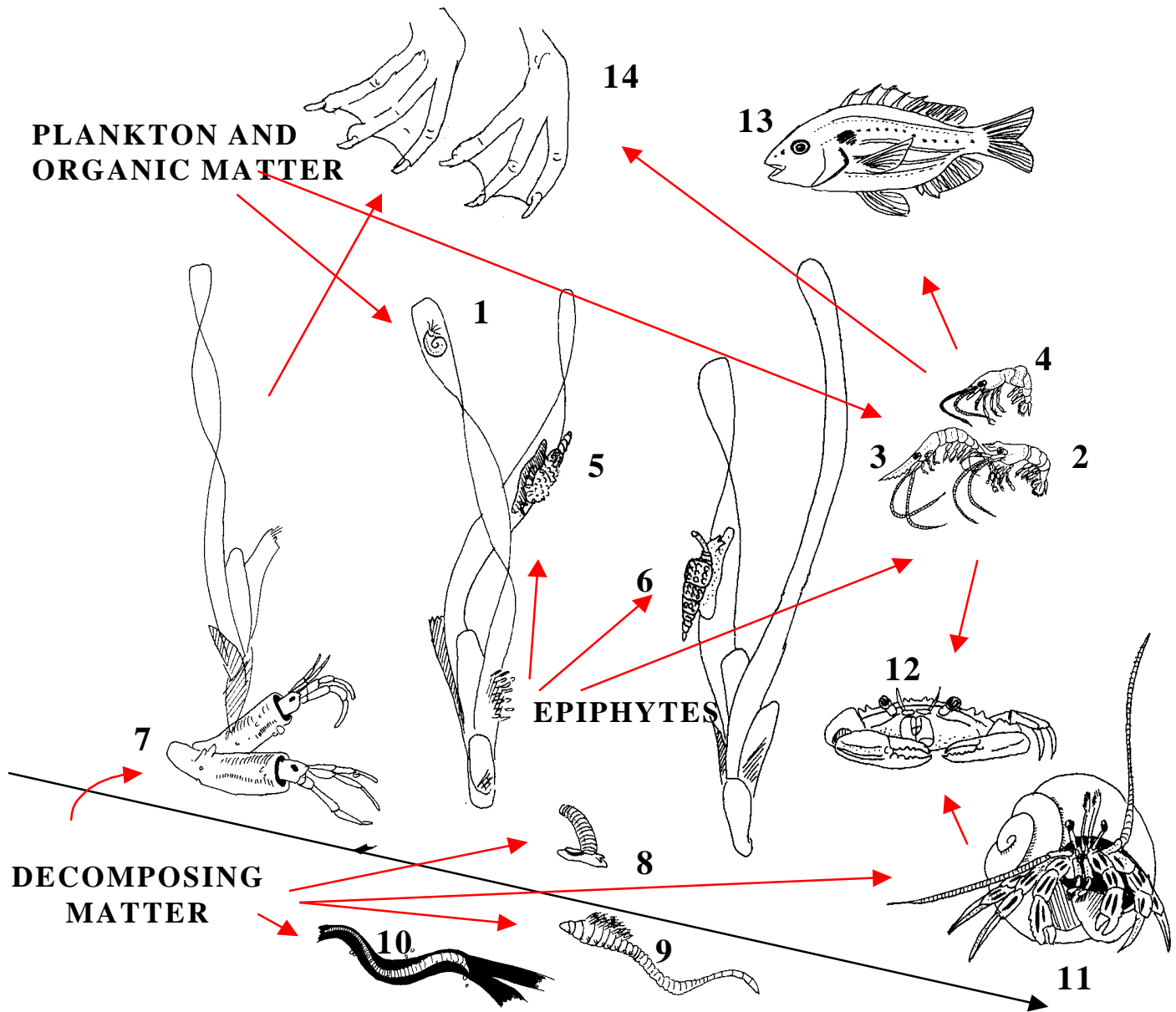
Fig. IV.2B. Seagrass habitat of the Bay Area. Seagrasses provide an important habitat for many fish and invertebrates, and contribute a major component of the decomposing matter that feeds deposit feeders. 2 – *Spirorbis* sp., 2 – *Palaemonetes* sp. (grass shrimp), 3 – *Tozeuma carolinese* (grass shrimp), 4 – *Hippolyte pleuracanthus* (grass shrimp), 5 – *Cerithium lutosum*, 6– *Diastoma varium*, 7 – *Grandidierella bonneroides*, 8 – *Caecum pulchellum*, 9–*Haploscoloplos foliosus*, 10 – *Capitella capitata*, 11- *Clibinarius vittatus* (hermit crab), 12 – *Callinectes sapidus* (blue crab), 13 – *Lagodon rhomboides* (pinfish), 14 - ducks

Many species can be found in the seagrass meadows. Among these are the tiny polychaete worm, *Spirorbis* sp., which filters plankton and organic matter from the water column. *Spirorbis* can be seen on seagrass blades as a small, white coil or circle. Grass shrimp graze on epiphtyic algae and detrital matter. There are three types of grass shrimp, the dominant *Palaemonetes* sp. (Fig. IV.2B.2), the arrow shrimp, *Tozeuma zostericola* (Fig. IV.2B.3), and the green, broken backed shrimp, *Hippolyte carolinensis* (Fig. IV.2B.4). The epiphytic algae is grazed by small snails, such as the white, sharp-pointed *Cerithium lutosum* (Fig. IV.2B.5) and the brown, round-knobbed *Diastoma varium* (Fig. IV.2B.6).

Many animals are supported by detrtitus trapped by the seagrass blades or beneath the sediment. These include the tube-building amphipod, *Grandidierella bonneroides* (Fig. IV.2B.7), small snails, such as *Caecum pulchellum* (Fig. IV.2B.8) and burrowing polychaetes. These polychaetes, such as *Haploscoloplos foliosus* (Fig. IV.2B.9) and *Capitella capitata* (Fig. IV.2B.10), process bulk sediment, extracting organic matter from non-organic mud.

At the top of the foodweb are several generalist crustaceans, such as the striped hermit crab, *Clibinarius vittatus* (Fig. IV.2B.11), and the blue crab, *Callinectes sapidus* (Fig. IV.2B.12). These animals eat everything they can find, from detritus to grass shrimp and worms. Many kinds of fish live in the seagrass meadows, but particularly visible are the pinfish, *Lagodon rhomboides* (Fig. IV.2B.13). In the winter, a variety of duck species move into the seagrass meadows (Fig. IV.2B.14). The ducks feed on small meiofauna, grass shrimp, or the roots and rhizomes of the seagrass itself. Larger predatory fish, such as a redfish, black drum, and spotted seatrout feed on the smaller fish and larger invertebrates that congregate in seagrass meadows.

Salt Marsh Habitat

Salt marshes are shallow or intertidal regions of the bay, often near a source of fresh water input, that are dominated by marsh grasses and plants, particularly *Spartina alterniflora* (Fig. IV.3A - IV.3B). In the CCBNEP Bay Area System, salt marshes can be found along the shores of all three estuaries, but are particularly abundant near river mouths in secondary bays. Nueces Bay has an extensive salt marsh in the Nueces Delta / Rincon Bayou area. Copano Bay also supports salt marshes in Mission and St. Charles Bays. Along the eastern coast of the United States, salt marshes extend for kilometers. In contrast, Texas has very small tidal ranges, so salt marshes in the CCBNEP Area only extend for a few meters from

Insects

Birds

Predator Fish

River and Runoff

Sun

Larvae of
Chironomidae
Corixidae
Deposit-feeding Insects

Fundulus sp.
Omnivore Fish

Spartina alterniflora
Marsh Grass

Microphytobenthos

Mediomastus sp.
Streblospio benedicti
Deposit-feeding Polychaetes

Detritus

Assiminea succinea
Littorina irrorata
Gastropods

Uca sp.
Deposit-feeding Crabs

Nutrients

Marsh Habitat Subsystem

Fig. IV.3A. The components of the Marsh Habitat Subsystem.

EPIPHYTES

DECOMPOSING MATTER

6 9 8 5 4 7 1 3 2
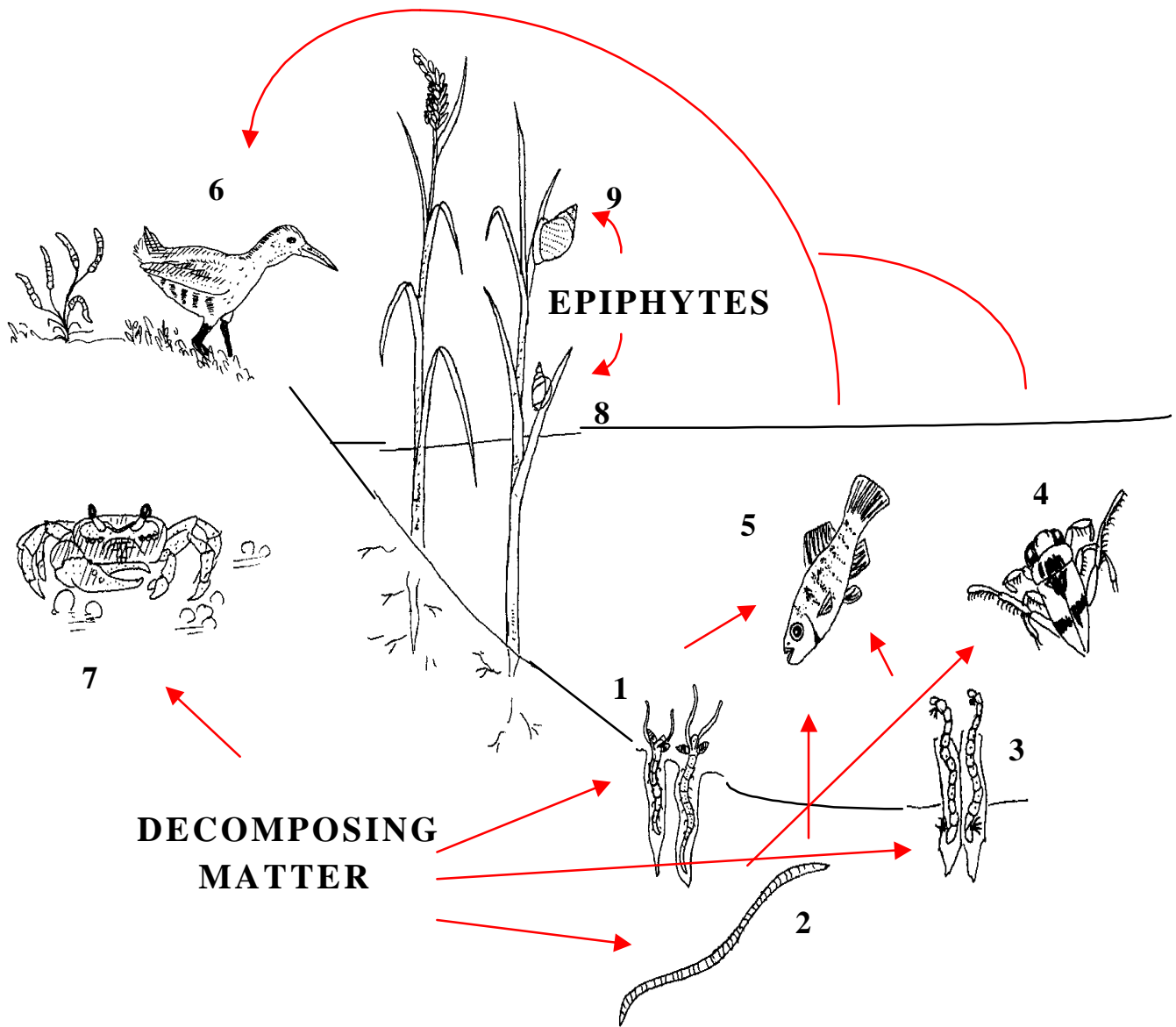
Fig. IV.3B. Salt marsh habitat of the Bay Area. Marshes along the shoreline, particularly near the mouth of rivers and creeks. Marsh grasses contribute organic matter to the Bay Area. 1– *Streblospio benedicti*, 2– *Mediomastus* sp., 3 – Chironomidae (midge) larvae, 4 – Corixidae (water boatsmen), 5- *Fundulus* sp. (killifish), 6- rails and other marsh birds, 7- *Uca* sp. (fiddler crab), 8- *Assiminea succinea*, 9- *Littorina irrorata* (marsh periwinkle).

the shoreline. In more tropical regions, mangroves, such as *Avicennia germinans*, gradually replace salt marsh grasses. The CCBNEP Area is near the northern extent of mangroves' range. However, in the period following several mild winters, mangroves are quite common, particularly along Redfish Bay.

Intertidal wetlands act as sediment traps, where soft sediment and peat become trapped between the salt marsh plants. Beneath the plants are strong reducing conditions, and often low oxygen levels. Areas with a higher fresh water inflow have higher producer diversity, higher rates of primary production and higher net community production. Because of the amount of dead and decaying plant matter, the detrital foodweb is important in salt marshes, and other habitats near salt marshes. Biomass of producers and consumers can be high, but species diversity can be low because of fluctuating salinity. Like seagrass beds, salt marshes are important nursery and feeding grounds for a variety of invertebrates and fish.

The ubiquitous polychaete, *Streblospio benedicti* (Fig. IV.3B.1), can be found in salt marshes. *Streblospio* filters plankton from the water or browses detritus with its tentacles. Another polychaete, common in salt marshes, and many other habitats, is the deposit feeder, *Mediomastus* sp. (Fig. IV.3B.2). Unlike most marine habitats, salt marshes also support some insects, particularly when salinities are low. Midge larvae (Chironomidae) behave much like polychates, feeding on detritus from their tubes (Fig. IV.3B.3). Water boatmen (Corixidae) are active swimmers, but feed mostly on detritus (Fig. IV.3B.4). Many small fish can be found in salt marshes. The many species of killifish (*Fundulus* sp.) feed on the abundant soft-bodied invertebrates in the marsh (Fig. IV.3B.5). These fish and their invertebrate prey are eaten by the diverse array of shore birds that frequent salt marshes, including rails, herons, egrets and ibis (Fig. IV.3B.6). Scurrying about on land, with the birds, can be found *Uca* sp., the fiddler crabs (Fig. IV.3B.7). *Uca* dig burrows in the soft mud in the high intertidal zone. They feed on algae and detritus that they collect by scooping up the mud into a feeding ball and scraping organic matter off of the ball with their mouth parts. The epiphytic algae that grow on *Spartina* are grazed by several species of snail, including the small, white *Assiminea succinea* (Fig. IV.3B.8) and the larger, striped periwinkle, *Littorina irrorata* (Fig. IV.3B.9).

Algal Mat Habitat

Algal mats are unusual features of the supratidal zone that occur in some locations around the CCNEP Bay Area. They occur when rain or wave surge collects in low spots near the shore,

often in areas with higher elevation than salt marshes. The trapped water is very shallow, and often becomes quite hot and saline. However, the water also allows a bloom of photosynthetic bacteria, called cyanobacteria or blue-green algae, that live on the sediment surface. These producers are very important to the bay ecosystem, because they have the ability to fix atmospheric nitrogen (N_2) into a form more usable by other producers and bacteria (NH_3, NO_3 or NO_2). When this material gets transported back into the estuaries, it represents a nutrient spike that can enhance primary productivity in the estuary. However, aside from the cyanobacteria, there are not many species that are endemic specifically to the algal mats.

Beach Habitat

There are two types of beach habitat in the CCBNEP Bay Area System (Fig. IV.4A - IV.4B). Bay shorelines that are not covered by salt marsh grasses can be considered beaches. However, bay beaches are not as diverse and are not as distinct a habitat as are oceanic beaches. Oceanic beaches are found on the Gulf of Mexico side of Padre, Mustang and San Jose Islands. While these habitats are not directly connected to the estuaries, there is interaction between the estuary and the adjacent beach. After storms, seagrass can be washed onto the beach, transporting energy from the bay to the oceanic environment. Also, many mobile animals, such as fish and crabs, move freely between the two ecosystems.

Tidal passes and beaches are directly exposed to strong currents and waves. Because of the high energy imparted by the water, most mud-sized particles have been carried away. Furthermore, because of the constant exposure to high energy, beach habitats are well oxidized and have a constant oceanic salinity (about 35 ppt). In the absence of mud, and high organic detritus, these habitats are home mostly to filter feeders. The community is often highly diverse and has a high biomass and productivity, due to the transport of food by currents.

The larger, more obvious animals include the mole crab, *Emerita portoricensis*, a relative of the hermit crab (Fig.IV.4B.1). *Emerita* buries itself up to its head in the sand and filters plankton and organic matter with its feathery antennae. Some polychate species, such as the tentacled *Scolepis squamata* (Fig.IV.4B.2), also rely on plankton brought in by the waves. These filter feeders are eaten by many species of juveline fish, particularly postlarval jacks (Carangidae) that hide in shallow water to escape predation (Fig.IV.4B.3). The small polychaetes are also eaten by larger, predatory polychaetes, such as *Lumbrineris* sp.
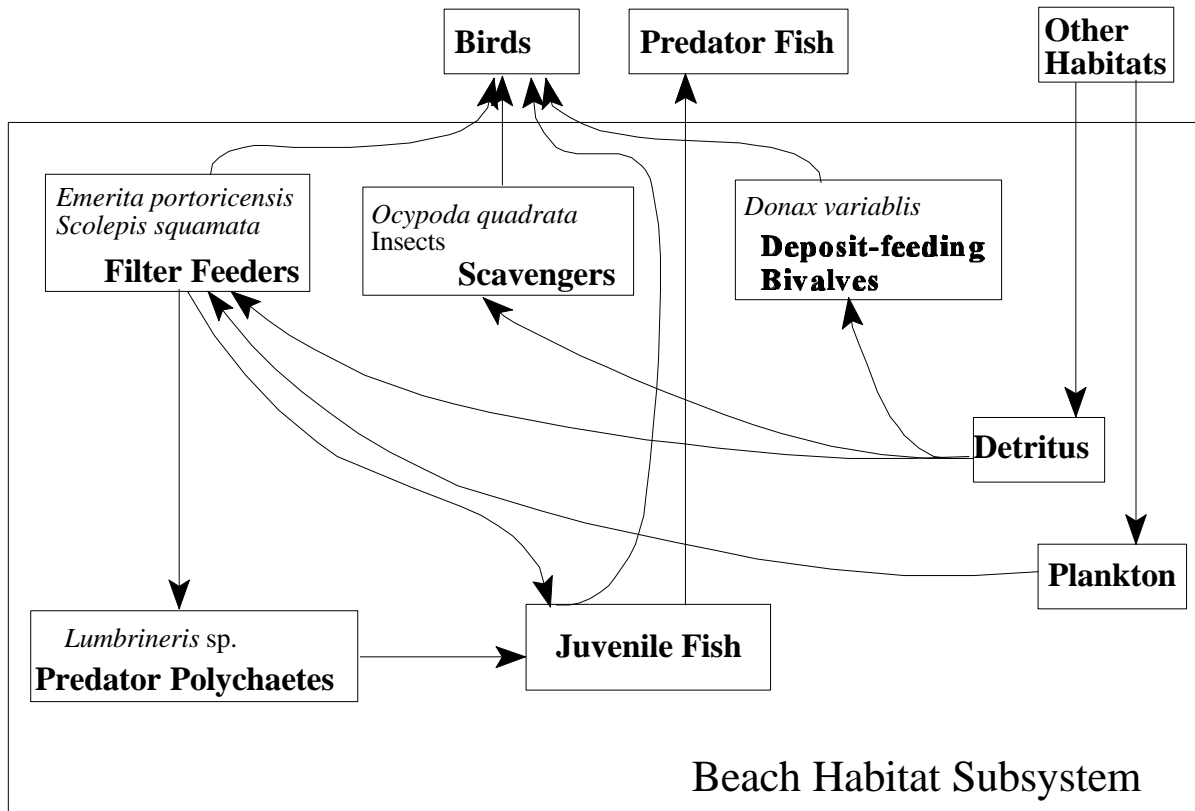
Fig. IV.4A. The component of the Beach Habitat Subsystem.

ANIMALS AND
DECOMPOSING
MATTER

PLANKTON

DECOMPOSING
MATTER

6

7

8

5

1

4

2

3
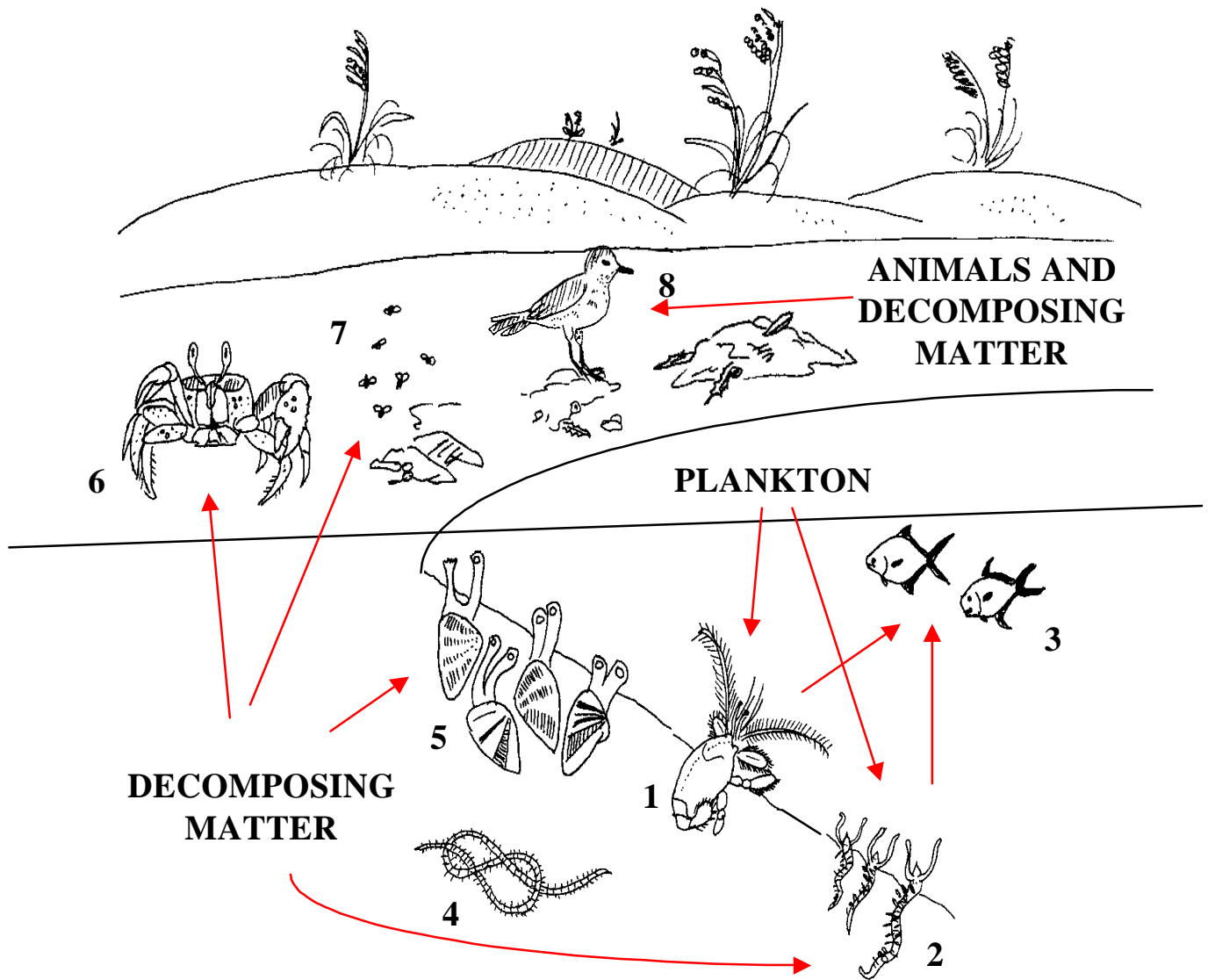
Fig. IV.4B. Beach habitat of the Bay Area. Beaches experience high energy, but still support many animal species. 1-*Emerita portoricensis* (mole crab), 2- *Scolepis squamata*, 3-juvenile Carangidae (jack fish) and other fishes, 4- *Lumbrineris* sp., 5-*Donax variabilis* (coquina clam), 6-*Ocypoda quadrata* (ghost crab), 7- Diptera (flies), 8- sandpipers and other shore birds.

(Fig.IV.4B.4). Another common and familiar resident of the beaches is the colorful coquina clam, *Donax variablis* (Fig.IV.4B.5). *Donax* bury themselves using their muscular feet and probe for food with their long siphons. Because of the waves and tides, a lot of detritus piles up on the beach itself. This detritus is mostly plant material, particularly *Sargassum* seaweed or sea grasses that are transported by tides out of the bay area after storms. While this decomposing matter may smell offensive, and is often cleaned from the beaches by humans, it serves as an important source of food for near coastal environments. Detritus is food for animals such as the elusive ghost crab, *Ocypoda quadrata* (Fig.IV.4B.6), amphipods, meiofauna or insects (Fig. IV.4B.7). Some of these smaller animals are eaten by the numerous shorebirds, such as sanderlings, sandpipers, turnstones and seagulls (Fig.IV.4B.8). In addition, buried debris can trap sand and is partly responsible for the beach accretion process during the summer and pre-hurricane seasons.

Water Column Habitat

The water column of the CCBNEP Bay Area refers to the water that fills all three estuaries (Fig. IV.5A - IV.5B). Although the water column covers a huge surface area, it is not very deep, and often only as productive as the bay bottom. Water column productivity is much lowere than in vegetated habitats. Typically, in marine environments, such as the Gulf of Mexico, the water column habitat is very deep, and more productive than the bottom. The water column of bays can become quite turbid as sediment is resuspended by wind or human activities. Because fresh water mixes with salt water in the bays, the salinities are typically brackish (10-25 ppt). However, when evaporation exceeds fresh water inflow and flushing by the ocean, salinities can become saltier than the ocean (> 35 ppt). The water column is usually well oxygenated. Mixing, due to the consistent high wind speeds, and shallow depths cause stratification of the bay water column to be a rare event. The foodweb consists of phytoplankton (one celled algae) being eaten by zooplankton, which are in turn eaten by fish. Primary production by phytoplankton in estuarine water can be relatively high. In temperate zones, there is a strong seasonal change (the spring and fall blooms), which is not as pronounced near the tropics.

There are two cycles of energy in the water column foodweb. One of these is called the "microbial loop." Small, flagellate algae (Fig.IV.5B.1) can photosynthesize, or ingest planktonic bacteria (Fig.IV.5B.2). Flagellates are a very diverse group of plankton that can travel short distances by beating their whip-like flagella. These small phytoplankton are eaten by small zooplankton, such as ciliated protists (Fig.IV.5B.3). When the small
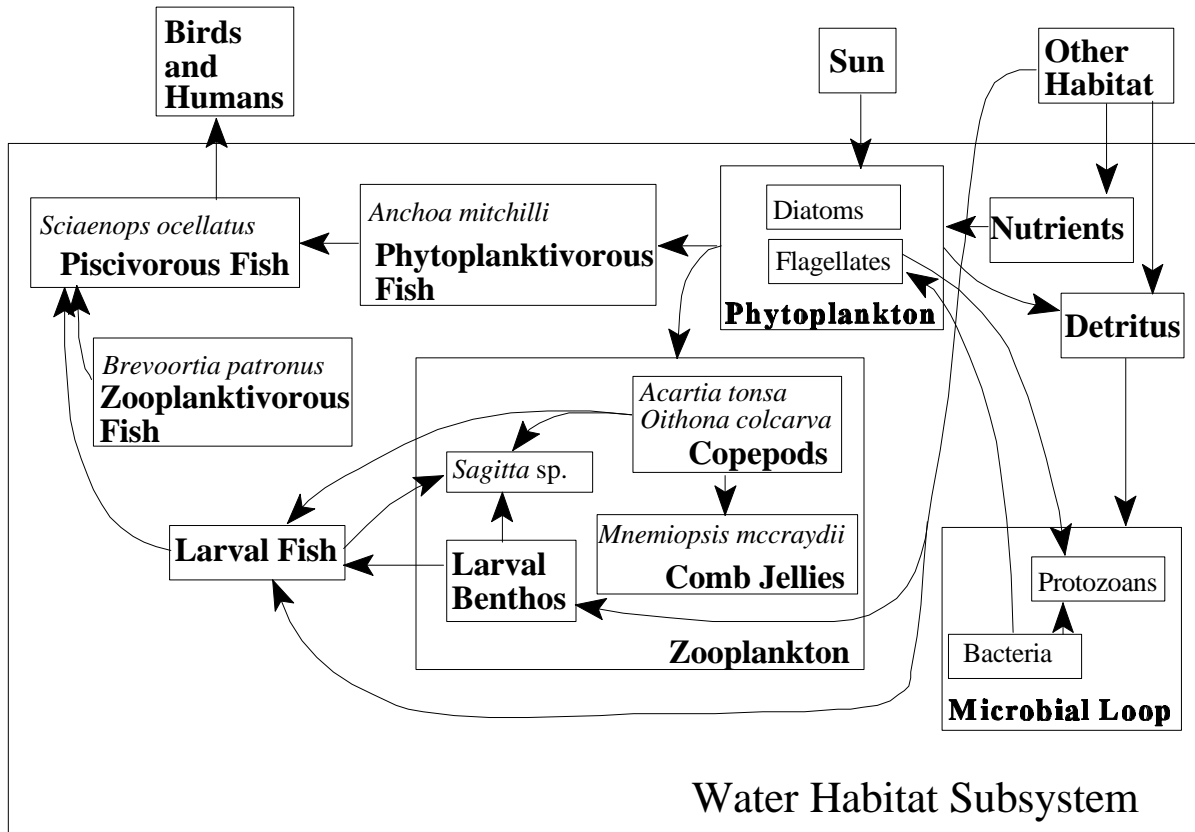
Fig. IV.5A. The components of the Water Habitat Subsystem.
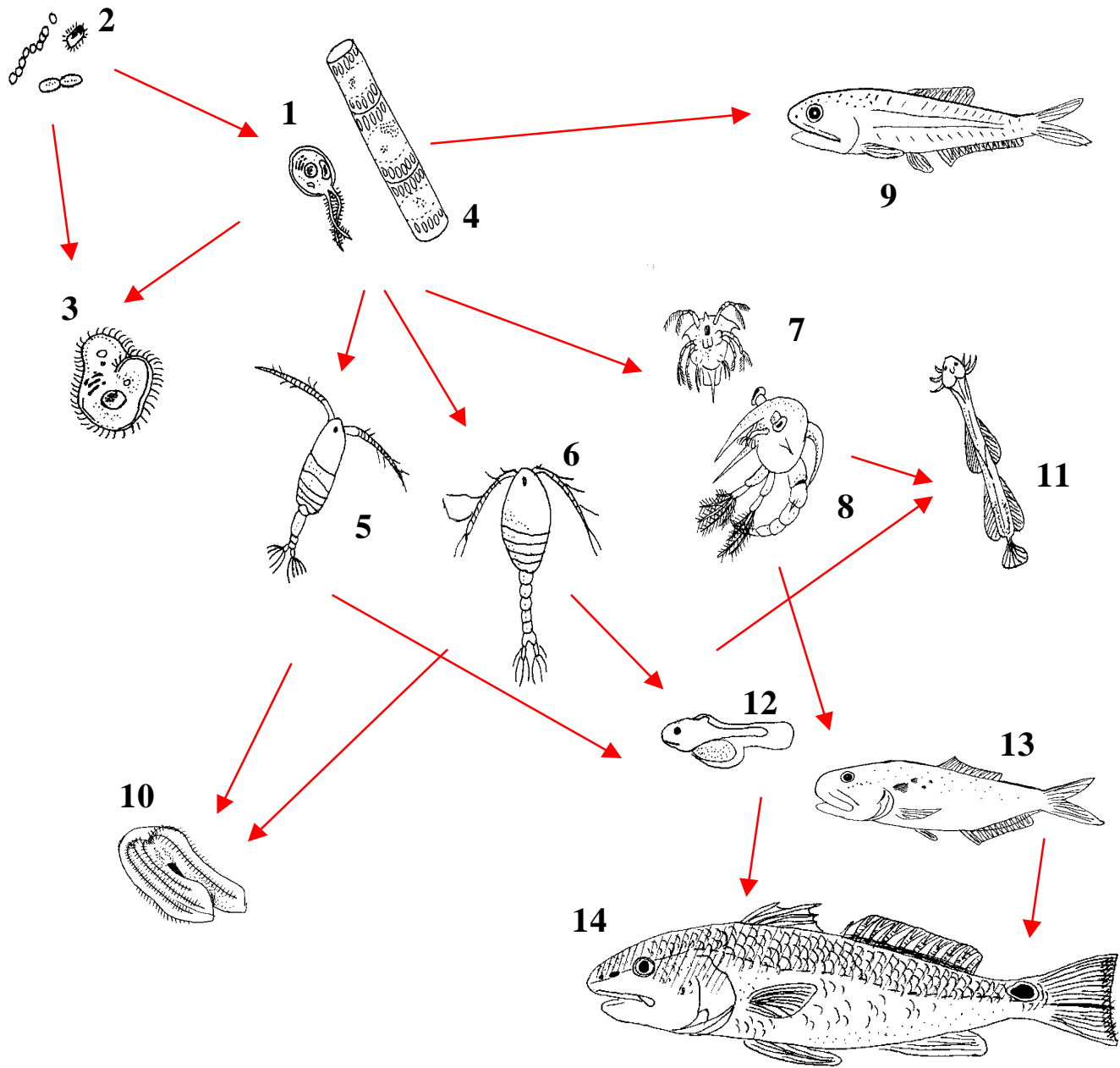
Fig. IV.5B. Water column habitat of the Bay Area. The water column contains many small animals and plants that are important food sources for larger animals. 1- flagellate phytoplankton, 2- bacteria, 3- ciliate, 4- diatom phytoplankton, 5- *Acartia tonsa* (calanoid copepod), 6 - *Oithona colcarva* (cyclopoid copepod), 7 - crustacean nauplius (larva), 8 - crab zoea (larva), 9- *Anchoa mitchilli* (bay anchovy), 10- *Mnemiopsis mccraydii* (comb jelly or ctenophore), 11 - *Sagitta* sp. (arrow worm or chaetognath), 12 - fish larva, 13 - *Brevoortia patronus* (bay menhaden), 14 - *Sciaenops ocellatus* (red drum) and other large fish.

phytoplankton and zooplankton die, they may be decomposed by bacteria in the water. Therefore, a small, but rapid foodweb cycle occurs among the small phytoplankton, small zooplankton and bacteria. Scientists are still unsure how much of this energy is available to other organisms, that is, it is unknown whether the microbial loop is a "link" or "sink."

A larger foodweb consists of the larger phytoplankton, such as diatoms (Fig.IV.5B.4), that are eaten by zooplankton. Diatoms have silicate shells that resemble pill boxes or petri dishes, and can be solitary or be joined together in long chains. There are two types of zooplankton, holoplankton, which spend their entire lives as plankton, and meroplankton, which are planktonic only as larvae. Holoplankton include many copepod crustaceans of the orders Calanoida (e.g., *Acartia tonsa*; Fig.IV.5B.5) and Cyclopoida (e.g., *Oithona colcarva*; Fig.IV.5B.6). Meroplankton include larval barnacles (or nauplii, Fig.IV.5B.7) and larval crabs (or zoea, Fig.IV.5B.8). There are also larger fish that eat phytoplankton, such as the large schools of bay anchovy, *Anchoa mitchilli* (Fig.IV.5B.9). Some zooplankton are eaten by larger zooplankton. The comb jelly, or ctenophore, *Mnemiopsis mccraydii* (Fig.IV.5B.10), filters out copepods with rows of comb-like projections. Comb jellies may, in turn, be eaten by larger jellyfish, such as the sea nettle, *Chrysaora quinquirecha*. Another zooplankton predator is the chaetognath, or arrow worm, *Sagitta* sp. (Fig.IV.5B.11). Many fish prey on zooplankton, including the larvae of many different species (Fig.IV.5B.12), and the adults of species such as the menhaden, *Brevoortia patronus* (Fig.IV.5B.13). Large, predatory fish, including the red drum, *Sciaenops ocellatus* (Fig.IV.5B.14), eat the plantkivourous fish.

Open Bay, Sandy Bottom Habitat

While most of the CCBNEP area has a muddy bottom, certain areas, particularly near shore, have sandier sediment (Fig. IV.6A - IV.6B). Sand can support larger animals that might sink in the soft mud. Sandy bottoms are often accompanied by stronger currents and higher water transparency in comparison with muddy water habitats. Attached algae, such as macroalgae, and benthic diatoms can yield high productivity in sandy bottoms. Because of the clear water, there are also many filter feeders in sandy sediment.

One of these filter feeders is the sandy bottom version of the tentacled polychaete, *Spiophanes bombyx* (Fig. IV.6B.1). Like its relatives, *Spiophanes* uses its palps to capture food from the water, or gather it from the sediment surface. A larger, stranger polychaete is *Chaetopterus variopedatus* (Fig. IV.6B.2). *Chaetopterus* builds a tube that is completely

Phytoplankton

Human

Sun

Microphytobenthos

Gobiosoma bosci
Fish

Callinectes sapidus
Crabs

Tellina sp.
Sipunculid worns
Deposit Feeders

Meiobenthos

Diopatra cuprea
Polychaetes

Nutrients

Busycon contrarium
Gastropods

Predators

Detritus

Mercenaria mercenaria
Chaetopterus variopedatus
Branchiostoma peridium
Phoronid worms
Spiophanes bombyx

Filter Feeders

Mineralizer Bacteria

Open Bay Sandy Bottom Habitat Subsystem

Fig. IV.6A. The components of the Open Bay Sandy Bottom Habitat Subsystem.
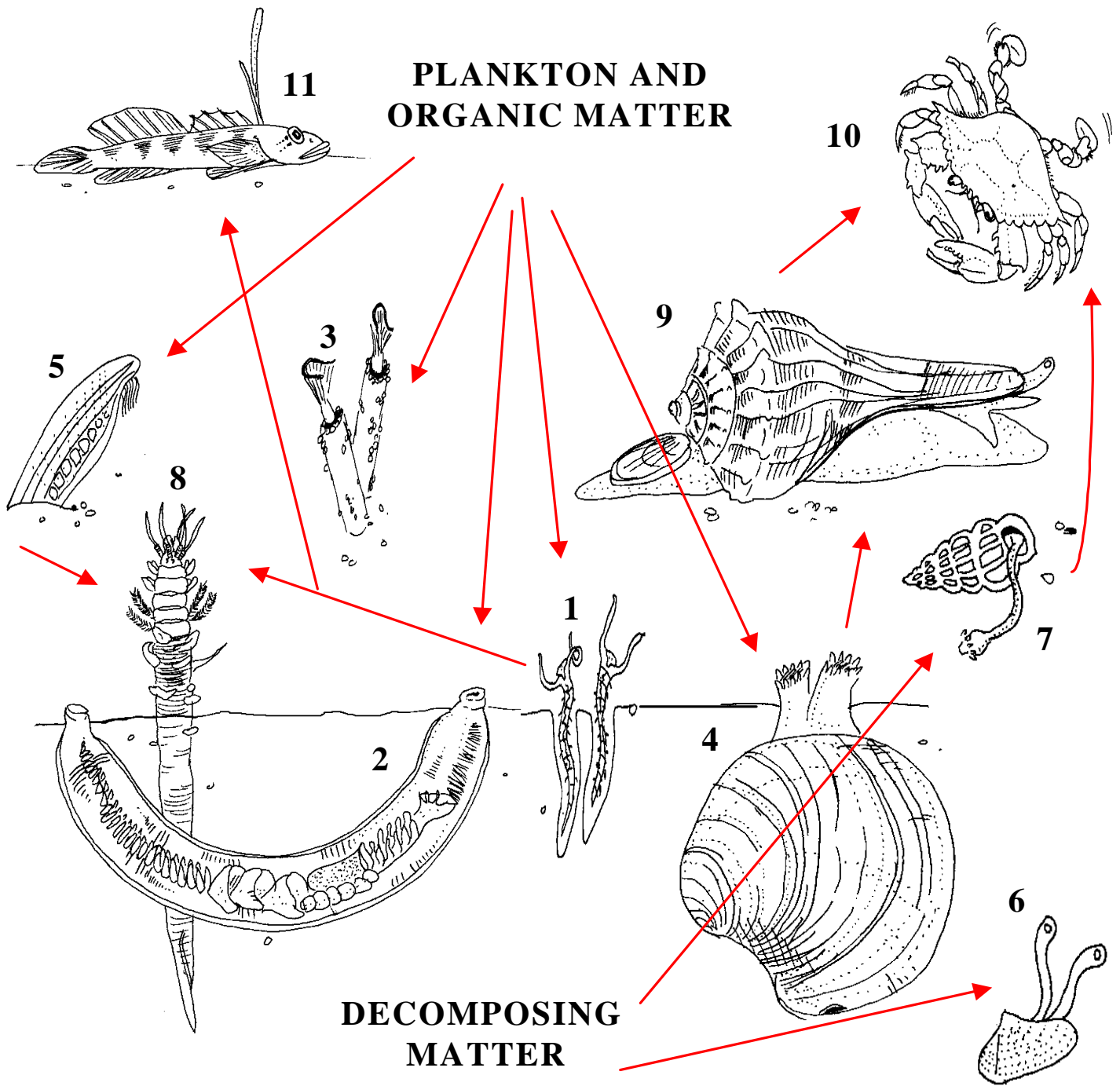
Fig. IV.6B. Sand bottom habitat of the Bay Area. Although not a large area, sandy bottoms can support many of the large, familiar invertebrates. 1- *Spiophanes bombyx*, 2- *Chaetopterus variopedatus*, 3- phoronid worms, 4- *Mercenaria camphechiensis* (quahog clam), 5 – *Branchiostoma peridium* (lancelet), 6- *Tellina* sp., 7- sipunculid worm (in a gastropod shell), 8- *Diopatra cuprea*, 9- *Busycon contrarium* (lightning whelk), 10-*Callinectes sapidus* (blue crab), 11- *Gobiosoma boscii* (naked goby).

buried in the sand. The worm stays inside the tube, using highly modified feet to pump in water and filter out organic matter. Another strange, tube worm is the phoronid (Fig. IV.6B.3), that filter feeds by using a U-shaped brush, somewhat like a barnacle. A more familiar filter feeder is the quahog clam, *Mercenaria campechiensis* (Fig. IV.6B.4). *Mercenaria* is quite large for a clam, and is capable of removing large ammounts of plankton from the water column. In more northern bays, *Mercenaria* can be very common, and is an important shellfishery. In the CCBNEP Area, these clams tend to be rare, occurring only in sandy sediment, but individuals can be quite large. Another filter feeder, less well known than the quahog, is the hemichordate, *Branchiostoma peridium* (Fig. IV.6B.5), that resembles a small fish. There are also deposit feeders in sandy sediment, such as the small clam, *Tellina* sp. (Fig. IV.6B.6). Another deposit feeder is the sipunculid worm (Fig. IV.6B.7). Sipunculids sometimes live in discarded gastropod shells, much like hermit crabs.

The many filter and deposit feeders support several invertebrate and invertbrate predators. The red-gilled worm, *Diopatra cuprea* (Fig. IV.6B.8) builds tubes of shells and detritus that are often found washed up on the beach. Despite the fact that it builds a tube, *Diopatra* is predatory, emerging from its tube to grab passing prey. The lightning whelk, *Busycon contrarium*, which in Texas, has a backwards-curving shell (Fig. IV.6B.9) is a large, well known snail that uses the edge of its shell and a rasping radula to feed on large clams, such as *Mercenaria*. Blue crabs, *Callinectes sapidus* (Fig. IV.6B.10), can be found in many habitats, including sandy bottoms. They tend to be opportunistic, eating any animals or detritus that they encounter. Another generalist predator is the naked goby, *Gobiosoma bocii* (Fig. IV.6B.11).

Open Bay, Muddy Bottom Habitat

By far, the most common benthic habitat in the CCBNEP system is the muddy bottom (Fig. IV.7A - IV.7B). Sediment underlying deeper water in Corpus Christi, Nueces, Redfish and Copano Bays is predominantly mud. In the Laguna Madre ecosystem, only Baffin Bay has a muddy bottom. Muddy bottoms occur in portions of bays where there is a lack of other physical features, such as grasses or oyster reefs. Movement of the water over the surface of the mud keeps the sediment oxygenated to about one centimeter depth. Below this region is a strongly reduced environment due to the absence of oxygen-generating producers. Mud is easily resuspended, and muddy bottoms may experience erosion or deposition of sediment. Therefore, turbidity tends to be high, which restricts the presence of producers and filter feeders. Deposit feeders, however, can be present in high abundance and diversity.

Phytoplankton

Human

Sun

Microphytobenthos

Mediomastus sp.
Ampelisca abdita
Penaeus aztecus
Tellina texana
Deposit Feeders

Meiobenthos

Pogonias cromis
Leiostomus xanthurus
Arius felis
Predator Fish

Nutrients

Detritus

Mulinia lateralis
Streblospio benedicti
Clymenella torquata
Filter Feeders

Mineralizer Bacteria

Open Bay Muddy Bottom Habitat Subsystem
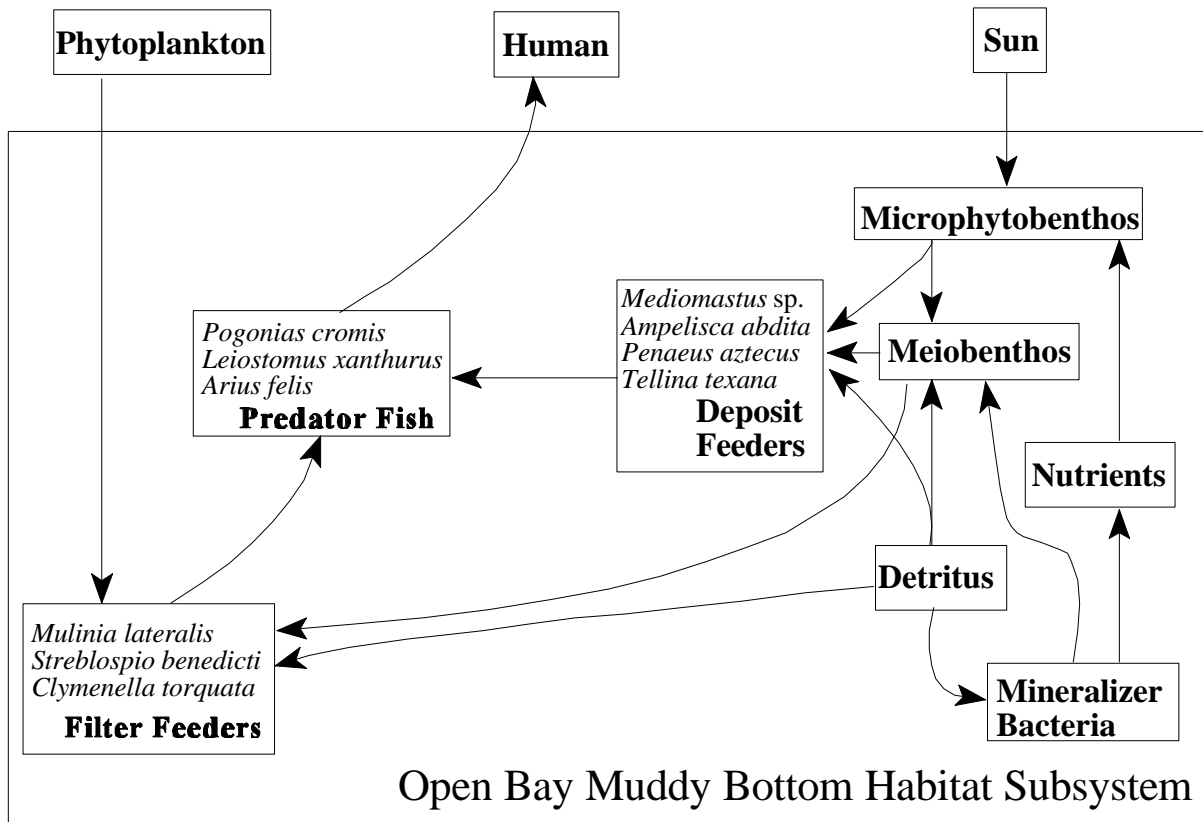
Fig. IV.7A. The components of the Open Bay Muddy Bottom Habitat Subsystem.

69
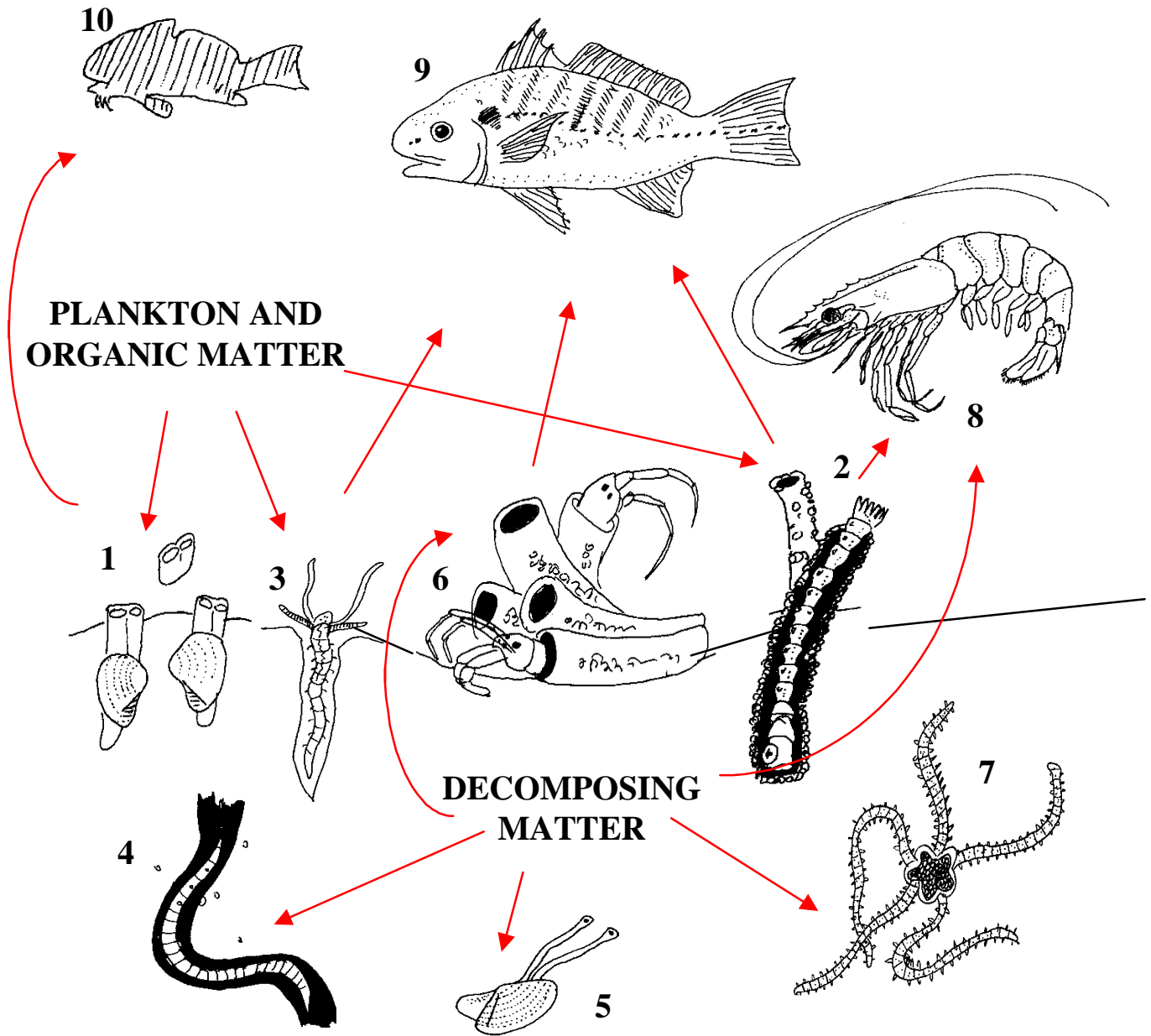
Fig. IV.7B. Muddy bottom of the Bay Area. Muddy bottoms are very common, and support a diverse array of species. 1- *Mulinia lateralis* (dwarf, surf clam), 2- *Clymenella torquata* (bamboo worm), 3- *Streblospio benedicti*, 4- *Mediomastus* sp., 5- *Tellina* sp., 6- *Ampelisca abdita*, 7- ophiuroid (brittle star), 8- *Penaeus aztecus* (brown shrimp), 9- *Leiostomus xanthurus* (spot), 10- *Pogonias cromis* (black drum) shown in background.

Biomass and metabolism are also relatively high.

The mudy bottom ecosystem is driven by two sources of carbon: phytoplankton and detrital matter. The filter feeders may eat phytoplankton in the water column, or detritus that is dissolved in the water. One of the dominant species is the dwarf surf clam, *Mulinia lateralis* (Fig. IV.7B.1). *Mulinia* is a small, white clam that can become so dense in certain areas that there is no space between a clam and its neighbors. Other filter feeders present are the bamboo worms of family Maldanidae, particularly *Clymenella torquata* (Fig. IV.7B.2). These polychaetes pump water through their tubes and extract food from it. An unusual characteristic of these worms is that their head is at the bottom of the tube. Because they pump water down to the bottom of the tube, these animals are important in turning over and aerating sediment, and returning sediment-bound nutrients to the foodweb. Another polychaete filter-feeder is the ubiquitous *Streblospio benedicti* (Fig. IV.7B.3). *Streblospio* uses its palps to capture organic matter in the water in strong currents or collect organic matter from the surface sediment when flow is lower.

Detritus, which can come from terrestrial organic matter transported by freshwater inflow, marine organic matter derived from marshes or seagrasses, and sedimented phytoplankton are the most important sources of carbon for muddy bottoms. There are three types of animals that utilize detritus: non-selective deposit feeders, selective deposit feeders, and omnivores. Non-selective deposit feeders include polychaetes such as *Mediomastus* sp., that resemble earthworms (Fig. IV.7B.4). These polychaetes process bulk sediment, extracting organic matter from the mud. Selective deposit feeders usually have tentacles to pick and choose specific particles of material for ingestion. In the CCBNEP Area, the dominant selective deposit feeders include bivalves, such as *Tellina* sp. (Fig. IV.7B.5) and *Macoma* sp., amphipods that build tubes, particularly *Ampelisca abdita* (Fig. IV.7B.6), and brittle stars (or ophiruoids, Fig. IV.7B.7). Omnivores include animals such as the edible shrimp, *Penaeus* sp., that eat detritus, microphytes, or any small animals they can catch (Fig. IV.7B.8). Many animals, particularly fish, eat the numerous invertebrates on the bottom. Spot, *Leiostomus xanthurus* (Fig. IV.7B.9), are well known for picking at animals in the sediment, particularly for biting off siphons or tentacles without killing the whole organism. *Mulinia lateralis* is the primary food source for black drum, *Pogonias cromis* (Fig. IV.7B.10), which collect mouths full of sediment and grind up shells with their pharyngeal teeth. Shrimp are eaten by a diverse assemblage of fish, such as catfish, *Arius felis*, red drum, *Sciaenops ocellatus*, and flatfish.

Phytoplankton

Human and Birds

Other Habitats

Sun

Pogonias cromis
Menippe adina
Predator Fish and Crab

Nutrients

Crassostraea virginica
Balanus sp.
Tunicates
Mussels

Filter Feeders

Nereids
Predator Polychaete

Detritus

Corophium sp.
Deposit Feeders

Thais haemastoma
Crepidiula fornicata
Epigrowth Feeders

Epiphytes

Oyster Reef Habitat Subsystem
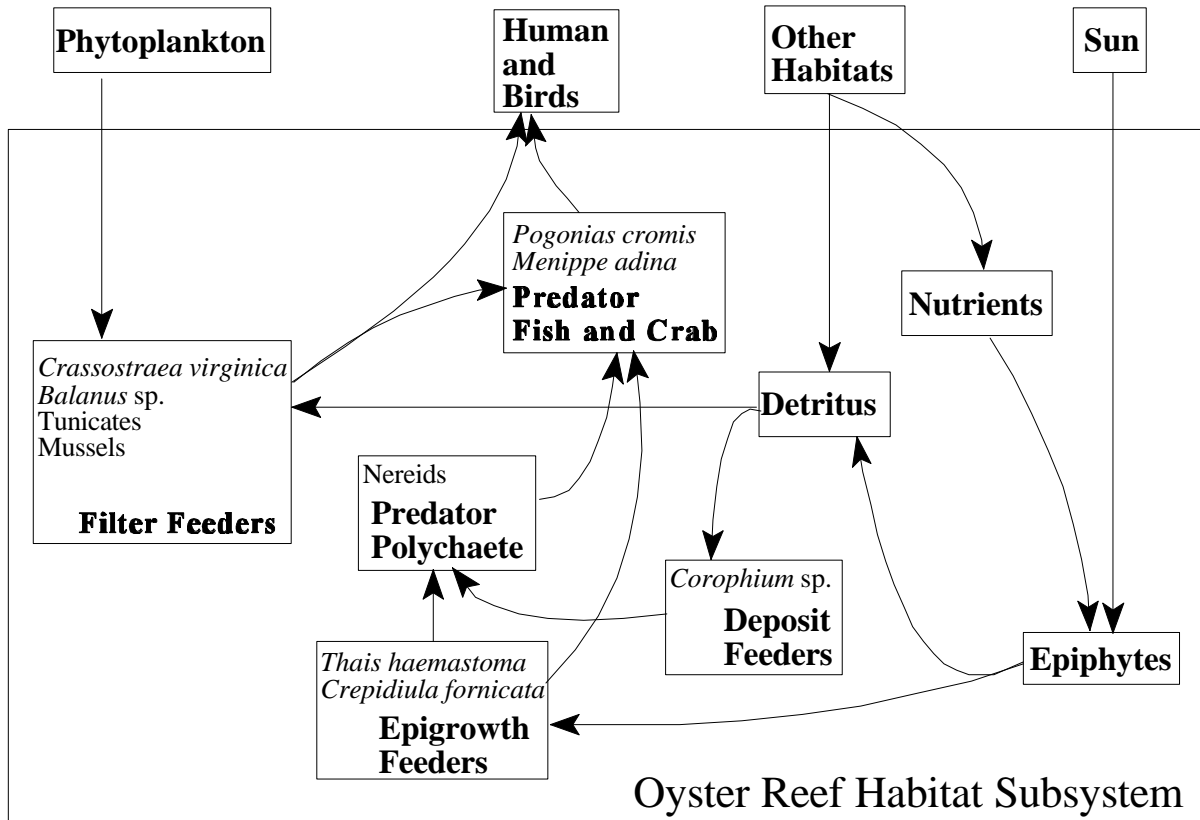
Fig. IV.8A. The components of the Oyster Reef Habitat Subsystem.

PLANKTON AND ORGANIC MATTER

11

12

DECOMPOSING MATTER

EPIPHYTES
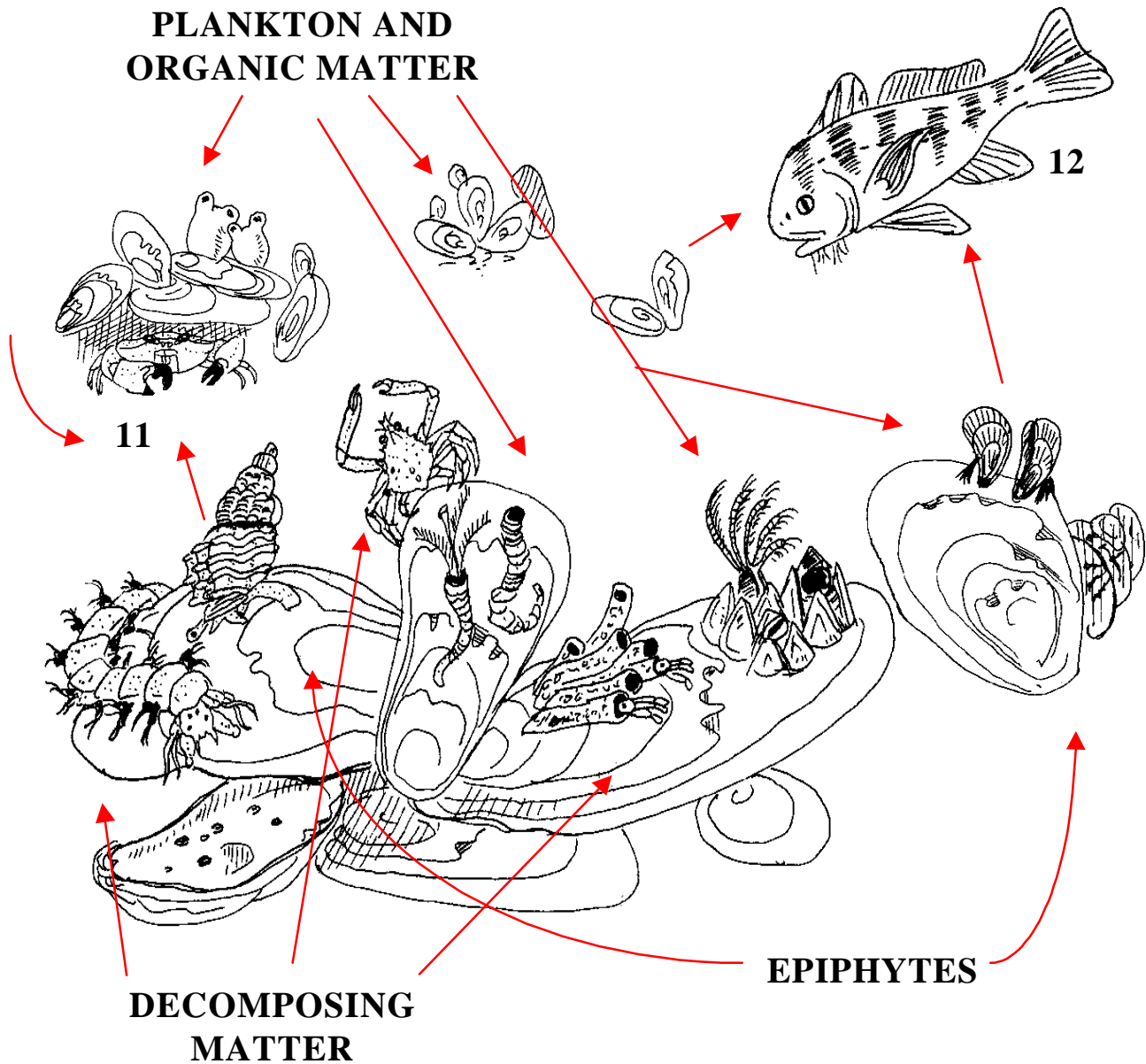
Fig. IV.8B. Oyster reef habitat of the Bay Area. In addition to providing an important fishery, oysters provide a hard substrate for a diverse array of other organisms. 1- *Crassostrea virginica* (oyster), 2- *Balanus* sp. (acorn barnacles), 3- serpulid polychaete worms, 4 - mussels, 5 - tunicates (sea squirts), 6- *Thais haemastoma* (rock snail), 7- *Crepidula fornicata* (slipper shell), 8- *Corophium* sp., 9- nereid polychaete, 10- *Libinia dubia* (spider crab), 11- *Menippe adina* (stone crab), 12- *Pogonias cromis* (black drum).

Oyster Reef Habitat

Oyster reefs are intertidal or subtidal areas of open bottom that have become covered with the living and dead shells of the oyster, *Crassostrea virginica* (Fig. IV.8A - IV.8B). In the CCBNEP Area, oysters flourish in shallow water of intermediate salinity. In Copano Bay and parts of Nueces Bay, oysters have formed extensive reefs. These reefs have two dramatic effects on the habitat. Both living oysters and dead shells provide a hard substrate for encrusting fauna, one of the only two natural hard bottom habitats in estuaries of the Texas coast. Furthermore, the physical structure of the reefs acts as a barrier to water flow, which can cause organic matter to settle out of the water on to the reef where it can fuel a detrital-based foodweb.

Many species in oyster reefs are filter feeders, including the oyster itself (*Crassostrea virginica*; Fig. IV.8B.1) and animals that encrust oyster shells. These include many species of barnacles, *Balanus* sp. (Fig. IV.8B.2), crustaceans that live in calcareous shells and filter water using modified feet. Some polychaetes, such as the members of the family Serpulidae (Fig. IV.8B.3), extend tentacles from calcaerous tubes. Other filter feeders, that actually pump water through their bodies, include various species of mussels (e.g. *Brachiodontes exustus*) (Fig. IV.8B.4), and tunicates (or sea squirts, Fig. IV.8B.5). Like the oysters, mussels filter plankton and organic matter out of the water using their gills as seives. Tunicates, which resemble lumpy bags with an incurrent and excurrent siphon, trap food from the water column using a fibrous net.

Deposit feeding encrusting fauna are also very diverse. Several mollusks, such as the rock snail, *Thais haemastoma* (Fig. IV.8B.6) and the slipper shell, *Crepidula fornicata* (Fig. IV.8B.7), attach to the oyster shells. Slipper shells settle on top of each other to facilitate reproduction. Slipper shells and rock snails graze on epiphytic algae that grow on oyster shells. Tube-building amphipods, *Corophium* sp. (Fig. IV.8B.8), feed on detrital material that settles on the reefs. They also use the material to construct their protective tubes.

With such a high biomass and diversity of food sources, several omnivore - predators can be found in the vicinity of oyster reefs. Nereid polychaetes and several species of crabs patrol the reefs searching for food. Nereids (Fig. IV.8B.9) are large, highly developed worms that have well-developed eyes, tentacles, and large jaws. The crabs include the spider crab, *Libinia dubia* (Fig. IV.8B.10) and the stone crab, *Menippe adina* (Fig. IV.8B.11). Stone crabs use their powerful claws to break open oyster and mussel shells, while spider crabs use their long arms to

grab smaller prey. Fish also frequent oyster reefs, either to hide among the shells, or to find food. The ubiquitous black drum, *Pogonias cromis* (Fig. IV.8B.12), use their pharyngeal teeth to crush shells of a variety of bivalve mollusks.

Scale of Benthic Invertebrates

Throughout the habitat section of this report, we have focused on invertebrate macrofauna, the large and more familiar animals, such as polychaete worms, mollusks and crustaceans (Fig. IV.9A. - IV.9B.). However, there are also many species of smaller invertebrates present in all of the habitats of the CCBNEP Study Area. Much less is known about these smaller invertebrates, despite the fact that they are very important components of the foodweb. Meiofauna are those animals between 63 and 500 μm in length. Meiofauna are extremely abundant in estuarine sediments, reaching densities of 10^6 m^{-2}. They are important food for some macrofauna, fish, such as spot, and birds, such as the green-winged teal and spoonbills. There are two trophic categories of meiofauna, deposit feeders and epigrowth feeders. Deposit feeders are dominated by nematode worms. In the CCBNEP Area, *Sabatieria hilarula* and *Viscosia macramphida* are two of the most common. Epigrowth feeders are animals that feed primarily upon benthic microalgae. Epigrowth meiofauna include both nematodes and shrimp-like harpacticoid copepods. In the CCBNEP Area, two typical, epigrowth feeding nematodes are *Chromadorita chitwoodi* and *Molgolaimus turgofrons*. Epigrowth feeding harpacticoids are also very diverse, and include such species as *Longipedia americana* and the *Coullana* sp. Microfauna are animals smaller than 63 μm, and are typically one-celled. In estuaries, ciliated protists, foraminifera, flagellates, and bacteria are the most common. These organisms are even more abundant than the meiofauna, but even less is known about them. The structure and dynamics of meiofauna and microfauna communities are serious data gaps in the CCBNEP Bay Area System. Readers should keep in mind that there are hundreds of undocumented meiofauna and microfauna species present in each of the CCBNEP habitats.

Summary

The different marine habitats in the CCBNEP Bay Area are defined by the physical structures, particularly vegetation, that can be found in each habitat (Fig. IV.1B). Seagrass beds are very diverse and productive, and serve as an important nursery ground for larval fish and invertebrates. Salt marshes are important sources of organic matter, and serve to buffer

Fish and Birds

Sun

Sabatieria hilarula
Viscosia macramphida
Deposit-feeders

Chromadorita chitwoodi
Molgolaimus turgofrons
Longipedia americana
Epigrowth Feeders

Meiofauna

Detritus

Streblospio benedicti
Mediomastus californionsis
Deposit-feeders

Streblospio benedicti
Mediomastus californionsis
Epigrowth Feeders

Macrofauna

Diatom

Bacteria

Nutrients

Microfauna

Relationship of Different Size of Benthos

Fig. IV.9A. Trophic relationships among different sizes of benthos.

MACROFAUNA

FISH AND BIRDS

MOLLUSK

CRUSTACEAN

MEIOFAUNA

NEMATODE

POLYCHAETE

HARPACTICOID COPEPOD

MICROFAUNA

FORAMINIFERA

CILIATES

DECOMPOSING MATTER

BACTERIA
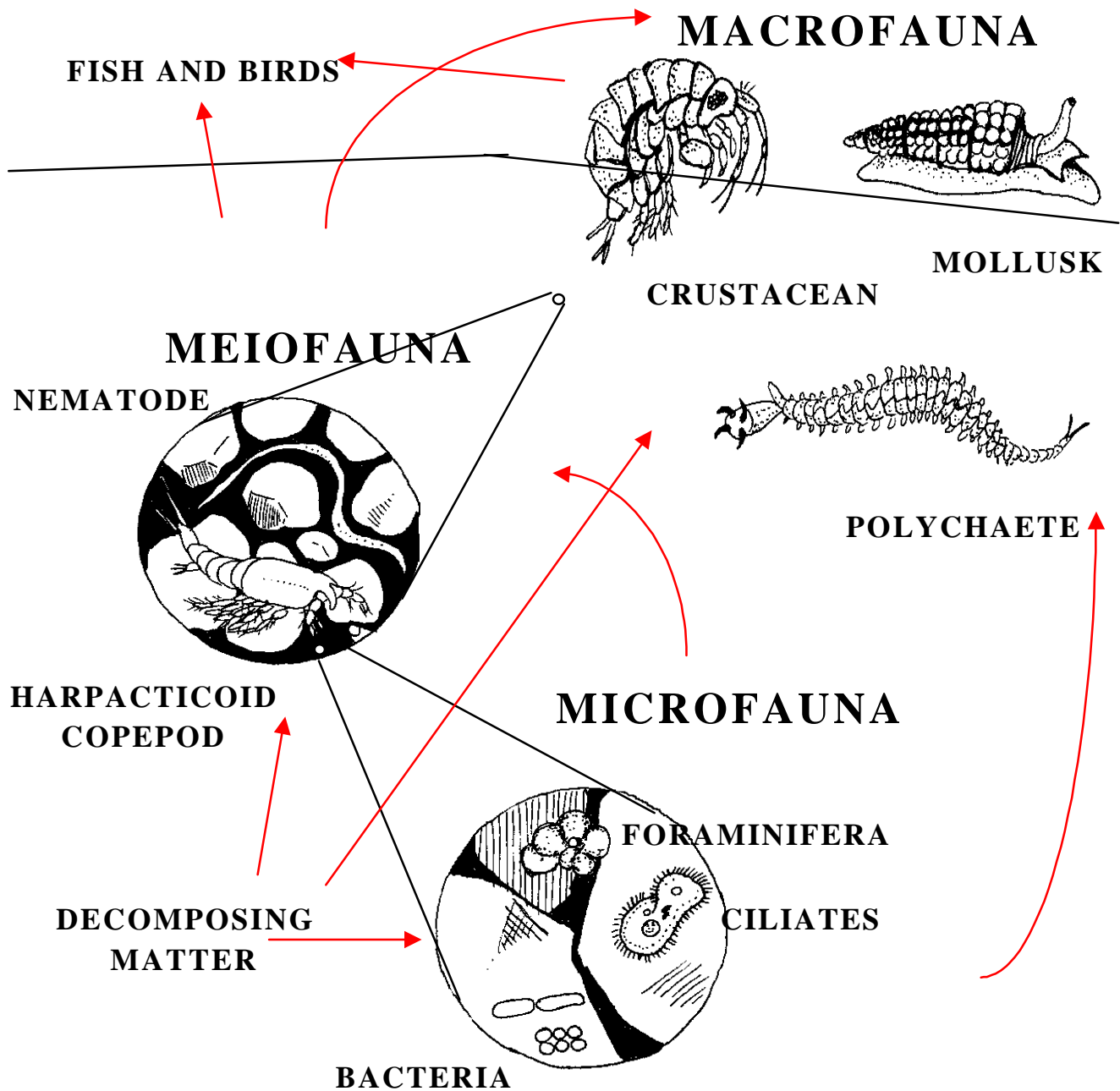
Fig. IV.9B. The relationship among the sizes of benthic invertebrates. It is important to remember that even though invertebrate macrofauna, such as large mollusks, crustaceans and polychaete worms are the most familiar, there is a diverse assemblage of smaller organisms as well that can be found in all of the CCBNEP Bay Area habitats. Meiofauna, particularly harpacticoid copepods and nematode worms, have very high productivity because of their great numbers and rapid growth rates. Smaller, one-celled microfauna, such as Foraminifera, ciliate protozoans, and even bacteria, are even more abundant. These small animals are important components of all benthic, marine habitats.

shorelines. Beach habitats experience high energy from wave impacts, but are still home to several species of animals. The water column refers to all of the water in the CCBNEP Area. Water column organisms that are at the mercy of the currents are called plankton. The larger animals, such as fish, that eat plankton, are called nekton. Sandy bottoms occur near shore, and can support large animals. Muddy bottoms are more common, but support smaller animals. Oyster reefs are very diverse, because the oyster shells provide a substrate and home for many different species. Although each habitat may seem distinct, there are many interconnections among the habitats. Water currents, waves and tides transport organic matter, energy and even animals between habitats. Many types of animals, such as the blue crab, can move among many different habitats.

V. ESTUARIES OF THE CCBNEP AREA

The three estuaries in the CCBNEP study area are the Mission-Aransas, Nueces and Laguna Madre Estuaries (Table V.1). Estuarine processes described in earlier chapters occur in all three estuaries. The primary factor affecting biological processes is temperature. Temperature changes mostly along latitudinal gradients. Therefore, temperature variation among the three estuaries is small, and consequently there is little difference in the rates of biological processes among the estuaries. The largest difference in biological processes among the estuaries is driven by other abiotic factors. The two dominant abiotic factors are undoubtely freshwater inflow and physiography. Freshwater inflow drives many key ecological processes (Figs. III.3A, III.3B). Therefore, differences in freshwater inflow will have a great effect upon the habitats of each system. The shape of the estuaries is important in determining the currents and exchange with the Gulf of Mexico. There are basically three bay systems and two lagoonal systems (Fig. I.1). Laguna Madre links Baffin Bay and Corpus Christi Bay. Red Fish Bay is actually a lagoonal system that links Corpus Christi Bay and Aransas Bay. Bays are dominated by deeper, muddy sediments. Lagoons are shallower, narrower, with less fetch, have clearer water and more seagrass beds. These habitat differences cause the ecological differences among the three systems. Another geological difference is Gulf passes, which are conduits for fisheries recruitment, and the exchange of nutrients and organic matter with the Gulf of Mexico. The same basic habitats and processes occur in all three estuaries, with minor differences among them.

Laguna Madre Estuary

Laguna Madre is three times the size of the other two estuaries. Therefore, it has more total energy flow, from the sun to the bay system and from the bay system to various sinks, than the other two systems ("1" and "4" in the Fig. III.2A). The higher energy flow from the sun to the bay area system for Laguna Madre means more energy input to the producer subsystem (Fig. III.3A) by increasing the photosynthesis of producers (Fig. III.5A). Laguna Madre has an average depth that is shallower than the other two estuaries and a larger surface area receiving sun light (Table V.1). The sun radiation per unit water volume is much higher in Laguna Madre than in the other estuaries, so the temperature storage is higher. This increases the energy flow level transport between subsystem and storage components (Fig. III.3A), by increasing all biophysiological process, such as synthesis rate, intake rate, decomposition rate, aging rate, respiration rate, migration rate, and

Table V.1. Comparison of characteristics of bays in the CCBNEP study area.

Variables	Mission-Aransas Estuary	Nueces Estuary	Laguna Madre Estuary
Primary Bay	Aransas Bay	Corpus Christi Bay	Laguna Madre
Secondary Bays	Copano Bay	Nueces Bay Oso Bay	Baffin Bay
Tertiary Bays	Mission Bay St Charles Bay Carlos Bay		Alazan Bay Cayo Del Grullo Laguna Salada
Rivers	Mission River Aransas River	Nueces River	
Creeks	Copano Creek Chiltipin Creek	Oso Creek	Petronila Creek San Fernando Creek Jarachinal Creek Los Olmos Creek
Size[a] (km^{-2})	540	500	1500
Average Depth at Mid-tide Level[a] (m)	2	2	1
Volume[b] (km^{-3})	1.08	1	1.5
Rainfall[c] ($cm \cdot y^{-1}$)	81	76	69
Combined Inflow[d] ($10^6\ m^3 \cdot y^{-1}$)	476	841	849
Net Inflow[d] ($10^6\ m^3 \cdot y^{-1}$)	190	509	-947
Surface Salinity[a] (‰)	11.2-17	14.8-31	30.3-34.4
Bottom Salinity[a] (‰)	12.3-19.3	16.6-30.6	31.3-37.0
Average Freshwater Inflow[a] ($m^3 \cdot s^{-1}$)	10	30	1
Maximal Monthly Mean Inflow[a] ($m^3 \cdot s^{-1}$)	15 (1964-1990)	50 (1939-1989)	5 (1965-1987)
Residence Time (y)	3.02[e]	0.46[e]	~ 1[f]
Open Bay Bottom[g]	common	common	intermediate
Marsh Habitat[g]	common	intermediate	rare
Algal Mat Habitat[g]	rare	intermediate	common
Water Column Habitat[g]	common	common	common
Grassbed Habitat[g]	rare	intermediate	common
Oyster Reef Habitat[g]	common	intermediate	rare
Beach Habitat[g]	intermediate	intermediate	common
Finfish Commercial Harvest[h] ($10^3\ kg \cdot y^{-1}$)	207	151	834
Shellfish Commercial Harvest[h] ($10^3\ kg \cdot y^{-1}$)	1453	544	147
Maximal Phytoplankton Abundance ($cell \cdot ml^{-1}$)	584[i]	1100[j]	1600[k]
Maximal Zooplankton Abundance ($10^5\ ind. \cdot m^{-3}$)	7[i]	500[l]	200[m]
Maximal Benthos Abundance ($10^2\ ind. \cdot m^{-2}$)	25[i]	72[n]	130[n]

[a]Orlando et al., 1993.
[b]Volume = surface area x depth
[c]Larkin and Bomar, 1983.
[d]Texas Department of Water Resources, 1982.
[e]Longley, 1994.
[f]See text. Terry Whitledge, per comm.
[g]Personal observations.
[h]Texas Parks and Wildlife, 1988.
[i]Holland et al., 1975.
[j]Murry and Jinnette, 1976.
[k]Hildebrand and King, 1978.
[l]Buskey, 1993.
[m]Buskey and Stockwell, 1993.
[n]Montagna and Kalke, 1995 (mollusks only).

reproduction rate (Fig. III.5A, III.7A and III.9A). The high energy flow in this creates the high rate of primary production. Phytoplankton primary production in Laguna Madre ranges from 2.68 to 4.78 g C $\cdot$ m^{-2} $\cdot$ d^{-1}, which is more than two times that of the other two estuaries (Odum and Wilson, 1962; Odum et al., 1963). The high ecological efficiency also results in the high abundances of the higher level consumers, such as benthic mollusks, and fishes (Table V.1). The benthic mollusk abundance in Laguna Madre (13,000 ind. $\cdot$ m^{-2}) is twice that of the other estuaries (2,500-7,200 ind. $\cdot$ m^{-2}). The commercial harvest of finfish in Laguna Madre (834 10^3 kg $\cdot$ y^{-1}) is about four times higher than the others (151-207 10^3 kg $\cdot$ y^{-1}). This biomass productivity is probably due to overall higher primary production in Laguna Madre.

Laguna Madre Estuary has a lower energy input from rivers, which provide nutrients, in comparison with the other two estuaries. Laguna Madre has a negative inflow balance (-947 $\cdot$ 10^6 m^3 $\cdot$ y^{-1}), which means the freshwater inflow is less than outflow, e.g., evaporation. The negative balance also accounts for hypersalinity in Laguna Madre. Flow of water from Nueces Estuary keeps the Laguna from evaporating entirely. Residence time for the water in Laguna, however, is very difficult to calculate because of its shallow depth, "negative" inflow, and its connection to Nueces Estuary (Table V.1).

Energy flow from ocean to the bay area system is higher for Laguna Madre than for the others ("3" in the Fig. III.2A), which mainly provides detritus. The detritus storage tank in Laguna Madre is expected to be much higher than in other estuaries, because there is high primary production due to an extensive seagrass habitat. The consumer subsystem is dominated by deposit feeding benthos. The input of seawater and less input from river also maintain a stable high salinity but low nutrients in Laguna Madre. The main limitation on producers' synthesis may be only nutrients (Fig. III.5A). However, less input from inflow reduces the human effects. So, Laguna Madre Estuary has a higher temperature storage, salinity storage and detritus storage and remains a more natural ecosystem than others.

Mission-Aransas and Nueces Estuaries

Nueces Estuary and Mission-Aransas Estuaries have a higher level of nutrient storage, kinetic storage and oxygen storage in comparison with Laguna Madre Estuary, because of more inflow from rivers and creeks per unit time (Fig. III.3A). However, phytoplankton primary production in Corpus Christi Bay is only 0.48-1.26 g C $\cdot$ m^{-2} $\cdot$ d^{-1} (Odum and Wilson, 1962; Odum et al., 1963; Flint, 1984; Stockwell, 1989). Other limitations rather than nutrient limitations are more

important in this estuary. Mission-Aransas Estuary has a series of oyster reefs in the primary bay, Aransas Bay, and secondary bay, Copano Bay. These reefs increase the kinetic energy by transfering the energy from river flow and ocean tide to water turbulence through changing the directions of tide, river flow, runoff, and currents. The water, turbulence, and sediment-derived turbidity decrease the available light for producers at the bottom. There is also a large biomass of filter-feeding mollusks (oysters). The high consumer biomass and increased turbulence may explain the fact that Mission-Aransas Estuary has a much lower phytoplankton standing stock (Table V.1), and a much lower seagrass standing stock (Dunton, 1994) than the other two estuaries. Oyster reefs can steer and slow water currents. As currents slow or are diverted, nutrients and organic matter can settle, or be trapped. The average water depth in Nueces and the Mission-Aransas Estuaries is 2 m (compared to 1 m for Laguna Madre) while the total area is half or one-third that of Laguna Madre (Table V.1). The amount of sun radiation per unit water volume is much lower than in Laguna Madre. This means a lower capacity for temperature storage and lower ecological efficiency than in Laguna Madre. This may explain the lower primary production rates and lower amount of consumer biomass (Table V.1).

The Mission-Aransas and Nueces estuaries have both river and creek sources while Laguna Madre has only creeks. The Mission-Aransas and Nueces Estuaries have an annual inflow balance (190-509 $\cdot$ 10^6 m^3 $\cdot$ y^{-1}) that is much higher than in the Laguna Madre. This indicates that energy flow from the land to the bay system is higher than in the Laguna Madre Estuary ("2" in the Fig. III.2A). However, the energy flow from the bay area system to ocean is also higher ("3" in the Fig. III.2A). The average rainfall of the three estuaries decreases from Mission-Aransas (81 cm $\cdot$ y^{-1}) to Nueces (76 cm $\cdot$ y^{-1}) to Laguna Madre (69 cm $\cdot$ y^{-1}) (Table V.1). Because Mission - Aransas recieves less inflow, the residence time of water in this estuary (3.02 y) is much longer than in Nueces Estuary (0.46 y) (Table V.1). The gradient of river inflow and average rainfall cause a lower salinity in the Mission-Aransas (12-19‰) and Nueces (17-31‰) estuaries than in Laguna Madre estuary (30-37‰). The salinity variation is higher in Mission-Aransas and Nueces Estuaries than Laguna Madre. High salinity variation makes these ecosystems more unstable than Laguna Madre (Fig. III.3A), by affecting population aging rates, respiration rates, reproduction rates and migration rates (Figs. III.5A, III.7A and III.9A). The Mission-Aransas and Nueces Estuaries are also more disturbed because there are more people living on their shores.

VI. ANTHROPOGENIC PROCESSES

The effects of human beings on a bay ecosystem are regulated by public policies, management of water and sediment, and management of living resources (Fig. VI.1A). Policy and management act as switches or dials by controlling forcing functions, which can stop or change the paths of relevant energy flows. The management of water and sediment quality can control the energy transport between the bay system and ocean, and from land to the bay system. The management of living resources can control the energy flow from the bay system to the land.

Summary

Human activities can impact the estuarine ecosystem in a variety of ways, most of which tend to have harmful effects on the productivity or diversity of the ecosystem (Fig. VI.1B). The specific factors that may lead to degradation of the estuarine ecosystem are discussed in the next section (VII. Priority Problems). However, many of these factors can be regulated, to some degree, by resource management. Water and sediment management can affect the influence of the river on the bay, and the degree of connection between the bay and the ocean. Water and sediment management can also control the amount of anthropogenic material that enters the bay ecosystem. Living resources management can regulate the extent of different habitats, such as salt marsh or seagrass meadows, and can control the loss of animals due to commercial harvests and recreational fishing.

Water and Sediment Quality Management

The control of water quality includes limiting pollutants being transported from land to river and from land to the bay. The control of sediment quality includes the changes in geological structures that may affect riverine input, outfall, runoff or currents between the bay and ocean. Changes in freshwater inflow or circulation within the system affect the level of energy in the various storage components in the bay system, such as oxygen, kinetic energy, salinity, detritus and nutrients (Fig. VI2.A). Changes in inflow and circulation can also affect the biotic subsystems of the bay ecosystem (Fig.VI. 3A, VI.7A-VI.9A). Pollutants can come from human activities, such as the waste materials from municipalities, industries, or farms. Pollutants can be classified as non-toxic or toxic pollutants (Fig. VI.3A-VI.5A). The toxic pollutants, including chemical discharges, can affect biotic systems by reducing their reproduction success, and increasing natural mortality and energy maintenance costs
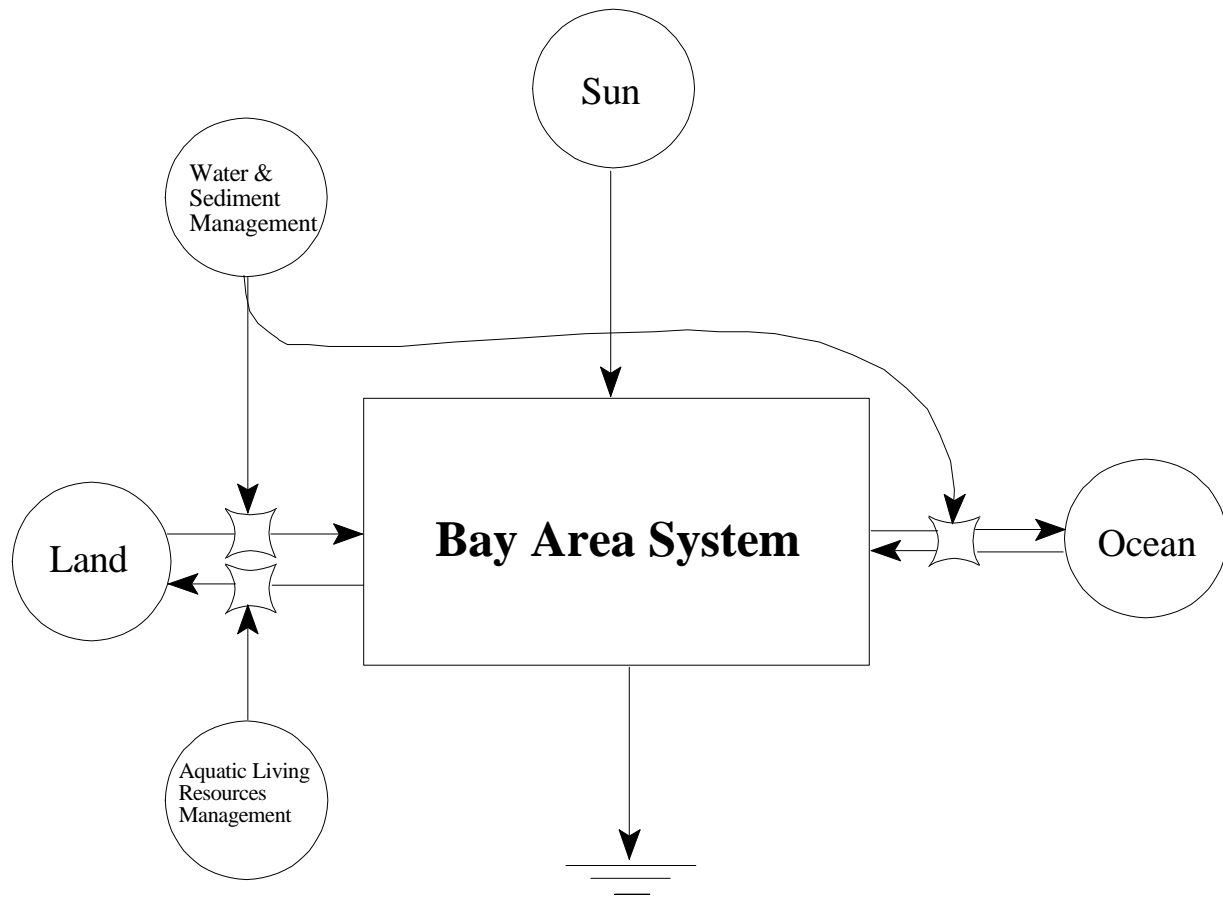
Fig. VI.1A. The role of public policy and resource management in the landscape and seascape of the Corpus Christi Bay National Estuary Program study area in terms of input and output from the Bay Area System. Policy and management acts as a switch by controlling the forcing functions.
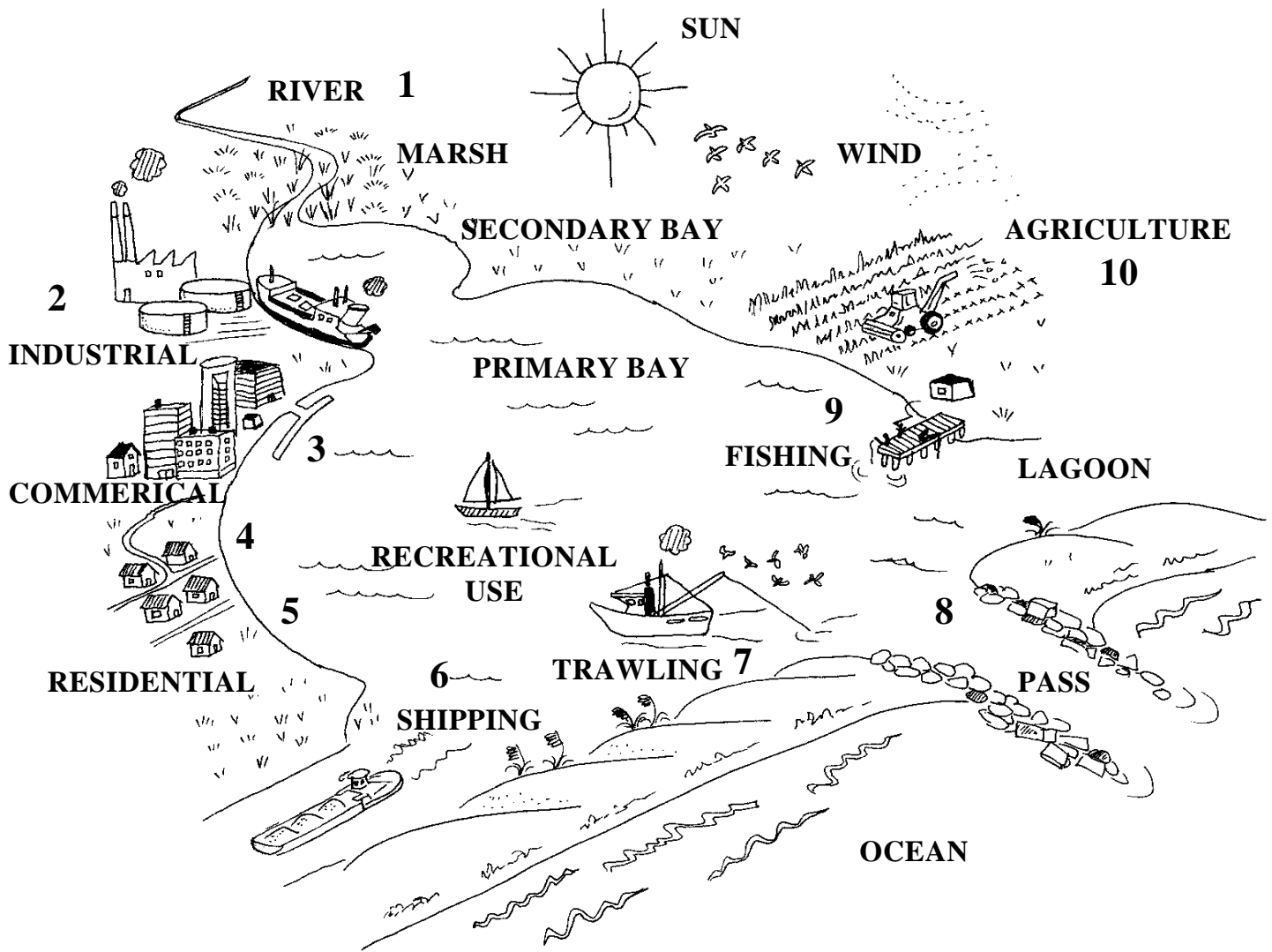
Fig. VI.1B. The role of humans in the CCBNEP Bay Area System. Human activities can impact the bay ecosystem in a variety of ways, most of which tend to have harmful effects on the productivity and diversity of the ecosystem. 1 – Impounding rivers cut off fresh water inflow to the bay. 2 – Industry can introduce toxic compounds to the air or water that can stress or kill many estuarine species. 3 – Construction on the shore of the bay destroys productive marsh habitats, and can increase turbidity. 4 – Runoff from cities can introduce contaminants to the bay and increase turbidity. 5 – Water treatment can bring high nutrients into the bay that may lead to eutrophication. 6 – Motor boats can scar seagrass beds and leak fuel. 7 – Trawling and dredging may disturb or kill the organisms living in sediment. Shrimping also produces by-catch. 8 – Creating or reinforcing passes, channels and causeways can alter estuarine circulation. 9 – Fishing may remove too many top predators from an ecosystem. 10 – Agriculture can introduce nutrients to the bay, through fertilizer or simple runoff, or can introduce toxins to the bay in the form of pesticides.
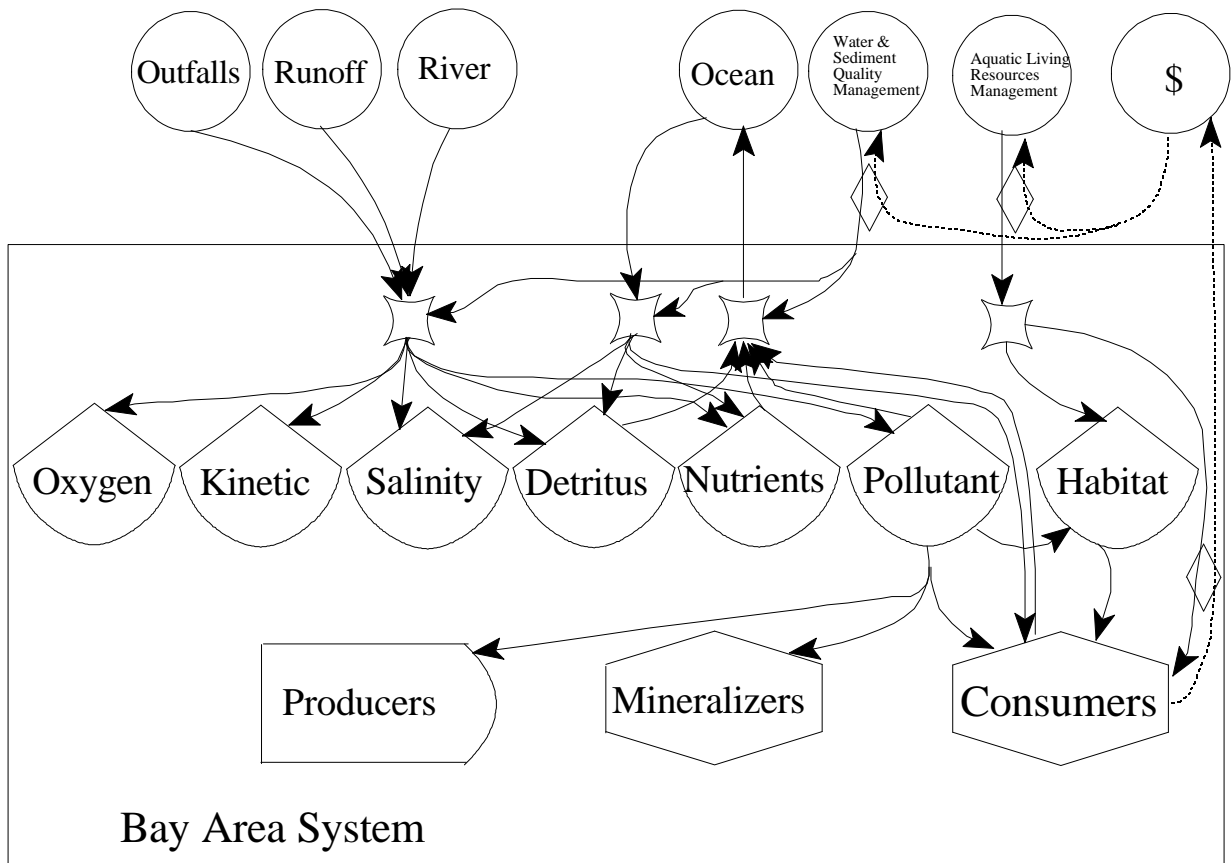
Fig. VI.2A. The role of the public management in the living and nonliving resources affecting the Bay Area System Component.
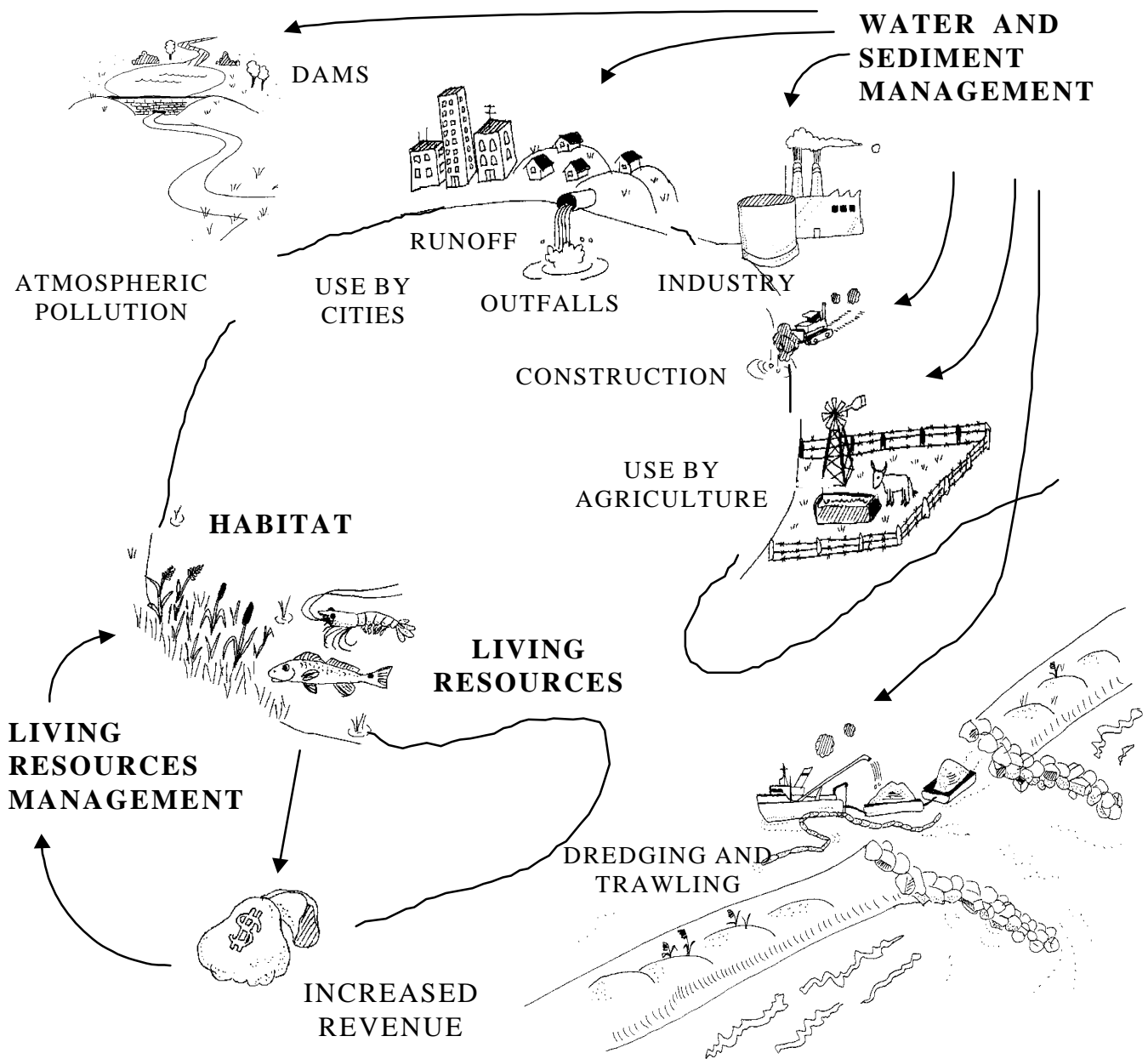
Fig. IV.2B. The role of public policy and resource management in the CCBNEP Bay Area System. Many of the negative human impacts on the Bay Area can be regulated by public education and management. It is difficult to directly regulate many of the subtle interactions that occur between organisms and their environment (for example, how many prey items a particular predator eats). However, some of the large scale processes that ultimately affect the various components of the Bay Area can, to some extent, be regulated (for example, the quantity of nutrients released into a bay by a wastewater treatment plant). Management of water and sediment resources can regulate such processes as the amount of fresh water inflow to a bay and the amount of pesticide used on crop land. Management of living resources can regulate such processes as habitat loss and fishery harvests.
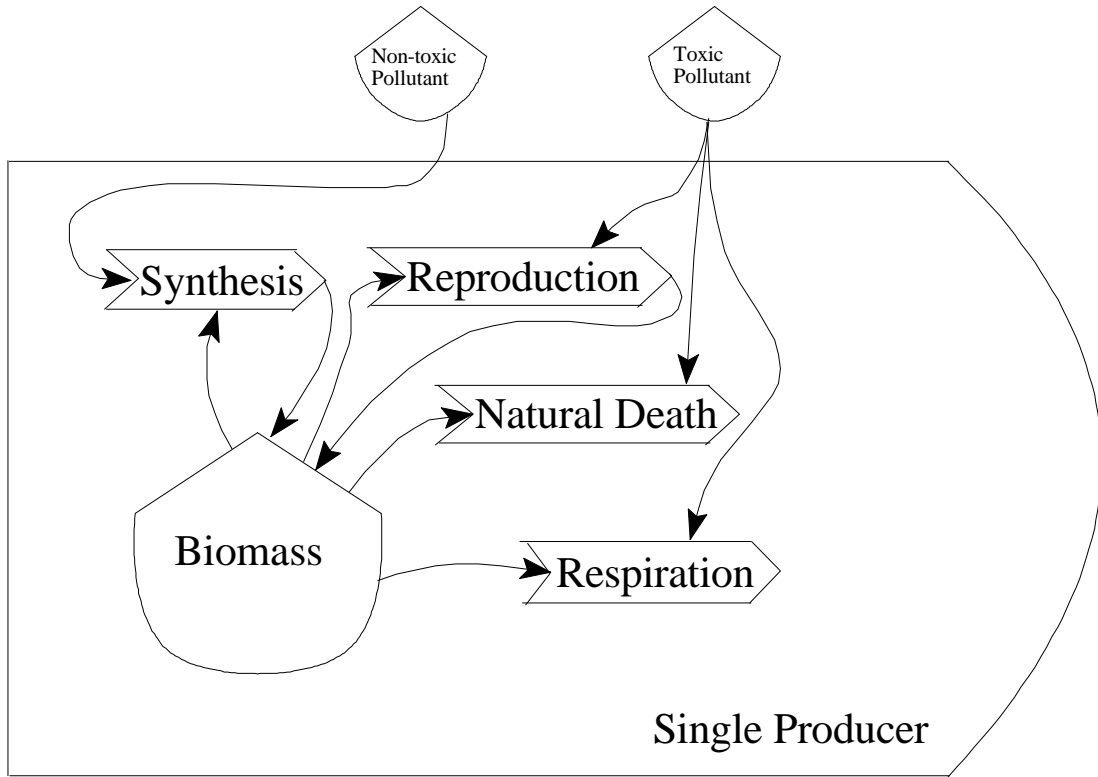
Fig. VI.3A. The role related to public policy resource management in a producer system.
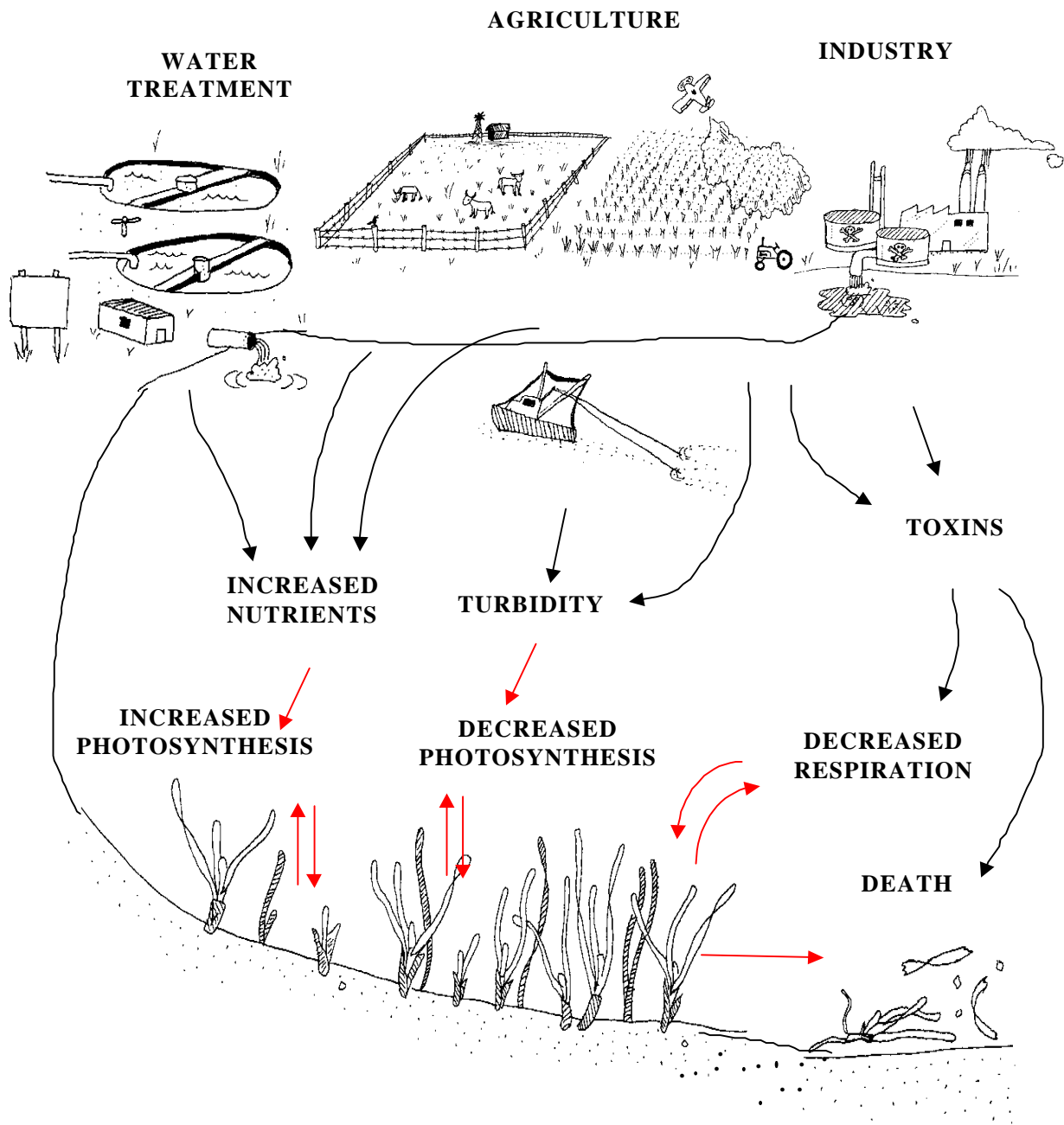
Fig. VI.3B. Human impacts upon a producer. Agricultural runoff, dredging and trawling can increase water turbidity. Runoff and wastewater effluent can increase nutrients in the bay. Pesticides and industrial pollutants can increase toxic compounds in the bay. All of these additions can impact producers in the bay. For example, photosynthesis of seagrass can be decreased by increasing water turbidity, or increased by increasing nutrient additions to the bay. However, too many nutrients can also lead to eutrophication, which may deplete the oxygen in the bay. Toxins in the water or sediment can increase the rate of respiration. The additional stress may require the plant to expend more energy, or even kill it.

due to detoxification of toxins in the environment. The non-toxic pollutants, such as nutrient inputs from sewers or increased temperature from power plants, can affect organisms metabolism and food supplies.

Living Resources Management

Living resource management includes the regulation of recreational and commercial fishing (including both finfish and shellfish) (Fig. VI.4A), such as limitations on the number, size, and species of fish caught, limitations on fishing tools (e.g., gill nets) as well as regulating the fishing season. The study of fish population biology and ecology can lead to rational fishery management, where people receive the optimal benefit from fishing while maintaining sustainable yields for the future. The optimal fishing season and size class may also be determined from the biological studies of fish populations. The management of living resources can also include the regulation of biotic or abiotic components of the fishery habitat (Fig. VI.4A). Management may create artificial habitats, or enhance natural habitats, such as oyster reefs, that increase the fish populations by increasing the subsystem that supports a fishery.

Pollutants

Pollutants can enter the system through human activities, including waste materials from municipalities, industries or agriculture. The non-toxic pollutants, such as nutrient additions due to point sources like sewage outfall, and non-point sources like agricultural runoff, may actually increase ecosystem productivity. However, increases in ecosystem productivity almost always occur coincident with changes in community structure leading to blooms of undesirable algal species and lower biodiversity in the ecosystem. When nutrient additions become high, high growth rates of bloom organisms, such as, phytoplankton and bacteria will cause oxygen depletion in a marine ecosystem. This process is known as hypoxia caused by eutrophication.

Summary

Human activities have the potential to affect the various subsystems of the bay ecosystem (Fig. VI.2B). Water and sediment management can affect everything from the amount of fresh water inflow and exchange with the Gulf of Mexico, to nutrient and toxic chemical additions. Living resource management can affect the extent of some habitats, such as salt
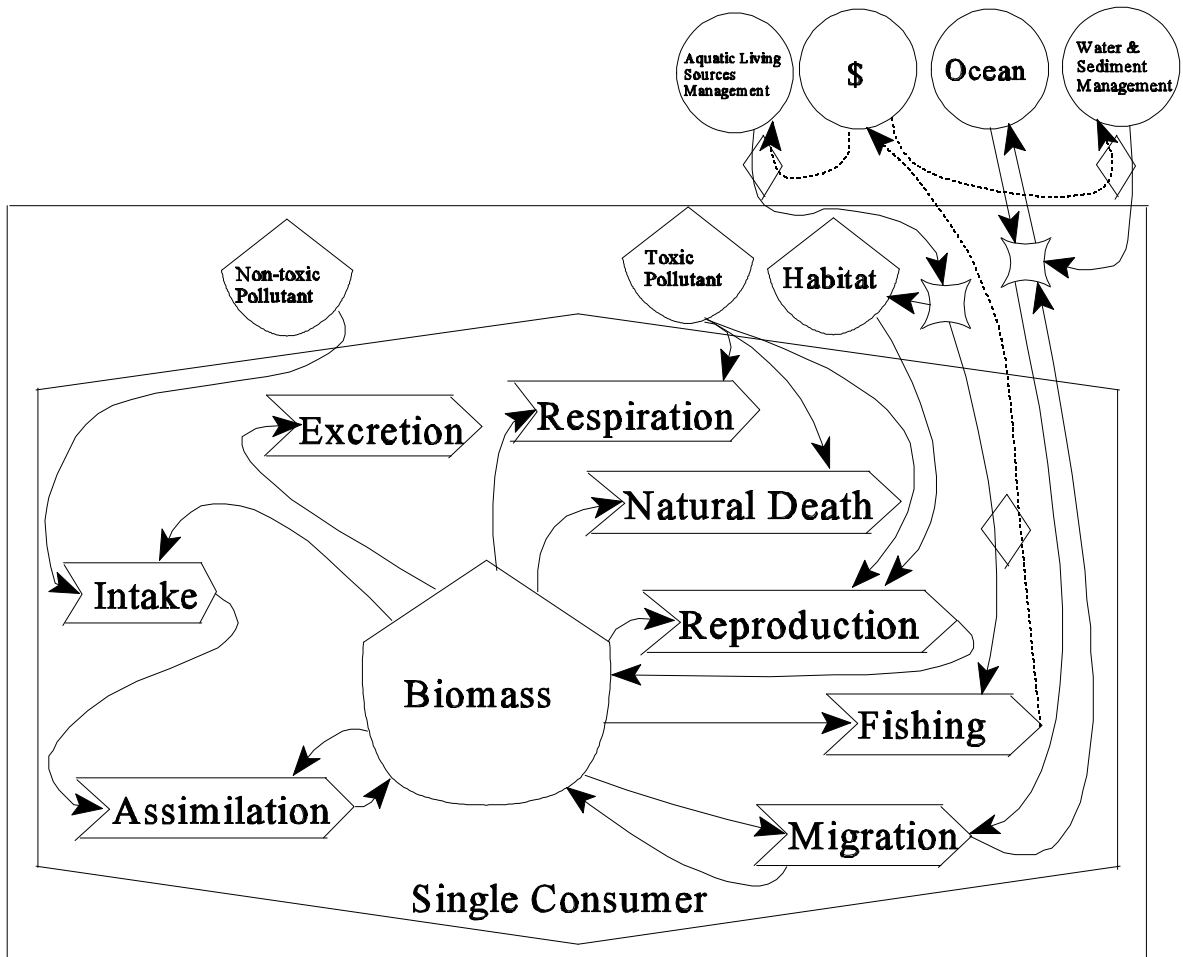
Fig. VI.4A. The role related to public policy resource management in a consumer system.

LIVING RESOURCES MANAGEMENT

WATER AND SEDIMENT MANAGEMENT

HABITAT

TOXINS

OUTFALLS

FISHING

NUTRIENTS

BIOMAGNIFICATION

MORE FOOD

CHANGES IN ESTUARINE CIRCULATION

DEATH

MIGRATION

REPRODUCTION
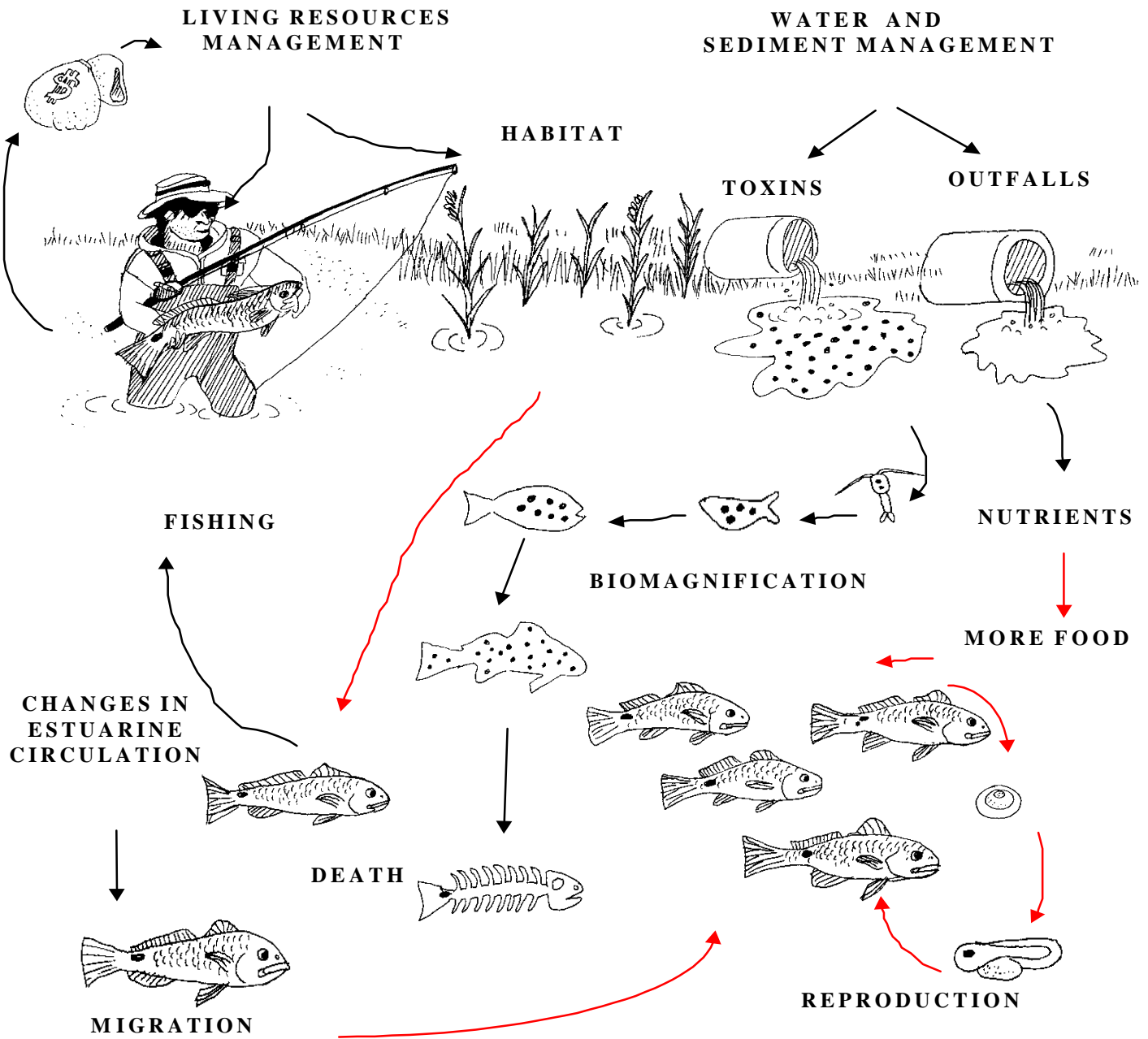
Fig. VI.4B. Human impacts upon a consumer. Consumers are not directly affected by nutrient levels. However, consumers are affected by abundance and distribution of producers, which are dependent upon nutrients. Consumers are at an even greater risk than producers from toxic compounds through biomagnification. There is also the possibility that the migration, and therefore the reproductive success, of some consumers may be altered by extensive changes to the flow of water in an estuary due to channels and barriers. The greatest threats to large consumers are over-fishing and loss of habitat. Many consumers, such as redfish, have very high larval mortality, and take years to reach reproductive age. Therefore, stocks of fish may take a long time to recover from losses to over-fishing. The loss of habitat is probably of even more importance to consumers. Many fish and invertebrates are dependent upon wetlands for food and to provide a nursery for their larvae. Management can affect the rate of loss of wetlands, and can also regulate fishing limits, as well as point and non-point sources of pollutants.
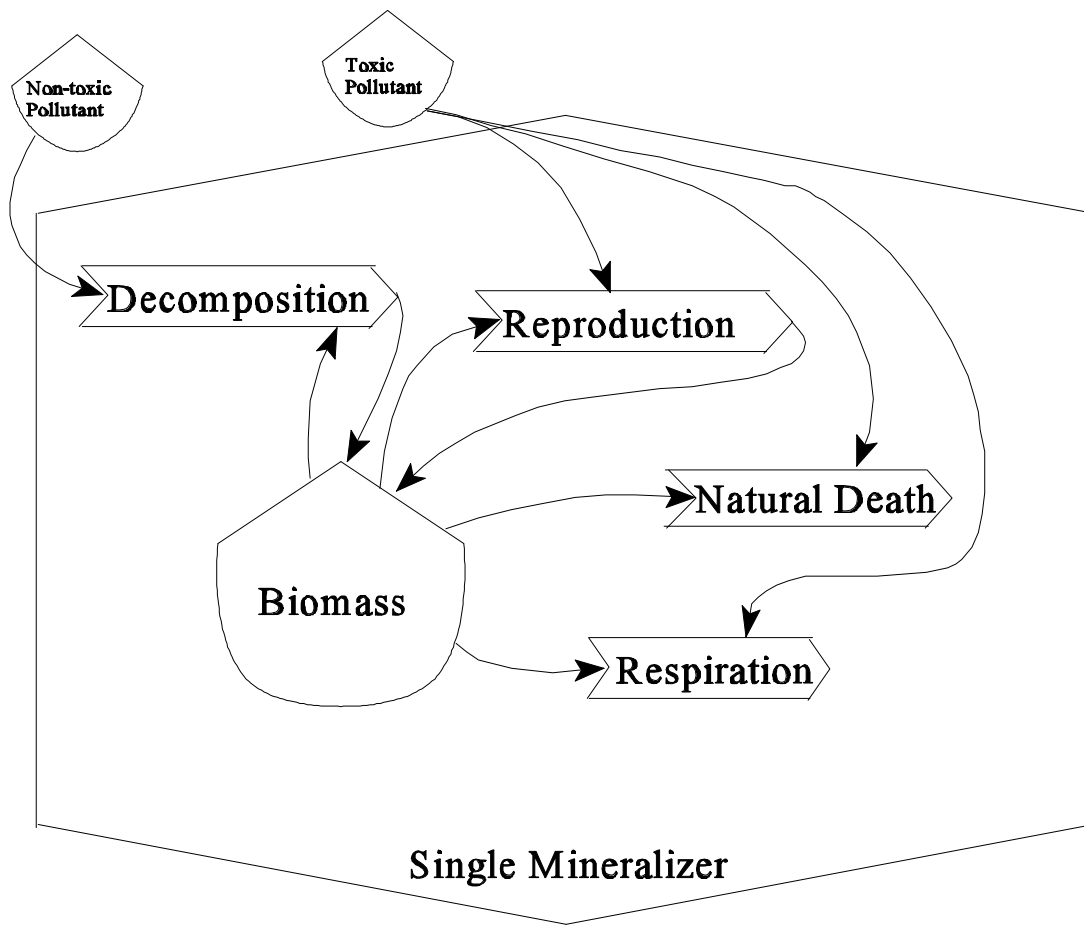
Fig. VI.5A. The role of public policy resource management in a mineralizer system.

HEAT

**INCREASED
DECOMPOSITION
RATE**

NUTRIENTS

DEATH

**DECREASED
RESPIRATION**

TOXINS
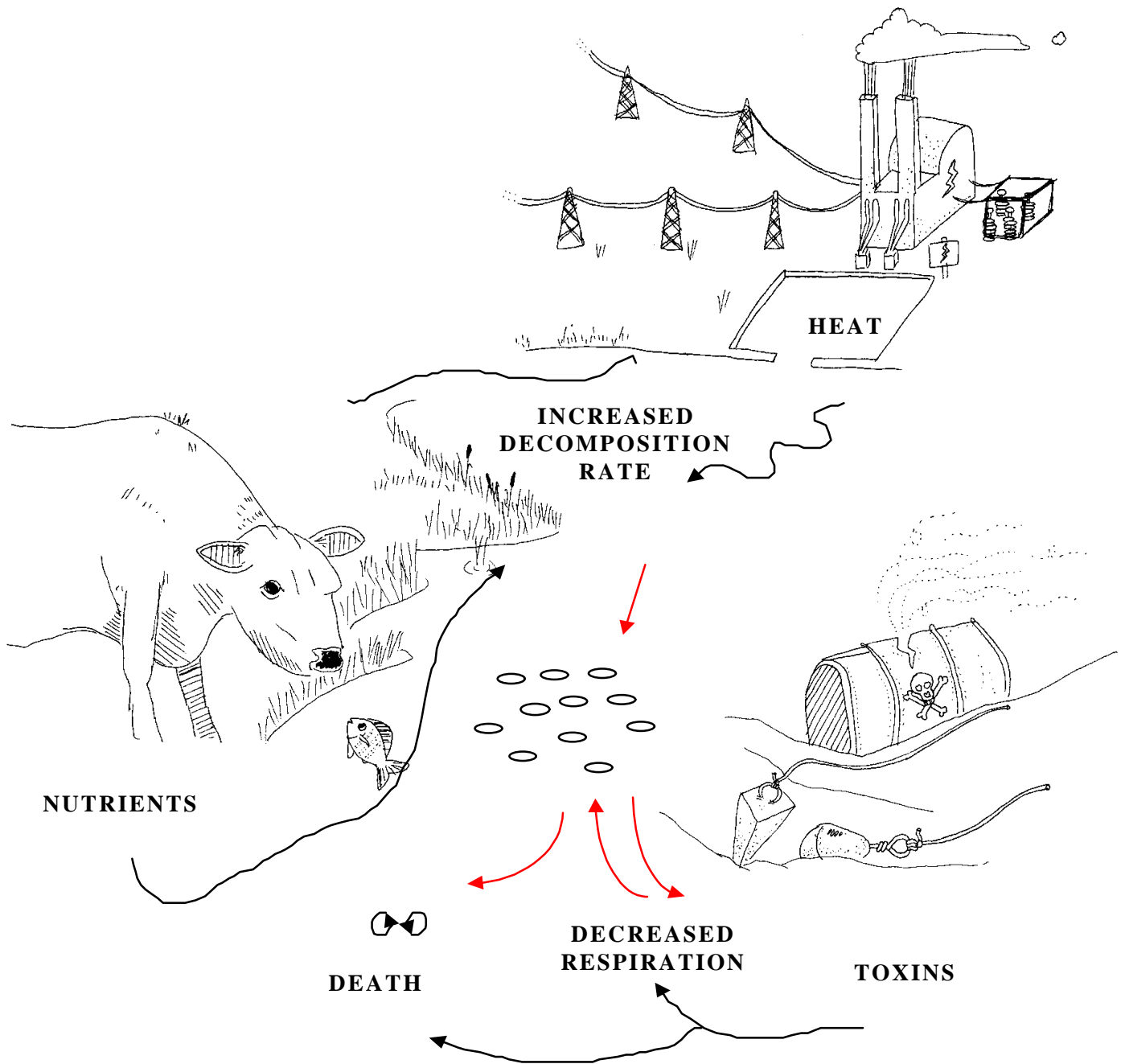
Fig. VI.5B. Human impacts upon bacteria. Because bacteria are important food sources, break down organic matter, and recycle nutrients, negative impacts upon bacteria can affect an entire ecosystem. Like all organisms, bacteria are sensitive to toxic compounds, such as hydrocarbons and heavy metals. Like producers, bacteria may also increase their production in the presence of increased nutrients. However, too many nutrients can cause eutrophication or nuisance plankton blooms. The metabolism of bacteria is very dependent upon water temperature. Cooling systems for power plants might significantly increase local water temperature.

marshes, and the numbers of individuals of certain commercial or recreational species. Producers can receive increased nutrient additions due to point sources, such as water treatment, or runoff of excess fertilizers applied to farmlands (Fig. VI.3B). While some degree of nutrient addition can benefit producers, such as seagrasses, too much can lead to alteration of the community structure and eutrophication. Eutrophication occurs when a body of water contains an excess of nutrients and organic material, to the extent that the ecosystem may deplete all available oxygen. Because producers need sunlight to photosynthesize, any decrease in water clarity can limit production. Turbidity can be increased by activities such as dredging, trawling, and by the input of sediment to the bay from terrestrial runoff. The addition of any toxic chemical, particularly pesticides, heavy metals and hydrocarbons, that might be produced by industry, can either stress producers, causing them to respire at higher rates, or even kill them.

While consumers are not as sensitive to nutrient additions or turbidity (Fig. VI.4B), they have another problem due to their position on the food chain. Although contaminants in the water may enter living tissues, they are often at concentrations too low to be threatening. However, a predator can gradually accumulate the contaminant burden from all different prey items that it eats. This phenomenon is known as biomagnification, and becomes more of a threat at higher trophic levels. In addition to biomagnification, some consumers also face losses in the form of predation from humans. Fishing efficiency can be so high that unrestricted fishing can quickly deplete an entire population past the point from which it may recover in subsequent years of recruitment.

Mineralizers can be constantly exposed to sediment-bound contaminants, because of their intimate association with the sediment, (Fig. VI.5B). Like producers, mineralizers are also sensitive to nutrient additions. A form of pollution that is often not considered is thermal pollution. Any activity that raises the water temperature, such as the input of cooling water from a power plant, can have a negative impact on the bay environment. High temperatures can quickly deplete a system of oxygen, or kill some sensitive species outright, replacing them with more tolerant, opportunistic species.

VII. PRIORITY PROBLEMS

The CCBNEP Bay Area System is located in a part of the country that is experiencing human population growth. Humans already impact the Bay Area in many different ways, most of which have the potential to decrease the diversity and productivity of the estuarine ecosystem. This impact will only intensify as the human population grows. In the CCBNEP Area, some of the impacts with a potentially negative effect are associated with estuaries in general, such as eutrophication, while others are specific to the local area, such as hypersalinity. The CCBNEP has identified several "Priority Problems" that may affect the three estuaries in the CCBNEP System. According to the CCBNEP Priority Problem Fact Sheet, "...these are problems in the definitional sense of the word, i.e., a problem being the focus for future investigation. The lists of concerns and contributing factors are meant to be inclusive of all potential problems - real or perceived - that are worthy of further scientific investigation." In many cases, the actual effect that these Problems have on the CCBNEP Bay Area System have not been fully explored by scientific methods, and represent a "data gap" in the CCBNEP, and therefore designing conceptual models to a level of detail comparable to the rest of this report is not currently possible.

Altered Freshwater Inflow Into Bays and Estuaries

The issue of freshwater inflow into Nueces Bay has received a great deal of political and media attention (Fig. VII.1). The Nueces River does not transport a great volume of water compared to other rivers in Texas, and yet is under considerable pressure from the growing population of the Coastal Bend and South Texas in general. People need water to drink, clean, water plants (particularly crops), and for industrial production. However, the organisms in Nueces and Corpus Christi Bays also need fresh water to live. Many of the animals that are commercially or recreationally important, such as shrimp and redfish, thrive in water that is less saline than the open ocean. Fresh water also brings nutrients into the bay that are needed by producers, just as crops and house plants need fertilizer. Seasonal inflow lowers salinity in a short period at time. These events are known to trigger reproduction and recruitment of many estuarine species.

Another concern specific to Nueces Bay is the alteration of flow of the Nueces River so that it no longer feeds into the Nueces Delta. The Delta supports an extensive salt marsh, which is an important source of nutrients and energy to the entire bay. There is currently a restoration program underway to enhance freshwater flow into the Delta by lowering

96

ALTERATION OF LOCATION OF TRIBUTARIES

IMPOUNDMENTS

ARID CLIMATE

LOSS OF SALT MARSH

LESS FRESH WATER INFLOW

LESS NUTRIENT INPUT

SALINITY INCREASES

LOSS OF ESTUARINE PRODUCTIVITY

WATER DEMAND OF CITIES

AGRICULTURE
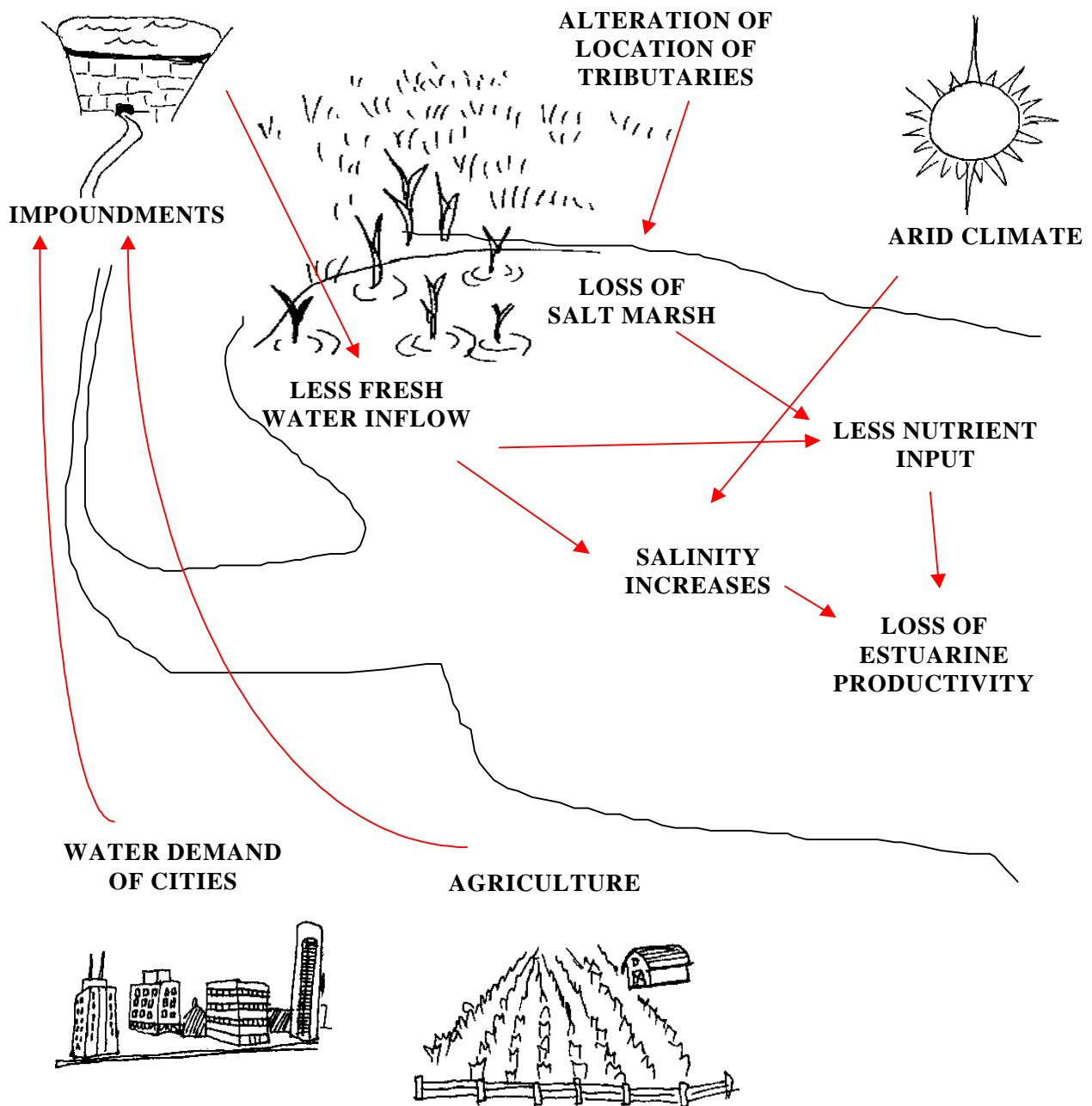
Fig. VII.1. Priority problems: altered freshwater inflow. Brackish water can support more productive organisms than marine water. Therefore, when fresh water inflow to an estuary decreases, the estuary generally becomes less productive. Fresh water can be diverted for a number of reasons, including industrial, residential and agricultural uses. Although humans need water too, it is important to remember that the only source of fresh water to an estuary is through rivers and creeks, particularly in an area with low rainfall, such as south Texas.

the banks of the Nueces River. This program should have positive benefits to the marsh and nursery habitat.

Loss of Wetlands and Estuarine Habitats

There are several reasons that salt marshes and other wetlands, such as seagrass beds, are so important to an estuarine ecosystem (Fig. VII.2). Wetlands: (1) provide critical habitat for fish, shellfish and wildlife, (2) provide a nursery ground for important commercial and recreational fish, (3) support a large and diverse estuarine foodweb, (4) filter and buffer residential, agricultural and industrial wastes, (5) buffer coastal areas against storm and wave damage, and (6) generate revenue and provide employment from recreational activities. Wetlands, however, can be lost through several human activities. Lower fresh water inflow decreases the size of salt marshes. Development along the bay shore may also remove salt marshes. Increasing the turbidity of the water can harm the productivity of seagrasses, or even cause the grass beds to disappear. Several factors contribute to turbidity, including natural factors, such as wind. Human activities that can increase turbidity include dredging, trawling, construction and run-off. The persistent brown tide in Laguna Madre also increases turbidity due to its high concentration. Scientists are still unsure as to whether the brown tide was caused or promoted by human activities. However, it is known that the brown tide thrives in periods of high ammonia, a nutrient that can be introduced through agricultural or residential run-off or water treatment.

Condition of Living Resources

The three estuaries in the CCBNEP are very productive, and support many different species. Several kinds of fish, such as redfish, speckled trout and flounder, are of economic importance to the area (Fig. VII.3). Other animals, such as the whooping crane, are threatened species with a limited range. Many of these animals are relatively large, and consequently at the top of the food chain. Therefore, they are extremely susceptible to changes in the environment that might have effects at any trophic level. For example, black drum are largely dependent upon bivalves for their food. If the bivalve populations in the CCBNEP Area are compromised, as may be happening due to the brown tide, then black drum populations might be consequently impacted.

Habitat loss and over-harvesting can also take their toll on estuarine wildlife. Species are adapted to live where they live. Consequently, habitat loss decreases the livable area of a

LOWER
FRESH WATER
INFLOW

DEVELOPMENT

LOSS OF
MARSH

LOSS OF
REVENUE

LESS FILTERING

LOSS OF
WETLANDS

LOSS OF
HABITAT

LESS BUFFERING
FROM STORMS

LOSS OF
ANIMALS

DISTURBED
BAY BOTTOM

NUTRIENT
INPUTS

LOSS OF
SEAGRASS

DREDGING

EUTROPHICATION

INCREASED
TURBIDITY

ALGAL
BLOOMS

TRAWLING
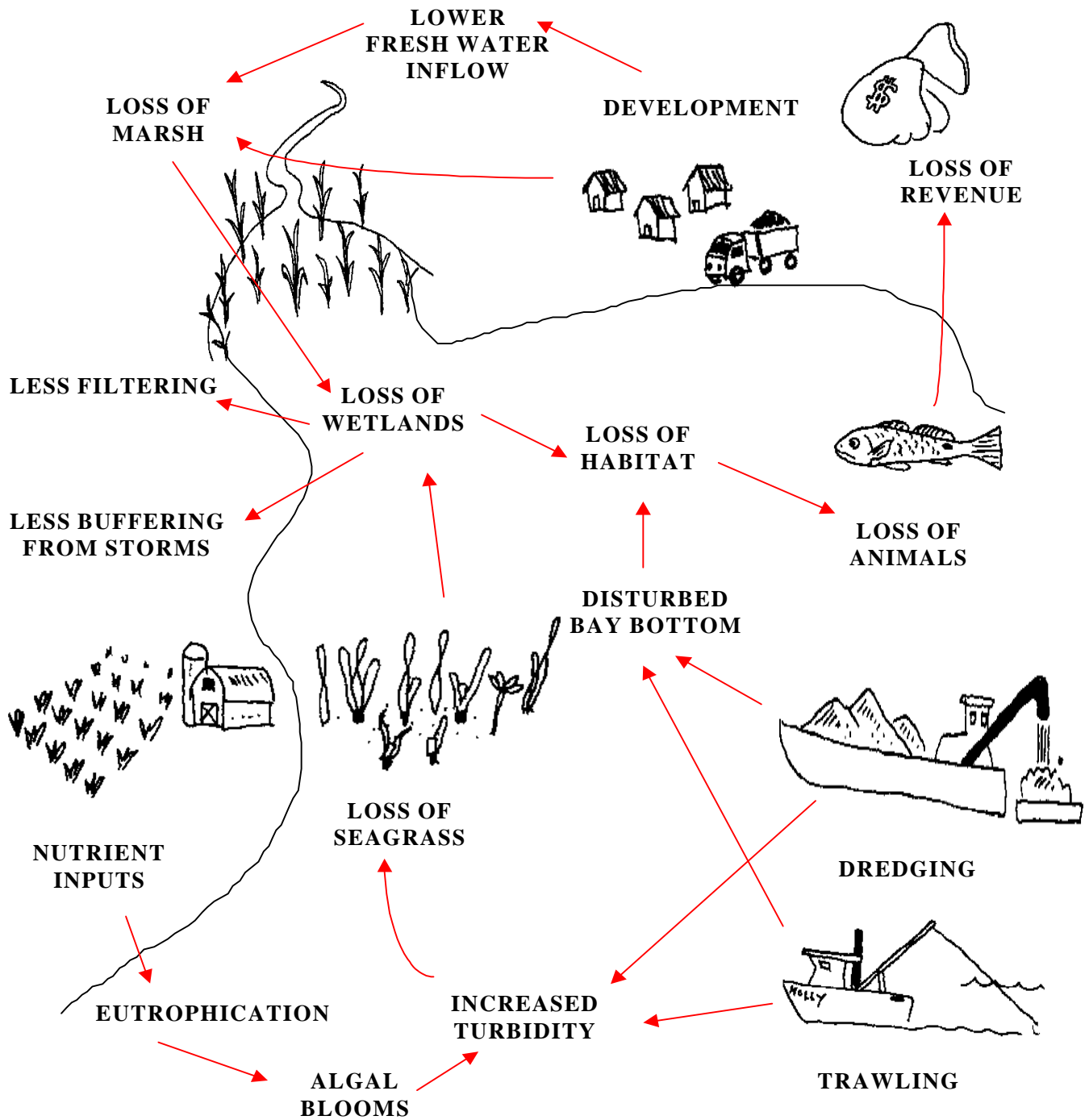
Fig. VII.2. Priority problems: loss of wetlands and estuarine habitats. Even if all other conditions are optimal, all estuarine species need a place to live. There are many factors that can limit habitat size. For example, restricting fresh water inflow can reduce the size of a salt marsh habitat. Increasing water turbidity can restrict the size of a seagrass bed habitat. Dredging or trawling over a muddy bottom can constantly disrupt the productivity of the organisms that live there. Because some estuarine species are important to the local economy, through tourism, recreational or commercial fishing, loss of habitat can have monetary consequences as well.

INCREASED NUTRIENTS

LOSS OF
PROTECTED
SPECIES

CONTAMINANTS

EUTROPHICATION

DREDGING / TRAWLING

LOSS OF
WILDLIFE

WATER
QUALITY
DEGRADATION

FEWER ANIMALS

LOSS OF
ECONOMICALLY
IMPORTANT
SPECIES

BROWN TIDE ?

LOSS OF
HABITAT

OVERFISHING
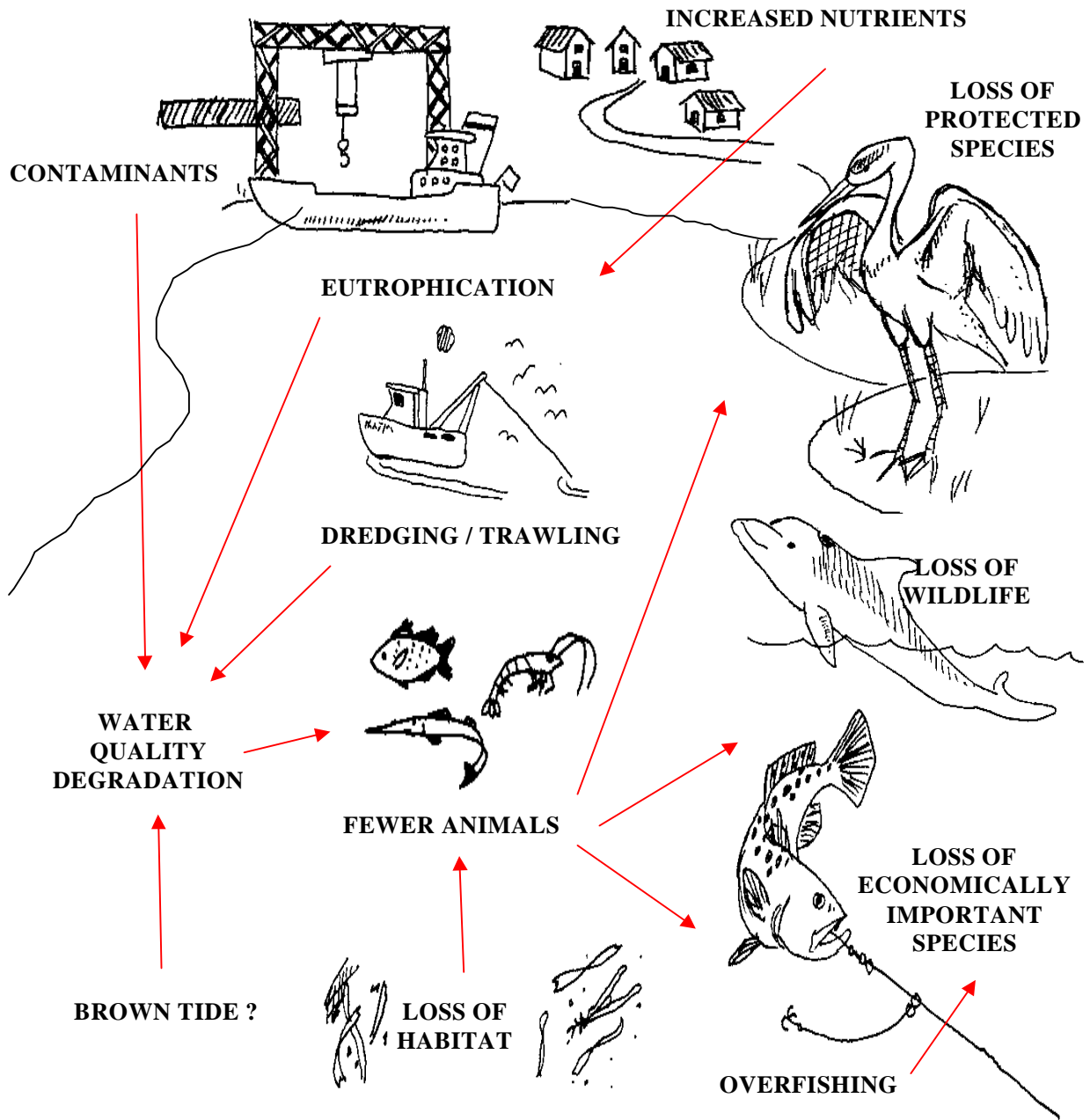
Fig. VII.3. Priority problems: condition of living resources. The CCBNEP Bay Area supports a diverse assemblage of wildlife, including some endangered or threatened species. These animals can decrease in number if they lose viable habitat or important food sources. These factors, combined with over-fishing, have caused some fish, such as snook and tarpon, that were once common to become much more scarce. Other animals, such as bottle-nosed dolphins, may be experiencing declines due to disease.

100

species. Over-fishing can hurt a population, because many of the animals require many years before they can become reproductive. Fish, such as tarpon and snook, sea turtles, and particularly the whooping crane have all declined in population, probably due to a combination of over harvesting and habitat loss. Other animals, such as the bottle-nosed dolphin, seem to experience periodic die-offs due to unknown reasons that may include pollution, plankton blooms, disease or perhaps old-age.

Degradation of Water Quality

All organisms that are dependent upon the CCBNEP Bay Area System, including humans, can be adversely affected by bad water quality (Fig. VII.4). For example, turbid water decreases photosynthesis by plants, while water that is contaminated by heavy metals can compromise the health of a variety of organisms. Water quality can be degraded in three main ways: it can become turbid, contaminated, or eutrophic.

Turbidity, in the shallow bays of the CCBNEP study area, is caused primarily by wind, but can be exacerbated by dredging or trawling the bottom. There are a variety of sources for potential contaminants. For example, the petrochemical industry alone can introduce contaminants in many ways, including: drill cuttings, produced waters from oil production, accidents and spills from transporting oil, and pipeline leaks. Runoff from industrial and residential areas is a major pathway for the introduction of non-point source contaminants to the bay. In the CCBNEP Area, air pollution may be another main source of contaminants to the water. Loss of wetlands can make contamination worse, because natural wetlands act as filters, removing some harmful chemicals from the water.

Eutrophication is caused when excessive nutrients are introduced into the bay. Nutrient sources include: agricultural runoff, water treatment plant effluents, and runoff from residential lawns. The nutrients cause an initial bloom of algae or bacteria. However, blooms of this magnitude can deplete the water of oxygen at night, which can limit secondary productivity or even kill animals such as fish.

Toxicity is another aspect of the degradation of water quality. Manufactured chemicals, called xenobiotic compounds, enter the bay from a variety of sources. Point sources, such as outfalls, discharge pipes, marinas, and platforms are easy to target for monitoring. Non-point sources, such as municipal, industrial, and agricultural runoff are difficult to quantify.

LESS FRESH
WATER INFLOW

ALTERED
ESTUARINE
CIRCULATION

ATMOSPHERIC
POLLUTION

CONSTRUCTION

LOSS OF
WETLANDS

LESS FILTERING
CAPACITY

TURBIDITY

DREDGING / TRAWLING

WATER
QUALITY
DEGRADATION

DISCHARGES

BROWN
TIDE ?

PIPELINES

SHIPPING AND
OTHER BOAT USE
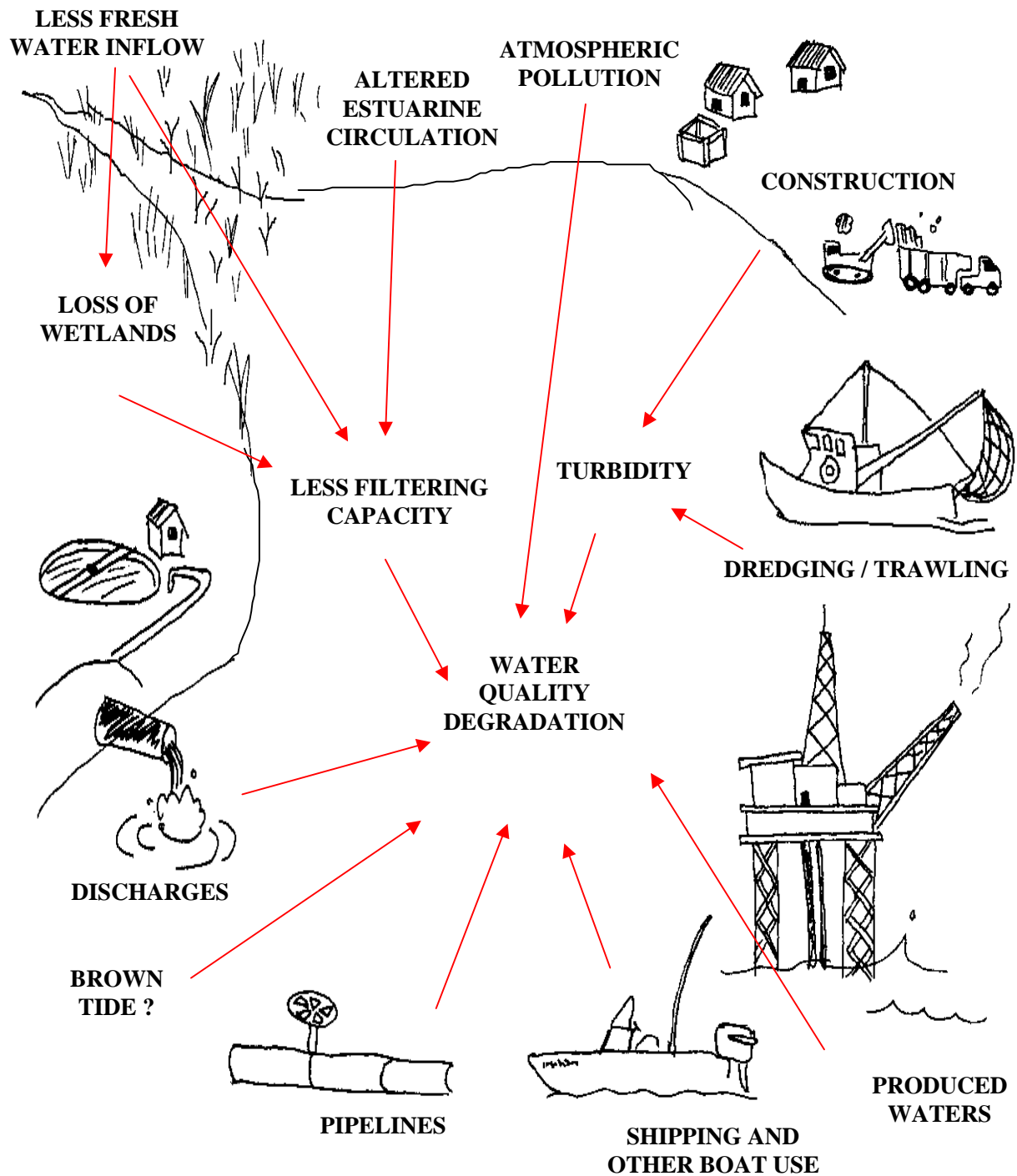
PRODUCED
WATERS

Fig. VII.4.   Priority problems: degradation of water quality. The most productive marine ecosystems thrive in areas of clear, clean water. Increasing the amount of contaminants or turbidity in the water can decrease productivity, or even human health. Human activities, such as agriculture, dredging and trawling can increase water turbidity, which limits photosynthesis. Limiting the flow of water in an estuary or limiting fresh water inflow can inhibit the natural properties that wetlands have to filter contaminants from water. Many human activities have the potential to contaminate water, from oil spills to runoff from streets following a storm.

Atmospheric deposition is another source of non-point pollution, and is very difficult to quanitfy. The main concern in agricultural and residential runoff is pesticides. Municipal and industrial runoff includes heavy metals and hydrocarbons.

Altered Estuarine Circulation

Although the CCBNEP estuaries are connected to the open ocean by passes, these passes allow only a small amount of water through them, relative to the total amount of water in the estuary. This is due to the microtidal range of the CCBNEP estuaries. The resdience time of water in South Texas Estuaries can be as great as several years (Table V.1). Circulation in CCBNEP estuaries is strongly influenced by winds especially the passages of fronts.

Small changes in the flow of water within an estuary in the CCBNEP area can have large effects on the estuary (Fig. VII.5). For example, limiting flow in some regions may prevent contaminants from becoming diluted throughout a bay. Low circulation can be responsible for relatively stagnant water, which can become hypoxic. Also, radically restructuring the pattern of water flow in a bay may have an effect on the many animals that migrate between bays and the ocean. The role of limited water flow on the persistence of the brown tide has been much discussed, but it not completely understood.

Under natural conditions, the locations and sizes of passes are changed constantly by wind and water currents, particularly during storms or hurricanes. Several channels, such as Aransas Pass and Mansfield Pass have been artificially maintained by granite jetties and regular dredging. However, several other channels that have not been maintained, such as Fish Pass, Newport Pass, Packery Channel, and Yarborough Pass have become closed. The size and location of channels does have an effect on circulation. One reason that Corpus Christi Bay passes may be difficult to maintain is that the deeper Aransas Pass currently directs all the circulation between the Gulf and the Bay. Another potential cause of passes silting over, is the low pressure head of freshwater inflow due to restricted inflows of the Nueces River to the Nueces Estuary.

Dredging channels through the bays is also a significant alteration from the natural condition. Dredging makes portions of the bays much deeper than they would be naturally. Although seagrass cannot grow in the deep channels, the channels do allow much more water to circulate through a bay. Dredging also creates spoil islands, which may inhibit the flow of water in some locations, but are also important roosting and nesting grounds for a variety
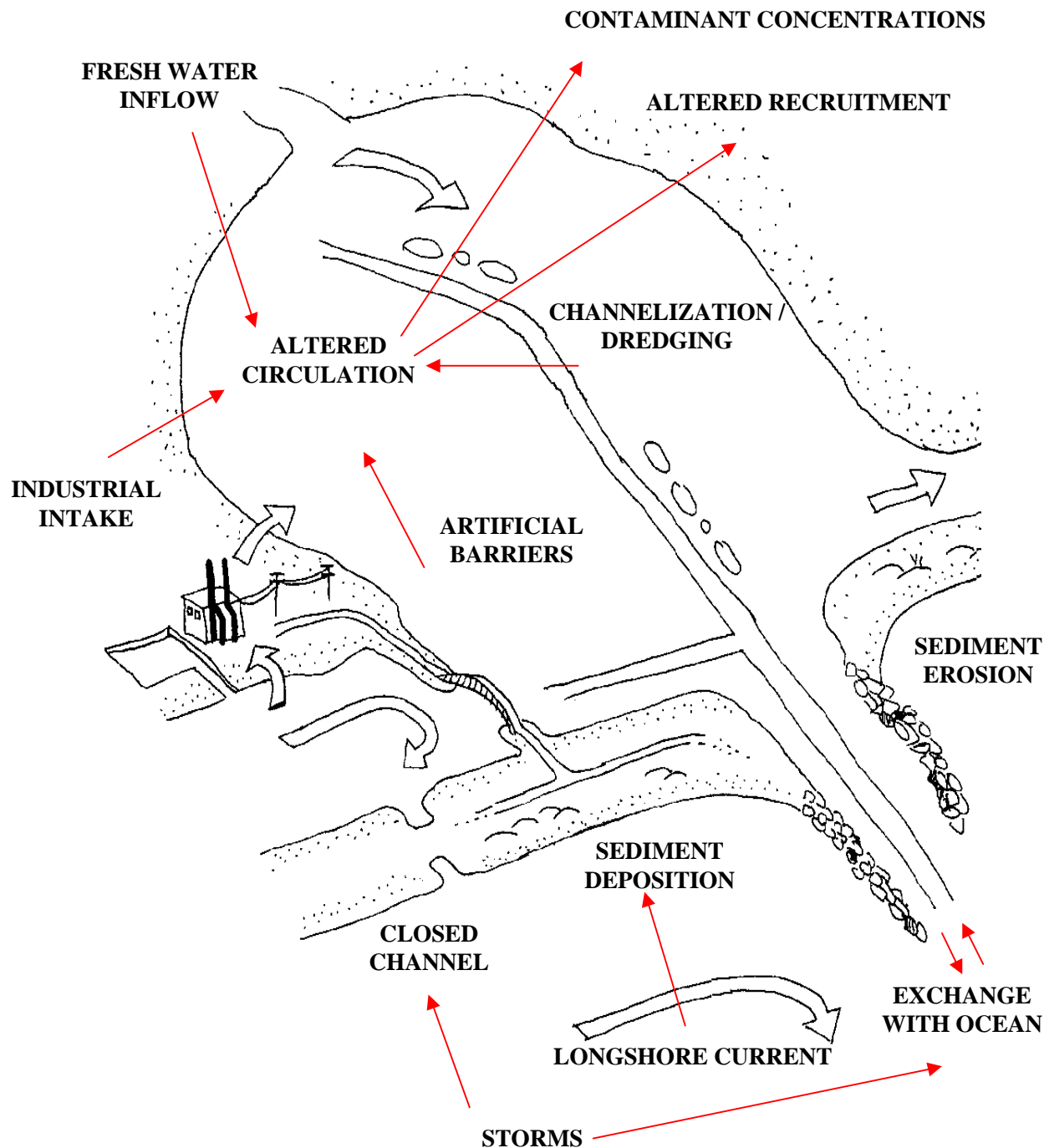
Fig. VII.5. Priority problems: altered estuarine circulation. Changing the flow of water in an estuary can have subtle effects upon the migrational patterns of some animals, the concentrations of contaminants in the water, and even nuisance plankton blooms, such as the brown tide. Creating channels and spoil islands to permit boat traffic creates unnatural features in the relatively shallow and unobstructed Bay Area. The creation of jetties, bulkheads and seawalls can have dramatic effects on the sediment transport by water. The consequences of altering estuarine circulation are not well understood, and warrants further scientific investigation.

of birds, such as black skimmers and white pelicans.

There are two other potential effects on estuarine circulation that are particular to the Nueces Estuary. The flow of the Nueces River has been diverted and greatly decreased by dams upstream. Therefore, the net flow of water from the river to the sea may have been changed. Secondly, industrial use of water can affect circulation. A CPL power plant draws cooling water in from the ship channel and returns it to Nueces Bay. The power plant in Flour Bluff draws water in from Laguna Madre, but returns it to Oso Bay. The magnitude of water moved in this manner is great, but the net flow of water from the Laguna to Corpus Christi Bay may not be greatly affected (Cheryl Brown, per. comm.)

Bay Debris

Debris is the most visible form of pollution: litter, garbage and refuse that is dumped or washed into the bay (Fig. VII.6). Although it takes a lot of plastic and other debris to elicit a toxic response, debris is dangerous for other reasons. Debris, particularly plastic, discarded nets and fishing line, can be dangerous to large animals that ingest or become tangled in it. It is said that a lost plastic or nylon net "fishes forever" as an unseen ghost net. Many of the gulls and terns that can be seen on the beach bear visible signs of bouts with discarded, tangled fishing line. Ingestion of plastic is a major problem for sea turtles. Discarded plastic may resemble jellyfish, a major food component for sea turtles. Necropsies performed on turtles that wash up on the beach frequently reveal the presence of ingested plastic that has blocked the animal's digestive system (Tony Amos, per. comm.).

Humans are also affected by bay debris. Occasionally, containers of toxic chemicals are brought in from the ocean or fall off of a bay-going barges. Medical waste, including discarded syringes, also appear from time to time. Even "harmless" debris can be detrimental to the area. A bay choked with garbage might be much less appealing to tourists, which could eventually hurt the local economy.

Some of the debris in the bays comes from boats. Recreational vessels, as well as the steady stream of transport ships that enter the CCBNEP Bay Area, may contribute to the debris problem, even accidently. A substantial portion of debris comes from recreational fishing, particularly tangled line, and lost lures and weights. Much of this material is accidently discarded when line becomes hung or tangled on rocks, reefs or even power lines. Debris is

PETROCHEMICAL
EXPLORATION AND
TRANSPORTATION

DECREASED
TOURISM ?

WASH OFF
FROM LAND

AESTHETICS

RECREATIONAL USE

ENTANGLEMENT

DEBRIS

INGESTION

BIOLOGICAL
DEBRIS

RED TIDES, FREEZES,
WEATHER

WIND

HUMAN HEALTH

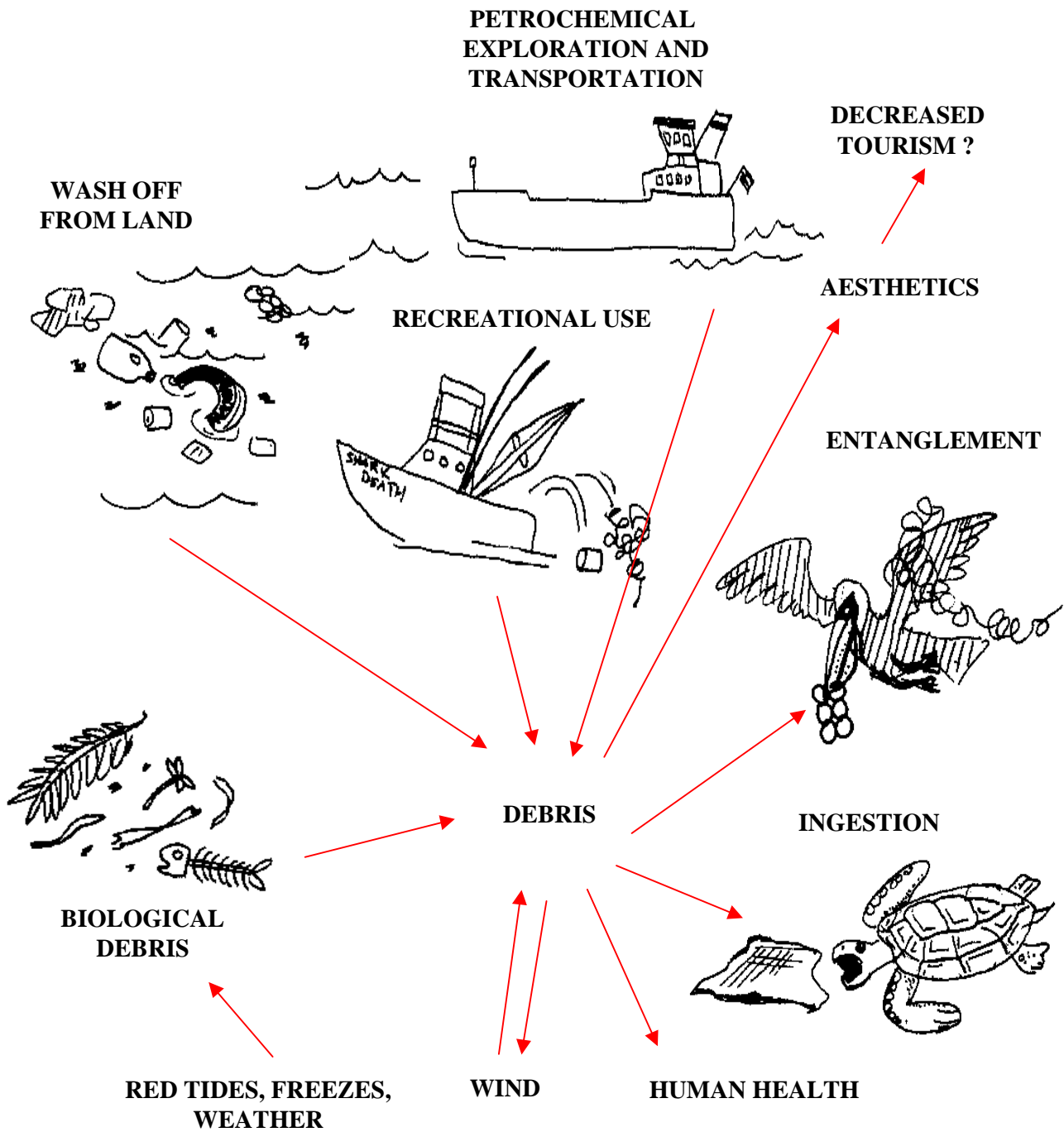Fig. VII.6. Priority problems: bay debris. Although not as insidious as chemical contaminants, debris can have detrimental effects upon the Bay Area. The loss of bird, sea turtle and marine mammal life due to entanglement in fishing line or ingestion of plastic has been well publicized. However, the build up of too much bay debris even has the potential to affect tourism, a major part of the economy in the CCBNEP Bay Area.

also brought into the CCBNEP Area from the Gulf of Mexico. Storms may carry debris off of ships or oil platforms, as can be seen from the hard hats and chemical drums that frequently wash up on the barrier islands. Furthermore, because of prevailing southeasterly winds, the CCBNEP Area also receives a lot of trash from Mexico and Central America. Not all debris is human made. There is also a lot of biological debris, particularly sloughed seagrass. A seagrass die off is a natural phenomenon that occurs in fall or winter. However, storms, heat waves, high turbidity, and algal blooms may also lead to vast quantities of dead seagrass. Because it is organic, seagrass and other biological debris are decomposed by bacteria causing the familiar "rotten eggs" along the Kennedy Causeway. The odor is caused by sulfide. Too much dead matter in the water can lead to a loss of oxygen, or too much sulfide and ammonia in the water. Sulfide and ammonia in high concentrations are toxic to marine animals. Seasonal freezes, which are periodic but infrequent in the CCBNEP Area, can cause fish kills that can also contaminate much of the bay as the fish decompose.

Public Health Issues

Many of the priority problems are concerned with impacts upon the estuarine flora and fauna of the CCBNEP Bay Area System. Obviously, loss of plant and animal life is not in the best interest of the human inhabitants of the CCBNEP Area because of losses in fisheries, tourism, recreational activity, and the qualify of life for CCBNEP residents. In addition to these indirect concerns, there are also some ways that the bay system may directly affect human health (Fig. VII.7). The two main concerns for humans are from contaminated water and contaminated seafood.

Although direct dumping of industrial and residential waste into the marine environment is a thing of the past, some dangerous compounds remain in the bay for many years. Bacteria, including many which are pathogenic, are associated with sewage and with runoff from farms. Some heavy metals, such as mercury, are toxic in even small doses. Mercury and other metals that are buried in the sediment can become resuspended, especially by dredging and trawling. The most susceptible areas to contamination by hydrocarbons and heavy metals are harbors or other areas that receive a lot of boat and ship traffic. The hydrocarbons come from spilled gas, diesel fuel, and oil. The metals originate from pilings and antifouling coatings. The city of Corpus Christi, and other towns along the CCBNEP Area are fortunate that their harbors are in much more pristine condition than many cities on

BIOACCUMULATION

CONTAMINATED SEAFOOD

DECLINE IN HUMAN HEALTH

TOXINS

PATHOGENS

DISEASE

POLLUTED WATER

TOXINS IN SEDIMENT

POINT SOURCES

RESUSPENSION

NON-POINT SOURCES
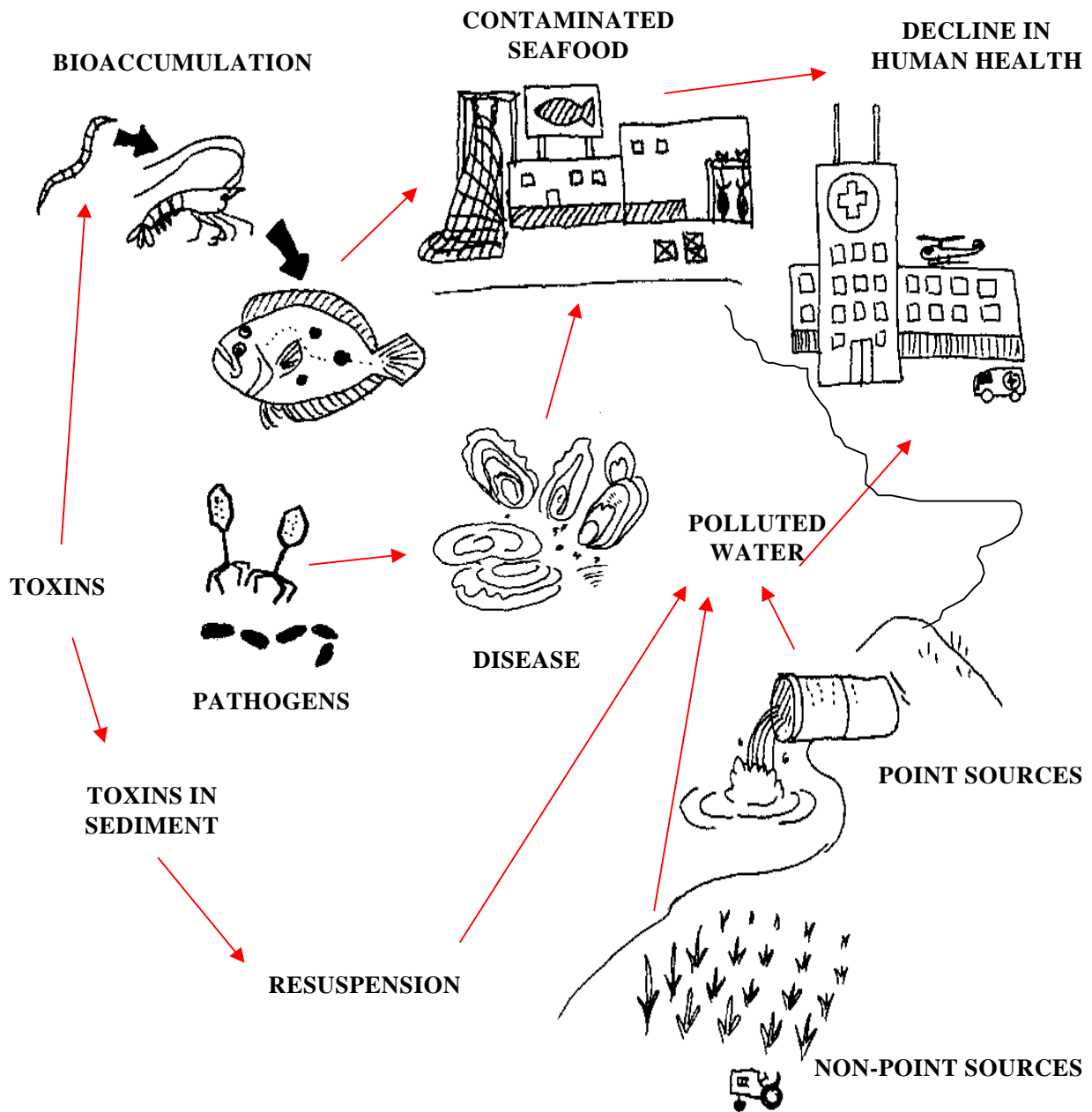
Fig. VII.7. Priority problems: public health. Even if the potential loss of production of the estuaries in the CCBNEP Bay Area is not considered, there are still several issues concerning the Bay Area that can impact human health. Illness and the loss of revenue due to shellfish poisoning by a variety of diseases and parasites is one obvious example. Eating seafood that has been contaminated by toxic waste may also be a potential problem. Of course, water itself may also become polluted as to be a direct danger to the public, as has regrettably happened in many east coast harbors.

the East Coast, and even some in the state of Texas.

Another threat to human health may come from all of the seafood that is produced in the area, including finfish, shrimp and oysters. Because humans are at the top of the food chain, we are extremtly susceptible to biomagnification, in which a contaminant becomes more concentrated as predators higher on the foodchain consume their prey. Seafood can also be a source of disease. Fish and shellfish can become infected while alive, or processed seafood may become contaminated during the time between collection and distribution to the consumer. The *Vibrio* bacteria that infects oyster beds in the summer is a well publicized example of a disease with the potential to affect humans.

Summary

The "Priority Problems" outlined by the CCBNEP are issues that have a real or perceived potential to negatively impact the Bay Area System. Many of these issues have not been fully explored, and may be further refined and developed by the CCBNEP as new information becomes available. In general, the greatest negative impacts that humans can have on the estuarine ecosystem come from contaminants or loss of habitat. Contamination may come from point sources, such as water treatment plants, or non-point sources, such as runoff. Habitat loss can come from alteration of the bay bottom, typically by dredging and trawling, development of wetlands and bay shorelines, and restricting fresh water inflow. The main effects of these contributing factors, as outlined by the CCBNEP, are altered freshwater inflow into bays and estuaries (Fig. VII.1), loss of wetlands and estuarine habitats (Fig. VII.2), condition of living resources (Fig. VII.3), degradation of water quality (Fig. VII.4), altered estuarine circulation (Fig. VII.5), bay debris (Fig. VII.6) and public health issues (Fig. VII.7). The CCBNEP will probably continue to devote resources to defining and refining these priority problems, as well as investigate ways in which people can minimize the negative impacts that they may produce as an important component of the estuarine ecosystem.

VIII. INFORMATION GAPS

In this project, a conceptual model of the CCBNEP Bay Area has been developed. In the strict sense of a conceptual model, there are few information gaps. There are few biological or ecological processes that are so poorly understood that a simplified conceptual model could not be developed. However, science knows less about microbial and biogeochemical processes than any other trophic level within the estuaries. A good example of the kind of problem this poses is the brown tide. Why has the brown tide persisted for so long? The answer may lie in the details of the nitrogen cycle. However, in most cases the lack of knowledge about the details of specific elemental cycles probably will not have a great influence on the success or failure of the CCBNEP.

On the other hand, it would be difficult to create quantitative models based on this conceptual model. The mathematical formulations that would be implied by the relationships between the boxes and arrows in the conceptual model would be a straight forward and relatively easy task. Parameterizing the quantitative model would be nearly impossible. Only cursory information exists on the major standing stocks (represented by storage tanks) in the conceptual models. Most of the information is summarized in Table V.1. Scanty data are available on the rates of processes (represented by bullets and diamonds) in the conceptual model (Table V.1). The data are particularly scanty in terms of spatial and temporal variability. Virtually nothing is known about the transformation coefficients (represented lines and arrows) in the conceptual models.

There are few estuaries in the world where quantitative estimates for most of these parameters exist. Chesapeake Bay is probably one of the best known estuaries in the world, but it differs from South Texas estuaries in many fundamental ways. Chesapeake Bay is surrounded by about 15 forested watersheds, where as Texas estuaries are bordered by only 1 or 2 agricultural or grassland watersheds. Municipal development in the CCBNEP area is trivial relative to the northeastern corridor. The Chesapeake is a large, deep, well-flushed, mesotidal system; whereas, South Texas estuaries are small, shallow, sluggish, and microtidal. Using parameters from the Chesapeake ecosystem would seem unwise.

Solving the problems identified for the CCBNEP area may require new quantitative data to be collected. The conceptual model can be used to identify the data needed. In some cases the data will be available in other characterization studies that were designed to summarize existing data.

IX. REFERENCES

Allendorf, P., 1981. Absorption of dissolved amino acids in the nutrition of benthic species. Kiel. Meeresforsch. 5: 557-565.

Alkemade, R., A. Wielemaker and M. A. Hemminga, 1993. Correlation between nematode abundance and decomposition rate of *Spartina anglica* leaves. Mar. Ecol. Prog. Ser., 99: 293-300.

Anderson, R. V., W. D. Gould, L. E. Woods, C. Cambardella, R. E. Ingham and D. C. Coleman, 1983. Organic and inorganic nitrogenous losses by microbivous nematodes in soil. Oikos, 40: 75-80.

Aruga, Y., 1965. Ecological studies of photosynthesis and matter production of phytoplankton. II. Photosynthesis of algae in relation to light intensity and temperature. Bot. Mag., Tokyo, 78: 360-365.

Banse, K., 1982. Mass-scaled rates of respiration and intrinsic growth in very small invertebrates. Mar. Ecol. Prog. Ser., 9: 281-297.

Billen, G. and C. Lancelot, 1988. Modelling benthic nitrogen cycling in temperate coastal ecosystems. In: Blackburn, T. H. and J. Sorensen (eds.). Nitrogen cycling in coastal marine environments. SCOPE. John Wiley and Sons, Chichester: 341-378.

Buskey, E. D., 1993. Annual pattern of micro- and mesozooplankton abundance and biomass in a subtropical estuary. J. Plankton Res., 15: 907-924.

Buskey, E. J. and D. A. Stockwell, 1993. Effects of a persistent "brown tide" on zooplankton populations in the Laguna Madre of South Texas. In: Smayda, T. J. and Y. Shimizu (eds.). Toxic Phytoplankton Blooms in the Sea: 659-666.

Carrada, G., T. Hopkins, Lj. Jeftiè and S. Morcos (eds.), 1983. Quantitative analysis and simulation of Mediterranean coastal ecosystems: The Gulf of Naples, a case study. Report of a workshop on ecosystem modeling Ischia, Naples, Italy 28 March to 10 April 1981 Organized by the United Nations, Educational, Scientific and Cultural Organization (UNESCO) and the Stazione Zoologica, Naples. 158 p.

Comida, G. W., 1968. Oxygen consumption in *Diaptomus*. Limnol. Oceanogr., 13:51-57.

Davis, J. H., 1940. The ecology and geologic role of mangroves in Florida. Carnegie Institution, Washington, Publ. No. 517: 303-412.

Day, J. W., C. A. S. Hall, W. M. Kemp and A. Yàñez-Arancibia (eds.), 1989. Estuarine Ecology. John Wiley & Sons, 558 p.

Dunton, K. H., 1994. Seasonal growth and biomass of the subtropical seagrass *Halodule wrightii* in relation to continuous measurements of underwater irradiance. Mar. Biol., 120: 479-489.

Elliot, J. M., 1971. Some methods for the statistical analysis of samples of benthic invertebrates. Freshwater Biological Association, Scientific Publication No. 25, 144 p.

Findlay, S. E. G. and K. R. Tenore, 1982. Effect of a free-living marine nematode (*Diplolaimella chitwoodi*) on detrital carbon mineralization. Mar. Ecol. Prog. Ser., 8: 161-166.

Flint, R. W., 1984. Phytoplankton production in the Corpus Christi Bay Estuary. Contrib. Mar. Sci., 27:65-83.

Gundersen, K., 1968. The formation and utilization of reducing power in aerobic chemo-autotrophic bacteria. Zeitschrift. Allg. Mikrobiol., 8: 445-457.

Heip, C., M. Vincx and G. Vranken, 1985. The ecology of marine nematodes. Oceanogr. Mar. Biol. Ann. Rev., 23:399-489.

Heyraud, M., 1979. Food ingestion and digestive transit time in the euphausiid *Meganyctiphanes norvegica* as a function of animal size. J. Plankton Res., 1: 301-311.

Hildebrand. H. and D. King, 1978. Abiological study of the Cayo del Oso and the Pita Island area of the Laguna Madre. Final Rep. to Central Power and Light Co. from Texas A& I University, Kingsville, 465 p.

Holland, J. S., N. J. Maciolek, R. D . Kalke, L. Mullins and C. H. Oppenheimer, 1975. A benthos and plankton study of the Corpus Christi, Copano and Aransas Bay systems. Final Rep. to Texas Water Development Board from Univ. Texas Marine Science Inst., Austin. 174 p.

Ikeda, T., 1970. Relationship between respiration rate and body size in marine plankton animals as a function of the temperature of habitat. Bull. Fac. Fish. Hokkaido Univ., 21: 91-112.

Ivlev, V. S., 1945. The biological productivity of waters. Usp. Sovrem. Biol., 19:98-120.

Jørgensen, B.B., 1980. Mineralization and the bacterial cycling of carbon, nitrogen and sulphur in marine sediment. In: Ellwood, D.C., J.N. Hedger, M.J. Latham, and J.H. Slater (eds.). Contemporary microbial ecology. Academic Press, London: 239-251.

Kerfoot, W. C., 1987. Predation: Direct and indirect impacts on aquatic communities. University Press of New England, 386 p.

Krebs, H. A., 1972. Some aspects of the regulation of fuel supply in omnivorous animals. Adv. Enzyme Regul. 10: 397-420.

Larkin, T. J. and G. W. Bomar, 1983. Climatic Atlas of Texas. Texas Department of Water Resources. Austin, Texas. 151 p.

Li, J., M. Vincx and P. Herman, In press. A model of nematode dynamics at the Westerschelde Estuary. Ecol. Modeling.

Longley, W. L. (ed.). 1994. Freshwater inflows to Texas bays and estuaries: ecological relationships and methods for determination of needs. Texas Water Development Board

and Texas Parks and Wildlife Department, Austin, TX. 386 p.

Lotka, A. J., 1925. Elements of physical biology. Baltimore, Md, Williams & Wilkins, pp. 460.

Malcolm, S.J. and S.O. Stanley, 1982. The sediment environment. In: Nedwell, D.B. and C.M. Brown (eds.). Sediment microbiology. Academic Press, London: 1-14.

Montagna, P. A. and D. Kalke, 1995. Ecology of Mollusca in the south Texas estuaries. Amer. Malacol. Bull. 11: 163-175.

Murray, L. S. and T. S. Jinnette. 1976. Studies of thermal loading on Nueces Bay, Texas. Rep. to Tex. Water Qual. Bd. from Central Power and Light Co., Corpus Christi. 70 p.

Nicholson , A. J. and V. A. Bailey, 1935. The balance of animal populations. Part 1. Proceedings of the Zoological Society of London, 24: 551-598.

Odum, H. T., 1971. Environment, Power, and Society. Wiley Interscience, New York. 331 p.

Odum, H. T., 1972. An energy circuit language. Systems Analysis and Simulation in Ecology vol. 2. In: B. C. Patten (ed.). Academic Press, New York: 139-211.

Odum, H. T., 1983. Systems Ecology. Wiley Interscience, New York, 644 p.

Odum, H. T. and R. Wilson, 1962. Further studies on reaeration and metabolism of Texas Bays, 1958-1960. Publ. Inst. Mar. Sci., U.T., 8:23-55.

Odum, H. T., R. P. Cuzon, R. J. Beyers and C. Allbaugh, 1963. Diurnal metabolism, total phosphorus, Ohle anomaly, and zooplankton diversity of abnormal marine ecosystems of Texas. Publ. Inst Mar. Sci., U.T., 9:404-453.

Orlando, S.P., Jr., L.P. Rozas, G. H. Ward, and C. J. Klein, 1993. Salinity characteristics of Gulf of Mexico Estuaries. Silver Springs, MD: National Oceanic and Atmospheric Administration, Office of Ocean Resources Conservation and Assessment. 209 p.

Parsons, T. R., K. Stevens and J. D. H. Strickland, 1961. On the chemical composition of eleven species of marine phytoplankton. J. Fish. Res. Bd., Canada, 18: 1001-1016.

Parsons, T. R., M. Takahashi and B. Hargrave, 1984. Biological oceanographic processes (3rd edition). Pergamon Press. 329 p.

Pennock, J. R. and J. H. Sharp, 1994. Temporal alternation between light- and nutrient-limitation of phytoplankton production in a coastal plain estuary. Mar. Ecol. Prog. Ser., 111: 275-288.

Platt, H. M. and R. M. Warwick, 1983. Free-living marine nematodes. Part I British Enoplids. Cambridge University Press. 307 p.

Poremba, K., 1994. Simulated degradation of phytodetritus in deepsea sediments of the NE Atlantic (47°N, 19°W). Mar. Ecol. Prog. Ser., 105: 291-299.

Prosser, C. L. (ed.), 1991. Environmental and metabolic animal physiology. Comparative animal physiology, 4th ed., John Wiley & Sons, Inc., Publication, pp. 578.

Redfield, A. C., 1934. On the proportions of organic derivatives in sea water and their relation

to the composition of plankton. James Johnstone Memorial Volume. Liverpool. 176 p.

Ruppert, E. E. and R. D. Barnes, 1993. Invertebrate zoology (6th edition). Saunders College Publishing. 1056 p.

Sand-Jensen, K., 1977. Effects of epiphytes on eelgrass photosynthesis. Aquat. Bot., 3:55-63.

Schiemer, F., 1982. Food dependence and energetics of free-living nematodes, I. Respiration, growth and reproduction of *Caenorhabditis briggsae* at different levels of food supply. Oecologia (Berlin), 54: 108-121.

Schiemer, F. and A. Duncan, 1974. The oxygen consumption of a freshwater benthic nematode, *Tobrilus gracilis* (Bastian). Oecologia (Berlin), 15: 121-126.

Sikora, J. P., W. B. Sikora, C. W. Erchenbrecher and B. C. Coull, 1977. Significance of ATP, carbon, and caloric content of meiobenthic nematodes in partitioning benthic biomass. Marine Biology, 44: 7-14.

Sommer, U., 1994. Are marine diatoms favored by high Si:N ratios? Mar. Ecol. Prog. Ser., 115: 309-315.

Stockwell, D. A., 1989. Effects of freshwater inflow on the primary production of a Texas Coastal Bay System. Nitrogen Processes Study (NIPS) (Final Report), The University of Texas Marine Science Institute, Technical Report No. TR/89-010. 180 p.

Texas Department of Water Resources. 1982. The influence of freshwater inflows upon the major bays and estuaries of the Texas gulf coast. Vol. 8. Executive Summary (Second Ed.). Texas Department of Water Resources, Austin, Texas. 133 p.

Texas Parks and Wildlife. 1988. Trends in Texas Commercial Fishery Landings, 1977-1987. Management Data Series, No. 149. Texas Parks and Wildlife Department, Coastal Fisheries Branch. Austin, Texas.

Vidal, J., 1980. Physioecology of zooplankton. III. Effects of phytoplankton concentration, temperature, and body size on metabolic rate of *Calanus pacificus*. Mar. Biol., 56: 195-202.

Whitledge, T. E., 1989. Nutrient distribution and dynamics in the Lavaca, San Antonio and Nueces/Corpus Christi Bays in relation to freshwater inflow. Nitrogen Processes Study (NIPS) (Final Report), The University of Texas Marine Science Institute, Technical Report No. TR/89-017. 211 p.

Wright, D. J. and D. R. Newall, 1980. Osmotic and ionic regulation in nematodes. In: Zuckerman, B. M. (ed.). Nematodes as Biological Models. Vol. II. Aging and other Models. Academic Press, New York: 143-164.

Zeuthen, E., 1970. Rate of living as related to body size in organisms. Polskie Archiwum Hydrobiologii, 17: 21-30.