

AD A132 389

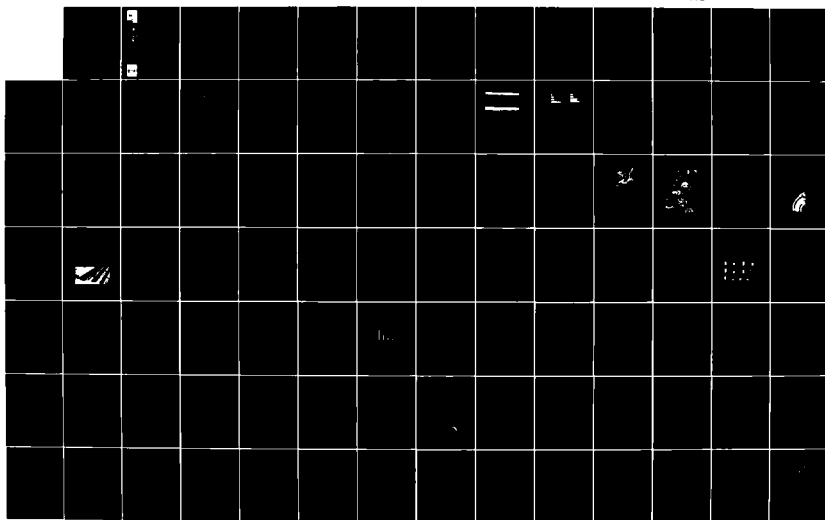
THE ROLE OF PHYSICAL CHEMICAL FACTORS IN STRUCTURING  
SUBTIDAL MARINE AND (U) ARMY ENGINEER WATERWAYS  
EXPERIMENT STATION VICKSBURG MS ENVIR... D R KENDALL  
JUN 83 WES/TR/EL 83-2

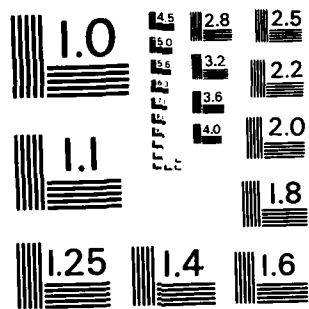
1/3

UNCLASSIFIED

F/G 5/1

NL



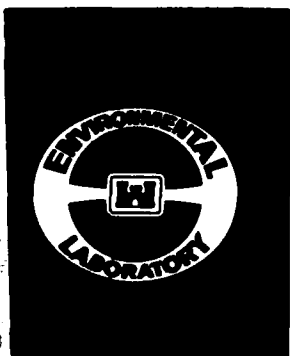
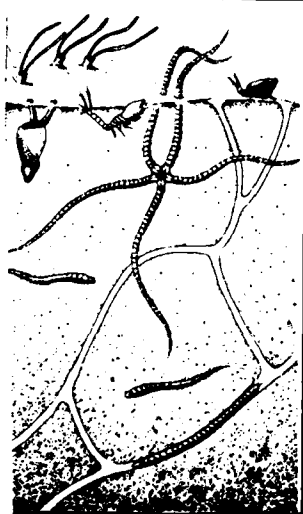


MICROCOPY RESOLUTION TEST CHART  
NATIONAL BUREAU OF STANDARDS - 1963-A



US Army Corps  
of Engineers

ADA132389



DTIC FILE COPY

TECHNICAL REPORT EL-83-2

12

# THE ROLE OF PHYSICAL-CHEMICAL FACTORS IN STRUCTURING SUBTIDAL MARINE AND ESTUARINE BENTHOS

by

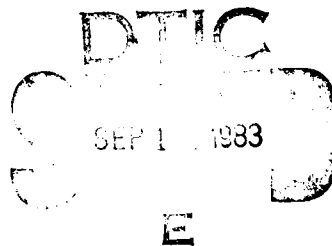
David R. Kendall

Environmental Laboratory  
U. S. Army Engineer Waterways Experiment Station  
P. O. Box 631, Vicksburg, Miss. 39180



June 1983  
Final Report

Approved For Public Release; Distribution Unlimited



Prepared for Office, Chief of Engineers, U. S. Army  
Washington, D. C. 20314

83 09 13 050

Destroy this report when no longer needed. Do not  
return it to the originator.

The findings in this report are not to be construed as an  
official Department of the Army position unless so  
designated by other authorized documents.

The contents of this report are not to be used for  
advertising, publication, or promotional purposes.  
Citation of trade names does not constitute an  
official endorsement or approval of the use of such  
commercial products.

The covers of U. S. Army Engineer Waterways Experiment Station  
(WES) engineering and scientific reports have been redesigned. Each  
WES Laboratory and support organization will have its own distinctive  
color imprinted on white coverstock. This standardizes WES publica-  
tions and enhances their professional appearance.

Unclassified

SECURITY CLASSIFICATION OF THIS PAGE (When Data Entered)

| REPORT DOCUMENTATION PAGE                                                                                                                                                                                                                                                                                                                                                                                                                                                                     |                                     | READ INSTRUCTIONS<br>BEFORE COMPLETING FORM                    |
|-----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|-------------------------------------|----------------------------------------------------------------|
| 1. REPORT NUMBER<br>Technical Report EL-83-2                                                                                                                                                                                                                                                                                                                                                                                                                                                  | 2. GOVT ACCESSION NO.<br>ADA132 389 | 3. RECIPIENT'S CATALOG NUMBER                                  |
| 4. TITLE (and Subtitle)<br>THE ROLE OF PHYSICAL-CHEMICAL FACTORS IN<br>STRUCTURING SUBTIDAL MARINE AND ESTUARINE<br>BENTHOS                                                                                                                                                                                                                                                                                                                                                                   |                                     | 5. TYPE OF REPORT & PERIOD COVERED<br>Final report             |
|                                                                                                                                                                                                                                                                                                                                                                                                                                                                                               |                                     | 6. PERFORMING ORG. REPORT NUMBER                               |
| 7. AUTHOR(s)<br>David R. Kendall                                                                                                                                                                                                                                                                                                                                                                                                                                                              |                                     | 8. CONTRACT OR GRANT NUMBER(s)                                 |
| 9. PERFORMING ORGANIZATION NAME AND ADDRESS<br>U. S. Army Engineer Waterways Experiment Station<br>Environmental Laboratory<br>P. O. Box 631, Vicksburg, Miss. 39180                                                                                                                                                                                                                                                                                                                          |                                     | 10. PROGRAM ELEMENT, PROJECT, TASK<br>AREA & WORK UNIT NUMBERS |
| 11. CONTROLLING OFFICE NAME AND ADDRESS<br>Office, Chief of Engineers, U. S. Army<br>Washington, D. C. 20314                                                                                                                                                                                                                                                                                                                                                                                  |                                     | 12. REPORT DATE<br>June 1983                                   |
|                                                                                                                                                                                                                                                                                                                                                                                                                                                                                               |                                     | 13. NUMBER OF PAGES<br>145                                     |
| 14. MONITORING AGENCY NAME & ADDRESS (if different from Controlling Office)                                                                                                                                                                                                                                                                                                                                                                                                                   |                                     | 15. SECURITY CLASS. (of this report)<br>Unclassified           |
|                                                                                                                                                                                                                                                                                                                                                                                                                                                                                               |                                     | 15a. DECLASSIFICATION/DOWNGRADING<br>SCHEDULE                  |
| 16. DISTRIBUTION STATEMENT (of this Report)<br>Approved for public release; distribution unlimited.                                                                                                                                                                                                                                                                                                                                                                                           |                                     |                                                                |
| 17. DISTRIBUTION STATEMENT (of the abstract entered in Block 20, if different from Report)                                                                                                                                                                                                                                                                                                                                                                                                    |                                     |                                                                |
| 18. SUPPLEMENTARY NOTES<br>Available from National Technical Information Service, 5285 Port Royal Road,<br>Springfield, Va. 22151.                                                                                                                                                                                                                                                                                                                                                            |                                     |                                                                |
| 19. KEY WORDS (Continue on reverse side if necessary and identify by block number)                                                                                                                                                                                                                                                                                                                                                                                                            |                                     |                                                                |
| Benthic habitat types                                                                                                                                                                                                                                                                                                                                                                                                                                                                         | Unconsolidated soft bottoms         | Substrate quality                                              |
| Habitat parameters                                                                                                                                                                                                                                                                                                                                                                                                                                                                            | Submerged aquatic vegetation beds   | Temperature                                                    |
| Subtidal                                                                                                                                                                                                                                                                                                                                                                                                                                                                                      | Rock/hard bottoms                   | Current velocity                                               |
| Estuarine                                                                                                                                                                                                                                                                                                                                                                                                                                                                                     | Reefs                               | Depth                                                          |
| Coastal marine                                                                                                                                                                                                                                                                                                                                                                                                                                                                                | Salinity                            | Vegetation quality                                             |
|                                                                                                                                                                                                                                                                                                                                                                                                                                                                                               |                                     | Water quality                                                  |
| 20. ABSTRACT (Continue on reverse side if necessary and identify by block number)                                                                                                                                                                                                                                                                                                                                                                                                             |                                     |                                                                |
| <p>This report represents a critical review of the literature on subtidal estuarine and coastal marine benthic habitats and the important measurable physical and chemical factors that influence community structure and production. It evaluates qualitative and quantitative trends in benthic community structure linked to physical and chemical environmental factors; it does not elaborate on the effects of important biological interactions such as competition and predation.</p> |                                     |                                                                |

(Continued)

DD FORM 1 JAN 73 1473 EDITION OF 1 NOV 65 IS OBSOLETE

Unclassified

SECURITY CLASSIFICATION OF THIS PAGE (When Data Entered)

Unclassified

SECURITY CLASSIFICATION OF THIS PAGE(When Data Entered)

20. ABSTRACT (Concluded).

There are four generally recognized benthic habitat types within the subtidal estuarine and coastal marine environment. They are: (1) unconsolidated soft bottoms, (2) submerged aquatic vegetation beds, (3) rock/hard bottoms, and (4) reefs. Measurable habitat parameters known to influence the qualitative and quantitative structure of subtidal benthic communities associated with one or all of the four broad habitat types are: (1) salinity, (2) temperature, (3) other water quality descriptors (dissolved oxygen, turbidity, pollution), (4) substrate quality, (5) vegetation quality, (6) current velocity, and (7) depth.

There are many qualitative trends apparent in the literature concerning macroinvertebrate-substrate-water quality relationships. These are discussed, contrasted, and compared, with exceptions noted from different geographical areas of the east, west, and gulf coasts. The literature generally shows that quantitative correlations are usually obscured due to (1) natural biological variability, (2) the integrated influences of substrate and water physical-chemical conditions, and (3) biological interactions including competition and predation. Some site-specific quantitative relationships have been observed, but they are exceptions generally limited to intensively studied benthic species of commercial, recreational, or ecological importance, such as the hard clam. Detailed quantitative studies of the effects of multiple environmental factors on low-interest benthic infaunas are severely lacking or rare.

A review of physical-chemical parameters suggests that it is extremely difficult to isolate the effects on the benthos of one habitat descriptor such as substrate quality at the present state of the art. Much has been written concerning species-specific animal-substrate relationships, but many species are generalists and defy classification based on substrate quality alone. Therefore, the inherent complexity of environmental factors acting in concert to structure benthic communities makes it difficult to determine qualitative changes in benthic communities occurring within any given habitat type. Qualitative changes in benthic community structure may alter the trophic support value of the benthic habitat to bottom feeding fishes, but these changes cannot be accurately quantified using present substrate and water quality data and existing information on benthic invertebrate-substrate quality relationships.

Unclassified

SECURITY CLASSIFICATION OF THIS PAGE(When Data Entered)

## PREFACE

This report furnishes U. S. Army Corps of Engineers District and field biologists with a contemporary critical review and synthesis document evaluating the role of physical-chemical factors in structuring subtidal marine and estuarine benthic habitats.

This document was prepared by Dr. David R. Kendall, Aquatic Habitat Group (AHG), Environmental Systems Division (ERD) of the Environmental Laboratory (EL), U. S. Army Engineer Waterways Experiment Station (WES). This work is a product of the Benthic Resources Assessment Technique (BRAT) Project under the Environmental Impact Research Program (EIRP). The project's Principal Investigator is Mr. John D. Lunz, AHG. Dr. Roger T. Saucier is the EIRP Program Manager; Mr. John Bushman is the Technical Monitor for this work at the Office, Chief of Engineers (OCE). This work was conducted under the supervision of Dr. Thomas Wright, Chief, AHG, Mr. Bob O. Benn, Chief, ESD, and Dr. John Harrison, Chief, EL. Critical reviews of this report were provided by: Mr. John D. Lunz; Drs. Donald F. Boesch, William D. Burbanck, Richard W. Heard, Terry McBee, Robin M. Overstreet, and Thomas D. Wright; and Mr. Bob O. Benn.

Commander and Director of WES during the conduct of this study and the preparation of this report was COL Tilford C. Creel, CE. Technical Director was Mr. F. R. Brown.

This report should be cited as follows:

Kendall, D. R. 1983. "The Role of Physical-Chemical Factors in Structuring Subtidal Marine and Estuarine Benthos," Technical Report EL-83-2, U. S. Army Engineer Waterways Experiment Station, Vicksburg, Miss.

|                    |                                            |
|--------------------|--------------------------------------------|
| Accession For      |                                            |
| NTIS GRA&I         | <input checked="checked" type="checkbox"/> |
| DTIC TAB           | <input type="checkbox"/>                   |
| Unannounced        | <input type="checkbox"/>                   |
| Justification      |                                            |
| By _____           |                                            |
| Distribution/      |                                            |
| Availability Codes |                                            |
| Dist               | Avail and/or<br>Special                    |
| A                  |                                            |

# CONTENTS

|                                                                                 | <u>Page</u> |
|---------------------------------------------------------------------------------|-------------|
| PREFACE. . . . .                                                                | 1           |
| CONVERSION FACTORS, INCH-POUND TO METRIC (SI) UNITS<br>OF MEASUREMENT . . . . . | 3           |
| PART I: INTRODUCTION. . . . .                                                   | 4           |
| Estuarine Environments . . . . .                                                | 5           |
| Coastal Marine Environments. . . . .                                            | 6           |
| Benthic Habitat Types. . . . .                                                  | 7           |
| Unconsolidated soft bottom . . . . .                                            | 9           |
| Submerged aquatic vegetation bed . . . . .                                      | 9           |
| Rock/hard bottom . . . . .                                                      | 9           |
| Reef . . . . .                                                                  | 10          |
| Habitat Descriptors. . . . .                                                    | 10          |
| PART II: ESTUARINE AND MARINE BENTHIC HABITATS. . . . .                         | 11          |
| Unconsolidated Soft Bottom Habitats. . . . .                                    | 11          |
| Submerged Aquatic Vegetation Beds. . . . .                                      | 18          |
| Rooted vascular plants . . . . .                                                | 19          |
| Kelp beds. . . . .                                                              | 23          |
| Rock/Hard Bottom Habitats. . . . .                                              | 26          |
| Reef Habitats. . . . .                                                          | 29          |
| Estuarine mollusk reefs . . . . .                                               | 29          |
| Coral reefs. . . . .                                                            | 32          |
| Worm reefs . . . . .                                                            | 36          |
| PART III: HABITAT DESCRIPTORS . . . . .                                         | 39          |
| Salinity . . . . .                                                              | 39          |
| Substrate Quality. . . . .                                                      | 54          |
| Vegetation Quality . . . . .                                                    | 73          |
| Temperature. . . . .                                                            | 82          |
| Current Velocity, Waves, and Storms. . . . .                                    | 93          |
| Depth. . . . .                                                                  | 103         |
| Water Quality. . . . .                                                          | 110         |
| Dissolved oxygen . . . . .                                                      | 111         |
| Turbidity. . . . .                                                              | 112         |
| Pollution. . . . .                                                              | 115         |
| REFERENCES . . . . .                                                            | 121         |

CONVERSION FACTORS, INCH-POUND TO METRIC (SI)  
UNITS OF MEASUREMENT

Inch-pound units of measurement used in this report can be converted to metric (SI) units as follows:

| <u>Multiply</u>                        | <u>By</u> | <u>To Obtain</u>            |
|----------------------------------------|-----------|-----------------------------|
| dynes/square centimeter                | 0.1       | pascals                     |
| Fahrenheit degrees                     | 5/9       | Celsius degrees or Kelvins* |
| feet                                   | 0.3048    | meters                      |
| knots (international)                  | 0.51444   | meters/second               |
| miles (U. S. statute)                  | 1.609347  | kilometers                  |
| parts per thousand ( <sup>o</sup> /oo) | 1.0000    | grams/liter                 |

---

\* To obtain Celsius (C) temperature readings from Fahrenheit (F) readings, use the following formula:  $C = (5/9)(F - 32)$ . To obtain Kelvin (K) readings, use  $K = (5/9)(F - 32) + 273.15$ .

THE ROLE OF PHYSICAL-CHEMICAL FACTORS IN STRUCTURING  
SUBTIDAL MARINE AND ESTUARINE BENTHOS

PART I: INTRODUCTION

1. U. S. Army Corps of Engineers construction and operational activities may affect substrate quality in estuarine and marine coastal environments. These substrate quality impacts directly affect benthic organisms and indirectly affect fish (commercial, noncommercial, and recreational or sport fish) dependent on the benthos for food. While fish and shellfish have historically been considered valuable natural resources, the extrinsic value of different benthic habitat types (and their associated benthos) is difficult to quantify in terms that have meaning to water resource planners attempting to evaluate substrate quality changes. The Benthic Resources Assessment Technique (BRAT), a methodology currently being developed by the U. S. Army Engineer Waterways Experiment Station (WES), will be used to quantify impacts of Corps activities on fish habitat quality using information describing benthic habitats in estuarine and marine coastal environments. The two objectives of BRAT are to: (a) design an aquatic habitat classification scheme, incorporating benthic ecological data, and (b) design an aquatic habitat evaluation methodology.

2. An underlying assumption of BRAT, a method which will assign "values" to different benthic habitats, is that one must first be able to distinguish different benthic habitats. In many cases distinct boundary areas for different habitat types are difficult to define due to the gradual transition from one habitat type to the next and the fact that most benthic environments exhibit patchiness within a relatively small area. If the substrate and water quality conditions influencing the boundary definitions are understood, field sampling, impact assessment, and construction and operations planning activities can be conducted more economically and effectively.

3. Benthic organisms are rarely if ever distributed uniformly in

time or space within a given aquatic environment. Individual benthic species exhibit seasonal life cycles and species-specific tolerances to environmental conditions. These largely determine their distribution spatially or temporally. Therefore, benthic species respond to environmental gradients and habitat patchiness and are distributed according to their individual ability to survive in any particular habitat type and water quality condition. Many studies have attempted to delineate the environmental and biological factors responsible for structuring benthic communities. Their results testify to the complexity of the relationships between the multiple environmental and biological factors and the folly of assuming simple correlations. Nevertheless, much has been learned concerning the distribution, composition, and secondary production of benthic communities.

4. This report summarizes the literature regarding benthic ecosystem structure and function. It shows the qualitative trends apparent in benthic invertebrate-substrate water quality relationships. It also shows the difficulty in quantifying the relationships between benthic invertebrates and substrate-water quality due to natural biological variability, biological interactions including predation and competition, and the integrated influences of substrate and water physical-chemical conditions.

#### Estuarine Environments

5. Estuarine environments broadly defined herein consist of all submerged (subtidal) benthic habitats, environments, and embayments that are usually semienclosed by land but have open, partly obstructed, or sporadic access to the open ocean, and in which ocean water is at least occasionally diluted by freshwater runoff from the land. This definition includes hypersaline bays, such as are found along the Texas coast, where the salinity may periodically be increased above that of the open sea.

6. Estuarine environments are bounded upstream by a zone in which the concentration of ocean-derived salts measures less than 0.5

parts per thousand ( $^{\circ}/\text{oo}$ )\* during the period of average annual low flow, and downstream by an imaginary line closing the mouth of a river, bay, or sound. Salinity patterns observed in a given estuarine system are generally gradational, ranging from high open-ocean salinities greater than  $30^{\circ}/\text{oo}$  near the mouth to less than  $0.5^{\circ}/\text{oo}$  at the headwaters. Salinities commonly exceed  $40^{\circ}/\text{oo}$  in hypersaline estuaries.

7. Large estuaries are best developed along the Atlantic and gulf coasts of the United States, while poorly developed on the Pacific coasts, where estuaries are more limited. Of the more than 500 estuaries in the United States, Chesapeake Bay represents the largest, ranging from 3 to 40 miles wide and 195 miles long. Along the Pacific coast of the United States, estuaries extend from Alaska south to San Francisco Bay. Glacier Bay, Puget Sound, Columbia River estuary, and San Francisco Bay represent the only sizeable estuaries found on the west coast; therefore, most of the examples and illustrations used to delineate benthic habitats and environmental factors that structure them will focus on the east coast and Gulf of Mexico estuarine system. Contrasts and comparisons among all areas will be made where applicable.

#### Coastal Marine Environments

8. Broadly defined, the marine coastal system considered in this report consists of those submerged benthic habitat types lying within the confines of the open ocean on the continental shelf and its associated high-energy coastline. These benthic environments are exposed to the waves and currents of the open ocean, and the ebb and flow of oceanic tides. Salinities generally exceed  $30^{\circ}/\text{oo}$  with little or no dilution except outside the mouths of estuaries. This definition will also include coastal bays with no appreciable freshwater inflows which support typically marine benthic species and communities.

---

\* A table of factors for converting inch-pound units of measurement to metric (SI) units is found on page 3.

9. The marine benthic system boundary limits considered by this report extend from the outer edge of the continental shelf shoreward to the outer limits of the estuarine system near bays or inlets and to the low tide line along adjacent coastlines. For the purpose of this discussion, only submerged benthic habitat types will be considered.

10. Comparisons of similar habitats and their associated faunas from the east, west, and gulf coasts of the United States at comparable latitudes and depths have shown general patterns of species replacement within similar ecotypes, which approach the parallel community concept (Table 1-1) originated by Thorson (1957) whereby similar types of communities have been found existing at comparable latitudes and depths in similar bottom types. Temperature fluctuations on the east coast are primarily caused by seasonal shifts in strongly flowing air masses, whereas on the west coast temperature fluctuations are primarily brought about by upwelling and injections of cold water from the sea (Odum and Copeland 1974). The stress severity of temperature on the east coast is greater than that occurring generally on the west coast at similar latitudes, resulting in a more diverse fauna on the west coast than the east coast (Sanders 1968).

11. Parts II and III of this report discuss in detail the generally recognized benthic habitat types and those measurable physical and chemical environmental conditions affecting benthos structure and productivity in estuarine and coastal marine environments. These are briefly outlined below.

#### Benthic Habitat Types

12. A modification of the system proposed by the U. S. Fish and Wildlife Service in their publication "Classification of Wetlands and Deepwater Habitats of the United States" (by L. M. Cowardin, et al. 1979) has been used herein to broadly classify the aquatic systems and their major benthic habitats. The following benthic habitats have been generally recognized within each aquatic system.

Table 1-1  
 Examples of Species Replacement: West and East Coast Niche Substitutions,  
 Gulf Coast Equivalents, and Tropical Types when Stressed  
 (after Odum and Copeland 1974)

| System Type             | Description of Role                                                          | Tropical Stressed            | Upper West Coast          | Gulf Coast                   | Upper East Coast             |
|-------------------------|------------------------------------------------------------------------------|------------------------------|---------------------------|------------------------------|------------------------------|
| Oligohaline river mouth | Clam with great capacity to burrow from cold and adapt to salinity variation |                              | <i>Mya arenaria</i>       | <i>Rangia</i>                | <i>Mya arenaria</i>          |
| Middle salinity estuary | Oyster reef niche                                                            | <i>Crassostrea virginica</i> | <i>Ostrea gigas</i>       | <i>Crassostrea virginica</i> | <i>Crassostrea virginica</i> |
|                         | General crab carnivore, moving in and out of varying salinity                | <i>Callinectes</i>           | Dungeness crab            | Blue crab                    | Green crab                   |
|                         |                                                                              |                              | Cancer                    | <i>Callinectes</i>           | Cancer                       |
| High-salinity estuary   | Top carnivore in bottom irregularities                                       | Lobster <i>Panulirus</i>     | King crab                 | Stone crab                   | Lobster                      |
| Kelp system             | Algal forests, bottom attached seaward of surf                               | --                           | <i>Paralithodes</i>       | <i>Menippe</i>               | Homarus                      |
|                         |                                                                              |                              | <i>Macrocystis</i>        | --                           | Laminaria                    |
| Beach and surf          | Deep digging clam adapted to heavy energies just seaward of breakers         | <i>Spisula</i>               | Razor clam                | <i>Spisula</i>               | Surf clam                    |
|                         |                                                                              |                              | <i>Siliqua</i>            |                              | <i>Spisula</i>               |
| Intertidal rocks*       | Surf zone sand dollar                                                        | <i>Mellita</i>               | Dendraster                | <i>Mellita</i>               | <i>Echinarachnius</i>        |
|                         | Grazers of intertidal rocks, periwinkles                                     | <i>Littorina ziczac</i>      | <i>Littorina planaxis</i> | <i>Littorina</i>             | <i>Littorina</i>             |
|                         | Intertidally protected filter feeders                                        | <i>Balanus amphitrite</i>    | Gooseneck barnacle        | <i>irrorata</i>              | <i>litorea</i>               |
|                         | barnacles, <i>Ulva</i>                                                       | <i>Ulva</i>                  | <i>Ulva</i>               | <i>Balanus eburneus</i>      | <i>Balanus</i>               |
| Coastal plankton        | Zooplankton-eater                                                            | Anchovy                      | Pacific herring, Sardines | <i>Ulva</i>                  | <i>balanoides</i>            |
|                         |                                                                              |                              |                           | Menhaden, Threadfin          | Atlantic herring, Alewives   |

\* Hedgepeth (1953, 1967).

#### Unconsolidated soft bottom

13. The unconsolidated bottom habitat type includes soft bottom habitats characterized by the lack of a stable surface for plant and animal attachment. This habitat type is generally found in lower energy environments than rock/hard bottoms, and may be unstable because of currents, tidal flows, and wave activity. The substrate characteristics (grain size, mineralogy) of soft bottom habitats in estuarine and marine coastal environments is largely a function of the sediment source and current velocity. Substrate types in unconsolidated soft bottom habitats include (a) gravel, (b) shell-sand, (c) sand, (d) mud, and (e) organic. Mud substrates may include admixtures of sand, silt, clay, shell, and organic material, although the finer particle sizes (silt and clay) usually predominate. Organic substrates are usually characterized by high organic content and strongly reducing conditions. Cobble-gravel and sand substrates are usually well oxygenated, while mud and organic habitats are characteristically oxygen deficient. Organic sediments with large concentrations of organic matter usually support an impoverished benthic community of low diversity.

#### Submerged aquatic vegetation bed

14. The submerged aquatic vegetation bed habitat type is characterized by rooted vascular plants (seagrasses, e.g. eelgrass and turtle grass) and macroalgae (kelp) attached to or rooted in the rock/hard bottom or unconsolidated soft bottom substrate. These vegetated substrates provide protection and a rich food supply for associated macroinvertebrate infaunal and epifaunal communities and are characteristically very productive benthic habitats.

#### Rock/hard bottom

15. The rock/hard bottom habitat type includes submerged benthic habitats with substrates consisting predominantly (75 percent or more) of stones, boulders, or bedrock which are unvegetated, or where vegetation covers less than 30 percent of the rock surface. This habitat also includes hard compacted clay bottoms which provide suitable substrates for sessile benthos. The stability of this type of benthic habitat allows for a rich diversity of generally sessile benthic

species (faunas and floras) to develop. This habitat type is usually characterized by high physical energy and saturated or nonsaturated dissolved oxygen conditions in surrounding waters. For purposes of this document, rock/hard bottom habitats will also include "artificial reefs" formed by the placement of man-made structures (tires, sunken vessels, etc.) which provide relief and a hard substrate for benthos.

#### Reef

16. The reef habitat type is characterized by ridgelike or mound-like structures formed by the colonization and growth of sedentary invertebrates. These structures are usually elevated above the surrounding substrate and tend to interrupt normal wave or current patterns. Biologically formed reefs found in estuarine environments are mollusk (oyster) and worm (sabellariid) reefs. Marine coastal reefs include coral and sabellariid reefs. The distribution of coral reefs is limited to tropical and subtropical marine environments.

#### Habitat Descriptors

17. Each habitat type will be discussed in terms of measurable habitat descriptors important to the structure and productivity of benthic macroinvertebrate communities. In estuarine and marine coastal environments, these descriptors include hydrologic regime affected by depth, currents, and wave energies and various parameters describing substrate, vegetation, and water quality, including salinity and temperature.

## PART II: ESTUARINE AND MARINE BENTHIC HABITATS

18. The following four submerged benthic habitats are described in this section.

- a. Unconsolidated soft bottom
- b. Aquatic vegetation bed
- c. Rock/hard bottom
- d. Reefs

These are generally recognized as discrete habitats within estuarine and coastal marine environments. Distinctions between variant estuarine and marine habitat examples are illustrated where appropriate, although some may overlap in both systems to some extent. In the following chapter measurable habitat descriptors affecting the distribution, composition, and production of benthos within each habitat type are discussed and evaluated.

### Unconsolidated Soft Bottom Habitats

19. On a spatial basis, unconsolidated soft bottom habitats make up the largest complex of subtidal benthic habitat types in estuarine and marine environments (Figure 2-1). Soft bottom habitats have been the object of much study, particularly with regard to animal-sediment relationships or community-sediment classifications. Ecologically distinct benthic communities have been described for marine soft bottom environments (Peterson 1913; Thorson 1957, 1958). Distinct community patterns have been delineated in the temperate marine coastal environment at comparable latitudes and varying depths (i.e., Parallel Communities (Thorson 1957)), although the distinct community dominance hierarchies observed at temperate latitudes do not appear to hold for warm temperate or tropical regions because of low dominance and high species evenness and diversity (Thorson 1971). Early investigators (Peterson 1913, Thorson 1957) have characterized sublittoral marine soft bottom habitats as being physically homogeneous, although recent studies have shown that the level bottom is "spatially heterogeneous,

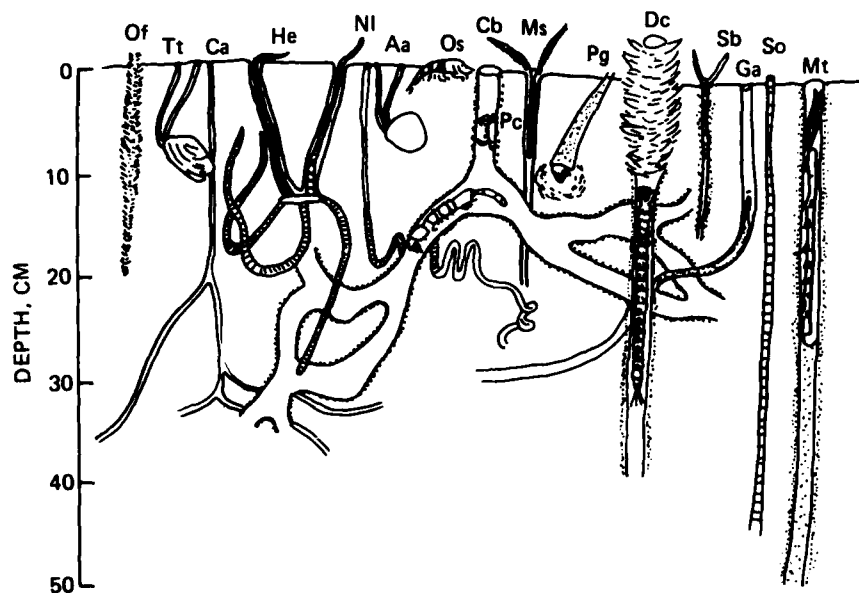


Figure 2-1. Vertical distribution of dominant macrobenthic species from the Georgia nearshore subtidal shelf environment. Legend: Aa = *Abra aequalis*; Ca = *Capitomastus* cf. *aciculatus*; Cb = *Callianassa biformis*; Dc = *Diopatra cuprea*; Ga = *Glycera americana*; He = *Hemipolis elongata*; Ms = *Megelona* sp.; Mt = *Mesochaetopterus taylori*; Nl = *Notomastus latericeus*; Of = *Owenia fusiformis*; Os = *Oxyurostylis smithi*; Pc = *Pinnixa chaetoptera*; Pg = *Pectinaria gouldi*; Sb = *Spiophanes bombyx*; So = *Spiochaetopterus oculatus*; Tt = *Tellina* cf. *texana* (after Dörjes and Howard 1975)

and consists of biologically produced microlandscapes" (Rhoads 1974). Comparable community delineations by substrate type (cobble-gravel, shell/sand, sand, mud, organic) are more difficult to establish in estuarine soft bottom environments due to marked patchiness in sediment quality and environmental gradients (fluctuations in salinity and temperature) along the axis of the estuary. In poikilohaline estuaries (estuaries having highly variable salinity), animal-sediment relationships may be difficult to define due to overriding effects of variable salinity on faunal composition and distribution within a given substrate type (e.g. sand). Dörjes and Howard (1975) concluded in a study of animal-sediment relationships along an environmental gradient in the

Ogeechee River estuary in Georgia that "the dependence upon sediment texture is superseded by dependences on salinity" and were forced to classify the distribution of benthic communities in this estuary based on salinity rather than sediment classification. However, a recent study by Burbanck (1981) in a poikilohaline subestuary in Delaware Bay, successfully classified infaunal groups based on their fidelity to and association with coarse-grained and fine-grained sediments. In relatively homeohaline environments with stable salinity fluctuations, animal-sediment relationships may be more easily defined. Sanders (1958, 1960) found relatively distinct animal-sediment relationships for macrobenthos in Buzzards Bay, Massachusetts, where salinity fluctuations were minimal (29.5-32.5 ‰). His studies showed that filter feeding infaunas were primarily associated with sand bottoms, while deposit feeding infaunas were primarily associated with muddy sediments. Sanders (1956) in a study of animal-sediment relationships in Long Island Sound found bottoms with silt-clay fractions in excess of 50 percent supported fewer individuals and species than coarser sediments. He found that substrates between 25 and 50 percent silt-clay were likely to support an abundance of deposit feeders, while coarser sediments less than 25 percent silt-clay supported the largest community with high concentrations of suspension feeding benthos. Similar animal-sediment relationships were also found in a poikilohaline estuary by Burbanck (1981). Rhoads and Young (1970) observed a similar segregation of deposit feeding and filter feeding benthos, and their study showed that deposit feeding benthos were able to exclude or inhibit the settlement of filter/suspension feeding benthos by creating an unstable, easily resuspended layer of biologically reworked sediments. They suggested that sediment instability and water turbidity maxima near areas of major deposit feeding aggregations successfully excluded suspension feeding groups, which suggestion they called the "Trophic Group Amensalism Hypothesis." Studies in a subtropical estuary (Bloom, Simon, and Hunter 1972) and a tropical lagoon (Aller and Dodge 1974) have confirmed the general validity of this hypothesis at lower latitudes.

20. Another factor complicating animal-sediment relationships on soft bottoms, especially relatively shallow ones (less than 20 m deep), is the relative instability of these habitats compared to vegetated bottoms, rock/hard bottoms, and reef habitats. Storms and seasonal changes in the amount of freshwater inflow modify estuarine sediment composition and benthic community structure by eroding or depositing sediments; benthic fauna associated with unconsolidated soft bottom habitats are thereby continually disrupted by changing sediments within their environment. Seascapes features such as sand waves, ripple marks, and a low level of bioturbation indicate a general instability of bottom sediments and their subsequent movement over the bottom which displaces and disrupts marine benthic communities. Relatively shallow, nearshore shelf benthic environments are subject to a greater frequency of disturbance than deeper midshelf-to-shelf edge benthic environments. Disturbances may be in the form of climatic variability (salinity, temperature, turbidity, etc.) and/or physical disruption of the bottom from currents, waves, dredging activities, and biological disturbance (Howard, Mayou, and Heard 1977; Dayton and Hessler 1972). Benthic faunas associated with shallow unconsolidated soft bottom habitats are continually being disrupted by changing sediments within their environment due to localized bathymetry and hydrographic conditions. Johnson (1972) has proposed an ecologically realistic concept of a benthic community as "a temporal and spatial mosaic, parts of which are at different levels of succession." From this viewpoint "the community is a collection of relics of former disasters." Therefore, it is not surprising that shallow sublittoral benthic infaunal communities rarely show close animal-sediment relationships over broad areas for a given habitat type and species, although they may show broad relationships for functional trophic groups as indicated by the Trophic Group Amensalism Hypothesis.

21. Studies of marine benthic community structure in shelf environments indicate that faunal changes occur along a continuum from nearshore to deepwater environments and that these changes are primarily related to bathymetric zones rather than to sediment compositional

changes (Day, Field, and Montgomery 1971; Buchanan, Sheader, and Kingston 1978; Flint and Holland 1980). In general, transect studies of shelf benthos from the east coast and Gulf of Mexico have shown that density and standing crops decrease from shallow to deep water, while species richness, species diversity, and equitability (lack of dominance) increase (Sanders 1968, Sanders and Hessler 1969; Day, Field, and Montgomery 1971; Flint and Holland 1980; Parker 1964; Boone, Granat, and Farrell 1978). Broad latitudinal studies of marine soft bottom benthic communities have found a general decrease in benthic standing crop biomass with latitude in relatively shallow nearshore environments (Emery and Uchupi 1972).

22. An intriguing discussion of soft bottom benthic community dynamics and production that has recently surfaced is based on the frequency of disturbance or perturbation. Benthos inhabiting muddy soft bottom habitats subjected to frequent disturbance (storms, current scour, dredged material disposal, environmental stress, etc.) characteristically differ markedly in their life history strategies from those infaunal benthos from relatively stable, undisturbed habitats; the former are called "opportunistic species" (Grassle and Grassle 1974), while the latter are termed "equilibrium species" (McCall 1977, 1978). Opportunistic species recolonizing muddy sediments after a disturbance are generally surface deposit feeders or suspension feeders living in the near-surface sediment layer. These fauna are generally small in size, exhibit erratic population density cycles caused by high reproductive potential (continuous recruitment), high mortalities, and short life spans. Equilibrium species may be deposit feeders or suspension feeders usually living deep within the sediment: they are generally larger in size, long lived, and have lower reproductive potentials (seasonal reproductive cycles) and planktotrophic larvae. Opportunistic species are better equipped to recolonize recently disturbed areas quickly due to their higher reproductive potential and life history strategies, whereas equilibrium species usually take much longer. Opportunistic species are also generally eurytopic (ubiquitous) compared with equilibrium species. This characteristic enables them to survive

in environmentally stressful or marginal environments. Table 2-1 illustrates the adaptive strategies of opportunistic species versus equilibrium species. Thus, the frequency of disturbance for a given sediment habitat type will influence the type of infaunas associated with that sediment type. Figure 2-2 illustrates the continuum of faunal structure over time and distance following a physical or pollution disturbance. The gross similarities of faunal structure are readily apparent between the two types of disturbances, illustrating the tendency for equilibrium-type species to be displaced and replaced by more eurytolerant opportunistic species following a perturbation. This figure also shows the succession of benthos and concomitant changes in the sediment oxidized layer from the pioneer community (opportunistic species) to the climax community (equilibrium species).

Table 2-1  
Benthic Adaptive Strategies (after McCall 1977)

| Disturbed Habitats                          | Undisturbed Habitats                          |
|---------------------------------------------|-----------------------------------------------|
| 1. Opportunistic species                    | 1. Equilibrium species                        |
| a. Many reproductions per year              | a. Few reproductions per year                 |
| b. High recruitment                         | b. Low recruitment                            |
| c. Rapid development                        | c. Slow development                           |
| d. Early colonizers                         | d. Late colonizers                            |
| e. High death rate                          | e. Low death rate                             |
| 2. Small size                               | 2. Large size                                 |
| 3. Sedentary                                | 3. Mobile                                     |
| 4. Deposit feeders (mostly surface feeders) | 4. Deposit and suspension feeders             |
| 5. Brood protection; lecithotropic larvae   | 5. No brood protection; planktotrophic larvae |
| 6. Eggs/female = $10-10^3$                  | 6. Eggs/female = $10^3-10^6$                  |

23. Generally speaking, the composition of sediments found in estuaries reflects the source of sediments (terrigenous or carbonate), bathymetry, and hydrography of the particular estuarine system. The distribution of sediments reflects the subtle changes in currents

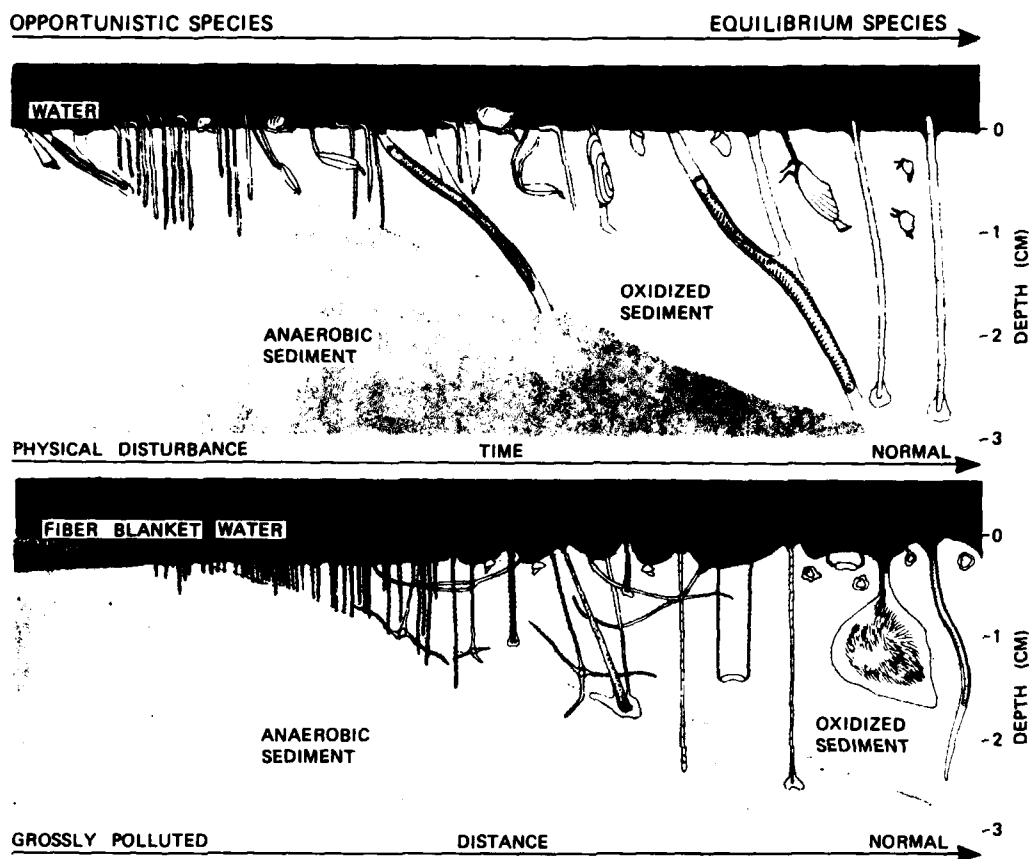


Figure 2-2. Unconsolidated soft bottom community continuum along a physical disturbance time scale and pollution distance gradient (after Rhoads, McCall, and Yingst 1978)

(tidal, wind generated, seasonal river flow) entering or leaving the system, all of which affect the quality and quantity of the associated benthos. Figure 2-3 shows the significance of bottom type and its covariable, current velocity, as they affect the distribution of the quahog (*Mercenaria mercenaria*) in a Maryland estuary.

24. Types of unconsolidated soft bottom habitats generally recognized based on sediment size classification are (a) gravel, (b) shell/sand, (c) sand, (d) mud, and (e) organic. All are indirectly related to current velocity and wave activity within each system. None of the categories of sediment are entirely distinct entities; each type grades

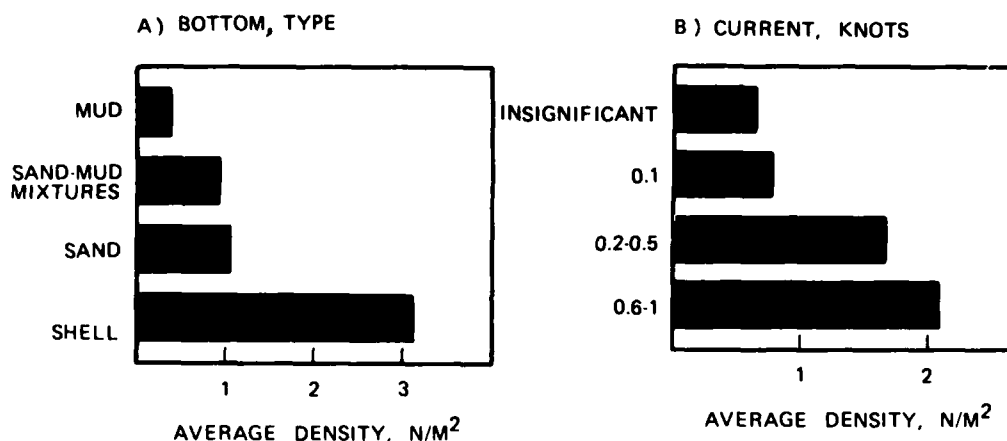


Figure 2-3. Relationship of the average density of *Mercenaria mercenaria* versus (a) bottom type; and (b) current velocity in Chincoteague Bay, Maryland (after Wells 1957)

into the next size category in a continuum based on varying admixtures of clay, silt, sand, shell, and organic matter contents, thereby making distinctions between gross habitat types difficult unless some objective classification scheme is used. Soft bottom infaunal species are rarely found distributed entirely or exclusively within any given sediment type; they are usually distributed along a gradient of varying sediment compositions (soft bottom habitat type), exhibiting peak abundances within a given sediment type, or they may be relatively ubiquitous with no discernible sediment affinities.

#### Submerged Aquatic Vegetation Beds

25. Aquatic vegetation beds are an important and distinct benthic habitat type in estuaries and marine coastal environments worldwide. The distribution of submerged aquatic vegetation is governed by temperature (depending on both latitude and season), salinity, substrate quality, currents, water quality, and bathymetry (depth). Submerged aquatic vegetation habitats found in estuarine and marine coastal environments are principally of two types: (a) rooted vascular plants (seagrasses) and (b) attached macroalgae (kelps). For purposes of this

discussion, macroalgae will be limited to those types forming quantitatively distinct zones in estuarine and marine coastal environments, such as the kelps (Phaeophyta).

#### Rooted vascular plants

26. Rooted vascular plants such as seagrasses are worldwide in distribution in shallow coastal and estuarine waters, in unconsolidated soft bottoms for the most part. They are very important habitats due to the protection they provide from erosion; their role in sediment accretion and stabilization; their high productivity; and their use as refuges and nursery and spawning areas by many commercial, recreational, and ecologically important species (Phillips 1980).

27. Seagrasses are flowering plants (Class: Monocotyledonae). Some 45 species have been described worldwide (Phillips 1980). In tropical to subtropical regions of the western Atlantic (i.e., from the Gulf of Mexico to North Florida on the Atlantic Coast) the dominant species is turtle grass, *Thalassia testudinum*. Other species from this same region are the shoal grass, *Halodule wrightii*; manatee grass, *Syringodium filiforme* (Cymodocea); and widgeon grass, *Ruppia maritima*. In temperate regions, the number of seagrass species diminishes. Of the five species reported, only two are significant, and they are eelgrass, *Zostera marina*, and widgeon grass. Both of these species are distributed widely along the Atlantic and Pacific coasts.

28. In oligohaline to freshwater zones of estuaries that are tidally influenced, other rooted vascular plants may be found, which also form extensive aquatic vegetation beds. A few species such as the tapegrass (*Vallisneria americana*) and the exotic eurasian watermilfoil (*Myriophyllum spicatum*) are known to support high densities of freshwater and estuarine animals (Burbanck and Burbanck 1967, Burbanck and Burbanck 1979, and Menzie 1980). Both species have a wide distribution in the eastern United States and have been reported in tidally influenced reaches of east coast and gulf coast estuaries (Burbanck and Burbanck 1967; Burbanck and Burbanck 1979; Radford, Ahles, and Bell 1968; Tarver et al. 1979; Menzie 1980; Desselle et al. 1978).

29. Rooted vascular plant species are almost exclusively found

on unconsolidated muddy sand bottoms, thus occupying a habitat virtually uncontested by benthic algae except for a few green algal families (Codiaceae and Caulerpaceae) in the tropics (Phillips 1978). However, two species of "surf grasses," *Phyllospadix torreyi* and *Phyllospadix scouleri* grow on rocky substrates down to 50 ft along the Northeast Pacific Coast; the latter species being distributed from Vancouver Island south to Mexico (Dawson 1956, Phillips 1978).

30. Subtropical and tropical seagrasses occur in waters of moderate current energy between 0.6- and 20-m depth in Puerto Rico, the Florida Keys, and south Texas (Odum 1974, Zieman 1975). In tropical areas of higher wave energy, seagrasses are displaced by coral and algal reef systems. This is due in part to adaptations to lower light intensities and currents and grazing by reef-associated animals (sea urchins, fish, etc.). Turtle grass requires high light intensity, and the maximum depth of large beds is generally around 10 m. *Thalassia* is considered to be a tropical marine plant, favoring relatively stable salinities from 20-35 ‰ and temperatures in the northern Gulf of Mexico ranging from 17° to 32° C (Zieman 1975, Phillips 1978). *Halodule* is much more euryhaline, having been reported from both hypersaline estuaries in Texas (Odum 1974) and lower salinity environments (Thorhaug 1981). This species appears to be primarily restricted to very shallow or lower salinity environments. This may be a consequence of its poor competitive ability with turtlegrass (Thorhaug 1981) or to its physiological adaptability in these environments. Widgeon grass (*Ruppia*) is also primarily restricted to low-salinity areas. Studies of turtle grass have shown that environmental factors are primarily responsible for blade (leaf) densities, standing crop biomass, and production within marine coastal environments (Zieman 1975).

31. Eelgrass forms the single most important temperate seagrass species. On the Pacific coast eelgrass extends from Port Clarence, Alaska (lat. 65° N), as far west as Atka Island (long. 175° W) and as far south as Agiopampo Lagoon, Mexico (lat. 26° N) (Phillips 1974). On the Atlantic Coast of North America, eelgrass extends from Hudson Bay, Canada, the southern tip of Greenland, and one locality in Iceland

(lat. 65° N) to Beaufort, North Carolina (Phillips 1974, Penhale and Smith 1977).

32. Eelgrass is a relatively eurytopic species, surviving the temperature range of 5° to 27° C, and salinities ranging between 10 and 30 ‰ are optimum for growth (Phillips 1974). *Zostera* activity has been correlated with temperatures and photoperiod, and both appear to be responsible for controlling growth and regulating reproduction in this species (Phillips 1974). Eelgrass occurs on tidal mud flats and in bays and estuaries at depths up to 5.4 m in turbid water and 30 m in clear water (Phillips 1974), although the general limit of dense eelgrass beds is 12-15 m in clear water. Along the open southern California Coast, eelgrass is often found on sandy bottoms in depths of 5 m or more. Substrate preferences for this species range from firm sand to soft mud, and distributions are apparently affected by current and wave energies and storm surges. Moderate currents of up to 3.5 cm/sec appear to enhance eelgrass growth, and the most luxuriant growth occurs within this range (Phillips 1980).

33. Representative annual production values for seagrasses range from 125 to 4000 g C/m<sup>2</sup>/year for turtlegrass, and 50 to 950 g C/m<sup>2</sup>/year for eelgrass (Phillips 1980). Table 2-2 illustrates some regional annual production estimates for representative seagrass species, and it is readily apparent that overall turtlegrass is approximately twice as productive as eelgrass (1000 g C/m<sup>2</sup>/year for subtropical seagrasses versus 480 g C/m<sup>2</sup>/year in temperate seagrasses) (McRoy and McMillan 1977).

34. This discrepancy may largely be a function of the length of the growing season (250 days for turtlegrass versus 120 days for eelgrass) (McRoy and McMillan 1977). Subtropical seagrass beds along the coast of Florida generally show a much less pronounced seasonal growth pattern due to less variable temperature and light intensity. Rooted aquatic vegetation such as eelgrass and turtlegrass are considered to be the chief producers of organic matter in shallow sublittoral waters (Carriker 1967). Eelgrass has been shown to be capable of pumping nutrients from subsurface sediments to surface waters, where they are exported, and it is likely that other seagrass species function in a

Table 2-2  
Comparative Average Productivities of Selected Seagrasses  
(After McRoy and McMillan, 1977)

| Species                             | Locality       | Productivity<br>g C/m <sup>2</sup> /day | Annual<br>Productivity<br>g C/m <sup>2</sup> |
|-------------------------------------|----------------|-----------------------------------------|----------------------------------------------|
| <b>Seagrasses</b>                   |                |                                         |                                              |
| <i>Thalassia testudinum</i>         | Puerto Rico    | 2.4-4.5                                 | 600-1125                                     |
| (assume growing season of 250 days) | Florida        | 0.35-16                                 | 88-4000                                      |
|                                     | Texas          | 0.9-9.0                                 | 225-2250                                     |
| <i>Halodule wrightii</i>            | North Carolina | 0.48-2.0                                | 72-240                                       |
| (assume growing season of 120 days) |                |                                         |                                              |
| <i>Zostera marina</i>               | Denmark        | 2.0-7.3                                 | 240-1095                                     |
| (assume growing season of 120 days) | Rhode Island   | 0.4-2.9                                 | 60-435                                       |
|                                     | North Carolina | 0.2-1.7                                 | 30-255                                       |
|                                     | Washington     | 0.6-4.0                                 | 90-600                                       |
|                                     | Alaska         | 3.3-8.0                                 | 495-1200                                     |
| <b>Epiphytes on seagrasses</b>      |                |                                         |                                              |
| <i>Zostera marina</i>               | Massachusetts  | --                                      | 20 <sup>a</sup>                              |
|                                     | North Carolina | --                                      | 73 (Detritus) <sup>b</sup>                   |
| <i>Thalassia testudinum</i>         | Florida        | --                                      | 200 <sup>c</sup>                             |

<sup>a</sup>After Marshall 1970.

<sup>b</sup>After Penhale and Smith 1977.

<sup>c</sup>After Jones 1968.

similar manner (McRoy and Barsdate 1970). Studies by Penhale and Smith (1977) indicate that as much as 15 percent of the total dissolved organic carbon (DOC) in the estuarine system near Beaufort, North Carolina, may be contributed by eelgrass and its associated epiphytes. The significance of seagrasses as a source of organic carbon has also been documented for the eastern Gulf of Mexico coastal zone (Iverson et al. 1979).

35. Epiphytes associated with seagrass ecosystems have been found to contribute substantial amounts of carbon (Table 2-2). Den Hartog (1970) has recorded 200 algal epiphyte species from turtlegrass, while Davis (1911) reported 42 species of epiphytes from eelgrass beds from Woods Hole, Massachusetts. Estimates of epiphyte production

within seagrass ecosystems range from 20 percent of the mean annual net production of turtlegrass in Florida ( $200 \text{ g C/m}^2/\text{year}$ ) (Jones 1968) to 25 percent of the annual production of eelgrass in North Carolina (Dillon 1971). A highly diverse faunal community is distributed within the seagrass substrate (infauna) or on the seagrass blades as encrusting or motile invertebrates (epifauna). Numbers of invertebrate species reported from tropical to subtropical seagrass communities range from 75 (stressed community) to 230 species, and 112 to 138 species in temperate eelgrass communities (O'Gower and Wacasey 1967, Young and Young 1977, Stoner 1980, Marsh 1973, Orth 1973, Phillips 1974). Studies by Burbanck and Burbanck (1967, 1979) and Menzie (1980) have also shown rooted aquatic vegetation beds in upper reaches of estuaries to be significant habitats for many freshwater and estuarine invertebrates. Seagrass communities are usually characterized as supporting a detritus-based food web, and relatively few animal species graze the seagrass blades directly (Phillips 1980). MacGinite (1935) in a quantitative study of trophic relationships of California seagrass communities found 95 percent of the species by weight to be detritus feeders.

#### Kelp beds

36. Large brown algae called kelp inhabit shallow marine waters of temperate zones of both the northern and southern hemispheres. Kelp are usually found seaward of the surf zone to depths less than 31 m, or in high salinity embayments with some swell and low-turbidity clear water (Figure 2-4). Kelp grows to 50 m in length on the Pacific Coast, with optimum growth occurring at water depths of 8-30 m. *Nerocystis*, an annual species, may reach lengths of 30 m in a single year (Thorson 1971). Another important genus, *Macrosystis* (giant kelp), is a perennial and grows to even greater lengths. Kelp beds may be 5 km wide along coasts, where they act as a protective buffer along marine coastal shallow water environments breaking up waves and subduing currents, thereby protecting shorelines from erosion. They grow as vertical standing underwater forests that wave and lash with the motion of the sea, supporting an immense production of associated epiphytes and invertebrates. The giant kelp is found on the Pacific Coast of North

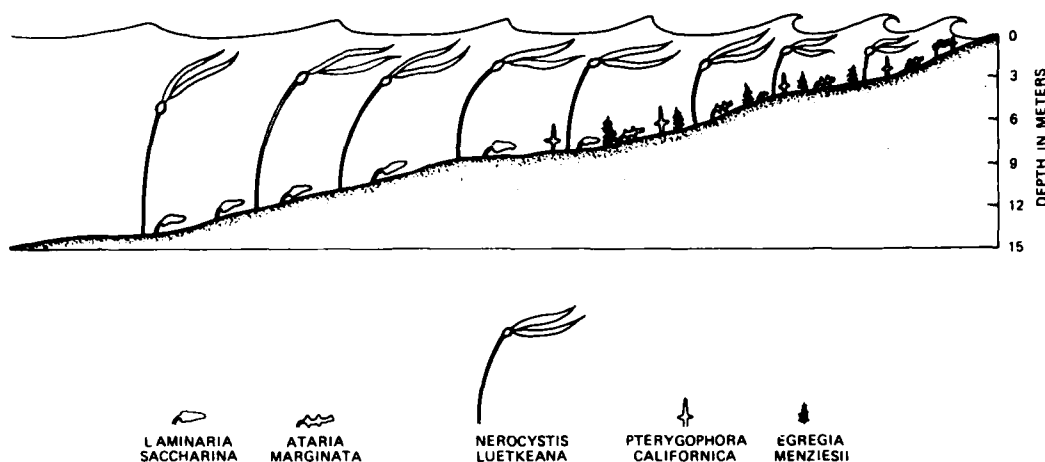


Figure 2-4. Schematic of a "typical" kelp bed in Puget Sound. Highly generalized representation of dominant kelp species. Horizontal axis and plant densities not to scale (after Phillips 1974)

America from lat. 27° N (west coast of Baja, California) to the Monterey Peninsula, California, and tolerates temperatures from 0° to 18° C, and salinities from 26.3-43.7 ‰. Kelp beds exhibit maximum development on hard rock bottoms and cool waters of the west coast. On the rocky temperate western Atlantic coast, *Laminaria* serves as a dominant kelp species. *Laminaria* may also dominate kelp beds on the Pacific coast. Other macroalgae make up significant portions of the kelp system and may be quantitatively significant as microhabitats for macroinvertebrates in the absence of the larger kelp dominants, as illustrated by Table 2-3. This table shows that sessile benthos may reach enormous biomass densities within algae/kelp beds. Some 114 algal species have been reported from giant kelp beds (Dawson, Neushul, and Wildman 1960). Production of giant kelp has been estimated at between 448 to 3138 g/m<sup>2</sup>/year averaging 1464 g/m<sup>2</sup>/year (dry-weight-organic matter) (Phillips 1974). Production of kelp is therefore similar in magnitude to coral reefs, freshwater springs, and seagrass systems (Phillips 1974). In contrast to seagrass systems, where the principal food web is detritus based, kelp systems exhibit both a grazing and detritus-based food web.

Table 2-3  
Comparison of the Standing Crops of the Chief Attached Plants and  
Sessile Animals from Two Locations\*

| Classification      | Under Canopy |                             |                            | Not Under Canopy |                             |                            | Mean Not<br>Under Canopy<br>Mean Under Canopy** |
|---------------------|--------------|-----------------------------|----------------------------|------------------|-----------------------------|----------------------------|-------------------------------------------------|
|                     | Frequency    | Range**<br>g/m <sup>2</sup> | Mean**<br>g/m <sup>2</sup> | Frequency        | Range**<br>g/m <sup>2</sup> | Mean**<br>g/m <sup>2</sup> |                                                 |
| Phaeophyceae        |              |                             |                            |                  |                             |                            |                                                 |
| <i>Cystoseira</i>   | 1.0          | 22-281                      | 90                         | 1.0              | 25-436                      | 200                        | 2                                               |
| <i>Egregia</i>      | 0            | 0                           | 0                          | 0.1              | 0-4                         | 0.4                        | --                                              |
| <i>Eisenia</i>      | 0.1          | 0-22                        | 2                          | 0.3              | 343-1865                    | 405                        | 200                                             |
| <i>Laminaria</i>    | 0.2          | 0-52                        | 6                          | 1.0              | 2.3-1758                    | 539                        | 90                                              |
| Juvenile            |              |                             |                            |                  |                             |                            |                                                 |
| <i>Macrocystis</i>  | 0            | 0                           | 0                          | 0.8              | P†-5.8                      | 0.9                        | --                                              |
| <i>Pterygophora</i> | 1.0          | 0.4-517                     | 124                        | 0.7              | 163-4258                    | 1263                       | 10                                              |
| Rhodophyceae        |              |                             |                            |                  |                             |                            |                                                 |
| Fleshy reds         | 0.6          | 0-25                        | 6                          | 1.0              | 0.5-476                     | 222                        | 37                                              |
| Calcareous reds     | 1.0          | 114-366                     | 209                        | 1.0              | 281-940                     | 658                        | 3                                               |
| All algae††         | 1.0          | 285-1058                    | 469                        | 1.0              | 810-6688                    | 3145                       | 7                                               |
| Sessile animals     | 1.0          | 193-923                     | 508                        | 1.0              | 129-999                     | 506                        | 1                                               |

\* One site was well beneath a dense *Macrocystis* canopy, which had been in existence for approximately a year, while the other site, 30 m away, extended out from the edge of the canopy and was free from any shading effects.

\*\* Mean values, ranges, and frequencies were computed from ten samples of area 1 m<sup>2</sup>, positioned randomly within the sampled location.

† P = present but less than 0.1 g.

†† Does not include adult *Macrocystis* or *Lithothamnion* (after North 1964).

Herbivores (e.g. sea urchins) are common and may be destructive to the kelp bed habitat. Kelp and associated algae serve as substrates and food for many sessile encrusting and motile invertebrates. Densities of motile invertebrates of up to  $100,000/m^2$  on blade surfaces of giant kelp have been reported by Wing and Clendenning (1959). Kelp blade surfaces are also generally heavily encrusted with bryozoans, hydroids, and other sessile species. Kelp beds also serve as critical foraging and reproductive habitats for many important commercial species such as lobster, abalone, crabs, and fish.

#### Rock/Hard Bottom Habitats

37. Estuarine distributions of hard bottom habitats are limited to areas where currents and waves are sufficient to maintain a surface free of sediment. Rocky substrates, oyster reefs, shell deposits, and other hard surfaces such as compacted clay bottoms seldom exist as clean surfaces in estuaries because of generally high rates of sedimentation (Day 1959, Percival 1929). Organisms attempting to settle must usually contend with sediment layers varying in thickness on top of hard surfaces (Carriker 1961). These habitats serve as "terra firma" for sessile macroinvertebrate communities sometimes referred to as "fouling communities." Fouling communities associated with hard bottom estuarine habitats are comprised of dominant sessile species such as mussels, bryozoans, barnacles, sea anemones, sea whips (e.g. *Leptogorgia*), hydrozoans, sponges, and tunicates (ascidians). These species in turn serve as substrates and microhabitats for many associated cryptic, motile, and boring organisms. Filter/suspension feeding is the primary trophic activity or mode of feeding for the dominant species groups within these communities. Epifaunal macroinvertebrates dominate these communities and are subjected to greater diel environmental stresses than infaunal communities inhabiting unconsolidated soft bottom habitats. Typical fouling communities are often contiguous with oyster communities, where relative proportions of dominant species contribute the only discernible differences.

38. Marine rock/hard bottom habitat. Marine hardgrounds exhibit wide but patchy distributions on Pacific, Atlantic, and Gulf shelf environments bordering the United States (Figure 2-5). Rocky substrates

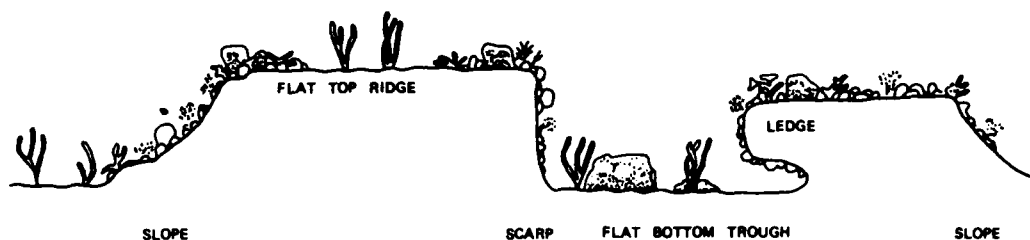


Figure 2-5. Cross section of a representative hard bottom community located 33 km due east of Sapelo Island, Georgia, in 19.8 m of water, and known locally as "Grays Reef" or "Sapelo Live Bottom" (after Hunt 1974)

comprising these hard bottom areas may vary widely in composition according to geographical region and local lithofacies. Hard bottom substrates from the southwest Atlantic have variously been described as recent to subrecent biostromal reef deposits; limestone conglomerates of carbonate shell and quartz sand, stone, sandy biomicrite; and "algal rocks including lithothamnion and coquinalithic deposits" (Menzies et al. 1966; Hunt 1974; Avent, King, and Gore 1977; Continental Shelf Associates 1979; Powles and Barans 1980; U. S. Department of the Interior Bureau of Land Management (BLM) 1978, 1981). Hard bottom habitats are limited to areas where an underlying rock/hard bottom substrate is near the sediment surface, allowing outcropping of exposed rock surfaces in areas where there is sufficient current or wave activity to maintain a sediment-free substrate. Sedimentation is generally not as great a problem as in estuarine environments, but shifting sand from adjacent unconsolidated soft bottoms (storms, currents) may alternately cover up existing low-relief hardbottoms and expose new rock surfaces. The discovery and increasing knowledge of the distributions of hardgrounds or hard bottom habitats have come about in recent years primarily as a

result of oil exploration activities and fisheries resource investigations on the continental shelves of the United States (Pearse and Williams 1951; Menzies et al. 1966; Cerame-Vivas and Gray 1966; Struhsaker 1969; BLM 1978, 1981; Parker, Colby, and Willis in press). Hardgrounds have generally been shown to exhibit discontinuous and patchy distributions, although some northeast-southwest-trending ridges and troughs have been recently described between Cape Hatteras, North Carolina, and Cape Canaveral, Florida (Hunt 1974; BLM 1978, 1981). Three discontinuous hard bottom regions were noted lying parallel to the coast as follows: inner shelf hardgrounds found in waters between 15 to 27 m deep (Jacksonville, Florida, to Charleston, South Carolina); middle shelf hardbottoms lying in waters between 28 to 55 m (Jacksonville, Florida, to Onslow Bay, North Carolina); and outer shelf banks (also referred to as "shelf edge reefs") in waters between 55 to 100 m (Hunt 1974, BLM 1978, Henry et al. 1980). Similar shelfedge features have been described in the Gulf of Mexico (Bright and Pequegnat 1974; Bright and Rezak 1976; Bright et al. 1976, 1978a,b; Edwards 1971; Ludwick and Walton 1957; Parker and Curray 1956). Rock outcrops observed on the southwest Atlantic shelf may exhibit vertical relief up to 15 m. Vertical relief is generally 2 m or less within the "inner shelf hardbottoms," and higher relief rock outcrops are usually restricted to the midshelf and outer shelf environments (Hunt 1974, Harris 1978, Henry et al. 1980). Hard bottom areas were estimated by Parker, Colby, and Willis (unpublished manuscript) to cover some 23.3 percent of the shelf between Cape Hatteras and Cape Canaveral, while those with vertical relief greater than 1 m covered approximately 7.4 percent. Hard bottom habitats with low-relief rock outcrop surfaces (less than 0.5 m) may be relatively ephemeral, transient entities in areas with shifting unstabilized sediments, frequent storm activity, and strong bottom currents.

39. Marine hard bottom habitats, also known as "live bottoms" and "reefs," support diverse communities of invertebrates, fish, and algae. Recent studies have identified 1175 invertebrate species and 150 algae species from various hard bottom habitats between North Carolina and

north Florida (Pearse and Williams 1951; Avent, King, and Gore 1977; BLM 1978, 1981). Structurally dominant animal taxa are attached (sessile) to the rock substrate and are predominantly filter/suspension feeders such as sponges, soft coral (alcyonarians), bryozoans, hydrozoans, tunicates, and polychaetes. These taxa serve as substrates or microhabitats for many motile epifaunas and cryptic species (crustaceans, mollusks, echinoderms, polychaetes, etc.). Descriptions of hard bottom communities from North Carolina southward indicate that many of the dominant sessile species and associated taxa common to these habitats are tropical in distribution, whereas adjacent soft bottom benthic communities are not. Many of these tropical species are existing in the northernmost extent of their ranges and are able to do so because of temperature-dampening influences of the Gulf Stream. Compared to adjacent unconsolidated soft bottom communities (Tenore et al. 1978, Hansen et al. 1981) on the southeastern United States continental shelf, hard bottom habitats or live bottom areas are much more productive and support larger populations of virtually every taxa. Fisheries resource investigations on the continental shelf of the southeastern United States have also shown that the live bottom habitats lying between 18 and 55 m are the only habitats in this region capable of supporting commercially exploitable demersal fish stocks (Bearden and McKenzie 1971, Struhsaker 1969, Barans and Burrell 1976, Powles and Barans 1980).

#### Reef Habitats

##### Estuarine mollusk reefs

40. Oyster reefs are primarily restricted to estuarine environments although they have been reported in marine coastal environments from North Carolina and the Gulf of Mexico off Louisiana. The eastern or American oyster (*Crassostrea virginica*) is the most widely distributed and commercially important reef-building mollusk species in North America. This species is distributed along the entire east coast of North America, from the Gulf of St. Lawrence, Canada, to Key Biscayne, Florida, to the Yucatan and West Indies (Bahr 1981), and has even been

reported from Brazil (Gunter 1951). The Pacific oyster (*Oystrea lurida*) replaces the Atlantic coast species (*C. virginica*) on the west coast, and the distributions of both species are shown in Figure 2-6.

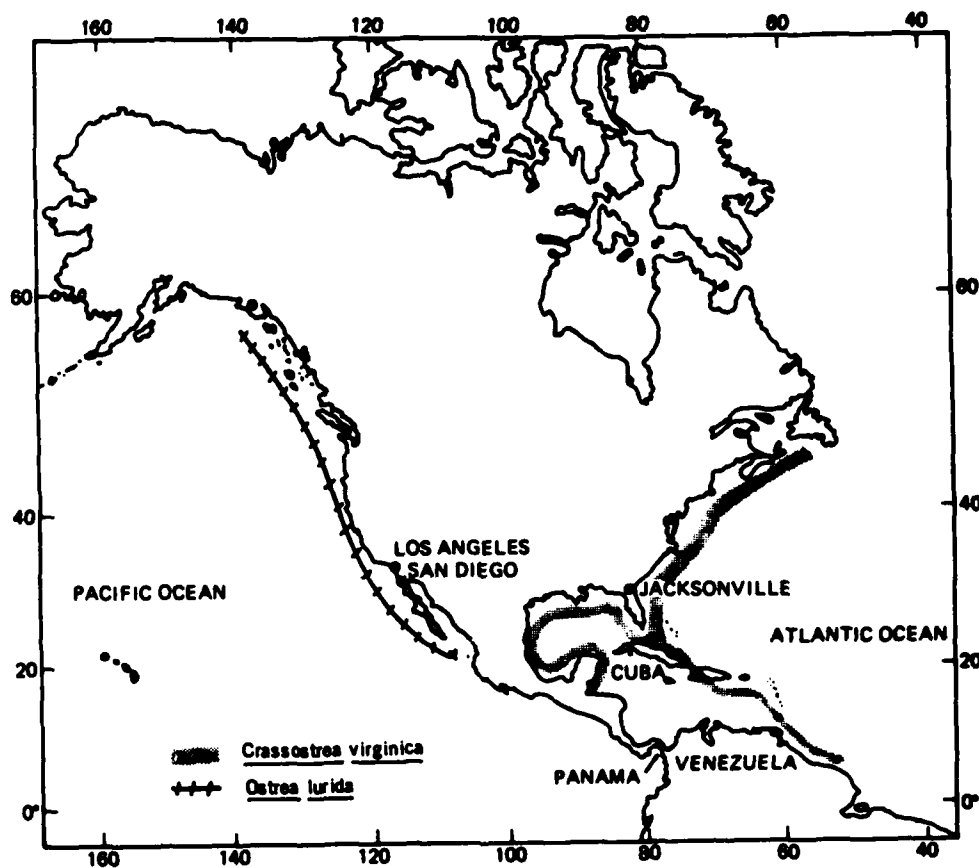


Figure 2-6. Oyster distribution patterns in North America (adapted from Ahmed 1975)

41. Ridge-shaped reefs of the edible oyster, *Crassostrea virginica*, characteristically develop from shell clusters at favorable shoreline or nearshore positions, growing out into passing currents and elongating at right angles to it. Branching or curving of the reef may occur as the current is deflected by the reef extension (Grave 1901, 1905) (Figure 2-7). Another class of reefs forms along a channel margin

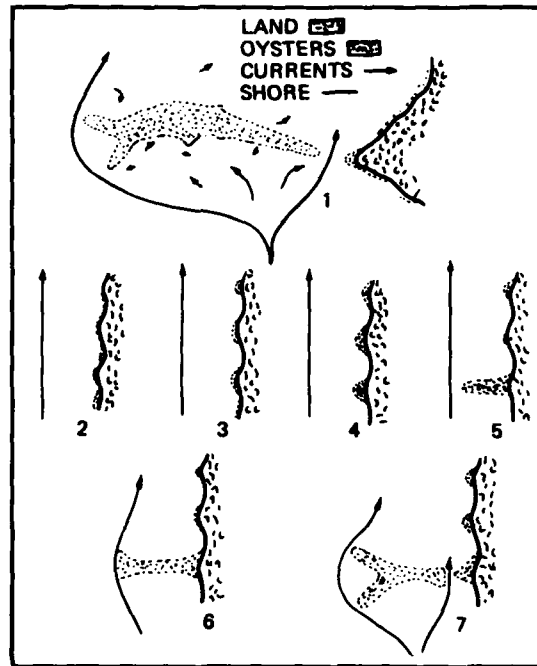


Figure 2-7. Oyster reef development in relation to current/tidal flow direction in a North Carolina estuary (after Grave 1901)

and elongates parallel to the dominant currents of the channel. Paired reefs of this type are common to many inner waterbodies such as central San Antonio Bay, Texas; Georgia tidal rivers; and the lower James River, Virginia. The characteristic reefs of most Atlantic estuarine rivers appear to be elevated ridges on large oval to quadrate oyster beds (Price 1954). Oyster reefs found along rivers of the Gulf coast are primarily restricted to their immediate banks (Price 1954).

42. Reefs along the gulf coast have been reported to exhibit a total shell depth of 18 ft or more, along with several interbedded layers of mud. Reefs in Texas bays may reach lengths of 1 to 2 miles, while a few have been reported at 4 to 5 miles in length. The longest oyster reef complex ever known was reported from Atchafalaya Bay, Louisiana, and was some 25 miles in length (Price 1954); this reef is no

longer viable due to altered hydrologic conditions from Mississippi River Channel diversion. Oysters have a wide distribution in estuaries from seawater (35 ‰) to oligohaline (3 ‰) zones and are found in a wide range of depths, with many reefs particularly well developed in the intertidal zone. They generally exhibit higher growth rates in higher salinity waters. Their distributions within estuaries are largely limited by predator pressure and diseases. Most predators are relatively stenohaline. Major oyster predators, such as the gastropods *Thais* spp. and *Urosalpinx* spp., have a lower salinity tolerance of 8 and 10 ‰, respectively (Gunter, Ballard, and Venkataramiah 1974). Other significant predators such as the stone crab (*Menippe mercenaria*), the boring clam (*Nartesia*), and the boring sponge (*Cliona celata*) are also distributed primarily in the higher salinity areas (Gunter, Ballard, and Venkataramiah 1974). Periods of high salinity coupled with high temperatures may result in mass mortality from the protozoan, *Perkinsus marinus* (Mackin 1951, Overstreet 1978). An oyster pathogen severely infecting oysters in the lower Chesapeake Bay and Delaware Bay is the sporozoan *Minchinia nelsoni* (or MSX). This disease causes high mortalities and has sharply reduced the size and distribution of oyster beds in the affected areas, although this pathogen also appears to have a lower salinity tolerance of 15 ‰.

43. Oysters provide a large substrate and habitat for epifaunal community associates. Bahr (1974) estimated that a minimum of 50 m<sup>2</sup> of surface area was available for epifaunal habitation for every square meter of reef area. Studies of oyster reefs have shown them to be faunally diverse communities (Figure 2-8). Wells (1961) has described some 303 invertebrate species associated with oyster reef habitats in the Newport River estuary, North Carolina.

44. The blue mussel, *Mytilus edulis*, may also form enormous reefs, especially at northern latitudes, where it hangs on the rocky substrates.

#### Coral reefs

45. Carbonate coral reef environments represent one of the most structurally complex and faunally and floristically diverse and



Figure 2-8. Oyster Community (after Hedgepeth 1953)

productive ecosystems on earth (Figure 2-9). Odum and Odum (1955), in a comprehensive study of the coral reef structure and function of a windward Pacific reef community, found the mean annual standing crop biomass of primary producers to be  $703 \text{ g/m}^2/\text{year}$ ; herbivores,  $132 \text{ g/m}^2/\text{year}$ ; and carnivores,  $11 \text{ g/m}^2/\text{year}$ . The primary production rate of the coral reef community was estimated at  $8760 \text{ g/m}^2/\text{year}$  (production-to-biomass (P/B) ratio = 12.5), although the net production is relatively low due to the high metabolic requirements (production-to-respiration ratio (P/R) = 1) of the community. Sessile benthos which are the structural, dominant species in coral reef communities are primarily autotrophic, and there are relatively few heterotrophic plankton feeders other than coral polyps (Odum and Odum 1955). Stony corals (Scleractinia and Hydrozoa) are major contributors to the calcium carbonate reef deposits, although calcareous red algae (Lithothamnium) may be of equal or greater importance, especially on the seaward side of the reef, where



Figure 2-9. Marine invertebrates inhabiting a coralline stone, illustrating the diversity of animals in coral reef habitats (from INVERTEBRATE ZOOLOGY by Robert D. Barnes. Copyright (c) 1980 by Saunders College/Holt, Rinehart and Winston. Copyright (c) 1963, 1968, 1974 by W. B. Saunders Company. Reprinted by permission of Holt, Rinehart and Winston, CBS College Publishing)

they are better able to tolerate the pounding surf (Odum 1971). It has been suggested (Odum 1971) that perhaps coral reefs could be more correctly referred to as "coral-algal reefs." The intimate association of the animal coral polyp with its symbiotic plant associate (Zooxanthellae) living within enables hermatypic (corals with symbiotic Zooxanthellae) or reef building corals to be essentially self-sustaining ecosystems (Johannes et al. 1970; Franzisket 1964; and Goreau, Goreau, and Goreau 1979). Reef-building corals (hermatypic) are found on the southeastern shores of the Americas, typically from Miami, Florida, southwest to the Dry Tortugas; the Caribbean Island, including Puerto Rico and the Virgin Islands; and the Pacific Islands, including Hawaii. Coral reef habitats are less common off the western shores of the Americas, and California and western Mexico have no extensive reef formations due to generally cooler waters. A few westward extensions of the West Indian reef system have been described from provinces or "salt domes near the shelf break" (Hedgepeth 1954, Bright et al. 1976) seaward of Texas and Louisiana in the northern Gulf of Mexico, known as the "Flower Garden Banks." To date some 253 invertebrate species and 103 fish have been described from this peculiar reef system. Reefs off Florida support an extremely diverse community of invertebrates, fish, and algae.

46. Coral reef habitats are stenotopic, delicately balanced ecosystems. Dominant coral reef species generally require stable temperatures, uniform salinities, and clear water, and surrounding waters usually exhibit low nutrient levels. Temperature ranges are critical for reef-building corals, and coral reefs are only found within a range of 16° to 36° C (Smith 1971). Optimum growth occurs within a narrow temperature range of 23° to 25° C. The observed critical salinity range for reef corals is 24 to 40 ‰, although reefs are generally found in oceanic salinities of 35 ‰. Corals may be exposed to temporary salinity reductions and physical abrasion after tropical storms and hurricanes. Reef-forming corals are generally restricted to depths of 90 m or less (Smith 1971; Goreau, Goreau, and Goreau 1979), and vigorous growth is generally limited to within 30 m of the surface. These corals

require high light intensities to support and maintain the symbiotic Zooxanthellae. Moreover, the fouling of reefs with sediment is particularly harmful to the delicate organisms making up the coral community, as their ability to remove sediment deposited on them is quite limited (Grigg 1970; Goreau, Goreau, and Goreau 1979). For this reason, and because of intolerances to salinity and temperature stresses, they are not as well developed in embayments and nearshore on the western Atlantic and gulf coasts. Reefs are generally located on the windward side of shorelines. The reefs of Florida and Hawaii are usually described as fringing reefs, although they differ somewhat from this definition. Florida's reefs are more aptly named bank reefs, built upon a shallow sea platform which was once the bottom of a shallow sea covering the southeastern portion of the United States (Smith 1971).

#### Worm reefs

47. Worm reefs are formed by massive colonies of polychaetes in the family Sabellariidae, which have a wide distribution on both east



Figure 2-10. Semischematic diagram of *Phragmatopoma lapidosa* Kingberg (after Kirtley and Tanner 1968)

and west coasts as well as the Gulf of Mexico (Figure 2-10). However, reef forming sabellarids are generally more commonly found in subtropical to tropical waters along the Atlantic Coast and the Gulf of Mexico, including the Virgin Islands and Puerto Rico. A sabellariid worm reef has also been reported from Delaware Bay (Wells 1970, Curtis 1978), although the polychaete forming this reef, *Sabellaria vulgaris*, does not form reefs throughout most of its geographical range, except off the north Florida Atlantic Coast (Figure 2-11). Reefs are constructed by large colonies of sabellariid worms living within individual tubes constructed of cemented sand grains. When found in estuaries they are generally restricted to higher salinity areas near the mouth, with sufficient current or wave activity and suitable sized particles for tube building. Scattered worm reefs reported from Baffin Bay, Texas, are of interest due to the high salinities of up to 80 ‰ reported from this hypersaline estuary (Hedgpeth 1954). Worm reefs are recognized as being an effective protection against beach erosion. Sabellariid reefs are known to occur between lat. 72° N and 53° S, and their widespread distribution indicates their stability potential along modern coastlines. The distribution of sabellariid reefs along the Florida coast are indicated by Figure 2-11. Because these animals depend on water turbulence for tube-building materials, food, and removal of metabolic wastes, the size and shape of the reefs is dependent upon prevailing local wave energy levels and water mass circulation properties (Kirtley and Tanner 1968). Littoral sabellariid reefs are found in belts of 100 m or more in width, lying parallel to the shoreline in elongated bands which are often cut by numerous surge channels; or they are found as rounded mounds (Figure 2-12). They are commonly found in depths of up to 5-10 m, although most are confined to depths of several meters (Multer and Milliman 1967). These reefs generally do not support as rich and diverse a fauna as do coral or mollusk (oyster/mussel) reefs.

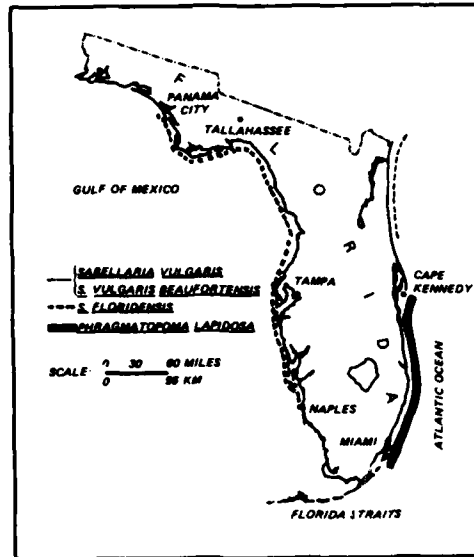


Figure 2-11. Distribution of sabellariid worm reefs along the Florida coast (after Kirtley and Tanner 1968)

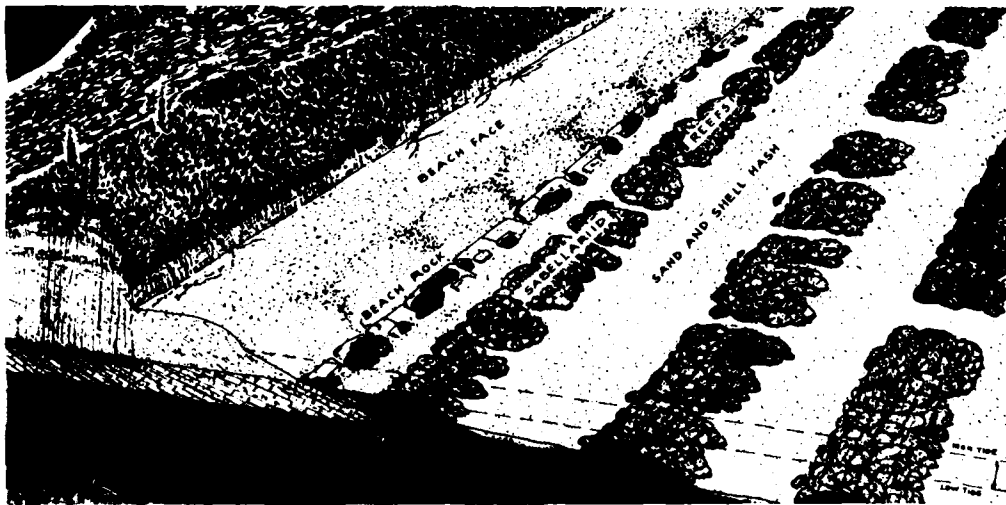


Figure 2-12. Schematic drawing showing the shape and distribution of sabellariid reefs (after Kirtley 1966)

### PART III

#### HABITAT DESCRIPTORS

48. The following chapter discusses the important measurable habitat parameters structuring estuarine and marine benthic habitat types in terms of their potential influence on the composition, density, and secondary production of benthic macroinvertebrates. Because of their importance, water quality descriptors such as salinity and temperature will be discussed separately in this report. Other water quality parameters, such as dissolved oxygen, turbidity, and general pollution, will be discussed in paragraphs 71 through 81 under the heading Water Quality. The important habitat descriptors in the estuarine and marine system are: (a) salinity, (b) substrate quality, (c) vegetation quality, (d) temperature, (e) current velocity, (f) depth, and (g) water quality.

#### Salinity

49. The significance of a water quality factor such as salinity in structuring benthic communities diminishes in coastal marine environments, while it is of major importance in estuarine environments. Salinity is regarded as a major factor delimiting the distributions of organisms along the axis of an estuary in every habitat class from freshwater to open-ocean salinities (Gunter, Ballard, and Venkataramiah 1974). Estuaries may be classified as homeohaline or poikilohaline, based on the relative magnitude of salinity fluctuations over a tidal cycle or between seasons at any given location within an estuary from limnetic (freshwater) to euhaline (seawater) zones. The rate and frequency of change of salinity in turn, dramatically affects the observed distribution of species along the salinity gradient (halocline), based on an individual species ability to tolerate the range of salinities encountered (Figure 3-1). Benthic faunas have been classified into ecological categories based on their observed distribution patterns in estuaries (Day 1967, Carriker 1967,

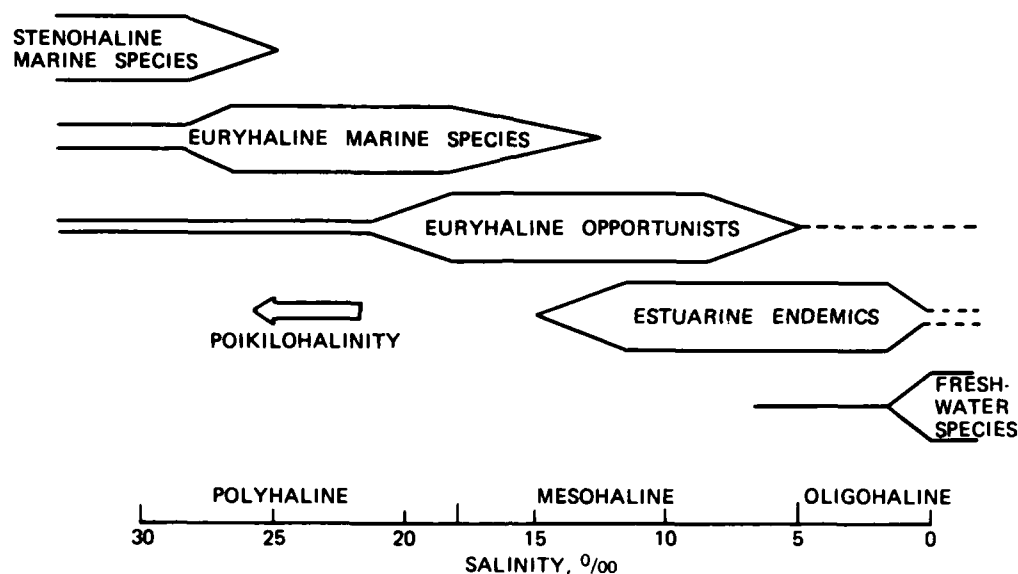


Figure 3-1. Schematic of the faunal and floral distributional classes along the halocline of a homeohaline estuary (after Boesch 1977b)

Boesch 1977b). These categories are as follows:

- a. Stenohaline marine. Marine species largely restricted to waters of high, relatively stable salinities near the mouth of the estuary.
- b. Euryhaline marine. Marine species exhibiting fairly broad salinity tolerances and distributions throughout an estuary.
- c. Euryhaline opportunistic. Marine species capable of exploiting environments where environmental stress is high (variable salinity, temperature, dissolved oxygen) and biotic interaction is generally low. This group is usually more abundant in salinities of 10-20 ‰, or in shallow habitats subject to frequent disturbance.
- d. Estuarine endemic. Organisms evolved from marine forms, but now restricted to estuaries and never found in the sea.

- c. Freshwater. Comprised of a few salt-tolerant examples of freshwater species derived from rivers, and restricted to low-salinity areas (upper reaches) of estuaries.
- f. Migratory. A variety of actively motile species (portunid crabs, shrimp, etc.), which move in and out of an estuary on feeding and spawning migrations.

50. In homeohaline estuaries, the salinity fluctuations are relatively stable and well defined over time, occurring around the boundaries of the "Venice Classification System," as depicted in Figure 3-1. Biotic distribution discontinuities or zones of more abrupt biotic change generally coincide within salinity limits of 30, 18, 5, and 0.5 ‰ for homeohaline estuaries. Therefore, faunal changes along the salinity gradient within homeohaline estuaries are gradual and relatively uniform along the axis of the salinity gradient, with a well-defined zonation of species from stenohaline marine to limnetic. A study by Boesch (1977b) of the Chesapeake Bay, a homeohaline estuary, showed a gradual and relatively constant change in macrobenthic species abundance along the salinity gradient, with somewhat accelerated changes occurring within the 20-15 ‰ range and in the 8-3 ‰ range, coinciding very closely with the Venice system.

51. The initial Classification scheme proposed by Carriker (1967) based on the "Venice System" for relatively homeohaline estuaries, has been modified by Boesch (1977b) to also include poikilohaline-type estuaries (Figure 3-1). In tidally and seasonally poikilohaline estuaries, the rate of change and magnitude of salinity fluctuations occurring within a reach or entire estuary do not fit into the classic "Venice System" salinity ranges. The degree of poikilohalinity, or rate and magnitude of salinity change, limit the distribution of stenohaline species (marine and freshwater). Lower limits of salinity tolerance delimit the distribution of faunas along the salinity gradient, and estuarine endemic and euryhaline opportunistic species will generally exhibit a much wider range of distribution in tidally and seasonally poikilohaline estuaries compared with homeohaline estuaries. For this reason the Venice Classification System as originally proposed

(Carriker 1967) is inappropriate for poikilohaline-type estuaries, and Boesch's (1977b) scheme is more appropriate. The terms poikilohaline and homeohaline may also be used to describe portions of an estuary based on the observed range of salinity changes over time for any given reach of an estuary. Faunal distribution patterns for any given location or reach of an estuary are generally limited by tidally and seasonally minimum salinity conditions rather than by average salinities (Boesch 1977b).

52. Salinity has also been shown to affect the infaunal and epifaunal components of the benthic fauna somewhat differently, as substrate (unconsolidated sediments) may moderate the short-term fluctuations in salinity. This causes the sediment interstitial salinity environment of the infauna to fluctuate less than the water column salinity environment of the epifauna (Sanders, Mangelsdorf, and Hampson 1965). These two benthic faunal components are recognized as being ecologically distinct (Thorson 1957).

53. Marine coastal environments on the other hand exhibit a much smaller range of salinity fluctuation compared to estuarine environments. Salinity fluctuations are closely linked by proximities to major river mouths (Emery and Uchupi 1972). Figure 3-2 shows the average monthly salinity and temperature fluctuations for seven coastal shelf stations. Small-scale changes in salinity are generally a response to seasonal river discharge rates, precipitation (storm) cycles, and temperature-regulated evapotranspiration. Changes in salinity are relatively small and decrease with increasing distance from river mouths as influences of river runoff diminish. Figure 3-3 shows the latitudinal salinity distribution and its relationship to precipitation minus evaporation. Figure 3-4 depicts the vertical (depth) and monthly distribution of salinity for five areas on the northwestern Atlantic shelf. It shows that salinities are generally much more stable near the bottom relative to the surface and usually vary little more than 1 ‰ over an annual cycle. Therefore, salinities encountered in marine coastal environments may only be critical to benthic habitats during exceptionally severe storms such as hurricanes, or in nearshore

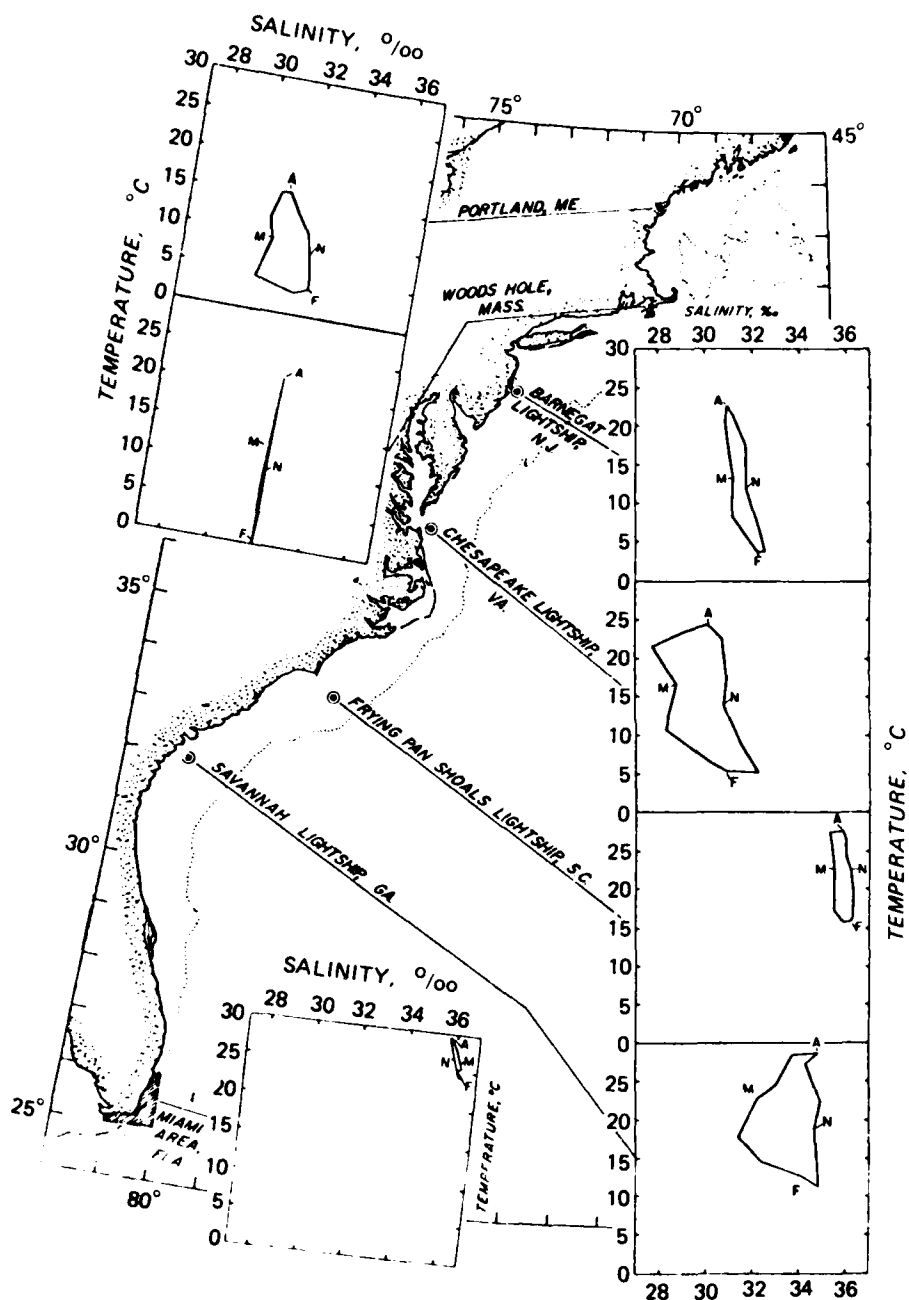


Figure 3-2. Polygons showing average salinities and temperatures at seven hydrographic stations in the northwestern Atlantic; M = May, A = August, N = November, and F = February (after Emery and Uchupi 1972)

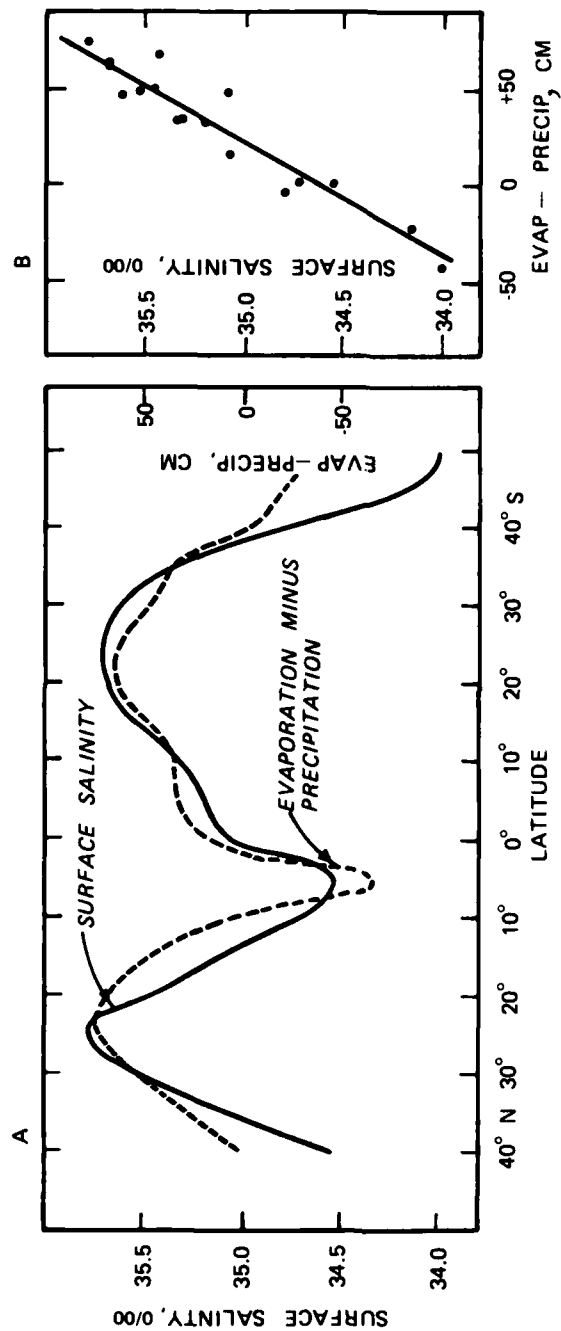


Figure 3-3. (A) Plots of (1) average surface salinity for all oceans and (2) the difference between evaporation minus precipitation, plotted against latitude. (B) A plot of the relationship between surface salinity and the difference between evaporation minus precipitation (after Sverdrup, Johnson, and Fleming 1942)

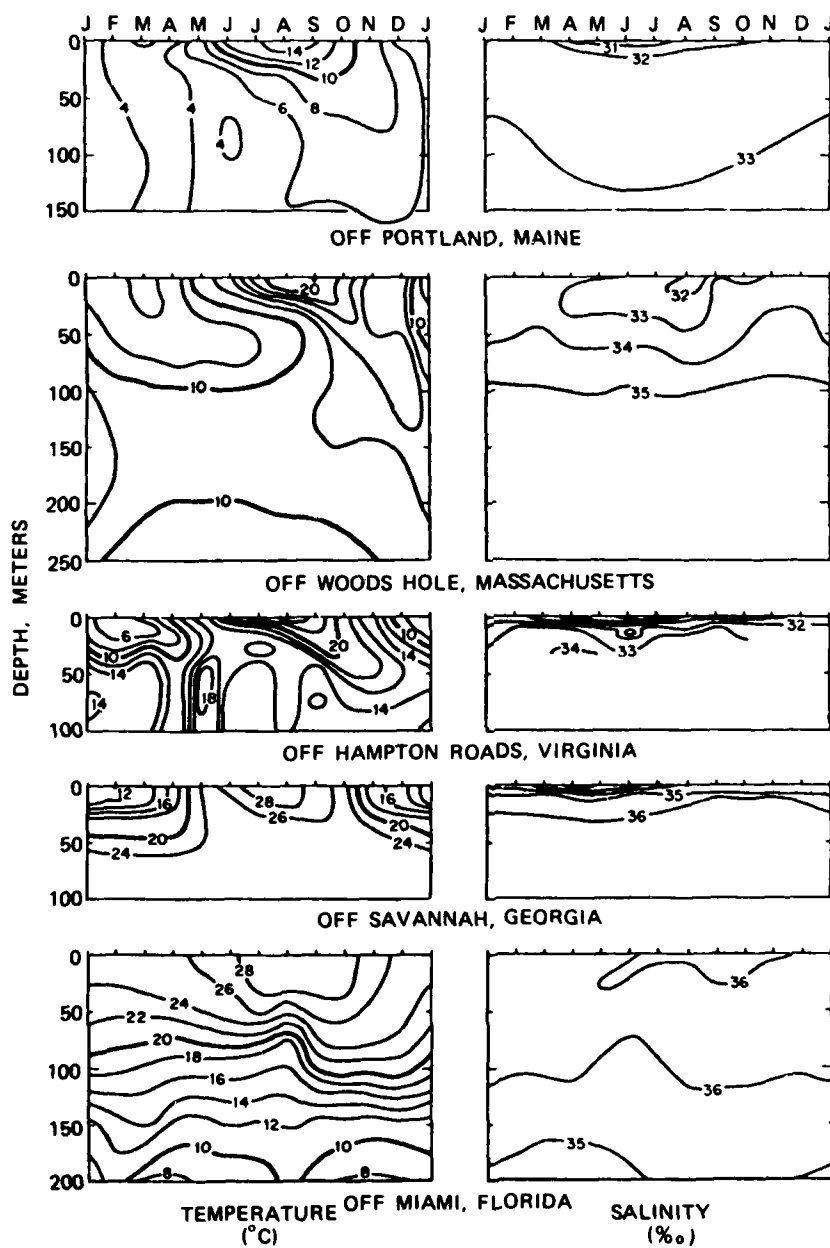


Figure 3-4. Vertical (depth) temperature ( $^{\circ}\text{C}$ ) and salinity ( $^{\circ}/\text{oo}$ ) profiles over time showing the seasonal/depth shifts in temperature and salinity from five areas on the northwestern Atlantic continental shelf (hydrographic stations depicted on map in Figure 3-2) (after Emery and Uchupi 1972)

areas subject to river mouth influences, or in areas affected by major currents like the Gulf Loop current.

54. The following discussion will summarize the effects of salinity within each estuarine benthic habitat type.

- a. Unconsolidated soft bottom habitats. Soft bottom communities are comprised of infaunal and epifaunal species. Sediments moderate or dampen short-term salinity fluctuations caused by tidal circulation or meteorological events, thereby creating a more hospitable environment for infaunal communities during short-term oscillations in salinity in overlying waters. Sediment interstitial salinities are in turn dependent to a large extent on grain-size composition (clay, silt, sand) because sediment porosity markedly influences the diffusion rate of water into and out of the sediments. Epifaunas living on the surface of unconsolidated soft bottom habitats are subjected to the full range of salinity fluctuations during a tidal cycle or storm event, and are more likely to encounter unfavorable salinities, especially in poikilohaline reaches of estuaries (Sanders, Mangelsdorf, and Hampson 1965; Burbanck and Burbanck 1967). This would explain the relatively impoverished epifaunas in mesohaline (5-18 ‰) and oligohaline (0.5-5.0 ‰) environments where salinity fluctuations are highest. In poikilohaline estuarine systems, the number of epifaunal species generally drops at a faster rate along the gradient of increasing salinity fluctuations, compared to infaunal species (Sanders, Mangelsdorf, and Hampson 1965). Nevertheless, the richness of total infaunal and epifaunal species decreases markedly along the salinity gradient from high to low salinity. Figure 3-5 illustrates the observed species richness, faunal density, and magnitude of tidal salinity change along the axis of a Georgia river estuary within sand bottom habitats. Figure 3-6 illustrates a similar gradient of species richness for individual taxa as a function of salinity along the axis of a tidally poikilohaline estuary. Stenohaline marine taxa such as echinoderms and bryozoans are quickly extinguished from the fauna, while all taxa show decreased species richness as salinity decreases. The obvious trend is one of decreasing species richness with increasing poikilohalinity and decreasing salinity. Similar faunal gradients of decreasing species in the mesohaline zone relative to the polyhaline zone have also been found in soft bottom habitats of the homeohaline Chesapeake Bay System (Boesch 1972, Nilsen et al. unpublished). Apparent observations of decreased total faunal abundances in the

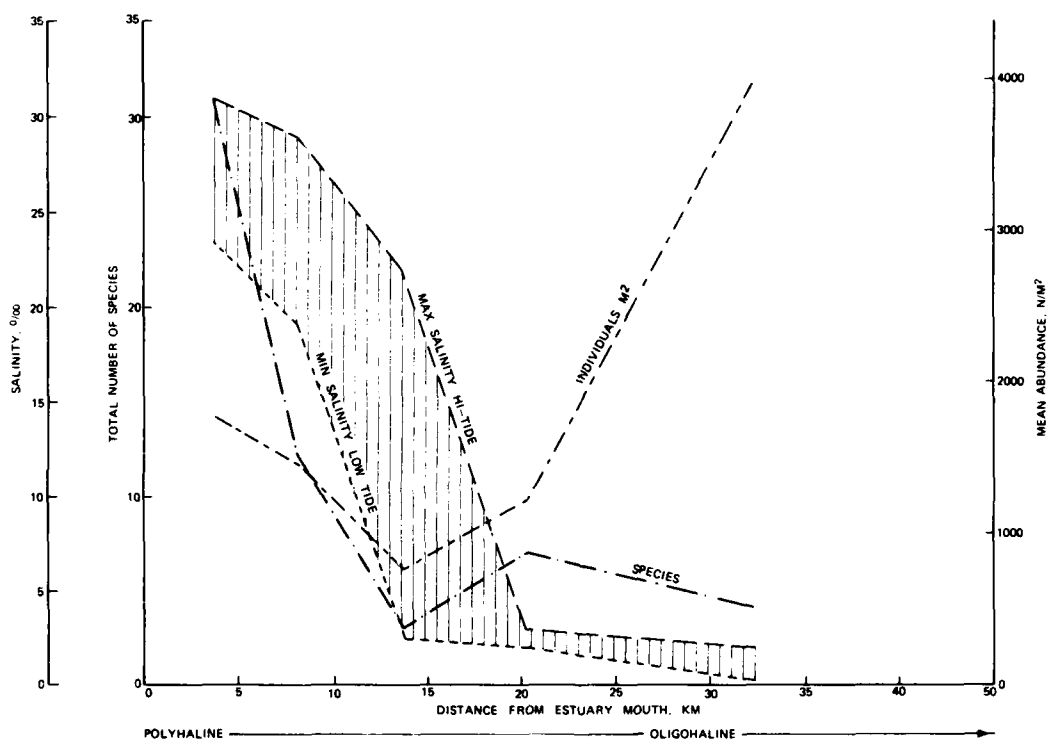


Figure 3-5. Macrobenthos distribution patterns in sand habitats (point bars) in the Ogeechee River Estuary, Georgia, along a halocline (after Howard, Elders, and Heinbokel 1975)

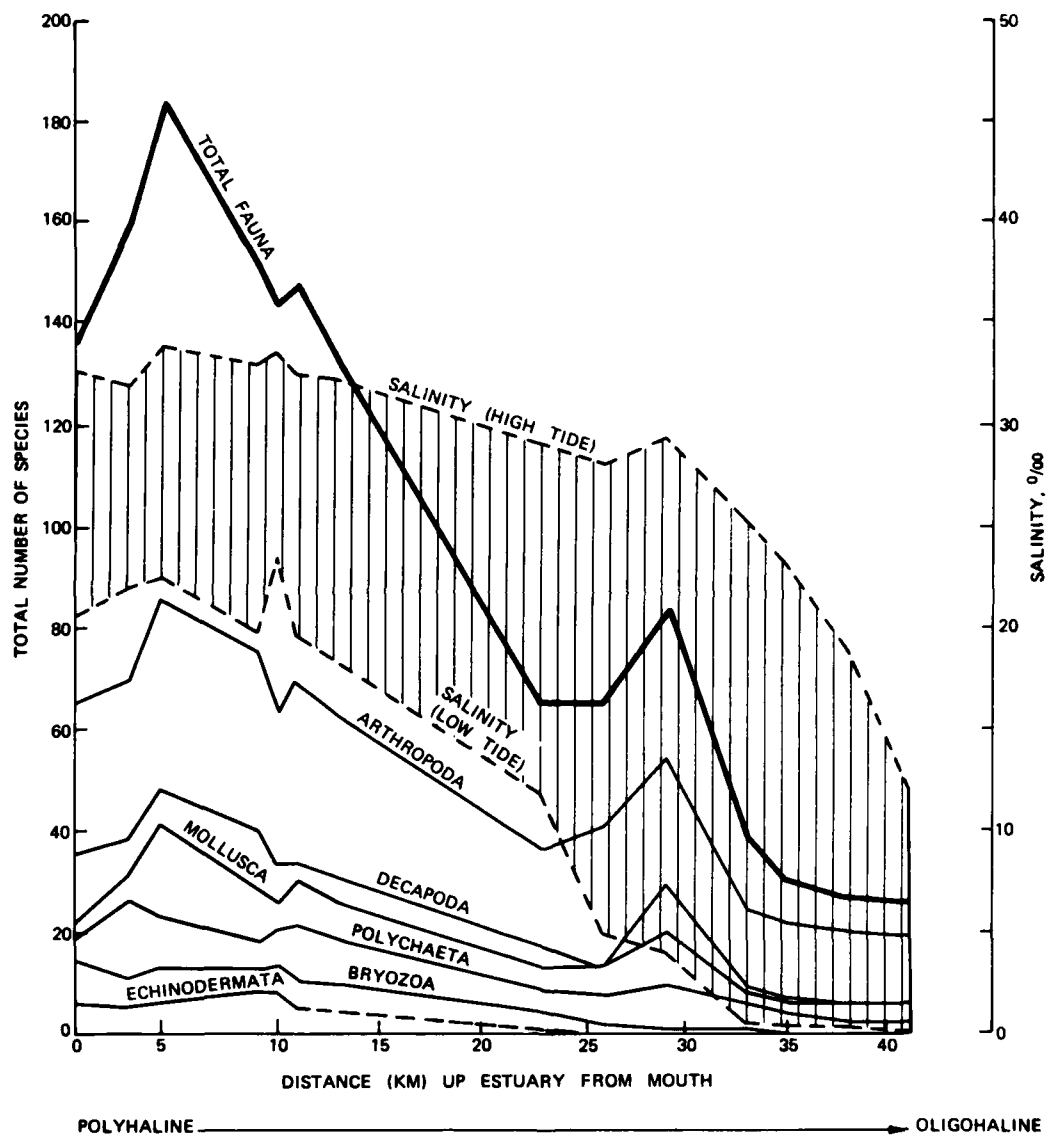


Figure 3-6. Macrobenthic invertebrate distribution along a salinity gradient in a poikilohaline estuary, Georgia (data from Howard and Frey 1975)

mesohaline zone depicted in Figure 3-5 may be an artifact of that particular study (Howard, Elders, and Heinbokel 1975) rather than a generally observed correlation; as other studies have shown no such trend (Boesch 1972, Kendall 1974,\*).

- b. Submerged aquatic vegetation habitats. The discussion of submerged aquatic vegetation habitats (paragraphs 28-32) showed that salinity was an important factor in delimiting the habitat boundaries of each vegetation type. Macrobenthos associated with vegetated habitats are in turn influenced by fluctuations in salinity along the axis of a habitat. Only a few studies have addressed the impact of variable salinity on macrobenthic communities from vegetated habitats. Figure 3-7 illustrates one such study for seagrass *Halodule wrightii* in the subtropical Indian River estuary, Florida (Young and Young

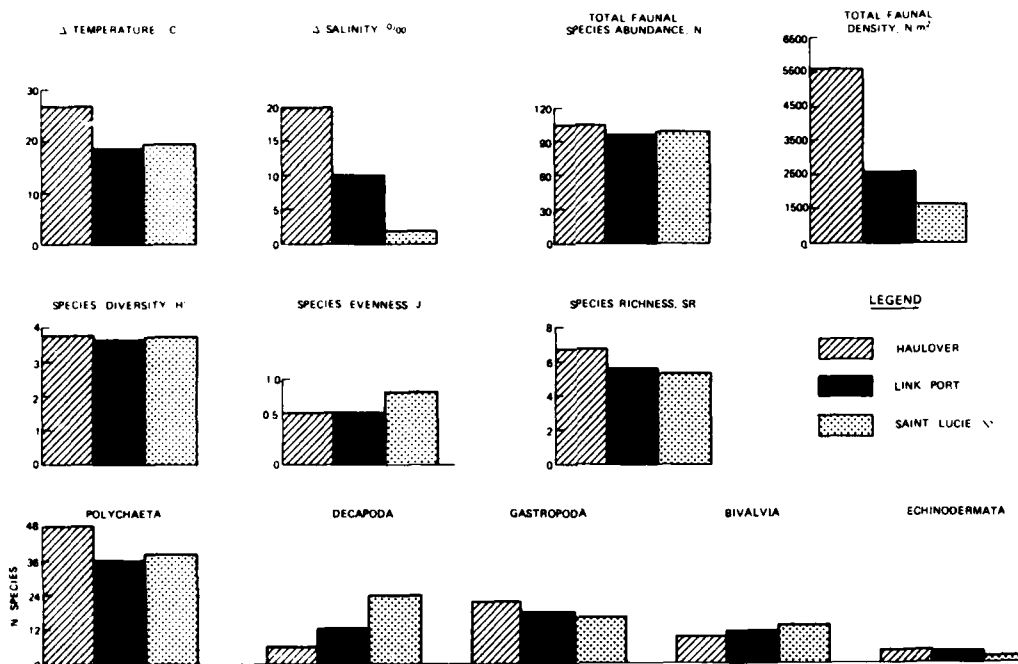


Figure 3-7. Effects of environmental stress (salinity and temperature) on uncaged areas of subtropical seagrass bed macrobenthic communities (data from Young and Young 1977). Note: see Pielou (1966a) for the equation used to derive species diversity ( $H'$ ), Margalef (1958) for the equation for species richness (SR), and Pielou (1966b) for the equation for species evenness ( $J'$ )

\* Personal Communication, 1981, D. F. Boesch, Director, Louisiana Universities Marine Consortium, Chauvin, La.

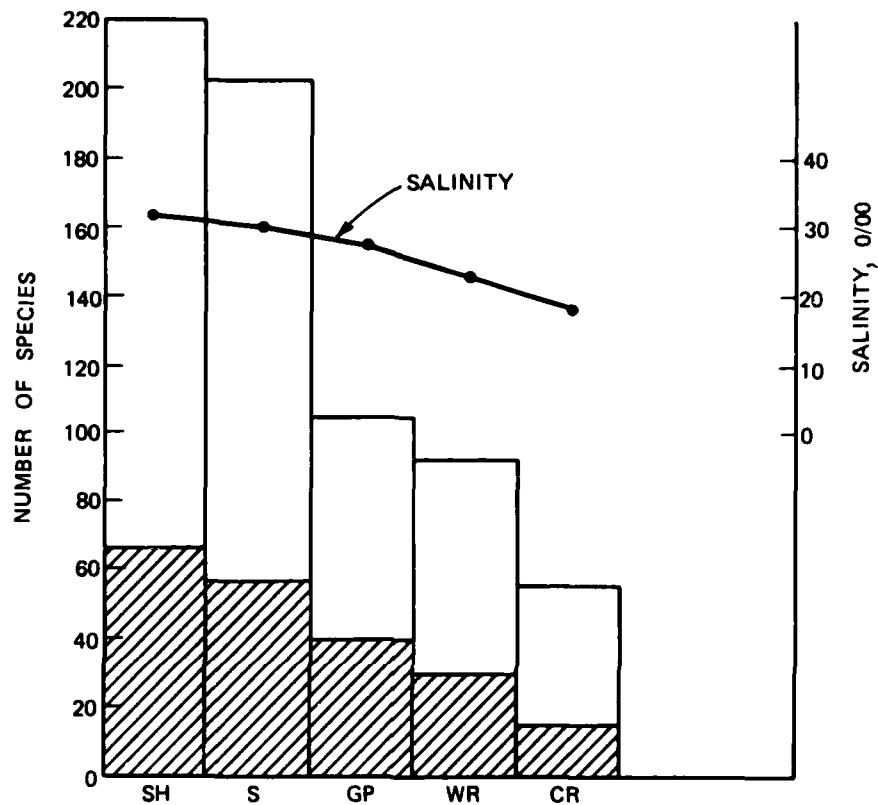
1977). This study showed that in the seagrass habitat stressed by variable salinity and temperature, the number of species and the values of indices for species diversity, evenness, and richness did not vary significantly from those of the more environmentally stable habitat; the structure of the community changed, however, favoring high densities of eurytopic opportunistic species at the environmentally stressed site (see Table 2-1). Note the subtle changes in the faunal composition at the three seagrass habitat sites, showing increased numbers of polychaete and gastropod species at the stressed site, while decapods and bivalves showed decreased numbers of species with increasing salinity and temperature stress. A study of eelgrass (*Zostera*) faunal species richness and abundance along an environmental gradient of fluctuating salinity and temperature by Orth (1973) showed decreased numbers of benthic infaunal species and generally decreased densities in lower salinity eelgrass habitats than in higher salinity habitats (Table 3-1). Subtle differences noted between the subtropical seagrass and temperate seagrass habitats from these two examples suggest caution should be exercised when attempting to extrapolate observed benthic community responses to environmental stresses (salinity and temperature) among similar types of seagrass habitats separated by large latitudinal ranges. Salinity-related impacts on community structure in seagrass habitats have been described by Orth (1974). He found lowered salinity levels following Tropical Storm Agnes (1972) caused marked reductions in faunal community structure in eelgrass beds.

Table 3-1  
Benthic Infaunas of *Zostera* Beds in the Chesapeake Bay-York River  
Estuary (Seasonal Distributions at Four Stations with  
Different Salinities (after Orth 1973))

| Station | Salinity<br>Range,* (‰) | Species (N) |        | Density (N/m <sup>2</sup> ) |        |
|---------|-------------------------|-------------|--------|-----------------------------|--------|
|         |                         | Spring      | Summer | Spring                      | Summer |
| A       | 19-24                   | 62          | 55     | 32,913                      | 14,725 |
| B       | 18-23                   | 56          | 50     | 24,333                      | 21,000 |
| C       | 16.5-22.5               | 48          | 42     | 8,696                       | 11,899 |
| D       | 12-20                   | 25          | 31     | 11,304                      | 4,754  |

\* Estimated from figure in Orth (1973).

- c. Reef habitat. Oyster reef habitats are widely distributed within estuaries between 35 and 3 ‰, although the most productive reefs are generally found in the mesohaline (5-18 ‰) to polyhaline zones (18-30 ‰) (Galstoff 1964). In some estuaries, such as Chesapeake Bay and Delaware Bay, outbreaks of oyster diseases (MSX, *Perkinsus*) and large predator populations may limit the oyster producing areas to salinities below 15 ‰. The distribution of benthos associated with oyster reefs clearly responds to salinity changes along the halocline of an estuary. A classic illustration of salinity effects on epifaunas and infaunas of oyster communities is shown in Figure 3-8 for the Newport River estuary in North Carolina (Wells 1961). Species abundance drops off sharply from euhaline to polyhaline/mesohaline environments. Freshets in the upper reaches of estuaries (<10 ‰) resulting from storms and/or abnormally high river inflows may cause high mortalities in oyster populations. A 6-week period of low-salinity water in the James River, Virginia, caused oyster mortalities approaching 90 percent in some oyster beds (Andrews 1973). Figure 3-9 shows a similar period of low-salinity water observed by Wells (1961) in the Newport River estuary after the passage of three hurricanes. This period of freshened water caused high mortalities in oyster community associates. Lowered salinity associated with large storm events may indirectly benefit oyster communities by temporarily ridding oyster reefs of stenohaline predators such as starfish and oyster drills (Wells 1961, Andrews 1973).
- d. Rock/hard bottom habitat. Epifaunas associated with estuarine rock/hard bottom habitats are generally similar in structure to those found in typical oyster reef communities, and a similar reduction in species abundance along the halocline of an estuary would be expected. Species recruitment to hard bottom habitats would also reflect the magnitude of the environmental stress. Figure 3-10 shows fouling community recruitment along an environmental stress gradient of increasing salinity and temperature fluctuations in a subtropical Florida estuary. The study shows a sharp reduction in fouling epifaunal species with decreasing salinities and increasing fluctuations in temperature and salinity (Mook 1980).



#### LEGEND

SH SHARK SHOAL

S SLUICEWAY

GP GALLANT POINT

WR WHITE ROCK

CR CROSS ROCK

▨ MEAN NUMBER OF SPECIES

□ TOTAL NUMBER OF SPECIES

Figure 3-8. Cumulative total and mean number of invertebrate species collected per sampling interval (monthly) and mean salinity for each oyster reef station in Newport River estuary, North Carolina (after Wells 1961)

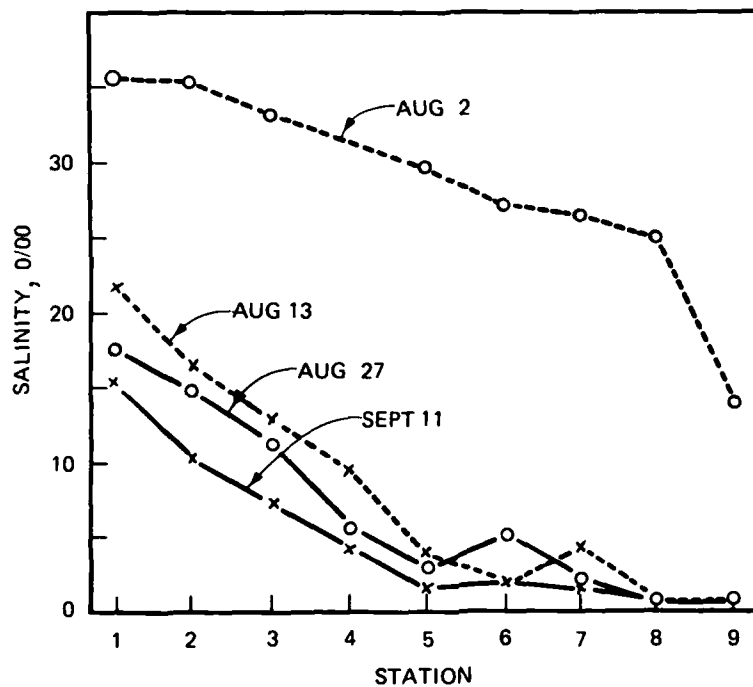


Figure 3-9. Salinity profiles from Newport River estuary, 1955. Hurricane Connie passed through on August 12, and Hurricane Diane on August 17 (after Wells 1961)

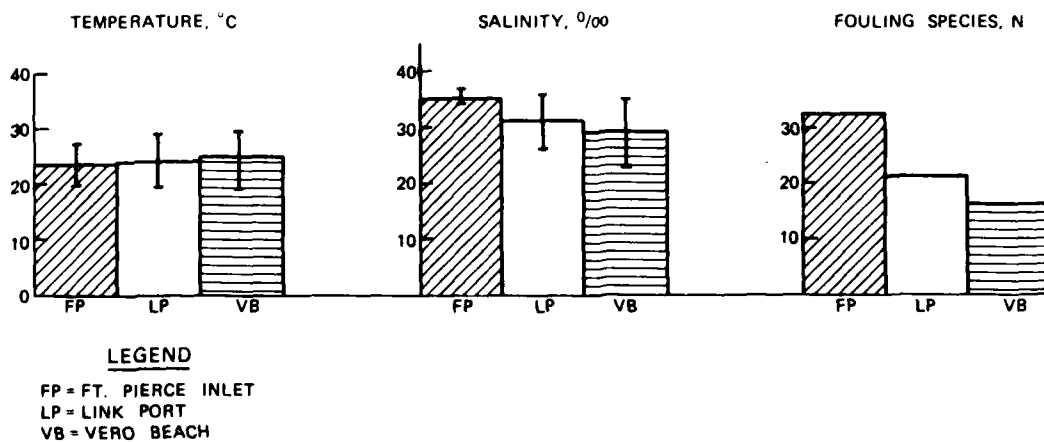


Figure 3-10. Fouling community settlement along an environmental stress gradient. Temperature and salinity are expressed as averages with ranges depicted (data from Mook 1980)

### Substrate Quality

55. Substrate quality parameters such as percent organic carbon, grain size distribution, sediment depth, shear strength, etc., are major factors influencing the distribution of marine benthic organisms (Peterson 1913; Jones 1950; Thorson 1955, 1957; Hedgepeth 1953) and have been demonstrated to be important factors for estuarine organisms as well (Sanders 1956, 1958, 1960; Rhoads and Young 1970; Young and Rhoads 1971; Wells 1957; Pratt 1953; Bloom, Simon, and Hunter 1972; McNulty, Work, and Moore 1962; Johnson 1970, 1972; Boesch 1973; Burbanck 1981). Although Muus (1967) has concluded that dominant estuarine benthic species are to a large extent eurytopic with respect to sediment type, many species and trophic groups show clear sediment affinities. Substrate composition and stability in unconsolidated and consolidated sediments will affect the types of benthos found on any particular bottom type. Substrates are vital as a source of attachment and as a food source for associated benthos. Sessile epifaunal benthos require consolidated, firm substrates for attachment. Burrowing, suspension feeding, and tube building infaunas modify the quality and may enhance the stability of unconsolidated sediments by binding inorganic and organic particles together as fecal pellets and pseudofeces, by the redistribution of sediments by feeding activities or tube building, and by the secretion of mucopolysaccharides (Fager 1964; Rhoads 1963, 1974). Benthic infauna may influence sediment stability and subsequent erodibility by reworking the near-surface sediment layers and increasing porosity due to subsurface burrowing activities (Biggs 1967; Rhoads 1974; Rhoads, Yingst, and Ulman 1978; Yingst and Rhoads 1978). The following discussion will illustrate the relationships between substrate and benthos within each habitat type.

- a. Unconsolidated soft bottom. Important sediment properties of soft bottom estuarine and marine sediments are particle size distribution, organic content and quality, and stability (shear strength). An important property of a sediment is its particle size distribution, which is a description or characterization of the sediment by discrete particle size classes as shown by the

Wentworth Grade Classification based on geometric class intervals (Table 3-2). A note of caution is in order concerning the mechanical analysis of sediments. Methods most frequently used are based on techniques borrowed from soil science that do not consider biological modifications of sediments following biogenic reworkings by deposit feeding and suspension feeding benthos (Rhoads 1974; Johnson 1974, 1977). Benthos may completely modify the physical characteristics of the sediment by binding silt and clay size particles into aggregate particles that behave as sand-size particles (McCall 1979, Levington 1977). Mechanical analyses of sediments destroy these aggregate particles and change the composition of the sediment to uniform unaggregated particles which may have little ecological meaning (Buchanan and Kain 1971; Morgan 1956; Rhoads 1974; Johnson 1974, 1977).

- (1) Sediments have been broken down into major qualitative (i.e., according to organic matter, carbon, calcium carbonate, and inorganic matter content) and particle size classes based on subjective and objective analyses. Pratt (1953) and Wells (1957) analyzed animal-sediment relationships in two estuaries based only on subjective visual/textural classification of sediments. Both found significant animal-sediment relationships using this approach (Figures 3-11 and 2-3). Objectively, particle size fractions of sediment may be classified into a sediment type using a classification scheme similar to Shepard (1954), whereby the three major size class fractions (clay, silt, sand) are plotted on a triangular graph, as shown in Figure 3-12.
- (2) The significance and quality of organic matter to organisms living in sediments cannot be ignored as it is utilized chiefly as food by deposit feeding benthos (Tenore 1975, 1977). Davis (1925), among others, felt that the association of various groups of animals with soils of particular textures is not so much influenced by the texture per se as by the food conditions of which the size of the soil particles is a correlated indication. Sanders (1956, 1958) suggested clay was the most valid sediment correlate for the distribution of deposit feeding organisms living on organic matter in or on fine-grained sediments (muds). Clays are much smaller than silt-size particles and therefore have a much larger surface area to bind organic matter serving as a primary source of food for deposit feeding benthos. Sanders (1956) found the largest populations of benthos in Long Island

Table 3-2  
Sediment Classification Schemes

| Sediment Particle Size Classification (after USEPA 1973) |                     |                                    |
|----------------------------------------------------------|---------------------|------------------------------------|
| Name                                                     | Particle Size<br>mm | U. S. Standard Sieve<br>Series No. |
| Boulder                                                  | >256                | --                                 |
| Rubble                                                   | 64-256              | --                                 |
| Coarse gravel                                            | 32-64               | --                                 |
| Medium gravel                                            | 8-32                | *                                  |
| Fine gravel                                              | 2-8                 | 10                                 |
| Coarse sand                                              | 0.5-2               | 35                                 |
| Medium sand                                              | 0.25-0.5            | 60                                 |
| Fine sand                                                | 0.125-0.25          | 120                                |
| Very fine sand                                           | 0.0625-0.125        | 230                                |
| Silt                                                     | 0.0039-0.0625       | 400                                |
| Clay                                                     | <0.0039             | Evaporate and weigh residue        |

Sediment Classification Using the Wentworth Scale\*\* with 2,  $\sqrt{2}$ , and  $\phi$   
Notation (After Buchanan and Kain 1971)

| Reduction (After Buchanan and Rahn 1977) |                                                |                  |        |
|------------------------------------------|------------------------------------------------|------------------|--------|
|                                          | 2 scale                                        | $\sqrt{2}$ scale |        |
|                                          | mm                                             | mm               | $\phi$ |
| Sand                                     | { 2<br>1<br>0.50<br>0.250<br>0.125             | 2                | -1     |
|                                          |                                                | 1.41             | -0.5   |
|                                          |                                                | 1                | 0      |
|                                          |                                                | 0.71             | +0.5   |
|                                          |                                                | 0.50             | +1.0   |
|                                          |                                                | 0.351            | +1.5   |
|                                          |                                                | 0.250            | +2.0   |
|                                          |                                                | 0.177            | +2.5   |
|                                          |                                                | 0.125            | +3.0   |
|                                          |                                                | 0.088            | +3.5   |
| Silt                                     | { 0.062<br>0.031<br>0.0156<br>0.0078<br>0.0039 | 0.062            | +4.0   |
|                                          |                                                | 0.044            | +4.5   |
|                                          |                                                | 0.031            | +5.0   |
|                                          |                                                | 0.022            | +5.5   |
|                                          |                                                | 0.0156           | +6.0   |
|                                          |                                                | 0.0110           | +6.5   |
|                                          |                                                | 0.0078           | +7.0   |
|                                          |                                                | 0.0055           | +7.5   |
| Clay                                     | { <0.0039                                      | 0.0039           | +8.0   |
|                                          |                                                | <0.0039          |        |

\* Standard sieves with 8- to 16-mm mesh are available.

\*\* Wentworth 1922.

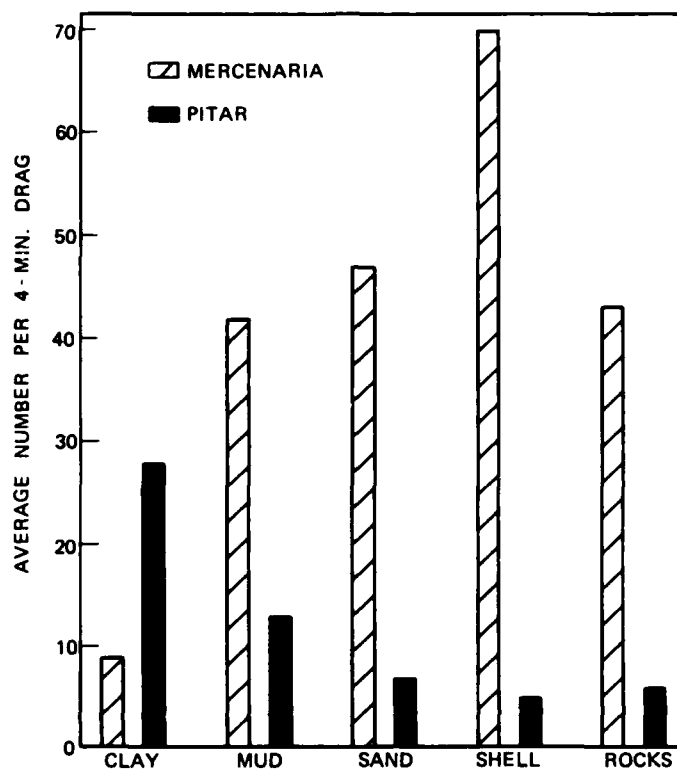


Figure 3-11. Abundance of two bivalve species as a function of sediment type (after Pratt 1953)

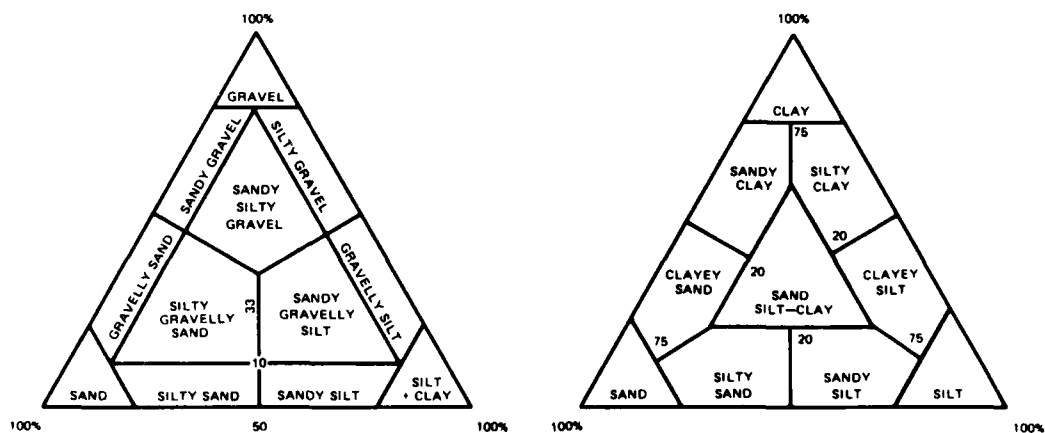


Figure 3-12. Triangular graphic methods of presenting data (after Buchanan and Kain 1971)

Sound in sediments with 13-25 percent silt and clay. Burbanck (1981) found higher dominance and lower species diversity and biomass in fine-grained sites than coarse-grained sediments in Delaware Bay. In carbonate sediments, clay may not be a good indicator of deposit feeding abundance, as illustrated by a recent study by Santos and Simon (1974). They compared deposit feeding polychaete distributions from carbonate sand bottoms in two seagrass and three unvegetated sand habitats in a subtropical Florida estuary and found no relationship between deposit feeding abundances and silt-clay content. Silt-clay levels were very low, 0.0-1.0 percent, although very high deposit feeding (polychaete) densities were found (averaging  $13,525/m^2$ ), three times those observed by Sanders in his study of Long Island Sound ( $4,430/m^2$ ). The high densities observed by Santos and Simon may have occurred because seagrass proximities to unvegetated sites provided a detrital food source (Figure 3-13). Levington (1977) attributed lower deposit feeding abundances in an unvegetated muddy-sand habitat in a Massachusetts estuary to resource (food) limitations. In estuarine unconsolidated soft bottom habitats, more or less optimum mixtures of clays, silts, fine sands, and organic matter support greater densities of macrobenthos than either clean coarse unstable sands and gravels at the mouths of estuaries or soft slurry muds in the quiet sheltered reaches of estuaries (Carriker 1967).

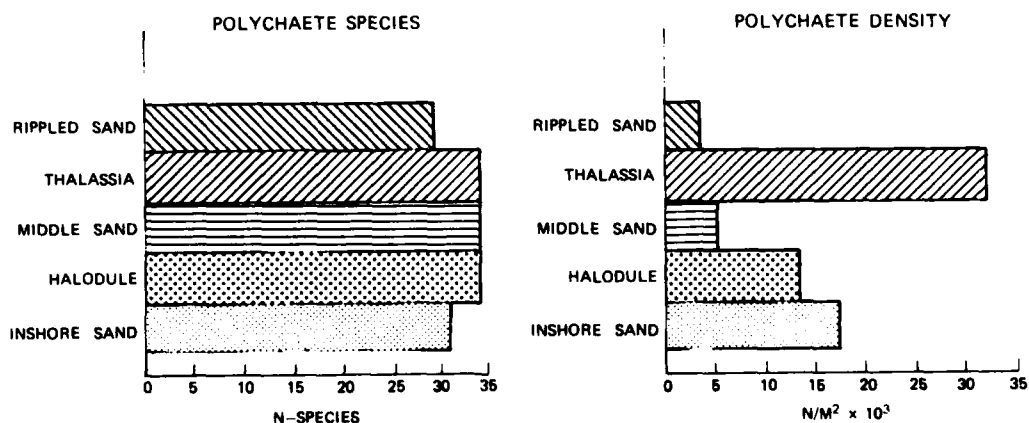


Figure 3-13. Interhabitat comparisons of infaunal polychaete structure (data from Santos and Simon 1974)

- (3) Extensive sampling of coastal marine shelf sediment environments from Nova Scotia to Mexico depicted in Table 3-3 gives some indication of qualitative changes in sediment encountered along a latitudinal gradient. Perhaps the most noticeable change found is in the relative amount of calcium carbonate material. The amount of biogenic calcium carbonate increases dramatically at lower latitudes near Key West, Florida, where it makes up an average of 55 percent of the sediments. Large rivers such as the Mississippi River make substantial contributions to shelf sediments as shown by Table 3-3, while sand makes up only 10 percent of the sediments in this region, the finer grain sizes comprising the bulk of the sedimentary material.
- (a) East, gulf, and west coast marine soft bottom textural gradients suggest there is a general increase in silt-clay and organic contents with increasing distance (depth) offshore, and a corresponding increase in sediment stability (Boone, Granat, and Farrell 1978; Emery and Uchupi 1972; Flint and Holland 1980). Substrate texture changes were closely linked with macrobenthic community structure changes in a transect study of benthic communities on the southern California continental shelf by Barnard and Hartman (1959). They identified three sediment texture/depth zones: sand (42-72 ft), silty-sand (90-150 ft), and mud (180-360 ft). Highest macrobenthic standing crops were found in the silty-sand habitats with mean biomass estimates of  $1370 \text{ g/m}^2$  (wet weight); decreasing shoreward and seaward in the other two substrate types, due to benthic community structure changes. However, textural gradients may vary substantially due to local sediment sources, currents, and bathymetry. Observed quantitative distributions of macrobenthos from different sediment types indicate that sediment quality does influence the standing crop of benthos, but that the relationships are complex and contradictory in some instances. Table 3-4 shows the observed standing crop biomass averages for nine sediment types ranging from gravel to clay within three latitudinal ranges. It can readily be seen that the observed distributions of benthos standing crop were not uniform with latitude or sediment type. Moreover, silty-sand

Table 3-3  
Average Properties of Shelf Sediments: Nova Scotia to Mexico  
(after Emery and Uchupi 1972)

|                               | Nova Scotia<br>to New York           | New York to<br>Cape Romain | Cape Romain<br>to Key West | Key West to<br>Mississippi<br>River | Mississippi<br>River to<br>Mexico |
|-------------------------------|--------------------------------------|----------------------------|----------------------------|-------------------------------------|-----------------------------------|
|                               | <u>Physical Composition, percent</u> |                            |                            |                                     |                                   |
| Sand                          | 65.0                                 | 100.0                      | 100.0                      | 91.0                                | 10.0                              |
| Silt                          | 2.0                                  | 0.0                        | 0.0                        | 0.0                                 | 0.0                               |
| Clay (<4μ)                    | 1.0                                  | 0.0                        | 0.0                        | 0.0                                 | 0.0                               |
| Silty clayey sand             | 5.0                                  | 0.0                        | 0.0                        | 3.0                                 | 26.0                              |
| Clayey sandy silt             | 5.0                                  | 0.0                        | 0.0                        | 6.0                                 | 13.0                              |
| Sandy silty clay              | 8.0                                  | 0.0                        | 0.0                        | 0.0                                 | 25.0                              |
| Sand-silt-clay                | 14.0                                 | 0.0                        | 0.0                        | 0.0                                 | 26.0                              |
|                               | <u>Chemical Composition</u>          |                            |                            |                                     |                                   |
| Calcium carbonate,<br>percent | 1.8                                  | 2.5                        | 17.8                       | 55.0                                | 6.3                               |
| Organic carbon,<br>percent    | 0.49                                 | 0.19                       | 0.16                       | 0.25                                | 0.53                              |
| Kjeldahl nitrogen,<br>percent | 0.097                                | 0.023                      | 0.030                      | 0.037                               | 0.070                             |
| Carbon/nitrogen<br>ratio      | 5.0                                  | 8.1                        | 5.2                        | 6.9                                 | 7.5                               |

Table 3-4  
Standing Crop\* of Benthic Animals, Nova Scotia to Key West (g/m<sup>2</sup>)  
 (after Emery and Uchupi 1972)

| <u>Sediment Type</u> | <u>Nova Scotia to New York</u> | <u>New York to Cape Romain</u> | <u>Cape Romain to Key West</u> |
|----------------------|--------------------------------|--------------------------------|--------------------------------|
| Gravel               | 277                            | n.d.**                         | n.d.                           |
| Sand-gravel          | 131                            | 21                             | n.d.                           |
| Glacial till         | 82                             | n.d.                           | n.d.                           |
| Shell                | 192                            | 574                            | 203                            |
| Sand-shell           | 81                             | 78                             | 70                             |
| Sand                 | 208                            | 81                             | 79                             |
| Silty sand           | 237                            | 771                            | 27                             |
| Silt                 | 164                            | 82                             | n.d.                           |
| Clay                 | 194                            | n.d.                           | n.d.                           |

\* Based upon about 1400 samples from depths between 0 and 200 m.

\*\* Not determined, mainly because of inadequate number of samples.

substrates showed both the highest benthic standing crop (771 g/m<sup>2</sup>) between New York and Cape Romain, South Carolina, and the lowest (27 g/m<sup>2</sup>) between Cape Romain and Key West. This makes quantitative and qualitative generalizations about any given sediment type difficult to make because other environmental factors besides grain size distributions are also likely to influence the benthos distributions and densities within any given sediment type. Broadly speaking, the distributions and densities of benthos become more stable from nearshore to deepwater environments, primarily as a response to increased environmental stability (Sanders 1968, 1969; Flint and Holland 1980). Sediment quality changes also occur, which may affect the benthos composition. For example, Jumars and Fauchald (1977) found relative increases in numbers of sessile polychaete species with increasing depths up to 400 m along a depth transect on the Pacific Coast, which were attributed to increasing

sediment stability. Observed spatial/depth sediment textural changes (i.e., increasing sediment stability, silt-clay content, organic content) on the Oregon shelf (mouth of the Columbia River) were also related to benthic faunal changes in biomass, density, and species diversity and richness, all increasing offshore (Boone, Granat, and Farrell 1978). Frankenberg and Leiper (1977) found high seasonal and spatial variability in nearshore littoral benthic communities on the Georgia shelf. Sediments in these relatively shallow (3.5- to 21-m) shelf environments are subject to frequent disturbances such as storms and greater climatic variability. Therefore, communities dominating these environments may reflect the "opportunistic life history 'strategies'" discussed by McCall (1977, 1978) (see Table 2-1). A study by Buchanan, Sheader, and Kingston (1978) found macrobenthos species diversity negatively correlated with silt content, although not with depth. They found biomass negatively correlated with depth, but not with sediment type.

- (4) A highly successful method for objectively analyzing and classifying complex animal-sediment relationships and species associations is the use of numerical classification procedures such as cluster analysis, ordination, and discriminant analysis (Clifford and Stephenson 1975, Boesch 1977a, Shin 1982). Boesch (1973) was able to identify habitat and species groups using numerical classification procedures for the macrobenthos in the Chesapeake Bay region (homeohaline estuary), and found sediment factors such as clay, silt, and the availability of hard substrates overwhelmingly responsible for the observed spatial patterns in benthos. He found epifaunas poorly developed on mud bottoms with high silt contents, relative to sand bottoms with more suitable substrates (i.e. shell). In general, he observed much higher diversities of infaunas and epifaunas on sand bottoms relative to mud bottoms, as shown in Table 3-5. Higher diversities frequently observed in sand bottoms may be a consequence of microhabitat complexity (e.g. variable grain sizes) (Sanders 1968, Boesch et al. in review).
- (5) In stressed (e.g. poikilohaline) estuaries animal-sediment relationships may not be as clearly

Table 3-5  
Soft Bottom Habitat Comparisons; Homeohaline Estuary  
(data from Boesch, 1973)\*

| <u>Habitats</u> | <u>Species<br/>Abundance</u> | <u>Density<br/>N/m<sup>2</sup></u> | <u>Species<br/>Diversity (H')</u> | <u>Species<br/>Richness (SR)</u> | <u>Species<br/>Evenness (J')</u> | <u>Number<br/>Stations</u> |
|-----------------|------------------------------|------------------------------------|-----------------------------------|----------------------------------|----------------------------------|----------------------------|
| Mud             | 23 ± 9<br>(9-29)             | 2525 ± 2756<br>(520-7780)          | 2.3 ± 0.9<br>(0.8-3.4)            | 3.8 ± 1.4<br>(1.7-5.7)           | 0.52 ± 0.19<br>(0.19-0.71)       | 6                          |
| Mud/Sand        | 40 ± 8<br>(31-55)            | 1403 ± 687<br>(735-2860)           | 4.0 ± 0.5<br>(3.2-4.8)            | 7.0 ± 1.1<br>(5.5-8.9)           | 0.75 ± 0.09<br>(0.64-0.86)       | 9                          |
| Sand            | 49 ± 11<br>(33-65)           | 3045 ± 1736<br>(730-8865)          | 4.0 ± 0.5<br>(2.9-4.9)            | 7.7 ± 1.4<br>(5.3-11.5)          | 0.72 ± 0.08<br>(0.57-0.84)       | 24                         |

\* Mean ± standard deviation (SD) (range of values observed at all stations).

defined due to overriding environmental stress factors (Dörjes and Howard 1975; see habitat type description, paragraph 19). In these systems, the source of the stress, e.g. salinity, current velocity, etc., may be more suitable for identifying faunal spatial distribution patterns using classification procedures. The multispecies structure of biological data may be explored and simplified using either of two different multivariate models. Each is capable of elucidating biological patterns that can be used in subsequent analyses of relationships with abiotic variables. In the case of large, spatially heterogeneous data sets, discrete (classification) models seem most tractable. When single gradients predominate (e.g., a stress gradient such as salinity, current, etc.), continuous models (ordination and discriminant analysis and correlation) tend to be more useful in data interpretation. Numerical classification techniques have also been used to identify benthic assemblages in coastal marine shelf environments in relation to sediment type, depth, environmental change, and current or water movements. Attempts to relate the benthic fauna distribution in terms of substrate particle size have usually failed to find sharp animal-sediment relationships using classification techniques on the South Atlantic and Northern Gulf of Mexico continental shelf (Day, Field, and Montgomery 1971; Flint and Holland 1980); this tool, however, has been successful in classifying benthos animal-sediment relationships in the Middle Atlantic Bight.\* Most investigations have generally found benthic faunal associations more closely related to depth than sediment textural changes, although some definite textural/faunal trends are apparent (Day, Field, and Montgomery 1971; Boesch 1973; Boone, Granat, and Farrell 1978; Flint and Holland 1980; Jumars and Fauchald 1977). Attempts at classifying animal-sediment relationships may be unsuccessful when sediment characterization studies are incomplete. Sediment characterizations based on simplistic measurements of only gross sediment composition (i.e., percent clay, silt, sand, organic content) may not be sufficient to distinguish subtle animal-sediment relationships, especially in shelf environments; in these environments sand particle size composition, for example,

---

\* Personal Communication, 1981, D. F. Boesch, Director, Louisiana Universities Marine Consortium, Chauvin, La.

may exhibit large variations within-habitat (i.e., according to where the particles occur on the crest or trough of a sand wave). It has been suggested (Boesch et al. in review) that these subtle variations in particle size distribution within a sand habitat may explain the large variations in species composition and abundance often observed in shelf environments.

- b. Aquatic vegetation bed. Substrate qualities are significant to and will affect the distribution of either submerged vascular plants and/or algae attached to the bottom. Seagrass species living in soft bottom environments generally require a reducing sediment environment, although the actual composition of sediments may be wide ranging. Both eelgrass and turtle grass require a strongly reduced sediment layer to become established (Phillips 1978, 1980; Zieman 1975). The Pacific surf grasses *Phyllospadix* spp, on the other hand, require a rock/hard substrate for attachment, as do the kelp bed communities found along the northwest Atlantic and Pacific Coasts. A delicate chemical equilibrium exists in sediments characteristic of seagrass beds, where strongly reducing conditions prevail below a 1-cm depth (Phillips 1978, 1980; Young and Young 1977; Zieman 1975). The oxidation of this strongly reduced layer from physical disruption of the sediments may render the sediments unsuitable for future growth of seagrasses. This was observed in a *Zostera* bed following eelgrass denuding by feeding swans (Wood 1959) and following destruction of eelgrass beds by cownose rays (Orth 1975). For high production, turtle grass beds appear to require reducing conditions in the sediments surrounding the rhizomes and roots (Phillips 1960). Substrate composition within and outside seagrass beds may vary from one location to another, and caution should be exercised when inferring substrate conditions from one seagrass habitat to another. The following example will illustrate the different sediment compositions observed within *Thalassia testudinum* beds from Bermuda and Florida, as a function of plant density. Figure 3-14 illustrates the sediment particle size, plant biomass, and faunal species richness and densities for a Florida turtle grass system. It shows no significant differences in sediment composition and faunal densities as plant densities increased (except faunal densities were much lower at the lowest plant density station) (Stoner 1980). There was also an apparent decrease in faunal biomass with increasing plant cover at the higher plant density stations (Stoner 1980). A study by Santos and Simon (1974) in another Florida estuary also found no sediment compositional

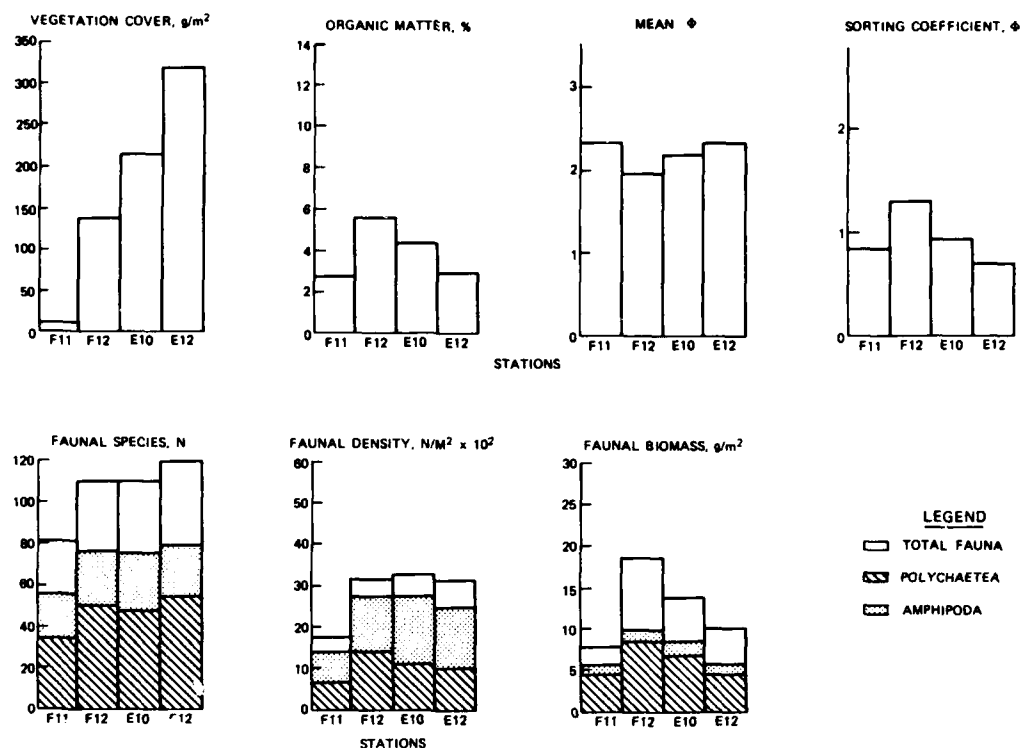


Figure 3-14. The role of seagrass biomass (*Thalassia*) in structuring macrobenthic assemblages (data from Stoner 1980)

differences between sand, *Thalassia*, and *Halodule* habitats, with mean grain sizes approximating those observed by Stoner (1980). However, Orth (1977a) found significant differences across the seagrass bed for both *Thalassia* in Bermuda and *Zostera* in Chesapeake Bay for sediment particle size and for organic matter and plant biomass (Figures 3-15 and 3-16). Clay and silt-size particles increased as plant biomass increased. These sedimentological differences were also correlated with increased faunal abundances in the finer grained sediments, but vegetation biomass was also a covariable. Figure 3-17 contrasts the large differences in faunal diversity and abundance observed between a *Thalassia* seagrass bed and an adjacent unvegetated sand habitat (Orth 1977a).

- (1) Seagrass species have been found growing in a wide variety of sediment compositions from mud to coarse sand. Eelgrass has been reported growing in a wide variety of substrates from pure firm sand to pure

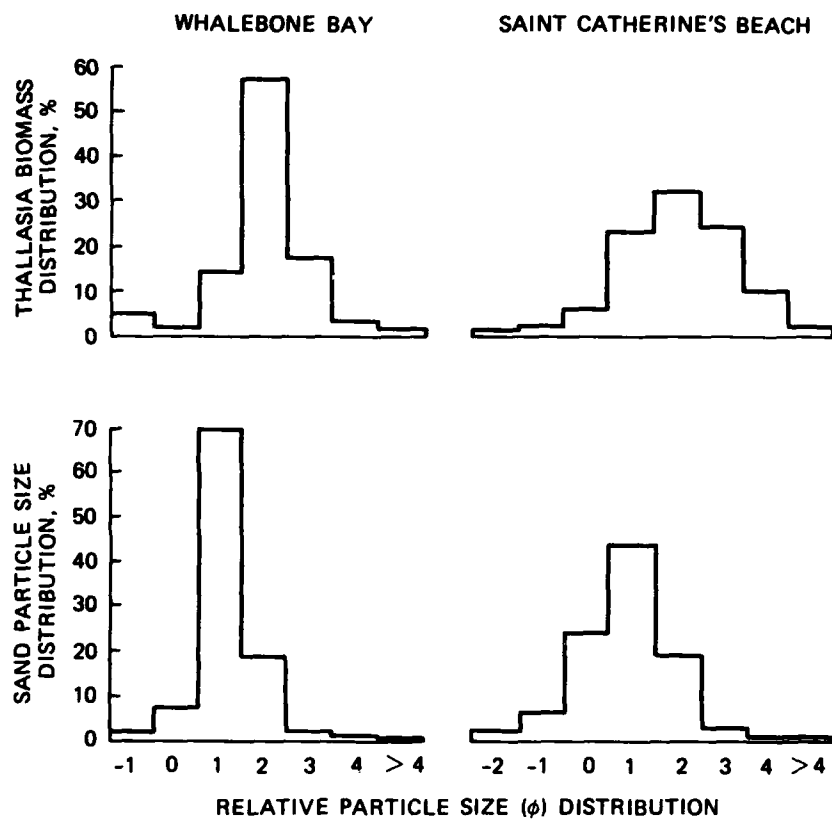


Figure 3-15. Sediment particle size versus *Thalassia* biomass distributions at two stations in Bermuda (after Orth 1977b)

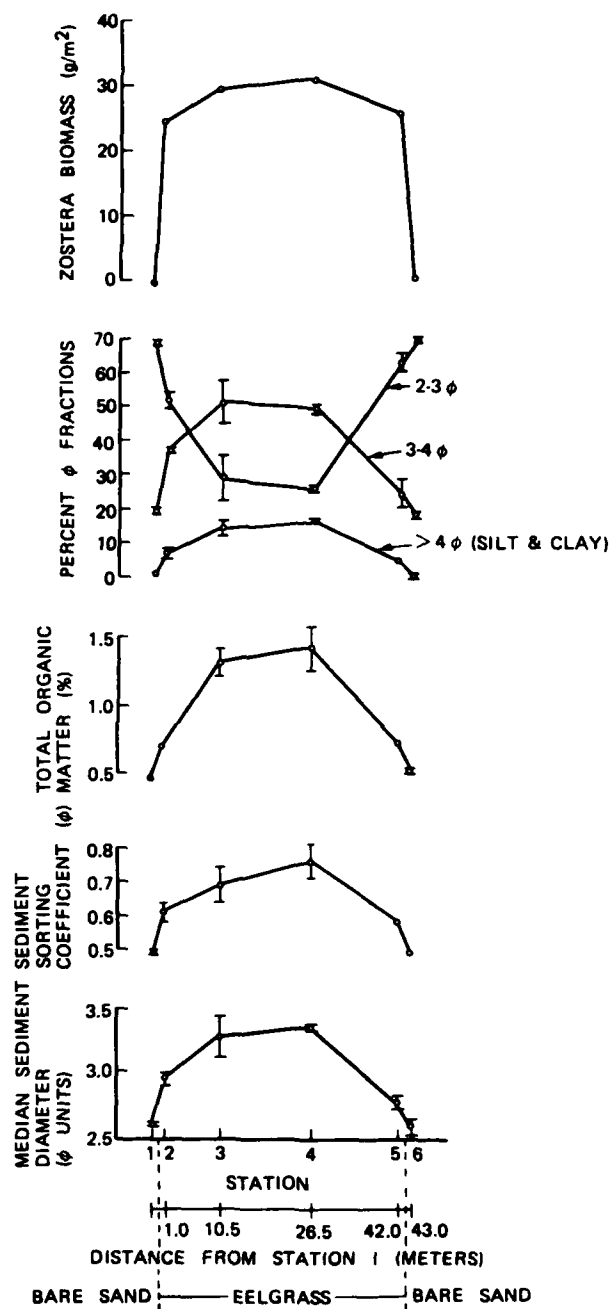


Figure 3-16. Sediment particle size distribution and eelgrass biomass gradients from a transect study across a seagrass bed (after Orth 1977a)

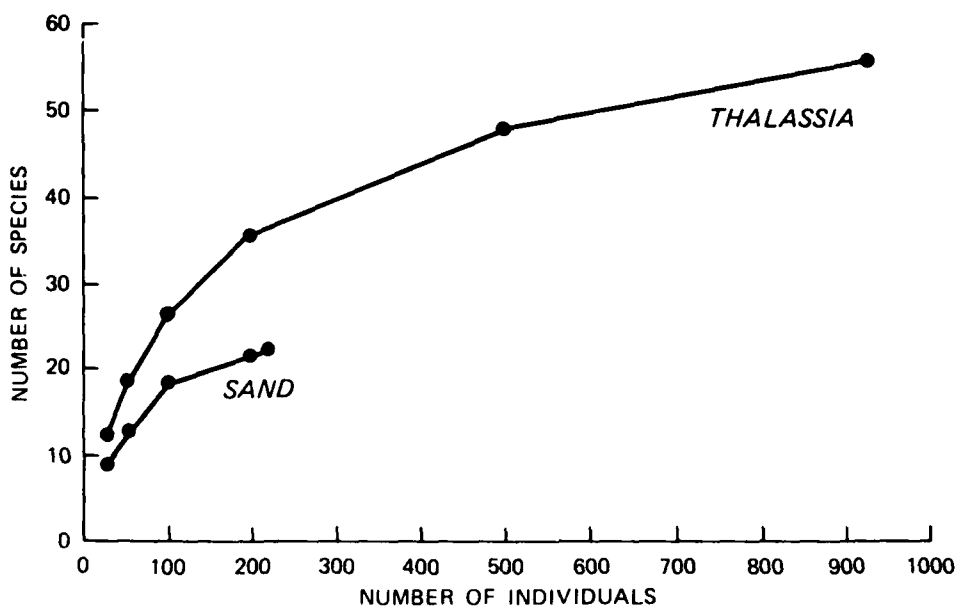


Figure 3-17. Rarefaction curves (Sanders 1968) for *Thalassia* and sand stations in Whalebone Bay (after Orth 1977a)

soft mud (Phillips 1974), although it appears to favor sandy substrates (greater than 70 percent sand) (Orth 1973, 1977a). Subtropical seagrasses in Florida are reported from fine to coarse sand (Stoner 1980, Santos and Simon 1974, Holm 1978, Young and Young 1977).

- (2) Sediment depth is critical to the growth of turtle grass which has a dense rhizomal and root system, and may bind the sediment to a depth of 1.2 to 1.8 m below the surface (Thorhaug 1981). Zieman (1972) has found turtle grass roots as deep as 4-5 m. This species does not grow well in shallow sediments. Figure 3-18 shows the effect of sediment depth on turtle grass standing crop biomass and associated macrobenthos. Figure 3-19 shows the relationship of sediment depth to turtle grass blade density and length (Zieman 1975). Other subtropical seagrass species (e.g. *Halodule* and *Syringodium*) have rhizome and root systems which only penetrate a few centimetres below the surface of the sediment (Thorhaug 1981). The lack of sufficient substrate depth has been cited by Thorhaug (1981) as a primary reason for the patchiness of turtle grass *Thalassia* in Florida waters.

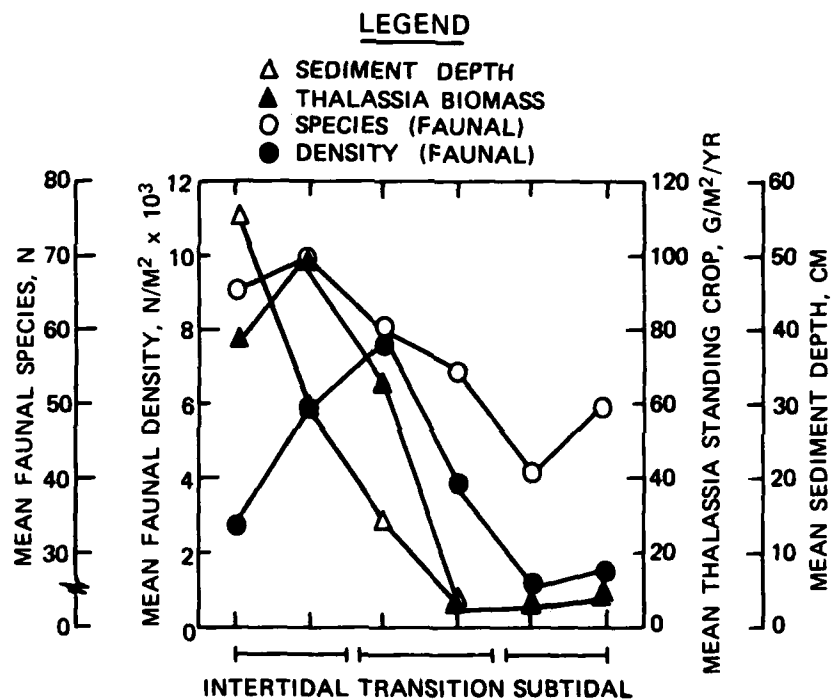


Figure 3-18. Mean macrobenthic faunal density and number of species along an environmental gradient of varying sediment depth and turtle grass (*Thalassia*) biomass (data from Holm 1978)

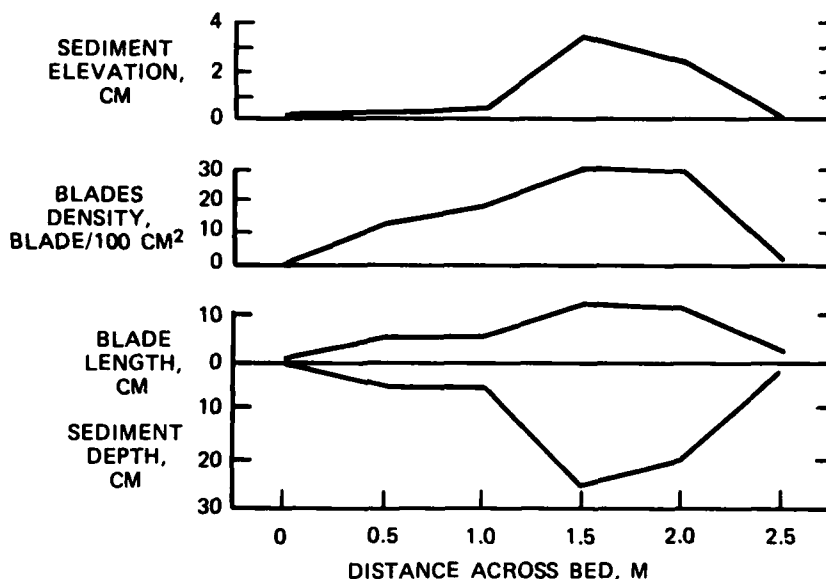


Figure 3-19. Relationships between depth of sediment, length and density of *Thalassia* blades, and sediment elevation caused by sediment stabilization in a bed off Key Largo, Florida (after Zieman 1975)

- (3) In kelp habitats, kelp survival depends on the presence of a suitable hard rock or compacted solid substrate. Shifting sand bottoms (storm or tidally induced) will cause the disappearance of this habitat type (Phillips 1974) if exposed surfaces are covered with sediment.
- c. Reef. Substrate quality is very important in determining the distribution of biological reefs. Oyster, coral, and worm (sabellariid) reefs are distributed in a wide variety of substrates from rock/hard bottoms to unconsolidated bottoms ranging from sand to mud. Oysters may grow equally well on a hard, rocky bottom or on semihard mud firm enough to support their weight. Shifting sand and soft mud are the only types of bottoms which are totally unsuitable for oyster communities (Galtsoff 1964). Planktonic larvae of oysters, coral, and sabellariids require the presence of a suitable hard substrate and usually settle on or near well-established populations of their own species. Larvae of these reef-building species do not successfully settle on unconsolidated sediments directly, as they would be smothered by fine, silt-size particles; these larvae generally settle on

shells, rock surfaces, or other suitable debris serving as "terra firma." The seaward extension or development of a fringing coral reef is dependent on the buildup of dead coral and algal sediments along its seaward edge. This is depicted in Figure 3-20, which shows the extension of reef as a function of the buildup of dead coral/algal rock and sediments on its seaward edge to depths of 90 ft or less (Smith 1971; Goreau, Goreau, and Goreau 1979). Sabellariid worm reef habitats are markedly affected by substrate quality in as far as the worms exert a bias in their choice of tube-building materials and their requirement for high energy environments (Scholl 1958, Kirtley and Tanner 1968, Rees 1976). The worms seize and sort suspended sand-size particles from the turbulent waters and fix appropriately shaped particles to their cylindrical tubes (Figure 2-10) with a special protein cement, which the animals secrete (Vovelle 1965). The worm reefs consist of agglutinated quartz grains, heavy mineral grains, small fragments of comminuted mollusk shells (shell hash), and other detrital fragments such as ostracods, foraminifera tests, fecal pellets, and sponge spicules (Kirtley and Tanner 1968). The availability of suitable substrates for the establishment of biological reefs is dependent on relatively high wave or current energy environments, and they are distributed accordingly.

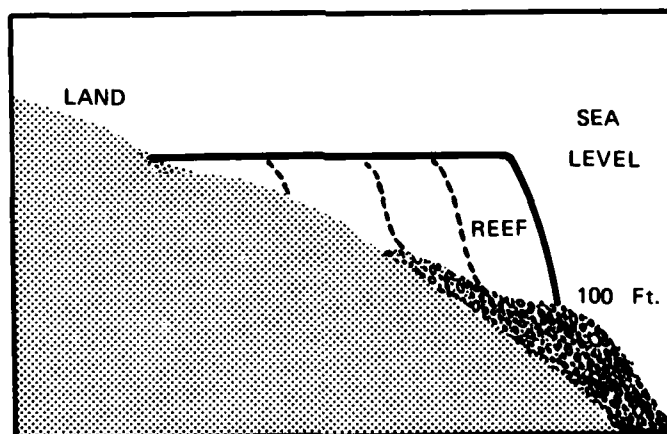


Figure 3-20. Schematic illustrating the growth and development of a fringing reef. Broken lines indicate successive stages of growth from left to right as coral broken by wave action builds up a base of dead coral substrate sufficiently shallow (less than 100 feet) to enable vigorous coral growth (after Smith 1971)

- d. Rock/hard bottom habitat. The availability of suitable hard substrates for the establishment of fouling or sessile benthic communities is largely regulated by current and wave energies necessary to maintain a relatively clean hard substrate. The distribution of rock/hard substrates in estuarine and coastal marine environments is generally limited to moderate to high current/wave energy areas with relatively low light intensities and/or high turbidity levels. Substrate factors such as texture, chemistry, orientation (vertical, horizontal, etc.), color, and cleanliness will affect settling of larvae onto hard substrates and thereby influence the community structure and composition.

#### Vegetation Quality

56. Qualitative vegetation factors such as blade density; blade size, length, and width; and root depth influence the distribution composition and structure of benthic communities associated with submerged vegetated habitats (i.e. seagrasses and kelp). Standing vegetation serves as both a substrate for attached sedentary and motile epifaunas and epiphytes and as a food source (directly grazed or indirectly consumed as detritus). Seagrasses are very important in stabilizing unconsolidated bottoms by binding the sediments with their roots and rhizomes. Seagrass blades serve as baffles to deflect currents and trap sediments, thereby reducing turbidity levels in water passing through a seagrass bed (Zieman 1975; Phillips 1974, 1978, 1980). Qualitative differences in seagrass species (i.e. blade size, length, and width) and vegetation densities in turn affect the qualitative and quantitative nature of associated macroinvertebrate communities by increasing the habitat structural diversity and complexity compared with unvegetated habitats (see Figure 3-17). Qualitative and quantitative differences in seagrass animal communities have been observed for tropical, subtropical, and temperate seagrass systems. For example, in subtropical seagrass habitats, Thorhaugh (1981) found the most abundant and diverse animal communities associated with turtle grass (*Thalassia*), followed by manateegrass (*Syringodium*), while shoalgrass (*Halodule-Diplanthera*) contained substantially lower animal biomass

and numbers of macroinvertebrate species. A comparative study of Florida turtlegrass, shoalgrass, and sand habitats by O'Gower and Wacasey (1967) found greater numbers of macroinvertebrate species in turtlegrass habitats, with decreasing species richness in shoalgrass and sand habitats. Densities of faunas were generally higher in shoalgrass habitats in this study than in turtle grass, while sand habitat densities varied appreciably between high and low current stress areas (Figure 3-21). Sharp qualitative differences in major taxa were apparent between vegetated and unvegetated-sand bottoms at both locations. Stoner (1980) studied the structure of seagrass benthic communities as a function of seagrass biomass and found significant faunal differences between heavily vegetated bottoms and a relatively bare sand bottom, although no significant differences were found between number of species, faunal densities, and faunal biomass with increasing vegetation cover (*Thalassia* density). Slight reductions in faunal biomass were

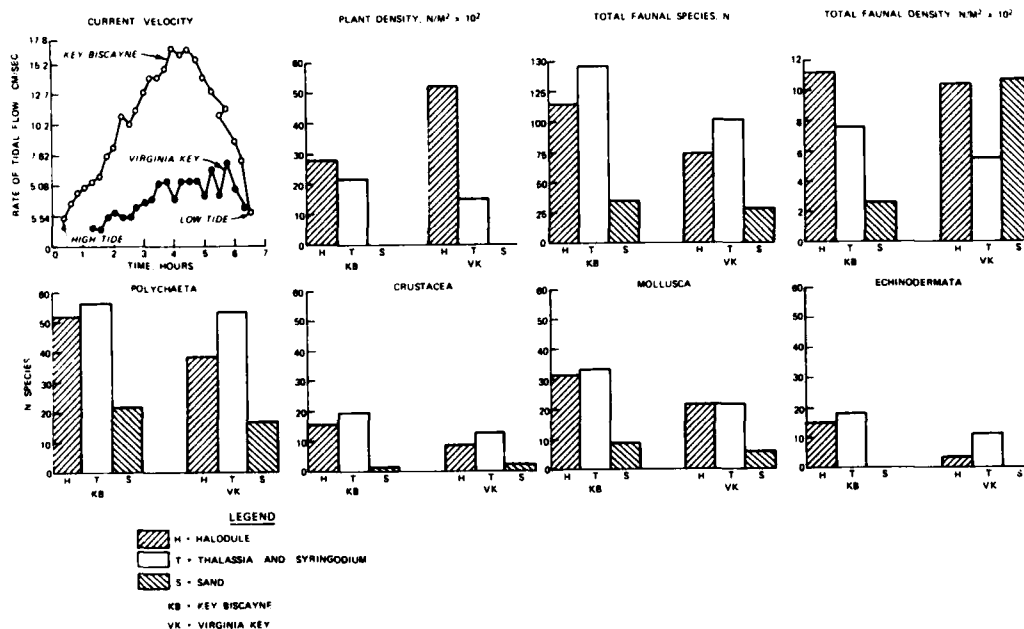


Figure 3-21. Comparative effects of current stress on macrobenthos from three habitat types in a subtropical marine coastal environment (data from O'Gower and Wacasey 1967)

observed as turtle grass biomass increased (Figure 3-14). In turtle grass beds, leaf density largely determines the ability of the community to reduce water flow, promote sedimentation, and stabilize the sediment surface (Zieman 1975). Stoner (1980) found faunal similarities within turtle grass habitats of different plant densities, which were distinct from the largely unvegetated site. Polychaetes and amphipods made up the bulk of the macrobenthic community in numbers of species, density, and biomass (Figure 3-14). This contrasts with Brook's (1978) study of turtle grass communities in Biscayne Bay, where he found low faunal similarity within five turtle grass habitats of similar plant densities ( $>3000$  blades/m<sup>2</sup>) and large differences in faunal composition and abundance among sites (Table 3-6). Macroinvertebrate densities ranged from 292-10,644/m<sup>2</sup>, while taxa compositions were highly variable among sites. Site descriptions for this study indicate varying sediment depths, sediment composition, and blade lengths of turtle grass, suggesting substrate quality may be more important than plant densities in structuring the turtle grass benthic communities at each site. Sediment depth has already been mentioned (see substrate quality, paragraph 55b(2)) as a limiting factor for turtle grass distribution and cover and may have a significant effect on the distribution and abundance of macrobenthic invertebrates, as was found by Holm (1978) in Biscayne Bay, Florida (Figure 3-18). Brook's study was conducted in the same bay, where differences in sediment depth and quality were not apparently related to turtle grass blade densities but may have been partially responsible for the observed faunal variability. In subtropical seagrass systems, blade density and length appear to be related to sediment depth, as shown in Figure 3-19. Increasing densities of seagrass leaves increase the surface area of the community and in turn offer greater substrate for epiphytes and epifaunas, as well as providing denser habitat for the organisms that use the grass beds as a nursery and for shelter (Zieman 1975).

57. Temperate seagrass beds dominated by eelgrass (*Zostera*) show marked seasonal changes in standing crop biomass and corresponding fluctuations in associated invertebrate and fish communities. Thayer.

Table 3-6

Comparative Macrofaunal Abundances in Turtle Grass Communities with High Blade  
Densities ( $>3000 \text{ m}^{-2}$ ), Biscayne Bay, Florida (after Brook 1978)

| Parameter                               | Beak Cut            | West Point       | Stations                            |                       |  | Murray Key          |
|-----------------------------------------|---------------------|------------------|-------------------------------------|-----------------------|--|---------------------|
|                                         |                     |                  | Featherbed Bank                     | Long Arsenicker       |  |                     |
| Blade length, cm                        | 30                  | 40               | 30-50                               | 25-40                 |  | >60                 |
| Sediment depth, cm                      | 5                   | --               | 25                                  | 10                    |  | 15                  |
| Sediment classification                 | Sand, coarse rubble | Floc. and rubble | Soft carbonate, flocculant material | Fine floc. and rubble |  | Fine floc. material |
| Total fauna:<br>no. of species (N)*     | 80                  | 61               | 38                                  | 72                    |  | 52                  |
| Total faunal<br>density, $N/\text{m}^2$ | 10,644              | 4286             | 292                                 | 1010                  |  | 4508                |
| Mollusks, %                             | 7                   | 25.5             | 52                                  | 32.5                  |  | 71.5                |
| Polychaetes, %                          | 31.3                | 10.5             | 20.5                                | 33.7                  |  | 14.5                |
| Crustaceans, %                          | 57.5                | 57.1             | 15.7                                | 24.4                  |  | 11.4                |

\* 161 macroinvertebrate species collected at all stations.

Adams, and LaCroix (1975) found a close relationship between eelgrass biomass and epifaunal invertebrate densities and fish biomass within a *Zostera* bed (Figure 3-22). Their study indicated that declines in invertebrate abundances were coincident with increases in fish biomass, particularly the pinfish, *Lagodon rhomboides*, within the eelgrass beds, suggesting heavy predator pressure on epifaunas during periods of highest eelgrass biomass. A trawling study by Orth and Heck (1980) and Heck and Orth (1980) in eelgrass beds from the Chesapeake Bay also found concomitant increases and decreases in numbers of fish and decapod crustacean species and their abundances which were directly correlated with temperature and eelgrass biomass changes throughout the year. Peak changes occurred during spring and summer, and lows during fall and winter. Marked differences were noted in eelgrass fish community structure between North Carolina and Chesapeake Bay, most notably in the scarcity of the pinfish (*L. rhomboides*) in Chesapeake Bay. This species is considered to be a major predator and determinant of epifaunal community structure in seagrass beds where it is abundant (Darnell and Wissing 1974, Orth and Heck 1980). Nocturnal abundances of fish and decapod crustacea were much greater than diurnal abundances, highlighting the significance of seagrass beds in providing refuges for relatively mobile species, such as shrimp, crabs, and fish. Relatively large variations in macroinvertebrate abundance have been observed between different eelgrass habitats, not unlike those found in tropical and subtropical seagrass habitats (Heck 1977, Young and Young 1977, Stoner 1980, Santos and Simon 1974, Brook 1978). Thayer, Adams, and LaCroix (1975) reported relatively low faunal densities and biomass from the Newport River estuary in North Carolina, averaging 923 individuals/m<sup>2</sup> and 7.5 g/m<sup>2</sup> (AFDW), respectively. However, Marsh (1973) observed mean epifaunal densities of 9600 m<sup>2</sup> in eelgrass beds from the York River in Virginia, while Orth (1973) reported a mean infaunal density of 15,000/m<sup>2</sup> in Chesapeake Bay. In every case, interhabitat comparisons between vegetated and unvegetated bottoms have shown markedly larger numbers of species, faunal abundances, and biomass within vegetated habitats. This was graphically illustrated in a study by Orth

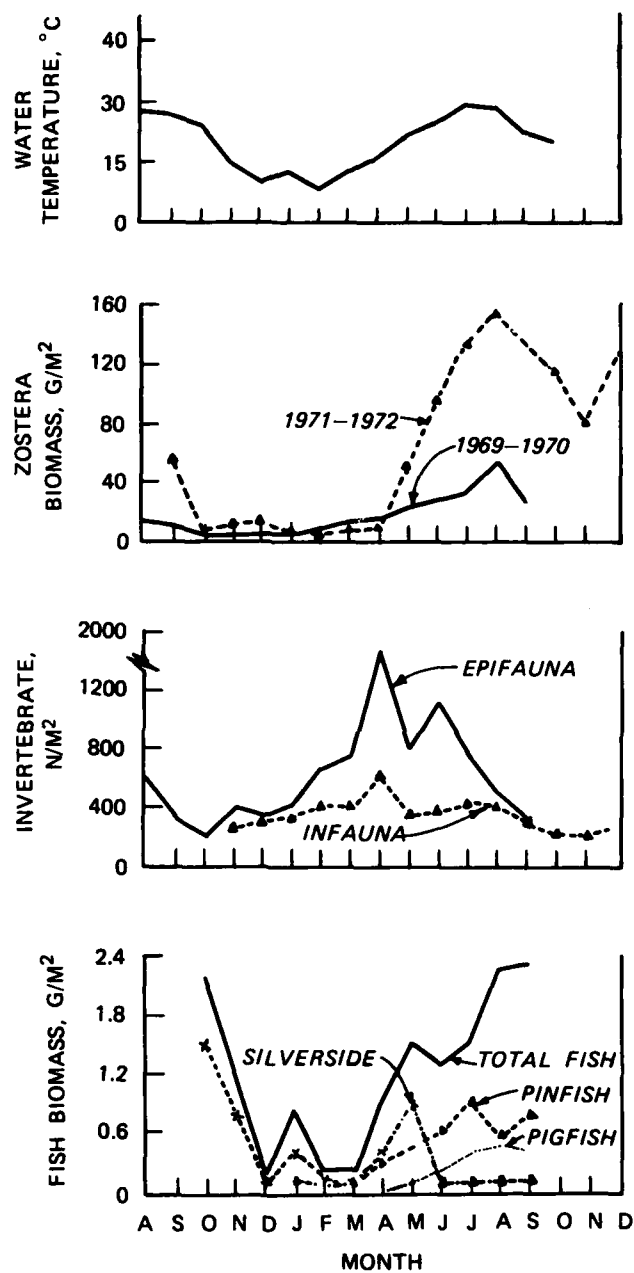


Figure 3-22. Seasonal distribution of water temperature, *Zostera* dry-weight biomass, mean epifaunal and infaunal densities, and major fish species biomass (after Thayer, Adams, and LaCroix 1975)

(1977a) of an eelgrass bed (Figure 3-23; Figure 3-16) and a turtlegrass bed (Figure 3-17). His study showed that numbers of faunal species and abundance increased as plant densities increased. Figure 3-24 shows the seasonal abundance and numbers of organisms per gram of *Zostera* at three different depth locations (Marsh 1973). This study indicates faunal densities increase on each *Zostera* blade as plant densities decline on a seasonal basis. Recent studies in transplanted eelgrass meadows from North Carolina (Fonseca et. al 1979; Kenworthy et al. 1980; Homziak, Fonesca, and Kenworthy 1982; Homziak, Fonseca, and Kenworthy

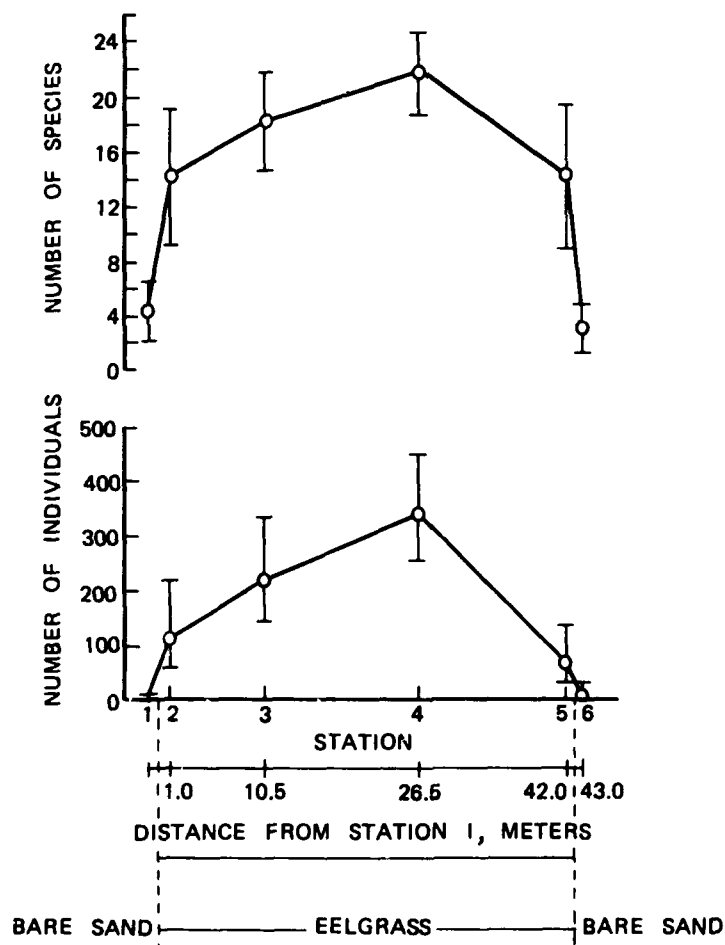
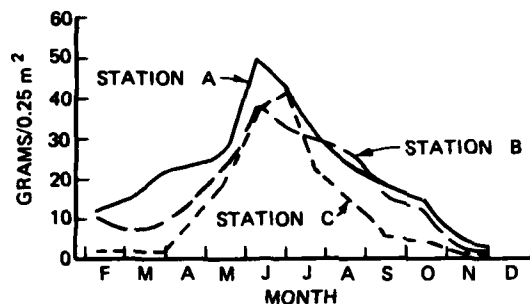
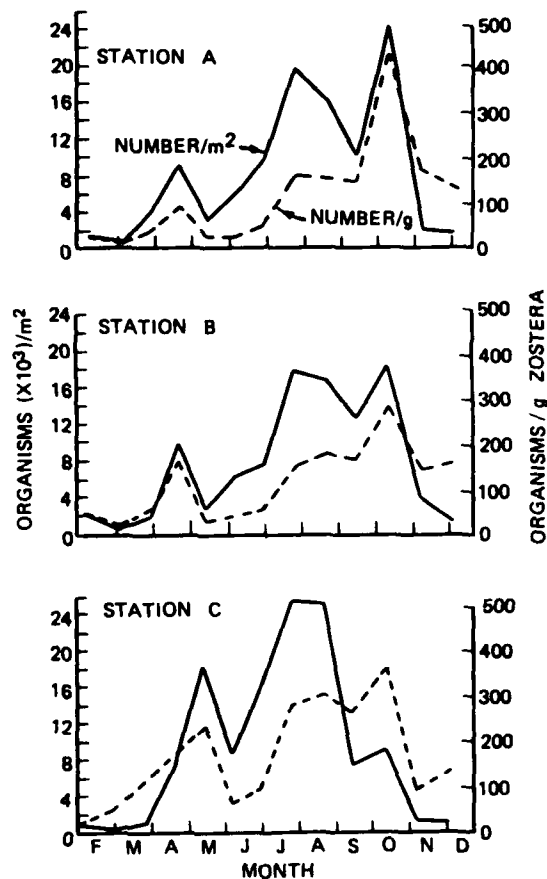


Figure 3-23. Mean and range of macrobenthic species and number of individuals collected at transect stations across an eelgrass bed (after Orth 1977a). Compare with Figure 3-16



a. ZOSTERA BIOMASS CHANGES



b. FAUNAL CHANGES

Figure 3-24. *Zostera* density-dependent faunal benthos changes: (a) seasonal *Zostera* biomass; (b) comparative seasonal changes in numbers of macrobenthos per gram of *Zostera* and macrobenthos density (number/m<sup>2</sup>) from three stations (A = 0.7 m; B = 1.2 m; C = 1.6 m) at three water depths (after Marsh 1973)

in review) have shed light on macrobenthic community structure and its development as a function of eelgrass shoot density. Homziak, Fonseca, and Kenworthy (1982) found macrofaunal density, number of species, and diversity positively but nonlinearly correlated with increasing eelgrass shoot density in a developing meadow. They also found a nonlinear decrease in dominance with increased shoot density. Another aspect of the same study (Homziak, Fonseca, and Kenworthy in review) demonstrated recruitment into and increased survival of juvenile hard clams (*Mercenaria mercenaria*) within transplanted eelgrass plots compared with unvegetated areas. Peterson (1982) found the clams *M. mercenaria* and *Chione cancellata* positively associated with *Halodule wrightii* cover in North Carolina, and high rates of mortality when vegetation was experimentally removed. High mortality rates were primarily attributed to predation.

58. The significance of seagrass in consolidating and stabilizing sediments is well established, and the loss or destruction of seagrass habitats may result in substantial substrate erosion (Phillips 1974, Zieman 1975, Christiansen et al. 1981). Physical destruction of stable eelgrass beds in the York River, Virginia, by the cownosed ray (*Rhinoptera bonasus*) caused marked decreases in faunal diversity and densities and the vegetation beds were replaced by unstable sand habitat (Orth 1975). Wilson (1949) noted that sand banks were lowered by 2 ft or more following the disappearance of eelgrass in England. The ability of seagrasses to stabilize and consolidate sediments is a function of their root and rhizome density and depth of penetration into the substrate. Species such as *Thalassia* and *Zostera* are important sediment stabilizers because of their wide distribution in tropical, subtropical, and temperate environments. Faunal changes following the disappearance of seagrass habitats have been much studied in the case of the rapid decline of eelgrass beds during 1931 along the Atlantic coasts of North America and Europe. In one year almost 99 percent of the standing stock of eelgrass was destroyed by a disease called "wasting disease." Epifaunas associated with eelgrass rapidly disappeared, while commercial fish and shellfish suffered large population

declines. Waterfowl dependent on this plant for food also suffered tremendous population declines (Phillips 1974, 1978).

### Temperature

59. Temperature is a major water quality factor structuring benthic communities in estuarine and marine systems (Gunter 1957, Hedgpeth 1957). The magnitude of diurnal and seasonal temperature changes generally increases from the tropics toward the arctic and from deepwater to shallow-water environments, while temperature fluctuations are generally more stable at the mouths of estuaries than at the upper reaches (Day 1951). Temporal shifts in temperature on the east coast are primarily caused by seasonal fluctuations in strongly flowing air masses, whereas west coast, temperature changes are primarily brought about by upwelling and injections of cold water from the sea (Odum and Copeland 1974). Seasonal temperature changes are generally greater on the east coast than on the west coast at similar latitudes. In marine coastal environments, away from high-energy beaches and salinity-shocked river mouths, salinity and high-energy wave stress diminish and latitudinal temperature and light programming become more important in the distribution and zonation of benthic communities (Odum and Copeland 1974).

60. Between the latitude of Alaska, where winter ice is prevalent, and the latitude of southernmost Florida are the temperate marine coastal ecological systems, characterized by sharp seasonal pulses in light energy and temperature. The magnitude of the seasonal pulse generally increases northward to Maine and southern Alaska. At tropical latitudes south of Florida, seasonal pulses in light energy and temperature diminish markedly and temperatures are relatively uniform. Figure 3-25 depicts average latitudinal temperature ranges for the Pacific and Atlantic Oceans and corresponding light intensity shifts. This demonstrates the close relationship between radiation income fluctuations in the oceans and corresponding temperature changes. Oceans in the northern hemisphere exhibit larger temperature fluctuations, particularly at higher latitudes, because seasonal shifts in prevailing wind

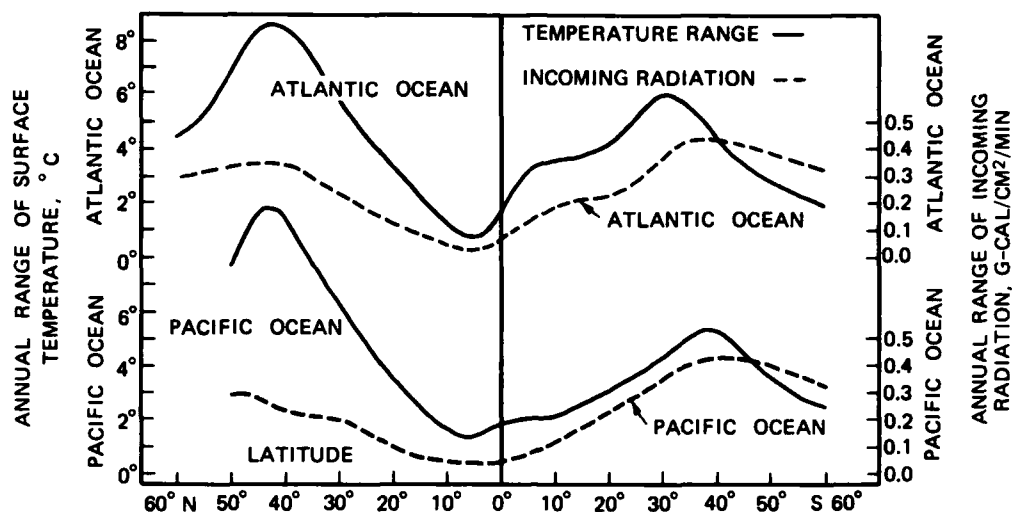
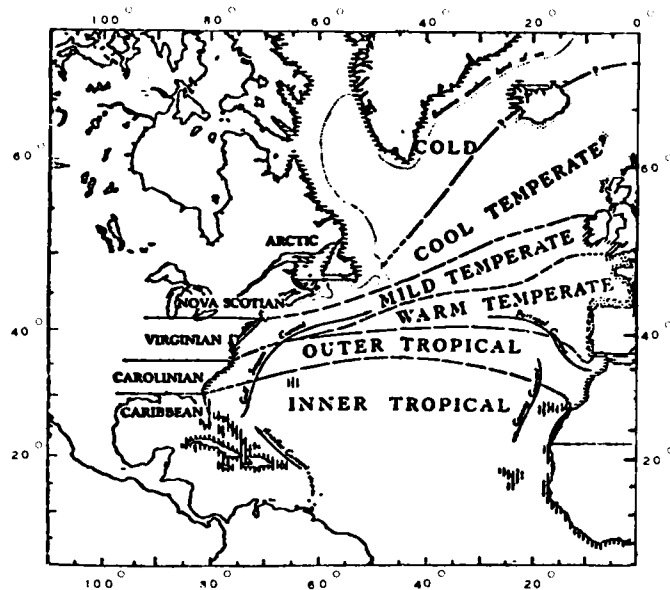


Figure 3-25. Average annual ranges of surface temperature in the Atlantic and Pacific Oceans plotted against latitude and corresponding ranges in the radiation income (after Sverdrup, Johnson, and Fleming 1942)

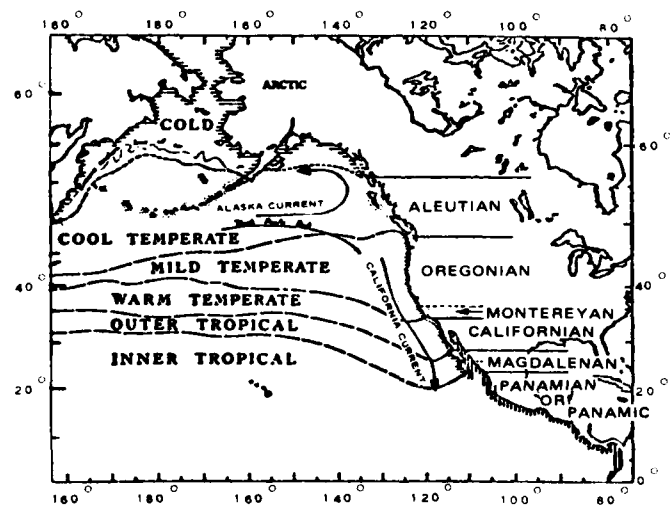
patterns blow cold winds from the continents toward the oceans and thereby greatly reduce winter temperatures (Sverdrup, Johnson, and Fleming 1942). Comparative annual variations in temperature at depth from different latitudes show generally increasing seasonal variations with increasing latitude (Figure 3-4). Bottom temperatures at depths of 15 to 44 m north of Cape Hatteras are generally more than 4° C cooler than surface waters between May and September (seasonal thermocline) (Emery and Uchupi 1972). Temperatures for coastal waters near Portland, Maine, range annually from 2.8° to 15.5° C ( $\Delta$  temperature = 12.8° C), while they range only from 24.4° to 29.6° C ( $\Delta$  temperature = 5.2° C) near Miami, Florida. For most of the northeast Pacific coast, mean high and low temperatures range from 9° to 14° C, with a mean annual range of only 5° C (Bourke, Glenne, and Adams 1971). Due to summer upwelling along the Pacific coast, lowest temperatures generally occur during summer (Bourke, Glenne, and Adams 1971).

61. The broad latitudinal distribution or range of benthic species is largely controlled by temperature, whereas salinity and

substrate quality largely determine their microdistributional patterns at a given latitude within an estuarine or marine system (Jones 1950, Thorson 1955, Hedgepeth 1957, Wells 1961). Biogeographical provinces or zones of faunal/floral similarity are based on faunal/floral distribution patterns in relation to temperature regimes to which many species are correlated due to physiological adaptations for maintenance, enzyme operation, seasonal programming of reproduction, and common access to genetic pools (Odum and Copeland 1974) (Figure 3-26). Broad regions of faunal overlap generally exist between contiguous biogeographical provinces. On the western Atlantic continental shelf, for example, south of Cape Hatteras, Gulf Stream eddies moderate temperature fluctuations near the seaward edge of the continental shelf such that many Caribbean (tropical) species range into what is generally characterized as the Carolinian Province (Pearse and Williams 1951). Tropical and polar organisms live in a relatively constant thermal range and have a limited ability to alter their metabolic responses to different temperatures outside their accustomed range in an adaptive or compensatory manner. In contrast, most temperate zone organisms are able to acclimate and have evolved homeostatic mechanisms enabling them to be partially insensitive to temperature fluctuations (Vernberg 1981). Figure 3-27 graphically depicts this metabolic temperature response pattern in tropical, polar, and temperate zone organisms. Seasonally programmed spawning and reproductive cycles become increasingly more common in faunas with increasing latitudes toward the arctic. Therefore, seasonally programmed faunal pulses (recruitment) are common at temperate and arctic latitudes. At temperate and boreal (northern) latitudes, seasonal spawning pulses of benthos occur in late spring and early summer. Sometimes a smaller peak may also occur in late summer to early fall. Migrations of animals coinciding with seasonal temperature changes often include many predators of estuarine and marine benthos (Day 1951). Migrations of invertebrates and fishes into deeper and warmer offshore waters in winter have also been reported (Kinne 1963). This contrasts sharply with tropical marine and estuarine ecosystems, where most species do not exhibit sharp seasonal reproduction and



a.



b.

Figure 3-26. Biogeographical provinces related to temperature regimes and faunal/floral similarities: (a) western north Atlantic; (b) eastern north Pacific (after Hall 1964)

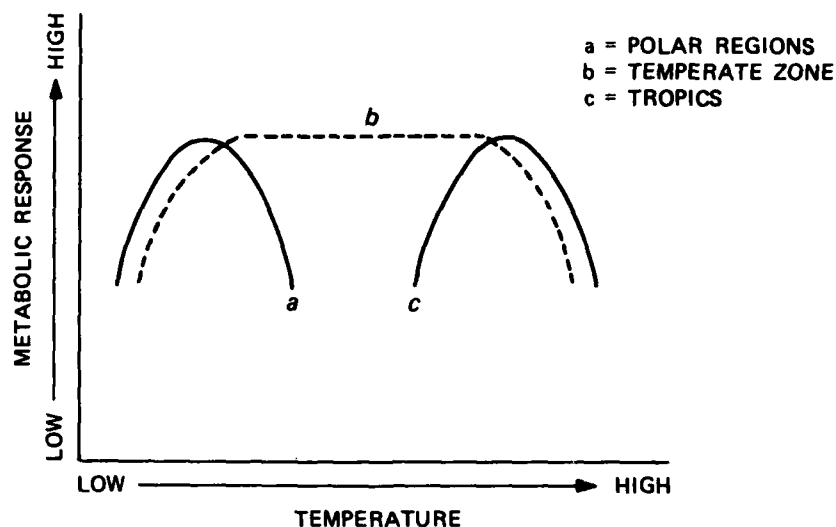


Figure 3-27. The generalized metabolic response to temperature of animals from different climatic regions

spawning cycles because of relatively stable temperature and light conditions. Recruitment of larvae at tropical latitudes is generally continuous throughout the year. There is also a generally recognized pattern of decreasing numbers of invertebrate species, especially epifaunal species, with increasing latitudes (i.e., from the tropics to the arctic) in marine coastal environments (Carriker 1967). It is likely that this same trend exists in estuaries as well, especially in shallow areas subject to temperature extremes and ice stress. Benthic species with pelagic larvae decrease in abundance generally from tropical latitudes to the polar regions. Thorson (1957, 1958, 1961) reports that 90 percent of tropical species exhibit pelagic (planktonic) larval stages, compared with approximately 67 percent in temperate marine coastal areas, dropping off to only a few species in polar waters. It is also likely that a similar latitudinal gradient in larval type (planktonic versus nonplanktonic) may be present in estuarine environments due to general increases in salinity and temperature stresses with increasing latitude. Species that brood their young (nonplanktonic, K-strategists) would be favored at lower temperatures characteristic of polar environments over those that release large numbers of

planktonic larvae (r-strategist)(Southwood 1977, Clarke 1979).

62. It is also generally recognized that organisms living in tropical marine and estuarine environments live much closer to their upper thermal limits than those living at temperate latitudes (Zieman 1970, Thorhaug 1981); at high arctic latitudes, however, ice stress may severely limit the distribution of epifaunas in shallow littoral areas less than 10 m deep (McRoy and Allen 1974). Thermal stress may be potentially more damaging to benthic organisms living at tropical latitudes compared with temperate latitudes, and the siting of power plants near tropical estuaries with resulting thermal releases may act as a severe stress (Odum 1971, Zieman 1970). Mortalities associated with cold temperatures have been reported for invertebrates and fish along the Georgia coast and estuaries (Dahlberg and Smith 1970), western Florida coast (Storey 1937, Springer and Woodburn 1960), Florida bay (Tabb, Daubrow, and Manning 1962) and the Texas coast (Gunter and Hildebrand 1951).

- a. Unconsolidated soft bottoms. Temperature ranges found in a given area will affect the distribution of benthos in soft bottom habitats. The temperature tolerances of individual species will determine the distributions observed. The number of infaunal species observed along the latitudinal gradient increases gradually toward the equator, although not nearly to the degree that epifaunal species increase (Thorson 1961,\*). In shallow estuarine and marine soft bottom habitats, temperature stresses may affect infaunal and epifaunal invertebrates differently. At arctic latitudes burrowing infauna may survive temperature extremes and ice stress, whereas epifauna may not. At lower latitudes, infauna may escape high temperatures by burrowing deeper within the sediments, whereas epifaunal invertebrates are subject to the full temperature regime. Estuaries and marine areas characterized by relatively poor water circulation during summer months may become thermally stratified, resulting in oxygen-poor reducing conditions in benthic environments. Biggs (1967) reported sediments in Chesapeake Bay below the 50-ft contour were generally oxygen deficient and reducing during the summer months, while those observed in depths less than 40 ft were oxygenated

---

\* Personal Communication, 1981, D. F. Boesch, Director, Louisiana Universities Marine Consortium, Chauvin, La.

continuously. Oxygen depletion has also been observed in the New York Bight (Boesch in press, Malone 1978). Thermal stratification with low oxygen levels will have a marked effect on the distribution of benthos in those areas, generally resulting in an impoverished benthic fauna or its complete elimination during the summer months (Holland, Mountford, and Mihursky 1977). Standing crops for benthos in unconsolidated sediment(s) in shallow marine coastal environments (10 m) average  $450 \text{ g/m}^2$  between Nova Scotia and New York, dropping to  $250 \text{ g/m}^2$  between New York and Cape Romain, and average  $100 \text{ g/m}^2$  between Cape Romain and Key West, Florida (Emery and Uchupi 1972). Thus, sharp contrasts in observed benthos standing crop exist along latitudinal gradients on the western north Atlantic shelf; similar, but less pronounced, biomass gradients probably occur along the West Coast as well.

- b. Submerged aquatic vegetation habitats. Temperature broadly delimits the geographical distribution of seagrass and macroalgae species (see paragraphs 30-32 and 36). Temperature, light intensity, salinity, and substrate quality are the factors principally responsible for the distribution of all the species making up vegetated bottoms. In subtropical and tropical estuaries, seasonal pulses of vegetation are less apparent than at temperate latitudes, where large temporal variations in submerged vegetation biomass occur. (See Figures 3-22 and 3-23 for an illustration of eelgrass temporal variations and corresponding variations in macroinvertebrate biomass.) Corresponding temporal variations in macroinvertebrate community structure are generally much greater in temperate eelgrass beds than in tropical seagrass beds. A recent study by Heck and Orth (1980) documented a temporal and latitudinal gradient in decapod crustacean abundances between Chesapeake eelgrass beds and tropical seagrass beds. They found that decapod crustacean abundances were positively correlated with plant biomass throughout the year and that total abundances of decapods were much greater in Chesapeake Bay eelgrass beds than those reported from North Carolina eelgrass habitats or Gulf of Mexico turtle grass habitats. Corresponding temporal variations in turtle grass biomass and associated epiphytes occur in subtropical estuarine and marine coastal environments, although vegetation is present throughout the year (Figure 3-28). Lethal temperature limits for subtropical-tropical seagrasses are only a few degrees above their ambient temperature, which is between  $32^\circ$  and  $34^\circ \text{ C}$  (depending

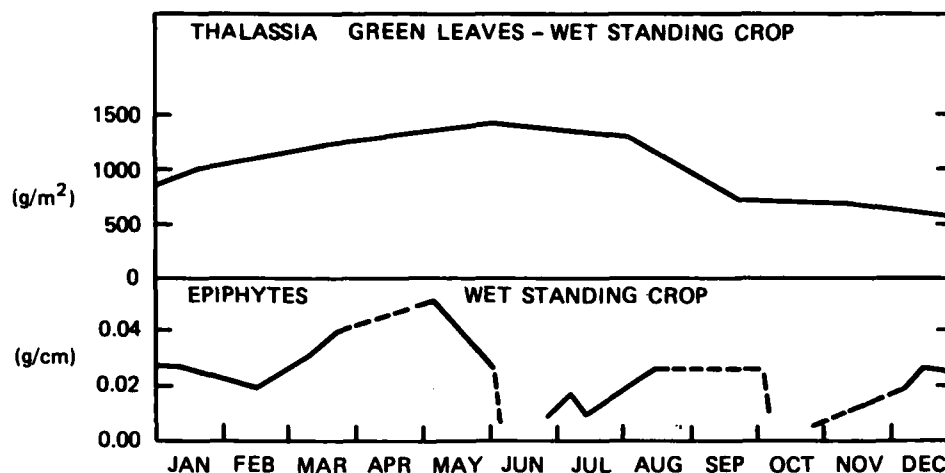


Figure 3-28. Seasonal biomass distribution of *Thalassia testudinum* and associated epiphytes from a south Florida estuary (after Jones 1968)

on geographical location) (Thorhaug 1981). Widgeon grass (*Halodule*) has an upper temperature limit of perhaps 1° C greater than turtle grass (*Thalassia*), while manatee grass (*Syringodium*) appears to be more sensitive than turtle grass, with an upper limit of between 30° and 33° C. The latitudinal distribution of marine kelp beds is limited by individual species tolerances to temperature (also by ice stress in Alaska (McRoy and Allen 1974)), while the seaward distribution is generally limited by available substrate, turbidity, and depth (Phillips 1974). Light intensity rather than temperatures per se regulate many aspects of kelp growth and development (North 1964, 1966).

- c. Reef habitat. The distribution of biological reefs (oyster and sabellariid) in estuaries is not generally limited by temperature, although temperature and light intensity may regulate spawning cycles. Oyster reefs exhibit wide distributions in Atlantic, Gulf, and Pacific estuarine environments. They generally exhibit wide temperature tolerances and are considered eurytopic species. Stenzel (1971) attributes the wide geographical range (8050 km, Figure 2-6) of the American oyster primarily to its tolerance to low temperature. Oysters are known to live in temperatures varying from 1° to 36° C throughout their geographical range (Galtsoff 1964). The northern limit of commercially harvested

oyster grounds is Long Island Sound (lat. 41° N) and the southern limit is close to Apalachicola Bay, Florida (lat. 30° N), although productive reefs also occur in Texas bays and in the Mississippi River Delta region (lat 29° N) (Galtsoff 1964). Oysters cease feeding at temperatures of 6° to 7° C. Maximum rates of feeding occur at about 25° to 26° C and decline rapidly above 32° C (Galtsoff 1964). Figure 3-29 shows the annual

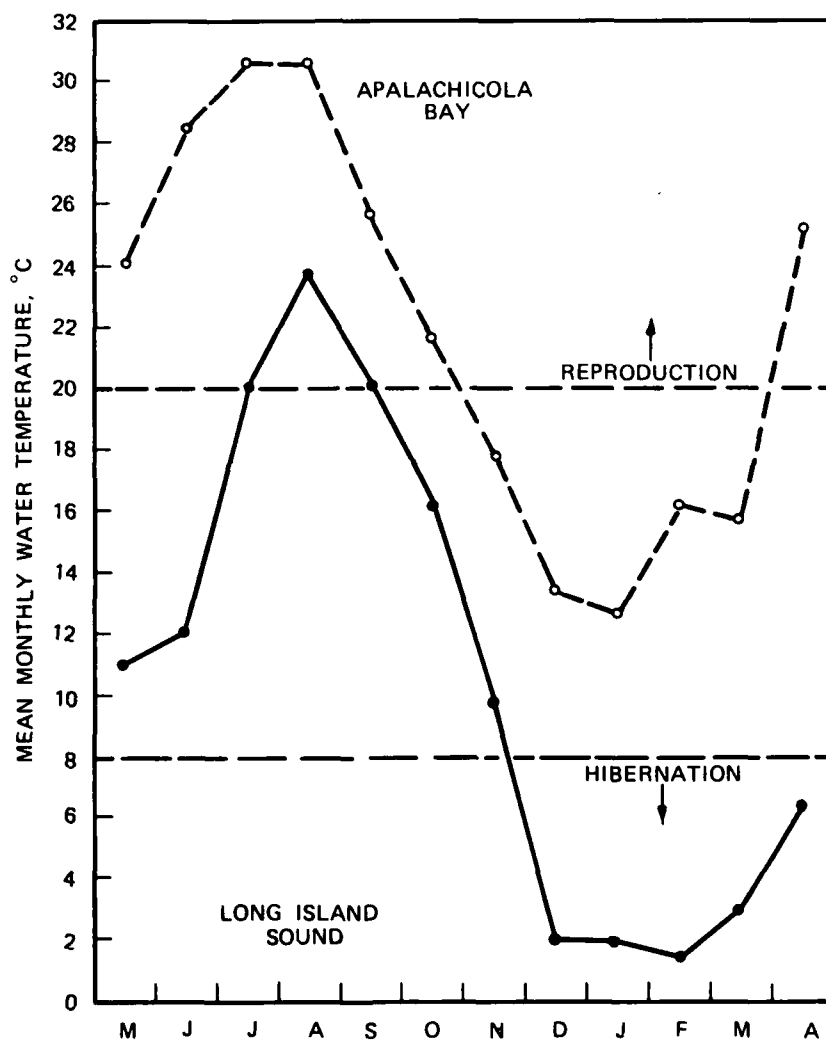


Figure 3-29. Mean monthly temperature cycles in Apalachicola Bay, Florida, and Long Island Sound, New York, illustrating seasonal oyster activity and reproductive cycles (after Galtsoff 1964)

temperature cycles for both Long Island Sound and Apalachicola Bay and illustrate the influences of temperature on oyster populations living at each location. Oysters in Apalachicola Bay continue to feed year round and may reproduce 7 months out of the year, spawning at temperatures of 20° C and above. At northern latitudes such as Long Island Sound, the period of feeding and growth is limited to about 6-1/2 months and the oyster reproduction season is limited to only around 2 months. An examination of thermal loading effects of power plant discharge waters on oyster reef communities from Crystal River, Florida, by Lehman (1974), concluded that an average annual water temperature increase of 4° C increased oyster biomass, metabolic rate, and turnover rate, but decreased the diversity of the oyster reef community. High temperatures during freshets may contribute to high oyster mortalities, whereas oysters may withstand long periods of low salinity at low temperatures (Galtsoff 1964).

- (1) Oyster distributions may be limited in estuaries by diseases and predator pressure. Most oyster predators and diseases are limited to salinities greater than 15 ‰. Oysters weakened by the sporozoan parasite *Perkinsus marinus* exhibit mortalities as high as 60 percent during periods of high salinity and temperature (Mackin 1951). Another disease called MSX (*Minchinia nelsoni*) has caused significant mortalities in oyster reefs in the lower reaches of Chesapeake Bay and Delaware Bay. High temperatures during summer months are responsible for significant mortalities in diseased oysters in these areas. Studies of oyster reef macroinvertebrate communities by Wells (1961) showed sharp temporal shifts in invertebrate species as a response to seasonally programmed life cycles. Figure 3-8 depicts the mean number of species collected at each station per sampling date compared with the cumulative total number of species observed throughout the year, illustrating the dynamic seasonal changes occurring within the structure of an oyster community as a consequence of temperature and salinity fluctuations. Figure 3-30 depicts the seasonal larvae set abundances of serpulids, oysters, and barnacles in a Texas estuary and illustrates the asynchrony in spawning cycles for some species (see also Figure 3-31). The distribution of biological reefs in marine environments are generally delimited by temperature, salinity, current and wave action, and turbidity. True coral reefs in particular are sharply limited

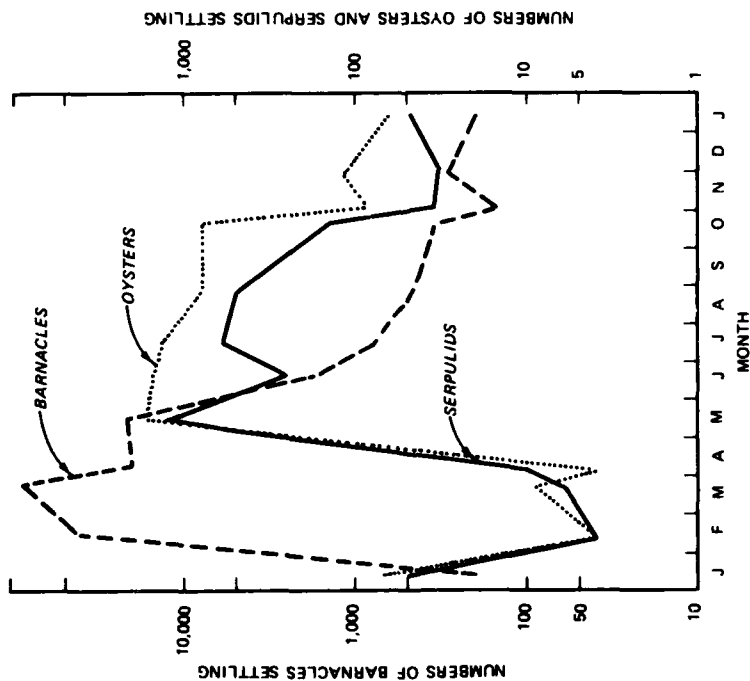


Figure 3-30. Seasonal spawning cycles (larvae set) for two reef-building species (oysters and serpulids) and one fouling species (barnacles) in Aransas Pass Inlet, Texas (after Behrens 1968)

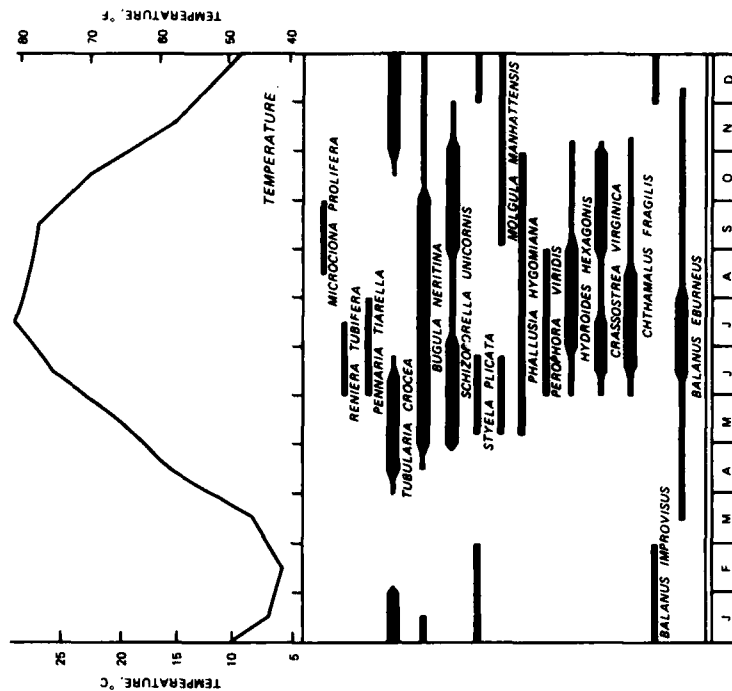


Figure 3-31. Seasonal abundance patterns of fouling community larvae set near Beaufort Inlet, North Carolina (data from Woods Hole Oceanographic Institute 1952)

AID A432 389 THE ROLE OF PHYSICAL CHEMICAL FACTORS IN STRUCTURING  
 SUBTIDAL MARINE AND... (U) ARMY ENGINEER WATERWAYS  
 EXPERIMENT STATION VICKSBURG MS ENVIR... D R KENDALL  
 UNCLASSIFIED JUN 83 WFS/TR/EI 83-2 F/G 5/1

THE ROLE OF PHYSICAL CHEMICAL FACTORS IN STRUCTURING  
SUBTIDAL MARINE AND... (U) ARMY ENGINEER WATERWAYS  
EXPERIMENT STATION VICKSBURG MS ENVIR... D R KENDALL  
JUN 83 WES/TR/EI 83-2 F/G 5/1

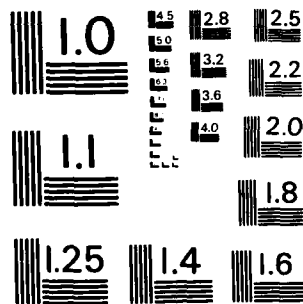
215

UNCLASSIFIED

F/G 5/1

NI

cont



MICROCOPY RESOLUTION TEST CHART  
NATIONAL BUREAU OF STANDARDS-1963-A

by temperature and are only found existing within a temperature range from 16° to 36° C, optimum growth occurring between 23° and 25° C (Smith 1971). Sabellariid worm reefs are distributed between latitudes 72° N and 53° S and generally exhibit wide tolerances to temperature within their individual species geographical ranges.

- d. Rock/hard bottom habitats. Temperature fluctuations are important in regulating the structure of rock/hard bottom communities by seasonally programming the life cycles of many of the dominant species associated with this habitat type (Figure 3-31). However, species dominance hierarchies associated with fouling/hard bottom communities have been found to shift in an unpredictable manner, responding to the availability of hard substrates, interspecific competition, and predation (Sutherland and Karlsen 1977, Sutherland 1981, Menge and Lubchenco 1981), more so than to temperature per se. Temperature extremes in arctic and tropical latitudes may in turn severely stress epifaunal hard bottom communities in shallow littoral environments by mechanical removal (ice) or by exceeding lower or upper thermal tolerances; as a consequence epifaunal communities are much more diverse and productive at lower latitudes (Thorson 1958, 1961; McRoy and Allen 1974). Recent studies of hard bottom (live bottom) habitats on the South Atlantic continental shelf have demonstrated seasonal as well as diurnal/nocturnal patterns in demersal fish species composition and abundance (BLM 1981). Species diversity and biomass of invertebrates found in these live bottom areas were found not to vary with respect to depth or latitude in the South Atlantic Bight (BLM 1981).

#### Current Velocity, Waves, and Storms

63. Water circulation plays an important role in structuring estuarine and marine benthic habitats and communities. The combined influences of freshwater inflow, tidal regime, wind, and oceanic forces result in specific patterns of water movement found in any coastal or estuarine system. The circulation of waters within an estuarine embayment or lagoon are responsible for transporting nutrients, plankton, and benthic larvae; flushing wastes from animals and plants; flushing the system of pollutants; controlling salinity; shifting sediments (eroding and deposition); and mixing the water masses (Clark 1974).

Naturally occurring storms of high intensity and relatively infrequent periodicity, such as hurricanes and tropical storms, may bring about large sudden changes in estuarine and marine benthic structure by sudden mass transport and redistribution of sediments, high wind and wave induced current velocities, and altered salinity patterns (Hayes 1978).

64. Circulation patterns in open ocean waters are dominated by large-scale forces which may have distant origins, such as massive currents like the Gulf Stream or California Current. Major currents of the North Atlantic and Pacific Oceans and the Gulf of Mexico (North Equatorial Current, Florida Current, Gulf Stream, North Atlantic Current, Labrador Current, Arctic Current, California Current, and Alaska Current) are responsible for regulating temperature and salinity in these oceans, which in turn control the currents (Emery and Uchupi 1972; Sverdrup, Johnson, and Fleming 1942) (Figure 3-32). Outwellings or eddies from these major currents onto the outer continental shelf may markedly affect primary production and benthos production in areas where they are known to occur, such as the South Atlantic (Atkinson 1977; Atkinson, Paffenhöfer, and Dunston 1978; Tenore et al. 1978; Hanson et al. 1981). Nearshore water circulation patterns, on the other hand, are largely controlled by tidal height, wind, waves, and land runoff.

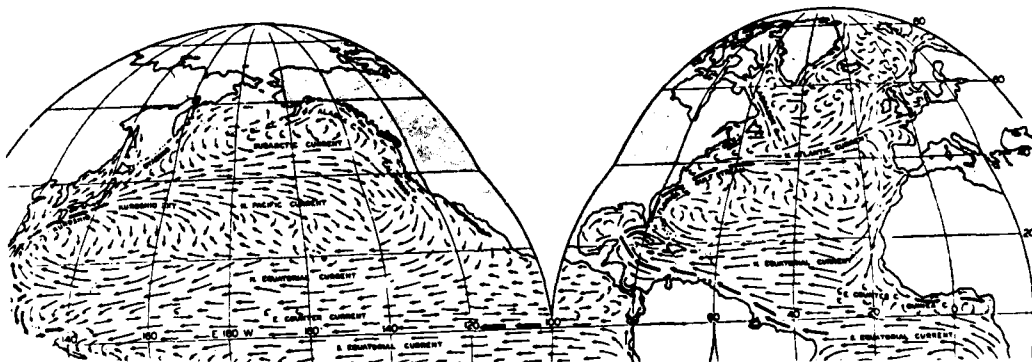


Figure 3-32. Average surface currents of the northern hemisphere of the world's oceans (modified after Sverdrup, Johnson, and Fleming 1942)

65. Upwelling of cold, nutrient-rich bottom waters onto continental shelves of the east, west, and gulf coasts may enhance productivity and affect benthos secondary production (Carpenter and McCarthy 1978, King 1958). Upwelling on the west coast occurs primarily in the spring and early summer and is usually induced by northerly winds, which through Ekman circulation drive surface waters offshore and cause an easterly movement of bottom waters onto the shelf. Upwelling areas are generally highly localized, and waters come from depths usually less than 200 m.

66. Residual, nontidal, and tidal currents occurring on the continental shelf may significantly modify benthic habitats. The general trend of these bottom currents for the northwestern Atlantic Coast suggest a dominantly southwestward movement, except between Cape Hatteras and Miami (Emery and Uchupi 1972). Large migrating sand waves several meters high are common on the western Atlantic shelf, with movements from northeast to southwest (Emery and Uchupi 1972), suggesting that bottom currents may be a significant factor in sediment transport in some shelf areas. Bottom features such as large sand waves, ripple marks, and degree of bioturbation give evidence of tidal bottom current intensity. Sediment patterns on shelves are controlled by bottom currents that transport sediments from their source areas. Generally the direction and speed of these bottom currents can be inferred from maps of clay and other minerals (Emery and Uchupi 1972). For example, the pattern of sediment grain-size distribution on the shelf of the northwestern Gulf of Mexico indicates a westward flow of bottom waters off Louisiana and a northeastward flow off southern Texas (Curry 1960). The distribution pattern of clay minerals along the entire Atlantic continental shelf indicates the bottom currents move sediments southwestward and into estuaries where general mixing of clays occurs (Hathaway 1972). The general transport of sediments from continental shelves into estuaries means that rivers are only able to contribute sediments to shelf environments during times of flood, when bottom currents are reversed (Emery and Uchupi 1972).

67. Tidal regimes are often the dominant force controlling water

movement in estuaries. Tidal cycles drive estuarine circulation patterns, and tidal amplitude may vary greatly with latitude as shown in Table 3-7. Within estuarine systems, tidal amplitudes generally decrease from the ocean landward through the inlet to the head of the estuarine basin (Clark 1974). Estuarine bathymetry also influences the magnitude of the water circulation patterns. Flushing rates are greater with increasing tidal range.

68. Circulation patterns in lagoons with little freshwater inflow and somewhat restricted inlet openings are largely controlled by wind. These types of lagoons are often poorly flushed and vulnerable to buildups of contaminants.

69. Current velocities generated by tides, wind, and storms are an important factor in structuring benthic communities associated with estuarine systems. Currents are important in delimiting the distribution of benthic habitat types. Storm-related impacts (disturbance) on benthic communities in soft bottoms may be largely controlled by water depth. McCall (1978) found storm-related disturbance to be a major controlling factor in benthos distribution in Long Island Sound. Current or wave stresses of 0.5 to 1 dyne/cm<sup>2</sup> are capable of entraining most fine-grained sediments from the bottom (Fukuda 1978; Rhoads, Aller, and Goldhaber 1977). Stresses of this magnitude are rare below 20 m (Figure 3-33), and McCall (1978) concluded that the combined stress effects of storms and the tidal system have little influence on the bottom below about 20 m in enclosed waters such as Long Island Sound. The actual depth beyond which wind-generated waves or current stress may disrupt the bottom is a function of the physical dynamics of the particular body of water and may be less than 20 m in a protected estuary or greater than 20 m in an open water body.

- a. Unconsolidated soft bottom habitats. Current velocity affects the distribution of sediment particle sizes in unconsolidated soft bottoms. Coarser sediments are associated with higher current environments, while fine-grained (mud) sediments are associated with lower energy environments. For example, a current velocity of 0.4 knot will shift ordinary sand along the bottom, while a current of 1 knot will shift fine gravel. A

Table 3-7  
Typical Tidal Characteristics of the Coastal Zone of the United States  
(after Clark 1974)

| Biophysical Region                  | Type of Tide        | Tidal Range, ft |        |          | Maximum<br>Tidal<br>Flood | Current<br>Velocity<br>Ebb |
|-------------------------------------|---------------------|-----------------|--------|----------|---------------------------|----------------------------|
|                                     |                     | Mean            | Spring | Diurnal* |                           |                            |
| <u>North Atlantic</u>               |                     |                 |        |          |                           |                            |
| Eastport, Maine (Bay of Fundy)      | Equal semidiurnal   | 18.2            | 20.7   |          | 3.5                       | 3.5                        |
| Isle de Haut, Maine (Penobscot Bay) |                     | 9.3             | 10.7   |          | 1.6                       | 1.7                        |
| Portsmouth Harbor, N. H.            |                     | 8.7             | 10.0   |          | 1.4                       | 2.1                        |
| Boston Harbor, Mass.                |                     | 9.5             | 11.0   |          | 2.0                       | 1.5                        |
| <u>Middle Atlantic</u>              |                     |                 |        |          |                           |                            |
| Dumpling Rocks (Buzzard Bay)        |                     | 3.7             | 4.6    |          | 0.9                       | 1.3                        |
| The Narrows (New York Harbor)       |                     | 4.5             | 5.5    |          | 2.0                       | 2.3                        |
| Cape May Harbor, N. J.              |                     | 4.4             | 5.3    |          | 2.1                       | 2.5                        |
| Virginia Beach, Va.                 |                     | 3.4             | 0.1    |          | 1.3                       | 0.9                        |
| <u>Chesapeake Bay</u>               |                     |                 |        |          |                           |                            |
| Wolf Trap Light (lower bay)         |                     | 1.0             | 1.2    |          | 1.8                       | 2.2                        |
| Point No Point (midbay)             |                     | 1.3             | 1.5    |          | 0.5                       | 0.7                        |
| Chesapeake Bay Bridge, Md           |                     | 0.8             | 0.9    |          | 0.8                       | 1.0                        |
| Washington, D. C. (Potomac River)   |                     | 2.9             | 3.3    |          | 0.7                       | 0.3                        |
| <u>South Atlantic</u>               |                     |                 |        |          |                           |                            |
| Wilmington, N. C. (Cape Fear River) |                     | 3.6             | 3.9    |          | 2.0                       | 2.7                        |
| Savannah River entrance, Ga.        |                     | 6.9             | 8.1    |          | 1.8                       | 3.0                        |
| Mayport, Fla. (St. Johns River)     |                     | 4.5             | 5.3    |          | 2.5                       | 3.5                        |
| Fort Pierce Inlet, Fla.             |                     | 2.6             | 3.0    |          | 3.0                       | 3.5                        |
| <u>Caribbean</u>                    |                     |                 |        |          |                           |                            |
| Miami Harbor, Fla.                  | Diurnal             | 2.5             | 3.0    |          | 2.2                       | 2.4                        |
| Key West, Fla.                      |                     | 1.3             | 1.6    |          | 1.2                       | 2.0                        |
| San Juan, P. R.                     |                     | 1.1             | 1.3    |          | **                        | **                         |
| Christiansted, St. Croix            |                     |                 |        | 0.8      | **                        | **                         |
| <u>Gulf of Mexico</u>               |                     |                 |        |          |                           |                            |
| St. Petersburg, Fla. (Tampa Bay)    |                     |                 |        | 2.3      | 0.3                       | 0.3                        |
| Pensacola Bay entrance, Fla.        |                     |                 |        | 1.1      | 1.8                       | 2.1                        |
| Barataria Bay, La.                  |                     |                 |        | 0.9      | 1.7                       | 1.7                        |
| Aransas Pass, Tex.                  |                     |                 |        | 1.7      | 1.6                       | 1.0                        |
| <u>Pacific Southwest</u>            |                     |                 |        |          |                           |                            |
| San Diego Bay entrance, Calif.      | Unequal semidiurnal | 3.9             |        | 5.6      | 1.2                       | 1.4                        |
| Monterey Bay, Calif.                |                     | 3.5             |        | 5.3      | **                        | **                         |
| San Francisco Bay entrance, Calif.  |                     | 4.0             |        | 5.7      | 3.3                       | 3.9                        |
| Point Arena, Calif.                 |                     | 4.0             |        | 5.8      | 1.3                       | 1.3                        |
| <u>Pacific Northwest</u>            |                     |                 |        |          |                           |                            |
| Humboldt Bay entrance, Calif.       |                     | 4.5             |        | 6.4      | 1.8                       | 2.3                        |
| Yaquina Bay entrance, Oreg.         |                     | 5.9             |        | 7.9      | 2.8                       | 2.6                        |
| Grays Harbor entrance, Wash.        |                     | 6.9             |        | 9.0      | 2.5                       | 2.2                        |
| Puget Sound (Elliott Bay), Wash.    |                     | 7.6             |        | 11.3     | **                        | **                         |
| <u>Alaska</u>                       |                     |                 |        |          |                           |                            |
| Juneau (Gastineau Channel)          |                     | 13.8            |        | 16.4     | 2.3                       | 2.3                        |
| Anchorage (Cook Inlet)              |                     | 25.1            |        | 28.1     | 3.3                       | 3.3                        |
| Goodnews Bay (Kuskokwim Bay)        |                     | 6.2             |        | 8.9      | 2.6                       | 2.4                        |
| Point Barrow                        |                     | 0.3             |        | 0.4      | **                        | **                         |
| <u>Pacific Islands</u>              |                     |                 |        |          |                           |                            |
| Honolulu, Hawaii (Oahu)             |                     | 1.2             |        | 1.9      | †                         | †                          |
| Hilo, Hawaii (Hawaii)               |                     | 1.6             |        | 2.4      | †                         | †                          |
| Apra Harbor, Guam                   |                     | †               |        | †        | 1.7                       | 3.4                        |
| Pago Pago Harbor, American Samoa    |                     | 2.5             |        | 4.0      | †                         | †                          |

\* For an unequal semidiurnal tide, the diurnal range is the extreme range over the two sequential tides in slightly over 1 day.

\*\* Weak and variable.

† No data.

Reference: The National Estuarine Inventory; Data source: U. S. Coast and Geodetic Survey.

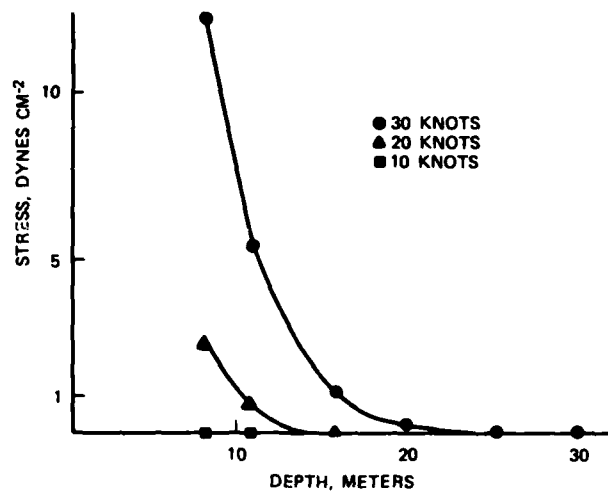


Figure 3-33. Average bottom shear stress as a function of wind speed and depth along a transect from New Haven, Connecticut, to Port Jefferson, New York (after McCall 1978)

current of 2.15 knots will move coarse gravel 2.5 cm in diameter, and 3.5 knots will move angular stones up to 3.8 cm in diameter (note 1 knot = 51.5 cm/sec) (Moore 1958). Therefore, currents largely determine the grain-size distribution of sediments. Figure 3-34 illustrates graphically the relationship between current velocity and its potential to deposit, transport, and/or erode sediments of various grain sizes. Areas characterized by high current velocities, such as harbor channels and coastal entrance channels, usually exhibit an impoverished benthic fauna due to the high degree of current stress associated with these areas. In estuaries and embayments, filter/suspension feeding groups are found primarily in higher energy coarse sediment environments, while deposit feeding benthos dominate the lower energy mud environments for the most part (Rhoads and Young 1970; Sanders 1958, 1960).

- (1) Wave-induced sediment disturbance may be very important in structuring shallow estuarine and marine benthic communities (McCall 1978; Rhoads, McCall, and Yingst 1978; Oliver et al. 1979). It is expected that effects of storms with higher wave frequencies and subsequent bottom disturbance (Figure 3-34) result in patterned distributions of benthic communities (i.e., the "spatial mosaic" discussed in paragraph 20) in relatively shallow (<20 m) shelf environments similar to those

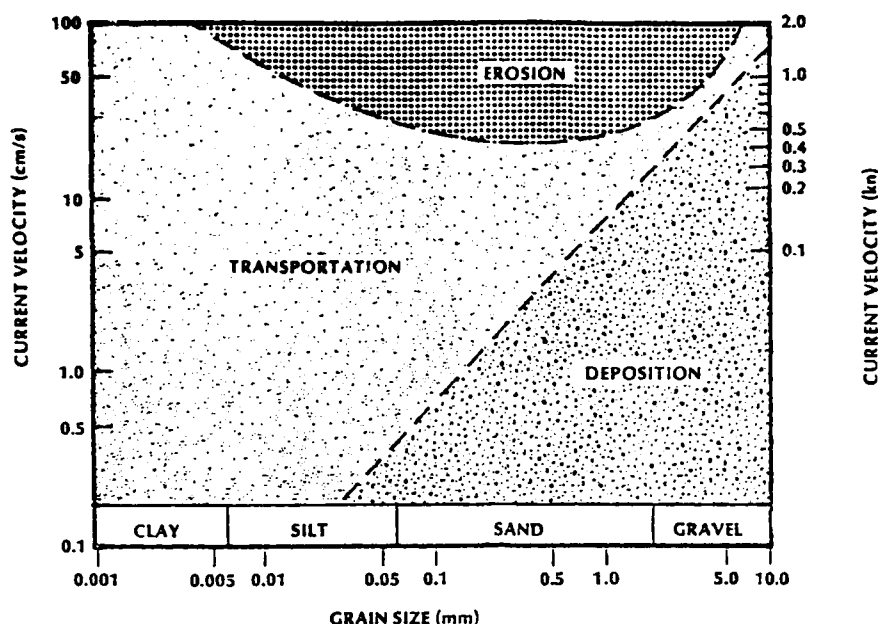


Figure 3-34. The relationship between current velocity and its potential to deposit, transport, or erode sediments of various grain sizes (after Moherek 1978)

observed in estuaries (McCall 1978; Rhoads, McCall, and Yingst 1978). For example, Frankenberg and Leiper (1977) found large spatial and temporal variations in nearshore (<21 m) marine benthic soft bottom community structure on the Georgia continental shelf. Recent studies by Oliver et al. (1980) observed nearshore faunal zonation on the continental shelf off Monterey, California, which were correlated with depth and wave-induced bottom disturbance. Benthos were classified into a shallow zone (<14 m) containing sediments frequently disrupted by wave activity, and this zone was primarily occupied by small, mobile, deposit feeding crustaceans. The deeper zone (>14 m) was dominated by sedentary polychaetes living in permanent tubes and burrows. These variations in faunal structure and animal motility patterns were correlated with water depth and the strength of the wave activity (Figure 3-35). The sedentary, tube-dwelling polychaete dwellers are unable to establish and maintain biogenic structures in areas subject to intense physical sediment movement, and thus they are largely restricted to areas of less intense

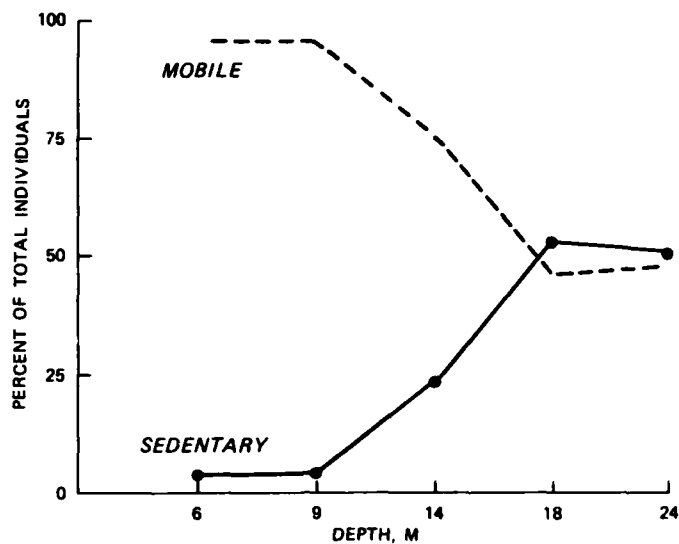


Figure 3-35. Variations in animal motility patterns along southern sandflats in Monterey Bay, Calif. (after Oliver et al. 1979)

wave activity (i.e. deeper waters). This same general pattern of zonations of benthic community structure in high-energy shallow shelf areas has also been documented for much of the temperate open coast of western North America (Carey 1965, 1972; Lie 1969; Lie and Kisker 1970; Barnard 1963; Van Blaricom 1978). It is likely that future studies will identify similar zonations of nearshore (<30 m) shelf benthos related to high-energy wave-induced sediment disturbance for the east and gulf coasts as well (Oliver et al. 1979). European coastal studies have also documented similar crustacean and polychaete dominated benthos assemblages related to wave exposure (Masse 1972; Rees, Nicholaidou, and Laskaridou 1977).

- (2) Adaptive life strategies of benthos associated with shallow water habitats subject to frequent disturbance differ markedly from those faunas characteristically found in relatively undisturbed soft bottoms (see Table 2-1). Communities dominated by opportunistic species are widespread, but generally dominate soft bottoms subjected to physical or pollution disturbances (McCall 1978) (see Figure 2-2). Their distributions are generally patchy in time and space, reflecting both life history strategies

and frequency of disturbance. Equilibrium species on the other hand are generally more evenly distributed, reflecting their much lower frequency of disturbance.

- b. Aquatic vegetation beds. Currents and storms effectively regulate the distribution and community structure of seagrasses in estuaries and coastal marine environments. Kelp beds, on the other hand, require moderately high wave energies (Phillips 1974). Seagrasses, particularly turtle grass, have been found to be particularly resistant to storm-related stresses, such as hurricanes. Observations by Thomas, Moore, and Work (1961), Oppenheimer (1963), and Phillips (1980) on the impact of hurricanes on turtle grass beds found that winds up to 175 mph (152 kn) had negligible effects on the vegetated beds. Eelgrass may be somewhat less resistant to wave exposure, although this species thrives in moderate current (up to 3.5 kn). Phillips (1972) observed eelgrass beds following a storm in Puget Sound, Washington (1- to 2-m waves for 2 days) with 40-kn winds and found that, although between 7 to 10 cm of sediment was removed exposing the rhizome mat, the eelgrass bed remained intact and subsequently recovered. Seagrass species such as turtle grass and eelgrass are therefore very important sediment stabilizers in shallow estuarine and coastal waters due to their ability to bind sediments and prevent erosion. This was documented by Orth (1977b) following a storm in Chesapeake Bay: up to 20 cm of sediment eroded from unvegetated sand banks, while little, if any, sediment disappeared from within an eelgrass meadow. The density, width, and length of leaves act as baffles that effectively trap sediments, particularly the finer grain sizes (Schubel 1973, Orth 1977a) (see Figures 3-15 and 3-16). Subtle changes in macrobenthos structure may be a consequence of seagrass beds subjected to current stress. O'Gower and Wacasey (1967) found higher numbers of species but lower species diversities and higher dominance (species equitability) in current stressed subtropical seagrass habitats (Figure 3-21).
- c. Reefs. Biological reefs (oyster, coral, and sabellariid) require sufficient water movements to maintain their structure. Currents transport the dissolved nutrients, suspended matter, and plankton over the oyster, coral, algal, and worm reefs thereby regulating the production of the reefs. Currents and waves regulate the structure of oyster reef communities (see paragraph 41), and mollusc and sabellariid reefs align themselves with prevailing currents or water movements within the estuarine and marine environment (Figures 2-7 and 2-11). Wave actions modify the shape of

colonies of individual coral species, and a single species may exhibit a number of different growth forms in varying current and wave energy environments. To maintain a flourishing oyster community there must be a continuous renewal of seawater running over the bottom (Galtsoff 1964). Adult oysters, living under optimum salinity and temperature conditions, pump water at a rate of 15 l/hr. Therefore, oysters cannot exist in areas of sluggish water in high population densities. Storms affect the distribution of all reefs by high current velocities, increased sedimentation rates, and altered salinity regimes, all of which may adversely affect the structure of reef communities by physical removal, burial, or mortalities. Wells (1961) studied the structure of oyster reef communities following the passage of three hurricanes in the Newport River, North Carolina. He found high mortalities in oyster communities primarily related to the drastically altered salinity regimes, although sediment redistribution and deposition on reefs also contributed to the mortalities. Sedimentation was cited by Engle (1948) as a major factor in oyster mortalities observed in Louisiana, Mississippi, and Alabama following a hurricane. Storms may also temporarily increase the diversity of coral species by localized disturbances (i.e., heavy sedimentation and physical abrasion), which open up bare substrates for colonizing fast growing "opportunistic" species. These areas will then undergo a localized succession, and the opportunistic coral and algal species will be gradually replaced by slower growing but more highly competitive species (Grassle 1973; Rogers, Suchanek, and Pecora 1982); storm-related disturbances thereby create spatial mosaics in coral reef community structure not unlike those observed in unconsolidated soft bottoms. In coastal marine environments, a particularly important role that coral and sabellariid reef habitats serve is that of shoreline stabilization by breaking up and dissipating wave and current energies nearshore.

- d. Rock/hard bottom habitats. The persistence of this habitat type and its associated communities is largely dependent on current and/or wave energies sufficiently strong enough to maintain a sediment-free surface. Faunas of this habitat type are especially sensitive to large storms and high current velocities which may increase sedimentation rates and suspended solids levels to unacceptable levels smothering filter/suspension feeding species, or physically dislodging attached sedentary forms from their hard substrates. Studies relating the growth of particular fouling species to current velocity may serve to illustrate the importance

of current stress to epifaunal invertebrates (Figure 3-36). When currents are too low, hard bottom community species do not receive enough food and aeration for internal metabolic activities and waste removal. Alternatively, when currents are too high the stress of attachment, feeding, and maintenance diminishes the amount of biological structure that can be maintained.

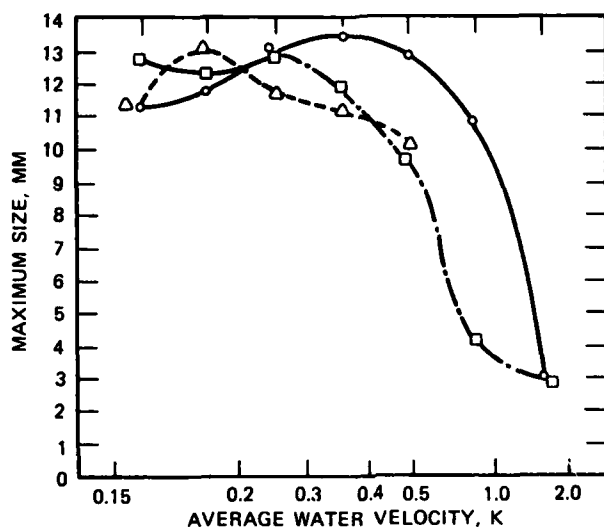


Figure 3-36. Current velocity effects on the growth of three species of barnacles, *Balanus amphitrite* (circles), *B. improvisus* (squares), *B. eburneus* (triangles) (after Doochin and Smith 1952)

### Depth

70. The bathymetry of a particular estuarine basin, coupled with freshwater inflow and tidal range, will determine the particular water circulation properties and types of substrates found. The significance of depth in regulating the frequency of physical disturbances to substrates has already been discussed (paragraph 69). In deep estuaries such as fjords, depth may also influence the standing crop of benthos found, although substrate quality changes also occur which may be a contributory factor. Figure 3-37 illustrates this relationship for an

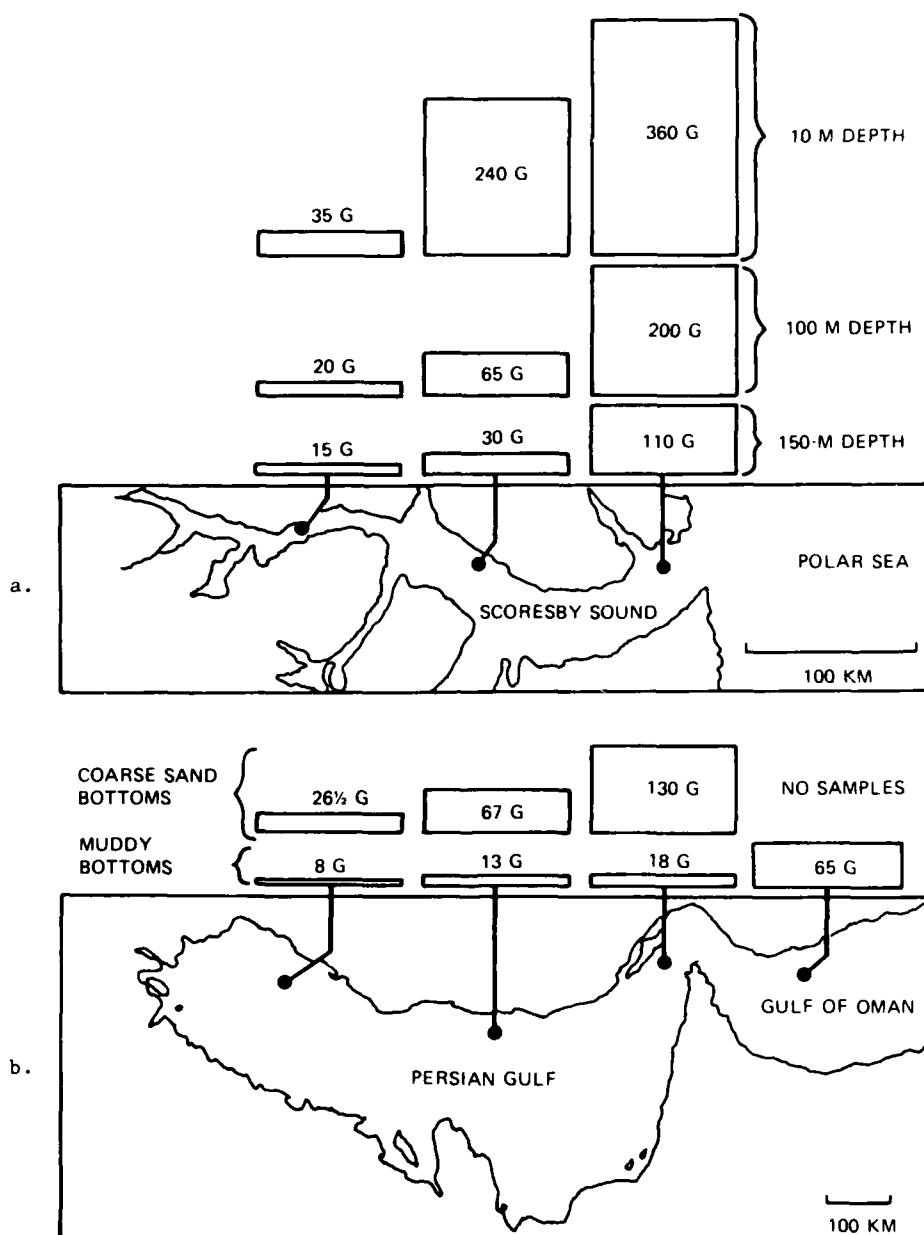


Figure 3-37. Macrobenthic infaunal biomass distribution according to (a) depth in a high-arctic fjord and (b) substrate quality in a tropical fjord (after Thorson 1957). Note: all biomass units are expressed as grams (G) per square meter

arctic fjord (Thorson 1957). There appears to be some relative decrease in benthic infaunal biomass with increasing depth and distance upstream from the mouth of the estuary. In coastal marine shelf environments, benthos community structure, species diversity, and standing crop also show generalized trends with depth. Studies have described a general species continuum of change along depth gradients from shallow water (20 m) to deep abyssal regions (Parker 1964; Sanders 1968; Sanders and Hessler 1969; Rowe, Polloni, and Horner 1974; Flint and Holland 1980). On a macroscale, benthos standing crop generally decreases from higher to lower latitudes and from nearshore shelf to outer shelf regions (Figure 3-38) as a consequence of decreasing primary production and food resources (Figure 3-39) (Emery and Uchupi 1972; Rowe, Polloni, and Horner 1974; Haedrich and Rowe 1977; Mills 1980). At depths of 1000 m or greater, benthos standing crop becomes relatively uniform and no latitudinal gradient is apparent (Figure 3-38). These trends are highly generalized, and localized variations in primary production (i.e. upwelling) for a region may alter this general pattern in the shelf environment. For example, an inverse depth-related distribution of macrobenthic biomass has been observed on the Georgia continental shelf (Figure 3-40) (Tenore et al. 1978, Hanson et al. 1981) and on the Washington continental shelf (Lie 1969). Tenore et al. (1978) found a relatively impoverished marine benthic community at nearshore shelf stations, which they attributed to low nutrient inputs and unfavorable sedimentary regimes. Nitrogen-rich Gulf Stream intrusions onto the shelf are common and may be responsible for the higher standing crops observed at outer shelf stations due to higher primary productivity in those areas (Tenore et al. 1978, Hanson et al. 1981). Flint and Holland (1980) identified three depth-related benthic infaunal assemblages in a transect study off the south Texas coast. Species diversity and equitability increased from shallow (22-m), middepth (36- to 49-m), to deepwater (78- to 131-m) shelf areas, primarily as a response to increased environmental stability. They concluded that environmental heterogeneity, including climatic variability (current velocity, waves, temperature, salinity), may be most important in

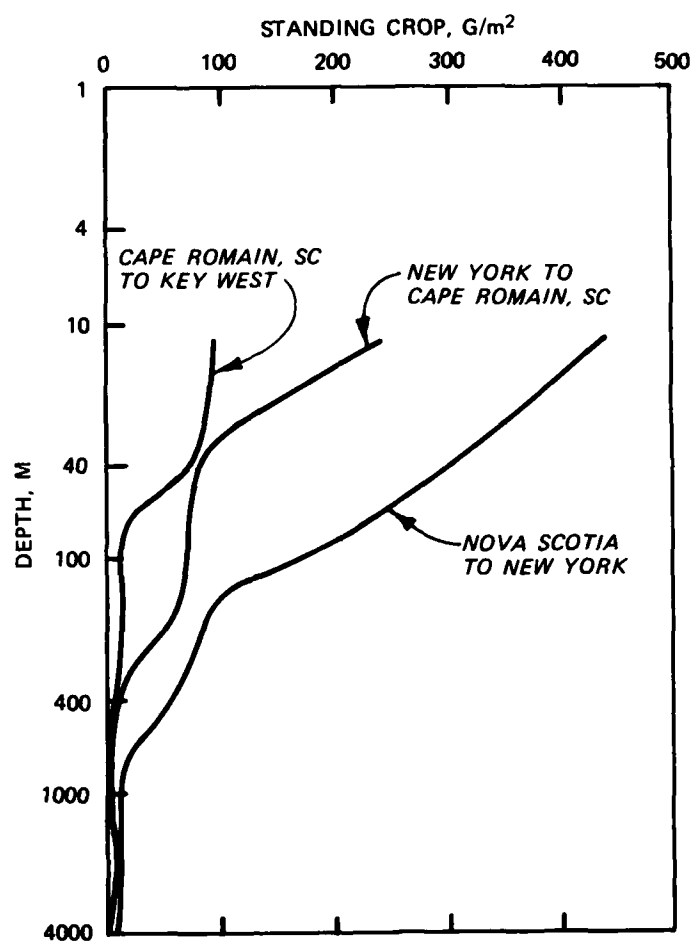


Figure 3-38. Highly generalized distribution gradients with depth of macrobenthos standing crop biomass for three latitudinal ranges of the ocean floor off the northwestern Atlantic coast (after Emery and Uchupi 1972)

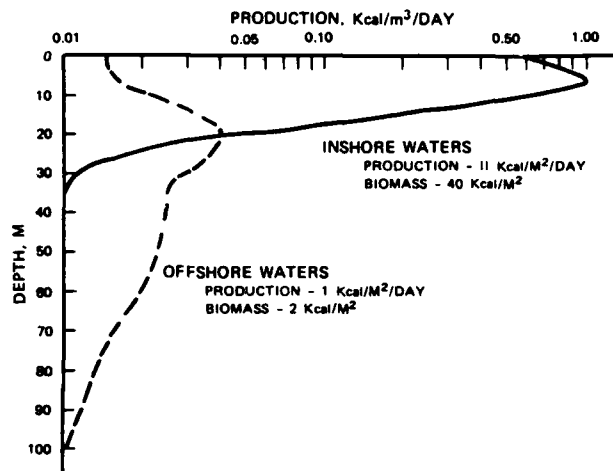


Figure 3-39. Comparison of the vertical distribution of primary production and biomass between inshore and offshore waters of the northeast Atlantic (after Currie 1958)

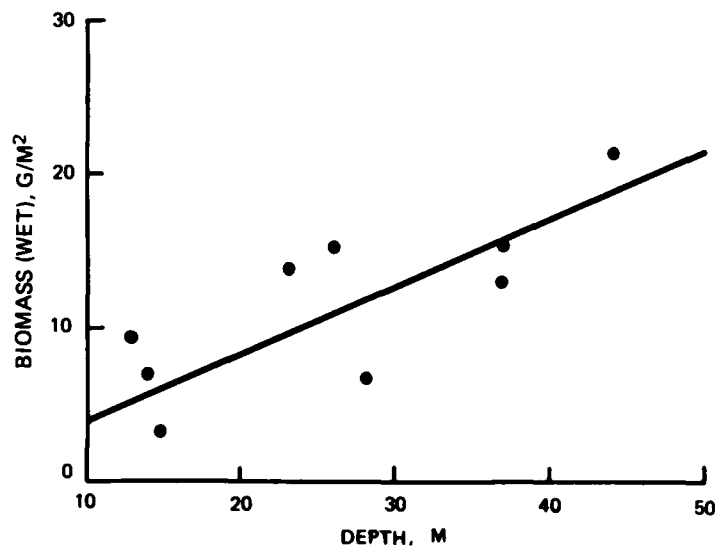


Figure 3-40. Scattergram and plot of a significant ( $p < 0.05$ ) regression line illustrating the relationship of macrobenthic biomass and depth across the Georgia continental shelf environment (data from Tenore et al. 1978)

controlling shallow-water benthos structure, while species interactions become progressively more important with increasing environmental stability (i.e. depth). Others have made similar observations and reached similar conclusions concerning the structure of benthic communities in nearshore and offshore shelf environments of the west and east coasts (Sanders 1968; Sanders and Hessler 1969; Day, Field, and Montgomery 1971; Boone, Granat, and Farrell 1978; Jumars and Fauchald 1977). Studies of benthic trophic structure along a gradient of increasing depth have shown some general trends. For example, Parker (1964) found decreasing compositions of suspension/filter feeding benthos and increasing compositions of deposit feeding benthos with increasing depth off California from shallow shelf to abyssal environments (Figure 3-41). Substrate instability due to wave-induced disturbance may alter this pattern in nearshore shelf areas along high-energy coastlines (see paragraph 69a(1)) (Figure 3-35).

- a. Unconsolidated soft bottom habitats. The trends outlined in the previous paragraph are all apparent in soft bottom habitats. Depth-related changes in sediment composition are also apparent. It is generally believed that environmental heterogeneity (i.e., difference in substrate, current velocity, temperature, dissolved oxygen, salinity, etc.) is primarily responsible for controlling benthic community structure (i.e., these are "physically accommodated communities") in temporally variable estuarine and shallow marine environments; whereas biological interactions become increasingly more important in environmentally stable environments (i.e., these are "biologically accommodated communities") (Sanders 1968, 1969). Thus, depth indirectly influences community structure by dampening or magnifying the variability of the other habitat descriptors, which in turn delimit the distribution and abundance of benthic species associated with soft bottoms.
- b. Aquatic vegetation bed. Decreasing light attenuation with depth sharply limits the seaward distribution of submerged attached marine macrophytes (seagrasses and algae). The compensation depth is limited by turbidity and generally increases with distance from shore, and all submerged aquatic vegetation bed habitats are generally restricted to depths of 31 m or less. Figure 3-42 illustrates the distribution of eelgrass and dominant bivalve species with depth and substrate

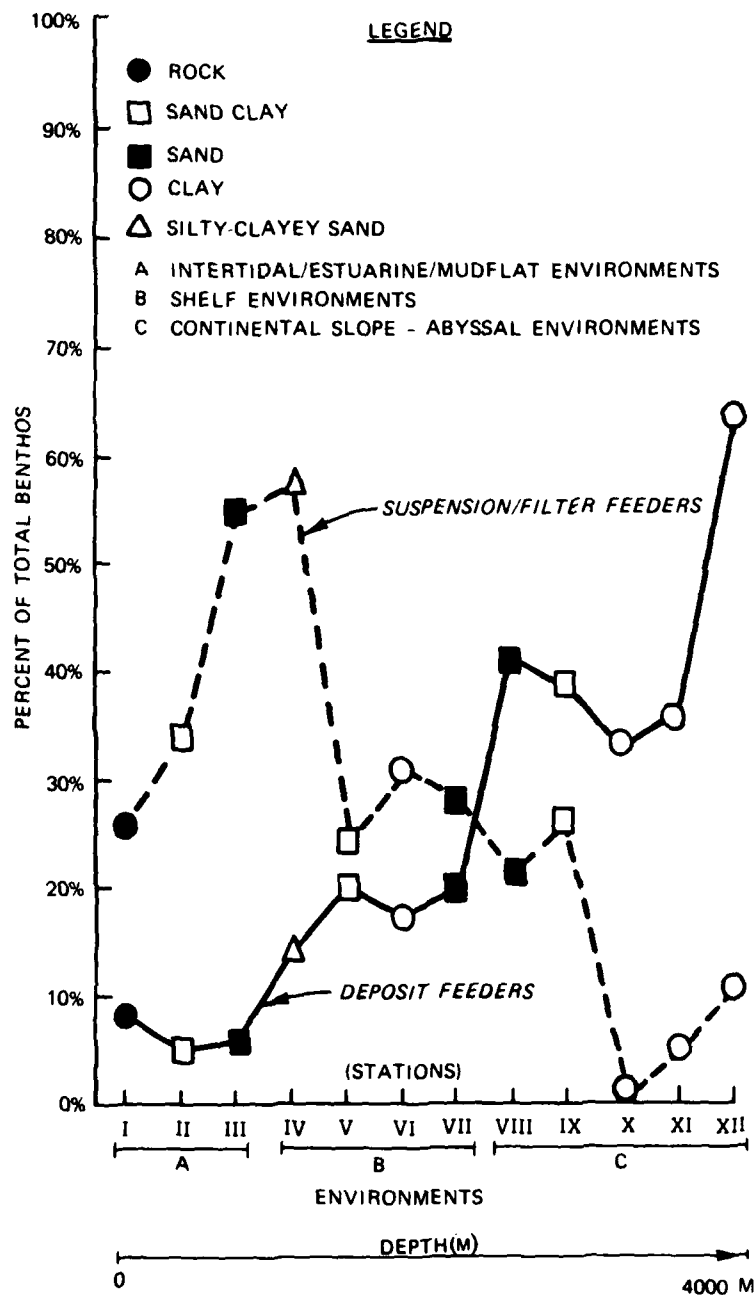


Figure 3-41. Distribution of two benthic feeding types in various sediment types along a gradient of increasing depth (after Parker 1964)

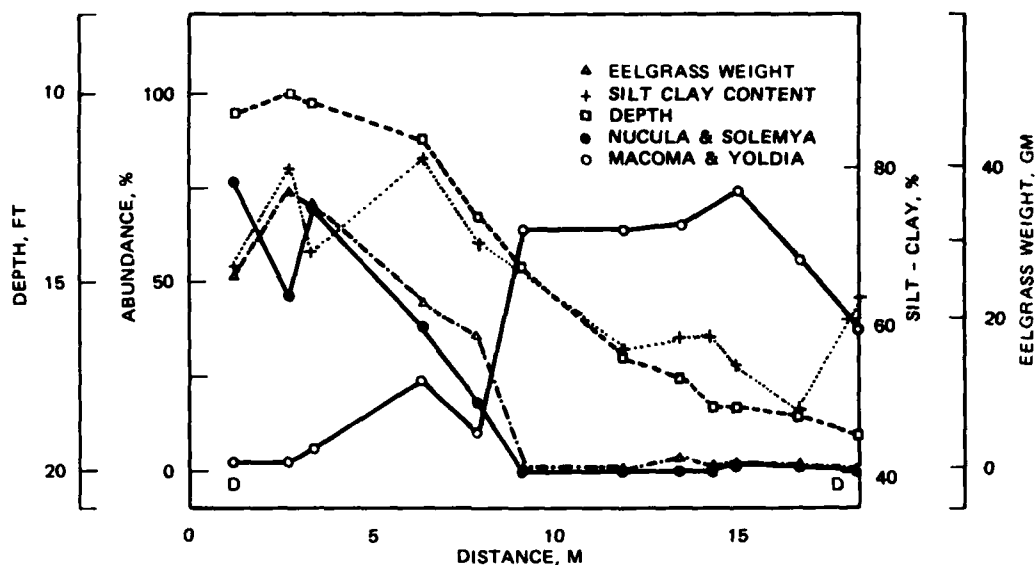


Figure 3-42. Distribution of dominant bivalve species, water depth, dry weight of eelgrass (per  $0.1 \text{ m}^2$ ), and percent silt-clay along a transect (after Levington 1977)

quality (silt-clay content) in a Massachusetts estuary.

- c. Reef habitats. Reef habitats are sharply delimited by depth, particularly true coral reefs. Symbiotic zooxanthellae require high light intensities, thereby restricting the depth regions of active coral growth to the upper 30 m or so from the surface. Other reefs such as sabellariid worm reefs are limited to relatively shallow nearshore high-energy environments between 2 and 10 m.
- d. Rock/hard bottom. This habitat is not depth limited, but is found whenever currents and wave activities are sufficient to maintain a clean, sediment-free surface. Benthic community dominants are generally sessile.

#### Water Quality

71. Water quality is of the utmost importance to all aquatic organisms. Various discrete, measurable aspects of water quality, such as salinity and temperature, have already been discussed as important parameters structuring estuarine and coastal marine benthic communities.

Therefore, this section will focus on a few important water quality parameters such as dissolved oxygen, turbidity, and general pollution which may significantly affect benthic community structure and function within estuarine and coastal marine environments.

#### Dissolved oxygen

72. Dissolved oxygen has long been shown to be a significant factor in delimiting the distribution of benthic faunas in aquatic environments. In seasonally stratified estuaries, such as Chesapeake Bay, seasonally hypoxic or anoxic conditions developing near the bottom have been observed to locally extinguish the benthic faunas occurring there (Biggs 1967; Holland, Mountford, Mihursky 1977; Taft et al. 1980). Fine-grained sediments with high organic matter content may lead to hypoxic or anoxic conditions in sediments and overlying waters. Oxygen depletion at the water-mud interface may result in complex changes in the solubility or concentrations of many elements basic to biological productivity (May 1973). Under anaerobic conditions, desorption of phosphate, hydrogen sulfide, carbon dioxide, ammonia, silicate, iron, and other metals may take place (Jitts 1959, Mortimer 1971). In strongly reducing environments desorbed metals generally form highly insoluble metal sulfides and precipitate out of solution; but these metals may be remobilized by processes such as sediment resuspension and/or bioturbation (e.g. by burrowing infaunas) of reoxidizing sediments (Troup and Bricker 1975). Oxygen depletion in sediments following a disturbance or pollution event may displace resident benthic species (equilibrium species) in favor of eurytopic opportunistic species (see Figure 2-2). May (1971) found 100 percent mortality in oysters from a reef in Mobile Bay following a 10-day period of low dissolved oxygen. Anoxic conditions resulting from a serious outbreak of the red tide organism *Gymnodinium breve* were responsible for the defaunation of benthos on the Florida west coast in Tampa Bay (Simon and Dauer 1977). Dissolved oxygen levels are generally not limiting to marine benthic communities except in areas subject to (a) seasonal thermoclines or haloclines (e.g., the Louisiana shelf), (b) upwellings, (c) nutrient enrichment from anthropogenic sources (sewage sludge), and

(d) large algal blooms (red tide). Oxygen depletion has been observed in the New York Bight in deeper areas below the seasonal pycnocline (temperature-related density gradient) at about 30 m (Boesch 1982, Malone 1978). A prolonged period of anoxia or hypoxia may lead to faunal extinctions in benthic habitats where they occur.

73. Nutrient levels in marine coastal environments generally decrease from nearshore to offshore and affect the primary production and benthic secondary production (Figures 3-38 and 3-39). Localized nutrient enrichment from natural or anthropogenic sources may increase benthic productivity. Tenore et al. (1978) and Hanson et al. (1981) attributed higher macrobenthos standing crops on the outer continental shelf to nutrient enrichment from Gulf Stream intrusions onto the Georgia shelf (Figure 3-40). Upwelling of slope water onto the outer continental shelf may be the primary source of inorganic nutrients in these areas (Carpenter and McCarthy 1978), while benthic regeneration of nutrients may be the primary source in estuaries and bays (Nixon, Oviatt, and Hale 1975). Offshore disposal of sewage sludge increases sediment nutrient levels and organic carbon content which may enhance benthos secondary production. A sewage sludge enriched area in the New York Bight apex is reported to support higher standing crops of macrobenthos than surrounding unaffected areas and nearby estuaries and bays, although the quality of the macrobenthos in the enriched area to demersal fish predators is questionable (McGrath 1974, Boesch 1982). An analysis of benthos structure in the enriched area and local fish feeding habits by Boesch 1982 suggests that only a small fraction of the resident benthos in the enriched areas is being utilized as prey by demersal predators, and that the overall trophic resource potential of the area may be reduced. High benthic standing crop biomass does not imply predator utilization, and may be instead the result of low-level predator cropping (Virnstein 1977, 1979; Reise 1977).

#### Turbidity

74. Turbidity is an expression of an optical property of a fluid caused by the presence of suspended matter such as clay, silt, finely divided organic and inorganic matter, plankton, and other microscopic

organisms. Increased turbidity and suspended solids loads in estuaries generally result in increased sedimentation, which affects benthic habitats. In estuaries, flocculation of silt-size particles generally takes place at the river estuary boundary (0-5 ‰) and is dependent on temperature, pH, and the types of sediments in suspension.

75. Studies of sedimentation in benthic communities such as oyster reefs have shown that deposits of silt or loose sediments as thick as 1 to 2 mm over a hard substrate or shell surface are sufficient to cause failure of setting oyster larvae and other larvae (Galtsoff 1964). Increased sedimentation in bays and estuaries has destroyed oyster reefs along the Texas coast (Galtsoff 1964) as a result of anthropogenic influences (soil erosion, deforestation, population increases).

76. Turbidity levels in water influence the depth of light penetration, which in turn affects the ability of plants to carry out photosynthesis. The depth at which oxygen production from photosynthesis equals oxygen consumption through respiration defines the compensation point; the compensation point in turn is approximately equal to that depth at which light penetration is 1 percent of the surface intensity. Water transparency or turbidity affects the compensation depth, which varies from less than 1 m in turbid estuaries to over 100 m in the nutrient-poor open ocean and decreases shoreward as a function of increased nutrient levels and primary production (Raymont 1963). High turbidity restricts the euphotic zone in estuaries, while suspended materials enhance the photosynthetic rate by providing large quantities of nutrients (Stern and Stickle 1978). Turbidity levels generally decrease from inshore to offshore except in areas of nutrient enrichment (upwelling, intrusions, sewage sludge disposal, etc.). Tenore et al. (1978) found a general decrease in suspended particulate matter offshore as a result of seawater dilution of coastal-derived suspended solids within the Georgia Bight (continental shelf). The depth distributions of aquatic vegetation bed habitats are turbidity limited. The maximum depth reported for kelp beds is around 31 m, while seagrasses such as eelgrass and turtlegrass are rarely found

below 10 and 20 m, respectively, in low-turbidity waters (Phillips 1974, 1978, 1980; Zieman 1975). Large benthic macrophytes such as kelp and seagrass beds may baffle currents, thereby trapping sediments and lowering turbidities. Filter/suspension feeding benthos such as oysters, other bivalves, barnacles, and tunicates may also play an important role in reducing turbidities by filtering suspended solids from the water column and depositing the material as feces and pseudofeces (Haven and Morales-Alamo 1967). Haven and Morales-Alamo (1967) found that oysters may produce up to 2422 kg/hectare/week of pseudofeces and feces. These biodeposits were found to consist of particles generally less than 3  $\mu$  in diameter, and were between 77-91 percent inorganic matter and between 4-12 percent organic carbon. Other types of benthos, such as surface feeding species, may increase near bottom turbidity levels as a result of their feeding activities (Rhoads 1973). Pumping rates in filter/suspension feeders are frequently reduced during periods of high concentrations of suspended solids which clog the animal's filtering apparatus. When turbidity levels remain at high levels, a filter feeding organism's growth rate will be reduced (Stern and Stickle 1978). Coral reef habitats are particularly sensitive to turbidity and siltation (Grigg 1970, Bok 1978). The effects of turbidity and suspended solids on aquatic organisms and associated environmental impacts have been extensively studied and reviewed under the Dredged Material Research Program (Stern and Stickle 1978; Hirsch, DiSalvo, and Peddicord 1978; Peddicord and McFarland 1978). These studies generally found that most species survived short-term levels of suspended solids associated with normal dredging and disposal operations, and that long periods of exposure were generally required to cause mortalities. Furthermore, contaminants bound by sediments are generally not readily available to biota (Luoma 1974; Kendall 1978; Windom and Kendall 1979; Neff, Foster, and Slowey 1978; Stern and Stickle 1978; Hirsch, DiSalvo, and Peddicord 1978; Peddicord and McFarland 1978), due to strong sorption by organic particulate matter and clay minerals. Dissolved contaminants rather than sediment-bound contaminants appear to be the major pathway for bioaccumulation and toxicity in aquatic organisms.

## Pollution

77. A comprehensive discussion of pollution effects on benthic communities is beyond the scope of this report. Much has been written in recent years concerning individual pollutants and their effects on aquatic organisms. Pollutants may be in the form of organic (sewage, hydrocarbon, pesticides) or inorganic (metals, radionuclides, chemicals) contaminants. Recent reviews by Reish et al. (1979); Pearson and Rosenberg (1978); Pearson 1982; and Pearson, Duncan, and Nuttall (1982) summarize much of the extensive pollution literature as it relates to estuarine and marine taxa, individual species, and benthic community responses. The Environmental Protection Agency's "Quality Criteria for Water" (Red Book) reviews the literature and critical levels for a number of priority pollutants, although a recent review of the Red Book by Thurston et al. (1979) has questioned the adequacy of critical levels established for many of the priority pollutants. In estuaries, the degree of eutrophication may have a significant effect on the toxicity and stimulatory and/or inhibitory effect of a given contaminant or group of contaminants at the population or species level. It is well known that dissolved organic carbon, suspended particulate organic matter, and clay minerals will chelate metals and organic pollutants and thereby alter and frequently reduce their toxicity and bioavailability (Luoma 1974; Linberg, Andren, and Harriss 1975; Smith 1976; Windom 1975; Kendall 1978; Neff, Foster, and Slowey 1978). Therefore, pollutants may be more toxic and/or bioavailable in oligotrophic aquatic environments than in eutrophic environments such as estuaries. This has been demonstrated for mercury, copper, and sewage pollution (Lewis, Whitfield, and Ramnarine 1972, 1973; Luoma 1974; Kendall 1978; Dauer et al. 1979; Dauer and Conner 1980).

78. Organic pollution as a result of nutrient enrichment from sewage effluents in low to moderate amounts may enhance the primary and secondary production of an aquatic system. Severe eutrophication from sewage sludge may increase the nutrient loads in the water column beyond a system's capacity to assimilate them. This nutrient overload stresses animal communities in these systems by lowering dissolved

oxygen (DO) levels and increasing biological and chemical oxygen demand. Lower DO levels may (a) in turn destabilize a community by reducing the species diversity and equitability to produce high dominance and (b) alter the productivity compared with a more natural, unenriched area. Sensitive, stenotopic species are selected against in favor of eurytopic, opportunistic species able to exploit marginally suitable habitats (Table 2-1). A classic example of severe water pollution was caused by duck farms in Long Island, New York, where indiscriminate dumping of duck manure into the bay resulted in an excessive buildup of nitrogenous wastes and large plankton blooms and a subsequent decline in shellfish populations in this area (Reidfield 1952, Ryther and Dunstan 1971). Organic pollutants such as sewage effluents and/or sludge have been much studied and their effects on benthos described. In general, four benthic faunal response zones are recognized as surrounding an organic effluent source (Reish 1973). The first zone, which is closest to the effluent source, is abiotic (grossly polluted); macrofauna are absent from this zone due to hypoxic or anoxic conditions. At a greater distance there exists a polluted zone characterized by a few very tolerant species; exploitation of enhanced organic material by a few eurytopic species may result in high population densities for these species. A third zone, lying between the polluted and normal zone, has been termed the enriched, hypertrophic, or transitory zone (Pearson and Rosenberg 1976, 1978; Reish 1973). In this zone the number of species, densities, and biomass may be increased above levels found in the normal, unaffected fourth zone. (See Figure 2-2 for a representation of a soft bottom benthic community's response to a pollution distance gradient.)

79. A study by McIntyre (1977) indicated that carbon input rates to the subtidal benthos were 55 times the natural rate at a sewage dump site. The enriched site had higher invertebrate densities ( $47,285/m^2$  versus  $1310/m^2$ ) and biomass ( $129.9\text{ g}/m^2$  versus  $40.5\text{ g}/m^2$  wet weight) than a similar but unaffected site, although the number of species found was lower at the enriched site (20 versus 33 species). A bio-stimulatory effect was also found in a study by Dauer and Conner (1980)

in Tampa Bay. They found individual polychaete densities, total biomass, and individual species numbers significantly greater at a moderately sewage-affected site.

80. Nutrient enrichment in the form of sewage effluent may have a biostimulatory effect, especially in nutrient-poor environments such as the open ocean (Dauer and Conner 1980). The greatest enhancement of biological productivity will occur within coarser sandy sediments compared to naturally organically rich, high clay-silt-content sediments. Dauer et al. (1979) found little enhancement of benthic productivity from sewage effluent in clayey-silt-type sediments, while Dauer and Conner (1980) found an almost four-fold increase in benthic productivity in sediments with low concentrations of fine-grain-size particles (2.67 percent silt-clay; 0.68 percent organic matter). Orth (1977b) found a similar relationship for eelgrass, *Zostera marina*, in low silt-clay-content sediments artificially enriched with fertilizer.

81. Environmental contamination from sewage and industrial effluents with metals, pesticides, PCB's, organic sludge, oil pollution, and radioactive wastes may adversely impact animal and plant communities by acute and chronic toxicity stress and by degrading habitats (Reish et al. 1979; Pearson and Rosenberg 1976, 1978). Synergistic or antagonistic effects of multiple contaminants may further compound the potential environmental impacts. Sublethal chronic effects of low-level exposure to multiple pollutants are not well understood (Malins and Collier 1981). Studies have shown that the effects of multiple pollutants in combination may be additive and consequently much more severe (Gray 1974, 1976; Braek, Jensen, and Mohus 1976; Vernberg, DeCoursey and O'Hara 1974). On the other hand, studies of estuarine benthos in Southwest England subjected to chronic metals pollution for 200 years from mining operations have demonstrated the remarkable ability of benthic communities to survive and adapt to toxic metal stresses; these communities show little discernible change in structure compared to nonmetal-contaminated estuaries (Bryan 1971, 1973, 1974; Bryan and Hummerstone 1971, 1973a, 1973b, 1977). Although the distribution and diversity of species in these heavily contaminated estuaries is fairly

normal, organisms found there are heavily contaminated with metals, and tissue concentrations may range two to three orders of magnitude higher than those from uncontaminated estuaries; these organisms may thus represent a potential hazard to man (Bryan 1974). Although food web-mediated bioamplification of contaminants has been demonstrated in terrestrial ecosystems (Woodwell, Wurster, and Isaacson 1967; Rudd, Craig, and Williams 1981), attempts to document its occurrence in aquatic ecosystems have generally failed except possibly in the case of mercury (Kendall 1978; Pentreath 1976a, 1976b, 1976c; Windom et al. 1976a; Windom and Kendall 1979; Gardner et al. 1975; Gardner et al. 1978; Irukayama 1967; Eisler 1978; Jernelöv and Lann 1971; Stickney et al. 1975; Huckabee and Blaylock 1972). The efficiency of food web transfers of mercury to predators may be largely a function of the chemical form of mercury in the prey. Jernelöv and Lann (1971) demonstrated preferential assimilation of methylmercury and excretion of inorganic mercury in fish. Analysis of benthos and nekton by Kendall (1978) have shown that infaunas generally contain relatively low levels of methylmercury (MeHg) (<30 percent) relative to predacious nekton species from the same areas. Others have verified this from other aquatic systems (Jernelöv and Lann 1971, Luoma 1974). Therefore, low transfer efficiencies of mercury are expected in fish feeding predominately on benthic invertebrate prey with low methylmercury body burdens. On the other hand, tertiary consumers feeding predominately on fish have been found to exhibit higher mercury-retention efficiencies because their teleost prey generally contain high levels of methylmercury relative to their total mercury burden (70-100 percent) (Rivers et al. 1972, Westöo 1973, Bishop and Neary 1974, Stickney et al. 1975, Gardner et al. 1975, Gardner et al. 1978, Windom et al. 1976b). This was experimentally verified by Pentreath (1976c) who found low assimilation of inorganic mercury by the *Plaice Pleuronectes platessa* fed inorganic mercury ( $^{203}\text{Hg}$ ) labeled *Nereis*, and high assimilation efficiencies from organic mercury ( $^{203}\text{MeHg}$ ) labeled *Nereis*. Therefore, as levels of methylmercury increase in prey relative to their total mercury burden, the efficiency of food web-mediated mercury transfers from prey to

predator species is expected to increase. This is illustrated in a study by Windom et al. (1976a), who found higher mercury but lower cadmium transfer efficiencies at higher trophic levels in marine fish collected from the Georgia embayment (continental shelf) (Figure 3-43).

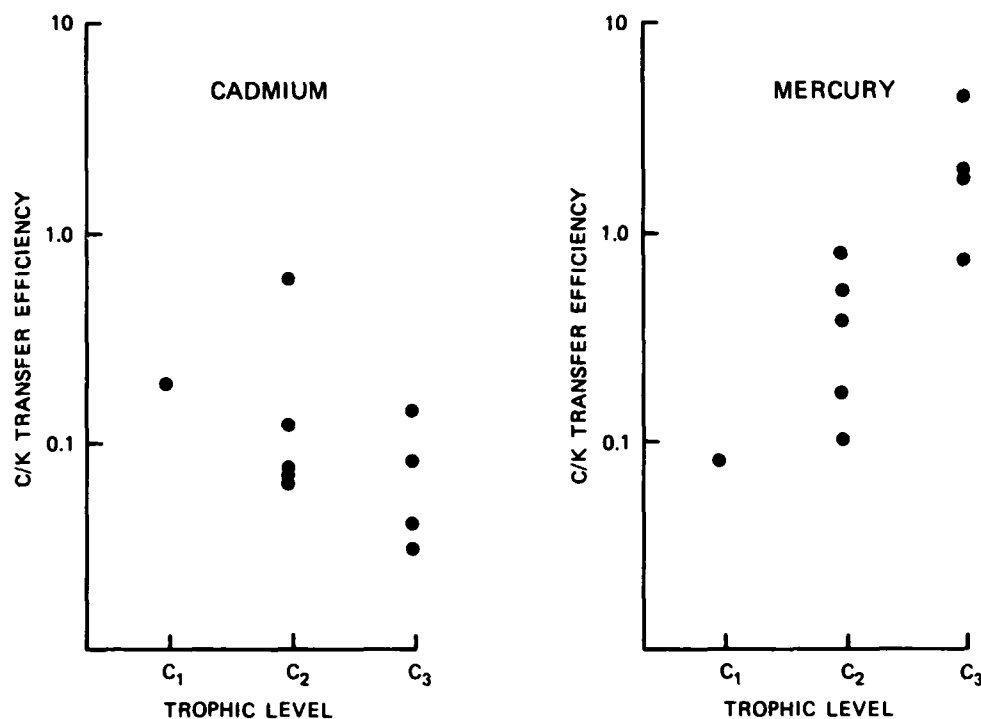


Figure 3-43. Cadmium and mercury transfer efficiencies in Georgia embayment food chains (after Windom et al. 1976a) (see Windom et al. (1976a) for an explanation of transfer efficiency (C/K) determinations)

Jernelöv and Lann (1971), summarizing experimental results from Sweden, found bottom feeding fish (i.e. invertebrate predators) assimilated less than 25 percent of their total mercury burden through the food web and the rest directly from the water. They found fish-eating aquatic predators accumulated as much as 60 percent of their total mercury burdens from their food (fish) and the remaining 40 percent directly from the water. Other studies have also demonstrated that food chain uptake of mercury may account for a significant percentage of the total

mercury body burden observed in fish (Huckabee and Blaylock 1972; Ratkowsky et al. 1975; Pentreath 1976a, 1976b, 1976c; Windom et al. 1976a). Therefore, conditions which promote or enhance the production and formation of monomethylmercury from inorganic mercury in aquatic ecosystems (Bisogni 1979) will lead to greater mercury bioaccumulation at lower trophic levels and subsequent potential biomagnification of mercury at higher trophic levels. Recent studies in Swedish lakes have found a negative correlation between methylmercury production and pH, with higher rates of monomethylmercury production at a lower pH (Landner and Larsson 1972; Jernelöv, Hansson, and Linse 1976; Hultberg 1977; Beijer and Jernelöv 1979). The rate of methylmercury formation is dependent on microbial activity and the bioavailability of mercury in sediment-bound versus dissolved forms (Jenson and Jernelöv 1969, Jernelöv 1970). The pH of the water will also determine whether mono- or dimethylmercury will be the dominant compound formed. Of the two forms, only monomethylmercury shows a strong affinity for biological tissue, the other being relatively innocuous in aquatic systems (Wallace et al. 1971; Kolb, Porcella, and Middlebrooks 1973). Mercury concentrations accumulated in biota as methylmercury may vary appreciably in different aquatic environments subjected to similar levels of pollution, but varying levels of eutrophication. Oligotrophic environments generally exhibit higher levels of methylmercury in resident biota than eutrophic environments (Beijer and Jernelöv 1979, Luoma 1974). Eutrophic aquatic environments such as estuaries generally exhibit higher pH's which may favor volatile dimethylmercury formation and a higher production of organic matter, which complexes the mercury thereby reducing its bioavailability. It should be apparent from the preceding discussion that complex processes govern the formation of organic and inorganic mercury species in aquatic environments, which formation in turn affects the observed environmental distributions and assimilation efficiencies of mercury in biota at any given location. Other metals also exhibit complex chemical forms which affect their distribution and availability to biota (Wood 1974).

# REFERENCES

- Ahmed, M. 1975. "Speciation in Living Oysters," Adv. Mar. Biol. 13:357-397.
- Aller, R. C., and Dodge, R. 1974. "Animal-Sediment Relations," J. Mar. Res. 32(2):209-232.
- Andrews, J. D. 1973. "Effects of Tropical Storm Agnes on Epifaunal Invertebrates in Virginia Estuaries." Chesapeake Sci. 14(4):223-234.
- Atkinson, L. P. 1977. "Modes of Gulf Stream Intrusion into the South Atlantic Bight Shelf Waters," Geophys. Res. Lett. 4:583-586.
- Atkinson, L. P., Paffenhöfer, G., and Dunston, W. M. 1978. "The Chemical and Biological Effect of a Gulf Stream Intrusion off St. Augustine, Florida," Bull. Mar. Sci. 28:667-679.
- Avent, R. M., King, M., and Gore, R. 1977. "Topographic and Faunal Studies of Shelfedge Prominences Off the Central Eastern Florida Coast," Int. Rev. Hydrobiol. 62(2):185-208.
- Bahr, L. M., Jr. 1974. "Aspects of the Structure and Function of the Intertidal Oyster Reef Community in Georgia," Ph.D. Dissertation, University of Georgia, Athens.
- \_\_\_\_\_. 1981. "The Ecology of Intertidal Oyster Reefs of the South Atlantic Coast: A Community Profile," prepared for National Coastal Ecosystems Team, U. S. Fish and Wildlife Service, FWS/OBS-81/15, Washington, D. C., 105 pp.
- Barans, C. A., and Burrell, V. G. 1976. "Preliminary Findings of Trawling on the Continental Shelf Off the Southwestern United States During Four Seasons (1973-1975)," S. C. Mar. Resour. Cent. Tech. Report 13, 16 pp.
- Barnard, J. L. 1963. Relationship of Benthic Amphipoda to Invertebrate Communities of Inshore Sublittoral Sands of Southern California," Pac. Nat. 3:439-467.
- Barnard, J. L., and Hartman, O. 1959. "The Sea Bottom Off Santa Barbara, California: Biomass and Community Structure," Pacific Naturalist 1(6):1-16.
- Barnes, R. D. 1980. Invertebrate Zoology, fourth edition, Saunders College, Philadelphia, 1089 pp.
- Bearden, C. M., and McKenzie, M. D. 1971. "An Investigation of the Inshore Demersal Fish Resources of South Carolina," South Carolina Wildlife Res. Dept. Tech. 2:19 pp.
- Behrens, E. W. 1968. "Cyclic and Current Structures in a Serpulid Reef," University of Texas Contr. Mar. Sci. 13:21-27.

- Beijer, K., and Jernelöv, A. 1979. "Methylation of Mercury in Aquatic Environments, Chapter 9," The Biogeochemistry of Mercury in the Environments, J. O. Nriagu, ed., Elsevier/North-Holland Biomedical Press, pp. 203-210.
- Biggs, R. B. 1967. "Sediments of Chesapeake Bay," Estuaries, Lauff, ed., (83):239-260, AAAS, Wash., D. C.
- Bishop, J. N., and Neary, B. P. 1974. The Form of Mercury in Freshwater in Fish, Proceedings International Conf. on Transport of Persistent Chemical Aquatic Ecosystems, Ottawa, Canada, pp. 25-29.
- Bisogni, J. J., Jr. 1979. "Kinetics of Methylmercury Formation and Decomposition in Aquatic Environments, Chapter 10," The Biogeochemistry of Mercury in the Environment, J. O. Nriagu, ed., Elsevier/North-Holland Biomedical Press, pp. 211-230.
- Bloom, S. A., Simon, G. L., and Hunter, V. D. 1972. "Animal-Sediment Relations and Community Analysis of a Florida Estuary," Mar. Biol. 13(1):43-56.
- Boesch, D. F. 1972. "Species Diversity of Marine Macrobenthos in the Virginia Area," Chesapeake Sci., 13:206-211.
- \_\_\_\_\_. 1973. "Classification and Community Structure of Macrobenthos in the Hampton Roads Area, Virginia," Mar. Biol., 21:226-244.
- \_\_\_\_\_. 1977a. "Application of Numerical Classification in Ecological Investigations of Water Pollution," U. S. Environmental Protection Agency, Ecological Research Series, EPA-600/3-77-033:114 pp.
- \_\_\_\_\_. 1977b. "A New Look at the Zonation of Benthos Along the Estuarine Gradient," Ecology of Marine Benthos, B. C. Coull, ed., University of South Carolina Press, Columbia, S. C., pp. 245-266.
- \_\_\_\_\_. 1982. "Ecosystem Consequences of Alterations of Benthic Community Structure and Function in the New York Bight Region," In: Ecological Stress and The New York Bight: Science and Management, G. F. Mayer, ed., Estuarine Research Federation, Columbia, S. C., pp 543-568.
- Boesch, D. F., Bowen, M. A., Gaston, G. R., Schaffner, L. C., Swartz, R. C., Peasce, J. B., Reid, R. N., Steimle, F. W., Jr., Ward, J. C., and Diaz, R. J. (in review). "The Macrobenthos of the New York Bight Region," Technical Report, National Oceanic and Atmospheric Administration.
- Bok, R. P. M. 1978. "Lethal and Sublethal Effects of Dredging on Reef Corals," Mar. Pollut. Bull., 9:14 pp.
- Boone, C. G., Granat, M. A., and Farrell, M. P. 1978. "Aquatic Disposal Field Investigations, Columbia River Disposal Site, Oregon; Evaluative Summary," Technical Report D-77-30, U. S. Army Engineer Waterways Experiment Station, CE, Vicksburg, Miss.

- Bourke, R. H., Glenne, B., and Adams, B. W. 1971. "The Nearshore Physical Oceanographic Environment of the Pacific Northwest Coast," Department of Oceanography, Oregon State University, Corvallis, Oreg., 127 pp.
- Braek, G. S., Jensen, A., and Mohus, A. 1976. "Heavy Metal Tolerance of Maine Phytoplankton, III. Combined Effects of Copper and Zinc Ion on Cultures of Four Common Species," J. Exptl. Mar. Biol. Ecol., 25:37-50.
- Bright, T. J., and Pequegnat, L. H., eds. 1974. "Biota of the West Flower Garden Bank," Gulf Publishing Co.
- Bright, T. J., and Rezak, R. 1976. "Fishing Banks of the Texas Continental Shelf," Proceedings: Colloquium on Snapper-Grouper Fishery Resources of the Western Central Atlantic Ocean, H. R. Bullis, Jr., and A. C. Jones, eds., Fla. Sea Grant Program, Rept. No. 17, pp. 248-288.
- Bright, T. J., Rezak, R., Bouma, A. H., Bryant, W. R., and Pequegnat, W. E. 1976. "A Biological and Geological Reconnaissance of Selected Topographic Features of the Texas Continental Shelf," Final Report prepared by Texas A&M Department of Oceanography for U. S. Dept. of the Interior, Bureau of Land Management, Outer Continental Shelf Office, New Orleans, La.
- Bright, T. J., Rezak, R., Gartner, S., McGrail, D., Pequegnat, W. E., and Treadwell, T. K. 1978a. "Northwestern Gulf of Mexico Topographic Features Study," Final Report prepared by Texas A&M Dept. of Oceanography for the U. S. Dept. of the Interior, Bureau of Land Management, Outer Continental Shelf Office, New Orleans, La.
- Bright, T. J., Rezak, R., Gartner, S., and Pequegnat, W. E. 1978b. "South Texas Topographic Features Study," Final Report prepared by Texas A&M Dept. of Oceanography for the U. S. Dept. of the Interior, Bureau of Land Management, Outer Continental Shelf Office, New Orleans, La.
- Brook, J. M. 1978. "Trophic Relationships in a Seagrass Community (*Thalassia testudinum*) in Card Sound, Florida," Fish Diets in Relation to Macrobenthic and Crystic Faunal Abundance, Bull. Mar. Sci. 28(1):211-217.
- Bryan, G. W. 1971. "The Effects of Heavy Metals (Other than Mercury) on Marine and Estuarine Organisms," Proc. Roy. Soc. Lond. B., 177:389-410.
- \_\_\_\_\_. 1973. "The Occurrence and Seasonal Variation of Trace Metals in the Scallops *Pecten maximus* (L.) and *Chlamys opercularis* (L.)," J. Mar. Biol. Ass. U. K., 53:145-169.
- Bryan, G. W. 1974. "Adaptation of an Estuarine Polychaete to Sediments Containing High Concentrations of Heavy Metals," Pollution and Physiology of Marine Organisms, F. J. Vernberg and W. B. Vernberg, eds., Academic Press, New York, pp. 123-135.

- Bryan, G. W., and Hummerstone, L. G. 1971. "Adaptation of the Polychaete *Nereis diversicolor* to Estuarine Sediments Containing High Concentrations of Heavy Metals. I. General observations and adaptation to copper," J. Mar. Biol. Ass. U. K. 51:845-863.
- \_\_\_\_\_. 1973a. "Adaptation of the Polychaete *Nereis diversicolor* to Estuarine Sediments Containing High Concentrations of Zinc and Cadmium," J. Mar. Biol. Ass. U. K. 53:839-857.
- \_\_\_\_\_. 1973b. "Adaptation of the Polychaete *Nereis diversicolor* to Manganese in Estuarine Sediments," J. Mar. Biol. Ass. U. K. 53:859-872.
- \_\_\_\_\_. 1977. "Indicators of Heavy Metal Contamination in the Looe Estuary (Cornwall) with Particular Regard to Silver and Lead," J. Mar. Biol. Ass. U. K. 57:75-92.
- Buchanan, J. B., and Kain, J. M. 1971. "Measurement of the Physical and Chemical Environment; Sediments," Chapter 3, Methods for the Study of Marine Benthos, IBP Handbook No. 6., N. A. Holme and A. D. McIntyre, eds., Blackwell Scientific Publ., Oxford and Edinburgh, pp. 30-58.
- Buchanan, J. B., Sheader, M., and Kingston, P. F. 1978. "Sources of Variability in Benthic Macrofauna of the South Northumberland Coast, 1971-1976," J. Mar. Biol. Assoc. U. K. 58:191-209.
- Burbanck, G. P. 1981. "Distribution of Estuarine Benthos in Relation to Physical-Chemical Factors," Ph.D. Thesis, University of Delaware, 275 pp.
- Burbanck, W. D., and Burbanck, G. P. 1967. "Parameters of Interstitial Water Collected by a New Sampler from the Biotopes of *Cyathura polita* (Isopoda) in Six Southeastern States," Chesapeake Sci., 8:14-27.
- Burbanck, W. D., and Burbanck, M. P. 1979. "Cyathura (Arthropoda: Crustacea: Isopoda: Anthuridae). Chapter 9," Pollution Ecology Of Estuarine Invertebrates, C. W. Hart and S. U. H. Fuller, eds., Academic Press, New York, pp. 293-323.
- Carey, A. G., Jr. 1965. "Preliminary Studies of Animal-Sediment Interrelationships off the Central Oregon Coast," Ocean Science and Engineering, Vol 1, pp. 100-110, Mar. Tech. Sec. Wash., D. C.
- \_\_\_\_\_. 1972. "Ecological Observations on the Benthic Invertebrates from the Central Oregon Continental Shelf," The Columbia River Estuary and Adjacent Ocean Waters, Bioenvironmental Studies, A. T. Pruter and D. L. Alverson, eds., Univ. Wash. Press, pp. 422-443.
- Carpenter, E. J., and McCarthy, J. J. 1978. "Benthic Nutrient Regeneration and High Rate of Primary Production in Continental Shelf Waters," Nature, 274:188-189.

- Carriker, M. R. 1961. "Interrelation of Functional Morphology, Behavior, and Autecology in Early Stages of the Bivalve, *Mercenaria mercenaria*," J. Elisha Mitchell Sci. Soc., 77:168-241.
- \_\_\_\_\_. 1967. "Ecology of Estuarine Benthic Invertebrates: A Perspective," Estuaries, G. H. Lauff, ed., AAAS Publ. (83):427-487.
- Cerame-Vivas, M. J., and Gray, I. E. 1966. "The Distribution Pattern of Benthic Invertebrates of the Continental Shelf of North Carolina," Ecology, 47(2):260-270.
- Christiansen, C., Christofferson, H., Dalsgaard, J., and Nornberg, P. 1981. "Coastal and Near-Shore Changes Correlated with Die-Back in Eel-grass (*Zostera marina*, L.)," Sed. Geol. 28:163-173.
- Clark, J. 1974. "Coastal Ecosystems: Ecological Considerations for Management of the Coastal Zone," The Conservation Foundation, Washington, D. C., 178 pp.
- Clarke, A. 1979. "On Living in Cold Water: K-Strategies in Antarctic Benthos," Mar. Biol., 55(2):111-119.
- Clifford, H. T., and Stephenson, W. 1975. "An Introduction to Numerical Classification," Academic Press, New York, 225 pp.
- Continental Shelf Associates. 1979. "South Atlantic Hard Bottom Study," Prepared for Bureau of Land Management, Contract AA551-CT8-25, Washington, D. C., 356 pp.
- Cowardin, L. M., Carter, V., Golet, T. C., and LaRoe, E. T. 1979. "Classification of Wetlands and Deepwater Habitats of the United States Office of Biological Services," Fish and Wildlife Service: FWS/DBS-79/31, U. S. Government Printing Office, Washington, D. C., 103 pp.
- Currie, R. I. 1958. "Some Observations on Organic Production in the Northeast Atlantic," Rapp. Proc. Verb. Cons. Int. Explor. Mer., 144:96-102.
- Curry, J. R. 1960. "Sediments and History of Holocene Transgression, Continental Shelf, Northwest Gulf of Mexico," Recent Sediments, Northwest Gulf of Mexico, F. B. Phleger and Tj. H. Van Andel, eds., American Assoc. Petroleum Geologist, pp. 221-266.
- Curtis, L. A. 1978. "Aspects of the Population Dynamics of the Polychaete *Sabellaria vulgaris* Verrill in the Delaware Bay," Estuaries, 1(2):73-84.
- Dahlberg, M., and Smith, F. 1970. "Mortality of Estuarine Animals Due to Cold on the Georgia Coast," Ecology, 51(5):931-933.
- Darnell, R. M., and Wissing, T. E. 1974. "Nitrogen Turnover and Food Relationships of the Pinfish *Lagodon rhomboides* in a North Carolina Estuary," Physiological Ecology of Estuarine Organisms, F. J. Vernberg, ed., Univ. South Carolina Press, pp. 81-110.

- Dauer, D. M., and Conner, W. G. 1980. "Effects of Moderate Sewage Input on Benthic Polychaetes Populations," Estuar. Coastal Mar. Sci., 10:335-346.
- Dauer, D. M., Robinson, W. W., Seymour, C. P., and Leggett, A. T., Jr. 1979. "The Effect of Nonpoint Pollution on Benthic Invertebrates in the Lynnhaven River System," Virginia Water Resources Research Center Bulletin, (117):112 pp, Blacksburg, Va.
- Davis, B. M. 1911. "Botanical Biological Survey of the Waters of Woods Hole Vicinity," Part I, Section #II. Bull. Bur. Fish., 31(1911):443-544.
- Davis, F. M. 1925. "Quantitative Studies on the Fauna of the Sea Bottom. II. Results of the Investigation in the Southern North Sea," 1921-1924, Gt. Brit. Fish. Invest., Ser. 2, 8(4):1-50.
- Dawson, E. Y. 1956. How to Know Seaweeds, William C. Brown Company, Publishers, 197 pp.
- Dawson, E. Y., Neushul, M., and Wildman, R. D. 1960. "Seaweeds Associated with Kelp Beds Along Southern California and Northwestern Mexico," Pacific Naturalist, 1(4):1-81.
- Day, J. H. 1951. "The Ecology of South African Estuaries," Trans. Roy. Soc. So. Africa, 33(1):53-91.
- \_\_\_\_\_. 1959. "The Biology of Langebaan Lagoon: A Study of the Effect of Shelter from Wave Action," Trans. Roy. Soc. So. Africa, 35:475-547.
- \_\_\_\_\_. 1967. "The Biology of Knysna Estuary, South Africa," Estuaries, G. H. Lauff, ed., AAAS publication (83):397-404.
- Day, D. H., Field, J. G., and Montgomery, M. P. 1971. "The Use of Numerical Methods to Determine the Distribution of Benthic Fauna Across the Continental Shelf of North Carolina," J. Anim. Ecol., 40:93-125.
- Dayton, P. K., and Hessler, R. R. 1972. "Role of Biological Disturbance in Maintaining Diversity in the Deep Sea," Deep-Sea Res., Pergamon Press, Inc., 19:199-208.
- den Hartog, C. 1970. "The Seagrasses of the World," North Holland Publ. Co., Amsterdam, 275 pp.
- Desselle, W. J., Poirrier, M. A., Rogers, J. S., and Cashner, R. C. 1978. "A Discriminant Functions Analysis of Sunfish (*Lepomis*) Food Habits and Feeding Niche Segregation in the Lake Pontchartrain, Louisiana, Estuary," Trans. Am. Fish. Soc., 107(5):713-719.
- Dillon, R. R. 1971. "Comparative Study of Primary Productivity of Estuarine Phytoplankton and Macrobenthic Plants," Ph.D. Dissertation, University of North Carolina, 112 pp.

- Doochin, H., and Smith, F. G. 1952. "Marine Boring and Fouling in Relation to Velocity of Water Currents," Bull. of Mar. Sci. Gulf Carib., 1:196-208.
- Dörjes, J., and Howard, J. D. 1975. "Estuaries of the Georgia Coast: Sedimentology and Biology. IV, Fluvial-Marine Transition Indicators in an Estuarine Environment," Ogeechee River-Ossabaw Sound, Senckenb. Marit. 7:137-179.
- Edwards, G. S. 1971. "Geology of the West Flower Garden Bank," Texas A&M Univ., Sea Grant Publ. TAMU-SG-71-215.
- Eisler, R. 1978. "Mercury Contamination Standards for Marine Environments," Energy and Environmental Stress in Aquatic Systems, Symposium, Augusta, Ga., Nov. 2-4, 1977, J. H. Thorp and J. W. Gibbons, eds., DOE/CONF-77114., pp. 241-272.
- Emery, K. O., and Uchupi, E. 1972. "Western North Atlantic Ocean: Topography, Rocks, Structure, Water, Life and Sediments," The American Association Petrol. Geol. Memoir, 17:1-532.
- Engle, J. B. 1948. "Investigation of the Oyster Reefs of Mississippi, Louisiana, and Alabama Following the Hurricane of Sept. 19, 1947," Fish and Wildl. Serv. Spec. Sci. Rept., 59:1-70.
- Fager, E. W. 1964. "Marine Sediments: Effects of a Tube-Building Polychaete," Science, 143(3604):356-359.
- Flint, W. R., and Holland, J. S. 1980. "Benthic Infaunal Variability on a Transect in the Gulf of Mexico," Estur. Coastal Mar. Sci., 10:1-14.
- Fonseca, M. S., Kenworthy, W. J., Homziak, J., Thayer, G. W. 1979. "Transplanting of Eelgrass and Shoalgrass as a Potential Means of Economically Mitigating a Recent Loss of Habitat," In: Cole, D. P., ed., Proceedings of the Sixth Annual Conference on Wetlands Restoration and Creation, Hillsborough Community College and Tampa Port Authority, Tampa, Florida, pp. 279-236.
- Frankenberg, D., and Leiper, A. S. 1977. "Seasonal Cycles in Benthic Communities of the Georgia Continental Shelf," The Ecology of Marine Benthos, B. Coull., ed., University of South Carolina Press, pp. 383-397.
- Franzisket, L. 1964. "Die Stoffwechselintensität der Rifffcorallen und ihre Ökologische, Phylogentische und Soziologische," Bedeutung. Z. Vergleich Physiol. 49:91-113.
- Fukuda, M. K. 1978. "The Entrainment of Cohesive Sediments in Freshwater," Unpublished Ph.D. dissertation, Case Western Reserve University, Cleveland, Ohio.
- Galtsoff, P. S. 1964. "The American Oyster, *Crassostrea virginica* Gmelin," Fish. Bull., Fish and Wildl. Serv., 64:1-480.

- Gardner, W. S., Kendall, D. R., Odom, R. R., Windom, H. L., and Stephens, J. A. 1978. "The Distribution of Methyl Mercury in a Contaminated Salt Marsh Ecosystem," Environ. Pollut., (15):243-251.
- Gardner, W. S., Windom, H. L., Stephens, J. A., Taylor, F. E., and Stickney, R. R. 1975. "Concentrations of Total Mercury and Methylmercury in Fish and Other Coastal Organisms: Implications to Mercury Cycling," Mineral Cycling in Southeastern Ecosystems, F. G. Howell, J. B. Gentry, and M. H. Smith, eds., Technical Information Center, Office of Public Affairs, U. S. Energy Research and Development Administration (ERDA), CONF-740513, pp. 268-278.
- Goreau, T. F., Goreau, N. I., and Goreau, T. J. 1979. "Corals and Coral Reefs," Sci. Amer., pp. 124-136.
- Grassle, J. F. 1973. "Variety in Coral Reef Communities, Chapter 8," Biology and Geology of Coral Reefs, Vol. II: Biology, O. A. Jones and R. Endean, eds., Academic Press, pp. 247-268.
- Grassle, J. F., and Grassle, J. P. 1974. "Opportunistic Life Histories and Genetic Systems in Marine Benthic Polychaetes," J. Mar. Res., 32:(2):253-284.
- Grave, C. 1901. "The Oyster Reefs of North Carolina," John Hopkins Circ. (151):9 pp.
- \_\_\_\_\_. 1905. "Investigations for the Promotion of the Oyster Industry of North Carolina," Rept. U. S. Fish. Comm., 1903, 29:247-341.
- Gray, J. S. 1974. "Synergistic Effects of Three Heavy Metals on Growth Rates of a Marine Ciliate Protozoan," Pollution and Physiology of Marine Organisms, F. J. Vernberg, and W. B. Vernberg, eds., Academic Press, New York, pp. 465-485.
- \_\_\_\_\_. 1976. "The Effects of Salinity, Temperature and Mercury on Mortality of the Trocophore Larvae of *Serpula vermicularia* L. (Annelida: Polychaeta)," J. Exptl. Mar. Biol. Ecol., 23:127-134.
- Grigg, D. I. 1970. "Some Effects of Dredging on Water Quality and Coral Reef Ecology," Caribbean Conservation Assoc. Environmental Newsletter, 1(2):22-27.
- Gunter, G. 1951. "The West Indian Tree on the Louisiana Coast, and Notes on Growth of the Gulf Coast Oysters," Science, 113:16-517.
- \_\_\_\_\_. 1957. "Temperature, Chapter 8," Treatise on Marine Ecology and Paleoecology, Vol. 1; Ecology, J. W. Hedgpeth, ed., Publ. by Geol. Soc. Amer. Memoir 67, Vol 1:159-184.
- Gunter, G., and Hildebrand, H. H. 1951. "Destruction of Fishes and Other Organisms on the South Texas Coast by the Cold, January 28-February 3, 1951," Ecology, 32:731-736.

- Gunter, G., Ballard, B. S., and Venkataramiah, A. 1974. "A Review of Salinity Problems of Organisms in United States Coastal Areas Subject to the Effects of Engineering Works," Gulf Research Reports, 4(3):380-475.
- Haedrich, R. L., and Rowe, G. T. 1977. "Megafaunal Biomass in the Deep Sea," Nature, 269:141-142.
- Hall, C. A. 1964. "Shallow Water Marine Climates and Molluscan Provinces," Ecology, 42(2):226-234.
- Hanson, R. B., Tenore, K. R., Bishop, S., Chamberlain, C., Pamatmat, M. M., and Tietjen, J. 1981. "Benthic Enrichment in the Georgia Bight Related to Gulf Stream Intrusions and Estuarine Outwelling," J. Mar. Res., 39(3):417-441.
- Harris, C. D. 1978. "Location and Exploration of Natural Reefs on Georgia's Continental Shelf," Georgia Dept. Natural Resources, Coastal Resources Program, Project No. F-31 (Final Report), Brunswick, Ga., 14 pp.
- Hathaway, J. C. 1972. "Regional Clay-Mineral in the Estuaries and Continental Margin of the United States East Coast," Estuaries, Symposium at Columbia, South Carolina, April 1969, Geol. Society of America Memoir. B. Nelson, ed.
- Haven, D. S., and Morales-Alamo, R. 1967. Aspects of Biodeposition by Oysters and Other Invertebrate Filter Feeders," Limnol. and Oceanogr., 11:487-498.
- Hayes, M. O. 1978. "Impact of Hurricanes on Sedimentation in Estuaries, Bays and Lagoons," Estuarine Interactions, M. L. Wiley, ed., Academic Press Inc., New York. pp. 323-346.
- Heck, K. L. 1977. "Comparative Species Richness, Composition, and Abundance of Invertebrates in Caribbean Seagrass (*Thalassia*) Meadows," Mar. Biol., 41:335-348.
- Heck, K. L., and Orth, R. J. 1980. "Structural Components of Eelgrass (*Zostera marina*) Meadows in the Lower Chesapeake Bay-Decapod Crustacea," Estuaries, 3(4):289-295.
- Hedgpeth, J. W. 1953. "An Introduction to the Zoogeography of the Gulf of Mexico with Reference to the Invertebrate Fauna," Publ. Inst. Mar. Sci. Texas, University of Texas, 3(1):110-224.
- \_\_\_\_\_. 1954. "Bottom Communities of the Gulf of Mexico," Gulf of Mexico, Its Origin, Waters, and Marine Life, P. S. Galtsoff, ed., U.S.D.I. Fishery Bulletin #89, Volume 55, pp. 203-214.
- \_\_\_\_\_. 1957. "Marine Biogeography, Chap. 13," Treatise on Marine Ecology and Paleoecology, Vol. 1: Ecology, J. W. Hedgpeth, ed., Publ. by Geol. Soc. Amer., Memoir 67. Vol. 1:359-382.
- \_\_\_\_\_. 1967. "Introduction to Seashore Life of the San Francisco Bay Region and the Coast of Northern California," Univ. Calif. Press, Berkeley, 136 pp.

- Henry, V. J., Jr., McCreery, C. J., Foley, F. D., and Kendall, D. R. 1980. "Ocean Bottom Survey of the Georgia Bight: Final Report to the U. S. Geological Survey Office of Marine Geology for FY 1979," Contract No. 14-08-0001-06266, 82 pp.
- Hirsch, N. D., DiSalvo, L. H., and Peddicord, R. 1978. "Effects of Dredging and Disposal on Aquatic Organisms," Technical Report DS-78-5, U. S. Army Engineer Waterways Experiment Station, CE, Vicksburg, Miss. 41 pp.
- Holland, A. F., Mountford, N. K., and Mihursky, J. A. 1977. "Temporal Variation in Upper Bay Mesohaline Benthic Communities: I. The 9-M Mud Habitat," Chesapeake Sci., 18(4):370-378.
- Holm, R. 1978. "The Community Structure of a Tropical Marine Lagoon," Estur. Coastal Mar. Sci., 7:329-345.
- Homziak, J., Fonseca, M. S., and Kenworthy, W. J. 1982. "Macrobenthic Community Structure in a Transplanted Eelgrass (*Zostera marina*) Meadow," Mar. Ecol. Prog. Ser. 9:211-221.
- \_\_\_\_\_. (in review). "The Settlement of the Bay Scallop (*Argopecten irradians*) and the Hard Clain (*Mercenaria mercenaria*) in an Artificially Established Eelgrass (*Zostera marina*, L.) Meadow," 24 pp.
- Howard, J. D., and Frey, R. W. 1975. "Estuaries of the Georgia Coast, U. S. A.: Sedimentology and Biology, II. Regional Animal-Sediment Characteristics of Georgia Estuaries," Senckenbergiana Marit., 7:33-103.
- Howard, J. D., Elders, C. A., and Heinbokel, J. F. 1975. "Estuaries of the Georgia Coast, U. S. A.: Sedimentology and Biology, V. Animal-Sediment Relationships in Estuarine Point Bar Deposits, Ogeechee River-Ossabaw Sound, Georgia," Senckenbergiana Marit., 7:181-203.
- Howard, J. D., Mayou, T., and Heard, R. 1977. "Biogenic Sedimentary Structures Formed by Rays," J. Sed. Petrol., 47(1):339-346.
- Huckabee, J. W., and Blaylock, B. G. 1972. "Transfer of Mercury and Cadmium from Terrestrial to Aquatic Ecosystems," Metal Ions in Biological Systems, S. K. Dhar, ed., Plenum Publish. Corp., New York, pp. 125-160.
- Hultberg, H. 1977. Unpubl. Rep., Swed. Water and Air Pollut. Res. Inst.
- Hunt, J. L., Jr. 1974. "The Geology and Origin of Gray's Reef, Georgia Continental Shelf," M. S. Thesis, University of Georgia, 83 pp.
- Irukayama, K. 1967. "The Pollution of Minamata Bay and Minamata Disease," Advances in Water Pollution Research; Proceedings of Third International Conference, Munich, Germany, Sep. 1966, Vol. 3, pp. 153-165, Discussion, pp. 165-180.

- Iverson, R. L., Harris, R., Bittaker, H. F., and DiDomenic, D. 1979. "Significance of Seagrasses as a Source of Organic Carbon for the Eastern Gulf of Mexico Coastal Zone," Am. Soc. Limnol. Oceanogr. Winter Meeting, 2-5 Jan 1979, Corpus Christi, Tex. (abstr.).
- Jensen, S., and Jernelöv, A. 1969. "Biological Methylation of Mercury in Aquatic Organisms," Nature, 223:753-754.
- Jernelöv, A. 1970. "Release of Methylmercury from Sediments with Layers Containing Inorganic Mercury at Different Depths," Limnol. Oceanogr., 15:958-960.
- Jernelöv, A., and Lann, H. 1971. "Mercury Accumulation in Food Chains," Oikos., 22:403-406.
- Jernelöv, A., Hansson, C., and Linse, L. 1976. "Mercury in Fish--An Investigation of the Effect of pH and Total Phosphorous on Concentration," (Swed.), Swed. Water Air Pollut. Res. Inst., p 282.
- Jitts, H. R. 1959. "The Absorption of Phosphate by Estuarine Bottom Deposits," Aust. J. Mar. Freshwater Res., 10:7-21.
- Johannes, R. E., Coles, S. L., and Kuenzel, N. T. 1970. "The Role of Zooplankton in the Nutrition of Scleractinian Corals," Limnol. Oceanogr., 15:579-586.
- Johnson, R. G. 1970. "Variations in Diversity Within Benthic Marine Communities," Amer. Naturalist, 104:(937):285-300.
- \_\_\_\_\_. 1972. "Conceptual Models of Benthic Marine Communities," Models in Paleobiology, T. J. M. Shopf, ed., Freeman and Cooper, San Francisco, pp. 149-159.
- \_\_\_\_\_. 1974. "Sediment-Water Interface in Coastal Environments," J. Mar. Res., 32(2):313-330.
- \_\_\_\_\_. 1977. "Vertical Variation in Particulate Matter in the Upper Twenty Centimetres of Marine Sediments," J. Mar. Res., 32(2):273-282.
- Jones, J. A. 1968. "Primary Productivity by the Tropical Marine Turtlegrass, *Thalassia testudinum* König, and Its Epiphytes," Ph.D. Thesis, Univ. Miami, Coral Gables, Fla., 196 pp.
- Jones, N. S. 1950. "Marine Bottom Communities," Biol. Rev., 25:283-313.
- Jumars, P. A., and Fauchald, K. 1977. "Feeding and Metabolism: Between-Community Contrast in Successful Polychaete Feeding Strategies," Ecology of Marine Benthos, B. Coull, ed., University South Carolina Press, Columbia, 20 pp.
- Kendall, D. R. 1974. "The Ecology of the Macrobenthos of a Tidal Creek, St. Simons Island, Georgia," M. S. Thesis, Emory University, Atlanta, Ga., 212 pp.

- Kendall, D. R. 1978. "The Role of Macrobenthic Organisms in Mercury, Cadmium, Copper, and Zinc Transfers in Georgia Salt Marsh Ecosystems," Ph.D. Thesis, Emory University, Atlanta, Ga., 241 pp.
- Kenworthy, W. J., Fonseca, M. S., Homziak, J., and Thayer, G. W. 1980. "Development of a Transplanted Seagrass (*Zostera marina* L.) Meadow in Back Sound, Carteret County, North Carolina," In: Cole, D. P., ed. Proceedings of the Seventh Annual Conference on the Restoration and Creation of Wetlands, Hillsborough Community College, Environmental Studies Center, in cooperation with Tampa, Florida, pp. 175-194.
- King, J. E. 1958. "Proceedings of the Ninth Pacific Science Congress," Vol. 16:98-107.
- Kinne, O. 1963. "The Effects of Temperature and Salinity on Marine Brackish Water Animals, I. Temperature," Oceanogr. Marine Biol. Ann. Rev., 1:301-340.
- Kirtley, D. W. 1966. "Intertidal Reefs of Sabellariidae (Annelida Polychaeta) Along the Coasts of Florida," M. S. Thesis, Florida State University, Tallahassee, Fla.
- Kirtley, D. W., and Tanner, W. F. 1968. "Sabellariid Worms: Builders of a Major Reef Type," J. Sed. Petrol., 38(1):73-78.
- Kolb, L., Porcella, D. B., Middlebrooks, E. J. 1973. "Ecological Implications of Dimethylmercury in an Aquatic Food Chain," PRWG-105-2, Utah Water Research Laboratory, Utah State Univ., 50 pp.
- Landner, L., and Larsson, P. O. 1972. "Biological Effects of Mercury Fall-Out into Lakes from the Atmosphere," Swed. Water Air Pollut. Res. Inst. Bull., p. 115.
- Lehman, M. E. 1974. "Oyster Reefs at Crystal River, Florida, and Their Adaptation to Thermal Plumes," Ph.D. Dissertation, Univ. of Florida, Gainesville, 197 pp.
- Levington, J. S. 1977. "Ecology of Shallow Water Deposit Feeding Communities," Ecology of Marine Benthos, B. Coull, ed., Univ. South Carolina Press., Quisset Harbor, Mass., pp. 191-227.
- Lewis, A. G., Whitfield, P. H., and Ramnarine, A. 1972. "Some Particulate and Soluble Agents Affecting the Relationship Between Metal Toxicity and Organism Survival in Calanoid Copepod, *Euchaeta japonica*," Mar. Biol., 17:215-221.
- \_\_\_\_\_. 1973. "The Reduction of Copper Toxicity in a Marine Copepod by Sediment Extract," Limnol. and Oceanogr., 18(2):324-325.
- Linberg, S. E., Andren, A. W., and Harriss, R. C. 1975. "Geochemistry of Mercury in the Estuarine Environment," Estuarine Research (I), L. E. Cronin, ed., pp. 64-107.
- Lie, U. 1969. "Standing Crop of Benthic Infauna in Puget Sound and Off the Coast of Washington," J. Fish. Res. Bd. Can., 26(1):55-62.

- Lie, U., and Kisker, D. S. 1970. "Species Composition and Structure of Benthic Infauna Communities Off the Coast of Washington," J. Fish. Res. Bd. Can., 27(12):2273-2285.
- Ludwick, J. C., and Walton, W. R. 1957. "Shelf-Edge, Calcareous Prominences in Northwestern Gulf of Mexico," Amer. Assoc. Petr. Geol. Bull., 41(9):2054-2101.
- Luoma, S. N. 1974. "Aspects of the Dynamics of Mercury Cycling in a Small Hawaiian Estuary," Ph.D. Thesis, University of Hawaii, 210 pp.
- MacGinitie, G. E. 1935. "Ecological Aspects of a California Marine Estuary," Amer. Midl. Natur., 16:629-765.
- Mackin, J. G. 1951. "Histopathology of Infection of *Crassostrea virginica* by *Dermocystidium marinum*," Mackin, Owen, and Collier, eds., Bull. Mar. Sci. Gulf and Carib., 1:72-87.
- Malins, D. C., and Collier, T. K. 1981. "Xenobiotic Interactions in Aquatic Organisms. Effects on Biological Systems," Aquatic Toxicology, 1:257-268.
- Malone, T. C. 1978. "The 1976 *Ceratium tripos* Bloom in the New York Bight: Causes and Consequences," NOAA Tech. Rept. NMFS Circ. 410, 114 pp.
- Margalef, R. 1958. "Information Theory in Ecology," Gen. System, 3:36-71.
- Marsh, G. A. 1973. "The *Zostera* Epifaunal Community in the York River, Virginia," Chesapeake Sci., 14(2):87-97.
- Marshall, N. 1970. "Food Transfer Through the Lower Trophic Levels in the Benthic Environment," J. H. Steele, ed., Marine Food Chains, Univ. Calif. Press, Berkeley, pp 58-59.
- Masse, d. 1972. "Quantitative Investigations of Sand-Bottom Macrofauna Along the Mediterranean North-West Coast," Mar. Biol., 15:209-220.
- May, E. B. 1971. "A Survey of the Oyster and Oyster Shell Resources of Alabama," Alabama Mar. Resources Bull., 4:53 pp.
- \_\_\_\_\_. 1973. "Extensive Oxygen Depletion in Mobile Bay, Alabama," Limnol. Oceanogr., 18(3):353-366.
- McCall, P. L. 1977. "Community Patterns and Adaptive Strategies of the Infaunal Benthos of Long Island Sound," J. Mar. Res., 35(2):220-266.
- \_\_\_\_\_. 1978. "Spatial-Temporal Distributions of Long Island Sound Fauna: the Role of Bottom Disturbance in a Nearshore Marine Habitat," Estuarine Interactions, M. Wiley, ed., Academic Press, New York, pp. 191-219.

- McCall, P. L. 1979. "The Effects of Deposit-Feeding Oligochaetes on Particle Size and Settling Velocity of Lake Erie Sediments," J. Sed. Petrol., 49(3):813-818.
- McGrath, K. 1974. "Benthic Macrofaunal Census of Raritan Bay-- Preliminary Results," Pap. 24, Hudson River Ecology, 3rd Symposium on Hudson River Ecology, March 22-23, 1973, Hudson River Environmental Society, Inc., 40 pp.
- McIntyre, A. D. 1977. "Effects of Population on Inshore Benthos," Ecology of Marine Benthos, Coul, ed., Baruch Libr. Mar. Sci (6): 301-318.
- McNulty, J. K., Work, R. C., and Moore, H. B. 1962. "Some Relationships Between Infauna of the Level Bottom and the Sediment in South Florida," Bull. Mar. Sci. Gulf Carib., 12(3):322-332.
- McRoy, C. P., and Barsdate, R. J. 1970. "Phosphate Absorption in Eelgrass," Limnol. Oceanogr., 15(1):6-13.
- McRoy, C. P., and Allen, M. B. 1974. "Ice Stressed Coasts. Chapter D-3A," Coastal Ecological Systems of the United States, Vol III. H. T. Odum, B. J. Copeland, and E. A. McMahan, eds., Conservation Foundation, Washington, D. C., pp. 17-36.
- McRoy, C. P., and McMillian, C. 1977. "Production Ecology and Physiology of Seagrasses," Seagrass Ecosystems: A Scientific Perspective, Chapter 3, C. P. McRoy and C. Helfferich, eds., M. Dekker, N. Y.
- Menge, B. A., and Lubchenco, J. 1981. "Community Organization in Temperate and Tropical Rocky Intertidal Habitats: Prey Refuges in Relation to Consumer Pressure Gradients," Ecol. Monog., 51(4):429-450.
- Menzie, C. A. 1980. "The Chironomid (Insecta: Diptera) and Other Fauna of a *Myriophyllum spicatum* L. Plant Bed in the Lower Hudson River," Estuaries, 3(1):38-54.
- Menzies, R. J., Pilkey, O. H., Blackwelder, B. W., Dexter, D., Huling, P., and McCloskey, L. 1966. "A Submerged Reef Off North Carolina," Int. Rev. Hydrobiol., 51:393-431.
- Mills, E. 1980. "The Structure and Dynamics of Shelf and Slope Ecosystems Off the Northeast Coast of North America," Mar. Benthic Dynamics., K. Tenore and B. Coull, eds., Univ. South Carolina Press., Columbia, South Carolina. pp. 25-47.
- Moherek, A. J. 1978. "Flume Experiments on Sand, Silt, and Clay Mixtures from the Offshore Dredged Material Disposal Site, Galveston, Texas," TR-D-78-34. U. S. Army Engineer Waterways Experiment Station, CE, Vicksburg, Miss.
- Mook, D. 1980. "Seasonal Variation in Species Composition of Recently Settled Fouling Communities Along an Environmental Gradient in the Indian River Lagoon, Florida," Estaur. Coastal Mar. Sci., 2:573-581.

- Moore, H. B. 1958. Marine Ecology, John Wiley and Sons, Inc., New York, 493 pp.
- Morgan, J. F. C. 1956. "Notes on the Analysis of Shallow-Water Soft Substrata," J. Anim. Ecol., 25:367-387.
- Mortimer, C. H. 1971. "Chemical Exchanges Between Sediments and Water in the Great Lakes--Speculation on Probable Regulatory Mechanisms," Limnol. Oceanogr., 16:387-404.
- Multer, H. G., and Milliman, J. D. 1967. "Geologic Aspects of Sabel-larian Reefs, Southeastern Florida," Marine Science Bulletin, 17:257-267.
- Muus, B. J. 1967. "The Fauna of Danish Estuaries and Lagoons--Distribution and Ecology of Dominating Species in the Shallow Reaches of the Mesohaline Zone," Meddel. Fra Danmarks Fiskeri og Hanunderogelser N. S., 5(1):1-316.
- Neff, J. W., Foster, R. S., and Slowey, J. F. 1978. "Availability of Sediment-Absorbed Heavy Metals to Benthos with Particular Emphasis on Deposit-Feeding Infauna," Technical Report D-78-42, U. S. Army Engineer Waterways Experiment Station, CE, Vicksburg, Miss., 186 pp.
- Nilsen, K. J., Diaz, R. J., Boesch, D. F., Bertelsen, R., and Kravitz, M. "The Biogenic Structure of Lower Chesapeake Bay Sediments," (unpublished), 130 pp.
- Nixon, S. W., Oviatt, O. A., and Hale, S. S. 1975. "Nitrogen Regeneration and the Metabolism of Coastal Marine Bottom Communities," Role of Terrestrial and Aquatic Organisms in Decomposition Processes, Anderson and Macfayden, eds., Blackwell, Oxford, England, pp 169-283.
- North, W. J. 1964. "Ecological Study of Kelp Beds in the Vicinity of San Elijo Lagoon, Calif.," State Water Quality Control Brd., Sacramento, 26 pp.
- \_\_\_\_\_. 1966. "Kelp Bed Restoration Activities," Annual Report, Kelp Hab. Imp. Proj., 1965-1966, California Inst. Tech., pp 5-30.
- Odum, E. P. 1971. Fundamentals of Ecology. W. B. Saunders Company, New York, 574 pp.
- Odum, H. T. 1974. "Tropical Marine Meadows," Chapter B-3, Coastal Ecological Systems of the U. S., Vol. 1, H. T. Odum, B. J. Copeland, and E. A. McMahan, eds., Conservation Foundation, Washington, D. C., pp. 442-487.
- Odum, H. T., and Copeland, B. J. 1974. "A Functional Classification of the Coastal Systems of the United States," Part I. Coastal Ecological Systems of the U. S., Odum, Copeland, and McMahan, eds., Conservation Foundation, Washington, D. C., pp. 5-103.
- Odum, H. T., and Odum, E. P. 1955. "Trophic Structure and Productivity of a Windward Coral Reef Community on Eniwetok Atoll," Ecol. Mongr., 25:(3):291-320.

- O'Gower, A. K., and Wacasey, J. W. 1967. "Animal Communities Associated with *Thalassia*, *Diplanthera*, and Sand Beds in Biscayne Bay. I. Analysis of Communities in Relation to Water Movements," Bull. Mar. Sci., 17(1):175-210.
- Oliver, J. S., Slattery, P. N., Hulberg, L. W., and Nybakk, J. W. 1979. "Relationships Between Wave Disturbance and Zonation of Benthic Invertebrate Communities Along a Subtide High-Energy Beach in Monterey Bay, California," Fishery Bull., 78(2):437-454.
- Oppenheimer, C. H. 1963. "Effects of Hurricane Carla on the Ecology of Redfish Bay, Texas," Bull. Mar. Sci., 13(1):59-72.
- Orth, R. J. 1973. "Benthic Infauna of Eelgrass, *Zostera marina*, Beds," Chesapeake Sci., 14(4):285-269.
- \_\_\_\_\_. 1974. "The Effects of Tropical Storm Agnes on the Benthic Fauna of Eelgrass, *Zostera marina*, in the Lower Chesapeake Bay," (abstract) p. D212, The Effects of Tropical Storm Agnes on the Chesapeake Bay Estuarine System, Davis, ed., Chesapeake Res. Const. Publ. 34.
- \_\_\_\_\_. 1975. "Destruction of Eelgrass, *Zostera marina*, by the Cownose Ray, *Rhinoptera bonasus*, in the Chesapeake Bay," Chesapeake Sci., 16(3):205-208.
- \_\_\_\_\_. 1977a. "The Importance of Sediment Stability in Seagrass Communities," Ecology of Marine Benthos, B. Coull, ed., University of South Carolina Press, Columbia, South Carolina, pp. 281-300.
- \_\_\_\_\_. 1977b. "Effect of Nutrient Enrichment on Growth of the Eelgrass, *Zostera marina*, in the Chesapeake Bay, Virginia," Mar. Biol., 44:187-194.
- Orth, R. J., and Heck, K. L., Jr. 1980. "Structural Components of Eelgrass (*Zostera marina*) Meadows in the Lower Chesapeake Bay-Fishes," Estuaries, 3(4):278-288.
- Overstreet, R. M. 1978. "Marine Maladies? Worms, Germs, and Other Symbionts from the Northern Gulf of Mexico," Mississippi-Alabama Sea Grant Consortium, MASGP-78-021, Gulf Coast Research Laboratory, Ocean Springs, Miss., 140 pp.
- Parker, R. H. 1964. "Zoogeography and Ecology of Macroinvertebrates of the Gulf of California and Continental Slope of Western Mexico," Symposium: Marine Geology of the Gulf of California (memoir 3), Van Andel and Shor, eds., Amer. Assoc. Petrol. Geol., Tulsa, Okla.
- Parker, R. H., and Curray, J. B. 1956. "Fauna and Bathymetry of Banks on Continental Shelf, Northwest Gulf of Mexico," Bull. Amer. Assoc. Petr. Geol., 40(10):2428-2439.
- Parker, R. O., Jr., Colby, D. R., and Willis, T. D. "Estimated Amount of Reef Habitat on U. S. South Atlantic and Gulf of Mexico Continental Shelf" (unpublished manuscript), National Marine Fisheries Service, Beaufort, N. C.

- Pearse, A. S., and Williams, L. G. 1951. "The Biota of the Reefs Off the Carolinas," J. Mitchell Sci. Soc., 67:133-161.
- Pearson, T. H. 1982. "The Loch Eil Project: Assessment and Synthesis with a Discussion of Certain Biological Questions Arising from a Study of the Organic Pollution of Sediments," J. Exp. Mar. Biol. Ecol., 57:93-124.
- Pearson, T. H., and Rosenberg, R. 1976. "A Comparative Study of the Effects on the Marine Environment of Wastes Cellulose Industries in Scotland and Sweden," Ambio, 5:77-79.
- \_\_\_\_\_. 1978. "Macrobenthic Succession in Relation to Organic Enrichment and Pollution of the Marine Environment," Oceanogr. Mar. Biol. Ann. Rev., 16:229-311.
- Pearson, T. H., Duncan, G., and Nuttall, J. 1982. "The Loch Eil Project: Population Fluctuations in the Macrobenthos," J. Exp. Mar. Biol. Ecol., 56:305-321.
- Peddicord, R. K., and McFarland, V. A. 1978. "Effects of Suspended Dredged Material on Aquatic Animals," Tech. Report D-78-29, U. S. Army Engineer Waterways Experiment Station, CE, Vicksburg, Miss., 102 pp.
- Penhale, P. A., and Smith, W. O. 1977. "Excretion of Dissolved Organic Carbon by Eelgrass (*Zostera marina*) and Its Epiphytes," Limnol. Oceanogr., 22(3):400-407.
- Pentreath, R. J. 1976a. "The Accumulation of Inorganic Mercury from Sea Water by the Plaice, *Pleuronectes platessa* L.," J. Exptl. Mar. Biol. Ecol., 24:103-119.
- \_\_\_\_\_. 1976b. "The Accumulation of Organic-Hg from Sea Water by the Plaice, *Pleuronectes platessa* L.," J. Exptl. Mar. Biol. Ecol., 24:121-132.
- \_\_\_\_\_. 1976c. "The Accumulation of Mercury from Food by the Plaice, *Pleuronectes platessa* L.," J. Exptl. Mar. Biol. Ecol., 25:51-65.
- Percival, E. 1929. "A Report on the Fauna of the Estuaries of the River Tamar and River Lynher," J. Mar. Biol. Assoc. U. K., 16:81-108.
- Peterson, C. G. J. 1913. "Evaluation of the Sea. II. The Animal Communities of the Sea Bottom and Their Importance for Marine Zoogeography," Report Danish Biol. Sta., 21:1-44.
- Peterson, C. H. 1982. "Clam Predation by Whelks (*Busycon* spp.): Experimental Tests of the Importance of Prey Size, Prey Density, and Seagrass Cover," Marine Biology, 66:159-170.
- Phillips, R. C. 1960. "Observations of the Ecology and Distribution of the Florida Seagrasses," Florida State Board of Conservation Marine Laboratory, Prof. paper series (2):1-72.

- Phillips, R. C. 1972. "Ecological Life History of *Zostera marina* L. (Eelgrass) in Puget Sound, Washington," Ph.D. Dissertation, University of Washington, 154 pp.
- \_\_\_\_\_. 1974. "Kelp Beds," Chapter C-11, Coastal Ecological Systems of the U. S., Vol. 2. Odum, Copeland, and McMahan, eds., Conservation Foundation, Washington, D. C., pp. 442-487.
- \_\_\_\_\_. 1978. "Seagrasses and the Coastal Marine Environment," Oceanus, 21(3):30-40.
- \_\_\_\_\_. 1980. Role of Seagrasses in Estuarine Systems, Proceedings of the Gulf of Mexico Coastal Ecosystems Workshop, U. S. Fish and Wildlife Service, P. L. Fore and R. D. Peterson, eds., FWS/OBS-80/30, pp. 67-93.
- Pielou, E. C. 1966a. "Shannon's Formula as a Measure of Specific Diversity: Its Use and Misuse," Amer. Natur., 100:463-465.
- \_\_\_\_\_. 1966b. "The Measurement of Diversity in Different Types of Biological Collections," J. Theor. Biol., 13:131-144.
- Powles, H., and Barans, C. A. 1980. "Groundfish Monitoring in Sponge-Coral Areas off the Southeastern United States," Mar. Fish. Rev., pp. 21-35.
- Pratt, D. M. 1953. "Abundance and Growth of *Venus mercenaria* and *Callcardia morrhuana* in Relation to the Character of Bottom Sediments," J. Mar. Res., 12(1):60-74.
- Price, W. A. 1954. "Oyster Reefs of the Gulf of Mexico," Department of Oceanography of the Agricultural and Mechanical College of Texas (27):491 pp.
- Radford, A. E., Ahles, H. E., and Bell, R. C. 1968. "Manual of the Vascular Flora of the Carolinas," Univ. North Carol. Press, Chapel Hill, 1183 pp.
- Ratkowsky, D. A., Dix, T. G., and Wilson, K. C. 1975. "Mercury in Fish in the Derwent Estuary, Tasmania, and Its Relation to the Position of the Fish in the Food Chain," Aust. J. Mar. Freshwater Res., 26:223-231.
- Raymont, J. E. G. 1963. Plankton and Productivity in the Oceans, MacMillian and Co., New York, 660 pp.
- Rees, C. P. 1976. "Sand Size Distribution in Tubes of *Sabellaria vulgaris* Verrill," Chesapeake Science, 17(1):59-61.
- Rees, E. I. S., Nicholaidou, A., and Laskaridou, P. 1977. The Effects of Storms on the Dynamics of Shallow Water Benthic Associations," Biology of Benthic Organisms, 11th European Symposium on Marine Biology, Galway, Oct. 1976, B. Keegan, P. Ceidigh, P. Boaden, eds., Pergamon Press, New York, pp. 465-474.

- Reidfield, A. C. 1952. "A Report to the Towns of Brookhaven and Islip, New York, on the Hydrography of Great South Bay and Moriches Bay," Woods Hole Oceanographic Inst., Ref. 52-26, 80 pp.
- Reise, K. 1977. "Predation Pressure and Community Structure of an Intertidal Soft-Bottom Fauna," Biology of Benthic Organisms, Pergamon Press, New York, pp. 513-519.
- Reish, D. J. 1973. "The Use of Benthic Animals in Monitoring the Marine Environment," J. Environ. Planning and Pollut. Control, 1:32-38.
- Reish, D. J., Rossi, S. S., Mearns, A. J., Oshida, P. S., and Wilkes, F. 1979. "Marine and Estuarine Pollution," J. WPCF, 51(6):1477-1517.
- Rhoads, D. C. 1963. "Rates of Sediment Reworking by *Yoldia limatula* in Buzzards Bay, Massachusetts, and Long Island Sound," J. Sed. Petrol., 33(3):723-727.
- \_\_\_\_\_. 1973. "The Influence of Deposit-Feeding Benthos on Water Turbidity and Nutrient Recycling," Amer. J. of Sci., 273:1-22.
- \_\_\_\_\_. 1974. "Organism-Sediment Relations on a Muddy Seafloor," Mar. Zool. Ann. Rev., 12:263-300.
- Rhoads, D. C., Aller, R. C., and Goldhaber, G. B. 1977. "Physical Properties and Chemical Diagenesis of the Estuarine Seafloor," Ecology of Marine Benthos, Coull, ed., pp. 113-138.
- Rhoads, D. C., McCall, P., and Yingst, J. 1978. "Disturbance and Production of the Estuarine Seafloor," The Amer. Sci., 66:577-586.
- Rhoads, D. C., Yingst, J., and Ulman, W. J. 1978. "Seafloor Stability in Central Long Island Sound. Part I. Temporal Changes in Erodibility of Fine-grained Sediments," Estuarine Interactions, M. Wiley, ed., Academic Press, New York. pp. 221-244.
- Rhoads, D. C., and Young, D. K. 1970. "The Influence of Deposit-Feeding Organisms on Sediment Stability and Community Trophic Structure," J. Mar. Res., 28(2):150-179.
- Rivers, J. B., Pearson, J. E., and Schultz, C. O. 1972. "Total and Organic Mercury in Marine Fish," Bull. Envir. Contam. Toxicol., 8(5):257-266.
- Rogers, C. S., Suchanek, T. H., and Pecora, F. A. 1982. "Effects of Hurricanes David and Frederick (1979) on Shallow *Heropora palmata* Reef Communities: St. Croix, U. S., Virgin Islands," B. Mar. Sci. 32(2):532-548.
- Rowe, G. F., Polloni, P. T., and Horner, S. G. 1974. "Benthic Biomass Estimates from the Northwestern Atlantic Ocean and the Northern Gulf of Mexico," Deep-Sea Research, 21:641-650.
- Rudd, R. L., Craig, R. B., and Williams, W. S. 1981. "Trophic Accumulation of DDT in a Terrestrial Food Web," Environmental Pollution (Series A) 25:219-228.

- Ryther, J. H., and Dunstan, W. M. 1971. "Nitrogen, Phosphorus, and Eutrophication in the Coastal Marine Environment," Science, 171(3975):1-7.
- Sanders, H. L. 1956. "Oceanography of Long Island Sound, 1952-1954. X. Biology of Marine Bottom Communities," Bulletin of the Bingham Oceanographic Collection, 15:345-415.
- \_\_\_\_\_. 1958. "Benthic Studies in Buzzards Bay. I. Animal-Sediment Relationships," Limnol. Oceanogr., 3(3):245-258.
- \_\_\_\_\_. 1960. "Benthic Studies in Buzzards Bay. III. Structure of Soft-Bottom Community," Limnol. Oceanogr., 5:138-153.
- \_\_\_\_\_. 1968. "Marine Benthic Diversity: A Comparative Study," Amer. Naturalist, 102:243-282.
- \_\_\_\_\_. 1969. "Benthic Marine Diversity and the Stability-Time Hypothesis," In: Diversity and Stability in Ecological Systems, Brookhaven Symposia in Biology: No. 22. pp. 71-81.
- Sanders, H. L., and Hessler, R. R. 1969. "Ecology of the Deep Sea Benthos," Science, 163:1419-1424.
- Sanders, H. L., Manglesdorf, P. C., Jr., and Hampson, G. R. 1965. "Salinity and Faunal Distribution in the Pocasset River, Massachusetts," Limnol. Oceanogr., 10 (suppl.): R216-R226.
- Santos, S. L., and Simon, J. L. 1974. "Distribution and Abundance of the Polychaetous Annelids in a South Florida Estuary," Bull. Mar. Sci., 24(3):669-689.
- Scholl, D. W. 1958. "Effects of Arenaceous Tube Building Polychaete upon the Sorting of a Bench Sand at Abalone Cove, California," Compass Magazine, 35:276-283.
- Schubel, J. R. 1973. "Some Comments on Seagrass and Sedimentary Processes," Review Paper, International Seagrass Workshop, Leiden, The Netherlands.
- Shepard, F. P. 1954. "Nomenclature Based on Sand-Silt-Clay Ratios," J. Sed. Petrol., 24(3):151-158.
- Shin, P. K. 1982. "Multiple Discriminant Analysis of Macrobenthic Infaunal Assemblages," J. Exp. Mar. Biol. Ecol. 59:39-50.
- Simon, J. L., and Dauer, D. M. 1977. "Reestablishment of a Benthic Community Following Natural Defaunation," The Ecology of Marine Benthos, Coull, ed., University of South Carolina, Columbia, pp. 139-154.
- Smith, F. G. W. 1971. "A Handbook of the Common Atlantic Reef and Shallow-Water Corals Reef of Bermuda, the Bahamas, Florida, the West Indies, and Brazil," University of Miami Press, 164 pp.
- Smith, R. G., Jr. 1976. "Evaluation of Combined Applications of Ultra-filtrations and Complexation Capacity Techniques to Natural Waters," Analytical Chemistry, 48(1):74-76.

- Southwood, T. R. E. 1977. "Habitat, the Templet for Ecological Strategies?" J. Anim. Ecol., 46:337-365.
- Springer, V. G., and Woodburn, K. D. 1960. "An Ecological Study of the Fishes of the Tampa Bay Area," Florida Brd. Cons. Mar. Lab. Prof. Paper Ser. 1:1-104.
- Stenzel, H. B. 1971. "Oysters," Treatise on Invertebrate Paleontology, K. C. Moore, ed., Part N, Vol. 3, Mollusca 6, Geological Soc. American Inc. and the Univ. of Kansas, Boulder, Colo., pp. N953-N1224.
- Stern, E. M., and Stickle, W. B. 1978. "Effects of Turbidity and Suspended Material in Aquatic Environments; Literature Review," Technical Report D-78-21, U. S. Army Engineer Waterways Experiment Station, CE, Vicksburg, Miss., 117 pp.
- Stickney, R. R., Windom, H. L., White, D. B., and Taylor, F. E. 1975. "Heavy-Metal Concentrations in Selected Georgia Estuarine Organisms with Comparative Food-Habit Data," Mineral Cycling in South-eastern Ecosystems (ERDA Symp.), pp. 257-267.
- Stoner, A. W. 1980. "The Role of Seagrass Biomass in the Organization of Benthic Macrofaunal Assemblages," Bull. Mar. Sci., 30(3): 537-551.
- Storey, M. 1937. "The Relation Between Normal Range and Mortality of Fish Due to Cold at Sanibel Island, Florida," Ecology, 19:10-26.
- Struhsaker, P. 1969. "Demersal Fish Resources: Composition Distribution and Commercial Potential of the Continental Shelf Stocks off the Southeastern United States," Fish. Ind. Res., 4(7):261-300.
- Sutherland, J. P. 1981. "The Fouling Community at Beaufort, North Carolina: A Study in Stability," The American Naturalists, 118(4):499-519.
- Sutherland, J. P., and Karlsen, R. H. 1977. "Development and Stability of the Fouling Community at Beaufort, North Carolina," Ecological Monogr., 47:425-446.
- Sverdrup, H. U., Johnson, M. W., and Fleming, R. H. 1942. The Oceans: Their Physics, Chemistry and General Biology, Prentice-Hall, Inc., Englewood Cliffs, New Jersey, 1060 pp.
- Tabb, D. C., Daubrow, D. L., and Manning, R. B. 1962. "The Ecology of Northern Florida Bay and Adjacent Estuaries," Florida Brd. Conserv. Tech. Ser. (39):79 pp.
- Taft, J. L., Taylor, W. R., Hartwig, E. O., and Loftus, R. 1980. "Seasonal Oxygen Depletion in Chesapeake Bay," Estuaries, 3(4):242-247.
- Tarver, D. P., Rodgers, J. A., Mahler, M. J., and Lazor, R. L. 1979. "Aquatic and Wetland Plants of Florida," Bureau Aquatic Plant Research and Control, Florida Dept. Natural Resources, 127 pp.

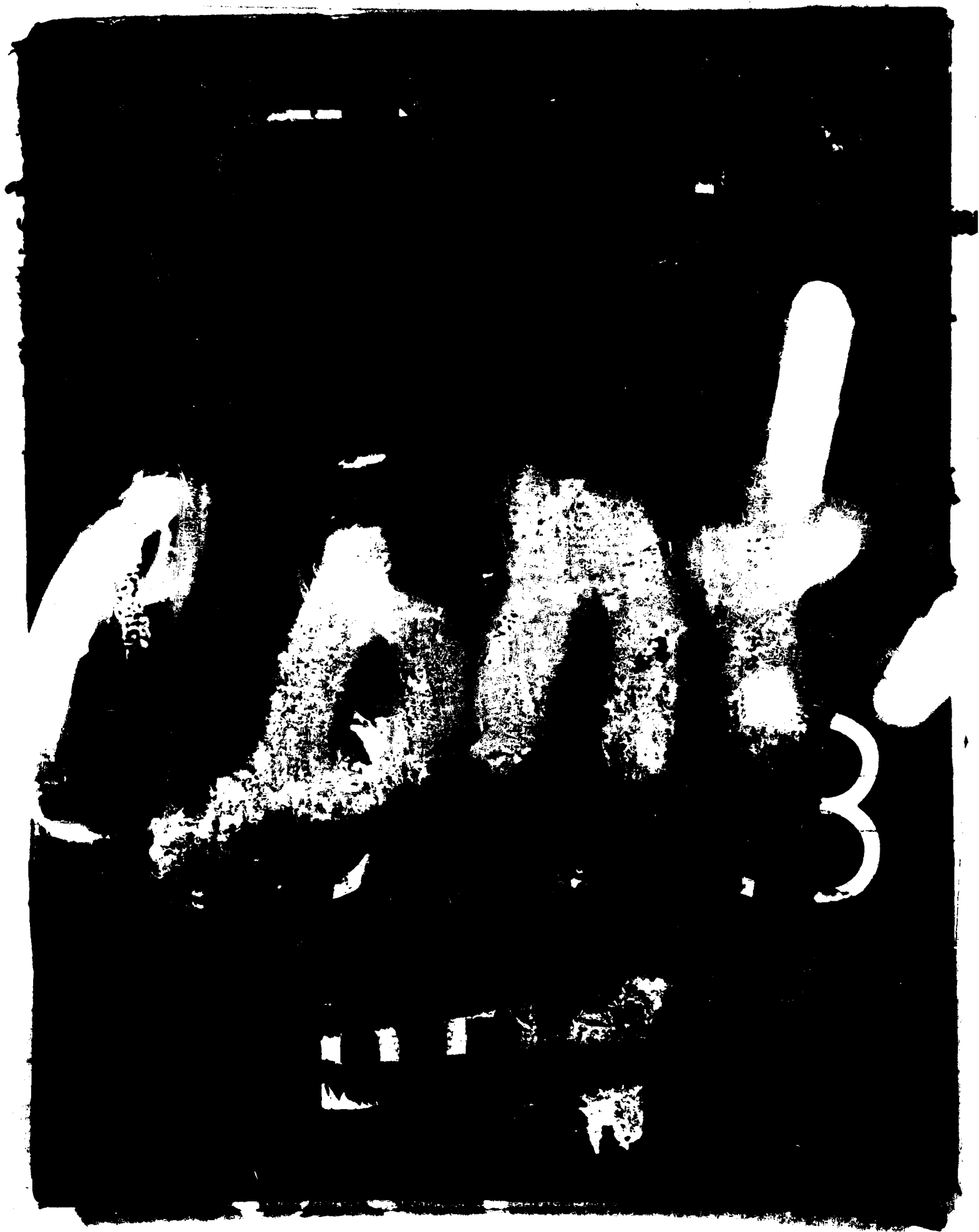
- Tenore, K. R. 1975. "Detrital Utilization by the Polychaete, *Capitella capitata*," J. Mar. Res., 33(3):261-274.
- \_\_\_\_\_. 1977. "Food Chain Pathways in Detrital Feeding Benthic Communities: A Review, with New Observations on Sediment Resuspension and Detrital Recycling," Ecol. Mar. Benthos, B. Coull, ed., Univ. South Carol. Press, Columbia, South Carolina, pp. 37-53.
- Tenore, K. R., Chamberlain, C. F., Dunstan, W. M., Hanson, R. B., Sherr, B., and Tietjen, J. H. 1978. "Possible Effects of Gulf Stream Intrusions and Coastal Runoff on the Benthos of the Continental Shelf of the Georgia Bight," Estuarine Interactions, M. L. Wiley, ed., Academic Press, New York, pp. 577-598.
- Thayer, G. W., Adams, S. M., and LaCroix, M. W. 1975. "Structural and Functional Aspects of Recently Established *Zostera marina* Community," Estuarine Research, Cronin, ed., Academic Press, Inc., 518-540.
- Thomas, L. P., Moore, D. R., and Work, R. C. 1961. "The Effects of Hurricane Donna on the Turtlegrass Beds of Biscayne Bay, Florida," Bull. Mar. Sci., 11(2); 191-197.
- Thorhaug, A. 1981. "Seagrasses in the Gulf of Mexico, Florida, and the Caribbean," Proc. U. S. Fish and Wildl. Ser., Wrksh:161-178.
- Thorson, G. 1955. "Modern Aspects of Marine Level-Bottom Animal Communities," J. Mar. Res., 14(4):387-397.
- \_\_\_\_\_. 1957. "Bottom Communities (Sublittoral or Shallow Shelf)," Geol. Soc. Amer. Mem., 67(1):461-537.
- \_\_\_\_\_. 1958. "Parallel Level Bottom Communities; Their Temperature Adaptation, and Their Balance Between Predators and Food Animals," Perspectives in Marine Biology, A. A. Buzzati-Traverso, ed., 68-82.
- \_\_\_\_\_. 1961. "Length of Pelagic Larval Life in Marine Bottom Invertebrates as Related to Larval Transport by Ocean Currents," Oceanography, M. Sears, ed., (67):455-474.
- \_\_\_\_\_. 1971. Life in the Sea, World University Library, McGraw-Hill Book Company, New York, 256 pp.
- Thurston, R. V., Russo, R. C., Fetterolf, C. M., Jr., Edsall, T. A., and Barber, Y. M., Jr., eds. 1979. "A Review of the EPA Red Book: Quality Criteria for Water," Water Quality Section AFS, Bethesda, Md., 313 pp.
- Troup, B. N., and Bricker, O. P. 1975. "Processes Affecting the Transport of Materials from Continents to Oceans," Mar. Chem. in the Coast. Envir., T. M. Church, ed., pp. 133-151.
- U. S. Department of the Interior Bureau of Land Management (BLM). 1978. "Final Environmental Impact Statement, Proposed 1978 Outer Continental Shelf Oil and Gas Lease Sale," South Atlantic OCS Sale No. 43, Washington, D. C.

- U. S. Department of the Interior Bureau of Land Management (BLM). 1981. "Final Report, South Atlantic OCS Area Living Marine Resources Study; Vol I-IV," Washington, D. C.
- U. S. Environmental Protection Agency. 1973. "Biological Field and Laboratory Methods for Measuring the Quality of Surface Water and Effluents," Environmental Monitoring Series, EPA 670/4-73-001, C. I. Weber, ed., Cincinnati, Ohio.
- \_\_\_\_\_. 1976. "Quality Criteria for Water," U. S. Government Printing Office, Washington, D. C., 256 pp.
- Van Blaricom, G. R. 1978. "Disturbance, Predation, and Resource Allocation in a High-Energy Sublittoral Sand-Bottom Ecosystem; Experimental Analyses of Critical Structuring Processes for the Infaunal Community," Ph.D. Thesis, Univ. California, San Diego, 328 pp.
- Vernberg, F. J. 1981. "Comparative Studies of Tropical and Temperate Zone Coastal Systems," Bull. Mar. Sci., 31(3):801-808.
- Vernberg, W. B., DeCoursey, P. J., O'Hara, J. 1974. "Multiple Environmental Factor Effects on Physiology and Behavior of the Fiddler Crab, *Uca pugnator*," Poll. Physiol. Mar. Organisms, F. J. Vernberg, and W. B. Vernberg, eds., Academic Press, New York, pp. 381-425.
- Virnstain, R. W. 1977. "The Importance of Predation by Crabs and Fishes on Benthic Infauna in Chesapeake Bay," Ecology, 58:1199-1217.
- \_\_\_\_\_. 1979. "Predation on Estuarine Infauna; Response Patterns of Component Species," Estuaries, 2(2):69-86.
- Vovelle, J. 1965. "Le tube de *Sabellaria alveolata* (L)--Annelide *Hermellidae*--et son ciment," Étude écologique expérimentale, histologique, et histochimique, Thesis Univ. Paris, 180 pp.
- Wallace, R. A., Fulkerson, W., Shults, W. D., and Lyon, W. S. 1971. "Mercury in the Environment: The Human Element," Oak Ridge Nat. Lab. U.S.A.E.C., Oak Ridge, Tenn., 61 pp.
- Wells, H. W. 1957. "Abundance of the Hard Clam, *Mercenaria mercenaria*, in Relation to Environmental Factors," Ecology, 38(1):123-128.
- \_\_\_\_\_. 1961. "The Fauna of Oyster Beds, with Special Reference to the Salinity Factor," Ecological Monographs, 31(3):239-266.
- \_\_\_\_\_. 1970. "*Sabellaria* Reef Masses in Delaware Bay," Chesapeake Sci., 11:258-260.
- Wentworth, C. K. 1922. "A Scale of Grade and Class Terms for Clastic Sediments," J. Geology, 30:377-392.
- Westöo, G. 1973. "Methylmercury as Percentage of Total Mercury in Flesh and Viscera of Salmon and Seatrout of Various Ages," Science, 181, 567-568.

- Wilson, D. P. 1949. "The Decline of *Zostera marina* at Salcombe and Its Effects on the Shore," J. Mar. Biol. Assoc. U. K., 28:395-412.
- Windom, H. L. 1975. "Heavy Metal Fluxes Through Salt Marsh Estuaries," Estuarine Research, L. E. Cronin, ed., 1:137-152.
- Windom, H. L., and Kendall, D. R. 1979. "Accumulation and Biotransformation of Mercury in Coastal and Marine Biota," The Biochemistry of Mercury in the Environment, J. O. Nriagu, ed., Elsevier-Holland Biomedical Press, pp. 303-323.
- Windom, H. L., Gardner, W., Dunstan, W. M., and Paffenhofer, G. A. 1976a. "Cadmium and Mercury Transfer in a Coastal Marine Ecosystem," Marine Pollution Transfer, (NSF workshop), H. L. Windom, and R. A. Duce, eds., Lexington Books, pp. 135-157.
- Windom, H. L., Gardner, W., Stephens, J., and Taylor, F. 1976b. "The Role of Methylmercury Production in the Transfer of Mercury in a Salt Marsh Ecosystem," Estur. Coastal. Mar. Sci., 4:579-583.
- Wing, B. L., and Clendenning, K. A. 1959. "Motile Invertebrates of *Macrocystis pyrifera* Fronds," Quarterly Prog. Rep. 1, Oct 31-Dec 1958, Kelp Invest. Prog. Univ. Calif. Inst. Mar. Res. IMR Ref. 59-6:4-18.
- Wood, E. J. F. 1959. "Some East Australian Seagrass Communities," Linnean Society New South Wales Proc., 84(2):218-226.
- Wood, J. M. 1974. "Biological Cycles for Toxic Elements in the Environment," Science, 183:1049-1052.
- Woods Hole Oceanographic Institute. 1952. "Marine Fouling and its Prevention," U. S. Naval Institute, 388 pp.
- Woodwell, G. M., Wurster, C. F., Jr., and Isaacson, P. A. 1967. "DDT Residues in an East Coast Estuary: A Case of Biological Concentration of a Persistent Insecticide," Science, 156:821-824.
- Yingst, J., and Rhoads, D. C. 1978. "Seafloor Stability in Central Long Island Sound: III. Biological Interactions and Their Potential Importance for Seafloor Erodibility," Estuarine Interactions, Wiley, ed., Academic Press, New York, pp. 245-260.
- Young, D. K., and Rhoads, D. C. 1971. "Animal-Sediment Relations in Cape Cod Bay, Massachusetts, I. A Transect Study," Mar. Biol., 11(3):242-254.
- Young, D. K., and Young, M. W. 1977. "Community Structure of the Macrobenthos Associated With Seagrass of the Indian River Estuary, Florida," The Ecology of Marine Benthos, Coull, ed., Univ. South Carolina Press (6):359-381.
- Zieman, J. C. 1970. "The Effects of a Thermal Effluent Stress of the Seagrasses and Macroalgae in the Vicinity of Turkey Point, Biscayne Bay, Florida," Ph.D. Thesis, Univ. Miami, Florida, 129 pp.

Zieman, J. C. 1972. "Origin of Circular Beds of *Thalassia* (Spermatophyta: Hydrocharitaceae) in South Biscayne Bay, Florida, and their Relationship to Mangrove Hammocks," Bull. Mar. Sci., Gulf and Caribbean 22:559-574.

\_\_\_\_\_. 1975. "Quantitative and Dynamic Aspects of the Ecology of Turtlegrass," Estuarine Research, Vol. 1, Cronin, ed., Academic Press, Inc., New York, pp. 541-562.



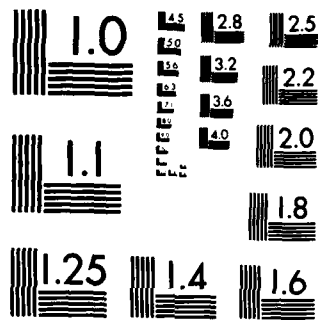
AD-A132 389

313  
THE ROLE OF PHYSICAL-CHEMICAL FACTORS IN STRUCTURING  
SUBTIDAL MARINE AND... (U) ARMY ENGINEER WATERWAYS  
EXPERIMENT STATION VICKSBURG MS ENVIR... D R KENDALL  
JUN 83 WES/TR/EL-83-2 F/G 5/1

UNCLASSIFIED

NL

|  |  |  |       |
|--|--|--|-------|
|  |  |  | END   |
|  |  |  | FILED |
|  |  |  | DTIC  |



MICROCOPY RESOLUTION TEST CHART  
NATIONAL BUREAU OF STANDARDS-1963-A

**SUPPLEMENTARY**

**INFORMATION**



DEPARTMENT OF THE ARMY  
WATERWAYS EXPERIMENT STATION, CORPS OF ENGINEERS  
P.O. BOX 631  
VICKSBURG, MISSISSIPPI 39180

REPLY TO  
ATTENTION OF

WESEV-I

11 March 1985

Errata Sheet

No. 1

THE ROLE OF PHYSICAL-CHEMICAL FACTORS IN STRUCTURING  
SUBTIDAL MARINE AND ESTUARINE BENTHOS

Technical Report EL-83-2

June 1983

1. Page 78, Figure 3-22: Replace title for Figure 3-22 with

Figure 3-22. Seasonal distribution of water temperature, *Zostera* dry-weight biomass, mean epifaunal and infaunal densities, and major fish species biomass (adapted from Vernberg 1981)

2. Page 86, Figure 3-27: Replace title for Figure 3-27 with

Figure 3-27. The generalized metabolic response to temperature of animals from different climatic regions (adapted from Vernberg 1981)

HYDRAULICS  
LABORATORY

GEOTECHNICAL  
LABORATORY

STRUCTURES  
LABORATORY

ENVIRONMENTAL  
LABORATORY

COASTAL ENGINEERING  
RESEARCH CENTER

**END**

**FILMED**

**5-85**

**DTIC**