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THE ECOLOGY OF INTERTIDAL OYSTER REEFS OF THE SOUTH ATLANTIC COAST: A COMMUNITY PROFILE

Fish and Wildlife Service

U.S. Department of the Interior

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PREFACE

This oyster reef community profile is the second in a developing series of profiles of coastal habitats. The purpose of this profile is to describe the structure and ecological function of intertidal oyster reefs in the salt marsh estuarine ecosystem of the Southeastern United States. The intertidal oyster reef habitat, as described here, is classified by Cowardin et al. (1979) as occurring in the Carolinian province, in the euhaline estuarine system, in the intertidal subsystem, in the reef class, and in the mollusk subclass, with the eastern oyster Crassostrea virginica as the dominance type.

This profile provides a handy reference which synthesizes the voluminous scientific literature on oysters and focuses on aspects of the less-studied oyster reef community. The profile also points out some of the many deficiencies in the current level of understanding of the oyster reef subsystem and of the entire estuarine ecosystem. If additional research efforts are thereby initiated, this profile will have been a success. (The observant reader will notice that in many instances where quantitative data were not available, extrapolations from other communities or educated judgments, or both, were necessary.)

The information in the profile will be useful to environmental managers, resource planners, coastal ecologists, marine science students, and interested laymen who wish to learn about the oyster reef community and its role in the coastal ecosystem. The format, style, and level of presentation should make this report adaptable to a diversity of needs, from the preparation of environmental assessment reports to supplementary reading material in college marine science courses.

This profile proceeds from a description of the estuarine setting (Chapter 1), to a discussion of oyster biology (Chapter 2), to a characterization of the oyster reef per se (Chapter 3), to a discussion of the development and role of the reef system in the coastal ecosystem (Chapter 4). Chapter 5 is a summary of the role of the oyster reef as expressed in three conceptual models, and Chapter 6 includes a brief synopsis of the first five chapters, along with implications for management.

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CONTENTS

Page

PREFACE iii
FIGURES vii
TABLES viii
ACKNOWLEDGMENTS ix

CHAPTER 1. COMMUNITY PROFILE BACKGROUND AND OBJECTIVES; DESCRIPTION OF THE COASTAL SETTING 1

1.1 Introduction and Objectives 1
1.2 General Characteristics of the South Atlantic Bight . . . 3
1.3 Estuarine Producers 8
1.4 Estuarine Consumers 10

CHAPTER 2. FUNCTIONAL OYSTER BIOLOGY AND AUTECOLOGY 17

2.1 Taxonomy and Evolution 17
2.2 Oyster Reproduction and Development. 20
2.3 Oyster Feeding, Digestion, and Assimilation 24
2.4 Stresses on Oyster Populations: Natural and Cultural. . . 28
2.5 Energy Summary 32

CHAPTER 3. OYSTER REEF DESCRIPTION AND SYNECOLOGY 37

3.1 General Reef Description 37
3.2 Reef-Associated Macrofauna 42
3.3 Reef Community Energetics 48
3.4 Reef Predation 53
3.5 Colonial Aspects of the Reef Community 55

CHAPTER 4. OYSTER REEF DEVELOPMENT, DISTRIBUTION, PHYSICAL EFFECTS, AND AREAL EXTENT 57

4.1 Reef Development 57
4.2 Distribution of Oyster Reefs in the Marsh Estuarine Ecosystem 58
4.3 Physical Effects of Oyster Reefs on the Marsh-Estuarine Ecosystem 61
4.4 Areal Extent of Oyster Reefs in the Coastal Ecosystem . . 62

CHAPTER 5. CONCEPTUAL MODELS OF THE INTERTIDAL OYSTER REEF COMMUNITY 65

5.1 Objectives and Level of Resolution 65
5.2 Regional Level Conceptual Model. 71
5.3 Drainage Unit Level Conceptual Model 71
5.4 Reef Level Conceptual Model. 74

CONTENTS (continued)

Page

CHAPTER 6. SUMMARY AND MANAGEMENT IMPLICATIONS AND GUIDELINES 79

6.1 Summary and Oyster Reef Significance 79
6.2 Management Implications and Guidelines 82

REFERENCES 84

APPENDIX: OYSTER BIOENERGETICS 93

FIGURES

Number Page

1a The study area (South Atlantic Bight) extends from Cape Fear, North Carolina, to Cape Canaveral, Florida 2
1b Tidal characteristics of the Atlantic and Gulf of Mexico coasts 2
2 Sedimentary regions of estuary 6
3 A comparison of primary productivity for different kinds of ecosystems 9
4 Model of energy flow in the Georgia salt marshes 12
5 Trophic spectrum of an estuarine community (Lake Pontchartrain Estuary, Louisiana). 15
6 The distribution of *Crassostrea virginica* 19
7 Anatomy of the oyster (*Crassostrea virginica*) and diagram showing the correct method of measuring the height, length, and width of oyster shells 21
8 Transverse section of the dorsal part of an adult *Crassostrea virginica* 22
9 A schematic representation of the rhythmic nature of the feeding process and extracellular and intracellular digestive mechanisms in oysters 25
10 Effects of turbidity on pumping rate 27
11 Effects of crude oil extract on *Mytilus edulis* carbon budgets calculated for 100-mg mussels held at 31 °/oo salinity under summer conditions (15° C,215 μg C/liter). . . 31
12 Summary of energy flow through intertidal reef oysters . . . 35
13 Diagrammatic section through oyster reef illustrating relative elevation with respect to mean tidal levels and corresponding fouling pattern on piling 38
14 Several generations of oysters (*C. virginica*) growing vertically on muddy bottom of Altamaha Sound, Georgia . . . 39
15 Seasonal oxygen consumption of reef community 49
16 Seasonal energy partitioning estimates for the entire reef community 52
17 Typical distribution of oyster reefs in small tidal creeks 60
18 Comparison of two systems of concentrated consumers whose survival depends on strong flows that bring in fuels and oxygen and outflow wastes: (a) reef of oysters and other marine animals characteristic of many estuaries; (b) industrialized city 66
19 Three hierarchical levels of oyster reef organization. . . . 67
20 Reef distribution in a single drainage basin, the Half Moon River Estuary, Wilmington Island, Georgia 68
21 Recent and historical reef distribution in the Duplin River Estuary, Sapelo Island, Georgia 69
22 Regional level conceptual model and explanation of symbols 72
23 Drainage unit level conceptual model 73
24 Reef organization conceptual model 75

FIGURES (continued)

Number | Page
A-1 Age-dependent annual production of soft tissue, shell organics, gonad output, and respiration in an oyster 95
A-2 Seasonal variation in water temperature affecting oyster reefs in South Carolina 96
A-3 Seasonal changes in size-frequency distribution of reef oysters in Georgia 99
A-4 Seasonal changes in intertidal oyster size-frequency distribution in South Carolina 100
A-5 Reef oyster height frequency relationship and cumulative biomass curves 102
A-6 Schematic representation of percentage distribution of potential food expressed in kilocalories for 1-year period in 1 m^2 of subtidal *Crassostrea gigas* population 104

TABLES

Number | Page
1 General effects of man-induced (cultural) stress on oysters 29
2 Pounds of meat and ex-vessel value (dollars) of oysters harvested in four South Atlantic States from 1973-1975 . . 33
3 Macrofauna found in Georgia oyster reefs 43
4 Mean annual frequency distribution of reef macrofauna . . 45
5 Ranked biomass of 16 major oyster species or groups of species and proportion of total macrofaunal biomass . . . 46
6 Ranking of macrofaunal metabolic dominance based on biomass 51
7 Community respiration in aquatic systems 54
8 Time scales relating ecosystem processes and components at the three conceptual levels of oyster reef organization and function 70
A-1 Conversion factors for oyster biomass units (intertidal oysters) 98
A-2 Comparison of two sets of oyster reef energy parameters collected within the study area 103

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This view of the intertidal zone at Sapelo Island, Georgia, shows the position of oyster reefs relative to the surrounding marshes and mudflats. Photo by Leonard Bahr, Louisiana State University.

CHAPTER 1

COMMUNITY PROFILE BACKGROUND AND OBJECTIVES;

DESCRIPTION OF THE COASTAL SETTING

1.1 INTRODUCTION AND OBJECTIVES

Oysters occupy a unique status among marine and estuarine invertebrates. As a group, they are the most widely studied and thus best known of all these animals, primarily because of their universal socioeconomic value. Some oyster species are prized for their flavor and high quality protein; some are valued for their pearls. Oyster shell calcium carbonate has long been used as a building material; e.g., "Tabby" houses of oyster shell were once common in coastal Georgia and South Carolina. Oyster shells are fed to chickens and are even the source of supplementary calcium in tablets for humans. Oysters of various kinds have been cultured for centuries, so, in a sense, some species qualify as domestic animals.

Much of the information gathered about oysters has been collected by scientists, but a significant amount has been collected by observant laymen, naturalists, and aquaculturists. The objectives of most of those observations, however, were to learn to grow more oysters in given areas faster and with fewer losses. In the vast oyster literature, there are relatively few "pure" ecological studies that treat the oyster objectively as an ecosystem component. For example, animals associated with oysters are usually referred to as "pest" species, as coyotes are to sheepherders. But just as no organism is autonomous, and all organisms operate within the framework of ecosystems, so the oyster's importance extends beyond its socioeconomic value.

The primary objective of this community profile is to describe the function of one species of oyster in a portion of its habitat. More specifically, we present a profile of a community associated with, dependent on, and dominated by the American or eastern oyster, *Crassostrea virginica* (Gmelin). The study area comprises the coast of the South Atlantic Bight between Cape Fear, North Carolina, and Cape Canaveral, Florida, (Figure 1a), as discussed in Section 1.2.

Because the range of the American oyster extends over a wide latitude (from 20° N to 54° N), the ecological conditions encountered are diverse and the "oyster community" is not uniform throughout the range (see Section 2.2). The present description applies primarily and specifically to those populations of oysters and associated organisms occurring in the intertidal zone in the Southeastern United States. In some portions of its range, particularly in the area being described (which has a large tidal range), the oyster builds massive, discrete reefs in the intertidal zone.

The vertical elevation of intertidal oyster reefs above mean low water is maximal within the central Georgia coastal zone, where mean tidal amplitude exceeds 2 m (2.2 m [7.2 ft] at Sapelo Island, approximately at the center of the South Atlantic Bight). Approximate isopleths or contours of the tidal range along the Atlantic and gulf coasts are indicated in Figure 1b. Local areas experience tidal variation because of local hydrologic effects. The most extensive contiguous oyster reefs occur in the South Carolina coastal zone. Oyster reefs diminish in size and significance south of Georgia and north of South Carolina, but there are intertidal patch reefs in northeastern Florida and southern North Carolina. Information reported in this document is applicable to reefs from Cape Fear, North Carolina, to Cape Canaveral, Florida, except as noted in the text.

The term oyster reef often is interchanged loosely with other terms for local estuarine areas inhabited by oysters, including oyster bar, oyster bed, oyster rock, oyster ground, and oyster planting.

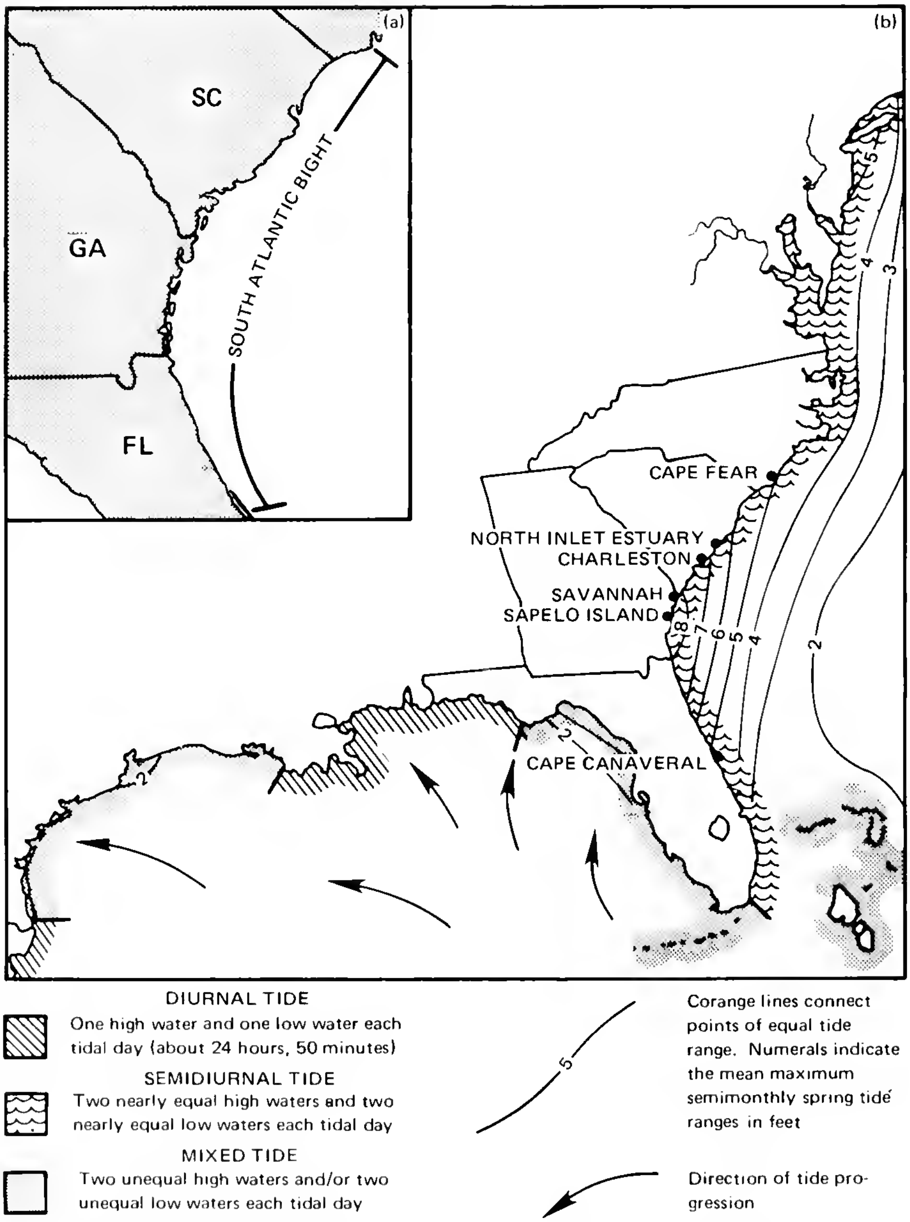

Figure 1. (a) The study area (South Atlantic Bight) extends from Cape Fear, North Carolina, to Cape Canaveral, Florida. (b) Tidal characteristics of the Atlantic and Gulf of Mexico coasts (adapted from U.S. Geological Survey 1970).

Throughout this document, oyster "reefs" are strictly defined as "the natural structures found between the tide lines that are composed of oyster shell, live oysters, and other organisms and that are discrete, contiguous, and clearly distinguishable (during ebb tide) from scattered oysters in marshes and mud flats, and from wave-formed shell windrows." Intertidal reefs, as defined here, are also distinct from natural and planted subtidal oyster populations.

Ecologists' opinions differ as to whether benthic communities (and some other communities) exist as tightly interactive and interdependent systems of organisms, or whether such communities are merely loose, chance associations to which member species belong solely by geographic accident. A proponent of the former argument long ago chose the oyster community as an example of a biocoenosis, or interactive community (Mobius 1883). Whether or not some species that occur in the oyster reef community are dispensable, the American oyster is the "keystone" species (or indispensable) in the sense intended by Paine (1969) when he coined the term.

Specific objectives of this report are as follow: (1) to synthesize a state-of-the-art systems view of the oyster reef community in the study area from existing literature; (2) to address the effects of various potential cultural and natural perturbations on the oyster reef subsystem, including pollution effects, physical alterations to the estuary, and natural changes; (3) to condense the above information into conceptual ecosystem models constructed at a level understandable by a variety of readers, including those inexperienced in using ecological models.

The American oyster is the quintessential or most typical estuarine animal. It can tolerate a wide range of salinity, temperature, turbidity, and oxygen tension, and therefore is adapted to the periodic and aperiodic changes in water quality that characterize estuaries. Some physiological and anatomical reasons for its adaptive plasticity are described in Chapter 2, which treats the autecology of the oyster. Other aspects of the success of the intertidal oyster are related to its colonial lifestyle and mutual interdependence and cannot be comprehended from information gathered for individual oysters. Chapter 3 is devoted to a discussion of the entire reef community. Chapter 4 discusses the reef's role in the coastal ecosystem and Chapter 5 presents three models expressing the reef's role. Chapter 6 summarizes the other chapters and gives implications for management.

This chapter's remaining sections describe the specific estuarine environment of the oyster reef community. They include the physical, chemical, and biological settings.

1.2 GENERAL CHARACTERISTICS OF THE SOUTH ATLANTIC BIGHT

The geographic area on which this profile primarily focuses is the portion of the South Atlantic Bight, extending along the southeastern coast of the United States between Cape Fear , North Carolina, and Cape Canaveral, Florida. This section of the southern coastal plain exhibits a continuum of change in coastal morphology, but is characterized by extensive lagoon-marsh systems and estuaries bound at their eastern extent by barrier island complexes. The morphology of coastal barrier island systems and extent of the lagoon-marsh are the results of a complex interplay of physical and biological processes.

In general, this area can be considered a mixed-energy coast (Hayes 1975) since coastal processes and morphologies are determined by the varying influence of both waves and tides. Wave and tidal conditions in this area are largely a function of the changing profile of the inner continental shelf (Hayden and Dolan 1979; Hubbard et al. 1979). Average wave heights decrease from a maximum of 1.2 m (4 ft) along the North Carolina coast to a minimum of 0.1 m (0.5 ft) along the central Georgia coast (Hubbard et al. 1979). Where the shelf is broad, nearshore wave heights are reduced through frictional loss caused by shoaling on the ocean floor shelf.

Shelf width, combined with the arcuate shape of the coastline, also influences tidal range. The southern coast of North Carolina is classified as a microtidal coastline (Davies 1964), with semidiurnal tides that range between 0 and 2 m

(0-6.5 ft). Tides at Masonboro Inlet on the southern coast of North Carolina range from 1.2 m (4 ft) to 1.4 m (4.5 ft) for mean and spring conditions, respectively (Vallianos 1975). Wind and wave processes are the principal forces dictating coastal morphology in microtidal coastal systems (Hayes 1975). Barrier islands in North Carolina tend to be long and narrow, and they contain relatively few tidal inlets. Lagoon-marsh systems are usually narrow (1.5 km or 0.6 mi), shallow, and densely vegetated (Cleary et al. 1979).

Farther south in South Carolina and Georgia, the coastal system has been classified as mesotidal (Davies 1964), having a tidal range between 2 and 4 m (6.5 and 13 ft). This coastline is characterized by short (20 to 30 km or 12 to 19 mi) barrier islands, with a wider central portion and narrow ends broken by numerous tidal inlets. In response to the higher tidal range, larger areas of lagoon-marsh are broken by extensive and complex networks of tidal drainage channels. Tidal inlets between barrier islands tend to be relatively deep (>10 m or 34 ft) and are flanked by extensive bars and spits.

Estuaries and lagoons with associated marsh, mudflat, and tidal drainage networks compose the dominant habitat of the American oyster, _C. virginica_, in the Southeastern United States. The term estuary from the Latin _aestus_, meaning tide (Schubel 1971), has been defined in various ways. Geologists tend to accept the strictly physical interpretation of Pritchard (1967), who defined an estuary as "a semi-enclosed coastal body of water which has a free connection with the open sea and within which sea water is measurably diluted with fresh water from land drainage." A broader, more ecological definition proposed by Cowardin et al. (1979) is "deep-water tidal habitats and adjacent tidal wetlands which are usually semi-enclosed by land, but have open, partially obstructed, or sporadic access to the open ocean and in which ocean water is at least occasionally diluted by fresh water runoff from the land." In this paper we define estuaries even more broadly to include all the ecological subsystems that interact to form the coastal marsh-estuarine ecosystem. In other words, to quote Odum et al. (1974), "It is the ecosystems rather than the estuarine waterbodies that are discussed ...here."

Pritchard (1967) subdivided estuarine waterbodies into four geomorphological types: (1) drowned river valleys; (2) fjord-type estuaries; (3) bar-built estuaries; and (4) estuaries produced by tectonic processes. All southeastern coastal plain estuaries fall into either the bar-built or the drowned river valley estuarine types.

General Estuarine Hydrography

Water circulation patterns are of primary significance in determining the physical and chemical conditions of the estuarine ecosystem. Water circulation strongly influences salinity, but it also directly influences sedimentation patterns, turbidity, temperature, and nutrient conditions. Estuaries with significant riverine sources of low salinity water are distinctly different in form and hydrographic character from those without such sources (Oertel 1974).

Classifications of estuarine water circulation patterns are based largely on the relative magnitude of either riverine or tidal influence (Ketchum 1951; Stommel 1951; Pritchard 1955, 1967, 1971; Bowden 1967) in conjunction with the geomorphology of the estuarine basin (Schubel 1971). Estuaries with large riverine sources of fresh water show a well-defined vertical salinity stratification. Fresh water overrides higher density salt water and forms an upper, freshwater layer. The entrainment of salt water from the lower layer into the upper, freshwater layer through eddy diffusion results in the mass movement of the saline bottom layer into the estuarine basin (Schubel 1971). This mechanism creates the salt-wedge type estuary as described by Pritchard (1971). A partially mixed estuary occurs when the tidal flow is sufficiently strong to prevent the river from dominating the circulation pattern (Schubel 1971). Turbulence generated by the movement of the saline bottom layer results in increased vertical mixing and moderate salinity stratification (Pritchard 1967). Many southeastern estuaries with relatively large freshwater sources (e.g., Altamaha and Ossabaw Sounds in Georgia and Charleston Harbor in South

Carolina) fall into this second, partially mixed classification at least seasonally.

Most estuaries in the study area are classified as vertically homogeneous (Pritchard 1967, 1971; Schubel 1971), where tidal mixing is the dominant physical process. These systems receive fresh water primarily though local precipitation via tidal creek drainage systems particularly during spring floods. Sapelo Sound, Georgia, and the lagoon-marsh complex adjacent to North Inlet, South Carolina (Finley 1975), are two examples of vertically homogeneous systems. Lagoon-marsh complexes in southern North Carolina are not fed by major streams (Cleary et al. 1979); therefore, they can also be considered vertically homogeneous.

In estuaries not directly influenced by large riverine sources, estuarine circulation patterns are largely determined by tides, wind, and by the water storage capacities of lagoon-marsh complexes (Oertel 1975). The lagoon-marsh complexes in Georgia, for example, are extensive and average 6.5 to 7.5 km (4.0 to 4.6 mi) in width. These areas store large volumes of water during high tide, and during tidal drainage they contribute significantly to water circulation and nutrient exchange within the estuarine ecosystem. These large lagoon marshes generally occupy a major portion of the watershed of the estuarine basins, and therefore direct rainfall is the major source of freshwater to these sytems (Tom Williams, Clemson University, Georgetown, South Carolina; pers. comm.)

Estuarine Sedimentation

The origin of sediments in estuaries and the processes that affect their distribution and deposition have been the subject of extensive research and scientific debate for over 25 years (Guilcher 1967). Estuarine sedimentation patterns are complex and influenced by tidal cycle, wind direction and duration, waves, seasonal riverine flooding, water storage capacity of lagoon-marsh complexes, and sediment availability. The biological animal-sediment interactions (bioturbation) and chemical factors are also important (Howard 1975). These factors may vary continuously in space, time, and intensity (Oertel 1974).

The processes of sedimentation can best be understood if the estuarine system is divided into three parts, based on generalized physical and hydrographic characteristics: (1) the lower sound and inlet entrance; (2) the middle region of the estuary, including the main rivers feeding the sound; and (3) smaller tidal creeks draining the marsh complex. Naturally occurring oyster reefs can be found in each of these main zones in the study area. The three estuarine sedimentation zones are illustrated in Figure 2.

The area of the lower sound and inlet entrance is influenced primarily by marine processes. Wind-wave and tidally generated currents exert the greatest influence in the lower sound, creating a relatively high energy sedimentary system. Where a sufficient sediment supply is present, this area is characterized by medium- to coarse-grained and commonly cross-bedded sands. Where the lower sound is less influenced by strong tidal currents, bottom sediments consist of a mixed medium- to fine-grained muddy sand. These sands become progressively finer grained and interbedded, or mixed with mud farther inland. This is particularly common in estuaries without fluvial sources of coarser-grained sediment. Near the mouth of the sound, influence of the adjacent shoreface is indicated by the increasing grain size and higher energy bedforms, sand ripples, etc. (Mayou and Howard 1975). Sandflats and mudflats frequently characterize the intertidal margins of the lower sound.

In estuarine systems characterized by large riverine freshwater input, the vertically stratified lower sections of the estuaries become natural traps for fine-grained sediment (Schubel 1971). Fine-grained sediment transported in the upper freshwater layer frequently will settle into the lower saline layer and then be carried back inland. Suspended sediment may, therefore, be transported back and forth many times within the lower section of an estuary before it is finally deposited (Postma 1967).

The middle region of the estuarine sedimentary environment includes the

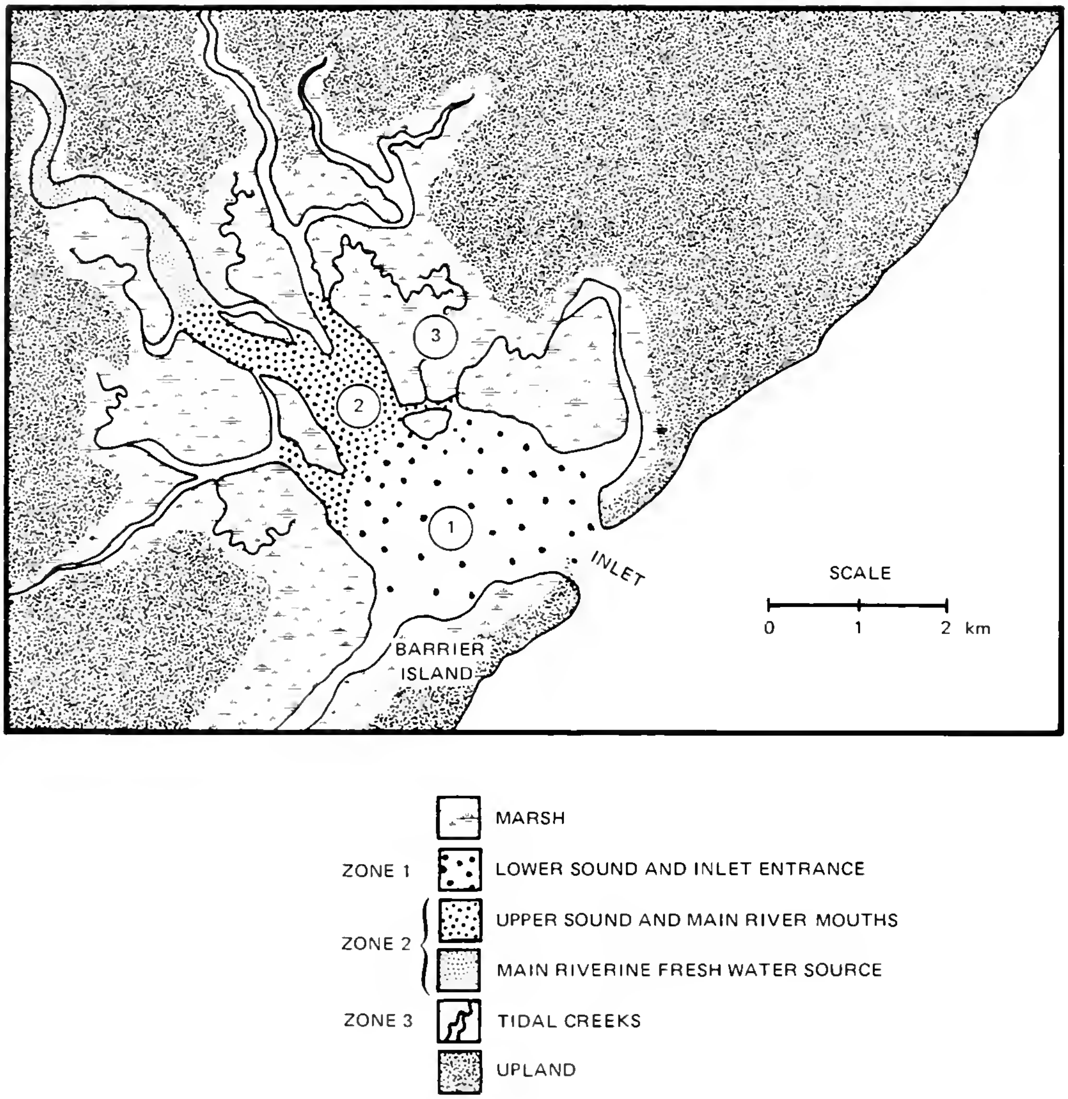

Figure 2. Sedimentary regions of estuary.

uppermost portion of the sound and the main rivers feeding the sound. This zone is influenced by both marine and riverine processes. Bottom sediments in the upper reaches of the estuary are characteristically muddy sands or interbedded fine-grained sands and muds. Farther inland, if the river transports a significant amount of coarse-grained material, bottom sediments contain a decreasing percentage of mud (Dorjes and Howard 1975). Turbidity levels are generally higher in this zone (the middle region) during all portions of the tidal cycle (Day 1951; Howard et al. 1975). These higher turbidity levels in part reflect the fact that tidal currents (especially ebb currents) attain the highest velocities in the middle regions of the estuary before they are slowed in the open sound. The importance of turbidity to oyster populations will be explained in Section 2.3.

The complex network of smaller tidal creeks that drain extensive areas of salt marsh forms the third division of the estuarine sedimentary environment. Tidal creeks exhibit highly sinuous channel patterns; laterally migrating point bars on the convex inner sides form depositional banks. The concave outer banks of tidal creeks are areas of net erosion, where water currents attain their highest velocities. This estuary zone can be classified as a low-energy, sedimentary environment. Current velocities in tidal creeks depend on the extent of marsh drainage area. Fine-grained mud-silts and, less frequently, fine sands are the most common bottom sediments. Despite the relatively fine grain size of bottom sediments in tidal creeks, the bottom includes all gradations, from extremely soft and organically rich to hard mud and clay (Galtsoff and Luce 1930). The degree of bottom sediment consolidation is a function of the interaction between depositional and erosion forces. Hard mud bottoms form in areas where tidal creeks erode into consolidated marsh sediment.

Physico-Chemical Environment

The chemical environment of the estuarine ecosystem is strongly influenced by local hydrography. The three general divisions (Figure 2) of the estuarine system used in the discussion of sedimentation also provide a convenient framework for a discussion of the chemical environment.

In the study area, estuaries are characterized by highly variable lateral and vertical salinity gradients. Within any particular estuary, however, salinity trends are best described by the degree of vertical mixing taking place between fresh and saline water masses. Three relatively well-defined salinity zones exist in the majority of estuarine systems: (1) a stable, well-mixed, and marine-dominated lower zone; (2) an unstable intermediate zone where large changes in the vertical salinity gradient occur with each tidal cycle; and (3) a stable upper region dominated by riverine fresh water influence (Howard et al. 1975). The juxtaposition of these three zones depends upon the interaction and relative magnitude of riverine and tidal influences. In the lower sound and inlet entrance, corresponding to zone 1, mean salinities are high, ranging from approximately 20 ^{o}/oo (parts per thousand) to 32 ^{o}/oo, and the water column tends to remain well mixed throughout the tidal cycle. In estuaries receiving large riverine inflows, the well-mixed, high-salinity zone may be displaced seaward several kilometers (Oertel 1974). The upper sound in the vicinity of the river mouths is influenced by both marine and riverine processes. Salinity in this region varies, ranging from 5 ^{o}/oo to over 20 ^{o}/oo, and strong vertical salinity gradients are common. Upstream of the river mouths (zone 3), salinities reflect riverine influence. The water column remains well mixed at all times, and salinities vary from 0 ^{o}/oo to 10 ^{o}/oo. Salinity variations in marsh tidal creeks correspond to that of the tidal water mass flooding the marsh. As might be expected, these values are lowered significantly during periods of local precipitation in the marsh and resultant runoff from adjacent uplands.

In general, thermal mixing of estuarine water masses occurs rapidly (Oertel 1974). Hence, over most of the lower sound, vertical temperature gradients in the water column are not pronounced and are subject to daily fluctuations (Oertel 1974). In summer, lower temperature ocean waters have a cooling influence on the estuary. Water temperatures in marsh creeks are slightly higher during ebb tide, the result of solar heating in the marsh during the tidal excursion over dark sediments with low albedo (reflectance).

Dissolved oxygen concentrations generally increase from the upper, riverine-dominated portion of the estuary to the lower sound and inlet. This pattern closely parallels that of salinity. Howard et al. (1975) found that during the summer dissolved oxygen values ranged from 4 to 6 microliters/liter for a portion of the Ossabaw Sound, Georgia. These relatively low values may reflect the consumption of oxygen during the oxidation of organic detritus in suspension in the upper section of the estuary. Frankenberg and Westerfield (1968) reported that the dissolved oxygen levels in estuarine waters in coastal Georgia were extremely sensitive to sediment disturbance; during the summer the oxygen demand of a single milliliter of disturbed sediment could deplete the dissolved oxygen contained within 986 ml of water.

Oertel (1976) described large temporal and spatial variations in turbidity in estuarine waters. These variations relate to riverine input, local resuspension of bottom sediments by tidal scour and waves, and trapping of fine-grained sediments in the lower portions of estuaries (Schubel 1971). Turbidity is greater in the upper reaches of the estuarine system than either farther upstream in the source river or farther seaward. This zone has been termed the "turbidity maximum" by Schubel (1968). Oertel (1976) found suspended sediment concentrations in the upper Wassaw ranging from 9.6 mg/liter to 585.6 mg/liter, averaging 46.6 mg/liter. Higher levels of turbidity were measured during spring tides. In tidal creeks, turbidity increases significantly during periods of local rainfall when the marshes are exposed at low tide (Settlemyre and Gardner 1975). Oertel (1976) found a consistent inorganic-organic ratio in suspended sediments in the upper estuary, averaging 70% inorganic material and 30% combustible organic detritus.

1.3 ESTUARINE PRODUCERS

The estuary is perhaps best known ecologically for its typically high net primary productivity. The productivity of estuarine systems relative to other ecosystems is illustrated in Figure 3. A detailed explanation of the high annual net productivity in southeastern estuaries was presented by Schelske and Odum (1962). They listed five essential factors: (1) tidal currents; (2) abundant nutrients; (3) rapid turnover and conservation of nutrients; (4) three separate groups of producers; and (5) year-round productivity. Factors 4 and 5 ensure that primary production occurs throughout the year; therefore, energy and nutrient sources are optimally exploited and net production is maximized. The three primary producers discussed by Schelske and Odum (1962) are emergent macrophytes, phytoplankton, and benthic algae. Another group recently has received scientific attention: chemosynthetic bacteria (Howarth and Teal 1979). Each group is briefly discussed below.

Emergent Macrophytes

The marsh-estuarine complexes within the study area are characterized by broad expanses of salt marshes dominated by two marsh grass species which compose a major portion of the annual primary production of these systems. These are the saltmarsh cordgrass (*Spartina alterniflora*) and the black needlerush (*Juncus roemerianus*). *Spartina* is dominant overall, and large continuous stands of this plant occur behind the barrier islands (Pomeroy and Wiegert 1980). The annual production cycle of these marshes peaks in late summer, followed by a long period of decay and gradual export of dead vegetation (detritus) into waterbodies or incorporation into peat deposits within the marsh.

In terms of overall primary production, the emergent macrophytes are considered to contribute a major portion of particulate carbon to the estuarine ecosystem. Pomeroy and Wiegert (1980) reported that *Spartina* production makes up 79% of the particulate organic matter annually produced by the entire marsh estuarine ecosystem. *Spartina* also produces dissolved organic matter that leaches into the water column during each tidal inundation. This leachate is thought to contribute significantly to the total carbon budget of the estuarine ecosystem (Turner 1978).

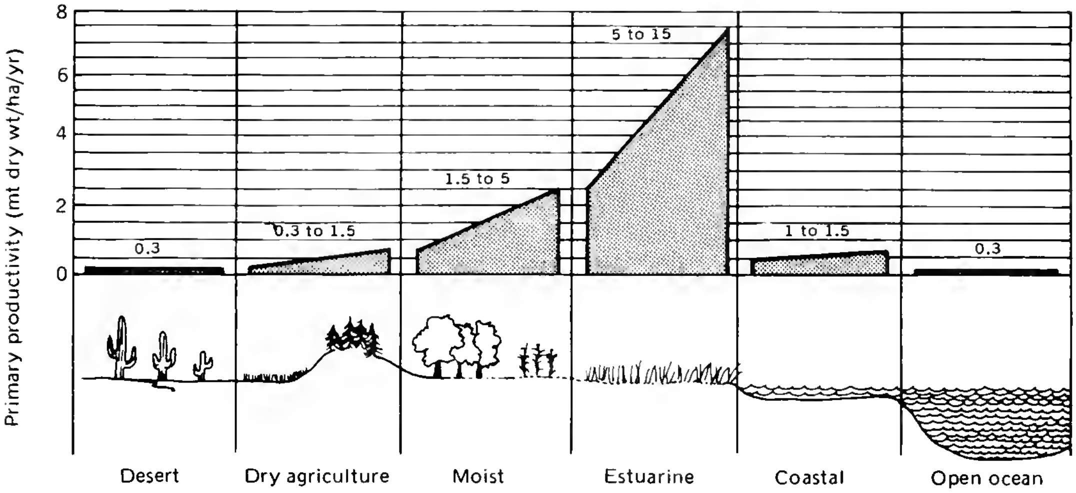

Figure 3. A comparison of primary productivity for different kinds of ecosystems (adapted from Teal and Teal 1969).

Estimated annual net production by emergent macrophytes in the study area has been reported at 980 $gC/m^2/yr$, when prorated for the entire marsh estuarine system (Pomeroy and Wiegert 1980). This number does not include leachate, however, making it a conservative estimate.

It should be noted that some controversy exists regarding the paradigm that emergent macrophytes are the primary source of particulate carbon in coastal ecosystems in the South Atlantic Bight. Arguments have been advanced (Haines 1976, 1977) that perhaps production by phytoplankton is more significant than that of emergent macrophytes. Counterarguments and hypotheses by Peterson et al. (1980) provide alternative interpretations of Haines' (1976, 1977) studies. Until more definitive research resolves this controversy, the paradigm is still viable.

Phytoplankton

The major phytoplanktonic producers in a "typical" estuary in Georgia were listed (Pomeroy and Wiegert 1980) as pelagic diatoms (and occasional benthic pennate diatoms swept up from the bottom into the water column), dinoflagellates and green flagellates. Their combined production rate was estimated as 125 $gC/m^2/yr$ (Pomeroy and Wiegert 1980) when prorated for the entire marsh water surface (water comprises about one-third of this area).

Benthic Algae and Epiphytes

The principal primary producers in the marsh sediments are benthic pennate diatoms. These organisms migrate vertically in the sediment, depending on the tidal stage and light conditions. They are often clearly visible on exposed creek banks as a golden sheen on the brown mud. Pomeroy and Wiegert (1980) reported that benthic algae account for about 11% of total net primary production in a marsh estuarine system in the study area, or 134 $gC/m^2/yr$, prorated for total estuarine area.

Another group of primary producers in the marsh-estuarine ecosystem is the community of epiphytic algae that inhabits the culms or stalks of marsh grass. This diverse community is not readily apparent but attracts grazers, especially the gastropod *Littorina irrorata*. In terms of production rates, the epiphytic community is relatively unimportant compared to *Spartina alterniflora* (Pomeroy and Wiegert 1980).

Chemosynthetic Bacteria: Mixotrophic and Photolithotrophic

Two groups of anaerobic microbial organisms inhabiting sediments within the salt marsh-estuarine system are the mixotrophic sulfate-reducing bacteria and the photolithotrophic bacteria, which have recently received scientific attention. The abundance of sulfate in salt marsh sediments makes this ion the obvious substitute for oxygen as the electron acceptor in the anaerobic respiration of many microbes. These organisms use dissolved organic matter as an energy source. Sulfate reduction is now recognized as an extremely important process in the salt marsh estuary (Fenchel and Riedl 1970; Howarth and Teal 1979). As sulfate is reduced (primarily by a bacterial group known as *Desulfovibrio*), the resulting sulfide diffuses upward. Its reducing "power" is subsequently used along with light as the energy source to fix atmospheric carbon dioxide by anaerobic bacteria. The release of the resulting organic matter from salt marsh sediments is probably augmented by tidal flushing and may be quite significant along creek banks.

A major implication of this overall process is that the initial carbon source for the sulfate reducers is leachate from the roots of macrophytes. Thus, the wetland macrophyte production is ultimately the source of this (unknown) amount of extra organic carbon that goes into the ecosystem.

1.4 ESTUARINE CONSUMERS

The following description of the consumers of the salt marsh estuarine ecosystem in the study area is necessarily incomplete because it describes only those groups of organisms that are considered dominant, functionally significant, or that directly affect the oyster reef community. These are bacteria, benthic infauna, zooplankton, nekton, and terrestrial consumers.

Bacteria

Two basic principles relate to the consumption of the net energy produced annually in the marsh-estuarine ecosystem. The first principle is that most energy produced by the dominant primary producer in the system (*Spartina alterniflora*) is not consumed directly by grazers. Instead, at least 90% (perhaps 95%) either leaches into the water column from living and dead plants as dissolved organic matter, or through various processes enters the system as detritus. Both forms of this organic matter are then attacked by microscopic decomposers or ingested directly by macroconsumers.

The second major principle of energy consumption in the salt marsh is that the decomposer community (aerobic and anaerobic) is large, diverse, and extremely active, consuming about 50% of the total energy flowing through the ecosystem, as shown in Figure 4 (Teal 1962). The decomposer community of the estuarine ecosystem can be divided conveniently into two groups: (1) aerobic heterotrophs (bacteria and fungi) which utilize inorganic matter in standing dead grass stalks, the water column, and aerobic sediments; and (2) anaerobic bacteria in anoxic (oxygen-poor) sediments. The activity of the aerobic group enhances the nutritive quality of both particulate and dissolved organic matter for the larger consumers. Particulate organic matter is colonized by the aerobic heterotrophs as it is gradually fragmented into detritus. Its nutritional value is enhanced by increasing the relative nitrogen composition of the particulate organic carbon (POC), as shown by Odum and de la Cruz (1967). This can be symbolized as follows: $POC + O_2 + NH_4^+ \rightarrow$ bacterial $POC\text{-}N + CO_2$. Dissolved organic carbon (plant leachates, etc.) can be assimilated by micro-heterotrophs and also converted into POC-N. Some aerobic bacteria are also critical elements of the nitrogen cycle, as discussed below.

Anaerobic decomposers function in a variety of roles in the salt marsh ecosystem. They are essential to the geochemical cycles that release plant nutrients in a continuous stream to the primary producers. The nitrogen cycle is especially important because evidence to date indicates that nitrogen is the limiting nutrient in the salt marsh (Valiela and Teal 1979). Since the decomposition of cellulose is nitrogen-limited (Pomeroy and Wiegert 1980), the decomposition of the large standing stock of organic matter in the system results in a competition for nitrogen between decomposers and primary producers.

Four groups of bacteria are involved in the nitrogen cycle. One group in the sediments (nitrogen fixers) converts atmospheric nitrogen to nitrate and nitrite ($N_2 \rightarrow NO_3^- + NO_2^-$); another group (the denitrifiers) reduces nitrates and nitrites to atmospheric nitrogen. A third group (ammonifiers) converts dead tissue into ammonia. A fourth group (nitrifiers) occupies the thin, oxidized layer around *Spartina* roots and converts ammonia from anaerobic sediments into nitrates directly usable by the plant.

The anaerobic zone in salt marsh-estuarine sediments extends upward almost to the sediment surface because of the enormous oxygen-depleting capacity (chemical oxygen demand) of these sediments. The metabolic activity of anaerobic bacteria is responsible for this oxygen demand.

Benthic Infauna

Other organisms in estuarine sediments include metazoan animals larger than bacteria but so small that studying them and documenting their functions are difficult. This group is called the meiofauna, and although it contains various phylogenetic groups and trophic positions, its overall role apparently is that of a trophic intermediary between bacteria and macroconsumers. Nematodes and other meiofauna appear to be major processors of bacterial tissue, and they are an important component of the food of many so-called deposit feeders (Sikora 1977; Bell and Coull 1979). Intertidal biomass of nematodes in creek banks in the study area has been measured at 6.4 g ash free dry weight (afdw)/ m^2 (Sikora et al. 1977).

Larger benthic organisms (macrobenthos) in salt marsh estuaries are usually divided into epibenthos and macro-infauna. Because oysters are epibenthos, we will omit further discussion of epibenthos

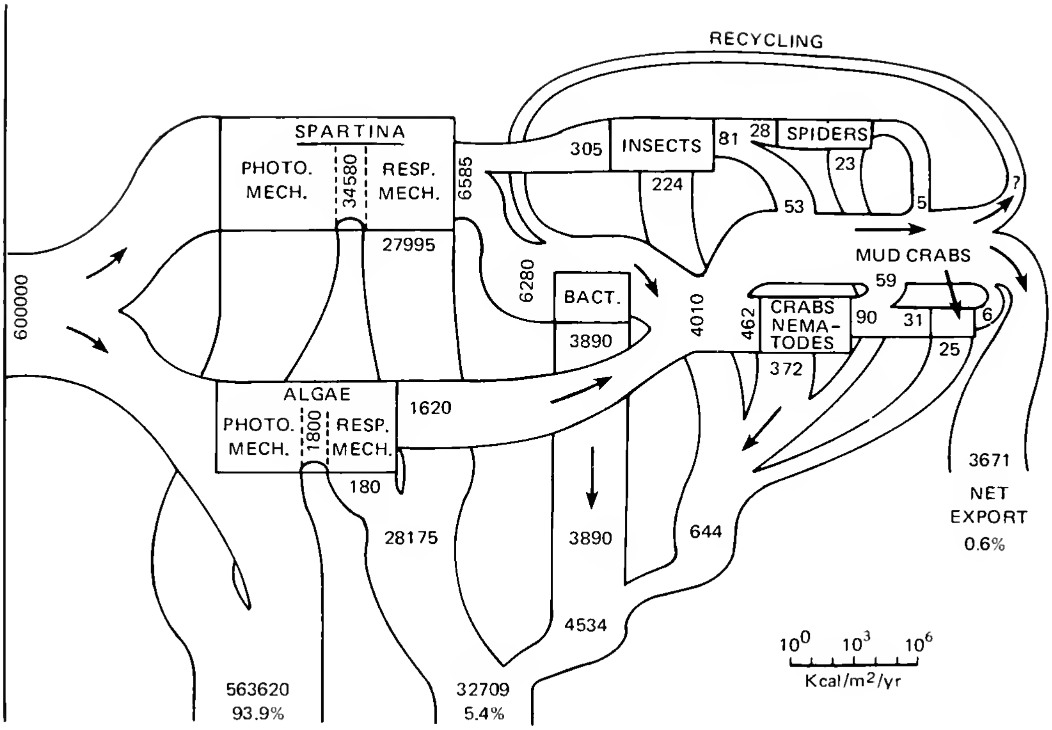

Figure 4. Model of energy flow in the Georgia salt marshes (adapted from Teal 1962).

until later. Macro-infauna are often divided into two functional groups, deposit feeders and suspension feeders. Theories have been developed to explain why often the two groups appear to be mutually exclusive in local areas (Rhoads and Young 1970; Levinton 1972).

Suspension feeders include clams and some tube-dwelling polychaetes (worms). Deposit feeders are often more motile, and some workers even include in the group those quasidemersal nektonic organisms that burrow into the bottom to feed, e.g., grass shrimp. Many polychaetes and gastropods (snails) are also deposit feeders. Another major category of the estuarine macrobenthic community is the predators, including some gastropods, turbellarians (flatworms), nemertines (round worms), and echinoderms (starfish).

Deposit feeders and demersal nekton are important in reworking the sediments by burrowing and plowing (bioturbation). This activity redistributes organic matter and other nutrients to the water column and introduces oxygen into the sediments. For example, one mullet can rework 45 m^2 of bottom area per year (Pomeroy and Wiegert 1980).

Conversely, suspension feeders (including oysters) filter particles from the water column and then deposit organic matter in the form of feces on the sediment where it becomes available to the decomposers. Krauter (1976) estimated that salt marsh macrobenthic organisms (in the marsh proper) deposit 1,709 g dry wt/m^2/ yr, which is 455 g of organic matter. He also calculated that 53% of the marsh's annual primary production could be processed through the feeding mechanisms of these organisms.

Zooplankton

Estuarine animals living suspended in the water column generally are classified as zooplankton if they are either so small or such weak swimmers that they are transported passively by water currents. The mobility of zooplankton typically is limited to vertical migrations in the water column; for example, a daily migration from the surface to bottom waters and back again is a commonly observed pattern among many forms. By altering their vertical elevation in the water column, zooplankters can use variations in food supply and use water movements in estuaries for dispersion by "riding" parcels of water masses as the latter traverse an estuary. For example, some species of zooplankton follow the salinity wedge on the bottom as the wedge progresses landward, or the surface layers of freshwater as they move seaward.

Zooplankton often are divided into holoplankton and meroplankton. Holoplankton spend their entire life cycles in the water column while meroplankton spend only their larval stages above the bottom. Holoplankton include microzooplankton, such as copepods and rotifers; and macrozooplankton, like euphausiids, ctenophora and other jellyfish. Meroplankton include larval finfish and decapods; and a large contingent of the larvae of many macrobenthic animals, including many polychaetes, barnacles, clams and mussels, and, of course, oyster larvae.

The functional importance of zooplankton in the estuarine ecosystem is partly expressed by a high turnover rate of planktonic species, by large populations, and by the very small average size of individual members. These three factors ensure that zooplankton process a large amount of the organic materials available in some estuaries, much of which represent the conversion of phytoplankton into the tissue of higher consumers. The zooplankton community as a group largely depends on phytoplankton as a carbon source, and thus tends to be more important (abundant) in estuaries dominated by phytoplankton, rather than in those where macrophyte production is of primary importance. The carbon pathway from phytoplankton to zooplankton to higher consumers is a significant trophic link in all estuaries, however, including those in the study area.

Although the oyster larvae are members of the zooplankton community, they are extremely vulnerable to predation by plankton feeders, including members of the macroplankton group, such as ctenophores. Some years ago in the New Jersey oyster grounds, oyster spatfall (larval recruitment) was reduced during years of large ctenophore populations (Nelson 1925). Meroplankton usually compose a greater portion of the zooplankton community during summertime when many clams, mussels, oysters, barnacles, crabs, polychaetes, and other benthic organisms are spawning. This input of living protein from the bottom into the water significantly increases the food supply of filter-feeding animals, both nektonic and epibenthic suspension feeders. Many of the latter probably cannibalize larvae of their own kind.

Nekton

The active swimmers in the estuary are divided into pelagic and demersal nekton. The pelagic nekton feeds in the water column, either on phytoplankton and detritus, on zooplankton (including oyster larvae), or on other nektonic forms. The bottom feeders or demersal nekton feed on adult benthos, including oysters and their associates. Darnell (1961) reported the feeding habits of some typical estuarine nekton (Figure 5).

Terrestrial Consumers

The other major group of consumers characteristic of the marsh-estuarine system is the large, diverse collection of "terrestrial" or land-based consumers. This group comprises insects and other small arthropods, including some fiddler crabs; pulmonate gastropods, especially *Littorina irrorata*; birds; reptiles (even alligators); and mammals, such as the rice rat, mink, otter, and raccoon. The specific members of this group that directly impinge on the oyster reef community are discussed in Chapter 3. The total biomass of terrestrial consumers, including the active primary consumers (plant hoppers and grasshoppers) that graze *Spartina* directly, was estimated at 1 g C/m^2 (Pomeroy and Wiegert 1980).

A view of the estuarine environment in which oyster reefs occur in coastal South Carolina. Photo by South Carolina Wildlife and Marine Resources Department.

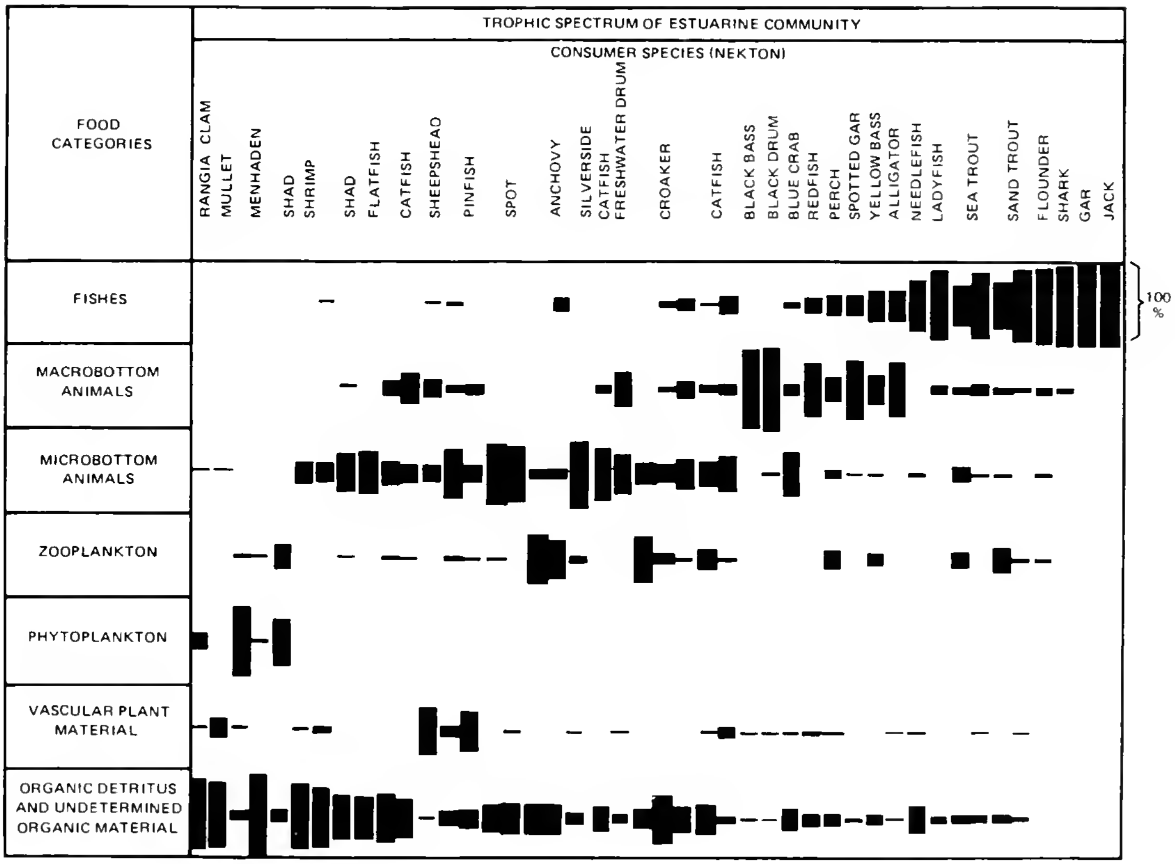

Figure 5. Trophic spectrum of an estuarine community (Lake Pontchartrain Estuary, Louisiana) (adapted from Odum 1971 after Darnell 1961).

This photograph depicts individual reef oysters occurring at the mean low water mark. Note the vertical orientation. Photo by Rhett Talbert, University of South Carolina.

CHAPTER 2

FUNCTIONAL OYSTER BIOLOGY AND AUTECOLOGY

This chapter summarizes the salient information on oyster biology, especially that relating to the functional position of the oyster in the estuarine ecosystem. Each aspect of oyster biology discussed here is presented as an aid to understanding this functional role.

A number of excellent treatises on oyster biology, including the monograph on the American oyster by Galtsoff (1964), preclude the necessity for another extensive treatment. Readers interested in more detail on subjects discussed here should refer to Galtsoff (1964) or other references cited in the chapter.

2.1 EVOLUTION AND TAXONOMY

The oyster evolved long ago from an ancestral mollusk into a highly reorganized and in some ways simplified form. The major evolutionary steps involved are summarized below as they were reconstructed by Yonge (1960):

(1) lateral compression of the body
(2) extension of the mantle to the margins of the shell
(3) division of the shell into halves (valves) separated by a noncalcareous ligament
(4) fusion of pallial muscles to form paired adductor muscles
(5) reduction of head and development of labial palps
(6) development of cilia on (paired) gills, and development of a gill feeding function in addition to their respiratory role
(7) probable reduction of metabolic requirements over that of ancestral forms
(8) loss of foot and byssus in the adult life stage
(9) loss of anterior adductor muscle
(10) rounding of the body
(11) development of a horizontal orientation with the left valve down in the adult form

The currently accepted formal classification of the American oyster is presented below, accompanied by the major morphological and ecological characteristics that apply to each category. There is currently some controversy about the classification of some oyster genera and species, and descriptors are not standardized, so that different workers have used shell morphology, geographical range, reproductive behavior, and larval shell morphology to classify oysters. New tools of biochemical genetics offer hope of resolving some of the controversial questions in oyster taxonomy.

For this report, the American oyster will be classified according to Abbott (1974) as follows:

Class Bivalvia (Pelecypoda)
Order Pterioida
Family Ostreidae
Genus _Crassostrea_
Species _virginica_

Each taxon will now be described briefly.

Class Bivalvia

This class includes clams, mussels, scallops and oysters. Some general characteristics are (1) a shell divided into two valves hinged dorsally by a ligament of conchiolin and connected by one or two adductor muscles; (2) a shell usually consisting of three layers: an outer organic horny matrix (conchiolin), a middle prismatic layer, and an inner nacreous or pearly layer; (3) a laterally compressed body; (4) either a small head or none at all; (5) a wedge- or hatchet-shaped foot (if present), (6) a mantle extending to the margins of the shell and forming a large mantle cavity, containing ciliated gills (ctenidia) that function in feeding, pumping, and respiration; (7) a crystalline style that releases amylase for starch digestion.

Order Pterioida

The order Pterioida is one of four orders of bivalves, each distinguished by the structure of its gills, and includes pearly and winged oysters, scallops, and the true oysters. These orders are characterized by paired gills that are greatly lengthened (compared to the ancestral type) and folded back on themselves to form four demibranchs interconnected by tufts of cilia. The mantles in these mollusks have taken over the sensory function of the molluskan head, including some visual or light-sensing capacity.

Family Ostreidae

This family includes a large number of edible and nonedible oysters. They are generally restricted to shallow coastal waters between 44° S and 64° N (Galtsoff 1964). Oysters have unequal valves with no hinge teeth except in the prodissoconch or larval shell. In all but their larval stages, oysters have completely lost their byssus (attachment filaments) and foot and have retained only the posterior adductor muscle, which is kidney- or crescent-shaped.

Genus Crassostrea

The oysters included in this genus are characterized by extremely variably shaped (ecomorphic) shells, depending on the substrate and current regimes of the habitat in which the oysters grow. Members of the genus *Crassostrea* are anatomically distinct from their counterparts in the genus *Ostrea*, in that *Crassostrea* are somewhat larger at maturity, with a deeper cupped left valve on which they ordinarily rest.[1] They also possess a distinctive asymmetrical space between the right mantle and gill plates, known as the promyal chamber. The promyal chamber is important because it probably permits greater pumping rates, an advantage in silt-laden water (Ahmed 1975). This chamber also functions in the reproductive success of this genus. Eggs of *Crassostrea* species are small (∿ 40 µ) and are released directly into the water, rather than being incubated within the mantle cavity, as those of the genus *Ostrea*. The promyal chamber allows for higher release velocity for eggs and is important for egg dispersal.

The production of free-living planktonic larvae is critical to members of the genus *Crassostrea* because it promotes genetic exchange over wide areas. Oyster larvae have been documented to travel at least 50 km (30 mi). Quayle (1969) and Stenzel (1971) estimated that they could disperse up to 1,300 km (800 mi).

Probably the most important characteristic of the genus *Crassostrea*, which has permitted almost worldwide distribution, is its ability to tolerate wide ranges of salinity, turbidity, temperature, and oxygen tension.

The morphology has changed little since the oyster arose during the Triassic period about 190 million years ago. The genus *Crassostrea* arose during the Cretaceous period (135 million years ago) (Stenzel 1971). Representatives of this genus characteristically occur in turbid estuaries with soft bottoms in the Indo Pacific area, Eurasia, Africa, and North and South America.

Crassostrea virginica

The Eastern or American oyster (*C. virginica*) is the species that builds the intertidal reefs focused on in this report. This species is distributed along the entire east coast of North America, from the Gulf of St. Lawrence in Canada to Key Biscayne, Florida, to the Yucatan and the West Indies; and it has been reported even in Brazil (Gunter 1951). Figure 6 (from Ahmed 1975) illustrates this 8,050-km (5,000-mi) range. *Crassotrea virginica* prevails over this immense range because of its tolerance to low temperature (Stenzel 1971).

Physiological, ecological, and biochemical data indicate that *C. virginica* has several distinct physiological races (Loosanoff and Nomejko 1955; Menzel 1955; Hillman 1964; Li and Fleming 1967; Ahmed 1975). On the other hand, Buroker et al. (1979) concluded that significant genetic distinctions occur only between populations of *C. virginica* from Nova Scotia and

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[1] Note, however, that reef oysters are usually oriented vertically with both left and right valves pointed upward.

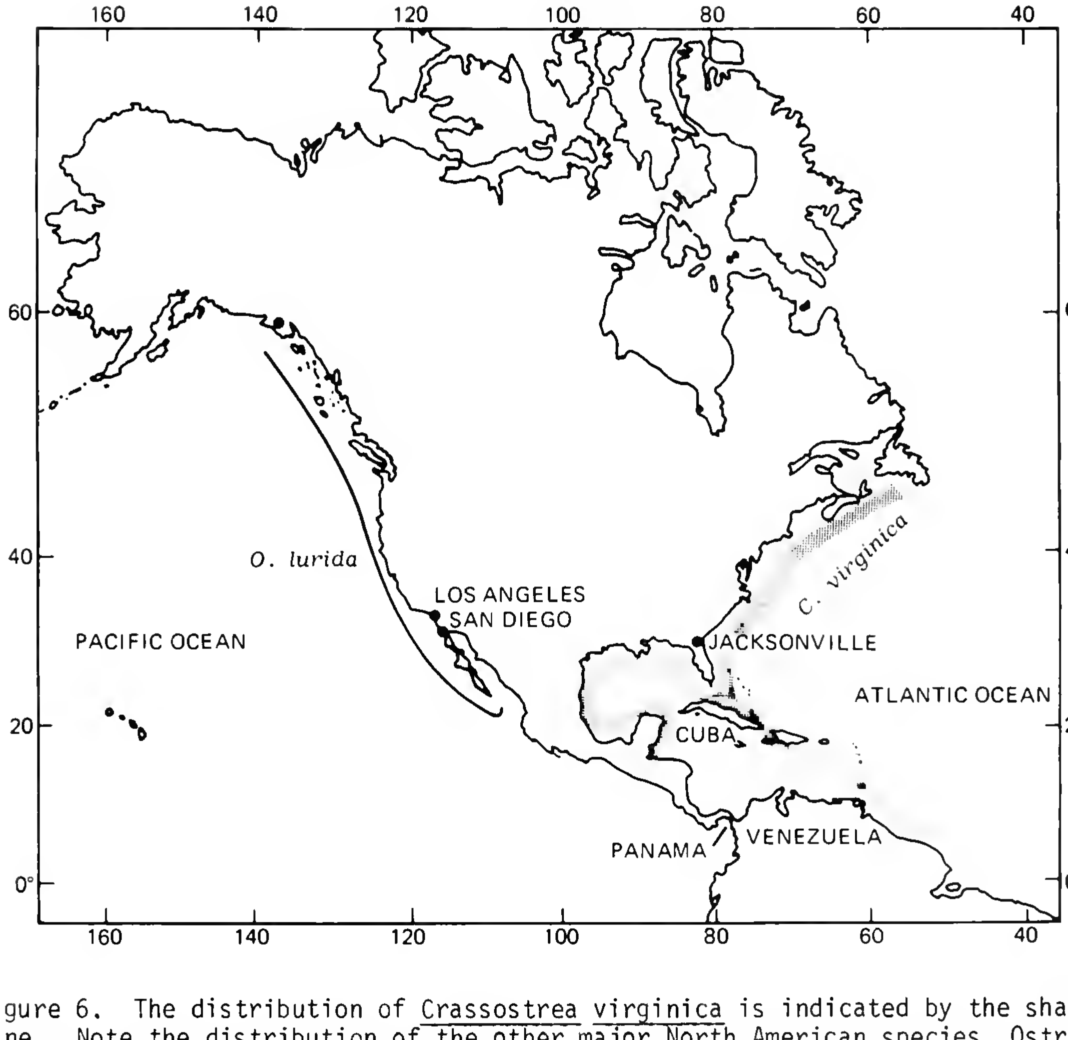

Figure 6. The distribution of Crassostrea virginica is indicated by the shaded line. Note the distribution of the other major North American species, Ostrea lurida, shown by the solid line on the west coast (adapted from Ahmed 1975).

west Florida. These researchers concluded that the two populations were only 82% genetically similar, approximately the level of similarity between C. virginica and C. rhizophorae. The latter two species are genetically close enough to have been successfully hybridized in the laboratory (Menzel 1968). Stauber (1950) postulated that C. virginica was discontinuously distributed on the east coast during prehistoric times, and that speciation was occurring before oyster culture activities by man removed the barriers to gene transfer.

N. E. Buroker (University of Maryland Marine Products Laboratory, Crisfield, Maryland; pers. comm.) indicates a single, large panmictic (genetically homogeneous) population exists between Cape Cod, Maryland, and Corpus Christi, Texas, with 96% to 99% genetic similarity. Levinton (1973) reported that six species of bivalve mollusks (not including oysters) showed an increase in genetic variability with an increase in intertidal elevation, corresponding to increasing environmental variability. This would be an interesting parameter to study in intertidal reef oyster populations.

Without further consideration of the evolutionary origins of the oyster, we will concentrate on the functional (ecological) classification of C. virginica between Cape Fear, North Carolina, and Cape Canaveral, Florida. From this point on, the generic term "oyster" will mean C. virginica, and "oyster reef" will refer to oyster reefs in the study area unless specified otherwise.

The general anatomy of the adult oyster appears in Figures 7 and 8 (adapted from Galtsoff 1964). Note the insert diagram in Figure 7 showing the proper way to describe oyster size.

2.2 OYSTER REPRODUCTION AND DEVELOPMENT

The oyster is dioecious (with separate sexes), but once a year some members of a given local population change their gender from male to female (protandry) or female to male (protogyny). This sexual lability is possible partly because of the simplicity of the oyster reproductive system, which lacks ducts, glands, or secondary sexual structures (Yonge 1960). Oysters develop functional gonads at a young age (2 to 3 months) and small size (less than 1 cm in height). Usually they tend to develop as males during their first season, with subsequent protandric change (to females) in following seasons (Menzel 1955). A small percentage of any given population (< 1%) functions as true hermaphrodites (Kennedy and Battle 1963), and this pattern seems to hold for other species in the genus Crassostrea (Asif 1979).

Some preliminary evidence indicates that populations of oysters under certain kinds of stress tend to develop a higher proportion of males than females, but this remains to be conclusively demonstrated (Amemiya 1936; Loosanoff and Nomejko 1955; Kennedy and Battle 1963; Bahr and Hillman 1964). It is interesting to speculate, however, that the stress encountered in the higher portions of the oysters' vertical range in the intertidal zone (the upper reef zone) could produce androgenous (predominantly male) colonies that would contribute little to the reproductive success of the population.

After oyster gonads reach maturity in a local population, a temperature (or salinity) shock triggers the emission of sperm from one or more males. The temperature at which oyster populations in different regions begin to spawn has been used in the past to distinguish physiological races. Atlantic coast and gulf coast oysters have thus been separated into 17° C, 20° C, and 25° C spawners (Yonge 1960). Reef oysters subject to very high summer temperatures are probably members of the last group.

The emission of sperm from male oysters occurs via the exhalent chamber of the mantle. A chemical constituent of the sperm (a protein pheromone) stimulates the females in the area to release eggs, and a spawning chain reaction can sweep dramatically over a dense population, turning the water white. Females expel eggs from the inhalent chamber rather than through the exhalent chamber. This process involves a preparatory contraction in portions of the mantle margins to reduce the size of the exhalent opening. Eggs then pass through

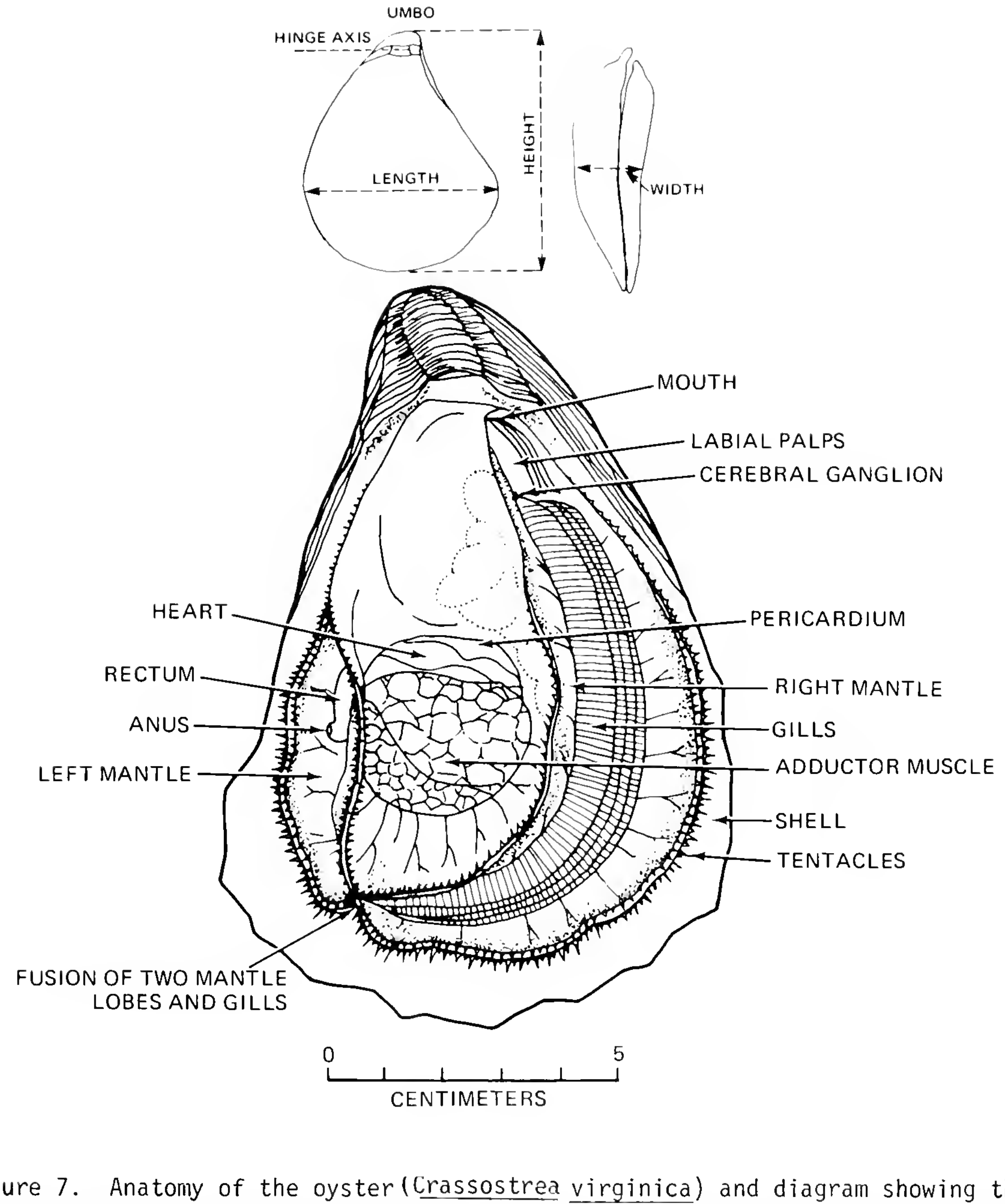

Figure 7. Anatomy of the oyster (*Crassostrea virginica*) and diagram showing the correct method of measuring the height, length, and width of oyster shells (from Galtsoff 1964).

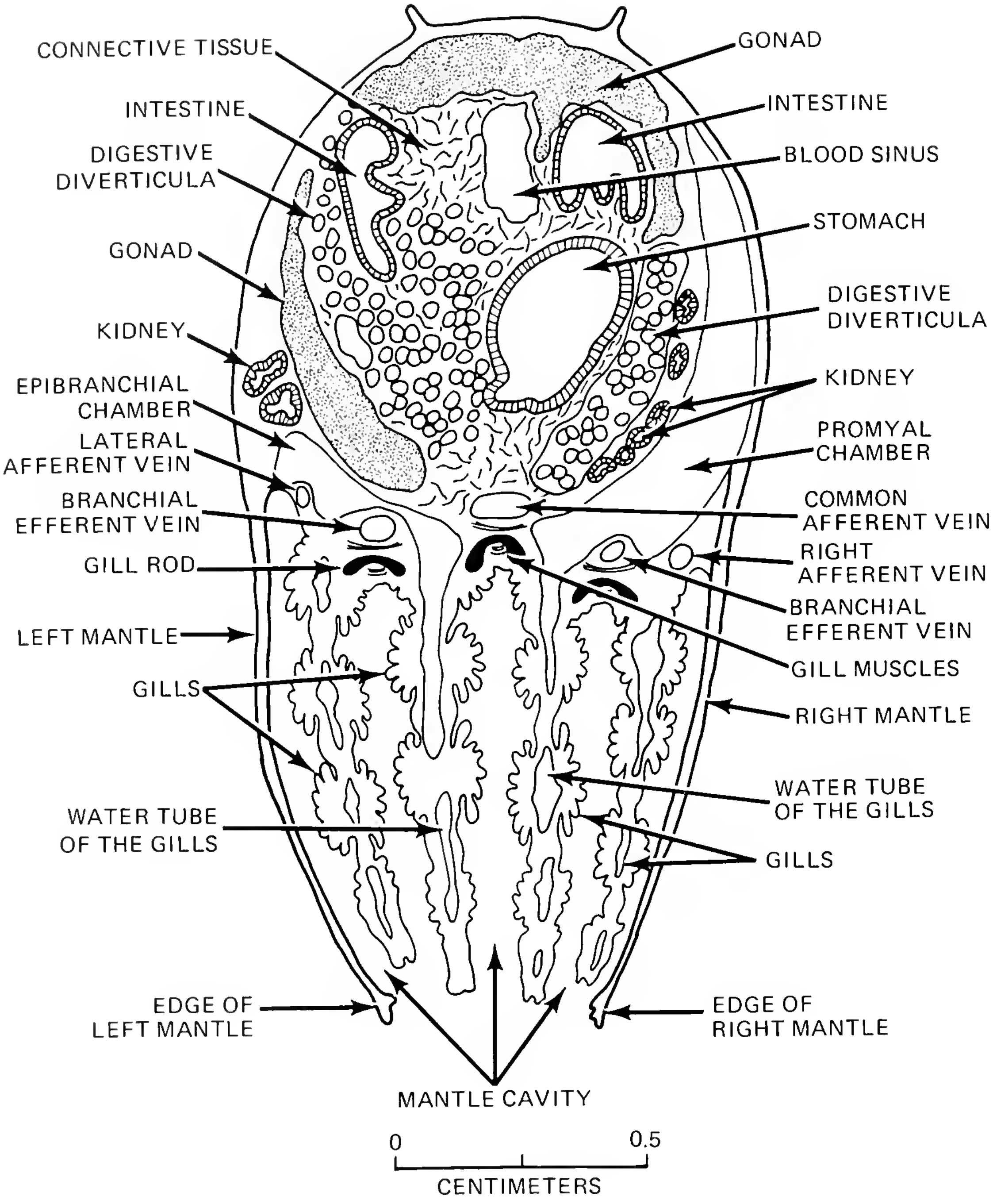

Figure 8. Transverse section of the dorsal part of an adult *Crassostrea virginica* (adapted from Galtsoff 1964).

the gill filaments (against the normal feeding current) and accumulate near the inhalent chamber. Rapid and repeated contractions of the adductor muscle then forcefully eject the eggs a considerable distance. The latter mechanism is also used to expel unwanted particulate material (pseudofeces) from the mantle cavity.

Fertilization occurs in the water column via chance encounters of eggs and sperm, and larval development ensues. Thus begins the free living phase of oyster larvae. These larvae function as zooplankters (meroplankton) in the water column, and probably are significant as a food source for planktivores in local areas.

After passing through blastula and gastrula stages, the young oyster develops into a trochophore larva characterized by a band of locomotory cilia called the prototroch. As development continues, the larval oyster secretes a pair of shells, and the prototroch becomes the larval velum, a ring of locomotory and feeding cilia characterizing the veliger larva. The first shelled larval stage is also termed the straight-hinge (veliger) stage.

The straight-hinge stage is succeeded by the umbo (veliger) stage, in which the larval "beak" on the left valve overhangs the hinge line. During the latter part of this stage, the larval oyster develops a foot and a byssus gland with which it will eventually attach itself to the substratum. With the development of the foot the larvae becomes known as a pediveliger. During the latter part of the pediveliger stage, the larval oyster develops a pair of darkly pigmented eyes. The presence of these eyes indicates that the free-swimming oyster is ready to attach and metamorphose into the adult form. At that time the larva is termed an eyed pediveliger.

Depending on water temperature and food availability, the larval life stage of C. virginica will last approximately 7 to 10 days. However, some larvae will remain planktonic for up to 2 months during cooler periods or in the absence of sufficient food. Early winter sets of oyster larvae in the northern Gulf of Mexico may be attributed to this phenomenon (Edwin W. Cake, Gulf Coast Research Lab., Ocean Springs, Mississippi; pers. comm.).

Feeding activities in larval oysters are generally well understood due to recent advances in commercial oyster culture. In the artificial conditions of an oyster hatchery, mixed cultures of various small "naked" flagellates (algae) produce adequate nutrition for the growing oysters. It is important to emphasize the value of mixed cultures, as opposed to monocultures, for oyster food sources. There are apparently synergistic reactions among various food items that are as yet unknown but that are very important to oyster growth (Epifanio 1979). This is hardly suprising because the diet of oyster larvae in the natural state is obviously far from a pure culture and probably includes bacteria and small detrital particles as well as algae and protozoa. The diet could also include dissolved organic matter.

After a variable planktonic period (about 2 weeks) from initial fertilization, the surviving oyster larvae prepare for settlement and metamorphosis. At this stage the "mature" larvae are significantly larger than the younger straight-hinge, early umbo, and late umbo stages; and they are experimentally separable by a 160-μ mesh sieve that retains the mature stages but not the immature (Hidu and Haskin 1971).

Several environmental factors influence the settlement of larval oysters, including the physico-chemical and biological factors discussed by Hidu and Haskins (1971). They maintained that light, salinity, temperature, and current velocity all affect "prospective" spat (newly settled oysters). Thorson (1964) proposed that the settling response of marine invertebrates is often cued by light. For example, oyster larvae tend to be photopositive throughout their larval life span but may become photonegative in response to a temperature increase. Late settling oyster larvae also tend to be more demersally distributed than earlier larvae, possibly because of their heavier shells.

Along the Atlantic coastal regions south of Virginia, spatfall appears to be denser in intertidal areas. Hidu and

Haskin (1971) related this phenomenon to a water temperature increase during flood tides over intertidal mudflats. The slack water areas of eddy currents also seem to favor heavier than average spatfall patterns (Roughley 1933). Spatfall will be discussed again in Chapter 4 when the distribution of reefs in an estuary is considered.

The biological cues to oyster larval settling are related to the fact that oyster larvae are gregarious and apparently respond to a waterborne pheromone or metabolite released by oysters that have already metamorphosed (Hidu and Haskin 1971). Larvae also seem to respond positively to a protein on the surface of oyster shells. This gregarious tendency is important to a reef-building (colonial) organism such as the oyster, which requires settlement in proximity for successful fertilization (Crisp and Meadows 1962, 1963). See Chapter 3 for additional details of gregarious behavior.

2.3 OYSTER FEEDING, DIGESTION, AND ASSIMILATION

The feeding organs of oysters are (1) the ciliated gills that provide the water currents (with the assistance of the mantle) and sort particles; (2) the palps surrounding the mouth that also play a role in the particle-sorting process; (3) the crystalline style, a semirigid clear rod composed of digestive enzymes that function in the mechanical breakdown of food particles; (4) the gastric shield against which the style rotates to grind food particles; (5) the stomach, in which food and digestive enzymes are mixed; and (6) the digestive diverticula surrounding the stomach, a group of blind-ending tubules with ducts leading to the stomach. The latter function in intracellular digestion.

The feeding of all filter-feeding bivalves (including oysters) had been assumed to be a continuous process in those organisms that are always submerged. The ciliary feeding currents and the production and erosion (dissolution) of the revolving crystalline style have been thought to occur continuously in undisturbed animals. This view was challenged by Morton (1973, 1977), who presented persuasive evidence that even in many subtidal bivalves, the feeding process is cyclic and discontinuous, affected by tidal and seasonal factors.

It is obvious that an intertidal oyster cannot feed when exposed during ebb tides, but an interesting aspect of Morton's hypothesis is that the feeding process is <u>necessarily</u> cyclic in subtidal as well as in intertidal bivalves. The implication of discontinuous ciliary suspension feeding with a tidal rhythym is that tidal and seasonal cycles were incorporated by ancestral bivalves in the evolution of their feeding process.

According to Morton (1977), the feeding of intertidal oysters occurs in three cyclic stages: (1) a feeding stage during which the oyster pumps water with ciliary currents produced by the gills; (2) an extracellular digestive stage, during which the crystalline style acts on ingested food that has been rolled into mucous strings; and (3) an intracellular digestive stage, during which small particles of food are further digested, absorbed, and assimilated within the digestive diverticula of the stomach. The three stages are illustrated in Figure 9. Note that the production of pseudofeces (consolidated particulate matter that is expelled without undergoing the digestive process) occurs during the active feeding cycle when rejected particles accumulate in the inhalent chambers. Fecal production results from the extracellular digestive and intracellular digestive processes, but feces and pseudofeces cannot be released except during inundation. Morton concluded that the three feeding cycles occur during two alternate phases: (1) food is collected, filtered, selected, and passed to the stomach; (2) food collection ceases and the accumulated material is digested.

The specific diet of intertidal oysters, like that of most estuarine consumers, is not clearly understood. The gills of the adult oyster have been reported to retain diatoms, dinoflagellates, and graphite particles from 2μ to 3μ but to pass 70% to 90% of <u>Escherichia coli</u> and 80% of graphite particles from 1μ to 2μ. On the other hand, Loosanoff and Engle

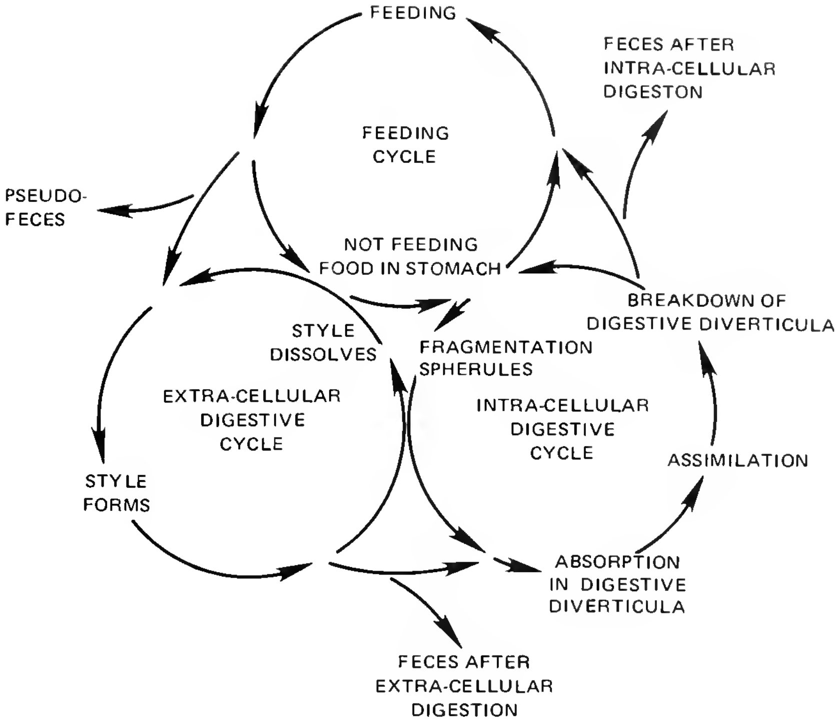

Figure 9. A schematic representation of the rhythmic nature of the feeding process and extracellular and intracellular digestive mechanisms in oysters (adapted from Morton 1973).

(1946) found ambiguous and variable results when examining the relation between particle size and retention on the gill in oysters. These results suggest that the filtering efficiency of oysters is not necessarily related to their pumping rate. The role of mucous in actually trapping food particles in oysters is unclear, as is the importance of dissolved organic material to the overall energy intake.

The assimilation of significant levels of dissolved organic matter (DOM) in oysters was documented by Collier et al. (1953), although the methods were criticized by Galtsoff (1964). Oysters probably "leak" some organic carbon (Johannes et al. 1969). Some workers feel that heterotrophic microorganisms (bacteria) represent the only significant consumers (and packagers) of DOM (Sottile 1973).

Feeding activity in oysters is highest at low concentrations of food; there is a negative correlation between pumping rate and turbidity (Loosanoff 1962). The effect of turbidity on the pumping rate is illustrated in Figure 10 (Loosanoff and Tommers 1948). Some ambiguity between laboratory and field studies exists however; for example, oysters held above the bottom, in the so-called maximum turbidity zone, grew more rapidly than those on the bottom in commercial beds in Buzzards Bay, Massachusetts (Rhoads 1973). Reef oysters may have a similar advantage in the study area. The average suspended load of particulate organic matter (POM) in a typical estuary in Georgia ranges between 4.6 and 15.8 mg/liter afdw (Odum and de la Cruz 1967). Hanson and Snyder (1979) reported extraordinarily high levels of suspended particulate organic carbon (POC) in the study area (0.02 to 0.1 gC/liter), equivalent to approximately 40 to 200 mg POM and much higher than the 1967 estimate of Odum and de la Cruz. High levels of suspended organic matter could reflect strong tidal currents.

Particulate organic matter is a mixture of marsh plant detritus, phytoplankton, benthic algae, bacteria, zooplankton (incuding oyster larvae), and DOM adsorbed onto clay particles. An intertidal oyster diet is a mixture of these items, some of which are not incorporated into oyster tissue while others are more assimilable. The presence of cellulolytic activity in the crystalline style of the oyster has been reported (Newell 1953), but the amount and kind of cellulose that can be used by the animal are unknown. Because the diet of the oyster includes dinoflagellates and other algae with cellulose tests (outer covering), the ability to digest such structural polysaccharides appears to be advantageous.

Results from laboratory experiments on oyster feeding are sometimes ambiguous or at least not directly applicable to oysters in their natural setting. For example, a study by Epifanio (1979) indicated that the gross chemical composition of experimental algal cultures fed to oysters (protein, lipid, carbohydrates, and ash) was less important to subsequent oyster growth than was the specific type of algae used. Oysters have even been shown to grow on cornstarch-supplemented diets (Ingle 1967).

A final note on the specific diet of intertidal oysters: in the only analyses of $\delta^{13}C$ (stable carbon isotope ratio test) of oyster tissue from the Duplin River, Georgia, Haines (1976) and Haines and Montague (1979) found the stable carbon isotopic ratio ranged from $-21^{\circ}/oo$ to $-24^{\circ}/oo$, typical of organic matter produced by phytoplankton. The interpretation indicates that oysters, even in small tidal creeks surrounded by Spartina, feed only on algae. We think this interpretation should be accepted cautiously due to discrepancies found in different tissues of shrimp. (Brian Frye, University of Texas Marine Science Institute, Port Aransas; pers. comm.)

The rate at which intertidal oysters ingest particulate matter is the product of four factors: (1) the average rate (volume/time) at which they can clear the water of POM of a favorable size range; (2) the concentration of suspended food in this size range; (3) the total time that a given oyster (or reef) is inundated; and (4) the percentage of inundation time that oysters filter water. Any significant uptake of DOM would add to this total rate. An energy budget for individual oysters is included in the Appendix and summarized in Section 2.5; energy requirements of a unit area of reef are discussed in Chapter 3.

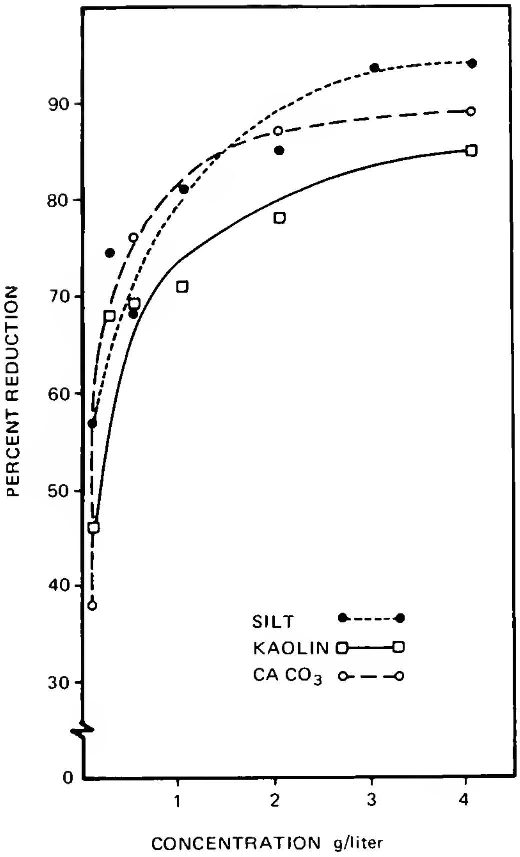

Figure 10. Effects of turbidity on pumping rate (adapted from Loosanoff and Tommers 1948).

2.4 STRESSES ON OYSTER POPULATIONS: NATURAL AND CULTURAL

Natural Stress

Much oyster literature concerns the variety of microscopic organisms that cause oyster mortalities. These pathogens have caused massive oyster die-offs in local areas and sometimes in broad regions, e.g., the infamous outbreak of the bacterium "MSX" (Minchinia nelsoni) in New Jersey, Delaware, and Virginia during the late 1950's and early 1960's. "Disease organisms" is an anthropomorphic and a pejorative phrase typically applied to organisms that appear to be harmful to animals and plants valued by man, and it often stands in the way of an objective functional approach to ecosystems. Oysters are ancient mollusks that undoubtedly have been competitive with, preyed upon, and parasitized by many species. Their survival to the present attests to the fact that they have maintained a complementary functional role within the estuarine ecosystem. As such, they have been subject to various ecosystem feedback regulators, including so-called "disease organisms" that maintain an oscillating stability in oyster population density. In the context of the present discussion, protozoan, fungal, bacterial, and other oyster parasites, commensals, and predators, such as oyster drills and oyster catchers, are considered oyster associates, or ecosystem regulators. These function under natural conditions to control excessive populations and regulate the distribution and density of oyster reefs themselves. It appears, however, that man-induced stresses on oysters may sometimes shift the balance in favor of the oyster regulator by creating subtle changes of temperature, oxygen, salinity, or pollution levels (Galtsoff 1964).

We are unaware of any studies attempting to distinguish between oyster vulnerability to "disease" in subtidal vs. intertidal habitats. Since oyster disease is often density-dependent, extremely dense intertidal reef populations may be more vulnerable than sparse communities. Reefs, however, persist in some areas for long periods (see Chapter 4), and oysters apparently have adapted better to the stress of intertidal existence than have the pathogens.

Oyster-associated organisms, including common oyster commensals, are discussed in Section 3.2. Usually, the occurrence and density of commensals are less in intertidal reef oyster populations than in subtidal oysters. Common commensals include the boring sponge (Cliona celata), the polychaete mud worm (Polydora websteri), and the pea crab (Pinnotheres ostreum). None of these organisms actually kills the oyster, but they do produce a stress. The boring sponge and the mud worm induce additional shell deposition; the pea crab lives within the oyster's mantle cavity and steals food and mucous from the gills, and perhaps even feeds on developing gametes (Galtsoff 1964).

Other natural stresses include low oxygen concentration, high temperature, excessive turbidity (sedimentation), either overabundance or shortage of appropriate food, crowding, and high wave energy or strong water currents. Oysters are remarkably tolerant of all these conditions, however. For example, a subtidal oyster population in the James River, Virginia, was relatively resistant to a severe freshet (flooding) associated with the 1972 tropical storm Agnes (Larsen 1974). They close tightly and respire anaerobically when exposed to the air or during low oxygen conditions (Hochacka and Mustafa 1972). Temperatures up to 40° C or more can be tolerated for short periods (see Section 3.1). Reef growth can accommodate slow, steady sedimentation but not sudden pulses of sediment. Oysters can withstand crowding, and as shown in Chapter 3, population density is important to their intertidal survival. Typically, intertidal reef oysters are not robust and fat, and do not contain high levels of glycogen. The natural stresses of their environment are reflected by the long narrow valves and watery tissue texture characteristic of "coon" oysters.

Man-related stress

Man-induced perturbations on oysters can conveniently be divided into eight classes (Table 1) as follows: (1) physical disturbances, especially sedimentation resulting from dredging and excessive boat traffic; (2) salinity changes due to freshwater diversion or local hydrologic alteration; (3) eutrophication or overenrichment of water from organic matter,

Table 1. General effects of man-induced (cultural) stress on oysters.

Stress	Effects	Sources
1) Sedimentation	Burial and anoxia of adult oysters, reduced availability of cultch for spatfall	Dunnington (1968)
2) Salinity increase over ambient concentrations	Increased predation and/or fouling	Van Sickle et al. (1976)
3) Eutrophication	Oxygen depletion in bottom water; toxic effects of blue green algae and other algae; excess POC, reducing water clearance efficiency	Redfield (1952)
4) Toxins	Sublethal effects, increased mortality, reduced resistance to natural stress, subtle changes in entire community, reduced gametogenesis	Galtsoff (1964) Watling (1978) Heck 1976 Tripp (1974)
5) Physical effects of pollutants	Impairment of feeding mechanism	Lund (1957b)
6) Thermal loading	Decreased community diversity, enhanced oyster production, increased respiratory cost	Lehman (1974) Kennedy and Mihursky (1972)
7) Overharvesting	Depletion of breeding stock and cultch and decrease in bottom stability	Numerous sources
8) Loss of wetlands	Loss of wetland-water interface prime reef habitat, decline of primary production	Numerous sources

sewage, and/or fertilizer; (4) toxins, including pulp mill sulfites, heavy metals, chlorinated hydrocarbons, organophosphates, radionuclides, and petroleum hydrocarbons; (5) physical impairment of feeding structures by oil; (6) thermal loading, primarily from power plants; (7) overharvesting; and (8) wetland loss due to development.

These perturbations can be lethal or sublethal for oysters, but even when sublethal, the oysters may be unfit for consumption either by humans or by other predators. Oysters, like most suspension feeders, efficiently concentrate suspended and dissolved constituents of the water column to levels several orders of magnitude above background concentrations (bioaccumulation). Human pathogens, pesticides, and heavy metals are prime examples. Greig and Wenzloff (1978) reported that oysters with high levels of heavy metals in their tissues did not purge or lose these metals rapidly when transferred to clean water.

Quantifying sublethal effects on oysters is complicated by the fact that oysters live at the water sediment interface, and most pollutant concentrations in sediments are different from those in water. While very low concentrations of some toxins in oysters, like dioxin, may be significant, the capability to detect these pollutants has been achieved only recently, so that much recent literature on pesticide residues in oysters and other organisms may be misleading (e.g., Bugg et al. 1967).

The effect of crude oil extracts on the carbon budget of Mytilus edulis, the edible mussel, is illustrated in Figure 11. As shown, carbon ingested and assimilated declines with increasing oil concentration. Comparable effects could be expected for the oyster.

The estuaries in the study area are presently not as severely impacted by man-induced (cultural) change as are some other oyster-producing areas, such as sections of the Louisiana and Florida coasts, Chesapeake Bay, and Long Island Sound. In addition, intertidal reefs are in some ways more resistant to man-induced perturbations (e.g., salinity intrusion and resultant susceptibility to predation) because of the periodic exposure due to tides. Conversely, intertidal reef existence is already stressful, and added stress may inhibit reef formation.

Effects of marsh alteration in Texas have decreased local oyster production (Moore and Trent 1971). Changes in hydrology and pollution have probably contributed to local declines in oyster reef density in the Savannah, Georgia, area. Historical change in intertidal oyster reefs in the study area, caused by both natural and cultural perturbations, is discussed in Section 4.2.

Harvest of Intertidal Oysters

Because this paper's overall objective is to describe the ecological function and importance of the oyster reef as a component of the coastal ecosystem in the study area, we include here only a brief discussion of several aspects of exploitation of reef oysters by man. More information on the present commercial harvest and potential for future exploitation may be found in Gracy and Keith (1972), Keith and Gracy (1972), and Gracy et al. (1978). These references are for South Carolina, where commercial harvest is concentrated in the study area.

(1) Oyster harvest by man has been an important cultural activity since long before recorded history (at least as early as 2000 B.C., Keith and Gracy 1972). Numerous oyster shell middens and shell rings of apparent ceremonial significance in the study area attest to the importance of the oyster in the diet of early coastal residents. Many oyster shells found in these artifacts are large and thick, which, when considered in light of the presence of many whelk and oyster drill shells, indicate that a significant portion of the prehistorically harvested oysters were of subtidal origin.

(2) Recent oyster harvest in the study area, however, is primarily concentrated on intertidal oyster populations. This harvest, both recreational and commercial, involves the very labor-intensive and time-consuming removal of clumps of oysters from exposed mud flats, an effort

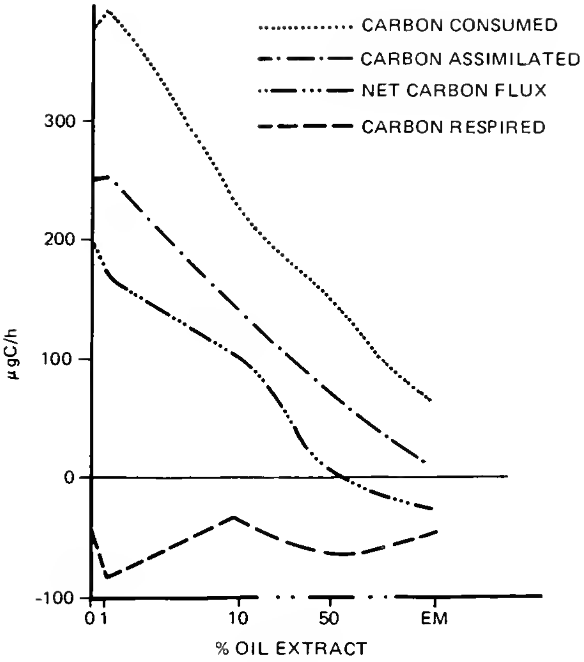

Figure 11. Effects of crude oil extract on Mytilus edulis carbon budgets calculated for 100-mg mussels held at 31°/oo salinity under summer conditions (15° C, 215µg C/liter) (adapted from Gilfillan 1975).

conducted done from small, flat-bottomed skiffs (bateaus).

(3) The majority of the (clumped) oysters collected today are of a quality that makes them less suitable for the raw bar trade than for canned oysters. Thus the oyster industry in the study area traditionally has been an oyster steam-canning industry.

(4) Of the intertidal oysters harvested, the most valuable, in terms of their shape, size, and condition, are found low in the intertidal zone rather than in mature reefs, or oyster rocks, as they are called locally.

(5) Oyster production or total harvest apparently peaked in the early 1900's and has steadily declined for numerous reasons as follows: over-harvesting and generally poor management; pollution, resulting in closing many local areas to oystering; labor problems, i.e., a dwindling number of people willing to work in the labor-intensive oyster industry; and changes in the hydrology of local area.

(6) Total oyster production from the study area (principally South Carolina) accounts for about 8% of total U. S. production (Lee and Sanford 1963). Table 2 from Gracy et al. (1978) summarizes recent oyster production from the study area and includes both subtidal and intertidal oysters. Presently it is unclear if the decline in intertidal oyster harvest indicates a decline in mature oyster reef density. For example, the closure of coastal areas to oystering because of pollution by human pathogens is in some respects beneficial to natural oyster reef populations that are thereby assured of nonexploitation. On the other hand, hydrologic changes accompanying marsh alteration and increased coastal activities are likely to be extremely damaging to the somewhat fragile reefs. In Section 4.2 we discuss the historical change in reef density in the study area.

In summary, the true mature oyster reef subunit of the coastal ecosystem in the study area is not of commercial interest because the reef oysters are of poor market quality. The exception to this is that high reef oysters can be removed and replanted lower in the intertidal zone. The increased efforts at oyster management in the study area could benefit natural reefs in that additional sources of oyster larvae could be created. The commercial exploitation of intertidal oysters ultimately will depend on the study area's economic climate. Increased mechanization that would solve the labor problem (Hixson 1975) is constrained by continual rise in energy costs.

2.5 ENERGY SUMMARY

A summary of estimates of energy flow in oyster reefs in the study area appears in Figure 12. These estimates were based on the most reliable available information (see the Appendix for details and rationale). The numbers shown in Figure 12 are the values for standing oyster biomass and for oyster respiration rate. The respiration estimate is particularly important as an index of oyster function because it represents the energy "tax" paid by reef oysters to support their other activities. The ratio between average biomass (kcal/m^2) and respiration (kcal/m^2/yr) gives the turnover time of the oyster portion of the reef as 0.38 yr (or 2.6 times/yr). This is the average time that any given organic carbon molecule "survives" as a constituent of oyster tissue before becoming oxidized to CO_2 and recycled. Gamete production represents another high energy expenditure, and the typical watery tissue of "coon" oysters in reefs is symptomatic of oysters that are continually spawned out (or subjected to a poor diet).

The extremely high ingestion and egestion (biodeposition) estimates are approximate but indicate the qualitative importance of reef oysters in the study area for transferring suspended organic matter to the reef surface. This process supports the high bacterial metabolism noted in Section 3.3, which in turn accelerates the rate of carbon flux through the ecosystem.

Table 2. Pounds of meat and ex-vessel value (dollars) of oysters harvested in four South Atlantic States from 1973-75 (National Marine Fisheries Service, NOAA, Department of Commerce, from Gracy et al. 1978).

State	1973		1974		1975	
	Pounds	Dollars	Pounds	Dollars	Pounds	Dollars
North Carolina	548,431	446,485	558,821	435,804	424,831	329,794
South Carolina	878,014	505,362	1,119,021	657,308	1,036,401	616,549
Georgia	105,998	65,122	64,664	36,040	44,062	25,613
Florida east coast	122,389	98,505	97,724	85,523	79,417	76,891
Total	1,654,832	1,115,474	1,840,230	1,214,675	1,584,711	1,048,847

Close-up view of oyster shell debris characteristic of the high energy beach shores at the mouth of large intertidal creeks. This shell provides a substrate for oyster spat settlement. Photo by Rhett Talbert, University of South Carolina.

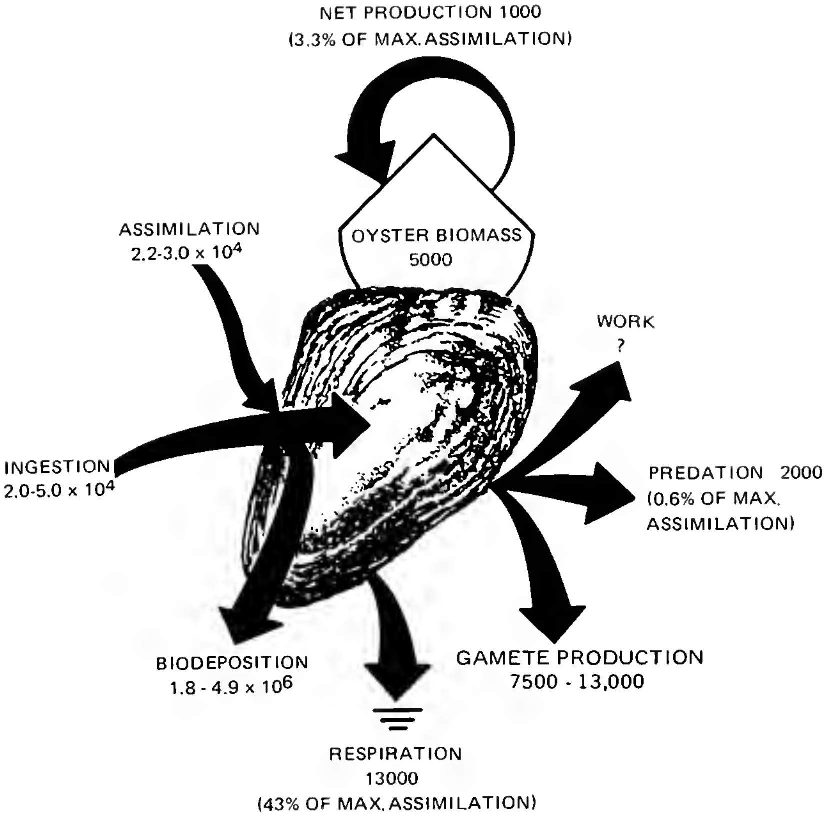

Figure 12. Summary of energy flow through intertidal reef oysters. Values are expressed in kilocalories per meter square per year.

Intertidal reefs in coastal South Carolina. Note the relatively flat top of the reefs in the background, a common feature indicative of the upper survival limit of the oysters in the intertidal zone. Photo by Rhett Talbert, University of South Carolina.

CHAPTER 3

OYSTER REEF DESCRIPTION AND SYNECOLOGY

The objective of this chapter is to detail the intertidal oyster reef community in the study area. The following sections will describe the reef, physically and biologically, to set the stage for Chapter 4 in which we discuss the relationship of the reef subsystem to the entire estuarine ecosystem.

Much of the material in this chapter was taken from Bahr (1974), the only available study that treats the entire reef community (in Georgia) quantitatively. Extrapolations of the results from Bahr (1974) to the entire study area should be made cautiously, and with the understanding that in South Carolina estuaries, oysters in reefs are less dense and net growth is more significant than is the case in Georgia (S. Stevens, University of Georgia, Sapelo Island; pers. comm.).

3.1 GENERAL REEF DESCRIPTION

Intertidal oyster reefs range in size from small scattered clumps to massive solid mounds of living oysters and dead shells. Reefs are limited to the middle portion of the intertidal zone, where minimum inundation time determines the maximum elevation of reef growth. Predation and siltation limit oyster populations in the lower intertidal and subtidal zones to scattered individuals.

The following passage by Dean (1892) describes intertidal oyster reefs or "ledges" in South Carolina at the turn of the century.

> Often at low tide the oyster ledges appear to the eye curiously like a low hedge of frosted herbage, grayish-green in color. A nearer view discloses branching clusters or clumps of oysters, densely packed together, whose crowded individuals now become modified or distorted according to their position on the cluster. The individuals that cap the cluster project upward like flat-tipped fingers, slender, narrow, and long, whose shape has given them throughout the South the names "cat tongues," "raccoon paws," or "raccoons." In many localities, as throughout the region of Skull Creek, the raccoon ledges, continuing for ages to encroach upon the stream bed, have formed vast oyster flats, acres, sometimes miles, in extent.

During exposure to the atmosphere (ebb tide), the surface of a reef dries and turns gray, but upon wetting, a living reef appears greenish-brown due to a thin film of algae. In contrast, piles of dead shells in the intertidal zone (wet or dry) generally are less colorful than are living reefs.

A section through a typical reef is depicted in Figure 13. The uppermost portion is level but slopes steeply at the edges. The living portion of a reef is thicker at the perimeter than in the center, where mud trapped by biodeposition and sedimentation smothers the oysters. This sedimentation results from suspended matter settling out as turbid water slows down while passing over a reef.

Often the surface of a reef is uniformly covered with oysters closely wedged together, so that it is difficult to remove an individual clump. Once a hole is made in a reef, however, adjacent oysters, lacking support, tend to fall toward the cavity and are readily removed. Most mature oysters are long and narrow, and virtually all are oriented with their growing edges facing upwards (Figure 14). These are the typical "coon oysters" described in Galtsoff (1964). They seem to grow toward the least disturbed water, like branches on a tree seeking light, and away from encroaching sediment beneath. A similar growth pattern on a much smaller scale was proposed for colonies of the freshwater bryozoan, Lophopodella carteri,

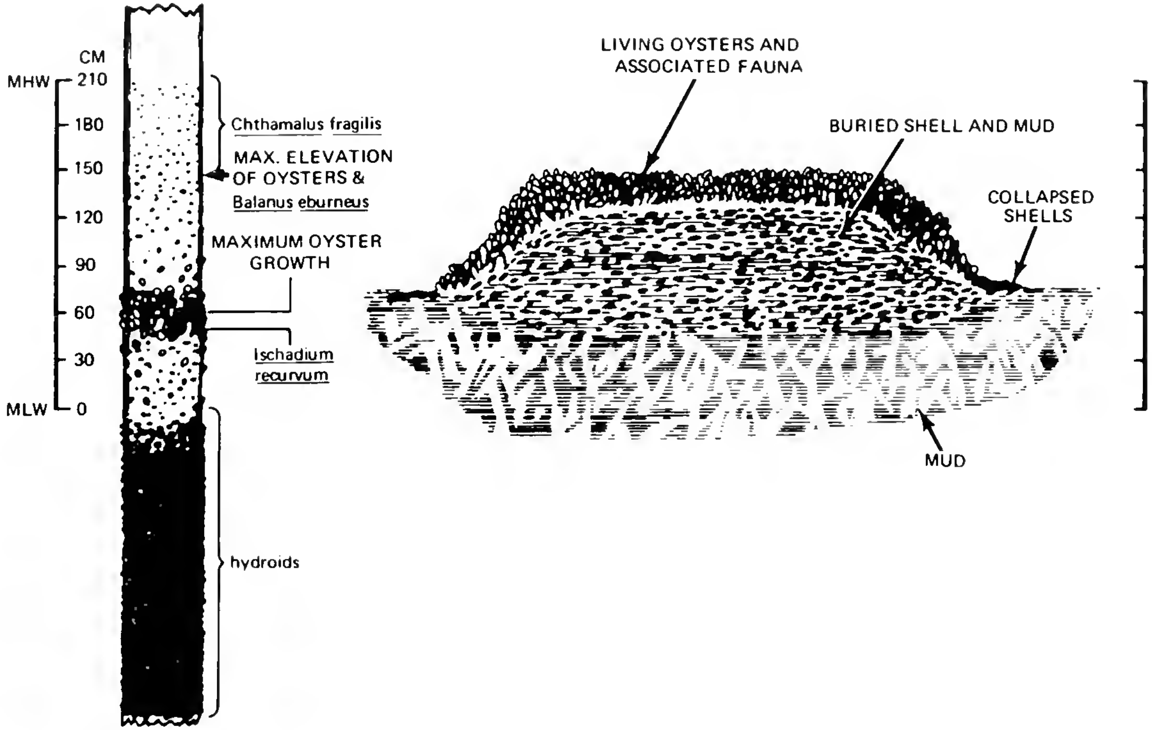

Figure 13. Diagrammatic section through oyster reef illustrating relative elevation with respect to mean tidal levels and corresponding fouling pattern on piling.

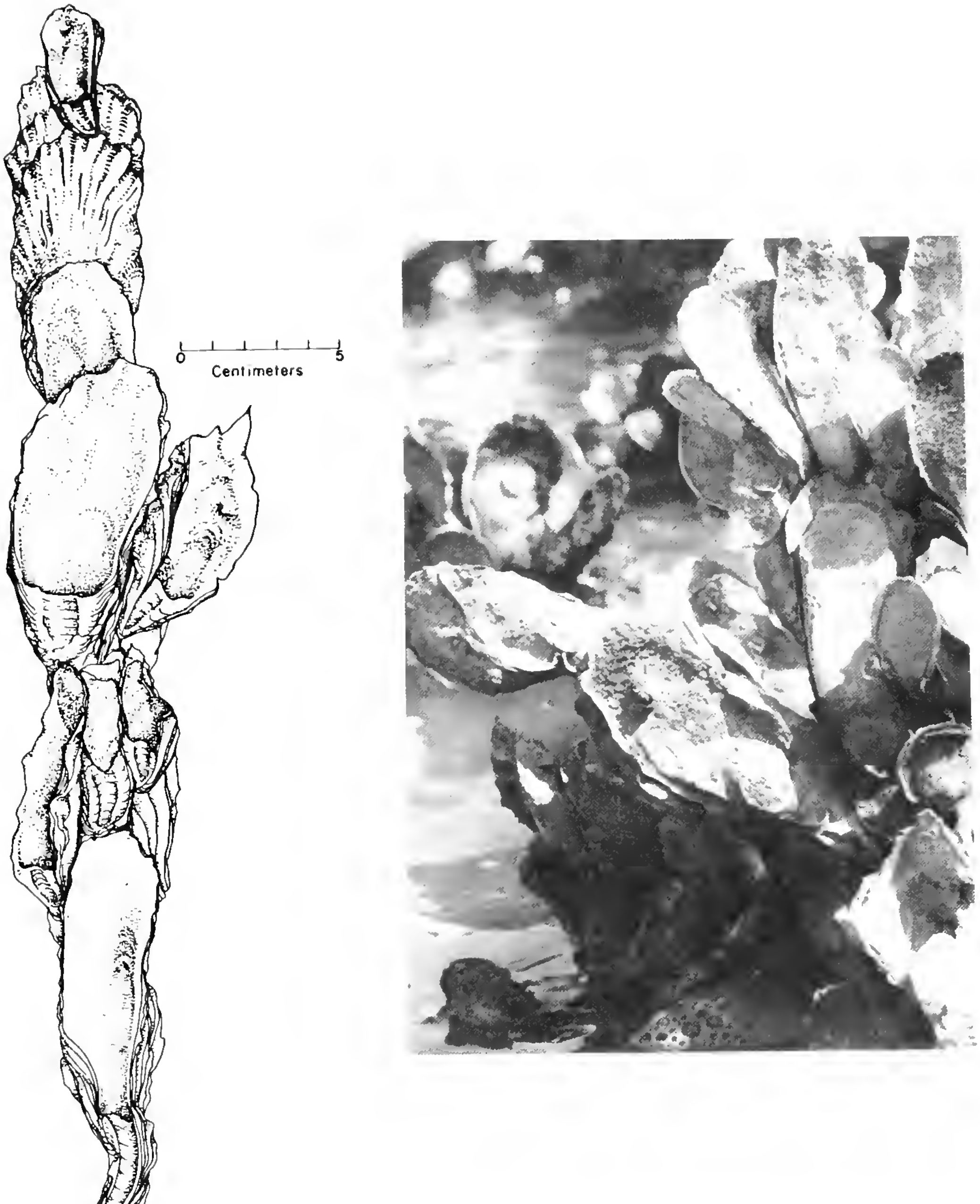

Figure 14. Several generations of oysters (C. virginica) growing vertically on muddy bottom of Altamaha Sound, Georgia (adapted from Galtsoff 1964). This growth pattern results in oyster clusters termed "coon" oysters as depicted in photo. Photo by Wiley M. Kitchens, U.S. Fish and Wildlife Service.

by Bishop and Bahr (1973). Bahr (1974) reported no evidence of orientation of individual oysters with respect to currents in reefs in Doboy Sound (in contrast to the studies by Lawrence 1971); but R. Frey (University of Georgia Marine Institute, Sapelo Island; pers. comm.) detected such orientation among oysters in reefs located in Blackbeard Creek, which is characterized by strong bidirectional currents.

All reefs studied at Sapelo Island, Georgia, were identical in height, 150 cm above mean low water (MLW), except the lower immature reefs, which presumably were still growing. Peak height appears to represent maximum equilibrium elevation, given present sea level and the local tidal amplitude. Generally flooding tides reach the lowest portion of the reefs approximately 2 hours following slack ebb, completely covering the uppermost oysters approximately 2 hours before peak flood. On an ebbing tide, the tops of the reefs become visible about 2 hours following peak flood, with the result that the tops of the reefs are inundated only 4 hours per tide, or 8 hours per day. The relationship between reef elevation and tidal amplitude is unknown for other areas.

Exposure to air during ebb tides allows the visible portion of a reef to dry. Only the upper layer (5-10 cm) of oysters and dead shells actually dries out, however. The underlying shell layer remains moist and appears reddish-brown when the dry shells are removed because a thin layer of detritus covers each shell. This lower layer of shells and living oysters appears to lack the film of algae characterizing the upper layer. A reef can thus be considered as consisting of three "horizons," one pale greenish-gray, one reddish-brown, and one silver-black, color characteristic of shells buried in an anaerobic environment high in ferrous sulfide (Wiedemann 1971). Fine scrape marks appear on many shells from the green and brown horizons, indicating that the organic film is constantly grazed. Mud crabs (Panopeus herbstii and Eurypanopeus depressus) graze these films on partially inundated reefs (Bahr 1974).

Oysters in the upper (green) horizon have sharper growing edges than those in the brown layer, indicating faster growth. Presumably this is a function of extreme crowding and sediment encroachment on the lower oysters. Many dead oysters are found in the black and lower brown horizons, with the valves still together, but full of silt and clay.

Approximately 61% (by volume) of the reef material collected from the upper surface down to the black horizon consists of living oysters, 21% consists of dead shells, and the remaining 18% consists of silt, clay, and nonoyster macrofauna.

Vertical Zonation

Although the three horizons described for the oyster reef are somewhat arbitrarily defined, there is a definite vertical change in reef macrofaunal composition. This is a result of interspecific tolerance to desiccation (drying) rather than a feeding limitation resulting from reduced inundation time. The pattern of zonation in the study area (Figure 13) is typified by the zonation pattern on dock pilings from the lower Duplin River examined after years of exposure to fouling organisms. From these pilings one can extrapolate the optimal elevations for oysters and other epifauna of the reefs.

At Sapelo Island, Georgia, oysters on pilings are virtually limited to an elevation (1.5 m above MLW) corresponding to the maximum elevation of reefs. One could assume that this pattern of vertical zonation would be compressed in areas of lower tidal amplitude. Oyster growth is maximal from about 60 to 70 cm above MLW, the elevation corresponding to the level of the sediment surface on which these reefs were located. Dean (1892), observing growth patterns on pilings, reported that oyster growth in South Carolina was maximal in the mid intertidal zone.

Populations of the barnacle Chthamalus fragilis dominate the upper 60 cm of tidal range. Other barnacles (Balanus) and two mussels (Ischadium and Guekensia) representative of the reef community occupy the lower intertidal and upper subtidal ranges on the pilings, which represent a zone extending beyond the lower limits of the reef. In fact, optimum elevation for these species appears to be below the limits of the reef zone. Wiedemann

(1971) remarked on the paradoxical restriction of the barnacle, C. fragilis, to the uppermost oysters in a reef or to blades of marsh grass above the maximum height of oyster reefs. Of the three species of barnacles in the reef community, C. fragilis is restricted to the upper, or green, horizon. Another related barnacle, C. stellatus, has been described as an obligate intertidal form for reasons of competition rather than physiology (Connell 1961; Barnes and Barnes 1969). The restriction of Chthamalus to the mid to upper intertidal zone was demonstrated by Connell to result, not from intolerance to constant inundation, but rather from competitive exclusion by Balanus spp. In the oyster reef community, where barnacle density is not as great as in Connell's study, oysters seem to assume the role of "squeezing out" all but the uppermost individuals of C. fragilis. Many well-preserved individuals of the latter species are found trapped and overgrown between adjoining oysters. Chthamalus fragilis represents the most obvious example of vertical zonation in the reefs, but other evidence of similar restrictions can be observed; e.g., anemones occur almost exclusively in the brown horizon.

Green and Hobson (1970) stated that a difference in elevation of 6 cm in the intertidal zone results in a significant effect on rates of mortality; however, they were describing an infaunal assemblage dominated by the little gem clam (Gemma gemma). The oyster reef displays a similar sensitivity at the upper limit of its intertidal range. At slightly lower elevations, however, these effects are buffered by the physical complexity and density of the reef, which trap and hold moisture above the level of the surrounding sediment.

Temperature Effects on Oyster Reefs

Oysters adjacent to a hole in a reef made by sampling often die after being dislodged from their normal position in the reef. Undisturbed oysters are normally oriented vertically, (with the ventral side upward) and those which collapse into a sampling site are usually horizontally oriented. The latter position results in exposure of a greater proportion of surface area to direct solar radiation, with little chance for mutual shading. The temperature of sediment within a reef varies widely with depth; e.g., temperatures were 35°C at the surface and 28°C at 6 cm depth during one measurement in October (Bahr 1974).

More critical than sediment temperature is the fact that the internal temperature of an oyster is a function of the orientation of the oyster with respect to direct solar radiation. For example, the internal temperature of a reef oyster in Georgia varied (in the same October observation) from 34°C to over 38°C, according to whether it was oriented vertically or horizontally (Bahr 1974). In full shade the temperature dropped to 31.5°C. This implies that mutual shading of crowded reef oysters is beneficial and important to the maintenance of temperatures within the tolerance limits of the oyster. In the summer when the angle (azimuth) of the sun is highest, significantly higher temperatures result on incident surfaces; therefore, high mortalities could easily result from the disruption of the angular orientation of reef oysters which provides the shading to protect the oysters. Copeland and Hoese (1966) reported mass mortalities of intertidal oysters in Texas during the summer. Hodgkin (1959) concluded that annual high mortalities of littoral fauna and flora near Fremantle, Australia, resulted from high temperature, which was a major factor in the maintenance of characteristic shore zonation. Thus, it appears that oyster reefs grow to elevations above that at which individual oysters could survive the rigors of temperature stress and minimal inundation time.

Lehman (1974) examined the effects of thermal loading from the discharge water of a local power plant on the oyster reef community at Crystal River, Florida. He concluded that an average annual increase of 4° C in the water surrounding experimental reefs (relative to unaffected reefs) caused an increase in oyster biomass, metabolic rate, and turnover rate, but a decrease in the diversity of the reef community.

Salinity Effects on Oyster Reefs

Although oysters are euryhaline and can tolerate low salinities, reefs are limited to areas with significant tidal amplitudes ordinarily associated with relatively high salinity coastal environments. The effect of long-term salinity changes on oyster reefs has not been reported (see Section 4.2). The reef life style allows oysters to invade the predator-rich, high salinity zones of estuaries. Predators are excluded because of the reef's daily exposure to the atmosphere resulting from the ebb and flood of the tides.

Reef Surface Area

The surface area of oysters and dead shells in a series of reef samples was measured by Bahr (1974). He calculated that at least 50 m^2 of surface area is available for habitation by epifauna for every square meter of overall reef area. The production of this large, highly irregular surface area is an important aspect of the functional role of the oyster. In the marsh-estuarine ecosystem that is relatively devoid of hard substrate, the oyster provides this limited resource for other oysters and for the associated macrofauna that will be described in the next section.

3.2 REEF-ASSOCIATED MACROFAUNA

A total of 42 species of macrofauna (or groups of related species) representing seven phyla are associated with the oyster reef community in Georgia (Table 3). This is only a fraction of the 303 species listed by Wells (1961) in his monograph on the fauna of subtidal and intertidal oyster beds, but slightly more than the 37 species found by Dame (1979) in South Carolina reef samples. Rarely present and thus not shown in Table 3 are unidentified species of boring sponges, bryozoans, hydroids, and mites; all of these, except mites, occur abundantly on subtidal oysters but only incidentally in the intertidal reef community. Probably a maximum of 50 macrofaunal species, including those not readily separable, occur in the community samples on which these numbers are based (Bahr 1974). Twenty-one species occurred in the majority of the samples; 17 occurred in 93% or more samples; 8 species occurred in every sample. Mean frequencies for each reef species over the entire sampling period and relative frequency of each species are listed in Table 4. The biomass and relative biomass of each major species or group of species are given in Table 5. No relationship between the size of reefs and the macrofaunal community was observed by Bahr (1974) although a theory exists that indicates a direct (positive) relationship between reef size and species richness (Simberloff 1974; Jackson 1977).

A comparison of the results of Dame's reef survey with the reef macrofauna data reported by Bahr (1974) indicates that Dame found slightly fewer species or groups of related species (Table 3). Dame also found a lower density of macrofauna, by an order of magnitude (about 3,300 individuals/m^2 compared to about 38,000/m^2 reported by Bahr). Some of these differences may result from differences in sampling technique since Dame sieved his oyster reef sediment samples through a 1.0-mm screen, whereas Bahr used a 0.5-mm mesh screen.

Lehman (1974) reported 31 species of invertebrate organisms or groups of related organisms from oyster reefs in Crystal River, Florida. Of these, only nine species were also found by Bahr (1974) to be associated with Georgia reefs. Lehman reported the total abundance of reef-associated organisms to be about 6,200/m^2 and oyster density to be about 3,800/m^2 in his control area. His estimate of biomass of oyster reef associated organisms was 135g/m^2 dry wt.

Specific groups of organisms that reside in oyster reefs in the study area will be discussed below.

Oyster Commensals

The relationship between the oyster pea crab (Pinnotheres) and the oyster represents inquilinism, an association slightly detrimental to the host species (Nicol 1960). Beach (1969) reported that Pinnotheres becomes increasingly rare in oysters in the higher portions of the intertidal zone. Dame (1970) found only about 1% incidence of pea crabs among intertidal oysters in South Carolina; likewise, Bahr (1974) found only a 3% incidence.

Table 3. Macrofauna found in Georgia oyster reefs (adapted from Bahr 1974).

Taxa
Mollusca
Pelecypoda
Crassostrea virginica (Gmelin)[a,b,c]
Guekensia demissa (Dillwyn)[a,b]
Ischadium recurvum (Rafinesque)[a,b,c]
Mya arenaria (Linnaeus)
Gemma gemma (Totten)[a]
Petricola pholadiformis (Lamarck)[a]
Gastropoda
Odostomia impressa (Say)[a,b]
Arthropoda
Insecta
Anurida maritima (Guerin)[a,b,c]
Cirripedia
Balanus improvisus (Darwin)[a,c]
Balanus eburneus (Gould)[a,b,c]
Chthamalus fragilis (Darwin)[a]
Decapoda
Eurypanopeus depressus (Smith)[a,b,c]
Panopeus herbstii (Milne-Edwards)[a,b,c]
Pinnotheres ostreum (Say)[a,b]
Sesarma cinereum (Say)[a]
Clibanarius vittatus (Bosc)[a]
Amphipoda
Melita nitida (Smith)[a,b]
Parhyale hawaiiensis
Gammarus palustris[a,b]
Isopoda
Cassidinidea lunifrons (Richardson)[a]
Edotea motosa (Stimpson)
Annelida
Polychaeta
Neanthes succinea (Frey and Leuckart)[a,b,c]
Nereiphyllis fragilis (Webster)[a,b]
Streblospio benedicti (Webster)[a,b]
Heteromastus filiformis (Claparede)[a,b]
Polydora websteri[a,b,c]
Tharyx setigera(Hartman)[a]
Spirorbis sp.
Sabellaria megaris[a]
Amphitrite ornata (Leidy)[a,b]
Marphysa sanguinea (Montagu)[a,b]
Lysidice ninetta
Syllidae (unidentified)
Dodecaceria sp.

Continued

Table 3. (Concluded)

Taxa
Annelida (continued)
Polychaeta (continued)
Lepidonotus sublevis(Verrill)
Polychaete (unidentified)
Polychaete (unidentified)
Polychaete (unidentified)
Nemertea
Nemertina (unidentified)[b]
Coelenterata
Anthozoa (unidentified)
Platyhelminthes
Turbellaria
Polyclad (unidentified)
Sipunculida
Sipunculid (unidentified)

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[a] Genus reported by Wells (1961).
[b] Species reported by Dame (1979).
[c] Species reported by Lehman (1974).

Table 4. Mean annual frequency distribution of reef macrofauna.

Species	Mean freq. (#/m^2)	Variance S	Standard deviation $s_{\bar{x}}$	% of total
Crassostrea virginica[a]	14666.9	4811.3	717.2	38.65
Guekensia demissa	514.8	459.5	68.5	1.36
Ischadium recurvum	5028.0	4051.0	603.7	13.25
Mya arenaria[a]	852.8	1577.7	235.2	2.25
Gemma gemma	1.3	-	-	-
Petricola pholadiformis	0.4	-	-	-
Odostomia impressa[a]	1643.5	1792.5	264.3	4.33
Anurida maritima[a]	5453.7	3626.4	1300.5	14.37
Balanus improvisus[a]	1063.9	1063.1	158.5	2.80
Balanus eburneus[a]	16.9	58.8	8.7	0.04
Chthamalus fragilis[a]	166.3	387.4	57.7	0.44
Eurypanopeus depressus[a]	1037.1	430.5	64.2	2.73
Panopeus herbstii[a]	103.1	75.0	11.2	0.27
Pinnotheres ostreum	24.5	33.5	5.0	0.06
Sesarma cinereum	0.1	-	-	-
Clibanarius vittatus	0.4	-	-	-
Melita nitida[a]	334.2	455.2	67.9	0.88
Parhyale hawaiiensis[a]	966.2	1278.4	190.6	2.55
Gammarus palustris[a]	5.2	-	-	-
Cassidinidea lunifrons[a]	323.5	171.6	25.6	0.85
Edotea montosa	1.3	-	-	-
Neanthes succinea[a]	1739.1	1778.3	268.1	4.58
Nereiphyllis fragilis[a]	78.0	60.9	9.0	0.21
Streblospio benedicti[a]	1362.4	1723.4	259.8	3.59
Heteromastus filiformis[a]	519.8	314.7	46.9	1.37
Polydora websteri[a]	359.3	436.4	65.1	0.95
Tharyx setigera	0.3	-	-	-
Spirorbis sp.	1.1	-	-	-
Sabellaria megaris	1.7	-	-	-
Amphitrite ornata	4.3	-	-	-
Marphysa sanguinea	5.2	-	-	-
Lysidice ninetta	1.3	-	-	-
Syllidae (unidentified)	0.4	-	-	-
Dodecaceria sp.	0.9	-	-	-
Lepidonotus sublevis	0.4	-	-	-
Polychaete (unidentified)	0.9	-	-	-
Polychaete (unidentified)	8.7	-	-	-
Polychaete (unidentified)	4.8	-	-	-
Nemertina (unidentified)[a]	204.0	194.8	29.0	0.54
Anthozoa (unidentified)[a]	1442.5	1376.6	205.5	3.80
Polyclad (unidentified)	7.8	-	-	-
Sipunculid (unidentified)	0.4	-	-	-
Total:	37,947.4			

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[a] Twenty-two species found in 93% of all samples and considered dominant. Brackets enclose groups of "similar" species that reduce major macrofauna members of the reef community to 16.

Table 5. Ranked biomass of 16 major oyster reef species or groups of species and proportion of total macrofaunal biomass.

Species or group of species	Mean biomass $(g/m^2 \pm 2\ s_{\bar{x}})$	% of total
Crassostrea virginica	969.6 ± 93.4	87.534
Guekensia demissa	83.7 ± 26.9	7.554
Ischadium recurvum	24.4 ± 13.0	2.200
Eurypanopeus depressus	13.5 ± 2.3	1.220
Panopeus herbstii	7.3 ± 4.4	0.656
Neanthes succinea	3.4 ± 1.6	0.304
Anthozoa (unidentified)	1.5 ± 0.5	0.131
3 Cirripedia species	1.4 ± 0.6	0.130
3 Amphipoda species	1.2 ± 0.5	0.106
Nereiphyllis fragilis	0.8 ± 0.5	0.069
Mya arenaria	0.3 ± 0.5	0.024
Odostomia impressa	0.3 ± 0.1	0.024
Nemertea (unidentified)	0.1 ± 0.0	0.013
Anurida maritima	0.1 ± 0.1	0.013
3 Polychaeta species	0.1 ± 0.1	0.013
Cassidinidea lunifrons	0.0 ± 0.0	0.001
Total	1,107.7	

Other inhabitants of shells of subtidal oysters were virtually nonexistent within reef oysters examined in the Georgia study, e.g., worms (Polydora spp.) were found free in the samples but not inside oysters. Boring sponges (Cliona spp.) were absent on intertidal oysters but abundant on subtidal oysters and dead shells. Infestation (with Cliona) results in shell deterioration in subtidal oysters due to shell erosion by Cliona. Infested (with Cliona) oysters are particularly vulnerable to predation, and the shells are fragmented into pieces which tend to be washed away rather than remaining in situ as substrate for further colonization. This is one of the principal reasons that subtidal reefs are absent in the study area. Guida (1976) discussed the abundance of Cliona spp. in subtidal oysters and oyster shells. No oyster drills or starfish were ever seen on the reefs examined. Parasitic gastropod, Odostomia impressa, was abundant, (up to $5,460/m^2$).

Insects

An interesting organism occurring in abundance on oyster reefs in the study area is a collembolan insect, Anurida maritima, a true marine insect (Miner 1951). The trophic role of a similar intertidal collembolan (Oudemansia esakii) in Hong Kong has been described as saprophagic on recently dead macrofauna, including oysters (Chan and Trott 1972). Anurida appears to be a true oyster associate since it is only observed on mud flats near oysters. The greatest concentrations are inside dead pairs of oyster shells, which often house masses of live insects along with large numbers of exuviae (shed exoskeletons). Small and covered with a nonwettable cuticle, Anurida is extremely buoyant and would be washed away during flood tides were it not for crevices in oyster shells which allow masses of them to cling together. As in the case of Oudemansia, Anurida probably emerges to the reef surface during ebb tide and retreats before flood tide. Dame (1979) reported a few Anurida ($\sim 6/m^2$) present in South Carolina reefs and Lehman (1974) reported Anurida from Florida reefs.

Barnacles

A marked vertical zonation of Chthamalus fragilis, one of three barnacle species identified from the reef community, has been noted in previous sections (see Section 3.1). Dame (1979) did not report C. fragilis on South Carolina reefs, which may indicate that these reefs were lower in the intertidal zone. Since total barnacle density on oyster reefs does not approach the density observed on pilings (Bahr 1974), it appears that unknown factors limit barnacle survival on intertidal reefs. It has been reported that Balanus eburneus reaches maximum density at a elevation of 9 to 14 m below sea level (Relini and Giordano 1969).

Mud Crabs

Two of the most characteristic members of the reef community are the common mud crabs Eurypanopeus depressus and Panopeus herbstii, observed by Bahr (1974) at mean densities of $1,037/m^2$ and $103/m^2$, respectively. They seem to remain quiescent in the brown horizon during exposure of the reefs but begin active feeding with tidal inundation. Feeding consists of using one or both chelae to scrape the film of algae and detritus from shells in the brown and green horizons. The "grazed" appearance of shells and the fact that neither algae nor detritus accumulates on shells indicate the proficiency of grazing. These two crabs are undoubtedly omnivorous, and Bahr (1974) noted Panopeus predation on small oysters on reefs and Eurypanopeus predation on amphipods in the laboratory. Dame (1979) reported much lower densities of mud crabs on South Carolina reefs; he found the two species in approximately equal densities.

Soft Shelled Clams

Common occurrence of small soft shell clams in the reef samples was noted by Bahr (1974) at densities ranging up to $6,460/m^2$. No adult clams have been observed in reef samples. It appears that clam spat (juveniles) settle on the reefs and survive only temporarily. Mya arenaria has not been reported to range successfully as far south as Georgia, although adult specimens have been found at Sapelo Island. Dame (1979) did not report finding Mya arenaria in South Carolina reefs.

Mussels

Kuenzler's (1961) study of the ribbed mussel Guekensia demissus (formerly called Modiolus) demonstrates that this animal's functional importance in the marsh system resides more in terms of nutrient (phosphorus) cycling than in energy flow. He estimated the mean density of Guekensia in the entire marsh at 7.82 animals/m^2, whereas in oyster reefs in Georgia, this mussel averaged over 500/m^2. Ischadium recurvum was found to be 10 times more numerous in reefs than was Guekensia (see Table 4), and together these two species contributed 9.5% of total macrofaunal biomass (112.08 g/m^2). Dame (1979) reported about 7 Guekensia/m^2 in South Carolina reefs and about 700 Ischadium/m^2, or two orders of magnitude greater than Guekensia.

Anemones

Anemones are sessile epibenthic suspension feeders that have soft bodies and are extremely vulnerable to dessication. Thus, they are not normally considered intertidal organisms. Their common occurrence in reef samples in Georgia (Bahr 1974) attests to the capacity of oyster reefs to retain water above MLW and to extend the vertical distribution of such creatures. Dame (1979) did not report any anthozoans in South Carolina reefs, but this group could have been overlooked in preserved samples.

Polychaetes

Polychaetes are generally one of the dominant groups in benthic systems because of their contribution to total biomass or to numbers, or both; but they are usually considered infauna, with some obvious exceptions such as the serpulids, which produce encrusting calcareous tubes. Smith (1971) found that polychaetes constitute the major portion of macrofauna in a sublittoral community near Sapelo Island. In the oyster reef community, polychaetes accounted for only 0.4% of the total biomass, most of which was contributed by one species, Neanthes succinea, which averaged 1,739 animals/m^2, compared to 281/m^2 in Long Island Sound (Sanders 1958).

The three most abundant small polychaetes, Polydora websteri, Heteromastus filiformis, and Streblospio benedicti, together comprised only about 0.01% of total macrofaunal biomass. There is a relative dearth of polychaetes in this reef system compared with other communities. This is perhaps related to the predominantly epibenthic nature of the reef community and to the absence of a substantial layer of aerobic sediment. Dame (1979) found significant numbers of Heteromastus in South Carolina reef samples, but he did not find many of the other two small polychaetes, probably because of the large mesh size used to screen his benthic samples.

Amphipoda

Amphipods are more numerous and diverse in sublittoral oyster beds than on intertidal reefs since, in the latter situation, tidal pools are not available to sustain them during ebb tides. Grackles were observed feeding on oyster reefs, probably preying on amphipods and mud crabs (Bahr 1974). Dame (1979) found relativity few amphipods in South Carolina oyster reef samples, and only one species, Melita nitida, was reported.

Accidentals

Hydroids, bryozoans, flatworms, and sponges, all commonly associated with subtidal oysters (Guida 1976), were so rarely encountered in Georgia oyster reefs as to be considered "accidentals" in the reef community.

3.3 REEF COMMUNITY ENERGETICS

The energy requirements, expenditures and an overall energy budget for reef oysters are discussed in the Appendix. The additional energy requirements of nonoyster members of the reef community are addressed in the following section. The data used are primarily those reported by Bahr (1974).

The best available estimate of total energy requirements of the reef community is the rate at which a unit area of reef consumes oxygen (community respiration rate). A sine curve fitted to oxygen consumption of the total reef community in Georgia for a 1-year period is depicted in Figure 15. The variation in community oxygen uptake ranged from approximately 6 to 50 gO_2/m^2/day over a temperature range of 9° to 30° C.

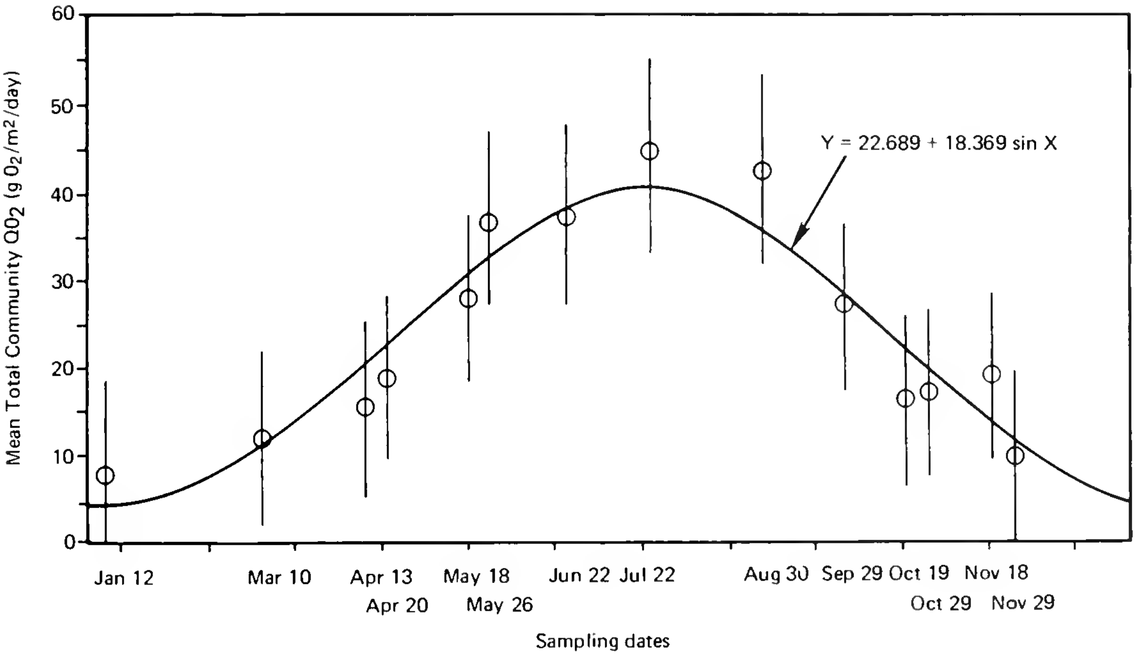


Figure 15. Seasonal oxygen consumption (QO_2) of reef community. Data points are average values for four samples with 95% confidence intervals (Bahr 1976).

The area beneath the curve in Figure 15 was integrated over a 1-year period to yield a total of 8,168 $gO_2/m^2/yr$ consumed by the oyster reef community, equivalent to 27,036 $kcal/m^2/yr$, assuming a respiratory quotient of 0.85. This estimate of the community metabolic energy demand by the reef community is conservative in that it is derived by multiplying hourly rates by 12 hours, with the assumption that little respiratory activity occurs during reef exposure at ebb tide. However, Lehman (1974) reported a significant metabolic rate of exposed oyster reefs by using an infrared gas analyzer to detect CO_2 released from enclosed reef samples. This measured rate was about 20% of the rate measured by oxygen changes during inundation. Total community metabolism in the Georgia reefs is partitioned among oysters, other macrofauna, small organisms, and chemical oxygen demand.

Macrofaunal Respiration

The contribution of each species of macrofauna to total community oxygen consumption at a given temperature is a function of its proportion to the total biomass, its size-frequency distribution, and the relationship between rate of respiration and size of an individual. Small rare species contribute little to total biomass and cannot contribute significantly to total oxygen uptake (QO_2); large rare species, on the other hand, can often alter total oxygen uptake (Smith 1971). Banse et al. (1969) and Pamatmat (1968) concluded that the most reliable method of estimating relative importance of various macrofaunal species in terms of total community respiration is to multiply mean ash free dry weight (afdw) per species by the density of that species in the community. By this criterion, the oyster reef community members were ranked in terms of macrofaunal metabolic importance, as shown in Table 6. The two species that comprised 95% of total biomass, *Crassostrea virginica* and *Guekensia demissa*, contributed 87.5% and 7.5% of total community biomass, respectively.

The respiration of oysters accounts for approximately 50% (48.1%), or about 13,000 $kcal/m^2/yr$ of the total reef community respiration. Total oxygen requirements (hence energy requirements) of nonoyster macrofauna was thus estimated to account for only 10% of the total reef requirements, about 800 $gO_2/m^2/yr$ or about 2,700 $kcal/m^2/yr$. This latter figure is similar to the total oxygen uptake rate of the subtidal soft bottom community near Sapelo Island (Smith 1971).

Nonoyster macrofauna were divided into 14 species or groups of related species, and estimates of the annual oxygen consumption rates were derived experimentally (Bahr 1974), as shown in Table 6.

Microbial and Meiofaunal Respiration

The metabolism of small consumer organisms represents 22% of the total reef community metabolism (Bahr 1974). This estimate is approximate since it is based on the difference between total community oxygen consumption and the sum of estimated macrofaunal and chemical oxidation rates.

The large surface area of an oyster reef (at least 50 times the area of a plane surface) provides a large surface for aerobic bacteria as well as for epifauna (see Section 3.1), and thus this estimated large energy requirement, 1,600 $gO_2/m^2/yr$ (5,400 $kcal/m^2/yr$), is not too improbable.

Chemical Oxidation

Bahr (1974) estimated that the proportion of total reef community oxygen uptake accounted for by the chemical oxidation of reduced compounds (20%) was only slightly lower than microbial metabolism. This estimate reflects the continual release of reduced compounds from the anaerobic decomposition of reef-derived organic matter.

Summary

The seasonal energy partitioning estimates for the entire reef community are depicted in Figure 16. To summarize, the reef community converts about 3×10^4 $kcal/m^2/yr$ to heat, which represents the net "cost" to the ecosystem of supporting the reef community. Systems theory would indicate that this cost is repaid by the reef community in the form of feedback services. For example, the reefs continually release plant nutrients, ammonia and phosphorus-containing compounds; they

Table 6. Ranking of macrofaunal metabolic dominance based on biomass (adapted from Bahr 1974).

Species or groups	Mean biomass (g/m^2± $2s_{\bar{x}}$)	% of total	Rank	Mean % of total macrofaunal respiration rate	Rank	Wt specific respiration rate (respiration rate x biomass)
Crassostrea virginica	969.6 ± 93.4	87.5	1	81.0	1	0.57
Guekensia demissa	83.7 ± 26.9	7.5	2	7.0	2	0.54
Ischadium recurvum	24.4 ± 13.0	2.2	3	2.3	4	0.61
Eurypanopeus depressus	13.5 ± 2.3	1.2	4	5.3	3	2.55
Panopeus herbstii	7.3 ± 4.4	0.6	5	1.5	5	1.33
Neanthes succinea	3.4 ± 1.6	0.3	6	1.1	6	2.13
Anthozoa (unidentified)	1.5 ± 0.5	0.1	7	0.1	11	0.72
3 Cirripedia species	1.4 ± 0.6	0.1	8	0.3	9	1.39
3 Amphipoda species	1.2 ± 0.5	0.1	9	0.5	7	3.05
Nereiphyllis fragilis	0.8 ± 0.5	0.1	10	0.4	8	3.19
Mya arenaria	0.3 ± 0.5	0.0	11	0.1	13	2.37
Odostomia impressa	0.3 ± 0.1	0.0	12	0.1	14	2.25
Nemertea (unidentified)	0.1 ± 0.1	0.0	13	0.1	15	3.00
Anurida maritima	0.1 ± 0.1	0.0	14	0.1	12	5.61
3 Polychaeta species	0.1 ± 0.1	0.0	15	0.2	10	8.84

Total	1,107.7	
Less oysters	138.0	
Suspension feeders	109.8	(80.2% of nonoyster macrofauna)
Deposit feeders	26.5	(19.3% of nonoyster macrofauna)
Others	0.7	(0.5% of nonoyster macrofauna)

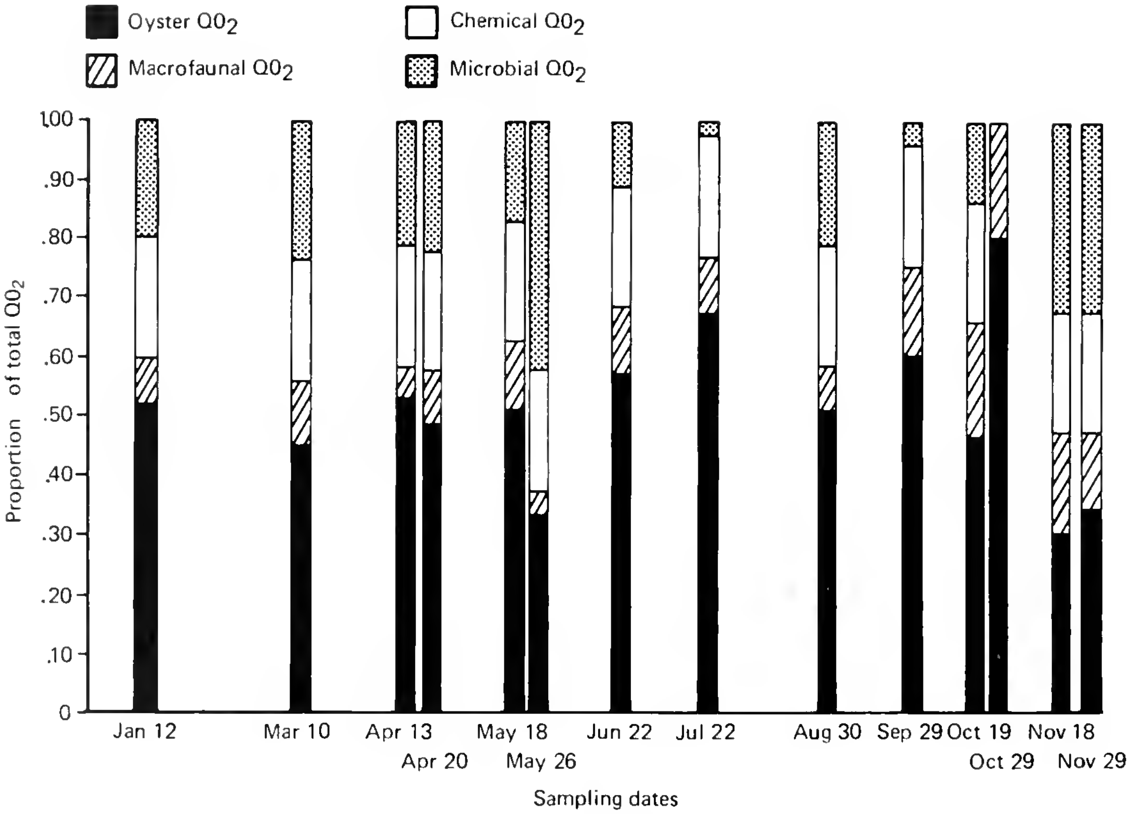


Figure 16. Seasonal energy partitioning estimates for the entire reef community (Bahr 1974). QO_2 = oxygen consumption rate.

significantly increase habitat diversity and provide substrate for epifauna, decomposers, and small nursery species (at least during flood tides). The 3×10^4 kcal/m^2/yr would require the total net production of about 5 m^2 of marsh estuary for each square meter of reef if total production were usable by the community. If only phytoplankton production were usable, the reef community would require at least 50 m^2 of marsh estuary for nutritional support (see Section 1.3).

A final point should be made about oyster reef energy requirements: the metabolic rate of this community ranks high among the values measured for the macrofaunal metabolism of benthic communities, exceeding even such systems as kelp beds. Table 7 summarizes the results of some representative benthic community metabolic measurements. Of particular interest is the 1974 study by Lehman, in which total reef community metabolism from gulf coast oyster reefs (Crystal River, Florida) was measured at 16 to 21 g O_2m^2/day at 31.7°C. Lehman's values for biomass were lower than those measured from Georgia reefs (119.5 g/m^2 dry wt vs. 970 g afdw/m^2), and his experimental temperature was about the same as the maximum experimental temperature used by Bahr (1974).

The increasing number of metabolic studies in which partitioning has been attempted have well established that macrofauna usually play a relatively minor role in total benthic community energy flow. Smith (1971), for example, determined that the proportion of total respiration rate attributable to macrofauna of a sublittoral community was equal to only 12.1%. Therefore, the oyster reef community is unique among benthic subsystems in that the oysters and other macrofauna conspicuously dominate community metabolism as well as community structure. Intertidal oyster reefs may be thought of as heterotrophic "hot spots" in the marsh-estuarine system.

3.4 REEF PREDATION

No quantitative information is available on the rate at which salt marsh consumers prey on the inhabitants of the intertidal reef community. From a qualitative standpoint, the predators include three groups: (1) small reef residents such as mud crabs; (2) strictly aquatic forms that migrate onto the reefs to feed during flood tides, e.g., the blue crab (Callinectes sapidus) and the sheepshead minnow (Cyprinodon variegatus); and (3) terrestrial animals that prey on exposed reefs during ebb tides, e.g., raccoons and wading birds. This "time sharing" arrangement by both aquatic and terrestrial predators, representing a "coupling" between the reef and adjacent ecosystems, would appear to wreak havoc on the reefs; but relatively little evidence of predation was ever detected in the reefs examined by Bahr (1974). Blue crabs were observed feeding on small oysters on partially exposed reefs; raccoon tracks were seen around reefs; and the most commonly observed reef predators were boat-tailed grackles (Cassidix mexicanus), seen picking unidentified organisms (probably small crustaceans, insects, and polychaetes) from recently exposed reefs.

Drinnan (1957) estimated that the European oystercatcher (Haematopus ostralegus) preyed on between 28.5 and 51 cockles per hour during active feeding, each cockle being between 23 and 30 mm in length. He concluded that about 22% of the total cockle population in his study area in Nova Scotia were removed as a result of this predation.

Butler and Kirbyson (1979) reported that the black oystercatcher (H. bachmani) can eat up to nine large oysters per hour, the oysters ranging from 80 to 160 mm. These birds feed primarily on single oysters, however, as opposed to American oystercatchers (H. palliatus) that feed on clumped or reef oysters (Tomkins 1947). The latter author observed predation on Crassostrea by oystercatchers on reefs near Savannah, Georgia, but no attempt at quantification was made. It was assumed from Tomkins' description of the feeding behavior of H. palliatus that only about 4 hr/day are available for feeding on intertidal oysters (2/hr/tide). Observations on the density of oystercatchers at Sapelo Island indicated fewer than one bird per reef, perhaps one per eight reefs, resulting in an estimated maximum of 25 oysters eaten by oystercatchers per reef per day (4 hr/ day x 1/8 bird/reef x 50 oysters/ hr/bird). If an average reef were approximately 25 m^2, a total loss of about

Table 7. Community respiration in aquatic systems.

System	Temperature range (° C)	Respiration (oxygen consumption) (g/m^2/day)	Author and method
1. Marine sediment	0-18	0.22-0.52	Kanwisher 1962, enclosed mud cores
2. Intertidal sand flat	6-25	0.07-2.4	Pamatmat 1968, bell jars
3. Kelp bed	17.5-18.5	33-37	McFarland and Prescott 1959, diurnal O_2 curve
4. Coral reefs	25-30	11-36	Odum et al. 1959, diurnal O_2 curve
5. Rocky intertidal (oysters, mussels, calcareous algae)	n.d.	10-50	Mishima 1966, bell jars
6. Intertidal mussel bed	n.d.	4.8-66.0	Nixon et al. 1971, upstream-downstream QO_2
7. Intertidal oyster reef	9-31	6-50	Bahr 1974, enclosed reef samples
8. Intertidal oyster reef	31.7	16-21	Lehman 1974, upstream-downstream QO_2
9. Sublittoral soft bottom	6.8-28.5	1.95-3.44	Smith 1971, enclosed cores
10. Salt marsh		28	Teal 1962, bell jars
11. Mud community in salt marsh	15-30	2.88	Teal and Kanwisher 1961, enclosed cores
12. Sediment community in salt marsh	n.d.	0.71	Pomeroy 1959, bell jars

0.1 g/m^2/day, or 40 g/m^2/yr (200 kcal/m^2/yr) could be estimated as sustained by intertidal oyster reefs from predation by birds. This estimate is obviously clearly approximate.

3.5 COLONIAL ASPECTS OF THE REEF COMMUNITY

The gregarious tendency of oyster larvae has obvious adaptive value in terms of the reproductive success of subtidal oyster populations. It is also of great adaptive value for intertidal reef oysters. Survival in the upper intertidal zone in the study area may depend on a crowded colonial life style.

The only single oysters (greater than 30 mm in height) or small clusters of oysters normally observed in the intertidal zone were either at the lower level of the zone (not much higher than 60 cm above MLW), or they were scattered among stalks of cordgrass (Spartina alterniflora), where they were shaded. The only way oyster reefs attain their maximum steady-state elevation, or mature stage, is via the slow process of reef accretion based on mutual support and self-shading.

On the other hand, oysters in the study area in the low intertidal zone or subtidal zone are characteristically heavily fouled and colonized with boring sponges, i.e., Cliona spp. These oysters are usually thick-shelled, with the stunted shape characteristic of slow growing oysters, particularly in high-salinity areas. It is obvious that relatively few oysters survive in the subtidal zone in these marsh-estuaries and that dead shells are rapidly eroded away by Cliona spp.

Oyster spatfall may be so dense in some low latitude areas that it constitutes a "fouling" situation. This condition (dense spatfall) has not been observed on an intertidal reef, however. Neither the density of barnacles nor oyster spat appears to be limited by space on a reef. This is perhaps not attributable to a lack of prospective spat but rather to the predatory effects of adult members of the reef community, especially filter feeders like mussels, barnacles, and oysters themselves. The vortices set up by the feeding currents of reef community filter feeders could make the reef surface a somewhat dangerous place to settle. This type of density-dependent feedback could explain the relatively even distribution of oysters in the mature reefs and the symmetrical form of the reefs.

American oyster catchers "loafing" on an oyster reef in South Carolina. These birds, rare over most of their range, are concentrated in coastal South Carolina and Georgia, feeding primarily on reef oysters. They are year-round residents and represent one of the major predators to the oysters. Photo by Wiley M. Kitchens, U.S. Fish and Wildlife Service.

"Fringing" reefs typical of those lining the shores of tidal creeks of high salinity estuaries in coastal South Carolina. Photo by Rhett Talbert, University of South Carolina

Oyster reefs interspersed in channels dissecting an intertidal mud flat. Photo by Rhett Talbert, University of South Carolina.

CHAPTER 4. OYSTER REEF DEVELOPMENT, DISTRIBUTION, PHYSICAL EFFECTS, AND AREAL EXTENT

4.1 REEF DEVELOPMENT

From a physical standpoint, a reef is a biologically constructed, wave-resistant or potentially wave-resistant structure. Worldwide, reefs range from mounds less than 1 m in height and diameter to massive structures 1,000 m across and 100 m thick (Pettijohn 1975). In general, reef morphology is a function of the constituent organisms and organism byproducts of which it is built, whether these organisms are corals, encrusting or sediment-binding algae, tube-building polychaetes, or oysters.

The thesis presented here is that the location of oyster reefs in the salt marsh-estuarine ecosystem is not accidental; rather, it is the result of interacting physical and biological processes that, if fully understood, would explain the natural distribution of reefs in a given area. Marshall (1954) concluded from a study of the distribution of oyster bars in Alligator Harbor, Florida, that physiographic conditions and predation were the most important factors.

In terms of physical conditions, a minimum stability is undoubtedly required; that is, a water current or wave energy regime above a certain threshold level will prevent the development of an intertidal oyster reef. At the same time, the development of a reef presumably affects the physical stability of an area by dampening current velocity and wave energy. To be viable, a reef also needs a minimum current velocity for the input of food and the export of waste products. The local reef area could thus be self-limited by its dampening influence on the current regime.

The following general model of oyster reef initiation, "ontogeny," and decline has four stages: (1) initial colonization, (2) clustering phase, (3) accretionary phase, and (4) maturation and senescence.

Initial Colonization

Initial reef formation begins with the settlement and growth of single oysters and small scattered oyster clusters within the lower intertidal zone. A suitable substrate must be present for the settlement of oyster spat and initial oyster growth in an area where water flow is sufficient to prevent stagnation (Galtsoff and Luce 1930). Suitable substrates may consist of either sand, firm mud, or clay. Shifting sand and extremely soft mud are the only bottom types totally unsuitable for oyster communities (Galtsoff 1964). Oyster larvae will attach to any hard object, such as fallen trees, driftwood, bushes, branches, old shell material, or discarded solid waste (bottles, cans, plastic, etc.) exposed in the intertidal zone. It is important that the areas be subject to little sediment deposition.

Clustering Phase

With time, additional generations of oyster larvae will settle in the area of the new reef and attach themselves to other live oysters and dead shell surfaces. This process results in the formation of distinct oyster clusters. A cluster is a small colony of three to seven generations of oysters, the majority of which are dead (Grave 1905). The oldest and lowest oysters in the cluster die from overcrowding and suffocation, but their shells remain to support the upward and outward growth of the cluster. This support is aided by the relatively flat shape and low specific gravity of oyster shells.

Accretionary Stage

Small oyster clusters increase in size through the settlement of additional spat and eventually coalesce, forming larger, massed oyster clusters (Grinnell 1971) that comprise the true constructional nucleus of the intertidal oyster reef. If environmental conditions remain stable, the newly formed reef accretes laterally and vertically within the intertidal zone. Dead shell material scattered around the reef aids in building up the channel floor or reef platform, paving the substrate for the reef to spread laterally (Wiedemann 1972). Lateral reef accretion generally occurs in a direction perpendicular to tidal currents so that the effectiveness of currents in transporting nutrients and removing fecal material is exploited (Grave 1905; Grinnell 1971).

On a still smaller scale, individual oysters on the reef surface tend to orient themselves so that their planes of commissure (i.e., opening between the valves) are alined roughly parallel to the current direction (Lawrence 1971). Lawrence (1971) found that either the anterior or posterior shell margin may face the oncoming current direction, a fact suggesting that this alinement is necessary for the hydrodynamic stability of the individual oysters. The macro-orientation of a reef with respect to the local current regime and the micro-orientation of its constituent oysters are only demonstrable where the currents are uni- or bi-directional. For example, most of the reefs examined by Bahr (1974) were located at the southern edge of Sapelo Island in Doboy Sound, an area with multidirectional currents, and no definite macro- or micro-orientation was observed.

Vertical accretion continues as long as the upper (living) layer of the oyster reef remains within the portion of the intertidal zone in which oysters are viable. Bahr (1976) found the maximal reef height for oysters to be a constant feature of the intertidal oyster reefs in Doboy Sound. No reefs in this area exceeded 72 cm above the surrounding mud surface or 1.5 m above mean low water.

At this stage of development, the reef consists of an approximately 1-m thick accumulation of live oysters, dead shell, and mixed shell and mud (Figure 13). The uppermost portion of the reef is level, sloping off steeply at the edges. The living portion of the reef is thicker at the edge than in the center because of mud trapped by the reef. The central core of the reef is composed of mixed dead shell and mud. If, for example, the reef is formed on a soft mud substrate, its weight will cause the entire structure to slowly subside or sink. Vertical upbuilding in a viable reef keeps pace with gradual subsidence, and the upper reef surface remains at a steady state with respect to mean water level. The reefs examined by Bahr (1974) were typical of this stage of development.

Senescent Stage

A senescent stage of intertidal oyster reef development is reached when the upper surface of the reef can no longer accrete vertically and the majority of live oysters populate only the flanks of the reef. The mature reef will have a barren central zone, or ridge in the case of long linear reefs, comprising dead shell and various sized fragments of shell. The barren central region has been referred to as a "hogback" (Gunter 1979) or flatland surface (Grinnell 1971). Gunter (1979) suggests that for gulf coast reefs the constant motion or saltation of fine shell "grit" in the central zone prevents the survival of new oyster spat, so that this area remains void of organisms. This "grit theory" would not hold, however, for the smaller, relatively sheltered reefs in the environment of the salt marsh estuary.

An extension to the senescent stage of reef development was proposed by Grave (1905). He suggested that with time, the barren central "flatland" surface would be built up with thicker accumulations of sand, mud, and shell debris, and would be colonized by Spartina. The reef would then become an oyster marsh island, with a length and width greater than that of the original oyster reef, and surrounded by a thin band of intertidal oysters. Little Egg Island in the mouth of the Altamaha River in Georgia may be an example of such an oyster-formed island.

4.2 DISTRIBUTION OF OYSTER REEFS IN THE MARSH-ESTUARINE ECOSYSTEM

This section includes some speculative material that remains to be confirmed by scientific study. There is, however, ongoing research at Sapelo Island, Georgia, that should help explain the observed distribution of reefs in the ecosystem

(S. Stevens, University of Georgia Marine Institue, Sapelo Island, Georgia; pers. comm.).

Present Distribution

Current speed and bottom roughness have been theorized as controlling the distribution of estuarine suspension-feeding macrobenthos (Wildish and Kristmanson 1979). The distribution of intertidal oyster reefs in the study area is described in terms of the three hydrographic zones of the estuary (see Section 1.2). The zones are (1) the lower sound and inlet areas between barrier islands; (2) the middle region of the estuary, including the major rivers feeding the sounds; and (3) smaller tidal creeks draining the marshes (Figure 2).

The typically high energy regime and sedimentary instability of the lower sound region render this zone the least favorable for reef development. Where reefs are found in the lower sound areas, they presumably indicate local pockets of shelter from storm surges.

From the lower to middle estuarine zone, wave energy is probably the controlling factor. The middle zone is characterized by an optimum current regime for reefs; the regime of the lower zone is too turbulent, and the upper zone is too sluggish. Oyster reefs, sometimes exceeding a kilometer in length, in the middle estuarine zone are predominantly (but not exclusively) oriented along the banks of rivers. Circular reefs and oyster reef islands also occur infrequently in this zone. Many reefs in the middle estuarine zone are near the entrances to small tidal creeks that feed the larger rivers. This orientation is not accidental and may indicate the importance of slight differences in current regimes, which are enhanced at the confluence of water bodies.

The complex network of tidal creeks and small rivers that drain the marshes is also an area of significant oyster reef development. The distribution of intertidal oyster reefs within this zone is perhaps the most consistent and predictable of the three estuarine subdivisions. The pattern of oyster reef development and tidal creek meander systems are strongly correlated. Oyster reefs are likely to occur in three zones within a tidal creek system (Figure 17): (1) on the concave outer banks of meander loops, (2) in areas immediately adjacent to smaller tidal tributaries, and (3) at points of tidal stream confluence.

The oyster reef tendency to develop on the concave outer banks of tidal creeks is predictable from the hydrography of stream meanders. The outer or cut-bank of the meander loop is the zone of highest current velocity within the channel. The sediment substrate, therefore, tends to consist of firm, consolidated mud, swept clean of soft mud and slime unsuitable as a spat settlement surface. Once the reef colony is established, these higher velocity currents provide nutrients and remove fecal matter. Keck et al. (1973) discussed this same relationship between meander morphology and oyster distribution in the Murderkill River, Delaware. Reefs in that region tend to form in areas adjacent to smaller tidal tributaries where important marsh-derived nutrients are. Oyster reefs at points of tidal stream confluence are also influenced by hydrographic factors. During flood tide, the confluence of flow between the two tidal creeks results in a zone of circular back-eddy formation located at the point bar (Figure 17). The turbulence associated with this process provides nutrients to the reef. During flood tide, the point bar is an area of relatively higher current velocity and little deposition.

Historical Changes in Reef Distribution

Four surveys of intertidal oyster reefs along the Georgia coast demonstrate changes in oyster distribution from 1889 to 1977. These are Drake (1891), Galtsoff and Luce (1930), Linton (1968), and Harris (1980). The survey results reveal two aspects of the change in oyster reef distribution over time: a change in total reef area, and local changes (increases or decreases) in specific areas.

Galtsoff and Luce (1930) reported few significant changes occurring in the distribution and extent of natural oyster beds between the years 1889 (Drake 1891) and 1925. They reported, however, a decline in the health of many intertidal

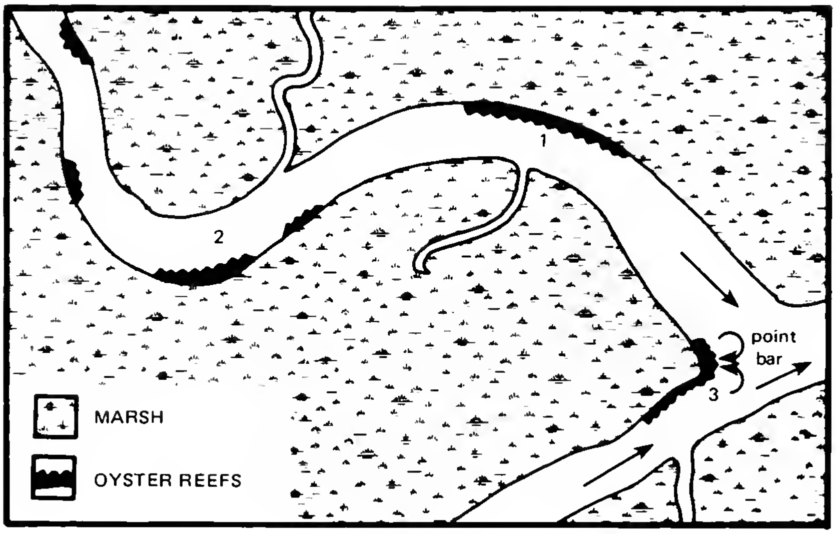


Figure 17. Typical distribution of oyster reefs in small tidal creeks. Zones are (1) concave outer banks of meander loops, (2) areas adjacent to tidal tributaries, and (3) tidal stream confluence.

oyster communities, noting in a number of cases, nothing but silt-covered, dead oyster shells remained of once-productive oyster reefs. This historical decline in the welfare of the intertidal oyster community is further supported by the most recent survey of Harris (1980). Total acreage of the intertidal oysters has decreased dramatically from approximately 688 ha (1,700 acres) in 1889 to less than 121 ha (300 acres) in 1977 (Harris 1980). Large areas of dead oyster shell were also reported in the 1977 survey. Harris related the steady decline of the Georgia commercial oystering industry to the decrease of total oyster acreage. In addition, there is reason to believe that the acreage figures reported by Harris (1980) are somewhat exaggerated, perhaps because they were partly based on aerial imagery that did not permit easy distinction between living reefs and dead shells. For example, Harris reported a total reef area of 9,632 m^2 in the Duplin River; Bahr (1974) reported 6,040 m^2 of living oyster reefs in the same river based on a ground-level survey.

Intertidal oyster populations in South Carolina have apparently also declined during the same period. We are unable at present to attribute this decline to any specific factor. It may be the result of a slow shifting of ecological conditions that reflect a natural successional pattern in the marsh-estuarine ecosystem (e.g., sea level change). Puffer and Emerson (1953) cited natural cyclic changes in environmental conditions--primarily temperature and salinity--as the cause of oyster reef death and subsequent repopulation in Aransas Bay, Texas. Alternatively, this decline may be the result of a man-induced perturbation of the marsh-estuarine ecosystem, such as dredging, waterway construction, pollution, or overharvesting.

It is easy to explain a decline in oyster reefs near population and industrial centers such as Savannah, Georgia, but it is much more difficult to account for a decline of reef area in the more pristine part of the Georgia coast near Sapelo Island.

The salinity of the Duplin River at Sapelo Island, Georgia, appears to have increased recently (B. J. Kjerfve, University of South Carolina, Columbia; pers. comm.). This salinity increase could be caused by a reduction in ground water inputs due to consumptive losses resulting from pumping for agricultural irrigation. This change could partly explain the gradual decline in viable oyster reef area in the Duplin River and in other parts of the study area, although, it is not clear how a salinity increase up to $25^{o}/oo$ or $30^{o}/oo$ would affect the reef community.

With respect to local changes in reef distribution, it is possible to find examples of reef area increases in some specific portions of the Georgia coast. For example, in Altamaha Sound, Georgia, oyster reefs have developed in areas farther inland in the lower sound than they occurred in 1889 (Figure 21). Associated with this shift in reef distribution is the accretion of marsh islands in southern Altamaha Sound. The accretion of marsh and marsh islands may relate to the sediment-trapping capacity of intertidal oyster reefs (Grave 1905; Wiedemann 1972; Stephens et al. 1976). The growth of intertidal oyster reefs farther inland of the lower sound may relate to shifting salinity conditions in Altamaha Sound.

In summary, reef distribution along the Georgia coast surprisingly has changed little over the last 90 years. Oyster reefs occur (in general) today in approximately the same locations where they occurred in 1889 (see Figure 21). The living oyster reef area, however, significantly has declined in the same period.

4.3 THE PHYSICAL EFFECTS OF OYSTER REEFS ON THE MARSH-ESTUARINE ECOSYSTEM

Hypothetically, reefs affect the physiography and hydrologic regime of salt marsh estuaries three ways: by modifying current velocities, both positively and negatively; by passively changing sedimentation patterns; and by actively augmenting sedimentation through biodeposition.

Interpretation of reef effects on the ecosystem over time from analyses of survey data of the last century is difficult because, although 90 years is a long biological time, it is short geologically.

For example, the average sediment deposition rate in the study area is less than 4 mm/yr (Letsch and Frey 1980). This means that from the years since the first reef survey in 1889, theoretically only about one-third of a meter of sediment has accumulated.

Oyster reefs undoubtedly dampen tidal current velocities over the entire ecosystem because of friction, but the magnitude of the drag coefficient of a unit area of reef is unknown, as is the overall effect. Reefs also augment current velocity in local areas by constricting tidal streams, but no quantitative data are available to detail the specific effects.

Grave (1905) noted that oyster reefs are wave- and current-resistant structures that exert a physical influence over the marsh system. He observed that small reefs originating at points along a tidal stream accrete laterally across the stream (into the current), and by displacing and constricting the current cause erosion of the opposite marsh bank. This process may result in the formation of marsh islands.

Passive sedimentation due to the presence of reefs is qualitatively obvious but has not been quantified. The magnitude of this effect would be related to the overall reduction in tidal current velocities and turbidity levels. Active sedimentation through biodeposition can be estimated (see Appendix). The biological process of aggradation increases the size of suspended particles and increases their effective settling rates. The dominant oyster reef zone's coinciding with the maximum turbidity zone in estuaries in the study area indicates that this effect may be significant. Lund (1957a) reported that oysters biodeposited or "self-silted" eight times the volume of sediment in test containers than would have deposited in the same time due to gravity alone. He calculated that a uniform single layer of oysters in a natural setting with relatively low turbidity water could biodeposit sediment at a rate of about 280 tons/acre/yr (6×10^4 g/m^2/ yr).

4.4 AREAL EXTENT OF OYSTER REEFS IN THE COASTAL ECOSYSTEM

The most obvious criterion by which to assess the importance of oyster reefs on the marsh-estuarine ecosystem is the relative proportion of reef surface area to the total surface area of the system. Planimetry on maps of the Georgia coastal zone (Galtsoff and Luce 1930) indicated that the total intertidal and subtidal zones of the entire area occupied approximately 1.8×10^9m^2. Of this area, approximately 75% was marsh and tidal creeks, and 25% was open water (wider than about 350 m). The linear extent of the oyster reefs measured about 403,000 m. If the average reef were estimated as 2 m in width, the total reef area in 1925 would have comprised about 8×10^5 m, or 0.04% of the marsh-estuarine area. If the mean reef width were 3 m, reef area would increase to 1.2×10^6 m^2, or 0.06%. Harris (1980) estimated that the total viable reef area in the Georgia coastal zone in 1977 was equal to 102 ha, or about 0.05% of the marsh-estuarine area. This presumably represents a decline from 1889, when Drake (1890) estimated that 6.8×10^6 square meters of reefs existed, or 0.3% of the total marsh estuarine zone was occupied by oyster reefs. In a detailed survey of the Duplin River drainage basin, Bahr (1974) estimated that about 0.06% of the marsh estuarine zone was occupied by viable reefs.

The absence of quantitative information about the areal extent of intertidal oyster reefs in South Carolina and northeastern Florida does not allow a comparison with Georgia. Apparently oyster reefs comprise a larger percentage of the marsh estuary in the South Carolina area than in Georgia, but the relative difference is unknown. A detailed analysis of the relationship between reef area and tidal amplitude in the study area would be interesting. A small area of the Savannah River basin in South Carolina surveyed by McKenzie and Badger (1969) indicated an extremely high oyster reef density (9%). Lunz (1943) reported an extremely high density of reefs along a 1-mi wide and 40-mi long strip surrounding the intracoastal waterway in South Carolina from Charleston to the Santee River. He reported that 33.6% of the total creek banks was lined with reefs. Lunz (1943) also reported that these reefs were populated by about 136 oysters/yd^2, (or about 114/m) of 2-inch (50-mm) or larger sized oysters. This represents a biomass of approximately 50 g/m^2 afdw, much lower than that for the more mature reefs described in Georgia. Lehman (1974) reported that oyster reefs in the Crystal River estuarine ecosystem in West Florida occupied about 3% of the total surface area.

To put these various estimates in perspective, it must be remembered that different survey techniques were used, and that some subjectivity is involved in distinguishing viable reefs from areas of dead shell. Whether or not a major decline in oyster reefs has occurred since 1899, the present proportion of reef area to marsh-estuarine area throughout the study area appears to be between 0.04% and 0.06%, with some local variation. The reef community's occupying such a small proportion of the total marsh-estuarine area may reflect both the very specific physicochemical requirements of the reef community and the limited productive capacity of the total system in supporting the high, heterotrophic demands of the oyster community.

An example of Spartina marsh invading the top levels of an oyster reef. Photo by Rhett Talbert, University of South Carolina.

CHAPTER 5. CONCEPTUAL MODELS OF THE INTERTIDAL OYSTER REEF COMMUNITY

5.1 OBJECTIVES AND LEVELS OF RESOLUTION

This chapter summarizes some conclusions, primarily qualitative, about the significance of oyster reefs to the coastal ecosystem in the study area. The summary is in the form of a set of three conceptual models that are explicit diagrammatic illustrations of the interactions among oyster reefs and other salt marsh ecosystem components. Conceptual models can provide succinct, qualitative expressions of the feedback pathways, forcing functions, and major interconnections characterizing a particular ecosystem. Conceptual models are usually over-simplifications of the real world, but their formulation may indicate deficiencies of information that can become future research goals. Conceptual models take a variety of forms, from simple box and arrow diagrams to detailed and complex "spaghetti" diagrams that are difficult to interpret. Figure 18 (from Odum 1971) illustrates one conceptual model of an oyster reef that compares it in functional terms to a city.

Oyster reef organization and function must be considered at different levels of space and time, and our conceptual models are presented at three (hierarchical) levels of resolution: a regional level, a drainage unit level, and a reef level (Figure 19). The regional level model treats the oyster reef system over the entire study area or a large portion of the study area. At the regional level, detailed reef community information is relatively unimportant compared with that of long-term geological processes affecting regional ecology. The relative proportions of salt marsh, open water, and total reef area and patterns of their spatial distribution are particularly significant at the regional level since these factors are regulated by long-term geological processes.

The second level of resolution is on a smaller and more detailed scale--that of a single marsh-estuarine drainage unit. For example, Figure 20 shows the oyster reef distribution in the Half Moon River estuary on Wilmington Island, Georgia. This tidal river and its surrounding salt marsh watershed exemplify a "typical" local drainage unit in which oyster reefs are distributed in a nonrandom pattern. At this intermediate scale of resolution, the reef community is more visible than at the regional level and presumably exerts a more profound short-term influence on the local ecosystem. Another example of the resolution achievable at this level may be seen in Figure 21. The information content at this scale is such that only broad spatial patterns of reef distribution within the marsh-estuarine ecosystem are discernable. The perspective, then, is an "overview." At scales smaller than this (greater resolution), the oyster reef system is obscured.

The third conceptual level of resolution is of a discrete reef and its immediate surroundings. At this level, a reef can be considered analogous to an individual in a "population" of reefs, each member being influenced by local forcing functions--hydrologic forces, short-term episodic events, and biological phenomena, such as spawning events and predation. An individual reef is subject to local phenomena, and its influence is primarily restricted to its immediate surroundings. The purpose of the third level conceptual model is to summarize the specific phenomena regulating the welfare of a given reef. The cumulative effects of the "population" of reefs in a drainage basin are addressed at the drainage unit level.

Some important differences among the above three conceptual levels of organization and function of oyster reefs in the study area are summarized in Table 8. The three different scales of resolution are discussed in Sections 5.2, 5.3, and 5.4.

Symbols used in the models were developed by H.T. Odum (1971) as a shorthand

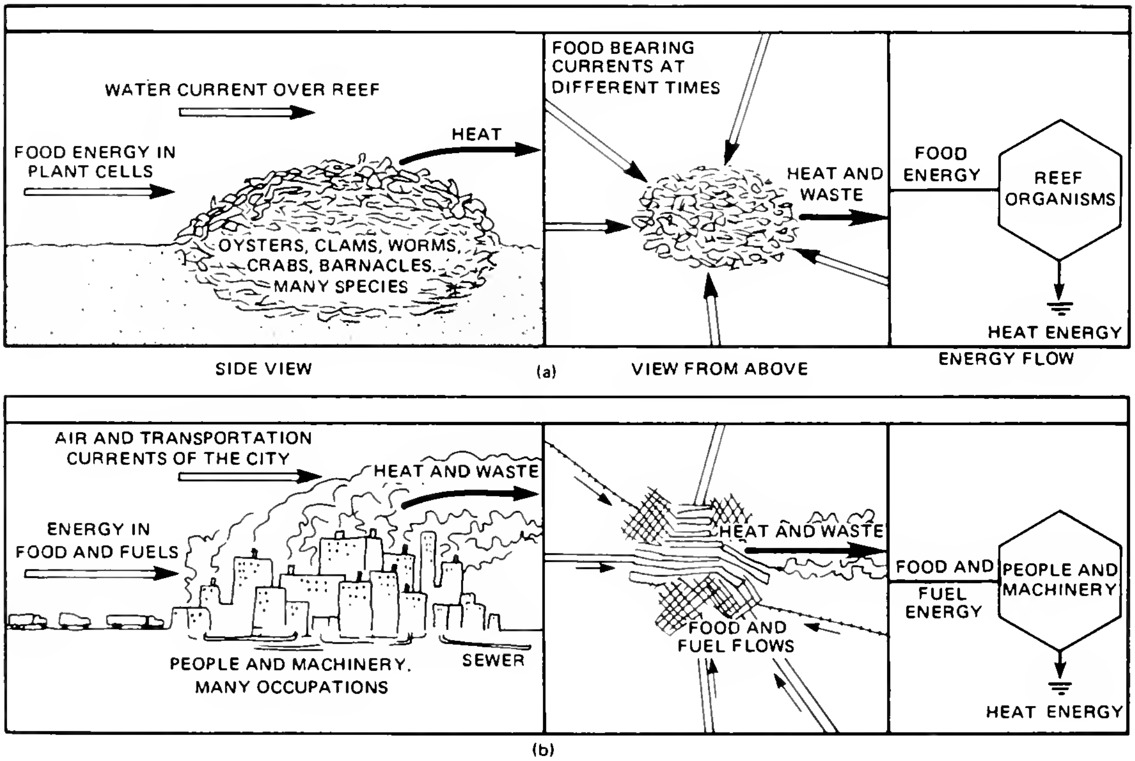


Figure 18. Comparison of two systems of concentrated consumers whose survival depends on strong flows that bring in fuels and oxygen and outflow wastes: (a) reef of oysters and other marine animals characteristic of many estuaries; (b) industrialized city (adapted from Odum 1971).

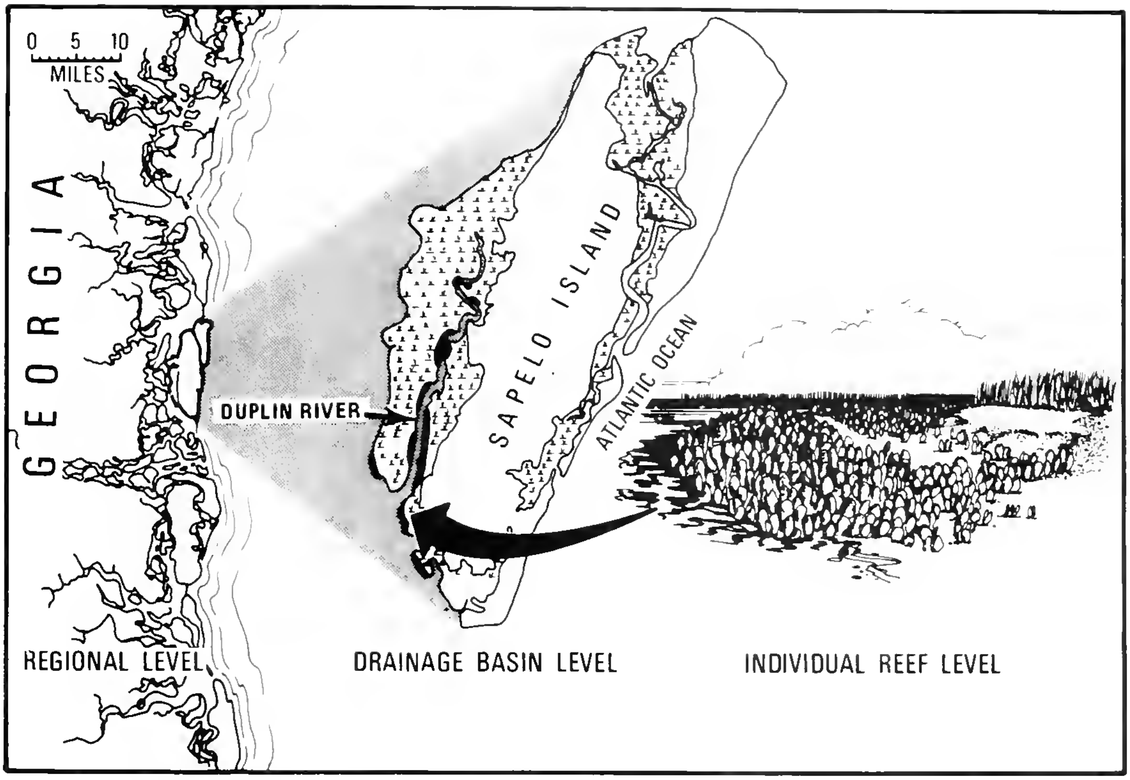


Figure 19. Three hierarchical levels of oyster reef organization.

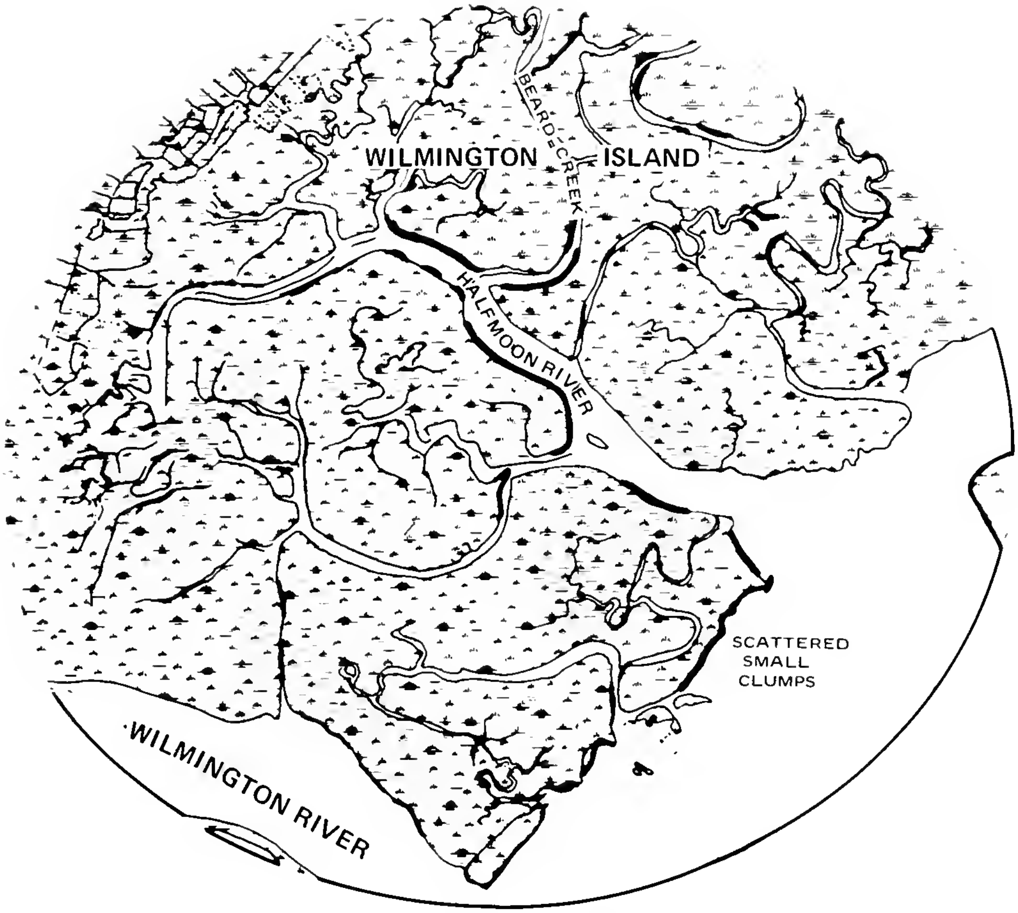


Figure 20. Reef distribution in a single drainage basin, the Half Moon River Estuary, Wilmington Island, Georgia. Reefs are indicated by bold, black lines.

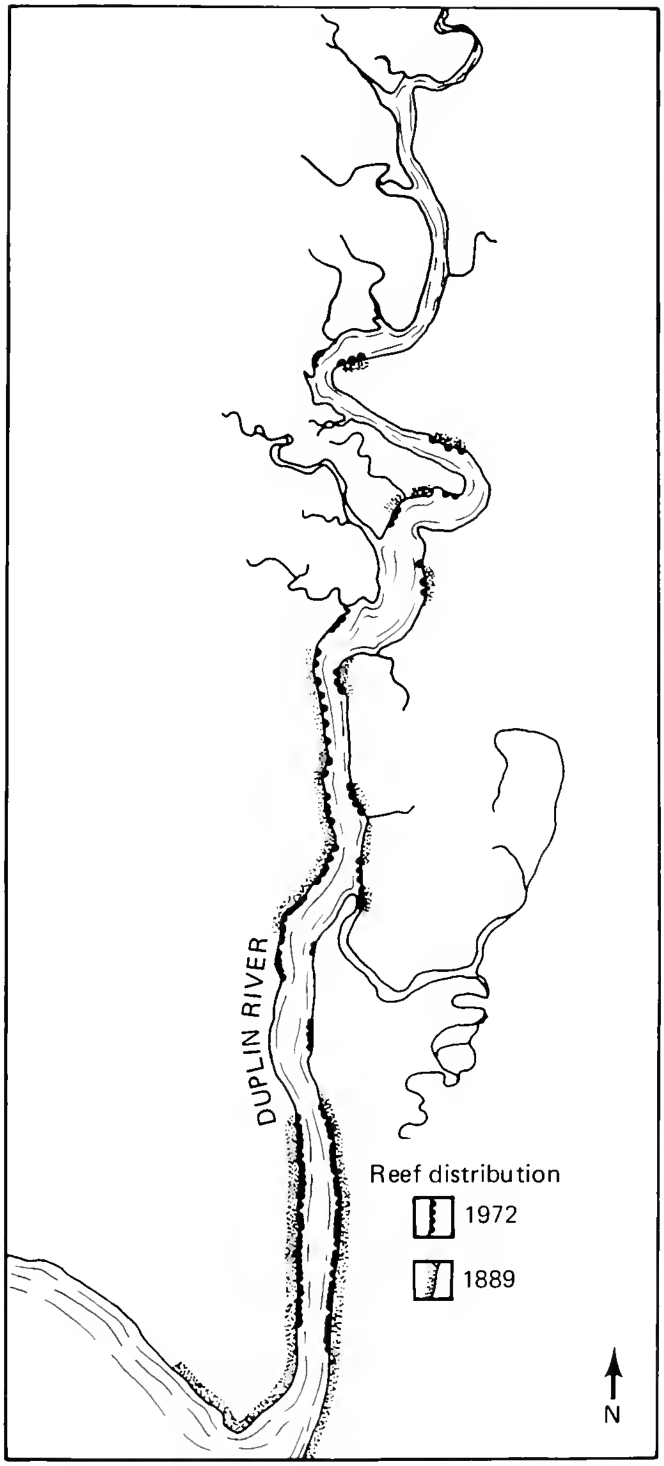


Figure 21. Recent and historical reef distribution in the Duplin River Estuary, Sapelo Island, Georgia (adapted from Bahr 1974 and Drake 1891).

Table 8. Time scales relating ecosystem processes and components at the three conceptual levels of oyster reef organization and function.

	Regional level	Drainage unit level	Reef level
	Approximate time scale		
Factors	1×10^2 to 1×10^4 yr	1 to 100 + yr	<1 to 25 yr
System components	Intertidal area Marsh area Reef area Mudflat area Water surface area	Wetland area Water area Phytoplankton biomass Reef area Reef biomass Suspended load	High (mature) reef area Low (mature) reef area Suspended load (POC and inorganic carbon) Reef biomass Predator component Oyster larvae Nutrient pool
Forcing functions	Sea level rise Latitude-tidal pattern Latitude-temperature regime Riverine sediment input Marine input-salts Marine inputs-storm energy	Solar insolation Tidal and wind-driven currents Sediment, marine or riverine	Local tidal regime (amplitude and period) Currents (tidal and wind) Temperature effects Sediment input POC input
Important system processes related to reefs	Areal trade offs among wetlands, waterbodies, and reefs	Physiographic changes in basin caused by reefs	Reef growth (vertical) Reef growth (lateral) Water clearance and biodeposition Mineralization and nutrient release Hydrologic damping by reefs

for expressing the functional connections in many different kinds of systems to compare these systems in thermodynamic (energy flow) terms. Odum calls the shorthand "energese," and it is becoming more popular, as evidenced by its increasing use in published reports. This shorthand "language" is flexible and information-rich, and it can be used in both qualitative conceptual models and in quantitative "working" models. The symbols are defined in Figure 22, taken from Odum (1971).

5.2 REGIONAL LEVEL CONCEPTUAL MODEL

The regional level model of oyster reef function in the study area is broad in its coverage and necessarily quite simple. At this level of resolution, oyster reefs were probably not a major factor in the geomorphological development of the area, although their wide surface distribution and largely unknown subsurface (fossil) distribution indicate that they indeed may have played a geological role. No one has as yet quantified the physical importance of oyster reefs to long-term coastal processes.

In Figure 22 we illustrate the theoretical role of oyster reefs at this broad regional scale. As indicated in Table 8, the time-scale of change at the regional level is in the geological range, outside the realm of control of environmental managers (although not immune to culturally induced alteration).

The major process symbolized in the regional scale conceptual model is the dynamic tradeoff in area between intertidal and subtidal zones. Oyster reefs primarily are distributed at the interface between these two zones, and thus the reef "fringe" partially reflects the outline of the marsh-water interface throughout the study area. Changes in the position of this outline are a function of such long-term processes as subsidence, sea level rise, and sedimentation regimes. For all practical purposes, reef distribution at the regional level can be considered spatially homogeneous.

Interactions between the intertidal and subtidal zones are described in the order of the work gates (1-4) shown in Figure 22.

(1) A gradual and persistent rise in sea level (about 4 mm/yr) has occurred since the relative stabilization of mean water level (MWL) following the last ice age. This has resulted in a constant encroachment upon the intertidal zone by open water. In the absence of other processes, the intertidal zone would eventually become open water.

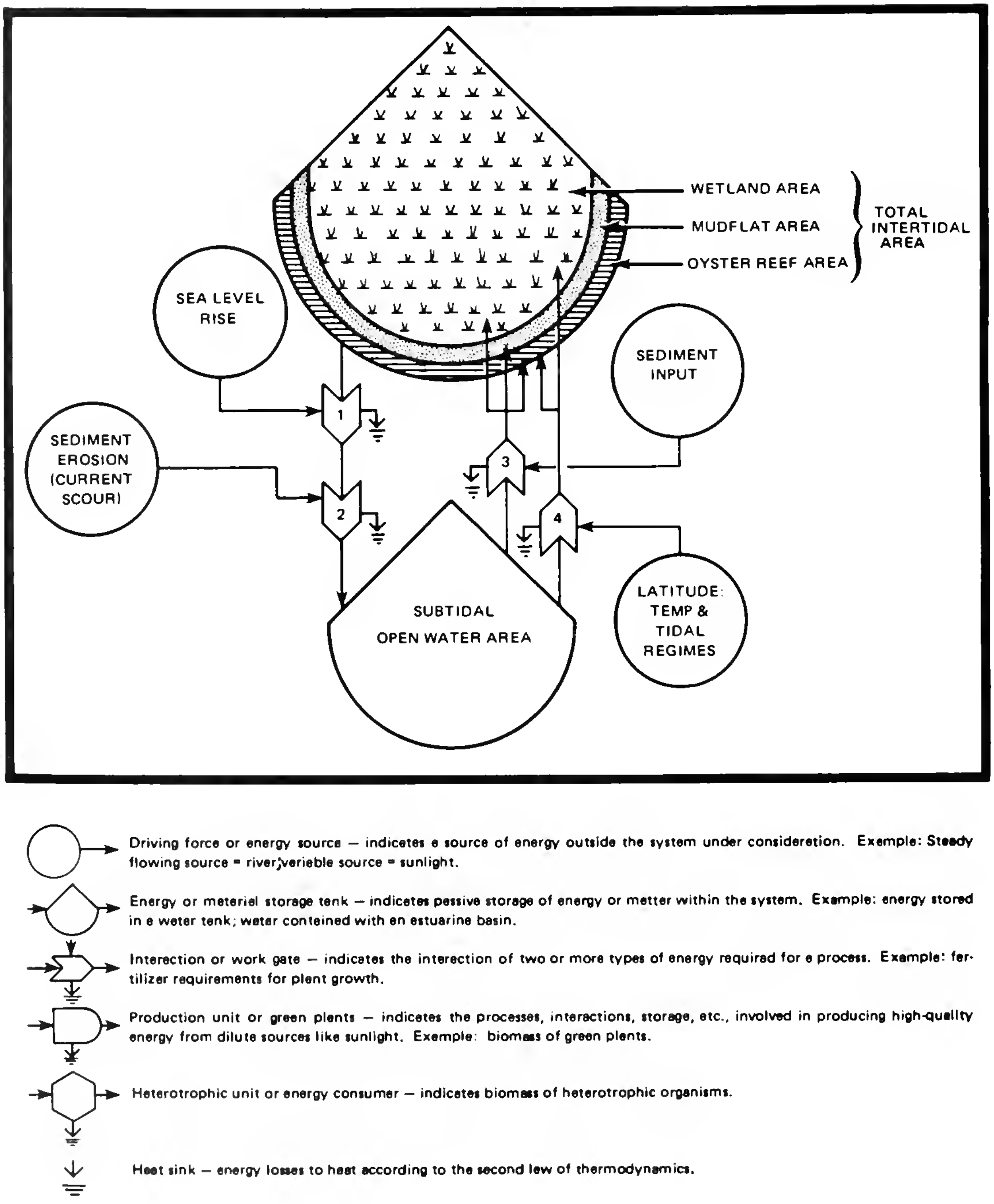
(2) The loss of intertidal area is accelerated by erosion from strong tidal currents and storm surges.

(3) Losses of intertidal habitat are offset in most undisturbed portions of the study area by inputs of sediment from rivers and/or from the marine system. This sedimentation process is augmented by increases in the volume of estuarine basins as a function of sea level rise. Mean water current velocities decline as volume increases, and sedimentation is enhanced.

(4) Latitude determines tidal amplitude in the study area, which, in conjunction with sediment sources, regulates the depositional patterns.

5.3 DRAINAGE UNIT LEVEL CONCEPTUAL MODEL

The components and interrelationships of a marsh estuary drainage unit including and affected by oyster reefs are shown in Figure 23. A major assumption at this level of resolution is that there is an optimum ratio of wetlands and open water which, in conjunction with tides, support the oyster reef area in a given drainage basin. One implication of this assumption is that relative reef area in a given drainage unit is limited by ecosystem level processes, (e.g., the relationship between the velocity of tidal currents, the cross-sectional area of tidal creeks, and the distribution of reefs). This thesis is



Driving force or energy source — indicates a source of energy outside the system under consideration. Example: Steady flowing source = river; variable source = sunlight.

Energy or material storage tank — indicates passive storage of energy or matter within the system. Example: energy stored in a water tank; water contained with an estuarine basin.

Interaction or work gate — indicates the interaction of two or more types of energy required for a process. Example: fertilizer requirements for plant growth.

Production unit or green plants — indicates the processes, interactions, storage, etc., involved in producing high-quality energy from dilute sources like sunlight. Example: biomass of green plants.

Heterotrophic unit or energy consumer — indicates biomass of heterotrophic organisms.

Heat sink — energy losses to heat according to the second law of thermodynamics.

Figure 22. Regional level conceptual model and explanation of symbols.

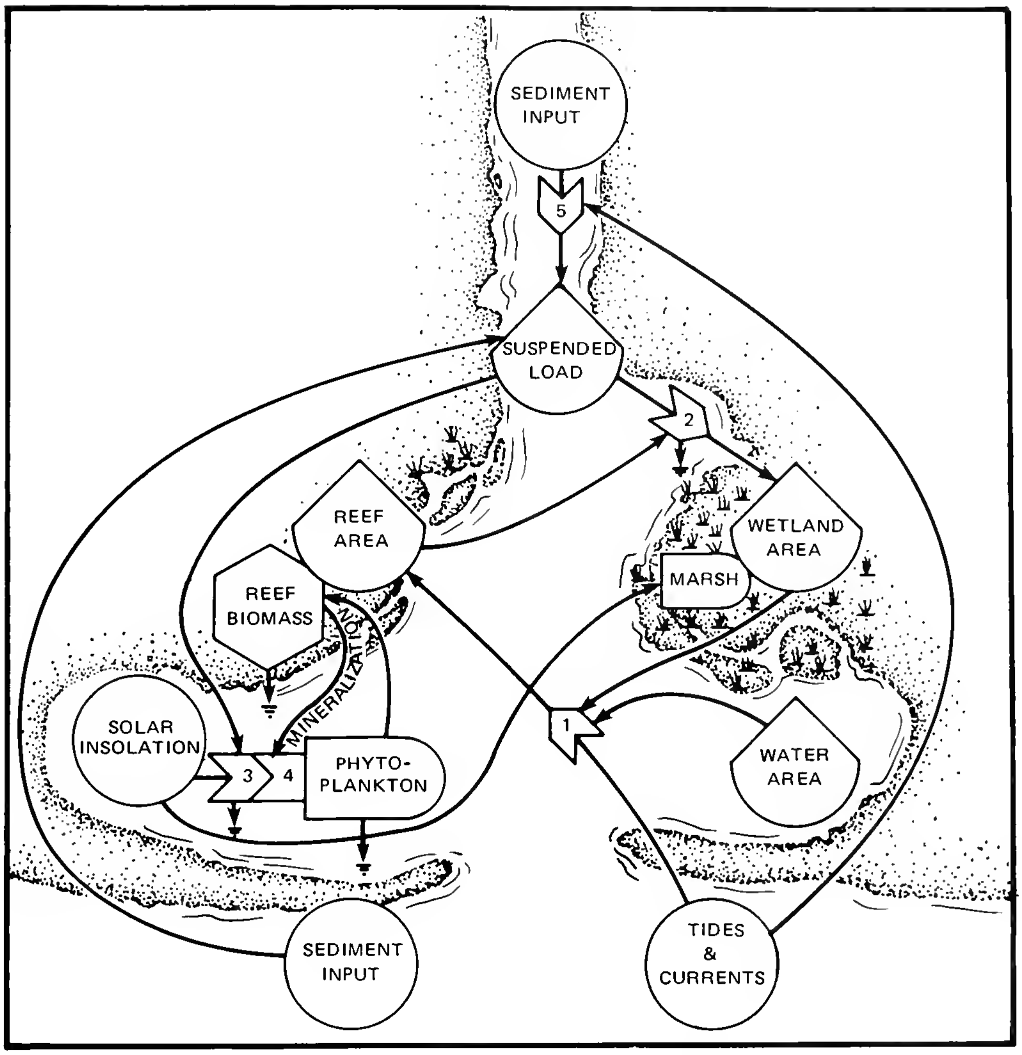


Figure 23. Drainage unit level conceptual model.

supported by the relatively static distribution of reefs within the Duplin River basin over time, shown in Figure 21.

Specific interactions shown in Figure 23 are described below:

(1) The local tidal regime is the primary forcing function for oyster reef distribution (and relative area) in a given salt marsh drainage unit. The tidal effect is shown interacting simultaneously with water area and wetland area. These respective components (water and wetlands) have a 1 to 2 ratio in the Georgia marsh-estuarine ecosystem (Pomeroy and Wiegert 1980). The pattern of distribution of oyster reefs in the Duplin River, as shown in Figure 21, is probably not a chance distribution. For example, oyster reefs are absent from the upper one-fourth of the basin, probably because of ecosystem level processes (e.g., a function of reduced current velocities in the upper reaches of the river).

(2) Oyster reef area in a given locale can affect local turbidity levels by filtration and biodeposition. By stabilizing and elevating sediment, wetland development can be enhanced. Marsh grass and oyster reefs have a reciprocal functional relationship in that reefs develop almost exclusively at the interface between wetland and water. There they subsequently grow and trap sediment, eventually becoming colonized by Spartina. The marsh invades formerly subtidal areas in this leapfrog fashion. For example, subsurface (fossil) oyster reefs occur in a pattern of increasing depth extending from an existing reef into the marsh. (S. Stevens, University of Georgia Marine Institute, Sapelo Island; pers. comm.).

(3) Suspended materials in water column inhibit the primary production by phytoplankton as a result of shading. Therefore, oyster reefs theoretically augment phytoplankton productivity by actively filtering these materials and thereby reducing turbidity.

(4) Oyster reefs in local areas also contribute to primary production (especially of phytoplankton and benthic algae) by rapidly mineralizing ingested organic matter into usable plant nutrients. Kuenzler (1961) showed that the regeneration of phosphorus by mussels in the salt marsh was more important than their role in energy transformation. Kitchell et al. (1979) discussed the roles of consumers in nutrient cycling. Oyster reefs by Interactions (3) and (4) can increase food availability, providing feedback in keeping with ecosystem theory, (e.g., Odum 1971).

(5) Tidal currents maintain extremely high suspended sediment loads in some study area estuaries, like the Duplin River (Hanson and Snyder 1979). The consequences of this siltation relate to Interactions (2) and (3).

5.4 REEF LEVEL CONCEPTUAL MODEL

The third conceptual model is shown in Figure 24, where reef development is expressed as growth in three dimensions: (1) upward toward the high intertidal zone, (2) downward toward the subtidal zone, and (3) lateral accretion.

The interactions involved in such changes are described below:

(1) Ingestion by oysters and other suspension-feeding members of the reef community is affected negatively by increased water turbidity (Section 2.3).

(2) Turbidity of estuaries in the study area is usually high and closely related to the high tidal current regime. Thus,

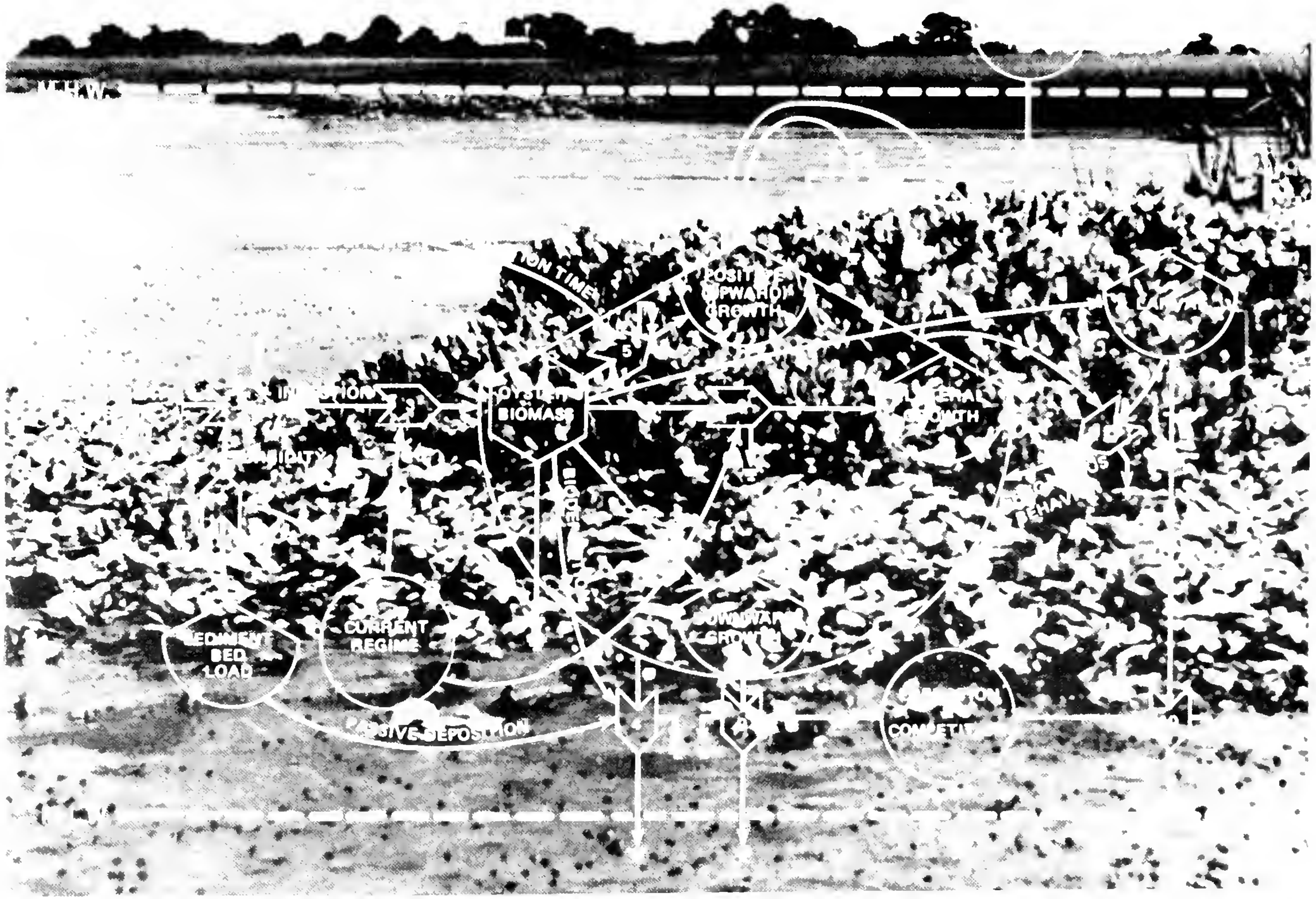


Figure 24. Reef organization conceptual model.

currents indirectly can reduce oyster feeding.

(3) Currents have been shown, however, to positively affect oyster ingestion (Walne 1972).Thus, an optimum low-current level probably exists to stimulate oyster feeding with a minimum of sediment erosion.

(4) Eroded sediments in the water column can settle out on a reef and bury the lower level oysters, causing a decline in reef viability. Sediment input by currents, coupled with a high rate of biodeposition, can suffocate all but the uppermost oysters in a reef.

(5) Oyster reef growth in a positive vertical direction is limited absolutely by the local tidal amplitude. The highest portions of the reefs examined at Sapelo Island were limited to 1.5 m above MLW, corresponding to a daily inundation time of only 8 hours, or conversely, to an exposure time of 16 hours.

(6) Lateral extension of oyster reefs apparently occurs at a rate limited by suitable substrate at the proper elevation in the intertidal zone, by water currents, and by available food.

(7) In addition to a minimum inundation time, vertical reef growth is also subject to temperature stress in the study area (extremely cold spells and hot spells during reef exposure).

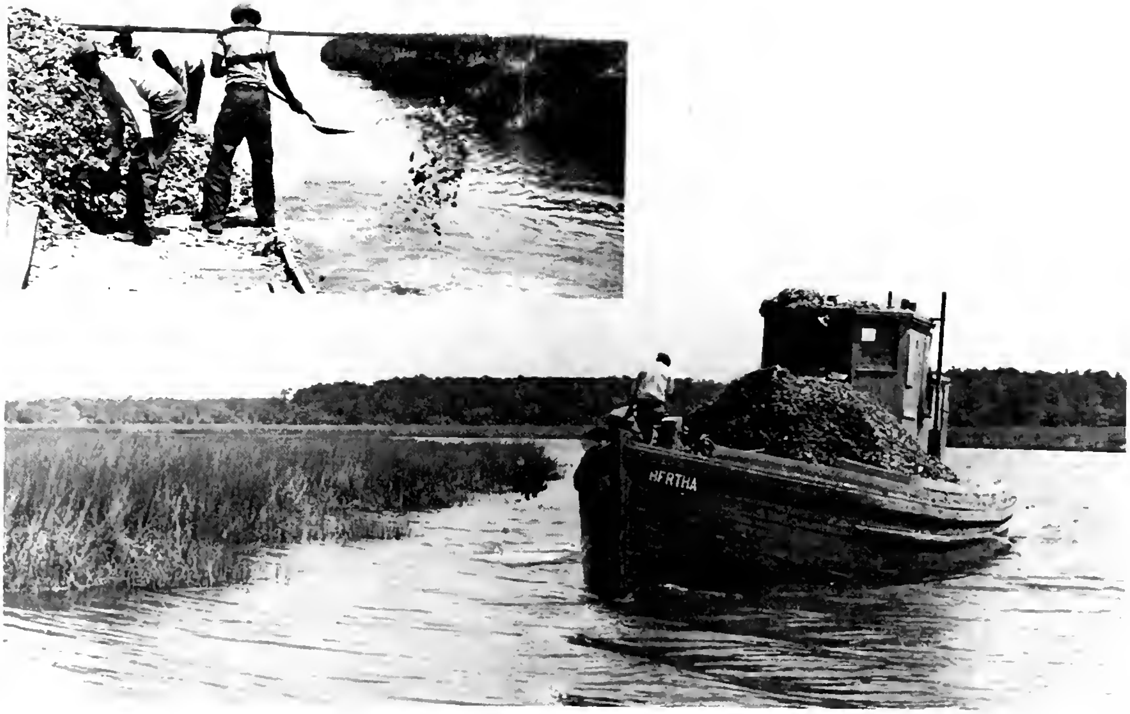
(8) Reef crowding appears to buffer temperature stress and to allow vertical reef accretion beyond the maximum level at which individual oysters survive.

(9) Downward extension of oyster reefs toward the subtidal zone appears limited by increased predation, fouling, and shell erosion by boring sponges.

(10) Predation by filter feeding organisms, nektonic, and epibenthic, reduces the available pool of oyster larvae and perhaps prevents overcrowding.

(11) The gregarious behavior of oyster larvae ensures a new crop of spat to replenish mortality losses and maintain the viability of existing reefs.

Immature reef at the mouth of an intertidal creek. Note the mature reefs in the background. Photo by Rhett Talbert, University of South Carolina.



The seeding of intertidal oyster beds with oyster shell to induce increased oyster spat settlement in areas that are being commercially harvested. Photo by South Carolina Wildlife and Marine Resources Department.

CHAPTER 6. SUMMARY AND MANAGEMENT IMPLICATIONS AND GUIDELINES

6.1 SUMMARY AND OYSTER REEF SIGNIFICANCE

The American oyster (Crassostrea virginica) is not only an extremely valuable commodity to man but is also a cosmopolitan, physiologically plastic, and ecologically interesting estuarine organism. Its natural range spans the Atlantic coast and much of the gulf coast, and its generic "brothers" exist in coastal systems worldwide.

One intriguing aspect of oyster behavior is its propensity, under certain conditions, to form massive, discrete, intertidal colonies, or reefs. The largest individual oyster reefs formed by the American oyster occur in open bays along the northern gulf coast. Some reefs are many kilometers in length; they consist mainly of dead shells, and their geometry is partially the result of reworking by storm surges.

In the South Atlantic Bight, tidal amplitude ranges from 1 m to over 3 m (3 to 10 ft), and oyster reefs occur in close association with extensive salt marshes characteristic of the area. Oyster reefs within this region achieve a greater elevation above mean sea level and a greater oyster density (in terms of numbers and biomass) than in any other coastal region. The structure and ecological function of these reefs are the subjects of the previous five chapters.

Whereas most oyster research has been carried out at the individual or population level of detail, this paper has emphasized the behavior of the oyster at the ecosystem level. The reef community described throughout this community profile exhibits characteristics and has ecosystem importance that could not be predicted from even "perfect" knowledge of the biology of individual oysters. Thus, just as a termite colony is more than a collection of termites, so an oyster reef shows emergent properties, including its capability of extending the intertidal range of the reef assemblage upward beyond the elevation at which individual oysters normally could survive. Oyster reefs possess the following characteristic properties: (1) individual oysters in a reef must grow with a strong vertical orientation to survive; (2) individual reefs strictly are limited to the intertidal zone, and the geometry of a given reef is strongly determined by mean water level, sediment stability, and current regime; and (3) patterns of reef distribution are discernable within drainage basins, such that reef density is usually maximal at intermediate channel widths and current velocities. In other words, if all living oysters in a drainage basin were redistributed either randomly or homogeneously throughout the ecosystem, a large portion of the function (and value) of the oyster community would be lost.

One primary ecosystem value of the oyster reef community relates to its physical, rather than its biological, properties. Mature reefs are stabilizing influences on erosional processes and may modify long-term changes in tidal stream flow and overall marsh physiography, although these effects have not been quantified yet.

The extent of the physical influence of reefs on the marsh system is a function of the average relative proportion of reef area to total intertidal area in a given drainage basin. The available estimates of this relationship vary, but about 0.05% of reef area to total intertidal area (marsh and water) may be a reasonable estimate.

Another aspect of the ecosystem value of oyster reefs relates, in natural estuarine areas, to reefs' being stable islands of hard substrate in an otherwise unstable soft muddy environment. These islands are essential habitat for some organisms, especially the sessile suspension-feeding epifauna usually limited by the available surface area. Reefs also provide a highly irregular surface with crevices that serve as havens for motile invertebrates; and some small fish use reefs for shelter during flood tides. Oyster reefs are

Photo indicates the "soupy" nature of the sediments that oft times support oyster reefs. The reefs represent a hard substrate "island" habitat in an otherwise soft-bottomed environment. Photo by Leonard Bahr, Louisiana State University.

densely populated with mussels, mud crabs, polychaetes, barnacles, and other macrofauna, and countless smaller metazoa, protozoa and bacteria.

The members of the oyster reef community are limited primarily to suspension and deposit feeding macrofaunal consumers. The trophic role of this macrofaunal community as a whole assimilates carbon derived from phytoplankton and detrital sources and makes it available to higher consumers, i.e, terrestrial and aquatic animals. Of the former, raccoons and birds like oyster catchers and grackles are predators on oyster reefs. Aquatic consumers that prey on healthy living oysters include the blue crab (Callinectes sapidus) and the black drum (Pogonias cromis). Many other aquatic carnivores undoubtedly visit oyster reefs during flood tides and prey on the host of small invertebrates residing there.

More important than the food web roles of oyster reef inhabitants in the salt marsh estuarine system is their role in mineralizing organic carbon and releasing nitrogen and phosphorus in forms usable by the primary producers. The significance of the energetic roles of the reef community is exemplified by the metabolic rates of the entire community being among the highest measured for any benthic community (27,000 kcal/m^2/yr). This rate is partly due to the great surface area in a reef, supporting a large population of aerobic bacteria, and to the high biomass of the resident macrofauna (up to 1,100 g afdw/m^2).

Each summer the reef community contributes a stream of high quality protein to the water column in the form of gametes and larvae of oysters and other resident macrofauna. These meroplankton (or larvae) are food for nektonic filter feeders, food for other benthic organisms, and recruits for the next generation of reef oysters and associates. Because reefs continually subside into the mud, new generations of oysters at the top are necessary to maintain the steady state elevation of the upper reef surface.

Oyster growth in mature reefs appears extremely slow, and some of the larger resident oysters probably are 5 to 10 or more years of age. They are typically long and narrow and usually display a watery condition with little glycogen reserves, a sign of stress or being spawned out.

Because oysters in reefs apparently live close to their stress tolerance threshold, further perturbation by man can easily destroy the entire reef community. Reefs are particularly susceptible to artificial hydrologic changes, such as those that follow the impoundment or diversion of waterbodies as large as coastal rivers or as small as individual tidal streams. Reefs primarily are found at the interface between wetland and open water, and the destruction of wetlands for any reason results in a decrease in this interface zone. Oysters and other benthic macrofauna are, of course, also connected to and depend upon wetland macrophytes via trophic pathways still not well understood.

Reef oysters are susceptible to the increasing array of man-made chemicals and heavy metals becoming more prevalent in coastal waters. They are also vulnerable to the eutrophic effects of fertilizer- and sewage-loading in coastal waters through the potential alteration of the composition of the natural phytoplankton community in a manner that may be less desirable or even toxic to oysters.

Reef oysters have evolved to tolerate high levels of turbidity, but increased sedimentation on top of natural levels can smother them. Dredging related to shell or phosphate mining, navigation or pipeline canals, or other construction activities in the coastal zone can drastically increase the natural sediment load in local areas. In addition, the artificial mixing of reduced bottom sediments with water above the bottom can deplete the water column of its dissolved oxygen.

Direct physical alteration of mature oyster reefs, e.g., by harvesting, can destroy an entire reef, even if the reef is only moderately disturbed. Harvest of intertidal oysters is productive only on immature oyster reefs low in the intertidal zone, where oysters are not as crowded as in mature reefs and where growth is more rapid. Thus, mature reefs are most valuable to the ecosystem and to society if they are left undisturbed, rather than harvested for their limited food value.

6.2 MANAGEMENT IMPLICATIONS AND GUIDELINES

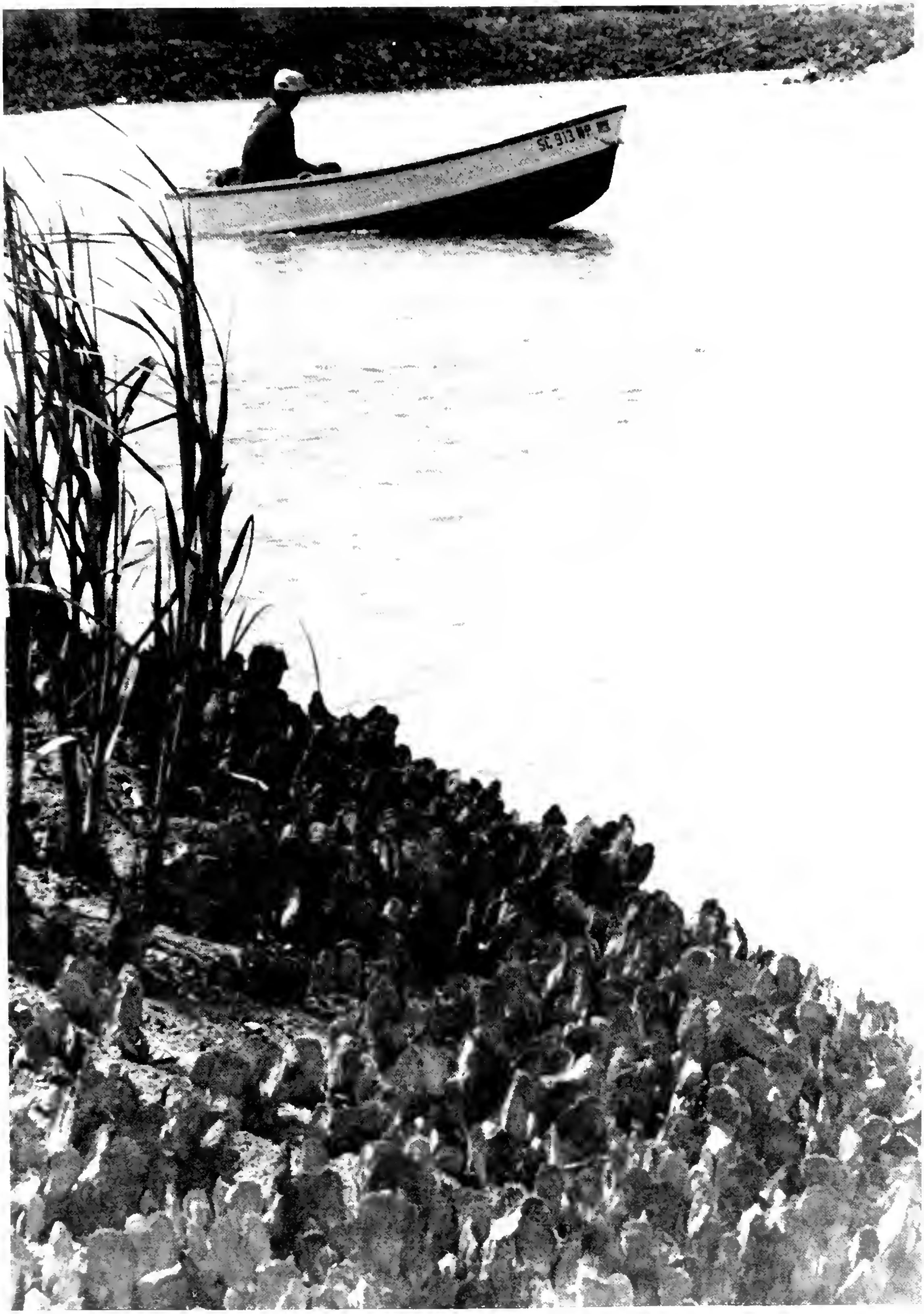
Clearly, the oyster reef component of the coastal ecosystem in the Southeastern United States depends on a healthy marsh-estuarine environment. Thus, the most logical recommendation for reef management is to mitigate increasing man-induced alterations on the marsh system to the extent possible. Changes in water flow, both surface and subsurface, appear to cause the most far reaching and cumulative damage to the entire system, and thus indirectly to the reef subsystem. See Table 1 for a summary of cultural stress on oysters.

The maintenance of high water quality is, of course, important to the continued viability of oyster reefs; and the introduction of urban, industrial, and agricultural pollutants from both point and non-point sources is to be avoided. Subtidal oysters normally can tolerate a fair amount of insult in terms of poor water quality before succumbing to many of the common pollutants. Such oysters usually become dangerous to eat before they die from chemical pollution. Reef oysters, on the other hand, are already stressed and may not be as hardy. At present, the oyster reef zone of the South Atlantic Bight appears relatively free of toxic chemicals and excess nutrients, except in the immediate vicinity of major population centers such as Savannah, Georgia, and Charleston, South Carolina.

Long-term effects of increasing freshwater pumping may pose a problem more serious than pollution for the marsh oyster reef system. Therefore, future urban, industrial, and agricultural requirements for freshwater need to be examined and their long-term effects on salinity distribution predicted, in order to understand the implications of development for the entire coastal ecosystem.

There have been several proposals and attempts to increase oyster reef area locally by spreading cultch along the fringe between marsh and water to induce oyster settlement. These efforts have been largely unsuccessful, implying that our thesis is valid; that is, the distribution of reefs relates to a specific set of conditions, especially with respect to water flow, and the proportion of a marsh drainage unit occupied by oyster reefs is not indefinitely expandable. The guideline derived from these observations is that artificial oyster reef development should be seriously attempted only at former reef sites.

In conclusion, the intertidal oyster reef subunit of the marsh estuarine ecosystem is an important component of the coastal zone in the Southeastern United States, and this subunit has declined in total area during the last 90 years. We can only guess at the consequences of the continued loss of reef area, but these effects could be both obvious and subtle, and could definitely result in an ecosystem less healthy, rich, and productive, and certainly less interesting from an aesthetic point of view.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APPENDIX: OYSTER BIOENERGETICS

Oysters, like all heterotrophic organisms, use energy in proportion to their growth rate, their reproductive investment, and their efforts to obtain food, remove waste, defend themselves against parasites and predators, and maintain a favorable osmotic balance. This section discusses the rates and partitioning of energy expenditures for individual intertidal oysters and the oyster population as a whole. The energy requirements of the entire reef, a prerequisite for understanding the dynamics of the oyster reef community, are estimated in Chapter 3.

Ecologists and environmental managers are beginning to realize the value of information regarding the rates and pathways of energy flow in communities of organisms and entire ecosystems. Energy units are interconvertible, and, therefore, the energy "cost" of totally different processes is the common denominator by which these processes can be compared objectively and ranked in terms of their ecological importance. The first ecologist formally to apply this principle to the study of ecosystems was Raymond Lindemann, who in 1942 published a landmark treatise on the partitioning of energy flow through an ecosystem (Lindeman 1942). Since then, it has become common practice to include energetics in ecological research. Good review sources on bioenergetics include Phillipson (1966) and Wiegert (1968).

The extant oyster literature includes several compilations of energy budgets for various species of oysters in different areas. Extrapolations from some of these studies are necessary to fill in energy budget data gaps for intertidal oysters in the study area.

The calculation of an energy budget for a population of organisms involves the use of one or another equation of the general form:

$$P_{(net)} = I-E-R-W \qquad (1)$$

$P_{(net)}$ = net secondary production rate, or growth of the population in a given time (including somatic growth, gamete production, and mortality losses)

I = ingestion rate

E = egestion and excretion rates

R = respiration or metabolic rate

W = the rate at which external work is performed by the organisms

The term W is usually ignored (Wiegert 1968), but for some animals (such as mound-building termites and reef oysters), work may be substantial because these organisms build vertical structures against gravity.

In mature populations, the production equation may attain a steady state, in which no net growth can be measured and annual energy inputs equal losses. Oyster reefs appear to attain this steady-state maturity when they achieve a critical vertical elevation relative to tidal stage or when oyster growth is equal to maintenance costs.

Before a rough energy budget for intertidal oysters is presented, the problems involved in compiling such a budget must be discussed. The terms in the energy budget Equation (1) are measured for an oyster population in the following ways. Net production $P_{(net)}$ is sometimes calculated by measuring the increase in size of experimental animals over a unit of time. This technique requires measuring the individual oysters. Another technique calculates time elapsed between age classes in the size-frequency distribution of a natural population. The latter technique is tedious since age classes quickly become indistinct because of continuous waves of spawning over the warm season.

Total production $P_{(gross)}$ includes gamete production (and release) as well as mortality and predation (and harvesting) between sampling periods. The growth rate of an oyster slows as its gamete production gradually begins to dominate its energy budget and as its respiratory rate "catches up" to its ingestion rate (Rodhouse 1978), as illustrated in Figure A-1.

Ingestion by oysters (I) is usually estimated by measuring the rate of clearance of particles in a suspension to which test animals are exposed for a unit of time. Walne's (1972) experiments using Crassostrea gigas and Ostrea edulis are exemplary in that realistic food concentrations and a wide range of sizes of oysters were used. In addition, Walne used flowing water conditions rather than the usual standing water experiments. Haven and Morales-Alamo (1970) also measured oyster ingestion in a flowing water system but did not use a wide size range of oysters.

Egestion (E) is measured by holding test oysters in trays in which feces and pseudofeces are collected and measured during a known time interval (Haven and Morales-Alamo 1967; Bernard 1974).

The respiration rate of oysters (R) is usually measured by documenting the rate of decline in dissolved oxygen in water in which oysters are immersed or by measuring the change of dissolved oxygen in water as it flows over a population of oysters. The rate of change of CO_2 is not as convenient to measure with oysters, partly because an infrared CO_2 analyzer is required, partly because oysters can fix CO_2 (Hammen 1969), and partly because they can respire anaerobically and release CO_2 from the dissolution of shell carbonate (Hochachka and Mustafa 1972).

One major problem in quantifying individual terms in the oyster energy budget equation is that most terms change in a nonlinear fashion as an oyster (or size class) grows. Small animals operate at higher metabolic rates than large animals. Another problem is that at least five environmental variables affect each term: (1) intertidal elevation, (2) water temperature, (3) levels of food and other suspended matter in the water column, (4) dissolved oxygen levels, and (5) current velocity. To further complicate the picture, the size of the animals and these other variables are interrelated in complex (nonlinear) ways.

Energy budgets are invariably simplified models because of these problems, and the present budget is no exception. Some comments about the variables used and assumptions made follow.

VARIABLES

Tide Stage

Oysters obviously cannot pump water to respire and feed unless they are immersed. Intertidal reef oysters are assumed to be inundated on the average of only 50% of any 24-hr day. Other workers have made similar assumptions on feeding duration, even for subtidal oyster populations. Bernard (1974) assumed 50%; Rodhouse (1978) assumed 70% feeding time.

Water Temperature

Temperature affects all biochemical reactions, including oyster energy consumption. Intertidal oysters are exposed to water temperatures that vary by a factor of about three, from 9° to 31°C (Dame 1970; Bahr 1974). The annual pattern of water temperature variation in coastal South Carolina is illustrated in Figure A-2 (Dame 1970). Over this temperature range oyster metabolism is estimated to vary by a factor of about eight (Bahr 1976).

Food and Other Suspended Matter

Loosanoff (1962) showed that food and other suspended matter significantly altered oyster ingestion rate. Excess turbidity, caused either by suspended organic or inorganic matter, reduces "oyster pumping." It can be assumed that suspended matter in the study area is close to optimum for intertidal oysters and that they are exposed to about 0.01 gC/liter or 0.04 kcal/ liter when inundated (Odum and de la Cruz 1967).

Dissolved O_2

Oyster respiration rates are unaffected by dissolved oxygen concentrations unless the concentration decreases below one-half saturation level (Ghiretti 1966). In other words, dissolved oxygen in estuaries in the study area should normally not affect respiration or feeding rates

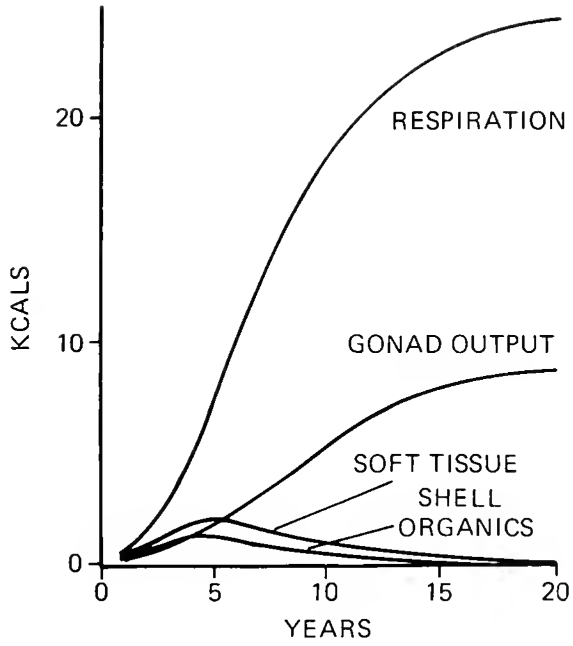

Figure A-1. Age-dependent annual production of soft tissue, shell organics, gonad output, and respiration in an oyster (adapted from Rodhouse 1978).

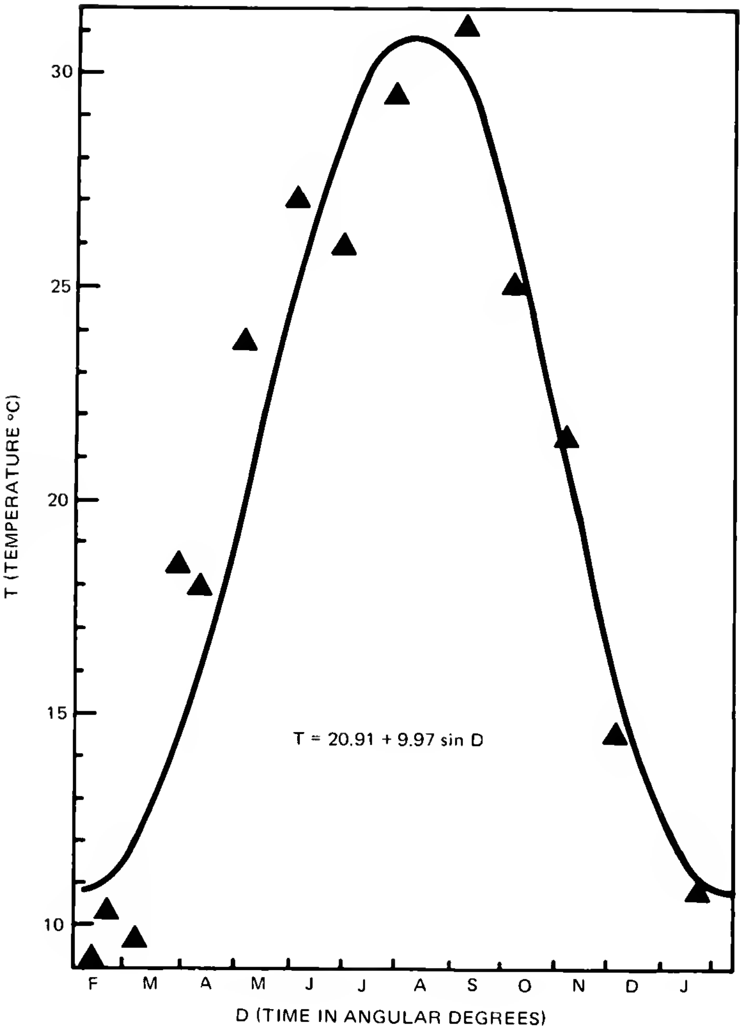

Figure A-2. Seasonal variation in water temperature affecting oyster reefs in South Carolina (adapted from Dame 1970).

but it could become a factor in dredged areas (Frankenberg and Westerfield 1968).

Current Velocity

A positive effect of current velocity on oyster feeding could be surmised from the fact that oyster reefs tend to grow outward toward the middle and more rapidly flowing portion of a tidal stream. Enhancement of oyster feeding as a function of increase in current velocity was demonstrated by Walne (1972).

Given the above assumptions, the additional information most important for the calculation of an energy budget for intertidal oysters is the size-frequency (or weight-frequency) distribution of reef populations and the effect of weight on the energy budget terms.

All of the terms in the energy budget equation for oysters are presumably affected by the size (or weight) of individuals by the following general equation:

$$F = a\,W^{b} \qquad (2)$$

where F = the process rate in energy or matter units
W = the biomass of the oyster (g or kcal)
a and b = constants (represent the effects of temperature and the surface area-to-volume ratio, respectively)

It is generally known that small oysters ingest, egest, respire, grow (and die) at higher rates than do large oysters, and that these rates increase in all oysters with increased temperature. Unfortunately, no general agreement exists in the bioenergetics literature concerning units of biomass. Table A-1 lists some conversion factors for oyster biomass that were compiled from various sources. The numbers are only approximate because the allometric relationships can change with gonadal state or with tidal elevation of the population. Dame (1972a) found that intertidal oysters in North Inlet, South Carolina, had a significantly higher ratio of shell weight to dry meat weight than subtidal oysters had.

Because small oysters process energy at relatively higher rates than large ones, it is important to document the size (biomass) frequency of intertidal oysters in the study area. Bahr (1974) separated reef oysters at Doboy Sound, Georgia, into 32 size classes at 5-mm intervals (2 to 157 mm). He found that the oyster population in the central (higher) portion of several old reefs typically showed a log normal distribution, especially during the late fall. Oysters in the smallest five size classes (up to 19 mm) dominated the population, and oysters above 100 mm were rare. Dame (1976) reported a similar size-frequency distribution of reef oysters in South Carolina, but with generally lower overall populations and reduced dominance of small size classes. Figures A-3 and A-4 illustrate the temporal changes in size-frequency distributions of reef oysters in these two respective studies.

The equation that describes the size-frequency distribution of reef oysters in Doboy Sound, Georgia (Bahr 1974) is as follows:

$$\log_{10} Y = -0.02\,X_i + 2.32 \qquad (3)$$

where Y = the number of oysters per 0.1 m^2 in size class X_i
X_i (i = 2, 7, 12...157) = 5-mm size class

The relation between individual oyster size and biomass from Bahr (unpublished data) is described by another regression equation as follows:

$$Y = 0.02\,X - 1.8 \qquad (4)$$

where Y = $\log_{10}$ afdw (g) of total oysters including shell,
X = height of each oyster in mm

The r^2 of this relationship is 0.84 with 78 degrees of freedom. The experimental animals were collected at eight different times, including all seasons.

To simplify the computation of the energy budget of the reef oyster population, Equations 3 and 4 were used to describe a typical reef oyster population, intermediate in both numbers and biomass. Thus, the numerical dominance of small oysters is offset by the higher biomass of (rare) large oysters, and oysters from 40 to 80 mm in height (mean 60 mm, or 0.25 g afdw) are functionally typical (See Figure

Table A-1. Conversion factors for oyster biomass units (intertidal oysters).

	Whole oyster	
Total wet wt	Wet shell wt	Wet meat wt
100%	72%	28%
Total dry wt	Dry shell wt	Dry meat wt
100%	97.1%	2.8%
Total afdw[a]	Shell afdw[b]	Meat afdw[b]
100%	42%	58%
	Meat only	
Wet wt	Dry wt	afdw[b]
100%	14.9%[a]	12.0[a]

[a] Gametes may comprise up to 50% of this proportion.

[b] afdw = ash-free dry weight.

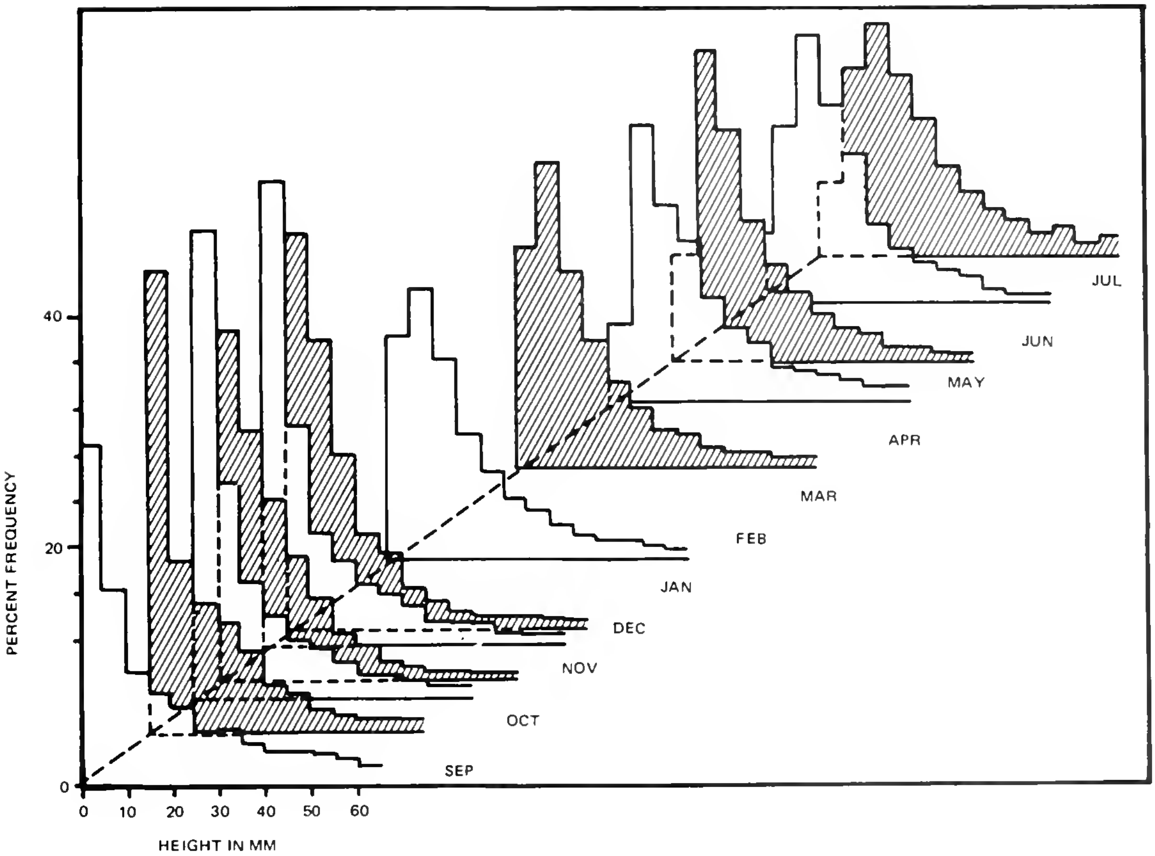

Figure A-3. Seasonal changes in size-frequency distribution of reef oysters in Georgia (Bahr 1976).

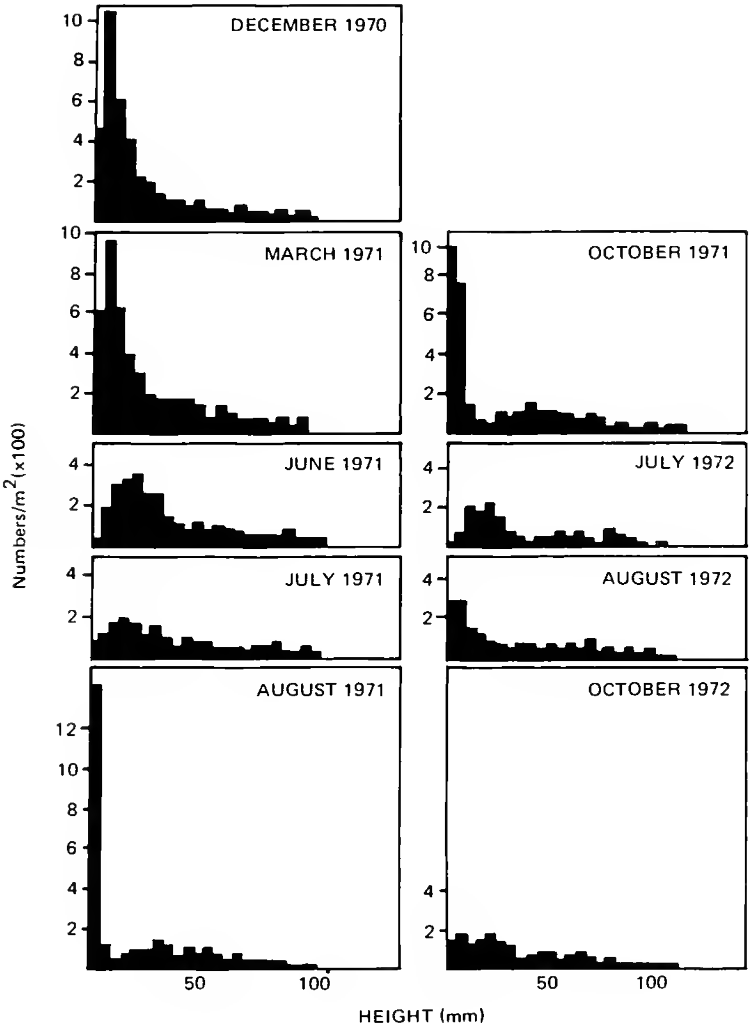

Figure A-4. Seasonal changes in intertidal oyster size-frequency distribution in South Carolina (adapted from Dame 1976).

A-5). The entire oyster biomass of the reef population is therefore considered here as divided among 0.25-g oysters. Bahr (1974) reported that the average biomass of the reef oyster population was 970 g/m^2 afdw (total wt); thus one can postulate a hypothetical reef populated by 60-mm oysters at a density of about 4,000 oysters/m^2. The dry meat weight of an oyster of 0.25 g total afdw would equal approximately 0.18 g (from Table A-1).

Before one estimates the value of the terms of Equation 1 for the "average" reef oyster population, it is appropriate to consider two independent studies that were conducted at approximately the same time and that attempted to measure certain aspects of the energy budget of oyster reefs. Bahr (1974, 1976) and Dame (1970, 1972a, 1972b, 1976, 1979) studied oyster reefs in Georgia and South Carolina, respectively. Significant differences between the studies are compared in Table A-2.

Some differences between the two sets of conclusions are explainable on the basis that test reefs in Dame's studies were significantly lower in the intertidal zone than were the reefs in Bahr's work, although the absolute elevation of Dame's reefs with respect to mean low water (MLW) was not reported. This elevation difference perhaps indicates a significant difference in inundation time, which could explain the higher production reported by Dame. In Dame's studies, oyster production estimates for large oysters were based on holding oysters in trays beneath a pier (presumably shaded) and therefore not in as stressful a setting as on a natural reef. A real difference probably existed in intertidal oyster reef production (higher in South Carolina). The active commercial harvest of South Carolina reef oysters is proof that net production of large oysters occurs there. Lunz (1943) reported that oysters can grow to 3 inches in 2 years in South Carolina reefs. Using a calorific coefficient of 3.3 kcal/g O_2, one can estimate that reef oysters respire the equivalent of 13,000 kcal/m^2/yr. The implication of this high metabolic rate is that the total biomass turns over on the average about once every 0.38 yr, or 2.6 times per year (13,000 kcal/m^2 /yr ÷ 5,000 kcal/m^2).

Energy expended for gamete production increases with the age of a particular oyster but remains about half the respiration rate (Figure A-1). Bernard (1974) estimated that a subtidal population of C. gigas expended as much energy on gamete production as on respiration (Figure A-6). Thus, between 7,500 and 13,000 kcal/m^2/yr of the energy assimilated by reef oysters would be converted to gametes and released into the water column. At least 99% of this energy "investment" would never reach "maturity" but would be consumed by other members of the salt marsh ecosystem.

The rate of external work (W) performed by oysters is the rate at which a unit weight of shell material is elevated above the mud surface, multiplied by its elevated distance. In energy terms this translates into the cost to oysters of producing the shell protein that comprises 1.3% of the total shell dry weight or about 400 g protein/m^2 (2,000 kcal/m^2). The maximum elevated distance is 1.5 m (see Section 3.1), but unfortunately we have no reliable estimate of reef growth rates. Bernard (1974) estimated that subtidal oysters (C. gigas) in British Columbia only expend about 10 kcal /m^2/yr on shell production. This is equivalent to (30 kcal/m^2/yr) for oysters in the study area, calculated by using Bernard's data but correcting for biomass differences between the two different populations. We suspect that this estimate is much too low. The rate of predation on oyster reefs is discussed in Section 3.4.

Energy Budget Summary

An energy budget for reef oysters is presented in the following paragraphs, and the rationale and values for the terms of the equations are discussed. Because of the method used in estimating net production [$P_{(net)}$] in the studies discussed above, we are inclined to agree with the conclusions of the Georgia study. Characteristically, net secondary production of reef oysters is low in the upper portion of high reefs and large oysters are quite old, perhaps even 5 to 10 years or more. In these reefs, somatic growth is balanced by mortality. In lower "immature" reefs, $P_{(net)}$ is undoubtedly significant. Because the South Atlantic Bight includes large areas of low "immature" reefs, especially

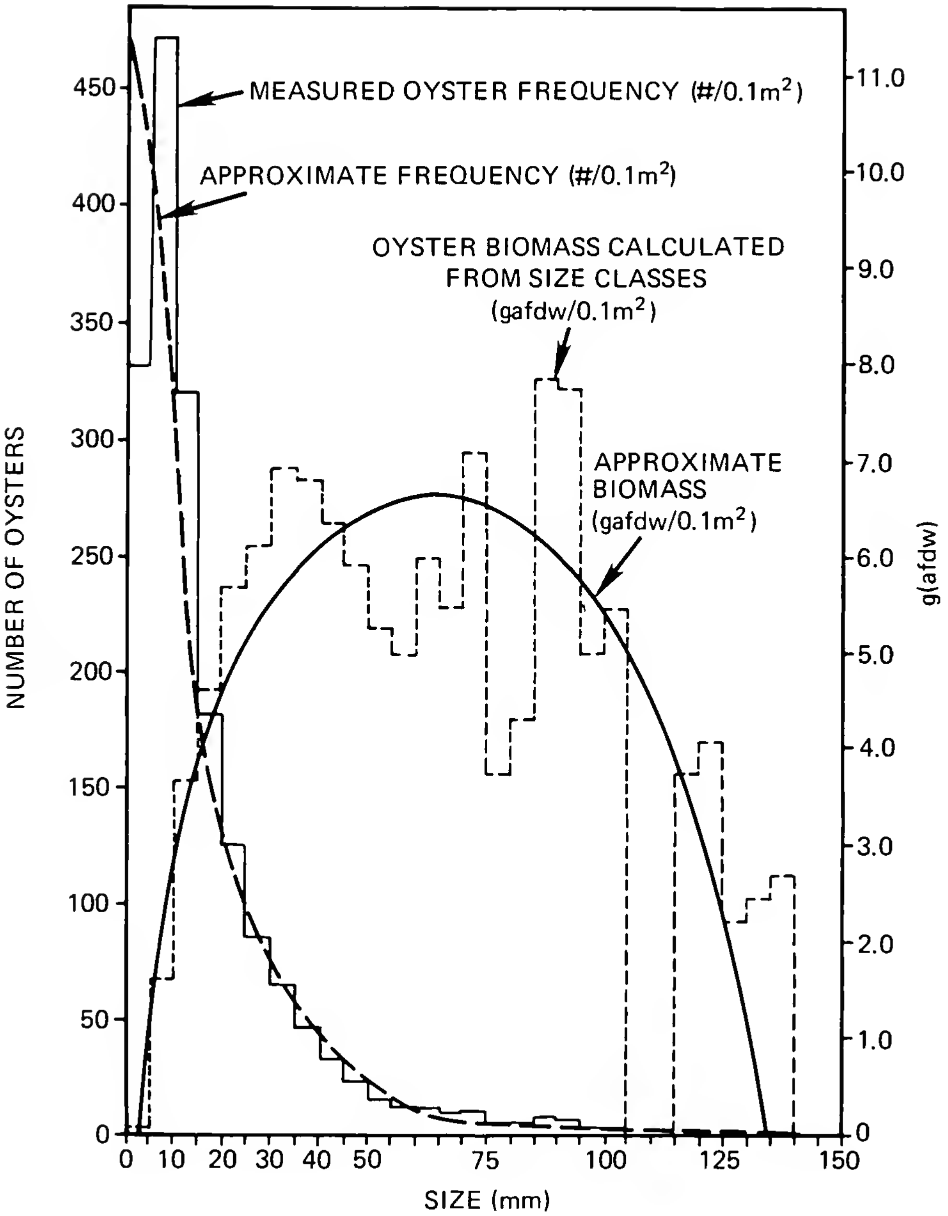

Figure A-5. Reef oyster height-frequency relationship and cumulative biomass curves.

Table A-2. Comparison of two sets of oyster reef energy parameters collected within the study area.[a]

Parameter	Sources Bahr (1974, 1976) Georgia	 Dame (1976) South Carolina
$P_{(gross)}$[b]	---	4,500/yr
$P_{(net)}$	0-1,000/yr [c]	3,460/yr
R	13,000/yr	6,000/yr
B[d]	5,000 (total oysters)	2,050 (meat)
F[e]	10,000-20,000	1,000-4,400

[a] All figures unless otherwise noted represent kcal/m^2 (rounded).

[b] Includes growth, mortality, and gonadal products.

[c] Minimum P from "old" high reef, maximum P from "young" low reef.

[d] B = biomass.

[e] F = oyster frequency (# /m^2).

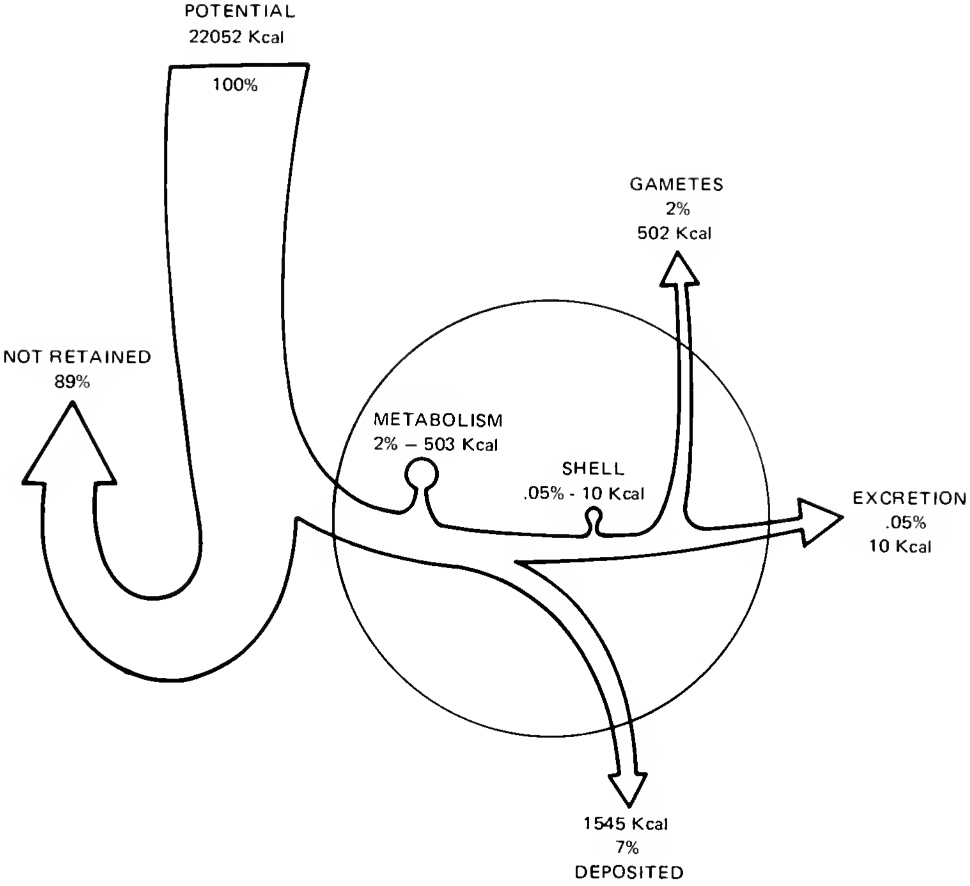

Figure A-6. Schematic representation of percentage distribution of potential food expressed in kilocalories for 1-year period in 1 m^2 of subtidal *Crassostrea gigas* population (adapted from Bernard 1974).

in South Carolina, we will assume the $P_{(net)}$ of 1,000 kcal/m^2/yr is a conservative estimate.

The ingestion rate (I) of a reef population, as expressed by the "functionally average" 60-mm oyster, approximates the ability of oysters in the population to filter about 100 ml of water per minute (extrapolated from values reported by Walne [1972] for *C. gigas* of the same height). The feeding experiments by Walne were carried out at temperatures approximating the median level for our study area (19° C). During one day (12 hours of pumping time), the oysters occupying a typical square meter of reef could filter 288,000 liters of water (4,000 oysters x 0.1 liter/min x 12 hr x 60 min). With an average POC load of 0.01 g/liter assumed (Odum and de la Cruz 1967), this would equal a potential maximum ingestion rate of 300 gC/m^2/day, or 1 x 10^6gC/m^2/yr (5 x 10^6 kcal/m^2/yr) if the oysters filtered at 100% efficiency. If filtration is 40% efficient (Haven and Morales-Alamo 1970), ingestion of organic carbon would occur at the rate of about 2 x 10^7 kcal/m^2/yr. Only a small fraction of this carbon would be assimilable, however. The remainder would be egested and biodeposited as feces or pseudofeces, or excreted as organic nitrogen. Mathers (1974) reported that large oysters of the species *C. angulata* could completely filter water at the rate of 54 ml/g (wet wt)/hr or about 0.45 liter/g (afdw)/hr. This translates to about 2 x 10^6gC/m^2/yr or 1.0 x 10^7 kcal/m^2/yr for reef oysters, twice the estimate of Walne (1972). These two estimates illustrate the approximate nature of this measurement.

Egestion, excretion, and pseudofecal production (E) by reef oysters can be expressed in terms of a reef population of 60-mm oysters. Bernard (1974) reported that large specimens of *C. gigas* (∿10 g dry wt of meat) produced about 5.9 x 10^4 kcal per oyster per year as biodeposits. If an extrapolation were made to the 60-mm reef oyster (dry meat weight = 0.18 g), we could conservatively predict that it would biodeposit the equivalent of 1,000 kcal/yr, or 4 x 10^6 kcal/m^2/yr for the entire oyster population. If one judges by the estimated maximum ingestion rate, however, (see above) this estimate is equal to 80% of ingestion, implying a 20% assimilation rate (A = I-E). This estimate may be high because only a small portion of the total of all ingested carbon can be assimilated by oysters.

Of the terms in Equation (1), respiration rates (R) are best known for reef oysters. Bahr (1974, 1976) calculated that the reef oyster population accounted for approximately 48% of the mean oxygen uptake of the total reef community, or about 3,900 gO_2/m^2/yr. This estimate was derived by combining individual oyster respirometry experiments (carried out seasonally at ambient temperatures and on different sized animals) with the relative proportion of the reef oyster biomass represented by each size class.

From data reported by Dame (1970) and Bahr (1974), the following equation describes the relationship between oyster oxygen uptake and biomass at the approximate median water temperature in the study area (20° C).

$$Y = 0.53X^{0.71} \qquad (5)$$

where Y = mg O_2 used per hour and
X = total afdw

Solving this equation for a functionally typical oyster of 0.25 g afdw, one would predict that a single oyster would consume 0.20 mg O_2/hr. When this figure is multiplied by 12 hours of inundation time/day, 365 days/yr, and 4,000 oysters/m^2, the resulting estimate of oxygen requirements is 3,500 g O_2/m^2/yr, very close to the above estimate of 3,900 g O_2/m^2/yr (Bahr 1974).

The final estimates of the parameters in the energy budget Equation (1) are presented in Section 2.5 and illustrated in Figure 12.

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16. Abstract (Limit: 200 words)

The functional role of the intertidal oyster reef community in the southeastern Atlantic coastal zone is described. This description is based on a compilation of published data, as well as some unpublished information presented as hypotheses.

The profile is organized in a hierarchical manner, such that relevant details of reef oyster biology (autecology) are presented, followed by a description of the reef community level of organization. Then the reef community is described as a subsystem of the coastal marsh-ecosystem (synecology). This information is also synthesized in a series of nested conceptual models of oyster reefs at the regional level, the drainage basin level, and the individual reef level. The final chapter includes a summary overview and a section on management implications and guidelines.

Intertidal oyster reefs are relatively persistent features of the salt marsh estuarine ecosystem in the southeastern Atlantic coastal zone. The average areal extent of the oyster reef subsystem in this larger ecosystem is relatively small (about 0.05%). This proportion does not reflect, however, the functional importance of the reef subsystem in stablizing the marsh, providing food for estuarine consumers, mineralizing organic matter, and providing firm substrates in this otherwise soft environment.

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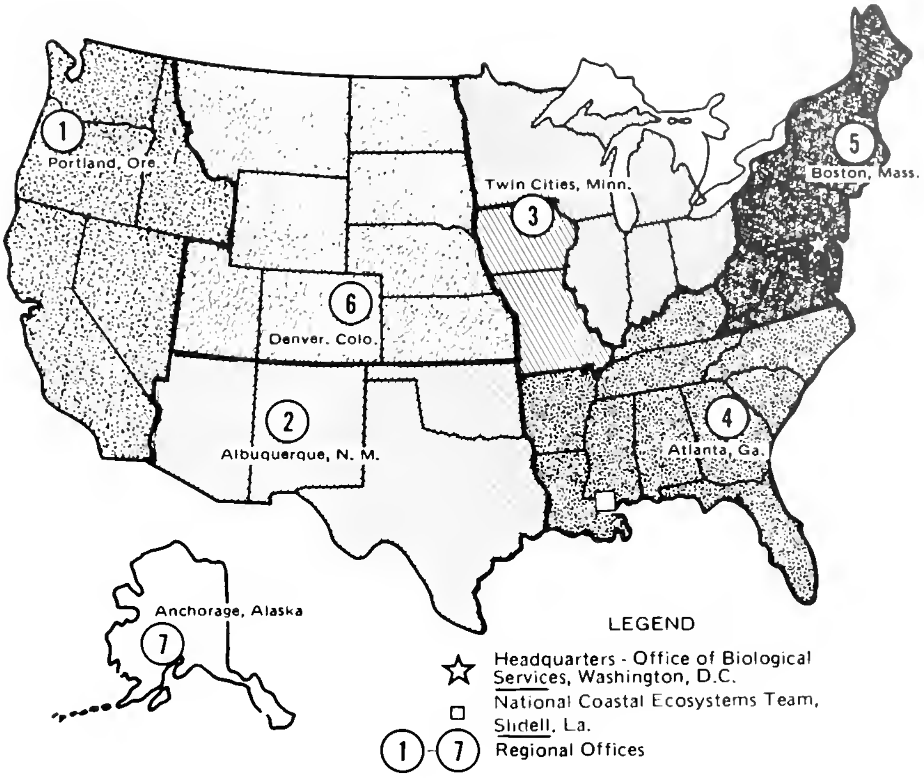

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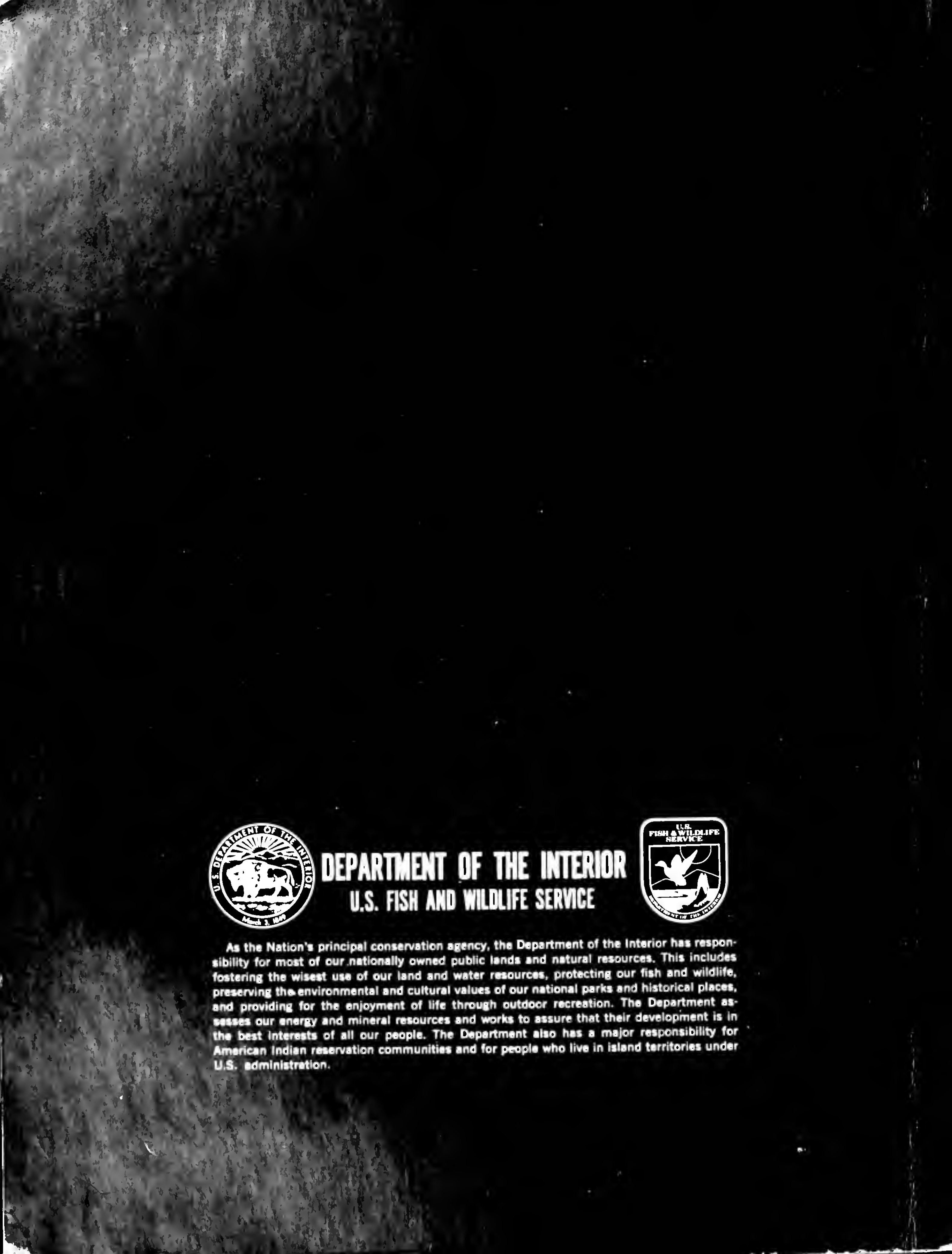

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