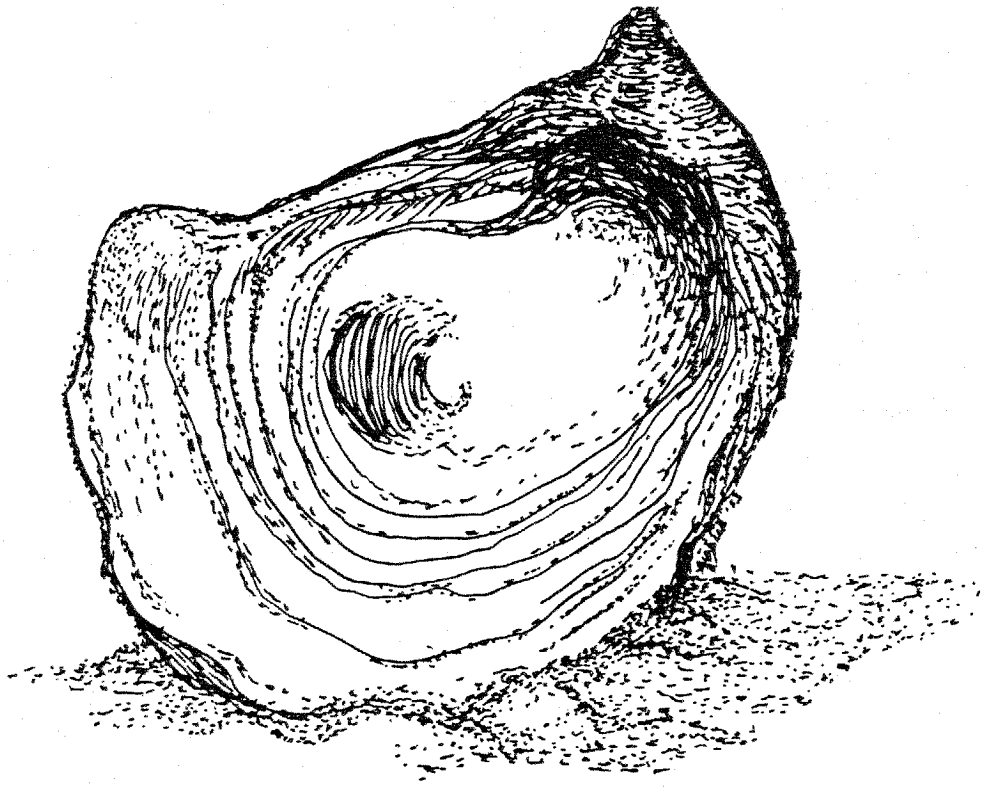
FWS/OBS-82/10.57
SEPTEMBER 1983

HABITAT SUITABILITY INDEX MODELS: GULF OF MEXICO AMERICAN OYSTER



Fish and Wildlife Service
U.S. Department of the Interior

FWS/OBS-82/10.57
September 1983

HABITAT SUITABILITY INDEX MODELS: GULF OF MEXICO AMERICAN OYSTER

by

Edwin W. Cake, Jr.
Oyster Biology Section
Gulf Coast Research Laboratory
Ocean Springs, MS 39564

Project Officer

Carroll L. Cordes
National Coastal Ecosystems Team
U.S. Fish and Wildlife Service
1010 Gause Boulevard
Slidell, LA 70458

Performed for
National Coastal Ecosystems Team
Division of Biological Services
Research and Development
Fish and Wildlife Service
U.S. Department of the Interior
Washington, DC 20240

This report should be cited as:

Cake, E.W., Jr. 1983. Habitat suitability index models: Gulf of Mexico American oyster. U.S. Dept. Int. Fish Wildl. Serv. FWS/OBS-82/10.57. 37 pp.

PREFACE

The habitat suitability index (HSI) model presented in this report on Gulf of Mexico stocks of the American oyster is intended for use in environmental impact assessment and habitat management. The model was developed from a review and synthesis of existing information based on methodology prescribed by the U.S. Fish and Wildlife Service (1981) and is scaled to produce an index of habitat suitability between 0 (unsuitable habitat) and 1 (optimal suitable habitat). Assumptions used to transform habitat use information in the HSI model and guidelines for model applications, including techniques for measuring the model variables, are described.

The HSI model presented herein is a hypothesis of species-habitat relationships, not statements of proven cause-and-effect relationships. The model has not been field-tested, but it has been applied to six hypothetical sets of data that are presented and discussed. For this reason, the U.S. Fish and Wildlife Service (FWS) encourages model users to convey comments and suggestions that may increase the utility and effectiveness of this habitat-based approach to fish and wildlife planning. Please send any comments or suggestions that you may have on the American oyster HSI model to:

National Coastal Ecosystems Team
U.S. Fish and Wildlife Service
1010 Gause Boulevard
Slidell, LA 70458

CONTENTS

ACKNOWLEDGMENTS

The development of this habitat suitability index model was evaluated by Winston Menzel, Florida State University Department of Oceanography, Tallahassee; and Gordon Gunter, Gulf Coast Research Laboratory (GCRL) Physiology Section, Ocean Springs, Mississippi. Their reviews, assistance, and cooperation are gratefully acknowledged. Carroll L. Cordes, Rebecca Howard, Michael Brody, and Gaye Farris, U.S. Fish and Wildlife Service (FWS) National Coastal Ecosystems Team, provided technical assistance in the formulation of the model and the preparation of this publication. Appropriate comments and suggestions were contributed by GCRL biologists Walter Brehm, William J. Demoran, and James T. McBee. The author gratefully acknowledges the reviews and suggestions received from the following individuals: Gerald Bodin, FWS, Lafayette, Louisiana; Michael Brim, FWS, Panama City, Florida; Philip A. Butler, Environmental Protection Agency Laboratory, Gulf Breeze, Florida; Mark Chatry and Ronald Dugas, Louisiana Department of Wildlife and Fisheries, St. Amant Marine Laboratory, Grand Terre; C. Austin Farley and Frederick G. Kern, III, National Marine Fisheries Service (NMFS), Northeast Fisheries Center Laboratory, Oxford, Maryland; Bruce G. Halstead, FWS, Houston, Texas; Dexter S. Haven, Virginia Institute of Marine Science, Gloucester Point; Clyde L. MacKenzie, Sandy Hook NMFS Laboratory, Highlands, New Jersey; and Donald Meineke, FWS, Corpus Christi, Texas. Funds for the formulation of the model and for the preparation of this publication were provided primarily by the Fish and Wildlife Service and secondarily by the Gulf Coast Research Laboratory. The author expresses his sincere appreciation to Lucia O'Toole, Cindy Dickens, and Linda Paulson for their assistance with typing and illustrations.

AMERICAN OYSTER (Crassostrea virginica [Gmelin])

INTRODUCTION

The American or eastern oyster (Crassostrea virginica [Gmelin]), a bivalve in the family Ostreidae, is an important commercial and recreational species along the Atlantic and Gulf of Mexico coasts of North America and other areas (U.S. Pacific coast and Hawaii) where it has been introduced (Galtsoff 1964). It evolved over the last 25 million years (Miocene and Pliocene epochs) from an ancestral, Atlantic-Pacific species that also gave rise to the Central American oyster of the Pacific coast, Crassostrea corteziensis (Hertlein) (Stenzel 1971). It evolved to fill a eurytopic niche in coastal estuaries where it forms massive reefs in nearshore bays, sounds, lagoons, and river mouths. Its existence depends on suitable substratum (cultch and firm bottom sediments) and acceptable salinity conditions. The location and distribution of oyster reefs in a salt marsh-estuarine ecosystem are not accidental; rather, they result from the interaction of many biological, chemical, geological, and physical processes (Butler 1954a; Marshall 1954; Bahr and Lanier 1981).

As a sessile (sedentary), benthic mollusk, the American oyster is susceptible to adverse natural and artificial environmental modifications and pollution within those estuarine habitats. That susceptibility is, however, tempered by its ability to withstand a wide range of ambient environmental conditions. When unfavorable environmental conditions prevail in one area, the species survives by establishing new populations in nearby areas that become suitable as environmental conditions change. Because of environmental disruption of estuarine ecosystems by human activities (e.g., dredging, filling, freshwater flow modifications, pollution discharges), oyster populations and their traditional habitats are being reduced. These human activities eliminate oyster reefs, cause flood deaths, permit high salinity predator invasions, and otherwise kill the oysters (and their larvae) or render them unfit for human consumption.

Adult American oysters form three principal reef types in the northern Gulf of Mexico: fringe, string, and patch. Reefs are classified by their configurations and location relative to the nearest shoreline (Price 1954; Stenzel 1971). Fringe reefs are adjacent to shore, usually parallel to both the shore and the predominant tidal currents, and are common along the sides of finger-like branches of estuaries. String (or linear ridge) reefs are usually long and narrow structures, forming series of echelons across the mouths of rivers, bays, and sounds and are located at right angles to tidal currents; they may also be controlled by tidal amplitude and wind currents. Patch (or tow-head) reefs exist in sounds, bays, and lagoons and they have irregular but fairly compact outlines; their size and location depend on the availability of suitable substrates (cultch) (Price 1954; Stenzel 1971). In high salinity areas incrustations of oysters may occur in intertidal locations or on shell out-croppings or other forms of solid substrate (e.g., jetties, groins, pilings, seawalls) (Menzel 1955).

Distribution

The American oyster occurs in nearshore, estuarine ecosystems from the Gulf of St. Lawrence in the Canadian maritime provinces to the Yucatan coast of Mexico, including the entire Gulf of Mexico coast (Galtsoff 1964; Abbott 1974). Butler (1954a) noted that approximately 3626 km^2 (1400 mi^2) of coastal waters in the Gulf of Mexico are suitable for and more or less populated with American oysters. Gunter (1951) believed that C. virginica occurred along the coast of Brazil, and Abbott (1974) considered the Brazilian oyster (C. brasiliana [Lamarck]) as a synonym of C. virginica. According to Stenzel (personal communication to Winston Menzel, Florida State University, Tallahassee), however, C. brasiliana is a valid species. South of the Yucatan Peninsula where no large rivers exist to produce the traditional estuarine habitat preferred by the American oyster, it is replaced by the Caribbean or mangrove oyster (C. rhizophorae [Guilding]) (Stenzel 1971). Successful hybridization studies by Menzel (1973), however, indicated that the American and Caribbean oysters are so closely related genetically that the Caribbean may be a subspecies (C. v. rhizophorae) of the American. The range of the American oyster may, therefore, extend throughout the Gulf of Mexico and Caribbean and perhaps along the northern coast of South America.

The American oyster has been introduced as a mariculture species to the Pacific coast of North America, the Hawaiian Islands, Japan, Australia, and the United Kingdom (Ahmed 1975), but with only limited success in most instances. The commercial hatchery production of this species and its ability to withstand extended transport may lead to a cosmopolitan range in the future. The species can, in fact, survive and flourish wherever environmental conditions approximate those of its traditional Atlantic or Gulf of Mexico coast habitat. Adverse competition, predation, and disease may be the only factors that prevent C. virginica from becoming established throughout the world's temperate to subtropic regions.

Life History Overview

Spawning. American oysters may spawn in the northern Gulf of Mexico during all but the coldest months (December through February) (Butler 1954a). Mature gametes are normally present in oysters from March through November but may occur during all winter months if water temperatures are high enough (Winston Menzel, Florida State University, Tallahassee; pers. comm.). Males are usually the first to spawn, and their spermatozoa and gamones stimulate other males and females to spawn. Eggs and sperm are liberated directly into the water column, and fertilization is external (Galtsoff 1964). Mature oysters spawn numerous times during their extended reproductive season in the northern Gulf of Mexico, but spawning is most prevalent in late May and early June (as water temperatures increase) and again in September (as water temperatures decrease) (Pollard, 1973). Whether the late spring spawning peak (Hayes and Menzel 1981) or the late summer-early fall spawning peak (McGraw 1980) is the more pronounced of the two depends on ambient conditions.

Fecundity depends on the size, state of maturation, and condition (health) of the female, and on the ambient water conditions. Various-sized females released from 15 x 10^6 to over 100 x 10^6 eggs during single, incomplete spawning events (Galtsoff 1930), and during one spawning season, large females may release more than 170 x 10^6 eggs (Galtsoff 1964). During heavy spawning, the

water over oyster reefs, especially shallow water reefs, may become "milky" with gametes (Galtsoff 1964). The duration of any spawning event depends on the physiological state of the oysters and the ambient water conditions (Galtsoff 1964).

Egg. The eggs of the American oyster are pear-shaped (55 to 75 µm by 35 to 55 µm) when spawned, but become globular after fertilization (Galtsoff 1964). Spawned eggs are demersal; they sink to the bottom and are transported by currents and waves; they remain demersal until the first free-swimming larval form develops (Galtsoff 1964).

The egg stage of the American oyster is brief. Embryological development begins immediately after fertilization. Depending on the condition of the egg, the ambient salinity, temperature, and oxygen content of the water, and other environmental factors, the embryo becomes a ciliated, trochophore larva in several hours (Winston Menzel, Florida State University, Tallahassee; pers. comm.).

Larva. Planktonic larvae of the American oyster develop within the estuarine water column and, depending on ambient water condition (e.g., salinity, temperature, and food availability), require about 2 weeks to metamorphose (Galtsoff 1964). The first recognizable larva is the trochophore, a ciliated, shell-less stage that lasts 24 to 48 hr, depending on the water temperature, and is 40 to 50 µm in its greatest dimension. The trochophore larva is free-swimming (drifting) and requires waterborne food particles.

The trochophore larva develops into the first of a series of free-swimming and feeding veliger larvae. The veliger larva is characterized by two semicircular folds or lobes bearing cilia (the velum) and a pair of thin, transparent shells (the prodissoconch). The velum is a locomotory and filter-feeding organ, and the prodissoconch encloses and protects the developing larva. The first veliger stage is known as the straight-hinge or D-stage larva; its length is 70 to 75 µm. Subsequent veliger stages are termed the umbo larva because of the pronounced umbone region of the prodissoconch, and the pediveliger because of the well-developed "foot." The pediveliger usually exceeds 300 µm in diameter and remains free-swimming. Just prior to metamorphosis (settling and attachment), the veliger develops two eye spots (that aid in selecting an acceptable location for attachment) and is termed an eyed-pediveliger. Shortly after metamorphosis, the newly attached oyster, the spat, loses its velum, foot, and eye spots as it begins a sedentary life (Galtsoff 1964).

Throughout larval development veligers are passively transported via water currents within their estuary. They are able to remain in water levels of acceptable salinity by migrating vertically into or out of the salt wedge produced by tidal currents (Carriker 1951; Galtsoff 1964; Wood and Hargis 1971). Many larvae are "lost" from their estuary into adjacent waters of the Gulf of Mexico or into otherwise unsuitable nearshore and low salinity areas. Many are also transported into adjacent estuarine areas (e.g., from the Louisiana marshes into the Mississippi Sound) and have a definite impact on the oyster recruitment and production in those areas. Large numbers are also consumed by or inadvertently killed by other filter-feeding invertebrates.

The abundance and planktonic dispersal of American oyster larvae ensure the species' survival in favorable areas of an estuary, even if traditional reef

areas become unacceptable because of adverse environmental conditions (e.g., pollution, estuarine modifications). Butler (1954a) reported that oyster larvae may constitute as much as 50% of the plankton volume in Mississippi Sound during the spawning season. Planktonic dispersal also ensures oyster survival in the event that adverse climatological conditions (e.g., flooding, drought) reduce large reefs to non-productive bottoms.

As the eyed-pediveliger larva nears the end of its planktonic development, it passively uses tidal currents, the salt wedge, and its ability to migrate vertically to "select" the optimal environment for metamorphosis (settling and attachment). It ceases to swim and creeps over the substrate with its foot until locating a suitable attachment point in an area of reduced light (inside of an empty shell, on the underside of a piece of cultch, or low in the water column). "Mature" larvae are normally sensitive to strong light and are slightly negatively phototactic (Nelson 1926; Ritchie and Menzel 1969).

At metamorphosis the mature larva attaches its left valve (shell) to the cultch with a small amount of cementing fluid (from its pedal byssus gland) that sets in a few minutes (Nelson 1924; Galtsoff 1964). Metamorphosing oyster larvae are gregarious and tend to attach in large groups on common cultch where other larvae have already attached or in the presence of mature oysters (Galtsoff 1964; Crisp 1967; Hidu 1969). Hidu et al. (1978) demonstrated that extrapallial (mantle) fluid from any oyster will act as a pheromone (attractant) in the gregarious setting of American oyster larvae. Once attached to the cultch, the tiny (300-µm) oyster is referred to as a spat during its initial growth phase. Butler (1954a) reported spatfall accumulations of up to 155/cm^2 (1000/inch^2) at Pensacola, Florida, during a single season.

Juvenile. A true juvenile stage, per se, does not really exist in the life cycle of the American oyster because gonadal development and gametogenesis begin within a few weeks of metamorphosis (Butler 1954a; Galtsoff 1964; Hayes and Menzel 1981), especially among early summer spat. Those that metamorphose during the fall may not undergo initial gametogenesis until the following spring (year 2).

During the spat stage, shell growth is rapid and depends on food availability, prevailing water temperatures, and the relative amount of feeding time available (especially among interidal oysters) (Stenzel 1971). The new shell follows the contour of the cultch material to which the spat is attached. The shell is relatively thin, but the mass of the cultch usually provides protection against most predators (e.g., blue and stone crabs) that crush the shells. Following the initial rapid growth phase, the spat shells begin to thicken and the shape of the young oyster begins to resemble that of the mature oyster. During this stage the oyster can be transplanted from "seed reefs" to grow-out areas without atmospheric exposure problems (e.g, desiccation, heating, cooling) and is often referred to as a seed oyster.

Adult. American oysters may become adults (i.e., sexually mature and capable of spawning viable gametes) within 4 to 12 weeks of settlement (metamorphosis), thereby permitting spawning by young of the year and production of two generations of oysters per year in the northern Gulf of Mexico (Menzel 1951; Hayes and Menzel 1981). Fecundity, however, is relatively low during that initial gametogenesis because of the oyster's size. Sexual maturation is primarily temperature-dependent (Galtsoff 1964), and a young-of-the-year oyster

setting in a Gulf of Mexico estuary during late summer or fall may not mature until its second year. Those that attach during spring or early summer will spawn during their first year (Hayes and Menzel 1981). One-year and older oysters will spawn in the northern Gulf of Mexico from about early spring through early fall (Butler 1954a; Hayes and Menzel 1981).

The American oyster exhibits protandrous hermaphroditism. Young oysters are predominantly males; but many precocious males become females during subsequent breeding seasons (Coe 1934; Galtsoff 1961, 1964). The primary gonad of a 12- to 16-week-old oyster from the middle U.S. Atlantic coast is bisexual and has oogonia and spermatogonia in the same follicles. Because the spermatogonia tend to proliferate more rapidly than the oogonia, the gonad becomes predominantly male in appearance. Even a "true male" retains a small number of oocytes. The transformation of a bisexual gonad into an ovary begins before the formation of spermatozoa, and spermatogenesis is thereby inhibited by growth of the oocytes (Galtsoff 1961, 1964). Of 1,070 yearling oysters examined from Long Island Sound and Great South Bay by Coe (1934), 81.2% were males, 7.0% were females, 11.0% were immature, and 0.8% were true hermaphrodites. (Functional hermaphroditism is relatively rare in C. virginica; Burkenroad [1931b] found that 1% of Louisiana oysters were hermaphrodites.)

After spawning, the gonad of C. virginica retains its bisexual potency and its sex may alternate (Galtsoff 1964). Sexual reversal is common among non-yearling oysters (Galtsoff 1961, 1964). During their second breeding season, the number of male oysters generally exceeds that of females, but the sex ratio approaches equality. Among 57 individuals of C. virginica studied by Needler (1942) for 4 years, a high proportion remained males while others changed sex at least once, and some changed sex every year. Galtsoff (1961) found that of 68 oysters that survived through their fourth breeding season, 18 altered their sex once, 10 changed twice, 2 changed three times, and 1 changed four times. The initial and final male-to-female sex ratios for Galtsoff's (1961) study were 2.9:1 and 1:1.8, respectively. Galtsoff (1961) also found that older oysters tended to be predominantly females, but he concluded that females survived longer than males rather than becoming females more often as older individuals.

Dorso-ventral shell growth ("length") of 75 mm (3 inches) or more is common for 1-year-old oysters in the northern Gulf of Mexico (McGraw 1980). Growth of oysters in the Gulf of Mexico continues throughout the winter (unlike that of more northern oysters), but may slow somewhat during severe winters. Growth slows considerably in large, older oysters when metabolic reserves are needed to maintain reproductive activities and soft parts (Stenzel 1971). After about 8 years the oyster's soft parts stop growing, and the volume of the mantle/shell cavity remains constant. Shell deposition, however, continues so that the shell thickens and its height ("length") and weight increases, but at a slower rate than previously (Stenzel 1971). Gulf of Mexico oysters will survive for 10 or more years provided that they do not succumb to harvesting, predation, diseases, or burial (caused by adverse sedimentation rates). Fossil Miocene species of Crassostrea have been aged (from annual growth layers within the hinge ligament) at up to 43 years for C. boureoissi (Remond) from California and 47 years for C. gryphoides (von Schlotheim) from Europe (Stenzel 1971).

SPECIFIC HABITAT REQUIREMENTS

American oysters occupy various estuarine habitats along the Gulf of Mexico coast depending on substrate (cultch) availability, bottom firmness, salinity, and current patterns (Butler 1954a). They occupy those habitats during all life stages. Since all oyster developmental stages normally occur within the environmental tolerance ranges of the adult, habitat requirements will be presented primarily for that stage. Other selected environmental requirements will be discussed because of their applicability to the proposed habitat suitability index model.

Spawning/Egg

Mass spawnings of gulf oysters occur when water temperatures reach or exceed approximately 25°C (77°F) (Hopkins 1931; Ingle 1951; Menzel 1955; Hayes and Menzel 1981). Spawning is synchronous: numerous adjacent oysters participate in response to short-term temperature fluctuations of ±5°C (±10.6°F) (Loosanoff and Davis 1963) and in response to gametogenic byproducts (gamones) that act as biochemical stimuli (Galtsoff 1964). Optimal spawning salinity ranges from 10 to 30 parts per thousand (ppt).

In addition to the ambient water conditions that control spawning, several artificial environmental perturbations may adversely affect spawning of mature oysters as well as affect other life stages. Spawning may be temporarily delayed by excessive turbidity (e.g., heavy silt loads, >50 Jackson Turbidity Units [JTU]) from flood waters or adjacent dredging and filling activities and from the untimely release of large volumes of freshwater from upstream flood-control structures (Galtsoff 1964; Davis and Hidu 1969).

High turbidities clog oysters' gills and interfere with respiration, filter-feeding, and ultimately spawning. The release of large volumes of toxic pollutants (e.g., hydrocarbons, chemical wastes, and industrial effluents) and the complete burial by dredge spoils may negate spawning because of physiological stress or mortality (Gunter 1953; Mackin 1961a; Mackin and Hopkins 1961; Mackin and Sparks 1961; May 1972; Woelke 1960a, 1960b). Toxic pollutants physiologically stress and may kill larvae and adults or suppress or prevent spawning of "ripe" adults if the pollutants are concentrated. Water-soluble oil fractions also stress and may kill oysters of all sizes and ages depending on length of exposure; nonsoluble fractions may coat and/or bury oysters and interfere with all life processes (Blumer et al. 1970; Julia Lytle, Environmental Chemistry Section, Gulf Coast Research Laboratory, Ocean Springs, MS, pers. comm.). Industrial wastes such as sulfite waste liquor in paper-mill effluents may interrupt reproduction and/or interfere with normal larval development (Hopkins et al. 1931; Woelke 1960b).

Gametes (eggs and sperm) are usually not subjected to deleterious water quality problems (e.g., low dissolved oxygen, low salinities, excessively high or low pH's) for the following reasons: (1) optimal spawning conditions generally prevail in the water surrounding sexually mature oysters in order for spawning to occur, (2) oyster eggs are normally fertilized shortly after spawning, and (3) larval development commences rapidly. If, however, some gametes do experience adverse water quality problems, their massive numbers and repetitious spawnings ensure survival and successful colonization of traditional bottoms when normal estuarine conditions return.

Larva

Salinity. As eurytopic organisms, American oyster larvae are able to withstand a wide range of ambient salinities. Their salinity tolerance depends on the salinity at which the parents were held during gametogenesis (Davis 1958). The salinity range for the development of normal, straight-hinge (D-stage) veliger larvae from eggs of low salinity oysters (8.7 ppt) was 7.5 to 22.5 ppt, whereas the range for eggs from oysters conditioned at 26.0 to 27.0 ppt was from 12.5 to above 35.0 ppt (Davis 1958). Larval growth is affected by reduced salinities; growth at 7.5 to 10.0 ppt is appreciably slower than that of sibling larvae reared at salinities of about 15.5 ppt (Calabrese and Davis 1970). Growth of oyster larvae is not inhibited, however, after a drop from 27.0 to 15.0 ppt (Davis 1958).

Metamorphosing oyster larvae will set (attach) at salinities between about 5 and 35 ppt with optimal setting occurring between 10 and 30 ppt and maximal setting at 18 to 22 ppt (Carriker 1951; Davis 1958; Calabrese and Davis 1970; Chatry and Dugas MS.). Chatry and Dugas analyzed 11 years (1971-1981) of spatset data from Louisiana and found that 85% of the spatset occurred between June and September when mean salinities ranged from 16 to 24 ppt. Setting intensities were consistently high (> 3 spat/cm^2) between 16 and 24 ppt with a peak of more than 12 spat/cm^2 between 20 and 22 ppt.

Temperature. Water temperatures that are considerably above or below the seasonal norms shorten or lengthen respectively, the normal 2-week larval development period. In cool water (15° to 20°C [59° to 68°F]), larvae may remain planktonic for 6 weeks or more under hatchery conditions (pers. observ.).

Food. The planktonic trochophore larvae require essentially the same optimal water quality as the spawned eggs, but in addition, they require waterborne food particles (e.g., algae, small detrital particles).

Oyster veliger larvae are primarily phytoplanktivores. With the aid of their velum (ciliated lobes), they filter small green algae, flagellates, detrital particles, and bacteria-laden particles over a size range of 1 to 3 µm from the water column (Galtsoff 1964). These foods are usually abundant in most estuaries when oyster larvae are present and are not normally limiting factors. Heavy concentrations of some algal species such as Chlorella may be deleterious to larvae that ingest the algae but receive no nutritional benefit from them (Galtsoff 1964).

Substrate. When the mature veliger larva is ready to metamorphose (attach to the substratum), a pair of eye-spots develop that aid the larva in "selecting" the proper (low) light conditions. At metamorphosis the larva requires clean, sediment-free cultch materials that are not heavily fouled with other encrusting organisms (e.g., bryzoans, barnacles, mussels, algae). It will attach to a variety of materials including occupied or empty oyster shells, calcareous remains of other mollusks, wooden materials, rocks, gravel, and solid refuse (Hedgpeth 1953; Butler 1954a; Lunz 1958; Galtsoff 1964; Gunter and Demoran 1971; MacKenzie 1977, 1981, 1983; Gunter 1979b). Optimal cultch material includes shells of live or recently dead oysters and calcareous remains of other estuarine mollusks (Butler 1954a; Galtsoff 1964; Gunter and Demoran 1971; MacKenzie 1977, 1981, 1983). Productive reefs usually contain 10% or more (by volume) of such shell materials (Hoskin 1972). A 1- to 2-mm (0.04- to

0.08-inch) layer of sediment on potential cultch will prevent the attachment of the mature larva (Galtsoff 1964; MacKenzie 1981, 1983).

Adult, Seed, and Spat

Butler (1954a) reported that successful colonies of oysters occur at depths from 0.3 m (1 ft) above mean low water to 12 m (40 ft). Once attached to solid substratum, the oyster cannot alter its habitat position. It remains on that reef, bed, piling, or rock until death or until transplanted elsewhere by oyster culturists, relayers, or management agencies. Because of its sessile nature, the oyster has evolved considerable tolerance with respect to such variables as salinity and temperature.

Except for differences in shell size and thickness, spat and small, immature seed oysters are not appreciably different from larger adult oysters on the same reef or in the immediate vicinity with regard to specific habitat requirements. They are subjected to the same ambient water conditions, respond to the same external stimuli, depend on the same water mass for food and waste transport, and are subjected to the same predators as adult oysters. Spat and small, single seed oysters that are not protected by large cultch are vulnerable to shell-crushing predators such as crabs and finfish (Menzel and Nichy 1958). The normally abundant spatfall that occurs in most optimal oyster habitats, however, usually ensures good survival even though predation of easily crushed or drilled spat is considerable.

Salinity. The normal salinity range for adult gulf coast oysters is 10 to 30 ppt, but they can survive in salinities from 5 to 40 ppt (Gunter and Geyer 1955, Butler 1954a, Galtsoff 1964; Stenzel 1971). The optimal salinity range for physiological purposes, food abundance, and stenohaline predator avoidance is probably closer to 10 to 20 ppt (Butler 1954a; Eleuterius 1977). Eleuterius found that productive oyster reefs in Mississippi Sound were subjected to salinity minima of 2 to 4 ppt, maxima of 18 to 22 ppt, and means of 10 to 16 ppt.

Crassostrea virginica can withstand depressed salinities of less than 5 ppt for brief periods; but feeding, growth, and reproduction are severely curtailed (Loosanoff 1952; Galtsoff 1964). Gunter (1950) found that oysters can survive salinities as low as 2 ppt for about a month and even survive in freshwater for several days. Water salinities in the normal oyster habitat may be reduced to zero or slightly above zero during floods or "freshets," and relief may be provided by the flood tide salt wedge. During periods of extremely depressed salinities, oysters remain tightly closed and survive via anaerobic respiration until the normal salinity regime is reestablished (depending on ambient water temperatures) or until they deplete their internal reserves and succumb (Galtsoff 1929, 1964; Butler 1949, 1952, 1954a; Gunter 1950, 1953; Andrews et al. 1958; May 1972). If the low salinity regime persists or if upland drainage modifications (e.g., dams, levees, canals) permanently alter the normal salinity regime, most of the oysters will die and the population will be reestablished in appropriate areas of the altered estuary. If a high salinity regime results from a prolonged drought or upland drainage modifications oyster populations and supporting cultch materials in the affected areas will be reduced or eliminated by high salinity, stenohaline predators including oyster drills, whelks, crabs, oyster leeches, and shell burrowing pests including pholad clams, sponges, polychaete worms (Gunter 1952; Galtsoff 1964).

Flood-related mass mortalities of oysters are not uncommon in many Gulf of Mexico estuaries which receive major river input (Galtsoff 1929; Butler 1949, 1952; Gunter 1950, 1953; May 1972). Affected reefs will normally receive a new spatfall during the next spawning season and will recover to preflood production levels within 2 to 3 years provided no new flooding occurs (W. J. Demoran, Fisheries Management Section, Gulf Coast Research Laboratory, Ocean Springs, Mississippi; pers. comm.). The timing and success of those subsequent spatfalls depend on whether or not the cultch materials have been silted over and on the proximity of unaffected brood stocks.

Temperature. American oysters inhabiting the Gulf of Mexico and the south Atlantic coast of the United States do not hibernate as do those north of Cape Hatteras, North Carolina (Galtsoff 1964). Oysters in northern latitudes that are subjected to water temperatures below about 8°C (46°F) become dormant and most of their physiological functions cease or are greatly reduced (Galtsoff 1964). Oysters south of Cape Hatteras are generally active throughout the winter and even exhibit considerable shell growth during the colder months even though gametogenic processes are reduced. Intertidal oysters or shallow subtidal oysters are occasionally subjected to freezing conditions during the passage of cold weather fronts, especially when such frontal passages coincide with spring low tides (Butler 1954a). Although oysters at latitudes north of Cape Hatteras can withstand freezing near-solid for 4 to 6 weeks (Nelson 1938; Kanwisher 1955), Gulf of Mexico oysters will succumb if subjected to temperatures less than 0°C (32°F) while exposed at low tide provided that condition persists for more than a day or so (McGraw 1980). Subtidal oysters, especially those on offshore patch reefs, will not be adversely affected by depressed winter temperature.

In certain areas during the summer, gulf coast oysters are occasionally exposed for 2 to 3 hr at low tides to elevated temperatures of 46° to 49°C (115° to 120°F) (Galtsoff 1964). Prolonged exposure at temperatures above 32° to 34°C (90° to 93°F) may kill the oysters outright or weaken them, permitting increased predation during subsequent tidal inundation (Nichy and Menzel 1960; Galtsoff 1964).

Food. All oysters (regardless of age) are filter-feeding planktivores and omnivores. They ingest a large assortment of small, waterborne particles including diatoms, flagellates, and bacteria (nannoplankton), detritus and silt, and dissolved molecules such as glucose (Nelson 1925; Yonge 1928; Galtsoff 1964). Food selection and ingestion are size-dependent; food particles range from 1 to 12 µm with a predominance in the 1- to 3-µm range (Haven and Morales-Alamo 1970).

Substrate. The American oyster requires firm and stable substrate conditions to attach, survive, and proliferate. The ideal bottom substrate consists of shell (reef) materials or mud-sand-shell mixtures that are firm enough to support the weight of large oysters without self-burial (Butler 1954a; Galtsoff 1964). Soft muds (> 80% silt and/or clay) that cannot support the weight of an empty shell and shifting sands (> 80% sand) that move easily with the currents and tend to clog the shells and ciliary mechanisms of affected oysters, are totally unsuitable for reef substrates since the oysters either settle into the substrate, are buried by currents and waves, or their gills are unable to function in filter-feeding and respiration. Soft, muddy bottoms may be gradually converted to acceptable bottoms by the oysters themselves, provided a few pieces

of cultch are available for initial colonization (Galtsoff 1964). Soft, unstable, and otherwise unsuitable bottoms can be stabilized and upgraded for oyster culture with the addition of oyster or clam shells or any other available and suitable cultch (e.g., gravel) (Gunter and Demoran 1970, 1971; Pollard 1973; Whitfield 1973; White and Perrett 1974).

Current and turbidity. Currents, particularly tidal currents, are important in the location, survival, and productivity of oysters in Gulf of Mexico estuaries. They transport food particles over the reefs, remove feces and pseudofeces, maintain proper salinities, and transport gametes and planktonic larvae within the estuary. Excessive currents prevent spat attachment as well as erode and/or eliminate the supporting substrate (sediment) base below the oysters. Insufficient currents permit adverse sedimentation that may bury oysters. Normal accumulations of riverborne sediments in the Matagorda Bay, Texas, destroyed 2430 to 2835 ha (6000 to 7000 acres) of oyster reefs between 1926 and 1962 (Galtsoff 1964). Adult oysters are more capable of withstanding adverse current conditions (especially sediment burial) than are young spat and seed oysters (Galtsoff 1964; Dunnington et al. 1970). During periods of adverse turbidity (e.g., those produced by storm waves, swift currents, and floods), oysters close their shells tightly for a week or more (depending on temperature conditions) until favorable conditions are reestablished.

Attached oysters are subjected to heavy concentrations of suspended particles (e.g., silt, clay, detritus), but can generally counteract them in several ways. Particles that are too large to ingest or that are small, but not acceptable as food items, are combined with mucous to form strands of pseudofeces and subsequently ejected from the oyster's mantle (shell) cavity via periodic, rapid shell closures (Galtsoff 1964). Large oysters, unlike small spat and seed, are not generally affected by normal estuarine sedimentation rates. Their growth rate and size permit them to avoid burial provided part or all of their shell margin is at or above the sediment/water interface. Tidal and storm currents normally flush most sediments from oyster reefs; however, in the absence of sufficient currents, natural sedimentation and/or biodeposited sediments may result in the burial and eventual death of affected oysters regardless of their size. When suspended sediment loads are too great for effective clearing via gill ciliary action, the oysters will close their shells until acceptable conditions return.

Davis and Hidu (1969) found that shell formation in C. virginica was impaired by suspended sediments between 0.125 and 0.188 g dry wt/l, and that growth and survival were reduced at concentrations above 0.75 g dry wt/l. Cardwell et al. (1976) found acute toxicities of natural sediments to larval Pacific oysters (C. gigas) at concentrations from as low as 0.1 to as high as 9.1 to 18.1 g dry wt/l.

Oysters can clear enormous amounts of suspended particles from the surrounding water column (Galtsoff 1964). Filtration and biodeposition activities may cause deleterious self-burial problems (Lund 1957a, 1957b; Stenzel 1971). Those particles consist of fine silts, clay-sized materials, oyster feces and pseudofeces, and other indigestible organic materials transported by waves and currents (Stenzel 1971). The ideal current represented by a steady, nonturbulent flow of water over an oyster bed, is strong enough to carry away feces, pseudofeces, and liquid and gaseous metabolites, and to provide oxygen and food (Galtsoff 1964).

Special considerations. Predators of the American oyster are abundant in the Gulf of Mexico and include numerous gastropod mollusks, decapod crustaceans, and molluscivorous finfish (Butler 1954a; Galtsoff 1964). Most are relatively stenohaline and naturally controlled by low-salinity regimes and occasional "freshets" in prime oyster habitats (Butler 1954a; Galtsoff 1964). The most destructive high salinity predators include the southern oyster drill (Thais haemastoma Linné), the stone crab (Menippe mercenaria [Say]), and the black drum (Pogonias cromis [Linnaeus]) (Moore 1907; Burkenroad 1931a; St. Amant 1938; Butler 1953, 1954b; Chapman 1955, 1958; Gunter 1955, 1979a; Menzel 1955; Menzel et al. 1957, 1966; Menzel and Nichy 1958; Nichy and Menzel 1960; Galtsoff 1964; Van Sickle et al. 1976; Cave 1978). During prolonged droughts, these and other high salinity predators move onto or settle (as juveniles) on productive reefs, and consume numerous oysters of all sizes. Drills consume oysters of any size, but prefer spat and seed oysters; crabs consume any size oyster they can break open with their chelipeds; and black drum consume any oyster that they can break loose, ingest, and crush with their strong pharyngeal apparatus and molariform teeth. Other low-to-moderate salinity predators such as turbellarian oyster leeches of the genus Stylochus, the blue crab (Callinectes sapidus Rathbun), the cownose ray (Rhinoptera bonasus [Mitchill]), and the sheepshead (Archosargus probatocephalus [Walbaum]) are of lesser importance, but may be significant when oyster production is naturally low (Butler 1954a; Gunter 1955; Menzel and Nichy 1958; Merriner and Smith 1979).

Oyster drills are the most important predators in the Gulf of Mexico and may destroy more than 50% of a population in waters with a mean salinity of 15 to 18 ppt in a given year (Burkenroad 1931a; St. Amant 1938; Schechter 1943; Butler 1953, 1954a, 1954b; Gunter 1955, 1979a; Galtsoff 1964; Van Sickle et al. 1976). Menzel et al. (1957) found an average of 2.75 oyster drills/m^2 on the depleted St. Vincent Bar in Apalachicola Bay, Florida, and concluded that drills (and stone crabs) were responsible for the 67% mortality that occurred over a one-month period.

The effects of the motile predators such as fish and crabs are more difficult to assess. The probability of predation by these organisms, however, increases with high salinity.

A major limiting factor for Gulf of Mexico oysters is the infectious protozoan pathogen Perkinsus (syn. Dermocystidium and Labyrinthomyxa) marinus (Mackin, Owen, and Collier). Severe mortalities from Perkinsus of more than 50% have been reported from Florida to Texas (Mackin 1953, 1962; Ray et al. 1953; Ray 1954, 1966; Dawson 1955; Quick and Mackin 1971; Beckert et al. 1972). Quick and Mackin (1971) and Quick (1972) devised an infection scale (code)* based on the relative concentration of stained hypnospores of P. marinus in oyster tissues cultured in a fluid thioglycollate medium. Quick and Mackin (1971) found that infections of P. marinus as low as "medium" may cause death, but most oysters do not succumb until "medium heavy" or "heavy" intensities are reached. They found that most lethal infections occur during elevated summer water temperatures. Those lethal infections are usually severe and rapid among adult oysters but spat and small seed oysters are generally unaffected.

---

*Quick and Mackin (1971) Perkinsus infection intensity code:
0 = negative, 1 = very light, 2 = light, 3 = light medium,
4 = medium, 5 = medium heavy, and 6 = heavy.

The estuarine habitat of the American oyster in the Gulf of Mexico has been adversely affected by several types of pollution including domestic sewage wastes, industrial chemical wastes, agricultural pesticide residues, hydrocarbon exploration and production effluents, and channel dredging spoils (Galtsoff 1964). Because insufficiently treated domestic sewage wastes pollute oyster reefs nearshore to population centers along the northern Gulf of Mexico, the U.S. Food and Drug Administration (under the National Shellfish Sanitation Program and its replacement organization, the Interstate Shellfish Sanitation Conference) and cooperating state shellfish sanitation control agencies close large areas of otherwise productive oyster bottoms to direct harvesting for human consumption. Depending on the levels of coliform indicator bacteria, those agencies classify shellfish-growing waters as Open (< 70 Most Probable Number [MPN] of bacteria per 100-ml water sample), Restricted (70 to 700 MPN/100 ml), and Prohibited (> 700 MPN/100 ml) (U.S. Public Health Service [USPHS] 1965). Although waters containing more than 70 MPN/100 ml of coliform bacteria produce large numbers of "healthy" oysters, the oysters cannot be harvested for direct human consumption unless cleansed of their "filth" (USPHS 1965). Domestic contaminants in estuarine waters may be a blessing for oysters. They generally increase the nutrient load of the water, promote oyster production, and restrict human exploitation.

Industrial and civil engineering wastes are also detrimental to oyster production (Galtsoff 1964). Toxic chemicals kill or otherwise interfere with normal physiological processes including reproduction and growth. Some such as mercury and kepone cause affected oysters to be toxic to humans. Channel dredging spoils bury and kill all affected oysters when deposited on or immediately adjacent to productive habitats. Highly toxic industrial pollutants in some areas such as Galveston, Mobile, and Escambia Bays have eliminated some productive reefs and rendered the oysters on many remaining reefs unsuitable for human consumption. The presence or absence of waterborne pollutants will not indicate the suitability of habitats for oyster survival and productivity in the future because all of those waters should be clean enough for shellfish production by mid-1983 if mandates of the U.S. Federal Water Pollution Control Act Amendments of 1972 (P.L. 92-500; 33 U.S.C. 1251 et seq.) are followed. Pollutants within sediments could, however, be deleterious to oysters in the future if those sediments are disturbed by natural phenomena (currents) or by dredging and filling.

HABITAT SUITABILITY INDEX (HSI) MODEL

Model Applicability

An HSI model incorporating all environmental variables that normally impact oyster habitat was not considered desirable because of practical and economic constraints. Such a model would be of little use in determining the suitability of a specific estuarine habitat at a given point in time because of the dynamic nature of most gulf coast estuaries. Instead, the model in this report provides the best estimate of a given habitat's suitability based on a minimum number of controlling variables that can be determined easily and inexpensively in the field and laboratory (pathogen variable). Those variables are applicable to all

Oysters cannot survive and flourish on pure sand bottoms (sand grains clog their gills and mantle cavity) or on soft, unconsolidated, muddy bottoms (into which they sink). As a general rule, substrates with 80% or more sand fractions or silt/clay fractions are unsuitable for oysters unless planted with cultch materials. The percentages of these components in sediment samples should be determined according to standard grain-size analytical procedures using soil testing sieves (see Folk 1968).

For purposes of intensive oyster population management, rather than habitat evaluation, additional variables affecting oyster survival can be included in this component. These variables are mean predator abundance (V_7) and mean disease intensity (V_8). Both variables were included to satisfy the requests of several oyster biologists who believed that they were required to complete the model.

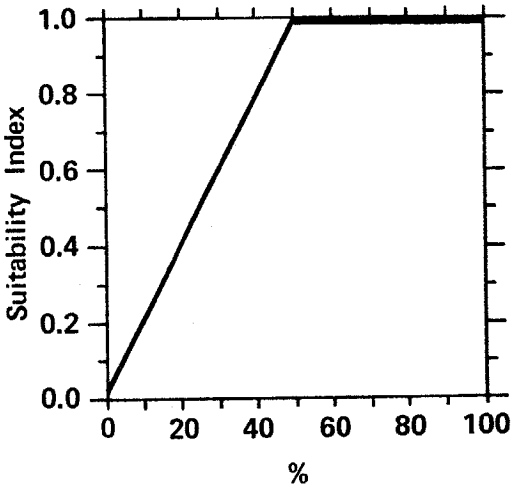
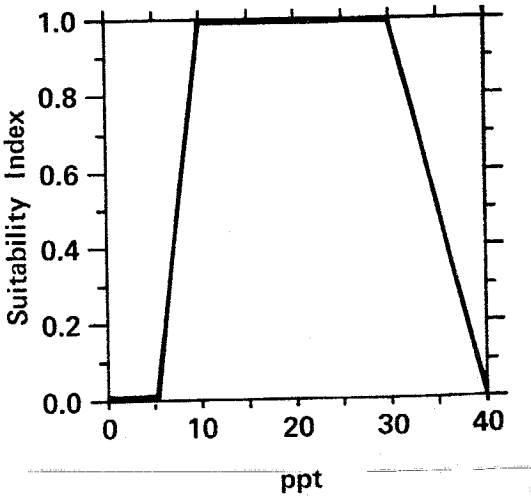
Oysters are killed in massive numbers by numerous predators including man, but none is more damaging than the southern oyster drill (Thais haemastoma). The relative abundance (mean number/m^2) of mature drills (>4 cm or 1.6 inches in length) is included as a model variable for this reason. Abundance levels of one or more drills/m^2 are considered unacceptable. Most other predators are very mobile and difficult to assess; their predatory effects are essentially covered by the salinity variable.

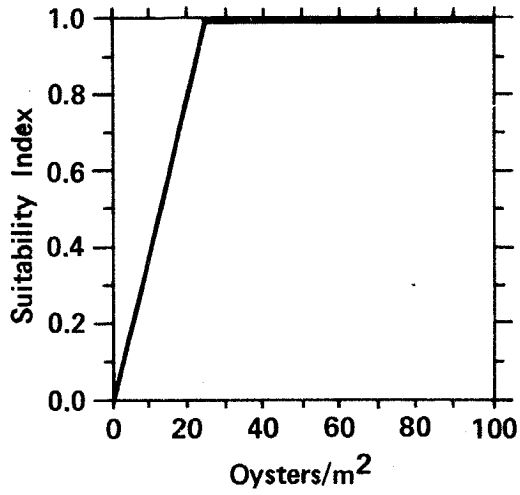
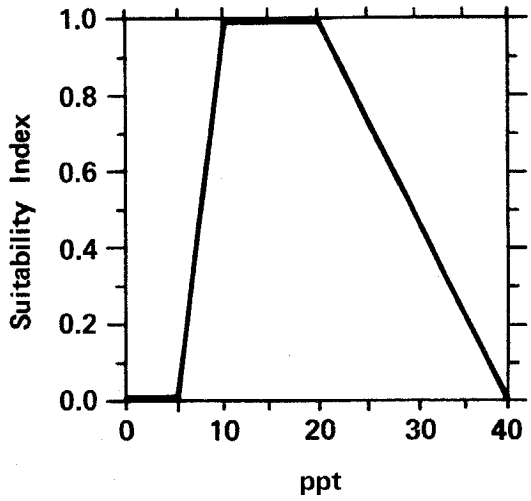
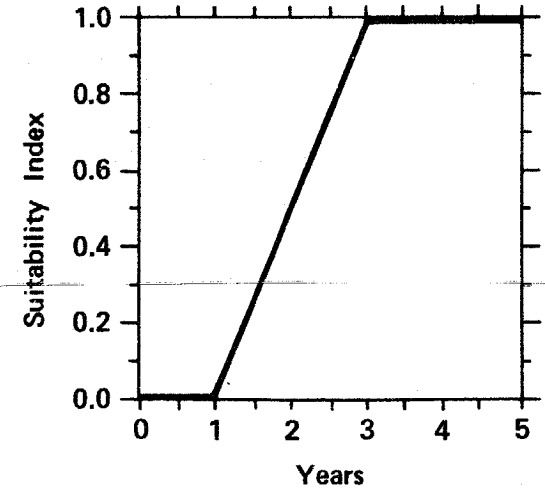
Mass mortalities of adult oysters that often exceed 50% frequently occur during elevated summer temperature regimes as a result of the protozan pathogen Perkinsus marinus (Mackin, Owen, and Collier) (vide: Levine 1978). Although other pathogens and parasites infect gulf coast oysters, none is more prevalent nor damaging than P. marinus. Its presence and prevalence are relatively easy to assess and its mean infection intensity is included as a model variable. The 10- to 14-day incubation period required for the laboratory assessment of this pathogen is its only drawback. The assay does require laboratory facilities including a microscope and proficiency in required assay procedures (Quick 1972).

Several habitat factors were not included in the model. A depth factor was omitted because the model is designed for subtidal, not intertidal habitats. Freshwater inputs other than killing floods are accounted for, at least partially, by the salinity variable. Food availability, water temperature, tidal, and wind effects were not considered to be as important as the variables included in the model. For instance, except in those intertidal areas where it may be exposed to freezing air temperatures or to excessive summer temperature (>40°C or 104°F), the American oyster survives over the wide water temperature range (5° to 35°C or 41° to 95°F) encountered in estuarine areas of the northern Gulf of Mexico and south Atlantic coast of the United States. Oyster veliger larvae are primarily phytoplanktivores. They filter small green algae, flagellates, detrital particles, and bacteria-laden particles over a size range of 1 to 3 μm from the water column with the aid of their velum (ciliated lobes) (Galtsoff 1964). These foods are usually abundant in most estuaries when oyster larvae are present and are not normally limiting factors.

Suitability Index (SI) Graphs for Model Variables

This section provides graphic presentations for the relationships between the habitat variables and the habitat suitability for the American oyster in estuarine (E) habitats in the northern Gulf of Mexico. The suitability index (SI) values can be determined directly from the graph of each variable. Those SI values range from 1.0, denoting optimal habitat, to 0.0, denoting unacceptable (or no) habitat. Table 1 gives sources and assumptions for the model variables.

Habitat	Variable		Suitability Graph
E	V_1	Percentage of bottom covered with suitable cultch.	
E	V_2	Mean summer water salinity.	

Habitat	Variable		Suitability Graph
E	V_3	Mean abundance of living oysters (gregarious factor).	
E	V_4	Historic mean water salinity.	
E	V_5	Mean interval between killing floods.	

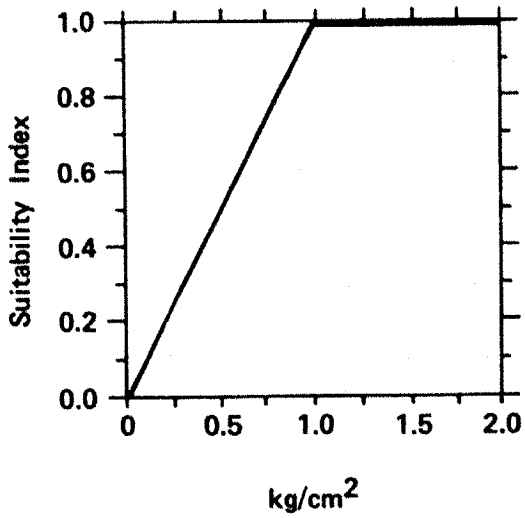
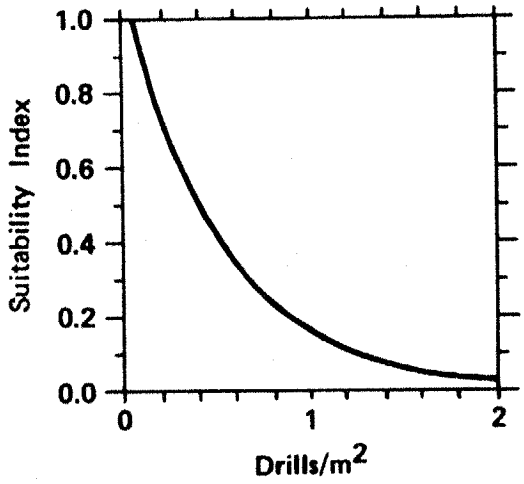
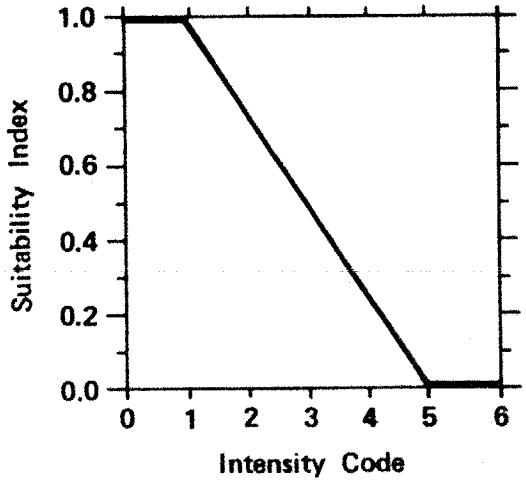
Habitat	Variable		Suitability Graph
E	V_6	Mean substrate firmness (penetrometer value).	
E	V_7	Mean predator abundance (southern oyster drills).	
E	V_8	Mean disease intensity (Perkinsus marinus).	

Table 1. Data sources and assumptions for American oyster habitat suitability indices.

Variable	Source	Assumption
V_1 Cultch availability	Hedgepeth 1953 Butler 1954a Lunz 1958 Galtsoff 1964 Gunter and Demoran 1971 Hoskin 1972 Pollard 1973 White and Perrett 1974 MacKenzie 1977, 1981, 1983 Gunter 1979b	Clean, unfouled cultch materials such as natural or planted shells are optimal for metamorphosing oyster larvae. Small shells, shell hash, gravel, rocks, and other solid material are suitable. Optimal coverage of bottom with cultch material is $\geq$50%. Cultch amounts and coverage may be increased by planting shells.
V_2 Mean summer salinity	Carriker 1951 Davis 1958 Calabrese and Davis 1970 Chatry and Dugas (MS.)	Metamorphosing oyster larvae will set (attach) at salinities between 5 and 35 ppt. Optimal setting occurs between 10 and 30 ppt and maximum setting occurs between about 18 and 22 ppt.
V_3 Gregarious factor	Galtsoff 1964 Crisp 1967 Hidu 1969 Keck et al. 1970 Veitch and Hidu 1971 Hidu et al. 1978	Oyster larvae set (attach) gregariously in the natural environment in response to waterborne pheromones, mantle fluid, metabolites, and shell leachates from living oysters and/or their remains. After spontaneous setting of spat on old cultch, their presence will stimulate more larvae to set in the immediate vicinity. Optimal abundance of oysters for this factor is set at $\geq 25/m^2$.
V_4 Historic mean water salinity	Gunter 1950, 1953, 1955 Loosanoff 1952 Butler 1954a Gunter and Geyer 1955 Galtsoff 1964 Stenzel 1971 Eleuterius 1977	Oysters survive over a salinity range of 5 to 40+ ppt but flourish within a range of 10 to 25 ppt provided predators, pathogens or shell pests are limited. The optimal historic salinity mean is between 10 and 20 ppt.

Table 1. Continued.

Variable	Source	Assumption
V_5 Frequency of killing floods	Galtsoff 1929, 1964 Butler 1949, 1952, 1954a Gunter 1950, 1953 Andrews et al. 1958 May 1972	Prolonged exposure to fresh water will kill 50 to 100% of the oysters in a given area. Significant mortalities occur with exposures of $\leq$2 ppt for several weeks. Recovery to preflooded population levels requires 2 to 3 years under optimal salinity conditions.
V_6 Mean substrate firmness	Butler 1954a Marshall 1954 Galtsoff 1964 Hoskin 1972 Bahr and Lanier 1981	Optimal substrates support the weight of an oyster and usually contain $\geq$10% (by volume) of shell or other material (e.g., rocks) and a mixture of sand, silt, and clay particles. Soft muds (>80% silt and/or clay) and shifting sands (>80% sand) are unsuitable for oysters unless cultch is planted. Penetrometer values of $\geq$1 kg/cm^2 are optimal for substrate firmness on oyster reefs.
V_7 Mean predator abundance	Burkenroad 1931a St. Amant 1938 Schechter 1943 Butler 1953, 1954a, 1954b Chapman 1955, 1958 Gunter 1955, 1979a Menzel et al. 1957, 1966 Galtsoff 1964	The southern oyster drill (Thais haemastoma) is the most destructive predator in the Gulf of Mexico and capable of killing >50% of the oysters on any reef with salinities of $\geq$18 ppt. Predation is a function of the drills' relative size and abundance. The total absence of drills is considered optimal, and the presence of $\geq$1 drill/m^2 of >4-cm length is considered unacceptable.
V_8 Mean disease intensity	Mackin 1953, 1961b, 1962 Ray et al. 1953 Ray 1954, 1966 Galtsoff 1964 Quick and Mackin 1971 Beckert et al. 1972 Quick 1972	The protozoan Perkinsus marinus is the most prevalent and lethal oyster pathogen in the Gulf of Mexico. It will kill >50% of the infected oysters on a given reef. Total absence of the pathogen is optimal for adult and seed oysters. Oysters with "medium heavy" to "heavy" infections (intensity codes of 5 and 6, respectively) will succumb.

Component Index (CI) Equations

To obtain component index values for the two life stages covered by this oyster model, the suitability index (SI) values for appropriate variables must be combined by using the following equations.

Life stages	Equations
Larval	$CI_l = (SI_{V1} \times SI_{V2} \times SI_{V3})^{1/3}$
	$(CI_l = [SI_{V1} \times SI_{V2}]^{1/2}$, if $SI_{V3} = 0)$
Adult, seed, spat	$CI_a = (SI_{V4} \times SI_{V5} \times SI_{V6})^{1/3}$
	(CI_a = 0, if the bottom substrate is composed of 80% or more sand fractions)

Modifier. The above equations describe typical use of the model to evaluate oyster habitat. For other uses, such as oyster management, one may wish to include variables V_7 and V_8 in the model. This changes the component equations for the adult, seed, spat life stages:

$$CI_a = (SI_{V4} \times SI_{V5} \times SI_{V6} \times SI_{V7} \times SI_{V8})^{1/5}$$

(CI_a = 0, if the bottom substrate is composed of 80% or more sand fractions)

HSI Determination

After obtaining the field data for the model, determine the suitability indices (SI) using the graphs provided earlier and calculate the component indices (CI) using the appropriate life stage equations. From the component indices determine the HSI as follows:

1) If the component index for the attached stage (CI_a) is the lowest component (i.e., if $CI_a < CI_l$), then $HSI = CI_a$.

2) If the component index for the attached stage (CI_a) is not the lowest component index (i.e., if $CI_a < CI_l$), then $HSI = (CI_l \times CI_a)^{1/2}$.

Six sample data sets from which suitability indices (SI), component indices (CI), and habitat suitability (HSI) values have been generated using the model equations are presented in Table 2. The data sets are representative of six typical estuarine habitats where oyster larvae may be expected to attach and grow: (1) a subtidal area of the mouth of river that experiences intermittent

Table 2. Calculations of suitability indices (SI), component indices (CI), and the habitat suitability indices (HSI) for six hypothetical data sets, using the oyster habitat variables (V) and model equations.

V_i	Data set 1		Data set 2		Data set 3		Data set 4		Data set 5		Data set 6	
	Data	SI	Data	SI	Data	SI	Data	SI	Data	SI	Date	SI
V_1 (%)	25	0.50	30	0.60	10	0.20	75	1.00	7	0.14	5	0.10
V_2 (ppt)	7	0.40	14	1.00	28	1.00	18	1.00	33	0.70	38	0.20
V_3 (No./m^2)	5	0.20	20	0.80	3	0.12	50	1.00	2	0.08	2	0.08
V_4 (ppt)	6	0.20	12	1.00	26	0.70	15	1.00	30	0.50	35	0.25
V_5 (yr)	1.5	0.25	2	0.50	3	1.00	3.5	1.00	>5	1.00	>5	1.00
V_6 (kg/cm^2)	0.5	0.50	0.4	0.40	1.2	1.00	1.5	1.00	0.9	0.90	0.8	0.80
V_7 (No./m^2)	0.0	1.00	0.0	1.00	0.1	0.84	0.4	0.49	1.3	0.10	2	0.03
V_8 (No.)	0.0	1.00	1	1.00	1	1.00	2	0.75	3	0.50	4	0.25
CI_1	0.34		0.78		0.29		1.00		0.20		0.12	
CI_a*	0.29		0.58†		0.89		1.00		0.77		0.58	
HSI*	0.29†		0.58†		0.51		1.00		0.39		0.26	
CI_a**	0.48		0.72		0.90		0.82		0.47		0.27	
HSI**	0.40		0.72†		0.51		0.82†		0.30		0.18	

*Excludes V_7 and V_8.

**Includes V_7 and V_8.

†(HSI = CI_a, if $CI_a < CI_1$).

flooding, (2) an inshore bayou surrounded by salt marshes, (3) an open sound bottom between a barrier island and the mainland, (4) a viable oyster reef in a typical bay or sound, (5) a barrier island pass connecting the sound and the Gulf of Mexico, and (6) a hypersaline lagoon on an offshore barrier island (Figure 2).

The data sets are not actual field measurements, but represent the values that one could expect to obtain in estuarine habitats occupied by the American oyster in the northern Gulf of Mexico. The HSI values that were calculated from these hypothetical data sets reflect the carrying capacity trends that the author believes are appropriate for estuarine habitats with the characteristics listed in Table 2.

Field Use of the Model

The level of detail required for a particular application of this model will vary depending on temporal, monetary, and accuracy constraints. Detailed evaluation of all habitat variables will result in the most reliable and repeatable HSI values. The use of previously collected data for one or more of the habitat variables should result in the satisfactory application of the model with minimum expense. Some of the data required for the model (e.g., prevalent salinity, mean flooding intervals) are frequently available from published sources (e.g., U.S. National Oceanic and Atmospheric Administration Weather Service and shellfish resource and/or management agencies in Gulf Coast States). Suggested techniques for measuring the model variables and references to consult for more detailed guidance are given in Table 3.

This model is not intended for the evaluation of open marine habitats, although small populations of oysters may occasionally occur in such areas for brief periods, especially on manmade structures (e.g., oil rigs). The model should not be used in those estuaries in which toxic industrial wastes have reduced habitat suitability, especially if those wastes are incorporated in the sediments of the oyster's traditional habitat. Large amounts of domestic sewage wastes may drastically reduce dissolved oxygen levels and/or promote excessive siltation in traditional oyster habitats thereby negating the applicability of this model. Extensive and operational freshwater control structures that are located upstream from the estuarine areas in question may also negate the applicability of this model.

This HSI model, with some minor modifications, should be applicable to selected locations along the Atlantic coast south of Cape Hatteras. American oysters that exist north of Cape Hatteras are physiologically dissimilar to those in the Gulf of Mexico (and south Atlantic coast). The differences include such temperature-related phenomena as gametogenesis, spawning, and hibernation. The primary difference between American oysters south of Cape Hatteras and those in the Gulf of Mexico is the intertidal reef-building characteristic of Atlantic populations caused by the extreme semidiurnal tidal ranges in that area (Bahr and Lanier 1981). Extreme tidal ranges expose large expanses of the bottom and produce considerable water movement (currents) and accompanying geophysical and physiological phenomena (e.g., large-scale sediment transport, atmospheric exposure, and desiccation). Before this HSI model can be applied to the Atlantic intertidal oyster populations, these variables would have to be incorporated into the model. Additional variables may include, but are not limited to, the elevation of the bottom relative to mean tide level, the location of the

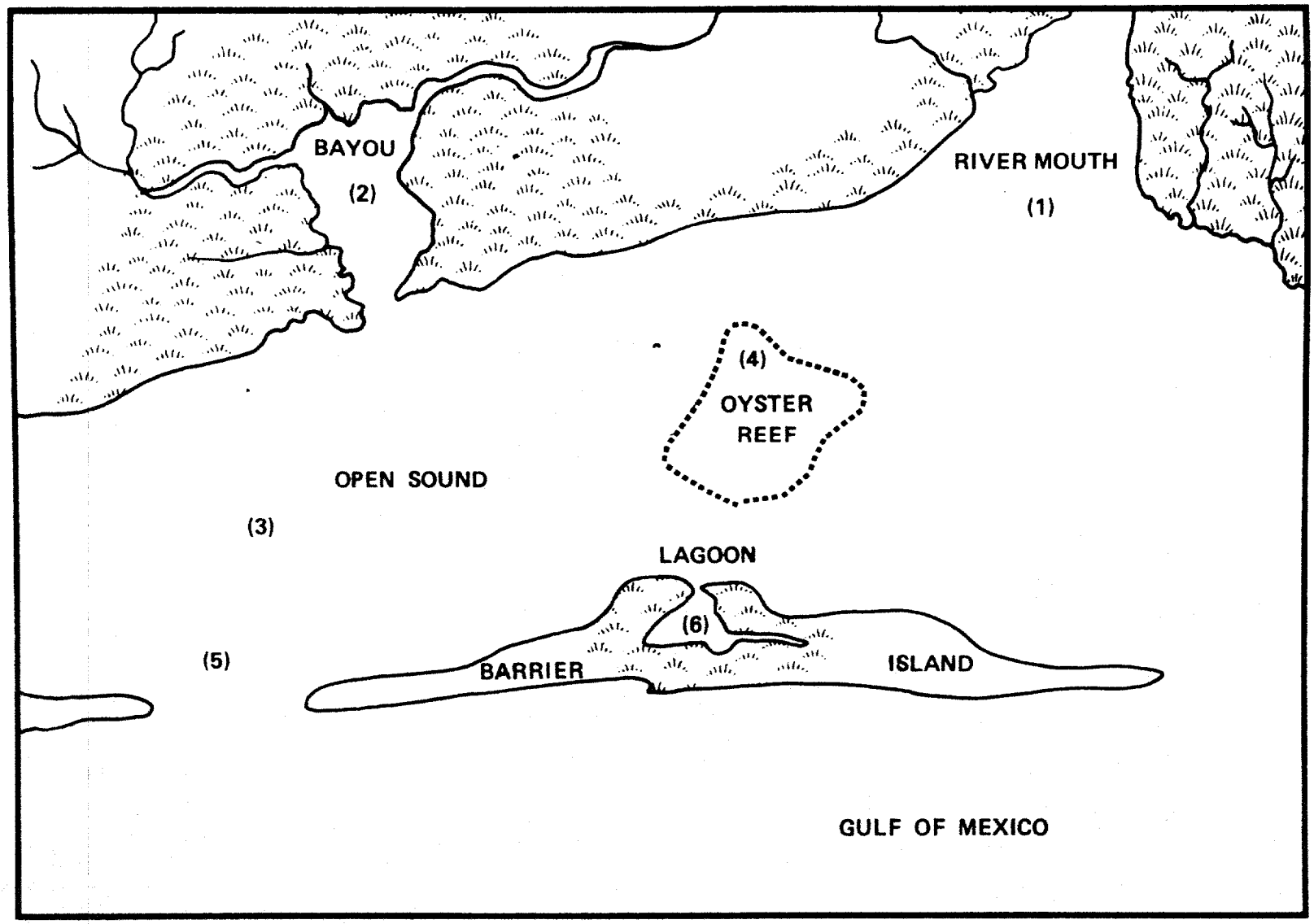


Figure 2. Hypothetical locations for oyster habitats in the northern Gulf of Mexico. Location numbers correspond to hypothetical data sets of Table 3.

Table 3. Description of oyster HSI model variables and suggested techniques for measuring variables for estuarine habitats.

V_i	Variable description	Suggested technique	Reference source
V_1	Percentage of bottom covered with suitable cultch	Field survey using hand-held probe or SCUBA; bottom grab or dredge samples.	May 1971 MacKenzie 1977, 1981, 1983 Haven et al. 1981
V_2	Mean summer water salinity	Field survey using hand-held, temperature-compensating AO Goldberg refractometer with direct-reading salinity scale.	Galtsoff 1964 Behrens 1965 Strickland and Parsons 1972
V_3	Mean abundance of living oysters	Field survey using SCUBA diving; selective sampling with oyster tongs; selective sampling with oyster dredge.	Keith and Cochran 1968 May 1971 MacKenzie 1977, 1981, 1983 Haven et al. 1981
V_4	Historic mean water salinity	Existing data, literature.	Galtsoff 1964 Stenzel 1971
V_5	Mean interval between killing floods	Existing data, literature.	Butler 1949, 1952 Gunter 1953
V_6	Mean substrate firmness	Existing geological surveys, literature; field surveys using pocket penetrometer* while SCUBA diving or test grab samples with penetrometer.	Miller 1961 Jumikis 1962 McMaster 1967 Smolowitz and Nulk 1982 Cordova (undated)
V_7	Mean predator abundance	Field survey using randomly placed quadrats and SCUBA; random sampling with grabs, dredges, tongs.	Brett 1964 Menzel et al. 1966 MacKenzie 1977, 1981, 1983 Breithaup and Dugas 1979
V_8	Mean disease intensity	Sample collection with SCUBA, dredge, grab, or tongs; laboratory assay with fluid thioglycollate medium and microscope.	Ray et al. 1953 Quick and Mackin 1971 Quick 1972

*Available from Soil Test, Inc., 2205 Lee Street, Evanston, IL 60202

area relative to tidal channels, and the mean exposure times of the intertidal areas. This HSI model should be applicable in subtidal areas of the southern Atlantic coast of North America.

Interpreting Model Outputs

The oyster HSI value determined by this model will not necessarily reflect the true population density of this species in a particular habitat within a given area because other unrelated controlling factors may be operating. Those factors may include, but are not limited to, human harvesting of the oysters and losses caused by tropical storms (erosion and burial).

In those areas where oyster population levels are controlled primarily by habitat-related factors, the model should be positively correlated with long-term mean population levels. That correlation, however, has not been tested.

The proper interpretation of the oyster HSI is simply one of numerical comparison. If two habitats have different HSI's, the one with the higher HSI should have the potential to support more oysters than the one with the lower HSI, given that the model assumptions have not been violated. If the HSI difference is based on the absence of suitable cultch materials, those materials may be planted, thereby increasing the lower HSI to or above that of the HSI in a habitat with insufficient cultch.

ADDITIONAL HABITAT MODELS

Bahr and Lanier (1981) formulated three conceptual models for intertidal oyster communities of the American oyster along the south Atlantic coast of the United States. Of the three (regional, drainage unit, and reef levels), the reef level model contains most of the components included in the habitat suitability index model proposed in this publication. Users of the proposed HSI model and those that attempt to modify the model for application to Atlantic coast populations of Crassostrea virginica should refer to those conceptual models for additional variables.

Butler (1954a) provided a "descriptive model" of major oyster habitats in the Gulf of Mexico and separated those habitats into four arbitrary, but distinctive, categories based on mean water salinities and estuarine locations. Those categories (estuarine head, midpoint, outer part, and mouth) and their relative characteristics are listed in Table 4. In those instances that Butler failed to provide relative values, this author either supplied the missing values or interpolated Butler's facts to determine them. The relative habitat suitability values are estimates based on the HSI values derived from hypothetical locations using the HSI model provided in this publication.

The author is aware of only one other mathematical model for evaluating the suitability of an estuarine habitat for the American oyster. Galtsoff (1964) proposed a simplistic model that he successfully used to evaluate oyster bottoms in some Gulf and south Atlantic states (Galtsoff 1959). Galtsoff chose five positive and five negative variables to input the model. Positive variables were bottom condition, water movement, water temperature, water quality (salinity), and food availability. Negative variables were adverse sedimentation, diseases, competition, predation, and water quality (pollution). The optimal

Table 4. Relative characteristics of major oyster habitats in the Gulf of Mexico (modified from Butler 1954a).

Characteristic	Estuarine location			
	Head	Midpoint	Outer part	Mouth
Salinity (ppt)				
Mean	10	15	25	30*
Range	0-15	10-20	10-30	20-35*
Population density	Sparse	Maximum	Moderate	Sparse
Spatfall accumulation	Low	Moderate to heavy	Moderate*	Low*
Spat survival	Fair*	Excellent*	Low	Low
Cultch availability	Low*	High*	Moderate	Low
Growth rate	Rapid to slow	Moderate to rapid	Rapid	Slow
Production potential*	Low*	Moderate to high*	Moderate*	Negligible*
Predator abundance	Low	Low to moderate*	Moderate	Maximum
Fouling organism abundance	Low	Moderate	Maximum	High*
Substrate suitability*	Low to moderate*	Moderate to high*	Moderate to high*	Moderate to low*
Probability of killing flood	High	Low to moderate	Low*	Negligible*
Annual mortality rate	High	Low to moderate	High	High
Commercial use	Seed grounds	Public reefs*	Bedding grounds	Spawning reservoir
Habitat suitability*	Low*	Maximum*	Moderate*	Low*

*Supplied by author or interpolated from Butler (1954a).

value for each positive variable is assigned a value of 10, and the relative degrees of variable inadequacies are assigned numerical values in descending order from 9 to 1. The complete absence of a negative factor refers to the optimal condition, and therefore, is designated as 0. The degrees by which negative factors adversely affect an oyster population are assigned numerical values in descending order from 9 (for 90% of negative influence) to 1 (denoting 10% or less of the expected harmful effect). The 0 value of a positive factor and the 10 value for a negative factor are omitted because under the proposed model such values denote the complete unsuitability of the habitat in question for the existence of a productive oyster population.

Galtsoff's proposed habitat evaluation model may be used as a substitute HSI model and is utilized by determining relative values for all ten variables and calculating an index with the following equation:

$$HSI = \Sigma f^{+} - \Sigma f^{-}$$

where Σf^{+} is the sum of all positive factors and Σf^{-} is the sum of all negative factors. According to Galtsoff's model, the theoretical optimal value for the ideal oyster habitat is 50 when all positive variables are optimal and all negative variables are absent. Galtsoff (1964) arbitrarily ranked the various degrees of oyster habitat suitability as follows:

SUITABILITY	INDEX RANGE
Excellent	41 to 50
Good	31 to 40
Average	21 to 30
Poor	11 to 20
Marginal	< 10

Galtsoff admitted that his proposed model was overly simplistic because it considered all of the variables (factors) as equally significant, but that is probably not true. He left it up to others to formulate an acceptable model for the American oyster. The author is confident that the HSI model presented herein should be applicable in assessing the suitability of actual and potential oyster habitats to which Galtsoff (1959) applied his model with similar, successful results.

REFERENCES

Abbott, R. T. 1974. American seashells. The marine Mollusca of the Atlantic and Pacific coasts of North America. 2nd. ed. Van Nostrand Reinhold Co., New York.

Ahmed, M. 1975. Speciation of living oysters. Adv. Mar. Biol. 13:357-397.

Andrews, J. D., D. Haven, and D. B. Quayle. 1958. Fresh-water kill of oysters (Crassostrea virginica) in James River, Virginia, 1958. Proc. Natl. Shellfish. Assoc. 49:29-49.

Bahr, L. M., and W. P. Lanier. 1981. The ecology of intertidal oyster reefs of the south Atlantic coast: a community profile. U.S. Fish Wildl. Serv. Biol. Serv. Program FWS/OBS-81/15. 105 pp.

Beckert, H., D. G. Bland, and E. B. May. 1972. The incidence of Labyrinthomyxa marina in Alabama. Ala. Mar. Resour. Bull. 8:18-24.

Behrens, E. W. 1965. Use of the Goldberg refractometer as a salinometer for biological and geological field work. J. Mar. Res. 2:165-171.

Blumer, M., G. Souza, and J. Sass. 1970. Hydrocarbon pollution of edible shellfish by an oil spill. Mar. Biol. (Berl.) 5:195-202.

Breithaup, R. L., and R. J. Dugas. 1979. A study of the southern oyster drill (Thais haemastoma) distribution and density on the oyster seed grounds. La. Wild Life Fish. Comm. Tech. Bull. 30. 20 pp.

Brett, C. E. 1964. A portable hydraulic diver-operated dredge-sieve for sampling subtidal macrofauna. J. Mar. Res. 22:205-209.

Burkenroad, M. D. 1931a. Notes on the Louisiana conch, Thais haemastoma Linn., in its relation to the oyster, Ostrea virginica. Ecology 12(4):656-664.

Burkenroad, M. D. 1931b. Sex in the Louisiana oyster, Ostrea virginica. Science 74(1907):71-72.

Butler, P. A. 1949. An investigation of oyster producing areas in Louisiana and Mississippi damaged by flood waters in 1945. U.S. Fish Wildl. Serv. Spec. Sci. Rep. Fish. No. 8:1-27.

Butler, P. A. 1952. Effects of floodwaters on oysters in Mississippi Sound in 1950. U.S. Fish Wildl. Serv. Res. Rep. 31:1-20.

Butler, P. A. 1953. The southern oyster drill. Proc. Natl. Shellfish. Assoc. 44:67-75.

Butler, P. A. 1954a. Summary of our knowledge of the oyster in the Gulf of Mexico. U.S. Fish Wildl. Serv. Bull. 89:479-489.

Butler, P. A. 1954b. The southern oyster drill. Proc. Natl. Shellfish. Assoc. 44:67-75.

Calabrese, A., and H. S. Davis. 1970. Tolerances and requirements of bivalve molluscs. Helgol. Wiss. Meeresunters. 20:553-564.

Cardwell, R. D., C. E. Woelke, M. I. Carr, and E. W. Sanborn. 1976. Sediment and elutriate toxicity to oyster larvae. Pages 684-718 in P. A. Krenkel, J. Harrison, J. C. Burdick III, eds. Dredging and its environmental effects: proceedings of the special conference; 1976 January 26-28 Mobile, Alabama. American Society of Civil Engineers, New York.

Carriker, M. R. 1951. Ecological observations on the distribution of oyster larvae in New Jersey estuaries. Ecol. Monogr. 21(1):19-38.

Cave, N. N. 1978. Predator-prey relationships involving the American oyster, Crassostrea virginica (Gmelin), and the black drum, Pogonias cromis (Linnaeus), in Mississippi Sound. M.S. Thesis. Southeastern Louisiana University, Hammond, La. 43 pp.

Chapman, C. R. 1955. Feeding habits of the southern oyster drill, Thais haemastoma. Proc. Natl. Shellfish. Assoc. 46:169-176.

Chapman, C. R. 1958. Oyster drill (Thais haemastoma) predation in Mississippi Sound. Proc. Natl. Shellfish. Assoc. 49:87-97.

Chatry, M., and R. J. Dugas. (Manuscript). Optimum salinity regime for oyster production on Louisiana's State seed grounds. St. Amant Marine Lab., La. Dep. Wildl. Fish., Grand Terre Isl., La. 70358. 10 pp.

Coe, W. R. 1934. Alternation of sexuality in oysters. Am. Nat. 68(716):236-251.

Cordova, F. J. (Undated). Field applications of the pocket penetrometer. Westville Engineering Company, Inc., Westville, Ind. 6 pp. (Source: Soiltest, Inc., 2205 Lee St. Evanston, IL 50202.)

Cowardin, L. M., V. Carter, F. C. Golet, and E. T. LaRoe. 1979. Classification of wetlands and deepwater habitats of the United States. U.S. Fish Wildl. Serv. Biol. Serv. Program FWS/OBS-79/31. 103 pp.

Crisp, D. J. 1967. Chemical factors inducing settlement in Crassostrea virginica (Gmelin). J. Anim. Ecol. 36(2):329-335.

Davis, H. C. 1958. Survival and growth of clam and oyster larvae at different salinities. Biol. Bull. (Woods Hole) 114(3):296-307.

Davis, H. C., and H. Hidu. 1969. Effects of turbidity-producing substances in seawater on eggs and larvae of three genera of bivalve mollusks. Veliger 11:316-323.

Dawson, C. E. 1955. Observations on the incidence of Dermocystidium marinum infection in oysters of Apalachicola Bay, Florida. Tex. J. Sci. 7(1): 47-56.

Dunnington, E. A., Jr., K. Leum, and D. MacGregor. 1970. Ability of buried oysters to clear sediments from the shell margin. Proc. Natl. Shellfish. Assoc. 60:2. (Abstr.)

Eleuterius, C. K. 1977. Location of Mississippi Sound oyster reefs as related to salinity of bottom waters during 1973-1975. Gulf Res. Rep. 6(1):17-23.

Folk, R. 1968. Petrology of sedimentary rocks. Hemphill's, Austin, Tex.

Galtsoff, P. S. 1929. Destruction of oyster bottoms in Mobile Bay by the flood of 1929. U.S. Bur. Fish. Doc. 1069:741-758.

Galtsoff, P. S. 1930. The fecundity of the oyster. Science 72(1856):97-98.

Galtsoff, P. S. 1959. Ecological evaluation of the usable productivity of bottom communities. International Oceanographic Congress (1959). Am. Assoc. Adv. Sci. Preprints:233-234. (Abstr.)

Galtsoff, P. S. 1961. Physiology of reproduction in molluscs. Am. Zool. 1(2):273-289.

Galtsoff, P. S. 1964. The American oyster Crassostrea virginica Gmelin. U.S. Fish Wildl. Serv. Fish. Bull. 64. 480 pp.

Gunter, G. 1950. The relationship of the Bonnet Carré Spillway to oyster beds in Mississippi Sound and the "Louisiana Marsh" with a report on the 1950 opening and a study of beds in the vicinity of the Bohemia Spillway and Baptiste Collette Gap. U.S. Army Corps of Engineers, New Orleans District, New Orleans, La. Mimeo. Rep. 66 pp.

Gunter, G. 1951. The species of oysters in the Gulf, Caribbean, and West Indian region. Bull. Mar. Sci. Gulf Caribb. 1(1):40-45.

Gunter, G. 1952. Historical changes in the Mississippi River and the adjacent marine environment. Publ. Inst. Mar. Sci. Univ. Tex. 2(2):119-139.

Gunter, G. 1953. The relationship of the Bonnet Carré Spillway to oyster beds in Mississippi Sound and the "Louisiana Marsh" with a report on the 1950 opening. Publ. Inst. Mar. Sci. Univ. Tex. 3(1):17-71.

Gunter, G. 1955. Mortality of oysters and abundance of certain associates as related to salinity. Ecology 36(4):601-605.

Gunter, G. 1979a. Studies of the southern oyster borer, Thais haemastoma. Gulf Res. Rep. 6(3):249-260.

Gunter, G. 1979b. The grit principle and the morphology of oyster reefs. Proc. Natl. Shellfish. Assoc. 69:1-5.

Gunter, G., and W. J. Demoran. 1970. Successful management of the oyster fishery by the State of Mississippi. Proc. Symp. Mollusca. Mar. Biol. Assoc. India. Part 3:899-905.

Gunter, G., and W. J. Demoran. 1971. Mississippi oyster culture. Am. Fish Farmer 2(5):8-12.

Gunter, G., and R. A. Geyer. 1955. Studies on fouling organisms in the northwestern Gulf of Mexico. Publ. Inst. Mar. Sci. Univ. Tex. 4(1):39-67.

Haven, D. S., and R. Morales-Alamo. 1970. Filtration of particles from suspension by the American oyster Crassostrea virginica. Biol. Bull. (Woods Hole) 139(2):248-264.

Haven, D. S., J. P. Whitcomb, and P. C. Kendall. 1981. The present and potential production of the Baylor Grounds in Virginia. Va. Inst. Mar. Sci. Spec. Rep. 243 in Appl. Mar. Sci. Ocean Eng. 1:1-167.

Hayes, P. F., and R. W. Menzel. 1981. The reproductive cycle of early setting Crassostrea virginica (Gmelin) in the northern Gulf of Mexico, and its implications for population recruitment. Biol. Bull. (Woods Hole) 160: 80-88.

Hedgpeth, J. W. 1953. An introduction to the zoogeography of the northwest Gulf of Mexico with reference to the invertebrate fauna. Publ. Inst. Mar. Sci. Univ. Tex. 3:107-224.

Hidu, H. 1969. Gregarious setting in the American oyster Crassostrea virginica (Gmelin). Chesapeake Sci. 10(2):85-92.

Hidu, H., W. G. Valleau, and F. P. Veitch. 1978. Gregarious setting in European and American oysters: response to surface chemistry vs. waterborne pheromones. Proc. Natl. Shellfish. Assoc. 68:11-16.

Hopkins, A. E. 1931. Factors influencing the spawning and setting of oysters in Galveston Bay, Texas. Bull. U.S. Bur. Fish. 47:55-58.

Hopkins, A. E., P. S. Galtsoff, and H. C. McMillan. 1931. Effects of pulp mill pollution on oysters. Bull. U.S. Bur. Fish. 47:125-186.

Hoskin, C. M. 1972. Oyster reef sedimentation, Biloxi Bay, Mississippi. Water Resour. Res. Inst., Mississippi State University. Compl. Rep. A-051-MISS. 35 pp.

Ingle, R. M. 1951. Spawning and setting of oysters in relation to seasonal environmental changes. Bull. Mar. Sci. Gulf Caribb. 1:111-135.

Jumikis, A. R. 1962. Soil mechanics. Van Nostrand Co., Princeton, N.J.

Kanwisher, J. W. 1955. Freezing in intertidal animals. Biol. Bull. (Woods Hole) 109(1):56-63.

Keck, R., D. Maurer, C. Kauer, and W. A. Sheppard. 1970. Chemical stimulants affecting larval settlement in the American oyster. Proc. Natl. Shellfish. Assoc. 61:24-28.

Keith, W. J., and H. S. Cochran, Jr. 1968. Charting of subtidal oyster beds and experimental planting of seed oysters in South Carolina. Contrib. Bears Bluff Lab. 48. 19 pp.

Levine, N. D. 1978. Perkinsus gen. n. and other new taxa in the protozoan phylum Apicomplexa. J. Parasitol. 64(3):549.

Loosanoff, V. L. 1952. Behavior of oysters in water of low salinities. Proc. Natl. Shellfish. Assoc., (Conv. Address) 1952:135-151.

Loosanoff, V. L., and H. C. Davis. 1963. Rearing of bivalve mollusks. Adv. Mar. Biol. 1:1-136.

Lund, E. J. 1957a. A quantitative study of clearance of a turbid medium and feeding by the oyster. Publ. Inst. Mar. Sci. Univ. Tex. 4(2):296-312.

Lund, E. J. 1957b. Self-silting, survival of the oyster as a closed system, and reducing tendencies of the environment of the oyster. Publ. Inst. Mar. Sci. Univ. Tex. 4(2):313-319.

Lunz, G. R. 1958. Unused oyster shell in South Carolina suitable for seed oyster production. Proc. Natl. Shellfish. Assoc. 48:44-51.

MacKenzie, C. L., Jr. 1977. Development of an aquacultural program for rehabilitation of damaged oyster reefs in Mississippi. Mar. Fish. Rev. 39(8):1-13.

MacKenzie, C. L., Jr. 1981. Biotic potential and environmental resistance in the American oyster (Crassostrea virginica) in Long Island Sound. Aquaculture 22:229-268.

MacKenzie, C. L., Jr. 1983. To increase oyster production in the Northeast United States. Mar. Fish. Rev. 45(3):1-22.

Mackin, J. G. 1953. Incidence of infection of oysters by Dermocystidium in the Barataria Bay area of Louisiana. Proc. Natl. Shellfish. Assoc. (Conv. Address) 1951:22-35.

Mackin, J. G. 1961a. Canal dredging and silting in Louisiana bays. Publ. Inst. Mar. Sci. Univ. Tex. 7:262-314.

Mackin, J. G. 1961b. Mortalities of oysters. Proc. Natl. Shellfish. Assoc. 50:21-40.

Mackin, J. G. 1962. Oyster disease caused by Dermocystidium marinum and other microorganisms in Louisiana. Publ. Inst. Mar. Sci. Univ. Tex. 7:132-229.

Mackin, J. G., and S. H. Hopkins. 1961. Studies on oyster mortality in relation to natural environments and to oil fields in Louisiana. Publ. Inst. Mar. Sci. Univ. Tex. 7:1-131.

Mackin, J. G., and A. K. Sparks. 1961. A study of the effect on oysters of crude oil loss from a wild well. Publ. Inst. Mar. Sci. Univ. Tex. 7:230-261.

Marshall, N. 1954. Factors controlling the distribution of oysters in a neutral estuary. Ecology 35(2):321-327.

May, E. B. 1971. A survey of the oyster and oyster shell resources of Alabama. Ala. Mar. Resour. Bull. 4. 53 pp.

May, E. B. 1972. The effect of floodwater on oysters in Mobile Bay. Proc. Natl. Shellfish. Assoc. 62:67-71.

McGraw, K. A. 1980. Growth and survival of hatchery-reared and wild seed oysters in Mississippi Sound and adjacent waters. Ph.D. Dissertation. University of Washington, Seattle. 234 pp.

McMaster, R. L. 1967. Compactness variability of estuarine sediments: an in situ study. Pages 261-267 in G. H. Lauff, ed. Estuaries. Am. Assoc. Adv. Sci. Publ. 83. Washington, D.C.

Menzel, R. W. 1951. Early sexual development and growth of the American oyster in Louisiana waters. Science 113(2947):719-720.

Menzel, R. W. 1955. Some phases of the biology of Ostrea equestris Say and a comparison with Crassostrea virginica (Gmelin). Publ. Inst. Mar. Sci. Univ. Tex. 4(1):69-153.

Menzel, R. W. 1973. Some species affinities in the oyster genus Crassostrea. Bull. Am. Malacol. Union, Inc. 1973:38. (Abstr.)

Menzel, R. W., and F. E. Nichy. 1958. Studies of the distribution and feeding habits of some oyster predators in Alligator Harbor, Florida. Bull. Mar. Sci. Gulf Caribb. 8(2):125-145.

Menzel, R. W., N. C. Hulings, and R. R. Hathaway. 1957. Causes of depletion of oysters in St. Vincent Bar, Apalachicola Bay, Florida. Proc. Natl. Shellfish. Assoc. 48:66-71.

Menzel, R. W., N. C. Hulings, and R. R. Hathaway. 1966. Oyster abundance in Apalachicola Bay, Florida, in relation to biotic associations influenced by salinity and other factors. Gulf Res. Rep. 2(2):73-96.

Merriner, J. V., and J. W. Smith. 1979. A report to the oyster industry of Virginia on the biology and management of the cownose ray (Rhinoptera bonasus Mitchill) in lower Chesapeake Bay. Va. Inst. Mar. Sci. Spec. Rep. Appl. Mar. Sci. Ocean Eng. 216:1-33.

Miller, C. E. 1961. A penetrometer for in situ measurements in marine sediments. D. S. Gorsline, ed. Proceedings, first national coastal and shallow water research conference, 1961 October, Tallahassee, Fla. National Science Foundation and Office of Naval Research.

Moore, H. F. 1907. Survey of oyster bottoms in Matagorda Bay, Texas. Rep. U.S. Comm. Fish., 1907. Doc. 610:1-86.

Needler, A. B. 1942. Sex reversal in individual oysters. J. Fish. Res. Board Can. 5(4):361-364.

Nelson, T. C. 1924. The attachment of oyster larvae. Biol. Bull. (Woods Hole) 46(3):143-151.

Nelson, T. C. 1925. The nannoplankton as a source of the oyster's food. Report of the Department of Biology, New Jersey Agriculture Experiment Station, New Brunswich, N.J., for the year ending 30 June 1924:197-199. (Published by the State, Trenton, N.J.)

Nelson, T. C. 1926. Report of the Department of Biology of the New Jersey Agriculture Experiment Station, New Brunswich, N.J., for the year ending 30 June 1925:281-288. (Published by the State, Trenton, N.J.)

Nelson, T. C. 1938. The feeding mechanism of the oyster. I. On the pallium and the branchial chambers of Ostrea virginica, O. edulis, and O. angulata, with comparisons with other species of the genus. J. Morphol. 63(1):1-61.

Nichy, F. E., and R. W. Menzel. 1960. Mortality of intertidal oysters in Alligator Harbor, Florida. Proc. Natl. Shellfish. Assoc. 51:33-41.

Pollard, J. F. 1973. Experiments to reestablish historical oyster seed grounds and to control the southern oyster drill. La. Wild Life Fish. Comm. Tech. Bull. 6. 82 pp.

Price, W. A. 1954. Oyster reefs of the Gulf of Mexico. U.S. Fish Wild. Serv. Fish. Bull. 89:491.

Quick, J. A., Jr. 1972. Fluid thioglycollate medium assay of Labyrinthomyxa parasites in oysters. Fla. Dep. Nat. Resour. Mar. Res. Lab. Leaf. Ser. 6(3):1-12.

Quick, J. A., Jr., and J. G. Mackin. 1971. Oyster parasitism by Labyrinthomyxa marina in Florida. Fla. Dep. Nat. Resour. Mar. Res. Lab. Prof. Pap. Ser. 13:1-55.

Ray, S. M. 1954. Biological studies of Dermocystidium marinum, a fungus parasite of oysters. Rice Inst. Pamphl. Spec. Issue. 114 pp.

Ray, S. M. 1966. Notes on the occurrence of Dermocystidium marinum on the Gulf of Mexico coast during 1961 and 1962. Proc. Natl. Shellfish. Assoc. 54: 45-54.

Ray, S. M., J. G. Mackin, and J. L. Boswell. 1953. Quantitative measurement of the effect of oyster disease caused by D. marinum. Bull. Mar. Sci. Gulf Caribb. 3(1):6-33.

Ritchie, T. P., and R. W. Menzel. 1969. Influence of light on larval settlement of American oysters. Proc. Natl. Shellfish. Assoc. 59:116-120.

Schechter, V. 1943. Tolerance of the snail, Thais floridana, to waters of low salinity and the effect of size. Ecology 24(4):493-499.

Smolowitz, R. J., and V. Nulk. 1982. The design of an electrohydraulic dredge for clam surveys. Mar. Fish. Rev. 44(4):1-18.

St. Amant, L. S. 1938. Studies on the distribution of the Louisiana oyster drill, Thais floridana haysae Clench. M.S. Thesis. Louisiana State University, Baton Rouge, La. 108 pp.

Stenzel, H. B. 1971. Oysters. Pages N935-N1224, Part N, Vol. 3, Mollusca 6, Bivalvia in R.C. Moore, ed. Treatise on invertebrate paleontology. Geological Society of America, Boulder, Colo.

Strickland, J. D. H., and T. R. Parsons. 1972. A practical handbook of seawater analysis. Fish. Res. Board Can. Bull. 167:1-310.

U.S. Fish and Wildlife Service (USFWS). 1981. Ecological services manual: standards for the development of habitat suitability index models (103 ESM). Division of Ecological Services, Fish and Wildlife Service, U.S. Department of the Interior, Washington, D.C.

U.S. Public Health Service (USPHS). 1965. National Shellfish Sanitation Program, manual of operations. Part 1. Sanitation of shellfish growing areas. USPHS Publ. No. 33:1-32 (1965 revision).

Van Sickle, V. R., B. B. Barrett, T. B. Ford, and L. J. Gulick. 1976. Barataria Basin: salinity changes and oyster distribution. La. Dep. Wild Life Fish. Tech. Bull. 20. 22 pp.

Veitch, F. P., and H. Hidu. 1971. Gregarious setting in the American oyster, Crassostrea virginica (Gmelin). I. Properties of a partially purified "setting factor." Chesapeake Sci. 12(3):173-178.

White, C. J., and W. S. Perret. 1974 Efforts to reestablish oyster tonging reefs in Lake Calcasieu, Louisiana. La. Wild Life Fish. Comm. Tech. Bull. 11. 15 pp.

Whitfield, W. K., Jr. 1973. Construction and rehabilitation of commericial oyster reefs in Florida from 1949 through 1971 with emphasis on economic impacts in Franklin County. Fla. Dep. Nat. Resour. Mar. Res. Lab. Spec. Sci. Rep. 38. 42 pp.

Woelke, C. E. 1960a. Preliminary report on laboratory studies on the relationship between fresh sulfite waste liquor and the reproductive cycle of the olympic oyster, Ostrea lurida. Wash. Dep. Fish. Res. Bull. 6:107-148.

Woelke, C. E. 1960b. Effects of sulfite waste liquor on the normal development of Pacific oyster (Crassostrea gigas) larvae. Wash. Dep. Fish. Res. Bull. 6:149-161.

Wood, L., and W. J. Hargis, Jr. 1971. Transport of bivalve larvae in a tidal estuary. Pages 29-44 in D. J. Crisp, ed. Fourth European malacology symposium. Cambridge University Press, Cambridge, U.K.

Yonge, C. M. 1928. The absorption of glucose by Ostrea edulis. J. Mar. Biol. Assoc. U.K. 15(2):643-653.

50272-101

REPORT DOCUMENTATION PAGE	1. REPORT NO. FWS/OBS-82/10.57	2.	3. Recipient's Accession No.

4. Title and Subtitle

Habitat Suitability Index Models: Gulf of Mexico American Oyster

5. Report Date

6.

7. Author(s)

Edwin W. Cake, Jr.

8. Performing Organization Rept. No.

9. Performing Organization Name and Address

Gulf Coast Research Laboratory
Oyster Biology Section
East Beach Drive
Ocean Springs, MS 39564

10. Project/Task/Work Unit No.

11. Contract(C) or Grant(G) No.

(C)

(G)

12. Sponsoring Organization Name and Address

National Coastal Ecosystems Team
Division of Biological Research
Research and Development
Fish and Wildlife Service
U.S. Department of the Interior
Washington, D.C. 20240

13. Type of Report & Period Covered

14.

15. Supplementary Notes

16. Abstract (Limit: 200 words)

A review and synthesis of existing information on the characteristics, life requisites, and specific habitat requirements were used to develop an estuarine habitat model for Gulf of Mexico stocks of the American oyster (Crassostrea virginica [Gmelin]). Eight habitat variables including two optional variables for oyster management and monitoring purposes were chosen, evaluated, and quantified into suitability index graphs. Those data were subsequently incorporated into a proposed Habitat Suitability Index (HSI) model for subtidal populations of the American oyster. The model can be easily modified for assessing and monitoring intertidal oysters from the Atlantic Coast of the U.S.

This is one in a series of publications developed to provide information on the habitat requirements of selected fish and wildlife species. The HSI model presented is designed to assist Fish and Wildlife personnel and interested state shellfish resource managers to assess environmental impacts of proposed estuarine activities and to assess, monitor, and upgrade oyster resources in coastal waters of the Gulf of Mexico. The HSI model is designed for use with Habitat Evaluation Procedures previously developed by the U.S. Fish and Wildlife Service.

17. Document Analysis a. Descriptors

Habitability
Invertebrates
Estuaries

b. Identifiers/Open-Ended Terms

Habitat
Habitat Suitability Index
American Oyster
Crassostrea virginica (Gmelin)

c. COSATI Field/Group

18. Availability Statement	19. Security Class (This Report)	21. No. of Pages
Unlimited	Unclassified	vi + 37
	20. Security Class (This Page) Unclassified	22. Price

(See ANSI-Z39.18)

OPTIONAL FORM 272 (4-77)
(Formerly NTIS-35)
Department of Commerce