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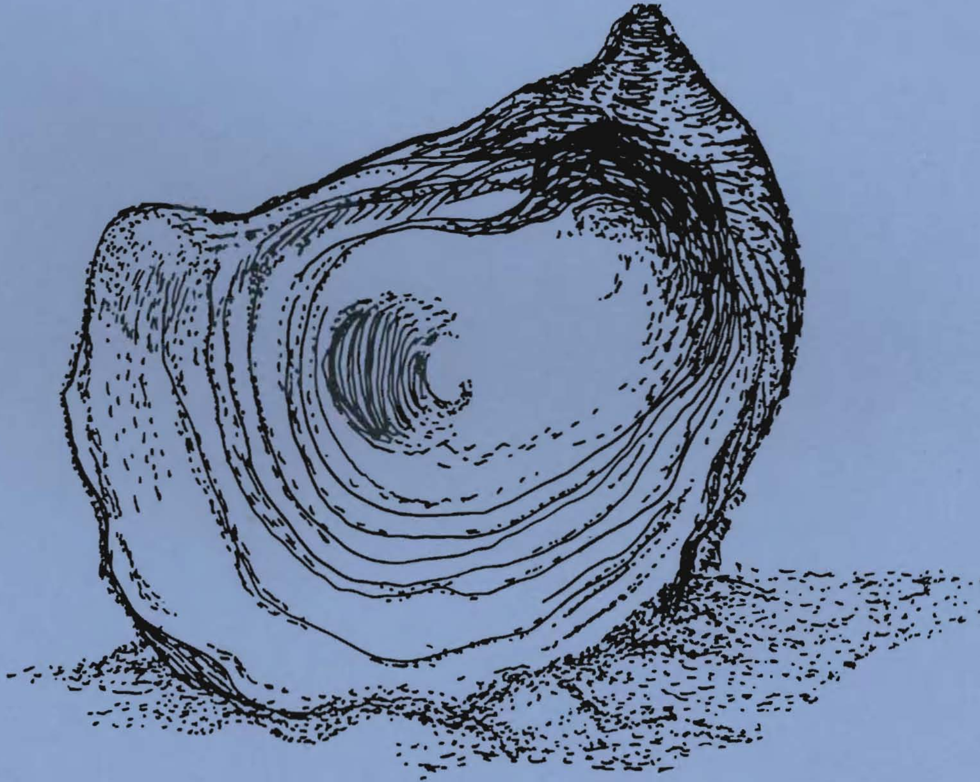
HABITAT SUITABILITY INDEX MODELS: GULF OF MEXICO AMERICAN OYSTER



Fish and Wildlife Service

U.S. Department of the Interior

This model is designed to be used by the Division of Ecological Services in conjunction with the Habitat Evaluation Procedures.

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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

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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

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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.

<u>Juvenile</u>. 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.

<u>Adult</u>. 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 water-borne 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.

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*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 habitats in the Gulf of Mexico where oysters normally exist and in those marginally acceptable habitats that may become more suitable in the future.

Geographic area. This oyster HSI model is intended for use in all subtidal estuarine areas of the Gulf of Mexico that comprise the Louisianian estuarine province as defined by Cowardin et al. (1979). Intertidal oysters were given only minor consideration in the formulation of this model because they are usually small and crowded, form small encrusting reefs, and are of little or no commercial value. Most of the suitable habitats for oysters along the gulf coast lie in relatively shallow water (< 10 m or 33 ft) and experience relatively small, mean diurnal tidal variations. It may be possible to apply the model to selected Atlantic coast habitats with some modifications.

Season. This HSI model was designed for application in all seasons. Measurements of larval variables, however, must be made for the time period that larvae are in the estuary.

Minimum habitat area. There is no known minimum habitat area for this species.

Verification level. Two biological experts reviewed, evaluated, and assisted in the development of the oyster HSI model: Dr. Winston Menzel, Department of Oceanography, Florida State University, Tallahassee; and Dr. Gordon Gunter, Director Emeritus, Gulf Coast Research Laboratory, Ocean Springs, Mississippi. The author is responsible, however, for the final version of this model.

Model Description

Overview. This HSI model for the American oyster is composed of two life stage components: (1) the settling larval stage (at metamorphosis) and (2) the postsettlement life stages (adults, seed, spat). The model considers the quality of the habitat for each of the two life stage components.

Gametes and fertilized eggs are free-drifting in the water column, but have been excluded from the model. Gametes typically are released only during optimal water conditions. Given their massive numbers, gametes are never limiting to the population. Fertilized eggs typically develop into the first swimming larval stage in several hours. Gametes and eggs have no habitat requirements beyond the water conditions which permit their parents to spawn.

When both components of the model are used, the model will produce one habitat suitability index for the entire life cycle. Suitability indices can be calculated for either the presettlement or postsettlement stages by using the individual components. Partial life cycle (HSI) values can also be calculated. Figure 1 illustrates how the HSI is related to the variables and life stages of the oyster.

Larval component. The habitat suitability of a given bottom area for metamorphosing (setting) oyster larvae is dependent on three variables: the presence of suitable cultch materials for setting (V_1), an appropriate salinity mean (V_2), and the presence of other oysters (V_3) (a gregarious factor). Cultch availability is probably the most important of the three, especially if all other conditions are acceptable. The salinity variable should already be accept-

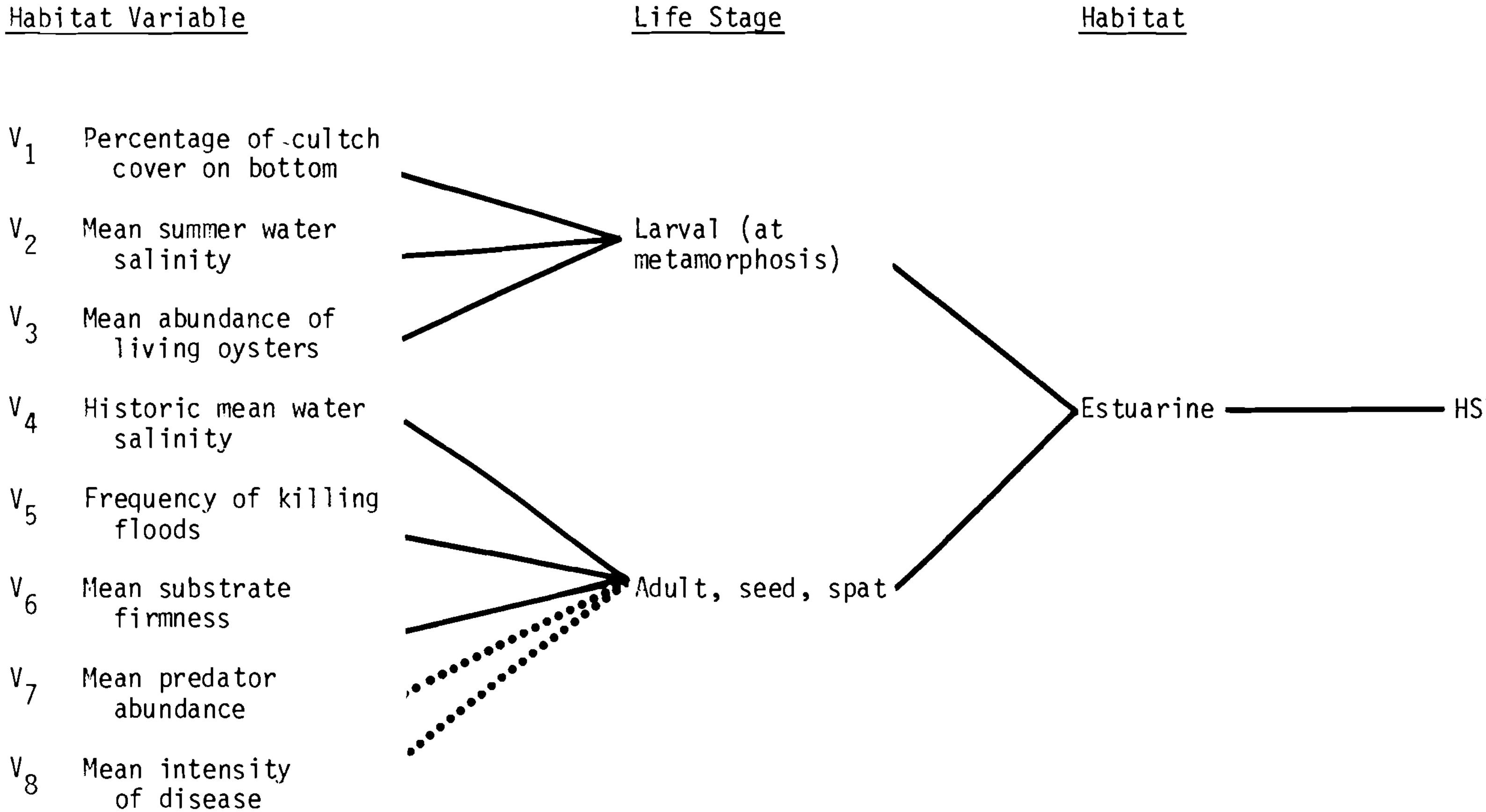


Figure 1. Tree diagram illustrating the relationship of habitat variables, life requisites, life stages, and habitat type to the Habitat Suitability Index (HSI) for Gulf of Mexico populations of the American oyster. For certain management applications, variables V_7 and V_8 should be included in the adult-seed-spat component.

able if the larvae are present and viable. The gregarious factor, while least important, is necessary for rapid setting of large numbers of spat on highly productive reefs and beds.

The larval component index is not designed to determine habitat suitability during the entire planktonic larval development. During that 10- to 14-day period, the eurytopic larvae are subject to ambient water qualities in the dynamic estuarine water mass. They are transported widely by tidal and wind currents and become well-dispersed. When attempting to determine habitat suitability, the planktonic trochophore and early veliger larvae are less important than the metamorphic eyed-pediveliger larvae immediately prior to setting because of their sheer abundance, extended spawning season, and relative eurytopicity. During that short interval (1 day or less) when the eyed-pediveligers are selecting suitable cultch and preparing to set (metamorphose), they are most vulnerable to the three subcomponent indices listed above. It is for this reason that the larval component of the oyster HSI is restricted, and yet important, in its application. The larval component index should be utilized primarily for determining short-term suitabilities of selected habitats, when the model user is attempting to predict spatfalls (mass attachment of spat), or when attempting to establish new oyster populations in otherwise suitable habitats by planting cultch materials. Even though the HSI of an oyster habitat may be temporarily unsuitable because of transitory water quality problems (e.g., depressed salinity, increased turbidity), that habitat should be acceptable during at least part of the extended spawning and setting season in the northern Gulf of Mexico.

Adult, seed, spat component. Two habitat variables contribute to water quality: prevalent water salinity and frequency of killing floods. The prevalent water salinity (V_4) affects the HSI of a given estuarine habitat, and is defined as the annual or historic salinity mean. If the prevalent salinity is too low (<5 ppt) for an extended period of time, oysters will die of osmotic stress; if the salinity is too high (>25 ppt) for an extended period of time, the oysters will be killed off by high salinity predators that invade the area. The best salinity range is considered to be 10 to 20 ppt.

The frequency of killing floods (V_5) is important in determining the long-term suitability of a given habitat, especially if that habitat is located near or within the mouth of a river with a history of frequent flooding. Flood waters will kill attached oysters directly via osmotic stress or indirectly via increased siltation over the reefs. Flood waters will also interfere with gametogenesis, spawning, feeding, growth, and the availability of exposed cultch (for metamorphosing juveniles). The importance of this variable is a function of the frequency of killing floods and the time required for oysters to recolonize the area in question. If those floods occur annually, the habitat is unsuitable. The suitability increases geometrically as the frequency decreases. (Oysters require 2 to 3 years to recover to preflood densities in Mississippi Sound.)

The substrate condition is described by a single variable: the firmness of the bottom substrate (V_6); it is important for support of large populations of oysters. The mean substrate firmness, as determined by a hand-held penetrometer, is a function of the substrate content. Substrates with a firmness of less than 1.0 kg/cm^2 are considered inappropriate for oyster survival and growth unless cultch materials such as clam and/or oyster shells, gravel, etc., are added to increase the firmness.

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.

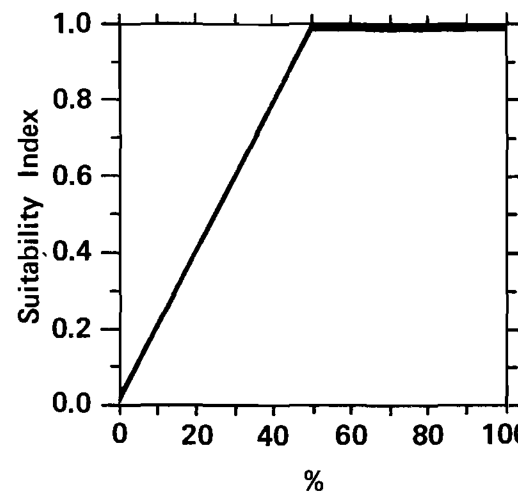
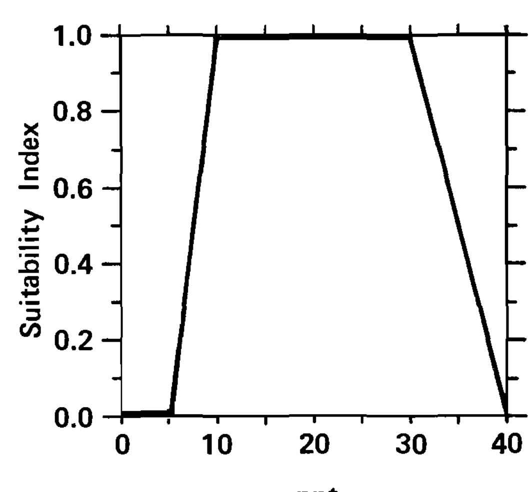
Oysters are killed in massive numbers by numerous predators including man, but none is more damaging than the southern oyster drill (Thais haemastoma). The relative abundance (mean number/m^2) of mature drills (>4 cm or 1.6 inches in length) is included as a model variable for this reason. Abundance 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.

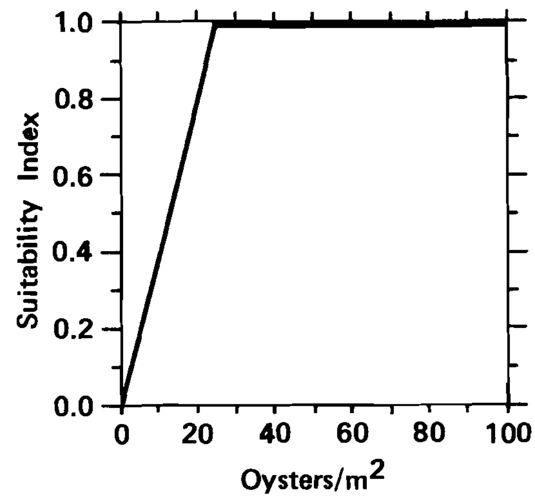
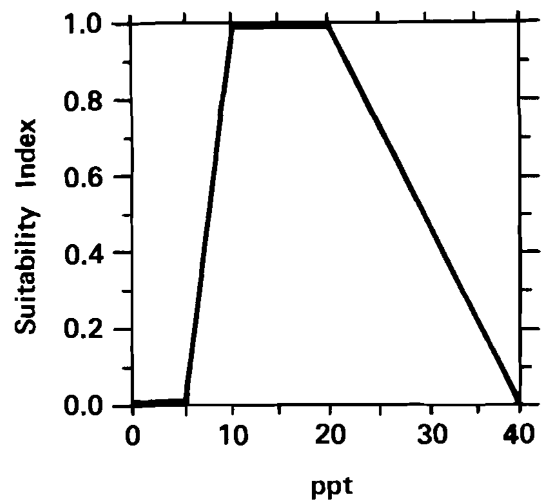
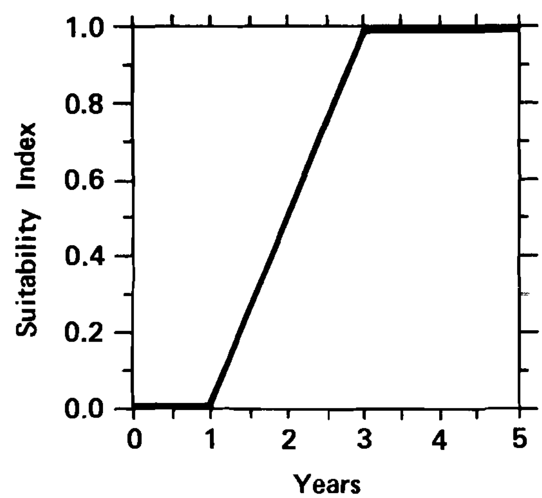
Mass mortalities of adult oysters that often exceed 50% frequently occur during elevated summer temperature regimes as a result of the protozan pathogen Perkinsus marinus (Mackin, Owen, and Collier) (vide: Levine 1978). Although other pathogens and parasites infect gulf coast oysters, none is more prevalent 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.	

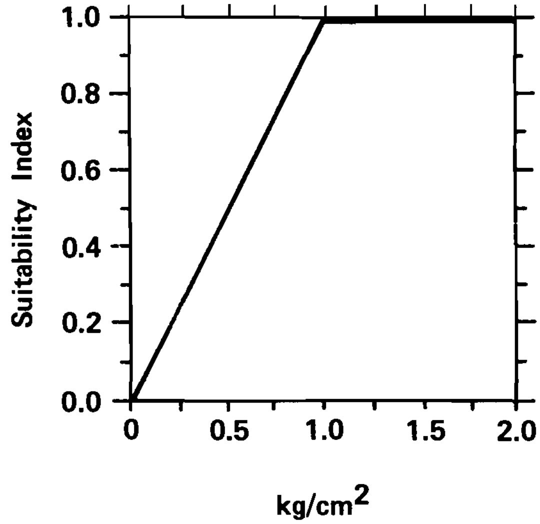
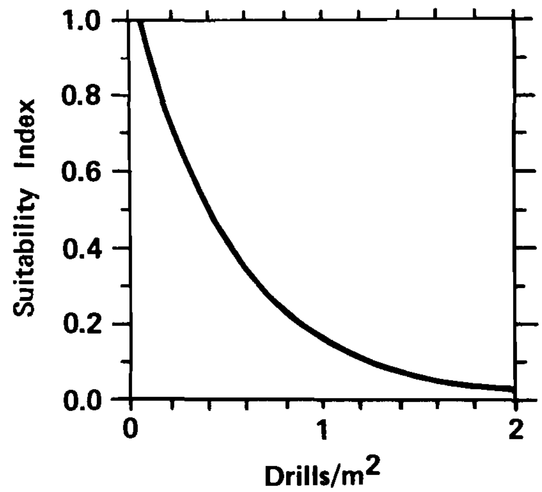
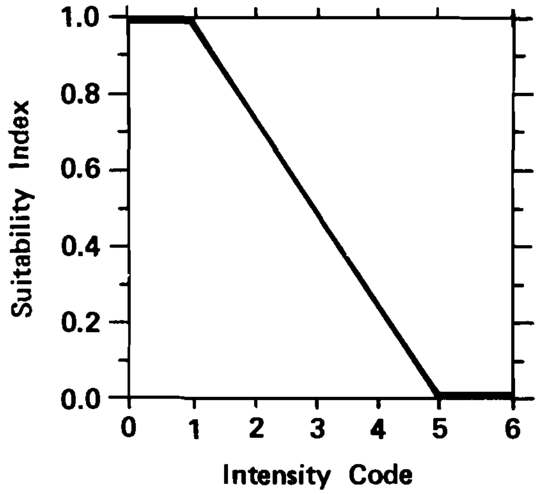
Habitat	Variable		Suitability Graph
E	V_6	Mean substrate firmness (penetrometer value).	
E	V_7	Mean predator abundance (southern oyster drills).	
E	V_8	Mean disease intensity (*Perkinsus marinus*).	

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 ≤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 ≥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 ≥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 ≥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 ≥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

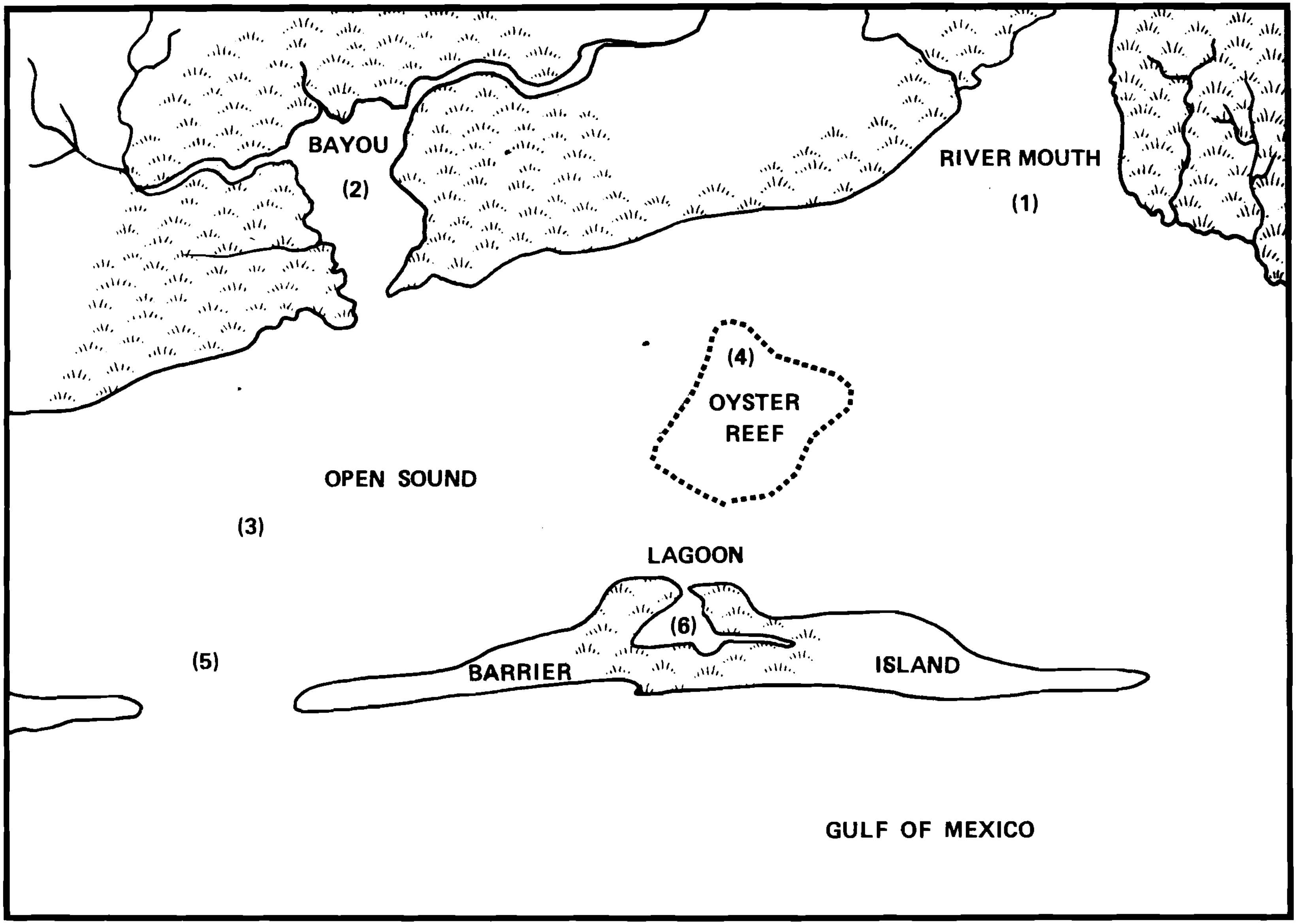


Figure 2. Hypothetical locations for oyster habitats in the northern Gulf of Mexico. Location numbers correspond to hypothetical data sets of Table 3.

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.

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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

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Invertebrates
Estuaries

b. Identifiers/Open-Ended Terms

Habitat
Habitat Suitability Index
American Oyster
Crassostrea virginica (Gmelin)

c. COSATI Field/Group

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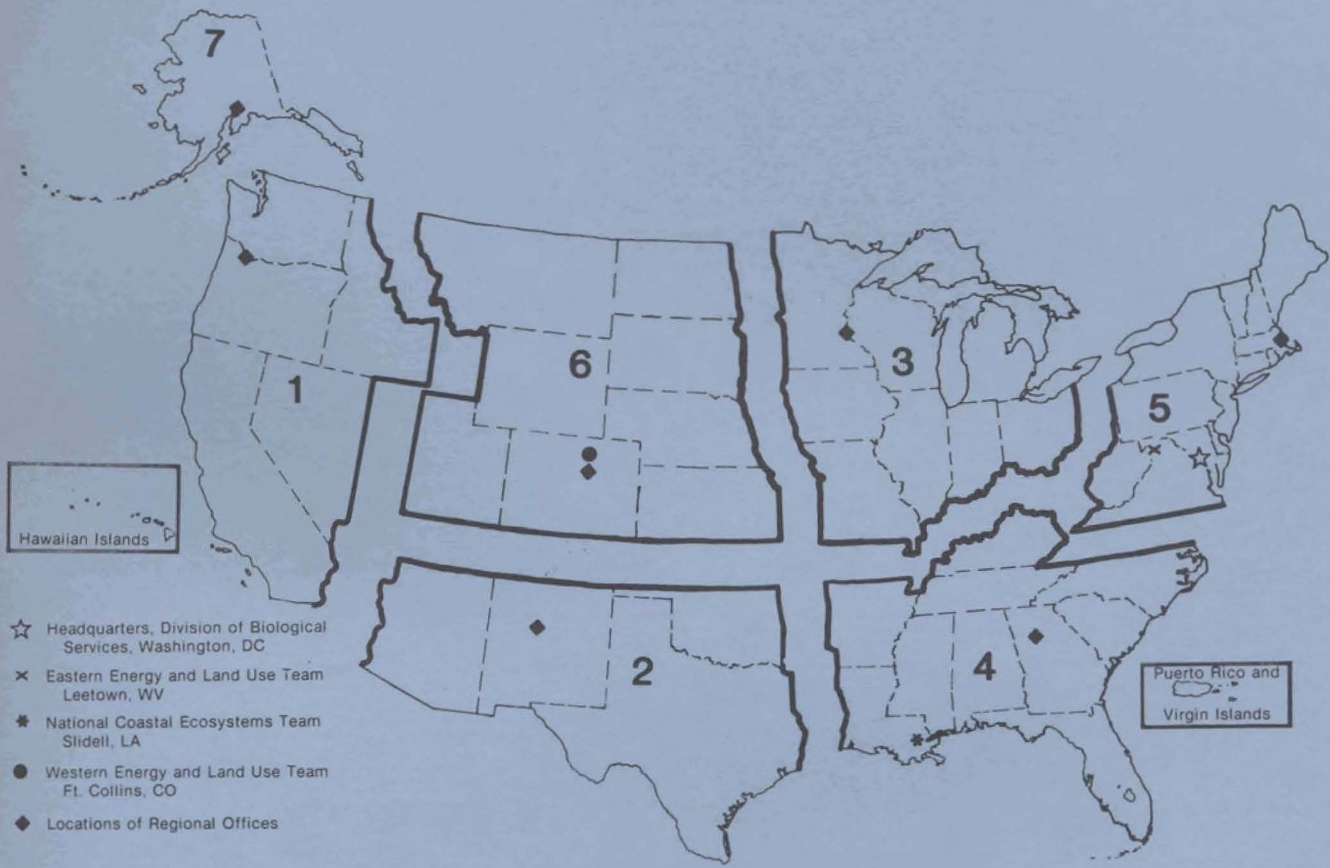

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U.S. Fish and Wildlife Service
Lloyd Five Hundred Building, Suite 1692
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