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Species Profiles: Life Histories and Environmental Requirements of Coastal Fishes and Invertebrates (South Atlantic)

AMERICAN OYSTER

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U.S. Department of the Interior

Coastal Ecology Group
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U.S. Army Corps of Engineers

CONTENTS

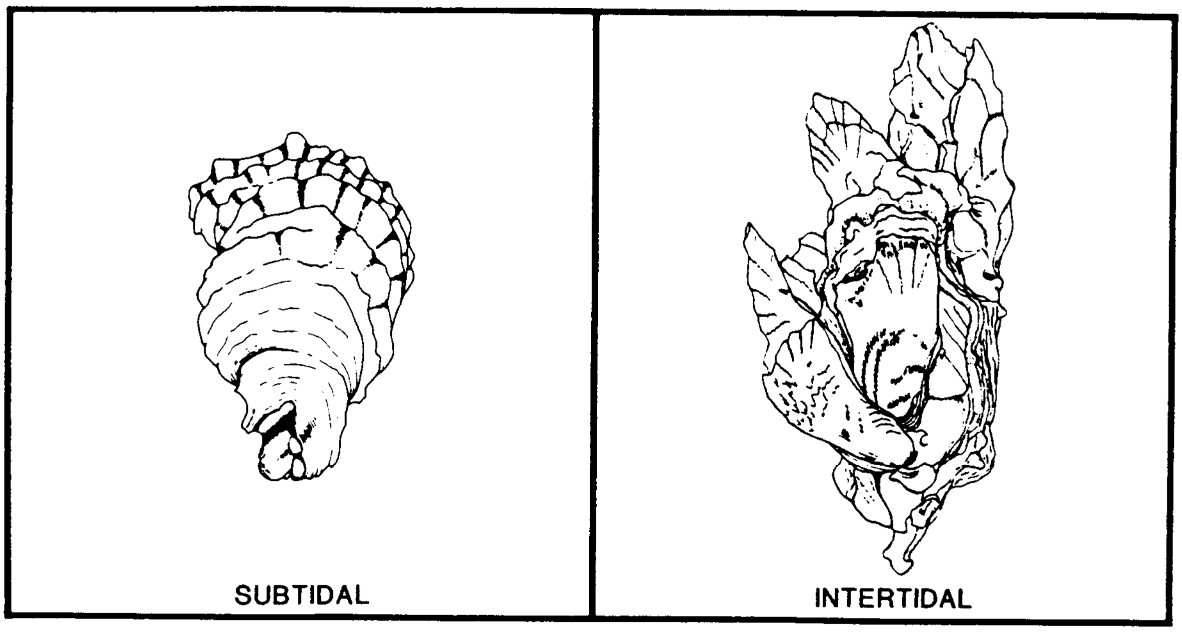

Figure 1. American oysters, *Crassostrea virginica*, from subtidal and intertidal habitats in the South Atlantic region.

AMERICAN OYSTER

NOMENCLATURE/TAXONOMY/RANGE

Scientific name............*Crassostrea virginica* (Figure 1)
Preferred common name.........American oyster
Other common names......Eastern oyster and when referring to long, thin shelled *C. virginica* growing intertidally, coon oyster
Class........................Bivalvia
Order........................Pteroidea
Family.......................Ostreidae

Geographic range: Found in sounds, bays, and estuaries from New Brunswick, Canada, to the Gulf of Mexico. Throughout most of its range, it grows subtidally; however, in the South Atlantic States from about the Newport River, North Carolina, south along the east coast of Florida, it occurs principally in dense, intertidal beds (Figures 2 and 3; Galtsoff 1964; Abbott 1974).

MORPHOLOGY/IDENTIFICATION AIDS

Shell weight and shape can be highly variable, ranging from heavy shell and fairly regular in subtidal single oysters to thin, elongated, and highly irregular in intertidal oysters (Figure 1). The left valve, which is attached to the substrate, is usually thicker and more deeply cupped than the right. The adductor muscle scar is located posteriorly and is generally pigmented; no hinge teeth are present. *Ostrea equestris*, or horse oyster, closely resembles *C. virginica*, but the muscle scar is more centrally located and not generally colored, and small denticles are present on either side of the right valve hinge. These denticles fit into corresponding depressions in the margin of the left valve. *Ostrea equestris* averages only about 5 cm in height, and therefore is not of commercial interest. It is most often found in higher salinity (35 ppt) than

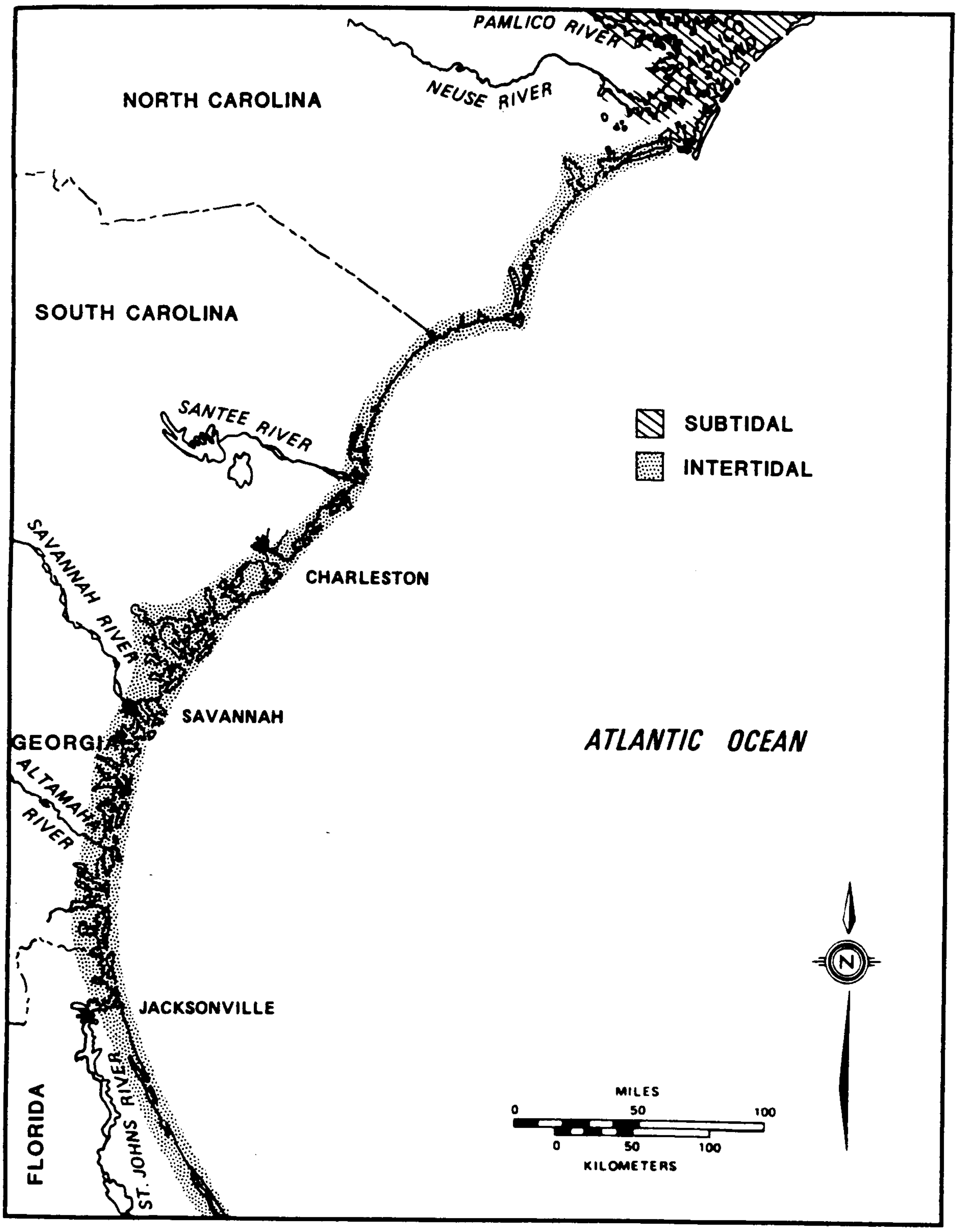

Figure 2. Distribution of predominantly subtidal and intertidal oysters in the South Atlantic region.

Figure 3. A typical intertidal oyster bar showing the dense growth common to these areas.

C. virginica, but both species may co-occur in salinities as low as 20-25 ppt (Menzel 1956; Yonge 1960; Galtsoff and Merrill 1962; Galtsoff 1964; Porter and Tyler 1974).

REASON FOR INCLUSION IN SERIES

The American oyster has been exploited commercially since the mid-19th century in the South Atlantic region and continues to support a prominent fishery in North Carolina and South Carolina (Burrell 1985a; Figure 4). It is also an important recreational species (Moore et al. 1984).

Vast intertidal reefs constructed by oysters are significant biologically and physically in estuaries of the South Atlantic region. Fishes, crabs and shrimp are among the animals that utilize the intertidal reefs while they are submerged for refuge and also as a source of food, foraging on the many reef dwelling species. Reefs, as they become established, modify tidal currents and this in turn affects sedimentary patterns. Further, the reefs contribute to the stability of stream bottoms and banks and to the bordering marsh as well (Wells 1961; Bahr and Lanier 1981; Cake 1983).

LIFE HISTORY

Spawning

Water temperature stimulates gametogenesis and spawning in the American oyster and critical temperatures vary over the geographical range. Spawning begins at 16.4 °C in Long Island Sound, 20.0 °C in more southerly areas, and 25 °C in the Gulf of Mexico (Loosanoff 1969). McNulty (1953) reported that South Carolina intertidal oysters

Figure 4. Intertidal oysters being picked by hand. This is the chief means of harvesting intertidal oysters.

spawned when surface temperatures ranged from 18.6 °C to 25 °C. Burrell et al. (1984) found that both subtidal and intertidal oysters were ripe throughout the year. Spawning was intermittent at salinities averaging 25 ppt or higher from May to November. In a lower salinity area (less than 20 ppt), spawning of subtidal oysters appeared to be restricted to one major period in midsummer (temperature above 30 °C), while intertidal oysters spawned during two major periods: one in early summer (>30 °C) and one in fall (>23 °C). Durant (1969) reported that the spawning season in Georgia lasted from May, when temperatures reached 23 °C, to November. In Apalachicola Bay, Florida, spawning, as indicated by the appearance of young oysters on planted shell, began the second week of April when temperatures reached 22.5-24.0 °C and continued through the second week of November. Mass spawning did not occur until temperatures reached 26.0 °C (Ingle 1951).

Spawning in females is triggered by release of sperm into the water column (Andrews 1979; Bahr and Lanier 1981). Oysters may spawn several times during a season; intermittent protracted spawning is typical in intertidal oysters. A rapid increase in temperature also often triggers spawning in oysters (Hidu and Haskins 1971; Dupuy et al. 1977). Intermittent spawning in intertidal oysters may result from greatly fluctuating temperatures on intertidal reefs. Lunz (1960) reported variations of 16 °C within a few minutes. Galtsoff (1964) estimated one female discharged 114.8 million eggs at a single spawning. Number of eggs released varies with size and condition of the female and number of spawns (Galtsoff 1964).

Eggs and Fertilization

Eggs of *Crassostrea virginica* are compressed and pear-shaped measuring from 55 to 75 µm in the long axis and 35 to 55 µm wide (Galtsoff 1964). Trochophore larvae develop within 6 to 9 h after egg fertilization, and metamorphose into straight hinge or veliger larvae at 12 to 16 h after fertilization (Galtsoff 1964; Dupuy et al. 1977). The straight hinge larvae and subsequent stages are planktonic and remain in the water column for up to 3 weeks, with planktonic time varying with available food, water temperature and salinity (Bahr and Lanier 1981; Cake 1983). Oyster larvae are transported throughout estuarine systems by tidal action. Larvae concentrate near the surface on rising tides and near the bottom on falling tides, thus increasing their chances of being more widely distributed in an estuary and not being swept out to sea (Carriker 1951; Haskins 1964; Wood and Hargis 1971).

The final larval stage, called the pediveliger or eyed larva, is approximately 300 μm in diameter and is characterized by a well-developed foot and two eye spots. The foot enables the larvae to crawl on the bottom to seek substrate suitable for attachment. The early sessile stage of the oyster is called spat and the process of attachment is called setting or spatfall. The pediveliger may explore several sites before permanently attaching the left valve to the final substrate with cement produced by a larval organ, the byssus gland.

Spat

Pediveligers rapidly lose many larval features after attachment. The foot and eye spots are lost and the velum is incorporated into parts of the alimentary system (Galtsoff 1964). Attachment substrate may be any hard substance such as glass, concrete, bits of rock or other shell. Oyster shell is most often chosen by the pediveliger. Oyster planters distribute molluscan shell called cultch for this purpose (Burrell 1985b). Larval set is stimulated by an increase in temperature (Lutz et al. 1970; Hidu and Haskins 1971). Bahr and Lanier (1981) reported that while oysters tend to be photopositive during larval stages, they may become photonegative as water temperature increases.

Heaviest spatfall may occur below mean low water in the South Atlantic States; however, survival is much greater at just above mean low water (Chestnut and Fahy 1953; McNulty 1953). Lower survival below mean low water may be a result of predation or of fouling by competitors and current-borne silt (Dean 1892; Chestnut and Fahy 1953; McNulty 1953; Linton 1969).

Adult

Once attached, oysters remain in the same location throughout life unless they are moved by man. In the South Atlantic States, oysters (with only a few exceptions) occur in intertidal beds that become established when conditions permit; that is, when salinity, current, food, supporting substrate, and turbidity are suitable (Burrell et al. 1981; Cake 1983). These beds provide habitat for numerous estuarine animals (Wells 1961; Dame 1972, 1979; Bahr and Lanier 1981; Cake 1983; Manzi et al. 1985). Stream channels are influenced by oyster reefs, which serve as either a stabilizing influence or modifying force as these reefs grow. Subtidal oyster beds do occur naturally but rarely in Southeastern States and provide habitat for other shellfish such as hard clams, Mercenaria mercenaria (Burrell 1977).

Adult oysters are usually dioecious, but sex changes are frequent. Generally, yearling oysters are predominantly males, but older oyster populations become preponderantly females. Even in oysters several years old, however, sex reversals are common and females may become males again or vice versa (Galtsoff 1964).

GROWTH

Ingle (1950) found that growth of American oysters in Florida exceeded 100 mm in 31 weeks; growth in length was greatest in the first 6 weeks after setting. Palmer (1976) recorded increases in average length of Georgia oysters over a 7-month period (November to June): in subtidal and intertidal animals, increases were 31.1 mm and 19.6 mm, respectively, when beginning sizes were 10-19 mm and 10.2 mm; subtidal oysters grew 3.0 mm when beginning size was 100 mm. Manzi et al. (1977) and Burrell et al. (1981) reported monthly growth of 1 to 4 mm in South Carolina oysters. Growth is continuous throughout the year, as far north as South Carolina, although it slows appreciably in midwinter in South

Carolina (Burrell et al. 1981). Growth appears to be most rapid in summer (Ingle 1950).

Growth appears to be greater in subtidal oysters than in intertidal oysters; however, this may be a result of crowding on intertidal beds (Burrell 1982). Gillmor (1982) found that oyster growth was better per unit immersion time at some depths below mean high water in the intertidal zone than in subtidal beds. Protracted spawning seasons may also retard growth in intertidal oysters because of energy demands for this activity (McNulty 1953). Lunz (1955), Anderson (1976), and Manzi et al. (1977) found that growth in salt ponds exceeded that in adjacent waterways.

COMMERCIAL HARVEST

The oyster industry has provided employment for many watermen in the South Atlantic States (Maggioni and Burrell 1982). In the early 1900's, annual landings generally exceeded 10 million pounds and peaked at nearly 20 million pounds in 1908. Production then declined steadily until 1970. From the mid-1970's to 1984, landings remained fairly steady at about 2 million pounds (Burrell 1982, 1985a; Figure 5). Several principal causes of this decline have been suggested:

1. Loss of labor to competing industries.
2. Growing area lost to production because of pollution, changes in salinity patterns caused by coastal development and changes in farming and forestry practices.
3. Management practices that do not encourage good husbandry.
4. Lack of modern technology in culture, harvest and processing sectors.

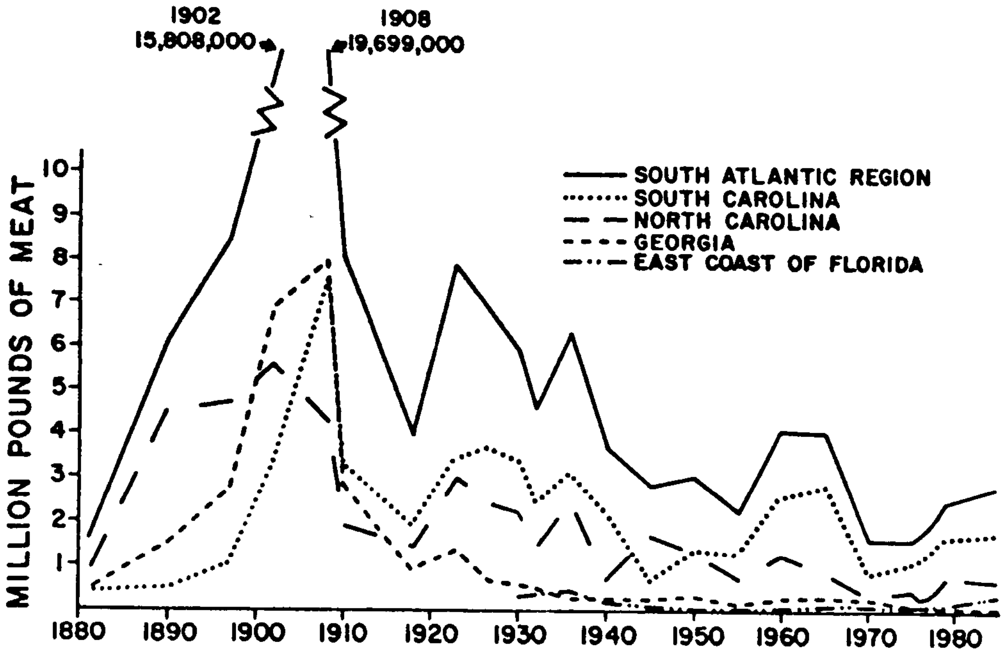

Figure 5. Oyster landings 1880-1984 for the individual States and for the region as a whole (Fishery Statistics of the United States, 1880-1979: fishery statistics offices for States involved, 1980-1984).

5. Laws that do not encourage increased investment in the industry.

6. Finally, and probably most importantly, the lack of markets for the intertidal oyster. This shellfish does not lend itself to raw shucking and must therefore be opened chiefly by steam. The meats are then canned as a cooked product that has a very limited demand and must compete with cheap imports. The number of canneries has dropped in South Carolina alone from 16 in 1905 to one today (Keith and Gracy 1972). The other viable market for intertidal oysters is sales to individuals or groups for oyster roasts. These roasts are traditional coastal social events and offer little potential for expanding the market.

Biological problems such as disease, recruitment failure, and predators influence production of southern intertidal oysters less than northern subtidal stocks. An overabundance of set and high survival is a greater problem for the southern oyster grower. The intertidal reefs tend to become overgrown with small and densely crowded oysters. Limited markets compound the problem because many more oysters are available on reefs than can be sold and, therefore, the reefs are not harvested regularly.

Oyster meat yield per volume of shell stock is lower in the South Atlantic States than in other oyster-growing areas because of the poor condition of the oysters due to a protracted spawning season, and because the crowded oysters in the intertidal zone are small, elongate, and thin shelled. Yield in Virginia oysters averaged 6.0 to 6.5 pints/ bushel raw shucked, while in South Carolina canneries the yield was only about 1 pint per bushel (Lunz 1950).

Each State of the South Atlantic region has a program of some sort designed to revitalize their oyster industry (Cowman 1982; Maggioni and Burrell 1982; Munden 1982). Mechanical harvesters are being used in North and South Carolina to move oysters from areas closed to harvesting and from very dense beds to public grounds in order to improve stocks in these areas. (Figure 6; Munden 1982; Manzi et al. 1985).

Population Dynamics

Sellers and Stanley (1984) reviewed mortality of larvae in subtidal growing areas. They noted that mortality varies greatly according to area, vulnerability to predators and intensity of set. Nelson (1925) noted that lobate ctenophores fed on oyster larvae and that abundance of ctenophores was inversely correlated with abundance of oyster set in New Jersey waters. Spat mortality is not a problem in the southern intertidal oyster; invariably more spat survive than are needed to repopulate reefs and, as mentioned, overcrowding and poor growth result. Mortality of spat in North Carolina and South Carolina increased with depth below mean low water (Chestnut and Fahy 1953; McNulty 1953). McKenzie (1981) calculated survival rates based on yearly changes in population; initial approximate spat density was 200 to $10,000/m^2$, at 1 to 2 years numbers fell to $300/m^2$, and at 3 to 4 years only $75/m^2$ remained. Burrell et al. (1981) observed in trays at several locations in South Carolina that yearly mortalities exceeded 50% in seed oysters 2 years old at transplanting and less than 22% in seed 1 year old at transplanting. In another study of South Carolina oysters (Manzi et al. 1977), adult oysters planted subtidally had survival rates of 85% to 91% in salt ponds and 92.5% to 94.5% in adjacent streams. Reisinger (1978) reported monthly mortalities ranging from less than 5% to 40% in a Georgia intertidal bed.

ECOLOGICAL ROLE

Larvae are planktivores feeding

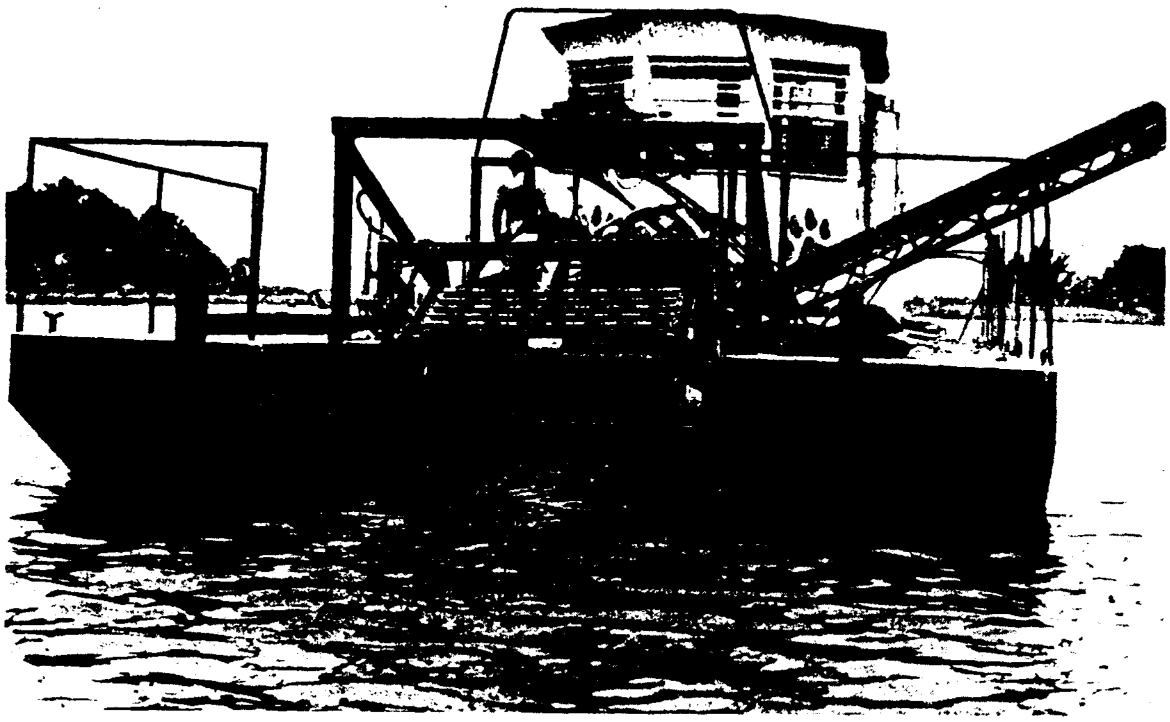

Figure 6. A mechanical intertidal oyster harvester being used to rehabilitate public oyster grounds in South Carolina.

principally on small naked flagellates and diatoms. Detrital particles and bacteria associated with particles, and possibly, dissolved organic compounds, may also be of nutritional importance to oyster larvae (Galtsoff 1964; Bahr and Lanier 1981; Cake 1983). Larvae are in turn consumed by a large number of predators that include copepods, ctenophores, jellyfish and the young of fish and crustaceans (Nelson 1925; Andrews 1979).

Adult oysters also feed primarily on phytoplankton. Preferred size of naked flagellates selected by oysters was reported by Haven and Morales-Alamo (1970) to be 3 to 4 µm. Under optimal conditions of temperature and salinity, an oyster pumps water at the rate of 15 l/h. (Galtsoff 1964). The daily volume of water filtered by intertidal oysters is not known, but presumably it is less than that of subtidal oysters for no other reason than intertidal oysters may spend half their lives out of water. The extensive salt marshes bordering tidal creeks serve as nutrient and organic detritus sinks and their flushing provides a rich food source for oysters (de la Cruz 1973; Manzi et al. 1977).

Intertidal oyster reefs provide habitat for countless infaunal and epifaunal species. Wells (1961) listed 303 species from both intertidal and subtidal reefs in North Carolina; Bahr (1974) reported some 42 species or groups associated with intertidal reefs in Georgia; and Dame (1979) found 37 species and Manzi et al. (1985) listed 89 species for South Carolina intertidal reefs. Dame (1979) reported the average number of individuals/m^2 to be 2,949, and Bahr (1974) 24,747/m^2 of associated animals living on intertidal oyster reefs in South Carolina and Georgia, respectively. Reefs also intercept tidal currents and may profoundly affect the suitability of adjacent areas for other species.

The density of oysters growing in intertidal reefs almost defies comprehension. Lunz (1960) counted 5,895 oysters, or 4.5 U.S. bushels, in an area of 1 yd^2. In another study, he reported an average of 135.9 2-inch oysters per square yard in 117 samples (Lunz 1943). Bahr and Lanier (1981) estimated that oysters alone accounted for approximately 87.5% of the biomass and 48.1% of the respiration on an oyster reef. Lunz's (1943, 1960) estimates suggest that this value appears reasonable.

Many theories have been put forth to explain the success of intertidal oysters in the South Atlantic States and the lack of success of subtidal oysters. These include avoidance of predators such as drills (*Eupleura caudata*, *Urosalpinx cinerea*), whelks (*Busycon carica*, *B. canaliculatum*), crabs (*Callinectes* sp. and family Xanthidae), starfish (*Asterias forbesi*), fish (*Rhinoptera bonasus*, *Pogonias cromis*), and flatworms (*Stylocus ellipticus*) (Battle 1892; Carriker 1955; Lunz 1960; Merriner and Smith 1979; Bahr and Lanier 1981; Sellers and Stanley 1984). Boring sponges (*Cliona* spp.) and annelid worms (*Polydora* spp.), which cause considerable damage to subtidal oysters, are not a problem in the intertidal zone (Lunz 1947).

Other reasons that may account for oyster reef concentrations in the intertidal zone are the presence of more suitable substrates, more available food, less turbidity, more suitable current velocities, higher spatfall, exclusion of some disease-causing organisms, and genetic differences leading to physiological selection (Lunz 1941, 1943; Haven and Burrell 1982; Burrell et al. 1984). Recent studies have shed light on two of these conjectures. No evidence of genetic differences between subtidal and intertidal oysters from the same South Carolina river system was determined in an electrophoretic study by Anderson and Weir (W. W. Anderson, Department of Molecular and Population Genetics, University of Georgia, Athens; pers. comm.). Burrell et al. (1984) found the incidence and intensity of infection of subtidal and intertidal oysters by the pathogen *Perkinsus marinus* to be of the same magnitude in two areas of South Carolina; thus this disease did not appear to be influenced by habitat elevation. Other oyster diseases, such as Delaware Bay disease caused by the haplosporidean *Minchinia nelsoni* and seaside disease caused by the haplosporidean *M. costalis* have not been reported south of North Carolina along the Atlantic coast.

Subtidal oysters compete for growing space with barnacles (*Balanus* spp.), scorched mussel (*Brachidontes exustus*), ribbed mussel (*Geukensia demissa*) and jingle shell (*Anomia simplex*). The distribution of intertidal oysters does not appear to be affected by these organisms (Dame 1970).

ENVIRONMENTAL REQUIREMENTS

The eastern oyster is a very successful estuarine animal and, as such, it tolerates widely varying salinities, temperatures, currents and turbidities (Andrews 1979). The intertidal oyster thrives in the most rigorous of habitats (Lunz 1960). Tolerance to extremes of one environmental condition is often modified by interaction of another condition such as an oyster's ability to survive low salinity in cold weather (Andrews et al. 1959). It is, therefore, difficult to precisely define environmental requirements.

Temperature

As a general rule, *C. virginica* requires temperatures above 19.5°C for egg development. Larvae develop properly above 20 °C and adults grow at temperatures 10 to 30 °C or higher (Galtsoff 1964; Burrell 1985b). Southern intertidal oysters are able to withstand summer temperatures above 43 °C when exposed to the sun and then sudden drops to 26 °C when the tide again covers the bed (Lunz 1960). Oysters are also exposed to winter air temperatures that may fall below freezing; even when these oysters are exposed several hours to these extremes, they apparently tolerate them well. However, mortality in several oyster beds in the McClellanville, South Carolina, area was almost 100% when air temperatures suddenly dropped 19 °C in 24 h after several weeks of above normal rainfall (Purvis 1983). The 1982 cold wave was the most severe for December in South Carolina's history, but lower than normal salinity caused by heavy rainfall may also have been a contributing factor to this mortality. Oyster growers in the area reported deaths from freezing were most unusual in these beds.

Salinity

Castagna and Chanley (1973) in a review of salinity requirements for life stages of oysters reported that egg cleavage occurred at 7.5 to 35 ppt with optimal development at 10 to 22 ppt, larvae developed at 5 to 39 ppt, and growth was best at 25 to 29 ppt. Metamorphosis occurred between 5.6 and 35 ppt. Spat grew best at salinities of 15 to 26 ppt (Chanley 1957). Adult oysters were produced commercially in Florida in areas where the salinity varied from 0 to 42.5 ppt (Ingle and Dawson 1950). Growth is most favorable at 14 to 30 ppt (Castagna and Chanley 1973).

Heavy rains in the watersheds of rivers feeding estuaries may on occasion cause catastrophic kills. This may be associated with tropical storms or higher than usual spring rains (Andrews et al. 1959; May 1972; Haven et al. 1976; Burrell 1977). Intertidal oysters in the South Santee River, South Carolina, suffered higher losses as a consequence of low salinity than did subtidal oysters in the same system. This would be expected because surface water would tend to be less saline than bottom water and intertidal oysters would be subject to fresher water for a longer period. However, mortalities among subtidal and intertidal oysters were near identical in an adjacent estuary at the same time (Burrell 1977). Oysters died from lack of oxygen in the James River, Virginia, in winter and early spring 1979-80 because freshwater covering the beds prevented the animals from feeding and respiring (Andrews 1982). This appears to be a fairly regular phenomenon in the Rappahannock River, Virginia, in wet years (Haven et al. 1976; Andrews 1982). Moderate salinities (those less than 15 ppt) for a significant period during the year may be beneficial in that most predators are excluded or their numbers greatly reduced and some disease organisms are kept out or their virulence is markedly weakened in these areas (Haven et al. 1978; Burrell et al. 1981).

Dissolved Oxygen

Oysters are tolerant of low dissolved oxygen, surviving at concentrations as low as 1 ppm (Andrews 1982). In laboratory studies, larvae ceased to swim and died after 3 days when oxygen concentration was 0.1 ppm and young spat died within a week; however, adult oysters survived much longer at the same concentration (Haven et al. 1978). Hourly oxygen uptake is low in oysters, 15.5 cc/kg dry wt., as would be expected for a sedentary animal (Nicol 1960). Furthermore, oysters probably use less than 10% of the oxygen available in the feeding currents passing over their gills (Galtsoff 1964).

Habitat

The preferred habitat for oysters in the South Atlantic region is from just below the mean low water level to about 1 m above mean low water (Sandifer et al. 1980). If all other conditions are suitable, a firm bottom is not necessary for a reef to become established. A few oysters may attach to a bit of shell or wood in a mudflat, and other oysters attach to them, pushing them into the mud and smothering them but providing substrate for subsequent spat. This process continues until the first set, long since dead, sinks deep enough into the mud to reach a sufficiently firm stratum to prevent further subsidence. Shells growing on top of the buried shell reach the surface of the mud and provide attachment area for subsequent crops of oysters. The reef then expands from this beginning. The underlying matrix supporting reefs is fairly fragile in places and its integrity can be damaged by heavy harvesting gear. Water currents must be strong enough to provide food. (Galtsoff (1964) estimated that water passing over an oyster reef should be renewed 72 times in a 24-h period.) Also, currents must wash away sediments and biodeposits of animals inhabiting the reef (Haven and Morales-Alamo 1966). Currents of too great a velocity can interfere with feeding and cause structural damage (Galtsoff 1964). Planting shell to establish an intertidal oyster reef can be a futile exercise in many cases because the shell may serve as a baffle in the current and collect sediment and that results in rapid silting over (Smith 1949).

Other Environmental Factors

A fairly large tidal range increases the intertidal area in the South Atlantic States because of little relief in coastal areas. This tide range is from about 1.5 to 2.1 m. These tides provide a mechanism for flushing adjacent marsh areas and enriching the oyster-growing water (Manzi et al. 1977). Because turbidity is high in southern estuaries, phytoplankton production is comparatively low; consequently marsh contribution to oyster nutrition is probably much more important here (Manzi et al. 1977).

Oysters, while tolerant of fairly turbid water, decrease pumping rate with increase in silt concentrations above 1.0 g/l and death may occur after long-term exposure. Egg survival was only 73% in water with a silt concentration of 0.25 g/l, and at 0.75 g/l growth of larvae was significantly affected (Loosanoff and Tommers 1948; Loosanoff 1962).

LITERATURE CITED

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

Anderson, W.D., III. 1976. A comparative study of a salt water impoundment with its adjacent tidal creek pertaining to culture of Crassostrea virginica (Gmelin). M.S. Thesis. Old Dominion University, Norfolk, Virginia. 65 pp.

Andrews, J.D. 1979. Pelecypoda: Ostreidae. Pages 293-341 In A.C. Giese and J.S. Pearse, eds. Reproduction of marine invertebrates. Vol. 5: Molluscs: Pelecypoda and lesser classes. Academic Press, New York.

Andrews, J.D. 1982. Anaerobic mortalities of oysters in Virginia caused by low salinities. J. Shellfish Res. 2(2): 127-132.

Andrews, J.D., D.S. Haven, and D.B. Quayle. 1959. Freshwater kill of oysters, Crassostrea virginica, in James River, Virginia. Proc. Natl. Shellfish. Assoc. 49: 29-49.

Bahr, L.M. 1974. Aspects of the structure and function of the intertidal oyster reef community in Georgia. Ph.D. Dissertation. University of Georgia, Athens.

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, Wash, D.C. FWS/OBS 81/15. 105 pp.

Battle, J.D. 1892. An investigation of coastal waters of South Carolina with reference to oyster culture. U.S. Fish. Comm. Bull. No. 10: 303-330.

Burrell, V.G., Jr. 1977. Mortalities of oysters and hard clams associated with heavy runoff in the Santee River system, South Carolina in the spring of 1975. Proc. Natl. Shellfish. Assoc. 67: 35-43.

Burrell, V.G., Jr. 1982. Overview of the South Atlantic oyster industry. Proceedings of the North American Oyster Workshop. World Maric. Soc. Spec. Publ. No. 1: 125-127.

Burrell, V.G., Jr. 1985a. Molluscan fisheries of the South Atlantic region of the United States. Natl. Shellfish. Assoc. Annu. Meet. Abstrs. p. 25.

Burrell, V.G., Jr. 1985b. Oyster culture. Pages 235-273 In J.V. Huner and E.E. Brown, eds. Crustacean and mollusk aquaculture in the United States. AVI Publ. Co., Westport, Conn.

Burrell, V.G., Jr., M.Y. Bobo, and J.J. Manzi. 1984. A comparison of seasonal incidence and intensity of Perkinsus marinus between subtidal and intertidal oyster populations in South Carolina. J. World Maricul. Soc. 15: 301-309.

Burrell, V.G., Jr., J.J. Manzi, and W.Z. Carson. 1981. Growth and mortality of two types of seed oysters from the Wando River, South Carolina. J. Shellfish Res. 1(1): 1-7.

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

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

Carriker, M.R. 1955. Critical review of biology and control of oyster drills Urosalpinx and Eupleura. U.S. Fish. Wildl. Serv. Spec. Sci. Rep. Fish. 148. 150 pp.

Castagna, M., and P. Chanley. 1973. Salinity tolerance of some marine bivalves from inshore and estuarine environments in Virginia waters on the western mid-Atlantic coast. Malacologia 12(1): 47-96.

Chanley, P.E. 1957. Survival of some juvenile bivalves in water of low salinity. Proc. Natl. Shellfish. Assoc. 48: 52-65.

Chestnut, A.F., and W.E. Fahy. 1953. Studies on the vertical distribution of setting of oysters in North Carolina. Proc. Gulf Caribb. Fish. Inst. 5: 106-112.

Cowman, C.F., Jr. 1982. A brief analysis of Georgia's oyster industry. Proc. North American Oyster Workshop. World Maric. Soc. Spec. Publ. No. 1: 128-131.

Dame, R.F. 1970. The ecological energies of growth, respiration and assimilation in the intertidal American oyster, Crassostrea virginica (Gmelin). Ph.D. Dissertation. University of South Carolina, Columbia.

Dame, R.F. 1972. The ecological energies of growth, respiration, and assimilation in the intertidal American oyster Crassostrea virginica. Mar. Biol. 17: 243-250.

Dame, R.F. 1979. The abundance, diversity and biomass of macrobenthos on North Inlet, South Carolina, intertidal oyster reefs. Proc. Natl. Shellfish. Assoc. 69: 6-10.

Dean, B. 1892. The physical and biological characteristics of natural oyster grounds of South Carolina. Bull. U.S. Fish. Comm. 10: 335-362.

De la Cruz, A.A. 1973. The role of tidal marshes in productivity of coastal waters. Assoc. Southeast. Biol. Bull. 20(4): 147-156.

Dupuy, J.L., N.T. Windsor, and C.E. Sutton. 1977. Manual for design and operation of an oyster hatchery. Va. Inst. Mar. Sci. Spec. Rep. Appl. Mar. Sci. Ocean. Eng. No. 142. 104 pp.

Durant, J.E. 1969. The effects of temperature and salinity upon the gonadal cycle of Crassostrea virginica (Gmelin) in Georgia waters. Pages 132-144 in T.L. Linton, ed. Feasibility study of methods for improving oyster production in Georgia. Compl. Rep. Proj. 2-10-R. Bur. Comm. Fish. P.L. 88-309.

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

Galtsoff, P.S., and A.S. Merrill. 1962. Notes on shell morphology, growth and distribution of Ostrea equestris Say. Bull. Mar. Sci. Gulf Caribb. 12(2): 234-244.

Gillmor, R.B. 1982. Assessment of intertidal growth and capacity adaptions in suspension-feeding bivalves. Mar. Biol. 68(3): 277-286.

Haskins, H.H. 1964. The distribution of oyster larvae. Pages 76-80 in

N. Marshall, ed. Proc. Symp. Exp. Mar. Ecol. Rhode Island (USA), Occas. Publ. No. 2: Narragansett Mar. Lab, Grad. School Oceanog., Univ. R.I.

Haven, D.S., and V.G. Burrell, Jr. 1982. The oyster...a shellfish delicacy. Marine Resources of the Atlantic coast, 2nd ed. Atlantic States Mar. Fish. Comm. Leafl. 11. 8 pp.

Haven, D.S., and R. Morales-Alamo. 1966. Aspects of biodeposition by oysters and other invertebrate filter feeders. Limnol. Oceanogr. 11(4): 487-498.

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., W.J. Hargis, Jr., and P.C. Kendall. 1978. The oyster industry of Virginia: its status, problems and promise, a comprehensive study of the oyster industry in Virginia. Va. Inst. Mar. Sci. Spec. Pap. Mar. Sci. No. 4. 1025 pp.

Haven, D.S., W.J. Hargis, Jr., J.G. Loesch, and J.F. Whitcomb. 1976. Shellfish emergency rehabilitation program. Va. Inst. Mar. Sci. Va. Mar. Resour. Comm. Compl. Rep. Mar. 1974-1975. 65 pp.

Hidu, H., and H.H. Haskins. 1971. Setting of the American oyster related to environmental factors and larval behavior. Proc. Natl. Shellfish. Assoc. 61: 35-50.

Ingle, R.M. 1950. Summer growth of the American oyster in Florida waters. Science 112(2908): 338-339.

Ingle, R.M. 1951. Spawning and setting of oysters in relation to seasonal environmental changes. Bull. Mar. Sci. Gulf Caribb. 1(2): 111-135.

Ingle, R.M., and C.E. Dawson, Jr. 1950. Variation in salinity and its relation to the Florida oyster. Salinity variation in Apalachicola Bay. Proc. Natl. Shellfish. Assoc. 16-19.

Keith, W.J., and R.C. Gracy. 1972. History of the South Carolina oyster. S.C. Wildl. Mar. Resour. Dep. Mar. Resour. Div. Ed. Rep. 1. 19 pp.

Linton, T.L. 1969. Inventory of intertidal oyster resources of Georgia. Pages 5-21 _In_ T.L. Linton, ed. Feasibility study of methods for improving oyster production in Georgia. Compl. Rep. Proj. 2-10-R. Bur. Comm. Fish. P.L. 88-309.

Loosanoff, V.L. 1962. Effects of turbidity on some larval and adult bivalves. Proc. Gulf Caribb. Fish. Inst. 14: 80-95.

Loosanoff, V.L. 1969. Maturation of gonads of oysters, _Crassostrea virginica_, of different geographical areas subjected to relatively low temperatures. Veliger 11(3): 153-163.

Loosanoff, V.L., and F.D. Tommers. 1948. Effect of suspended silt and other substances on rate of feeding in oysters. Science 107: 69-70.

Lunz, G.R., Jr. 1941. _Polydora_, a pest in South Carolina oysters. J. Elisha Mitchell Sci. Soc. 57(2): 273-283.

Lunz, G.R., Jr. 1943. The yield of certain oyster landings in South Carolina. Amer. Midl. Nat. 30(3): 806-808.

Lunz, G.R., Jr. 1947. *Callinectes* versus "Ostrea." J. Elisha Mitchell Sci. Soc. 63(1): 81.

Lunz, G.R., Jr. 1950. Production and yield of the oyster canning industry of South Carolina. Contrib. Bears Bluff Lab, No. 9. 14 pp.

Lunz, G.R., Jr. 1955. Cultivation of oysters in ponds at Bears Bluff Laboratories. Proc. Natl. Shellfish. Assoc. 46: 83-87.

Lunz, G.R., Jr. 1960. Intertidal oysters. Wards Nat. Sci. Bull. 34(1): 3-7.

Lutz, R.A., H. Hidu, and K.G. Drobeck. 1970. Acute temperature increase as a stimulus to setting in the American oyster, *Crassostrea virginica*. Proc. Natl. Shellfish. Assoc. 60: 68-71.

Maggioni, G.J., and V.G. Burrell, Jr. 1982. South Carolina oyster industry. Proceedings of North American Oyster Workshop. World Maric. Soc. Spec. Publ. No. 1: 132-137.

Manzi, J.J., V.G. Burrell, Jr., and W.Z. Carson. 1977. A comparison of growth and survival of subtidal *Crassostrea virginica* (Gmelin) in South Carolina salt marsh impoundments. Aquaculture 12: 293-310.

Manzi, J.J., V.G. Burrell, Jr., K.J. Klemanowicz, N.H. Hadley, and J.A. Collier. 1985. Impacts of a mechanical harvester in intertidal oyster communities in South Carolina. Final Report. Coastal Energy Impact Program, Office of the Governor, Columbia, S.C. 31 pp.

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

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

McNulty, J.K. 1953. Seasonal and vertical patterns of oyster setting off Wadmalaw Island, S.C. Contrib. Bears Bluff Lab. No. 15. 17 pp.

Menzel, R.W. 1956. Some additional differences between *Crassostrea virginica* and *Ostrea equestris* in the Gulf of Mexico. Proc. Natl. Shellfish. Assoc. 46: 76-82.

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. No. 216. 33 pp.

Moore, C.J., H. Mills, and D. Cupka. 1984. Recreational shellfish gathering in South Carolina 1980-81. S.C. Wildl. Mar. Resour. Dep. S.C. Mar. Resour. Cent. Tech. Rep. No. 37. 9 pp.

Munden, F.H. 1982. A review of the North Carolina oyster rehabilitation program. Proceedings of the North American Oyster Workshop. World Maric. Soc. Spec. Publ. No. 1: 138-151.

Nelson, T.C. 1925. On the occurrence and food habits of ctenophores in New Jersey inland coastal waters. Biol. Bull. 48: 92-111.

Nicol, J.A.C. 1960. The biology of marine animals. Pitman House, London, U.K. 707 pp.

Palmer, B.A. 1976. Coastal fisheries oyster research (second annual report). Georgia Department of Natural Resources, Game and Fish

Division, Coastal Fisheries Office. Part II. 14 pp.

Porter, H.J., and J. Tyler. 1974. Seashells common to North Carolina. N.C. Dep. Nat. Econ. Res. Div. Comm. Sportfish. Inf. Ser. 36 pp.

Purvis, J.C. 1983. Climatological data. South Carolina, December. Dep. Comm. NOAA. Natl. Climatic Data Center, Asheville, N.C. 1983 (12): 1-19.

Reisinger, E.A., Jr. 1978. Demonstrate revitalization of oyster beds by resurfacing and reseeding. Fourth quarter report and summation of fifth year's work 1977-1978. Coastal Plains Regional Commission, Charleston, S.C. 25 pp.

Sandifer, P.A., J.V. Miglarese, D.R. Calder, J.J. Manzi, and L.A. Barclay, eds. 1980. Ecological characterization of the sea island coastal region of South Carolina and Georgia. Vol. 3: Biological features of the characterization area. U.S. Fish Wildl. Serv. Biol. Serv. Program. FWS/OBS-79/42. 620 pp.

Sellers, M.A., and J.G. Stanley. 1984. Species profiles: life histories and environmental requirements of coastal fishes and invertebrates (North Atlantic) -- American oyster. U.S. Fish. Wildl. Serv. FWS/OBS-82/11.23. U.S. Army Corps of Engineers, TR EL-82-4. 15 pp.

Smith, R.O. 1949. Summary of oyster farming experiments in S.C. 1939-1940. U.S. Fish Wildl. Serv. Spec. Sci. Rep. No. 63. 20 pp.

Wells, H.W. 1961. The fauna of oyster beds, with special reference to the salinity factor. Ecol. Monogr. 31(3): 239-266.

Wood, L., and W.J. Hargis, Jr. 1971. Transport of bivalve larvae in a tidal estuary. Pages 29-44 In D.J. Crisp, ed. Marine biology. Fourth European Symposium. Cambridge University Press.

Yonge, C.M. 1960. Oysters. Willmer Brothers and Haram, Ltd. London. 209 pp.