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

AMERICAN OYSTER
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AMERICAN OYSTER

by

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PREFACE

This species profile is one of a series on coastal aquatic organisms, principally fish, of sport, commercial, or ecological importance. The profiles are designed to provide coastal managers, engineers, and biologists with a brief comprehensive sketch of the biological characteristics and environmental requirements of the species and to describe how populations of the species may be expected to react to environmental changes caused by coastal development. Each profile has sections on taxonomy, life history, ecological role, environmental requirements, and economic importance, if applicable. A three-ring binder is used for this series so that new profiles can be added as they are prepared. This project is jointly planned and financed by the U.S. Army Corps of Engineers and the U.S. Fish and Wildlife Service.

Suggestions or questions regarding this report should be directed to one of the following addresses.

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U.S. Fish and Wildlife Service
NASA-Slidell Computer Complex
1010 Gause Boulevard
Slidell, LA 70458

or

U.S. Army Engineer Waterways Experiment Station
Attention: WESER-C
Post Office Box 631
Vicksburg, MS 39180
## CONVERSION TABLE

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ACKNOWLEDGMENTS

I thank Ronald Dugas and John Manzi for their reviews and many helpful suggestions. I am grateful to Louise Hammes for typing the manuscript, Karen Swanson for drafting the figures, and George Steele and William Anderson for photographic assistance. Thanks also go to Nancy Peacock for computer assistance.
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......................... Ostreidae

**MORPHOLOGY/IDENTIFICATION AIDS**

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).

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 aequastria*, 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 aequastria* 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.
**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
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 Lanler 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 Lanler 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 settling 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 (Chesnut 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; Chesnut 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; Cale 1983). These beds provide habitat for numerous estuarine animals (Neils 1961; Dame 1972, 1979; Bahr and Lanier 1981; Cale 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 (McNuilty 1953). Lunz (1955), Anderson (1976), and Manzl 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; Meggionl 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 (Cheesnut and Fazy 1953; McNulty 1953). McKenzie (1981) calculated survival rates based on yearly changes in population; Initial approximate spat density was 200 to 10,000/m², at 1 to 2 years numbers fell to 300/m², and at 3 to 4 years only 75/m² 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
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; Manzl 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 Manzl et al. (1985) listed 89 species for South Carolina intertidal reefs. Dame (1979) reported the average number of

Figure 6. A mechanical Intertidal oyster harvester being used to rehabilitate public oyster grounds in South Carolina.
Individuals/m² to be 2,949, and Bahr (1974) 24,747/m² 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 yd². In another study, he reported an average of 135.9 2-inch oysters per square yard in 117 samples (Lunz 1943). Bahr and Lanler (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 (Euplerura caudata, Urosalpinx cinerea), whelks (Busycon carica, B. canaliculatum), crabs (Callinectes sp. and family Xanthidae), starfish (Asterias forbesi), fish (Rhinoptera bonasus, Pogonias cromis), and flatworms (Stylurus ellipticus) (Battle 1892; Carriker 1955; Lunz 1960; Merriner and Smith 1979; Bahr and Lanler 1981; Sellers and Stanley 1984). Boring sponges (Cliona spp.) and annelid worms (Polychaeta 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. costella, have not been reported south of North Carolina along the Atlantic coast.

Subtidal oysters compete for growing space with barnacles (Balanus spp.), scorched mussel (Brachiodonites exustus), ribbed mussel (Geukensia demissa) and jingle shell (Anomalina 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
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 mud-flat, 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 (Manzl 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 (Manzl 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 Tammers 1948; Loosanoff 1962).
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Species Profiles: Life Histories and Environmental Requirements of Coastal Fishes and Invertebrates (South Atlantic) -- American Oyster

Abstract (Limit: 200 words)
Species profiles are literature summaries of the taxonomy, morphology, range, life history, and environmental requirements of coastal species. They are designed to assist in environmental impact assessment. The American oyster, Crassostrea virginica, is an important commercial and recreational species. Spawning occurs continuously in warmer months. Larvae are planktonic and are distributed throughout estuaries by tidal currents. After a 2- to 3-week planktonic stage, larvae permanently attach to a solid substrate. In the South Atlantic region, this solid substrate is usually the shell of other oysters growing in the intertidal zone. This gregarious behavior results in formation of massive intertidal reefs that are a prominent feature of high salinity bays, creeks and sounds in the region. These reefs serve as habitat and foraging grounds for other species. Oysters tolerate salinity from about 5 ppt to above 40 ppt and temperatures from below freezing to nearly 50°C.
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