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Species Profiles: Life Histories and Environmental Requirements of Coastal Fishes and Invertebrates (Gulf of Mexico)

AMERICAN OYSTER

Coastal Ecology Group
Waterways Experiment Station

Fish and Wildlife Service

U.S. Department of the Interior

U.S. Army Corps of Engineers

Species Profile: Life Histories and Environmental Requirements
of Coastal Fishes and Invertebrates (Gulf of Mexico)

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.

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CONVERSION TABLE

Metric to U.S. Customary

Multiply	By	To Obtain
millimeters (mm)	0.03937	inches
centimeters (cm)	0.3937	inches
meters (m)	3.281	feet
kilometers (km)	0.6214	miles
square meters (m^2)	10.76	square feet
square kilometers (km^2)	0.3861	square miles
hectares (ha)	2.471	acres
liters (l)	0.2642	gallons
cubic meters (m^3)	35.31	cubic feet
cubic meters	0.0008110	acre-feet
milligrams (mg)	0.00003527	ounces
grams (g)	0.03527	ounces
kilograms (kg)	2.205	pounds
metric tons (t)	2205.0	pounds
metric tons	1.102	short tons
kilocalories (kcal)	3.968	British thermal units
Celsius degrees	1.8(°C) + 32	Fahrenheit degrees

U.S. Customary to Metric

inches	25.40	millimeters
inches	2.54	centimeters
feet (ft)	0.3048	meters
fathoms	1.829	meters
miles (mi)	1.609	kilometers
nautical miles (nmi)	1.852	kilometers
square feet (ft^2)	0.0929	square meters
acres	0.4047	hectares
square miles (mi^2)	2.590	square kilometers
gallons (gal)	3.785	liters
cubic feet (ft^3)	0.02831	cubic meters
acre-feet	1233.0	cubic meters
ounces (oz)	28.35	grams
pounds (lb)	0.4536	kilograms
short tons (ton)	0.9072	metric tons
British thermal units (Btu)	0.2520	kilocalories
Fahrenheit degrees	0.5556(°F - 32)	Celsius degrees

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ACKNOWLEDGMENTS

Figure 1. American oyster from soft substrate with juvenile attached (Galtsoff 1964).

AMERICAN OYSTER

NOMENCLATURE/TAXONOMY/RANGE

Scientific name . . . . . Crassostrea
   virginica (Gmelin)
Preferred common name . . . American
   oyster (Figure 1)
Other common name . . . Eastern oyster
Class . . . . . . Bivalvia (Pelecypoda)
Order . . . . . .Mytoloida (Pteroidea)
Family. . . . . Ostreidae

Geographic range: The American oyster lives in estuaries and behind barrier islands; it is abundant along the gulf coast from Florida to Texas (Figure 2). The Gulf of Mexico has about 3600 km² (1400 mi²) of habitat suitable for the American oyster (Butler 1954). Its range extends to the Yucatan Peninsula of Mexico and to Venezuela. Along the east coast of North America, it occurs from the Gulf of St. Lawrence, Canada, to Key Biscayne, Florida. This species was introduced with limited success to Japan, Australia, Great Britain, Hawaii, and the west coast of North America, but it has not become abundant (Ahmed 1975). The American oyster is most abundant in the Gulf of Mexico, Chesapeake Bay, and Long Island Sound.

MORPHOLOGY/IDENTIFICATION AIDS

The left valve is almost always thicker and heavier than the right, and more deeply cupped (Yonge 1960; Galtsoff 1964). The oyster is cemented to the substrate on its left valve. Hinge teeth are absent, but a buttress on the right valve fits into a depression on the left. There is no gap between the valves when fully closed.

Shell shape is variable. On hard bottoms, beaks (umbones) usually are curved and point toward the posterior, whereas in silty environments or on reefs, umbones are usually straight. Solitary oysters from hard substrates are rounded and ornamented with radial ridges and foliated processes, whereas

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Figure 2. Distribution of American oyster in the Gulf of Mexico.

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those from soft substrates or reefs are more slender and sparsely ornamented. Shell thickness also depends on environment. Oysters on hard substrates have thicker and less fragile shells than those on soft substrates. The "index of shape" ((height + width)/length) varies from 0.5 to 1.3 in southern populations and from 0.6 to 1.2 in northern populations.
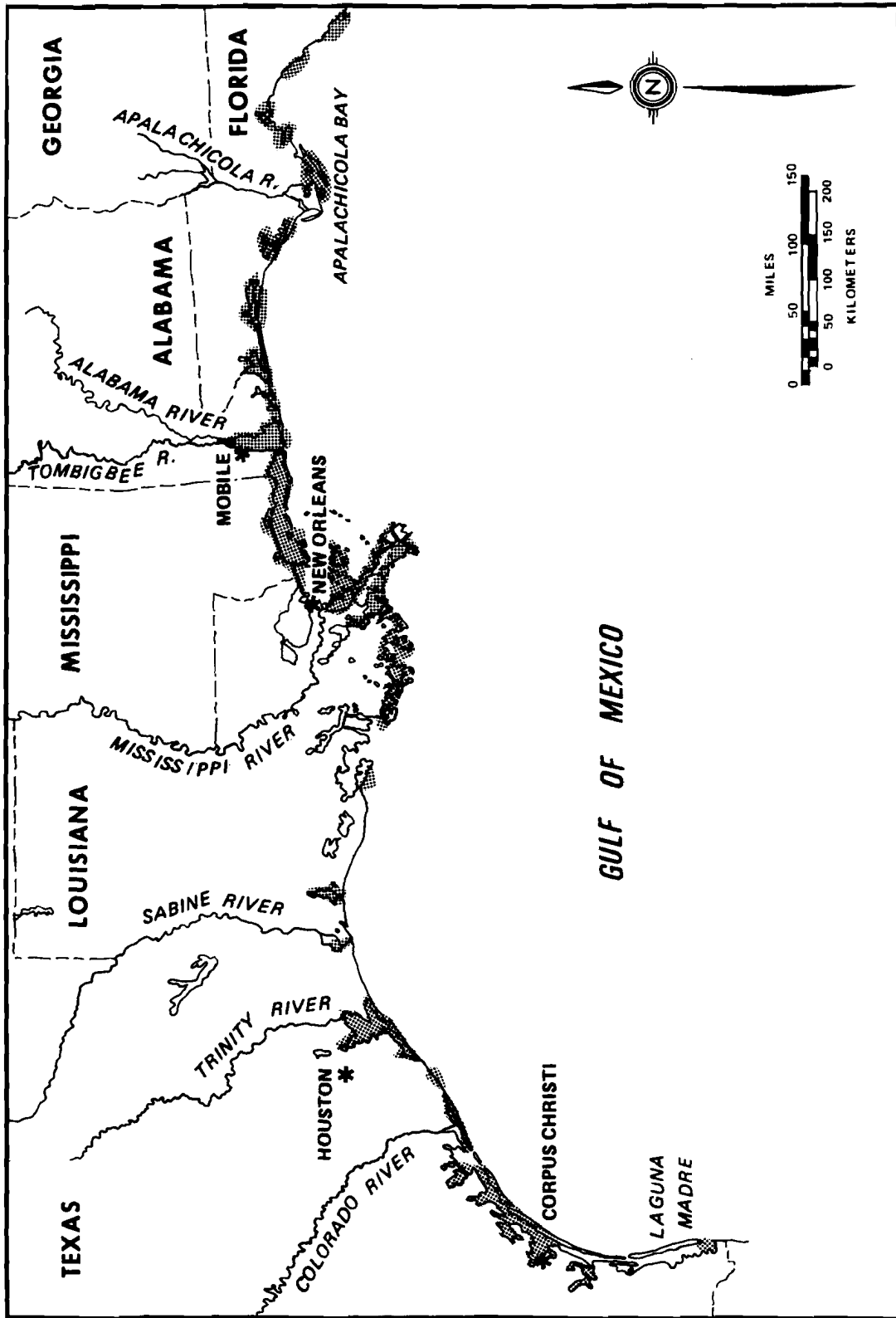
The shell grows along a dorsal-ventral axis, but the angle of the axis is not permanent and may change several times over the lifespan of an individual, resulting in a zigzag pattern. The growth axis may change as much as 90°. The shell of oysters 3- to 5-years old is usually 10 to 15 cm long. Although tissue mass reaches an upper limit, the shell continues to grow over the lifespan of an oyster (Stenzel 1971). Throughout this review shell height is termed length.

The American oyster is monomyarian (anterior adductor muscle has been lost). The interior of the shell has a purple-pigmented adductor muscle scar situated slightly posterior and ventral. A second muscle scar, of the Quenstedt's muscle, is situated ventral to and a short distance from the hinge. The purple pigmentation on the adductor muscle scar distinguishes the American oyster from similar species. In the mangrove oyster (C. rhizophorae) and Pacific oyster (C. gigas) the muscle scar is lightly pigmented and in C. rivularis it is unpigmented. The shell of the mangrove oyster is less plicated than that of the American oyster. There are no other species of Crassostrea sympatric with the American oyster in the Mid-Atlantic region. Species of Crassostrea are distinguishable from species of Ostrea by the promyal chamber, which is well developed in Crassostrea species, but not in Ostrea. By trapping saltwater, this chamber may allow the American oyster to tolerate wider fluctuations in salinity in estuaries.

Crassostrea species are oviparous (gametes are released into the water), whereas Ostrea species incubate fertilized eggs in the mantle cavity. The morphology of larval stages is described by Kilgen and Dugas (1984). Advanced Crassostrea larvae are distinguished from the larvae of other bivalves by length-width measurements, and an asymmetric umbo. The morphology of the dentition on the hinge distinguishes the larvae of the American oyster from other bivalves (Lutz et al. 1982).

REASON FOR INCLUSION IN SERIES

The American oyster supports an important commercial fishery from the Gulf of Mexico to the Gulf of St. Lawrence, and is an important mariculture species. More oysters are processed than any other single fishery product in the United States, and over 10,000 people work in the oyster industry. Oysters are valued as a luxury food item and are the keystone species of a reef biocoenosis that includes several hundred species (Wells 1961). Because oysters inhabit estuaries, they are particularly vulnerable to urban and industrial disturbances (Cake 1983).

LIFE HISTORY

Spawning

Gametogenesis and spawning are stimulated by changes in water temperature (Hopkins et al. 1954; Kaufman 1978; Andrews 1979). Spawning temperature differs among populations. Based on spawning temperatures, Stauber (1950) recognized three physiological races: one from the Gulf of Mexico that spawns when water temperatures are near 25 °C, and two from the east coast that spawn at 16 °C and 20 °C. In the Gulf of Mexico, the temperature must be constantly above 20 °C for spawning, and above 25 °C for mass spawnings (Schlesselman 1955). In the

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Apalachicola River estuary, Florida, the oyster does not spawn until water temperature reaches 22.5 °C and mass spawning occurs at 26 °C (Ingle 1951).

The American oyster in the northern Gulf of Mexico spawns from March through November according to Butler (1954) and from April to October according to Hayes and Menzel(1981). In Louisiana, spawning peaks occur in late May, early June, and September (Pollard 1973). In Mississippi, most oysters spawn from May to October and spawning intensity is greatest in June (MacKenzie 1977). In Galveston Bay, Texas, spawning begins in early April about the time water temperatures exceed 20 °C and continues at least until the end of August (Hopkins 1931). Spat setting indicates that the American oyster probably spawns in all months in shallow warm bays in Texas (e.g., Redfish Bay) with the exception of July and August (Copeland and Hoese 1966). Water temperatures exceeding 35 °C in those months may limit the extent of spawning.

Spawning does not depend directly on tidal cycles (Loosanoff and Nomejko 1951), but sunlight may warm the water during low tide and stimulate spawning (Drinnan and Stallworthy 1979).

The timing and intensity of spawning is initiated by males that release their sperm and a pheromone into the water. The females spawn when sperm enter their water transport system (Andrews 1979), or when phero- mone stimulates females to release their eggs in a mass spawning (Bahr and Lanier 1981). Each female produces 23 million to 86 million eggs per spawning; the number is propor- tional to the size of the individual (Davis and Chanley 1955). Egg counts of 15 million to 115 million were cited by Yonge (1960). Females may spawn several times in one season (Davis and Chanley 1955). The egg hatches 6 h after fertilization at water temperatures near 24 °C (Loosanoff 1965a).

Larvae

Oyster larvae are meroplanktonic and remain in the water column for 2 to 3 weeks after hatching (Bahr and Lanier 1981). During this period the larvae pass through several stages of development (Carriker and Palmer 1979; Kilgen and Dugas 1984). After the blastula (3.2 h), gastrula (4.5 h), and trochophore (10 h) stages (Parrish 1969), the larvae secrete a straight- hinge shell and develop a ring of locomotory cilia called the velum. This straight-hinge larva or prodisso- conch I is about 75 μm in diameter. It develops into a prodissoconch II larva (also termed an eyed larva or pediveliger), which is characterized by a pronounced umbone. This larva is a vigorous swimmer, and has a pair of pigmented eyes and an elongate foot with a large byssal gland (Andrews 1979). Mean diameter of prodissoconch II larvae is 0.3 mm.

Young larvae (prodissoconch I) in Little Egg Harbor, New Jersey, stay in the water column about 1 m below the surface (Carriker 1951). Older larvae (prodissoconch II) are near the bottom of the estuaries during flood tide and rise nearer the surface during the ebb tide. Andrews (1979) questioned these findings because in the laboratory, older larvae are stimulated to swim by increased salinities and inhibited by decreased salinities (Haskin 1964). Swimming velocity increased threefold when salinity was increased 0.5 ppt/h (Hidu and Haskin 1978). Upward swim- ming is nearly 1 cm/sec (Andrews 1979). These behavioral traits may result in selective tidal transport so that larvae position themselves in the estuary. Generally, larvae are transported toward the head of an estuary against a net downstream flow (Seliger et al. 1982), presumably because they use these behavioral responses. Currents carry larvae considerable distances: 6.5 km in Alligator Harbor, Florida (Marshall 1954), and 10 km in Louisiana (Gunter

1951). Oyster larvae drift westward along the coast of the Gulf of Mexico (Buroker 1983).

Juveniles

Two to three weeks after hatching, oyster larvae commence a period of crawling in a circular pattern, presumably seeking a solid surface for attachment (Andrews 1979). In Long Island Sound the first set is 18 days after the first spawning (Loosanoff and Nomejko 1951). In Galveston Bay, Texas, setting was first seen 2 months after spawning when the larvae were about 0.2 mm long (Hopkins 1931). After attachment with a droplet of liquid cement exuded from a pore in the foot, they lose the velum and foot and are called spat (spat are newly settled oysters). Shells are preferred as attachment sites, but stones and other firm surfaces may be used. Spat that set during the first 3 days after metamorphosis may grow faster than those setting later (Losee 1979). Metamorphosis may be delayed if suitable substrate is not located (Newkirk et al. 1977). Burke (1983) defined settlement as the behavior of dropping to the bottom, in contrast to metamorphosis, which is the irreversible developmental process.

Several factors influence the setting behavior of larvae. Hidu and Haskin (1971) believed that rising water temperatures over tidal flats during flood tides stimulate setting. In the laboratory, rising temperatures trigger setting (Lutz et al. 1970). Swimming larvae have positive phototaxis, which becomes negative with an increase in temperature (Bahr and Lanier 1981). Light inhibits setting in tanks (Shaw et al. 1970), and oysters prefer to set on the undersides of shells (Ritchie and Menzel 1969). More oysters settle in the subtidal zone than elsewhere in Delaware Bay (Hidu 1978). In shallower water, settlement is greatest on artificial substrate held away from the bottom because siltation inhibits setting (Andrews 1979).

Oyster larvae set in established oyster beds and in other habitats with firm substrate and suitable salinities. Crisp (1967) postulated that larvae are attracted to the proteinaceous surface of the periostracum of adult shells and observed that larvae did not settle on shells that had been treated with bleach. Hidu (1969) demonstrated, however, that a water-borne factor, perhaps a pheromone, stimulates larvae to settle on oyster shells. Currents also influence setting patterns: settlements in Delaware Bay are heaviest where tidal currents cut through salt marshes (Keck et al. 1973). Juveniles 26 to 75 mm in height and 7 to 14 months old are designated as seed oysters (Chatry et al. 1983).

Adult

Because adult oysters are sessile, their distribution depends on where the larvae set and on subsequent survival of the spat. Oysters typically live in clumps called reefs or beds, in which they are the dominant organism. The mass of shells sometimes alters currents and increases deposition of particulates so that the local environment is modified.

Adults are dioecious, but often change gender, exhibiting protandrous hermaphroditism (Bahr and Lanier 1981). The gender and the process of sex inversion are genetically determined by perhaps three loci (Haley 1977). Typically the young adults are predominantly males; subsequent sex inversion with age increases the number of females. Sex ratios in the James River Estuary, Virginia, change from 90% males at 1 year of age to 80% females in older oysters (Andrews 1979). In Louisiana, 76% of oysters were males if attached to older oysters and 46% were males if attached to dead shells (Menzel 1951). Oysters may become sexually mature in

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the Gulf of Mexico 4 weeks after attachment (Menzel 1951). Those oysters that mature during the first summer of life, however, do not contribute significantly to the year class because of the relatively low number of eggs that they produce (Hayes and Menzel 1981).

GROWTH CHARACTERISTICS

American oysters grow fastest during their first 3 months of life (Bahr 1976). Butler (1954) stated that oysters in the gulf region grow about 50 mm/year. In Apalachicola Bay, Florida, oysters reach 25 mm in 5 weeks, and 100 mm in 31 weeks (Ingle 1950). In a second study, oysters were 4 mm at 1 week of age, 8 mm at 2 weeks of age, and 27 mm at 5 weeks of age (Ingle and Dawson 1952). For comparison, oysters in Pensacola Bay, Florida, rarely exceed 75 mm of growth in their first year (Butler 1954). In Louisiana, oysters grew at the rate of 0.26 to 0.30 mm per day during the first growing season (Gunter 1951). Oysters in Louisiana usually reach 30 mm in length in 3 months, 55 to 60 mm in 1 year, 85 to 95 mm in 2 years, and 105 to 115 mm in 3 years (Mackin 1961a). There is variation in growth rate in Louisiana: the time to reach 70 mm was 45 weeks at Grand Pass, 25 weeks in upper Bastian Bay, and 12 weeks in lower Bastian Bay (Owen 1953a). Instantaneous monthly growth coefficients ranged from 0.42 to 0.84 (Gillmor 1982).

Growth is influenced by temperature, salinity, intertidal exposure, turbidity, and food. Growth is greatest in August and September after spawning, when glycogen reserves are restored (Loosanoff and Nomejko 1949; Price et al. 1975). Growth in the gulf region is continuous throughout much of the year, though it may be interrupted by unusual cold periods or by spawning. Growth is slow during spawning because most of the energy is used for gamete production instead of adding body biomass. In Louisiana,

the glycogen content of oysters declines to support gonad maturation in April and reaches lowest levels during spawning in May, June, and July (Hopkins et al. 1954). Butler (1953) noted an increase in biomass after spawning without an increase in shell length. Oysters expend as much as 48% of their annual energy budget in reproduction (Dame 1976).

Growth of oysters depends on environmental conditions and their position and density in the oyster reef. Fluctuating environments may promote better growth. For example, oysters in fluctuating salinity within normal ranges tend to grow better than oysters under a relatively constant salinity (Pierce and Conover 1954). Oysters exposed for short periods during the tidal cycle grow about the same rate as those continuously submerged (Gillmor 1982). Long exposure out of water, however, reduces growth. Oysters in reefs exposed about 20% of the time may grow about twice as fast as those exposed 60% of the time. The growth rate of the oyster is directly related to phytoplankton density. Oysters grow faster in nutrient-rich salt ponds than in tidal creeks where primary productivity is lower (Manzi et al. 1977). Individuals in populations of oysters of high density grow slower than those at low density (Copeland and Hoese 1966). Crowding, however, may prevent spawning and thus indirectly lead to increased growth (Butler 1953).

A Walford plot predicts that oysters in South Carolina would cease growing when 140-mm long (Dame 1971); however, oysters 200-mm long occur.

COMMERCIAL SHELLFISHERIES

The American oyster has traditionally supported a valuable shellfishery along the entire gulf coast. The shellfisheries are concentrated in bays and estuaries (Figure 2). The landings in the Gulf States combined average about 8,000

metric tons (18 million pounds) annually (Table 1). Oyster production has been relatively stable; the landings since 1950 have varied only from 10 million to 27 million pounds. The landings of oysters in the Gulf of Mexico are about a third of the U.S. landings. The landings for the individual States vary by an order of magnitude (Table 2). Louisiana has the largest shellfisheries for oysters; annual landings are about 9 million pounds (4,000 metric tons). The west coast of Florida has the second largest fishery, about half that of Louisiana. Poor year classes lead to reduced harvests. Louisiana had poor harvests in 1979, 1980, and 1981; Florida in 1973 through 1976; and Texas in 1974, 1975, 1978, 1979 and 1981. Alabama and Mississippi have the same trends as Louisiana.

Table 1. Oyster landings (thousands of pounds; meat weight) by geographic region for the years 1950-1982. (From U.S. Dep. Commer., Natl. Mar., Fish. Serv., NOAA, Natl. Fish. Stat. Program. Annual summaries of oyster landings.)

Year	New England	Mid-Atlantic	Chesapeake	South Atlantic	Gulf of Mexico
1950	4,727	18,170	29,954	3,033	12,292
1951	1,970	17,410	29,598	3,783	11,519
1952	2,209	16,767	34,418	4,111	14,637
1953	1,038	14,462	36,946	4,019	12,836
1954	735	13,377	41,587	3,811	11,443
1955	619	9,848	39,227	2,260	13,881
1956	506	8,466	37,064	3,656	13,513
1957	405	7,981	34,234	3,069	14,307
1958	276	4,296	37,530	2,651	10,408
1959	387	1,392	33,322	3,516	13,721
1960	500	1,154	27,111	4,119	16,098
1961	453	1,921	27,500	3,984	18,240
1962	294	2,362	19,939	3,850	18,838
1963	452	951	18,274	4,837	24,139
1964	195	1,356	22,098	3,527	23,385
1965	340	757	21,188	4,082	19,156
1966	408	917	21,232	3,657	17,182
1967	323	1,190	25,798	3,160	21,747
1968	195	1,538	22,679	2,965	26,739
1969	152	1,322	22,157	1,830	19,765
1970	190	1,413	24,668	1,626	17,714
1971	190	1,965	25,557	1,846	20,266
1972	129	3,335	24,066	1,868	18,260
1973	181	3,181	25,400	1,656	14,914
1974	644	2,739	25,021	1,841	14,878
1975	600	3,274	22,640	1,585	19,295
1976	201	3,566	20,964	1,704	21,569
1977	905	2,412	18,014	1,861	19,670
1978	887	2,415	21,531	2,138	18,212
1979	1,129	3,038	20,428	2,441	15,289
1980	200	2,635	21,777	2,279	16,548
1981	26	2,396	22,153	2,786	17,079
1982	1,195	2,352	18,134	2,650	24,158

Table 2. Oyster landings (thousands of pounds; meat weight) for the Gulf States, 1930-82 (From U.S. Dep. Commer., Nat. Mar. Fish. Serv., NOAA, Natl. Fish. Stat. Program. Summation of annual reports.)

Years	Florida[a]	Alabama	Mississippi	Louisiana	Texas	Total
1930	1,501	287	4,896	4,846	1,157	12,688
1931	1,406	769	3,438	3,590	982	10,185
1932	1,109	859	5,222	2,978	981	11,149
1934	1,357	392	4,904	5,592	1,312	13,556
1936	917	992	5,771	5,743	823	14,246
1937	817	1,235	12,894	8,048	1,190	24,184
1938	858	1,359	2,241	10,222	1,356	16,036
1939	742	1,358	7,706	13,586	987	24,380
1940	669	936	2,270	12,412	1,297	17,584
1945	1,496	1,606	265	9,884	719	13,970
1950	873	2,070	508	8,715	125	12,292
1951	681	2,191	28	8,164	456	11,519
1952	542	1,842	23	11,402	828	14,637
1953	564	1,450	318	9,435	1,068	12,835
1954	668	739	976	8,361	699	11,444
1955	630	1,581	1,731	9,396	543	13,881
1956	856	770	846	10,056	986	13,514
1957	710	1,291	862	10,489	953	14,306
1958	795	458	579	8,265	311	10,407
1959	1,415	895	333	9,667	1,411	13,722
1960	1,931	1,169	2,391	8,311	2,396	16,098
1961	3,255	509	3,241	10,139	1,096	18,239
1962	4,592	443	3,073	10,160	1,210	18,840
1963	4,282	995	4,679	11,563	2,618	24,138
1964	2,793	1,005	4,829	11,401	3,357	23,385
1965	3,789	492	2,695	8,343	4,836	19,155
1966	4,157	1,304	2,232	4,764	4,725	17,183
1967	4,578	2,087	3,786	7,742	3,553	21,747
1968	5,317	1,212	3,786	13,112	3,302	26,739
1969	4,912	481	1,430	9,178	3,764	19,765
1970	3,573	279	548	8,639	4,675	17,714
1971	3,529	250	1,215	10,528	4,744	20,266
1972	3,231	106	1,220	8,805	3,935	18,260
1973	2,409	591	612	8,953	2,349	14,914
1974	2,653	733	276	9,972	1,244	14,878
1975	2,134	638	1,080	13,687	1,756	19,295
1976	2,602	1,236	1,516	12,334	3,881	21,569
1977	4,072	1,549	1,384	10,065	2,600	19,670
1978	5,780	760	682	9,081	1,909	18,212
1979	6,048	454	272	7,561	954	15,289
1980	6,445	55	21	6,806	3,221	16,548
1981	7,179	1,330	321	7,298	1,221	17,079
1982	4,833	1,497	2,576	12,441	2,811	24,158

[a]Gulf coast only.

Oysters are taken by handpicking of clumps from reefs (Bahr and Lanier 1981), hand and patent tonging, and dragging and dredging (Korringa 1976). In Louisiana, oysters are taken mostly with dredges (Pausina 1971). Tonging is limited to water 4-m deep or less; dredging requires a larger vessel (Maghan 1967). In Mississippi coastal waters, the method used depends on the type of fishery. In the Mississippi Sound near Bay St. Louis and Pass Christian, oysters are taken by dredging or with tongs; in Biloxi Bay and Graveline Bayou they are dredged for transplantation to grow out sites; and near Horn Island they are taken by hand for food and recreation (Ogle 1979). In Alabama, tonging and handpicking are the only legal means of taking oysters; this is because the major reefs are close to shore in shallow waters (Mark S. Van Hoose, Alabama Department of Conservation and Natural Resources, pers. comm.). Power equipment has made capture more efficient but it also increases the potential for depleting the beds.

The American oyster is the dominant species in mariculture in the United States. In 1980, the yield of oysters in mariculture was 10,753 metric tons (about 24 million lb) valued at $37 million, which was about 55% of the total U.S. shellfishery harvest (19,250 metric tons; 42.4 million lb). The equivalences between different values reported for harvest are: 1 bu = 35 1 = 32 kg total weight = 7.8 pints of meats = 3.4 kg meat weight (Pruder 1975).

The market quality of the meat varies with the season. The yield of oyster meat per shell is highest in March before reproduction and lowest in the summer in Texas (Gunter 1942) and Florida (Rockwood and Mazek 1977). The reduced yields during spawning periods correspond to a reduced condition index following spawning (Hopkins et al. 1954; Lawrence and Scott 1982).

Even 'wild' oysters are often cultivated by altering the substrate. Oyster shells (cultch) placed in suitable habitat lacking substrate promote settlement of the larvae (Whitfield and Beaumariage 1977). Suitable habitat can be created by redepositing buried shells on the surface (May 1976) but only if the bottom is relatively hard at the site of deposition (Eckmayer 1977). Dredging is effective in rehabilitating oyster reefs if the bottom is relatively hard (Eckmayer 1977).

Population Dynamics

A vast majority of the eggs and larvae produced by American oysters perish before setting. Following spawning, oyster larvae are abundant plankters, ranging from 2.0 to 5.5 per liter in Virginia coastal waters (Andrews 1979; Seliger et al. 1982). In the Mississippi Sound, one half of the zooplankters in the summer are oyster larvae (Butler 1954). Abundance is greatest after high tide (Andrews 1979). The daily mortality of larvae is about 10% (Drinnan and Stallworthy 1979).

Newly set spat usually are dense on suitable substrates. For example, in Apalachicola Bay there is an average of 2.5 spat set per shell (Ingle 1951), or 100 spat/m^2 of surface area (Menzel et al. 1966). In Alabama, there are only 0.06 spat/m^2 in Bayou Cour and 0.17/m^2 in Shellbank Bayou (Eckmayer 1977), where there is intensive shrimping, low DO, and siltation (Mark S. Van Hoose, pers. comm.). Ten miles away in Kings Bayou, spat density is 1.2 to 10.8/m^2. In Louisiana, the daily rate of setting after peak spawning is as much as 90 spat/shell (Hopkins 1955). Chatry et al. (1983) observed sets of 10 to 1,890 oysters/m^2 in Louisiana.

The early mortality of spat has not been studied in the gulf region. In Massachusetts, the mortality during

the first month ranges from 79% to 99% (Krantz and Chamberlin 1978). Typical annual mortality of spat is 60% in Louisiana (Mackin 1961a); mortality is usually 90% to 99% at specific seed grounds (Chatry et al. 1983). Annual mortality of seed oysters is 6% to 11% (Owen 1953a). Spat survival is less in dense sets than in sparse sets in Louisiana (Chatry et al. 1983) and Chesapeake Bay (Webster and Shaw 1968). Mortality tends to be greater in small seed oysters than in large ones. Production of seed oysters is not closely correlated with the number of spat (Chatry et al. 1983).

The mortality of oysters in gulf coastal waters varies greatly depending upon the rate of freshwater inflow and predator abundance. In Texas, the mortality of oysters from seed to adult (1 year) is 90% (Gunter 1955). Under optimal conditions, the monthly mortality is 2% to 4% in Louisiana (Gunter 1953). Mackin (1961a) cited 60% as the annual mortality under prevailing conditions of salinity and predators. Based on the number of newly dead oysters, Ogle (1979) estimated that the monthly mortality in Mississippi ranged from 6% to 36%. In Louisiana, newly dead oysters made up 5% to 80% of the population with an average of 27% (Owen et al. 1951). An entire population of oysters in some areas may be killed by excessive freshwater inflow (and low salinities) from the Mississippi and Pearl Rivers (Gunter 1953; Schlesselman 1955; MacKenzie 1977), or by high water temperatures in isolated bays in Texas (Copeland and Hoese 1966).

ECOLOGICAL ROLE

Larvae feed largely on plankton, particularly small, naked flagellates (chrysophytes) (Guillard 1957). At moderate water temperatures, larval growth is best with a diet of naked flagellates, whereas at temperatures above 27 °C naked algae are scarce and

chlorophytes are more abundant as food (Davis and Calabrese 1964). Bacteria are not eaten by larvae (Davis 1953).

Oyster larvae are food for a wide variety of filter feeders (Andrews 1979).

Adult oysters filter large quantities of brackish water. They most effectively filter particles in the 3- to 4-μm size range (Haven and Morales-Alamo 1970). Naked flagellates are the most important food although bacteria are sometimes consumed, presumably because they are attached to detritus. For each gram of dry weight of tissue, an oyster held at 21 °C filters 1.5 l/hr, with a maximum of 1.9 l/hr (Palmer 1980). At temperatures above 25 °C about 8 l/hr are filtered (Langefoss and Maurer 1975). The volume of water filtered per hour is about 1500 times the volume of the oyster's body (Loosanoff and Nomejko 1946). The filtration rate is independent of the available food supply, the stage of tide, or the time of day. If food is absent, however, the valves are closed much of the time (Higgins 1980).

The American oyster is the dominant species in the oyster reef community. Over 40 macrofaunal species or groups live in oyster beds (Bahr and Lanier 1981), and the total number of species in an oyster community may exceed 300 (Wells 1961). On the oyster reef, oysters are responsible for as much as 88% of the respiration (Bahr and Lanier 1981).

Oysters are susceptible to a variety of diseases and parasites and are preyed upon by several species (Galtsoff 1964). The bacterial diseases Vibrio and Pseudomonas sometimes kill oysters. The protozoan pathogen Perkinsus marinus infects oysters from Delaware to Mexico. In Texas, the index of stress was in direct relation to the level of infection (Soniat and Koenig 1982). In Florida, infections of the

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protozoan become lethal only during elevated summer water temperatures (Quick and Mackin 1971). In Texas, the protozoan parasite Labyrinthomyxa marina is thought to kill 10% to 50% of the adult oysters (Hofstetter 1977). Disease epidemics are common in the gulf region (Mackin 1961b). In Louisiana, all oysters in some locations are infected with the gregarine parasite Nematopsis ostrearum, and in Florida 95% are infected (Owen et al. 1951). The parasite, however, did not directly cause mortality.

Predators often limit the abundance of oysters. The southern oyster drill, Thais haemastoma, is responsible for the majority of oyster deaths in Louisiana, Mississippi, and Alabama. Other common predators are the lightning whelk (Busycon contrarium), the blue crab (Callinectes sapidus), and the stone crab (Menippe mercenaria) (Marshall 1954; Menzel and Nicky 1958; Cake 1983). All sizes of oysters are killed by oyster drills, which bore through the shells with a combination of chemical dissolution of the shell and drilling (radular rasping). Blue crabs prefer small oysters; stone crabs will crush any size of oyster that they can manipulate, as will several species of xanthid mud crabs. The southern oyster drill often kills without drilling by rasping a minute gap between the valves and protruding the proboscis into the mantle cavity (McGraw and Gunter 1972; Gunter 1979b). The crown conch (Melongena corona) is a predator of oysters along Florida's west coast. The southern oyster drill has been reported to kill 50% of the oysters of productive reefs and 100% in nonproductive reefs near Pass Christian, Mississippi (Chapman 1959), and 50% to 85% of the oysters in Louisiana (Schlesselman 1955). Southern oyster drills have densities of 20/m² in some oyster reefs (Hopkins 1955), and a single drill can consume up to 4 spat/hr (Butler 1954), or up to one adult oyster every 8 days

(Gunter 1979b). On St. Vincent Bar in Apalachicola Bay, Florida, there were 2.8 drills/m², which together with stone crabs destroyed 67% of the oysters in one month (Menzel et al. 1957). The drill and the stone crab cause serious mortality in Texas (Gunter 1955) and Florida (Menzel et al 1966).

Menzel et al. (1966) consider the stone crab to be the main enemy of oysters in Florida. The density of the stone crab in Louisiana is 1/m² and each potentially consumes 219 oysters per year. In laboratory experiments, a blue crab ate 19 oyster spat/day, but did not consume adults unless they were weakened (Menzel and Hopkins 1956). The black drum (Pogonias cromis), southern eagle ray (Myliobatis goodei), and cownose ray (Rhinoptera bonasus) may destroy an oyster reef by eating the spat (Schlesselman 1955).

The oyster crab Pinnotheres lives in the mantle cavity and may damage the gills of oysters (Schlesselman 1955). The widespread boring sponge Cliona, and the boring clam (Diplothyra smithii) weaken the oyster's shell and lower market quality (Schlesselman 1955). Spat are preyed upon by the flatworm Stylochus ellipticus (MacKenzie 1970; Christensen 1973). The sea anemone (Diadumene leucolena) consumes 0.6 to 4.9 oyster larvae per minute in the laboratory and also feeds on larvae in the natural environment (Steinberg and Kennedy 1979).

Major competitors for space on substrate are the slipper shells (Crepidula spp.) and the jingle shells (Anomia spp.) as well as barnacles and other oysters that set on adult shells (MacKenzie 1970). The hooked mussel (Ischadium recurvum) competes with oysters for space and food in Louisiana (Schlesselman 1955). A heavy set of the barnacle Balanus improvisus can seriously reduce the area of hard surface available to

oysters (Ingle 1951). According to Ingle (1951), slipper shells and the hooked mussel are not serious competitors with oysters in Apalachicola Bay, Florida. Young oysters may be smothered by the excreta of polychaete worms of the genus _Polydora_, or by excreta of adult oysters (Stenzel 1971). Blooms of red tide (_Cochlodinium heterolobatum_) at concentrations of 500 cells/ml kill oyster larvae (Ho and Zubkoff 1979).

ENVIRONMENTAL REQUIREMENTS

The American oyster typically lives in shallow, well-mixed estuaries, lagoons, and oceanic bays where it tolerates widely fluctuating water temperatures, salinities, and concentrations of suspended solids (Andrews 1979). Because of tolerance to these fluctuations, precise environmental requirements alone or in combination are difficult to define.

Temperature

In laboratory tests, embryos develop normally at temperatures between 20 and 30 °C but abnormalities increase progressively when temperatures decline to 15 °C or rise to 35 °C (MacInnes and Calabrese 1979). On the other hand, Dupuy (1975) in his experiments reported that embryo abnormalities could be as high as 2% at 25 °C and 12% at 30 °C. The growth of larvae may be impaired by water temperatures of 30 °C and higher, and even a brief exposure for 10 min at water temperatures near 40 °C retards growth (Hidu et al. 1974). In other tests, growth was fastest and survival highest at water temperatures of 27.5 to 32.5 °C (Davis and Calabrese 1964). These tests were all conducted on oyster stocks from the Atlantic coast and exact temperature ranges may not apply to oyster embryos or larvae from the Gulf of Mexico.

Adults exist within a range of water temperatures from -2 °C in New England to 36 °C in the Gulf of Mexico. During low tide, oysters may be exposed to and survive air temperatures below freezing or above 49 °C (Galtsoff 1964). Excessively high temperatures cause mortality; water temperatures above 35 °C for the whole tidal cycle in Indian River bay, Delaware, are known to have killed some oysters (Tinsman and Maurer 1974). The critical thermal maximum determined in the laboratory for the American oyster is 48 °C (Henderson 1929). Oysters tolerate freezing of their tissues, and revive after thawing (Loosanoff 1965a). Gulf coast oysters, however, apparently are not as tolerant of freezing (Cake 1983).

Optimum water temperatures for growth, reproduction, and survival of American oysters range from about 20 to 30 °C, and the response of oysters to temperature changes and extremes depend on an interaction of environmental conditions. The rate that water is pumped through the oyster's gill system is determined by temperature. A water temperature range of 20 to 25 °C results in favorable pumping rates for supplying needs for oxygen, food, and waste disposal (Collier 1951). Oysters are relatively inactive below 7 °C and pumping is greatly reduced. Although the threshold for feeding by Chesapeake Bay oysters in the laboratory is 3 °C (Haven and Morales-Alamo 1966), few New England oysters feed at temperatures below 8 °C and growth ceases (Price et al. 1975). Some growth has been reported in Long Island Sound in the winter when water is unseasonably warm and food is available (Ruddy et al. 1975). Growth of Long Island Sound oysters is possible between 6 and 32 °C and fastest near 26 °C (Galtsoff 1964). The exposure of Florida adults to a 35 °C water temperature accelerated gametogenesis and spawning, but the exposure prevented subsequent spawning in that year (Quick 1971).

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Differences in thermal requirements of oysters from different areas have led to the postulation that races may be separated on the basis of temperature requirements (Ahmed 1975). Spawning temperatures for three distinct races were reported by Stauber (1950): 16 °C for the northern race (New England), 20 °C for the mid-Atlantic race, and 25 °C for the Gulf of Mexico race. For instance, oysters spawn in Galveston Bay, Texas, after temperatures exceed 25 °C (Hopkins 1931), and mass spawnings in Apalachicola Bay, Florida, do not take place until temperatures exceed 26 °C (Ingle 1951). Additional evidence for the existence of physiological races was reported by Menzel (1955), who found that ciliary activity continues at 0 °C in northern oysters but ceases at 6 °C in southern oysters. Andrews (1979) believes there are other races as well, but genetic studies do not closely support the existence of physiological races. Buroker et al. (1979) found that all oysters studied were genetically identical, except those from Nova Scotia and Florida. These populations were 82% similar, about the level of similarity between the American and mangrove oysters, which can successfully hybridize (Menzel 1968). According to Groue and Lester (1982), oysters in Laguna Madre, Texas, are genetically distinct from four other gulf populations. Measurement of isozymes in the genetic studies, however, may not validate these findings.

Salinity

Adult oysters in the Gulf of Mexico normally occur at salinities between 10 and 30 ppt but they tolerate a salinity range of 2 to 40 ppt (Gunter and Geyer 1955); outside this range, they die or discontinue feeding and reproduction. In the Mississippi Sound, salinities among productive reefs range from 2 to 22 ppt (Eleuterius 1977). The optimum salinity range of the American oyster in Long Island Sound is 10 to 28 ppt (Loosanoff 1965a), but most oysters from Long Island Sound survive 3 ppt for up to 30 days in the laboratory (Loosanoff 1965b). High mortality was reported during extended exposure of oysters to freshwater (<2 ppt salinity) during spring floods in Mississippi Sound and Louisiana marshes (Gunter 1953), in Mobile Bay, Alabama (May 1972), and in the Santee River, South Carolina (Burrell 1977). Many oysters died in the Beaufort Inlet, North Carolina, after exposure to 5 ppt for about a month (Wells 1961). Oysters in one Louisiana reef died after 14 days at 6 ppt (Anderson and Anderson 1975), although most oysters in Louisiana coastal waters tolerate lower salinities: Gunter (1953) reported that a salinity of less than 2 ppt for 14 days killed only 12% of a population of oysters.

Oysters apparently tolerate higher salinities in Texas than elsewhere. In Laguna Madre, a saltwater bay that often has unusually high salinities, oysters spawn and grow in salinities greater than 40 ppt (Breuer 1962). In Redfish Bay and Harbor Island, Texas, mass mortality occurred at a salinity of 40 ppt but the oysters also were exposed to a water temperature of 37 °C (Copeland and Hoese 1966).

Salinity requirements or tolerance vary from place to place for different life stages and activities. In the Gulf of Mexico, best growth and reproduction is in oyster reefs with a salinity of 12 to 30 ppt, but oyster abundance is greatest at 10 to 20 ppt (Butler 1954). In Long Island Sound, salinities above 7 ppt are required for spawning (Loosanoff 1948). Unusually high freshwater inflow in Mobile Bay, Alabama, inhibits the maturation and spawning of oysters (May 1972). Excessively low salinity inhibits gonadal maturation in oysters in Chesapeake Bay (Butler 1949) and Long Island Sound (Loosanoff 1953). Reproductive failure may be a direct

effect of salinity or it might be indirectly caused by insufficient feeding at low salinity.

In the laboratory, Atlantic coast embryos develop normally at salinities of 16 to 30 ppt (MacInnes and Calabrese 1979). Atlantic coast larvae tolerate salinities of 3 to 31 ppt (Carriker 1951), but grow fastest and survive best at salinities above 12 ppt (Davis and Calabrese 1964). Larvae in a New Jersey estuary move to the halocline (the boundary between low salinity water and deeper high salinity water) where salinities are above 5 ppt (Carriker 1951). The minimum salinity for good production of larvae in Galveston Bay, Texas, is about 20 ppt, probably because food is more abundant at these salinities (Hopkins 1931). In general, spat setting is less at lower salinities (Menzel et al. 1966). In a 10-year study at three sites near Breton Sound, Louisiana, optimum salinities for spat production were 6 to 8 ppt in May and 3 ppt in June and July (Chatry et al. 1983). Optimum salinities for the growth of spat are 15 to 22 ppt (Chanley 1957).

Heavy freshwater inflow sometimes greatly benefits oyster populations by killing predators that cannot tolerate low salinity water (Owen 1953b; Marshall 1954). For example, the southern oyster drill and the whelk (Busycon carica) die at salinities below 11 ppt (Wells 1961), and stone crabs succumb at salinities below 15 ppt (Menzel et al. 1966).

Substrate

The preferred habitats in the Gulf of Mexico are shallow bays, mud flats, and offshore sandy bars (Butler 1954; Copeland and Hoese 1966; Menzel et al. 1966). Oysters grow equally well on rocky bottoms or on mud with a consistency that will hold the oyster on the surface. Although most oyster reefs are on firm bottoms (Price

1954), they may also be abundant on mud bottoms surrounding the reefs (Butler 1954; Menzel et al. 1966). Oysters from muddy substrates are more slender than those from hard substrates (Galtsoff 1964). Maximum setting is on horizontal surfaces (Clime 1976). In Galveston Bay, Texas, oysters thrive on bottoms that are 17% to 100% sand (Harry 1976). The weathering of shells produces grit which is thought to clean oyster shells of fouling organisms (Gunter 1979a).

Currents

Currents are particularly important to American oyster larvae and adults. For maximum feeding, the volume of water immediately above an oyster bed must be renewed by a moderate current 72 times every 24 h (Galtsoff 1964). Tidal flows of 156 to 260 cm/sec or higher are needed for optimum growth in Mississippi (Veal et al. 1972). Currents are necessary for removal of feces and pseudofeces to prevent burial of the oyster reef (Lund 1957; Stenzel 1971). Currents on the sites of oyster bars in Beaufort Inlet and the Newport River estuary in North Carolina are 11 to 66 cm/sec (Wells 1961). Turbulent currents that carry sand and pebbles, however, can damage oysters by eroding shell surfaces (Galtsoff 1964). A velocity of 150 cm/sec was observed to cause unattached oysters to tumble along the bottom of Long Island Sound (MacKenzie 1981). In Delaware Bay, oysters are most abundant in areas of scour where currents keep the oyster beds free of sediments (Keck et al. 1973).

Oxygen

The hourly oxygen consumption is 39 ml/kg for a whole animal including the shell or 303 ml/kg of wet tissue (Hammen 1969). Oxygen consumption

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increases with increasing temperature (Figure 3); Q_{10} values (the factor by which a reaction velocity is increased by an increase in temperature of 10 °C) range from 1.2 to 2.3 for gill tissue and 2.7 to 4.2 for mantle tissue (Bass 1977). Oysters are facultative anaerobes and are able to survive daily exposure to low oxygen. In 1971, low oxygen killed oysters and reduced the setting of spat in Mobile Bay, Alabama (May 1972). Oxygen consumption is zero when the valves are closed (Hammen 1969), but an oxygen debt builds up.
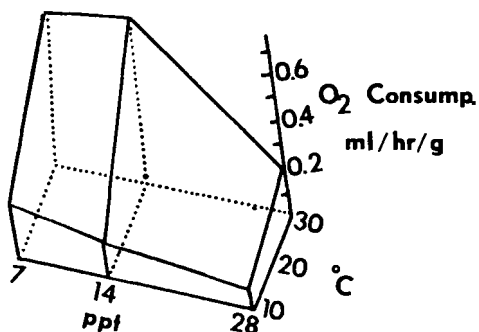

Figure 3. Oxygen consumption in the American oyster as a function of salinity and temperature (Shumway 1982).

Suspended Solids and Sedimentation

Extreme conditions, such as those associated with large storms, can practically destroy an oyster reef. The large decrease in oyster meat landings in Alabama from 1979 to 1980 is a result of Hurricane Frederick which struck Alabama in September 1977. The storm killed oysters by covering some reefs with mud and washing the substrate off others (Mark S. Van Hoose, pers. comm.). Suspended solids may clog gills and interfere with filter feeding and respiration (Cake 1983). Oysters tolerate water with suspended solids, but the pumping rate decreases. In the laboratory, pumping is reduced 70% to 85% over the range 0 to 1 g/l, depending on the nature of the suspended sediment (Loosanoff and Tommers 1948). In natural environments oysters apparently develop and grow better in waters with high concentrations of suspended solids than in waters with low concentrations (Rhoades 1973).

If covered with sediment, oysters die in 1 week at 20 °C and in 2 days at 25 °C (Dunnington 1968). The mortality of oysters covered with 2 to 5 cm of sediment near one dredging site in Louisiana increased by 48% (Rose 1973). In Alabama, however, muddy water from dredging generally did not harm nearby oyster reefs because currents and gravity carried the muddy water away from the elevated oyster reefs (May 1976).

Other Environmental Requirements

Oyster embryos develop normally within a pH range of 6.75 to 8.75 (Calabrese and Davis 1966), and develop abnormally at a pH above 9.0 and below 6.5. Larvae tolerate the same pH range as embryos but growth is fastest at a pH of 8.25 to 8.5.

Oysters occur at depths of 0.3 m above to 12 m below mean low tide (Butler 1954).

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16. Abstract (Limit: 200 words)

Species profiles are literature summaries of the taxonomy, morphology, life history, and environmental requirements of coastal aquatic species. They are designed to assist in environmental impact assessment. The American oyster, Crassostrea virginica, is an important commercial species. Spawning occurs repeatedly during warmer months with millions of eggs released. Embryos and larvae are carried by currents throughout the estuaries and oceanic bays where they occur. The surviving larvae cement themselves to a solid object, where they remain for the remainder of life. Unable to move, they must tolerate changes in the environment that range from -2 to 36 °C (air temperature), 2 to 40 ppt salinity, and clear or muddy water. The density and occurrence of adults is limited by predators, chiefly oyster drills, whelks, fish, and crabs.

17. Document Analysis   a. Descriptors

Estuaries   Fisheries   Oxygen consumption
Oysters   Salinity   Life cycles
Growth   Temperature
Feeding Habits   Suspended sediments

b. Identifiers/Open-Ended Terms

American oyster   Spawning
Crassostrea virginica
Salinity requirements
Temperature requirements

c. COSATI Field/Group

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