The Cultivation of American Oysters
(Crassostrea virginica)

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Oyster culture is the oldest form of bivalve culture and oysters were probably the first cultured shellfish. The United States leads all countries in the quantity of oysters produced, and the American oyster, (Eastern oyster), (Crassostrea virginicus) represents 80 percent of the total production. American oysters belong to the Phylum Mollusca, Class Bivalvia (Pelecypoda), Order Mytiloida (Plerioida) and the Family Ostereidae. The geographic range is eastern North America from Canada south to the Gulf of Mexico. These oysters live in estuaries and behind barrier islands. Oysters are found on a reef or water bottom where there is a mixture of fresh and saline water.

Oysters are composed of two very different parts which are the soft body mass and the outside shell which serves to protect it. The shape of the shell is influenced by environmental conditions. Oysters grown on soft mud tend to sink into the mud and must grow lengthwise in order to keep the bill above the mud. These oysters are called “coon” or “snapper” oysters. Where the bottom is firm

and the oysters are not overcrowded, oysters develop broad, well-cupped shells. Overcrowding results in long, thin-shelled oysters. Oyster reefs are most abundant along the Gulf of Mexico, South Atlantic and Long Island Sound.

Reproduction and development

Oysters are dioecious, with sexes separate; however, they exhibit alternate sexuality. Oysters usually begin life as a male, change to female then possibly back to male. This phenomenon is known as protandric hermaphroditism. In the first spawning season most young individuals are males. After the second spawning season the numbers of individuals in the total population of each sex are almost equal. Protandry takes place in the intervals between spawning seasons. Functional hermaphrodites (both male and female) are found among adult oysters. Hermaphroditism constitutes less than 1 percent of the adult population, but is found in 99 percent of all oyster population areas.

Oyster spat are predominantly male. The sex ratio after the breeding season is influenced by environmental conditions and physiological stress. Oysters that settle in unfavorable environments or experience physical injury do not tend to develop as females. Functioning as a female requires more energy for gonad development, and coping with environmental or physiological stress may limit the amount of energy that can be invested in female gonad development.

The sexual cycle begins with spawning which is triggered by water temperature. Gametogenesis, the maturation of ova and sperm, follows the spring’s increase in temperature culminating in ripeness when water tem-

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peratures trigger the spawning threshold. The American oyster spawns at temperatures greater than 16°C (60.7°F). The temperature that stimulates spawning differs among each population.

Three physiological races are based on spawning temperatures. They are found along the northern Gulf of Mexico, the mid-Atlantic coast and the Appalachicola River. Oysters in the Gulf of Mexico system spawn when water temperatures are near 25°C. Temperatures must be above 20°C for spawning and above 25°C for mass spawning. East Coast oysters spawn between 16° and 20°C. In the Appalachicola River estuary, Florida oysters spawn when water temperatures reach 22.5°C with mass spawning occurring at 26°C. The time of spawning occurs between March and November for all three races. Water temperatures above 35°C may limit the extent of spawning. Spawning does not depend directly on tidal cycles except in shallow bays where the water may warm up rapidly during low tide and stimulate spawning. Oysters can be artificially induced to spawn in laboratories and hatcheries where exact control of temperature or chemical stimulation is possible. Addition of fresh or frozen sperm or egg material is also used when artificial spawning of oysters is induced.

Other factors also influence the onset of spawning. Salinity influences spawning, and most spawning occurs when salinities remain higher than 10 ppt. Phytoplankton may stimulate oysters to spawn by chemical induction. Under natural conditions, simultaneous release of sperm and eggs into the water is essential to successful reproduction. The presence of sperm and egg in the water column may trigger other oysters to spawn as a hormonal response. Females may require stronger stimulation in the form of specific chemical stimulation from male sperm to ensure that eggs are not dis-charged without the presence of sperm. Dianthin in oyster sperm triggers spawning in other oysters.

The next stage in the reproductive cycle is the fertilization of the egg by the sperm which are released at the time of spawning by the female and male, respectively. During this stage the female produces millions of eggs. The ripe eggs of the American oyster are pear-shaped, but become globular after fertilization. Spawned eggs are heavier than water and quickly settle to the bottom where they are transported by currents and waves. The egg stage is brief, remaining emersed until development, which begins immediately after fertilization (Figure 1).

**Larval development**

After fertilization, cell division proceeds rapidly and within hours, the swimming trochophore stage is formed and the oysters are called veliger larvae. Within 24 hours two thin valves have been formed, and within 48 hours, the shell fully encloses the body and the elementary organ systems have been formed. Through larval development, the hinge changes into more adult-like, rounded protuberances. The early umbonal stage has a well-developed mouth, esophagus, stomach, intestine and rudimentary gills. Larval shells do not contain as much calcium carbonate as adults. They are lower in density and are transparent, allowing microscopic examinations of soft body parts. Soon veliger larvae form a distinctive ciliated organ called the velum, which is used for swimming and feeding. During swimming the veliger projects between the shell halves. Large cilia around the margin of the velum are for swimming; smaller cilia covering the base carry food particles to the mouth. As development continues, descriptive names are used that refer to the most conspicuous morphological changes associated with each stage.

Larval development generally lasts 10 to 21 days depending on culture techniques. The pelagic larvae of oysters act to distribute the species. Currents are the major influence on the dispersal of oyster larvae in the wild. Their swimming ability is insufficient to counter the force of currents. They generally swim upward at a rate of 1 cm/sec. This behavior trait results in tidal transport generally toward the head of an estuary where currents may transport larvae more than 5 miles.

When the veliger develops two eye spots that are on each shell, it is called an eyed-pediveliger. The eye spots aid in selecting an acceptable location for attachment. Soon after, a ciliated, muscular foot is formed. These pediveligers become bottom oriented, crawling on substrate to find a suitable site to cement or set. At this time they are negatively phototropic (response to light), generally setting on darkened surfaces using their cement glands. Once set, metamorphosis of internal organs occurs and the velum, eye spots and foot are lost. Once a small amount of cementing fluid is excreted from the edge or bill of the larval shell, the “spat” become sedentary filter-feeders through adulthood.

Several factors influence setting behavior of oysters. Dominant factors include temperature combined with the maturity of the pediveliger. As the eyed-pediveliger larva nears the end of its planktonic development, it passively uses tidal currents, the salt wedge and its ability to migrate vertically to “select” the optimum environment for metamorphoses. Rising water temperatures over tidal flats during flood tides stimulate setting. Cooling or warm temperatures may affect the rate of setting by as much as 10 days. In shallow water, setting occurs mostly on artificial substrates held away from the bottom since siltation inhibits setting.

The length of the larval period depends on water temperature
Figure 1. Life cycle of the Eastern oyster, Crassostrea virginica.
and food supply but will generally last 8 to 12 days under well-fed hatchery conditions, longer in "brown water" culture. Trochophore larvae are about 60-70 microns in length. Veliger larvae are about 200 microns. Larvae become eyed at about 265 to 270 microns, while pediveligers range from 285 to 320 microns in length.

Proper temperatures (above 20°C or 68°F) are needed for development. Mature oysters grow well at 10°C to 30°C (50°F to 80°F) or higher, but the most favorable temperatures are 77°C to 79°F. Salinities also have an affect on development. Gonadal and larval development takes place best above 10 ppt salinities. Oysters grow best in the intertidal zone to depths greater than 30 meters (98 feet).

The ideal salinity range for growth and development is 10 to 22 ppt. Salinity below 10 ppt inhibits spat set. Seed oyster production does well within a salinity range from 10 to 15 ppt. A range from 15 to 25 ppt is optimum for gonadal development.

Growth

The American oyster’s rate of growth is fastest during their first three months of life. Oysters grow about 10 mm/month. Growth is highest during the first six months after setting and gradually declines throughout the life of the oyster. Growth is influenced by many factors. One major factor is the availability of food. Available food must be of the right size and quality. Food consists of algae, bacteria, detritus and other minute organisms that are 10 microns or less. Increased temperature and salinity will also increase the rate of growth. Decrease in growth is caused by longer intertidal exposure and increased turbidity.

Growth is continuous throughout the year with the exception of unusually cold periods or spawning. Growth is slow during gametogenesis because most of the energy is used for gamete production instead of adding body mass. Increase in biomass after spawning may occur without an increase in shell length, when glycogen reserves are restored. Glycogen is used as a fast access energy storage system that is used during gonadal development. Transplanting seed oysters (≥ 1 inch) from lower to higher salinity also stimulates fast growth.
Whether in a natural reef or aquaculture setting, under optimum growing conditions, the oysters reach market size in 9 to 12 months of age. Oyster growth is influenced by temperature and varies seasonally. Maximum growth usually occurs from fall through spring. During spring and early summer, growth is slow because most energy is used for gamete production. In the warm, nutrient-rich water of the Southern Atlantic Coast and the Gulf Coast, the American oyster can be harvested at 9 months off bottom, but more typically is harvested at 18-24 months of age when cultivated on bottom. The American oyster is 300 to 320 microns (0.01 inch) at metamorphosis and at harvest is approximately 3 inches (120 mm) shell length, having a meat weight of 60 to 85 grams. Oyster growth is more rapid in the warmer waters of the Gulf of Mexico than the cooler waters of the Mid and Northern Atlantic coast where it may take 4 to 5 years for an oyster to reach marketable size. Growth is also affected by salinity, food availability, periods of exposure to air and population density.

Farming

The primary method of farming oysters is the shell-cultch method. Oysters are farmed extensively with the majority of most seed oysters produced on state-owned or public water bottoms where little or no cultivation is done. The object of oyster bottom culture is to replace the reef where age classes are kept separated on different grounds. The ideal situation is where breeding grounds are completely separated from growing areas.

Before the application of shell, the reefs or beds should be cleaned to remove as much debris as possible for best production. Planting shell or cultch is the most commonly used management strategy to maintain and increase oyster production. Shells and/or cultch provide a clean hard substrate for oyster setting and growth.

Planting cultch is not a simple matter of evenly spreading hard materials (usually shells) along the bottom. The oyster farmer must also understand the life history of the oyster and optimum environmental conditions for growth at the culture site. Seasonal temperatures through generations of salinity cycles as well as the reproductive cycle are generally learned. Knowing the density of oyster larvae in plankton samples is also important information that can be used to determine how much cultch to spread in a given area.

Site selection for planting cultch is very critical. The most important factor is planting cultch on or near existing oyster reefs. Other important factors to consider are bottom conditions (firmness), water depth (shallow), sediment types, turbidity, and tidal and flow patterns. Oysters are most successful in shallow bays and on mud flats. They can survive on relatively dense mud that is firm enough to support their weight. Soft mud and shifting sand are not suitable for oysters. Water temperature and salinity should be considered as well as historical catch data in the area.

The timing of cultch planting is critical. If planted too early, shells may become fouled by other marine organisms, or if too late, peak oyster larvae production may have passed. In either case, setting densities and ultimate production will be reduced.

Application of cultch should be relatively thin on established reefs; however, thicker applications or even piles may prove best on soft water bottoms. Piled cultch catches more spat and can then be further dispersed by high velocity water currents, or mechanical spreading.

Timing and method of application of cultch is significantly more important than the type of cultch used. Oyster shells are the most widely used cultch because of their availability and low cost. Clam shells (Rangea cuneata) have also been used extensively and in large volumes because single oysters are generally produced.

Availability has reduced their use in recent years because of environmental damage caused by the dredging operations for clam shells.

There are disadvantages in attempting to establish an oyster bed by planting cultch. The area selected must be conducive to good oyster production where good setting substrate is the limiting factor. Conflicts may occur with other uses of water bottoms such as shrimping, oil and gas operations, and dredge material disposal.

The best oyster farming techniques employ the proper seeding of oyster beds. Two areas are typically used, one for seeding and one for growing. Excluding predation the major sources of mortality are from siltation. Competition for space causes poor growth. Proper site selection can eliminate or reduce mortalities from siltation.

Selecting seed ground

The following factors should be considered in the selection of seed ground. The amount of suitable ground at various tidal levels is proportional to the amount of seed to be planted. The bottom should be firm enough to support oysters and as mentioned above where the proper substrate may be the limiting factor. Seed at lower levels are more susceptible to attack by predators such as starfish, crabs and drills. In the Southeast (Carolinas, Georgia and Atlantic Florida), there is also less time available to farm seed when the level of low and high tide occurs. This is not a problem in the Gulf of Mexico because the tidal fluctuations are not as great.

There are disadvantages in selecting seed available to growers of Eastern oysters, wild seed and hatchery seed. Wild seed is produced naturally, usually acquired from public reefs during an oyster season. Leases are sometimes cultivated for seed as well. The essential feature is that the control...
of reproduction development and growth is under natural forces. Oyster farmers that use wild seed are at the mercy of the elements. Hatchery seed for the American oyster is from controlled production and availability is limited. There are only a few vendors of hatchery produced seed along the range of the American oyster.

The spreading of seed may be done either from a boat or directly on the ground at low tide. Often boat seeding requires some redistribution. There are no strict rules as to the density at which seed is planted. It depends on many factors such as seed availability and wave action. Seed oysters can be placed in more saline waters that result in better growth but at the same time increasing the incidence of mortality from predation.

Production and seed availability can be increased by providing a controlled environment during initial development, using hatcheries and remote setting. Hatcheries are very site specific requiring high quality water conditions. Broodstock acquisition and management of algal culture for larval food and appropriate hatchery management skills are also needed for successful larval culture.

Easily accessible or near-shore estuarine areas may provide a more suitable environment for setting and growth. Near-shore estuarine areas have been used in Louisiana for seed production using remote setting. This method utilizes oyster larvae from a hatchery to produce seed using tanks of filtered seawater containing a suitable cultch. The tank's water is aerated to provide even larval dispersal. Setting occurs over 48 to 72 hours with a 20 percent setting success typically guaranteed by commercial hatcheries. A common “recipe” includes adding approximately 100 larvae per oyster shell, resulting in an average of 20 spat per shell after setting; about 14 seed per shell after a 30 day near-shore nursery period; and culminating in about 3 market oysters per shell, if all goes well.

The advantages of remote setting are consistent seed production, the purchase of specific quantities, matching settlement time to natural food availability, and reduced price. Some of the disadvantages of remote setting are more labor intensive operations, increased risk of disseminating disease, and higher production costs compared to using wild seed.

Oysters may be cultivated in ponds. Pond cultivation systems require the control and monitoring of salinity, temperature, dissolved oxygen and other water quality parameters. Optimum growing conditions should be maintained as well as the detection of diseases and chemical and bacteriological contamination. A high quality natural food supply may be difficult to maintain. This technique is experimental and not viable oyster aquaculture.

There are some disadvantages to pond culture. Spawning and young can cause water quality and system design problems by fouling and clogging equipment. It is very likely that difficulties related to monitoring water quality for public health purposes will occur. Pond culture in lowland areas (marsh) may be impossible with the new wetland regulations and the initial expense of highland pond construction unless polyculture is attempted.

Another method of growing oysters is off-bottom or suspension culture. This technique utilizes the water column, typically over soft bottom, to suspended substrate and/or seed oysters. Oysters exhibit faster growth with this technique. The disadvantages are that the systems are more labor intensive, production costs are greater and the water column cannot be used by other commercial or public interest.

### Purging

Oyster beds that are found to be contaminated due to the presence of biological pathogens or chemicals are closed to harvest and these beds become restricted. Oysters from these areas cannot be directly harvested to enter the market for human consumption without using a suitable and approved cleansing or purging technique.

A technique called “relaying” can be utilized, whereby oysters from restricted areas are moved and transferred to approved areas or banks. The concept applied is that when oysters are moved to areas of better environmental conditions they “purge” themselves of the contaminants found in the restricted areas. Relaying is accomplished by respeding the oysters on new bottoms or suspending the oysters using various types and methods of containerization. The oyster must remain in these relayed areas for a minimum of 11 days, or until a test shows that indicator coliform bacteria have been purged to acceptable levels. Increased use of relaying could increase production but is cost prohibitive during times of high oyster production in approved growing areas. Other disadvantages include compliance with regulatory controls, increased manpower needs, and suspended containers that remove submerged lands from public use.

Depuration is another technique in which contaminated oysters are allowed to purge themselves of contamination under more controlled conditions. It involves onshore facilities. Oysters from contaminated areas may be purified in special tanks through which large quantities of pure water are passed. Contaminated oysters are placed in tanks of water that for this purpose are prepared by several methods including the use of ultraviolet rays, which destroys the bacteria.

The advantages of depuration are the reduction in bacterial count and purging of sand and grit. The disadvantages of depuration are increased cost and labor intensity. The success of treatment in removing viruses and *Vibrio* sp. may be inadequate to insure safe-
ty from disease following consumption. There is a lack of standards and knowledge of the process for removing these pathogens and heavy metals. This technique is used with greater success in European countries but has not received general acceptance in the United States. As the population of the U.S. expands, more coastal waters will be used for disposal of waste, reducing the areas for oyster culture. With time depuration techniques may be more widely accepted.

**Predation and disease**

Disease and predation can limit oyster production. All oysters are very susceptible to predation but off-bottom cultured oysters are less susceptible. Oyster eggs, early embryos and larvae are eaten in large numbers by protozoans, ctenophores, jellyfish, hydroids, worms, other bivalves, barnacles and crabs, as well as juvenile and adult fish. Larvae are also parasitized by the protozoans which cause extensive mortality. A trematode worm, *Bucephalus cuculus*, inhabits the gonads of oysters.

Predation represents a serious threat to oyster populations with severe consequences to commercial harvest. Most oyster predators such as gastropods (oyster drill or conch), starfish and many species of fishes such as black drum live on or near the bottom. The conch is probably the most serious predator. This small snail can eat almost a hundred oysters a day. Black drum have pharyngal plates in their throat which can crush the shells of oysters, causing the destruction of newly planted reefs. Oysters that remain in high salinity areas throughout the summer generally encounter high mortalities from oyster drill predation and infections from the parasite *Perkinsus marinus*.

Although fouling is generally minimal, fouling organisms are usually distinctly zoned primarily by salinities. Barnacles and algae are the major intertidal fouling organisms. Oyster planting can be located to minimize the major effects of fouling organisms.

Another important constraint to oyster culture is the problem of disease. Bacterial diseases are known to affect oysters; however, their influence has not been determined on oyster populations. Bacterial infections can and do kill oysters at all stages of development. Bacteria, such as *Vibrio* sp. and *Pseudomonas* sp., are found in water which infects and kills both larve and adult oysters. There are few effective methods for controlling disease among oysters at this time but the best tool to use today is the education of the farmer.

**Managing the environment**

The survival of oysters is negatively affected by many factors. Pollutants such as heavy metals, petroleum hydrocarbons, pesticides, chlorine derivations, sewage, freshwater runoff and other pollutants may destroy oyster populations and oyster reefs. Sewage, both point and non-point source, contributes to bacterial contamination. Heavy metals affect oysters during all stages of their life cycle. Heavy metal contamination causes stress that reduces their ability to withstand diseases and parasites. It can lead to mortality of embryos and larvae, reduce growth of larvae and spat, reduce spat setting and cause shell thinning.

As industrial activities increase, pollution by heavy metals can cause the consumer concern because of its detrimental effects on public health. Oil pollution increases oyster mortality and reduces the quality for human consumption. Oil pollution reduces oyster feeding which interferes with reproduction success, reduces growth and lowers resistance to parasites.

Since bivalves are sedentary animals that filter their food from water, the success of bivalve culture depends on the environmental management of estuaries and coastal areas where the bivalve is cultured. When choosing a bivalve culture site two important factors to consider are the quality and quantity of fresh water. When fresh water enters the estuaries and coastal areas it carries organic material and pollution from upstream. As coastal activities (recreation, tourism and shipping) increase the effluents and residues, they may directly or indirectly increase the pollution burden. Since these factors influence the site, care must be taken when managing it.

Oysters also need fresh water and nutrients for growth and reproduction. Concentrations of chlorine and chlorine derivatives as low as 0.005 ppm can cause reduced pumping rates, due to reduced ciliary activity. Exposure to a chlorine concentration between 0.12 and 0.16 ppm adversely affects oyster growth, food intake and reproduction. Chlorine concentrations greater than 0.16 ppm are toxic, and when exposed to chlorine concentrations greater than 1 ppm oysters close their valves. This is significant if domestic water supplies containing chlorine are part of the effluent entering an estuary.

There are numerous freshwater diversion projects being proposed to rebuild wetlands and halt salt water intrusion. Since fresh water is important to oyster setting, growth and survival by providing nutrients and its gradual influence in salinity changes, production from many reefs could be increased if the freshwater influx was increased and controlled. The disadvantages of freshwater diversion are the low cost benefit ratio because of high construction cost and impacts to oyster reefs in close proximity to the project. Biological changes may occur in the area of the diverted water and the area receiving the diverted water. The production of some species may be enhanced at the expense of others and the total environmental impacts and benefits may be difficult to measure. Oyster reefs located closest to the
diversion project may be destroyed by decreased water quality, increased sedimentation or a complete change to a freshwater environment. Harvesting may be restricted as a result of increased contamination.

In the marine environment, pollution standards for both water and oysters should be established to protect the consumer and produce a healthier product. On the administrative and political level regulations must be changed to improve the environment in order to deliver a quality product. These regulations might encourage the oyster farmer to produce a better product while market prices are kept in line with production costs. Regulations pertaining to oyster culture are not the same in each coastal state. Be sure to check the regulations in your state.

Harvesting

Before harvesting oysters, health of the oyster bed has to be determined. Oyster bed health can be determined by quality and complex interaction of changing environmental factors, primarily salinities, circulation, temperature, water quality, bacterial count and food supply.

Oysters are harvested by a variety of methods. In areas where oyster reefs are exposed during low tide, individual oysters may be handpicked. This technique has no commercial significance. In shallow areas, oysters may be harvested by tongs. Tonging is one of the oldest methods utilized to harvest oysters. Tongs work like a pair of post hole diggers with handles that are at least 10 feet long. The harvesting end is similar to two rakes that scoop the oysters off the bottom and hold them in a basket when closed. The harvested oysters are then emptied into a boat or container. If the handles are long enough tongs can be used in water up to 25 feet deep. In some regions this may be the only legal technique for harvesting oysters. A good oyster tongs may harvest 25 to 30 bushels per day.

Oysters are also harvested by dredging from oyster boats. Dredges are metal baskets with a row of spike-like teeth. When dragged over oyster beds, dredges uproot the oysters from the bed and force loose oysters into the basket. Mechanical winches hoist the heavy load on board. Mechanical dredges are also used that harvest 1 to 2 bushels per drag. Suction dredges are also used and are efficient in clearing bottoms of 10,000 bushels per day. However, environmentalist have fought this technique as this is the same technique used to harvest clam shells for cultch. Another dredge used to harvest oysters is the escalator dredge, which is very effective in shallow water.

Oysters can be harvested and processed year-round and oyster meat yield varies with the season. Winter oysters, “fat” oysters, are cream colored due the presence of glycogen and may yield eight pounds per sack (1.5 bushels). Summer oysters are milky in appearance due to spawning condition and may yield four pounds/sack with an average of six pounds/sack.

Marketing

After predation, disease and environmental conditions are met, the farmer has to ask questions on how he will market his product. The success of oyster production depends on the methods used, and what applies in one area may not apply to others. Those individuals in charge of oyster culture must adapt production strategies to the local situation, and the farmer must assume some of the responsibility for sanitary control and improved production methods. Production methods will have to be improved in order to enhance the marketability of oysters.

The market price of oysters is affected by relationship between production and market demand. When demand is high the price of oysters goes up and when production is high the price goes down. Producing a high quality product improves the possibility that the market demand will be greater. Negative publicity on oyster quality has a serious effect on the sale of raw oysters, which is a major market.

Oysters are marketed in two forms. They are marketed as shucked meats and sold in halfpint, pint and gallon containers. They are also sold live in the shell or on the half shell for immediate consumption. Live oysters may be sold by the dozen, peck, bushel, tub, basket, sack or by count. Live oysters may be singles, doubles, or clusters and all may be combined in one container. Oysters in sacks may be kept live for two weeks if the temperature is maintained between 35 to 40°F. The oysters should never be allowed to dry out.

Shucked oysters in gallon containers are graded as extra large (no more than 160 oysters/gallon), large or extra select (more than 160 but no more than 300 oysters/gallon), small or standard (more than 300 but no more than 500 oysters/gallon) and very small (more than 800 oysters/gallon). Nothing should be in the container other than oysters since the law prohibits the addition of any ingredients including water or oyster juice.

American oysters are the basis for important industries along the Atlantic and Gulf Coast. The future of this industry is in serious jeopardy because of soft markets for raw products, and changes in habitat due to tidal and salinity changes as well as habitat destruction due to silting, coastal erosion and subsidence. Other important factors are changes in water quality due to increased pollution levels from industrial and domestic sources.