CMFRI
bulletin 38

JANUARY 1987

OYSTER CULTURE—STATUS AND PROSPECTS

Edited by : K. NAGAPPAN NAYAR AND S. MAHADEVAN

CENTRAL MARINE FISHERIES RESEARCH INSTITUTE
(Indian Council of Agricultural Research)
P.B. No. 2704, Cochin 682 031, India

2

ECOLOGY OF OYSTER BEDS

S. MAHADEVAN[1] AND K. NAGAPPAN NAYAR[1]

INTRODUCTION

The oysters of the world are grouped into one family Ostreidae. Within this family are 3 groups or genera *viz., Ostrea, Crassostrea* and *Pycnodonta.* The genus *Ostrea* which is widespread through most part of the world is generally considered to be adapted to clear waters with little sediment and high salinity. *Crassostrea* exist in estuaries where the silt load is high and salinity variable and generally low. *Pycnodonta* is a tropical open sea form and thrives in high salinity. They are less abundant. In each of these genera are a number of species, about 100 species throughout the world The various species inhabit coastal waters within the broad belt of the seas, limited by the latitudes 22°S and 64°N. Patchy settlement cover many square miles of bottom of littoral and intertidal zones. They also thrive above the bottom attached to rocks and underwater structures, submerged branches and trunks of fallen trees, concrete embankments and piles and miscellaneous objects in the sea shore. These aggregations of live oysters and empty shells are termed as *oyster beds* or *oyster bottoms* or *oyster reefs.* Once they are densely settled they become important to man as source of food.

Oysters have some common factors in whichever country they are found. Description of oyster bottoms usually provide information about their location, nature of bottom and depth. The oyster bed is an example of 'biocoenosis' or a social community (Mobius, 1883) of living beings, a massing of individuals with ideal conditions governing their existence. This community character of the biocoenosis is affected as also the oyster by the changes in the factors of environment—natural or man made. The well being of oyster population is closely linked up with factors such as the character of bottom, water movements, salinity of water, temperture and abundance of planktonic food. Excessive sedimentation, extreme turbidity of water and pollution caused in the oyster bed areas due to techno-economic activities of man are some of the adverse factors disturbing the established biological balance. Predation, competition and out-break of enzootic and epizootic diseases also spell disaster to the oyster life and surrounding cohabiting organisms. In spite of these natural and man made disasters the oyster possesses some amount of flexibility in physiological adaptations to tolerating fairly wide range of salinity and temperature variation, feeding flexibility and prolificity of breeding and self defensive mechanisms for self perpetuation and survival.

The 'Oyster' is scientifically the best known marine animal in the world (Nelson, 1938). Baughman (1948) has provided a complete annotated bibliography of oysters and recently Joyce Jr. (1972) has updated all publications by listing 4,117 referenes. When compared to the voluminous data and knowledge available from the above and other equally important publications like that of Breisch and Kennedy (1980) brought out subsequently on the ecology of oysters it should be admitted that the attention paid in India to the study of oyster in general and ecology in particular appears very limited. This is partly due to the fact that till 1975 oyster did not figure prominently in our piroity areas of Research and Development. From the Indian point of view and interest species of *Crassostrea* are more important as the genus *Ostrea* is not reported to occur along the Indian coastline. Some investigations of importance and interest have been conducted in the early years on the Indian backwater oyster *Crassostrea madrasensis* (Preston) and *C. gryphoides.* Hornell (1910a, 1910b), Paul (1942), Rao

[1] *Present address :* CMFRI, Research Centre, Tuticorin-628 001.

(1951, 1956, 1983) Rao and Nayar (1956) and Durve (1962, 1967) have given information on the oyster biology and ecology.

Proper understanding of the ecology of the oyster bed is very essential in order to evaluate the influence of different physical, chemical and biological environmental factors and their interaction. This will help in future management of oyster fishing and farming. Most of the information on the oyster ecology given presently is drawn from works on *Crassostrea* species outside Indian waters. But it is unavoiadable to mention here and there about *Ostrea* species also for similarity and comparison. It is hoped that informations provided here will stimulate further interest in India where oyster resources are now known to be considerable and oyster farming is one of the priority areas in our efforts to produce more protein food from the sea and brackish water.

Substratum

Oysters grow equally well on a hard rocky bottom or semihard mud firm enough to support their weight. Shifting sand and mud appear to be unsuitable. Where oozy silt covers the bottom oysters suffer or die. (Bennet, 1946). With the exception of these extreme conditions oysters adapt themselves to a variety of bottoms. They thrive on shore rocks and underwater structures which are left exposed at low tides. Climate controls the survival since no oyster can survive several hours of exposure to below or above ambient temperature. Therefore very little settlement and growth is seen very near surface ; those clumps seen with dead oysters jutting above water level during low tides in estuarine zones or pillars of bridges represent the stock which have settled down when water level was adequate till seasonal vageries bring down water level leaving live oysters exposed to atmosphere resulting in the death of continuously exposed oysters.

In some estuaries the soft muddy bottom has been naturally improved by dead shell remains which give some firmness. Dead oyster shells dropping from clusters help the bed to grow horizontally or vertically. Galtsoff (1964) indicated an arbitrary scale from 0-10 to indicate the suitability of oyster bottom to oyster.

Habitat

It is difficult to state categorically that *Crassostrea* is an estuarine form just because it thrives well under estuarine conditions. It thrives equally well in sea water also. *C. madrasensis* lives and grows along Tuticorin coast (Tamil Nadu) and in salinities of 33-35‰ in the sea. It is known that Puerto Rico species, *C. rhizophorae* thrives at salinities 33-44‰ (Mattox, 1949). As stated by Fischer (1948) many so-called estuarine species have a wide ecological range and may endure salinities of oceanic water well. No doubt many oyster beds do especially well in estuarine waters bceause drills, starfishes and boring sponge cannot stand reduced salinities thereby indirectly helping oyster survival. Brackish water areas include all dynamically stable environment of lagoons, lakes etc. in which sea water diluted by freshwater is not necessarily influenced by tidal movements. On the other hand the estuarine environment is unstable. This makes it all the more difficult for expansive beds of oysters in the estuarine system. This accounts for the presence of several mounds of dead oyster shells found in the estuarine bar mouth region due to seasonal salinity variations.

Very often setting grounds of oyster spat are seen far above the spawning ground. In the distribution and abundance of oysters it can be said that sheltered bays often have a varied population of marine organisms as a result of wave action. Along open coasts, freshwater and sediment brought to the sea from rivers and streams are dispersed readily. Water movement is relatively weak, (Lewis, 1964) with the result that silt accumulates. A high percentage of animals with rock habitat are filter feeders. Water, high turbidity and the deposition of mud over the individuals tend to eliminate these animals from their habitats.

Light

Fischer (1948) has stated that little is known on the physiological influence of sunlight on oysters. Oyster spat settlement is greater in the darker under surface of objects than in areas which are less dark. It has also come to notice that in the discharge of spawns mature oysters react positively to darkness. Sun exposed oysters formed a thicker harder and more deeply cupped shell than those growing in the dark (Medcof and Needler, 1949).

Current

The areas with swift current are said to affect larval set and this is the reason why oyster spat are found at the bottom where the current action is weak than the surface where the action of current is greater in general. Tidal currents may carry away oyster larvae with it dispersing them in areas unsuitable for larval set or exposing them to plankton feeding animals.

Turbidity

Reports on the effects of turbidity on shellfishes in general are sometimes contradictory. It has been maintained that excessive turbidity inhibits the feeding mechanism thus restricting the growth. Lunz (1938) maintains that mortality of oysters is not increased by turbid conditions. Loosanoff and Tommers (1948) studied the effect of suspended solid material on feeding rate of oysters and concluded that oysters are vrey sensitive to suspended silt and there is an inverse proportion between concentration of sediment and rate of pumping. They state that even 0.1 g/l did seriously reduce the rate of pumping (to 40 % of normal). If 3-4 g were added per litre of water only 4 % of normal quantity of water was pumped. Very high concerntration may inhibit pumping completely. Dead and dying oysters found in turbid waters invariably contain large amount of silt in their gills (Loosanoff, 1962). Korringa (1952) also found that silt and other substances producing turbidity, kaolin or chalk, at low concentration as 0.1 mg/1 bring about reduction in water pumping. Oysters are normally not bothered by ordinary sediment but in some years of heavy spillway discharge there is 100 % mortality. On the one hand there is a view that some turbidity in the water in which the larvae are living during metamorphosis may be desirable aginst U.V. light shielding these from U.V. radiation in shaded areas. There is a second view that the settling of turbid material to the bottom of a body of water prevents effective attachment of spat. Even 1 or 2 mm thick sediment is sufficient to prevent satisfactory oyster set (Galtsoff, 1964).

Loosanoff and Engel (1947) state that the rate of pumping may be influenced by the density of microorganisms present in the water. There are definite concentrations above which the density of microorganisms begin to interfere with the rate of pumping; not only it decreases but the oysters become sluggish. Dangerous quantities were 75,000/ml for smaller *Nitzchia* sp. and 2,00,000/ml for small *Chlorella* sp. This may be due to metabolic products of micro-organisms having inhibiting influence, probably caused by the bacteria which abound in such dense concentration and which live on organic excretion produced by the planktonic organisms. Water containing low concentration of small diatoms and dinoflagellates running over a bottom in a non-turbulent flow is ideal.

Water movements

Free exchange of water is essential for growth to remove gaseous and liquid metabolites and faeces and to provide oxygen and food. This is very essential for the dispersal of the oyster larvae in order to expand the beds. Estuaries are ideal in this regard. As the oyster closes its shell tightly underwater or exposed to air, many processes come to a standstill e.g., digestion. This process is said to be carried on anaerobically in closed oyster as long as glycogen reserves are available (Dugal, 1940). It is stated that *Crassostrea* is more hardy than *Ostrea* and can stand 24 days of exposure and live.

pH

In the case of C. *virginica* the pH of tidal estuary which forms the principal habitat must not fall below 6.75. The species does not reproduce successfully in waters where the pH remained above 9.00. The rate of pumping is normal at 7.75; in 6.75—7.00 vigorous first and then declines; at 6.5—4 decreases by 10 % of normal.

Temperature

Almost all workers who have studied oysters from temperate waters have found that growth is confined to the periods when water temperatures are higher. Davis and Calabrese (1964) concluded that maximum growth results at a particular temperature since growth rate is affected by the type of food organisms available at different temperatures. Data on ecological range of adult oysters show that many oysters are killed by prolonged cold spells although *C. virginica* withstands —5°C. High temperature also causes death showing distress after 34°C. Functioning of adductor is weakened at 40°C and mortality results. The temperature regime affects the life of the oyster by controlling the rate of transport, feeding, respiration, growth, gonad formation and spawning. The oyster can adjust its pumping rate quickly to sharp and sudden changes in temperature (Loosanoff, 1950b). While it is recognised that temperature affects biological processes organismic response patterns to the natural environments are multidimensional. Most of the experimental studies devoted to the analysis of temperature effects have been conducted under simplified laboratory conditions. While such unifactorial approaches are useful there is need for the study of response to multivariable factor intensity patterns. Water temperature is known to influence the filtering activity i.e., the volume of water oyster pumps through its gills (Loosanoff, 1950a). From 28°—32°C the rate of pumping is as much as 37 L/hr. Normally 5—25 L/hr is pumped.

Reproduction tends to be confined to narrower thermal ranges than majority of other life processes.

The American oyster can feed and grow at much lower and higher temperature than are required for spawning. Once certain conditions such as appropriate physiological condition and nutritional demands are satisfied the time of reproduction is often decisively affected by temperature. Spawning of the oyster, *C. virginica* can be delayed by ripe or near ripe individuals being transferred to subnormal temperatures (Loosanoff and Davis, 1950). That is to conclude that temperature although high enough to permit gamete maturation is too low to induce spawning.

The time required for the larvae to reach the setting stage for *C. virginica* ranges in laboratory conditions from 10—12 days at 30°C—32°C to 36—40 days at 20°C (Davis and Calabrese, 1964). In the larvae of *O. edulis* the temperature range for satisfactory growth (70% or more) ranges at 27‰ salinity from 17.5°C—30°C. (Davis and Calabrese, 1964). Approximate setting time are 26 days at 17.5°C, 14 days at 20°C, from 8—12 days at 25°, 27.5°C and 30°C. According to Korringa (1941) larvae of *O. edulis* have a pelagic life of 6 days at 22°C—23°C, 9—10 days at 18°C—21°C and 13—14 days at 16°C—17°C. In the case of *C.gigas* the percentage of eggs developing to the shelled stages has a tendency to decrease sharply at temperature above the optimum (23°C—25°C) and decrease slowly at temperature below the optimum (Cahn 1950, Galtsoff 1964, Sato 1948, 1967). In *C. madrasensis* the spat settlement was achieved within 15-20 days at lower temperature range of 27°C—30°C although the optimum temperature was not decided upon (Nayar *et al.*, 1984). Medcof and Needler (1941), Thorson (1946), Korringa (1952) and Carriker (1946, 1951, 1961) give further information regarding thermal responses of lamellibranch larvae.

Enzymes required for molluscan larvae for digesting naked dinoflagellates are reported to be active at a lower temperature than are enzymes necessary to digest forms with more resistant cell walls. The temperature allowing maximum growth in larvae of *C. virginica* lies between 30°C—32.5°C at higher salinities and 27.5°C at low salinity of 7.5‰.

SALINITY

Oysters like many other euryhaline organisms are able to live in seawater of wide range of salinity. Many have reported on adverse effects upon oysters of too low or too high salinities but statements are contradictory. The oyster can isolate itself from outside environment by closing its values tightly and survive adverse conditions provided they do not last indefinitely. Ranson (1943) noted damage below 13‰ when oodemic tissues are developed with vacuolisation of the epithelial cells and a sharp increase in leucocytes. Below 7‰ degeneration of tissue progresses. It has been observed that in Courtallayar river mouth, ranges below 10% slowly kill the Madras backwater oysters during north-east monsoon floods. In the Vaigai estuary at Athankarai the entire oyster population suffer total mortality when the salinity shoots up beyond 40‰ due to solar evaporation of the impounded water near the closed bar mouth. Unstable salinity regime characterises the tidal rivers and appears to be an important ecological factor.

Loosanoff (1950a) stated that sharp changes from low to high salinity can be withstood without physiological injuries and that it is tissue starvation due to prolonged low salinity exposure which leads to death. It is apparent that critical salinity values are to be determined for each area separately. Changes in salinity have not been known to induce spawning in the American or European oysters. Butler (1949) observed inhibition of gametogenesis in 90% of *C. virginica* in a low salinity area and attributed to inability of oysters to feed under low salinity conditions. Chestnut (1946) observes that in places where salinity is very low feeding often stops during low tide. Under tropical conditions of our coasts the temperature of the sea or the backwaters are maintained high throughout the year. Rao (1951) felt that a drop in density of water due to rains acts as a stimulating agent factor in the spawning of the Madras oyster in the east coast backwaters of South India.

Salinities between 5—8‰ are considered as an ecological boundary and referred to as 'horohalinicum'. This has been analysed by Khlebovich (1969) who found that the larvae of *C. virginica* tolerate salinity reductions down to 5-8‰. Adult requires higher salinities. In the case of *C. gigas* the formation of the larval shells is retarded in suboptimal salinities. Dupuy *et al.* (1977) reared the larvae of *C. virginica* and *C. gigas* to setting stage in 9-11 days at salinities 17.5‰—20.0‰. Hopkins (1937) found correlation between the periods of setting and periods of high salinity in *Crassostrea virginica* and that the larvae depended on a salinity of about 20.0‰ as a stimulus to develop the setting stage. In the case of *C. madrasensis*, Nagappan Nayar *et al.* (1984) found that the larvae reached the eyed stage from 13th to 15th day at salinities of 30.5‰. This was delayed further in higher salinities thereby indicating the role of salinity in larval development.

Larval food

Appreciation of nannoplankton organisms as food for marine larvae is increasing. That non-coloured flagellates like *Monas* may constitute a suitable food for oyster larvae under natural conditions is expressed by Imai and Hatanaka (1950). Needler (1941) and Blanco *et al.* (1951) have also expressed opinion that nannoplankton plays essential role in oyster larval development.

Fouling

It is of very great importance to understand the oyster bed associated organisms and the epifauna since they play a decisive role in the well being of oysters. Apart from abiotic factors which affect the oysters, heavy mortalities of oysters in the bed are caused by biological factors like predation, competition and disease outbreak.

The polychaete worm *Polydora* sp. is often mentioned as an agent causing damage. This worm selects the shell of the oyster as a habitat and diverts the energy of the oyster to shell secretion for countering the effect of mud blisters formed by the polychaetes. The shells are often honeycombed by the worms and become brittle. The infestation makes the animal vulnerable to secondary invasion by microorganisms. Similarly the boring sponge *Cliona* though not a true parasite excavates galleries in the calcareous shell of the oyster for shelter. This results in heavy mortality at times of heavy infestation by reduced resistence of oyster against pathogenic organisms (Old, 1941). In the case of English and Dutch oyster beds, the slipper limpet *Crepidula fornicata* is considered a serious pest (Korringa, 1952) by occupying space meant for young oysters.

Pollution

Pollution plays an important role in the ecology of oyster beds from the biological point of view. In coastal waters contamination of water by domestic sewage and trade waters are common. The sewage covers the bottom with a sludge which smothers the oyster bed affecting the oxygen content of the water and greatly increasing the bacterial load of the water. The degree of pollution is determined by *Escherichia coli* found in the water. Where the MPN is in excess of 70 per ml the area is unsafe. Similarly the disposal of radio-active waste in the sea presents a new threat. Excess heavy metals in water like Mercury and Zinc tend to get accumulated in oyster flesh and beyond certain level prove to be lethal. Sulphite waste liquor of pulp mills has caused damage. Odlaug (1949) found that in 1,000 p.m. concentration the oysters suffered greatly due to perhaps impairment of mucus feeding sheets and also gill lamellae forming indentations (Mackernan, Tartar and Tollefson, 1949). Oysters developing abnormal fibres in the adductor muscle (Galtsoff, Chipman, Engel and Calderwood, 1947). As a sedentary animal not capable of locomotion after setting the oyster is vulnerable to environmental changes thus affecting its equilibrium or steady state. Factors of environment act jointly and the combined action of several factors produce a far greater effect than that by a single factor. A thorough understanding of all these is essential in the ecological studies of oyster bed. Some pollutants contain highly toxic substances and cause mortalities among marine populations. Others are not so toxic to have lethal effects on adults but decrease the rate of survival of their larvae. Davis (1961) found DDT to be one of the most toxic with 0.05 ppm causing 90% mortality of oyster larvae. The normal ecological environment may be so changed, that some planktonic organisms useful to shellfish as food disappear and are replaced by microorganisms not useful but even harmful.

Diseases and parasites

Extensive studies have been made on the mortality of oysters in natural beds caused by the pathogenic fungus *Parkinsus marinus* (Dermo), the haplosoridians *Minchinia nelsoni* (MSX) and *M. coastalis* (SSO) in the case of *C. virginica*. Similarly in France and other European coastal beds *Marteilia refringens* causes large-scale mortalities. In India, so far, such pathogens do not seem to occur ; but a suspected case of Dermo in *C. madrasensis* is being carefully studied. Mahadevan (1980) has catalogued most of the prominent oyster diseases reported from all over the world. Apart from MSX, SSO and Dermo diseases the list includes *Ostracobiabe implexa* (*C. virginica*) *Myotomus ostrearum* (*C. virginica*, *C. gryphoides*), *Nocardia*, (*O. edulis*) *Nematopsis ostrearum* (*C. virginica*) *Hexamita nelsoni* (*O. edulis*, *O. lurida*), *Sphaenophyra*, (*C. virginica*) *Nosema dollfusi* (*C. virginica*), *Orchitophyra stellarum* (*C. virginica*) and *Ancistrosoma pelseneeri* (*C. virginica*) as of considerable importance as disease causing agents. Crustacean parasites like *Mytilicola intestinalis* in *C. gigas* and helminths (cestodes and trematodes) also cause debility to the oysters.

Predation is next to disease causing agents in eliminating oysters from beds. Crabs in the oyster beds crack off the edges of oyster shells which leads to death of oysters ; particularly the spat are more vulnerable. Predatory gastropods known as drills play havoc to oyster population. *Urosalpinx cinerea* in Atlantic coast is a classic example. In *C. madrasensis* beds the gastropod *Cymatium cingulatum* destroys the spat and adults. Although *Thais* and *Rapana* are also known to be dangerous their threat is much less to *C. madrasensis*. The havoc played by these differs from one geopgraphical area to the other. Control measures have been evolved and followed with certain amount of success but the problem always continues in the natural beds resulting in losses of natural population.

REFERENCES

BAUGHMAN, J. L. 1948. An annotated Bibliography of oysters with pertinent material on mussels and other shellfish and an Appendix on pollution. *Tex. A & M. Res. Found College Station*. 794 pp.

BENNETT, H. H. 1946. Stream pollution by erosion silt. In 'pollution of Navigable waters'. Hearing before the committee on rivers and harbours, House of representatives, in the Congress, 1st session, Govt. printing office, Washington D.C., pp. 318-327.

BLANCO, G. J., D. K. VILLALUZ, AND H. R. MONTALBAN. 1951. The cultivation and biology of oysters at Bacoor Bay, Luzon. *Philipp. J. Fish.*, 1 : 35-53.

BUTLER, P. A. 1949. Gametogenesis in the oyster under conditions of depressed salinity. *Biol. Bull.*, 96 : 263-269.

BREISCH LINDA, L. AND VICTOR S. KENNEDY 1980. A selected bibliography of world wide oyster literature. Sea Grant Program (UM. SG. TS-80-11). A Maryland Sea Grant Publication. University of Maryland ; 309 pp.

CAHN, A. R. 1950. Oyster Culture in Japan. *Fish. Leafl. Wash.*, 283 : 1-80.

CALDERWOOD, H. N. AND A. R. ARMSTRONG 1941. Determination of glycogen in oysters. *J. Ass. of Argic. Chem. Wash.*, 24 : 154-165.

CARRIKER, M. R. 1946. A brief critical survey of the evidence for the horizontal movements of oyster larvae. *Conv. natl. shellfish. Ass. New York*, June 5-7, 1946, pp. 28-32.

CARRIKER, M. R. 1951. Ecological observations on the distribution of oyster larvae in New Jersey estuaries. *Ecol. monog.*, 21 : 19-38.

CARRIKER, M. R. 1961. Inter-relation of functional morphology, behaviour and autoecology in early stages of the bivalve *Mercenaria mercenaria*. *J. Elisha Mitchell Scient. Society*, 77 : 168-241.

CHESTNUT, A. F. 1946. Some observations on the feeding of oysters with special reference to the tide. *Con. Shellfish Ass. New York*, June 5-7, 1946 : 22-27.

DAVIS, H. C. 1941. Effects of some pesticides on eggs and larvae of oyster *Crassostrea virginica* and Clams *Venus mercenaria* *Comm. Fish. Rev.*, 23 (12): 8-23.

DAVIS, H. C. 1961. Effects of some pesticides on eggs and larvae of oysters (*Crassastrea virginica*) and clams (*Venus mercenaria*). *Comm. Fish. Rev.* 23 (12) : 8-23.

DAVIS, H. C. AND A. CALABRESE. 1964. Combined effetcs of temperature and salinity on development of eggs and growth of larvae of *M. mercenaria* and *C. virginica*. *U.S. Fish. and Wildlife Serv., Fish. Bull.* 63 : 643-55.

DUGAL, L. P. 1940. Le glucose come agent de resistance a pasphyxie chez *Ostrea virginica*. Ann. ACFAS, 6 : 114

DUPUY, J. L., N. J. WINDSOR AND C. E. SUTTON 1977. Manual for design and operation of an oyster seed hatchery for the American oyste. *Crassostrea virginica* VIMS, Gloucester Point, Virginia, Spl. Rep. ; 142 : 1-104.

DURVE, V. S. AND D. V. BAL 1962. Preliminary observations on the growth of spat of the oyster *Crassostrea gryphoides* (Schlotheim). *J. mar. biol. Ass. India* ; 4 (2) : 200-213.

DURVE, V. S. 1967. On the nomenclature of two Indian backwater oysters. *J. mar. biol. Ass. India* ; 9 (1) : 173-178.

FISHER, P. H. 1948. Donnees Sur la resistance et Sur la Vitalite des mollusques. *J. Conchyoliol.*, 88 : 100-140.

GALTSOFF, P. S. 1964. The American oyster *Crassostrea virginica* (Gmelin). *U.S. Fish. and Wildlife Serv., Fish. Bull.*, 64 : 1-480.

GALTSOFF, P. S., W. A. CHIPMAN, J. B. ENGLE AND H. N. CALDERWOOD. 1947. Ecological and physiological studies of the effect of pulp mill wastes on oysters in the Yark river, Virginia. *Fish. Bull. U.S.*, 51 : 59-186.

HOPKINS, A. E. 1937. Experimental observations on spawning, larval development and setting in the Olympia oyster, *Ostrea lurida*. *Bull. U.S. Bur. Fish.*, 48 : 439-503.

HORNELL, J. 1910 a. An attempt to ascertain the principal determining factor in oyster spawning in Madras backwaters. *Madras Fish. Bull.*, 4 : 25-31.

HORNELL, J. 1910 b. The practice of oyster culture at Arcachon (France) and its lessons for India. *Madras Fish. Bull.*, 4 : 25-31.

IMAI, T. AND M. HATANAKA. 1950. Studies on marine noncoloured flagellates, *Monas* sp. favourite food of larvae of various marine animals. I. Preliminary research on cultural experiments. *Sci. Rep. Tohok Univ., Biology* 18 : 304-315.

JOYCE, E. A. 1972. A Partial Bibliography of Oysters, with annotations. Marine Research Lab., Florida Dept. of Natural Resources, st. Petersburg, Florida : 846 pp.

KHLEBOVICH, V. V. 1969. Aspects of animal evolution related to salinity and internal state. *Mar. Biol.*, 2 : 338-345.

KORRINGA, P. 1941. Experiments and observations on swarming, pelagic life and setting in the European flat oyster *Ostrea edulis. L. Arch. neerl Zool.*, 5: 1-249. University of Amsterdam (Thesis, 1940).

KORRINGA, P. 1952. Recent advances in oyster biology. *Qly. Rev. of Biology*, 27 (4): 266-308 and 339-35.

LEWIS, J. R. 1964. *The ecology of rocky shores.* English Universities Press, London.

LOOSANOFF, V. L. 1950 a. On behaviour of oysters transferred from low to high salinities. *Anat. Rec.* 108, Abstr. 147.

LOOSANOFF, V. L. 1950 b. Rate of water pumping and shell movements of oysters in relation to temperature. *Anat. Rec.* 108, Abstr. 229.

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

LOOSANOFF, V. L AND DAVIS. 1950. Spawning of oystars at low temperatures. *Science*, 111 : 521-522.

LOOSANOFF, V. L. AND J. B. ENGLE. 1947. Effect of different concentrations of microorganisms on the feeding of oysters (*O. virginica*). *Bull. U.S. Fish.*, 42 : 31-57.

LOOSANOFF, V. L. AND F. D. TOMMERS. 1948. Effect of suspended silt and other substances on rate of feeding of oysters. *Science*, 107 : 69-70.

LUNZ, G. R. 1938. The effects of the flooding of the Santae River in April 1936 on oysters in the Cape Romain area of South Carolina. U.S. Engr. off.

MCKERNAN, D. L., V. TARTAR AND R. TOLLEFSON 1949. An investigations of the decline of the native oysters industry of the State of Washington, with special reference to the effects of sulphite pulp mill waste on the olympia oyster. (*Ostrea lurida*). Dept. Fish. Wash. State *Biol. Bull. Rep.*, 49a : 115-165.

MAHADEVAN, S. 1980. Shell fish diseases and their control. In: Edible molluscs. *Proc. Summer Inst.*, C.M.F.R.I. publication Sept. 1980 ; 122-131.

MATTOX, N. T. 1949. Studies on the biology of the edible oyster, *Ostrea rhizophorae* Guilding, in Puerto Rico, *Ecol. Monogr.*, 19 : 339-356.

MEDCOF, J. C. AND A. W. H. NEEDLER 1941. The influence of temperature and salinity on the condition of oysters (*Ostrea virginica*). *J. Fish. Res. Bd. Can.*, 6: 498-505.

MOBIUS, K. 1883. XXVII. The oyster and oyster culture—Translated by H. J. Rice by permission of the author From the book published in 1887. Die auster and die Austernwinthschaft Verlag Von Wiegandt Hempel and Parey, Berlin : 126 pp. U.S. Commission of Fish and Fisheries, Part 8. Report of the Commissioner for 1880. appendix H-pp. 683-751.

NAGAPPAN NAYAR, K.. M. E. RAJAPANDIAN, A. D. GANDHI AND C. P. GOPINATHAN. 1984. Larval rearing and production of spat of the oyster *Crassostrea madrasensis* (Preston) in an experimental hatchery. *Indian J. Fish.*, 31 (2) : 233-243.

NEEDLER, A. W. H. 1941. Oyster farming in Eastern Canada. *Bull. Fish. Res. Bd.* Canada, 60 : 1-83.

NELSON, T. C. 1938. The feeding mechanism of the oyster. I. On the pallium and the branchial chambers of *Ostrea virginica, O. edulis* and *G. angulata*, with comparisons with other species of the genus. *J. Morph.*, 63 : 1-61.

ODLANG, 1949. Effects of stabilised and unstabilised waste sulphite liquor on the Olympia oyster, *Ostrea lurida. Trans. Amer. micr. Soc.*, 65 : 311-317.

OLD, M. C. 1942. The taxonomy and distribution of the boring sponges (Clionidae) along the Atlantic coast of North America *Contr. Chesapeake biol. lab.*, 41 : 1-30.

PAUL, M. D. 1942. Studies on the growth and breeding of certain sedentary organisms in the Madras harbour. *Proc. Indian Acad. Sci.*, 15 : 1-42.

RANSON, G. 1943. La Vie des Huitres. Histoire Naturelles, I. 260 pp. Gallimard, Paris.

RAO, K. V. 1951. Observations on the probable effects of salinity on spawning, development and setting of the Indian back. waters oyster *Ostrea madrasensis* Preston. *Proc. Indian Acad. Sci.*, 33-B : 231-56.

RAO, K. V. 1956. Seasonal gonadal changes in the adult backwater oyster *Ostrea* (*Crassostrea*) *madrasensis* Preston from Ennur near Madras. *Proc. Indian Acad. Sci.*, 37 : 332-336.

RAO, K. V. 1983. Induced spawning of the adults and laboratory rearing of the larvae of the edible oyster *Crassostrea madrasensis* (Preston). *Proc. Symp. Coastal Aquaculture* ; Part 2: Molluscan culture : 479-483.

RAO, K. V. AND K. NAGAPPAN NAYAR. 1956. Rate of growth of spat and yearlings of the Indian backwater oyster *Ostrea madrasensis* Preston. *Indian J. Fish.*, 6 : 231-260.

SATO, T. 1948. Relation between growth of oyster larvae and water temperature and the specific gravity of the upper layer of water. *Quart. J. Fish. Inst.*, 1 : 90-110.

SATO, T. 1967. Oyster. Yogyogakukakuron, Tokyo : Koseisha Koseikaku.

THORSON, G. 1946. Reproduction and larval development of Danish marine bottom invertebrates with special reference to the planktonic larvae in the Sound (Oresund). Meddleraer Fra Kommissionen for Denmarks Fiskeri-Og Harundersogelser, Serie : plankton, bind 4, nr. 6 : 523 pp. C. A. Reitzels. Forlag, Copenhagen.