ICLARM STUDIES AND REVIEWS 13

The Biology and Culture of Tropical Oysters

C. L. Angell

ICLARM
INTERNATIONAL CENTER FOR LIVING AQUATIC RESOURCES MANAGEMENT

The Biology and Culture of Tropical Oysters

The Biology and Culture of Tropical Oysters

C.L. ANGELL
210-35th Avenue East
Seattle, Washington 98112
USA

1986

INTERNATIONAL CENTER FOR LIVING AQUATIC RESOURCES MANAGEMENT
MANILA, PHILIPPINES

The Biology and Culture of Tropical Oysters

C.L. Angell

1986

Published by the International Center for Living Aquatic Resources Management, MC P.O. Box 1501, Makati, Metro Manila, Philippines with financial assistance from the International Development Research Centre of Canada through ICLARM's Selective Information Service project

Printed in Manila, Philippines

Angell, C.L. 1986. The biology and culture of tropical oysters. ICLARM Studies and Reviews 13, 42 p. International Center for Living Aquatic Resources Management, Manila, Philippines.

ISSN 0115-4389
ISBN 971-1022-24-9

Cover: Wild *Crassostrea rhizophorae* attached to mangrove roots, Dominican Republic. Photo by C.L. Angell.

ICLARM Contribution No. 315

Contents

29 Sept. 1982

This review complements the work of the Thailand Fisheries Department-ICLARM project on Applied Research on Coastal Aquaculture 1982-1985, which was funded by the German Agency for Technical Cooperation.

The first review in this series is "The Biology and Culture of Marine Bivalve Molluscs of the Genus *Anadara*" by M.J. Broom. 1985. ICLARM Studies and Reviews 12, 37 p.

ABSTRACT

Oysters with potential for aquaculture are found throughout the tropics and subtropics, but few species have been cultured and in only a few tropical countries. This monograph reviews the biology, ecology and culture techniques, both experimental and commercial, used in the tropics; describes the problems associated with tropical oyster farming; and points out research needs to develop further this form of aquaculture.

Three oyster genera are discussed in the review: *Ostrea*, *Crassostrea* and *Saccostrea*. The advantages and disadvantages of various species of each genus with regard to aquaculture are described.

INTRODUCTION

Oysters are found throughout the tropics and subtropics and are commonly harvested from wild populations. In spite of their adaptability to cultivation, oyster farming has developed in only a few tropical countries. The expansion of oyster culture has been hindered by limited awareness of its potential among fishery development promoters and the need for more widespread dissemination of information on the technology of oyster culture, processing and marketing. Hopefully this publication will contribute to overcoming some of these obstacles.

The oyster is probably the most studied invertebrate organism and much is known of its biology in temperate waters. Galtsoff (1964) provides an excellent coverage of its general biology, based on the American oyster, *Crassostrea virginica*. Quayle (1975) has provided an extensive bibliography dealing with tropical oyster biology and culture. More recently Breisch and Kennedy (1980) produced a bibliography covering the entire subject of oyster taxonomy, biology and culture with over 3,000 citations.

The taxonomy and phylogeny of tropical oysters remain confusing in some areas, but the application of modern methods of protein electrophoresis and hybridization using state-of-the-art hatchery technology will help to clarify these relationships. Identification keys based on regional species groupings would be most useful for oyster culture developers, but are beyond the scope of this paper.

While much of the biology of tropical oysters is comparable to that of their temperate counterparts, the effects of their warm environment on reproductive cycles are not well understood. Temperature may play a minor role in stimulating gonad maturation, as will be pointed out in following sections. Oysters, particularly of the genus *Crassostrea*, must adapt themselves to the sometimes rapidly changing salinity and heavy silt loads brought about by the monsoonal climate of much of the tropics.

Tropical oyster farmers are confronted with the difficulty of predicting spatfall from populations of oysters that may be spawning continuously. Sometimes they must avoid excessive setting. Fouling is a serious problem in the tropics and culture systems must be evolved which can economically overcome it.

Many of these problems are compensated for by the extremely fast growth (compared to temperate species) of tropical oysters. The farmer can usually obtain market-size oysters in less than one year, often in as little as six months, and with the continuous spatfall common in many areas, can produce a steady flow of product for customers.

Although disease has not been a serious problem in tropical oyster culture, siltation and pollution have reduced production and pose a continuing public health hazard that must be addressed if the industry is to thrive. Problems of both technology and infrastructure have to be overcome.

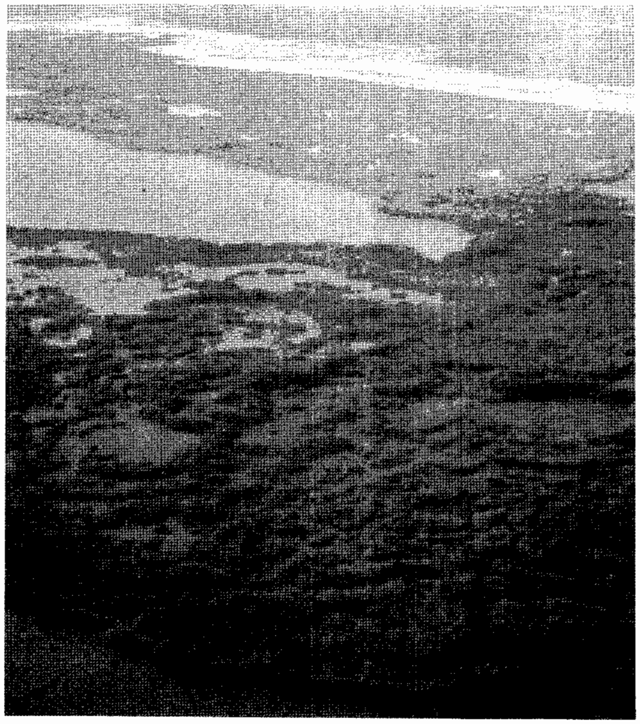
Oyster production is slowly increasing (Table 1), but tropical production is still dominated by a few countries, most notably Mexico, and its production comes mainly from one species, *Crassostrea virginica*. However, the potential is great. Culture technology utilizes low-cost materials and is adaptable to rural development.

Table 1. Oyster production in tonnes by country, year and species, 1978-1983. (FAO 1984)

Country	Species	1978	1979	1980	1981	1982	1983
Kenya	*Ostrea* sp.	1	3	1	1	2	0
Mexico	*Ostrea* sp.	1,740	2,495	2,606	4,244	4,509	3,294
	Crassostrea virginica	33,591	36,059	41,303	37,706	30,397	32,723
Cuba	*C. rhizophorae*	2,100	2,700	2,012	2,525	2,577	2,370
Venezuela	*C. rhizophorae*	803	0	16	575	1,240	755
Dominican Republic	*C. rhizophorae*	43	5	1	2	23	23
Columbia	*Crassostrea* sp.	49	56	52	56	53	19
Senegal	*Crassostrea* sp.	123	92	149	136	124	124
Sierra Leone	*Crassostrea* sp.	1,092	950	980	940F	900	900
Brazil	*Crassostrea* sp.	377	135	178	149	212	440
Indonesia	*Crassostrea* sp.	186	912	605	573	1,981	1,866
Thailand	*Crassostrea* sp.	221	562	5,410	7,856	3,690	3,477
Total		40,326	43,969	53,313	54,763	45,708	45,991

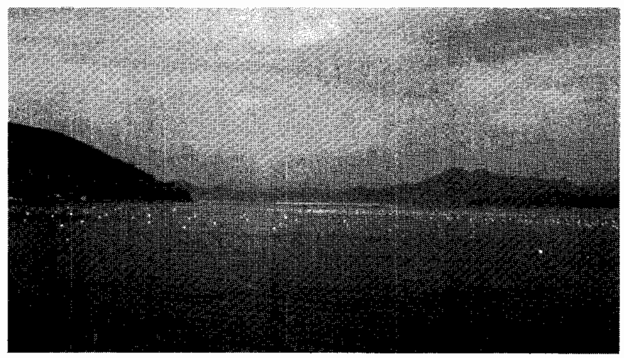
THE SPECIES AND GEOGRAPHIC DISTRIBUTION OF CULTURED TROPICAL OYSTERS

The following discussion is not intended to be an exhaustive review of the taxonomy of living tropical oysters, but rather a survey of some of the more readily available literature dealing principally with species which are now cultivated or that have potential. The potential for culture of a



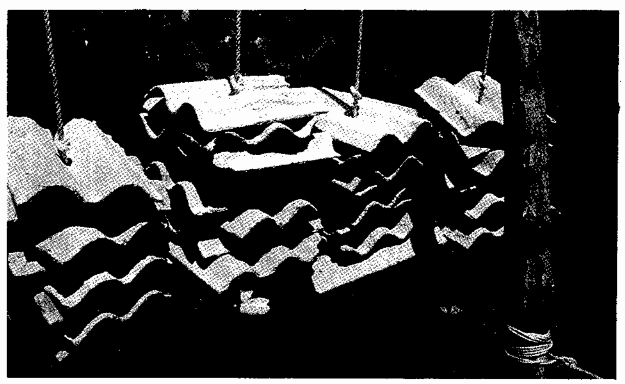
1

2



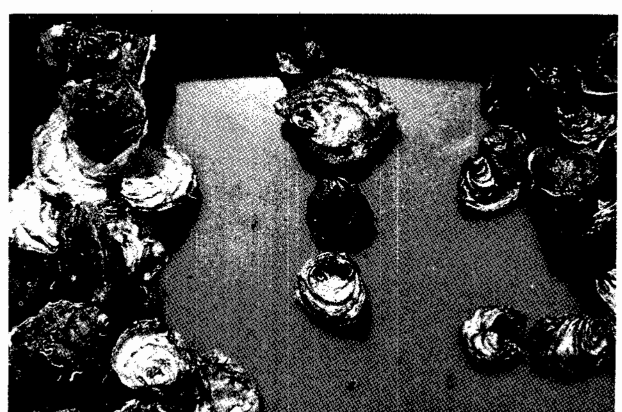
3

1. *Rhizophora mangle* mangroves in Las Marites Lagoon, northeastern Venezuela. This is the natural habitat of *C. rhizophorae*. 2. Cement slabs used for both spat collection and grow-out. The slabs are planted in the soft bottom of Deep Bay, Hong Kong, for the culture of *C. gigas*. 3. An example of longline oyster culture using a single mainline and styrofoam floats, Cholla Nam Do, South Korea. 4. Spat collectors made of cement-palm composite, Ambon, Indonesia. 5. Hatchery-produced single spat of *C. belcheri*, Thailand. 6. Using a simple tool to twist galvanized wire for hanging culture of *C. gigas*. Twists serve as cultch separators.



4

6



5

particular species is based primarily on biological and technical criteria, since there are few data available on markets and marketing. Experimental results may indicate potential in those species which have been subject to study. In other cases the size achieved by wild specimens and the extent of their distribution may show their promise for aquaculture. Some species are considered unsuitable for farming because of their small size or restricted range.

Genera

The three genera of interest to aquaculturists are *Ostrea*, *Crassostrea* and *Saccostrea*. Stenzel (1971) placed the tuberculated oysters in the genus *Saccostrea* on the basis of their chomata, deep umbonal cavity and tendency to form rudistiform or cornucopia-like shapes. Ahmed (1975) considered the separation from the genus *Crassostrea* valid and remarked on the difference in habitat as further evidence of their generic separation. Dinamani (1976) was able to differentiate larvae of *Saccostrea* from those of *C. gigas* on morphological differences in their shells (Fig. 1). Several other characteristics used for comparison are listed in Table 2.

Table 2. Comparative features of three oyster genera from Glude (1971), Ahmed (1975) and Stenzel (1971).

Characteristics	Genus *Ostrea*	*Crassostrea*	*Saccostrea*
Chomata (denticles)	present	absent	present
Promyal chamber	absent	present	present
Umbonal cavity	absent	moderate	deep
Sexual development	protandrous hermaphrodite	dioecious	dioecious
Spawning mode	larviparous	oviparous	oviparous
Turbidity tolerance	low	high	moderate
Salinity preference	stenohaline	euryhaline	stenohaline
Shape	subcircular, flat	somewhat elongated and cupped	cornucopiate or rudistiform
Shell margins	crenulated in some species	not crenulated	crenulated
Valves	equal	upper valve smaller	upper valve smaller
Size	small to moderate	may be large	small to moderate
Range	All tropical seas	All tropical seas except Polynesia and Melanesia	Indo-Pacific

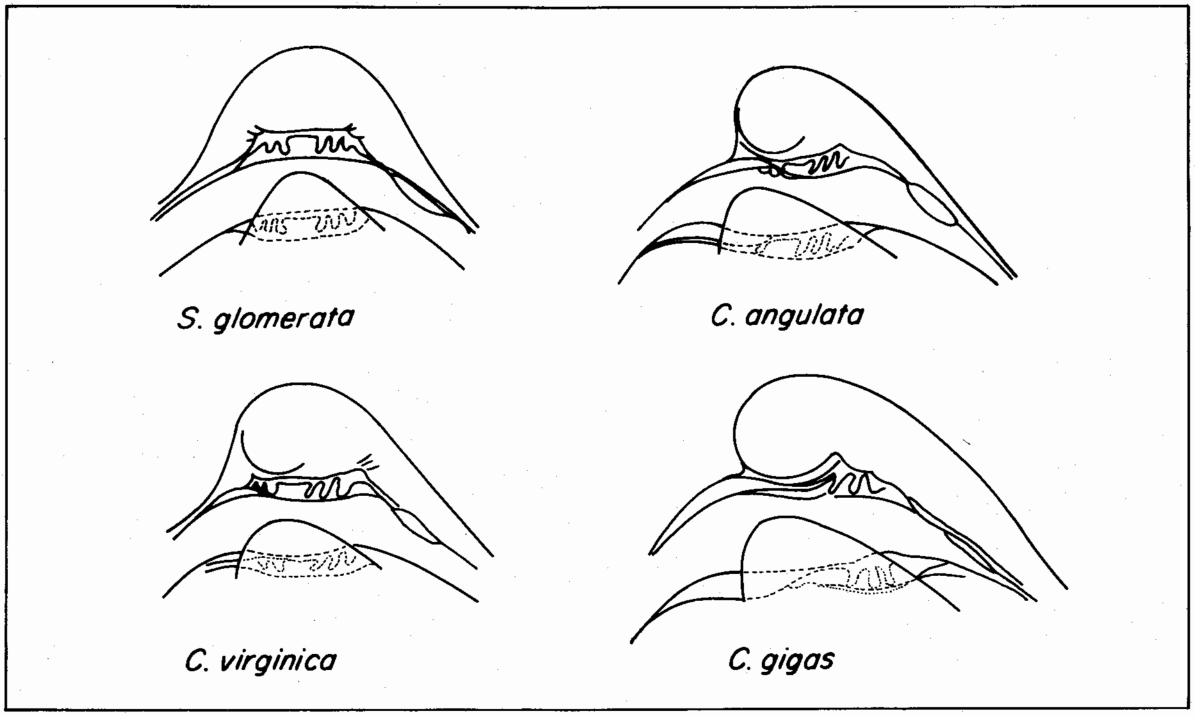


Fig. 1. Comparisons of the umbonal region of the prodissoconchs of four oyster species (after Dinamani 1976).

Species

OSTREA

Species of this genus are widely distributed in tropical seas and some are of commercial importance, either cultured or harvested from wild stocks (Table 3). Most are not presently farmed, but may have potential.

O. equestris and *O. frons* are found in the Gulf of Mexico, Antilles and West Indies (Gunter 1951). However, *O. frons* is too small for consideration as an aquaculture candidate. Gunter (1951) found specimens of *O. equestris* on oil platforms in the Gulf of Mexico that had grown to 72-mm shell height in one year which indicates culture might be possible in high salinity water such as occurs in the more southern range of the species. However, without hatchery production, spat supply might limit potential.

Two species, *O. iridescens* and *O. palmula*, are of commercial importance on the west coast of Mexico and one of them, *O. palmula*, is commercially cultured (Cardenas 1984). *O. iridescens* is a large oyster, sometimes reaching 25 cm (Olsson 1961) and should be a candidate for aquaculture. *O. megadon* is found subtidally as deep as 110 m from Baja California to Peru (Hertlein and Strong 1946). Nothing is known of its biology or aquaculture potential and there appear to be no records of its use for food.

O. stentina is found in the Mediterranean from Portugal to Angola, but appears rather small for culture (Nickles 1950, 1955). Nickles (1950) also reported the occurrence of *O. folium* from Morocco to Gabon, where it is harvested from wild stocks in some parts of its range. This species is also reported from Australia and Malaysia (Thomson 1954; Ng 1980). However, the correct identity of Nickles' *O. folium* needs to be verified. Comparing the descriptions of Nickles (1950) and Thomson (1954), there are differences in the width of the hinge plate and shape of the lower valve. Nickles (1950) described the presence of clinging hooks ("crampons"), not mentioned in Thomson's description. *O. folium* has been experimentally cultured in Malaysia (Ng 1979).

Glude (1971) encountered a small *Ostrea*, *O. nomades*, in Palau, Truk, American Samoa, French Polynesia and the Cook Islands. It is also said to occur in the New Hebrides (Thomson 1954). However, due to its small size it is not likely to offer any potential for culture.

Table 3. Tropical species of *Ostrea* with their range and aquaculture status.

Species	Range	Aquaculture potential: Experimental	Commercial	Harvest wild stocks	Location or taxonomic reference
O. equestris	Gulf of Mexico		unknown		Gunter 1951
O. iridescens	Gulf of California to Peru		potential	+	Hertlein and Strong 1946; Olsson 1961
O. palmula	Gulf of California to Ecuador		+	+	Hertlein and Strong 1946; Olsson 1961
O. stentina	Portugal to Angola		doubtful		Nickles 1950; Nickles 1955
O. folium	Australia to Malaysia; Morroco to Gabon	+	potential		Nickles 1950; Thomson 1954; Ng 1980
O. megadon	Gulf of California to northern Peru		unknown		Hertlein and Strong 1946
O. nomades	South Pacific; northern Australia		none		Thomson 1954; Glude 1971
O. trapezina	Northern Australia		none		Thomson 1954

+ Indicates existing experimental or commercial culture, or harvesting of wild stocks.

CRASSOSTREA

The *Crassostrea*-type oysters are the most important commercial species and have the greatest development potential due to their tolerance of estuarine conditions and usually abundant spatfall. Many of them have been experimentally and commercially cultured in the tropics (Table 4). *C. gigas* and *C. virginica* have been the object of numerous attempts at introduction into tropical waters. Potential exists for transplantation of several species within the tropical zone.

C. virginica extends from the coast of Mexico, where it forms the most important fishery in lagoons, as far south as Brazil (Gunter 1951). It occurs along the continental shores of its range and

Table 4. Tropical species of *Crassostrea* with their range and aquaculture status.

Species	Range	Aquaculture potential: Experimental	Aquaculture potential: Commercial	Harvest wild stocks	Location or taxonomic reference
C. virginica	Continental coasts from Mexico to Venezuela		+		Gunter 1951
C. rhizophorae	Antilles, West Indies, Venezuela to Brazil	+	+	+	Gunter 1951
C. paraibanensis	Northeastern Brazil	+	+		Singaraja 1980b
C. brasiliana	Brazil	+	potential	+	Singaraja 1980b
C. corteziensis	Gulf of California to Panama		+	+	Olsson 1961
C. fischeri	Baja California to Ecuador		unknown	+	Olsson 1961
C. columbiensis	Baja California to Chile		limited	+	Hartlein and Strong 1946
C. gasar	Senegal to Angola		potential	+	Nickles 1955
C. madrasensis	Southeast India to South China Sea coasts		potential	+	Ranson 1967 Asif 1979
C. ariakensis	Southern Japan to Pakistan		+	+	Wakiya 1929
C. gryphoides	West coast of India		potential	+	Durve 1965
C. tulipa	Senegal to Angola	+	potential	+	Nickles 1950
C. iredalei	Philippines		+		Carreon 1969
C. belcheri	South China Sea coasts	+	potential		Ranson 1967

does not inhabit the Caribbean islands. *C. guyanensis* and *C. lacerata* reported from Venezuela by Macsotay (1974) were considered to be subspecies of *C. virginica* by Ahmed (1975).

C. rhizophorae is found from Florida to Venezuela, including the Antilles and West Indies (Gunter 1951; Ruiz 1969). It may reach Brazil, but according to Singaraja (1980b), is identical to *C. brasiliana* in the northeastern part of that country.

C. paraibanensis was described as a new species by Singaraja (1980b). It is apparently confined to northeastern Brazil and is notable for its tolerance of very low salinity. This large oyster is commercially cultured by bottom and raft culture in the Paraiba River estuary (Singaraja 1980a).

The range of *C. brasiliana* extends into subtropical areas of Brazil, where spat collection techniques were developed with the objective of repopulating overfished natural banks (Akaboshi and Bastos 1977).

On the tropical Pacific coast of Latin America, *C. corteziensis* is an important species which is both harvested from wild populations and cultured (Cardenas 1984). This species extends from the Gulf of California to Panama (Olsson 1961). Other *Crassostrea* species found on the same coast are *C. fischeri* and *C. columbiensis* (Olsson 1961). Both species are harvested from wild populations throughout their range (Olsson 1961; Cardenas 1984).

No indigenous species of *Crassostrea* were reported by Glude (1971) in his extensive survey of Pacific Island oysters. Those oysters referred to by Glude (1971) as *Crassostrea* should be placed in the genus *Saccostrea* using the criteria of Stenzel (1971).

Several *Crassostrea* species of commercial importance are found throughout Southeast Asia (Table 4). *C. iredalei* is widely distributed in the Philippines and is commercially farmed (Carreon 1969). *C. ariakensis* ranges from southern Japan to coasts bordering the South China Sea, including Hong Kong, Vietnam, Amoy province of China, and Sabah, Malaysia (Ranson 1967). It is cultured in parts of Deep Bay, Hong Kong, where low salinity prevails (Mok 1974a). *C. belcheri* is a large, rapidly growing oyster found in the South China Sea region including the Philippines, Vietnam, the Malaysian states of Sabah and Sarawak, and the Indonesian islands of Java and Sumatra (Ranson 1967). This species has been experimentally cultured in Sabah and shows strong potential for commercial development (Chin and Lim 1977).

The taxonomy of *Crassostrea* species in India requires clarification. The two species of commercial importance are reported to be *C. madrasensis* and *C. gryphoides* (Durve and Bal 1962; Rao 1951). However, there is disagreement as to whether "gryphoides" is a valid name for a living oyster species and "cuttakensis" has been proposed (Ahmed 1975). Hornell (1951) maintained both were identical to *C. virginica* (his "virginiana") and should be so named. In following discussions the species names as used by Durve and Bal (1962) and Rao (1951) are used.

While references to *Crassostrea* species in tropical East Africa were not found, *C. gasar* and *C. tulipa* occur on the western coasts (Nickles 1950, 1955). Both species range from Senegal to Angola and are harvested from wild populations (Nickles 1950; Kamara 1982b). *C. tulipa* has been experimentally cultured (Kamara 1982a, 1982b).

SACCOSTREA

The most widely distributed species is *S. cucullata*, which is found throughout the Indian Ocean and tropical western Pacific (Rabesandratana 1971; Ray 1977) (see also Table 5). However, the original description of the species was from the Atlantic, raising doubts about its applicability to oysters in the Indo-Pacific (Glude 1971). *S. cucullata* has been commercially cultured in French Polynesia (Aquacop 1982) and the Philippines (Blanco et al. 1951; Blanco 1956). It is also harvested from natural stocks throughout its range (Ray 1977; Glude 1984).

S. commercialis is found from Victoria in Australia to Thailand (Thomson 1954; Saraya 1982), although there is some question about its correct identity in Thailand (Mr. Kosol Mutarasint, Dept. of Fisheries, Bangkok, pers. comm.). *S. commercialis* is farmed extensively in Thailand, particularly along the coast of the Gulf of Thailand (Saraya 1982) and from Victoria to Queensland, Australia (Thomson 1954). Genetic studies by Buroker et al. (1979a) showed that *S. glomerata* should be considered a subspecies of *S. commercialis* and Dinamani (1976) found no differences in their larval

Table 5. Tropical species of *Saccostrea* with their range and aquaculture status.

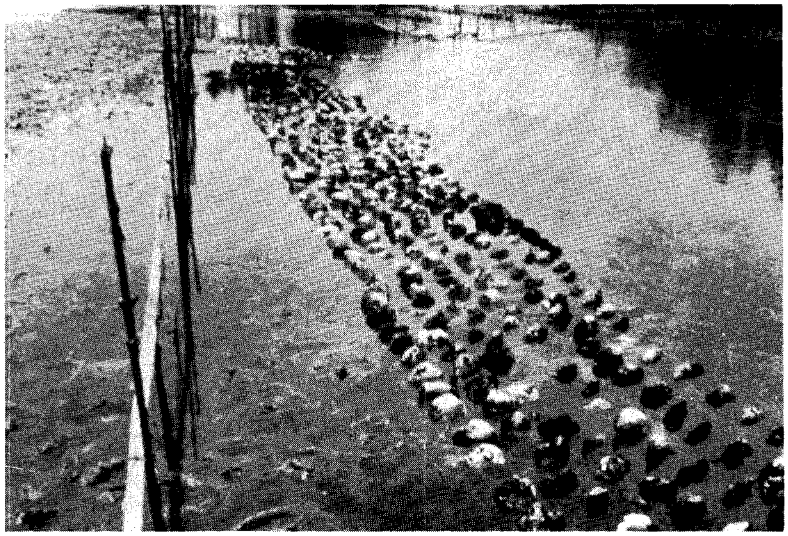
Species	Range	Aquaculture potential: Experimental	Commercial	Harvest wild stocks	Location or taxonomic reference
S. cucullata	Indo-Pacific	+	+	+	Ray 1977
S. commercialis (glomerata)	Southern Australia to Thailand	+	+		Thomson 1954
S. mordax (amasa)	Northern Australia to Western tropical Pacific	+	potential		Thomson 1954 Glude 1971
S. lugubris	South China region east to New Guinea	+	+		Ranson 1967
S. echinata	Philippines, Indonesia and western Pacific Islands	+	+	+	Thomson 1954 Carreon 1969 Glude 1971
S. malabonensis	Philippines		+		Carreon 1969
S. palmipes	Philippines		+		Carreon 1969
S. tuberculata	Western Australia, Philippines		unknown		Thomson 1954 Carreon 1969
S. manilai	Philippines		unknown		Buroker et al. 1979b

shells. Further genetic studies by Buroker et al. (1979b) indicated *S. commercialis* and *S. cucullata* are non-sibling species.

S. mordax, the pink or coral oyster, ranges from northern Australia through the western tropical Pacific (Thomson 1954; Glude 1971) and has been experimentally cultured in Queensland, Australia, by Bryson (1977), although he designated it *amasa.* Glude (1971) found Gould's type specimens to be identical with pink oysters he collected in Fiji and based on this and Thomson's description, proposed Gould's original *mordax* replace *amasa* as the correct species name.

Ranson (1967) reported the range of *S. lugubris* from the South China Sea region eastward to Papua New Guinea. It is commercially farmed in Thailand (Bromanonda 1978) and harvested from wild stocks in the Philippines (Lopez and Gomez 1982).

One of the species which has shown promise for development from experimental culture is *S. echinata* (Aquacop 1982; Angell 1984; Braley 1984; Glude 1984). It may have potential for culture in high salinity water throughout its range; in the Philippines it is commonly harvested from wild

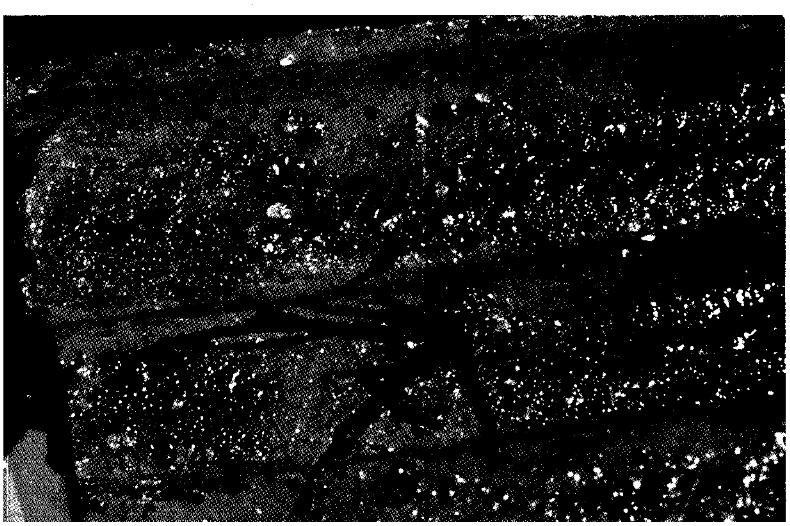


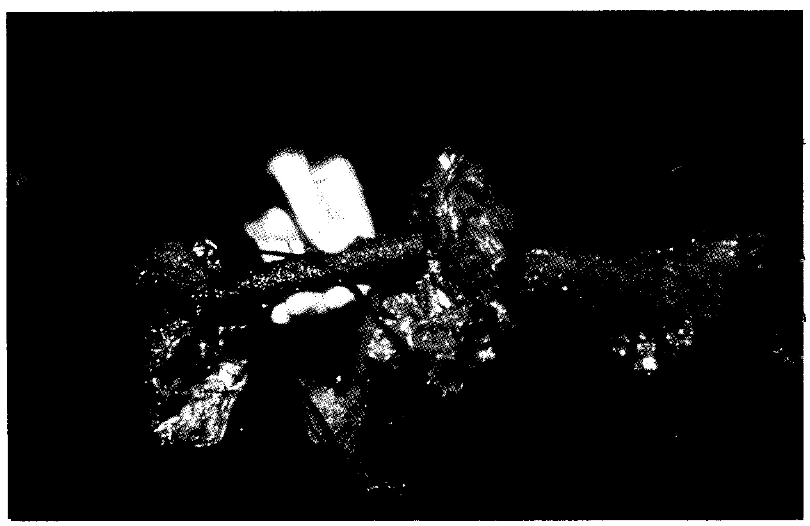
2

1

3

1. Rack culture of *S. commercialis* in southern Thailand. Spat are reared here for about 3 months and then sold to grow-out operators. 2. Spat collection of *S. commercialis* using old *Placuna* shells. Spat are reared on the shell for a month, removed and transferred to growing racks as in Plate 1. 3. Two-month old *C. gigas* grown by hanging culture, Hong Kong. 4. Spat of *S. echinata*, Ambon, Indonesia. 5. Hanging culture of *C. gigas* showing use of rubber hose spacers.





stocks (Lopez and Gomez 1982). *S. echinata* is widely distributed from the tropical waters of Australia (Thomson 1954) through the Philippines and the western Pacific Islands (Carreon 1969; Glude 1971).

Several other *Saccostrea* species are cultured commercially in the Philippines, including *S. malabonensis* and *S. palmipes* (Blanco et al. 1951). These species were described by Carreon (1969), but no record of their occurrence outside the Philippines was obtained. The description and comparison of soft parts as used by Carreon (1969) should be extended to a wider range of species (see Fig. 2 for application to Philippine species). In addition to these, *S. tuberculata* and *S. manilai* are also found in the Philippines (Carreon 1969; Buroker et al. 1979b). *S. tuberculata* ranges as far south as Australia (Thomson 1954), but its commercial status is unknown. The proper naming of this species requires further study of the soft parts, particularly the union of auricles and the position of the rectum and shape of anal fold. Thomson (1954) claimed *S. tuberculata* is very close to *S. cucullata*, while Glude (1971) proposed that it should be considered an ecomorph of *S. mordax*, principally because of the common yellow mantle rim, also described by Carreon (1969). *S. manilai* was identified as a sibling species of *S. malabonensis* by Buroker et al. (1979b) using genetic markers identified by protein electrophoresis.

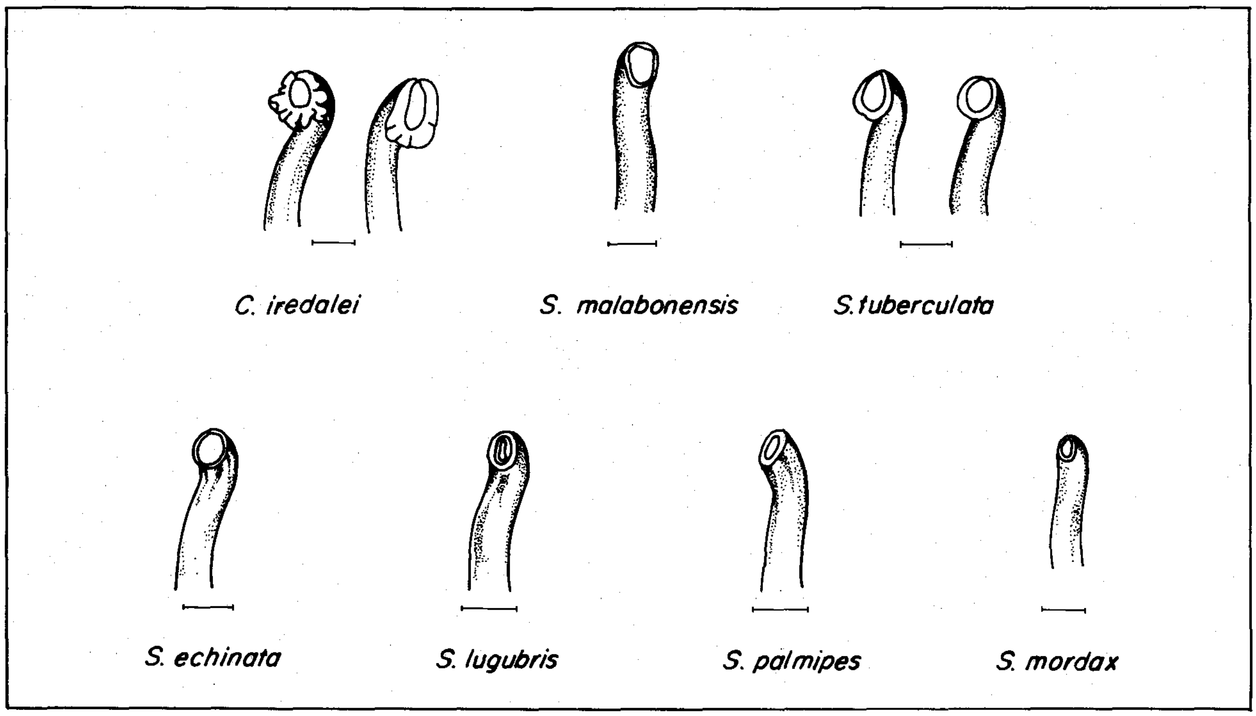


Fig. 2. Anal fold configurations of several species of Philippine oysters (after Carreon 1969). Horizontal lines represent 1 mm.

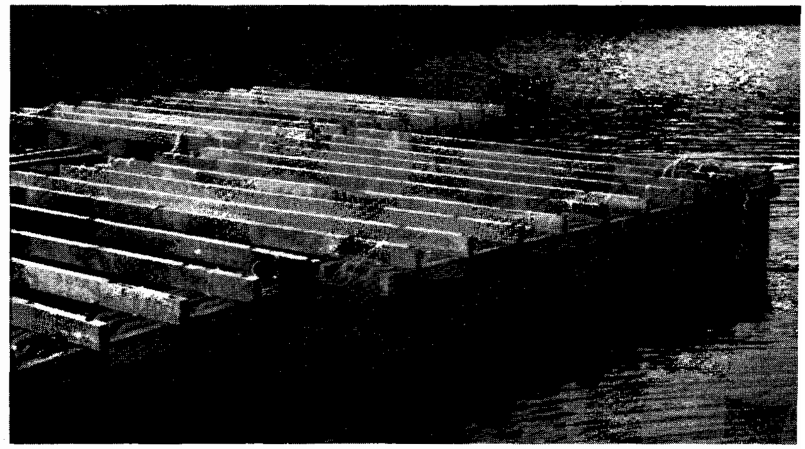
ECOLOGY OF WILD POPULATIONS

Physical Environmental Factors

TIDE

Most species of tropical oysters are intertidal and tend to concentrate in narrow bands or form dense banks at a tidal height where dessication, fouling and predation are minimized. A few species are predominantly or wholly subtidal, including *O. trapezina* (Thomson 1954), *C. paraibanensis* (Singaraja 1980b), and *O. megadon* (Hertlein and Strong 1946).

2

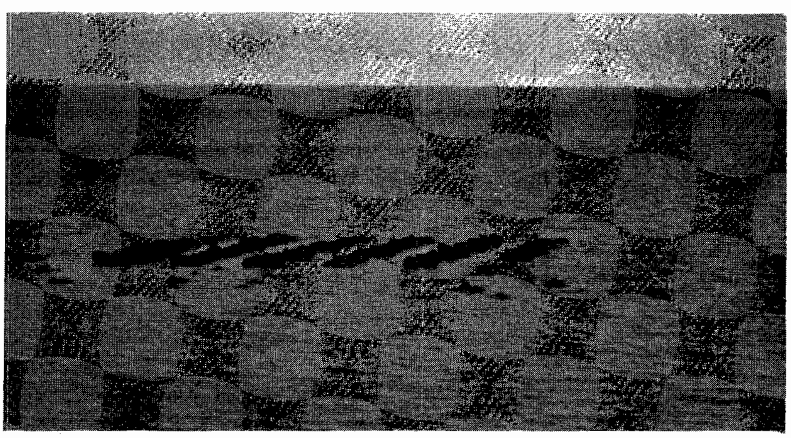


1

3

1. Rafts constructed of timber and discarded chemical carboys. The carboys have a useful life of about five years under tropical conditions. These rafts withstood a severe hurricane. 2. Tree branches used as spat collectors for *S. commercialis*, southern Thailand. 3. Spat of *C. rhizophorae* on cement-coated plywood cultch, St. Croix, U.S. Virgin Islands. 4. Small-scale intertidal rack culture of *S. commercialis*, inner Gulf of Thailand. 5. Grow-out operation using intertidal rack culture, southern Thailand. 6. Oyster products for sale at a family-operated stand along the Bangkok-Chantaburi highway. Products include oyster sauce and pickled oyster meats.

5



4

6

In some of its range, *S. cucullata* is attached to mangrove roots and is submerged most of the year (Pinto and Wignarajah 1980), while in other areas it may form dense intertidal banks (Rabesandratana 1971).

In the Caribbean, *C. rhizophorae* is nearly always found attached to mangrove roots in narrow intertidal bands, reflecting the small tidal range in the much of the Caribbean Sea (Farfante 1954; Nikolic and Melendez 1968). However, Saenz (1965) noted an indirect effect of salinity on vertical distribution of this species. Where it is found in oceanic salinity, the vertical range of *C. rhizophorae* is restricted to the intertidal zone due to excessive fouling below low water, but where the salinity is less than 30 ppt, the oyster can be found subtidally.

The tolerance of tropical oysters to desiccation and their susceptibility to heavy fouling when continuously immersed directly influence culture technology and these effects are discussed later.

SALINITY AND TEMPERATURE EFFECTS

The salinity and temperature ranges reported for several species are shown in Table 6. In many cases, the extremes occur only sporadically and are of short duration; an oyster may tolerate such conditions for brief periods, but if subjected to them long enough would experience mortality. For example, Lopez and Gomez (1982) found that *S. lugubris* and *S. echinata* would withstand 41°C, but such an extreme temperature occurs only briefly during ebb tide. The normal range in the tropics is 2-7°C, increasing considerably in the subtropics. For example, *C. rhizophorae* is subjected to a much greater temperature fluctuation in the northern part of its range (northwestern Cuba) than further south (see Table 6).

Low salinity and heavy siltation following monsoonal rains may cause mass mortalities of oysters. DeBuen (1957) investigated the problems confronting oyster culture in the lagoons of the Gulf coast of Mexico, pointing out the mass mortalities of spat associated with the rainy season. Spat set during the dry season when the salinity was 26 to 37 ppt suffered complete mortality six months later at a salinity of 4 ppt. Bottom cultured oysters in Mexican lagoons may die due to siltation during flooding, but those near the lagoon mouths are much less subject to mortalities and frequently form dense banks or reefs.

Although very high mortality is associated with low salinity during the rainy season, *C. gasar* survived in laboratory experiments in clear freshwater as long as 10 days (Sandison 1966). Setting of this species was very weak below 10 ppt and peaked at around 30 ppt. Heavy siltation associated with monsoon rains probably affected setting and survival during periods of low salinity. The author speculated that water movement could have an influence, since oysters on exposed mangrove roots suffered high mortality, while those in sheltered positions survived.

Given the lack of laboratory data, the effect of salinity on gonad maturation is unclear. Where a correlation has been demonstrated in nature, it may reflect changes in nutrition, rather than salinity *per se*. Maturation in *C. rhizophorae* in northeastern Venezuela is more pronounced during periods of lower salinity and reduced temperature (Angell 1973). These conditions correspond with the upwelling season along that coast; presumably primary production and hence the availability of nutritious phytoplankton improve. It has also been reported that high carbohydrate content of these oysters corresponds with the upwelling season (Ruiz et al. 1969).

Rao (1951) found that 22.3 ppt was the optimum salinity for egg development of *C. gryphoides* under laboratory conditions and its natural spawning did not begin until this salinity had been reached. In the Bombay area, most spawning in this species occurs between 13.2 and 28.6 ppt (Durve 1965).

S. lugubris and *S. echinata* in the western Philippines spawn throughout the year but exhibit peaks (Lopez and Gomez 1982). Gamete development coincides with periods of high temperature and high salinity (second and third quarters), while spawning takes place between the wet and dry seasons when temperature and salinity are relatively low.

Chin and Lim (1975) reported that *C. belcheri* in Malaysia spawns at the onset of the rainy season, implying maturation takes place during the dry season when salinity tends to be high. They noted condition index was high during periods of reduced salinity fluctuations (less than 2.5 ppt), but declined when variations reached 5 ppt during heavy rainfall. The authors attributed the decline in condition index to spawning.

Hong Kong is subtropical, but growth and maturation of *C. gigas* there and their relationship with environmental parameters are interesting in light of attempts to introduce *C. gigas* to tropical waters. The work of Mok (1973, 1974a) pointed to periods of rapid shell growth alternating with

Table 6. Salinity and temperature ranges of several tropical and subtropical oyster species.

Species	Salinity (ppt)	Temp (°C)	Reference
S. cucullata			
Sri Lanka	9 – 27	26 – 32	Pinto and Wignarajah 1980
Madagascar	30 – 35	24 – 32	Rabesandratana 1971
Indonesia	30 – 34	28 – 30	Fatuchri 1976
C. rhizophorae			
Cuba	22 – 40	18 – 34	Farfante 1954
Venezuela	37 – 39	27 – 30	Angell 1973
Puerto Rico	11 – 35	24 – 27	Watters and Prinslow 1975
Colombia	15 – 30	27 – 33	Wedler 1970
St. Croix	34 – 37	25 – 32	Forbes 1973
C. virginica			
Mexico	3 – 12	20 – 30	De Buen 1957
Hawaii	22 – 32	21 – 27	Sakuda 1966a
S. lugubris			
Thailand	1 – 30	27 – 31	Bromananda 1978
Philippines	26 – 36	24 – 41	Lopez and Gomez 1982
S. echinata			
Indonesia	16 – 30	27 – 31	Angell 1984
Guam	30 – 35	29	Braley 1984
Philippines	26 – 36	24 – 41	Lopez and Gomez 1982
C. gasar			
Nigeria	20 – 30	25 – 30	Ajana 1980
C. parabainensis			
Brazil	3 – 23	24 – 30	Singaraja 1980b
C. gryphoides			
India	3 – 40	19 – 33	Durve 1965
C. madrasensis			
India	0 – 41	26 – 31	Virabhadra and Nayar 1956
C. gigas			
Hong Kong	2 – 32	11 – 31	Mok 1973
Israel	41	12 – 34	Hughes-Games 1977
Fiji	26 – 36	24 – 31	Ritchie 1977
Hawaii	31 – 36	22 – 28	Brick 1970
C. belcheri			
Malaysia	22 – 28	27 – 31	Chin and Lim 1975

maturation and spawning, the latter being stimulated by increasing temperature. Maximum shell growth occurred during the months of highest salinity (20-28 ppt) and lowest temperature (15-16°C) at the end of February. During this period the percentage of developing gonads was very low, but as water temperature began increasing at the end of February, gonad activity increased and peaked during April and May. The first spawning occurred in May when water temperature had reached about 24°C. Spawning in Deep Bay peaked between June and August when salinity varied from 2 to 13 ppt and temperature ranged from 26 to 31°C. There was little or no shell growth during this period.

The effect of salinity on growth may also reflect changes in the nutritional quality or abundance of food organisms or materials. There appear to be few attempts to link food availability, much less quality to oyster growth in the tropics. Ruiz et al. (1969) compared the carbohydrate content of oysters from two different Venezuelan lagoons, Laguna Grande and Bahia de Mochima. The higher turbidity of Laguna Grande appeared to indicate more fertile water to which the authors attributed the greater carbohydrate content of oysters there.

In the Caribbean, *C. rhizophorae* shows similar growth rate depression as a result of freshwater intrusion (Forbes 1973). In Salt River Inlet, St. Croix, the growth rate of this species was low or zero during months of low salinity. The overall salinity range is about 33.9 to 37.3 ppt. In contrast to *C. gigas* in Hong Kong, spawning occurs throughout the year (Forbes 1973). Low salinity predominates between July and November in Cuba, ranging from 13 to 16 ppt, increasing thereafter until March, the high range being between 33 and 35 ppt. The growth rate of *C. rhizophorae* is also highest during the period of increasing salinity (Farfante 1954), which is concurrent with a fall in temperature from 30 to 25°C.

C. madrasensis exhibited higher growth in the Adyar estuary whenever exchange with the Bay of Bengal increased, as indicated by higher salinity within the estuary (Rao and Nayar 1956). On the other hand, *C. gryphoides* grew best in moderate salinity. Shell growth was retarded during periods of high salinity and was totally absent when low salinity water prevailed (Durve and Bal 1962).

The condition index of *C. virginica* in Pearl Harbor tends to follow the pattern of salinity change, increasing with increasing salinity and vice versa. Silt associated with low salinity is heavy enough to influence growth (Sakuda 1966a).

An exception to the direct correlation of growth and salinity is the growth of *C. paraibanensis* reported by Singaraja (1980a). This large oyster can reach a shell height of 16 cm in 14 months and its growth rate does not seem to be affected by prolonged exposure to low salinity and accompanying silt.

Studies such as the above suggest that adequate nutrition for growth and maturation of tropical oysters requires food sources which are more abundant in higher salinity water. This water may intrude into estuaries and lagoons from the adjacent sea or a larger embayment. High runoff would dilute intruding seawater, alter temperature, salinity and light penetration affecting the growth of phytoplankton, as well as the species composition of the phytoplankton community. In the case of lagoons, detritus, which may be an important constituent of the oyster's diet (Odum and Heald 1975), could also be flushed out to sea. The influence of heavy silt loads has already been mentioned.

Temperature changes appear to have much less influence on growth and gonad maturation within the tropical zone, and even occasionally outside it (Farfante 1954). However, controlled laboratory experiments will be required to determine the combined effects of nutrition, temperature and salinity.

Maturation and Spawning Cycles

Changes in the condition index (usually the ratio between meat weight, either dry or wet, and internal shell volume) can be used to predict the onset of spawning by oyster populations. The condition index is relatively easy to measure and also has commercial application since oysters are more marketable when their condition index is high. Other measures, such as carbohydrate or glycogen content of soft parts, are more direct indicators of gonad state, but their measurement requires more sophisticated laboratory equipment.

As gonad maturation proceeds, the glycogen content of the soft parts, excluding the adductor muscle, declines and reaches a minimum during the spawning season (Imai 1971). The condition index is usually measured as the ratio of meat weight to internal shell volume. Both wet and dry meat weight are used; the latter reduces the within-sample variation. The condition index increases during maturation as the mass of the gonad increases, declining sharply after spawning. Percentage edibility as used by Durve (1964) closely followed the spawning cycle of *C. gryphoides.* To measure percentage edibility (expressed as the ratio of meat weight to total weight), meats were extracted and preserved in 5% seawater formalin for eight days to allow their weights to stabilize.

Seasonal variations in carbohydrate, fats, lipids and ash content of populations of *C. rhizophorae* were followed by scientists at the Universidad del Oriente, Cumana, Venezuela (Ruiz et al. 1969; Ruiz 1975). Although spawning of *C. rhizophorae* occurs throughout the year, seasonal cycles were evident in some of the constituents. Percentages by weight of the above constituents are influenced by nutrition and reproduction and the relationship between them is complicated by the continuous spawning of this species. Studies by Ruiz et al. (1969) and Ruiz (1975) showed both long- and short-term cycles. The long-term cycles, observed over three years, may reflect changes in the seasonal upwelling that occurs along northeastern Venezuela. Short-term cycles were influenced by spawning and persisted for 6-7 months. The cycles of carbohydrate and ash content as percentage dry weight were clear and inversely correlated. Short-term cyclical changes in protein and fat were much less apparent, particularly their correlation with carbohydrate cycles (Ruiz 1969). Peak spawning on Margarita Island occurred from December through February (Angell 1973). During this same period, fat and protein content fell while carbohydrate and ash as percentage of dry weight did not follow any consistent pattern (Ruiz 1975). Under the conditions that are found in northeastern Venezuela and in view of continuous spawning, it may be that histological sections are required to get an accurate picture of spawning activity.

C. madrasensis on the southwestern coast of India clearly shows the shift to lipids in the ovary during maturation, with a corresponding decline in carbohydrate (Stephen 1980).

Sakuda (1966a, 1966b) investigated both spawning and condition indexes of *C. virginica* and their seasonal variations in West Loch, Pearl Harbor, Hawaii. As indicated by partially spawned gonads, spawning was most intense between April and September. Correspondingly, the condition index declined during this period, reaching a minimum in July, and began to increase again as the percentage of immature (recovering) gonads increased.

Working with *C. gryphoides* near Bombay, Durve (1964) observed similar seasonal cycles in the percentage edibility and condition index. Minima in both parameters corresponded with the peak spawning period, between July and September.

Direct observation of gonadal maturity states requires the preparation of histological sections, usually stained with hematoxylin and eosin. The method is laborious, which restricts the sample size to 25 or 30 specimens. However, through careful subsampling, one should get a realistic picture of trends in the population under study. Sections are classified on the basis of categories established by the presence of oogonia or spermatogonia, amount of mature oocytes present, follicle wall thickness and fullness, and indications of phagocytosis of unspent gametes. Periods of sex change and hermaphroditism are easily detected as well. Maturation has been documented in several populations of tropical oysters using these methods. *C. rhizophorae* of Margarita Is., Venezuela, exhibited peaks of spawning activity in January, April, August and December (Angell 1973). In the Philippines, *S. echinata* reached peak activity during the first and last quarters of the year, with a smaller peak about mid-year (Lopez and Gomez 1982). In the same study, intensity of spawning activity in *S. lugubris* varied between the two years of the study. Peaks were more pronounced during the second year, occurring within two months of each other. Maturation and spawning of *C. gryphoides* near Bombay appear to be influenced by salinity so that only one spawning period occurs during the summer monsoon. Maturation proceeds during the winter. Durve (1965) found histological evidence of partial spawnings, but spawning had been completed by the end of the monsoon. *Crassostrea* species in Deep Bay, Hong Kong, spawn only during the warm months from May through October (Mok 1973). Cyclical spawning was indicated by peaks at approximately monthly intervals and evidence was also found of partial spawning.

Hermaphroditism and Sex Change

A number of studies have shown the presence of hermaphroditic specimens of tropical *Crassostrea* species. Seasonally changing sex ratios have been observed which indicate sex changes were occurring. In the case of *C. rhizophorae*, females predominate, sometimes reaching almost 90% of the population (Angell 1973). Hermaphroditic gonads are found in small numbers, from 0.3 to 1.6%, depending on the species. Seasonality in their occurrence was observed in Venezuelan mangrove oysters, where they occurred during months of below average temperature. In Cuba, females of *C. rhizophorae* tended to be larger than males (Farfante 1954). Seasonal differences were observed, but there was no indication these were significant. However, the size difference may be indicative of protandrous hermaphroditism. Among Pakistan oysters including *C. ariakensis, C. madrasensis, S. glomerata* and *S. cucullata*, males predominate slightly in smaller size classes, but the sex ratio favors females in larger oysters (Asif 1979). A similar phenomenon occurs among *C. gryphoides* in India, where sex change in favor of females occurs principally during the monsoon season (Durve 1965). Histological evidence substantiates this because gonads can be seen with varying proportions of oocytes and spermatocytes, indicating the transition from one sex to the other (Angell 1973).

Larval Distribution and Abundance

Regular sampling of oyster larvae has proven useful to oyster growers in the northern hemisphere to indicate when their cultch should be put out to collect spat. Timing is critical since cultch placed out too long before setting-size larvae appear will become fouled with resultant loss in set. If too late, the major period of spatfall may be missed. Some cultching areas, particularly in the Pacific Northwest of the USA, have irregular setting and in some years a low larval count will be read as a signal not to deploy cultch or reduce the quantity rafted. The Washington State Fisheries Department has been issuing regular reports on larval abundance during the spawning seasons in Dabob and Willapa Bays for many years (Westley 1968).

Detailed studies of this type over a sufficiently long period of time have not yet been done in tropical areas, but there are reports on larval abundance, seasonality and relation to setting intensity. Frequently setting is too intense, which results in stunting or slow growth. Sampling which attempts to relate larval abundance to oversetting would be valuable to growers in some areas, but requires quantitative techniques.

It is better to count pediveliger larvae, particularly those which have developed eyespots because the early veliger larvae of many bivalve species are very difficult to identify positively. Sampling of larvae has usually been done by surface tows, although a series of vertical samples would be more representative. In the San Blas area of Mexico, Cortez-Guzman and Martinez-Guerrero (1979) found that pediveliger larvae of *C. colombiensis* peaked during October and November and in January and were absent from April to June, August and September. Barnacle larvae were also sampled, due to competition with oyster larvae for cultch space. They found the abundance of barnacle larvae alternated with cycles of abundance of oyster larvae, but barnacle larvae were totally lacking during periods of very low salinity (0-5 ppt). The data were used to determine the best cultching sites. On the basis of larval abundance and growth rates, the authors advised that two or three harvests per year would be possible.

In Lagos Harbor, salinity is the dominant influence on the distribution and abundance of oyster larvae (Sandison 1966). As the optimum salinity for *C. gasar* larvae was around 30 ppt, they were restricted to areas in the harbor that had waters near that value.

Larvae of *C. rhizophorae* are present in Larestinga Lagoon, Venezuela, throughout the year, but peak during January and February. In that location, there did not seem to be a significant correlation between larval abundance and setting intensity (Angell 1973). This might be due to the location chosen for placing cultch during the above study, since extreme variations were found in setting density between different locations. Small-scale circulation phenomena such as tidal eddies strongly influence the distribution of larvae, resulting in irregular setting patterns within a lagoon or bay. Counts were of total numbers of oyster larvae, rather than pediveligers only, which could have affected the statistical correlation between larval counts and setting intensity.

Lambert and Polk (1971) counted barnacle and *Polydora* larvae as well as oyster larvae. They found the larvae of these oyster pests to be present year-round, but with cyclical variations in abundance. This aspect of plankton sampling might be more widely used, particularly with regard to barnacle larvae, since during heavy barnacle sets cultch can be rendered useless.

Setting

Perhaps more than any other aspect of oyster biology, setting behavior is of primary importance to the tropical oyster culturist. An understanding of its cycles enables the farmer to obtain commercially adequate sets, or in some cases avoid excessive setting with its consequent stunting or high mortality. Most biological studies of the potential of oyster culture in the tropical environment have dealt with some aspect of setting or "spatfall". In areas with temperature or salinity extremes, such as Hong Kong or the monsoonal coasts of India, setting may be highly cyclical, alternating with periods of very low or zero spatfall. In other regions, such as the Caribbean, spatfall is continuous, although peaks are usually present. Often the problem in such situations is oversetting and how to avoid it.

Cultch materials and their deployment are discussed in more detail in the section on culture techniques, but a few comments on materials might be in order here. As one might expect, oyster shell is used whenever available. Otherwise, a variety of substrates have been tried, including mahogany, glass, tiles, mangrove roots, plastic film, asbestos-cement (Eternit) and other cement composites, scallop shell, bamboo, rocks and concrete pipe. The two overriding requirements are spat attraction and economy.

Horizontally suspended collectors usually collect more spat on their lower surfaces because of siltation of the upper surface. Setting density also varies with depth. *C. rhizophorae* consistently sets most densely near the surface in eastern Venezuela's hypersaline lagoons (Angell 1973). Spat density declines sharply at 1 m and increases somewhat at 2-m depth. In Lagos Lagoon, setting of *C. gryphoides* is most intense at 75- to 100-cm depth (Ajana 1979). Vertical distribution there could be affected by low salinity surface runoff.

Setting may be very localized due to the effects of eddies or other aberrations in tidal currents. A distance of a few tens of meters can result in dramatic differences in spat density. The attraction of larvae to areas where adults or spat are established has been long been noted by commercial growers. The influence of pheromones in gregarious setting has been demonstrated by Hidu et al. (1978) to explain this phenomenon.

Data are limited as to what constitutes a "commercial" set, that is, one that will result in optimum growth and survival. As might be expected, results vary widely. In Hong Kong, the first spatfall occurs in June with about 128 spat/shell (Mok 1973). Counts in this study were made on the inside of the shell only due to the small size of spat and the difficulty of finding them on the rough outer shell surface. The surface area of the shells was not given. At that time of year, temperature and salinity are about 30.7°C and 10 ppt, respectively. Spatfall occurs every month until October. Farfante (1954) observed setting of *C. rhizophorae* throughout the year in Cuba. Tiles used in the study were 625 cm^2 and averaged 14.5 spat per month ($232/m^2$). In Cienaga Grande, Colombia, setting was tied to the end of the rainy season and ranged from 3,000 to 10,000 $spat/m^2$, depending upon the material used (Wedler 1980). Bonnet et al. (1975) found the equivalent of 8,000 $spat/m^2$ in Guyana using cement-coated egg cartons. A density of greater than nine per oyster shell is considered adequate for commercial purposes in the Philippines (Blanco et al. 1951).

Chin and Lim (1975) were able to define parameters for a suitable setting density for *C. belcheri* in Sabah, Malaysia. Fifty to eighty spat per 64 cm^2 of oyster shell produced the best growth and survival ($7{,}800\text{-}12{,}500/m^2$). Peak spatfalls had to be avoided to prevent excessive setting. These spat densities were correlated with larval counts in the plankton of 6,000-60,000 per 1,000 m^3 of water.

If predation is limited and spat are left unthinned, one may observe the type of curve shown in Fig. 3. This pattern has been observed with *C. rhizophorae* in the Caribbean and *S. echinata* in eastern Indonesia (Angell and Tetelepta 1982). The descending leg of the curve follows a typical mortality relationship of the type

$$N_t = N_o e^{-rt}$$

where N_t is the number of oysters at time t, N_o the number at the peak density and r is the mortality rate. Thus, under certain conditions spat may exhibit density-dependent mortality (Angell 1974). It may be that the density of spat on the lower leg of the curve represents the optimum density for maximum growth and survival, although this hypothesis has yet to be tested.

Growth

The elevated water temperatures of the tropics can produce high oyster growth rates if adequate food is available. An outstanding example is *C. paraibanensis* which may reach a shell height of 15 cm in one year (Singaraja 1980a). In some of the lagoons of northeastern Venezuela, naturally occurring mangrove oysters are stunted from excessive setting and exposure, but if cultured, they may reach the market size of 6 cm in less than six months (Angell 1974).

Growth curves for *C. rhizophorae* from several Caribbean locations are shown in Fig. 4. For about the first six months, rates are similar for the locations shown, all of which were lagoons or shallow bays. The year-round setting of *C. rhizophorae*, fast growth and small market size enable farmers to obtain several crops a year in the Caribbean region.

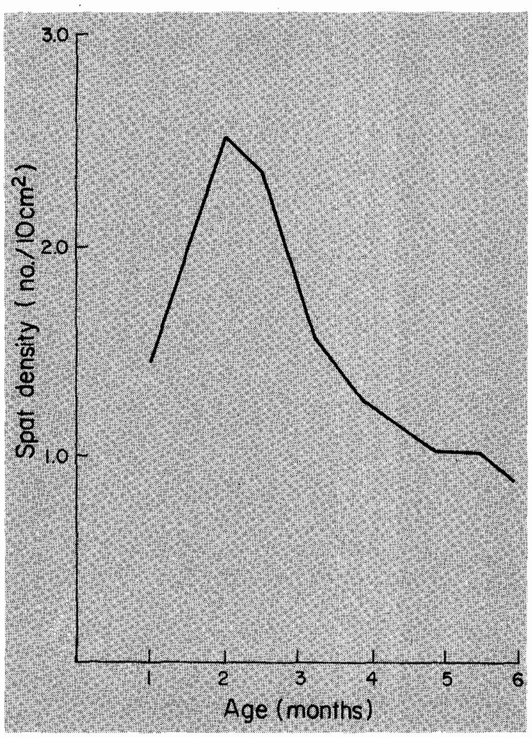


Fig. 3. Survival of spat of *C. rhizophorae* in St. Croix, S.S. Virgin Islands (Angell and Tetelepta 1982).

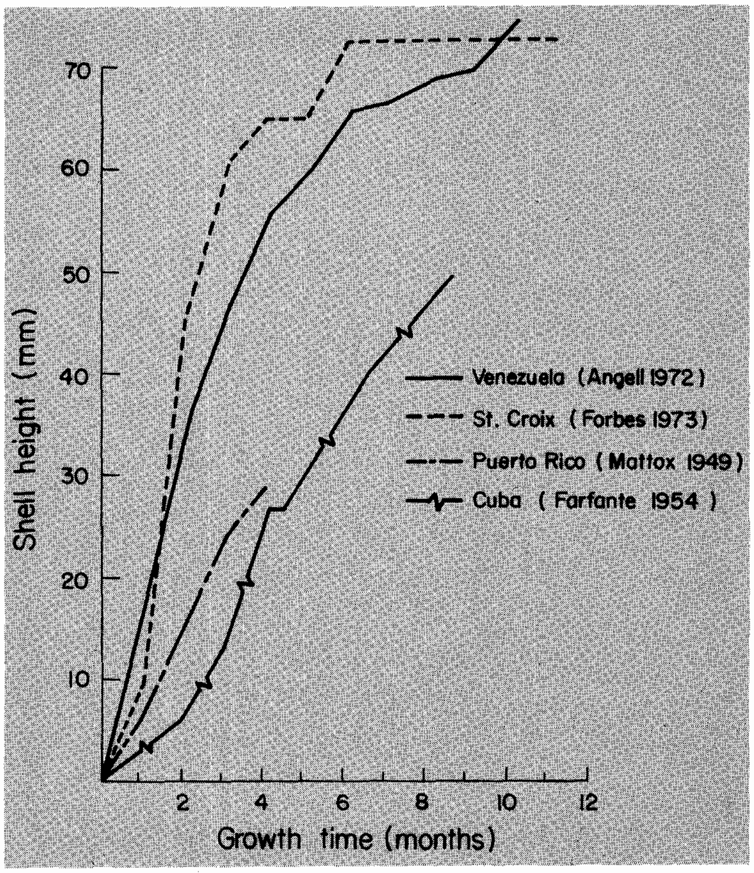


Fig. 4. Some representative growth curves for *C. rhizophorae* from the Caribbean.

Wide differences in growth rates between species and locations occur as would be expected due to the influences on growth of water conditions, culture systems and the inherent growth potential of a species (Fig. 5). However, data given by Silas et al. (1982) indicate that *C. madrasensis* may do better in locations other than that represented in Fig. 5, as it was found to reach an average shell height of over 86 mm in one year. *S. lugubris* is commercially cultured in Thailand and has a growth rate similar to that of experimentally reared *C. belcheri* in Sabah, Malaysia (Fig. 6).

The typical growth pattern for tropical oysters reflected in these figures is one of a very rapid increase in shell height for the first six to twelve months. Practically, this means a very rapid turnover for the tropical osyter farmer, provided adequate sources of spat are available.

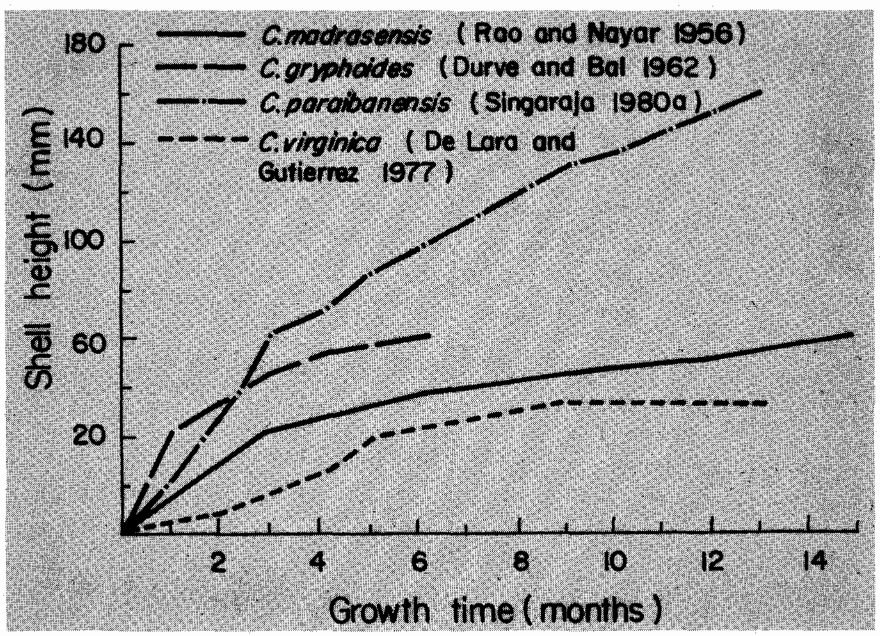


Fig. 5. Growth curves for several experimentally cultured tropical oysters.

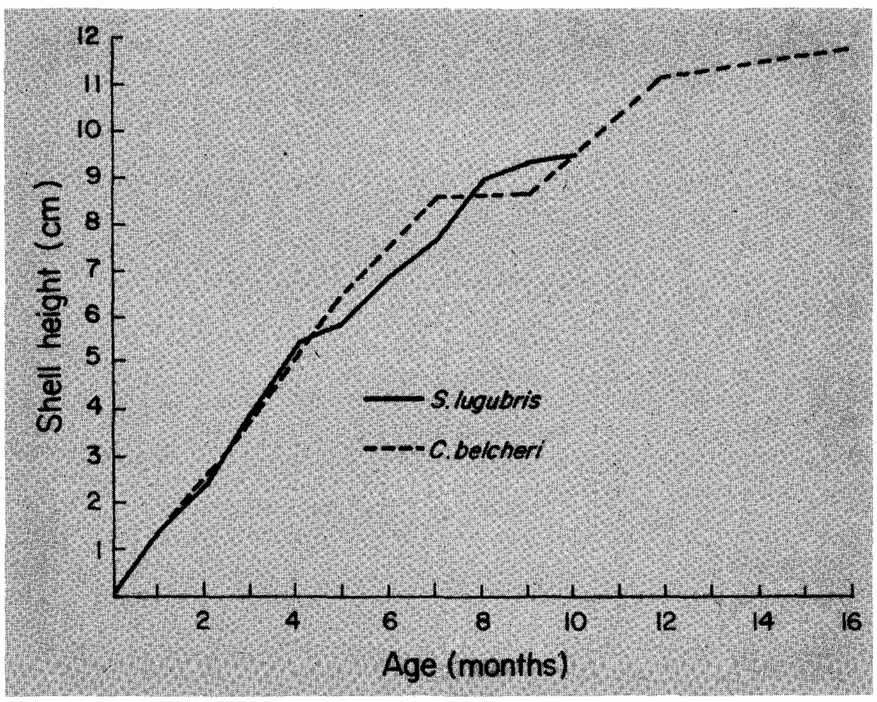


Fig. 6. Growth curves for *Saccostrea lugubris* (Bromanonda 1978) in southern Thailand and *Crassostrea belcheri* (Chin and Lim 1975) in Sabah, Malaysia. The curve for *C. belcheri* uses data taken from a scaled photograph.

The growth performance of the Pacific oyster, *C. gigas*, is interesting because it is one of the few species that have been introduced to tropical areas as an exotic. Although these attempts have failed (Glude 1984), the Pacific oyster may yet play a role in tropical oyster development in view of the possibility of hybridization. It is cultured in Hong Kong, where it is native, but the southern extension of its range on the coast of China is not clear. Some representative growth curves for *C. gigas* are illustrated in Fig. 7. The data are from introductions to sites ranging from Venezuela to Mauritius. However, it should be pointed out that most of these introductions have experienced high mortality (see sections on culture techniques and exotic species). The effect of a total die-off of larger oysters after 13 months of growth is reflected in the curve from Mauritius (Fig. 7). In some cases, condition may also be poor in spite of good shell growth (Brusca and Ardill 1974).

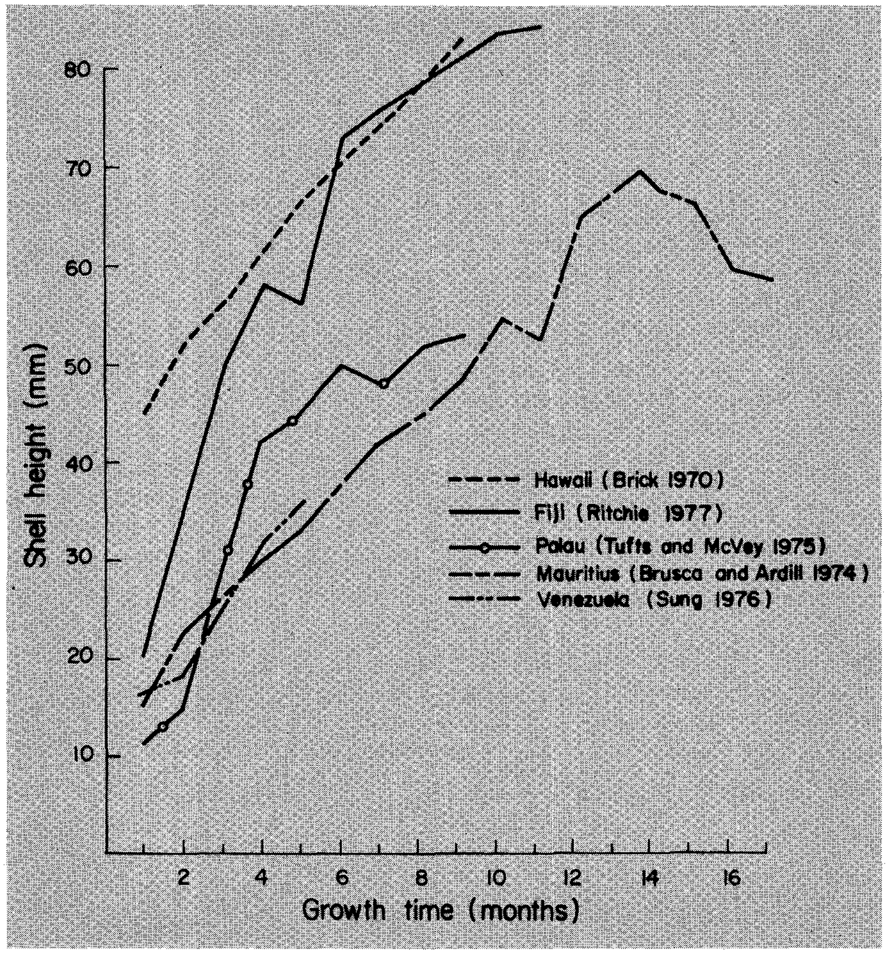


Fig. 7. Growth curves for *C. gigas* transplanted to tropical sites.

CULTURE SYSTEMS

Although experimental oyster culture has been attempted in many tropical countries, commercial farming is limited to a few. Notable examples can be found in the Philippines and Thailand. Oyster farmers are confronted with many of the problems facing other small agricultural producers. Among their difficulties are poor market development, expensive transport or inadequate infrastructure, lack of technical assistance and in some cases poorly defined ownership of the intertidal zone.

Oyster farming involves four basic operations: cultching, nursery, grow out and harvest. Processing and marketing are also often done by the farmer and his family. Cultch is the material upon which the oyster larvae attach or "set". "Collector" is a more frequently used term, particularly in Latin America. Individual pieces of cultch may conveniently be referred to as collectors. Oysters set on a variety of substrates and the farmer's choice is dictated by the suitability of available materials and cost, as well as by the type of culture system in use.

If spat are maintained for a time on cultch material and then transferred to a grow-out system, that period can be termed the nursery phase. Spat are often reared to market size on their original cultch so that there is no distinct nursery phase.

The methods used to produce marketable oysters (grow-out system) include bottom culture, racks, rafts, trays and stakes. The system is determined not only by the animal's biology, but also by environmental factors and material costs.

The harvest method naturally depends upon the culture system and is usually labor intensive. Multiple cropping is often possible.

Bottom Culture

Bottom culture is limited to areas where the sea floor is firm enough to support some kind of cultch and where siltation is not excessive. It is a very old method, having existed in Hong Kong's Deep Bay for at least 150 years (Bromhall 1958). Cultch may be angular rocks, concrete pipe, cement slabs or bars. If the bottom is firm enough, old oyster shell may be used. Cultch is placed directly on the bottom, or if slabs are used, planted in it. Morton (1975) described oyster farming in Deep Bay based on *C. gigas* and *C. ariakensis*. The tiles are initially planted in the upper intertidal zone for spat collection. At the end of the spatting season, the tiles are transferred to beds deeper in the intertidal zone. Spat are grown to market size directly on these collectors. During the grow-out period, tiles must be periodically replanted to prevent the oysters from being smothered by silt. Oysters are harvested between four and six years of age, depending on demand. Most are sold as shucked meats. The oyster grounds of Deep Bay are divided into several family plots, which are either farmed by the owner or rented to tenant farmers. The area of Deep Bay under actual culture has not been documented and yields are not available. However, total production figures indicate that they have been dropping, and this has been attributed to pollution and siltation (Mok 1974b; Morton 1975).

Bromanonda (1978) provided data on the productivity of Thai oyster farms which raise *S. lugubris*. Farmers collect spat on concrete pipes, later transferring the juveniles to grow-out pipes, cementing them in place. This procedure prevents crowding and results in better meat condition. The average production is 45 oysters per pipe, or 75,000 per 0.16 ha (one *rai*). A market-size oyster is 7 cm and a few can be harvested between four and five months of age. At eight months, 99% are harvestable.

Most oyster culture in Mexico uses some form of bottom culture (Lizarraga 1974). Spat of *C. virginica* are collected in the extensive lagoons of the Gulf of Mexico coast using suspended cultch. A variety of materials are used among which are strung oyster shells, limed tiles and limed egg cartons. The cultch is placed on racks in the collecting areas. Cultching is timed with the appearance of pediveliger larvae in spring and late summer to early autumn. Spat are kept on the collectors for two or three months, by which time they measure 2-3 cm and must be planted on the beds. The spat-bearing cultch is transferred to the growing areas and scattered. The bottom sediments on the beds consist of fossil shell deposits or shell scattered on the bottom near shucking operations. Oysters reach 8-10 cm after a growing period of 9-14 months. Oyster culture is the main fishery of these lagoons.

Bottom culture of *C. corteziensis* is practiced on the Pacific coast of Mexico in the states of Sonora, Sinaloa and Nayarit (Lizarraga 1974). The spat collecting system follows the French method (Bardach et al. 1972) using limed tiles, but occasionally shell strings are used. Tiles are placed directly on the bottom, while shell strings are suspended on racks. The spat are kept on the cultch for two or three months until attaining a shell height of 2-4 cm, after which they are separated and planted on hard bottom. Spat density ranges from 2,000 to 10,000 per tile. The shell cultch, containing 50 shells per string, will collect 400 to 1,500 spats per string. The seasonal setting pattern is similar to that of *C. virginica* on the Gulf coast. *C. corteziensis* requires 9-12 months to reach the market size of 8-11 cm.

There is some bottom culture in the Philippines (Young and Serna 1982). Cultch may be old oyster shell, stones or rocks, boulders, logs, and even tin cans. When an adequate set has been collected, the cultch is transplanted to the subtidal growing areas and harvested 8-12 months later by divers. Although little investment is required, the method is not very productive due to high mortality and the difficulty of harvesting.

The culture of *C. brasiliana* shows promise in the Sao Paolo region of Brasil. Akaboshi and Bastos (1977) developed spat collection techniques to provide a basis for the development of commercial culture and to supply seed for the restocking of overfished natural beds. Scallop shells were strung on wire, 100 per string, and placed directly on the bottom in 3-7 m depth. Barnacles were a major pest and it was found that their set was much reduced directly over the sea floor. Oyster larvae were sampled and test cultch examined to determine when cultching should be done. Counts of more than 45 spat/100 cm^2 and the presence of larvae greater than 280 microns with eyespots in the plankton were established as criteria for cultching. Spatted cultch was transplanted to the intertidal zone after 15 days for "hardening". The daily exposure insured that only the hardiest spat survived. The spat were grown to market size either in trays placed on the bottom in 1-2 m of water or suspended from longlines.

Stake Culture

Stake culture is common in the Philippines and was described by Blanco (1956). At the time of his report, 65 ha were being farmed in the Dagat-Dagatan lagoon. Several species were cultured, including *S. cucullata*, *C. iredalei* and *S. malabonensis*. Several modifications were in use, based on the type of cultch. The bamboo stakes were 60 cm long, driven into the soft bottom of the intertidal zone. Two of the modifications used oyster shell strung on galvanized wire and then hung on the tip of the stake, differing only in the manner in which the cultch was tied to the stake. In the third modification, the stake was split and several tin cans with their ends removed were slid down onto the stake. However, the tin cans rusted quickly and were not very attractive to larvae. It required 9-12 months to produce a market-size oyster, depending on species and setting time. An oyster bed of 5,000 m^2 contained 31,500 stakes and could produce about 8,600 liters of shucked meats. The lagoon has since been converted to low-cost housing.

The lattice method is intermediate between stake and rack culture (Fig. 8). The lattices are constructed of bamboo poles 5-9 cm in diameter in the form of an inverted "V" and tied together with galvanized wire (Ablan 1955). The useful life of the bamboo is 1-2 years. Lattice rows are placed 5 m apart and in depths of less than 1 m at low tide, and can also be suspended from floats in deeper water. *S. malabonensis*, *C. iredalei* and *S. palmipes* are cultured by this method.

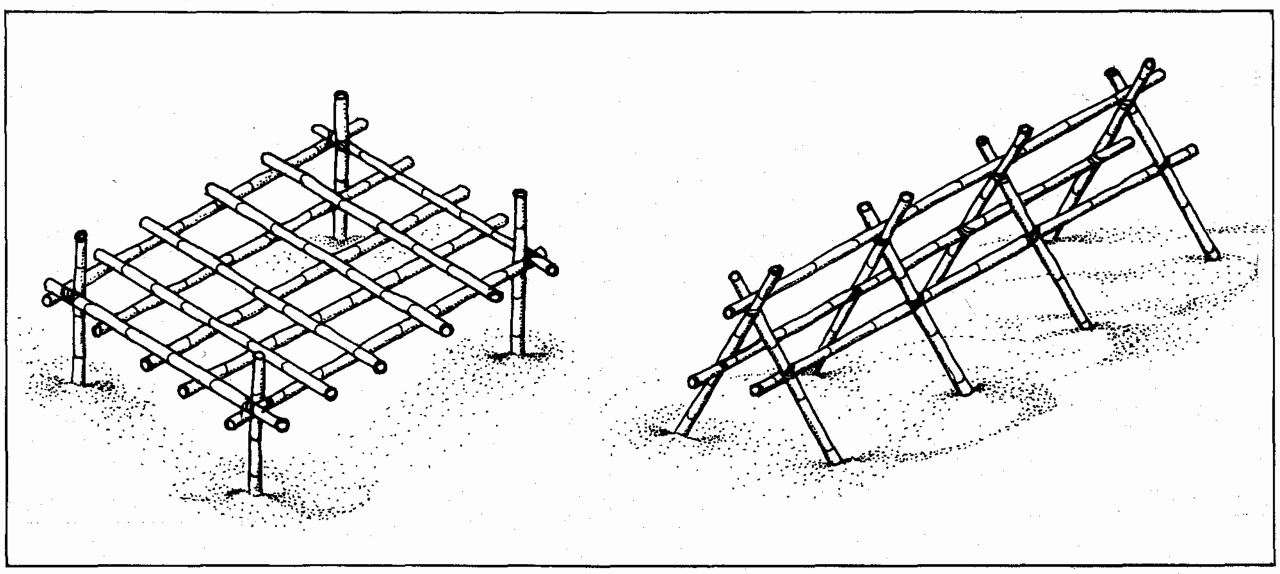


Fig. 8. Two methods of setting up intertidal lattice culture as used in the Philippines (after Ablan 1955).

Intertidal Rack Culture

The principle advantages of the rack method are the reduced fouling and predation obtained by placing the cultch off the bottom, intensifying production by using more vertical space and low cost relative to raft culture.

A commercially viable system of intertidal rack culture has been developed in Cuba (Nikolic et al. 1976). Collectors made from the tips of branches of mangroves are suspended from horizontal supports termed "stockades" (Fig. 9). The stockades may be planted below low water, but the height of the collectors is adjusted seasonally so that they are in the lower 35-40 cm of the intertidal zone. The collectors are spaced 35-40 cm apart and last about nine months. Nikolic et al. (1976) advised a farm size of 7,500 collectors, of which 3,750 would be under harvest. Annual production from such a farm was estimated at 26.2 t of oysters in shell. Harvesting begins five or six months after the first set and continues for two or three more months. One collector can produce 5.2 kg or about 374 marketable oysters, representing 80% of the total set. Undersized oysters can be transferred to intertidal trays. Alternatively, oysters can be selectively harvested from the collectors as they reach market size. Lepoureau (1978) recommended three harvests for each of the two major spatfalls, most being taken from the autumn set and the remainder from the spring set.

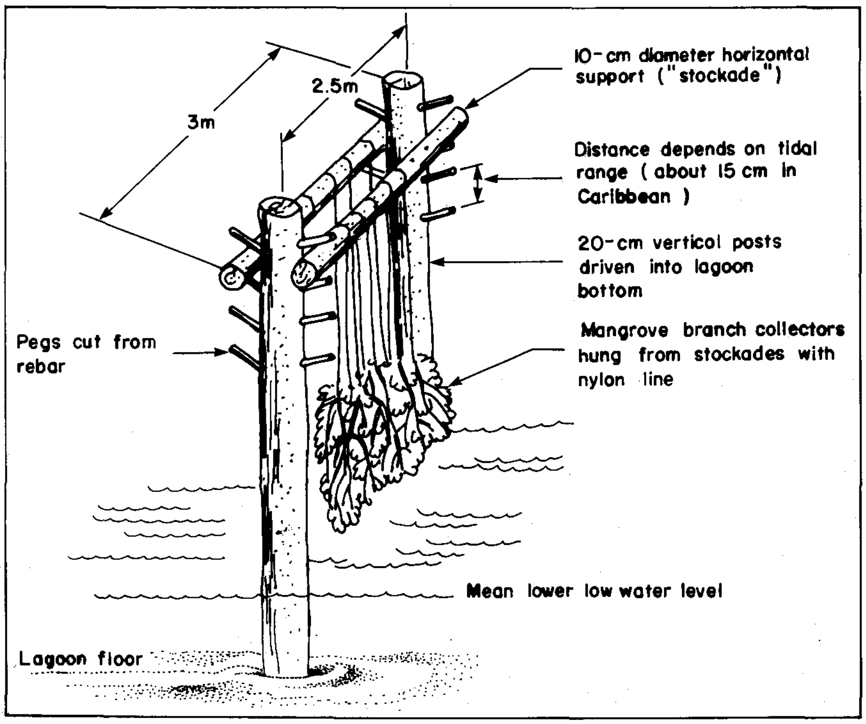


Fig. 9. Intertidal rack culture developed by Nikolic et al. (1976).

The system appears to be a good one, requiring very little capital investment. Since the collectors are taken from the growing tips of mangrove branches, no damage would be done to the trees. It is well suited to many Caribbean islands where the tidal range is very limited and mangroves completely occupy the shoreline.

A similar method is used in the Philippines, except that oyster or coconut shell is used for the cultch (Young and Serna 1982). The cultch is strung on synthetic rope, separated by knots or bamboo spacers. The strings are hung 25 cm apart. In a variation of the technique, cultch-bearing strings 20 m long are suspended in four parallel rows. Old tires may also be hung from horizontal poles or ropes.

Bryson (1977) reported on his experimental culture of *S. mordax* and *S. echinata* using intertidal rack culture. Asbestos-cement tiles fabricated from broken-up roofing were used as cultch and suspended from intertidal "fences". The system was designed to take advantage of tropical waters and offshore islands along the Queensland coast. Spat are left on closely spaced cultch for three or four months, after which the distance between collectors is increased to about 10 cm. The oysters are removed and transferred to permanently submerged trays after 18 months on the cultch. Another three months in the trays is required to produce market-size oysters. If spatfall is light, the cultch can be suspended from longlines. The submerged phase of culture improves meat condition and adds shell growth. In the case of *S. echinata*, the thick mantle or "black lip" disappears. One of the problems experienced was excessive setting which could be overcome to some degree by shifting the collectors to other locations.

Silas et al. (1982) tried intertidal culture of *C. madrasensis* combining mortar-coated tiles for spat and trays for grow-out. Spat density depended on season and location, varying from 2 to 35 per tile. The spat were removed from the cultch after about two months of growth and placed in rearing cages suspended from poles in the intertidal zone for intermediate rearing to about five cm. In the final rearing stage the oysters were transferred to trays measuring 90 x 60 x 15 cm at a density of 150-200 oysters per tray. After a total growing time of one year, they had reached a height of between 9 and 11 cm. One tray produced about 24 kg of product.

A similar system was developed by Chin and Lim (1975) to culture *C. belcheri* in Sabah. Asbestos-cement strips were used as cultch, followed by transfer to trays. The total rearing period was 18 months, when the oysters reached about 14 cm with a meat weight of 14-21 g. Larval counts were used to indicate when cultching should start. Cultching was carefully timed to avoid barnacle sets, which were associated with reduced turbidity and current velocity. The condition index of oysters ranged from 50 to 150, falling between 115 and 135 when water conditions were favorable. Annual production of oyster meat was estimated at 18 t/ha.

Banten Bay on the west coast of Java has potential for developing oyster and mussel culture. Fatuchri (1976a, 1976b) investigated spatfall and growth of *S. cucullata* using intertidal methods. Cultch was fabricated from cement-coated coconut shell and suspended from racks on strings of 10-15 collectors. One month after cultching, spat were transferred to plastic trays on racks. The oysters were later thinned and placed in larger wire baskets. A size range of 40 to over 60 mm shell height was attained after one year, with an average of 50 mm. Boring organisms proved to be pests in the basket phase and caused high mortality. The author considered the growth rate slow and recommended trying other species. However, marketability depends on a combination of consumer preference, processing technology and the costs of operating a particular system. The introduction of a fast growing species such as *C. belcheri* might prove justified in this situation.

Raft Culture and Longline Culture

The success of the Japanese in developing raft culture stimulated interest in many countries because of the fast growth rates and high productivity obtained in Japan. However, there has been little development of the technique outside of that country. In the tropics, high costs and heavy fouling have hindered the spread of raft culture beyond a few experimental installations.

Cultch may be a problem when there is no existing oyster fishery or culture industry. Cement-coated plywood has been used in Puerto Rico (Watters and Martinez 1976) and mortar-coated asbestos-cement in Venezuela (Angell 1974). These coatings are attractive to larvae, facilitate harvesting and reduce shell breakage. In both these locations, cultch was hung from grow-out rafts and spat reared to market size without further handling. Several treatments to control fouling have been tested in northeastern Venezuela (Angell, unpublished data). The most effective were brine and quicklime dips, although brine did not kill barnacles. The lime dip could also be used to reduce spat density since it killed spat less than about two weeks old. Air drying is a simple method, but is ineffective against barnacles. The quicklime treatment was employed about once every 4-6 weeks and proved to be cost effective.

Rafts should be as simple as possible. The greatest cost is usually the floats. While styrofoam is effective, it must often be protected from borers by some type of covering. In some areas, steel drums may be cheap enough to use, although they must be adequately painted with antifouling compound and rust preventive. Technically viable alternatives include fiberglass and ferrocement.

Ferrocement buoys have been used for experimental mussel culture in the Philippines and are easily constructed from materials readily available (Telosa 1979).

C. tulipa has been farmed using the raft method in Sierra Leone (Kamara 1982b). Raft frames are made of bamboo and oil drums liberally painted with asphalt serve as floats. The rafts are anchored in depths of 6-10 m at low tide. Oyster shell is readily available from the oyster fishery and can be used as cultch. Each cultch string holds 160 shells, which are later separated at about 2-cm intervals on the growing ropes. One cultch string yields nine growing ropes. Spat density is often over 100 per shell and setting is year round. Growth averages 1 cm and 1 g per month, enabling harvesting after seven months of grow-out. Rafts produced 90-230 g of meats per string, depending on location (Kamara 1982a). Those located more seaward in higher salinity had higher production. Bacterial testing was used to insure product safety and, in fact, consumers preferred raft cultured to wild oysters and were willing to pay a higher price for them.

Raft culture has shown possibilities in Puerto Rico, where Watters and Martinez (1976) developed a production system for *C. rhizophorae*. Their raft used two styrofoam floats and a timber frame 3 x 4.3 m. The cultch was fabricated from plywood panels 41 x 61 cm, coated with cement. Fouling was controlled by overnight drying once a month. The minimum profitable yield was 60 oysters per collector. With a growth rate of 1 mm per day, some oysters could be harvested after two months.

There are a few examples of combining tray and raft culture. Bonnet et al. (1975) worked with an unidentified *Crassostrea*-like oyster in French Guyana. Oysters are common in the river mouths along the coast, but their condition is very poor. For the experiment, spat were collected near the creek mouths using cement-coated egg cartons which were mounted on wooden tiles of 0.18 m^2. Spat set only on the undersides of the tiles and counts varied from 200 to 1,600 per collector. Spat were separated and moved to trays suspended from rafts or fixed on intertidal racks in marine waters. In both cases, meat condition was superior to that of oysters kept on intertidal racks in the rivers. Oysters reared in marine waters took 17 months to reach 75 mm shell height on the rafts and 57 mm on the racks in marine waters, while those kept in the river had reached 41 mm in the same period. Mortality measured over a one-year period varied considerably between the three sites: 32.2% for the rack-reared sample, 1.8% for the rafted trays and 83.3% for those kept in the river. The authors stated that the meat condition of sea-cultured oysters was as good as that of oysters farmed in Europe and they encouraged commercial development.

Declining production of *C. gigas* in Deep Bay, Hong Kong, stimulated interest in developing alternative culture systems. Mok (1974b) experimentally cultured oysters in Tung Chung Bay, just off Lantau Island. The site was chosen for its hydrological similarity to Deep Bay. Originally, spat-bearing slate tiles were transferred from Deep Bay to trays suspended from rafts. Some tiles were also planted in the bottom for comparison. The spat had been maintained in Deep Bay for one or two years and ranged from 21 to 24 mm at the time of transplantation. Growth levelled off after eight months in the Bay, but the raft-cultured oysters survived better and grew faster than their bottom-cultured counterparts. In succeeding experiments by Mok (1974b), spat were collected in Tung Chung Bay using either strung oyster shell or cement-coated corrugated paper. Spat set on shell was restrung for growth, while the others were separated after three months of growth on the cultch and put in plastic trays hung from the rafts. In two years the tray-reared oysters were 131 mm long with 82.1% survival. They had grown faster and had better shape than those kept on the strings. The bottom-cultured oysters had been heavily preyed upon by oyster drills, especially during periods of high salinity. The author recommended scaling up to a pilot operation in view of the positive results. Typhoons, frequent in the Hong Kong area, pose an obvious problem for raft culture, but a well constructed raft could survive if sheltered from direct exposure.

An innovative variation on raft culture was introduced by Ng (1979) in Malaysia. Rafts at Langkawi Island were fitted with polyethylene net panels as cultch for setting *O. folium*. This material was superior to roofing tiles, asbestos cement sheets and bamboo screens. One of the most interesting results was the negligible fouling on the net collectors compared to the other materials. Setting of *O. folium* was correlated with the onset of the rainy season and spat grew to a marketable size of 6-7 cm in 8-10 months.

Longline culture was developed in Japan to extend oyster culture to exposed waters as near-shore areas became polluted or overcrowded (Imai 1971). It is now widely used in South Korea, even in sheltered locations and is suitable for mussels and certain seaweeds as well as oysters. Two of the method's advantages are economy of construction and ease of maintenance, particularly if ferro-cement buoys are used (Telosa 1979). Fig. 10 illustrates schematically how a longline system can be set up. A series of buoys are tied together with 10-mm synthetic rope and anchored parallel to the direction of prevailing winds. The mooring should be made as taught as possible and concrete blocks can be used if the sea floor is soft. The cultch-bearing strings are hung from the main lines.

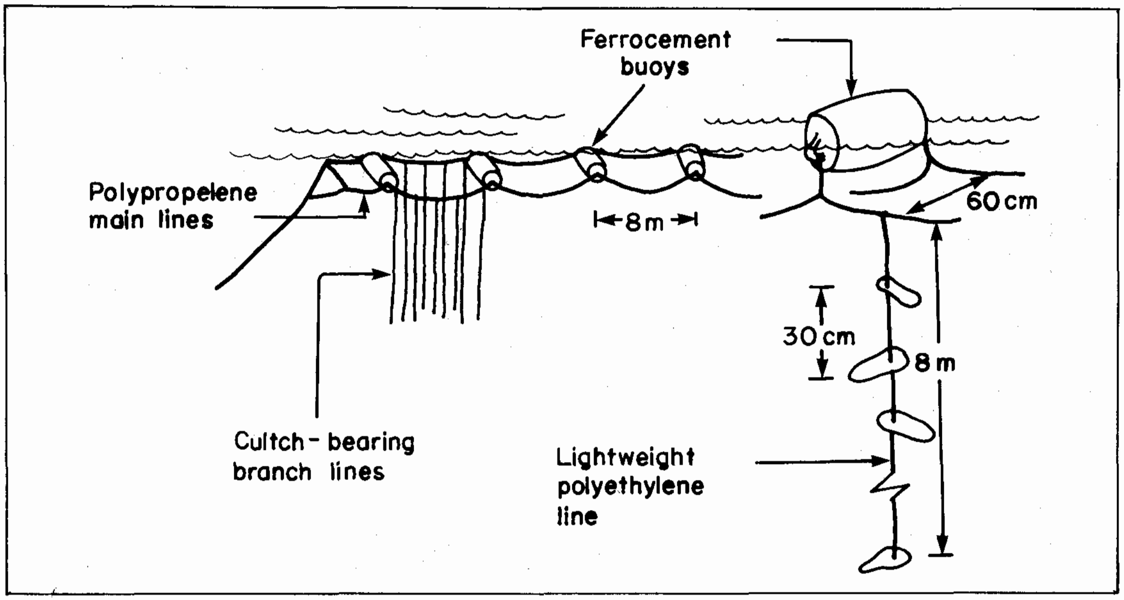


Fig. 10. Longline system using double mainlines and ferrocement buoys (after Imai 1971).

DISEASES AND MASS MORTALITIES

Diseases of tropical oysters are poorly known and with the exception of Hong Kong, there are no reports of mass mortalities from farming areas. This is partly due to the limited development of tropical oyster culture and the lack of biologists trained in the diagnosis of shellfish diseases.

No viral or bacterial diseases of tropical oysters have been reported to date and very limited and inconclusive evidence of protozoan infection exists. An amoeba, *Hartmanella tahitiensis*, was found in the tissues of oysters in Tahiti, French Polynesia (Cheng 1970). However, it may have been a facultative parasite, attacking only moribund oysters. *Hartmanella* is common in soil and may have originated in the heavy freshwater runoff that was causing morbidity in the oysters examined in the above study.

Labyrinthomyxa marina is a serious fungal parasite of oysters in Florida and although it has not been reported from tropical oysters, deserves mention here since infections are associated with warm water. It causes up to 50% mortality in *C. virginica* in Florida and is most infectious during the summer (Quick and Mackin 1971).

Several trematodes infect or prey upon oysters. *Bucephalus haimeanus* attacks the gonads of *C. madrasensis* but infects only a small percentage of oysters (Samuel 1976; Mohan 1978). It is found in all tissues of heavily infected specimens and its sporocysts may completely occupy the gonad. Mohan (1978) observed no gonadal activity in heavily infected oysters at a time when healthy oysters were in various stages of maturation and spawning. The primary infection site is the mantle and an infection rate of 1.7-3.5% was found to occur during periods of relatively low temperature and salinity.

Stylochus inimicus is a predatory flatworm that has caused extensive damage among Florida oysters (Pearse et al. 1938). It lays eggs at temperatures above 15°C and cannot tolerate salinity below 6 ppt.

Echinocephalus sinensis is a nematode which has infected as much as 31% of *C. gigas* in Hong Kong (Ko et al. 1975). It more heavily attacks older oysters and inhabits the genital ducts, causing desquamation with the possibility of direct damage to the gametes. A ray, *Aetobates flagellum*, is thought to be the definitive host. Infection of oysters by *E. sinensis* may pose a public health hazard as it has been found capable of infecting cats and rhesus monkeys.

Serious pest of raft-cultured oysters in tropical waters are spionid polychaetes. Infestation may be extremely heavy, reaching 100%. The worms may also establish themselves in intertidal oysters. Skeel (1979) found *Polydora websteri*, *P. haswelli*, *P. hoplura* and *Boccardia chilensis* attacking intertidal cultures of *S. commercialis* in Australia. The larval worms bore into the oyster shell and upon reaching the inner nacre, the oyster reacts to the irritant by secreting a layer of conchiolin over the site of contact with mantle tissue, forming a "mud blister". The conchiolin is eventually covered with calcareous material, but mud blisters seriously affect marketability.

Stick culture in the intertidal zone controls *Polydora* infestation by drying the young stage of the worm before it can bore deep into the shell. If oysters in subtidal trays are placed where there are fast currents or are washed regularly with high pressure spray, infestations can be controlled. Australian oyster farmers dip sticks in hot water to kill excess spat, which also kills the worms. Other effective treatments include phenol and 70% brine dips (Skeel 1979). Dipping oysters in a 15% (by weight) suspension of quicklime is also effective (Angell 1974). Spionid polychaetes are not true parasites since they do not consume host tissues or fluids but heavy infestations probably stress the oysters, particularly during or shortly after spawning.

Sinderman (1974) suggested several ways that disease may be controlled or limited. Among those that are practical for tropical oyster culture are the following: Environmental manipulation—remove old dead shell; selectively remove intermediate hosts if known; selective use of chemicals, for example, as dips. Stock manipulation—transfer oysters to low salinity water; plant at low density; suspend oysters at specific depths or tidal heights; replace susceptible species with resistant ones; manipulate planting time to avoid attack by disease organisms; breed resistant stock through a hatchery program.

EXOTIC SPECIES

International transplantations of bivalves have had significant impact on the development of shellfish industries in North America and Europe. The oyster industry on the west coast of North America is based on *Crassostrea gigas* which was introduced from Japan during the early twentieth century and for many years farmers depended upon imported Japanese seed. The same species has been introduced to France, the United Kingdom, Ireland, Spain, Germany and the Netherlands, among others (Mann 1983).

In this section reports of the introductions of non-endemic species to and within tropical regions are reviewed. Apparently, no commercial production has resulted from these attempts, with the exception of Baja California (Olivares 1975). However, as knowledge of the biology and growth potential of tropical oysters improves, introduction of exotics may increase. Mann (1978) listed the motivations for past introductions of exotic species in temperate climates, which have included the following:

- economic pressures accompanying the depletion of a native fishery through overfishing or degradated environment;
- the devastation of a fishery by disease;
- the absence of a native fishery and the creation of a new fishery by filling an apparently vacant ecological niche.

It is the last mentioned which has stimulated most introductions in the tropics.

The Pacific oyster, *C. gigas*, has been the most frequently introduced exotic oyster species in the tropics. The oysters often experience very high mortality after a period of quite rapid growth. In some cases, the low survival may be due more to the culture system than some inherent problem with the oysters. Fouling control and protection from predators are particularly important in this regard. However, the growth rate may be so fast that they reach market size before high mortality begins. Physiological stress may be the cause of mortality as the gonad mass increases and maturation proceeds at a high rate in the warm water. Two-year old *C. gigas* in Japan suffer several physiological disorders during summer that lead to mass mortalities (Imai 1971). There is experimental evidence that the rapid depletion of carbohydrate reserves during gonad maturation at high temperatures may severely stress the animal (Mann 1979). This situation does not occur with *O. edulis* and Glude (1984) has suggested that more trial introductions in tropical waters are warranted.

C. gigas was introduced on a small scale to Fijian waters by a pearl farmer in 1969 (Ritchie 1977). Marketable oysters were obtained in less than one year. Later experiments by the fisheries department with tray culture produced harvestable oysters in 12-15 months. Initial trials were expanded with the importation of two tonnes of spatted cultch from Japan. These were raft cultured, but clusters of market-size specimens were separated after about seven months and placed in trays to improve their condition. After holding in the trays for two weeks, shell shape and meat condition had improved enough to permit marketing.

Heavy mortality began during the 10th month, and by the 16th month survival was 12%. In spite of the heavy mortality of cultured oysters, *C. gigas* was reported to have established itself on mangrove roots in Laucala Bay (Ritchie 1977). These experiments demonstrated that marketable Pacific oysters can be produced, but the question remains as to the economic viability of farming this species in Fiji, particularly if the industry has to depend upon imported seed.

The Micronesian Mariculture Demonstration Center attempted raft and tray culture of *C. gigas* in Palau (Tufts and McVey 1975). Survival varied considerably according to site and method used. Mortality was attributed to fouling and predation. An interesting system was developed utilizing rabbitfish (*Siganus* sp.) to control fouling. Compared to controls without rabbitfish, survival was doubled after three months of growth and the rabbitfish were a marketable product as well (Hasse 1974).

Sung (1976) transplanted Korean spat of *C. gigas* to Venezuela and reared them in Cocineta Lagoon in the northwestern corner of the country. Spatted shell cultch was strung and suspended from floats. Initial mortality was high, particularly among larger spat, but stabilized two months after planting. Survival remained about 20% for the next three months, when the trial was terminated. The primary objective of the work was testing the feasibility of transplanting spat from Korea to Venezuela. More extensive growth trials and a pilot project would be required to assess the economic feasibility of culturing *C. gigas*. Since *C. rhizophorae* and *C. virginica* occur in that part of Venezuela, the rationale for introducing *C. gigas* is not clear. There is a serious disease risk involved because spores of an organism similar to *Minchinia nelsoni* have been reported to occur in Korean oysters (Rosenfield and Kern 1978). This organism caused devastating mortalities in Delaware Bay oyster populations of *C. virginica* (Sinderman 1974).

Akaboshi (1979) imported a small amount of *C. gigas* seed from Japan to Sao Paulo state in Brazil. Both suspended and bottom tray culture were tried. Two locations were tested, one estuarine and the other open sea. Suspended culture was used in the latter. Growth and survival were better in the open sea location and market-size oysters were obtained in five months. However, Akaboshi (1979) believed both environments appeared promising for the development of commercial culture.

C. gigas was introduced to Mauritius waters, along with *C. virginica* and *O. edulis* (Brusca and Ardill 1974) using seed produced in a California hatchery. Spat were reared in wooden and wire trays suspended from rafts. The pattern of growth and mortality was comparable to the Fijian experiment, although early mortality was considerably higher. In Mauritius, oysters of one year and older had very poor survival. Several predators, including a drill (*Cymatium* sp.) and a flatworm (*Stylochus* sp.) attacked the oysters, which were also infected with *Polydora*. Histological examination did not reveal any pathogenic organisms. However, the authors attributed the poor results to inadequate nutrition, as there was little phytoplankton in the inshore waters where the tests took place. They concluded that commercial cultivation of the exotic species they tested was probably not feasible and that work should concentrate on the native *S. cucullata*.

The Pacific oyster was introduced to Gulf of California waters in about 1973 using seed from Washington State (Olivares 1975). Some commercial culture is now underway with seed obtained from Washington hatcheries. These gulf waters have a subtropical temperature regime and it may be that a prolonged period of lower temperature allows the oyster to accumulate enough glycogen reserves to sustain it during the spawning season.

Yao and Ryu (1982) transplanted hardened spat of *C. gigas* from Chungmu, South Korea, to Ambong Bay in Sabah, Malaysia. The spat were planted in the bay midway through the rainy season as water temperature increased from 28.5 to 31.1°C. Condition index and meat weight declined during the experiment, although there was an increase in shell height. Survival had declined to 38% after five months of trial, when the experiment was terminated. Their results seemed to follow the usual experience with introductions of *C. gigas* to tropical waters. As with other introductions of *C. gigas* from Korea to tropical areas which have indigenous species that can be cultured (*C. belcheri* in this case), the motivation is unclear. The disease risk has also been mentioned.

Brick (1970) attempted to use traditional fishponds in Hawaii for the tray culture of *C. gigas* and *C. virginica*. Problems were experienced with *Stylochus* predation and high turbidity. Overall mortality was about 59% over a 10-month trial period. It would require about 14 months to produce a market-size oyster of 7.5 cm shell height. However, to achieve adequate environmental conditions within the ponds, considerable renovation would have been necessary. Present attempts to develop oyster culture in Hawaii have centered on land-based intensive systems, which do not appear commercially viable (Goldstein 1984).

C. virginica (source unknown) was introduced to Hawaii as long ago as 1871 and became established in some lagoons and bays (Lee et al. 1983). Pearl Harbor, Oahu, Hawaii, could serve as a source of seed but has experienced mass mortality thought to be due to a fungal infection (Lee et al. 1983).

Introductions of adult *C. virginica* from Pensacola, Florida, to Puerto Rico failed after repeated attempts (Mattox 1952). The experiment was motivated by concern for the heavily harvested native wild stocks of *C. rhizophorae*. All attempts experienced total mortality after a few months, but the causes were undetermined. Introduction of *C. virginica* to Mauritius suffered the same fate and failure was attributed to a combination of high temperature and salinity and low food availability (Brusca and Ardill 1974).

In summary, *C. virginica* can establish itself in tropical waters, as shown by the example of Hawaii, but if there is adequate reason for introducing an exotic species, success would seem to be much more likely if one of the Southeast Asian species of *Crassostrea* is used.

O. edulis has been the object of several introductions to tropical waters, but results to date are inconclusive (Glude 1984). Funes and Olivares (1979) had promising results in the Gulf of California, but did not give the source of seed. Tray culture was used with an initial planting density of 373 oysters/m^2 and after nine months of growout gross production (wet meat weight) varied between 2.6 and 4.1 kg/m^2; survival was 45%.

Culture trials with *O. edulis* were attempted in the coastal waters of Mauritius using seed from a California hatchery (Brusca and Ardill 1974). Some of the transplants grew well for a few months, but eventually all died. The authors attributed the outcome to high temperature. However, *O. edulis* was successfully introduced in Fiji and grew rapidly to market size (Glude 1984). California hatchery-produced seed introduced into the artificial upwelling system at St. Croix, U.S. Virgin Islands, grew from 3 mm to 8 cm in 13 months with 80% survival (Sunderlin et al. 1976). The water temperature ranged from 22 to 29°C. It appears that if nutritionally adequate food is available, *O. edulis* can grow well at relatively high water temperatures. In a comparative study, 8 mm seed of *O. edulis* was planted in Salt River Inlet, St. Croix, and suffered total mortality after four months due to siltation, fouling and predation (Sunderlin et al. 1976).

The potential for polyculture of oysters and fish or shrimp in brackishwater ponds (tambaks) has received little attention to date. Such systems may have wide application, particularly in the tambaks of Java where multiple cropping is a long-established tradition. Some of the tambaks have lost their freshwater supply and have become too saline for optimum shrimp growth. The extensive system of drainage and supply canals might also provide opportunities for oyster culture. In this regard, the results reported by Hughes-Games (1977) show that such development might be feasible.

C. gigas was cultured in fishponds and their outlets on the Gulf of Eilat, Israel, where both salinity and temperature can reach high levels. Seed for the experiments was obtained from Conway, N. Wales, U.K. The Gulf of Eilat region is subtropical, with a wide range of temperature, 12 to 34°C, but salinity is uniformly high, 41 to 42 ppt. Oysters in the ponds increased in weight from 4 to 79 g in one year, while those in the outlets reached 92 g. Shading proved beneficial in the harsh climate of the region. There were no fouling problems in the pond-reared oysters, but silt and accumulated faeces had to be washed off those kept in the outlet trough. Meat quality was considered excellent throughout the study and in spite of the temperature range encountered during the course of the trials, there was never any sign of gonad development. The author emphasized that the ponds were supplied by water from a beach well, which eliminated potential fouling organisms and predators.

C. rhizophorae was cultured in high salinity shrimp ponds in northeastern Venezuela supplied by water from an adjacent lagoon (Angell unpublished data). The attempt had to be abandoned because of heavy fouling by serpulid polychates. Fouling is influenced by many factors, so it would be worthwhile to extend these kinds of trials to further explore polyculture possibilities. Perhaps polyculture with rabbitfish or similar herbivorous browsers could control fouling.

There have been few attempts to transplant exotics within the tropical zone. *S. cucullata* and *S. echinata* were introduced to Sasa Bay, Guam, from the Solomon Islands and their growth and reproduction were monitored (Braley 1984). *S. echinata* matured and spawned and recently set spat were noted in the study area. It was estimated to take 6-9 months for *S. echinata* to reach a market size of greater than 40 g using intertidal tray culture. Apparently, the growth of *S. cucullata* was too slow to offer any commercial potential.

S. echinata was introduced to Tahitian waters from New Caledonia in 1978 because farms of the native *S. cucullata* had become infested with *Polydora* worms (Aquacop 1982). Hatchery production of seed was successful and a pilot-scale growout operation produced several hundred kilos of oysters, which required two years to reach marketable size. The biggest problem was consumer dislike for *S. echinata* due to its "bitter" taste. Attempts are underway to cross *S. cucullata* with *S. echinata* in hopes of obtaining an acceptable taste while retaining resistance to *Polydora* infestation.

Several attempts were made to introduce *C. iredalei* to Fiji using seed from Manila, Philippines (Ritchie 1977). Both trials were of short duration, but the species appeared to have potential. Mortality was attributed to poor shipping, handling and acclimatization; even so, growth was between 0.5 and 1.2 cm per month.

Some species in Southeast Asia which are presently cultured commercially might prove successful in other regions with similar environmental conditions. *C. belcheri*, *S. lugubris* and *C. iredalei* grow rapidly with high survival in the intertidal zone. *C. paraibanensis* in Brazil merits further investigation of its potential both in Brazil and other countries as it can withstand very low salinity.

HYBRIDIZATION AND SELECTIVE BREEDING

The development of bivalve shellfish hatchery technology has opened new possibilities for improving oyster production. Although some progress has been made, most of the possibilities are still just that (Menzel 1971). Bivalve hatcheries are now playing an important role in commercial oyster production in the USA, but are just beginning to be introduced in tropical and subtropical regions. Examples are Mexico (Haro et al. 1983), Thailand (Angell, unpublished data) and Malaysia (Dr. Wong Tat-Meng, Universiti Sains, Penang, Malaysia, pers. comm.).

Menzel (1971) listed the benefits that can be achieved only through hatchery breeding:

- *Growth.* Better growth can be achieved through selecting fast growing strains or physiological races of the same species or by interspecific crosses. Hybrids can be developed that will be better adapted to specific environmental conditions. For example, a hybrid which could grow rapidly in high salinity would be beneficial in many tropical areas. Hybrids could be selected for shell thickness to resist borers.

- *Disease resistance*. The inheritability of disease resistance has been demonstrated in the Pacific oyster, *C. gigas* (see Beattie et al. 1978).
- *Resistance to physiological stresses*. The effect of high temperature on survival of *C. gigas* has been noted. Hybridization with a high-temperature tolerant species could enable the oyster farmer to take advantage of the fast growth rate of *C. gigas*.

Selected interspecific crosses of oysters that have been cultured commercially or experimentally in tropical waters are summarized in Table 7. Several attempts to cross *Saccostrea* and *Crassostrea* species have been made, but only a few have been successful. Dinamani (1984) reported hybridizing *S. glomerata* females with males of *C. gigas*. The F_1 s grew to maturity and produced viable larvae which were back-crossed. The practical benefits of this hybrid are still unknown.

Thai biologists succeeded in obtaining viable hybrids of *S. lugubris* and *C. belcheri* (Angell unpublished data). The hybrid larvae had better hatchery survival than those of either parent. Both reciprocal crosses were viable, but the female *C. belcheri* with male *S. lugubris* were hardier.

Table 7. Selected hybridizations of *Crassostrea* and *Saccostrea* oysters.

Cross male	x	female	Fertilization	Viable F_1 Larvae	Viable F_1 Adults	Fertile F_1	Reference
C. belcheri		*S. lugubris*	+	+	+	*	Angell (unpubl.)
S. lugubris		*C. belcheri*	+	+	+	*	Angell (unpubl.)
C. gigas		*S. glomerata*	+	+	+	+	Dinamani 1984
C. gigas		*S. echinata*	+	—	—	—	Imai and Sakai 1961
S. echinata		*C. gigas*	+	—	—	—	Imai and Sakai 1961
C. rhizophorae		*C. virginica*	+	+	+	*	Menzel 1969
C. gigas		*C. rhizophorae*	+	+	+	*	Menzel 1969
S. commercialis		*C. gigas*	—	—	—	—	Menzel 1969
C. gigas		*S. commercialis*	—	—	—	—	Menzel 1969

*Not determined.

PROCESSING AND MARKETING

Research and development programs promoting tropical oyster culture have clearly been dominated by biological considerations, with very little attention directed towards the solution of processing and marketing problems. The marketing of oysters and oyster products follows traditional methods. In Southeast Asia, oysters may be dried, brined, pickled, or processed into sauce, as well as being sold fresh. In Latin America, sales are exclusively of the fresh product.

In the Philippines, the major market is Manila where the majority of sales are for whole oysters (Young and Serna 1982). Occasionally they are shucked, particularly if the shells are beginning to gape. The meats are packed in plastic bags with freshwater and stored on ice. Preservation includes salting, pickling, canning, smoking and freezing. Farmers may sell through wholesalers or directly at roadside stalls. If through wholesalers, markup at the retail level over farm price is about 100%. Wholesalers may do retailing as well, usually in urban markets. Institutional buyers include hotels and restaurants. There are the beginnings of a modest export industry to Singapore.

Roadside stalls are common in the oyster growing regions of Thailand, where shucked meats are sold in plastic bags, as in the Philippines. Pickled oysters are usually sold along with the fresh shucked product. *S. commercialis* is most commonly involved in this type of trade. *C. belcheri* and *S. lugubris* grown in southern Thailand are trucked to Bangkok, where they are a luxury food in restaurants. Thailand has good infrastructure connecting major cities including road, rail and air; potential exists for expanding sales provided improved transport systems for shellfish are developed. Cockles *(Anadara granosa)* are currently being marketed as far north as Chiengmai, although often in poor condition. Both products would benefit from improved transport.

There is no oyster farming as yet in Nigeria, but presumably cultured oysters would be handled in the same way as those from the existing fishery (Ajana 1980). Oysters are steamed in tins for 10-15 minutes, drained, rinsed, salted and smoked. The processed meats are skewered on sticks of a dozen oysters for retailing. Shells are used for building material and in poultry feeds. Oysters are simply steamed and retailed by the fishermen's wives in Sierra Leone. The meats are sold by volume in the local markets or along the roadside (Kamara 1982b). These processing methods have the advantage of reducing or eliminating bacterial contamination. Goldmintz et al. (1978) found that in-shell steam pasteurization at 60°C reduced both total plate count and coliforms by 99.5 and 99.9%, respectively. Shelf life of pasteurized oysters was considerably extended and organoleptic test results were positive.

Smoking followed by drying might be applicable to oysters and would be a suitable method for many tropical coastal areas. Mangrove wood is excellent for smoking and is readily available near most oyster farm sites. Mussels processed with this technique can be stored for up to six months (Silas et al. 1982). Canning alone or in combination with smoking is another possibility, although of more limited marketability due to cost.

Salafranca (1952) investigated the effects of salt, vinegar and heat on coliforms in Philippine oysters from waters near Manila. The concentrations of salt and vinegar needed to bring about an appreciable reduction in coliforms would render the product unpalatable. Boiling for 10 to 15 minutes was the only method that resulted in safe levels of coliforms. However, such treatment considerably reduced the appeal of the oyster meats.

Many tropical estuaries with oyster culture potential are likely to carry hazardous levels of human pathogens, making the public health problem a serious concern. Singapore has placed sanitary standards on imported seafood, which has resulted in the use of depuration by at least one Philippine exporter (Poquiz and Rice 1982). It is unlikely, though, that depuration will become widespread unless more attention is paid to developing economically feasible systems. Uniform enforceable national standards would have to be established to encourage private sector development of depuration facilities. Relaying to clean waters might be possible in some areas, although operating costs would be increased. Perhaps a more practical alternative is to develop domestic markets for processed oysters, or improve existing processing methods.

The level of fecal bacteria is highly seasonal in some estuaries, rising to hazardous levels during the rainy season (Leung et al. 1975). Morton and Shortridge (1976) found coliform counts fluctuated with the tidal cycle, rising considerably during low tide exposure. They suggested that harvesting be restricted to high tide to reduce the risk of contamination.

It is certainly in the interest of the industry to ensure the safety of its product. If widespread disease outbreaks occur as a result of consuming contaminated oysters, the effect could be devastating to the oyster farmers. In some Southeast Asian countries, consumers are already becoming wary of shellfish. Although the history of fishermen's cooperatives is hardly promising, some form of community approach to depuration should be encouraged. It is unlikely that individual oyster farmers could bear the expense of an installation.

ECONOMICS OF TROPICAL OYSTER CULTURE

Detailed and comprehensive economic studies of tropical oyster culture are few, even in those instances where there has been some development. Young and Serna (1982) provide some figures on costs and profitability of oyster farming in the Philippines. They compared four methods of culture: stake, hanging, lattice and broadcast. Earnings on sales varied from 10 to 73%. Broadcasting was the least profitable and hanging culture the best but also required the highest capital investment. Data on stake culture provided by Blanco (1956) indicated that labor amounted to 65% of operating costs.

Economic or financial analysis of pilot or demonstration projects should be encouraged to show development potential and indicate where refinements might be made. Although the results of such studies may be preliminary, they can be useful for comparative purposes.

An analysis of an intertidal rack system for the small-scale culture of *S. echinata* in Ambon, Indonesia, showed a 27% rate of return on investment (Angell 1984). Chin and Lim (1975) estimated the returns from farming *C. belcheri* based on the operation of an experimental farm. Although they considered the initial investment costs to be high, the rapid turnover due to high growth rates meant the initial investment could be recovered at the end of the second year of operation. Labor amounted to 8% of the cost of production.

Watters and Martinez (1976) estimated that raft culture of *C. rhizophorae* in Puerto Rico could be profitable. If capital costs were amortized in one year, a small profit would accrue at the end of the first year and better than 100% return on investment achieved by the end of the second year.

Experimental raft culture of *C. tulipa* was evaluated by Kamara (1982a) and it was found that yield was not high enough to keep the break-even price below the selling price of oysters harvested from wild stocks. The cost of the rafts was depreciated in one year and the opportunity costs for labor were not counted in the study. Perhaps the enterprise could become profitable by increasing raft size, improving raft construction to allow depreciation over a longer time period and better fouling control.

RESEARCH NEEDS

Several broad areas for applied research can be identified: biology, culture technology, processing and marketing, and economics.

Biology

The basic biology of tropical oysters and differences with that of temperate species have been reasonably well documented. For those regions where the speciation of oysters has not been examined with modern techniques, such as South and Southeast Asia and West Africa, the clarification of intra-specific affinities would be of value. In some countries, such as Indonesia and the coastal states of Africa, national surveys of species, the environments they inhabit and their suitability for culture should be made.

Further testing and evaluation of exotic introductions or transplants of indigenous species to new culture sites are needed, particularly in the Pacific Islands.

Culture Technology

Through the experience gained during the past two decades, it is evident that some techniques are more likely to prove successful than others. In most situations, including countries which support an industry, some form of intertidal rack culture seems to be most effective. Studies can concentrate on developing more cost-effective methods in terms of both materials used and techniques. The seed supply situation seems to vary considerably between countries, some reporting an abundance while others experience shortages. In some cases, there may be an abundant source within a country, but expansion may be limited by the lack of a seed collection industry. Alternatives include the development of such an industry or the construction of hatcheries. Oyster hatchery technology has developed to the point that it is rather standard and provided water quality is good, there should not be any technical impediments. However, the advisability of embarking on any sort of hatchery development should be based on a thorough economic analysis of the industry. A hatchery might be justified as a public investment where seed supplies are inadequate to expand culture or intensify existing practices. Hatcheries have the additional advantage of being able to produce a wide variety of bivalve seed which can be used to stimulate the development of new culture industries, for example, scallop farming. Hatcheries should also be incorporated into any program of exotic introductions to ensure that only disease-free F_1 progeny are planted in growing areas (Mann 1983). The phytoplankton cultured in a typical oyster hatchery can also be used to rear shrimp and fish larvae. Thus, one could envision a seed production facility for crustaceans and bivalves centered around an intensive phytoplankton culture system. Such multiple use should greatly improve hatchery economics. Experience in Thailand indicates there are sites where water quality is compatible with multiple use. A government-operated seed center at Prachuap Khirikahn presently produces shrimp and seabass fry and the spat of *S. cucullata*, *Perna canaliculatus*, *S. lugubris*, *C. belcheri* and their hybrids on a pilot scale. Single oyster seed produced in the hatchery can be readily integrated into existing Thai culture systems. From an investor's point of view, hatchery production of spat provides a predictable source of raw material. The use of eyed larvae has not yet been attempted in the tropics, but if spat and growout sites are some distance apart, costs can be reduced when eyed larvae are used for setting directly at the growout site, thus avoiding the transport of large amounts of cultch. Predictability of supply and reduction of transport costs are two reasons why hatchery-produced eyed larvae are replacing natural setting on the U.S. west coast (Beattie 1983).

The development of cost-effective cultch would be beneficial where supplies of old shell are limited or non-existent. The use of composites such as cement-palm fiber, could be applied in some cases. The increased useful life of these materials may compensate for their added expense (Djausal 1980).

Processing and Marketing

As remarked above, one solution to the problem of unsanitary oysters is some form of heat processing. Market research and development will play a crucial role, particularly in those countries where trade in such products is limited or unknown. Traditional market channels could be encouraged to utilize pasteurized oyster meats through stimulating consumer demand. Urban centers in many developing countries now boast modern supermarkets which could provide retail outlets for properly packaged products and at the same time greatly expand distribution.

Depuration is already in use on a very limited scale in Southeast Asia, but could increase where the "half shell" trade is sufficiently developed or system costs can be held low enough to attract private investment. Either pasteurization or depuration would greatly improve consumer confidence, a prerequisite to expanded sales.

Economics

While a number of studies have been made of oyster biology and technology, the same cannot be said of the economics of the industry. Ultimately, the potential for the development of tropical oyster farming will depend upon its profitability. There is need now for detailed comparative economic studies of various culture and marketing systems, both pilot and industrial scale. Such studies are needed to guide development planning, both in the public and private sectors.

DEVELOPMENT PROBLEMS AND POTENTIAL

Tropical oyster culture has a number of advantages as an element of rural development:

- Simple technology, using locally available materials.

- Labor intensive operations.
- Low capital investment.
- Minimum environmental impact.
- The product contributes to improved nutrition.

Oysters are consumed by local people almost everywhere they occur naturally and many beds are severely depleted. Why isn't culture more widespread? The obstacles to expansion are not much different in several aspects from those facing any new industry in developing economies. The importance of market development has already been mentioned. Many countries face severe shortages of qualified personnel, particularly in fisheries and aquaculture development. Sometimes the organizational setting for implementing demonstration and development is not clear, especially at the local level. Since coastal dwellers are often amongst the poorest segments of society, even the modest amounts of financing required for oyster culture are often not available. Sometimes funds may be nominally available, but procedures and/or criteria for granting loans are unsuitable for the economic and social situation of the potential farmer. These include unnecessary bureaucracy, unreasonable collateral and excessive down payments.

The mechanism by which research results are translated into development bears consideration. Ideally, a process develops in which research leads to pilot-scale trials designed to indicate financial feasibility. If pilot results are positive, a widespread demonstration program can be undertaken at the village (producer) level. Provided adequate technical assistance and financing is available, development may then proceed. But technical assistance must include marketing as well as technical elements.

Adequate funding must be available for the demonstration phase, which must be of sufficient duration to have an impact. Rarely will the production of one crop be sufficient as it may take several years to work out problems and stimulate community interest. Even after the demonstration phase has terminated, extension staff must be assigned to assist with both production and marketing on a continuous basis. The demonstration phase is invaluable in serving as a training mechanism for extension agents and farmers once the major production problems have been worked out.

It is also important that an oyster farming project be carried out within the proper institutional framework. This will vary from country to country and may have to involve several ministries or directorates-general if all the necessary activities are not found within one particular government structure. Interagency communications are often not well developed and will require special effort.

In the village, it is crucial to identify innovative individuals and often this must be the first step in the development process. Oyster culture lends itself to very small-scale operations and may involve an entire family. Women may be involved in maintenance, harvesting, processing and marketing and should not be overlooked in any development scheme.

Land tenure and user conflicts may hinder oyster farming in some areas. Land tenure is less of a problem in traditional societies because coastal resources are usually considered to be a community asset. An individual may be granted rights to establish an oyster farm through traditional law. In Polynesian cultures, communities control marine resources, particularly within the lagoon; individuals are granted rights to occupy sections of the lagoon or to fish at certain times and places through the traditional leadership. Outsiders who attempt to usurp this right will be rejected by the community, as has happened in the Cook Islands (Julian Dashwood, Dept. of Fisheries, Cook Islands, pers. comm.). This type of exclusive community right may render entrepreneural development impossible. The possibility of community activity, as through cooperatives, always exists but usually proves difficult to develop in practice. Mexico has a long history of cooperative involvement in oyster harvesting and culture but the cooperatives have experienced problems in expansion and intensification due to lack of technical expertise and shortages of funds (Haro et al. 1983). However, producers may group together in informal associations as brackishwater pond farmers do in Indonesia. Governments may grant farming rights through leasing, as is the case in Thailand and Malaysia for cockle farms.

User conflicts may pose problems, since intertidal areas most suitable for oyster culture are often exploited by artisanal fishermen and their families. Care must be taken to resolve or avoid user conflicts before a project begins. Chin and Lim (1977) mention difficulties with illegal trawlers entering shallow bays where oyster culture and spat collection could be developed. It may be advisable to employ the services of rural sociologists and anthropologists during the early stages of a project in the hope that they can anticipate potential problems of this type.

Kamara et al. (1974) pointed out that pollution and interference with navigation are additional constraints on oyster culture development. Pollution is indeed a serious threat and has caused problems in several Southeast Asian countries. Waste dumped into rivers by pineapple canneries in Thailand has seriously affected small-scale oyster production in the southern part of the country; the inner Gulf of Thailand is so heavily impacted by runoff from the Chao Phrya River that it is useless for shellfish farming. Jakarta Bay, Indonesia, is very polluted and there is concern that "Minimata" disease may manifest itself due to mercury contamination. Outbreaks of gastroenteritis in Singapore were traced to oysters imported from the Philippines (Young and Serna 1982), which emphasizes the ever-present threat of intestinal diseases that can be carried by oysters and other bivalves reared and harvested in polluted water.

Paralytic shellfish poisoning (PSP) from consumption of bivalve shellfish is of increasing concern, particularly in Southeast Asia where sporadic outbreaks have been documented. Maclean (1979) attributed PSP poisoning in Papua New Guinea, Brunei and Malaysia to blooms or "red tides" of the dinoflagellate *Pyrodinium bahamense*, later determined to be *P. bahamense* var. *compressa* (Steidinger et al. 1980). A recent study demonstrated the toxicity of *Pyrodinium* in Palau (Harada et al. 1982). PSP including occasional deaths could be traced back at least until the 1950s in Papua New Guinea, but the outbreaks in Brunei and Malaysia (Sabah and Sarawak) occurred for the first time in 1976. PSP and deaths from eating shellfish have occurred sporadically since then. The Philippines experienced its first major *Pyrodinium* red tide with associated poisonings in 1983. The large mussel industry in the affected area in the Samar Sea was closed for nearly a full year, since sampled mussels remained toxic during that time. Pollution does not seem to be a factor causing *Pyrodinium* blooms. However, red tides from other dinoflagellates are increasing at alarming rates in polluted areas of Hong Kong and Japan. Summaries of all these phenomena in Southeast Asia are given in White et al. (1984) and Maclean and White (1985). Much more research is needed to determine the environmental conditions that lead to blooms of PSP organisms in tropical waters.

Besides the obvious health hazard, outbreaks of PSP could deal a devastating blow to shellfish culture development. Public health agencies may be the appropriate vehicle for monitoring programs, but extensive training will be required in the detection of causative organisms and in the use of monitoring techniques.

References

Ablan, G.L. 1955. Lattice method of oyster culture. Philipp. J. Sci. 2(2): 197-201.

Ahmed, M. 1975. Speciation in living oysters, p. 357-397. *In* F.S. Russell and M. Yonge (eds.) Advances in marine biology, vol. 13. Academic Press, London.

Ajana, A. 1979. Preliminary investigation into some factors affecting the settlement of the larvae of the mangrove oyster, *Crassostrea gasar*, in the Lagos Lagoon. Malacology 18: 271-275.

Ajana, A.M. 1980. Fishery of the mangrove oyster, *Crassostrea gasar*, Adanson in the Lagos area, Nigeria. Aquaculture 21: 129-137.

Akaboshi, S. 1979. Notas sobre o compartamento da ostra japonesa *Crassostrea gigas* (Thunberg 1795) no litoral do estado de Sao Paolo, Brasil. Bol. Inst. Pesca 6: 93-104.

Akaboshi, S. and A.A. Bastos. 1977. El cultivo de la ostra *Crassostrea brasiliana* Lamarck en la region lagunar de Cananeia, Sao Paolo, Brasil. *In* La acuicultura en America Latina. Food and Agriculture Organization FIR/R159.1 (Es), V.1: 148-158.

Angell, C.L. 1973. Maduracion gonadica y fijacion de *Crassostrea rhizophorae* en una laguna hipersalina del nororiente de Venezuela. Mem. Soc. Cienc. Nat. La Salle 33(93): 216-240.

Angell, C.L. 1974. Crecimiento y mortalidad de la ostra de mangle cultivada *(Crassostrea rhizophorae)*. Separata #49, Estacion de Investigaciones Marinas de Margarita, Fundacion La Salle de Ciencias Naturales, Caracas.

Angell, C.L. 1984. Culturing the spiny oyster, *Saccostrea echinata*, in Ambon, Indonesia. J. World Maricult. Soc. 15: 433-441.

Angell, C.L. and J. Tetelepta. 1982. Oyster culture in the mangrove forest ecosystem, p. 177-189. *In* A.Y. Kostermans and S.S. Sastroutomo (eds.) Symposium on Mangrove Forest Ecosystem Productivity in Southeast Asia. Biotrop Spec. Publ. No. 17.

Aquacop. 1982. French Polynesia, p. 31-33. *In* F.B. Davy and M. Graham (eds.) Bivalve culture in Asia and the Pacific. International Development Research Council, Ottawa, Canada.

Asif, M. 1979. Hermaphroditism and sex reversal in the four common oviparous species of oysters from the coast of Karachi. Hydrobiologia 66(1): 49-55.

Bardach, J.E., J.H. Ryther and W.O. McLarney. 1972. Aquaculture—the farming and husbandry of freshwater and marine organisms. John Wiley & Sons, New York.

Beattie, H.J. 1983. Overview of oyster culture on the Pacific coast. *In* Proceedings of the North American Oyster Workshop. World Maricult. Soc. Spec. Publ. 1: 11-15.

Beattie, H.J., W.K. Hershberger, K.K. Chew, C. Mahnken and E.F. Prentice. 1978. Breeding for resistance to summertime mortality in the Pacific oyster *(Crassostrea gigas)*. University of Washington Sea Grant WSG 78-3.

Blanco, G.J. 1956. The stake (patusok) method of oyster farming in the Dagatdagatan Lagoon, Rizal Province. Philipp. J. Fish. 4(1): 21-30.

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(1): 35-53.

Bonnet, M., M. Lemoine and J. Rose. 1975. Une overture nouvelle pour les cultures marines l'ostreiculture en Guyane. Sci. Pêche, Bull. Inst. Peche Marit. No. 249.

Braley, R.D. 1984. Mariculture potential of introduced oysters *Saccostrea cucullata tuberculata* and *Crassostrea echinata* and a histological study of reproduction of *C. echinata*. Aust. J. Mar. Freshwat. Res. 35: 129-141.

Breisch, L. and V.S. Kennedy. 1980. A selected bibliography of worldwide oyster literature. University of Maryland Sea Grant Publ. No. UM-SG-TS-80-11.

Brick, R.W. 1970. Some aspects of raft culture of oysters in Hawaii. University of Hawaii, Institute of Marine Biology Tech. Rep. No. 24.

Bromanonda, P. 1978. Study on some biological aspects and culture of oyster. Thai Fish. Gaz. 31(3): 202-228.

Bromhall, J.D. 1958. On the biology and culture of the native oyster of Deep Bay, Hong Kong, '*Crassostrea* sp.' Hong Kong Univ. Fish. J. 2: 93-107.

Brusca, G. and D. Ardill. 1974. Growth and survival of the oysters *Crassostrea gigas, C. virginica* and *Ostrea edulis* in Mauritius. Rev. Agri. Sucri. Ile de Maurice 53: 111-131.

Bryson, R.K. 1977. Tropical oyster farming—a valuable new industry. Aust. Fish. November: 2-6.

Buroker, N.E., W.K. Hershberger and K.K. Chew. 1979a. Population genetics of the family Ostridae I. Intraspecific studies of '*Crassostrea gigas*' and '*Saccostrea*'. Mar. Biol. 54(2): 157-169.

Buroker, N.E., W.K. Hershberger and K.K. Chew. 1979b. Population genetics of the family Ostreidae 2. Interspecific studies of the genera '*Crassostrea*' and '*Saccostrea*'. Mar. Biol. 54(2): 171-184.

Cardenas, E.B. 1984. Status of molluscan aquaculture on the Pacific coast of Mexico. Aquaculture 39: 83-93.

Carreon, J.A. 1969. The malacology of Philippine oysters of the genus '*Crassostrea*' and a review of their shell characters. Proc. Nat. Shellfish. Assoc. 59: 104-115.

Cheng, T.C. 1970. '*Hartmannela tahitiensis*' new species: an amoeba associated with mass mortalities of the oyster '*Crassostrea commercialis*' in Tahiti, French Polynesia. J. Invertebr. Pathol. 15(3): 405-419.

Chin, P.K. and A.L. Lim. 1975. Some aspects of oyster culture in Sabah. Fish. Bull. Minist. Agric. Rural Dev. 5: 1-13.

Chin, P.K. and A.L. Lim. 1977. Oyster culture development in Sabah. Sabah Soc. J. 6(3): 107-115.

Cortez-Guzman, A.S. and A. Martinez-Guerrero. 1979. Identificacion y quantificacion de larvas pediveligas de '*Crassostrea corteziensis*' Hertlien y balanides en los esteros de San Blas, Nayarit, Pacifico de Mexico. Annu. Cent. Cienc. Mar. Limnol. Univ. Nac. Auton. Mexico 6: 37-52.

DeBuen, F. 1957. Crisis ostricolas y su recuperacion. Secretaria Maritima, Direccion General Pesca y Industrias Conexas. 44 p.

De Lara, A.R. and M.E. Gutierrez, 1977. Algunos aspectos sobre el cultivo de *Crassostrea virginica* Gmelin en el sistema lagunar Carmen-Machona-Redonda, Tabasco, Mexico. La acuicultura en America Latina, vol. 1. Food and Agriculture Organization Inf. Pesca No. 159: 196-202.

Dinamani, P. 1976. The morphology of the larval shell of *Saccostrea glomerata* (Gould, 1850) and a comparative study of the larval shell in the genus *Crassostrea* Sacco, 1897 (Ostreidae). J. Moll. Stud. 42: 95-107.

Dinamani, P. 1984. Oyster hybridization work continues. Shellfish Newsl. 21: 13-14.

Djausal, A. 1980. Pipa sabut semen. Pusat Teknologi Pembangunan. Institut Teknologi Bandung, Bandung, Indonesia.

Durve, V.S. 1964. On the percentage edibility and the index of condition '*Crassostrea gryphoides*' (Scholtheim). J. Mar. Biol. Assoc. India 6(1): 128-134.

Durve, V.S. 1965. On the seasonal gonadal changes and spawning in the adult oyster '*Crassostrea gryphoides*' (Schlotheim). J. Mar. Biol. Assoc. India 7(2): 328-344.

Durve, V.S. and D.V. Bal. 1962. Preliminary observations on the growth of the spat of the oyster '*Crassostrea gryphoides*' (Schlotheim). J. Mar. Biol. Assoc. India 4(2): 206-213.

FAO. 1984. Yearbook of fishery statistics, catches and landings, 1983. FAO Fish. Ser. V. 56.

Farfante, I.P. 1954. El ostion comercial en Cuba. Centro de Investigaciones Pesqueras Contribucion No. 3. Cuba.

Fatuchri, M. 1976a. Study on the growth of local oyster '*Crassostrea cucullata*' Born in Banten Bay. Mar. Fish. Res. Rep. Indonesia (No. 1): 47-54.

Fatuchri, M. 1976b. Perkiraan waktu pemijahan tiram (*Crassostrea cucullata* Born) di perairan Teluk Banten. Mar. Fish. Res. Rep. Indonesia (No. 1): 37-46.

Forbes, M. 1973. Setting and growth of *Crassostrea rhizophorae*. College of the Virgin Islands, St. Croix Campus, U.S. Virgin Is. Mimeo.

Funes, V.G. and R.I. Olivares. 1979. Analysis comparativo de produccion del ostion europeo *(Ostrea edulis)* en dos localidades de Baja California. Cienc. Mar. 6(1&2): 19-26.

Galtsoff, P.S. 1964. The American oyster. U.S. Fish Wildl. Serv. Fish Bull. V. 64.

Glude, J.B. 1971. Identification of oysters of the South Pacific Islands. National Marine Fisheries Service, Seattle, Wash., USA. Mimeo.

Glude, J.B. 1984. The applicability of recent innovations to mollusc culture in the western Pacific Islands. Aquaculture 39: 29-43.

Goldmintz, D., R.C. Ernst and J. Rasekh. 1978. Development of a pasteurized oyster product. Proceedings 3rd Annual Tropical and Sub-tropical Fisheries Technology Conference of the Americas. New Orleans.

Goldstein, B.B. 1984. The commercial cultivation of *Crassostrea gigas* in a land-based, tropical, managed food chain. Aquaculture 39: 393-402.

Gunter, G. 1951. The species of oysters of the Gulf, Caribbean and West Indian region. Bull. Mar. Sci. Gulf and Caribbean 1(1): 40-45.

Harada, T., Y. Oshima, H. Kamiya and T. Yasumoto. 1982. Confirmation of paralytic shellfish toxins in the dinoflagellate *Pyrodinium bahamense* var. *compressa* and bivalves in Palau. Bull. Jap. Soc. Sci. Fish. 48(6): 821-825.

Haro, B.H., E.P. Nunez, A.F. Mattus and M.A. Landin. 1983. The development and perspective of oyster culture in Mexico. *In* Proceedings of the North American Oyster Workshop. World Maricult. Soc. Spec. Publ. 1: 64-69.

Hasse, J. 1974. Utilization of rabbitfishes 'Siganidae' in tropical oyster culture. Prog. Fish-Cult. 36(3): 160-162.

Hertlein, L.G. and A. Strong. 1946. Molluscs of Mexico and Central America. Zoologica 31(5): 54-55.

Hidu, H., W.G. Valleau and F.P. Veitch. 1978. Gregarious setting in European and American oysters—response to surface chemistry vs. waterbone pheromones. National Shellfisheries Association V. 68: 11-16.

Hornell, J. 1951. Indian molluscs. Bombay Nat. Hist. Soc.: 58-60.

Hughes-Games, W.L. 1977. Growing the Japanese oyster *(Crassostrea gigas)* in subtropical seawater fishponds. I. Growth rate, survival and quality index. Aquaculture 11: 217-229.

Imai, T. 1971. Aquaculture in shallow seas: progress in shallow sea culture. National Technical Information Service PB 280 493-T.

Imai, T. and S. Sakai. 1961. Study of breeding the Japanese oyster, *Crassostrea gigas*. Tohoku J. Agric. Res. 12(2): 125-171.

Kamara, A.B. 1982a. Preliminary studies to culture mangrove oysters, *Crassostrea tulipa*, in Sierra Leone. Aquaculture 27: 285-294.

Kamara, A.B. 1982b. Oyster culture in Sierra Leone, p. 91-107. *In* Smith and Peterson (eds.) Westview special studies in agriculture and aquaculture science and policy. Westview Press, Boulder, Colorado.

Kamara, A.B., K.B. McNeil and D.B. Quayle. 1974. Tropical mangrove oyster culture: problems and prospects, p. 334-348. *In* Food and Agriculture Organization Conference on Aquaculture, Kyoto, Japan.

Ko, R.C., B. Morton and P.S. Wong. 1975. Preliminary studies on *Echinocephalus sinensis* (Nematoda: Spiruroidea), an unusual parasite from the oyster *Crassostrea gigas* Thunberg 1793 (Mollusca: Bivalvia) in Hong Kong. Pacific Science Association, Special Symposium on Marine Sciences, Hong Kong.

Lambert, F. and P. Polk. 1971. Observations sur l'ostreiculture a Cuba 1. Composition du plankton. Hydrobiologia 38(1): 9-14.

Lee, K.W.F., J.S. Corbin and W.A. Brewer. 1983. Oyster culture in Hawaii and various United States Pacific Island territories. *In* Proceedings of the North American Oyster Workshop. World Maricult. Soc. Spec. Publ. 1: 70-85.

Lepoureau, J.A. 1978. Proporciones en cosechas comerciales de ostion de cultivo en Cuba y su comparacion con patrones teoricos. 2nd Symposium, Latin American Aquaculture Association, Mexico.

Leung, C., B.S. Morton, K.F. Shortridge and P.S. Wong. 1975. The seasonal incidence of faecal bacteria in the tissues of the commercial oyster *Crassostrea gigas* Thunberg 1793 correlated with the hydrology of Deep Bay, Hong Kong. Proceedings of the Pacific Science Association Special Symposium on Marine Science, Hong Kong.

Lizarraga, M. 1974. Tecnicas aplicadas en el cultivo de moluscos en America Latina. La acuicultura en America Latina. Food and Agriculture Organization, Inf. Pesca No. 152 V2: 96-105.

Lopez, M.D. and E.D. Gomez. 1982. Reproductive cycles of the oysters *Crassostrea echinata* and *C. lugubris* in Calatagan, Batangas, Philippines. Kalikasan 11(1): 57-73.

Maclean, J.L. 1979. Indo-Pacific red tides, p. 173-178. *In* D.L. Taylor and H.H. Seliger (eds.) Toxic dinoflagellate blooms, vol. 1.

Maclean, J.L. and A.W. White. 1985. Toxic dinoflagellate blooms in Asia: a growing concern, p. 517-520. *In* Anderson, D.M., A.W. White and D.G. Baden (eds.) Toxic dinoflagellates. Proceedings of the Third International Conference on Toxic Dinoflagellates, St. Andrews, New Brunswick, Canada, 8-12 June 1985. Elsevier Publishing Co., Inc., New York.

Macsotay, O. MS. 1974. Estudios sobre especies de ostras del genero *Crassostrea*, fosiles y vivientes del Cenozoico al reciente.

Mann, R. 1978. Exotic species in aquaculture: an overview of when, why and how. *In* R. Mann (ed.) Exotic species in mariculture. MIT Press, Cambridge, Mass.

Mann, R. 1979. Some biochemical and physiological aspects of growth and gametogenesis in *Crassostrea gigas* (Thunberg) and *Ostrea edulis* L. grown at sustained elevated temperatures. J. Mar. Biol. Assoc. U.K. 59: 95-110.

Mann, R. 1983. The role of introduced bivalve mollusc species in mariculture. J. World Maricult. Soc. 14: 546-559.

Mattox, N.T. 1950. Report on attempted introduction of the Virginia oyster, *Crassostrea virginica* into the waters off Puerto Rico. Proc. Gulf Caribb. Fish. Inst. 2: 46-47.

Mattox, N.T. 1952. Report on the attempted introduction of the Virginia oyster *Crassostrea virginica* into the waters of Puerto Rico. Proc. Gulf and Caribb. Fish. Inst. 2: 12-14.

Menzel, R.W. 1955. Some phases of the biology of *Ostrea equestris* Say and a comparison with *Crassostrea virginica* (Gmelin). Publ. Inst. Mar. Sci. Univ. Texas 4: 69-153.

Menzel, R.W. 1969. Cytotaxonomy of clams *(Mercenaria)* and oysters *(Crassostrea)*. Symposium on Mollusca, Mar. Biol. Assoc. India. Pt. 1: 75-84.

Menzel, R.W. 1971. Selective breeding in oysters, p. 81-92. *In* K.S. Price and D.R. Maurer (eds.) Artificial propagation of commercially valuable shellfish. University of Delaware, Newark, Delaware.

Mohan, J.M. 1978. Observations on the larval trematode *'Bucephalus'* sp. parasitic in the oyster, *'Crassostrea madrasensis'*. J. Invertebr. Pathol. 32(3): 381-383.

Mok, T.K. 1973. Studies on spawning and setting of the oyster in relation to seasonal environmental changes in Deep Bay, Hong Kong. Hong Kong Fish. Bull. 3: 89-101.

Mok, T.K. 1974a. Observations on the growth of the oyster *'Crassostrea gigas'* Thunberg in Deep Bay, Hong Kong. Hong Kong Fish. Bull. 4: 45-53.

Mok, T.K. 1974b. Study of the feasibility of culturing the Deep Bay oyster *Crassostrea gigas* Thunberg, in Tung Chung Bay, Hong Kong. Hong Kong Fish. Bull. 4: 55-56.

Morton, B. 1975. Pollution of Hong Kong's commercial oyster beds. Mar. Pollut. Bull. 6(8): 117-122.

Morton, B. and K.F. Shortridge. 1976. Coliform bacteria levels correlated with the tidal cycle of feeding and digestion in the Pacific oyster *(Crassostrea gigas)* cultured in Deep Bay, Hong Kong. Proc. Natl. Shellfish. Assoc. 65: 78-83.

Ng, F.O. 1979. Experimental culture of flat oyster *(Ostrea folium)* in Malaysian waters. Malay. Agric. J. 52(2): 103-113.

Ng, F.O. 1980. Occurrence of a flat oyster *Ostrea folium* in Malaysian waters. Malay. Agric. J. 52(3): 308-314.

Nickles, M. 1950. Mollusques testaces marins de la cote occidentale d'Afrique. Manuel oest Africains: 178-184.

Nickles, M. 1955. Scaphopodes et lamellibranches recoltes dans l'Quest Africain. Atlantide 3: 192-237.

Nikolic, M. and S.A. Melendez. 1968. El ostion del mangle *Crassostrea rhizophorae* guilding 1828. Esperimentos iniciales in el cultivo. Notas Sobre Investi. 6, Centro Invest. Pesq. Cuba.

Nikolic, M., A. Bosch and S.J. Alfonso-Melendez. 1976. A system for farming the mangrove oyster, *'Crassostrea rhizophorae'* Guilding. Aquaculture 9(1): 1-18.

Odum, W.E. and E.J. Heald. 1975. The detritus-based food web of an estuarine mangrove community, p. 265-286. *In* L.E. Cronin (ed.) Estuarine research, Academic Press, New York.

Olivares, P.I. 1975. El ostion japones *('Crassostrea gigas')* en Baja California. Cienc. Mar. 2(1): 58-59.

Olsson, A.A. 1961. Mollusks of the tropical eastern Pacific, Panamic-Pacific pelecypods. Paleont. Res. Inst.: 171-175.

Pearse, A.S. and G.W. Wharton. 1938. The oyster leech *'Stylochus inimicus'* Palombi associated with oysters on the coasts of Florida. Ecol. Monogr. 8: 605-655.

Pinto, L. and S. Wignarajah. 1980. Some ecological aspects of the edible oyster, *'Crassostrea cucullata'* (Born) occuring in association with mangroves in Negombo Lagoon, Sri Lanka. Hydrobiologia 69: 11-19.

Poquiz, W.M.R.N. and M.A. Rice. 1982. Oyster depuration: one answer to polluted estuaries. ICLARM Newsl. 5(3): 14.

Quayle, D.B. 1975. Tropical oyster culture—a selected bibliography. IDRC-052e. International Development Research Centre, Ottawa, Canada.

Quick, J.A. and J.G. Mackin. 1971. Oyster parasitism by *'Labyrinthomyxa marina'* in Florida. Florida Department of Natural Resources, Research Marine Laboratory Professional Paper No. 13: 1-55.

Rabesandratana, H. 1971. *'Crassostrea cucullata'* var. *'cornucopiae'* oyster beds in the extreme south of Madagascar. Tethys Supplement No. 1: 141-160.

Ranson, G. 1967. Les especies d'huitres vivants actuellement dans le monde, definies par leurs coquilles larvaires ou prodisso-conchs. Etud des collections de quelques-un de grand Musees d'Histoire Naturell. Rev. Trav. Inst. Peche Marit. 31(2): 127-199; 31(3): 205-274.

Rao, K.V. 1951. Observations on the probable effects of salinity on the spawning, development and setting of the Indian backwater oyster, *'Ostrea madrasensis'* Preston. Curr. Sci. 22: 377-378.

Rao, K.V. and K.N. Nayar. 1956. Rate of growth in spat and yearlings of the Indian backwater oyster *'Ostrea madrasensis'* Preston. Indian J. Fish. 3(2): 231-260.

Ray, H.C. 1977. Contribution to the knowledge of the molluscan fauna of Maungmagan, Lower Burma. Indian Museum, Calcutta.

Ritchie, T.P. 1977. Fiji oyster culture. Food and Agriculture Organization Report No. FI:DP FIJ/73/016/2.

Rosenfield, A. and F.G. Kern. 1978. Molluscan imports and the potential for the introduction of disease organisms. *In* R. Mann (ed.) Exotic species in mariculture. MIT Press, Cambridge, Mass.

Ruiz, J.B. 1969. Notas sobre aspectos biologicos de las ostras. Lagena 23 & 24: 48-68.

Ruiz, J.B. 1975. Variacion mensual de la composicion quimica del ostion del mangle en Laguna Las Marites (Venezuela). Bol. Inst. Oceanogr. Universidad del Oriente, Venezuela 14(1): 117-127.

Ruiz, J.B., J. Benetiz and T. Okuda. 1969. Variacion estacional de la composicion quimica del ostion, *'Crassostrea rhizophorae'* (Guilding) en la Laguna Grande y la Bahia de Mochima. Bol. Inst. Oceanogr. Universidad del Oriente, Venezuela 8(1&2): 46-52.

Saenz, B.A. 1965. El ostion antillano *Crassostrea rhizophorae* Guilding y su cultivo experimental en Cuba. Notas Sobre Invest. Pesq. 6, Centro Invest. Pesq. Cuba.

Sakuda, H.M. 1966a. Condition of American oyster *'Crassostrea virginica'* in West Loch, Pearl Harbor, Hawaii. Trans. Am. Fish. Soc. 95(4): 426-429.

Sakuda, H.M. 1966b. Reproductive cycle of American oyster *'Crassostrea virginica'* in West Loch, Pearl Harbor, Hawaii Trans. Am. Fish. Soc. 95(2): 216-218.

Salafranca, E.S. 1952. The effect of salt, vinegar and heat on the coliforms in oysters. Philipp. J. Fish. 2(1&2): 90-105.

Samuel, D. 1976. A digenic trematode infection in the edible oyster *Crassostrea madrasensis* (Preston). Indian J. Fish. 23(1/2): 379-389.

Sandison, E.E. 1966. The effect of salinity fluctuations on the life of Gryphea gasar in Lagos harbor, Nigeria. J. Anim. Ecol. 35(2): 379-389.

Saraya, A. 1982. Thailand, p. 73-78. *In* F.B. Davy and M. Graham (eds.) Bivalve culture in Asia and the Pacific. International Development Research Centre, Ottawa, Canada.

Silas, E.G., K. Alagarswami, K.A. Narahimhan, K.K. Appukuttan and P. Muthiah. 1982. India, p. 34-43. *In* F.B. Davy and M. Graham (eds.) Bivalve culture in Asia and the Pacific. Workshop Proceedings. International Development Research Centre, Ottawa, Canada.

Sinderman, C. 1974. Oyster mortalities and their control, p. 349-361. *In* Food and Agriculture Organization, Conference on Aquaculture, Kyoto, Japan.

Singaraja, K.V. 1980a. Some observations on spat settlement, growth rate, gonad development and spawning of a large Brazilian oyster. Proc. Natl. Shellfish. Assoc. 70(2): 190-200.

Singaraja, K.V. 1980b. On the taxonomy, ecology and physiology of a giant oyster, *Crassostrea paraibanensis*, new species. Bull. Mar. Sci. 30(4): 833-841.

Skeel, M.E. 1979. Shell-boring worms (Spionidae: Polychaeta) infecting cultivated oysters in Australia. Proc. World Maricult. Soc. 10: 529-533.

Steidinger, K.A., L.S. Tester and F.J.R. Taylor. 1980. A redescription of *Pyrodinium bahamense* var. *compressa* (Böhm) stat. nov. from Pacific red tides. Phycologia 19(4): 329-334.

Stenzel, H.B. 1971. Oysters. *In* K.K. Moore (ed.) Treatise on invertebrate paleontology. Part N, vol. 3. Mollusca 6. Geol. America Inc. and the University of Kansas, Boulder, Colorado USA.

Stephen, D. 1980. The reproductive biology of the Indian oyster, *Crassostrea madrasensis* (Preston) I. Gametogenic pattern and salinity. Aquaculture 21: 139-146.

Sunderlin, J.B., W. Tobias and O.A. Roels. 1976. Growth of the European oyster, *Ostrea edulis* Linne in the St. Croix artificial upwelling mariculture system and in natural waters. Proc. Natl. Shellfish. Assoc. 65: 43-48.

Sung, K.K. 1976. Growth of transplanted Pacific oyster, *Crassostrea gigas*. Bull. Natl. Fish. Univ. Busan 16(2): 42-48.

Telosa, R.T. 1979. Ferrocement bouys for mussel culture. J. Ferrocement 9(3): 129-133.

Thomson, J.M. 1954. The genera of oysters and the Australian species. Aust. J. Mar. Freshwat. Res. 5: 132-168.

Tufts, D. and J.P. McVey. 1975. MS. Offbottom culture of *Crassostrea gigas* (Thunberg) in Palau, Western Caroline Islands. Micronesian Mariculture Demonstration Center.

Virabhadra, R. and K.N. Nayar. 1956. Rate of growth of spat and yearlings of the Indian Backwater oyster, *Ostrea madrasensis* Preston. Indian J. Fish. 3(2): 231-260.

Wakiya, Y. 1929. Japanese food oysters. Jap. J. Zool. 2(1): 359-367.

Watters, K.W. and P.A. Martinez. 1976. A method for the cultivation of the mangrove oyster in Puerto Rico. Agric. Fish. Contrib. Dept. of Agric. Commonwealth of Puerto Rico.

Watters, K.W. and T.E. Prinslow. 1975. Culture of the mangrove oyster *Crassostrea rhizophorae* Guilding, in Puerto Rico. Proc. World Maricult. Soc. 6: 221-233.

Wedler, E. 1970. Experimental spat collecting and growing of the oyster *Crassostrea rhizophorae* Guilding in the Cienaga Grande de Santa Marta, Columbia. Aquaculture 21: 251-259.

Westley, R.E. 1968. Relation of hydrography and *Crassostrea gigas* setting in Dabob Bay, Washington. Proc. Natl. Shellfish Assoc. 58: 42-45.

Yao, S.K. and H.Y. Ryu. 1982. The growth of Pacific oyster *Crassostrea gigas* transplanted into Ambang Bay in Malaysia. Bull. Korean Fish. Soc. 15(1): 42-46.

Young, A. and E. Serna. 1982. Philippines, p. 55-68. *In* F.B. Davy and M. Graham (eds.) Bivalve culture in Asia and the Pacific. Workshop Proceedings, Singapore. International Development Research Centre, Ottawa, Canada.

White, A.L., M. Anraku and Hooi K-K., editors. 1984. Toxic red tides and shellfish toxicity in Southeast Asia. Southeast Asian Fisheries Development Center, Bangkok, Thailand and International Development Research Centre, Ottawa, Canada.

OTHER TITLES IN THIS SERIES:

- Theory and management of tropical multispecies stocks: a review, with emphasis on the Southeast Asian demersal fisheries. D. Pauly. 1979. Reprinted 1983. ICLARM Studies and Reviews 1, 35 p.
- A research framework for traditional fisheries. I.R. Smith. 1979. Reprinted 1983. ICLARM Studies and Reviews 2, 40 p.
- Review of breeding and propagation techniques for grey mullet, *Mugil cephalus* L. C.E. Nash and Z.H. Shehadeh, Editors. 1980. ICLARM Studies and Reviews 3, 87 p.
- Philippine municipal fisheries: a review of resources, technology and socioeconomics. I.R. Smith, M.Y. Puzon and C.N. Vidal-Libunao. 1980. Reprinted 1981, 1983. ICLARM Studies and Reviews 4, 87 p.
- Food potential of aquatic macrophytes. P. Edwards. 1980. ICLARM Studies and Reviews 5, 51 p.
- Applied genetics of tilapias. G.W. Wohlfarth and G. Hulata. Second edition, 1983. ICLARM Studies and Reviews 6, 26 p.
- Caribbean coral reef fishery resources. J.L. Munro, Editor. 1983. ICLARM Studies and Reviews 7, 276 p.
- Fish population dynamics in tropical waters: a manual for use with programmable calculators. D. Pauly. 1984. ICLARM Studies and Reviews 8, 325 p.
- Indonesian marine capture fisheries. C. Bailey, A. Dwiponggo and F. Maharudin. 1986. ICLARM Studies and Reviews 10.
- A hatchery manual for the common, Chinese and Indian major carps. V.G. Jhingran and R.S.V. Pullin. 1985. ICLARM Studies and Reviews 11, 191 p.
- The biology and culture of marine bivalve molluscs of the genus *Anadara*. M.J. Broom. 1985. ICLARM Studies and Reviews 12, 37 p.

Write to the Editor, ICLARM, MC P.O. Box 1501, Makati, Metro Manila, Philippines for ordering information.

INTERNATIONAL CENTER FOR LIVING AQUATIC RESOURCES MANAGEMENT

The International Center for Living Aquatic Resources Management (ICLARM) is an autonomous, nonprofit, international scientific and technical center which has been organized to conduct, stimulate and accelerate research on all aspects of fisheries and other living aquatic resources.

The Center was incorporated in Manila on 20 January 1977 and its operational base was established in Manila in March 1977. The interests of ICLARM are primarily in tropical, developing countries worldwide.

ICLARM is an operational organization, not a granting or funding entity. Its program of work is aimed to resolve critical technical and socioeconomic constraints to increased production, improved resource management and equitable distribution of benefits in economically developing countries. It pursues these objectives in the fields of aquaculture, traditional fisheries and resource assessment and management through cooperative research with institutions in developing and developed countries. The Center also has active education and training and information programs.

Policies are set by a Board of Trustees with members drawn from the international community. Direction of ICLARM, under the policies set by the Board, is the responsibility of the Director General.

The ICLARM core staff consists of internationally recruited scientists drawn from diverse disciplines in the biological and social sciences. In addition, provision is made for interns, consultants and visiting fellows, contributing to breadth of competence and flexibility. The core program and core staff are supported by private foundations and governments.