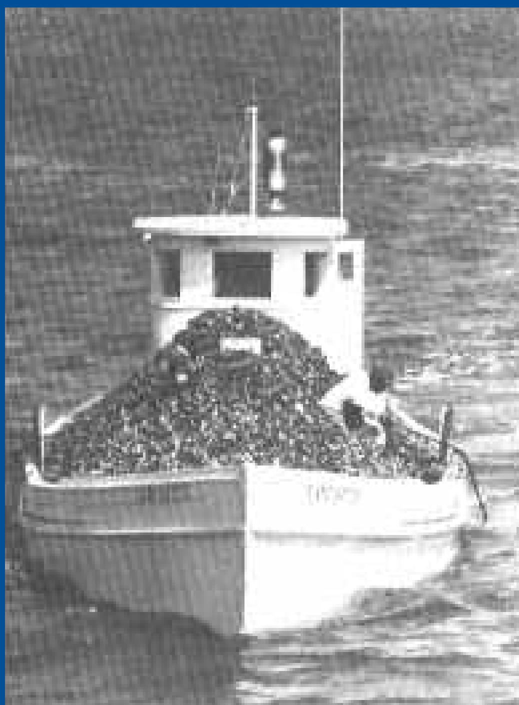
Maryland's Oysters Research and Management

By Victor S. Kennedy and Linda L. Breisch



A Maryland Sea Grant Publication
University of Maryland
College Park

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Contents

ILLUSTRATION AND PHOTO CREDITS

Page	
cover	top left photo: R. DeGast. top right, bottom photo: Skip Brown, Maryland Sea Grant Program.
xx,166,174,230	Skip Brown.
68	Photomicrograph by A.L. Zachary.
88,89,90,91,92	Lippson, A.J. The Chesapeake Bay in Maryland: An Atlas of Natural Resources.
94	Churchill, E.P., Jr. The Oyster and the Oyster Industry of the Atlantic and Gulf States.
98	R. DeGast.
102	Burgess, R.H. This was Chesapeake Bay. Cornell Maritime Press, Inc. Cambridge, MD. pg. 136.
112	Map of Chesapeake Bay prepared by S. Harpe.
145	top, bottom photo: Skip Brown. middle photo: Al Daneggar.
149	Sieling, F.W. Maryland's Commercial Fishing Gears. II. The Oyster Gears.
154	M.W. Fincham, Maryland Sea Grant Program.

LIST OF FIGURES

Preface

This critical review, Maryland's Oysters: Research and Management, is intended for fishery resource managers, researchers and students of marine biology. It joins a previous publication, *A Selected Bibliography of Worldwide Oyster Literature*, a comprehensive bibliography of the literature on the biology and ecology of oysters including the eastern oyster, *Crassostrea virginica*.

The goal of this series is improved planning both for research on the biology and ecology of the eastern oyster and for management of the oyster fishery of the Chesapeake Bay. Resource managers need an up-to-date review of the existing literature to make the most effective decisions on issues such as catch limits, sustainable yields, harvesting techniques, fishing season dates, shell planting and seed planting. Researchers and research managers need a current overview that illuminates the crucial questions remaining to be answered in order to achieve a more complete understanding of the species and to improve management of this valuable commercial fishery. Though thousands of published papers and dozens of books describe one or two aspects of oyster biology and ecology, only a few publications have tried to synthesize this extensive literature into an overall, analytical examination of the species. Since Korringa's review was published in 1952, only partial reviews of selected aspects of oyster biology have appeared. Recognizing the need for a current bibliography and review, the University of Maryland Sea Grant Program and the Tidewater Administration of the Maryland Department of Natural Resources decided to cosponsor this series of publications.

Our review considers the eastern oyster and its fishery in some depth, emphasizing the Maryland resource. We consider the biology and ecology of the oyster, with a view to delineating those areas of uncertain knowledge which require further research. We then trace the historical decline of the Maryland fishery and, in so doing, discover that environmental factors alone have not been the only cause of this decline. Sociological and political factors have been significant as well. We describe Maryland's oyster grounds and discuss current management of the oyster fishery in Maryland. At the end of the report, there is an annotated bibliography of references to research on Chesapeake Bay populations of *C. virginica* and important associated organisms.

In general, this review considers mainly those reports that deal with the Chesapeake Bay oyster and the industry it supports. However, because no research is accomplished in an information vacuum, we refer to work performed elsewhere when its insights prove valuable.

During the preparation of this review, it became obvious to us that solid groundwork had been laid in earlier, comprehensive reviews of the literature. There is no need to reiterate this material in detail. Thus, the following publications provide extensive background material that our review seeks either to supplement or to apply to the special case of Chesapeake Bay oysters:

1. Recent Advances in Oyster Biology. P. Korringa. 1952. Quart. Rev. Biol. 27: 266-308; 339-365. An extensive review of the biology of oysters of the genera *Crassostrea* and *Ostrea*.

2. The American Oyster *Crassostrea virginica* Gmelin. P. S. Galtsoff. 1964. Fish. Bull. 64: 1-480. A detailed and important text, strong in anatomy and physiology, but with only limited discussion of ecology.

3. Oysters. H. B. Stenzel. 1971. Treatise on Invertebrate Paleontology, N3(6)) Bivalvia, pp. N953-N1224. A detailed description of oysters, emphasizing phylogeny and paleontology.

4. Speciation in Living Oysters. M. Ahmed. 1975. Adv. Mar. Biol. 13:357-397. Considers aspects of oyster taxonomy, speciation, and genetics.

5. Farming the Cupped Oysters of the Genus *Crassostrea*. P. Korringa. 1976. Elsevier, New York. 224 pp. A review of oyster culture.

6. Manual for Design and Operation of an Oyster Seed Hatchery. J. L. Dupuy, N. T. Windsor and C. E. Sutton. 1977. VIMS Spec. Sci. Rep. No. 142. 111 pp. A *vade mecum* for oyster hatcheries, developed from work in Chesapeake Bay.

7. Diseases of Oysters. V. Sprague. 1971. Ann. Rev. Microbiol. 25: 211-230. A general review of oyster pathology studies, with recommendations for future work.

8. Disease Diagnosis and Control in North-American Marine Aquaculture. C. Sindermann (ed.). 1977. Elsevier, New York. 330 pp. A summary of information on diseases and their control.

9. The Oyster Industry of Virginia: Its Status, Problems and Promise. A Comprehensive Study of the Oyster Industry in Virginia. Haven, D. S.,

W. J. Hargis, Jr. and P. C. Kendall. 1978. Va. Inst. Mar. Sci., Spec. Pap. Mar. Sci. 4: 1-1024. A detailed study of factors influencing oyster production in Virginia.

Access to these materials should provide resource managers with most of the information necessary for directing research, supporting oyster culture, and managing the oyster resource in the Bay. Our review addresses matters specific to the Bay oyster resource in general and to Maryland oyster populations in particular.

V.S.K.
L.L.B.

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The following people read sections of the review and provided helpful comments: Brian Bradley, Dave Cargo, Gene Cronin, Elgin Dunnington, James Engle, Roger Newell, Gary Newkirk, Sally Otto, Fred Sieling and Chris Valenti. George Krantz has provided helpful information and insight during numerous discussions of Maryland oyster biology over the past few years. Dan Levine developed the photomicrographs of gonad tissue. We are grateful to the University of Maryland Sea Grant Program and the Maryland Department of Natural Resources for financial support during the production of this review.

Introduction

In the Chesapeake Bay, one of the world's most fertile food-bearing estuaries, the American oyster (*Crassostrea virginica*) remains the most valuable seafood crop. And the most controversial.

Over the last century, the history of that fishery in Maryland shows a record of booms and slumps and partial recoveries. Harvests that averaged more than 10 million bushels a year during the late 19th century have averaged 2 to 3 million bushels a year during this century. Even at those levels, the contemporary fishery helps support 4,000 watermen who dredge and tong oysters out of the northern bay from early fall through late winter. In most years, their work brings in more than $15 million a year in dockside sales and generates another $30 million for the state's economy through shucking, packing, shipping, and selling. The oyster harvest outranks all other Maryland seafood catches combined, including crabs, clams, menhaden, striped bass, bluefish, white perch, and a dozen other species regularly fished from the Bay.

At present, hand tongers, patent tongers, and dredgers take oysters off nearly 1,000 public oyster bars spread over 215,000 underwater acres. Most watermen work as hand tongers, using long, lowsided tongboats equipped with a small cabin forward and an open cockpit aft for dumping and culling each day's catch. They spend their days at hard, physical labor, anchored over bars where they wrestle oysters up from the bottom with long, wooden-shafted tongs tipped with metal rakes for scooping oysters. A growing number of watermen have equipped their boats with patent-tonging rigs that feature power-driven winches; a small number have even taken to the water in scuba diving gear. Only a handful of watermen still sail their skipjacks. These graceful, wide-beamed sailboats—perhaps 30 are left—are the last survivors of a commercial sailing fleet that once numbered in the hundreds.

During the last two decades, the oyster fishery has changed from a "wild harvest" controlled only by natural cycles to a "put-and-take" harvest dependent in part on human efforts to replenish the oyster supply. On the public fishing grounds, state management officials now organize a major seed and shell planting program every spring, an effort that helps offset erratic sets of new oysters. On private fishing grounds, a few oystermen now lease Bay bottom and plant seed and shell to farm their own oysters. During the next two decades the fishery may change again, with more small oyster farms starting up outside the public fishing grounds now worked by watermen in skipjacks and tongboats and scuba diving suits.

For the Maryland fishery, however, nearly all change stirs controversy. When harvests decline, when oyster divers begin using scuba gear, when resource managers alter seeding plans, when oyster leasing increases, watermen and scientists and fishery managers begin arguing about the causes and effects, the costs and benefits of change. The history of the Maryland fishery, then, is a record of abundance and decline, of evolution and controversy. It is also a record of increased research and management efforts to understand those declines and to replenish those harvests.

Out of those efforts, a considerable body of knowledge about the biology of *Crassostrea virginica* and about the management of that species in the northern Chesapeake has developed — albeit in somewhat disorganized form. Most of the biological articles are scattered in dozens of scientific journals; much of the crucial management information is scattered in the "grey literature" of technical reports, administrative memoranda, and annual summaries long buried in office files or university archives.

In this book, biologists Vic Kennedy and Linda Breisch sketch that history and review that scientific and technical literature. Their goal in developing this publication was to assist current research and management efforts designed to improve our understanding of this species and to sustain a fishery that so many Marylanders have depended on for so long.

There are lessons, painful and positive, in all that history, research, and management. In tracing the record of the Chesapeake oyster fishery, the authors found sobering examples of overfishing, poor conservation, and environmental degradation. They also found encouraging evidence on the resilience of the oyster and the ecosystem, on the positive effects of active oyster management, on the potential for increased harvest in the future.

In their history of the early fishery, four themes recur:

1. **The decline of the early fishery was predominantly a result of overfishing and ineffectual conservation efforts.**

The Maryland oyster harvest began thousands of years ago with the Indians who roamed the Bayshore on foot and by canoe, before vanishing about two hundred years ago, leaving little but Indian names to mark the rivers and great piles of oyster shells to mark the sites of their ancient villages. Among the colonists who came after, a major commercial fishery developed late, and only after Connecticut watermen early in the 19th century began dredging the northern Chesapeake for seed oysters to replenish their own overfished waters. When railroads and refrigeration made oysters a favored food in fashionable, big city restaurants, Marylanders began taking their most plentiful shellfish seriously. Watermen began building boats and buying dredges, and legislators began passing laws keeping Maryland oysters for Maryland residents.

In the post-war prosperity of the 1870's the demand for oysters soon outraced the supply, pumping up prices and profits, turning Bayshore villages into boomtowns, and sparking battles between Marylanders and Virginians, tongers and dredgers, oystermen and the Oyster Police. From 1870 to 1900, Maryland watermen sailing slant-masted log canoes, pungys, bugeyes, and skipjacks dredged and tonged oysters out of the Maryland Chesapeake at better than 10 million bushels a year. In 1875, they hauled home 14 million bushels; in 1885, 15 million. The Chesapeake Bay, in good years, was producing more meat than all the cattle farms of Maryland, Delaware, and Virginia. The great oyster hunt was on.

Watermen went out in small boats, in log canoes, in anything that could float. The hunt, according to one observer, was "simply a scramble," carried on with "regard neither for the laws of God or man," with tongers battling dredgers and both battling the Oyster Police—a scramble complete with night poaching, daylight rustling, running gun battles, and massive overfishing of the oyster grounds.

Those boom times faded with the century. The catch records of the 20th century show a sharp drop during the first decades, followed by a long decline during which the annual harvest averaged only 2.5 million bushels over half a century. The heydays of the wild harvest were over.

2. Political considerations, rather than limited biological knowledge, have frequently hampered efforts to improve fishery management.

Inspired by the huge harvests and sudden declines of the late 19th century, by the smaller booms and slumps and recoveries of the 20th century, the Maryland General Assembly has periodically established different commissions and boards and departments, stocked them with scientists and resource managers, and instructed them to oversee management of the resource and its harvesters. Over the last century, however, legislators in the General Assembly have always exerted the major influence on regulation of the fishery, ignoring in many cases the recommendations of the boards and commissions and departments they established. Naturally sensitive to the immediate concerns of watermen and seafood processors, legislators have passed many laws affecting management of the oyster resource which have little basis in biological or economic reality.

Wise management of any resource, stress the authors, depends upon close links between gathering information through laboratory and field study and applying the information to management questions. It also depends upon a supportive socio-political structure that leaves management to an informed group of managers.

3. The key management steps that have helped sustain the public fishing grounds have been: conserving available shell stock for replanting as cultch, protecting spat through cull laws, and expanding and protecting natural seed areas.

The early efforts to manage a wild but endangered fishery included the 1890 cull law that required watermen to throw back undersized oysters and shells with spat and young oysters. Throwing back the small oyster expanded the potential brood stock; throwing back the shell also provided a better base or cultch for the setting of new oysters. Later harvest declines during this century inspired laws requiring shucking houses to make 10 percent of their shucked shell available for replanting as cultch. The shell tax later grew to 20 percent, then 50 percent of available shell, before dropping to 25 percent—the current level.

The oyster seed for the current planting program comes in the form of shell dotted with young oyster spat. Watermen dredge these off the bottom of the state's 1,200 off-limits seed acres for replanting along public fishing grounds. Those new oysters reach market size two to three years later.

Fresh shell for the program comes from local shucking houses; old shell is dredged up from beneath the sediments covering long-abandoned oyster beds. Planted along the seed grounds and along the public fishing grounds, all this shell forms a clean, hard cultch for oyster larvae to settle on during the summer spawning season. These newly set oysters will grow to market size three to five years later. In a very literal way, this planting program helps lay the foundation for future harvests.

In recent decades shell planting and seed planting proved their effectiveness dramatically. When heavy fishing and disease drove harvests down to 1.6 million bushels during the mid 1960's, the Maryland Department of Chesapeake Bay Affairs stepped up seeding and shell plantings. boosting harvests to a 10-year average of 2.7 million bushels a year from 1966 to 1975. Those same efforts, though diminished in recent years because of rising costs, have helped sustain harvests above 2 million bushels, despite a decade and a half of poor natural reproduction.

What now threatens the oyster harvest and the way of life it supports is a series of oyster reproductive failures that could negate the oyster repletion effort and extend the fishery's historical decline. After significantly poor natural sets of new oysters in 1966, 1967, 1970, and 1971, Tropical Storm Agnes struck the Bay in 1972, causing enormous freshwater run-off, silting up oyster beds in the northern waters and diluting salinities. From 1965 through 1976, natural oyster reproduction was 72 percent lower than the average rates for the previous 27 years. If the supply of new oysters is not replenished soon, either by nature or by man, and if watermen continue to fish off the remaining oysters, the Bay harvest will soon decline again as it did during the early decades of this century.

4. Private oyster culture should have the stimulating effect here that it has had elsewhere. It should help revitalize the industry and increase yield and economic benefit for all involved.

By 1906, when the oyster harvest was down to 4.5 million bushels, leasing—first legalized in 1830—was tried on a large, half-hearted scale. The legislature commissioned a thorough survey of Maryland's oyster beds, and watermen began signing up for plots. Most of them, however, kept fishing the public bars while they waited to see if anyone else could learn how to plant and grow oysters successfully.

In the contemporary fishery many watermen continue to oppose private leasing, fearing eventual control of the fishery by large corporations rather than by independent, self-employed watermen. As a result less than 10,000 acres are currently leased; many of those leased areas are not under active cultivation; and a moratorium on new leases has been established by the state legislature, pending completion of a new survey of the state's oyster beds. The few planters who actively cultivate their leases with shell and seed oysters produce more bushels per acre than do watermen fishing the public bars.

Their current production, however, stands well below what would be possible under active oyster farming similar to what now works in countries like France, Holland, and Japan, in other states like Oregon, or in other estuaries like Long Island Sound. From this review of the aquaculture literature it is clear that effective farming techniques are being developed and that the natural environment in many parts of the northern Bay is ideal for this form of animal husbandry.

Managing Maryland's public fishing grounds can also be called a form of farming. And it requires the kind of detailed technical information now applied so successfully on most American farms. Most farmers now working the land rely on an immense amount of information about soil conditions and carrying capacity, about crop rotations and growth rates and nutrient needs, about fertilizers and herbicides and pesticides, about resistance to disease and response to genetic manipulations.

Most fishery managers, however, have much less to work with. As this review makes clear, a core of useful information is available and applicable to many of the major management issues—indeed, some of that information has been available for several decades. But the kind of precise management that could adjust strategies to different conditions in different parts of the estuary must draw on much more detailed information on dozens of key questions.

For our current understanding of oyster biology, say the authors, the areas of greatest ignorance concern: (1) the biology and behavior of oyster larvae while they float and feed in the water between spawning and spat set; (2) the food needs for those larvae and for juveniles and adults, and the food sources now available around the estuary; (3) oyster genetics, an infant science that may hold the key to breeding healthier, faster-growing oysters; (4) disease among natural and hatchery-spawned populations; and (5) the effect of pollutants—especially chlorine, heavy metals, and petrochemicals—on all stages of oyster growth. Our understanding of these issues ranges from primitive to poor.

For many of the environmental factors affecting oyster productivity we know a little more; our understanding ranges from poor to almost adequate—adequate, at least, for status quo management. To boost harvests, however, fishery managers need more detailed information about the oyster's habitat, especially about: (1) the health, location, and abundance of brood stock in the Bay; (2) the best sources and best uses of seed oysters, fresh shell, and dredged shell; and (3) the best bottom areas for spat settlement and for spat growth and reproduction.

If oyster managing is a form of farming, if Maryland's oyster fishery is ever to blossom as richly as its land farms have over the last half century, then resource managers will need the kind of detailed biological and technical bonanza that came out of this country's massive investment in agricultural research.

The immense agricultural productivity of recent decades arrived slowly. It followed an era of overfarming for tobacco, depleted soil conditions, and ineffectual cultivation, an era that forced a westward migration for many 19th century Marylanders and inspired during the depth of the Civil War the federal creation of this country's land grant college system. Year by year, experiment by experiment, decade by decade, those land grant colleges and the experimental farms established on them built an information base that created and still supports our current agricultural abundance.

The historical decline of the Maryland oyster fishery, then, has clear parallels in recent agricultural history, and those parallels support a qualified optimism about the future of the fishery. If research efforts continue, if they focus on the key questions important to management, if current management programs can achieve greater freedom from political restraints than their predecessors did, if cheaper sources of seed oysters can be developed, if private farming can succeed—then Maryland's oyster harvests may recover as dramatically as did its agricultural harvests.

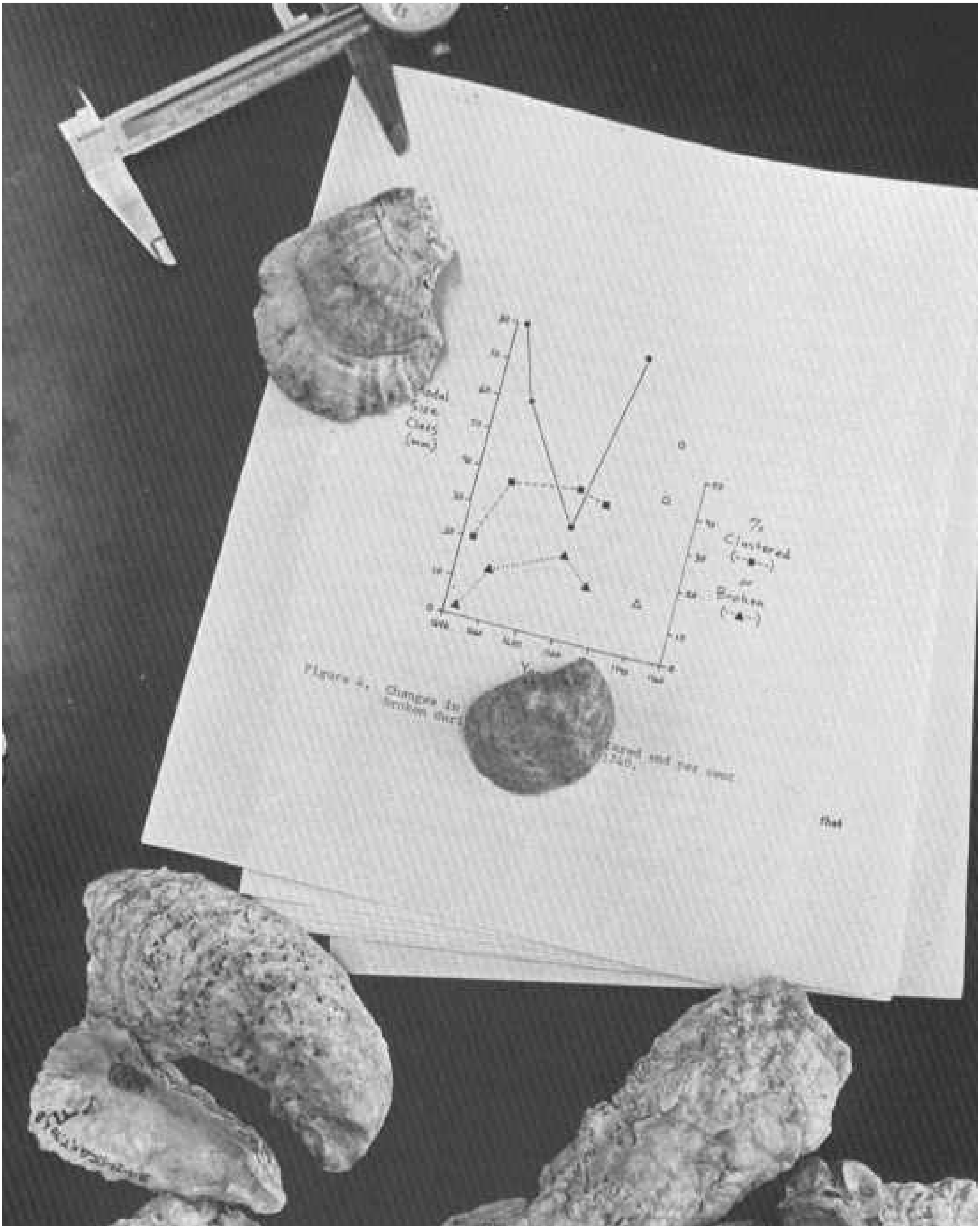
A better basis for optimism—again a qualified optimism—comes from the present, not the past. It comes from some of the findings of this review and from some of the recent behavior of the Chesapeake ecosystem. In reviewing the research records, the authors found evidence the oyster is a resilient animal, able so far to withstand heavy fishing pressures and large environmental variations without passing its "breaking point" as a viable commercial species. They also found that oyster management efforts, especially seed planting, can help sustain the fishery during periods of poor reproduction and that many oyster researchers still believe careful cultivation of the public fishing grounds and the growth of private farming could combine to increase the state's annual oyster harvest several fold.

The best reason for optimism comes from the Chesapeake itself, from the rich productivity and strong recuperative powers of this large, crowded estuary. In 1980, after 15 years of poor sets of new oysters, the Chesapeake Bay responded with one of the best crops of new oysters in the last 40 years. In 1981, it nearly duplicated that crop.

The Bay, despite depredations by humans and hurricanes, remains an impressive oyster growing ground. In many areas, it still has the temperatures, tidal circulations, and salinity levels that help spawning and growth. In most areas, it has shallow waters that help sunlight work on bacteria, detritus and plankton to build fertile food chains. The Bay retains such rich potential for oysters, in fact, that the well-managed harvests of the future could one day resemble the “wild harvests” of the past.

M. W. Fincham
Editor

Biology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It's a wery remarkable circumstance, sir," said Sam, "that poverty and oysters always seems to go together."

"I don't understand, Sam," said Mr. Pickwick.

"What I mean, sir," said Sam, "is, that the poorer a place is, the greater call there seems to be for oysters. Look here, sir; here's a oyster stall to every half-dozen houses. The streets lined vith 'em. Blessed if I don't think that ven a man's wery poor, he rushes out of his lodgings and eats oysters in reg'lar desperation."

—Pickwick Papers, C. Dickens (1836)

Biology of the Oyster

Sam Weller was speaking of the flat oyster (*Ostrea edulis*) and the poor in England. At that time, about 500 million oysters were sold at Billingsgate every year, resulting in a cheap and readily available foodstuff (Gross and Smyth 1946). However, the production of the fishery declined throughout Europe until the oyster became too expensive for the poor. Eventually, flat oysters were maintained mainly by culture in areas representing only a portion of their former range. In discussing this decline, Gross and Smyth (1946) felt that two major and interrelated causes for the decline were (1) overfishing and (2) the resultant consequence of a severely reduced population of oysters. Briefly, unrestrained fishing led to a severe reduction of oyster populations, the loss of young and immature oysters, and destruction of oyster beds. The decline was exacerbated by pollution. Cultivation of beds was initiated, but the resource remained depleted. Although a variety of factors were implicated in this lack of response to cultivation, Gross and Smyth (1946) felt that, because flat oyster populations had been depleted so greatly, they were thus much less resilient to various adverse environmental factors. They postulated that the flat oyster populations had been so ravaged as to fall below a critical minimum, with the trend towards extinction continuing even after the fishing mortality was lessened.

It is not clear if the eastern oyster would be similarly susceptible to overfishing and environmental degradation. Though there is still much cause for concern, we believe that the Chesapeake Bay oyster resource might be more resilient. But that resilience, we also believe, depends on effective management strategies. We are convinced that the best management of any natural resource occurs when there is linkage between gathering of information by field or laboratory study and subsequent application of this information in resource management. Optimal management depends upon thorough understanding of the biology of the resource. We begin, then, with a general outline of oyster biology, emphasizing *Crassostrea virginica* and noting those areas requiring further research. Unless otherwise indicated, the word "oyster" refers to *Crassostrea virginica*.

This section of the review considers the general biology and ecology of the eastern oyster, *Crassostrea virginica*, with comparative information for other species provided on occasion. Some aspects of oyster biology (e.g., genetics, effects of heavy metals) which have recently been reviewed elsewhere are dealt with briefly to avoid unnecessary repetition. Those matters which bear further investigation, either for academic interest or because of their practical (applied) importance, are so indicated. During the review, the reader should remember that reports of oyster performance under certain environmental conditions may reflect only the response of the local population being studied. It is possible that such responses might have been different if oysters from more northerly or southerly populations, or from different conditions of salinity, turbidity, etc., had been studied. Eastern oysters generally inhabit dynamic estuarine environments and are broadly eurytopic. Thus, that which holds for oysters taken from one environment and tested under controlled laboratory conditions may not hold for oysters from a different environment. Indeed, the topic of physiological adaptations of oysters throughout their broad distributional range has only been investigated cursorily and might be a productive area for further research.

ENVIRONMENTAL FACTORS

Temperature

Oysters are ectotherms (poikilotherms), ranging in distribution from the Gulf of St. Lawrence in Canada to the Gulf of Mexico and the West Indies (Abbott 1975). Thus they are probably subject to a temperature range of about 0°C or slightly below to about 36°C, although oysters exposed in air at low tide in southern regions have attained body temperatures of 46°-49°C (Galtsoff 1964). Copeland and Hoese (1966) reported apparent high-temperature-related mortality of intertidal oysters in central Texas.

Crassostrea virginica has a maximum rate of ciliary activity of about 25°-26°C. Above 32°C, ciliary activity is disrupted, whereas feeding may cease below 6°-7°C (Galtsoff 1964, but see Loosanoff 1958 below). Nelson (1928a) demonstrated that in New Jersey waters ciliary activity and shell opening virtually ceased below 5.6°C. Heartbeat activity is also temperature dependent (Fen" 1965), with frequency of beat highest at 24°C, declining steadily until reaching 10°C. Collier (1954) recorded shell movement and pumping rate of 66 oysters over long periods of time (from 3-24 weeks) and related his findings to temperature. He concluded that *C. virginica* is fundamentally a cool-water animal with an optimum temperature range for pumping, growth, and survival of 15° to 25°C.

Loosanoff (1958) studied oyster behavior at different temperatures. Some oysters from Long Island Sound pumped at temperatures as low as 1°C. Fifteen percent of those held between 2°-3°C and 50% of those held between 3°-4°C formed pseudofeces. However pumping rates were low below 8°C, increasing as temperatures rose to 16°C and maintaining a fairly constant rate between 16° and 28°C. There was a further rate increase as temperature rose to 32°C, with the rate dropping at temperatures above 34°C. A maximum pumping rate of 37,500 cc h^{-1} occurred at 24°C. Loosanoff noted that oysters were able to adjust rapidly to temperature change.

Given the differences in temperature effects on ciliary activity, pumping and feeding noted by different authors, it is possible that oysters in different parts of their range have different environmental tolerances.

Effects of elevated temperatures have been studied with regard to shell deposition, gonadal development, and biochemical constituents of oyster bodies (Ruddy et al. 1975). Oysters grown in the warm-water effluent of a power plant (temperatures ranged from 7.0 to 12.4°C higher than ambient) produced thicker shells and developed gonad four months earlier than did control oysters held near the power plant intake. In spite of the accelerated gonadal ripening, spawning occurred just one month earlier among the oysters in the heated effluent. In winter and spring, oysters in the effluent had higher concentrations of protein and carbohydrate and a higher condition index than did the control oysters. In summer, there was no difference in condition index or protein and carbohydrate concentrations between the experimental and control groups, although in some cases in late summer, control oysters were slightly superior to experimental oysters in these measures. This could indicate that the artificial elevation of temperature over summer extreme temperatures might be unfavorable (see also Quick 1971).

With regard to reproduction, as temperature increases in spring, gametogenesis accelerates, resulting in development and maturation of sperm and eggs and thickening of gonadal epithelium (Kennedy and Battle 1964). Spawning of ripe gonads may be initiated as a result of a rapid rise in temperature (but see section on Reproduction). The spawning of oysters in hatcheries and laboratories both out-of-season and in-season depends on this reaction to temperature increase (Loosanoff and Davis 1963). In cool northern waters, the reproductive season is truncated; it may last only a few weeks. In warm southern waters, spawning may be spread out over most of the year. This subject is discussed more completely in the section on Reproduction.

Temperatures lethal to oysters were determined by Henderson (1929) and Fingerman and Fairbanks (1957), but their experimental procedures did not produce data that were ecologically useful. No other studies on temperatures lethal to adults, or to spat, have been reported for *C. virginica*. However, some research has been done on temperature and larval survival. Hidu et al. (1974) subjected fertilized eggs, ciliated gastrulae, and two-day-old veliger larvae to temperature increases for periods from 10 seconds to 16 hours. Mortality increased with increasing temperature and exposure time. Fertilized eggs were least resistant to higher temperatures, followed by ciliated gastrulae; veliger larvae were most tolerant.

Diaz (1973) used techniques different from Hidu et al. (1974) for exposing developmental stages for five seconds to 10°, 15° and 20°C increases. He reported that mortalities 48 h after exposure were higher for older stages, but he performed no tests for statistical significance.

In nature, temperature influences larval development. For example, in Bideford River, Canada, Medcof (1939) found that the time it took oyster larvae to reach 365 µm in length depended on water temperature: 30 days at 19°, 26 days at 20°, and 24 days at 21°C. Davis and Calabrese (1964) found the temperature range for maximum growth for *C. virginica* larvae to be between 30.0 and 32.5°C at salinities ranging between 10.0 and 27.5 ppt. At 7.5 ppt, maximum growth occurred at 27.5°C. In these experiments, larvae reached setting stage in 10-12 days at 30° to 32.5°C and 36-40 days at 20°C. If larvae were reared to setting size and then transferred to lower temperatures, the percentage of successful metamorphosis declined correspondingly; however, some setting did occur at 12.5°C. Diaz (1973) noted that a five-second exposure to a 20°C increase permanently impaired larval growth, in contrast to the lack of effect of exposure to 10° and 15°C increases for five seconds.

Increased temperatures (below lethal levels) influence setting success of pediveligers. Lutz et al. (1970) found that increase in temperature from 24° to 29°C for 4 h increased the percentage of larvae that set. Setting was also influenced by the age of larvae and degree of temperature increase in Diaz' (1973) experiments. Setting values 30 days after exposure were significantly lower for larvae exposed to five-second increases of 15° and 20°C than they were for larvae exposed to 0° and 10°C increases.

Limited research into temperature effects on larval activity has been conducted. Hidu and Haskin (1978) studied swimming rates of *C. virginica* trochophores and straight-hinge and eyed veliger larvae in small experimental containers. As experimental temperatures increased from 15°C to 20°C and 25°C, swimming speeds for the larval stages generally increased, with swimming speeds of the earlier stages increasing at a greater rate than those of the older stages.

Research into larval responses to temperature (and especially to interactions with salinity) needs additional attention, in order to provide understanding of larval behavior in the field. In addition, the chronic effects of elevated temperatures (such as those around industrial waste-heat effluents) on juvenile and adult oyster condition and susceptibility to disease have not been thoroughly studied. From the point of view of aquaculture, it is important to understand the role of temperature in, for example, shell deposition, growth of body meat, efficiency of food conversion, stimulation of gametogenesis out of season, and effect on larval vigor of sublethal stress on adults. Depending upon the optimal end-point desired in raising oysters (for ease of shucking, rapid growth to market size, maximal efficiency in using food, superior gamete production, resistance to various environmental stressors, or some combination of these or other characteristics), temperature may have an important influence, either alone or (more likely) in concert with other environmental factors such as food, oxygen, salinity, or water movement. Similarly, in the field, temperature may interact synergistically with other environmental variables such as salinity, tidal exposure, food supply, oxygen availability, sediment load, current flow, and more recently, the panoply of chemicals derived from human waste disposal. Sorting out all of these interactions remains to be accomplished.

Salinity

It is characteristic of oysters of the genus *Crassostrea* to thrive in estuarine environments, although they can also tolerate marine conditions. Korringa (1957) briefly reviewed reports of the distribution of *Crassostrea* species, noting that they were euryhaline, with some found in salinities up to 44 ppt (e.g., *C. rhizophorae* in Puerto Rico). *Crassostrea margaritacea* lives in the South African intertidal zone in salinities approaching 36 ppt. *Crassostrea gigas* seed oysters grow in Mangoku-Ura inlet in Japan at 32-33 ppt. *Crassostrea madrasensis* occurs near Madras, India, at 30 ppt or more. More recently, Stephen (1980) reported *C. madrasensis* to be surviving and reproducing in an Indian estuary with an annual salinity range of 3-33 ppt.

Crassostrea virginica thrives in waters as varied as central Chesapeake Bay (mesohaline) and the higher salinities of Connecticut's Long Island Sound (28 ppt), North Carolina (30 ppt), and Texas (36 ppt). Copeland and Hoese (1966) described oyster populations in a hypersaline bay on the central Texas coast where salinities reached 43.5 ppt. They suggested that salinity values of 45 ppt were responsible for the lack of oysters in areas to the south of Corpus Christi, Texas. Castagna and Chanley (1973) reviewed a number of studies on salinity tolerance of *C. virginica*. Some important aspects of the effects of salinity are described below.

Laboratory Studies

Loosanoff (1953) undertook to answer a number of questions concerning the physiological effects of low salinity on *Crassostrea virginica*, using Long Island Sound oysters acclimated to about 27 ppt. His results are the most comprehensive to date and are presented in detail.

He found that mortality in oysters subjected to fresh water and lower salinities increased with temperature increase. Some oysters which did survive long periods in low salinity conditions (up to 115 days — presumably by remaining closed most of the time) were normal when examined histologically. However, others became emaciated and appeared to be under attack by bacteria Oysters held in low salinities often began building a second shell inside the original shell (see also section on Chemicals-Chlorine). Loosanoff found no differences in salinity tolerance among oysters of different ages, including spat.

If their bills were damaged to allow for ingress of water, oysters would press their mantles over the artificial opening. Oysters held for up to 30 days in low salinities experienced mortality similar to that of undamaged controls held in the same salinities.

Oysters could feed at levels as low as 5 ppt (such low salinity levels were tolerated if temperatures were cool) but no feeding was ever observed at 3 ppt or below. At 5 ppt, feces were composed mainly of blood cells, with the fecal ribbons thin and white or greenish in color. After extended exposure to 5 ppt, oysters seemed to adapt better and more of them fed, albeit abnormally.

The crystalline style disappeared in oysters held in low salinities. This is a sign that feeding was not occurring. Regeneration of the style occurred soon after the oysters were returned to normal salinities. In one case, after 20 days in fresh water, oysters formed a crystalline style (1 mm diameter) within an hour after being returned to normal salinity. When exposed to 3 ppt or lower, oysters retained feces and pseudofeces within their shell, presumably as a result of the shell's rarely being opened.

Little or no growth occurred at 5 ppt or less. Growth was retarded at 7 ppt but was unaffected at 12 ppt.

Using histological preparations, Loosanoff found that fresh water and 3 ppt resulted in the total inhibition of gametogenesis. At 5 ppt, gametogenesis was arrested in about 50% of the sample. The remainder of the sample exhibited depressed gametogenesis; however, males were more advanced in their development than were females. At 7.5 ppt, ripe spermatozoa and a few ripe eggs were noted, but development was retarded. At 10 ppt and 12 ppt, oysters were ripe, with some starting to spawn. In the control (at 27 ppt), most specimens began spawning during the experiment.

Oysters were held in ambient conditions and allowed to grow until the gonads began enlarging (about three weeks before the normal onset of spawning) and were then placed in lower salinities. Fresh water, 3 ppt and 5 ppt prevented further gonad development. At 5 ppt, males became more developed than did females. At 7.5 ppt, 10 ppt, and 12 ppt, normal gametogenesis proceeded, with some oysters spawning at 7.5 ppt and with more intense spawning in higher salinities.

Oysters which were just about to spawn when placed in low salinities did so at 7.5 ppt, 10 ppt and 12 ppt, but managed only feebly at 5 ppt and not at all in 3 ppt or in fresh water.

Pumping rate (method of assessment not stated) was strongly affected by sharp reductions of salinity from 27 ppt. After about six hours, these reductions were 24% at 20 ppt, 89% at 15 ppt, 91% at 10 ppt and 99.6% at 5 ppt. However, after additional exposure to the lower salinities, pumping rates began to increase somewhat.

Rapid changes from low to high salinities had little effect, with oysters opening and rapidly beginning to feed, forming a crystalline style, and expelling feces and pseudofeces.

Finally, oysters accustomed to living in lower salinities were more tolerant of the effects of even lower salinity (as measured by shell-closing behavior or by pumping behavior) than were oysters used to living in higher salinities.

A number of studies on salinity effects have been performed on oyster gill tissue. Vernberg et al. (1963) measured ciliary activity of excised, isolated gill pieces of *C. virginica* under different conditions of temperature and salinity. Tissue from warm-acclimated oysters (25°C) survived low salinities (4, 5, 6 and 9 ppt) better than did tissue from cold-acclimated oysters (10°C) when exposed for 24 or 48 hours. Ciliary activity was slowed greatly at 4 ppt and stopped at 3 ppt. Prior to experimentation, the whole oysters had been held at 30 ppt.

Van Winkle (1968, 1972) studied effects of salinity on ciliary activity and oxygen consumption of oyster gill tissue. In his initial experiments (1968), he found that oxygen consumption of tissue was relatively constant over a 5 to 30 ppt range for oysters collected from a salinity range of 25 to 30 ppt. In a later study, Van Winkle (1972) found that there was an initial inhibition of ciliary activities at experimental salinities which were appreciably different (higher or lower) from acclimation salinities. However, recovery began after about 0.5 to 2.5 h, if the differences between experimental and acclimation salinities were not too great. The lowest salinity value (7 ppt) permitting “normal” ciliary activity of gill tissue of oysters acclimated to low salinity (11-13 ppt) was close to the value determined elsewhere for “normal” activity of whole oysters. Compared with high salinities, ciliary activity at low levels decreased, whereas oxygen consumption either remained constant or increased. This would indicate that, while low salinities resulted in decreased ciliary activity and concomitant decreased oxygen consumption, intracellular ionic regulation or other low-salinity-mediated activity might increase oxygen consumption.

With regard to larval survival and growth in different salinities, Davis (1958) noted that the optimum salinity and the salinity range for development of *C. virginica* eggs to straight-hinge larvae appeared to be influenced by the salinity level experienced by the parents during gametogenesis. Thus, adult acclimation at 26.0-27.9 ppt resulted in zygotes which developed over a salinity range of 12.5-35 ppt, with an optimal development at about 22.5 ppt. Acclimation of parents to about 9 ppt resulted in zygotes which developed within a range of 7.5-22.5 ppt and optimally between 10.0-15.0 ppt. Optimal larval growth occurred at 17.5 ppt for larvae whose parents were held at 26.0-27.9 ppt. This compared with 22.5 ppt for larvae from parents held at about 9 ppt (based on one experiment only). Thus it is not clear how parental acclimation salinity affects larval growth.

Using older larvae (165 µm long) from parents acclimated to 26.0-27.0 ppt, Davis (1958) found good growth at 12.5, 15.0, and 17.5 ppt and in the controls (26.0-27.0 ppt). At 10 ppt, growth was half as good as that in the controls; at 7.5 ppt, it was one-quarter. Setting was good at 12.5, 15.0, and 17.5 ppt. A few spat set at 10.0 ppt, but at 7.5 ppt no larvae survived to metamorphosis (contrarily, Prytherch (1934) found that *C. virginica* larvae would metamorphose at 5.6 ppt). No experiments were made with larvae from parents held in low salinity conditions.

Based on this research, Davis (1958) speculated that oyster populations in areas with salinities below 10 ppt may depend on the influx of nearly full-grown larvae from higher salinity areas, which would then proceed to set in the lower salinity environment. Although no data have been collected on survival and growth for low-salinity progeny, Davis's speculation may need to be considered in central and upper Chesapeake Bay. Eastern Bay and the lower Choptank River are the northernmost regions with consistently good spat settlement success. Both have salinities generally above 10 ppt during the spat settlement period, and contrast with the Chester River further up-Bay which is not self-supporting in terms of spat settlement (Engle 1948, 1956; Beaven 1951).

Chanley (1958) placed recently set spat (0.3-0.5 mm long) directly into salinities ranging from 2.5 ppt to “full salinity” (not specified) at 21°-24°. At 2.5 ppt, all spat died within two weeks; at 5 ppt, half of the sample died. Spat at 7.5 and 10.0 ppt grew slowly compared with those in higher salinities. In a second experiment, spat (1.0-1.4 mm) were transferred gradually to experimental conditions over a week. From 15.0-22.5 ppt, growth was good. It was poorer at 10.0 ppt, 12.5 ppt, and at full salinity, and poorest at 7.5 and 5.0 ppt. At 2.5 ppt, only 19% survived compared with 66% at 5 ppt and 80-100% at the remaining salinities. At 2.5 ppt. average length was shorter. Thus, spat were more resistant to salinity effects than were larvae (Chanley 1958, Davis 1958) but reacted much the same as adults (Loosanoff 1953). Larvae grew well at 12.5 ppt and higher. Spat and adults grew slowly from 5.0-12.0 ppt and grew normally from 12-27 ppt.

Salinity also affects the temperature tolerance of oyster larvae (Davis and Calabrese 1964). At all salinities tested except 7.5 ppt (i.e., l0.0, 12.5, 15.0, 17.5, 20.0, 22.5, 25.0 and 27.5 ppt), the optimum temperature for larval growth was between 30.0 and 32.5°C. At 7.5 ppt, the optimum was 27.5°C. No well-defined optimum growth salinity was delineated; growth depended upon the experimental temperature. Reduced salinities reduced the temperature range that eggs and larvae could tolerate for development and growth.

Haskin (1964) and Hidu and Haskin (1978) attempted experimental studies on salinity effects on *C. virginica* larval swimming behavior, as part of an effort to relate such behavior to field distributions of larvae in estuaries. Hidu and Haskin (1978) found that larvae responded to hourly salinity increases of 0.5 ppt by more rapid swimming activities (about three times non-directed swimming speeds). They believed that these speeds were sufficient to place larvae above the bottom, allowing them to use whatever tidal transport systems might be available (see section on Water Circulation).

Field Studies

Descriptions of deleterious effects of floodwaters on *Crassostrea virginica* can be found for a variety of locations (e.g., Alabama: May 1971, 1972; Louisiana: Van Sickle et al. 1976; Mississippi: Butler 1952; Mexico: Garcia Sandoval 1972; see review in Galtsoff 1964).

In Chesapeake Bay, the “Head of the Bay” is that section north of a line drawn from Sandy Point, Maryland, to the Chester River. It is a region of wide seasonal and annual fluctuations in salinity. These fluctuations are the result of variations in stream-flow from the enormous watershed of the Susquehanna River (Beaven 1947). At one time, a number of oyster bars were found in this region, extending as far north as 39°l9’N (Beaven 1947, Meritt 1977). Few of those beds are still able to produce oysters, in part because low salinities inhibit recruitment.

From 1944 to 1946 graphic examples of the effects of low salinities on oyster populations in this region occurred (Engle 1947). Salinity decreased from 10 ppt in February 1944 to fresh water by May, increasing again to 15 ppt by October. This resulted in slight retardation of gonad development and no larval settlement. However, adult oyster growth was better than usual, perhaps because of an input of nutrients that stimulated plant growth (see section on Rainfall). Salinities of about 15 ppt persisted through February 1945. In March, a rapid, early thaw in the Susquehanna River basin lowered salinities to freshwater levels. They climbed to 7 ppt in April but May rains dropped them back to freshwater levels. There was a gradual increase to 6 ppt through August and a rise to 9 ppt in September. For the rest of the year, salinities were between 5 ppt and 7 ppt. That winter, oyster mortalities in the Head of the Bay involved 50% to 90% of the stock. Body tissues were edematous and virtually transparent and the oysters gaped readily.

Butler (1949) studied the effects of these low salinities on gametogenesis, using oysters from Tolchester Beach area, across the Bay from Baltimore harbor. He compared them with oysters from the more southerly Eastern Bay (personal communication), a region of higher salinity relatively unaffected by the increased freshwater input from the Susquehanna River. In the surviving low salinity population, gametogenesis was inhibited in 90% of the animals when salinities stayed below 6 ppt. As salinities rose, gametogenesis quickened but did not attain the level of the higher salinity group until 3-4 months later. Butler (1949) felt that the retardation of gametogenesis was probably due to variations in food supply (either because of depressed feeding activity or changed plankton structure), rather than to direct inhibition of gametogenesis by low salinity. The actual reason for this retardation has not been demonstrated.

In another instance (winter 1957 and spring 1958), excess rainfall led to deep penetration of freshwater over oyster beds in the important James River seed area (Andrews, et al. 1959). This led to mortalities as high as 90% between May 1 and June 15. Oysters from the upriver part of the seed beds were more resistant to low salinities than were oysters downriver. Oysters which were exposed to freshwater beginning in winter entered a low metabolic state. Heartbeat stopped, as did ciliary activity. Mantle sensitivity was dulled or lost. Slow conditioning of oysters at low salinities in cool or cold weather thus induced a state of "narcosis." This conserved glycogen stores and allowed for long-term endurance of low salinities. Apparently such a narcotized state was unattainable at higher temperatures.

Beneficial Aspects of Low Salinity

Lower salinities can be helpful to oysters. Many diseases and parasites are inhibited by low salinity. For example, in Apalachicola Bay, Florida, salinity reduction resulted in elimination of species such as oyster drills and stone crabs (both are oyster predators and are less euryhaline than oysters) with the result that the oyster beds returned to an earlier, higher level of productivity (Menzel et al. 1966). Similarly, on natural seed oyster beds in Delaware Bay, drill populations were depleted over the period of 1967 to 1973, apparently in part as a result of lower salinities (Haskin and Tweed 1976). This decline in drills allowed for better spat survival than in periods when the predators were more abundant.

Because of its lower salinity regime, Maryland's Chesapeake Bay is generally free of drills and starfish, which destroy large numbers of spat in higher salinity environments, such as Virginia. While there are important predators in Maryland (see section on Competitors, Pests, and Predators), the greater freedom from predation should lead to higher oyster survival, an important factor in both natural productivity and productivity due to oyster farming activities. Finally, some important diseases such as that caused by *Minchinia nelsoni* seem to recede with declining salinity (Sprague et al. 1969). This, too, enhances the fitness of Maryland's Chesapeake Bay as a region of oyster survival and production.

Rainfall

Grave (1912) discussed lack of rainfall in relation to food and "fattening" of oysters. He concluded that oyster food volume was greatly reduced by drought and was rapidly restored by copious rainfall. His conclusion was based on evidence of poor condition in oysters during droughts and of better condition after rainfall. Further, plankton samples showed changes in types and proportions of phytoplankters (we assume he meant phytoplankton when he used the term "food quality") in years of different rainfall amounts. He postulated that there was a relationship between rainfall, erosion, organic sediment, (natural) plant fertilizers, and growth of aquatic plant life (including oyster food).

Nelson (1921) in his studies of oysters in New Jersey found that increased rainfall was correlated with oyster "fatness." Later, he produced additional evidence that periods of prolonged rainfall helped "fatten" oysters (Nelson 1924). His colleague Martin (1923) found that oyster stomachs after rain contained freshwater algal species (e.g., *Nitzchia* sp., *Euglena* sp.) which were presumably washed from the nearby land.

Engle (1947) reported on the effects of fresh water runoff from the Susquehanna River in spring 1944 on oysters in upper Chesapeake Bay. While gonad development was slightly retarded and spatfall was nonexistent, the oysters' growth was better than usual and undersized oysters quickly reached market size. Beaven (1955) mentioned that preliminary studies indicated that abundant nutrients from runoff, coupled with suitably higher salinities so that gonad growth was not retarded, might provide suitable conditions leading to successful set.

Reimold and Daiber (1967) noted that total phosphorus concentrations in rainwater near Lewes, Delaware, increased from spring through summer and decreased in fall. They postulated that the increased supply of this plant nutrient might provide an extra source of nutrient into estuaries in spring and summer.

We believe that Beaven's (1955) suggestion of a link between nutrient input via runoff and later successful spat settlement bears further investigation. For example, the late winter and early spring of 1980 was quite wet (personal observations). This wet period was followed by a summer of low rainfall in which salinities rose to levels similar to those prevalent in the early to mid-1960's when spat settlement was higher than in the 1970's. The summer of 1980 saw some enormous sets of oysters in various sectors of the Bay (as well as large numbers of sea nettles, *Chrysaora quinquecirrha*—see section on Competitors, Pests, and Predators). Is it possible that the wet spring resulted in increased nutrient input into the Bay, developing an extensive food supply to fatten adult oysters and later to nourish larvae before settlement? Did the increased salinities result in larvae being retained further up into tributaries, rather than being flushed out into the mainstem of the Bay where, presumably, there was less shell on the bottom available for settlement? (Anecdotal reports noted sea nettles further up into tributaries than in recent years, demonstrating the penetration of higher salinity waters.) These matters require elucidation.

Sediment and Dredging

Oysters of the genus *Crassostrea* thrive in shallow estuarine waters and can be found even on rather soft muddy bottoms (Korringa 1957). Such environments are subject to erratic increases in turbidity and sedimentation due to the effects of wind, currents, land runoff, etc. Adaptation for existence in such a silt-laden environment is obviously essential. Menzel (1955) elaborated on the presence of such adaptations in *Crassostrea virginica*.

Species of *Crassostrea* are more tolerant of turbid conditions than are species of *Ostrea* (Nelson 1938, Jørgensen 1966, Moore 1977). A number of morphological, anatomical and behavioral adaptations enable *Crassostrea* spp. to deal with turbidity. The left, attached valve forms a deep bowl which raises the edge of the shell off the substratum (Green 1968). The presence of the promyal chamber, absent in *Ostrea* spp., and the subsequent posterior displacement of an adductor muscle capable of rapid and powerful contractions enable *C. virginica* forcibly to eject a stream of water washing out the accumulated sediment in the mantle cavity and on the gills (Nelson 1938, Menzel 1955). The mantle edges in *Crassostrea* spp. often contract to form grooves, or pseudosiphons, to restrict the inhalent and exhalent currents. The tentacles on the contracted mantle edges intermesh and screen out large, inedible particles. The larger palps of *Crassostrea* spp. allow a more extensive sorting of collected materials (Nelson 1960, Foster-Smith 1978). *Crassostrea* spp. can form copious pseudofeces in highly turbid water (Menzel 1955) while *Ostrea* spp. form no pseudofeces unless the particles are too large for ingestion or the alimentary canal is gorged. Furthermore, in high turbidities, *Crassostrea* spp. close their valves, while *Ostrea* spp. remain with their valves open (Foster-Smith 1978).

Nelson (1923b) found *Crassostrea virginica* to be capable of feeding rapidly in waters containing up to 0.4g (dry weight) of suspended matter per liter. Nelson (1938, 1960) described the efficient gill filtration system that allows for this, including the promyal chamber which is characteristic of oviparous oysters (genus *Crassostrea*). The promyal chamber allows for the egress of nearly all the water passing the right gill anterior to the adductor muscle. This is a short route (compared with the route through the epibranchial chamber of larviparous oysters of the genus *Ostrea*) and allows the oyster to expel material forcibly from the shell's interior. The presence of an enlarged "quick" muscle allows for vigorous and frequent shell movements which aid in the ejection of feces and pseudofeces.

Nelson (1960) reported that fat oysters were common on tidal flats in Delaware Bay at a site where "waters for days at a time are so laden with silt that a Secchi disc disappears in less than six inches." He described the stomachs of these fat oysters as being well filled with recently filtered diatoms and protozoa, along with nauplii and other larvae and numerous sand grains. He concluded that *C. virginica* is able to feed in the presence of heavy loads of suspended silt (however, see Loosanoff (1962) and Loosanoff and Tommers (1948) below).

Even with an efficient mechanism for tolerating the often heavy silt load of estuaries, oysters can be overwhelmed and buried by heavy sedimentation (Nelson 1960). Indeed, oysters may add to the problem by burying themselves in their own pseudofeces (Lund 1957a). In general, oysters do best on bottoms that are firm, such as those of shell, rock, and firm or sticky mud. Sand bottoms are subject to shifting activity, resulting in abrasion and valve injury. In addition, sand movement destroys young spat of the flat oyster, *O. edulis* (Shelbourne 1957), so, presumably, young *C. virginica* spat would also be at risk in sandy environments. Shifting light mud may cause death by suffocation.

Loosanoff and Tommers (1948) provided quantitative estimates of pumping rates by *C. virginica* from Long Island Sound in the presence of various concentrations of turbidity-creating substances. Feeding was most efficient when the water contained little suspended material. Additional studies reported by

Loosanoff (1962) showed that even for short exposures (3 to 6 h), oysters demonstrated sensitivity to turbidity caused by a variety of particulate materials (fine silt from Milford Harbor, Connecticut; kaolin; powdered chalk; $CaCO_3$; Fuller's earth). As turbidity increased, the rate of water pumping dropped, reaching zero in high concentrations of suspended material. Over a 48 h period in high concentrations of silt, pumping rate was 90% of normal. Upon return to clean sea water, these oysters took longer to recover than did oysters held in the same silt concentrations for shorter periods. Loosanoff (1962) assumed that the longer exposure period resulted in tissue damage to the filtering apparatus. He offered the caveat that the Long Island Sound oysters under study normally live in comparatively clear water. This may explain the apparent contradiction between his findings and those of Nelson (1960). Loosanoff recommended additional study of oysters from a variety of habitats with different turbidity conditions for comparative purposes to determine if there are varying abilities to tolerate silt conditions. This still remains to be done.

Eggs of *C. virginica* are sensitive to silt (Davis and Hidu 1969b). Concentrations of 0.25 g L^{-1} resulted in 27% mortality. At 0.59 g L^{-1}, 69% died. From 1 g L^{-1} and above, mortality ranged from 97% to 100%. The authors concluded tentatively that the larger particles present in silt were primarily responsible for the mortalities.

As little as 0.5 g L^{-1} of silt led to nearly 20% mortality in eastern oyster larvae after 12 days of exposure (Davis and Hidu 1969b). Fifty percent mortality occurred between 1.0 and 1.5 g L^{-1} of silt, with 100% mortality at 3 g L^{-1}. Oddly, larvae of the flat oyster (*O. edulis*) were more tolerant of silt than were larvae of the eastern oyster Travis and Hidu 1969b; Moore 1977), yet the latter inhabits a more turbid environment (Korringa 1957). Because there is a lack of detailed information on larval feeding and how it differs among species, there is no explanation for this paradox. Larvae of both the eastern and flat oysters suffered reduction in growth in 0.75 g L^{-1} silt. At 2 g L^{-1} growth stopped. To place their results in an environmental perspective, Davis and Hidu (1969b) noted that eastern oyster larvae tolerated turbidity levels higher than those normally encountered in nature. However, they felt that excessive turbidity caused by activities such as dredging might be detrimental to *C. virginica*.

Effects of Dredging and Spoil Disposal

Because of the active depositional characteristics of estuaries, navigational channels rapidly fill in, necessitating maintenance dredging. The effects of dredging on oysters have been studied by various investigators and will be briefly reviewed here. Morton (1977) provides a literature review of ecological effects of dredging and dredged spoil disposal.

Lunz (1938, 1942) studied the effects of dredging the intracoastal waterway in South Carolina and Florida He concluded that oysters were harmed by spoil or high turbidity only if buried and smothered. Ninety-four percent of an experimental population of oysters survived even in the dredge discharge. Spawning and spat setting were apparently not hindered. Wilson (1950) measured the effects of dredging in Copano Bay, Texas. As expected, heavier particles settled out near the dredge. Suspended materials moved in the direction of the current. Turbidity above background levels was noted generally from 300-900 feet (90-275 m) from the dredge (on one occasion, such higher turbidity levels were measured 1800 feet (550 m) from the dredge). Oysters were affected by chronic exposure to high concentrations of suspended silt (in a manner unspecified by May (1973) on whom we depended for this annotation). Wilson found no correlation between amount of spat set and amount of suspended material in laboratory tanks, nor between spat set and distance from the dredge.

Ingle (1952) performed a fall-winter study of dredging operations in Mobile Bay, Alabama Oysters suspended in trays from the stern of a working dredge suffered about 8% mortality in 5 weeks (10/19/51-11/26/51). Oysters suspended from a barge anchored an average of 225 feet (70 m) from a dredge suffered 5% mortality in the same period. Other oysters held within 600 feet (185 m) of the dredge suffered 9% mortality in a 26 day period in November, compared to 0% mortality in a similar sample held 1/4 mile away. Living oysters were trawled (shrimp trawl) from locations within 75-225 feet (20-70 m) from where the dredge was working in October 1951 and February 1952. Ingle (1952) concluded that all potentially deleterious particles would settle within 900-1200 feet (275-370 m) downstream of an active dredge. (One shortcoming of his study is the fact that oysters in winter may be less susceptible to chronic exposure to sediment than in warmer months when their metabolism is higher).

Breuer (1962) noted that shell dredging in South Bay, Texas, had resulted in loss of oyster populations. Deposition of spoil caused the region to become shallower, altering circulation patterns that had previously allowed for flushing of wastes from the oyster reefs. Hellier and Kornicker (1962) monitored hydraulic channel dredging in Redfish Bay, Texas, using colored gravel chips. They concluded that 22-27 cm of sediment might be deposited within 1/2 mile (800 m) of the dredge. Effects at greater distances were negligible.

Mackin (1962b) found that canal dredging in Louisiana carried silt to a maximum distance of 1,300 feet (400 m). At distances greater than a few hundred feet, turbidity generally did not exceed turbidity that might occur under maximum normal conditions. Turbidity levels outside the influence of direct spoil deposit did not harm oysters. Harrison (1967) reported in a study on dredging and spoil disposal in lower Chesapeake Bay that there were no measurable effects on oyster beds 0.8-2.0 miles (0.5 - 1.2 km) from the dredge site. Sediment deposition on the monitored beds appeared to be natural rather than caused by the dredging operation. Masch and Espey (1967) studied shell dredging in Galveston Bay, Texas, with somewhat more sophistication than had been employed in earlier studies. They found that bottom topography (including oyster bed topography) influenced movement of density layers of suspended sediment. Thus, control of dredging effects was not simply a matter of determining distance from the dredging operation. Type and amount of sediment involved were important, as were amount of sediment being worked at any one time, local conditions of circulation, and bottom and oyster reef topography.

May (1973) evaluated a variety of studies on estuarine dredging. He concluded that attention to bottom topography and type of sediment being dredged could alleviate potential damage to oyster reefs. Those reefs that are raised above the bottom should be especially less susceptible to smothering by sediments because tidal currents would tend to keep them clean.

Rose (1973) examined sediment-induced damage to market oysters in a bayou in southern Louisiana. A bucket dredge operation deepened a canal in close proximity to a planted oyster lease, with spoil disposal resulting in radical blockage of the bayou's width. Rose estimated that oyster mortality within 600 m (2000 feet) of the spoil bank was higher (57%) than on the unaffected part of the lease (17%). Sediment was about 2-15 cm thick on oysters in the affected area

These selected references indicate that there appears to be a certain amount of location-specific impact of large-scale dredging on *C. virginica*. As Masch and Espey (1967) indicated, local conditions of bottom topography could influence movement of sediment-laden waters. Thus, before broad statements can be made about any one area's response to dredging, one needs to know the type of sediment, the circulation in the area, the amount of sediment suspended and redistributed, and the topography of the local oyster grounds and their surroundings. Note that those oyster reefs which project above the bottom are usually well situated to have sediment washed off by currents before smothering occurs (May 1973). However, in areas where the oyster beds have been so heavily fished that they do not project very far from the bottom, smothering might happen more readily. This may lead to barrenness of formerly productive but heavily overfished oyster grounds, with loss of exposed shell and consequent failure of recruitment.

As previously noted, the early life stages (eggs, larvae) are probably the most sensitive to sedimentation (e.g., Davis and Hidu 1969b). Thus, extensive dredging during the reproductive season when the young planktonic stages are present would probably be detrimental. Similarly, higher summer temperatures and consequent higher metabolism of spat and adult oysters may put them at risk from sediment coverage that they might better tolerate in colder periods. Compared with acute, non-smothering exposure of short duration, chronic exposure to higher sediment levels is probably more of a problem to oysters because of the impact on pumping and feeding (Loosanoff 1962).

Turning now to consideration of the effects on oysters of hydraulic dredging in Chesapeake Bay for clams, the effects should be scaled down compared with those described earlier because such dredging does not occur around the clock or with the same intensity (measured as volume of sediment distributed in a local environment) as does navigation-related dredging. Further, one would not expect toxic materials to be released, since the clams are presumably living in clean substrate. Thus the main effects will be those involved with suspension of sediment and its deposition on oysters. Again, summer should be the more sensitive period. Manning's (1957) study on the effect of hydraulic dredging for clams near a concentration of oysters was performed in a region of high current velocity (0.1-0.9 knots on ebb). In quieter environments, deposited sediments may not be washed off oysters quickly. On the other hand, the sediments would not be carried as far. Manning's data certainly indicated that effects of dredging on oysters 75 feet (23 m) or more away should be negligible.

Water Circulation

Oysters are sessile organisms, becoming fixed in position on the estuarine floor a few weeks after fertilization occurs. Thus, any natural dispersal that occurs within the estuary must involve the free-floating planktonic larvae. The influence of water movements and the role of the larvae (whether active or passive) in such dispersal have been matters of considerable research interest and controversy. Work by the Nelsons in New Jersey and Delaware waters led to the initial descriptions of planktonic distributions of oyster larvae in the water column and to hypotheses of the role played by larvae in influencing these distributions (J. Nelson 1912, 1916, T.C. Nelson 1923a, Nelson and Perkins 1931). Discussion of their results and those of others will follow. First, some relevant aspects of estuarine circulation will be considered.

Estuarine Circulation

In estuaries, there is a net removal of water to the sea. This should also tend to remove entrained organisms. In Canada, Rogers (1940) noted that larvae of *Balanus improvisus* (barnacle), *Sagitta elegans* (arrow worm), and *Osmerus mordax* (smelt) could be found far upriver in the Miramichi River and St. John River estuaries. The former two species did not breed as far up as their larvae were found. The barnacle and arrow worm larvae were more abundant near the bottom and presumably entered the estuary with encroaching salt water. Later, Bousfield (1955) elaborated on aspects of retention of barnacle larvae in the Miramichi estuary. The smelt larvae entered the estuary from fresh water spawning grounds (Rogers 1940). The larval smelt appeared to have a diurnal migration pattern. They were found in deeper (more saline) water during the day and near the surface (fresher water) at night. Thus they could remain in the system by travelling up-estuary in the salt water inflow and down-estuary in the fresher water outflow.

Ketchum (1954) elaborated on the relation between circulation and planktonic populations in estuaries. He considered the flushing rate of the estuary to have great significance in relation to the reproduction rate of plankton. If more young were flushed from the estuary than were produced by the adult stock or than were supplemented by migration or washing in from outside the estuary, the population would decline. Ayers (1956) coupled such physical oceanographic considerations with assumptions concerning soft clam (*Mya arenaria*) spawning and mortality to provide reasons for the anomalous history of soft clam production in Barnstable Harbor, Massachusetts.

Application to Oysters

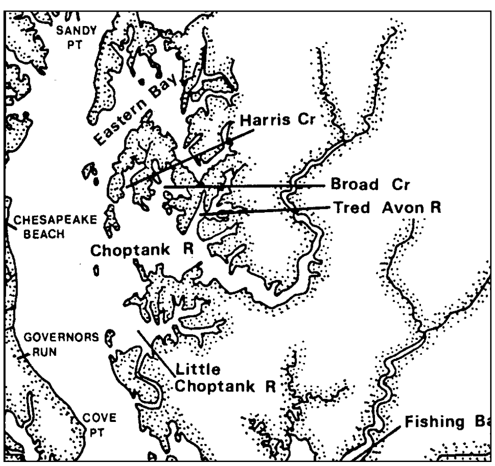
Research on estuarine circulation in relationship to oyster biology has not been extensive. Curiously, pioneering research was performed in the early 1950's in both Australia and in Chesapeake Bay. In Australia, oysters (scientific name not given but probably *Saccostrea commercialis*) may be found in a variety of estuaries (Rochford 1951, 1952). In some Australian estuaries, adult oysters are stunted and grow poorly, but spatfall is consistently good. In others, oysters grow and fatten rapidly but spatfall is indifferent. In a few cases, both good growth and good spatfall occur in the same estuary. This situation parallels that in Chesapeake Bay where some rivers have stunted adult populations yet experience good spatfall (e.g., James River and Broad Creek in the Choptank River) whereas other rivers support good growth but experience poor spatfall (e.g., Patuxent River). The reasons for these differences are not clear. Rochford (1951) implicated phosphate concentrations in the estuary as affecting adult growth, but no further studies on Australian estuaries in relation to oyster spatfall and growth were performed after 1952 (Rochford, personal communication).

In Chesapeake Bay, hydrographic conditions in James River (a major oyster seed area) during the summer of 1950 were measured by Pritchard (1953) and related to distribution of oyster larvae. He found that ebb velocities were greater at the water surface and decreased with depth. Flood velocities were lower at the surface and increased to a point near the estuary bottom; thereafter, increasing friction resulted in a slowing of water movement. As a result of the distribution of salinity and of the circulation pattern in the James River, there was a net horizontal flow down-estuary at the surface and a net horizontal flow up-estuary in the bottom waters. This return flow is thought to provide a mechanism for larval recruitment to upriver oyster beds. Thus, larvae entrained in the deeper more saline waters flowing upstream from the beds near the mouth of the river could replenish upriver beds. Also, slow upwelling of deeper water over shallow bars would concentrate larvae over bars on the northeast side of the river (Andrews 1979). These bars are in fact more productive than those on the southwest shore.

Manning and Whaley (1954) extended this kind of research to the (then) highly productive St. Mary's River at the mouth of the Potomac River. They sampled zooplankton over four periods during one summer (June 26 to July 20, 1951), exposed bags of shell for approximately weekly intervals from June 11 to October 15, and made hydrographic and meteorological observations during the study. Spat settlement was greatest upriver, decreasing downriver. They claimed that their hydrographic observations revealed that longitudinal circulation was such that the two-layered system of Pritchard (1953) existed in the upper St. Mary's River with a weak net up-estuary movement in the middle portion. Thus, net upstream transport of oyster larvae could occur with the upper river acting as a "larval trap." Near the mouth of the river, circulation was such that larvae from the lower river would probably be lost to the Potomac River. Apparently the pattern of longitudinal circulation at the time of the study was strongly influenced by prevailing southerly winds. If one looks closely at their results, however, it is obvious that the circulation pattern that they described is not tenable. According to their scheme, no water leaves the upper part of the river, yet it must if the river is not to overflow its banks in that region. W. Boicourt (Chesapeake Bay Institute, personal communication) has checked their raw data (on file as CBI Data Report No. 11) and notes that their experimental design and survey techniques were not suitable or sufficient to allow for the conclusion they drew. Thus, the hydrodynamics of the St. Mary's River system remain unclear and we do not yet know with any certainty why this area was such an excellent spat settlement environment.

During summer 1967, Carter (1967) studied the Manokin River, Maryland, to determine the optimum placement of planted shell to ensure successful settlement of oyster larvae produced by the disease-resistant brood stock in that river. Carter interpreted his hydrographic measurements to show that the circulation pattern appeared to be similar to that of the St. Mary's River (Manning and Whaley 1954). Again, no path existed for outflow from the upriver segment according to his postulated scheme of circulation. A tracer study using Rhodamine WT dye indicated that passively drifting oyster larvae would be expected to occur upriver from the dye release point. Based on this work, Carter (1967) made recommendations regarding placement of brood stock and natural cultch on the bottom of the Manokin River.

These three studies provided indications that, at least in the areas studied, local circulation patterns may "trap" larvae or move them upriver from the main broodstock concentration. However, until 1979 (see below) no attempt had been made to examine tributaries with poor spat settlement to determine if water movements are different from those of tributaries with good spat settlement. If they were not different, some other explanation for the poor spat settlement would be required.



Two tributaries near the mouth of the Choptank River (Broad Creek and Tred Avon River) historically have been areas with good and poor spat settlement success, respectively (Kennedy 1980). Both are physically oriented in the same general direction and are subject to similar environmental influences (insolation, wind, rainfall). Broad Creek is slightly more saline and cooler than Tred Avon River in summer (Kennedy 1980), but the differences are small and are not expected to be important to larval survival. Gametogenesis (gonad development, spawning period, sex ratios) was similar for oysters sampled from both rivers in 1977 and 1978 (Kennedy, personal observations). This suggested that the observed differences in spat settlement might be due either to biological factors causing differential larval availability or mortality, or to physical processes reducing larval availability in Tred Avon River (by increased flushing or by preventing influx of larvae from sources outside the tributary).

A study involving use of current meters and fluorescent dye was performed in both tributaries in summer 1979 during late June-early July when larvae were becoming abundant in the region. In brief, Broad Creek was found to be a more dynamic system and sensitive to wind action. Larvae produced within the system could be retained by the estuarine circulation therein. Also, additional larvae could readily enter Broad Creek from the mainstem Choptank River. Contrarily, while Tred Avon River had an estuarine circulation pattern in its upper half (surface outflow, bottom inflow), at its mouth the flow of lower-salinity Choptank River water tended to establish a three-layer system which would block influx of larvae (except perhaps on the bottom) to the Tred Avon River. Larvae produced within the system would probably be retained, whereas those from the mainstem Choptank would probably be prevented from entering in any numbers. Thus, Tred Avon River might be an area of poor spat settlement because brood stock numbers on the upriver grounds might be too low to provide sufficient larvae and because there may be no addition of larvae from outside the river.

Current Speed

Speed of current flow inshore is less than the speed in deeper mid-river channels. Shelbourne (1957) demonstrated the relationship between current velocity and natural oyster (*O. edulis*) abundance on cross-river transects by showing (his Fig. 8) that, as current speed increased towards mid-river, the average number of oysters per standard haul decreased. Almost no such information is available for Chesapeake Bay. However, limited data on crude current measurements in relation to oyster beds are provided in Grave (1912). For example, in the Magothy River north of Baltimore (where oyster beds still could be found shortly after the turn of the century) current speeds attained 0.17-0.25 mph (7.6-11.2 cm sec^{-1} in the main channels and 0.04-0.14 mph (1.8-63 cm sec^{-1}) over the oyster beds. These beds were, with one exception, located near the shore. In the other limited observations mentioned by Grave (1912), water velocities were always lower over oyster bars than in the main channel. On the other hand, as Grave (1912, p.220) indicated, the most productive oyster bars were those “over which the best circulation of water is maintained,” while “the bars situated on bottoms where good currents are not present were invariably poorly stocked.” Similarly, Keck et al. (1973) found dense oyster populations to be associated with the outside of large meanders in the estuarine portion of rivers emptying into Delaware Bay. These are areas of increased water velocity and decreased sediment deposition.

No data are available concerning optimum current speeds for settlement of spat and for growth. Prytherch (1929) mentioned (with little supporting evidence) that *C. virginica* larvae drop to the bottom if current speed exceeds 0.34 mph (l5.2 cm sec^{-1}). Yet Perkins (1931, 1932) found larvae to be swimming actively at speeds up to and exceeding 0.48 mph (21.3 cm sec^{-1}). In studying larvae of *O. edulis*, Korringa (1941) collected larvae at the surface in current velocities up to 0.9 mph (40 cm sec^{-1}) during one series of samples. Other samples showed there were larvae in the water column at velocities exceeding 2.2 mph (100 cm sec^{-1}) in some places. Korringa (1941) concluded that *O. edulis* did not drop to the bottom under these conditions. Of course, it is not clear if the larvae were swimming to maintain themselves at the surface speeds or if they had been tossed there by turbulence caused by the tidal currents themselves.

The effects of current speed on larval distribution (i.e., their ability to orient in the water column) and behavior need further investigation. This will be referred to later.

Wind Effect

Shallow estuarine environments may be strongly influenced by wind. Manning and Whaley (1954) described the influence of prevailing southerly winds on the pattern of longitudinal circulation in St. Mary's River. Perkins (1932) found wind-blown currents to influence vertical distribution of oyster larvae. Nelson (1953) described research in oyster larval abundance and behavior in waters off Cape May shores of Delaware Bay. He noted that sets were sparse when strong offshore winds continued blowing during the spawning season. On the other hand, southerly winds were generally associated with good sets. Depending on wind direction, then, larvae were thus entrained in the wind-induced currents and ended up being blown away from or onto the New Jersey shore.

Eddies

Shelbourne (1957) quoted Kandler (1928) and Orton (1937) as believing that the phenomenon of high oyster (*O. edulis*) set under eddies was due to an accumulation of larvae within the system. Shelbourne, instead, found no accumulation of larvae within these eddies, on either the ebb or flood tides. The heavy oyster set under eddies is presumably due to the reaction of the eyed pediveligers to reduced current within the eddy, rather than to some physical concentrating mechanism (Shelbourne 1957). Andrews (1955a) noted that there were "pockets" or turns in the James River (Jail Point), York River (Gloucester Point), and Rappahannock River (Towles Point) in which set was frequently highest for the whole river.

Conclusions

It is not yet clear how Chesapeake Bay tributaries may be classified with regard to their suitability for serving as larvae traps. Circulation patterns in the James River, Manokin River, Tred Avon River, and Broad Creek have been described as the result of dependable studies. Circulation patterns in all four tributaries seem to be such that larvae would be expected to be moved upriver while they are in the water column. However, the Tred Avon River would appear to be dependent upon its upriver oyster populations for its larval supply because of a circulation pattern at its mouth that would tend to block entrance of quantities of larvae from outside (i.e., from the Choptank proper) to supplement the upriver populations.

Presumably Eastern Bay, Little Choptank River, and Honga River, all good setting areas, also possess circulation patterns enhancing larval influx and retention. It is not clear why the Patuxent River or the lower Potomac River above its mouth do not have better success with spat settlement.

Larval behavior may be such that larvae can take advantage of estuarine circulation patterns to enhance their retention within tributaries. Such behavior is reviewed in the section on Larval Biology and Spat Settlement.

Dissolved Oxygen

Limited experiments have been performed to evaluate the effects of low dissolved oxygen on oysters, whether measured in terms of survival, physiological activity of one kind or another, reproduction, spat settlement, etc. Sparks et al. (1958) examined the comparative utilization of oxygen by *C. virginica* and found that oysters survived for up to five days in water containing less than 1.0 ppm oxygen. Presumably they underwent anaerobic metabolism during that time (Galtsoff 1964).

Usuki (1962) found that cilia of isolated gill tissue of *C. gigas* stopped beating after two hours in anaerobic conditions, but recovered quickly when aerobic conditions were restored. Even with ciliary movement having ceased, gill tissue survived for as long as a day under anaerobic conditions.

In discussing reasons for decline in spatfall in the Rappahannock River, Haven et al. (1978) remarked on the development of an oxygen deficiency in the lower river's deeper regions. They noted that the impact of such a development on larval survival and setting has not been studied carefully. They speculated that oxygen-poor water may be an important factor in larval mortality in this region. The effects of various levels of dissolved oxygen on oyster larval mortality or settlement success needs elucidation.

Light

Responses to light by larvae of 141 species of invertebrates, including oysters, have been summarized by Thorson (1964). For oysters, there are some contradictory indications of the effects of light on larval behavior.

Hopkins (1937) found similar numbers of larvae of *Ostrea lurida* on undersurfaces of both clear and darkened glass plates and concluded that they did not select shade for settlement. Cole and Knight-Jones (1939) found larvae of *O. edulis* setting preferentially on the underside of dark plates rather than clear plates. In five experimental periods of daylight, about five times as many *O. edulis* spat settled on the undersides of dark plates as on clear plates; in three experimental periods of darkness, there was no difference between setting beneath clear or dark plates. However, there was a marked tendency for *O. edulis* larvae to attach to the inner concave surfaces of oyster shell during daylight compared with attachment in darkness. The conclusion was that light stimulated swimming, bringing the larvae into contact with more potential setting surfaces. Cole and Knight-Jones (1949) found larvae of all classes of *O. edulis* to be concentrated in deeper water during periods of bright sunshine.

Cranfield (1968) studied settlement in the New Zealand oyster, *Ostrea lutaria*. He concluded tentatively that light stimulates these larvae to swim in still water. At low light intensities in still water, larvae tended to swim up toward the light. In dim light and still water, the larvae settled mainly on undersurfaces. In darkness and still water, larvae settled mainly on upper surfaces. In the presence of currents and light, larvae settled mainly on upper surfaces.

Nelson (1916) noted that larvae of *C. virginica* were found near the bottom of the water column at night, then rose at dawn. His son (Nelson 1926) reported that light stimulated eyed pediveliger larvae to move. When they encountered shade, they became inactive. Younger larvae without eyespots were not sensitive to light. On the other hand, Prytherch (1934) stated that *C. virginica* larvae were unresponsive to light.

For *C. virginica*, Nelson (1953) indicated that at Cape May, New Jersey, a preponderance of larvae set on the upper rather than the lower surface of shell substrate in 1952, unlike the situation in earlier years. He stated that larvae exposed to light would crawl to the edge of test shells, move to the shaded underside, and attach. He noted that in 1952 light penetration of the inshore waters off Cape May was much decreased compared to normal, apparently because of high phytoplankton concentrations. He felt that the resultant decreased light transmission may have led to less stimulation of the larvae to crawl to undersurfaces and set, leading to the preponderance of setting on the upper surfaces that year.

Medcof (1955) studied *C. virginica* settlement in a clear, tideless body of water. Settlement on spat collectors was higher by day than by night (see also Cole and Knight-Jones (1939) above). He concluded that the larvae "preferred" to settle on lower rather than upper surfaces, but that light stimulated them to settle.

Ritchie and Menzel (1969) studied the influence of light on *C. virginica* larvae in the laboratory. They illuminated experimental shell substrate from above and below and allowed larvae to settle. Control shells received illumination from above, none from below. At 50 footcandles of illumination, the ratio of set on the two different undersurfaces was 4:96 (experimental : control surfaces). When footcandles were decreased to 25, the corresponding ratio was 20:80. The authors concluded that the eyed larvae were light sensitive and that there was a "preference" for non-illuminated surfaces.

Shaw et al. (1970) performed laboratory experiments with *C. virginica* larvae and concluded that settling was encouraged by darkness and partially inhibited by light. This is contrary to Medcof's (1955) field observations.

More sophisticated study of phototaxis and other effects of light on larval behavior is needed. Effects of interaction of light and other environmental factors also need to be clarified.

Fewer studies on the effect of light on adult oysters seem to have been done. Loosanoff and Nomejko (1946) studied feeding of oysters in relation to tidal stages and to light. They found that percentages of full stomachs were similar in field samples collected by day or by night. Medcof and Kerswill (1965) found that shading increased the linear growth of *Crassostrea virginica* about 150%, but reduced the thickness-to-length ratio of their shells. Light exposure increased the index of condition, specific gravity, fluting, and pigmentation of shell. The authors postulated that light reduced the ability of the mantle to produce marginal shell but increased its ability to produce pigments.

pH

In a study of *O. edulis* setting behavior, Cole and Knight-Jones (1949) felt that they had found a relationship between the vertical distribution of spatfall and pH. They noted that under conditions of constant pH in culture tanks, spatfall tended to be more intense near the surface, but, as pH rose, it tended to become more intense near the bottom. This situation and other aspects of pH involvement in spat settlement seem not to have been studied further.

Prytherch (1929) observed that *C. virginica* spawned at pH 7.8 to 8.2 in Long Island Sound. He concluded that low pH inhibited oyster spawning.

Loosanoff and Tommers (1947) found that pumping rate in adult *C. virginica* was normal at pH 4.4. At pH 4.25, oysters remained open about 76% of the time but pumped about 90% less water than did controls. At pH 6.75 and 7.00, oysters initially pumped more than did the controls, but the rate gradually declined to become less than in the controls.

Galtsoff (1964) reported that pH had a pronounced effect on *C. virginica* respiration. At pH 6.5, oxygen consumption was 50% of normal, decreasing to 10% at pH 5.5.

Calabrese and Davis (1966) found normal embryonic development of *C. virginica* at pH 6.75 to 8.75. Survival of larvae was more than 68% in the range of 6.25 to 8.75. For oyster larvae, the lower limit for survival was pH 6.00. Normal growth of oyster larvae occurred from pH 6.75 to 8.75. At levels below pH 6.75, growth dropped rapidly. Abnormal development of eggs and mortality of larvae increased rapidly at pH 9.00 to 9.50. The authors concluded that successful recruitment of oysters requires a pH above 6.75. High concentrations of silt were found to lower seawater pH below 6.75 to 6.40. Thus, heavy silt (or any pollutant lowering pH in tidal estuaries) may lead to failure of oyster recruitment. Calabrese and Davis (1969) also noted that *C. virginica* would not spawn below pH 6.0 or above pH 10.0.

Chemicals

With (1) the post-war growth of the chemical industry, (2) greater reliance on petroleum products for transportation, fertilizers, and consumer goods, and (3) increased use of pesticides for health and agricultural purposes, output of chemical materials has increased and diversified immensely. Dumping or leaking of chemicals into sewage systems, runoff into irrigation or drainage ditches, and spillage during ship transportation all contribute to deposition of increasing amounts of chemicals into estuaries.

When these anthropogenic materials contact oysters, they may be lethal; they may exert sublethal effects; they may be concentrated in amounts dangerous to human health when oysters are eaten; or they may have a mix of influences. Direct lethal effects might involve larvae rather than adults, with possible effects on recruitment. Indirect effects might include loss of larval or adult food supply; inhibition of the "gregarious" settling response exhibited by larvae in the presence of adults and newly settled spat; contamination of settling surfaces with consequent loss of attraction to larvae; increased susceptibility to disease, pests or predation; decreased fecundity of adults; loss of larval vigor; poor growth; and elimination of spawning cues.

To complicate matters further, results of chemical contamination in nature may differ from results predicted by laboratory experiments because of synergistic effects resulting from interactions among chemicals mixing in the water column in the vicinity of oysters. Thus, although some studies on effects of a variety of chemicals on various life history stages of oysters have been performed, much remains to be done to test chemicals, individually and in combination, in order to estimate direct and indirect influences on oyster survival and reproduction.

Chlorine

Chlorine is used as a disinfectant of effluents in sewage treatment plants and as a biocide to combat fouling of condenser tubes in steam-electric power plants (Whitehouse 1975; Brungs 1976). Its increasing use in estuarine environments is a matter of concern (Gentile et al. 1976).

In an early study, Galtsoff (1946) found that in the presence of chlorine in quantities greater than 1 mg L^{-1}, oysters will respond by closing their valves, as they do to other environmental irritants. At concentrations as low as 0.05 mg L^{-1}, pumping rates are reduced.

As understanding of the chemistry of chlorine in aqueous solutions grew, it was found that chlorine added to seawater results in a variety of compounds. These compounds are generally lumped under the heading of chlorine-produced oxidants (CPO). The toxicity of these materials has been under recent study. For example, adult oysters (5-12 cm long) were subjected to a variety of chronic bioassays using CPO during fall, winter, and spring seasons in a salinity range of 23.3-26.6 ppt and a temperature range of 11.2-27.0°C (Scott and Vernberg 1979). Survival was generally enhanced in winter and spring compared with fall exposure. Concentrations of 0.12 to 0.16 mg L^{-1} of CPO led to a reduction of 50% or more in fecal production in all three seasons. In any season, condition and gonadal indices were always significantly higher for control than for experimental oysters, even for those held in concentrations which were sublethal. Condition index generally declined as exposure time to CPO increased. Growth rates were affected in that the mantle apparently withdrew further into the shell upon CPO exposure and began to deposit new shell inside the old (this may also happen at low salinities—Loosanoff 1953). Temperature seemed to be a factor in the effects of CPO exposure on mantle respiration. Scott and Vernberg (1979) concluded that chronic exposure to CPO material was highly toxic to *C. virginica* at higher concentrations. Sublethal concentrations resulted in severe reactions. Seasonal environmental factors also affected the toxicity of CPO.

Effects of CPO materials on oyster larvae have been studied by Roosenburg et al. (1980). Straight-hinge veliger larvae (48-60 h old) were more sensitive to CPO than were pediveliger larvae (over 14 days old), especially over longer exposure times. Mortality of both larval stages was directly related to increased CPO concentration and exposure time. Concentrations resulting in 50% mortality of straight-hinge larvae were estimated to be 0.3 ppm CPO at 48 h, 0.08 ppm at 72 h, and 0.06 ppm at 96 h. Concentrations causing 50% mortality were not determinable for pediveliger larvae because the larvae did not reach 50% mortality within the maximum period of experimental exposure (96 h).

Haven et al. (1978) postulated that the decline of oyster production in some Virginia rivers was due to chlorination. They implicated chlorine in the James River by placing mature oyster larvae in water collected from the vicinity of the Warwick River sewage treatment plant. These larvae stopped swimming, whereas control larvae in water from the York River (relatively unchlorinated) were unaffected.

Field information on chlorine and CPO concentrations in all productive or formerly productive areas of Maryland's Chesapeake Bay (e.g., St. Mary's River, Eastern Bay, the lower Choptank River) and in relatively unproductive areas (Tred Avon River, Chester River) might be instructive. It would seem to be important to measure levels of CPO concentrations in the Bay on or near oyster grounds to determine if human population increase and concomitant building of sewage treatment plants are resulting in discharge of chlorine-treated water to the point that oysters are being affected. This would be especially important in summer when larvae are present in the water column and could be in contact with CPO.

Heavy Metals

Increased industrial activity has led to increased release of toxic substances, including heavy metals, into the environment. This material may be discharged directly into estuarine and marine environments or may arrive there via water runoff. Many of these substances can be concentrated by oysters and thus become a potential hazard to organisms which feed on oysters. Further, these materials may exert a lethal or sublethal effect on different stages of the life cycle of oysters, with consequent influence on population abundances. Although some studies on heavy metals and their effects on oysters were performed several decades ago (e.g., Prytherch 1934, Chipman et al. 1958), most are more recent, reflecting both the increasing severity of heavy metal pollution and the improvement of technology for studying effects of heavy metals. A relatively comprehensive, recent summary of the effects of heavy metals on marine and estuarine bivalves is Cunningham's (1979), which provides greater detail than does our summary. Her review should be consulted for more information. A general discussion of heavy metal tolerance in aquatic organisms is provided by Bryan (1976).

The following (not all-inclusive) list of references indicates the major materials involved in studies of the effects of heavy metals on various species of oysters:

Aluminum

Crassostrea virginica - Calabrese et al. (1973)

Arsenic

Crassostrea virginica - Calabrese et al. (1973)

Cadmium

Ostrea sinuata - Brooks and Rumsby (1967)
Crassostrea commercialis - Mackay et al. (1975)

Crassostrea virginica - Calabrese et al. (1973); Casterline and Yip (1975); Engle and Fowler (1977); Frazier (1975, 1976); Greig et al. (1975); Shuster and Pringle (1969); Zaroogian and Cheer (1976); Zaroogian (1980)

Chromium

Crassostrea virginica - Calabrese et al. (1973); Preston (1971); Shuster and Pringle (1969)

Copper

Ostrea edulis - Coombs (1974)
Crassostrea gigas - Ruddell and Rains (1975)

Crassostrea commercialis - Mackay et al. (1975); Wisely and Thick (1967)

Crassostrea virginica - Calabrese et al. (1973, 1977); Engle and Fowler (1977); Frazier (1975, 1976); Greig et al. (1975); Maclnnes and Calabrese (1978, 1979); Prytherch (1934); Roosenburg (1969); Ruddell and Rains (1975); Shuster and Pringle (1969); Windom and Smith (1972)

Iron

Crassostrea virginica - Frazier (1975, 1976); Windom and Smith (1972)

Lead

Crassostrea virginica - Calabrese et al. (1973); Greig et al. (1975); Zaroogian et al. (1979).

Manganese

Crassostrea virginica - Calabrese et al. (1973); Frazier (1975, 1976)

Mercury and Mercury Compounds

Crassostrea commercialis - Wisely and Thick (1967)

Crassostrea virginica - Calabrese et al. (1973); Cunningham (1972, 1976); Cunningham and Tripp (1973, 1975a, b); Kopfler (1974); Maclnnes and Calabrese (1978); Mason et al. (1976)

Nickel

Crassostrea virginica - Calabrese et al. (1973, 1977)

Silver

Crassostrea virginica - Calabrese et al. (1973, 1977); Greig et al. (1975), Maclnnes and Calabrese (1978); Thurberg et al. (1974); Windom and Smith (1972)

Zinc

Ostrea edulis - Coombs (1972, 1974)

Crassostrea commercialis - Mackay et al. (1975); Wisely and Thick (1967)

Crassostrea gigas - Boyden et al. (1975); Brereton et al. (1973); Ruddell and Rains (1975)

Crassostrea virginica - Calabrese et al. (1973); Chipman et al. (1958); Frazier (1975, 1976); Greig et al. (1975); Maclnnes and Calabrese (1978); Romeril (1971); Shuster and Pringle (1969); Windom and Smith (1972); Wolfe (1970).

A survey of a number of oyster studies (Cunningham 1979) reveals that the presence of many heavy metals results in mortality of embryos (e.g., Calabrese et al. 1973) and larvae (Boyden et al. 1975), reduced growth of larvae (e.g., Brereton et al. 1973, Calabrese et al. 1973) and spat (Cunningham 1976), reduced spat settlement (Boyden et al. 1975), thinning of shell over time (Frazier 1976), and changes in oxygen consumption (Thurberg et al. 1974). Concentrations of heavy metals per unit weight in body tissues usually decrease with increasing size, age, and weight; however, total body residue can increase at the same time (Cunningham 1979). Spawning of gametes may result in a drop in the total body residue of metals (Frazier 1975, Cunningham 1979).

In terms of exposure (Cunningham 1979), as exposure "time" increases, tissue residues tend to increase until a saturation level is reached. Similarly, saturation may be attained after "concentration" of a heavy metal has reached a specific level. Beyond that concentration, no further uptake occurs but mortality may increase.

With regard to collection sites, a gradient of tissue residues of Cu, Zn and Cd with location has been reported for *C. commercialis* in Australia (Mackay et al. 1975). They noted that concentrations increased with distance upstream in Australian estuaries.

Synergistic interactions of various heavy metals have been reported (e.g., Mackay et al. 1975; Frazier 1976), but more information is needed. The influence of salinity as a synergistic factor needs elucidating. One would also expect that temperature stress would exacerbate any deleterious influence of heavy metals.

Because the early life history stages (eggs, embryos) of oysters tend to be the least resistant to extremes of various environmental factors (Cunningham 1979), their use as bioassay material for water quality studies has been proposed (Woelke 1972). The incidence of abnormal development can be followed for specified periods of time (e.g., 48 hours). The ease of spawning oysters and the sophisticated facilities that have developed for larval culture make such bioassay attempts reasonably simple.

In one such study, Calabrese et al. (1973) examined the effects of 11 heavy metals on embryos of *C. virginica*. They divided these into three categories according to LC_{50} values derived in their experiments. The three categories (with the LC_{50} value in ppm inside parentheses) were a) Most toxic: Mercury (0.0056), Silver (0.0058), Copper (0.103) and Zinc (0.31); b) Relatively toxic: Nickel (1.18), Lead (2.45) and Cadmium (3.80); c) Non-toxic: Arsenic (7.5), Chromium (10.3), Manganese (16.0) and Aluminum (75).

With regard to the monitoring of incidence of heavy metals in Chesapeake Bay, the body burdens of various heavy metals in oysters have been reported by Bender et al. (1972) and Drifmeyer (1974). Presumably such monitoring activities will continue in order to record any unusual increase in heavy metal content before it becomes a health hazard.

Petroleum Hydrocarbons

With the increase in spills and pollution resulting from world demand for and transport of petroleum products, there has been an increase in concern about the effects of these materials on marine and estuarine organisms, including oysters. Numerous symposia and study sessions have been convened to discuss these matters (see, for example, National Academy of Science 1975, Johnson 1977, Varanasi and Malins 1977, Wolfe 1977, Anderson 1979, Neff 1979). A bibliography on biological effects of pollution in the marine environment has recently been compiled (Filion-Myklebust and Johannessen 1980). For administrators and policy makers, Evans and Rice (1974) have produced a brief review of the effects of oil on marine ecosystems which has transfer value to Chesapeake Bay. A recent overview on impact of oil and oil dispersants in the marine environment is provided by Gunkel and Gussmann (1980).

In their review paper, Evans and Rice (1974) summarized the potential damage to organisms by petroleum pollution using Blumer's (1970) classification. Such damage could result from:

1. Direct mortality by covering and asphyxiation.
2. Direct mortality from contact poisoning.
3. Direct mortality from water soluble toxic components carried from the pollution scene.
4. Mortality of generally more sensitive juvenile stages.
5. Destruction of food sources, resulting in starvation of higher trophic levels.
6. Lowered resistance and death resulting from stress induced by sublethal pollutant levels.
7. Concentration of carcinogens and mutagenic chemicals into marine organisms.
8. Low level disruption of normal behavior patterns resulting in aberrant and unsuccessful migration, feeding, mating activity, etc.

Some of these factors have been studied, but others, especially those listed under items 5, 6 and 8 (above) need more and deeper investigation.

As early as 1935, Galtsoff et al. (1935) reported on effects of crude oil pollution on oysters in Louisiana. Mackin and Sparks (1962) studied the effects of a two-week-long oil spill in the oyster producing area of Louisiana. Additional assessment of effects of field exposures has occurred (e.g., Blumer et al. 1970, Ehrhardt 1972, R.D. Anderson 1975, Lake and Hershner 1977, Bravo et al. 1978).

Such spills may not be lethal to oysters, but chronic exposure to petroleum hydrocarbons leaking from sediments where they have been trapped might lead to population decline by impairing adult ability to reproduce or larval ability to settle.

Problems of assessing the effects of exposure of aquatic organisms to petroleum hydrocarbons derive from the fact that such materials are composed of a variety of components of varying toxicity. For example, J.W. Anderson (1975) determined concentrations of oil-derived hydrocarbons in oyster tissues after exposure of whole oysters to oil-in-water dispersions of four kinds of test oil. He noted the presence of a variety of paraffins, naphthalenes, and other compounds (he listed 17) in varying proportions, depending upon the oil source. Similarly, Ehrhardt (1972) found a complex mix of hydrocarbons in tissues of oysters from a heavily contaminated reef at the entrance to the Houston ship channel in Galveston Bay. Such an intricate mixture of substances in oil leads to the necessity for careful study of the effects of its components as well as of the varying types of oil.

Temperature of water and other factors influence the kinds of degradation products produced after a spill. Some products may be less harmful than others. For example, results of 96 h bioassays with adult oysters (Anderson and Anderson 1975) revealed that crude oils (South Louisiana, Kuwait) were less toxic than were partially refined oils (No. 2 fuel oil, Venezuela Bunker C).

As noted, oysters exposed to a number of test oils accumulate a variety of different hydrocarbons in their tissues, with naphthalenes being concentrated to the greatest extent (J.W. Anderson 1975). Upon return to oil-free conditions, oysters may rapidly release these hydrocarbons, complete depuration taking from 10 to 52 days (Anderson et al. 1974). Speed with which depuration occurs may vary with experimental conditions. Blumer et al. (1970) also monitored accumulation of petroleum hydrocarbons in oyster tissue, finding that they seemed to be retained in the tissues rather than being released under "clean" conditions. Stegeman and Teal (1973) held oysters for 49 days in running seawater and low concentrations of No. 2 fuel oil. The oysters accumulated up to 334 ppm total petroleum hydrocarbons and released nearly 90% of that in two weeks under "clean" conditions. However, even after 4 weeks, 34 ppm still remained.

In another study, after eight hours exposure to approx. 400 ppm No. 2 fuel oil in a flow-through system, oysters contained up to 312 ppm petroleum hydrocarbons, with paraffins the major component. Depuration occurred rapidly for the first three hours, before slowing. Paraffin was discharged most rapidly (Neff et al. 1976).

Such accumulations of petroleum hydrocarbons can be influenced by lipid content of the exposed animal. Stegeman and Teal (1973) exposed "high lipid content" oysters (1.62%) and "low lipid content" oysters (0.95%) to No. 2 fuel oil (approx. 406 ppm hydrocarbon) at 20°C in flowthrough conditions. The first group concentrated hydrocarbons to 334 µg/g wet weight compared with 161 µg/g for the second group, suggesting that hydrocarbons may be held in lipid deposits. In clean water, oysters lost 90% of their accumulated hydrocarbons in 2 weeks. Up to a concentration of 450 µg L^{-1} there was a direct correlation between concentration of hydrocarbon in the experimental water and extent of uptake into oysters. At 900 µg L^{-1}, the test oysters remained closed.

Physiologically, petroleum hydrocarbons exert a variety of influences. Chipman and Galstoff (1949) found that crude and diesel oils inhibited ventilation and reduced valve closure. Lund (1957b) found filtration rate to be sensitive to petroleum products. On the other hand, Mackin and Hopkins (1961) found heartbeat and shell movements of oysters to be unaffected by exposure to 0.1% concentration of water-soluble fractions. J.W. Anderson (1975) found little effect on growth over 105 days after exposure to a 1% oil-seawater dispersion for 96 hours. Anderson and Anderson (1975) found no long-term effects on pericardial fluid of oysters when transferred from 20 ppt to 10 ppt and 30 ppt in the presence of a 1% oil-water dispersion of South Louisiana crude or No. 2 fuel oil (although oysters exposed to the latter adjusted more slowly).

Anderson (1979) summarized a number of findings. The range of toxicity of crude oil and No. 2 fuel oil to marine organisms (96 hour LC_{50} tests) spanned about 1 to 20 ppm crude oil in water and 0.4 to 0.6 ppm No. 2 fuel oil. Lower temperatures (4°-10°C) generally depressed LC_{50} values to the lower end of the range. Larval stages may be more sensitive than the adult. In addition, oysters may be more resistant to crude oil toxicity in winter than in summer (Anderson and Anderson 1976). This may be related to differences in oyster condition between the two seasons.

With regard to fertilization and developmental success, oysters were adversely affected in proportion to water-soluble fraction concentration in the range of 0.001 to 1 ml L^{-1} (1-1000 ppm) when exposed to Prudhoe Bay, Nigerian, and Kuwait crude oils (Renzoni 1975).

In a recent study, Barszcz et al. (1978) found that chronic exposure to crude oils in estuarine ponds resulted in apparent starvation of test oysters. This suggested that the oils interfered in some undetermined manner with food ingestion or utilization. The tissues of test animals became clear, watery, and emaciated, unlike the condition of control animals. Histological observations revealed tissue (hyaline) degeneration. Germinal epithelial tissue was reduced and follicular development was inhibited or lacking, indicating a decline in reproductive potential; this correlates with Renzoni's (1975) observations. Finally, the incidence of parasitism was much higher in oil-treated oysters than in controls, indicating that the former were in poor health with lowered resistance, exposing them to greater risk of infection.

Additional study of sublethal effects of various petroleum hydrocarbons on adult and larval growth, reproduction, larval survival, settlement success, and spat survival is desirable. A recent thesis by Noyes (1978) has apparently reported on some aspects of this (not seen by us), but information is needed for oysters growing in low salinity habitats such as Maryland's Chesapeake Bay.

Pesticides

Increasing concern about effects of pesticides on ecosystems and their biological components has led to numerous studies and reviews (e.g., see Edwards

1973a,b; Brown 1978). The importance of chlorinated hydrocarbons to agriculture, and examples of their application have been described by Snelson (1977). There appears to be no foreseeable alternatives to use of these materials in the near future, and much of it will undoubtedly run off into the tributaries and collect in Chesapeake Bay. In a recent review, Ernst (1980) indicated that estuaries are regions of special concern because of their higher accumulations of pesticides (see also Duke and Dumas 1974, Nimmo 1979).

Kerr and Vass (1973) have written a helpful discussion of pesticide residues in aquatic invertebrates including the oyster. They considered the mobilization of pesticides in the environment and their concentration in food webs. In brief, to become a problem the pesticide (or other contaminant) must be introduced into the environment in appreciable quantities, it must be relatively resistant to degradation, and it must have an affinity for biological systems (consider how readily body lipids concentrate DDT). Kerr and Vass (1973) detailed the processes of translocation of contaminants to water and to estuarine and marine environments. Although industrial and domestic out falls provide appreciable contaminant loads, conventional forestry and agricultural practices, and disease vector control programs result in the major portion of aquatic contamination (Butler 1971, Kerr and Vass 1973).

Given the proximity of many estuaries to human population centers (Odum 1970), it is obvious that estuarine organisms such as oysters may be subject to contact with a diversity of contaminants. It appears that the major source of water-borne material such as pesticides is available in the water column in the form of suspended particulate matter (Kerr and Vass 1973). Oysters pump such material over their gill surfaces during respiration and feeding. Thus, even if they do not ingest the contaminated material, their body tissues, and especially the gills with their network of blood vessels, come into contact with it. Kerr and Vass (1973) develop this subject in more detail for aquatic invertebrates.

The amount of contaminant accumulated in the bodies of oysters varies with location (Butler 1971) and, obviously, with proximity to a source. For example, low levels of PCB's and organochlorine insecticides have been measured in *C. virginica* from Mexican coastal lagoons that are relatively remote from industrial or domestic pollution (Rosales et al. 1979). In contrast, PCB levels in oysters from the polluted Raritan Bay region of New Jersey are higher (Stainken and Rollwagen 1979).

Kerr and Vass (1973) listed representative residue levels for a variety of aquatic invertebrates. Values for *C. virginica* have been extracted from their paper and are listed in Table 1.

Additional information on residue levels can be found in a number of reports; for example, Wilson and Forester (1978 - Aroclor 1254), Butler (1966, 1973 - DDT and other chemicals), and Sprague and Duffy (1973 - DDT). The extent to which some pesticides are concentrated by oysters is given in Table 2.

Table 1. Representative residue levels of some pesticides in *Crassostrea virginica* (after Kerr and Vass 1973). ND = No Data.

Chemical	Residue µg/kg (wet wt)	Range µg/kg (wet wt)	Remarks
ΣDDT	60	<30-710	Median, 2.5 yr, 6 States
	15	< 10-30	Mean, 2 sites, Canada
	51	ND-150	Representative estimate, 8 sites in Texas
Aldrin	3	ND-30	Mean for 10 samples
	<10	<10-30	Median, 2.5 yr, 6 States
BHC-Lindane	4	ND-10	Representative estimate, 10 samples
Chlordane	10	<10-500	Median, 2.5 yr, 6 States
Dieldrin	<10	<10-10	Median, 2.5 yr, 6 States
	4	ND-10	Representative estimate, 10 samples
	10	<10-30	Median, 2.5 yr, 6 States
	17	ND-39	
Endrin	5	ND-20	Median, 1 yr, 2 sites
	<10	<10-70	
Heptachlor	1	ND-<10	Representative estimate, 10 samples
	<10	ND	Median, 2.5 yr, 6 States
Heptachlor epoxide	<10	ND	Median, 2.5 yr, 6 States
Methoxychlor	<10	ND	Median, 2.5 yr, 6 States
Campechlor	80	<10-1000	Median, 2.5 yr, 6 States ates

Table 2. Experimental conditions of exposure of *C. virginica* to pesticides, concentration factors of material in oyster bodies, and notes on effects on growth and pathology. EC_{50} = estimated con centration reducing shell deposition by half in 96 h. MEC = minimum effective concentra tion affecting oyster growth in 24 h.

Chemical		Concentration (Exposure Period)	Concentration Factor	EC50 (µg/L)	MEC ppm	Remarks
Aldrin		-	-	-	0.1	Butler et al. 1962.
Arochlor	1016	-	-	10.2		Hansen et al. 1974.
	1254	1 ppb (30 wk)	101,000	-	-	No effect on growth. Lowe et al. 1972.
		5 ppb (24 wk)	85,000	-	-	Growth reduced. Histopathological damage. Lowe et al. 1972.
		5 ppb (6 mo)	-	-	-	Abnormal infiltration of leucocytes in connective tissue. Nimmo et al. 1975.
BHC		(28 d)	218	-	-	Schimmel et al. 1977b.
Chlordane		-	-	6.2	-	4.7 µg/l retarded shell growth. Parrish et al. 1976.
					0.01	Butler et al. 1962.
DDD		-	-	-	1.0	Butler et al. 1962.
DDT*		-	-	-	0.1	Butler et al. 1962.
		1 ppb (4 d)	-	-	-	Shell growth inhibited by 20%. Butler 1974.
		10 ppb (7 d)	70,000	-	-	Butler 1974.
o-Dichloro- benzene		-	-	-	1.0	Butler et al. 1962.
Dieldrin		-	-		0.1	Butler et al. 1962.
		-	-	12.5	-	Parrish et al. 1974.
		0.001-0.1 ppm	5100-5400	-	-	No histopathological damage. Emanuelson et al. 1978.
Endrin		-	-	-	0.1	Butler et al. 1962.
		-	-	14.2		4.9 µg/L retarded shell growth. Schimmel et al. 1975.
		0.1 µg/L (168 h)	-	1670	-	Mason and Rowe 1976.
		50 µg/L (168 h)	-	2780	-	90% mortality. Mason and Rowe 1976.

Table 2 continued.

Chemical	Concentration (Exposure Period)	Concentration Factor	EC_{50} (µg/L)	MEC ppm	Remarks
Heptachlor	-	-	-	0.01	Butler et al. 1962
	-	2800-21,300	1.5	-	Schimmel et al. 1976
	-	-	-		
Kepone	(19d)	-	10,000	-	Bahner et al. 1977
Mirex	-	73,700	-	-	Not more lethal than controls. Tagatz et al. 1976
Parathion*	1 ppb	-	-	-	No effect on tissues or health. Lowe et al. 1971
	-	-	-		
PCB isomers	(1 mo)	1200-48,000	-	-	Vreeland 1974
Rotenone	-	-		-0.01	Butler et al. 1962
Sevin	-	-	-	1.0	Butler et al. 1962
Sodium Pentachlorophenate	2.5 ppb (28 d)	78	-		Schimmel et al. 1978
	25.0 ppb (28 d)	41	-	-	Schimmel et al. 1978
	-	-	-40[a]	-	Borthwick and Schimmel 1978
	-	-	76.5[b]	-	Schimmel et al. 1978
Toxaphene*	-	-	-	0.1	Butler et al. 1962
	-	9000-15,200	16.0	-	Schimmel et al. 1977a

* At 1 ppb, each of these 3 substances had no significant effect on oysters. However, all 3 together led to weight loss and changes in tissue morphology and histopathology (Lowe et al. 1971)

a 48h EC_{50}

b 192 h EC_{50}

Additional studies on combinations of common pesticides are needed. Further, does salinity stress (e.g., in oysters in the upper reaches of the Bay and its tributaries) lessen resistance to pesticide effects? Information concerning experimental effects of pesticides on oyster growth and tissue pathology is provided in Table 2.

With regard to oyster larvae, Calabrese (1972) noted that "safe" levels of pesticides (and this can be extended to other chemical agents) would be those levels that did not affect embryonic survival (zygotes to two-day-old veligers) or growth and survival of the planktonic larvae older than two days. Slow growth for these floating stages prolongs their pelagic existence and thus their exposure to predators. "Safe" levels should be determined for common pesticides and also for the phytoplanktonic food of larvae (and adults). For example, Ukeles (1962) found that the tolerance of larval food organisms to pesticides was lower than the tolerance of the larvae themselves.

The most extensive surveys of pesticide effects on survival and growth of *C. virginica* larvae were performed by Davis (1961) and Davis and Hidu (1969a). The test chemicals of the latter survey included 17 insecticides, 12 herbicides, one nematocide, four solvents, and 18 miscellaneous bactericides, fungicides, and algicides. However, some of the tests were incomplete and much remains to be learned. In general, some chemicals affected embryos more than they did larvae; for other chemicals, the opposite was true. Some pesticides such as Endrin and Dieldrin gave variable results within replicates, demonstrating the necessity of strict quality control during experimentation.

Chesapeake Bay monitoring programs have been described briefly by Munson and Huggett (1972). These programs need to be continued to provide early warning of possible public health hazards like the Kepone contamination of the James River.

However, in addition to the problem of contamination of a human food product there is the concern about the effect of pesticides on adult and larval oysters themselves. For example, Tripp (1974) described experiments on effects of two organophosphate pesticides (Abate and Dibrom) on survival, gametogenesis and spawning of *C. virginica*. Exposures 300 to 400 times the pesticide concentrations that might normally be experienced in the field produced no significant increase in mortality. Pesticide-treated oysters did not mature rapidly (although lack of food was probably a compounding factor), and spawning was inhibited under field conditions. Further experiments on well-fed oysters subjected to high concentrations of these two pesticides found no important inhibition of maturation or spawning, suggesting a synergistic effect of lack of food and presence of pesticide load. Experiments which involve a variety of pesticides commonly used around Chesapeake Bay and an assessment of their sublethal effects on reproduction and growth can be valuable and more should be performed.

Synergistic effects of exposure to combinations of pesticides were noted by Lowe et al. (1971), who found that low levels (1 ppb) of DDT, toxaphene, and parathion did not significantly affect the growth of *C. virginica* However, a mix (1 ppb each) of the three insecticides resulted in significant weight loss after nine months. Histopathological changes also occurred in tissues and a mycelial fungus attacked experimental oysters.

Detergents

Alkyl-benzene sulfonate (ABS) detergents, which are only slowly degraded by bacteria, have been generally replaced by biodegradable linear alkylate sulfonate (LAS) detergents. However, oyster embryos and larvae appear to be no more tolerant to LAS detergents and their degraded products than they are to ABS detergents; indeed the former may be more toxic (Calabrese 1972). Growth of oyster larvae was not affected by LAS concentrations of 0.0025 to 0.25 mg L^{-1} but was sharply affected above 0.25 mg L^{-1}. Larval survival was reduced significantly at concentrations of 0.5 to 1.0 mg L^{-1} of LAS. Concentrations of 0.1 mg L^{-1} resulted in 36% mortality of test larvae, and many survivors were abnormal in size or shape. Calabrese (1972) concluded that efficient sewage treatment plants would have to produce enough effluent to approach 15% of the total volume of receiving water before oyster larval development, survival, and growth was affected by detergent materials.

Concluding Statement

Given the number of industrial, agricultural and household chemicals which arrive in Chesapeake Bay daily, the evaluation of their effects on each life stage of the oyster is an immense task. It is exacerbated by possible synergistic effects, compounded by any differential responses caused by oyster condition, size, age, disease, and parasite burden. The role of environmental factors such as salinity, temperature, or dissolved oxygen also should not be overlooked. In addition to increasing our knowledge of the effects of these factors on survival of oyster life history phases, there is a need for more information on sublethal effects on oyster growth, reproduction, larval viability, spat settlement and growth, disease resistance and on oyster food organisms.

FEEDING AND NUTRITION

A shucked oyster's market value depends upon a high condition index, i.e., a large amount of stored glycogen, lipid and germinal tissue in proportion to internal shell volume. This in turn depends upon its feeding behavior, nutrition, and reproductive state (Korringa 1952). Successful culturing efforts in either field or hatchery require a thorough understanding of filter-feeding activities, ingested food ration, and nutritional requirements of oysters, including both biochemical aspects and the relative food value of different diets. Although a great deal of current research is dedicated to the definition and description of oyster feeding behavior and nutrition, complete understanding has not yet been achieved.

Sources of Comparison Error

Apparent contradictions in the literature relating to feeding and nutrition may be due to differences between the species of oysters or food organisms studied or to the experimental techniques used. Feeding habits of *Ostrea* spp. and *Crassostrea* spp. vary greatly due to morphological, anatomical, and behavioral differences (Nelson 1938, Menzel 1955). Attempts to generalize about oyster feeding processes from findings on specific species may result in conflicting interpretations. A number of morphological, anatomical, and behavioral adaptations enable *Crassostrea* spp. to cope more efficiently with large amounts of suspended particulate matter than can *Ostrea* spp (see section on Sediment and Dredging).

Conclusions based on field observations of littoral oysters should not automatically be extended to include sublittoral populations, since digestive rhythms that are imposed in one environment may be lacking in the other (Loosanoff and Nomejko 1946, Winter 1978). The many variables involved in feeding experiments make comparisons (i.e. temperature, density) between different experiments difficult (Wilson 1978). Equal food rations must be maintained when testing the effect of these variables on feeding. Laboratory apparatus itself may seriously alter the results. Filtration capabilities of oysters in small, closed volumes of water may differ widely from those in large or constantly flowing volumes, even if initial concentrations of suspended material are identical in each case (Loosanoff and Engle 1945).

Techniques used to study functions of the oyster's gills and palps, such as removal of one valve (Nelson 1938, Jørgensen 1976, Bunde and Fried 1978), insertion of a glass window into a valve (MacGinitie 1941, Foster-Smith 1975, 1978), or the observation of young oysters which have set on glass slides (the "glass oyster" techniques of Nelson 1923b, 1938, Menzel 1955), can influence experimental results and their interpretation. For example, if a valve is removed or the shell broken, the gill cilia remain in motion regardless of the contraction of the adductor muscle, which would normally close the valves and cause ciliary action to cease (Menzel 1955).

Slight variations in culturing techniques produce algal cells of differing chemical composition and perhaps differing nutritional value (Saddler and Taub 1972, Breese et al. 1977, Flask and Epifanio 1978, Wilson 1979). Bacterial flora (Miller and Scott 1967a), algal cell concentration, and algal physical form (Ukeles 1971) may not be consistent. Cultured algae may not be directly comparable to natural or wild food sources. Furthermore, the condition of the larvae and their nutritional requirements may vary from one study to another (Wilson 1978). However, if care is taken, some comparisons may be made while allowing for these possible influences.

Filter-Feeding Mechanisms

Adult

The mechanical process of feeding in adult oysters is well documented (Nelson 1938, 1960, Korringa 1952, Menzel 1955, Jorgenson 1966, 1975, 1976, Owen 1974, Winter 1978). Galtsoff (1964) provides an excellent and detailed look at the anatomy and physiology of the gills, so his efforts will not be repeated here. Briefly stated, particles carried on streams of water pass through the gills and become entrapped, bound in mucus and transferred towards food-collecting furrows. Masses of collected food are conveyed in strings of mucus to the labial palps where particulate matter is sorted, either to be passed on to the mouth or rejected as pseudofeces. Figure 1 shows the major feeding organs of the oyster.

Role of Mucus. The role of mucus in particle retention and sorting is not completely understood. Much of the diet of different species of oysters may consist of very small particles, some smaller than 2 µm, although retention efficiencies are greater with particles in the size range of 3 to 10 µm (Haven and Morales-Alamo 1970; Kusuki, *C. gigas*, 1977b; Møhlenberg and Riisgard, *O. edulis*, 1978). Critical size for retention of particles in *C. virginica* corresponds to the distance between the laterofrontal cilia, or approximately 1.5 to 3.7 µm (Jørgensen 1966).

MacGinitie (1945) postulated that extremely minute particles are strained from the water by means of a mucous sheet previously secreted by a portion of the gills. Bernard (*C. gigas*, 1974a) noted the presence of a thick (approx. 12 µm thick and 20 µm wide) mucous band overlying the frontal cilia on each gill filament. He believed this band functioned in entrapment of particles, much like MacGinitie's mucous sheet. Other investigators have rejected this idea, labelling the mucous sheet as either a response to physical or chemical stimuli (Nelson 1960), as an artifact of experimental technique (Foster-Smith 1975), or as a method of gill cleaning (Jørgensen 1976). Nelson (1960) argued that a mucous

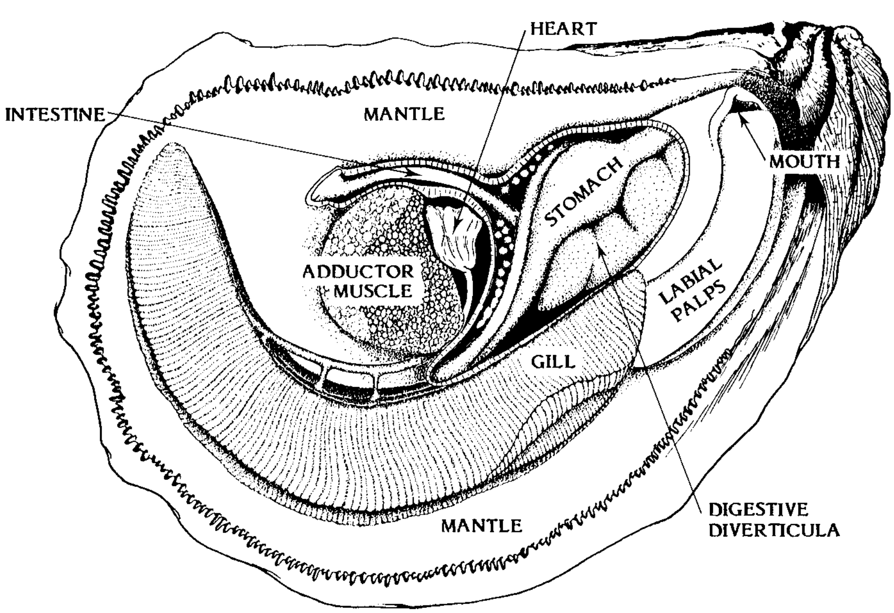


Figure 1. Diagrammatic sketch of an oyster showing internal parts. (From Ashbaugh, B.L., l951)

sheet created in advance would interfere with cilia and their pumping function. Jørgensen (1976) questioned the entire role of mucus in particle retention, observing that only a minor part of the algal cells collected by the gills become entrapped. He reported that the majority of the retained particles were carried on water currents above the ciliary tracts. Foster-Smith (1975) suggested that instead of a mucous sheet being employed, the cilia of filterfeeding bivalves are "branched" like those in *Mytilus* sp. (Winter 1978) and are capable of trapping minute particles. Moore (*Mytilus edulis*, 1971) and Ribelin and Collier (1977), using scanning electron microscopy, did in fact determine that each cirrus of the cirri has 3-10 pairs of fringing cilia. Since the average spacing between each cilium is less than 0.7 µm, filtration of particles smaller than 1 µm should be possible.

Particle Sorting. Particle sorting by differential mucous secretions is another controversial aspect of oyster feeding. The majority of mucous glands on the gills lie between the two rows of cilia. Many researchers have stated that the amount of mucus secreted depends upon the degree of mucous gland stimulation by particles, with large particles evoking more copious mucous secretions than small particles (Menzel, *C. virginica*, *O. edulis*, 1955; Nelson, *C. virginica*, *O. edulis*, 1960; Bernard, *C. gigas*, 1974a; Foster-Smith 1978). Sorting takes place on the ciliated and deeply ridged labial palps. It is postulated that on these palps selection of food particles is dependent upon the size and density of the particle-mucus mass (Jørgensen 1966). Large, inorganic particles are made yet larger by addition of more mucus from glands located on palp ridges (Nelson 1960) and are transported on surface ciliary tracts to be rejected as pseudofeces. Smaller organic particles follow a deeper, sinuous path of ciliary tracts towards the mouth. Final acceptance or rejection of particles is determined mainly by the amount of mucus secreted by the gills and palps.

Bernard (*C. gigas*, 1974a) and Foster-Smith (1975) questioned the concept of a prominent role of mucus in particle selection. Labial palp pairs are usually studied as separate surfaces rather than as a single entity. Therefore, the reported ciliary activity may have been distorted and misunderstood (Bernard 1974a). Bernard suggested that palps are predominantly mucus-reducers with the ability to reject the entire mucus-particle load on their surfaces. Foster-Smith (1975) observed that loose particles presented to palps are sorted before being bound in mucus. This aspect of feeding in oysters requires further study.

Qualitative Selection Active selection of food particles on a qualitative rather than quantitative basis is poorly understood. Winter (1978) asserted that filter-feeders have no selective abilities, save those dealing with particle-mucus size and quantity. The very nature of mucus-embedded particles would seem to reduce the effectiveness of qualitative selection (Foster-Smith 1975). However, the ability of some bivalves to select their food actively has recently been confirmed by Kiørboe et al. (1980). They found that mussels (*Mytilus edulis*) were able to select algal particles in preference to silt particles (average silt particle size was 9.6 µm). It appears likely that *Crassostrea* spp. may also have selective capabilities (Grave 1916; Morse 1944), since stomach contents do not correspond to phytoplankton composition in the water column. For instance, Grave (1916) seldom found the small diatom *Rhizosolenia* sp. (species not given) in oyster alimentary tracts, although this species was abundant in the overlying sea water.

Behavior of particle-mucus masses on the labial palps as described by Menzel (1955) may provide a mechanism for selection of mucus-embedded particles. Individual particles break off a particle-mucus mass and are sorted at the apex of the palps, with food particles directed towards the mouth and non-food particles carried back to the mass for eventual rejection as pseudofeces. Menzel further noted that particles accepted as food may be larger than those rejected as pseudofeces. Loosanoff (1949a) reported that, while yeast cells offered to oysters were rejected, plankton organisms of the same size and shape mixed in with the yeast cells were readily accepted. Similarly, he observed that oysters selectively rejected as pseudofeces the small (2-3 µm in diameter) purple sulfur bacteria, *Chromatium perty*, from a mixed algal culture. Bernard (1974a) objected that in Loosanoff's experiment, selection was not taking place on the palps but that irritation of the gills by hydrogen sulfide in the culture media may have caused rejection of the bacteria He further postulated that preferential digestion of bacteria in the stomach would disguise bacterial remains in the feces.

Other investigators have reported that oysters are capable of detecting small differences in potential food material (Dwivedy 1973a,b; Mathers, *O. edulis* and *C. angulata*, 1974b; Epifanio and Ewart 1977). Epifanio and Ewart (1977 suggested that *Isochrysis galbana* was selectively filtered from suspension by *C. virginica*, since both smaller algae (*Thallasiosira pseudonana*) and larger algae (*Carteria chuii*) were removed at a lower rate.

Loosanoff's (1949a) suggestion that food selection depends upon the nature of secretions of different organisms reaching the palps assumes the presence of chemoreceptors on the palps. Galtsoff (1958a) mentioned the existence of numerous sensory cells with long processes on the palps. Nelson (1960) noted that the palps responded to mechanical, electrical, and chemical stimulation as well as to light intensity. More recently, electrical responses which occur after chemical stimulation of the sensory cells have been measured (Dwivedy 1973a,b). These "taste" cells respond to all four major taste categories (i.e., saline, sweet, bitter, and sour). Saline and sweet substances, by stimulating the least rejection responses, are considered the most preferred substances, while bitter and sour (i.e., acidic) substances are the most stimulating and therefore the least preferred. It is advantageous for a marine animal to accept saline substances; otherwise, seawater itself would provoke copious mucus secretions.

Success or failure of algal or artificial diets may depend upon their "taste" qualities. More research is needed to determine the importance of taste as an aid to food selection in oysters.

Larvae

The larval feeding process and how metamorphosis affects it are understood only in a most rudimentary way. Cilia of the velum direct food particles towards ciliary tracts or food grooves at the base of the velum (Yonge 1926, Jørgensen 1966). Particles appear to be embedded in mucus and sorted, accepted particles being carried on to the mouth while rejected particles are dropped off at the "foot rudiment." Ciliary mechanisms concerned with elimination of surplus material are well developed (Menzel 1955). Strathmann and Liese (1979), using high speed microcinephotography to study feeding *C. virginica* larvae, observed that the spacing of cilia did not determine the minimum size for captured particles. Other mechanisms must be in operation in addition to such sieving.

At metamorphosis, palps grow rapidly from the apical region of the velum and take over the velum's function as the food collecting organ (Jørgensen 1966). Juvenile palps are of a relatively large size (Menzel 1955).

Digestion

After being sorted on the gills and palps, food is carried in a mucous string to the alimentary canal with further sorting by the caecum occurring in the stomach (Menzel 1955, Nelson 1960, Jørgensen 1966). Menzel (1955) reported that the passage of a particle through the digestive system can be very fast. Transport of food particles to the palps may take less than five seconds. The food may reach the stomach in 40 seconds and can be deposited in feces in less than 16 minutes. This speed of transport does not necessarily mean that the particle has been subjected to the normal digestive processes.

The actual digestive process has not yet been satisfactorily determined. Whether digestion is largely intracellular, through leucocytes and cells lining the digestive diverticula (Nelson 1938), or extracellular, occurring in the stomach by the mechanical turning and chemical dissolution of the crystalline style (George 1952), or some combination of the two processes (Morton, *C. gigas* 1977; Mathers 1973) is still unresolved. Purchon (1968) and Owen (1974) provide a discussion of this subject.

Another poorly understood aspect of oyster biology, but one that has important aquacultural implications, is whether or not sublittoral oysters feed and digest food continuously. Jørgensen (1975) felt that digestion is potentially a continuous process in sublittoral bivalves. Undisturbed *C. virginica* maintain a fairly constant current of water through their valves, which are open 90% of the time. However, feeding or filtration rates do not necessarily equal pumping rates (Korringa 1952, Lund 1957b, Winter 1978). Langton and Gabbot (*O. edulis*, 1974) found that endogenous rhythms of digestion in intertidal oysters are lost under a continuous feeding regime in the laboratory. Continuously fed oysters may have a higher rate of growth (Winter 1978). On the other hand, Epifanio and Ewart (1977) reported that with steady, high concentrations of food, oysters exhibited periods of low filtration rates occurring simultaneously with periods of maximum digestive activity. Consequently they recommended use of a batch, or "pulsed," supply of food in aquaculture. Morton (*O. edulis*, 1971, 1973) and Purchon (1971) also agreed that feeding and digestion are rhythmic and discontinuous. Mathers (1972) suggested that discontinuous feeding may be an adaptation to an estuarine life style in which food may only be present during certain tidal stages.

Some investigators believe that digestion is dependent upon food availability, with feeding and digestion stimulated by high levels of suspended food followed by quiescent periods until the next stimulating high food level (Langton and Gabbott, *O. edulis*, 1974; Wilson and LaTouche, *O. edulis*, 1978). In intertidal waters, this cycle corresponds with the tidal cycle (Morton, *C. gigas*, 1977; Winter 1978), although the influence of tidal rhythms on sublittoral oysters has been disputed (Wilson and LaTouche, *O. edulis*, 1978). Langton and McKay (*C. gigas*, 1974, 1976) reported consistently higher growth in spat with a discontinuous feeding regime. This feeding method creates an initially high concentration of food which appears to stimulate oysters to filter the water at maximum rate. In addition, it enforces a digestive rhythm upon oysters including a "rest" period which may provide a net energy saving and allow for an increase in growth (Langton and McKay 1976).

The initial fecal masses are composed almost entirely of unutilized "food," or live algal cells, loosely bound in mucus (Dinamani 1969). Those feces have a different texture, color, and form with a higher mucus content than those produced later. This may confirm the existence of an initial preparatory phase in digestion corresponding to the stimulation of style dissolution.

Evidence confirming or rejecting the presence of a diel pattern of feeding in oysters is still inconclusive. Many investigators have reported existence of photoreceptors in the mantle of oysters (Nelson 1938, Menzel 1955, Lund and Powell 1957, Nelson 1960, Bernard, *C. gigas*, 1974a). These photoreceptors have been linked to the pumping mechanism, with a decrease in illumination causing an inhibitory response in pumping activity (Lund and Powell 1957). In field studies, Nelson (1923a) reported a period of inactivity for *C. virginica*, with the major portion of inactivity occurring during darkness. However, Loosanoff and Nomejko (1946) found no such pattern.

Current studies in Delaware are testing the effects of continuous and discontinuous feeding regimens over broad ranges of algal concentrations and temperatures (C. Valenti 1981, University of Delaware, personal communication). Further studies are needed to determine if feeding and digestion are continuous or if there is a rhythmic alternation between these two activities.

Larval digestion is similar to that of adults, with a continuity of structure and function of organs from the larval to the adult phase (Miller, *O. edulis*, 1955). The gut is shorter in larvae than in adults, tending to reduce digestive efficiency (Walne, *O. edulis*, 1965). Recently, Babinchak and Ukeles (1979) used epifluorescence microscopy to study uptake, lysis, and digestion or rejection of algal cells. By following autofluorescence of chlorophyll a and its derivatives through the larval body, they were able to determine whether or not larval oysters were capable of digesting particular algal cells. The process of food consumption as well as digestion occurred more rapidly with the increasing age of the larvae.

Environmental Effects

Rate of water transport through the oyster is directly dependent upon the activity of the cilia, the changes in the size of the ostia, or interfilimentar spaces in the gills, and the changes in the size of the inhalent and exhalent apertures (Moore 1977). These in turn are affected by environmental factors such as salinity, temperature, pH and suspended silt or food concentrations. Most of these factors have been discussed in the section on Environmental Factors.

Food Concentration

Food concentration has been shown to play a major role in the determination of filtration rates of bivalves. From a low threshold concentration upwards, filtration rate increases rapidly and then is kept constant up to a food concentration at which a maximum of food is ingested (Winter, *Mytilus edulis*, 1978). As soon as this maximum ingestion rate is reached, filtration rate decreases continuously in such a way that the amount of food ingested is kept constant (Ukeles 1971). At higher food concentrations, production of pseudofeces begins and fecal production tends to decline (Wisely and Reid, *C. commercialis*, 1978). At still higher food concentrations, however, filtration and ingestion rates are drastically reduced (Malouf, *C. gigas*, 1971; Kusuki, *C. gigas*, 1977a; Winter 1978). Loosanoff and Engle (1947) listed threshold concentrations for different algae, above which the density began to interfere with feeding of 4- to 6-year old oysters. These threshold concentrations were proportional to algal size. For *Chlorella* sp. (approx. 5 µm in diameter), *Nitzchia closterium* (size not given), and *Euglena viridis* (60 µm long), threshold densities were 2,000,0000 cells ml^{-1}, 70,000 to 80,000 cells ml^{-1}, and 3,000 cells ml^{-1} respectively. Where food concentrations normally remain below incipient limiting levels, feeding rates and growth vary directly with food levels (Jørgensen 1975). For a given set of physical parameters, food concentration controls growth rate much the same as concentrations of reactants control the rate of a chemical reaction (Walker and Zahradnik 1977). Only in euphotic waters would food levels begin to hinder feeding mechanisms (Jørgensen 1975).

Loosanoff and Engle (1947) found that at very high algal concentrations, not only did pumping rates decrease, but often the oysters became sluggish in response to stimuli. These effects persisted even after most algal cells were filtered from the medium. They hypothesized that perhaps either toxic metabolites excreted from dense algal concentrations or the highly concentrated nutrients used to culture the algae were the cause of the problem. The decrease in pumping rates with aging of the water as reported by Ray and Aldrich (1961) may similarly be explained as due to toxic metabolites. Increased bacterial populations associated with unutilized components in algal cultures aggravated by high temperatures may result in oyster mortalities (Heller and Taub 1971; Lipovsky and Chew, *C. gigas*, 1973, 1974).

While field studies have shown that areas of highly sustained phytoplankton production-dependent upon adequate nutrient supplies-result in good oyster condition (Westley, *C. gigas*, 1964), extreme phytoplankton production or algal blooms result in poorer oyster condition or death (Davis and Chanley 1956, Jørgensen 1966). Manzi et al. (1977), conducting studies in salt marsh impoundments and their associated tidal creeks, reported an inverse relationship between nutrient concentrations and oyster growth. In field situations, toxicity of high algal concentrations may be alleviated by hydrographic conditions (Westley, *C. gigas*, 1964). For example, unstratified water with rapid exchange may prevent toxins from accumulating, except in extreme algal blooms, while stratified deep or shallow waters with little mixing may tend to concentrate toxins.

Loosanoff and Engle (1945) suggested that seasonal control of phytoplankton populations determines oyster condition. In northern latitudes, phytoplankton is less abundant from October to December, coinciding with the period of greatest oyster fattening. If oysters can use low food concentrations more efficiently than they can high food concentrations, this coincidence is not surprising. However, this fattening could be due more to the reproductive cycle (oysters at this time storing up energy for future spawning) than to seasonal food concentrations.

Maximum daily ration of food for *Crassostrea virginica* depends upon the species of algae in the diet (Epifanio and Ewart 1977), size of the algal cell itself (Loosanoff and Engle 1945, 1947), and, for larval feeding, larval size (Rhodes and Landers 1972). For a 15-gram whole weight oyster in laboratory culture, Epifanio and Ewart (1977) recommended a food ration of 4 mg algal dry weight per gram whole weight of oyster per day for diets consisting of algal species *Thalassiosira pseudonana* and *Carteria chuii*. For diets of *Isochrysis galbana* (a much smaller alga) nearly four times this amount was recommended. In larval diets of *Isochrysis galbana*, and for larval densities of 15 larvae ml^{-1}, Rhodes and Landers (1972) advised increasing food ration from approximately 1,667 algal cells per larva per day (2.5 µl packed cells L^{-1}) to 21,667 cells per larva per day (32.5 µl packed cells L^{-1}) as the larvae increase from 74 µm to 246 µm in length.

Dissolved Substances

“Wild” oysters grow at a much greater rate than do oysters reared under optimum aquacultural conditions with phytoplankton and particulate organocarbon concentrations similar to natural concentrations (C. Valenti 1981, personal communication). Dissolved substances may be among the factors responsible for this growth difference. Ukeles (1971), reviewing the literature, found reports documenting the presence in seawater of substantial amounts of naturally occurring dissolved substances including phosphate and calcium ions, amino acids, carbohydrates, and lipids. Several experiments indicate that oysters absorb and utilize at least some dissolved substances (Ukeles 1971). Bamford and Gingles (1974) found that glucose and galactose were absorbed against a gradient in the gills. The mantle may be metabolically active as well and may provide another important pathway for the uptake of dissolved substances (Bamford and Gingles 1974, Moore 1977). Both radioactive chromium (Preston 1971) and labelled palmitate, a dissolved fatty acid (Bunde and Fried 1978), were accumulated more readily by soft-body surfaces than by ingestion.

Ukeles (1971) suggested that oysters are obligate phagotrophs, ingesting most of their food in particulate forms, though able to fill some of their needs by absorbing solutes. The role of soluble substances in nutrition of natural oyster populations needs further clarification but, considering the normally low level in most habitats, the total contribution to the oyster energy budget is likely to be small. However, bivalves also lose organics in the form of ammonia-nitrogen, the byproduct of protein catabolism, and amino acids are excreted during hypo-osmotic salinity stress, so the net flux of dissolved organics must be considered (R. Newell, 1981, Horn Point Environmental Lab, personal communication).

Nutrition

The nutritional requirements of adult and larval oysters have been studied intensively. Use of artificial feeds in both larval and adult culture have been investigated by many researchers (e.g., Ukeles 1976). However, nutritional requirements of oysters (both adult and larval) in the field, and food availability and fluxes are research topics which have been explored only superficially.

Larval Nutrition. *Crassostrea virginica* larvae are quite selective in their choice of food and often perish before metamorphosis because of the absence of the proper quality and quantity of planktonic food (Korringa 1952). Naked flagellates and nannoplankton appear to be important food sources for larval oysters, although similarly sized bacteria do not seem to be utilized (Davis 1953). Davis (1953) found that of 13 species of bacteria tested, including a sulfur bacterium, none were utilized by oyster larvae. However, Hidu and Tubiash (1963) found circumstantial evidence that *Mercenaria mercenaria* and perhaps *C. virginica* larvae may use certain bacteria as food. Cultures were treated with an antibody (dihydrostreptomycin-streptomycin) sulfates and inoculated with a mixed flora of marine bacteria The bacterial flora induced by the antibiotic appeared to produce greater clam larval growth than did bacteria-free cultures. However, clam larvae may be able to utilize a greater variety of food than oyster larvae (Ukeles 1971).

Ukeles (1971) in a review of the literature discusses further the role of bacteria in oyster nutrition. Non-toxin producing bacteria may reduce the toxicity of some species of algae (e.g. *Prymnesium parvum*). On the other hand, large numbers of innocuous bacteria may reduce the food value of a given algal species. Since the quantity of bacteria introduced with food culture is not negligible (Prieur and LeRoux 1975), the bacterial impact could be important.

Different size ranges of phytoplankton are important for different sizes of *C. virginica* larvae. Straight-hinge larvae selected phytoplankton in the 1 to 10 µm range, early and late umbo larvae selected algal cells up to 18 µm, and eyed larvae selected cells up to 30 µm (Mackie 1969). Guillard (1958) found that small naked flagellates were necessary for oyster larvae and adequate for juvenile oysters. The latter are able to use some food organisms (e.g., cryptomonads, *Skeletonema costatum*, *Actinocyclus* sp.) which are useless to larvae. Ukeles and Sweeney (1969) found that numbers of discharged trichocysts or surface structures of dinoflagellates could impair feeding of small *C. virginica* larvae (approx. 75 µm) by blocking their mouths (which are less than 10 µm wide).

In addition to selection of the best food for larval oysters, the diet of the parent stock must also be considered in oyster culture. Helm et al. (1973) found that larval vigor in *O. edulis* was positively correlated with the proportion of lipid which larvae had received from the parent. Parent oysters in a density of approximately one adult per 3 liters of water and receiving an algal supplement of $10x10^6$ cells L^{-1} of *Tetraselmis suecica* produced healthier, more vital larvae than those receiving no supplement. This is perhaps of more importance to *O. edulis* larvae which do not feed in the early stages of metamorphosis (Miller and Scott 1967b; Holland and Spencer 1973). Nevertheless, it should be considered for the culture of larvae of *Crassostrea* spp. as well.

The best single-species diet for *C. virginica* larvae has been reported to be either *Isochrysis galbana* or *Monochrysis lutheri* (Davis and Guillard 1958). Walne (*O. edulis*, 1970) found that *Monochrysis lutheri*, *Chaetoceros calcitrans*, *Tetraselmis suecica*, *Skeletonema costatum* and the algae *Dunaliella tertiolecta* and *Phaedoactylum tricornutum*, when assimilated, produced better larval growth at low food densities than did *I. galbana*. *Hemiselmis virescens* was found to induce some growth, but not as well as *I. galbana* Wilson (1978) also found *P. tricornutum* to be similar in food value to the *I. galbana* controls in his study for *C. gigas* D-veligers. However, most larvae may be unable to digest the cell wall of *P. tricornutum* (Davis and Guillard 1958).

High concentrations of *Chlorella* sp. have been found to have adverse effects on larvae, i.e., either decreasing growth rate or increasing mortality (Walne, *O. edulis*, 1963; Helm, *O. edulis*, 1977; Babinchak and Ukeles 1979). Davis (1953) and Walne (*O. edulis*, 1965) reported that *Chlorella* sp. were of little or no value to larvae. Presence and thickness of food cell walls as well as degree of toxicity of metabolites appear to be important factors in determining food value of microorganisms (Davis and Guillard 1958). Davis and Calabrese (1964) found *C. virginica* larvae to show significant growth at low temperatures while on a diet of naked chrysophytes such as *Monochrysis lutheri* and *Isochrysis galbana*. Diets consisting of chlorophytes with cell walls such as *Chlorella* sp. produced less growth in larvae at low temperatures. Davis and Calabrese (1964) hypothesized that the enzyme systems needed to break down cell walls were inactive at these low temperatures. Guillard (1958) found *Chlorella* isolate "A," *Amphidinium cartera*), *Gymnodinium* sp. and *Prymnesium parvum* to be toxic to oyster larvae.

Mixtures of different algae have been shown to promote more rapid growth than single algal diets (Davis and Guillard 1958; Dupuy 1975; Sunderlin et al., *C. gigas*, 1976, Helm, *O. edulis*, 1977). Davis and Guillard (1958) found that mixtures of the chrysophytes *Isochrysis galbana* and *Monochrysis lutheri*, and the chlorophytes *Dunaliella euchlora* and *Platymonas* sp. produced more rapid growth than did an equal amount of any of those foods separately. A mixed diet of *I. galbana* and *Tetraselmus suecica* was also found to promote growth superior to that achieved with single food diets (Helm, *O. edulis*, 1977). The enhanced growth of larvae fed a mixture of species may be due to deficiencies in nutritionally important components in one species being remedied by other species in the mixture (Winter 1978). Natural populations of phytoplankton are usually mixtures of different algal species and only rarely comprise a single species (Jørgensen 1966).

In addition to nanno- or phytoplankton, oyster larvae have been observed to accumulate dissolved organic carbon (Fankboner and DeBurgh, *C. gigas*, 1978). This accumulation is up to 25% greater in pediveligers than in juveniles. Davis and Chanley (1954) reported that the addition of vitamins (e.g., riboflavin) to a "poor" food such as *Chlorella* sp. enhanced growth of both *C. virginica* and *O. edulis* larvae. Nutritional value of a "good" food was enhanced to a lesser extent.

Adult Nutrition. Adult oysters in the field have been found to contain, by gut analysis, diatoms and algal spores (McCrady 1874); the free-living nematode *Chromadora* sp. (Nelson, *O. edulis*, 1933); diatoms and other algae, dinoflagellates, tintinnids, silico-flagellates, ostracods, eggs and larvae of m marine invertebrates, pollen grains from land plants, detritus, sponge spicules, and sand grains (Morse 1944); diatoms and blue-green algae (Flint 1956); diatoms, algae, and peridinians (Noor-Udin, *Crassostrea* sp., 1962) and phytoplankton and zooplankton (Hariati, *C. cucullata*, 1976). Extremely small nannoplankton such as naked flagellates are often difficult to identify in gut analyses since they tend to decompose rapidly into amorphous, gelatinous masses (Martin 1923); thus they may be under-represented.

Current research by G. W. Patterson in Chesapeake Bay is investigating the link between lipid composition of oysters and that of algal populations. Sterols, in particular, are important dietary elements associated with rapid growth, reproductive processes, and larval vigor. Berenberg and Patterson (1981) have found that oyster sterol composition reflects dietary steroL Isomers of sterols isolated from oysters indicated that marine algae, diatoms in particular, rather than detritus from terrestrial plants formed the major portion of the oysters' diet. Currently, Patterson (personal communication) is comparing the sterol composition of oysters from both good and poor spat set areas and good and poor growth areas to determine the physiological effects of sterol composition. In addition, the sterol compositions of algal species known to be “good” oyster foods will be compared with species known to be inadequate to determine a nutritional basis for observed food differences.

Much work is being done to determine relative food values of different ingested materials, especially algae. Detritus is not considered to be a valuable adult oyster food (Glancy 1944, Jørgensen 1975). Glancy (1944) discounted the importance of detritus for oyster fattening because its presence was more or less constant in Great South Bay, New York, while oyster fattening varied widely from year to year. He found a correlation between fattening of oysters with presence of the diatoms *Skeletonema* sp., *Chaetoceros* sp. and *Thalassiosira* sp. Nelson (1947a) similarly reported a correlation between oyster fattening and large numbers of the diatom *Skeletonema costatum* in New Jersey waters. At high food levels, *Thalassiosira pseudonana* and *Skeletonema costatum* induced higher feeding levels while the same levels of *Dunaliella tertiolecta* depressed feeding rates (Tenore and Dunstan 1973). Epifanio (1979b), comparing nutritional effects of different algal species, found diets of *Isochrysis galbana* and *Thalassiosira pseudonana* to produce high growth while *Carteria chuii* and *Platymonas suecica* produced the least growth in *C. virginica*. Diets containing a combination of algae (both *I. galbana* and *T. pseudonana*) were found to promote greater growth than did diets consisting of only a single species. Epifanio (1979b) concluded that this indicated synergism in relative food values of the algal species. He hypothesized that relative food values may be a result of either deficiencies in some growth-promoting micronutrients or differences in digestibility of the substances.

Differences in algal response to the crystalline style as it dissolves in the stomach may explain differences in digestibility (Dean 1958, Davis and Calabrese 1964). Dean (1958) found *Crytomonas* sp. and *Monochrysis* sp. to be more sensitive to the style and its enzymes while *Isochrysis* spp. were less sensitive. He speculated that a “resistance” to digestion by some algae may be the cause of different nutritive values.

Dunaliella sp. and *Chlamydomonas* sp. have been described as “poor” foods for oysters (Tenore and Dunstan 1973, Jørgensen 1975). Tenore and Dunstan (1973) further noted that green algae (i.e., *Dunaliella* sp. or *Chlamydomonas* sp.) tend to be dominant forms in polluted or eutrophicated water. In addition, diatoms (i.e., *Thalassiosira* sp. and *Skeletonema* sp.) are adversely affected by organochlorine compounds (i.e., DDT or PCB) while the green alga *Dunaliella* sp. is relatively insensitive. Therefore, polluted waters may encourage the growth of “poor” oyster food organisms while discouraging that of “good” food organisms.

Feeding activities of oysters in Chesapeake Bay were found to fall into distinct periods coinciding with the seasons and characterized by a particular alga (Morse 1944). In autumn, 80% of the oysters’ food was a small diatom, *Cyclotella striate*. Winter was a period of hibernation, with feeding resuming in spring. The diatoms *Cerataulina bergonii* and *Nitzschia striate* formed a greater part of the oysters’ diet in spring, although *C. striate* was still important. While ingested algal species must obviously be present in the phytoplankton, mere presence in the water column did not guarantee ingestion. Morse reported that on April 25, 1944, *C. striate* and *C. bergonii* made up 5% and 79%, respectively, of the plankton in the water column, but 50% and 37% respectively of the ingested food in the oyster stomach. Large or bulky cells were not eaten (e.g., *Chaetoceras* sp., *Ceratium* sp. and *Rhizosolenia* sp.).

No recent literature exists on oyster diets in Chesapeake Bay. It would be interesting to see whether these algal species still form a major part of the oyster's diet, or if there have been changes in algal populations and consequently in diets.

Artificial Foods Populations of phytoplankton often fluctuate in their nutritional value and are frequently inadequate to provide healthy, good quality oysters (Glancy 1944, Saddler and Taub 1972, Breese et al. 1977, Flaak and Epifanio 1978, Wilson 1979). Efforts are underway to find suitable food supplements to remedy nutritional deficiencies and to increase glycogen content.

As early as 1951, tidal mud flats were fertilized with a mixture of super-phosphate and linseed oil, yielding a better quality or "fatter" oyster (Korringa 1952). Discovery of a naturally occurring carbobydrate-like substance that stimulated feeding rates (Collier et al. 1950) encouraged efforts to find food supplements. More recent efforts involve addition of various substances such as dried algae, yeast, glucose, dextrose, and finely ground cornstarch, cornmeal, or ricemeal to culture media Diets of dried algal preparations, while suitable for clam larvae, resulted in little or no growth of oyster larvae (Hidu and Ukeles 1962). Epifanio (1979a) compared yeast and algal diets for *C. virginica* and determined that growth of soft tissue of oysters decreased with amount of yeast in the diet. Willis et al. (1976) also determined that yeast does not enhance oyster quality since it is generally ejected undigested in the feces. A sugar, D-fructose, was found to be absorbed against an apparent concentration gradient by *C. gigas* spat (Schulte and Lawrence 1977). This suggests that dissolved sugars may be possible nutrient sources. Glucose enabled unfed oysters to live an average of 68.2 days longer than oysters given no glucose (Gillespie et al. 1965). However, Swift et al. (1975) found glucose to supply only a negligible portion of adult oysters' nutritional needs.

Haven and Turgeon (1968) and Turgeon and Haven (1978), comparing the effects of dextrose and cornstarch diet supplements on *C. virginica*, found that cornstarch significantly increased glycogen content, while dextrose had a lesser influence. Further, they noticed a seasonal pattern to the effects of the carbohydrate supplements. This seasonal effectiveness of diet supplements with an increase in tissue weights occurring in autumn had been noticed by previous investigators (Haven 1965; Sayce and Tufts, *C. gigas*, 1968; Willis et al. 1976). This pattern follows the natural seasonal cycle of oyster fattening in temperate waters. Oysters generally have a higher glycogen content in the fall, winter, and spring months than in summer months when gametogenesis uses up stored energy. However, by using the artificial fattening process and varying the optimum feeding rate, high quality oysters with a high glycogen content can be obtained in the summer as well (Willis et al. 1976).

Optimum feeding concentrations of supplemental, artificial foods seem to range from 2 to 4 mg L^{-1} (Wisely and Reid, *C. commercialis*, 1978), although feeding levels lower than this may be preferable in larval culture (Lund, *C. gigas*, 1973). Gillespie et al. (1966) found that varying concentrations of cornmeal supplements yielded different results. Higher concentrations produced greater glycogen content while lower concentrations gave superior shell growth and dry weight increase. Oysters may grow more rapidly and show higher glycogen content when fed diets richer in carbohydrates than in protein (Flaak and Epifanio 1978). Dunathan et al. (1969) found cornmeal and ricemeal to promote good growth, but they thought that perhaps other food constituents in addition to carbohydrates were contributing to the glycogen gain. Castell and Trider (1974) found that the type and amount of lipid in the diet was important in glycogen production. Diets containing cod liver oil, high in linolenic acid, produced oysters with a higher condition index (or higher meat weight to shell weight ratio) than did diets containing corn oil, which is low in linolenic acid.

Gabbott et al. (1975) tested the feasibility of a micro-encapsulated diet for *Crassostrea gigas*, An ideal microcapsule would have the following characteristics: small in size; non-toxic, impermeable wall; enzyme soluble or pH labile (i.e. easily digested); neutral buoyancy in seawater; containing a complete aqueous and oil based diet. The nylon-protein microcapsule studied by Gabbott et al. (1975) was 5 to 1,000 µm in size. In growth experiments using *C. gigas* spat smaller than 1 cm in length, the most suitable size range for capsules was less than 25 µm in diameter (compare this with cell sizes of typical algal foods: *Tetraselmis suecica*, 8.6 µm *Isochrysis galbana*, 4.8 µm; *Monochrysis lutheri*, 3.9 µm). The nylon-protein capsule wall, while non-toxic and susceptible to proteolytic digestion by spat, was flawed in that it was permeable to small molecules and could contain only particulate or macro-molecular components. In these experiments, the capsules contained a protein-starch-cholesterol mixture. Gabbott et al. (1975) found growth of *C. gigas* spat limited on this particular micro-encapsulated diet, presumably because it lacked vitamins and fatty acids. The researchers suggested further studies using micro-capsules as supplements to algal diets, the essential vitamins being provided by algal cells.

Sublethal Effects of Inadequate Food. Laboratory studies have demonstrated that one of the dominant factors affecting energy available for somatic and germinal growth of suspensionfeeding bivalves is food availability (Thompson and Bayne 1974, Winter and Langton 1975, Widdows 1978a,b). When food supply is deficient, even though a bivalve population may not suffer much mortality from starvation, significant sublethal effects may occur leading to reduced larval vigor and hence depressed recruitment and subsequent decline in population size. For example, blue mussels, *Mytilus edulis*, when stressed by variation in environmental factors such as elevated temperatures or reduced food ration, produce fewer and smaller eggs in smaller follicles than those formed in mussels in control, unstressed situations (Bayne 1975). Eggs from stressed adults also have significantly less lipid and protein, and the larvae have more developmental defects and grow more slowly.

Studies on *O. edulis* have found larval vigor (estimated in terms of percentage yield of spat and of growth rate) to decline (compared with vigor of larvae from better-fed adults) when adults were held in conditions of low food availability (Helm et al. 1973). Presumably, sublethal stress reduces the amount of energy available to be budgeted among various physiological processes (maintenance, growth, reproduction, activity) with fecundity and larval viability being negatively affected. This in turn can have an impact on the numbers of larvae surviving to set. Thus, subtle influences such as inadequate food supply may have major impacts on oyster populations. The exact role of food in influencing fecundity and larval vigor in *C. virginica* has not been ascertained.

Energy Budgets

The subject of energy budgets and flows in oyster populations is in its infancy; yet it is important in a thorough understanding of oyster physiology. Studies have been performed on *O. edulis* in Europe (Newell et al. 1977, Rod house 1978, 1979) and *C. gigas* in Canada (Bernard 1974b). For *O. edulis*, Newell et al. (1977) found energetic costs to rise sharply with temperature increase. Thermal optimum for clearance rates ranged between 15° to 18°C with a decline thereafter. Maximum filtration efficiency was attained at 20°C, a temperature which allowed for maximum scope for growth and reproduction. The authors concluded that the normal food rations available in local inshore waters in summer should allow for a positive index of energy balance in the populations they studied. Rodhouse (1978, 1979) was able to estimate values (in terms of energy consumed) for somatic tissue production (6% of energy consumed), gonadal output (6%), respiration (29%), excrete (28%), and feces (31%). Of the material filtered by *O. edulis*, 52% was deposited as feces and pseudofeces, rendering it available to deposit feeders and decomposers.

With regard to *C. virginica*, Dame (1972, 1976) studied ecological energetics of intertidal oyster populations in South Carolina. Much of the oysters' assimilated energy was used in growth, both somatic and gonadal. About 30% of the standing crop energy of the population was tied up in an energy sink, the shell. Reproductive energy varied from 0 to 48% of total production, depending on season. For the population sampled (comprising 1000-4400 individuals m^{-2} with a biomass of 1548-2513 kcal m^{-2}), production was high (P = 4132 kcal m^{-2} yr^{-1}), as was energy flow (A = 9788 kcal m^{-2} yr^{-1}) and net growth efficiency (P/A(100) = 42%). *C. virginica* outperformed other intertidal molluscs for which these values had been obtained elsewhere. These intertidal oysters in South Carolina appeared to be the most important primary consumer in the study area. Similarly, Bahr (1976) found the oyster reef community of Sapelo Island, Georgia, to be an important primary consuming entity.

These studies on *C. virginica* involved intertidal oysters in warm temperate southern locations. Similar evaluation of energy budgets needs to be performed on the sublittoral oyster populations of Chesapeake Bay. Newell (1981, Horn Point Environmental Lab, personal communication) is currently studying the influence of food availability and salinity stress on Chesapeake Bay oysters. This research will culminate in an energy budget which will allow predictions to be made about how variations in the salinity or the quantity or quality of the suspended particulate food will affect the energy available for growth and reproduction in oysters.

Animal husbandry has progressed with increased understanding of optimal conditions for food utilization and energy partitioning by domestic organisms. The same should be true with regard to oysters if they are to be cultured efficiently.

GROWTH

The morphology, structure, and chemical composition of oyster shell and the physical processes by which the oyster increases in shell diameter are described in detail by Galtsoff (1964). Briefly, the oyster's mantle secretes a substance called conchiolin which in time becomes calcified. Since much of the conchiolin secretion occurs at the mantle's edges, the shape and position of the mantle determines the shell shape. Factors which cause the mantle to retract for prolonged periods, e.g., water-borne sediment in a swift current, may make shell deposition difficult at the shell periphery and may result in a deformed shell (Cole and Waugh, *O. edulis*, 1959; Ruddy et al. 1975).

Loosanoff and Nomejko (1949) performed the first series of intensive studies on growth of *C. virginica* on a year-round basis, using oysters from Milford Harbor, Connecticut. There was no increase in size, volume, or weight during winter months (December-March) in the wild. However, if temperatures were artificially elevated in these months, growth occurred. During the eight-month natural growing season, most rapid growth in length occurred from May through July. Increase in width was most rapid in June and depth increase was greatest in July. Volume increases were greatest in August and September. Thus, the major increases in length and width occurred in the first half of the growing period, whereas depth and volume increased most in the second half. Spawning did not interfere with growth.

Unlike the situation in Connecticut, growth in Apalachicola Bay, Florida, oysters was found to be continuous throughout the year (Ingle and Dawson 1952). Growth rates were higher than they were for northern populations of oysters, with spat attaining a size in five weeks that was not attained by northern spat for a year. Gametogenesis or spawning did not appear to affect growth in these Florida oysters. Studies elsewhere in Florida (Dawson 1955) found growth rates to be less than those reported for Apalachicola Bay but still greater than for northern populations.

Beaven (1950, 1953a) performed experiments on oyster growth in Chesapeake Bay, including transplanting seed oysters from grounds within the

Bay and from sources elsewhere along the East Coast of the United States to various areas of the estuary. He noted significant differences in average growth rates among different oyster bars within Maryland, among groups of seed from different areas, and from year to year on the same bar where the same type of seed was planted. The most rapid growth observed by Beaven (1950) occurred in upper Pokomoke Sound. A heavy set on planted cultch resulted in many oysters which grew to three in. (7.5 cm) by late fall of the year and to six in. (15 cm) by their second fall. Contrarily, oysters in the Head of the Bay region above the Chester River-Sandy Point transection were found to grow slowly, presumably due to low salinity and consequent inhibition of feeding. Oysters in the Patuxent which had been planted as seed and which were about 2 1/2 years old when sampled were found to be larger in the upper river than in the lower river (Beaven 1953a). In general, in Maryland's Chesapeake Bay, oysters on most grounds reached market size by the end of their third growing season.

In a series of transplant experiments, Beaven (1950) found that oysters transplanted from Bay waters with salinities around 12 ppt to Chincoteague Bay (20-30 ppt) survived better and outgrew controls planted at Solomons, Maryland. However, Shaw (1966 b) found that oyster spat transferred from 12 ppt (Broad Creek) grew at similar rates in Chincoteague Bay (30 ppt) and Tred Avon River (12 ppt).

Oysters from outside Chesapeake Bay had variable mortality rates when transplanted to Solomons, depending upon their environment of origin (Beaven 1950). Oysters from the higher salinities of Long Island Sound had mortalities of 58% by the second year, whereas oysters from Gull Rock, North Carolina (an area similar in salinity variation to Solomons) experienced only 5% mortality.

Further experiments using South Carolina seed oysters (Beaven 1953b) revealed that survival of these oysters from higher salinity, intertidal habitats was poor in central Chesapeake Bay, better in the lower Bay, and best in Chincoteague Bay in areas relatively free from oyster drills. Transplantation in summer resulted in lower mortality than for fall transplants. Drill predation was heavy in certain areas.

With regard to factors influencing shell deposition, Loosanoff and Nomejko (1955) found that damage to the shell edge of *C. virginica* caused a rapid rate of shell deposition as the filed or broken areas were repaired. Once repairs were completed, the shell deposition rate returned to normal. There was no relationship between amount of shell removed and final length attained.

Growth and fattening (i.e., increase in glycogen levels) of oysters are dependent upon food source, some diets stimulating growth while others are inhibitory (see section on Feeding and Nutrition). In general, a high biomass is correlated with high oyster production (W. D. Anderson 1979). While spawning interrupts fattening (Korringa 1952, Mann 1979), shell growth during spawning may continue, given an adequate food source (Loosanoff and Nomejko 1949, Korringa 1952). For larvae, growth rate at different temperatures may be dependent on food type available (Davis and Calabrese 1964).

Among the environmental influences on growth are temperature, salinity, water velocity, waterborne sediments, population densities, pollution from anthropogenic chemicals, disease and predation, and perhaps pH, dissolved oxygen, and light intensity. These influences are treated briefly below (see also other sections in this review.)

Temperature and Salinity

Seasonal fluctuations of temperature and salinity can affect oyster growth. Beaven (1950, 1953a) found that growth of *C. virginica* in Maryland was generally greater in fall (although this may not have resulted directly from influence of temperature). Adult *C. virginica* from Milford Harbor, Connecticut, grew in the laboratory in the temperature range 13.0 to 22.0°C, the optimum growing temperature being 15°C (Loosanoff and Nomejko 1949).

Mann (1979), experimenting with the reactions of adult *C. gigas* to thermal effluents in England, reported no growth advantage for this species of oyster at temperatures above 15°C. He concluded that high temperatures favored *C. gigas* growth, but lower temperatures stimulated greater absolute meat production.

Davis (1958) suggested that *C. virginica* larvae spawned from oysters whose gonads matured at low salinities survived better and grew faster at salinities under 10 ppt than did larvae from oysters conditioned at 26.0-27.0 ppt. He found the salinity range for normal development of larvae from lowsalinity conditioned oysters to be 7.5 to 22.5 ppt whereas the range for larvae from oysters held at 26-27 ppt was 12.5 to above 35.0 ppt.

Davis and Calabrese (1964) found optimum temperatures for larval growth to range between 30.0°C and 32.5°C at all salinities tested (over a range of 7.5 to 27.0 ppt) except 7.5 ppt, where the optimum was 27.5°C. They reported no well-defined optimum salinity for larval growth at any temperature because of variability in results. The range of temperatures tolerated by larval oysters narrowed as salinities decreased. Growth to setting size varied from 10-12 days in the temperature range of 30.0°C to 32.5°C to 36-40 days at 20.0°C.

Water Velocity

A slight decrease in water circulation only slightly affects *C. virginica* growth, but when circulation is greatly reduced, the oyster's growth rate is very low (Kerswill 1949). Perhaps there is a low limit of water flow below which adequate food is not supplied or waste products are not cleared away. On the other hand, high water velocities may result in abnormal shell growth. Cole and Waugh (*O. edulis*, 1959) and Ruddy et al. (1975) both noted that, in strong currents, oysters may increase shell deposition, but most growth occurred in the thickening of the shell, giving the oysters a spherical or "dumpy" appearance.

The deformed shell shape may be due to sediments borne on swift currents which, by bombarding the mantle edge, do not allow the mantle to deposit new conchiolin at its edge.

Population Densities

There are discrepancies in the literature concerning the effect of population densities on oyster growth. Cole and Waugh (1959) found the shell growth of *O. edulis* unaffected by contact with adjacent oysters. Sheldon (1968), however, reported a reduced growth of meat for *O. edulis* at the densities used by Cole and Waugh. Increased competition for food resources may result in low meat production, but the reason for uninhibited shell growth is unclear.

High larval densities in laboratory or hatchery culture may depress growth rate. Helm and Millican (1977) reported that for *C. gigas* larvae cultured under optimal conditions of temperature and salinity, food supply became the limiting factor in growth. High densities might not interfere with growth if an adequate supply of food was available.

Anthropogenic Chemicals

Davis (1961) and Davis and Hidu (1969a) tested several types of pesticides on embryonic and larval *C. virginica*. Some compounds were more inhibitory to embryonic development than to larval survival and growth while others reduced larval growth and had no or little effect on embryos. These studies stressed the need to test a pesticide on all life history stages as well as on food organisms before considering a substance safe. Davis (1961) found some pesticides, i.e., guthion and parathion, to increase larval growth at low levels (0.025 to 0.05 ppm and 0.025 ppm, respectively) although they were toxic at higher levels (1.0 ppm). He postulated that the pesticides reduced bacterial growth, resulting in increased larval growth rates.

Pesticides may reduce oyster growth by inhibiting the process of shell deposition. Eisler and Weinstein (1967) found that some pesticides interfered with calcium uptake in quahaugs although effects on shell deposition were not studied. The herbicide 2,4-D BEE, however, did not adversely affect shell growth of *C. virginica* in the quantities tested by Rawls (1977).

Limited exposures of adult oysters to petrochemicals does not seem to affect them adversely. Anderson (1977b) exposed *C. virginica* from the Gulf of Mexico to various types of oils. A four-day exposure to a 1% oilwater-dispersion mixture (approx. 40 µg/ml) did not reduce growth rate. He found the oyster to be the most resistant organism in his study.

Disease and Predation

Oysters infected by disease organisms may have reduced growth rates. Menzel and Hopkins (1955b) reported that *Dermocystidium* sp. infections reduced the growth of *C. virginica*, the size of the growth reduction being proportional to the intensity of the infection. Early infections by the parasite *Bucephalus* sp. appeared to stimulate growth, although advanced infections arrested growth.

Brown (1973) studied the effects of 156 types of bacteria on the growth of *C. virginica* embryos and larvae. As one might expect from results of research involving other environmental factors, embryos and younger larvae were more susceptible to disease and infection than were mature larvae. Brown (1973) hypothesized that older larvae were protected from bacterial infections by a better developed shell or increased tolerances to bacteria.

Shell-boring predators and pests may cause oysters to divert energy away from oyster growth and focus it on shell repair. Stunted oyster growth can be the result of heavy pest infestations.

Other Environmental Factors

Medcof and Kerswill (1965), studying the effects of light on *C. virginica* found shading to increase linear shell growth but decrease its thickness. Meat production increased when oysters were exposed to light. Perhaps the oyster's mantle, displaying photophobic tendencies, was unable to extend itself to deposit new shell along the valve edges. Increased meat production in this experiment may have been the result of increased algal production in the unshaded compartments.

Hydrogen-ion levels (pH) may influence the growth of oysters by affecting the chemistry of the shell material. Calabrese and Davis (1966) found *C. virginica* larvae to grow within the pH range of 6.75 to 8.75, with optimum growth at 8.25 to 8.50.

Applied Aspects

An oyster population with a high growth rate is desirable in both open water and in pond or hatchery farming endeavors. Market-sized oysters produced in the shortest period of time mean a reduction of the time that an oyster, cultured in open water, is exposed to predation, disease, and the vagaries of nature. For aquaculturists growing oysters in ponds or hatcheries, a fast growth rate can mean a shorter period of maintenance, resulting in reduced capital and labor costs. There is some evidence that the fastest growing *C. virginica* larvae become not only the earliest setting larvae, but the fastest growing spat as well (Losee 1979), but this relationship may not hold after a year or two (see section on Genetics). According to Losee, selection for these fast growers might be achieved by limiting spat collection to the first days of the spat settlement period. The long-term utility of collecting only the earliest setting larvae needs to be evaluated further.

In a study of population genetics, Singh and Zouros (1978) found the condition of increased heterozygosity to be associated with increased weight of individual oysters. They postulated that faster growth rates may be obtained by crossing oyster stocks from different geographical regions. A later paper (Zouros et al.

1980) firmly established the correlation between heterozygosity and growth rate (weight at the age of one year). The relation of this phenotypic character to overall fitness is unclear and the practical applications (if any) need to be developed.

In summary, the physical process of shell growth by the oyster is well documented, although the causes of deformed shells are still unclear. The genetic and nutritional aspects of growth are areas which need further research. Among the environmental factors influencing growth, temperature and salinity have been studied extensively. Other factors, however, such as current velocities and population densities, are not completely understood and need more study. Growth patterns of larval oysters and factors influencing growth are less well known than for adults.

With regard to Maryland waters, the reasons for differences in oyster growth between regions of the Bay, or from year to year are unknown. Such information is important for sound management. If areas supporting poor growth cannot be conditioned to support better growth, they will not be as suitable for oyster farming or seed planting. The reasons for good growth in different areas need to be determined. In addition, the carrying capacity of areas used for seed planting need to be established.

REPRODUCTION

Crassostrea virginica is an alternative hermaphrodite (Fretter and Graham 1964), reproducing by shedding sperm and eggs into the water column where fertilization occurs.

Details of the reproductive organs of oysters, cellular aspects of egg and sperm development, fertilization and cleavage, and the morphological changes that occur during larval development and metamorphosis are well presented by Galtsoff (1964). Andrews (1979) added to and updated Galtsoff's work in his own recent review of reproduction in Ostreidae. Our review will not reiterate this material but will examine selected aspects of reproduction briefly, highlighting areas requiring further study.

Gametogenesis and Spawning

Annual Reproductive Cycle

Many temperate zone invertebrates (including C. virginica) reproduce in annual cycles. Given the seasonality of temperate environments, it is adaptive for species to breed when environmental conditions are optimal for development and growth of the larvae. General synchrony of gametogenesis and spawning is also important for those invertebrates like oviparous oysters which broadcast eggs and sperm into the water column for external fertilization.

The pattern of gametogenesis in C. virginica has been thoroughly described by Kennedy and Battle (1964). Figure 2 shows the gametogenic stages for female and male oysters. Briefly, during fall and winter, the germinal epithelium is in an indifferent state. Although metabolic activities at the cellular level undoubtedly continue, follicular development, oocyte and spermatocyte formation and growth, etc., do not proceed. In spring, gonadal development commences with proliferation of germinal epithelium, and enlargement and anastamosing of follicles. Maximum follicular proliferation occurs just prior to spawning. Gamete release occurs in late spring or summer, with perhaps two or more waves of spawning over the period. As spawning ends, follicles shrink, amoebocytes invade the reproductive tissues, and the quiescent state resumes.

This pattern of gametogenesis was established by Kennedy and Battle (1964) for oysters near their northern range, in Prince Edward Island, eastern Canada. Further to the south, the pattern is modified by the ripening phases occurring earlier in the calendar year, the spawning period being extended until it encompasses most of spring, summer, and fall, and the indifferent stage being truncated. Thus, Loosanoff (1965) found Long Island Sound oysters to spawn between late June to early September, which compares with late June to August in Prince Edward Island (Kennedy and Battle 1964), March-April to October in Florida (Ingle 1951), and February-March to October-November in Hawaii (Sakuda 1966). In Florida, there appeared to be no mass release of spawn by the entire population of oysters, as happens in eastern Canada and Long Island Sound (Ingle 1951).

Factors Influencing Gametogenesis

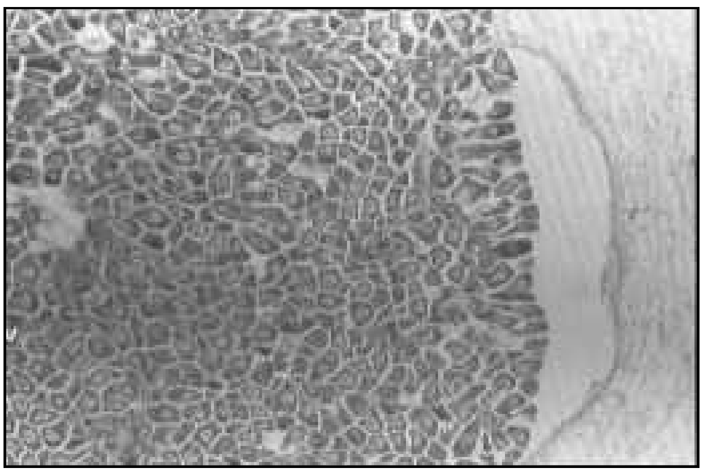
For some marine and estuarine organisms, the timing of such reproductive events has been shown to be coordinated with aspects of the external environment which act as cues (see Sastry 1975 for review). For example, salinity, temperature, day length, and abundance of food may serve as cues or stimulants (Giese 1959). Note that the influence of salinity on gametogenesis (perhaps as a result of its influence on feeding) is considered in the section on salinity.

Sastry (1979) made an extensive review of the literature on reproduction in bivalve molluscs. He concluded that studies on environment-organism interactions in relation to the course of reproductive cycles are limited in number. His own studies on the bay scallop, *Argopecten irradians*, are probably the most detailed and informative of the genre (Sastry 1963, 1966 1968, 1970, Sastry and Blake 1971). In brief, he found that of the possible exogenous factors (those external to the animal) that might be involved, temperature and food supply are strongly implicated as environmental controllers of the reproductive cycle of bay scallops. Because of the lack of information on C. virginica and because temperature and food might interact to control oyster reproduction, we briefly describe Sastry's findings for the bay scallop.

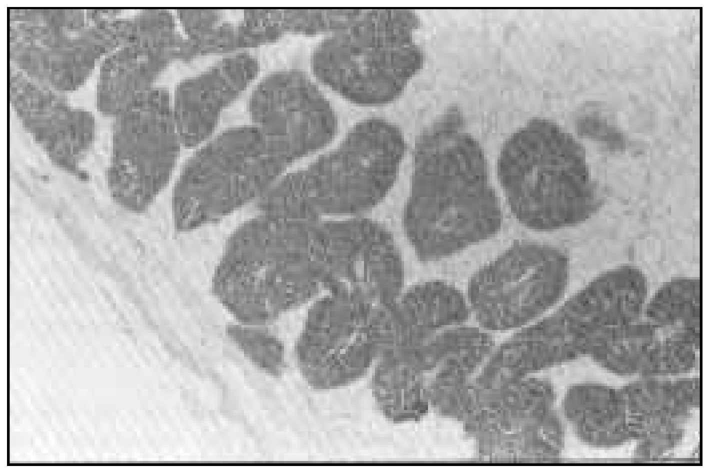
The period of gonad growth for *A. irradians* at Beaufort, N.C., coincides with the time when phytoplankton production is at an annual high (Sastry 1966). Sastry found that the sequential events of the reproductive cycle (e.g., vegetative phase, early growth phases of gametes, resting stage, etc.) were affect

A. Female early development.

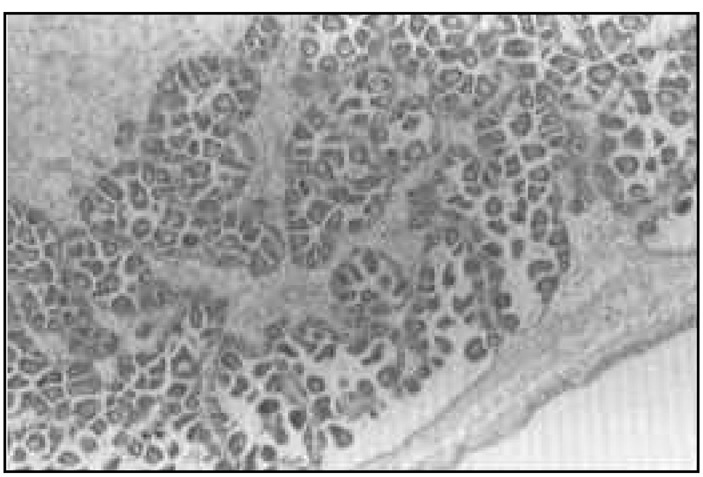
B. Male early development.



C. Female later development.

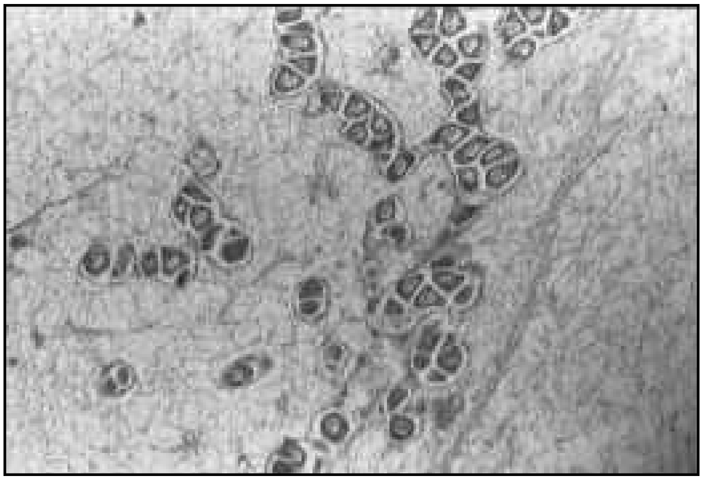


D. Male later development.



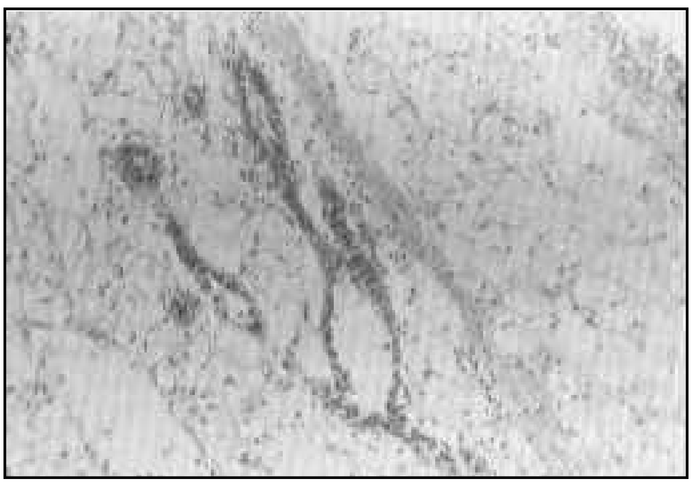
E. Female spawning.

F. Male spawning.

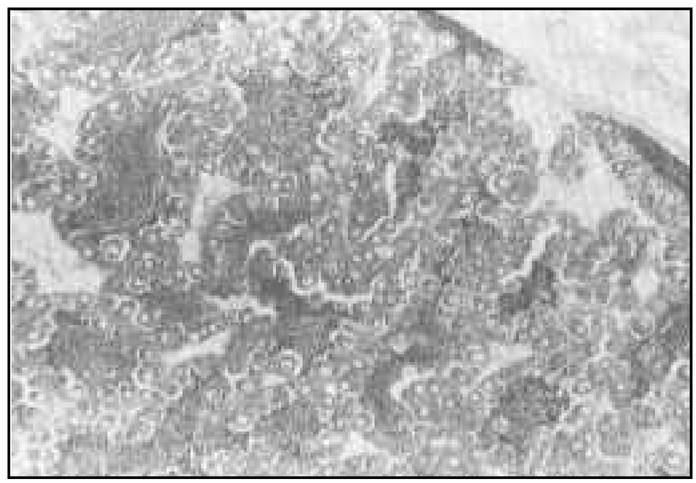


G. Female spent.

H. Male spent.



I. Indeterminate, overwintering.



J. Hermaphrodite.

Figure 2. Gametogenic stages for female and male *Crassostrea virginica*.

In early female development, small developing eggs with a clear internal space line the follicle walls (A). In later development, large numbers of mature eggs pack the follicles (C), prior to spawning. Spawning results in the release of most mature eggs (E). The end of the spawning period finds few eggs remaining in the shrinking follicles (G). Overwintering follicles are lined with tiny immature eggs (I).

Male oyster gonads develop similarly, with immature sperm forming densely-staining masses in follicles (B). Later development results in enlarged follicles (D), followed by sperm release during spawning (F) and fol licle shrinkage (H). The hermaphrodite gonad contains both eggs and sperm intermingled in follicles (J).

differently by temperature in the absence of food. Scallops in the vegetative phase (which occurs early in the cycle) and in the resting stage (occurring late in the cycle after spawning) seemed to require both a suitable temperature and an adequate food supply before gonad growth occurred. In poor food conditions, tissue reserves seemed to be used for maintenance metabolism rather than for gametogenesis. After certain minimum reserves had accumulated in the gonad, it appeared that food supply was less critical. Gonad maturation occurred at a temperaturedependent rate. However, even when the minimal gonadal reserves were present, in the continued absence of food the gonad did not develop as extensively as it did in the presence of adequate food.

In another study, Sastry (1968) found that, if resting stage scallops were held at 15°C under conditions of adequate food, the early gametogenic stages developed but oocytes did not enter the normal growth phase. At 20°C with no food, resting stage scallops failed to begin gonad growth. On the other hand, at 20°C with adequate food, oocyte growth began. Even in the presence of abundant food, the reproductive cycle seemed to require that a certain minimum temperature prevail before oocyte growth began.

Both Sastry (1979) and Andrews (1979) in their reviews of reproduction of bivalves in general and of oysters in particular indicated that little information exists on the effects of the interactions of various environmental variables on oyster reproduction. Most of the information concerns temperature effects, mainly on *Crassostrea virginica*. For example, Loosanoff and Engle (1942) studied oysters in Long Island Sound and noted that this area contained different groups of oysters with different temperature requirements for spawning. Stauber (1950) reviewed the literature on spawning and temperature and concluded that there were probably three physiological races of C. virginica along the western Atlantic coast. He noted that oysters spawned at similar times of the year over this range despite the different water temperatures prevailing in the different areas. In 1951, Loosanoff and Nomejko showed that temperature requirements for gonad development and spawning of northern oysters (from Massachusetts and Connecticut) were lower than for southern oysters (from New Jersey and Virginia).

Loosanoff and Davis (1952) studied the effects of different temperatures on (well-fed) oysters from Long Island Sound. They found that 10°C was not sufficient for normal gametogenic activity in most oysters. Ripening and spawning did occur at 15.8°C and above. Males ripened faster than females in the range between 15.0° to 30.0°C. The average time required at different temperatures for production of mature gametes ranged from 26.5 days at 15.0°C to 4.9 days at 30.0°C. Loosanoff and Davis developed an equation to estimate the average time in days (D) needed for mature gamete development as follows:

$$D = 4.8 + 4205\ e^{-0.3554}T$$

where T is temperature and e is the base of the natural logarithms. Kaufman (1979) later modified this equation as follows:

$$D = kT^{(b+a\,\lg T)}$$

where k, a and b are coefficients derived from Loosanoff and Davis' data and 15°C ≤ T≤ < 30°C. Kaufman indicated that the modified equation could be used to determine times of first spawning and mass spawning, as well as of mature gamete development.

Loosanoff (1969) reported on additional studies of gonad maturation at low temperature for oysters from widely separated populations. This work was performed in Connecticut. In general, low temperatures inhibited or prevented gonadal maturation in oysters from southern regions but not so for northern oysters. For example, some oysters from Long Island Sound which were kept in Milford Harbor, Connecticut, for three months and then exposed to 12°, 15°, or 18°C, were able to ripen even at 12°C, with a male being induced to spawn after 68 days at 12°C and a female after 78 days. New Jersey, Virginia, South Carolina, and Florida oysters were not able to ripen at 12°C. Similarly, at the higher holding temperatures (15°, 18°C), Long Island Sound oysters ripened, with many spawning, whereas oysters from more southerly locations ripened slowly if at all, and few spawned.

In Delaware Bay, Maurer and Price (1968) and Price and Maurer (1971) studied requirements for holding and conditioning local oysters to spawn out of season and developed information on the number of degree-days required to elicit spawning in 50% of the population tested. Within the range of 12° to 22°C, 450 degree-days (sum of the daily exposure temperatures above 12°C) were required. When Price and Maurer (1971) compared the time for 50% of Delaware Bay oysters to ripen with data for Long Island Sound oysters (using Loosanoff and Davis' (1952) equation) at 15°, 20°, and 25°C, they found that the northern oysters ripened about 6 to 7 times faster than Delaware Bay oysters. The reasons for this difference are not clear and need to be determined. The data collected by Price and Maurer (1971) in their study were used to develop a proposed temperaturetime schedule for holding, conditioning, and spawning Delaware Bay oysters all year round in hatcheries. Similar information would be needed for Maryland hatcheries and the transferability of Loosanoff and Davis' (1952) data or Price and Maurer's (1971) data has not been demonstrated.

These past studies on the role of temperature in oyster gonad development and spawning are of course well known and have been put to use by those interested in the aquaculture of oysters (e.g., Loosanoff and Davis 1963, Hidu et al. 1969, Breese and Malouf 1975, Dupuy et al. 1977).

Studies of effects of nutritional factors have usually focused on growth of adult oysters, not on reproduction. Thus, the above-mentioned research projects on temperature effects have paid little attention to the interaction of food and temperature on oyster gametogenesis (see Andrews 1979, Sastry 1979). However, such information is of importance in understanding the nutritional aspects of oyster biology for aquacultural purposes, to explain poor reproductive success in nature, and for use in development of energy budgets and assessment of stress effects (Bayne 1975, 1976, Newell et al. 1977). In addition, the role of neurosecretion and of the mobilization of nutrient materials within the body of the oyster need study (Sastry 1979).

Spawning

Beyond the interaction of food and temperature as they may influence gametogenesis lies their role in triggering spawning. As mentioned earlier in this section, temperature affects spawning and the manipulation of temperature in hatcheries provides for spawning of conditioned oysters which are used as brood stock (Loosanoff and Davis 1963). However, oysters from areas south of New Jersey are difficult to condition and spawn (Loosanoff and Nomejko 1951, Hidu et al. 1969). Dupuy et al. (1977) were able to condition oysters for spawning using appropriate food and temperature conditions (see also Hidu et al. 1969). However, the situation as it exists in the field is not clearly understood. Do oysters spawn as a result of a slow steady temperature increase to a certain level, or as a result of a rapid change after a certain gametogenic condition is attained? Medcof (1939) felt that spawning was preceded by sudden rises in water temperature. Butler (1954) suggested that changing temperatures were more important than some "critical" level being attained. In addition Butler was quoted by Nelson (1955, 1957) as stating that adequate water temperatures (25°C) had often been reached at Pensacola, Florida, for a number of weeks before the local oysters spawned. It appeared that a spring phytoplankton bloom was necessary to stimulate spawning. Nelson (1955) also noted that Long Island Sound oysters in July 1954 had not spawned even though temperatures were sufficiently high. Nelson speculated (1955, 1957) that some sort of material (a vitamin, or pectin, or other carbohydrate) might be released by phytoplankton, thus stimulating spawning.

Just recently, the subject of induced spawning of commercial bivalves by exposure to phytoplankton has been investigated by Breese and Robinson (1981). They found they could stimulate razor clams (Siliqua patula) to spawn in the hatchery by holding them in a concentration of Pseudoisochrysis paradoxa (2-2.5 million cells ml^{-1}). Traditional methods of eliciting spawning (temperature change, chemical stimulation) had previously been unsuccessful. Subsequent experiments led to induced spawning of a number of bivalves, including C. gigas and C. rivularis, upon exposure to phytoplankton species. The nature of the stimulant responsible for these responses, and its presence and activity in the wild remain to be determined.

Note that a few other molluscs have been found to spawn naturally in synchrony with phytoplankton blooms. Five chiton species found on the west coast of North America spawn in the spring when phytoplankton populations are increasing (Himmelman 1980). Thorson (1936) found that two species of Greenland bivalves spawned during a phytoplankton bloom before temperatures increased. No information on oysters was reported by Andrews (1979) in his review, nor have we noted any reports on spawning response to algal blooms. However, Miyazaki (1938) found a substance in *Ulva* sp. that stimulated spawning in *C. gigas*, with a dose of 1 ml of a 1 ppt solution being effective.

The study of the possible influence of food materials or their byproducts on oyster spawning is obviously necessary to provide basic information on C. virginica's reproductive biology.

Adult Stress and Larval Viability

Bayne (1975) reviewed the subject of bivalve reproduction under environmental stress. Stressors included such factors as elevated temperatures or decreased food ration. Of interest here were his findings of the effects of stress in adults on larval development and viability. Under thermal and nutritive stress, blue mussels, *Mytilus edulis*, were less successful in fertilization and embryogenesis and larval growth rate was reduced compared with control animals.

Bayne et al. (1978) carried their study on *Mytilus edulis* further. They found that high temperature and/or lack of food led to mussels producing fewer, smaller eggs, in smaller follicles, than did mussels not under stress. There was no attempt at measurement of spat settlement success or spat survival but one might surmise that small eggs might result in less viable spat (if any) being produced.

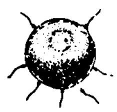
The point of these studies is that the nutritional and other well-being of adult bivalves, presumably including C. virginica, may have an impact on their offspring. Such an important relationship affecting ecological fitness requires intensive study in Chesapeake Bay. Might it be one factor involved in the recent years of poor spat settlement? Certainly such laboratory studies as those of Bayne and his colleagues, coupled with assessment of adult, larval, and spat condition in the field and of food materials available to adults in nature would be very enlightening. Perhaps some biochemical index might emerge as a means of predicting potential larval vigor in the field from assessment of adult condition.

Sex Ratios and Changes

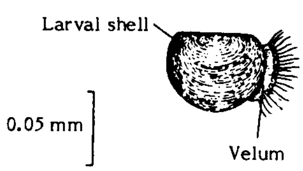
As mentioned, *Crassostrea virginica* is an alternative hermaphrodite which means that the species has the ability to change sex during its lifetime. This subject has been well investigated by Coe who provided a summary of available information in 1943. The timing of this sex change is erratic. When first mature, oysters are protandric, with more than 70% of the new spawners in some areas functioning as males. As the oysters age, the proportion of functional females increases, with a tendency towards an excess of females occurring among older oysters. Sexual change seems to occur between spawning seasons when the gonad appears quiescent (when scrutinized microscopically).

Needler (1932) marked oysters of known sex in 1930 and examined four survivors in 1931. One was found to have changed from male to female. A more extensive survey was performed by Galtsoff (1964) over a five-year period using oysters that were four years old at the start of his experiments. In that time, the sex ratio of males to females changed from 1.9:1 at the beginning of the experiment to 0.8:1 at the end. It was not clear if the increasing predominance of

Unfertilized egg.



Fertilization.



Straight-hinge larva.

females was due to more frequent sex changes from male to female (rather than the reverse) or to greater survival rate of female oysters. This needs further investigation. Thirty one of the 68 survivors at the end of the fourth breeding season had changed sex at least once over the experimental period (Galtsoff 1964). Eighteen had changed once, 10 twice, 2 three times and 1 four times. The reasons for such changes and the factors influencing any change are not known.

Coe (1943) postulated that temperature and nutritive conditions with in the body might influence such change, with physiological state in each breeding season affecting sexual phase. He indicated that some studies had noted that rapid growth in yearling oysters was linked with presence of functional female gonad. Slower growing yearling oysters were predominantly male.

Information on effects of physiological state on oyster sex is very limited and inconclusive. We have gathered some scattered data. For example, Amemiya (1929) found a ratio of 100 female *C. gigas* (two years old) to 73 males on good fattening grounds and 100 females to 155 males on poor fattening ground. Amemiya (1935) also found that in groups of *C. gigas* having a portion of the gills removed immediately after spawning, there arose a slightly larger ratio of males in each group than in untreated controls. Awati and Rai (1931) found that a sample of *C. cucullata* infested with pea crabs contained 10% females and 83% males compared with 56% females and 41% males in a sample with no pea crabs. Pea crabs live in the mantle cavity and may interfere with feeding or cause some stress reaction. Kennedy and Battle (1964), in studying oysters in 1961 and 1962 in Prince Edward Island, found a higher percentage of males in both younger and older age groups than did Needler (1932) in her earlier studies in the same bay. They attributed this difference to excessive silting and prolific growth of eelgrass (with resultant inhibition of oyster growth during their later study. Chronic damage (by filing) to the shell of C. virginica results in a higher male to female ratio (Bahr and Hillman 1967, Davis and Hillman 1971). For example, in a group of oysters with shell filed weekly, there were 14 females and 36 males, compared with 24 females and 20 males in the control (unfiled) group.

Perhaps these examples indicate that, if there is insufficient food supply, or if some factor such as pea crab infestation or shell damage results in shunting energy elsewhere from gamete production, maleness is favored. The whole subject of energy mobilization in oysters requires elucidation, especially in light of potential stress from pollution.

Additional questions concerning sex ratios can be posed. For example, one of us (VSK) has studied histological slides of over 6,000 oysters collected from 18 oyster bars in Maryland's Chesapeake Bay in 1977 and 1978 (unpublished data). Of the 29 determinations of sex ratios of oyster populations on these oyster bars for two summers, only 3 exceeded a ratio of 2 females per male (they were 2.4:1, 3.1:1 and 3.1:1). Two determinations were 0.9 females per male, not significantly different from a 1:1 ratio. The remaining 24 determinations ranged between 1.0 and 2.0 females per male, with only 8 being significantly different from a 1:1

ratio. These findings are significant in that, from about 1966 to 1979, recruitment of young (male) oysters to the oyster grounds, as measured by spat settlement, has been poor (Krantz and Meritt 1977, personal observation). Thus, one would expect that the surviving oyster populations would, as they aged, become overwhelmingly female. That this has not happened may indicate that oyster populations can maintain a relatively balanced ratio; if so, what cues do they depend on?

Burkenroad (1931b) noted that in a sample of oysters averaging 74 cm long and growing singly (i.e., not close to one another) there were 131 females and 34 males (3.9:1) whereas for similar sized oysters growing in clumps of two or more so that their valve margins were < 4 cm apart, there were 27 males and 46 females (1.7:1). Needler (1932) reported that her preliminary observations indicated that males tended to remain male in the presence of females. Further study of this subject would be interesting and worthwhile. As oyster farming develops, it would be useful to know if a certain ratio of females to males is optimum (recall the fact that few bulls or roosters are required for satisfactory fertilization of cows or hens). If so, food supply and other environmental conditions might be manipulated to provide for this optimum ratio in an oyster farming situation.

LARVAL BIOLOGY AND SPAT SETTLEMENT

Crassostrea virginica reproduces by shedding sperm and eggs into the water column where fertilization occurs. The resulting pelagic larvae are planktotrophic, feeding upon phytoplankton and growing through various larval stages over a period of two or three weeks. As the larvae mature, it is believed that the older stages tend to remain near the estuarine bottom (Carriker 1967). Eventually, the settling stage, called the pediveliger (Carriker 1961), spends time crawling on the bottom, apparently testing the substrate for suitability as a settlement surface. If conditions are acceptable, the pediveliger cements its left valve to the substrate and metamorphoses (Medcof 1961). Figure 3 illustrates some of the life history stages of oyster larvae.

The length of the larval period in the water column is temperature (and perhaps food) dependent. Longer periods in the plankton increase exposure of larvae to predation and the risks associated with a pelagic existence. Thus, increasing time spent in the water column will result in increasing loss of larvae (Korringa 1941).

Unfortunately, because oyster larvae are so small (averaging about 275-315 µm at metamorphosis - Loosanoff and Davis 1963), much of their biology in the field is poorly known. It has not yet been possible to follow a larval brood from fertilization to settlement. Some information is available about larval behavior in aquaculture and laboratory situations, but such findings may not always be directly applicable to the field. We need further information concerning larval behavior and survival in nature.

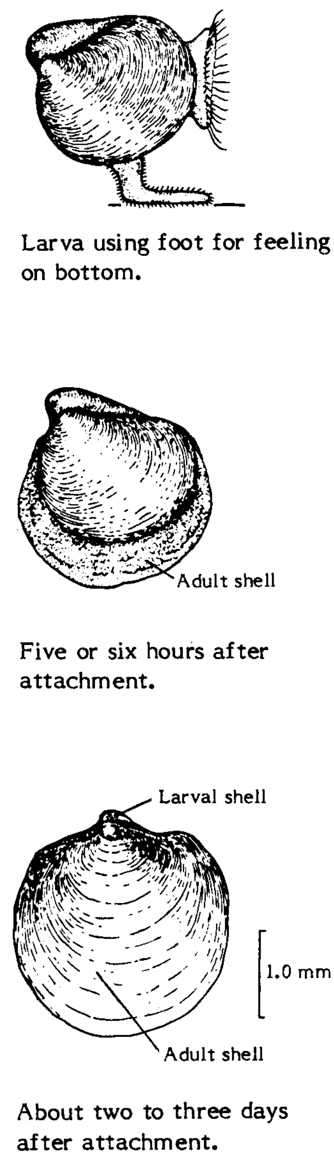
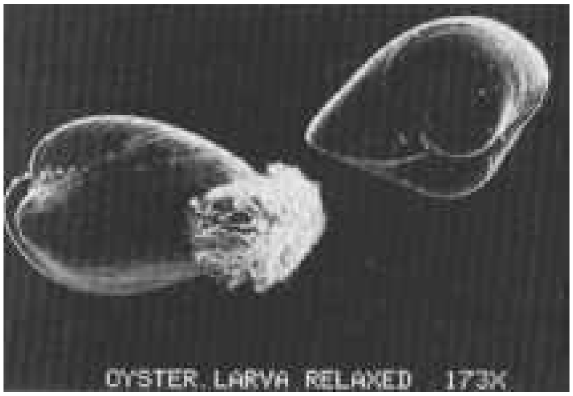


Figure 3. Early development stages of the oyster. (From C.L. Newcombe and R.W. Menzel, 1945)

However, this depends on planktonic sampling methods which have major difficulties associated with them. For example, pumps are generally to be recommended over plankton nets because the latter rapidly fill with ctenophores and cnidarians, especially in Chesapeake Bay. The intake of pumps can be screened somewhat to exclude these gelatinous zooplankters. Pump intakes can also be positioned at chosen depths to sample a discrete water layer.



In terms of sample size, it should be noted that in many regions older larval stages may be so sparse as to make quantitative sampling difficult if not unreliable (Galtsoff 1964). For example, Pritchard (1953) calculated that the large commercial sets in James River, Virginia, required only about one late-stage oyster larva per 100 liters. Thus, better sampling methods than previously used would be necessary to provide more reliable samples. Further, such studies require that experienced personnel be available for sample sorting as identification of bivalve larvae can be very difficult (Galtsoff l958b). The early stages of bivalve larvae are notoriously similar, although examination of hinge teeth will probably result in more reliable identification (perhaps at the expense of speed in sorting the many samples necessary for a thorough study).

An example of these logistical problems is provided by the study of larval distributions in the James River by Wood and Hargis (1971). Five vessels and fifty people were involved in an intensive week-long sampling program, with plankton pumps on the ships collecting samples at four different depths in the channel and at two different depths in shallow water. Because of the size of the program, logistics and scheduling had to be arranged for in advance of the expected spawning season; as the time approached, it appeared that the oyster spawning season was delayed. It was not possible to reschedule the study, and as a result, the peak of larval production was apparently missed. In the samples, taken hourly during the study, identification of oyster larvae was slowed down because of the similarities among the 17 early stage bivalve species that were identified. Mature oyster larvae (the most readily identifiable stage) were scarce, even though about 300 liters of water were pumped for each sample.

Even with this immense effort, Wood and Hargis (1971) only reported on results from a 24-hour period. Their interpretations have been disputed by Andrews (1979) who discussed a separate set of similar data from the same survey. Thus, the difficulties associated with collecting enough data to allow for successful analysis and clear interpretation of oyster larval distribution in relation to water circulation are apparent.

What follows is a summary of work that has been performed in this area of research.

Larval Field Behavior

One of the major research efforts on oyster larval biology has been that of the Nelsons and their students. J. Nelson began his research in 1889 and continued until his death in 1916. His son, T. C. Nelson, began to work with his father in 1908 and continued this research until his own death. From 1889 to 1932, an almost unbroken series of annual reports was produced by these two scientists, providing information on their extensive research activities in Little Egg Harbor and Barnegat Bay, N.J., and in Delaware Bay.

The results of their studies on behavior and movements of oyster larvae have been summarized elsewhere (Carriker 1947, Nelson 1953, 1955). Their initial work was in Little Egg Harbor. In 1916 they found that there was a progressive increase in larval abundance starting at the mouth of the inlet and moving upstream, whereas the bulk of the parent oysters were near the mouth. Sampling showed oyster larvae leaving the inlet with the last of the ebb tide and returning on early flood. Additional studies in Barnegat Bay showed that young larvae were carried up to 1 or 2 miles to sea but after one week of age they began returning to the Bay, being found upstream by the time they were ready to set.

In Barnegat Bay, strong vertical stratification was noted in quiet weather. At times, a lowering of a sampler through the halocline (area of sharpest change in salinity) in the water column by as little as 8 inches (20 cm) led to a doubling of salinity concentration. Generally, oyster larvae were found concentrated on top of the halocline (e.g., in one sample 66,110 larvae were on top and 102 below, near bottom). In unstratified conditions, larvae were often distributed homogenously in the water column, being concentrated by the current at its level of greatest velocity.

Horizontal distribution of larval groups was uneven, and they could be found in definite lanes upstream and downstream from adult populations, with little lateral distribution. Heaviest sets tended to occur in these lanes. In areas with strong tidal currents (such as Little Egg Harbor), most larvae were found on the flood. In regions with weakened tidal currents (such as Barnegat Bay), there were about equal numbers of larvae on flood and ebb. Youngest larvae tended to be homogeneously distributed throughout the water column, with older larvae near the bottom. Earlier larval stages occurred further downstream, with older larvae more numerous upstream.

The “Nelson School” attributed these larval distributions to behavioral mechanisms that allowed older larvae to rise during flood and sink during ebb tides. The proposed stimuli were salinity changes together with tidal changes and increased current speeds. Preliminary experiments found that older larvae became more active and swam up in the water column when salinity increased. Lowered salinity led to decreased activity and settlement downward. Currents moving over larvae caused them to swim upward.

Carriker (1951a) reported on an extensive series of plankton studies performed over a number of summers. He pumped samples from a variety of depths in different estuaries in New Jersey. He also sampled a number of complete tidal cycles. In three out of four study areas, he found more larvae of all stages during flood tides than during ebb tides. Although eyed larvae (the stage preceding settlement) were scarce in most samples, he did find more of them on or near the bottom during ebb tide than than he found at flood tide. He also collected more larvae directly on the bottom than off bottom during ebb tide. Using information on tidal current velocity in Delaware Bay, he showed that on an average spring flood tide, inert particles would only be carried 7 nautical miles upstream from spawning adults, yet larvae were found to set 20 miles upstream from the adults. Further, given that the ebb tide runs longer than flood in Delaware Bay, larvae would be expected to be carried 0.8 miles downstream in each succeeding ebb (a total of 20 miles in 2 weeks) if they were transported as inert particles. Yet, because larvae have been found to set upbay, this would indicate that they swim actively for longer periods during flood than during ebb.

In 1953, Pritchard made the first attempt to relate oyster larval distribution to hydrographic conditions. He studied the James River, Virginia, an area with consistently dependable spat settlement and seed production. He described a circulation pattern involving outflow of lighter, fresher water on the surface and inflow of denser saltier water on the bottom. His postulation was that this return flow in the deeper layers could serve to replenish upriver beds with larvae from downstream spawning beds. The high seed oyster production on the shallow bars of the northeast side of the river could be attributed to slow upwelling of deeper waters over these grounds. Pritchard also noted that samples of larvae over time on one planktonsampling station showed concentration peaks which were more pronounced than one would expect if larvae were just passively suspended in the water. He proposed that the larvae may have been “swarming,” thus retaining a more compact configuration for the population.

Manning and Whaley (1954) undertook a similar study of St. Mary’s River, a tributary at the mouth of the Potomac River that, at the time, experienced very fine sets. They determined that the river acted as a larval trap, due to its sluggish circulation and the prevailing southerly winds (see section on Water Circulation for a caveat concerning their study). They also found older larvae to be more predominant in the lower water column.

In Delaware Bay, Kunkle (1957) found that early stages were almost uniformly distributed vertically during all phases of the tidal current cycle. Late stage larvae tended to congregate on or near the bottom during low slack and high slack as well as during the ebb tide. During early flood and maximum flood, late stage larvae were generally homogeneously distributed vertically. In late flood there was a tendency to concentrate near the bottom. Haskin (1964) provided additional data collected by Kunkle but not reported in his 1957 note. In 1956 in Delaware Bay, samples collected over a tidal cycle showed that as the tide ebbed, eyed larvae disappeared from surface waters more rapidly than from bottom waters, with lowest counts occurring at slack low water. On the flood, larval counts increased, with surface numbers more than double off-bottom values at full flood.

In the extensive survey referred to earlier, Wood and Hargis (1971) attempted to obtain information on field distribution of larvae over many tidal cycles. Their report covers results for a 24 h period. In their sampling area, coal particles of a size similar to oyster larvae (44-210 µm) and of similar density were common (due, apparently, to the proximity of a coal-loading facility). The distribution of these passively transported particles and of bivalve larvae differed in time and space. Coal particle maxima usually coincided with current speed maxima, regardless of current direction. The maximum number of larvae coincided in most cases with salinity increases that accompany flood tide. Wood and Hargis (1971) concluded that larvae in the deeper channel and northeast shoal waters were transported upstream, whereas larvae in the southwest shoal waters were carried seaward.

Not everyone is in accord with the interpretations by the “Nelson School” of the studies reported above. Andrews (1979) disagreed with Wood and Hargis (1971) conclusions. Arguing that oyster larvae are predominantly distributed passively, he discussed a different set of data from the same survey from which Wood and Hargis (1971) derived their results. These data revealed regular rhythms of bivalve larval abundance with tidal stage. Larvae were about five times as abundant between maximum flood and maximum ebb compared with the other half of the tidal cycle. Surface and bottom samples had fewer bivalve larvae than did those collected at mid-water depths. Oyster larvae (which were the major component of the larval populations) did not increase in size during the twelve-day sampling period (they were predominantly straight-hinge larvae). This would indicate steady recruitment over the period, rather than the presence of a single brood of siblings. Weekly replacement of cultch placed on a grid of 19 stations revealed that spat settlement increased or decreased synchronously throughout the river from week to week. Swarms of larvae apparently became riverwide before setting indicating constant dispersal. Andrews (1979) noted that upriver and inshore sections of the swarm became less dense.

Andrews (1979) indicated that the estuaries studied by various investigators in the past differ (often widely) in physical characteristics and hydrographic regimes. There are shallow, stratified lagoons in New Jersey salt marshes; shallow, clear, still, lake-like estuaries of Bras d’Or, Canada; deep, turbulent and open waters of Long Island Sound; muddy, tidal river estuaries such as the James River and Delaware Bay; and trap-type low-flushing tributaries such as St. Mary’s, Great Wicomico, and Piankatank rivers of Chesapeake Bay. The different flushing, tidal, stratification, and wind regimes of these regions may strongly influence larval abundance and distribution and thus make comparative sampling difficult.

Other researchers, primarily those working with the European oyster, have questioned the conclusions of the “Nelson School.” Korringa (1941) found different distribution patterns in his own studies of *O. edulis* larvae in the Oosterschelde oyster grounds of the Netherlands. This environment, however, differs from the areas studied in New Jersey; it is a region of strong tidal currents and, because of tidal ebb and flow, much movement of water into and out of the system. Korringa (1952) continued to be skeptical about interpretations of data collected on C. virginica, remarking that even Carriker's (1951a) extensive study did not lead him to "...deduce from Carriker's data that his oyster larvae in any stage of development tend to travel into the headwaters of the estuary by performing rhythmical vertical migrations." More recently, deWolf (1973, 1974) performed an extensive study of barnacle larval dispersal in the Dutch Wadden Sea and concluded that larval retention in estuaries can be attributed to mechanical processes alone, with no need to appeal to larval swimming behavior patterns as an additional mechanism. He extended his remarks to include bivalve larvae.

One of the problems raised by critics of the "Nelson School" concerns the possible cues stimulating larval behavior to take advantage of estuarine transport mechanisms which might exist for carrying material upstream. If larvae are capable of swimming actions which result in their entrainment in appropriate water masses for retention in estuaries, they must have some means of sensing environmental cues. Our knowledge of oyster larval response to various environmental factors is extremely limited. However, some research has been conducted on larval response to salinity, one of the factors which changes with the tidal cycle. As mentioned, Nelson (1912) noted more oyster larvae in the water during flood periods than during ebb periods. Nelson and Perkins (1931) were the first to show that oyster larvae respond to increases in salinity by swimming. Haskin (1964) demonstrated increased activity in oyster larvae as salinity increased from 7 to 14 ppt. Hidu and Haskin (1978) reported on experiments on swimming speeds of oyster larvae in different salinities and temperatures. They noted two kinds of larval behavior. A slow spiral swim seemed to be associated with remaining in position in the water column. Maximum speed for this activity was 5 cm min^{-1} (0.08 cm sec^{-1}). Upward or downward movements could be performed at speeds up to 14 cm min^{-1} (0.23 cm sec^{-1}). At these speeds, larvae could move 7 to 8 m vertically in an hour, which would allow them to exploit tidal transport systems. Larval speed was also a function of size, with the largest-eyed larvae moving upward nearly three times faster than early larval stages (straight-hinge, early umbo). The authors used this ontogenetic difference to explain Kunkle's (1957) observations by postulating that the younger stages were poor swimmers and thus subject to relatively passive distribution through the water column whereas the older larvae were better able to affect their position by swimming in response to salinity changes.

The problem with the experiments of Haskin (1964) and Hidu and Haskin (1978) is that they were performed using very small experimental chambers (2 x 2 x 2 cm) cut out of paraffin blocks or made from 1.4 cm diameter glass tubes. Such small chambers may affect larval swimming behavior. Experiments are needed using larger water columns and chambers which can allow for normal swimming activity. Temperature, light, and pressure effects on larvae should be assessed and then effects of varying salinity levels and rate of change of salinity should be studied to determine if there is a 'salinity response' by oyster larvae and if that response is equivalent to what might actually be experienced in nature."

Larval Settlement

Mature larvae develop a pair of eyes (whose function is in dispute) and a foot containing a byssal gland. When ready to set, the larvae swim about with the foot extended to grip any solid surface. When contact is made, the larvae (pediveligers) crawl on the surface and, if it is suitable, attach by the left valve. At this stage, they are called spat. Larvae may be stimulated to settle by temperature (Lutz et al. 1970). They respond to the proteinacious component of the surface of oyster shells (Crisp 1967); they also exhibit rugotropism, settling in small pits and irregularities of surfaces (Galtsoff 1964). They appear to settle more readily in shade than in light (Ritchie and Menzel 1969). Hidu (1969) and Hidu et al. (1978) have demonstrated the presence of a water-borne "gregarious factor" which appears to be released by newly settled spat, thus attracting additional pediveligers to the vicinity. Figure 4 illustrates the settlement of spat.

Figure 4. Oyster shells with spat. (From Lippson, 1973)

Settlement behavior in relation to light intensity, surface angle, and current speed has been studied by a number of investigators using a number of oyster species. Contradictory results have been obtained (Cranfield 1968) which may be due to experimental conditions. Information concerning C. virginica is contained in Table 3 and shows similar variability in results. More attention to settlement behavior is needed to reach firm conclusions concerning the factors attractive to larvae and responsible for stimulating settlement.

Numerous field studies of settlement have been performed. Prytherch (1929) reported that set distribution was uneven and that it varied in intensity according to water depth and distance from the spawning population. On planted beds in Connecticut in 1925 he found that spat were most abundant on shells planted over the spawning bed and within about 100 m of its center. The commercially important set in the vicinity of this bar occurred mainly within 300 m of the bed with spat abundance ranging from 5-6 per shell on the outer edge of the bed to about 200-300 per shell in the central area of the bar. Prytherch (1929) felt this showed that larvae remained close to the place where they were spawned. However, there was no evidence that the oysters which settled were the same which had been spawned in that region and, since larvae exhibit a "gregarious" response to spat and adults, they might have originated elsewhere.

Table 3. Settlement surface preferences (upper, under) of *Crassostrea virginica* spat on different kinds of material and in different light conditions (where known).

Surface Upper	Under	Settling Material	Remarks	Authority
			In 8 yr of experimentation, no influence of light on setting was noted. No documentation given.	Prytherch 1934
	+	Glass, sand-blasted	9 feet below surface, 2 ft above bottom, Pensacola, Fla. See Butler 1955.	Pomerat & Reiner 1942
	+	Shell	More and larger spat on under surface in shell bags in field (S.C.).	Smith 1949
	+	Shell	Shell bags in field, 4-5 feet for 7 days. Upper side not silted (Md.).	Sieling 1951
+		Cement board	In field at 1 to 8 ft in 1 ft intervals. Also, setting seemed higher by day than by night (Fla.).	Butler 1955 (4-yr. study)
	+	Cement board	In field, at 9 ft, one inch above bottom. 50% of the set occurred on this bottom plate.	“
	+	Glass, sand-blasted	Could not duplicate Pomerat and Reiner’s obser vations although experi ments were performed in the same location.	“
	+	Concrete-coated cardboard	In field, at various depths in 2.3 m of clear calm water. Spatfall increased with depth and was heavier by day than by night. No fouling or silting occurred (Canada).	Medcof 1955

Table 3 cont'd.

Surface: Upper	Surface: Under	Settling Material	Remarks	Authority
	+	Shell	In open Pyrex dishes in the lab (Va.)	Crisp 1967
		?	Field studies. Set-tiny heaviest 0400 0830, then 1630-1940, then 0830-1630; then 1940-1600. Under con stant illumination, lar vae preferred dark ened areas (N.C.).	Chestnut 1968
	+	Shell	In lab. If under-surfaces were illu-minated, setting de-creased greatly (Fla.).	Ritchie & Menzel 1969
			In laboratory, set-ting was encouraged by darkness and par-tially inhibited by light (Canada)	Shaw et al. 1970
+		Cement board panels	In field suspended throughout the water column; collected weekly. Delaware Bay, N.J.	Hidu 1978
+		Asbestos plates	Three sampling levels in water column ($\simeq$ 3 m) in Mobile Bay, Ala. Peak Secchi disk visibility: 1.5-2.8 m.	Lee 1979
+		Asbestos cement plates	Held 10-20 cm above bottom in depths ranging from 1 to 3 m. Collected weekly. Choptank River tributaries, Maryland.	Kennedy 1980

Prytherch (1929) noted that larvae in Milford Harbor attached from low slack water through the first two hours of flood tide. He claimed that a velocity of 20 ft min^{-1} (10 cm sec^{-1}) inhibited setting. In areas without current, spat evenly covered collectors on all sides, but above 10 cm sec^{-1} spat settled mostly on the lee or protected side. Galtsoff et al. (1930) found the zone of heaviest setting to coincide with the level of low slack water.

Korringa (1941, 1952) considered settlement in *O. edulis* in Holland. He believed that two important factors governed settlement success. One was the number of mature larvae available to settle per unit volume of water and the second was the current velocity at the time of settlement. Of lesser importance, but still of significance, were the suitability of the bottom and the presence of predators.

Truitt (1929, 1931) found oyster shell to be more suitable as cultch in Chesapeake Bay, attracting more larvae than did glass, gravel, slag, or wood. He also noted (1931) that in areas of the Bay with abundant oyster larvae, a rich spatfall occurred (e.g., Seminary Bar in St. Mary's River; Dry Rock in Tar Bay (where 11,400 larvae were counted in one 50 gallon sample); Crab Alley and Mill Hill in Eastern Bay).

The predators of larvae will be discussed in the section on Competitors, Pests, and Predators and need not be dealt with here except to note that predation on larvae is extremely high and deserves greater study. Korringa (1941) determined for *O. edulis* larvae in a dynamic estuary in Holland that only about 250 larvae out of each one million produced survived to metamorphose. Of these, 95% expired before winter. This compares well with Waugh's (1972) estimate of 93% mortality for *O. edulis* spat after 1 year. Estimates of larval mortality of C. virginica appear not to have been published. However, Nelson and Chestnut (1945) noted that only about 1 of 630 spat per square inch survived its first year under crowded conditions. Estimates of mortality of larvae and spat would be useful in managing oyster stocks in the Bay. It would also help to know how to increase survival of young spat.

Larval Food

The natural food of larval oysters, as well as such useful knowledge as feeding rates under different conditions, is one major area requiring research. Optimal feeding regimes for rearing oyster larvae in hatcheries have been developed. However, natural diets may differ from laboratory diets. Further, it is not yet clear why some areas (e.g., Patuxent River in Maryland) are excellent for fattening of adults and not especially good for spat settlement, whereas other regions (e.g., James River, Virginia; Broad Creek, Maryland) are excellent areas for spat settlement. Nelson (1950a) noted that such information was missing for New Jersey waters but suggested the answer may be related to presence or absence of suitable food materials. Presumably the appropriate nannoplankton food for oyster larvae is not necessarily useful for adults, whereas diatoms and dinoflagellates might lead to fat adults but be of little use to larvae. Davis (1953) found certain species of flagellates and not others to be useful for larval growth and survival in the laboratory. Again, it is not clear what the larvae feed on in their natural environment. Nor is it clear what is available for them to feed on in Chesapeake Bay, as the nannoplankton communities are poorly known. It is important to establish a long-term study of nannoplankton (indeed, phytoplankton in general) seasonality in relation to oyster larval abundance and spat settlement success. D. Waugh (unpublished presentation to the International Council for the Exploration of the Sea - 1957) noted that studies in England showed correlation between nannoplankton crop failure and poor larval growth, and between abundant nannoplankton and good larval growth. Further, he noted the rapid (few days to a week or two) “blooming” and decrease of populations of different nannoplankton species. This leads to the need to establish clearly which species is present at critical periods in the oyster's larval life rather than depending upon gross indices such as chlorophyll a content or volume of plant cells, etc. Further, he noted that the failure of oyster spatfall in 1955 was correlated with the presence of a toxic flagellate. This ties in with Loosanoff's (1974) observations that toxic species of phytoplankton may be implicated in larval mortalities on the east coast of North America.

In his unpublished report just quoted, Waugh pointed out that four rivers supporting oyster fisheries in England varied widely in the reliability with which oysters grew and fattened. He postulated that an understanding of nannoplankton production would help explain such differences. In Australia, Rochford (1951, 1952) began a study of estuaries which also differed greatly in ability to set or grow oysters. His work on this ceased in 1952, unfortunately, but he felt that phosphorus was an important factor influencing the differences between rivers (personal communication). The point is that different oyster producing areas of the world have some regions where spat set is reliable and other regions where adult growth is excellent. There must be a general answer to the world-wide similarities of oyster grounds in terms of adult growth versus larval survival and spat settlement. We postulate that the phytoplankton in different regions (e.g., Broad Creek versus Tred Avon River versus Patuxent River in Maryland) may be responsible for the differences in adult growth or spat settlement (whether the phytoplankton serves as food or a source of toxin). This whole subject requires long-term attention.

Larval Disease

We have little knowledge of larval disease, especially disease in the natural environment. This has been remarked on by Loosanoff (1974). Bivalve larvae are highly susceptible to disease organisms, but information on field mortalities is lacking.

GENETICS

Taxonomic Aspects

The taxonomy of oysters has been the center of some attention. Some of the more pertinent papers are those of Gunter (1950, 1951) and Menzel (1974), and review papers by Stenzel (1971) and Ahmed (1975). Hillman (1964, 1965) found indications of intraspecific genetic differences in *Crassostrea virginica* from Long Island Sound, Delaware Bay, Virginia and several sections of Chesapeake Bay, and Louisiana Estimates of genetic variation have been made by intraspecific studies of *Crassostrea gigas* and *Saccostrea commercialis* and interspecific studies of *Crassostrea* and *Saccostrea* (Buroker et al. 1979a,b respectively). Buroker (1980) also used data on genetic variation in species of *Crassostrea* and *Saccostrea* to test the trophic resource stability theory.

Applied Genetics

With regard to genetic studies as applied to oyster "farming," we are not much further advanced than when Nelson (1947b) considered the topic of selective breeding of oysters. However, genetic research on C. virginica is being carried on at two research centers: Milford, Connecticut (by Longwell and Stiles), and Halifax, Canada (by Newkirk and Haley).

In any successful breeding program, the resultant product depends on exploitable genetic variation, the presence of which must first be determined. Sources of genetic variability can include (a) that which is present within the population under consideration (b) that which exists between populations of the same species, and (c) genetic differences between species (Newkirk and Haley 1977).

Exploitation of this genetic variation normally requires selection for the superior individuals possessing the trait in question, e.g., for fast growth, prolific breeding, environmental resistance. The analogy with domestic animal and plant breeding programs is obvious. However, as Wilkins (1981) indicates, there is greater potential for genetic improvement of aquaculture candidates than for modern domestic livestock because of greater genetic variability and fecundity, and relative ease of fertilization and interspecific crossings. In addition to the use of selection in "selective breeding," a program of cross-breeding individuals from genetically different populations to produce offspring superior to the parents can be initiated. The strategies involved and the problems associated with cross-breeding are briefly and clearly stated in Newkirk and Haley (1977). In general, selective breeding is costly and time-consuming and requires a long-term commitment of money and manpower if it is to be successful. Such programs have worked well with domestic organisms (Roosenburg 1976) with the support of both governmental and breeder-organization financing. At present, only governmental support would appear to be forthcoming for oyster breeding studies but the need is great and the potential returns are large.

The general topics of oyster genetics and their application to breeding have been reviewed by Longwell and Stiles (1970, 1973), Longwell (1976), Newkirk (1980), and Wilkins (1981). These references, especially Newkirk's and Wilkins', should be consulted to provide detail and entry to the literature.

In general, a number of points are becoming clear. The first step in initiating an aquaculture program involves defining the breeding goal (e.g. disease resistance, enhanced larval or spat survival, better growth rate or food conversion efficiency) and ways of measuring it (Wilkins 1981). Variation must be present for the chosen character and the variation must be measurable to allow for monitoring genetic improvement. Such improvement will depend on aspects of the breeding scheme, the heritability of the desirable character, and biological and environmental influences upon the character.

There appears to be considerable interpopulation and intrapopulation genetic variation available. This is important because it provides the raw material for a selective breeding program. However, phenotypic variability and year-to-year environmental variation are also high; consequently, a number of generations may have to be raised to demonstrate the success of any breeding program, and the raising of these generations may be plagued with difficulties. Thus the need for patience (Longwell 1976).

Heritability of desirable characters must be determined. For example, with regard to the heritability of larval growth rates, current estimates are high (Newkirk et al. 1977, Losee 1978), indicating additive genetic variance which is available for exploitation in a selective breeding program. A positive relationship has been found between fast growth and early setting in larvae and fast growth in the resulting spat (Losee 1979). If this relationship were to hold for growth to market size, this would allow the breeder to select for fast growth during the larval stage when animal numbers are highest, individuals are cheapest to produce, and handling is simple and inexpensive. Culling of the slowly growing larvae would result in savings in space, food, and handling expense. However, Newkirk has cautioned (personal communication) that the relationship between larval growth rate and spat growth rate may not be important in improving growth to market size. Indeed, he has evidence that the positive correlation between fast growing larvae and fast growing spat does not hold past the first season. His work was with *Ostrea edulis*, however, whereas the earlier work (Haley and Newkirk 1978, Losee 1979) was on *Crassostrea virginica* The subject needs further clarification.

Selection for disease resistance has occurred in nature. This is true for resistance to Malpeque Bay disease in Canadian oysters (Logic et al. 1961) and MSX in Delaware oysters (Newkirk 1980). However, artificial selection for resistance to MSX in hatchery-reared stock has increased resistance more rapidly than has been true for natural selection of wild populations (Haskin and Ford 1978).

Studies similar to those cited above need to be encouraged in Chesapeake Bay. Newkirk (1980) reports that (1) the observed genetic variation in and between oyster populations is encouraging because future breeding programs will require such variability; (2) inbreeding depression may be a problem in hatcheries in spite of large numbers of brood stock, and must be guarded against (see also Wilkins 1981); (3) the rapid response to artificial selection for disease resistance is encouraging because disease resistance is generally thought to have a low heritability. Perhaps this indicates that the oyster will respond rapidly and vigorously to other breeding efforts, e.g., for growth, survival, environmental resistance.

DISEASES AND PARASITES

The overwhelming importance of disease in oyster populations was illustrated dramatically by the onset of infection by the haplosporidan *Minchinia nelsoni* Haskin, Stauber and Mackin (MSX) which depleted oyster populations in Delaware Bay in 1957-1958 (Haskin et al. 1965, 1966). As a result of this epizootic, oyster production in Delaware Bay declined from 7.5 million pounds of meat to less than 100,000 pounds (Sindermann and Rosenfield 1967). By 1959, *M. nelsoni* was found to be present in Chesapeake Bay (Andrews 1966, Andrews and Wood 1967) where it had serious impact on oyster populations in Virginia and in the more saline portions of Maryland (Farley 1975).

The disease has abated in both Bays and it appears that disease-resistant populations have developed from the survivors of the original epizootic (Haskin and Canzonier 1969, Otto et al. 1975). The disease did have one salutary effect as Sprague (1971) has indicated. Its presence and devastating impact forced the organization of annual oyster mortality conferences to improve dissemination of knowledge in an effort to ameliorate the effects of the disease. These conferences evolved into shellfish pathology conferences and a merger of shellfish and insect pathologists led to the formation of the Society for Invertebrate Pathology. Thus the study of oyster disease has progressed from a state of neglect to a state of healthy activity (Sprague 1971). Further evidence of this development may be found by taking notice of the relatively recent production of various reviews and bibliographies (Mackin 1961a,b, 1962a, Sindermann and Rosenfield 1967, Sindermann 1968a,b, Sprague 1970, 1971) and at least four major books (Cheng 1967, Sindermann 1970, 1977, Snieszko 1970).

Because of the relatively recent understanding of the importance of diseases in shellfish mortalities, there are few adequate, well-financed programs aimed at providing a base of information for future comparison with epizootic conditions. There is little information on background levels of disease and parasites in populations not presently subject to epizootics. It often takes some crisis to release sufficient funds for any sort of adequate study. In an effort to provide for some disease monitoring, the Maryland Department of Natural Resources (DNR) has a project called Marine Animal Disease Investigations (MADI) which receives a grant from National Marine Fisheries Service (NMFS). This project continues the work of a study initiated in the early 1960's by the then U.S. Bureau of Commercial Fisheries of Oxford, Maryland, to monitor the presence of infectious and noninfectious disease of several species of molluscs in Chesapeake Bay. With regard to oysters, its major emphases include: *Perkinsus marinus Minchinia nelsoni*, rickettsial and chlamydial infections, gill xenomas (ciliated thigmotrichs); physiological stress syndrome; neoplasia. However, because of limited boat facilities available to MADI, since 1974 the Center for Environmental and Estuarine

Studies has provided samples of oysters from a number of oyster bars whenever possible. In the past, sampling has generally occurred during two periods of the year, one in spring and one in fall.

This limited sampling effort, while useful, puts a constraint on the extent of this important oyster disease program. It does provide for satisfactory monitoring of the presence of *P. marinus* but limits assessment of the seasonal progress of other diseases, such as parasite burdens. Burton (1963) has indicated the importance of periodic histological examination of oyster tissue by referring to the situation prevalent during the 1957 epizootic in Delaware Bay. Because of lack of periodic collection of oyster tissues in previous (relatively disease-free?) years, it was not possible to compare the infestation of newly observed microparasites noted in weak and dead oysters with their occurrence in earlier years.

The following diseases or parasites are encountered in Chesapeake Bay, Maryland:

A. *Minchinia nelsoni* (MSX). We have already described the effects of this haplosporidan parasite in Delaware and Chesapeake Bays. Plasmodia enter the oyster through the epithelial lining of the gill and inner palp. Proliferation begins here and continues throughout the animal as the disease advances. There is an intense cellular response characterized by hyaline hemocytes infiltrating the affected areas of connective tissue and circulation systems. After infection, heavy congestion appears in the affected tissue. Farley (1968) stated that "extensive destruction of gametic tissue by *M. nelsoni* was seen microscopically." Major progress in the identification of the causative organisms occurred in the early 1960's with the naming of the organism (Haskin et al. 1966) and the clarification of the association between its plasmodium and pre-spores and spores (Barrow and Taylor, 1966, Couch et al. 1966). The spores have been described in electron microscope studies by Rosenfield et al. (1969). Aspects of the epizootiology of the disease in Virginia have been described by Andrews (1964, 1966).

Otto et al. (1975) have stated that prevalence of this disease had decreased to zero in Maryland waters of Chesapeake Bay before the time their regular sampling program ceased in 1972. However, since then occurrences have been noted. For example, with Sea Grant support, one of us (VSK) collected more than 6,700 individual oysters from 18 oyster bars over a 19-month period as part of a study of oyster gametogenesis. During the preparation of histological slides, cursory observations revealed appreciable occurrences of *M. nelsoni* in higher salinity waters. For example, in Manokin River in September 1977, 8% of the sample was affected by *M. nelsoni*. In October 1977, the prevalence of MSX was 8% in Nanticoke River and 4% on Sharkfin Shoal, Tangier Sound. Project MADI continues to monitor for this disease.

B. *Perkinsus marinus*. This significant disease inhibits normal gonad development (Mackin 1951, Menzel and Hopkins, 1955b). It infects oysters from the

Atlantic and Gulf coasts of the United States. First described by Mackin et al. (1950), its distribution, pathogenicity, and epidemiology have been studied intensively (Andrews, 1955b, Andrews and Hewatt 1957, Sprague 1971). Otto and Krantz (1976) have reported an epizootic of this disease on oyster bars in higher salinity waters of Maryland. This disease is readily studied by culture techniques (Ray 1966) and is monitored by Project MADI.

C. *Bucephalus cuculus*. This trematode infects digestive diverticula and gonads of the oyster (Hopkins 1957, Cheng and Burton 1965). Young sporocysts apparently pass through the intestinal wall and move to the digestive gland via blood vessels. As the sporocysts age and anastamose, they infiltrate connective tissue and most major organs including the gonads (Cheng and Burton 1965). In heavy infections, sporocyst branches may be tightly packed in the area normally occupied by gonads (Cheng and Burton 1965) and normal gonadal development is correspondingly prevented (Feng and Canzonier 1970). During the previously mentioned gametogenesis study (by VSK), this trematode was present on all oyster bars surveyed, with as much as 22% prevalence in some samples. On some oyster bars, the trematode was present throughout the 1977 survey period whereas in others it appeared as oysters entered the regression stage in autumn after spawning. The percentage and degree of infection (Douglass 1975) and range of this parasite is of interest because heavy infestation effectively sterilizes the oyster (Feng and Canzonier 1970).

D. Hyperparasites of *Bucephalus cuculus*. The trematode may be infected by hyperparasites. Mackin and Loesch (1955) have noted the occurrence of just such an organism (whether sporozoan or haplosporidan is not clear). Such hyperparasites have been noted rarely in Maryland waters (Sprague 1970). Another relatively uncommon hyperparasite is *Nosema dollfusi* (Sprague 1964).

E. Other Infectious and Noninfectious Diseases. A variety of rarer parasites and conditions may be noted in Maryland oysters.

1. Neoplasia. The study of neoplasia and related disorders in molluscs has intensified in recent years (Couch 1969, Farley 1969, 1976a,b, Newman 1972, Frierman 1976, Harshbarger et al. 1979). Their tissue origin, host cellular response, and presence or absence of parasitic involvement is of interest to researchers in this fairly new field of molluscan research. During our gametogenesis survey, in a histological preparation of a monthly sample from Eastern Bay a neoplasm was observed which is probably of hematopoietic origin.

2. “Ovacystis.” A lytic virus morphologically similar to papillomavirus has been found in germinal tissues of C. virginica (Farley 1976a, 1978). It appears in abnormally large basophilic, Feulgen-positive cells in gonadal tissue.

3. *Nematopsis ostrearum*. Cysts of this gregarine parasite have been described by Prytherch (1940) from *C. virginica*. Galtsoff (1964) reports

the parasite as widely distributed in oysters along the Atlantic coast of the U.S. but there is no correlation between its presence and oyster mortality. The cysts are easily recognized in histologic section. In addition to *N. ostrearum*, a gregarine-like parasite of oysters has been described by Sawyer et al. (1975).

4. *Sphenophyrya* sp. Xenomas (Weissenberg 1968) with bodies of a ciliated thigmotrich resembling *Sphenophyrya* sp. have been found in gills and mantle of C. virginica (Otto et al. 1979). They are easily identified. No mortalities have been reported as a result of this parasite's presence. It is probably rare.

5. *Ancistrocoma pelseneeri*. This cilate parasite is not common but can be identified easily when found in gill or mantle tissue. It is known to cause mortality in Chesapeake Bay. Sprague (1970) has described it briefly.

6. Physiological stress syndrome. Factors such as severe winter weather conditions, polluted water, and limited food supply may be associated with an observable cellular response which can be determined in histologic section. The syndrome has been seen on several shellfish beds in 1974, 1975, and 1976 in late winter and early spring samples and can appear as early as late autumn and post-spawning period (Otto, personal communication).

7. Rickettsial and chlamydial intracytoplasmic inclusions. Recent papers by Harshbargar et al. (1977) and Otto et al. (1979) deal with these organisms which have been noted in Chesapeake Bay bivalves (as well as in molluscs worldwide). They have not been associated with molluscan mortalities or implicated in human disease, although related species are known pathogens. Definitive identification of these molluscan cytopathologic agents is underway.

Larval Disease

Loosanoff (1974) reviewed a wide variety of factors that had, at one time or another, been thought to be responsible for sudden and mass mortalities of oyster larval populations. He felt that no one factor was necessarily ever completely responsible for such mortalities. However, he did note that disease was one of the least studied factors that might result in such mass mortalities in nature, with only a few studies having been performed on fungal and bacterial pathogens. The situation has not improved much since he wrote.

What research activity there is has concentrated mostly on bacterial pathogens (Guillard 1959, Tubiash et al. 1965, 1970, Brown 1973, Tubiash 1975). One of the most serious diseases afflicting hatchery-reared oysters is vibriosis caused by bacteria of the genus *Vibrio* (Tubiash et al. 1970, Brown and Losee 1978, Elston and Leibovitz 1980). A useful recent review of economically important diseases of larval bivalves has been provided by Elston (1979).

Given the vagaries of sampling discrete populations of larval oysters in the field, studies of disease in wild populations will be difficult. Further, it will probably continue to be difficult to attribute mass mortalities of larval oysters to any factor, including disease. One may not be sure if the decline in abundance of larvae over time is due to mortality or to physical removal from the sampling area by water circulation patterns. Probably, therefore, the most productive research will focus on hatchery populations, although researchers face the problem that they are dealing with unnatural monocultural situations in which disease is readily and rapidly transferred.

Because of the relative newness of oyster disease studies, basic information is still lacking on many disease organisms and parasites, including life cycles, transmission modes, synergistic effects of interactions (involving *M. nelsoni* and *P. marinus*, for example), environmental influences on disease prevalence, and implications for human health or health of commercial species in the Bay.

COMPETITORS PESTS, AND PREDATORS

As populations of oysters decline in Chesapeake Bay, efforts are increasing to augment natural oyster recruitment with hatchery-produced spat transplanted to natural or artificial beds. The oyster's competitors and predators, while always a nuisance, are now becoming weeds and pests threatening these new aquacultural crops. In order to control these enemies of the oyster, it is crucial to understand their biology, their methods of attack on the oyster, and how they may be efficiently eliminated.

Competitors

Since little is known of oyster larval nutritional requirements in the natural environment (see section on Feeding and Nutrition) very little can be said about competition for larval food resources. There must be some competition for food among planktonic organisms, but the direct effect of planktonic competitors on larval oysters is unknown. Nelson (1928b) reported that scientists in Conway, Wales, noticed heavier spat set in laboratory tanks in which the goby *Gobius microps* was also present. It was thought that the reduction in numbers of copepods by the fish left more food resources for the larval oysters.

More is known about competition for settlement space; in this case, the oysters' competitors are usually referred to as fouling organisms. Shaw (1967)—see also Kennedy 1980—studied seasonal fouling in Broad Creek, a tributary in central Chesapeake Bay, and found that bryozoans (*Membranipora tenuis* and *Conopeum tenuissimum*), barnacles (*Balanus improvisus*), mussels (*Ischadium recurvum*), flatworms (*Stylochus ellipticus*), and settling oysters compete for settlement space over the summer months.

In addition to competing with oyster larvae for settlement space, barnacles may ingest mature larvae. Steinberg and Kennedy (1979) found that *Balanus improvisus* greatly reduced the number of oyster larvae in laboratory test containers. The presence of partially digested oyster larvae in the gut of a large barnacle implied that reduction in larval numbers was due at least in part to ingestion by the barnacles and not merely to mechanical damage caused by their beating cirri.

A widespread space (and perhaps food) competitor of adult oysters in the low salinity waters of Chesapeake Bay is the mussel *Ischadium recurvum* (= *Brachidontus recurvus*). Oysters encrusted with mussels have a deformed shell shape and poor condition (Engle and Chapman 1951). Oyster condition improves if the mussels are removed.

In more saline waters, space available for oyster settlement may already be occupied by young starfish, one of the oyster's more destructive predators (Galtsoff 1964). The starfish *Asterias forbesi* has a reproductive season slightly preceding that of the oyster in New England. In Long Island Sound, *A. forbesi* spawns approximately two weeks before the oyster (Loosanoff et al. 1955) and, with a setting season of approximately the same length as the oyster, it settles out of the water before the oyster.

Crepidula fornicata (slipper limpet) along the Atlantic coast can be a serious competitor with oyster larvae for settlement space. Adult *C. fornicata* can alter hard substrates, preferred by oyster spat, to muddy bottom through the accumulation of their feces and pseudofeces (Barnes et al. 1973). In addition, this organism may ingest large numbers of young oyster larvae. Although the larvae may not be digested, they may be deposited in sticky feces from which they cannot escape (Korringa 1949, 1952).

Control of Competitors

Control of fouling on spat collectors or cultch by the application of chemicals has produced promising but inconclusive results. Walne (1956) recommended the immersion of collectors with oyster spat in a solution of 4 ppt of hydrated copper sulfate, followed by a 1-2 hour drying period. Waugh and Ansell (1956) used a spray of 0.03 mg DDT cm^2 for successful control of barnacles (*Elminius modestus*). While oyster spat settlement was doubled, early growth of oyster spat was temporarily inhibited by this treatment. MacKenzie (1961b) demonstrated that many competitors can be killed by a five-second immersion in a 98 to 100% salt solution followed by a period of storage in air, the length of storage dependent upon the species being eliminated. Dipping oyster shells into certain oils containing large amounts of tetra-chloro-benzene, such as Polystream and Polychlor, prevented fouling and increased oyster setting in Long Island Sound (Loosanoff 1961). Similarly, Haven and Whitcomb (1969) found increased spat set on Polystream-treated cultch in lower Chesapeake Say. Shaw and Griffith (1967) reported higher spat set on shells treated with Polystream and Drillex in Chincoteague Bay, Maryland, and in the Tred Avon River, but not in Tangier Sound or Broad Creek (the latter three locations are in Chesapeake Bay, Maryland). Studies in the central Chesapeake Bay area using test panels treated with Polystream and Drillex did not result in reduced fouling (Shaw 1967). Control of fouling on oyster cultch in Chesapeake Bay is a topic which requires further study.

Crepidula sp. can be controlled by mechanical, chemical, and biological methods. Mechanical cleaning by dredging and sorting is feasible but expensive (Korringa 1949). Loosanoff (1961) suggested the use of underwater plows to control both *Crepidula* sp. and the mussel *Mytilus edulis* on Long Island Sound oyster beds. *C. fornicata* may also be controlled by immersion in a seawater and corrosive sublimate (1:25,000) solution for two hours. While young oysters detect the poison and close their valves, *C. fornicata* appears unaware of it and accumulates it (Korringa 1949). MacKenzie (1961b) recommended dipping oysters in a 1.0% copper sulfate solution followed by a period of storage in air to control mussels and *Crepidula* sp., the lethal material entering these pests more readily than it does oysters. This method, MacKenzie cautioned, should not be used on oysters smaller than 22 mm, as it is also lethal to them.

Planting of young mussels on unused, slipper limpet-infested beds was mentioned by Korringa (1949) as one possible biological control used by European mussel farmers. Growing mussels soon smother the slipper limpets. After the mussels are harvested, the beds can be re-used for oyster culture.

A degree of natural control of some oyster competitors may be achieved by the preference of the starfish *Asterias rubens* for *Crepidula*, *Mytilus* and *Elminius* spp. rather than for oysters (Hancock 1955).

Pests

The pea crab, *Pinnotheres ostreum* Say, is found inside oysters and robs them of their filtered food. While still in a developing stage, the crab invades oyster spat (Christensen and McDermott 1958). The mature crab lives in the mantle cavity on the oyster's gills and feeds on mucous strings of food collected by the oyster. Pea crabs weaken oysters and promote poor oyster condition (Sandoz and Hopkins 1947, Korringa 1952, Haven 1958, Nelson 1960). In addition to interfering with the feeding mechanism of their hosts, pea crabs usually cause gill erosion and may interfere with oyster growth (Christensen and McDermott 1958). Awati and Rai (1931) found fewer females than males among pea-crab infested oysters (*Ostrea cucullata*). Thus, pea crabs may influence sex ratio in oysters, with older oysters more affected than younger ones due to increased infestation (Christensen and McDermott 1958).

Mud-blister worms, *Polydora websteri* and possibly *Boccardia hamata* (Larsen 1978) in Chesapeake Bay, are other pests which can be detrimental to oysters in low salinity, muddy environments (Lunz 1941). The pelagic stage of *P. websteri* establishes itself between the pallium and shell of oysters. It accumulates a mass of mud around itself and the oyster responds by secreting shell to cover the mud-worm complex. While Loosanoff and Engle (1948) and Medcof (1946) asserted that the infestation has no effect on oyster fatness, heavily infested oysters may indeed be in poorer condition and more susceptible to disease (Korringa 1952). Skeel (1979) stated that some oysters infested with *P. websteri* may become so weakened that they die. Moreover, shells of infested oysters are often brittle and break easily during transportation after harvesting or while under attack by crabs. Such brittle shells are also hard to shuck, making them undesirable to commercial buyers. Market value of infested oysters is lowered because the blisters are unappetizing, especially if they break and release mud over the oyster meats (Medcof 1946). Suspension of oysters in trays may reduce but not completely eliminate mudworm infestations. Off-bottom culture may also provide favorable environmental conditions for oyster growth, counteracting any adverse effects of mudworm infestation (Loosanoff and Engle 1948).

A pest in lower Chesapeake Bay and the Atlantic coast, the boring sponge *Cliona* sp. cannot tolerate salinities below 10 ppt (Hopkins 1962). The sponge makes holes in oyster shell by a chemical mechanism (Cobb 1969) to provide itself with shelter. Oysters respond by continuously secreting shell to prevent penetration by the sponge (Korringa 1952). Oyster condition becomes poorer as the oyster becomes weakened and exhausted.

The boring clam, *Diplothyra* (=*Martesia*) *smithii*, although more common in southern waters, has been found occasionally in Tangier Sound, Chesapeake Bay (Galtsoff 1964). This clam drills a cavity in the shell of the oyster, which responds by depositing new shell layers so that the shell is never completely perforated. The boring clam is a minor pest, its major effect being weakening of the oyster's shell structure.

Control of Pests

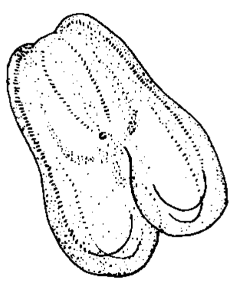
Pinnotheres ostreum can be controlled by exposing the oysters to 10 mg L^{-1} of 95% technical Sevin for 24 hours. The pea crabs are then ejected by the unharmed oysters. Although crabs are highly sensitive to Sevin, oysters can be exposed to as much as 100 mg L^{-1} without apparent injury (Andrews et al. 1969). *Polydora* sp. can be controlled by bathing oysters in fresh water for 16 hours or in a solution of seawater and an ammonium salt of dinitro-ortho-cresol solution for three hours (Korringa 1952). MacKenzie (1961b) recommended storing oysters in air for three hours after an immersion of five seconds in a completely saturated salt solution. *Cliona* sp. have many natural enemies including gastropods and crabs on the oyster reef (Guide 1976). Where natural predation is not a sufficient control, Korringa (1952) suggested a fresh water bath to rid oysters of sponges. A five-second dip in a saturated salt solution followed by three hours' exposure to air (MacKenzie 1961b), or a 30-second dip followed by a one-hour exposure (Loosanoff 1961) is also an effective control, resulting in complete mortality of sponges.

Predators

Predators of Larvae

Loosanoff (1959) reported that large ciliated protozoans of the family Condylostomidae could ingest as many as six lamellibranch larvae at a time in the laboratory. He suggested that related species or related families of these organisms in nature, such as the widespread and numerous Folliculinidae, could be capable of destroying many bivalve larvae. Another possible predator mentioned by Korringa (1952) in his review on oysters is the mosquito larva (*Aedis togoi*). Whether the mosquito species present in Chesapeake Bay marshes have any appreciable effect upon oyster larval numbers in natural or cultured populations is an area for possible further study.

In 1915, Kincaid reported that the ctenophore *Pleurobrachia* sp. ingests large numbers of oyster larvae. Nelson (1925a,b), after several years of research in Barnegat Bay, New Jersey, postulated that the ctenophore, *Mnemiopsis leidyi* exerted a major influence over C. virginica numbers as a result of predation. He counted as many as 125 straight-hinge oyster larvae in the digestive cavities of single ctenophores. In 1921 and 1922, large sets of oysters occurred while few or no *Mnemiopsis leidyi* were present in Barnegat Bay. Contrarily, in 1923, there were swarms of *M. leidyi* present (25-40 m^{-3}) and poor oyster set. However, Loosanoff (1974) reported that he had not noted any strong correlation between numbers of ctenophores and oyster larvae in Long Island Sound. He cited an example of a year (1944) when numbers of ctenophores and settled spat were both very high.

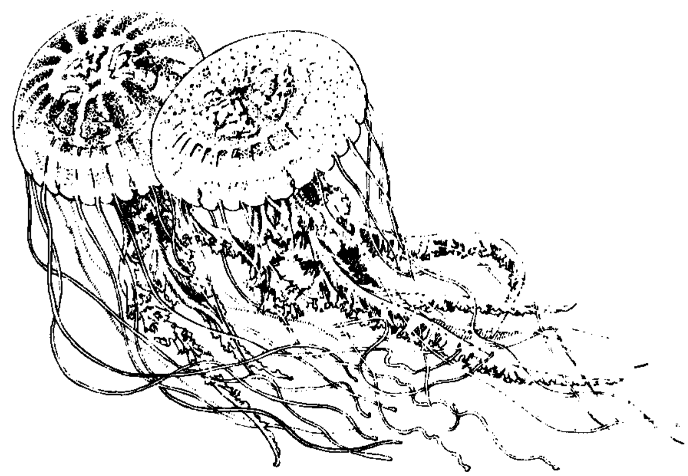


Mnemiopsis leidyi

Additional studies on *Mnemiopsis leidyi* have provided evidence that the species may be responsible for a varying fraction of zooplankton mortality (Bishop 1967, Burrell 1968, Kremer 1979). However, no particular attention was paid to the impact on bivalve larval numbers in these studies, although Kremer (1979) noted elevated feeding rates by the ctenophore on zooplankton prey dominated by calanoid copepods or cladocerans as compared to prey dominated by cyclopoid copepods and veliger larvae. Burrell and Van Engel (1976) studied the predation by *M. leidyi* on zooplankters in the York River estuary. While primarily interested in predation upon crustacean plankters, they nevertheless noticed an inverse relationship between the numbers of bivalve larvae and the volume of ctenophores present.

Sea nettles, *Chrysaora quinquecirrha*, widely distributed in salinities higher than 5 ppt, have been reported to feed on oyster larvae (Loosanoff 1974). The sea nettle is also a heavy feeder on *Mnemiopsis leidyi* (Cargo and Schultz 1967, Burrell 1968, Miller 1974, Burrell and Van Engel 1976), as is the atentaculate ctenophore, *Beroe ovata* (Burrell 1968, Burrell and Van Engel 1976). Truitt and Mook (1925) commented that "an intimate relationship exists between ctenophore, jellyfish, and oyster larvae." In 1925, numbers of *C. quinquecirrha* appeared in Chesapeake Bay in quantities greater than in living memory. Similarly, in late summer, masses of *M. leidyi* were present in surface waters, being rare in bottom samples (the sea nettles were also found predominantly near the surface). Coincidentally, the normal top to bottom ratio of larval distribution was altered. In past samples it had been 3:1 in favor of the surface waters. In 1925, it was 5:4. Truitt and Mook (1925) attributed the change to heavy feeding by the gelatinous zooplankters on oyster larvae near the surface. That year, precipitation from June to September was two-thirds normal and the temperature was consistently warm (although not record-breaking). Spat settlement that year was poor. In addition, at least in shell planting regions, the bottom was covered with mats of tunicates in an unusual outbreak of these creatures.

In 1930, Truitt again reported a heavy infestation of sea nettles in the Bay. That same year the spatfall was the greatest in years and rainfall in the Chesapeake drainage belt was the lowest in recorded history. In the stomodaeum of a specimen of *M. leidyi* from Tar Bay, 113 whole veligers plus fragments were counted. Truitt noted that over a period of years of observation, ctenophores were almost persistently present in the Bay whereas sea nettles were erratic in numbers, being abundant for a couple of years and then absent for a period.

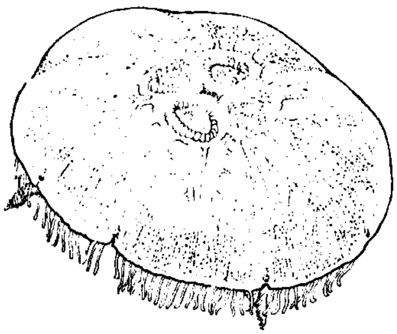


Chrysaora quinquecirrha

In 1931, sea nettles again appeared in vast numbers (Truitt 1931), being even more abundant than in 1930. Spatfall was also very good throughout the Bay. The drought of 1930 broke in the summer of 1931, but salinities remained higher than usual. No mention was made of ctenophore numbers in this report.

Thus, good spat sets occurred at the same time as sea nettle numbers and salinities were high. In more recent times, sea nettles were very abundant off Chesapeake Biological Laboratory pier in 1962 and 1964, with lesser but high numbers present in 19 63, 1965, and 1966 (Cargo and Schultz 1967). These years also had relatively high spat sets (Meritt 1977) compared with other recent periods of time. These relationships are not always close; for example, the peak of sea nettle abundance (Cargo and Schultz 1967) was 1964 whereas the peak of oyster spat set (Meritt 1977) was 1965. The excellent spat set of 1980 in central Chesapeake Bay was also accompanied by an abundance of sea nettles (personal observation).

However, sea nettle numbers and oyster larvae numbers may both be responding to other factors (e.g., higher salinities) rather than the oyster larval numbers being affected by sea nettle predation on ctenophores. Unfortunately, it does not appear that ctenophore abundances were measured for 1980 when spat settlement was excellent (nor for earlier years for comparison). The relationship between these gelatinous zooplankton and oyster larvae should be investigated further.



Aurelia aurita

Moon jellyfish, *Aurelia aurita*, widespread throughout Chesapeake Bay, may also prey on larval oysters. Drinnan (1975) noticed that large concentrations of this jellyfish in the spatfall areas of Cape Breton, Canada, coincided with heavy larval mortalities. The effect this organism has on Chesapeake Bay larval oysters is not documented and is an other area for additional study. We expect that predation pressure by *A. aurita* is small because numbers of the jellyfish are low in the Bay.

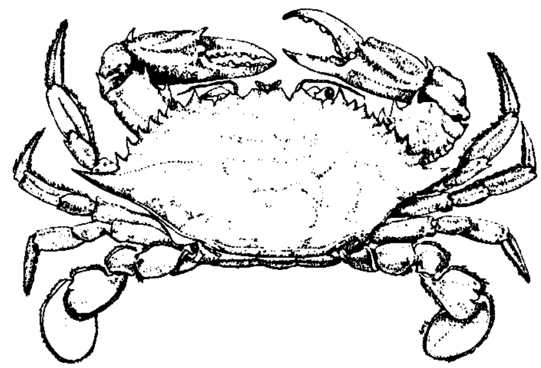
MacKenzie (1977b) found sea anemones, *Diadumene leucolena* (another organism found living on oyster shell throughout the Bay), to consume large numbers of oyster larvae. He reported that an anemone can capture and consume all the oyster larvae that touch its tentacles at the rate of more than one larva per minute. Steinberg and Kennedy (1979) found feeding rate to increase as size of the anemone increased, larger individuals being capable of consuming an average of more than four larvae per minute. Since mature larvae may tend to congregate near the bottom prior to setting, sea anemones may be highly destructive to pediveligers. MacKenzie (1977b) suggested that sea anemones could be controlled by spreading quicklime (CaO) in a fashion similar to that used on starfish.

Filter-feeding molluscs (oysters, mussels, clams, limpets) may ingest oyster larvae in the process of filtration and feeding (Korringa 1949, Drinnan 1975). Drinnan (1975), noting that mackerel guts have been found to contain oyster larvae, postulated that filter feeding fish may also be oyster larvae predators. Herring-like fishes such as menhaden may possibly feed on larval oysters present in the plankton in Chesapeake Bay. The magnitude and impact of this predation on oyster larvae populations are not documented and require further study.

Predators of Spat and Adult Oysters

Many predators of adult oysters are effectively barred from much of upper and central Chesapeake Bay because of intolerance to the characteristically low salinities prevailing there. Salinities in the Maryland portion of the Bay are seldom above 20 ppt, with spring salinities much lower than this, depending upon runoff from the Susquehanna River (Lippson 1973).

Flatworms. An extremely important predator on oyster spat is the polyclad turbellarian flatworm, *Stylochus ellipticus* (Loosanoff 1956, Webster and Medford 1959). It occurs widely throughout Chesapeake Bay and its tributaries and can survive a slow decrease in salinity from 32 ppt to 2.9 ppt (Landers and Toner 1962). *S. ellipticus* exhibit a marked prey preference, which appears to be directly related to prey density (Christensen 1973, Parsons 1973). Although there may be a natural preference for barnacles (Christensen 1973), a high density of oysters may result in *S. ellipticus* learning to prefer oysters as prey (Landers and Rhodes 1970). *Stylochus ellipticus* can be controlled by dipping infested oyster seed in a saturated salt solution (Provenzano 1959, MacKenzie 1961b), although reinfestation is a problem., *Crustaceans*. Blue crabs (*Callinectes sapidus*), so abundant in Chesapeake Bay, are no threat to healthy adult oysters, but do feed on dead, thin-shelled or weakened adults (Lunz 1947, Menzel and Hopkins 1955a, Menzel and Nichy 1958). Lunz (1947) reported that *C. sapidus* was the most serious oyster predator at Wadmalaw Island, South Carolina, killing more oysters than all other pests combined. He noticed the greatest mortality among young oysters, but even adult, clustered (and therefore thin-shelled) oysters were susceptible to their attack. *Callinectes sapidus* and xanthid crabs are important predators on oyster spat in Chesapeake Bay. Krantz and Chamberlin (1978) found cultchless spat produced in oyster hatcheries to be especially susceptible to blue crab predation. The Dupuy technique of culturing cultchless spat produces oysters with a thin lower valve. Blue crabs are able to manipulate cultchless spat and penetrate this weaker area easily.



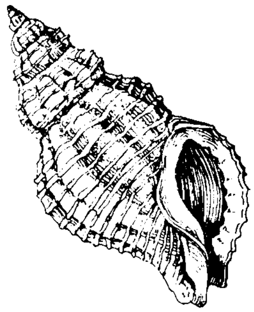
Callinectes sapidus

In New Jersey, *Panopeus herbsti* and *Eurypanopeus depressus* readily destroyed young, thinshelled oysters (McDermott 1960). McDermott (1960) postulated that crowding of spat may make them more vulnerable to crab attack. In Chesapeake Bay, *Rhithropanopeus harrisii*, which prefers lower salinities (Ryan 1956), is a probable predator of oyster spat (Krantz and Chamberlin 1978).

Some crabs such as *Menippe mercenaria* are serious predators of adult oysters (Gunter 1955, Menzel 1955, Menzel and Hopkins 1955a, Menzel and Nichy 1958, Menzel et al. 1957). Even a small 5 cm stone crab can crush the shells of large, marketable oysters. Menzel et al. (1957) considered *M. mercenaria*, along with the southern drill, *T. haemastoma*, to be the principal causes of depletion of an oyster bar in Apalachicola Bay, Florida. However, *M. mercenaria* may be limited to areas with salinities higher than 1215 ppt (Menzel et al. 1966).

Crab predation on spat may be controlled by covering young oysters with wire mesh (Walne and Davies 1977). Hatchery-reared *C. gigas* spat were placed in trays elevated five cm off the sea bed and covered by 36 mm or 12.5 mm galvanized mesh. Walne and Davies (1977) reported that growth increased and mortality decreased in mesh-covered spat compared with the uncovered controls. They attributed this result to reduced predation by the crab *Carcinus maenas*. These protective measures are expensive, however.

Crab predation may also be controlled by chemical means. MacKenzie (1961b) found complete mortality of mud crabs after immersion in a saturated salt solution followed by an exposure of 1.5 hours in air. Obviously, this works only if oysters are being cultured in trays. Chemically-treated baits can be used to poison undesirable species (Loosanoff 1961). Crabs are highly sensitive to the pesticide Sevin, while oysters appear to be unaffected by quite high dosages (Andrews et al. 1969). However, such insecticides would have limited use in



Urosalpinx cinerea

Eupleura caudata

areas such as Chesapeake Bay where crab production is also a highly valued industry.

Gastropods. Dominant drill species vary regionally, with *Urosalpinx cinerea* and *Eupleura caudata* common along the northeast and middle Atlantic coastline (MacKenzie 1961a, Wood 1968), *Thais haemastoma* found along the southern and Gulf coastlines (Chapman 1956, Cooley 1962), and *Thais lamellosa* and *Tritonalia (Ocenebra) japonica* distributed along the West coast (Galtsoff 1964).

The oyster predators *U. cinerea* and *E. caudata* cannot tolerate salinities below 19 ppt and 20 ppt, respectively (Lippson 1973). Exposure to low salinities of 10 ppt in fluctuating salinity experiments caused a decrease in predation rates by *Thais haemastoma* (Garton & Stickle 1980) and a high mortality rate in *U. cinerea* even though these low salinity levels were interspersed with higher, more tolerable salinity levels (Zachary and Haven 1973). In waters of higher salinities, such as lower Chesapeake Bay and along the Atlantic and Gulf coasts, oyster drills are a major oyster predator (Gunter 1955, Menzel 1955, Andrews 1956, Menzel et al. 1957).

Urosalpinx cinerea is chemically attracted to its prey (Carriker 1957, Pratt 1978), preferring young and rapidly growing oysters (Haskin 1950, Huguenin 1977). Fast growing, thin-shelled oysters of marketable size are lost to drill predation on Virginia's Eastern Shore (Andrews 1956). *Urosalpinx cinerea* attaches itself to an oyster's shell and begins to secrete a chemical substance from its accessory boring organ. By alternating short periods of rasping with long periods of chemical activity, the oyster drill excavates a hole through which it inserts its proboscis to feed upon the oyster (Carriker and Van Zandt 1972, Carriker and Chauncey 1973). This drill is a relatively short-lived species, most populations in Delaware Bay not living more than one to two years (Haskin 1969). However, young, newly hatched drills may cause extensive damage to oyster spat (Korringa 1952, Andrews 1956).

In addition to shell boring capabilities, *Thais haemastoma* may secrete a ciliary-inhibiting substance which paralyzes the oyster, causing the bivalve to gape open while the snail continues to feed (McGraw and Gunter 1972). However, two earlier accounts, one by Burkenroad (1931a) and the other by Chapman (1956), observed that the valve of the oyster remained closed until approximately 3/4 of the oyster had been devoured, the adductor muscle being one of the last tissues to be eaten.

In some studies, oyster drills have shown a preference for mussels (Burkenroad, *T. haemastoma*, 1931a) or for mussels and clams (Chew and Eisler, Ocenebra japonica, 1958) in place of oysters. However, Haskin (1950) found *U. cinerea*, when given a choice, consumed three times as many oysters as mussels. A possible explanation for this discrepancy involves the concept of ingestive conditioning. Wood (1968), while working with *U. cinerea*, found that the drill tended to prefer food organisms upon which it had previously fed. The relative abundance of a given prey species can therefore affect prey selection.

Other gastropod enemies of adult C. virginica, perhaps present only in lower Chesapeake Bay, are *Odostomia* sp. and *Busycon contrarium*. The snail *Odostomia impressa* ranges along the Atlantic coast from Massachusetts Bay to the Gulf of Mexico. Maurer and Watling (1973) occasionally found *O. impressa* in tributaries of Delaware Bay, although most snails were found on Delaware Bay oyster beds. Wells (1961) reported a low salinity tolerance threshold level of 11 ppt for *O. impressa* from North Carolina waters. *Odostomia impressa* prefers older, larger oysters as prey rather than spat or small oysters (Hopkins 1956, Loosanoff 1956). It begins to feed by attaching itself along the outside margin of an oyster shell. Whenever the oyster opens its valves to feed, the snail inserts its proboscis between the valves and pierces the oyster's mantle with its buccal styles to suck the oyster's blood. Oysters smaller than 0.4 in (1.0 cm) may eventually die and the snail leaves to find another victim. Larger oysters exhibit deformed shell shapes and abnormal growth after such attacks (Loosanoff 1956).

The whelk, *Busycon contrarium*, is another destructive predator of oysters (Carriker 1951b, Korringa 1952, Menzel and Nichy 1958, Nichy and Menzel 1960). A related species, *B. carica*, from North Carolina was found to tolerate salinities down to 11 ppt (Wells 1961). Attracted by prey effluent, *B. contrarium* chips away at the edges of the oyster shell until it is able to force the valves apart to feed on the meat.

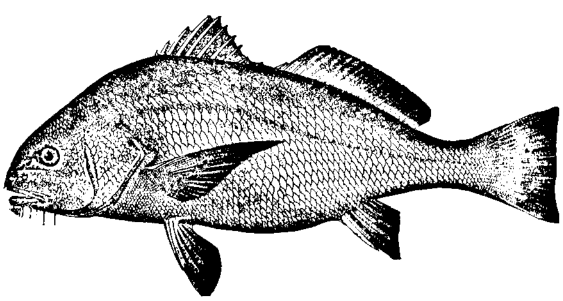
Several methods have been tested to control drill predation on oyster beds. Handpicking with bounties paid per gallon of drills may be an efficient method on intertidal beds (Andrews 1956), but other methods more feasible for subtidal, deep-water oyster beds are being developed. Modified plows or dredges can be used to turn over layers of bottom sediments, burying drills under a fatal depth of six cm of material (Loosanoff and Nomejko 1958). While 92% of drills can be killed with this method, oysters themselves have only limited abilities to clear moderate amounts of sediments from the shell margin (Dunnington et al. 1970). Furthermore, drills are small, 1.5 to 2.5 cm in diameter, and can escape from conventional dredges (Korringa 1952).

Trapping drills on oyster beds is a method of control studied in Virginia (Andrews 1956, McHugh 1956, 1957). Traps are placed over an oyster reef and stocked with fresh bait. Traps fished and rebaited weekly were found to be the most biologically and economically feasible (McHugh 1956) because a decline in the rate of catching became significant after the first week. Traps can be expected to produce a minimum level of drill abundance of approximately 0.11 drills yard^{-1} (0.12 drills m^{-1}) (Stauber 1943).

Various types of barriers around cleaned oyster beds can be used to control drills and other gastropods to a certain extent but such barriers are expensive. Marshall (1954) found lower mortalities in oysters protected by cages in Alligator Harbor, Florida. Cole (1951) suggested a barrier of clean mud around oyster beds, but *U. cinerea* has been found to travel at least 10 m in response to current direction and prey effluent to reach its prey (Pratt 1978). Barriers of chemically impregnated grease (Chambers, *Ocenebra japonica*, 1970) or heavy oils of ortho-, pare-, and tetra-chloro-benzene (Loosanoff et al. 1960) can block the passage of drills. Physical contact with pesticides such as Polystream (a mixture of chlorinated benzenes) and Sevin (methyl carbamate) can incapacitate drills, resulting in their death either directly or indirectly by increasing their vulnerability to predation (Davis et al. 1961). MacKenzie (1971) reported a mortality rate of 85% for *E. caudata* and 66% for *U. cinerea* after Polystream was applied to oyster beds at a rate of 9.5 kl treated sand ha^{-1}. Drill mortality was higher when treatments were applied in spring. At that time, immediately after hibernation, drills may be weakened and more susceptible to the insecticide (Wood and Roberts 1963). Because Sevin is also extremely toxic to crabs (Wood and Roberts 1963), its use in or near Chesapeake waters with valuable populations of blue crabs should be limited or avoided. Drills are highly sensitive to contact with copper ions and avoid crossing metallic copper (Glude 1957, Huguenin 1977). Strips of copper incorporated into bottom mounted fences surrounding oyster beds or around vertical supports of frames used in string or tray cultures may effectively bar the passage of adult drills.

Barriers have only a limited effectiveness because some drills such as *T. haemastoma* have a freeswimming larval stage during which they are able to bypass barriers (Burkenroad 1931a, Pollard 1973). Other drills (e.g., *U. cinerea* and *E. caudata*) may not have a pelagic stage yet they are still capable of migrating over great distances and possibly over barriers by either attaching themselves to bits of floating debris (Carriker 1957, Huguenin 1977) or to other animals such as the horseshoe crab *Limulus polyphemus* (MacKenzie 19 62).

Fish. Some fish are also capable of feeding on adult oysters. *Gobiosoma bosci* follows a volatile compound to oysters and is induced to feed by the presence of another unknown substance (Hoese and Hoese 1967). Nelson (1928b) reported that a single *G. bosci* had taken up residence in the promyal chamber of a C. virginica, with a subsequent enlargement of that organ. It was not apparent whether the enlargement was due to feeding or movement by the fish. *G. bosci* feeds mainly on small crustaceans (copepods and amphipods) and small polychaete worms (Nelson 1928b, Cory 1967) and may only be a scavenger of dead or diseased oysters (Hoese 1964).



Pogonias cromis

Fish in Chesapeake Bay which are probable predators on oyster spat are oyster toadfish, *Opsanus tau*; croaker, *Micropogon undulatus*; spot, *Leiostomus xanthurus*; and cow-nosed ray, *Rhinoptera bonasus* (Krantz and Chamberlin 1978). *Opsanus tau* also preys to a great extent upon mud crabs in New Jersey waters (McDermott 1964); thus, it may be more of an oyster benefactor than an oyster predator. While oysters may grow to a size at which most potential predators are unable to attack them, cow-nosed rays may be able to consume even adult, market-sized oysters (Smith and Merriner 1978). Barriers around oysters may provide only limited success in controlling cow-nosed ray predation, the rays at times being able to swim over these fences (Villadolid and Villaluz 1938). Mesh covers may be more successful, but it has as yet not been proven that they are practical, especially in an open public fishery. Drumfish (*Pogonias* sp.) may be a predator in the more saline portions of Chesapeake Bay. Ranging from New Jersey to the Gulf, drumfish are known to be very destructive to young oysters (Churchill 1920). In Alabama, drumfish are reported to be capable of destroying single planted oysters, but not clustered oysters of the natural reefs (Engle 1945a).

Echinoderms. Starfish (*Asterias* sp.) are intolerant of salinities below 15 ppt and are therefore not usually found in the upper or central areas of Chesapeake Bay.

Appropriate Control Strategies

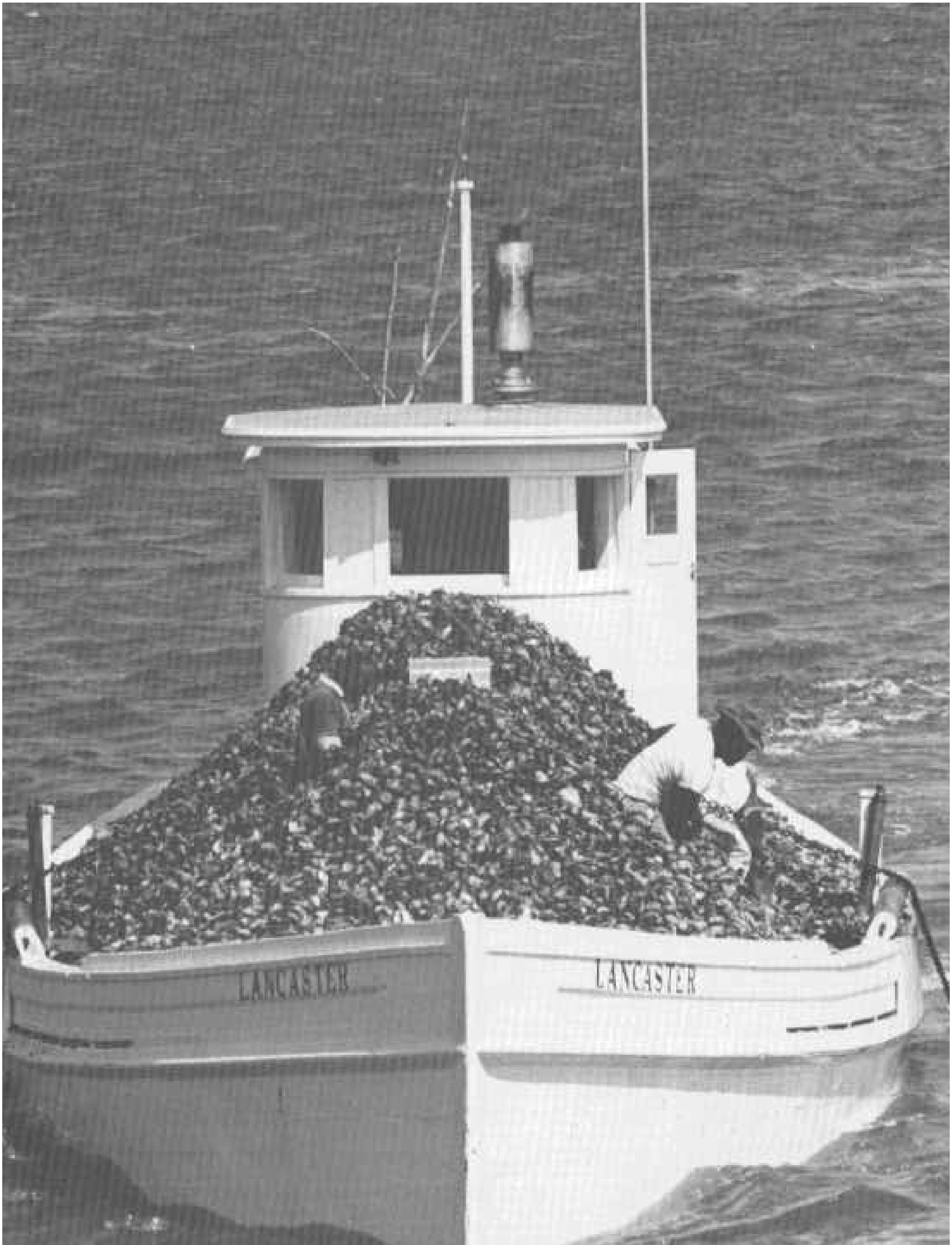
Not all of the control methods for oyster competitors and predators described above are appropriate for a predominantly public oyster fishery such as that existing in northern Chesapeake Bay. Many control strategies would appear to be more suitable for cooperative efforts on private rather than public oyster beds. Fences and chemical barriers are obviously more suitable for small, defined and closely-monitored private oyster grounds than for large, amorphous public areas. Mechanical methods such as starfish mopping and drill dredging and plowing as well as some chemical controls, i.e., immersion of dredged oysters and shell in chemical solutions, are labor-intensive activities (Loosanoff 1961). MacKenzie (1961b) reported that it took two deckhands three hours to dip 150 bushels of bottom material into a chemical bath. While this effort may be worthwhile on a privately-controlled oyster bed, how many fishermen will exert this amount of labor only to have the treated oysters harvested from a public bed by someone else? Some cooperation is necessary even among individual aquaculturists on their leased or private oyster beds. As Churchill (1920) said of starfish mopping, “It is little avail for a planter to attempt to keep his beds free from starfish, unless his neighbor does likewise.”

Possible control strategies for public oyster grounds might include those that require limited labor and intermittent or infrequent applications to large areas. These methods may include predator traps, biological controls, and perhaps bottom treatments to prevent predator invasion. Traps, such as drill traps, once installed need only to be fished and rebaited periodically to be biologically feasible (McHugh 1956). Biological controls could be supported by encouraging the recruitment of natural predators and parasites of oyster enemies. Chemical treatment of public oyster beds, if applied infrequently, may perhaps be economically sponsored by public resource management agencies. Cost-benefit analyses would have to be conducted to confirm this.

Summary

For the most part, the literature which exists on oyster competitors, pests, and predators deals primarily with those affecting juvenile and adult oysters. Knowledge of the competitors of larval oysters is restricted to those organisms which compete for settlement space since little is known of larval nutritional requirements in their natural environment. Methods of controlling the fouling of spat collectors or cultch in Chesapeake Bay need improvement. Strategies for the control of many competitors, pests, and predators of oysters depend upon (1) mechanical methods (e.g., mops, dredges, plows, traps, fences); (2) chemical methods (i.e., chemical baths, bottom treatments with chemicals, chemically impregnated barriers, spatcollector treatments); and (3) biological methods (i.e., the parasites and predators of oyster enemies and pests). Some of these methods are more appropriate for private or leased oyster beds than for public beds.

Management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Managing Maryland's Oyster Industry

For more than 150 years, management of Maryland's oyster resource has been the subject of varying degrees of controversy. Different commissions and boards and departments have been established to oversee the general management of the resource and its harvesters. But the Maryland General Assembly has had the major influence on its use, through the various laws it has promulgated. Because legislators are sensitive to the concerns of watermen and processors, many laws have been passed which have affected management of the oyster resource but which have had no sound basis in biological or economic reality.

In this section, we trace first a general history of the fishery, in the belief that "Those who cannot remember the past are condemned to repeat it." It is instructive to note that 1981 is the centenary of an insightful report by Lieutenant Francis Winslow who carefully surveyed the oyster grounds of Pocomoke and Tangier Sounds. Winslow recommended the appointment of an investigative and regulatory commission for oversight and management of the then declining resource. Thus, the Oyster Commission was formed in 1882. It produced the first of at least six major reports (the rest from five other commissions or committees of one kind or another) that were written during the next century detailing the decline of the Maryland oyster and the actions that might halt and reverse that decline.

Our historical survey is followed by a physical description of the Bay's oyster grounds in Maryland, as they were and are. Then we survey the rehabilitation measures that have been proposed in the past by many investigators. There is a certain similarity to the reports which we will focus on to demonstrate that there has been long and general agreement over the past 100 years as to what the rehabilitative measures should be. For that reason also, we do not really make any recommendations of our own. We let the weight of past statements speak for themselves. Finally, we conclude with considerations of aspects of oyster farming or cultivation.

Throughout this section, we rarely refer to the situation concerning the Potomac River oyster resource. Because this river is totally in Maryland, yet with its southerly bank being Virginia territory, the management of the oyster resource

An oyster buyboat dredges up spat-holding shell from the state's oyster seed grounds for replanting on the public fishing grounds, an important part of the annual oyster repletion program managed by the Maryland Department of Natural Resources.

and its partitioning among watermen of the two states has been, until recently, a matter of long-standing controversy (Ingersoll 1881, Stevenson 1894, Power 1970). The mainstem of the river is administered by the Potomac River Fisheries Commission, a bi-state organization, whereas the tributary creeks come under the administration of the respective state resource agencies. A description of the oyster grounds and the fishery, along with management recommendations, is included in Davis et al. (1976).

HISTORICAL BACKGROUND

When the first European settlers arrived in the Chesapeake Bay region, they encountered a cornucopia of biological resources, not the least of which was the oyster. Reports of this bounty are described by Wharton (1957) in his historical treatment of colonial Virginia's fishing activities. Two examples are impressive: He quotes William Strachey who wrote in 1612,

> "Oysters there be in whole banks and beds and those of the best. I have seen some thirteen inches long. [The Indians]...hang the oysters upon strings...and [dry them] in the smoke, thereby to preserve them all the year."

He also quotes a Swiss visitor, Francis Louis Michel, who wrote in 1701,

> "The abundance of oysters is incredible. There are whole banks of them so that the ships must avoid them. A sloop, which was to land us at Kingscreek, struck an oyster bed, where we had to wait about two hours for the tide. They surpass those in England by far in size, indeed they are four times as large. I often cut them in two, before I could put them into my mouth."

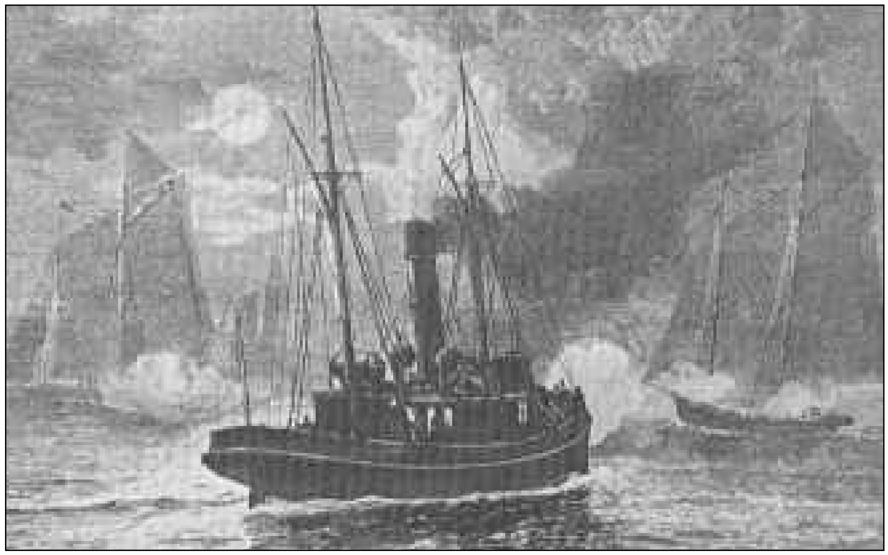
The presence of such bounty presumably was welcome to those dependent on a subsistence existence in the early days of the colonial period, although some "Kent Islanders," in the Clairborne suit of 1680 related hardships so severe that: "...their supply of provisions becoming exhausted, it was necessary for them, in order to keep from starvation, to eat the oysters taken from along the shores" (Stevenson 1894). However, as immigrant populations increased and tongs and then dredges appeared, inroads into the oyster population began. Quantitative production data were apparently not collected until about 1839, when the yield in Maryland was 710,000 bushels. Soon, many of the large reefs in Tangier Sound were discovered and the fishery expanded greatly (Stevenson 1894).

Meanwhile, the oyster beds of New England had become badly depleted throughout the 18th Century by overfishing (Ingersoll 1881, Sweet 1941). The center of the U.S. oyster industry had been in Connecticut; from there, apparently beginning about 1808 (Stevenson 1894), dredge schooners traveled to New Jersey and Virginia. In 1811, Virginia passed legislation prohibiting dredging in its waters, forcing the fleet north up the Bay to Maryland. Concern about such fishing led the Maryland legislature in 1820 to enact its earliest oyster-related law, prohibiting both oyster dredging in the state and the transport of oysters from the state in ships not wholly owned for the preceding year by Maryland residents (Stevenson 1894, Grave 1912, Nichol 1937). This fact (Grave 1912), coupled with the building and improvement of transportation systems such as the Baltimore and Ohio railway and national turnpikes (Nichol 1937) and the desire to be closer to the principal source of supply (Sweet 1941), led established Northern oyster packers to open branch plants in Baltimore in the mid-1830's. These plants exported increasing quantities of oysters to western communities. The demand on Maryland oyster resources thus rose, with the number of processing establishments (including raw packers and steam packers or canners) in Baltimore increasing from one in 1836 to 80 in 1868 (Nichol 1937). By 1869-1870 the oyster harvest amounted to about nine million bushels.

Associated with this great increase in harvest were changes in legislation concerning harvesting techniques and fishing regulations (Stevenson 1894, Grave 1912). In 1836 (Dorchester and St. Mary Counties) and 1840 (Somerset County), burning oysters for agricultural fertilizer (lime) was prohibited. In 1846, Worcester County established a closed season (April 13 to September 1), the first in Maryland and one of the earliest in America. In 1852, Worcester County banned the removal of any shell from its reefs. In 1854, the use of small dredges (scrapes) was allowed in certain waters of Somerset County with a license that cost $15; it was the first oyster license law in Maryland and one of the first in the nation. Similar laws were enacted in 1870 and 1874 with regard to certain waters in Dorchester and Talbot Counties, respectively. In 1865, the old general oystering laws were abolished and a new set enacted, including adoption of a state-wide license system governing tongers, scrapers, and dredgers. However, the revenue anticipated as a result of this General License Law was not forthcoming because of its unpopularity with watermen, so, in 1868, a State Fishery Force ("Oyster Police") was established. For the first decade or so, the "Oyster Navy" was maintained by the licensing revenue, but thereafter the fees were insufficient to underwrite all costs (Grave 1912).

In terms of oyster culture, in 1865 and 1867, legislation was enacted to allow individuals to plant oysters on five-acre plots of barren bottom. This was an increase from the one-acre provision of a similar law passed in 1830 (Stevenson 1894, Power 1970). Grave (1912) noted, however, that the 11,000 or more acres of bottom that were preempted in this way were used mainly to hold oysters ("bedding") rather than for the growing or culturing of young oysters.

A major problem facing those who wished to manage the oyster resource scientifically a century ago was the recalcitrance and suspicion of watermen and their local elected representatives towards such management attempts. This, indeed, remains a problem even today, when the resource has declined to a fraction of its potential. In 1905, Brooks noted that no one would risk oyster farming on leased bottom because dredgers and tongers did not recognize private property rights on oyster grounds. Numerous incidents involving theft of oysters from leases occurred in early years (Brooks 1905, Green 1916) although this problem declined in severity with the strengthening of the oyster police force.



Maryland State Fisheries' patrol boat in an engagement with oyster pirates in 1886

However, a prevailing attitude in tidewater communities has been that oysters were, and are, a common property resource and that no one, especially non-Marylanders, should be allowed private control over good oyster grounds. Coupled with this has been a concern that private corporations might take advantage of leasing laws and occupy large tracts of oyster grounds, denying access to independent watermen. Further, packing houses might stock oysters on leased ground to ensure a constant, reliable supply, using its own employees to harvest this stock as needed and bypassing the oystermen. Watermen have always feared that they would eventually lose out in any competition with big business for oyster grounds.

Finally, there remains a concern that oyster farming activities would lead to such an increase in oyster production that supply would far exceed demand. Watermen have feared the depressed prices that might result from glutted markets; thus, they have consistently pressured their representatives to protect their perceived interests. As a result (as will be shown below), sound management practices have been delayed or hindered by Tidewater legislators who have held great power in the legislative bodies which enact regulations governing the oyster fishery.

Intensive Biological Studies

Oyster harvests continued to increase to a peak of 14 million bushels in 1874. A five-year decline followed, the harvest reaching 10 1/2 million bushels in 1879. This decline resulted in the commissioning of a survey of oyster grounds in Pocomoke and Tangier Sounds, Maryland, in 1877-79 under the direction of Lieutenant Francis Winslow of the U.S. Coast and Geodetic Survey (Winslow 1882). These two sounds had very extensive oyster beds then subject to intensive fishing pressure. This thorough survey, using a coast-survey schooner, delineated a large area of the beds and estimated the number of oysters they held. The character of the bottom beneath the beds and the condition of sedimentation were determined, temperatures and specific gravities of surface and bottom waters were measured, and spat collectors (tiles) were deployed to study settlement of oysters and their growth rates. (All but one of 24 bundles of these tiles were destroyed by vandals, demonstrating the early resistance of oystermen to any attempts to study the resource scientifically). The information collected in this survey provides insight into conditions prevailing on oyster grounds a century ago when only a few major areas had been fished intensively. Winslow (1881) summarized his findings:

1. The once-compact beds had been enlarged by dredging, which dragged oysters off the rocks and on to the surrounding soft bottom, and by culling, which dropped shell and undersized oysters overboard onto new ground.

2. In spite of such a real enlargement, the number of oysters had declined since the fishery began, as documented from 1878 to 1879 on certain beds in both Sounds.

3. Unfished oyster beds were found in Chesapeake Bay waters adjoining the sounds. They had distinct and contrasting characteristics when compared with deteriorating oyster beds in the sounds. Overworked beds generally had much mud or sand among the shells which in turn were infested with worms and were broken and bored in many places; oysters were found singly or in clumps of two or three and were large and broad, not long and thin; the meat was plump. Unfished beds contained oysters in clusters of three to fifteen, with clean shells free from worms and often with large red sponges attached. The mature oysters were long and narrow with thin sharp bills and long, thin bodies.

4. Unfished beds were hard, requiring greater force to dredge the oysters from the main body of the bed than was required on previously worked oyster beds. Broken shell and debris made up about 30% of the material dredged up from unfished grounds. On worked beds, this percentage was higher, reaching 97% on some beds in Pocomoke Sound.

5. In 1879, all oysters examined were classified into two mature classes and two young classes. Over 20,000 oysters were measured and classi-

fied from unfished beds. The ratio of young to mature oysters was 3:2. Over 100,000 oysters were collected from fished beds in the sounds and a ratio of 3:6 was noted. Thus, on unfished beds the young outnumbered the mature oysters, whereas on fished beds the reverse was true.

6. In Pocomoke Sound in 1879, the number of oysters per square yard on every bed was considerably less than in 1878 and was also much lower than the number per square yard in the unfished beds of the Bay.

Winslow (1881) recommended two actions. The first involved placing materials such as ballast, water pipes, and shells on appropriate bottom in the direction of tidal currents to serve as spat settlement areas which could extend the beds. This cultch would be exposed late in spring to ensure its cleanliness. Mature oysters would be added with this material to aid in providing for and attracting spat. The second recommendation involved appointment of a commission of "intelligent individuals" having specialized knowledge of the oyster and its industry which was to be allowed considerable power (free of political interference) to regulate dredging, protect spat and young oysters, close beds when necessary, destroy predators, and expose cultch in order to rehabilitate oyster grounds.

In 1882, an Oyster Commission comprising three men, including Dr. W. K. Brooks of Johns Hopkins University, was appointed "to examine the oyster beds and to advise as to their protection and improvement" (Brooks 1905). Brooks had earlier discovered that Crassostrea *virginica*, unlike the European *Ostrea edulis*, expelled its gametes into the water where external fertilization and development occurred (Brooks 1880) and he was very familiar with the eastern oyster and its fishery. However, not everyone considered Brooks to be knowledgeable. He noted (1905):

> "I speak on this subject with the diffidence of one who has been frequently snubbed and repressed; for while I am myself sure of the errors of the man who tonged oysters long before I was born, and who loudly asserts his rights to know all about it, it is easier to acquiesce than to struggle against such overwhelming ignorance, so I have learned to be submissive in the presence of the elderly gentleman who studied the embryology of the oyster when years ago as a boy he visited his grandfather on the Eastern Shore, and to listen with deference to the shucker as he demonstrates to me at his raw-box, by the aid of his hammer and shucking-knife, the fallacy of my notions of the structure of the animal."

The Oyster Commission made a survey of oyster beds throughout Maryland's portion of the Bay and noted a rapid deterioration. In 1882, they found an average ratio of 1.3 bushels of oysters to each bushel of shell. This was a decrease from Winslow's ratio of 1.9 bushels in 1879 and from Lugger's ratio of 3.7 bushels in 1876 (Winslow 1884). Similarly, Winslow's survey of Tangier Sound in 1878-79 recorded about one oyster in every 2.3 yd^2. In 1883, Brooks found only one oyster per 4.2 yd^2 in the same sound (Winslow 1884). Thus the decline in oyster landings was found to parallel the decline in and deterioration of the oyster grounds in the Bay.

Oyster Culture Recommended

The Oyster Commission recommended conservation measures, the establishment of a system of oyster farming, and also a system of private oyster culture beyond that envisaged in the Five Acre Planting Law (Brooks 1905, Grave 1912). But in 1884-85, about 15 million oysters were harvested, apparently due to an excellent set of oysters in 1883 (Stevenson 1894). It was the peak harvest ever for the Bay and it served to encourage state legislators to ignore the Commission's recommendations (Grave 1912). The catch thereafter declined to its present low level, with only a few periods of slight increase.

The legislature did pass the Cull Law of 1890, which Grave (1912) considered to be the most efficient method ever devised for the protection of natural oyster beds. Among other things, the law required that shells with spat and young oysters be thrown back ("culled") on the beds from which they were dredged. It also set a minimum legal size of 2 1/2 inches for market oysters. Maryland was one of the first states to attempt the enforcement of such a law (Stevenson 1894).

As catches continued to decline at the turn of the century, a Baltimore attorney, B. H. Haman, defended the concept of oyster culture and submitted bills on this matter to the legislature. He was backed by farmer's clubs and organizations which favored the Oyster Commission's recommendations. However, delegates from the tidewater counties derided these bills, expecting the fishery to repeat its 1885 rebound (Grave 1912). But the decline had set in, resulting in the closing of a number of packing houses in Baltimore as the export source steadily withered away (Nichol 1937). As Commissioner Brooks (a strong supporter of private culture) noted in the preface of the second edition (1905) of his important report on the results of the Oyster Commission:

> "...the oyster grounds of Virginia and North Carolina, and those of Georgia and Louisiana, are increasing in value, and many of our packing houses are being moved to the south, but there is no oyster farming in Maryland, and our oyster beds are still in a state of nature, affording a scanty and precarious livelihood to those who depend upon them."

These comments came fifteen years after the first edition appeared with its extensive recommendations.

Thus, by 1906, the time was ripe for passage of the Haman Oyster Bill. The law, as amended in 1912, allowed individual leases up to 30 acres in county waters (except Tangier Sound where 100 acres was the limit) and up to 500 acres in the Bay beyond county boundary limits. Though it was made largely ineffectual by amendments by its opponents (Grave 1912), the Haman Law did provide for a Shell Fish Commission in 1906 (one of its members was C. Grave, a student of W. K. Brooks). As the oyster catch continued to decrease, the Shell Fish Commission in 1908 and then in 1910 attempted to persuade the legislature to amend the Haman Law to allow for successful oyster farming. Instead, the Commission's recommendations were ignored, and the 1910 Reshelling Act was passed. It provided for a one cent per bushel tax to provide a fund for the reshelling of certain depleted bars. The courts declared it unconstitutional (Grave 1912). In 1914, the Maryland General Assembly passed the Shepherd Act to allow for resurveying of disputed bottom and to distinguish between "natural" and "barren" grounds, with the result that additional acreage was reclassified to "natural" oyster bar and not available for leased ground. These procedures have greatly hindered granting of oyster leases (Power 1970).

Continued Decline

In 1906, the Shell Fish Commission embarked on an ambitious six-year survey of the natural oyster bars of the state in cooperation with the U.S. Coast and Geodetic Survey. It was called the Maryland Oyster Survey, and was under the control of C. C. Yates, who published a series of very important reports dealing with distribution of oyster beds in different regions of the Bay.

The Maryland Oyster Survey was the last extensive biological and environmental survey of Maryland's oyster bars until the last decade or two. After six years' work, it resulted in publication of 17 official documents and 43 large-scale charts, for a total of 2400 printed pages and 400 square feet of charts (Yates 1913). This was coupled with a comprehensive technical report by the Board of Shell Fish Commissioners (Grave 1912).

All of this material supplemented the earlier work of the 1882-1884 Oyster Commission (Brooks 1905) and the Winslow survey of 1878-79. In addition, the economic, historical, and social aspects of the fishery had been treated by Ingersoll (1881) and Stevenson (1894).

This tremendous accumulation of information, although incomplete in some details of the life history of oysters (for example, the behavior of oyster larvae and the factors affecting spat settlement were unknown), was undoubtedly sufficient for arresting the decline in production and for restoring the former economic strength of the industry, including the oyster packing industry. However, the efforts at rehabilitation were of minimal value because the socio-political roots of the problem were ignored or only partially considered.

In 1916, the Maryland Conservation Commission was created, consolidating the Shell Fish Commission, Fish Commissioners, the State Game Warden, and the State Fishery Force (Oyster Police) under one administration (Earle 1932). The sailing vessels of the State Fishery Force were replaced by a steamer and power boats.

In 1922, legislation allowed for annual, extensive placement of shell as cultch on depleted oyster bars, but funds were limited. Funds were supplemented in 1927 by an act requiring oyster packers to make 10% of their shucked shells available for state use. Work boat gasoline taxes and a small appropriation allowed for the establishment of an annual rehabilitation fund. By 1932, the State was planting about one million bushels of oyster shell on natural bars as cultch (Earle 1932). However, due to the nature of local politics, in which watermen were consulted on the placement of shell, the initial planting activities were generally failures, with but few exceptions (Truitt and Mook 1925, Beaven 1945).

In 1931, construction of the Chesapeake Biological Laboratory was begun, providing a base for the work on oysters of R. V. Truitt and later of G. F. Beaven and other associates. In conjunction with the laboratory, an experimental "oyster farm" was established in the Honga River (State Planning Commission 1935). This was a 1000-acre area of bottom which was established as a reserve for experimental use by the laboratory. It was in a region which had proven to have numerous oyster larvae in the water, although the oyster grounds had been badly overfished. Over a three-year period, 42,000 bushels of shell were planted on one 50-acre section. About 4,000 bushels of seed were harvested in fall 1934 from a four-acre patch within the planted section. It was estimated that 50,000 bushels of seed had set where oysters had not been produced for years (State Planning Commission 1935). Dr. Truitt continued research in this area for a few more years but then the experimental region was turned over to public use as a tonging bar, apparently against Dr. Truitt's advice and to the ultimate detriment of the area and the seed program (Wharton 1959).

In their report of 1935, the State Planning Commission noted that the 51% decline in oyster yield in Maryland from 1910 to 1932 resulted from "...a continuation of the unsound conditions and short-sighted policies that have characterized and controlled the industry's operations over a long series of years." They noted that the decline could be traced to overfishing, the wholesale export of seed oysters out of state (for example, in 1879 over two million bushels of seed oysters were shipped north from Maryland), and the failure to return adequate supplies of cultch to the Bay. This had resulted in the destruction of the canning industry with a loss of $750,000, a loss of employment for watermen and canning industry workers, and a dependence on other states for large, high-quality oysters. Their recommendations included:

1. Resurveying of oyster bars for effective policing, determination of developmental areas, and guidance in formulation of conservation policies. They estimated such a survey to require one year.

2. Developing seed areas such as Eastern Bay, upper Honga River, and the Head of the Bay (the latter area now no longer suitable due to the depletion of oyster grounds and the danger of high mortalities from fresh-water runoff from the Susquehanna River).

3. Planting of two-thirds of the seed developed on seed areas in public bars of proven ability with the remainder being made available for private use.

4. Planting of shells as cultch on suitable grounds having sufficient brood stock.

5. Amending leasing laws to allow a lease to include 250 acres of ground, and removal of limitations on who holds a lease (note that Powers (1970) declared that such discrimination is unconstitutional).

6. Increasing potential lease areas.

Finally, the State Planning Commission's report (1935) described some successes and failures in the state's shell planting activities. On Harris Rock, where 60,000 bushels had been planted, little or no set resulted over a five-year period. On Carrol's Bank, a good oyster ground in the Patuxent River, shells were planted on top of oysters, smothering them and injuring the bar. On the other hand, 9,000 bushels planted on Middleground Bar in the Patuxent yielded one bushel of oysters for each bushel of shell planted, a ratio also attained on the experimental area in the Honga River. The report urged that shell plantings be made with an understanding of conditions in the area being restored. Further, the greatest benefit from shell planting came in areas which produced Maryland's least desirable oysters (presumably stunted, although this was not stated) due to an abundance of brood oysters and, therefore, of spat. In ravaged Tangier Sound, shell plantings were generally a failure at the time because of limited numbers of brood oysters. The State Planning Commission (1935) recommended that every shell taken from Maryland waters be returned in order to meet the great need for restoration of the oyster grounds.

In 1942, the Tidewater Fisheries Commission undertook a large seedgrowing and transplanting operation (Maryland Commission 1948). This was to be made self-supporting by collection of ten to twenty cents per bushel of oysters taken from planted bars. From 1940 to 1946, 211,000 bushels of oysters were harvested. The planted seed had cost the State $96,000. Taxes recovered were $42,000 (Maryland Commission 1948).

In 1947, the shell tax on shucking houses was increased to 20% of the shell produced during shucking of the catch (Maryland Board of Natural Resources 1951). Apparently the idea was that shells of oysters are containers which belong to the state and which must be returned to the water (Maryland Board of Natural Resources 1951). In 1951, new legislation required that the state receive 20% of all shells shucked by commercial establishments, plus the option to purchase an additional 30% (Maryland Board of Natural Resources 1952). Only Baltimore City shucking houses were exempt, because of the ban on storing shells within city limits. In 1953, the state was empowered to collect 50% of all shells produced by packers, etc. (Maryland Board of Natural Resources 1955). However, even this amount was not enough to provide for the appropriate level of shelling activity, and efforts were made to find quantities of dredged shell to supplement the fresh shell (Maryland Board of Natural Resources 1960).

In the early 1960's, state resource managers again recognized that overfishing was rapidly depleting the resource. They reported that many small oysters were being sold and that much shell was being lost. Scarcity was causing high prices, and undersized oysters were sold readily (Maryland Board of Natural Resources 1962). In 1961, the state implemented an oyster repletion program with oyster shells from non-producing areas of the Bay being dredged and distributed over public oyster beds. By 1963, the amount of fresh shell planted by the state was the smallest for many years, due in part to the sale of oysters to out-of-state buyers (Maryland Board of Natural Resources 1963).

In spite of the well-demonstrated need to retain shell as cultch, in 1965 Maryland passed a law that reduced the percentage of fresh shell that packers were required to make available to the state from 50 percent to 25 percent (Maryland Board of Natural Resources 1965). What is more, the packers had the option of keeping the shell and paying the state cash for it instead. In the early 1960's, large deposits of old "fossil" shell had been found and were being dredged at the state's behest to supplement the planting program that had previously depended exclusively on fresh shell. Presumably, with the supply of old shell then available, packers were free to find other markets for their fresh shell. In a recent study, Cabraal and Wheaton (1981) determined that fresh shell was a better cultch material than dredged shell. This seems to be the only economic study detailing the benefits that accrue to the state from its purchase and planting of dredged old shell. The concept that the state owns the "container" from which the processor is privileged to extract oyster meat apparently fell out of style in the mid-1960's. Some statistics on shell planting activity are available in Suttor and Corrigan (1968) and Outten (1980).

Current Management

Management of the contemporary oyster fishery is the responsibility of the Tidewater Fisheries Administration of the Maryland Department of Natural Resources. Their shellfish effort includes traditional management practices such as:

1. Establishing fishing seasons, catch limits, and harvesting gear.

2. Granting licenses for harvesting from the public grounds and leasing plots for private planting.

3. Resolving conflicts between oystermen and clammers, between dredgers and tongers, or tongers and divers.

4. Keeping records on annual harvests and on recruitment of new oysters on public fishing grounds, seed areas and private planting plots.

5. Reviewing with the Maryland Department of Health and Mental Hygiene the public health quality of shellfish beds.

6, Transporting oysters from shellfish beds closed because of potential pollution to unpolluted growing and harvesting areas.

7. Organizing an annual oyster seeding and shell planting program to rehabilitate the fishing grounds.

8. Planning and participating in research efforts designed to improve efficiency and harvest productivity.

In addition, the Maryland oyster management program is currently conducting a resurvey of all the state's traditional and potential oyster grounds, the first new survey since the Maryland Oyster Survey of 1906. The resurvey will establish the extent and character of the fishing grounds and may provide a basis for re-instituting the awards of new leases for oyster farming. The General Assembly in 1972 declared a moratorium on the award of new leases, pending completion of the survey (Jensen 1981).

The annual oyster seed and shell planting program is considered one of the most important management practices for maintaining levels of production during periods of poor natural reproduction (Ulanowicz et al. 1980). The major sources of shell for this effort are: (1) fresh shell acquired from local shucking houses under the current shell tax, and (2) dredged shell dug up from beneath the sediment covering "fossil" beds of shell in the northern Bay. During the 1960's and 1970's, the state was normally contracting for the dredging, washing, and replanting of 5 million bushels of dredged shell a year.

Those "fossil" shells provide the vast bulk of the shell planting effort, outranking fresh shells during the late 1970's by more than nine to one (Cabraal 1978). In 1976, for example, dredged shell totaled 90 percent of the new cultch, fresh shell only 9.6 percent. For dredged shell, 4.4 million bushels went to permanent plantings along the public fishing grounds, 560,000 bushels went to seed areas. For fresh shell, 531,000 went to the public grounds, only 1900 to seed areas.

Nearly all the oyster seed for the program comes from 1200 acres of off-limits seed areas that have proven highly productive in the past for spat settlement (Cabraal 1978). Every spring the Tidewater Fisheries Administration organizes a major seed planting program, contracting with watermen who dredge spat-carrying shell off the seed areas and replant them along the open fishing grounds. In a very literal way, this shell and seed planting program lays the foundation for future harvest.

To organize this effort every spring, fishery managers draw up a distribution plan that outlines where in the Bay the seed and shell will go. They review the plan with committees of watermen and consider a variety of factors including economic conditions in each county, the number of watermen living in each county, the number of shell bushels and seed bushels planted in each region in recent years, the biological condition of the waters, and the number of oysters harvested there (Cabraal 1978). Their plan usually combines economic, political, and biological factors.

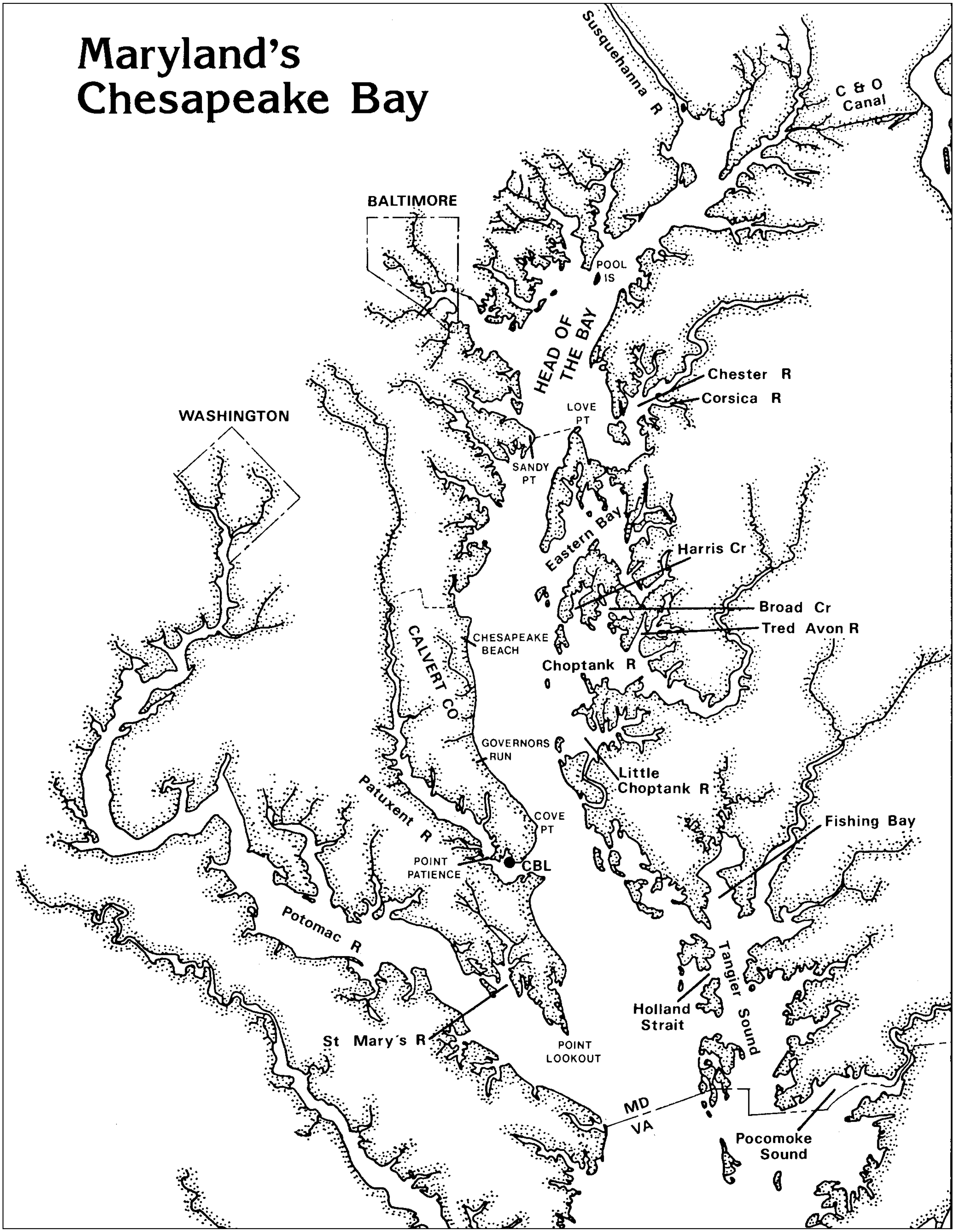
New studies of the seeding and shelling program are analyzing the regional productivity of these plantings and developing models useful in identifying the most biologically productive and cost-effective distribution plans (Cabraal and Wheaton 1981; D. Swartz, Sea Grant Marine Advisory Program, pers. comm., 1981). While some of these studies question the effectiveness of past dredge shell plantings, they all reaffirm the role of seed plantings in sustaining harvests.

The value of seed plantings has stimulated new research work on developing cheaper sources of seed. Cooperative research projects have been investigating new seed hatchery technology, ground-based oyster growout troughs or “raceways,” and new spat-catching devices for seed areas. Cooperating organizations have included the Department of Natural Resources, the University of Maryland Center for Environmental and Estuarine Studies, and the University of Maryland Sea Grant Program. Spurring interest in this work are rising costs and erratic sets of new oysters, factors which led to declines in the numbers of seed oysters planted during the last half of the 1970’s. Annual plantings for these years averaged half the annual averages for the preceding decade (D. Swartz, pers. comm., 1981).

Funds for the seed and shell planting effort come from: (1) license fees charged to watermen and planters; (2) an oyster tax collected from processors on each bushel purchased from harvesters; and, when these sources fail to cover the costs, (3) a commitment of funds from the state treasury. In a fairly typical year, 1976, the costs for the program totaled $1.31 million, not counting overhead costs such as salaries of state employees and their expenses for transportation, equipment replacement and maintenance (Department of Natural Resources, Commercial Fisheries Newsletter, 1976). In the 1970’s, these planting programs required annual subsidies from state funds ranging from $250,000 to $500,000 (J. Bandolin, Maryland Tidewater Administration, pers. comm. to D. Swartz, 1981).

Four Problem Areas

As mentioned, the mass of data collected and analyzed by diligent researchers over a 30-year period from about 1880 to 1910 led to a number of conclusions concerning management of the industry which, if implemented, would probably have kept the oyster fishery as a highly productive enterprise.



Maryland's Chesapeake Bay
Susquehanna R
C & O Canal
BALTIMORE
POOL IS
HEAD OF THE BAY
Chester R
Corsica R
WASHINGTON
LOVE PT
SANDY PT
Eastern Bay
Harris Cr
Broad Cr
Tred Avon R
CHESAPEAKE BEACH
CALVERT CO
Choptank R
GOVERNORS RUN
Little Choptank R
Patuxent R
COVE PT
Fishing Bay
POINT PATIENCE
CBL
Potomac R
Tangier Sound
Holland Strait
St Mary's R
POINT LOOKOUT
MD
VA
Pocomoke Sound

Woven throughout these early reports, and extending into the later literature, are four dominant refrains:

1. The decline of the fishery is predominantly a result of overfishing and ineffectual conservation efforts.

2. It is important to protect spat, to conserve the available shell stock as cultch, and to expand and protect natural seed areas.

3. Oyster culture by means of leasing should have the stimulating effect it has had elsewhere (e.g., Connecticut, Louisiana). It should help revitalize the industry and increase yield, with economic benefit to all involved.

4. Many efforts to improve the industry by preventing overfishing, implementing biologically sound shell planting efforts, enforcing cull laws, and encouraging private oyster culture have been hampered by the determined resistance of watermen and Tidewater politicians.

These points will re-occur in the section dealing with management and rehabilitation. Figure 5 summarizes the reported landings for the past 140 years and indicates the periods of major legislation, biological surveys and studies, and environmental factors affecting the resources. We turn now to a general description of Maryland's oyster grounds, including information on past and present conditions.

DESCRIPTION OF MARYLAND'S OYSTER GROUNDS

Stevenson (1894) noted that oyster reefs in Maryland were found generally along the shores of Chesapeake Bay and its tributaries, extending mainly in the direction of the current. Reefs were most abundant at the mouths of estuaries and in locations with sudden depth changes.

Before oyster harvesting became extensive, Maryland oysters were generally found on "hard" bottom (Grave 1912). They were usually not found inshore on shallow sandy bottoms because this material tends to shift easily with breaking waves. However, in quieter waters and areas with larger particles such as gravel and shell fragments, oysters could be found to low water mark. Thus, oysters were found inshore in Smith's Creek in the Potomac River (quiet waters), and along the Bay shore between the Patuxent and Potomac rivers where gravel and stones provided stable substrate suitable for spat settlement, even above low water mark. However, within this latter region, near Point No Point, no oysters grew along a 1.2 mi. (2 km) stretch of shore, apparently because this region's sandy bottom shifted with storms, smothering any cultch material or spat which might be present.

Oysters thrived on bottoms of sticky mud. As the bottom became softer and muddier (e.g., towards the channel) oysters tended to be found in "lumps," or iso-

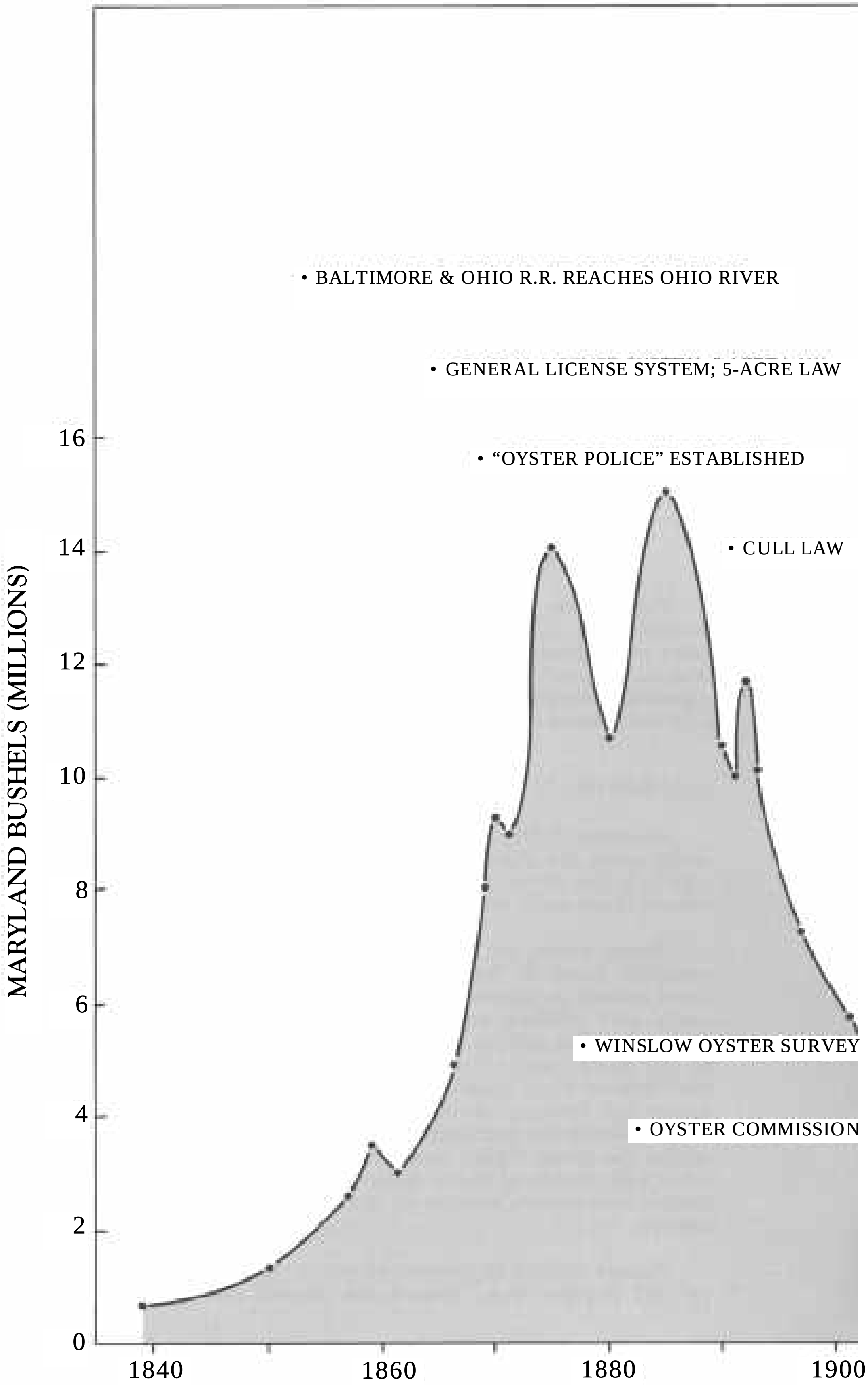


Figure 5. Reported landings of oysters in Maryland over the past 14 decades, in millions of bushels (approx. 1.3 times standard U.S. bushel). The harvest period for oysters begins

c. 1852: Baltimore & Ohio Railroad Reaches Ohio River. Expanded the oyster market to western communities; northern oyster packers opened plants in Baltimore.

1865: General License System; Five-Acre Law. State-wide license system regulated oystermen; leasing law allowed oyster planting on five-acre plots.

1868: "Oyster Police." Collected license fees, enforced fishing restrictions, and protected private grounds.

1877-79: Winslow Oyster Survey. Documented expansion of oyster beds and decline in number of oysters in Pocomoke and Tangier Sounds.

1882: Oyster Commission. Surveyed Maryland oyster beds; recommended conservation measures and oyster farming.

1890: Cull Law. Set minimum legal size for market oysters; required return of shells with spat and young oysters to natural oyster bars.

1906: Haman Oyster Culture Law; Shellfish Commission. Increased leasing allowance, a proposal rendered ineffectual by later legislation; commissioned Maryland Oyster Survey (Yates Survey).

1906-12: Yates Survey of Natural Oyster Bars. Conducted extensive biological and environmental surveys of Maryland's oyster bars.

1916: Maryland Conservation Commission. Consolidated Shell Fish Commission, Fish Commissioners, State Game Warden, and State Fishery Force (Oyster Police) into one agency.

1922: Shell-Planting Legislation. Initiated annual placement of shell as cultch for depleted oyster bars.

1927: Ten-Percent Shell Tax. Required oyster processors to make 10 percent of their shucked shell available for state use in planting.

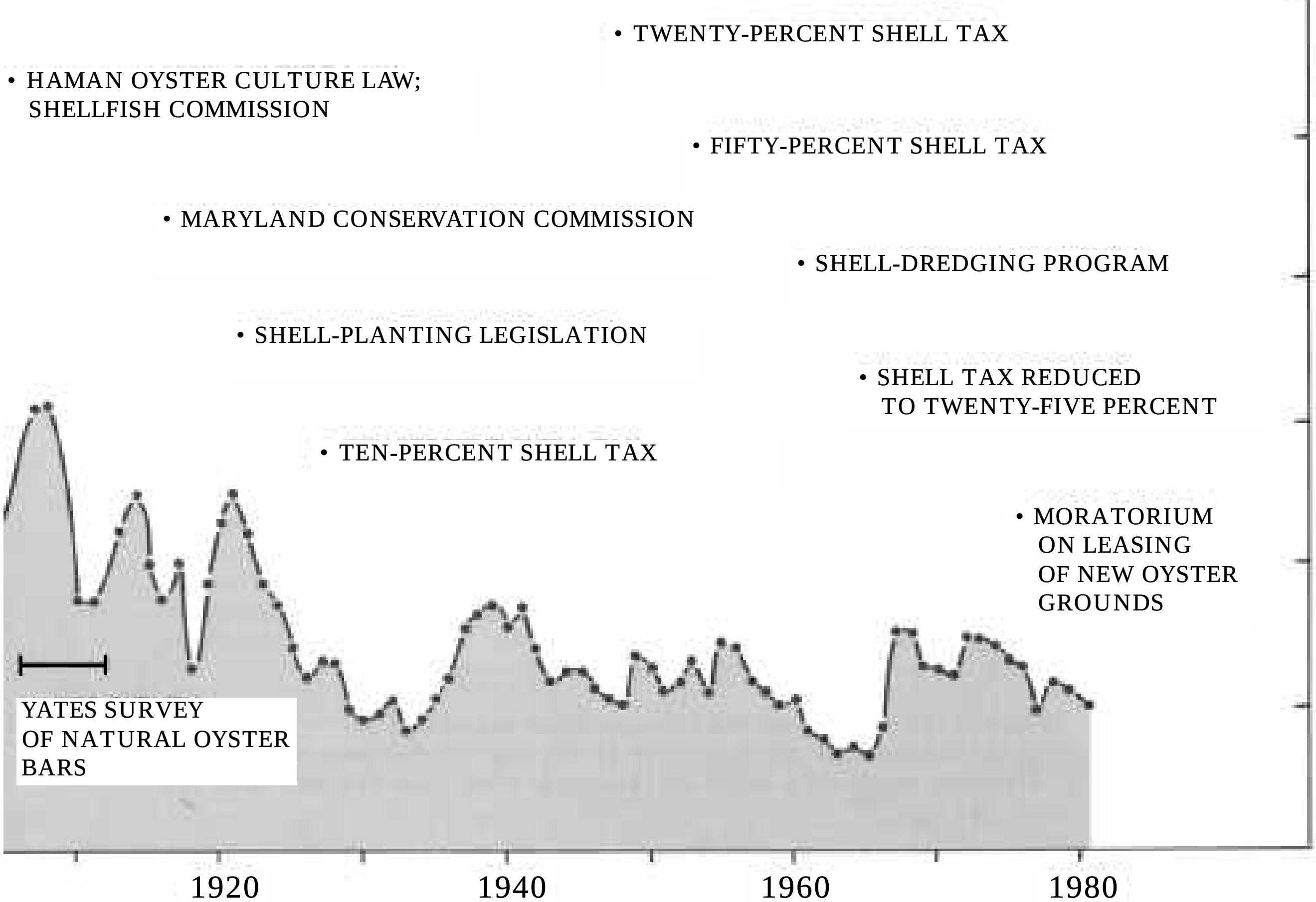
1947: Twenty-Percent Shell Tax. Increased shell tax on processors.

1953: Fifty-Percent Shell Tax. Increased shell tax again, but the supply still proved insufficient.

1961: Shell-Dredging Program. Initiated new oyster repletion program using old shells dredged from non-producing areas

1965: Twenty-Five Percent Shell Tax. Reduced shell tax; allowed processors the option of cash payment, in place of shell.

1972: Moratorium on New Leases. Suspended awards of new leases of oyster grounds pending completion of new survey of state oyster grounds.

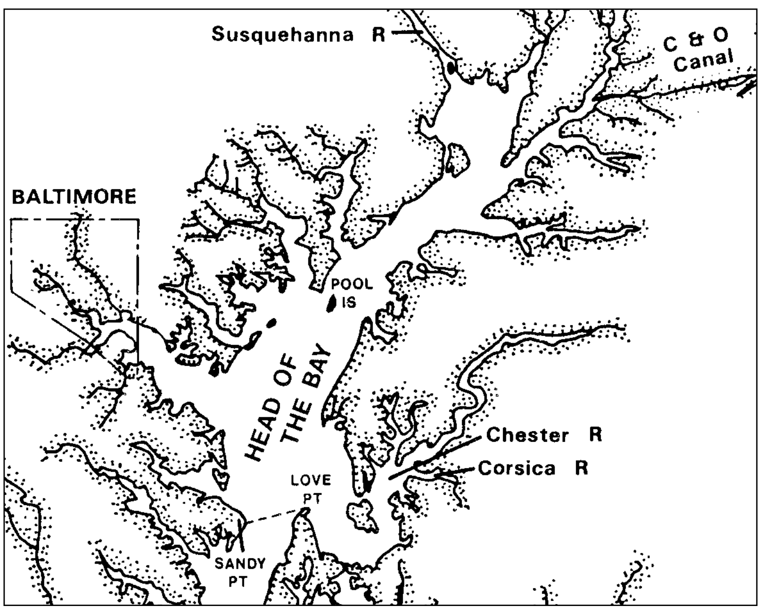


at the end of the old year and extends into the new. The time line refers to the new year (for example, 1961 denotes the 1960-1961 harvest period). Important events in the history of managment in Maryland are noted. (After Grave 1912, modified) lated concentrations. These patterns have since been modified by harvesting practices. Dredging has tended to expand beds by dragging shell onto barren ground where it has served as a base for new spat settlement. Thus beds in many locations (e.g., Choptank River, Tangier Sound) grew greatly in area in the early days of dredging.

As part of the effort to understand the oyster and its fishery, we briefly describe Maryland's Chesapeake Bay oyster grounds as they are grouped into a series of locations. Historical changes are noted. Reference to recent spat settlement success, including the 1980 situation, involves personal communications from Dr. G. Krantz of Horn Point Environmental Laboratories. Page 112 provides a map of Maryland's portion of Chesapeake Bay.

Head of the Bay, Including Chester River

This area is located north of an imaginary line drawn from Sandy Point on the western shore to Love Point on the east. In the past, it yielded many small oysters which were used extensively by Baltimore canners (Grave 1912). The region is subject to irregular fresh-water flooding by Susquehanna River runoff. Some of the most extensive flooding in this region had devastating impacts on the oyster resource in 1928 (Truitt 1929) and 1936, 1943, 1945, and 1946 (Beaven 1947).

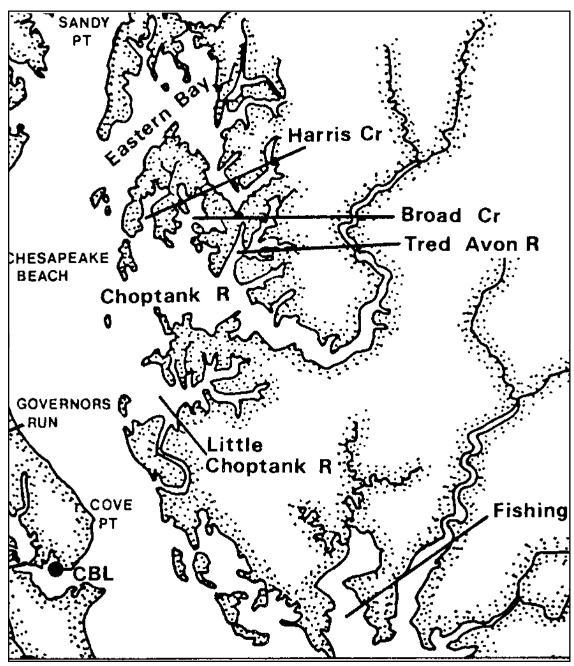


Stevenson (1894) commented that oysters used to be abundant as far north as "Pool" Island, with some even found at the mouth of the Susquehanna River. He attributed their disappearance to changes in freshwater inflow caused by more intense cultivation of farmland, timber harvesting, and ditching, with attendant rapid runoff. By 1912, the area of oyster grounds had been decreased by fishing activities (Grave 1912). Poor or irregular spat settlement did not allow for suitable recovery from fishing. The normal low salinity regime probably inhibited feeding at times, resulting in small oysters and in poor spawning and spat settlement success; accumulation of oysters in this region was always slow at best (Engle 1948). Sieling (1950a) also commented on the poor spat settlement of the region.

Grave (1912) noted that the Chester River contained oysters extending from about the six-foot depth contour to the edge of the deep water channel. The beds occupied a width of about one-third mile (0.5 km) from the river mouth up to the Corsica River. Thereafter the width decreased to about one-quarter to one-eighth mile (0.4-0.2 km). Oysters extended upriver about 25 miles (40 km) from Love Point, with few breaks in the distribution. Many bars extended for some distance upon very soft mud bottoms as lumps rather than as continuous populations. Engle noted in 1948 that the setting in Chester River was insufficient to keep the oyster grounds stocked by natural means. Few of the natural bars appeared to be workable in 1980, with no spat noted on the four oyster beds surveyed by Dr. Krantz in 1980. Indeed, no spat were noted by Dr. Krantz in the rest of the Head of the Bay environment in 1980. Two large oyster beds at the mouth of the river have been silted over (H. Seliger, Johns Hopkins University, personal communication). This is a characteristic of overfished, unproductive oyster beds (Winslow 1881).

Eastern Bay

Grave (1912) noted that this region had numerous contiguous oyster bars. The most productive bars were generally in areas of good water circulation; poorly stocked grounds were found in areas of poor circulation. Over time, setting has been consistent and heavy in the area, so shelling has been performed in the past (approx. 2000 bu/acre annually) to provide substrate for spat settlement and growth to seed size for transplantation (Engle 1948). Sieling (1950a) felt that Eastern Bay may have been potentially the largest seed area in the state. For example, on shell plantings in 1947, there were 2000 spat per bushel; in 1948, there were 776 (Sieling 1950a). Millhill Bar was set aside in about 1941 as 150 acres of originally barren bottom which then received annual cultch plantings (Engle 1956). If set exceeded 500 spat per bushel (about one spat/shell) the seed was transplanted to growing grounds next spring. Interestingly, on four bars from 1946 to 1954, spat settlement intensity increased from east to west in eight of the nine seasons (Engle 1956). This pattern was generally repeated in the high 1980 set (Krantz, personal communication). The cause of this pattern is not clear.



Choptank River and Little Choptank

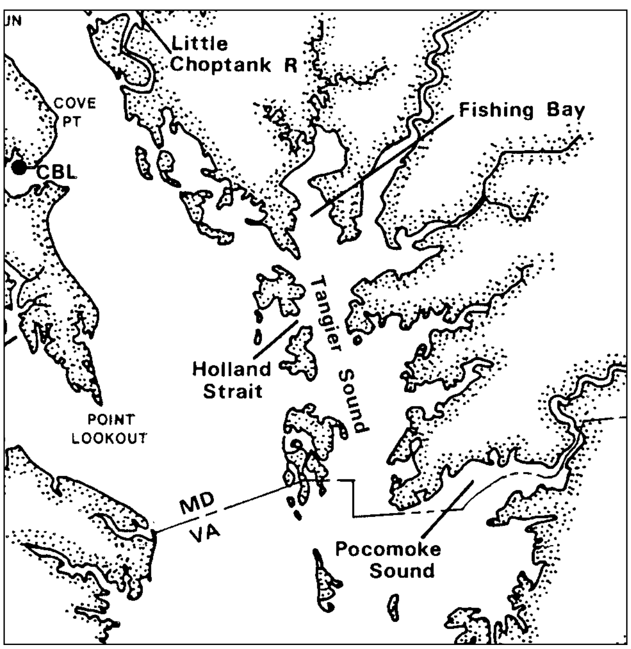
Choptank River oysters were so attractive to the consumer and so famous as to be known on the market as "Choptanks" (Stevenson 1894), just as there were "Kettle Bottoms," "Parker Moores," and "Chincoteagues." The bottom of the river was mainly "hard." Dredging had been performed in the river since 1870 and oysters more or less covered the bottom from shore to shore (Grave 1912), although they accumulated in separate "lumps" in the muddy mid-river channels. Grave (1912) attributed the general continuity of the grounds to the effects of dredging.

In Broad Creek and Harris Creek, some natural beds were so overstocked that the oysters were stunted (Grave 1912), a situation still true today. These oysters were then used for planting. Grave (1912) noted that the proportion of the total bottom area in these two creeks that was covered with oysters was unusually large, although he provided no data to support this statement. On Great Bar, Broad Creek, a square yard of bottom contained an average of 36 oysters below the 2.5 in (64 cm) market size and 12 above, for a total of about 394 bushels per acre (212 bushels of seed and 182 bushels of market oysters). Some Harris Creek grounds were apparently even more prolific.

In 1948, Engle was still able to include the lower Choptank and some of its tributaries in the category of locations with setting adequate to allow for natural restocking of the fished bars.

Tangier Sound and Fishing Bay

This area was surveyed by Winslow a century ago (1882) when it was being fished intensively and declining in yield. Stevenson (1894) noted a decrease in average oyster size over the size available 20 years earlier. Grave (1912) said that conditions on natural bars in this region gradually improved as one moved north from the Maryland-Virginia line. He attributed failure of the lower grounds to be replenished naturally to the excessive removal of cultch. Illegal out-of-season dredging of shell and seed oysters for sale to Virginia planters occurred here. He recommended private culture as a means of preventing this activity.

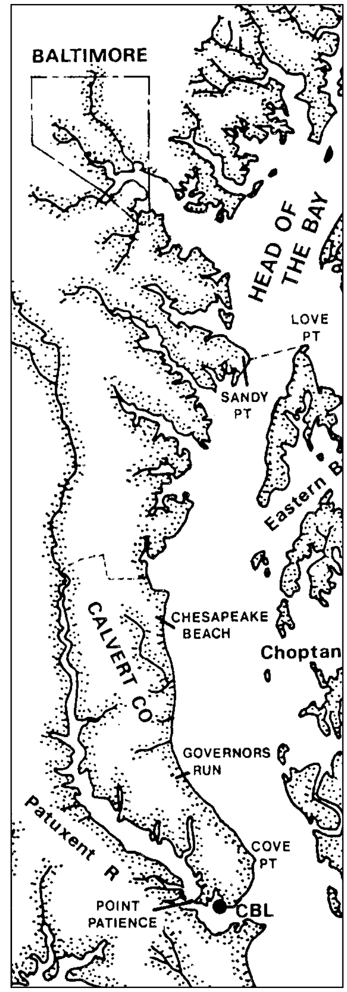


By 1948, Holland Straits had become the site of a state seed area receiving about 2000 bushels of cultch per acre (Engle 1948). Engle indicated that Fishing Bay was a region where setting was adequate to restock fished grounds. Sieling (1950a) warned that too much broodstock was being removed from this area, with depressed spat settlement resulting.

This area, and the following, were badly affected by the diseases MSX and *Perkinsus marinus* ("Dermo") in the 1960's.

Pocomoke Sound

This area was also surveyed by Winslow (1882). The oyster-producing bottoms were a mix of sand and mud (sticky and hard) with patches of hard sand, gravel, clay, and soft black mud. Clams were abundant in the soft mud (Grave 1912). Grave noted that since Winslow's survey, more than 5800 acres of ground had been over-fished to exhaustion. It appeared that reefs in this area did not become naturally restocked even if left alone. Many became silted



over and unfished until even the names were lost from memory. Still, in 1950 Sieling could declare it a self-sustaining area (although a shadow of its former self) with over 300 spat per bushel on natural cultch in 1947 and about 200 per bushel in 1948. It too was ravaged by disease in the 1960's and became a center for disease studies (Farley 1975).

Western Shore

This area includes the "Bay-shore grounds" or Bay bars of Stevenson (1894). In 1894 the oyster bars were almost continuous along the shore, extending in width to one and one-half miles (2.4 km) offshore in some areas. Oysters from Anne Arundel shore to Point Lookout were large and plump, and among the finest in Maryland; however, their abundance fluctuated widely (Stevenson 1894). On the other hand, Grave (1912) reported that Bay oysters off Calvert County were of inferior quality and that the Bay grounds had been dredged to the point of barrenness. The 1935 report of the State Planning Commission noted that the area between Cove Point and Chesapeake Beach had once produced fine oysters. However, a survey in November 1934 yielded the following figures for a series of test dredges over a three-eighths to one-half mile (0.6-0.8 km) distance:

Governors Run - 2-11 large oysters per haul.
Flag Pond - 12-21 oysters of mixed size.
Daddy Dare's Wharf - 20-37 oysters of mixed size.

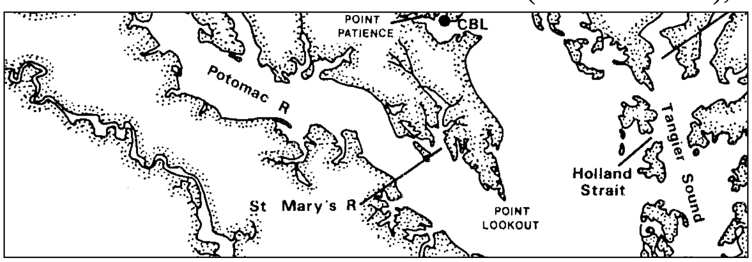
The surveyors noted that three to four bushels of oysters would have been taken from a productive ground over those same haul lengths. Further, Chesapeake Biological Laboratory scientists estimated the area to be capable of producing one and three-quarter million bushels per year (State Planning Commission 1935). Engle (1948) reported that large portions of the western shore did not have sufficient setting to keep the bars stocked by natural means. Beaven (1950) indicated that setting was very poor on the upper western shore (and in the major tributaries except near their mouths). Because earlier workers did not describe spat settlement, it is not clear if poor sets have always been prevalent on the western shore. However, these once productive grounds probably had self-sustaining sets because of the presence of plentiful brood stock and cultch.

Patuxent River

In 1894, oyster reefs in this river extended 24 miles (39 km) from the mouth upstream to the southern border of "Prince George" County, having apparently extended even farther 25 years earlier (Stevenson 1894). Even in 1894, to a greater extent than elsewhere in Maryland, the Patuxent was the site of "laying down," or holding oysters to grow and await favorable markets. Grave (1912) noted that oysters from above Point Patience were superior to those below. In this deepest region of central Chesapeake Bay, oysters thrived even at 120-130 ft (37-40 m), with dense stocks in the hole near Point Patience. Grave (1912) noted that during one year of the 1906-1912 survey of the Board of Shell Fish Commissioners, there were few, if any, places along the Atlantic coast where oyster food was more abundant than in this river (no data given). He attributed this to the presence of widespread muddy bottoms and organic material transported downstream from the extensive marl beds. The Patuxent has the reputation of being an area of good growth but poor settlement (Engle 1948, Sieling 1950a), so Grave's (1912) observations are important and the subject needs further investigation (see section on Feeding and Nutrition).

Potomac River, Including St. Mary's River

The largest oysters in Maryland ("Kettle Bottoms") were once fished from the Potomac (Stevenson 1894). In his 1912 report, Grave did not mention anything about the spat settlement in St. Mary's River (nor elsewhere in the Bay for that matter). However, in the past it has been intensive and consistent (Engle 1948, 1956, Sieling 1950a) with the result that a state seed area was established in this Potomac tributary. Sieling (1950a) noted the abundance of adult oysters in the river which did not grow to a large size, presumably because of overcrowding. (This was and is also true of Broad Creek and Harris Creek (p. 118) and the James River (Andrews 1951), all good setting areas.) Unfortunately, in recent years, spat settlement success in St. Mary's River has been poor, as it has been elsewhere in the Potomac, except near the river mouth (Davis et al. 1976). This low setting success has hampered rehabilitation efforts. It appears that oyster abundance depends on the rare heavy set which may occur only every 10-15 years (Davis et al. 1976).



REHABILITATION MEASURES

As noted in the section on the historical background of Maryland's oyster fishery, Chesapeake Bay oyster stocks are not the only ones to have become depleted. Oyster populations in New England declined greatly by the early 1800's (Ingersoll 1881, Sweet 1941). Thereafter, in states from New Jersey north, a system of private cultivation was encouraged, with consequent revival of the industry (Sweet 1941, Christy 1964). In addition, various rehabilitation measures have been undertaken in different regions of North America (Galtsoff 1943, Engle 1945b, Nelson 1950b, Pollard 1973, Whitefield 1973, Little and Quick 1976, MacKenzie 1977a). It is worth noting that no region on the Atlantic or Gulf Coast of the United States appears to have managed its eastern oyster resource so well that rehabilitation has been unnecessary. Frequently the resource has been overexploited greatly before any remedial measures have been taken.

Oyster populations from Chesapeake Bay south were less rapidly depleted than those in the northeast, to a large extent (at least initially) because of a greater resource base, fewer people living in the area, and less pollution. However, overfishing and disease led inexorably to population decline. In Maryland, Grave (1912) indicated that Pocomoke Sound's depleted oyster grounds had not recovered quickly when left alone after there were too few oysters to maintain commercial interest. He felt that so much shell had been removed that inadequate amounts of cultch remained. Thus, active rehabilitation measures were necessary to enhance recovery of the oyster resource. That continues to be true today.

Much of the information necessary for satisfactory management of Maryland's oyster resource had been accumulated by about 1912 (see the section on Historical Background). Winslow (1881, 1882, 1884) had described the deterioration of the extensive and prolific oyster beds in Tangier and Pocomoke Sounds, attributing much of the decline to unregulated overfishing. The oyster industry had been thoroughly reviewed by Ingersoll (1881) and Stevenson (1894). The biology of the oyster had been subjected to extensive study by scientifically trained investigators (Brooks et al. 1884, Brooks 1905, Grave 1912). Although many aspects of oyster biology remained to be explained, the essential core of information for enlightened management was there. Unfortunately, as Wallace (1952) indicated in his critique of biological research on oysters, political considerations, rather than limited knowledge, have frequently contributed to declines in fisheries in North America and elsewhere (see also Adams 1968). Socio-political considerations have strongly affected management decisions in Maryland. Therefore, it is important that our available biological insights be marshalled to support appropriate management actions.

In contemplating management practices to be applied to Chesapeake Bay, it would appear sensible to consider the Bay from the same perspective that a farmer would apply to management of his land or farm animals. He would need to know the carrying capacity of the farmland, the nutrients available and nutrients required, where the good soil and poor soil was located, the yields to be expected from one soil versus another, or from one food supply versus another, reproductive capacity and health needs of the crops or stock, etc. If he were seeking to reclaim marginal farmland, the obvious tactic would be to start with the best section, clear it of weeds, fertilize it, and carefully nurture it until it was good farmland. Then he could move on to the less suitable land. It would be a waste of resources (unless they were not limited) to take a scatter-shot approach, diluting the effort and the return and perhaps misusing the good land at the same time.

Similarly with the Bay, one needs to know where good growing and good seed areas are located. These then must be tended and protected. The fact that a once reliable spatting region like St. Mary's River has apparently become an area of limited spatfall is disturbing. Such regions are the buffers needed to provide seed resources required for gradual upgrading of other regions, and seed is the limiting resource in public or private oyster harvesting in the Bay.

Similarly, we would wonder at the farmer who harvested his plants or animals before they were fullgrown, or who destroyed the soil or the rangeland in the process. That is what has happened in the Bay and no rehabilitation activity will be really successful until destructive practices are curtailed.

We can take as an instructive example the efforts at rehabilitation of the Long Island Sound oyster resource which have recently been described by MacKenzie (1981). As a result of an extensive study of the area from 1966 to 1972, MacKenzie concluded that oysters in Long Island Sound had the potential of covering the bottom of the Sound in a few years under optimal environmental conditions. This potential was due to early oyster maturity (by the second year), high fecundity of the parents, reasonably widespread setting success, and good post-setting survival under field culture. Limiting factors included low temperatures, lack of clean shell cultch for setting, a suite of predators and competitors, and presence of silt. MacKenzie found oyster survival to be high on cultivated beds because predators, competitors, and suffocation by silt could be controlled to a large degree by oyster farmers. MacKenzie felt that few oysters in the Sound would survive without such bed culture.

Such culture has been increased in Long Island Sound since 1966 (MacKenzie 1981). Oyster growers spread shells every year on setting beds. They controlled major predators like starfish and oyster drills by use of quicklime (starfish) and harvesting by suction dredge (drills). Growers avoided oyster mortalities from suffocation by silt by transplanting seed in March-April rather than in May-June as had once been the practice. This apparently lifts oysters above the winter-deposited silt before temperatures are warm enough to increase metabolism with its attendant respiratory and water pumping demand. As a result of these culturing activities, by 1972 (when MacKenzie's study ended), oyster yield in Connecticut had increased 85-fold over the 1966 yield. Off New Haven alone, production rose from 10 million oysters in 1966 to one billion oysters in 1972. Although MacKenzie had no further data for Connecticut yield after 1972, he did show that production in New York increased from 46 metric tons of oyster meat in 1967 to 956 metric tons in 1975. Thus, this study demonstrates the excellent effects of careful cultivation of private oyster grounds through use of simple measures such as annual provision of clean cultch at the right time and control of predators and of smothering by silt. To an extent, some similar measures are being taken by the state in Maryland's Chesapeake Bay. However, private culture could enhance this by allowing for more careful attention to specific areas by those with a financial investment in the success of the private ground.

Management Recommendations Since 1884

Various investigators and resource managers working in Chesapeake Bay published conclusions concerning appropriate management strategies. We will now describe their findings and recommendations developed over the past century. Some major points have been made again and again, and we hope that their reiteration in our report will help convince readers of the utility of these long-recommended actions.

Brooks et al. (1884) visited 59 oyster bars, made 326 examinations, measured and counted all the oysters upon 120,958 yd^2 (101 km^2) of oyster bottom, and concluded that the average density of oysters was one oyster per 4.2 yd^2 (3.5 m^2). This was a decline from the average of 1 per 2.3 yds^2 (1.9 m2) found by

Winslow in 1879 (Winslow 1884). They recommended annual surveying and marking of oyster grounds by the Oyster Police (as they were then known). They advocated that oyster beds should be closed where and when necessary to allow for rehabilitation and growth, and that the opening or closing of areas be decided upon by trained experts.

In his “popular treatise” on the oyster based on the earlier work of the Oyster Commission, Brooks (1905) advanced reasons for declining spat set: scarcity of mature oysters to furnish spawn; wanton destruction of large numbers of spat by watermen ignoring culling laws; and lack of clean shell on beds as cultch. (Note that Waugh (1972) found for *Ostrea edulis* in England that the number of spat setting per unit area was related to available shell area and was limited by the number of available larvae).

Grave (1910) expressed the opinion that Maryland localities differed greatly in the quantities of oyster food available, with different diatom species being found in different areas. He declared that oyster beds in sluggish waters were most easily injured by overfishing whereas those in swifter moving water recovered quickly, presumably because the currents cleansed the cultch of sediment. He suggested that those prolific oyster bars with an overabundance of stunted oysters of less than market size be designated as seed oyster bars. Oyster planters could purchase this seed and the cull law need not apply to them. The areas he singled out for this treatment were found in the Head of the Bay, Broad Creek, Harris Creek, and Tar Bay. After 1916, the Conservation Commission of Maryland did set aside choice locations as “Reserve Areas” for experimentation in transplantation.

Grave (1912) made a number of additional recommendations. He noted that in order to obtain spat, fresh cultch should be strewn on somewhat elevated bottom washed with strong currents at certain tidal stages. The freshness of the cultch would prevent formation on the shell of material unattractive to pediveligers as they crawled on the shell surfaces. The currents would keep the cultch clean. One bushel of shell would cover 20-25 ft^2 (1.8-2.3 m^2) of bottom with a one-shell-thick layer. An acre could be covered with 1700 bushels of shell but 2500 bushels per acre were recommended on good spatting grounds provided the set were moved to growing grounds and spread more thinly within the year. Apparently, experiments to determine suitable methods of planting shells had been performed, including placing them in rows or ridges across and parallel to currents. Grave concluded that broadcasting shell was more satisfactory and economical than planting in piles (considering the difficulty for larvae to penetrate the piles or ridges to settle on the interior shells).

In 1921, Truitt lamented the shifting of oyster shell and small oysters to shell piles on shore. Oyster shell was in demand for lime, road material and chicken grit, a situation deplored earlier by Brooks (1905). In addition, apparently the entry of motorized boats into the fishery tended to eliminate sailboats which used oyster shell as ballast. In the past, this ballast had been dumped onto the grounds as the catch was brought on board the sailboats. With the decline in sailboat numbers, shell was not being returned to the grounds. Truitt recommended the return of shells systematically and abundantly according to an informed design based on knowledge of prime setting areas and of factors such as survival, growth and “fattening” for each proposed area to be shelled.

Truitt (1929) demonstrated the importance of shell as a settlement substrate by comparing spat settlement thereon with other material such as pebbles, cinders, coal lumps, glass, brickbats, and twigs or chips of various trees. Oyster shell was settled upon by about twice as many spat as was glass. The remaining materials had very few spat. Thus, oyster shell was the obvious choice as cultch.

In 1931, Truitt expanded upon his recommendations, urging shell planting in suitable places and noting deficiencies in selecting planting sites. It appeared that no attention was being paid to:

> “1. whether or not there is brood stock present to assure reproduction,
>
> 2. whether, once set, the young survive,
>
> 3. whether the areas selected are, essentially, breeding (setting) grounds or growing and fattening grounds,
>
> 4. whether plantings should be made on the basis of expediency as to season or at the time young (larvae) oysters are in the water and at what concentrations, and
>
> 5. whether salinity differences in the several regions affect growth and survival.”

In general, shell distribution was highly dependent on the desires of local watermen. No scientific information was collected to any extent nor was it given attention if it was (Truitt 1931). Today, local committees of watermen advise the management agency as to shell distribution, and, in a number of instances, shell is placed in biologically unsuitable areas (personal observations).

Beaven (1945) outlined Maryland’s oyster problem succinctly, indicating that the essentials of successful oyster culture included:

Stable bottom with good circulation of water containing adequate food

Suitable quantities of brood stock for spawning and larval production

Adequate supplies of clean cultch

Spat that are not so crowded as to prevent good growth

Pest- and predator- (and disease-) free conditions

Harvesting at the right time when the oysters are optimal for marketing

Beaven (1945) emphasized that the natural bars in Maryland should be studied on a more or less individual basis, due to their great variation in suitability for settlement, growth, etc. He indicated that we need to know the abundance of natural brood stock now available in the Bay, the numbers of brood oysters needed per acre for optimal spat production in a given locality, the extent of larval dispersion, and the best position of brood oysters in relation to the cultch. What concentration of cultch is optimal? Should cultch be distributed randomly and widely, or in windrows, or in some other configuration (see Grave 1912)? What levels of spat mortality occur in different localities? These questions asked in 1945 are still unanswered for the most part. In a related vein, evaluating the decline of the European oyster industry, Korringa (1946) noted that in the Dutch Oosterschelde, at least 10 million oysters were needed if enough spat were to be produced in an average summer. Such insight resulted from years of intensive study. No such information is available for Chesapeake Bay.

With regard to shell planting, it may be important to add a certain number of adult oysters to the shell after it has been laid on the bottom. Quantitative study of such practice has apparently not been made for C. virginica, but Knight-Jones (1951) provided some insight for *O. edulis*. When a shelled patch was stocked with oysters, nearly three times as many spat were recorded from it as from a shelled patch that had not been stocked with adult oysters. Similarly, there were always more spat on densely stocked grounds, usually about two times as many as were found on neighboring grounds with fewer oysters. Knight-Jones attributed this to the tendency of oyster spat to settle gregariously in the presence of adults and recommended that reclamation of derelict ground include the relaying of older oysters. Crassostrea *virginica* also demonstrates gregarious setting behavior (Hidu 1969, Hidu et al. 1978) so that Knight-Jones' work is worthy of repetition in the field with the eastern oyster.

Galtsoff (1943) provided a valuable statement of principles of oyster management for increased production. This paper should still be consulted for sound information on management and cultural practices. He warned against uninformed and indiscriminate planting of oyster shell and described some instances of careless management. For example, in different geographic regions, shell was planted in areas with no record of good spat settlement (this happens in Maryland), or where it was rapidly fouled. In some places, shells were dumped in large piles in the mistaken hope that tides and currents would distribute them. In Florida, *Ostrea equestris* was thought to be year-old C. virginica and was transplanted as seed by the thousands of bushels. Obviously, it is important to understand the dynamics of the local environment and to plant shells at the proper time in the proper configuration and in an appropriate location.

Galtsoff (1943) also discussed private oyster cultivation and management of public grounds. He concluded that natural oyster beds cannot produce as many oysters as can cultivated bottoms. The natural population is a mix of ages which may interfere with one another. Spat and seed on the adults may compete for food and oxygen. Harvesting, culling, and processing all can cause mortality of spat. A well-cultivated bed can harbor a population of single-age oysters in an appropriate concentration to utilize ambient food, thus fattening quickly. The population need not be disturbed by dredging until it is to be harvested as a group. The bottom can then be replanted with spat, a process which Galtsoff showed is more advantageous than the planting of 2-3 year old seed (he expected a return of one bushel of oysters per bushel of seed compared to 4-7 bushels of oysters per bushel of spat).

Galtsoff (1943) recommended that badly depleted grounds be rehabilitated by planting, and that planted grounds should be closed to fishing until oysters reach market size. When the ground is opened, all oysters should be removed to prepare the ground for the next planting. A distinction should be made between setting and growing grounds and no shells should be planted on the latter except to reinforce the bottom if necessary. Grounds should be rotated for harvesting depending on the time needed by the oysters to grow to market size. He stated that the cost of such a program should be borne by those who benefit economically from it, i.e., the harvesters and packers. As Alford (1973) pointed out, the Maryland oyster program is very heavily subsidized. Galtsoff (1943) showed how an appropriate assessment per bushel of oysters could be implemented. He recommended a system of checking records that was established in Louisiana. We believe that appropriate and effective mechanisms suitable for local conditions in Maryland should be developed.

As Galtsoff (1943) indicated, any program of management requires thorough knowledge of local grounds and an understanding of the behavior of oysters in each area. He reiterated this in his 1945 note on rehabilitation of Chesapeake Bay oyster resources (Galtsoff 1945). In a move in this direction, the Maryland Commission on the Conservation of Natural Resources (1948) provided a thorough survey of the Maryland oyster resource. They noted that in good seed areas, one bushel of shells would catch enough spat to yield about three-quarters of a bushel of seed the next year at 600-1000 seed oysters per bushel. They claimed that about 3000 bushels of shell were needed to plant one acre of seed area and that 2250 bushels of seed should result. This in turn should yield 2250-6750 bushels of mature oysters when planted in a growing area at a density of 500 bushels of seed per acre.

We can conclude from these reports that the haphazard placement of cultch or seed is wasteful, just as the indiscriminate spreading of seed by a farmer over his farm (roads, ditches, barnyard, and woodlot as well as ploughed fields) would be a waste. The oyster grounds should be as carefully studied as farmland would be. The requirements of the oyster crop should be as well known as are the requirements of agricultural crops.

With regard to such generalizations as can be made about Chesapeake Bay oyster grounds, Engle (1948) pointed out that there was (1) a wide range of intensity of setting from one location to another, (2) a tendency for more regularity in setting from one year to another in certain areas, (3) a tendency for more regular and heavier setting on the Eastern Shore, and (4) a tendency for heavier setting at the mouths of rivers and down-Bay than upstream or in the Head of the Bay region. Three categories of regions could be established. One included areas with consistent heavy setting. A second comprised areas with adequate setting when cultch was added. The third included areas in which setting was insufficient to replace harvestable stock. Areas in the first category (Eastern Bay, Holland Straits in Tangier Sound, St. Mary's River) had been developed as seed areas on which 2000 bushels of shell per acre were placed yearly. Locations in the second category included Fishing Bay, Tangier Sound, and Choptank River including its lower tributaries. Planting of cultch could be practiced here if money and shell were sufficient. The third region included much of the western shore, the Patuxent River and the Chester River. Here the planting of cultch would probably be a waste of time, shell, and money until the better regions of the Bay had been carefully cultivated and more regions had been made self-sustaining. When that had occurred, perhaps the regions of poor setting could be treated to improve settlement.

A report to the General Assembly of Maryland made similar points (Chesapeake Biological Laboratory 1953). Natural oyster bars are the sites most favorable for oyster growth because they have been established by natural processes over the centuries. Overfishing, removal of natural cultch, and heavier siltation due to clearing of land had combined to smother many natural beds under layers of mud. Yet water conditions over oyster grounds in 1953 appeared to be as favorable for oyster survival, growth, and quality as they had been 70 years earlier. (We believe that this is probably still true for large areas of oyster grounds today, especially on the Eastern Shore; however an extensive survey of water quality to determine this is very desirable).

The 1953 report also noted three categories of natural oyster grounds. Again there were the seed areas (often shallow and semi-enclosed bodies of water) in which settlement was usually excellent but in which growth was poor due to crowding. The seed oysters should be harvested and moved elsewhere to grow. Then there were self-sustaining bars with suitable setting to replace harvested oysters (e.g., Eastern Shore tributaries). These could continue to produce well if small oysters and sufficient shells were returned to the bottom and if overharvesting was prevented. The third category included growing bars where set was poor but growth was excellent (the Bay proper and the larger tributaries). For this latter category, it was felt that strong currents favored oyster growth but acted to disperse larvae. Such bars should be seeded regularly to maximize production.

The 1953 report noted that the above categories were an attempt to impose clear-cut distinctions on a fluid situation. Patterns of growth and setting in the Bay are dynamic and changeable. Thus, management strategies should also be flexible and would require extensive carefully collected and up-to-date information to be most effective. They would require large expenditures of time and money to have any impact and the 1953 report urged the expansion of private farming to help with this.

Finally, it seems reasonable to end this review of management recommendations with those made in 1966 (Quittmeyer 1966) by a knowledgeable team of consultants (an oyster biologist, two business administration professors, a sociologist, an economist, and a political scientist) to the Seafood Advisory Committee of Wye Institute (see also section on Private Culture and Oyster Farming). This team considered the Maryland oyster industry with care and their recommendations are clear, comprehensive, and seem to be consistent with available knowledge. In the recommendations, listed below as they appeared in the 1966 report, references to “Department of Chesapeake Bay Affairs” have been replaced by “Tidewater Administration” of the Department of Natural Resources. Similarly, “Natural Resources Institute of the University of Maryland” has been replaced by “Center for Environmental and Estuarine Studies” or “Center.” Expertise regarding oyster biology is now shared by workers at Chesapeake Biological Laboratory and Horn Point Environmental Laboratories, both in the Center. Seed oysters may no longer be readily available from St. Mary’s River, as that region has deteriorated since 1966

> “With awareness of the attitudes of watermen in Maryland, from a biological standpoint the following steps can be recommended on the oyster fishery:
>
> a. Continue the state-operated shell planting and seed-oyster operation.The scale of these operations is already large and can provide quantities of seed oysters.
>
> b. Give the Tidewater Administration full authority to determine, designate and use seed areas regardless of location, county lines, and local sentiment.
>
> c. Authorize the Tidewater Administration to dispose of seed oysters by sale or transplanting to areas of their choosing. This would provide a beginning to a self-sustaining industry.
>
> d. Open all public grounds to oystermen of the State. Tradition and public opinion notwithstanding, public oyster beds should not be opened for marketing before 1 October each year. This will tend to insure quality to the consumer and good yields to the producer.
>
> e. Impose a uniform tax on all marketed

oysters, which would at least pay for the cost of seed production and transplantation.

f. Encourage private planting by removing restrictive laws on renting barren bottom and by selling seed oysters by competitive bids. The Tidewater Administration with advice from the Center for Environmental and Estuarine Studies should have wide authority to determine utilization of bottoms.

g. Explore the possibility of rehabilitating deep Bay beds, particularly on the Western Shore of the lower Bay, by renting for 10 or 20 years at competitive bids, large tracts of 1,000 acres or more of good public bottom for modern management. Rentals of no less than $100 per acre per year should be expected. Seed oysters should be made available and no restrictions made on source or type of management, except to meet public health standards.

h. Grant authority to the Tidewater Administration to determine during the impending survey of public grounds those which are productive or which can be made so and open all marginal bottoms to private leasing.

i. Authorize the State to sell or plant shells for private companies at cost on unused or inferior rented bottoms in seed areas. Initiation of private seed production will provide some insurance against spatfall failures and help stabilize seed production.

j. Re-examine and determine policy in regard to dredging of buried shells for shell-planting programs. Establish criteria for determining whether a bottom is more properly used to grow oysters or supply buried shell. A deep conflict between use of existing shell deposits as a source of cultch and potential use as beds for growing oysters is arising because most shell deposits underlie recently depleted productive bottoms. The demand for buried shell may cause irreparable harm.

k. Provide the Center with expanded capabilities to pursue their research and advisory responsibilities to the Tidewater Administration in its many management decisions, monitoring of setting, and ecological research.

l. Encourage watermen to become participants in a more diversified system by executing the planting and transplanting with modern equipment—light dredges if needed, etc.—for the state.

m. Re-evaluate the Potomac River Compact seeking to rectify the political settlement which defies effective management. The river has extensive high-quality oyster-growing bottoms but lacks seed oysters. These could be obtained from tributaries such as St. Mary's River and Great Wicomico River. Neither Virginia nor Maryland has shown positive attitudes toward the Potomac oyster fishery.

n. Convince the people of Maryland and Virginia that a management system for Chesapeake Bay with very few limitations between states would provide the most effective and flexible fisheries industry to the benefit of all residents of the region."

Scientific Management

It is appropriate to comment on the serious inadequacy of information available in Maryland for scientific management of the sort applied to shellfish stocks elsewhere. A very useful introduction to the problems of estimation of population dynamics and its application to management of shellfish stocks is provided by Hancock (1979) in a paper presented to a shellfish management symposium (other useful papers appear in that same symposium). His paper considers assumptions of various fishery models, their application to various fisheries, and some of the associated pitfalls. Methods of managing fisheries are briefly considered (unrestricted fishery, management by specific regulations, management by effort limitation, management by catch quota). He notes the shortcomings and uncertainties of managing shellfish stocks. Hancock's experience is firsthand, deriving from his work with cockles (*Cardium edule*), a commercial bivalve fished in the United Kingdom (Hancock 1965, 1967). He built on his studies of this species to provide generalized insights into population parameters and their interrelationships (e.g., between stock and recruitment) for exploited marine bivalves in general (Hancock 1973, Hancock and Simpson 1962). His insights are applicable to oyster management.

Managing oyster populations successfully requires information concerning oyster abundances on the grounds, annual magnitude of recruitment (spat set and survival), natural mortality and fishing mortality, growth, and age at first maturity. These estimates are not all easily obtained. Growth and age at first maturity can be determined fairly well, but variations with location in the Bay need to be taken into account. Fishing mortality can be estimated from landings, which should include details of catch-per-unit effort and of location of the fishing effort (to aid in management of specific regions where necessary). Magnitude of spat settlement is presently being assessed yearly in the Bay. Natural mortality estimates are more difficult to make but can be derived with some effort. It would be helpful to understand the dispersal of larvae from one region to another.

Given this information, suitable management decisions concerning opening or closing areas to fishing, catch limitations, length and timing of season, placement of seed and cultch, etc. could be made and defended vigorously. Introduction of such a program, coupled with an increase in rental of Bay bottom for private culture, might proceed slowly but deliberately and become more refined over a few years.

For an example of the application of biological knowledge and catch information to modelling an oyster fishery, we can turn to the *Ostrea lutaria* fishery in Foveaux Strait, New Zealand. Allen (1979) was able to make use of the extensive body of knowledge that had been collected concerning the species' life history, including information on spawning and recruitment, growth, and natural mortality. He coupled this with information on fishing mortality and distribution of fishing effort. The result was a yield model for the fishery. Although the estimates of the various parameters involved were not accurate enough to provide estimates of optimal catch levels from year to year, the model was used to examine the relative advantages of fixed and varying annual catch quotas. A variable quota was found to provide the highest average catch under the model's assumptions. It also provided a good level of protection against catastrophes which might result from overfishing a low-level population. Allen (1979) discussed the various shortcomings of his model, but none were incapable of being overcome. Presumably, the New Zealand model is now being tested and refined.

Fishery models are valuable tools to managers of shellfisheries and finfisheries around the world. In Chesapeake Bay, they would help provide rational bases for proposing and implementing various management strategies that would protect and enhance the oyster resource, to the benefit of all concerned. Power (1970) provided a broad review of legislation affecting the Maryland oyster industry. As others have done, he noted the fact that wise management of Maryland's oyster resource has been hindered by legislative responses to the concerns of watermen. He urged that the management agency be given broad authority to manage the fishery. The resultant range of choice necessary for effective management and the freedom from outdated laws and from having to deal with a cumbersome legislative process would permit bold initiatives. The appropriate mix between public and private oyster grounds could be attained. There would be greater freedom to explore advantageous Maryland-Virginia cooperation in oyster management.

We feel Power's conclusions are correct. If high production is the proper objective of management, there is no evidence that it will be best achieved by retaining controlling decisions in the legislative branch of government. There is much evidence that a biological resource can best be managed by trained biologists whose decisions are based on research findings, field sampling, and continuous interaction with experienced watermen, rather than on politically expedient factors.

Biological Aspects of the Oyster Cull Law in Maryland

The following report to a Meeting of the Advisory Committee to Tidewater Fisheries on December 6, 1951, is included because it covers a number of interesting matters and because of the late Mr. Beaven's extensive experience with the biology of Maryland oysters.

Biological Aspects of the Oyster Cull Law in Maryland
by G. Francis Beaven
(Reported to Meeting of Advisory Committee to Tidewater Fisheries)
(December 6, 1951)

"The aim of any cull law is to insure the retention of sufficient juveniles in a natural population to replace the adults which are cropped or eliminated by natural causes. The effective operation of such a measure is essential on any oyster bottom which is to continue in production entirely or largely through the results of natural repopulation.

"The optimum size at which an oyster or other animal is taken is partly determined by the point where increments of future growth to the total crop become offset by losses due to the increased mortality among the older individuals. The market value at a given size and the ease of handling and processing are other factors to be considered in establishing the most profitable size at which the oysters should be taken. In an industry such as the poultry industry it frequently is more profitable to market the crop as broilers and replace the stock with a new crop than to carry the animals on to maturity. The same principle may at times be applied to oysters.

"Since rate of growth, rate of mortality, marketability and other factors are quite variable over the areas where oysters are grown, it is difficult to establish the best size at which a minimum limit should be set. For this reason cull laws have not been uniform everywhere and contention arises as to the wisdom of the limitations which have been established.

"The present Maryland law requires that all oysters less than three inches in length shall be returned to the beds upon which they grew while harvesting operations are in progress. It is true that in most instances the crop would produce better returns if the three inch oysters were permitted to remain on the bottom and attain a larger size. At times very young and thin shelled oysters at three inches in length are practically worthless for shucking. On the other hand, in some areas the single round deep cupped oysters which occur may contain considerably larger meats at 2 1/2 inches than do many much longer oysters growing under crowded conditions. Hence the establishment of the three inch limit represents something of a compromise.

"The rate of growth of Maryland oysters often has been given as one inch per year. This figure is a very broad approximation. Occasional spat on planted shells under exceptionally favorable growth conditions in Maryland have been found to slightly exceed three inches in length at the end of the initial growing season when the oysters are less than six months old. Oysters known to be less than eighteen months old similarly have been found at times to exceed six inches in length. In certain seed areas oysters fail to reach three inches after many seasons of growth and only a small proportion ever reach market size. Furthermore, the rate of growth is much more rapid when oysters are young and decreases greatly with increasing age. Typically, however, most Maryland oysters on good growing bottom will have reached three inches in length when they are three years old.

"The established three inch cull law under Maryland conditions serves to ensure that oysters typically too small for shucking are returned to the bars where they may be expected to continue rapid growth without undue mortality. Since the proportion of undersize oysters in the oystermen's catch increases as he continues removal of the market sized individuals the point eventually is reached where it is not profitable for him to continue harvesting even though a number of large oysters still are present. This tends to ensure future well balanced populations with sufficient brood stock for new generations. In those areas where environmental conditions consistently favor a rate of natural reproduction sufficiently high to replace the oysters harvested, the strict enforcement of the three inch cull law has served to maintain production on a self-sustaining basis. With continued vigorous enforcement of this law, and the presence of adequate cultch, continued yields at minimum rehabilitation costs can be expected. It should be pointed out, however, that much of Maryland's bottoms do not receive sufficient set of young oysters to repopulate the bars under normal harvesting practices even though the cull law is enforced. Production on such bottoms can be maintained by bringing in seed oysters from areas where setting is high.

"Some years ago Dr. Thurlow Nelson of New Jersey pointed out a condition under which enforcement of a cull law may be detrimental. It is a known fact that rate of individual growth among oysters may vary quite widely. Among an even aged set some individuals will grow rapidly and produce giants while some will grow slowly and produce runts. It is probable that the offspring of the fast growers will contain a high proportion of similar fast growers and that the offspring of runts will contain a high proportion of runts. Under conditions where all have an equal chance to mature the practice of removing the fast growers and putting back the runts may finally result in the development of a slow growing population of runts on the bar. Such a condition is reported to have occurred in Europe. According to Dr. Korringa of Holland, the oyster growers there practice a very intensive method of cultivation. Seed are produced on tile and transplanted many times so that all of the set have an equal opportunity to grow. When the age of harvest is reached the Dutch growers carefully go over their plantings and remove all of the small slow growing individuals for sale first. As long as an oyster shows vigorous growth it is returned to the beds so that in the end only the fastest growers and largest oysters are left and these are used for brood stock on the seed beds before they are finally marketed. Over the years these planters have developed oysters which grow more rapidly and attain a larger size than do oysters of the same species grown in France where the practice has been to harvest all oysters as soon as they reach market size with runts remaining indefinitely on the beds.

"Under Maryland conditions, where setting has remained high enough to maintain natural production and especially in the areas where seed is produced, it is likely that natural competition through crowding serves to eliminate most runts and that the fastest growers have the best opportunity of reaching maturity. Thus far there is no indication of an adverse effect of the cull law upon oyster growth in Maryland. The present practice of transplanting seed from thickly populated areas to bars where natural reproduction does not maintain sufficient populations should serve to eliminate the runts which might tend to develop there naturally. Variations of growth among oysters on different bars in Maryland and of oysters from different sources when planted on the same bar are being studied by the Department of Research and Education and by agencies elsewhere. If superior races of oysters should be discovered they can be introduced for brood purposes. Thus far the oysters produced in Maryland seed areas have been found to grow best under Maryland conditions. Checks should continue to be made on the growth rate in isolated self maintaining areas to determine whether any tendency towards developing slow growing varieties may occur.

“While enforcement of the cull law thus appears highly desirable on Maryland’s natural rocks there are two weaknesses in the law as written which are apparent. The term “all oysters” under three inches may be understood to include every oyster which has attached. Many of the younger oysters are too small to be recognized except by a trained person using special techniques. On a self-sustaining bar there must be quite an excess of spat to offset natural mortality. During early fall a bar of this type in good condition should have one or more spat ranging down below one inch in length attached to every large oyster. These are too small to be knocked off without killing them. If the large oysters are returned to the bottom with the spat on them then it is not possible to harvest any others at all from the bar which is manifestly absurd. Until recent years few watermen or inspectors recognized spat below one inch in size when culling oysters. This practice is sound but leaves open the question as to whether or not the cull law is really being complied with. There are practical objections to making exceptions of small oysters say under one inch in length. It might be that the provision to cull out all visible small oysters should remain in the law but that the provision to throw back large oysters with small ones attached which cannot be separated without killing them should be dropped. It is doubtful that many large oysters are ever returned to the bottom under the existing law for it would be practically impossible to prove that a young oyster had been killed in removing it from a large one when only the large ones are left at inspection. The inspector, of course, would still count as illegal any large oyster bearing a small one which could be knocked off without killing it. Some such revision may be desirable in view of the recent more widespread recognition of small spat by both oystermen and inspectors.

“The second weakness of the cull law is its application to privately planted beds. In many cases such beds are on bottoms which are not dependent upon natural set for their production. Seed produced in high setting areas is transplanted to the beds and grown to market size. Unlike production on natural rocks the new crops are not dependent upon the small oysters and shell culled off, but upon replanting with seed of known count in such concentration that a good crop can be produced. When such a planter is forced to cull his crop then he does not want the small oysters and shell put back on the ground from which he is harvesting them, for their presence there interferes with complete harvesting of the large oysters and it is desirable to have the ground cleaned up as completely as possible before replanting. He may choose to cull out the small oysters for replanting on another bed if their value as seed will offset the cost of the operation. In many instances the undersize oysters and shells are few and the cost of culling would greatly exceed the value of the small oysters as seed. To cull such stock adds greatly to the planter’s cost of production. Hence it is to his advantage to let any undersize oysters and shell go on to his shell pile and thence back to seed beds for further seed production. In this manner he can produce more oysters per year which is the goal of any management procedure. Not all planters operate in the manner described for some are fortunate enough to have bottoms which may produce in a manner similar to the self sustaining natural rocks. However, the application of the cull law to planters who operate on a crop rotation basis serves to limit his production rather than increase it."

PRIVATE CULTURE AND OYSTER FARMING

Bottom Rental

Current harvesting practices for oysters in Maryland's Chesapeake Bay may be placed in the anthropological category of hunting and gathering. Oyster fisheries which thrive elsewhere—in Europe and Japan (Korringa 1976), in Long Island Sound (MacKenzie 1981)—represent the more advanced category of farming. For nearly a century, scientists and informed managers have urged the state of Maryland to open areas of the Bay to private oyster farming; yet the acreage of oyster ground under lease now is minimal: 651 lease holders control about 9,000 acres of bottom (Jensen 1981). This limited area amounts to three percent of the 279,000 acres of oyster ground reserved for public or private use (Jensen 1981). The small proportion is somewhat ironic; in 1830, Maryland followed New Jersey (1820) and Rhode Island (1827) and became one of the first states to recognize private cultivation of oysters when it passed a law permitting one-acre sites for that purpose (Stevenson 1894).

In 1905, Brooks pointed out that demand had outrun the natural supply of oysters. He noted that some harvesting and processing activities added to the depletion of the fishery and suggested that oyster farming could alleviate these problems. For example, spat and seed oysters still attached to market oysters ended up on shell piles outside shucking houses, their death inevitable. A planting industry would find such attached oysters suitable as seed. They would be sold to the planter rather than to the shucking house. Where once the full-grown oyster was the economic prize and the attached small oysters were of no commercial value, now the attached oysters could be of more value than the large oysters and cull laws would be unnecessary. Again, Brooks indicated that the rampant violation of culling laws of his time could be avoided if the harvested shell, spat, and seed could be sold to planters. Similarly, if a demand for oyster shell by oyster planters who would use it as cultch arose, the loss of this valuable resource could be stemmed.

After his extensive six-year survey of Maryland's oyster grounds, Yates (1913) felt very optimistic:

> "It now seems not only reasonable but probable that within the next generation the citizens of Maryland will be leasing and cultivating a probable 100,000 and a possible 300,000 acres of so-called "barren bottoms" where oysters do not now grow in commercial quantities; that the

> more than 200,000 acres of natural oyster bars now reserved for the use of the oystermen as a result of the Maryland Oyster Survey will be so conserved and developed that they will produce as they have done before ore, twice the amount they now yield; and that the oyster industry of Maryland will then be based on an annual production of 20,000,000 bushels of oysters where now it is barely 5,000,000..."

Yates was wrong, not because the Bay was becoming less capable of yielding such quantities of oysters but because sociological and political factors lead to mismanagement and the discounting of biological realities. Dr. R. V. Truitt, the former director of Chesapeake Biological Laboratory, consistently pointed out the potential productivity of the Bay, with its oyster catch in the past having surpassed the beef production of the states surrounding the Bay (Nichol 1937). He felt that farming could have led to the level of productivity aspired to by Yates, for the reasons alluded to by Brooks (1905).

Economists have also been interested in private culture as a rational way of increasing oyster yield. Fairbanks (1932) presented an extensive discussion on the subject, tracing its history in Maryland and making recommendations that it be pursued vigorously. Similarly, Wheatley et al. (1959) suggested that oyster productivity in Virginia's York River could be increased by renting additional ground. Abrahamson (1961) discussed the economic aspects of markets for middle Atlantic oysters.

Wharton (1963) briefly described the natural history of the oyster, harvesting and marketing activities, and oyster laws and their enforcement. He concluded that a history of lack of concern for conservation measures had led to the oyster decline, coupled with the effects of inadequate law enforcement, unhelpful watermen's attitudes, and increased demand that came with improved transportation facilities and packaging techniques. Over time, he noted, Bay-area politicians had dictated oystering policy in compliance with the watermen's wishes. He felt that the state's newly initiated intensive rehabilitation program might help increase production on public beds, but he found it restrictive and costly, requiring controls and higher taxes. The biggest problem, however, was the state's deaf ear to numerous recommendations to allow greater private cultivation.

In a thorough analysis of the oyster fishery in Maryland, Christy (1964) discussed the common property approach to natural resources in general— its effects on the resource, its economic consequences, and its associated public costs. He then dealt with the supply and demand for oysters, before considering the characteristics of Maryland's industry. He considered alternative management strategies and suggested the institution of "exclusive use" rights. This would eliminate the problems of congestion on or overfishing of good areas. Oyster beds would produce economic rent and there would be an economically proper allocation of capital and labor resources. Innovative technology would be encouraged and the public would not to have to bear the costs of cultivation and management. Oyster production could be adjusted with respect to demand. To achieve this goal in the face of opposition by oystermen, he suggested the imposition of gradual restrictions on the number of producers by using direct license limitation and monetary disincentives.

In an informative presentation, Glude (1966) suggested that three criteria be employed to evaluate successful management of commercial fisheries: (1) that the resource be harvested at a profit; (2) that the resource be maintained at a level which produces the maximum sustained economic yield; (3) that each participant in the fishery be provided the opportunity to obtain an adequate share of the harvest. Using these criteria, he determined that management of the oyster fishery in Washington State was successful whereas management of the Maryland oyster fishery was not. The public grounds in Maryland are under heavy fishing pressure, so individual incentive to practice conservation is weak. The catch is restricted only by allowing use of inefficient harvesting methods. Development of private oyster farming has been hindered. Efforts to improve management and the fishery have been hampered by opposition from the fishing industry. Thus the limitations to improved production are social and political. Glude quoted his “Great Law of Fishing” by stating that “Fisheries that are unlimited become unprofitable.” He concluded that the situation could be changed only by “courageous experimentation to develop improved management techniques, and a well-planned system of public education.”

In 1966, the Seafood Advisory Committee of Wye Institute received a report on the Chesapeake Bay fisheries of Maryland from an independent research group of consultants (Quittmeyer 1966; see also section on Rehabilitation Measures). Based on the extensive study performed by the research group, the Seafood Advisory Committee strongly recommended a system of private culture of all oyster grounds except seed areas. The grounds should be apportioned into tracts of a size sufficient to attract private capital and management. Great flexibility in managing such grounds should be allowed to the farmers. The leasing program should be phased in gradually to avoid disruption to self-employment of individual watermen. The interests of these individuals should be recognized and respected but the greater interest of the Maryland taxpayer who subsidizes the oyster industry must also be recognized. The management agency should have the freedom to classify oyster grounds as “seed,” “self-sustaining,” and “growing grounds” and would be allowed to restrict entry to the fishery. The scarce and vital seed areas (mostly on the Eastern Shore) should be designated and used only for that purpose. Access to the common resource should be limited to those seriously desiring to make a living from its harvest and efficiently equipped to make that harvest and help repay the cost of repletion. These actions, coupled with increased rehabilitation of grounds, would result in more oysters per unit of effort, raising the income of watermen. If the recommendations in the report were followed, the committee predicted a doubling of production in five years. The recommendations have thus far not been followed.

Again, Maryland's situation was analyzed by Alford (1973). He discussed oyster bars as a common property resource and described the resulting overexploitation arising from a lack of conservation incentives. He reviewed private oyster culture in the Bay and the restrictive Maryland laws concerning private bottom rental, and described the political influence of Maryland watermen on management efforts. Despite this, in 1965, the private oyster grounds, which then comprised 16% of the oyster-producing bottom of Chesapeake Bay, produced 42% of the total catch. He claimed that another 176,000 acres of cultured bottom in Maryland could provide 10 million pounds of oyster meat if the beds produced as well as those in Virginia did. He noted that between 1960 and 1966, the state of Maryland spent $7 million on oyster propagation, while the industry generated $400,000 from taxes and license fees. In another paper, Alford (1975) put forth a suggestion for interstate cooperation in the oyster industry. He discussed the oyster fishery in general and emphasized the special problems associated with the division of the Bay between Maryland and Virginia. He suggested a variety of mechanisms for increasing inter-state cooperation in order to bolster productivity. This cooperation would include allowing Virginia planters to rent bottom in Maryland waters, and would allow Marylanders access to the (then rich) seed beds of the James River.

Agnello and Donnelley reported on economic and legal factors affecting the oyster industry of the mid-Atlantic (1975a, b). They discussed the impact of three forces (economic, biological, legal) in the decline of the middle Atlantic oyster industry (1975a). A supply and demand model of the oyster industry was developed and the authors concluded that common property characteristics of the industry have harmed the industry's progress. Evidence of overfishing exists in common property states, with sub-optimal exploitation of the oyster resource. This is especially true in Chesapeake Bay states which the authors compared with Delaware Bay states where private culture is more common. They noted (1975b) that allowing for a mix of private and common property rights would result in higher ex-vessel prices and more stable intraseasonal price movements.

The ability of oyster grounds to yield increased harvests under even the most elementary of culture conditions is described by MacKenzie (1981) for Long Island Sound. Because growers began providing more clean shell cultch, kept removing two dominant predators from oyster beds, and took steps to prevent smothering by silt, yield in Connecticut increased 85 times from 1966 to 1972.

Part of the problem associated with common property resources appears to involve the fact that no one who participates in the fishery has any incentive to reduce his catch or cultivate the grounds, since there is no guarantee that other participants would do the same. This dilemma has been referred to as the "tragedy of the commons" by Hardin (1968), and this analysis has been applied to the Maryland oyster industry by Power (1970 — however, see Godwin and Shepard, 1979, for another perspective on the "tragedy of the commons").

Sometimes, pursuit of the common resource can be counterproductive to the common good and leave those dependent on the resource fearful for their stability. In late 1980, for example, a Maryland waterman told the Easton *Star-Democrat* newspaper that divers (as a new harvesting technique) were cleaning the bottom of oysters, leaving few for spawning. Faced with this dilemma, the watermen felt little recourse:

> "But if everyone else is doing it, then I'm going to put a diver on my boat, too. What else can I do? As long as the oyster business is being ruined anyway, I've got to get what I can, there's no other way."

It is understandable yet disheartening to note that this watermen's view of and response to the problem are not unique. Indeed, as the section on Historical Background suggests, watermen and their representatives remain unconvinced of the destructive power of overfishing or of the usefulness of private culture as an alternative way to bolster oyster-bed productivity. The very subject of rental of oyster ground has traditionally been an emotional one: though he did not mention the state, Galtsoff (1958b) reported being physically threatened after a small town meeting where he advocated private oyster leasing.

Maryland enjoys a unique situation because Chesapeake Bay has been a prolific producer of oysters. Its lower salinity habitats preclude most diseases, pests, and predators that deplete oyster grounds in higher salinities. Yet the industry is a shadow of what it was —and what it might be. Commenting on the problems of getting scientific insights incorporated into social action, Bowman (1940) used the Maryland oyster industry as an example. He cited the large amount of scientific material collected on the oyster and Brooks' recommendations concerning the management of the industry. He said that the legislators had ignored all these data and recommendations, preferring to consult "practical" oystermen. He described the results as a failure.

There appear to be three main reasons for watermen's resistance to private development of Maryland oyster grounds. Two have been voiced for some time (Commission of Tidewater Fisheries 1948), but the third appears to be more recent.

The first objection is that privately cultivated oysters will increase the harvest so much as to depress the market, bringing down the price of publicly harvested oysters. The 1948 Commission noted that farmed oysters from the Bay proper (it did not then recommend leasing tributary grounds) would be larger animals, and thus not directly competitive with standard oysters from the tributaries. It also noted that Maryland once marketed an annual production of 12-15 million bushels to an American population half the size of that in 1948; proper marketing, it said, should be able to sell any increase from private cultivation.

The second objection stems from the fear of encroachment by big business and the possibility that the traditional, individualistic way of life of the people who work on the water will be endangered. If, as a matter of social policy, it appears important to maintain productive tonging bars, or to encourage dredging by sailboat, or to maintain a “tidewater way of life,” suitable legislation could be enacted to sustain these things, while at the same time encouraging private cultivation. The economic advantage that would accrue to tidewater communities from private cultivation—increased supply and demand for oysters, year-round work opportunities, the circulation of more money within the communities—as outlined in earlier references, appears to be substantial.

The third, and apparently more recent, argument is that a potential major bottleneck in increasing oyster production lies with actual processing of the catch rather than with harvesting. Some watermen have claimed that the lack of shuckers and processing machinery will “back up” the distribution of the supply, and overload the present processing capacity. But this may be a chicken-before-the egg complaint. Presumably, any increase in private farming would result in slowly increasing oyster yield. That in turn would stimulate more intensive research into shucking and processing machines. Oysters are basically solid meat within a hinged calcium-carbonate box. Yet crab processors now use a machine which picks meat out of many shell compartments in a crab body. Processing blue crab meat seems more difficult than removing oyster meat in that the meat lies within these various compartments and the shell breaks easily. We expect that the major problem of opening oyster shells will be solved, especially if a growing supply and growing demand-encouraged by better marketing and production-can be counted on by food processors.

Oyster Aquaculture in Maryland

Farming oysters has been underway in a number of nations for many years, with excellent results (Korringa 1941, 1976). For example, around 1860 France started to study methods of improving spat collection and began leasing oyster grounds. Many European countries and some areas of the United States followed suit. In Holland in the late 1800’s, the oyster grounds were withdrawn from the free fishery and private culture began; this led to an unexpected revival of the oyster industry there. Not all problems were solved, and some regions continued to decline.

In most instances, oyster farming has followed the decline of natural oyster populations. Thus, although Maryland watermen have resisted the concept of renting oyster grounds for nearly a century, it would seem inevitable that a system allowing for rational utilization of the Bay’s oyster growing potential must eventually prevail. As noted earlier, Dr. R. V. Truitt, former director of Chesapeake Biological Laboratory and a long-term investigator of oyster biology in the Bay, was fond of comparing the Bay’s oyster producing potential with the production of dressed beef from terrestrial farms. For example, in his foreword to a report by Nichol on the oyster-packing industry of Baltimore (Nichol 1937), Truitt noted that the oyster yield (as he wrote) had averaged about two million bushels over the past few years, compared with a yield of 15 million bushels in the previous century. The difference of 13 million bushels in terms of shucked meat was equivalent to a herd of 160,000 head of large steers, each dressing 600 pounds including meat and bone. Truitt noted that this quantity of beef exceeded that produced on Maryland's farms at the time. Thus, the decline in oyster production was greater than Maryland's beef production, yet the potential productivity of the Bay with regard to oyster production was not being tapped. The same situation exists today. Even though pollution has undoubtedly affected a greater proportion of Bay waters than in Truitt's day, one would expect the Bay to be able to sustain a greater harvest than it presently does if management and harvesting practices were changed to take advantage of what we know about oyster biology.

Bottom Culture

Should farming of oysters be encouraged in Maryland, it could take two directions. The first is the rental of Bay bottom (preferably good areas rather than the marginal grounds now available) to entrepreneurs who would undertake to cultivate it to produce maximum yield, just as a farmer cultivates his land. And, just like the farmer, the oyster grower would need to apply principles common to animal husbandry or plant production. For such activities, the oyster farmer would need to understand the fertility of his grounds. He would have to assess the food supply available for seed oysters and adults if he hoped to rear seed to market size. If he decided to depend on natural set to provide him with seed (a riskier proposition), he would need to understand the past history of the region with regard to dependability of set. Presumably, the state would have delineated those areas of the Bay that had dependable set and those that were good for fattening and growth. Once natural set or purchased seed were in place, the farmer would have to monitor for pests and disease organisms (fortunately a lesser problem in most of Maryland's waters than in higher salinity areas of the Bay). Because of capital and (especially) labor costs, it might be necessary to automate systems for cultivating the bottom, eliminating pests, evaluating oyster growth and condition, and harvesting each year's crop. Presumably, good husbandry practices would include complete harvest of all oysters from the bottom at the appropriate time, followed by reconditioning of the bottom as necessary. Further, a system of rotation of "cropland" might be necessary as it is on land. The carrying capacity of the grounds (i.e., number of oysters optimal for good growth per hectare) would need to be determined. In other words, a thorough knowledge of local grounds and of the behavior of oysters in each locality would be required. Such information should be readily available if correct management principles were being followed, for how can we manage what we do not understand? The absence of such information might discourage individuals from undertaking oyster farming; it would certainly slow down such an undertaking. But eventually a core of information would accumulate as more and more people became involved in oyster farming. The general subject of molluscan farming is explored further by Loosanoff (1972).

So far we have been speaking of on-bottom culture. Off-bottom culture of oysters often results in greater yields, fewer pest problems, and easier harvesting.

However, it also is beset with legal difficulties and it can be very labor intensive. Little exploration of this topic has occurred for Maryland's waters (Shaw 1966a, 1969, 1970, 1972; Shaw and Merrill 1966) but it appears that off-bottom culture in Maryland might be made commercially feasible, although more detailed economic analyses are necessary. A more general summary of the subject of oyster culture from rafts in east coast estuaries is provided by Aprill and Maurer (1976). More recently, Walker and Gates (1981) reported on an innovative approach to string oyster culture in Narragansett Bay, using saltmarsh ponds with artificially prolonged tidal flows. Economically, the internal rate-of-return ranged from 6.8% to 26.3%, with room for improvement.

Aquaculture or Seed Culture

The second direction possible in oyster farming is the employment of aquaculture techniques to spawn and rear seed which can then be placed in the Bay to grow to market size or which can be sold to other oyster farmers. The lack of seed in Chesapeake Bay is a major problem facing resource managers. Aquaculture technology is well advanced and several books are available for general use (e.g., Walne 1974, Korringa 1976), and a number of regional "hatchery manuals" have been produced (e.g., Pacific oyster - Breese and Malouf 1975; New Zealand oysters - Curtin 1979).

With regard to Chesapeake Bay, Dupuy et al. (1977) have produced a detailed, useful manual for rearing oyster larvae in hatcheries. In Maryland, Hidu et al. (1969) reported on a series of trial experiments in the low salinity (10-20 ppt) area of Solomons. They considered conditioning and spawning of adults, rearing of larvae, and handling of spat, and made numerous recommendations, concluding that commercial hatcheries appeared to be biologically feasible in the Chesapeake Bay area.

Some of the conclusions and recommendations of Hidu et al. (1969) can be summarized as follows:

1. *Conditioning and Spawning*. Low salinity stocks of Chesapeake Bay oysters can be conditioned starting in February by placement in running Bay water (0.5 L min^{-1} per dozen oysters) at 24-26°C. Parallel brood-stocks can be established at two-week intervals. Visual inspection of gonads of selected oysters would indicate success of this regime. Four or five weeks after conditioning started, spawning can be attempted. In late spring or summer, field stock can be collected and held at 20-22°C for a week before spawning is attempted. Spawnable oysters can be held in late fall through winter at 20-22°C in running water.

2. *Larval Rearing*. The technical details of culturing fertilized eggs and larvae, of changing water and feeding larvae, etc., need not be repeated here. Essentially, scrupulous cleanliness is required, a suitable temperature regime is necessary for good growth of larvae but not bacteria,

screening of larvae for size is necessary for selection of rapid growers, and sufficient food and antibiotics are needed for larval growth and control of bacteria.

3. *Handling of Spat*. Young spat (a few days to a few weeks old) need protection from predators (crabs, drills, flatworms) in the field. (For example, Krantz and Chamberlin (1978) studied blue crab predation on cultchless oyster spat. From an examination of broken oyster shell taken from field plots and of shells destroyed by blue crabs in laboratory tanks, they concluded that high mortalities (79-99%) of spat (size range 6 mm-25 mm) occurring within one month of planting in the field were probably attributable to blue crab predation.) Spat undoubtedly must be held in a hatchery or outdoor troughs (usually a costly action) until they reach a size sufficient to resist attack by predators or should be placed in the field in cooler months when predators are less active or are absent.

In addition to biological considerations, economic factors involved in hatchery operations must be carefully considered. A pilot-scale hatchery operation has been underway at Horn Point Environmental Laboratories to provide insight into labor, energy, and capital costs for such a commercial scale facility. Unfortunately the hatchery was built by the state in an area which was declared to be less than optimal by oyster biologists who were consulted (salinities are lower than those found at better sites in Maryland's Chesapeake Bay). In spite of its sub-optimal location, operation of the hatchery has yielded some information on manpower and operational requirements (Lipschultz and Krantz 1978). Labor was the major cost component, although the study year (1976) was one in which energy costs were much less than they are at present. The data need updating, but the model is a useful first step in the important project of estimating costs of hatchery activity. It is encouraging that a number of commercial oyster hatcheries (albeit small ones) have operated in Maryland for a number of years.

Some recent papers on West Coast aquaculture practices by Lannan (1980a,b,c) and Lannan et al. (1980) provide excellent examples of the sort of information that is needed in Maryland concerning broodstock management of C. virginica for hatchery use. These papers consider larval survival of *C. gigas* in hatcheries and attempt to optimize such survival by various biologically sound practices such as broodstock conditioning and selected mating. Lannan (1980a) found substantial variation in larval survival. The variation was due to genetic and non-genetic factors. The non-genetic factors appeared to be subtle environmental differences in the rearing systems. Genetic influences involved regulation of gametogenesis and timing of spawning. Lannan et al. (1980) showed that, to achieve maximum larval survival, gametes needed to be released at a certain optimal stage. Time-course conditioning trials revealed an optimum conditioning interval during which the proportion of viable gametes is at a maximum. Matings which occurred before or after this optimum interval resulted in reduced gamete viability. This was reflected in reduced setting success.

Clockwise from top: Oyster cultivation in trays by an individual waterman. Young oysters in raceways at a research-oriented, pilot-scaled hatchery at Horn Point Environmental Laboratories. Setting-tables containing spat and cultch in the State-run oyster hatchery at Deal Island.

Careful observation could determine if such optimum intervals exist for C. virginica If they do, one would need to know the annual gonadal cycle of one's brood stock to take advantage of them. Then one would choose the appropriate conditioning regime, including temperature. Finally, the optimum conditioning interval at the chosen temperature would have to be determined empirically, depending upon the season. In addition, the suitability of various parental lines would need to be determined (Lannan 1980b). It may be that some lines reach optimal spawning condition at a period that is different from other lines. The mating of lines reaching optimal spawning condition at the same general time period would produce better larval survival and spat settlement than would the mating of lines not in synchrony.

Finally, the legal aspects of closed-cycle aquaculture have been examined by Bockrath and Wheeler (1975). They discuss potential problems with such systems in Maryland which may result from the wording of Maryland legislation that was developed before such aquacultural systems were envisaged. The principal problems include vagueness in the wording of some statutes regulating the natural fishery, apparent inhospitality to corporate investment in fishery resource activity, and the lack of any reference to such systems in the laws which deal with private oyster culture. The authors conclude that entirely new statutes are needed if Maryland wishes to encourage closed-system mariculture development.

A Glutted Market

We have referred to the concern of watermen and processors that the potential exists for markets to become glutted if oyster production rises above present levels. They appear to feel that increased supply of oysters will outstrip demand, resulting in depressed prices.

Though economists can provide better detailed analysis of this potential, we can take note that past demand for oysters was much greater than it is now. For example, Nichol (1937) pointed out that theater-goers in Baltimore once ended their evening with oyster stew in oyster parlors, and that oyster suppers were an elite form of hospitality, especially at Thanksgiving and Christmas. Engle (1966) commented that he recollected having oysters as a family meal at least once a week, and that they traditionally appeared in the dressing of holiday fowl and as oyster stew on Easter morning. Yet, as the population increased, oyster production and consumption decreased, leading to the loss of the tradition of eating oysters at home or as aperitifs when dining out. Bryan (1949) noted that in 1912, per capita consumption was five times what it was in 1949; when the U.S. population was half that of 1949, Maryland sold seven times the number of oysters in the 1949 harvest at a profit.

It seems reasonable to conclude that scarcities and resultant high prices lead to the loss of the habit of eating oysters. This would seem to hurt industry more than the "problem" of having plenty of oysters available at moderate prices. Suitable marketing strategies should be able to expand demand for such a nourishing food as oysters, especially if prices were moderate and competitive with other meat sources. New methods of preparing oysters might also serve to attract potential customers who would otherwise refuse to eat oysters in their more traditional raw or stewed form.

SPATFALL PREDICTION

Each spring in Maryland's portion of Chesapeake Bay, the Department of Natural Resources pays contractors to have large quantities of oyster shell dumped overboard at different locations (Outten 1980). This shell serves as cultch for oyster larvae which require hard surfaces when they settle to begin their benthic existence. Since Maryland's most recent program of shell and seed planting began, 120 million bushels of shell and seed have been handled at a cost of about $24 million (Outten 1980). The cost of planting an acre of bottom with shell varies from $550 to $700 (Outten 1980).

Some of the shell ("fresh") is purchased from oyster packers, who are under no obligation to sell to the state. Obviously, not all of the fresh shell which is removed from the Bay annually in the oyster harvest is returned, since oysters are exported in-shell. Additional use is made of "dredge" or "fossil" shell mined from deposits located in the muddy bottom of the Bay. These finite resources will eventually run low because dredged shells are an exhaustible resource (Outten 1980) and the amount of fresh shell returned to the Bay is less than the amount harvested. Given the cost to the state and the continued depletion of shell resources, it is important that the cultch be used carefully in order to get the maximum return (in spat settlement) for the money expended.

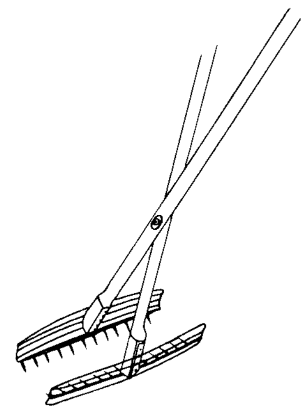
The importance of cultch material has long been understood by oyster farmers and biologists. In 1855 in Connecticut, shells for catching spat were deployed on the northern shore of Long Island Sound (Galtsoff et al. 1930). Brooks (1905) remarked that part of the reason for a decline in the oyster resource in Chesapeake Bay was the absence of enough clean shell on beds as cultch. He advocated an end to the use of shells from shucking houses as road-building and lime-production material; they should be returned to the Bay as cultch. Galtsoff et al. (1930) claimed that reasons for the decline in the annual crop of oysters on the U.S. East Coast included the failure to return sufficient quantities of shell to the oyster beds. In Europe, planting of oyster shell as cultch material had been practiced for decades (Korringa 1941).

It has also been common knowledge that placement of the cultch in the water must be timed carefully. If the cultch is placed too early-before the larvae are ready to settle—it may become fouled by bacterial slimes which are unattractive or repellent to larvae, or by invertebrates which compete for setting space with or prey upon the mature oyster larvae (Nelson 1908, Sieling 1951, Manning 1953, Beaven 1955, Engle 1956, Wisely et al. 1978, Steinberg and Kennedy 1979). Indeed, Korringa (1941) claimed that, after about 12 days, cultch becomes unsuitable for settling by larvae of the European oyster, *Ostrea edulis*. However, no such time limit for cultch in Maryland's Chesapeake Bay has been determined (Sieling 1951, Manning 1953, Beaven 1955, Engle 1956). Obviously, if cultch is placed too late to catch the peak or peaks of larval settlement, the money involved in its placement will have been wasted and the planted shell may become so fouled that, when the next year's settlement period occurs, the shell may only be minimally attractive.

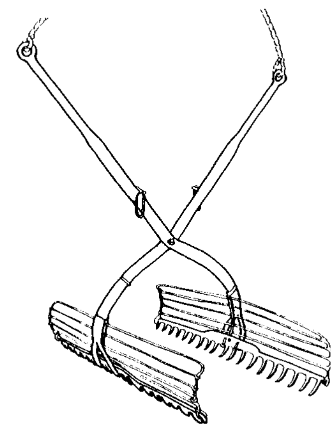
The period of main oyster settlement in any region is notoriously variable, which means that the placement of shell according to the convenience of human suppliers or management personnel may result in placement too early or too late in the season. For example, as part of Sea Grant-supported research in the summers of 1977 to 1979, one of us (VSK) monitored the periods of spat settlement in two tributaries of the Choptank River, i.e., Broad Creek and Tred Avon River (Kennedy 1980). In Broad Creek, two peaks of settlement occurred in 1977, in late July and late August. In 1978, a small peak of settlement occurred in early August. In 1979 there were two peaks again, this time in mid-June and early July, with few spat being found thereafter. In Tred Avon River in 1977, spat numbers were very low until a small peak of settlement occurred in late September which was later than settlement occurred in Broad Creek. In 1978, almost no spat were noted on plates in Tred Avon River during the period of study. There were three peaks of abundance in 1979 (late May, mid-June, early July), after which settlement was negligible. From this information it is obvious that, if cultch was planted in these areas in June as a matter of economic and logistical convenience, it would have arrived "too early" in 1977 and 1978 in both tributaries. It would have been "on time" in 1979, although it would have missed the first peak of spat settlement in Tred Avon River. Thus, it would seem desirable to have a method of predicting the proper time to place the cultch.

This is not a new insight. In 1874, Winslow (based on his work in North Carolina and Connecticut) stated "...thousands of dollars could be saved annually by the oystermen if they would determine with any approximate accuracy the date when attachment of the young oysters would occur." (quoted by Korringa 1941). In New Jersey, J. Nelson (1909) tried to predict the probable date of setting of C. virginica by studying the stages of development of larvae in the water. His son, T. C. Nelson (1917), stated that it was possible to predict setting time in New Jersey waters within two days of the event. The French initiated such studies in the 1920's, followed by the Dutch in the 1930's (Korringa 1941). In Holland, Dutch oyster farmers paid close attention to the studies and predictions of the government supported biologists when preparing to place spat collectors in the field (Korringa 1941). The application of such predictive techniques has spread to western Canada ("...In British Columbia no cultch is exposed before a forecast predicts a spatfall of commercial intensity." Quayle and Terhune 1967b, p. 1); Japan (Wisely et al. 1978); New Zealand (Dinamani and Lenz 1977); and the northwestern U.S. (Lindsay et al. 1959).

In all these areas, hydrographic conditions and aspects of larval activity and distribution tend to differ. For example, in British Columbia 95% of the oyster larvae (*C. gigas*) occur between the surface and a depth of 10 ft (3 m) (Quayle and Terhune 1967a), unlike the situation with C. virginica in Barnegat Bay and Delaware Bay (Nelson 1953,1955, Kunkle 1957). In the state of Washington, setting of *C. gigas* larvae and the predictability of setting vary with the presence of a stable, warm surface layer of water (Westley 1968). The variability of hydrographic conditions and larval distribution in other regions has been discussed by Korringa (1941).

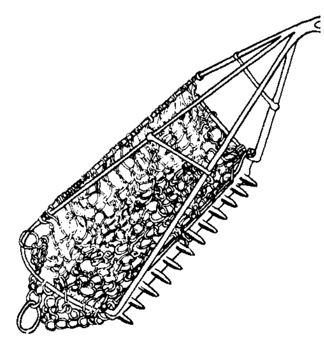

Oyster tongs

It is, therefore, not a foregone conclusion that one can predict spat settlement details wherever one might choose to do so. In the state of Washington, it is considered necessary to (a) measure hydrographic conditions; (b) determine when spawning occurs; (c) observe distribution and abundance of larvae; (d) follow progress of larval groups in plankton; (e) make setting predictions by using present findings and comparing them with past data; and (f) evaluate predictions by observations on eventual distribution and abundance of set (Lindsay et al. 1959). The possibility of transference of this predictive ability to Chesapeake Bay has not been demonstrated.


Patent tongs

If the state of Maryland finds it increasingly important to conserve money and shell in its planting program, as we believe it undoubtedly will, it will be important to know when to place the cultch for maximum benefit. This is no more or no less than what is done elsewhere. Second, if private farming of oyster bottom increases in the state, as we believe it must if the industry is to thrive, then oyster farmers in Maryland will be no less in need of predictions for collecting commercial quantities of spat than are their compatriots elsewhere around the world. Indeed, given the logistical difficulty Maryland would face in stockpiling shell and placing it overboard in a limited period of time, it is clear that the most efficient system would involve a large number of individual oyster farmers who would see that their own smaller holdings were shelled at the right time.

FISHING GEAR


Oyster dredge

The commercial oyster fishery in Chesapeake Bay relies upon fishing gear which has not changed, or has changed very little except for the use of patent tongs, in more than sixty years (See Figure 6). The origins of at least one gear type, hand tongs, can be traced back to the traditional gear used in fisheries on the west coast of England and imported by the early colonists (Carey 1970). The three main methods used on the public oyster grounds of the Bay are dredging, patent tonging, and hand tonging. Both Churchill (1920) and Sieling (1950b) have written excellent reviews of these fishing methods and gear, the latter containing especially good drawings and photographs. These types of gear vary in efficiency, the oyster dredge being the most efficient device of the three (Sieling 1950b; Maryland Board of Natural Resources 1953). However, all three of these fishing methods are less efficient and more labor-intensive than other methods involving use of escalator and hydraulic dredges (NOAA, Office of Fisheries Development, 1977a,b). A mechanical escalator harvester, developed from a conventional Maryland soft clam dredge, can harvest 500 bushels of oysters an hour while being operated by only two people (Haven et al. 1979).

Tonging oysters before 1919.

Dredging oysters from a skipjack in 1980.

Tonging oysters in 1980.

Figure 6.

The more efficient methods, while frequently illegal or restricted on public grounds for conservation reasons (Sieling 1950b), can often be used by growers on private or leased oyster grounds in other states (NOAA, Off. Fish. Dev., 1977b). Oyster farmers on the Pacific Northwest and Long Island Sound use large, barge-mounted dredges which effectively harvest oyster beds. Some hydraulic dredges can yield an average of 1,400 bushels per day per man (NOAA, Off. Fish. Dev., 1977a). In addition, studies at Willapa Bay on the West Coast are continually seeking to improve oyster cultivation methods by developing new methods or techniques, or new uses for existing equipment. For example, the use of the traditional English pasture harrow on oyster beds has been found to increase spat settlement, control fouling growth, and prepare the oysters for harvesting (Sayce and Larson 1966).

In a recent paper, Haven (1981) described modern gear that can increase harvest efficiency; the gear included automatic culling machines, mechanized seed planters, and oyster harvesters.

DREDGING IN OYSTER CULTIVATION

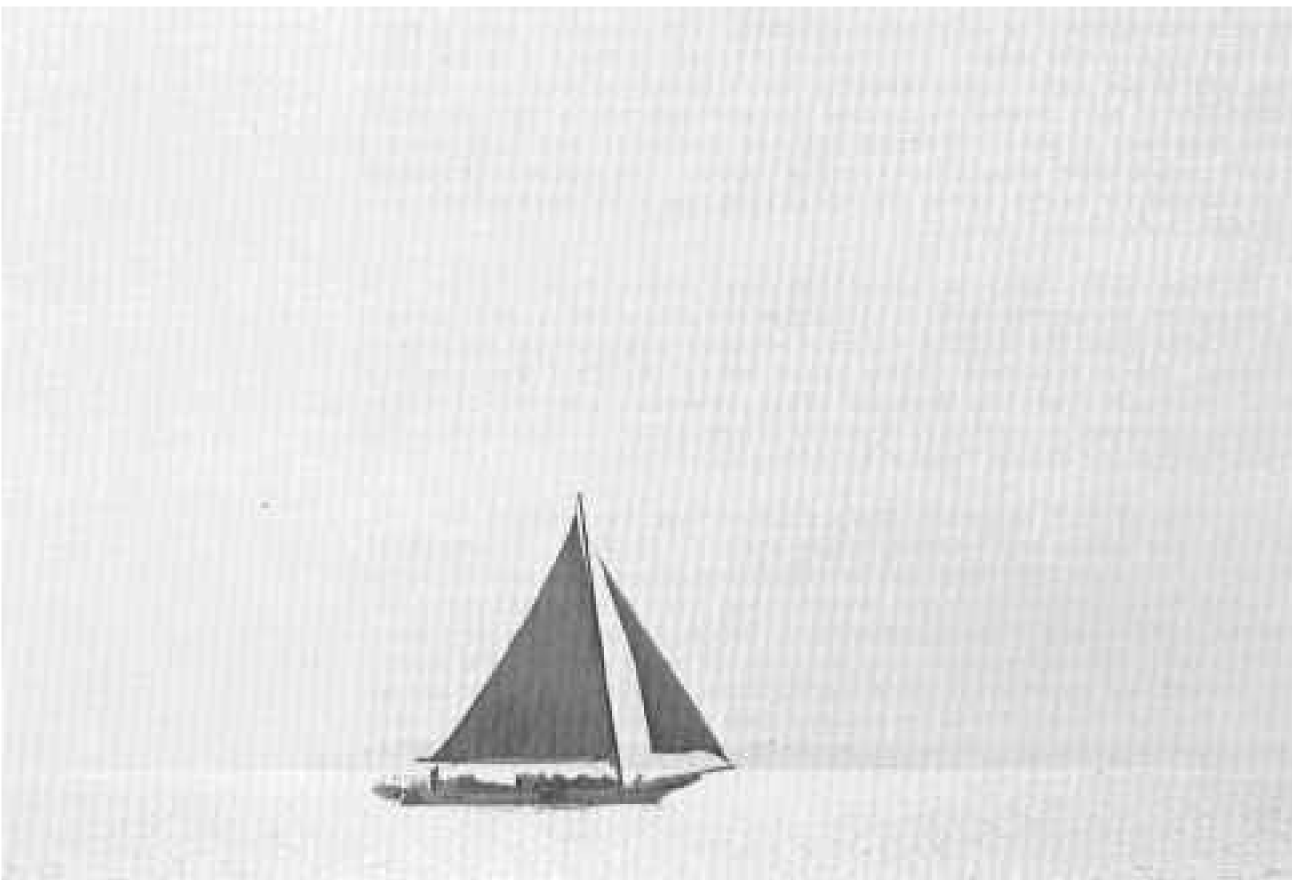
Ingersoll (1881) considered the advantages and disadvantages of dredging as a management or cultivation practice. The consensus among those who had studied the subject was that, if properly conducted at the right time and in the right place, dredging was a beneficial practice. Undisturbed oyster bars tended to become consolidated into a rigid structure which was hard to work. Dredging broke up the “rock” and scattered the oysters over a wider area, thus extending the bar. The provision of greater area allowed for better oyster growth and may have provided greater surface area for spat settlement.

Winslow (1881, 1882) concurred with these observations. By the time of his survey, the oyster grounds in Tangier and Pocomoke Sounds had doubled in area from the original compact vertical configuration because of dredging. Given moderate fishing effort before the Civil War, the beds were continually improving (Ingersoll 1881). However, after the Civil War, dredging increased in intensity, resulting in a depletion of about 80% in Pocomoke Sound and 66% in Tangier Sound (Ingersoll 1881).

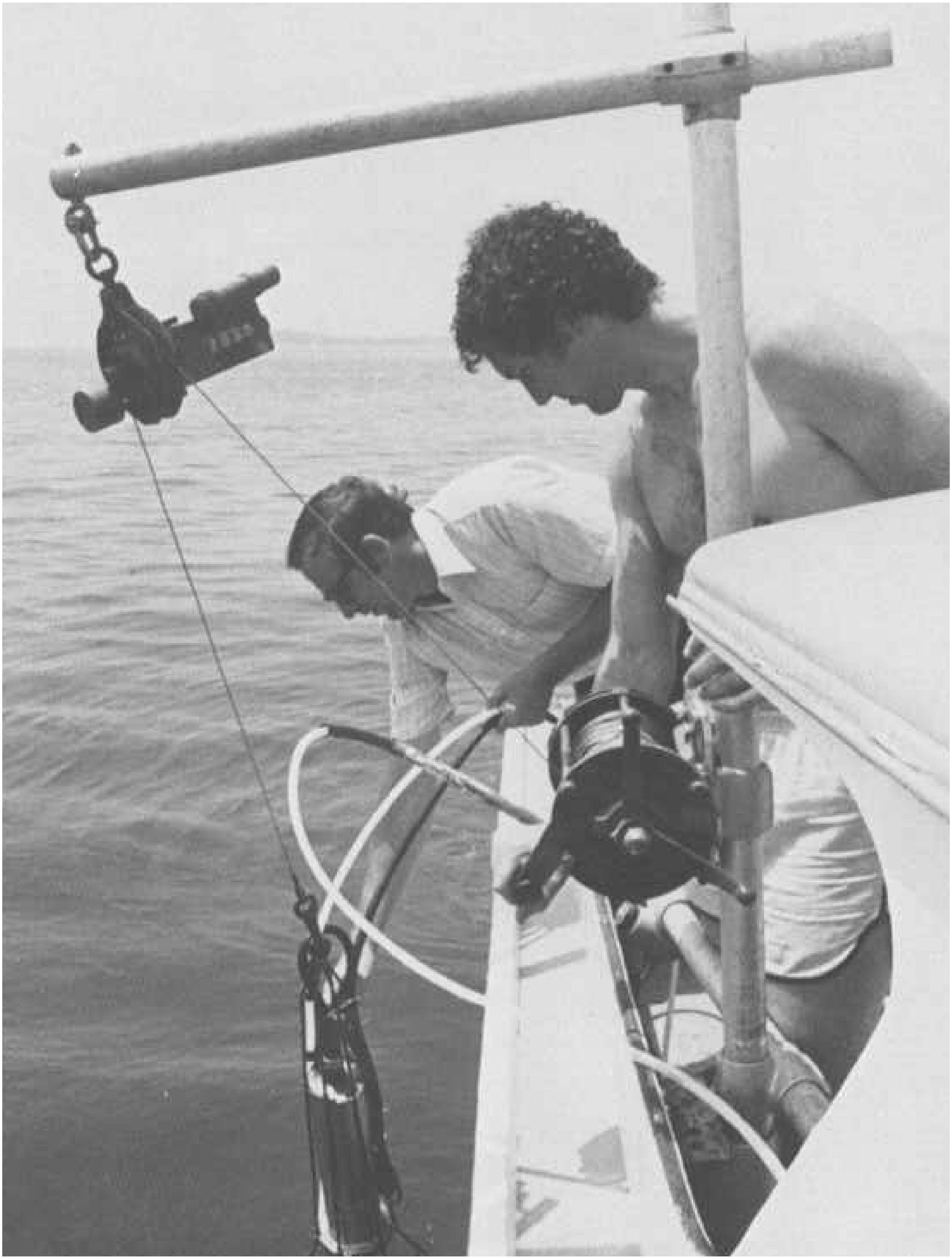
Because of such depletion, many claimed that the dredgers were responsible for killing and crushing young oysters. However, Brooks (1905) disputed this claim and noted that private leaseholders who farmed oysters in Connecticut used much larger dredges than were used in Maryland, apparently with benefit to their oyster beds. Brooks presented his own observations that, although dredges may break or kill small oysters, the number was limited and probably of little significance. Because the spat are attached flat on the substrate, he thought they thereby avoided being damaged. As they grow they project more and more above the substrate but by then their structural strength should have increased.

The subject of using dredging as a cultivation tool was explored in some detail on *Ostrea edulis* beds in England by Waugh (1972) with conclusions contrary to those of Brooks (1905). In England, it was the practice to use harrows to turn shells over to kill epifauna and expose clean surfaces for spat settlement. Over a number of years, Waugh performed a variety of field experiments using harrows. He found that, while oyster condition on harrowed beds was not affected, growth was significantly less compared with that on control beds. He cautioned against harrowing without care on stocked grounds because of the shell damage that might ensue. Shell damage results in slowed growth. On grounds that had been shelled, harrowing did not appear to result in increased recruitment. There seemed to be no increased mortality because of harrowing.

Waugh's (1972) work appears to be the most extensive reported. Its transferability to the situation with Crassostrea *virginica* is not clear. Our impression is that American oysters tend to have stronger shells than do flat oysters, thus they may be subject to less mechanical damage from dredging or bagless dredging. The subject needs further careful experimentation in Chesapeake Bay. Note that the pasture harrow has been used in Washington state with the result that settlement of *C. gigas* larvae has been enhanced (Sayce and Larson 1966).



Research



Questions for Further Research

The commercial importance of Crassostrea *virginica* has stimulated much research into its biology and management in North America. Numerous studies of varying degrees of thoroughness and quality have been performed over the past century (Breisch and Kennedy 1980). Yet, many questions, some more important than others, remain.

That we have such a shortfall in knowledge after so much research attests to the immensity of the job of understanding even one species and its niche in nature. The complexity of interaction in a system such as Chesapeake Bay is great. The broad role of a dominant species such as the oyster requires careful, extensive, and lengthy analysis. This creature initially has a role as a pelagic larva which may become food for any of a variety of pelagic or benthic predators. As a pediveliger it competes with other epifaunal species for limited hard substrate. As a settled oyster its shell becomes that hard substrate. As it grows it filters great quantities of water, preys on or at least filters out plankton, consolidates sediment, and produces fecal and pseudofecal material which smothers some creatures and serves as food for others. By concentrating trace materials, it may serve as a sink for pollutants. It is a target for parasites and disease organisms. As a commercial species, its harvest supports an important economic infrastructure involving thousands of people.

These and other facets of the oyster's life and role in estuarine ecology and human culture have formed the basis for this report. We have drawn together a number of questions that remain to be answered, questions that indicate areas that need more study. We have tried to avoid trivial questions but have included a number that are of "academic" or basic interest because, we believe, the best management depends on a great depth of understanding of the oysters' biology and ecological relationships.

The questions are grouped roughly according to the order of sections of our review. However, a number of questions (e.g. the influence of low salinity on feeding and thus on gametogenesis, spawning success and resultant larval vigor) cut across that listing (in the example just given, the question involves salinity,

Scientists an a research vessel obtain a water sample to study the movements of oyster larvae in the plankton.

food and nutrition, reproduction, and larval biology). Such questions appear in the section we think most appropriate. There may be some overlap.

Oyster Biology

There is need for research into physiological adaptations of eastern oysters to various environmental factors throughout their distributional range (Canada to the Gulf of Mexico). The results could be significant for aquacultural activities, if the environmental plasticity and resilience of various oyster stocks can be exploited in culture. Studies might include responses to temperature, salinity, and sediment load. Other studies would consider disease resistance, growth, rapidity of attaining maturity, fecundity, spawning stimuli, larval vigor, feeding efficiency, etc. over a wide geographic range. The genetic exploitability of such adaptations could then be investigated.

Temperature

What are the upper and lower lethal temperature limits for adults, spat, and larvae? How does temperature influence physiology or activity-feeding, growth, condition, susceptibility to disease, larval swimming, and settlement in the field-over the distributional range of C. virginica? In terms of aquaculture, for specific geographic regions or broodstocks of oysters, what influence does temperature have on shell deposition, increase in meat weight, food conversion efficiency, resistance to parasites and disease, sublethal stress in adults and resultant larval vigor?

Is spawning initiated by temperature change, either slow or rapid increase? Is it influenced by temperature only in some areas of the oysters' range and by other factors (e.g. food supply) elsewhere? Why is it apparently easier to spawn oysters from more northerly populations (say New Jersey north) than from more southerly populations (below Chesapeake Bay)?

Salinity

What mechanisms are involved in the apparent influence of adult acclimation salinity on salinity tolerances of larvae? How does salinity affect larval, spat, and adult growth and gametogenesis and spawning in adults? Is it by the imposition of physiological stress, or by some indirect influence either by inhibiting oyster feeding (Butler 1948), or by leading to changes in phytoplankton that are unacceptable to oysters?

In Chesapeake Bay, does recruitment to oyster populations in low salinity regions (<10 ppt) depend on influx of mature larvae from higher salinity areas (Davis 1958)?

Rainfall

In Chesapeake Bay, does copious late winter-early spring rainfall followed by late spring-summer drought conditions lead to enhanced nutrient input and phytoplankton growth, followed by excellent larval survival and retention in good setting areas?

Sediment

In Chesapeake Bay, how does silt affect survival of all life history stages of oysters? Are there seasonal effects which might prove detrimental, for example, by combining stress from high temperature or low salinity with stress from silt coverage? If so, how could this stress be mitigated in oyster farming? Has the apparent increase in siltation in Chesapeake Bay in recent decades been a factor in oyster resource depletion?

Dissolved Oxygen

In Chesapeake Bay, what role do low levels of dissolved oxygen play in affecting larval survival and settlement? Are areas of poor spat settlement success the result of low dissolved oxygen levels during summer?

Light

What is the role of light in stimulating or inhibiting larval behavior? Do larval responses to light alter with age, or with variation in other environmental factors such as temperature, salinity, pressure, etc? Have apparent changes in turbidity and therefore light transmission in Chesapeake Bay altered larval behavior (swimming, settlement) and, if so, how?

pH

Does heavy siltation, which is reputed to result in lowered pH, thereby affect oyster recruitment (Calabrese and Davis 1966)?

Chemicals

The influence of a wide range of anthropogenic chemicals needs to be measured for all life history stages of the eastern oyster. Both direct effects (toxic levels leading to death) and indirect effects through inhibition of feeding or respiration, etc. need to be known. Effects on growth, reproduction, and spat settlement need to be understood. As with natural environmental stress, chemicals may stress adults with resultant production of larvae with reduced vigor. Synergistic effects need to be assessed.

In addition to direct effects on the animals themselves, we need to understand the influence of chemicals on quantity and quality of oyster food. Chemicals which may not directly affect oysters in any measurable fashion may have a major impact if they affect the oysters' food source deleteriously.

Is chlorine so harmful to oysters that its increased use in Chesapeake Bay has contributed to population declines?

What control mechanisms are involved in manganese dynamics in relation to shell deposition, feeding and spawning in oysters (Frazier 1976)?

What are the synergistic effects involving different metals with each other and with other kinds of pollutants (e.g. PCBs, petroleum hydrocarbons, etc.)? What is the role of salinity in such synergisms, or in heavy metal uptake in general? Is there a transfer of metals and accumulated toxins from female oysters to their eggs? If so, what is the result on fertilization and subsequent growth of the young? Ultimately, is the reproductive performance of the population affected? What are the effects on oyster populations of chronic sublethal stress caused by heavy metals and other toxins? Are there mutagenic and other genetic effects as a result of exposure to heavy metals?

Food and Nutrition

What do larval and adult oysters feed on in Chesapeake Bay today? Has their diet changed appreciably from that reported by Morse in 1944? Is there a seasonal pattern of diet with different dominant species of algae? Has there been a change or decline in phytoplankton species, similar to that observed in submerged aquatic vegetation populations? Have conditions favored less nutritious algal species at the expense of "good" algal species? Have suspended silt concentrations in Chesapeake Bay increased over time to the point that they adversely affect oyster feeding mechanisms?

Are there great variations in the carbohydrate content in natural populations of phytoplankton as there are in laboratory cultures? Are these variations seasonal? How do they affect oyster condition and growth? What are the relative food values of both natural and artificial diets? What are the rates of ingestion of these foods?

What are the biochemical aspects of nutritional requirements? Can vitamin supplements of artificial or natural diets increase growth rates and oyster condition? How are dissolved substances accumulated? Do they have an important nutritional role? Are dissolved substances which are adsorbed onto inert suspended particles made more or less accessible to oysters? Can oysters "taste" their food and, if so, how does this ability affect their choice in natural and artificial diets? Is carbohydrate in the diet more important than protein, or are there some other factors involved?

How do larval feeding mechanisms differ from those of adults? How do these mechanisms change in metamorphosis? What is the mechanism of digestion in both larval and adult oysters? Is it mainly intracellular or extracellular? How is it affected by environmental conditions? Are feeding and digestion continuous or is there a rhythmic alternation between these two activities? In the culturing of oysters, is a continuous feeding regime preferable to one employing batch feeding? What is the role of mucus in feeding and how is it affected by environmental factors including pollution?

Does the diet of Crassostrea sp. parent stocks greatly affect the viability of larvae and spat as it appears to do in *Ostrea* sp. (Helm et al. 1973)?

Growth

What causes the differences in average growth rates among different oyster bars within Maryland, or within bars from one year to the next, or among groups of seed from different areas (Beaven 1950, 1953a)? Specifically, with regard to good seed areas such as James River, Va. or Broad Creek, Md., why are the resident oysters stunted and slow-growing (Andrews 1955)?

Reproduction

Given the demonstrated impact on larval vigor of stress on adult *Mytilus edulis* and *Ostrea edulis* during gametogenesis, what are the effects of natural and anthropogenic stresses on adult Crassostrea *virginica* in terms of larval vigor?

What is the role of food in the process of oyster gametogenesis and in stimulating spawning? How does temperature interact with food supply in controlling reproductive activity? If there are interactions, do they vary with latitude?

How do environmental conditions affect sex ratios? It appears that Chesapeake Bay oysters maintain balanced or nearly-balanced sex ratios in the face of long-term diminution of recruitment of young (which are mainly males). How do they accomplish this? What cues are available to indicate sex ratios on established oyster bars? What sex ratios are optimal for spawning and fertilization?

What causes varied widths of gonad layers from year to year (Galtsoff 1938)? Why do some areas such as James River, Va. do so well in producing spat, yet have such apparently poorly conditioned brood stock (Andrews 1951)? Similarly, how do Florida grounds containing oysters with low glycogen content manage to produce so much spat (Ingle 1951)? What is the relationship (if any) between thickness of gonads and reproductive success?

Why are oysters from southern populations (Chesapeake Bay south) so difficult to spawn in the laboratory (Hidu et al. 1969, Dupuy and Rivkin 1973)? Are their spawning stimuli different in nature from stimuli that cause northern oysters to spawn?

Larval Biology

What is the mortality rate of oyster larvae in Chesapeake Bay (Carter 1967)? How does the rate vary from year to year, or with location? What are the principal causes of larval mortality and do these causes vary annually or are they consistent from year to year? From an oyster farming point of view, can larval survival be enhanced in nature, and if so, at what cost?

How widely are larval broods spread in nature? Do they settle in the vicinity of the adults which produced them? Is there widespread mixing among larvae from different spawning populations, either within a tributary system or up and down the Bay?

How do oyster larvae react to various current speeds? What is their swimming behavior like in the field? Are they able to sense cues that would allow them actively to take advantage of estuarine transport mechanisms and be carried upstream, or are they transported passively?

What factors influence setting in Chesapeake Bay? Why does setting occur at consistently high levels in one area and consistently low levels in another? Why is setting so successful in some years (e.g. 1980) and not in others (e.g. 1978)? Are there features about oyster shells, other than the shell proteins, which attract pediveligers to settle? If so, can settlement be augmented by enhancement of these features? Why are some kinds of bacterial films on cultch apparently attractive to pediveligers while other films are not?

What are the larval concentrations to be found over various kinds of Bay bottom? Are they similar over both good setting areas and barren bottom, indicating that good setting areas have suitable quantities of cultch and barren bottoms do not? If a barren area has sufficient quantities of larvae in the overlying water (how much is sufficient?) does it need only application of cultch to become a good setting area?

Genetics

What trait or traits need to be selected for in Chesapeake Bay oysters? Is there an interaction between traits such that improvement in one, e.g. shell growth, results in loss in another, e.g. meat yield?

Given adequate quantities of cheap wild seed, what is involved (in terms of expense) in developing higher quality hatchery seed that will outperform the wild seed, e.g. in growth, meat yield, survival? How much better than natural seed does hatchery seed have to be in order to justify hatchery production economically?

What level of heterosis ("hybrid vigor") may be expected from crossbreeding different oyster strains for rearing in Chesapeake Bay?

Can we control the sex of oysters so that sterile animals can be produced? If so, would these sterile oysters be superior in growth characteristics or meat quality now that energy would not be diverted to gonad production?

Is it possible to select for low-salinity tolerant oysters so that the Upper Bay could be reseeded? If it were possible, would it be desirable or economically feasible?

Can genetic selection in oysters be enhanced by use of mutagenic agents? Is polyploidization (increase in the number of chromosomal sets) applicable to oysters, and if so, what useful characters (enhanced growth rate, greater mature size or weight, more efficient conversion of food) might result?

We know relatively little about oyster genetics. Research into this field needs to be expanded if aquaculture is to be successful.

Disease and Parasites

For Chesapeake Bay, the long term incidences of diseases and parasites need to be monitored as they are now by Project MADI, sponsored by DNR. In addition, methods of transmittal need to be established for some diseases and parasites. Interaction of certain diseases (e.g. "MSX" and "Dermo") need to be studied. The study of disease should be performed with attention to the-role of disease in the ecology of oysters. Perhaps more understanding of susceptibility on the part of oysters will accrue if the animals' niche is also considered during research into parasites and disease.

Larval diseases, both in the hatchery and in the field, are little known and need attention.

Studies of disease in oysters are in their infancy, yet are of great importance. Monetary support should be adequate and consistent.

Competitors, Predators and Pests

What are the major competitors of larval oysters for food? Is such competition of an intensity to affect larval survival significantly? If so, can these competitors be controlled to ensure an adequate food supply for oyster larvae? Would it be economically possible to do so?

What is the nature and extent of the proposed sea nettle-ctenophore-oyster larvae interaction? If such a relationship exists and if it is deleterious to larval survival, can anything be done to counter the deleterious effect? What is the influence of potential predators such as filter-feeding fish, moon jellyfish (*Aurelia aurita*), mosquito larvae, folliculinids, which are mentioned in the review? In general, how greatly do predators of oyster larvae affect recruitment and population maintenance in Chesapeake Bay?

What effects do chemicals used for predator control, such as quicklime, have on other estuarine organisms? Do chemical barriers or treatments adversely affect other important organisms? What predator and competitor controls are truly feasible for a public fishery where a free resource is less likely to be carefully maintained?

Rehabilitation

What is the abundance of natural brood stock now available in different locations of Chesapeake Bay? Is it increasing or declining? If it fluctuates annually, why, and how important are these fluctuations in affecting future harvests? Is brood stock presently too dispersed in the Bay to allow for adequate stimulation of adults to spawn? Is there an optimal brood stock concentration to ensure adequate spawning (or, how many brood oysters are required for a given area of bottom)? If so, do different areas have different optimal concentrations? Do young or old oysters make the best brood stock?

What is the best position of brood oysters in relation to cultch? On the cultch? Upstream or downstream? Some distance away? What are the best concentrations of cultch shells on different bottom types? Is setting rate enhanced by allowing large brood reserves to accumulate in designated seed areas where dispersal of larvae to other water masses would be at a minimum (assuming they are greatly dispersed at all)?

Why are (or were) certain oyster grounds capable of producing an excellent set consistently (e.g. James River, Holland Straits, St. Mary's River, Eastern Bay, Fishing Bay, Tangier Sound, Broad Creek and Harris Creek in the Choptank River)? Why are some of these setting areas not suitable for rapid growth and fattening of oysters? Why was and is the Chester River a poor setting area? Why are other areas (e.g. Patuxent River) good for growing market oysters but not for spat settlement? (for background—see Galtsoff 1958, Engle 1948). Can any area of the Bay be made into a good seed area, given adequate material to firm up the bottom and adequate cultch for settlement? What is the optimum density for maximum survival and growth of newly settled spat, juveniles or adults? Do such optimal densities vary with region? What are the natural mortality levels for larvae, spat and juveniles in different areas?

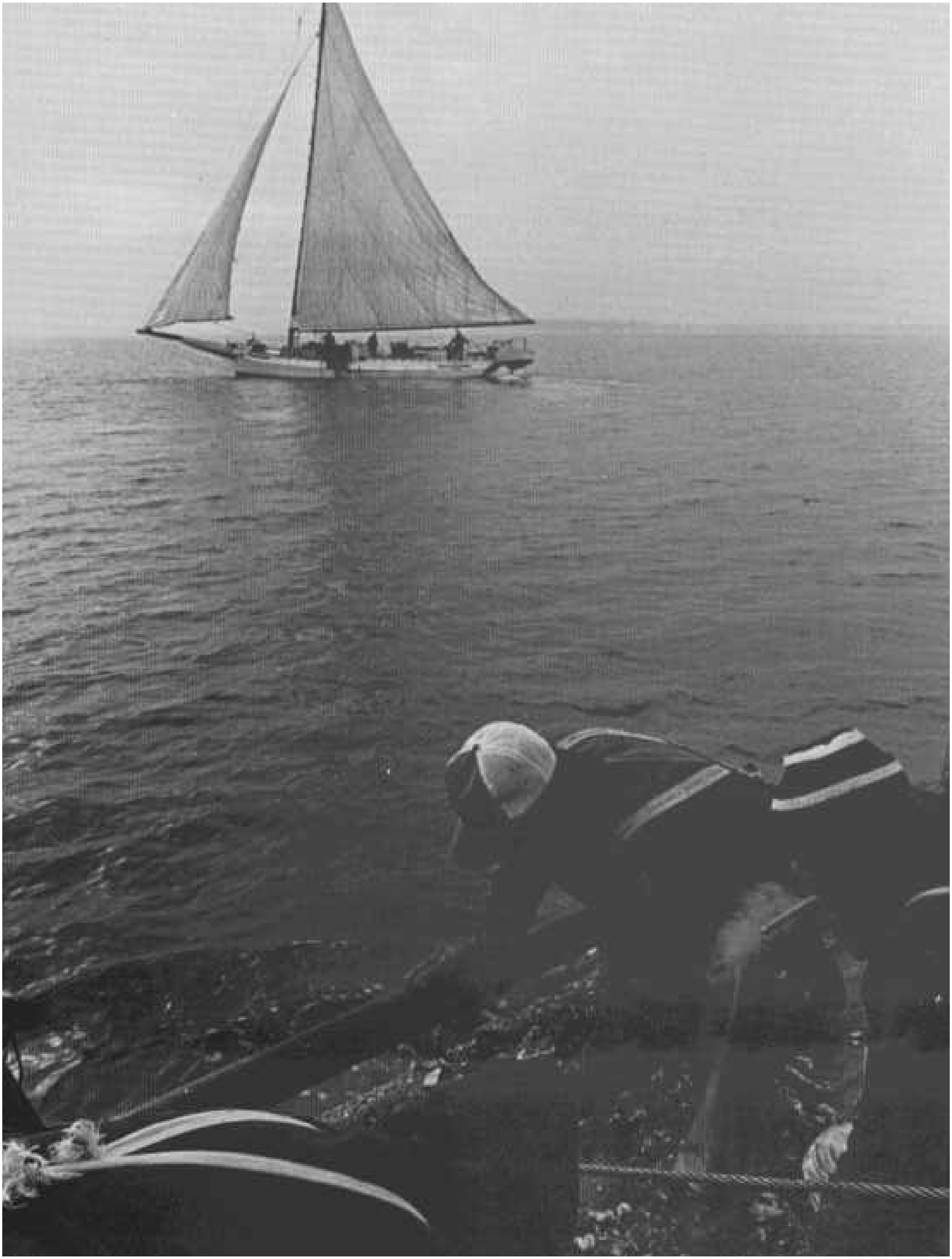
How are growth and mortality affected by handling and transporting spat or seed oysters within the Bay? What sort of damage is caused to spat by harvesting activities? In oyster farming, what is the optimum time for harvesting oysters? That is, should they be harvested just after they have first spawned, or would it be better to wait for another year or two? Should they be harvested when they have reached their maximum growth rate and before it slows? How would the latter affect possible future contributions of these oysters to recruitment?

What is the annual magnitude of recruitment in any area? What is the level of fishing mortality and catch per unit effort in the Bay? Are variable annual quotas more suitable than fixed quotas for management of Bay oysters? Would a limited entry fishery result in better management for greater yield? What is the projected yield that would accrue if widespread rental of oyster grounds was practiced in Maryland?

What kinds of automated systems for handling farmed oysters in the field and for processing them on-shore are economically feasible? If oyster farming were to become a viable enterprise in Maryland, what economic and marketing steps could be taken to prevent an over-supply of oysters?

There is need for development of a wider variety of food products incorporating oysters, in order to stimulate consumer demand.

Summary



Summary

The commercial importance of Crassostrea *virginica* has stimulated much research into its biology and management in North America. This report reviews the extensive documentation of this research and delineates areas of uncertain knowledge which require further study. In addition, the history of oyster management in Maryland is reviewed and instructive lessons are drawn from earlier experiences.

In this review, we do not wish to separate research insights from management requirements, even though the framework of the report includes separate sections on oyster biology and on management. We are convinced that the best management of any natural resource occurs when there is linkage between gathering of information by field or laboratory study and subsequent application of this information in resource management. Optimal management depends upon thorough understanding of the biology of the resource. It also requires a supportive socio-political structure that leaves management to a skilled and informed group of managers insulated from well-meaning but uninformed political interference.

The efficient management of oyster resources can be likened to dryland farming, where it is vital to know the land and its carrying capacity, the kinds and quality of nutrients available and the best areas for supporting different agricultural crops. With regard to the crop, knowledge of nutrient requirements, productivity and growth rates, environmental requirements and tolerances, reproductive capacity, disease susceptibilities, and response to genetic manipulations is indispensible. Proper methods of cultivation, harvesting, and marketing must be determined. Long term goals must not be sacrificed for short-term ephemeral gains. Productive farms are the result of informed management; the same approach must apply to public and private management of oyster resources.

Status of Our Understanding of Oyster Biology

Concerning oyster biology, responses to environmental factors such as temperature, salinity, sediments, and dissolved oxygen have been measured to a degree that allows reasonable understanding. While the core of information nec-

Watermen on a skipjack cull through their catch, throwing back undersized oysters, empty shell and spat-holding shell, a conservation measure that provides cultch and stock for future harvests.

essary for merely adequate management exists, improved management requires answers to numerous intriguing questions. We know that C. virginica is a very tolerant animal, possessing broad resistance to a variety of environmental stresses. This is generally true of estuarine animals, which face stress from summer heat and winter cold in their relatively shallow habitat, from constantly varying (tidally and seasonally) salinity levels, and from sediments that are readily suspended by wind activity. We believe that the eastern oyster is ecologically resilient. An example of this resilience is evident in the excellent level of spat settlement in certain areas of Chesapeake Bay in 1980. This occurred after some years of poor spat settlement Bay-wide, and under conditions of relatively low quantities of oysters because of over-harvesting. However, while the oyster resource was able to respond to suitable (but unknown) environmental conditions, the fact is that even the most resilient organism has its “breaking point.” We do not know how much more resilient C. virginica is, nor how much more stress it can tolerate. Thus, efforts for rehabilitation must continue.

There is need for a more thorough understanding of five major areas of oyster biology:

1. *Larval Biology.* The biology, ecology and behavior of oyster larvae are poorly understood. Their small size and the difficulties of sampling field populations continually and accurately are primarily responsible for this. We need to understand larval dispersal patterns, i.e. how far a brood drifts from its parental stock; the influence of water movements, salinity changes, temperature, light and pressure on larval behavior in the water column; factors concentrating or dispersing larvae; factors influencing settlement either positively or negatively; the relationship of larval abundance to settlement success; whether the absence of suitable cultch is a limiting factor in settlement in some areas of Chesapeake Bay; larval food requirements and whether these are being met; the impact of predators, parasites and disease on larval abundances and ultimately on settlement success.

2. *Feeding and Nutrition.* The natural food supply and nutritional requirements of all life history stages of Chesapeake Bay oysters need to be determined. Have there been changes in natural food species in the Bay over time, similar to changes in submerged aquatic vegetation? Have conditions favored less nutritious or less acceptable species at the expense of suitable food species? If there have been such changes, are they influencing gametogenesis and larval vigor? Are the variations in suitability of different areas of the Bay for settlement or growth related to differences in food quality or quantity?

   With regard to hatchery culture, more research into suitable food species for a lower salinity environment such as central Chesapeake Bay appears to be needed. Cheap and nutritionally dependable food material such as micro-encapsulated diets that can be stored and delivered in optimal quantity needs to be developed.

3. *Genetics.* Our understanding of oyster genetics is primitive compared with our knowledge of domestic animals and plants. Selective breeding of oysters is an infant science. For aquacultural purposes in Chesapeake Bay, what trait or traits need to be selected? Are there interactions between traits such that improvements in one (e.g., shell growth) result in loss in another (e.g., meat yield)? How much of an improvement over natural selection can we expect to attain by experimental selection for desirable traits and how much will it cost in terms of time, energy, space and money? How responsive are oysters to genetic manipulation? Do positive results in selecting for a desirable trait in larvae (e.g., in terms of rapid growth) persist in later life?

4. *Disease.* The role of disease in the ecology of oysters and the impact of non-catastrophic disease on population levels and environmental resistance need to be investigated. Interactions of certain diseases and methods of disease transmittal need to be established. Larval diseases, both in the hatchery and in the field, have not been studied to any extent.

5. *Pollutants.* Because estuaries are semi-enclosed bodies of water which are generally (a) shallow, (b) subject to surface runoff, (c) used as transportation arteries, and (d) in close proximity to high concentrations of people, they are particularly exposed to pollution. In many parts of the world, they are terminal sewers. Pollutants tend to be concentrated in estuaries, either by estuarine circulation systems or by adsorption onto sediments. Thus, quantities of anthropogenic chemicals, among them chlorine compounds, heavy metals, and petrochemicals, may come into contact with oysters. The influences of these materials on all life history stages of C. virginica remain to be evaluated. In addition to direct effects on oysters, we need to know the influence of pollutants on the food species of larval and settled oysters, and on contamination of the settlement substrate. Synergistic effects of various pollutants have not been studied to any extent.

Management and Rehabilitation

Improved management and rehabilitation of the oyster fishery requires thorough study of the following:

1. *Brood Stock.* What is the abundance of natural brood stock now available in different areas of the Bay? Is it increasing or declining? Is there an optimal brood stock concentration that ensures adequate spawning? Is population age distribution a factor in determining this optimal concentration, i.e., does one age group contribute more gametes than another age group?

2. *Cultch and Seed Supply.* The supply of seed oysters is a limiting and critical factor in rehabilitation and management. Those areas of the Bay consistently producing adequate quantities of seed should be pro-

tected and expanded. A private oyster farming industry would encourage growth of a seed industry.

Numerous informed observers have stated that fresh shell should not be exported or used for anything other than for replenishment of the bottom. How much cultch is now available in the Bay, and how much is optimal? What are the best concentrations on different bottom types or in different locations? Can any area of the Bay be made into a good seed area, given suitable firm bottom and adequate cultch for settlement?

3. *Growing and Setting Areas*. The best areas still available for settlement and growth need to be determined and protected. It is not clear why some areas are conducive to setting but are not suitable for rapid growth and fattening, and vice versa, but the reasons must be clearly understood in order to utilize areas effectively. The development of good seed and good growing areas depends upon a clear understanding of the environment and on the biological responses of oysters to the environment.

Historical Roots of Declining Yield

While tracing the historical decline of the Maryland oyster fishery, we discovered that factors other than environmental ones have had a major impact on this decline. Throughout the past century, four dominant themes recur:

1. The decline of the fishery is predominantly a result of overfishing and ineffectual conservation efforts.

2. It is important to emphasize the need to conserve the available shell stock as cultch, to protect spat and encourage their best growth, and to expand and protect natural seed areas.

3. Private oyster culture should be encouraged because it should have the stimulating effect it has had elsewhere. It should help revitalize the industry and increase yield with increased economic benefit to all involved.

4. Political considerations, rather than limited biological knowledge, have frequently been the cause of fishery declines elsewhere. In Chesapeake Bay, efforts to improve the industry by preventing overfishing, implementing shell planting efforts, enforcing cull laws and encouraging private oyster farming have been hampered by resistance from watermen and their political representatives.

As early as 1882, the Oyster Commission headed by W. K. Brooks recommended an expansion of the private oyster culture system. Rental of oyster beds has been strongly supported by researchers and some resource managers over the last hundred years. However, strong opposition from watermen's groups and their representatives has blocked any expansion of the current small leasing program.

To help alleviate the fear of private culture, economic studies and suitable marketing strategies need to be developed. If prices were moderate and competitive with other meat sources, would market demand expand? Can the small entrepreneur be protected from the interests of large businesses?

We are now entering into the second century of informed insight into oyster biology in Maryland, since the Oyster Commission was formed in 1880. One hundred years of biological research have passed with much of this research funded erratically and poorly. We know enough to manage the resource as hunters, but not as farmers. Yet, after 100 years of continued decline of the Maryland resource, resistance to appropriate management strategies continues. The catch has declined from 10 to 15 million bushels a year to the present 2 to 3 million bushels. Yet, informed observers have consistently estimated that four to ten times the present level of harvests could be sustained with suitable management, and with development of private oyster farming as an essential element of that management.

We believe that the biological resilience of the resource and the presence of large areas of relatively unpolluted oyster ground could indeed lead to an increase in productivity and thus benefit tidewater communities that presently defend the status quo. The realization of these benefits, however, depends not on political fiat but on informed management which must in turn be based upon the best available biological information. The problems of depleted oyster harvests in Maryland are not simply biological in nature but also sociological and political.

References

References Cited

Abbott, R. T. 1975. American Seashells. Second Edition. Van Nostrand, New York. 568 pp.

Abrahamson, J. D. 1961. Economic aspects of markets for middle Atlantic oysters. Proc. Gulf Carib. Fish. Inst. 13: 128-131.

Adams, D. A.. 1968. The State's role in management of sea resources. Proc. Natl. Shellfish. Assoc. 58: 19-22.

Agnello, R. J. and L. P. Donnelley. 1975a. The interaction of economic, biological, and legal forces in the middle Atlantic oyster industry. Fish. Bull. 73: 256-261.

Agnello, R. J. and L. P. Donnelley. 1975b. Prices and property rights in the fisheries. Southern Econ. J. 42: 253-262.

Ahmed, M. 1975. Speciation in living oysters. Adv. Mar. Biol. 13: 357-397.

Alford, J. J. 1973. The role of management in Chesapeake oyster production. Geogr. Rev. 63: 44-54.

Alford, J. J. 1975. The Chesapeake oyster fishery. Ann. Assoc. Amer. Geographers 65: 229-239.

Allen, R. L. 1979. A yield model for the Foveaux Strait oyster (*Ostrea lutaria*) fishery. Rapp. P.-v. Reun. Cons. Int. Explor. Mer. 175: 70-79.

Amemiya, I. 1929. On the sex-change of the Japanese common oyster *Ostrea gigas* Thunberg. Proc. Imp. Acad., Japan 5(7): 284-286

Amemiya, I. 1935. Effect of gill excision upon the sexual differentiation of the oyster (*Ostrea gigas*). Rept. Jap. Assoc. Adv. Sci. 10: 1025 and Jap J. Zool., Trans. Abstr. 6(4): 84-85.

A handtonger dumps his catch on the culling board. Handtonging remains the most widely used harvesting technique in the northern Chesapeake Bay.

Anderson, J. W. 1975. Laboratory studies on the effects of oil on marine organisms: An overview. Amer. Petrol Inst. Publ. 4249: 1-70.

Anderson, J. W. 1977a. Responses to sublethal levels of petroleum hydrocarbons: Are they sensitive indicators and do they correlate with tissue contamination? In: D. Wolfe (ed.), Fate and Effects of Petroleum in Marine Ecosystems and Organisms, pp.95-114. Pergamon Press, New York.

Anderson, J. W. 1977b. Effects of petroleum hydrocarbons on the growth of marine organisms. Rapp. P.-v. Reun. Cons. Int. Explor. Mer. 171: 157-165.

Anderson, J. W. 1979. As assessment of knowledge concerning the fate and effects of petroleum hydrocarbons in the marine environment. In: W. B. Vernberg, A. Calabrese, F. P. Thurberg and F. J. Vernberg (eds.). Marine Pollution: Functional Responses, pp.3-21. Academic Press, New York.

Anderson, J. W., J. M. Neff, B. A. Cox, H. E. Tatem and G. M. Hightower. 1974. The effects of oil on estuarine animals: toxicity, uptake and depuration, respiration. In: F. J. Vernberg and W. B. Vernberg (eds.). Pollution and Physiology of Marine Organisms, pp.285-310. Academic Press, New York.

Anderson, R. D. 1975. Petroleum hydrocarbons and oyster resources of Galveston Bay, Texas. In: American Petroleum Institute, Proceedings of a Joint Conference on Prevention and Control of Oil Spills, March 25-27, 1975. A. P. 1., Washington, D.C. pp. 541-548.

Anderson, R. D. and J. W. Anderson. 1975. Oil bioassays with the American oyster Crassostrea *virginica* (Gmelin). Proc. Natl. Shellfish. Assoc. 65: 38-42.

Anderson, R. D. and J. W. Anderson. 1976. Effects of salinity and selected petroleum hydrocarbons on the osmotic and chloride regulation of the American oyster, Crassostrea *virginica*. Physiol. Zool. 48: 420-429.

Anderson, W. D. 1979. A comparative study of a saltwater impoundment and its adjacent tidal creek pertinent to culture of Crassostrea *virginica* (Gmelin). Proc. World Maricult. Soc. 10: 649-671.

Andrews, J. D. 1951. Seasonal patterns of oyster setting in the James River and Chesapeake Bay. Ecology 32: 752-758.

Andrews, J. D. 1955a. Setting of oysters in Virginia. Proc. Natl. Shellfish. Assoc. 45: 38-46.

Andrews, J. D. 1955b. Notes on fungus parasites in bivalve mollusks. Proc. Natl. Shellfish. Assoc. 45: 157-163.

Andrews, J. D. 1956 Trapping oyster drills in Virginia. Part 1. The effect of migration and other factors on the catch. Proc. Natl. Shellfish. Assoc. 46: 140-154.

Andrews, J. D. 1964. Oyster mortality studies in Virginia. IV. MSX in James River public seed beds. Proc. Natl. Shellfish. Assoc. 53: 65-84.

Andrews, J. D. 1966 Oyster mortality studies in Virginia. V. Epizootiology of MSX, a protistan pathogen of oysters. Ecology 47: 19-31.

Andrews, J. D. 1979. Pelecypoda: Ostreidae. In: A. C. Giese and J. S. Pearse (eds.). Reproduction of Marine Invertebrates. V. Molluscs: Pelecypods and Lesser Classes, pp.293-341. Academic Press, New York.

Andrews, J. D., D. S. Haven and D. B. Quayle. 1959. Fresh-water kill of oysters (*Crassostrea virginica*) in James River, Virginia, 1958. Proc. Natl. Shellfish. Assoc. 49: 29-47.

Andrews, J. D. and W. G. Hewatt. 1957. Oyster mortality studies in Virginia II. The fungus disease caused by *Dermocystidium marinum* in oysters of Chesapeake Bay. Ecol. Monogr. 27: 1-26.

Andrews, J. D., D. Turgeon and M. Hreha. 1969. Removal of pea crabs from live oysters by using Sevin. Proc. Natl. Shellfish. Assoc. 59: 1.

Andrews, J. D. and J. L. Wood. 1967. Oyster mortality studies in Virginia VI. History and distribution of *Minchinia nelsoni*, a pathogen of oysters, in Virginia Chesapeake Sci. 8: 1-13.

Aprill, G. and D. Maurer. 1976 The feasibility of oyster raft culture in east coast estuaries. Aquaculture 7: 147-160.

Awati, P. R. and H. S. Rail 1931. *Ostrea cucullata* (the Bombay oyster). Indian Zool. Memoirs V.3; 107 pp. (Not seen, quoted from Christensen and McDermott 1958).

Ayers, J. C. 1956 Population dynamics of the marine clam, *Mya arenaria* Limnol. Oceanogr. 1: 26-34.

Babinchak, J. and R. Ukeles. 1979. Epifluorescence microscopy: a technique for the study of feeding in Crassostrea *virginica* veliger larvae. Mar. Biol. 51: 69-76.

Bahner, L. H., A. J. Wilson, Jr., J. M. Sheppard, J. M. Patrick, Jr., L. R. Goodman and G. E. Walsh. 1977. Kepone bioconcentration, accumulation, loss and transfer through estuarine food chains. Chesapeake Sci. 18: 299-308.

Bahr, L. M., Jr. 1976 Energetic aspects of the intertidal oyster reef community of Sapelo Island, Georgia (USA). Ecology 57: 121-131.

Bahr, L. M. and R. E. Hillman. 1967. Effects of repeated shell damage on gametogenesis in the American oyster Crassostrea *virginica* (Gmelin). Proc. Natl. Shellfish. Assoc. 57: 59-62.

Bamford, D. R. and R. Gingles. 1974. Absorption of sugars in the gill of the Japanese oyster, Crassostrea *gigas*. Comp. Biochem. Physiol. 49A: 637-646.

Barnes, R. S. K., J. Coughlan and N. J. Holmes. 1973. A preliminary survey of the macroscopic bottom fauna of the Solent, with particular reference to *Crepidula fornicata* and *Ostrea edulis*. Proc. Malacol. Soc. London 40: 253-275.

Barrow, J. H., Jr. and B. C. Taylor. 1966. Fluorescent-antibody studies of haplosporidian parasites of oysters in Chesapeake and Delaware Bays. Science 153: 1531-1533.

Barszcz, C., P. P. Yevich, L. R. Brown, J. D. Yarbrough and C. D. Minchew. 1978. Chronic effects of three crude oils on oysters suspended in estuarine ponds. J. Envir. Pathol. Toxicol. 1: 879-895.

Bayne, B. L. 1975. Reproduction in bivalve molluscs under environmental stress. In: F. J. Vernberg (ed.). Physiological Ecology of Estuarine Organisms, pp.259-277. Univ. S. Carolina Press, Columbia, S.C.

Bayne, B. L. 1976 Aspects of reproduction in bivalve molluscs. In: M. L. Wiley (ed.). Estuarine Processes, Vol. 1, pp.432-448. Academic Press, New York.

Bayne, B. L., D. L. Holland, M. N. Moore, D. M. Love and J. Widdows. 1978. Further studies on the effects of stress in the adult on the eggs of *Mytilus edulis*. J. Mar. Biol. Assoc. U. K. 58: 825-841.

Beaven, G. F. 1945. Maryland's Oyster Problem. Educ. Series No. 8. Maryland Board of Natural Resources, Dept. Res. and Ed., Solomons Island, Md., 14 pp.

Beaven, G. F. 1947. Effect of Susquehanna River stream flow on Chesapeake Bay salinities and history of past oyster mortalities on upper Bay bars. Proc. Natl. Shellfish. Assoc. (1946): 38-41.

Beaven, G. F. 1950. Growth observations of oysters held on trays at Solomons Island, Maryland. Proc. Natl. Shellfish. Assoc. (1949): 43-49.

Beaven, G. F. 1951. Recent observations on the season and pattern of oyster setting in the middle Chesapeake area. Proc. Natl. Shellfish. Assoc. (1950): 53-56.

Beaven, G. F. 1953a. Some observations on rate of growth of oysters in the Maryland area. Proc. Natl. Shellfish. Assoc. 43: 90-98.

Beaven, G. F. 1953b. A preliminary report on some experiments in the production and transplanting of South Carolina seed oysters to certain waters of the Chesapeake area. Part 2. Proc. Gulf Carib. Fish. Inst. 5: 115-122.

Beaven, G. F. 1955. Various aspects of oyster setting in Maryland. Proc. Natl. Shellfish. Assoc. (1954): 29-37.

Bender, M. E., R. J. Huggett and H. D. Slone. 1972. Heavy metals—an inventory of existing conditions. J. Wash. Acad. Sci. 62: 144-153.

Berenberg, C. J. and G. W. Patterson. 1981. The relationship between dietary phytosterols and the sterols of wild and cultivated oysters. Lipids (in press).

Bernard, F. R. 1974a. Particle sorting and labial palp function in the Pacific oyster Crassostrea *gigas* (Thunberg, 1795). Biol. Bull. 146: 1-10.

Bernard, F. R. 1974b. Annual biodeposition and gross energy budget of mature Pacific oysters Crassostrea *gigas*. J. Fish. Res. Bd. Canada 31: 185-190.

Bishop, T. W. 1967. Feeding rates of the ctenophore *Mnemiopsis leidyi* Chesapeake Sci. 8: 259-261.

Blumer, M. 1970. Scientific aspects of the oil spill problem. Presented at NATO Conference, Brussels, 6 Nov. 1970, 21 pp. WHOI, Woods Hole, Ma. (Not seen. Referred to by Evans and Rice, 1974).

Blumer, M., S. Souza and J. Sass. 1970. Hydrocarbon pollution of edible shellfish by an oil spill. Mar. Biol. 5: 195-202.

Bockrath, J. and D. Wheeler. 1975. Closed-cycle mariculture in Maryland, Virginia, and Delaware: An examination of the adaptability of existing fishery laws to new technology. William and Mary Law Review 17: 85-107.

Borthwick, P. W. and S. C. Schimmel. 1978. Toxicity of pentachlorophenol and related compounds to early life stages of selected estuarine animals. In: K. R. Rao (ed.). Pentachlorophenol, pp. 142-146 Plenum Press, New York.

Bousfield, E. L. 1955. Ecological control of the occurrence of barnacles in the Miramichi estuary. Bull. Nat. Mus. Canada 137: 1-69.

Bowman, I. 1940. Science and social effects: Three failures. Sci. Monthly 50: 289-298.

Boyden, C. R., H. Watling and I. Thornton. 1975. Effect of zinc on the settlement of the oyster, Crassostrea *gigas*. Mar. Biol. 31: 227-234.

Bravo, H., S. Salazar, A. V. Botello and E. F. Mandelli. 1978. Polyaromatic hydrocarbons in oysters from coastal lagoons along the eastern coast of the Gulf of Mexico, Mexico. Bull. Environ. Contam. Toxicol. 19: 171-176.

Breese, W. P., P. L. Dunaghay, R.E. Malouf and L. F. Small. 1977. Algal chemostats and oyster larvae. Proc. Natl. Shellfish Assoc. 67: 125.

Breese, W. P. and R. E. Malouf. 1975. Hatchery Manual for the Pacific Oyster. Agric. Expt. Stn. Spec. Rep. No. 443, Oregon State U. Publ. ORESU-H-75-002. Corvallis, OR. 22 pp.

Breese, W. P. and A. Robinson. 1981. Razor clams, *Siliqua patula* (Dixon): gonadal development, induced spawning and larval rearing. Aquaculture 22: 27-33.

Breisch, L. L. and V. S. Kennedy. 1980. A Selected Bibliography of Worldwide Oyster Literature. University of Maryland Sea Grant Publication No. UM-SG-TS-80-11. College Park, MD. 309 pp.

Brereton, A., H. Lord and J. S. Webb. 1973. Effect of zinc on growth and development of larvae of the Pacific oyster, Crassostrea *gigas*. Mar. Biol. 19: 96-101.

Breuer, S. P. 1962. An ecological survey of the lower Laguna Madre of Texas, 1953-1959. Publ. Inst. Mar. Sci., Univ. Texas 8: 153-185.

Brooks, R. R. and M. G. Rumsby. 1967. Studies on the uptake of cadmium by the oyster, *Ostrea sinuata*. Aust. J. Mar. Freshw. Res. 18: 53-61.

Brooks, W. K. 1880. Development of the American oyster (*Ostrea virginica* L.). Studies from the Biological Laboratory, Johns Hopkins University, Baltimore, Md., Vol. 4(1): 1-81.

Brooks, W. K. 1905. The Oyster. A Popular Summary of a Scientific Study. The Johns Hopkins Press, Baltimore, Md. 225 pp.

Brooks, W. K., J. I. Waddell and W. H. Legg. 1884. Report of the Oyster Commission of the State of Maryland. J. B. Ehlers and Co., Baltimore, Md. 193 pp.

Brown, A. W. A. 1978. Ecology of Pesticides. John Wiley and Sons, New York. 525 pp.

Brown, C. 1973. The effects of some selected bacteria on embryos and larvae of the American oyster, *Crassostrea virginia*. J. Invert. Pathol. 21: 215-223.

Brown, C. and E. Losee. 1978. Observations on natural and induced epizootics of Vibriosis in Crassostrea *virginica* larvae. J. Invert. Pathol. 31: 41-47.

Brungs, W. A. 1976. Effects of Wastewater and Cooling Water Chlorination on Aquatic Life. EPA-600/3-76-098. US EPA, Environmental Research Lab, Duluth, MN. 52 pp.

Bryan, G. W. 1976 Some aspects of heavy metal tolerance in aquatic organisms. In: A. P. M. Lockwood (ed.). Effect of Pollutants in Aquatic Organisms, pp. 7-34.

Bryan, J. Y. 1949. The vanishing oyster. The South Atlantic Quarterly 48(4): 546-556

Bunde, T. A. and M. Fried. 1978. The uptake of dissolved free fatty acids from seawater by a marine filter feeder, Crassostrea *virginica* Comp. Biochem. Physiol. 60A: 139-144.

Burkenroad, M. D. 1931a. Notes on the Louisiana conch, *Thais haemastoma* Linn., in its relation to the oyster, *Ostrea virginica*. Ecology 12: 656- 664.

Burkenroad, M. D. 1931b. Sex in the Louisiana oyster, *Ostrea virginica*. Science 74: 71-72.

Buroker, N. E. 1980. An examination of the trophic resource stability theory using oyster species of the family Ostreidae. Evolution 34: 204-207.

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

Buroker, N. E., W. K. Hershberger and K. K. Chew. 1979b. Population genetics of the family Ostreidae. II. Interspecific studies of the genera *Crassostrea* and *Saccostrea* Mar. Biol. 54: 171184.

Burrell, V. G., Jr. 1968. The ecological significance of ctenophore *Mnemiopsis leidyi* (A. Agassiz) in a fish nursery ground. M.S. Thesis, College of William and Mary, Williamsburg, VA. 61 pp.

Burrell, V. G., Jr. and W. A. Van Engel. 1976 Predation by and distribution of a ctenophore, *Mnemiopsis leidyi* A. Agassiz, in the York Estuary. Est. Coastal Mar. Sci. 4: 235-242.

Burton, R. W. 1963. Distribution of oyster microparasites in Chesapeake Bay, Maryland, 1959-1960. Proc. Natl. Shellfish. Assoc. 52: 65-74.

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

Butler, P. A. 1952. Effect of Floodwaters on Oysters in Mississippi Sound in 1950. U. S. Fish Wildl. Serv., Res. Rep. 31. 20 pp.

Butler, P. A. 1955. Selective setting of oyster larvae on artificial cultch. Proc. Natl. Shellfish. Assoc. 45: 95-105.

Butler, P. A. 1956 Reproductive cycle in native and transplanted oysters. Proc. Natl. Shellfish. Assoc. 46: 75.

Butler, P. A. 1966. Fixation of DDT in estuaries. Trans. N. Amer. Wildlife Conf. 31: 184-189.

Butler, P. A. 1971. Influence of pesticides on marine ecosystems. Proc. Roy. Soc. Lond. B. 177: 321-329.

Butler, P. A. 1973. Organochlorine residues in estuarine mollusks, 19651972. National Pesticide Monitoring Program. Pest. Monitor. J. 6: 238-362.

Butler, P. A. 1974. Trends in pesticide residues in shellfish. Proc. Natl. Shellfish. Assoc. 64: 77-81.

Butler, P. A., A. J. Wilson, Jr. and A. J. Rich. 1962. Effects of pesticides on oysters. Proc. Natl. Shellfish. Assoc. 51: 23-32.

Cabraal, R.A. 1978. Systems analysis of the Maryland oyster fishery: production management and economics. Ph.D. Dissertation, Agri. Eng. Univ. Md. 318pp.

Cabraal, R.A. and F.W. Wheaton. 1981. Production functions for the Maryland oyster fishery. Trans. Amer. Soc. Agric. Eng. 24(1): 248-251,254.

Calabrese, A. 1972. How some pollutants affect embryos and larvae of American oyster and hardshell clam. Mar. Fish. Rev. 34: 66-77.

Calabrese, A., R. S. Collier, D. A. Nelson and J. R. Maclnnes. 1973. The toxicity of heavy metals to embryos of the American oyster, Crassostrea *virginica*. Mar. Biol. 18: 162-166.

Calabrese, A. and H. C. Davis. 1966 The pH tolerance of embryos and larvae of *Mercenaria mercenaria* and Crassostrea *virginica*. Biol. Bull. 131: 427-436

Calabrese, A. and H. C. Davis. 1969. Spawning of the American oyster, Crassostrea *virginica*, at extreme pH levels. Veliger 11: 235.

Calabrese, A., J. R. Maclnnes, D. A. Nelson and J. E. Miller. 1977. Survival and growth of bivalve larvae under heavy-metal stress. Mar. Biol. 41: 179-184.

Carey, G. G. 1970. Maryland Folklore and Folklife. Tidewater Publ., Cambridge, Md. 98 pp.

Cargo, D. G. and L. P. Schultz. 1967. Further observations on the biology of the sea nettle and jellyfishes in Chesapeake Bay. Chesapeake Sci. 8: 209-220.

Carriker, M. R. 1947. A brief critical survey of the evidence for the horizontal movements of oyster larvae. Proc. Natl. Shellfish. Assoc. (1946): 28-32.

Carriker, M. R. 1951a. Ecological observations on the distribution of oyster larvae in New Jersey estuaries. Ecol. Monogr. 21: 19-38.

Carriker, M. R. 1951b. Observations on the penetration of tightly closing bivalves by *Busycon* and other predators. Ecology. 32: 73-83.

Carriker, M. R. 1957. Preliminary study of behavior of newly hatched oyster drills, *Urosalpinx cinerea* (Say). J. Elisha Mitchell Sci. Soc. 73: 328-351.

Carriker, M. R. 1961. Interrelation of functional morphology, behavior, and autecology in early stages of the bivalve *Mercenaria mercenaria*. J. Elisha Mitchell Sci. Soc. 77: 168-241.

Carriker, M. R. 1967. Ecology of estuarine benthic invertebrates: A perspective. In: G. H. Lauff (ed.). Estuaries, pp.442-487. Amer. Assoc. Adv. Science, Washington, D.C.

Carriker, M. R. and H. H. Chauncey. 1973. Effect of carbonic anhydrase inhibition on shell penetration by the muricid gastropod *Urosalpinx cinerea*. Malacologia 12: 247-263.

Carriker, M. R. and D. Van Zandt. 1972. Predatory behavior of a shellboring muricid gastropod. In: Winn, H. E., and B. L. Olla (eds.). Behavior of Marine Animals. V. I. Invertebrates, pp.l57-244. Plenum Press, New York.

Carter, H. H. 1967. A Method for Predicting Brood Stock Requirements for or Oyster (*C. virginica*) Producing Areas with Application to the Manokin River. Chesapeake Bay Institute, Spec. Rep. 13. 46 pp.

Castagna, M. and P. E. Chanley. 1973. Salinity tolerance of some marine bivalves from inshore and estuarine environments in Virginia waters on the western mid-Atlantic coast. Malacologia 12: 47-96.

Castell, J. D. and D. J. Trider. 1974. Preliminary feeding trials using artificial diets to study the nutritional requirements of oysters (*Crassostrea virginica*). J. Fish. Res. Bd. Can. 31: 95-99.

Casterline, J. I. and G. Yip. 1975. The distribution and binding of cadmium in oyster, soybean, and rat liver and kidney. Arch. Envir. Contam. Toxicol. 3: 319-329.

Chambers, J. S. 1970. Recent research on control of oyster drills. Proc. Natl. Shellfish. Assoc. 60: 13.

Chanley, P. E. 1958. Survival of some juvenile bivalves in water of low salinity. Proc. Natl. Shellfish. Assoc. 48: 52-65.

Chapman, C. R. 1956 Feeding habits of the southern oyster drill, *Thais haemas - toma*. Proc. Natl. Shellfish. Assoc. 46: 169-175.

Cheng, T. C. 1967. Marine molluscs as hosts for symbioses with a review of known parasites of commercially important species. Adv. Mar. Biol. 5: 1-424.

Cheng, T. C. and R. W. Burton. 1965. Relationships between *Bucephalus* sp. and Crassostrea *virginica*: histopathology and sites of infection. Chesapeake Sci. 6: 3-16

Chesapeake Biological Laboratory. 1953. The Commercial Fisheries of Maryland (A Special Report to the General Assembly of Maryland). Board of Natural Resources, Department of Research and Education, Solomons, MD. (Ches. Biol. Lab. Educ. Ser. No.30). 45 pp.

Chestnut, A. F. 1968. Setting behavior of oyster larvae. In: T. L. Linton (ed.). Proceedings of the Oyster Culture Workshop. Marine Fisheries Division, Brunswick, Ga. Contrib. 6: 32-34.

Chew, K. K. and R. Eisler. 1958. A preliminary study of the feeding habits of the Japanese oyster drill, *Ocinebra japonica.* J. Fish. Res. Bd. Canada 15: 529-535.

Chipman, W. A. and P. S. Galtsoff. 1949. Effects of oil mixed with carbonized sand on aquatic animals. U. S. Fish Wildl. Serv. Spec. Sci. Rep. 1: 1-52.

Chipman, W. A., T. R. Rice and T. J. Price. 1958. Uptake and accumulation of radioactive zinc by marine plankton, fish and shellfish. Fish. Bull. 58: 279-292.

Christensen, A. M. and J. J. McDermott. 1958. Life-history and biology of the oyster crab, *Pinnotheres ostreum* (Say). Biol. Bull. 114: 146-179.

Christensen, D. J. 1973. Prey preference of *Stylochus ellipticus* in Chesapeake Bay. Proc. Natl. Shellfish. Assoc. 63: 35-38.

Christy, F. T. 1964. The exploitation of a common property natural resource: the Maryland oyster industry. Ph.D. Thesis, University of Michigan, Ann Arbor, MI. 222 pp.

Churchill, E. P., Jr. 1920. The oyster and the oyster industry of the Atlantic and Gulf coasts. U. S. Comm. Fish., Rep. App., Burl Fish Docu. 890: 1-51.

Cobb, W. R. 1969. Penetration of calcium carbonate substrates by the boring sponge, *Cliona*. Amer. Zool. 9: 783-790.

Coe, W. R. 1943. Sexual differentiation in mollusks. I. Pelecypods. Quart. Rev. Biol. 18: 154-1 64.

Cole, H. A. 1951. The British oyster industry and its problems. Rapp. Cons. Explor. Mer. 128: 7-17. (Not seen, quoted from Korringa, 1952).

Cole, H. A. and E. W. Knight-Jones. 1939. Some observations and experiments on the setting behavior of larvae of *Ostrea edulis*. J. Cons. Explor. Mer. 14: 8 6-105.

Cole, H. A. and E. W. Knight-Jones. 1949. The setting behaviour of larvae of the European flat oyster *Ostrea edulis* L., and its influence on methods of cultivation and spat collection. Fish. Invest., London. Ser. II, 17: 1-39.

Cole, H. A. and G. D. Waugh. 1959. The problem of stunted growth in oysters. J. Cons. Perm. Int. Explor. Mer. 24: 355-365.

Collier, A. 1954. A study of the response of oysters to temperature, and some long range ecological interpretations. Proc. Natl. Shellfish. Assoc. (1953): 13-38.

Collier, A., S. M. Ray and W. Magnitzky. 1950. A preliminary note on naturally occurring organic substances in sea water affecting the feeding of oysters. Science 111: 151-152.

Commission of Tidewater Fisheries. 1948. Report on the oyster problem in the Chesapeake Bay, pp. 27-39. In: Fourth Annual Report, Md. Board of Nat. Res., Annapolis, Md.

Cooley, N. R. 1962. Studies on *Parorchis acanthus* (Tremtoda: Digenea) as a biological control for the southern oyster drill, *Thais haemastoma*. Fish. Bull. 62: 77-91.

Coombs, T. L. 1972. Distribution of zinc in oysters, *Ostrea edulis*, and its relation to enzyme activity and to other metals. Mar. Biol. 12: 170-178.

Coombs, T. L. 1974. The nature of zinc and copper complexes in the oyster, *Ostrea edulis*. Mar. Biol. 28: 1-10.

Copeland, B. J. and H. D. Hoese. 1966. Growth and mortality of the American oyster, Crassostrea *virginica*, in high salinity shallow bays in central Texas. Publ. Inst. Mar. Sci. 11: 149-158.

Cory, R. L. 1967. Epifauna of the Patuxent River Estuary, Maryland, for 1963 and 1964. Chesapeake Sci. 8: 71-89.

Couch, J. A. 1969. An unusual lesion in the mantle of the American oyster, Crassostrea *virginica*. Natl. Cancer Inst. Monogr. 31: 557-562.

Couch, J. A., C. A. Farley and A. Rosenfield. 1966 Sporulation of *Minchinia nel - soni* (Haplosporida, Haplosporidiidae) in Crassostrea *virginica* (Gmelin). Science 153: 1529-1531.

Cranfield, H. J. 1968. An unexploited population of oysters, *Ostrea lutaria* Hutton, from Foveaux Strait. Part II. Larval settlement patterns and spat mortality. New Zealand J. Mar. Freshw. Res. 2: 183-203.

Crisp, D. J. 1967. Chemical factors inducing settlement in Crassostrea *virginica* (Gmelin). J. Anim. Ecol. 36 329-335.

Cunningham, P. A. 1972. The effects of mercuric acetate on the adults, juveniles, and larvae of the American oyster, Crassostrea *virginica*. M.S. Thesis, Univ. Delaware, Newark, DE. 77 pp.

Cunningham, P. A. 1976. Inhibition of shell growth in the presence of mercury and subsequent recovery of juvenile oysters. Proc. Natl. Shellfish. Assoc. 66: 1-5.

Cunningham, P. A. 1979. The use of bivalve molluscs in heavy metal pollution research. In: W. B. Vernberg, A. Calabrese, F. P. Thurberg and F. J. Vernberg (eds.), Marine Pollution: Functional Responses, pp. 183-221. Academic Press, New York.

Cunningham, P. A. and M. R. Tripp. 1973. Accumulation and depuration of mercury in the American oyster, Crassostrea *virginica*. Mar. Biol. 20: 14-19.

Cunningham, P. A. and M. R. Tripp. 1975a. Factors affecting accumulation and removal of mercury from tissues of the American oyster, Crassostrea *virginica*. Mar. Biol. 31: 311-319.

Cunningham, P. A. and M. R. Tripp. 1975b. Accumulation, tissue distribution, and elimination of $^{203}HgCl_2$ and $CH_3{}^{203}HgCl$ in the tissues of the American oyster, Crassostrea *virginica*. Mar. Biol. 31: 321-334.

Curtin, L. 1979. Oyster hatchery pilot scheme. Setting up, operation, and future role of hatcheries. New Zealand Ministry of Agriculture and Fisheries, Tech. Rep. 155: 1-16.

Dame, R. F. 1972. The ecological energies of growth, respiration and assimilation in the intertidal American oyster Crassostrea *virginica*. Mar. Biol. 17: 243-250.

Dame, R. F. 1976. Energy flow in an intertidal oyster population. Est. Coastal Mar. Sci. 4: 243-253.

Davis, H. C. 1953. On food and feeding of larvae of the American oyster *C. virginica* Biol. Bull. 104: 334-350.

Davis, H. C. 1958. Survival and growth or clam and oyster larvae at different salinities. Biol. Bull. 114: 296-307.

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

Davis, H. C. and A. Calabrese. 1964. Combined effects of temperature and salinity on development of eggs and growth of larvae of *M. mercenaria* and *C. virginica*. Fish. Bull. 63: 643-655.

Davis, H. C. and P. E. Chanley. 1956. Effects of some dissolved substances on bivalve larvae. Proc. Natl. Shellfish Assoc. 46: 59-74.

Davis, H. C. and R. L. Guillard. 1958. Relative value of ten genera of microorganisms as foods for clam and oyster larvae. Fish Bull. 58: 293-304.

Davis, H. C. and H. Hidu. 1969a. Effects of pesticides on embryonic development of clams and oysters and on survival and growth of the larvae. Fish. Bull. 67: 393-404.

Davis, H. C. and H. Hidu. 1969b. Effects of turbidity-producing substances in sea water on eggs and larvae of three genera of bivalve mollusks. Veliger 11: 316-323.

Davis, H. C., V. L. Loosanoff and C. L. MacKenzie, Jr. 1961. Field tests of chemical methods for the control of marine gastropods. U. S. Fish. & Wildl. Serv. (Milford, Conn.) Bull 25(3): 3-9. (Not seen, quoted by Wood and Roberts, 1963).

Davis, J., D. Haven, K. G. Drobeck and E. A. Dunnington. 1976 Plans for Management of the Fisheries of the Tidal Potomac River. University of Maryland, Chesapeake Biological Laboratory, Solomons, Md. CEES Ref. No. 76-123CBL. 38 pp.

Davis, N. W. and R. E. Hillman. 1971. Effect of artificial shell damage on sex determination in oysters (Abstract). Proc. Natl. Shellfish Assoc. 61: 2.

Dawson, C. E. 1955. A study of the oyster biology and hydrography at Crystal River, Florida. Inst. Mar. Sci. Univ. Texas 4: 281-302.

Dean, D. 1958. New property of the crystalline style of Crassostrea *virginica*. Science 128: 837.

de Wolf, P. 1973. Ecological observations on the mechanisms of dispersal of barnacle larvae during planktonic life and settling. Neth. J. Sea Res. 6: 1-129.

de Wolf, P. 1974. On the retention of marine larvae in estuaries. Thalassia Jugoslavica 10: 415-424.

Diaz, R. J. 1973. Effects of brief temperature increases on larvae of the American oyster (*Crassostrea virginica*). J. Fish. Res. Bd. Canada 30: 991-993.

Dinamani, P. 1969. A note on feeding and excretion in bivalves. Veliger 11: 198-199.

Dinamani, P. and P. A. Lenz. 1977. Some aspects of spatfall of the New Zealand rock oyster during 1974. Veliger 20: 17-26

Douglass, W. R. 1975. Host response to infection with *Bucephalus* in *Crassostrea virginica* (Abstract). Proc. Natl. Shellf. Assoc. 65: 1.

Drifmeyer, J. E. 1974. Zinc and copper levels in the eastern oyster Crassostrea *vir - ginica* from the lower James River. J. Wash. Acad. Sci. 64: 292-294.

Drinnan, R. E. 1975. Oysters - disease, predation, parasites and competitors. In: Proc. Bras D'Or Lakes Aquacult. Conf., College of Cape Breton Press, Sydney, Canada.

Duke, T. W. and D. P. Dumas. 1974. Implications of pesticide residues in the coastal environment. In: F. J. Vernberg and W. B. Vernberg (eds.). Pollution and Physiology of Marine Organisms, pp.l37-164. Academic Press, New York.

Dunathan, J. P., R. M. Ingle and W. K. Havens, Jr. 1969. Effects of Artificial Foods upon Oyster Fattening with Potential Commercial Applications. Fla. DNR, Mar. Res. Lab., Tech. Serv. (No. 58); 39 pp.

Dunnington, E. A., Jr., K. Leum and D. MacGregor. 1970. Ability of buried oysters to clear sediment from the shell margin. (Abstract). Proc. Natl. Shellfish. Assoc. 60: 2-3.

Dupay, J. L. 1975. Some physical and nutritional factors which affect the growth and setting of the larvae of the oyster, Crassostrea *virginica* in the laboratory. In: F.J. Vernberg (ed). Physiological Ecology of Estuarine Organisms, pp.319-331. Univ. So. Carolina Press, Columbia, S. C.

Dupuy, J. L., N. T. Windsor and C. E. Sutton. 1977. Manual for Design and Operation of an Oyster Seed Hatchery for the American oyster Crassostrea *virginica*. Va. Inst. Mar. Sci., Spec. Rep. No. 142. Gloucester Pt., Va. 111 pp.

Dwivedy, R. C. 1973a. Instrumentation and technique of electrophysical studies of chemoreceptors on labial palps of the American oyster. Trans. Amer. Soc. Agric. Eng. 16: 367-370.

Dwivedy, R. C. 1973b. A study of chemoreceptors on labial palps of the American oyster using microelectrodes. Proc. Natl. Shellfish. Assoc. 63: 20-26.

Earle, S. 1932. The fisheries of Chesapeake Bay. Trans Amer. Fish. Soc. 62: 43-49.

Edwards, C. A. 1973a. Persistent Pesticides in the Environment, Second Edition. CRC Press, Cleveland, Ohio. 170 pp.

Edwards, C. A. (ed.). 1973b. Environmental Pollution by Pesticides. Plenum Press, New York. 542 pp.

Ehrhardt, M. 1972. Petroleum hydrocarbons in oysters from Galveston Bay. Environ. Poll. 3: 257-271.

Eisler, R., and M. D. Weinstein. 1967. Changes in metal composition of the quahog clam, *Mercenaria mercenaria*, after exposure to insecticides. Chesapeake Sci. 8: 253-258.

Elston, R. 1979. Economically important larval bivalve diseases and their control. Riv. Ital. Pisic. Ittiop. A, XIV, No. 2: 47-51.

Elston, R. and L. Leibovitz. 1980. Pathogenesis of experimental vibriosis in larval American oysters, Crassostrea *virginica*. Can. J. Fish. Aquat. Sci. 37: 964-978.

Emanuelson, M., J. C. Lincer and E. Rifkin. 1978. The residue uptake and histology of American oysters (*Crassostrea virginica* Gmelin) exposed to dieldrin. Bull. Environ. Contam. Toxicol. 19: 121-129.

Engle, J. B. 1945a. Alabama program of rehabilitation. Proc. Natl. Shellfish. Assoc. (1944). 3 pp.

Engle, J. B. 1945b. The Condition of the Natural Oyster Reefs and Other Public Oyster Bottoms of Alabama in 1945 with Suggestions for Their Improvement. U. S. Fish. Wildl. Serv., Spec. Sci. Rep. 29: 1-42. (Not seen, quoted by Korringa, 1952)

Engle, J. B. 1947. Commercial aspects of the upper Chesapeake Bay oyster bars in the light of recent oyster mortalities. Proc. Natl. Shellfish. Assoc. (1946): 42-46.

Engle, J. B. 1948. Distribution of setting guides the Maryland oyster program. Proc. Natl. Shellfish. Assoc. (1947): 16-20.

Engle, J. B. 1956 Ten years of study on oyster setting in a seed area in upper Chesapeake Bay. Proc. Natl. Shellfish. Assoc. 46: 88-99.

Engle, J. B. 1966 The molluscan shellfish industry. Current status and trends. Proc. Natl. Shellfish. Assoc. 56: 13-21.

Engle, J. B. and C. R. Chapman. 1951. Oyster condition affected by attached mussels. Proc. Natl. Shellfish. Assoc. 42: 70-78.

Engle, D. W. and B. A. Fowler. 1977. Copper and cadmium induced changes in the metabolism and structure of molluscan gill tissue. In: W. B. Vernberg, A. Calabrese, F. P. Thurberg and F. J. Vernberg (eds.), Marine Pollution: Functional Responses, pp. 239-256. Academic Press, New York.

Epifanio, C. E. 1979a. Comparison of yeast and algal diets of bivalve molluscs. Aquaculture 16 187-192.

Epifanio, C. E. 1979b. Growth in bivalve molluscs: nutritional effects of two or more species of algae in diets fed to the American oyster Crassostrea *virginica* (Gmelin) and the hard clam *Mercenaria mercenaria* (L). Aquaculture 18: 1-12.

Epifanio, C. E. and J. Ewart. 1977. Maximum ration of four algal diets for the oyster Crassostrea *virginica* Gmelin. Aquaculture 11: 13-29.

Ernst, W. 1980. Effects of pesticides and related organic compounds in the sea. Helgolander Meeresunters. 33: 301-312.

Evans, D. E. and S. D. Rice. 1974. Effects of oil on marine ecosystems: a review for administrators and policy makers. Fish. Bull. 72: 625-638.

Fairbanks, W. L. 1932. The oyster industry of Maryland. Chapter 9 in The Fisheries of Maryland. Baltimore Association of Commerce. Baltimore, Md., pp. 96-139.

Fankboner, P. V. and M. E. DeBurgh. 1978. Comparative rates of dissolved organic carbon accumulation by juveniles and pediveligers of the Japanese oyster Crassostrea *gigas* Thunberg. Aquaculture 13: 205-212.

Farley, C. A. 1968. *Minchinia nelsoni* (Haplosporida) disease syndrome in the American oyster, *Crassostrea virginica*. J. Protozool. 15: 585-599.

Farley, C. A. 1969. Probable neoplastic disease of the hematopoietic system in oysters, Crassostrea *virginica* and *Crassostrea gigas* Natl. Cancer Inst. Monogr. 31: 541-555.

Farley, C. A. 1975. Epizootic and enzootic aspects of *Minchinia nelsoni* (Haplosporida) disease in Maryland oysters. J. Protozool. 22: 418-427.

Farley, C. A. 1976a. Ultrastructural observations on epizootic neoplasia and lytic virus infection in bivalve mollusks. Prog. exp. Tumor Res. 20: 283-294.

Farley, C. A. 197 6b. Proliferative disorders in bivalve mollusks. Mar. Fish. Rev. 38(10): 30-33.

Farley, C. A. 1978. Viruses and virus-like lesions in marine mollusks. Marine Fisheries Review Paper 1337: 18-20.

Feng, S. Y. 1965. Heart rate and leucocyte circulation in Crassostrea *virginica*. Biol. Bull. 128: 198-210.

Feng, S. Y. and W. J. Canzonier. 1970. Humoral responses in the American oyster (*Crassostrea virginica*) infected with *Bucephalus* sp. and *Minchinia nelsoni*. In: S. F. Snieszko (ed.), A symposium on Diseases of Fishes and Shellfishes, pp.497-510. Amer. Fish. Soc., Spec. Publ. No. 5.

Filion-Myklebust, C. and K. 1. Johannessen. 1980. Biological Effects of Oil Pollution in the Marine Environment: A Bibliography. Int. Council Explor. Sea, C. M. 1980/E: 31. 145 pp. (Available from FOH's Laboratory of Ecotoxicology, University of Oslo, P.O. Box 1064, Blindern, Oslo 3, Norway).

Fingerman, M. and L. D. Fairbanks. 1957. Heat death and associated weight loss of the oyster Crassostrea *virginica*. Tulane Stud. Zool. 5(4): 55- 68.

Flaak, A. R. and C. E. Epifanio. 1978. Dietary protein levels and growth of the oyster Crassostrea *virginica* Mar. Biol. 45: 157-163.

Flint, L. H. 1956 Notes on the algal food of shrimp and oysters. Proc. La. Acad. Sci. 19: 11-14.

Foster-Smith, R. L. 1975. The role of mucus in the mechanism of feeding in three filter-feeding bivalves. Proc. Malac. Soc. London 41: 571-588.

Foster-Smith, R. L. 1978. The function of the pallial organs of bivalves in controlling ingestion. J. Moll. Stud. 44: 83-99.

Frazier, J. M. 1975. The dynamics of metals in the American oyster, Crassostrea *virginica*. I. Seasonal effects. Chesapeake Sci. 16: 162-171.

Frazier, J. M. 1976 The dynamics of metals in the American oyster Crassostrea *virginica*. II. Environmental effects. Chesapeake Sci. 17: 188-197.

Fretter, V. and A. Graham. 1964. Reproduction. In: K. M. Wilbur and C. M. Yonge (eds.). Physiology of Mollusca, Vol. 1, pp.l27-164. Academic Press, New York.

Frey, D. G. 1944. Oyster conservation problems on the Potomac River. Proc. Natl. Shellfish. Assoc. 35: 3 pp.

Frierman, E. M. 1976 Occurrence of hematopoietic neoplasms in Virginia oysters (*Crassostrea virginica*). Mar. Fish. Rev. 38(10): 34-36

Gabbott, P. A., D. A. Jones and D. H. Nichols. 1975. Studies on the design and acceptability of microencapsualted diets for marine particle feeders. II. Bivalve molluscs. Proc. European Symp. Mar. Biol. 10: 127-141.

Galtsoff, P. S. 1943. Increasing the production of oysters and other shellfish in the United States. U. S. Fish Wildl. Serv., Fish. Leaflet 22: 1-14.

Galtsoff, P. S. 1945. Problems of rehabilitation of Chesapeake Bay oyster resources. Proc. Natl. Shellfish. Assoc. 35: 3 pp.

Galtsoff, P. S. 1946 Reaction of oysters to chlorination. U.S. Fish Wildl. Serv. Rep. 11: 1-28.

Galtsoff, P. S. 1958a. Observations on muscle attachments, ciliary motion, and the pallial organ of oysters. Proc. Natl. Shellfish Assoc. 48: 154- 1 61.

Galtsoff, P. S. 1958b. The past and future of oyster research. Proc. Natl. Shellfish. Assoc. 48: 8-22.

Galtsoff, P. S. 1964. The American Oyster Crassostrea *virginica* Gmelin. Fish. Bull. 64: 1-480.

Galtsoff, P. S., H. F. Prytherch and H. C. McMillin. 1930. An experimental study in production and collection of seed oysters. Bull. U.S. Bur. Fish. 46: 197-263.

Galtsoff, P. S., H. F. Prytherch, R. S. Smith and V. Koehring. 1935. Effects of crude oil pollution on oysters in Louisiana waters. U.S. Burl Fish., Bull. No. 48: 143-210.

Garcia Sandoval, S. 1972. Dinamica de los bancos ostricolas en relacion con factores del ambiente y el control ejercido mediante obras hidraulicas en la laguna de Pueblo Viejo, Ver., Mexico. Memorias, IV Cong. Nac. Oceanogr. (Mexico) Mexico, D. F., Mexico. pp. 429-442.

Garton, D. and W. B. Stickle. 1980. Effects of salinity and temperature on the predation rate of *Thais haemastoma* on *Crassostrea virginica* spat. Biol. Bull. 158(1): 49-57.

Gentile, J. H., J. Cardin, M. Johnson and S. Sosnowski. 1976. Power Plants, Chlorine, and Estuaries. EPA-600/3-76-055. USEPA, Environmental Res. Lab., Narragansett, Rl. 28 pp.

George, W. C. 1952. The digestion and absorption of fat in lamellibranches. Biol. Bull. 102: 118-127.

Giese, A. C. 1959. Comparative physiology: Annual reproductive cycles of marine invertebrates. Ann. Rev. Physiol. 21: 547-576

Gillespie, L., R. M. Ingle and W. K. Havens. 1965. Glucose nutrition and longevity in oysters. Quart. J. Fla. Acad. Sci. 27: 279-288.

Gillespie, L., R. M. Ingle and W. K. Havens. 1966 Nutritional Studies with Adult Oysters. Fla. DNR, Mar. Res. Lab., Tech. Serv. 51. 26pp.

Glancy, J. B. 1944. Observations on the fattening of oysters in Great South Bay, New York. Proc. Natl. Shellfish. Assoc. 35; 9 pp.

Glude, J. B. 1957. Copper, a possible barrier to oyster drills. Proc. Natl. Shellfish. Assoc. 47: 73-82.

Glude, J. B. 1966 Criteria of success and failure in the management of shellfisheries. Trans. Amer. Fish. Soc. 95: 260-263.

Godwin, R. K. and W. B. Shepard. 1979. Forcing squares, triangles and ellipses into a circular paradigm: The use of the commons dilemma in examining the allocation of common resources. West. Poll Quart. 32(3): 265-277.

Grave, C. 1910. The resources of Maryland for oyster production. Report of the Oyster Commission to the General Assembly of Maryland. pp. 167-180.

Grave, C. 1912. A manual of oyster culture in Maryland. Fourth Rep. Board Shell Fish Commissioners. Baltimore, Md. pp. 279-348.

Grave, C. 1916 The process of feeding in the oyster. Science 44: 178-181.

Green, B.K. 1916 Seventh Report of the Shell Fish Commission of Maryland, 1914 and 1915. Kohn and Pollock, Inc., Baltimore, Md. 78 pp.

Green, J. 1968. The Biology of Estuarine Animals. Univ. of Wash. Press, Seattle. 401pp.

Greig, R. A., B. A. Nelson and D. A. Nelson. 1975. Trace metal content in the American oyster. Mar. Pollut. Bull. 6: 72-73.

Gross, F. and J. C. Smyth. 1946 The decline of oyster populations. Nature 157: 540-542.

Guida, V. G. 1976 Sponge predation in the oyster reef community as demonstrated with *Cliona celata* Grant. J. Exp. Mar. Biol. Ecol. 25: 109-122.

Guillard, R. R. 1958. Some factors in the use of nannoplankton cultures as food for larval and juvenile bivalves. Proc. Natl. Shellfish. Assoc. 48: 134-142.

Guillard, R. R. 1959. Further evidence of the destruction of bivalve larvae by bacteria. Biol. Bull. 117: 258-263.

Gunkel, W. and G. Gussmann. 1980. Oil, oil dispersants and related substances in the marine environment. Helgolander Meeresunters. 33: 164-181.

Gunter, G. 1950. The generic status of living oysters and the scientific name of the common American species. Amer. Midl. Naturalist 43: 438-449.

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

Gunter, G. 1955. Mortality of oysters and abundance of certain associates as related to salinity. Ecology 36: 601-605.

Haley, L. E. and G. F. Newkirk. 1978. Selecting oysters for faster growth. Proc. Ann. Mtg. World Mariculture Society 8: 557-564.

Hammer, R. C. 1948. Present status of the Chesapeake Bay oyster bars in Maryland. Proc. Natl. Shellfish. Assoc. (1947): 8-10.

Hancock, D. A. 1965. The determination of natural mortality and its causes in an exploited population of cockles (Cardium edule L.). Fish. Invest. Ser. 2. Vol. 24 (2): 1-40.

Hancock, D. A. 1967. Growth and mesh selection in the edible cockle (*Cardium edule* L.). J. Appl. Ecol. 4: 137-157.

Hancock, D. A. 1973. The relationship between stock and recruitment in exploited invertebrates. Rapp.P. v. Reun. Cons. Int. Explor. Mer 164: 113-131.

Hancock, D. A. 1979. Population dynamics and management of shellfish stocks. Rapp. P.-v. Reun. Cons. Int. Explor. Mer. 175: 8-19.

Hancock, D. A. and A. C. Simpson. 1962. Parameters of marine invertebrate populations. In: E. D. LeCren and M. W. Holdgate (eds.). The Exploitation of Natural Animal Populations, pp. 29-50. Blackwell, Oxford .

Hansen, D. J., P. R. Parrish and J. Forester. 1974. Arochlor 1016: Toxicity to and uptake by estuarine animals. Envir. Res. 7: 363-373.

Hardin, G. 1968. The tragedy of the commons. Science 162: 1243-1248.

Hariati, T. 1976 Stomach content analyses of local oyster (*Crassostrea cucullata* Born) from Banten Bay. (In Indonesian, English summary). Indonesian Mar. Fish. Res. Rep., (No. 1): 87-95.

Harrison, W. 1967. Environmental effects of dredging and spoil deposition. Proc. First World Dredging Conf., New York, NY. pp. 535-559.

Harshbarger, J. C., S. C. Chang and S. V. Otto. 1977. Chalamydiae (with phages), mycoplasmas and rickettsiae in Chesapeake Bay bivalves. Science 196: 666-668.

Harshbarger, J. C., S. V. Otto and S. C. Chang. 1979. Proliferative disorders in Crassostrea *virginica* and *Mya arenaria* from the Chesapeake Bay and intranuclear virus-like inclusions in *Mya arenaria* with germinomas from a Maine oil spill site. Haliotis 8: 243-248.

Haskin, H. H. 1950. The selection of food by the common oyster drill, *Urosalpinx cinerea* Say. Proc. Natl. Shellfish. Assoc. 41: 62-68.

Haskin, H. H. 1964. The distribution of oyster larvae. Proc. Symp. Exp. Mar. Ecol., Univ. Rhode Island, Occas. Publ. 2: 76-80.

Haskin, H. H. 1969. Population dynamics of oyster drills on a Delaware Bay oyster ground. Proc. Natl. Shellfish. Assoc. 59: 3.

Haskin, H. H. and W. J. Canzonier. 1969. Recent evidence of MSX - resistance in various stocks of oysters. (Abstract). Proc. Natl. Shellf. Assoc. 59: 4.

Haskin, H. H., W. J. Canzonier and J. L. Myhre. 1965. The history of "MSX" on Delaware Bay oyster grounds, 1957-1965. (Abstract). Am. Malacol. Union Inc., Ann. Rep. 32: 20-21.

Haskin, H. H. and S. E. Ford. 1978. Mortality patterns and disease resistance in Delaware Bay oysters. (Abstract). Proc. Natl. Shellfish. Assoc. 68: 80

Haskin, H. H., L. A. Stauber and J. G. Mackin. 1966 *Minchinia nelsoni* n. sp. (Haplosporida, Haplosporidiidae): Causative agent of the Delaware Bay oyster epizootic. Science 153: 1414-1416.

Haskin, H. H. and S. Tweed. 1976. Oyster Setting and Early Spat Survival at Critical Salinity Levels on Natural Seed Oyster Beds of Delaware Bay. Final Report. Water Resources Res. Inst., Rutgers Univ., New Brunswick, N.J. 66 pp.

Haven, D. S. 1958. Effects of pea crabs, *Pinnotheres ostreum*, on oysters, Crassostrea *virginica*. Proc. Natl. Shellfish. Assoc. 49: 77-86

Haven, D. S. 1965. Supplemental feeding of oysters with starch. Chesapeake Sci. 6: 43-51.

Haven, D. S. 1981. Modernizing the Oyster Industry, pp. 47-54. In. D. Webster (ed.). Oyster Culture in Maryland 1980: A Proceedings. Univ. Maryland Coop. Ext. Serv., College Park, Md. Rep. UM-SG-MAP-81-01.

Haven, D. S., W. J. Hargis and P. C. Kendall. 1978. The Oyster Industry of Virginia: Its Status, Problems and Promise. Virginia Inst. Mar. Sci. Spec. Papers Mar. Sci. (No. 4). 1024 pp.

Haven, D. S. and R. Morales-Alamo. 1970. Filtration of particles from suspension by the American oyster. Biol. Bull. 139(2): 248-264.

Haven, D. S. and K. W. Turgeon. 1968. Influence of small quantities of cornstarch and dextrose on glycogen levels of Crassostrea *virginica*. (Abstract Proc. Natl. Shellfish. Assoc. 58: 4.

Haven, D. S. and J. P. Whitcomb. 1969. Treatment of Shell with Polystream to Increase Survival of Oysters (*Crassostrea virginica*) in Virginia VIMS Spec. Sci. Rep. No. 54; 6 pp.;

Haven, D. S., J. P. Whitcomb and Q. C. Davis. 1979. A mechanical escalator harvester for live oysters and shell. Mar. Fish. Rev. 41: 17-20.

Heller, J. and F. B. Taub. 1971. The production of extracellular products by the marine alga *Monochrysis lutheri* as a nutrient source for bacteria Proc. Natl. Shellfish Assoc. 61: 8.

Hellier, T. R., Jr. and L. S. Kornicker. 1962. Sedimentation from a hydraulic dredge in a bay. Publ. Inst. Mar. Sci. Univ. Texas 8: 212-215.

Helm, M. M. 1977. Mixed algal feeding of *Ostrea edulis* larvae with *Isochrysis galbana* and *Tetraselmis suecica*. J. Mar. Biol. Assoc. UK. 57: 1019-1029.

Helm, M. M., D. L. Holland and R. R. Stephenson. 1973. The effect of supplementary algal feeding of a hatchery breeding stock of *Ostrea edulis* L. on larval vigor. J. Mar. Biol. Assoc. UK. 53: 673684.

Helm, M. M., and P. F. Millican. 1977. Experiments in the hatchery rearing of Pacific oyster larvae (*Crassostrea gigas* Thunberg). Aquaculture 11: 1-12.

Henderson, J. T. 1929. Lethal temperatures of lamellibranchiata. Contr. Canad. Biol. 4(25): 397-411.

Hidu, H. 1969. Gregarious setting in the American oyster Crassostrea *virginica* (Gmelin). Chesapeake Sci. 10: 85-92.

Hidu, H. 1978. Setting of estuarine invertebrates in Delaware Bay, New Jersey, related to intertidal-subtidal gradients. Int. Rev. Ges. Hydrobiol. 63: 637-661.

Hidu, H., K. G. Drobeck, E. A. Dunnington, Jr., W. H. Roosenburg and R. L. Beckett. 1969. Oyster Hatcheries for the Chesapeake Bay Region. NRI Spec. Rep. 2, Natural Resources Institute, U. Md., Solomons, Md. 18 pp.

Hidu, H. and H. H. Haskin. 1978. Swimming speeds of oyster larvae Crassostrea *virginica* in different salinities and temperatures. Estuaries 1: 252-255.

Hidu, H., W. H. Roosenburg, K. G. Drobeck, A. J. McErlean and J. A. Mihursky. 1974. Thermal tolerance of oyster larvae Crassostrea *virginica* Gmelin, as related to power plant operation. Proc. Natl. Shellfish. Assoc. 64: 102-110.

Hidu, H. and H. S. Tubiash. 1963. A bacterial basis for the growth of antibiotic treated bivalve larvae. Proc. Natl. Shellfish. Assoc. 54: 25-39.

Hidu, H. and R. Ukeles. 1962. Dried unicellular algae as food for larvae of the hard shell clam, *Mercenaria mercenaria.* Proc. Natl. Shellfish. Assoc. 53: 85-101.

Hidu, H., W. G. Valleau and F. P. Veitch. 1978. Gregarious setting in European and American oysters—Response to surface chemistry vs. waterborne phenomena. Proc. Natl. Shellfish. Assoc. 68: 11-16.

Hillman, R. E. 1964. Chromatographic evidence of intraspecific genetic differences in the eastern oyster, Crassostrea *virginica*. Syst. Zool. 13: 12-16.

Hillman, R. E. 1965. Chromatographic studies of allopatric populations of the eastern oyster, Crassostrea *virginica* Chesapeake Sci. 6: 115-116.

Himmelman, J. H. 1980. Reproductive cycle patterns in the chiton genus *Mopalia* (Polyplacophora). Nautilus 94: 39-49.

Hoese, H. D. 1964. Studies on oyster scavengers and their relation to the fungus, *Dermocystidium marinum*. Proc. Natl. Shellfish. Assoc. 53: 161-174.

Hoese, H. D. and D. Hoese. 1967. Studies on the biology of the feeding reaction in *Gobiosoma bosci*. Tulane Stud. Zool. 14: 55-73.

Holland, D. L. and B. E. Spencer. 1973. Biochemical changes in fed and starved oysters, *Ostrea edulis* L., during larval development, metamorphosis, and early spat growth. J. Mar. Biol. Assoc. UK. 53: 287-298.

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

Hopkins, S. H. 1956 *Odostomia impressa* parasitizing southern oysters. Science 124: 628-629.

Hopkins, S. H. 1957. Our present knowledge of the oyster parasite "*Bucephalus*." Proc. Natl. Shellfish. Assoc. 47: 58-61.

Hopkins, S. H. 1962. Distribution of species of *Cliona* (boring sponge) on the Eastern Shore of Virginia in relation to salinity. Chesapeake Sci. 3: 121-124.

Huguenin, J. E. 1977. The reluctance of the oyster drill (*Urosalpinx cinerea*) to cross metallic copper. Proc. Natl. Shellfish. Assoc. 67: 80-84.

Ingersoll, E. 1881. The History and Present Condition of the Fishing Industries. The oyster industry. U. S. Census Bureau, 10th Census. Dept. of Interior. Washington, D. C. 251 pp.

Ingle, R. M. 1951. Spawning and setting of oysters in relation to seasonal environmental changes. Bull. Mar. Sci. Gulf Carib. 1: 111-135.

Ingle, R. M. 1952. Studies of the effect of dredging operations upon fish and shellfish. Fla. State Bd. Conserv., Tech. Ser. No. 5: 1-25.

Ingle, R. M. and C. E. Dawson, Jr. 1952. Growth of the American oyster Crassostrea *virginica* (Gmelin) in Florida waters. Bull. Mar. Sci. Gulf Carib. 2: 393-404.

Jensen, W. P. 1981. Leased bottom and the Maryland oyster fishery, pp. 117-127. In: D. Webster (ed.). Oyster Culture in Maryland 1980: A Proceedings. Univ. Maryland Coop. Ext. Serv., College Park, Md. Rep. UM-SG-MAP-81-01.

Johnson, F. G. 1977. Sublethal biological effects of petroleum hydrocarbon exposure: bacteria, algae, and invertebrates. In: D. C. Malins (ed.), Effects of Petroleum on Arctic and Subarctic Marine Environments and Organisms, pp. 271-318. Academic Press, New York.

Jørgensen, C. B. 1966 Biology of Suspension Feeding. Pergamon Press, Oxford. 357 pp.

Jørgensen, C. B. 1975. Comparative physiology of suspension feeding. Ann. Rev. Physiol. 37: 5779.

Jørgensen, C. B. 1976. Comparative studies on the function of gills in suspension feeding bivalves, with special reference to effects of serotonin. Biol. Bull. 151: 331-334.

Kandler, R. 1928. Untersuchungen uber die Biologie der Auster, Nr. 3. Verbreitung der Austernbrut im Wattenmeer. Wiss. Meeresunt. Abt. Helgoland 17: 1.

Kaufman, L. F. 1979. Dependence of the time of gamete maturation and spawning on environmental temperature in the Virginia oyster Crassostrea *virginica*. Hydrobiological Journal 14(4): 29-30.

Keck, R., D. Maurer and L. Watling. 1973. Tidal stream development and its effect on the distribution of the American oyster. Hydrobiologia 42: 369-379.

Kennedy, A. V. and H. I. Battle. 1964. Cyclic changes in the gonad of the American oyster Crassostrea *virginica* (Gmelin). Can. J. Zool. 42: 305-321.

Kennedy, V. S. 1980. Comparison of recent and past patterns of oyster settlement and seasonal fouling in Broad Creek and Tred Avon River, Maryland. Proc. Natl. Shellfish. Assoc. 70: 36-40.

Kerr. S. R. amd W. P. Vass. 1973. Pesticide residues in aquatic invertebrates. In: C. A. Edwards (ed.), Environmental Pollution by Pesticides, pp. 134-180. Plenum Press, New York.

Kerswill, C. J. 1949. Effects of water circulation on the growth of quahaugs and oysters. J. Fish. Res. Bd. Can. 7: 545-551.

Ketchum, B. H. 1954. Relation between circulation and planktonic populations in estuaries. Ecology 35: 191-200.

Kincaid, J. 1915. Oyster culture in Washington. Trans. Second Ann. Mtg. Pacific Fisheries Soc.

Kiørboe, T., F. Møhlenberg and O. Nøhr. 1980. Feeding, particle selection and carbon absorption in *Mytilus edulis* in different mixtures of algae and resuspended bottom material. Ophelia 19(2): 193-205.

Knight-Jones, E. W. 1951. Aspects of the setting behaviour of larvae of *Ostrea edulis* on Essex oyster beds. Rapp. Proc. v. I.C.E.S. 128(2): 3034.

Kopfler, F. 1974. The accumulation of organic and inorganic mercury compounds by the eastern oyster, Crassostrea *virginica*. Bull. Environ. Contam. Toxicol. 11: 275-280.

Korringa, P. 1941. Experiments and observations on swarming, pelagic life and setting in the European flat oyster, *Ostrea edulis* L. Arch. Neerl. Zool. 10: 1-249.

Korringa, P. 1946 A revival of natural oyster beds? Nature 158: 586-587.

Korringa, P. 1949. *Crepidula fornicata* as an oyster-pest. J. Cons. Perm. Int. Explor. Mer., Rapp. P.V. Reun. 128: 55-59.

Korringa, P. 1952. Recent advances in oyster biology. Quart. Rev. Biol. 27: 266-308; 339-365.

Korringa, P. 1957. On the supposed compulsory relation between oviparous oysters and waters of reduced salinity. Ann. Biol. 33: 109-116

Korringa P. 1976 Farming the Cupped Oysters of the Genus *Crassostrea*. Elsevier, New York. 208 pp.

Krantz, G.E. and J. F. Chamberlin. 1978. Blue crab predation on cultchless oyster spat. Proc. Natl. Shellfish. Assoc. 68: 38-41.

Krantz, G. E. and D. W. Meritt. 1977. An analysis of trends in oyster spat set in the Maryland portion of the Chesapeake Bay. Proc. Natl. Shellfish. Assoc. 67: 53-59.

Kremer, P. 1979. Predation by the ctenophore *Mnemiopsis leidyi* in Narragansett Bay, Rhode Island. Estuaries 2: 97-105.

Kunkle, D. E. 1957. The vertical distribution of oyster larvae in Delaware Bay. Proc. Natl. Shellfish. Assoc. 48: 90-91.

Kusuki, Y. 1977a. On measurement of the filtration rates of the Japanese oyster. (In Japanese, English summary). Bull. Jap. Soc. Sci. Fish. 43: 1069-1976.

Kusuki, Y. 1977b. Retention of small particles by the gills of the Japanese oyster. (In Japanese, English summary). Bull. Jap. Soc. Sci. Fish. 43: 1391-1396

Lake, J. L. and C. Hershner. 1977. Petroleum sulfur-containing compounds and aromatic hydrocarbons in the marine molluscs *Modiolus demissus* and Crassostrea *virginica*. In: American Petroleum Institute, Proceedings 1977 Oil Spill Conference (Prevention, Behavior, Control, Cleanup), March 8-10, 1977. pp. 627-632. A.P.I., Washington, D. C.

Landers, W. S. and E. W. Rhodes, Jr. 1970. Some factors influencing predation by the flatworm, *Stylochus ellipticus* (Girard), on oysters. Chesapeake Sci. 11: 55- 60.

Landers, W. S. and R. C. Toner. 1962. Survival and movements of the flatworm, *Stylochus ellipticus*, in different salinities and temperatures. Biol. Bull. 123: 146-153.

Langton, R. W. and P. A. Gabbot. 1974. The tidal rhythm of extracellular digestion and response to feeding in *Ostrea edulis*. Mar. Biol. 24: 181-187.

Langton, R. W. and G. U. McKay. 1974. The effect of continuous versus discontinuous feeding on the growth of hatchery reared spat of Crassostrea *gigas* Thunberg. Journal du Conseil 35: 361-363.

Langton, R. W. and G. U. McKay. 1976. Growth of Crassostrea *gigas* spat under different feeding regimes in a hatchery. Aquaculture 7: 225-233.

Lannan, J. E. 1980a. Broodstock management of Crassostrea *gigas*. I. Genetic and environmental variation in survival in the larval-rearing system. Aquaculture 21: 323-336.

Lannan, J. E. 1980b. Broodstock management of Crassostrea *gigas*. III. Selective breeding for improved larval survival. Aquaculture 21: 347-351.

Lannan, J. E. 1980c. Broodstock management of Crassostrea *virginica*. IV. Inbreeding and larval survival. Aquaculture 21: 353-356.

Lannan, J. E., A. Robinson and W. P. Breese. 1980. Broodstock management of Crassostrea *gigas* II. Broodstock conditioning to maximize larval survival. Aquaculture 21: 337-345.

Larsen, P. F. 1978. *Boccardia hamata* (Polychaeta: Spionidae): A potential pest of the American oyster in the James River, Virginia. Estuaries 1: 183-185.

Lee, C. 1979. Seasonal and spatial study of oyster spat in Mobile Bay and East Mississippi Sound. M.S. Thesis, Univ. Alabama, Dauphin Island, Alabama. 90 pp.

Lindsay, C., R. E. Westley and C. S. Sayce. 1959. Prediction of oyster setting in the State of Washington. Proc. Natl. Shellfish. Assoc. 49: 59-70.

Lipovsky, V. P. and K. K. Chew. 1973. Laboratory control of Pacific oyster mortality by manipulation of temperature and nutrient concentration. Proc. Natl. Shellfish Assoc. 63: 3.

Lipovsky, V. P. and K. K. Chew. 1974. Why "fat" oysters die: a theory on mortality in southern Puget Sound. Proc. Natl. Shellfish Assoc. 64: 13.

Lippson, A. J. 1973. The Chesapeake Bay in Maryland: An Atlas of Natural Resources. Johns Hopkins Univ. Press, Baltimore and London. 56 pp.

Lipschultz, F. and G. Krantz. 1978. An analysis of oyster hatchery production of cultched and cultchless oysters utilizing linear programming techniques. Proc. Natl. Shellfish. Assoc. 68: 5-10.

Little, E. J. and J. A. Quick, Jr. 1976 Ecology, resource rehabilitation, and fungal parasitology of commercial oysters, *Crassostrea virginica* (Gmelin), in Pensacola Estuary, Florida. Fla. Mar. Res. Publ. No. 21: 1-89.

Logie, R. R., R. E. Drinnan and E. B. Henderson. 1961. Rehabilitation of disease-depleted oyster populations in eastern Canada. Proc. Gulf Carib. Fish. Inst. 13: 109-113.

Longwell, A. C. 1976. Review of genetic and related studies on commercial oysters and other pelecypod mollusks. J. Fish. Res. Bd. Canada 33: 1100-1107.

Longwell, A. C. and S. S. Stiles. 1970. The genetic system and breeding potential of the commercial American oyster. Endeavour 29: 94-99.

Longwell, A. C. and S. S. Stiles. 1973. Oyster genetics and probable future role of genetics in aquaculture. Malacol. Rev. 6: 151-177.

Loosanoff, V. L. 1932. Observations on Propagation of Oysters in James and Corrotoman Rivers and the Seaside of Virginia. Virginia Commission of Fisheries, Newport News, Va. 45 pp.

Loosanoff, V. L. 1949a. On the food selectivity of oysters. Science 110: 122.

Loosanoff, V. L. 1949b. Vertical distribution of oyster larvae of different ages during the tidal cycle. Anat. Rec. 105(3): 591-592.

Loosanoff, V. L. 1953. Behavior of oysters in water of low salinity. Proc. Natl. Shellfish Assoc. (1952): 135-151.

Loosanoff, V. L. 1956 Two obscure oyster enemies in New England waters. Science 123: 1119-1120.

Loosanoff, V. L. 1958. Some aspects of behavior of oysters at different temperatures. Biol. Bull. 114: 57-70.

Loosanoff, V. L. 1959. *Condylostoma*, an enemy of bivalve larvae. Science 129: 147-148.

Loosanoff, V. L. 1961. Recent advances in the control of shellfish predators and competitors. Proc. Gulf Carib. Fish. Inst. 13: 113-128.

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

Loosanoff, V. L. 1965. Gonad development and discharge of spawn in oysters of Long Island Sound. Biol. Bull. 129: 546-561.

Loosanoff, V. L. 1969. Maturation of gonads of oysters, Crassostrea *virginica*, of different geographical areas subjected to relatively low temperatures. Veliger 11: 153-163.

Loosanoff, V. L. 1972. Research requirements for development of molluscan farming in the United States. Progress in Fishery and Food Science 5: 165-179.

Loosanoff, V. L. 1974. Factors responsible for the mass mortalities of molluscan larvae in nature: a review. Proc. Ann. Meetg. World Mariculture Soc. 5: 297-309.

Loosanoff, V. L. and H. C. Davis. 1952. Temperature requirements for maturation of gonads of northern oysters. Biol. Bull. 103: 80-96

Loosanoff, V. L. and H. C. Davis. 1963. Rearing of bivalve mollusks. Adv. Mar. Biol. 1: 1-136

Loosanoff, V. L. and J. B. Engle. 1942. Accumulation and discharge of spawn by oysters living at different depths. Biol. Bull. 82: 413-422.

Loosanoff, V. L. and J. B. Engle. 1945. Feeding and fattening of oysters. Proc. Natl. Shellfish. Assoc. 35; 7pp.

Loosanoff, V. L. and J. B. Engle. 1947. Effect of different concentrations of microorganisms on the feeding of oysters (*O. virginica*). Fish. Bull. (No. 42): 57 pp.

Loosanoff, V. L. and J. B. Engle. 1948. *Polydora* in oysters suspended in the water. Biol. Bull. 85: 69-78.

Loosanoff, V. L., J. B. Engle and C. A. Nomejko. 1955. Differences in intensity of setting of oysters and starfish. Biol. Bull. 109: 75-81.

Loosanoff, V. L., C. L. MacKenzie Jr. and L. W. Shearer. 1960. Use of chemical barriers to protect shellfish beds from predators. U. S. Fish. Wildl. Serv. Fish. Bull. 23(6): 2-10.

Loosanoff, V. L. and C. A. Nomejko. 1946. Feeding of oysters in relation to tidal stages and to periods of light and darkness. Biol. Bull. 90: 244-264.

Loosanoff, V. L. and C. A. Nomejko. 1949. Growth of oysters, *O. virginica* during different months. Biol. Bull. 97: 82-94.

Loosanoff, V. L. and C. A. Nomejko. 1951. Existence of physiologically different races of oysters, Crassostrea *virginica*. Biol. Bull. 101: 151-156.

Loosanoff, V. L., and C. A. Nomejko. 1955. Growth of oysters with damaged shell edges. Biol. Bull. 108: 151-159.

Loosanoff, V. L., and C. A. Nomejko. 1958. Burial as a method for control of the common oyster drill, *Urosalpinx cinerea,* of Long Island Sound. Proc. Natl. Shellfish. Assoc. 48: 83-89.

Loosanoff, V. L. and F. D. Tommers. 1947. Effect of low pH upon the rate of water pumping of oysters, *Ostrea virginica*. Anat. Rec. 99: 668-669, abstr. 245.

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

Losee, E. 1978. Influence of heredity on larval and spat growth in Crassostrea *virginica*. Proc. Ann. Mtg. World Maricult. Soc. 9: 101-107.

Losee, E. 1979. Relationship between larval and spat growth rates in the oyster (*Crassostrea virginica*). Aquaculture 16: 123- 126:

Lowe, J. I., P. R. Parrish, J. M. Patrick, Jr. and J. Forester. 1972. Effects of the polychlorinated biphenyl Aroclor 1254 on the American oyster Crassostrea *virginica*. Mar. Biol. 17: 209-215.

Lowe, J. I., P. D. Wilson, A. J. Rick and A. J. Wilson, Jr. 1971. Chronic exposure of oysters to DDT, toxaphene and parathion. Proc. Natl. Shellfish. Assoc. 61: 71-79.

Lund, D. S. 1973. Feeding studies with Pacific oyster larvae. Proc. Natl. Shellfish. Assoc. 63: 8.

Lund, E. J. 1957a. Self silting by the oyster and its significance for sedimentation geology. Publ. Inst. Mar. Sci. Univ. Texas 4: 320-327.

Lund, E. J. 1957b. Effect of bleedwater, “soluble fraction” and crude oil on the oyster. Publ. Inst. Mar. Sci., Univ. Texas 4: 328-341.

Lund, E. J. and E. Powell. 1957. Note on the reflex inhibition of water propulsion by the oyster. Publ. Inst. Mar. Sci., Univ. Texas 4: 293-295.

Lunz, G. R., Jr. 1938. Oyster Culture with Reference to Dredging Operations in South Carolina. Rep. U. S. Engineers, Charleston, S.C. 135 pp.

Lunz, G. R., Jr. 1941. *Polydora*, a pest in South Carolina oysters. J. Elisha Mitchell Sci. Soc. 57: 273-283.

Lunz, G. R., Jr. 1942. Investigation of the effects of dredging on oyster leads in Duval County, Florida. Handbook of Oyster Survey. Intracoastal Waterway. Spec. Rep., U. S. Army Corps of Engineers, Jacksonville, Fla.

Lunz, G. R., Jr. 1947. *Callinectes* versus *Ostrea*. J. Elisha Mitchell Sci. Soc. 63: 81.

Lutz, R. A., H. Hidu and K. G. Drobeck. 1970. Acute temperature increase as a stimulus to setting in the American oyster Crassostrea *virginica* (Gmelin). Proc. Natl. Shellfish. Assoc. 60: 68-71.

MacGinitie, G. E. 1941. On the method of feeding of four pelecypods. Biol. Bull. 80: 18-25.

MacGinitie, G. E. 1945. The size of the mesh openings in mucous feeding nets of marine animals. Biol. Bull. 88: 107-111.

Maclnnes, J. R. and A. Calabrese. 1978. Response of embryos of the American oyster, Crassostrea *virginica*, to heavy metals at different temperatures. In: D. S. McLusky and A. J. Berry (eds.): Physiology and Behavior of Marine Organisms. Proc. 12th Europ. Mar. Biol. Symp. pp. 195-202. Pergamon Press, New York.

Maclnnes, J. R. and A. Calabrese. 1979. Combined effects of salinity, temperature, and copper on embryos and early larvae of the American oyster, Crassostrea *virginica* Arch. Environm. Contam. Toxicol. 8: 553-562.

MacKenzie, C. L., Jr. 1961a. Growth and reproduction of the oyster drill *Eupleura caudata* in the York River, Virginia. Ecology 42: 317-338.

MacKenzie, C. L., Jr. 1961b. A practical chemical method for killing mussels and other oyster competitors. Comm. Fish. Rev. 23: 15-19.

MacKenzie, C. L., Jr. 1962. Transportation of oyster drills by horseshoe “crabs”. Science 137: 36-37.

MacKenzie, C. L., Jr. 1971. Control of oyster drills, *Eupleura caudata* and *Urosalpinx cinerea*, with the chemical Polystream. Fish. Bull. 68: 285-297.

MacKenzie, C. L., Jr. 1977a. Development of an aquacultural program for rehabilitation of damaged oyster reefs in Mississippi. Mar. Fish. Rev. Paper 1259. pp. 1-13.

MacKenzie, C. L., Jr. 1977b. Sea anemone predation on larval oysters in Chesapeake Bay (Maryland). Proc. Natl. Shellfish. Assoc. 67: 113-117.

MacKenzie, C. L., Jr. 1981. Biotic potential and environmental resistance in the American oyster (*Crassostrea virginica*) in Long Island Sound. Aquaculture 22: 229-268.

Mackay, N. J., R. J. Williams, J. L. Kacpezac, A. J. Collins and E. H. Auty. 1975. Heavy metals in cultured oysters, *Crassostrea commercialis* from the estuaries of New South Wales. Aust. J. Mar. Freshw. Res. 26: 31-46

Mackie, G. 1969. Ouantitative studies of feeding in the oyster, Crassostrea *vir - ginica*. Proc. Natl. Shellfish. Assoc. 59: 6-7.

Mackin, J. G. 1951. Histopathology of infection of Crassostrea *virginica* by *Dermocystidium marinum*. Bull. Mar. Sci. Gulf and Carib. 1: 72-87.

Mackin, J. G. 1961a. Status of research on oyster diseases in North America. Proc. Gulf Carib. Fish. Inst. 13: 98-109.

Mackin, J. G. 1961b. Mortalities of oysters. Proc. Natl. Shellf. Assoc. 50: 21-40.

Mackin, J. G. 1962a. Oyster diseases caused by *Dermocystidium marinum* and other microorganisms in Louisiana. Publ. Inst. Mar. Sci., Univ. Texas 7: 132-229.

Mackin, J. G. 1962b. Canal dredging and silting in Louisiana bays. Publ. Inst. Mar. Sci. Univ. Texas. 7: 262-314.

Mackin, J. G. and S. H. Hopkins. 1962. Studies on oysters in relation to the oil industry. Publ. Inst. Mar. Sci. Univ. Texas 7: 3-131.

Mackin, J. G. and H. Loesch. 1955. A haplosporidan hyperparasite of oysters. Proc. Natl. Shellf. Assoc. 45: 182-183.

Mackin, J. G., H. M. Owen and A. Collier. 1950. Preliminary note on the occurrence of a new protistan parasite, *Dermocystidium marinum* n. sp. in Crassostrea *virginica* (Gmelin). Science 111: 328-329.

Mackin, J. G. and A. K. Sparks. 1962. A study of the effect on oysters of crude oil loss from a wild well. Publ. Inst. Mar. Sci. Univ. Texas 7: 230-261.

Malouf, R. 1971. The food consumption and growth of the larvae of the Pacific oyster, Crassostrea *gigas* Proc. Natl. Shellfish. Assoc. 61: 10.

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

Manning, J. H. 1953. Setting of oyster larvae and survival of spat in the St. Mary's River, Maryland, in relation to fouling of cultch. Proc. Natl. Shellfish. Assoc. (1952): 74-78.

Manning, J. H. 1957. The Maryland Soft Shell Clam Industry and Its Effects on Tidewater Resources. Md. Dept. Res. Educ., Resource Study Rep. No. 11: 25 pp.

Manning, J. H. and H. H. Whaley. 1954. Distribution of oyster larvae and spat in relation to some environmental factors in a tidal estuary. Proc. Natl. Shellfish. Assoc. 45: 56-65.

Manzi, J. J., V. G. Burrell and W. Z. Carson. 1977. A comparison of growth and survival of subtidal Crassostrea *virginica* (Gmelin) in South Carolina salt marsh impoundments. Aquaculture 12: 293-310.

Marshall, N. 1954. Factors controlling the distribution of oysters in a neutral estuary. Ecology 35: 322-327.

Martin, G. W. 1923. Food of the oyster. Bot. Gaz 75: 143-169.

Maryland Board of Natural Resources. 1951. 8th Annual Report. Annapolis, Md. 182pp.

Maryland Board of Natural Resources. 1952. 9th Annual Report. Annapolis, Md. 207pp.

Maryland Board of Natural Resources. 1953. The Commercial Fisheries of Maryland. A Report to the General Assembly of Maryland. Md. Dept. Resource Educ., Educ. Ser. No. 30. 45 pp.

Maryland Board of Natural Resources. 1955. 12th Annual Report. Annapolis, Md.. 201 pp.

Maryland Board of Natural Resources. 1960. 17th Annual Report. Annapolis, Md. 165 pp.

Maryland Board of Natural Resources. 1962. 19th Annual Report. Annapolis, Md. 142 pp.

Maryland Board of Natural Resources. 1963. 20th Annual Report. Annapolis, Md. 190 pp.

Maryland Board of Natural Resources. 1965. 22nd Annual Report. Annapolis, Md. 210 pp.

Maryland Commission on Conservation of Natural Resources. 1948. Report to the Governor of Maryland. 91 pp.

Masch, F. D. and W. H. Espey, Jr. 1967. Shell Dredging as a Factor in Sedimentation in Galveston Bay. Center for Research in Water Resources. Univ. of Texas at Austin. Tech. Rep. HYD 06 6702; CRWR-7. 168 pp.

Mason, J. W., J. H. Cho and A. C. Anderson. 1976. Uptake and loss of inorganic mercury in the eastern oyster, Crassostrea *virginica*. Arch. Environ. Contam. Toxicol. 4: 361-376.

Mason, J. W. and D. W. Rowe. 1976. The accumulation and loss of dieldrin and endrin in the eastern oyster. Arch. Environ. Contam. Toxicol. 4: 349-360.

Mathers, N. F. 1972. The tracing of a natural algal food labelled with a carbon 14 isotope through the digestive tract of *Ostrea edulis* L. Proc. Malacol. Soc. London 40: 115-124.

Mathers, N. F. 1973. A comparative histochemical survey of enzymes associated with the processes of digestion in *Ostrea edulis* and *Crassostrea angulata* (Mollusca: Bivalvia). J. Zool. London 769: 169-179.

Mathers, N. F. 1974. Some comparative aspects of filter feeding in *Ostrea edulis* and *Crassostrea angulata* (Mollusca, Bivalvia). Proc. Malacol. Soc. London 41: 89-97.

Maurer, D. and K. S. Price, Jr. 1968. Holding and spawning Delaware Bay oysters (*Crassostrea virginica*) out of season. I. Laboratory facilities for retarding spawning. Proc. Natl. Shellf. Assoc. 58: 71-77.

Maurer, D. and L. Watling. 1973. Studies on the oyster community in Delaware: The effects of the estuarine environment on the associated fauna. Int. Rev. Ges. Hydrobiol. 58: 161-201.

May, E. B. 1971. A survey of the oyster and oyster shell resources of Alabama. Alabama Mar. Resource Bull. 4: 1-53.

May, E. B. 1972. The effect of floodwater on oysters in Mobile Bay. Proc. Natl. Shellfish. Assoc. 62: 67-71.

May, E. B. 1973. Environmental effects of hydraulic dredging in estuaries. Ala. Mar. Res. Bull. 9: 185.

McCrady, J. 1874. Observations on the food and reproductive organs of *Ostrea virginica*, with some account of *Bucephalus cuculus* nov. sp. Proc. Boston Soc. Natur. Hist. 16: 170-192.

McDermott, J. 1960. The predation of oysters and barnacles by crabs of the family Xanthidae. Proc. Penn. Acad. Sci. 34: 199-211.

McDermott, J. 1964. Food habits of the toadfish, *Opsanus tau* (L.), in New Jersey waters. Proc. Penn. Acad. Sci. 38: 64-71.

McGraw, K. A. and G. Gunter. 1972. Observations on killing the Virginia oyster by the Gulf oyster borer, *Thais haemastoma*, with evidence for a paralytic secretion. Proc. Natl. Shellfish. Assoc. 62: 95-97.

McHugh, J. L. 1956. Trapping oyster drills in Virginia. II. The time factor in relation to the catch per trap. Proc. Natl. Shellfish. Assoc. 46: 155-168.

McHugh, J. L. 1957. Trapping oyster drills in Virginia. III. The catch per trap in relation to condition of bait. Proc. Natl. Shellfish. Assoc. 47: 83-102.

Medcof, J. C. 1939. Larval life of the oyster (*Ostrea virginica*) in Bideford River. J. Fish. Res. Bd. Canada 4: 287-301.

Medcof, J. C. 1946. The mud-blister worm, *Polydora*, in Canadian oysters. J. Fish. Res. Bd. Can. 6: 498-505.

Medcof, J. C. 1955. Day and night characteristics of spatfall and of behavior of oyster larvae. J. Fish. Res. Bd. Canada 12: 270-286.

Medcof, J. C. 1961. Oyster farming in the Maritimes. Fish. Res. Bd. Canada Bull. 131: 1-158.

Medcof, J. C. and C. J. Kerswill. 1965. Effects of light on growth of oysters, mussels, and quahaugs. J. Fish. Res. Bd. Canada 22: 281-288.

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: 70-153.

Menzel, R. W. 1974. Portuguese and Japanese oysters are the same species. J. Fish. Res. Bd. Canada 31: 453-456

Menzel, R. W. and S. H. Hopkins. 1955a. Crabs as predators of oysters in Louisiana. Proc. Natl. Shellfish. Assoc. 46: 177-184.

Menzel, R. W. and S. H. Hopkins. 1955b. The growth of oysters parasitized by the fungus *Dermocystidium marinum* and by the trematode *Bucephalus cuculus*. J. Parasitol. 41: 333-343.

Menzel, R.W., N. C. Hulings and R. R. Hathaway. 1957. Causes of depletion of oysters in St. Vincent Bar, Apalachicola Bay, Florida. Proc. Natl. Shellfish. Assoc. 48: 66-71.

Menzel, R. W., N. C. Hulings and R. R. Hathaway. 1966. Oyster abundance in Apalachicola Bay, Florida in relation to biotic associations influenced by salinity and other factors. Gulf Res. Rept. 2: 73-96.

Menzel, R. W. and F. E. Nichy. 1958. Studies of the distribution and feeding habits of some oyster predators in Alligator Harbor, Florida. Bull. Mar. Sci. Gulf Carib. 8: 125-145.

Meritt, D. W. 1977. Oyster Spat Set on Natural Cultch in the Maryland Portion of the Chesapeake Bay (1939-1975). Univ. Maryland, Center for Environmental and Estuarine Studies, Spec. Rep. No. 7. 111 pp.

Millar, R. H. 1955. Notes on the mechanism of food movement in the gut of the larval oyster, *Ostrea edulis*. Quart. J. Micr. Sci. 96: 539-544.

Millar, R. H. and J. M. Scott. 1967a. Bacteria-free culture of oyster larvae. Nature 216: 1139-1140.

Millar, R. H. and J. M. Scott. 1967b. The larvae of the oyster *Ostrea edulis* during starvation. J. Mar. Biol. Assoc., UK. 47: 475-484.

Miller, R. J. 1974. Distribution and biomass of an estuarine ctenophore population, *Mnemiopsis leidyi* (A. Agassiz). Chesapeake Sci. 15: 1-8.

Miyazaki, I. 1938. On a substance which is contained in green algae and induces spawning action of the male oyster. Bull. Jap. Soc. Sci. Fish. 7: 137-138.

Møhlenberg, F. and H. U. Riisgard. 1978. Efficiency of particle retention in 13 species of suspension feeding bivalves. Ophelia 17(2): 239-246.

Moore, H. J. 1971. The structure of the latero-frontal cirri on the gills of certain lamellibranch molluscs and their role in suspension feeding. Mar. Biol. 11: 23-27.

Moore, P. G. 1977. Inorganic particulate suspensions in the sea and their effects on marine animals. Oceanogr. Mar. Biol. Ann. Rev. 15: 225-363.

Morse, D. C. 1944. Some observations on the food and feeding of oysters in Chesapeake Bay. Proc. Natl. Shellfish. Assoc. 55: 17-19.

Morton, B. S. 1971. The diurnal rhythm and tidal rhythm of feeding and digestion in *Ostrea edulis*. Biol. J. Linn. Soc. 3: 329-342.

Morton, B. S. 1973. A new theory of feeding and digestion in the filterfeeding lamellibranchia. Malacologia 14: 63-79.

Morton, B. S. 1977. The tidal rhythm of feeding and digestion in the Pacific oyster, Crassostrea *gigas* (Thunberg). J. Exp. Mar. Biol. Ecol. 26: 135-151.

Munson, T. D. and R. J. Huggett. 1972. Current status of research on the biological effects of pesticides in Chesapeake Bay. Chesapeake Sci. 13 (Supplement): S154-S156.

National Academy of Science. 1975. Petroleum in the Marine Environment. Washington, D. C. 107 pp.

Needler, A. B. 1932. Sex reversal in *Ostrea virginica*. Contr. Can. Biol. Fish. 7: 285-294.

Neff, J. M. 1979. Polycyclic Aromatic Hydrocarbons in the Aquatic Environment. Sources, Fates and Biological Effects. Applied Science Publishers, London. 262 pp.

Neff, J. M., D. Dixit, B. A. Cox and J. W. Anderson. 1976. Accumulation and release of petroleum-derived aromatic hydrocarbons by marine animals. Mar. Biol. 38: 279-289.

Nelson, J. 1908. Report of the Biologist. Observations on the fixation of oyster spat at Barnegat, N.J., 1907. Rep. Biol. Dept. New Jersey Agric. College Expt. Stn., pp. 207-282.

Nelson, J. 1909. Report of the Biologist. Studies on natural oyster propagation at Barnegat, 1908. Rep. Biol. Dept. New Jersey Agric. College Expt. Stn., pp. 151-191.

Nelson, J. 1912. Report of the Biologist. Observations of natural propagation of oysters at Barnegat, N. J. in 1911. Rep. Biol. Dept. New Jersey Agric. College Experiment Stn. pp. 271-309.

Nelson, J. 1916 Report of the Department of Biology. New Jersey Agric. College Experiment Stn. pp. 239-260.

Nelson, T. C. 1917. Report of the Assistant Biologist. Rept. Dept. Biol. New Jersey Agric. College Expt. Stn., pp. 401-433.

Nelson, T. C. 1921. Report of the Department of Biology. Rep. N.J. Agric. College Expt. Sta. for 1920: 319-355.

Nelson, T. C. 1923a. Report of the Biologist. Rep. Dept. Biol. New Jersey Agric. College Experiment Stn., pp. 321-351.

Nelson, T. C. 1923b. The mechanism of feeding in the oyster. Proc. Soc. Exp. Biol. Med. 21: 166-168.

Nelson, T. C. 1924. Report of the Department of Biology for the year ending June 30, 1923. N. J. Agric. Coll. Experiment Stn., pp. 195-209.

Nelson, T. C. 1925a. Report of the Department of Biology. N. J. Agric. Coll. Experiment Stn., pp. 237-248.

Nelson, T. C. 1925b. On the occurrence and food habits of ctenophores in New Jersey inland coastal waters. Biol. Bull. 48: 92-111.

Nelson, T. C. 1926. Report of the Department of Biology. New Jersey State Agricultural Experiment Station. pp. 281-288.

Nelson, T. C. 1928a. On the distribution of critical temperatures for spawning and for ciliary activity in bivalve molluscs. Science 67: 220-221.

Nelson, T. C. 1928b. On the association of the common goby (*Gobiosoma bosci*) with the oyster, including a case of parasitism. Nat. Hist. 28: 78-84.

Nelson, T. C. 1933. On the digestion of animal forms by the oyster. Proc. Soc. Exp. Biol Med. 30: 1287- 1290.

Nelson, T. C. 1938. The feeding mechanisms of the oyster. I. On the pallium and branchial chambers of *Ostrea virginica*, *O. edulis* and *O. angulata* with comparisons with other members of the genus. J. Morphol. 63: 1-61.

Nelson, T. C. 1947a. Some contributions from the land in determining conditions of life in the sea. Ecol Monogr. 17: 337-346

Nelson, T. C. 1947b. On the need for developing new strains of oysters through selective breeding of domestic stock, cross breeding with other species and the introduction of species from other areas. Proc. Natl. Shellfish. Assoc. (1946): 1-7.

Nelson, T. C. 1950a. What can science offer the oyster grower? Proc. Natl. Shellfish. Assoc. (1949): 9 pp.

Nelson, T. C. 1953. Some observations on the migrations and setting of oyster larvae. Proc. Natl. Shellfish. Assoc. 43: 99-104.

Nelson, T. C. 1955. Observations of the behavior and distribution of oyster larvae. Proc. Natl. Shellfish. Assoc. 45: 23-28.

Nelson, T. C. 1957. Some scientific aids to the oyster industry. Amer. Sci. 45: 301-332.

Nelson, T. C. 1960. The feeding mechanism of the oyster. II. On the gills and palps of *Ostrea edulis*, *Crassostrea virginica* and C. *angulata* J. Morphol. 107: 163-191.

Nelson, T. C. and A. Chestnut. 1945. Some observations on the transplantation of two weeks old set and of older oysters. Proc. Natl. Shellfish. Assoc. (1944): 3 pp.

Nelson, T. C. and E. B. Perkins. 1931. Annual Report of the Department of Biology, July, 1929-June 30, 1930. New Jersey Agric. Experiment Sta. Bull. 522: 3-47.

Newell, R. C., L. G. Johson and L. H. Kofoed. 1977. Adjustment of the components of energy balance in response to temperature change in *Ostrea edulis*. Oecologia 30: 97-110.

Newkirk, G. F. 1980. Review of the genetics and the potential for selective breeding of commercially important bivalves. Aquaculture 19: 209-228.

Newkirk, G. F. and L. E. Haley. 1977. The role of natural populations in the genetic improvement of species used in aquaculture. Proc. Ann. Mtg. World Maricult. Soc. 8: 567-578.

Newkirk, G. F., L. E. Haley, D. L. Waugh and R. W. Doyle. 1977. Genetics of larvae and spat growth rate in the oyster, Crassostrea *virginica*. Mar. Biol. 41: 49-52.

Newman, M. W. 1972. An oyster neoplasm of apparent mesenchymal origin. J. Natl. Cancer Inst. 48(1): 237-243.

Nichol, A. J. 1937. The Oyster-Packing Industry of Baltimore. Its History and Current Problems. Bulletin, Chesapeake Biological Laboratory, Univ. Md. 32 pp.

Nichy, F. E. and R. W. Menzel. 1960. Mortality of intertidal and subtidal oysters in Alligator Harbor, Florida. Proc. Natl. Shellfish. Assoc. 51: 33-41.

Nimmo, D. R. 1979. Pesticides: Their impact on the estuarine environment. In: W. B. Vernberg, A. Calabrese, F. P. Thurberg and F. J. Vernberg (eds.). Marine Pollution: Functional Responses, pp.259-270. Academic Press, New York.

Nimmo, D. R., D. J. Hansen, J. A. Couch, N. R. Cooley, P. R. Parrish and J. I. Lowe. 1975. Toxicity of Arochlor 1254 and its physiological activity in several estuarine organisms. Arch Environ. Contam. 3: 22-39.

NOAA, Office of Fisheries Development, NMFS. 1977a. A Comprehensive Review of the Commercial Oyster Industries in the United States. NOAA-NMFS, Washington, D.C. 63 pp.

NOAA, Office of Fisheries Development, NMFS. 1977b. The Molluscan Shellfish Industries and Water Quality: Problems and Opportunities. NOAA-NMFS, Washington, D.C. 46 pp.

Noor-Udin. 1962. An account of the food of oysters of Karachi Coast together with a note on fattening and their behavior to some ecological and hydrographical factors. Agr. Pakistan 13: 427-444.

Noyes, G. S. 1978. Effects of petroleum on adults and larvae of the American oyster, Crassostrea *virginica* Gmelin. Ph.D. Thesis, Rutgers University. Diss. Abstr. Int., V.39/II-B: 5277.

Odum, W. E. 1970. Insidious alteration of the estuarine environment. Trans. Amer. Fish. Soc. 99: 836-847.

Orton, J. H. 1937. Some interrelations between bivalve spatfalls, hydrography and fisheries. Nature 140: 505.

Otto, S. V., J. B. Hammed and A. Rosenfield. 1975. Decline of *Minchinia nelsoni* in Maryland waters of Chesapeake Bay. (Abstract). Proc. Natl Shellfish. Assoc. 65: 5.

Otto, S. V., J. C. Harshbarger and S. C. Chang. 1979. States of selected unicellular eucaryote pathogens, and prevalence and histopathology of inclusions containing obligate procaryote parasites, in commercial bivalve mollusks from Maryland estuaries. Haliotis 8: 285-295.

Otto, S. V. and G. E. Krantz. 1976 An epizootic of "Dermo" disease in oysters in the Maryland portion of the Chesapeake Bay. (Abstract). Proc. Natl. Shellf. Assoc. 67: 121.

Outten, W. 1980. Maryland's State seed program. In: D. Webster (ed.). Oyster Culture in Maryland '79. A Conference Proceedings. Coop. Ext. Serv., Univ. Maryland, College Park, Md. pp. 15-24.

Owen, G. 1974. Feeding and digestion in the bivalvia. Adv. Comp. Physiol. Biochem. 5: 1-35.

Parrish, P. R., J. A. Couch, J. Forester, J. M. Patrick, Jr. and G. H. Cook. 1974. Dieldrin: effects on several estuarine organisms. Proc. 27th Ann. Conf. Southeast. Assoc. Game Fish Comm. pp. 427-434.

Parrish, P. R., S. C. Schimmel, D. J. Hansen, J. M. Patrick, Jr. and J. Forester. 1976. Chlordane: effects on several estuarine organisms. J. Toxicol. Environ. Health 1: 485-494.

Parsons, A. D. 1973. Prey selection in the oyster leech, *Stylochus ellipticus*. (Abstract). Proc. Natl. Assoc. Shellfish. 63: 4-5.

Perkins, E. B. 1931. A study of oyster problems in Barnegat Bay. Ann. Rep. Dept. Biol., New Jersey Agric. Coll. Experiment Stn. (July 1, 1929-June 30, 1930).

Perkins, E. B. 1932. Progress of oyster investigations in Barnegat Bay during 1930. Rep. Dept. Biol. New Jersey Agric. Coll. Experiment Stn. (July 1, 1930-June 30, 1931).

Pollard, J. F. 1973. Experiments to re-establish historical oyster seed grounds and to control the southern oyster drill. La. Wildl. Fish. Comm., Tech. Bull. 6: 1-82.

Pomerat, C. M. and E. R. Reiner. 1942. The influence of surface angle and of light on the attachment of barnacles and their sedentary organisms. Biol. Bull. 82: 14-25.

Power, G. 1970. More about oysters than you wanted to know. Maryland Law Review 30: 199-225.

Pratt, D. M. 1978. Homing in *Urosalpinx cinerea* in response to prey effluent and tidal periodicity. Veliger 20: 30-32.

Preston, E. 1971. The importance of ingestion in chromium-51 accumulation by Crassostrea *virginica*. J. exp. Mar. Biol. Ecol. 6: 47-54.

Price, K. S., Jr. and D. Maurer. 1971. Holding and spawning Delaware Bay oysters (*Crassostrea virginica*) out of season. II. Temperature requirements for maturation of gonads. Proc. Natl. Shellfish. Assoc. 61: 29-34.

Prieur, D. and S. LeRoux. 1975. The comparative growth of some algal populations and their associated bacteria in laboratory cultures. Proc. European Symp. Mar. Biol. 10: 345-355.

Pritchard, D. W. 1953. Distribution of oyster larvae in relation to hydrographic conditions. Proc. Gulf Carib. Fish. Inst. 1952: 123-132.

Provenzano, A. J., Jr. 1959. Effects of the flatworm *Stylochus ellipticus* Girard on oyster spat in two salt water ponds in Massachusetts. Proc. Natl. Shellfish. Assoc. 69: 83-88.

Prytherch, H. F. 1929. Investigation of the physical conditions controlling spawning of oysters and the occurrence, distribution and setting of the oyster larvae in Milford Harbor, Connecticut. Bull. U. S. Burl Fish. 44: 429-503.

Prytherch, H. F. 1934. The role of copper in setting, metamorphosis, and distribution of the American oyster, Crassostrea *virginica*. Ecol. Monogr. 4: 49- 107.

Prytherch, H. F. 1940. The life cycle and morphology of *Nematopsis ostrearum*, sp. nov., a gregarine parasite of the mud crab and oyster. J. Morphol. 66: 39-65.

Purchon, R. D. 1968. The Biology of the Mollusca. Pergamon Press, New York. 560 pp.

Purchon, R. D. 1971. Digestion in filter feeding bivalves—a new concept. Proc. Malacol. Soc. London 39: 253-262.

Quayle, D. B. and L. D. B. Terhune. 1967a. A plankton sampler for oyster larvae. J. Fish. Res. Bd. Canada. 24: 883-885.

Quayle, D. B. and L. D. B. Terhune. 1967b. The hydrodynamics and field trial results of a perforated pipe plankton sampler. Fish. Res. Bd. Canada, Manuscript Rep. Ser. (Biological), N. 887: 1-32.

Quick, J. A., Jr. 1971. Symposium on a preliminary investigation: The effect of elevated temperature on the American oyster Crassostrea *virginica* (Gmelin). Florida Dept. Nat. Res., Res. Mar. Lab., Prof. Paper 13: 1-190.

Quittmeyer, C. L. 1966 A Report on the Chesapeake Bay Fisheries of Maryland. Seafood Advisory Committee of Wye Institute, Centreville, Md. 68 pp.

Rawls, C. K. 1977. Field studies of shell regrowth as a bioindicator of eastern oyster (*Crassostrea virginica* Gmelin) response to 2, 4-D BEE in Maryland tidewaters. Chesapeake Sci. 18: 266-271.

Ray, S. M. 1966 A review of the culture method for detecting *Dermocystidium marinum*, with suggested modifications and precautions. Proc. Natl. Shellfish. Assoc. 54: 55-69.

Ray, S. M. and D. V. Aldrich. 1961. Oyster studies. U. S. Fish. Wildl. Serv., Burl Comm. Fish., Circ. (No. 129): 72-74.

Reimold, R. J. and F. C. Daiber. 1967. Eutrophication of estuarine areas by rainwater. Chesapeake Sci. 8: 132-133.

Renzoni, A. 1975. Toxicity of three oils to bivalve gametes and larvae. Mar. Poll. Bull. 6: 125-128.

Rhodes, E. W. and W. S. Landers. 1972. Growth of oyster larvae, *Crassostrea virginica*, of various sizes in different concentrations of the chrysophyte, *Isochrysis galbana*. Proc. Natl. Shellfish. Assoc. 63: 53-59.

Ribelin, B. W. and A. Collier. 1977. Studies on the gill ciliation of the American oyster, Crassostrea *virginica* (Gmelin). J. Morph. 151: 439-450.

Ritchie, T. P. and R. W. Menzel. 1969. Influence of light on larval settlement of American oysters. Proc. Natl. Shellfish. Assoc. 59: 116-120.

Rochford, D. J. 1951. Studies in Australian estuarine hydrology. I. Introductory and comparative features. Aust. J. Mar. Freshw. Res. 2: 1-117.

Rochford, D. J. 1952. The application of studies on estuarine hydrology to certain problems in Australian oyster biology. Rapp. et Proces - verbaux des Reunion 131: 35-57.

Rodhouse, P. G. 1978. Energy transformations by the oyster *Ostrea edulis* L. in a temperate estuary. J. Exp. Mar. Biol. Ecol. 34: 1-22.

Rodhouse, P. G. 1979. A note on the energy budget for an oyster population in a temperate estuary. J. Exp. Mar. Biol. Ecol. 37: 205-212.

Rogers, H. M. 1940. Occurrence and retention of plankton within the estuary. J. Fish. Res. Bd. Canada 5: 164-171.

Romeril, M. G. 1971. The uptake and distribution of ^{65}Zn in oysters. Mar. Biol. 9: 347-354.

Roosenburg, W. H. 1969. Greening and copper accumulation in the American oyster, Crassostrea *virginica*. Proc. Natl. Shellfish. Assoc. 59: 91-103.

Roosenburg, W. H. 1976. Can the oyster industry learn from livestock breeders? Proc. Natl. Shellfish. Assoc. 66: 95-99.

Roosenburg, W. H., J. C. Rhoderick, R. M. Block, V. S. Kennedy, S. R. Gullans, S. M. Vreenegoor, A. Rosenkranz and C. Collette. 1980. Effects of chlorine-produced oxidants on survival of larvae of the oyster Crassostrea *virginica*. Mar. Ecol. Prog. Ser. 3: 93-96

Rosales, M. T. L., A. V. Butello, H. Bravo and E. F. Mandelli. 1979. PCBs and organochlorine insecticides in oysters from coastal lagoons of the Gulf of Mexico, Mexico. Bull. Environ. Contam. Toxicol. 21: 652-656.

Rose, C. D. 1973. Mortality of market-sized oysters (*Crassostrea virginica*) in the vicinity of a dredging operation. Chesapeake Sci. 14: 135.

Rosenfield, A., L. Buchanan and G. B. Chapman. 1969. Comparison of the fine structure of spores of three species of *Minchinia* (Haplosporida, Haplosporidiidae). J. Parasitology 55: 921-941.

Ruddell, C. L. and D.W. Rains. 1975. The relationship between zinc and copper and the basophils of two crassostreid oysters, Crassostrea *gigas* and *Crassostrea virginica*. Comp. Biochem. Physiol. 51A: 585-591.

Ruddy, G. M., S. Y. Feng and G. S. Campbell. 1975. The effect of prolonged exposure to elevated temperatures on the biochemical constituents, gonadal development and shell deposition of the American oyster, Crassostrea *virginica*. Comp. Biochem. Physiol. 51B: 157-164.

Ryan, E. P. 1956 Observations on the life histories and the distribution of the Xanthidae (mud crabs) of Chesapeake Bay. Amer. Midl. Nat. 56: 138-162.

Saddler, J. B. and F. B. Taub. 1972. Chemical variability of algal shellfish feeds. Proc. Natl. Shellfish. Assoc. 62: 6-7.

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

Sandoz, M. and S. H. Hopkins. 1947. Early life history of the oyster crab, *Pinnotheres ostreum* (Say). Biol. Bull. 93: 250-258.

Sastry, A. N. 1963. Reproduction of the bay scallop, *Aequipecten irradians* Lamarck. Influence of temperature on maturation and spawning. Biol. Bull. 125: 146-153.

Sastry, A. N. 1966 Temperature effects in reproduction of the bay scallop, *Aequipecten irradians* Lamarck. Biol. Bull. 30: 118-134.

Sastry, A. N. 1968. Relationships among food, temperature and gonad development of the bay scallop, *Aequipecten irradians* Lamarck. Physiol. Zool. 41: 44-53.

Sastry, A. N. 1970. Environmental regulation of oocyte growth in the bay scallop, *Aequipecten irradians* Lamarck. Experientia 26: 1371-1372.

Sastry, A. N. 1975. Physiology and ecology of reproduction in marine invertebrates. In: F. J. Vernberg (ed.), Physiological Ecology of Estuarine Organisms, pp. 279-299. Univ. S. Carolina Press. Columbia.

Sastry, A. N. 1979. Pelecypoda (excluding Ostreidae). In: A. C. Giese and J. S. Pearse (eds.). Reproduction of Marine Invertebrates, Vol. V, pp. 113-292. Academic Press, New York.

Sastry, A. N. and N. J. Blake. 1971. Regulation of gonad development in the bay scallop, *Aequipecten irradians* Lamarck. Biol. Bull. 140: 247-283.

Sawyer, T. K., M. W. Newman and S. V. Otto. 1975. A gregarine-like parasite associated with pathology in the digestive tract of the American oyster, Crassostrea *virginica*. Proc. Natl. Shellf. Assoc. 65: 15-19.

Sayce, C. S. and C. C. Larson. 1966 Willapa oyster studies—Use of the pasture harrow for the cultivation of oysters. Comm. Fish. Rev. 28(10): 21-26

Sayce, C. S. and D. F. Tufts. 1968. The supplemental feeding of *Crassostrea gigas* in the laboratory. Proc. Natl. Shellfish. Assoc. 58: 14.

Schimmel, S. C., P. R. Parrish, D. J. Hansen, J. M. Patrick, Jr. and J. Forester. 1975. Endrin: Effects on several estuarine organisms. Proc. 28th Ann. Conf. S. E. Assoc. Game Fish. Comm pp. 187-194.

Schimmel, S. C., J. M. Patrick, Jr. and L. F. Faas. 1978. Effects of sodium pentaphlorophenate on several estuarine animals: toxicity, uptake, and depuration. In: K. R. Rao (ed.). Pentachlorophenol, pp. 147-155. Plenum Press, New York.

Schimmel, S. C., J. M. Patrick, Jr. and J. Forester. 1976. Heptachlor: Toxicity to and uptake by several estuarine organisms. J. Toxicol. Envir. Health. 1: 955-965.

Schimmel, S. C., J. M. Patrick, Jr. and J. Forester. 1977a. Uptake and toxicity of Toxaphene in several estuarine organisms. Arch. Envir. Contam. Toxicol. 5: 353-367.

Schimmel, S., J. M. Patrick, Jr. and J. Forester. 1977b. Toxicity and bioconcentration of BHC and Lindane to selected estuarine animals. Arch. Envir. Contam. Toxicol. 6: 355-363.

Schulte, G. J. and A. L. Lawrence. 1977. Uptake of D-Fructose from seawater by Pacific oyster spat. Amer. Zool. 17: 860.

Scott, G. I. and W. B. Vernberg. 1979. Seasonal effects of chlorine-produced oxidants on the growth, survival and physiology of the American oyster, Crassostrea *virginica* (Gmelin). In: W. B. Vernberg, F. P. Thurberg, A. Calabrese and F. J. Vernberg (eds.), Marine Pollution: Functional Responses, pp.415-435. Academic Press, New York.

Shaw, R., D.C. Arnold, and W. B. Stallworthy. 1970. Effects of light on spat settlement of the American oyster (*Crassostrea virginica*). J. Fish. Res. Bd. Canada 27: 743-748.

Shaw, W. N. 1966a. Advances in the off-bottom culture of oysters. Proc. Gulf Carib. Fish. Inst. 19: 108-115.

Shaw, W. N. 1966b. The growth and mortality of seed oysters, Crassostrea *vir - ginica*, from Broad Creek, Chesapeake Bay, Maryland, in high- and low-salinity waters. Proc. Natl. Shellfish. Assoc. 56: 59-63.

Shaw, W. N. 1967. Seasonal fouling and oyster setting on asbestos plates in Broad Creek, Talbot County, Maryland, 1963-65. Chesapeake Sci. 8: 228-236

Shaw, W. N. 1969. The past and present status of off-bottom oyster culture in North America. Trans. Amer. Fish. Soc. 98: 755-761.

Shaw, W. N. 1970. Raft production of seed oysters in upper Chesapeake Bay. Proc. Natl. Shellfish. Assoc. 60: 11.

Shaw, W. N. 1972. An off-bottom culture demonstration at Oxford, Md. Proc. Natl. Shellfish. Assoc. 62: 7.

Shaw, W. N. and G. T. Griffith. 1967. Effects of Polystream and Drillex on oyster setting in Chesapeake Bay and Chincoteague Bay. Proc. Natl. Shellfish. Assoc. 57: 17-23.

Shaw, W. N. and A. S. Merrill. 1966. Setting and growth of the American oyster, Crassostrea *virginica*, on navigation buoys in the lower Chesapeake Bay. Proc. Natl. Shellfish. Assoc. 56: 67-72.

Shelbourne, J. E. 1957. The 1951 oyster stock in the Rivers Crouch and Roach, Essex and the influence of water currents and scour on its distribution: with an account of comparative dredging experiments. Fish. Invest., London. Ser. II, Vol. 21: 1-27.

Sheldon, R.W. 1968. The effect of high population density on the growth and mortality of oysters (*Ostrea edulis*). J. Cons. Perm. Int. Explor. Mer. 31(3): 352-363.

Shuster, C. N. and B. H. Pringle. 1969. Trace metal accumulation by the American oyster, Crassostrea *virginica*. Proc. Natl. Shellfish. Assoc. 59: 91-103.

Sieling, F. W. 1950a. Intensity and distribution of oyster set in Chesapeake Bay and tributaries. Proc. Natl. Shellfish. Assoc. (1949): 28-32.

Sieling, F. W. 1950b. Maryland's Commercial Fishing Gears. II. The Oyster Gears. Md. Bd. Natl. Res. Educ. Ser. No. 25. 24 pp.

Sieling, F. W. 1951. Influence of seasoning and position of oyster shells on oyster setting. Proc. Natl. Shellfish. Assoc. (1950): 57-61.

Sindermann, C. J. 1968a. Bibliography of Oyster Parasites and Diseases. U.S. Fish Wildl. Serv., Spec. Sci. Rep., Fisheries, No. 563. 13 pp.

Sindermann, C. J. 1968b. Oyster Mortalities, with Particular Reference to Chesapeake Bay and the Atlantic Coast of North America. U. S. Fish Wildl. Serv., Spec. Sci. Rep., Fisheries, No. 569. 10 pp.

Sindermann, C. J. 1970. Principal Diseases of Marine Fish and Shellfish. Academic Press, New York. 369 pp.

Sindermann, C. J. (ed.). 1977. Disease Diagnosis and Control in North American Marine Aquaculture. Elsevier, New York. 330 pp.

Sindermann, C. J. and A. Rosenfield. 1967. Principal diseases of commercially important marine bivalve molluscs and crustacea. Fish. Bull. 66: 335-385.

Singh, S. M. and E. Zouros. 1978. Genetic variation associated with growth rate in the American oyster (*Crassostrea virginica*). Evolution 32: 342-353.

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

Smith, J.W. and J. V. Merriner. 1978. Biology and Identification of Rays in the Chesapeake Bay. VIMS Educ. Ser. No. 20; 22 pp.

Smith, R. O. 1949. Summary of Oyster Farming Experiments in South Carolina, 1939-1940. U. S. Fish Wildl. Serv. Spec. Sci. Rep. 63. 20 pp.

Snelson, J. T. 1977. The importance of chlorinated hydrocarbons in world agriculture. Ecotoxicol. Environ. Safety 1: 17-30.

Snieszko, S. F. (ed.). 1970. A Symposium on Diseases of Fish and Shellfishes. Amer. Fish. Soc., Spec. Publ. No. 5. Washington, D. C. 526 pp.

Sparks, A. K., J. L. Boswell and J. G. Mackin. 1958. Studies on the comparative utilization of oxygen by living and dead oysters. Proc. Natl. Shellfish. Assoc. 48: 92-102.

Sprague, J. B. and J. R. Duffy. 1971. DDT residues in Canadian Atlantic fishes and shellfishes in 1967. J. Fish. Res. Bd. Canada 28: 59-64.

Sprague, V. 1964. *Nosema dollfusi* n. sp. (Microsporidia, Nosematidae) a hyperparasite of *Bucephalus cuculus* in *Crassostrea virginica*. J. Protozool. 11: 381-385.

Sprague, V. 1970. Some protozoan parasites and hyperparasites in marine bivalve molluscs. In: S. F. Snieszko (ed.), A Symposium on Diseases of Fishes and Shellfishes, pp.551-526. Amer. Fish. Soc., Spec. Publ. No. 5.

Sprague, V. 1971. Diseases of oysters. Ann. Rev. Microbiol. 25: 211-230.

Sprague, V., E.A. Dunnginton, Jr. and E. Drobeck. 1969. Decrease in incidence in *Minchinia nelsoni* in oysters accompanying reduction of salinity in the laboratory. Proc. Natl. Shellfish. Assoc. 59: 23-26.

Stainken, D. and J. Rollwagen. 1979. PCB residues in bivalves and sediments of Raritan Bay. Bull Environ. Contam. Toxicol. 23: 690-697.

State Planning Commission. 1935. Conservation Problems in Maryland. Unpublished report of the Sub-Committee on Conservation. A. Wolman, Chairman. Maryland Energy Relief Administration. 64 pp.

Stauber, L. A. 1943. Ecological studies on the oyster drill, *Urosalpinx cinerea*, in Delaware Bay, with notes on the associated drill, *Eupleura caudata*, and with practical consideration of control methods. Unpublished manuscript, Oyster Res. Lab., Rutgers Univ., New Brunswick, N.J. (Not seen, quoted from Andrews, J. D. 1956.)

Stauber, L. A. 1950. The problem of physiological species with special reference to oysters and oyster drills. Ecology 18: 523-527.

Stegeman, J. J. and J. M. Teal. 1973. Accumulation, release and retention of petroleum hydrocarbons by the oyster Crassostrea *virginica*. Mar. Biol. 22: 37-44.

Steinberg, P. D. and V. S. Kennedy. 1979. Predation upon Crassostrea *virginica* (Gmelin) larvae by two invertebrate species common to Chesapeake Bay oyster bars. Veliger 22: 78-84.

Stenzel, H. B. 1971. Oysters. In: R. C. Moore (ed.). Treatise on Invertebrate Paleontology, Part N, Vol. 3, Mollusca 6, Bivalvia, pp.N953-N1224. Geol. Soc. America, Boulder, CO.

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

Stevenson, C. H. 1894. The oyster industry of Maryland. Bull. U. S. Fish Commission for 1892. pp. 205-297.

Strathmann, R.R. and E. Liese. 1979. On feeding mechanisms and clearance rates of molluscan veligers. Biol Bull. 157: 524-535.

Sunderlin, J. B., P. T. Baab and E. M. Patry. 1976. Growth of clam and oyster larvae on different algal diets in a tropical artificial upwelling mariculture system. Proc. Ann. Meetg. World Maricult. Soc. 7: 215-228.

Suttor, R. E. and T. D. Corrigan. 1968. economic effects of regulations in Maryland oyster fishery. U. S. Fish Wildl. Serv., Rep. No. 845, pp. 38-41.

Sweet, G. 1941. Oyster conservation in Connecticut: Past and present. Geogr. Rev. 31(4): 591-608.

Swift, M. L., K. Conger, J. Exler and S. Lakshmanan. 1975. Uptake of glucose and orthophosphate by the American oyster. Life Sci. 17: 1679-1684.

Tagatz, M. E., P. W. Borthwick, J. M. Ivey and J. Knight. 1976. Effects of leached Mirex on experimental communities of estuarine animals. Arch. Envir. Contam. Toxicol. 4: 435-442.

Tenore, K. R. and W. M. Dunstan. 1973. Comparison of rates of feeding and biodeposition of the American oyster, Crassostrea *virginica*, fed different species of phytoplankton. J. Exp. Mar. Biol. Ecol. 12: 19-26.

Thompson, R. J. and B. L. Bayne. 1974. Some relationship between growth, metabolism and food in the mussel, *Mytilus edulis*. Mar. Biol. 27: 317-326.

Thorson, G. 1936. The larval development, growth and metabolism of arctic marine bottom invertebrates. Meddr. Grønland 100: 1-155.

Thorson, G. 1964. Light as an ecological factor in the dispersal and settlement of larvae of m marine bottom invertebrates. Ophelia 1: 167-208.

Thurberg, F. P., A. Calabrese and M. A. Dawson. 1974. Effects of silver on oxygen consumption of bivalves at various salinities. In: F. J. Vernberg and W. B. Vernberg (eds.), Pollution and Physiology of Marine Organisms, pp. 67-78. Academic Press, New York.

Tripp, M. R. 1974. Effects of organophosphate pesticides on adult oysters (*Crassostrea virginica*). In: F. J. Vernberg and W. B. Vernberg (eds.). Pollution and Physiology of Marine Organisms, pp. 225-236. Academic Press, New York.

Truitt, R. V. 1921. A policy for the rehabilitation of the oyster industry in Maryland. Annual Report (1920), Md. Conserv. Committee (5 pp.).

Truitt, R. V. 1929. Chesapeake biological inquiry, 1929. Seventh Ann. Rep. Conserv. Dept. State of Maryland, Baltimore, Md., pp. 39-69.

Truitt, R. V. 1930. Chesapeake biological inquiry, 1930. Eighth Ann. Rep. Conserv. Dept. State of Md., Baltimore, Md., pp. 34-35.

Truitt, R. V. 1931. Recent Oyster Researches on Chesapeake Bay in Maryland. Chesapeake Biological Laboratory, Publ. No. 3. 28 pp.

Truitt, R. V. and P. V. Mook. 1925. Oyster problem inquiry of Chesapeake Bay. Third Ann. Rep. Conserv. Dept. State of Maryland, pp. 25-35. Baltimore, Md.

Tubiash, H. S. 1975. Bacterial pathogens associated with cultured bivalve mollusk larvae. In: W. L. Smith and M. H. Chanley (eds.). Culture of Marine Invertebrate Animals, pp. 61-71. Plenum Press, New York.

Tubiash, H. S., P. E. Chanley and E. Leifson. 1965. Bacillary necrosis, a disease of larval and juvenile bivalve molluscs. I. Etiology and epizootiology. J. Bacteriol. 90: 1036-1044.

Tubiash, H. S., R. R. Colwell and R. Sakazaki. 1970. Marine vibrios associated with bacillary necrosis, a disease of larval and juvenile bivalve molluscs. J. Bacteriol. 103: 272-273.

Turgeon, K. W. and D. S. Haven. 1978. Effects of cornstarch and dextrose in oysters. Veliger 20: 352-358.

Ukeles, R. 1962. the effect of several toxicants on five genera of marine phytoplankton. Appl Microbiol. 10: 532-537.

Ukeles, R. 1971. Nutritional requirements in shellfish culture. In: Price, K.S. and D. L. Maurer (eds). Artificial propagation of commercially valuable shellfish, pp.43-69. Univ. Delaware; Newark, DE.

Ukeles, R. 1976. Views on bivalve larvae nutrition. In: K. S. Price, Jr., W. N. Shaw and K. DS. Danberg (eds.). Proceedings of the First International Conference on Aquaculture Nutrition, pp. 127-162. Univ. Delaware Sea Grant College Program, Newark, DE.

Ukeles, R. and B. M. Sweeney. 1969. Influence of dinoflagellate trichocysts and other factors on the feeding of Crassostrea *virginica* larvae on *Monochrysis lutheri*. Limnol. Oceanogr. 14: 403-410.

Ulanowicz, R. E., W. C. Caplins and E. A. Dunnington. 1980. The forecasting of oyster harvest in central Chesapeake Bay. Est. Coastal Mar. Sci. 11: 101-106

Usuki, I. 1962. The stoppage and the recovery of the movement of cilia in oyster gill kept under the absence of O_2. Sci. Repts., Tohoku Univ., Ser. 4, Biology 28(2/3): 85-95.

Van Sickle, V. R., B. B. Barrett, L. J. Galick and T. B. Ford. 1976 Barataria Basin: Salinity Changes and Oyster Distribution. La Wildl. Fish. Comm., Tech. Bull. 20. Center for Wetland Resources, L.S.U., Baton Rouge, LA. 22 pp.

Van Winkle, W., Jr. 1968. The effects of season, temperature and salinity on the oxygen consumption of bivalve gill tissue. Comp. Biochem. Physiol. 26: 69-80.

Van Winkle, W., Jr. 1972. Ciliary activity and oxygen consumption of excised bivalve gill tissue. Comp. Biochem. Physiol. 42A: 473-485.

Varanasi, U. and D. C. Malins. 1977. Metabolism of petroleum hydrocarbons: Accumulation and biotransformation in marine organisms. In: D. C. Malins (ed.). Effects of Petroleum on Arctic and Subarctic Marine Environments and Organisms, pp. 175-270. Academic Press, New York.

Vernberg, F. J., C. Schlieper and D. Schneider. 1963. The influence of temperature and salinity on ciliary activity of excised gill tissue of mollusks from North Carolina. Comp. Biochem. Physiol. 8: 271-285.

Villadolid, D. V. and D. K. Villaluz. 1938. Animals destructive to oysters in Bacoor Bay, Luzon. Philippine J. Sci. 67: 393-396

Vreeland, V. 1974. Uptake of chlorobiphenyls of oysters. Environ. Poll. 6: 135-140.

Walker, N. P. and J. M. Gates. 1981. Financial feasibility of high density oyster culture in saltmarsh ponds with artificially prolonged tidal flows. Aquaculture 22: 11-20.

Walker, P. N. and J. W. Zahradnik. 1977. Kinetics of food utilization of oysters. Trans. Amer. Soc. Agric. Eng. 20: 795-798.

Wallace, D. H. 1952. A critique of present biological research on oysters. Proc. Gulf Carib. Fish. Inst. 5: 132-136

Walne, P. R. 1956. Destruction of competitive organisms on artificial oyster-spat collectors. Cons. Perm. Int. Explor. Mer., J. Cons. 12: 75-76

Walne, P. R. 1963. Observations on the food value of seven species of algae to larvae of *Ostrea edulis*. I. Feeding experiments. J. Mar. Biol. Assoc., UK. 43: 767-784.

Walne, P. R. 1965. Observations on the influence of food supply and temperature on the feeding and growth of the larvae of *Ostrea edulis.* Min. Agric. Fish. Food, Fish. Invest., UK, Ser. II (No. 24): 1-45.

Walne, P. R. 1970. Studies on the food value of nineteen genera of algae to juvenile bivalves of the genera *Ostrea*, *Crassostrea* and *Mytilus*. Fish. Invest. Ser. 2. 26(5): 62 pp.

Walne, P. R. 1974. Culture of Bivalve Molluscs. Fifty Years' Experience at Conwy. Fishing News (Books) Ltd., Surrey, England. 173 pp.

Walne, P. R. and G. Davies. 1977. The effect of mesh covers on the survival and growth of Crassostrea *gigas* Thunberg grown on the sea bed. Aquaculture 11: 313-321.

Waugh, G. D. 1972. Settlement of *Ostrea edulis* (L.), in relation to the cultivation of oyster grounds. Fish. Invest., London, Ser. 2, 27: 1-29.

Waugh, G. D. and A. Ansell. 1956. The effect, on oyster spatfall, of controlling barnacle settlement with DDT. Ann. Appl. Biol. 44: 619-625.

Webster, J. R. and R. Z. Medford. 1959. Flatworm distribution and associated oyster mortality in Chesapeake Bay. Proc. Natl. Shellfish. Assoc. 50: 85-89.

Weissenberg, R. 1968. Intracellular development of the microsporidan *Glugea anomata* Moniez in the hypertophying migratory cells of the fish *Gasterosteus aculeatus* L., an example of the formation of "Xenoma" tumors. J. Protozool. 15: 44-57.

Wells, H. W. 1961. The fauna of oyster beds, with special reference to the salinity factor. Ecol Monogr. 31: 241-266

Westley, R. E. 1964. Some relationships between Pacific oyster (*Crassostrea gigas*) condition and environment. Proc. Natl. Shellfish. Assoc. 55: 19-33.

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

Wharton, B. H. 1963. The Maryland Oyster Industry. Thesis submitted to the Stonier Graduate School of Banking, Rutgers University, New Brunswick, N.J. 64 pp.

Wharton, G. W. 1959. Oyster Conference, 7 January 1959, University of Maryland, College Park., Unpublished transcript of the conference. 82 pp. Available in library of Chesapeake Biological Laboratory, Solomons, Md.

Wharton, J. 1957. The Bounty of the Chesapeake. Fishing in Colonial Virginia Univ. Press of Virginia, Charlottesville, Va. 78 pp.

Wheatley, J. J., C. L. Quittmeyer and L. A. Thompson. 1959. The Economic Implications of the York River Industry. Bureau of Population and Economic Research, University of Virginia, Charlottesville, VA. 119 pp.

Whitehouse, J. W. 1975. Chlorination of Cooling Water: A Review of Literature on the Effects of Chlorine on Aquatic Organisms. Central Electricity Generating Labs., Memo. No. RD/L/M 496. 22 pp.

Whitfield, W. K., Jr. 1973. Construction and rehabilitation of commercial oyster reefs in Florida from 1949 through 1971. Fla. Dept. Nat. Resources, Mar. Res. Lab., Spec. Sci. Rept. No. 38: 1-42.

Widdows, J. 1978a. Combined effects of body size, food concentration and season on the physiology of *Mytilus edulis*. J. Mar. Biol. Assoc. U.K. 58: 109-124.

Widdows, J. 1978b. Physiological indices of stress in *Mytilus edulis*. J. Mar. Biol. Assoc. U.K. 58: 125-142.

Wilkins, N. P. 1981. The rationale and relevance of genetics in aquaculture: An overview. Aquaculture 22: 209-228.

Willis, S. A., W. K. Havens and R. M. Ingle. 1976. Quality Improvement of Oysters, Crassostrea *virginica* (Gmelin), Using Artificial Foods. Fla. DNR, Mar. Res. Lab. (No. 20); 22 pp.

Wilson, A. J. and J. Forester. 1978. Persistence of Aroclor 1254 in a contaminated estuary. Bull. Environ. Contam. Toxicol. 19: 637-640.

Wilson, J. H. 1978. The food value of *Phaeodactylum tricornutum* Bohlin to the larvae of *Ostrea edulis* L. and Crassostrea *gigas* Thunberg Aquaculture 13: 313-323.

Wilson, J. H. 1979. Observations on the grazing rates and growth of *Ostrea edulis* L. larvae when fed algal cultures of different ages. J. Exp. Mar. Biol. Ecol. 38: 188-199.

Wilson, J. H. and R. W. LaTouche. 1978. Intracellular digestion in two sublittoral populations of *Ostrea edulis* (Lamellibranchia). Mar. Biol. 47: 71-77.

Wilson, W. B. 1950. The effects of sedimentation due to dredging operations on oysters of Copano Bay, Texas. M.S. Thesis, Texas A&M Univ., College Station, TX. 128pp. (Not seen; quoted by May, 1973).

Windom, H. L. and R. G. Smith. 1972. Distribution of iron, magnesium, copper, zinc and silver in oysters along the Georgia coast. J. Fish. Res. Bd. Canada 29: 450-452.

Winslow, F. 1881. Deterioration of American oyster-beds. Pop. Sci. Monthly 20: 29-43; 145-156.

Winslow, F. 1882. Report on the Oyster Beds of the James River, Virginia, and of Tangier and Pocomoke Sounds, Maryland and Virginia. Appendix 11, Rep. U. S. Coast and Geodetic Survey for 1881. Washington, D. C. 87 pp.

Winslow, F. 1884. Present condition and future prospects of the oyster industry. Trans. Amer. Fish. Soc. 13: 148-163.

Winter, J. E. 1978. A review on the knowledge of suspension-feeding in lamellibranchiate bivalves, with special reference to artificial aquaculture systems. Aquaculture 13: 1-33.

Winter, J. E. and R. W. Langton. 1975. Feeding experiments with *Mytilus edulis* L. at small laboratory scale. In: G. Persoone and E. Jaspers (eds.). Proc. Europ. Mar. Biol. Symp. 10: 565-581.

Wisely, B. and R. A. P. Thick. 1967. Mortality of marine invertebrate larvae in mercury, copper and zinc solutions. Aust. J. Mar. Freshw. Res. 18: 63-72.

Wisely, B., R. Okamoto and B. L. Reid. 1978. Pacific oyster (*Crassostrea gigas*) spatfall prediction at Hiroshima, Japan, 1977. Aquaculture 15: 227-241.

Wisely, B. and B. L. Reid. 1978. Experimental feeding of Sydney rock oysters (*Crassostrea commercialis = Saccostrea cucullata*). Part I. Optimum particle sizes and concentrations. Aquaculture 15: 319-332.

Woelke, C. E. 1972. Development of a receiving water quality bioassay criterion based on the 48 hour Pacific oyster, Crassostrea *gigas* embryo. Wash. Dept. Fisheries, 9: 1-93.

Wolfe, D. A. 1970. Zinc enzymes in Crassostrea *virginica*. J. Fish. Res. Bd. Canada 27: 59-69.

Wolfe, D. A. 1977. Fate and Effects of Petroleum Hydrocarbons in Marine Ecosystems and Organisms. Pergamon Press, New York. 478 pp.

Wood, L. 1968. Physiological and ecological aspects of prey selection by the marine gastropod *Urosalpinx cinerea* (Prosobranchia: Muricidae). Malacologia 6: 267-320.

Wood, L. and W. J. Hargis, Jr. 1971. Transport of bivalve larvae in a tidal estuary. In: D. J. Crisp (ed.). Fourth Europ. Mar. Biol. Symp. Cambridge Univ. Press, pp. 29-44.

Wood, L. and B. A. Roberts. 1963. Differentiation of effects of two pesticides upon *Urosalpinx cinerea* Say from the Eastern Shore of Virginia. Proc. Natl. Shellfish. Assoc. 54: 75-85.

Yates, C. C. 1913. Summary of Survey of Oyster Bars of Maryland 1906-1912. U. S. Coast and Geodetic Survey, Washington, D.C. 81 pp.

Yonge, C M. 1926. Structure and physiology of the organs of feeding and digestion in *Ostrea edulis*. J. Mar. Biol. Assoc. UK. 14: 295-386

Zachary, A. and D. S. Haven. 1973. Survival and activity of the oyster drill *Urosalpinx cinerea* under conditions of fluctuating salinity. Mar. Biol. 22: 45-52.

Zaroogian, G. E. 1980. Crassostrea *virginica* as an indicator of cadmium pollution. Mar. Biol. 58: 275-284.

Zaroogian, G. E. and S.Cheer. 1976. Accumulation of cadmium by the American oyster, Crassostrea *virginica* Nature 261: 408-409.

Zaroogian, G. E., G. Morrison and J. F. Heltshe. 1979. *Crassostrea virginica* as an indicator of lead pollution. Mar. Biol. 52: 189-196.

Zouros, E., S. M. Singh and H. E. Miles. 1980. Growth rates in oysters: An overdominant phenotype and its possible explanations. Evolution 34: 856-867.

Annotated Bibliography

Annotated Bibliography
Of Chesapeake Bay Oyster Literature

Abrahamson, J. D. 1961. Economic aspects of markets for middle Atlantic oysters. Proc. Gulf Carib. Fish. Inst. 13: 128-131.

Examined economic aspects of the oyster industry in post-World War II years. Concluded that oyster production had not met demand, with a consequent decrease in per capita consumption. The supply had set the limit on national consumption. At the same time, prices rose steadily and the industry prospered. However, the market could absorb a greater production. Limits to increased production include loss of oyster grounds, and loss of oysters to disease and predators. Recommended more rental of grounds and increased culture of oysters.

Agnello, R. J. and L. P. Donnelley. 1975a. The interaction of economic, biological, and legal forces in the middle Atlantic oyster industry. Fish. Bull. 73: 256-261.

Discussed the oyster industry along the U.S. East Coast and presented a supply and demand model of the industry. Included consideration of the industry in Chesapeake Bay, concluding that there was evidence of overexploitation in the common property states, with suboptimal use of the natural resource. A footnote indicates that an unpublished study concluded that oystermen's income in 1969 would have increased by about 50% if all coastal states had relied on rental of oyster grounds.

Agnello, R. J. and L. P. Donnelley. 1975b. Prices and property rights in the fisheries. Southern Econ. J. 42: 253-262.

In this general survey of the effects of property right structures on ex-vessel prices and harvest quantities of fisheries, the authors showed that, for or the eastern oyster, common property rights are associated with lower prices and incomes compared with private property right structures. If all oyster resources were declared common property, the harvesters would tend to bring more oysters to market early in the season with unstable prices result-

Watermen unload the day's catch at a seafood processing house
In Cambridge, Maryland.

ing. A combination of common grounds and private holdings should tend to smooth intraseasonal price movements.

Alford, J. J. 1973. The role of management in Chesapeake oyster production. Geogr. Rev. 63: 44-54.

Discussed the role of public misuse of the common property resource of oysters in leading to the persistent and continuing decline of the productivity of the fishery. Described the history of private oyster culture in the Bay. Suggested the imposition of higher oyster taxes on oyster harvesters to overcome the deficits in taxpayer-supported seed and shell planting programs, and tighter controls on harvesting.

Alford, J. J. 1975. The Chesapeake oyster fishery. Ann. Assoc. Amer. Geographers 65: 229-239.

Reviewed both general aspects of oyster ecology in Chesapeake Bay and the effects of pollution. Discussed and compared Maryland and Virginia laws and practices concerning public use versus private rental of oyster bars. Considered the idea that all oyster bottoms be turned over to private culture but concluded that this was not a completely satisfactory answer. Declared that the Chesapeake oyster fishery should be managed as a single unit, with Virginia seed moved to Maryland waters where Virginia production methods (private culture) would be established to supplement production from natural public beds.

Andrews, J. D. 1949. The 1947 oyster strike in the James River. Proc. Natl. Shellfish. Assoc. (1948): 61-66.

Three bars were studied in 1947. Characteristic setting rates prevailed for each bar. No advantage was found for any particular time of shell planting. Settlement was good throughout the river and, although mortalities were high, the set was effective. On the best bar (Wreck Shoal), an average of 314 spat per shell settled during the season, with 14 spat per shell still alive in November 1947.

Andrews, J. D. 1951. Seasonal patterns of oyster setting in the James River and Chesapeake Bay. Ecology 32: 752-758.

In the James River, Virginia, setting was usually continuous for about 90 days, with the period extending from early July to early October. Setting was consistent from year to year with no failures noted during this study. Ninety percent of the set occurred after the first of August, in contrast to other areas of the Bay where setting was generally earlier. Setting peaked in early September. The late set may have been related to the small size of brood oysters or to the scarcity of net plankton.

Andrews, J. D. 1955a. Setting of oysters in Virginia. Proc. Natl. Shellfish. Assoc. 45: 38-46.

Oyster settlement in Virginia waters was generally prolonged from July to early October, depending upon location. Setting was continuous in the James River, nearly so in the York River, but often discontinuous in the Rappahannock River. One peak of setting often occurred in mid-July, with a second in August or September. The later set was more important in the James River and slightly less so in the York River. The early set was most consistent and important in the Rappahannock and perhaps also in Maryland. In any particular season, timing and intensity of setting was similar within any one river system, suggesting that the same broods of larvae provided spatfall for the whole river. Survival rate increased as the strike decreased, or with decreasing salinities up-river, or as the setting season progressed. In Virginia, setting was heaviest near the mouths of rivers, decreasing progressively upriver. It was also heaviest on the left side of the channel (facing downriver); most natural oyster beds were located on this side. Andrews believed that size of brood stock may not be important because the poorly conditioned small oysters of the James produced consistently good sets in contrast to the fat, large Rappahannock oysters which produced generally poorer sets. Andrews stated that there were turns in the rivers ("pockets") which tended to trap larvae.

Andrews, J. D. 1955b. Notes on fungus parasites in bivalve mollusks. Proc. Natl. Shellfish. Assoc. 45: 157-163.

In 1953-54, twelve of sixteen bivalve species were found to be infected with a fungus resembling *Dermocystidium marinum*. These infections disappeared in late winter and early spring. There seemed to be differences among oysters from different areas with regard to their susceptibility to the fungus disease.

Andrews, J. D. 1956. Trapping oyster drills in Virginia. I. The effect of migration and other factors on the catch. Proc. Natl. Shellfish. Assoc. 46. 140-154.

Various attempts to control oyster drills were reviewed briefly. A drill trapping program in the York River revealed some information on behavior, abundances, and lengths of *Eupleura caudata* and *Urosalpinx cinera*. The relative importance of resident and migratory drill populations was not resolved, nor was it demonstrated satisfactorily that trapping was a useful pest control strategy.

Andrews, J. D. 1964. Oyster mortality studies in Virginia. IV. MSX in James River public seed beds. Proc. Natl. Shellfish. Assoc. 53: 65-84.

Between 1959 and 1961, the disease MSX resulted in the death of half of Virginia's privately-planted oyster stock. MSX appeared in the James River

seed beds in fall 1960, apparently in relation to saltwater influx along the channel. The disease spread with time, disappearing at the period of lowest salinities. Persistence of the disease in the James River seed area appeared to depend on importation of infective material from saltier waters at the mouth of the River. Thus serious losses result from planting of infected seed in high salinity waters.

Andrews, J. D. 1965. Infection experiments in nature with *Dermocystidium marinum* in Chesapeake Bay. Chesapeake Sci. 6: 60-67.

The effects of proximity of fungus-infected oysters on epizootiology in isolated disease-free oysters was studied in the York River, Virginia. It appeared that proximity to an infected population led to infection of the disease-free specimens. The fungus was active in warm weather and persisted by chance survival through the winter. The fungal pathogen seemed to depend solely on transmission from oyster to oyster for its spread.

Andrews, J. D. 1966. Oyster mortality studies in Virginia. V. Epizootiology of MSX, a protistan pathogen of oysters. Ecology 47: 19-31.

From 1959 to 1963, the pathogen MSX caused high mortalities in oysters in high salinity areas of Chesapeake Bay. Oysters imported from disease-free locations in winter and spring became infected in early summer and died in late summer. Oysters imported in late summer apparently became infected shortly thereafter. However, infections were subclinical until the following spring (May). Mortalities occurred throughout the year but were highest in warmer months. Prevalence of MSX did not decline as the oyster populations died off, resulting in about half of Virginia's oyster beds ceasing production.

Andrews, J. D. 1967. Interaction of two diseases of oysters in natural waters. Proc. Natl. Shellfish. Assoc. 57: 38-49.

In 1965, the author induced and monitored a localized epizootic of the fungal disease *Dermocystidium marinum* in the York River. During the experiments, an epizootic of the sporozoan disease MSX (caused by *Minchinia nelsoni*) persisted, resulting in about 50% mortality in the experimental oyster populations. The author found that imported disease-free oysters in lower York River became infected with *D. marinum* in one to three years. However, during this time, MSX was causing high mortalities and resulting in declines in oyster populations. Thus, *D. marinum* was prevented from becoming epizootic because it depends on direct transmission, and distances of 15 to 100 feet between populations seemed to result in slowed infection rates.

Andrews, J. D. 1968. Oyster mortality studies in Virginia. VII. Review of epizootiology and origin of *Minchinia nelsoni*. Proc. Natl. Shellfish. Assoc. 58: 23-36.

Intensive epizootics of *Minchinia nelsoni* continued in lower Chesapeake Bay, with high mortalities during the initial year of exposure to the disease. Density of oyster population did not seem to be important for disease activity. It appeared that resistance to the disease can be acquired. The author speculated on the origin of the virulent pathogen and implicated seed transplants in the outbreak and spread of the disease.

Andrews, J. D. 1971. Climatic and ecological settings for growing shellfish. In: Price, K. S. Jr., and D. L. Maurer (eds.), Proc. Conf. on Artificial Propagation of Commercially Valuable Shellfish Oysters, pp. 97-107. University of Delaware, Newark, DE.

Reviewed some aspects of hydroclimates and their effects on distribution and biology of commercial bivalves, including Crassostrea *virginica*. Application was made of this information for culture purposes.

Andrews, J. D. 1973. Effects of Tropical Storm Agnes on epifaunal invertebrates in Virginia estuaries. Chesapeake Sci. 14: 223-234.

Passage of Tropical Storm Agnes in June 1972 led to establishment of low-salinity regimes in areas of Chesapeake Bay that did not normally experience such salinities for any extended period of time. Oligohaline species such as oysters were severely stressed and some mortality resulted. However, populations were not exterminated. Oyster drills were largely eliminated from large areas of their habitat, including, apparently, all of the Rappahannock River. Given the lack of a pelagic larval stage for *Urosalpinx cinerea* and *Eupleura caudata*, return of drills to their former habitats was expected to be slow.

Andrews, J. D. 1979. Oyster diseases in Chesapeake Bay. Mar. Fish. Rev. 41(1): 45-53.

The author reviewed three major oyster diseases which affect Virginia oysters: *Dermocystidium* (=*Perkinsus*) *marinum*, *Minchinia nelsoni* and *Minchinia costalis*. The former is a disease of oysters in higher salinity habitats (15 ppt) which is fatal in warm water conditions. It is a “contact” pathogen. *Minchinia nelsoni* (MSX) is also a problem in higher salinities, with oyster mortalities reaching 20-50% annually. Oyster strains resistant to MSX were found to have developed. *Minchinia costalis* affects oysters in salinities above 30 ppt.

Andrews, J. D. and M. Frierman. 1974. Epizootiology of *Minchinia nelsoni* in susceptible wild oysters in Virginia, 1959 - 1971. J. Invert. Pathol. 24: 127-140.

This oyster disease had been studied in Virginia since 1959. It appeared not to be contagious in trays. Mortalities, prevalence and seasonal patterns of disease activity were described. Size, age, source and history of oysters, and timing of exposure all were found to affect disease activity.

Andrews, J. D., D. Haven and D. B. Quayle. 1959. Fresh-water kill of oysters (*Crassostrea virginica*) in James River, Virginia, 1958. Proc. Natl. Shellfish. Assoc. 49: 29-49.

In winter and spring, 1958, fresh water invaded the upper part of the James River seed area, resulting in the deaths of many oysters between May 1 and June 15. Death rates reached 90%. It appeared that oysters could be "conditioned" in nature to such fresh-water inundations if temperatures were low. A "narcotized" condition of no heartbeat or ciliary motion and no mantle sensitivity would result as long as shell closure occurred. Once "broken" at higher temperatures, the "conditioning" appeared to be lost.

Andrews, J. D. and W. G. Hewatt. 1957. Oyster mortality studies in Virginia II. The fungus disease caused by *Dermocystidium marinum* in oysters of Chesapeake Bay. Ecol. Monogr. 27: 1-26.

This is an extensive discussion of research performed on oysters and the seasonally virulent disease caused by the fungus, *Dermocystidium marinum*. The epidemiology of the disease was studied extensively and the results are presented.

Andrews, J. D. and J. L. McHugh. 1957. The survival and growth of South Carolina seed oysters in Virginia waters. Proc. Natl. Shellfish. Assoc. 47: 3-17.

South Carolina oysters were held in Virginia waters and mortality and growth were monitored. These southern oysters were susceptible to winter low temperatures. They grew no better than did native oysters and yields were smaller. They were more resistant to fungal disease (*Dermocystidium* (=*Perkinsus*) *marinum*).

Andrews, J. D. and J. L. Wood. 1967. Oyster mortality studies in Virginia VI. History and distribution of *Minchinia nelsoni*, a pathogen of oysters, in Virginia Chesapeake Sci. 8: 1-13.

In 1959, the sporozoan, *Minchinia nelsoni*, was the cause of an epizootic among York River, Virginia, oysters. By 1960, high mortality had occurred

on all lower Chesapeake Bay oyster grounds. A record-breaking drought from 1963-1965 allowed for the extension of the epizootic further up Chesapeake Bay and its tributaries. Oyster grounds in Virginia were classified into four groups according to intensity of MSX activity.

Andrews, J. D., J. L. Wood and H. D. Hoese. 1962. Oyster mortality studies in Virginia III. Epizootiology of a disease caused by *Haplosporidium costale* Wood and Andrews. J. Insect Path. 4: 327-343.

An epizootic disease on the seaward side of the Eastern Shore peninsula of Virginia (Seaside) was associated with *H. costale*. The disease caused oyster mortality in May-June. Oysters transplanted from James River, Virginia to Seaside suffered higher mortalities after a year of acclimation than did native oysters. On the Bay side of the peninsula, *Dermocystidium marinum* caused mortalities in late summer. Neither disease was found where the other occurred.

Bahner, L. H., A. J. Wilson, Jr., J. M. Sheppard, J. M. Patrick, Jr., L. R. Goodman and G. E. Walsh. 1977. Kepone bioconcentration, accumulation, loss and transfer through estuarine food chains. Chesapeake Sci. 18: 299-308.

Experiments in static and flow-through bioassays indicated that oysters would concentrate kepone both from water and from kepone-contaminated *Chlorococcum* algae. Oysters concentrated kepone up to 10,000 times exposure concentrations within 19 days. They cleared the chemical from their bodies rapidly. No kepone was detected within 7-20 days from the end of exposure for oysters that had been held in kepone-dosed water and within 10 days from the end of exposure to kepone-contaminated algae.

Bahr, L. M. and R. E. Hillman. 1967. Effects of repeated shell damage on gametogenesis in the American oyster, Crassostrea *virginica* (Gmelin). Proc. Natl. Shellfish. Assoc. 57: 59-62.

Two groups of oysters held in Patuxent River water were treated by having their growing edges filed repeatedly over time. One of these groups and an untreated control were held in filtered river water (unfed). The other filed group and a control were held in unfiltered river water (fed). After 8 months, histological preparations were made of the gonads of all four groups. Unfed oysters had less developed gonads than did fed oysters. The filed and undamaged groups were generally similar, although it seemed that lack of food depressed gametogenesis in unfed filed oysters to a greater extent than in the unfed controls. Both filed groups (fed and unfed) had a higher proportion of male oysters than did the undamaged groups.

Barrow, J. H., Jr. and A. C. Taylor. 1966. Fluorescent-antibody studies of haplosporidian parasites of oysters in Chesapeake and Delaware Bays. Science 153: 1531-1533.

A fluorescent antibody was produced against the haplosporidian parasite of oysters, *Minchinia nelsoni*. No reaction occurred with *Minchinia costalis*, indicating that the two species were antigenically distinct.

Beaven, G. F. 1945. Maryland's oyster problem. Maryland Board of Natural Resources, Dept. of Research and Education, Solomons Island, Md., Educational Series, No. 8: 1-14.

Discussed the problem of depletion of the oyster resource, which was then less than one-fifth of the production at its peak in the 1880's. Described instances where local politics or pressure from watermen concerning shell plantings led to management action which was a waste of money and oyster shell. Recommended remedial action involving oyster culture and private leasing.

Beaven, G. F. 1947. Effect of Susquehanna River stream flow on Chesapeake Bay salinities and history of past oyster mortalities on upper Bay bars. Proc. Natl. Shellfish. Assoc. (1946): 38-41.

North of Kent Island, quantities of slow-growing small oysters used to be available for canning purposes. Production on the bars was erratic and heavy mortalities often occurred. These mortalities were linked, not to pollution from Baltimore, but to periods of long-term depression of salinity as a result of high run-off from the Susquehanna River.

Beaven, G. F. 1948. Observations on fouling of shells in the Chesapeake area. Proc. Natl. Shellfish. Assoc. (1947): 11-15.

Principal fouling organisms included bryozoans, barnacles, hooked mussels, tunicates, sponges, tube worms, folliculinids, hydroids, algae and bacteria Bryozoans and barnacles appeared to be the major species with the potential of inhibiting settlement of oysters. Boring sponges eroded shell, leading to decrease in "cultch efficiency." An organic film of diatoms, algae and bacteria may also have deterred settlement. Experiments comparing spat settlement on new shell plantings with settlement on the previous year's plantings revealed greater set on the newer shell.

Beaven, G. F. 1950. Growth observations of oysters held on trays at Solomons Island, Maryland. Proc. Natl. Shellfish. Assoc. (1949): 43-49.

Growth rate was found to vary with region in Chesapeake Bay. For example, in some seed areas in Maryland, few oysters reached legal size even by 6 years

of age. In contrast, in Pocomoke Sound, a heavy oyster set led to many individuals being 3” long by the end of the setting year and 6” long by the second fall. Wide variations in growth of seed oysters after transplanting to other bars, or from year to year, were described. This study followed growth of oysters from 9 locations in Maryland, Virginia, New Jersey, Connecticut and North Carolina which were held in trays at Solomons from 1947 to 1949. In general, growth was greater in fall than in spring and very poor in summer 1948. Mortality was greater for oysters transplanted from higher salinity water. There was greater growth variation among individuals within a group than for between-group averages. All groups contained small oysters (“runts”) which made little noticeable growth during the two years of study.

Beaven, G. F. 1951. Recent observations on the season and pattern of oyster setting in the middle Chesapeake area. Proc. Natl. Shellfish. Assoc. (1950): 53-59.

Set in 1949 was somewhat better than average, with setting very poor along the upper western shore and in the major rivers except near their mouths. However, in the productive St. Mary’s River, setting intensity increased upriver. Spat counts on planted shell were generally higher than on old cultch in the same areas. Similarly, newly planted shell usually received heavier set than older, heavily fouled shell. Plankton sampling coupled with use of shell bags for spat enumeration indicated that areas with limited spatfall had few larvae present. Comparisons between the Solomons region and St. Mary’s River revealed an extended period (June-October) of light setting at Solomons versus a peak 2- to 3-week period in St. Mary’s River. At Solomons, many oysters retained their spawn into fall or early winter, whereas in St. Mary’s River, nearly all oysters were spawned out after the July setting peak and remained thin until cold weather. Areas of high setting typically were somewhat landlocked with limited water exchange. Brood stock was generally found in densely populated groups, probably being more abundant in proportion to water volume than in poorer setting areas.

Beaven, G. F. 1952. A preliminary report on some experiments in the production and transplanting of South Carolina seed oysters to certain waters of the Chesapeake area. Proc. Gulf Carib. Fish. Invest. 5: 115-122.

The author described a major problem in Maryland: that of securing a sufficient supply of seed oysters. The resources in the upper Bay and upper Potomac River had been destroyed by recurring freshets. Sale of James River seed was periodically banned to out-of-state buyers. Pamlico Sound stock had been depleted and its sale restricted. Thus, use of newly-set spat as seed oysters had expanded as “shell plants” were scattered in good growing areas by the State. The author studied the survival and growth of South Carolina

seed oysters. Survival was negligible at Solomons or Crisfield when transplanted in November, but was better for seed transplanted in July. Survival was also good in parts of Chincoteague Bay. Survival was generally better in higher salinities.

Beaven, G. F. 1953. Some observations on rate of growth of oysters in the Maryland area. Proc. Natl. Shellfish. Assoc. 43: 90-98.

Reiterated the existence of significantly different growth among the State's oyster bars, among groups of seed from different sources, and from year to year on the same bar. Often in winter there was a recession in length Growth was greater in fall than in spring. Growth in seed areas was generally lower than on growing bars. In the Patuxent River, growth in the upper river was greater than in the lower river. In general in Maryland, it took three years for oysters to reach legal size (3" or 76 mm). However, in some areas, some individuals reached 3" in a year and 6" in two. Quick growing oysters were thin-shelled and easily broken. Growth was more rapid in Chincoteague Bay than in Chesapeake Bay (none of these data were compared statistically).

Beaven, G. F. 1955. Various aspects of oyster setting in Maryland. Proc. Natl. Shellfish. Assoc. 45: 29-37.

Grouped Maryland oyster beds into three classifications: (1) bars on which high quality oysters grew but on which recruitment did not replace harvest losses. Many such bars were depleted and needed to be maintained by seed plantings; (2) limited areas of self-sustaining bars where recruitment balanced harvest losses. These produced most of Maryland's natural yield (at the time of writing); (3) a small number of bars which received intensive sets resulting in overcrowded oysters which could be used as seed oysters. Setting rate in Maryland increased from the upper limit of oyster growth down to the Virginia border, and from upper to lower reaches of tributaries with fairly large stream flow. In many small estuaries in the Bay with little or no drainage or salinity gradient, setting typically was heavier in their upper reaches than near their mouth. Setting was greater on the eastern shore compared with western shore. Setting variations were common from bar to bar, or from one part of a bar to another (better along the shallow or inshore margin of a bar than along its deeper edges). Maryland setting extended from late May into October with a marked peak of about two weeks' duration from late June to September (usually in July). In a few places the principal set occurred in fall. Oysters in tributary and shallow waters usually were the first to spawn, with those in deeper or open water spawning later. Many scattered oysters on deep bars of the Bay or large tributaries may not spawn. Barnacle sets inhibited successful oyster set. The limited areas of high oyster set were believed to be comparatively free from heavy growths of bryozoans and barnacles. Presence of larger quantities of brood stock in the more numerous eastern shore tributaries may have increased the setting

potential of the area. Periods of high salinity and fertile water seemed to be favorable for production and growth of oyster larvae. Semi-enclosed areas with slow water movement seemed to lead to high setting and abundant brood stock. This could occur behind or between islands or in sluggish tributaries. Presence or absence of suitable larval food may have influenced setting success. Historically, setting intensity seemed to have declined with time.

Bender, M. E., R. J. Huggett and H. D. Slone. 1972. Heavy metals—an inventory of existing conditions. J. Wash. Acad. Sci. 62: 144-153.

Oysters were surveyed from February to May 1971 in Virginia's Chesapeake Bay and were analyzed for presence of zinc, copper and cadmium. Oysters were also collected in fall 1970 and spring and summer 1971 for mercury determinations. Human influences in some of the metal values noted were discussed.

Bockrath, J. and D. Wheeler. 1975. Closed-cycle mariculture in Maryland, Virginia, and Delaware: An examination of the adaptability of existing fishery laws to new technology. William and Mary Law Review 17: 85-107.

Recent rapid advances in closed-cycle mariculture technology may place strains on laws which were promulgated to regulate natural fisheries at a time when such technology was undreamt of. It appears that Delaware has drafted fishery laws which would readily accommodate closed cycle mariculture of molluscs. In Maryland and Virginia, somewhat ambiguous wording and intent of some aspects of the law (i.e., enactments dealing with leasing of subtidal land) make for uncertain application of these statutes to closed-cycle mariculture. This discourages development of any new industry. The adoption of new statutes would be necessary to encourage closed-cycle mariculture in these two states.

Boon, D. D. 1972. The red pigment in discolored oysters and soft-shelled clams from the Chesapeake Bay. Chesapeake Sci. 13: 334-335.

In winter 1970-71, some oysters from Chesapeake Bay had a red discoloration. This was caused by a red pigment which appeared to be a carotenoid, presumably derived from a plant in the oysters' food.

Boon, D. D. and M. C. Tatro. 1971. Blowing oysters for increased salt content. Chesapeake Sci. 12: 51-52.

Washing oysters in fresh water agitated by air ("blowing") resulted in loss of salt content. Blowing oysters in salt solution restored this salt, which added to consumer appeal. However, oysters blown in salt water lost some of their initial weight.

Breisch, L. L. and V. S. Kennedy. 1980. A Selected Bibliography of Worldwide Oyster Literature. Maryland Sea Grant No. UM-SG-TS-80-11. College Park, Md. 309 pp.

This extensive volume of material covers literature on numerous species of oysters from around the world and includes over 3,700 entries.

Brooks, W. K. 1879. Abstract of observations upon artificial fertilization of oyster eggs and embryology of American oysters. Amer. J. Sci. 18: 425-427.

An early report that oyster eggs could be fertilized and developed into the larval stage in the laboratory.

Brooks, W. K. 1891. The Oyster. A Popular Summary of a Scientific Study. The Johns Hopkins Press. 225 pp. (Second edition, 1905).

In this comprehensive, semi-popular account of his research, Brooks described the anatomy, development and artificial cultivation of oysters. He discussed the problem of continued decline in oyster catch in Chesapeake Bay, relating this to overfishing. He encouraged private cultivation of oysters, providing many cogent arguments to show the sensibility of renting oyster beds, the results of which could answer many of the problems facing the fishery. The problems still exist and his recommendations are still valid.

Burrell, V. G., Jr. and W. A. Van Engle. 1976. Predation by and distribution of a ctenophore, *Mnemiopsis leidyi* A. Agassiz, in the York River estuary. Est. Coastal Mar. Sci. 4: 235-242.

The tentaculate ctenophore, *Mnemiopsis leidyi*, occurred in the York River estuary during a 22 month study period (Aug. 1965-May 1967). Numbers of small plankters varied inversely with ctenophore volume, suggesting a negative (predatory) effect of the ctenophores on the plankters. Bivalve larvae (not identified, but presumably including oyster larvae) were found in 13% of the ctenophore stomodaea examined.

Burton, R. W. 1963. Distribution of oyster microparasites in Chesapeake Bay, Maryland, 1959-1960. Proc. Natl. Shellfish. Assoc. 52: 65-74.

The author examined 663 oysters collected from 165 oyster beds in 1959 and 1960. The parasites included *Nematopsis ostrearum* (in 82 oysters), *Bucephalus cuculus* (in 12), *Hexamita* sp. (in 4), *Ancistrocoma* sp. (in 4), *Dermocystidium marinum* (in 13), and “MSX” (in 12). Bacteria in dense concentrations were also found in seven oysters. The author concluded that upper Chesapeake Bay was relatively free of oyster parasites.

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

Extensive flooding of upper Chesapeake Bay by Susquehanna River water in summer 1945 and spring 1946 led to fresh water covering oyster beds in this area for protracted periods. Histological studies revealed that gametogenesis was inhibited in 90% of the surviving population of oysters until salinities exceeded 6 ppt. Thereafter, oyster condition improved rapidly, but gametogenesis lagged behind that of a control higher-salinity population by 3-4 months. This suppressed gonadal activity was attributed by Butler to variations in food availability, perhaps due to salinity inhibition of feeding activity.

Butler, P. A. 1949b. Effects of flood conditions on the production of spawn in the oyster. Proc. Natl. Shellfish. Assoc. (1948): 78-81

In 1948, floods in upper Chesapeake Bay caused extensive oyster mortality. In May, a bushel of dredged shell contained 50 - 100 oysters, but by October it was necessary to examine 2-3 bushels to obtain 25 live oysters. The shells were clean because of death of fouling organisms. From May-July, gonads (examined microscopically) generally were resting or indifferent for 50% of the samples, in early development phase for 40%, and ripe for 10%. In August, ripening accelerated and larvae were collected in plankton samples. This occurred as salinities started to increase to 6 ppt and then gradually to 13 ppt. Butler suggested that low salinities inhibited feeding and thus gonad development.

Butler, P. A. 1956. Reproductive cycle in native and transplanted oysters. Proc. Natl. Shellfish. Assoc. 46: 75.

Six-month-old Chesapeake oysters were transferred to Pensacola, Florida, and held for one year. Gonad histology and reproductive behavior were observed for the transplanted population and compared with gametogenesis and spawning in native populations in Chesapeake Bay and Pensacola. The transplanted oysters began spawning and mass spawning occurred at a temperature that was 5°C above that for the parent stock. The spawning period was extended from the normal period of 3 1/2 months for native Chesapeake oysters to 5 months for transplanted oysters.

Cabraal, R. A. 1978. Systems analysis of the Maryland oyster fishery: production management and economics. Ph.D. dissertation, Agricultural Engineering, University of Maryland. 318 pp.

Developed a big-economic model of the Maryland oyster fishery. A computerized data bank of economic, production, and management information on the fishery was organized (a computer listing is included in an appendix).

Factors affecting the productivity of the fishery were evaluated. Oyster population sizes of Eastern Bay, Chesapeake Bay mainstem, Potomac River, Patuxent River, Tangier Sound, and other areas were estimated using the Leslie and DeLury equations. Production functions, relating catch to effort, lagged spatfall, and seed and shell plantings were developed for all regions. Quality of available data and the effectiveness of resource management policies within the fishery were evaluated. Fresh shell was judged the most successful planting material. The demand equation indicated that oysters had a unitary demand elasticity.

Cabraal, R. A. and F. W. Wheaton. 1981. Production functions for the Maryland oyster fishery. Trans. Amer. Soc. Agri. Eng. 24: 248-251, 254.

Using seed planting, shell planting, spatfall and fishing effort data, production functions were developed for or Eastern Bay, Chesapeake Bay mainstem, Potomac River, Patuxent River, and Tangier Sound. Results from these functions were then used to analyze the effectiveness of state operated seed and shell planting programs. The repletion program was found to have significantly increased oyster production although with varying degrees of success. The effectiveness of fresh shell versus seed planting in terms of both dollar and harvestable bushels of oysters returned was assessed. Fresh shell plantings were the most successful planting material.

Calder, D. R. and M. L. Brehmer 1967. Seasonal occurrence of epifauna on test panels in Hampton Roads, Virginia. Int. J. Oceanol. Limnol. 1: 149-164.

Asbestos fiber panels were submerged to a depth of 5 m. While oysters settled from August to October, they were a minor fouling species.

Carter, H. H. 1967. A Method for Predicting Brood Stock Requirements for or Oyster (*C. virginica*) Producing Areas with Application to the Manokin River. Chesapeake Bay Institute, The Johns Hopkins University, Spec. Rep. 13. 46pp.

In an effort to determine the optimum relative positions of brood stock and planted cultch in order to establish a seed bed in the Manokin River, the author performed a dye study to follow current patterns over a 14-day period in July-August 1967. Using the results obtained from drogue studies, the tracking of the spread of the fluorescing dye, and examination of river discharge and salinity data, the author determined that the Manokin River could be divided into three different areas with different circulation patterns. Upstream, the river mode was important, with outflow at the surface and salinity-mediated inflow on the bottom. At the mouth of the river, wind

effects were important, with surface inflow and bottom outflow. A transition area occurred between the upriver and river-mouth areas. The Manokin system was thus similar to that described for St. Mary's River on the Potomac. The author was able to recommend a site for placement of brood stock and a more upriver site for placement of cultch.

Castagna, M. and P. Chanley. 1973. Salinity tolerance of some marine bivalves from inshore and estuarine environments in Virginia waters on the western mid-Atlantic coast. Malacologia 12: 47-96.

The oyster, C. virginica, was included in this compendium of information. Selected references describing its salinity tolerances were discussed. The authors did not treat C. virginica experimentally as they did other species in this report.

Chesapeake Biological Laboratory. 1953. The Commercial Fisheries of Maryland (A special report to the General Assembly of Maryland). Board of Natural Resources, Dept. of Research and Education, Solomons Island, MD. 45 pp.

This special report was prepared in response to a joint resolution of the Maryland General Assembly (1951) calling for general information on the fisheries of the state. Concerning the oyster, the report declared that the best methods of culture would yield 40 million bushels of oysters. The limiting factors to such production were not biological, but social and political. Depletion of oyster grounds was attributed to overfishing as a major factor, with other factors (siltation, increased fresh-water runoff up-Bay, pollution of some areas) having a lesser influence. The report recommended encouragement of private cultivation, conservation of shell for cultch, expansion of a seed-production program, and continued research to provide knowledge for appropriate management of the resource.

Christensen, D. J. 1973. Prey preference of *Stylochus ellipticus* in Chesapeake Bay. Proc. Natl. Shellfish. Assoc. 63: 35-38.

The hypothesis of "ingestive conditioning" in *S. ellipticus* was investigated in 1969 using oysters and barnacles. When flatworms were segregated on the basis of prey utilized at the time of collection (i.e., worms feeding on oysters vs. worms feeding on barnacles), barnacle eating flatworms did not feed on oysters, even when no other choice was available. Oyster-eating flatworms fed on oysters or barnacles, but to a greater extent on oysters. Only rarely did oyster-eating worms feed on barnacles if oysters were available. The author concluded that barnacles were the preferred prey under most circumstances because some worms became conditioned to the lack of oysters but not to the lack of barnacles.

Christy, F. T. 1964. The exploitation of a common property natural resource: the Maryland oyster industry. Ph.D. Dissertation Univ. of Michigan. 222 pp.

Discussed common property natural resources in general (effects on the resource, economic consequences, associated public costs). Considered Maryland's oyster industry and its characteristics, and discussed the consequences of the public fishery. Considered alternative management strategies and recommended consideration of "exclusive use" rights. This would allow economically proper allocation of capital and labor resources. Innovative technology would be encouraged. The public would not bear the costs of cultivation and management. Suggested gradual restriction on the number of producers through use of direct license limitation and monetary disincentives.

Colwell, R. R., S. G. Berk, G. S. Sayler, J. D. Nelson, Jr., and J. M. Esser. 1975. Mobilization of mercury by aquatic microorganisms. In: T. C. Hutchinson (ed.), Proc. Int. Conf. on Heavy Metals in the Environment. Institute for Environ. Studies, Univ. Toronto, pp. 831-843.

A simplified food chain involving bacteria and C. virginica was established in the laboratory. Concentrations of ^{203}Hg were found to be 200 times greater in tissue from organisms held in an environment containing mercury-metabolizing bacteria than in controls without these bacteria

Colwell, R. R. and G. S. Sayler. 1977. Effects and Interactions of Polychlorinated Biphenyl (PCB) with Estuarine Microorganisms and Shellfish. USEPA. Ecological Research Series. EPA-600/3-77-070. Gulf Breeze, Fl. 45 pp.

PCBs were found to be present in samples of Chesapeake Bay surface water and sediment. Number of bacteria grown in presence of PCB was found to be positively correlated with presence of PCS in the water or sediment. Acute PCB stress led to a decrease in depuration of *E. coli* and *Salmonella typlimurium* by the oyster C. virginica, although net accumulation of these bacteria was not affected.

Commission of Tidewater Fisheries. 1948. Report on the oyster problem in the Chesapeake Bay. Fourth Ann. Rep. Md. Board of Nat. Res., Annapolis, Md. pp. 27-39.

The Commission blamed the long-term decline in oyster production on harvesting oysters at a rate exceeding the rate of replenishment by natural reproduction. The state oyster-farming program involved in development of seed areas was described. The 20¢ bushel tax on harvested oysters was judged to be insufficient to support the seed enhancement program. A long-term, appropriately funded rehabilitation program was considered to be necessary

in order for the oyster fishery to increase in productivity. However, the Commission recognized the political difficulties in such a long-term program. They suggested as an alternative that depleted oyster grounds be opened to private cultivation. They noted that other oyster-producing states had been unsuccessful in sustaining a public fishery and had resorted to private oyster farming. Such private management would allow private moneys to be substituted for state subsidies. Seed production and seed transfer could be enhanced; supply of market oysters could be stabilized. A private oyster farmer could probably devote more care and attention to his holdings compared with the more general attention the state could afford to provide.

Cory, R. L. 1967. Epifauna of the Patuxent River estuary, Maryland, for 1963 and 1964. Chesapeake Sci. 8: 71-89.

Panels of wood and of black asbestos-cement placed 0.1 m above the bottom at 6 stations along the Patuxent River collected very few oysters, despite the presence of beds of oysters in the river.

Crisp, D. J. 1967. Chemical factors inducing settlement in Crassostrea *virginica* (Gmelin). J. Anim. Ecol. 36: 329-335.

Experiments on oysters cultured in York River, Virginia, revealed that the removal of shell periostracum and outer layers of organic matrix rendered oyster shell less favorable for spat settlement. Body extracts made shell somewhat more favorable for settlement. This was related by the author to gregariousness of settlement in this species, with the larvae presumably recognizing both soluble material coming from living oysters and the insoluble organic layer of the shell. Oyster larvae settled preferentially on the underside of shells and on the smooth inner surf ace.

Drifmeyer, J. E. 1974. Zn and Cu levels in the eastern oyster, Crassostrea *virginica*, from the lower James River. J. Wash. Acad. Sci. 64: 292-294.

In 1973, oysters from the Craney Island area of the lower James River contained up to 10,000 ppm zinc and 584 ppm copper, with average levels of 3,915 ppm zinc and 180 ppm copper. This was an increase over data collected in 1971.

Dunnington, E. A., Jr. 1968. Survival time of oysters after burial at various temperatures. Proc. Natl. Shellfish. Assoc. 58: 101-103.

Oysters were buried 3” deep in containers held in running salt water at five temperature ranges. At less than 5°C, oysters lived over 5 weeks while buried. At 10°-15°C, mortality occurred at 3 weeks, increasing thereafter. At 15°-20°C, most oysters survived for 1 week but all had died after 2 weeks.

Over 25°C, mortality occurred after 2 days, becoming almost total within a week. In declining temperatures (24° to 18°C), the pattern resembled that at 25°C.

Dupuy, J. L. and S. Rivkin. 1970. Cultch-free spat present and future. Proc. Ann. Workshop World Mariculture Soc. 1: 157-158.

This paper introduced the vertical use of frosted Mylar sheets for attachment of newly setting spat.

Dupuy, J. L. and S. Rivkin. 1972. The development of laboratory techniques for the production of cultch-free spat of the oyster, Crassostrea *virginica*. Chesapeake Sci. 13: 45-52.

Methods for successful conditioning and spawning of Chesapeake Bay oysters in 4-6 weeks were outlined. In addition, two methods of producing cultch-free spat were described. The first method was of value in relatively clear estuarine areas. It involved periodic use of small underwater jets of Bay water (every 2 hours) to remove spat from setting trays. The second method was employed in regions with high siltation and fouling. Oyster spat settled on Mylar sheets which, after a few weeks, were shaken over and dipped into a container of water to release the spat.

Dupuy, J. L., S. Rivkin and F. D. Ott. 1973. A new type of oyster hatchery. Proc. Ann. Workshop World Mariculture Soc. 4: 353-368.

Hatchery techniques were described for (a) conditioning oysters to spawn when desired all year; (b) raising oyster larvae year round, with setting in 14 days; (c) production of cultch-free spat (20-25 mm long) for field planting. A continuous flow system (20 liters min^{-1}) for production of pasteurized algal medium used to promote growth of three new algal species (oyster larval food) was described.

Dupuy, J. L., N. T. Windsor and C. E. Sutton. 1977. Manual for Design and Operation of an Oyster Seed Hatchery for the American Oyster Crassostrea *virginica*. Virginia Institute for Marine Science, Spec. Rep. No. 142. 111 pp.

This is an extensive manual outlining steps and procedures for rearing oysters from the initial conditioning of adults to holding of spat. Described are culture facilities, algal culture techniques, and personnel and economic matters.

Earle, S. 1932. The fisheries of Chesapeake Bay. Trans. Amer. Fish. Soc. 62: 43-49.

In this brief report, the author recounted some of the history of the oyster fishery, including the earlier confrontations between scoff-law dredgers and the oyster police, and some of the remedies undertaken to halt the production decline of oysters.

Engle, J. B. 1947. Commercial aspects of the upper Chesapeake Bay oyster bars in light of the recent oyster mortalities. Proc. Natl. Shellfish. Assoc. (1946): 42-46.

Considered reproduction, setting and mortality of oysters from beds in the “Head of the Bay” region (north of a line drawn from the Chester River to Sandy Point). Low salinities in 1944 and 1945 retarded gonad development, inhibited spawning, discouraged setting and resulted in extensive mortality. In 1944, as salinities rose in summer and fall, growth was better than usual.

Engle, J. B. 1948. Distribution of setting guides the Maryland oyster program. Proc. Natl. Shellfish. Assoc. (1947): 16-20.

Summarized results of a research program in Chesapeake Bay: (1) there was a wide range of setting intensity from one area to another; (2) setting was more regular in some areas than in others; (3) setting tended to be heavier on the eastern side of the Bay than on the western side; (4) setting seemed to be heavier in lower portions of rivers and the Bay than upstream or in the “Head of the Bay” (above the present Bay bridge) section. Consistently good sets in three areas (St. Mary’s River, Holland Straits in Tangier Sound, Eastern Bay) led to their receiving intensive shelling to encourage seed production. This was important because large portions of the oyster area did not receive adequate natural set and overfishing had depleted oyster bars. In addition to the seed production areas, cultch was placed in areas of Fishing Bay, Tangier Sound and the Choptank River and tributaries to allow for spat settlement to restock the beds.

Engle, J. B. 1951. The condition of oysters as measured by the carbohydrate cycle, the condition factor and the percent dry weight. Proc. Natl. Shellfish. Assoc. 41: 20-25.

A wide range of quality of oyster meat could be found from one location to another, and even on different parts of one oyster bar. The glycogen cycle in Chesapeake Bay followed a cyclic or seasonal pattern. The glycogen level dropped in late spring as gametogenesis occurred. As spawning occurred the lowest glycogen level was reached. After spawning ended, glycogen reaccumulation occurred. Engle recommended that oyster harvesting begin after mid-October to allow for glycogen buildup.

Engle, J. B. 1956. Ten years of study on oyster setting in a seed area in upper Chesapeake Bay. Proc. Natl. Shellfish. Assoc. 46: 88-99.

Reviewed an extensive State and Federal research program designed to reverse the decline in Maryland's oyster industry. Current seed areas were Millhill in Eastern Bay, Cinder Hill in Holland Straits, Seminary Bar and Gravelly Run in St. Mary's River, and Punch Island in Chesapeake Bay. Most of these seed areas were in tributaries. Indicated that the minimum spatfall which could be moved economically as seed was 500 spat per bushel or about 1 spat per shell. These counts were determined in the fall after summer mortalities had occurred. Weekly plankton sampling in Eastern Bay revealed a positive correlation of numbers of spat set and average number of late-stage larvae per 100 litres of water pumped. Noted positive correlation of spat set with "cleanliness" (fouling condition) of shell (older shell had fewer spat; however, no statistical treatment was applied and some of the figures seem very similar - ed.)

Engle, J. B. 1958. The seasonal significance of total solids of oysters in commercial exploitation. Proc. Natl. Shellfish. Assoc. 48: 72-78.

Over a ten-year period, percent dry weight and total solids of oyster samples were measured at least monthly. Lowest solids regularly occurred in August; highest solids occurred in November-December. During a period of unusually low salinity (Aug. 1946), solids reached their lowest point. For best harvesting, the times for optimum quality of oysters were late fall and late spring.

Engle, J. B. 1966. The molluscan shellfish industry: Current status and trends. Proc. Natl. Shellfish. Assoc. 56: 13-21

A brief review of the U.S. shellfish industry, focusing on the varieties of oysters, clams and scallops. With regard to the oyster, the decline in production in Chesapeake Bay and the increase in production in the Gulf and Pacific regions were described. As to Chesapeake Bay, Engle mentioned the change from the time when George Washington and other landowners bought or gathered oysters to provide for their slaves' food, through the period when oysters were commonly eaten at home (often at least once a week) or when dining out, to the time of writing when such customs were not being maintained.

Engle, J. B. and C. R. Chapman. 1952. Oyster condition affected by attached mussels. Southern Fisherman (August): 28-30.

On some oyster grounds in Chesapeake Bay, the hooked mussel, *Ischadium* (=*Brachidontes*) *recurvum*, forms dense colonies attached to live oysters. The authors found that oysters with attached mussels were characteristically more elongate than were mussel-free controls. More meat, relative to shell,

was produced in mussel-free oysters, with these oysters having a condition factor about 28% better than the condition factor of oysters with attached mussels.

Engle, J. B. and A. Rosenfield. 1962. Progress in oyster mortality studies. Proc. Gulf Carib. Fish. Inst. 15: 116-124.

A short historical and technical review of disease-induced mortality in Chesapeake Bay oysters, including descriptions of the research underway at the NMFS Laboratory at Oxford, Md.

Fairbanks, W. L. 1932. The Fisheries of Maryland. Maryland Development Bureau, Baltimore Association of Commerce, Baltimore, MD. 140 pp.

With regard to the oyster fishery, the report urged the extension of private culture as a sound business practice. A brief overview of the history of oyster grounds rental from 1906 to 1930 includes statistics on numbers of leaseholders, acres of bottom rented, distribution by county, size of holdings, production from the grounds, etc. The problems of seed oyster production was also reviewed. The poor condition of seed beds was attributed to the past practice of exporting large quantities of oysters in the shell, with immature oysters included, leading to the depletion of the seed beds and associated cultch. Some recommendations included providing the Conservation Department full authority to resurvey and reclassify disused oyster grounds in order to allow for greater production through private culture; more money and authority for the Conservation Department to use in development of large areas of seed beds; an increase in maximum area of bottom that could be rented for private culture; repeal of the prohibition on corporations and joint-stock companies with regard to rental of oyster grounds for private culture; amend the leasing laws to require actual planting of shells, oysters or cultch on private bottom within specific time periods and in specific quantities.

Farley, C. A. 1975. Epizootic and enzootic aspects of *Minchinia nelsoni* (Haplosporida) disease in Maryland oysters. J. Protozool. 22: 418-427.

This disease was studied for an 8 year period (1961-1968) using oysters from Marumsco Bar, Pocomoke Sound, Maryland. The author reviewed the life cycle stages, gross pathology and histopathologic aspects of the disease. He discussed mortality, incidence and prevalence and related these to environmental factors such as salinity and temperature. Genetic resistance to the disease appeared to be increasing during the period of study.

Frazier, J. M. 1972. Current status of knowledge of the biological effects of heavy metals in the Chesapeake Bay. Chesapeake Sci. 13 (suppl.): S149-S153.

A brief summary of studies concerning heavy metal uptake, concentrations, and effects on Chesapeake Bay organisms, including Crassostrea *virginica*.

Frazier, J. M. 1975. The dynamics of metals in the American oyster, Crassostrea *virginica*. I. Seasonal effects. Chesapeake Sci. 16: 162-171.

Hatchery reared oysters maintained in the Rhode River estuary were sampled monthly from September 1971 to May 1973 and seasonal dynamics of Mn, Fe, Zn, Cu and Cd were determined. Concentrations of Mn and Fe in soft tissues were found to be correlated with the deposition of shell, whereas concentrations of the other three metals were not. Thus, the aspects of Mn and Fe metabolism in the oyster were closely involved with processes of shell growth. The rapid discharge of Zn, Cu and Cd in summer and fall implicated reproductive activities such as spawning with the seasonal variation of these metals in oyster tissue.

Frazier, J. M. 1976 The dynamics of metals in the American oyster, Crassostrea *virginica*. II. Environmental effects. Chesapeake Sci. 17: 188-197.

Hatchery reared oysters were held in the Rhode River estuary (September 1972-August 1973) at two locations—one with little human impact (controls) and one subject to much human activity with metal contamination resulting. Growth of both populations was similar, but the metal-exposed population had shells which became significantly thinner (16%) than those of controls. Metal uptake by soft tissues was rapid in summer and fall but was slower in spring. Concentrations of Zn and Cu in soft tissues were higher in metal-exposed oysters than in controls.

Frey, D. G. 1945. Oyster Conservation Problems on the Potomac River. Proc. Natl. Shellfish. Assoc. Vol. 35: 3 pp.

The Potomac River oyster fishery was initially regulated and managed as a result of the compact of 1785 between Maryland and Virginia. However, it was not until 1912 that suitable laws were enacted by both states to regulate the fishery (these included a 2 1/2” cull law and establishment of an upriver seed area). In 1928, the U. S. Bureau of Fisheries was requested to survey the river’s oyster bars. These were found to be much depleted, with the result that dredging was prohibited starting in 1931. In November 1942, the U.S. Fish and Wildlife Service began a resurvey of the oyster bars in the Potomac,

finishing in July 1943. The survey found that stocks were still low (about 10 bushels of marketable oysters per acre on average) although large oysters had increased 10-fold and small oysters 20-fold since 1928. Oysters were found to be unevenly distributed over the larger oyster beds, with larger concentrations occurring on small sections of the bed. Setting appeared to be greater towards the mouth of the river. The author recommended that more cultch be applied in the good setting areas of the lower river, and that the clustered oysters in these areas be broken up. Small oysters should be planted to grow in the upper part of the river. The author concluded that the small increase in oyster abundance from 1928 to 1943 demonstrated that, even with decreased fishing pressure, the oyster bars cannot regain their former productivity by themselves, thus the need for remedial management.

Frierman, E. M. and J. D. Andrews. 1976. Occurrence of hematopoietic neoplasms in Virginia oysters (*Crassostrea virginica*). J. Natl. Cancer Inst. 56: 319-324.

Seventy cases of a rare neoplastic disease were noted during an intensive survey of trayed populations of oysters in Virginia waters. The disease occurred in oysters from a wide geographic range. There was a suggestion of seasonality, with most cases appearing from July to November at salinities from 10-22%. The disease may be associated with inbreeding.

Galtsoff, P. S. 1945. Problems of rehabilitation of Chesapeake Bay oyster resources. Proc. Natl. Shellfish. Assoc. Vol. 35: 3 pp.

Briefly described the decline of the oyster industry in Chesapeake Bay. For example, in Baltimore alone, the value of the oysters produced declined from about $4 million in 1880 to about $1 1/2 million in 1936-37. Galtsoff attributed the decline to a disregard of the fundamentals of the basic principles of conservation. He recommended that an effective system of exploitation and management begin. He briefly described the Bay-wide cooperative efforts between Maryland, Virginia and federal governments that had begun. The U.S. Fish and Wildlife Service had established a field headquarters in Annapolis and at Cambridge, and careful studies of the very low salinity conditions in the upper Bay and of spawning and setting patterns in the central Bay were underway.

Galtsoff, P. S., W. A. Chipman, Jr., J. B. Engle and H. M. Caldewood. 1947. Ecological and physiological studies of the effect of sulfate pulp mill wastes on oysters in the York River, Virginia. Fish Wildl. Serv., Fish. Bull. 43: 60-176.

Studies of the effects on oysters of effluent from a pulp-mill were performed from 1935. Results indicated that the upper part of the York River was an

unhealthy environment for oysters. Superficially, ecological conditions appeared suitable. However, presence of pulp-mill waste reduced the number of hours oysters were open and decreased pumping rates. Filtration rates varied in proportion to pulp-mill effluent concentration.

Glude, J. B. 1966. Criteria of success and failure in the management of shellfisheries. Trans. Amer. Fish. Soc. 95: 260-263.

Evaluated characteristics of successfully managed commercial fisheries for shellfish. Concluded that the oyster fishery in Maryland was managed unsuccessfully because of unlimited entry, inefficient harvesting techniques and limitations on private culture of oyster grounds.

Grave, M. 1912. A manual of oyster culture in Maryland. Fourth Report, Board of Shell Fish Commissioners. pp. 279-348.

A general treatment of physical and biological conditions which directly or indirectly affect oysters. A history of Maryland oyster production and an extensive section on oyster food are included.

Green, B. K. 1916 Seventh Report of the Shell Fish Commission of Maryland 1914 and 1915. Kohn and Pollock Inc., Baltimore, MD. 78 pp.

In a very brief review of oyster legislation, the commission considered private culture and rental of ground. At the time, any rented ground was used to “bed” oysters for growth and future sale. Aspects of the struggle to open more and better grounds to private culture were discussed. During the recent extensive survey of oyster grounds (1906-1912), full copies of the survey were filed in the county seat and there was a period available for challenging the survey findings. In 1912 there was a great increase in rental applications. This was followed by mounting protests by watermen that natural (not barren) oyster grounds were being rented. Much of this problem was caused by their having ignored the appeal period. However, other protests were found to be valid but, unfortunately, the watermen’s representatives had earlier insisted that the findings of the 1906-1912 survey be fixed and final. They had believed that natural grounds were shrinking in area and wanted to have a fixed survey to keep as large an area for their own use as possible. They refused to adhere to the agreed-upon rules and brought pressure on the Shell Fish Commission. Other watermen destroyed the property and stole the oysters of certain lessees. One such case was detailed by R. H. Spedden of St. Mary’s County. As a result of the pressure, further legislation (Shepherd Bill) was passed to modify the private culture laws to provide for greater flexibility in designating grounds as natural oyster beds or as private culture grounds.

Gregory, R. H., R. T. Hill and J. A. Hope, Jr. 1958. Bacteriological studies of harvesting and processing of oysters in Virginia. Proc. Natl. Shellfish. Assoc. 48: 30-43.

Oysters were examined from June 1955 to April 1956 using samples from lower Chesapeake Bay, Mobjack Bay and the mouths of the York and Rappahannock Rivers. The oysters were processed in packing plants. Shucking was found to cause an increase in the bacterial content of oysters. The bacterial content decreased during packing.

Hammer, R. C. 1948. Present status of the Chesapeake Bay oyster bars in Maryland. Proc. Natl. Shellfish Assoc. (1947): 8-10.

Blamed the decline of oyster yield in Maryland from 12 1/4 million bushels in the late 1800s to 2 1/2 million bushels (1946) on overfishing, which led to the result that many bars were completely devoid of oysters and cultch. Production was almost entirely due to more consistent spat sets on shallow bars in tributaries. The Say dredging bars once supported 1000 dredge boats and yielded 50 bushels of oysters per acre. By 1946 48 Bay dredgers remained, harvesting one bushel per acre. Provided data on costs of and yields from state shell planting action. Recommended private culture of oyster bars to help restore Bay's productivity.

Harshbarger, J. C., S. C. Chang and S. V. Otto. 1977. Chlamydiae (with phages), mycoplasmas, and rickettsiae in Chesapeake Bay bivalves. Science 196: 666-668.

Electron microscopy studies of Chesapeake Bay oysters revealed the presence of chlamydia-like organisms, rickettsia-like organisms and mycoplasma-like organisms. The former were observed to have phages present.

Haven, D. S. 1959. Effects of pea crab *Pinnotheres ostreum* on oysters Crassostrea *virginica*. Proc. Natl. Shellfish. Assoc. 49: 77-86

Condition indices were determined for tray-held oysters and oysters from the natural bottom. The latter were tested for condition in June 1956 (prior to spawning season); August 1956 (post-spawning); December 1956 (after full fattening); May 1957. The former were tested in December 1957. Measurements included volume, wet and dry mean weight, and shell cavity volume. During the seasons of maximum fatness (late spring, late fall, winter), oysters containing pea crabs had less meat by weight and lower condition index than did crab-free oysters. In August 1956 (post-spawning), condition indices for both groups of oysters were similar. Monthly samples of oysters from 1953 to 1958 revealed incidences of pea crab infestations varying from 6-22% in James River, 12-21% in York River, and 7-16% in Rappahannock River.

Haven, D. S. 1962. Seasonal cycle of condition index of oysters in the York and Rappahannock Rivers. Proc. Natl. Shellfish. Assoc. 51: 42-61.

Oysters collected annually from Wreck Shoals oyster bed in James River were held on the bottom or in trays elevated off the bottom in the York and Rappahannock Rivers. Each month, 25 oysters from stations in both rivers were processed either as a group or individually, and condition indices were determined. Incidence of pea crab and *Dermocystidium marinum* infestation were noted. In winter, York River tray and bottom oysters generally had a lower condition index than did Rappahannock tray or bottom oysters. Bottom oysters in both rivers often had a consistently lower index than did tray oysters. Rappahannock oysters generally had high indices of condition in late spring, followed by a decline in summer and a return to high values in fall. Peak condition was reached in York River in late spring, followed by a decline in summer and no quality increase in fall. The winter of 1960-61 produced a six-year high in quality and yields for oysters from public oyster grounds in both rivers, and for the experimental oysters held in trays and on the bottom in both rivers. Presence of *Dermocystidium marinum* or *Pinnotheres ostreum* was not responsible for condition index differences between tray and bottom oysters.

Haven, D. S. 1965. Supplemental feeding of oysters with starch. Chesapeake Sci. 6: 43-51.

The author added cornstarch or wheat flour to provide supplemental food for James River oysters held in flowing York River water. This influenced meat weight but generally not oyster air weight or shell cavity size. Reducing water volume flow or filtering incoming water inhibited meat development. Added starch tended to compensate for these restrictions. Under estuarine conditions, tissue weights may be influenced by quantities of starch in planktonic algal cells more than by the species or volume of plankters ingested.

Haven, D. S. 1980. Virginia seed sources. In: D. Webster (ed.). Oyster Culture in Maryland ‘79. A Conference Proceedings. Md. Coop. Ext. Service, pp. 25-30.

A brief review of Virginia’s seed resource.

Haven, D. S., W. J. Hargis, Jr., and P. C. Kendall. 1978. The Oyster Industry of Virginia: Its Status, Problems and Promise. Va. Inst. Mar. Sci., Spec. Papers in Mar. Sci. No. 4. 1024 pp.

An extensive survey of the history, economics, fishery, culture, biology and ecology of oysters in Virginia, with recommendations for management and rehabilitation.

Haven, D. S., J. P. Whitcomb, J. M. Zeigler and W. C. Hale. 1979. The use of sonic gear to chart locations of natural oyster bars in lower Chesapeake Bay. Proc. Natl. Shellfish. Assoc. 69: 11-14.

A microphone encased in a PVC tube, suspended from an A-frame, and towed over the bottom of Chesapeake Bay was used as a means of detecting shell material. The information collected was used in conjunction with other data to chart oyster bottoms in Virginia.

Hewatt, W. G. and J. D. Andrews. 1954. Oyster mortality studies in Virginia. I. Mortalities of oysters in trays at Gloucester Point, York River. Texas J. Sci. 6: 121-133.

During the warm months of summer and fall, oysters growing in trays in York River, Virginia, suffered high mortality. Studies of this mortality began June 1950. The fungus, *Dermocystidium marinum*, was implicated. It caused seasonal variations in mortality.

Hewatt, W. G. and J. D. Andrews. 1956. Temperature control experiments on the fungus disease, *Dermocystidium marinum*, of oysters. Proc. Natl. Shellfish. Assoc. 46 129-133.

In summer 1954, oysters from the James River (a fungus-free area) and the Rappahannock River (a diseased area) were collected. They were twice exposed to minced oyster tissues from fungus-infected oysters, then divided into groups held at 15°C, 28°C and in ambient seawater (26°-30°C). Over a 6-week period, there was a 10% mortality at 15°C compared with 99% mortality at 28°C. Mortality was 53% in ambient seawater. Mortalities were greater in oysters from the fungus-free river.

Hidu, H., K. G. Drobeck, E. A. Dunnington, Jr., W. H. Roosenburg and R. L. Beckett. 1969. Oyster Hatcheries for the Chesapeake Bay Region. Univ. of Maryland, Natural Resources Institute, Spec. Rep. No. 2. 18 pp.

The authors performed trials to determine feasibility of hatchery technology for rearing oysters to supplement natural recruitment. They reviewed some history and discussed the general recalcitrance of southern populations of oysters, including those of Chesapeake Bay, to spawn under artificial conditions. Unlike their more northerly counterparts, southern oysters do not respond well to attempts to initiate spawning by chemical or thermal stimulation, or both. However, properly conditioned Chesapeake Bay oysters will spawn eventually, appear to be able to spawn periodically during the summer, and may even be spawned in the fall. The authors provided information on rearing larvae and for handling spat.

Hidu, H., W. H. Roosenburg, K. G. Drobeck, A. J. McErlean and J. A. Mihursky. 1974. Thermal tolerance of oyster larvae, Crassostrea *virginica* Gmelin, as related to power plant operation. Proc. Natl. Shellfish. Assoc. 64: 102-110.

Fertilized eggs, ciliated grastrulae, and two-day-old veliger larvae of Chesapeake Bay oysters were subject to temperature increases for periods ranging from 10 seconds to 16 hours. Percentage mortality increased with increasing temperature and time of exposure. Fertilized eggs were most sensitive to higher temperatures, with veliger larvae most tolerant. The application of these findings to entrainment in power plant cooling water systems was discussed.

Hillman, R. E. 1964. Chromatographic evidence of intraspecific genetic differences in the eastern oyster, Crassostrea *virginica*. Syst. Zool. 13: 12-18.

Paper partition chromatography was used to determine patterns of free amino acids or small peptides in samples of oysters from Long Island Sound and James River, Virginia. Under the experimental conditions, one reproducible difference in these patterns was obtained. The author regarded this as evidence of intraspecific genetic differences between the two populations.

Hillman, R. E. 1965. Chromatographic studies of allopatric populations of the eastern oyster Crassostrea *virginica*. Chesapeake Sci. 6: 115-121.

The author extended his 1964 study of genetic differences among oyster populations by adding material from Delaware Bay, Louisiana, Long Island, Virginia, and parts of Chesapeake Bay. A new chromatographic technique was used and described. No data were given, but the author reported qualitative differences occurring in chromatograms, which he interpreted as indirect evidence for metabolic differences among the oyster populations.

Hoese, H. D. 1964. Studies on oyster scavengers and their relation to the fungus *Dermocystidium marinum*. Proc. Natl. Shellfish. Assoc. 53: 161-174.

Traces of this parasitic fungus were found in the stomach of the snail *Urosalpinx cinerea*, the body and guts of the fishes *Gobiosoma bosci*, *Chasmodes bosquiences* and *Opsanus tau* and the body and setae of the crab *Neopanope texana* and *Rhithropanopeus harrisii*. All had previously fed on infected oysters. In the presence of fishes which had been fed infected oyster tissue, some healthy oysters became lightly infected. In a field study, killed oysters placed on the bottom in a tidal inlet of Chesapeake Bay were eaten by scavengers in less than 24 hours when temperatures exceeded 24°C. Above 18°C, tissue never had a chance to decay because of rapid

scavenging. The author surmised that the parasites in the infected oysters must pass through the guts of scavengers, hastening transmittal of fungal spores to other oysters in the vicinity.

Hopkins, S. H. 1962. Distribution of species of *Cliona* (boring sponge) on the Eastern Shore of Virginia in relation to salinity. Chesapeake Sci. 3: 121-124.

Four species of *Cliona* were found to occur in Chesapeake Bay waters off Virginia's Eastern Shore. The most abundant boring sponge in high salinity waters of Virginia (*C. celata*) was least abundant in the lower salinities of Bayside creeks. *C. truitti* was most abundant in Bayside creeks. Its abundance increased as salinity decreased.

Hussong, D., R. R. Colwell and R. M. Weiner (in press). Seasonal concentration of coliform bacteria by Crassostrea *virginica*, the eastern oyster in Chesapeake Bay. J. Food Protection.

Oysters, water and sediment samples from Tolly Point and Eastern Bay were collected from February 1977 to October 1978. Total coliforms remained at low densities over this time period. However, coliform MPN counts in oysters rose significantly in the fall (October - early November) of each year (approx. 13°C). These increases, and a smaller increase at Tolly Point in late spring/early summer, were not the result of increases in coliforms in the water column. The resultant concentration of coliforms by oysters is unexplained.

Ingersoll, E. 1881. The History and Present Condition of the Fishing Industries. The Oyster Industry. U. S. Census Bureau, Tenth Census, Dept. of the Interior, Washington, D.C. 251 pp.

An extensive treatment of the oyster industry in the U.S. (and Canada's maritime provinces) encompassing fishery statistics, processing and shipping industries, and even aspects of the sociology of oystermen. The Maryland and Virginia industries were described in some detail (pp. 156-187).

Jensen, W. P. 1981. Leased bottom and the Maryland oyster fishery. In: D. Webster (ed.). Oyster Culture in Maryland 1980: A Proceedings. University of Maryland Cooperative Extension Service, College Park, Md. pp. 117-127.

A brief discussion of the status of the Maryland leased bottom program, extent of bottom presently in lease (9,000 acres by 651 leaseholders), extent that could be made available under present law (about 25,000 acres of ground suitable for oyster cultivation), and current state policy towards expansion of private holdings.

Kennedy, V. S. 1980. Comparison of recent and past patterns of oyster settlement and seasonal fouling in Broad Creek and Tred Avon River, Maryland. Proc. Natl. Shellfish. Assoc. 70: 36-46.

Settlement of oyster spat, barnacles, encrusting bryazoans, and some additional invertebrates was studied for three summers (1977-1979) in these lower Choptank River tributaries. Results were compared with a similar study in this area in 1961 to 1966. In contrast to the earlier results, in 1977-1979 oysters settled predominantly on upper surfaces, perhaps as a result of increased turbidity or decreased light penetration in the intervening years. Average numbers of oyster spat were lower than in 1961 to 1966. Barnacles and bryozoan colonies settled predominantly on under surfaces, as before. Numbers of hooked mussels settling were lower than in the past. As before, Broad Creek had a higher incidence of oyster settlement than did Tred Avon River, which continued at its former low level.

Kraeuter, J. and O. S. Haven. 1970. Fecal pellets of common invertebrates of lower York River and lower Chesapeake Bay, Virginia. Chesapeake Sci. 11: 159-173.

The authors describe the fecal pellets of 70 species of Chesapeake Bay invertebrates, including the oyster, Crassostrea *virginica*.

Krantz, G. E. and J. V. Chamberlin. 1978. Blue crab predation on cultchless oyster spat. Proc. Natl. Shellfish. Assoc. 68: 38-41.

Blue crab predation on oyster spat reared on and then removed from Mylar plastic sheets was studied by providing the spat to blue crabs in aquaria. Shell chipping and crushing by the crabs was described.

Krantz, G. E. and D. W. Meritt. 1977. An analysis of trends in oyster spat set in the Maryland portion of the Chesapeake Bay. Proc. Natl. Shellfish. Assoc. 67: 53-59.

From 1939 to 1975, there was a general trend of declining spat settlement in Chesapeake Bay, Maryland, although there had been some short periods of good spat settlement (e.g., 1943, 1945, 1965). Tropical Storm Agnes which flooded the Bay with freshwater in 1972 obviously influenced oyster mortality, reproduction and recruitment. However, the available data showed that this and other natural disasters were not totally to blame for the decline in recruitment. Other possible factors, including overfishing, were considered. A recommendation that shellfish hatchery oysters be used to supplement natural set on selected oyster bars was made.

Lackey, J. B., C;. Vander Borgh, Jr., and J. B. Glancy. 1953. General character of plankton organisms in waters overlying shellfish-producing grounds. Proc. Natl. Shellfish. Assoc. (1952): 152-156.

Study locations included Woods Hole; Milford, Long Island; and, in Chesapeake Bay: Solomons, the Patuxent River and St. Mary's River. Of several hundred plankton samples collected since 1948, the lowest number of organisms was 300,000 liter^{-1} (over Thomas Bar, Solomons, Md.) with the greatest abundance being over 300,000,000 liter^{-1}. In St. Mary's River (an excellent setting ground but a poor fattening area) there was a large plankton assemblage with relatively few diatoms and dinoflagellates compared with other locations. There were large numbers of various small flagellates, including very small green flagellates. The authors felt that the small flagellates are good larval food, with diatoms and dinoflagellates a better food for adults. The other Chesapeake locations were also lower in diatoms but had more dinoflagellates than did St. Mary's River. The authors concluded that inshore waters were able to produce sufficient plankton to maintain large shellfish populations, that kind and not abundance was critical, and that smaller flagellates were best for larvae.

Larsen, P. F. 1974. Structural and functional responses of an oyster reef community to a natural and severe reduction in salinity. In: Proc. First Int. Congress of Ecology, Structure, Functioning and Management of Ecosystems. Cntr. Agric. Publ. Docu. Wageningen (Neth.), pp. 80-85.

In June 1972, Tropical Storm Agnes inundated Chesapeake Bay, with resultant flooding causing sharp drops in salinity. This study involved the James River estuary, Virginia. Samples on 8 oyster reefs before and after the freshet indicated decreases in numbers of species and densities of individuals following the storm. Down-estuary sites lost their less euryhaline species, whereas up-estuary sites showed less change, presumably due to greater adaptabilities and tolerances to salinity stress of the associated organisms.

Larsen, P. F. 1978. *Boccardia hamata* (Polychaeta: Spionidae): A potential pest of the American oyster in the James River, Virginia. Estuaries 1: 183-185.

Boccardia hamata is a boring species of spionid polychaete which was found in large numbers in oyster reefs of the James River, Virginia. It had not been reported in such high numbers before, either in Chesapeake Bay or elsewhere on the Atlantic coast.

Lawler, A. R. 1969. Occurrence of the polyclad *Coronadena mutabilis* (Verrill, 1873) in Virginia. Chesapeake Sci. 10: 65-67.

Coronadena mutabilis, like the polyclad *Stylochus ellipticus*, was found in association with oysters. This report concerns its presence at two new locations, both in lower Chesapeake Bay. It was not observed to feed on C. virginica during the course of the study.

Lewis, T. B. and G. Power. 1979. Chesapeake Bay oysters: Legal theses on exotic species. In: R. Mann (ed.) Exotic Species in Mariculture, pp. 265-305. MIT Press, Cambridge, Mass.

The authors reviewed oyster laws in the Chesapeake Bay area, especially recent court decisions concerning county residency requirements. They recommended that Maryland's oyster management program move to protect its property interest in state oyster grounds, and to encourage widespread cultivation of privately managed oyster beds. The introduction of a new (exotic) species of oyster would need to be preceded by statutory changes in Maryland's law.

Lewis, T. B. and I. E. Strand, Jr. 1978. Douglas v. Seacoast Products, Inc.: The legal and economic consequences for the Maryland oystery. Maryland Law Review 38: 1-36.

The authors reviewed possible consequences of a U.S. Supreme Court decision concerning use of federally licensed vessels by non-residents or aliens in a Virginia fishery. The implication was that a federal vessel license allows non-residents to harvest oysters in Maryland on the same terms as residents, restrictive-entry state laws notwithstanding. The authors compared the Supreme Court decision with a Maryland judgment which struck down county residency requirements for the taking of oysters and crabs. Their conclusion was that public oyster bars may be in danger of even greater fishing pressure without the protection of state residency restrictions. They recommended a restructuring of the state management program and encouragement of private culture of oyster bars.

Lipschultz, F. and G. Krantz. 1978. An analysis of oyster hatchery production of cultched and cultchless oysters utilizing linear programming techniques. Proc. Natl. Shellfish. Assoc. 68: 5-10.

A system of linear equations and a computer optimization program were used to compare manpower and operational requirements in a large-scale hatchery. The model was used to determine the best production schedule and use of equipment, to compare hatchery production of cultched and cultchless spat, and to evaluate the suitability of the design of an oyster hatchery operating in Chesapeake Bay. The model allowed for manipulation of various aspects of hatchery procedure and equipment use to determine the

most economic (in terms of labor, energy and dollars) production scheme. Cost of production of cultched spat was estimated to be 44% less than for cultchless spat. Design errors in the hatchery were noted and production bottlenecks were identified.

Loosanoff, V. L. 1932. Observations on Propagation of Oysters in James and Corrotoman Rivers and the Seaside of Virginia. Virginia Commission of Fisheries, Newport News, Va. 46 pp.

This report is a description of the results of extensive studies undertaken from spring to fall, 1931. The author made many observations on temperature and salinity, including the use of recording thermometers at two stations in Chesapeake Bay. Plankton samples were collected (usually at slack tide) nearly every day in the James River, with occasional samples made elsewhere. Spat settlement was monitored on shell in wire bags. In the James River, oyster spawning began in late May-early June and extended until October. General spawning occurred at 26°C (bottom), not at 20°C (a "critical temperature" of early investigators). Straight-hinge larvae were collected from late May to mid-October but umbo larvae were very rare. Setting extended from mid-June to mid-October with peaks in mid-August and mid-September. The heaviest setting occurred near the bottom and decreased towards high water mark. The author recommended that oyster cultivation be encouraged in the Corrotoman River and in Virginia's seaside waters.

Loosanoff, V. L. 1969. Maturation of gonads of oysters, Crassostrea *virginica*, of cliff Brent geographical areas subjected to relatively low temperatures. Veliger 11: 153-163.

The author studied gametogenesis in oysters collected from a number of locations along the U.S. Atlantic coast (including lower York River, Virginia) and held in Long Island Sound waters (Milford Harbor). Over a 2 1/2-month period, beginning January 15, groups of oysters were held at 12°, 15° and 18°C and their gonadal maturation was assessed periodically using histological techniques. At 12°C, the gonads of Virginia oysters had not progressed past winter stages, even after 78 days of conditioning. At 15°C, Virginia gonads were in the early development stage after 72 days, even though most appeared to be feeding. At 18°C, the Virginia oysters continued to be in the early stages of development, even after 71 days of conditioning.

Lovelace, T. F., H. Tubiash and R. R. Colwell. 1968. Quantitative and qualitative commensal bacterial flora of Crassostrea *virginica* in Chesapeake Bay. Proc. Natl. Shellfish. Assoc. 58: 82-87.

Water, mud, oyster mantle fluid, and oyster gill tissue were examined from material collected every 6 weeks from Marumsco Bar in Pocomoke Sound,

and from Eastern Bay. Salt-requiring bacteria appeared to be a significant part of the bacterial flora of both areas. On Marumsco Bar, 81% of water, mud and animal samples were composed of *Vibrio*, *Pseudomonas* and *Achromobacter* spp. In Eastern Bay, these bacteria comprised just 46%, with *Cytophaga/Flavobacterium* spp. dominant. Eastern Bay was considered to harbor a "balanced" population.

MacKenzie, C. L., Jr. 1977. Sea anemone predation on larval oysters in Chesapeake Bay (Maryland). Proc. Natl. Shellfish. Assoc. 67: 113-117.

Diadumene leucolena is a sea anemone which is commonly found attached to oyster shell in Chesapeake Bay, Maryland. It was found to feed on oyster larvae in the laboratory and presumably feeds on these larvae in nature.

Mackin, J. G. 1951. Histopathology of infection of Crassostrea *virginica* (Gmelin) by *Dermocystidium marinum* Mackin, Owen, and Collier. Bull. Mar. Sci. Gulf Carib. 1: 72-87.

In late summer, 1949, high mortality occurred among oysters in the Rappahannock River, Virginia. Histological sections of survivors revealed the presence of the fungus *Dermocystidium marinum*.

Manning, J. H. 1953. Setting of oyster larvae and survival of spat in the St. Mary's River, Maryland, in relation to fouling of cultch. Proc. Natl. Shellfish. Assoc. 43: 74-78.

Wire bags of oyster shell which had been held beneath the laboratory pier at Solomons, Maryland, for varying periods of time were moved on July 2 to St. Mary's River in time for the major period of spatfall. Counts of barnacles, bryozoan colonies and oyster spat at varying periods until November were made. Barnacle fouling appeared to inhibit oyster setting. Heavily fouled cultch caught only about 25% as many spat as did cultch which was relatively free of barnacles during the spatfall period. Light to moderate bryozoan fouling had no apparent influence on oyster set.

Manning, J. H. 1957. The Maryland Soft Shell Clam Industry and its Effects on Tidewater Resources. Md. Dept. Res. Educ., Resource Report No. 11. 25 pp.

This report contains the results of an experiment performed in Cox Creek, Queen Anne's County, to determine the effects of hydraulic clam dredging on oysters. An experimental plot was established. It contained oysters unevenly distributed over a generally shelly bottom, An approximately 0.25 acre plot at the north end of the experimental area was dredged thoroughly

on the ebbing tide (0.1-0.9 knots) for 9.5 hours in late August 1956. This was done after all oysters from within 4 randomly-placed 20 ft rectangles on each of 7 parallel transects had been removed by divers. The transects were established at intervals of 25, 50, 75, 100, 200, 300 and 400' from the experimental area. About 1" of sediment was deposited down-current 25' from the dredged area and about 0.6" was deposited 50' away. About 4 months later, the 7 transects and the experimental (dredged) area were resampled as before. Numbers of oysters collected after dredging were not significantly different from those collected before dredging, except in the dredged area and on the transect 25' away, where numbers were higher before dredging. The author concluded that no damage from the results of hydraulic dredging would be expected at a distance 75' down-current from the dredging area, assuming currents up to 1 knot (a high velocity for most parts of the oyster areas of the Bay).

Manning, J. H. and H. H. Whaley. 1955. Distribution of oyster larvae and spat in relation to some environmental factors in a tidal estuary. Proc. Natl. Shellfish. Assoc. 45: 56-65.

The authors sampled plankton and measured spatfall, current velocities, salinity and temperature in St. Mary's River, a tributary of the Potomac River, in June and July 1951. The sluggish circulation of the river seemed to produce three main sub-regions: Area I, the lower river, had wind-induced circulation with surface inflow and bottom outflow; Area II, middle river, had a very weak net upstream water movement; Area III, upper river, had a 2-layer system of upper-level outflow and lower-level inflow. Spat settlement was highest in Area III, decreasing downstream. Contrarily, 88% of the charted oyster bars lay in Area I, 9% in II and 3% in III. Plankton sampling at various depths indicated a tendency of oyster larvae as they mature to be found at progressively greater depth. Thus the authors postulated that Area I would lose early stage larvae to Area II and later stage larvae to the Potomac River. Area II larvae would slowly be carried upstream to Area III, which in turn would act as a "larval trap."

Marasco, R. J. 1973. An appraisal of the alternative earning power of the Maryland oystermen. Proc. Natl. Shellfish. Assoc. 63: 47-52.

Oystermen of the communities of Rock Hall and Crisfield-Smith Island on the Eastern Shore and of Shadyside and Avenue on the Western Shore were studied by personal interview. Oystermen from the Eastern Shore communities would appear to have more difficulty finding employment outside the fishing industry than would the oystermen from the Western Shore.

Marshall, N. 1954. Changes in the physiography of oysters bars in the James River, Virginia. Proc. Natl. Shellfish. Assoc. 44: 113-121.

The author compared data from depth surveys on transects across selected public oyster bars in lower James River. These bars had been surveyed for depths at different times from 1854-1855 onward to the late 1940's. At most points, depth comparisons indicated an increase in depth with an average loss of about a foot in elevation of oyster grounds. Most of the formerly emergent or intertidal oyster shoals which had been noted in the 1871-73 surveys (17,000 yards in area) had disappeared in the late 1940's (100 yards left). The author calculated (roughly) that the oyster fishery would have been responsible for less than about half the depth increase. Thus, presumably both natural and fishery influences resulted in dynamic changes in oyster bar physiography.

Maryland Commission on Conservation of Natural Resources. 1948. Report to the Governor of Maryland. 91 pp.

The Commission recommended oyster farming and presented estimates of the yields in seed or harvestable oysters per bushel of shell or seed that was planted in the proper area. They noted that the 1948-49 increase in the shell tax to 20% of fresh resin shell was insufficient and stressed the need to have all shell returned to the State.

McHugh, J. L. 1956. Trapping oyster drills in Virginia. II, The time factor in relation to the catch per trap. Proc. Natl. Shellfish. Assoc. 46: 155-168.

Experiments on trapping oyster drills using seed oysters as bait were performed at Gloucester Point, Va. in summer 1953 and spring and summer 1954. *Urosalpinx cinerea* was the most common drill trapped, being about 22 times more common at the experimental location than was *Eupleura caudata*. For both species, the rate of being trapped declined with time. This decline was not statistically significant for *U. cinerea* over the first week, thus traps could be lifted weekly rather than daily with little loss of catching efficiency compared with lifting them more frequently. Significantly lower catches occurred for *E. caudata* in traps fished weekly compared with traps fished daily.

McHugh, J. L. and J. D. Andrews. 1955. Computation of oyster yields in Virginia. Proc. Natl. Shellfish. Assoc. 45: 217-239.

Oysters were held in trays suspended from the Virginia Fisheries Laboratory Pier, Gloucester Point, Va., for 4 years. Data on mortality and growth were collected at closely-spaced intervals. Rather than the normal yield of one bushel of market oysters for one bushel of planted seed (typical for Chesapeake Bay), the tray-held oysters yielded three bushels of market oys-

ters for each bushel of seed placed in the trays. The authors calculated Walford growth curves and determined seasonal growth patterns, mortality rates, and the instantaneous rate of mortality. Yields were then computed.

Merrill, A. S. and K. J. Boss. 1966. Benthic ecology and faunal change relating to oysters from a deep basin in the lower Patuxent River, Maryland. Proc. Natl. Shellfish. Assoc. 56: 81-87.

Oysters were found in substantial numbers in 120-130 feet of water in a deep basin near the mouth of the Patuxent River. Their condition was not as good as that of shallow water (10') oysters. In June, oysters from 10', 65' and 130' were ripe. By December, shallow water oysters had spawned, but some oysters from 65' and 130' (30% and 40% respectively) were only partly spawned. Deep-water oysters grew more slowly than their shallow-water counterparts.

Morse, D. C. 1945. Some observations on the food and feeding of oysters in Chesapeake Bay. Proc. Natl. Shellfish. Assoc. 35: 3 pp.

In 1943-44, Patuxent River oysters were collected biweekly during periods of oyster activity and less frequently in winter. Stomach contents were collected from about 10 oysters in the field and preserved immediately. Plankton samples were generally collected at the same time. Stomach contents included diatoms, dinoflagellates, tintinnids, silicoflagellates, ostracods, unidentified eggs and larvae and land pollen. Red pigmentation of the meats on one occasion was due to the dinoflagellate *Exuviella apora*. Seasonal patterns in feeding were evident. In autumn, until the weather turned cold, the diatom *Cyclotella striate* dominated in stomach samples (up to 80% of the food). It was accompanied by other diatoms and by dinoflagellates. After mid-November, feeding declined until it halted in mid-December. No food was noted in stomachs sampled at water temperatures less than 5°C. In mid-March when bottom temperatures passed 5°C, diatoms predominated, with *Cerataulina bergonii* and *Nitzchia seriata* comprising up to 90% of the stomach contents. After mid-April, *Cyclotella striata* reappeared. Below 10-12°C, few food organisms were found in the stomachs although some oysters had crystalline styles. Above 20°C, oysters were fat and full of diatoms. Comparison with plankton samples revealed that oysters rejected the large spring diatoms such as *Rhizosolenia* and large *Chaetoceras*, larger dinoflagellates (*Ceratium*), and copepods (however, parts of these organisms were found to be ingested). The nanoplankton appeared to be important, as evidenced by the numbers of *Cyclotella* ingested in fall and spring.

Munson, T. O. and R. J. Huggett. 1972. Current status of research on the biological effects of pesticides in Chesapeake Bay. Chesapeake Sci. (Supplement) 13: S154-S156.

A brief summary of the limited number of studies concerning pesticides and their effects on Chesapeake Bay ecosystems and organisms, including C. virginica. In Virginia, a number of stations had been established for monitoring of pesticides (DDT, dieldrin, PCB, etc.). A few studies had been performed in Maryland. Although EPA was there monitoring fish, no other Bay-wide monitoring was being performed.

Newcombe, C. L. . and R. W. Menzel. 1945. Future of the Virginia oyster industry. Commission of Fisheries of Virginia, Contrib. No. 22: 1-11. Reprinted from The Commonwealth 12(4) 1945.

A general, illustrated essay on the biology of oysters in Virginia, with a summary of research needs.

Nichol, A. J. 1937. The Oyster-Packing Industry of Baltimore. Its History and Current Problems. Chesapeake Biological Laboratory Bulletin, Solomons Island, MD. 32 pp.

An extensive illustrated history of the Maryland oyster industry, especially that which centered around Baltimore, from colonial days when oysters were eaten only because of fear of starvation, through the boom days of the late 1800's, to the depressed market in the mid 1930's. The author saw a solution to the depressed market in the guarding and replenishing of the supply. "This will come in Maryland when the oystermen of Chesapeake Bay realize that their excessive independence has worked against their best interest, economically and socially, while at the same time, it has been dissipating a treasure which belongs not alone to them but to all the people of the State."

Orbach, M. K.. 1980. Fishery cooperatives on the Chesapeake Bay: advantage or anachronism. Anthropol. Quart. 53: 48-55.

Discussed cooperative activity among Bay watermen over time and attempted to explain rise and fall of cooperatives and unions in the Bay area.

Outten, W. 1980. Maryland's state seed problem. In: D. Webster (ed.). Oyster Culture in Maryland '79. A Conference Proceedings. Md. Coop. Ext. Serv., pp. 15-24.

A brief review of the state seed program.

Pfitzenmeyer, H. T. 1972. Molluscs of the Chesapeake Bay. Chesapeake Sci. 13 (Suppl): S107-S115.

This is a brief review of research performed on the ecology and biology of Chesapeake Bay molluscs, including Crassostrea *virginica*.

Power, G. 1970. More about oysters than you wanted to know. Maryland Law Review. 30: 199-225.

An extensive study of legal aspects of the public and private oyster fishery in Maryland. Reviewed history of state regulation of the industry and of the attempts to allow private cultivation of oyster ground. Concluded that discriminators in Maryland law which excluded non-residents and corporations from the fishery were generally unconstitutional, and that a successful judicial attack on these discriminations might stimulate general reform of existing oyster laws. Recommended encouragement of greater private cultivation of oyster grounds and the granting of broad management authority to the Fish and Wildlife Administration (now Tidewater Administration). The latter action would free the Administration from anachronistic laws and would abolish the current hold the legislature has over the industry.

Pritchard, D. W. 1953. Distribution of oyster larvae in relation to hydrographic conditions. Proc. Gulf Carib. Fish. Invest. 5: 123-132.

Oscillatory tidal currents produce a typical coastal plain estuarine circulation pattern in which ebb velocities are relatively large at the surface, decreasing with depth, while flood velocities are relatively small at the surface, increasing with depth, and then decreasing as bottom friction exerts an influence. This leads to a two-layered circulation pattern, with a surface of no net motion at some mid-depth. Salt balance in the James River, Virginia, is maintained primarily by the mean horizontal advection and the vertical mixing term. Mean vertical advection and the horizontal mixing term are of lesser or no importance, respectively. Pritchard proposed that distribution of oyster larvae could be influenced by the described hydrographic conditions. For example, the northeast side of the James River had higher production of oyster seed than did the southwest shore. This could be attributed to slow upwelling of deeper waters over the shallow northeast bars. However, field sampling was difficult because the counting of oyster larvae is onerous. Further, Pritchard calculated that only 1 larva per 100 litres of water was required to achieve the large observed sets. A sampling program involving samples of 100 litres obviously would be inadequate. Examination of the results of a field sampling program indicated that larval distributions were more compact and concentrated than were predicted on the assumption that oyster larvae were passively distributed in the same manner as dissolved material, e.g., dye. Dye studies in estuaries seemed to indicate that dissolved or suspended materials spread more quickly than did oyster larvae.

Quittmeyer, C. L. 1966. A Report on the Chesapeake Bay Fisheries of Maryland. Seafood Advisory Committee of Wye Institute, Centreville, Md. 68 pp.

This privately-commissioned report was prepared by an independent research group of consultants, including an oyster biologist, two business administrators, a sociologist, an economist, and a political scientist. They studied other fisheries in addition to the oyster fishery. However, with regard to the latter, they reiterated the conclusion of "generations of studies and reports," i.e., encourage private cultivation of the resource to complement the public fishery. They felt that if this were done, a doubling of production would occur in five years. Further, oyster grounds should be classified as "seed, self-sustaining, and growing grounds," with appropriate management of the different grounds. They compiled a list of 14 steps or actions based on biological understanding which they regarded as necessary for enhancement of oyster production.

Rawls, C. K. 1977. Field studies of shell regrowth as a bioindicator of eastern oyster (*Crassostrea virginica* Gmelin) response to 2,4-D BEE in Maryland tidewaters. Chesapeake Sci. 18: 266-271.

Eurasian watermilfoil can be controlled by application of the butoxyethanol ester of 2,4dichlorophenoxy-acetic acid (2,4-D BEE). To determine its effect on oysters, new growth was filed from the edges of oysters which were then held in trays in field environments to which three different quantities of the herbicide were applied. There was no evidence that oyster shell regrowth or replacement was adversely affected by the herbicide in the amounts used.

Roosenburg, W. H., J. C. Rhoderick, R. M. Block, V. S. Kennedy, S. R. Gullans, S. M. Vreenegoor, A. Rosenkranz and C. Collette. 1980. Effects of chlorine-produced oxidants on survival of larvae of the oyster Crassostrea *virginica* Mar. Ecol. Prog. Ser. 3: 93-96

Effects of chlorination on straight-hinge veliger larvae and pediveliger larvae were studied over time in flowing estuarine water. Larval mortality was directly related to increased concentrations of chlorine-produced oxidants (CPO) and extended exposure time. Pediveliger larvae were generally more resistant to CPO than were straight-hinge larvae, especially with lower exposure time. Equations for predicting mortality under different conditions of time and CPO concentrations were developed.

Sayler, G. S. J. D. Nelson, Jr. and R. R. Colwell. 1975. Role of bacteria in bioaccumulation of mercury in the oyster Crassostrea *virginica.* Appl. Microbiol. 30: 91-96.

In an experimental system, mercury concentrations in tissue of oysters dosed with mercury metabolizing bacteria were 200 times greater than in tissues of oysters in control conditions. Mercury accumulation was significantly higher in gill and visceral tissues than in other tissues.

Sayler, G. S., J. D. Nelson, Jr., A. Justice and R. R. Colwell. 1976. Incidence of Salmonella spp., *Clostridium botulinum*, and *Vibrio parehaemolyticus* in an estuary. Appl. Envir. Soc. Microbiol. 31: 723-730.

During the sampling period, September 1974 - December 1974, C. virginica was found to be free of pathogens which were found in water or sediment samples. As water temperatures fell from 23.8°C to 6.2°C, bacteriological quality of the oyster generally improved.

Sawyer, T. K., M. W. Newman and S. V. Otto. 1975. A gregarine-like parasite associated with pathology in the digestive tract of the American oyster, Crassostrea *virginica*. Proc. Natl. Shellfish. Assoc. 65: 15-19.

An amoeboid or gregarine-like parasite was found to be associated with seasonal pathology of the digestive tract in oysters from Connecticut and Maryland waters.

Shaw, W. N. 1966. The growth and mortality of seed oysters, Crassostrea *virginica*, from Broad Creek, Chesapeake Bay, Maryland, in high- and low-salinity waters. Proc. Natl. Shellfish. Assoc. 56: 59-63.

Seed oysters from Mulberry Point bar, Broad Creek, were held off-bottom in trays or strung on wires in Tred Avon River (low salinity) and Chincoteague Bay (high salinity). Over a two-year observation period, shell growth was similar in both areas. In the second year, high mortality occurred in Chincoteague Bay, apparently unrelated to high salinity.

Shaw, W. N. 1967. Seasonal fouling and oyster setting on asbestos plates in Broad Creek, Talbot County, Maryland, 1963-65. Chesapeake Sci. 8: 228-236.

Weekly setting frequencies of oysters, bryozoans, barnacles, mussels, and flatworms were observed on asbestos-cement plate collectors. The barnacles, bryozoans and flatworms set predominantly on plate undersurfaces. Oysters and mussels preferred the undersurface when plate collectors were 4” apart, but settled predominantly on upper surfaces when the plates were 1” apart. It was recommended that shells be planted in Broad Creek during the first week of July to serve as cultch for spat that should become available at that time.

Shaw, W. N. 1969. Oyster setting in two adjacent tributaries of Chesapeake Bay. Trans. Amer. Fish. Soc. 98: 309-314.

Over a 5-year period (1962-66), oyster setting in Broad Creek, Choptank River, was consistently greater than in adjacent Tred Avon River, as measured by spat settlement weekly on asbestos plates and seasonally on oyster shell. Setting generally began in June, peaked in July, and ended in September. Broad Creek appeared to be a suitable area for expansion of a seed reserve.

Shaw, W. N. and G. T. Griffith. 1967. Effects of Polystream and Drillex on oyster setting in Chesapeake Bay and Chincoteague Bay. Proc. Natl. Shellfish. Assoc. 57: 17-23.

Significantly more oysters were caught on Polystream-treated and Drillex-treated shells compared with untreated controls when both were suspended either intertidally or on the bottom of Chincoteague Bay. In Tred Avon River, Polystream-treated shells held off-bottom caught more oysters than did controls. On the other hand, no significant differences were found in Tangier Sound and Broad Creek, Chesapeake Bay. Fouling organisms apparently were not affected by treatment of shell with the two chemicals.

Shaw, W. N. and A. S. Merrill. 1966. Setting and growth of the American oyster Crassostrea *virginica* on navigation buoys in the lower Chesapeake Bay. Proc. Natl. Shellfish. Assoc. 56: 67-72.

Oysters were collected from navigation buoys over a 7-year period. Growth of oysters setting on newly placed buoys was very rapid and mortalities were low. These results suggest that off-bottom culture of oysters in lower Chesapeake Bay might be commercially feasible.

Sieling, F. W. 1950. Intensity and distribution of oyster set in Chesapeake Bay and tributaries. Proc. Natl. Shellfish. Assoc. (1949): 28-32.

Counts of oyster spat using one-half bushel random samples from oyster bars were used to monitor oyster set (which was low in 1947 and 1948). Best area was the eastern shore of the Bay from Love Point to Tangier Sound. Average values of spat per bushel on dredging bars were: 1947 - eastern shore 61.2; western shore 2.2; upper Bay 5.5; 1948 - eastern shore 15.5; western shore 3.4; upper Bay 0.3. Best sets were in tributaries of the Choptank River, Tangier Sound, Eastern Bay and St. Mary's River. In Eastern Bay, 2002 spat per bushel were recorded on planted shell in fall 1947. Slag which had been planted as cultch in the Eastern Bay seed area yielded 2280 spat per bushel. Counts in 1948 were lower. The Patuxent River continued to be a poor setting area, as was the Potomac River (except for St. Mary's River).

Sieling, F. W. 1951. Influence of seasoning and position of oyster shells on oyster setting. Proc. Natl. Shellfish. Assoc. (1950): 57-61.

Experiments in St. Mary's River revealed that the majority of oyster larvae settled on the underside of oyster shell held horizontally in wire mesh bags. Barnacles exhibited the same preference whereas bryozoans seemed to show no preference. Although inconclusive, experiments also indicated that clean shell obtained slightly more spat than did shell that was fouled with barnacles and bryozoans.

Sindermann, C. J. 1968. Oyster Mortalities, with Particular Reference to Chesapeake Bay and the Atlantic Coast of North America. U. S. Fish. Wildl. Serv., Spec. Sci. Rep. - Fisheries, No. 569. 10 pp.

Reviewed oyster mortalities, including those resulting from MSX in Chesapeake Bay.

Sindermann, C. J. and A. Rosenfield. 1967. Principal diseases of commercially important marine bivalve mollusca and crustacea. Fish. Bull. 66: 335-385.

In the course of this review, the authors used as examples incidents of disease noted in species taken from Chesapeake Bay.

Smith, R. S. 1953. A water quality survey of Hampton Roads shellfish areas. Proc. Natl. Shellfish Assoc. (1952): 121-134.

The authors described the pollution history of the Hampton Roads area of Virginia's Chesapeake Bay. The implementation of sewage treatment led to improvement of water quality in the late 1940's. The authors' own survey led to a recommendation for the reopening of three areas to oyster fishing.

Sprague, V., E. A. Dunnington, Jr., and E. Drobeck. 1969. Decrease in incidence of *Minchinia nelsoni* in oysters accompanying reduction of salinity in the laboratory. Proc. Natl. Shellfish. Assoc. 59: 23-26

Sick oysters collected from a population heavily infected by *M. nelsoni* were held for about 6 months at 7-8 ppt, 14-16 ppt, and 19-22 ppt. Continuing histological monitoring indicated that incidence of infection in these salinities was 5.5%, 63.1% and 88.8%, respectively. This information provided some corroborative evidence that the parasite responsible for the infection does not thrive at lower salinities.

State Planning Commission. 1935. Conservation Problems in Maryland. Unpublished Report of Sub-Committee on Conservation, A. Wolman, Chairman. Maryland Emergency Relief Administration. 64 pp.

The 51% decline in oyster yield in Maryland from 1910 to 1932 has resulted from "a continuation of the unsound conditions and short-sighted policies that have characterized and controlled the industry's operations over a long series of years." Among the reasons for the decline were overfishing, wholesale export of seed oysters out-of-state (e.g. over 2 million bushels in 1879), and failure to return cultch to the oyster grounds. This led to loss of a $750,000 canning industry with resultant loss of employment for workers. Larger-sized oysters also became uncommon and other states filled the demand. Previous shell-planting and seed-planting efforts were reviewed. Private culture was declared to be an important rehabilitation measure. For example, from 1929-1932 in the U.S., 47% of the volume and 68% of the value of Atlantic and Gulf state landings came from private beds. Harvested oysters from private culture sold for $0.99 per bushel compared with $0.47 per bushel for publicly harvested oysters.

Steinberg, P. D. and V. S. Kennedy. 1979. Predation upon Crassostrea *virginica* (Gmelin) larvae by two invertebrate species common to Chesapeake Bay oyster bars. Veliger 22: 78-84.

Prefeeding and feeding behavior of the sea anemone *Diadumene leucolena* in the presence of oyster larvae was described. As larval density increased, sea anemone feeding rates increased, with larger individuals generally feeding at a greater rate than smaller individuals. Few larvae survived in the presence of sea anemones. Also, numbers of surviving larvae decreased significantly in the presence of the barnacle *Balanus improvisus*.

Stevenson, C. H. 1894a. The oyster industry of Maryland. U. S. Fish Comm. Bull. No. 12: 203-298.

The author discussed the oyster industry in Maryland from many angles, from the operations of the oystermen through to the processing of the shucked oyster. In addition, the mass of regulations that had built up since 1820 were briefly but completely considered.

Stevenson, C. H. 1894b. A bibliography of publications in the English language relative to oysters and the oyster industries. U. S. Comm. Fish, Report of the Commissioner (1892), pp. 305-359. Washington, D.C.

This formed the most complete oyster bibliography of the time.

Suttor, R. E. and T. D. Corrigan. 1970. The Chesapeake Bay Oyster Fisheries: an Econometric Analysis. U. Maryland, Agricultural Experiment Station, Rep. No. MP-740. 50 pp.

An econometric (five-equation recursive) model was developed to analyze and project landings, price, employment and income in Maryland and Virginia oyster fisheries. Certain projections concerning landings and income were made using the model. An increase in oyster taxes to generate increased state revenues for program management was found not to hinder landings. The oyster seeding program was found to lead to increases in landings and employment, to the benefit of oystermen.

Suttor, R. E., T. D. Corrigan and R. H. Wuhrman. 1968. The Commercial Fishing and Seafood Processing Industries of the Chesapeake Bay Area. U. Maryland, Agricultural Experiment Stn., Rep. No. MP-676. 81 pp.

Described the commercial fishing and seafood processing industries in Chesapeake Bay, with emphasis on economic trends. An economic analysis of the oyster industry was recommended, with focus on evaluation of the effects of seeding of public oyster beds. The writers stated that the goals of the oyster management program were not clear-were they to increase oyster production, to increase employment or to increase income to watermen? These goals may be conflicting. The impact of private culture on income and retail oyster prices needed to be examined, according to the authors.

Truitt, R. V. 1921. A policy for the rehabilitation of the oyster industry in Maryland. Ann. Rep. (1920), Maryland Conservation Commission, pp. 1-5.

Maryland's oyster grounds had been generally destroyed by constant working with limited attention paid to restoring them to their former state of cultch and brood abundance. The replacement of sail boats by motor boats resulted in elimination of the shell ballast once dumped from the former as oysters were harvested and taken aboard. Solutions included an organized and systematic return of shell to natural bars. Shell should be placed only where it is known that spat settlement is reliable and where aspects of survival and growth of spat, as well as adult fattening prospects, are well understood. Truitt bemoaned the loss of shell to lime dealers, road builders and chick-grit sellers. Yet it was not clear that oystermen and oyster dealers supported the need to return shell to the bottom. Further, the legislature refused to provide the additional funds necessary for other than stopgap conservation measures.

Truitt, R. V. 1927. Aspects of the Oyster Season in Maryland Involving Labor Conflicts Detrimental to both Seafood and Cannery Industries, with Special Reference to the Latter. Maryland Ag. Expt. Station. 15 pp.

Truitt noted that the tremendous historical oyster depletion was due to overworking of oyster beds (one-fifth total oyster grounds completely exhausted with one-third nearly exhausted), removal of cultch and too small a legal size (resulting in mortality of unshucked seed dumped on shell piles). Further, at the time of writing, the oyster season began in September. This resulted in spat mortality from harvesting, mortality or loss of quality from heat spoilage, poor meat quality due to the fact spawning season had just ended, and competition of oyster harvesting with September vegetable canning labor needs. Tongers, dealers, dredgers and vegetable canners all recommended banning oyster harvesting in September.

Truitt, R. V. 1929. Biological contributions to the development of the oyster industry in Maryland. Ph.D. Dissertation American University, Washington, D.C. 56 pp.

Prepared during a period of harvest decline, this report concluded that, because salinity, temperature and pollution values (low) in Maryland's Chesapeake Bay had remained essentially unchanged over 3 or 4 decades, overfishing was the probable reason for the decline. Truitt compared various materials for suitability as cultch. Oyster shell caught about twice as many spat (33 per basket of shell) as did glass (1 to 5 in^2 in area), which caught about 16 spat per basket. Numbers of spat on other substrates (per basket) were: cinder and coal lumps - 4; 3/8" to 1/2" diameter pebbles - 3; egg-sized brickbats - 3; twigs or chips of various trees - 0 to 1. Thus Truitt recommended use of shell as a spatting substrate. He also estimated larval abundance in the water, finding a positive correlation of larval number to spat settlement. Spawning occurred from June to October, with the main peak usually in July (in 1925—an excellent year for spat—there was an additional larger peak in September). He established the fact that oyster fecundity increased with increasing age. Intense summer storms were shown to lead to the presence of fewer oyster larvae in the water (for reasons unknown). Truitt indicated that his findings on the importance of shell to successful oyster spat settlement had led to legislation requiring return of 10% of all harvested shell to the Bay. Similarly, his findings that oysters in their second year produced only small quantities of gametes had led to the establishment of a 3" market size limit.

Truitt, R. V. 1931a. The oyster and the oyster industry of Maryland. State of Maryland Conservation Dept., Conservation Bull. 4:1-48.

The biology of the oyster was described in non-technical terms, followed by a description of the past and present (to 1931) condition of oyster produc-

tion in Maryland. There was a good description of various oyster fishing gears. In the section on oyster farming, Truitt indicated that the fact that legislative bodies were involved in management action had been detrimental to use of potentially productive grounds that were Iying fallow. As to seed planting, he noted that seed running 700-800 per bushel required 300-400 bushels per acre for optimum yield. Seed of this size should yield 2-3 bushels for each one planted. Grounds rounds should not be planted continuously, but should be rotated. Four acres of oyster ground can produce about 4,000 bushels of oysters in three years. Truitt recommended an enlightened program of private culture to encourage scientific farming.

Truitt, R. V. 1931b. Recent Oyster Researches on Chesapeake Bay in Maryland. Official Publication, Chesapeake Biological Laboratory, Solomons, Md. 28 pp.

This report summarized findings from 1918 to 1930 on oyster studies in Maryland. This research progressed in spite of the opposition of watermen to investigation of factors governing oyster abundance. Apparently they felt that natural restoration had to be depended upon. Truitt noted that two factors were responsible for oyster decline. The first was reduction of brood stock and the second was removal of cultch. Oysters of too small a size had been harvested. Based on the results of past work, the market size was raised from 2 1/2 inches to 3 inches. Also, legislation had been passed reserving 10% of shucked shell for planting by the state. Unfortunately, shell planting site selection did not consider (1) presence of brood stock to assure reproduction; (2) spat survival; (3) if the planting grounds really were good setting grounds or if they were better for growing and fattening; (4) whether shell was actually the best substrate and how it should be placed on the bottom; (5) when planting should occur; and (6) the effects of local salinity regime on growth and survival. Since watermen were asked to provide recommendations for sites for shell planting, these sites were generally barren bars, rather than even moderately producing beds.

Research showed that larval concentrations over once productive areas (e.g., Great Rock, Cornfield Harbor, Flag Pond, Governor's Run, Dry Rock in Tar Bay) never exceeded 9 larvae per 200 liters of water. One to three larvae were more typical. Contrarily, on Seminary Bar, Crab Alley, Mill Hill, etc., hundreds of larvae (e.g., 11,400 in 50 gal. at Dry Rock, July 1, 1924) per sample were collected. Areas of intermediate larval densities included lower Honga River, Fishing Bay, Holland Straits, Poplar Island Narrows, and Buoy Rock. Truitt stated that such information is vital for proper shell planting and that testing for spat settlement success is important before large plantings are made.

It was not determined just what brood stock concentrations were needed to provide for 400+ spat per bushel (the arbitrary level for commercial production) but it was known that breeding success was higher if the adults were close together as on Seminary Bar, Dry Rock, Crab Alley and Mill Hill. Setting and survival was also found to vary within the seasons and from year to year. Further, high brood stock levels alone did not assure a satisfactory strike in all regimes of the Bay. Shells planted in June did not foul sufficiently to prevent a strike.

For shell planting in open water, Truitt recommended no less than 1,000 bushels per acre, with 1,200-3,500 bushels per acre optimum. Heavy concentrations of brood stock rather than scatterings seemed desirable. Research indicated that oyster shell was the most efficient, abundant and inexpensive cultch that could be used.

Truitt, R. V. 1945. The oyster. Maryland Board of Natural Resources. Dept. of Research and Education, Solomons Island, Md., Educational Series No. 7: 1-12 (Reprinted from Bios, 15(3); Oct. 1944).

In this lay guide to oyster biology, the author indicated that the 15 million bushels of oysters harvested in 1883 in Maryland would have yielded about 15 million gallons or 120 million pounds of oyster meat. This is the equivalent of about 200,000 dressed beef steers, the entire yield from New Jersey, Delaware, Maryland and West Virginia farms (at the date of writing) combined.

Truitt, R. V. and P. V. Mook. 1925. Oyster problem inquiry of Chesapeake Bay. Third Ann. Rep. Conservation Dept., State of Maryland. Baltimore, Md. pp. 25-55.

This report describes studies on prevalence of oyster larvae in plankton, spawning of adult oysters, temperature effects on spawning and larval production, experimental planting of shell as cultch, and the possible relationships among abundances of sea nettles, ctenophores and oyster larvae.

Tubiash, H. S., R. R. Colwell and R. Sakazaki. 1970. Marine vibrios associated with bacillary necrosis, a disease of larval and juvenile bivalve mollusks. J. Bacteriol. 103: 272-273.

Bacillary necrosis of larval and juvenile oysters was determined to be caused by members of the bacterial genus *Vibrio.*

Tubiash, H. S., S. V. Otto and R. Hugh. 1973. Cardiac edema associated with *Vibrio anguillarum* in the American oyster. Proc. Natl. Shellfish. Assoc. 63: 39-42.

The incidence of "cardiac vibriosis" (greatly enlarged and edematous pericardia) in over 10,000 oysters from Chesapeake Bay which were examined between 1967-1970 was 0.04% (4 animals). The animals were collected in the Manokin, St. Mary's and South Rivers. Examination of the pericardial fluid revealed heavy concentrations of gram-negative motile rods resembling *Vibrio* anguillarum.

Ulanowicz, R. E., W. C. Caplins and E. A. Dunnington. 1980. The forecasting of oyster harvest in central Chesapeake Bay. Est. Coastal Mar. Sci. 11: 101-106.

Forty years of data on oysters were analyzed with a multivariate analysis. Variations in spat density and seed plantings explained 56% of the variation in annual harvest. Spat density varied directly as the cumulative high salinity during the spawning season and inversely as the harvest of the previous season. The analysis allowed for the estimation of oyster harvest four years into the future.

Vaughn, M. W. and A. W. Jones. 1964. Bacteriological survey of an oyster bed in Tangier Sound, Maryland. Chesapeake Sci. 5: 167-171.

From August to October 1959, water, oyster and mud samples were collected irregularly from three cliff Brent sections of Hall's Bar, Tangier Sound, and examined for populations of bacteria, including coliforms and *E. coli*. Mud samples had higher plate counts than did oyster samples, which in turn were higher than water samples. Plate counts were low as were coliform counts. No. *E. coli* were detected.

Webster, J. R. 1953. Operations and problems of an oyster census on Swan Point Bar, Upper Chesapeake Bay. Proc. Natl. Shellfish. Assoc. (1952): 113-120.

Swan Point bar on the upper Eastern Shore was once self-sustaining and productive until prolonged lower salinities occurred in 1945 and 1946. The State began seeding the bar annually beginning in 1947. The author discussed problems associated with a census attempt on the bar using a handscrape (small oyster dredge).

Webster, J. R. and R. Z. Medford. 1961. Flatworm distribution and associated oyster mortality in Chesapeake Bay. Proc. Natl. Shellfish. Assoc. 50: 89-95.

Sampling of oyster beds for age studies of oysters in Chesapeake Bay, Maryland, produced evidence of *Stylochus ellipticus* presence on 73 widely scattered locations. Greatest numbers were noted in the lower Potomac River and its tributaries (although the survey was not quantitatively performed). No other species was collected (identifications were by Dr. L. H. Hyman, Amer. Mus. Nat. Hist). The worms were occasionally found in empty spat "boxes" (hinged valves with no oyster meat present). In a field experiment using bags of oyster shell in the Potomac River (Smith Creek), 95% of the worms collected from the bags when they were harvested in the fall were found in fresh spat boxes. The authors concluded that this flatworm was probably a cause of spat mortality.

Webster, J. R. and W. N. Shaw. 1968. Setting and First Season Survival of the American Oyster, Crassostrea *virginica*, Near Oxford, Maryland, 1961-62. U. S. Fish Wildl. Serv., Spec. Sci. Rep. Fisheries. No. 567, 6 pp.

Spat monitoring in 1961 and 1962 revealed that settlement was greater in Broad Creek than in Tred Avon River, adjacent tributaries of the Choptank River. First-season survival rates varied from 1 to 27%. Three times more spat were caught on shells clumped in bags than on shells broadcast on the bottom.

Wharton, B. H. 1963. The Maryland oyster industry. Thesis, Stonier Graduate School of Banking, Rutgers - The State University. 64 pp.

A general review of oyster biology and the commercial industry. Concluded that having 3 million Marylanders support 5,000 oystermen to the tune of 1 million dollars annually was inequitable and suggested that private culture of oyster grounds would help improve productivity. Blamed a history of lack of concern for conservation, inadequate law enforcement and the undue political influence of tidewater politicians for the decline in oyster production.

Wharton, J. 1957. The Bounty of the Chesapeake. Fishing in Colonial Virginia Univ. Press of Virginia, Charlottesville, Va. 78 pp.

A compilation of historical accounts of the past immense bounty of the Chesapeake Bay, especially Virginia waters. Although fishes were emphasized, oysters were mentioned as being in such accumulations as to be a navigational hazard in places. In the colonial period, oysters were generally preserved by pickling.

Wheatley, J. J., C. L. Quittmeyer and L. A. Thompson. 1959. The Economic Implications of the York River Oyster Industry. Bureau Pop. and Econ. Res., U. Virginia, Charlottesville, Va. 119 pp.

At the time of writing, overfishing had led to stock depletion in the York River, per capita oyster consumption had declined, and floods, pollution and disease had made inroads into the resource. The authors suggested the need to encourage consumer consumption coupled with increased production of oysters by opening new areas to fishing, renting ground, developing new seed areas and encouraging efficiency and conservation simultaneously. An aquaculture experimental program was recommended.

Wheaton, F. W. 1970. An engineering study of the Chesapeake Bay area oyster industry. Proc. Natl. Shellfish. Assoc. 60: 75-85.

Operational research techniques were used in development of an operations-process chart of the Chesapeake Bay oyster industry. Information was collected using personal interviews, time studies and on-site observations. The time studies found that an average oyster shucker shucked 7.7 oysters per minute or produced about 1.7 gallons of oysters meat per hour. Economic data were used to determine that an oyster processor could economically invest $33,000 in a machine which could shuck 60 oysters per minute. Such a machine would help solve processing problems caused by a declining pool of human oyster shuckers.

Winslow, F. 1881. Deterioration of American oyster-beds. Pop. Sci. Monthly 20: 29-43; 145-156.

Winslow based this semi-popular report on his own research in 1878 and 1879 on the oyster beds of Tangier and Pocomoke Sound and on the research by Brooks into artificial propagation of the oyster. At the time of his commissioned study, the oyster beds in the two Sounds had been heavily fished, to the point of great decline. In addition, the beds occupied a much greater area of the bottom than before, a fact Winslow proved to be due to the dredging and culling activities of the fishermen. He described the differences between unfished beds (clustered oysters, with clean shells, often with attached tufts of red sponge; the oysters being long and narrow with thin sharp bills and thin bodies) and fished beds (single oysters predominated, being broader and thicker than on unfished beds and with fatter bodies; shells dirty, with little attached sponge and more worms and boring clams in association). As evidence of deterioration in quality and fecundity of an oyster bed he listed: (1) the above description of a worked bed; (2) a ratio of small to mature oysters that was greater than 2:1 or less than 1:1; (3) a large (greater than 50%) amount of debris (shell, etc.); (4) decreasing numbers of oysters on the bar every year; (5) marked changes in the fauna of the bed. For rehabilitation, he recommended use of cultch (stones, earthenware, water pipes, shell) to extend old beds. Cultch should be placed on suitably hard bottom in the direction of currents from established beds. Mature oysters should be deposited with the shell to provide larvae. Cultch should be placed late in the spring to ensure its cleanliness. A commission of intelligent and knowledgeable (concerning oysters) people with considerable power and insulation from politics was recommended to be appointed to (1) prevent exhaustive dredging and the wasting of young growth by their being dredged or removed from the beds with market oysters, and to (2) provide for cleansing the beds of fouling organisms, pests and predators. He warned against inattention and misuse of the resource, which would result in a situation similar to the overfishing and destruction of European oyster stocks.

Winslow, F. 1882. Report on the oyster beds of the James River, Virginia Coast Survey Report for 1881. U. S. Navy, Washington. 87 pp. Reviewed in Science 1883, Vol. 2, No. 34, pp. 440-443.

Dredging extended the area of otherwise vertical oyster beds by spilling cultch over on mud making increased surface area available for spat settlement. Further dredging "thins out" the oysters and allowed for far better, more well-shaped growth. Reviewer remarked that dredging had been carried on in Chesapeake "to a disastrous extent." Oyster laws were ignored and flouted in the eyes of the "oyster police." Winslow determined the area of numerous oyster beds and approximate quantity of oysters per square yard over much of this area. Reviewer predicted the precipitous decline of the oyster beds, resulting in 40,000 people becoming unemployed. The reviewer deplored the vandalism by watermen of experimental tile-collectors, thermometers, etc., that had been deployed by Winslow in his study. From the surviving tiles it could be concluded: (a) in 1879, spat settlement on tiles set out July 9 had occurred by mid-July, continuing for about a month; (b) 50% mortality occurred within 6 weeks by unknown predators or factors; (c) attachment was greater on the concave underside of the tiles (which apparently were on or near the bottom); (d) growth rate was rapid, with some oysters being 2" long after 3 months.

Winslow, F. 1884. Present condition and future prospects of the oyster industry. Trans. Amer. Fish. Soc. 13: 148-163.

Winslow reviewed the continued deterioration of the oyster industry, especially that of Chesapeake Bay, which employed 75% of Americans in the U. S. industry and 67% of the capital and provided 77% of the harvested oysters. Evidence of continued depletion (decreasing numbers of oysters per square yard; decreasing bushels of oysters per bushel of shell; increasing price per bushel) was presented. Because of pressure from the watermen to preserve the status quo, the response of legislators of both states to the problem of declining catch was limited to the addition of a few more police boats. Winslow recommended an encouragement of private oyster culture. The state could not afford to culture oysters because of costs. Although Maryland employed 10 times as many people and produced 10 times as many oysters as did any other state (except Virginia), and although the gross value of the product was 2-4 times as large as elsewhere and the capital was 5 times as great, and there were at work 2-3 times as many vessels as other states, the percentage of capital returned was the smallest of all states. The yield per acre was only 40 bushels, compared with 120 bushels per acre in New England where the private industry prevailed. In conclusion, Winslow lamented, "The goose will be killed; the golden eggs will be laid no more. And the vast fleet of pungies and canoes, and multitudes of men and women will have no employment beyond picking out the pinfeathers of the inanimate carcass."

Wood, L. and W. J. Hargis, Jr. 1971. Transport of bivalve larvae in a tidal estuary. In: D. J. Crisp (ed.), Fourth European Mar. Biol. Symposium, pp. 29-44. Cambridge Univ. Press.

An extensive plankton sampling survey in James River, Virginia was accomplished in late August-early September 1965. Hourly samples were collected from 2-4 depths on five stations around the clock for 7 days. Mature bivalve larva were found in negligible quantities. Passive coal particles seemed to exhibit four concentration maxima which were related to the time of maximal tidal current. Concentration minima occurred at or near slack tide. Contrarily, bivalve larvae concentrations were bimodal at or near slack water after maximum flood. Minimum larval concentrations occurred on the slack following ebb. The authors claimed that larval maxima coincided in most cases with the salinity increase which accompanies flood tide.

Yates, C. 1913. Summary of Survey of Oyster Bars of Maryland (1906-1912). Government Printing Office. 75 pp.

From 1906 to 1912 the Maryland Shell Fish Commission, headed by Dr. Caswell Grave of Johns Hopkins University, cooperated with the U. S. Bureau of Fisheries, the U. S. Bureau of Chemistry and the U. S. Coast and Geodetic Survey to perform the Maryland Oyster Survey. During this period, over 200,000 acres of natural oyster bars were surveyed, technically defined and charted (along with over 40,000 acres of crab bottom and 506 acres of clam beds); in addition, over 1/2 million acres of oyster bottoms suitable for oyster culture (by leaseholders) were determined. At a cost of about $200,000, this survey involved 1112 triangulation stations; 159,530 soundings; 11,006 oyster investigation stations for examination of bottom, etc.; 3,060 miles of examination of shell bottoms with chain apparatus; 8,600 hydrographic positions plotted; 63 large-scale leasing charts prepared; 900 printed pages of Maryland Shell Fish Commission reports; 1,560 printed pages in U.S.C.G.S. publications; and 43 charts of public oyster grounds. Given the annual landings in Maryland of 5 million bushels of oysters at that time, the cost was about 4 cents a bushel. This summary presented some of the highlights of this immense and informative effort.

Annotated Bibliography Index