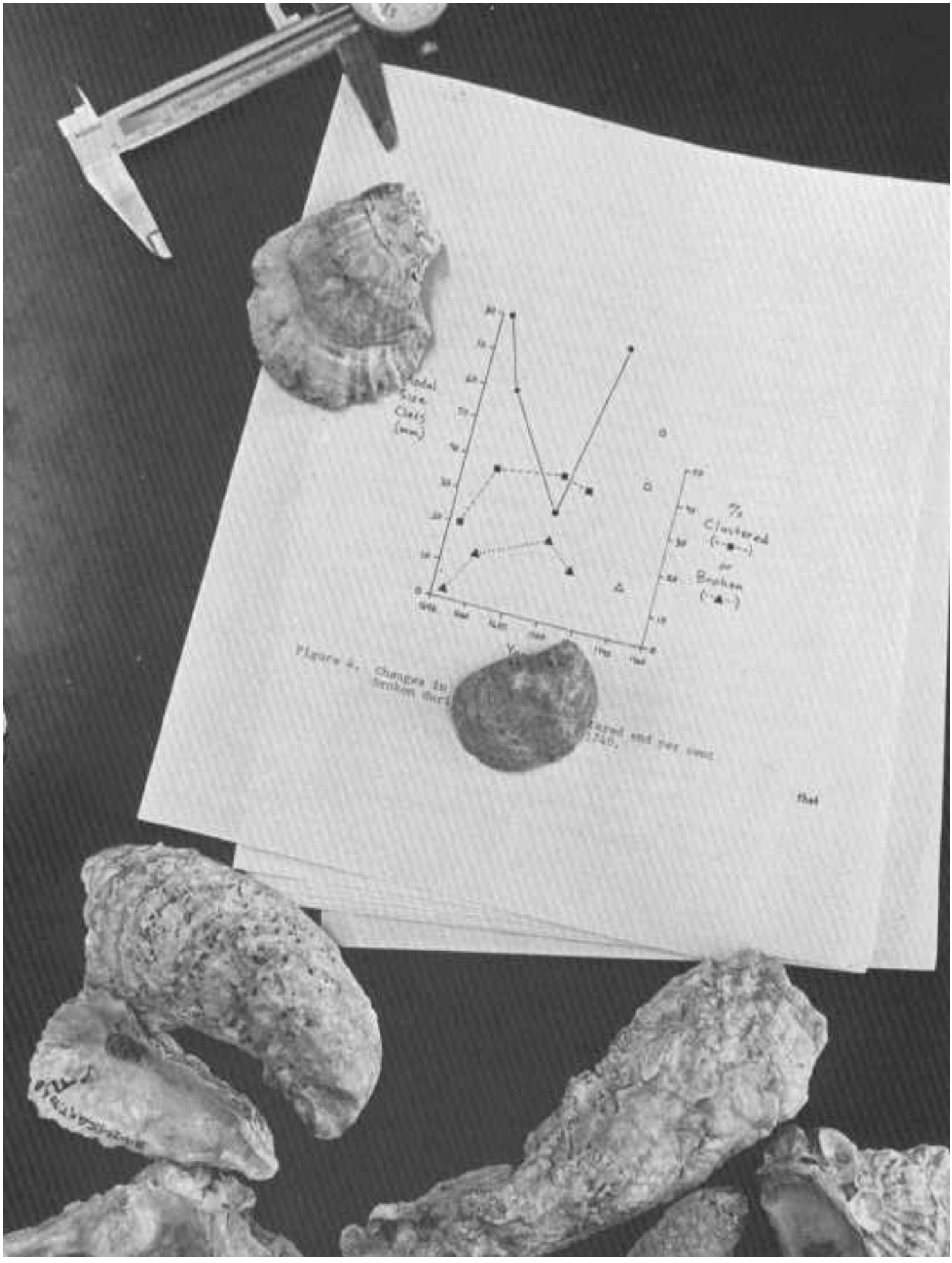
Biology



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

"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 despera - tion."

—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).

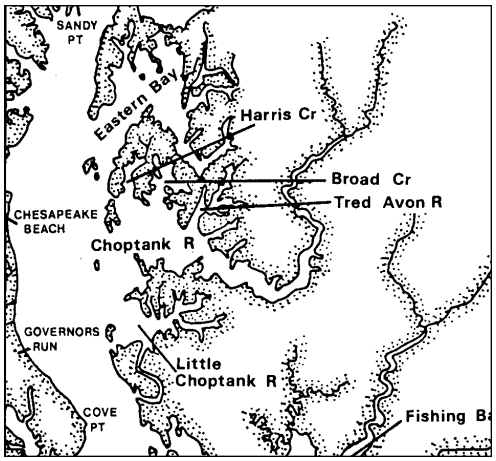
In Chesapeake Bay, hydrographic conditions in James River (a major oyster seed area) during the summer of 1950 were measured by Pritchard (1953) and related to distribution of oyster larvae. He found that ebb velocities were greater at the water surface and decreased with depth. Flood velocities were 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 reten-

tion. 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 experi-

mental 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); MacInnes 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 ventiliation 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 concentration reducing shell deposition by half in 96 h. MEC = minimum effective concentration 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

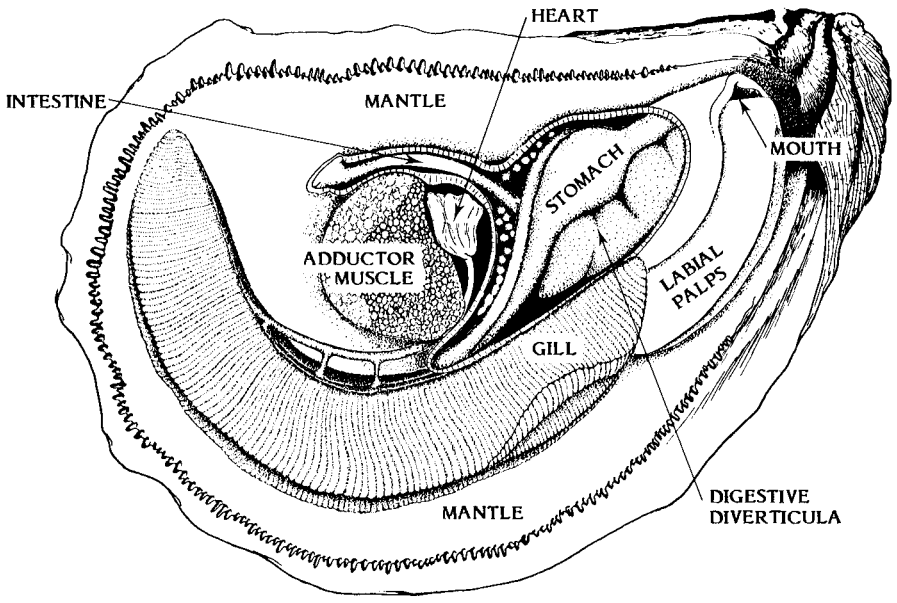


Figure 1. Diagrammatic sketch of an oyster showing internal parts. (From Ashbaugh, B.L., l951)

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 capa-

bilities (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 epifluo-

rescence 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 sim-

ilarly 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, carbo-

hydrates, 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 con-

trol, 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

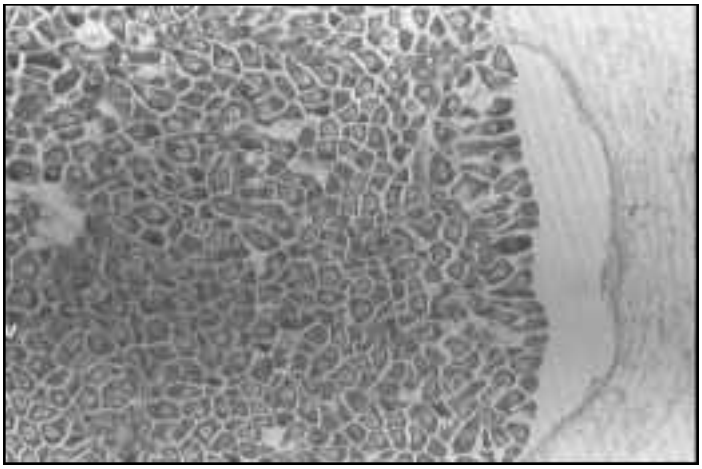
For some marine and estuarine organisms, the timing of such reproductive events has been shown to be coordinated with aspects of the external environment which act as cues (see Sastry 1975 for review). For example, salinity, temperature, day length, and abundance of food may serve as cues or stimulants (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.

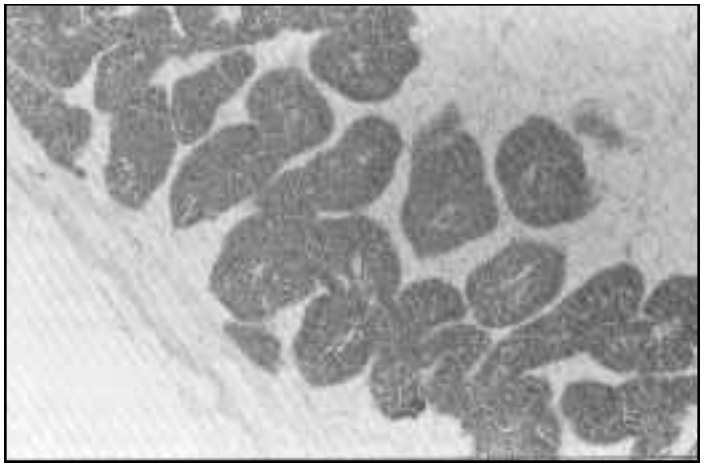
The period of gonad growth for *A. irradians* at Beaufort, N.C., coincides with the time when phytoplankton production is at an annual high (Sastry 1966). Sastry found that the sequential events of the reproductive cycle (e.g., vegetative phase, early growth phases of gametes, resting stage, etc.) were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

A. Female early development.

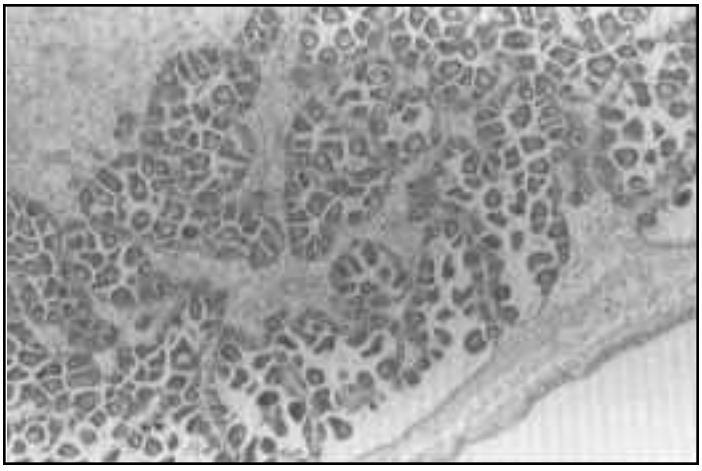
B. Male early development.



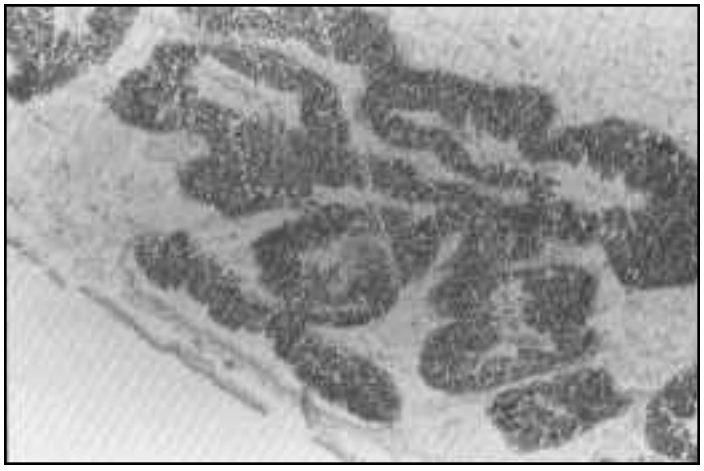
C. Female later development.



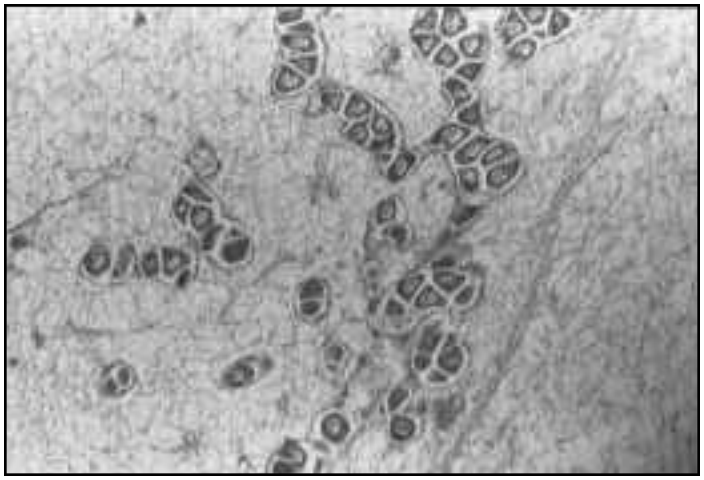
D. Male later development.



E. Female spawning.

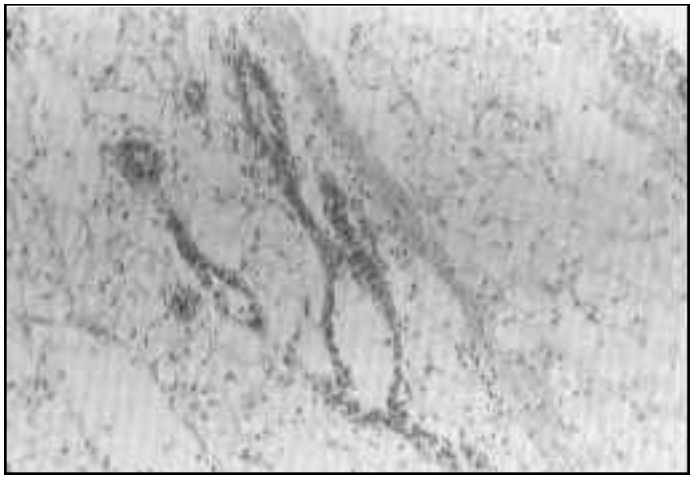


F. Male spawning.

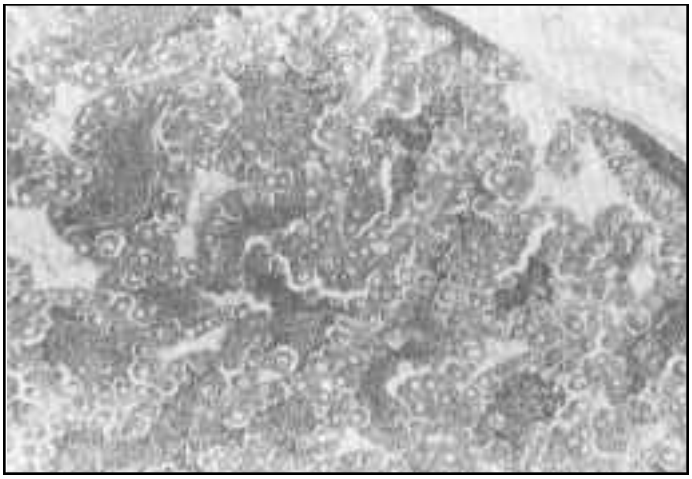


G. Female spent.

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:

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

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 $15°C \leq T \leq < 30°C$. 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 neurose-

cretion 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.

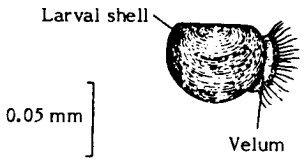
Sex Ratios and Changes

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.

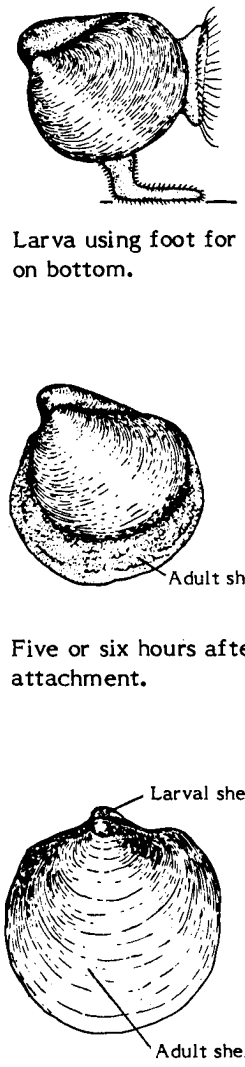


Figure 3. Early development stages of the oyster. (From C.L. Newcombe and R.W. Menzel, 1945)

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		Settling		
Upper	Under	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		Settling		
Upper	Under	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 (≃ 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 resis-

tance 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 vib-

riosis 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 mudworm 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

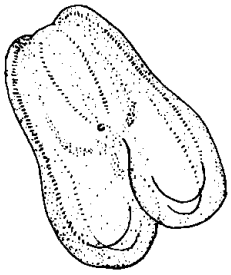
Pinnotheres ostreum can be controlled by exposing the oysters to 10 mg L^{-1} of 95% technical Sevin for 24 hours. The pea crabs are then ejected by the unharmed oysters. Although crabs are highly sensitive to Sevin, oysters can be exposed to as much as 100 mg L^{-1} without apparent injury (Andrews 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.



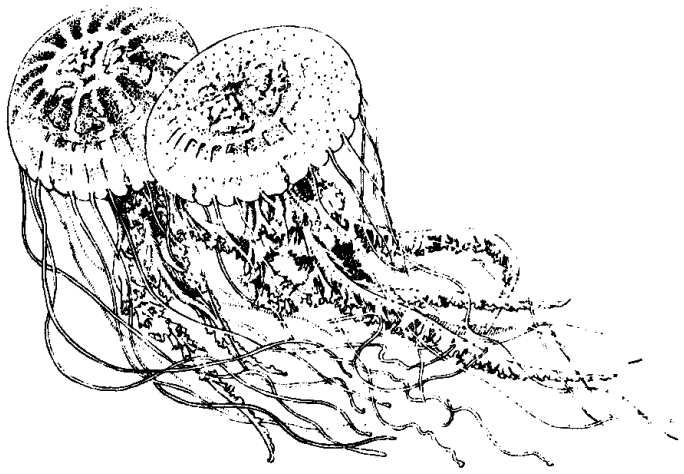
Mnemiopsis leidyi

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.

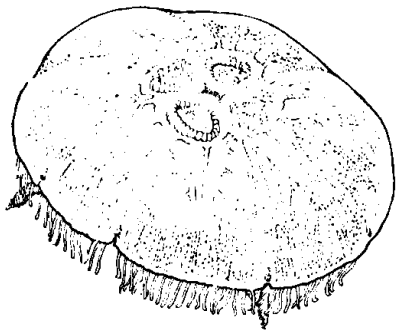


Chrysaora quinquecirrha

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.

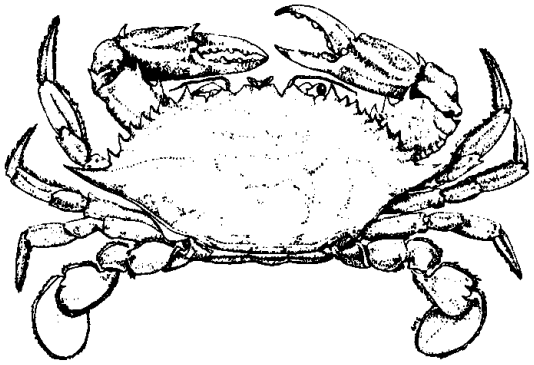
Filter-feeding molluscs (oysters, mussels, clams, limpets) may ingest oyster larvae in the process of filtration and feeding (Korringa 1949, Drinnan 1975). Drinnan (1975), noting that mackerel guts have been found to contain oyster larvae, postulated that filter feeding fish may also be oyster larvae 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.



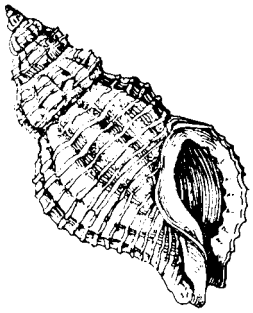
Callinectes sapidus

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).

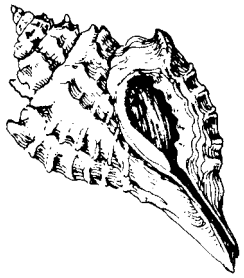
Some crabs such as *Menippe mercenaria* are serious predators of adult oysters (Gunter 1955, Menzel 1955, Menzel and Hopkins 1955a, Menzel and Nichy 1958, Menzel et al. 1957). Even a small 5 cm stone crab can crush the shells of large, marketable oysters. Menzel et al. (1957) considered *M. mercenaria*, 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).

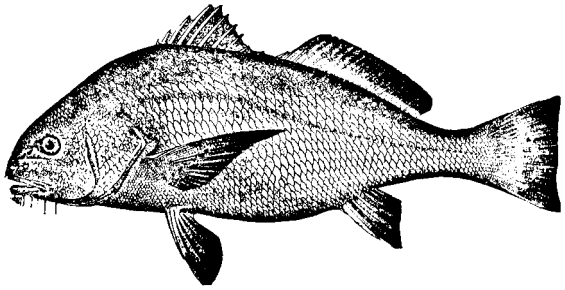
Trapping drills on oyster beds is a method of control studied in Virginia (Andrews 1956, McHugh 1956, 1957). Traps are placed over an oyster reef and stocked with fresh bait. Traps fished and rebaited weekly were found to be the most biologically and economically feasible (McHugh 1956) because a decline 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.