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Chapter 13

Natural Environmental Factors

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INTRODUCTION

Gunter (1957) wrote, "temperature is the most important single factor governing the occurrence and behavior of life," a point reiterated by Kinne (1970) who stated that, "with regard to life on earth, temperature is, next to light, the most potent environmental component." It can act directly on the organism as a factor affecting physiological performance, and it can also be a factor in evolution of the species, acting as a selective force in speciation. Prytherch (1928) stated that, "in the environment of the oyster, temperature is the most important factor as it controls, either directly or indirectly, the growth and reproduction of the organism." In the eastern oyster, *Crassostrea virginica*, as in many other organisms, the processes of reproduction, development, and growth are intimately linked seasonally to climatic conditions and to the availability of energy resources. In addition, thermal effluent may, in many instances, induce detrimental changes in reproduction, gametogenesis, fecundity, and larval development. Conversely, heated effluents from power plants have been of benefit to oyster growers in their efforts to extend the growing season.

For estuarine species, salinity is also an important and influential factor, limiting distribution of many aquatic organisms (Gunter 1961; Wells 1961). Butler (1949c) suggested that the single most important factor affecting oyster populations is salinity. Salinity variations in estuaries may be diurnal, seasonal, or spatial and changes may be gradual or abrupt.

Of all the abiotic factors that can affect the biology of an estuarine organism such as *C. virginica*, the synergistic effects of temperature and salinity probably have the most profound effects. As pointed out by a number of researchers (e.g., Alderdice 1972; Vernberg and Vernberg 1972), two or more environmental variables working in concert can have more profound biological consequences than any one of those factors acting independently.

Temperature or salinity affect virtually every aspect of oyster biology including feeding, respiration, utilization of food reserves, gonadal development and time of spawning, parasite-disease interactions, predation rates, growth, and distribution. Temperature and salinity can affect rate functions, can be the trigger that initiates a process, or can be a threshold factor such that a particular temperature-salinity combination is necessary for continuation of specific processes. Further, effects can vary with specific stages of the oyster's life cycle.

In addition to temperature and salinity variations, oysters experience other environmental factors such as variations in seston concentrations, light, and pH. There is an extensive literature available on the effects of all of these factors on marine invertebrates, and only those studies that specifically pertain to *C. virginica* are discussed here. This review will elucidate the physiological and behavioral mechanisms that allow the eastern oyster to survive and flourish under often harsh estuarine conditions.

DISTRIBUTION, TOLERANCE, AND SURVIVAL

Adult oysters are highly tolerant of extremes in ambient temperatures and are commonly found in waters where the annual range is from –2° to 36°C (Butler 1954; Gunter 1954; Galtsoff 1964). Loosanoff and Engle (1940) reported an elevated body temperature of 35.7°C for oysters immersed in shallow (25 cm) tidal pools; only 12 h later on the following tide, the water temperature was 22°C lower. In some shallow-water habitats, emersed oysters can be frozen solid in the winter and, if not disturbed, will thaw out and survive when covered by water (Loosanoff 1965). If frozen oysters are shaken or dropped, however, death occurs. Henderson (1929) reported a thermal death point for *C. virginica* of 48.5°C and Fingerman and Fairbanks (1956, 1957) noted appreciable death and weight loss in oysters exposed to temperatures above 41°C. Galtsoff (1964), however, reported that oysters can survive intertidal temperatures of 46° to 49°C when emersed at low tide. This finding was supported by Ingle et al. (1971) who reported survival of intertidal Gulf oysters at 49.5°C even when temperatures between 44° and 49.5°C were sustained for 3 h. Further, Vernberg et al. (1963) demonstrated that excised gills survived for 100 min at 44°C.

Rate of change of temperature seems to have a greater effect than temperature level per se, i.e., the slower the rate of temperature increase, the lower the upper lethal temperature. Oysters can also be killed by short exposure to high temperatures or longer exposure to lower temperatures. Fingerman and Fairbanks (1957) demonstrated experimentally that the rate of thermal increase can greatly influence the final median tolerance levels. Oysters acclimated to 24°C and exposed to increases of 0.74°C h^{-1} suffered 50% mortality at 41°C. In contrast, oysters exposed to an increase of 13.2°C h^{-1} experienced 50% mortality at 47.5°C. Quick (1971) reported 54% mortality after 5-d exposure to 35°C in oysters acclimated to 16°C. A direct relationship between the survival time of buried oysters and temperature was reported by Dunnington (1968). He found that under these anaerobic conditions oysters survived for 2 d in summer (25°C) and for over 5 weeks in winter (< 5°C) and attributed the differential survival rates to a reduced metabolic rate at low temperature.

As with temperature, oysters have a wide tolerance of salinity. Commercial production occurs in areas with annual salinity variations from 0 to 42.5 ppt (Ingle and Dawson 1950a, b, 1953). The species normally occurs from about 5 to 40 ppt (Galtsoff 1964; Wallace 1966) and Menzel et al. (1966) gave a range of 1.2 to 36.6 ppt. Amemiya (1926) reported the lower and upper salinity limits for this species to be 1.5 and 39 ppt. Loosanoff (1953a) and Wells (1961) gave minimum values for normal survival of 7.5 ppt and 7 ppt, respectively. Several authors set the minimum salinity for indefinite survival at 4 to 5 ppt (Arnold 1868; Ryder 1885; Belding 1912; Loosanoff 1932). The optimum salinity range is generally considered to be about 14 to 28 ppt (Moore 1900; Butler 1949c; Chanley 1958; Galtsoff 1964) although this optimum range can vary geographically. R. Newell (University of Maryland, pers. comm.) suggested that intermediate salinities of about 15 to 18 ppt represent a physiologically optimum range.

Gunter (1950, 1953) noted that although *C. virginica* is uncommon below 5 ppt, it can survive salinities as low as 2 ppt for a month, or even fresh water for several days when water temperatures are low. Self-sustaining populations occurred where salinities were as low as 0.2 to 3.5 ppt for five consecutive months annually (Butler 1952), and permanent oyster communities flourished in 10 to 30 ppt (Butler 1954). Distinct types of oyster reefs occur at different salinity regions in the Gulf of Mexico (Butler 1954). Reefs near the head of an estuary experience salinity ranges of 0 to 15 ppt (average 10 ppt) annually, and because of high annual mortality rates, the populations are sparse. Oysters from low-salinity areas tend to be small and rounded with smooth whitish shells, and spatfall is low and growth slow. Where salinity fluctuates from 10 to 20 ppt (average 15 ppt), populations tend to be dense as a result of high reproductive ability, availability of oyster shell upon which larvae can metamorphose, and low concentration of predators. Near the mouth of a typical Gulf Coast estuary with a salinity of about 25 ppt, growth rates are usually high and reproductive potential is at its maximum; however, competition and predation are also

maximal. Where the estuary opens into high-salinity Gulf waters, oysters are sparse, growth is slow, and mortality is high. Suitable cultch is lacking and the high concentration of predators leads to low spat survival. The commercial importance and reproductive capacity of oyster beds in these high salinity regions are negligible.

Long-term exposure to high salinities can also be detrimental. Eastern oysters can survive in open ocean waters for some time; however, they usually do not reproduce or grow well, although there are exceptions. W. Menzel (late of Florida State University, pers. comm.) observed rapid growth, profuse spawning, and spatfall in salinities of 35 ppt and higher at Port Aransas, Texas. Breuer (1962) described a commercial population of *C. virginica* at Port Isabel in the lower Laguna Madre, Texas, that spawned and grew rapidly in a range of 32 to 42 ppt. Moreover, some spat survived salinities of 1.4 to 4.2 ppt in this same location as evidenced by successful propagation during periods of flood and reduced salinities. Breuer (1962) suggested that this Texas population might constitute a new physiological race because its salinity tolerance is lower than for *C. virginica* from northern populations. The possibility that populations of oysters have different salinity optima warrants further investigation.

Few data exist on effects of salinity on juvenile oysters. Loosanoff (1953a) found that juvenile oysters (spat) could resist reduced salinities as efficiently as do adult oysters. In a later study, Chanley (1958) showed that juvenile oysters less than 1 year old (0.3 to 2.2 mm) from Chesapeake Bay survived waters of 5 ppt and that the optimum salinity for growth of recently set oysters was 15 to 22.5 ppt. Juveniles differed somewhat from larvae in their salinity requirements and responded to reduced salinities as did adults, i.e., with no growth below 5 ppt, slow growth below 12 ppt, and normal growth from 12 to 27 ppt.

The effect of salinity on mortality rate in eastern oysters is highly dependent on ambient temperature as shown by variable survival during spring floods and heavy rains, mostly in the southern portions of the range. Oyster mortality from excessive freshwater runoff is fairly common, as has been reported by numerous authors (see Baughman 1948; Galtsoff 1972; Joyce 1972). Specific areas most frequently affected include the mouth of the Mississippi River (Gunter 1950, 1953; Butler 1952), the upper reaches of the Chesapeake Bay (Beaven 1946; Engle 1946; Andrews et al. 1959), the Santee River in South Carolina (Lunz 1938; Burrell 1977), and areas of Louisiana (Owen 1953; Andrews et al. 1959; Dugas and Perret 1975). The situation is exacerbated because these periods of runoff usually coincide with periods of high temperature and increased metabolic energy demands. Major mortalities in Chesapeake Bay also occurred after Tropical Storm Agnes in 1972 (Cory and Redding 1976; Haven et al. 1976). In some areas, it is the combination of high temperature and high salinity that causes mass mortalities of oysters, as in southeast Louisiana (Owen 1953) and Texas (Copeland and Hoese 1966).

In Long Island Sound, oysters survived in freshwater or at 3 ppt for 70 and 115 d when water temperatures ranged from 8° to 12°C; at the same salinities, all oysters died within 15 d when the temperature ranged between 23° and 27°C (Loosanoff 1948). Andrews et al. (1959) reported that oysters conditioned to low salinity and low temperature combinations were able to withstand low salinities in a state of "narcosis" for as long as closure was continuously enforced by fresh water or other factors.

The tolerance or susceptibility of oysters to pollutants can be exacerbated by temperature and salinity stresses, especially in the early stages of development. Mandelli (1975) exposed juvenile and adult oysters to diluted desalination brines and found that both groups were adversely affected by copper concentrations in the water (19 to 43 μg Cu L^{-1}) and that spring and summer mortalities (elevated temperatures) were higher than those in autumn and winter. MacInnes and Calabrese (1979) reported an influence of temperature in the toxic effects of heavy metals on oyster embryos, with the highest susceptibility to metal toxicity at either 20° or 30°C and the lowest toxicity at 25°C. They also demonstrated that, while interaction of temperature and salinity on survival of embryos and larvae was only significant at high concentrations of copper, low concentrations of copper produced intolerable stress during periods of persistently low salinities and low or high temperatures. They also showed that veliger larvae were more tolerant to temperature and salinity changes than were de-

veloping embryos. A synergistic effect of temperature on the toxicity of free chlorine and chloramine to oyster larvae (7-d old) was also demonstrated by Capuzzo (1979); also see Capuzzo, Chapter 15.

Larval Distribution

Distribution of oyster larvae and their behavior during development is governed by a number of factors, not the least of which is salinity; their response to these factors, coupled with tidal currents, plays a most significant role in their distributional patterns. For years, scientists have debated whether or not horizontal or vertical distribution of oyster larvae and their retention in estuaries at spawning are controlled by active swimming in response to environmental factors, or whether purely mechanical forces of strong currents and turbulences at mid-tides keep larvae in suspension. Some authors believe that oyster larvae are carried at random by currents and exhibit no differential vertical position with tidal stage, whereas others believe that there is a response by larvae to increased salinity and propose this increased swimming as a mechanism in estuarine movement.

Julius Nelson (1908, 1909, 1911 to 1917) found more larvae in the water column during flood than ebb currents. He postulated that larvae were more active during increasing salinities and therefore would tend to rise more during flood currents and be carried up the estuary, i.e., he postulated that the oyster larvae overcome strong, non-tidal seaward drift by rising and swimming on the flood tides and settling to the bottom during ebb tides. His ideas were later confirmed by Nelson (1931) and other authors (Carriker 1951; Kunkle 1957; Haskin 1964; Wood and Hargis 1971).

Nelson (1931) summarized a long-term study of factors that affect vertical distribution of oyster larvae. Oyster larvae tended to be concentrated at the top of the halocline. The sharper the transition zone between the overlying brackish water and the underlying saline water, the more marked the concentration of larvae. The concentration was deemed to be a passive, physical effect with no evidence for any active selection of an optimum salinity by larvae. Nelson and Perkins (1931) were the first to demonstrate increased activity of oyster larvae exposed to increased salinities. They concluded that oyster larvae are usually found at a point midway between the surface and bottom in the water column and that this area of greatest concentration could not be correlated with fluctuation in temperature, pH, or salinity, but rather with areas of greatest current velocity. They believed that, in the absence of a halocline, oyster larvae are most abundant in numbers where current is strongest; where salinity gradients are present, the greatest numbers of oyster larvae were found just above the halocline. Thus, Nelson and Perkins (1931) demonstrated that it is a combination of larval swimming activity, salinity, current, and halocline presence that determines vertical distribution of larvae in the estuary. In the presence of a halocline, larval swimming is stimulated as larvae sink into the more saline water, which causes them to rise into the less saline overlying water. If no halocline is present, or if it moves with the tidal current, larvae are distributed in proportion to speed of the current, being most abundant where current is most rapid (see also J. Nelson 1917). When current is negligible, larvae are found in greatest numbers on the bottom. Contrary to the conclusion of Nelson and his colleagues, Prytherch (1928, 1934) concluded that larvae remain on the bottom during most of the tidal cycle and that they remain within several hundred meters of spawning beds. However, Prytherch's conclusions were not supported by other research.

Loosanoff (1932) found that larvae in the water column were most abundant at and around slack water, i.e., when current velocity was at its minimum, and were practically absent during the peak of flood and ebb. Larvae were most numerous near the bottom during late ebb and least abundant at the beginning of flood tide. These observations led Loosanoff to conclude that oyster larvae swim only during periods of weak tidal currents and remain on the bottom during most of their existence. Later, Loosanoff (1949) did not find any significant correlations between larval number and stage of the tidal cycle; he concluded that larvae do not settle during ebb tides and are thus rapidly dispersed in tidal currents.

Carriker (1947) provided a most insightful survey of the literature extant on evidence for the horizontal movements of oyster larvae. He agreed with previous workers' findings that larvae, especially older stages, rise on the flood and sink on the ebb tide. He concluded by pointing out that much more exhaustive work had to be done both in the laboratory and in the field before this question could be resolved. His detailed field study of larval distribution in New Jersey waters and of larval movements with respect to tidal cycles demonstrated that mature and eyed larvae can be present close to the bottom in relatively large numbers during the ebb tide. Within the larval "swarm," larvae were heterogeneously distributed, with the swarms tending to remain in definite "lanes" or areas (see also Nelson 1952). Carriker concluded that salinity gradients as well as current velocities are influential in larval movements, based on evidence that different larval stages exhibited different vertical distributional patterns, i.e., younger stages tended to sink near or onto the bottom on ebb tide and swim upward on the flood. He also showed that younger stages ebbed and flowed passively with the tide, with older stages tending to sink onto the bottom on the ebb and rise into the water on the flood. Finally, Carriker (1947) determined that relatively large numbers of mature and eyed larvae were present on the bottom during ebb tide. These observations led him to conclude that older larvae tend to migrate into headwaters of estuaries to set beyond the distance made possible by tidal conveyance alone, as a result of an active vertical movement by the larvae. These findings were disputed by Korringa (1952) and Verwey (1966) who believed that swimming movements of the larvae were not important, though Carriker's studies were supported by subsequent research (see below).

Pritchard (1953) provided a detailed study of hydrographic conditions prevailing in the James River, Virginia, and he predicted the distribution of oyster larvae. His theoretical predictions did not agree with observed distributions of oyster larvae, so he suggested that oyster larvae could not be considered simply as passive particles. Rather, they appeared to exhibit some ability to remain closely grouped, independent of the physical character of the circulation and mixing processes.

In contrast to earlier studies, Loosanoff (1949) found no relationship between stratification of larvae and tidal stages in Milford Harbor, Connecticut, and no evidence that larvae in advanced stages of development were more common near the bottom. He believed that oyster larvae do not descend to the bottom during periods of rapid tidal flow but are widely dispersed by tidal currents. These data supported earlier findings of Prytherch (1928) and Galtsoff et al. (1930) who reported the distribution and abundance of oyster larvae in Milford Harbor to be extremely irregular.

Andrews (1954) believed that too much attention had been given to larval activity and too little to the physical system of currents, tides, wind, and turbulence. He believed that larvae are distributed passively with their own active motion essentially limited to vertical migrations. Further support for the passive particle theory came from Manning and Whaley (1954) who concluded that the estuarine circulation system, which provides a means of slow upstream transport and ensured retention of larvae, was apparently the major factor in determining horizontal distribution of oyster larvae and spatfall in St. Mary's River, Maryland. They also suggested that water density can be a controlling factor in larval vertical distribution. This suggestion, though, is in keeping with previous studies in that it is just this vertical migration and activity that ensures distribution via physical means.

Kunkle (1957) found that older larval stages tended to congregate on or near the bottom at both slack and ebb tides, but were in the water column during early and maximum flood. Young larvae (up to 8-d old) were uniformly distributed throughout the water column on both ebb and flood tides. His work thus strongly confirmed that of the Nelsons and Carriker reported above.

Haskin (1964) extended this work with extensive field studies coupled with laboratory experiments. His experiments were designed to determine whether or not salinity is indeed an adequate stimulus to induce activity changes in oyster larvae (Nelson 1931). He

demonstrated that larvae disappeared from surface waters as the tide ebbed and later increased with the flood tide. His data provided strong evidence that there is a different distribution of older stage larvae on flood and ebb tides (Fig. 1). His laboratory data further indicated that large changes in salinity (although greater than those normally experienced in the field [Fig. 2A]) were definitely correlated with increased swimming activity. Under conditions of more subtle salinity changes, there was still a strong, though not as pronounced, pattern of activity change as the salinity varied (Fig. 2B). Although Haskin's (1964) data do not prove conclusively that salinity accounts for vertical distribution of oyster larvae over the tidal cycle, they do demonstrate that salinity can play an important role in regulating larval activity. The accumulated data lend support to the possible role of "ebb tide eddies" as larval traps, evidence for which is found in heavy spatfalls that commonly occur in mouths and lower tributary streams of estuaries (Nelson 1931).

Wood and Hargis (1971) found that coal particles, present in nearly all their samples from the James River, Virginia, had a density similar to that of oyster larvae. Wood and Hargis (1971) took advantage of this built-in "control" and compared distributions of oyster larvae with those of the coal particles. The temporal pattern in concentration maxima was different between larvae and coal particles so Wood and Hargis (1971) concluded that selective swimming by the larvae must be involved. Their data suggest (Fig. 3) that fluctuations in abundance of coal particles coincide with variations in tidal current velocities, whereas those of bivalve larvae coincide with increases in salinity. They claimed that larvae can swim vertically at speeds of 60 cm min^{-1}. With currents of up to 480 cm min^{-1} present in the region, this behavior alone is not sufficient to provide any advantage in distribution. Larvae could, however, rise in the water column through about 10 m of water in 15 min at this rate,

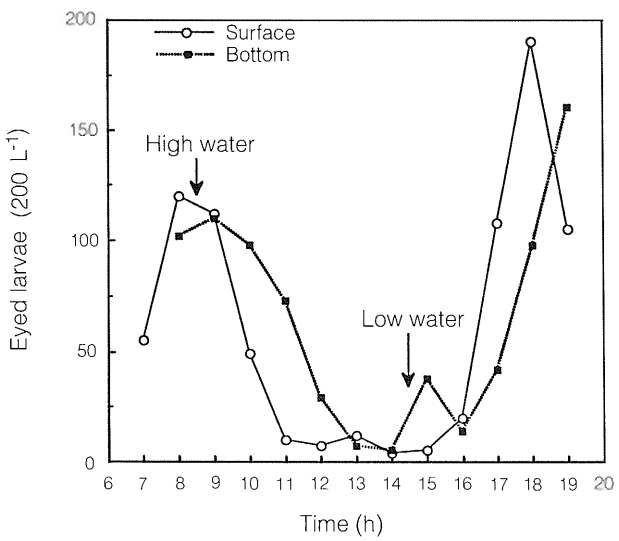


Figure 1. Numbers of eyed larvae collected during tidal cycle observations at the Paris Green Station, Delaware Bay, on August 20, 1956. After Haskin (1964).

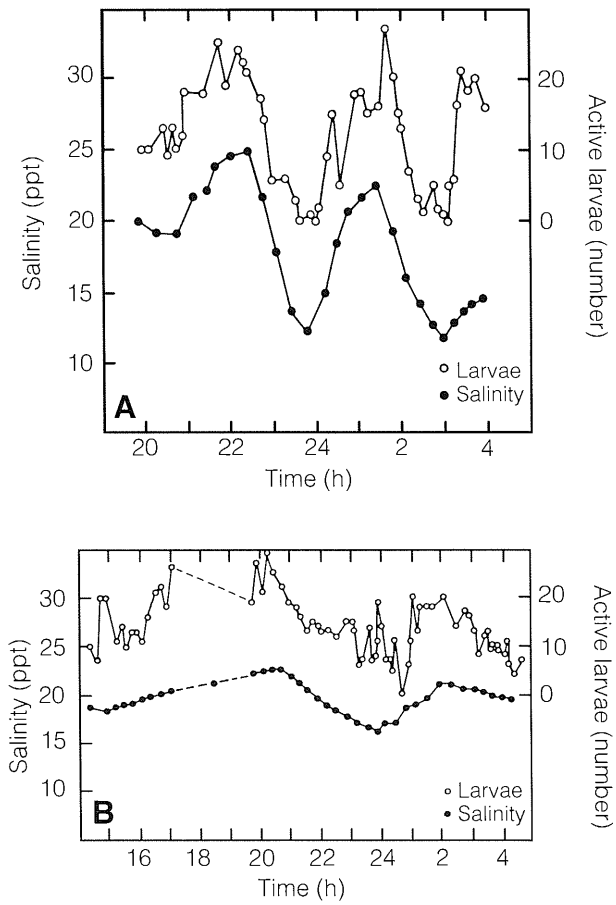


Figure 2. (A) Swimming activity of eyed larvae in response to salinity changes, August 21, 1958 and (B) swimming activity of eyed larvae in response to salinity changes during laboratory experiments, August 30, 1958. After Haskin (1964).

which is sufficient speed to allow them to capitalize on tidal changes in water flow. During tidal ebb (salinity decreases), larvae descend to the bottom where currents are weakest. When the tide floods, larvae stimulated by increased salinities may then swim up into surface waters to be carried upstream. Wood and Hargis (1971) concluded that bivalve larvae are not transported passively, but exhibit an active swimming response that results in movement upriver. These researchers also demonstrated that the swimming behavior was correlated with increases in salinity, not with increasing current speed as had been sug-

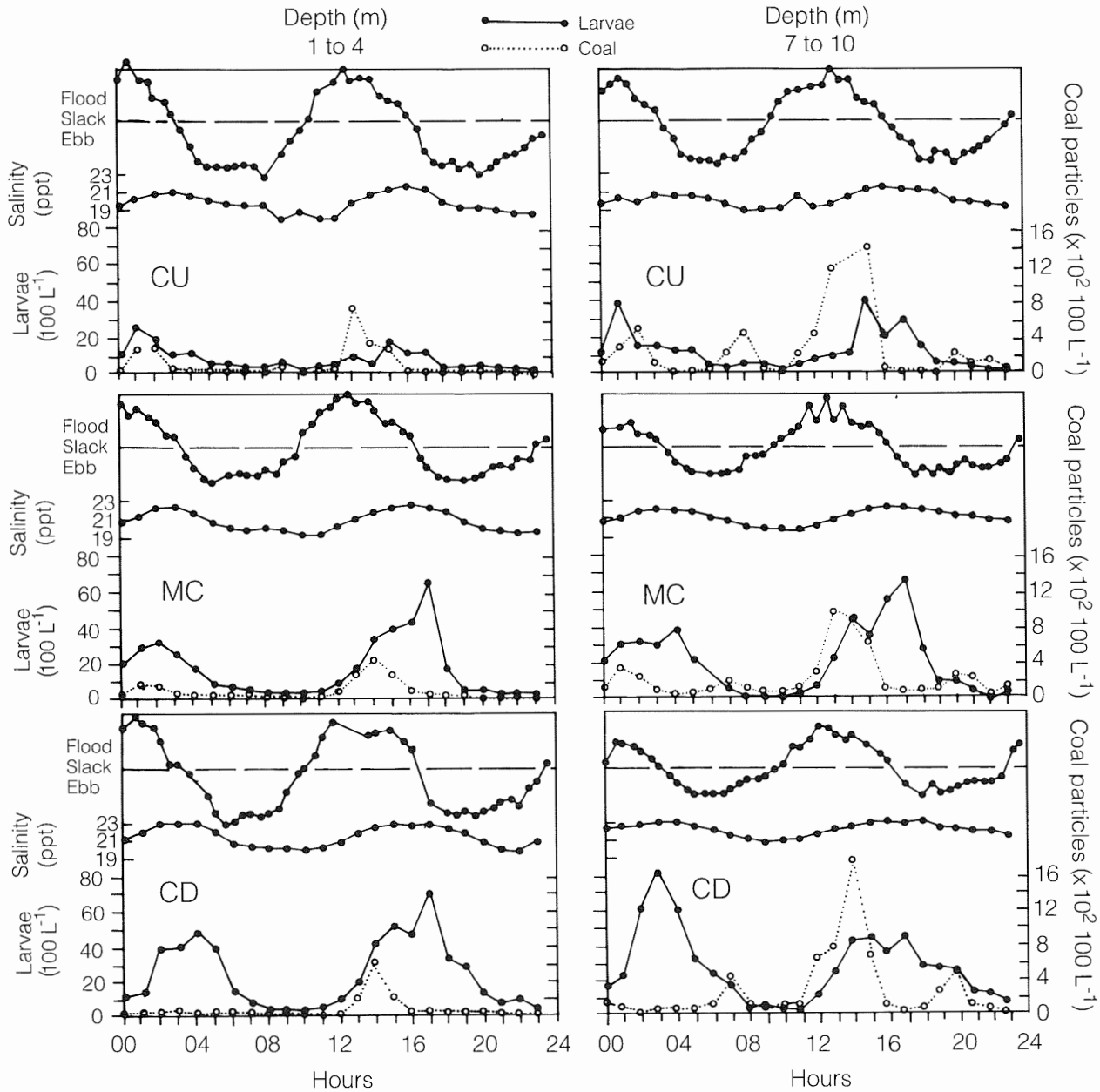


Figure 3. Hourly measurements of relative flow (upper curve), salinity (middle curve), and density of larvae and particles (two lowest curves) averaged for each of three channel stations [CU, MC, CD] in James River, Virginia, over average depths of 1 to 4 m (left) and 7 to 10 m (right). After Wood and Hargis (1971).

gested previously. Menzel (1955) suggested that late umbo larvae of *C. virginica* are really influenced by salinities in relation to the specific gravity of the larvae themselves, so that in high salinities (>35 ppt) they tend to "float" near the surface. This might help to explain intertidal spatfall in high-salinity areas.

Hidu and Haskin (1978) monitored swimming speeds of oyster larvae of various stages in response to differing salinities. Straight-hinge larvae (75 μm shell length) swam vertically between 0.6 and 2 cm min^{-1}, whereas eyed larvae (300 μm) swam at 5 cm min^{-1}. Hidu and Haskins (1978) demonstrated that larvae could move up or down at a rate of up to 14 cm min^{-1}; at these speeds they could move through a linear distance of 7 to 8 m h^{-1}, an ample speed to place larvae well above the bottom in time to "take advantage of" available tidal transport systems. Much higher swimming rates of 67 cm min^{-1} were reported by Wood and Hargis (1971). Different swimming speeds of different larval stages reported by Hidu and Haskin (1978) can partially explain some of the differences of vertical position noted in the work of Kunkle (1957) and others.

Temperature effects on vertical distribution have not been as widely studied as those of salinity. Nelson (1908, 1916) speculated that high water temperatures caused larvae to rise to the surface whereas low temperatures tended to drive them deeper into the water column; however, Nelson and Perkins (1931) found no correlation between temperature and larval distribution. For further discussion of larval behavior see Kennedy, Chapter 10.

REPRODUCTION PATTERNS

Gametogenesis and spawning in oysters are directly correlated with water temperature. In addition, the condition index (the ratio between dry meat weight and shell cavity volume; Grave 1912; Hopkins 1937) of oysters is strongly influenced by season and environmental factors and not solely by temperature. Major changes associated with variation in condition are a function of the gametogenic cycle. For further discussion of the gametogenic cycle in eastern oysters, see Thompson et al., Chapter 9.

Coe (1936) first discussed the role of temperature in determining sex in *C. virginica.* In the northern part of its range, the oyster appeared to be mainly or wholly protandric, but in somewhat warmer waters a higher proportion of young oysters functioned as females during their first breeding season (end of Year 1). Coe (1934) suggested that more favorable conditions for rapid growth of young oysters led to omission or abortion of the initial male phase and that localities and seasons in which 1-year old oysters attained the largest mean size usually had the largest proportion of females in the first breeding season. From North Carolina southward, young eastern oysters of both sexes reached functional maturity within the same reproductive season that they settled. Animals from Connecticut to North Carolina increased not only in mean size of individuals, but also in the proportion of females in yearling populations under favorable conditions (Coe 1936).

A number of authors have proposed various equations to predict maturation of gametes at a given temperature. Loosanoff and Davis (1952) maintained oysters at experimental temperatures ranging from 10° to 30°C in an effort to determine the number of days needed for formation of the first physiologically mature gametes of each sex. They found that almost no gametogenic activity took place at 10°C, whereas a temperature of 15°C proved adequate for ripening and spawning in some animals. Their equation for the prediction of average times needed for development of mature gametes in 50% of the oysters at different temperatures is:

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

where D is the average time needed, T is temperature (°C), and e is the base of natural logarithms. Development time ranged from 26.5 d at 15°C to 4.9 d at 30°C (mature gametes); however, calculated data did not always coincide with empirical data. Loosanoff and Davis (1952) suggested that the amount of glycogen in oysters at the beginning of gonadal development could control the quantity of spawn produced.

Price and Maurer (1971) were able to predict the exposure temperature necessary for laboratory maturation of eastern oyster gametes from Delaware Bay. They found that these oysters required 6 to 7 times as long to ripen at temperatures between 12° and

22°C as did oysters from Long Island Sound. The cumulative temperature exposure was more significant in the ripening of Delaware Bay oysters than exposure to "high" temperatures per se, and ripening did not occur at 12°C and below. Their equation is:

$$D = \frac{700}{T\text{-}12}$$

where D is exposure time in days and T is the daily mean exposure temperature within the approximate range of 12° to 22°C. Their equation was specific in that it was only applicable to Delaware Bay oysters removed from the field in winter and spring before ambient water temperatures had risen above 12°C. They estimated that the average number of days for 50% of eastern oysters to produce ripe gametes was 150 d at 15°C, 56 d at 20°C, and only 35 d at 25°C.

Kaufman (1978) proposed a revised version of the formula given by Loosanoff and Davis (1952) such that:

$$D = kT^{(b + a \cdot \log T)}$$

where D and T are the same as in Loosanoff and Davis' equation; k, a, and b are coefficients, the values of which were determined from the experimental data of Loosanoff and Davis (1952):

Event	k	a	b
Time of appearance of mature gametes	10288	– 0.29	–1.96
Time of first spawning	348×10^8	3.84	–13
Time of mass spawning	36×10^{18}	7.68	–24

The revised formula allows accurate description of the maturation rate of gametes as a function of ambient temperature, and it can be used to predict both when spawning will be initiated and the time of mass spawning. Kaufman's (1978) calculations for *C. virginica* over temperature changes of 1°C (15° < T < 30°) and the experimental data of Loosanoff and Davis (1952) are in agreement.

Kaufman (1978) further concluded, based on calculations using his revised formula, that at lower temperatures, a slight temperature change in the environment causes a more significant change in the rate of gametogenesis than at higher temperatures: at 20° ≤ T ≤ 30° all three processes had a Q_{10} of 2, in agreement with van't Hoff's rule, whereas at 15°C ≤ T ≤ 21°C, the figures deviated significantly from the rule. Thus, the time at which the first ova appear increases by a factor of four while the time at which the first spawning occurs is reduced by a factor of five and the time of mass spawning is reduced by a factor of eight.

Salinity is also known to affect gametogenesis, condition index, and spawning in oysters, although to a lesser degree than temperature. Like the effects of temperature, those of salinity also vary among populations. Amemiya (1926) reported normal egg development from 18 to 40.1 ppt, with optimal development in the range of 19.3 to 35.1 ppt. Davis (1958) found egg cleavage from 7.5 to 35 ppt, with normal development from 10 to 22.5 ppt.

Gametogenesis is arrested or depressed at low salinities. Loosanoff (1953a, b) showed that normal gonadal development proceeded in salinities near 7.5 ppt and he placed the lower limit somewhere between 7.5 and 5 ppt. Calabrese and Davis (1970) reported mature gonads and spawning activity at 27.5 ppt, but eggs did not develop at 10 ppt. At 12.5 ppt they rarely developed to the straight hinge larval stage. Larvae reared to the setting size at 27.5 ppt could successfully complete metamorphosis in salinities as low as 9 to 10 ppt. Successful spawning has been reported at salinities ranging from 32 to 42 ppt in the lower Laguna Madre, Texas (Breuer 1962). Butler (1949c) found that gametogenesis was inhibited in oysters held in brackish water for long periods, but that the condition was reversible if oysters were returned to normal conditions. He, too, recorded a lower limit of about 6 ppt for successful gametogenesis and suggested (as did Loosanoff 1953a, b) that the marked variation and suppression of gonadal activity at low salinities could also be caused by variations in food availability. Further, oysters apparently do not "fatten" or increase proportionally in dry weight when

salinity drops below 20 ppt in Canadian waters (Medcof and Needler 1941; Medcof 1946). Ingle and Dawson (1953) suggested that the low glycogen content and poor quality of oysters from Apalachicola Bay, Florida, could be due to great ranges in salinity to which oysters were exposed.

The glycogen content of *C. virginica* is intimately linked to the reproductive cycle which in turn is strongly affected by season. Generally, condition index and glycogen content decline during the breeding season and at elevated temperature. This is a result of more rapid conversion of glycogen to glucose in response to elevated metabolic demands (see Mitchell 1917; Medcof and Needler 1941; Medcof 1946; Galtsoff et al. 1947; Chipman 1948; Menzel and Hopkins 1952; Lee et al. 1960; Haven 1962; Sakuda 1966). In a comprehensive review, Walne (1970) summarized data available on condition index in various oyster species including *C. virginica*. He found that the median condition index increased exponentially with the latitudinal location of the species or population and suggested that populations in cooler waters generally tend to be in better condition than those from warmer waters. Figures 4 and 5 summarize data on seasonal variations in the proportion of glycogen and in condition indices for *C. virginica*, respectively.

Condition index is often high in winter and declines to a lower level in summer once spawning has occured. Condition indices vary among populations. Engle (1958) reported meats in Chesapeake Bay to be thinnest in summer, with an increase in condition index during winter. In contrast, Galtsoff et al. (1947), working in a different section of the Bay, reported higher indices in summer than in winter. Galtsoff et al. (1947) demonstrated that glycogen content of oysters from the York and Piankatank Rivers in Virginia varied seasonally, but that quantitative variations were different between the two areas. They further demonstrated that the glycogen content of York River oysters decreased from the mouth of the river towards its head; the process was reversed in the Piankatank River, where oysters from upper parts of the river were richer in glycogen than those from the lower part of the river. They also showed that transplanting oysters with low glycogen content from an environment where oysters generally grew poorly to an environment where oyster growth and condition was better could increase the glycogen content of the transplanted oysters.

Swift and Ahmed (1983) showed that eastern oysters exhibit some regulatory mechanism for maintaining concentrations of glucose, total Lowry-positive substances (LPS), and triacylglycerols in the hemolymph. Over a 27-d period of starvation, oysters purchased commercially (Washington, D.C.) and held at constant temperatures and salinities maintained concentrations of their hemolymph glucose and LPS; environmental extremes, however, caused variations in these hemolymph constituents (Swift

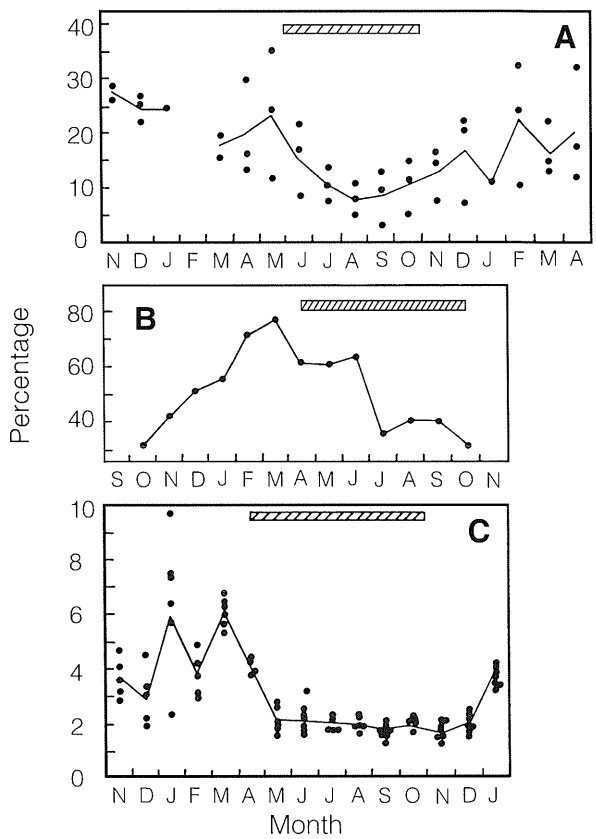


Figure 4. Seasonal variation in the percentage of glycogen (or carbohydrate) in the tissues of *C. virginica*. Data from (A) Galtsoff et al. (1947), (B) Lee et al. (1960), and (C) Menzel and Hopkins (1952). Hatched bar indicates approximate time of spawning. After Walne 1970.

and Ahmed 1983). Oysters maintained at 4°C had significantly higher concentrations of hemolymph glucose and LPS than did oysters held at 20°C. Oysters maintained at low salinity (12 ppt) had significantly lower concentrations of glucose in their hemolymph and concentrations of LPS than animals kept at either 18 or 24 ppt.

Seasonal changes in protein and carbohydrate content of oyster hemolymph have also been reported. Fisher and Newell (1986) showed in laboratory experiments that temperature, salinity, and nutrition did not play a major role in affecting concentrations of these constituents, thus indicating good short-term regulation. They did find, however, that there were large differences in hemolymph constituents between oysters taken from different localities. They attributed these differences to long-term differences in environmental condition or to population differences. They

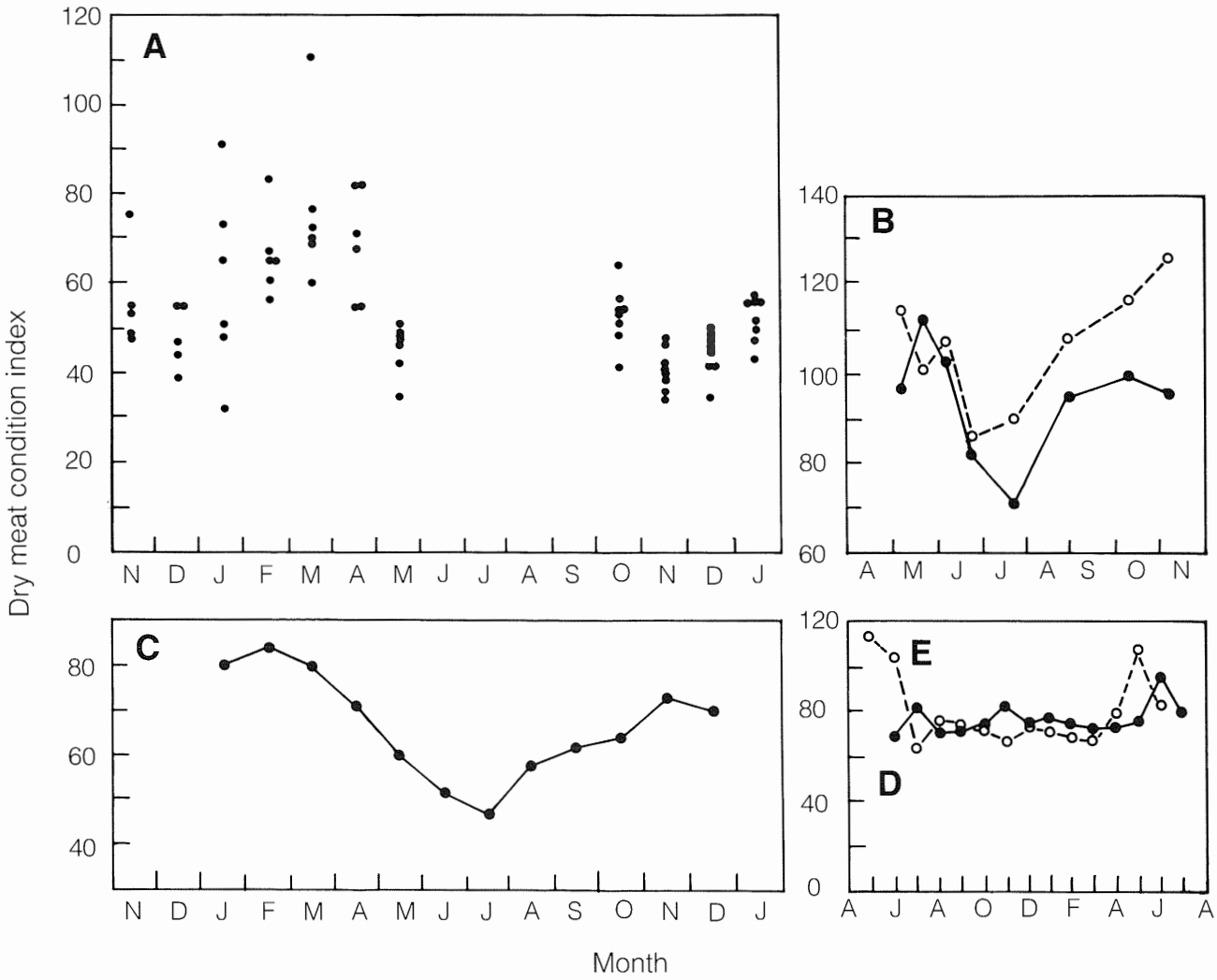


Figure 5. Seasonal variation of the dry meat condition index in *C. virginica.* Data from (A) Menzel and Hopkins (1952) and (B) Medcof (1946), in which solid circles and full line are samples from the upper part of the Bideford River, Prince Edward Island, and open circles and broken line are for samples from the lower part of the river. Additional data are from (C) Sakuda (1966) for oysters in Hawaii, (D) Haven (1962) in the York River (•), and (E) Haven (1962) in the Rappahannock River (o). Data from Haven (1962) are composite curves of four years' observations. After Walne (1970).

also suggested that the relationship between hemolymph protein and carbohydrate concentrations is linked to the reproductive cycle and stressed the importance of establishing good controls before using hemolymph composition to assess effects of other variables such as parasitism or environmental stress.

SPAWNING

Temperature is undoubtedly the single most important factor governing spawning of eastern oysters. For many years, the concept of a "critical temperature" for spawning was believed to apply to oysters in general. Nelson (1928b) wrote that oysters spawn after water temperature reaches 20°C "over all parts of their range, with no adjustment to the extremes of their distribution" (see also Townsend 1893; Stafford 1913; Churchill 1921; Gutsell 1924; Nelson 1924a; Prytherch 1924). This was supposedly confirmed in the laboratory by Galtsoff et al. (1930), but as will be demonstrated later, his results were a direct consequence of geographic location.

The proposition that ambient water temperatures must attain 20°C in order for eastern oysters to spawn has since been refuted by several authors (Loosanoff 1932; Galtsoff 1938; Loosanoff and Davis 1950; Stauber 1950b; Loosanoff and Nomejko 1951; Bardach et al. 1972). Indeed, Nelson (1931) wrote that spawning of ripe gonads is triggered by a rapid rise in temperature but is not determined by a specific critical temperature as others had originally suggested. This belief was reiterated by Medcof (1939) who stated that spawning occurs with rising temperatures "which may or may not reach 20°C." It is now well established that there is a fairly direct relationship between latitude and the minimal temperature required for spawning (with some exceptions), and the existence of physiological races based on these differences. Although minor, irregular spawnings are known to take place in most populations, a required minimal temperature must be reached before a major, mass spawning will occur. In general, oysters in more southern portions of their range exhibit longer spawning periods than their more northern counterparts and mass spawning temperatures are considerably higher, e.g., 26°C in Apalachicola Bay versus only 17°C in Long Island Sound (Fig. 6). The major period of spawning (spring) reported for Mexican oysters by Garcia and Ramirez (1981) is very short; however, minor spawnings also occurred during winter and summer.

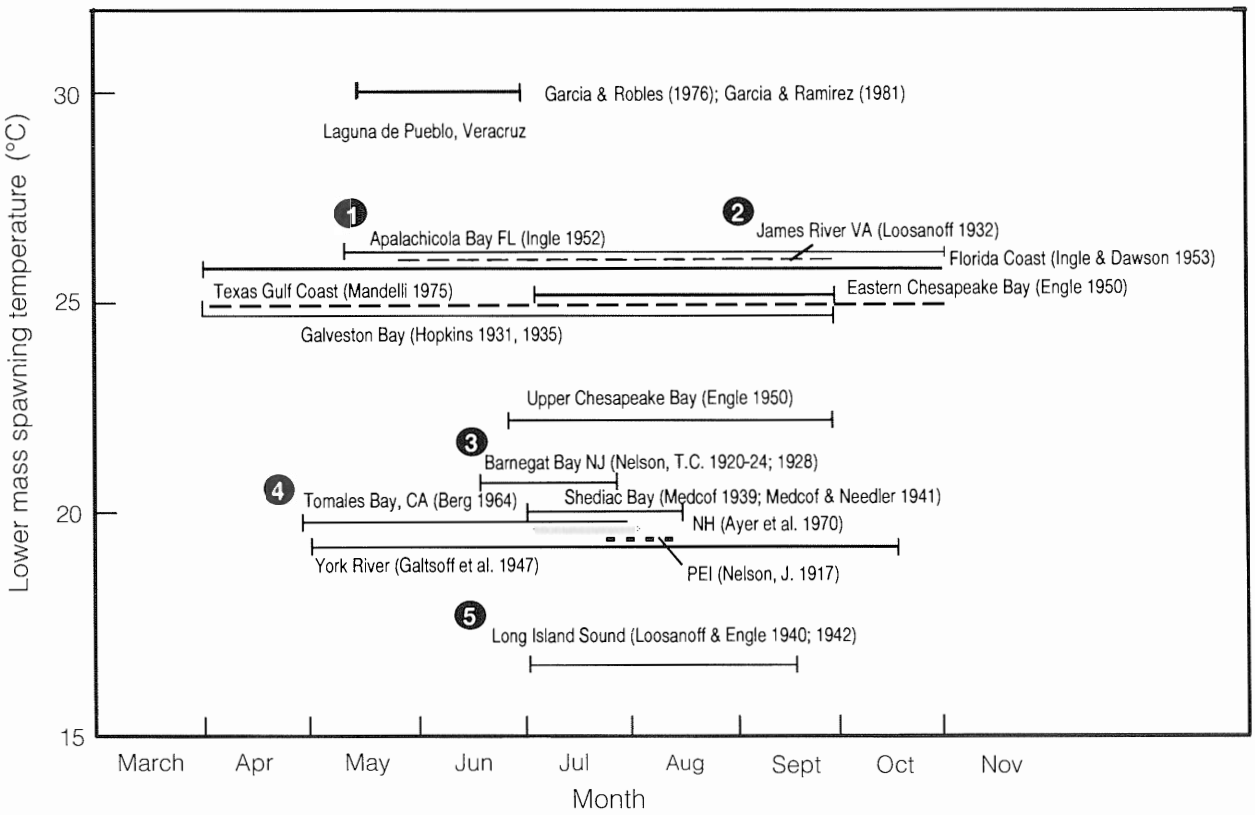
Temperature is not always the only critical factor governing spawning. For example, Matthiessen (1971) reported that although water temperatures in parts of Nova Scotia, New Brunswick, and Prince Edward Island in Canada became sufficiently high during the summer to stimulate spawning, overall the conditions necessary for successful reproduction were marginal and inconsistent from year to year.

Dependence of spawning on temperature has had major ramifications for hatcheries. Loosanoff (1945a) first proposed the "conditioning" of oysters out of season by exposure to increased temperatures. Loosanoff and Davis (1951) were able to delay spawning activity in *C. virginica* from Long Island Sound by transporting nearly ripe oysters to Boothbay Harbor, Maine, where temperatures were adequate to permit continued gametogenesis but too low to stimulate spawning. These eastern oysters could then be used in autumn when ripe oysters from natural populations were unavailable to hatcheries. The ability to control gametogenesis and to induce spawning has assured the supply of oyster larvae on nearly a year-round basis.

The increasing number of electricity-generating power plants built during the 1960s and 1970s prompted a number of studies on effects of heated effluent on various phases of oyster biology. Roosenburg (1969) found significantly higher initial oyster mortalities near a power plant in Maryland when oysters were placed in the effluent between May and September, presumably due to weakened conditions brought about by gametogenic activity or spawning. Similar results were reported by Quick (1971), who found that condition of oysters before exposure to elevated temperatures was critical to their reproduction at the high temperature. Oysters in good condition and not spawning were better able to maintain or improve their condition when exposed to elevated temperatures than those not in good condition. Winter mortalities of oyster spat were significantly reduced in a heated effluent in New Hampshire (Ayer et al. 1970).

Tinsman and Maurer (1974a, b) reported both beneficial and detrimental effects of exposure to thermal effluents. They found that meat weights and condition indices were low during warm months, but more favorable winter conditions in the effluent allowed both body weight and condition of oysters to improve and exceed the weight and condition of oysters from control areas. They also noted increased rates of meat growth and shell heights throughout the study in the heated effluent.

Oysters kept in heated effluents in Connecticut during winter and spring were superior in growth and biochemical composition compared with control oysters, and gonadal development began about 4 months earlier (Ruddy et al. 1975). Protein, carbohydrate, and condition index increased by 56%, 109%, and 22% respectively in winter and spring, and thicker shells were produced. Ruddy et al. (1975) estimated that the growing season could be extended from the normal 6-month period to about 9 months and at the same time allow oysters to take advantage of the spring phytoplankton bloom that normally occurs when water temperatures are still too low for oysters to feed efficiently under normal conditions. Interestingly, even



1 Assuming larval period of approximately 2 weeks; Ingle (1952) reported spat settlement into the second week of November.

2 Temperature was above 20°C for several months; Loosanoff (1932) speculated that other factor(s) influenced spawning

3 Mean average temperature 24 h before spawning ranged from 21.6° to 23.4°C for the years 1924 to1927; temperature continued to increase throughout spawning season.

4 *Crassostrea virginica* introduced; although spawning occurred, successful propogation of larvae was lacking.

5 Spawning in shallow water completed by mid-August; only deep water oysters (lower temperature) spawned through September.

Figure 6. Lower mass spawning temperature for *C. virginica* from various geographic locations.

larvae of oysters from Long Island Sound, conditioned and spawned at 26.0 to 27 ppt was 17.5 ppt (Fig. 8). Optimal salinity for growth of larvae from Hodges Bay, Maryland (8.7 ppt), conditioned and spawned at 26 to 27 ppt, appeared to be about 22.5 ppt. Although not conclusive, it appeared that larvae from Maryland oysters did not tolerate lower salinities than did larvae from Long Island Sound oysters conditioned at the same salinity. Davis (1958) reported a minimal salinity for successful metamorphosis of 10 ppt for larvae of unstated parentage. Similar results were reported by Chanley (1958) who found some growth of recently metamorphosed larvae at 5 ppt, but optimal growth between 12.5 and 25 ppt.

Davis and Calabrese (1964) studied the combined effects of temperature and salinity on development of eastern oyster eggs and larval growth. Rates of growth and development were poor at the extremes of temperature ranges and satisfactory survival rates (70% or better) were limited to temperatures of 27.5° to 32.5°C and salinities of 10 to 27.5 ppt. As salinity decreased, the tolerated range of temperatures narrowed. Optimal temperature for larval growth was between 30° and 32.5°C for all salinities except 7.5 ppt where the optimum was 27.5°C. Conversely, there was no well-defined optimal salinity for larval growth at any temperature as maximal growth occurred in salinities varying from 15 to 27 ppt at some temperatures and from 20 to 27 ppt at 17.5°C. Thus, the effect of reduced salinities on larvae was to reduce the range of temperature tolerance.

Loosanoff (1965) provided further data on larval growth and development at various temperatures and salinities in Long Island Sound. He reported that no eggs developed into normal, straight-hinge larvae at 15.5°C, about 97% developed to fully formed, straight-hinge stage at 17.7°C, most fertilized eggs developed normally at 30°C, and only about 50% of the eggs developed to the straight-hinge stage and many were abnormal at 33.3°C. Optimal salinity for egg development was 22.5 ppt; some normal larvae developed at 15 ppt and at 35 ppt; below 22.5 ppt, the percentage of normally developed larvae decreased. Optimal salinity for larval development from eggs was about 17.5 ppt. Good larval growth was recorded at 15 ppt, with appreciably slower growth at 12.5 ppt and almost no growth at 10 ppt. The older larvae were better able to withstand low salinity. Wright et al. (1983) also studied thermal tolerance of larval stages of *C. virginica* and found that larval mortality generally increased with exposure to higher temperature and with increased exposure time at any one temperature. Nevertheless, at temperatures as high as 40° to 41°C, straight hinge larvae sustained low mortality (11%) when exposed for up to 1 h.

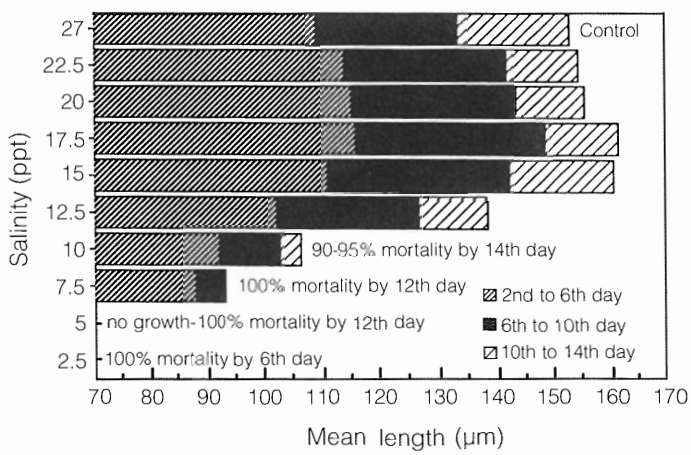


Figure 8. Growth of oyster larvae at different salinities. Samples from each of the duplicate cultures at each salinity were taken on the 6th, 10th, and 14th days. The lengths (µm) of one hundred larvae from each sample were measured. After Davis (1958).

Diaz (1973) found that growth of larval eastern oysters was not affected by brief temperature increases of 10° or 15°C, but a 20°C increase resulted in permanently impaired growth of surviving larvae.

Loosanoff (1965) collected oysters from Chesapeake Bay at 8.7 ppt and spawned them. Some eggs developed into normal larvae at 10 ppt and even at 7.5 ppt, although abnormally small individuals were common at the latter salinity. Optimal salinity for development of eggs in this group of oysters ranged between 12 and 15 ppt, with a salinity of about 22 ppt being the upper limit for normal development.

Hidu et al. (1974) demonstrated that the fertilized egg and ciliated gastrula were considerably more temperature sensitive than later stages of larval development. Time of exposure greatly affected the temperature tolerance of the larvae in that longer exposures led to increased mortality.

Amemiya (1926) studied effects of salinity on early development of *C. virginica* cultured over the salinity range of 12.3 to 52.1 ppt; 24.5 to 29.8 ppt was the optimum salinity for development, and the range of 22 to 33 ppt was favorable. He provided a description of larval development at 24 separate salinities to which the reader is referred for details. He also reported that only a small proportion of oyster larvae develop normally between 31 and 34 ppt. MacInnes and Calabrese (1979) reported 25°C and 26 ppt as the optimum temperature and salinity for normal embryonic development.

Although temperature and salinity have a direct effect on larval growth, availability of suitable food items to support growth is also of considerable importance. Davis and Calabrese (1964) grew larvae on monocultures of the unicellular algae, *Dunaliella euchlora* and *Chlorella* sp., and on a mixture containing *Chlorella* sp., *Dicrateria* sp., *Isochrysus galbana*, and *M. lutheri*. Although there was a distinct effect of temperature on growth rate regardless of food supply, oyster larvae fed the mixture of four algal species showed highest growth rates (Fig. 9).

In a further experiment to determine upper and lower limits for growth of oyster larvae, Davis and Calabrese (1964) found no growth at 15°C, minimal growth at 17.5°C, and maximal growth at 30° and 33°C (Fig. 10). A re-evaluation of these data by Lough (1975) gives a clear expression of the combined effects of thermal and salinity variations on oyster larvae. Lough (1975) used response-surface techniques to show that maximal survival of 2-d old

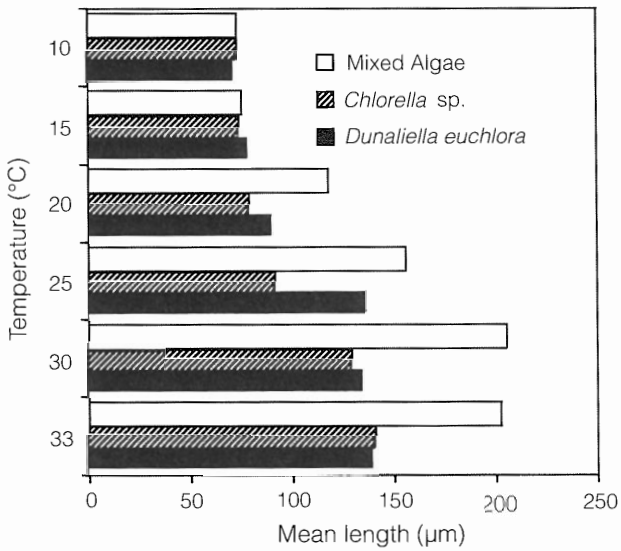


Figure 9. Growth of oyster larvae receiving different foods and reared at different temperatures. Plots are based on mean length of 100 larvae from each temperature at each measuring period. After Davis and Calabrese (1964).

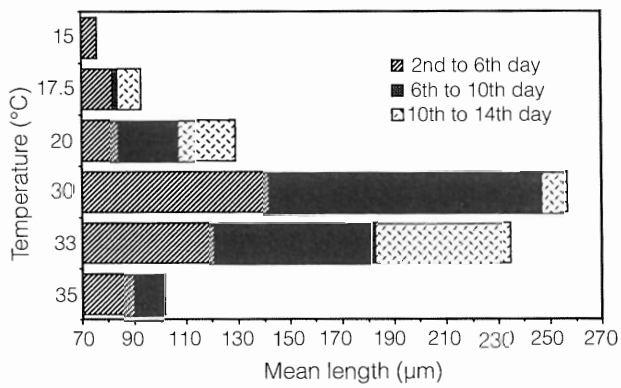


Figure 10. Growth of oyster larvae receiving a mixture of foods and reared at high and low temperatures. Plots based on mean length of 100 larvae from each duplicate culture at each temperature at each measuring period. Many of the larvae kept at 30° and 33°C set between the 10th and 14th days and were not included in the 14-d samples. After Davis and Calabrese (1964).

larvae (80% contour, Fig. 11A) occurred between 19° and 30.5°C and 19 and 30 ppt. Maximal survival after 8 d (60% contour, Fig. 11B) occurred above 21°C and between 8 and 30.5 ppt, with a much higher tolerance to higher temperature and a wider salinity range than the 2-d old larvae demonstrated. Maximum growth (100% response contour) (Fig. 11C) was estimated to occur above 33°C and 19 ppt. Differences between survival and growth at 8 d indicated that a significantly higher salinity range is required for optimal growth than for optimum survival. Lough (1975) estimated that the optimal (80% contour) temperature and salinity conditions for maximizing both larval survival and growth are above 30°C and between 18 and 35 ppt.

Generally speaking, within the zone of tolerance, the higher the temperature the faster the development of eggs and growth of larvae. Because factors apart from temperature can also affect these processes, it is probably best to define optimal conditions for development as those at which mortality is lowest, rather than those at which development is fastest. Development of eastern oyster eggs and larvae is considered further by Eble in Chapter 2 and Thompson et al. in Chapter 9.

Adult Growth

Growth rate of adult eastern oysters is as strongly affected by temperature and latitude (Table 1) as are egg and larval development. Butler (1953) believed that a clear-cut differential in oyster growth exists at different latitudes and that differences in shell growth do not necessarily reflect differences in tissue or meat yield. Measurement of shell volume provides a more critical evaluation of growth than does shell height. As an example, 2-year old oysters from a South Carolina clustered reef yielded about 1.2 kg of meats per bushel (average height ~75 mm, Butler 1953). Oysters grown individually in the same area can require 3 years to attain the same size, but the yield increases to ~3.4 kg per bushel.

As a rule, growth is more rapid in warm waters such as those of the Gulf of Mexico where a marketable oyster (90 mm) can be grown in 2 years. In northern waters, e.g., Long Island Sound, 4 to 5 years are required to attain the same size. Butler (1953) pointed out, however, that oysters growing in the Chesapeake region tend to grow faster and produce more meat per unit time than oysters growing north or south of this region. Loosanoff and Nomejko (1949) in observations of monthly shell growth rates for oys-

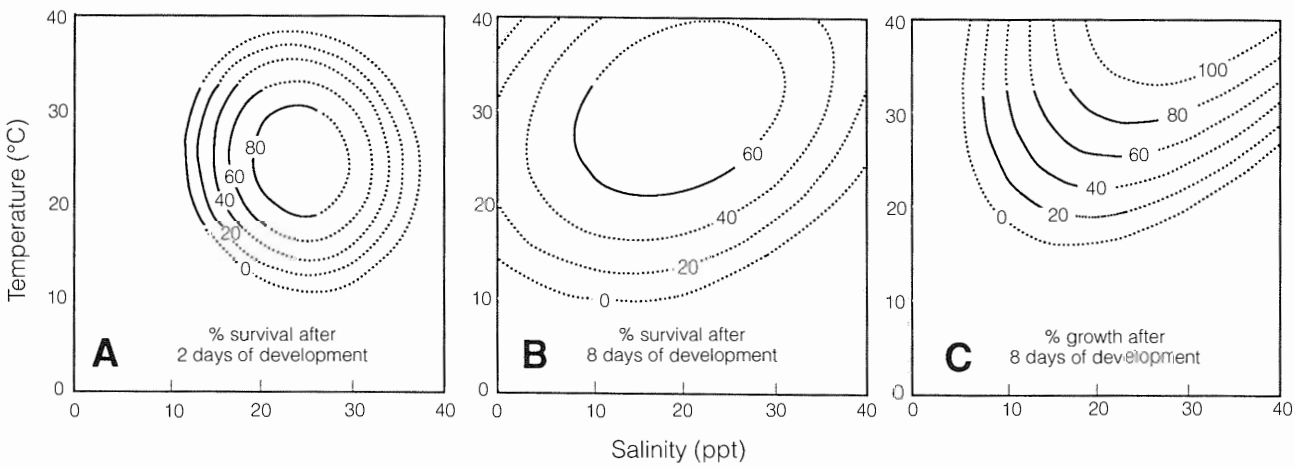


Figure 11. Response surface estimation of percent survival of *C. virginica* larvae (A) after 2 d of development and (B) after 8 d of development at experimental temperature and salinity combinations given in Davis and Calabrese (1964) and (C) response surface estimation of percent growth of veliger larvae after 8 d of development at these temperature-salinity combinations. Contours extrapolated beyond the experimental data are given as dotted lines. After Lough (1975).

Table 1. Summary of growth rate studies on *Crassostrea virginica* (Gmelin) and time required to produce equivalent growth at Apalachicola rate. From Ingle and Dawson (1952).

Place	Linear growth	Elapsed time	Time required in Apalachicola	Reference	
Canada	Setting to 2 in	24 mo	5 mo	Stafford	1913
Long Island	1.4 to 3 in	6 mo*	12 wk*	Moore	1905
Long Island Sound	Setting to 4.5 in	4 yr[1]	1.4 yr[1]	Churchill	1921
New Jersey	3.7 to 4.2 in	12 mo	6 mo	Nelson	1922
Chesapeake Bay	0.8 in	44 d	42 d	Ryder	1885
Chesapeake Bay	1.5 in	12 mo	3.5 mo	Ryder	1885
Chesapeake Bay	3.5 in	23 mo	15 mo	Ryder	1885
Chesapeake Bay	Setting to 0.75 in	3 mo	1.5 mo	Winslow[2]	1913
Beaufort, NC	Setting to 1 in	2 mo	2 mo	Osborn	1883
North Carolina	3.4 to 4.3 in	2 mo	.....	Glaser	1905
North Carolina	5.2 to 5.9 in	2 mo	.....	Glaser	1905
North Carolina	7.2 to 7.6 in	2 mo	.....	Glaser	1905
North Carolina	Seed to market size	2 yr	.....	Higgins	1940
North Carolina	Setting to 3 in	6 mo*	4 mo*	Higgins	1940
South Carolina	Marketable size	One season	.....	Dean	1892
South Carolina	Setting to 1.5 in	2-3 mo*	7 wk*	Moore	1905
South Carolina	Setting to 2.5 in	6-7 mo	6.2 mo	Moore	1903
Tarpon Springs, FL	Setting to good sized	10 mo	.....	Brice	1896
Louisiana	Setting to 1 in	6 wk*	5 wk*	Moore	1899
Louisiana	Setting to 3.5 in	18 mo	15 mo	Moore	1899
Louisiana	Setting to 4 or 6 in	23 mo	17 mo[1]	Moore	1899
Louisiana	Setting to 3.1 in	10.3	9 mo	Gunter	1951
Louisiana	Setting to 4 in	39 wk*	31 wk*	Menzel	1951
Texas	Setting to 3.7 in	12 mo[3]*	28 wk[3]*	Gunter	1951

* Maximum growth rate.

[1] Time refers to 4 inches growth.

[2] See Stafford 1913.

[3] The data of Gunter (1995) are not easily compared with Apalachicola Bay findings inasmuch as the oysters he observed were growing under unusual ecological conditions and his samples were small.

ters in Long Island Sound, found that growth was limited to about 8 months of the year, although most individuals showed growth increases only during 6 or 7 months; no growth occurred after the point of induction of cold coma in the Milford Harbor area. If the water temperatures were maintained above the point of cold coma, growth would continue. There was a strong relationship between changes in rate of increase in shell volume and changes in water temperature.

Ingle and Dawson (1950a, b; 1952) and Copeland and Hoese (1966) reported exceptionally rapid growth of oysters from Apalachicola Bay, Florida, and south Texas. Growth was continuous throughout the year and basic growth curves remained the same despite seasonal environmental changes, i.e., oysters that set in autumn had very nearly the same growth curves as those that set in the spring. Reported growth rates are faster than for any other oyster populations; both sets of authors attributed high growth rates to high

temperature. Ingle and Dawson's (1950a, b; 1952) estimates were based on shell size and may not necessarily reflect tissue growth. The authors summarized growth data over the entire geographic range of *C. virginica* (Table 1); their recorded values for Apalachicola Bay (column 4) remain among the highest known.

Only Loosanoff (1953a, 1965) and Shaw (1966) have provided data on effects of salinity on growth rate. Loosanoff (1953a, 1965) noted that oysters adapt rapidly to salinity change, but that growth was stunted at 7.5 ppt and almost nonexistent at 5 ppt. He suggested that 10 ppt was the minimum salinity at which adult oysters grew at a normal rate. Shaw (1966) transplanted seed oysters from low-salinity waters in Chesapeake Bay to a low-salinity area (Broad Creek in Chesapeake Bay; 8 to 16 ppt, average 12 ppt) and a high-salinity area (Chincoteague Bay; 17 to 35 ppt, average 30 ppt). Over a two-year period, shell growth rate was similar in both areas.

Activity

There have been few studies concerned with effects of temperature and salinity on valve activity or closure in *C. virginica*, with most data collected as a by-product of other studies. Galtsoff (1946) subjected oysters exposed in air for 24 h at 5°C to temperatures of 22°C and found irregular shell movements accompanied by a complete cessation of pumping until the third or fourth day after transfer, after which normal pumping resumed. Loosanoff (1953a) noted that at the lowest salinities tested (0 to 5 ppt), valve movement and water transport were abnormal and growth was inhibited (see also section on growth). Valvular activity also becomes irregular above 30°C, with some eastern oysters closing their valves completely, and with pumping activity frequently inhibited (Loosanoff 1958). There was a reduced rate of pumping even during periods when valves were open. Between 34.1° and 36°C, these symptoms became exaggerated and oysters remained closed about 67% of the time above 36.1°C. When oysters were exposed to a sudden increase in temperature, there was an immediate opening of the valves and inhibition of pumping (Loosanoff 1958). Galtsoff (1964) stated that while temperature has no direct influence on the duration of shell opening, lowered salinity results in partial or complete contraction of the adductor muscle and a slowing or cessation of water current through the gills.

Numerous authors have reported mass mortalities due to fresh water flooding, predominantly in southern United States waters. Flooding is a common phenomenon in these regions, and in some areas low salinity flood conditions can last up to a month. Oysters are thus left inundated in fresh water at high temperatures, and mortalities up to 100% are not uncommon. The magnitude of the effect(s) of environmental perturbations (such as salinity changes) on oysters depends on the range of fluctuations and abruptness of these changes (see Hand and Stickle 1977). The ability of oysters to withstand such changes in salinity is enhanced by their ability to close the shell valves when exposed to extreme conditions such as protection from sudden freshwater input from floods and freshets.

Salt sensitivity at the mantle margin would be an advantage to oysters as an early warning system. Hopkins (1932), developed a method for studying the latent period of reactions of *C. virginica* to chemical stimulation. He monitored the latent period of reaction of tentacles on the oyster mantle to 21 different salts (most of the chlorides, iodides, bromides, nitrates and sulphates of potassium, sodium, ammonium, lithium, and magnesium) and was able to group the different ions according to their stimulating efficiency. He found that effectiveness of an ion as a stimulant depends in a direct manner on its atomic weight and that sensory stimulation of oyster tentacles by the salts is primarily a function of the cations present. He gave the following order of stimulating efficiency: cations, $K > NH_4 > Na > Li$; anions, $I > Br > NO_3 > Cl$. It is not clear what role this sensitivity might play in stimulating valve closure during exposure to various salinities, but it may confer an advantage.

Valve closure can only serve as a temporary means of protection against such adverse environmental conditions as reduced salinities. Even a slight contraction of the valves will result in a reduced rate of water flow that will in turn affect the rate of feeding and gas ex-

change (see below). Long-term valve closure will result in eventual mortality, especially when coincidental with high temperatures.

A distinction must be made between pumping rate (the velocity of water movement through the mantle cavity) and filtration rate (the amount of water completely cleared of particles larger than a specified size per unit time). Obviously, the two are intimately related, but not necessarily synonymous. If animals are not actively pumping, feeding cannot occur; conversely, even though some pumping activity can be underway, feeding still may not occur, especially at very low temperatures.

In an early study of pumping rate in *C. virginica*, Galtsoff (1928 a,b) calculated a maximum pumping rate of 3.9 L h^{-1} for a 76 to 102 mm oyster at 25°C (Fig. 12). Nelson (1938) disagreed with Galtsoff's findings, believing that Galtsoff's method interfered with activity and that the correct rate was actually a much higher value of 26 L h^{-1}. Subsequent studies (Loosanoff 1950a, 1958; Loosanoff and Nomejko 1946) reported values similar to those given by Nelson. While it is possible that Galtsoff's experimental design resulted in low values for pumping rates, it is also possible that other factors were responsible for differences.

Several authors have demonstrated that pumping rate is affected by both temperature and salinity. Most of our knowledge of pumping activity in *C. virginica* is from the work of Loosanoff (1958). His data show that pumping rate increased steadily as temperature rose from 8° to 28°C (Fig. 12). Pumping was reduced or non-existent below 2°C, whereas above 34°C oysters began to show distress that resulted in a marked decrease in pumping rate and abnormal shell movements. Highest flow rates were measured at about 29°C. Even though the absolute values for pumping rate measured by Loosanoff (1958) and Galtsoff (1928a) differ, they are in agreement that the upper temperature range of 35°C is the limit for normal pumping activity. W. Menzel (pers. comm.) observed oysters open and pumping at temperatures of 36° to 37°C. Other temperature values for maximal pumping rate are given by Nelson (1936) and Collier (1959) as 30°C and 20° to 25°C, respectively. It appears that optimal levels are sustained in the region of 25°C regardless of acclimation temperature of oysters.

Loosanoff (1953a) studied effects of salinity on pumping activity. Exposure to an abrupt reduction from 27 ppt to 20, 15, 10, and 5 ppt resulted in a decrease in pumping rate of 24, 89, 91, and 99.6% respectively for about 6 h after transfer. Thereafter, normal pumping activity resumed and there were no long-term effects on pumping rate. Oysters conditioned to live in lower salinities ceased or resumed pumping water and closed or opened their valves at lower salinity concentrations than did oysters from higher salinities.

Pumping rate of *C. virginica* is affected by a number of factors other than salinity and temperature. Nelson (1936) stated that pumping is increased during active shell secretion and by addition of fresh oyster sperm to incurrent water of the male oyster; the increase is typically from 5.9 to 11 L h^{-1}. No response occurs in female oysters unless they are induced to spawn, at which time water flow is markedly reduced. Subsequent research by Nelson and Allison (cited by Galtsoff 1964) suggests that pumping activity in spawning female oysters is actually enhanced although efficiency of particle retention on the gill is reduced. Nelson (1936) suggested that reduced pumping by females reduces the likelihood of retaining eggs on the gills whereas increased pumping by males permits wider and more rapid dissemination of sperm.

Eastern oysters can feed and grow at temperatures much lower and higher than required for spawning (Gunter 1957). Studies that deal specifically with the effects of temperature and salinity on feeding in *C. virginica* are scant. Galtsoff (1928a) reported that no current was produced and no feeding took place at or below 5°C. This statement was later modified by Loosanoff (1958; see below) but the generalization remains true. Prytherch (1928) concluded that gonadal development was dependent on the amount of food consumed by oysters and that, in years when ambient temperatures were above normal, higher rates of spat production due to the increased feeding activity and subsequent gonadal development might be expected.

Loosanoff (1953a, 1958, 1965) provided the most detailed studies of effects of temperature and salinity on feeding activity. He fed 90 oysters on a

culture of *Chlorella* sp. at 2° to 3°C and found that only one produced true feces, whereas 15% produced pseudofeces (Loosanoff 1958); at 3° to 4°C, about 50% of the oysters produced pseudofeces but still only one produced feces. Between 5° and 6°C, 11 of the 90 oysters expelled feces and over 75% produced pseudofeces. Thus, feeding occurs below 5°C only as an exception and the ability to produce pseudofeces may be a function of ciliary activity (as demonstrated by Galtsoff [1928a] who showed that frontal cilia are able to transport particles at a temperature of 3°C, whereas lateral cilia generally only produce a feeding current when the ambient temperature is about 5°C).

In terms of salinity, no feeding was seen in oysters maintained at 3 ppt or lower (Loosanoff 1953a; 1965). Animals exposed to 5 ppt exhibited abnormal activity, and their feces often appeared white or greenish and were composed principally of blood cells. Oysters were, however, producing both feces and pseudofeces, indicating that feeding activity and ingestion were not totally impaired. Loosanoff (1958, 1965) again demonstrated that oysters stopped feeding and "hibernated" [sic] below 5°C. Feeding rate increased rapidly between 13.9° and 27.8°C, with a further, less rapid increase up to 32.2°C. Above 33.8°C, a marked decrease in pumping rate was noted (Fig. 12) and shell movements became abnormal.

Davis and Calabrese (1964) demonstrated that the ability of oyster larvae to digest food is temperature dependent and that some food items are more easily digested at lower temperatures than others. Thus, naked flagellates were more easily digested than were algae with cell walls. No similar studies exist for adults, but it seems reasonable to assume that temperature must affect digestion rate in adults as it does in other species of bivalves (Bayne and Newell 1983 and references therein).

HEART RATE

Heart beat increases with increased temperatures within the range of 5° to 30°C (Fig. 13), depending on geographic location (Federighi 1929; Prytherch, cited in Higgans 1931; Stauber 1940; Stauber, unpublished cited in Stauber 1950a; Menzel 1955, 1956; Feng 1965). Dimock (1967) reported that salinity affects *C. virginica* heart activity by interfering with osmotic balance of heart tissue and with the activity of acetylcholinesterase in the heart (decreased salinity inhibits acetylcholinesterase activity, the extent of the inhibition being influenced by the oyster's ambient salinity).

Feng (1965) found a simple linear relationship between number of leucocytes in suspension in the hemolymph and the temperature of the external medium (Fig. 14). He suggested that leucocytes are nearly 100% settled out at 0°C because the heart is probably quiescent at this temperature. The number of leucocytes in suspension was strongly influenced by the heart rate, which was affected in turn by temperature or other stimuli. Feng and Van Winkle (1975) subsequently used *C. virginica* from two populations (New Jersey and Connecticut) and found that the time of acclimation to low salinities did not significantly affect recovery of heart beat for either stock, although the time of acclimation was very short (4 to 5 h versus 18 h). Above 10°C, heart beat of New Jersey oysters was

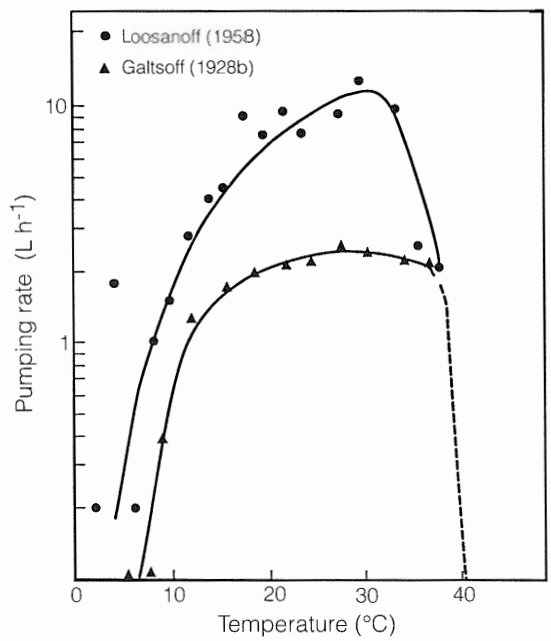


Figure 12. Pumping rate of *C. virginica.* Data taken from Loosanoff (1958) (plotted as upper level of each 2°C temperature interval tested) and Galtsoff (1928b). No size specified in Galstoff (1928b). Loosanoff (1958) gives size range as 100 to 110 mm length; 80 to 85 mm width; 30 to 35 mm depth; 85 to 100 ml volume; he provided no information on sample sizes.

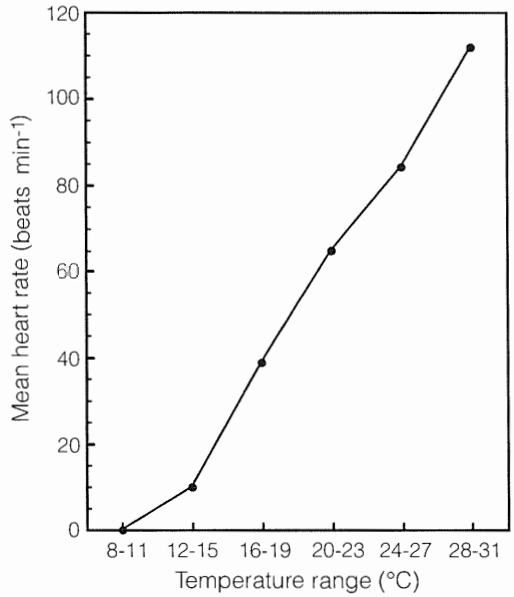


Figure 13. Average rate of heart beat min^{-1} at various temperature ranges for *C. virginica*. After Menzel (1956).

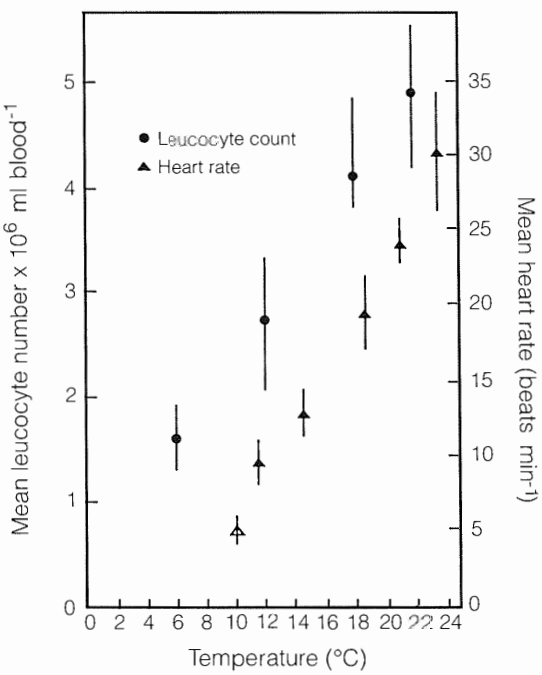


Figure 14. The effect of temperature on leucocyte numbers and heart rate of oysters. Each point represents average heart rate of three determinations on 10 oysters. The mean leucocyte count in heart blood at 6°, 12°, 18°, and 22°C is obtained from a group of 21 oysters. The vertical lines are ranges of the means. After Feng (1965).

less inhibited after a gradual decrease (3 to 4 d) in salinity from 5 to 10 ppt than after an abrupt decrease in salinity. Oysters from Connecticut exhibited a maximal rate of heart beat at intermediate salinities (14 and 19 ppt) at 20° to 30°C with heart rate relatively insensitive to salinity at lower temperatures (5° and 10°C). Feng and Van Winkle (1975) further concluded that the effect of salinity on heart rate is probably not very strong in that it is readily masked at low temperatures. Again, acclimation periods in this study were short and results should be considered as acute responses rather than acclimation responses to reduced salinity.

The only information available on effects of temperature on accessory hearts is given in a personal communication by Stauber (cited in Feng 1965) who stated that the two accessory hearts are as temperature-dependent as the systemic heart.

RESPIRATION

Surprisingly few data are available on effects of temperature or salinity on respiration rate in *C. virginica*. Galtsoff (1964) reported no significant change in respiratory rate after 3 d of acclimation to water of lowered salinity, although he based this conclusion on only nine individuals and a salinity change of 31.6 to 24.1 ppt.

A number of studies followed that of Galtsoff (1964) in which authors reported on the effects of temperature and salinity on excised tissues, with conflicting results. Van Winkle (1968) reported that oxygen consumption ($\dot{V}O_2$; volume respired per unit time) of excised gill tissue was relatively constant over a range of temperatures (10°, 18°, and 26°C) and salinities (5, 10, 15, 20, and 30 ppt) during both summer and winter. Percy et al. (1971) monitored $\dot{V}O_2$ in excised mantle, adductor muscle, and gill tissue of eastern oysters from Trinity Bay, Newfoundland. Respiration rates of gill tissue increased during exposure to dilute salinities, remained constant for mantle tissue, and declined for adductor muscle. All tissues exhibited an increased $\dot{V}O_2$ with increased temperature. Respiratory maxima for both mantle and adductor muscle were about 32°C, whereas gill $\dot{V}O_2$ increased continuously up to 40°C. There were also marked seasonal effects on $\dot{V}O_2$.

Wegener (1971) reported that the $\dot{V}O_2$ of gill tissue from eastern oysters collected at Beaufort, North Carolina, was unaltered by osmotic stress. Bass (1977) also reported on the effects of temperature and salinity on the metabolism of excised gill, mantle, and adductor muscle from Chesapeake Bay oysters. He demonstrated that cold-acclimated gill tissue showed good acclimatory ability, whereas mantle tissue showed little and muscle none. Gill and mantle showed partial acclimation and muscle none when acclimated to warm temperatures. When exposed to dilute seawater, gill and mantle tissues showed elevated respiration rates and muscle tissue did not change. None of the tissues exhibited any alterations in respiration rates when exposed to increased salinities. In contrast, Percy et al. (1971) found an increased respiration rate in both gill and mantle tissue when exposed to dilute salinities and no change in adductor muscle for Newfoundland oysters. Bass (1977) also showed that cold-acclimated tissues were, on average, better able to acclimate to perturbations of temperatures than warm-acclimated tissues.

The data available for $\dot{V}O_2$ in whole oysters are limited, and it is clear that the responses of individual tissues are not always applicable to whole oysters (see Shumway 1982 for review). Shumway and Koehn (1982), in the only comprehensive study to date of the combined effects of temperature and salinity on respiration in *C. virginica*, measured the acclimated and acute rates of oxygen consumption under nine temperature-salinity regimes. They presented a series of multiple regression equations relating acclimation and exposure temperature and salinity to standard $\dot{V}O_2$ measured in starved oysters. As acclimation salinity decreased, the effect of exposure temperature became more pronounced and the effect of exposure salinity decreased. As acclimation temperature increased, the effect of exposure salinity decreased and the effect of exposure temperature increased (Table 2; Fig. 15). The overall multiple regression equation is:

$$R = 0.0015 + 0.0004\ T_a - 0.0019\ S_a + 0.0178\ T_e - 0.0049\ S_e$$

where $R = \dot{V}O_2$ (ml O_2 0.4 $g^{-1}h^{-1}$); T_a and S_a = acclimation temperature and salinity; and T_e and S_e = experimental temperature and salinity. This regression is significant at $p < 0.001$ and explains almost 92% of the total variance in $\dot{V}O_2$. Interaction terms, T_eS_a and T_aS_e, are negligible. Little evidence exists for any temperature regulation, even after three weeks of acclimation.

Values of Q_{10} for warm-acclimated individuals were higher than those for cold-acclimated individuals when exposed to low experimental temperatures, the only exception being oysters acclimated at 7 ppt and exposed to 28 ppt (Shumway and Koehn 1982). At any given experimental salinity, highest Q_{10} values were observed between 20° and 30°C. The multiple regression relating Q_{10} to acclimation and exposure salinity and temperature is:

$$Q_{10} = 4.401 - 0.003S_a + 0.0674T_a - 0.1457T_r - 0.0082S_e$$

where T_r = mean of the temperature range considered; and S_a, S_e, and T_a are as before. Although the regression was significant at $p < 0.001$, it only accounts for 36% of the observed variation in Q_{10}, indicating that other factors also influence Q_{10} values (e.g., acclimation time, starvation, or phase of gametogenic cycle). Finally, Shumway and Koehn (1982) demonstrated that oysters regulated $\dot{V}O_2$ when exposed to declining oxygen tensions at all temperature-salinity combinations tested; however there was no clear pattern of response between exposure conditions and ability to regulate $\dot{V}O_2$. Generally, the degree of regulation decreased with increased temperature or decreased salinity.

Widdows et al. (1989) found that the tolerance of *C. virginica* larvae to anoxia increases with developmental stage and body size. Like juvenile and adult oysters, oyster larvae maintained rates of heat dissipation and oxygen uptake independent of PO_2 down to low critical pressures of oxygen. Further, prodissoconch larvae maintained relatively high rates of heat dissipation under anoxic conditions (34% of normoxic rate), whereas pediveliger and juveniles lowered their anoxic rates of heat dissipation to 3% of the normoxic rate.

Newell (pers. comm.) studied oysters from both a high (30 ppt) and low (10 ppt) salinity environment in Chesapeake Bay and found that those from

the high-salinity population had significantly lower clearance rates coupled with higher metabolic rates than those from the low-salinity population. There was no evidence that oysters held in 6 ppt seawater had acclimated to low salinity after a 14-d acclimation period, supporting the contention of Shumway and Koehn (1982) that the degree of regulation of respiration rate decreases with decreased salinity.

Shumway and Koehn (1982) found no evidence for capacity adaptation or acclimation in oxygen consumption of starved *C. virginica*. It is, however, undoubtedly the possession of this rather "elastic" or "euryplastic" (Alderdice 1972) physiology that allows *C. virginica* to use available oxygen over a wide range of temperature-salinity combinations and thus to sustain an energy gain from a constantly fluctuating environment.

OSMOTIC REGULATION

The effects of salinity on osmotic and ionic regulation in marine and estuarine invertebrates have been the subject of numerous reviews (see Spaargaren 1979 and references therein; Burton 1983). Most marine bivalve molluscs have little, if any, capability for extracellular osmotic regulation and *C. virginica* is no exception. It is poikilosmotic, i.e., an osmotic conformer with no ability for osmotic regulation of the extracellular fluid (hemolymph). When exposed to waters of increased or decreased salinities, the hemolymph becomes concentrated or diluted to remain in osmotic equilibrium with the surrounding seawater. This lack of extracellular regulation puts a burden on cells with regard to maintenance of cell volume compatible with cell function and maintenance of cellular constituents. Newell (pers. comm.) demonstrated that although eastern oysters are tolerant of extended exposure to low salinities, they are physiologically stressed by such conditions.

Loosanoff (1953a) found that the body fluids of *C. virginica* are isosmotic with the external medium as long as shell valves remain open. Fingerman and Fairbanks (1955a, b, 1956) reported that the species

Table 2. Multiple regression equations relating $\dot{V}O_2$ (R; ml O_2 0.4 g^{-1} h^{-1}) of *C. virginica* from Long Island Sound to acclimation (T_1, S_1) and experimental (T_2, S_2) temperatures and salinities (r = correlation coefficient). From Shumway and Koehn (1982).

Acclimation condition			
S_1 (ppt)	T_1 (°C)	Regression equation	r
28	10	$R = 0.0160 + 0.0140\,T_2 - 0.0095\,S_2$	0.950
	20	$R = 0.1050 + 0.0133\,T_2 - 0.0085\,S_2$	0.910
	30	$R = 0.0181 + 0.0202\,T_2 - 0.0107\,S_2$	0.859
14	10	$R = -0.0048 + 0.0153\,T_2 - 0.0037\,S_2$	0.965
	20	$R = -0.0902 + 0.0189\,T_2 - 0.0024\,S_2$	0.984
	30	$R = -0.0286 + 0.0210\,T_2 - 0.0074\,S_2$	0.913
7	10	$R = -0.0597 + 0.0192\,T_2 - 0.0022\,S_2$	0.994
	20	$R = -0.0779 + 0.0175\,T_2 - 0.0006\,S_2$	0.986
	30	$R = -0.1580 + 0.0211\,T_2 + 0.0001\,S_2$	0.977

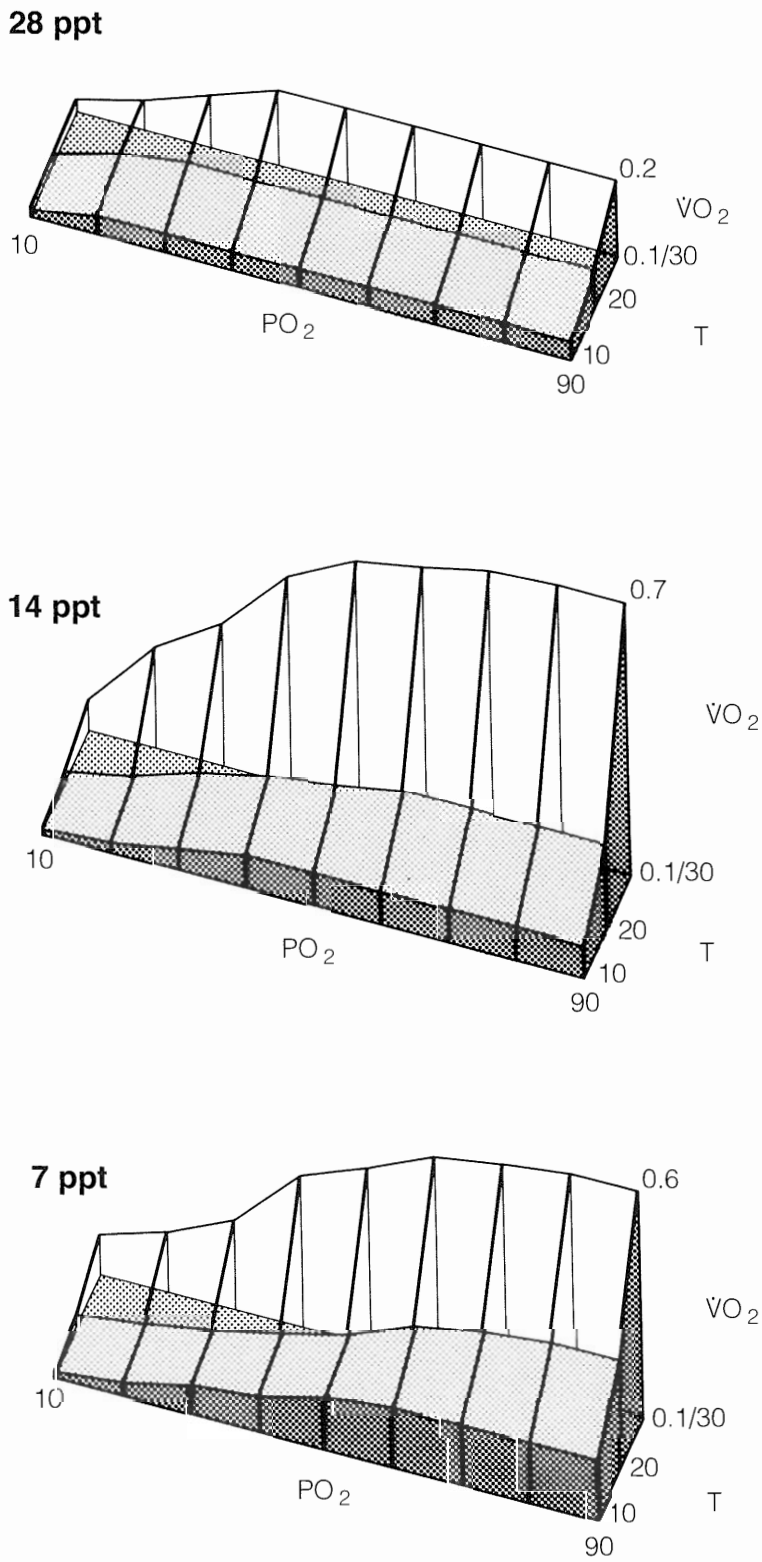


Figure 15. Graphic representation of the combined effects of temperature (T, °C), salinity (28, 14, and 7 ppt) and declining oxygen tension (PO_2) on rate of oxygen consumption $\dot{V}O_2$ (ml O_2 h^{-1}) for a standard oyster of 0.4 g dry weight. After Shumway and Koehn (1982).

has a limited ability to osmoregulate; however, this conclusion was based on hemolymph analyses taken only 4 to 8 h after transferral of oysters adapted to 17 ppt into salinities ranging from 10 to 36 ppt. Galtsoff (1964) stated that, if a salinity change of 10 ppt is maintained for several hours, it reduces the amount of time *C. virginica* remains open and pumping. He also showed that oysters attained osmotic equilibrium in about 120 h when transferred from 31 or 32 ppt to 16.7 or 17.7 ppt. It seems likely that oysters used by Fingerman and Fairbanks (1955a, b, 1956) had closed their valves in response to the salinity change and thus gave the impression of osmotic regulation. These researchers stated in their summary (1955b) that "oysters must be free to open and close their shells for weight and volume regulation. Oysters prevented from completely closing their shells lost weight both in and out of water due to secretion of body fluids." Anderson and Anderson (1974, 1975) demonstrated quite clearly that osmotic and chloride ion concentration of body fluids of the oyster conformed to those of ambient seawater over the non-lethal range of salinities (Fig. 16).

Hand and Stickle (1977) exposed *C. virginica* to simulated tidal fluctuations of salinity of 20 to 10 to 20 ppt and 15 to 10 to 15 ppt and monitored pericardial fluid osmolality and concentrations of Cl^-, Na^+, Mg^{++}, K^{++}, Ca^{++} and ninhydrin-positive substances during both short-and long-term experiments. Their results reconfirmed that oysters are osmotic conformers and that their pericardial fluid remained slightly hyperosmotic to the surrounding seawater (Fig. 17). They also demonstrated that oysters exposed to gradual fluctuations of salinity remain open and pumping for a greater percentage of time than do oysters exposed to sudden and abrupt salinity alterations. Hand and Stickle (1977) suggested that oysters close their valves to partially dampen the osmotic stress imposed when faced with continuous salinity fluctuations for prolonged periods.

In the absence of any extracellular osmotic regulation of the hemolymph, the cells must bear the burden of volume regulation. During the late 1950s and early 1960s, attention became focused on the role of intracellular free amino acids (FAAs), and their function in osmotic regulation by marine invertebrates has been studied extensively (Duchateau et al. 1952; Simpson et al. 1959; Jeuniaux et al. 1961; Bricteaux-Gregoire et al. 1962, 1964a, b). Lynch (1965) and Lynch and Wood (1966) collected eastern oysters from areas of various salinities (i.e., field acclimatized animals) and measured concentrations of 20 free amino acids and ammonia in adductor muscles (Figs. 18, 19). The total concentration of FAAs of the muscle tissue increased proportionally with increased salinity, with taurine, glycine, alanine, and proline accounting for most of the observed increases. Interestingly, concentration changes of individual free amino acids were not proportional to the salinity changes. Histidine was the only FAA that exhibited a decrease in concentration with increased salinity over a portion of the range tested. Lynch and Wood (1966) suggested that alterations in Na:K ratios associated with salinity changes could play a role in regulation of the free amino acid concentration.

Wegener (1971) used isolated mantle tissue as well as whole oysters acclimated in the laboratory to half-strength seawater (17 to 19 ppt) to study by-

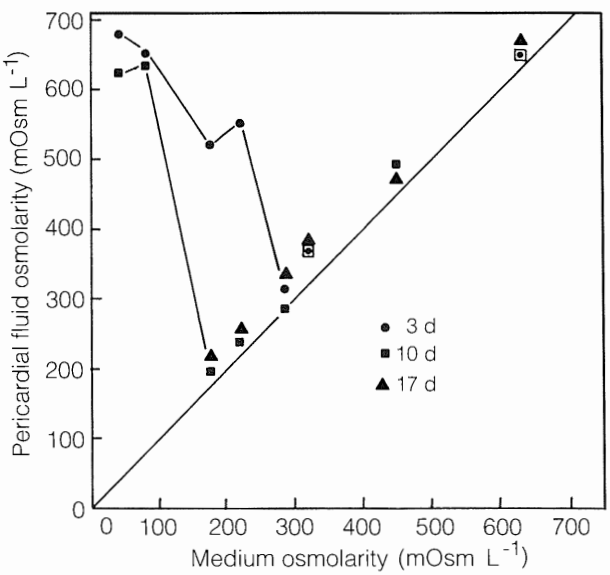


Figure 16. Relationship between osmolarity of the medium and that of oyster pericardial fluid. Each point represents the average osmolarity after 3, 10, and 17 d of three oysters transferred from 620 mOsm L^{-1} to the various media. The isosmotic line is shown. Data points are connected for convenience. After Anderson and Anderson (1975).

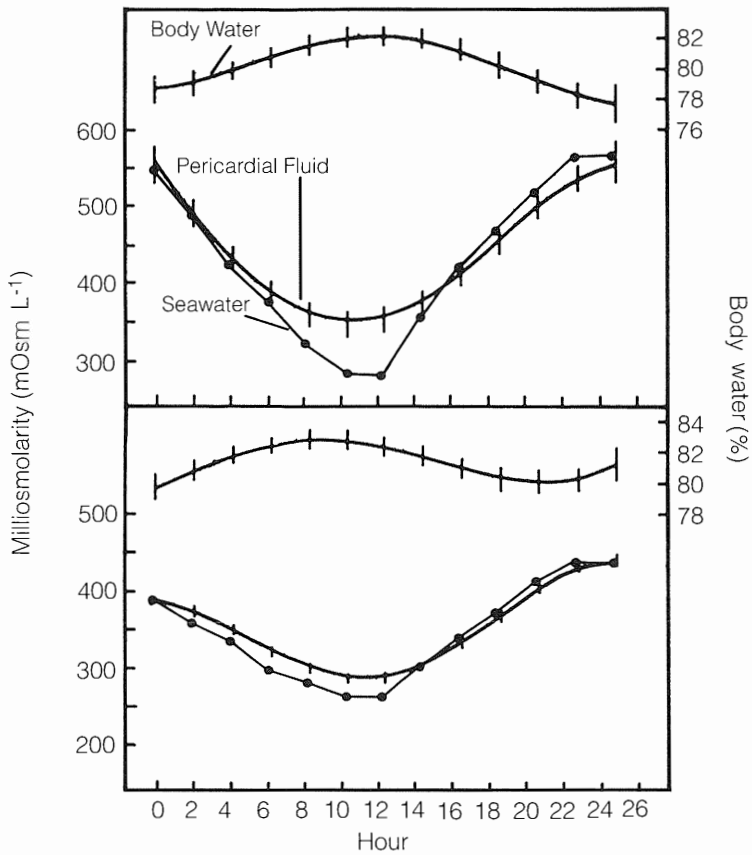


Figure 17. Curves for percent body water and pericardial fluid milliosmolality for 20-10-20 ppt (above) and 15-10-15 ppt (below) diurnal experiments. Actual seawater milliosmolality values are denoted by circles. Vertical lines represent 95% confidence intervals at each sample point along the regression lines. After Hand and Stickle (1977).

products of amino acid metabolism and the fate of both precursors and individual amino acids during salinity stress. Her values for total FAA concentrations are similar to those of Lynch (1965) and taurine was again found to be the most abundant free amino acid. Wegener (1971) found that both whole oysters and isolated gill tissue maintained a constant cell volume when exposed to reduced salinity and that measured changes in ammonia excretion rates of isolated mantle tissue indicated a shift in amino acid metabolism. Adjustments of the FAA pool were shown to be rapid, occurring within less than 3 h of exposure to reduced salinity. Conversely, FAAs were rapidly synthesized by isolated mantle in response to increased external osmotic pressure. When tissues were exposed to 17 ppt seawater, there was an immediate decrease in the incorporation of pyruvate-1-^{14}C in FAAs and a concomitant release of a portion of the FAA pool and some metabolic by-products, including FAAs, NH_3, $^{14}CO_2$, and a non-FAA fraction known to originate from alanine-U-^{14}C. The FAAs released accounted for about 30% of the net reduction in the tissue FAA pool of free amino acids in animals acclimated in 50% seawater. Powell et al. (1982) demonstrated that factors other than salinity changes, including anoxia, turbidity, and drilling effluents, can cause alterations of the FAA pool in *C. virginica*. Their results with regard to salinity induced changes are in agreement with those of the two previous studies mentioned; again, taurine was the most prominent FAA present.

Pathways of synthesis and degradation of FAAs are controlled by ionic concentration of intracellular fluid that in turn is determined by ambient salinity

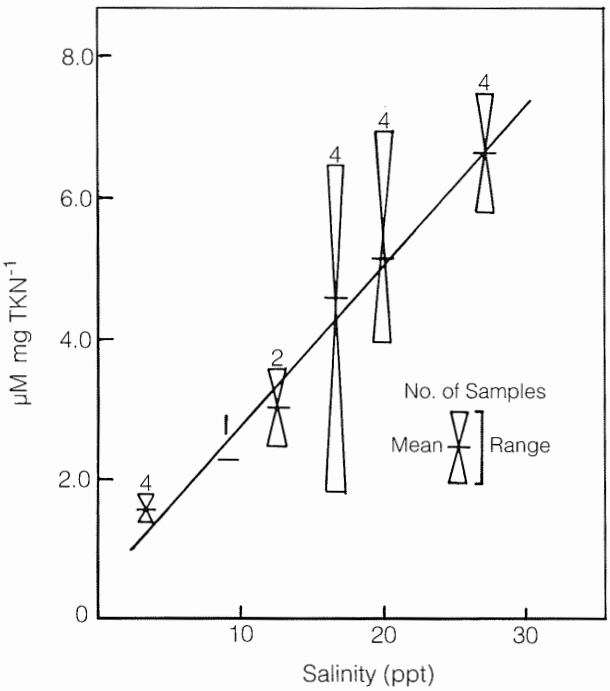


Figure 18. Mean concentration of total free amino acids in adductor muscle of *C. virginica* from various salinities. After Lynch (1965). TKN = Total Kjeldahl nitrogen.

and hemolymph concentration (Gilles 1969). Following the studies discussed above that demonstrated a relationship between salinity and concentration of free amino acids, other studies were undertaken to determine the effect(s) of salinity on enzymes implicated in amino acid metabolism. For example, Sarkissian (1974) studied citrate synthase (an enzyme reversibly inhibited *in vitro* by increasing ionic strength) in *C. virginica* and found that catalytic activity was affected by increased concentration of salt, with the apparent K_m increasing approximately six-fold, i.e., citrate synthase was slightly inhibited by salt. Sarkissian and Gomolinski (1976) demonstrated that malate dehydrogenase from the oyster was not significantly affected by changes in ionic strength of the reaction mixture.

Wickes and Morgan (1976) examined the effects of salinity on glutamate dehydrogenase (GDH), pyruvate kinase (PK), and glutamate-oxaloacetate transaminase (GOT) activity, in adductor muscle and gill tissue of eastern oysters. There was no measurable effect of salinity on PK, suggesting that it does not play a regulatory role in the build-up of FAAs in *C. virginica* during isosmotic intracellular regulation. Activity of GOT, however, increased substantially with increased ionic concentrations. Because they could not demonstrate an increase in aspartic acid with salinity in adductor muscle, Wickes and Morgan (1976) speculated that a direct pathway exists for synthesis of alanine from decarboxylation of aspartic acid, whereby aspartic acid formed from oxaloacetate could immediately undergo decarboxylation to form alanine. In turn, this process would prevent build-up of aspartate as the result of increased GOT activity and would lead to an increased concentration of alanine. This pathway for alanine synthesis remains to be demonstrated. Activity of GDH showed a high positive correlation with salinity in adductor muscle but GDH activity was absent in gill tissue.

In the only other similar study on eastern oysters, Cripps (1977) studied effects of salinity on six enzymes, including GOT, PK, MDH, glutamate dehydrogenase (GDH), lactate dehydrogenase (LDH), and phosphoenolpyruvate carboxykinase (PEPCK) in gill, adductor muscle, and mantle tissue. His results were in general agreement with Wickes and Morgan (1976) and he pointed out that responses of individual tissues were variable for acute salinity stress.

In other related studies, Feng et al. (1970) reported seasonal variations in hemolymph FAAs as well as a shift in the FAA pool in eastern oysters induced by parasitic infestations of *Bucephalus* sp. and *Haplosporidium* (=*Minchinia) nelsoni*. These alterations could conceivably interfere with osmoregulatory capabilities of infected oysters under some conditions. Prusch and Hall (1978) calculated diffusional water permeabilities (P_d) for eight different marine bivalve species and found that *C. virginica* had one of the lowest P_d values of any species studied, $3.01 \pm 0.28 \times 10^{-5}$ cm s^{-1}. This low permeability to water movement undoubtedly aids the ability of *C. virginica* to resist desiccation in high intertidal areas.

The role of amino acids in intracellular osmotic regulation is complicated, and there are obviously numerous mechanisms operating simultaneously. Data reported for *C. virginica* are similar to, although not in total agreement with, data reported for other bivalves with regard to their osmotic regulation and amino acid pools (Lange 1963, 1972; Shumway et

al. 1977; Shumway and Youngson 1979). The ability of eastern oysters to cope with a wide amplitude of salinity variation at the cellular level represents but one more means by which they have successfully invaded estuaries.

GENETIC ADAPTATIONS TO ENVIRONMENTAL STRESSORS

The existence of physiological races that are geographically separated has been demonstrated quite

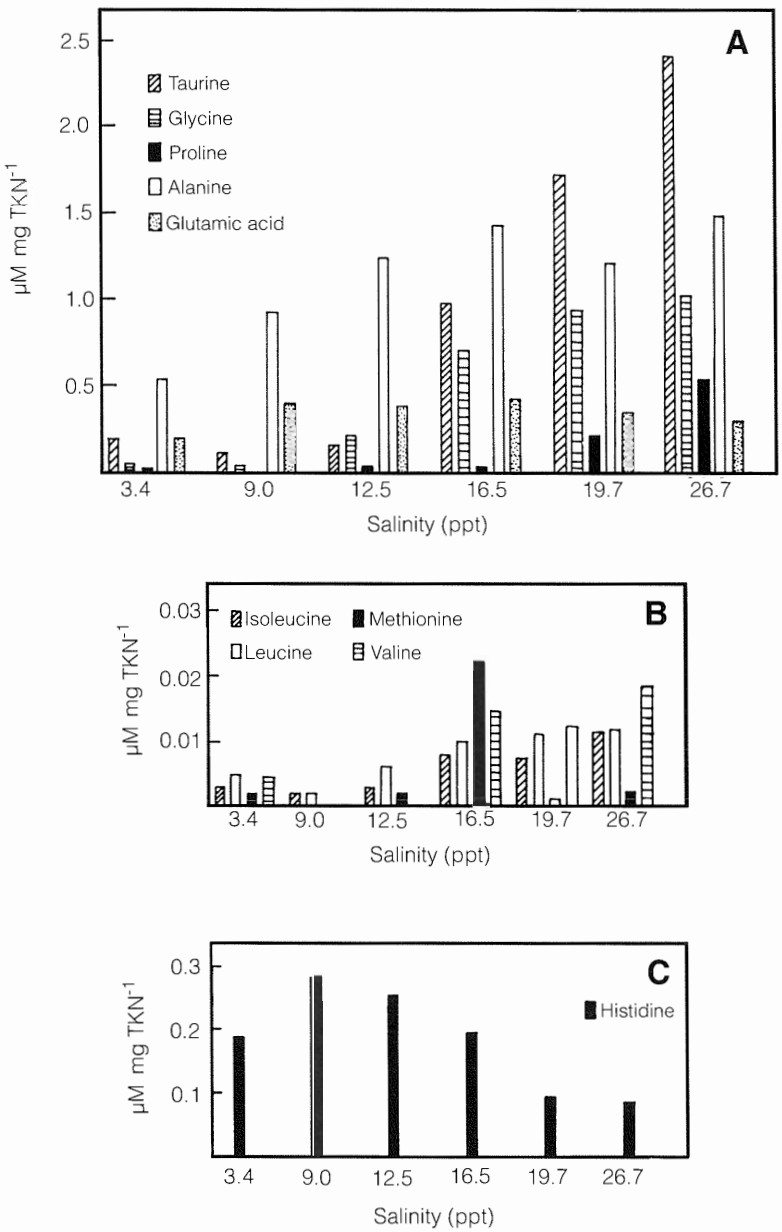


Figure 19. Mean concentrations (µM mg TKN^{-1}) of (A) taurine, glycine, proline, alanine, and glutamic acid; of (B) isoleucine, leucine, methionine, valine; and of (C) histidine in adductor muscle of *C. virginica* from various salinities. TKN [Total Kjeldahl nitrogen]. After Lynch (1965).

clearly, and differences can exist between populations located in close geographic proximity. Longwell (quoted in Loosanoff 1969) stated that "there is sufficient justification for the interesting speculation that genetic differences play a role in the differences in gametogenic activities of South Carolina oysters exposed to the same temperatures that failed to elicit a response from the other southern groups studied." Unfortunately, the prospect is still speculative. Newell and co-workers (pers. comm.) found significant differences in attributes such as scope for growth, feeding rate, and oxygen consumption between oyster populations from high and low-salinity areas; however, they were unable to demonstrate any difference between the two populations through electrophoretic analyses of nine enzyme loci. The question remains as to whether or not separated populations of oysters exhibiting different tolerances to various environmental factors represent merely physiological races or are in fact genetically separate units.

Newkirk et al. (1977) showed that two populations of *C. virginica* exhibited genetic differences in regard to tolerance of reduced salinities and that some of the genetic variation was non-additive. In a more complete study, Newkirk (1978) used oysters from four populations and found evidence of overdominance in survival in one of their hybrids, although there were no significant differences in survival among the populations. Salinity also affected the expression of differences in growth rate demonstrated among populations. Non-additive genetic effects in the hybrid crosses were also seen, but direction and magnitude were dependent upon salinity. Expression of survival differences seen between populations was dependent on the environment in which larvae were reared and whether larvae were from a pure or a hybrid cross. Interestingly, there was as much difference in survival between populations from the same estuary as there was between populations from geographically isolated populations. Even though Newkirk (1978) was able to demonstrate evidence for genotype-environment interaction on growth rate, the presence of non-additive effects interacting with the environment precluded assigning these survival differences either to adaptation to particular environments or isolation of the populations.

Koehn and Shumway (1982) showed that more heterozygous individuals of *C. virginica* were at an energetic advantage compared to their homozygous siblings when exposed to temperature or salinity stress. They found that the metabolic energy demand of high temperature and low-salinity was over twice as great for multiple locus homozygous individuals as for the most heterozygous individuals, and concluded that homeostasis represents a magnification of inherent genetic differences between individuals.

PARASITES, PREDATORS, AND DISEASES

Although salinity per se can affect distribution of oysters, the indirect role of salinity on the incidence of parasites, predators, and diseases can also control the distribution of eastern oysters. The estuarine habitat and associated freshwater influxes can have lethal effects on stenohaline carnivorous gastropods, starfish, and other pestilential taxa. It has been noted that high temperature and salinity combinations generally tend to increase the threat of disease and predation. For further discussion of effects of diseases of and predation on eastern oysters, see Ford and Tripp, Chapter 17 and White and Wilson, Chapter 16, respectively.

One of the most severe diseases of oysters (Dermo) is caused by the protistan parasite *Perkinsus marinus*, and is most prevalent in oysters exposed to conditions of high temperature and salinity (Mackin et al. 1950; Mackin 1951, 1956, 1961; Hewatt and Andrews 1956; Andrews and Hewatt 1957; Quick 1971; Quick and Mackin 1971; Ogle and Flurry 1980). The infectious agent was first erroneously described as a fungal disease by Mackin et al. (1950) and initially named *Dermocystidium marinum* (later changed to *Labyrinthomyxa marina*, Levine 1958; see Mackin and Ray 1966). The relationship between this parasite and high temperature and salinity conditions was quickly established (Mackin 1951), as was the incidence of high mortalities of infected oysters during warm summer months (Mackin 1953; Hewatt and Andrews 1954). Ray and Chandler (1955) established that temperatures above 20°C favored development of the disease in the Gulf of Mexico.

In a later study, Mackin (1956) more clearly defined the effects of salinity on Dermo. He demonstrated conclusively that low temperature-salinity combinations retarded parasite development and concluded that oysters can exist and grow vigorously in salinities slightly lower than the minimum tolerated by Dermo. He hastened to point out, however, that the margin of tolerance is so narrow that, for practical purposes, it does not exist. He summarized his results and others as follows: in the estuary there is generally a positive correlation of high salinity with high incidence and weighted incidence of the disease, although infection by *P. marinus* is reduced at low salinity. The salinity tolerance range of the parasite is wide, in some instances varying from 8 to 50 ppt. From laboratory experiments, he concluded, that, while there can be a retarding effect of low salinity per se, the disease may nevertheless develop in oysters at these low salinities and there is probably no physiological handicap for *P. marinus* produced by low salinities. He suggested that dilution of infective particles by freshwater inflow, coupled with the preponderance of ebb over flood current rates, tended to eliminate infective cells in low-salinity areas and to concentrate them in high-salinity areas.

Hewatt and Andrews (1956) found that oysters infected by *P. marinus* all died within about four weeks at 28°C. When infected oysters were held at 15°C, infection was arrested and mortalities caused by the disease were negligible. Hewatt and Andrews (1956) also suggested that oysters taken from an endemic area were less susceptible to infection by Dermo than were oysters collected from nonendemic waters. Andrews (1965) later showed that temperatures above 25°C were necessary to cause high mortalities, and that *P. marinus* growth is dependent on warm seasons.

Soniat (1985) studied the quantitative relationship between intensity of infection by *P. marinus* and the interaction of water temperature and salinity in Galveston Bay. Although the temperature-salinity interaction explained more variability in weighted incidence of *P. marinus* than either temperature or salinity alone, most variability was still unexplained. Soniat (1985) suggested that this variability was probably the result of individual differences in resistance to infection.

Other diseases known to show chronic infections only at high salinities are *Haplosporidium costalis* (SSO) and *Haplosporidium nelsoni* (MSX), with the latter tolerating a wide range of temperatures and posing a serious and increasing threat to oyster populations (Andrews 1967, 1988; Andrews and Ray 1988). Newell (1985) demonstrated a marked reduction in clearance rate and condition index of *C. virginica* with systemic infections of MSX. He also noted that there were no differences in the rate of oxygen consumption between infected and uninfected oysters. Decreased feeding rates coupled with sustained metabolic rates lead to a decreased condition index and imparts a severe physiological stress on oysters (Newell 1985). Barber et al. (1988a, b) demonstrated that condition index and fecundity in *C. virginica* are a function of the infection intensity of MSX. Uninfected individuals have higher values than epithelially infected individuals, which in turn have higher values than systemically infected individuals. The condition indexes of oysters with gill infections of MSX and systemic infections were 13% and 31% lower than uninfected oysters, respectively. Fecundity was reduced in oysters with gill infections (35% reduction) and systemic infections (81% reduction) and Barber et al. (1988a, b) concluded that reduced fecundity is most likely the result of metabolic stress whereby MSX reduces food intake and competes for energy reserves. These authors also demonstrated that all biochemical components (lipid, glycogen, protein) generally decreased in concentration with increasing MSX infection, intensity, and duration. Thus, even at sublethal levels, meat yield and recruitment potential of *C. virginica* are reduced by the presence of MSX.

Fisher and Newell (1986) provided a possible explanation for the marked seasonal trends in infection by diseases such as Dermo, SSO, and MSX. They suggested that high salinity reduces the oysters' defense capacity, leaving them more susceptible to pathogenic parasites. Fisher and Newell (1986) studied effects of salinity on granular hemocytes in *C. virginica* from Chesapeake Bay. These oyster hemolymph cells are responsible for most phagocytic activity that provides the primary line of defense against foreign particles. Fisher and Newell (1986) demonstrated that increases in acute salinity retarded activity of hemocytes and that decreases in acute salinity

enhanced hemocytic activities. They speculated that differences in hemocyte activities found between high and low-salinity areas could provide oysters with greater disease resistance, i.e., oysters that are able to maintain maximal hemocytic activity can be at an advantage when faced with possible infection. This topic has been treated in greater detail by Cheng in Chapter 8.

In addition to parasites and diseases, many oyster predators are also limited to more saline waters (Grave 1905; Butler 1954; Wells 1961; Maurer and Watling 1973). Indeed, Gunter (1955) proposed that one advantage conferred to eastern oysters living in less saline estuarine water was reduced predation and competition. Probably the most completely studied of these predators are the drills, *Thais haemastoma*, *Thais lapillus*, *Urosalpinx cinerea*, and *Eupleura caudata*. These species constitute one of the largest groups of predators on oysters and as such their tolerance and functional capabilities have been studied by numerous authors (see Carriker 1955; Hanks 1957; Manzi 1970; Zachary and Haven 1973; Bayne and Scullard 1978).

Manzi (1970) exposed drills (*Eupleura caudata* and *Urosalpinx cinerea*) to 12 salinity-temperature combinations, and showed that feeding rates on oyster spat increased with each increase in salinity and temperature. Maximum rates were measured at the highest salinity (26.5 ppt) and temperature (25°C) tested; little or no feeding was seen at 12.5 ppt. Manzi (1970) concluded that this salinity is near the lower limit for feeding. He further showed that at all temperature and salinity combinations studied, *U. cinerea* consumed more oyster spat than did *E. caudata*.

Garton and Stickle (1980) found that both predation and ingestion rates of *T. haemastoma* feeding on eastern oysters are sensitive to temperature and salinity, and that the temperature threshold for predation is between 10 and 12.5°C; no feeding occurs below 7.5 ppt. Garton and Stickle (1980) also exposed drills to diurnal tidal fluctuations of salinity, more closely representing the estuarine environment than did previous studies, and demonstrated that drills had predation rates significantly lower than those at the optimal constant salinity of 20 ppt at 30°C; however, there were no significant differences among salinities at 20°C. Predation and ingestion rates in fluctuating salinity cycles were not significantly different from rates for drills at constant acclimation salinities of 10 and 30 ppt. Garton and Stickle (1980) were able to show that *T. haemastoma* can tolerate changes in its physiology that accompany changes in environmental temperature and salinity and are able to function as an efficient oyster predator under these conditions.

Various other oyster predators are also known to be limited in their distribution by salinity. The starfish, *Asterias forbesi*, has a lower salinity threshold of about 16 to 18 ppt (Loosanoff 1945b; Wells 1961) as does the whelk, *Fasciolaria hunteria* (Wells 1961). In Virginia, Hopkins (1962) reported on the distribution of species of the boring sponge, *Cliona* spp., on the eastern shore of Virginia in relation to salinity. He found that *Cliona celata* was most abundant in high-salinity bays and the least abundant in lower salinity, whereas *Cliona truitti* was the most abundant species in low salinity areas and became increasingly prominent as salinity decreased (see also Old 1941). The flatworm, *Stylochus ellipticus*, is also a predator of oysters (Loosanoff 1956) that is tolerant of low salinities.

Various species of crabs also pose a threat to oysters. The commensal pea crab, *Pinnotheres* sp., frequently occurs in oysters in high-salinity water on the Atlantic coast but is uncommon in Gulf waters (Butler 1954). MacKenzie (1970) showed that mud crabs (family Xanthidae) prey on oyster spat and Little and Quick (1976) reported that prolonged periods of high salinity (greater than 25 ppt) foster proliferation of xanthid crabs, among other species. The stone crab *Menippe mercenaria* preys on eastern oysters but is not tolerant of low salinities and is eliminated by freshwater intrusion (Menzel et al. 1966). Menzel et al. (1966) also reported that the blue crab, *Callinectes sapidus,* becomes a more serious predator when large oysters are weakened by high temperatures.

Finally, the sea anemone, *Diadumene leucolena,* is a predator of oyster larvae in the Chesapeake Bay region (MacKenzie 1977; Steinberg and Kennedy 1979). Clearly, the fact that oysters can tolerate lower salinities than those that inhibit predators has aided in the proliferation of oysters in the upper reaches of estuarine systems.

LIGHT, pH, AND TURBIDITY

Orton (1929) first suggested that oysters do not feed during late night or early morning hours. Loosanoff and Nomejko (1946) studied the possible effects of tidal stage and periods of light and darkness on the feeding activity of about 1,400 *C. virginica.* In darkness, the percentage of oysters with full stomachs was comparable to that of the individuals examined in daylight, the oysters fed actively, and the average rate of pumping was comparable to that by day. Shell valves remained open 94% of the time during daylight and darkness and the oysters were feeding all or most of the time when their shells remained open. Thus, no experimental evidence exists to support the early theory that oysters feed only by day, and it is now generally accepted that light has no discernable effect on their feeding activity.

Light has, however, been shown to affect other aspects of oyster biology. Medcof and Kerswill (1965) reported that shading increases linear shell growth of oysters about 150% but reduces the ratio of thickness to length. Further, exposure to light increases plumpness of meats, specific gravity of the body tissue, and shell fluting and pigmentation. These results are in agreement with those reported previously by Medcof (1949). No physiological mechanisms were suggested for these differences.

Medcof (1955) indicated that light favors setting of *C. virginica* larvae. Ritchie and Menzel (1969) and Shaw et al. (1970), however, demonstrated that eyed larvae of *C. virginica* are light sensitive and that larval setting is encouraged by darkness and partially inhibited by light (Fig. 20). Larval behavior is covered in greater detail by Kennedy in Chapter 10.

Early data on the effects of pH on the biology of *C. virginica* are anecdotal. Based on a few field observations, Prytherch (1928) suggested that spawning is inhibited by low pH. Loosanoff and Tommers (1948) demonstrated that pH affects pumping rate such that oysters kept in waters of pH 4.25 pump only 10% as much water as control animals at 7.75 pH, even though the oysters remain open about 75% of the time. Calabrese and Davis (1966, 1969, 1970) demonstrated that the minimum and maximum pH levels at which the oyster will spawn are 6.0 and 10.0, respectively. Moreover, they found that oyster eggs and sperm released outside the range of pH 6.0 to 10.0 lose their viability rapidly within 2 to 4 h, with the lowered viability due to a combination of pH and aging (Fig. 21). The pH range for normal embryonic development is 6.75 to 8.75, with a lower pH limit of 6.00 for larval survival. Normal growth was found over the pH range of 6.75 to 8.75 and growth rate decreased rapidly at pH levels below 6.75. Optimum pH for growth of oyster larvae is 8.25 to 8.5.

The effect of varying quantities of suspended material (seston) on the biology of *C. virginica* has been a matter of discussion for many years, yet seston remains one of the least studied environmental variables. Suspended materials may be natural (floods, storms) or anthropogenic (dredging) in origin. Opinions of researchers have ranged from the claim that oysters feed only in clear waters (Kellogg 1915,

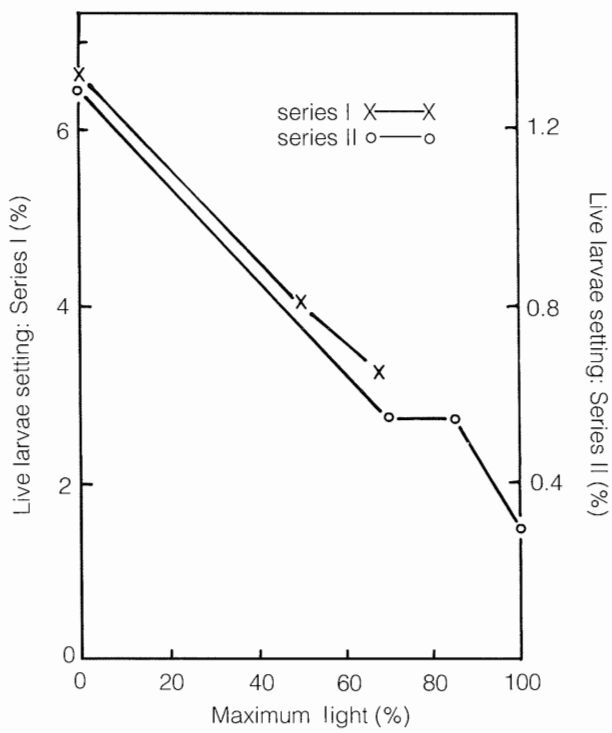


Figure 20. Effects of light on numbers of oyster larvae setting. Total spat setting over 3 to 4 d expressed as percent of living larvae present, plotted against the proportion (%) of each 24 h period during which tanks were illuminated. After Shaw et al. (1970).

1916) to that of oysters being unaffected by highly turbid waters (Grave 1916), and have provided the basis for several debates in the early literature. Nelson (1921c) demonstrated that oysters fed in waters of high levels of seston (up to 0.4 g dry weight L^{-1}). Loosanoff and Engle (1947a) presented evidence indicating that Kellogg (1915, 1916), Grave (1916), and Nelson (1921c, 1951) were all partially correct in their conclusions. They supported Kellogg's (1915, 1916) contentions that oysters feed most efficiently in clear waters; however, they also found that oysters can feed in water containing relatively large numbers of microorganisms, although under such conditions the rate of feeding is decreased. If the concentration of planktonic organisms is too great, feeding ceases. A more detailed account (Loosanoff and Engle 1947b) provided data on the effects of high concentrations of microorganisms on feeding and pumping by *C. virginica*. The changes in feeding activity of oysters in response to increases in seston concentration are discussed by Newell and Langdon in Chapter 5.

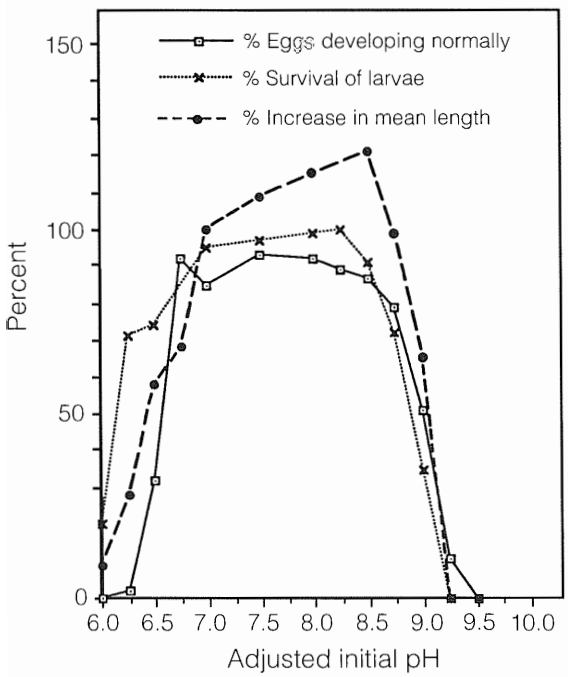


Figure 21. The pH tolerance of oyster embryos and larvae as indicated by percentage of eggs that developed normally, survival of larvae, and increase in mean length. After Calabrese and Davis (1966).

The effects of turbidity (silt or seston concentration) on the activity patterns of oysters has been the focus of several studies, especially in relation to dredging activities. Increased concentrations of suspended materials can induce a reduction in pumping rate, a clogging of the gill apparatus, a subsequent reduction in growth rate, and death. As pointed out by Stern and Stickle (1978), although the effects of turbidity and suspended material may not necessarily be lethal, quite often the associated sedimentation may smother and kill both juvenile and adult oysters.

Lunz (1938) performed a field study during the dredging of the Intracoastal Waterway of South Carolina. Unless adult oysters were completely buried, their mortality near the dredging activity was no higher than in areas remote from the dredging operations and there was no evidence of changes in the physiological condition of the oysters. The intensity of setting of oysters adjacent to the dredging operations did not differ from setting intensity in areas remote from such activities. Lunz (1938) concluded that dredging apparently had no effect on spawning and setting success. Much subsequent work has found deleteriuous effects of siltation on cultch cleanliness. Even a thin layer of silt reduces spat settlement as reviewed by Mackenzie in Chapter 21.

Loosanoff (1948) and Loosanoff and Tommers (1948) demonstrated that concentrations of silt (0.1 g L^{-1}; note that this is over four times the maximum levels commonly observed in estuarine waters) caused a 57% reduction in pumping rate of adult oysters in Long Island Sound. The reduction in the average pumping rate was more than 80% at 1 gL^{-1} and 94% in concentrations of 3 and 4 g L^{-1}. Similar results were shown for kaolin and chalk. Fuller's earth at a concentration of 0.5 g L^{-1} reduced the rate of pumping by 60% (Fig. 22). Although the efficiency of feeding was greatly reduced, the oysters could ingest small quantities of particles in very turbid waters. This finding supports the earlier statement of Nelson (1921b) that oysters could feed in turbid waters.

Loosanoff and Tommers (1948) also demonstrated that the shell movements of oysters in turbid waters were greater in amplitude and of a different type than those under normal conditions. Movements in

turbid waters were usually associated with the expulsion of large amounts of pseudofeces. Loosanoff and Tomers (1948) speculated on the possibility of physiological races of oysters with varying degrees of tolerance to turbidity. These findings were confirmed by the work of Hsiao (1950) who reported that the more turbid the water, the more irregular the respiratory and feeding movements of the shells of *C. virginica*. A reduction in the turbidity was followed immediately by increased shell movement. Hsiao (1950) also showed that in very turbid seawater, where the silt was allowed to settle on the oysters, there was an immediate cessation of shell movement for 16 to 19 h. The animals subsequently attempted to reopen their shells in an effort to remove the silt. If the silt deposits remained for more than 3 d, death resulted.

Engle (1958) found no detrimental effects of suspended silt on eastern oysters hung in baskets adjacent to dredging activities in Chesapeake Bay. He suggested that dredging might provide an increased supply of organic detritus that would in turn increase the condition of the oysters. McKinney and Case (1973) reported similar results for oysters suspended in experimental cages in San Antonio Bay, Texas, although populations on the bottom were killed by the accumulation of dredged particles. Mackin (1956, 1962) and Mackin and Hopkins (1961) found that turbidities up to 0.7 g L^{-1} were not harmful to eastern oysters and that it was apparently impossible to maintain a suspension of high concentration long enough to cause mortality of oysters. They did report an inverse relationship between turbidity and mortality of oysters; however, these differences in mortality rates were probably more a function of salinity than turbidity (see also Butler and Engle 1950; Gunter 1953; Cory and Redding 1976). Mackin (1956) also stated that high turbidities neither enhance nor depress the effect of Dermo disease.

The most detailed studies on the effects of turbidity on pumping and shell valve activity in eastern oysters is that of Loosanoff (1962). He demonstrated that 0.1 g L^{-1} of silt can noticeably affect the behavior of adult oysters. The average reduction in rate of pumping was 57%; however, occasionally the oysters appeared to be stimulated and pumped faster. In silt and kaolin concentrations ranging from 0.1 to 4 g L^{-1}, rate of change in pumping ranged from −100 to +18%, with average reductions ranging from 57 to 94% for silt and from 46 to 85% for kaolin. Over a similar range of concentrations of chalk, the rates of change ranged from −12 to −94%, with average reductions of 38 to 89%. At 0.5 g L^{-1}, Fuller's earth reduced pumping by an average of 60%.

In addition to the reductions in pumping rates, the oysters formed and discharged large quantities of pseudofeces containing silt and increased their shell-valve activity, presumably in association with the rapid expulsion of the pseudofeces. In heavy concentrations of silt, oysters closed their shells entirely for extended periods of time, sometimes remaining closed for a pe-

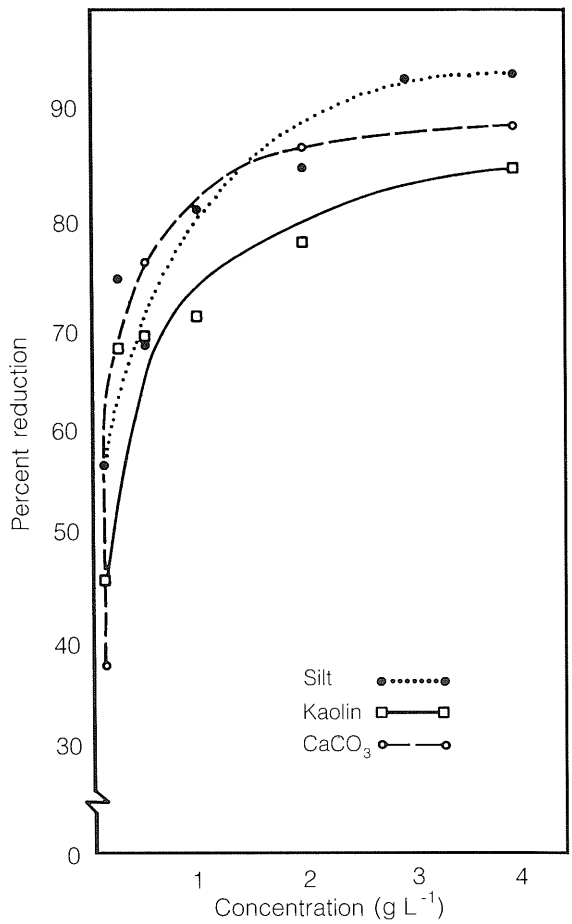


Figure 22. Percent reduction in pumping rate of eastern oysters subjected to different concentrations of turbidity-creating substances. After Loosanoff (1948).

riod of several weeks. Loosanoff (1962) concluded that oysters "feed most efficiently in relatively clear water."

Of equal or greater importance than the effects of seston on adult oysters is its effect(s) on eggs and larval stages. Davis (cited in Loosanoff, 1962) and Davis and Hidu (1969) showed clearly that silt was harmful to oyster eggs. Egg mortality was 27% at concentrations of 0.25 g L^{-1} of silt and 69% at 0.5 g L^{-1}. Silt was more harmful to oyster eggs than either kaolin or Fuller's earth. Oyster larvae could withstand highly turbid water (2 g L^{-1} silt and up to 4 g L^{-1} of either kaolin or Fuller's earth) for up to 14 d.

Carriker (1986) has recently reviewed the available literature concerning the effects of silt on planktonic stages of *C. virginica* ranging from eggs and spermatozoa to pediveligers. His review demonstrates the paucity of information on this topic. He suggests that the free swimming trochophore and veliger stages may be particularly vulnerable to the presence of silt that could clog the highly sensitive feeding apparatus. He also points out that there are undefined, yet beneficial, concentrations of silt for embryos (below 0.25 g L^{-1}) and for veligers (0.75 g L^{-1}), but that the optimum range of particle concentrations for the differing stages of development has not been determined. Clearly, the effects of silt and turbidity on oyster larvae require further research.

SUMMARY

In conclusion, a fundamental requirement of the eastern oyster is the mixture of salt water with fresh water from land drainage (Butler 1954). In light of their sessile nature, oysters are particularly susceptible to environmental perturbations and yet they thrive in the often harsh and constantly fluctuating environs of the estuary. Through an array of physiological and behavioral mechanisms, oysters are highly tolerant of different habitats and environmental variations. It is the possession of a rather plastic physiology, acquired through geologic ages of adaptation, that has allowed the eastern oyster to tolerate estuarine conditions and flourish under such unpredictable conditions and to establish itself as one of the true estuarine species.

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