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THE REPRODUCTIVE CYCLE OF EARLY SETTING *CRASSOSTREA VIRGINICA* (GMELIN) IN THE NORTHERN GULF OF MEXICO, AND ITS IMPLICATIONS FOR POPULATION RECRUITMENT

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Abstract

Oysters which set early in the spawning season reach sexual maturity and spawn before the end of their first year. The early sexual development in the southern latitudes is the result of both an extended growing season and an increased instantaneous rate of growth. Widespread spawning of oysters older than one year occurs twice during the reproductive season, with a period of renewed development in between. Spawning by young-of-the-year oysters is of minimal importance to population recruitment during the year they set.

Introduction

Numerous studies have been conducted to determine the annual reproductive cycle of *Crassostrea virginica* at various locations throughout its range. The majority of these studies were conducted along the northern Atlantic coast and clearly demonstrate that in the northern latitudes only one generation of oysters is produced annually. In contrast, several authors (Burkenroad, 1931; Coe, 1938; Menzel, 1951; Butler, 1954) have suggested the possibility of multiple generations within each year in this species' southern range.

The present paper reports on field studies conducted to describe the reproductive cycle and breeding patterns of *C. virginica* in southern latitudes. Of particular interest was when spawning occurred in oysters which had set early in the breeding season.

Materials and Methods

Sampling sites

In April 1978 two sampling stations were established in the northeastern Gulf of Mexico. One site, Turkey Point, was near the mouth of a small stream and the other, Alligator Harbor, in a neutral estuary. Temperature and salinity were measured at each station before sampling.

Sampling the established oyster populations

Each station had a fairly discrete, well established oyster population along the vertical walls of private boat docks. These oysters were sampled to monitor the gonad condition of the established populations and were the progenitors for establishing the young-of-the-year populations.

At first, we sampled the established populations at each station weekly. Later, when the young population was established, sampling was approximately biweekly.

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On each sampling date groups of attached oysters were obtained from a randomly selected area.

Samples were returned to the laboratory on ice and stored at 4°C until processed.

Sampling the young-of-the-year populations

As cultch material holders, we built wooden racks, each holding a maximum of 30 asbestos shingles (hereafter panels; each 30 cm × 60 cm) 5 cm apart. Grooves cut in the racks allowed removal and addition of panels. To minimize predation, the racks were held off the bottom.

A full rack was positioned near the established oyster population at each station on 20 May 1978. This was the first time the water temperature exceeded 25°C at both sites and corresponds to the expected time of the spring mass spawning (Hopkins, 1931; Ingle, 1951; Menzel, 1955). After 1 week under water, each panel had received an abundant fall of spat. This served as the young-of-the-year populations for the remainder of the study. Alternate panels were removed from these racks on 26 September to provide unrestricted space for further growth.

Sampling young populations began after the spat had reached about 20 mm in shell height because sizes smaller than 20 mm were impossible to process reliably. We know of no practical method to determine exactly which spat settled first, so we used the traditional method of selecting the largest specimens as the oldest (those in the initial set) (Ingle and Dawson, 1952; Menzel, 1955).

After the spat were large enough for sampling, collections were approximately biweekly, by removing the panel furthest from the dock. The panel, with oysters attached, was brought to the laboratory on ice and stored at 4°C until processed.

Sample processing

Within 72 h of sampling, we arbitrarily selected from the established populations 25 oysters larger than the largest specimen from the young population, to insure that only oysters from previous years' setting would be sampled. Each of these oysters was separated, measured (sensu Galtsoff, 1964), shucked, weighed, and fixed whole in Bouin's fixative.

The largest 25 specimens on each panel were individually labeled and maintained separately throughout the laboratory procedure outlined above.

After at least 72 h in Bouin's fixative, a 5–10 mm section was removed from mid-way between the anterior end of the oyster and the anterior side of the adductor muscle perpendicular to the anterior-posterior body axis. Standard histological preparations were made, following Humason (1967).

Slide analysis

We used the quantitative method for evaluating the gonadal condition of oysters described by Tinsman *et al.* (1976), with slight modifications. After determining the percent gonad and gonad density for each specimen, a follicle index was calculated by multiplying these measurements together. This index measures the area devoted to germinal tissue in each oyster cross section, which in turn measures the oyster's gonadal development (Tinsman *et al.*, 1976).

Each specimen also was examined with a light microscope (250×) to assign it to a particular stage of development by the more traditional procedure (Loosanoff and Engle, 1942).

Determination of setting patterns

A second cultch-holding rack was constructed for each station and positioned adjacent to the rack for holding the developing spat. Each week a clean panel was inserted into the rack to provide fresh setting material, and the panel exposed during the previous week was removed and examined to determine the density of spat attachment. Random coordinates were used to place a 7 cm × 7 cm transparent plastic grid on the panel. A stereoscope (10×) with an extendible arm was used to determine the number of spat in four areas on each side of the panel.

Statistical analysis

A distribution-free multiple comparison test based on Kruskal-Wallis rank sums was used to determine significant differences between the mean follicle indexes within each population (Hollander and Wolfe, 1973).

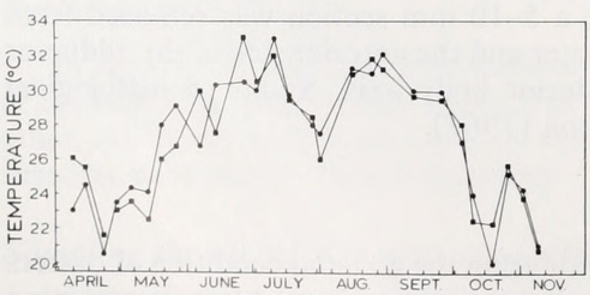
RESULTS

Temperature

Figure 1 shows water temperature patterns at the Turkey Point and Alligator Harbor sites. The seasonal temperature changes at both stations were similar, with the largest difference on any sampling date about 3°C. Between 20 May and 5 October the temperature remained above 25°C. The temperature drop of about 6°C at both stations in July is attributed to increased storms and rainfall. A low of 20°C and a high of 33°C were recorded during the experiment.

Salinity

Due to the nature of the locations, salinity fluctuated more at Turkey Point than at Alligator Harbor. On every sampling date except one (29 July), the salinity at Turkey Point was lower than that at Alligator Harbor. Both stations experienced slightly higher salinity from September to November. The salinity varied from 15.0 to 32.3‰ at Turkey Point and from 27.0 to 33.7‰ at Alligator Harbor.



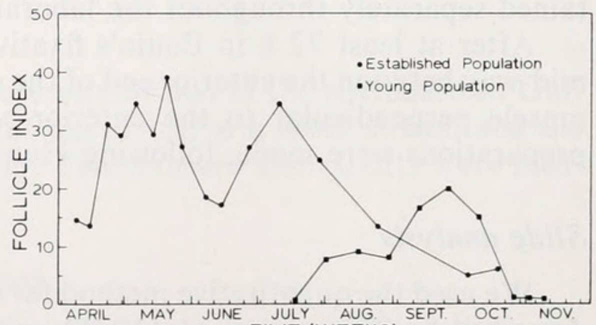


FIGURE 1. (Left.) Surface water temperature at each station for all sampling dates. Measurements were made with a stick thermometer read to the nearest 0.1°C. Circles = Turkey Point, squares = Alligator Harbor.

FIGURE 2. (Right.) Gonadal condition of the established and young populations at Turkey Point. Each point is the median follicle index of the 25 specimens for that date (except the mid-July young population point, which is the median of 15 specimens). The median gave the best representation of the central tendency of the data due to skewed distributions.

Growth

Growth of the young populations was initially faster at Alligator Harbor than at Turkey Point. However, little growth was observed at the former from mid-August through September, resulting in a smaller average size at Alligator Harbor by the end of the experiment (9 November). Turkey Point had an initially slower, but overall a more steady rate of growth.

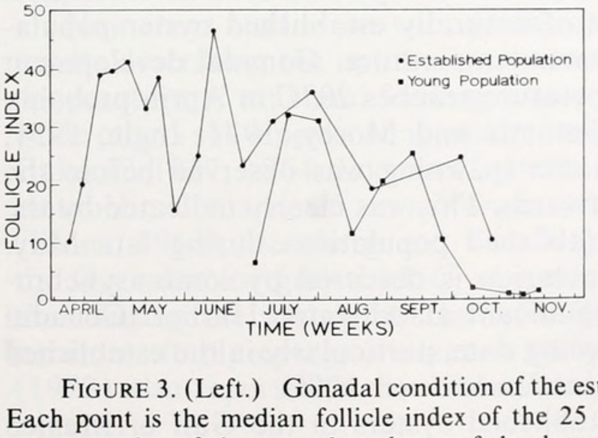
If setting is assumed to have occurred on the first day the cultch material was set out (20 May), an average growth rate of 0.79 mm/day at Alligator Harbor and 0.45 mm/day at Turkey Point was recorded for the 25 fastest growing individuals from setting until the initial sampling (3 and 18 July, respectively). By the end of the experiment, the average size of the 25 largest individuals from the young population at Alligator Harbor was 65.9 mm, a daily growth rate of 0.38 mm. At Turkey Point the average shell length of the 25 largest individuals at the end of the study was 84.1 mm, a growth of 0.47 mm/day.

The fastest growing oyster early in the study was one in Alligator Harbor, which reached 43 mm in the 44 days from when setting could have first occurred, a growth rate of 0.98 mm/day. Toward the end of the study one Turkey Point specimen had reached 105.0 mm in 166 days. This represents a growth rate of 0.63 mm/day.

Follicle index

The follicle index data, which measure gonadal development, are presented in graphic form in Figure 2 (Turkey Point) and Figure 3 (Alligator Harbor). The established populations at both stations followed similar trends over the study period, rising during April and early May, declining in late May and early June, recovering again until mid- to late July, and finally declining until the project ended in November. The large, statistically significant peak on 14 June at Alligator Harbor appears to be anomalous: It does not follow the trend at Turkey Point, nor does the developmental stage data support it as an indication of the population trend.

Statistical analyses of the follicle index data for the established populations support the stated interpretations except for one point: The drop in the index at



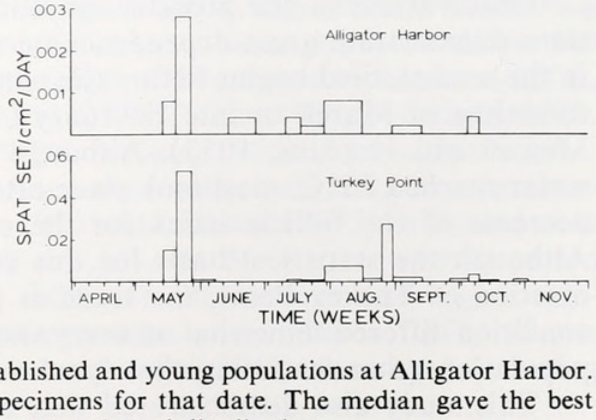


FIGURE 3. (Left.) Gonadal condition of the established and young populations at Alligator Harbor. Each point is the median follicle index of the 25 specimens for that date. The median gave the best representation of the central tendency of the data due to a skewed distribution.

FIGURE 4. (Right.) Oyster setting patterns at both stations. Each bar represents the average number of oyster spat counted in eight randomly chosen 49 cm^2 areas on the panel exposed during the period covered by the width of the bar. Note scale differences.

Turkey Point from 20 May to 14 June is not significant, whereas the corresponding decrease at Alligator Harbor is significant.

The follicle index for the young-of-the-year populations also changed similarly at the two sampling sites. Both sites' indexes increased sharply in July and early August. This rise was followed by a small decrease at Turkey Point and a large one at Alligator Harbor. Both indexes rose again until mid- to late September, when they peaked, and then declined steadily until the project ended. Statistical analyses confirmed the significance of the trends stated above, except for the slight decrease at Turkey Point in late August. The decline at Alligator Harbor during this period was significant.

Developmental stage

The percent of individuals in five general stages of development, determined by traditional techniques, yield some additional information to support the more quantitative results. Data from the established population show that gonads were active throughout the duration of the study. At least some of these oysters spawned from the end of April to the end of October.

The developmental-stage data for the two young populations show active gonads in Alligator Harbor from early July to early November and at Turkey Point from early August to early November. Most of the spawning appears to have occurred during September and October, although some did take place as early as August or even July at Alligator Harbor, and as late as November.

Setting patterns

Figure 4 summarizes the setting data from both stations. The overall setting trends at both stations are fairly similar. A large setting peak occurred during the period 20 May–27 May at both stations. Setting continued at a much lower level until late July and mid-August when a smaller setting peak occurred. After August, some light setting was recorded at both stations until the project ended in early November.

Discussion

Examination of gonads from over 1300 *C. virginica* specimens enabled the first quantitative determination of this species' reproductive cycle in the Gulf of Mexico.

Observations of the gonadal condition of naturally established oyster populations demonstrate great dependence on water temperature. Gonadal development in the area studied begins before the temperature reaches 20°C in April, probably sometime in March or late February (Gennette and Morey, 1971; Ingle, 1951; Menzel and Hopkins, 1953). Although some spawning was observed before the water reached 25°C, most took place afterwards. This was clearly indicated by the decrease of the follicle index for the established populations during late May. Although the statistical basis for this conclusion is obscured by some asynchronization at Turkey Point, the trend is significant at Alligator Harbor. Gonadal condition differed somewhat on every sampling date, particularly in the established populations, demonstrating that synchronization is never 100%.

This study also demonstrated that established oysters in the Gulf of Mexico begin new development of gametes after the initial spring spawning, as previously suggested by Hopkins *et al.* (1953), and Gennette and Morey (1971). This continues as the dominant trend during the summer, as long as the temperature remains high.

Temperature fluctuations of 5–10°C also can induce spawning (Loosanoff and Davis, 1963). During late July to early August, a temperature drop large enough to induce spawning was recorded. This temperature change appears to have begun the steady late-summer decline of the follicle index, indicative of increased spawning. In years when this temperature change does not occur, widespread spawning may not begin again until the fall temperature decline in September.

This study is the first to describe the reproductive cycle of young-of-the-year *C. virginica.* The results clearly support the hypothesis that two generations are produced in this area each year. Increases in the follicle index as well as the presence of more advanced developmental stages indicate that early setting oysters ripen at both stations during the summer. This process appears to have been slightly enhanced at Alligator Harbor, where growth was also faster at first. Active gonads were found there 2 weeks earlier than at Turkey Point.

Some of these young oysters spawned during mid-summer, apparently in response to temperature fluctuation. This suggests that some specimens were mature enough for natural spawning to occur only 12 weeks after attachment. When the temperature rose again, it appears that gonadal development resumed, as it had in the established oysters after the spring spawning. The September fall temperature decline initiated large-scale spawning in the young oysters. The reproductive cycle for these young oysters includes active gonads from late June or early July until late October. These oysters spawn to some degree throughout this period, mostly in late September and early October.

Orton (1920) and Giese (1959) have stated that the occurrence of more than one generation each year in the warmer areas of a species' distribution could be due to accelerated development and/or an extended period when conditions are suitable for gonadal development. Which permits or causes multiple generations to occur in *C. virginica* in the warmer areas of its distribution is not known.

Numerous reports on the growth rate of *C. virginica* in various areas of its distribution demonstrate that oysters grow faster in the warmer areas (Gunter, 1951; Ingle, 1950; Ingle and Dawson, 1952; Loosanoff, 1965a; Maurer and Aprill, 1973; Shaw and Merrill, 1966). Pruder *et al.* (1976), presenting theoretical growth expectations for a mariculture operation based on the fastest growth data available in the north, calculated a maximum growth rate equal to about half that recorded in our study. Dame (1972) also showed that in South Carolina the instantaneous growth rate for all sizes examined is fastest during summer. Data in the literature support the idea of faster instantaneous growth rates in the southern latitudes.

Numerous studies on various aspects of oyster physiology present conflicting results describing the optimal environment for oysters. Some studies indicate the temperature of maximal feeding, water pumping, or heart rate to be about 25°C, while others show peaks at approximately 30–35°C (Collier, 1954; Federighi, 1929; Galtsoff, 1927, 1964; Loosanoff, 1958, 1965b; Nelson, 1935). Although the basal metabolic demand of many organisms increases with increasing temperature (Kinne, 1963), Vernberg and Vernberg (1970) and Dame (1972) indicated that the Q_{10} value for growth of *C. virginica* is much lower during the warmer period than during the winter months. Low Q_{10} values at intermediate and higher temperatures imply energy utilization without excessive waste (Dame, 1972). Dame (1972) also reported higher assimilation rates for South Carolina oysters during summer.

The importance of a longer season of suitable growing conditions cannot be overlooked when examining the causes of rapid development of southern oysters. However, it appears that these locations also present a more favorable environment for increased rates of instantaneous growth and assimilation than do northern locations. These faster rates are of paramount importance for promoting the observed rapid sexual development.

Although many factors affect oyster setting, the amount of spawning activity ultimately determines setting potential and the maximum possible recruitment to an oyster population. Comparing the spawning and setting data of the young and established populations at each station gives some idea of relative contributions to recruitment.

Most of the setting recorded in this study occurred during the spring, in late May. This peak can be attributed solely to oysters attached in previous years. Setting later in the season, however, may be due to additional spawning by the older oysters and/or spawning of the sexually developed young-of-the-year oysters. The results of this study demonstrate that not only are the older oysters solely responsible for early setting, but they contribute most of the gametes that result in later setting. Numerous studies of setting patterns in northern areas, where early sexual development does not occur, have shown a bimodal distribution of setting activity (Chestnut, 1948; Chestnut and Fahy, 1952; Hopkins, 1937; Loosanoff, 1966; McNulty, 1953; Shaw, 1967). These studies support the hypothesis that older oysters can spawn several times during the reproductive season or that some spawn early while others spawn later in the season (Galtsoff, 1964). The present study indicates significant spawning by the older oysters both in the spring and the fall, with continual light spawning throughout the summer. Also, the observation of renewed sexual development in older oysters during the summer provides these specimens with more potential for spawning in the fall than if renewed gametogenesis had not occurred.

Although the young oysters undoubtedly contribute to the mid-summer setting peak (as demonstrated by the presence of spawning individuals), no significant peak was observed when most of them were spawning in response to the fall temperature decrease. Thus, the young oysters, although spawning by the end of their first year, make little significant contribution to the overall population recruitment during that year. This is undoubtedly due to their relatively smaller size and fewer numbers compared to oysters from previous years.

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