GROWTH AND SURVIVAL IN NEWLY SETTLED SPAT OF THE MANILA CLAM, TAPEȘ JAPONICA

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ABSTRACT

Substrate abundances of adult Manila clam, Tapes japonica, were manipulated in July 1976 on a portion of beach dug commercially in the southern region of Puget Sound, Washington. Differences in clam spat growth and survival were measured between samples taken from substrates having varying levels of adult clam abundance.

The clam spat settled at 0.206 mm long. Initial growth of clams settling in the fall was much slower than for clams settling in the summer, 9 months versus 2 months, respectively, to reach approximately 2.5 mm long. Summer settling clams form a visible growth checkmark by October of their first year at approximately 5-8 mm. Fall settling clams form their first visible checkmark during their second October at approximately 14-16 mm. The length of clams was found to be significantly less for clams growing in substrates with natural or high adult clam abundances versus those from substrates with no adult clams.

Only 1.2% of the initial population of clams that settled in September 1976 survived until June 1977. The most likely cause of this mortality was by meiofaunal predators, particularly nematodes. By June, no difference in survival rates was detectable between clams from substrates that contained no adult clams versus those from substrates with natural or high adult clam abundance.

Clam spat movement occurred along the beach and may have contributed to the high spat mortality.

The Japanese little-neck or Manila clam, Tapes japonica Deshayes, is a native to Japanese and Korean waters, but was introduced into Puget Sound, Wash., along with the Pacific oyster, Crassostrea gigas, in the 1930's (Quayle 1964). It has since become an important part of the commercial Puget Sound hard-shell clam fishery with approximately 1 million lb harvested annually. It has also been so heavily utilized by the sport fishery that the populations on some Puget Sound beaches have been almost eliminated.

The majority of research on the Manila clam has been performed in Japan (see Tamura 1966 for a review of the Japanese literature). Because the water temperatures and climate in Puget Sound are cooler than those in most of the Japanese study areas, the results published by the Japanese with respect to spawning times, growth, and population numbers can be misleading when applied to clam populations in this area. Studies conducted on the west coast of the United States and Canada dealt with gonad development (Holland and Chew 1974), planktonic larval stages (Quayle and Bourne 1972), and growth and/or survival after settling and after some arbitrary body size, usually based on sieve retention, had been reached (Jones 1974; Glock 1978; Lukas2). Nosho and Chew (1972) made the only attempt to investigate early settling stages of the Manila clam. However, due to the sieve size they used, they were unable to detect newly settled spat. The lack of early life history information is probably related to the difficulty in sorting out newly settled spat from gravel samples, and in specific indentification. Loosanoff et al. (1966) found it difficult to identify pelagic larvae to species and cited this as a reason for incomplete life histories of many pelecypods. Quayle (1952) found that identification of spat was even more difficult than the identification of planktonic larvae.

I began a study in the summer of 1976 to describe the growth and survival of Manila clams from settling size to formation of the first growth ring. In addition, since the study was located in an area with large numbers of adult Manila clams, I investigated the possibility that the pres-
ence of adults may influence or be associated with spat growth and survival.

METHODS

In 1976 a study site was chosen in southern Puget Sound on a narrow estuary called Little Skookum Inlet (Figure 1). The site was on intertidal land from which Manila clams were commercially harvested. There was easy access to the beach, but because of its private ownership, the probability of people tampering with the experimental plots was low.

Plot Construction

To study the possible influence of adult clams on the growth and survival of spat, I constructed plots in which I experimentally manipulated the beach material to yield different concentrations of adult clams. Each plot contained four treatments, as follows:

Treatment 1. No adult clams and new substrate. All beach material was removed to a depth of 15 cm to ensure removal of adult clams. Gravel from the high intertidal (+3 m) was then carried down to fill the excavated hole to the existing beach level.

Treatment 2. No adult clams and old substrate. All beach material was removed to a depth of 15 cm and then sifted through a 12 mm mesh screen to remove the adult clams. All screened material and any large rocks retained on the screen were then returned to the excavated hole and enough additional screened material was added from residue of Treatment 1 to bring the treatment level to the same height as the beach.

Treatment 3. Moderate adult clam density (control). A shovel blade was inserted vertically, 15 cm into the substrate on the edge of the treatment. The handle was pulled back and forth 3 or 4 times until the surface above the blade was loosened. The shovel blade was inserted and agitated around the perimeter of the treatment until the entire surface area of the plot had been disturbed. No clams were added to or subtracted from the treatment, and no counts of naturally occurring clams in the treatment were made prior to the settling experiments.

Treatment 4. High adult clam density. This treatment was disturbed in the same manner as Treatment 3. In addition, enough adult clams between 2.0 and 5.0 cm in length were placed on the surface of the treatment to create a surface density of approximately 480/m². This density was the number of clams necessary to completely cover the surface area.

In all cases, the day following the construction of Treatment 4, no clams remained on the beach surface, and a large number of new siphon holes were apparent. In no case were any adult clams found in Treatments 1 or 2, and it was thus assumed that the clams added to Treatment 4 buried within the treatment and did not move to adjacent treatments or outside the plot. I as-
assumed that any predation on the clams before they were able to bury within the substrate did not substantially affect the magnitude of the adult clam density, as compared with the other treatments.

I constructed Plots A, II, and III in July 1976, and Plots R, S, and T in July 1977 at a tidal height ranging from +0.25 m to +0.75 m (MLLW datum), as determined by the height of the nearby oyster dikes (Figure 1). For Plots A, R, S, and T, wooden lath stakes were driven into the ground to delineate 2 x 2 m squares, that were then subdivided by stakes into four rows and four columns. The result was sixteen 0.25 m² subareas in each plot. Four replicates of Treatments 1-4 were then constructed within each plot to form a 4 x 4 Latin square array of treatments. For Plots II and III, stakes were driven into the ground to delineate a 1.5 m wide by 12.0 m long plot. Treatments 1-4 were randomly assigned to sub­areas within the plot so that the resulting configuration consisted of four different 1.5 x 1.5 m treatments, separated by 1.5 m spaces between each treatment, within each plot.

A continuously recording thermograph was buried 1 cm below the surface gravel next to Plot A in October 1976. The recording tape was re­placed monthly.

The large plots were constructed to minimize possible edge effects caused by the close proximity of treatments to each other. To further minimize possible edge effects, samples were taken only from the inside 0.25 m² area of each treatment in both the large and small plots.

Sampling

To check for newly settled clams, each week I took two or three gravel samples beside each plot by twisting a 20.28 cm² clear plastic tube 2 cm deep into the beach. A small hand trowel was then shoved down beside and rotated under the tube as it was removed from the gravel, preventing any material from falling out. The contents of the tube were then transferred to a bottle or plastic bag. A 10% formaldehyde solution with a concentration of 0.01% phloxine B dye was then added to the container.

In the laboratory, I washed the gravel samples through a series of Tyler³ sieves. Sieving down to

³Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA

mesh size of 0.149 mm was necessary to insure retention of the smallest, newly settled spat in freshly preserved samples. The residue from the finest sieve was placed in a Petri dish under a compound dissecting scope (50×) and examined for clam spat.

In 1976, when a large larval settlement was detected from the weekly gravel samples, I sampled all of the treatment areas in each plot. I constructed a sampling template from a piece of 1.91 cm thick plywood that had the inside 0.125 m² removed. Seine twine was stretched over the opening to form a 5 x 5 grid with each square 5.72 cm on a side.

For each individual treatment area in a plot, five squares in the grid were randomly selected as the sample sites from which to take cores. After removing the cores, the holes were filled to beach level with gravel taken from beside the plot, at a depth of 4 cm, in order to avoid introducing newly settled spat to the plots.

To follow the growth and survival from settling size, I took 10 cores per treatment in November and December 1976 and in January, March, and April 1977 from Plots A and II. The location of the cores within each treatment was randomly selected, excluding all core areas previously utilized. In June 1977 the remaining core areas in the different treatments were sampled. For each sampling period, all cores in each treatment were sieved in the laboratory, the clams were counted, and a height and length measurement was taken on the first 30 clams encountered per treatment.

Sample Sizes

Twenty core samples per treatment were taken immediately after newly settled clams were observed. Using methods given by Elliott (1971), I determined that the number of clam spat per core per treatment had a negative binomial distribution. The counts were transformed (log₁₀X) and a mean and variance computed. These numbers were utilized in Elliott's formula for the determination of sample sizes. A standard error equal to 20% of the mean and a 95% confidence were used. The results showed that a sample size of 5 for each treatment would have been sufficient. Based on this and the amount of time necessary to process each core, 10 cores per treatment were chosen as the sample size for subsequent sampling periods.
Summer Sampling in 1977

To follow the growth of the 1976 fall settlement for 1 yr, three random 0.25 m², 3 cm deep gravel samples were taken from near Plot A in early August 1977, and again in the middle of September. No treatment effect determinations were possible due to a lack of sufficient study plots. Material was preserved by freezing, instead of by a formaldehyde solution. In the laboratory the material was thawed and washed through Tyler sieves (1.190 mm minimum mesh size), and then the residue on the screens was placed in a large cake pan. The clams were sorted by eye, and a height and length measurement was taken on all clams.

Core samples taken from Plots R, S, and T, in the summer and fall of 1977 to test for larval settlement were used as the basis for determining the growth of the clam spat that settled in July 1977.

RESULTS

Growth

To test for possible changes in the height-length ratio due to growth, a linear regression was run on log₁₀-transformed height versus length measurements for clams from settling size through 1 yr. Correlation was high (r = 0.997) and thus only length measurements were used to express results. A plot of clam lengths determined from samples taken after the initial settlement in September 1976 through the following 12 mo is shown in Figure 2.

The average length of newly settled clams was 0.206 mm (N = 129; SE = 0.01). The clam spat that settled in September 1976 grew about 2.5 times their settling length in 2 mo. Little growth occurred between November and January; growth commenced again by the middle of March. By June the spat had attained a length of 2.17-2.7 mm.

In contrast to the growth of the fall settlement, the clams that settled in July 1977 attained an average length of 2.82 mm (N = 47; SE = 0.12) by the middle of September. This was a growth of 13.5 times their size at settling in 2 mo and was slightly larger than the size reached in 9 mo by clams from the fall settlement.

Growth rings were laid down in October. Clams that settled in July attained an average length of 6.16 mm (N = 42; SE = 0.51) by this time. Clams that settled in the fall also formed rings their first October, but since they were so small, the mark was not discernable by the following summer. By September 1977 the clams from the fall settlement had attained an average length of 14.93 mm (N = 110; SE = 0.26). Approximately 0.5 mm growth occurred before the end of October, at which point their first growth ring was visible. Clams that settled in July were about 23 mm long 1 yr later.

No differential growth was detectable until June 1977 between clams that settled in fall 1976 into the different experimental treatment substrates. A Kruskal-Wallis rank sums test on clams sampled in June detected a significant difference (P < 0.001) between those sampled from substrates with no adult clams and those from substrates with adult clams. The treatments were ranked by the average length of clams that each contained (Treatment 2 had the largest clams; Treatment 3 had the smallest). A series of one-tailed Mann-Whitney pairwise comparisons (pairwise P < 0.05) were performed to test which treatments differed significantly (Hollander and Wolfe 1973). The following were the results (no significant difference between pairs underlined in common):

2 1 4 3
Clams from substrates with no adults (Treatments 1, 2) averaged 2.70 mm ($N = 55; \text{SE} = 0.08$) long, and clams from substrates with moderate (Treatment 3) and high (Treatment 4) adult clam abundances averaged 2.17 mm ($N = 39; \text{SE} = 0.08$).

**Survival**

The density of newly settled clams sampled from 105 cores ranged from 19 to 93, with a mean of 54.3. Only 1.2% of the clams (equivalent to 250-450/m$^2$) survived until June 1977, 9 mo after the fall 1976 settlement (Figure 3). The largest loss in clams occurred during the first 2 mo after settling when the density decreased by 57%. During the third, fourth and next 2 (combined) mo after settling, the average density decrease from the previous sampling period was 34%, 56%, and 35%, respectively. A Kruskal-Wallis test on the June data detected no differential ($P>0.50$) survivorship between clams that had settled into substrates with adult clams versus those that settled into substrates with no adult clams.

**DISCUSSION**

**Growth**

There has been a great disparity in the reported size of 1-yr-old Manila clams. Three areas in Japan have reported three different lengths: in Hokkaido, 8 mm (Yamamoto and Iwata 1956); in the Inland Sea, 18 mm (Ohba 1959); and in Ariake Bay (South Japan), 27 mm (Tanaka 1954). Rodde et al. (1976) grew Manila clams to 34 mm in 1 yr under hatchery conditions with high temperatures and nutrient rich water. Nosho and Chew (1972) estimated that Manila clams in Hood Canal, Wash., were 24 mm at the end of 1 yr. These conflicting reports have created some difficulties for scientists in attempting to determine the age of Manila clams found in Puget Sound beaches. The fact that I found two sizes of clams that resulted from settlements only a few months apart makes this understandable. In some cases, others have based growth data on checks in the shell without studying the early stages of growth. However, without the knowledge about the time of year that a clam cohort settled and the period of growth until the formation of the first visible checkmark, the determination of the age of a clam can be difficult.
corresponded to the temperatures found in Little Skookum Inlet during the winter months (Table 1). The growth for the summer settling clams was much higher, and other studies with Manila clams of the same settling size have reported similar or higher initial growth. Yoshida (1953) found clams settling in early June reached 0.9 mm by the end of July. Clams raised in 22°-29° C water under hatchery conditions, with an optimal food supply, were 5 mm 90 days after settling (Rodde et al. 1976). The small size at settlement for the Manila clam and the slow initial growth of clams that settled in the fall underscores the necessity to use a small mesh size when sampling for spat so as not to possibly mask a large part of their early life.

In addition to a difference in the growth rates between summer and fall settling clams, the lengths of clams that I recovered in June were significantly greater ($P < 0.001$) in treatments without adult clams than in treatments with adult clams. A similar decreased growth with increased densities has also been shown for larger Manila clams in other studies. Sagara (1952) found this for clams >30 mm, but indicated that clams <20 mm were not affected by density. Ohba (1956) found decreased growth in 10-12 mm clams and related it to competition for food. In other studies, Hancock (1973) found reduced growth with Cardium edule in areas of overpopulation and a marked reduction in size in locally overcrowded areas. Finally, in a hatchery-rearing experiment with 14 mm Manila clams, Langton et al. (1977) found that growth increased with ration size in crowded conditions. A decrease in available food to juveniles was implicated as the controlling factor that caused the decrease in clam growth observed in treatments with adult clams, as compared with those in treatments without adults. There were not sufficient study plots available to determine whether this differential growth continued during the summer. The results of these experiments indicates that the harvest of adult clams from a beach will allow for a better growth of undersized clams. This result coincides with the general view of commercial Manila clam harvesters in Puget Sound (Taylor^{4}).

**Survival**

Approximately 1.2% of the clams that settled in September 1976 survived until June 1977. Japanese studies on Manila clams have reported similar low levels of survivorship 4-9 mo after initial settlements. Ikematsu (1957) found that spat densities of 5,000/m² in March were only 1.0% of the 500,000/m² he found the previous November. Ohba (1959) estimated settling densities of 25,000/m² in October, but found only 8.0% of that (2,000/m²) by the following June. In studies on a number of clam species other than Manila clams, Muus (1973) reported that regardless of clam densities at settling, the number of clams recovered per unit area decreased rapidly until a density of several hundred per square meter was approached. The level of survivorship from the fall settlement was similar to these studies but although it was low, the number of spat that it represented (250-450/m²) was more than 2.5 times greater than the density of adults (approximately 100/m²) considered as an adequate level at which a beach can be dug commercially (Taylor see footnote 4).

Not only was the survivorship from the fall settlement low, but the majority of the clam spat mortality occurred during the first 2 mo after settling (57%) and only about 10% of the clams survived to 0.7 mm long (6 mo). One or more of a number of factors are usually identified as causes of high mortality in biological populations. In the case of benthic marine invertebrates, Hancock (1970) stated that survival after settlement will depend upon: a) environmental conditions, notably temperature; b) food supply, which may be affected by intra- and interspecific competition; c) space competition; d) parasites and disease; e) ac-

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**TABLE 1.**—The daily average and the extreme substrate temperatures (1 cm below surface) between sampling periods for the Manila clam in Little Skookum Inlet, Wash., at the +0.6 m tide level.

<table>
<thead>
<tr>
<th>Sampling period</th>
<th>$N$</th>
<th>Average (°C)</th>
<th>Extremes</th>
</tr>
</thead>
<tbody>
<tr>
<td>1976:</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Oct. 24-Nov. 20</td>
<td>30</td>
<td>11.6</td>
<td>10.5-12.5</td>
</tr>
<tr>
<td>Nov. 20-Dec. 20</td>
<td>30</td>
<td>9.7</td>
<td>6.5-10.5</td>
</tr>
<tr>
<td>Dec. 20-Jan. 16, 1977</td>
<td>27</td>
<td>7.8</td>
<td>4.0-9.0</td>
</tr>
<tr>
<td>1977:</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Jan. 16-Feb. 2</td>
<td>17</td>
<td>8.6</td>
<td>3.0-9.0</td>
</tr>
<tr>
<td>Mar. 11-Apr. 8</td>
<td>28</td>
<td>9.5</td>
<td>5.5-20.0</td>
</tr>
<tr>
<td>Apr. 8-May 6</td>
<td>28</td>
<td>12.2</td>
<td>11.0-18.5</td>
</tr>
<tr>
<td>May 6-June 4</td>
<td>29</td>
<td>12.8</td>
<td>12.0-20.0</td>
</tr>
<tr>
<td>June 4-July 4</td>
<td>30</td>
<td>15.6</td>
<td>14.5-28.0</td>
</tr>
<tr>
<td>July 4-6</td>
<td>3</td>
<td>16.7</td>
<td>16.5-21.5</td>
</tr>
<tr>
<td>July 30-Aug. 4</td>
<td>6</td>
<td>17.8</td>
<td>16.5-19.0</td>
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<td>Aug. 25-Sept. 21</td>
<td>27</td>
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<tr>
<td>Sept. 21-Oct. 12</td>
<td>21</td>
<td>15.6</td>
<td>10.0-16.5</td>
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</table>
WILLIAMS: GROWTH AND SURVIVAL OF MANILA CLAM SPAT

cidential ingestion of newly settled young (of some molluscs by adults of the same or different species; f) physical damage or disturbance; and g) predation. Most of the above factors did not appear to be significant in this study.

a) Yoshida (1953) experimented with 1.0-3.8 mm Manila clams and found a survival of 90% or greater in water temperatures averaging 7° C. The water temperatures at Little Skookum averaged 8.9°-12.7° C during winter and probably were an insignificant cause of mortality, except during the coldest part of January (Table 1). Low water temperature probably attributed to the slight increase in clam spat mortality observed at this time.

b) When Cahn (1951) surveyed the Japanese Manila clam fishery, he cited starvation under overcrowded conditions of newly settled spat as a probable cause of death. The survival rate in this study, however, remained fairly equal between treatments with no adult clams and those with high adult clam densities. Thus, the expected cropping of the food supply to spat that settled among the adults did not appear to affect the spat’s survival. In addition, almost nothing is known about the food requirements of newly settled spat, so adequacy of food supply as a controlling factor would be difficult to determine.

c) Lack of sufficient space for growth between two consecutive year classes was proposed by Hancock (1973) as one of the largest factors controlling survival of newly settled spat in C. edule. He proposed that space requirements for growth of shells would conflict in two adjacent year classes, with the smaller cockles being forced from the substrate as they grew. In nonadjacent year classes, 0-group cockles could maintain their position between shells of older adult clams. This hypothesis was based on clams first observed when 10 mm long. Space limitation did affect survival of the spat in this study, because their size was quite small compared with the space available for growth.

d) There was no evidence of parasites and/or disease in either the adult stocks or the newly settled spat.

e) Under experimental conditions, Kristensen (1957) found that inhalation by adult cockles of newly settled spat could cause death of the small spat, even when the larvae were discharged soon afterward. Hancock (1973), however, did not feel that the presence of adults adversely affected survival of settled young in his studies at Burry Inlet, but he felt that mortalities were related to oyster catcher, Haematopus ochchmani, predation. Since he did not look at the spat until 5 mo after they had settled, it would be difficult to determine at which stage in their early life history the largest mortality occurred. In the present study, the largest initial settlement occurred in Treatment 1, but by April this treatment had not only the lowest survival but also the lowest absolute density of the four treatments. If mortality was caused by ingestion by adults, then a higher density would have been expected for Treatment 1, which contained no adults.

f) Shellbourne (1957) studied small oysters and found that shifting surface sands subjected newly settled spat and juveniles to increased mortality due to abrasion. Quayle (1952) felt the largest cause of mortality for the spat of Venerupis pullulastra was the unsuitability of the substrate. Glock (1978) planted small (2-4 mm) hatchery-reared Manila clams on a southern Puget Sound beach and then covered some of the area with protective mesh covering. He had a much higher survival rate under the areas with plastic mesh, and attributed this in part to stabilization of the sediment. He also found predation rates to be low. In this study, the Treatment 1 areas in Plots A, II, and III were readily observable through the third month after settling, due to a slight difference in color of the gravel brought down from the high intertidal area. This observation indicated that any movement of the surface gravel must have been slight in order not to mask the visible differences of this treatment. In the laboratory, I subjected the spat to considerable mechanical agitation during the process of washing and sieving; however, only a few of the thousands of spat that I observed had damaged shells. I also found some unbroken, empty clam shells that were equal in size to live clams sampled, but never a number of shells equivalent to the mortality observed. I concluded that abrasion did not cause substantial mortalities in this study.

g) Thorson (1966) felt that the biological factor with the greatest effect on survival of newly settled larvae was predation. Muus (1973) came to the conclusion after a very complete study on the early life history of newly settled bivalves in Denmark. Since the largest mortality in this study occurred when the spat were quite small, it seemed most probable that if predation were the cause, then the majority of the loss would be to
meiofaunal predators (defined as organisms that are retained on sieves 0.04-0.1 mm and passed through sieves 0.5-1.0 mm (McIntyre 1969; Coull 1973), that were nearly the same size. Swedmark (1964) listed turbellarians, coelenterates, and nematodes as interstitial predators. Thorson (1966) cited studies that have shown turbellarians, nematodes, and harpacticoid copepods to be predators on newly settled spat. Although only a few turbellarians and no coelenterates were recovered during the study period, a large number of nematodes and harpacticoids were included in each core sampled. In spite of the citation by Thorson, the harpacticoids in this study were not likely to have eaten even the smallest clam spat, as these particular species are considered almost exclusively detritus feeders (Sibert et al. 1977; Illg5). The degree to which nematodes may have accounted for loss in clam spat is unknown. Although larger predators (shore crabs, drilling snails, sea stars, fish, birds) may account for significant predation losses on larger clams, their effect on survival of the newly settled spat was probably low. Large, active predators would not likely have expended the energy to forage for the small spat that would have provided little energy in return.

Of all the above factors listed, I concluded the major cause for the large loss in spat that I observed was due to predation by meiofaunal predators. Since some empty clam shells were found on the beach and vigorous sieving in the laboratory did not damage the shells of the spat, only predation could have accounted for both the high mortalities and the destruction or removal of shells. I assumed that nematodes were the dominant predator.

Movement of Clams on the Beach

Two experiments were performed (November 1976 and May 1977) to test for movement of small clams on the beach. In each case, 2 cm of surface gravel was removed from a plot that was 0.25 m², to insure that no small clams remained. One month after the start of each experiment, core samples were taken and small clams were found in the center of each plot that had been previously clam free. It was not known whether this movement was active or passive. Active movement implies that clams physically moved (probably by foot action) across the beach. Passive movement implies physical transport of clams across the substrate, with or without movement of surface gravel. In the present study, byssus threads were detectable on clams as small as 0.45 mm long. This indicated that they had the ability to attach to the substrate which would decrease their susceptibility to movement by currents. To the contrary, Sigurdsson et al. (1976) proposed that some postplanktonic bivalve larvae use their byssus threads as a method for dispersal. The method of transport would be analogous to the gossamer flight by young spiders. Either of these two methods for utilization of byssus threads may have been used by some of the clam spat at the study site.

Baggerman (1953), with C. edule, found that transportation of clams over the substrate may have been an important factor in the final distribution of clams. In this study, transportation may have played an important part in the growth and survival of the spat. Growth was shown to be significantly greater in treatments without adult clams than in treatments with adult clams. The adults thus may have directly caused a decrease in growth of juveniles by decreasing the availability of food, and/or indirectly they may have influenced clam spat to actively seek new substrates in which to resettle to avoid competition. Additionally, in the process of resettlement, clam spat may have become susceptible to a larger number of predators.

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5Paul Illg, Department of Zoology, University of Washington, Seattle, WA 98195, pers. commun. February 1977.
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