The influence of adults on the settlement of spat of the clam, Tapes japonica

by John G. Williams[1]

ABSTRACT

Substratum abundances of adult Manila clams (*Tapes japonica*) were manipulated in July 1976 on a portion of a beach located in the southern region of Puget Sound, Washington. Differences in larval settlement of clam spat were measured between samples taken from substrata having different abundances of adult clams.

Significantly more clam spat settled in areas with no, or moderate, adult clam abundances than in areas with high adult clam abundances. The cause for the difference appeared to be related to the ingestion of larvae by adults and/or a preference of larvae to settle away from the adults. However, even in dense assemblages of adults, larvae were not prevented from settling.

1. Introduction

Successful habitat selection by invertebrate larvae and the variables involved have been discussed by a number of authors (Thorson, 1957, 1966; Levinton, 1972; Muus, 1973; Crisp, 1974; Doyle, 1975, 1976; Eagle, 1975; Heip, 1975; Moore, 1975; Woodin, 1976). Larval discrimination between substrata decreases as larvae delay metamorphosis (Knight-Jones, 1953; Bayne, 1965; Thorson, 1966; Johannessen, 1973; Doyle, 1975), but the consensus of the literature is that larvae seek specific cues indicating a suitable substratum, and that these cues are related to the presence of adult organisms in some way.

Some researchers have found that consistently higher settlement occurs on substrata where there have been previous settlements. This was found in species of oysters (Bayne, 1969; Hidu and Haskin, 1971; Keck *et al.*, 1971; Veitch and Hidu, 1971; Gillmor and Arakawa, 1976), polychaetes (Wilson, 1953; Moore, 1975), barnacles (Crisp and Meadows, 1962; Larman and Gabbott, 1975), and clams (Keck *et al.*, 1973). Woodin (1976) states that preferential larval settlement of infaunal organisms seems to be due to the presence of particular micro-organisms, rather than the presence of adults of the larval species. Wilson also believed this to be the case in *Ophelia* larvae.

1. Washington Cooperative Fishery Research Unit, College of Fisheries, University of Washington, Seattle, Washington 98195.

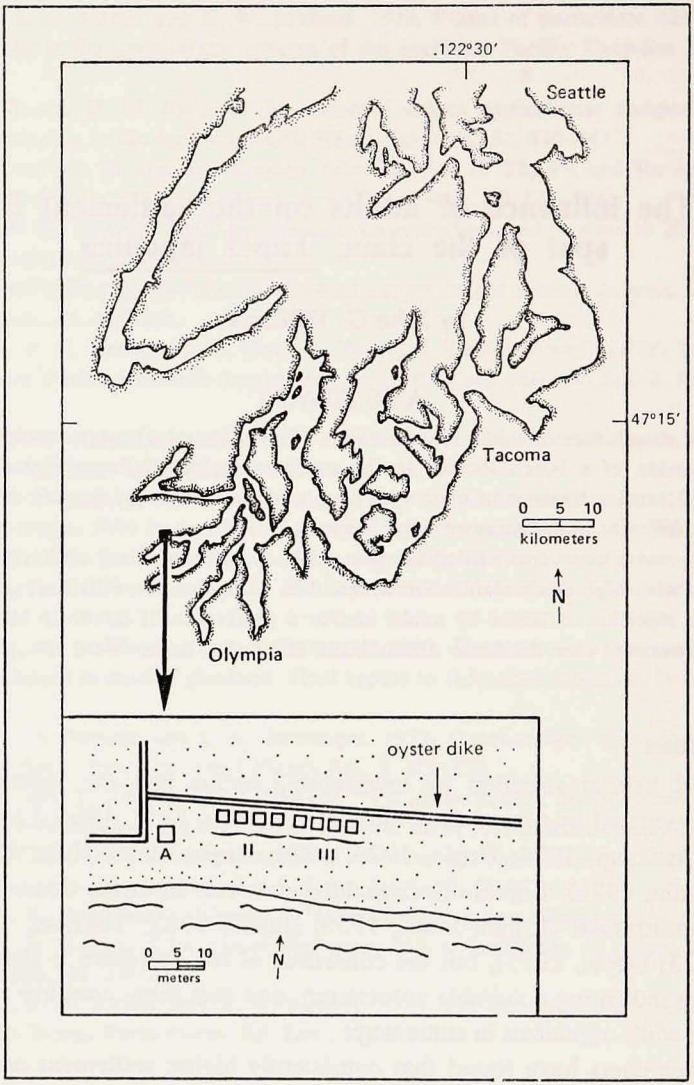

Figure 1. Diagrammatic representation of the study site for the Manila clam on Little Skookum Inlet in southern Puget Sound, Washington, on a minus tide (MLLW). Plot A was a 2 × 2 m square divided into 16 0.25 m² sections. Plots II and III each contained four 1.5 × 1.5 m sections in a row.

Successful survival to adulthood may also depend upon the ability of larvae to detect the presence of adults, as adults may compete with or prey on larvae. However, there have been few field experiments on the influence of filter-feeding adults on settling larvae. This is particularly true for clam species. Clam studies have usually been conducted by fisheries researchers primarily interested in recruitment and

growth to harvestable sizes. They generally used screens too large (1-2 mm) to retain newly settled spat in order to simplify the processing of large amounts of sediment. Small organisms, the size of settling clams, are studied by meiobenthos researchers but, as clam spat are only a temporary part of the meiobenthos, they are not studied in as much detail as are the permanent meiofauna. In addition, there is difficulty in making specific identifications. Loosanoff *et al.* (1966) found it difficult to identify pelagic larvae to the species level, and cited this as a reason for our incomplete knowledge of life histories of many pelecypods. Quayle (1951) found the identification of spat even more difficult than the identification of planktic larvae.

Many workers have speculated on the causal mechanisms for settlement, recruitment, and survival based on information gained from clams retained on 1-mm or larger sieve mesh sizes (Fitch, 1965; Hughes, 1970; Hancock, 1970, 1973; Holland and Dean, 1977; Johannessen, 1973; Paul and Feder, 1973; Wendell *et al.*, 1976; Woodin, 1976). Woodin (1976) formulated hypotheses to explain spatial patterns of abundance based upon adult-larval interactions in dense infaunal assemblages. She hypothesized that, in dense infaunal assemblages of filter feeders, no larvae could successfully settle. She based her prediction on the research of Fitch (1965) and Hancock (1970). However, neither of these studies could have detected newly settled spat as the former used a 1-mm mesh screen and the latter sampled five months after settlement, when spat were greater than 5-mm in length.

Because Woodin (1976) based her prediction on the inadequacy of early life history information, I chose the Manila clam to study the influence of infaunal filter-feeding adults on settling larvae. I formulated three alternative hypotheses that were then tested in the field: (1) Manila clam settlement is independent of adult clam density, (2) the presence of adults is positively correlated with Manila clam settlement, and (3) the presence of adult clams is negatively correlated with Manila clam settlement.

2. Study site

In 1976, a study site was chosen on a narrow tidal estuary in southern Puget Sound, Washington, called Little Skookum Inlet, from which approximately 285,000 pounds of Manila clams are harvested annually (Fig. 1). The actual site was on 10° sloping intertidal beach that had not been harvested for more than one year. There was easy access to the beach, but due to its private ownership, the probability of people tampering with the experimental plots was low.

3. Methods and Materials

Plots were constructed at the site during the first three weeks of July 1976 at a tidal height ranging from +0.25-0.75 m (MLLW datum), as determined by the

height of the nearby oyster dikes (Fig. 1). Within each plot, the beach material was experimentally manipulated to yield different concentrations of adult clams. Each plot contained four treatments as follows:

Treatment 1. All beach material was removed to a depth of 15 cm to ensure removal of adult clams. Sediment from the high intertidal (+3 m) level was then carried down to fill the excavated hole to the existing beach level.

Treatment 2. All beach material was removed to a depth of 15 cm and then sifted through a 12-mm mesh screen to remove 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 added from the residue of Treatment 1 to bring the level to the height of the beach.

Treatment 3. This treatment was used as a reference. A shovel blade was inserted vertically, 15 cm into the substratum, on the edge of the treatment. The handle was pulled back and forth three or four 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 settling experiments.

Treatment 4. This treatment was disturbed in the same manner as Treatment 3. In addition, enough adult clams between 3.0 cm and 5.0 cm in length were placed on the surface of the treatment to completely cover the visible surface area of the plot. This created a surface density of approximately 480/m^2.

In all cases, on the day following 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 thus it was assumed that the clams added to Treatment 4 buried within the treatment and did not move to adjacent treatments or outside the plots.

To determine the range of normal or ambient density of adult clams at the study site, sixteen random 0.25 m^2 areas were sampled near the plots and counts of all clams greater than 12 mm were made. Densities ranged from 55 to 130 with a mean of 93 ($N = 16$, S.D. = 24.4), thus the artificially high density created in Treatment 4 was at least double the normal adult density of clams.

Plot A was constructed by driving wooden lath stakes into the ground to delineate a 2×2 m square. This square was, in turn, equally subdivided by stakes into four rows and columns resulting in sixteen 0.25 m^2 subareas. Four replicates of each treatment were then constructed within the subareas to form a 4×4 Latin square array. For plots II and III, stakes were driven into the ground to delineate 1.5 m wide by 12.0 m long plots. Treatments 1-4 were randomly assigned to subareas within each plot so that the resulting configuration consisted of four different 1.5×1.5 m treatments, separated by 1.5 m spaces between each treatment, within each plot.

The large plots were constructed to minimize the variable of edge effects that possibly could have occurred in Plot A where all of the small treatment substrata were touching. To further minimize possible edge effects, samples were only taken from the inside 0.125 m^2 area of each treatment in both the large and small plots.

To check for newly settled spat, beginning the middle of July, I took two or three sediment samples at weekly intervals beside each plot by twisting a 5.08 cm I.D. clear plastic tube 2 cm deep into the beach substratum. A small hand trowel was then shoved down beside, and rotated under, the tube as it was removed from the substratum, preventing material from falling out. The contents of the tube were 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, the gravel samples were washed through a series of Tyler sieves. Sieving down to a mesh size of 0.149 mm was necessary to ensure retainment of the smallest spat in freshly preserved samples. The residue from the smallest screen was washed into a black Petri dish, swirled around in a circular motion to allow the heavier sediment particles to sink below the lighter organic material, and placed under a dissecting microscope at 50×. The material was illuminated from above, and the pink-stained clam spat were easily detected against the dark background. This was a modification of a sorting method used by Hamilton (1969).

A large larval settlement was detected from the weekly sediment sample taken on September 21st. During the next two days, I took five random cores (5.08 cm I.D. and 2 cm deep) from the inside 0.125 m^2 area from each of the sixteen treatment squares in Plot A and from each treatment in Plots II and III. A few cores from each treatment within each plot were sieved in the lab within the first week after the samples were taken, and counts of newly settled clams were made. For each treatment in Plot A, the length of the first twenty-five to thirty clams observed under the microscope at 50× were measured to the nearest 0.005 mm by the use of an ocular micrometer. The majority of the cores were sieved more than one month after they were taken. Most of the cores in Plots II and III and a couple from Treatment 3 of Plot A were sieved and counted before I realized that the counts were averaging less than those counts obtained in freshly preserved samples. A 0.072 mm mesh sieve was added to the sorting process and a considerable number of clam spat were found with shells that had disintegrated enough to allow them to pass through the 0.149 mm mesh screen. All subsequent cores handled in the lab were sifted down to the smaller sieve size, and the number of newly settled spat was considered to be the sum of the clams found on the 0.072 mm and 0.149 mm screens.

Although each core sampled 20.28 cm^2 of surface area, the amount of substrate available for settling larvae in Treatment 3 and 4 was potentially decreased by the amount of area physically occupied by the siphons of the adult clams. Photographic

slides of clam siphons in the substrate were taken. Measurements determined the maximum area displaced by both the inhalent and exhalent siphons to be 20.68 mm^2 and 10.67 mm^2, respectively. Based on the average number of adult clams each core sample in Treatments 3 and 4 would contain, the percentage of area available to settling clams was decreased by 1.6% and 3.3%, respectively. All counts of clams in Treatments 3 and 4 were thus increased by these percentages.

One sediment sample was taken from each of Treatments 1 and 2 of Plot A for grain-size analysis four months after its construction. The gravel and sand-size fractions were analyzed using standard dry-sieving techniques; the silt and clay-size fractions were analyzed using standard pipetting techniques (Krumbein and Pettijohn, 1938).

4. Results

Wilcoxson Rank Sum tests were performed to detect differences in the densities of newly settled spat between treatments in Plot A with those in Plots II and III (Hollander and Wolfe, 1973). No significant differences ($p > 0.05$) were found. Edge effects due to the size of the plots were considered to be insignificant and all like treatments in the different plots were thus combined for analysis.

The average length of newly settled clams ranged from 0.197 mm to 0.207 mm. A Kruskal-Wallis test (Hollander and Wolfe, 1973) detected a significant difference ($p < 0.01$) in the average length of clams that settled into the different treatments (Table 1). A series of Mann-Whitney U pairwise comparisons (Hollander and Wolfe, 1973) were performed to test which treatments differed significantly (Table 2).

The average density of clam spat ranged from approximately 18,600-31,200/m^2. A Kruskal-Wallis test detected a significant difference ($p < 0.001$) between densities of clams in the different treatments (Table 3). Mann-Whitney U pairwise com-

Table 1. Kruskal-Wallis Test. H_o: No difference in the mean length of clams sampled from different experimental substrata.

Treatment	High intertidal substratum, no adult clams	Low intertidal substratum, no adult clams	Low intertidal substratum, ambient adult clam density	Low intertidal substratum, high adult clam density
n	30	32	29	23
Mean length (mm)	0.207	0.201	0.201	0.197
Standard deviation	0.01	0.02	0.02	0.01
Mean rank	73.9	54.2	56.5	42.0
N = 114				
	H_o: rejected	$\chi^2 = 14.49$	$p < 0.005$	

parisons were performed to test which treatments differed significantly (Table 4). The average density of clams was significantly different between all treatments with the exception of Treatment 2 compared with Treatment 3.

A series of Kruskal-Wallis tests were performed to determine if the density of clams per core within each treatment varied for the different positions of that treatment in the Latin square design of Plot A. No significant differences ($p > 0.05$) were detected between clam densities within Treatments 2-4. A significant difference ($p < 0.05$) was detected in the density of clam spat sampled per core from

Table 2. Mann-Whitney U pairwise comparisons. H_o: No difference in mean length of clams between experimental treatments.

Treatment	U	Z-value	2-tailed p	H_o
1 vs 2	646.5	2.4636	< 0.05	rejected
1 vs 3	583.0	2.3722	< 0.05	rejected
1 vs 4	521.5	3.2940	< 0.01	rejected
2 vs 3	439.5	−0.3915	> 0.05	not rejected
2 vs 4	453.5	1.5708	> 0.05	not rejected
3 vs 4	429.0	1.9275	> 0.05	not rejected

Table 3. Kruskal-Wallis Test. H_o: No difference in the density of clams sampled from different experimental substrata.

Treatment	High intertidal substratum, no adult clams	Low intertidal substratum, no adult clams	Low intertidal substratum, ambient adult clam density	Low intertidal substratum, high adult clam density
n	25	22	23	22
Mean density/core	63.3	55.1	48.7	37.8
Standard deviation	13.4	14.0	16.4	12.6
Mean rank	65.7	52.0	41.4	24.5
N = 92				
	H_o: rejected	$\chi^2 = 29.71$	$p < 0.0001$	

Table 4. Mann-Whitney U pairwise comparisons. H_o: No difference in the density of clams sampled from different experimental treatments.

Treatment	U	Z-value	2-tailed p	H_o
1 vs 2	177.5	−2.0801	< 0.05	rejected
1 vs 3	135.0	−3.1496	< 0.01	rejected
1 vs 4	52.0	−4.7567	< 0.001	rejected
2 vs 3	197.0	−1.2722	> 0.05	not rejected
2 vs 4	94.0	−3.4747	< 0.001	rejected
3 vs 4	161.0	−2.0902	< 0.05	rejected

Treatment 1 substrates, located in the different rows of the Latin square array (Table 5). A series of Mann-Whitney U pairwise comparisons were performed to test which rows significantly differed (Table 6). The top three rows (closest to the oyster dike) did not differ from each other. Only row d (closest to the water) differed from the two middle rows (b and c) in the Latin square design. This small amount of difference was assumed to not bias the results.

5. Discussion

Based on the results of this study, my hypotheses that the presence of adult clams is independent of, or positively correlated with, the level of Manila clam settlement are rejected. A negative correlation was found between the number of newly settled spat and density of adult clams. Fewer clams settled in treatments with adult clam concentrations than in treatments without adults, although the difference between Treatment 3 (with adults) and Treatment 2 (without adults) was not statistically significant. Even in the treatment with the highest density of adults, there was nonetheless a large larval settlement (ca. 18,200/m^2); thus the hypothesis of Woodin (1976) that no larvae can successfully settle in areas with high infaunal abundance of filter feeders is also rejected.

Treatment 4, with double the normal adult clam abundance, had significantly fewer spat. Two mechanisms related to adult abundance may have accounted for this: (1) some larvae in close proximity to adults were directly inhibited from successful settlement and/or (2) the larvae selectively settled away from the adults. Some research has indicated that adult populations of benthic invertebrates can cause substantial larval mortality. Thorson (1957) estimated that an adult mussel can filter out 100,000 larvae in 24 hours. Kristensen (1957) found that spat of *Cardium edule* were inhaled by adults during feeding, wrapped in mucus, and discharged as pseudofeces. This entanglement in mucus caused high mortality. Similar causes of death were also observed by Mileikovsky (1974) with other invertebrates. In this study, larvae may have been filtered from suspension by clam siphons as they approached the substrate in the process of settling. It was unknown whether

Table 5. Kruskal-Wallis Test. H_o: No difference in the density of clams sampled from Treatment 1 substrata in different rows of experimental Plot A.

Row	a	b	c	d
n	5	5	5	5
Mean density/core	58.6	70.2	72.8	48.0
Standard deviation	6.5	10.9	16.4	7.0
Mean rank	9.6	14.2	14.2	4.0
N = 20				
H_o: rejected	$\chi^2 = 10.14$		$p < 0.05$	

this was the major cause of the difference in larval settlement detected. Neither could it be determined whether or not larvae actively settled away from the adults. Hypothetically, larvae may elect not to settle on a substratum if adult clam siphons are detected directly or some evidence resulting from the presence of clams is detected. The former implies an ability to detect adults without being inhaled, and the latter implies an ability to detect a concentration gradient away from the adults of some substance, be it bacterial metabolites, adult metabolites, or food. As larval settlement differed between, but not within, the treatments of the Latin square array in Plot A, it indicated that adult metabolite concentrations were minimal cues for settlement, except possibly in the area immediately adjacent to the exhalent siphons.

Not all of the differences in settlement between treatments could be accounted for entirely by the presence or absence of adult clams. There were significant differences in settlement between Treatments 1 and 2, but neither of them had adults. In all treatments, but particularly in those without adults, the settling larvae may have been influenced by other macrofaunal components in the substrate or by the meio- or interstitial-faunal community in the sediment which has been stated to be related to grain size composition (McIntyre, 1969; Swedmark, 1964; Williams, 1972). However, the grain size between Treatments 1 and 2 did not appear to differ (Table 7). No estimates of packing or porosity of the sediment were made for any of the treatments. Neither were quantitative measures made of the microfloral, macrofloral, or meiofaunal composition. During construction of the study plots, the only macrofaunal organisms observed besides Manila clams, were two other filter feeding clams (*Prototheca* sp. and *Saxidomus* sp.) and two detritus feeders: a small (<2.0 cm) clam (*Macoma* sp.) and a ghost shrimp (*Callianassa* sp.). The incidence in Treatment areas 3 and 4 of *Protheca, Saxidomus,* and *Macoma,* based on the number removed from Treatment areas 1 and 2, was approximately 3, 0.25, and 2, respectively. Compared with Manila clams, the effect of these few clams on settling was assumed to be inconsequential. Due to the depth of ghost shrimp burrows, none were removed during construction of the plots. Burrows were assumed to be randomly dispersed throughout the treatments, with a maximum of two bur-

Table 6. Mann-Whitney U pairwise comparisons. H_o: No difference in the density of clams sampled from Treatment 1 substrata in different rows of experimental Plot A.

Treatment row	U	Tabled 2-tailed p $n_1 = 5, n_2 = 5$	H_o
d vs c	24	< 0.05	rejected
d vs b	24	< 0.05	rejected
d vs a	22	> 0.05	not rejected
c vs b	14	> 0.05	not rejected
c vs a	18	> 0.05	not rejected
b vs a	21	> 0.05	not rejected

rows observed in any one treatment area. Thus no direct cause other than high adult abundances of clams could be related to any of the differences in larval settlement detected between treatments.

Although settling occurred three months after construction of the treatment substrata, there were no apparent changes in the integrity of the plots. No clam siphons or holes were observable in, and no adults were taken with sample cores from Treatments 1 and 2. The abundance of adult clams within each treatment substratum was thus assumed to be unchanged from the time of initial construction.

No account could be made for the differences in length of newly settled spat detected between treatments on the basis of the data obtained.

The large larval settlement of clam spat observed in this study can not be considered an anomaly. Ikematsu (1957) reported Manila clam settlements ranging from 200,000 to 1,800,000/m^2. McIntyre (1969) reported 72,000/m^2 0-year old *Cardium edule,* but made no mention of their size. Ohba (1959) predicted Manila clam settlements in Japan to be approximately 25,000/m^2 based on numbers of larger spat that he collected. Muus (1973) found clam spat levels of 5,000-8,000/m^2, in a number of species, although the smallest sieve used (0.246 mm) probably missed the newly settled spat. None of these studies correlated their findings to adult clam abundances, but the high levels of settlement that they found and the results of this study indicate that infaunal filter feeding adults can not preclude successful settlement of larvae. Thus patterns of dense infaunal abundances of filter feeders must be based on some other mechanism.

Table 7. Grain size analysis of two sediment samples taken from Treatments 1 and 2 from experimental Plot A in Little Skookum Inlet, Washington.

Samples	PHI Units	Size in mm	Composition (%)
Treatment 1	<−2.0	>8	31.3
	−2.0 to 0.0	2-8	29.9
	0.0 to 1.0	1-2	9.6
	1.0 to 2.0	0.5-1.0	12.0
	2.0 to 4.0	0.062-0.5	9.0
	>5.0	<0.062	8.2
Treatment 2	<−2.0	>8	29.5
	−2.0 to 0.0	2-8	25.5
	0.0 to 1.0	1-2	13.0
	1.0 to 2.0	0.5-1	14.2
	2.0 to 4.0	0.062-0.5	10.3
	>5.0	<0.062	7.5

Acknowledgments. Thanks to K. K. Chew, J. L. Congleton, P. A. Jumars, and P. L. Illg for their advice and assistance. Daniel B. Quayle helped with the identification of young Manila spat.

Office space and materials for field work were provided by R. R. Whitney, Leader, Washington Cooperative Fishery Research Unit at the University of Washington. Michael Shepard, T. Schink, and R. Carter provided assistance with the field work. My special thanks to J. Taylor who allowed me to use his beach for this study. His wisdom gained from years of commercial clam and oyster harvesting provided me with valuable insight into the biology of the Manila clam.

Editorial comments by two anonymous reviewers were helpful in the preparation of this manuscript.

REFERENCES

Bayne, B. L. 1965. Growth and the delay of metamorphosis of the larvae of *Mytilus edulis* (L). Ophelia, *2,* 1–47.

—— 1969. The gregarious behavior of the larvae of *Ostrea edulis* at settlement. J. Mar. Biol. Assoc. U.K., *49,* 327–356.

Crisp, D. J. 1974. Factors influencing the settlement of marine invertebrate larvae, *in* Chemoreception in Marine Organisms, P. T. Grant and A. M. Mackie, eds., Academic Press, London, 105–141.

Crisp, D. J. and P. S. Meadows. 1962. The chemical basis of gregariousness in cirripedes. Proc. R. Soc. B., *156,* 500–520.

Doyle, R. W. 1975. Settlement of planktonic larvae: a theory of habitat selection in varying environments. Amer. Natur., *109,* 113–126.

—— 1976. Analysis of habitat loyalty and habitat preference in the settlement behavior of planktonic marine larvae. Amer. Natur., *110,* 719–730.

Eagle, R. A. 1975. Natural fluctuations in a soft-bottom community. J. Mar. Biol. Assoc. U.K., *55,* 865–878.

Fitch, J. E. 1965. A relatively unexploited population of Pismo clams *Tivela stultorum* (Mawe, 1923). Proc. Malac. Soc. Lond., *36,* 309–312.

Gillmor, R. B. and K. Y. Arakawa. 1976. Some field experiments on settling in *Crassostrea gigas.* Mukaishima Mar. Biol. Station, Hiroshima Univ. Contr. No. 133, 14 pp.

Hamilton, A. L. 1969. A method of separating invertebrates from sediments using longwave ultraviolet light and fluorescent dyes. J. Fish. Res. Board Can., *26,* 1667–1672.

Hancock, D. A. 1970. The role of predators and parasites in the fishery for the mollusc *Cardium edule* L., *in* Dynamics Numbers Population, P. J. den Boer and G. R. Gradwell, eds., Proc. Adv. Study Inst. Osterbrook, 419–439.

—— 1973. The relationship between stock and recruitment in unexploited invertebrates. Cons. Perm. Int. Explor. Mer. Rapp. P.-V. Reun., *164,* 113–131.

Heip, C. 1975. On the significance of aggregation in some benthic marine invertebrates, *in* Proc. 9th Europ. Mar. Biol. Symp., H. Barnes, ed., Aberdeen Univ. Press, 527–538.

Hidu, H. and H. Haskin. 1971. Setting of the American oyster related to environmental factors and larval behavior. Proc. Nat'l. Shellfish Assoc., *61,* 35–50.

Holland, A. F. and J. J. Dean. 1977. The biology of the stout razor clam *Tagelus plebeius*: I. Animal sediment relationships, feeding mechanisms, and community biology. Chesapeake Sci., *18,* 58–66.

Hollander, M. and D. A. Wolfe. 1973. Nonparametric statistical methods. John Wiley and Sons, New York. 503 pp.

Hughes, R. N. 1970. Population dynamics of the bivalve *Scrobicularia plana* (Da Costa) on an intertidal mudflat in North Wales. J. Anim. Ecol., *39,* 333–356.

Ikematsu, W. 1957. Ecological studies on the clam *Tapes japonica* (Reeve) II. On setting season and growth in early young state (in Japanese, English summary). Bull. Jap. Soc. Scient. Fish., *22,* 736–741.

Johannessen, O. H. 1973. Population structure and individual growth of *Venerupis pullastra* (Montagu). Sarsia, *52,* 97–116.

Keck, R., D. Mauer, J. C. Kauer, and W. A. Sheppard. 1971. Chemical stimulants affecting oyster larval settlement in the American oyster. Proc. Nat'l. Shellfish. Assoc., *61,* 24–38.

Keck, R., D. Mauer, and R. Malout. 1973. Factors influencing the settling behavior of larval hard clams, *Mercenaria mercenaria.* Proc. Nat'l. Shellfish. Assoc., *64,* 59–67.

Knight-Jones. 1953. Decreased discrimination during settling after prolonged planktonic life in larvae of *Spirorbis borealis.* J. Mar. Biol. Assoc. U.K., *22,* 337–345.

Kristensen, I. 1957. Differences in density and growth in a cockle population in the Dutch Wadden Sea. Arch. Neerl. Zool., *12,* 350–453.

Krumbein, W. C. and F. J. Pettijohn. 1938. Manual of sedimentary petrology. Appleton-Century-Croft, Inc. New York. 549 pp.

Larman, V. N. and P. A. Gabbott. 1975. Settlement of cyprid larvae of *Balanus balanoides* and *Elminius modestus* induced by extracts of adult barnacles and other marine animals. J. Mar. Biol. Assoc. U.K., *55,* 183–190.

Levinton, J. 1972. Stability and trophic structure in deposit-feeding and suspension-feeding communities. Amer. Natur., *106,* 472–486.

Loosanoff, V., H. Davis, and P. Chanley. 1966. Dimensions and shapes of larvae of some marine bivalve molluscs. Malacol., *4,* 351–435.

McIntyre, A. D. 1969. Ecology of marine meiobenthos. Biol. Rev., *44,* 245–290.

Mileikovsky, S. A. 1974. On predation of pelagic larvae and early juveniles of marine bottom invertebrates by benthic adult invertebrates and their passing alive through their predators. Mar. Biol., *2,* 303–311.

Moore, P. G. 1975. Habitat selection in marine animals. Mar. Behav. Physiol., *3,* 97–100.

Muus, K. 1973. Settling, growth and mortality of young bivalves in the Øresund. Ophelia, *12,* 79–116.

Ohba, S. 1959. Ecological studies in the natural population of a clam, *Tapes japonica,* with special reference to seasonal variations in sizes and structure of the population and to individual growth. Biol. J. Okayama Univ., *5,* 13–42.

Paul, A. J. and H. M. Feder. 1973. Growth, recruitment, and distribution of the littleneck clam, *Protothaca staminea,* in Galena Bay, Prince William Sound, Alaska. Fish. Bull., *71,* 665–677.

Quayle, D. B. 1951. Structure and biology of the larvae and spat of *Venerupis pullastra* (Montagu). Trans. R. Soc. Edinb., *62,* 25–297.

Swedmark, B. 1964. The interstitial fauna of marine sand. Biol. Rev., *39,* 1–42.

Thorson, G. 1957. Bottom communities, *in* Treatise on Marine Ecology and Paleoecology. The Geol. Soc. Amer. Mem., J. W. Hedgpeth, ed., Vol. 67, pt. 1, 461–535.

—— 1966. Some factors influencing the recruitment and establishment of marine benthic communities. Netherlands J. Sea Res., *3,* 267–293.

Veitch, F. P. and H. Hidu. 1971. Gregarious setting in the American oyster *Crassostrea virginica* Gmelin: I. Properties of a partially purified "setting factor". Chesapeake Sci., *12,* 173–178.

Wendell, F., J. DeMartini, P. Dinnel, and J. Siecke. 1976. The ecology of the gaper clam or horse clam, *Tresus capax* (Gould 1850), in Humboldt Bay, California. Calif. Fish and Game, *62,* 41–64.

Williams, R. 1972. The abundance and biomass of the interstitial fauna of a graded series of shell-gravels in relation to the available space. J. Anim. Ecol., *41,* 623–646.

Wilson, D. P. 1953. The settlement of *Ophelia bicornis* Savigny larvae. J. Mar. Biol. Assoc. U.K., *31,* 413–438.

Woodin, S. A. 1976. Adult-larval interactions in dense infaunal assemblages: patterns of abundance. J. Mar. Res., *34,* 25–41.

Received: *15 August, 1979;* revised: *12 August, 1980.*