SOME ASPECTS OF THE ECOLOGY OF A BIVALVE MOLLUSK IN KANEHOE BAY, OAHU, HAWAII

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INTRODUCTION

The bivalve, *Tapes philippinarum* Adams and Reeve, 1867, was introduced in Hawaii around 1900 (Bryan, 1918). The clam originally came from Japan where, according to Cahn (1951), it is one of the most important commercial species of shellfish. It is cultured in bays throughout Japan, Korea, and the Philippines. *Tapes* was accidentally introduced to the Pacific coast of North America when Japanese oysters, *Crassostrea gigas*, were brought there early in the century (Bonnot, 1935). The clam spread rapidly and is now one of the more important commercial clams there.

*Tapes philippinarum* is a member of the family Veneridae and appears in the literature under a variety of names including *T. semidecussata* Adams and Reeve 1864, and *T. japonica* Deshayes, 1853. Various generic names are also applied: *Venerupis*, *Venus*, *Ruditapes* and *Paphia*. The clam has been identified for me as *Tapes philippinarum* by Dr. E. A. Kay, who compared Hawaiian shells with type material at the British Museum (Natural History) and will be so called throughout this paper. A common name, the Japanese littleneck clam, is almost universally accepted; "Asari" is the Japanese name.

The most extensive work concerning life history and ecology of *Tapes* was done by Cahn (1951) who summarizes the Japanese literature. Its natural history and shell
pattern were described by Shaw (1950). Other references are limited to mention of its first appearance on the Pacific Coast (Keen, 1947; Kincaid, 1947a, 1947b; Neave, 1944).

After its introduction to Hawaii the clam apparently spread rapidly in shallow bays on Oahu and was used extensively as food. Bryan (1918) reported that it became well established in the Kalihi and Moanalua mud-flats. Ostergaard, (1930) and Dall, (1938) confirmed its successful establishment. Edmondson, (1946) also stated that after its introduction, *Tapes philippinarum* multiplied rapidly in shallow bays about Oahu and was common in Honolulu fish markets.

Distribution of *Tapes* throughout the islands today is poorly known, but its abundance appears to have declined since the initial spread. The beds in the Kalihi, Moanalua, and Pearl Harbor mud-flats have disappeared (personal communication -- Mr. Sam Okamura, Hawaii Institute of Marine Biology, and Mr. Henry Sakuda, State Division of Fish and Game). Kaneohe Bay, Oahu is the only area where there are enough for exploitation.

The earliest recorded planting in Kaneohe Bay occurred in 1920 (Dall, 1938). The clam became successfully established and, though there is no documented information, presumably spread considerably. At present it is abundant on the shallow water reef platforms of
the southeast Bay and is harvested extensively during a short clam season regulated by the State Division of Fish and Game.

The waters of southeastern Kaneohe Bay have undergone change recently because of extensive building ashore which has increased the flow from the two streams which empty here (Bathen, 1968). In addition, two recently constructed sewer outfalls discharge treated sewage into the southeast section. Exchange with ocean water is slow leading to accumulation of sewage and water from run-off (Bathen, 1968). Accompanying these changes have been undocumented reports of atypical phytoplankton blooms, an increase in the abundance of *Tapes*, and a decrease in the population of the brachiopod *Lingula reevii*. These changes could be caused by increased run-off and pollution in this sector of the bay although there is no documentation.

With these factors in mind, this study was made to: (1) to collect relevant ecological data particularly on the distribution and growth of clams in various parts of the bay in order to determine what limits distribution, and any effects pollution may have on the clam beds; (2) to determine interaction of *Tapes* with other species, particularly predators and *L. reevii*, a co-occurring filter feeder; and (3) to study the effects of harvesting on abundance and population structure.
METHODS

Preliminary Survey

*Tapes philippinarum* occurs on a series of shallow water reef platforms (avg. depth 1m) which extend around the periphery of southeastern Kaneohe Bay (Fig. 1). A preliminary survey of the area was conducted during June-August of 1967 to determine the distribution of the clams. Transects were run across the platforms from reef edge to shore at 100 meter intervals. The position of the transects was first selected from aerial photographs and subsequently located in the field. A fifty meter rope marked at ten meter intervals was used to measure distance. Environmental factors, particularly sediment type and distribution of *Lingula reevii*, were also recorded. Mr. W. S. Worcester, who is concurrently investigating the brachiopod, collaborated on the survey.

Notes were taken every fifty meters. If substratum type or relative abundance of *Tapes* and *Lingula* changed at intervals of less than 50m, these changes were measured where they appeared. To maintain precision, all field observations were made by Mr. Worcester and recorded by me. Whenever possible, field work was done at low tide while the reef platforms were exposed.
Figure 1. Southeast Kaneohe Bay showing reef platforms and Clam Beds 1-7 (stipled areas). Approximate scale: 1 cm = 250 m
Quantitative Sampling

Each clam bed was staked out prior to sampling and paced off to roughly determine overall dimensions and shape, and a drawing was made of each bed. Sampling was done randomly and by transects. The locations of random samples were selected using a co-ordinate system with the X axis running the length of the bed and the Y axis across. Paired numbers from a table of random digits were used to position each sample. Measurement of the distance from the axes to sample positions were paced off. Stratified samples were taken at five meter intervals along transects across the bed. The number of samples varied from ten to forty depending on the size of the bed. Samples were taken by inserting a \( \frac{1}{20} \text{m}^2 \) quadrat into the bottom. The substrate from the top 10 cm (the clams do not live much below 7 cm) was removed and passed through a screen of 5 mm mesh. The material retained by the screen (broken shells, pebbles, and live clams) was placed in a plastic bag marked to indicate the sampling point. Samples were frozen for later study.

RESULTS AND DISCUSSION

Preliminary Survey

The reef platforms are flat except for a narrow band of dead, broken coral heads along the perimeter of each platform. At the perimeter the reef slopes sharply to the bottom of the bay. Substrate behind and among the coral
heads is predominantly a mixture of calcareous sand, shells and gravel. The sediment in many inshore areas, especially around the mouths of streams, is mud.

The clams occur in aggregations or beds generally close to the fringe of the reef platforms and near deeper water (Fig. 1). I found beds in various types of substrate as did Shaw (1950). Although beds could be found in bottom varying from rubble to mud, they were predominantly located in a sand, shell, gravel mixture as Cahn (1951) found. The borders of beds were not related to visible changes in substratum. Thus the type of bottom does not appear to be an important factor in distribution.

Clam beds were usually in quiet water and near elevated areas such as bars. This suggests that distribution may be related to water velocity or the larvae may have an optimum settling depth. In Japan the larvae settle only where the current is gentle (Cahn, 1951).

Movement and Behavior

Normally the adult Tapes are found entirely buried in the bottom, the anterior end down with the siphon ends just above the surface. Among twenty individuals studied for a month in the laboratory no movements were observed other than initial burial in the sand. Once buried, the only activity observed was protrusion and withdrawal of the siphons associated with pumping and ejection of
pseudofeces from the mantle cavity. If the clams were covered with more sand, they moved upwards and reburied if uncovered. Actively burrowing individuals could bury themselves in less than ten minutes. If the water was allowed to stagnate they would come to the surface and rebury if supplied with clean water.

In the field, the young, and frequently the adults were found attached by a byssus to a small pebble or dead shell, indicating that the clams remain stationary for some period of time.

**Predators**

Large numbers of broken shells in the clam beds suggest that crabs are probably the most important predators on *Tapes*. Predation by crabs on bivalves is well known (Shoup, 1968). Many species are able to crush the shell with their chelipeds.

Two crabs, *Calappa calappa* and *Thalamita* sp., were observed feeding on *T. philippinarum* in the laboratory. *Calappa* searches for clams from the surface of the substrate, probing its first two pairs of ambulatory legs into the sand until a clam is located. It then unearths the clam and rolls it over several times using the chelae and first two pairs of legs. Then, the crab breaks the shell; the heavy teeth on the right cheliped were not used as described by Shoup (1968) for *Calappa*. Clams of all sizes could be opened, although larger clams required
more time. In some cases, the larger clam shells were not totally crushed. Rather, the tips of the shell were chipped as if the crabs had only gradually gained access to the soft parts.

To determine predation rates of *Calappa*, fifty clams ranging in shell length from 10-30 mm were placed in four separate compartments in a tank supplied with running water and allowed to bury themselves in the bottom. Four *Calappa* specimens ranging in size from 65-75 mm across the carapace were introduced into the tank, one specimen per compartment. Every two days the crabs were removed and placed in an alternate tank with 50 clams in four compartments as previously described. The soil in the first tank was screened and the clams counted. Then additional clams were added to make the number up to fifty. Two days later the crabs were returned to the first tank and so on for a total of 20 days.

One crab ceased feeding while molting and the data for it were discarded. The three remaining crabs ate a total of 354 clams for an average of 5.9 clams/crab/day. Probably because the crabs were hungry the rate was higher at first and declined for the first six days after which the crabs ate a relatively constant number of clams/day. Thus the rates for the last 14 days, 6.3, 3.6, and 3.0 clams per day are probably more appropriate for the field.
Thalamita burrowed in the sand for clams and was also able to break open all sizes of clams. In another similar experiment one Thalamita ate an average of 5.2 clams/day for 20 days.

Neither Calappa nor Thalamita were observed actually breaking open shells of Tapes in the field. However, on several occasions, both species were found holding intact clams. Thalamita is more common on the reef flats in the vicinity of the clam beds, and is probably the more important of the two predators. Their estimated abundance near Bed 1 was about 4 crabs/10 m² or more. This indicates a consumption of approximately 2 clams/m²/day or about 700 clams/m²/yr. Mean clam density for Bed 1 was approximately 3000 clams/m² before clam season, and thus Thalamita could conservatively account for a 23% yearly mortality.

Crabs probably play an important role in Tapes distribution by limiting the clams to areas where recruitment is sufficient to sustain such predation. Transplants of clams from Bed 1 to several areas of the Bay were unsuccessful probably because of crab predation. Several months after transplanting, the only sign of clams were broken shells. In the beginning of the growth study some boxes were left uncovered. The clams were almost completely lost within 30 days and crabs were primarily if not entirely responsible. This suggests that crabs exert a considerable influence on distribution and that before a new clam
bed can be established there must be sufficient numbers and recruits, or control of crabs.

The gastropod Natica marochiensis was also found to prey on Tapes. This snail was first discovered in a growth box (Station 3) in which nine clams had been consumed over a maximum period of 30 days. It was brought into the laboratory and placed in a tank with 25 clams. The snail attacked clams by enfolding the clam in its foot and boring a small, circular hole, generally in the umbonal region. One clam was regularly consumed every three days for a period of 18 days. Although larger clams were available, clams attacked were 20 mm or less in length, indicating that smaller clams are taken more readily than larger ones. This observation is supported by field samples in which shells with drill holes similar to those of Natica were 28 mm or less in length. However this predator was not commonly observed and is probably a minor cause of mortality in the beds.

**Salinity**

It has been suggested that Tapes appears to be restricted to brackish water in the Hawaiian Islands and is easily killed by either fresh or sea water (Bryan, 1918; Dall, 1938). Bryan recorded an instance when a flood presumably killed an entire population on the Ewa mud flats. My observations indicate that normal sea water does not adversely affect Tapes. I have kept the clams for several
months in aquaria containing normal sea water (34.8 o/oo) and the clams occur naturally in salinities of 31-35 o/oo in Kaneohe Bay (Bathen, 1968).

To investigate the effects of reduced salinity, the clams were placed in water ranging from 0 to 35 o/oo. Filtered sea water was obtained from the well at Coconut Island and diluted with tap water. Dilutions were made assuming a salinity of 35 o/oo and were accurate to ±0.5 o/oo based on salinometer measurements. Intervals of 5 o/oo were initially selected. For each salinity ten clams, ranging in length from 10 to 30 mm, were placed in a one-half gallon jar, each supplied with an air stone.

Within nine days, all clams in fresh and 5 o/oo water were dead. Within 13 days, eight out of ten clams at 10 o/oo had died, but the remaining two survived for 29 days. All the clams in the 15-35 o/oo categories survived for 41 days when they began to die sporadically; but at least half of the clams remained in each category at the end of 50 days when the experiment was terminated. Since the interval of 10-15 o/oo was the critical range, experiments were conducted at salinities of 11.5 and 13.5 o/oo. All the clams at 11.5 o/oo died eight days later but all at 13.5 o/oo survived for 38 days. When experiments were run at 12, 13 and 13.5 o/oo the clams at 12 and 13 o/oo died within eight days while those at 13.5 o/oo survived. This experiment was repeated and results were similar.
These results indicate that adult *Tapes* can tolerate salinities ranging from 35 o/oo or greater to around 13.5 o/oo for prolonged periods. This agrees with their distribution in the field. The clams are not found in areas of pure or nearly pure fresh water. Thus it is likely that continuous low salinities, at the mouths of streams for example, limit their distribution.

**Settling of Larvae**

Changes of size frequency with time of clams in Bed 1 (Fig. 2 B, C) indicated that settling of larvae occurred between February and June 1968. The 24 February sample (Fig. 2 B) was unimodal showing one size class, while the 26 June sample was bimodal, the mode at 8 mm representing newly settled individuals.

The lower mode shifted to 16 mm by 28 August 1968, (63 days later) suggesting a growth rate of about 4 mm/month for these young clams. If the growth rate from settling to 8 mm is similar, greatest settling occurred approximately two months before the 26 June sampling, probably in late April. The larger clams (15 mm) of this size class probably settled in February and the smaller (3 mm) in June.

Other evidence suggested the clams were settling as early as February. On 13 February 1968, Mr. Worcester sifted some substratum in the vicinity of Clam Bed 1 through a 1/16 inch mesh sieve. The particles passing
Figure 2. Size distribution of T. philippinarum in samples taken from Clam Bed 1 during 1967-1968.
Figure 2. (continued) Size distribution of T. philippinarum in samples taken from Clam Bed 1 during 1967-1968.
through the sieve were used for substrate in a laboratory tank for a growth study of *L. reevii*. A month later he noticed small clams among the brachiopods suggesting that newly settled clams small enough to pass through the sieve were in the substratum at the time it was obtained. However, the substrate had been kept in running sea water, and clam larvae may have come in through the water system. To check this possibility, the clams were removed from Mr. Worcester's tank, and a new tank containing sediment from Bed 1 that had been sifted through a 1/16 inch mesh screen was set up. Clams never reappeared in Mr. Worcester's tank but did appear in the new tank. This indicated that clams were already present in the substrate he sifted on 13 February and thus that larvae were settling in the field as early as February.

The soil in the June 26th sample was examined under a microscope for newly settled larvae. No individuals under 3 mm were found, indicating that settling was largely finished. The shift in modes between the June and August samples, with no new size clams appearing, further indicates that settling was probably over by June. Thus settling occurred in the Spring probably between February and June with a peak in April-May.

**Size at First Maturity**

The gonads of fifty clams ranging in size from 9.1 to 35.0 mm but mostly between 15 - 25 mm in length were
examined to determine the size at first maturity. The gonad, when developed is milky white in color and situated in the viscera just above the foot. I found sperm in males from 16.1 mm and longer and eggs in females for sizes 18.2 mm and longer. Below these sizes, the gonads were poorly developed, and no sperm or eggs were found. Thus 16.1 mm and 18.2 mm in length are probably the minimum length at maturity. In general the gonads of specimens 20 mm and over were better developed than those under this length, indicating that the clams start maturing just under 20 mm and are mature by the time they reach this size.

Weight Relationships

Maximum shell length in millimeters was related to total weight in grams by the equation, $W = 1.75 \times 10^{-3} L^{3.06}$ as determined by linear regression on the logarithms of length and weight from 500 individual measurements of clams 11-38 mm long.

The relation of body weight to total weight was determined from 27 samples totaling 214 clams taken during 1966 from various parts of Kaneohe Bay. The total weight of all the clams in each sample was measured and recorded. Then the clam bodies were removed, dried on a paper towel and weighed. The average body weight-total weight ratio for the 27 samples was 0.31. The range was 0.21-0.39. The 95% confidence intervals were 0.29-0.33.
Spatial Distribution and Density Within a Clam Bed

Density of clams in Bed 1 at random points and along transects is shown in Fig. 3A. The average density within the bed was 30 clams/dm² for random points and 29/dm² for the transect data. The range for the random points was large (1-66/dm²) and the index of dispersion (Fisher, 1925) was 433 indicating an aggregated distribution (p<0.01).

The transects (Fig. 3B) show a peak of density in the central area and high densities for the random points are likewise concentrated in the interior. The density drops off sharply on the seaward edge and more gradually shoreward. The equation $D = A e^{- Ky}$ was used to describe the sampling data in which:

- $D$ = density
- $A$ = amplitude of the curve
- $y$ = distance along the y axis
- $k$ = a constant which positions the maxima of the curve
- $e$ = the base of Naperian logarithms

This equation was suggested by Dr. H. A. Loomis of the Hawaii Institute of Geophysics who also provided a computer program to determine the curve of best fit. For fitting, all transects and random sampling points were scaled to twenty meters in length and best fit was determined by iterating values of $A$ and $K$. The scaled data and calculated curve for Bed 1 are shown in Fig. 3C. The curve provides an objective and useful means of describing
Figure 3. (A) Diagramatic representation of Clam Bed 1 before clam season showing axes, transects, sampling points and the number of clams/dm² at each sampling point. (B) Clam density plotted across the width (Y-axis) of Bed 1. Transect points are connected by lines and show a peak density in the central area of the Bed (Transact 1, Transact 2, Transact 3). (C) Curve of best fit plotted through the density points—width (Y-axis) has been standardized to 20 meters to provide a uniform boundary for the points to fall to zero.
the population density data.

This asymmetrical profile of clam density may be produced by crab predation. The crabs live in burrows on the shoreward side of the clam bed. I did not observe burrows in the bed or on the hard reef material of the seaward side. Crabs venturing into the bed to feed would encounter clams on the periphery first. Thus predation would be expected to be heaviest on the periphery of the bed and decline toward the interior. In the absence of predation the clam bed might have a symmetrical density profile.

The density profile may also be related to water depth. Clam Bed 1 was situated on a slightly elevated slope and, as previously mentioned, clam beds are often located in elevated areas such as sandbars. This slope might produce the density profile, if the larvae have an optimum settling depth.

**Comparative Growth Study**

To observe growth rates of *T. philippinarum* in different areas, masonite boxes containing sediment were placed on the bottom at various points in Kaneohe Bay from November 1967 to July 1968. The boxes were 40 x 40 x 20 cm deep, with numerous holes bored through the walls to allow water circulation. The tops were covered with one-half inch mesh screen to prevent entrance of predators. Each box contained 50 clams 10-20 mm in length. Sediment in the
boxes was standardized—three parts sand, one part shells and pebbles, a composition reported by Cahn (1951) to be best for growth. The boxes were placed at the following stations (Fig. 4):

1. Coconut Island. Depth 1 meter.
3. Kaneohe Marine Corps Air Station sewer outfall—approximately 5 meters from the flume. Depth 7 meters.
5. Clam Bed No. 6—approximately 10 meters north of Kaneohe Stream. Depth 1 meter.
6. The fish pond immediately north of Kaneohe Stream. Depth 0.5 meter.

Boxes placed at five other sites were lost or destroyed.

Shell length was measured to the nearest 0.1 mm at 30 day intervals with a Vernier caliper. The clams were not individually marked and thus the changes in average size provide estimates of average growth only. Total weight was also measured for the clams at Station 1.

The stations were located at different depths. Depth does not appear to affect growth, however, because at four different stations where growth was steady, the clams grew at approximately the same rate. None of the boxes were exposed at low tide. Owing to loss or destruction of growth boxes I had to replace some of them during the
Figure 4. Kaneohe Bay, showing station locations.
course of study. Consequently, the data are not completely homogeneous.

The first five months of growth data are shown in Table I for all stations except 3 (only 3 months are available). At Stations 3-6 the clams grew steadily as well as faster than at the other stations. The clams at Station 1 and 2 grew slowly and growth fluctuated from month to month. The clams at Station 7 survived but did not grow.

Pratt and Campbell (1956) measured growth rates of *Venus mercenaria* in different localities of Narragansett Bay, R. I. over a five year period using retrievable boxes containing clams in a constant substrate. Growth rates varied up to threefold in different localities, and there was a positive correlation between growth rate and concentration of phytoplankton. This appears to be the case for *T. philippinarum* in Kaneohe Bay. The southeast Bay is polluted, turbid, and has a higher standing crop of phytoplankton and other particulate matter resulting in rapid steady growth at Stations 3-6. The clams at Station 1 grew more slowly and also erratically. The erratic growth was probably related to variation in phytoplankton as Station 1 was in a poorly circulated dredged channel where the water varied from very clear to quite turbid with phytoplankton. The clams at Station 7 survived for three months but did not grow. After three months they were removed to Station 6.
Table I. Average growth increments at different stations for clams of initial shell length 10-20 mm.

<table>
<thead>
<tr>
<th>Station</th>
<th>Date From</th>
<th>Date To</th>
<th>Initial Mean Length, mm</th>
<th>Final Mean Length, mm</th>
<th>Increase, Per Mean Length, mm</th>
<th>Growth Per Month, mm</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>11/6/67</td>
<td>4/8/68</td>
<td>17.6</td>
<td>25.7</td>
<td>8.1</td>
<td>1.6</td>
</tr>
<tr>
<td>2</td>
<td>11/3/67</td>
<td>4/5/68</td>
<td>16.9</td>
<td>29.1</td>
<td>12.2</td>
<td>2.4</td>
</tr>
<tr>
<td>3</td>
<td>2/16/68</td>
<td>5/17/68</td>
<td>16.0</td>
<td>27.0</td>
<td>11.0</td>
<td>3.9*</td>
</tr>
<tr>
<td>4</td>
<td>2/16/68</td>
<td>7/17/68</td>
<td>15.4</td>
<td>32.0</td>
<td>16.6</td>
<td>3.3</td>
</tr>
<tr>
<td>5</td>
<td>2/16/68</td>
<td>7/17/68</td>
<td>16.3</td>
<td>31.7</td>
<td>15.4</td>
<td>3.1</td>
</tr>
<tr>
<td>6</td>
<td>11/6/67</td>
<td>4/6/68</td>
<td>16.3</td>
<td>32.6</td>
<td>16.3</td>
<td>3.2</td>
</tr>
<tr>
<td>7</td>
<td>3/3/68</td>
<td>6/1/68</td>
<td>19.0</td>
<td>19.0</td>
<td>0.0</td>
<td>0.0</td>
</tr>
</tbody>
</table>

*Only three months growth data are available at Station 3 which accounts for the high average value.
and, fresh clams were placed at Station 7 to ensure that the difference was not due to the original clams having been somehow damaged. The new clams at Station 7 did not grow either but the original clams which had been moved to Station 6 began to grow and after 60 days the mean shell length had increased 1.8 mm. There is probably insufficient nutrition for growth at Station 7 where the water is clear and more oceanic.

Other factors may have affected growth at Station 2. Station 2 was located among mangroves where there are considerable fluctuations in environmental conditions (Walsh, 1963). Temperature or salinity may have varied enough to retard growth but not enough to be fatal.

Sediment composition has a definite effect on growth rates of *T. philippinarum*. To test the effect of substrate on growth, one box at Station 6 was partitioned and the standard substrate (p. 21) was placed in one half, and a mixture of shells and pebbles in the other. Clams growing in the mixture of shells and pebbles without sand grew consistently slower than clams in the standard substrate (56% as fast over a four month period). At the same location clams in mud grew 83% as fast as clams in the standard sediment; however, this box was destroyed after two months and this figure may not be reliable. The clams did not grow without substrate. Previous work showed that *Mya arenaria* (Swan, 1952; Spear and Glude, 1957) and *Venus*
mercenaria (Pratt, 1953) grow faster in sand than in silt or mud when other factors are controlled. The sediment factor or factors responsible for this effect and their modes of operation are not understood.

**von Bertalanffy Growth Curve**

The von Bertalanffy growth curve was used to extrapolate and scale my growth data because it is known to describe shellfish growth fairly well (von Bertalanffy, 1957). The equation for the curve is usually written:

\[
L_t = L_\infty[1-e^{-k(t-t_0)}]
\]

where \(L_t\) is the shell length at time \(t\), \(L_\infty\) the maximum attainable size, \(k\) a constant related in its derivation to catabolism, and \(t_0\) a correction on the time axis.

Because growth and initial size were similar at Stations 3-6, all measurements from there were pooled in order to have the curve represented by the greatest number of clams. \(K\) and \(L_\infty\) were evaluated by plotting the regression of shell length at time \(t+1\) minus length at time \(t(L_{t+1} - L_t)\) on length at time \(t(L_t)\) where \(L_\infty\) is the \(Y\) intercept and slope is \(e^{-k-1}\) (Fig. 5). Estimates of slope and intercept were determined by linear regression. \(t_0\) was evaluated by substituting values for \(t_1\), \(t_2\), \(t_3\) and taking an average. Resulting plot and original data are shown in Fig. 6.

Using these constants, sizes were calculated for ages up to approximately 48 months (Fig. 6). This approximation
Figure 5. Method of fitting the von Bertalanffy equation to data. The slope of the line obtained from the regression on shell length at time $t + 1$ minus shell length at time $t$ ($L_{t+1} - L_t$) on the length at time $t$ ($L_t$) gives an estimate of $e^{-k} - 1$. The Y-intercept gives an estimate of $L_{oo}$. 

Slope = $e^{-k} - 1$
Figure 6. von Bertalanffy growth curve of shell length in *T. philippinarum*. Calculated and observed points are shown above. Number of clams representing each calculation: points 1-3, 242 clams; points 3-6, 198 clams; points 6-9, 43 clams.
stems from not having a precise estimate of the initial age of the experimental clams. They were probably about four months old based on the 4 mm/month estimate of growth rate of young clams described on p. 13. The calculated curve is close to observed points where data are available and predicts an \( L_\infty \) of 63 mm. The largest clam I found, 58 mm, was only slightly smaller. Thus the calculated curve appears fairly reliable.

The curve shows that starting at approximately 16 mm. *T. philippinarum* would reach a length of 44 mm at \( t_{12} = 1 \) year, 56 mm at \( t_{24} = 2 \) years, 60 mm at \( t_{36} = 3 \) years, and 62 mm at \( t_{48} = 4 \) years (4 months should be added to each time to get an estimate of total age). Clams in Bed 1 were all 4 mm or smaller indicating that they were between one and two years old. However, growth rates in the boxes were probably higher than in the crowded natural beds (see next section). Thus the larger clams found in nature may be considerably older than predicted.

If the lengths at each time are converted to weight, an S shaped curve is produced (Fig. 7). The curve indicates that weight increases rapidly from \( t_1 \) to about \( t_{28} \) growing from less than 1 gm to approximately 43 gm. Growth is considerably slower afterwards reaching only 51.5 gm at \( t_{36} \). **Growth in Clam Bed 1**

The shift in modes from 19 to 27 mm between 24 February 1968, and 28 August 1968, gave an approximate value for
Figure 7. Growth in weight of *T. philippinarum*. The curve was obtained by converting the shell lengths of Figure 6 into weight by the equation, $W = 1.75 \times 10^{-4} L^{3.06}$. 
growth in Bed 1 (Fig. 2 B, D). Thus in six months, the clams grew 8 mm or an average of 1.3 mm/month.

The growth ring associated with clam season from 1 December 1967 to 31 January 1968, (see next section) provided another means of estimating growth. Shell length at the ring and total shell length were measured for 100 clams from the 28 August 1968, sample. The difference between the two values varied considerably and ranged from 4.1 to 15.3 mm with a mean of 10.6 mm. The variation did not correlate with initial size, i.e. smaller clams growing faster than larger ones, but seemed to be due to individual variability in growth rate. This indicates a growth of 10.6 mm over about seven months or 1.5 mm/month which agrees fairly well with the value obtained from the shift in modes.

Growth estimates were also obtained from marked clams released into Bed 1. On 26 June 1968, two size classes of 100 clams each ranging from 22-24 mm and 25-27 mm were marked with enamel paint and released; the clams were obtained from Bed 1 and marked the same day. Of the original 200 clams, 34 were recovered on 28 August 1968, 19 from the 22-24 and 15 from the 25-27 mm size classes. The clams from the 22-24 mm size class ranged from 25.4 to 27.7 with a mean of 25.2 mm. The previous mean was 22.2 mm indicating a growth of 3.0 mm over 63 days, about 1.5 mm/month. The 15 clams recovered from the 25-27 mm class
ranged from 27.6 to 31.0 mm with a mean of 29.5 mm. The previous mean was 28.0 mm indicating a growth rate of about 1.7 mm/month. For clams of initial length 22.0 and 26.0 mm the growth curve predicts increases of 6.2 and 5.7 mm respectively over 60 days. This gives growth rates of 3.1 and 2.9 mm/month which is considerably faster than that observed in the marked clams.

Whatever the method, the growth rate, 1.3 to 1.7 mm/month, indicated for the clams in Bed 1 was considerably lower than growth in the boxes at Stations 3-6. Average growth was 20 mm for a six month period beginning at 19.8 mm at these stations, an average of approximately 2.9 mm/month or roughly twice the growth rate of Bed 1.

Since Bed 1 is very close to Station 3, I doubt that a difference in water properties would account for the dissimilarity of growth rates.

Crowding may be the reason for the different growth rates. Tapes populations in Japan are usually very dense per unit area and, if the young clams are allowed to remain in this crowded condition, shortage of food causes mortality and retarded growth among the survivors (Cahn, 1951). Artificial culture methods in Japan involve gathering the young clams and transplanting them to better conditions. As a result, the clams grow rapidly and become marketable within one or two years. In Hawaii, as in Japan, T. philippinarum occurs in dense beds. Mean density was 30 clams/dm².
in Bed 1 before clam season but ranged upward to 71/dm$^2$. Density in the growth boxes was only 5-6/dm$^2$ and the clams were evenly distributed as compared to the clumped conditions of Bed 1. Thus conditions in the boxes were probably better for growth.

**Effects of Harvesting**

Bed 1 was chosen to illustrate the effect of harvesting because more was known about its dimensions and density than those of any other clam bed. It had the highest density and underwent more exploitation than any other because of its accessibility to the clam diggers. Many of the other beds were in front of private property and could only be reached by boat. The mean densities before and after clam season for the remaining beds are given in Table II. Bed 2 actually showed an increase in density. It consisted of small clams and was evidently left alone by the clam diggers. The rise in density may be attributed to either sampling error or larval settling.

Clam season was first opened in 1966 but I did no sampling until the second season which ran from 1 December 1967-31 January 1968. During the latter season, I frequently heard diggers comment that the clams were more "bunched" than in 1966 and that the clams and clam beds were smaller. After the second season was over, I noticed a considerable reduction in the size of Bed 1. Length, approximately 100 meters, remained the same; however,
Table II. Mean clam density for samples taken from Clam Beds 1-7 before and after Clam Season.

<table>
<thead>
<tr>
<th>Bed Number</th>
<th>Mean Before, Clams/dm²</th>
<th>Mean After, Clams/dm²</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>32</td>
<td>14</td>
</tr>
<tr>
<td>2</td>
<td>24</td>
<td>28</td>
</tr>
<tr>
<td>3</td>
<td>9</td>
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<td>0.5</td>
<td>0.2</td>
</tr>
<tr>
<td>6</td>
<td>8</td>
<td>1</td>
</tr>
<tr>
<td>7</td>
<td>2</td>
<td>1</td>
</tr>
</tbody>
</table>
width was considerably reduced ranging from 12-30 meters before clam season but only 5-22 meters at the end of the season. Generally in the field, where clams were more numerous, they were smaller in size. To illustrate this relationship, each sample taken from Bed 1 before clam season was weighed and the weight divided by the total number of clams in the sample. Fig. 8 shows that as the number of clams increases, the average size or weight decreases. Clams were less dense on the periphery of the bed and hence had a greater average size. People looking for the larger clams would be expected to work on the periphery and did so in practice. Consequently, the periphery was "clammed out" first, compressing the bed around the high density interior where clams were smaller. This accounts for the "bunching" and possibly smaller clam sizes.

Size frequency distributions before and after clam season for the clams in Bed 1 are shown in Fig. 2A, B. The legal minimum length for clams is one inch (approximately 25 mm) and it can be seen that clams above this length were almost entirely eliminated. The average weight of the clams in the samples from Bed 1 before season was 1.7 grams, after clam season 1.1 grams, a 35% reduction.

Mean density in Bed 1 before clam season was 30 clams/dm², after 14/dm² -- a reduction of 47%.
Figure 8. The relationship of average weight/clam/sample to the total number of clams/sample taken from Clam Bed 1.
Certain areas of clam Bed 1 underwent greater reduction in numbers than others and to show this graphically, the bed was divided into three sections (Fig. 9). A curve, described on p. 18, was fitted to the sampling points in each section before and after clam season (Fig. 10). The curves show that the middle area (section 2) was nearly clammed out. This section also underwent the greatest reduction in area (Fig. 9). Peak curve densities of 49, 51, 66 clams/dm² before clam season, dropped to 26, 9, and 35 clams/dm², reductions of 48, 83, and 46% respectively.

The curves and samples indicate a reduction in density of approximately 50% which brings to light a common practice among clammers. In Fig. 2A approximately 15% of the clams were greater than 25 mm or one inch in length; yet the samples indicate approximately 50% of the clams were removed. Obviously, the clammers were removing or destroying, exposing to predation, clams smaller than the legal size limit and doing this to a considerable extent.

A prominent growth ring was observed among clams surviving the season. The ring was not present among clams before season and was absent among specimens from unclammed areas. The ring indicates an interruption in growth and probably is due to the disturbance from clammers. I have induced rings in Tapes by bringing them into the laboratory for about a week and returning them
Figure 9. Diagrammatic plan of Clam Bed 1 before (dashed line) and after clam season (solid line). Approximate scale: 1 cm = 7 m
Figure 10. Population density curves from Sections 1, 2, and 3 of Clam Bed 1 before and after clam season. A, C, E, before season; B, D, F, after season. For explanation see text.
to the field. The extent of growth interruption is not possible to assess from modal shifts (Fig. 2A, B) because the clammers were removing small clams.

The effect of clamming on the clam population was considerable if not extreme. Clammers were removing clams below the legal limit, density was reduced approximately 50%, growth was interrupted, and bed size was compressed around the high density interior. Clam season was reopened in the Fall of 1968 (2 September - 31 October). On 14 October 1968, I examined the area of Bed 1 and could find no clams at all.

The clams are obviously being over-exploited and unless something more is done to regulate harvest, the yield of even moderate sized clams will become nearly zero. On the basis of the data collected I would suggest the following:

1. Scattering of clams in crowded areas. This could be done by the clammers themselves or even more systematically with less damage to clams by workers using an hydraulic rake.

2. Better regulation of size collected. If clams below 18-20 mm are removed, reproduction might be affected. Clammers might be required to submit their catch to a sieve to separate clams below 25 mm. Those clams passing through the sieve could then be scattered.
3. Establishment of new clam beds. It would be advantageous to fence off and trap out the crabs in the area to be seeded before transplanting.
SUMMARY

A general ecological study was made of the bivalve, *Tapes philippinarum* in Kaneohe Bay, Oahu, Hawaii. Data from the general ecology study are summarized as follows:

1. The clams occur in aggregations or beds generally on the periphery of the shallow water reef platforms of southeastern Kaneohe Bay. Clam distribution is possibly related to substratum, circulation, depth, and salinity.

2. Two species of crab and a gastropod were observed feeding on the clam in the laboratory. Field observations indicate that crabs are the most important predators on *T. philippinarum*.

3. The larvae settled in the Spring probably between February and June with peak settling in April-May.

4. Gonad examinations indicate a minimum size at maturity of shell length 16.1 mm (males) and 18.2 mm (females), and that the clams are mature by 20 mm.

5. Shell length was related to total weight by the equation \( W = 1.75 \times 10^{-4} L^{3.06} \). Body weight is approximately 29-33% of total weight.

6. Clam beds in general have an interior core of high density with numbers decreasing away from
the interior. A curve was used to express this density distribution.

7. Most of the clams occur in crowded conditions; as density increases the average clam weight or size decreases.

Growth rates of *Tapes philippinarum* were observed over a nine month period in various localities of Kaneohe Bay using retrievable boxes containing clams in a standard substrate. Growth rates of clams in Bed 1 were determined by sampling, ring analysis, and releasing marked individuals into the bed. The results are summarized as follows:

8. Average growth rates varied with locality with stations in the southeast Bay showing the most rapid growth. Nutrition was probably the ecological factor responsible for these variations.

9. A von Bertalanffy growth curve was calculated from growth data of several stations.

10. Average growth rates in Clam Bed 1 were about half of those observed in the experimental boxes in the southeast section of the Bay.

11. When different sediments were used in pairs the clams grew faster in a substratum of 3 parts sand, 1 part shells and pebbles than in a mixture of shells and pebbles or mud.
Studies were made of the clam beds before and after clam season. In one bed, chosen for extensive observation because of its high population density and heavy exploitation by the public, the following effects were noted:

12. Bed dimensions, especially width were considerably reduced. Clammers tend to work on the periphery of the bed because the clams are larger there. Thus, the periphery of the bed becomes clammed out first, compressing the bed around the high density interior. This leaves the remaining clams crowded where conditions for growth may be poor.

13. Virtually all clams above the legal size limit (25 mm) were taken and the average weight of the clams dropped from 1.7 to 1.1 grams, a 35% reduction.

14. Population density curves and sampling showed a reduction in population density of approximately 50%. The samples taken before clam season showed only about 15% of the clams were above 25 mm in length, indicating clammers were removing or destroying clams smaller than the legal size limit.
15. A growth ring not present on clams before clam season or on clams from unclammed areas indicates a disruption of growth during clam season.

16. Several regulations are suggested to insure the continued harvest of clams.


