SETTLEMENT AND GROWTH OF FOULING ORGANISMS AT
ALAMEDA MARINA, SAN FRANCISCO BAY, CALIFORNIA

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By
Christopher P. Ehrler
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ABSTRACT

Settling periods and maximum growth of fouling organisms at Alameda Marina, San Francisco Bay, California, were examined from January 1, 1975 to April 21, 1976. Plastic plates suspended in a rack were exposed at a constant depth and retrieved at one, two, six and twelve month periods. Organisms settling during these periods were identified and size and numbers of certain species were recorded. Particular seasons of settlement were inferred from when the species attached to the plates. Settlement times and growth rates of these organisms at Alameda Marina were compared with findings of other investigators. A direct correlation was noted between water temperature and (1) the total number of attached species, (2) the total number of attached individuals of six species, and (3) the growth rate of eight species. In addition, a correlation was found between salinity and numbers and growth for a few species.

The Index of Similarity was used to make a comparison between the total number of species that attached after one and six or twelve month periods. The data indicated that organisms did not disappear as the community developed, and settlement was dependent on when the larvae or spores were in the water. This development of the community was interpreted as a seasonal progression, instead of a true succession.
INTRODUCTION

Many studies have been undertaken on different aspects of the biology of fouling organisms, plants and animals that attach to and grow on submerged man-made objects. There are nearly 2,000 species of fouling organisms from at least the following groups: Bacteria, Fungi, Algae, Protozoa, Porifera, Cnidaria, Platynhelminthes, Nemertea, Rotifera, Bryozoa, Brachiopoda, Annelida, Arthropoda, Mollusca, Echinodermata, Tunicata and Pisces (Woods Hole Oceanographic Institute 1952). In some studies, submerged artificial test panels have been used to accurately determine the season of settlement (Coe 1932; Goodbody 1961; Nair 1967) and growth rates (Nair 1967) of these organisms.

Several factors have been found to affect the settlement of these organisms on fouling surfaces. The physico-chemical factors include type, color, texture, orientation, and depth of the substrate, presence of silt, water current moving over the substrate, time of year, length of submergence, water temperature and salinity. The biological factors include concentration of larvae, growth after attachment and longevity of the breeding season (Visscher 1929; Woods Hole Oceanographic Institute 1952).

Some of these investigations have attempted to determine if the fouling community developed via a true succession or by a seasonal progression. For true succession to occur
(1) earlier organisms in the community must be essential to the attachment of later ones, and (2) organisms must disappear as the development of the community progresses (Shelford 1930). Scheer (1945) showed that when bacteria were present on glass plates, there was increased settlement of hydroids. He also found that the settlement sequence did not depend on when the plates were exposed, and thus development must have been via true succession. Many investigators (Shelford 1930; McDougall 1943; Reish 1964; and others) have found that settlement depends on when the larvae or spores of any organism are in the water column, and that the presence of one organisms is not essential for the attachment of another.

To my knowledge, only one study has been carried out on the fouling organisms of San Francisco Bay, that of Graham and Gay (1945). They found the community on wood to be dominated by Tubularia crocea (Cnidaria), Polydora ligni (Annelida), Corophium insidiosum (Amphipoda), Balanus improvisus (Cirripedia) and Mytilus edulis (Pelecypoda). The settlement of most of the organisms in this study appeared to be related to the changes in water temperature.

The purpose of my study was to answer the following four questions: (1) What was the season of settlement of the fouling organisms at Alameda Marina, San Francisco Bay? (2) What was the growth rate of certain of these fouling organisms? (3) Was the season of settlement or growth rate related to either water temperature or salinity changes?
(4) Did the development of the community take place via a true succession or by a seasonal progression?
MATERIALS AND METHODS

The study was carried out from January 1, 1975 until April 21, 1976 at Alameda Marina, Alameda, California. This Marina is located on the Oakland Estuary, across from Government Island (Figure 1). The area was chosen because fouling organisms are abundant and present throughout the year, and it was within one mile of Graham and Gay's (1945) study site.

Experimental fouling surfaces, 10 x 10 cm, were constructed of 5 mm thick black acrylic sheeting. The plates were sandblasted to roughen the surface (crevices about 0.1 mm wide and deep), and thus aid in the attachment of organisms (Pomerat and Weiss 1946). A total of twenty-four numbered plates were used for the entire study.

Five sets of plates were used, with three replicates per set in the rack (see below) at all times. These five sets were as follows: (A) plates that were exposed for one month, (B) and (C) plates that were exposed for two months, (D) plates that were exposed for six months, and (E) plates that were exposed for twelve months. Two plate types, (B) and (C), were needed for two months exposure so that one set could be collected at the end of each monthly period. It should be noted that 'one month' in this study consisted of exactly four weeks. Table 1 illustrates the chronological sequence of placement and replacement of the plates.
The plates were held in a rack constructed of rigid, white one inch PVC tubing filled with concrete to create a negative bouyancy (Figure 2). The rack was held together with waterproof PVC glue and stainless steel hose clamps. The rack held fifteen randomly positioned plates oriented vertically at a constant distance of 5 cm from each other. Stainless steel cable (5 mm diameter) was used to suspend the rack at a constant depth of 76 cm from an eyebolt which was screwed in on the underside of the dock. The other end of the cable hooked to the rack via a brass swivel which enabled the rack to turn with water movement (Figure 3). A swivel and cable were also attached to the underside of the rack for security reasons. This cable was hooked to a second eyebolt, also attached to the underside of the dock. The distance between the two eyebolts was approximately one meter.

Each 'month' the appropriate set of 1,2,6 and/or 12 month plates were collected from the rack and clean, randomly selected plates were used to replace the collected plates. The fouled plates were returned to the laboratory in a carrying chamber. Photographs were taken of both front and back of each plate, and within two days, all organisms were identified and listed, and size and number of certain species (called quantified species) were recorded. While in the laboratory, the water in the carrying chamber was aerated, and the temperature was kept within ± 1°C of the temperature at the study site.
During the study, representative examples of species were removed from the plates and fixed in 10% neutral formaldehyde. The plates were then scraped clean with a razor blade and placed in a freshwater bath for one week. The plates were then used again at a later date in the study.

Water temperature and salinity were monitored at a depth of 10 cm throughout the study. Temperature was determined by use of a thermometer, and salinity was determined by use of a Goldberg T/C Refractometer (AO Instrument Company, Buffalo, New York; accuracy = ± 1°/oo).

The total number of individuals of many species that attached to the one and two month plates was determined. Certain species were not quantified, but from the presence or absence of each species it was possible to determine when they settled.

In an effort to determine the maximum growth rate of the quantified species, the mean size of the three largest individuals of each species on one and two month plates was calculated. It was assumed that the largest individuals of each species attached on the day the clean plates were placed in the water. Size of encrusting animals (bryozoans and colonial tunicates) was determined with a planimeter and expressed as total area covered (mm²). Areas under 25 mm² were estimated. Size of upright animals (barnacles, mussels and simple tunicates) was determined by use of a micrometer.
and expressed in mm. Figure 4 shows the parts of the body of the erect species that were measured. Simple tunicates were relaxed before measuring.

The Mann-Whitney test was used to determine if the total number of attached individuals and their mean size were statistically similar on both front and back of the one and two month plates. Siegel's (1956; p.125) formula was used, and the calculated Z values were compared as in Zar (1974; p.112). Zar (1974) notes that the critical values of t and Z are equal for large samples, and for $\alpha = 0.05$, $t$ and $Z = 1.960$.

Multiple correlations (Zar 1974) were carried out to determine if the total number of attached species, or the numbers or growth of individuals of the quantified species, had any relationship with either temperature and/or salinity changes.

A comparison was made between the total number of species that attached after different lengths of submergence to determine if the development of the fouling community took place via a true succession or by a seasonal progression. This comparison was made by use of the Index of Similarity ($S$):

$$S = \frac{2c}{a+b} \times 100$$

where $a =$ number of species in month A, $b =$ number of species in month B and $c =$ number of species in common to A and B (Sorenson 1948). A high similarity between overlapping periods
of long and short submergence would show that organisms do not drop out as the community develops, and no one organism was essential for the settlement of another. Thus such a high similarity would indicate that community development was via a seasonal progression. A low similarity between all overlapping periods of long and short submergence would mean that organisms were dropping out as the community developed and may indicate that one organism was essential to the attachment of another (development takes place via a true succession).
RESULTS

The season of settlement of the fouling organisms at Alameda Marina is shown in Figure 5. The solid lines denote settlement on both one and two month plates, while a dotted line signifies settlement only on two month plates. Only a diatom film (probably composed of both bacteria and diatoms) and Melosira sp. attached throughout the entire study, the rest of the species settled over only part of the year. Certain species (ex. Zoothamnium sp., Obelia longissima) did not attach during the summer, while many others (ex. Corophium sp., Mytilus edulis) did not settle during the fall or winter.

The front and back of the plates were found to be statistically similar in relation to the total number and mean growth of all individuals of the quantified species on the one and two month plates (Table 2). Thus, data from the front and back of three plates in a set ($N = 6$) could be used together, and the total number of settled individuals and their maximum growth rates could be determined.

Figures 6 to 16 represent the total number of individuals and the mean size ± 1 S.E. of the three largest individuals of the quantified species: the bryozoans Membranipora membranacea, Cryptosula pallasiana, Smittoidea prolifica, the barnacle Balanus improvisus, the mussel Mytilus edulis, and the tunicates Botryllus sp., Botrylloides sp., Molgula manhattensis, Ascidia ceratodes, and Ciona intestinalis. Many
of the attached colonial tunicates could not be identified to genus due to their small size, and were placed in an additional category, Family Botryllidae. Figure 17 shows the total number of attached Mercierella enigmatica. No growth data was collected for this species.

Multiple correlations were calculated to determine if water temperature or salinity changes (Figure 18) had a significant effect on the total number or average growth of all attached individuals of the quantified species (Table 3). The number of attached C. pallasiana, B. improvisus, Botryllus sp., Botrylloides sp., Family Botryllidae and A. ceratodes, and growth of C. pallasiana, B. improvisus, Botryllus sp., Botrylloides sp., Family Botryllidae, Molgula manhattensis, C. intestinalis and A. ceratodes were directly correlated with water temperature. The relationship with salinity shows some significant positive (C. intestinalis, Botrylloides sp. and Family Botryllidae) and negative (M. membranacea and M. edulis) correlations for numbers and growth.

Table 4 shows that there is a direct correlation between the total number of attached species and temperature. Salinity does not have a statistically significant effect.

Some Index of Similarity (S) values are shown in Table 5. There is a high similarity between certain 1 and 6 or 12 month periods, such as June 1 month and June 6 month plates and August 1 month and December 6 or 12 month plates. Little similarity is seen between different 1 month periods, such as January 1 month and August 1 month plates. It should
be noted that in all comparisons between 1 and 6 or 12 month
periods, there was one month of submergence in common to
both plate types. In other words, while the August 1 month
plates were in the water, so were the December 6 month plates.
DISCUSSION AND COMPARISON

Algae

Coe (1932) working at La Jolla, California, found that algae settled year round. The settlement of algae is usually best near the surface of the water (Pyefinch 1950). In the present study, a diatom film and Melosira sp. attached year round, while only during the spring were a few Enteromorpha sp. and Ulva lobata found attached to the plates (Figure 5). The docks at Alameda are covered with large quantities of these algae, and the limited algal attachment on the plates was probably due to the lack of a minimum quantity of light at the depth of the rack, caused by shading from the dock and a nearby boat, by the turbidity of the water, and by the vertical orientation of the plates.

Protozoa

Coe (1932) and Graham and Say (1945) found that protozoans settle year round. My study shows that protozoans were always found attached to the plates, but no one species was present throughout the year (Figure 5). Allen and Wood (1950) in Australia, and Ganapathi et al. (1958) in the Indian Ocean, found that Zoothamnium sp. settled year round. At Alameda, it only settled from November to May (Figure 5). Zoothamnium sp., Folliculina sp. and Stentor sp. did not attach during the summer at Alameda and might be limited by
warm water. The suctorian and unidentified protozans (all ciliates) were able to settle during these warmer water periods. *Stentor* sp. appears to also be limited by colder water temperatures, and thus did not settle at either of the extremes of temperature at Alameda (Figures 5, 18).

**Porifera**

Nair (1962) working in Norway and Coe (1932) found that sponges attach during the warmer water periods. *Scypha* sp. at Alameda, followed this pattern, probably being limited by cold water (Figures 5, 18). Kajihara *et al* (1975) in Japan, found that *Halichondria panacea* settles from May to August, while *Halichondria bowerbankia* at Alameda, attached for a longer period of time, April to December (Figure 5). Fell (1970) found that *Haliclona eshais* has two periods of reproduction at the Berkeley Yacht Harbor, San Francisco Bay, spring and fall. Settlement of *Haliclona* sp. at Alameda appears to follow the same pattern (assuming season of settlement reflects period of reproduction), with the fall period lasting longer than the spring period (Figure 5).

**Cnidaria**

Visscher (1928) working on the East Coast of the United States, found that hydroids settled from January to April, while Coe (1932) found that *Obelia dichotoma* attached from August to May. *Obelia longissima* at Alameda, settled from November to June (Figure 5).
**Syncoryne** sp. and the unidentified hydroid only settled in the cool water periods of 1976, having not been seen in 1975 (Figure 5). The unidentified hydroid consisted of small, less than 1 mm tall, single upright polyps, interconnected by a stolon-like structure. A hydromedusa was contained inside each polyp. The hydromedusae were small, less than 1 mm across, and had four short tentacles. No feeding polyps were seen.

**Platyhelminthes**

Egg cases from an unidentified flatworm were found on many plates (Figure 5). The adult flatworms were white in color, with two dark anterior eyespots. Four to six young were found in each egg case.

**Annelida**

**Mercierella enigmatica** settled from April to August at Alameda (Figure 17), while Kajihara et al (1975) found it attached in Japan from May to November. No adults of this species were seen at or near Alameda Marina, but large populations live in Lake Merritt, a brackish lake in Oakland that connects with the Oakland Estuary via a canal. The individuals on the plates might have been recruited from Lake Merritt.

**Polydora ligni** lives in a tube which it constructs out of silt and debris (Graham and Gay 1945). It might be that not enough of this type of material was found on the 1 month
plates for tube construction, individuals thus only being found on two month plates (Figure 5).

Bryozoa

Membranipora tenuis settled from April to November in North Carolina (Maturo 1959). At Alameda, M. membranacea attached from February to June, with peak settlement from April to late May (Figure 6). It is not known why this species did not attach again in the second year.

M. membranacea appears to have about the same growth rate (Figure 6) as M. pilosa in Woods Hole (Parker 1924), but much slower than Membranipora sp. in India (Paul 1942).

Cryptosula pallasiana has two settlement periods in North Carolina, April to June and October to November (Maturo 1959), but in Norway, it settles continuously from April to December (Nair 1962). At Alameda, it attached from February to August and from October to November (Figure 7).

Settlement of Smittoidea prolifica is during the warmer water periods, with peak settlement from mid-June to mid-July (Figure 8).

Settlement of Bugula californica in Japan took place from May to August (Kajihara et al 1975), in North Carolina, it attached from April to December (Maturo 1959). Maturo (1959) also found that this species began to settle when the water temperature rose to 15°C. At Alameda, this species did not settle until the temperature reached 19°C (Figures 5, 18).

Coe (1932) and Maturo (1959) found that Bugula neritina
began to attach when the water temperature rose to 15 - 16°C (April) and continued until the end of fall (November, December). It did not settle until the temperature reached 20°C (July) at Alameda (Figures 5, 18). It continued until December.

*Tricellaria occidentalis* has not been listed as a fouling organism by either the Woods Hole Oceanographic Institute (1952) or Ryland (1965), yet it is the dominant erect bryozoan in the fouling community at Alameda (Figure 5). It is limited by the colder water temperatures during the winter at Alameda.

Settlement of *Bowerbankia gracilis* appears to be limited by high summer water temperatures (Figures 5, 18). Settlement of *Alcyonidium polyoum, Farrella elongata* and *Electra crustulenta* was rare and limited to spring and summer (Figure 5).

The unidentified bryozoans (Figure 5), both erect and encrusting, were small (1 and 2 zooid) and probably young individuals of the dominant species.

**Arthropoda**

Graham and Gay (1945) found that *Balanus improvisus* attached from March (temperature 15°C) to October. At Alameda, it started to settle in March (Figure 9) at a temperature of 11°C (a possible explanation for this difference will be discussed later). The growth of this barnacle at Alameda (Figure 9) is within the range that Graham and Gay (1945)
found, an average growth of 4.4 mm in 30 days.

The amphipod Corophium insidiosum began to settle when the temperature reached 15°C at Oakland (Graham and Gay 1945). At Alameda, Corophium sp. (Figure 5) began to attach at a temperature of 11 to 12°C (see below for a possible explanation).

**Mollusca**

Settlement of *Mytilus edulis* is from June to August in Long Island Sound (Engle and Loosanoff 1944) and Maine (Fuller 1946) and from March to May at Oakland (Graham and Gay 1945). At Alameda, settlement appears to take place from March until June and again in August and October (Figure 10). *Mytilus edulis* exhibits a crawling behavior (Harger 1968) and it is possible that the large *M. edulis* found on the plates of June 18, August 13, October 10, 1975 and March 24, 1976 might have crawled onto the plates. If so, settlement at Alameda takes place from March to June.

The growth of this species, minus the very large individuals, ranges from 4 to 9 mm per month. A similar range has been found in other studies (Graham and Gay 1945; Fuller 1946; Reish 1964).

Settlement of *Ostrea lurida* at Alameda, did not begin until the water temperature reached its maximum, 20°C (Figures 5, 18). Coe (1932) found that this species began to attach at LaJolla, California, after the temperature had reached only 16°C, while McDougall (1943) found that *Ostrea virginica*
in North Carolina, did not begin to spawn until the water reached 20°C.

**Entroprocta**

Maturo (1959) found that *Barentsia laxa* in North Carolina settled from July (water temperature 28°C) to October. At Alameda, *Barentsia* sp. did not attach until the temperature had dropped to 16°C (Figures 5, 18).

**Ascidians**

Millar (1958) in Scotland, found that *Botryllus schlosseri* began to attach when the water temperature was 8°C (April). At Alameda, *Botryllus* sp. does not settle until the temperature reached 11°C (Figures 11, 18). The growth rate of *Botryllus* sp. at Alameda was within the ranges for both *B. schlosseri* (Parker 1924) and *B. gouldii* (Grave 1933). The growth rate of this species was much less on the July plates than on the June or August plates (Figure 11). It might be that on the July plates, individuals did not start to settle on the first day the plates were placed in the water, and thus did not have the entire 'month' period in which to grow.

The difference between the settlement of *Botrylloides* sp. on the 1 and 2 month plates (Figure 12) might be due to the inability of identifying small (young) individuals. They have to attain a certain size (age) in order to be identified. Thus, more and larger individuals were seen after two months.
than one.

There was usually fewer Family Botryllidae individuals on the two month than one month plates (Figure 13). This might be due to the ability of identifying larger colonies, and reclassifying them into one of the two genera of colonial tunicate.

McDougall (1943) found that high summer temperatures tended to stop reproduction in *Molgula manhattensis*. This is a possible explanation for the absence of this species on the September one month plates (Figure 14).

*Ciona intestinalis* attached from April to November in Norway (Gulliksen 1972) and from May to October in Alamitos Bay, California (Reish 1964). At Alameda, this species did not settle until July of 1975, yet in 1976, it started to attach in early March (Figure 15). This species was not found attached to the docks of this Marina until July, 1975, and thus may have been introduced to this Marina at that time.

Attachment of *Ascidia ceratodes* (Figure 16) and *Styela clava* (Figure 5) appears to be limited to warmer water periods (Figure 18). Settlement and growth of *A. ceratodes* decreases as the temperature decreases.

Graham and Gay's (1945) study and results differed in a number of respects from the present study. They used 16 in$^2$ (100 cm$^2$) wooden panels suspended vertically at a constant depth just below the water's surface. It has been found (Aleem 1957) that wood and plastic have about the same suitability for attachment and growth of organisms.
Ectocarpus sp., Vaucheria sp., Eteone lighti, Eteone californica and Tubularia crocea attached in 1945, but not in the present study. I have found no specimens of the algae or annelids and only one T. crocea attached to the docks at Alameda.

Polydora sp., Corophium sp. and Balanus improvisus were found in both studies, but in 1945, the numbers of these three that attached were statistically much higher than in 1975-76.

No bryozoans or ascidians attached to the plates or were seen on nearby docks in 1945, yet they now dominate the community at Alameda. Obelia longissima and Ostrea lurida were also not present in 1945.

The reason for the differences in the two studies is not known, but may be due to a number of factors. Graham (personal communication) noted that there was considerable pollution from a sanitary sewer in the area of their study. The decomposition of this sewage might have decreased the dissolved oxygen content in the water to a level which would support only relatively few types of organisms. In 1945, the California State Department of Public Health ordered an end to the discharge of raw sewage into San Francisco Bay waters (San Francisco Bay Conservation and Development Commission 1969b), and in recent years, extensive improvements in the treatment of industrial and municipal wastes have greatly reduced the amount of pollution in the Bay (San Francisco Bay

Patrick, Hohn and Wallace (1954) found low diatom density in polluted river water, with large numbers of individuals of each species (low diversity), while in unpolluted water there were more species, but less individuals of each species (high diversity). If this also happens for macroscopic organisms, it could explain some of the differences seen between the two studies now under comparison. In the more polluted case, 1945, there was a large number of individuals of a few species, while in 1975-76, there was less pollution, and fewer individuals of a large number of species.

It is also possible that many organisms had not been introduced into the Oakland Estuary by 1945, and thus the differences seen between the two studies are due to the introduction of new species and interspecific competition for available niches.

Variations occur during the year in both the number of attached individuals and growth rate of fouling organisms, and they have been found to be regulated by water temperature (Orton 1920; Coe and Allen 1937; Nicol 1960). In the present study, temperature was correlated with the total number of attached species, the total number of attached individuals of six species and the growth rate of eight species.

It is known that spawning in many marine organisms is triggered by a certain temperature, which varies with species (Vernberg and Vernberg 1972). Within any one species, the breeding season will vary in different parts of its range.
depending on the temperature variation at different latitudes (Crisp 1957). This is the probable reason why certain species in my study started to settle at a different temperature than was indicated by other investigators. It is not certain why two species (Balanus improvisus and Corophium sp.) started to attach at different temperatures at Oakland (Graham and Gay 1945) and Alameda. It is possible that the increased amount of pollution in 1945 put an added stress on these organisms, the adult and/or larval stages, and thus they did not begin to settle until a slightly higher temperature.

Sastry (1963, 1968) found that scallops in Massachusetts start spawning when the temperature increases, while more southern scallops spawn only as the temperature rises. It appears in my study that all species begin to settle as the temperature is increasing.

Nair (1967) found that salinity variations played a major role in settlement and growth of the major fouling organisms in Cochin Harbor, India. Orton (1920) found that salinity had no affect on the breeding of many marine organisms. I found that salinity and the number or growth of attached individuals were only correlated for a few species.

The presence and growth of the attached species might also be affected by certain biological factors. Predation could have affected the number of attached individuals. Coe (1932) found that "even during the season when young barnacles are daily attaching themselves to the blocks, the rate of
mortality may exceed the increment owing to new arrivals, with a possible decrease in the population following an early maximum". This could also happen to other young organisms. Flatworms, caprellid amphipods, nudibranchs and fish, which were seen on the plates or in close proximity to them, might have eaten and thus decreased the number of attached individuals.

Competition for food and space could also limit the number of individuals and their growth rate. Coe (1932) found that there was a definite competition for food among newly attached individuals. The amount of food, if limited, can greatly affect the growth rate of organisms (Coe and Allen 1937; MacGinitie and MacGinitie 1968). Possible competition for food was not examined in this study.

Competition for space can also affect marine organisms. Connell (1961) found that the lower limits of Chthamalus stellatus in the rocky intertidal is limited by competition for space with Balanus balanoides. In my study, overgrowing by colonial organisms was only noticed twice, but in each instance the bottom organism was dead. This overgrowing could affect the number or size of individuals.

The monopolization of limited resources has been found to affect community development. There will start to be interspecific competition (interference) for the limited resource as the number of individuals and species (diversity) increases. As the competitively successful species become dominant, the less successful will drop out of the community,
and the diversity will decrease (Grigg and Maragos 1974). In the present study, competition for space was never intense enough, even on the twelve month plates, so that there was a decline in the number of attached species. A comparison of the climax community on the docks and that on the twelve month plates shows that the number of species on the plates might decline as development continues.

Grigg and Maragos (1974) while working on coral diversity in Hawaii, found that during the succession of a biologically accommodated community, the diversity would be expected to increase steadily, reaching a peak value at or near the climax. Also, competition and predation would "provide regulation and therefore confer stability to the community". Physically controlled communities usually show a diversity peak at an intermediate stage. The development of the fouling community at Alameda fits in between these two extremes, showing characteristics of both biologically accommodated and physically controlled communities.

Odum (1971) states that succession is composed of "an orderly process of community development that involves changes in species structure and community process with time". Scheer (1945) at Newport Harbor, California, found that the developmental sequence of organisms on experimental panels leading to a climax community was not dependent on the time of year. This does not happen at Alameda. Interpretation of the Index of Similarity values shows that earlier organisms were not
essential for settlement of later ones, organisms did not disappear as the development of the community took place, and settlement was dependent on when the larvae or spores are present in the water. Thus, development of the community was via a seasonal progression and not a true succession. These were also the findings of Coe (1932) and Coe and Allen (1937) at La Jolla, California, Weiss (1948) in Biscayne Bay, Florida, Kawahara (1962, 1963, 1965) in Japan, and others.

In conclusion, it is hoped that this study will aid others in understanding certain aspects of the biology of some of the organisms in San Francisco Bay. Additional studies of this type must be carried out to determine more about the life histories of individual species, the year-to-year fluctuations in the species composition, the seasonal variation in growth under different environmental situations, and interactions between different populations. Only then can any far-reaching conclusions be drawn.
LITERATURE CITED


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Figure 1. Map of San Francisco Bay. Parallel straight lines symbolize water. Insert shows Alameda Marina (A), Oakland Estuary (B) and Government Island (C). At point D, Latitude is $38^\circ 00'$ N and Longitude is $120^\circ 00'$ W. Total scale equals 4 miles.
Figure 2. Rack with fifteen plates in place. Scale equals 15 cm.

a) Restraints are attached to the rack with stainless steel bolts and keep the plates from falling out of the rack.
Figure 3. Suspension of rack, side view. Scale equals 15 cm.
Figure 4. Measurement of upright species. Scales represent parts of body measured. Measurements expressed in mm in text.
Ascidia ceratodes

Ciona intestinalis

Molgula manhattensis

Mytilus edulis

Balanus improvisus
Figure 5. Settlement times of the fouling organisms at Alameda Marina. Solid line indicates settlement on 1 and 2 month plates; dotted line, settlement only on 2 month plates.
<table>
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- **Diatom film**
- **Melosira sp.**
- **Entermorpha sp.**
- **Ulva lobata**
- **Zoothamnium sp.**
- **Folliculina sp.**
- **Stentor sp.**
- **Suctorian**
- **Unidentified protozoans**
- **Halichondria bowerbankia**
- **Haliclona sp.**
- **Scypha sp.**
- **Obelia longissima**
- **Syncoryne sp.**
- **Unidentified hydroid**
- **Flatworm egg cases**
- **Polydora sp.**
- **Mercierella enigmatica**
- **Tricellaria occidentalis**
- **Bugula californica**
- **Bugula neritina**
- **Membraniopora membranacea**
- **Cryptosula pallisiana**
- **Smittioidea prolifica**
- **Bowerbankia gracilis**
- **Alcyonidium polyom**
- **Farrella elongata**
- **Electra crustulenta**
- **Unidentified bryozoans**
- **Corophium sp.**
- **Balanus improvisus**
- **Balanus crenatus**
- **Balanus sp.**
- **Mytilus edulis**
- **Ostrea lurida**
- **Barentsia sp.**
- **Botryllus sp.**
- **Botrylloides sp.**
- **Family Botryllidae**
- **Molgula manhattensis**
- **Ascidia ceratodes**
- **Styela clava**
- **Ciona intestinalis**
Figure 6. Numbers and growth of Membranipora membranacea with season. For Figures 6 to 16, the top graph indicates the total number of individuals and the bottom graph shows the mean size ± 1 S.E. of the three largest individuals that settled on three 1 and three 2 month plates (total plate area for each month equals 600 cm²). Solid line represents 1 month plates; dashed line, 2 month plates. Arrow point indicates that error bar extends up above scale.
Figure 7. Numbers and growth of *Cryptosula pallasiana* with season. For explanation, see legend Figure 6.
Figure 8. Numbers and growth of *Smittoidea prolifica* with season. For explanation, see legend Figure 6.
Figure 9. Numbers and growth of *Balanus improvisus* with season.

For explanation, see legend Figure 6.
Figure 10. Numbers and growth of *Mytilus edulis* with season.

For explanation, see legend Figure 6.
Figure 11. Numbers and growth of *Botryllus* sp. with season. For explanation, see legend Figure 6. Arrow points indicate that error bars extend up above scale.
Figure 12. Numbers and growth of *Botrylloides* sp. with season.
For explanation, see legend Figure 6.
Figure 13. Numbers and growth of Family Botryllidae with season. For explanation, see legend Figure 6.
Figure 14. Numbers and growth of *Molgula manhattensis* with season. For explanation, see legend Figure 6.
Figure 15. Numbers and growth of *Ciona intestinalis* with season. For explanation, see legend Figure 6.
Figure 16. Numbers and growth of *Ascidia ceratodes* with season. For explanation, see legend Figure 6.
Figure 17. Number of *Mercierella enigmatica* with season.

Total number of attached individuals that settled on three 1 and three 2 month plates (total plate area for each month equals 600 cm²). Solid line represents 1 month plates; dashed line, 2 month plates.
Collection dates
Figure 18. Salinity and water temperature at Alameda Marina.
<table>
<thead>
<tr>
<th>MONTH DATE</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>6</th>
<th>7</th>
<th>8</th>
<th>9</th>
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<th>12</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
</tr>
</thead>
<tbody>
<tr>
<td>1 month plates (A)</td>
<td>P→R→R→R→R→R→R→R→R→R→R→R→R→R</td>
<td>P→R→R→R→R→R→R→R→R→R→R→R→R→R</td>
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<tr>
<td>2 month plates (B)</td>
<td>P→R→R→R→R→R→R→R→R→R→R→R→R→R</td>
<td>P→R→R→R→R→R→R→R→R→R→R→R→R→R</td>
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</tr>
<tr>
<td>2 month plates (C)</td>
<td>P→R→R→R→R→R→R→R→R→R→R→R→R→R</td>
<td>P→R→R→R→R→R→R→R→R→R→R→R→R→R</td>
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</tr>
<tr>
<td>6 month plates (D)</td>
<td>P→R→R→R→R→R→R→R→R→R→R→R→R→R</td>
<td>P→R→R→R→R→R→R→R→R→R→R→R→R→R</td>
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<tr>
<td>12 month plates (E)</td>
<td>P→R→R→R→R→R→R→R→R→R→R→R→R→R</td>
<td>P→R→R→R→R→R→R→R→R→R→R→R→R→R</td>
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</table>

P = Placement of plates
R = Replacement of plates
Table 2. Comparison, using Mann-Whitney test, between total number and mean growth of the individual quantified species found on front versus back of plates, during the entire study. 51-one month plates (3 per month, 17 months) and 48-two month plates (3 per month, 16 months) were used.

<table>
<thead>
<tr>
<th>ORGANISM</th>
<th>MONTHS OF SUBMERGENCE</th>
<th>Z VALUES FOR NUMBERS&lt;sup&gt;a&lt;/sup&gt;</th>
<th>Z VALUES FOR GROWTH&lt;sup&gt;a&lt;/sup&gt;</th>
</tr>
</thead>
<tbody>
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<td>0.331</td>
<td>NO DATA</td>
</tr>
<tr>
<td>enigmatica</td>
<td>2&lt;sup&gt;c&lt;/sup&gt;</td>
<td>0.478</td>
<td>NO DATA</td>
</tr>
<tr>
<td>Membranipora</td>
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<td>0.046</td>
<td>0.163</td>
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<tr>
<td>membranacea</td>
<td>2</td>
<td>0.259</td>
<td>0.239</td>
</tr>
<tr>
<td>Smittoidea</td>
<td>1</td>
<td>0.049</td>
<td>0.030</td>
</tr>
<tr>
<td>prolifica</td>
<td>2</td>
<td>0.573</td>
<td>0.523</td>
</tr>
<tr>
<td>Cryptosula</td>
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<td>1.389</td>
<td>1.301</td>
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<tr>
<td>pallasiana</td>
<td>2</td>
<td>1.121</td>
<td>0.274</td>
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<tr>
<td>Balanus</td>
<td>1</td>
<td>0.295</td>
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<td>improvisus</td>
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<td>0.598</td>
<td>0.766</td>
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<tr>
<td>Mytilus</td>
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<td>0.272</td>
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<td>edulis</td>
<td>2</td>
<td>1.130</td>
<td>0.422</td>
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<td>Botryllus sp.</td>
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<td>0.367</td>
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<td>2</td>
<td>0.304</td>
<td>0.998</td>
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<td>Botryllioides sp.</td>
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<td>0.849</td>
<td>0.535</td>
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<td></td>
<td>2</td>
<td>0.348</td>
<td>0.664</td>
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<td>Botryllidae</td>
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<td>Molgula</td>
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<td>0.500</td>
<td>0.703</td>
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<tr>
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<tr>
<td>Ascidia</td>
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<tr>
<td>ceratodes</td>
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<td>1.046</td>
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<sup>a</sup> Z values were calculated by the method of Siegel (1956).
<sup>b</sup> critical value (α=0.05, D.F.=51) = 1.960 (see Zar 1974, p.112)
<sup>c</sup> critical value (α=0.05, D.F.=48) = 1.960 (see Zar 1974, p.112)

No significant difference is seen in the above values.
Table 3. Multiple correlations: total number and average growth of each quantified species on 3-one and 3-two month plates versus temperature and salinity (average during period of submergence). There was 17-one and 16-two month periods.

<table>
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<tr>
<th>ORGANISM</th>
<th>MONTHS OF SUBMERGENCE</th>
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<th>CORRELATION COEFFICIENTS OF GROWTH VERSUS</th>
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<tr>
<td></td>
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<td>SALINITY</td>
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<td>Mercierella</td>
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<td>enigmatica</td>
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<td>-0.302</td>
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<td>Membranipora</td>
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<td>-0.050</td>
<td>-0.767*</td>
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<td>membranacea</td>
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<td>-0.184</td>
<td>-0.827*</td>
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<tr>
<td>Cryptosula</td>
<td>1</td>
<td>0.483*</td>
<td>0.076</td>
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<tr>
<td>pallasiana</td>
<td>2</td>
<td>0.566</td>
<td>0.259</td>
</tr>
<tr>
<td>Smittoidea</td>
<td>1</td>
<td>0.343</td>
<td>0.034</td>
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<tr>
<td>prolifica</td>
<td>2</td>
<td>0.418</td>
<td>-0.139</td>
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<tr>
<td>Balanus</td>
<td>1</td>
<td>0.567*</td>
<td>0.029</td>
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<tr>
<td>improvisus</td>
<td>2</td>
<td>0.499</td>
<td>-0.214</td>
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<tr>
<td>Mytilus</td>
<td>1</td>
<td>0.138</td>
<td>-0.617*</td>
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<tr>
<td>edulis</td>
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<td>-0.059</td>
<td>-0.293</td>
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<td>Botryllus sp.</td>
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<td>Family</td>
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<td>0.482*</td>
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<tr>
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<td>0.549</td>
<td>0.594</td>
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Table 3. (cont.)

<table>
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<th>ORGANISM</th>
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<th>CORRELATION COEFFICIENTS OF GROWTH VERSUS TEMPERATURE</th>
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<tbody>
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<td>0.477</td>
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<td>0.396</td>
<td>0.758</td>
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<tr>
<td>Ciona intestinalis</td>
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<td>0.312</td>
<td>0.536*</td>
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<td>2</td>
<td>0.382</td>
<td>0.526</td>
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<td>Ascidia ceratodes</td>
<td>1</td>
<td>0.803*</td>
<td>0.682*</td>
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<td>0.522</td>
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</table>

* - significant difference

a) critical value of $r_{0.05(2),15} = 0.482$ (from Zar 1974)
b) critical value of $r_{0.05(2),14} = 0.497$ (from Zar 1974)
Table 4. Multiple correlations: total number of attached species on 3-one and 3-two month plates versus temperature and salinity (average during period of submergence) over the entire study. There was 17-one and 16-two month periods.

<table>
<thead>
<tr>
<th>MONTHS OF SUBMERGENCE</th>
<th>CORRELATION COEFFICIENTS OF NUMBERS VERSUS TEMPERATURE</th>
<th>SALINITY</th>
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<tbody>
<tr>
<td>1^a</td>
<td>0.901*</td>
<td>0.199</td>
</tr>
<tr>
<td>2^b</td>
<td>0.834*</td>
<td>0.301</td>
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</tbody>
</table>

* - significant difference

a) critical value of \( r_{0.05(2),15} = 0.482 \) (from Zar 1974)
b) critical value of \( r_{0.05(2),14} = 0.497 \) (from Zar 1974)
Table 5. Index of Similarity (S) expressed in percent. All collections referred to were made in 1975.

\[
S = \frac{2 \times \text{number of species in common to both months}}{\text{number of species in month A plus number of species in month B}} \times 100
\]

<table>
<thead>
<tr>
<th>MONTH</th>
<th>S</th>
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<td>Jan (1)</td>
<td>100.0</td>
<td>19.0</td>
<td>9.1</td>
<td>66.7</td>
<td>20.0</td>
<td>8.7</td>
<td>8.7</td>
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<tr>
<td>June (1)</td>
<td>100.0</td>
<td>64.2</td>
<td>41.7</td>
<td>80.0</td>
<td>57.9</td>
<td>68.4</td>
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<tr>
<td>Aug (1)</td>
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<td>46.6</td>
<td>50.0</td>
<td>87.2</td>
<td>76.9</td>
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<tr>
<td>Dec (1)</td>
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<td>46.7</td>
<td>46.7</td>
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<tr>
<td>June (6)</td>
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<td>Dec (6)</td>
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<tr>
<td>Dec (12)</td>
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</table>

(1) = 1 month submergence
(6) = 6 months submergence
(12)=12 months submergence
MONTH: refers to the month in which the plates were collected and analysed. For example, June (1) plates placed May 21 and collected June 18.