THE GENERAL ECOLOGY AND GROWTH OF A SOLITARY ASCIDIAN, CORELLA WILLMERIANA [1]

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The diverse assemblage of marine organisms growing on boat hulls, floating docks and other man-made installations is commonly termed the fouling community. Many practical investigations into the development and control of these communities have been undertaken (see Anon., 1952, for review). Ecological study of the fouling communities has been hampered, however, by the lack of information on the life cycles, growth and survival rates, and other properties of the individual species forming this complex (Grave, 1933; Berrill, 1950; Abbott, 1957; Moore, 1958).

One group which may form an important, even dominant, part of the fouling complex, but which has received very little attention, is the Ascidiacea. Scattered ecological data on this group can be found in a few papers, for example those by Huntsman (1921) on *Chelyosoma,* and Just (1934), Hŭus (1937), and Millar (1953) on *Ciona.* Although certain aspects of ascidian population ecology have been studied by Millar (1952, 1954) and Goodbody (1961a, 1961b, 1962, 1963, 1965), a detailed study of the growth of many individuals of a single population is lacking.

Of the thirteen species of solitary ascidians that occur in the Puget Sound region of the Pacific Northwest coast of the United States, one of the more common occurring on marina floats is *Corella willmeriana* Herdman (which will hereafter be referred to as *Corella*). This small (2–3 cm. in height), fairly transparent animal breeds throughout the year. The eggs are shed into the atrial chamber, where they are fertilized and develop into the free-swimming tadpole stage before being released. The aims of this study were to determine the growth rate of the young post-larval stages of *Corella* in the field, the approximate size at sexual maturity and the average life span. Observations on predation and on interspecific competition for space have been included, since it is the relative interplay between all these factors that determines the establishment, persistence, and general success of any species population characteristic of fouling communities.

Material and Methods

Study area and apparatus

Field observations were carried out at the Bremerton Yacht Club on Phinney Bay, adjacent to the city of Bremerton, Washington, from April 24, 1966, to April 15, 1967. These floats, although composed of such diverse materials as creosoted

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and fiberglass-covered styrofoam, wood, and rubber (old airplane fuel tanks), harbor a luxuriant growth of marine animals, including usually a large population of *Corella*. In order to study the growth rate and settling preferences of the young post-larval stages of *Corella*, two frames of polyvinyl chloride were constructed (Fig. 1). Each frame held 32 8.3 × 10.2 cm. glass plates 1 mm. in thickness, arranged on four sides of the frame, four pairs of plates per side. The plates were suspended vertically in pairs so that organisms could settle on only one surface of

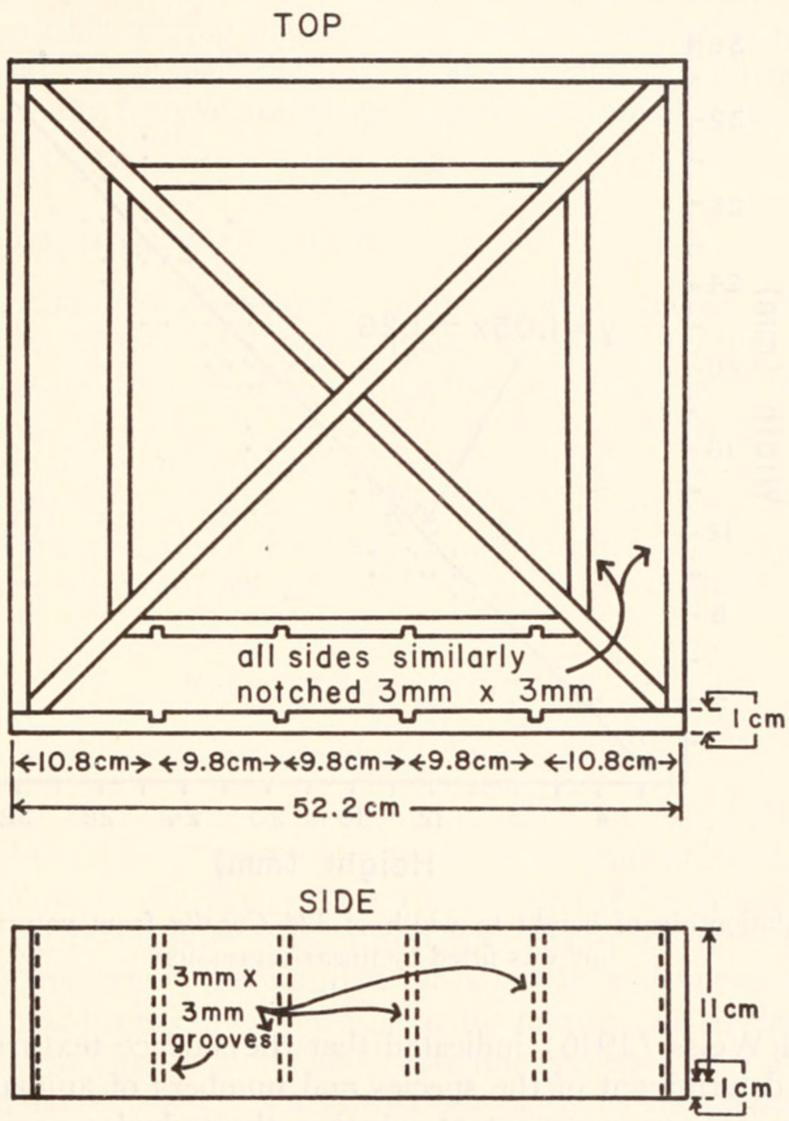

FIGURE 1. Diagram of settling frame.

each plate. The frames (designated A and B) were suspended about 24 cm. below the water surface by nylon rope and plastic-coated wire from the walkway on the floats.

On April 23–24, 1966, a large number of new creosoted styrofoam floats were placed in the water at the Bremerton Yacht Club by the management. Since this was the date on which the two frames were initially submerged, a good opportunity was provided for comparing each month the extent of fouling of the floats and frames. It was hoped that this would give some indication of the effect (or lack of effect) of different substrates on settlement intensity and pattern.

Replacement schedule for the glass plates

A record of the first month's growth of the newly settled *Corella* was obtained for each month of the year by replacing monthly four plates from each frame. For submergence times of 2–11 months, two plates were removed from each frame each month. The remaining eight plates in each frame were left in the water for 12 months. The schedule of the particular plates to be replaced was decided before the frames were placed in the environment by using a random numbers table.

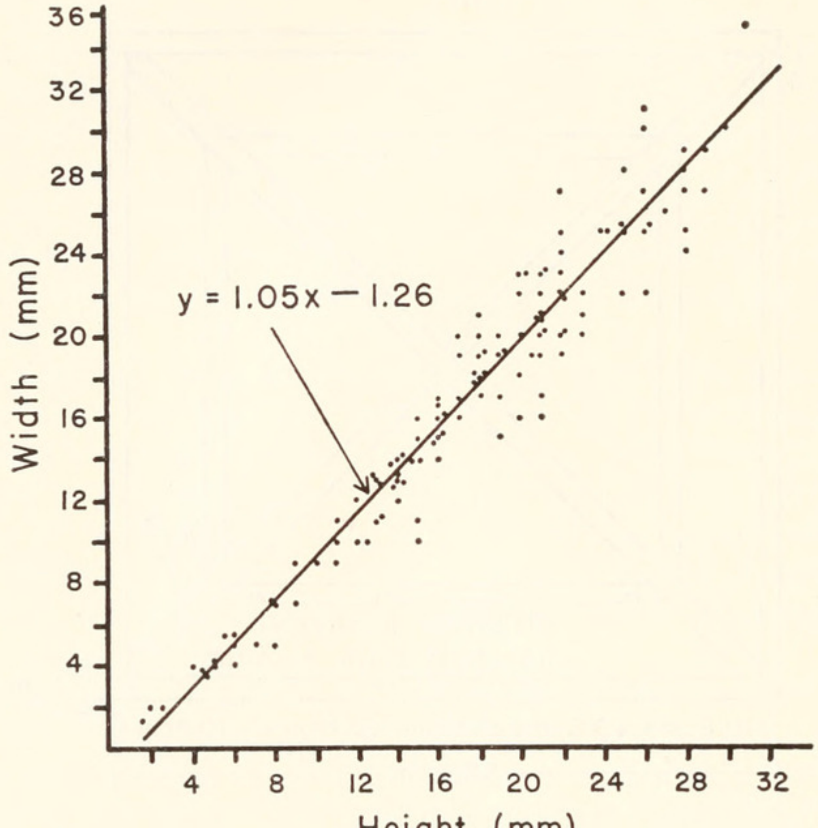

FIGURE 2. The relationship of height to width of 124 *Corella* from natural populations. The line was fitted by linear regression.

Pomerat and Weiss (1946) indicated that the surface texture of the substrate is an important determinant of the species and numbers of animals that will settle. In order to determine to some extent whether the tadpoles preferred to settle on smooth or roughened glass, four of the eight plates replaced each month had a smooth surface exposed for settlement, as did eight of the sixteen plates left in the frames for the entire year. The remaining plates were roughened on one side with coarse carborundum paper.

On 8/20/66 it was discovered that both the nylon rope and plastic coated wire supporting frame A had been cut. The frame was retrieved from the bottom a month later and after cleaning, a new set of glass plates was installed and the frame submerged on 9/25/66. The schedule of replacement of the glass plates was begun again from the beginning, but time did not permit an additional year of study of frame A from the date of its resubmergence. Thus only from April through July was settlement on the two frames comparable.

As each plate was removed from its frame it was immediately isolated in a clear water-filled plastic sandwich box. These were transported back to the laboratory in an ice chest and examined with a binocular dissecting microscope without ever being removed from the boxes. In this way the organisms which had settled on the plates were disturbed as little as possible, and if anything was dislodged, it was kept with that plate. During the replacement of plates and examination of the frames each month, the frames were raised to the surface of the water but were never removed from the water, thus minimizing any undue disturbance and possible tearing off of organisms. The water in which the frames were suspended was fairly sheltered, and tidal currents, though present, were not swift. Therefore, many *Corella* and other organisms were able to remain tenuously attached to the frame.

Method of size measurement of Corella

The measure of individual size used in the growth studies was determined as follows. The height of *Corella* shows a linear relationship (Fig. 2) to its width, as measured across the two siphons. Therefore, although both height and width are a valid measure of size, the latter was used because it was easier to make and entailed a minimum of disturbance to the animals. Newly metamorphosed *Corella* possesses paired atrial siphons (which later fuse to form one atrial siphon) and a single branchial siphon. For newly metamorphosed individuals, the width was measured from the branchial siphon across one of the atrial siphons.

Results and Discussion

General description of changes occurring on settling frames

The two settling frames were placed in the water on April 24, 1966. During the first two months of submergence, large clumps of filamentous diatoms, hydroids, and barnacles developed. By June 19 a few specimens of *Corella* were large enough to be seen easily on the frames, the largest measuring 4.5 mm. in width. After three months' submergence the number of *Corella* had increased greatly; the largest were 12 mm. in size and were sexually mature, as evidenced by the full sperm duct in all the largest individuals and the presence of a few eggs floating in the atrial chamber of some. Large masses of hydroids (mostly *Obelia* spp.) and the colonial ascidian *Distaplia occidentalis* were also present, though the number of barnacles and filamentous diatoms had declined. In August, frame A was missing, but *Corella* was very abundant on frame B, and the largest individuals, now four months old, measured 30 mm., a size near maximum for float populations of this species. *Distaplia* colonies were numerous, and the colonies of another colonial tunicate, *Diplosoma macdonaldi* (formerly *D. pizoni*) had begun to appear.

At the September sampling, most of the hydroids on frame B had disappeared, as had most of the largest *Corella*. Some empty entire and torn tests were found still attached to the frame and to some of the glass plates submerged since April. The cause of death of most of the *Corella* is not known. It was most likely not environmentally caused, because hundreds of 1–2-month-old *Corella* on the frame and plates appeared perfectly normal and healthy. A small percentage of the mortality was caused by flatworms of the genus *Eurylepta;* this will be discussed later.

Very few sexually mature specimens of *Corella* were observed on frame B in October; most of the population measured about 1 cm. in width or less. The largest of these had become sexually mature by the end of November, and throughout December, January, and February large clumps of mature *Corella* dominated the surface of frame B and those plates which had been in the water for 4–6 months. Very little growth of *Distaplia* occurred during the winter months; most of the individuals had disappeared or had died back to an apparently quiescent base. On the other hand, colonies of *Diplosoma* grew rapidly between December and March, covering most of the bare space (including a large part of the plates replaced each month) and overgrowing the *Corella* to some extent. Between November and February, when large numbers of *Corella* tadpoles were settling on the clean plates each month, many specimens 300 μ or less in size were found beneath the spreading *Diplosoma* colonies. The overgrown individuals near the edge of the colonies were often still alive, but those near the center of the colonies had died. Figure 3 shows three tracings made of a glass plate removed from frame B and suspended in running sea water in the laboratory for two months. The *Diplosoma* has eventually grown around the *Corella* without growing over them; in all cases there is a space surrounding the *Corella.* These events are similar to those which occurred on the floats and frame B at Bremerton; *Diplosoma* usually grew around rather than over organisms larger than 1 cm. in height.

By March a few of the largest *Corella* had disappeared from frame B, especially those nearest the top edge of the frame and plates. This may have been due to low surface salinity, caused by the heavy rainfall during the winter months which resulted in a surface layer of fresh water that could be seen floating over and mixing to some extent with the salt water underneath. At the completion of these observations in April, 1967, nearly all the adult *Corella* had disappeared from frame B. This second wave of mortality is believed to be due to the large masses of filamentous diatoms that had accumulated on frame B starting in March and increasing tremendously in April. Thick mats of the diatoms were found attached to the siphonal end of the remaining adult *Corella,* and in some the branchial basket was clogged to a variable extent. Large sheets of *Diplosoma* were still present, and *Distaplia* had reappeared. Hydroid growth was negligible.

The changes occurring on the creosoted floats were quite similar to those occurring on frame B, with a few exceptions. When initially submerged, in April of 1966, barnacles settled thickly on the floats (nearly all of these fell off a few months later), but relatively few settled on the frames and virtually none on the glass plates. Most of those that did settle on the frames had fallen off after three months. Large populations of *Corella* colonized both the frames and the new floats during the summer of 1966, but after the large adult mortality in September, younger individuals did not replace them so rapidly or completely on the floats as on frame B. During the winter months the anemone *Metridium senile* became very dense on the floats and grew tall enough to extend beyond the *Corella* present there. On frame B, in contrast, specimens of *Corella* were always larger and more numerous than *Metridium.* It appears that the smooth surface of the polyvinyl chloride frames provided a substrate somewhat more suitable for *Corella* than for some of the other species present in the area.

After frame A was resubmerged in September, filamentous diatoms and hydroids were the first to appear, though not so thickly or in so short a time as in the spring. The diatoms were gone by November, although the hydroids (mainly *Obelia* spp.) continued to increase in numbers and length steadily until

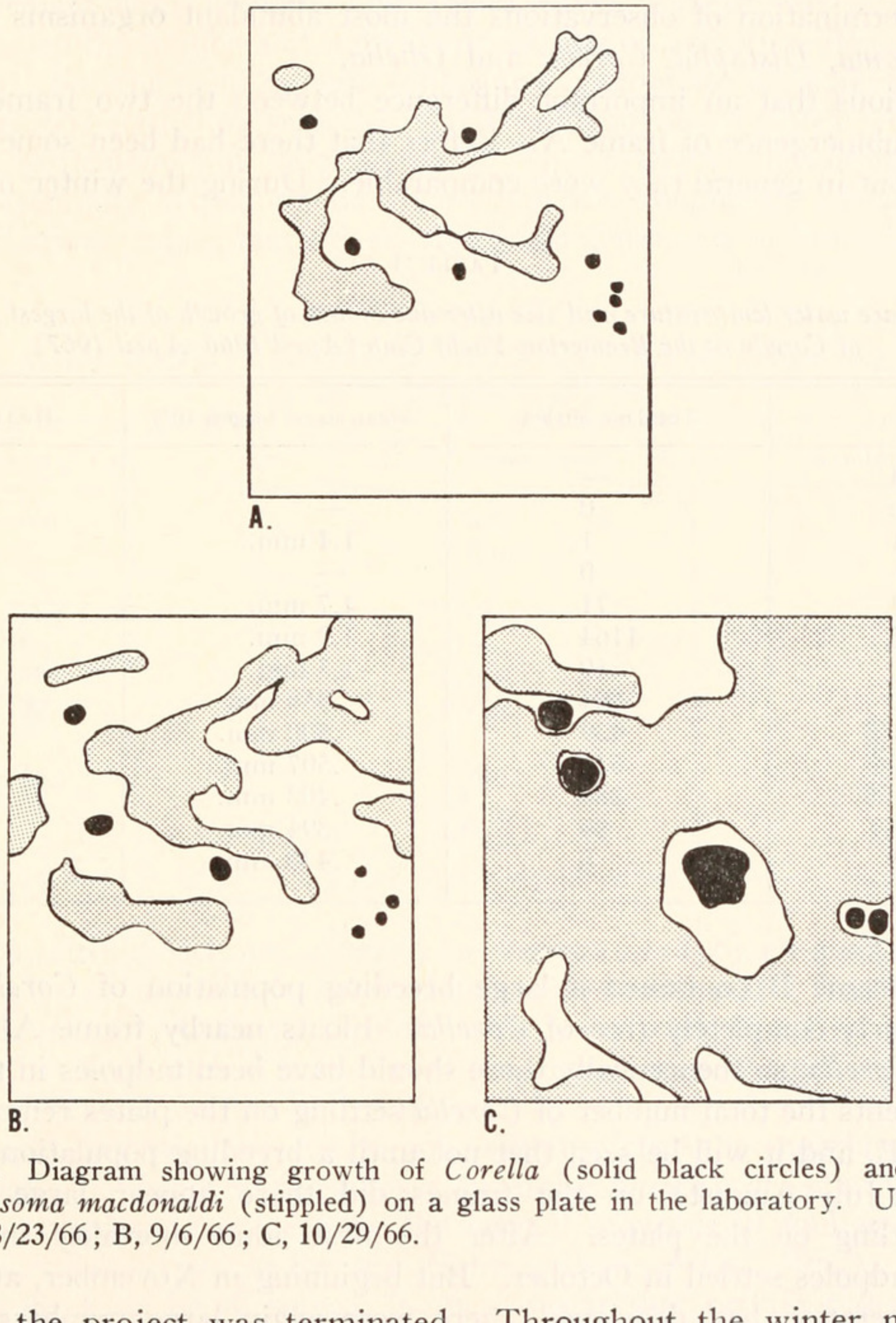

FIGURE 3. Diagram showing growth of *Corella* (solid black circles) and the colonial ascidian *Diplosoma macdonaldi* (stippled) on a glass plate in the laboratory. Unutilized space is blank. A, 8/23/66; B, 9/6/66; C, 10/29/66.

April, when the project was terminated. Throughout the winter months large parts of the frame and plates were covered by broad flat colonies of *Diplosoma*. *Corella* was not observed on frame A or its plates until January. In February about three or four mature individuals 2–2.5 cm. in size were observed, suggesting that there were a few young unnoticed *Corella* present before January. Even in March only about a dozen were observed, and most of them had not yet reached reproductive size. By April these were mature and healthy-looking. Almost no filamentous diatoms had accumulated, possibly because frame A was in a shadier location and subject to faster water currents than frame B. Large numbers of laminarians and *Agarum* sp. were found growing on the upper edges of frame A in March, and although most of them were removed so as not to cover the frame completely, they had grown back again in April; several had reached a length of one meter. *Distaplia* colonies appeared in November but grew very little until the beginning of March. By the end of April the colonies had increased in size, and at the termination of observations the most abundant organisms on frame A were *Diplosoma, Distaplia, Corella* and *Obelia*.

It is obvious that an important difference between the two frames developed after the resubmergence of frame A. Before that there had been some quantitative differences, but in general they were comparable. During the winter months, how-

Table I

Surface water temperature and size after one month of growth of the largest 10% of Corella at the Bremerton Yacht Club (April 1966–April 1967)

Date	Total no. settled	Mean size of largest 10%	H_2O temp. (° C.)
April 24	—	—	11
May 21	0	—	12
June 18	1	1.4 mm.	15
July 16	0	—	16
Aug. 20	71	1.7 mm.	17
Sept. 25	1164	1.9 mm.	14.5
Oct. 22	10	1.5 mm.	11.5
Nov. 20	604	.356 mm.	11
Dec. 18	439	.500 mm.	9.5
Jan. 22	525	.507 mm.	8
Feb. 19	284	.402 mm.	8
March 19	89	.394 mm.	8
April 15	6	.430 mm.	10

ever, while frame B contained a large breeding population of *Corella,* frame A remained nearly completely free of *Corella.* Floats nearby frame A possessed at least a few *Corella,* so theoretically there should have been tadpoles in the plankton. Table I presents the total number of *Corella* settling on the plates removed monthly from frame B, and it will be seen that not until a breeding population had become established (July–August) on the frames did there appear large numbers of tadpoles settling on the plates. After the first adult mortality in September, only a few tadpoles settled in October. But beginning in November, after a second breeding generation had developed, there were again large numbers of tadpoles settling. When the second wave of adult mortality occurred in the spring of 1967, the number of tadpoles settling decreased sharply, in spite of the fact that the *Corella* on frame A and some of the marina floats were still alive and healthy. Thus it seems to be extremely local recruitment of tadpoles that accounts for the presence of nearly all of the individuals on frame B. Nair (1962) has made a similar observation for compound ascidians in his extensive paper on marine fouling.

Seasonal fluctuations in settlement and growth rate of young Corella

Because of the small size of the plates and the fact that frame A had to be restarted, the variation on plates from frame B submerged for longer than one month was too great to permit any realistic evaluation of the growth rate of *Corella* older than one month. Fair numbers of tadpoles settled on the plates which were replaced monthly, although this number fluctuated widely from month to month (Table I).

In agreement with Pomerat and Weiss (1946), there was a significant difference between the numbers of individuals settling on smooth and roughened plates each month. For the eight months considered appropriate for making these paired observations, 662 settled on smooth and 1405 on roughened plates. The hypothesis of random settlement was rejected by χ^2 ($p << 0.01$), indicating that *Corella* either preferentially settled on or adhered to the roughened surfaces. Between plates of different surface texture, no significant difference in individual size of the

Table II

Number of newly settled Corella 200 µ in size or less on plates submerged for varying lengths of time

Month of analysis	Duration of submergence	Number of *Corella*
Nov.	1 mo.	549
	7 mo.	0
Dec.	1 mo.	200
	2 mo.	48
	4 mo.	4
	8 mo.	0
Jan.	1 mo.	169
	3 mo.	14
	9 mo.	5

largest 10% settling each month could be demonstrated, by an analysis of variance. Therefore, size measurements from all four one-month plates from frame B were pooled each month. Only the largest 10% were used, based on a statement by Moore (1958) that such a measure of the few largest should give a reasonable indication of growth for the entire period.

One might question the validity of assuming that the monthly size measurements actually represent in most cases an entire month's growth. Many projects have been carried out to determine the normal sequence in fouling of denuded or clean surfaces submerged in the sea (Scheer, 1945; Anon., 1952). Although this problem is far from being solved, it does appear that certain types of organisms settle first (usually bacteria, diatoms and suctorians) and other organisms settle later, even if ready-to-settle larval stages have been present in the water for the entire time. *Corella* tadpoles, however, apparently prefer to settle on bare surfaces, as evidenced by the number of newly settled tadpoles observed on plates submerged for varying lengths of time (Table II). (Similar data have been collected on a larger scale by Goodbody (1965) for *Ascidia nigra,* which also shows a marked preference for unfouled surfaces.) The indications are, then, that *Corella* will settle immediately on clean surfaces such as glass, supporting the assumption that the largest specimens represent a full month's growth. The close relationship between size of the breeding population on the frames and number of young *Corella* on the one-month plates is further support for this assumption. It might have been better to submerge panels on which tadpoles had been allowed to settle in the laboratory and for which the exact age was thus known, but this was unfeasible for the present study and would have introduced other problems of analysis.

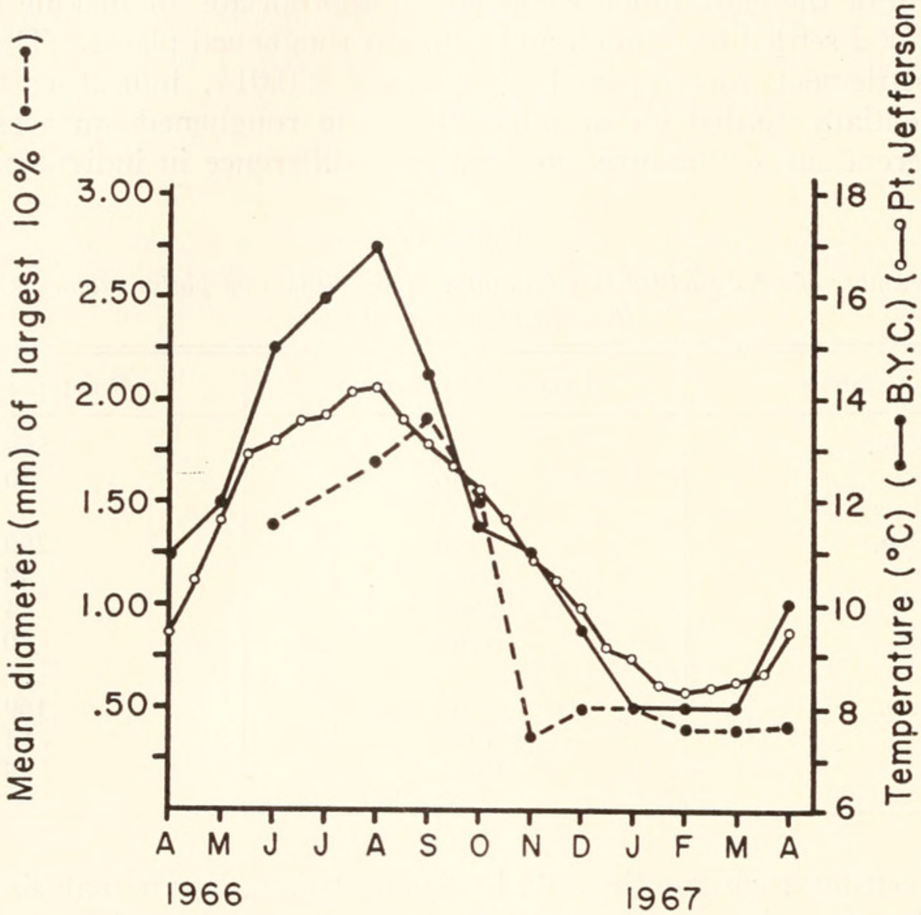

FIGURE 4. A comparison of surface water temperatures at Pt. Jefferson and the Bremerton Yacht Club with the size attained by *Corella* after one month of growth.

In order to determine whether there were seasonal fluctuations in the growth rate of the young stages of *Corella,* the average size attained in one month by the largest 10% of the newly settled individuals for each month throughout the year was measured (Table I). It should be noted that some of the figures are more reliable than others, being based on larger sample sizes. For instance, in October very few mature individuals were present on frame B, and a total of only ten *Corella* was counted on all four of the one-month plates removed that month. In order to obtain a reasonable size value for such a small sample, the size given (1.5 mm.) is an average for the three largest individuals. In April of 1967 only six *Corella* settled on the one-month plates, and the size given is the largest of those six. The mean size for November is abnormally small, probably because it represents less than a whole month's growth. The breeding stock of *Corella* on frame B was very small until those individuals which were still immature in October grew to reproductive size, sometime before November 20. Thus recruitment of the tadpoles to the plates throughout the month of November was unlikely; the 604 individuals on the one-month November plates probably represent settlement for only the prior two weeks or so.

In Figure 4 the size values for the first month's growth of *Corella* for each month of the year have been plotted against temperature. Since surface temperature readings were taken only once a month at Bremerton, it was thought that these readings might show enough variability to mask average seasonal trends. Therefore, along with the Bremerton temperature readings are plotted average bimonthly surface temperature readings for Point Jefferson (Megia, 1956). The Point Jefferson and Bremerton curves agree fairly well, although as might be expected, higher summer temperatures occur in the inshore waters at Bremerton. Figure 4 shows that there is a strong correlation between the initial month's post-larval growth and temperature. Seasonal food supply is very likely also an important factor here, but it was not measured in the present study. The correlation between morphological changes occurring after metamorphosis and the rate of growth of *Corella* is currently being investigated.

Predation on Corella

Eurylepta leoparda Freeman, a cotylean polyclad flatworm, was found inside a few adult *Corella* on the settling frames and floats at Bremerton during the September, November, December, March, and April visits. The worms were 1–3 cm. in length; laboratory observations (about 20–25) showed that they always entered the *Corella* by rolling into a tube as they passed through the branchial (incurrent) siphon (never the atrial siphon). Once inside the *Corella,* the flatworms unrolled themselves and usually ingested the branchial basket first; then they might either leave the individual through a siphon or continue devouring the remainder of the internal organs within 3–7 days, finally leaving only an empty test. Ingestion occurred by extrusion of the pharynx and sucking in of the food material. Generally only one flatworm was found inside a *Corella* at Bremerton, but occasionally there were two, and in the laboratory three or four often moved into the same *Corella.*

There are very few references concerning predation on ascidians. The polyclad flatworm *Cycloporus papillosus* feeds on the colonial tunicates *Botryllus* and *Botrylloides* (Jennings, 1957), and several species of molluscs have been observed to feed on simple and colonial ascidians (Thompson and Slinn, 1959; Miller, 1961; Barrett and Yonge, 1964; Ghiselin, 1964). Goodbody (1963) states that young *Ascidia nigra* are "undoubtedly" eaten by flatworms and by young polychaetes. To my knowledge, there is only one recorded observation of a flatworm feeding on adult simple ascidians. Crozier (1917) reported that *Pseudoceros crozieri* was found in the branchial sac of *Ascidia curvata* and *A. nigra* as well as on colonies of *Ectinascidia turbinata.* According to Crozier, each of the three sets of flatworms taken from the three species of ascidians would feed only on the particular species on which it had originally been found, that is, there were three "physiological varieties" of *Pseudoceros crozieri.* A few feeding experiments carried out with *Eurylepta leoparda* indicate that it will feed only on adult *Corella* and not on *Ascidia callosa, Chelyosoma productum,* or *Diplosoma macdonaldi,* three other species of ascidians presented as food. Conversely, other species of polyclads that have been collected have not been observed to feed on *Corella.* Interestingly, *E. leoparda* has been found only with the Bremerton population of *Corella.* In other local areas, such as Edmonds and Friday Harbor, this flatworm is apparently absent from the *Corella* populations, which show much more marked fluctuations in numbers than does the Bremerton population.

Conclusions

Corella's position in the successional sequence in fouling communities appears to be the following. It is apparently a primary colonizer, since the tadpoles have been shown to settle preferentially on clean, unfouled surfaces. It is a "fugitive" species; the tadpoles settle on new or denuded surfaces and grow quickly to sexual maturity. As they die off, however, colonial ascidians may take over the space, overgrowing small *Corella,* particularly during the winter, and thus preventing the maintenance of stable populations of *Corella.* Tadpoles tend to settle in the immediate vicinity of the adult *Corella,* however, thus prolonging the length of time that *Corella* can exist before being replaced.

The dominant organisms on the older floats (submerged for five years or more) are *Metridium senile, Eudistylia vancouveri, Mytilus edulis* and *Pyura haustor.* All of these species, with the exception of *M. senile,* settled sparsely on the frames; only at the termination of observations were they beginning to become more evident. Judging from observations of the older floats, had the frames been left submerged these species would probably have continued to increase in abundance. On the older floats there is, however, a seasonal sloughing off of some of these organisms. These spots are usually then colonized by *Corella.* The populations of *Corella* in shady locations are able to survive the spring period of diatom overgrowth better than other populations and may be partially responsible for the summer recolonization by *Corella* of the denuded areas.

Summary

1. A one-year field study of the ecology of the solitary ascidian *Corella willmeriana* Herdman was conducted between April, 1966, and April, 1967, at the Bremerton Yacht Club, Bremerton, Washington, where two polyvinyl chloride frames containing glass plates were examined at monthly intervals.

2. The results indicate that *Corella* is a primary colonizer, preferring to settle on clean surfaces. Growth is rapid during the summer, when sexual maturity, corresponding to a size of 12 mm., may be attained in three months and life span is approximately five months. Individuals grow at a slower rate and live longer during the winter; the life span then is seven or eight months.

3. Very young specimens of *Corella* are frequently overgrown during the winter by the colonial ascidian *Diplosoma macdonaldi.* The causes of death of adult *Corella* are not completely known, although a small percentage of them are eaten by the polyclad flatworm *Eurylepta leoparda.* A luxuriant spring growth of filamentous diatoms may cause death of adult *Corella* by smothering them.

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