Notes on the natural history of the Sabellariid polychaete Phragmatopoma californica

Dean Ernest Griffin

University of the Pacific

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NOTES ON THE NATURAL HISTORY OF THE
SABELLARIID POLYCHAETE PHRAGMATOPOMA CALIFORNICA

A Thesis
Presented to
the Faculty of the Department of Biological Sciences
University of the Pacific

In Partial Fulfillment
of the Requirements for the Degree
Master of Science

by
Dean Ernest Griffin
February, 1964
This thesis, written and submitted by

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Dated January 25, 1964
# TABLE OF CONTENTS

<table>
<thead>
<tr>
<th>Section</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>INTRODUCTION</td>
<td>1</td>
</tr>
<tr>
<td>METHODS AND MATERIALS</td>
<td>4</td>
</tr>
<tr>
<td>FIELD OBSERVATIONS</td>
<td>7</td>
</tr>
<tr>
<td>Location of the field station</td>
<td>7</td>
</tr>
<tr>
<td>Geology of the field station</td>
<td>7</td>
</tr>
<tr>
<td>Distribution of <em>Phragmatopoma californica</em></td>
<td>8</td>
</tr>
<tr>
<td>Quadrats</td>
<td>9</td>
</tr>
<tr>
<td>Associated fauna</td>
<td>13</td>
</tr>
<tr>
<td>EXPERIMENTAL OBSERVATIONS</td>
<td>17</td>
</tr>
<tr>
<td>Observations and experimentation on the worm tubes</td>
<td>17</td>
</tr>
<tr>
<td>Determination of population density</td>
<td>21</td>
</tr>
<tr>
<td>LABORATORY OBSERVATIONS</td>
<td>24</td>
</tr>
<tr>
<td>External anatomy</td>
<td>24</td>
</tr>
<tr>
<td>Opercular disk and stalk</td>
<td>24</td>
</tr>
<tr>
<td>Thorax</td>
<td>26</td>
</tr>
<tr>
<td>Abdomen</td>
<td>27</td>
</tr>
<tr>
<td>Cauda</td>
<td>27</td>
</tr>
<tr>
<td>Observations of feeding and the anatomy of the digestive system</td>
<td>27</td>
</tr>
<tr>
<td>Observations of feeding</td>
<td>28</td>
</tr>
<tr>
<td>Digestive system</td>
<td>29</td>
</tr>
<tr>
<td>Reproduction</td>
<td>33</td>
</tr>
</tbody>
</table>
# LIST OF FIGURES

<table>
<thead>
<tr>
<th>Figure</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Profile of the field station</td>
<td>5</td>
</tr>
<tr>
<td>2. Reconstruction of altered tube masses</td>
<td>20</td>
</tr>
<tr>
<td>3. Determination of population density</td>
<td>23</td>
</tr>
<tr>
<td>4. External anatomy of <em>Phragmatopoma californica</em></td>
<td>25</td>
</tr>
<tr>
<td>5. Internal anatomy of <em>Phragmatopoma californica</em></td>
<td>25</td>
</tr>
<tr>
<td>6. Photomicrograph of cross section taken through tentacles</td>
<td>31</td>
</tr>
<tr>
<td>7. Photomicrograph of cross section taken through mouth showing typhlosole</td>
<td>31</td>
</tr>
<tr>
<td>8. Photomicrograph of cross section showing convolutions of the esophagus</td>
<td>32</td>
</tr>
<tr>
<td>9. Photomicrograph of cross section taken through esophagus anterior to stomach</td>
<td>32</td>
</tr>
<tr>
<td>10. Photomicrograph of cross section taken through the stomach</td>
<td>34</td>
</tr>
<tr>
<td>11. Photomicrograph of cross section taken through the abdomen</td>
<td>34</td>
</tr>
<tr>
<td>12. Photomicrograph of cross section taken through the cauda</td>
<td>35</td>
</tr>
<tr>
<td>13. Population density of <em>Sabella media</em></td>
<td>40</td>
</tr>
</tbody>
</table>
INTRODUCTION

In the coves and crevices at Natural Bridges State Park, Santa Cruz, California, one can find large masses of worm tubes constructed of sand. These tube masses often cover areas of several square feet. The tubes are usually straight and packed together in large masses. The individual tubes are about one-fourth of an inch in diameter and may be up to two and one-half feet long. The worm responsible for these masses of tubes is a small polychaete, Phragmatopoma californica.

Phragmatopoma californica is one of the two representatives in the family Sabellariidae found along the central Pacific coast. The other species is Sabellaria cementarium, which is often found with Phragmatopoma. Both worms construct their tubes with small grains of sand cemented together by mucus. The family Sabellariidae belongs to the Polychaeta Sedentaria.

Very little work has been done on Phragmatopoma californica. Hartman (1944) prepared a monograph on the sabellariids, including an account of morphology, larval characters, and distribution of Phragmatopoma. Okuda (1938) reviewed the sabellariids of Japan. Aspects of the morphology of sabellariids have been studied by Quatrefages (1848) and Meyer (1887, 1888). Dales (1952) has published a detailed account of the life cycle, including descriptions
of each larval stage of *Phragmatopoma californica*. Studies of the formation of polychaete tubes have largely been made on the serpulids and larger sabellids.

Hanson (1948) has studied the formation of serpulid tubes. He found that the tubes of the serpulid *Salmacina incrustans* branch, and that each branch contained a separate individual. This condition has not been observed in *Phragmatopoma*. Hanson has also described a number of anatomical structures found to contain mucus. Some of these structures are used in tube construction. Unfortunately, the sections prepared for this report were unsatisfactory for examination of these structures. Headley (1956a, 1956b) has studied tube formation in serpulids. Since the calcareous tubes of serpulids are formed in a manner quite different from sabellariid tubes, data pertaining to the actual tube construction will not be considered in this report. Headley does, however, present useful staining methods for the detection of mucus, using Southgate's mucicarmine or Meyer's mechaematein.

The interrelationship of the circulatory system and food transport in the serpulids has been investigated by Hanson (1948, 1950a, 1950b). In serpulids as well as in sabellids the alimentary canal is surrounded by a branch of the circulatory system called the gut sinus. Blood is propelled anteriorly into an enlarged dorsal vessel by
antiperistaltic movements of the gut muscles which may surround the sinus or both the gut and sinus. Hanson believes that such movements would interfere with food transport and concludes that the food bolii are transported by means of cilia as well as "other mechanisms". No observations of this nature have been made on Phragmatopoma.

Very little work has been done on the natural history of local sabellariids. It is therefore the purpose of this paper to present data pertaining to the natural history of the sabellariid polychaete, Phragmatopoma californica. Such data will include notes of the reproduction, feeding, tube building habits, and associated biota of this polychaete as well as a description of its digestive system.
METHODS AND MATERIALS

A small cove, whose walls were covered with worm tubes, was chosen for field observations. A series of reference points was established on the wall of this cove. The most shoreward point at which the worms were found was marked "I". Similar markings were made at five foot intervals towards the sea, the last of which IX, is located near the mouth of the cove. This reference system and the distribution of worm tubes on the cove wall is illustrated in Figure 1. Field observations were aided by the establishment of three quadrats. The quadrats were located at reference points I, II, and III.

Observations of the structure and construction of the worm tubes were made. Experimental work on the worm tubes consisted mostly of removing the hood-like structures found at the tube openings and rotating large blocks of worm tubes 180°. At each of the five foot intervals the hood-like structures were removed from a thirty-six square inch portion of the population. The surrounding worm tubes were unaltered and thereby served as controls. The reconstruction of the altered tubes was then observed and recorded. Large blocks of worm tubes, about one foot in diameter, were rotated 180° and wired back to the substrate from which they were removed. Again, the surrounding, unaltered tubes served as controls. It was found necessary to use one-half
Figure 1  Profile of the field station showing the distribution of *Phragmatopoma californica*

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<thead>
<tr>
<th>Feet from V</th>
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<th>15</th>
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<th>35</th>
<th>40</th>
<th>45</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sand to top of tube mass, inches</td>
<td>39</td>
<td>42</td>
<td>46</td>
<td>45</td>
<td>45</td>
<td>40</td>
<td>43</td>
<td>20-46</td>
<td>52</td>
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<td>Sand to bottom of tube mass, inches</td>
<td>31</td>
<td>24</td>
<td>36</td>
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<td>18</td>
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<td>16</td>
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</tr>
<tr>
<td>Substrate surface conditions</td>
<td>Long horizontal crevices</td>
<td>Smooth, uniform surface</td>
<td>Surface irregular</td>
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</tr>
</tbody>
</table>
inch mesh wire nailed completely around the block to keep it from washing away.

Small clumps of worm tubes were collected and transported to the laboratory where they were placed in salt water aquaria. Tubes containing living worms were placed in finger bowls filled with sea water and observed under a dissecting microscope. Observations were made on the anatomy and feeding habits of Phragmatopoma californica as well as the organisms found on or within the worm tubes. Dissections were made on the larger specimens to observe their gross internal anatomy.

Further anatomical studies were made by preparing sections of this polychaete. Two specimens were fixed in Bouin's solution and imbedded in paraffin. A series of sections, fifteen micra thick, were prepared. The sections were then stained for six minutes in a 0.5% methylene blue solution. Dehydration was first attempted by using a series of alcohols with increasing concentrations. Poor results were obtained by using this technique as methylene blue is soluble in alcohol. Excellent results were obtained, however, by using an acetone/xylene sequence. The stained slides were first placed in 100% acetone, then into 75% acetone/25% xylene, 50% acetone/50% xylene, 25% acetone/75% xylene, and finally into 100% xylene. The slides remained in each solution for fifteen minutes.
FIELD OBSERVATIONS

Location of the field station: Field observations were made at Natural Bridges State Park, located approximately 4 miles north of Santa Cruz, California. The exact location of the field station can be found on the Santa Cruz Quadrangle, U. S. Geological Survey, at 36° 56' 50" North and 122° 3' 46" West.

Geology of the field station: A large terrace of Monterey sandstone occupies the northern boundary of Natural Bridges State Park. This highly jointed terrace extends three to twelve feet above the beach. Field observations were made in a small cove in the sandstone. A large stack is found in the center of the cove. The upper portions of the cove and stack walls are perpendicular to the beach while the lower portions are concave due to the weathering action of sea water and sand. Similar conditions exist in all of the surrounding coves. The walls of the cove extend seven to eight feet above the cove floor.

The sandstone found here is difficult to work with. When nails are driven into this rock, it has a tendency to crack. If nails are successfully driven into the rock they form eddies in the water which tend to erode the surrounding rock. Consequently, marker nails at lower levels are washed away within a period of one week.

There is evidence to indicate that the surf is
often very rough. One often finds mussel shells, *Mcro-
cystis*, *Esperia*, and *Zostera* scattered high on the beach. *Zostera* and mussel shells have been found tightly wedged into crevices four feet above the cove floor. A great deal of sand can be suspended in swift currents of water. This sand, in addition to being a factor in erosion, has a pronounced effect on the organisms living in the lower concave areas. The cove floor gradient of 3.5° is an important factor in the movement of particles. Rocks with a diameter of two and one-half inches are easily moved up this slope.

**Distribution:** The coastal distribution of *Phragmatopoma californica* extends south to Ensenada, Mexico. The northern limit could not be found in the literature. The author has observed *Phragmatopoma californica* as far north as Shell Beach State Park, California. *Sabellaria cementarium*, which is often found with *Phragmatopoma*, is found as far north as Nanaimo, British Columbia. Both worms are found from the intertidal zone to a depth of forty fathoms (Hartman, 1944).

The worms at Natural Bridges State Park are found attached to cove walls at approximately the midtide level and in some cases in the lower tide pools. The dense tube masses are generally found from fifteen to thirty inches above the sand. Small tube masses are often found in
concavities in the substrate. Differences in the size and location of these concavities often affects the distribution of the worm tubes.

**Quadrats:** Observations on the tube growth and faunal associations were aided by the establishment of three quadrats located at reference points I, II, and III, (Figure 1, Page 5). These quadrats were laid out March 3, 1960. Weekly observations were made until May 22, 1960, while less frequent observations were made during the summer and fall of 1960. The following is a brief description of physical and faunal aspects of each quadrat.

**Quadrat #1:**

**Physical aspects**

- **Size:** 12" x 12"
- **Substrate:** sandstone
- **Slope of substrate:** 20°
- **Surface conditions:** irregular with many crevices and pits
- **Inches above cove floor:** 6 (located in concave portion of cove wall)

**Fauna:** *Phragmatopoma californica* occupied the upper half of the quadrat. Striped shore crabs, *Pachygrapsus crassipes*, were found in crevices between the worm tubes. Small sea anemones were found in the lower portion of the
quadrat. On March 10, 1960 large numbers of the sabellid polychaete, *Sabella media*, were observed settling in the area. Nearly the whole quadrat was covered by these worms. The majority of *S. media* were found on the tubes of *Phragmatopoma*, while some were found in surrounding crevices.

Remarks: Within a short period of time this quadrat was largely destroyed by the abrasive action of waves and sand. By April 19, 1960 the sand level in the cove had risen twelve inches, thereby covering most of the quadrat. All of the worm tubes on the lower portion of the cove wall were sandblasted into a shapeless mass. Microscope slides attached to the substrate adjacent to the quadrat to determine what organisms were settling in the area, were often broken and washed away. An interesting relationship was observed in this quadrat between *Phragmatopoma* and *Sabella media*. This relationship will be discussed under "associated fauna" of this report.

Quadrat #2

Physical aspects:

Size = 6" X 10"

Substrate = sandstone

Slope of substrate = 90° to -30° in the lower 2/3 of the quadrat
Surface conditions = smooth on vertical surface
becoming rough below

Inches above cove floor = 31

Fauna: The upper border of the quadrat was formed
by the bottom of a large mass of *Phragmatopoma* tubes.
This border served as a reference point from which
measurements could be taken to determine the downward
growth of the colony. A small portion of the colony
extended 4 3/4 inches into the quadrat. The upper limit
of the quadrat was bordered with the limpets *Acmese
scabra*, *A. persona* and *A. digitalis*. Limpets were
seldom found in the other portions of the quadrat.
On March 10, 1960 young specimens of *Balanus* were
found on both the quadrat and slides placed adjacent
to the quadrat. The barnacles occurred in great
numbers. On March 10th the population density was
approximately 90 per square inch. The majority of
these barnacles were washed away. Solitary specimens
of *Mitella polymorpha* were found in the lower portion
of the quadrat. Sea anemones were also found in this
region.

Remarks: Throughout the field observations the fauna
present and its distribution remained relatively constant.
The lower border of the worm tubes, which served as the
upper border of the quadrat, remained stationary. The distribution of neighboring tubes was seriously affected by the bait gathering activities of fishermen. During the winter of 1961, large sections of the cove wall on which the quadrat was located crumbled into the sea.

Quadrat #3

Physical aspects

Size = transect 5 inches long; one inch wide
Substrate = sandstone
Slope of substrate = 20°
Surface conditions = smooth
Inches above cove floor = 4.0

Fauna: The small concavity in which the transect was established was mostly filled with sabellariid tubes. Those tubes occupying the seaward wall of the concavity opened into the concavity while those tubes occupying the lee side opened upwards. The majority of the tubes were on the floor of the concavity. These tubes were 5 1/8 inches long. Acmea scabra and A. digitalis were found adjacent to the tubes as in quadrat number two. Large numbers of young balanoids were found settling on the slides placed adjacent to the transect.

Remarks: The purpose of the transect was to measure the growth of the worm tubes. Throughout the field
observations the length of the tubes remained constant. One should not conclude from this data that the worm tubes do not grow in length. Tube growth was observed in neighboring regions and in areas where the tubes had been experimentally altered. It is interesting to note that Acmee was found bordering the tube masses in both quadrats numbers one and two. A further discussion of this distribution may be found under "Associated Fauna". Slides set out in this area were, like the slides in nearby areas, often broken and washed away.

Associated fauna: The biotic relationships of Phragmatopoma merit an ecological study of their own. The following is a brief discussion of the animals found associated with Phragmatopoma.

The most conspicuous animal found with Phragmatopoma is Pachygrapsus crassipes. Pachygrapsus is found in small pits in the tube masses. The outer portions of these pits are often quite narrow while the inner portions are usually enlarged by the crabs. Three such pits were found in quadrat number one.

On March 10th small sabellid polychaetes, Sabella media, were seen settling on both the tubes of Phragmatopoma and surrounding, unoccupied substrate. Their population density rose to ten per square inch in both areas. Most
specimens of *S. media* that settled on the exposed rock were soon washed away.

The population density of those worms settling on the sabellariid tubes remained relatively constant. Quantitative observations were made on *S. media* in quadrat number one. A transect was laid out from the bottom to the top of the quadrat. The lower four inches of the transect crossed unoccupied substrate while the upper eight inches crossed a mass of *Phragmatopoma* tubes. The number of *S. media* was counted at one inch intervals. The results of these observations are seen in Figure 13, Page 40. The rough sand tubes of *Phragmatopoma* seem to offer some degree of protection to *Sabella media*. A similar association exists between *Phragmatopoma* and the sabellid, *Pseudopotimilla intermedia*. *P. intermedia* was found in small cracks or holes between the sand tubes of *Phragmatopoma*. In spite of the strong wave action in the cove, the population density of *P. intermedia* remained constant. Other sessile forms found on the sabellariid tubes included the serpulid polychaete, *Serpula vermicularis* and *Syncrura mirabilis*, a small hydroid with capitate tentacles.

Abandoned *Phragmatopoma* tubes are often occupied by errant polychaetes and nemerteans. The largest nemertean found, *Micrura pardalis*, was often seen with its body folded
in such a manner that both its head and tail were situated just inside the tube orifice. Large numbers of errant polychaetes were found both on and within the sabellariid tubes. The most conspicuous of these polychaetes was the brilliantly colored phyllodocid, *Anaiticles williamsi*.

The limpets, *Acmaea scabra*, *A. persona*, and *A. digitalis* were commonly seen adjacent to the lower border of the sabellariid tube masses. These forms were common elsewhere although their density remained highest in the vicinity of the sabellariid tubes. It is interesting to note that the distribution of those limpets adjacent to the worm tubes followed every irregularity of the lower tube mass border.

For the most part this distribution was observed along tube masses located at approximately the higher low water mark. The substrates on which the limpets were found was, in all cases, moist and covered with mucus. To be sure, the majority of this mucus is produced by the limpets themselves. The distribution of this mucus, however, may well be affected by the presence of *Phragmatopoma*. It is possible that a small amount of the mucus is derived from the feeding and tube building activities of *Phragmatopoma*. The substrate immediately below the tube masses is somewhat protected from wave shock. Furthermore, the worm tubes case a shadow on this portion of substrate during most of
the day. It should also be noted that the substrate in the region of higher low water seems to be little affected by the abrasive action of sand. It should be noted, however, that this pattern of distribution does not occur in all of the tube masses.
EXPERIMENTAL OBSERVATIONS

Observations and experimentation on the worm tubes:

Phragmatopoma californica constructs tubes of sand cemented together with mucus. These tubes overlap each other so as to form large, thick, encrusting areas over rocks at the low tide line, only the open ends of the tubes being exposed. Tube masses fifteen feet long and three feet in width have been observed at Natural Bridges State Park. The individual tubes may measure up to two and one-half feet long. The smooth inner surface of each tube is lined with a smooth layer of small flat sand grains cemented together with mucus. This layer is surrounded by larger sand particles which make up the bulk of the tube. The orifice of each tube is enlarged thereby providing a protected area for the tentacular crown of the worm. A curious hood-like structure is found at the orifice of each tube. The location of the orifice hood was found to be dependent upon the worm's location in the tube mass. Those worms located in the upper portion of the tube mass orient their hoods on the upper portion of the tube orifice while those worms in the lower portion orient their hoods on the lower portion of the orifice. Worms located in the vertical, outermost regions, perpendicular to the sand bottom, orient their hoods toward the sea.
In diagramatic form the hoods are seen as follows:

Experimental work on hood orientation was done at Natural Bridges State Park. Observations have shown that if the orifice hoods are removed they are reconstructed in their original position. Thirty-six square inch plots were laid out at five foot intervals corresponding to the reference points described above. The orientation of the hoods in each plot was observed and recorded. The orifice hoods in each plot were then carefully removed. When the plots were next observed, twenty-four hours later, the hoods had been reconstructed in their original position.

Does hood orientation depend upon the height of the tube above the sand level or the location of the tube
in the tube mass? What effect does the slope and curvature of the tube mass have on hood orientation? To help answer these questions a second experiment was performed on a large, uniform tube mass. Three plots, 12" X 12", were established at 13", 29", and 19", above the cove floor respectively. The orientation of the hoods in each plot was observed and recorded. The surrounding tubes served as a control. A >-shaped groove was carved horizontally into each plot. The slope of the lower surface of the groove would correspond to the slope of the upper portion of the entire tube mass while the upper portion of the groove would correspond to the lower portion of the tube mass. When the plots were next observed, one week later, the hoods had been reconstructed. Those worms on the lower groove surface had constructed their hoods above the tube orifice as do the worms on the upper portion of the tube mass, while those on the upper groove surface had constructed their hoods below the tube orifice as do the worms in the lower portion of the tube mass (Figure 2.)

Worms in the vertical, outermost portion of the tube mass construct their hoods on the seaward side of the tube orifice. On May 7, 1960 a block of worm tubes approximately 12" X 12" was removed from the cove wall, rotated 180°, and wired back in place. The location of each hood was then
Figure 2

Cross Section

Plot number one

Plot number two

Plot number three
recorded. The surrounding tubes served as a control. By the next observation, May 14, 1960, the hoods had been rearranged. The hoods that faced shoreward had shifted to their original seaward position. The screen will be left in place as a reference point to measure tube growth.

Two small clumps of worm tubes were placed in an aquarium for a period of one month. The hoods were removed from one clump; the other clump, which was unaltered, served as a control. The hoods were not reconstructed in the experimental group, indicating that a current and/or suspended sand may be necessary for hood construction.

The present report does not attempt to investigate the mechanism by which sabellarid tubes are constructed. For such data the reader is referred to the papers of Vovelle (1957, 1958a, 1958b).

**Determination of population density:** Until recently no adequate means for determining the population density of *Phragmatopoma californica* had been devised. Previous methods involved counting the tube orifices (van Fossen, 1959), and breaking open a large number of worm tubes and counting the worms present (Collon, 1959). The former method is inaccurate as there is no way of determining which tubes are unoccupied. The latter method is not only time consuming (nine hours were spent breaking open tubes!),
but causes unnecessary damage to the population. I have devised a method whereby the population density of\nPhragmatopoma can be determined indirectly in a matter of\nminutes. The area in which the population density is to be\ndetermined is carefully measured and marked. Nails are\nthen pushed into the tubes at each corner of the plot to\nserve as markers. The hoods on the worm tubes within the\nplot are then carefully removed. The hoods will be\nreconstructed during the next high tide. Since each worm\nreconstructs its hood, the number of hoods replaced is\indicative of the number of living worms present;\nunoccupied tubes remain unhooded (Figure 3).

In this manner 384 worms were counted in an area\nof 36 square inches. The tubes were then checked by opening\nthem. The count obtained by opening the tubes verified\nthe indirect count.
Figure 3. Determination of population density. The orifice hoods have been removed from the tubes in the 36 square inch plot. Population density is determined by counting the number of reconstructed hoods.
External anatomy of Phragmatopoma californica:
The body of P. californica is of four body regions: an anterior opercular disk and stalk, a thorax, an abdomen, and a cauda. Differentiation is distinct in these regions. P. californica measures 40-60 mm. long (Figure 4).

1. Opercular disk and stalk: The dark colored operculum of P. californica is composed of three rows of horny opercular palaeae. Their distal ends meet to form a loose cone. The dark color of this cone is a characteristic separating P. californica from Saballaria cementarium which has an amber colored cone (Light 1957, Hartman 1944). Since the opercular palaeae are not attached at their distal ends they can be spread or contracted at will, thus allowing the worm to move deep within its tube. The outer palaeae are linear while the middle and inner palaeae are L-shaped. These palaeae are arranged in three concentric and almost complete rings. Sections reveal they arise from two pairs of paleal sacs, the outer and middle rows from one, the inner row from the other. The paleal sacs are embedded in the dorsal muscle of the most anterior segments and pass back into the second segment or the first parathoracic segment, one pair passing back slightly farther than the other. Dales (1952) believes the opercular palaeae are derived from the notochaetae of the first segment.
FIGURE 4

A general view of Phragmatopoma californica, showing the external anatomy of the adult. 4X.

FIGURE 5

A general view of Phragmatopoma californica, showing the internal anatomy of the adult. 4X.

1. Esophagus
2. Mesentery
3. Stomach
4. Abdomen
The opercular stalk is situated just posterior to the opercular disk. In living specimens the stalk has a greenish tint. The opercular stalk may be heavily streaked with oblique black stripes but is never spotted as in *Sabellaria cementarium*, with which *Phragmatopoma* sometimes occurs (Hartman, 1944).

The prostomium is almost concealed by the above structures. The tentacles remain small while the palpi are modified into a large tentacular crown.

2. **Thorax**: The thorax includes the portion posterior to the oral aperture; it includes two anterior thoracic and three (or four) parathoracic segments, each except the first with biramous appendages, dorsal and ventral cirri, and simple branchiae (Hartman, 1944).

The widely separated notopodia and neuropodia of the thoracic parapodia have attracted the attention of many workers. Long capillary setae emerge from lobes on the ventro-lateral portion of the worm. Such setae are usually associated with notopodia. It may be argued that they are neurosetae because of their ventral position, however sections reveal that they arise in a more dorsal position. Furthermore, the large dorso-lateral setae arise near the ventral nerve cord. This suggests that the notosetae and neurosetae are actually reversed, not only in the abdomen,
as Hartman had suggested, but throughout the segmental region of the body (Dales, 1952).

Pratt (1951) maintains that all of the setigerous segments constitute the thorax while the cauda of Hartman represents the abdomen.

3. Abdomen: The abdomen is marked by the increase in size of the notopodia, which, in the anterior segments, cover the whole side of each segment. The size of the notopodia decrease posteriorally. The ventrally located neuropodia are highly stalked, each giving rise to long capillary setae. The dorsal cirri in both the thoracic and abdominal segments have been modified into filamentous branchiae. Upon close examination of these highly vascularized branchiae one finds small clumps of cilia along their anterior surface. A large groove runs down the ventral surface of the abdomen. When the worm is in its tube the cauda is folded anteriorly and occupies this groove.

4. Cauda: The cauda is a small segmented portion of the body measuring approximately 20% of the total body length. There are no parapodia or setae present. The anal aperture is at its posterior terminus.

Observations of feeding and the anatomy of the digestive tract: Sabellariids obtain their food by means of a ciliary-mucoid filtering system. The prostomial palpi
of these worms are modified into large tentacular crowns which serve to filter plankton from the sea water. The plankters coming in contact with the tentacles are entrapped in mucus and transported to the mouth by means of cilia. The following notes were obtained while watching Phragmatopoma feed in the laboratory.

**Observations of feeding:** Newly obtained worms, still in their tubes, were placed in a finger bowl containing fresh sea water. The worms were then placed under a dissecting microscope for observation. Those worms covered by the sea water extended their tentacles and began feeding. The tentacular crown of each worm is protected by the enlarged walls of the tube orifice and orifice hood. The tentacles are supplied with fine bands of cilia. Mucus production in the tentacular crown of Phragmatopoma seems to be sparse. Copepods and nematodes were often seen coming in contact with the tentacular crown, however they were able to work themselves free from the mucus.

*Phragmatopoma* is offered a fresh supply of food with each tide. Plankters come in contact with Phragmatopoma by virtue of the tidal currents or, in quiet pools, by ciliary currents produced by the worm itself. The ciliary currents are produced by the tentacular cilia and clumps of cilia on the anterior surface of each branchia. Wells (1951) reports
that some tubicolous polychaetes produce water currents in their tubes by undulatory movements of the body. Such movements may aid water circulation in the tubes of Phragmatopoma. These movements have not been observed while Phragmatopoma was in its tube; the movements can be seen, however, by removing the worm from its tube and placing it in a dish of sea water. The water currents were traced by adding fine carmine particles to the water just in front of the worms while they were still in their tubes. The water appears to circulate throughout the entire length of the tubes as carmine particles were found in all parts of the tubes when they were later opened. These currents are thought to be instrumental in both feeding and respiration.

Microscopic plankters carried by the ciliary currents were observed coming in contact with the tentacular crown where they became entangled in mucus. If by chance a copepod or nematode moves too far into the tentacular crown the worm suddenly withdraws into its tube, covering the entrance with its operculum. It is questionable whether these forms are swallowed or move to the deeper portions of the worm tube.

Digestive system: The prostomium of Phragmatopoma has been partly or wholly concealed by the development of the operculum and modified palpi. The enlarged palpi emerge
as flattened lobes on either side of the opercular stalk; large numbers of tentacles are formed at their distal ends (Figures 5 and 6). The mouth, located at the base of the enlarged palpi, is bordered by the rami of the neuropodia of the first segment. Small capillary seta emerge from each ramus.

The esophagus extends from the mouth to segment V. It is supported by a number of fibers inserted on the walls of the large thoracic coelom. Two membranous sacs of unknown function are located in the mid-esophageal region. A muscular stomach occupies the first three segments of the abdomen (segments VI through VIII). The unbranched intestine extends through the remaining portion of abdomen and cauda. The anus is at the posterior terminus of the cauda (Figure 4, Page 25).

Cross sections reveal a ciliated typhlosole in the anterior portion of esophagus (Figure 7). The typhlosole is soon replaced by a series of convolutions. The convolutions just posterior to the typhlosole are relatively small while those in the posterior two-thirds of the esophagus are quite large. The lumen in this region is thus reduced to a system of small channels (Figure 8). The straight, narrow channels extend to a region just anterior to the muscular stomach. The diameter of the lumen increases markedly as
FIGURE 6

Photomicrograph of a cross section of *Phragmatopoma californica* showing the two enlarged palpi which are modified into a tentacular crown. Stained with methylene blue, 40X.

1. Opercular palea in opercular stalk
2. Tentacle
3. Palpus

FIGURE 7

Photomicrograph of a cross section of *Phragmatopoma californica* taken just posterior to the mouth. A typhlosole is found directly above the mouth. Stained with iron hematoxylin, 40X.

1. Opercular palea
2. Typhlosole
3. Neurosetae
FIGURE 8

Photomicrograph of a cross section of *Phragmatopoma californica* showing the highly convoluted nature of the esophagus. Stained with methylene blue, 40X.

1. Branchia
2. Opercular palea
3. Mesentery
4. Esophagus

FIGURE 9

Photomicrograph of a cross section of *Phragmatopoma californica* showing the enlarged esophagus just anterior to the stomach. Stained with methylene blue, 40X.

1. Branchia
2. Opercular palea
3. Mesentery
4. Esophagus
it enters the enlarged stomach (Figure 9). The muscular stomach is quite large; both the dorsal and ventral surface of the stomach lie just beneath the integument. The nerve cords lie ventrally on either side of the stomach. The greater part of the stomach is made up of a circular band of muscle fibers. There are no grinding structures. The structure of the stomach may be seen in Figure 5, Page 25 and in Figure 10. Segment IX marks the beginning of the intestine. The diameter of the intestine is slightly smaller than that of the stomach. The large band of muscle fibers seen in the stomach is not seen in the intestine. Instead, one finds a highly developed submucosa surrounded by a thin layer of muscle fibers (Figure 11). The serosa in the posterior portion of the abdomen extends ventrally to surround the ventral blood vessel. There are no intestinal diverticula. The diameter of the intestine remains constant as it enters the cauda but steadily decreases posteriorly. The lumen is much smaller in the posterior region due to the presence of large convolutions which somewhat resemble those found in the esophagus (Figure 12).

Reproduction: Observations on the sexual activity of Phragmatopoma californica were made from February 1960 to May 1960. Phragmatopoma, like the majority of tubicolous polychaetes, casts its sex products into the sea where
Photomicrograph of a cross section of *Phragmatopoma californica* showing the stomach. The submucosa is surrounded by a large layer of circular muscle fibers. Stained with methylene blue, 40X.

1. Branchia
2. Circular muscle fibers
3. Submucosa

**FIGURE 10**

Photomicrograph of a cross section of *Phragmatopoma californica* showing the intestine. The submucosa is highly developed while the layer of circular muscle fibers is greatly reduced. Stained with methylene blue, 40X.

1. Branchia
2. Submucosa
3. Visceral peritonium

**FIGURE 11**
Figure 12

Photomicrograph of a cross section of *Phragmatopoma californica* showing the posterior portion of the intestine and the internal structure of the cauda. Stained with methylene blue, 40X.

1. Eggs in coelomic cavity
2. Neuropodium with fragments of neurosetae
3. Cauda
fertilization occurs by chance meeting of the eggs and sperm.

In periods of ripeness the sex of *Phragmatopoma californica* can be determined by color. The females are purple in the ovigerous condition while the males are white. This coloration is caused by purple color of the matured eggs and the white, milky sperm showing through the integument. Sex determination should not be made solely on the basis of coloration, as females were found with white eggs in the early part of March. Eggs were first seen on March 10th, at which time they were white. By the latter part of March the eggs had turned purple. These mature eggs were measured and found to be about 75 microns in diameter. The parapodia of *P. californica* are often swollen due to the presence of large numbers of eggs or sperm (Figure 12). The worms were still ripe in the latter part of May when the field observations were terminated. The color of the worms, however, was fainter than previously observed.

Ripe females were removed from their tubes and placed in a hypotonic solution. The worms were then observed under a dissecting microscope. Eggs were seen streaming from a pore located at the ventral base of each parapodium in the abdominal region. Similar observations were made on male worms. The sperm were discharged from a pore located at the
dorsal base of each parapodium in the abdominal region. The factors causing Phragmatopoma to discharge its sex products in nature are, to the author’s knowledge, unknown. Sperm were seen flowing from one tube after a small tube mass was disturbed by mechanical shock. The flow of sperm was slow and steady followed by a series of strong rhythmic discharges. The small clump of tubes was held in such a position that the sperm would drift into the surrounding tubes, but the other worms did not discharge their sex products.

Young worms were found in the latter part of March occupying the lee sides of pits dug into the older tube masses. Since the purple color of the eggs is indicative of maturation it would seem unlikely that the new individuals developed from the newly matured sex products as the eggs were just turning purple when the new individuals were found. Furthermore, the larvae spend approximately two months in the plankton, which would indicate fertilization took place sometime prior to February.

The eggs of Phragmatopoma may be fertilized in the laboratory. For a description of the techniques employed in fertilizing the eggs and a description of the larval development of Phragmatopoma californica the reader is referred to Dales (1952).
DISCUSSION

The apparent reversal of noto- and neurosetae is quite common in the sedentary polychaetes. Both Dales (1952) and the author have noted that the ventrally located neurosetae of Phragmatopoma arise from sacs well above the ventral nerve cord while the dorso-lateral, spear-shaped parathoracic setae arise near the nerve cord. It may be argued that the latter type setae are actually neurosetae. In support of this hypothesis it may be pointed out that in less advanced families large specialized setae tend to be characteristic of the neuropodium rather than the notopodium while only the more advanced families have uncini on the dorsal lobe in the anterior part of the body.

The author is inclined to agree with Hartman (1944), and Dales (1952), who suggest that the notosetae and neurosetae of Phragmatopoma are reversed. Although sections of sabellariids do suggest that the noto- and neurosetae have been in fact transposed, there is as yet no real evidence that such transposition has occurred, either in this family or in the anterior region of sabellids and serpulids. It is probably safer in these instances to call the setae which emerge from the notopodium and the notosetae, and those emerging from the neuropodium and the neurosetae, although further research may show that the reversal has in fact taken place.
Phragmatopoma tubes seem to offer some degree of protection to sessile organisms. Large numbers of the sabellids, Sabella media and Pseudopotamilla intermedia were found in pits and crevices in the rough sand tubes of Phragmatopoma. Large numbers of S. media were also found in the root systems of Zostera. Since the density of S. media that settled on unprotected substrates decreased markedly while the density of those individuals settling on the sabellariid tubes remained high the author would conclude that the sabellariid tubes do indeed offer protection from being washed away. For a quantitative expression of this argument the reader is referred to Figure 13.

It is known that the young worms are capable of constructing complete tubes while the adults can only repair damaged tubes. Hartman (1944) believes that the cauda is used to repair or construct new tubes. Perhaps the cauda is used in the reconstruction of damaged orifice hoods in the exact position from which they were removed. It would be interesting to watch the tube building activities of worms whose cuada had been experimentally removed. Many questions regarding the construction and functions of various worm tube structures remain unanswered.

Observations of the tube orifice hoods in the field station as well as surrounding coves and surge channels indicate
Figure 13 The number of *Sabella media* along a transect taken through quadrat number one

Number of *Sabella media* per square inch

Transect in inches
that the orientation of the hoods is dependent upon the slope of the surface of the tube mass. It is also concluded that damaged orifice hoods will be immediately reconstructed in their original position or, if the slope of the tube mass has been altered, in a position corresponding to the hoods of worms located on similar slope angles. The reconstruction of orifice hoods is so precise that the author feels this phenomenon may be used to determine population densities as described above.

Those worms located in that portion of the tube mass whose surface is perpendicular to the cove floor orient their hoods on the seaward side of the tube orifice. This condition was observed on both the north and south sides of the field station. Hence, the hoods may be on either the right or left side of the tube orifice. In both natural and experimental observations, the hoods in this region were always constructed on the seaward side of the tube orifice. It is therefore not unreasonable to assume that the surf currents may affect the orientation of these hoods.

The hoods and the enlarged tube orifices offer the worm some protection from wave shock. Furthermore, the hoods tend to set up eddies in the water as it comes in contact with the tubes. Such eddies would swirl water directly into the tube orifice. Such an arrangement would,
in addition to protecting the worms from wave shock, produce currents whereby food would be brought in direct contact with the tentacular crown of *Phragmatopoma*.

In the author's opinion, any observations on the feeding habits of an organism should be supplemented by studying the anatomy of the feeding and digestive organs. Serial sections taken through *Phragmatopoma californica* revealed a large ciliated typhlosole in the anteriormost portion of the esophagus. The typhlosole increases the surface area of the esophagus coming in contact with the incoming water and mucus entrapped food. Hence, a large ciliated surface is available to help ingest food particles and pass them along the esophagus. The stomach of *Phragmatopoma californica* is highly muscular. In contrast to a number of polychaetes, this muscular organ is devoid of grinding structures. It appears that the stomach does not function as a grinding organ, but as a pumping organ serving to draw water and plankters into the alimentary canal.

There seems to be a relationship between the amount of mucus produced in the tentacular crown and the structure of the esophagus. As stated above, the mucus production in the tentacular crown of *Phragmatopoma californica* is sparse. Hence only the smaller plankters become entangled in the mucus.
In the majority of cases the larger forms are able to work themselves free from this mucus. The convoluted nature of the posterior three-fourths of the esophagus probably acts as a filtering device, allowing only the smaller food particles to pass. If, however, the mucus production were sufficient to capture larger plankters, they would be filtered out by the esophagus. The possibility exists that the ciliated typhlosole also acts to discharge large particles if they should by chance enter the esophagus. This may be accomplished by a reversal in the metachronal waves of the cilia.
SUMMARY

1. Studies of the natural history of the sabellariid polychaete, Phragmatopoma californica were conducted over a period of two years.

2. A field station was established in a small cove located along the northern boundary of Natural Bridges State Park, Santa Cruz, California. A discussion of the physical factors of the environment and their effects on the cove fauna may be found in the "Field Observations" section of this report.

3. The sabellariids construct large masses of tubes of sand grains cemented together with mucus. Both natural and experimental observations were made to determine the manner in which these tubes are made. It was concluded that the position of the hood-like structures located on the tube apertures is dependent upon the slope of the tube mass surface as well as the position of individual worms with respect to the sea.

4. A new method for determining the population density of Phragmatopoma californica is presented. This method involves the alteration of a measured portion of tube mass followed by observations on its subsequent reconstruction.
5. A number of animals were observed living both on and within the tubes of **Phragmatopoma californica**. The rough, irregular surface of these sabellariid tubes is considered as a factor influencing the population density of sessile forms settling upon them.

6. The external anatomy of **Phragmatopoma californica** is reviewed in the "Laboratory Observations" section of this report. The body of **Phragmatopoma californica** is divided into four body regions: i) the opercular stalk and disk, ii) the thorax, iii) the abdomen, and iv) the cauda. The characters separating **P. californica** from **Sabellaria cementarium**, the sabellariid commonly found with **Phragmatopoma**, are discussed.

7. The feeding habits of **Phragmatopoma** were observed in the laboratory. The plankters upon which **Phragmatopoma** feeds are brought to the worm by means of tidal currents and/or ciliary currents produced by the worm itself. Only the smaller plankters are captured; the larger forms were seen working themselves free from the mucus produced in the tentacular crown of the worms.

8. The feeding observations are supplemented with a description of the alimentary canal. This work was facilitated by studying serial sections.
9. The sex products of *Phragmatopoma californica* are briefly discussed. It is commonly held that the sex of *P. californica* can be distinguished by the color of the ovigerous region; the females are purple while the males are white. The females were found to be white in the early part of March; their color, however, changed to purple by the latter part of the month.
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