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# Spawning periodicity and habitat of the palolo worm *Eunice viridis* (Polychaeta: Eunicidae) in the Samoan Islands

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## Abstract

The relationship between the phase of the moon and the emergence of the epitokous segments of the palolo worm *Eunice viridis* Gray has been known to the natives of the Samoan Islands for centuries. They predict the date and time of day when the emergence occurs so that they can be ready to catch the worms. This phenomenon is one of the best known examples of lunar periodicity. It was first described scientifically at the end of the last century. My own investigations concern the occurrence of the worms in the reef, in which they gnaw long tunnels through the massive blocks of coral limestone at levels characterized by the occurrence of symbiotic algae. Apparently the algae are the main sources of nutrition for the worms. The casting off of the epitokous segments occurs at the third quarter of the moon in October or November. An analysis of known dates on which the swarms of worms have appeared permitted a precise method of prediction to be formulated. The causality of this periodicity is discussed.

## Introduction

Since the end of the last century, the polychaete *Eunice viridis* Gray has become a classic example of a marine animal exhibiting lunar periodicity. A clear correlation can be observed between the swarming period and a certain phase of the moon. The first scientists who visited the Samoan Islands learned from the natives about the appearance of the "palolo" – the name of the worm in the Samoan language – during three days of the third quarter moon in October or November. Even today, the epitokous parts of these worms are a favourite food of the Samoans who collect them above coral reefs surrounding the islands (McNeill, 1954; Miller *et al.*, 1955; Miller and Pen, 1959). The natives have a long tradition of preparing for the appearance of the palolo, and they have also discovered that certain environmental clues help them to predict the "palolo days".

Early descriptions of this phenomenon, which occurs with great regularity, were provided by Gray (1847), MacDonald (1858), and Whitmee (1875). Later, Collin (1897), Ehlers (1898), Friedländer (1898a, b, 1899a, b, c), Powell (1882), Krämer (1899a, b, 1903), and Stair (1897, 1916) described it in more detail. In 1904, Friedländer published a summary of the information available on the palolo. Other witnesses of the emergencies were Horst (1904), MacIntosh (1905), Becke (1909), and Woodworth (1903a, b, 1907). The publications provoked discussion mainly concerning the explanation of the lunar periodicity (see e.g. Brunelli and Schoener, 1905; McKay, 1953).

Since then a lunar rhythm has been noted in a number of different polychaetes, as well as in other marine animals and plants. For summaries see Caspers (1951), Korringa (1957), and Neumann (1981). Several reports concern the distribution and the spawning behavior of *Eunice viridis* in other parts of the Pacific (Corney, 1922; Berrill, 1948, Burrows 1945, 1955).

My first report on my own observations on the Samoan Islands during 1959 was published in 1960 and 1961. After von Haffner (1961) based his morphological studies on specimens I collected, Hauenschild *et al.* (1968) published a comprehensive investigation on the anatomy and sexual development of the Samoan palolo from Faga'itua Bay, Tutuila. In the meantime, I had the opportunity to continue collecting empirical data on palolo emergence, to examine the specimens collected from Tutuila and Upolu in more detail, and to analyze the correlations between swarming and environmental factors.

Much of my data was taken from the notes of Mr. M. Haleck who lived in Pago Pago for more than 40 yr. Further valuable data were found in the missions of the Marist Brothers. Notes for Tutuila were provided by Brothers Hermann and Michael. In the Mission Moamou on Upolu, the notes of the late Brother Briand had been preserved and made available to me by Brother Labrecque.

Brother Henry had made notes on the "palolo days" on Upolu during the years from 1925 to 1931.

The data from 1964 to 1982 were provided by several residents of Upolu. Dr. K. J. Marschall of the Biological Laboratories, Vaoala/Apia, sent me a list of the palolo swarming dates he had personally observed and recorded since 1964 on Upolu and Savaii, including additional information for 1977 through 1982 provided by Mr. A. Phillipps, Director of the Department of Fisheries in Apia. These dates were compared with a list from Br. T. Lynch, St. Joseph's College, Apia, who compiled information on the palolo emergence from 1977 to 1982 off Manua, Tutuila, Upolu and Savaii. All the lists also included exact statements as to the time of day the swarming started. Thus, the compilation of the swarming dates in Table 2 is quite complete for the last two decades and provides a chance to check the accuracy of the palolo rules worked out in 1961.

## Methods

### Determining the hour of the palolo emergence

Collin (1897), Friedländer (1898 a, b, 1899 a, b, c), and Krämer (1899 a, b, 1903) reported that the palolo emergence begins at 4.00 hrs and the main catch is made at about 5.00 hrs. While this is correct for the islands of Upolu and Savaii, it is not true for the more eastern islands of Tutuila and Manua. Friedländer and Krämer themselves wrote that, in Tutuila, the catch begins at midnight. Friedländer (1898, p 339) mentioned that there is a difference between the two western islands, the main swarming in the westernmost one, Savaii, being a little later after sunrise. I have reports that on the Upolu reefs, the main catch is also between 5.30 and 7.00 hrs. It seems that the first appearance of the palolo and the main swarming near Savaii is about one hour later than near Upolu (Fig. 1).

The recent information from K. J. Marschall and A. Phillipps from Apia confirms the commencement of the palolo emergence near Manua at about 20.00 hrs, off Tutuila at 1.00 hrs and off Upolu and Savaii at 4.00 to 5.00 hrs.

I learned from my inquiries on Tutuila that the swarming of the palolo from the reefs begins shortly after midnight. During the days of the palolo emergence in 1959, I had the chance to observe the times exactly in Matuu Bay, west of Pago Pago on the island of Tutuila. The first palolo were observed at 0.30 hrs Samoan Standard Time, i.e. 0.07 hrs sun time. The epitokous segments of the worms, about 20 cm long (Fig. 2), appear quite suddenly, and 30 min later the highpoint of the swarming is reached (Fig. 3). At the beginning, the worms emerge in dense crowds; later, they become more evenly distributed by the waves. There is a flat reef in the bay which may be approached from the coast. I have heard reports from Samoan fishermen that along the outer side of the reef, the worms have been seen rising in great abundance from

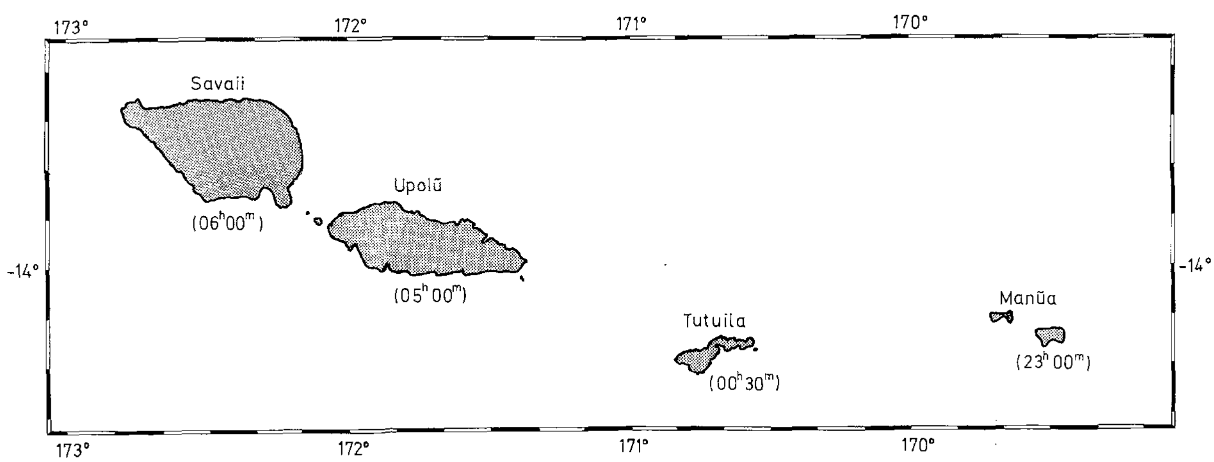


**Fig. 1.** Map of the Samoan Islands with records of the starting time of the palolo emergences (Samoan Standard Time)

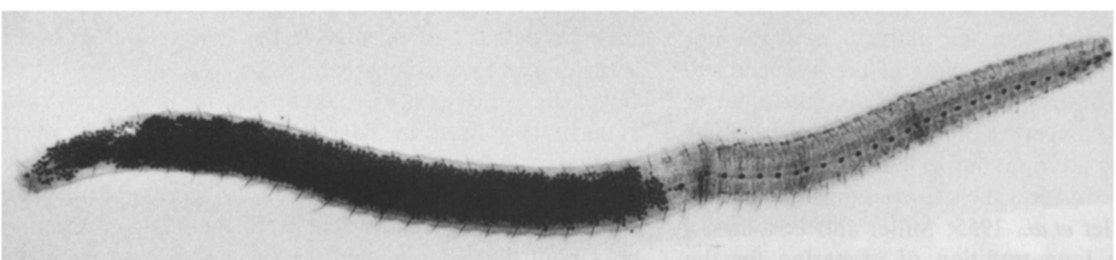

**Fig. 2.** *Eunice viridis.* A female with atokous segments (left) and epitokous segments (right) filled with eggs

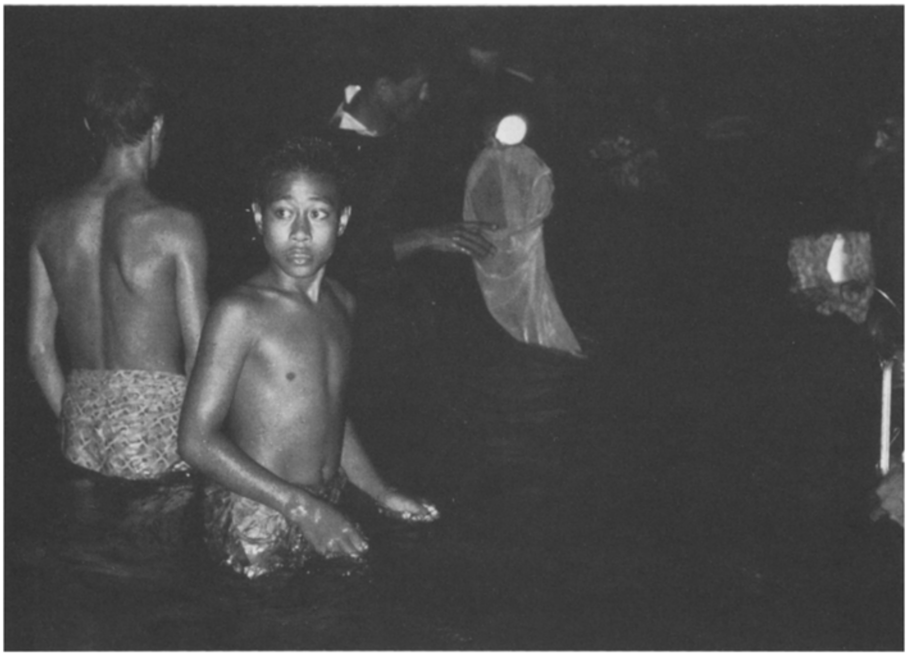

**Fig. 3.** Capture of the palolo in the reef area of Matuu Bay off Tutuila at 1:00 hrs

**Fig. 4.** Capture of the palolo in the reef area off Apia, Upolu, at 6:00 hrs

deeper parts of the coral. The epitokous parts are readily broken by the waves, and the water is soon filled with the blue-green eggs.

As previously mentioned, the maximum number of palolo appear about 30 min after the beginning of the swarming. It seems that the total number of worms does not increase thereafter, and so we must suppose that the emergence from the reefs is limited to about 30 min. The worms are continually torn into smaller pieces, and after about two hours, the catch is no longer productive. The short pieces, emptied of eggs and sperm, are washed away by the waves.

The reports from Upolu and Savaii both agree that the catch is limited to about two hours in the early morning, at about sunrise, so it is finished by 6.00 or 7.00 hrs (Fig. 4). I have heard a few reports by Samoans, however, that sometimes the collecting period is longer: in some years more than four hours. Presumably, this is due to differences in weather, mainly wind and waves, which distribute the palolo pieces at different rates.

## Occurrence of the palolo swarming in October and November

As indicated in Table 1, the palolo emergence is limited to three days, and the main swarming occurs on the second day. Also the dates from 1964 to 1982, compiled in

**Table 1.** Compilation of all known dates on the palolo emergence in the Samoan Islands from 1843 to 1960. Dates of third quarter moon in Samoan time (UTC – 11 h) provided through the courtesy of Mr. K.-H. Gaida, Deutsches Hydrographisches Institut, Hamburg

| Year | 3rd quarter moon | | Palolo emergence | | Other months | Reference |
|---|---|---|---|---|---|---|
| | Oct. | Nov. | Oct. | Nov. | | |
| 1843 | 16 | 14 | 15/16 | | | St |
| 1862 | 15 | 14 | 15/16 | 14/15 | | Wh |
| 1864 | | | 23 | 21 | | Wh |
| 1865 | 11 | 9 | 12/13 | | | Wh |
| 1866 | 30 | 28 | 31 | 1 | | Wh |
| 1867 | 19 | 18 | 21 | | | Wh |
| 1868 | 8 | 7 | 8/9 | 8 | | Wh |
| 1872 | 23 | 22 | 24 | | | Wh |
| 1873 | 12 | 11 | | 11/12 | | Wh |
| 1874 | 31 | 30 | 31 | 1 | | Wh; Co |
| 1881 | 14 | 13 | | | 21. III. | Co |
| 1893 | 31 | 29 | 31 | 1 | | Co |
| 1894 | 21 | 19 | 21/22 | | | Fr |
| 1895 | 11 | 9 | 10/11 | 8/9 | | Fr |
| 1896 | 29 | 27 | 28/29 | | | Fr; Kr |
| 1897 | 18 | 17 | 16/17/18 | 15/16 | | Kr |
| 1898 | 7 | 6 | | 4/5 | | Kr |
| 1925 | 9 | 8 | | 7 | | C-4 |
| 1926 | 27 | 26 | 28 | | | C-4 |
| 1927 | 17 | 15 | 17 | | | C-4 |
| 1928 | 5 | 4 | | 4 | | C-4 |
| 1929 | 24 | 23 | 25 | | | C-4 |
| 1930 | 14 | 13 | 14/15 | | | C-1; C-4 |
| 1931 | 4 | 2 | | 2 | | C-1; C-4 |
| 1932 | 22 | 20 | 21/22 | 19/20/21 | | C-1; Bu |
| 1933 | 11 | 10 | 10/11 | | | C-1 |
| 1934 | 29 | 28 | 28/29 | | | C-1 |
| 1935 | 18 | 17 | 18/19 | | | C-1 |
| 1936 | 7 | 5 | | 5/6 | 5/6 XII. | C-1; Bu |
| 1938 | 15 | 14 | 16 | 13/14/15 | | C-1; Bu |
| 1940 | 23 | 22 | 23/24 | | | C-2; Bu |
| 1942 | 31 | 30 | 31 | | | C-2 |
| 1943 | 20 | 19 | 20 | | | C-1 |
| 1944 | 8 | 7 | (8/9) | 7/9 | | C-1; C-2 |
| 1945 | 27 | 26 | 28 | | | C-1 |
| 1946 | 17 | 15 | 16/17/18 | 14/15/16 | | Bu; C-1; C-5 |
| 1947 | 6 | 5 | (6/8) | 4/5/6 | | Bu; C-1; C-5 |
| 1948 | 25 | 23 | 24/25 | | | C-1; C-5 |
| 1949 | 14 | 13 | | 12/13 | | C-5 |
| 1950 | 3 | 2 | | 3 | | C-5 |
| 1951 | 22 | 21 | 21/22 | 21 | | C-5 |
| 1952 | 10 | 9 | | 9 | | C-5 |
| 1953 | 29 | 27 | 28/29 | | | C-2; C-5 |
| 1954 | 18 | 16 | 17/18/19 | | | C-3; C-5 |
| 1955 | 8 | 6 | 8/9 | 7 | | C-3; C-5 |
| 1956 | 26 | 24 | 25/26/27 | | | C-3; C-5 |
| 1957 | 16 | 14 | | 14/15 | | C-5 |
| 1958 | 5 | 4 | | 2/3/4 | | C-3; C-5 |
| 1959 | 24 | 23 | 24/25/26 | 22/23 | | C-6 |
| 1960 | 12 | 11 | 11/12 | 10/11 | | C-7 |

(a) Literature
Wh = Whitmee (1875)
St = Stair (1897)
Co = Collin (1897)
Fr = Friedländer (1809)
Kr = Krämer (1899)
Bu = Burrows (1955)
Ha = Hauenschild *et al.* (1968)

(b) Unpublished records
C-1 = Brother Briand/Upolu
C-2 = Brother Heslin/Tutuila
C-3 = Brother Schwehr/Savaii
C-4 = Brother Henry/Upolu
C-5 = Max Haleck/Tutuila
C-6 = Personal observations 1959
C-7 = Later information

**Table 2.** Compilation of dates on the palolo emergence in the Samoan Islands from 1964 to 1983

| Year | 3rd quarter moon | | Palolo emergence | | Reference |
|---|---|---|---|---|---|
| | Oct. | Nov. | Oct. | Nov. | |
| 1964 | 27 | 25 | 27/28 | – | M |
| 1965 | 17 | 15 | – | ? | M |
| 1966 | 7 | 5 | – | 5 | M |
| 1967 | 26 | 24 | 25 | 24 | M |
| 1968 | 14 | 12 | 13 | 12 | M |
| 1969 | 3 | 1 | | ? | M |
| 1970 | 21 | 20 | 21 | 19/20 | M |
| 1971 | 10 | 9 | – | 9/10 | M |
| 1973 | 18 | 16 | 19 | | M |
| 1974 | 8 | 6 | 8 | | M |
| 1975 | 27 | 25 | 27 | | M |
| 1977 | 4 | 3 | (4?) | 3 | P+L |
| 1978 | 23 | 22 | 23/24 | 21/22 | P+L |
| 1979 | 12 | 11 | 12 | | P+L |
| 1980 | 30 | 28 | 30/31 | – | M+P+L |
| 1981 | 19 | 18 | 19/20 | 19 | M+P+L |
| 1982 | 9 | 7 | – | 8 | M+P+L |
| 1983 | 28 | 26 | 28/29 | – | M |

Source of information:
M = Karl-Joseph Marschall, Apia
P = Alfons Phillipps, Apia
L = Br. Thomas Lynch, Apia

Table 2, clearly coincide with the third quarter of the moon.

In several cases the emergence of the palolo was recorded from all Samoan Islands from Manua in the east to Savaii in the west. Sometimes subsequent days of emergences after the main swarming have been mentioned. During some years, emergences were recorded off only one or two islands. It is apparent that this is due to a lack of information from other places. It can be stated that the palolo days are identical on all islands of the archipelago.

Tables 1 and 2 include only dates on which the palolo has been definitely reported. Thus, disregarding years for which I have no dates at all, when the palolo swarmed in October and there is no date reported for November, this implies that swarming occurred only in October.

There is a particular difficulty in the collection of swarming dates for previous years on the island of Tutuila because it occurs here shortly after midnight. It is not always certain, therefore, whether the observer did not report the date of the day on which he started from home. However, I have tried to correct this error as much as possible, and the dates supplied by Mr. Haleck are not subject to this error. For Upolu and Savaii the dates are certain because the swarming is in the early morning.

My own observations, as already mentioned, were made in 1959 on Tutuila. The palolo days that year were October 24 to 26. On October 24th very few Samoans had gone palolo fishing, but they were very successful. On the second day, the main swarming occurred. The bay was crowded with people, and they all brought home rich catches. On the third day, there was very little emergence, and this appears to be the case frequently. In 1959, the third day was stormy, and large waves on the coral platform scattered the worms. However, the swarming itself probably involved fewer individuals than on the first two days.

In earlier times the natives tried to find worms, both before and after this swarming period, and it seems quite certain that no palolo emergence occurs except on these three days.

According to the Admirality Tide Table (Vol. 3, 1984), on the date of the third quarter moon high tides occur between midnight and 2.00 hrs and between 9.00 and 21.00 hrs. Low tide at Apia occurs 21 min later than at Tutuila and 8 min earlier than at Savaii. Therefore, there is a maximum difference of 29 min between the high tides at Tutuila in the west and Savaii in the east. The corresponding differences for the low tides are 4, 8 and 12 min, respectively. The average tidal ranges are 1.0 m for spring tides and 0.6 m for neap tides.

The time differences between the tides in the Samoan islands and the ranges of spring and neap tides are too small to be correlated with the hours of palolo emergence. Differences in weather conditions, cloud cover and wave action before and during the times of palolo swarming influence that habitat much more than lunar illumination or exposure of the reefs.

During the year of my investigations on Tutuila Island, 1959, the following tidal data during the palolo days Oct. 24 to 26 were provided by the Pago Pago Tide Tables:

| October 24 | | October 25 | | October 26 | |
|---|---|---|---|---|---|
| time | m | time | m | time | m |
| 00.33 | 0.64 | 01.32 | 0.70 | 02.26 | 0.76 |
| 07.05 | 0.15 | 07.55 | 0.09 | 08.39 | 0.09 |
| 13.24 | 0.64 | 14.16 | 0.70 | 15.02 | 0.76 |
| 19.15 | 0.24 | 20.12 | 0.18 | 21.01 | 0.12 |

The third quarter moon occurred at 09.22 hrs on October 24.

Evidently, the palolo swarming on the Tutuila reef starts at the end of the nocturnal flood tide, about four to five hours after low tide.

## Correlation with the third quarter of the moon

As shown in Table 1, the palolo swarming is strictly correlated with the third quarter of the moon. The calendar dates of the monthly third quarter are different each year, corresponding to the difference between the length of the solar and synodic months.

It has been clearly demonstrated that the palolo do not emerge in September. Because swarming coincides with the third quarter of the moon, it must occur 10 to 11 d earlier each year, until in some subsequent year, it must be postponed until the following third quarter, 29 to 30 d later. The critical day before which no palolo swarming is possible and the latest date on which it can occur were still to be determined. Therefore an analysis was made to develop rules for predicting quite precisely the dates of the palolo swarming in future years.

## The palolo rules

Based on the empirical data listed in Table 1, regularities in the dates of swarming correlated with the moon phases permit the prediction of the palolo emergence in future years. Based on past dates of occurrence, the method of prediction seems accurate.

(a) The swarming never occurs before October 8th. If the third quarter of the moon is on October 7th or earlier, the palolo appears during the next quarter of the moon, i.e. on November 6th or a few days earlier. In such years, there is no palolo emergence during October. In Table 1, some earlier dates (October 4th to 7th) are given in brackets. These, however, relate to a few reports of a small swarm near Savaii. No dates so early have been recorded on Upolu and Tutuila.

(b) An emergence in October does not always occur if the third quarter of the moon falls between October 8th and 18th. Very often in such years, there is no emergence in October, or at most, a very minor one.

(c) The worms will certainly emerge in October if the third quarter moon comes after October 18th.

(d) An emergence in November is certain if the third quarter moon appears before November 7th. This swarming period is not followed by a second one (see point a).

(e) A third quarter moon between November 8th and 17th provokes a major palolo emergence, which may follow an earlier one between October 8th and 18th (see point b).

(f) A minor emergence in November is possible until the 23rd of the month, although the main swarm has occurred in October (see point c).

The relationships are presented graphically in Fig. 5.

As shown in Table 1, every 19 yr, the palolo emergence occurs on the same dates (e.g. October 24th in 1940 and 1959). This would appear to be an example of the Metonic Cycle, which is exactly 19 years. After this period, the same relative positions of the sun and moon to the earth occur on the same solar date (in 19 tropical years = 6 939.75 d there are 235 synodical months = 6 939.69 d).

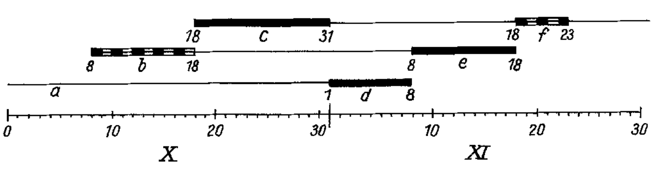


**Fig. 5.** The distribution of palolo emergence dates in October and November according to palolo rules a – f. Solid bars: definite emergence periods. Broken bars: possible emergence periods

## Causes of periodicity

Empirically, the swarming periods are sufficiently analyzed. The palolo rules seem exact enough to predict the days when the epitokous worms appear in the open water. However, this does not explain the causes of swarming.

First, we have to ask which environmental factor governs the periodicity. Hauenschild, in several papers, showed that the lunar periodicity of the nereid *Platynereis dumerilii* depends on a lunar rhythm synchronized with the periodic change in the nightly moonlight as zeitgeber. His experiments with *Eunice viridis* on Samoa were unsuccessful. In his paper (Hauenschild *et al.,* 1968), he stated that a full year of synchronized sexual development within a whole population does not occur because the duration of the spawning periods varies between 12 and 13 synodic months. Therefore, the periodicity of spawning cannot be based on an endogenic annual rhythm. There must be an external zeitgeber which correlates the onset of sexual maturity in fully grown specimens shortly before the emergence date, perhaps by synchronizing endogenic rhythms.

Due to the fact that season (October/November), date (last quarter of the moon), and local hour of the day are exactly fixed, there must be a hierarchy of annual, lunar and diurnal zeitgeber (Hauenschild *et al.,* 1968, p 292).

## Behavior of the worms in the coral rocks

During my stay in Samoa, I collected numerous whole palolo worms from the reef, where they live in branching tunnels throughout the compact coral blocks. They are concentrated at a particular level, about 3 to 5 cm below the surface, corresponding to the blue-green coloured layer of symbiotic algae (Figs. 6 and 7). All tunnels have contact with the surface.

Hauenschild *et al.* (1968) suggested that these tunnels originate from sipunculids living in the coral. The polychaetes would therefore be secondary inhabitants of abandoned tunnel systems. In my opinion, this would mean a full dependence of the palolo on the activity of other boring animals and would not explain its abundance. Furthermore, the strong mandibles of *Eunice viridis* indicate the probability that the worms gnaw their tunnels themselves. This requires further investigation.

As already mentioned, the tunnels are mostly in the layer of symbiotic algae. If the worms do not regularly leave the tunnel system to feed at the coral surface, it could be hypothesized that they feed at least partly on these algae, and only at the time of reproduction do the epitokous segments swarm into the open water. However, it must be mentioned that Hauenschild *et al.* (1968) reported that the palolo worms are primarily nocturnal and apparently extend their anterior and posterior ends temporarily out of the tunnels to feed and defecate. These authors believe that the worms may be influenced directly by periodic changes in the nocturnal light conditions.

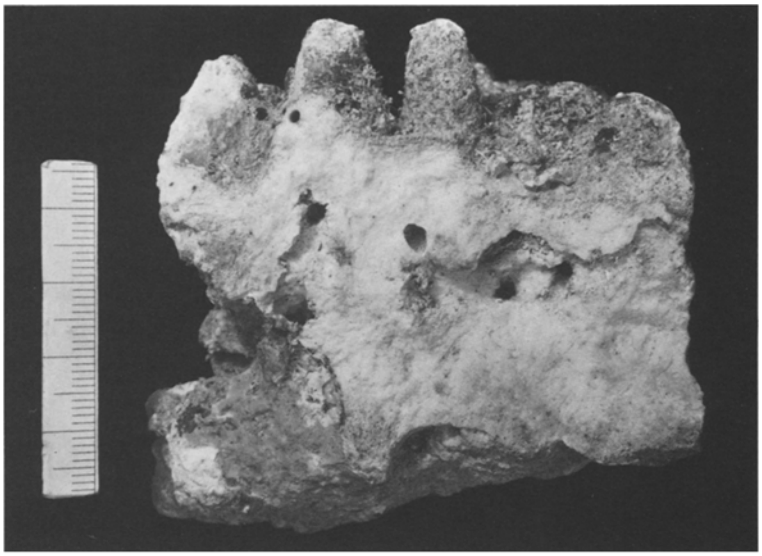

**Fig. 6.** Level of palolo tunnels in living coral rocks. Left: Scale in cm

**Fig. 7.** A palolo worm partly out of its tunnel

Possible timing determinants

As I learned in Samoa, mucus discharge has been found in the water of the coral area two days before the palolo spawning. In 1930, Brother Henry of the Marist Mission reported that on the first day "the sea is covered with a limy matter containing all sorts of sea annelids, etc., which gives the water an agitated or even muddy aspect". This could be a mass production of larvae, perhaps by the coral species themselves or by other marine taxa. If this is correct, the liberation of the epitokous palolo segments could be a reaction to the lunar periodicity of another animal. Perhaps indirect guidance could better explain the seasonal, synodic and diurnal regularity of the palolo phenomenon. Hauenschild *et al.* (1968) also discussed the possibility of an indirect impulse through photobiological changes of fodder plants.

It is difficult to conceive of a direct influence by the moonlight on the sexual maturity of the *Eunice viridis* worms in the coral rocks. Assuming that parts of the worms leave the tunnel at night, the influence of the moonlight is limited both temporally and in intensity by the weather conditions. Clear or cloudy nights do not affect the spawning date. A moonlight penetration to the tunnel level in the rocks is not considered possible. Thus, neurosecretory impulses must be induced by an external zeitgeber as Hauenschild *et al.* (1968) emphasized.

Hauenschild *et al.* (1968) described the sexual maturation. Females which had been isolated from the reef on 22 October 1966 or later (palolo emergence: 5 November) continued their sexual development in the laboratory, and males that had been collected one to two months earlier also became sexually mature. In all palolo worms taken from the reef before October 22 sexual development was totally inhibited. The same was true for all headless posterior fragments, even those isolated on October 22nd in a nearly mature state. Only three such fragments completed their sexual maturation after regeneration of a new head. "This result and other facts suggest the existence of a hormone in the head which induces sexual maturation in the posterior end of the worms". This was confirmed by histological investigations (see also Hofmann, 1969). Those maturing worms that had been fixed one month before spawning contained about 10 times as much neurosecretory material in their brains than specimens collected earlier. These observations show that the maturation of the palolo in the reef starts about one month before emergence. Nevertheless, this does not help to explain the simultaneous breeding during one to three days after the third quarter of the moon in October or November and the east to west shift of the time of day near the Samoan Islands from ca 20.00 hrs off Manua to 1.00 hrs off Tutuila and 4.00 hrs off Upolu and Savaii. No tidal differences could be detected, and the exact phase of the moon at all the islands is effectively the same.

The empirical rule for the palolo swarming is well established. The question of the external zeitgeber for the relative importance of the annual, lunar and diurnal regulation of the phenomenon will require further observation and experimental study.

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