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https://doi.org/10.5109/23802

出版情報：九州大学大学院農学研究院紀要. 29 (2/3), pp.157-165, 1984-12. Kyushu University
バージョン：
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J. Fac. Agr., Kyushu Univ., 29(2・3), 157-165 (1984)

Reproduction of Ulvaceous Algae with Special Reference to the Periodic Fruiting

III. Six-Day Periodicity in the Fruiting of *Ulva pertusa* on the Noto Peninsula

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(Received October 16, 1984)

Fertile plants of *U. pertusa* appear en masse at intervals of six days at Nago and Ushitsu on the Noto Peninsula, Japan. This alga is scarcely exposed to the air even at low tides throughout the summer because of a small tidal range. Although occasional fruiting may occur, outbursts of fertile plants seem to be predictable. Both gametophytes and sporophytes seemed to be present in approximately equal numbers at Nago. At Ushitsu, however, the fertile gametophytes always predominated over the fertile sporophytes in number. Fertile sporophytes cannot be separated from fertile gametophytes by the colors of their respective fertile areas. Daily integrated radiation at the level of *Ulva* colonies was not always proportional to that on the surface, particularly under conditions of increased turbidity. This alga seems to have an endogenous rhythm in its fruiting, but some exogenous factors may affect its periodicity.

INTRODUCTION

In a previous paper we reported on the fruiting of *Ulva pertusa* at Tsuyazaki, northern Kyushu, and showed that this alga usually fruited during neap tides insted of spring tides (Sawada and Watanabe, 1974). Since it seemed to be accepted that many of the ulvaceous algae in Japan produced swarmers during spring tides (Ohno and Arasaki, 1967; Chihara, 1969), the result obtained at Tsuyazaki was entirely unexpected one. To investigate whether or not such a phenomenon occurred only in northern Kyushu, observations were made at Shibukawa on the Seto Inland Sea. As tidal conditions were comparable with those at Tsuyazaki, a similar result was surmised. Though this alga there became fertile during neap tides, details were apparently different with respect to the development of fertile blades in each generation (Okuda, 1975).

Obtaining these results, the Noto Peninsula was chosen as the third place to continue this study. The Noto Peninsula is situated in the central part of Japan on the Japan Sea and has a very small tidal range throughout the year. In some doorway regions to the Japan Sea as Tsuyazaki, tidal range is about 2 m during a spring tide series, as it is on the Pacific coast,

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and this alga undergoes alternate emersion and submersion. On the Noto Peninsula, however, the tidal range is about 35cm during the summer spring tide series, leaving this alga underwater in general. It is evident that the semilunar rhythmicity in the fruiting of this alga, either during spring tides or neap tides, is based chiefly on the tidal conditions including a submergence-exposure factor. It is of interest to make an investigation on how this rhythmicity was retained or modified by this alga under subtidal conditions. In this paper the fruiting of this alga with a six-day periodicity that does not seem to be related to the tides will be described.

MATERIALS AND METHOD

Observations were made on successive days at Nago[1)] and Ushitsu[2)] in 1970 and 1972, respectively. In 1970, the Noto Marine Laboratory of the University of Kanazawa was available from August 21 through September 14. Nago is located about 3 km northeast of the Laboratory and was visited at least once a day. *Ulva pertusa* was at that time one of the most abundant species growing on the breakwaters and scattered stones. All of the materials were collected inside the breakwaters, where this alga formed dense communities from near the surface to the bottom, the water being around 70cm deep at low tide. Collections were made only when fertile plants were recognized. Because of the small tidal range, materials were easily collected at any time during the day. Nago was reached at about sunrise on the first few days only to confirm that the liberation of swarmers would not occur so early in the morning, and it was found later that even a collection at 10 o'clock was not too late. When a burst of fertile plants appeared, thalli of well over 100 were collected and put together into cloth bags, while if only some fertile ones were dotted, a few of them were collected, making the same collecting effort throughout the study period.

In the laboratory, a piece of fertile area of each plant was given a rinse and placed in a separate Petri dish of seawater. If liberation of swarmers did not occur, water in dishes was replaced with fresh seawater or stirred by finger to induce liberation. One drop of seawater with dense swarmers was placed on a slide, fixed with osmic acid, stained with crystal violet, and examined through a microscope to determine if the swarmers were biflagellated gametes or quadriflagellated zoospores.

In 1972, the second investigation was resumed at Ushitsu 10 km west of Nago, where the Fisheries Experimental Station of Ishikawa Prefecture was located. *Ulva* colonies were found on the breakwaters just in front of the Station during my stay from August 16 through September 4.

Solar radiation was measured in two ways. In 1970, a Bellani radiation integrator was set in the grounds of the Marine Laboratory on August 22 and measurement was continued through September 13. In 1972, an underwater photosynthetic irradiance sensor (PSZ-1, Toshiba) was placed on August 15

[1)] 長尾, [2)] 宇出津.

among *Ulva* colonies, where plants were most densely populated. The water level of the sensor was about 30cm deep at low tide and about 60cm at high tide. A few plants were exposed at low tide, but most plants were distributed through about 40cm below the sensor. A Bellani radiation integrator was also set in the grounds of the Station on August 16, and both were kept in place through September 3.

RESULTS

Nago

Prior to this investigation in 1970, two preparatory trips to Nago were taken in April and July of that year to make sure there was enough material. Very few *Ulva* thalli were found and some species of *Enteromorpha* were thriving on April 18. On July 28, *U. pertusa* was affluent and seemed to suffice for the present purpose. Observations were planned to continue long enough to cover 2 successive quarters of the moon, inferring some semilunar-related phenomena from the results in Tsuyazaki and Shibukawa. This alga did not show any indication of fading during the observations. The surface water temperature ranged from 25.0 to 28.6-C.

Fertile thalli were as distinct as those in Tsuyazaki or Shibukawa by the colors of their marginal areas, and an enormous amount of such plants appeared at intervals of 6 days (Table 1). The figure 100 in Table 1 indicates an uncountable number, a large quantity of fertile blades, while figures under 100 represent a small, negligible quantity of such ones. The first fruiting burst occurred on August 24 without any signs of fruiting the day before. Sporophytes and gametophytes seemed to grow in approximately equal numbers. No fertile thalli were observed on the following 2 days, and only a few fertile ones were dotted among the *Ulva* colonies on the next 3 days. Sporophytes could not be separated from gametophytes by the color of their fertile areas, though they could be at Tsuyazaki.

In a surprise development on August 30, the second outburst took place 6 days after the first one. More fertile blades turned out to be sporophytes on microscopic examination. Although fertile blades were only a few on September 1, 32 plants out of 34 were gametophytes, and fewer fertile blades were observed through September 4. The third outburst appeared unexpectedly on September 5 and the substrate there was densely covered with fertile blades. Predominance of sporophytes over gametophytes was resumed on this day. Less fertile blades were found on the following day, but as the figure 96 shows they were still quite abundant, and gametophytes predominated over sporophytes.

The next fruiting burst occurred on September 12, not after 6 days but 7 days. Predominance of sporophytes over gametophytes was most remarkable on this day. Some fertile plants appeared on the following day and gametophytes strikingly outnumbered sporophytes, a recurrence of the dominancy reversal as on September 6.

Table 1. Rise and fall of fertile plants of *Ulva pertusa* at Nago on the Noto Peninsula, 1970.

Date	Moon's age	Integrated radiation (cal/cm² SWR)	Number of plants examined		
			Total	Gametophyte	Sporophyte
Aug. 21	18.9	—	0	0	0
22	19.9	—	0	0	0
23	20.9	523	0	0	0
24	21.90	410	100	53	47
25	22.9	449	0	0	0
26	23.9	293	0	0	0
27	24.9	510	12	0	12
28	25.9	353	17	8	9
29	26.9	385	1	1	0
30	27.9	405	100	41	59
31	28.9	244	4	2	2
Sept. 1	0.2.	527	34	32	2
2	1.2	521	5	5	0
3	2.2	311	0	0	0
4	3.2	527	0	0	0
5	4.2	362	100	45	55
6	5.2	318	96	75	21
7	6.2	502	12	12	0
8	7.2	507	42	21	21
9	8.2◐	450		1	0
10	9.2	180	6	3	3
11	10.2	520	0	0	0
12	11.2	189	100	37	63
13	12.2	319	86	76	10
14	13.2	—	0	0	0

Ushitsu

According to a preparatory observation at Ushitsu on July 29, 1972, it appeared that *Ulva* colonies would flourish till early in September. They faded away, however, so earlier that only a small amount of *Ulva* thalli was left in the last observation period. The surface water temperature ranged from 24.2 to 28.2°C.

On August 16, a fruiting burst occurred as is shown in Table 2. There was a considerable unbalance in number between sporophytes and gametophytes, and the latter overwhelmingly outnumbered the former. Dominancy reversal was recorded in Nago in 1970, with gametophytes outnumbering sporophytes on the second day. However, because of the abundance of fertile plants at Ushitsu on this day, the 16th, it did not seem to be the second day of the fruiting period. It was impossible to separate gametophytes from sporophytes by the colors of fertile areas. No fruiting was observed on the following day. Some fertile plants, being less than '100' but still not an inconsiderable amount, appeared on the 18th, 19th, and 20th. On each of those 3 days gametophytes were always dominant over sporophytes.

Table 2. Rise and fall of fertile plants of *Ulva* ***pertusa*** at Ushitsu on the Noto Peninsula, 1972.

Date	Moon's age	Integrated radiation: surface (cal/cm² SWR)	Integrated radiation: under-water (cal/cm² PhAR)	Integrated radiation: ratio: under-water / surface	Number of plants examined: Total	Number of plants examined: Gameto-phyte	Number of plants examined: Sporo-phyte
Aug. 16	6.9	—	186.6	—	100	95	5
17	7.90	605	188.6	0.31	0	0	0
18	8.9	585	169.5	0 29	80	52	28
19	9.9	530	155.5	0: 29	76	48	28
20	10.9	104	23.4	0.23	64	39	25
21	11.9	220	53.3	0. 24	0	0	0
22	12.9	238	53. 0	0.22	100	89	11
23	13.9	576	178.8	0.31	36	36	0
24	14.9	580	172.8	0.30	0	0	0
25	15.90	190	50.2	0. 26	0	0	0
26	16.9	65	4.4	0.07	0	0	0
27	17.9	577	140.3	0.24	100	0	0
28	18.9	85	4.1	0.05		89	11
29	19.9	549	158.8	0.29	0	0	0
30	20.9	402	109.7	0.27	0	0	0
31	21.90	282	47.8	0.17	0	0	0
Sept. 1	22.9	400	87.7	0.22	0	0	0
2	23.9	543	147.3	0.27	48	44	4
3	24.9	549	147.5	0.27	0	0	0
4	25.9	—	—	—	0	0	0

The second fruiting of '100' occurred on August 22, 6 days after the first one as expected. Gametophytes outnumbered sporophytes 89 to 11. On the following day, fertile plants were few and all of the 36 examined were gametophytes. The next big fruiting occurred on August 28, 6 days after the second one as anticipated. It was an exact copy of the result on August 22, gametophytes and sporophytes being 89 and 11, respectively. No fertility was observed the following 5 days.

Around the end of August, as *Ulva* colonies rapidly became sparse and thalli small, they seemed to be in the last stage of growing. On September 2, 5 days after the preceding fruiting, a small amount of fertile plants appeared. Fruiting was expected to occur on September 3, but it was found neither on the 3rd nor the 4th, and *Ulva* thalli were about to disappear. Again on this day gametophytes outnumbered sporophytes remarkably.

DISCUSSION

A new moon and a full moon, or its first quarter and last quarter come alternately at intervals of 14.8 days. As the fruiting of *U. pertusa* occurs during neap tides both in Tsuyazaki and Shibukawa, the fruiting matches semilunar cycles. On the Noto Peninsula, however, outbursts of fertile plants seem to occur every

6 days. On the afternoon of August 30, fertile plants being collected around half past six in the morning, the second visit to Nago was made around one o'clock. About one half of the thalli liberated swarmers at that time and whitish appendages were still found at their marginal areas. According to Professor K. Nishida of the University of Kanazawa, such colorless appendages were found on the afternoon of August 18. Fruiting must have occurred on that day, dating back 6 days from the first encounter with the outburst on the 24th.

There are some reports on fortnightly fruiting in ulvaceous algae and many of them refer to the fruiting during spring tides. According to Ohno and Arasaki (1967), *U. pertusa* produces swarmers for several days during spring tides in an April-August period. *U. lobata* liberated swarmers during spring tides, gametophytes early in a series and sporophytes late in a series (Smith, 1947). Fertile fronds of *U. fenestrata* and *U. scagelii* (Chihara, 1968) and *U. arasakii* (Chihara, 1969) were found only for a few days during spring tides. Subbaramaiah (1970) reported that *U. fasciata* liberated swarmers for 3 days regularly coinciding with spring tides. Both *U. arasakii* and *U. fasciata* maintained a fortnightly rhythm in fruiting even under laboratory conditions. Such a periodic fruiting during spring tides was also reported for *Enteromorpha intestinalis* (Christie and Evans, 1962) and *E. flexuosa* and *E. compressa* (Ohno *et al.,* 1981).

Fruiting during neap tides, instead of spring tides, was reported for *U. pertusa* (Sawada and Watanabe, 1974; Okuda, 1975) and for *Monostroma nitidum* (Ohno, 1972). Tokuda and Arasaki (1967) reported that 2 species of *Monostroma* liberated swarmers when the lowest tide in a day came early in the morning. This day generally falls 2 or 3 days after quarters of the moon.

All the algae mentioned above are periodic and semilunar in fruiting. Six-day periodicity of *U. pertusa* on the Noto Peninsula never seems to be derived from a semilunar or lunar-related cycle. Plants there may have an endogenous rhythm, but external factors such as a small tidal range, or lack of exposure to the air might drive this alga to become fertile every 6 days. According to Ohno (1972), a semilunar periodicity of *M. nitidum* was observed only for fronds in their natural habitat, and it was less distinct for ones on fixed culture nets, while those on floating culture nets showed no periodicity. Here also environmental factors seem to be influencing periodic fruiting.

Besides these ulvaceous algae, *Halicystis ovalis* (*Derbesia marina*) under natural conditions is reported to discharge gametes usually toward the end of each spring tide series, and the same bi-weekly periodicity was observed on the plants in laboratory cultures (Hollenberg, 1936). On the other hand, according to Page and Kingsbury (1968) and Page and Sweeney (1968), an endogenous rhythm controls gamete formation in *H. parvula* (*D. tenuissima*), and the period of this rhythm is 4-5 days under laboratory conditions. Beth (1962) made field observations on another siphonaceous alga, *Halimeda tuna,* and found a 4–5-day periodicity in gametangial formation. He noted that there were varying period lengths between (2 ?) 3 and more than 14 days, but an underlying large period of about 28 days could be detected. *Ulva pertusa* may show other rhythmicities depending on its localities or culture conditions.

Whenever fertile plants appeared at Ushitsu, gametophytes always outnumbered sporophytes. In the previous study at Nago, in 1970, plants of both generations seemed to be present in approximately equal numbers. Sporophytes sometimes outnumbered gametophytes on outbursting days, but on the following day or the next, gametophytes dominated sporophytes in number. As fertile plants among male, female, and zoosporic ones on the Noto Peninsula cannot be selectively collected, it was strongly assumed that there was only a small quantity of sporophytes at Ushitsu, at least during the summer months.

Arasaki (1946) reported on ulvaceous algae along the Pacific coasts of Mie and Aichi Prefectures. According to him, vegetative plants of *U. pertusa* are found throughout the year in that region, but zoospores are obtained from December through May, and gemetes from March through July. Such a time lag is indicated for 7 species out of 9 among *Ulva* and *Enteromorpha*. Some modified shifts may occur in different regions, and long-term observation is desirable at each locality.

Through the investigations at Tsuyazaki and at Shibukawa, light intensity seemed to be influential on fruiting. Fertile plants generally appeared 5 or more straight days during neap tides there, but they were usually very small in number after wet weather. No fertile plants appeared, unexpectedly, at Nago on September 11. As it was rainy on the preceding day, it was assumed that the accumulation of materials necessary for fruiting was not enough owing to the low level of integrated radiant energy.

It is, however, difficult to read a critical level, if any, as the Bellani radiation integrator was set at the Marine Laboratory apart from the collection site. Also, according to the later measurements at Ushitsu, the radiation integrated underwater was not always proportional to that integrated at the surface. Solar radiation was measured in two ways, short wave radiation for the surface and photosynthetically active radiation underwater. The underwater/surface -ratio is supposed to be constant, and the ratio was about 0.3 in general when the water was clear. But when the muddy sea bottom was stirred due to a rough sea, it was only 0.07 on the 26th, and 0.05 on the 28th of August. Along the rocky shores where the water is clear, a pyranometer for surface use furnishes us with much information, but in the inlets where increased turbidity is suspected, direct measurement with underwater light sensors is required.

Plants were distributed in a range of about 70–80 cm both at Nago and Ushitsu. Only a few of them were exposed at low tides, but most of them were not exposed during my investigations. There was no significant difference in the fruiting time between those growing deeper and near the surface. Such is the case with ***Halimeda tuna,*** whose gametangial formation occurs simultaneously in communities near the surface as well as at depths of 20 and 40 m (Beth, 1962). Recording solar radiation at two levels, near the surface and among deeper colonies, will contribute to the future laboratory cultures.

ACKNOWLEDGEMENTS

I would like to express my sincere thanks to Professor Emeritus K. Mashiko, then director of the Marine Laboratory, the University of Kanazawa, and to Mr. K. Tomi, then director of the Fisheries Experimental Station, Ishikawa Prefecture, for providing working facilities and for their interest. I am particularly indebted to the late Dr. M. Ikemori of the Marine Laboratory, the University of Kanazawa, for supporting me in arranging my schedule and taking me to the right places for collecting materials. I am also grateful to Professor K. Nishida of the University of Kanazawa for the profitable suggestion in his casual talk, and to Assistant Professor 0. Hirota of the Crop Husbandry Laboratory, Kyushu University, for his valuable comments on measuring solar radiation.

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