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# The life history of *Gloiosiphonia capillaris* (HUDSON) CARMICHAEL (Rhodophyceae, Cryptonemiales)[2)]

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The life history of the red alga *Gloiosiphonia capillaris* (HUDSON) CARMICHAEL from Oshoro Bay, Hokkaido in Japan was studied by laboratory culture experiments and periodic field observations. Carpospores obtained from field-collected plants germinated in culture to form prostrate discs. Upright thalli originated directly from erect filaments of the discs under short-day conditions. No tetrasporangia were observed in the discs. The upright thalli produced carpogonia and spermatangia under long-day conditions, then, carposporophytes developed, and released viable carpospores. Thus, *G. capillaris* from Oshoro Bay lacks a tetrasporophytic phase in the life history. However, it is uncertain whether the life-history pattern is like *Lemanea* or apomictic because of the absence of cytological evidence. A correlation was found between growth and reproduction in culture and its seasonal pattern in nature.

*Key Index Words*: *Cryptonemiales*; Gloiosiphonia; *photoperiodism*; *Rhodophyceae*; *life history*; *taxonomy*.

EDELSTEIN (1970), who cultured carpospores of *Gloiosiphonia capillaris* from Nova Scotia, Canada, reported the occurrence of small crustose tetrasporophytes in the life history. Similar crustose tetrasporophytes were also found for *G. capillaris* from Punta Baja, Mexico (WEST pers. comm.). However, according to other investigators (GOOR 1923, NEWTON 1931, KYLIN 1956, TAYLOR 1957, FUNAHASHI 1966, 1967, NODA 1971), the tetrasporangia were formed on upright thalli. Thus some controversy is evident regarding the reproductive patterns in this species. It is well known that several species of the Florideophycidae possess two types of life history in different populations (UMEZAKI 1977, for review). The purpose of our present study was to clarify this question and we have conducted laboratory culture experiments of *Gloiosiphonia capillaris* from Oshoro Bay, Hokkaido in Japan and field observations on the same locality.

## Materials and Methods

Fertile cystocarpic plants were collected in Oshoro Bay on May 25, and May 29, 1977 (Fig. 1). We examined these plants carefully and did not find any tetrasporangia. The excised fertile branches were washed in sterile seawater using small writing brushes and put in an icebox at about 5°C for 5-10 min. They were placed in Petri dishes (7.5 cm × 1.8 cm) containing 30 m$\ell$ of PES culture medium (PROVASOLI

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1968). Liberated carpospores were rinsed quickly in medium using finely-drawn glass capillary pipettes under a dissecting microscope and then inoculated onto several drops of culture medium on slide glasses placed on the bottom of Petri dishes (9 cm ×2 cm). The Petri dishes were placed under culture conditions tested. The carpospores attached to slide glasses 24–48 hr after inoculation and then about 50 mℓ of culture medium were introduced into the Petri dishes. After 7 days the slides were transferred to culture vessels (6.5 cm×8.0 cm) containing 200 mℓ of medium.

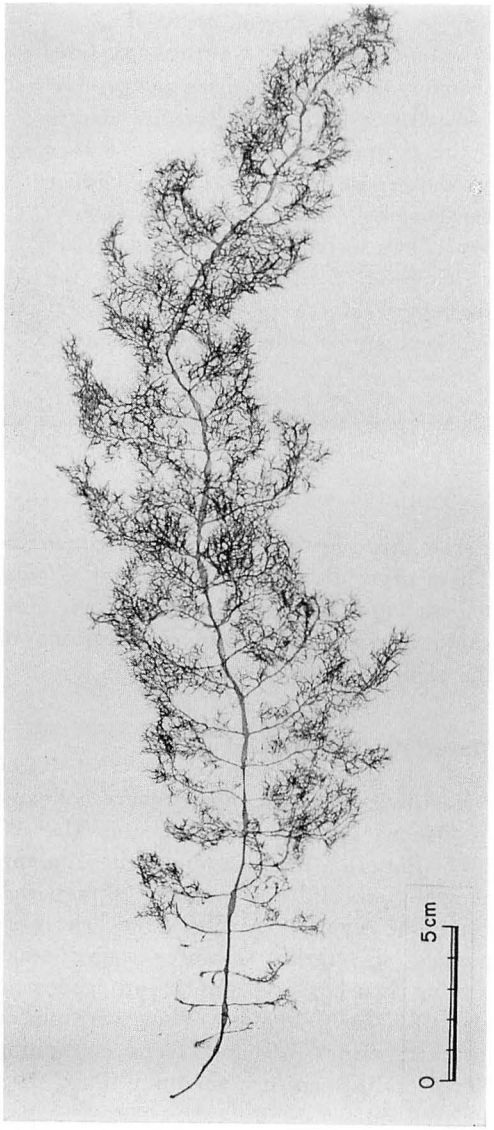


Fig. 1. Cystocarpic plant of *Gloiosiphonia capillaris* collected in Oshoro Bay on May 29, 1977 (SAP 032130).

Carpospore germination tests were done as follows. Excised and washed fertile branches were immersed for 30–60 min in Petri dishes (7.5 cm×1.8 cm) containing 30 mℓ of culture medium. Then, the branches were removed and the Petri dishes were placed under culture conditions tested. Cultures were checked 3 and 5 days after inoculation under an inverted microscope (Olympus CK).

Sterile plants were collected on April 21, 1977 at the same locality mentioned above and apical fragments of the branches were used for culture experiments. Tips of the lateral branches were washed and transferred with a glass capillary pipette under a dissecting microscope. The excised tips (about 200 μm in length) were rinsed and introduced individually into screw cap tubes (1.8 cm×13.5 cm) each containing 10 mℓ of medium. Eighteen days after inoculation they were transferred to culture vessels (6.5 cm×5.0 cm) containing 100 mℓ of medium and later transferred to larger vessels (6.5 cm×8.0 cm) containing 200 mℓ of medium. Six fragments derived from three field-collected plants (two fragments per one plant) were placed in separate vessels under each condition tested. To eliminate diatoms germanium dioxide was added to a concentration of 5 mg/ℓ (WEST 1972).

The cultures were maintained in freezer-incubators illuminated with cool-while fluorescent lamps (2500–3000 lux). The temperatures and photoperiods were regulated in the following combinations: 5°C, 16 : $\overline{8}$ (light and dark cycle); 5°C, 8 : $\overline{16}$; 10°C, 16 : $\overline{8}$; 10°C, 8 : $\overline{16}$; 15°C, 16 : $\overline{8}$; 15°C, 8 : $\overline{16}$; 20°C, 16 : $\overline{8}$; and 20°C, 8 : $\overline{16}$. These will be shown in the text as 5 L, 5 S, 10 L, 10 S, 15 L, 15 S, 20 L and 20 S, respectively. In the germination tests and apical fragment cultures 20 S was excluded. The culture medium was changed monthly.

Periodic field observations were made in Oshoro Bay from March 1977 to February 1978 in order to obtain information on the

life history in the field. Additional field observations were also made in the same locality during March 1978 and April 1979.

## Results

*Culture experiments with carpospores*: Liberated carpospores are globular and yellowish red in color and average 20 μm diameter (Fig. 2, A). The carpospore germination tests were made with seven of the eight culture conditions stated above. The germination rate was low (0.0–2.2%) at lower temperature conditions and high (13.5–24.7%) in higher temperatures (Table 1). A few spores attached to the

Table 1. Percentage germination of the carpospores under seven conditions tested

| Conditions | 5S | 5L | 10S | 10L | 15S | 15L | 20L |
|---|---|---|---|---|---|---|---|
| Germling number | 0 | 0 | 8 | 13 | 51 | 69 | 156 |
| Counted spore number | 600 | 600 | 600 | 600 | 607 | 511 | 631 |
| Germination rate (%) | 0.0 | 0.0 | 1.3 | 2.2 | 8.4 | 13.5 | 24.7 |

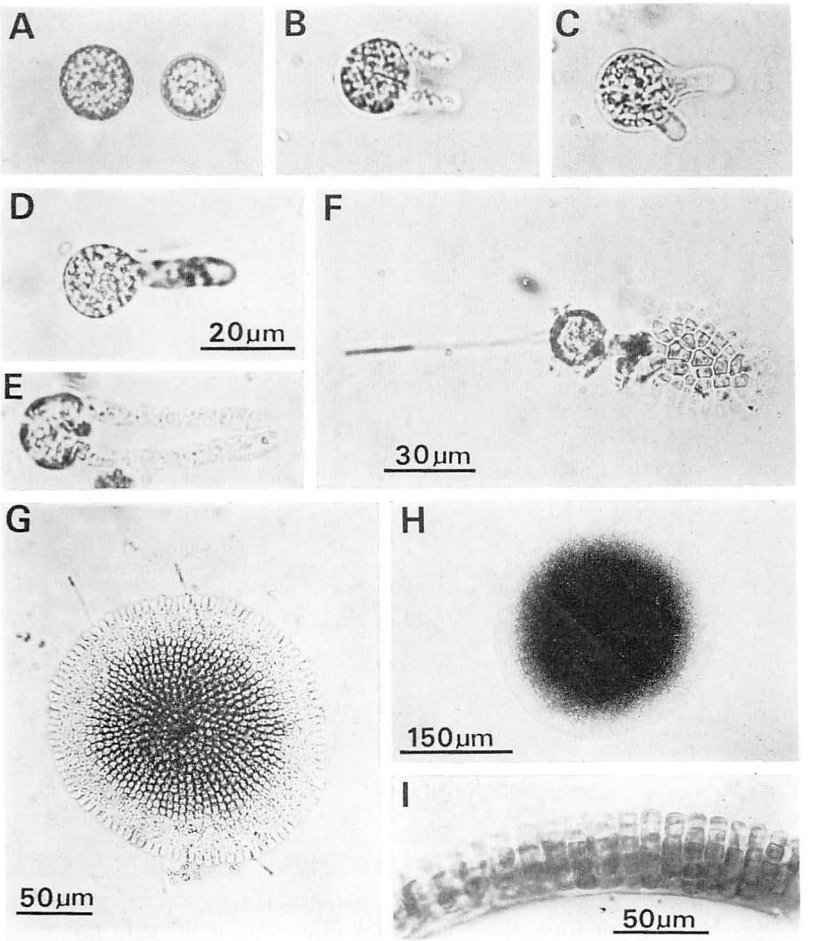


Fig. 2. Carpospores and their germination. A. Two carpospores. B–I. Carpospore germlings grown at 15 L: B–D, two-day old; E, four-day old; F, seven-day old; G, seventeen-day old; H–I, one-month old (I, section through a disc). Scale in D applies also to A–C and E.

substrate at 5 L and 5 S, but they did not germinate. No apparent difference in development was found at these culture conditions.

Carpospores isolated by glass capillary pipettes were first cultured at 15 L and 20 L. The spores germinated and grew into prostrate discs in a manner similar to that previously reported for this species (ROSENVINGE 1917, EDELSTEIN 1970) and shown in Fig. 2, B–G. The discs reached 50–340 $\mu$m (average 210 $\mu$m) in diameter at 15 L (Fig. 2, H) and 60–300 $\mu$m (average 170 $\mu$m) in diameter at 20 L after one month from inoculation. They are 5 cells thick at the center of the discs (Fig. 2, I) and becomes thinner toward the growing margin.

Two-month-old cultures maintained at

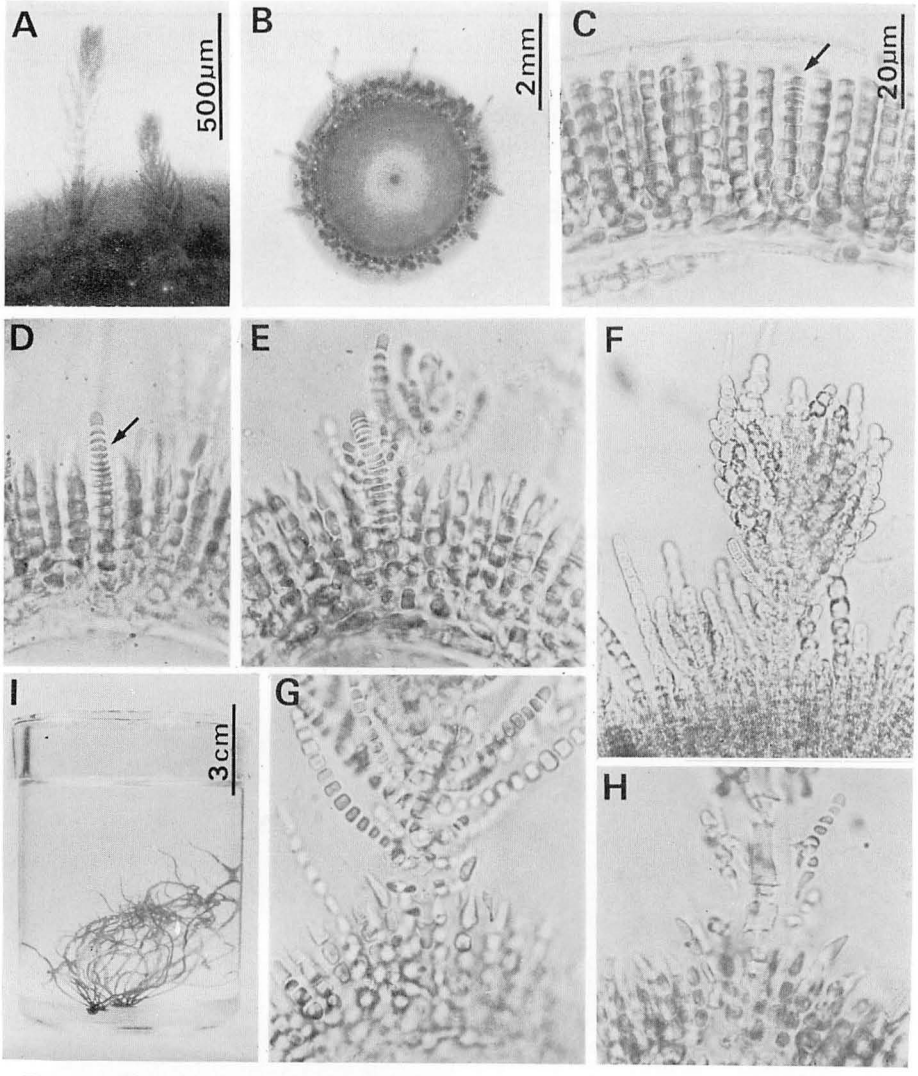


Fig. 3. Upright thalli derived from carpospore germlings. A–H. Young upright thalli arising from three-month-old discs grown at 15 L for 2 months and then transferred to 10 S (A, B, surface view; C–H, sections through discs; arrows indicate primordia of axial filaments). I. Habit photograph of seven and a half-month old plants grown at 15 L for 2 months and then transferred to 10 S. Scale in C applies also to D–H.

15 L and 20 L were divided into eight groups (each divided into four) and grown under four different temperatures and two different light regimes stated above. One month later, the discs transferred to 5 S, 10 S and 15 S formed upright thalli (Fig. 3, A, B). Each disc formed a slightly elevated ring of erect axes, 1.5–2.3 mm broad, around the margin (Fig. 3, B). The upright thalli issued only within the ring. The developmental sequence of the upright thalli was followed in sections through the discs. Specially differentiated erect filaments (primordia of axial filaments), which consisted of short cells, originated terminally on ordinary erect filaments of the disc (Fig. 3, C, D ; 4, A). They grew into axial filaments of the upright thallus and bore lateral filaments of limited growth (Fig. 3, E–H ; 4, B). The axial filaments and lateral filaments became embedded in a mucilaginous matrix and young thalli with uniaxial construction were formed. This process is similar to that reported for the development of upright thalli in this species (OLTMANNS 1904). No reproductive structures were observed in these discs which formed the upright thalli.

The upright thalli rapidly developed into *G. capillaris* plants similar to those found in the field (Fig. 3, I). Several erect thalli were detached from the base and transferred to 15 L 4 months after their initiation. Spermatangia and carpogonia were formed on the same plant at 15 L one year after transfer (Fig. 5, A, B). Female fertile branch system is borne on the first, second, or third cells of lateral branches of limited growth which issue from the central axial cells. The fertile branch system is composed of a carpogonial branch, 3–7 cells in length, and an auxiliary cell branch, 4–7 cells in length, both of which originate

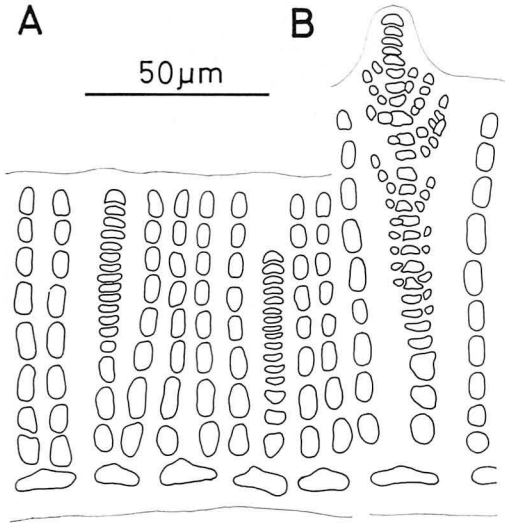


Fig. 4. Sections through three-monthold discs grown at 15 L for 2 months and then shifted to 10 S, showing the origin of upright thalli. A. Two primordial filaments consisting of short cells. B. More advanced stage than A.

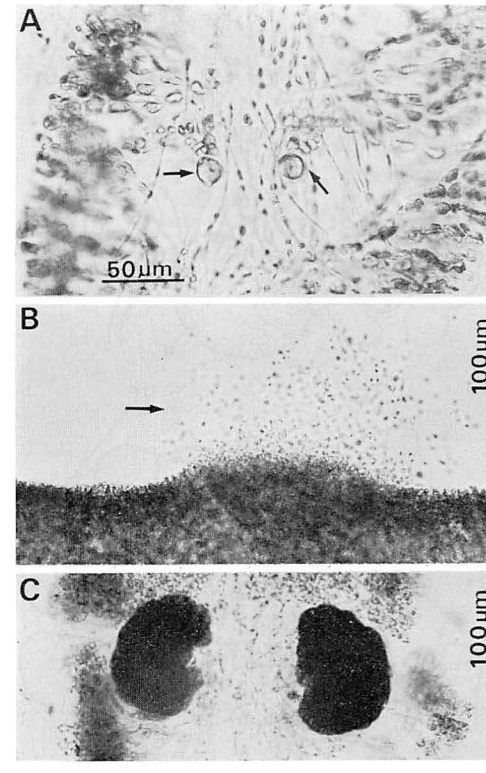


Fig. 5. Sexual reproductive structures and cystocarps borne on upright thalli. A. Longitudinal section of the thallus, showing two fertile branches: arrows indicate auxiliary cells. B. Surface view of the thallus, showing liberated spermatia (arrow). C. Longitudinal section of the thallus, showing two cystocarps.

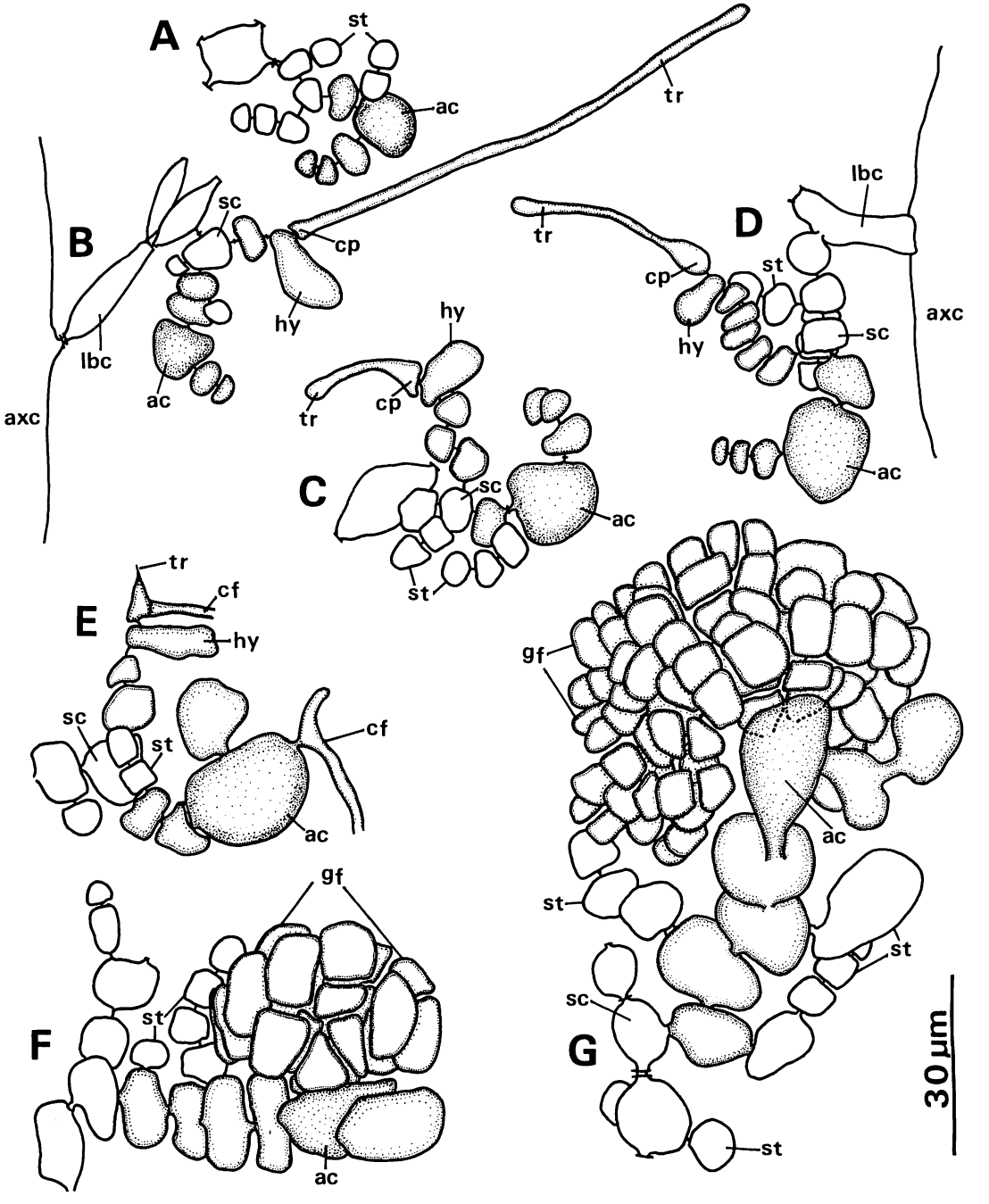


Fig. 6. Female fertile branch system before fertilization (A–D) and gonimoblast development (E–G) of cultured plants. A. Fertile branch composed of an auxiliary cell branch. B–D. Fertile branches with various carpogonial branches; B, with three cells; C, with five cells; D, with seven cells. E. Early stage in gonimoblast development; note a connecting filament issuing from the carpogonium (the trichogyne disintegrated) and another connecting filament penetrating into the auxiliary cell. F–G. Gonimoblast filaments issuing from the auxiliary cells; note the pit-connections between the cells of auxiliary cell branches becoming wider. ac, auxiliary cell; axc, cell of axial filament; cf, connecting filament; cp, carpogonium; gf, gonimoblast filament; hy, hypogenous cell; lbc, cell of lateral branch; sc, supporting cell; st, sterile branchlet; tr, trichogyne.

from a common supporting cell (Fig. 6, B–D). At times the fertile branch is composed of only an auxiliary cell branch (Fig. 6, A). Short sterile branches issue from some cells of the fertile branches (Fig. 6, A–D). The supporting cell is hardly distinguishable from the cells of the auxiliary cell branch and proximal one or two cells of the fertile branch. The gonimoblast development was observed one month later (Fig. 6, E–G). A presumably fertilized carpogonium produces a connecting filament (Fig. 6, E). Then, the connecting filament penetrates into an auxiliary cell (Fig. 6, E). The presumably diploid auxiliary cell bears gonimoblast filaments (Fig. 6, E–G). The cells of the fertilized auxiliary cell branch increase in size, and the pit connections between them become widen (Fig. 6, F, G). These developmental sequences are similar to those reported previously for this species based on field materials (SCHMITZ 1883, OLTMANNS 1898, OKAMURA 1914, SJÖSTEDT 1926, KYLIN 1930, EDELSTEIN 1972). Mature cystocarps appeared subsequent one month later (Fig. 5, C) and released carpospores which germinated and grew into prostrate discs.

The prostrate discs derived from carpospores of field-collected plants and cultured at 5 L, 10 L, 15 L, 20 L, and 20 S did not form upright thalli or any reproductive organs even after one year, although they formed slightly elevated rings near the margin in all culture conditions except at 20 L.

*Culture experiments with apical fragments of branches*: The majority of isolated apical tips of branches regenerated and grew into plants similar in morphology to that of the naturally occuring plants. However, main axes of some plants divided dichotomously and bore few branches. The length of the plants was measured every ten days from 18 days after inoculation for 5 months and the data is shown in Fig. 7. The plants grew more rapidly at 10–20°C than at 5°C and they grew best in long-day conditions. The plants cultured at 20 L formed spermatangial sori after 3 months from inoculation, and those cultured at 15 L and 10 L formed them after 4 months. They grew slowly from these periods and bore cystocarps about one and a half month later. However, the plants maintained at 5 L and short-day conditions did not become fertile even after 8 months, although they were longer than the plants which bore cystocarps.

All of the plants cultured at 10 L, 15 L and 20 L bore spermatangia and carpogonia on the same thallus as did the Canadian and the Mexican *G. capillaris* (EDELSTEIN and MCLACHLAN 1971, WEST pers. comm.). The self-fertilization might occur in the monoecious gametophytes of this species,

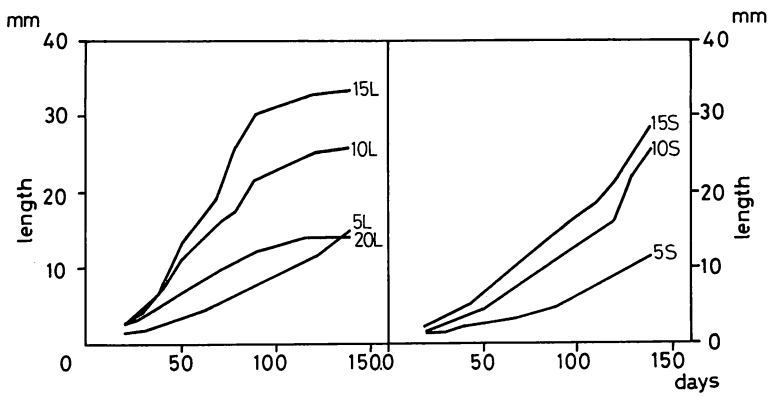


Fig. 7. The growth of upright thalli derived from apical fragments of branches; the mean lengths of 6 individuals in each culture condition are plotted.

as each plant derived from three field-collected plants was cultured separately throughout this experiment.

*Field observations*: This alga grows on rocks near the low-water mark and in tide pools in Oshoro Bay. Periodic field observations were made from March 1977 to February 1978. The results are summarized in Fig. 8. Young sterile plants were found in mid-March when the periodic observations were started. The plants increased in size until June (increasing in abundance until late-April) and they disappeared by mid-July. They grew slowly from late-May to mid-June when they reached reproductive maturity. This agrees fairly well with the results of culture experiments mentioned above. Monoecious plants with spermatangial sori and carpogonia were first found in mid-April. Cystocarps were first evident in mid-May and they increased in abundance until mid-June. Plants bearing tetrasporangia and the prostrate discoid stage of upright gametangial plants were not observed, although we carefully searched during the years 1977–1979.

A correlation may be drawn between the appearance of upright thalli and reproductive responses of this alga in cuture and its observed seasonal periodicity in nature. Upright thalli were formed under short-day conditions at 5–15°C in culture. In nature upright thalli first occur during mid-March when the day lengths were about 11 hours and the seawater temperatures were 4–5°C. In this period the observed upright thalli in nature were 2–25 cm in length. This may suggest that the initials of upright thalli appeared before mid-March. The reproduction occurred under long-day conditions at 10–20°C in culture and that was found in mid-April to June when the day lengths were about

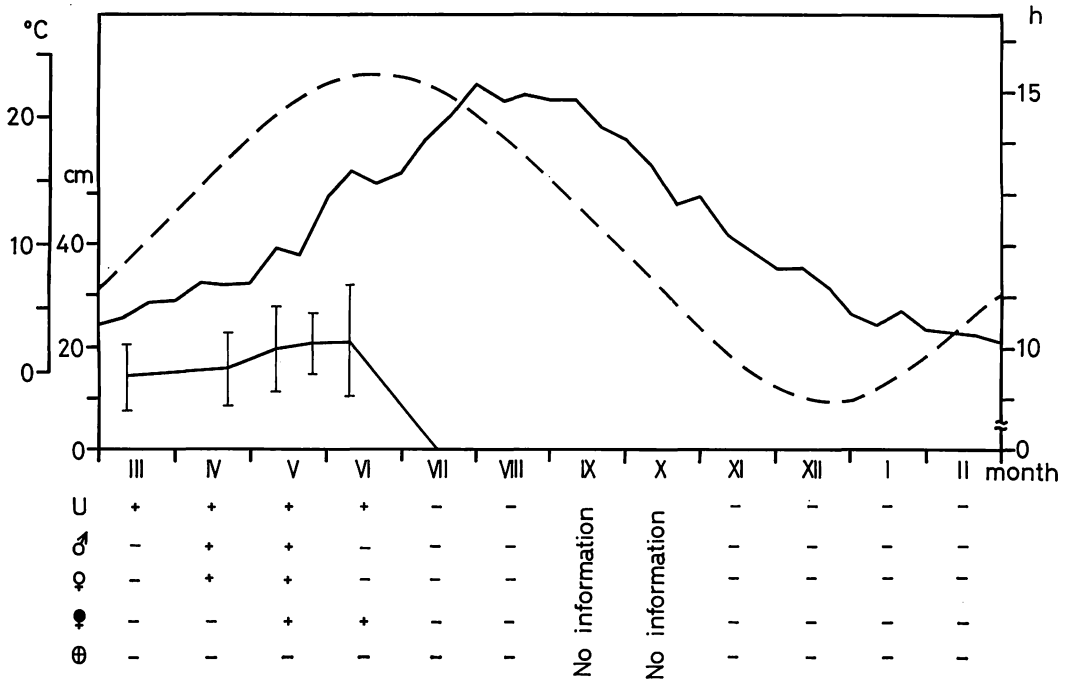


Fig. 8. Summary of phenological data on *Gloiosiphonia capillaris* in Oshoro Bay from March 1977 to February 1978 correlated to average monthly surface seawater temperatures and day lengths; means and±standard deviation of lengths of upright thalli are given. U, upright thalli, ♂, spermatangia; ♀, carpogonia; ♀, cystocarps; ⊕, tetrasporangia; solid line, surface seawater temperatures; dashed line, day lengths.

13–15 hours and the seawater temperatures were 7–15°C in nature.

## Discussion

The observed life history pattern of *Gloiosiphonia capillaris* from Oshoro Bay, Hokkaido in Japan is summarized as follows. The carpospore germlings grew into upright monoecious gametophytic thalli without intervention of a tetrasporophytic phase. This pattern of life history is different from that of the North American *G. capillaris* (EDELSTEIN 1970, EDELSTEIN and MCLACHLAN 1971, WEST pers. comm.) and the Californian *G. verticillaris* FARLOW (WEST pers. comm.). In the latter two, the carpospore germlings grew into crustose tetrasporangial plants from which tetraspores were liberated and germinated into upright gametophytes. There are two possible explanations for the former pattern of life history. (1) The tetrasporangium formation is suppressed and meiosis occurs in the initials of primordial filaments of upright gametophytic thalli as in the case of *Lemanea* (MAGNE 1967 a, 1967 b). (2) Fertilization does not occur but carposporophytes develop by apomixis just as they do in *Gigartina* subgenus *Mastocarpus* (CHEN *et al.* 1974, EDELSTEIN *et al.* 1974, MASUDA and UCHIDA 1976, POLANSHEK and WEST 1977, WEST *et al.* 1978). We did not obtain cytological evidences of fertilization, but observed connection between the carpogonium and the auxiliary cell suggests that fertilization between a spermatium and a carpogonium does occur. The observed gonimoblast development is normal in this genus and similar to that reported by several investigators (SCHMITZ 1883, OLTMANNS 1898, OKAMURA 1914, SJÖSTEDT 1926, KYLIN 1930, EDELSTEIN 1972). In our opinion the former hypothesis is the most likely, although it is still a matter of conjecture without cytological evidence of meiosis occurring somatically.

Whether the hypothesis just-mentioned is true or not, it is clear that *Gloiosiphonia capillaris* from Oshoro Bay lacks a tetrasporophytic phase and has monoecious gametophytes and carposporophytes in the life history. *G. capillaris* possesses two different types of life history between the North American and the Japanese populations. This situation is similar to that of *Pikea californica* in the Dumontiaceae. The North American *P. californica* exhibits an alternation of upright gametophytes and crustose tetrasporophytes (SCOTT and DIXON 1971), whereas the Japanese plants lack tetrasporophytes (CHIHARA 1972). Even though both populations of *G. capillaris* and *P. californica* have morphological similarities, respectively, there is a possibility that they are different species. Further comparative studies of the both populations are necessary. According to CHIHARA (pers. comm.), the Japanese *G. capillaris* includes two or three different species as pointed out by SEGAWA and OHTA (1951), CHIHARA and his colleagues are conducting a taxonomic study of them.

We examined two herbarium specimens of *Gloiosiphonia capillaris* on loan from the Herbarium of University of California, Berkeley, on which FUNAHASHI's report (1966) was based. These were collected from Vladivostok on the coast of the Sea of Japan by A. KUZNETSOV on June 20, 1927 (*Kuznetsov* 466) and June 14, 1928 (*Kuznetsov* 0–294). The former specimen is cystocarpic, but tetrasporangia were observed in the latter specimen between the cortical cells. They are ellipsoid measuring 60–85 μm in length and 35–45 μm in diameter, and divided cruciately. However, this specimen is different in gross morphology from the former specimen which is similar to the plants from Oshoro Bay. The specimen *Kuznetsov* 0–294 shows a somewhat resemblance to *Hyalosiphonia caespitosa* OKAMURA belonging to the Dumontiaceae, but we could not identify exactly it with any of known species. Thus, certain reports on the tetrasporangia borne on upright thalli seem to include those of other species.

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**諸星裕夫*・増田道夫： 紅藻イトフノリ (*Gloiosiphonia capillaris*) の生活史**

北海道忍路湾の紅藻イトフノリの生活史を培養実験とフィールド観察によって調査した。果胞子は発芽して最初盤状体に生長した。これらのうち短日条件に移行したものだけが直立体を形成した。直立体は盤状体を構成する直立糸から直接形成され，四分胞子嚢はみられなかった。配偶子嚢は長日条件においてのみ形成され，造果器と精子嚢を同一個体に生じた後，果胞子体が発達し，果胞子が放出された。このように，忍路湾のイトフノリの生活史は雌雄同株の配偶体と果胞子体からなっていることが判明した。フィールド観察では直立体の出現と生殖器官の形成に季節的周期性がみられ，培養実験の結果と一致した。(060 札幌市北区北 10 条西 8 丁目 北海道大学理学部植物学教室 *現在の宛名，107 東京都港区赤坂 7-1-16 ブリストル・マイヤーズ株式会社 学術部)