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Dominance of female gametophytes in field populations of *Cutleria cylindrica* (Cutleriales, Phaeophyceae) in the Tsugaru Strait, Japan

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The sex ratio (ratio of male to female gametophytes in field populations) of *Cutleria cylindrica* Okamura (Cutleriales, Phaeophyceae) in the Tsugaru Strait, Japan varies in different localities. Female gametes from localities where the sex ratio was about 1 : 1 showed high fertilization rates ($\bar{X} = 71\%$). By contrast, female gametes from localities where female gametophytes were dominant (> 90%) showed lower fertilization rates ($\bar{X} = 9\%$). In culture, female gametes from the former localities developed parthenogenetically to form the *Aglaozonia*-stage, which in turn formed neutral plurilocular sporangia. Gametes from the other localities developed directly into the *Cutleria*-stage, which in turn formed female gametangia. Zygotes developed into the *Aglaozonia*-stage, which produced unilocular sporangia and neutral plurilocular sporangia. Unispores developed directly into male and female gametophytes in a ratio of about 1 : 1. Neutral plurispores developed into the *Aglaozonia*-stages. These results indicate that sex-ratio variations in the populations of *C. cylindrica* are caused mainly by differences in life-history pattern. In culture, male gametes may occasionally develop into the *Aglaozonia*-stage by androgenesis; however, the effect of this process on the sex ratio in field populations is negligible. The occurrence of plurilocular sporangia in the *Aglaozonia*-stage plants was confirmed in field plants.

INTRODUCTION

When meiosis and cytokinesis proceed normally in algae that have sporic meiosis, the male: female ratio of spores should be 1 : 1 since sexual plants are haploid and sex is probably determined by a pair of alleles (van der Meer 1986; DeWreede & Klinger 1988) or by a pair of sex chromosomes (Evans 1965).

Species of the genus *Cutleria* (Cutleriales, Phaeophyceae) have a heteromorphic life history in which an alternation between erect gametophytes (*Cutleria*-stage) and prostrate sporophytes (*Aglaozonia*-stage) takes place (Falkenberg 1879). While *C. adspersa* (Roth) De Nortaris, *C. cylindrica* Okamura, and *C. multifida* (Turner) Greville have dioecious gametophytes, *C. monoica* Ollivier is monoecious (Fritsch 1945, p. 159). The sex ratio between male and female gametophytes in the dioecious species would be expected to be roughly 1 : 1.

Cutleria cylindrica occurs along the coasts of Japan, Korea (Cotton 1906) and California (La Claire 1982). In Japan, male and female gametophytes have been generally reported from latitudes lower than approximately 38°N (e.g. Okamura 1936; Noda 1987). However, *C. cylindrica* also occurs in the Tsugaru Strait, about 400 km north of the general limit of distribution (Takamatsu 1938). In this area, Sasaki *et al.* (1987) reported the dominance of female gametophytes at Shiriuchi and Ishizaki. Our own observations on some populations agree with this report; however, we also found populations with both male and female gametophytes. We report here on the sex composition, the life history and fertilization rates of plants from different populations.

In the present paper, we use the term 'sex ratio' as meaning 'ratio of fertile male and female gametophytes in field populations' (= 'quarternary sex ratio' in Pianka 1983, p. 159). We use the term '*Aglaozonia*-crust' to describe a large crust having a conspicuous marginal growth zone, thereby distinguishing it from a small disk lacking marginal meristematic cells. By the terms 'parthenogenesis' and 'androgenesis' we mean the

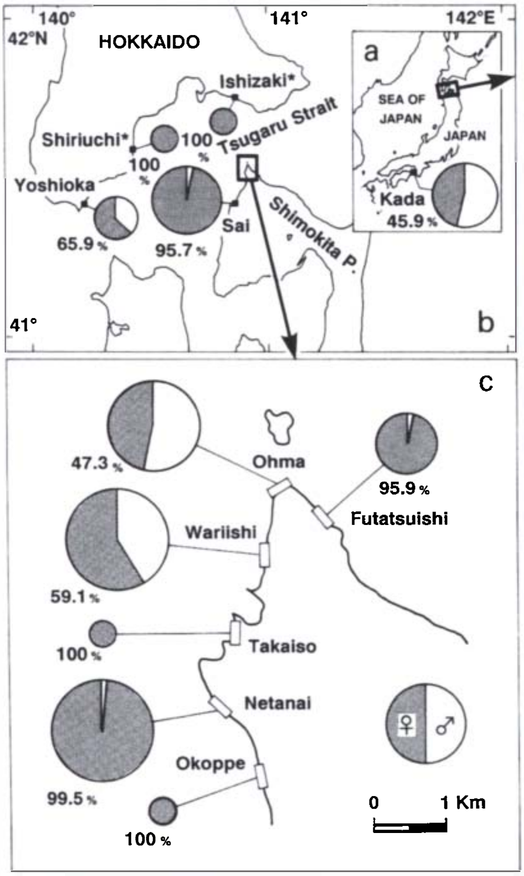

Fig. 1a–c. Sites in Japan at which the sex ratio of *Cutleria cylindrica* was studied and culture material was collected. The percentages of female gametophytes in the populations are shown. Diameter of each circle is proportional to the number of individuals examined. Information from Ishizaki and Shiriuchi (asterisks) is based on Sasaki *et al.* (1987).

direct development of female and male gametes without fertilization respectively (Ramirez *et al.* 1986).

MATERIALS AND METHODS

Sex ratio in field populations

Table 1. Sex ratio in the field populations of *Cutleria cylindrica* in Japan

Locality	Date of collection	Female gametophytes (%)	[Total gametophytes]
Futatsuishi	18.v.1988	95.9	[73]
Kada	1.v.1988	45.9	[85]
Netanai	22.iii.1988	99.5	[202]
Ohma	22.iii.1988	54.5	[101]
	18.v.1988	36.4	[66]
Okoppe	22.iii.1988	100	[12]
Sai	17.v.1988	95.7	[94]
Takaiso	22.iii.1988	100	[9]
Wariishi	22.iii.1988	55.2	[125]
	18.v.1988	66.2	[68]
Yoshioka	16.v.1988	65.9	[44]

In order to investigate sex ratios in field populations of *Cutleria cylindrica* approximately 800 gametophytes were collected in March and May 1988 at the localities listed in Table 1 (Fig. 1a, b, c). Additional investigations were made at Ohma, Wariishi and Netanai from April 1986 to April 1990 (Table 2). Plants were fixed in 5–10% Formalin-seawater and transported to the laboratory. The sex of individual plants was determined by examination of gametangia by light microscopy.

Rate of fertilization

In order to determine fertilization rates, two kinds of crossing experiments were carried out using mature individual gametophytes collected from separate tufts. In the first, male and female gametes were collected separately by means of their positive photoaccumulation, and mixed on a slide glass in the combinations given in Table 3. For this experiment, male gametophytes collected at Ohma (Ohm 1–3) and female gametophytes collected at Ohma (Ohm 4–7) and Netanai (Net 1–6) on 20 January and 18 May 1988, and 9 May 1989 were used. In the second crossing experiment, mixtures of fertile male and female gametophytes (*c.* 4 cm in length) were incubated in darkness overnight. After exposure to light male and female gametes were released and fertilization occurred. For these experiments, plants from the locations listed in Table 4 were collected on 14 March 1990. Fertilization rates were determined by counting settled female gametes with

Table 2. Sex ratio in the field populations of *Cutleria cylindrica* in Japan at different times

Date of collection	Female gametophytes (%) [Total number of gametophytes]		
	Ohma	Wariishi	Netanai
27.iv.1986	–	61.0 [100]	100 [100]
9.v.1989	55.6 [9]	–	100 [10]
1.ii.1990	61.5 [13]	76.9 [13]	92.3 [26]
14.iii.1990	28.6 [18]	–	92.9 [14]
27.iv.1990	58.8 [17]	–	100 [10]

Table 3. Zygote formation between male gametes from Ohma (Ohm 1–3) and female gametes from Ohma (Ohm 4–7) or Netanai (Net 1–6)

Female gametophyte × Male gametophyte (Date of collection)	Percentage of zygotes (%) [Total number of female gametes]
Ohm 4 (20.i.1988) × Ohm 1 (20.i.1988)	94.0 [216]
Ohm 5 (18.v.1988) × Ohm 2 (18.v.1988)	72.2 [367]
Ohm 6 (9.v.1989) × Ohm 3 (9.v.1989)	85.0 [107]
Ohm 7 (9.v.1989) × Ohm 3	62.8 [78]
Net 1 (20.i.1988) × Ohm 1	2.9 [624]
Net 2 (18.v.1988) × Ohm 2	1.2 [1978]
Net 3 (9.v.1989) × Ohm 3	7.7 [13]
Net 4 (9.v.1989) × Ohm 3	0 [6]
Net 5 (9.v.1989) × Ohm 3	24.7 [247]
Net 6 (9.v.1989) × Ohm 3	14.2 [148]

two stigmata (regarded as zygotes), and one stigma (regarded as unfused gametes) using light microscopy.

Culture experiments

Unialgal cultures were established from gametes or meristems of gametophytes collected at Ohma and Netanai on 18 May 1988, using PESI medium (Tatewaki 1966). Culture conditions were 5°C, LD (16 : 8 h); 5°C, SD (8 : 16 h); 10°C, LD; 10°C, SD; 15°C, LD; 15°C, SD; 20°C, LD; and 20°C, SD, under white fluorescent light of about 30 μmol photons m^{-2} s^{-1} (10°C) or 50 μmol photons m^{-2} s^{-1} (5°C, 15°C and 20°C). Most observations were made under long day conditions at 10, 15 and 20°C. The development of zygotes as well as unfused male and female gametes was followed. Unilocular and plurilocular sporangia formed on the crustose thalli were isolated together with several vegetative cells below them. Spores were cultured separately at 20°C, LD. Parthenogenetic development of female gametes was followed in the fertilization rate studies (Ohm IV–VII, IX–XIII, XV, Net I–X) (Table 5). Additionally, development of unfused female gametes was studied in plants from Wariishi (War I, IV, V, VII, VIII, XI–XV) collected on 1.ii.1990 (Table 5).

Field sporophytes

Crustose plants referable to the *Aglaozonia*-stage of *Cutleria cylindrica* were collected at Ohma on 4.xii.1990 and were compared with the cultured crustose stage. For morphological observations,

Table 4. Percentages of zygotes and total numbers of female gametes examined (in brackets) in crossing of fertile male sori from Ohma (Ohm I, II, VIII, XVII) and female sori from Ohma (Ohm IV, VI, X–XIII) or Netanai (Net I–IV, VI–X)

Female gametophyte	Male gametophyte			
	Ohm I	Ohm II	Ohm VII	Ohm XVII
Ohm IV	49.3 [144][1]	34.0 [100]	49.0 [100]	70.0 [100]
Ohm VI	81.5 [124]	85.0 [100]	72.0 [100]	72.0 [100]
Ohm X	87.4 [143]	47.4 [116]	95.5 [133]	90.7 [151]
Ohm XI	74.0 [100]	33.0 [100]	72.0 [100]	72.0 [100]
Ohm XII	84.0 [100]	93.0 [100]	81.0 [100]	85.0 [100]
Ohm XIII	79.5 [127]	25.0 [120]	92.6 [121]	90.4 [125]
Net I	4.4 [159]	0.7 [151]	5.0 [140]	0.6 [179]
Net II	6.6 [167]	7.5 [107]	1.6 [123]	2.2 [139]
Net III	2.3 [173]	0 [120]	3.3 [123]	6.5 [108]
Net IV	14.5 [131]	10.0 [100]	0 [108]	26.7 [120]
Net VI	4.4 [114]	26.7 [150]	64.1 [131]	15.0 [100]
Net VII	13.7 [124]	1.1 [179]	0.5 [184]	0.8 [123]
Net VIII	7.2 [111]	5.7 [174]	0.7 [131]	9.2 [141]
Net IX	3.5 [141]	6.3 [111]	0.9 [111]	1.6 [122]
Net X	12.0 [100]	1.6 [126]	19.0 [100]	22.0 [100]

[1] Total numbers examined in brackets.

Table 5. Development in culture of female gametes from Ohma (Ohm IV–VII, IX–XIII, XV), Netanai (Net I–X) and Wariishi (War I, IV, V, VII, VIII, XI–XV).

Strain	Type of life history	Strain	Type of life history	Strain	Type of life history
Ohm IV	het[1]	Net I	dir[2]	War I	dir
Ohm V	het	Net II	?[3]	War IV	het
Ohm VI	het	Net III	dir	War V	het
Ohm VII	?	Net IV	?	War VII	?
Ohm IX	?	Net V	?	War VIII	dir
Ohm X	het	Net VI	dir	War XI	dir
Ohm XI	het	Net VII	dir	War XII	dir
Ohm XII	het	Net VIII	dir	War XIII	het
Ohm XIII	het	Net IX	dir	War XIV	?
Ohm XV	het	Net X	dir	War XV	dir

[1] Heteromorphic life history; [2] Direct life history; [3] Unknown.

the plants were fixed, embedded and sectioned as described by Kawai (1989).

RESULTS

Sex ratio in field populations

There is no obvious difference in the appearance of male and female gametophytes (Fig. 2). Fertile filaments (Fig. 3) are arranged in sori on the erect thalli and bear pedicellate gametangia. Female gametangia are dark brown, cylindrical with conspicuous constrictions between loculi, 60–140 × 18–25 μm and have 6–15 × 2–4 loculi in lateral view. Female gametes contain 6–8 chloroplasts; a chloroplast with a stigma is associated with the flagellar base (Figs 4, 5). Male gametangia are pale in colour, cylindrical with slight constrictions between loculi, 40–270 × 12–15 μm and composed of 10–58 × 3–6 loculi. Male gametes contain a single chloroplast with a stigma (Fig. 6). Both male and female gametes are released through a pore in each loculus. Male and female gametangia were never observed on the same plant.

The sex ratio of the gametophytes varied considerably in different localities (Fig. 1, Table 1). Results of additional investigations made during April 1986 to April 1990 at Ohma, Wariishi and Netanai are shown in Table 2.

Rate of fertilization

Settled female gametes from Ohma and Netanai gametophytes attracted male gametes of the Ohma gametophytes (Fig. 7). However, zygote formation differed (Tables 3, 4). In the first crossing experiment, 62.8–94.0% of the female gametes from Ohma fused with male gametes from Ohma (Figs 8–11) while only 0–24.7% female gametes from Netanai fused with male gametes from Ohma. In the second crossing experiment, the average fertilization rate between the female and male gametes of Ohma was 71% (25–96%, SD = 21%) and the average fertilization rate between Netanai female gametes and Ohma male gametes was 9% (0–64%, SD = 12%).

Life history of Ohma plants

PARTHENOGENESIS: Female gametes (9.4–12.7 × 7.1–8.8 μm) from Ohma gametophytes (Fig. 4) showed positive phototaxis and mostly settled within 1 h. They germinated parthenogenetically within a few days (Fig. 12). Most developed into small disks (< 0.2 mm in diameter) composed of irregularly arranged rounded cells, having one to several phaeophycean hairs in the centre within 2 weeks at 10°C, LD; 15°C, LD or SD; and 20°C, LD or SD; and within 6 weeks at 5°C, LD or SD; and 10°C, SD (Fig. 13). Meristematic cells formed at the margin of the disks, which developed into *Aglaozonia*-crusts (1–5 mm in diam-

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Figs 2–11. *Cutleria cylindrica* in the field and in culture (scale on Fig. 4 applies to Fig. 5 and Fig. 6; scale on Fig. 7 applies to Figs 8–11).
Fig. 2. Habit of female gametophyte collected at Ohma on 20.i.1988.

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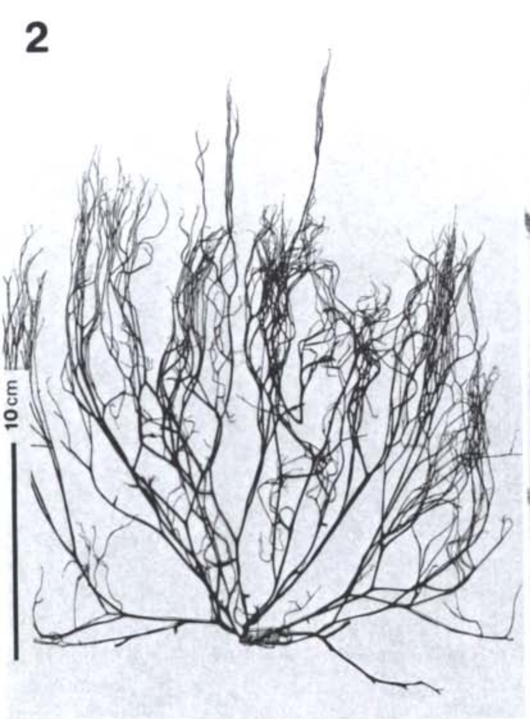

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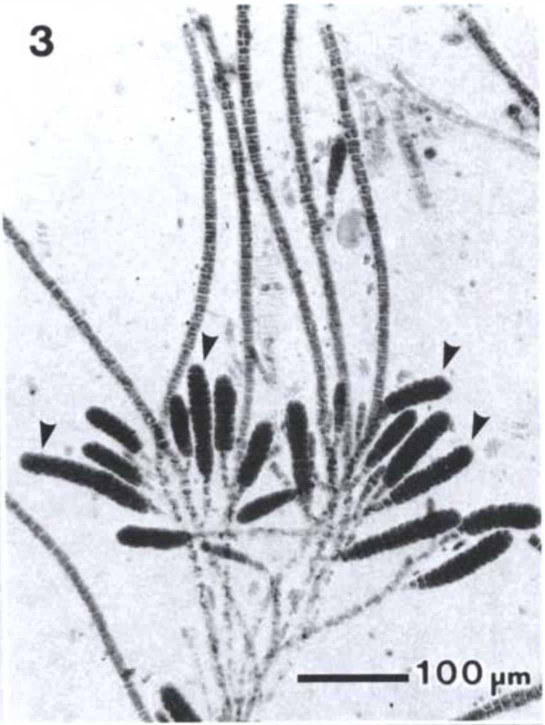

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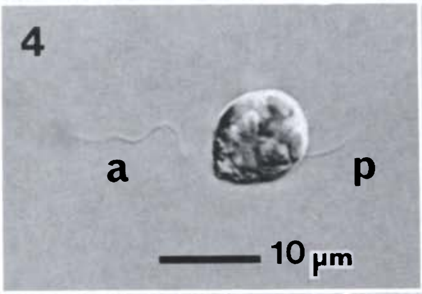

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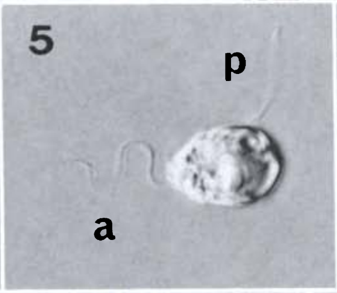

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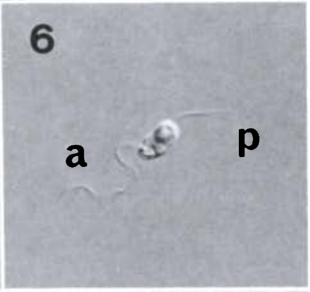

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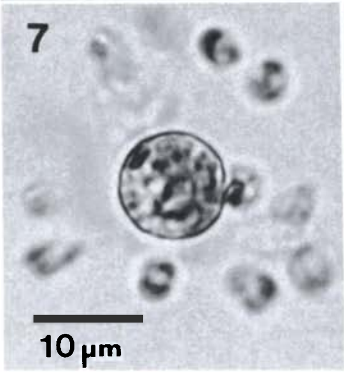


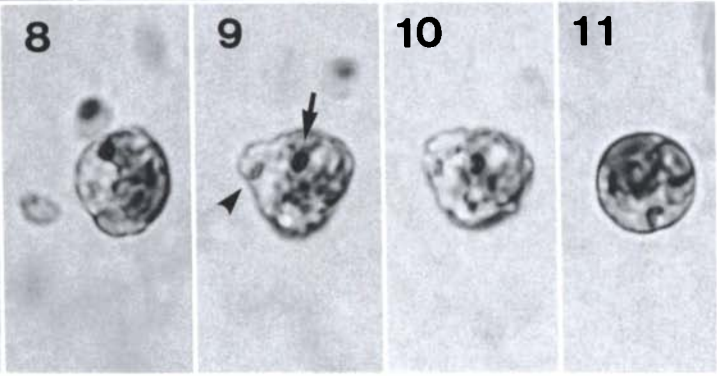
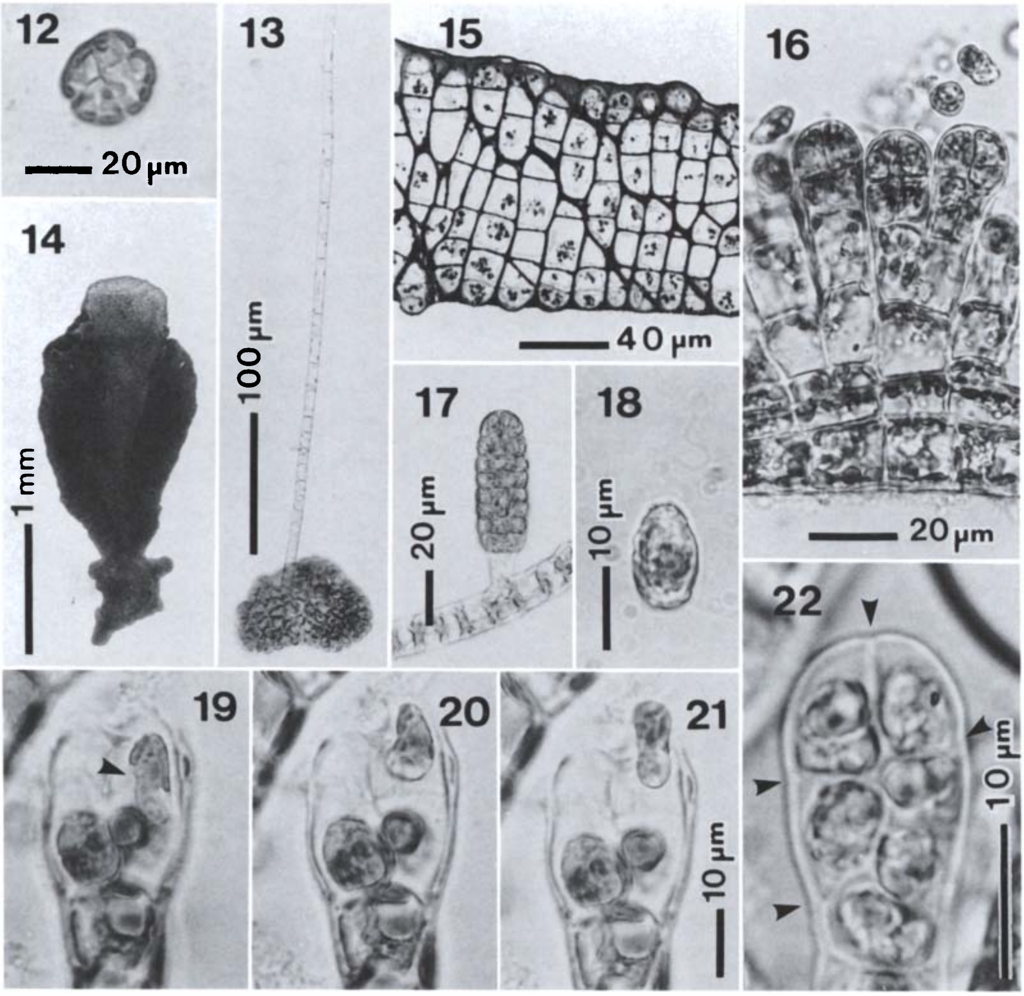


Fig. 3. Female gametangia (arrowheads) in sorus on a female gametophyte from Ohma.
Fig. 4. Female gamete from Ohma (a, anterior flagellum; p, posterior flagellum).
Fig. 5. Female gamete from Netanai.
Fig. 6. Male gamete.
Fig. 7. Female gamete attracting male gametes.
Figs 8–11. Successive stages of plasmogamy between an Ohma male gamete and an Ohma female gamete. Arrow and arrowhead show stigmata from female and male gamete, respectively.



Figs 12–22. Parthenogenetic development of *Cutleria cylindrica* from Ohma female gametes in culture (10°C, LD) (scale on Fig. 21 applies to Fig. 19 and Fig. 20).

Fig. 12. Germling of unfused female gamete.

Fig. 13. Phaeophycean hair on a disk.

Fig. 14. *Aglaozonia*-crust.

Fig. 15. Vertical section of *Aglaozonia*-crust.

Fig. 16. Vertical section of *Aglaozonia*-crust with neutral plurilocular sporangia.

Fig. 17. Female gametangium.

Fig. 18. Neutral plurispore.

Figs 19–21. Successive stages of spore release from a neutral plurilocular sporangium. Note the constriction of the spore passing through the pore in the septum wall (arrowhead) and release pores in the terminal portion of the sporangium.

Fig. 22. Neutral plurilocular sporangium. Note the slight constrictions on the septum walls (arrows).

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Figs 23–33. Development of *Cutleria cylindrica* from zygotes and unispores in culture (scale on Fig. 30 applies to Fig. 31).

Fig. 23. Zygote showing two stigmata.

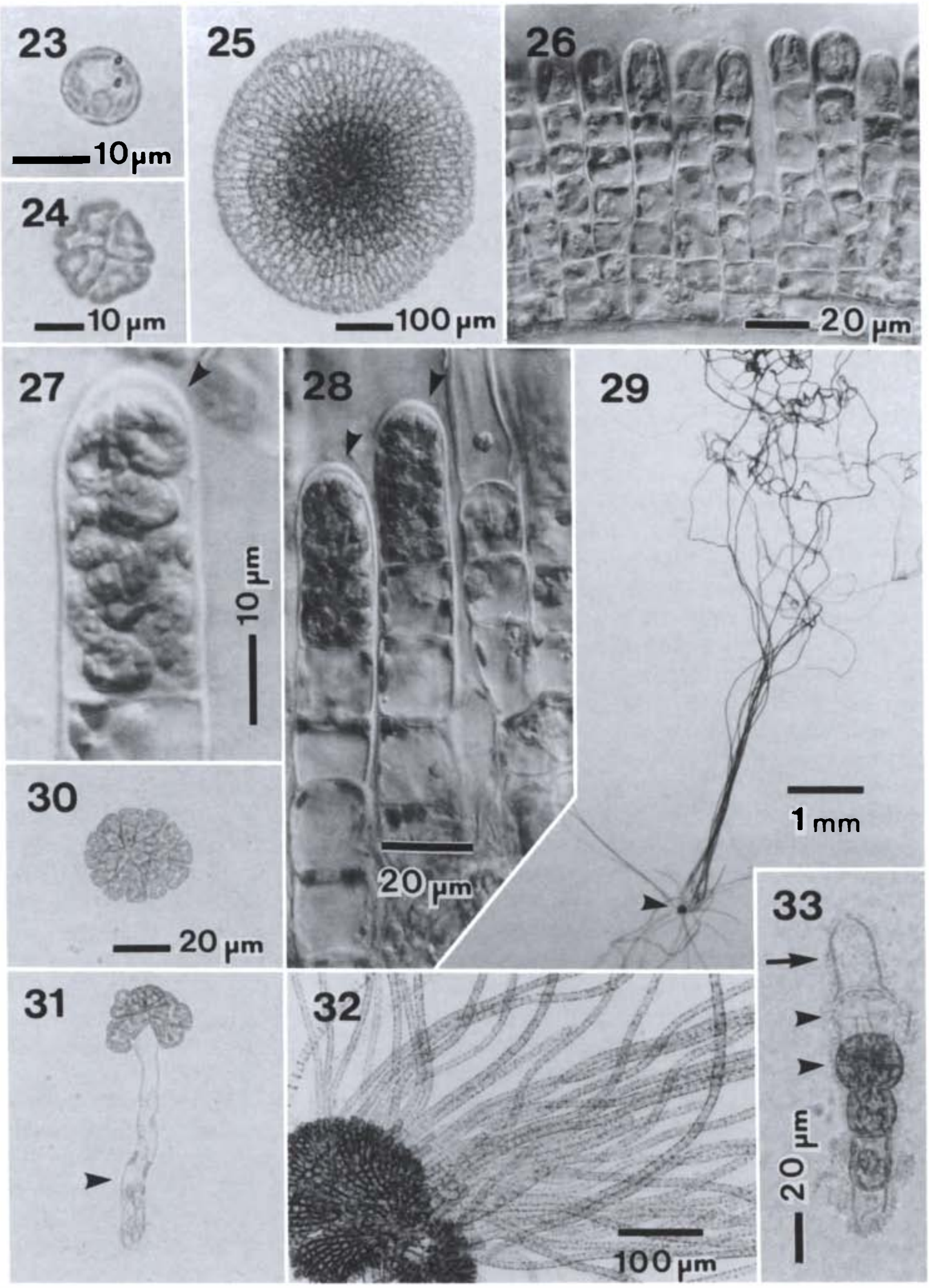

Fig. 24. Germling of zygote at 10°C, LD.
Fig. 25. *Aglaozonia*-crust derived from a zygote at 10°C, LD.
Fig. 26. Vertical section of *Aglaozonia*-crust derived from a zygote at 20°C, LD.
Figs 27, 28. Unilocular sporangia on upright filaments at 20°C, LD. Note the cap structures at the tips (arrowheads).
Fig. 29. Gametophytic plant derived from a unispore at 20°C, LD. Arrowhead shows the disk.
Figs 30, 31. Germlings of unispores, some with rhizoidal cells (arrowhead) at 20°C, LD.
Fig. 32. Gametophytic erect filaments formed on a disk derived from a unispore at 20°C, LD.
Fig. 33. Isolate of upright filament with a unilocular sporangium (arrow). Note transformation of the supporting cells into plurilocular sporangia (arrowheads) at 20°C, LD.

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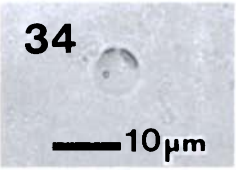

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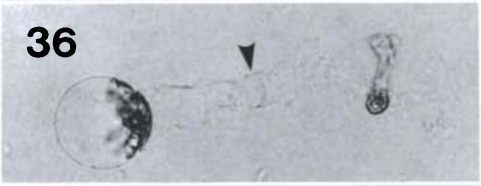

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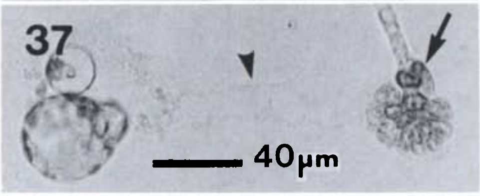

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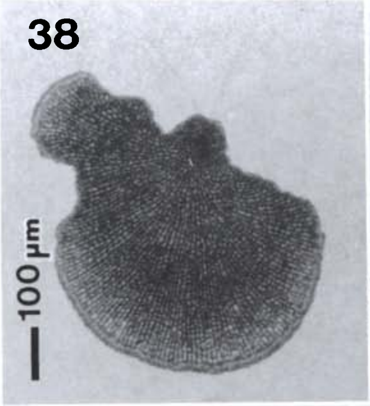

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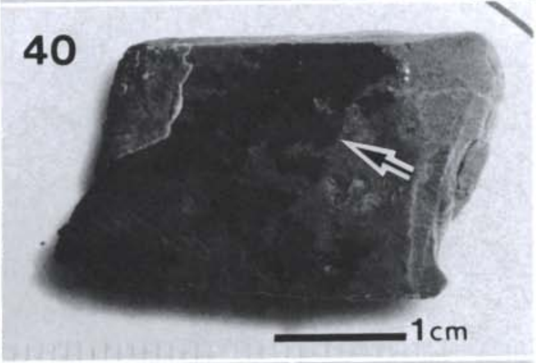

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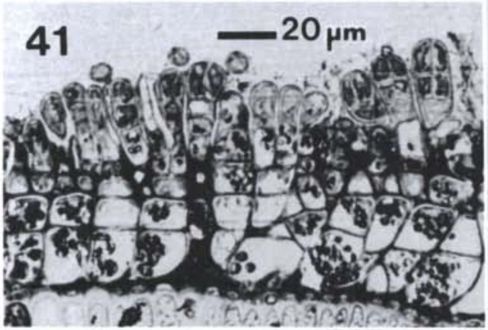

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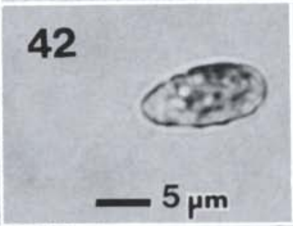

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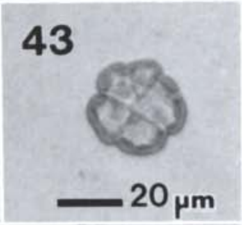

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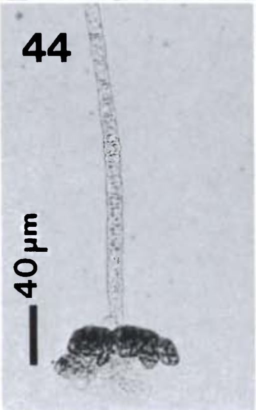

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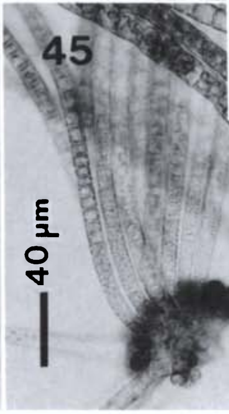

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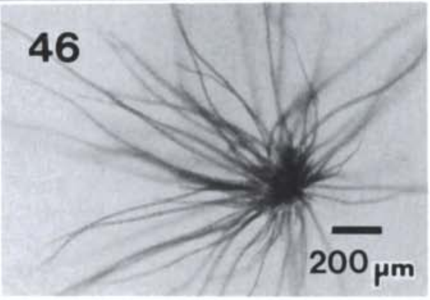

Figs 34–46. *Cutleria cylindrica* in the field and in culture.

Figs 34, 35. Germination products of male gametes increasing in size at 10°C, LD.

Figs 36, 37. Enlarged male gamete cells provided with a sheath-like structure (arrowheads). Arrow shows a disk derived from a cell left in the sheath-like structure.

Fig. 38. *Aglaozonia*-crust derived from a male gamete at 10°C, LD.

Fig. 39. Male gametangia on the erect filaments on the *Aglaozonia*-crust derived from a male gamete at 10°C, LD.

Fig. 40. *Aglaozonia*-crusts on a stone collected at Ohma on 4.xii.1990 (arrow).

Fig. 41. Vertical section of the *Aglaozonia*-crust collected at Ohma on 4.xii.1990 with neutral plurilocular sporangia.

Fig. 42. Plurispore from a neutral plurilocular sporangium on the Ohma *Aglaozonia*-crust.

eter) within 12 weeks (Fig. 14). The crusts were composed of pigmented cortical cells and 2–5 layers of colorless medullary cells (Fig. 15). Most of the female gametes from Ohma (Ohm IV–VI, X–XIII, XV) developed into such *Aglaozonia*-crusts (Table 5).

PLURILOCULAR SPORANGIA: Upright filaments of 2–5 cells were formed on the surface of *Aglaozonia*-crusts at 10–20°C, LD or SD. Their uppermost cells were transformed into cylindrical plurilocular sporangia with slight constrictions (Figs 16, 22). Plurilocular sporangia were 16–27 × 13–19(24) μm and composed of 2–4 × 2–4 loculi in lateral view. Plurispores (11.7–14.6 × 7.1–8.5 μm) (Fig. 18) were released individually through pores at the apex of the sporangium (Figs 19–21). Plurilocular sporangia often regenerated from the supporting cells of empty sporangia. Although the plurispores had a similar appearance to female gametes, their phototactic response was weak and they did not attract male gametes after settlement. These plurispores are thus considered to be asexual. They developed into *Aglaozonia*-crusts of up to 1 cm in diameter, except at 5°C LD or SD. The crusts derived from female gametes as well as those from neutral plurispores produced polystichous erect filaments at 20°C, LD or SD but rarely at 10°C, LD or SD; and 15°C, LD or SD. The erect filaments grew well at 20°C, LD or SD and formed lateral female gametangia (Fig. 17) resembling those of field gametophytes. The erect filaments further developed into parenchymatous thalli resembling the field gametophytes after a month at 20°C, LD. Culture results from the unfused Ohma female gametes are summarized in Fig. 47.

ZYGOTE DEVELOPMENT: Zygotes (Fig. 23) of the Ohma gametophytes germinated (Fig. 24) and developed into *Aglaozonia*-crusts (Fig. 25). They formed upright uniseriate filaments on the crust at 10–20°C, LD or SD (Fig. 26). The terminal cells of the uniseriate filaments were transformed into plurilocular sporangia at 10°C, LD; and 15°C, LD or SD. However, they formed both plurilocular and unilocular sporangia at 20°C, LD or SD. The plurilocular sporangia resembled those formed on the crusts derived from parthenogenetic gametes. The plurispores released from them developed into *Aglaozonia*-crusts. Supporting cells of the unilocular sporangia were often progressively transformed into plurilocular sporangia (Fig. 33). Their spores also formed *Aglaozonia*-crusts.

Unilocular sporangia are cylindrical, 25–31(40) × 15–18(–22) μm (Figs 27, 28) and contain 8 or 16 unispores (8.8–11.2 μm in length). Unispores developed into microscopic disks (Figs 30, 31) and formed erect gametophytic filaments (Fig. 32) which often became entangled with each other (Fig. 29), and formed male or female gametangia within 2 months at 10°C, LD. Six of the 12 gametophytes derived from a unilocular sporangium were female. Culture results from the zygotes of Ohma gametes are summarized in Fig. 47.

ANDROGENESIS: Male gametes are 5.0–7.1 × 2.6–3.5 μm (Fig. 6). Rarely, unfused male gametes developed into *Aglaozonia*-crusts at 10 and 20°C, LD. About 3% of settled male gametes ($n = 3851$) became enlarged, the number of chloroplasts increased (Figs 34, 35), and a large spherical or cylindrical cell up to 40 μm in diameter was formed. A few smaller cells were cut off by unequal divisions into a sheath-like membranous structure (Figs 36, 37). The smaller cells developed into *Aglaozonia*-crusts (Fig. 38). The fate of the large cells was not followed. Neutral plurilocular sporangia were formed on the crusts at 10°C, LD or SD; 15°C, SD; and 20°C, LD. Their plurispores (11.1–13.2 × 6.1–7.7 μm) developed into *Aglaozonia*-crusts forming polystichous erect filaments on the cortex, which formed male gametangia at 10°C, LD (Fig. 39).

The life history in culture of Ohma plants is summarized in Fig. 48.

Life history of Netanai plants

Unfused female gametes from Netanai (10.6–13.7 × 7.6–8.8 μm, Fig. 5) germinated (Fig. 43) and developed into small disks (Fig. 44) in the same way as Ohma female gametes. However, these disks did not form marginal meristematic cells and remained less than 0.2 mm in diameter. Many polystichous erect filaments issued from the disks within 8 weeks in all culture conditions (Figs 45,

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Fig. 43. Germling from unfused Netanai female gamete at 10°C, LD.
Fig. 44. Disk derived from a Netanai female gamete with a phaeophycean hair at 10°C, LD.
Fig. 45. Disk derived from a Netanai female gamete, forming many erect filaments at 10°C, LD.
Fig. 46. Gametophyte originating from an unfused Netanai female gamete at 10°C, LD.

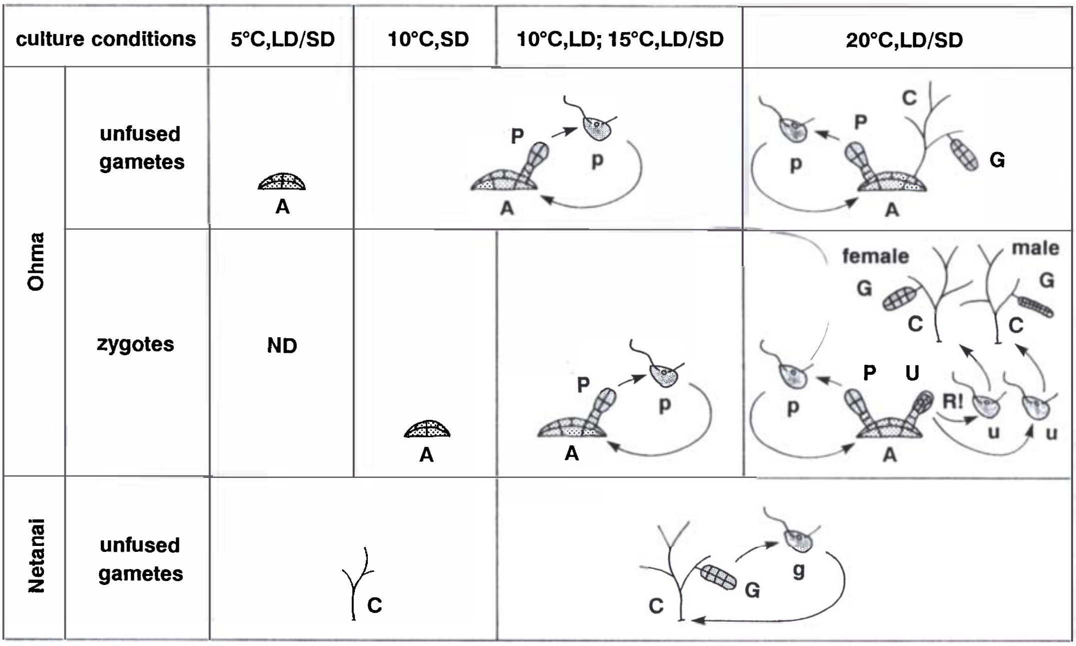

Fig. 47. Diagrammatic summaries of culture results from unfused gametes and zygotes from Ohma and unfused gametes from Netanai (A, *Aglaozonia*-stage; C, *Cutleria*-stage; G, gametangia; g, gametes; ND, no data; P, neutral plurilocular sporangia; p, neutral plurispores; R!, putative meiosis; U, unilocular sporangia; u, unispores).

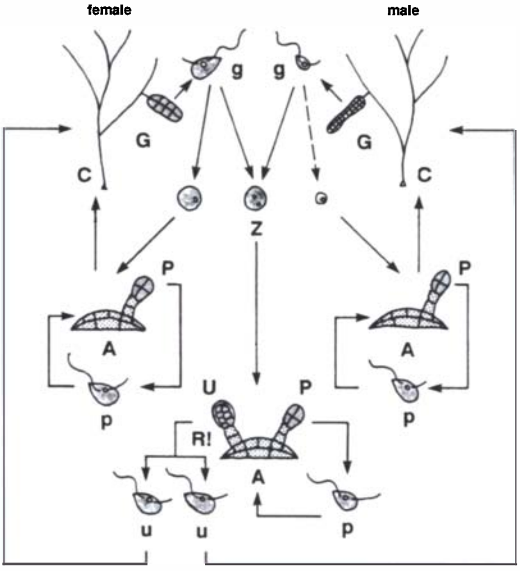

Fig. 48. Diagrammatic summary of the life history of Ohma plants (solid arrows, usual pathway; broken arrow, rare pathway; A, *Aglaozonia*-stage; C, *Cutleria*-stage; G, gametangia; g, gametes; P, neutral plurilocular sporangia; p, neutral plurispores; R!, putative meiosis; U, unilocular sporangia; u, unispores; Z, zygote).

46), and female gametangia formed on the erect filaments at 10°C, LD; 15°C, LD or SD; and 20°C, LD or SD. The female gametes from most of the gametophytes from Netanai (Net I, III, VI–X) developed into erect gametophytic filaments (Table 5). These results are summarized in Fig. 47.

Life history of Wariishi plants

Some of the female gametes from the Wariishi female gametophytes (War IV, V, XIII) developed into *Aglaozonia*-crusts, and the remainder (War I, VIII, XI, XII, XV) developed into gametophytic erect filaments (Table 5).

Morphology of field *Aglaozonia*-crusts

Aglaozonia-crusts collected in the field are dark brown, are attached to stones (arrow, Fig. 40) or crustose algae, and are provided with marginal meristematic cells. The crusts are composed of a cortex of 1–3 cell layers and a medulla of 2–5 cell layers (Fig. 41). Plurilocular sporangia (Fig. 41) are formed which are similar in morphology to those found on cultured crusts. They are cylindrical with slight constrictions, 21–27 × 12–18 μm, and composed of 2–4 × (1)2–4 loculi in lateral view. The plurispores (Fig. 42) developed into *Aglaozonia*-crusts at 10 and 20°C, LD. Unilocular sporangia were not found in the field material.

DISCUSSION

Our investigations of *Cutleria cylindrica* gametophytes show that the sex ratios in field populations vary from area to area. Reinke (1878) observed that the sex ratio of male to female gametophytes in a population of *C. multifida* was 3 : 2; however, Thuret (1850), Church (1898), Fletcher (1987) and Womersley (1987) reported a dominance of female gametophytes in populations of *C. multifida* at various localities and explained it by the frequent occurrence of parthenogenesis in female gametes. The following sex ratios have been reported in other species of marine algae: 1 : 1 (male : female) in *Cystoseira osmundacea* (Turner) C. Agardh (Schiel 1985); 1 : 1 and 1 : 2 depending on localities in *Dumontia contorta* (S.G. Gmelin) Ruprecht (Kilar & Mathieson 1978); 1 : 3 to 1 : 12 in *Bangia atropurpurea* (Roth) C. Agardh (Sheath *et al.* 1985).

There are clear differences in the parthenogenetic developmental pattern of female gametes between Ohma and Netanai plants. The female gametes from Ohma developed into haploid sporophytes, whereas those from Netanai developed into gametophytes. In Europe, the life history of *Cutleria multifida* has been studied by several authors. Falkenberg (1879, p. 423) noted that in Italy, female gametes did not germinate without fertilization. Thuret (1850, pl. 31, fig. 3) found that in France, unfused female gametes developed into young filamentous *Cutleria*-stage plants. Church (1898, pl. 8, figs 11–14, pl. 9, figs 15–21) found that in England, female gametes developed into young *Aglaozonia* plants. These reports suggest that *C. multifida* in Europe may have different life-history strategies.

The relatively high fertilization rates (71 ± 21%) in Ohma gametes suggest that sexual reproduction is common in the field. The resulting zygotes probably form diploid sporophytes, as observed in culture. Zygotic sporophytes are expected to produce equal numbers of male and female gametophytes by means of meiosis, which would explain the sex ratio at Ohma (male : female is roughly 1 : 1). As observed in culture, parthenogenesis of female gametes may occur and development into haploid sporophytes takes place. However, the number of female gametophytes that originates from them is relatively small, and parthenogenesis has little impact on the sex ratio.

By contrast, the relatively low fertilization rates (9 ± 12%) between male gametes from Ohma and female gametes from Netanai suggest that at Netanai sexual reproduction may be rare. Accordingly, gametophytes are formed more frequently by parthenogenesis of female gametes, and thus female gametophytes are dominant at Netanai.

The ratio of male to female gametophytes was 2 : 3 at Wariishi, which is located between Ohma and Netanai. This ratio can be explained as an overlapping of the Ohma and Netanai populations, which is supported by the occurrences of both direct and heteromorphic life histories in culture.

The seasonal range of seawater temperature in the Tsugaru Strait is rather large, because the area is influenced both by the Tsushima warm current and by the Kurile cold current. At Ohma, the average temperature for September 1986 reached 22°C, but in March 1987 it was 6°C. In order to expand the distribution of *Cutleria cylindrica* in this area, the direct life history is perhaps more favourable for survival than the heteromorphic life history. In the direct life history the plants can produce new gametophytes at temperatures as low as 10°C, which makes it possible for a new population to be established in a short time. In the heteromorphic life history, the formation of unilocular sporangia on the sporophyte is restricted at temperatures of 15°C or lower. This means that gametophyte formation occurs during much shorter periods in the Tsugaru Strait than in warmer waters. Accordingly, many of the populations in the Tsugaru Strait probably show the direct type of life history.

Neutral plurilocular sporangia formed on *Aglaozonia*-crusts have not been reported in *Cutleria* to date. Their occurrence was also confirmed for *Aglaozonia*-crusts in the wild. These plurilocular sporangia superficially resemble female gametangia on the gametophytes, but their plurispores are released from terminal pores, while in female gametangia each gamete is released from an individual pore. In addition, the neutral plurilocular sporangia are shorter than female gametangia.

Matsue & Chihara (1985) reported that in *Cutleria cylindrica, Aglaozonia*-crusts derived from zygotes formed unilocular sporangia in culture, but no morphological details were given. We show here that the unilocular sporangia of *C. cylindrica* form terminally on short upright filaments of the *Aglaozonia*-crusts. In *C. multifida*, unilocular sporangia are sessile, arising directly on the cortical cells of the sporophytic thalli (Reinke 1878; Kuckuck 1899; Fletcher 1987; Womersley 1987). Only Yamanouchi (1912) has reported (in *C. multifida*) that the terminal cells of the upright filaments of the crusts are transformed into unilocular sporangia. Our observations on *C. cylindrica* agree with those of Yamanouchi (1912) in *C. multifida*.

In our culture experiments, unfused male gametes of *Cutleria cylindrica* could develop into *Aglaozonia*-crusts by androgenesis. However, considering the very low germination rate, this process is unlikely to influence the sex ratio of the population. Androgenesis of male gametes in cultures of brown algae has been reported in the Ectocarpales (Müller 1967), Scytosiphonales (Clayton 1979, 1980), Desmarestiales (Ramirez *et al.* 1986) and *Akkesiphycus lubricus* Yamada et Tanaka (Kawai, unpublished observations). However, the significance of androgenesis in field populations is not well known.

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