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Morphology and reproduction of Asiatic *Ulva pertusa* (Ulvales, Chlorophyta) in Thau Lagoon (France, Mediterranean Sea)

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Abstract — A detailed study of vegetative and reproductive phases of several populations of a common species of *Ulva* from Thau Lagoon (France, Mediterranean Sea) showed that the material is in good agreement with Asiatic *Ulva pertusa* Kjellman. Since October 1994, the date of its first observation in Thau Lagoon, *U. pertusa* has developed abundant reproductive populations. It is highly probable that this species was introduced at Thau along with oyster transfers from the Pacific. *Ulva pertusa* is new to the Mediterranean Sea.

France / marine algae / Mediterranean Sea / species introduction / *Ulva pertusa*

Résumé — Morphologie et reproduction de l'algue asiatique *Ulva pertusa* (Ulvales, Chlorophyta) dans l'étang de Thau (France, Méditerranée). Une étude détaillée des stades végétatif et fertile de plusieurs populations d'une espèce d'*Ulva* commune dans l'étang de Thau (France, Méditerranée) a montré qu'elle appartenait à l'espèce asiatique *Ulva pertusa* Kjellman. Depuis octobre 1994, date de sa première observation dans l'étang de Thau, *U. pertusa* a développé des populations importantes et fertiles. L'espèce a probablement été introduite à Thau avec des importations d'huîtres en provenance du Pacifique. *Ulva pertusa* est une espèce nouvelle pour la Méditerranée.

algues marines / introduction d'espèces / France / Méditerranée / *Ulva pertusa*

INTRODUCTION

Thau Lagoon, France, has developed into one of the major hotspots of marine macrophyte introductions in the Mediterranean Sea (Verlaque, 2001). Among the pool of exotic species recently reported, there is an *Ulva* that differs from the Atlantic and Mediterranean species in both vegetative and reproductive

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features. A study of Japanese specimens of *Ulva pertusa* Kjellman has enabled us to attribute the alga from Thau lagoon to that species, which occurs in the extensive Indo-Pacific area and is now reported for the first time in the Mediterranean Sea. The present paper describes the general morphology of *U. pertusa* from Thau Lagoon. It is clear that a comparison between the Mediterranean populations and specimens of *U. pertusa* originating from various regions using molecular taxonomic tools will be invaluable to confirm the identity of this *Ulva*, but the aims of this study are to quickly warn phycologists about a newly introduced species that could spread along the Mediterranean and European coasts, and to give several morphological characters to identify it.

MATERIALS AND METHODS

Observations and sampling in Thau Lagoon (7000 ha, mean depth: 3.8-4.5 m, max. depth 10 m, Fig. 1) were undertaken from October 1994 to October 2000. All samples were hand-collected and preserved in buffered 4 % formaldehyde-seawater. Material for microscopic examination was sectioned manually with a razor blade and stained in 1 % aqueous aniline blue, washed, and then acidified by the addition of a drop of 1 N hydrochloric acid. Fixed material was studied under light and phase contrast microscopes. Photomicrographs were made using a Nikon Optiphot-2®. Liquid-preserved specimens and exsiccata, referenced "F" and "H" + n°, respectively, were deposited in the Verlaque Herbarium, UMR Dimar COM, Marseilles, France.

Material studied: JAPAN. The Marine Algae of the Seto Inland Sea, Kobe University, col.: S. Enomoto, det. T. Yoshida, **n° 002-1** (collection n° 0191), loc. Taka-shima, Ehime-ken (N 33°56'.8, E 132°38'.3), Aug. 27, 1987; **n°002-2** (collection n°3057), loc. Kamaguchi, Awaji-shima, Hyôgo-ken (N 34°28'.9, E 134°57'.5), May 22, 1993.

THAU LAGOON. **H.3223-3226,** Marseillan, 8 October 1994; **F.1374 & H.2655-2658,** Bouzigues & Parcs A, September 1995; **H.2647-2650,** between Bouzigues & Mèze, 20 June 1996, fertile gametophytes; **H.2651-2654**, Moure Blanc, 20 June 1996; **H.2659**, Marseillan & Parcs C, 20 June 1996; **H.3227,** Marseillan, 8 October 1997; **H.3228,** between Mèze & Bouzigues, 8 October 1997; **H.3229,** Moure Blanc, 8 October 1997; **H.3230,** Parcs B, 11 May 1998; **H.3231**, Marseillan, 17 June 1998; **H.3221-3222**, without locality, 31 July 1998; **H.3232-3235**, Moure Blanc, 18 October 2000, fertile gametophytes.

RESULTS

***Ulva pertusa* Kjellman**

Figs 2-11

Reference: Kjellman (1897): 4-10, pl. 1, figs1-5, pl. 3, figs 1-8. Type locality: Hakodate, Yenoshima and Yokohama.

Description: thallus membranous, bright dark green, thick and tough, 10–20(-30) cm high, usually perforated with variously sized irregular openings, sometimes split longitudinally into several fragments when old, undulate at mar-

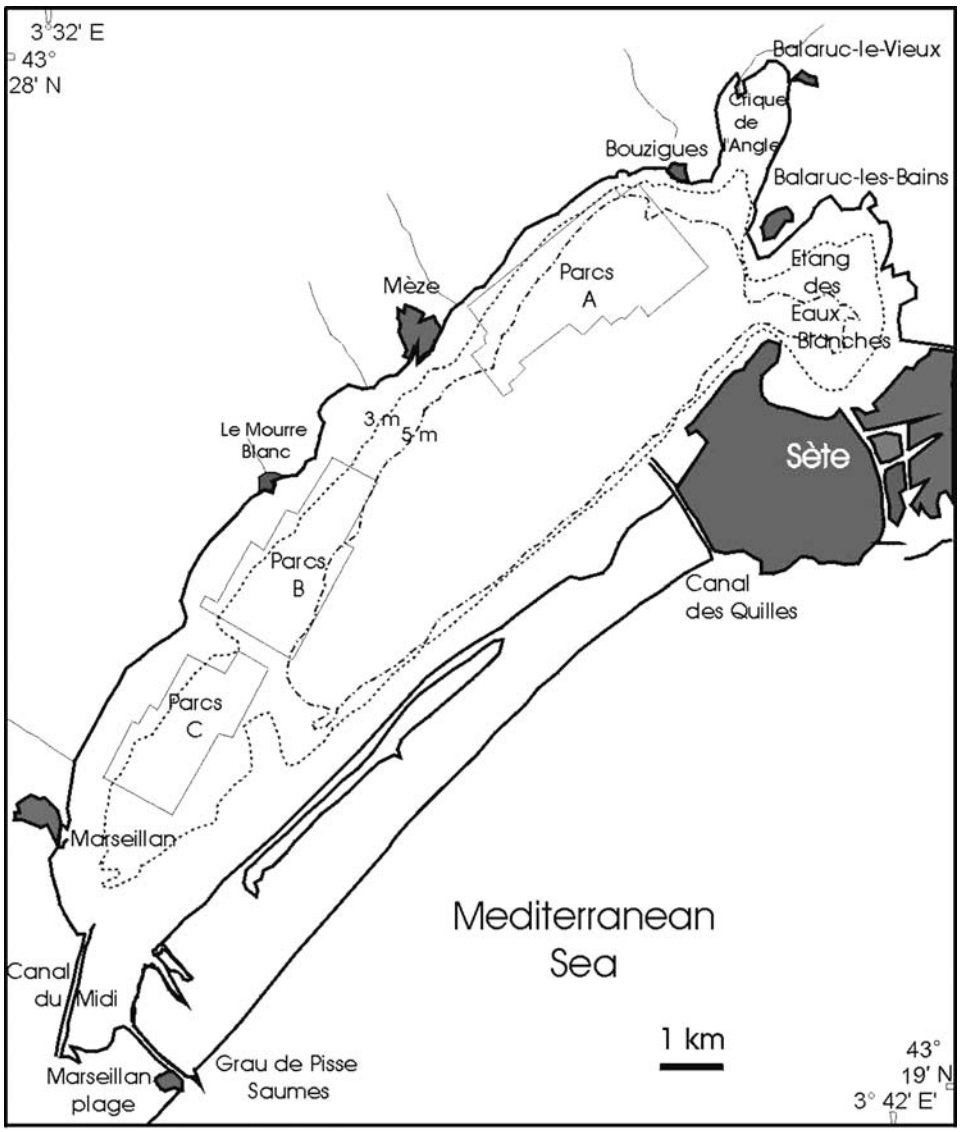

Fig. 1. Thau Lagoon with location of oyster farming zones (Parcs A, B & C).

gin, without microscopic marginal teeth; lower part of the basal region without a central cavity; membrane distromatic, the two layers of cells closely united throughout, 490-500 µm thick just above the holdfast where the surface is concentrically wrinkled, soon becoming thinner above, 156 µm thick in the rhizoidal part, 90-115 µm and 60-70 µm thick in the lower and mid parts, respectively; margin thin, membranous, (34) 40-54 µm thick; cells in surface view irregularly arranged, except very locally, isodiametric to elongate, rounded, rarely slightly polygonal, 10–22 × 8-18 µm, each with (1-) 2 (-3) pyrenoids; in cross-section, cells

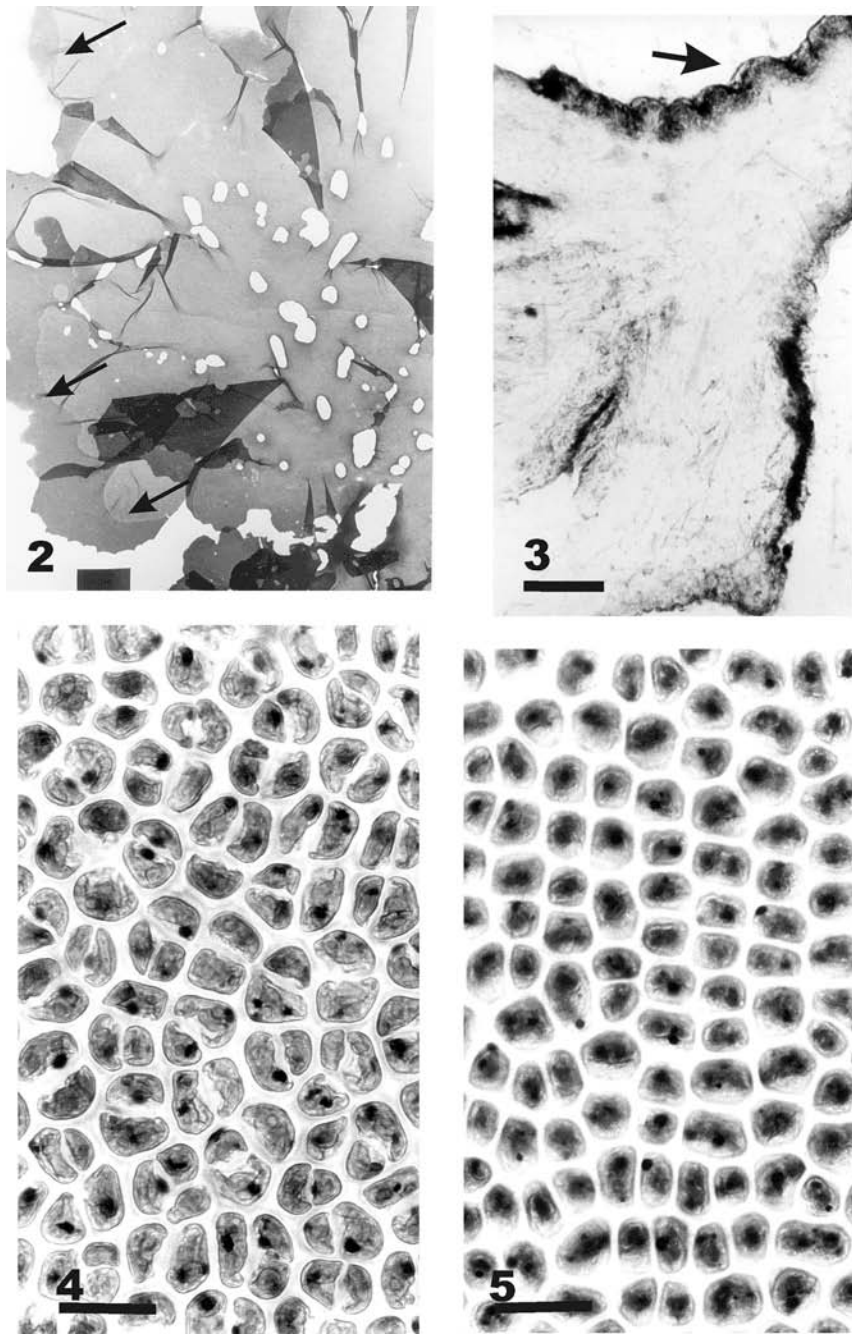

Fig. 2-5. Fig. 2. Fertile thallus. Arrows: linear rim of fertile cells. Scale bar = 1 cm. Fig. 3. Longitudinal section of the basal portion of thallus. Arrow: wrinkles. Scale bar = 250 µm. Figs 4-5. Surface views of cells without and with local arrangement, respectively. Scale bars = 30 µm.

cylindrical, about 2 times as high as broad, 30–44 × 12–18 (-20) µm, never with a spindle-shaped form and tapered ends, in the lower portion, becoming shorter and subcubical above, 22-25 × 12–15 µm, almost as long as broad in the marginal portion, 18–22 × 15–20 µm; when fertile, the margin of the frond transformed into a broadly linear rim of olive-yellow coloured sori; fertile cells in surface view 17–23 × 10–14 µm, opening by teat-like pores, with up to 32 biflagellate gametes, 9.5–11.5 × 7.5 µm, per fertile cell.

Ecology: *Ulva pertusa* is abundant from spring to autumn (May-October) along the north coast of Thau Lagoon, from Bouzigues to Marseillan, and in oyster farming zones (Parcs A, B & C) (Fig. 1). We have no observations for winter. It grows between the water surface and 1 m depth, on rocky substrates and hard structures. Fertile gametophytes were observed from May to October.

DISCUSSION

Hitherto, 16 species belonging to the genus *Ulva* have been reported for the north-east Atlantic Ocean and Mediterranean Sea (Bliding, 1968; Ardré, 1970; Koeman & Van den Hoek, 1981; Hoeksema & Van den Hoek, 1983; South & Tittley, 1986; Lawson & John, 1987; Gallardo *et al.*, 1993; Dion *et al.,* 1998; Benhissoune *et al.*, 2001). Of these, only 9 taxa possess mostly two or more pyrenoids per cell: *U. armoricana* Dion, de Reviers *et* Coat, *U. bifrons* Ardré, *U. elegans* Gayral *nom. inval.*, *U. fasciata* Delile, *U. popenguinensis* P. Dangeard, *U. rhacodes* (Holmes) Papenfuss, *Ulva rotundata* Bliding, *Ulva rigida* C. Agardh[1] and *Ulva scandinavica* Bliding. They differ from the specimens of the Thau Lagoon in having one or several of the following features:

– Thallus with an irregular outline, margin dentate (often double) (*U. rhacodes*),

– Small plant (up to 4 cm in height), initially entire and spathulate, later developing a stipe and becoming obovate, often lobed or bifid (*U. popenguinensis*),

– Thallus divided into long, ribbon-like, lanceolate segments (*U. elegans, U. fasciata*),

– Basal part less thick and not concentrically wrinkled (all species),

– Margin with tooth-like protuberances (*U. armoricana, U. bifrons, U. popenguinensis, U. rigida, U. rhacodes, U. rotundata, U. scandinavica*),

– Plants having a metallic gloss, cells in apical and middle regions very big in surface view (up to 35 x 24 µm) (*U. rotundata*),

– Polygonal cells, in surface view (*U. armoricana, U. rotundata*),

– In cross-section, dimorphic two layers of cells (*U. bifrons*),

– In cross-section, cells with a spindle-shaped form and tapered ends in the lower portion (*U. rigida*),

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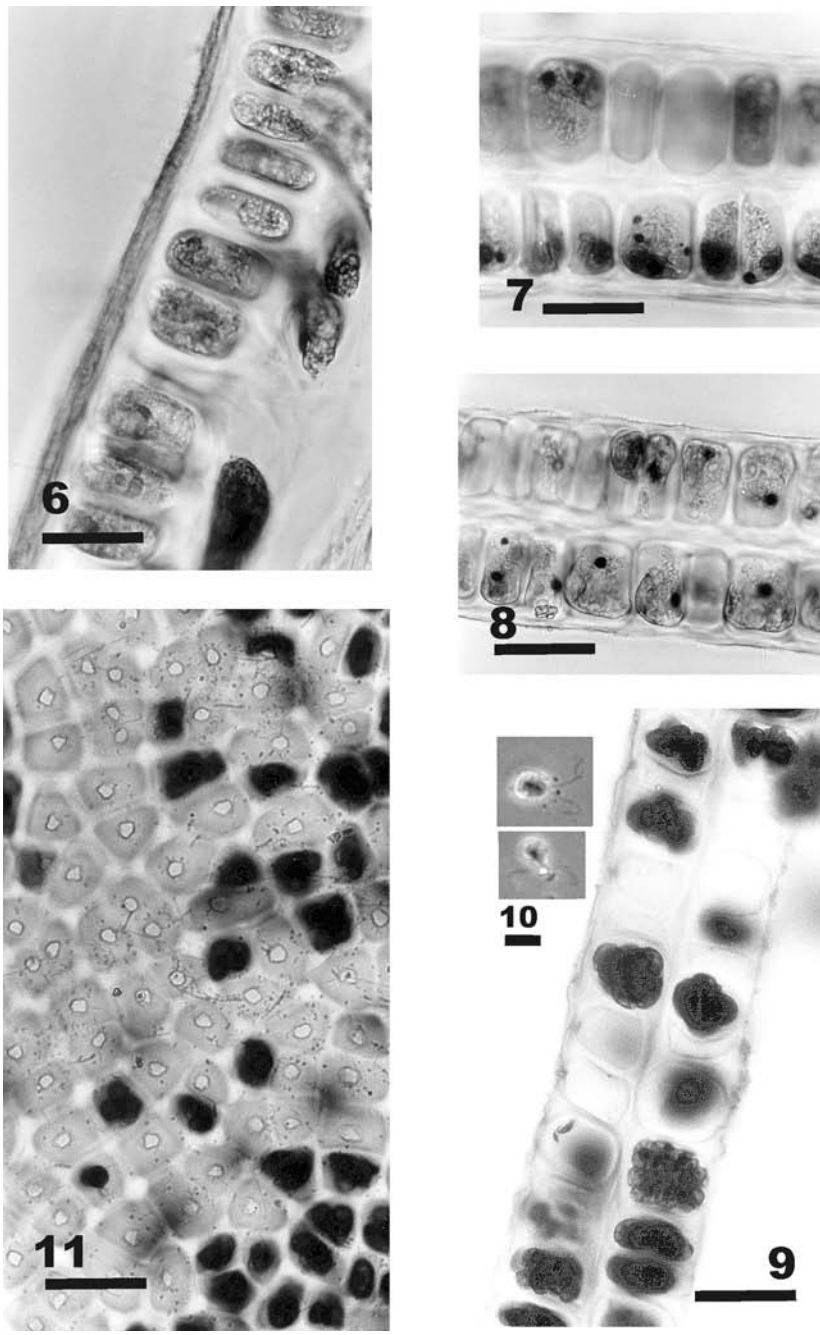
1. As Gallardo *et al.* (1993), we do not follow Phillips (1984, 1988), who considers that *U. rigida* C. Agardh and *U. rigida sensu* Bliding are two distinct species and attributes the latter to *U. laetevirens* Areschoug. Unlike Bliding's concept of the species, *U. rigida* C. Agardh *sensu* Phillips from Australia is in disagreement with the protologue (C. Agardh, 1823: 410-411) and further contribution to the type description (J.G. Agardh, 1883: 168-173, Fig. 119-122) of the European species by the lack of marginal teeth (see also comments in Phillips, 1988: 448). The other feature considered by Phillips (1988) (*i.e.* the cell shape in section of the basal region) requires further investigations on the lectotype of *U. rigida*.



Figs 6-11. Longitudinal sections of thallus. Fig. 6. Rhizoidal region of thallus. Fig. 7. Lower part of thallus. Fig. 8. Upper part of thallus. Fig. 9. Linear rim of fertile cells. Scale bars = 30 μm. Fig. 10. Two 2-flagellate gametes in phase contrast microscopy. Scale bar = 10 μm. Fig. 11. Surface view of filled and emptied fertile cells. Scale bar = 30 μm.

On the other hand, no differences were observed in comparing our specimens with *Ulva pertusa* from Japan. All specimens share the same combination of characters, thus allowing *U. pertusa* to be readily distinguished from the other members of the genus. These characters include

(i) thallus lobed and more or less perforated,
(ii) lack of tooth-like marginal protuberances,
(iii) basal part of thallus with surface concentrically wrinkled and without a central cavity,
(iv) thickness: *ca* 500µm thick, just above the holdfast, 156-90µm and 50-40 (-34) µm, in the lower and marginal parts, respectively,
(v) cell shape in transverse section, just above the rhizoidal region, cylindrical,
(vi) cells not ordered, except very locally,
(vii) (1-) 2 (-3) pyrenoids per cell,
(viii) fertile cells arranged in broadly linear rim,
(ix) up to 32 biflagellate gametes per fertile cell. This high number of gametes produced per cell has previously been reported for *U. pertusa*, while 4–16 gametes per fertile cell is more typical for the genus (Yabu & Tokida, 1960).

Prior to this study, in April and September 1984, Ben Maiz collected at Thau (Localities: Mèze and Bouzigues, respectively) an *Ulva* sp. with thallus without tooth-like protuberances, 85-160 µm and 45-60 µm thick at the middle and marginal parts, respectively, cells not or scarcely ordered, about 7-14 x (9-) 12-16 (-19) µm with (1-) 2 (-3) pyrenoids (Ben Maiz, 1986). This could be the first observation of *U. pertusa* in the lagoon. If so, the species could have been introduced into Thau Lagoon as early as 1971-1977 along with massive official importations of Japanese oysters from the Pacific (Grizel & Héral, 1991), as was probably also the case for *Chrysymenia wrightii* (Harvey) Yamada, *Dasya sessilis* Yamada, *Desmarestia viridis* (O.F. Müller) J.V. Lamouroux, *Laminaria japonica* Areschoug, *Lomentaria hakodatensis* Yendo, *Sargassum muticum* (Yendo) Fensholt, *Sphaerotrichia divaricata* (C. Agardh) Kylin, *Undaria pinnatifida* (Harvey) Suringar (see Verlaque, 2001). In Europe, *Ulva pertusa* has also been introduced recently in The Netherlands, at least since 1995 (H. Stegenga, pers. comm.).

Ulva pertusa Kjellman occurs in an extensive Indo-Pacific area and is common in the North-West Pacific: China, Japan, Korea, and the Philippines (Okamura, 1921; Dong & Tseng, 1984; Lee & Kang, 1986; Silva *et al.*, 1987, 1996; Yoshida, 1998). Its northern and southern latitudinal range limits in Asia seem to be southern Sakhalin-southern Kuril Islands and Indonesia-Singapore, respectively (Nagai, 1940; Tokida, 1954; Wei & Chin, 1983; Silva *et al.*, 1996). The seasonal range of sea-surface temperatures tolerated by *U. pertusa* is very wide, from about 0°C to 16-18°C along the Okhotsk coasts and from 27-28°C to about 30-31°C at Singapore (Tokida, 1954; Wei & Chin, 1983). The patterns of the photosynthesis-temperature curve imply the existence of at least 2 enzyme systems, one of which was heat-resistant and the other heat-susceptible (Mizusawa *et al.,* 1978). In laboratory, *U. pertusa* survives after 24 hr freezing at –15°C (Terumoto, 1960).

In Japan, *Ulva pertusa* is ranked among the most common seaweeds, both on natural and man-made substrata, and in the intertidal and sublittoral zones (Takamatsu, 1939; Noda, 1987; Chihara, 1990; Tokuda *et al.*, 1994). In particular, it grows in coastal lagoons comparable to Thau Lagoon, such as Lake Nakaumi (southwestern Honshu) (Kunii & Minamoto, 2000) and Lake Saroma (Hokkaido) (Iwamoto, 1960). It tolerates a wide range of salinity, from 17-18 PSU in a coastal lagoon to an open-sea salinity (Iwamoto, 1960; Floreto *et al.,* 1994). According to

Floreto *et al.* (1993), its growth rate is highest at low temperature (15°C), high light intensity (48-64 µE m^{-2} s^{-1}) and high salinity (35 PSU). On the Izu peninsula, its optimum temperature for photosynthesis is 25-30°C (Yokohama, 1972). At 19-22.5°C, the fronds can increase up to about 775% during 1 week (Ohno, 1977). The main factor limiting its growth is considered to be climatic condition, above all water temperature**,** together with nutrient salt supply (nitrogen) (Matsukawa & Umebayashi, 1987, 1988). The ecological requirements of *Ulva pertusa* in Japan are consistent with the data of Thau Lagoon (water temperature range: 4-27°C and salinity range: 27 to 40 PSU, Jouffre & Amanieu, 1991). In the intertidal zone of southern Hokkaido, *Ulva pertusa* is a common and dominant species, especially under sheltered conditions such as where protected by breakwaters. Its frequent reproduction in temperate areas (from spring to autumn according to Okamura, 1921; Sawada, 1972) is considered to support its position as a dominant species in this marine vegetation (Saito *et al.*, 1977). Moreover, its output of gametes is high (32 gametes per gametangia) and the gametes can develop by parthenogenesis (Yamada & Saito, 1938; Yabu & Tokida, 1960). Molecular analysis of *Ulva* thalli of green tides have shown a high degree of homology (92%) between the ITS sequences of some Japanese populations and those of *U. pertusa* of Korea (Niwa *et al.*, 2001). Consequently, *U. pertusa* would appear to have the capacity to colonize large areas in the temperate European regions both in the Mediterranean Sea and Atlantic Ocean.

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