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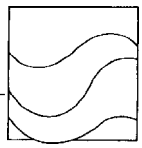

Checklist of the macroalgae of Thau Lagoon (Hérault, France), a hot spot of marine species introduction in Europe

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Abstract – A checklist of macroalgae in Thau Lagoon (Hérault, France), based on literature records and new collections, is given. Using present-day taxonomy, 196 taxa and stadia of macroalgae have been identified to date. Sixty of these were no longer found in the samples, 36 were new to the lagoon, and the taxonomic identity of 15 species was amended. Twenty-five new introduced taxa were identified, giving a total of 45 introduced macroalgae for the flora (23% of total). Among these, 17 taxa and several genera (*Acrothrix, Chondrus, Dasysiphonia* (?), *Prionitis*) are new to the Mediterranean Sea and 12 are new to Europe. The majority (43 taxa) may originate from the Pacific region, having arrived either directly or via other aquaculture sites. A highly probable vector of macroalgae introductions is the transfer of oysters, which appears, at present, to be the main vector of macrophyte introductions in the Mediterranean Sea, surpassing the Suez Canal. Thau Lagoon is revealed to be one of the major hot spots of marine species introduction in the Mediterranean Sea, Europe, but also in the world. This result is worrying as Thau is also an important exportation centre of living molluscs towards other French aquaculture sites and abroad. Therefore, the numerous exotic macroalgae, which have been acclimatized in the lagoon, have a high probability of being diffused throughout Europe and other Mediterranean countries. At present, the hard substrates of the Thau Lagoon are clearly dominated by the introduced species to the detriment of indigenous flora. The fate of these species in the Mediterranean Sea and Europe is unpredictable. It is probably not very realistic to hope that the accidental introductions linked to aquaculture activities will stop. A set of recommendations exists, however, that might contribute to limit the phenomenon.

Résumé – Inventaire des macroalgues de l'étang de Thau (Hérault, France), un lieu privilégié d'introduction d'espèces marines en Europe. Un inventaire des macroalgues de l'étang de Thau (Hérault, France), basé sur les travaux antérieurs et de nouveaux échantillonnages, est présenté. En fonction de la taxonomie actuelle, 196 taxa et stades de macroalgues ont été retenus, 60 d'entre eux n'ont pas été retrouvés dans les récoltes, 36 sont nouveaux pour l'étang et l'identité de 15 espèces a été précisée. Vingt-cinq nouveaux taxa exotiques ont été identifiés, ce qui donne un total de 45 macroalgues exotiques pour la flore (23% du total). Parmi ces algues, 17 taxa et plusieurs genres (*Acrothrix, Chondrus, Dasysiphonia* (?), *Prionitis*) sont nouveaux pour la Méditerranée et 12 pour l'Europe. La majorité de ces espèces (43 taxa) proviendraient du Pacifique, directement ou indirectement via d'autres sites aquacoles. La raison la plus probable de cette situation est le transfert d'huîtres qui apparaît, à présent, comme le principal vecteur d'introduction de macrophytes en Méditerranée, surpassant le canal de Suez. L'étang de Thau se révèle comme un des plus importants sites d'introduction de macroalgues marines en Méditerranée, en Europe mais également dans le monde. Ce résultat est préoccupant car Thau est aussi un important centre d'exportation de mollusques vivants vers d'autres sites

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aquacoles français ou étrangers. Par conséquent, les nombreuses macroalgues exotiques qui se sont acclimatées à Thau, ont une forte probabilité d'être diffusées ailleurs en Europe et dans d'autres pays méditerranéens. Actuellement, les substrats durs de l'étang sont dominés par les espèces exotiques, au détriment des algues indigènes. Le devenir de ces espèces en Méditerranée et en Europe reste imprévisible. Il est probablement irréaliste d'espérer arrêter les introductions accidentelles liées aux activités aquacoles, cependant, un ensemble de recommandations pourrait contribuer à limiter le phénomène. © 2001 Ifremer/CNRS/IRD/Éditions scientifiques et médicales Elsevier SAS

Mediterranean Sea / Thau Lagoon / macroalga / checklist / introduced species

Méditerranée / étang de Thau / inventaire / macrophytes / espèces introduites

1. INTRODUCTION

Aquaculture, as well as the fouling and deballasting of water, represent some of the more important sources of species introduction in the marine environment (Zibrowius, 1991; Boudouresque and Ribera, 1994). With a standing stock and annual production reaching 25 000 t and 12 000–13 000 t of oysters, respectively, Thau Lagoon (7000 ha, mean depth: 3.8–4.5 m, maximum 10 m deep, water temperature range: 4–27°C; salinity range: 27 to 40, Jouffre and Amanieu, 1991, *figure 1*) is by far the leading site of mollusc shellfish aquaculture in the Mediterranean Sea (Hamon and Tournier, 1990; Trousselier et al., 1991). Faced with successive oyster diseases, the professionals in this field have, since 1961, been forced to resort to imported species (Pichot, 1991; Hamon and Pichot, 1994): the Portuguese oyster *Crassostrea angulata* (Lamarck), from 1961 to 1971, and the Japanese oyster *Crassostrea gigas* (Thunberg), from 1971.

As the breeding of these two species is not of a level to allow the collection of larva in the Mediterranean Sea, production has been wholly dependent on the importation of adults or spat. The first importation of non-Mediterranean *Ostrea edulis* took place between 1920 and 1929, and the oysters originated from England and Ireland (Grizel, 1994). The massive importation of *Crassostrea gigas*, however, occurred from 1971 to 1976 with 280 million oysters directly imported from Japan (Grizel and Heral, 1991). Since 1976, the only spat officially authorized to enter Thau Lagoon is that produced in the Atlantic, but illicit importations from other regions have occurred in the past and probably still do. As a result of the failure in decontamination processes and/or quarantine of these authorized or non-authorized imports, an increasing number of species introductions have occurred in Thau Lagoon. In the framework of the pluridisciplinary

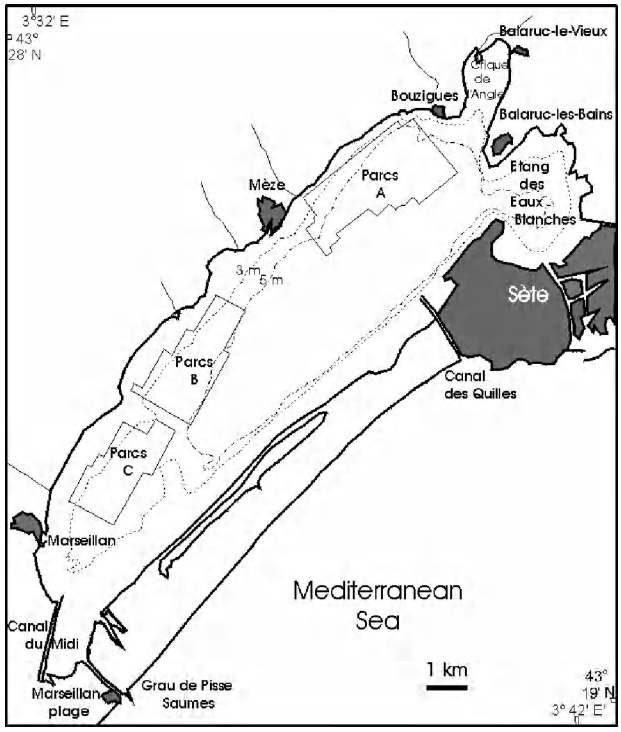


Figure 1. The Thau Lagoon with location of oyster farming zones A, B and C.

'*Programme national d'écologie côtière*' (PNEC), we have carried out a re-evaluation of the macroalgae checklist in Thau Lagoon (Verlaque, 2000). The aims of this present study were: 1) to emend the bibliographic checklist, 2) to sample and identify new species, exotic or not, 3) to analyse the introduced species flora, and 4) to warn the phycologists about a new and abundant contingent of introduced algae that could spread along the European and Mediterranean coasts.

Table I. Total number of taxa and stadia of marine macroalgae listed in Thau Lagoon

Classes	Total	Not observed during present study	New taxa	Amended taxa
Rhodophyceae	99	30	19	9
Fucophyceae	55	16	13	2
Chlorophyta	42	14	4	4
Total	196	60	36	15

2. MATERIALS AND METHODS

A first checklist (Ben Maiz et al. 1988), two theses (Ben Maiz, 1986a; Gerbal, 1994) and a synthesis of the introductions of macroalgae in the Mediterranean Sea (Verlaque, 1994) provided valuable information concerning the evolution of the macroalgal flora in Thau Lagoon since 1892. Using present-day taxonomy, these studies were amended and complemented by the bibliographic analysis of the following works: Huber (1892), Calvet (1905), Pavillard (1905), Sudry (1910), Hamel (1930), Hamel (1939), Valet (1958), Lauret (1967), Ville (1968), Dubois (1969), Lauret (1970), Dubois (1972), Anonymous (1980), Pérez et al. (1981), Verlaque (1981), Anonymous (1982), Critchley et al. (1983), Belsher et al. (1984), Pérez et al. (1984), Boudouresque et al. (1985), Gerbal et al. (1985), Lauret et al. (1985), Pellegrini et al. (1985), Riouall (1985), Riouall et al. (1985), Ben Maiz (1986a, b), Gerbal (1986), Ben Maiz et al. (1986, 1987), San Martin (1987), Verlaque and Riouall (1989), Belsher (1991), Dubois and Lauret (1991), De Casabianca et al. (1994), Gerbal (1994), Gerbal and Verlaque (1995), Latala (1995), Verlaque (1996), Verlaque and Latala (1996), De Casabianca et al. (1997a–c), De Casabianca and Posada (1998), Lamy et al. (1998), Marinho-Soriano et al. (1998), Laugier et al. (1999). Those records that could not be attributed to any valide present taxa were not considered here, i.e. *inquirandae* in Ben Maiz et al. (1988), and some incompletely determined taxa.

New observations and sampling were performed in September–October 1994, September 1995, June 1996, October 1997 and May–June 1998. All samples were hand-collected from more than 70 stations evenly distributed in Thau Lagoon, and preserved in buffered 4% formaldehyde–seawater. Fixed material was studied under stereoscopic and light microscopes and subsequently dried. Voucher specimens were deposited in the Verlaque Herbarium (UMR Dimar Com, Marseille, France). We also re-examined some specimens misidentified or incompletely identified by Ben Maiz.

3. RESULTS

3.1. Checklist of macroalgae

Until now, 196 taxa and stadia of macroalgae have been recorded from Thau Lagoon, 60 of which were not found in our samples, 36 were new to the lagoon, and the taxonomic identity of 15 species was amended (appendix *and table I*). The taxa which were not found in the samples taken here belong to either cold season flora, such as *Bangia, Porphyra, Ectocarpus* (season not sampled in the present study), or exotic species which failed their acclimatization, or to a group undergoing extinction due to the extensive environmental changes experienced in the lagoon since 1900 (increase in the exchanges with the sea, extension of aquaculture facilities, increased urban development, industrial and agricultural pollution, accidental introduction of species, etc.).

3.2. Exotic flora

Hitherto, a total of 45 species are considered to be introduced (23% of total). To analyse this exotic flora, its origins, vectors and degree of acclimatization, each taxon was considered as a function of its date of discovery and subsequently, for each year, based on alphabetical order. Three periods of species introduction were distinguished: 1) before 1971, date of the first official importation of *Crassostrea gigas* from Japan, 2) from 1971 to 1988, period during which studies were carried out following these importations, and 3) from 1993 to 1998 (present study). For each taxon, a brief natural world distribution (with the exception of areas where the species is considered to be introduced) is given according to Tseng (1984), South and Tittley (1986), Silva et al. (1996) and other more limited references. For Pacific species, their occurrence in Korea and Japan is established based on Lee and Kang (1986) and Yoshida (1998). Dates of first and most

recent observations are indicated, the uncertain data and the species newly identified or amended are labelled by question marks and asterisks, respectively.

3.2.1. Before 1971

– *Leathesia difformis* (Linnaeus) Areschoug (Corynophlaeaceae, Fucophyceae). Cosmopolite, in the all temperate seas (including Japan and Korea). 1905 (? Calvet, 1905, as *L. tuberiformis*)–1979 (Verlaque, 1981)–Not observed during the present study.

– *Colpomenia peregrina* (Sauvageau) Hamel (Scytosiphonaceae, Fucophyceae). Indian Ocean–Pacific (including Japan). < 1918? and 1957 (Ville, 1968)–1998.

– * *Polysiphonia harveyi* Bailey (Rhodomelaceae, Rhodophyceae) (*figure 2*). Atlantic–Southeast Asia (including Japan and Korea, as *P. japonica* Harvey). 1958? (Lauret, 1967, as *P. mottei*)–1998. Described from Connecticut along the East Coast of USA (Bailey, 1848), *Polysiphonia harveyi* Bailey is considered to be an old introduction in Europe, probably during the last century (see Maggs and Hommersand, 1993). In fact, *P. harveyi* may be *P. japonica* Harvey (1857), a widespread Asiatic alga (Eno et al., 1997; Maggs and Stegenga, 1999). At the time of its discovery in Thau Lagoon, the species was considered to be a new species (*P. mottei* Lauret, 1967). In the Mediterranean Sea, the species has been recorded only once as *P. harveyi* (Tuscan Archipelago, Papi et al. 1992), but frequently as *P. mottei* (Gómez Garreta et al., 2001). *P. harveyi* is probably an introduction of long standing in the Mediterranean Sea.

– *Polysiphonia paniculata* Montagne (Rhodomelaceae, Rhodophyceae). East Pacific. 1967 (Lauret, 1970)–Not observed during the present study.

– *Codium fragile* (Suringar) Hariot (Codiaceae, Chlorophyta). Indian Ocean–Pacific (including Japan and Korea). 1967 (Lauret, 1967)–1998.

3.2.2. 1971–1988

– *Undaria pinnatifida* (Harvey) Suringar (Alariaceae, Fucophyceae). Southeast Asia (including Japan and Korea). 1971 (Anonymous, 1980) – 1998.

– *Porphyra yezoensis* Ueda (Bangiaceae, Rhodophyceae). East Asia (including Japan and Korea). 1975 (Anonymous, 1982, as *P. tenera*) – Not observed during the present study.

– *Laminaria japonica* Areschoug (Laminariaceae, Fucophyceae). East Asia (including Japan and Korea). 1976 (Pérez et al., 1984) – 1989 (unpublished data) – Not observed during the present study.

– *Chrysymenia wrightii* (Harvey) Yamada (Rhodymeniaceae, Rhodophyceae). East Asia (including Japan and Korea). 1978 (Ben Maiz et al., 1987) – 1998.

– *Desmarestia viridis* O.F. Müller (Desmarestiaceae, Fucophyceae). North Atlantic–East Asia (including Japan and Korea). 1978 (Verlaque, 1981) – 1998.

– *Rhodophysema georgii* Batters (Rhodophysemataceae, Rhodophyceae). Atlantic–North Pacific (including Japan). 1978 (Verlaque, 1981) – Not observed during the present study.

– *Lomentaria hakodatensis* Yendo (Lomentariaceae, Rhodophyceae). North Pacific (including Japan and Korea). 1979 (Ben Maiz and Boudouresque, unpublished data) – 1998.

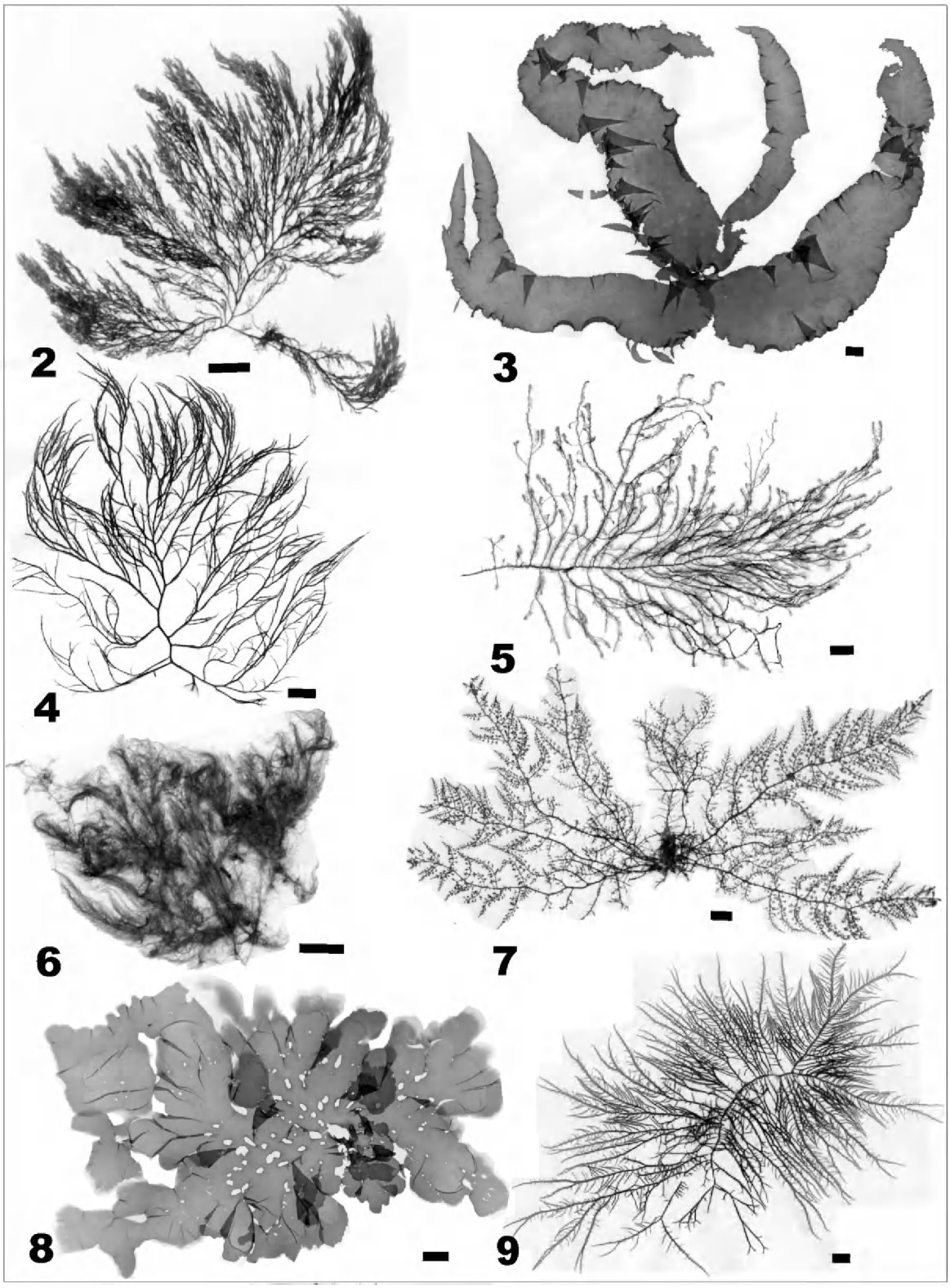
– *Sargassum muticum* (Yendo) Fensholt (Sargassaceae , Fucophyceae). Japan. 1980 (Pérez et al., 1984) – 1998.

– *Chorda filum* (Linnaeus) Stackhouse (Chordaceae, Fucophyceae). Atlantic–North Pacific (including Japan and Korea). 1981 (Riouall, 1985) – 1998.

– *Sphaerotrichia divaricata* (C. Agardh) Kylin (Chordariaceae, Fucophyceae). East Asia (including Japan and Korea)–North Atlantic (Japanese origin established by Peters et al., 1992). 1981 (Riouall, 1985) – 1998.

– * *Grateloupia* cf. *turuturu* Yamada (Halymeniaceae, Rhodophyceae) (*figure 3*). Japan and Korea. 1982 (Riouall et al., 1985, as *G. doryphora*) – 1998. In 1982,

Figure 2. *Polysiphonia harveyi* Bailey (H.2872, Bouzigues, October 1994).
Figure 3. *Grateloupia* cf. *turuturu* Yamada (H.2633, Bouzigues, September 1990).
Figure 4. *Agardhiella subulata* (C. Agardh) Kraft and M. J Wynne (H.2866, Bouzigues, November 1988).
Figure 5. *Dasya* sp. (H.2869, Bouzigues, December 1998).
Figure 6. *Derbesia rhizophora* Yamada (H.2823, Parcs A, May 1998).
Figure 7. *Laurencia okamurae* Yamada (H.2809, Parcs C, June 1998).
Figure 8. *Ulva pertusa* Kjellman (H.2658, Parcs A, September 1995).
Figure 9. *Grateloupia* sp. (H.2871, Mèze-Bouzigues, September 1995). (Scale bars = 10 mm).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Riouall et al. (1985) found a large foliaceous alga, which they identified as *G. doryphora* (Montagne) Howe, a Southeast Pacific species described from Peru (Montagne, 1839, as *Halymenia* (?) *doryphora*). This species was first recorded in Europe, in 1969 (England, Farnham and Irvine, 1973). Since 1969, it has spread along the American and European Atlantic coasts (Cabioch et al., 1997; Eno et al., 1997; Villalard-Bohnsack and Harlin, 1997), in the western Mediterranean Sea (De Masi and Gargiulo, 1982; Giaccone et al., 1985; Riouall et al., 1985; Rull Lluch et al., 1991) and in the Adriatic Sea (Gargiulo et al., 1992). Different authors have suggested that its introduction in Europe should be attributed to the oyster transfers from Japan made by France as early as 1966 (Farnham, 1980; Ribera and Boudouresque, 1995; Farnham in Eno et al., 1997). Unfortunately, *G. doryphora* occurs neither in Japan (Yoshida, 1998) nor in Korea (Lee et Kang, 1986). On the other hand, *G.* cf. *turuturu* Yamada, a species described from Hokkaido (Yamada, 1941) that is endemic to these two countries, is in good agreement with the introduced alga until now attributed to *Grateloupia doryphora.* While awaiting further investigation, and in light of its probable Asiatic origin, we have preferred to tentatively regard this alga as *G.* cf. *turuturu.*

– * *Agardhiella subulata* (C. Agardh) Kraft et M. J Wynne (Solieriaceae , Rhodophyceae) (*figure 4*). Atlantic–Mediterranean Sea–Pacific (?). 1984 (Ben Maiz et al., 1986, as *Solieria chordalis*) – 1998. *Agardhiella subulata* has been described from the northeastern America coast (Agardh, 1822, *s. n. Sphaerococcus subulatus*), but a possible Pacific origin cannot be excluded for European populations (see Maggs in Eno et al., 1997). It was first introduced in Great Britain prior to 1973 (Farnham and Irvine, 1979). It may also occur in Spain, although this record needs to be confirmed (Eno et al., 1997). In the Mediterranean Sea, it was first observed in 1987 in Mar Piccolo di Taranto (South Italy; Cecere, 1989) and then in Sicily (Perrone and Cecere, 1994). These authors considered it as either an introduced species or a new example of a Tethys relict. In Thau Lagoon, it has probably been introduced with oyster transfers from the Atlantic. *Agardhiella subulata* is new to France.

– * *Dasya* sp. (Dasyaceae, Rhodophyceae) (*figure 5*). 1984 (Ben Maiz et al., 1986, as *Dasya hutchinsiae*) – 1998. Although common in the lagoon, this alga has not yet been identified to the species level. The specimens differ from the Atlantic and Mediterranean species of *Dasya* (*D. hutchinsiae* included) by the peculiarity of their reproductive features, which are very close to those of a Pacific taxonomic group. We regard it as a Pacific species probably introduced in the 1970s along with massive importations of Japanese oysters. This alga is new to Europe and the Mediterranean Sea.

– * *Derbesia rhizophora* Yamada (Bryopsidaceae, Chlorophyta) (*figure 6*). Japan. 1984 (Ben Maiz et al., 1986, as *Derbesia* sp.) – 1998. Described from the Ehime Province (Yamada, 1961), *D. rhizophora* seems to be an endemic Japanese species. Its introduction in Thau Lagoon probably occurred as early as the 1970s along with the massive importations of Japanese oysters. *Derbesia rhizophora* is new to the Mediterranean Sea and Europe.

– *Griffithsia corallinoides* (Linnaeus) Batters (Ceramiaceae, Rhodophyceae). Atlantic–Pacific (including Japan and Korea). 1984 (Ben Maiz et al., 1986) – 1998.

– * *Laurencia okamurae* Yamada (Rhodomelaceae, Rhodophyceae) (*figure 7*). East Asia (including Japan and Korea). 1984 (Ben Maiz et al., 1986, as *Laurencia coronopus*) – 1998. Described from Japan (Satsuma, Hizen, Bungo, Nagato, Kii, and Awa Provinces, Yamada, 1931), *L. okamurae* is widespread in Asia (Japan, Korea, the Philippine Islands, China, Taiwan). Its introduction in Thau Lagoon probably occurred as early as the 1970s along with the massive importations of Japanese oysters. *Laurencia okamurae* is new to the Mediterranean Sea and Europe.

– * *Ulva pertusa* Kjellman (Ulvaceae, Chlorophyta) (*figure 8*). Indian Ocean–Northwestern Pacific (including Japan and Korea). 1984 (Ben Maiz et al., 1986, as *Ulva* sp.) – 1998. Described from Japan (Hakodate, Yenoshima and Yokohama, Kjellman, 1897), *U. pertusa* is widespread in the Indo–Pacific. Its introduction in Thau Lagoon probably occurred as early as the 1970s along with the massive importations of Japanese oysters. *Ulva pertusa* is new to the Mediterranean Sea and Europe.

– * *Grateloupia* sp. (Halymeniaceae, Rhodophyceae) (*figure 9*). 1985 (Ben Maiz et al., 1986, as *Grateloupia dichotoma*?) – 1998. This very polymorphic alga has not yet been identified to the species level. The specimens differ from the Atlantic and Mediterranean species of *Grateloupia.* Due to the peculiarity of its features and the high number of species described from Pacific, this alga is tentatively regarded as a species possibly introduced from this region. It is new to Europe and the Mediterranean Sea.

– *Halothrix lumbricalis* (Kützing) Reinke (Elachistaceae, Fucophyceae). North Atlantic–East Asia (including Japan). 1985 (Ben Maiz et al., 1986) – 1998.
– *Monostroma obscurum* (Kützing) J. Agardh (Monostromataceae, Chlorophyta, see Burrows, 1991). Atlantic–North Pacific (including Japan and Korea, as *Ulvaria fusca* Ruprecht and *U. obscura* (Kützing) Gayral). 1985 (Ben Maiz et al., 1986, as *Monostroma grevillei*) – 1998.
– *Pilayella littoralis* (Linnaeus) Kjellman (Pilayellaceae, Fucophyceae). Atlantic–Pacific (including Japan and Korea). 1985 (Ben Maiz et al., 1986) – Not observed during the present study.
– * *Polysiphonia atlantica* Kapraun et J. Norris (Rhodomelaceae, Rhodophyceae). North Atlantic–Indian Ocean–Pacific (including Korea). 1985 (Ben Maiz et al., 1986, as *Lophosiphonia scopulorum*) – 1998. Described from the eastern USA (Belize, Kapraun and Norris, 1982), *P. atlantica* is widespread throughout the world. It was recorded in the North Atlantic, from North Carolina to Brazil and from the British Isles to Morocco, the Indian Ocean and the Pacific (Maggs and Hommersand, 1993). The species has been frequently recorded in the Mediterranean Sea (Gómez Garreta et al., 2001), but only once from France (Pyrénées Orientales, Knoepffler et al., 1990, *s. n. P. macrocarpa* Harvey). We consider it to be an introduced species in Thau. The vector of introduction may be either maritime traffic or oyster transfers.
– *Antithamnion pectinatum* (Montagne) Brauner ex Athanas and Tittley (Ceramiaceae, Rhodophyceae). Pacific (including Japan and Korea). 1988 (Verlaque and Riouall, 1989 as *A. nipponicum* Yamada et Inagaki) – 1998.

3.2.3. 1993–1998

– *Grateloupia lanceolata* (Okamura) Kawaguchi (Halymeniaceae, Rhodophyceae) (*figure 10*). Japan and Korea. 1993–1998. Described from Japan (Kii Province, Okamura, 1935, as *Aeodes lanceolata*), *G. lanceolata* appears to be endemic to Japan and Korea. Since its description, it has been placed in a new genus (*Pachymeniopsis* Yamada in Kawabata, 1954, 1962), and then transferred to the genus *Grateloupia* (Kawaguchi, 1997). The alga was probably introduced in Thau Lagoon along with transfers of Asiatic oysters. In light of the high risk of confusing it with *G.* cf. *turuturu*, the exact date of its introduction remains undetermined (during the 1970s or more recently). Ongoing molecular studies confirm the specific distinction between the two foliaceous *Grateloupia* from Thau (Villalard-Bohnsack, personal communication). *Grateloupia lanceolata* is new to the Mediterranean Sea and Europe.
– *Ahnfeltiopsis flabelliformis* (Harvey) Masuda (Phyllophoraceae, Rhodophyceae) (*figure 11*). East Asia (including Japan and Korea). 1994–1998. Described from Japan (Shizuoka Province, Harvey, 1857, as *Gymnogongrus flabelliformis*), *A. flabelliformis* is widespread in the Pacific (former USSR, China, Japan, Korea, Vietnam, the Philippine Islands, Hawaii, Peru). The alga was probably introduced in Thau Lagoon along with the recent transfers of Asiatic oysters. *Ahnfeltiopsis flabelliformis* is new to the Mediterranean Sea and Europe.
– *Chondrus giganteus* Yendo f. *flabellatus* Mikami (Gigartinaceae, Rhodophyceae) (*figure 12*). Japan. 1994–1998. Described from Japan (Aomori Province, Mikami, 1965), *Chondrus giganteus* f. *flabellatus* appears to be endemic to the north of the Japan. The material from Thau has already been described in detail (Verlaque and Latala, 1996). The alga was probably introduced in Thau Lagoon along with recent transfers of Asiatic oysters. *Chondrus giganteus* f. *flabellatus* is new to the Mediterranean Sea and Europe.
– *Lithophyllum yessoense* Foslie (Corallinaceae, Rhodophyceae) (*figure 13*). North Pacific (including Japan). 1994–1997. Described from Japan (Foslie, 1909), *L. yessoense* is the dominant species of the isoyake areas (barren grounds dominated by encrusting Corallinaceae), which lie at depths of between 0 and 20 m in the Southwestern Hokkaido (Noro et al., 1983). The alga has several adaptations that allow it to successfully outcompete the other algae and thus form extensive encrusting communities: 1) grazer-resistance (calcification and epithallial shedding), 2) anti-fouling mechanism sufficient to prevent the overgrowth of fleshy algae (epithallial shedding and deep-layer sloughing), 3) high capacity of regeneration, and 4) low iron requirement (Masaki et al., 1981, 1984; Fujita et al., 1992; Tokuda et al., 1994; Susuki et al., 1995; Fujita, 1999). Consequently, *L. yessoense* should be considered to be a potentially invasive species. The alga was probably introduced in Thau Lagoon along with recent transfers of Asiatic oysters. *Lithophyllum yessoense* is new to the Mediterranean Sea and Europe.
– *Prionitis patens* Okamura (Halymeniaceae , Rhodophyceae) (*figure 14*). Japan and Korea. 1994–1996. Described from Japan (Aichi Province, Okamura, 1899), *P. patens* is an endemic species from Japan and Korea (Lee and Kang, 1986; Kawaguchi, 1989). The alga was probably introduced in Thau Lagoon along with recent trans-

fers of Asiatic oysters. *Prionitis patens* is new to the Mediterranean Sea and Europe.

– *Scytosiphon dotyi* Wynne (Scytosiphonaceae, Fucophyceae) (*figure 15*). North Pacific. 1994. Described from California (Wynne, 1969), *S. dotyi* is widespread in the North Pacific. It was introduced in the North Atlantic, along the east coast of England (Fletcher, 1987), and in the Mediterranean Sea where it has been recorded from Trieste (Giaccone, 1978) and Venice Lagoon (Curiel et al., 1996a). The alga was probably introduced in Thau Lagoon either directly with transfers of Asiatic oysters or indirectly via other sites of shellfish aquaculture. *Scytosiphon dotyi* is new to France.

– *Chondria coerulescens* (J. Agardh) Falkenberg (Rhodomelaceae, Rhodophyceae) (*figure 16*). North Atlantic–Mediterranean Sea. 1995–1997. Described from Brittany (Agardh, 1863; *s. n. Chondriopsis coerulescens*), *C. coerulescens* occurs along the eastern Atlantic coast, from England to Morocco (Maggs and Hommersand, 1993). In Thau Lagoon, it was probably introduced along with oyster transfers from the Atlantic. In the Mediterranean Sea, it has been often recorded except from France (Gómez Garreta et al., 2001).

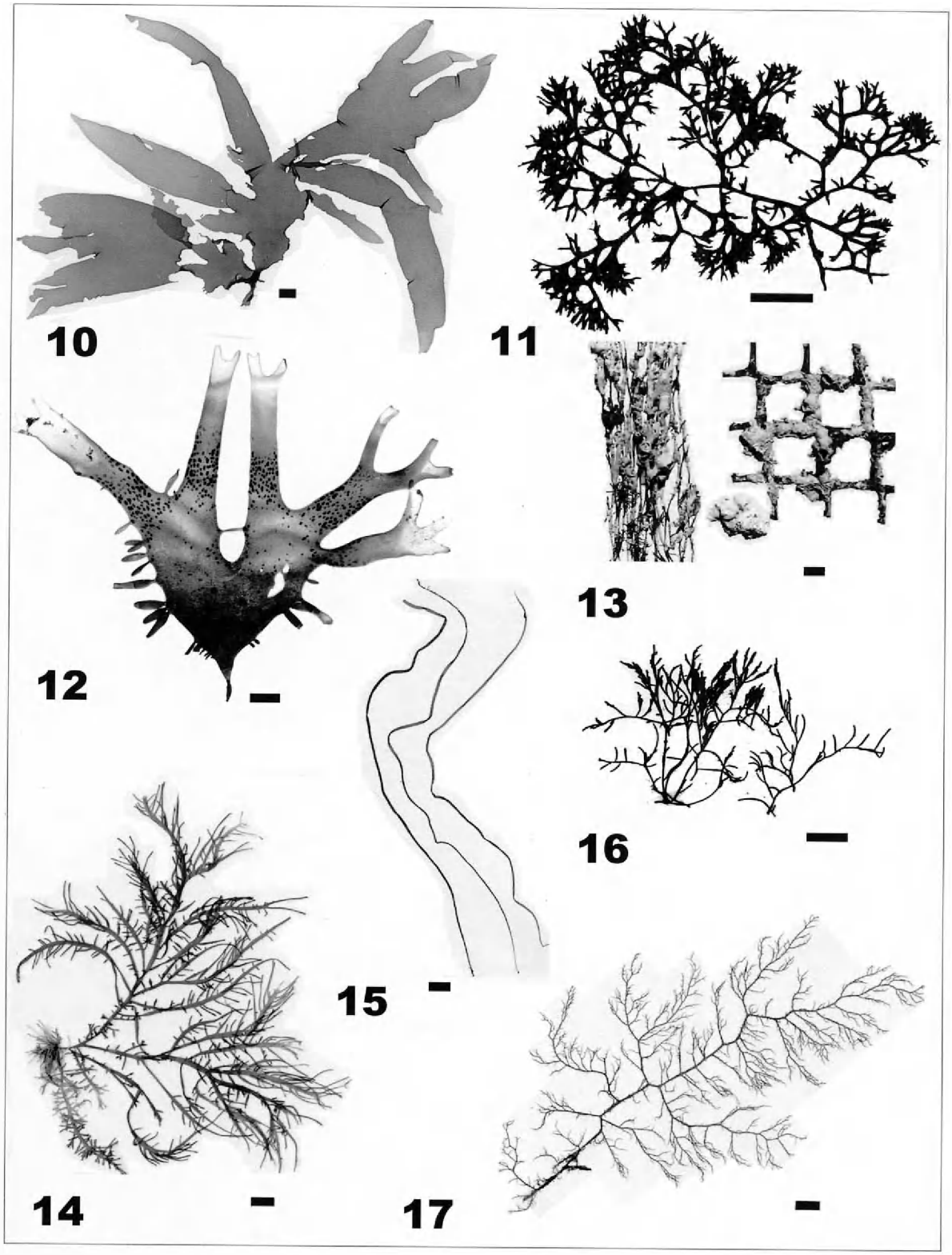
– *Hypnea valentiae* (Turner) Montagne (Hypneaceae, Rhodophyceae) (*figure 17*). Tropical and subtropical seas (including Japan and Korea, as *H. charoides* Lamouroux). 1996–1998. Described from the Red Sea (Turner, 1809, as *Fucus valentiae*), *H. valentiae* is widespread throughout the world. In Japan and Korea, it is recorded as *H. charoides* Lamouroux (Tanaka, 1941; Lee and Kang, 1986; Yoshida, 1998), although Asiatic descriptions are in good agreement with the *H. valentiae* diagnosis but not at all with those of the authentic *H. charoides* from New Zealand (Lamouroux, 1813) and present in Tasmania and South Australia (Womersley, 1994). In the eastern Mediterranean basin, it was recorded from the Island of Rhodes, where it was considered to be a Lessepsian immigrant (Aleem, 1948), Greece (Gerloff and Geissler, 1971), Syria (Mayhoub, 1976, as *H. hamulosa* Lamouroux) and Egypt (Aleem, 1993). In Thau Lagoon, the probability of a Lessepsian origin is extremely low. An Asiatic origin attributable to the transfers of oysters is more probable. *Hypnea valentiae* is new to the western Mediterranean Sea and France.

– *Grateloupia filicina* (Lam.) C. Agardh var. *luxurians* Geep *et* Geep (Halymeniaceae, Rhodophyceae) (*figure 18*). Pacific. 1997–1998. Described from Australia (New South Wales, Geep and Geep, 1906), *G. filicina* var. *luxurians* was first observed in Europe in 1947 (Great Britain, Farnham and Irvine, 1968). Since then, it has been recorded from the Spanish Atlantic Coast (López-Rodríguez and Cremades, 1991) and Brittany (Cabioch et al., 1997). The alga was probably introduced in Thau Lagoon with oyster transfers either directly from Pacific or indirectly via other sites of shellfish aquaculture. *Grateloupia filicina* var. *luxurians* is new to the Mediterranean Sea.

– *Herposiphonia parca* Setchell (Rhodomelaceae, Rhodophyceae) (*figure 19*). Indian Ocean –Pacific (including Japan and Korea). 1997. Described from Tahiti (Setchell, 1926), *H. parca* was later found in Japan where it was considered to be a new species (*H. terminalis*; Segi, 1954). The alga was probably introduced in Thau Lagoon with recent transfers of Asiatic oysters. *Herposiphonia parca* is new to the Mediterranean Sea and Europe.

– *Polysiphonia morrowii* Harvey (Rhodomelaceae, Rhodophyceae) (*figure 20*). North Pacific (including Japan and Korea). 1997–1998. Described from Japan (Hokkaido, Harvey, 1856), *P. morrowii* was first recorded in Europe, in 1993, at Gorishoek, The Netherlands, as *P. senticulosa* Harvey (1862), a species from the state of Washington (Maggs and Stegenga, 1999). The conspecificity of *P. senticulosa* and *P. morrowii* has been proposed by Yoon (1986). The alga is now common in a large part of the North Sea, where it is locally abundant in the oyster ponds of Yerseke Oesterbank (Maggs and Stegenga, 1999). The alga was probably introduced in Thau Lagoon either directly with transfers of Asiatic oysters or indirectly via other sites of shellfish aquaculture. *Polysiphonia morrowii* is new to the Mediterranean Sea and France.

Figure 10. *Grateloupia lanceolata* (Okamura) Kawaguchi (H.2870, Parcs A, May 1998).
Figure 11. *Ahnfeltiopsis flabelliformis* (Harvey) Masuda (H.2865, Marseillan, May 1998).
Figure 12. *Chondrus giganteus* Yendo f. *flabellatus* Mikami (H.2867, Bouzigues, May 1998).
Figure 13. *Lithophyllum yessoense* Foslie (B.962, Bouzigues, September 1995).
Figure 14. *Prionitis patens* Okamura (H.2607, Bouzigues, October 1995).
Figure 15. *Scytosiphon dotyi* Wynne (H.2874, Balaruc, October 1994).
Figure 16. *Chondria coerulescens* (J. Agardh) Falkenberg (H.2868, Mèze-Bouzigues, September 1995).
Figure 17. *Hypnea valentiae* (Turner) Montagne (H.2679, Marseillan, June 1996). (Scale bars = 10 mm).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– *Rhodothamniella* cf. *codicola* (Børgesen) Bidoux et F. Magne (Rhodothamniellaceae, Rhodophyceae). Atlantic–Indian Ocean–Pacific (including Japan and Korea). 1997. Described from the Canary Islands (Børgesen, 1927, as *Acrochaetium codicola*), *Rhodothamniella codicola* has been recorded in all the warm temperate seas. In light of the high risk of confusing it with other species, which grow as epiphytes on *Codium* spp., however, this worldwide distribution should be re-evaluated (Bidoux and Magne, 1989). *A. codicola* was recorded from Japan and Korea as *Rhodochorton codicola* (Børgesen) Nakamura or *Audouinella codicola* (Børgesen) Garbary (Nakamura,1944; Lee and Kang, 1986; Yoshida, 1998), but it may be the epiphytic form to *Rhodochorton rhizoideum* Drew, another Asiatic species (Bidoux and Magne,1989). While awaiting new information, we have tentatively attributed our material to *R. codicola*. This species was probably introduced into the Mediterranean Sea during the Second World War along with its host *Codium fragile* (Bidoux and Magne, 1989; Verlaque, 1994). Its introduction in Thau Lagoon may have been as early as that of *C. fragile*.

– *Acrothrix gracilis* Kylin (Acrotrichaceae, Fucophyceae) (*figure 21*). North Atlantic–North Pacific (including Japan). 1998. Described from Sweden (Kylin, 1907), *A. gracilis* is native to a large area of the North Atlantic and North Pacific (Forward and South, 1985; Wynne, 1987). In Japan, it lives with a sister-species, *A. pacifica* Okamura et Yamada in Yamada (1932), that differs in the occurrence of sexual reproduction only known in vitro (Arasaki, 1948; Ajisaka, 1979). In view of the weak taxonomic significance of this feature, we have preferred to consider our material as *A. gracilis*. In Thau Lagoon, it was probably introduced along with oyster transfers from the Atlantic or Pacific. *Acrothrix gracilis* is new to the Mediterranean Sea.

– *Cladosiphon zosterae* (J. Agardh) Kylin (Chordariaceae, Fucophyceae) (*figure 22*). Northeastern Atlantic–Mediterranean. 1998. Described from the Baltic Sea (J. Agardh, 1841, as *Myriocladia zosterae*), *C. zosterae* is widespread along the European Atlantic coast, from Norway to the Bay of Biscay (South and Tittley, 1986). It was recorded in the Mediterranean Sea from Sicily (Battiato and Ponte, 1975), then Sardinia (Cossu et al., 1992), the Adriatic Sea (Giaccone, 1978) and Turkey (Guner et al., 1983–1984). In Thau Lagoon, it was probably introduced along with oyster transfers from the Atlantic. *Cladosiphon zosterae* is new to the Mediterranean coast of France.

– *Dasysiphonia* (?) sp. (Dasyaceae, Rhodophyceae) (*figure 23*). East Asia (including Japan and Korea), as *Heterosiphonia japonica* Yendo *pro parte*. 1998. This alga was often recorded from Asia as being *Heterosiphonia japonica* Yendo. Its features, however, are in poor agreement with either the genus *Heterosiphonia* Montagne (1842) or any other genus of Dasyaceae. The most closely related genus is *Dasysiphonia* Lee and West (1979), although this alga might justify the description of a new genus according to Stegenga and Choi in De Jong et al. (1998). In Europe, *Dasysiphonia* (?) sp. was first observed in 1994, in former oyster ponds from The Netherlands (Stegenga, 1997), and then in 1995 near Roscoff, Brittany (Maggs and Stegenga, 1999). An apparently identical red alga is now rather common along the Galician Coast, especially in aquaculture areas, and may have been introduced there as early as 1990 (Cremades in Maggs and Stegenga, 1999). The alga was probably introduced in Thau Lagoon either directly with transfers of Asiatic oysters or indirectly via other sites of shellfish aquaculture. *Dasysiphonia* (?) sp. is new to the Mediterranean Sea.

– *Pterosiphonia* sp. (Rhodomelaceae, Rhodophyceae) (*figure 24*). 1998. Although common in the lagoon, this alga has not yet been identified to the species level. The specimens differ from the Atlantic and Mediterranean species of *Pterosiphonia*. It is tentatively regarded as a species possibly introduced from the Pacific. The alga is new to Europe and the Mediterranean Sea.

– *Ulva fasciata* Delile (Ulvaceae, Chlorophyta) (*figure 25*). Cosmopolite in warm seas (including Japan). 1998. Described from the Egyptian Mediterranean Coast (Alexandria, Delile, 1813), *U. fasciata* occurs along the

Figure 18. *Grateloupia filicina* (Lam.) C. Agardh var. *luxurians* Geep *et* Geep (H.2698, Marseillan, June 1996).
Figure 19. *Herposiphonia parca* Setchell (H.2764, Parcs B, October 1997).
Figure 20. *Polysiphonia morrowii* Harvey (H.2873, Marseillan, May 1998).
Figure 21. *Acrothrix gracilis* Kylin (H.2813, Parcs B, May 1998).
Figure 22. *Cladosiphon zosterae* (J. Agardh) Kylin (H.2863, Mèze, June 1998).
Figure 23. *Dasysiphonia* (?) sp. (H.2841, Parcs A, May 1998).
Figure 24. *Pterosiphonia* sp. (H.2875, Parcs A, May 1998).
Figure 25. *Ulva fasciata* Delile (H.2771, Étang des Eaux Blanches, July 1998). (Scale bars = 10 mm).

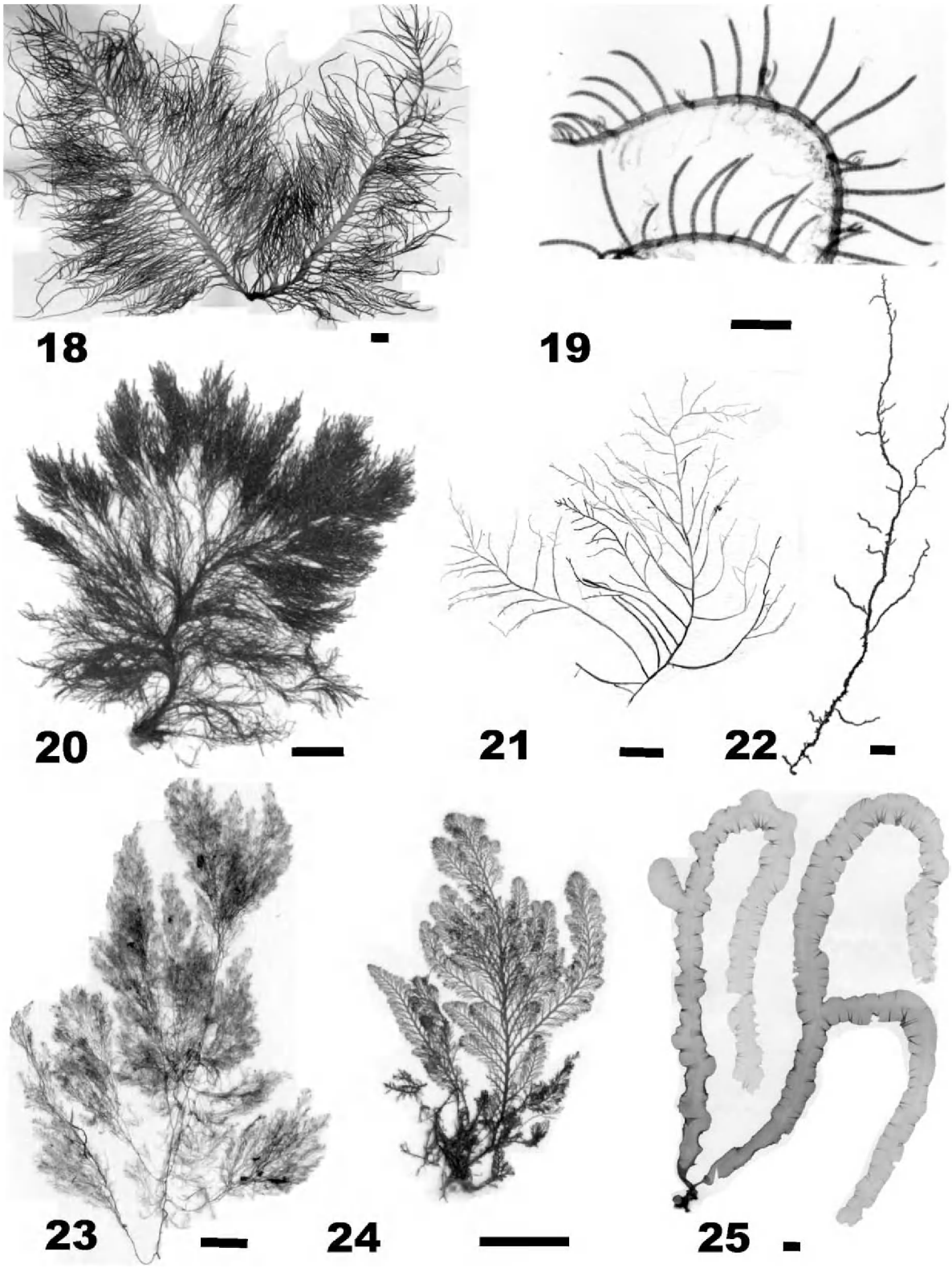
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Table II. Number and native regions of the introduced algae listed from Thau Lagoon.

Period	Total	Indo–Pacific	Indo–Pacific or Atlantic	Indo–Pacific, Atlantic or Mediterranean	Atlantic or Mediterranean	Atlantic
Before 1971	5	4	1	–	–	–
1971–1994	23	14	8	1	–	–
1994–1998	17	11	2	2	1	1
Total	45	29	11	3	1	1

south coasts of the Western Mediterranean Sea, the Adriatic Sea and in the Eastern Mediterranean Basin (Gallardo et al., 1993). In Thau Lagoon, it may have been introduced either by maritime traffic from southern mediterranean populations or by oyster transfers from the Pacific. The material from Thau is in good agreement with the Asiatic specimens. *Ulva fasciata* is new to France.

3.2.4. Number, origins, vectors, acclimatization and incidence of exotic flora

Before 1961, date of the first massive importation of Portugese oysters from the Atlantic, only 53 taxa of macroalgae had been recorded from Thau Lagoon (Ben Maiz et al., 1988, amended). Since 1961, the macroalgal flora has never stopped increasing. Based on literature records and the original data of the present study, the evolution in the number of introduced algae reported from Thau Lagoon is given in *table II*. Among the 45 species which are considered to be introduced, 25 are identified here for the first time from Thau Lagoon and 17 taxa are new to the Mediterranean Sea (of which 12 are new to Europe). Eight introduced species had previously been misidentified or incompletely identified. Among the newly introduced algae, *Acrothrix gracilis*, *Chondrus giganteus, Dasysiphonia* (?) sp. and *Prionitis patens* belong to genera recorded for the first time in the Mediterranean Sea.

A Pacific origin, either direct or via other aquaculture sites, is clear for 29 introduced species and probable for 14 others, giving a total of 43 taxa (95.5% of the exotic flora). The two last species (*Chondria coerulescens* and *Cladosiphon zosterae*) have a probable Atlantic origin (*table II*). For some species, such as *Codium fragile, Monostroma obscurum, Polysiphonia atlantica, P harveyi, P paniculata* and *Ulva fasciata*, an introduction attributable to maritime traffic, via the harbour of Sète, cannot be excluded. For the other species, however, the most probable vector is through oyster transfers for the following reasons:

– the only countries where a large majority of these species live together are Japan (35 species) and Korea (27 species), which are the two major oyster exporters in the world;
– an introduction by ships can be excluded, as the newly identified Asiatic algae have never been observed on ship hulls or in any of the Mediterranean or Atlantic harbours;
– there are massive and recurrent oyster importations (spat and adults) in Thau Lagoon;
– introduced species have all been discovered in, or close to, the oyster farming zones, with the exception of *Polysiphonia paniculata,* collected in the *Canal du Rhône* in Sète, *Ulva fasciata*, collected in the *Étang des Eaux Blanches*, and *Agardhiella subulata*, now present throughout the lagoon;
– similar observations have already been made for the introduced species previously recorded in other European localities (Cabioch and Magne, 1987; Rismondo et al., 1993; Curiel et al., 1995; Curiel et al., 1999a, b; Cabioch et al., 1997; Maggs in Farnham, 1997; Stegenga, 1997; Cremades in Maggs and Stegenga, 1999; Maggs and Stegenga, 1999);
– the major vector implicated in the introduction of marine macrophytes in the Atlantic and North Sea is also oyster transfer (Eno et al., 1997; Maggs and Stegenga, 1999; Reise et al., 1999);
– the accidental introduction of various invertebrates along with oyster transfers also occurs in Thau Lagoon (Zibrowius, 1991, 1994, and personal communication).

The newly identified Asiatic species may have arrived indirectly from other Mediterranean or Atlantic aquaculture facilities (e.g. *Agardhiella subulata, Dasysiphonia* (?) sp., *Polysiphonia morrowii, Scytosiphon dotyi*), although some of these were probably directly introduced with more or less recent importations of oysters from the Pacific. This hypothesis is based on the following observations:
– twelve algae are new to Europe and the Mediterranean Sea (*Ahnfeltiopsis flabelliformis, Dasya* sp., *Derbesia rhizophora, Chondrus giganteus, Grateloupia lan-*

ceolata, G. sp., *Herposiphonia parca, Laurencia okamurae, Lithophyllum yessoense, Prionitis patens, Pterosiphonia* sp., *Ulva pertusa*) and ten of these, at least, are recorded here for the first time outside of their natural geographical area (*Acrothrix gracilis, Ahnfeltiopsis flabelliformis, Derbesia rhizophora, Chondrus giganteus, Grateloupia lanceolata,. Herposiphonia parca, Laurencia okamurae, Lithophyllum yessoense, Prionitis patens, Ulva pertusa*);

– several of these algae were discovered in the farming zone A (*figure 1*), a widely investigated zone during the 1980s, thus excluding the possibility of an introduction before 1976, date of the last massive official importations of oysters from Japan;

– young thalli of *Ahnfeltiopsis flabelliformis, Lithophyllum yessoense* and *Prionitis patens* grew on aquaculture oyster pockets thrown onto the bottom (*figure 13*);

– since 1976, illicit importations of oysters from eastern Asia have probably been carried out, as was the case in the early 1990s (Affaires maritimes de Sète, personal communication).

On the 45 introduced species listed from Thau Lagoon, only 6 (*Laminaria japonica, Leathesia difformis, Pilayella littoralis, Polysiphonia paniculata, Porphyra yezoensis* and *Rhodophysema georgii*) were not observed during the present study. Some of these were recorded during the cold season, which may explain their absence during the spring and autumn sampling periods of the present study. Most of the other introduced species developed reproductive populations. An appraisal of the ecological and economic impact of the exotic flora in Thau Lagoon is not easy because of the poorly documented data before the introductions. However, some species, such as *Ahnfeltiopsis flabelliformis, Chrysymenia wrightii, Colpomenia peregrina, Codium fragile, Desmarestia viridis, Grateloupia* spp., *Lomentaria hakodatensis, Monostroma obscurum, Polysiphonia harveyi, Sargassum muticum* and *Undaria pinnatifida,* have proliferated to the detriment of the Mediterranean species. The hard substrates of the lagoon are strikingly dominated by the introduced species. The frequency and abundance of many indigenous algae, including *Cladophora* spp., *Codium bursa, Colpomenia sinuosa, Cystoseira barbata, C. schiffneri, Grateloupia filicina* var. *filicina, Gymnogongrus griffithsiae* and *Polysiphonia* spp., have clearly decreased since the 1970s. On soft substrates, the dominance of introduced species is less noticeable (Verlaque, 2000). Similarly, large-sized introduced species, such as *Desmarestia viridis, Grateloupia* spp., *Sargassum muticum* and *Undaria pinnatifida,* proliferate on the aquaculture facilities (pillars, ropes and oysters) and thus reduce available light, water circulation and nutrient supplies to the detriment of oyster growth. In light of both the high number of introduced species in Thau Lagoon and the limited time elapsed since their introduction, an equilibrium state in the lagoon is probably far from being reached and the fate of this exotic flora within the lagoon and, if the case arises, in other Mediterranean or Atlantic regions is unpredictable.

4. CONCLUSION

The inadequacy of current French and European legislations concerning the transfer of living marine animals is such that oyster transfers occur with the accidental introduction of marine species. Since the 1960s, and as is true in other aquaculture sites of the Mediterranean, Thau Lagoon is wholly dependent on the massive importation of oysters. In light of the recent evolution of the introduced flora, this lagoon appears to be an important Mediterranean site of acclimatization, directly or via other farming regions, of exotic macroalgae. Approximately twenty years after the accidental introduction of a first contingent of Pacific algae along with massive importations of *Crassostrea gigas* from Japan, the discovery of new and massive introductions of Asiatic algae in Thau Lagoon provides evidence that recent illicit importations of oysters (in the form of spat or living adults) from the Pacific have occurred. The high number of oyster farms (800) and the difficulty in controlling the origin of all the oysters immersed in the lagoon has probably increased the risk of these importations.

In 1994, a bibliographic review suggested a total of 85 more or less probable introductions of marine macrophytes to the Mediterranean Sea (Verlaque, 1994). The main vector of introduction was the Suez Canal with 18 to 33 Lessepsians immigrant macrophytes (Boudouresque and Ribera, 1994; Verlaque, 1994; Ribera and Boudouresque, 1995; 22 to 26 taxa according to Boudouresque, 1999). With 25 new species introductions, Thau Lagoon has, at present, 45 introduced species (23% of total flora). This value is impressive when compared to the value of only 14 introduced marine algae (12% of total flora) found in Venice Lagoon, another important Mediterranean aquaculture site (Sfriso, 1987; Rismondo et al., 1993; Curiel et al., 1996a and b, 1999a and b). Like

Table III. Number of macroalgae taxa listed in different Mediterranean lagoons.

Lagoons	Area (ha)	Rhodophyceae	Fucophyceae	Chlorophyta	Total	References
Diana	550	26	7	13	46	De Casabianca et al., 1972–1973
Urbino	750	19	6	13	38	De Casabianca et al., 1972–1973
Mar Piccolo	2072	61	13	27	101	Cecere et al., 1991
Bages-Sigean	5240	20	4	24	48	Mercier, 1973
Mar Chica	11 400	62	18	31	111	González and Conde, 1991
		62	21	30	113	González-Garcia and Conde-Poyales, 1995
Mar Menor	13 500	29	19	27	75	Pérez-Ruzafa, 1990
Berre	15 500	13	4	23	40	Riouall, 1972
Venice	58 700	72	18	20	110	Pignatti, 1962
		53	11	37	101	Sfriso, 1987, amended
	Channels	59	22	28	109	Curiel et al., 1999b
Salses–Leucate	5400	40	11	18	69	Verlaque, 2000
Thau, before 1961	7000	22	9	17	48	Ben Maiz et al., 1988, amended
1986		84	44	37	165	Gerbal, 1994, amended
1998		99	55	42	196	Present study

for Venice, most introduced species from Thau have a Pacific origin and the most probable vector of introduction is oyster transfer. The present study clearly shows that oyster transfer is the number one vector of macroalgae introduction in the Mediterranean Sea, before the Suez Canal. This is especially true when one considers that the exotic algae identified in Thau Lagoon only represent the 'tip of the iceberg'. Indeed, due to both the size of the lagoon (7000 ha) and the extent of the aquaculture facilities (2500 farming tables, 80 000 metallic pillars and more than 3.5 millions aquaculture ropes), it is highly probable that other unsuspected introduced species remain to be discovered. Moreover, a number of algal introductions have probably passed undetected because they belong to cryptic species or pre-existing Mediterranean species. In the latter case, this leads to the introduction of exotic genotypes, which are difficult to detect. This hypothesis is corroborated by the abnormally high number of macroalgae reported from Thau Lagoon in comparison with other Mediterranean lagoons (*table III*).

Elton (1958) said: "the greatest agency of all that spreads marine animals to new quarters of the world must be the business of oyster culture". The present study shows this remark is also relevant to marine algae. Similar conclusions have also been made in the Atlantic and North Sea (Eno et al., 1997; Maggs and Stegenga, 1999; Reise et al., 1999). The numbers of introduced macroalgae recorded along the European Atlantic coasts and in the North Sea are 28 and 20 taxa, respectively (Ribera and Boudouresque, 1995; Reise et al., 1999). Therefore, Thau Lagoon is quickly becoming not only the most important site of macroalgae introduction in the Mediterranean Sea, but also in Europe. In terms of marine macrophyte introductions, Thau Lagoon is probably one of the world's 'hot spots', as it comes far before other major introduction sites, including New Zealand (21 introduced marine macrophytes), Australia (20) and San Francisco Bay (6) (Ribera and Boudouresque, 1995; Carlton, 1996). This result is worrying as Thau Lagoon is also an important exportation site of living bivalve molluscs (*Crassostrea gigas, Ostrea edulis, Mytilus galloprovincialis, Tapes* spp.) towards other French regions and abroad. In light of the legislation currently in force, the numerous introduced algae present in Thau Lagoon have a high-probability of being diffused throughout Europe and other Mediterranean countries. As the fate of an introduced species is unpredictable at best, it would be well advised to set up an international watch of all the introduced species acclimatized in Thau Lagoon. Moreover, it is probably not very realistic to hope that the accidental introductions linked to aquaculture activities will stop. There exists a set of recommendations that might contribute to limit this phenomenon, however, namely by increasing the awareness of shellfish producers concerning the risks associated with uncontrolled importation (harmful species, diseases), by producing spat in hatcheries and, in the case of living species importation, by following a decontamination processes and/or quarantine as proposed by the International Council for the Exploration of the Sea (Grizel, 1994; Wallentinus, 1994; Ribera and Boudouresque 1995).

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APPENDIX: CHECKLIST OF MACROALGAE OF THE THAU LAGOON. Symbols and abbreviations: +, taxa recorded from Thau and not observed again during the present study; ° taxa previously misidentified or incompletely identified; *, taxa collected for the first time in the lagoon.

RHODOPHYCEAE – Bangiophycideae

\+ *Bangia atropurpurea* (Roth) C. Agardh
Erythrotrichia carnea (Dillwyn) J. Agardh
* *E. investiens* (Zanardini) Bornet
* *E. simplex* Dangeard

RHODOPHYCEAE – Florideophycideae

Acrochatium daviesii (Dillwyn) Nägeli
A. mediterraneum (Levring) Boudouresque
A. reductum (Rosenvinge) Papenfuss
\+ *A. savianum* (Meneghini) Nägeli
\+ *A. secundatum* (Lyngbye) Nägeli
A. virgatulum (Harvey) Batters
\+ *Acrosorium venulosum* (Zanardini) Kylin
° *Agardhiella subulata* (C. Agardh) Kraft *et* M.J. Wynne
\+ *Aglaothamnion tenuissimum* (Bonnemaison) Feldmann-Mazoyer
* *Ahnfeltiopsis flabelliformis* (Harvey) Masuda
Alsidium corallinum C. Agardh
Antithamnion cruciatum (C. Agardh) Nägeli
° *A. pectinatum* (Montagne) Brauner *ex* Athanasiadis *et* Tittley
\+ *Callithamnion corymbosum* (Smith) Lyngbye
\+ *C. tetragonum* (Withering) Gray ?
Centroceras clavulatum (C. Agardh) Montagne
Ceramium ciliatum (J. Ellis) Ducluzeau
\+ *C. codii* (H. Richards) Feldmann-Mazoyer
\+ *C. flaccidum* (Harvey *ex* Kützing) Ardissone
C. secundatum Lyngbye
C. strictum sensu Harvey
* *Champia parvula* (C. Agardh) Harvey
Chondracanthus acicularis (Roth) Fredericq
* *Chondria capillaris* (Hudson) M.J. Wynne
* *C. coerulescens* (J. Agardh) Falkenberg
C. dasyphylla (Woodward) C. Agardh
* *Chondrus giganteus* Yendo f. *flabellatus* Mikami
Chrysymenia wrightii (Harvey) Yamada
Chylocladia verticillata (Lightfoot) Bliding
Corallina elongata Ellis *et* Solander
° *Dasya* sp.
\+ *Peyssonnelia dubyi* Crouan *et* Crouan
° *Phymatolithon lenormandii* (Areschoug) Adey
\+ *Plocamium cartilagineum* (Linnaeus) Dixon
Pneophyllum fragile Kützing
° *Polysiphonia atlantica* Kapraun *et* J. Norris
\+ *P brodiaei* (Dillwyn) Sprengel
P denudata (Dillwyn) Greville *ex* Harvey
P elongata (Hudson) Spengel
\+ *P flocculosa* (C. Agardh) Endl.
\+ *Porphyra leucostica* Thuret
\+ *P yezoensis* Ueda
Sahlingia subintegra (Rosenvinge) Kornmann
Stylonema alsidii (Zanardini) K. Drew
* *Dasysiphonia* (?) sp.
\+ *Gastroclonium clavatum* (Roth) Ardissone
Gelidium crinale (Turner) Gaillon
\+ *G. pusillum* (Stackhouse) Le Jolis
Gracilaria bursa-pastoris (S.G. Gmelin) P. C. Silva
G. dura (C. Agardh) J. Agardh
G. gracilis (Stackhouse) Steentoft *et al.*
Gracilariopsis longissima (S.G. Gmelin) Steentoft *et al.*
° *Grateloupia* cf. *turuturu* Yamada
G. filicina (Lamouroux) C. Agardh var. *filicina*
* *G. filicina* (Lamouroux) C. Agardh var. *luxurians* A. Gepp *et* E.S. Gepp
* *G. lanceolata* (Okamura) Kawaguchi
° *G.* sp.
Griffithsia corallinoides (Linnaeus) Trevisan
Gymnogongrus griffithsiae (Turner) Martius
Halopitys incurva (Hudson) Batters
* *Halymenia floresia* (Clemente) C. Agardh
* *Herposiphonia parca* Setchell
Hypnea musciformis (Wulfen) Lamouroux
* *H valentiae* (Turner) Montagne
\+ *Jania rubens* (Linnaeus) Lamouroux
° *Laurencia microcladia* Kützing
° *L. okamurae* Yamada
* *Lithophyllum yessoense* Foslie
* *Lithothamnion* sp.
Lomentaria clavellosa (Turner) Gaillon
L. hakodatensis Yendo
\+ *Lophosiphonia obscura* (C. Agardh) Falkenberg
Nemalion helminthoides (Velley) Batters
Nitophyllum punctatum (Stackhouse) Greville
Osmundea ramosissima (Oeder) Athanasiadis
\+ *P setigera* Kützing
\+ *P subulata* (Ducluzeau) J. Agardh
* *Prionitis patens* Okamura
Pterocladiella capillacea (S.G. Gmelin) Santelices *et* Hommersand
\+ *P melanoidea* (Schousboe *ex* Bornet) Santelices *et* Hommersand
\+ *Pterosiphonia pennata* (C. Agardh) Sauvageau
* *P* sp.
Pterothamnion plumula (J. Ellis) Nägeli
\+ *Radicilingua reptans* (Kylin) Papenfuss

+ *P. furcellata* (C. Agardh) Harvey
° *P. harveyi* Bailey
* *P. morrowii* Harvey
+ *P. opaca* (C. Agardh) Moris *et* De Notaris
+ *P. paniculata* Montagne
+ *P. sertularioides* (Grateloup) J. Agardh

* "*Acinetospora crinita* (Carmichael *ex* Harvey) Sauvageau" stadium
* *Acrothrix gracilis* Kylin
+ "*Aglaozonia parvula* (Greville) Zanardini" stadium
Chorda filum (Linnaeus) Stackhouse
+ *Cladosiphon cylindricus* (Sauvageau) Kylin
* *C. mediterraneus* Kützing
* *C. zosterae* (J. Agardh) Kylin
* *Cladostephus spongiosus* (Hudson) C. Agardh f. *verticillatus* (Lightfoot) C. Agardh
Colpomenia peregrina (Sauvageau) Hamel
+ *C. sinuosa* (Martens *ex* Roth) Derbès *et* Solier
Cutleria multifida (Smith) Greville
* *Cylindrocarpus microscopicus* Crouan *et* Crouan
Cystoseira barbata (Goodenough *et* Woodward) C. Agardh f. *barbata*
C. barbata f. *aurantia* (Kützing) Giaccone
+ *C. schiffneri* Hamel
Desmarestia viridis O.F. Müller
Dictyota dichotoma (Hudson) Lamouroux
° *D. fasciola* (Roth) Lamouroux
D. linearis (C. Agardh) Greville
+ *Ectocarpus fasciculatus* Harvey
E. siliculosus (Dillwyn) Lyngbye var. *siliculosus*
+ *E. siliculosus* (Dillwyn) Lyngbye var. *dasycarpus* (Kuckuck) Gallardo
+ *E. siliculosus* (Dillwyn) Lyngbye var. *pygmaeus* (Areschoug) Gallardo
+ *Elachista stellaris* Areschoug
+ *Feldmannia* sp.
* *Giraudia sphacelarioides* Derbès *et* Solier
Halothrix lumbricalis (Kützing) Reinke
+ *Hincksia fuscata* (Zanardini) P. C. Silva

Acetabularia acetabulum (Linnaeus) P.C. Silva
Acrochaete inflata (Ercegovic) Gallardo *et al.*
+ *Blastophysa rhizopus* Reinke
* *Bolbocoleon piliferum* Pringsheim
Bryopsis plumosa (Hudson) C. Agardh
Chaetomorpha aerea (Goodenough *ex* Dillwyn) Kützing
C. linum (O. F. Müller) Kützing
° *C. mediterranea* (Kützing) Kützing
+ *Chaetosiphon moniliformis* Huber
Cladophora albida (Nees) Kützing
+ *C. battersii* van den Hoek
+ *C. coelothrix* Kützing
+ *C. dalmatica* Kützing
C. hutchinsiae (Dillwyn) Kützing
+ *C. laetevirens* (Dillwyn) Kützing
C. lehmanniana (Lindenb.) Kützing
° *C. liniformis* Kützing
C. ruchingeri (C. Agardh) Kützing
R. thyzanorizans (Holmes) Papenfuss
+ *Rhodophysema georgii* Batters
* *Rhodothamniella* cf. *codicola* (Børgesen) Bidoux *et* F. Magne
Rytiphloea tinctoria (Clemente) C. Agardh
+ *Seirospora giraudyi* (Kützing) De Toni

FUCOPHYCEAE
H. granulosa (J. E. Smith) P. C. Silva

H. mitchellae (Harvey) P. C. Silva
H. sandriana (Zanardini) P. C. Silva
+ *Kuckuckia spinosa* (Kützing) Kuckuck
+ *Kuetzingiella* sp.
+ *Laminaria japonica* Areschoug
+ *Leathesia difformis* (Linnaeus) Areschoug
* *Myriactula* sp.

Myrionema orbiculare J. Agardh
M. strangulans Greville
* *Padina pavonica* (Linnaeus) Thivy
Petalonia fascia (O. F. Muller) Kuntz
+ *Pilayella littoralis* (Linnaeus) Kjellman

Punctaria latifolia Greville
P. tenuissima (C. Agardh) Greville
Sargassum muticum (Yendo) Fensholt
* *Scytosiphon dotyi* Wynne
S. lomentaria (Lyngbye) Link
* *Sphacelaria cirrosa* (Roth) C. Agardh
S. rigidula Kützing
+ *S. fusca* (Hudson) S.F. Gray ?
Sphaerotrichia divaricata (C. Agardh) Kylin

Stictyosiphon adriaticus Kützing

* *Stilophora rhizodes* (Turner) J. Agardh
* *Streblonema* sp.
° *Stypocaulon scoparium* (Linnaeus) Kützing
Undaria pinnatifida (Harvey) Suringar

CHLOROPHYTA
+ *Codium bursa* (Linnaeus) C. Agardh
C. fragile (Suringar) Hariot
° *Derbesia rhizophora* Yamada
Enteromorpha clathrata (Roth) Greville
E. compressa (Linnaeus) Nees
E. flexuosa (Wulfen *ex* Roth) J. Agardh
E. intestinalis (Linnaeus) Nees
E. prolifera (O. F. Müller) J. Agardh var. *prolifera*
+ *Entocladia leptochaete* (Huber) Burrows
* *E. viridis* Reinke
+ *Eugomontia sacculata* Kornmann
Monostroma obscurum (Kützing) J. Agardh
Phaeophila dendroides (Crouan *et* Crouan) Batters
+ *Rhizoclonium riparium* (Roth) Harvey
* *Sporocladopsis* sp.
+ *Ulothrix* sp.
* *Ulva fasciata* Delile
+ *U lactuca* Linnaeus

	C. sericea (Hudson) Kützing	°	*U. pertusa* Kjellman
+	*C. socialis* Kützing		*U. rigida* C. Agardh
	C. vagabunda (Linnaeus) van den Hoek	+	*Valonia aegagropila* C. Agardh

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