Polyopes lancifolius (Halymeniales, Rhodophyta), a new component of the Japanese marine flora introduced to Europe

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Polyopes lancifolius (Harvey) S. Kawaguchi & H.W. Wang has been recorded for the first time in Europe, during the summer of 2008. A small population was discovered in the Gulf of Morbihan (northeast Atlantic, France). This is the first observation of P. lancifolius outside its native range. Vegetative and reproductive morphological features are compared with previous descriptions. rbcL sequences show no divergence from Japanese populations. Imports of Pacific oysters Crassostrea gigas (Thunberg 1793) are likely to be responsible for its accidental introduction into the Gulf of Morbihan, either directly from northwest Pacific regions or indirectly (secondary dispersal) by transfers from another European oyster farming site. The history of previous algal introductions from Japan suggests that if it becomes successfully established at Morbihan, the species is likely to spread to other European coastal areas.

KEY WORDS: Polyopes lancifolius, marine algae, species introduction, Japan, France, Brittany

INTRODUCTION

Over the past few decades, various macroalgae have been introduced to coasts of the English Channel and Brittany (Gruet 1976; Farnham 1980; Cabioch & Magne 1987; Maggs & Guiry 1987; Floc’h et al. 1996; Maggs & Stegenga 1999; Rueness & Rueness 2000; Rueness 2005; Sjøtun et al. 2008). Once the exotic status and origin of these species had been accurately established, the introductions were invariably traced to the North Pacific (mainly Korea and Japan).

During the summer of 2008, one of us (ALR) found an unknown red algal species in the Gulf of Morbihan (Brittany, France). Despite previous shore surveys (e.g. for the French benthic network REBENT, http://www.rebent.org), it had never been observed before in the area. Its general habit exhibited strong similarities to the genus Grateloupia C. Agardh (1822). However, its characteristically ‘furry’ aspect was distinctly different from native Grateloupia species and North Pacific species of the genus already established in Europe (Farnham & Irvine 1968, 1973; Cabioch et al. 1997; Verlaque et al. 2005). Japan supports a wide range of Grateloupia species, some of which resemble the Morbihan specimen (Yoshida 1998), but a member of another genus, Polyopes lancifolius (Harvey) S. Kawaguchi & H.W. Wang (= Grateloupia okamurae Yamada), is also generally similar in aspect. In this study, we identify the new introduction as P. lancifolius by molecular taxonomy and compare morphologically the European specimens with Japanese P. lancifolius. We also discuss the likely transport vector, provenance and future spread of this new introduction.

MATERIAL AND METHODS

Specimen collection and herbaria

Field observations and sampling in the Gulf of Morbihan were carried out on 31 August and 4 September 2008 and 28 February and 26 March 2009. Samples were hand collected and dried as herbarium specimens. Specimens used in the molecular analyses were preserved in silica gel prior to DNA isolation.

Rehydrated material was studied under the light microscope. Material was sectioned manually with a razor blade. Transverse sections were stained with 1% aqueous Aniline Blue, washed, and then acidified by the addition of a drop of 1 N HCl. Photomicrographs were made using a Nikon Optiphot-2®.

The following samples were studied (see Fig. 1 for details of the collection site): P. lancifolius (Harvey) S. Kawaguchi & H.W. Wang. Gulf of Morbihan, Toulindac (47°36′N, 2°52.5′W), coll. A. Le Roux, H8080, 31 August 2008, tetrasporophyte; H8081–8084, 4 September 2008, tetrasporophytes; H8085–8091, 4 September 2008, female gametophytes; H8092–8094, 28 February 2009; H8095, 26 March 2009.

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The above material has been deposited in the Verlaque Herbarium, HCOM, Marseille, France. Herbarium abbreviation follows Thiers (2009).

Molecular and phylogenetic analyses

Dry samples (e.g. c. 1 cm lengths of the cylindrical extensions covering the main blades) were rehydrated in distilled water. After removing excess water (and potential epiphytes or biofilm) on tissue paper, samples were submerged in liquid nitrogen (using a disposable 1.5 ml Eppendorf tube) and ground with a plastic micropestle. Qiagen DNeasy Plant Minikits (Qiagen Ltd, Crawley, UK) were used for DNA extractions. The \( rbcL \) gene was amplified according to Freshwater & Rueness (1994) and Freshwater et al. (1994). Two overlapping DNA fragments were amplified using the following pairs of primers: F8 (5'-GGTGTAATTCCATACGCTAAAATG-3') and R1150 (5'-GCATTTGTCCGCAGTGAATACC-3') and F753 (5'-GGAAATATGATGAAAG-AGC-3') and rbcSstart (5'-GTTCCTTGTGTTAAATCTCAC-3'). Purification and sequencing of the PCR products were outsourced to Macrogen (Seoul, Korea). The sequences obtained with the second pair of primers include a partial sequence of the rubisco spacer between the \( rbcL \) and the \( rbcS \); this part of the sequences was excluded from the analyses.

\( rbcL \) sequences were obtained for five specimens (H8080, H8081, H8088, H8093 and H8095) and have been deposited in GenBank (Table 1). The newly obtained sequences were aligned with the closest NCBI BLAST hits and a diversity of Halymeniales sequences as well as Chondracanthus acicularis (Roth) Fredericq, a member of the sister order Gigartinales, for use as an outgroup. Sequences were aligned by eye using BioEdit 7.0.4.1 (Hall 1999).

The \( rbcL \) data set, trimmed to a 1254 bp alignment, was analysed with Bayesian inference (BI) and maximum likelihood (ML) using MrBayes v3.1.2 (Ronquist & Huelsenbeck 2003) and PhyML v2.4.4 (Guindon & Gascuel 2003), respectively. BI and ML trees were computed under a general time-reversible model with a proportion of invariable sites and gamma distribution, as determined by the Akaike information criterion in PAUP/Modeltest 3.6 (Posada & Crandall 1998; Swofford 2002).

BI analyses consisted of two parallel runs of four incrementally heated chains and 3 million generations with sampling every 1000 generations. A burn-in sample of 2000 trees was removed before constructing the majority rule consensus tree. For the ML trees, the reliability of each internal branch was evaluated on the basis of 1000 bootstrap replicates.
Table 1. List of species used in rbcL analyses, with GenBank accession numbers. New accession numbers associated with this study are given in bold.

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Collection site</th>
<th>Voucher specimen, collection date or reference</th>
<th>GenBank accession number</th>
</tr>
</thead>
<tbody>
<tr>
<td>Aedes ulviformis F. Schmitz</td>
<td>South Africa</td>
<td>Hommersand &amp; Fredericq (2003)</td>
<td>AF385638</td>
</tr>
<tr>
<td>Carpolpetis phyllophora (J.D. Hooker &amp; Harvey) F. Schmitz</td>
<td>Victoria, Australia</td>
<td>Kawaguchi et al. (2004)</td>
<td>AB116364</td>
</tr>
<tr>
<td>Chondracanthus acicularis (Roth) Fredericq</td>
<td>Roscoff, France</td>
<td>Hommersand et al. (1994)</td>
<td>U02938</td>
</tr>
<tr>
<td>Cryptonemia borealis Kylin</td>
<td>Washington, USA</td>
<td>Gavio &amp; Fredericq (2002)</td>
<td>AF488812</td>
</tr>
<tr>
<td>Grateloupa asiatica Kawaguchi &amp; H.W. Wang</td>
<td>Yamaguchi, Japan</td>
<td>Kawaguchi et al. (2001)</td>
<td>AB055486</td>
</tr>
<tr>
<td>G. doryphora (Montagne) M.A. Howe</td>
<td>Lima, Peru</td>
<td>Figuerola et al. (2007)</td>
<td>AF488817</td>
</tr>
<tr>
<td>G. filicina (J.V. Lamouroux) C. Agardh</td>
<td>Livorno, Italy</td>
<td>Kawaguchi et al. (2001)</td>
<td>AB055472</td>
</tr>
<tr>
<td>G. lanceola (J. Agardh) J. Agardh</td>
<td>Malaga, Spain</td>
<td>Figuerola et al. (2007)</td>
<td>AM422897</td>
</tr>
<tr>
<td>G. lanceolata (Okamura) Kawaguchi</td>
<td>Fukuoka, Japan</td>
<td>Kawaguchi et al. (2001)</td>
<td>AB055477</td>
</tr>
<tr>
<td>G. minima P.L. Crouan &amp; H.M. Crouan</td>
<td>Esposende, Portugal</td>
<td>De Clerck et al. (2005)</td>
<td>AJ868471</td>
</tr>
<tr>
<td>G. subpectinata Holmes</td>
<td>Wakayama, Japan</td>
<td>Faye et al. (2004)</td>
<td>AB114208</td>
</tr>
<tr>
<td>Halymenia floridana J. Agardh</td>
<td>Brazil</td>
<td>Gavio et al. (2005)</td>
<td>AY294361</td>
</tr>
<tr>
<td>Halymenia formosa Harvey ex Kützing</td>
<td>Pupukka, Hawai’i</td>
<td>Figuerola et al. (2007)</td>
<td>AM422899</td>
</tr>
<tr>
<td>Pachymenia carnosa (J. Agardh) J. Agardh</td>
<td>South Africa</td>
<td>Hommersand &amp; Fredericq (2003)</td>
<td>AF385640</td>
</tr>
<tr>
<td>Polyophyes affinis (Harvey) Kawaguchi &amp; H.W. Wang</td>
<td>Liaoning, China</td>
<td>Kawaguchi et al. (2002)</td>
<td>AB084528</td>
</tr>
<tr>
<td>P. hakalaensi (Tilden) I.A. Abbott</td>
<td>Hilo, Hawaii</td>
<td>Kawaguchi et al. (2003)</td>
<td>AB096712</td>
</tr>
<tr>
<td>P. lancifolius (Harvey) Kawaguchi &amp; H.W. Wang</td>
<td>Kochi, Japan</td>
<td>Kawaguchi et al. (2002)</td>
<td>AB084543</td>
</tr>
<tr>
<td>P. lancifolius (Harvey) Kawaguchi &amp; H.W. Wang</td>
<td>Present study: H8080, H8081, H8088, H8093, H8095</td>
<td></td>
<td>GQ303331, GQ303332, GQ303333, GQ303334, GQ303335</td>
</tr>
<tr>
<td>P. polyideoides Okamura</td>
<td>Tainan</td>
<td>Hommersand &amp; Fredericq (2003)</td>
<td>AF385643</td>
</tr>
<tr>
<td>P. tasmanicus (Womersley &amp; J.A. Lewis)</td>
<td>Swansea, Tasmania</td>
<td>Kawaguchi et al. (2002)</td>
<td>AB084545</td>
</tr>
<tr>
<td>P. tosaensis Kawaguchi &amp; Masuda</td>
<td>Kochi, Japan</td>
<td>Kawaguchi et al. (2003)</td>
<td>AB096716</td>
</tr>
</tbody>
</table>

RESULTS
Phylogenetic analyses
The rbcL sequences of the Morbihan specimens (H8080, H8081, H8088, H8093 and H8095) were identical. The data set consisted of 24 sequences belonging to 22 species of Halymeniales and one species of Gigartinales used as outgroup. Consensus trees resulting from the BI and ML analyses were largely congruent. The Halymeniales species present in the data set are clearly discriminated into at least four strongly supported clades: (1) Aedes and Pachymenia; (2) Grateloupa; (3) Carpolpetis, Cryptonemia and Halymenia; and (4) Polyophyes (Fig. 2). Molecular analyses clearly show that the Morbihan specimens belong to the same clade as species of the genus Polyophyes, including specimens determined as Polyophyes constrictus (Turner) J. Agardh (Hommersand & Fredericq 2003), the type species of the genus. Although phylogenetic relationships between Polyophyes species are not clearly resolved, the present specimens strongly cluster with P. lancifolius from Japan with no divergence in the rbcL sequences between the Japanese specimens of P. lancifolius and the French material.

This is an addition to the seaweed flora of Europe, so we here provide nomenclatural information for P. lancifolius, with a description of the European material.

Polyophyes lancifolius (Harvey) S. Kawaguchi & H.W. Wang

BASIONYM: Gigartina lancifolia Harvey (1860, p. 332).

TYPE LOCALITY: Hakodate Bay (Hokkaido Prefecture), Japan.

HOMOTYPIC SYNONYMS: Grateloupa lancifolia (Harvey) Okamura 1899, nom. illeg. (non G. lancifolia Kützing 1867), G. okamurae Yamada 1941 (as ‘okamura’), Sinkoraena okamurae (Yamada) H.-B. Lee et al. 1997, nom. illeg. (the specific epithet lancifolius ought to have been adopted since available under the genus Sinkoraena, S. lancifolia (Harvey) H.-B. Lee et al in H.-B. Lee 1997, comb. inval. [the combination was validated by H.-B. Lee (1998, p. 163)].

HETEROTYPIC SYNONYM: Grateloupa horrida Okamura (1893, p. 99, pl. 5: figs 1, 2), nom. illeg. (non G. horrida Kützing 1849).

Description of Morbihan specimens
Thalli dark purplish-red in colour and cartilaginous in texture, occurring as caespitose clumps of up to 10 axes, attached to the substratum by a small discoid holdfast or a
large flat one (c. 5 mm in diameter) giving rise to many axes; in summer, fertile specimens producing young primary axes, linear-lanceolate, simple or once- to twice-dichotomously branched, cylindrical to compressed, up to 6 cm long and 1–2 mm wide, with short marginal, cylindrical to compressed, proliferations; mature blades linear-lanceolate, 15–40 cm long, 2–4 cm wide and 350–500 μm thick, with proliferations densely clothing all surfaces and margins (Fig. 3); proliferations simple, up to 10–12 mm at the margin, shorter at the surface of blades, to dichotomously branched once, up to 20 mm long, and provided with marginal proliferations; proliferations cylindrical to lanceolate, compressed, with a constricted base (Fig. 4); in late winter, long proliferations, up to 10 cm, arising from old thalli (Fig. 5), young specimens differing from old individuals by their long linear-lanceolate blades, 10–22 cm × 1 cm (dried specimens), without any proliferations (Figs 6, 7); thalli not adhering to paper on drying.

Cortical cells in surface view circular to ovate in outline, 4–5 μm in diameter (Fig. 8); thalli multiaxial and composed of a compact cellular cortex and a filamentous medulla (Figs 9, 10); outer cortex consisting of moniliform, anticlinal filaments, up to eight cells long; outer cortical cells elliptical to cylindrical; inner cortical cells stellate (Fig. 10).

Gametophytes and tetrasporophytes isomorphic; sexual reproductive structures only on proliferations of female gametophytes; carpogonial ampullae with a two-celled carpogonial branch; auxiliary cell ampullae cup-shaped (Aeodes-sensu Chiang 1970) (Fig. 11); mature cystocarps spherical to ovoid, not protruding, 200–300 μm in diameter (Figs 12–14); ostiole more or less protruding (Figs 12, 13); spermatangia not

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**Fig. 2.** Maximum likelihood tree based on rbcL sequence data, showing the phylogenetic relationships of Polyopes spp. and related genera within the order Halymeniales inferred from rbcL gene sequences (1254 bp) (outgroup: Chondracanthus acicularis, order Gigartinales). Numbers above branches indicate ML bootstrap values, and numbers below branches indicate posterior probabilities from the Bayesian phylogenetic analysis. Branch lengths are drawn proportional to the amount of sequence change.

Fig. 8. Surface view of the thallus (H8087, female gametophyte). Bar = 10 µm.
Fig. 9. Transverse section of cortex (H8087). Bar = 20 µm.
Fig. 10. Longitudinal section of cortex (H8087). Bar = 20 µm.
Fig. 11. Transverse section of the cortex showing an auxiliary cell ampulla (H8087). Bar = 20 µm.
Fig. 12. Transverse section of a blade through two mature cystocarps (H8087). Bar = 100 µm.
Fig. 13. Transverse section of a cystocarp through the ostiole (H8087). Bar = 20 µm.
Fig. 14. Transverse section of a cystocarp showing the basal portion with the fusion cell (H8087). Bar = 20 µm.
Fig. 15. Mature cruciately divided tetrasporangium embedded in the outer cortex (H8080). Bar = 20 µm.


Fig. 3. Habit of fertile tetrasporophyte (H8080). Bar = 1 cm.
Fig. 4. Portion of axis showing proliferations (H8080). Bar = 0.5 cm.
Fig. 5. Habit of old specimen with long proliferations (H8092). Bar = 1 cm.
Figs 6, 7. Habit of young specimens with long narrow blades and no surface outgrowths (H8095 and H8093). Bars = 1 cm.
Table 2. Comparison of diagnostic features between *Polyopes lancifolius* and northeast Atlantic *Grateloupia* species.

<table>
<thead>
<tr>
<th>Species</th>
<th>Habit</th>
<th>Branching pattern</th>
<th>Axes</th>
<th>Texture</th>
<th>Marginal proliferations</th>
<th>Surface proliferations</th>
<th>Medullary structure</th>
<th>Location of reproductive structures</th>
<th>Tetrasporangia</th>
<th>Mature auxiliary cell</th>
<th>Mature cystocarp</th>
<th>Native regions</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>P. lancifolius</em></td>
<td>Discoid holdfast and erect axes, to 15–30 cm high</td>
<td>Linear-lanceolate, simple or once to twice dichotomously branched at the base</td>
<td>Cylindrical to foliaceous, 2–4 cm broad, 350–500(–700) μm thick</td>
<td>Cartilaginous</td>
<td>Usually abundant</td>
<td>Usually abundant</td>
<td>Compact</td>
<td>Predominantly over proliferations</td>
<td>10–12(–15) × (20–)25–30 μm</td>
<td>Oblong, conspicuously larger than ampullary cells (200–)200–300(–320) μm in diameter</td>
<td>To 250 μm in diameter</td>
<td>NW Pacific</td>
</tr>
<tr>
<td><em>Grateloupia minima</em> (P.L. &amp; H.M. Crouan)</td>
<td>Horizontally expanded crust with erect axes to 2–4(–10) cm high</td>
<td>Simple to 2–4 times dichotomously branched</td>
<td>Cylindrical to compressed, 0.8–1.0(–1.5) mm broad, (150–)200–300(–700) μm thick</td>
<td>Firm</td>
<td>Common, constructed at the base, simple</td>
<td>Absent</td>
<td>Hollow to very laxly constructed</td>
<td>Over the entire thallus except for the basal portion</td>
<td>18–25 × 40–45 μm</td>
<td>Oval, larger than ampullary cells</td>
<td>To 250 μm in diameter</td>
<td>NE Atlantic</td>
</tr>
<tr>
<td><em>Grateloupia montagnei</em> (P.L. &amp; H.M. Crouan)</td>
<td>Horizontally expanded crust with erect fertile papillae, up to 2 mm high</td>
<td>Unbranched</td>
<td>Terete and ovate/obovate, 500 μm in diameter</td>
<td>Cartilaginous</td>
<td>Absent</td>
<td>Absent</td>
<td>Compact</td>
<td>Toward tips</td>
<td>10–18 × (25–)35–38 μm</td>
<td>Oval, larger than ampullary cells</td>
<td>75–100 μm in diameter</td>
<td>NE Atlantic</td>
</tr>
<tr>
<td><em>Grateloupia subpectinata</em> Holmes</td>
<td>Discoid holdfast and erect axes, to 15–70 cm high</td>
<td>Once or twice pinnate</td>
<td>Compressed to flattened, to 4.5–10 mm broad, up to 1.3 mm thick</td>
<td>Soft and mucilaginous</td>
<td>Numerous, constructed at the base, simple</td>
<td>Occasional to common 5–14 cells thick (2–5 cells)</td>
<td>Loosely to densely constructed</td>
<td>Over the entire thallus except for the basal portion</td>
<td>13–16(–20) × 30–55 (–60) μm</td>
<td>Oval, larger than ampullary cells</td>
<td>120–250(–300) μm in diameter</td>
<td>Pacific</td>
</tr>
<tr>
<td><em>Grateloupia turuturu</em> Yamada</td>
<td>Discoid holdfast and erect axes, up to 100 cm high</td>
<td>Simple or irregularly divided</td>
<td>Linear-lanceolate, foliose, up to 20 cm broad, 225–400(–650) μm thick</td>
<td>Soft and gelatinous</td>
<td>Absent to occasional, foliaceous</td>
<td>Absent to occasional 5–6(–10) cells thick (3–4 cells)</td>
<td>Loosely constructed</td>
<td>Over the entire thallus except for the basal portion</td>
<td>13–16(–20) × 30–55 (–60) μm</td>
<td>Oval, slightly larger than ampullary cells</td>
<td>205–300(–350) μm in diameter</td>
<td>NW Pacific</td>
</tr>
</tbody>
</table>

observed; tetrasporangia elongate-ellipsoid, 23–30 μm long and 10–12 μm wide, decussately cruciately divided, and predominantly scattered over proliferations; tetrasporangia terminal, arising laterally from cortical cells in the fourth to fifth cortical layers from surface, without differentiation of nemathecia (Fig. 15).

Ecology and seasonality

*Polyopes lancifolius* was observed in August and September 2008 as well as in February and March 2009 on the shore at Toulindac. Attached living specimens were found in the intertidal zone, growing on isolated pebbles partly buried in sand and in a neighbouring habitat with pebbles partly embedded in silt, under the *Fucus serratus* Linnaeus belt. Individuals growing on pebbles were found on a stretch of shore around 300 m in length. Drifting fragments were frequently found in a radius of 800 m around the attached population. The presence or absence of the species in the subtidal zone in this locality has yet to be confirmed.

Epiphytic organisms (members of the Ceramiales and animals such as bryozoans, annelids and small ascidians) were found on the oldest parts of the thalli. The small proliferations on the surface of the thallus also tend to trap sediment.

**Fig. 16.** Distribution of *Polyopes lancifolius* S. Kawaguchi & H.W. Wang in the northwest Pacific (compiled from Harvey 1860; Suringar 1873; Noda 1987; Nam *et al.* 1996; Lee *et al.* 1997; Kawaguchi *et al.* 2002; Guiry & Guiry 2009).

**DISCUSSION**

Identity of the introduced *Polyopes* in the Gulf of Morbihan

European specimens from the Gulf of Morbihan agree with the descriptions of *P. lancifolius* from the northwest Pacific Ocean (Suringar 1873, as *Gigartina lancifolia*; Okamura 1908, as *Grateloupia lancifolia*; Noda 1987, as *G. okamura*; Tokuda *et al.* 1994, as *G. okamura*; Lee *et al.* 1997, as *Sinkoraena okamura*), and no differences in the molecular marker considered here were observed between our specimens and Japanese populations (Kawaguchi *et al.* 2002). Consequently, the species discovered in the Gulf of Morbihan is attributed to *P. lancifolius*. The species and the genus are newly introduced to European shores. Table 2 shows a comparison of diagnostic features between *P. lancifolius* and northeast Atlantic species (native or introduced) of the genus *Grateloupia*.

Transport vector, origin and risk of invasion

The presence of *P. lancifolius* in the Gulf of Morbihan is to date the most recent exotic addition to the European macroalgal flora. In France, the Morbihan is one of the leading Atlantic regions of oyster culture, with an annual production of *Crassostrea gigas* (Thunberg 1793) that reached
10,532 t in 2001 (Girard et al. 2005). In the Gulf of Morbihan, the collection site (Toulindac) is located close to large oyster farming areas. In the absence of effective antifouling treatments, oyster shells usually carry propagules of a wide range of seaweed species (Mineur et al. 2007), and it is now widely recognised that oyster import and transfer between farming areas is one of the most important vectors for seaweed introductions (e.g. Maggs & Stegenga 1999; Reise et al. 1999; Wallentinus 2002; Ribera-Siguan 2003; Verlaque et al. 2007). Several species of Halymeniales from northeast Asia have been introduced into Europe via this vector (Verlaque et al. 2005). The discovery of P. lancifolius in the Gulf of Morbihan in 2008 is consistent with a recent accidental introduction, directly from Asia or indirectly via other European shellfish farming sites, by oyster transfers.

In the northwest Pacific, P. lancifolius has a wide latitudinal distribution, from Hokkaido to Taiwan (Guiry & Guiry 2009) (Fig. 16). In Japan and Korea, it grows attached to rocks adjacent to sandy substrata at and just below low-tide level in areas of moderate wave energy (Okamura 1908; Noda 1987; Tokuda 1994; Lee et al. 1997). Therefore, P. lancifolius seems to be eurythermal. Consequently, if successfully established in the Gulf of Morbihan, P. lancifolius is likely to spread to other European areas.

By comparison, two other Halymeniales species, Grateloupia turuturu Yamada and Grateloupia subpectinata Holmes, both originating from Japan (Verlaque et al. 2005), have extended their distribution after their initial introduction into the Channel area to most European Atlantic coasts (G. turuturu from Portugal to the Netherlands; G. subpectinata from Spain to northern France) in just a few decades (Farnham & Irvine 1968; Stegenga 1997; Bárbara et al. 2002; Araújo et al. 2003). Moreover, both species have been introduced into temperate lagoons in the western Mediterranean Sea (e.g. lagoon of Venice, Thau Lagoon) (Gargiulo et al. 1992; Verlaque et al. 2005, respectively). As most secondary introductions of these two species are likely to have followed pathways of oyster transport in Europe (see Mineur et al. 2007), it is reasonable to think that if P. lancifolius successfully establishes self-sustaining populations, it would extend its distribution in a similar way. Prevention or at least mitigation should involve treatment of oyster shells (such as hot-water or brine treatment; see Mineur et al. 2007) before any transfer from the area of original introduction. As P. lancifolius is supposedly restricted to a small area, eradication could be considered at this stage (Simberloff 2009).

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