

# A concise review of the red macroalgae *Chondracanthus teedei* (Mertens ex Roth) Kützing and *Chondracanthus teedei* var. *lusitanicus* (J.E. De Mesquita Rodrigues) Bárbara & Cremades

Leonel Pereira<sup>1</sup> · Paulo Silva<sup>2</sup>

Received: 27 May 2020 / Revised and accepted: 19 August 2020 / Published online: 11 September 2020  
© Springer Nature B.V. 2020

## Abstract

*Chondracanthus teedei* is a small red alga, whose fronds are cartilaginous membranous, dark crimson to red black, turning yellow-green due to decay. The main frond axes, due to their broad branches, reach 1 cm in the oldest portions in the case of the *lusitanicus* variety. Originally described in Portugal, *C. teedei* is found widespread in the Atlantic, Mediterranean, Black Sea and Indian Ocean. This cosmopolitan species is typical of lower intertidal and shallow subtidal habitats, of sciophilous habitats in semi-exposed or protected areas, and tolerates the presence of mud and sand. Its composition may vary according to the geographical location of origin, and the time of year when it is collected. It has relatively high levels of protein (14.66%), ash (28.68%), fibres (2.21%), lipids (1.82%) and moisture (86.73%), making this alga able to be considered for its implementation as food. In addition, *C. teedei* var. *lusitanicus* produces hybrid carrageenans belonging to the lambda family (xi-theta hybrid carrageenans), in the case of tetrasporophytes, and kappa-iota-mu-nu hybrid carrageenans, in the case of female gametophytes and non-fruited thalli. The carrageenans extracted from this species have antifungal and antiviral activities, and the dry ground biomass of *C. teedei* has potential to be used in cosmetic formulations.

**Keywords** *Chondracanthus teedei* · Variety *lusitanicus* · Taxonomy · Distribution · Cultivation · Biotechnological potential · Gastronomy · Utilisation

## Identity

## Nomenclature

## Valid scientific names

Hommersand et al. (1993) transferred this species to the genus *Chondracanthus*; *Chondracanthus teedei* (Mertens ex Roth) Kützing (basonym: *Ceramium teedei* Mertens ex Roth; synonym: *Gigartina teedei* (Mertens ex Roth)

J.V. Lamouroux). *Chondracanthus teedei* was originally described from Portugal (Guiry 1984), is widespread in the northeastern Atlantic, Mediterranean and the Black Sea (Ardré 1970, Orfandis 1993). It has also been reported from Japan (Mikami 1965), the Indian Ocean (Silva et al. 1996) and Brazil (Ugadam 1975). In France, Spain and Portugal, the species is frequent in the lower intertidal zone on sheltered habitats. Rodrigues (1958) described it as a new variety, *C. teedei* var. *lusitanicus* (Rodrigues) Bárbara and Cremades (basonym: *Gigartina teedei* (Roth) J.V. Lamouroux var. *lusitanica* Rodrigues). Ardré (1970) and Bárbara and Cremades (1996) reported this variety in several Portuguese localities and the North West coast of Spain (Ría de A Coruña), respectively (Pereira and Mesquita 2004, Gaspar et al. 2019).

Nomenclatural synonyms (after Guiry and Guiry 2020)

Homotypic synonyms of *Chondracanthus teedei*:

*Ceramium teedei* Mertens ex Roth 1806

*Gigartina teedei* (Mertens ex Roth) J.V. Lamouroux 1813

*Sphaerococcus teedei* (Mertens ex Roth) C. Agardh 1817

*Fucus teedii* (Mertens ex Roth) Turner 1819

✉ Leonel Pereira  
leonel.pereira@uc.pt

Paulo Silva  
paulo.s.14@gmail.com

<sup>1</sup> Marine and Environmental Sciences Centre (MARE), Department of Life Sciences, University of Coimbra, 3000-456 Coimbra, Portugal

<sup>2</sup> UCIBIO-REQUIMTE, Departamento de Química, Faculdade de Ciências e Tecnologia, Universidade NOVA de Lisboa, 2829-516 Caparica, Portugal

*Chondroclonium teedii* (Mertens ex Roth) Kützing 1845

*Mammillaria teedei* (Mertens ex Roth) Kuntze 1891

Homotypic synonym of *Chondracanthus teedei* var. *lusitanicus*:

*Gigartina teedei* var. *lusitanica* J.E. De Mesquita Rodrigues 1958

## Origin of species name

*Chondracanthus* comes from the Greek words *chondrus* (cartilage) and *akanthos* (thorn, alluding to its spiny appearance); and *teedei* derives from the name of its collector, the British Tedde.

## Vernacular names

Japan: Cata-nori (Smith 1904), Shikin-nori (Chapman and Chapman 1980).

Sicily: Måuru (Pérez-Lloréns et al. 2018).

Portugal: Musgos (Pereira and Correia 2015, Pereira 2016).

## Taxonomy

### Affinities and diagnosis

*Chondracanthus teedei* belongs to the family Gigartinaceae of the order Gigartinales, red algae (class Florideophyceae, phylum Rhodophyta). The genus *Chondracanthus* belongs to a well-defined group within Gigartinaceae, which have cystocarps in which gonimoblasts tend to penetrate the surrounding envelope, as in the genera *Rhodoglossum* and *Gigartina* (Hommersand et al. 1999).

Thalli of *Chondracanthus* are composed of one or more erect axes from a discoid or crustose holdfast, the erect axes initially cylindrical and either remaining cylindrical or becoming compressed or flattened; axes repeatedly pinnately branched or foliaceous and either simple or basally or marginally proliferous, often bearing numerous vegetative or reproductive branchlets, or sparsely to thickly covered by vegetative or reproductive papillae (Hommersand et al. 1993).

Currently, there are 28 species names in AlgaeBase, as well as 1 infraspecific name. Of the species names, 23 have been flagged as accepted taxonomically based on the listed literature under the species name (Guiry and Guiry 2020).

### Infraspecific name

The specimens present in Buarcos Bay (Figueira da Foz, Portugal) show very evident differences in relation to the specimens present in the English Channel (French coastline), in Biscay (Spain), or in the Mediterranean.

Due to the existence of a set of distinctive characteristics, in relation to *C. teedei*, the specimens present in Buarcos Bay were included in a distinct taxon (Fig. 1a–i), called *Chondracanthus teedei* var. *lusitanicus* (Rodrigues 1957, 1958, Bárbara and Cremades 1996).

## Morphology and anatomy

### External morphology

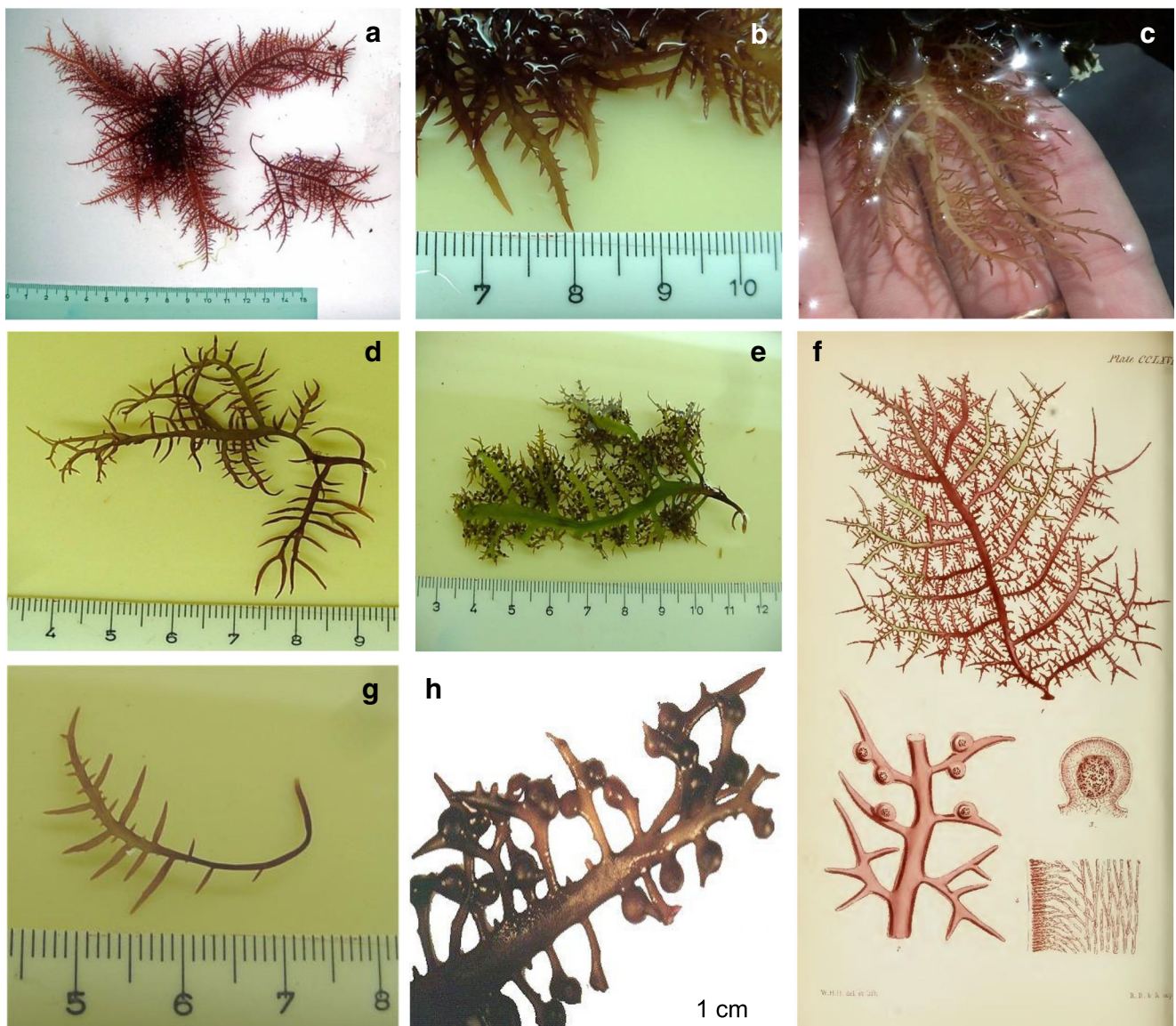
*Chondracanthus teedei* (Fig. 1a–h) is very easily identifiable, developing fronds which can reach 15 cm in height, in tufts from a small basilar disc that connects them to the substrate; the main axes, attenuated for both ends, end in a point and branches branch out once, twice or three times; the terminal ramuli are small, with prickly appearance (spine-like) and horizontally patent. Cystocarps (Fig. 1 e, f and h), few in number, usually solitary, sessile and globose, are produced in the pinnules or in the enlarged part of the margins of the branches, and the tetrasporangial sori also have a marginal location (Pereira 2004).

*Chondracanthus teedei* present flattened main axes, regularly pinnately branched (Guiry 1984; Zinoun 1993; Zinoun et al. 1993). The fronds, cartilaginous membranous, have a purplish-violet colour that darkens by desiccation, becoming greenish-yellow through decay (Fig. 1 h and i) (Rodrigues 1957; Gayral 1982; Guiry and Maggs 1985).

In *C. teedei* var. *lusitanicus* (Fig. 2a–f), the main axes of the fronds, as well as their branches, are broader (reaching 1 cm in the older portions) and, therefore, the plants look more robust, often reaching 20 cm in height; the branching is more dense and luxuriant and the pinnula develops not only on the margins of the branches but also on their surface; the pinnula is patent, simple—rarely bifid—and very sharp, giving fronds a prickly appearance; cystocarps, globose and sessile are very numerous (Rodrigues 1957, 1958; Pereira 2004). This variety is confused sometimes with the red alga *Calliblepharis jubata* (Pereira 2010; Pereira 2020b).

### Anatomy and cytology

Thallus of multiaxial construction has two types of filaments: undetermined and determined growth. Filaments are determined in the medullary region, with elongated, hyaline cells, with a starry outline, with 7 to 41 µm in diameter, and anastomosed. The occasional presence of medullary cells of circular contour, with 17 to 34.5 µm in diameter and walls with thickening between 2 and 6 µm (Fig. 3 a and e). Filaments of determined growth are located laterally, forming the cortex; on the inside with hyaline cells of irregular contour, turning to elliptical and rounded, towards the edges; cells in the inner



**Fig. 1** *Chondracanthus teedei*: non-fructified thalli collected in Roscoff, France (**a**, **b**); tetrasporic thalli collected in Baleal, Portugal (**c**, **d**); female thallus collected in Baleal, Portugal (**e**); illustration from William H.

Harvey (Plate CLXXXI, *Phycologia Britannica*, 1846–1951) (**f**); non-fructified thallus collected in Baleal, Portugal (**g**), and cystocarps detail (**h**)

layers of the cortex 4 to 10.5  $\mu\text{m}$  high by 3.5 to 9  $\mu\text{m}$  wide; outermost cells 4 to 12  $\mu\text{m}$  high by 2.5 to 5  $\mu\text{m}$  wide. Cortex near the base and in the median region of the thallus with 6 to 7 ( $\pm 2$ ) layers of cells; apical region with 5 to 6 layers of cells (Fig. 3b–d) (Rodrigues 1957; Guiry 1984; Braga 1985; Pereira et al. 2007).

Ultrastructural features during carposporogenesis (Fig. 3f), in addition to typical features of the Rhodophyta (chloroplasts with peripheral thylakoid and non-associated internal thylakoids, extra-plastidial floridean starch grains, etc.), show well-developed Golgi apparatus which are very active with an abundance of dictyosomes and cored vesicles. As already mentioned, this

would appear to play a key role in the genesis of fibrillar vacuoles and subsequent cell wall formation (Fig. 3g) (Pereira 2004).

## Genetic data

### Molecular analysis

Recently, the specimens recognised as *C. teedei* from Bermuda has been assigned to a new species, *Chondracanthus saundersii*, using the ribulose-1,5-bisphosphate carboxylase/oxygenase (RuBisCo) gene (RbcL) marker (Schneider and Lane 2005).



**Fig. 2** *Chondracanthus teedei* var. *lusitanicus*: fertile female gametophytes, with cystocarps, collected in Buarcos, Portugal (a, b); tetrasporic thalli (c, d); non-fertile thalli (e, f)

Yang et al. (2015), using molecular data (cytochrome *c* oxidase I gene—COI and RbcL), reported that many samples classified in North Pacific as *C. teedei* are, in fact, specimens of *Chondracanthus chamissoi*, previously known as an endemic species in Chile. In their study,

specimens from Spain and Brazil were grouped as *C. teedei*, refuting for now the presence of *C. chamissoi* in these two countries.

According to Rocha-Jorge et al. (2018), sequences of *rbcL* were obtained for four samples of *C. teedei* and comparing the

samples of *C. teedei* sequenced from Brazil with the ones available from France and Spain, there was an intraspecific variation of 14 base pairs (1%).

## Distribution, ecology and metabolism

### Distribution

Originally described from Portugal, *C. teedei*, is widespread in the northeastern Atlantic, Mediterranean and the Black Sea (Ardre 1970; Guiry 1984; Orfandis 1993). It has also been reported from Japan (Mikami 1965), the Indian Ocean (Silva et al. 1996), Venezuela (Taylor 1942, 1960) and Brazil (Joly 1957, 1965, Ugadim 1975). According to Yang et al. (2015), *C. teedei* is found in the Atlantic and not in the western Pacific region, being absent in Korea and Japan (Fig. 4).

In the eastern Atlantic the species is found from southwest England to south South Africa, and in the Azores and Cabo Verde Islands (Dizerbo 1974; Dixon and Irvine 1977). In the British Isles, it is confined to south Devon and Cornwall (Parke 1952; Dixon and Irvine 1977).

Ardre (1970), Bárbara and Cremades (1996), Pereira and Mesquita (2004), Araújo et al. (2009) and Pereira (2020a, b) reported the variety *lusitanicus* in several Portuguese localities (Viana do Castelo, Castelo do Neiva, A-Ver-o-Mar, Aguçadoura, Mindelo, Lavadores, Aguda, Buarcos Bay, Peniche) and the northwest coast of Spain (Galicia - Ría de A Coruña; Lugo, San Ciprián; Pontevedra, Ría de Vigo) (Fig. 4).

### Vertical distribution

This comopolitan species is typical of the lower intertidal and shallow subtidal habitats of sciophilous habitats in semi-exposed or protected areas, supporting the presence of mud and sand (Pérez-Lloréns et al. 2016). In France, Spain and Portugal, the species is frequent in the lower intertidal zone on sheltered habitats (Pereira and Mesquita 2004). In Brazil, plants growing in intertidal zone, on rocks, are protected from the waves (Rocha-Jorge et al. 2018).

### Coverage, biomass and plant size

Despite not being a harvested seaweed, it is surprising that, among the carrageenophytes studied by Pereira and Mesquita (2004) and Pereira (2013), *C. teedei* var. *lusitanicus* is the one which had the highest values of average length with  $7.7 \pm 0.4$  cm ( $n = 100$ ) in summer and a minimum of  $2.9 \pm 0.2$  cm ( $n = 100$ ) in winter, and coverage (Fig. 5). The biomass (dry weight) values ranged between  $110 \pm 1.9$  g m<sup>-2</sup> ( $n = 8$ ) in summer and  $594 \pm 10.5$  g m<sup>-2</sup> ( $n = 8$ ) in late spring. Biomass and length showed low values in autumn and winter, a small

increase occurred in early spring, and the highest values were recorded in early summer (Pereira et al. 2013).

## Accompanying species

### Flora

According to Pereira (1994, 2004), *C. teedei* var. *lusitanicus* constitutes one of the dominant algal species in Buarcos Bay (Portugal), and in the studied area, there are several species of red (Rhodophyta) and green (Chlorophyta) algae, some of them maintaining a neighbourhood relationship (species that live nearby) and others an epiphytic (growing on another plant but not parasitic) relationship. Three species of Rhodophyta always appear in the samples of *C. teedei* var. *lusitanicus*: *Osmundea pinnatifida*, *Corallina officinalis* and *Ceramium* sp. With the first two species, *C. teedei* var. *lusitanicus* maintained a neighbourhood relationship, while with the latter, a hostess relationship. The chlorophyte *Ulva rigida* was always present in the samples, as a neighbour and in some cases as an epiphyte.

In addition to these species, other species were also associated, as mentioned below: *Ulva clathrata*, *U. compressa*, *Cladophora* spp. (Chlorophyta), *Chondria coeruleascens*, *Chondria dasyphylla*, *Chondrus crispus*, *Gigartina pistillata*, *Gracilaria multipartita*, *Gymnogongrus crenulatus* and *Polysiphonia* spp. (Rhodophyta) (Pereira 2004).

### Epi-endophytes

Tsekos (1982) described the fine structure of bacteria-induced galls on the field material of *C. teedei* (as *Gigartina teedii*).

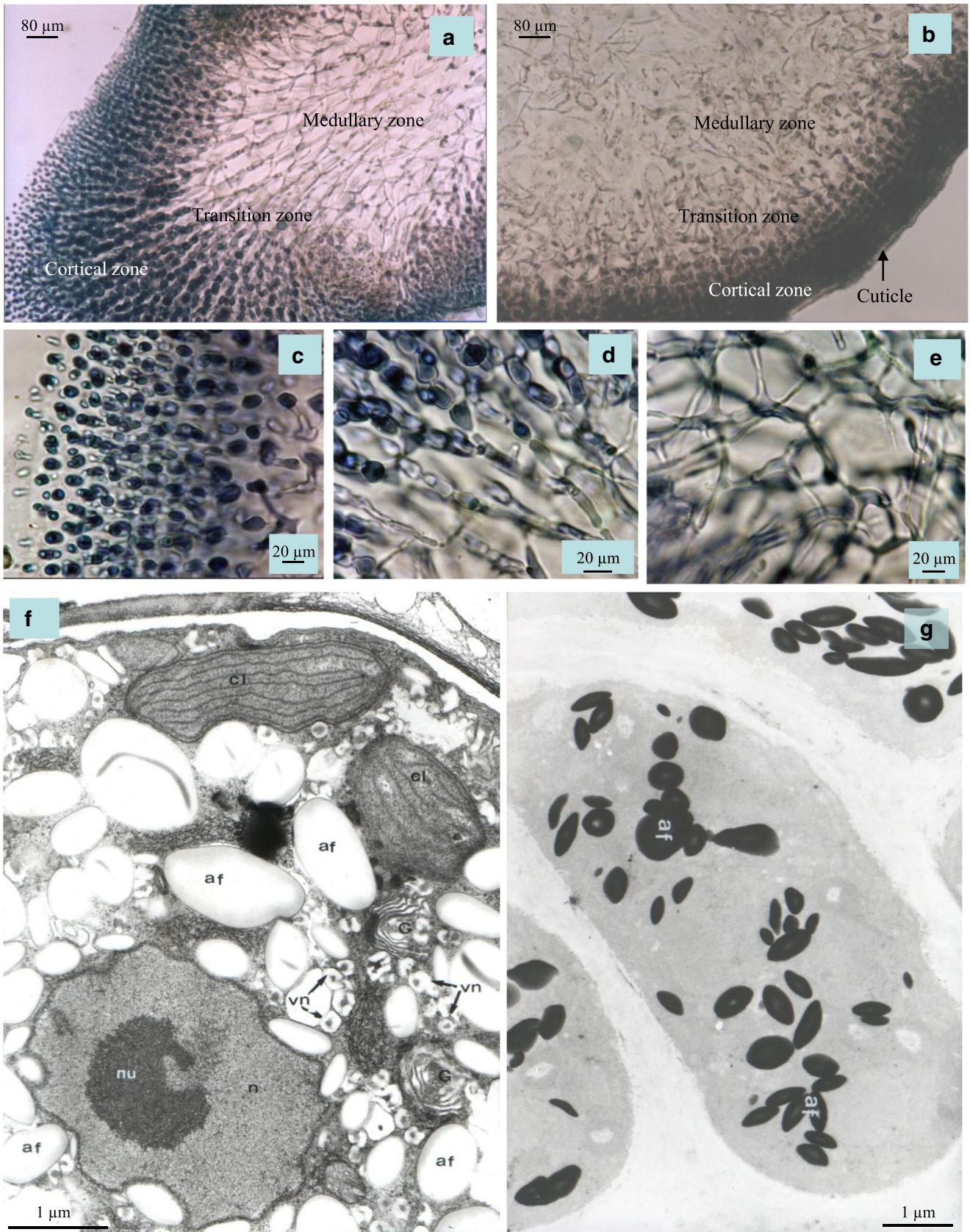
Guimarães (2006) made the first reference to *Colaconema infestans* (Colaconemataceae, Rhodophyta) in Brazil from Espírito Santo State, which was found as endophytic in *C. teedei*.

## Life history

### Life cycle

*Chondracanthus teedei* and *C. teedei* var. *lusitanicus* have an isomorphic triphasic life cycle (see Fig. 6) (Guiry 1984; Braga 1985, 1990; Guiry et al. 1987; Pereira 2012, 2013; Contador et al. 2020).

This cycle is the typical one for most Florideophyceae, in which the diploid zygote develops directly in situ, parasitizing the female gametophyte, giving rise to a second phase, with reduced vegetative structure, the carposporophyte, a carpospore producer. Carpospores, in turn, give rise to a third phase of independent life, the tetrasporophyte, whose vegetative



◀ **Fig. 3** *Chondracanthus teedei* var. *lusitanicus*: optical microscope observations of thallus cross-sections (**a**, and **b**); details of cortex (**c**), transition zone (**d**) and medulla (**e**); staining with lactophenol blue (**a–e**). Cytology (**f**): electron microscope observations of floridean starch (af), chloroplasts (cl), Golgi (G), nucleus (n), nucleolus (nu) and cored vesicles (vn); note the abundance of florid starch grains that give a positive reaction to the “Thiery test” (G) (after Pereira 2004)

apparatus is in most cases morphologically identical to that of gametophytes, although diploid. The tetrasporophyte has tetrasporangial sori that release, after meiosis, tetraspores that will originate new gametophytes. This three-phase cycle then comprises the succession of a haploid generation (gametophyte) and two diploid generations (carposporophyte and tetrasporophyte) (Hommersand et al. 1999).

According to Braga (1980, 1990), there always seems to be a higher proportion of gametophytes than tetrasporophytes. However, a population of *C. teedei* var. *lusitanicus* from Buarcos Bay (Figueira da Foz, Portugal) has shown to have a larger percentage of fertile tetrasporophytes than fertile female gametophytes (Pereira and Mesquita 2004; Pereira 2004). In Buarcos Bay population, the non-fructified thalli were dominant in all samples; the percentage varied from 43% (early autumn) to 82.5% (early summer). The female

gametophytes were present in all samples, varying the proportion of 3% (late autumn) to 29% (late summer). The tetrasporophytes were also present in all samples, with a maximum of 32.5% in autumn and a minimum of 4% in summer. As compared to fructified thalli, namely, the female gametophytes bearing cystocarps ( $9.6 \pm 1.7\%$ ,  $n = 17$ ), the tetrasporophytes are, generally, more abundant ( $21 \pm 1.7\%$ ,  $n = 17$ ). The average percentage of non-fertile thalli was  $69.4 \pm 2.2\%$  ( $n = 17$ ) (Pereira 2013).

## Reproductive structures and reproduction

*Chondracanthus teedei* var. *lusitanicus* tetrasporophytes (Fig. 7) exhibit tetrasporangial sori with the appearance of dark red spots, prominent in the thallus, on the main axis and lateral branches (Fig. 7a). Sori, with cruciately divided tetrasporangia (Fig. 7c and d), are released by rupturing of the cortex and old sori, after tetraspore liberation, are filled with medullary filaments (Guiry 1984; Pereira 2004; Pereira et al. 2007).

In Fig. 7 (panels b and c) (semi-thin sections at the level of tetrasporangial sorus), the regions most intensely stained by



**Fig. 4** World distribution of *Chondracanthus teedei* (red dots are records of occurrence) and *Chondracanthus teedei* var. *lusitanicus* (blue dots are records of occurrence). Adapted from the Ocean Biogeographic Information System (OBIS 2020), incorporating all records included in

OBIS and complemented with geographical distribution data of works cited in AlgaeBase (Guiry and Guiry 2020), and validated for these species

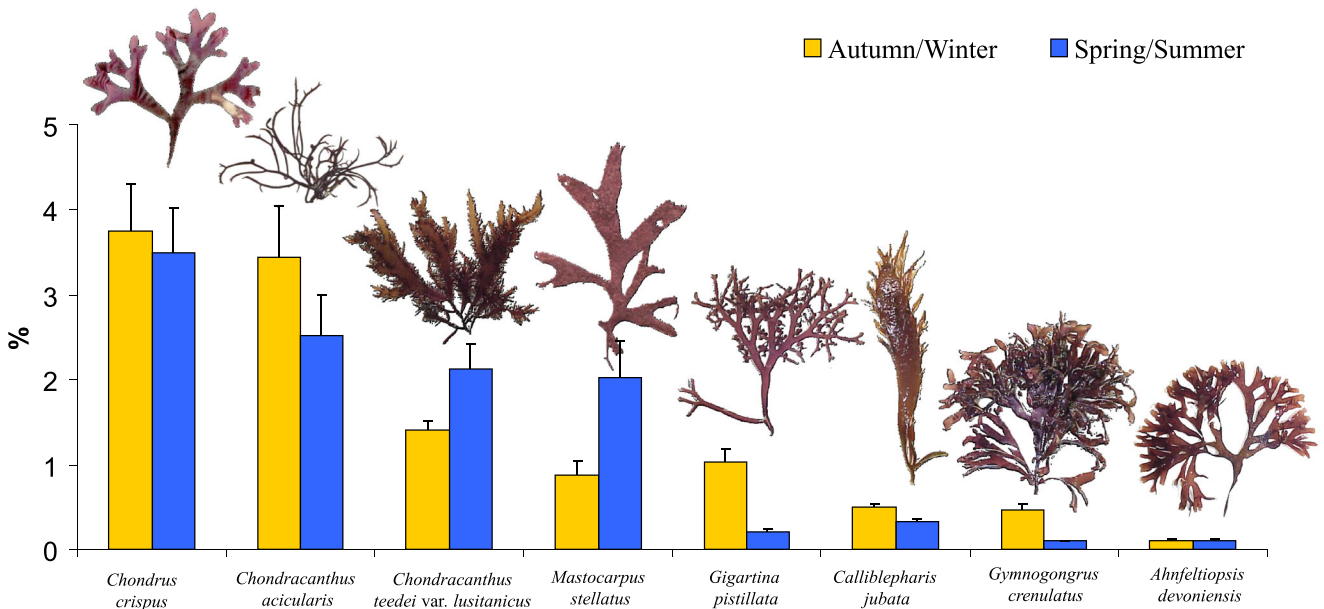


Fig. 5 Carrageenophytes coverage in Buarcos Bay, in the Autumn/Winter and Spring/Summer periods (mean ± standard error, n = 46)

toluidine blue were located in the intercellular spaces, especially in the cortical zone. The ultrastructure of tetrasporogenesis (Fig. 7 e and h) in *C. teedei var. lusitanicus* can be summarised as follows: the nucleus with a well-developed nucleolus, contains little condensed chromatin; chloroplasts, in addition to their typical non-association with internal and peripheral thylakoids, show several areas of DNA and electron-dense inclusions; in addition to floridean starch

grains, which represent the most abundant cellular component, a large part of the remaining cytoplasm is occupied by very active dictyosomes producing numerous vesicles with a dense core (cored vesicles). As in tetrasporogenesis in *Chondria capillaris* (formerly *Chondria tenuissima*) (Tsekos et al. 1985; Pereira et al. 2007), the ultrastructure of *C. teedei var. lusitanicus* during tetrasporogenesis shows straight, large

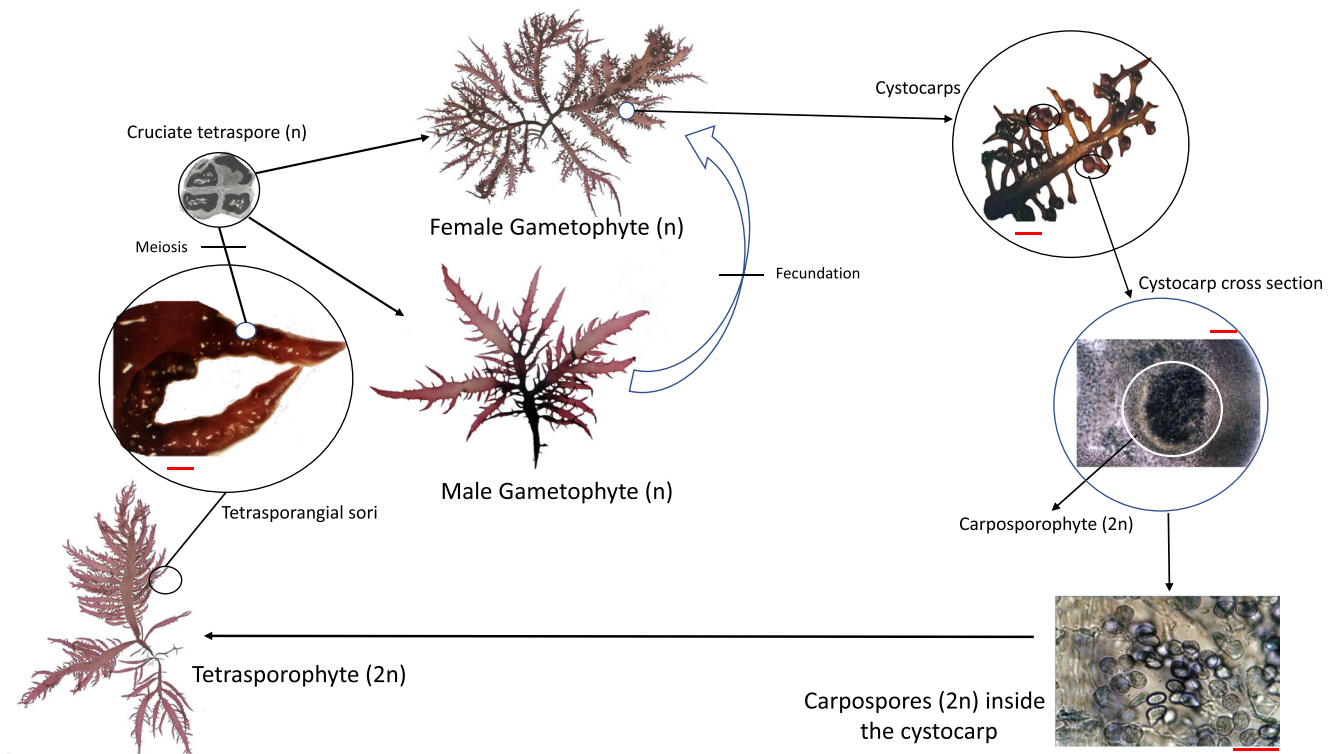


Fig. 6 Triphasic, isomorphic, life cycle of *Chondracanthus teedei var. lusitanicus* (scale bars in red = 100 μm)



dictyosomes which produce cored vesicles, an abundance of starch grains and form fully developed chloroplasts (Fig. 7h).

*Chondracanthus teedei* var. *lusitanicus* female gametophytes (Fig. 8a–f) present prominent spherical cystocarps (Fig. 8a), producing carpospores (Fig. 8b–d). The thallus transverse section shows a multiaxial structure (see Fig. 3a–e), like that of tetrasporophyte one. In general, carposporangial ultrastructure (female gametophyte) is not significantly different from that observed during tetrasporogenesis (tetrasporophyte), before cell division (Fig. 8e and f) and similar to that described in *C. teedei* by Tsekos and Schnepf (1983).

By analysing the ultrastructure of the cells involved in carposporogenesis, we can see that in the auxiliary cell and gonimoblast, it is possible to observe plastids with a homogeneous stroma a central region with gonophores and a plastidial envelope with a peripheral thylakoid or, more rarely, without an internal lamellar structure. After the appearance of the first internal membrane system, the formation of thylakoids begins, structures that are in contact with or are derived from the peripheral thylakoid (Fig. 8f) (Tsekos 1981).

## Chemical composition

### Average composition

#### Organic constituents

The average composition of *C. teedei* is important because, according to Schwochow and Zanboni (2007), macroalgal composition may vary with the time of year when it is collected. In a comparison carried out with native Brazilian macroalgae for implementation in food, *C. teedei* had the following levels of protein (14.66%), ash (28.68%), fibres (2.21%), lipids (1.82%) and humidity (86.73%) (Bastos et al. 2012). Despite the variability, it is verified that the biomass in this study yields acceptable values that can be implemented in food since its protein content is higher than *K. alvarezii* and its fat content is lower than *C. teedei* while the fibre content is higher (Menezes et al. 2015).

*Chondracanthus teedei* var. *lusitanicus* volatile compounds were identified by Moreira-Leite (2017) with mass spectrometry analysis (GC-MS), and 21 substances were confirmed in fresh *C. teedei* var. *lusitanicus* (Fig. 9). According to the author, “Musgos”, *C. teedei* var. *lusitanicus* vernacular name, have a mild mushroom and earthy aroma. The three profiles analysed were dominated by trans-2-nonenal, 2,4 decadienal and  $\beta$ -ionone; however, the marked presence of hexanal (capric aldehyde), representing 71.87% of the highest peak area and 16.50% of the total relative area of the chromatogram, should be highlighted. This aldehyde has a sweet, citrus and floral aroma, and, together with the cucumber

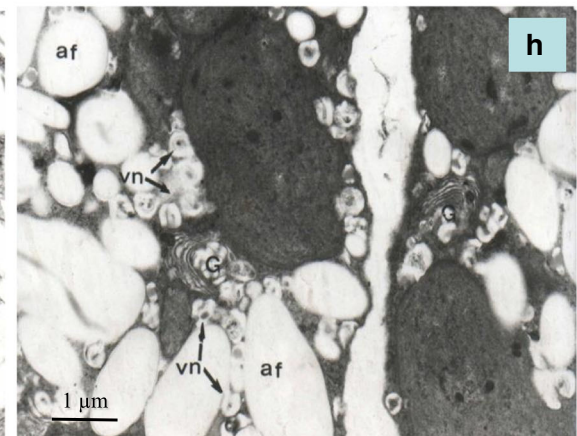
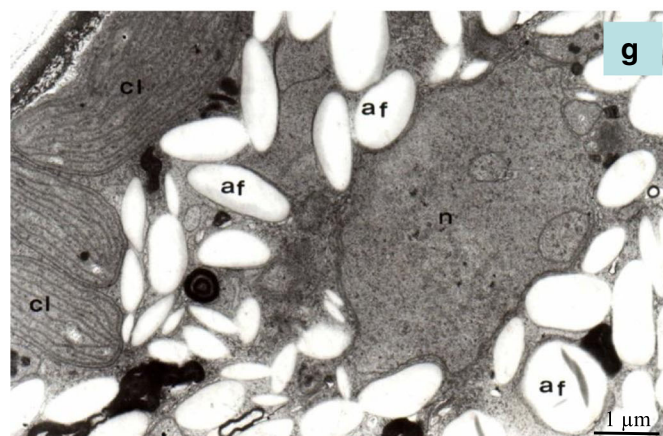
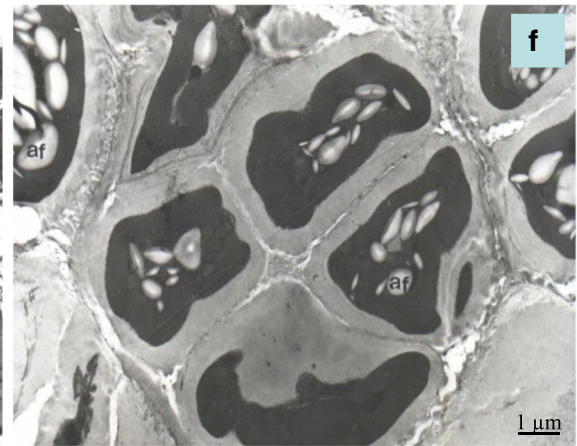
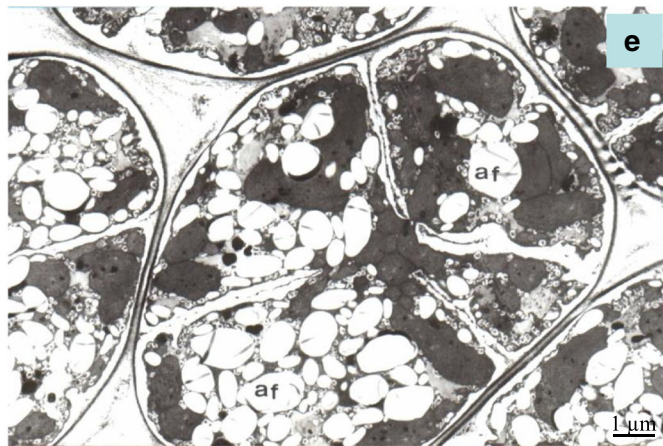
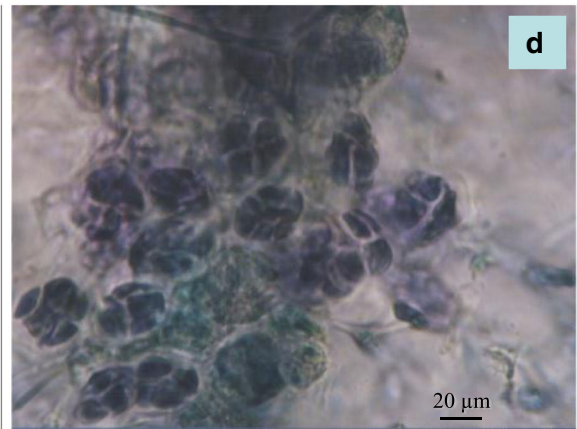
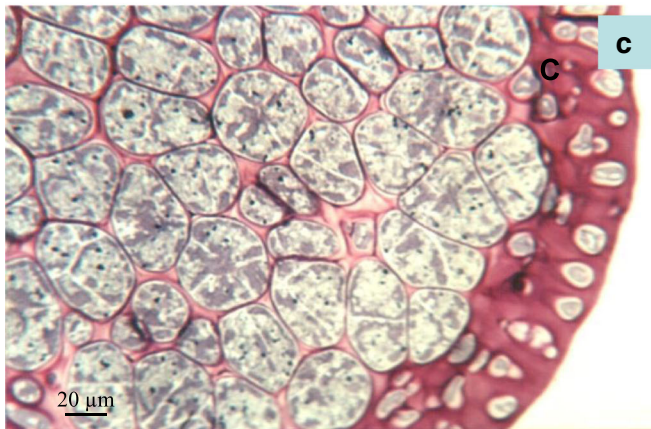
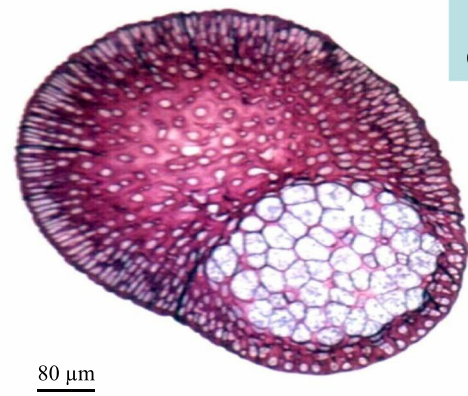
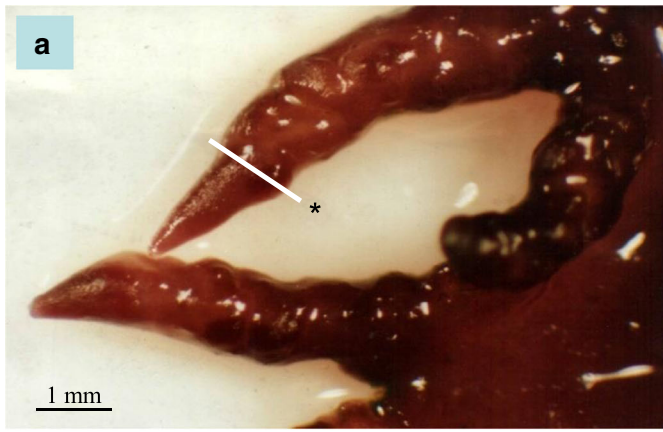
aldehyde, it adds a certain freshness to the seaweed. “Musgos” seem suitable for preparing salads with seaweed (see Fig. 10), due to their pleasant texture and neutral flavour. However, the presence of bromoform was detected in the sample analysed, which suggests some caution in the consumption of *C. teedei* var. *lusitanicus*.

## Source of hydrocolloids and sulphated polysaccharides

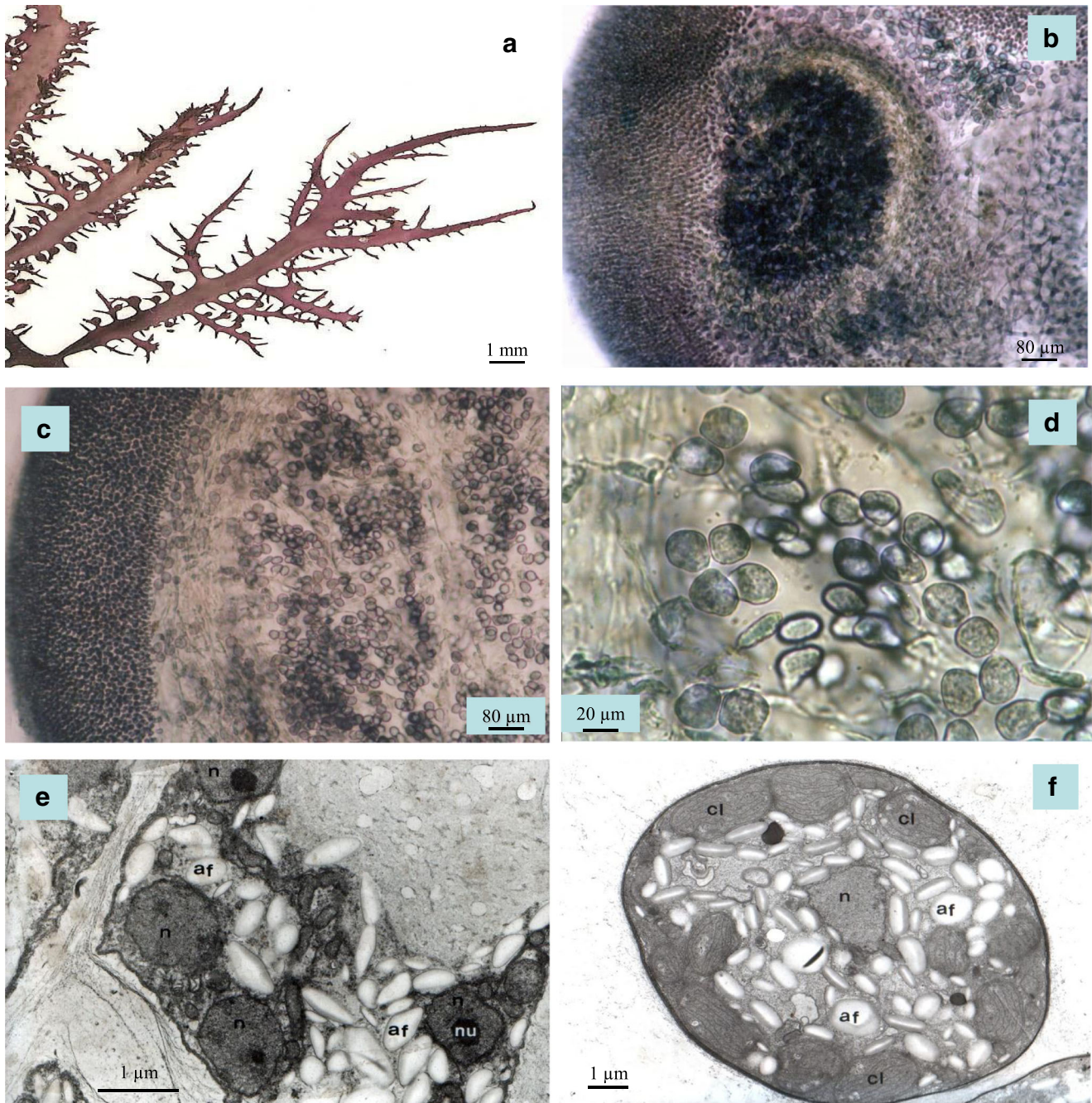
### Carrageenans

Carrageenan is an industrially important hydrocolloid produced by several species of red algae (Gigartinales, Rhodophyta), generically called “carrageenans” (van de Velde and de Ruiter 2002; Pereira and van de Velde 2011; Pereira 2018a). Carrageenans are a family of linear, sulphated and water-soluble galactans. composed of alternating  $\beta$ -D-galactopyranose (G units) and 4  $\alpha$ -D-galactopyranose bonds (D units) or 3,6-anhydrous-4- $\alpha$ -D-galactopyranose bond (DA units), forming the disaccharide unit of repeat carrageenan. The most common types of carrageenans are traditionally identified by a Greek prefix and, more recently, by the letter codes developed by Knutsen et al. (1994). The three most commercially important carrageenans are called iota-, kappa- and lambda-carrageenan. The letter codes of these types of carrageenan are G4S-DA, G4S-DA2S and G2S-D2S, 6S, respectively. Kappa-carrageenan is present mainly in species belonging to the genera *Hypnea* (Cystocloniaceae) and *Kappaphycus* (Solieriaceae) and species belonging to the genus *Euclima* (Solieriaceae), are the main source of iota-carrageenan (Craigie 1990; Chopin et al. 1999; Rudolph 2000). Kappa/iota-hybrid carrageenans are found in gametophytic phases of several species of Gigartinaceae and Phylloporaceae families (Pereira and Mesquita 2003; Pereira et al. 2009a, b). Carrageenans mu and nu, found in native phycocolloid samples, are the biological precursors of kappa and iota-carrageenan, respectively (Bixler et al. 2001). In vivo, iota and kappa-carrageenan are formed enzymatically from the precursors of carrageenans by a sulphohydrolase (Wong and Craigie 1978; de Ruiter et al. 2000). *In vitro*, these precursor residues are converted into gelling carrageenan corresponding to the treatment alkali. Alkali extraction is commonly used in the commercial production of kappa and iota-carrageenan, in order to increase the 3,6-anhydrous-D-galactose content as it results in a product with enhanced gelling properties (van de Velde et al. 2002a; Aguilan et al. 2003). The tetrasporic phase of Gigartinaceae produces carrageenans of the lambda family.

With respect to carrageenan in Gigartinales, the most important modulators of quality and chemical composition at seasonal and geographical levels are mainly abiotic factors (e.g. light, temperature, water motion and oxygen depletion,



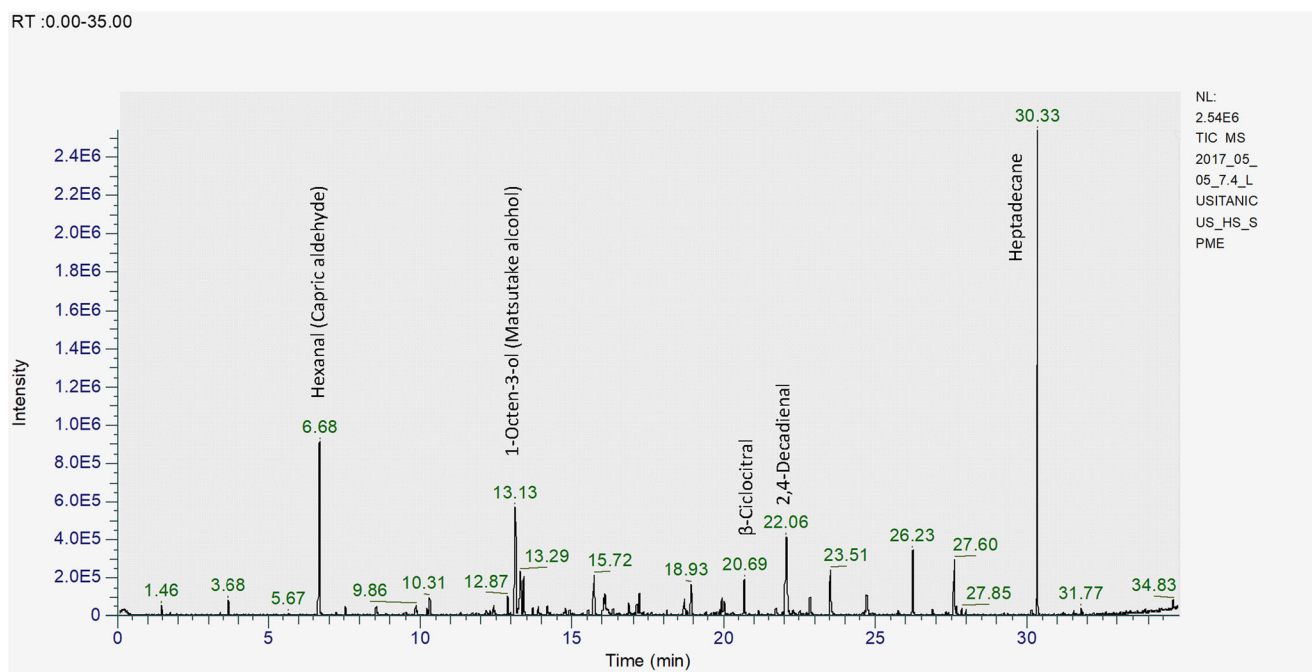
◀ **Fig. 7** *Chondracanthus teedei* var. *lusitanicus*: fructified tetrasporophyte, with tetrasporangial sori, collected in Buarcos Bay, Portugal (a–h); detail of branches with tetrasporangial sori (a); branch cross-section at the level of tetrasporangial sori, according to the orientation shown in panel a (b); detail of tetrasporangia and tetraspores (f–g). Staining with Toluidine blue (b, c). Cytology: electron microscope observations of floridean starch (af), chloroplasts (cl), Golgi (G), nucleus (n) and cored vesicles (vn) (after Pereira 2004)



**Fig. 8** *Chondracanthus teedei* var. *lusitanicus*: fructified female gametophyte, with cystocarps, collected in Buarcos, Portugal (a–f); detail of branches with cystocarps (a); cystocarp cross-section (b); carpospores within cystocarps (c, d); staining with lactophenol blue (b–d).

nutrients, salinity) and oceanographic conditions (e.g. currents, upwelling) (Periyasamy and Subba Rao 2017; Campbell et al. 2019). In most species from temperate zones, including those from *Chondracanthus* genus, there is evidence of increased culture yields in spring and summer (Pereira and Mesquita 2004; Pereira and van de Velde 2011; Pereira 2013). Consequently, the environmental conditions are important factors to be considered, both in terms of culture

Ultrastructure of the female gametophyte showing partially a multinucleate cell (e) and some aspects of the carpospore differentiation (f); af—floridean starch grains, cl—chloroplast, n—nucleus, vn—cored vesicles (adapted from Pereira 2004)



**Fig. 9** GC-MS chromatogram of *Chondracanthus teedei* var. *lusitanicus* (after Moreira-Leite 2017, with permission)

and in population conservation planning for this group of red macroalgae (Contador et al. 2020).

In spite of not being a harvested seaweed, as previously mentioned, it is surprising that, among the Buarcos Bay carrageenophytes, *C. teedei* var. *lusitanicus* is one of those which presents the highest values of average carrageenan yields, with  $34.9 \pm 1.0\%$  ( $n = 13$ ) (Fig. 11) (Pereira and Mesquita 2004).

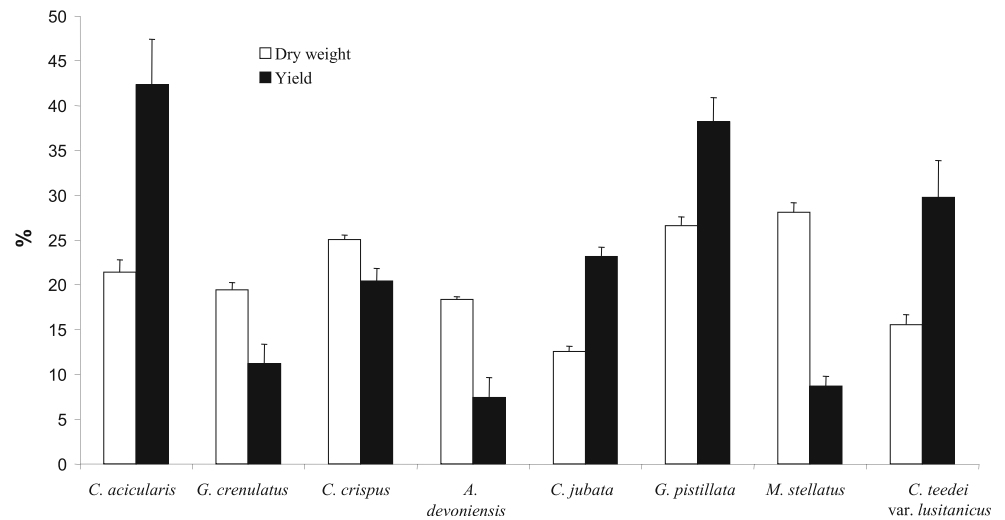
In relation to the phycocolloid nature, spectroscopic analysis showed that the two phases in the life cycle of *C. teedei* var. *lusitanicus* seem to present a variation similar to that



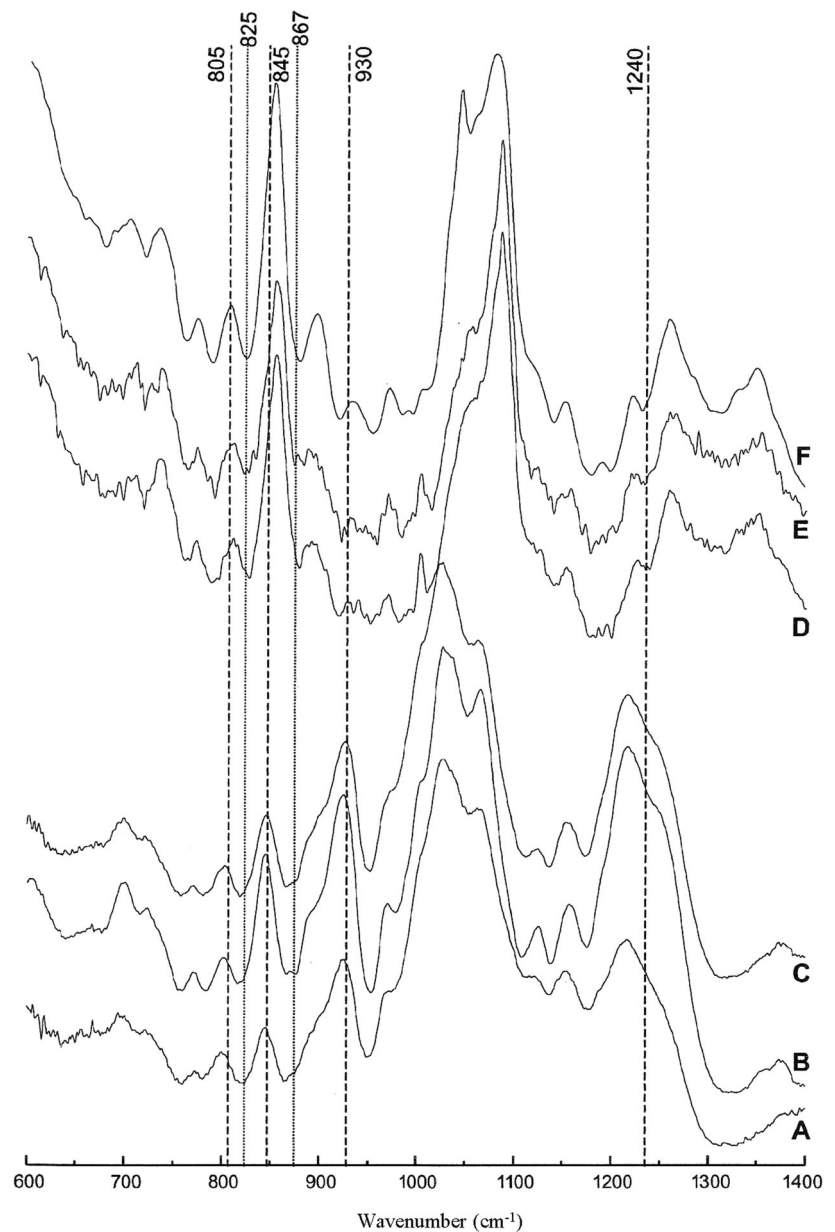
**Fig. 10** Coriander seaweed salad—mixture of unconventional algae (*Laminaria ochroleuca*, *Pelvetia canaliculata*—brown algae, and *Chondracanthus teedei* var. *lusitanicus*—red alga), seasoned with floor of olive oil, garlic and coriander. After Moreira-Leite 2017, with permission

existing in other species of *Chondracanthus* genus (see Chopin et al. 1999; Pereira and Mesquita 2004): the gametophytic stages yield carrageenans of the kappa family (hybrid kappa/iota/mu/nu carrageenan), while the tetrasporophytic stages produce carrageenans of the lambda family (hybrid xi/theta-carrageenan). Figure 12 shows the FTIR and FT-Raman spectra of ground seaweed samples (A, D), native carrageenan (B, E) and alkali-extracted carrageenan (C, F) of *C. teedei* var. *lusitanicus* female gametophytes. All spectra show a band at  $845 \text{ cm}^{-1}$ , which is assigned to D-galactose-4-sulphate (G4S) and a band at  $805 \text{ cm}^{-1}$ , which indicates the presence of 3,6-anhydro-D-galactose-2-sulphate (DA2S). The presence of a strong band at  $930 \text{ cm}^{-1}$  in the FTIR spectra, weak in FT-Raman spectra, indicates the presence of 3,6-anhydro-D-galactose (DA) in all samples (Chopin et al. 1999; Pereira et al. 2003; Pereira et al. 2009a). The broad signal in FTIR, between  $1210$  and  $1260 \text{ cm}^{-1}$ , was characteristic of sulphate esters in general (Chopin et al. 1999). Additional peaks at  $867 \text{ cm}^{-1}$  (galactose and D-galactose-6-sulphate = G/D6S),  $825 \text{ cm}^{-1}$  (galactose and D-galactose-2-sulphate = G/D2S) and  $820 \text{ cm}^{-1}$  (G/D6S), with little intensity, correspond to the presence of carrageenan precursors (mu and nu) in the samples of ground seaweed (A) and native carrageenan (B) (Chopin et al. 1999). The presence of bands at  $825$  and  $867 \text{ cm}^{-1}$ , corresponding to the existence of precursors, is more evident in the FT-Raman spectra (D, E). Figure 13 shows the FTIR and FT-Raman spectra of ground seaweed samples (A, D), native carrageenan (B, E) and alkali-extracted carrageenan (c, f), from the non-fructified thalli. These spectra are compared to the ones presented for female gametophytes, which showed a strong absorbance at  $1240$

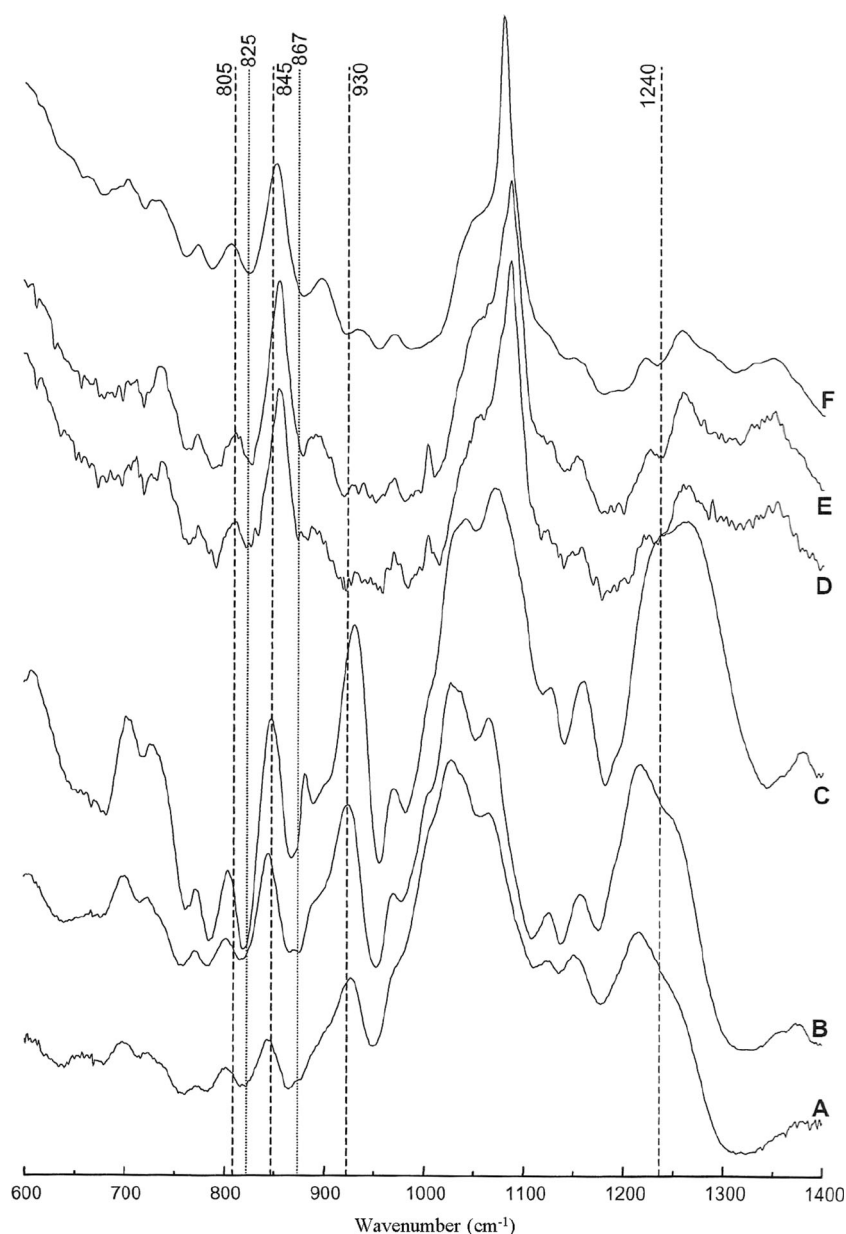
**Fig. 11** Carrageenophytes dry weight expressed as the percentage of fresh weight and carrageenan yields expressed as the percentage of dry weight (mean ± standard error,  $n = 13$ ) (after Pereira 2004)



**Fig. 12** FTIR and FT-Raman spectra of ground seaweed samples (A, D), native carrageenan (B, E) and alkali-extracted carrageenan (C, F) of *C. teedei* var. *lusitanicus* female gametophytes (after Pereira 2004)



**Fig. 13** FTIR and FT-Raman spectra of ground seaweed samples (A, D), native carrageenan (B, E) and alkali-extracted carrageenan (C, F) of *C. teedei* var. *lusitanicus* non-fructified thalli (after Pereira 2004)

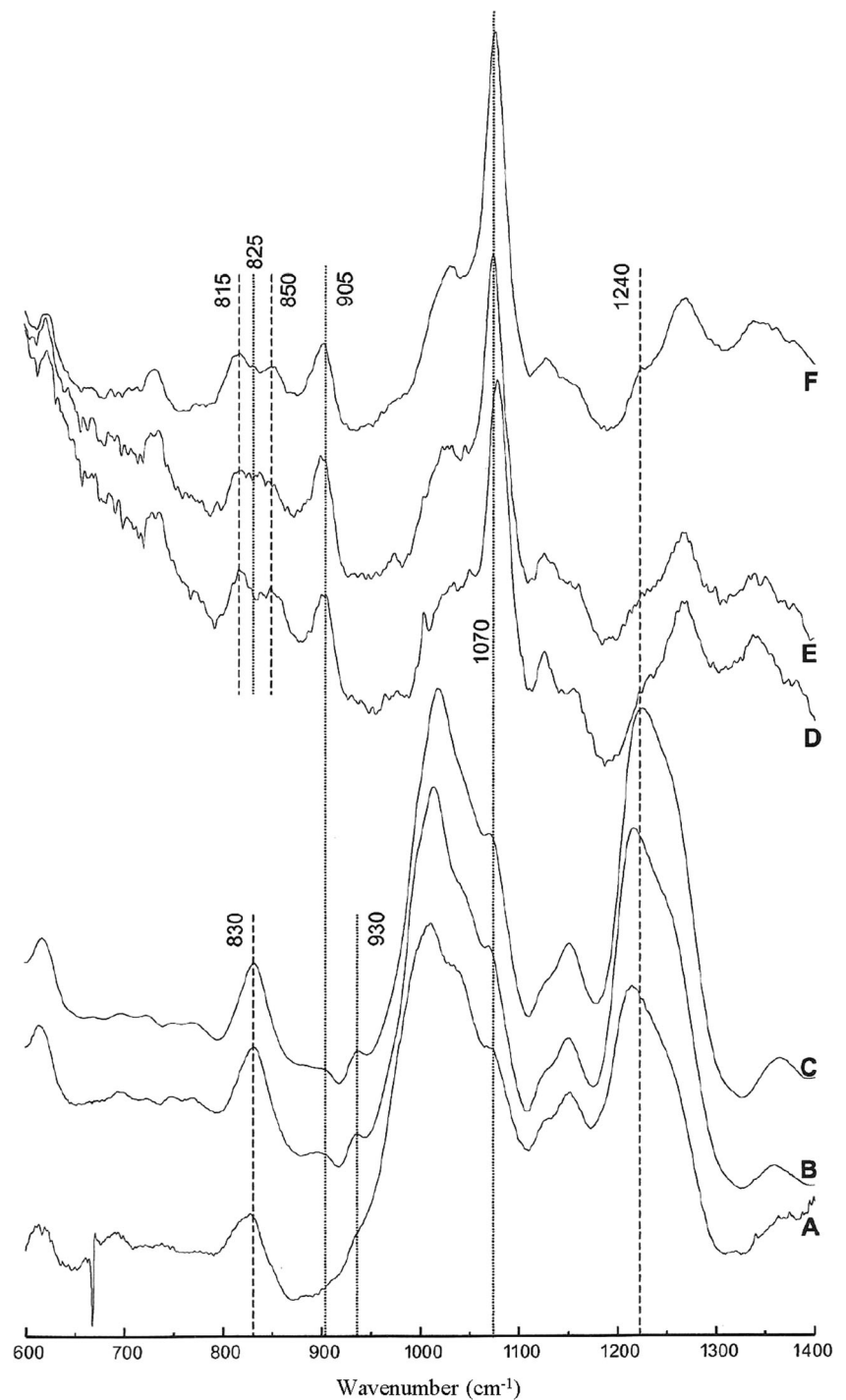


$\text{cm}^{-1}$  for sulphate esters and three other bands at  $805 \text{ cm}^{-1}$  (DA2S), at  $845 \text{ cm}^{-1}$  (G4S) and  $930 \text{ cm}^{-1}$  (DA). The ground seaweed (G) and native carrageenan (H) showed additional peaks at  $820 \text{ cm}^{-1}$  (G/D6S),  $825 \text{ cm}^{-1}$  (G/D2S) and  $867 \text{ cm}^{-1}$  (G/D6S), the last ones, more evident in the FT-Raman spectra (D, E), corresponded to the precursors. The FTIR and FT-Raman spectra of tetrasporophytes samples of *C. teedei* var. *lusitanicus* are shown in Fig. 14: ground samples (A and D), native carrageenan (B and E) and alkali-extracted carrageenan (C and F). The infrared spectra of all samples showed a strong absorbance at  $1240 \text{ cm}^{-1}$  for sulphate esters and a narrow peak between  $825$  and  $830 \text{ cm}^{-1}$  (G/D2S). In addition to these signals of larger intensity, three shoulder peaks at  $905 \text{ cm}^{-1}$  (DA2S),  $930 \text{ cm}^{-1}$  (DA) and  $1070 \text{ cm}^{-1}$  (DA) appear in all the FTIR spectra, related to the presence of

theta-carrageenan. All Raman spectra (Fig. 14 (D and F)) present strong absorbance at  $1070 \text{ cm}^{-1}$ , which corresponds to C–O of 3,6-anhydrogalactose (DA), and three other near bands in the spectral region of  $815$ – $850 \text{ cm}^{-1}$ , related with the high sulphate contents (Pereira et al. 2003). The presence of  $815$  and  $850 \text{ cm}^{-1}$  peaks (Fig. 14 (D and F)) allows us to conclude that the main constituent fraction is an xi-carrageenan (Pereira et al. 2003). The  $825 \text{ cm}^{-1}$  and  $905 \text{ cm}^{-1}$  peaks, present in all Raman spectra (Fig. 14 (D and F)), correspond to the presence of theta-carrageenan.

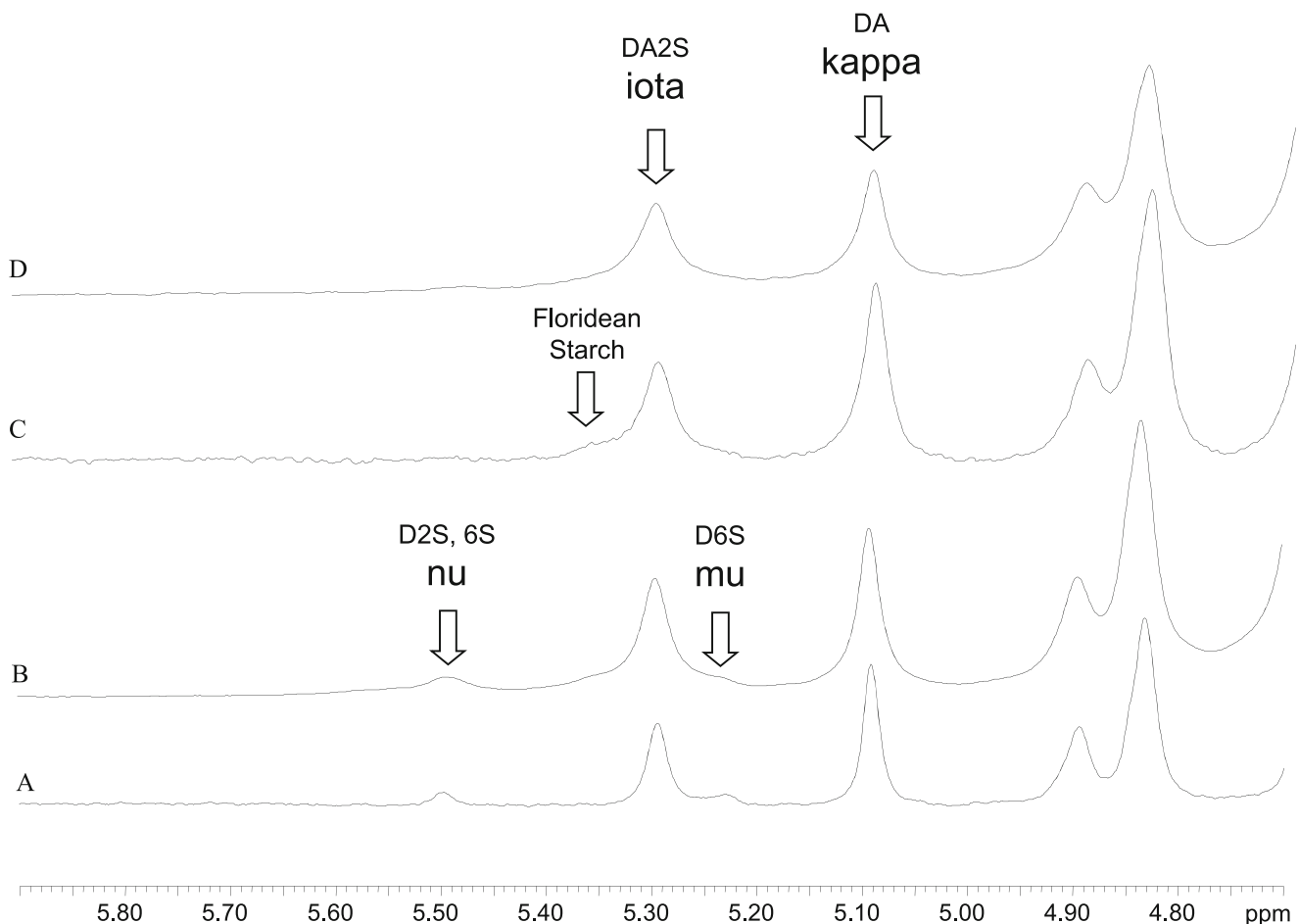
The  $^1\text{H-NMR}$  spectra of native and alkali-modified carrageenans from *C. teedei* var. *lusitanicus* female gametophytes and non-fructified thalli revealed, in the anomeric protons zone, two major signals at  $5.11 \text{ ppm}$  and  $5.32 \text{ ppm}$  (Fig. 15 (A–C)). These signals correspond to the anomeric protons of

**Fig. 14** FTIR and FT-Raman spectra of ground seaweed samples (A, D), native carrageenan (B, E) and alkali-extracted carrageenan (C, F) of *C. teedei* var. *lusitanicus* tetrasporophytes (after Pereira 2004)



the 3,6-anhydro- $\alpha$ -D-galactose (DA; kappa-carrageenan) and the 2-sulphated 3,6-anhydro- $\alpha$ -D-galactose (DA2S; iota-carrageenan), respectively. Minor components detected in the spectra of the native carrageenans (Fig. 15 (A and B)) gave a signal at 5.52 ppm and were assigned to the anomeric proton of the  $\alpha$ -D-galactose 2,6-disulphate (D2S, 6S; nu-carrageenan) and 5.25, assigned to the  $\alpha$ -D-galactose-6-sulphate (D6S; mu-carrageenan) (Ciancia et al. 1993; Stortz et al. 1994; van de Velde et al. 2002a; Pereira and

Mesquita 2004; van de Velde et al. 2004). In addition to the carrageenan signals, the spectrum of the alkaline-extracted female gametophyte sample showed a minor signal with a chemical shift of 5.37 ppm. This signal is assigned to floridean starch, which is a usual and natural impurity of carrageenan samples (Knutsen and Grasdalen 1987; Van de Velde et al. 2002a, b, 2005). The <sup>13</sup>C-NMR spectra of native and alkaline extracted carrageenan, from tetrasporophytes, show signals



**Fig. 15**  $^1\text{H-NMR}$  spectra of native (A, B) and alkali-extracted (C, D) carrageenans of *C. teedei* var. *lusitanicus* female gametophytes (A, C) and non-fertilized thalli (B, D). The letter code refers to the nomenclature developed by Knutsen et al. 1994 (after Pereira 2004)

at 105.44 and 94.94 ppm, relative to the anomeric carbons of xi-carrageenan, and 102.57 and 97.81 pp, relative to the anomeric carbons of theta-carrageenan (Fig. 16).

## Management and production

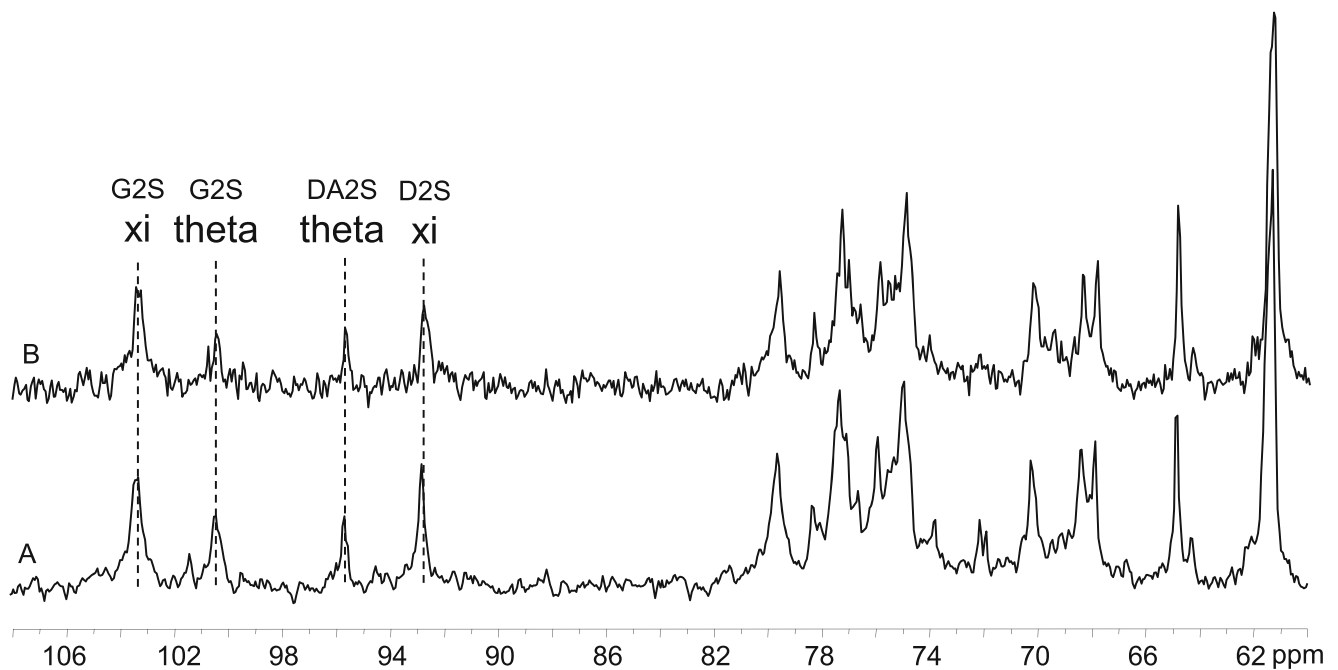
### Cultivation

Laboratory cultivation tests with this species have been done mainly to determine its life cycle (Guiry 1984; Braga 1985, 1990), or to assess tolerance to temperature changes (Guiry et al. 1987), to assess the response to different types and intensity of radiation (Schmidt et al. 2012). In the cultivation trials performed by Zinoune (1993) and Zinoune et al. (1993), the environmental factors that influenced the growth of *C. teedei* and the production of carrageenans were determined. From the perspective of *C. teedei* culture as a source of carrageenans, the results obtained in Zinoune's experiments showed that it is possible to manipulate the metabolism of this species. The variation in the level of nutrients, the temperature, the

photoperiod and the intensity/quality of the lighting determine the concentration and the final quality of the carrageenans produced. Following the work carried out by Ortega (2015), Love (2018) proceeded to optimise the cultivation of *C. teedei*, evaluating the effects of irradiance, temperature, salinity and nutrient enrichment. According to (Barbosa 2019), the highest growth rate was under enrichment of the red-light radiation spectrum, but the study suggests that monochromatic irradiance did not encourage the synthesis of compounds of economic interest in *C. teedei* during the experimental period.

Domestication of the oceans is widely regarded as a possible solution to increase food and could be one of the next most important developments in human history. By 2050, the edible bioresource biomass will have to satisfy the 9 billion people predicted to live on the planet. Seaweed aquaculture can help to address global challenges related to nutrition, health and sustainable circular bio-economy. Today, there is growing need for development, improvement and diversification of seaweed aquaculture practices in Europe, a continent characterised by its large coastal territory and large range of climates (Barbier et al. 2019).





**Fig. 16**  $^{13}\text{C}$ -NMR spectra of carrageenans of *C. teedei* var. *lusitanicus* tetrasporophytes (A—native, B—alkali-extracted). Letter codes refer to the nomenclature of Knutsen et al. (1994), after Pereira (2004)

Species of the red algal genus *Chondracanthus* (Gigartinales, Rhodophyta) have been considered a target for exploitation because of its importance as a source of raw material for the carrageenan industry as well as food industry as a sea vegetable. *Chondracanthus* is represented in Brazil, as well in the Iberian Peninsula, by four species, among which *C. teedei* is of special interest in view of its size, distribution and abundance. As the natural population is not large enough to support a commercial exploitation, the alternative remains on its mariculture. However, it is well known that success in a sustainable and commercial cultivation of a natural resource can only be achieved if based on solid biotechnological background that leads to the domestication of the targeted species (Bastos et al. 2012; Bastos 2013; Barbier et al. 2019). The cultivation of *C. teedei* var. *lusitanicus* made by Soares (2015) in an Integrated Multitrophic Aquaculture (IMTA) system showed better results than the laboratory cultivation. The highest relative growth rate ( $2.04 \pm 1.9\% \text{ day}^{-1}$ ) and productivity ( $53.1 \pm 1.2 \text{ g (dw) m}^{-2} \text{ day}^{-1}$ ) were achieved at a cultivation density of  $8 \text{ g L}^{-1}$ .

In Andalusia (south of Iberian Peninsula), seaweed cultivation is occurring in earthen ponds, by the rope system, for *Ulva* sp., *Gracilaria* sp., *Gracilariopsis longissima* and *C. teedei* (Ortega 2015; Love 2018; Barbier et al. 2019; Bermejo et al. 2020)

### Impacts of NIS introduced by aquaculture species

Although aquaculture continues to be an important economic driver in many coastal areas, the aquaculture industry has had

a long history as a major vector for the introduction of non-indigenous species (NIS) around the world (Grosholz et al. 2015). Using the NEMESIS list of non-native algae and mollusc species introduced in California, Grosholz et al. (2012) searched the peer-reviewed scientific literature and created a database of studies on the impacts of mollusc and macroalgal species. *C. teedei* was intentionally introduced for aquaculture purposes (Grosholz et al. 2012).

## Utilisation

### Human food

With the succession of culinary movements, chefs started to incorporate values of yore, even though there was apparently a break with the past. In this way, both the “New Cuisine” and the “Fusion Cuisine” have brought about the adoption of some standards, referring to dietetics and the use of oriental products by the West, paving the way for the consumption of algae. Seaweeds are complete foods through nutritional optics. However, Atlantic species are little studied and, in the West, their consumption as food is not very usual. Although there is a great opportunity for genetic selection and improvement of the species, considering their use in food, the same way it happened with the terrestrial plants (Moreira-Leite 2017). According to the same author, it is therefore necessary to investigate which of the species may be suitable for food, highlighting their organoleptic properties, and also to develop techniques for their conservation and use in gastronomy.

Today, seaweed consumption in Portuguese and Spanish homes is growing thanks to the gastronomic bloom driven by some celebrity chefs and because of the growing belief that the nutritional properties of seaweeds make them appropriate for inclusion as part of a healthy and well-balanced diet (Pérez-Lloréns et al. 2016, 2018). It has resulted in countless workshops and/or master classes such as that offered by the renowned Basque Culinary Center, where some avant-garde Spanish chefs are invited to give lectures such as “Seaweeds, the flavour of the sea into the kitchen”. It also positively contributed to the rise of new companies that gather and pack seaweeds such as Suralgas, “la Huerta Marina or Conservas Mar de Ardora”, retailers (Terra Verda or Ecoveritas) or public markets (“La Mar de Algas in Madrid or Javier Morcillo in Valencia”), as well as funding research projects focused on mariculture of seaweed species (*Gracilariopsis longissima* and *C. teedei* (Ortega 2015; Bermejo et al. 2020) with culinary potential such as the Ealga project in Cádiz Bay (Spain) and Alga4Food in Portugal (Mouritsen et al. 2019; Noronha et al. 2020).

As a way to incorporate less conventional algae (as is the case with *C. teedei*) into the recipes, a coriander salad was developed, which takes more advantage of the crunchy and gelatinous textures of the algae, and also of its colour, than of the flavour itself (Moreira-Leite 2017). Another recipe was proposed by the “elBulli” restaurant team, a marinated spherical quail with oysters and “musgos” (*C. teedei*) (Adrià et al. 2011).

*C. teedei* is highly prized in certain regions of Sicily, where it is popularly known as “máru”. In summer, there is a high demand for this seaweed during popular festivals. It is carefully harvested by hand, washed with seawater and sold on the streets in stalls specially set up by fishermen, who dress them with lemon juice and salt and serve them on paper plates. The famous Sicilian poet Vincenzo de Simone (1879–1942) refers to this seaweed in his poetry entitled “La Sicilia” (Pérez-Lloréns et al. 2016).

### Pharmacological, biological and nutraceutical activities

In general, carrageenan serves as a gelling agent (carrageenans from the kappa family), stabilising and viscosity agent (lambda family carrageenan) in food products, pharmaceutical formulations, cosmetics and drilling fluid for oil wells (Hotchkiss and Trius 2007; Ortiz et al. 2009).

#### Antifungal activity

There are still few studies about antifungal sulphated polysaccharides described in the literature. However, some recent studies demonstrated that these macromolecules possess antifungal activity or induce resistance against fungal

pathogens (Souza et al. 2018). According to Soares et al. (2016), carrageenan extracts from red alga *C. teedei* var. *lusitanicus* promoted morphological alterations on *Aspergillus fumigatus* and *Alternaria infectoria* after exposure to 0.15 mg mL<sup>-1</sup> of kappa/iota and to 0.1 mg mL<sup>-1</sup> of xi/theta carrageenan, respectively. In addition, the chitin cell wall content of *A. fumigatus* decreased significantly. According to the authors, these changes were associated with a decrease of the  $\beta$ -glucan content. Nevertheless, the mechanisms involved in the antifungal activity of sulphated polysaccharides are unclear. Carrageenans extracted from *C. teedei* var. *lusitanicus* were studied in order to determine their potential antifungal activity (Soares 2015; Soares et al. 2016; Pereira 2018b). FTIR-ATR and FT-Raman spectroscopic analysis confirmed the presence of a hybrid kappa/iota-carrageenan belonging to the gametophytic phase and a hybrid xi/theta-carrageenan in the tetrasporophytic phase (Pereira and Mesquita 2004; Pereira and van de Velde 2011; Pereira 2013; Pereira et al. 2019). Kappa/iota and xi/theta-carrageenan induced the formation of swollen hyphal segments in *A. infectoria*, upon exposure to 125  $\mu$ g mL<sup>-1</sup> and 60  $\mu$ g mL<sup>-1</sup>, respectively. The observed phenotype was similar to those induced by antifungals targeting the fungal cell wall. When exposed to 87.5  $\mu$ g mL<sup>-1</sup> of kappa/iota-carrageenan, *A. fumigatus* hyphae became shortened and highly branched, a phenotype commonly observed in response to antifungals. These morphological alterations were associated with a decrease of the  $\beta$ -glucan content in *A. infectoria* after exposure to 150  $\mu$ g mL<sup>-1</sup> of kappa/iota and to 100  $\mu$ g mL<sup>-1</sup> of xi/theta-carrageenan. On the other hand, the chitin cell wall content of *A. fumigatus* decreased significantly upon exposure to 150  $\mu$ g mL<sup>-1</sup> of both extracts, which triggered an increase in the content of  $\beta$ -glucan. Overall, this work shows that carrageenans extracted from *C. teedei* var. *lusitanicus* cause alterations on the *A. fumigatus* and *A. infectoria* cell walls, indicating a marked antifungal activity (Soares 2015; Soares et al. 2016; Pereira 2018a).

#### Antiviral activity

The data obtained in Soares (2015) and Soares et al. (2016) works revealed that the viral infection by Lentivirus was reduced upon exposure to a pre-treatment with extracts from female gametophytes (FG) and tetrasporophytes (T) of *C. teedei* var. *lusitanicus*. Although the inhibitions were not statistically significant, FG (producers of kappa/iota-hybrid carrageenan) and T (producers of xi-carrageenan) of *C. teedei* var. *lusitanicus* extracts was able to reduce 14% of the virus infection, and the Tetra extract was able to reduce, approximately, 35% of the virus infection (Pereira 2018b).

## Cosmetic ingredients

*Chondracanthus teedei* powder obtained from the dried, ground alga has been assessed to be used as skin-conditioning agents (Cherian 2020).

## Source of plant growth regulators

Plant growth regulators (PGRs) are organic substances that influence the physiology and development of plants at very low concentrations. Many of the good results observed in the use of seaweed in the fertilisation of plants for agricultural use were due to the fact of cytokinins, auxins and abscisic acid (ABA) were common constituents in red seaweeds (Pereira et al. 2019). *Chondracanthus teedei* is a producer of auxin, cytokinins, indole-3-acetic acid (IAA), indole-3-acetamide (IAM) and ABA (Yokoya et al. 2010) and, therefore, it is a good candidate for obtaining an effective agricultural biostimulant.

**Funding information** Leonel Pereira had the support of Foundation for Science and Technology (FCT), within the scope of the project UIDB/04292/2020 – MARE - Marine and Environmental Sciences Centre.

## References

- Adrià F, Adrià A, Soler J (2011) La Historia de elBulli – Toda nuestra historia desde 1961 hasta 2011. Available on: [http://www.elbulli.com/historia/version\\_imprimible/1961-2011\\_es.pdf](http://www.elbulli.com/historia/version_imprimible/1961-2011_es.pdf) (accessed on 23 May 2020)
- Aguilan JT, Broom JE, Hemmingson JA, Dayrit FM, Montañó MNE, Dancel MCA, Niñuevo MR, Furneaux RH (2003) Structural analysis of carrageenan from farmed varieties of Philippine seaweed. *Bot Mar* 46:179–192
- Araújo R, Bárbara I, Tibaldo M, Berceibar E, Tapia PD, Pereira R, Santos R, Pinto IS (2009) Checklist of benthic marine algae and cyanobacteria of northern Portugal. *Bot Mar* 52:24–46
- Ardre F (1970) Contribution a l'étude des algues marines du Portugal. I. La flore. *Port Acta Biol (B)* 10:137–560
- Bárbara I, Cremades J (1996) Seaweeds of the ria de A Coruña (NW Iberian Peninsula, Spain). *Bot Mar* 39:371–388
- Barbier M, Charrier B, Araújo R, Holdt SL, Jacquemin, Rebours C (2019) In: Barbier M, Charrier B (eds) PEGASUS - Phycomorph European guidelines for a sustainable aquaculture of seaweeds. COST Action FA1406, Roscoff, 194 pp.
- Barbosa IM (2019) Efeitos da Qualidade de radiação na Fisiologia de *Chondracanthus teedei* (Gigartinales, Rhodophyta). Graduação em Oceanografia. Universidade Federal de Santa Catarina, Brazil, 51 pp
- Bastos E (2013) Bases biológicas para a domesticação de uma alga vermelha nativa de valor econômico: *Chondracanthus teedei*. Master Thesis, Universidade Federal de Santa Catarina, Departamento de Botânica, Santa Catarina, Brazil, 92 pp
- Bastos E, Felix M, Rover T, Horta PA, Hayashi L, Oliveira EC (2012) Caracterização nutricional das macroalgas *Chondracanthus teedi* (Gigartinales, Rhodophyta) e *Kappaphycus alvarezii* (Solieriaceae, Rhodophyta) do sul do Brasil. XIV Congresso Brasileiro de Ficologia. Universidade Federal de Santa Catarina, Brazil
- Bermejo R, Cara CL, Macías M, Sánchez-García J, Hernández I (2020) Growth rates of *Gracilariopsis longissima*, *Gracilaria bursapastoris* and *Chondracanthus teedei* (Rhodophyta) cultured in ropes: implication for N biomitigation in Cadiz Bay (Southern Spain). *J Appl Phycol* 32:1879–1891
- Bixler HJ, Johndro K, Falshaw R (2001) Kappa-2 carrageenan: structure and performance of commercial extracts: II. Performance in two simulated dairy applications. *Food Hydrocoll* 15:619–630
- Braga M (1985) Taxonomia e Biologia de *Gigartina teedii* (Roth) Lamouroux (Rhodophyta, Gigartinales) no Litoral do Estado de São Paulo. Masters Thesis. Instituto de Biociências da Universidade de São Paulo, Brazil, 161 pp
- Braga MRA (1990) Reproductive characteristics of *Gigartina teedii* (Roth) Lamouroux (Rhodophyta, Gigartinales), a turf-forming species: field and laboratory culture studies. *Bot Mar* 33:401–410
- Campbell I, Macleod A, Sahlmann C, Neves L, Funderud J, Øverland M, Hughes AD, Stanley M (2019) The environmental risks associated with the development of seaweed farming in Europe - prioritizing key knowledge gaps. *Front Mar Sci* 6:1–22
- Chapman VJ, Chapman DJ (1980) Seaweeds and their Uses. Springer, Dordrecht, 334 pp. <https://doi.org/10.1007/978-94-009-5806-7>
- Cherian P (2020) Safety assessment of red algae-derived ingredients as used in cosmetics. Scientific literature review for public comment. *Cosmetic Ingredient Review*, Washington 24 pp
- Chopin T, Kerin BF, Mazerolle R (1999) Phycocolloid chemistry as a taxonomic indicator of phylogeny in the Gigartinales, Rhodophyceae: a review and current developments using Fourier transform infrared diffuse reflectance spectroscopy. *Phycol Res* 47:167–188
- Ciancia M, Matulewicz MC, Finch P, Cerezo AS (1993) Determination of the structures of cystocarpic carrageenans from *Gigartina skottsbergii* by methylation analysis and NMR spectroscopy. *Carbohydr Res* 238:241–248
- Contador CB, Massad IP, Contreras-Porcía L, Zapata J, Castañeda F, Ramírez ME, Gil-Kodaka P (2020) Concise review of genus *Chondracanthus* (Rhodophyta: Gigartinales). *J Appl Phycol* 32: 773–785
- Craigie JS (1990) Cell walls. In: Cole KM, Sheath RG (eds) *Biology of the Red Algae*, vol 5. Cambridge University Press, Cambridge, pp 221–257
- de Ruyter GA, Genicot S, Kloareg B, Penninkhof B, Potin P, Richard O, Rudolph B (2000) Sulphohydrolases, corresponding amino acid and nucleotide sequences, sulphohydrolase preparations, processes, and products thereof. World Patent Application WO2000068395A3
- Dixon PS, Irvine LM (1977) Seaweeds of the British Isles. Rhodophyta - Part 1: Introduction; Nemaliales; Gigartinales (Vol 1). Intercept Scientific, Medical and Technical Publications, London, pp 264.
- Dizerbo AH (1974) La repartition des *Gigartina* (Gigartinales, Gigartinaceae) du Massif Armoricain. *Bull Soc Phycol Fr* 19:88–94
- Gaspar R, Pereira L, Sousa-Pinto I (2019) The seaweed resources of Portugal. *Bot Mar* 62:499–525
- Gayral P (1982) Les algues de côtes Françaises (Manche & Atlantique). Éditions Doin, Paris, pp 21–29
- Grosholz ED, Crafton RE, Fontana RE, Pasari JR, Williams SL, Zabin CJ (2012) Aquatic invasive species vector risk assessments: an analysis of aquaculture as a vector for introduced marine and estuarine species in California. University of California at Davis - Bodega Marine Laboratory & Department of Environmental Science and Policy, California 77 pp
- Grosholz ED, Crafton RE, Fontana RE, Pasari JR, Williams SL, Zabin CJ (2015) Aquaculture as a vector for marine invasions in California. *Biol Invas* 17:1471–1484
- Guimarães SMPB (2006) A revised checklist of benthic marine Rhodophyta from the State of Espírito Santo, Brazil. *Bol Inst Bot* 17:143–194

- Guiry MD (1984) Structure, life-history and hybridization of atlantic *Gigartina teedii* (Rhodophyta) in culture. *Br Phycol J* 19:37–55
- Guiry MD, Guiry GM (2020) AlgaeBase. World-wide electronic publication, National University of Ireland, Galway. Available on: [https://www.algaebase.org/search/genus/detail?genus\\_id=110&session=abv4:AC1F0F3E0c94034533Yo4AC33DC0](https://www.algaebase.org/search/genus/detail?genus_id=110&session=abv4:AC1F0F3E0c94034533Yo4AC33DC0) (accessed on 17 May 2020).
- Guiry MD, Maggs CA (1985) Notes on Irish marine algae: 7 *Gigartina teedii* (Roth) Lamour. (Rhodophyta). *Ir Nat J.* 11:490–493
- Guiry MD, Tripodi G, Lüning K (1987) Biosystematics, genetics and upper temperature tolerance of *Gigartina teedii* (Rhodophyta) from the Atlantic and Mediterranean. *Helgol Meeresunters* 41:283–295
- Hommersand MH, Guiry MD, Fredericq S, Leister GL (1993) New perspectives in the taxonomy of the Gigartinales (Gigartinales, Rhodophyta). *Hydrobiologia* 260:105–120
- Hommersand MH, Fredericq S, Wilson Freshwater D, Hughey J (1999) Recent developments in the systematics of the Gigartinales (Gigartinales, Rhodophyta) based on rbcL sequence analysis and morphological evidence. *Phycol Res* 47:139–151
- Hotchkiss S, Trius A (2007) Seaweed: the most nutritious form of vegetation on the planet? *Food Ingredients – Health and Nutrition* 1/2:22–33. Available on: <https://www.foodmanufacture.co.uk/Article/2007/04/27/Seaweed-the-most-nutritious-form-of-vegetation-on-the-planet> (accessed on 27 May 2020)
- Joly AB (1957) Contribuição ao conhecimento da flora ficológica marinha do Baía de Santos e Arrendores. *Bolm Fac Filos Ciênc Univ S Paulo - Botanica* 14:1–196
- Joly AB (1965) Flora marinha do litoral norte do estado de São Paulo e regiões circunvizinhas. *Bolm Fac Filos Ciênc Univ S Paulo - Botanica* 21:1–267
- Knutsen SH, Grasdalen H (1987) Characterization of water-extractable polysaccharides from Norwegian *Furcellaria lumbicalis* (Huds) Lamour (Gigartinales, Rhodophyceae) by IR and NMR-spectroscopy. *Bot Mar* 30(6):497–505. <https://doi.org/10.1515/botm.1987.30.6.497>
- Knutsen SH, Myslabodski DE, Larsen B, Usov AI (1994) A modified system of nomenclature for red algal galactans. *Bot Mar* 37:163–169
- Love R (2018) Optimisation of the culture of the red alga *Chondracanthus teedei*. Effects of irradiance, temperature, salinity and nutrient enrichment. *Doble grado en Ciencias de mar y Ambientales. Facultad de Ciencias de Mar y Ambientales. Universidad de Cádiz, Spain*, 48 pp
- Menezes BS, Coelho MS, Meza SLR, Salas-Mellado M, Souza MRAZ (2015) Macroalgal biomass as an additional ingredient of bread. *Int Food Res J.* 22:812–817
- Mikami H (1965) A systematic study of the Phyllophoraceae and Gigartineae from Japan and its vicinity. *Scient Pap Inst Algal Res Hokkaido Univ* 5:181–185
- Moreira-Leite, B (2017) *Novas Alternativas para o Uso de Macroalgas da Costa Portuguesa em Alimentação*. MSc Thesis. Instituto Superior de Agranomia, FCT, Universidade Nova de Lisboa, Lisboa, 301 pp
- Mouritsen OG, Rhatigan P, Pérez-Lloréns JL (2019) The rise of seaweed gastronomy: phycogastronomy. *Bot Mar* 62:195–209
- Noronha J, Diniz M, Mata P, Pereira L, Milinivic J, Campos B, Moreira-Leite B, Salgado A, Gabriel P (2020) ALGA4FOOD - Algas na Gastronomia - Desenvolvimento de técnicas inovadoras de conservação e utilização. Chemistry Department, Faculty of Sciences and Technology, NOVA University, Lisbon. Available on: <https://alga4food.wixsite.com/> (accessed on 22 May 2020)
- OBIS (2020) Ocean Biogeographic Information System. Intergovernmental Oceanographic Commission of UNESCO. Available on: <https://obis.org/taxon/145624> (accessed on 24 May 2020)
- Ortega CLC (2015) *Cultivo de algas mediante sistema de cuerdas en la bahía de Cádiz*. Grado en Ciencias del Mar. Universidad de Cádiz, Spain, 41 pp
- Ortiz J, Uquiche E, Robert P, Romero N, Quiral V, Llantén C (2009) Functional and nutritional value of the Chilean seaweeds *Codium fragile*, *Gracilaria chilensis* and *Macrocystis pyrifera*. *Eur J Lipid Sci Technol* 111:320–327
- Parke M (1952) *Flora of Devon*, vol 2. Pt 1. The marine algae, The Devonshire Association, Torquay, 77 pp
- Pereira L (1994) *Ecologia das Macroalgas Marinhas – Estudo Ecológico duma População de Gigartina teedii da Baía de Buarcos*. Universidade de Coimbra, Coimbra, MSc Thesis, pp 27–31
- Pereira L (2004) *Estudos em macroalgas carragenófitas (Gigartinales, Rhodophyceae) da costa portuguesa: aspectos ecológicos, bioquímicos e citológicos*. PhD Thesis, Universidade de Coimbra, Coimbra, 293 pp
- Pereira L (2010) *Littoral of Viana do Castelo – Algae (Bilingual)*. Câmara Municipal de Viana do Castelo, 68 pp. ISBN 978-972-588-217-7
- Pereira L (2012) Cytological and cytochemical aspects in selected carrageenophytes (Gigartinales, Rhodophyta). In: Heimann K, Katsaros C (eds) *Advances in Algal Cell Biology*. Walter De Gruyter, Berlin, pp 81–104
- Pereira L (2013) Population studies and carrageenan properties in eight Gigartinales (Rhodophyta) from western coast of Portugal. *Sci World J* 2013:939830–939811
- Pereira L (2016) *Edible seaweeds of the world*. CRC Press / Taylor & Francis Group, Boca Raton, pp 448
- Pereira L (2018a) Biological and therapeutic properties of the seaweed polysaccharides. *Int Biol Rev* 2(2):1–50
- Pereira L (2018b) *Therapeutic and Nutritional Uses of Algae*. CRC Press / Taylor & Francis Group, Boca Raton, pp 560
- Pereira L (2020a) *Chondracanthus teedei*—Portuguese Seaweeds Website, available online on: [http://www.flordeutopia.pt/macoi/spec\\_list\\_detail.php?spec\\_id=32&searchSpecies=chondracanthus+teedei+%28mertens+ex+roth%29+k%FCtzing](http://www.flordeutopia.pt/macoi/spec_list_detail.php?spec_id=32&searchSpecies=chondracanthus+teedei+%28mertens+ex+roth%29+k%FCtzing) (accessed on 21 May 2020)
- Pereira L (2020b) *Chondracanthus teedei* var. *lusitanicus*—Portuguese Seaweeds Website, available online on: [http://www.flordeutopia.pt/macoi/spec\\_list\\_detail.php?spec\\_id=30&searchSpecies=chondracanthus+teedei+var.+lusitanicus+%28rodrigues%29+b%Elrbar+%26+cremades](http://www.flordeutopia.pt/macoi/spec_list_detail.php?spec_id=30&searchSpecies=chondracanthus+teedei+var.+lusitanicus+%28rodrigues%29+b%Elrbar+%26+cremades) (accessed on 21 May 2020)
- Pereira L, Correia F (2015) *Algas Marinhas da Costa Portuguesa—Ecologia, Biodiversidade e Utilizações*. Nota de Rodapé Edições, Paris, pp 340
- Pereira L, Mesquita JF (2003) Carrageenophytes of occidental Portuguese coast: 1-spectroscopic analysis in eight carrageenophytes from Buarcos bay. *Biomol Eng* 20:217–222
- Pereira L, Mesquita JF (2004) Population studies and carrageenan properties of *Chondracanthus teedei* var. *lusitanicus* (Gigartinales, Rhodophyta). *J Appl Phycol* 16:369–383
- Pereira L, van de Velde F (2011) Portuguese carrageenophytes: carrageenan composition and geographic distribution of eight species (Gigartinales, Rhodophyta). *Carbohydr Polym* 84:614–623
- Pereira L, Sousa A, Coelho H, Amado AM, Ribeiro-Claro PJA (2003) Use of FTIR, FT-Raman and <sup>13</sup>C-NMR spectroscopy for identification of some seaweed phycocolloids. *Biomol Eng* 20:223–228
- Pereira L, van de Velde F, Mesquita JF (2007) Cytochemical studies on underutilized carrageenophytes (Gigartinales, Rhodophyta). *Int J Biol Biomed Eng* 1:1–5
- Pereira L, Amado AM, Critchley AT, van de Velde F, Ribeiro-Claro PJA (2009a) Identification of selected seaweed polysaccharides (phycocolloids) by vibrational spectroscopy (FTIR-ATR and FT-Raman). *Food Hydrocoll* 23:1903–1909
- Pereira L, Critchley AT, Amado AM, Ribeiro-Claro PJA (2009b) A comparative analysis of phycocolloids produced by underutilized *versus*

- industrially utilized carrageenophytes (Gigartinales, Rhodophyta). *J Appl Phycol* 21:599–605
- Pereira L, Gheda FS, Ribeiro-Claro PJA (2013) Analysis by vibrational spectroscopy of seaweed polysaccharides with potential use in food, pharmaceutical and cosmetic industries. *Int J Carbohydr Chem* 2013:537202:7
- Pereira L, Bahcevandziev, Joshi NH (eds) (2019) Seaweeds as plant fertilizer, agricultural biostimulants and animal fodder. CRC Press, Boca Raton, pp 224
- Pérez-Lloréns JL, Hernández I, Vergara IJ, Brun FG, León Á (2016) Las Algas Se Comen? Un Periplo por la Biología, las Curiosidades y la Gastronomía. Servicio de Publicaciones de la Universidad de Cádiz, Cádiz, pp 336
- Pérez-Lloréns JL, Hernández I, Vergara IJ, Brun FG, León Á (2018) Those curious and delicious seaweeds. A fascinating voyage from biology to gastronomy. Servicio de Publicaciones de la Universidad de Cádiz, Cádiz, pp 384
- Rocha-Jorge R, Nauer F, Silva IB, Fujii MT, Necchi O Jr, Le Gall L, Oliveira MC (2018) Diversity of *Chondracanthus* (Gigartinales, Rhodophyta) on the Brazilian coast based on molecular and morphological evidences. *Braz J Bot* 41:889–900
- Periyasamy C, Subba Rao P (2017) Growth rate and carrageenan yield of cultivated *Kappaphycus alvarezii* (Doty) Doty in the coastal waters of Bay of Bengal at Chepala Timmapuram, Andhra Pradesh, east coast of India. *J Appl Phycol* 29:1977–1987. <https://doi.org/10.1007/s10811-017-1099-1>
- Rodrigues JEM (1957) Contribuição para o conhecimento das algas marinhas da baía de Buarcos. Publicações do XXIII Congresso Luso-Espanhol, Separata do Tomo V:1-15
- Rodrigues JEM (1958) A new variety of *Gigartina teedii* (Roth) Lamouroux. *Bol Soc Brot* 32:91–94
- Rudolph B (2000) Seaweed products: red algae of economic significance. In: Martin RE, Paine CE, Flick Jr, George J, Lynn MD (eds) . *Marine & Freshwater Products Handbook*. Technomic, Lancaster, pp 515–529
- Schmidt E, Pereira B, Pontes C, dos Santos R, Scherner F, Horta P, de Paula M, Latini A, Maraschin M, Bouzon Z (2012) Alterations in architecture and metabolism induced by ultraviolet radiation-B in the carrageenophyte *Chondracanthus teedei* (Rhodophyta, Gigartinales). *Protoplasma* 249:353–367
- Schneider CW, Lane CE (2005) Notes on the marine algae of the Bermudas. 7. Additions to the flora including *Chondracanthus saundersii* sp. nov. (Rhodophyta, Gigartinales) based on rbcL sequence analysis. *Phycologia* 44:72–83
- Schwachow RQ, Zanboni AJ (2007) O estuário da Laguna dos Patos: um exemplo para o ensino de ecologia no nível médio. *Revista Cadernos de Ecologia Aquática* 2:13–27
- Silva PC, Basson PW, Moe RL (1996) Catalogue of the benthic marine algae of the Indian Ocean. University of California Publications, Berkeley, pp 1–1259
- Smith HM (1904) The seaweed industries of Japan. *Fish Bull (USA)* 24: 133–181
- Soares F (2015) Antifungal, antibacterial and antiviral activity of *Chondracanthus teedei* var. *lusitanicus* (Gigartinales, Rhodophyta). MSc Thesis, University of Coimbra, Coimbra, Portugal, 154 pp
- Soares F, Fernandes C, Silva P, Pereira L, Gonçalves T (2016) Antifungal activity of carrageenan extracts from the red alga *Chondracanthus teedei* var. *lusitanicus*. *J Appl Phycol* 28:2991–2998
- Souza RB, Frota AF, Silva J, Alves C, Neugebauer AZ, Pinteus S, Rodrigues JAG, Cordeiro EMS, Almeida RR, Pedrosa R, Benevides NMB (2018) *In vitro* activities of kappa-carrageenan isolated from red marine alga *Hypnea musciformis*: Antimicrobial, anticancer and neuroprotective potential. *Int J Biol Macromol* 112: 1248–1256
- Stortz CA, Bacon BE, Chemiak R, Cerezo AS (1994) High field NMR spectroscopy of cystocarpic and tetrasporic carrageenans from *Iridaea undulosa*. *Carbohydr Res* 261:317–326
- Taylor WR (1942) Caribbean marine algae of the Alan Hancock Expedition, 1939. *Rep Allan Hancock Adam Exped* 2:1–193
- Taylor WR (1960) Marine algae of the eastern tropical and subtropical coasts of the Americas. The University of Michigan Press, Ann Arbor 870 pp
- Tsekos I (1981) Growth and differentiation of the Golgi apparatus and wall formation during carposporogenesis in the red algae, *Gigartina teedii* (Roth) Lamour. *J Cell Sci* 52:71–84
- Tsekos I (1982) Tumour-like growths induced by bacteria in the thallus of a red alga, *Gigartina teedii* (Roth) Lamour. *Ann Bot* 49:123–126
- Tsekos I, Schnepf E (1983) The ultrastructure of carposporogenesis in *Gigartina teedii* (Roth) Lamour - (Gigartinales, Rhodophyceae) - auxiliary cell, cystocarpic plant. *Flora* 173:81–96
- Tsekos I, Reiss HD, Schnepf E (1985) Occurrence of particle tetrads in the vacuole membrane of the marine red algae *Gigartina teedii* and *Ceramium rubrum*. *Naturwissenschaften* 72:489–490
- Ugádim Y (1975) Algas marinhas bentônicas do litoral sul do estado de São Paulo e do litoral do estado do Paraná. III. divisão Rhodophyta (2): Cryptonemiales, Gigartinales e Rhodymeniales. *Bolm Botânica, Univ S Paulo* 3:115–163
- van de Velde F, de Ruiter GA (2002) Carrageenan. In: Steinbuechel A, de Baets S, Vandamme EJ (eds) *Biopolymers, polysaccharides II: polysaccharides from eukaryotes (Biopolymers, Vol. 6)*. Wiley-VCH, Weinheim, pp 245–274
- van de Velde F, Knutsen SH, Usov AI, Rollema HS, Cerezo AS (2002a) <sup>1</sup>H and <sup>13</sup>C high resolution NMR spectroscopy of carrageenans: application in research and industry. *Trends Food Sci Technol* 13: 73–92
- van de Velde F, Rollema HS, Grinberg NV, Burova TV, Grinberg VY, Tromp RH (2002b) Coil-helix transition of iota-carrageenan as a function of chain regularity. *Biopolymers* 65:299–312
- van de Velde F, Pereira L, Rollema HS (2004) The revised NMR chemical shift data of carrageenans. *Carbohydr Res* 339:369–383
- van de Velde F, Antipova AS, Rollema HS, Burova TV, Grinberg NV, Pereira L, Tromp RH, Rudolph B, Grinberg VY (2005) The structure of kappa/iota-hybrid carrageenans II. Coil-helix transition as a function of chain composition. *Carbohydr Res* 340:1113–1129
- Wong KF, Craigie JS (1978) Sulfohydrolase activity and carrageenan biosynthesis in *Chondrus crispus* (Rhodophyceae). *Plant Physiol* 61:663–666
- Yang MY, Macaya EC, Kim MK (2015) Molecular evidence for verifying the distribution of *Chondracanthus chamissoi* and *C. teedei* (Gigartinales, Rhodophyta). *Bot Mar* 58:103–113
- Yokoya NS, Stirk WA, Van Staden J, Novák O, Turečková V, Pěňčík A, Strnad M (2010) Endogenous cytokinins, auxins, and abscisic acid in red algae from Brazil. *J Phycol* 46:1198–1205
- Zinoun M (1993) Études Biochimiques des Polysaccharides Parietaux Produits par Deux Gigartinales (Rhodophycées) des Cotes de La Manche, *In Situ* et en Cultures Contrôlées: *Calliblepharis jubata* et *Gigartina teedii*. These de Doctorat de Sciences. Université de Technologie de Compiègne, France, pp. 6-11, 142-207
- Zinoun M, Cosson J, Deslandes E (1993) Influence of culture conditions on growth and physicochemical of carrageenans in *Gigartina teedii* (Rhodophyceae, Gigartinales). *Bot Mar* 36:131–136