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# Concise review of the red macroalga dulse, *Palmaria palmata* (L.) Weber & Mohr

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## Abstract

*Palmaria palmata*, commonly referred to as *dulse*, is a well-known and highly valued red macroalga distributed along the North Atlantic shores within a latitude range of approximately 40 to 80 °N. It is a species of commercial importance with historical records of use as food dating back several centuries to the current harvesting of dulse by hand-picking on the foreshore in Western Europe as well as Canada (New Brunswick and Nova Scotia) and USA (Maine). Because the demand for *P. palmata* increases and future sustainable commercial developments cannot rely solely on wild-harvested biomass, significant efforts have been made by research and industrial actors to cultivate the species. The low rates of spore release and germination, high mortality and epibiont contaminations remain major bottlenecks and point towards the need for optimized hatchery methods to enable upscaling the biomass production. The present review summarizes the available knowledge related to the biology, including the unique life history of the species among the Rhodophyta, the ecology as well as the nutrient composition and quality of *P. palmata* as food. Recent advances in taxonomy and cultivation techniques are reported along with a status of regulations for the commercial harvest of wild populations. An outlook on future industrial perspectives using biomass of *P. palmata* is also given.

**Keyword** Rhodophyceae; Red algae; Taxonomy; Distribution; Management; Production; Applications; Market value; Cultivation

## Morphological description

The name of the red macroalga *Palmaria palmata* reflects the characteristic shape of the plant consisting of flattened oblong lobes expanding from the middle of the frond as the shape of a hand or a palm. The fronds arise from a disc-shaped holdfast prolonged by a short stipe (Fig. 1).

Individuals can grow up to a size of 50 cm-long but usually between 10 and 20 cm. Observations of the species on the North-eastern coast of North America report a length up to 50 cm with wide individual branches that may have marginal proliferations in old damage specimens (Sears 1998). Broader fronds (length and width > 50 cm) may be observed on Eastern Canadian shores (L. Le Gall, pers. observation) compared to those growing on Atlantic European shores.

The texture of the fronds is somewhat leathery when the plant is old. New plants have a distinct fresh red colour while older plants are often darker with a reddish-brown colour. Individuals may turn greenish or even bleach due to higher temperatures and increased sunlight exposure during the early summer months, causing changes in pigment composition. Distinct morphotypes of *P. palmata* i.e. with finely dissected blades and numerous divisions as shown in Fig. 1, can be observed in more sheltered and silty areas of semi-exposed shores. These morphotypes are known as the varieties *sobolifera* and *sarniensis*. However, the validity of this varietal designation is questioned by studies showing the

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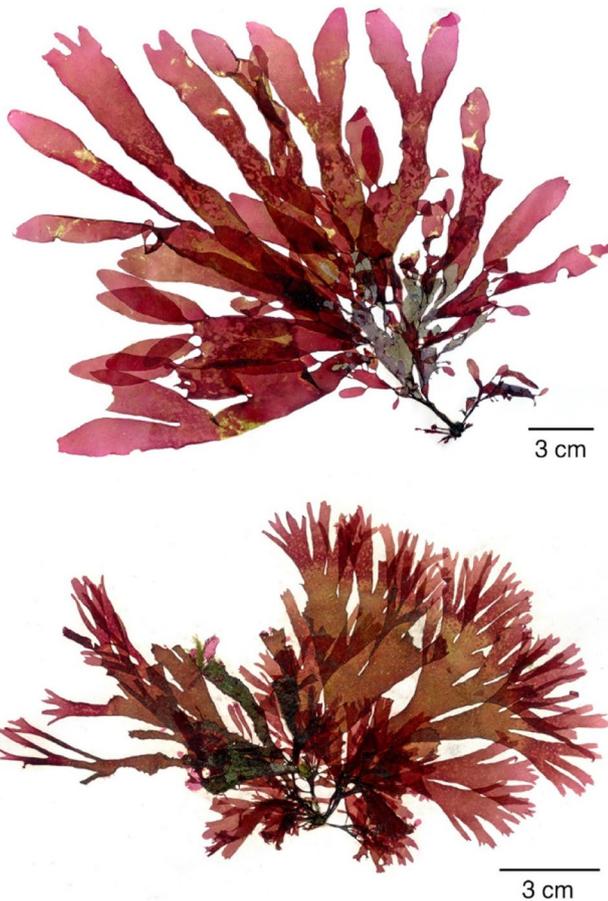
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**Fig. 1** Herbarium samples of two morphotypes of *Palmaria palmata* collected in Western Brittany, France. Top: typical plant, collected at Plougastel-Daoulas (Brittany, France). Bottom: Plant referred to as belonging to the *sarniensis-sobolifera* complex, collected at Le Conquet (Brittany, France)

production of viable hybrids from individuals of the *sarniensis-sobolifera* complex and typical *palmata* plants (van der Meer 1987), and the low genetic divergence across these entities based on nuclear genes (Kraan and Guiry 2006). These results highlight the morphological plasticity of the species under the influence of environmental factors.

## Nomenclature

### Scientific name and synonyms

The currently accepted name for the species is *Palmaria palmata* (Linnaeus) Weber & Mohr 1805. Homotypic synonyms are listed by Guiry and Guiry (2022) and include:

- Fucus palmatus* Linnaeus 1753
- Ulva palmata* (Linnaeus) Withering 1796

- Ceramium palmatum* (Linnaeus) Stackhouse 1797
- Delesseria palmata* (Linnaeus) Lamouroux 1813
- Sarcophylla palmata* (Linnaeus) Stackhouse 1816
- Halymenia palmata* (Linnaeus) Agardh 1817
- Sphaerococcus palmatus* (Linnaeus) Wahlenberg 1826
- Rhodymenia palmata* (Linnaeus) Greville 1830
- Isomenia palmata* (Linnaeus) Bachelot de la Pylaie 1830

### Vernacular names

The English common name “*dulse*” is the most employed to refer to the species also in other languages. This vernacular name as well as the alternative “*dillisk*” is closely related to “*duileasc*” (Gaelic) (Mouritsen et al. 2013) and “*tellesk*” (Breton). Other vernacular names include “*creannach*” (Gaelic), “*søl*” or “*söl*” (Norwegian/Danish and Icelandic) (Østgaard and Indergaard 2017), “*goëmon à vache*” (French, translated from the Breton “*bezhin saout*” meaning “cattle’s seaweed”) (Garineaud 2018) and “*botelho-comprido*” (Portuguese).

## Taxonomy and phylogeny

### Taxonomy

*Palmaria palmata* was first described by Linnaeus in 1753 under the name *Fucus palmatus*. It was later designated as *P. palmata* by the German naturalists Friedrich Weber and Daniel M.H. Mohr in 1805. In 1830, Greville grouped many red membranaceous species including *P. palmata*, in the genus *Rhodomencia* (currently *Rhodymenia*). The species was then known as *Rhodymenia palmata* (Linnaeus) Greville, until Guiry (1974) proposed to reinstate the genus *Palmaria* (over which *Rhodymenia* had been conserved) after observing morphological, anatomical and reproductive features (e.g. the absence of carposporophytic generation and the presence of a stalk cell involved in the production of the tetrasporangia). He proposed to place *Palmaria* along with *Halosaccion* and *Leptosarca* in a new family (Palmariaaceae). A few years later, a new order (Palmariales) was proposed to accommodate the Palmariaaceae (Guiry and Irvine 1978). Further studies of the life history (van der Meer and Chen 1979; van der Meer and Todd 1980) and ultrastructural features of the species (Pueschel 1979; Pueschel and Cole 1982), supported Guiry’s revision that was later confirmed by molecular studies (Harper and Saunders 2002). *Palmaria palmata* was included in two pioneer phylogenies published in 1994, inferred from the analysis of plastid *rbcL* sequences (encoding the large subunit of the ribulose-1,5-biphosphate carboxylase/oxygenase enzyme or RuBisCo) (Freshwater et al. 1994) and gene sequences encoding small subunit ribosomal RNA (SSU rDNAs) (Ragan et al. 1994). The latter

marker established the Palmariales as closely allied to the Nemaliales and Acrochaetales, which was at the time, an unexpected result. Subsequent phylogenies (e.g. Harper and Saunders 2002; Le Gall and Saunders 2007; Saunders et al. 2018) confirmed this relationship.

Recent studies based on molecular-genetic data supported the transfer of related species of *P. palmata*, namely *P. mollis*, *P. callophyloides*, *P. marginicrassa* and *P. stenogona*, to the genus *Devaleraea* (Saunders et al. 2018; Skriptsova and Kalita 2020; Skriptsova et al. 2022). Six species are currently accepted under the *Palmaria* genus, including *Palmaria decipiens* (Reinsch) Ricker from the Macquarie Island (Southern Pacific), *Palmaria georgica* (Reinsch) Ricker from the Southern Atlantic, *Palmaria integrifolia* Selivanova & Zhigadlova from the Russian Pacific coast, *Palmaria hecatensis* Hawkes from the Northern Pacific, *Palmaria moniliformis* (Blinova & Zinova) Perestenko from the Russian Far East and *P. palmata* from the North Atlantic (Guiry and Guiry 2022). The currently accepted taxonomy for *P. palmata* is given in Table 1. The monotypic nature of the *Palmaria* genus, with only one representative in the Northern Atlantic, was hypothesized by Skriptsova and Kalita (2020). Further studies investigating the phylogenetic relationships between *P. palmata* and the other currently accepted species of the *Palmaria* genus are required to verify this hypothesis.

## Phylogeny and population structure

During the last three decades, genetic-molecular methods allowed for detailed investigations of the phylogenetic relationships of red algae (Freshwater et al. 1994; Ragan et al. 1994). Lindstrom et al. (1996) investigated the radiation of the Palmariaceae based on the comparative analysis of non-coding sequences (ITS) of rDNA from 12 species across the North Atlantic and North Pacific. Four distinct clades across species were identified. *Palmaria palmata* (type variety) and *P. palmata* var. *sarniensis-sobolifera* appeared as an isolated clade and the most divergent from the others. Based on estimates of the divergence rate of ITS sequences, the authors postulated that the species derived from a palmariacean ancestor which occurred in the Pacific during the late Miocene-Pliocene i.e. about 12 million years before present. While several species radiated in the North Pacific, *P.*

**Table 1** Currently accepted classification for *P. palmata*

Kingdom	Plantae
Phylum	Rhodophyta
Class	Floridophyceae
Subclass	Nemaliophycidae
Order	Palmariales
Family	Palmariaceae
Genus	<i>Palmaria</i>
Species	<i>Palmaria palmata</i>

*palmata* dispersed in the Atlantic approximately 3.5 million years ago, corresponding to the opening of the Bering Strait.

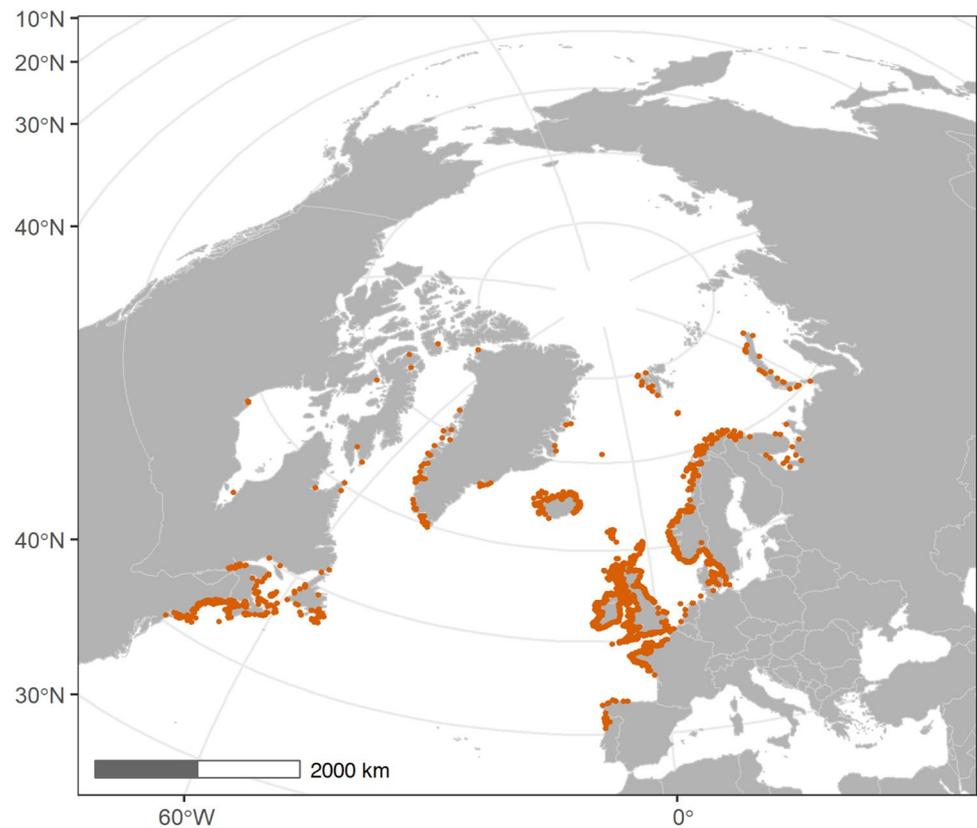
A phylogeographic study by Provan et al. (2005), later confirmed by Li et al. (2015), showed that glaciation events of the mid-Pleistocene (0.13–0.78 million years before present) have shaped the biogeography of *P. palmata*, like other macroalgal species. Populations have persisted in a series of refugia (e.g. the English channel, Western coast of Ireland, North America, Iceland) during periods of unfavourable climatic conditions, then recolonized new areas. Genetic data from Arctic populations (Southern Greenland and Hudson Bay, Canada) revealed that these Arctic collections of *P. palmata* are extensions of Northwest Atlantic populations (Saunders and McDevit 2013; Bringloe et al. 2020). The analysis of plastid DNA of specimens collected along the coast of Europe revealed relatively large intraspecific variation and more specifically a genetic divergence between Northern/Eastern populations on the one hand and Western populations on the other hand (Provan et al. 2005). The divergence between populations across the Atlantic was inferred from crossing studies of Irish and Canadian isolates producing viable hybrids which however produced poorly viable tetraspores (van der Meer 1987). Both isolates were then regarded as belonging to a single species in the process of splitting into sibling species. Divergence among European and American populations was later confirmed by genetic studies of Provan et al. (2005), Li et al. (2015), Bringloe and Saunders (2018) as well as Saunders et al. (2018) who nevertheless observed genetic similarities in Canadian specimens with European ones, suggesting that migration from the Northeast to the Northwest Atlantic has occurred at least once. A divergence time of approximately 1 million years between populations from both sides of the Atlantic was estimated by Bringloe and Saunders (2018).

## Distribution

### Geographic distribution

Based on the taxonomic studies cited above, the distribution of *P. palmata* is primarily confined to the North Atlantic coasts within a latitude range of approximately 40 to 80 °N. The species has been observed from Long Island (Provan et al. 2005) to the Devon Island (GBIF 2022) on the Western Atlantic shores and from Northern Portugal (Fernández-Mendoza et al. 2002; Araújo et al. 2009; GBIF 2022) to the far reaches of the Barents Sea i.e. Spitzbergen and Novaya Zemlya (Guliksen et al. 1999; Fredriksen et al. 2019; Marambio and Bischof 2021; Mikhaylova 2021) in the Eastern Atlantic. It is also present along the shores of Atlantic islands e.g. Faroe Islands and Iceland (Fig. 2). However, it was explicitly deleted from the list of species found in the Azores, and considered

**Fig. 2** Distribution of *Palmaria palmata* based on observation and collection reports of the species from the Ocean Biodiversity Information System (OBIS 2022) and Global Biodiversity Information Facility (GBIF 2022) databases, distribution sources from AlgaeBase (Guiry and Guiry 2022) as well as records of observations from the cited literature and personal observations from the authors. According to recent taxonomic studies, *P. palmata* is primarily confined to the North Atlantic. Therefore, records of the species as here presented exclude the relatively few registrations in the Pacific Ocean. See details in the text (“Geographic distribution” subsection)



misidentified in previous floristic inventories (Tittley and Neto 2005). Registration of the species in Greenland includes historical identifications (Rosenvinge 1898, 1983; Jónsson 1904) and herbarium specimens in the National History Museum of the University of Copenhagen, as well as more recent observations (Pedersen 1976; Hansen and Johansen 1998; Krause-Jensen et al. 2020), mainly along the West Coast from 60°N (Cape Farewell) to 78°N, but also along the Eastern coast (S. Wegeberg and O. Geertz-Hansen, unpubl. observations). The species has also been reported in the Russian Arctic along the Murman Coast, the White Sea and both Western (Barents Sea) and Eastern coasts (Kara Sea) (Mikhaylova 2021; GBIF 2022). It is even reported in a checklist further East on the Russian Arctic coastline i.e. from the Kara Sea to the Western part of the Chukchi Sea and the Wrangel Island (but not observed in the Laptev Sea) (Vinogradova 1999). Observation records should be verified genetically to confirm the presence of *P. palmata* in these regions.

The morphology of *P. palmata* is similar to that of closely related species, e.g. *Devaleraea mollis* (formerly assigned to the *Palmaria* genus) and *P. hecatensis*. Therefore, misidentifications may occur. Distribution records of *P. palmata* in the North Pacific including Southern Alaska, Aleutian Islands, Kuril Islands and Russian shores of the Sea of Japan, are now largely attributed to the confusion with sibling species, as supported by genetic studies (Kraan and Guiry

2006; Skriptsova and Kalita 2020). Recent genetic analyses resolved the previously identified *P. palmata* from Japan as a new species, namely *Devaleraea inkyuleei* (Skriptsova et al. 2022). Although some Arctic specimens (from Greenland and the Canadian Arctic) appear to originate from Western Atlantic populations (Saunders and McDevit 2013; Bringloe et al. 2020), the question whether *P. palmata* is present in the northerly reaches of the Pacific region (Northern Alaska and Russian Far East) remains unanswered. Additional phylogeographic studies are needed to resolve the population genetic structure of *P. palmata* across the arctic as well as phylogenetic relationships with closely related species.

The currently available distribution records of *P. palmata* in AlgaeBase (Guiry and Guiry 2022) include relatively recent references to the species in tropical waters including the Galapagos islands, the Pacific coast of Mexico, Ghana, and Southeast Asia. However, reports from these checklists have not been genetically verified. Given the cold-water preference of the species and the induction of fertility at low irradiance (see “Reproduction” section), these reports most likely arise from misidentifications. The distribution range of *P. palmata* is likely to be affected by the current scenario of climate change resulting in increasing sea temperatures. The species may face local extinctions in areas near its thermal tolerance limit e.g. Northern Portugal, North-western Spain, due to global warming.

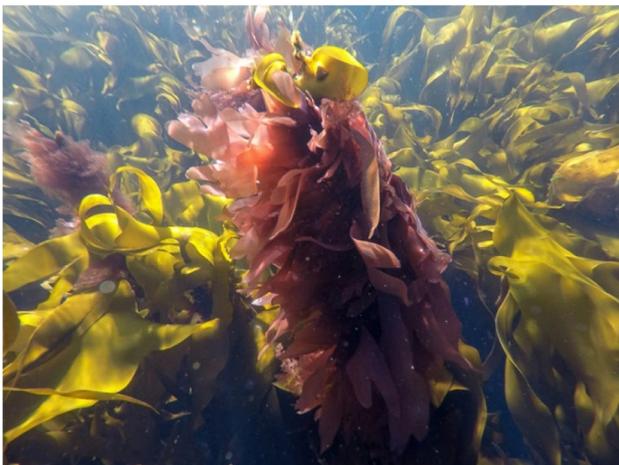
## Local vertical distribution

Throughout its distribution range, *P. palmata* is found attached to bedrock and boulders in the intertidal and subtidal zones, in both sheltered and moderately exposed shores. It is also commonly found as an epiphyte on other macroalgae, especially on the stipes of the kelp *Laminaria hyperborea* (Fig. 3) and *Laminaria digitata*, and fronds of *Fucus serratus* and *Cystoseira baccata* (Faes and Viejo 2003; Garbary et al. 2012). As for other marine photosynthetic organisms, light is a major factor limiting its vertical distribution. Although the species is more abundant in the first 10 m below the surface, it can be observed down to a maximum depth of approximately 20 m in offshore shoals with exceptionally clear waters. In the intertidal zone, exposure to drought stress at low tide as well as grazing by molluscs are the main factors governing the upper distribution limit (Cabioch et al. 2006). In subtidal environments, Hawkins and Harkin (1985) observed the rapid colonization of open substrates by *P. palmata*, in areas where the macroalgal canopy was removed indicating that the competition with kelps restricts this species to a primarily epiphytic habitat in such ecosystems.

## Environmental requirements and stressors

### Temperature

Temperature is one of the most critical abiotic factors directly affecting photosynthetic performance, growth and reproduction. *Palmaria palmata* is distributed across Arctic and warm temperate environments with sea temperatures from near 0 °C up to over 20 °C and variable thermic



**Fig. 3** Epiphytic *Palmaria palmata* growing on a stipe of *Laminaria hyperborea* (Remøya, Norway). Photograph by Annelise Chapman

amplitudes (Martínez and Rico 2002; Karsten et al. 2003; Le Gall et al. 2004b). Based on cultivation studies of wild-collected material, the optimal growth temperature ranges between 6 and 12 °C (Morgan and Simpson 1981b; Corey et al. 2012) depending on the origin of the strain. Reduced productivity is reported above 14 °C (Corey et al. 2013) and increased mortality of the biomass at 21 °C (Matos et al. 2006). *Palmaria palmata* was shown to be less resistant to oxidative stress caused by elevated temperatures (> 20 °C) and hypo- and hyper salinity compared to a proliferative macroalgal species of the subtidal zone i.e. *Grateloupia turuturu* (Liu and Pang 2010). This was attributed to the lower efficiency of antioxidant enzymatic systems to scavenge reactive oxygen species (ROS) upon stress.

### Salinity

*Palmaria palmata* is often associated with habitats characterized by relatively stable salinity conditions (30 – 40 PSU). However, it is also found in the intertidal zone where it may be exposed to rapid variations in salinity (due to precipitation). Some populations are exposed to a seasonal decrease in seawater salinity due to e.g. large discharge of ice-melting water in boreal and arctic regions. A strong photosynthesis inhibition and mortality at 15 PSU was reported for *P. palmata* from Spitzbergen under controlled conditions (Karsten et al. 2003). In contrast, the specific growth rate of individual fronds originating from Danish inner-waters and cultivated in tanks was maximal at 15 PSU compared to 25 and 35 PSU (Schmedes and Nielsen 2020b) suggesting that ecotypes of *P. palmata* are adapted to a wide range of salinity conditions.

### Irradiance

As other plants exposed to high photosynthetically active radiation (PAR) and ultraviolet (UV) radiation, *P. palmata* can regulate its photosynthetic activity in response to diurnal variations in light conditions. Photoinhibition is a photoprotective mechanism to avoid photodamage resulting from the formation of ROS upon high PAR and UV irradiation (Hanelt and Nultsch 1995; Karsten et al. 2003; Marambio and Bischof 2021). As for other macroalgal species, inhibition of the photosynthetic activity of *P. palmata* is mainly caused by the UV-B wavelengths (Pakker et al. 2000; Karsten et al. 2001). The physiological adaptation to photooxidative stress involves reversible damage to light-harvesting pigments i.e. phycoerythrin, phycocyanin and chlorophyll *a*, leading to the dissipation of the absorbed excess energy in the form of heat and enables rapid recovery after the offset of stressful conditions (Hanelt and Nultsch 1995). Chronic photoinhibition entails DNA damage and the alteration of a key subunit of the photosystem II (i.e. D1

protein) requiring de novo synthesis and a longer recovery process (Pakker et al. 2000). Such damage may negatively affect physiological functions and the growth of the plant. The photoreactivation from DNA damage in *P. palmata* (like in higher plants) involves enzymatic reactions which are highly temperature-dependant.

Seasonal studies of the photosynthetic pigments of *P. palmata* report a decrease in chlorophyll *a* and light-harvesting pigments during the summer months (Hanelt and Nultsch 1995; Marambio and Bischof 2021), correlating with field observations of greenish or bleached *P. palmata* thalli. In culture conditions and under nitrogen depletion, bleaching of *P. palmata* fronds occurs at irradiance level above 200  $\mu\text{mol photons m}^{-2} \text{s}^{-1}$  PAR after 2–3 weeks, which can lead to the fragmentation of the thallus (Edwards 2007). However, fronds fully recover their red pigmentation within seven days after adding one pulse of *f*/2 growth medium under laboratory conditions (Schmedes & Nielsen 2020a, b). Pigment accumulation in *P. palmata* grown under high nitrogen concentrations is also influenced by light quality. Higher concentrations of chlorophyll *a* and  $\beta$ -carotene were measured in individuals grown under white or blue light, compared to red light (Parjikolaei et al. 2013).

Light-acclimation by photoinhibition is habitat-specific with a lower ability of subtidal populations to down-regulate photosynthesis. This was highlighted in a comparative study of the photosynthetic performance of several arctic macroalgal species exposed to natural PAR and UV radiation where *P. palmata* showed greater tolerance to radiation stress compared to species bound to deeper-water habitats (Karsten et al. 2001). Light-acclimation is also affected by other abiotic stress factors such as fluctuations in salinity (Karsten et al. 2003) and temperature (Marambio and Bischof 2021). In addition, *P. palmata* synthesizes and accumulates photo-protective molecules, namely mycosporine-like amino acids (MAAs) to protect from oxidative stress and degradation of biomolecules (DNA, proteins) from UV radiation (Karsten and Wiencke 1999; Lalegerie et al. 2020).

## Nutrients

Macroalgae extract nutrients from their surrounding environment by uptake across the thallus area. Both ammonium ( $\text{NH}_4^+$ ) and nitrate ( $\text{NO}_3^-$ ) are nitrogen sources for macroalgal growth although *P. palmata* has a greater affinity for  $\text{NH}_4^+$  (Morgan and Simpson 1981a; Corey et al. 2013). Under controlled conditions, Lubsch and Timmermans (2020) revealed a synchronized pulse-like pattern of both  $\text{NO}_3^-$  and phosphate ( $\text{PO}_4^{3-}$ ) uptake with intervals of about 7 days which, according to the authors, can be a physiological response to intra- and interspecific competition. Nitrogen, phosphorus and carbon (*P. palmata* is able to use both  $\text{CO}_2$  and  $\text{HCO}_3^-$ ) can be stored to support growth under

situations of nutrient limitation. Besides nutrient availability, irradiance plays an important role in nutrient storage in *P. palmata*. Higher nitrogen and phosphorus levels but lower soluble carbohydrate contents were measured in individuals acclimated to low irradiance compared to plants grown under high irradiance (Morgan and Simpson 1981a; Martínez and Rico 2002). Part of the nitrogen is stored in the form of phycoerythrin (involved in light absorption) to improve photosynthesis under low irradiance and to enhance growth under optimal nutrient conditions (Martínez and Rico 2002).

## Biotic factors

The growth of *P. palmata* and colonization of substrates is limited by competitive interactions with other macroalgal species. Following canopy removal experiments, Hawkins and Harkin (1985) reported *P. palmata* as one of the early colonizers of open rocky substrate although the species may later be overtopped by more rapidly growing kelp species e.g. *L. digitata*. Grazing is a major factor structuring macroalgal communities and affecting biomass density (Cabioch et al. 2006). Various gastropods e.g. sea hare (*Aplysia punctata*), sea snail (*Littorina littorea*), abalone (*Haliotis tuberculata*), limpets (*Patella* spp.), as well as sea urchins and amphipods, may feed on adult and juvenile fronds of *P. palmata*.

*Palmaria palmata*, especially old individuals, is commonly affected by epiphytes such as filamentous red (e.g. *Acrochaetium secundatum*) (Sanderson 2015) and brown algae (Ectocarpaceae) (Sanderson et al. 2012; Badis et al. 2019), competing with the host plant for nutrients and light. In addition, colonization by epibionts e.g. encrusting bryozoan (*Membranipora membranacea*) can result in mechanical stress and tissue damage to the host plant and may reduce the reproductive output. In temperate coastal waters, epibionts typically settle during late spring and early summer. Temperature changes from winter to summer greatly affects the population dynamics of bryozoan and colonization of macroalgal fronds (Saunders et al. 2010).

The cellular invasion of a sibling species i.e. *D. mollis*, by an oomycete parasite (*Petersenia palmariae*) was described in detail by Poeschel and van der Meer (1985). Spore infection by an intracellular oomycete was later reported by Sanderson (2015) from a *P. palmata* culture maintained in tanks. Further investigation of this endoparasite by Badis et al. (2019) using microscopy and molecular methods described the infection of spores and young gametophytes of *P. palmata* by a novel oomycete species i.e. *Olpidiopsis palmariae*. *Olpidiopsis* is an abundant and widespread genus including known pathogens of cultivated red macroalgae (e.g. *Pyropia* spp.) and causing substantial economic loss in the Asian macroalgae industry (Badis et al. 2020). Such

infections may be a major cause of unexplained spore mortality in *P. palmata* cultures (see the “Cultivation” section).

## Reproduction and growth

### Life history

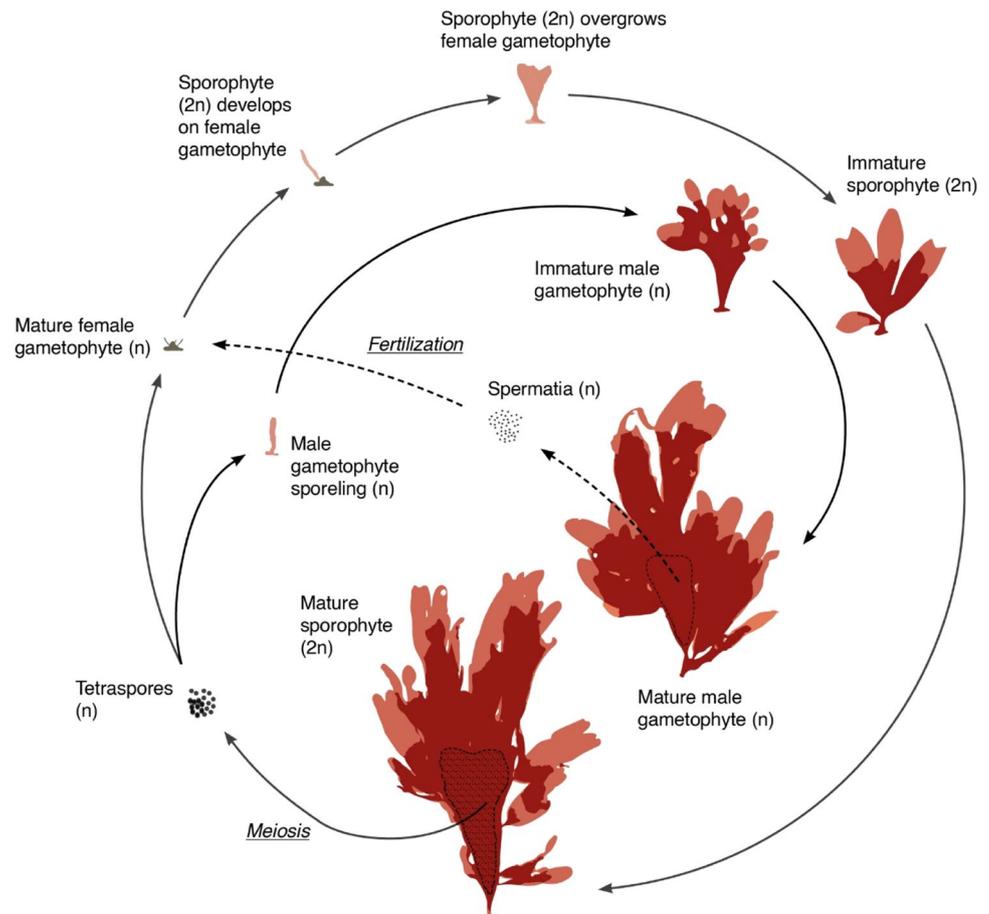
*Palmaria palmata* is considered pseudo-perennial since the fronds grow, reproduce and senesce from a holdfast that survives multiple years. It has a complex heteromorphic diplohaplontic life history (Fig. 4) which is unique among the Rhodophyta and had remained a mystery for phycologists for a long time. Blade-like male gametophytes and tetrasporophytic thalli were described by van der Meer and Chen (1979) but the life history of *P. palmata* was first revealed by van der Meer and Todd (1980), by crossing a red-pigmented female gametophyte with a mutant green male. After fertilisation and development, a green diploid tetrasporophyte could be observed attached to the red-pigmented female haploid thallus. The life history of *P. palmata* has been further described in the scientific literature focusing on improving

the cultivation of the species (van den Hoek et al. 1995; Werner and Dring 2011a; Grote 2019).

According to van der Meer and Todd (1980), haploid tetraspores develop within the sori of the frond of diploid tetrasporophytes through meiosis. The haploid tetraspores germinate into either microscopic female or blade-like male gametophytes of a similar morphology to diploid tetrasporophytes. The female gametophyte develops oogonia with trichogynes (i.e. hair-like structures) to catch spermata (i.e. non-motile male gametes) released from a mature male gametophyte (at least one year old). The zygote resulting from the fertilization of a female gamete by a spermatium grows into a diploid tetrasporophyte from the encrusting female gametophyte, which is overgrown at an early stage as the tetrasporophyte develops its own discoid holdfast.

The life history of most red algal species (e.g. Gigartinales, Bangiales) often includes different morphologies between the tetrasporophyte and the gametophyte (male and female). Further, as opposed to the commonly observed pattern within the Rhodophyta, the carpogonium (female sexual organ) does not develop into a carposporophyte following fertilization, i.e. a diploid microscopic structure releasing diploid carpospores into the environment from which

**Fig. 4** Life cycle of *Palmaria palmata* as described by van der Meer and Todd (1980). The dashed-line areas on mature sporophyte (with dotted fill) and gametophyte fronds indicate tetrasporangial (i.e. sorus) and spermatangial tissues respectively



multiple tetrasporophytes may develop, allowing amplification of the zygote (Fredericq and Hommersand 1990). Instead, the fertilised carpogonium of *P. palmata* develops into a single tetrasporophyte, which is already attached to the substrate (van den Hoek et al. 1995). Hence, the life history of *P. palmata* differs from that of most red algae.

## Fertility and phenology

Like the majority of macroalgal species, *P. palmata* relies on the production and release of spores for the reproduction, dissemination and colonization of substrata. To become fertile and induce the maturation of spores, *P. palmata* has specific environmental requirements regarding temperature and light conditions, which influence the timing of reproduction in situ (phenology).

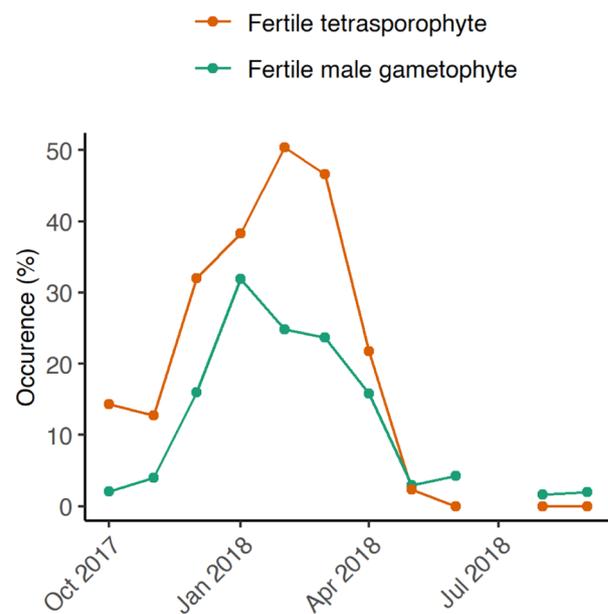
The development and maturation of tetrasporangial tissue (Fig. 5) is triggered by short day conditions, i.e. 8 h of light per day and a temperature of 10 °C or below (Pang and Lüning 2006; Schmedes and Nielsen 2020a). However, development of tetrasporangia was reported under a photoperiod of 12:12 h (light:dark) but at a lower irradiance, i.e. 5 to 10  $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ , than used in the abovementioned studies (Werner and Dring 2011a). This suggests that a prolonged low exposure to PAR is the actual trigger of fertility induction in *P. palmata*. This photoperiodic control of the spore development combined with a rather specific temperature requirement narrows the

reproductive window, as well as the distribution of the species to temperate and arctic regions which are characterized by a strong seasonality. As argued by Pang and Lüning (2006), this timing may be a strategy to ensure a vigorous vegetative growth in spring under optimal irradiance and daylength conditions.

The seasonality of tetrasporophyte and male gametophyte maturation has been investigated in several studies. In mid-Norway (Trondheimsfjord), mature tetrasporophytes were found from October to May, with the occurrence of mature specimens peaking from December to February (up to 50% of all individuals, Fig. 6). Mature male gametophytes were observed during a slightly shorter time frame, i.e. from November to April, with a peak in January (Bøe 2019; Schmedes 2020). Monthly samples of *P. palmata* in the Isle of Man revealed a similar pattern of mature tetrasporophytes and male gametophytes being observed from November to July (Kain 1982). This is also supported by observations of mature specimens (tetrasporophytes and male gametophytes) from late autumn to late spring along the Eastern coast of the North Atlantic (Faes and Viejo 2003; Le Gall et al. 2004a; Pang and Lüning 2006; Edwards 2007; Werner and Dring 2011a; Schmedes and Nielsen 2020b) and Greenland (Rosenvinge 1898; Jónsson 1904). However, Bird and McLachlan (1992) describes *P. palmata* as fertile in summer to late autumn for the Maritime Provinces



**Fig. 5** Fertile tetrasporophyte of *Palmaria palmata*. Tetrasporangial tissues are visible as marble-like structures on the distal part of the frond. These tissues may also appear on the basal or middle parts. Photograph by Peter Schmedes



**Fig. 6** Year-round reproductive status of *Palmaria palmata* thalli collected at Storsteinan (Trondheimsfjord, Norway) between October 2017 and September 2018. The points represent the percentage of occurrence of fertile male gametophytes and tetrasporophytes over  $n$  sampled individuals ( $n$  ranging from 141 to 266 per sampling date). Data from Bøe (2019) and Schmedes (2020)

of Canada, although “well-developed and fertile fronds are found throughout the year”.

### Sori and spore development

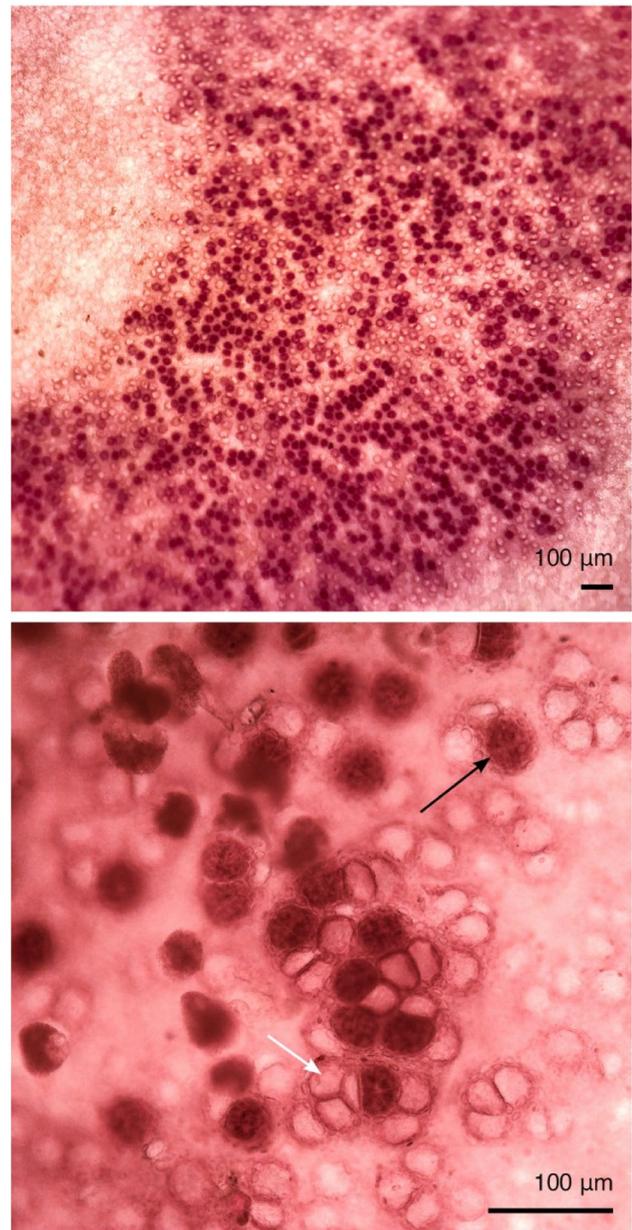
The formation of sori in *P. palmata* appears to be governed by meristematic tissues as observed in kelp species (e.g. *L. digitata*, *Saccharina latissima*) in which the meristem produces inhibitors of sporangium development during the season of rapid growth (Buchholz and Lüning 1999; Pang and Lüning 2004b). In these species, suboptimal growth conditions under low irradiance and temperature result in the decrease in the production of these inhibitors leading to sori formation. Likewise, isolating the meristem from the rest of the blade induces the development of sporangia (Pang and Lüning 2004b). Titlyanov et al. (2006) observed a similar pattern in *P. palmata* where the formation of tetraspores in submeristematic fragments was stimulated by isolation from the meristem. However, cutting the marginal edges (meristem) of *P. palmata* fronds does not systematically result in sorus formation (P. Schmedes, pers. observation). Micrographs of fertile tissue of *P. palmata* are shown in Fig. 7.

Sporangium formation is initiated by the differentiation of outer cortex cells into sporangial initials i.e. tetrasporocytes, and stalk cells (Pueschel 1979). Tetrasporocytes undergo meiosis in a cruciate cleavage to form four tetraspores. Although the knowledge related to tetrasporangial formation is limited, available information reveals that cleavages in Rhodophyta generally occur either successively or simultaneously i.e. the first cleavage is completed before the next or all cleavages are completed at the same time (Pueschel and Cole 1982). *Palmaria palmata*, on the other hand, is characterized by an intermediate process in which the second cleavage starts just before the completion of the first division (Pueschel 1979). Following the release of tetraspores, the primary stalk cells form new stalk cells and tetrasporocytes, and the entire process of tetrasporogenesis is then repeated.

High levels of tyramine have been measured in fertile sporophytic tissue compared to the concentrations measured in non-fertile fronds suggesting that this biogenic polyamine is involved in tetrasporogenesis in *P. palmata* (Schmedes 2020). Low levels of putrescine were measured and both spermine and spermidine were not detected, in contrast with studies reporting the influence of these polyamines in the maturation of reproductive structures in other red algae species (Guzmán-Urióstegui et al. 2002; García-Jiménez and Robaina 2012). More research is needed to properly understand the physiological mechanisms of sorus formation and maturation in *P. palmata*.

### Spore dispersal

Mature spores released to the surrounding environment are rather large (approx. 30  $\mu\text{m}$ ) and not motile (Le Gall et al.



**Fig. 7** Microscopic views (top: 100x, bottom: 250x) of a maturing *Palmaria palmata* sorus bearing fertile tetrasporangia containing 4 tetraspores (black arrow) to be released at full ripeness. Hyaline cells (white arrow) are sporangia undergoing maturation. Photographs by Peter Schmedes

2004b). Therefore, their dispersal is governed by hydrodynamic conditions. Norton (1992) suggested that small macroalgal species (compared to e.g. large kelps) release their propagules quite close to the substratum thus limiting the distance of dispersal. Under controlled laboratory conditions, the spores settle and firmly attach to the substratum after 6 h (Le Gall et al. 2004b). However, the settlement process of macroalgal spores and colonization of new substrates may be adversely affected by abiotic factors such as turbidity

(Vadas et al. 1992). The drifting of vegetative material of *P. palmata* as well as organic substrates (e.g. stipes of *L. hyperborea*) following storm events may allow the dispersion of the species over larger distances. However, due to the single non-motile spore releasing phase in its life cycle, the dispersibility of *P. palmata* is considered low. Studies highlighting the geographically structured genetic patterns among populations (see “Taxonomy and phylogeny” section and references therein) support the relatively poor dispersion ability of the species.

## Growth

The vegetative growth of *P. palmata* from spore germination has been described in the literature (Le Gall et al. 2004b; Pang and Lüning 2006). Spore settlement is facilitated by the development of a mucilage covering the entire spore and consolidating the attachment to the substrate. The first cell divisions occur in a plane perpendicular to the substratum then in all 3 dimensions resulting in a hemispherical attachment disc from which the frond develops from a single apical cell (Deniaud et al. 2006). As observed in higher plants, the morphogenesis is governed by cortical microtubules during mitosis marking the site of future cellular cleavage and regulating the position of relevant organelles such as the Golgi apparatus, involved in the synthesis of cell-wall polysaccharides (Le Gall et al. 2004c). During germination and the first stages of germling development, the biosynthesis of the cell-wall matrix, mainly composed of xylose, occurs concurrently to the degradation of starch granules (floridean starch) contained in the spores. Young sporeling growing close to each other will often coalesce at an early stage resulting in individuals with several fronds. This may be a strategy from the plant to enhance photosynthetic efficiency and increase germling survival (Deniaud et al. 2006). The vegetative growth of *P. palmata* (both sporophyte and male gametophyte) is supported by meristematic cells located in marginal tissues of the fronds. New fronds can also grow from marginal proliferations on old thalli (Fig. 8). Clusters of meristematic tissues (wart-like structures) can also be observed scattered in the cortical layer of the thallus (Titlyanov and Titlyanova 2006).

In wild populations the growth rate is maximal between May and July then decreases to eventually become negative in summer because of frond breakage. This is due to a combination of factors such as high irradiance, high temperature, low nutrients, grazing by invertebrates and the presence of epibionts on the surface of the fronds (Faes and Viejo 2003). Plant density (intra- and interspecific competition), grazing and wave impact are important factors for the mortality of young *P. palmata* plants. Recorded maximal growth rates range from 0.9 to 1.5% day<sup>-1</sup> in Northern Ireland and Northern Spain respectively (Faes and Viejo 2003) and was



**Fig. 8** Vegetative growth of new fronds of *Palmaria palmata* from old thalli fragments. Photograph by Peter Schmedes

estimated to over 4% day<sup>-1</sup> in the Bay of Fundy (Canada) (Lukeman et al. 2012).

## Chemical and nutrient composition

Due to the commercial interest for *P. palmata* mainly in food application, the chemical composition and nutrient content of the species have been studied extensively. Table 2 provides an overview of the proximate composition and levels of important nutritional elements in *P. palmata* including potentially toxic compounds. Like most macroalgal species, the moisture content of *P. palmata* is very high and accounts for up to 88% of the fresh biomass. As generally observed in macroalgae, the moisture content of *P. palmata* is highest during winter and spring (Rødde et al. 2004).

## Carbohydrates

Carbohydrates make up to 74% of the dry weight (DW) of *P. palmata*. Figure 9 illustrates the seasonal variation in the carbohydrate composition of *P. palmata*. Xylans, which are the primary component of the cell-wall of this species, are essentially composed of  $\beta$ -(1  $\rightarrow$  4)- and  $\beta$ -(1  $\rightarrow$  3)-linked D-xylose units in a proportion of about 4:1 (Lahaye et al. 1993; Deniaud et al. 2003). Being indigestible, xylans are regarded as the main source of dietary fibres in *P. palmata* and are present in both water-soluble and insoluble forms (Fig. 9). Minor amounts of cellulose (i.e. insoluble glucans, about 3% DW) are also found as structural carbohydrates. This species also contains water-soluble low molecular weight carbohydrates mainly in the form of floridoside ( $\alpha$ -D-galactopyranosyl-(1–2)-glycerol) and to a lesser extent floridean starch (amylopectin-like glucan).

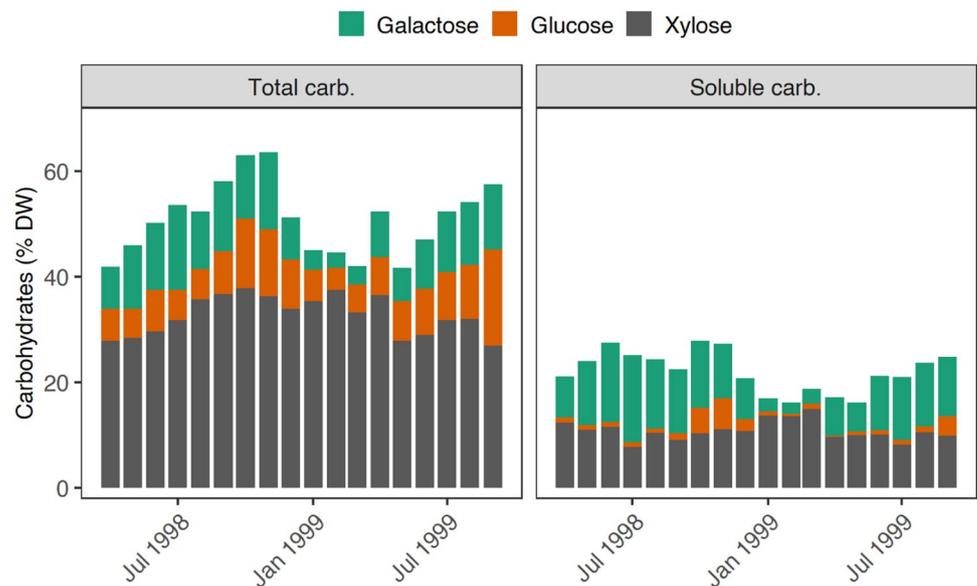
**Table 2** Chemical composition of *Palmaria palmata* reported in the literature

Variable	Unit	Reported values
Moisture	% WW	80 – 88 <sup>[1,2]</sup> ; 82 <sup>[3]</sup> ; 84 <sup>[4]</sup> ; 88 <sup>[5]</sup>
<i>Carbohydrates</i>		
Total	% DW	42 – 64 <sup>[1]</sup> ; 38 – 74 <sup>[2]</sup> ; 38 <sup>[4]</sup> ; 25 <sup>[5]</sup>
Xylans	% DW	24 – 35 <sup>[1]</sup> ; 23 <sup>[4]</sup> ; 19 <sup>[5]</sup>
Floridoside	% DW	3 – 25 <sup>[1]</sup>
<i>Protein</i>		
Total	% DW	11 – 18* <sup>[1]</sup> ; 12 <sup>[3]</sup> ; 15* <sup>[4]</sup> ; 18 <sup>[5]</sup> ; 8 – 9 <sup>[6]</sup> ; 19 <sup>[7]</sup> ; 7–19* <sup>[8]</sup>
EAAAs	% total AA	39 <sup>[3]</sup> ; 33 <sup>[6]</sup> ; 36 <sup>[7]</sup> ; 27 <sup>[8]</sup> ; 44 <sup>[9]</sup>
Phycocerythrin	mg g <sup>-1</sup> DW	2.2 – 7.5 <sup>[5]</sup> ; 5 – 18 <sup>[10]</sup>
<i>Lipids</i>		
Total FA	% DW	0.4 – 3.8 <sup>[2]</sup> ; 1.3 <sup>[3,6]</sup> ; 0.37 <sup>[11]</sup> ; 0.35 – 1.84 <sup>[12]</sup> ; 1.80 <sup>[13]</sup>
Σ Saturated FA	% total FA	28.3 <sup>[11]</sup> ; 22.3 – 57.8 <sup>[12]</sup> ; 60.5 <sup>[13]</sup>
Σ MUFA	% total FA	8.7 <sup>[11]</sup> ; 6.1 – 16.2 <sup>[12]</sup> ; 10.7 <sup>[13]</sup>
Σ PUFA	% total FA	62.9 <sup>[11]</sup> ; 3.1 – 61.8 <sup>[12]</sup> ; 28.8 <sup>[13]</sup>
Σ ω-6	% total FA	8.4 <sup>[11]</sup> ; 0.7 – 4.2 <sup>[12]</sup> ; 2.1 <sup>[13]</sup>
Σ ω-3	% total FA	54.5 <sup>[11]</sup> ; 2.2 – 60.8 <sup>[12]</sup> ; 25.5 <sup>[13]</sup>
<i>Minerals</i>		
Ash	% DW	15 – 27 <sup>[1]</sup> ; 12 – 37 <sup>[2]</sup> ; 42 <sup>[3]</sup> ; 35 <sup>[5]</sup> ; 21 – 23 <sup>[6]</sup>
Na	mg g <sup>-1</sup> DW	11 – 23 <sup>[1]</sup> ; 26 <sup>[5]</sup> ; 3.2 <sup>[11]</sup>
K	mg g <sup>-1</sup> DW	48 – 87 <sup>[1]</sup> ; 106 <sup>[5]</sup> ; 28 <sup>[11]</sup>
Ca	mg g <sup>-1</sup> DW	2.4 – 7.9 <sup>[1]</sup> ; 3.6 <sup>[3]</sup> ; 2.5 <sup>[11]</sup>
Mg	mg g <sup>-1</sup> DW	2.3 – 3.2 <sup>[1]</sup> ; 5.3 <sup>[3]</sup> ; 1.2 <sup>[11]</sup>
Cu	mg kg <sup>-1</sup> DW	4.9 <sup>[3]</sup> ; 4.1 <sup>[11]</sup>
Fe	mg kg <sup>-1</sup> DW	100 <sup>[3]</sup> ; 73 <sup>[11]</sup>
I	mg kg <sup>-1</sup> DW	260 <sup>[3]</sup> ; 74 <sup>[5]</sup> ; 220 <sup>[11]</sup> ; 15 – 790 <sup>[14]</sup>
Mn	mg kg <sup>-1</sup> DW	11 <sup>[3]</sup> ; 4.1 <sup>[11]</sup>
Se	mg kg <sup>-1</sup> DW	0.14 <sup>[3]</sup> ; 0.1 <sup>[11]</sup>
Zn		29 <sup>[3]</sup> ; 42 <sup>[11]</sup>
<i>Heavy metals</i>		
Cd	mg kg <sup>-1</sup> DW	0.06 <sup>[5]</sup> ; 0.05 – 1.6 <sup>[11,14]</sup> ; 0.02 – 2.46 <sup>[15]</sup>
Hg	mg kg <sup>-1</sup> DW	0.003 <sup>[11]</sup> ; <0.043 <sup>[14]</sup> ; 0.004 – 0.314 <sup>[15]</sup>
Pb	mg kg <sup>-1</sup> DW	0.14 <sup>[11]</sup> ; <0.039 – 1.1 <sup>[14]</sup>
As (iAs)	mg kg <sup>-1</sup> DW	(0.18) <sup>[5]</sup> ; 9.2 (0.02) <sup>[11]</sup> ; (0.02 – 1.03) <sup>[14]</sup> ; 7.19 – 12.03 <sup>[15]</sup>
<i>Vitamins</i>		
A (retinol)	mg kg <sup>-1</sup> DW	15.9 – 270 <sup>[16]</sup>
B1 (thiamine)	mg kg <sup>-1</sup> DW	0.7 – 40 <sup>[16]</sup> ; 3 <sup>[17]</sup>
B2 (riboflavin)	mg kg <sup>-1</sup> DW	4.27 – 19.1 <sup>[16]</sup> ; 10 <sup>[17]</sup> ; 7 – 88 <sup>[18]</sup>
B3 (niacin)	mg kg <sup>-1</sup> DW	10 – 83 <sup>[16]</sup> ; 100 <sup>[17]</sup> ; 15 – 35 <sup>[18]</sup>
B6 (pyridoxine)	mg kg <sup>-1</sup> DW	5 – 18 <sup>[18]</sup>
B12 (cobalamine)	μg kg <sup>-1</sup> DW	90 – 240 <sup>[16]</sup> ; 230 <sup>[17]</sup>
C (ascorbic acid)	mg kg <sup>-1</sup> DW	63 – 2000 <sup>[16]</sup> ; 39 – 690 <sup>[19]</sup>
D (calciferols)		n.d
E (tocopherols)	mg kg <sup>-1</sup> DW	14.5 <sup>[11]</sup> ; 22 – 162 <sup>[16]</sup>
K (phyloquinone, menaquinone)	mg kg <sup>-1</sup> DW	2 – 17 <sup>[12]</sup>
Kainic acid	mg kg <sup>-1</sup> DW	0.22 – 130 <sup>[12]</sup> ; <7 – 560 <sup>[20]</sup>

References: [1] Rødde et al. (2004); [2] Morgan et al. (1980b); [3] Mæhre et al. (2014); [4] Jard et al. (2013); [5] Stévant (2019); [6] Bikker et al. (2020); [7] Bjarnadóttir et al. (2018); [8] Galland-Irmouli et al. (1999); [9] Munda and Gubenšek (1976); [10] Guihéneuf et al. (2018); [11] Biancarosa et al. (2018); [12] Mouritsen et al. (2013); [13] Sánchez-Machado et al. (2004); [14] Duinker et al. (2020); [15] Roleda et al. (2019); [16] Kraan (2013); [17] MacArtain et al. (2007); [18] Ryzhik et al. (2021); [19] Nielsen et al. (2021); [20] Jørgensen and Olesen (2018). Abbreviations: DW, dry weight; WW, wet weight; AA, amino acid; EAA, essential amino acid; FA, fatty acid; MUFA, monounsaturated fatty acid; PUFA, polyunsaturated fatty acid; n.d., no data

\*Corrected values for the protein content using the nitrogen-to-protein factor of 4.7

**Fig. 9** Variation in the carbohydrate composition of *Palmaria palmata* harvested in Norway (Trondheimsfjord). Data from Rødde et al. (2004)



Floridoside accounts for below 5% of the DW during winter and up to 25% during the summer months (Rødde et al. 2004). Deniaud et al. (2006) revealed higher carbohydrate levels in sporophytes compared to gametophytes collected at the same period. Floridoside is associated with immunostimulating activity in response to antigens with potential therapeutic applications (Courtois et al. 2008).

### Proteins and amino acids

The protein content of *P. palmata* is one of the main reasons for the commercial interest for this species for both food and feed applications. The protein content of *P. palmata* is high compared to levels reported in most of other edible brown species e.g. *Undaria pinnatifida* and *S. latissima* (ca. 10% DW) (Jard et al. 2013; Mæhre et al. 2014; Stévant 2019) while it is comparable to those reported in *Ulva* sp. (10–26% DW) and lower than levels measured in *Pyropia* sp. (33–47% DW) (Fleurence 1999). Levels up to 35% DW have been reported (Morgan et al. 1980b) although such high values are often derived from a standard nitrogen-to-protein conversion factor of 6.25, overestimating the real protein content due to significant sources of non-protein nitrogenous compounds e.g. nitrate, which can be as high as 18% of the total nitrogen content (Morgan et al. 1980b). A factor of 4.7 was found appropriate to estimate the protein content of *P. palmata* (7–19% DW, Table 2) from the total nitrogen content (Bjarnadóttir et al. 2018). In wild harvested individuals, higher protein contents are found during the winter season (Galland-Irmouli et al. 1999; Rødde et al. 2004) while high levels can be achieved in tank cultivation under low irradiance and high nitrogen supply (Morgan and Simpson 1981a). This is correlated with high levels of proteinaceous

water-soluble pigments, i.e. mainly phycoerythrin and to a lesser extent phycocyanin during the winter compared to summer months (Guihéneuf et al. 2018). The relatively high proportion of essential amino acids (EAAs, Table 2) reflects the nutritional potential of proteins from *P. palmata*. Glutamate and aspartate are the most abundant amino acids in *P. palmata*. The species also contains substantial amounts of alanine, arginine, glycine, serine, leucine and valine as well as EAA that are often limiting in plant food sources i.e. methionine, lysine, threonine, tryptophan (Morgan et al. 1980b; Galland-Irmouli et al. 1999; Mouritsen et al. 2013; Bjarnadóttir et al. 2018). However, some amino acids are present in low levels or may even be seasonally absent in the profile e.g. cysteine and histidine (Galland-Irmouli et al. 1999). It should be noted that ca. 10% of the total amino acid content of dulse is in the form of free amino acids (Mæhre et al. 2015; Aasen et al. 2022). Peptides and MAAs from *P. palmata* are suggested as natural antioxidants in various commercial applications following reported bioactivity in the scientific literature (Yuan et al. 2009; Harnedy et al. 2017).

### Lipids

In *P. palmata*, lipids are distributed among neutral, polar and free fatty acids (FA) as respectively 36%, 37.5% and 26.5% of the total FA (Foseid et al. 2020). Despite a low total lipid content compared to typical plant lipid sources, mono- and polyunsaturated fatty acids (MUFAs and PUFAs) are highly represented as described in Table 2. The lipid fraction of *P. palmata* is rich in long-chain  $\omega$ -3 PUFA, namely eicosapentaenoic acid (EPA), which may account for over 50% of the total lipids (Mouritsen et al. 2013; Lopes et al. 2019). However, it does not contain any significant amounts of

docosahexaenoic acid (DHA) making *P. palmata* an interesting raw material for the production of high purity EPA concentrates (Mishra et al. 1993). Besides, antioxidant activity was reported from the EPA-rich polar lipid fraction of *P. palmata* (Lopes et al. 2019). Geographical location, age of the plant as well as storage of the harvested material greatly affect the lipid profile of the species (Mouritsen et al. 2013). As for other phytochemical constituents, lipids are varying according to seasons or environmental conditions. Schmid et al. (2017) measured significantly higher total FA content in *P. palmata* harvested in May (1.3% DW) compared to October (0.7% DW). The same authors also reported a notably low  $\omega$ -6/ $\omega$ -3 ratio varying from 0.08 to 0.24 across seasons (Schmid et al. 2017). A high  $\omega$ 6/ $\omega$ 3 ratio typical of Western diets (in a range between 15 and 17) is associated with the occurrence of chronic diseases including cardiovascular diseases, cancer, inflammatory and autoimmune diseases. Edible macroalgae, that are generally characterized by a ratio of 1 or below, and particularly *P. palmata*, have the potential to provide a more balanced  $\omega$ -6/ $\omega$ -3 ratio as recommended by international authorities.

### Minerals and ash content

The species is a rich source of minerals (reflected by the ash content) including both macro (Na, K, Ca and Mg) and microelements (e.g. Fe, I, Mn). The ash content is generally lowest during the summer and autumn months and highest during winter and spring (Rødde et al. 2004). *Palmaria palmata* contains higher levels of K compared to Na which is interesting in a nutritional perspective given that diets rich in Na are associated with health risks such as high blood pressure and cardiovascular diseases. It should be noted that the iodine content of *P. palmata* is in the upper range of values reported from red macroalgal species but lower than those of kelp species (Duinker et al. 2020). Reports of the iodine content of commercially available macroalgae, particularly from the Laminariaceae (e.g. *S. latissima*, *L. digitata*) have recently raised concerns from national food safety authorities regarding potentially negative health effects of excessive iodine intakes. Although the iodine content of *P. palmata* may reach values within the range of those measured in brown macroalgae (i.e. up to 790 mg kg<sup>-1</sup> DW measured from screening 26 samples across Norway; Duinker et al. (2020)), average values are lower than the iodine levels found in commercial kelp species and the weekly consumption of a few meals containing *P. palmata* will not expose the consumer to excessive iodine intakes.

### Vitamins

There are several available reports of the vitamin content of dulse (see references in Table 2) but studies comparing

the vitamin levels of edible macroalgal species with dietary reference intakes and with other food sources are scarce. In a meta-analysis of available data on the vitamin C content of macroalgae, Nielsen et al. (2021) concluded that most species (including *P. palmata*) are not a rich source of vitamin C compared to other plants (e.g. rosehip, parsley, broccoli) and that normal consumption will not contribute significantly to the recommended nutrient intake for this compound. This contrasts with historical records of dulse being consumed by Norwegian Vikings during expeditions at sea to protect against scurvy (Mouritsen et al. 2013). It is therefore more likely that the combined consumption of seafood rich in vitamin C (e.g. shellfish, fish roe) effectively prevented this widespread disease among seafarers rather than the consumption of dulse alone. On the other hand, dulse appears to be a good source of vitamin B, particularly B<sub>1</sub> (thiamine), B<sub>2</sub> (riboflavin) and B<sub>12</sub> (cobalamin) (MacArtain et al. 2007; Kraan 2013). As animal products are the most common dietary sources of vitamin B<sub>12</sub>, vegetarians and vegans may therefore be at risk of vitamin B<sub>12</sub> deficiency. Based on maximum levels measured in *P. palmata* i.e. 240 µg kg<sup>-1</sup> DW (Table 2), the daily consumption of 1 g dried material will cover 10% of the recommended nutrient intake of 2.4 µg day<sup>-1</sup> established by the World Health Organization (WHO 2005). Dulse may therefore represent an alternative dietary source of vitamin B<sub>12</sub>. Among the fat-soluble vitamins (i.e. A, D, E and K), *P. palmata* is particularly rich in β-carotene (up to 456 mg kg<sup>-1</sup> DW; Kraan 2013), known as provitamin A (precursor to vitamin A) as well as vitamin K (Mouritsen et al. 2013). To the authors' knowledge there are no records of the vitamin D content of *P. palmata*.

### Potentially toxic compounds (PTEs)

*Palmaria palmata* may accumulate potentially toxic elements (PTEs) such as heavy metals present in the environment either naturally or from anthropogenic activities. Prasher et al. (2004) revealed a greater affinity of *P. palmata* for lead (Pb) and cadmium (Cd) compared to other metals, but the reported concentrations of Pb and Cd in the literature for this species are generally lower than the maximum limit allowed in food supplements in the European Union (EU) (3.0 mg kg<sup>-1</sup> DW for both metals, EU 1881/2006) (Duinker et al. 2020). However, Desideri et al. (2016) reported a Pb level of 4.4 mg kg<sup>-1</sup> DW in a commercial *P. palmata* sample (of unknown origin) indicating that elevated levels may be achieved. Similarly, there are numerous reports of relatively low levels of mercury (Hg) in edible macroalgae including *P. palmata*, below the threshold value of 0.1 mg kg<sup>-1</sup> DW (maximum level in food supplements, EU 1881/2006) (Biancarosa et al. 2018; Duinker et al. 2020). Roleda et al. (2019) investigated seasonal, interannual and geographical variations in contaminants in several edible

macroalgal species. Despite an average Hg content in *P. palmata* ( $0.063 \text{ mg kg}^{-1} \text{ DW}$ ) below the threshold, the authors reported maximum levels ( $0.314 \text{ mg kg}^{-1} \text{ DW}$ ) exceeding the limit. Hence, further attention must be given to monitor the contaminant levels of commercially sold products from *P. palmata*. Inorganic arsenic (iAs) is another PTE that can be found in marine macroalgae. The levels found in *P. palmata* are below the French recommendation of  $3 \text{ mg kg}^{-1} \text{ DW}$  (ANSES 2018) and therefore considered safe in the context of using this species in food applications. Kainic acid is an amino acid which is structurally similar to glutamate, but which can be neurotoxic at high doses. It can be found in variable concentrations in *P. palmata* typically from below the detection limit to relatively low levels (up to  $560 \text{ mg kg}^{-1} \text{ DW}$ , Table 2). Although these levels are much lower than concentrations inducing damages to neurons, Ramsey et al. (1994) measured exceptionally high levels i.e. exceeding  $10,000 \text{ mg kg}^{-1} \text{ DW}$  in a dwarf mutant of *P. palmata* (not a natural strain). Further research is therefore needed to establish human safety standards and identify the factors affecting the biosynthesis and accumulation of this compound in *P. palmata*.

## Exploitation of wild stocks

### Historical uses

Dulse is one of the few macroalgal species that is associated with ancient eating traditions in Europe and North America, with documented uses from centuries back. The use of *duileasc* as food was mentioned in the Brehon laws of Ireland from the fifth century (Rhatigan 2009). Later records from the twelfth century and onward describe the collection, drying and trading of dulse by coastal communities in Ireland, mostly from the Northern and Western coasts, and Scotland (Delaney et al. 2016; Mac Monagail et al. 2017). The species was considered a seasonal staple food, often used as a condiment served with e.g. bread, whey milk and butter, or traded at local markets and fairs. In coastal Norway, *søl* could be eaten either fresh or dried, together with dried fish (Østgaard and Indergaard 2017). Similar uses were reported from historical records from Iceland from the eighth century (Kristjánsson 1980). The fronds were handpicked during the summer, rinsed and spread over the fields for sun-drying. They were then stored in closed barrels to be consumed the rest of the year. Dulse was even used as a trading commodity and medieval legal texts established rights to dulse-rich shores in Iceland (Mouritsen et al. 2013) reflecting the importance of this species during ancient times. There are only limited written records of ancient traditions of eating *P. palmata* in Brittany but the similarity of Breton vernacular

names (e.g. *tellesk*, *terlesk*) with Irish names (*duileasc*, *dilisk*) suggest a common origin (Garineaud 2018). Another Breton name i.e. *bezhin saout* (cattle's seaweed) reflects its use as fodder for livestock. *Palmaria palmata* has also been used as food for over a century by populations along the Northwest Atlantic coast including the state of Maine (USA) and the Canadian Maritime Provinces. Although the species may have been eaten by the Indigenous People of the Maritimes, it is not mentioned in available written records. Tradition for eating this species in North America would most likely originate from its use in the British Isles.

Dulse was known for its bioactive properties and besides being consumed as a sea vegetable, it was also used for specific purposes. Preparations based on boiled dulse were given to children and animals in e.g. Ireland and Wales as a treatment against worms. Anthelmintic effect was later correlated to kainic acid content in *P. palmata*. More generally, dulse provided nutrients to local communities in Northern Atlantic Europe, especially in periods of food scarcity. This has led to some extent to negative associations of eating macroalgae with poverty and famine. There has been in recent decades a renewed interest for using edible species, and particularly *P. palmata*, as a natural, sustainable, healthy and tasty food ingredient with a great potential in culinary applications.

### Harvesting and regulatory frameworks

The current commercial exploitation of *P. palmata* both in Europe and North America largely relies on harvesting wild populations (Chopin and Ugarte 1998; Mac Monagail et al. 2017). On both sides of the Atlantic, the species is collected at low tide in a way that a portion of the frond is left on its substrate to ensure regrowth and perennity of this activity. It is then mainly dried locally to be sold either in the form of whole blades, flakes or powder by small local businesses or by wholesalers. This activity is seasonal i.e. from late spring to autumn (Chopin and Ugarte 1998; Rhatigan 2009) and generally characterized by a low level of mechanization limiting the quantity available to the market. In most cases, harvesting *P. palmata* on the shore is combined with other activities e.g. fishing, farming, foraging shellfish or other macroalgal species (Chopin and Ugarte 1998; Mesnildrey et al. 2012). The amount of harvestable biomass is also limited by interannual variations in population stocks (which may be low due to unfavourable natural conditions) and the accessibility of harvesting sites either by land or by boat. Besides, increasing the commercial use of *P. palmata* based on wild catches may increase pressure on natural populations. These limitations are currently hampering market developments based on wild *P. palmata* biomass.

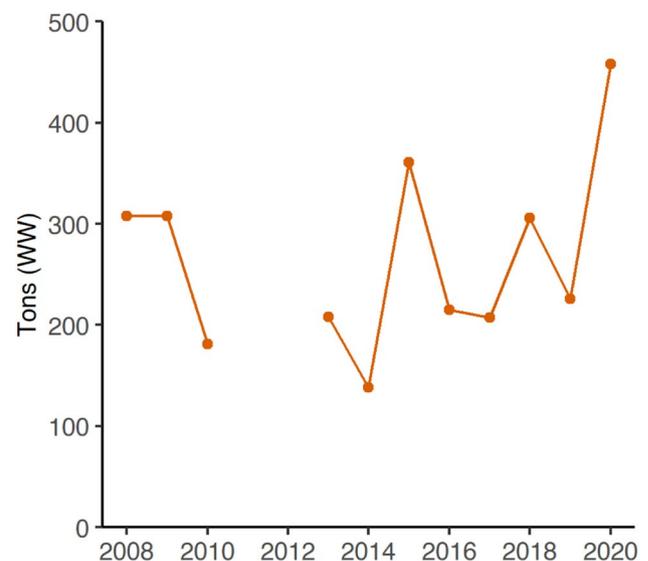
There is currently no systematic reporting of the harvested quantities of dulse from wild populations to the

Food and Agriculture Organization (FAO). This is most likely due to different regulations for harvesting macroalgae on the foreshore across countries. In Canada, *P. palmata* is commercially harvested in the Bay of Fundy, mainly along the shores of Grand Manan Island in New Brunswick. Annual landings in New Brunswick during the period 1982 – 2002 ranged from 38 to 100 dry tonnes (i.e. approximately 380 to 1000 t wet weight, WW) (Chopin and Ugarte 1998). Lower amounts (2 dry tonnes or ca. 20 wet tonnes) were also harvested on the South-eastern coast of Nova Scotia (Garbary et al. 2012). Unlike the industrial exploitation of wild bladder wrack (*Ascophyllum nodosum*) beds which is subject to harvesting licences and monitoring of the resource, there is at present no regulation applied to the commercial wild harvest of *P. palmata* in Canada. Based on a resource assessment before and after harvest and modelling the growth of *P. palmata* during the summer and spring seasons (> 4% growth per day), the removal of 50% of the standing crop on harvesting sites each month was considered sustainable for the resource (Lukeman et al. 2012). In the state of Maine, USA, harvesting macroalgal biomass from wild beds for commercial use is subject to a specific permit issued by the state's Department of Marine Resources (DMR). Harvesters must report their activity to the DMR monthly including harvesting areas, species and landings (State of Maine DMR 2003). However, only the landings for combined macroalgae species are available from DMR's database. The DMR is in the process of establishing a management plan for Maine's harvested macroalgae including *P. palmata*. Until such a plan is implemented, the Maine Seaweed Council (MSC, network of commercial and recreational harvesters) created guidelines outlining the best practices for a sustainable harvest. Based on the knowledge of its members, the council advises that a maximum of 75% of the *P. palmata* biomass at a given site may be sustainably harvested (above the holdfast) to allow for regrowth of the stock (MSC 2022).

In Ireland, the 1933 Foreshore Act prohibits the removal of beach material; hence, a licence from the Department of Housing, Local Government and Heritage is required to harvest macroalgae on the foreshore. Although no data is available regarding annual quantities of *P. palmata* collected, these volumes are assumed to be minimal (< 30 t WW, L. Watson, pers. comm.). In Scotland and Norway access to the macroalgal resource may be given by landowners upon a lease or a fee (NETALGAE 2012). *Palmaria palmata* is also commercially harvested in Iceland but the newly established Icelandic regulatory framework does not address the exploitation of this species (Maack 2019). Official monitoring of the resource does not currently exist in these countries.

In contrast, harvesting is more strictly regulated in France. Dulse is collected mainly in North-western Brittany

(Finistère), where fronds grow up to 60 cm whereas fronds are smaller and thinner further East (*sobolifera-sarniensis* morphotype in Côte d'Armor) and regarded less attractive for food applications. Harvesting of *P. palmata* is allowed from April to December. However, it is not collected during the summer months due to sun-bleaching giving the fronds a white-yellow tint. The commercial harvest of this species, as for other hand-picked macroalgal species, is subject to an annual authorization delivered by local county authorities. Specific decrees may be issued by these authorities to adjust e.g. harvesting areas for resource management purposes as well as minimum cutting heights (normally set to 25 cm) (Mesnildrey et al. 2012; Philippe 2013). Information including the quantities harvested and the location must be reported monthly to the authority by professionals holding an authorization (Philippe 2013). The obtained data for hand-picked dulse in France reveals large interannual variations in the harvested volumes ranging from 138 to 458 t (WW) (Fig. 10) reflecting variations in biomass availability due to abiotic and biotic factors such as grazing from gastropods. Ongoing work in collaboration with research institutions, local authorities and professionals evaluates the biology and the distribution of commercially exploited species including *P. palmata* as well as the effects of the harvesting activities on local standing stocks to define and implement management measures and optimize the harvesting effort (CRPMEM 2021). According to a study of the European market for sea vegetables, France alone produced 90% of the dulse consumed in Europe in 2013, while



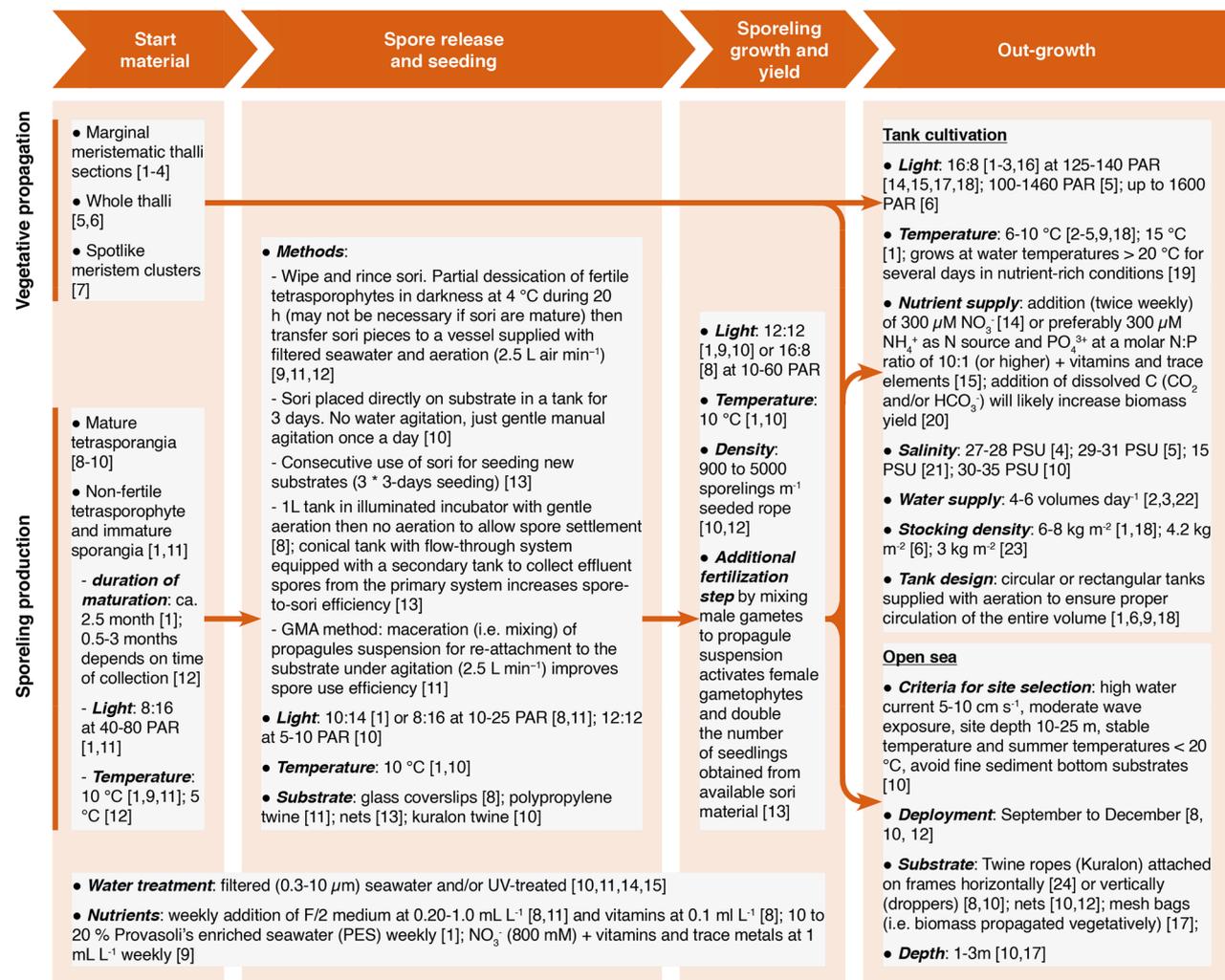
**Fig. 10** Annual harvest of *Palmaria palmata* from wild populations in France, exclusively in Brittany. Data from Mesnildrey et al. (2012), CRPMEM (2020) and Chambre Syndicale des Algues et Végétaux Marins (J.B. Wallaert, pers. comm.)

the remaining 10% came from Ireland, Iceland and North America (BIM 2014).

Systematic reporting of annual landings of wild-harvested *P. palmata* at a local scale (i.e. harvesting sectors) and national level is a prerequisite for establishing management schemes for the sustainable exploitation of this resource. Meanwhile on both sides of the Atlantic, the demand for dulse from industrial retailers is currently outstripping the supply. Therefore, significant efforts have been made during the past decades to cultivate the species to allow for an increased and more consistent supply of *P. palmata* than available from wild populations.

## Cultivation

*Palmaria palmata* can be cultivated either in tanks under controlled conditions in land-based facilities, or at sea following the deployment of seeded substrates (e.g. twine ropes, nets) on cultivation rigs in open-waters. A detailed description of the culture conditions from relevant studies until 2017 is available in a comprehensive review by Grote (2019). The present section provides a summary of the experimental research conducted since 1980 as well as insights on the current status of dulse aquaculture and recent improvements of cultivation techniques (i.e. after 2017).



**Fig. 11** Summary of different methods and optimal conditions for the cultivation of *Palmaria palmata* based on published studies. Light conditions are given as the photoperiod (light:dark) and the irradiance (PAR, in μmol photons m<sup>-2</sup> s<sup>-1</sup>). References: [1] Pang and Lüning (2006); [2] Morgan and Simpson (1981a); [3] Morgan and Simpson (1981b); [4] Titlyanov et al. (2006); [5] Corey et al. (2014); [6] Pang and Lüning (2004a); [7] Titlyanov and Titlyanova (2006); [8] Edwards and Dring (2011); [9] Le Gall et al. (2004b); [10] Wer-

ner and Dring (2011a); [11] Schmedes et al. (2019); [12] Schmedes (2020); [13] Schmedes and Nielsen (2020a); [14] Corey et al. (2012); [15] Corey et al. (2013); [16] Sagert and Schubert (2000); [17] Martínez et al. (2006); [18] Kim et al. (2013); [19] Levinsen (2020); [20] Grote (2019); [21] Schmedes and Nielsen (2020b); [22] Evans and Langdon (2000); [23] Matos et al. (2006); [24] Sanderson et al. (2012)

The main bottlenecks to achieve commercial production are also identified. Key features for the cultivation of *P. palmata* following different strategies i.e. vegetative propagation or sporeling production, and the optimal conditions for the successive steps of the process based on the state-of-the-art knowledge, are summarized in the Fig. 11.

### Cultivation techniques

Small scale experiments of *P. palmata* cultivation have been carried out in tanks based on the vegetative propagation of juvenile fronds (Morgan et al. 1980a), whole adult thalli (Pang and Lüning 2004a; Corey et al. 2014), apical meristematic thallus pieces (Morgan and Simpson 1981a, b; Pang and Lüning 2006), marginal proliferations (Titlyanov et al. 2006; Schmedes and Nielsen 2020b) and isolated meristematic fragments (Titlyanov and Titlyanova 2006) as starting material for land-based cultivation. While acceptable growth rates have been achieved under experimental settings e.g. 8–12% day<sup>-1</sup> (Morgan and Simpson 1981b; Pang and Lüning 2004a; Sanderson 2015; Manríquez-Hernández et al. 2016), the main bottlenecks for establishing a commercially viable cultivation based on vegetative propagation are related to the difficulty of building up high stocking densities of biomass free of epiphytes on a large scale and maintaining such growth rates over time while avoiding losses of biomass from unintended sporulation events. The vegetative growth of *P. palmata* has also been tested at sea by inserting thalli into cultivation ropes (Browne 2001; Bak 2019) although this method is time-consuming and individuals may detach from the action of waves and currents, limiting its viability on a commercial scale. Alternatively, fronds can be placed into mesh bags attached to vertical ropes as reported by Martínez et al. (2006) but self-shading under high stocking densities will limit growth rates.

Other methods for the cultivation of *P. palmata* requires the seeding of growth substrates either using released tetraspores (Browne 2001; Le Gall et al. 2004b; Sanderson 2006; Edwards 2007; Werner and Dring 2011a; Schmedes 2020) or by direct seeding using germinated gametophytes (Schmedes et al. 2019). These methods have gained increasing attention since they may allow the production of biomass on a larger scale through a hatchery step, as for the cultivation of other species of commercial interest, e.g. *S. latissima*. However, the biology of *P. palmata* and cultivation technology are more complex than those of kelp species (Redmond et al. 2014), which limits the development of commercial cultivation operations despite an increasing demand for this species from several markets including the food sector.

Experimental open-water cultivation of *P. palmata* has been demonstrated using vertical droppers or nets attached to longlines suspended below the surface (Sanderson 2006; Edwards 2007; Edwards and Dring 2011; Sanderson et al.

2012; Schmedes 2020). Data from the literature reports appropriate seedling densities for open-water cultivation of *P. palmata*, ranging from 9 to 50 individuals cm<sup>-1</sup> substrate (Werner and Dring 2011a; Schmedes 2020). Besides, deploying well-grown seedlings (minimum size 3–8 mm) (Werner and Dring 2011b; Sanderson et al. 2012) during the autumn or early winter (instead of summer) (Werner and Dring 2011b) are strategies promoting the growth of *P. palmata* against epiphytes and fouling competitors such as other macroalgae (e.g. *Ectocarpus* spp., *Ulva* spp., *S. latissima*) and hydroids. Epiphytes affect not only the growth but may also compromise the quality of the biomass to be used in commercial applications (e.g. food) and should therefore be avoided. Tank cultivation on land allows for a greater control over epiphytes and other competitors provided that the supplied seawater is treated (mechanical filtration, UV-treatment).

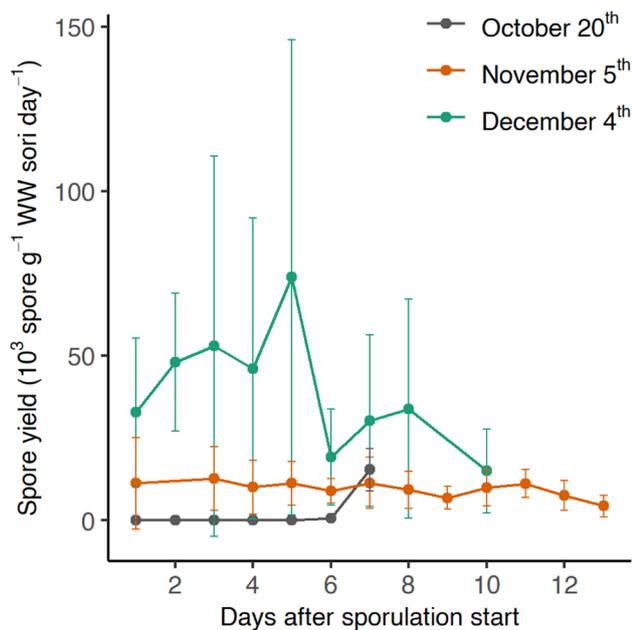
Variable biomass yields from *P. palmata* cultivation at sea have been reported in the literature but differences in seedling density and size at deployment, local growth conditions, cultivation time and farming configuration makes the comparison of these figures difficult. Based on the overview of reported numbers by Grote (2019), 0.5 to 1 kg WW per meter longline appears a realistic baseline estimate of the expected biomass yield of *P. palmata* cultivated at sea. The use of high-density substrates such as nets or textile sheets, extended hatchery time and multiple sequential harvests will result in higher yields per unit area (Werner and Dring 2011a; Schmedes 2020). Furthermore, relatively high growth performance of *P. palmata* may be achieved in integrated multitrophic aquaculture (IMTA) systems where the species is grown using nutrient effluents from finfish production either in land-based facilities (Matos et al. 2006; Kim et al. 2013; Corey et al. 2014; Grote 2016; Levinsen 2020) or aquaculture sites at sea (Sanderson et al. 2012) highlighting the bioremediation potential of the species.

### Bottlenecks related to spore availability and mortality

Without control on the fertility of the raw material, the seeding of growth substrates and subsequent sporelings growth is restricted by the seasonal occurrence of mature fertile tetrasporophytes from wild stocks (Fig. 6). In some areas, e.g. regions with low tidal range where *P. palmata* is mainly found subtidal, the low accessibility to fertile raw material may represent an additional challenge. Besides, the spore yield of *P. palmata* is relatively low. Edwards (2007) revealed the variability of spore production from a natural Irish population and estimated the number of spores per individual between 7 and 36 × 10<sup>6</sup> which is several orders of magnitude lower than other macroalgal species e.g. *L. digitata*, *Saccharina longicuris* releasing 9 to 20 × 10<sup>9</sup> spores

per square meter colonized substrate (Chapman 1984). Thus, a relatively large amount of wild-harvested fertile material is necessary to seed substrates and achieve an appropriate density of seedlings for successful out-growth. Furthermore, the results from a sampling campaign of mature tetrasporophytes in Norway confirm the variability in spore yield from natural populations and show that the number of spores obtained from tetrasporangial tissue is affected by the time of collection of fertile material (Fig. 12). This suggests that the availability of potent spore donors is somehow limited even though fertile individuals can be found during an extended period.

Another major hurdle to the mass cultivation of *P. palmata* sporelings is spore mortality typically ranging from 60 to 90% (Werner and Dring 2011a, c). Unexplained seeding failures may be attributed to the infection of spores and young gametophytes by the intracellular oomycete *O. palmariae* (Sanderson 2015; Badis et al. 2019), highlighting the possibility of substantial yield-limiting epidemic outbreaks in commercial cultivation of *P. palmata*. Besides, the contamination of cultures in tanks by endophytes, epiphytic filamentous brown (*Ectocarpus* spp.) and red algae (*Acrochaetium secundatum*) as well as microalgae is common and may affect the growth and survival of seedlings (Werner and Dring 2011a; Sanderson 2015). Cleaning procedures



**Fig. 12** Spore release from fertile tetrasporophytes of *Palmaria palmata* collected during the autumn 2017 near Storsteinan (Trondheimsfjord, Norway) as a function of the duration of sporulation (days). Small pieces of cleaned sori were dissected and submerged into well-plates containing 5 mL filtered seawater and daily transferred to new wells prior to spores counting. Values are given as mean ± standard deviation ( $n=6$ ). Data from P. Schmedes (unpublished data)

consisting in 1-min bath treatments in sodium hypochlorite (NaOCl, from 0 to 1.2%) were not suitable for the disinfection of wild-collected reproductive material due to tissue damage (at 1.2%) or limited contaminant removal at 0.6% and lower concentrations (Bak 2019). In a study of Kientz et al. (2011), efficient removal of *P. palmata* epibionts was achieved following exposure to a mixture of 50% ethanol and 1% NaOCl for 30 s. However, the effect of this procedure on spores and seedlings survival was not investigated. Other methods using e.g. potassium iodide (KI) may also be suited and should be tested systematically.

Collecting fertile tetrasporophytes at the peak of sorus occurrence (January to March, Fig. 6) for spore release and further seeding of substrate implies a temporal overlap and shortening of the growth season because the optimal time for deploying seeded substrates in open-sea cultivation sites ranges from the autumn to late winter and harvesting the following spring (Werner and Dring 2011a, b; Schmedes 2020). Some successful attempts to induce fertility and subsequent spore release in *P. palmata* have been reported by isolating submeristematic thalli fragments exposed to short days (8 h:16 h, L:D) and 10 °C with a maturation time varying from 1.5 to 2.5 months (Pang and Lüning 2006; Titlyanov et al. 2006). Recent work documented the sequential effects of short days (8 h:16 h) and high nutrient on the induction of tetrasporogenesis (Schmedes 2020). In this study, spore formation occurred only at 5 °C and was not observed at 10 °C suggesting that local populations require specific combinations of environmental factors triggering the onset of sporogenesis. Furthermore, the response time to obtain mature sori from vegetative wild individuals highly depends on time of collection and sporogenesis may become evident after 0.5 to 3 months, but the emergence of mature sori may extend up to 4 to 6 months (Schmedes 2020). Gaining control over the fertility of *P. palmata* would allow the year-round production of spores and seedlings as well as flexibility to accommodate the hatchery phase according to optimal deployment time.

### Recent improvements of existing protocols

Optimizing hatchery conditions to promote spore release, dispersal then attachment to the substrate is critical for the viable commercial cultivation of *P. palmata*. In a recent study, Schmedes and Nielsen (2020a) developed a new system based on conical seeding tanks in a flow-through system in which fertile material is placed above the substrate (nets) and equipped with a secondary tank to recover unattached spores. The consecutive use of sorus material (5 to 15 g WW); i.e. 3 times 3-days seeding period, successfully seeded nets (equivalent to 54 m linear rope) resulting in an average seedling density of 9 individuals per centimetre. The authors observed that an average of only 16% of the released spores attached to the substrate while the remaining were recovered in the

secondary tank and germinated into male and female gametophytes after settlement. Homogenisation of the propagule suspension (i.e. the mixture of aggregated spores and young seedlings) and transfer to agitated seeding tanks allowed the gametophytes to establish discoid reattachment and spores to settle on the substrate in a secondary seeding trial. The procedure is referred to as the GMA-method (germinate, macerate, agitate) (Schmedes et al. 2019). Moreover, 50% of all released spores in a single batch will germinate into female gametophytes which will not develop further unless fertilized. An additional step consisting in mixing male gametes to the propagule suspension allows to fertilize the female gametophytes resulting in a doubling of the number of seedlings on a seeded substrate. These combined methods provide substantial improvements in spore-use efficiency compared to the high requirements of previous protocols for fertile material, i.e. 150 g of sorus tissue for seeding the equivalent of 82 m linear twine (Werner and Dring 2011a).

## Commercial developments

There is currently no large-scale cultivation of *P. palmata*. A Portuguese company (AlgaPlus Ltd) runs a semi-commercial land-based production of *P. palmata* (max. 2 t WW year<sup>-1</sup>, H. Abreu, pers. comm.) from the vegetative propagation of acclimated strains since 2013. Other land-based pre-commercial growth trials are being conducted in Eastern Canada (e.g. Acadian Seaplants Ltd). A few other companies e.g. in USA (Springtide Ltd, Maine Fresh Sea Farm Ltd) and Denmark (OceanWide Seaweed ApS) are currently developing methodologies for the commercial production of spores and seedlings and subsequent deployment at sea. Further efforts are needed to develop a sustainable and profitable industry based on *P. palmata* cultivation. These include securing stable seed supplies, improve spores and seedlings survival and identify the conditions maintaining a high productivity in land- and sea-based cultivation operations. Technical adjustments of the cultivation settings e.g. turning off tank aeration during the dark hours, may provide substantial reductions in energy costs without affecting the growth of *P. palmata* (Caines et al. 2014). Cultivation protocols and technology adapted to this species must be developed to reduce the costs per ton produced (Werner and Dring 2011a) and to make the production of *P. palmata* an economically viable activity in Europe and North America.

## Commercial applications

### Direct food applications and sensory profile

Food is the main commercial application for *P. palmata*. In fact, it is one of the most popular species among Western

consumers and high-end chefs. The increased interest for dulce and edible macroalgae in general is supported by current trends promoting local, sustainable, healthy and vegetarian/vegan foods. Besides its remarkable nutritional profile (see section on “[Chemical and nutrient composition](#) and [Table 2](#)), dulce is highly appreciated for its unique flavour profile and is used either directly as a snack or in various food preparations (Rhatigan 2009; Mouritsen et al. 2013; Chapman et al. 2015). It is often sold to the consumer in dry form (whole fronds, flakes) or as an ingredient in products (spreads, herbal tea mixes, breads, seaweed salt, mustard). It may also be found in fresh salted form.

Umami is the most typical flavour reported in the literature from sensory descriptions of *P. palmata* (Mouritsen et al. 2012; Chapman et al. 2015). Umami is the fifth basic taste (along with sweet, salty, sour and bitter) and is described as a savoury, long-lasting flavour of broth and meat. It is elicited primarily by free glutamate and to a lesser extent free aspartate, which are abundant in typical umami-rich foods e.g. dried and aged Japanese kelp *kombu* (*Saccharina japonica*), cured meat, soy sauce and aged cheese (Ninomiya 1998). The levels of free glutamate measured in *P. palmata* (1 to 4 mg g<sup>-1</sup> DW) vary depending on the origin of the raw material and physiological status of the plant (Mouritsen et al. 2012). Although these levels are lower than those found in *kombu* (up to 16 mg g<sup>-1</sup> DW), the umami response does not depend solely on the free glutamate content but also on other flavour-active compounds e.g. 5'-ribonucleotides (guanylate, inosinate and adenylate), small peptides and glutamate derivatives (Zhao et al. 2016) which have not yet been studied in *P. palmata*. In culinary applications, umami is found to enhance the flavour of other ingredients that do not contain appreciable amounts of glutamate such as vegetables. Several collaborations between scientists and chefs have distinguished *P. palmata* as a promising ingredient providing not only flavour but also a pleasing visual appearance to a wide range of dishes such as ice cream, bread and pasta (Mouritsen et al. 2012, 2019; Chapman et al. 2015) (Fig. 13).

As for other foods, the organoleptic quality of *P. palmata* is greatly affected by post-harvest processing steps, storage conditions and preparation methods. Freshly harvested dulce, often considered less palatable than dried material, is described by fresh marine aromas while it is associated with green aromas following freezing then thawing (Le Pape et al. 2002) and with fishy and fish meal notes in its dry form (Michel et al. 1997; Stévant et al. 2020b). The light rehydration of dried *P. palmata* fronds and subsequent storage for several weeks or months develop distinct sweet, rich and complex flavours including umami and notes of honey and liquorice (Chapman et al. 2015; Stévant et al. 2020b). This flavour development is correlated with a higher level and diversity of volatile compounds in lightly rehydrated



**Fig. 13** Examples of food dishes containing *Palmaria palmata* prepared during a cooking workshop in Norway described in Chapman et al. (2015). Top: dulse tagliatelle with chicken breast. Bottom: clip fish (i.e. salted and dried cod) brandade with dulse. Photographs by Pierrick Stévant

(referred to as semi-dried) dulse compared to the dry material (Stévant et al. 2020b), and with the hydrolysis of soluble proteins into smaller peptides (Stévant et al. 2020a). A more tender texture of the fronds was also reported from this maturation process, reflecting structural alteration from endogenous (e.g. enzymatic) degradation of cell-wall polysaccharides (xylans). A specific preparation, consisting of deep-frying dried and smoked dulse fronds, has recently received media attention since it was found to produce flavours and texture similar to pork bacon (Mouritsen et al. 2019). This highlights the potential of dulse in culinary innovations to create distinct flavours and textures using different processing methods.

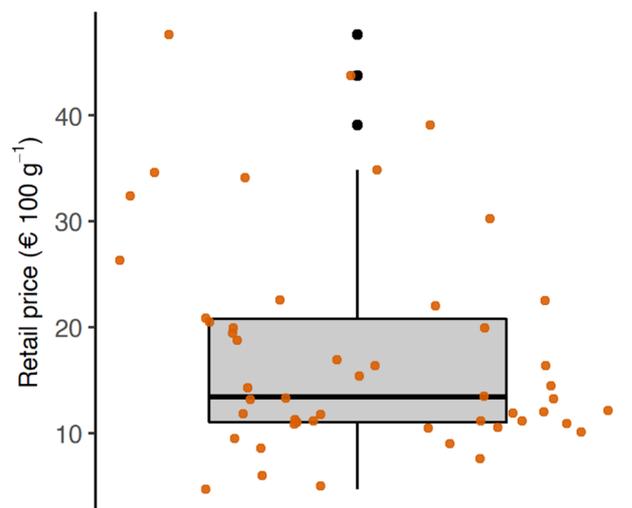
### Market value

The renewed interest from Western consumers for macroalgae and particularly *P. palmata* has led to an increasing demand for this species, primarily from food manufacturers, exceeding the current production based on wild-harvested biomass. This can explain the relatively high bulk retail value

(business-to-business) of dried dulse which was reported to range from 16 to 19 € kg<sup>-1</sup> approximately ten years ago (Walsh and Watson 2011; Werner and Dring 2011a) and is now estimated between 40 and 75 € kg<sup>-1</sup> (H. Abreu, pers. comm.). As a comparison, statistics from the Norwegian directorate of Fisheries (2022) for the national macroalgae production reports a sales value of 2 to 4 € kg<sup>-1</sup> for the cultivated kelps *S. latissima* and *A. esculenta* between 2019 and 2021 (original values expressed in NOK, 1 NOK = 0.099 €). Based on an online search of dried dulse products, the current median consumer retail price of dried dulse is estimated to 13.40 € 100 g<sup>-1</sup> ( $n=50$ , Fig. 14). Despite large variations (min = 4.68, max = 47.60 € 100 g<sup>-1</sup>) which may reflect different marketing strategies and differences in consumers' willingness-to-pay for such products across countries, this estimate is in the upper range of reported prices for dried edible macroalgae including several species (Le Bras et al. 2015).

### Ingredient in human and animal nutrition

There are few written historical records of dulse being used to feed livestock during ancient times, e.g. in Iceland (Hallsón 1964). The relatively high protein content of *P. palmata*, reaching levels of typical protein-rich plant material (e.g. pulse, beans and soy), and a favourable amino acid profile (high proportion of EAA, Table 2) has driven the interest for its commercial exploitation in animal nutrition. However, the



**Fig. 14** Boxplot and overlaid scatter plot of the consumer retail value of dehydrated *Palmaria palmata* based on an online search (conducted in September 2022) including 50 products consisting of dried raw material (whole, flaked or powdered) from France ( $n=9$ ), Ireland ( $n=9$ ), Canada ( $n=7$ ), United Kingdom ( $n=7$ ), USA ( $n=6$ ), Norway ( $n=3$ ), Portugal ( $n=2$ ), Denmark ( $n=2$ ), Iceland ( $n=2$ ), Spain ( $n=2$ ) and from unknown origin ( $n=1$ ). 68% of the products were labelled “organic”. Original prices in USD, CAD, GBP, DKK, ISK and NOK were converted in € according to exchange rates in September 2022

results from in vitro assays revealed the rather low digestibility of proteins from *P. palmata*, both from algal powder and water-soluble extracts (Galland-Irmouli et al. 1999; Bikker et al. 2020). This is due to the ionic interactions of cell-wall polysaccharides (xylans) with proteins and the high viscosity of aqueous extracts, reducing the protein bioaccessibility to proteolytic enzymes. Results from a mink feeding trial supported the findings from in vitro assays and revealed the low apparent amino acid digestibility (especially histidine) of dried and milled *P. palmata* fronds added to the diet, and a lower body weight of the animals (minks) fed with this diet compared to a control containing fish meal (Krogdahl et al. 2021). In contrast, the inclusion of up to 15% *P. palmata* into salmon smolt diets did not significantly affect fish growth (feed conversion ratio, specific growth rate) or health parameters (hematological, immunological and hepatic functions) (Wan et al. 2016).

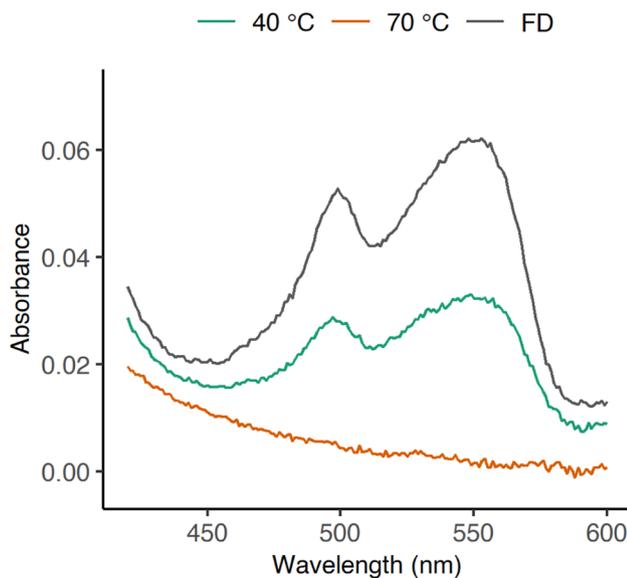
Processing steps such as boiling (Mæhre et al. 2015), freshwater-soaking and fermentation using a *Trichoderma* strain (Marrion et al. 2003) has been shown to improve the digestibility of proteins from *P. palmata*, as a result of the partial removal or degradation of xylans. Water extraction procedures are typically used to recover proteins from dulse. Since xylans also impair the aqueous extraction of proteins, several protocols including an enzymatic pre-treatment step using xylanase have been tested and resulted in higher extraction yields (Joubert and Fleurence 2008; Harnedy and FitzGerald 2013; Bjarnadóttir et al. 2018; Naseri et al. 2020). Bjarnadóttir et al. (2018) and Naseri et al. (2020) obtained a higher protein concentration and proportion of EAA (approximately between 40 and 50%) in the solid phase from the extraction of enzyme-treated *P. palmata* samples compared to levels found in the aqueous phase. A protein concentrate obtained from a similar protocol was shown to have a higher apparent digestibility in minks compared to diets containing whole *P. palmata* (Krogdahl et al. 2021). The authors concluded that such a protein concentrate may have a potential as animal feed ingredient, although it should be combined with other protein-rich sources in feed formulations to compensate for some limiting amino acids. A pilot-scale protein extraction of dulse using xylanase increased the protein content from 12% (initial raw material) to 28% DW in the final product, i.e. the solid fraction after extraction (Aasen et al. 2022). Since existing feed protein ingredients (e.g. from soybean) have a relatively low price, the economic viability of a feed protein concentrate from *P. palmata* will greatly depend on associated production and processing costs. The use of high quantities of enzymes in an industrial setting may not be viable economically. The recovery of valuable compounds (e.g. minerals, pigments, soluble carbohydrates) from side streams (e.g. liquid fraction) can add value to the harvested biomass and create an economic incentive for the use of dulse in animal nutrition.

Schiener et al. (2017) proposed the simultaneous recovery of the protein- and lipid- enriched solid residue on the one hand, and liquid extract containing carbohydrates (mainly xylans) and minerals on the other hand, after enzymatic treatment of *P. palmata* under acidic conditions. No commercial application was suggested for the latter extract, but it is likely to contain water-soluble flavour compounds, e.g. free amino acids, peptides (Stévant et al. 2020b) and phycoerythrin pigment (Dumay et al. 2013), and may have potential as a flavour extract or food colorant. However, commercial development of commodity products from dulse (e.g., feed or food ingredients) are limited by raw material availability, as well as production and process efficiency, to be competitive with existing alternatives. Fermentation (ensiling), even without the addition of a commercial start culture, appeared to be an efficient method for the conservation and fractionation of *P. palmata* biomass, in which nearly up to 50% of the initial fresh weight containing up to one third of the total dry matter can be separated into a liquid fraction (Gallagher et al. 2021). The effluent formation from this process can be improved by additional processing steps such as screw-pressing, wilting or chopping. The commercial potential of the solid and liquid components of fermented dulse in human and animal nutrition have not yet been explored.

## Other industrial applications

Dulse is characterized by relatively high levels of phycoerythrin pigment, especially during the winter season (Table 2). This water-soluble pigment has industrial applications as colorant in food and cosmetic products and as fluorescent marker in immuno-assays (Sekar and Chandramohan 2008). Microalgae such as *Porphyridium cruentum* are the main commercial source of phycoerythrin. Protocols have also been developed for the optimized extraction and purification of the phycoerythrin from *P. palmata* (Galland-Irmouli et al. 2000; Dumay et al. 2013) but have not been implemented commercially. The results from a drying experiment of *P. palmata* indicates that the phycoerythrin is rather sensitive to degradation upon processing of the biomass, as illustrated by the reduced absorption spectra of extracts from air-dried compared to freeze-dried samples (Fig. 15). Appropriate post-harvest treatments and storage methods that maintain the integrity of the compound and maximize extraction yields must be established for future commercial exploitation of phycoerythrin from *P. palmata*.

The antioxidant activity of aqueous and ethanol-soluble extracts from *P. palmata* and the potential of these extracts as natural antioxidant has been studied extensively. Antioxidant activity is associated with various molecules such as phenolic compounds (Yuan et al. 2005; Suwal et al. 2019), although found at lower levels in *P. palmata* compared to brown macroalgae (Roleda et al. 2019), as well as peptides



**Fig. 15** Absorption peaks of phycoerythrin from *Palmaria palmata* extracts obtained from air-dried samples at 40 and 70 °C and freeze-dried (FD) samples. Data from Stévant (2019)

(Wang et al. 2010; Harnedy et al. 2017) and polysaccharides (Suwal et al. 2019). The bioactivity of extracts can be enhanced by enzymatic treatments using proteases (Wang et al. 2010; Harnedy et al. 2017) or polysaccharidase (i.e. hemicellulose) under high hydrostatic pressure (Suwal et al. 2019). A protein hydrolysate from *P. palmata* associated with renin inhibitory bioactivity (i.e. reducing the risk of hypertension) was successfully added to a bread which retained bioactivity following the baking process (Fitzgerald et al. 2014). In a recent study, Lopes et al. (2019) revealed the antioxidant activity of a polar lipid-rich extract from dulse. These results highlight the potential of *P. palmata* and derived products to be used as functional ingredient to extend the shelf-life and improve the health value of foods. On the other hand, the results from a human intervention study suggest that the daily consumption of 5 g dulse (incorporated into a bread) for 4 weeks stimulates inflammation, increases serum triglycerides and alters thyroid function (Allsopp et al. 2016). However, these metabolic changes remained within the normal clinical range and were unlikely to impact health. Further studies of this kind including larger sample sizes and longer interventions may confirm these results and provide information on the medium to long-term impact of dulse consumption.

*Palmaria palmata* is also rich in photoprotective molecules, namely MAAs (see “environment requirements and stressors”) showing antioxidant activity (Yuan et al. 2009) and anti-proliferative properties on human cells (Athukorala et al. 2016) when isolated in aqueous methanol extracts.

Moreover, these compounds are suggested as a biocompatible alternative to the use of synthetic UV radiation filters in sunscreens and cosmetic formulations, which are associated with negative impacts on marine ecosystems (Lawrence et al. 2018). Besides, the antioxidant properties of dulse can also be applied to edible films and coatings for the food industry. Albertos et al. (2019) successfully incorporated 1% powdered dulse in a chitosan-based edible films, delaying the oxidation and microbial spoilage of fish burgers.

Technical solutions based on low-cost technologies must be developed for the production, preservation and processing of *P. palmata* to enable future commercial developments with this species. Applying circular principles such as cultivation in IMTA systems, use of industrial surplus heat for biomass processing, valorisation of waste streams in biorefinery processes, will increase the profitability and the environmental sustainability of new products based on dulse.

## Conclusions

*Palmaria palmata* is a common red macroalgae species of the Northern Atlantic shores. Owing to remarkable nutritional features and unique flavours, dulse has traditionally been harvested and used as food among coastal communities in Western Europe and North America. The recent interest from Western consumers for natural foods and the (re)discovery of macroalgae as a source of nutrients, bioactive compounds and flavours has shed light on the potential of dulse in gastronomy and as a functional ingredient in the food industry. Other than food, *P. palmata* may enter the composition of commercial formulations e.g. animal feed, cosmetic products, as an alternative to ingredients associated with negative environmental impacts (e.g. soy protein concentrate, synthetic antioxidants). Hence, the increasing demand for dulse biomass from industrial actors.

This review highlights the current lack of adapted resource management schemes for the exploitation of wild biomass in relevant countries, including the reporting of annual landings to the FAO. Increasing our understanding of the biology, taxonomy and distribution of the species will provide a basis for effective decision-making for conservation purposes and sustainable harvest. However, significantly increasing the harvesting pressure on wild populations is not considered sustainable. Instead, *P. palmata* may be cultivated in land-based facilities and/or at sea, either vegetatively or by seeding growth substrates with tetraspores and germinated gametophytes. However, there are major bottlenecks limiting the commercial cultivation of dulse, including the low rate of released spores, high mortality and contamination from epiphytes and endophytes. Establishing cultivation protocols for the industrial production of *P. palmata* as

well as efficient biomass processing methods is the key to enable commercial developments in food and other applications in the future.

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**Data availability** The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

## Declarations

**Competing interests** The authors have no competing interests to declare that are relevant to the content of this article.

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