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Marine fungal abilities to enzymatically degrade algal polysaccharides, proteins and lipids: a review

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Abstract
Over the last decades, metabolites with biotechnological application produced by marine resources and notably macroalgae have seen increasing interest. Among these metabolites, many require the use of efficient extraction processes to reach a sufficiently high yield for industrial development. One of the more promising extraction processes currently used is the extraction assisted by enzymes, which can be coupled with other extraction techniques. However, most of the commercial enzymes used for the extraction of molecules of interest from marine material are enzymes obtained from terrestrial microorganisms and with limited substrate specificity. The efficiency of the extraction could then be increased by using more specific enzymes according to the targeted matrix. Marine fungi are particularly promising for the production of degradation enzymes and their interest recently increased, but they are still less studied than marine bacteria. A state of the art on the degradation enzymes from marine fungi is proposed, and more specifically on polysaccharide, protein and lipid degradation enzymes.

Keywords Seaweeds · Marine fungi · Enzymatic activities · Polysaccharidases · Proteases · Lipases

Introduction

Marine fungi were first defined in 1961, based on their ability to grow in seawater conditions (Johnson and Sparrow 1961). After two decades, this definition was modified due to the ability of some fungal strains to grow under conditions comparable with those found in marine environments (Kohlmeyer and Kohlmeyer 1979). These authors then defined obligate and facultative marine fungi: the former needing marine or estuarine conditions to sporulate and the latter being fungal strains isolated from terrestrial habitats able to grow and sporulate in marine conditions. Even though this definition has been widely used in the last decades, it has some ambiguities considering those fungal strains isolated from the marine environment but able to grow under terrestrial conditions which are considered as facultative fungi. "True" marine fungi have been then linked only with obligate marine fungi, discriminating the facultative ones, leading to an underestimation of the whole marine fungal biodiversity. Moreover, some facultative marine fungi isolated from the marine environment are characterized by clear adaptations in the marine environment and have developed interactions with marine microbial communities, but still could not be considered as real marine fungi (Pang et al. 2016; Rédou et al. 2016). The currently used definition has been given by Pang et al. (2016) and describes three ways to consider a fungal strain as a marine fungus: "(1) it is able to grow and/or sporulate (on substrata) in marine environments; (2) it forms symbiotic relationships with other marine organisms; or (3) it is shown to adapt and evolve at the genetic level or be metabolically active in marine environments".

Fungal strains have been found in every marine environment investigated. Fungi seem to be widespread in the marine environment, including the water column, sediments, driftwood, algae, invertebrates and mammals (Tisthammer et al. 2016; Amend et al. 2019). Marine fungi isolated from sponges and algae are particularly well documented compared with those isolated from other marine habitats. Indeed, sponges correspond to the most studied substrate, and algae correspond to the second most studied one for marine fungal isolation (Rédou et al. 2016). Studies can have different criteria to separate fungal strains according to habitat diversity. For example, Hugues (1974) separated marine fungal communities according to the climate, temperature

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and biogeographical zones (arctic, antarctic, temperate, subtropical, tropical). Geographic location seems indeed to have an influence on the marine fungal distribution, but the use of environmental factors like water depth would be more pertinent (Tisthammer et al. 2016). In most studies, the distinction can then be established between coastal and deep-sea marine fungi because of the different characteristics of such habitats (temperature, light, pressure, biological diversity…) (Manohar and Raghukumar 2013; Satyanarayana et al. 2019). Then, it appears that deep marine sediments have lower diversity than coastal ones, but with many cultivable fungal strains belonging to species also found in terrestrial environments (Manohar and Raghukumar 2013; Rédou et al. 2016). However, other deep-sea habitats such as hydrothermal vents seem to be characterized by a high fungal diversity (Rédou et al. 2016). Coastal environments such as mangroves or coral reefs also show a high fungal diversity (Manohar and Raghukumar 2013; Satyanarayana et al. 2019). All putative marine fungal habitats are not studied equally: coastal, water column and hydrothermal vents environments would be less studied than deep-sea regions (Satyanarayana et al. 2019). Beyond an absolute underestimation of global marine fungal diversity, the less studied marine regions would then putatively appear wrongly as having poor fungal diversity than more studied regions.

The phyla Ascomycota and Basidiomycota are the most represented considering the fungal strains isolated from marine environments (Manohar and Raghukumar 2013; Rédou et al. 2016; Amend et al. 2019) and a predominance of Ascomycota has been highlighted in several studies (Satyanarayana et al. 2019). Among these Ascomycota, several orders are particularly represented in marine fungi such as Microascales, Pleosporales, Eurotiales and Saccharomycetales (Jones et al. 2019). At the genus level, *Aspergillus*, *Cladosporium*, *Fusarium*, *Gliocladium*, *Microsphaeriopsis*, *Paecilomyces*, *Penicillium*, *Phoma*, *Phomopsis*, *Trichoderma* and *Ulocladium* seem to be particularly represented (Bugni and Ireland 2004). In response to the increasing studies on marine fungal diversity, a database on marine fungi (www.marinefungi.org) has been created recently and provides classification details and descriptions of marine fungi (Jones et al. 2019).

Concerning algicolous fungal diversity, the great majority belong to Ascomycota (Menezes et al. 2010; Suryanarayanan 2012; Gnavi et al. 2017; Olafsson 2017; Garzoli et al. 2018; Nicoletti and Andolfi 2018; Kamat et al. 2020). Among these Ascomycota, species belonging to several genera such as *Aspergillus*, *Cladosporium* and *Penicillium* are dominant and exhibit a broad algal host specificity (Suryanarayanan 2012; Raghukumar 2017; Abdul Malik et al. 2020). They cope particularly easily with environmental factors (such as saline conditions), exhibit easy cultivable potential and high growth rates compared with other fungal species (Bugni and Ireland 2004; Suryanarayanan 2012). Some other species are restricted to only several different hosts (Raghukumar 2017), and several fungal species are so adapted to their macroalgal host metabolites that they cannot grow in their absence. This is the case of *Acremonium fuci* of which spore germination is possible only in the presence of tissue of the macroalga *Fucus serratus* (Suryanarayanan 2012; Nicoletti and Andolfi 2018).

Algicolous fungi can develop various kinds of interactions with their algal host. Fungi are often linked with infections and diseases in the marine environment and are then characterized as parasites (Bugni and Ireland 2004; Suryanarayanan 2012; Raghukumar 2017; Nicoletti and Andolfi 2018; Menaa et al. 2020). These parasitic fungi can either be characterized as obligate or facultative (opportunistic), and can be restricted to several hosts, suggesting coevolution between hosts and pathogens (Raghukumar 2017). Some mutualistic relationships can exist between fungi and the macroalgal host, with benefits to both organisms (Bugni and Ireland 2004; Raghukumar 2017; Nicoletti and Andolfi 2018; Menaa et al. 2020). For example, the brown alga *Ascophyllum nodosum* and the fungus *Mycosphaerella ascophylli* cannot be found separated in nature (Bugni and Ireland 2004). Some other mutualistic fungi allow to their host to cope with desiccation (Raghukumar 2017). Marine fungi also often develop on dead macroalgal biomass and are described as saprobes (Suryanarayanan 2012; Raghukumar 2017; Nicoletti and Andolfi 2018; Menaa et al. 2020).

However, the diversity of algicolous fungi and their interactions with the algal hosts are probably still not enough studied, notably compared with bacteria, to establish clear tendencies (Suryanarayanan 2012; Garzoli et al. 2018; Menaa et al. 2020). The role of these marine fungi in the degradation of macroalgal biomass is also not well established (Gomaa et al. 2015). Further fungal community inventory need to be performed, notably considering red and green seaweeds on which fungal diversities are less documented than brown seaweeds (Suryanarayanan 2012; Raghukumar 2017; Garzoli et al. 2018). Moreover, even if the use of molecular-based protocols is increasing, most studies on algicolous fungal diversity has been performed on the cultivable community which is known to represent less than 2% of the total fungal diversity (Garzoli et al. 2018). It would therefore be important to complement culture-based studies with molecular-based studies to exhibit a more exhaustive fungal diversity. Moreover, these studies on fungal diversity should also be performed on varied seaweed structures and organs which could harbour differences in fungal diversity, and in varied seasons which can influence the diversity of fungal communities (Suryanarayanan 2012).

Marine fungi, particularly algicolous ones, can be considered as sources of new compounds of biotechnological interest which cannot be found in their terrestrial counterparts

(Bugni and Ireland 2004; Raghukumar 2008). They are notably known as producers of antiviral, antifungal, antibacterial or anticancer natural products (Jones et al. 2019). More specifically, several fungal strains isolated from macroalgae exhibit promising bioactivities such as antioxidant (Suryanarayanan et al. 2010; Suryanarayanan 2012; Hong et al. 2015; Sarasan et al. 2017; Kamat et al. 2020), antimicrobial (Zhang et al. 2009; Suryanarayanan et al. 2010; Flewelling et al. 2013; Hong et al. 2015; Sarasan et al. 2017; Kamat et al. 2020), antitumor (Sarasan et al. 2017; Kamat et al. 2020), antialgal or antiinsect (Suryanarayanan et al. 2010; Suryanarayanan 2012) activities. Marine environments differ from terrestrial ones by several physicochemical factors, such as salinity, pressure, lightning condition or temperature (Zhang and Kim 2010; Bonugli-Santos et al. 2015). Marine organisms need to cope with these factors notably with the synthesis of enzymes adapted to high concentrations of salinity but also to high temperatures (Shah et al. 2019). Marine enzymes also have substrate affinities which differ from the ones of terrestrial enzymes (Trincone 2011; Arnosti et al. 2014). According to the targeted substrate, marine enzymes could then exhibit higher performances than terrestrial ones. Several marine oxidoreductases also exhibit higher resistance to organic solvents, besides the tolerance of high concentrations of salinity (Trincone 2011). These marine enzymes, such as polysaccharidases, proteases and lipases, have gained interest over several years in their corresponding industrial applications (Zhang and Kim 2010). Several bioprocesses such as ethanol production from marine algal biomass, need a desalinization step when terrestrial enzymes are used. The use of halophilic enzymes derived from the marine environment would then allow this desalinization step to be ignored (Trincone 2011). Treatments of various effluents are also more effective by using marine enzymes compared with terrestrial ones (Raghukumar et al. 2004). Marine enzymes are also increasingly used in several other domains such as medicine, food supplements, beverages and production of chemicals (Shah et al. 2019).

Fungal enzymes are currently particularly well represented in biotechnological applications. A recent report by de Vries et al. (2020) shows that more than 50% of commercial enzymes with biotechnological interest have been obtained from fungi. Besides their high enzymatic activities (Schatz 1984; Grant and Rhodes 1992), fungi possess the advantage, compared with bacteria, to excrete enzymes in the external medium. This enzymatic external excretion allows the recovery of enzymatic crude extract without supplementary extraction protocol.

The use of fungi isolated from marine environments in biotechnologies and the finding of new natural products has been increasing since the 1990s (Rédou et al. 2016; Sarasan et al. 2017; Nicoletti and Andolfi 2018). Among these natural products, enzymes of degradation (of polysaccharides, proteins, lipids, nucleic acids…) from marine fungi are of particular interest compared with their terrestrial counterparts due to their higher specific activity (Balabanova et al. 2018a) or because they are active under particular conditions such as high salinity, high pressure, acid and alkaline pH (Pointing et al. 1998; Huang et al. 2004; Wang et al. 2007; Atalla et al. 2013; Mzui and Ch 2018; Ogaki et al. 2019). Even if marine fungi seem to be characterized by several advantages compared with marine bacteria according to enzyme production, marine bacterial enzymes are largely better documented than marine fungal ones (de Vries et al. 2020).

Polysaccharidases have numerous interests in several industrial fields. More specifically, the use of this kind of enzyme on algal biomasses is particularly interesting in food industries, biofuel production, pre- and probiotic production, cosmetics and pharmaceutics, paper and textile industries, and for bioplastic production (Nicoletti and Andolfi 2018; de Vries et al. 2020). Marine polysaccharides, particularly sulfated polysaccharides from marine algae, can exhibit interesting activities that seem to be increased when the polysaccharide is partially degraded, highlighting another interest about polysaccharidases (Synytsya et al. 2015; de Vries et al. 2020). Proteinases and lipases are also degrading enzymes with industrial application even if polysaccharides degrading enzymes are more diverse because of the great diversity of natural polysaccharides.

The majority of enzymes of interest from marine fungi correspond to polysaccharide degrading enzymes, such as cellulases, xylanases or amylases. A first part will then briefly describe the structures and functions of the principal macroalgal polysaccharides targeted by these fungal enzymes. Nevertheless, several studies have also studied marine fungal proteases and lipases (Damare et al., 2012). This review aims to summarize data and literature available on the algal polysaccharide, protein and lipid degrading enzymes secreted by marine fungi. Several of these references have been published from the 1980s even if the majority of them have been obtained during the last decade. Characteristics such as optimal temperature and pH, specific activity or enzymatic molecular weight are particularly focused on.

Principal polysaccharides found in marine macroalgae

Seaweed polysaccharides can have three main different roles for the alga: some polysaccharides have a role of structuring of the cell and are mainly found in the cell wall, some other polysaccharides have a role of food stock for the alga and some other are found in the cell matrix with several roles

among which the prevention of desiccation (Usov 2011; Synytsya et al. 2015). These latter polysaccharides have other protective effect for the alga and are in part responsible of the algal flexibility (Percival 1979). Almost all of them are sulphated polysaccharides and are deeply studied for their application in human health (Kuznetsova et al. 2020). Moreover, many of these sulphated polysaccharides are widely used in other domain such as food, cosmetic or pharmaceutical industries thanks to their gelling and thickening properties (Renn 1997; Jiao et al. 2011; Dobrinčić et al. 2020; Kuznetsova et al. 2020).

Chlorophyceae

Chlorophyceae have a physiology and polysaccharide composition more similar to terrestrial plants than the Rhodophyceae and Phaeophyceae. This similarity is for example highlighted by the presence of starch as food reserve in the Chlorophyceae but not in the Phaeophyceae or Rhodophyceae (with the exception of Floridean starch) even when it shows several differences with terrestrial starch (Percival 1979). Principal structural polysaccharides of the Chlorophyceae are xylan, mannan and cellulose (Percival 1979; Hong et al. 2014).

Sulphated polysaccharides from green seaweed have heteregeneous structures particularly complex and numerous compared with other seaweed (Jiao et al. 2011). Their functions are diverse and can enhance the flexibility as well as the resistance of the alga. They also have a role of defence against pathogens and allow water retention (Percival 1979). The best known of the sulphated polysaccharides of green seaweeds is certainly ulvan, for which precise structure can change according to the considered algal species, the environment or the season (Jiao et al. 2011; Synytsya et al. 2015; Kuznetsova et al. 2020). Other sulphated polysaccharides from green seaweeds, such as sulphated rhamnan, galacotan, arabinogalactan or mannan, have been studied (Wang et al. 2014).

Rhodophyceae

The main polysaccharide with a food reserve function in the Rhodophyceae is floridean starch. It differs from terrestrial or green seaweed starch by the absence of amylose, consisting of small granules kind of amylopectin (Percival 1979; Usov 2011).

Xylan is particularly represented in red seaweeds, with several forms that are not observed in green or brown seaweeds (Synytsya et al. 2015). Moreover, this polysaccharide has a role of food storage in red seaweeds in addition to the structural role also observed in green and brown seaweeds (Percival 1979). Another structural polysaccharide, also found in green and brown seaweeds, is cellulose although it generally only represents about 10% of the cell wall (Usov 2011). The other main structural polysaccharide found in Rhodophyceae is mannan, which can be found in the cell matrix as is xylan (Usov 2011).

One main group of water-soluble sulphated polysaccharides in the Rhodophyceae, the sulphated galactans, is separated into two subgroups: agarans and carrageenans (Ahmadi et al. 2015). The latter exists mainly in three different forms namely ι-, κ- and λ-carrageenans according to their sulphation level (Usov 2011; Kuznetsova et al. 2020). Both agarans and carrageenans are composed of galactose residues, but the former is more precisely composed of L-galactose and the latter is composed of D-galactose (Jiao et al. 2011; Usov 2011; Synytsya et al. 2015). Hybrid polysaccharides with agaran and carrageenan parts have been observed in some red algae (Jiao et al. 2011; Usov 2011). As for the Chlorophyceae, there is a great diversity of sulphated polysaccharides in Rhodophyceae, such as sulphated xylogalactan or xylomannan for example (Jiao et al. 2011).

Phaeophyceae

Laminarin is the principal storage product for brown seaweeds and is one of the most important carbon sources in marine environments (Percival 1979; Sanjeewa et al. 2017). Contrarily to Rhodophyceae and Chlorophyceae, Phaeophyceae do not synthetize starch as a storage product but form laminarin. Laminarin structure consists in a chain of 1,3-linked β-D-glucose residues with several branched β-D-glucose residues (Ahmadi et al. 2015; Sanjeewa et al. 2017; Dobrinčić et al. 2020).

Alginate is the most abundant polysaccharide found in brown seaweeds and is located in the cell wall (Ahmadi et al. 2015; Synytsya et al. 2015). It is structurally composed of β-D-mannuronic acid and α-L-guluronic acid with varying proportions resulting in a diversity of alginates (Synytsya et al. 2015; Dobrinčić et al. 2020; Kuznetsova et al. 2020). Cellulose has also been described in brown seaweeds with a structural function.

Fucans are the main sulphated polysaccharides situated in the algal matrix in the Phaeophyceae. They have a great structural diversity, and algal species can even be composed of different kinds of fucans (Jiao et al. 2011; Ahmadi et al. 2015). Fucose is the main component of fucans, but the structural complexity and diversity of this polysaccharide are due to the additional presence of monosaccharides such as glucose, galactose, xylose, mannose or uronic acids (Jiao et al. 2011; Sanjeewa et al. 2017; Kuznetsova et al. 2020). "Simple fucoidans" are only composed of a chain of sulphated fucose residues, but many other forms of fucoidans have been described with great heteropolysaccharidal and structural diversity (Synytsya et al. 2015; Sanjeewa et al. 2017; Dobrinčić et al. 2020).

Generally, the characterization and the precise description of seaweed polysaccharides is difficult to establish because of a great amount of derivatives and diversity even in the same species, and because of the effect of several factors such as the season or the algal age on their structure.

Enzymes of polysaccharide degradation from marine fungi

As in several other scientific domains, comparison of enzymatic activity values from a publication to another can be difficult because of a diversity in methodologies. Indeed, even if the dinitrosalicylic acid (DNS) method is the most widespread method of measuring polysaccharidase activity, some other methods can be used. Moreover, the substrate used for the activity can vary. Another source of diversity is fungal culturing methods, which differ widely in the literature because of fungal growth conditions. Those are defined by many variables (substrate, ionic solution, temperature, pH, solid/liquid medium…) and are responsible for different enzyme production. For example, according to the aim of the study, the substrate on which fungi are grown before enzymatic extraction can be a commercial preparation of polysaccharide targeted by an enzyme of interest, an alga (from which fungi can be isolated) pre-processed and incorporated into the medium, or food industry by-products of economic interest. On the other hand, in some studies the crude enzymatic activity is measured, while in others the enzymatic extract will be purified, using once again very diverse methods (Raghukumar et al. 2004; Li et al. 2007; D'Souza-Ticlo et al. 2009; Qianqian et al. 2011; Singh et al. 2011; Wu et al. 2011; Rong et al. 2015; Jmel et al. 2020). Here, we will describe all marine fungal enzymatic activities referenced in the literature degrading polysaccharides with few comparisons due to the reasons mentioned above.

As enzymatic mechanisms are complex and generally monospecifically studied, it can be assumed that the same enzyme can exhibit various activities, and consequently a fungal strain can also have various enzymatic activities. For example, cellulose belonging to the glucan polysaccharide family, a cellulase could also be described as glucanase. In this review, we describe activities as published in the literature.

A representative part of the whole data detailed further is synthesized in Table 1, focusing on data obtained from 2000 organized in four groups: firstly glucanase, secondly galactanases, thirdly other polysaccharide hydrolases and fourthly polysaccharide-degrading enzymes with a non-hydrolytic mechanism. When data were available supplementary information has been given, being enzymatic activity, specific activity, enzymatic kinetics (V_m and K_m), molecular weight, and optimal temperature and pH. The ranges of enzymatic activities (and specific activities) were elaborated by selecting the highest activities of every study. There can be an important gap between the highest activity values reported, but this can be explained by the fact that they come from diverse studies, with many variables which could have an impact on the enzymatic activity.

Then, in order to highlight the diversity of some of these variables, the marine fungal species, their principal natural origins and the substrates used for their enzymatic production are summarized in Table 2. These data, such as Table 1, focus on the best polysaccharide-degrading marine fungal strains of every study and on the literature published from 2000.

The diversity of activities, of optimal pH and temperature, along with the marine fungal species that may be particularly promising for polysaccharide degradation, as well as other several tendencies, are further discussed in detail.

Hydrolases

Glucan degradation

The majority of studies dealing with marine fungal enzymes degrading polysaccharides concern glucans. Among these studies, many describe enzymes with glucanase or glucosidase activities but without specific association with a particular polysaccharide—most enzymes involved in polysaccharide degradation are not specific and can degrade several types of polysaccharides with different efficiencies. Thus, a glucanase could both degrade glucans and xyloglucans, and this ability is a characteristic participating in its classification in the Glycosyl Hydrolases families (Maclachlan and Brady 1994; Segato et al. 2017; Zhao et al. 2019). Natural algal glucans targeted by marine fungal enzymes of degradation are laminarin, cellulose and starch. Their structures and the general mode of action of glucanases are presented in Fig. 1. The use of commercial preparations of cellulose for fungal growth to measure glucan degradation capacities is particularly widespread compared with other natural glucans such as laminarin, or amylose (Fig. 1b).

Glucanases can be classified according to two principal operating modes allowing the degradation of glucan into glucosides, small chains of glucose residues. Endoglucanases represent enzymes allowing degradation of polymers of glucan targeting osidic linkages into the chain, while exoglucanases specifically hydrolyze the ends of the polysaccharide chain (Fig. 1a). In order to completely degrade glucosides into glucose molecules, organisms degrading glucans need to synthesize glucosidases. As for glucanases, glucosidases can target either glucoside α- or β-linkages and thus defined as α-glucosidases and β-glucosidases (Fig. 1a).

Table 1 Summary of marine fungal enzymes degrading polysaccharide described from 2000 and their principal characteristics. Only data concerning highest enzymatic activities obtained from the studies or bringing information on enzymes characteristics (Vm, Km, molecular weight, optimal temperature and pH) are presented (1 U = 1 µmol min^{-1})

Polysaccharide-degrading specificity	Highest enzymatic activity (U mL^{-1})	Highest specific activity (U mg^{-1})	*Vm*	*Km* (mM)	Molecular weight (kDa)	Optimal temperature (°C)	Optimal pH	References
Glucosidase	0.22–80	110	381.1 (U mg^{-1})	0.140	107	35–70	4–7	Elyas et al. 2010; Ravindran et al. 2010; Hong et al. 2015; Lee et al. 2015, 2019; Karray et al. 2016; Méndez-Líter et al. 2018; Patyshakuliyeva et al. 2020
Cellulase	0.15–21.4	0.011–30.1	0.57 (U L^{-1})	0.070	56–67	40–60	4–7.5	Ravindran et al. 2010; Xue et al. 2012a; Torres and dela Cruz 2013; Li et al. 2014; Trivedi 2015, p. 201; Hong et al. 2015; Rong et al. 2015; Lee et al. 2015, 2019; Karray et al. 2016; Ghazal Mustafa et al. 2016; Patyshakuliyeva et al. 2020; Jmel et al. 2020
Laminarinase	0.22	0.010–13.5		0.002–0.005	54–56	40–60	4.4–7.5	Burtseva et al. 2003, 2006; Balabanova et al. 2018b; Patyshakuliyeva et al. 2020
Amylase		297.3–120 × 10^3	0.25 (mg min^{-1} mL^{-1})	0.059	98	30–60	4.5	Li et al. 2007; Burtseva et al. 2010; Gonçalves et al. 2013
Galactosidase		42 × 10^3						Burtseva et al. 2010
Agarase	0.182–7.69	20			39–44	40–50	7–8	Kawaroe et al. 2015; Gomaa et al. 2015, 2017; Furbino et al. 2018; Fawzy 2020
Carrageenase	0.015–17.49							Furbino et al. 2018; Patyshakuliyeva et al. 2020
Xylosidase	0.01	0.0024						Thirunavukkarasu et al. 2015; Patyshakuliyeva et al. 2020
Xylanase	2.924–629.6	2.2–10 × 10^3	2688 (U mg^{-1})		18–38	25–55	3.5–9	Raghukumar et al. 2004; Hou et al. 2006; Torres and dela Cruz 2013; Del-Cid et al. 2014; Thirunavukkarasu et al. 2015; dos Santos et al. 2016; Korkmaz et al. 2017; Wu et al. 2018; Patyshakuliyeva et al. 2020
Fucosidase	0.00185							Shvetsova et al. 2014
Fucoidanase	0.006–4	0.25–0.3 × 10^3	2.02–6.55 (mg min^{-1} mL^{-1})	0.036–0.139	64–180	40–60	6–7	Burtseva et al. 2010; Qianqian et al. 2011; Wu et al. 2011; Gomaa et al. 2015, 2019; Hifney et al. 2019; Patyshakuliyeva et al. 2020
Mannosidase		5.5 × 10^3						Burtseva et al. 2010
Alginate lyase	24–860	67.24–85		0.227	95	35	6.5	Burtseva et al. 2010; Singh et al. 2011; Gomaa et al. 2015, 2019

Table 2 Summary of marine fungal species exhibiting polysaccharide-degrading abilities described from 2000, along with their environmental origin and the substrates used for their growth and enzymatic production. Only the best polysaccharide-degrading strains of each study are reported

Polysaccharide-degrading specificity	Fungal origins	Fungal identifications	Substrates for fungal growth	References
Cellulolytic	Mangrove debris (wood, leaves), macroalgae (*Agarum* sp., *Fucus* sp., *Sargassum* sp., *Ulva* sp.), marine sediments, seawater	*Arthrinium saccharicola, Aspergillus* sp., *A. niger, Aureobasidium pullulans, Candida* sp., *Chaetomium* sp., *Cladosporium sphaerospermum, Fusarium equiseti, Penicillium chrysogenum, P. madriti, Phomopsis* sp., *Scopulariopsis brevicaulis, Trichoderma paraviridescens*	Macroalgae (*Ulva lactuca*, *U. fasciata*, *Agarum clathratum*), purified substrates (cellulose, carboxymethyl cellulose), raw materials (cotton seeds, rice bran, wheat bran)	Elyas et al. 2010; Ravindran et al. 2010; Xue et al. 2012a; Torres and dela Cruz 2013, p. 2; Li et al. 2014; Trivedi 2015; Hong et al. 2015; Rong et al. 2015; Lee et al. 2015, 2019; Balabanova et al. 2018b; Patyshakuliyeva et al. 2020
Laminarinolytic	Macroalgae (*Fucus* sp.), marine sediments	*Beauveria felina, Chaetomium indicum, Penicillium brevicompactum*	Macroalgae (*Laminaria digitata*), laminarin, rice bran	Burtseva et al. 2003; Balabanova et al. 2018b; Patyshakuliyeva et al. 2020
Amylolytic	Marine sediments, ocean depths	*Aureobasidium pullulans, Penicillium solitum, Scopulariopsis brevicaulis*	Starch, rice bran	Li et al. 2007; Burtseva et al. 2010; Gonçalves et al. 2013; Balabanova et al. 2018b
Agarolytic	Macroalgae (*Palisada perforata, Georgiella confluens*), marine sediments, seawater	*Beauveria felina, Cladosporium* sp., *Curvularia lunata, Dendryphiella arenaria, Hypocraceae* sp.	Macroalgae (*Gelidium latifolium, Palisada perforata*), agar, rice bran	Kawaroe et al. 2015; Gomaa et al. 2015, p. 20, 2017; Balabanova et al. 2018b; Furbino et al. 2018; Fawzy 2020
Carrageenanolytic	Macroalgae (*Iridaea cordata, Fucus* sp.), marine sediments	*Beauveria felina, Clonostachys rosea, Penicillium* sp.	Macroalgae *(Laminaria digitata)*, carrageenan, rice bran	Balabanova et al. 2018b; Furbino et al. 2018; Patyshakuliyeva et al. 2020
Xylanolytic	Mangrove leaves and sediments, macroalges (*Fucus* sp., *Sargassum wightii*), marine sponge (*Dragmacidon reticulatum*), marine sediments	*Aspergillus tubingensis, A. ustus, Beauveria felina, Cladosporium* sp., *Penicillium chrysogenum, Phoma* sp., *Trichoderma harzianum, T. paraviridescens, T. pleuroticola*	Macroalgae *(Ulva lactuca)*, purified xylan (from beechwood, birchwood, oat, rice), rice bran	Raghukumar et al. 2004; Hou et al. 2006; Torres and dela Cruz 2013, p. 201; Del-Cid et al. 2014; Thirunavukkarasu et al. 2015; dos Santos et al. 2016; Korkmaz et al. 2017; Balabanova et al. 2018b; Wu et al. 2018; Patyshakuliyeva et al. 2020
Fucoidanolytic	Macroalgae (*Fucus* sp., *Padina pavonica, Palisada perforata*), marine sediments	*Beauveria felina, Cladosporium salinae, Dendryphiella arenaria, Fusarium* sp., *Trichoderma paraviridescens*	Macroalgae (*Cystoseira trinodis, Laminaria digitata, Sargassum* sp.), fucoidan (from *Sargassum latifolium, Fucus vesiculosus*), rice bran	Qianqian et al. 2011; Wu et al. 2011; Gomaa et al. 2015, p. 20, 2019; Balabanova et al. 2018b; Hifney et al. 2019; Patyshakuliyeva et al. 2020
Mannanolytic	Marine sediments	*Beauveria felina*	Rice bran	Balabanova et al. 2018b
Alginolytic	Marine macroalgae (*Cystoseira myrica, Dictyota dichotoma, Palisada perforata*), marine sediments	*Acrophilophora* sp., *Aspergillus oryzae, Beauveria felina, Dendryphiella arenaria, Setosphaeria rostrata*	Macroalgae (*Sargassum* sp.), sodium alginate, rice bran	Singh et al. 2011; Gomaa et al. 2015, 2019; Balabanova et al. 2018b

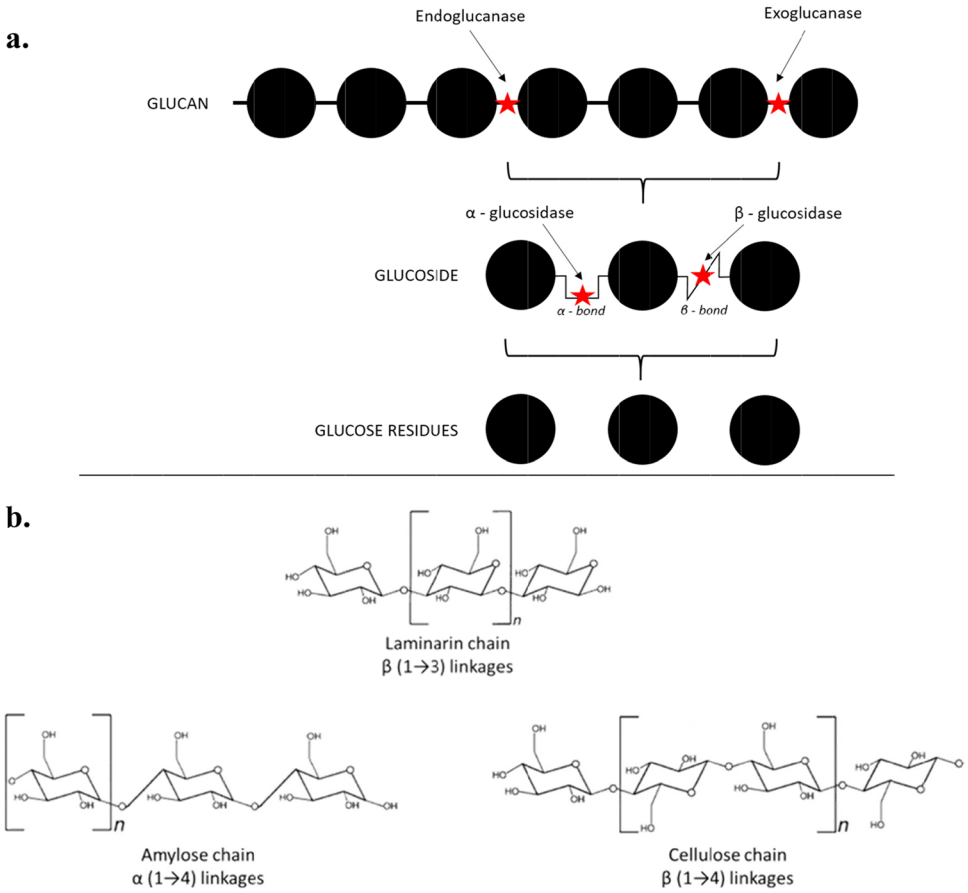

Fig. 1 **a.** General mechanisms of glucan degradation with glucanases with a first step of degradation in glucosides followed by a second step of degradation of glucosides in glucose residues. Disks represent glucose, red stars represent link breaking by the corresponding enzyme. **b.** Structural composition of natural glucans targeted by marine fungal enzymes (adapted from Allen et al. (2001); Kadokawa (2012); Olsson and Westm (2013))

Studies dealing with the characterization of glucan degrading enzymes from marine fungi (endoglucanases, exoglucanases and glucosidases) describe strains isolated from diverse habitats such as water column, marine sediments, mangrove, sponges, algae… However, concerning algae, studies principally describe fungal communities of brown algae (Burtseva et al. 2003, 2006; Hong et al. 2015; Lee et al. 2015, 2019; Patyshakuliyeva et al. 2020). That can be explained by two phenomena. First, enzymes obtained from fungi isolated from brown algae are more studied than enzymes obtained from fungi isolated from other algal families. Furthermore, the glucanase family includes enzymes targeting the most common polysaccharides composing brown algae such as cellulose or laminarin.

All studies characterizing glucanase activities perform assays on these kinds of polysaccharides as substrates. These glucanases activities and properties will be discussed further according to their substrate, being cellulose, laminarin and starch.

However, concerning glucosidases, studies are mostly performed using p-nitrophenyl-b-D-glucopyranoside (pNPG) as substrate, which is not specific with any natural polysaccharide but has colorimetric properties allowing the enzymatic assays. Moreover, marine fungal glucosidases are less studied than marine fungal glucanases.

Nevertheless, an important diversity of marine fungal strains exhibit β-glucosidase activities (Pointing et al. 1999; Hong et al. 2015; Lee et al. 2015; Patyshakuliyeva et al. 2020). Among marine fungal strains in which β-glucosidase activity has been studied, the genera *Arthrinium*, *Penicillium*, *Hypoxylon*, *Trichoderma*, *Aspergillus* and *Fusarium* seem particularly interesting because their β-glucosidase activity has been exhibited in several studies (Pointing et al. 1999; Burtseva et al. 2010; Hong et al. 2015; Lee et al. 2015, 2019; Patyshakuliyeva et al. 2020).

The optimal temperatures of most β-glucosidases obtained from marine fungi range from 50 to 60 °C (MacDonald and Speedie 1982; MacDonald et al. 1985; Ravindran et al. 2010; Karray et al. 2016). However, some β-glucosidases activities from marine fungi are optimal at 70 °C (Méndez-Líter et al. 2018) or at 35 °C (Elyas et al. 2010). Optimal pH ranges from 4 to 7 (Elyas et al. 2010; Ravindran et al. 2010; Karray et al. 2016; Méndez-Líter et al. 2018). Concerning salinity, a strain of *Aspergillus niger* isolated from seawater was characterized by an optimal NaCl concentration of 6% for its β-glucosidase activity (Xue et al. 2012b).

Cellulases

Cellulose is the most abundant natural polysaccharide and is widely present in terrestrial as well as marine plants. This polysaccharide is made of D-glucose linked in a chain by β-1,4 bonds (Fig. 1b). The interests in the characterization of new cellulose-degrading enzymes are multiple. Three main kinds of cellulase are found in fungi with different and complementary functions (Acharya et al. 2008). Endoglucanases hydrolyze the internal chain of the cellulose releasing multiple smaller chains, exoglucanases target the reducing and non-reducing ends of the cellulose chain resulting in cellobiose production and β-glucosidases release glucose residues from cellobiose. All of these enzymatic activities have been studied in marine fungi (Pointing et al. 1999; Ravindran et al. 2010; Hong et al. 2015; Lee et al. 2015, 2019; Patyshakuliyeva et al. 2020). However, according to the study and considering the methodology applied, the detailed enzymatic activity may not be more specific about and limited to "cellulase" activity, corresponding in fact to the cellulolytic complex or parts of it. Using cellulase for enzymatic hydrolysis could be of great interest in complex biological matrices due to the wide spectrum of efficient substrates that can be degraded.

Species belonging to fungal genera *Trichoderma* and *Aspergillus* are of particular interest considering their cellulase production, and other fungal genera such as *Penicillium* and *Humicola* are also known as cellulase producers (Kuhad et al. 2011; Gupta et al. 2015; Imran et al. 2016; Kunamneni 2016; Kavanagh 2017; Balabanova et al. 2018a; Shah et al. 2019; Singh et al. 2021). However, several other marine fungi produce only a low level of cellulase, or no cellulase at all, due to their specificity for a non-cellulose substrate (Balabanova et al. 2018a). When cultured on non-marine substrates, marine fungi have cellulolytic activities comparable with terrestrial fungal strains (Balabanova et al. 2018a).

Cellulase enzymes represent the third place in industry share (15%) after amylase (25%) and protease (18%) (Singh et al. 2021), and the industrial interest of these enzymes has greatly increased during the two past decades (Bhardwaj et al. 2021).

Cellulases have application in the food industry and particularly in the production of plant juices and oil (they can be used in collaboration with xylanase and pectinase for extraction and clarification) as well as in baking (increasing bread quality) (Kuhad et al. 2011; Imran et al. 2016; Kunamneni 2016; Kavanagh 2017; Shah et al. 2019; Siqueira et al. 2020; Srivastava et al. 2020; Bhardwaj et al. 2021; Ejaz et al. 2021; Singh et al. 2021). Cellulases have various other applications in industries such as laundry detergents (Vala et al. 2019; Barzkar and Sohail 2020), textiles (Trivedi et al. 2016; Vala et al. 2019; Barzkar and Sohail 2020; Singh et al. 2021), leather (Trivedi et al. 2016) and pharmaceutics (Singh et al. 2021). They are also used in the pulp and paper industry, particularly in the bleaching process as an alternative to traditional chlorine chemicals which exhibit disadvantages in terms of health and environment (Raghukumar 2008; Trivedi et al. 2016; Vala et al. 2019; Singh et al. 2021).

These cellulases also have applications directly linked with macroalgal uses. Indeed, these enzymes can be used in the degradation of seaweed wastes to produce plant biofertilizers in agriculture (Barzkar and Sohail 2020; Singh et al. 2021). They have also gained interest in the production of third-generation biofuels, allowing saccharification of macroalgal biomass (Vala et al. 2019; Barzkar and Sohail 2020). Marine fungi are particularly promising in biofuel production compared with marine bacteria or commercial enzymes (Trivedi et al. 2016; Vala et al. 2019). For example, species of *Aspergillus* have been particularly studied for the production of bioethanol from green seaweeds (Ghazal Mustafa et al. 2016; Karray et al. 2016; Girisha et al. 2017), but other genera are also studied for this bioethanol production, like *Trichoderma* or *Cladosporium* (Trivedi 2015; Girisha et al. 2017).

Advantages of marine microbial enzymes compared with terrestrial ones have already been mentioned. Marine microbial cellulase presents a particularly interesting stability at high or low temperatures, high pressure and salinity, and acid or alkaline pH (Barzkar and Sohail 2020).

Most of the studies of cellulolytic activities of marine fungal strains concern carboxymethyl cellulase (CMCase) (Meyers and Reynolds 1959; Torres and dela Cruz 2013; Li et al. 2014; Rong et al. 2015; Trivedi 2015; Karray et al. 2016). Carboxymethyl cellulose (CMC) is a modified cellulose produced with alkali cellulose and monochloroacetic acid (Hollabaugh et al. 1945) and is notably more soluble than classic kinds of cellulose and is easier to use as a carbon substrate. As CMC is not found in nature and fungal cellulases allow the degradation of CMC, CMCase activity is usually measured for the screening of cellulase activity. Indeed, some studies mention a "cellulase activity" when using CMC as enzyme substrate (Meyers and Reynolds 1959; Torres and dela Cruz 2013; Li et al. 2014; Trivedi 2015). Cellulolytic activities obtained using CMC as substrate will then be considered as cellulase in the present paragraph. The use of such pure cellulose substrates generally allows better cellulase production than by using other raw substrates (e.g., rice straw, wheat straw or sugarcane bagasse), but pure substrates can also be characterized by a low solubility and structural complexity, and they are more expensive (Bhardwaj et al. 2021). Some studies then aim to determine the preferred raw substrate to obtain the highest enzymatic activity. For example, the use of cotton seeds in culture allowed the highest exoglucanase, endoglucanase and β-glucosidase activities to be obtained by solid

fermentation of a strain of *Chaetomium* sp. isolated from mangrove wood (Ravindran et al. 2010).

As cellulases are glucanases allowing the degradation of cellulose, these cellulases can exhibit more specific endo-, exoglucanase or glucosidase activities. However, several cellulases can exhibit both endo- and exoglucanase activities (Gupta et al. 2012). Of the marine fungal cellulolytic enzymes, endoglucanases appear to be particularly well documented and represented compared with exoglucanases or glucosidases (Luo et al. 2005).

Marine fungal cellulases can be obtained from strains isolated from various habitats such as algae (Hong et al. 2015; Lee et al. 2015; Trivedi 2015; Patyshakuliyeva et al. 2020), sponges (Baker et al. 2009), mangrove habitats (Pointing et al. 1999; Ravindran et al. 2010; Torres and dela Cruz 2013), sediments (Balabanova et al. 2018b) and seawater (Li et al. 2014; Rong et al. 2015).

Optimal temperature and pH for cellulase activity can depend on the nature of considered cellulase (endoglucanase, exoglucanase or β-glucosidase) and the marine fungal species (Pointing et al. 1999). Generally, cellulase activities seem to be highest with a temperature ranging from 50 to 60 °C (MacDonald and Speedie 1982; MacDonald et al. 1985; Pointing et al. 1999; Ravindran et al. 2010; Santos et al. 2020) with several exceptions of optimal temperatures at 40 °C, notably for CMCase activities (Rong et al. 2015; Trivedi 2015). Optimal pH values for marine fungal cellulase generally are about 5–6, with several optimal pH values at 4 or even 9 (Meyers and Reynolds 1959; Pointing et al. 1999; Ravindran et al. 2010; Peng et al. 2011; Rong et al. 2015; Trivedi 2015; Santos et al. 2020). Rong et al. (2015) have characterized the molecular size of a marine fungal CMCase obtained from the *Aureobasidium pullulans* 98 strain, isolated from seawater in China, with a result of 67 kDa. A marine fungal strain of *Aspergillus terreus* has been described as producing a smaller cellulolytic enzyme (endoglucanase), at 56 kDa (Jmel et al. 2020).

The evolution of cellulase activity according to the concentration of NaCl was observed for a strain of *Ulocladium chartarum* isolated from salt marshes in Egypt. The cellulase activity slightly increases from 10 to 30 g L^{-1} NaCl in the culture medium (0.215 and 0.259 U mL^{-1} respectively) then decreases with 40 g L^{-1} NaCl (0.124 U mL^{-1}) (Sallam et al. 1988). Some other fungi have an increasing cellulolytic capacity with a salinity increasing (*Savoryella lignicola*, *Stagonospora* sp., *Trematosphaeria striatispora*), while the opposite is observed for others (*Helicascus kanaloanus*, *Lignincola laevis*) (Pointing et al. 1998).

As mentioned, strains of *Aspergillus* seem to be particularly well represented in studies dealing with marine fungal cellulases (Ravindran et al. 2010; Xue et al. 2012a; Karray et al. 2016; Girisha et al. 2017; Santos et al. 2020). Moreover, *Aspergillus* strains exhibited higher cellulase specific activity (18.6 U mg^{-1}) than species of *Penicillium* or *Rhizopus* (Ghazal Mustafa et al. 2016). Recently, an endoglucanase obtained from an *Aspergillus terreus* strain isolated from the green alga *Ulva* sp. was potentially interesting by its high specific activity (30.1 U mg^{-1}) and its high thermostability (Jmel et al. 2020). The use of this enzyme, compared with other commercial endoglucanases, is characterized by a higher degradation capacity of the alga *Ulva* sp. because this endoglucanase targets specifically the complex structure of the alga (Jmel et al. 2020). Even if *Aspergillus* sp. strains exhibit CMCase activities, it does not mean that these activities are always particularly high. As an example, fungi isolated from mangrove leaves in the Philippines showed that the highest CMCase activity was reached by a *Phomopsis* sp. strain (21.4 U mL^{-1}), while that of an *Aspergillus* sp. strain was 7.8 U mL^{-1}. *Colletotrichum* sp., *Penicillium* sp. and *Paecilomyces* sp. strain activities were also higher than that of *Aspergillus* sp. (Torres and dela Cruz 2013). *Aspergillus* is a genus widespread in the terrestrial environment, where cellulose is particularly present. It is difficult to know if terrestrial fungal strains have inherited and developed their cellulose-degrading capacity from the marine fungal strains having colonized the land, or if this ability has appeared in terrestrial fungal strains which would then colonize marine habitats. Interestingly, cellulase activities exhibited by *Penicillium* strains were almost as high as *Aspergillus* ones, *Penicillium* also being ubiquitous and widespread in terrestrial environments (Ghazal Mustafa et al. 2016). In a screening study of marine fungal strains associated with the brown alga *Agarum clathratum*, it has been shown that among the 233 isolated strains, belonging to 89 species, the highest cellulase activity was observed from *Penicillium madriti* with values higher than 0.5 U mL^{-1} (Lee et al. 2019). Fungi belonging to *Penicillium* genus are generally characterized by a good halotolerance, which is highlighted by Lee et al. (2015) where a strain of *Penicillium chrysogenum* was characterized by an increase of cellulase activity of 126% at 0.5 mM NaCl compared with no salt medium. However, the most active species was *Trichoderma hamatum* exhibiting a cellulase activity of 0.57 U mL^{-1} (Lee et al. 2015). In a recent study, a strain of *Trichoderma paraviridescens* exhibited a cellulase activity of 0.15 U mL^{-1}, being 2 to 10 times higher than those of other strains belonging to *Cladosporium*, *Epicoccum*, *Clonostachys*, *Penicillium* and *Rhizopus* genera (Patyshakuliyeva et al. 2020). Some other marine fungal species exhibit interesting cellulolytic activities, including *Hypoxolon oceanicum* (Pointing et al. 1999) and *Arthrinium* sp. (Hong et al. 2015). In addition to filamentous fungi, yeasts are also reported for cellulolytic activity such as strain of *Aureobasidium* (Torres and dela Cruz 2013; Rong et al. 2015; Karray et al. 2016). Moreover, some strains of *Candida* isolated from seawater in China exhibited higher CMCase activity (1.311 U mL^{-1}) than the

filamentous *Ascomycota* sp. and *Cladosporium* sp. (respectively 1.133 U mL^{-1} and 0.843 U mL^{-1}) (Li et al. 2014).

Several factors have been found to be responsible of variation of cellulolytic activities, in addition with the nature of the substrate previously discussed (Table 2). The optimal incubation period has an impact on cellulase activity of *Scopulariopsis brevicaulis*, which was more than two times higher after 7 days than 4 days of incubation, unlike *Beauveria felina* which exhibited low and no cellulase activity after 4 and 7 days, respectively (Balabanova et al. 2018b). Two main kinds of industrial fungal fermentations exist, being based on liquid media (submerged fermentation) or solid media (solid-state fermentation). Fungal enzyme production seems higher with fermentation performed on solid media (Viniegra-González et al. 2003; Hölker et al. 2004; Dutta et al. 2008; Ravindran et al. 2010; Rodríguez-Jasso et al. 2013). The activity of cellulolytic enzymes was also influenced by the amount of cellulose available and by the presence or absence of other enzymes such as the β-glucosidase which induced endoglucanase synthesis. Indeed, it has been observed that specific inhibition of β-glucosidase in the *Trichoderma reesei* QM9414 resulted in an inhibition of its endoglucanase activity (Kubicek 1987). Besides the enzymatic activity, growth rate also greatly influences the biotechnological potential of marine fungal strains, which can be limited considering strains with slow growth (Baker et al. 2009). Moreover, in order to enhance the activity of fungal enzymes, mixed cultures are being currently developed (Singh et al. 2021). Indeed, fungi not only excrete cellulase for the degradation of lignocellulosic compounds but a large set of enzymes with multiple polysaccharide targets. Different kinds of cellulase are usually used synergistically because of the lower efficiency obtained with a unique cellulase (Imran et al. 2016). Mixed cultures reduce the chance of contamination of the culture medium and can enhance enzyme production and efficiency (Bhardwaj et al. 2021; Singh et al. 2021).

Laminarinases

Some 1,3-β-glucanases can specifically target laminarin which is a polysaccharide composed of a linear chain of glucose linked in majority with β-1,3 bonds (Fig. 1b). The main sources of laminarinases are bacteria, fungi and algae (Huang et al. 2021). The principal biotechnological function of laminarinase is the production of laminarin-derived oligosaccharides which are more soluble in water than native polysaccharides and can exhibit several bioactivities of interest such as antioxidant, prebiotic, immunoregulatory, anti-inflammatory, radioprotective and antitumor activities (Trincone 2018; Usoltseva et al. 2020; Jagtap and Manohar 2021, p. 2021; Huang et al. 2021). These laminarinases also have applications in food industries (in brewing or wine making) (Usoltseva et al. 2020), in agriculture (as plant biocontrol agents) (Trincone 2018; Usoltseva et al. 2020) or in cosmetics (Huang et al. 2021). They are also used in the conversion of algal biomass into fermentable sugars for the production of bioethanol, but only a few studies have been performed on the subject since 2018 (Perez et al. 2018; Trincone 2018; Usoltseva et al. 2020; Huang et al. 2021; Rocher et al. 2021). Indeed, practical use of these laminarinases is just beginning (Usoltseva et al. 2020).

A diversity of fungal strains degrade laminarin, including several particularly promising ones such as strains of *Dendryphiella salina*, whose capacity of degrading laminarin has been described in several studies with enzymatic activities up to 0.032 U mL^{-1} (Schatz 1984; Grant and Rhodes 1992). *Cercospora salina* has been reported to exhibit a specific activity of 34 U mg^{-1} (Chesters and Bull 1963). A strain of *Penicillium brevicompactum* showed an activity of 0.22 U mL^{-1} (Patyshakuliyeva et al. 2020).

While optimal pH for the laminarinase activity of *D. salina* was 4.6 (Grant and Rhodes 1992), this enzymatic activity from *Chaetomium indicum* and *Trichoderma aureviride* was stable for pH in the range 4.5–7.5 (Burtseva et al. 2006). This suggests that marine fungal laminarinases tend to be preferentially active in acidic pH values. The optimal temperature for the laminarinase activity of *Chaetomium indicum* and *T. aureviride* has been recorded at 45 and 40 °C, respectively (Burtseva et al. 2006). An exoglucanase activity observed in a marine strain of *C. indicum* has been associated with an enzyme of 54 kDa (Burtseva et al. 2003). This exoglucanase shows a higher substrate affinity for laminarin than for other tested substrates (i.e. agar, laminarin oligosaccharides, glucose, etc.).

The incubation period for fungal growth before the measurement of the enzymatic activity seems to impact laminarinase activity. For example, *Beauveria felina* laminarinase specific activity was two times higher at 7 days of incubation (0.0100 U mg^{-1}) than at 4 days (0.5×10^{-3} U mg^{-1}) (Balabanova et al. 2018b). However, enzymatic specific activity increasing with the fungal incubation time is not observed for all enzymes. The opposite tendency characterized the fucoidanase and fucosidase activities. On the other hand, substrate nature does not seem to always influence the enzymatic activity of fungal strains. Enzymatic activities, including laminarinases, obtained from strains cultivated on *Laminaria* or *Ulva* matrices did not show significant differences (Patyshakuliyeva et al. 2020). This study demonstrated that most fungal strains grow preferentially on an algal matrix-based medium than a glucose-based medium. Growing on an algal medium could be of interest when specific algal degrading enzymes are targeted further.

Amylases

Starch has two principal components, namely amylose (a linear polysaccharide made of α-1,4 linked glucose units (Fig. 1b) and amylopectin (a polysaccharide made of an α-1,4 linked glucose backbone with α-1,6 linked glucose branching). Starch is not particularly represented in marine algae. Some green algae have been studied for starch and belong to the genus *Ulva*. Furthermore, one class of red seaweed (Bangiophyceae) is characterized by starch granules (Love et al. 1963; Percival 1979; Yu et al. 2002). Even if some data concerning amylases obtained from marine fungi are presented below, none of these fungi are indicated as isolated from an alga. Strains of interest have been isolated from sponges (Mohapatra et al. 1998), marine sediments (Gonçalves et al. 2013; Balabanova et al. 2018b), deep-sea (Li et al. 2007) or are taken from marine microorganism collections (Burtseva et al. 2010; Wang et al. 2016). However, amylases obtained from marine environments could have interests in the treatment of terrestrial starch which is the main source of starch (Prabhu et al. 2019), because of their particular characteristics.

The starch saccharification process performed by amylases is used in several industries such as textile (notably during the desizing process) (Homaei et al. 2016a; Trincone 2018; Vashist et al. 2019; Ahmed et al. 2020), leather (Trincone 2018), food (notably in bakery) (Homaei et al. 2016a; Suriya et al. 2016; Barone et al. 2019; Vashist et al. 2019; Ahmed et al. 2020), feed (by enhancing the protein concentration) (Vashist et al. 2019; Ahmed et al. 2020), detergent (Suriya et al. 2016; Trincone 2018; Ahmed et al. 2020), fermented beverages and distilleries (Homaei et al. 2016a; Vashist et al. 2019; Ahmed et al. 2020), paper industry (Homaei et al. 2016a; Suriya et al. 2016; Vashist et al. 2019), pharmaceutics (Trincone 2018, p. 20; Barone et al. 2019; Ahmed et al. 2020) and chemicals (Trincone 2018; Barone et al. 2019; Ahmed et al. 2020). Amylases are also used in waste treatment (Trincone 2018; Vashist et al. 2019), in biofuel production from starch biomass (Homaei et al. 2016a; Suriya et al. 2016; Barone et al. 2019) and in the processing of glucose and fructose syrups (Homaei et al. 2016a; Suriya et al. 2016). The use of amylase in industries using traditional chemicals can replace these, which has health and environmental benefits (Barone et al. 2019).

Fungal sources of amylases mainly belong to the genera *Aspergillus*, *Penicillium* or *Rhizopus* (Kango et al. 2019).

The optimal temperature for the activity of amylases obtained from marine fungi seems to be similar to those for other glucanase enzymes (60 °C) (Mohapatra et al. 1998; Li et al. 2007). Indeed, even if all glucan degrading enzymes can degrade different specific polysaccharides, it can be expected that they all have similarities in their global mechanism, including the temperature of activity. However, an amylase obtained from a strain of *Penicillium solitum* isolated from marine sediments of Antarctica exhibited its highest activity according to the enzymatic zone of clearance on solid culture medium at a temperature of 30 °C. However, without a higher tested temperature, it is difficult to define any optimal temperature (Gonçalves et al. 2013). Nevertheless, the cold active ability of this *P. solitum* amylase could have interests in cold processes in the pharmaceutic, cosmetic and chemical industries (Gonçalves et al. 2013).

It seems that optimal pH for the activity of amylases is acidic, with pH values ranging from 4.5 to 5 (Mohapatra et al. 1998; Li et al. 2007). This tendency of acid functioning enzymes obtained from marine fungi seems globally shared between all kinds of enzymes.

Of the 15 strains of marine fungi obtained from a microorganism collection (Marine microorganisms of the Pacific Institute of Bioorganic Chemistry) showing an amylase activity, the two most active strains belonged to the species *Penicillium chrysogenum* (Burtseva et al. 2010). Moreover, the majority of strains exhibiting amylase activity belonged to *Penicillium*. The amylase ability of this genus is also highlighted by Gonçalves et al. (2013) who showed a promising amylase activity from a strain of *Penicillium solitum*. Interestingly, the *Penicillium* genus is also widespread in terrestrial plants, in which starch is commonly present (Ellis et al. 1998; Belyuchenko 2016).

Amylase activity was obtained from two strains of *Scopulariopsis brevicaulis* and *Beauveria felina* isolated from marine sediments. The highest specific activity (0.5×10^{-3} U mg^{-1}) was observed after 7 days of incubation in *S. brevicaulis*, with a value more than twice higher than the one obtained after 4 days of incubation (0.2×10^{-3} U mg^{-1}) (Balabanova et al. 2018b). Other marine fungal strains of *Aureobasidium pullulans*, *Mucor* sp. and *Pestalotiopsis* sp. have shown promising amylase activites (Mohapatra et al. 1998; Li et al. 2007; Wang et al. 2016).

An amylase specific activity of 120×10^{3} U mg^{-1} has been obtained from a strain of *Penicillium chrysogenum* (Burtseva et al. 2010). The addition of laminarin in the fungal culture medium seems to increase amylase activities (as well as most other enzyme activities) in a strain of *Penicillium canescens* (Burtseva et al. 2010).

Few studies dealing with marine amylases are available compared with terrestrial ones and marine amylases are poorly characterized. However, it has been shown that an amylase obtained from the marine yeast *Aureobasidium pullulans* was characterized by a molecular weight of 98 kDa and composed of two subunits of 65 and 33 kDa (Li et al. 2007).

It seems that marine amylases are more tolerant to salinity than terrestrial ones (Mohapatra et al. 1998). In this study, the amylase reached its optimal activity with 2% NaCl, and a salinity increase to 9% halves this activity.

The high salinity would be part of extreme conditions for which marine amylases and more generally marine enzymes may present an important interest notably in starch saccharification.

Several marine fungal strains belonging to *Calcarisoprium*, *Tritirachium*, *Bartalinia*, *Penicillium*, *Scopulariopsis* and *Pestalotiopsis* grew on starch similar to their growth on glucose, showing the efficiency of amylases produced. A strain of *Pestalotiopsis* sp. exhibited the best affinity with starch (Wang et al. 2016).

The production of amylases by marine filamentous fungi seems to be less important than by those obtained by marine bacteria or marine yeasts. Indeed, considering 161 marine strains isolated from Antarctica (sediments, plants, algae, water, animal faeces, ice, etc.) tested at 20 °C (151 bacteria, 31 yeasts and 10 filamentous fungi), any filamentous fungi exhibited amylase activity contrarily to bacteria and yeasts, among which 51% and 3%, respectively, exhibited amylase activity (Loperena et al. 2012).

Galactan degradation

Galactans are polymers of galactose, as glucans correspond to glucose polymers. However, galactans are less common than glucans in nature; therefore, they are less studied and data dealing with galactan degrading enzymes in the literature are fewer than those for glucan degrading ones. Nevertheless, several algal galactan molecules are targeted by marine fungal enzymes, namely agarose and carrageenan. Their structures and the general mode of action of galactanases are presented in Fig. 2.

As for cellulose and more widely glucan degradation, galactan degradation occurs by the action of three types of enzymes: endogalactanases, exogalactanases and galactosidases. The first two target respectively the side chain and the end of the galactan molecule (Fig. 2a). The name of galactanase is defined according to the nature of the targeted galactan, i.e. agarases and carrageenases which will respectively cleave agar and carrageenan. The third, the galactosidases, are responsible for the degradation of galactosides into galactose units (Fig. 2a) (Yoshimi et al. 2017).

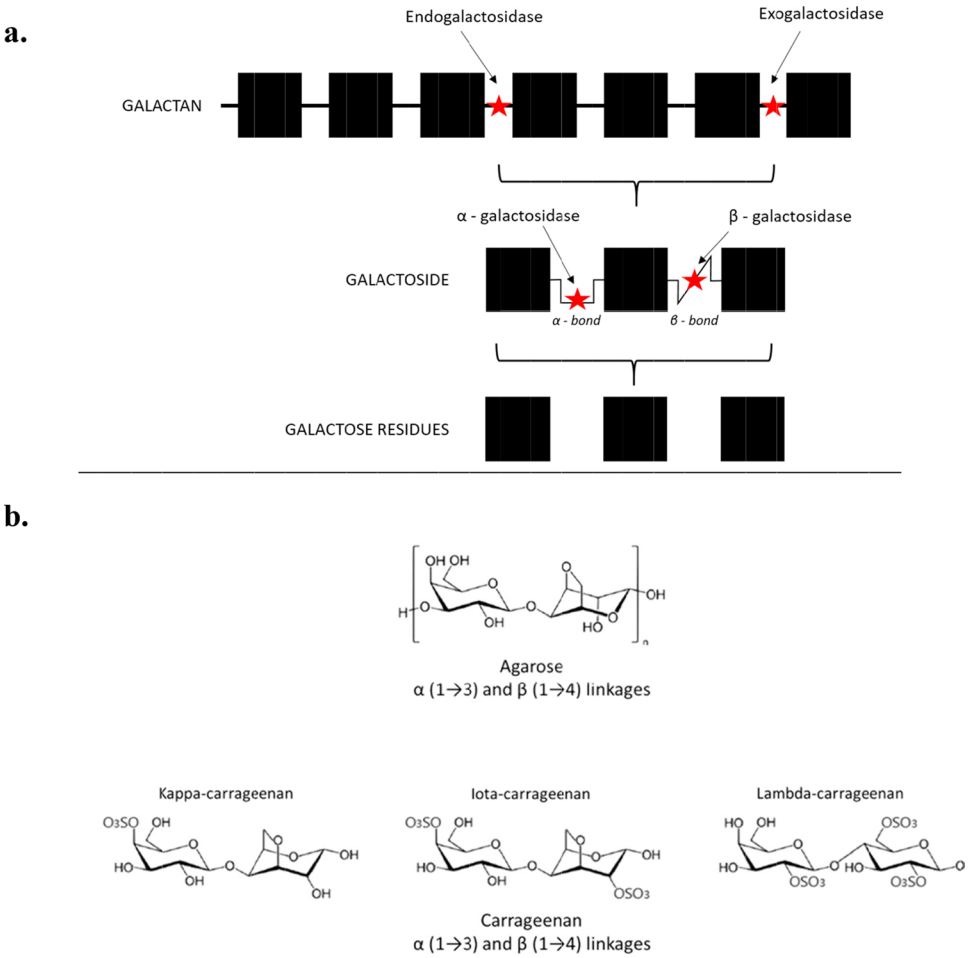

Fig. 2 **a.** General mechanisms of galactan degradation with galactanases with a first step of degradation in galactosides followed by a second step of degradation of galactosides in galactose residues. Squares represent galactose, red stars represent link breaking by the corresponding enzyme. **b.** Structural composition of natural galactans targeted by marine fungal enzymes (adapted from Henares et al. (2010); Ven and Rani (2012))

Galactosidases

The α-galactosidase, β-galactosidase and α-AcN-galactosaminidase specific activities found in *Beauveria felina* raged from 1.2×10^{-3} to 2.4×10^{-3} U mg^{-1}. Interestingly, the α-galactosidase activity was twice as high after 4-day incubation than after 7-day incubation, showing that some enzymatic activities seem to decrease after a short period of incubation (Balabanova et al. 2018b). *Scopulariopsis brevicaulis* also exhibited β-galactosidase and α-AcN-galactosaminidase specific activities, respectively 2.5×10^{-3} and 1.7×10^{-3} U mg^{-1} (Balabanova et al. 2018b).

In a study screening some enzymatic activities from marine fungal strains belonging to the three genera *Aspergillus*, *Geomyces* and *Penicillium*, only *Penicillium* strains showed β-galactosidase activity (although not all *Penicillium* strains exhibited enzymatic activity). A strain of *Penicillium implicatum* exhibited a noticeable β-galactosidase specific activity (42×10^3 U mg^{-1}), at least twice higher than the β-galactosidase activity of the other tested strains of *Penicillium* (Burtseva et al. 2010).

Agarases

Agar is composed of two structures, namely agarose (a polysaccharide constituted by a repetition of a disaccharide made of D-galactose and 3,6-anhydro-L-galactopyranose (Fig. 2b) and agaropectin (a mixture of smaller sulfated molecules), and is widely used in many industries (agronomy, cosmetics, pharmacology, microbiology…) because of its gelling and thickening properties (Armisén et al. 1991; Armisén and Gaiatas 2009). As for carrageenan, agar is produced by red seaweeds (Armisén et al. 1991; Armisén and Gaiatas 2009).

Industrial processes entailing the use of agarases can be performed by native or recombinant enzymes. Agaro-oligosaccharides and neoagaro-oligosaccharides are then obtained after agarose hydrolysis by native and recombinant agarases respectively (Jahromi and Barzkar 2018; Trincone 2018). These oligosaccharides can exhibit several bioactivities such as prebiotic, anti-obesity, anti-diabetic, immunomodulatory, skin whitening, skin moisturizing, anti-inflammatory, antioxidant, antibacterial and antitumor activities (Jahromi and Barzkar 2018; Vashist et al. 2019; Park et al. 2020; Jagtap and Manohar 2021). These bioactivities have particular interests in industries such as pharmaceutical, cosmetic, medical or food (Muffler et al. 2015; Beygmoradi and Homaei 2017; Jahromi and Barzkar 2018; Birolli et al. 2019; Vashist et al. 2019; Park et al. 2020). These agarases are also used in molecular biology for the recovering of DNA fragments in agarose gels (Muffler et al. 2015; Beygmoradi and Homaei 2017; Jahromi and Barzkar 2018; Trincone 2018) and are promising in the production of biofuel (Martin et al. 2014; Park et al. 2020).

Agarases have direct applications on seaweed, being used for the preparation of algal protoplasts for genetic engineering (Jahromi and Barzkar 2018; Trincone 2018), for the control of red algal blooms (Beygmoradi and Homaei 2017), for the prevention of biofouling (Beygmoradi and Homaei 2017) or for the recovery of algal compounds of interest such as unsaturated fatty acids, pigments or vitamins by the hydrolysis of the algal cell wall (Jahromi and Barzkar 2018).

Marine agarases generally exhibit thermostability as well as halostability which can be worthwhile in several industries (Jahromi and Barzkar 2018). There is a great gap between knowledge in marine bacterial enzymes and marine fungal enzymes, with few data on the latter, which highlights great opportunities in these research fields (Gomaa et al. 2017; Birolli et al. 2019).

As for carrageenan, galactan units of agar polymers are linked by β and α alternated bonds (Fig. 2b), which explain the differentiation between α-agarases and β-agarases (Flament et al. 2007; Gomaa et al. 2017). Marine fungal strains of the genera *Beauveria*, *Scopulariopsis* and *Cladosporium* have been described as degrading agar (Gomaa et al. 2015; Balabanova et al. 2018b; Furbino et al. 2018). Moreover, the majority of agarolytic marine fungal strains isolated from algae are associated with red seaweeds, although some also have been isolated from brown seaweeds (Gomaa et al. 2015, 2017; Furbino et al. 2018; Fawzy 2020).

The optimal temperature of agarases obtained from marine fungi ranges from 40 to 50 °C (Kawaroe et al. 2015; Gomaa et al. 2017; Fawzy 2020). The optimal pH, contrarily to glucanases, seem to be more alkaline for agarases, ranging from 7 to 8 (Kawaroe et al. 2015; Fawzy 2020).

According to Balabanova et al. (2018b), isolates *Beauveria felina* and *Scopulariopsis brevicaulis* exhibited agarase specific activities of 0.4×10^{-3} U mg^{-1} and 0.04×10^{-3} U mg^{-1}, respectively. These activity values seem particularly low compared with other enzymes screened in this study for these fungal strains. Among nine marine fungi isolated obtained from macroalgae, a strain of *Cladosporium* sp. isolated from the red seaweed *Georgiella confluens* exhibited the highest agarase activity (6.55 U mL^{-1}) (Furbino et al. 2018).

The first described fungal agarase came from a strain of Hypocreaceae, isolated from seawater and using the red seaweed *Gelidium latifolium* as a substrate for the fungal incubation (Kawaroe et al. 2015). Two bands of proteins were obtained by SDS-PAGE, at 39 and 44 kDa. To the best of our knowledge, it is the first reference describing the molecular weight of a marine fungal agarase, but it seems that this agarase molecular weight is close to those found for marine bacteria (Kawaroe et al. 2015).

Gomaa et al. (2015) obtained agarase activities from marine fungi isolated from several seaweeds, principally red seaweeds. The fungal isolates were incubated using *Palisada*

perforata as carbon substrate, and interestingly, the highest agarase activities obtained corresponded to marine fungi isolated from *P. perforata*. The highest agarase specific activity was reached by a *Curvularia lunata* strain (isolated from *P. perforata*) at 20 U mg^{-1}. Other marine strains of *Aspergillus terreus*, *Setosphaeria rostrate* and *Dendryphiella arenaria* also showed promising agarase activities. According to Gomaa et al. (2015), the studied algicolous fungi exhibited higher agarase activities than other non-algicolous fungi, highlighting the adaptation of these closely related fungi to their algal substrate. Moreover, the agarase and amylase activities of marine fungi associated with *P. perforata* seem to have a synergetic influence, allowing a more efficient degradation of the alga.

Carrageenases

Carrageenan is a polymer of galactose residues alternatively linked with α-1,3 and β-1,4 bonds (Fig. 2b). Three main types of carrageenans are found according to their structural organization and sulfation degree and correspond to kappa-, iota- and lambda-carrageenan (De Ruiter and Rudolph 1997) (Fig. 2b). Carrageenans are of particular interests in some industries (agronomic, cosmetics, pharmaceutics…) due to their numerous properties like gelling and thickening (Necas and Bartosikova 2013; Campbell and Hotchkiss 2017; Furbino et al. 2018). These carrageenans are only produced by red seaweeds (De Ruiter and Rudolph 1997; Rocha de Souza et al. 2007), but some marine fungi isolated from brown seaweeds show carrageenase activity (Furbino et al. 2018; Patyshakuliyeva et al. 2020). This observation highlights the fact that marine fungal species can be characterized by enzymatic strategies allowing them to develop on different substrates.

One of the main industrial use of carrageenase is the synthesis of oligosaccharides from carrageenan polysaccharides (Ghanbarzadeh et al. 2018; Zhu et al. 2018a). Indeed, carrageenan exhibits interesting bioactivities, but its therapeutic use is limited by the low tissue-penetrating ability and bioavailability due to high molecular weight and viscosity. Oligosaccharides have similar bioactivities and exhibit better bioavailability and solubility (Ghanbarzadeh et al. 2018). These oligosaccharides have antitumor, antiviral, anticoagulant, immunoregulatory and antioxidant activities (Chauhan and Saxena 2016; Beygmoradi and Homaei 2017; Ghanbarzadeh et al. 2018; Trincone 2018; Zhu et al. 2018a; Vashist et al. 2019; Jagtap and Manohar 2021). Carrageenases are used in several industries such as the food, detergent, textile, pharmaceuticals and chemicals industries (Chauhan and Saxena 2016; Beygmoradi and Homaei 2017; Ghanbarzadeh et al. 2018; Zhu et al. 2018a; Birolli et al. 2019) and can also be used as plant defence stimulators in agriculture (Ghanbarzadeh et al. 2018), and seem promising for bioethanol production (Chauhan and Saxena 2016; Ghanbarzadeh et al. 2018; Zhu et al. 2018a).

Carrageenases also have application in marine biotechnology and environment. Indeed, they are used in seafood processing (Beygmoradi and Homaei 2017), for the isolation and preparation of algal protoplasts (Chauhan and Saxena 2016; Ghanbarzadeh et al. 2018; Zhu et al. 2018a), in the treatment of seaweed wastes (used as industrial raw material and as depolluting agents) (Chauhan and Saxena 2016; Ghanbarzadeh et al. 2018; Zhu et al. 2018a), in the prevention of red algal blooms (Chauhan and Saxena 2016) and in the recovery of compounds of interest such as proteins from macroalgae (Chauhan and Saxena 2016).

Some marine fungal genera are regularly studied for their carrageenase activities, such as *Beauveria*, *Penicillium* or *Cladosporium* (Balabanova et al. 2018b; Furbino et al. 2018; Patyshakuliyeva et al. 2020). Carrageenase activity has been measured in both *Beauveria felina* and *Scopulariopsis brevicaulis* (Balabanova et al. 2018b). The tendency of *B. felina* to reach its maximum carrageenase enzymatic activity level early (4 days of incubation) has been observed, as for the α-galactosidase activity. The maximum carrageenase activity of *S. brevicaulis* is reached after 7 days of incubation. However, with values of 0.02×10^{-3} and 0.13×10^{-3} U mg^{-1} obtained after an incubation of 7 days respectively for *B. felina* and *S. brevicaulis*, carrageenase specific activity is particularly low compared with other screened enzymatic activities (Balabanova et al. 2018b).

Of the four algae from which fungi have been isolated and screened for their carrageenase activity, three belonged to the Rhodophyceae (*Georgiella confluens*, *Iridaea cordata*, *Palmaria decipiens*) and one to the Phaeophyceae (*Ascoseira mirabilis*) (Furbino et al. 2018). This observation suggested that carrageenase activity is mostly found in Rhodophyceae-associated fungi, which are characterized by presence of carrageenan unlike Phaeophyceae and Chlorophyceae. Considering the marine fungal strains exhibiting carrageenase activity, the genus *Penicillium* was the most represented. Furthermore, a *Penicillium* sp. strain isolated from the red alga *I. cordata* exhibited the highest carrageenase activity (17.5 U mL^{-1}), at least twice higher than the other strains (Furbino et al. 2018). In another study, among fungi isolated from the brown alga *Fucus* sp., the strain characterized by the highest carrageenase activity (0.015 U mL^{-1}) was a strain of *Clonostachys rosea* (Patyshakuliyeva et al. 2020). The other carrageenase activities of the study ranged from 0.0045 to 0.0115 U mL^{-1}. It is important to highlight the fact that there are many variables (i.e. fungal species, fungal isolation, conservation, incubation, enzymatic extraction protocol, activity measurement…) which could explain these different carrageenase activities between both studies. Nevertheless, it may be interesting to perform studies to determine if marine fungi isolated from red seaweeds are

more interesting with respect to carrageenase activity than marine fungi isolated from brown seaweeds.

Other hydrolases

Even if many polysaccharides targeted by marine fungal polysaccharidases belong either to glucans or galactans, several other polysaccharides can be also hydrolyzed, such as xylan, fucan and mannan. Their structures and the global hydrolyze mechanism which allows the degradation of these polysaccharides are presented Fig. 3.

Xylan degrading enzymes

Xylan is a polymer of xylose residues linked by β-1,4 osidic bonds, putatively branched with α-arabinofuranose or α-glucuronic acids residues (Fig. 3b). Xylan is particularly represented in red seaweeds and is widely distributed in terrestrial plants, in both dicotyledons (such as beechwood) and monocotyledons (such as corn) (Synytsya et al. 2015; Jensen et al. 2018; Hsieh and Harris 2019).

Xylan degrading enzymes can be separated between xylanases and xylosidases. Xylanases (endo- and exoxylanases) target the xylan chains to produce xylosides, oligosaccharides of xylan, while xylosidases degrade these xylosides to produce xylose (Fig. 3a).

Xylan is a principal component of the polysaccharide cell wall of some plants and algae. The main sources of xylanases for industrial uses are fungi and bacteria (Burlacu et al. 2016). Among fungi, several genera are particularly promising for xylanase production, such as *Aspergillus*, *Trichoderma*, *Penicillium* and *Fusarium* (Motta et al. 2013; Burlacu et al. 2016; Bajaj and Mahajan 2019; Singh et al. 2019). Fungal xylanase activities are generally higher than bacterial ones (Burlacu et al. 2016).

Xylanases, including marine ones, can be used in numerous industries and applications, such as food (notably for extraction and clarification of fruit juices, wine, brewing, bakery, dairy, marine food, extraction of coffee, plant oils

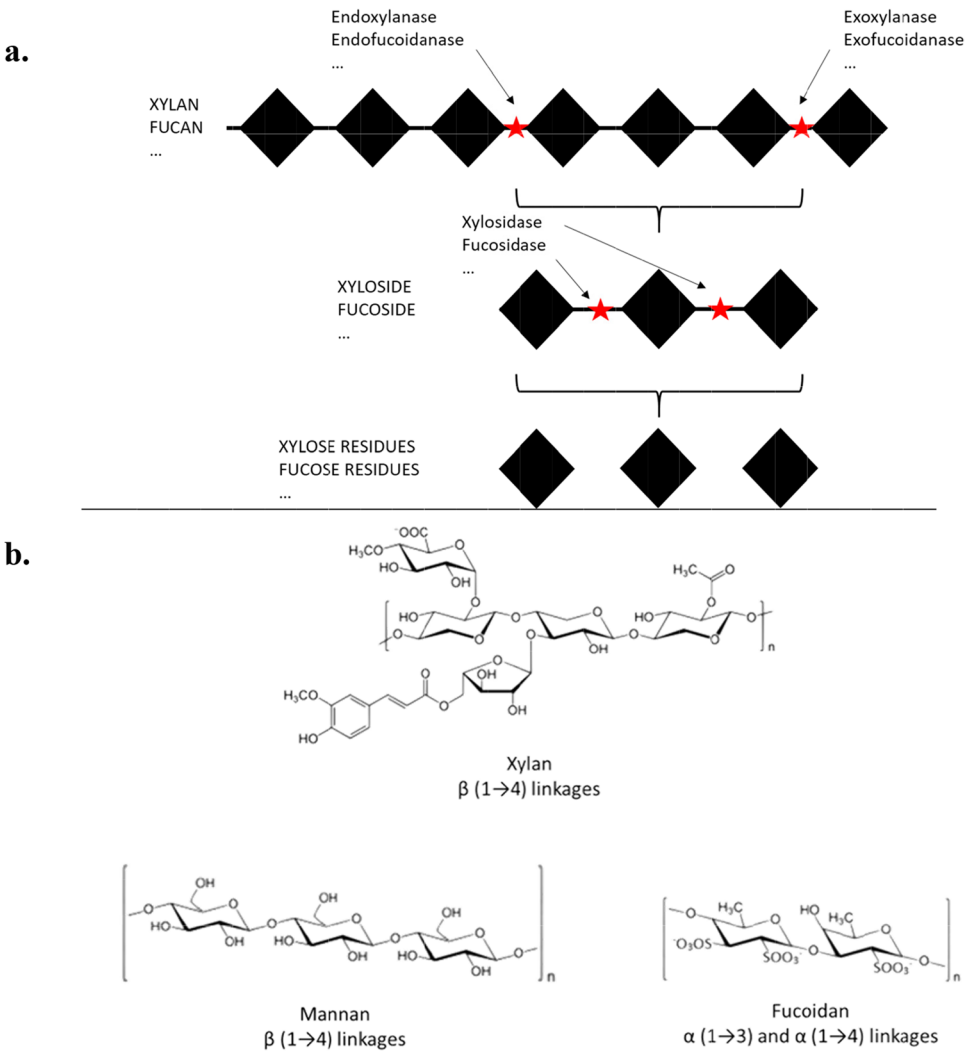

Fig. 3 **a.** General mechanism of other polysaccharide degradation with hydrolases with a first step of polysaccharide degradation in "osides" followed by a second step of degradation of "osides" in "oses". Diamonds represent sugar residues (xylose, fucose and mannose), and red stars represent link breaking by the corresponding enzyme. **b.** Structural composition of natural other polysaccharides targeted by marine fungal enzymes (adapted from Rogowski et al. (2014); Anbuchezhian et al. (2015); Bonechi et al. (2017))

and starch) (Polizeli et al. 2005; Burlacu et al. 2016; Beygmoradi and Homaei 2017; Trincone 2018; Alokika and Singh 2019; Singh et al. 2019; Vashist et al. 2019; Qeshmi et al. 2020), pulp and paper biobleaching (Raghukumar et al. 2004; Polizeli et al. 2005; Burlacu et al. 2016; Beygmoradi and Homaei 2017; Alokika and Singh 2019; Singh et al. 2019; Vashist et al. 2019; Qeshmi et al. 2020), textile (Polizeli et al. 2005), animal feed (including fish feed) (Polizeli et al. 2005; Burlacu et al. 2016; Alokika and Singh 2019; Singh et al. 2019; Vashist et al. 2019; Qeshmi et al. 2020), biofuel production (notably in the saccharification of seaweed biomass) (Burlacu et al. 2016; Trincone 2018; Alokika and Singh 2019; Singh et al. 2019; Qeshmi et al. 2020), detergent (Burlacu et al. 2016), waste treatment (Burlacu et al. 2016; Trincone 2018), plant biocontrol (Burlacu et al. 2016), chemicals (Polizeli et al. 2005) and pharmaceutics (Polizeli et al. 2005; Alokika and Singh 2019; Birolli et al. 2019; Singh et al. 2019; Qeshmi et al. 2020).

Marine xylanases are mostly obtained from bacteria and fungi, being particularly interesting in terms of high temperature and pH tolerance (Qeshmi et al. 2020). These marine xylanases can be used for the production of algal protoplasts (Qeshmi et al. 2020) and for the extraction of soluble metabolites of interest, such as the R-Phycoerythrin extracted from red algae for example (Dumay et al. 2014).

These xylan degrading enzymes from marine sourced microorganisms are poorly studied compared with terrestrial ones. Moreover, marine fungal xylan degrading enzymes seem more efficient than marine bacterial ones (Haltrich et al. 1996; Bergquist et al. 2002; Polizeli et al. 2005; Thirunavukkarasu et al. 2015). These observations can explain the interest concerning xylan degrading enzymes from fungi isolated from marine environments for their use in industries.

Xylanases

The optimal temperature for xylanase activity in marine fungi ranges from 45 to 55 °C (Raghukumar et al. 2004; Torres and dela Cruz 2013; Del-Cid et al. 2014; dos Santos et al. 2016; Korkmaz et al. 2017; Wu et al. 2018). However, a cold-adaptive xylanase obtained from a marine strain of *Penicillium chrysogenum* has shown an optimal temperature of 25 °C (Hou et al. 2006), highlighting the high diversity considering the specificities even in the same enzyme family. In general, polysaccharide degrading enzymes from marine fungi seem to have optimal pH values slightly acidic as is also the case concerning xylanases with optimal pH values varying between 5 and 6 (Hou et al. 2006; Del-Cid et al. 2014; Thirunavukkarasu et al. 2015; dos Santos et al. 2016; Korkmaz et al. 2017; Wu et al. 2018). A xylanase obtained from a marine strain of *Aspergillus* sp. showed optimal activity at pH 3.5 (Raghukumar et al. 2004). Nevertheless, several xylanases from marine fungi can also be characterized by optimal pH values more neutral or even slightly alkaline (Torres and dela Cruz 2013).

Xylanases can be obtained from marine fungi isolated from different habitats like marine sponges (Del-Cid et al. 2014; dos Santos et al. 2016; Korkmaz et al. 2017), marine sediments (Hou et al. 2006; Korkmaz et al. 2017; Wu et al. 2018), mangroves (Raghukumar et al. 1994, 2004; Torres and dela Cruz 2013; Wu et al. 2018) and seaweeds (Thirunavukkarasu et al. 2015; Patyshakuliyeva et al. 2020). Among marine fungal xylanases, most of them have been obtained from filamentous fungi, but some marine yeast strains seem to present interesting xylanase activities (Duarte et al. 2013); Torres and dela Cruz 2013).

Among the marine fungal strains characterized by a promising xylanase activity, the genera *Trichoderma* and *Aspergillus* seem to be particularly efficient for xylan degradation (Raghukumar et al. 2004; Torres and dela Cruz 2013; Thirunavukkarasu et al. 2015; dos Santos et al. 2016; Korkmaz et al. 2017; Patyshakuliyeva et al. 2020). Indeed, terrestrial strains of these two genera are currently mainly used for the production of commercial xylanases (Torres and dela Cruz 2013; Korkmaz et al. 2017). The important xylan degrading capacity of a marine *Trichoderma harzianum* should be due to its high xylanase and xylosidase activities. The presence of 2% of NaCl in the culture medium increased the xylanase activity of this strain compared with no salt control culture, showing the adaptability of *T. harzianum* to its marine environment (Thirunavukkarasu et al. 2015). Marine strains of *Trichoderma* are not only promising for the production of xylanases and xylosidases but also glucanases and β-glucosidases (Patyshakuliyeva et al. 2020). Indeed, xylanase-producing marine fungi seem to generally synthesize also cellulases (Luo et al. 2005). These two kinds of enzymes have complementary activities in the degradation of natural polysaccharides. According to Patyshakuliyeva et al. (2020), marine fungi do not need to exhibit enzymatic activities perfectly complementary with the polysaccharides of the substrate to allow its degradation. Indeed, the presence of enzymes targeting polymers which are widespread in algal cell walls (like xylanases or cellulases) would be sufficient to allow the fungal growth on diverse algal biomasses (Patyshakuliyeva et al. 2020). In the study of Thirunavukkarasu et al. (2015), the second most important xylanase producer was an *Aspergillus terreus* strain isolated from a seagrass (*Cymodocea serrulata*), with specific activity values of 0.7 U mg^{-1}. In addition to the fact that *Aspergillus* is a genus particularly interesting for xylanase production, the study of dos Santos et al. (2016) highlighted also the importance of fungal culture condition to optimize the enzymatic activity (with an increase of xylanase activity from 49.4 to 629.6 U mL^{-1} thanks to culture optimization). Other marine fungal strains of the genera *Penicillium* or *Cladosporium*, for example, are described in several studies exhibiting xylanase

activities of interest (Hou et al. 2006; Torres and dela Cruz 2013; Del-Cid et al. 2014; Patyshakuliyeva et al. 2020).

Several xylanases obtained from marine fungi of genera such as *Phoma*, *Penicillium*, *Cladosporium*, *Trichoderma* or *Paecilomyces* showed better activity in the presence of NaCl concentrations close to those of seawater than without any salinity (Raghukumar et al. 2004; Torres and dela Cruz 2013; Korkmaz et al. 2017; Wu et al. 2018). A strain of *Trichoderma pleuroticola* (08CK001) was characterized by a sixfold xylanase production in a culture medium supplemented with 24.4% artificial seawater (Korkmaz et al. 2017).

An important factor of fungal culture conditions impacting xylanase activity is the substrate used. Pure xylan is the most evident substrate to enhance the xylanase activity, but for large-scale enzymatic production, this substrate is not economically viable. Other kinds of substrates of interest in the enhancement of enzymatic activities include agricultural by-products or co-products (Table 2). Considering a marine *Cladosporium* sp. strain screened by Del-Cid et al. (2014), the highest xylanase activities were obtained using beechwood and birchwood xylans (specific activities of 200 and 160 U mg^{-1}, respectively), but the most promising alternative substrate was the wheat bran.

Marine fungal strains characterized by xylanase activity can produce several xylanases. It is the case for an *Aspergillus niger* strain isolated from mangrove (Raghukumar et al. 2004), which appears to have two different xylanases (13 and 18 kDa). The enzyme molecular weight differs according to the fungus. A marine fungal xylanase obtained from a strain of *Penicillium chrysogenum* was characterized by Hou et al. (2006) with a molecular weight of 38 kDa. This molecular weight is about two times higher than both xylanases obtained from *Aspergillus niger* (18 and 13 kDa) characterized by Raghukumar et al. (2004). A xylanase produced by a mangrove fungal strain of *Phoma* sp. has an intermediate theoretical molecular weight of 24.4 kDa (Wu et al. 2018).

Xylosidases

There are fewer studies on xylosidases from marine fungi than on xylanases. This can be explained in part by the fact that some studies characterize the general xylanolytic activity, degrading the xylan to xylose, whereas others make the distinction between the activities of the different actors of the xylan degrading complex (principally endoxylanases, exoxylanases and xylosidases).

Due to this lack of studies available in the literature, no data have been found on optimal temperature and pH of marine fungal xylosidase, as well as data on enzyme molecular weight. However, concerning salinity tolerance, xylosidase specific activity increased respectively by 3.2, 2.1 and 1.8 with 1.5, 2 and 2.5% NaCl compared with media without supplemented NaCl in *Trichoderma harzianum* strain MTCC10344 isolated from *Sargassum wightii* (Thirunavukkarasu et al. 2015). Another study on *T. harzianum*, *Curvularia tuberculata*, *Gonatophragmium mori* and *Aspergillus terreus* marine strains, showed that the xylosidase specific activity was maintained from 0 to 1.2 M NaCl, without any significant increase (Sengupta et al. 2017).

Thirunavukkarasu et al. (2015) found that the marine fungal strain showing the most important xylosidase specific activity (2.4×10^{-3} U mg^{-1}) was *Trichoderma harzianum*. This genus seems to be particularly interesting with respect to xylosidase activity (Thirunavukkarasu et al. 2015; Sengupta et al. 2017; Patyshakuliyeva et al. 2020). In the study of Patyshakuliyeva et al. (2020), the *Trichoderma paraviridescens* strain CBS 143,790 FP-027-C5 isolated from *Fucus* sp. was characterized by the greatest xylosidase activity (0.01 U mL^{-1}) compared with the other screened marine fungal strains. Some of these strains seem to exhibit a little preference for the use of *Ulva lactuca* as a substrate compared with *Laminaria digitata*.

Fucoidanases

Fucoidans are sulfated polysaccharides principally constituted of fucose alternatively linked by α (1 → 3) and α (1 → 4) bonds (Fig. 3b) and they are mainly found in brown macroalgae (Morya et al. 2012; Zayed and Ulber 2019).

Endo- and exo-fucoidanases degrade fucoidan and respectively target the backbone and the ends of the polymeric chain, resulting in oligosaccharides themselves degraded in monosaccharides (fucose) by fucosidases (Fig. 3a).

The presence of fucoidanase in marine fungi was discussed in 2009 (Holtkamp et al. 2009), but here we provide information from several more recent studies. However, despite the biotechnological potential of fucoidans, studies on the properties of fucoidanases are scarce because of the limited description of microbial producers of this enzyme (Gurpilhares et al. 2016; Balabanova et al. 2018a).

Besides the role of fucoidanases in the description of fucoidan structures (Kusaykin et al. 2015), recent studies exhibited bioactivities of fucoidan oligosaccharides obtained with fucoidanases and fucosidases such as anticancer (Trincone 2018) and immunoregulatory activities (Jagtap and Manohar 2021). Moreover, fucosylated oligosaccharides can be involved in physiological processes such as immune response, signal transduction, early embryogenesis, growth regulation, apoptosis, adhesion of pathogens, extravation of leukocytes and maturation and interaction of gametes. Fungal fucosidases are mainly synthesized by *Aspergillus*, *Fusarium* and *Penicillium* genera (Guzmán-Rodríguez et al. 2019). Considering all the enzymes described in the present review, fucoidan-degrading enzymes are certainly the ones for which properties and industrial applications are the least studied.

Habitats of fucoidanase producing marine fungi seem to be limited to red and brown macroalgae (Gomaa et al. 2015, 2019; Hifney et al. 2019; Patyshakuliyeva et al. 2020), and marine sediments (Qianqian et al. 2011; Wu et al. 2011; Balabanova et al. 2018b).

Optimal temperatures of marine fungal fucoidanase range from 40 to 60 °C (Qianqian et al. 2011; Wu et al. 2011; Hifney et al. 2019). The optimal pH values are slightly acidic to neutral, ranging from 6 to 7, which is a little less acidic than other marine fungal enzymes previously discussed (Qianqian et al. 2011; Wu et al. 2011; Hifney et al. 2019). Concerning optimal salinity, a culture optimization protocol for *Dendryphiella arenaria* enzymatic production showed that increasing NaCl concentrations have a negative impact on fucoidanase production. However, fungal growth could be inhibited without supplemented NaCl. Thus, a salinity of 1.5% NaCl seems to allow the best fucoidanase activity (Gomaa et al. 2019).

Dendryphiella seems to be a particularly interesting marine fungal genus for fucoidanase activity (Wu et al. 2011; Gomaa et al. 2019; Hifney et al. 2019). However, marine strains belonging to other widespread fungal genera such as *Penicillium*, *Trichoderma*, *Aspergillus* or *Cladosporium* have also been described for their fucoidanase activities (Burtseva et al. 2010; Gomaa et al. 2015; Patyshakuliyeva et al. 2020).

Among the six marine fungal strains isolated from the brown alga *Fucus* sp., fucoidanase activity was detected in *Trichoderma paraviridescens* strain CBS 143,790 FP-027-C5 (6×10^{-3} U mL^{-1}) and *Rhizopus oryzae* strain CBS 143,788 FP-027-B4 (4.5×10^{-3} U mL^{-1}) (Patyshakuliyeva et al. 2020). Gomaa et al. (2015) observed the highest fucoidanase specific activity (18 U mg^{-1}) in a *Cladosporium salinae* strain isolated from *Padina pavonica*. Interestingly, all of the isolated strains were grown on a *Sargassum*-based medium, but marine fungal strains isolated from *Sargassum* sp. did not show the highest enzymatic activities (Gomaa et al. 2015). Indeed, the three most active strains were isolated from the red seaweeds *Padina pavonica* and *Palisada perforata*. Thus, a specific association with the alga does not seem to necessarily allow a better degradation compared with fungi isolated from other habitats, at least concerning fucoidan degradation (Gomaa et al. 2015).

The molecular weight of marine fungal fucoidanase seems to be variable. Two fucoidanases have been characterized with molecular weights of 64 kDa and 180 kDa, obtained respectively from marine strains of *Fusarium* sp. (Qianqian et al. 2011) and *Dendryphiella arenaria* (Wu et al. 2011).

According to Gomaa et al. (2019), the main factors allowing a better fucoidanase activity were the supplementation with fucoidan and urea in the culture media. Even if the increase of salt seemed to exert a negative impact on fucoidanase activity, it was also necessary for the growth of the studied fungal strain *Dendryphiella arenaria* isolated from *Palisada perforata.*

Fucosidases

As previously mentioned, fucosidases allow the release of monosaccharides from the oligosaccharides produced by fucoidanases degrading fucoidans. These enzymes are still poorly explored considering marine fungi. As for some other enzymatic activities poorly explored in marine fungi such as xylosidases or mannanases, no data are available for fucosidase on optimal temperature, pH values and molecular weights.

Shvetsova et al. (2014) have reported the growth of a *Fusarium proliferatum* strain on a solution of algal fucoidans. The marine origin of this strain is not clear, but the fucosidase activity was measured and reached 1.85×10^{-3} U mL^{-1}. In another study, the marine fungal isolates *Beauveria felina* and *Scopulariopsis brevicaulis* exhibited fucosidase activities (Balabanova et al. 2018b).

Mannanases

Mannan is a linear polysaccharide composed of mannose residues linked by β-1,4 linkages (Fig. 3b). This polysaccharide is produced by terrestrial plants but also by marine algae and bacteria (Frei and Preston 1964; Huizing and Rietema 1975; Recalde et al. 2012; Kokoulin et al. 2020). The backbone of this polysaccharide is randomly hydrolyzed by mannanases with the production of β-1,4-manno-oligomers. The hydrolysis of both these oligomers and mannan molecule, with the release of mannose residues, is realized by mannosidase which targets the non-reducing ends of these molecules (Fig. 3a) (Malgas et al. 2015).

No data on marine mannanases has been found and only a few studies describing enzymatic activities of marine fungi have measured mannosidase activity (Burtseva et al. 2010; Balabanova et al. 2018b). Indeed, mannanase from the marine environment was first mentioned in 2006 from the abalone *Haliotis discushannai* (Ootsuka et al. 2006; Trincone 2018).

However, the use of mannan-degrading enzymes is well described, and they have applications in numerous industries such as pulp and paper in the biobleaching process (Dhawan and Kaur 2007; van Zyl et al. 2010; Chauhan et al. 2012), detergent (Dhawan and Kaur 2007; van Zyl et al. 2010; Chauhan et al. 2012), food (in the hyodrolysis of coffee extracts, oil extraction from coconut, maceration and clarification of fruit juices) (Dhawan and Kaur 2007; van Zyl et al. 2010; Chauhan et al. 2012; Kango et al. 2019), animal feed (notably as fish feed additive) (Dhawan and Kaur 2007; van Zyl et al. 2010; Chauhan et al. 2012; Kango et al. 2019),

textile (Dhawan and Kaur 2007) and pharmaceutics (manno-oligosaccharides and mannoses residues synthesized by mannanases are of interest as prebiotics and in urinary tract infection, or in several abdominal disorders) (van Zyl et al. 2010; Chauhan et al. 2012). They also have supplementary applications in oil, gas or biofuel industry (van Zyl et al. 2010; Chauhan et al. 2012), and as antifouling by removing bacterial biofilms (Chauhan et al. 2012).

Among the fungal producers of mannanases, the best ones belong to the genera *Aspergillus*, *Agaricus*, *Trichoderma* and *Sclerotium* (Dhawan and Kaur 2007; Kango et al. 2019).

According to Balabanova et al. (2018b), the mannosidase activity of *Beauveria felina* is higher after 7 days of incubation than after 4 days of incubation. The mannosidase specific activity after 7 days of incubations was comparable between the two marine fungal species tested (*B. felina* and *Scopulariopsis brevicaulis*) with values respectively at 1.5×10^{-3} and 1.4×10^{-3} U mg^{-1}. Mannosidase activity has also been detected in two marine fungal strains of *Penicillium chrysogenum* and *P. canescens* grown on a fucoidan-based medium (Burtseva et al. 2010).

Lyases

The great majority of marine fungal polysaccharidases described in the literature belong to the hydrolase family. However, one important polysaccharide, alginate, is degraded by other kinds of enzymes characterized by a lyase catalytic reaction.

Alginate lyases

Alginases, also known as alginate lyases, allow the degradation of alginate. These enzymes target the β-1,4 linkages between the β-D mannuronic acid and α-L-guluronic acid units constituting alginate (Fig. 4). Alginate lyases are produced by several marine organisms including brown seaweeds, marine molluscs, bacteria, viruses, cyanobacteria and fungi (Zhu et al. 2018b; Dharani et al. 2020; Gao et al. 2021). They can be used as antibiotics due to their ability to degrade the polymeric substances found in some bacterial biofilms (Dharani et al. 2020; Cao et al. 2021; Gao et al. 2021). Alginate lyases have also application in biofuel production by the saccharification of brown seaweed biomass (Beygmoradi and Homaei 2017; Trincone 2018; Zhu et al. 2018b; Dharani et al. 2020) and in production of oligosaccharides with many application notably in plant biocontrol (promoting plant growth, conferring plant resistance, inhibition of pathogen growth, being environmental-friendly fertilizer and biopesticide) (Zhu et al. 2018b; Dharani et al. 2020; Zhang et al. 2020; Cao et al. 2021) and in pharmaceutics (immunomodulatory, anti-inflammatory, antimicrobial, antioxidant, anticoagulant, prebiotic, antitumor,

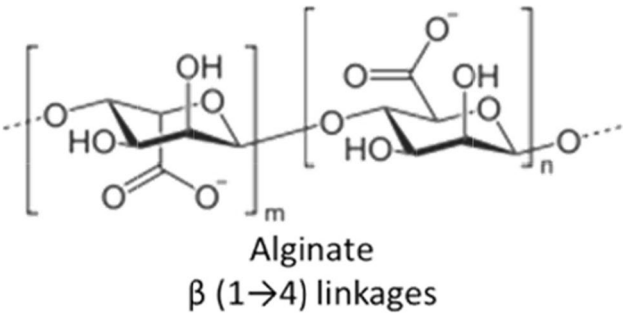

Fig. 4 Structure of alginate (from Claudio-Rizo et al. (2018))

anti-hypertensive, antidiabetic and neuroprotective activities) (Beygmoradi and Homaei 2017; Trincone 2018; Dharani et al. 2020; Zhang et al. 2020; Cao et al. 2021; Gao et al. 2021; Jagtap and Manohar 2021). They can also be used for the production of food additives (Beygmoradi and Homaei 2017; Dharani et al. 2020; Cao et al. 2021).

A marine fungal strain of *Paradendryphiella salina* (isolated from *Fucus serratus*) only differs from terrestrial strains by the presence of alginate lyase concerning the degradation of brown algae (Pilgaard et al. 2019). This highlights marine fungal adaptation at the species level, with an enzymatic activity linked to the specific habitat of the marine strain.

The optimal temperature for marine fungal alginase activity seems to be lower than for other marine fungal polysaccharide degrading enzymes. The highest alginase specific activity of a marine strain of *Aspergillus oryzae* (67.2 U mg^{-1}) was obtained at 35 °C (Singh et al. 2011). The tendency of slightly acidic preference generally observed for polysaccharide degrading enzymes of marine fungi also characterizes alginases. The optimal pH ranges from 6 to 6.5 according to the species and the studies (Wainwright and Sherbrock-Cox 1981; Singh et al. 2011).

Two fungal genera, *Dendryphiella* and *Aspergillus*, have been reported to exhibit alginase activity (Wainwright and Sherbrock-Cox 1981; Schaumann and Weide 1990; Burtseva et al. 2010; Singh et al. 2011; Gomaa et al. 2015, 2019). Gomaa et al. (2015) obtained the highest alginase specific activity of 85 U mg^{-1} with strains of *Acrophilophora* sp. and *Setosphaeria rostrata*. Interestingly, these two active strains were isolated from brown and red seaweed, respectively. Thus, even if alginate is particularly present in brown seaweeds, the difference of alginate degrading capacity between these two strains isolated from red and brown seaweeds remains unclear (Gomaa et al. 2015). Nevertheless, it is quite difficult to compare enzymatic activities of marine fungal strains which are obtained from different habitats. Indeed, many studies are focused on the activity of one marine fungal species or genus.

In general, marine fungi are able to grow with NaCl, but at high concentrations, enzymes are inhibited. The impact of salinity on alginate degradation depends on the fungal species. The alginate degrading capacity of *Dendryphiella arenaria* is inhibited by 1% NaCl, while a salinity ranging from 1 to 3% NaCl stimulates *Dendryphiella salina* alginate degrading capacity (Wainwright and Sherbrock-Cox 1981). These results for *D. arenaria* should be discussed with another study showing that a 4% NaCl concentration was optimal to obtain the highest alginase activity (24 U mL^{-1}) (Gomaa et al. 2019). These results suggest intraspecific variability or could be due to variations between protocols and assays.

One alginate lyase of *Aspergillus oryzae* has been characterized and is constituted of two subunits of 40 and 50 kDa (Singh et al. 2011).

Lyases in marine fungal species are poorly documented, except for some studies on alginate lyases. One strain of *Thalassochytrium gracilariopsidis* isolated from *Gracilariopsis* sp. presented an α-glucan lyase (Nielsen et al. 2000). However, considering promising enzymes such as ulvan lyases (currently studied for biofuel production from green seaweed), no data are available from marine fungi, and almost all studies describe marine bacterial activities.

Enzymes of protein degradation from marine fungi

Proteases can generally be differentiated between exopeptidases (peptidases) and endopeptidases (proteinases) (Kango et al. 2019). On the basis of the functional group of their active site, proteases can be subgrouped into cysteine, aspartic, serine and metallo-proteases (Kango et al. 2019).

Fungal proteases have several benefits against bacterial ones and major fungal protease producers belong to *Aspergillus*, *Cephalosporium*, *Fusarium*, *Rhizopus* and *Penicillium* genera (Naveed et al. 2021).

Proteases, including marine ones, are used in food industry (cheese manufacturing, baking, brewing and dairy industries, fruit juice and coffee processing and meat tenderization) (Muffler et al. 2015; Srilakshmi and Madhavi 2015; Homaei et al. 2016b; Duarte et al. 2018; Mzui and Ch 2018; Vashist et al. 2019; Naveed et al. 2021), in detergent industry (Zhang and Kim 2010, 2012; Muffler et al. 2015; Srilakshmi and Madhavi 2015; Homaei et al. 2016b; Beygmoradi and Homaei 2017; Mzui and Ch 2018; Vashist et al. 2019; Barzkar and Sohail 2020; Naveed et al. 2021), in leather industry (Zhang and Kim 2010, 2012; Muffler et al. 2015; Srilakshmi and Madhavi 2015; Homaei et al. 2016b; Beygmoradi and Homaei 2017; Mzui and Ch 2018; Barzkar and Sohail 2020; Naveed et al. 2021), in pharmaceutics (treatments of several disorders such as ulcers, cancer, cystic fibrosis, cardiac and digestive disorders, and inflammation and exhibiting antioxidant, anticancer and antibacterial bioactivities) (Zhang and Kim 2010, 2012; Muffler et al. 2015; Srilakshmi and Madhavi 2015; Homaei et al. 2016b; Beygmoradi and Homaei 2017; Duarte et al. 2018; Mzui and Ch 2018; Barone et al. 2019; Vashist et al. 2019; Barzkar and Sohail 2020; Naveed et al. 2021), in cosmetic industry (as skin peeling and softening) (Vashist et al. 2019; Naveed et al. 2021), in textile industry (silk degumming) (Srilakshmi and Madhavi 2015; Homaei et al. 2016b; Duarte et al. 2018; Mzui and Ch 2018; Vashist et al. 2019; Naveed et al. 2021), in chemical industry (Barone et al. 2019; Naveed et al. 2021) and in waste management (Muffler et al. 2015; Vashist et al. 2019; Naveed et al. 2021). Marine proteases are also used in contact lens cleansing, in marine waste treatment and as antifouling and antibiofilm agents (Barzkar and Sohail 2020).

However, data on the characterization or application of marine fungal proteases are still limited; the first study describing a protease from an endophytic marine fungus was published in 2014 (Budiarto et al. 2014).

Marine fungal proteases are of particular interest for their ability to be active in extreme conditions such as salinity, some proteases being active with values up to 3.5 M NaCl (Lario et al. 2015), and low temperatures, several proteases exhibiting an optimal temperature of 25 °C (Pazgier et al. 2003; Turkiewicz et al. 2003; Zhu et al. 2009; Mzui and Ch 2018). They can also be active in acidic (Li et al. 2010; Lario et al. 2015) or alkaline (Zhu et al. 2009; Jasmin et al. 2010; Mzui and Ch 2018) conditions, some proteases exhibiting optimal activities with pH values ranging from 3.5 to 11.

Proteolytic enzymes from marine fungi are less documented than polysaccharide degrading enzymes (Mzui and Ch 2018). As for the previous subsections, enzymatic activities are not easily comparable between studies, because of the diversity of fungal species, habitats and used methodology to obtain activities. However, contrarily to the numerous substrates putatively used for the study of polysaccharide degrading enzymes, the majority of marine fungal protease assays are carried out using casein (or azocasein). The substrate is of course adjusted according to the targeted protease activity. Thus, gelatin or keratin are used in the case of gelatinase or keratinase studies, respectively (Pisano et al. 1964; El-Gendy 2010). Nevertheless, most of the studies cited in this review only measure the marine fungal protease activity without substrate specificity.

Marine fungi exhibiting protease activities have been isolated from various habitats such as algae (Chaud et al. 2016), sediments (Chellappan et al. 2006), corals (El-Gendy 2010) or column water (Li et al. 2010). Among the studies characterizing marine fungal proteases, several have focused on marine yeasts belonging to genera like *Rhodotorula*, *Aureobasidium*, *Leucosporidium* or *Metschnikowia* (Pazgier et al. 2003; Turkiewicz et al. 2003; Chi et al. 2007;

Li et al. 2010; Duarte et al. 2013; Lario et al. 2015; Chaud et al. 2016). Considering marine filamentous fungi, common genera have been studied such as *Aspergillus* (Damare et al. 2006; Kamat et al. 2008) or *Penicillium* (Zhu et al. 2009; El-Gendy 2010; Park et al. 2016; Wang et al. 2016). However, species such as *Xylaria psidii* and *Engyodontium album* have been described by several studies for their protease activity (Chellappan et al. 2006, 2011; Jasmin et al. 2010; Budiarto et al. 2014; Indarmawan et al. 2016).

Marine fungal proteases are generally characterized by an optimal temperature between 45 and 60 °C (Chellappan et al. 2006, 2011; Damare et al. 2006; Chi et al. 2007; El-Gendy 2010; Lario et al. 2015). However, other marine fungal proteases have been studied because of their lower optimal temperature. Then, several marine fungal species have shown their highest protease activity at 40 °C (Li et al. 2010), 35 °C (Zhu et al. 2009), 25 °C (Pazgier et al. 2003; Turkiewicz et al. 2003) or even 10 °C (Chaud et al. 2016). Cold environments such as polar zones as the Antarctic are of particular interest in the targeting of cold-adapted marine fungal proteases.

Optimal pH for marine fungal proteases seemed to be very variable from acidic to alkaline values according to the species, while an acidic tendency characterized polysaccharide degrading enzymes. Proteases (subtilase or keratinase) optimal activities have been observed at neutral pH (Pazgier et al. 2003; Turkiewicz et al. 2003; El-Gendy 2010; Budiarto et al. 2014; Samuel et al. 2018), while other optimal activities have been observed between pH values 9 and 11 (Chellappan et al. 2006, 2011; Damare et al. 2006; Chi et al. 2007; Zhu et al. 2009; El-Gendy 2010). Interestingly, marine fungal (yeast) species of *Rhodotorula* or *Metschnikowia* contain proteases with acidic optimal pH values of 4–5 and 3.5, respectively (Li et al. 2010; Lario et al. 2015; Chaud et al. 2016). To the best of our knowledge, no marine filamentous fungal protease with acid affinity has been reported in the literature.

Most of the described marine fungal proteases have a molecular weight ranging from 30 to 40 kDa (Pazgier et al. 2003; Turkiewicz et al. 2003; Chellappan et al. 2006, 2011; Damare et al. 2006; Zhu et al. 2009; El-Gendy 2010; Jasmin et al. 2010; Lario et al. 2015). El-Gendy (2010) purified a smaller keratinase of 19 kDa from a marine *Penicillium* sp. isolate, while a 71 kDa extracellular protease has been described from an isolate of *Xylaria psidii* (Budiarto et al. 2014). Interestingly, an isolate of this species has been described to express three proteases of 56.6, 89.1 and 162.2 kDa (Indarmawan et al. 2016).

The effect of the carbon source for fungal growth seems to have an impact on protease activity. However, protease activities depend on marine fungal species screened. Maltose is the preferential carbon source for protease production by *Colletotrichum capsici* and *Curvularia lunata* (Samuel et al. 2018), while glucose and corn starch allow the highest protease activity of *Metschnikowia reukaufii* (72.5 U mL^{-1}) and *Aureobasidium pullulans* (7.2 U mL^{-1}), respectively (Chi et al. 2007; Li et al. 2010). It does not seem to be one specific interesting carbon source for enzymatic production. However, each fungal isolate has different affinities when agroindustrial residues such as rice, wheat or barley straw are used as substrate (El-Gendy 2010).

The effect of NaCl on marine fungal protease activity depends on the species considered. Some protease activities decrease at once with the adding of NaCl (Chellappan et al. 2011; Chaud et al. 2016), but others keep activity at low NaCl concentrations from 0.1 to 1 M (Damare et al. 2006) or even with a high amount of NaCl such as 3.5 M maintaining 40% of the initial activity (Lario et al. 2015). However, it is important to know that seawater does not only contain NaCl but many other salts and minerals. Marine fungal growth with supplemented artificial seawater is greater than with NaCl enriched medium (Chaud et al. 2016).

The protease activity is different considering the marine fungal species but the substrate used for enzymatic assays can also have a great influence. As mentioned above, casein is the main substrate used for protease activity measurement. Indeed, it has been shown that compared with haemoglobin, gelatin or bovine serum albumin (BSA), proteolytic activity was higher using casein as a substrate (Chellappan et al. 2011). On the other hand, more than half of the marine filamentous fungi screened by Loperena et al. (2012) were characterized by a gelatin degrading capacity but no casein degrading capacity. A large spectrum of substrate potentially targeted by the proteases increase their application and their interest (Chellappan et al. 2011).

Enzymes of lipid degradation from marine fungi

Different types of lipolytic enzymes can be found in microorganisms, such as lipases, esterases or phospholipases, targeting respectively long and medium triglycerides, short triglycerides and phosphoglycerides (Albayati et al. 2020). These hydrolyses result in the production of shorter molecules such as free fatty acids and glycerol notably. They can be either in activated or inactivated forms (Patnala et al. 2016; Geoffry and Achur 2018).

Microbial lipases have numerous advantages, being easily modified genetically, and exhibit a great diversity of characteristics and specificity (Filho et al. 2019). Among these microbial lipases, fungal ones are particularly promising for industrial use because of their ease of production, specificities and stabilities (Navvabi et al. 2018; Filho et al. 2019; Chandra et al. 2020; Melani et al. 2020). The most cited fungal genera for lipase production are *Aspergillus*,

Trichoderma, *Rhizopus*, *Penicillium*, *Mucor*, *Geotrichum* and *Fusarium* (Navvabi et al. 2018; Melani et al. 2020). Lipases from marine environments are particularly promising even if they are less studied than terrestrial ones (Patnala et al. 2016; Mzui and Ch 2018; Navvabi et al. 2018; Filho et al. 2019).

Lipases, including marine ones, are mainly used in food and nutrition (particularly in fat and oil industry, for the production of a cocoa butter equivalent, in the bakery industry, in dairy industry, in egg processing, in fruit juices, for fish preservation or as biosensors) (Zhang and Kim 2010, 2012; Patnala et al. 2016; Beygmoradi and Homaei 2017; Navvabi et al. 2018; Filho et al. 2019; Vashist et al. 2019; Chandra et al. 2020; Melani et al. 2020). They are also used in the wastewater treatment (Basheer et al. 2011; Patnala et al. 2016; Filho et al. 2019; Vashist et al. 2019; Chandra et al. 2020; Melani et al. 2020), animal feed (Navvabi et al. 2018), detergent (Zhang and Kim 2010, 2012; Beygmoradi and Homaei 2017; Navvabi et al. 2018; Chandra et al. 2020), paper production (Zhang and Kim 2010, 2012; Navvabi et al. 2018; Vashist et al. 2019; Chandra et al. 2020), textile (Navvabi et al. 2018; Vashist et al. 2019; Chandra et al. 2020), leather (Vashist et al. 2019; Chandra et al. 2020), pharmaceutics (treatment of cardiovascular diseases, obesity, anxiety, inflammation and pain) (Beygmoradi and Homaei 2017; Navvabi et al. 2018; Barone et al. 2019; Vashist et al. 2019; Chandra et al. 2020; Melani et al. 2020), cosmetics (Zhang and Kim 2010, 2012; Vashist et al. 2019; Chandra et al. 2020), agriculture (Beygmoradi and Homaei 2017; Chandra et al. 2020) and biofuel production (Navvabi et al. 2018; Filho et al. 2019; Chandra et al. 2020; Melani et al. 2020).

Substrates used for the lipolytic assays are principally either olive oil or paranitrophenol derivatives (paranitrophenol palmitate or p-nitrophenyl laurate). The different enzymatic substrates are then chosen according to their availability and using easiness and do not necessarily correspond to the lipidic substrate specifically targeted by the studied enzyme. However, activity values from a study to another are still uneasily comparable.

Marine fungi are generally more resistant to physicochemical constraints than their terrestrial counterparts (Patnala et al. 2016; Navvabi et al. 2018). Among these resistances, marine fungal lipases can be characterized by a salinity tolerance (Huang et al. 2004; Geoffry and Achur 2018) and can be cold-adapted (Wang et al. 2007; Mzui and Ch 2018; Wentzel et al. 2019). Lipases, producing glycerol from lipids, are of particular interest for cold resistance and cell survival because of the cryoprotectant effect of this compound (Duarte et al. 2013). A study of extracellular enzymes produced by microorganisms in Antarctica has shown that 40% of filamentous fungi were producing lipases when incubated at 4 °C, while only 13% of yeasts produced this enzyme (Loperena et al. 2012). This observation needs to be compared with another study on marine yeasts isolated in Antarctica in which 46% of yeasts isolates were able to produce lipases with incubation at 15 °C (Duarte et al. 2013).

Most of the marine fungal species described as lipolytic have been isolated from seawater near India (Potumarthi et al. 2008; Basheer et al. 2011; Lanka et al. 2016; Geoffry and Achur 2018) or Antarctica (Loperena et al. 2012; Duarte et al. 2013; Wentzel et al. 2019). However, some lipolytic marine fungi have also been isolated from sediments, seaweed or fish (Wang et al. 2007; Farha and Hatha 2019). According to Duarte et al. (2013), a majority of lipase producing marine yeasts have been isolated from lichens and marine sediments (compared with other animal or algal sources). Almost half of the studies on marine fungal lipases have described yeast lipases from species like *Aureobasidium pullulans*, *Rhodotorula mucilaginosa* or *Candida* sp. (Wang et al. 2007; Liu et al. 2008; Potumarthi et al. 2008; Duarte et al. 2013; Li et al. 2014; Wentzel et al. 2019). Marine filamentous fungi with lipase activity belong mainly to common genera such as *Penicillium*, *Cladosporium*, *Aspergillus* or *Fusarium* (Basheer et al. 2011; Li et al. 2014; Lanka et al. 2016; Wang et al. 2016; Geoffry and Achur 2018).

The optimal temperatures for marine fungal lipases are lower than those observed for proteases and most of the polysaccharidases. Indeed the highest optimal temperature, observed in *Geotrichum marinum*, *Aspergillus awamori* and several yeast species, only reached 40 °C (Huang et al. 2004; Wang et al. 2007; Basheer et al. 2011). The variation of optimal temperature is particularly low compared with proteases or polysaccharidases, with a lower optimal temperature for lipase activity at 35 °C (Wang et al. 2007; Liu et al. 2008). The few studies characterizing the optimal temperature for marine fungal lipases could explain the weak variation observed.

Optimal pH values of marine fungal lipases seem also to be constant from a study to another with optimal pH values neutral and varying between 6 (for *Rhodotorula mucilaginosa*) and 8.5 (for *Aureobasidium pullulans* and *Fusarium solani*) (Wang et al. 2007; Liu et al. 2008; Geoffry and Achur 2018). Optimal pH values ranging from 7 to 8 have been observed for lipases extracted from *Aspergillus awamori*, *Geotrichum marinum* and several yeast species (Huang et al. 2004; Wang et al. 2007; Basheer et al. 2011).

Three marine fungal lipases have been purified and their molecular weight characterized. Lipases from *Aureobasidium pullulans* and *Geotrichum marinum* have similar molecular weights of 63.5 and 62 kDa respectively (Huang et al. 2004; Liu et al. 2008), and a lipase from *Aspergillus awamori* has a molecular weight of 90 kDa (Basheer et al. 2011).

Even if lipases are not the most described enzymes from marine fungi, it seems that this enzymatic activity is particularly high in several cases. Indeed, an isolate of *Penicillium* sp. has been tested on several enzymatic activities including gelatinase, amylase, phytase, pectinase and lipase. The lipolytic activity seemed to be the most important compared with other enzymes like amylase or cellulase, based on the enzymatic zone of clearance on a solid culture medium (Farha and Hatha 2019). This kind of promising marine fungal lipolytic activity has also been detected in four marine fungi isolated in China (*Cladosporium* sp., *Rhodosporidium* sp., *Candida* sp. and unidentified *Ascomycota*) which have exhibited lipolytic activity higher than cellulase activity. In this study, the highest lipase specific activity was obtained for *Candida* sp. strain PKU Y8 with 21.94 U mL^{-1} (Li et al. 2014). A strain of *Leucosporidium scottii* was characterized by the highest lipase activity of 0.23 U mL^{-1} (Duarte et al. 2013). Among nine marine yeast producing lipases, *Candida intermedia* and *Pichia guilliermondii* showed the highest specific activities of 0.042 and 0.0436 U mg^{-1}, respectively (Wang et al. 2007).

As lipases are induced by lipidic substrates (Basheer et al. 2011), several studies have reported the influence of different oils as the main carbon source in the fungal culture medium. Peanut oil (Liu et al. 2008) or rice bran oil (Basheer et al. 2011) have shown particularly interesting results with a lipase production higher than using other lipidic substrates. In the first report of lipase produced by marine-derived yeasts, olive oil resulted in the highest lipase specific activity in five of the nine screened strains, with values up to 0.2 U mg^{-1}, compared with other lipidic substrates such as lard, peanut oil and soybean oil (Wang et al. 2007). Supplementation with 1% of molasses also seemed to induce the lipase activity of a *Rhodotorula mucilaginosa* isolate (Potumarthi et al. 2008).

Conclusion

Marine microorganisms are of obvious biotechnological interest and have applications in many diverse industries. Among them, bacteria are still clearly more documented than fungi, but there is increased interest in fungi. Indeed, new marine fungal metabolites are regularly and currently discovered, highlighting the richness of these organisms.

This review provided an overview of polysaccharide, lipid and protein degrading enzymes obtained from marine fungi. Because of the great diversity of marine polysaccharides, and especially marine algae, and because of their numerous applications, marine fungal polysaccharidases begin to be well documented compared with proteases and lipases. Fungi from different marine habitats have shown a wide variety of polysaccharidases, some being specifically necessary for fungal growth and development, while others apparently inherited from terrestrial ancestors.

Few data on polysaccharidases, proteases and lipases of marine fungi are available compared with marine bacterial ones, but this scope of research is growing. Unfortunately, enzymatic activity values, as well as kinetic parameters, are not easily comparable between studies, principally because of differences in fungal growth protocols or because of the use of various units of activity. Standardization of protocols and assays would permit better data comparisons, but several issues exist. For example, methods are continuously evolving to allow better and sharper results, fungal strains can have different substrate affinity for a same enzyme and it can lead to a loss of information from previous studies with non-standardized results.

Fungal genera such as *Aspergillus*, *Penicillium*, *Cladosporium* or *Trichoderma* seemed to be particularly well represented considering the highest polysaccharidase activities. This could be partially explained by their ease of isolation and growth in lab conditions. It should then be interesting to go further in the characterization of other marine polysaccharidases of *Aspergillus*, *Penicillium*, *Cladosporium* or *Trichoderma* species because there should be enough data in the literature to discuss the results. On the other hand, it is important to not only focus on easy growing species because this ability is not obligatory linked with high and interesting polysaccharidase activities.

Marine fungal polysaccharidases exhibit optimal temperatures of about 40–60 °C and pHs ranging from 4 to 7, with some exceptions. They are generally characterized by molecular weights ranging from 40 to 60 kDa, with some heaviest enzymes about 100 kDa. Marine fungal polysaccharidases are also particularly studied for their resistance against saline conditions. In most cases, low concentrations of NaCl ranging from 1 to 3% resulted in high enzymatic activities, whereas high NaCl concentrations have inhibitory effects. When cultured on non salted media, the growth and development of marine fungi are generally lower than by using saline conditions, leading to a loss of enzymatic activity. This can be explained by the marine adaptation of the studied fungal strains.

This review focused on marine fungal polysaccharidases targeting macroalgal polymers, but marine fungi, notably the ones isolated from macroalgae, can exhibit other polysaccharidase activities. Several data and reports exist on hydrolases such as pustulanases, dextranases, pectinases or chitinases. Other enzymes such as oxidoreductases, involved in the degradation of lignocellulosic substrates and particularly the ones found in mangroves, are also well documented, being laccases, manganese-peroxidases and lignin-peroxidases.

Most of the marine fungal species studied for polysaccharidase activities have been isolated from marine sediments or

marine algae. However, even if fungal strains have a marine origin, they can be able to produce enzymes active in the presence of terrestrial substrate. Indeed, most of the marine fungal species have also terrestrial counterparts from which they could have inherited abilities to degrade terrestrial polysaccharides. This observation explains the fact that in several studies cited in this review, marine fungal growth is carried out on terrestrial agricultural by-products such as rice or wheat bran for example. Indeed, their ability to degrade terrestrial polysaccharides, added to their particularly interesting resistance to extreme physicochemical conditions compared with their terrestrial counterparts, explains the great interest of marine fungi for agricultural by-product valorization.

Data on marine fungal proteases and lipases are still very scarce. Predominant marine filamentous fungal genera cited above for polysaccharidase activities such as *Penicillium* or *Aspergillus* are also represented in studies on proteases and lipases. Optimal temperatures for marine fungal proteases seem more diverse than for polysaccharidases even if there is still a tendency around 40–60 °C. Lipase optimal temperature seems lower, with the highest optimal activity around 40 °C. Contrarily to polysaccharidases, marine fungal proteases seem to be characterized by neutral to alkaline optimal pH, while marine fungal lipase optimal pHs seem to be generally neutral. Molecular weights of protease are generally about 30–40 kDa, a little lower than polysaccharidases. On the contrary, the smallest marine fungal lipase has been characterized with a molecular weight of 62 kDa. All conclusions, observations and tendencies concerning marine fungal lipases and proteases need to be qualified considering the small amount of available data.

Many fields of application linked to enzyme use still need to be optimized, highlighting a great interest in the development of research on specific and highly active enzymes. Moreover, studies on marine fungal enzymes targeting specific polysaccharides such as mannan are still scarce, as are studies on proteases or lipases. Many unexplored marine habitats could then be sources of fungal species characterized by a production of new enzymes of great interest.

These studies could enhance the applications which already exist in numerous industries such as human food, animal feed, agriculture, cosmetics, pharmaceutics, chemicals, detergent, textile, leather, pulp and paper, biofuels or in waste management. They could also potentially allow the development of new biotechnologies, notably in applied phycology. Indeed, marine fungal enzymes, and particularly algicolous ones, would be of particular interest in the specific degradation of macroalgal polysaccharides. This degradation process occurs in several applications such as the extraction of bioactive molecules from macroalgae, the treatment of seaweed wastes notably for the production of fertilizers in agriculture, the production of biofuels of third generation, the preparation of protoplasts for algal genetic engineering, the prevention of algal bloom or biofouling. This implication of marine fungal enzymes in algal biotechnologies is particularly both recent and promising.

It has been shown in this review that marine fungi are a great source of enzymes responsible for the degradation of polysaccharides, proteins and lipids. These enzymes are produced by a wide variety of fungi and are promising because of their high activities. Assuming that marine fungi associated with a specific alga would exhibit a particularly promising ability to degrade this alga, studying the fungal community and its enzymatic potential on algae of biotechnological interest would enhance the efficiency of these technologies. Moreover, several processes such as the use of synergistic enzymes or marine fungal co-cultures can enhance the enzymatic degradation potential. Still, two economic challenges remain, being the low reusability potential of enzymes, and their production prices, along with a continuous need of discovery of new physicochemically stable enzymes.

Declarations

Conflict of interest The authors declare no competing interests.

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