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REVIEW

Exopolysaccharides from marine bacteria: production, recovery and applications

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Abstract

Ocean represents an unusual diversity of life. The largest proportion of microbial diversity has been found in the oceanic and terrestrial subsurface respectively. Marine habitats are inhabited by several microbial populations adapted to these ecosystems. Among these populations, bacteria are one of the important and dominant inhabitants of such environments. Marine bacteria themselves or their products such as enzymes, exopolymers, pigments, antimicrobial compounds, and biosurfactants represent a wide range of applications in food, textile, and pharmaceutical industries as well as in many environmental processes. This review aims to present the exopolysaccharide production from marine bacteria and its possible biosynthesis along with recovery of these polymers using various methods. Finally, the applications of these polymers, particularly in the field of bioremediation, are also discussed.

Keywords Biosynthesis · Exopolysaccharides (EPS) · Marine bacteria · Recovery · Structure of EPS

Introduction

About 71% of the Earth's surface is covered with oceans having an average depth of 3.8 km and an average pressure of 38 MPa (van Eldik and Hubbard 1996). Temperatures at deep-sea surfaces and the upper surfaces of the sea are different. The different conditions that prevail in the marine ecosystems are responsible for the existence of various extreme habitats, such as salt lakes, marine salterns, deep-sea, volcanic and hydrothermal marine areas as well as in the sea ice in Polar Regions, where organisms grow in such extreme conditions and flourish (Casillo et al. 2018). The marine organisms have developed unusual metabolic processes and defensive mechanisms for their survival under such extreme conditions, which might have resulted in the ability to produce novel bioactive compounds in comparison to other natural habitats (Chi and Fang 2005). Marine microorganisms produce many organic substances and one such product is exopolysaccharide (EPS) (Abreu and Taga 2016). There has been a growing interest in the isolation and identification of new marine microorganisms capable of producing polysaccharides. These polymers participate in the maintenance of marine environments by contributing to several processes like sedimentation, particle formation, cycling of dissolved metals and dissolved organic carbon (Verdugo 2012).

Although microbial cells require up to 70% of the total energy for EPS production, but once formed it benefits the microbes in multiple ways. EPS helps the organisms to grow and survive under adverse environmental conditions (Poli et al. 2010). Apart from these, EPS play a vital role in nutrient uptake, aggregation, adhesion to surfaces, and biofilms formation (Dave et al. 2016; Shukla and Dave 2018). EPS possess active and ionisable functional groups and non-carbohydrate substituents like amine, sulfhydryl, carboxyl, hydroxyl, phosphate, and sulphate groups that are responsible for the negative charge of the polymer. Due to this property, various heavy metals can bind to EPS by ion exchange, complexation, and entrapment like mechanisms (Gupta and Diwan 2017). Loaec et al. (1998) and Wuertz et al. (2000) have described the role of EPS producing heavy metal resistant isolates from deep-sea hydrothermal vents and purified EPS for metals and toxic substances binding ability.

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Now a days the focus is to isolate novel marine microorganisms for the production of EPS with diverse properties. Different genera of marine bacteria such as *Alteromonas, Bacillus, Cobetia, Colwellia, Geobacillus*, *Halomonas, Hyphomonas, Idiomarina, Pseudoalteromonas, Pseudomonas, Polaribacter, Rhodococcus, Shewanella, Vibrio, Exiguobacterium, Kocuria, Pontibacter, Planococcus, Marinobacter* have been reported as EPS producers (Le Costaouec et al. 2012; Kumar et al. 2004; Lelchat et al. 2015; Carillo et al. 2015; Arena et al. 2009; Bouchotroch et al. 2000; Arias et al. 2003; Quintero et al. 2001; Martínez-Cánovas et al. 2004; Saravanan and Jayachandran 2008; Wu et al. 2016a, b; Sun et al. 2015; Urai et al. 2006; Vinogradov et al. 2005; Bramhachari and Dubey 2006; Upadhyay et al. 2016). Genera of halophilic archaea *Thermococcus*, *Sulfolobus, Haloarcula*, and *Haloferax* are also reported for EPS production by Poli et al. (2011).

The increasing commercial importance of marine microbial EPS has stimulated the efforts in the development of rapid and efficient techniques for their recovery and purification. The presence of microbial cells, medium ingredients in the fermentation broth, as well as its high viscosity, often causes problems in the recovery of EPS (Yang et al. 1998; Kumar et al. 2007). The steps involved in EPS recovery and purification are the removal of microbial cells and protein followed by precipitation, dialysis and lyophilisation of EPS (Smith and Pace 1982; Laroche and Michaud 2010; Castillo et al. 2015). Elucidations of chemical compositions and structures of EPS are necessary to establish their structure-function relationship. But the precise characterization of the EPS is a challenge to researchers because of its structural complexity (Chowdhury et al. 2011). Although the chief components of EPS are carbohydrates, it is difficult to derive their unique monomer linkage patterns and biochemical properties (Jiao et al. 2010). Thus acid hydrolysis, Fourier-transform infrared spectroscopy (FTIR), high-performance liquid chromatography (HPLC), methylation analysis, gas chromatography with mass spectroscopy (GC–MS), and ^{1}H- and ^{13}C-NMR (one and two dimensions) have been used for chemical characterisation of EPS (Liang and Wang 2015). The development of purification techniques and sophisticated analytical approaches permit researchers to provide an insight into primary structures and conformation of polysaccharides, which are important to acquire information about complete polymeric structures.

This review highlights the EPS production ability of various marine bacteria, chemical structure and biosynthetic mechanisms of EPS and their applications. The content also explores distinct strategies of metal remediation through marine bacteria and their EPS. To understand the mechanism behind metal ion uptake through EPS, it is essential to know its chemical structure and properties. The properties and structural aspects can be studied from purified EPS. Thus, the extraction, purification and recovery of EPS by various methods has also been illustrated.

EPS production by marine bacteria

In case of domain Bacteria, several species of Gram-positive bacteria such as *Bacillus*, *Lactobacillus, Streptococcus, Diplococcus, Leuconostoc* and Gram-negative bacteria such as *Pseudomonas, Xanthomonas, Enterobacter, Azotobacter, Klebsiella*, and *Rhizobium* are reported for EPS production (Sutherland 1972; Jekins and Hall 1997). Various marine bacteria are also reported for EPS production and some examples are depicted in Table 1.

Although extensive research has been carried out in this field, further investigations will result in identification of novel EPS producing organisms, new products with novel characteristics within the marine environment of the deep-sea hydrothermal vents, the Arctic and the Antarctic regions.

Chemical structure of EPS

EPS are chemical compounds that are synthesized as secondary metabolites by different microorganisms and are secreted as slime or jelly-like material outside the cell-wall. Polysaccharide chains of EPS vary from 103 to 108 kDa and contain sub-unit configurations that may also have species-specificity (Sutherland 1985). EPS are organic macromolecules and are formed by polymerization of simple building blocks of monosaccharides, uronic acids, amino sugars linked by glycosidic bonds, amino acids linked by peptide bonds, nucleic acids, phospholipids and humic substances. In a polymer they are arranged as repeating units (Frølund et al. 1996; Dignac et al. 1998; D'Abzac et al. 2010). EPS carry organic substituents such as acetyl, succinyl, or pyruvyl group or inorganic substituent such as sulphates. EPS are homo- or heterogeneous compounds having mono-, di-, and oligosaccharides along with some non-carbohydrate substituents (Sutherland 1985; Whitfield 1988). The bond angles of polysaccharides govern the relative orientation of adjacent sugar residues in a chain and determine the shape of EPS. In solution, EPS may have single-, double- or triple-helical conformation, which makes polysaccharides semi-rigid. Their helix is stabilized by an intermolecular hydrogen bond. Poor intramolecular interactions between polymer segments lead to aggregation and finally precipitation or gelation of EPS in organic solvents (Jekins and Hall 1997). Polysaccharides mostly possess negative charge, but occasionally they also have neutral and positive charges depending upon the constituents of the repeated units (Neu and Poralla 1990). The diversity of bacterial polysaccharides

Table 1 Properties and applications of various EPS produced by marine bacteria

Isolate	Source of isolation	EPS composition	Properties and application of EPS	References
Halomonas eurihalina H96	Saline soils	Sulphated EPS, Uronic acid	NR	Béjar et al. (1998)
Hyphomonas strain MHS-3	Marine sediments in Puget Sound	*N*-Acetyl galactosamine	Metal-binding capacity (gold)	Quintero et al. (2001)
Halomonas maura	Solar saltern of Asilah, Morocco	Manan	Pseudoplastic behaviour	Bouchotroch et al. (2001) and Arias et al. (2003)
Vibrio alginolyticus	Sea water	Glucose, xylose and amino sugars (RibN, AraN)	Pseudoplastic properties	Muralidharan and Jayachandran (2003)
Halomonas strain CRSS	Salt lake in Cape Russell, Antarctica	Mannan, xylo-mannan, fructo-glucan (composed of glucose, fructose, glucosamine and galactosamine)	NR	Poli et al. (2004)
Helomonas ventosae	Saline soils, Spain	NR	NR	Martínez-Cánovas et al. (2004)
Enterobacter cloacae	Marine sediments of the coastal area, Bhavnagar, India	NR	Biosorption of cadmium copper, cobalt and hexavalent chromium	Iyer et al. (2004) and Iyer et al. (2005)
H. ventosae strains Al12T and Al16	Saline soils in Jaén, Spain	Glucose, mannose and galactose	Emulsifying activity	Mata et al. (2006)
H. anticariensis strains FP35T and FP36	Saline soils of endorheic wetland, Fuente de Piedra, Málaga, Spain	Glucose, mannose and galacturonic acid	Pseudoplastic behaviour	Mata et al. (2006)
Vibrio harveyi strain VB23	Mandovi and Zuari estuaries, Goa, India	Galactose, glucose, rhamnose, fucose, mannose, ribose, arabinose, xylose	Emulsifying properties	Bramhachari et al. (2006)
Pseudoalteromonas sp. SM9913	Deep-sea sediment	Glucose, galactose, xylose, and arabinose	Biosorption ability and flocculation property	Qin et al. (2007)
Rhodococcus erythropolis PR4	Pacific Ocean, Japan	Mucoidan (glucose, glucosamine, mannose and glucuronic acid)	NR	Urai et al. (2007)
		FACEPS (galactose, glucose, mannose and glucuronic acid, stearic palmitic acids)	Emulsifying property	
Vibrio furnissii strain VB0S3	Mandovi and Zuari estuaries, Goa, India	Glucose, galactose, rhamnose, fucose, mannose, arabinose, ribose	Acidic EPS, emulsifying properties	Bramhachari et al. (2007)
Zoogloea sp. KCCM10036	Surface layer of the seaweed *Undaria* sp., Korea	NR	Flocculating properties	Lim et al. (2007)
Pseudoalteromonas ruthenica	Seawater samples of the vicinity of the Bay of Bengal, India	Mannose, uronic acids	Pseudoplastic behaviour	Saravanan and Jayachandran (2008)
Colwellia psychrerythraea 34H	Arctic marine sediments	Amino sugars, uronic acids	Cryoprotectant polymers	Marx et al. (2009)
Geobacillus thermodenitrificans	Marine vent, Vulcano Island, Italy	mannose and glucose	Molecular weight of 400 kDa	Arena et al. (2009)
Alteromonas macleodii subsp. fijiensis biovar deepsane HYD 657	Deep-sea hydrothermal vent polychaete annelid *Alvinella pompejana*	Fucose, rhamnose, glucose, galactose, mannose, glucuronic acid, galacturonic acid with Sulphate, lactate and pyruvate groups	Use in cosmetic preparations	Le Costaouec et al. (2012)

Table 1 (continued)

Isolate	Source of isolation	EPS composition	Properties and application of EPS	References
Polaribacter sp. *SM1127*	Arctic brown alga *Laminaria*	Rhamnose, fructose, mannose, glucose and amino sugars	High viscosity and anti-oxidant activity, Cryoprotectant	Dong et al. (2012)
Alteromonas sp. JL2810	Seawater (South China)	Rhamnose, mannose, and galacturonic acid	Metal-binding capacity	Zhang et al. (2015)
Cobetia marina DSMZ 4741	Littoral seawater, USA	Ribose and a 7, 8-pyruvilated Kdo (pyruvate substitution on its 3-deoxy-d-manno-oct-2-ulosonic acid (KDO) residue)	NR	Lelchat et al. (2015)
Pseudomonas stutzeri 273	Marine sediments	Glucose, galactose, rhamnose, mannose and amino sugars	Antioxidant, anti-biofouling properties	Wu et al. (2016a, b)
Bacillus licheniformis SR5	Sea sediment of Alang, Bhavnagar, India	Glucose, galactose and fructose	Metal sorption capacity	Upadhyay (2017)
Bacillius altitudinis MSH2014	Sediments around the mangrove trees in Ras Mohamed area, Red Sea Coast, Sinai Peninsula, Egypt	Mannouronic acid, glucose, and sulphate	Antitumor activities against two cancers cells EACC and lung cancer A-549 Antibacterial and antifungal properties	Mohamed et al. (2018)
Alteromonas and Thalassospira	Surface water, northern Gulf of Mexico	Protein rich EPS	Oil degradation capacity	Bacosa et al. (2018)
Brevundimonas subvibrioides MSA1, *Bacillus thuringiensis* E4, *Bacillus amyloliquefaciens* MGA2, *Pseudomonas fluorescens* SGA3, and *Advenella kashmirensis* NRC-7	Marine sediment, Mediterranean and Red Seas	Glucose, mannose, galactose, glucouronic acid, and mannouronic acid with sulphat group	Anti-proliferative activities against hepatocellular carcinoma cells (HepG2)	Asker et al. (2018)
Pseudoalteromonas sp. MER144	Antarctic seawater	Glucose, galactose, mannose, glucosamine, arabinose, galacturonic acid, glucuronic acid	Heavy metal (mercury and cadmium) tolerance	Caruso et al. (2018)
Alteromonas sp. PRIM-28	Malpe region in the West coast of India	Mannuronic acid, glucose and *N*-acetyl glucosamine	Cell proliferation and wound healing	Sahana and Rekha (2019)
Alcaligenes, Halomonas	Seawater (Mauritius)	Glucose, fructose with sulphate group	Antibacterial properties	Aullybux et al. (2019)
Marinobacter sp. W1-16	Antarctic surface seawater	Glucose, mannose, galactose, galactosamine, galacturonic acid, glucuronic acid	Emulsifying, cryoprotective and heavy metal binding properties	Caruso et al. (2019)

NR not reported

is eight folds higher in comparison to plant polysaccharides (Jekins and Hall 1997). Bacterial polysaccharides have constant and reproducible physicochemical properties, desired degree of purity and more diverse structural properties as compared to plant polysaccharides. In contrast to plants, cellulose produced by bacteria has more purity and a wider range of applications because of the absence of lignin and hemicellulose. Moreover, the bacterial cellulose provides high absorbent capacity and tensile strength as compared to the cellulose obtained from plants (Kambourova et al. 2015). In traditional applications, some bacterial EPS like xanthan gum or gellan gum can directly replace polysaccharides obtained from plants such as guar-gum or pectin, as well as carrageenan or alginate produced by algae, because of improved physical properties of bacterial EPS (Fialho et al. 2008; Rehm 2010). An EPS produced by *Pseudomonas elodea* was identified as gellan and it was recommended as a food additive by Japan, the United States and Europe (Prameela et al. 2018). It was categorized as high acyl (HA) and low acyl (LA) gellan depending upon the degree of acylation (Fallourd and Viscione 2009). Gellan gum forms a gel at low concentrations and it is highly biocompatible and biodegradable. A mixture of xanthan and gellan has been used instead of alginate to encapsulate the probiotic cells as they showed high resistance toward acidic conditions (Sun and Griffiths 2000). Due to these distinct physical properties, they have been used largely.

Classification of EPS

Bacterial polysaccharides normally include lipopolysaccharides (LPS), peptidoglycans, teichoic acids (TA) capsular polysaccharides (CPS), and EPS. Mostly the CPSs are made up of repeating oligosaccharide units and are heteropolysaccharides in nature. LPSs contain repeating units of core oligosaccharide, and an acylated disaccharide (lipid A). Peptidoglycans are made up of repeating disaccharide units called *N*-acetylglucosamine (NAG) and *N*-acetyl muramic acid (NAM). TA possesses mono- or oligosaccharides, or ester-bound amino acids with polyolphosphates and glycosylpolyolphosphates fragments. EPS are categorized as homo- and hetero-polysaccharides based on their chemical composition (De Vuyst and De Vin 2007). Figure 1 shows various classes of bacterial polysaccharides.

Homopolysaccharides are made up of only one type of sugar molecule and are categorized based upon their chemical composition such as type of linkage and monomeric units present in EPS. Various examples of homopolysaccharides are α-D-glucans, β-D-glucans, fructans and polygalactan, etc. (Ruas-Madiedo et al. 2002). Heteropolysaccharides possess repeating units of more than one type of sugars such as D-glucose, D-galactose, L-rhamnose, *N*-acetylglucosamine (GlcNAc), *N*-acetylgalactosamine (GalNAc) or glucuronic acid (GlcA). Moreover, some EPS also contain the non-carbohydrate substituents such as phosphate, sulphate, glycerol and acetyl. Homo- and heteropolysaccharide have a different

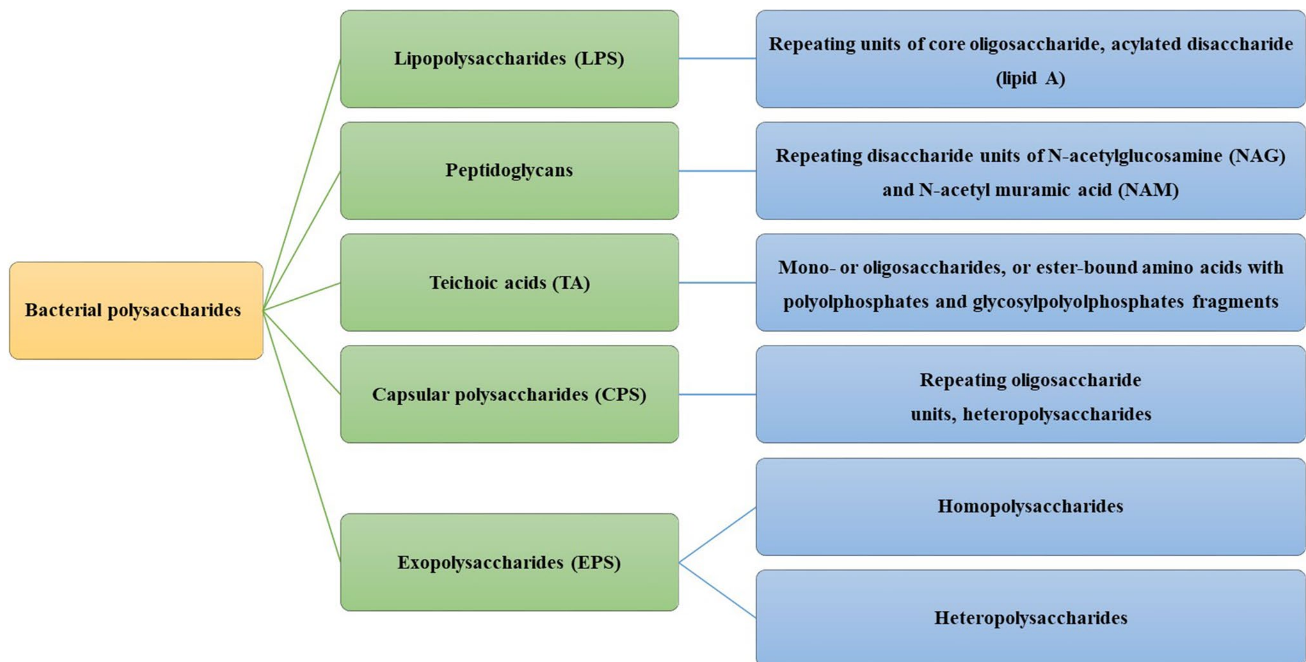

Fig. 1 Classification of bacterial polysaccharides

chemical structure and linkages. The site of their synthesis and synthetic enzymes are also different. They possess mainly β-1,4- or β-1,3 linkages which are highly rigid and more flexible α-1,2 or α-1,6 linkages (Nwodo et al. 2012). Further detail of their synthesis is given in the next part.

Biosynthesis of EPS

Several studies have been carried out to understand the EPS biosynthesis mechanisms in bacteria. Pathway of EPS biosynthesis differs from genus to genus and is an energy-dependent process. The production and utility of substrate molecule also differ based on the organisms and types of EPS produced. In most cases, EPS are synthesized at the cell membrane and then exported from the cell. The only exceptions are homo-polysaccharides, which are synthesized extracellularly. The activated precursor monosaccharide is transferred from the substrate to growing polysaccharide by various enzymes. The sugars of polysaccharides are then assembled in a particular linkage pattern such as α and β. In the cyclic structure of monosaccharide, when the –OH is situated below the plane of the ring then α linkage occurs and when the –OH is placed above the plane then β-linkage forms. Janczarek (2015) has reported the production of succinoglucan and galactoglucan by *S. meliloti*. Succinoglucan represented the repeating units of D-glucose and D-galactose which were joined by β-1,3; β-1,4 and β-1,6 linkages. Whereas galactoglucans contained the same sugar units, which are joined by α-1,3 and β-1,3 linkages.

In intracellular EPS biosynthesis, the substrate entered the bacterial cell first and then it is catabolised by periplasmic oxidation or intracellular phosphorylation (Freitas et al. 2011). Biosynthesis of EPS mainly involves glycosyltransferases, which link sugars from intracellular nucleotide sugars to a lipid carrier molecule. The availability of sugar nucleotides affects greatly the biosynthesis of certain EPS namely alginate, gellan, etc. Biosynthesis of other EPS such as levan, alternan, reuteran, mutan and dextran is catalyzed extracellularly by levansucrase, alternansucrase, reuteransucrase, and mutansucrase and dextransucrase, respectively, from sucrose (Whitfield 1988; Boels et al. 2001; Patel et al. 2010).

The intracellular mechanism requires charged and energy-rich precursor monosaccharide in the form of nucleotide diphosphate/monophosphate sugar (NDP/NMP-sugar) for the synthesis of a biomolecule as simple sugar molecules cannot carry out the synthesis. The synthesis is carried out by phosphorylated sugars normally in the form of sugar-1P but rarely in the form of sugar-2P or sugar- 6P. The synthesis of sugar molecules follows an independent pathway. Then, these sugar molecules from activated NDP/NMP-sugar moieties get transferred to undecaprenyl phosphate (C55-P) with the help of enzyme glycosyltransferase (Sutherland 2001). In the assembly and transport of Gram-negative bacterial EPS the lipid intermediate pathway plays an important role, it is also reported that sometime it has also been utilized by Gram-positive bacteria. In Gram-positive bacteria, there is translocation of backbone chain to the cell surface after assembly of repeating moieties at the lipid carrier. Published literature provides evidence for the involvement of ATP-binding cassette (ABC) transporter-dependent pathway, Wzx/Wzy-dependent pathway and synthase-dependent pathway for the biosynthesis of EPS in marine bacteria (Cuthbertson et al. 2010; Ates 2015; Sara Pereira et al. 2015; Parkar et al. 2017). Gram-negative bacteria usually follow either ABC transporter-dependent or Wzx–Wzy dependent pathway but *Pseudomonas aeruginosa* follows the synthase-dependent pathway. The overall process of polymerization, chain length control, detachment from lipid and finally in the export of EPS is catalyzed by several enzymes.

The Wzx/Wzy-dependent pathway takes place in the cytoplasm and several membrane proteins play an important role in the synthesis of EPS. In this pathway, many distinct repeating units which are generally attached to a undecaprenol diphosphate anchor at the inner membrane are assembled by numerous glycosyltransferases and translocated across the cytoplasmic membrane by a Wzx protein known as flippase. Before they will be exported to the cell surface, their polymerization occurs at the periplasmic space by Wzy protein, and Wzz protein controls the length of the repeating units. Polymerized repeat units have been transported from the periplasm to the cell surface. This transportation is dependent upon the additional proteins allotted to the polysaccharide co-polymerase (PCP) and the outer membrane polysaccharide export families. The completely synthesized and exported EPS either secrete as slime or it gets attached to the cell surface as capsular polysaccharide material. EPS assembled by the Wzx/Wzy pathway contain a variety of sugars and thus they are classified as heteropolymers. The genes for the flippase (Wzx) and the polymerase (Wzy) are located within the extracellular polysaccharide operons in all strains which use this pathway (Schmid et al. 2015).

Synthase-dependent pathway not only secrets a complete polymer strand outside the membrane and the cell wall but it is often operated for the assembly of homopolymers. This pathway is independent of flippase. The process of polymerization and translocation are performed by single synthase protein (Islam and Lam 2014).

The capsular polysaccharide (CPS) biosynthesis is carried out by the ABC transporter dependent pathway. This pathway is also dependent on phosphoglycosyl transferases, which are relatively similar to that of the Wzx/Wzy-dependent pathway. The involvement of single phosphoglycosyl transferase containing operon in biosynthesis results in homopolymers and heteropolymers products, when multiple

phosphoglycosyl transferases are used. The process occurs due to the ABC transporter proteins (which are present across the inner membrane), periplasmatic proteins of the polysaccharide co-polymerase (PCP) and proteins of outer membrane polysaccharide export (OPX) families (Willis and Whitfield 2013; Gupta and Diwan 2017; Parkar et al. 2017).

Recovery and purification of EPS

Pre-treatment

The processing and recovery costs of EPS are fairly less when it is extracted directly from the fermentation broth without any pre-treatments. The resultant product has a higher viscosity than that obtained from powder product and it can be dissolved easily. But in such products, impurities of microbial cells, medium constituents and colour are present. The presence of bacterial cells and colour impurities are usually undesirable from the application point of view (Smith and Pace 1982; Sutherland 1983). The main aim of any recovery process is the removal/lysis of microbial cells and precipitation of EPS from the fermentation broth. Purification of EPS is carried out either in the broth itself or after recovery (from the broth) to improve some aspects of the quality and performance of EPS for a given application (Leroy and De Vuyst 2016). Various steps involved in EPS recovery and purification are summarized in Fig. 2.

Cell removal

The first step in EPS downstream process is the removal of microbial cells from the fermentation broth. EPS might occur as either capsular or slime polysaccharides. The slime polysaccharides are loosely bound to the cell surface and can be extracted by centrifugation or by ultra-centrifugation. The speed and duration of the centrifugation depend upon the viscosity of fermentation broth (Morin 1998; Mende et al. 2013; Notararigo et al. 2013; Kreyenschulte et al. 2014). The capsular polysaccharides are firmly attached to the cell, thus various chemical and physical pre-treatments (alkaline pre-treatments with sodium hydroxide or heat treatments) are needed before centrifugation (Notararigo et al. 2013). The fermentation broth can be filtered, centrifuged or ultracentrifuged before polysaccharide recovery to remove cells and associated material at laboratory level studies (Stredansky et al. 1999). But at an industrial scale, the above mentioned procedures cannot be used effectively due to the large volume and highly viscous nature of the broth. This demands the development of alternative methods for cell removal. Several mechanical, chemical and thermal treatments have been established to lyse, deactivate or remove cells from the broth. Different chemical treatments when performed at high pH generally affect the structural properties of the product whereas enzymatic treatments increase the cost of downstream processes. Mostly the physical treatments such as pasteurization or sterilization are used to kill the microbial cells (Smith and Pace 1982; Garcia-Ochoa et al. 1993;

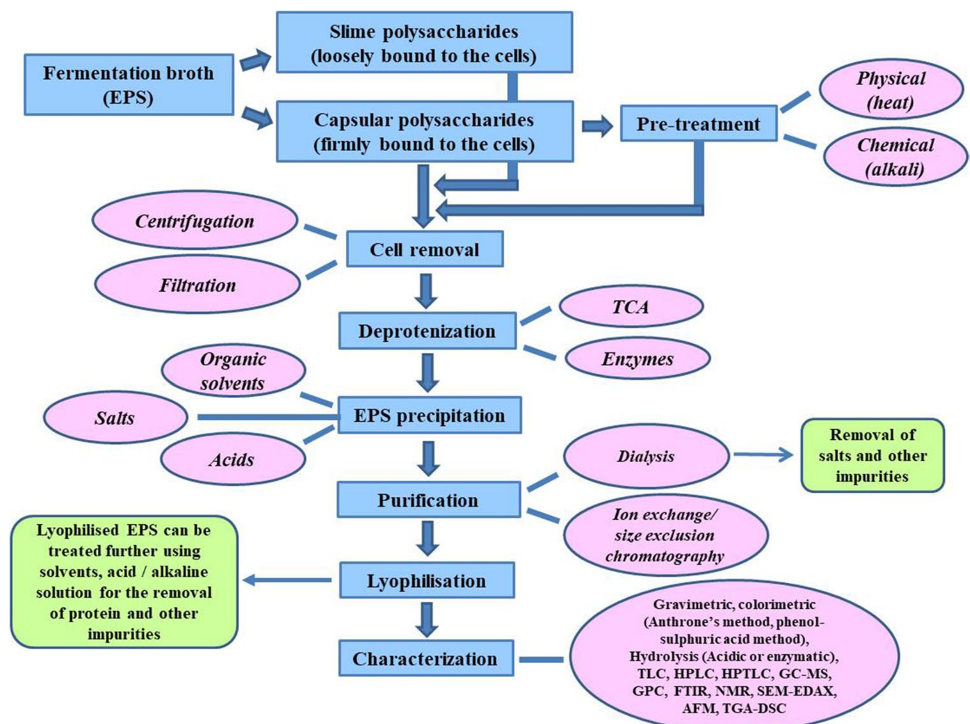

Fig. 2 Schematic diagram of the production, recovery, purification and characterization of exopolysaccharides (EPS)

Mende et al. 2013; Notararigo et al. 2013). Thermal treatments decrease the viscosity of broth, inactivate some of the enzymes and also kill the microbial cells and enhance EPS detachment from the cells. Capsular polysaccharides can also be extracted using autoclaving and various alkali treatments. Several other methods like boiling of fermentation broth for 15 min in water, heating at 60 °C in a mixture of phenol and water or in saline solution and sonication have also been used (Smith and Pace 1982; Freitas et al. 2011; Kreyenschulte et al. 2014; Leroy and De Vuyst 2016). Mechanical methods make use of centrifugation, ultracentrifugation, and filtration of fermentation broth. Stredansky et al. (1999) used activated charcoal to remove cells, colour impurities and odour from fermentation broth.

Deproteinization

The presence of protein with polysaccharide directly affects the purity of EPS hence it is required to perform deproteinization. Protein removal from the fermentation broth or crude EPS can be carried out using various chemicals such as trichloroacetic acid (TCA) and enzymes like proteases. TCA treatment results in co-precipitation of about 50% of the EPS with the medium proteins along with other impurities. It has been suggested to wash the TCA precipitate at least once to improve EPS recovery (Rimada and Abraham 2003). Various treatments used for the deproteinization of EPS are illustrated in Table 2.

Precipitation of EPS from the fermentation broth

After performing pre-treatment steps described above, recovery of EPS can be carried out using various organic solvents, salts and acids. The lower alcohols (methanol, ethanol, isopropanol) and acetone can be added to the fermentation broth to decrease the solubility of EPS and also to remove some impurities. Colo et al. (1997) have reported the use of ultrafiltration of fermented broth for better precipitation of EPS.

Some anionic polysaccharides in solution may be precipitated using acids. The anionic polysaccharides get precipitated upon the action of protons present in acid. The addition of salts in sufficient concentration also causes precipitation or complex coacervation due to the binding of the cations of the added salt to the ionized groups of EPS. This leads to charge reversal when all the available anionic groups are bound to cations. Polyvalent cationic salts (calcium, aluminium, and quaternary ammonium salts) are more effective in precipitation of EPS as compared to monovalent salts like sodium and potassium chloride (Pace and Righelato 1981). Solvents and salt in combination promote precipitation by decreasing the water affinity of the polymer and by increasing its affinity to bind cations. Thus, EPS precipitates wita-Ochoah lesser amounts of solvents (Garci et al. 1993). Various treatments used for EPS precipitation are showed in Table 3.

Partial purification of EPS

EPS precipitation treatments mostly follow the procedure of dialysis and lyophilisation. Number of researchers (Górska-Frączek et al. 2013; Marcial et al. 2013; Notararigo et al. 2013; Donnarumma et al. 2014; Ismail and Nampoothiri 2014; Shao et al. 2014; Fontana et al. 2015; Upadhyay 2017; Vaishnav 2017) have suggested to follow the steps like dissolution of EPS in deionized water, dialysis against water for 2–4 days at 4 °C, optional treatment with activated charcoal to decolourize, washing with anhydrous ethanol, acetone, and ether and finally lyophilisation

Table 2 Treatments used for deprotienization of EPS

No.	Deproteinizing agent	Condition used	References
1.	Trichloroacetic acid (TCA)	4–20% w/v under agitation or stirring	Zhang et al. (2013), Shao et al. (2014), Fontana et al. (2015) and Leroy and De Vuyst (2016)
		15% TCA (crude ethanol-treated freeze dried EPS)	Ahmed et al. (2013)
		TCA treatment after threefold precipitation with isopropanol	Park et al. (2013)
		TCA treatment between 2 ethanol precipitation step	Suzuki et al. (2013) and Yilmaz et al. (2015)
		TCA treatment followed by 2 times ethanol precipitation	Marcial et al. (2013)
2.	Acid	Acidification of complex media with 12 M HCl followed by heating the broth at 70 °C	Enikeev (2012)
3.	Enzyme	Digestion with proteases followed by inactivation through heating	Leroy and De Vuyst (2016)
		Protease containing buffer followed by phenol:chloroform:isoamyl alcohol (25:24:1)	Bajaj et al. (2007), Górska-Frączek et al. (2013) and Leroy and De Vuyst (2016)
4.	Organic solvent	Sevag reagent (chloroform: *n*-butanol) (4:1)	Shang et al. (2013)

Table 3 Treatments used for EPS precipitation

No.	Treatments	Details	References
1.	Solvents	Acetone	Sutherland (1990) and Mende et al. (2013)
		Ethanol, methanol	Enikeev (2012), Ahmed et al. (2013), Górska-Frączek et al. (2013), Marcial et al. (2013), Notararigo et al. (2013), Zhang et al. (2013), Ismail and Nampoothiri (2014), Shao et al. (2014) and Fontana et al. (2015)
		Isopropanol	Galindo and Albiter (1996) and Park et al. (2013)
2.	Combination of solvents	Acetone and ethanol	Donnarumma et al. (2014)
3	Salts	Mixture of salts and alcohols	Garcia-Ochoa et al. (1993)
		NaCl, KCl, $MgSO_4$, MgO, $CaCl_2$, cetrimide, Al_2O_3	Kennedy and Bradshaw (1984) and Pace and Righelato (1981)
5.	Acids	HCl for alginate (for anionic polysaccharides)	Smith and Pace (1982) and Margaritis and Pace (1985)

of EPS. The dialysis of EPS is mainly important to remove small molecules such as salts and other impurities that are present in the material. Dialysis membranes with a molecular weight of 6000–8000 Da are suggested for dialysis, as EPS fractions of low molecular mass may otherwise be lost in the dialysis water and finally the content of dialysis bag is lyophilized (Rimada and Abraham 2003).

The lyophilized EPS can be treated further for the removal of proteins and other impurities. It can be done by using 80% v/v ethanol solution with 0.1% v/v formic acid to solubilize the protein followed by washing with 96% v/v ethanol (Tuinier et al. 1999; Ruas-Madiedo and de los Reyes-Gavilán 2005). The dissolution of lyophilized EPS in 0.3 M NaOH followed by centrifugation can also help to eliminate extra contaminants (Notararigo et al. 2013). EPS purification steps generally include size exclusion chromatography, ion-exchange chromatography or preparative SDS-PAGE (Notararigo et al. 2013; Zhang et al. 2013; Shao et al. 2014; Fontana et al. 2015).

When the ultimate aim is to quantify EPS production, some of these purification steps are less important as they affect the final yield of the product. For example, when protein removal is conducted using different chemicals and enzymes, these might react with EPS components and lower down the yield (Rimada and Abraham 2003). Purification method becomes an important criterion when EPS characterization is considered. At that time purity of EPS becomes the first concern as compared to its yield. If the product is pure then it will be less difficult to elucidate its structure. Therefore, the use of complex and non-complex media should be decided from the beginning of the experiment, as the EPS produced using complex media require extensive pretreatment procedures whereas the EPS recovered from non-complex media require simple deproteinization method before the centrifugation step.

Applications of EPS from marine microorganisms

In 1960s microbial polymers were explored for their applications in various fields, and since then there has been a remarkable increase for their commercial applications. Microbial polysaccharides are mainly used in the field of agriculture, pharmaceutical, food, textile, detergent, paper, paint, and petroleum industries. They are also used in processes like bioremediation, as a tool in drug delivery and cancer therapy, as well as for formulation of various culture media (Quesada et al. 1993; Dave et al. 2016; Vaishnav et al. 2016). Technological advancement has led to the discovery of the utility of microbial biopolymers to man (Nwodo et al. 2012). Microbial polymers help the organisms for attachment, biofilm formations, stabilization, aggregation and to maintain structural integrity (Lorenz et al. 1988). The EPS interacts with water molecules and change the rheological properties by increasing stability, thus can be used in the formulation of many pharmaceutical and cosmetic products. Most of the toothpaste making industries utilizes EPS as a binding and thickening agent (Tabibloghmany and Ehsandoost 2014).

Recently the applications of EPS from marine bacteria are increasing in various fields as they offer a great diversity of polysaccharides. Marine bacteria produce EPS having unique composition and properties. These bacterial polymers are reported to have anti-oxidant, antitumor, antimicrobial and immune-modulatory properties (Mohamed et al. 2018). The non-toxic EPS of marine microorganisms has been used for several medical applications such as in wound dressing and in drug delivery (Sutherland 1998; Otero and Vincenzini 2003; Rehm 2010; Laurienzo 2010). The spirulan produced by *Arthrospira platensis*

and EPS from *Spirulina* has been used in the treatment of pulmonary metastasis and as an anti-inflammatory agent in many drugs (Wu et al. 2016a, b). *Vibrio diabolicus*, a marine bacterium has been reported for the production of "Hyalurift" polysaccharides having properties that are similar to hyaluronic acid and known for its restoration of bone integrity (Nwodo et al. 2012; Onesti et al. 2013). Romano et al. 2007) and de Morais et al. 2010) have suggested the use of microbial polysaccharides for bone integrity. A marine *Pseudomonas* sp. is reported to produce sulphated polysaccharide B-1, which showed cytotoxic activity against human cancer cell lines (Matsuda et al. 2003). EPS secreted by *Bacillus licheniformis* and *Geobacillus thermodenitrificans* has been used as an immunemodulatory agent for therapeutic purposes (Arena 2004). An acidic EPS released by *Alteromonas* sp. strain 1545 has interesting rheological properties and may be used as a thickening agent (Talmont et al. 1991); EPS secreted by *A. madeodii* sub sp. *fijiensisbiovar* has found application in cosmetics (patent number 94907582-4). The EPS secreted by *Hahella chejuensis* gen. nov., sp. nov., has emulsifying properties (Lee et al. 2001); polymer produced by *Cyanothece* sp. ATCC 51142 has the capability of gel formation and use in food industries (Shah et al. 2000). Kumar et al. (2007) isolated *Planococcus maitriensis*, which produced an EPS having biosurfactant properties. Microbial EPS are extensively used for Microbial Enhanced Oil Recovery (MEOR) and transport of polyaromatic and aliphatic hydrocarbons. The marine *Pseudomonas* sp. strain S9 was found to produce EPS in nutrient availability as well as in nutrient starvation conditions (Wrangstadh et al. 1990). An EPS capable of binding heavy metals was produced by the *Alteromonas* strain 1644 isolated from *Alvinellidae* collected from the East Pacific Rise (Bozzi et al. 1996). The *Pseudoalteromonas* strain SM9913 was isolated from deep-sea sediments in the Gulf of the Yellow Sea (China). EPS of this strain showed flocculating and biosorptive capacity (Qin et al. 2007; Li et al. 2008). Muralidharan and Jayachandran 2003) described the physicochemical properties of bioadhesives produced by marine biofouling bacterium, *Vibrio alginolyticus*. The EPS of Artic marine bacterium *Polaribacter* sp. SM1127 showed antioxidant activity, moisture-retention ability and protective property on human dermal fibroblasts (HDFs) at low temperature. EPS has also promoted the skin wound healing and prevented the frostbite injury in Rat Skin (Sun et al. 2020).

Heavy metal remediation using marine bacteria and their EPS

Biosorption is one of the mechanisms through which organisms remove or accumulate heavy metals. It is a rapid and passive process of metal uptake for which the cells need not be in a live state. Biosorption is a physicochemical process, which includes various mechanisms such as adsorption, absorption, intracellular or extracellular accumulation, redox reaction, ion exchange, surface complexation and precipitation (Gadd 2010). Agricultural waste such as rice straw, wheat straw, soya bean straw, coconut husks, waste tea, waste coffee powders, dried plant leaves, wool, cork biomass, and cottonseed hulls are used for metal removal. Sewage, sludge and microbial cells such as bacteria, fungi and algae have been also used for their metal- binding capacity under various conditions (Abbas et al. 2014). Microbial EPS have the ability to bind with anion and cations, resulting in a candidate of choice for the bioremediation process (Saikia et al. 2013). In some remediation processes EPS modified by chemical processes such as acetylation, methylation, phosphorylation, and sulfonylation are used (Desbrieres et al. 2018). Acetylation of EPS decides the selectivity of metal-binding (Sutherland 1983). The metal binding property of the EPS plays a significant role for metal remediation from the wastewater (Choi and Yun 2006).

The reports of Gupta and Diwan (2017) demonstrated almost 85–95% of zinc, copper and chromium removal using consortium developed from activated sludge. They also reported that many Gram-negative bacterial consortia could remove 75–78% of zinc, lead, chromium, nickel, copper, cadmium, and cobalt within two hours. Immobilized EPS of *Chryseomonas* and *Paenibacillus polymyxa* showed the removal of cadmium, cobalt, copper, and lead (Ozdemir et al. 2005; Acosta et al. 2005). Dead cell-bound EPS of *Bacillus cereus, Bacillus pumilus, Pentoea agglomerans* showed 85.5–89% of chromium removal (Sultan et al. 2012). EPS of *Acidithiobacillus ferrooxidans* helps the organisms to bind with the mineral and thus extract metals from the sulphide ores (Yu et al. 2011). Salehizadeh and Shojaosadati (2003) reported the biosorption of copper (74.9%), lead (98.3%) and zinc (61.8%) by the EPS of *Bacillus firmus*. The EPS produced by *Azotobacter chroococcum* XU1 showed the sorption of lead (40.48%) and mercury (47.87%) (Rasulov et al. 2013). The EPS of *Ensifer meliloti*, showed 89, 85 and 66% of lead, nickel and zinc ion reduction respectively (Lakzian et al. 2008).

Various marine bacteria are also reported for their metal removal ability. The specific structure and high uronic acid content impart an enhanced anionic property to marine bacterial EPS which may be responsible for metal removal. EPS of *Marinobacter* sp. showed sorption of metals like lead and copper (Bhaskar and Bhosle 2006). EPS from marine *Enterobacter cloacae* demonstrated the sorption of cadmium (65%), copper (20%) and hexavalent chromium (75%) (Iyer et al. 2004, 2005). *Halomonas* sp. associated with marine micro-alga was also reported to chelate metals such as calcium, aluminium, iron, and magnesium (Gutierrez et al. 2012). The EPS secreted by the *Pseudoalteromonas*

sp. SM9913 showed the adsorption of Fe^{2+} (85.00%), Zn^{2+} (58.15%), Cu^{2+} (52.77%), Co^{2+} (48.88%), Mg^{2+} (30.69%), Mn^{2+} (25.67%) and Cr^{6+} (5.15%) (Qin et al. 2007). Details regarding the EPS producing organisms and their metal removal efficiency are enlisted in Table 4.

Future prospects

The marine biopolymers contribute only a small portion to the current polymer market. Mainly the high production costs of the EPS affect the profit margin at market level. The high production costs are mainly due to the use of expensive and specific nutrients in the preparation of fermentation media; this generally contributes about 30% of the cost for the fermentation process. To make the processes cost effective, cheaper alternative substrates such as cane molasses, sugarcane bagasse, corn steep liquor, fruit peels, potato peels etc. should be used for the large scale production. Some biopolymers like xanthan, curdlan, dextran, gellan have been produced by solid state fermentation using raw substrates like spent malt grains, vegetable and fruit wastes, citrus peels, olive mill waste water etc. But it requires lots of efforts to scale-up the process from lab level to industrial level for the production of a commercial product using cheaper or solid substrates (Poli et al. 2011; Casillo et al. 2018).

Although marine microbial EPS have been studied in recent times for their various industrial applications, there have been only a few reports highlighting their production and recovery. More detailed research in this field is needed to understand the properties of EPS in depth. To achieve the higher EPS yields, the marine bacterial strains can be improved using genetic engineering (use of mutagenic strains, gene manipulations) and also EPS having specific properties and structures can be produced using the same.

The present methods that are used for structural determination of EPS are labor-intensive and tedious. So suitable modifications can be incorporated in the existing protocols or novel strategies can be developed to make the process simpler. Moreover, the EPS extraction methods can be suitably modified in a cost-effective manner which would significantly lower down the overall cost of the downstream processes.

Table 4 Application of marine bacterial EPS for metal remediation

EPS producing marine bacteria	Metal ions	Sorption capacity (mg/g)	References
Idiomarina fontislapidosi F23^T	Cu^{2+}	16.30	Mata et al. (2008)
	Pb^{2+}	40	
	Co^{2+}	8	
Idiomarina ramblicola R22 ^{T}	Cu^{2+}	26.25	
	Pb^{2+}	44.65	
	Co^{2+}	10	
Psuedoalteromonas sp. strain TG12	Na^{+}	154.5	Gutierrez et al. (2008)
	Mg^{2+}	31.0	
	K^{+}	10.6	
	Sr^{2+}	2.7	
	$Fe^{2+/3+}$	0.14	
Salipiger mucosus A3^T	Cu^{2+}	15.7	Llamas et al. (2010)
	Pb^{2+}	43.5	
	Co^{2+}	8.7	
Desulfovibrio desulfuricans	Cu^{2+}	98.2	Kim et al. (2015)
	Ni^{2+}	90.1	
	Cr^{6+}	99.8	
EPS M1	Cu^{2+}	400	Deschatre et al. (2015)
	Ag^{+}	256	
Alteromonas sp. JL2810	Cu^{2+}	140.8 ± 8.2	Zhang et al. (2017)
	Ni^{2+}	226.3 ± 3.3	
	Cr^{6+}	251.2 ± 5.1	
Bacillus licheniformis SR5	Hg^{2+}	200	Upadhyay et al. (2017)
Bacillus xiamenensis PbRPSD202 (Live cells)	Pb^{2+}	216.75	Mohapatra et al. (2019)
Bacillus xiamenensis PbRPSD202 (Dead cells)	Pb^{2+}	207.4	

Conclusions

The review intends to provide information on EPS producing marine bacteria, their unique properties, purification methods and applications in various fields. This also provided an insight of novel marine biopolymers of applied interest. There are several methods for recovery, extraction and purification of EPS, but they need to be considered critically depending upon the source of production and biochemical nature of the EPS. All the purification and recovery methods are having one or the other limitation and no universal extraction method is available due to wide variety of EPS specially from marine bacteria. Thus for the potential biotechnological and industrial applications of these polymers, further developments in the methods used for their recovery and purification are needed. Marine bacterial EPS can be a good source for metal remediation, MEOR as well as in the field of medicine thus can play role in maintaining environmental sustainability.

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Compliance with ethical standards

Conflict of interest We all the authors have no conflict of interest for publishing this review.

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