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Marine bacterial extracellular polysaccharides: A review

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ABSTRACT

Marine ecosystems are of great importance to humans since evolution. Conventionally, polysaccharides were isolated from plants, algae, *etc.* As science advanced, various sources of exopolysaccharides have been found. Exopolysaccharides have wide applications in food, medical, pharmaceutical and environmental industries which lead to the exploration of more aspects regarding extracellular polymeric substances (EPS). Various marine bacteria, such as *Bacillus, Halomonas, Planococcus, Enterobacter, Alteromonas, Pseudoalteromonas, Vibrio, Rhodococcus*, *etc.*, have been extensively studied for the marine EPS isolation and its characterization. In this review, the composition, biosynthesis of EPS, along with major sources of EPS and potential applications have been discussed.

1. Introduction

Marine biotechnology has been one of the emerging and key areas of research since 1940s due to diverse functional areas (marine natural products for medicine, marine nutraceuticals, marine bioenergy, marine bioremediation). Moreover, marine organisms have the capacity to produce unique bioactive compounds which can be utilized for human and industries. Bioactive compounds from marine sources have found various implications in the progress of mankind due to their diverse biological properties such as anticancer, antiviral, *etc*. In addition to bioactive compounds, extracellular polysaccharides from marine organisms have found to be beneficial in various industries.

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Due to diverse biological properties and physiological parameters, exopolysaccharides has been found to be implicated in various industries such as food, textile, *etc.* (Table 1)[1]. Significant studies of microbial extracellular polymeric substances (EPS) have been carried out extensively for decades, which further enhances the researches to figure out the mechanism of EPS biosynthesis providing divergent directions to the study of EPS. EPS have been isolated from many natural sources such as soils, fresh water, hydrothermal vents, *etc*. Researchers focus on isolating EPS producing microorganisms from marine sources as many marine microbes are useful for the human. Thus, this leads to new insights in exploring the EPS production from marine bacteria and other microbes. This review article focuses on the new insights of exopolysaccharides from marine bacteria, along with its chemical properties and applications in the industries.

Table 1
Various commercial applications of EPS.

EPS	Producer bacteria	Commercial applications
Kelcogel/ gelrite	*Sphingomonas paucimobilis*	Gelling, Stabilizing agent in food industry
Xanthan	*Xanthomonas campestris*	Viscofying agent
Emulsan	*Pseudomonas fluorescence*	Emulsifiers
Dextran	*Streptococcus mutans*, *Leuconostoc mesenteroides*	Purification
Curdlan	*Agrobacterium* and *Rhizobium* spp.	Antithrombotic

Adapted and modified from the table made by Madhuri and Prabhakar[1].

2. Classification and chemistry of bacterial EPS

On the basis of structural composition, microbial EPS can be classified into three groups[2] which are depicted in the following Figure 1. Homo-EPS consist of single type of monosaccharide usually α-D-glucans, β-D-glucans, fructans and other polygalactan. Hetero-EPS consist of different types of monosaccharides mainly, D-glucose, D-galactose, L-rhamnose and their derivatives[3,4]. The differences arise between the homopolysaccharides on the basis of their primary structures such as patterns of main chain bonds, molecular weights and branch structures[4].

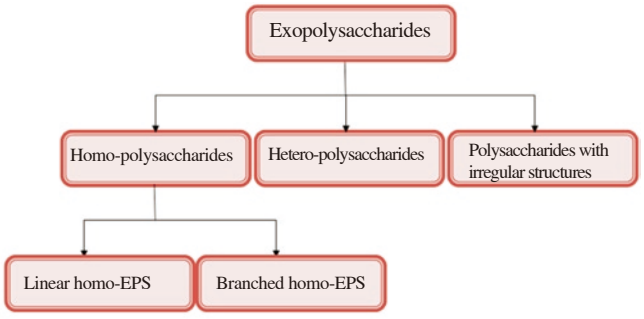

Figure 1. Classification of EPS on the basis of structures.

Furthermore, on the basis of their functions[5], EPS were classified into 7 groups, including the constructive or structural, sorptive, surface active, active, informative, redox active, and nutritive.

Exopolysaccharides consist of linear, branched repeating units of sugars or sugar derivatives. These sugar units are mainly glucose, galactose, mannose, N-acetylglucosamine, N-acetyl galactosamine and rhamnose in variable ratios[6]. In addition to sugar moieties, some non-carbohydrate substituents such as acetate, pyruvate, succinate and phosphate are also present[7]. The typical composition of bacterial EPS is tabulated in Table 2.

Table 2
Typical components of bacterial EPS.

Components	Examples
Pentose sugars	D-arabinose, D-ribose, D-xylose
Hexose sugars	D-glucose, D-galactose, D-mannose, D-allose, L-rhamnose, L-fucose
Amino sugars	D-glucosamine, D-galactosamine
Uronic acids	D-glucuronic acids, D-galacturonic acids, D-mannuronic acid
Organic substituents	Acetate, succinate, pyruvate, glycerate, hydroxybutanoate
Inorganic substituents	Sulfate, phosphate

Adapted and modified from researches of Kenne and Lindberg[8] and Laurienzo[9].

3. Possible biosynthesis pathways of marine bacterial EPS

Extracellular polysaccharides biosynthesis is a complex process due to the involvement of various enzymes. Various studies have been carried out to figure out the exact mechanisms of biosynthesis of EPS in bacteria, but mechanisms of biosynthesis of EPS in the marine bacteria have still remained unclear. Generally, the precursor sugars are synthesized and activated inside the cell and the polymerization takes place in the inner cell membrane. Several reviews and studies suggested three possible biosynthesis pathways of EPS in marine bacteria, namely Wzx/Wzy-dependent pathway, ATP-binding cassette (ABC) transporter-dependent pathway, and synthase-dependent pathway (Figure 2).

3.1. Wzx/Wzy-dependent pathway

The Wzx/Wzy-dependent mechanism has been widely studied in Gram-negative bacteria especially for heteropolysaccharide production[10]. Wzx/Wzy-dependent pathway occurs in the cytoplasm with the help of series of the membrane-spanning proteins[11]. The initiation of the pathway occurs through the initiator protein known as phosphoglycosyl transferases which harbours the first osidic residue to the undecaprenyl phosphate resulting in the sugar repeat units linked to undecaprenyl pyrophosphate[12,13]. These undecaprenyl pyrophosphate-linked sugar repeat units are then flipped across the cytoplasm to the periplasm of the inner membrane using Wzx protein known as flippase, where these repeating units are then polymerized by Wzy protein, namely, polymerase, through a putative catch and release mechanism[14]. Wzy mediated polymerization is carried out at the negative terminus end of the growing chain and the length of the repeating unit is controlled by another protein known as Wzz.

3.2. ABC transporter-dependent pathway

ABC transporter-dependent pathway of EPS biosynthesis is quite similar to the Wzx/Wzy-dependent pathway since the initiation of EPS biosynthesis takes place with the action of various phosphoglycosyl transferases in the cytoplasm[15]. The only difference between the Wzx/Wzy-dependent pathway and the ABC transporter-dependent pathway is the export of sugar linked moieties from the cytoplasm to the periplasm of the inner membrane. Export of sugar linked repeated moieties occurs due to the ABC transporter proteins spanning the inner membrane and the periplasmic polysaccharide co-polymerase and outer membrane polysaccharide export families[16-18]. Polysaccharides produced through this pathway carry a conserved glycolipid at the reducing end composed of phosphatidylglycerolandapoly-2-keto-3-deoxyoctulosonicacid linker[14].

3.3. Synthase-dependent pathway

The unique feature of synthase-dependent pathway is the secretion of the complete polymer strands across the membranes and the cell wall which is independent of a flippase[14]. The polymerization as

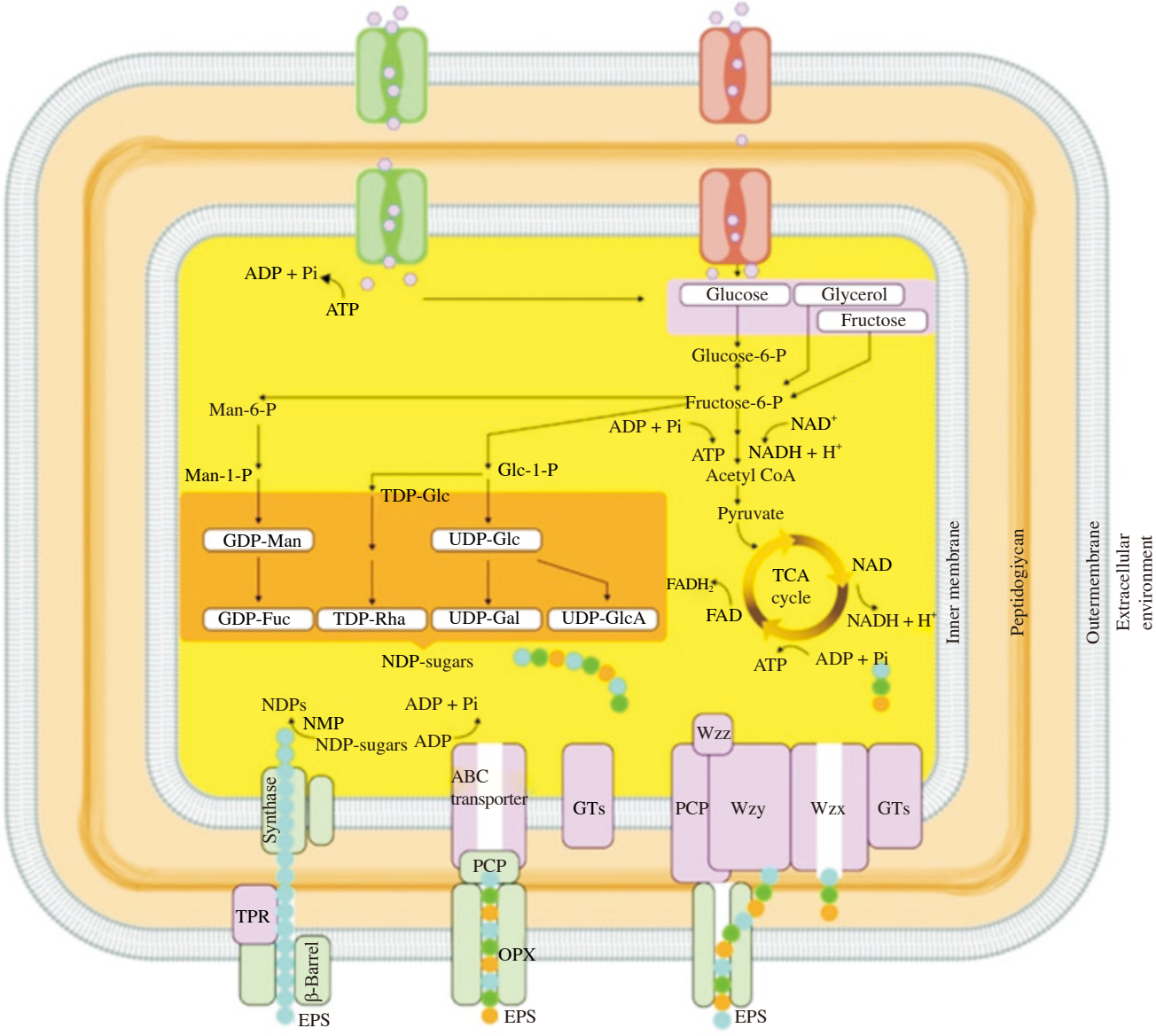

Figure 2. Possible pathways of EPS biosynthesis in marine bacteria[7].

ATP: Adenosine tri-phosphate; ADP: Adenosine di-phosphate; FAD: Flavin adenine dinucleotide; NAD: Nicotinamide adenine dinucleotide; GDP: Guanosine di-phosphate; GDP-Fuc: Guanosine di phosphate-fucose; TDP: Thymidine di phosphate; TDP-Rha: Thymidine di phosphate-rhamnose; NMP: Nicotinamide mono phosphate; UDP: Uridine di phosphate; TPR: Tetratricopeptide repeats; TCA: Tri carboxylic acid; Man-1-P: Mannose 1'-phosphate; TDP-Glc: Thymidine di phosphate-glucose; Glc-1-P: Glucose 1'-phosphate; UDP-Glc: Uridine di phosphate-glucose; GDP-Man: Guanosine di phosphate-mannose; UDP-Gal: Uridine di phosphate-galactose; UDP-GlcA: Uridine 5'-diphosphoglucuronic acid; NADH: Nicotinamide adenine dinucleotide (reduced form); $FADH_2$: Flavin adenine dinucleotide (reduced form); GTs: Glycotransferases; OPX, Outer membrane polysaccharide export.

well as the translocation process is performed by a single synthase protein[11]. Synthase-dependent pathways are often utilized for the assembly of homo-polymers requiring only one type of sugar precursor.

Most of the enzymatic steps for exopolysaccharide precursor biosynthesis occur inside the cell while the polymerization/ secretion is localized in the cell envelope. The genes involved in the different biosynthesis pathways encode various types of glycosyl transferases, polymerizing and branching enzymes, as well as enzymes responsible for addition of substituents or modifications of sugar moieties[14]. The genes encoding these enzymes can be found in most of the EPS producing microbes clustered within the genome or on large plasmids[11]. EPS biosynthesis gene clusters are often located on plasmids[19,20].

4. EPS producing marine bacteria

Marine bacteria, such as *Bacillus, Halomonas, Planococcus, Enterobacter, Alteromonas, Pseudoalteromonas, Vibrio, Rhodococcus*, *etc*,, are the primary EPS producers and have been extensively studied till date[21]. Most of the EPS producing marine bacteria are Gram-negative in nature, while very few are Gram-positive. It was observed that marine bacterium *Saccharophagus degradans* (*S. degradans*) produced EPS in high amounts from several carbohydrates sources including starch and xylose. Thus, the production of EPS from *S. degradans* was enhanced by nutritional limitation[22]. *Vibrio furnissii* strain VB0S3 was isolated and characterized from coastal regions of Goa and showed to produce highest EPS in batch cultures during the late exponential growth

phase[23]. *Planococcus maitriensis* Anita I was isolated from the coastal sea water area of Bhavnagar, India[19]. This bacterium was able to produce an EPS which can be further used for bioremediation, enhanced oil recovery and cosmetic applications. *Enterobacter cloacae*, isolated from marine sediments in India produced an acidic EPS that showed excellent emulsifying properties as comparable to other commercial gums[24]. EPS production by *Pseudoalteromonas* CAM025 and CAM036, isolated from Antarctica sea water and sea ice were described[25]. Marine bacteria such as *Halomonas maura, Halomonas ventosae*, and *Halomonas alkaliantarctica* were isolated and evaluated for the EPS production[26-28]. Some exopolysaccharide producing marine bacteria have been tabulated in Table 3.

Table 3

Some exopolysaccharide producing marine bacteria.

Marine bacteria	Sources	References
Planococcus maitriensis Anita I	Coastal sea water of Bhavnagar District, India	[19]
S. degradans	-	[22]
Vibrio furnissii strain VB0S3	Coastal region of Goa	[23]
Enterobacter cloacae	Marine sediments	[24]
Halomonas spp.	-	[26]
Halomonas anticariensis	-	[27]
Halomonas ventosae	-	[27]
Alteromonas haloplanktis KMM 156	-	[29]
Alteromonas infernus (*A. infernus*)	Deep sea hydrothermal vent	[30,31]
Alteromonas macleodii 2MM6	Intertidal zone of Halifax, Nova Scotia	[32]
Bacillus licheniformis (*B. licheniformis*)	Volcano island	[33,34]
Bacillus marinus	Marine sediment	[35]
Bacillus strain B3-15	Shallow water, marine hot spring	[36]
Bacillus strain B3-72	Shallow vent	[37]
Bacillus thermoantarcticus	Ischia island	[37]
Geobacillus sp.	-	[37]
Desulfovibrio sp. strain Indl	Indonesian coast	[38]
Flavobacterium uliginosum	-	[39]
Hahella chejuensis	-	[40]
Pantoea sp. BM39	Seafloor sediments	[41]
Pseudoalteromonas atlantica	-	[42,43]
Pseudoalteromonas sp. strain S9	Marine sediment	[44-46]
Pseudomonas sp strain NCMB 2021	Madilyn fletche Halifax, Nova Scotia	[47]
Rhodococcus erythropolis PR4	-	[48]
Shewanella colwelliana	Eastern oyster	[49]
Vibrio alginolyticus	Marine fouling material	[50]
Vibrio parahaemolyticus	Marine water	[51]
Zunongwangia profunda SM-A87		[52]

5. Potential applications of marine bacterial EPS

Bacterial EPS have been implicated in industries such as pharmaceutical, biomedical, food, bioremediation and so on due to their stringent physical and chemical parameters. The applications of EPS in industries are mainly determined by their physical and chemical properties[19]. Rheological, emulsifying, solidifying properties of bacterial exopolysaccharides have been the key properties for the diverse applications. In addition to EPS extracted from terrestrial bacteria, marine bacteria have found their role in the pharmaceutical and biomedical industries (Table 4).

5.1. Medical and pharmaceutical applications

EPS secreted by *B. licheniformis* and *Geobacillus thermodenitrificans* are evaluated and it is found that they are powerful stimulators of Th1 cell mediated immunity[54]. Thus, these can be potentially used as immunomodulatory agent for therapeutic purposes. Following sulfation and depolymerisation of EPS produced by *A. infernus*, the EPS derivatives can be used in the treatment of lipemia and arteriosclerosis[55,56]. HE800 EPS produced by *Vibrio diabolicus* was found to be strong bone healing material without any inflammatory and hypersensitivity reactions[57]. It was demonstrated that HE800 EPS enhanced collagen structuring in engineering connective tissue model and promoted fibroblast settled in extracellular matrix. Furthermore, it was observed that during collageneous matrix building, the addition of HE800 EPS, increased and accelerated collagen fibrils formation with 67 nm periodic striations[58]. Polysaccharide B1 from the marine bacterium, *Pseudomonas* sp., was found to be more cytotoxically active to the central nervous system and lung cancer cell lines since the EPS induced apoptosis in the cells[59,60].

Table 4

Some potential biotechnological applications of marine bacterial EPS.

Marine bacteria	Biotechnological applications
A. infernus strain GY785	Anticoagulant activity, increased the viability and proliferation of chondrocytes, cartilage tissue engineering
Alteromonas macleodii subsp. *fijiensis*	Thickening agent in food industry, detoxification of waste water, bone healing, treatment of cardiovascular diseases, protection of sensitive skin against chemical, mechanical and UVB aggressions
B. licheniformis B3-15	Antiviral activity
Bacillus thermodenitrificans strain B3-72	Immunomodulatory and antiviral activity
Geobacillus sp. strain 4004	Pharmaceutical applications
Paracoccus zeaxanthinifaciens subsp. *payriae*	Bioremediation of toxic metals
Polaribacter sp. SM1127	Food, cosmetic, pharmaceutical, biomedical
Pseudoalteromonas strain 721	Gelling properties
Pseudoalteromonas strain CAM025	Cryoprotection
Pseudoalteromonas strain CAM036	Trace metal binding
Pseudoalteromonas strain SM9913	Flocculation behaviour and biosorption capacity
Vibrio diabolicus strain HE800	Bone regeneration

Adapted and modified from researches of Poli *et al.*[34] and Donato *et al.*[53].

5.2. Environmental applications

It has been found that the EPS produced by marine bacteria have strong affinity for heavy metals and thus EPS can be used for bioremediation of heavy metals from the environment. It was found that the strong interaction of EPS produced by *Altermonas* sp. strain 1644 between divalent and monovalent cations[56,61]. The EPS produced by *A. infernus* also showed a very strong affinity for lead, cadmium, and zinc[62].

6. Recent advances

In vitro studies conducted in Italy found that the EPS1-T14 produced by marine bacterium, *B. licheniformis* T-14 inhibited the biofilm formation of clinical isolates *Escherichia coli* 463, *Klebsiella pneumoniae* 2659 , *Pseudomonas aeruginosa* 445 and Staphylococcus *aureus* 210 to a considerable extent dependent on the dosage and concentrations of the EPS1-T14[63]. According to them, this antibiofilm activity of EPS1-T14 was due to the surfactant properties of EPS1-T14 which could influence bacterial cell surface hydrophobicity and thereby interfere with the initial adhesion step, which was essential for the biofilm formation. Authors also suggested that the presence of fructose and fucose in the EPS1-T14 could interfere with the surface lectins of various bacteria such as *Pseudomonas aeruginosa*, thereby interfering with the assembly of adhesions in the cell wall. Thus, EPS1-T14 could be fascinating anti-adhesive drug in medical and non-medical prospects, which needs further researches and studies.

7. Conclusion

Due to the rheological, emulsifying and solidifying properties of exopolysaccharide, it has become one of the most fascinating fields of research in terms of marine science. Bone regeneration activity of some EPS has facilitated enormous researches in order to explore the pros and cons of the EPS as bone regeneration agent. Antitumor and antiulcer activities of marine EPS can be further explored in terms of its mechanisms and other aspects. These various activities of EPS have facilitated the enormous findings to figure out the enhanced production of these EPS by modifying the organisms using genetic engineering principles. Thus, EPS can be more fascinating as the EPS from marine sources is an emerging field.

Conflict of interest statement

We declare that we have no conflict of interest.

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