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Potential Sanitary Impacts on Shellfish Aquaculture by the Marine Invasive Sponge *Celtodoryx ciocalyptoides*

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Abstract

Marine invasive species represents one of the major threats affecting biodiversity by altering marine habitat functionality, aquaculture economy by degrading seawater quality and even health by introducing pathogens. In this study, the polysaccharidic extract of the non-indigenous marine sponge *Celtodoryx ciocalyptoides* was evaluated on biofilm formation by pathogenic bacteria including *E. coli* and Vibrio splendidus. Effect of this extract was investigated on different stages of bacterial colonization: adherence and biofilm formation. Results indicated that this polysaccharide extract was able to enhance biofilm formation by *E. coli*, *Pseudoalteromonoas* sp., and *Vibrio splendidus* and to inhibit biofilm formation by *Paracoccus* sp. Due to the abundance of this marine invasive species and its distribution near French shellfish areas, it is feared that this species may represent a new threat to the bacteriological quality and economy of shellfish production areas.

Keywords: Biofilm; Polysaccharide; Invasive species; *Celtodoryx ciocalyptoides*; *Vibrio splendidus*; *Escherichia coli*

Introduction

Shellfish farming is particularly sensitive to the degradation of the seawater quality. Among biological pollutants, faecal bacteria such as *E. coli* are a major public health concern through bivalve consumption. Due to the increasing demographic pressure on the coastline, wastewater treatments are rapidly becoming insufficient. Among other bacteriological strains, pathogenic bacteria belonging to Vibrio species are known to cause host-tissue lesions in various marine shellfishes. For example, *Vibrio splendidus* related strains were found associated with mortality outbreaks of the Pacific oyster Magallana gigas [1]. One of the reasons for the persistence of pathogens as reservoirs in the marine environment might be their resilience in the form of biofilm on biotic or abiotic surfaces.

Biofilm formation is a succession of several stages: reversible and irreversible attachment of plank-tonic bacteria onto a surface, growth, and cell dispersal. It is defined as a dynamically and structurally com-plex microbial community in which microbial cells are embedded into a self-produced matrix made of extra-cellular polymeric substances [2]. This matrix is composed of a complex and polar mixture of organic sub-stances such as polysaccharides, proteins and nucleic acids. This form of life confers advantages to bacteria in terms of growth, protection from antimicrobial agents, enzymatic activity, communication and lateral gene transfer [3]. In the shellfish industry, bacterial infections that lead to the formation of biofilms pose a serious sanitary and economical threat [4,5].

The marine invasive sponge *Celtodoryx ciocalyptoides* was discovered in 1996 in the river of Etel (France), in the nearby Golfe du Morbihan and simultaneously around Oesterschelde (Netherlands) [6,7], two European regions where shellfish culture represents an important economic activity. This marine sponge species probably originates from the Chinese Yellow Sea and is thought to have been introduced in North-East Europe by the transfer of the Pacific Oyster Magallana gigas during the 60's to aquaculture farms [7]. Competing successfully for space with other sessile invertebrates, *C. ciocalyptoides* is considered as an invasive marine species [6]. After a mass mortality during the winter 2003, sponges recovered with a covering rate 5 times higher than in 2003. Between 2011 and 2014, we estimated its covering rate about 29.3% of the rocky reef of the Etel river (Morbihan, France) [8]. Extending its cover over artificial and natural substrates, *C.*

cio-calyptoides spreading area seems to enlarge along the French Atlantic coast. This IS was also discovered in 2012 in the river of Penerf, in 2014 in the port of Le Havre [9] and in 2016 in front of Lorient on the Tanche wreck (Sauleau, pers. comm.) where it has probably found optimal conditions (light, temperature, nutrients, lack of predation, biodiversity loss, etc.) to proliferate. In 2017, in the port of Le Havre, specimens were not found any more (Breton, pers. comm.). Regression of its covering rate was also observed by scuba divers in the ria of Etel between 2017 and 2019. However, since 2021, this sponge showed a rapid population growth on the rocky substrate forming once again a huge mat (Sauleau, pers. comm.). In addition to this bloom-bust dynamic, the marine sponge *C. ciocalyptoides* is characterized by the secretion of sulfated polysaccharides [10]. Due to the large amounts of polysaccharides secreted by the invasive sponge, their potential role in the invasion process cannot be excluded.

Since polysaccharides are known to play a role in biofilm formation by bacteria [11], we hypothesized that this invasive sponge favours biofilm formation by bacteria during bloom phase. To investigate the interaction of the invasive marine sponge *C. ciocalyptoides* with its microbial environment, we studied the impact of the sponge polysaccharides enriched mucus on the biofilm formation by 4 different bacterial strains present in the surrounding seawater including *E. coli* and *V. splendidus*. Other roles of those polysaccharides in the marine environment are also discussed.

Materials and Methods

Bacterial strains and culture media

Four bacterial strains were used in this study. *Escherichia coli* DH5-*α* strain *(E. coli)* (Biomedal) was grown at 37°C on Lysogeny Broth (LB) medium composed of 10 g/L NaCl, 5 g/L yeast extract and 10 g/L tryp-tone in distilled water. *Paracoccus* sp. 4M6 (P. 4M6) and *Pseudoalteromonas* sp. 3J6 (P. 3J6) strains were isolated from the marine environment in the Golfe du Morbihan (Brittany) as previously described [12]. *Vibrio splendidus* 02/041 *(V. sp.)* strain was isolated from *Crassostrea gigas* at Argenton (Brittany) [13]. The *V. splendidus* 02/041, *Paracoccus* sp. 4M6 and *Pseudoalteromonas* sp. 3J6 strains were grown on Lysogeny Broth Salt (LBS) medium composed of 20g/L NaCl, 5g/L yeast extract and 10g/L tryptone in distilled water. Bacteria were cultivated 24h at 20°C with shaking (120rpm). Bacterial growth was studied in 24-well microplates Costar® containing 2mL of medium. Microplates were placed on a rotary shaker at 120rpm at 20°C. Growth was monitored over time by measuring the absorbance at 600 nm every 30 minutes.

Extraction and purification of sponge polysaccharides

The marine sponge *C. ciocalyptoides* was collected by SCUBA diving in the Ria of Etel (Brittany, France) during spring and transported to the laboratory within cooled bags containing seawater. Fresh sponges (3.5kg) were simply squeezed upon a funnel to extract 1L of a mucus. This viscous solution was then extracted from seawater by absolute ethanol precipitation (1:1 v/v) at 5°C overnight. After centrifugation (8000rpm, 5min. at 4°C), the precipitate was then dissolved in distilled water in a water bath at 35°C, desalted on a 6-8 kDa dialysis membrane tubing (Spectra/PorTM, SpectrumTM) and lyophilized (Cryotec) to yield 2g (0.33% dry weight) of a polysaccharide enriched fraction (EPS). Protein content (less than 2%) was determined by the Bradford's method using bovine serum albumin as the standard. Powder was stored at – 20°C until biological evaluation.

Antibacterial assays

The disc diffusion method was used to evaluate the bactericidal effect of the polysaccharidic fraction. Briefly, on Petri dishes seeded with E. coli DH5-*α*, *V. splendidus* 02/041, *Pseudoalteromonas* sp. 3J6 or *Paracoccus* sp. 4M6, 10*μ*L of a solution of 20mg/mL polysaccharides in distilled water were loaded onto 9 mm cellulose disc. The plates were incubated at 20°C for 48h. Presence of clear halos around the discs indicates growth inhibition. Experiments were performed in triplicate. Results (data not shown) indicated no bactericidal effects at a concentration of 20mg/mL.

Bacterial adherence and biofilm formation

For bioassays, polysaccharides were dissolved in culture media at a maximal concentration of 20 mg/mL and sterilized by filtration through 0.20*μ*m membranes. As previously described [14], adherence and biofilm were realized on glass coverslips in a 3 independent channels of adherence or flow cells (channel dimensions, 1x4x40 mm, Technical University of Denmark Systems Biology, Denmark). The adherence step consisted in injecting in each flow cell 0.5mL of a post-exponential bacteria culture adjusted at 0.5 OD600 with ASW (Artificial Sea Water at 35g/L) (Sigma-Aldrich) without (control) or with EPS (20mg/mL) and let incubated at room temperature (20°C) for 2h without flow to allow bacterial attachment on a sterilized glass coverslip. After incubation, the samples were rinsed 3 times with ASW to eliminate non-adherent bacteria.

After the adherence phase previously described, the second step consisted in passing a flow of medium (without polysaccharide) in the chamber of adherence at 0.5mL/h for 48h at 20°C to let the formation of a biofilm.

Adherence and biofilm analysis

Adherence and biofilm formation were observed by CLSM (Confocal Laser Scanning Microscopy) using a TCS-SP2 system (Leica Microsystems, Germany) with a 60x oil immersion objective. Bacteria were observed with SytoTM 9 Green Fluorescent Nucleic Acid Stain (Invitrogen) at 5*μ*M (Excitation/Emission (nm): 485/498) during 20min. Channels were observed by CLSM in all their length and nine images were taken at regular intervals using the Leica Confocal® software. At least 6 series of observations

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were realized each time and all the tested strains were replicated three times. A minimum of 18-image stacks was obtained for each strain with or without EPS.

Statistical analysis

Adherence (%), biomass (i.e. the volume of bacteria/glass surface, $\mu m^3/\mu m^2$), average thickness (μm) and maximum thickness (μm) of biofilm were calculated by the Comstat2® software (www.comstat.dk). All statistical analyses were performed with RStudio (R version 4.1.0). The non-parametric Mann-Whitney test was conducted to examine the influence of the polysaccharidic fraction on adherence and biofilm formation by bacteria. Statistical significance was accepted at p-value < 0.01.

Results and Discussion

As expected, the 4 bacterial strains adhered on a glass surface in control conditions (Figure 1). To evaluate the sponge EPS effect, the polysaccharide enriched fraction was dissolved in culture media and evaluated on the adherence step. At a non-bactericidal concentration of 20mg/mL, results indicated for the 4 bacteria strains significant differences of adherence between the 2 conditions (i.e. with or without polysaccharides) (Figures 1 & 2). In the presence of EPS, the adherence of *E. coli* DH5-*α*, *Pseudoalteromonas* sp. 3J6 and *V. splendidus* 02/041 were significantly increased (p-value < 0.01). Among those 3 bacterial strains, the strongest effect was observed on *Vibrio splendidus* adherence which increased by 125% followed by E. coli adherence which increased by 102%. The *Pseudoalteromonas* sp. 3J6 adherence increased moderately but significantly by 33%. In contrast, the adherence by *Paracoccus* sp. 4M6 was significantly reduced by 28% (p-value < 0.01).

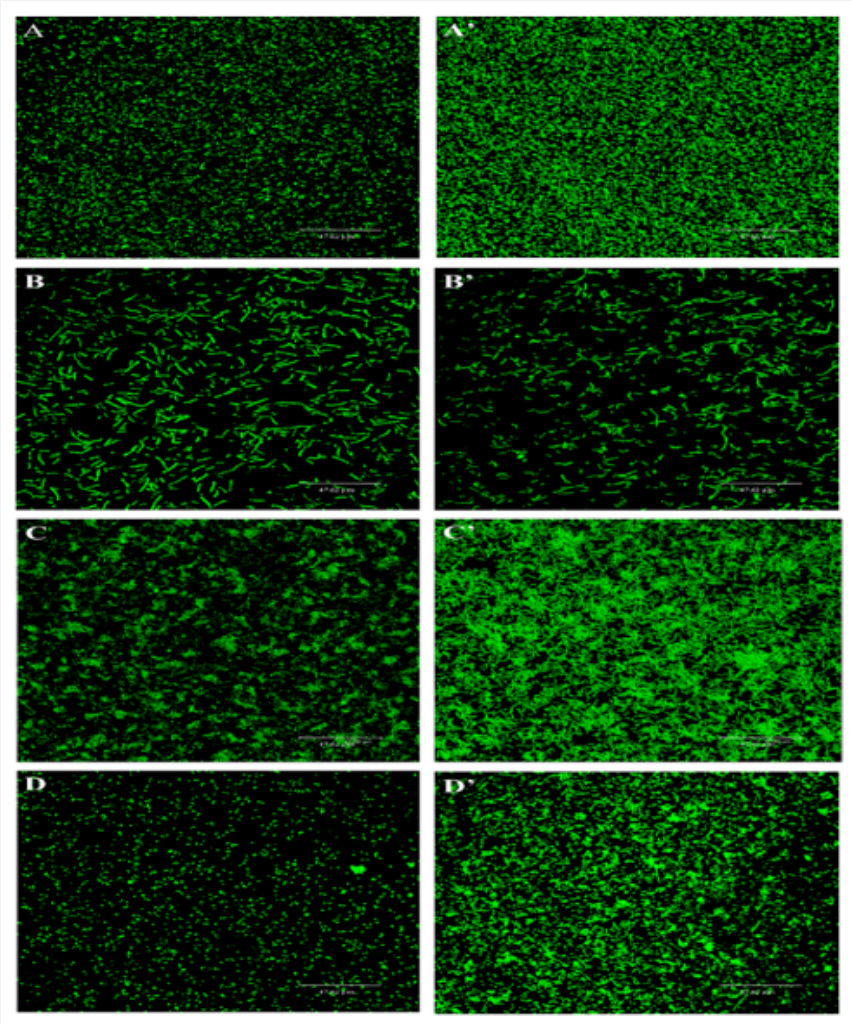

Figure 1: Confocal laser scanning microscopy images of adherence of A) E. coli DH5-α, B) Paracoccus sp. 4M6, C) Pseudoalteromonas sp. 3J6 and D) V. splendidus 02/041 without (left, control) or with (A', B', C' and D', respectively) sponge polysaccharides, after 2h of contact onto glass surface and staining with SytoTM 9 green.

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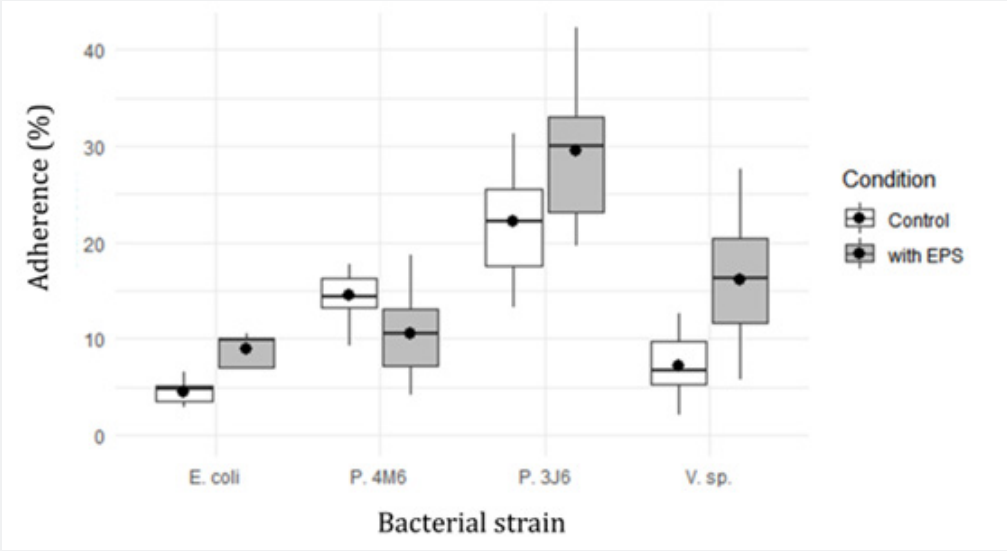

Figure 2: Bacterial adherence (%) on glass surface without (control) or with sponge polysaccharides (E. coli = E. coli DH5-α, P. 4M6 = Paracoccus sp. 4M6, P. 3J6 = Pseudoalteromonas sp. 3J6, V. sp. = Vibrio splendidus).

In presence of polysaccharides, both biomass and thickness of the strains *E. coli* DH5-α, *Pseudoalteromonas* sp. 3J6 and *V. splendidus* 02/041 were significantly increased (Figure 3 & Table 1) (p-value < 0.01). In contrast, biofilm formation by *Paracoccus* sp. 4M6 was significantly reduced (p-value < 0.01).

Table 1: Biofilm growth in flow-cell chambers for 48h after a 2h adherence step without (control) or with sponge polysaccharides (EPS) (*E. coli* = *E. coli* DH5-α, P. 4M6 = *Paracoccus* sp. 4M6, P. 3J6 = *Pseudoalteromonas* sp. 3J6, V. sp. = *Vibrio splendidus*).

	Control			With EPS		
Strain	Biomass ($\mu m^3/\mu m^2$)	Average Thickness (μm)	Maximum Thickness (μm)	Biomass ($\mu m^3/\mu m^2$)	Average Thickness (μm)	Maximum Thickness (μm)
E. coli	1.85±0.81	14.4±3.86	21.7±2.46	4.23±2.76	19.34±5.02	33.29±7.67
P. 4M6	8.64±2.67	31.08±9.7	46.5±10.24	0.09±0.06	9.24±2.43	19.22±3.76
P. 3J6	12.99±9.15	31.65±14.84	51.28±13.11	27.24±5.19	47.15±9.48	56.62±11.48
V. sp.	1.43±1.56	22.74±14.66	40.13±16.55	15.8±8.35	75.52±30.78	131.5±29.72

In aqueous environment, any biotic or abiotic surface is overgrown by bacterial biofilm followed by micro- and macro-foulers within days or weeks. Most of the time, this phenomenon occurs in several distinct stages: reversible attachment of planktonic bacteria, irreversible attachment and EPS secretion, biofilm maturation, detachment [15,16]. To limit biofouling and exhibit clean surface, soft-bodied marine invertebrates such as marine sponges produce antibiofilm natural substances. For example, pyrrole-2-amino-imidazole alkaloids such as oroidin isolated from Agelasidae are considered as an interesting source for biofilm modulators [17]. Polysaccharides from various natural sources also showed antibiofilm activities [18,19]. Among those polysaccharides, chitosan is probably the most promising antibiofilm polymer due to its biodegradable and biocompatible properties [20]. Other marine sources such as sponges and/or their associated micro-organisms also produce antibiofilm polysaccharides [21]. For example, a highly anionic polysaccharide isolated from a Spongia officinalis associated strain of Bacillus licheniformis was shown to inhibit adherence and biofilm formation of bacterial strains [22]. A sponge-associated Enterobacter strain isolated from the Brazilian sponge *Oscarella* spp. was also shown to produce polysaccharides inhibiting biofilm formation by *Staphylococcus* spp. [23]. In our study, the sulphated polysaccharide enriched fraction secreted by the marine sponge *C. ciocalyptoides* showed antibiofilm activities against the commensal bacteria *Paracoccus* sp. 4M6. As many natural compounds isolated from marine invertebrates, polysaccharides secreted by *C. ciocalyptoides* are probably produced by sponge associated micro-organisms rather than the sponge itself. In our case, the sponge associated micro-organism responsible for the production of those polysaccharides still remains unknown. In contrast, the same polysaccharidic fraction was shown to promote *E. coli*, *Pseudoalteromonoas* sp., and *Vibrio splendidus* biofilm formations. Polysaccharides are the major component of the extracellular matrix in many bacterial biofilms and are necessary for their formation and stabilization. While

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polysaccharides production by bacteria often correlated with their own biofilm formation, data concerning the promotion of biofilm formation by polysaccharides from exogenous origin are scarce. Since in the shellfish industry bacterial infections that lead to the formation of biofilms pose a serious threat to the economy, further studies are needed to understand the exogenous factors that modulate biofilm formations.

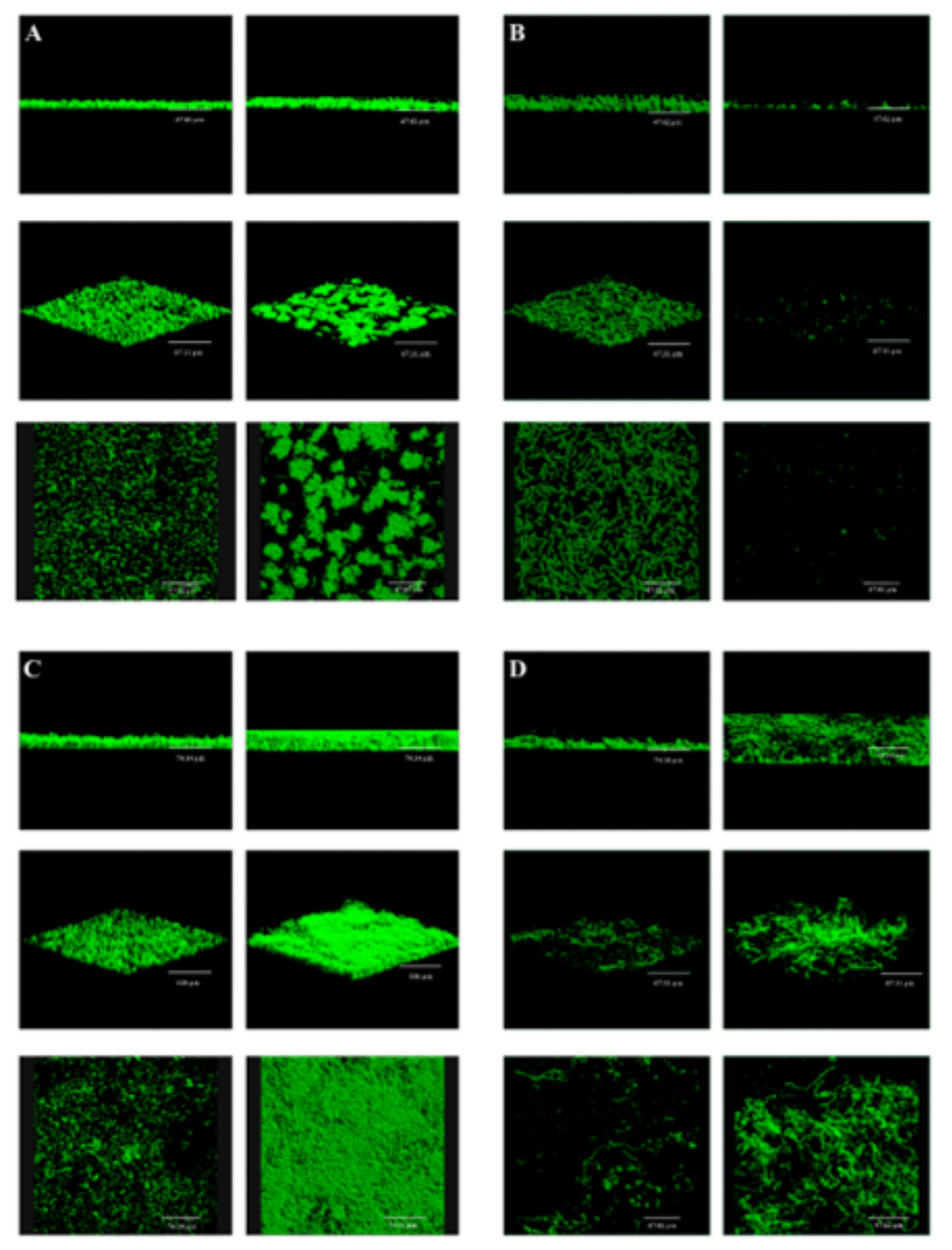

Figure 3: Confocal laser scanning microscopy images of biofilm formation by A) E. coli DH5-α, B) Paracoccus sp. 4M6, C) Pseudoalteromonas sp. 3J6 and D) V. splendidus 02/041 in a flow-cell chambers for 48 h after a 2 h adherence step without (left, control) or with (right) sponge polysaccharides. Strains were stained with Syto 9. Projections in the x-y plane are presented. Images are representative of at least 3 independent experiments.

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In most cases, invasive species modify habitats, change community structure, impact ecosystem ser-vices and threat socio-economic activities [24-27]. In addition, invasive species can act as a competent host for native pathogens thus amplifying transmission dynamics of pathogens populations [28]. Ultimately that can lead to increased infection levels in native hosts defined as "parasite spillback" [29] with economic and sanitary consequences including on aquaculture [30]. Due the invasive character of the marine sponge *Cel-todoryx ciocalyptoides* and its close distribution to shellfish areas [6-8], it is feared that *C. ciocalyptoides* polysaccharides may represent an additional threat to shellfish aquaculture by promoting biofilm formation by pathogens.

From an ecological point of view, it is of interest to understand the interaction between the marine sponge *C. ciocalyptoides* and environmental bacteria including pathogens. It has been reported that some marine organisms can tolerate bacterial epibiosis and even use this epibiotic biofilm as a second skin [31]. It will be worthy to study how well adapted organisms to disturbances such as invasive species mediate interactions with bacterial epibiosis to confer novel advantages in their novel and changing environment. For example, the genus *Pseudoalteromonas* is frequently associated with marine invertebrates and displays several biological activities [32]. Interestingly, in our study, the polysaccharidic fraction obtained from *C. ciocalyptoides* was shown to enhance biofilm formation by *Pseudoalteromonas* sp. 3J6. One other hypothesis to explain the invasiveness of the marine sponge *C. ciocalyptoides* could be that the sponge produces sufficient amounts of sulfated polysaccharides to cover biotic or abiotic substrates and favour biofilm formation thus facilitating sponge larvae settlement or sponge cells confluence by cell-cell adherence and recognition [33,34]. Sulfated polysaccharides from the marine sponge *Hymeniacidon heliophila* are known to be involved in cell-cell adherence and recognition in sponges forming small cellular aggregates or primmorphs [35,36]. Whatever, the ecological role of this polysaccharide fraction and its potential contribution to the invasiveness process of this exotic sponge species remain unclear.

Conclusion

In this study, the polysaccharide enriched fraction secreted by the marine sponge *C. ciocalyptoides* showed antibiofilm activities against the commensal bacteria *Paracoccus* sp. 4M6 by reducing both bacterial adherence and biofilm biomass and thickness. In contrast, the polysaccharide enriched fraction was shown to promote *E. coli*, *Pseudoalteromonoas* sp. 3J6, and *Vibrio splendidus* biofilm formations. The consequence is that this sponge-polysaccharides secretion may impact seawater quality through pathogens spillback with sanitary and economic impacts on shellfish farming in the context of a changing climate. Since *C. ciocalyptoides* can be viewed as a reservoir or a vector of biological contaminants, further strategies to control the expansion of *C. ciocalyptoides* are required.

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