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Cultivable microbiota associated with *Aurelia aurita* and *Mnemiopsis leidyi*

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Abstract

The associated microbiota of marine invertebrates plays an important role to the host in relation to fitness, health, and homeostasis. Cooperative and competitive interactions between bacteria, due to release of, for example, antibacterial substances and quorum sensing (QS)/quorum quenching (QQ) molecules, ultimately affect the establishment and dynamics of the associated microbial community. Aiming to address interspecies competition of cultivable microbes associated with emerging model species of the basal animal phyla Cnidaria (*Aurelia aurita)* and Ctenophora (*Mnemiopsis leidyi*), we performed a classical isolation approach. Overall, 84 bacteria were isolated from *A. aurita* medusae and polyps, 64 bacteria from *M. leidyi*, and 83 bacteria from ambient seawater, followed by taxonomically classification by 16S rRNA gene analysis. The results show that *A. aurita* and *M. leidyi* harbor a cultivable core microbiome consisting of typical marine ubiquitous bacteria also found in the ambient seawater. However, several bacteria were restricted to one host suggesting host-specific microbial community patterns. Interbacterial interactions were assessed by (a) a growth inhibition assay and (b) QS interference screening assay. Out of 231 isolates, 4 bacterial isolates inhibited growth of 17 isolates on agar plates. Moreover, 121 of the 231 isolates showed QS-interfering activities. They interfered with the acyl-homoserine lactone (AHL)-based communication, of which 21 showed simultaneous interference with autoinducer 2. Overall, this study provides insights into the cultivable part of the microbiota associated with two environmentally important marine non-model organisms and into interbacterial interactions, which are most likely considerably involved in shaping a healthy and resilient microbiota.

KEYWORDS

Aurelia aurita, cultivation, gelatinous zooplankton, *Mnemiopsis leidyi*, quorum quenching

1 | INTRODUCTION

The marine environment covers more than 70% of the world's surface and harbors approximately 3.6×10^{28} microorganisms (Amann, Ludwig, & Schleifer, 1995; Flemming & Wuertz, 2019; Magnabosco et al., 2018; Whitman, Coleman, & Wiebe, 1998). Marine microbial communities are highly diverse and have evolved under a variety of ecological conditions and selection pressures (Haubold & Rheinheimer, 1992). Those microbes are also known to form beneficial symbiotic relationships with various marine multicellular hosts, for example, sponges, corals, squids, and jellyfishes, and are assumed to produce unique biologically active compounds important for the homoeostasis of the host, which are additionally often pharmacologically valuable compounds (Bosch & McFall-Ngai, 2011; McFall-Ngai et al., 2013). Recently, the potential role of associated microbiota became an important research focus in the fields of zoology, botany, ecology, and medicine, since each multicellular organism can be regarded as an entity with its associated microbes as a so-called "metaorganism" or "holobiont." The microbes most likely have crucial functions for fitness and health of the host (Bosch & McFall-Ngai, 2011; McFall-Ngai et al., 2013), in addition to their function for the ecological role of the metaorganism in the respective environment. The role of bacteria during the development of various organisms, such as humans, as well as their importance for the host's resilience in the control of pathogens and prevention of inflammatory diseases, has been intensively studied in recent years (reviewed in (Sommer, Anderson, Bharti, Raes, & Rosenstiel, 2017)). These studies also showed that the interactions within a metaorganism are complex. In order to understand this complexity, research studies addressing the impact of the microbiota on a host have mostly utilized well-studied model organisms, such as the *Drosophila* and mouse model. To understand the long-term evolutionary origin of the metaorganism, however, additional (model) organisms are urgently needed (Dawson & Martin, 2001; Jaspers, Fraune, et al., 2019). Here, evolutionarily ancient organisms, which are located at the base of the metazoan tree of life, are expected to provide important insight into host–microbe interactions. Two basal metazoan species, which are widely distributed in marine environments, partly due to their large adaptability (Dawson & Jacobs, 2001; Jaspers, Huwer, Weiland-Bräuer, & Clemmesen, 2018), are the moon jellyfish *Aurelia aurita* and the comb jelly *Mnemiopsis leidyi* (Figure 1a). Their ecological impacts are widely recognized (Bayha & Graham, 2014; Jaspers, Huwer, Antajan, et al., 2018), but the characterization of their associated microbial communities and interactions lacks behind; however, the relatively simple morphology with only two tissue layers as surfaces for microbial colonization definitely allows for such studies.

A. aurita is one of the most widely distributed Scyphozoans (Cnidaria) featuring a complex life cycle. In its diphasic life cycle, *A. aurita* alternates between a free-living pelagic medusa and a sessile polyp (McFall-Ngai et al., 2013). In its different successive stages of

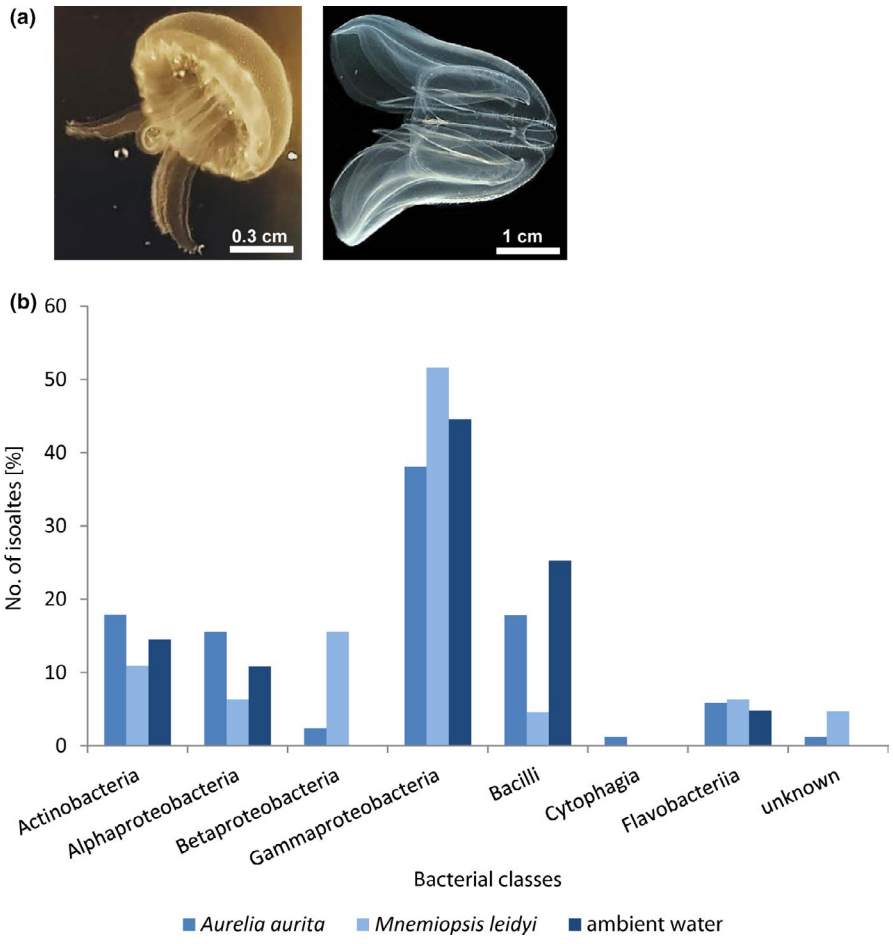

FIGURE 1 Taxonomic classification of isolates. (a) *Aurelia aurita* (left panel) and *Mnemiopsis leidyi* (right panel) (b) Bar plot represents classification of bacterial isolates to class level in percentage.

life cycle—planula larva, sessile polyp, pelagic ephyra, and medusa—*A. aurita* is adapted to different marine environmental factors, for example, salinity, temperature, and food spectrum (Fuqua, Winans, & Greenberg, 1996). In a recent study, we disclosed that those different life stage and different compartments of a medusa as well as different subpopulations harbor distinct, specific microbiota (Weiland-Brauer, Neulinger, et al., 2015). The comb jelly *M. leidyi* (Ctenophora) is one of the most successful invasive marine species worldwide (Bayha & Graham, 2014). *M. leidyi* features an unusual mode of reproduction so-called dissogony (Jaspers et al., 2012), where small larval stages before metamorphosis are already sexually reproducing, while they also reproduce again after metamorphosis in the adult stage as simultaneous hermaphrodites (Sasson & Ryan, 2016). Although those jellies possess only two tissue layers for bacterial colonization, interactions at those interfaces can be manifold and take place between the host and the colonizing bacteria and among the bacteria.

Current molecular high-throughput techniques, like deep sequencing, are preferred methods to analyze such complex microbial communities and interactions (Lagkouvardos, Overmann, & Clavel, 2017). They enable the identification of microbes, normally missed by cultivation-based approaches, and ultimately allow for a broader picture of the entire environmental network (Lagkouvardos et al., 2017). However, these metagenomics-based approaches lack the possibility for additional experimental manipulation studies. Although the cultivation of certain bacteria is still challenging, several recent studies showed that the cultivation of host-associated bacteria is urgently needed to better study and understand their function in a metaorganism context (Esser et al., 2018).

Consequently, this study aimed to isolate bacterial colonizers of *A. aurita* and *M. leidyi* to disclose potentially specific microbial community patterns of these gelatinous zooplankton species compared to the ambient seawater as well as to compare the cultivable community pattern to the reported microbial diversity based on 16S rRNA amplicon sequencing. The generation of such a bacterial archive of isolates is crucial for future colonization experiments. Finally, it was also intended to elucidate interbacterial interactions, for example, potential bacterial competition and quorum quenching (QQ) activities. Such bioactive compounds might be important for the maintenance of a healthy microbiota by defending competitors or pathogens due to inhibition of their growth or interference with their cell–cell communication.

2 | MATERIALS AND METHODS

2.1 | Sampling of *A. aurita* and *M. leidyi*

Individual *A. aurita* (Linnaeus) medusae (with mean size umbrella diameter of 22 cm) were sampled from one location in the Kiel Bight, Baltic Sea (54°32.8′N, 10°14.7′E), in June 2015 using a dip net. Accordingly, *M. leidyi* (Agassiz) adults (mean size of 4 cm) were sampled from the same location in May 2017. The animals were immediately transported to the laboratory and washed thoroughly with autoclaved artificial seawater to remove nonassociated microbes. Additionally, individuals were kept in artificial seawater (Tropical Marine Salts, 18 practical salinity units (PSU)) for ten days before thoroughly washing with autoclaved artificial seawater to remove nonassociated microbes and considered as husbandry individuals. In addition, *A. aurita* polyps of subpopulations Baltic Sea, North Sea, and North Atlantic (Roscoff) were kept in artificial seawater (Tropical Marine Salts, 18 PSU (Baltic Sea) and 30 PSU (North Sea, North Atlantic)) in 2-L plastic tanks originating from natural polyps sampled in the respective locations almost 15 years ago. Prior to bacterial enrichment and isolation, polyps were not fed with freshly hatched (unmanipulated) *Artemia salina* for at least three days to ensure empty guts and consequently least possible contamination with microbes. Moreover, 1L ambient water (Baltic Sea 54°32.8′N, 10°14.7′E; artificial seawater 18 and 30 PSU) was filtrated (0.22 µm pores, Millipore, 45 mm diameter) to enrich bacterial cells for further isolation.

2.2 | Bacterial enrichment and isolation

Bacterial enrichment and isolation were performed with sterile cotton swabs from the surface of the umbrella of native and kept *A. aurita* as well as *M. leidyi* individuals (in total 10 medusae of each phylum were sampled), homogenized single *A. aurita* polyps of different subpopulations, and filters derived from ambient seawater filtration. In order to ensure high diversity during the isolation procedure, swabs, 100 µL of homogenized animal tissues, and ¼ of a filter were streaked/plated onto three different solid media (Marine Bouillon (Sizemore & Stevenson, 1970), R2A (Reasoner & Geldreich, 1985), Plate Count Medium (Buchbinder et al., 1951)) and all plates were incubated at 4, 20, and 30°C, respectively, for at least 16 hr up to one week (for 4°C incubations). Obtained single colonies were picked and purified by streaking at least three times on the respective agar plates and incubated at the initial incubation temperature. Morphologically similar colonies (i. a. colony size, colony color, and colony shape) from different samples as well as morphologically different colonies from all samples were grown in the respective liquid medium at the respective incubation temperature. Pure cultures were stored as glycerol stocks (10%) at −80°C and subsequently were taxonomically classified by 16S rRNA analysis.

2.3 | Nucleic acid isolation

High-molecular weight genomic DNA of bacteria was isolated from 5 ml overnight cultures using the Wizard Genomic DNA Isolation Kit (Promega) according to the manufacturer's instructions.

2.4 | 16S rRNA gene analysis

16S rRNA genes were PCR-amplified from 50 ng isolated genomic DNA using the bacterium-specific primer 27F (5′-AGAGTTTGATCCTGGCTCAG-3′) and the universal primer

1492R (5′-GGTTACCTTGTTACGACTT-3′) (Lane, 1991) resulting in a 1.5-kb bacterial PCR fragment. The fragment sequences were determined by the sequencing facility at the Institute of Clinical Molecular Biology, University of Kiel, Kiel, Germany (IKMB), using primer 27F (Phred quality score of 20). Sequence data are deposited under GenBank accession numbers MK967003–MK967227.

2.5 | Growth inhibition assay (modified after (Moran, Crank, Ghabban, & Horsburgh, 2016))

First, all 231 isolated bacterial strains were grown on MB agar plates at 30 °C overnight (Moran, Crank, Ghabban, & Horsburgh, 2016). Out of those 231 strains, 203 formed compact bacterial lawns on the agar plates under the selected growth conditions and were subsequently used for the growth inhibition assay as follows. First, agar disks with a diameter of 5 mm were cut out of those incubated agar plates comprising the respective living bacterial strain at the surface. Second, agar disks were placed in prepared accurately fitting cavities of freshly generated agar plates (screening plates) on which bacterial strains to be tested have been plated (100 µl of an overnight culture). All 203 strains were tested against each other. Screening plates were incubated overnight at 30°C. Growth inhibition zones were detected, and the assay was verified with at least two biological replicates each with two technical replicates of initially identified inhibiting bacterial strains. Finally, inhibition zones were measured from the center of the agar disk to the edge of the halo. Moreover, an isolate was defined to have a growth-promoting effect on the strain present on the agar disk when this bacterium was overgrowing the edge of the agar disk.

2.6 | Identification of quorum sensing-interfering activities (QQ activities) of isolates

Quorum quenching assays with bacterial isolates were performed as described in Weiland-Bräuer, Kisch, Pinnow, Liese, and Schmitz (2016); Weiland-Brauer, Pinnow, and Schmitz (2015). Briefly, QQ screening plates were prepared as follows: LB agar containing 0.8% agar at 50°C was supplemented with final concentrations of 100 µM N-(β-ketocaproyl)-L-homoserine lactone (Sigma-Aldrich, Munich, Germany), 100 g/mL ampicillin, 30 g/mL kanamycin, and 10% (vol/vol) exponentially growing culture of the reporter strain AI1-QQ.1. LB agar plates were coated with the top agar mixture. AI-2 quorum quenching plates were prepared similarly, but the agar was supplemented with final concentrations of 50 mM 4-hydroxy-5-methyl-3-furanone (Sigma-Aldrich, Munich, Germany), 100 g/mL ampicillin, 30 g/mL kanamycin, and 5% (vol/vol) exponentially growing culture of the reporter strain AI2-QQ.1. After 10 min of solidifying the top agar, 5 µL of the test substances was applied, followed by overnight incubation at 37°C. QQ activities were visualized by growth of the respective reporter strain. Preparation of cell-free cell extracts and culture supernatants from isolates was performed after growth of bacterial isolates in 5 mL of the respective isolation medium (MB, R2A, and PCA) overnight at the respective isolation temperature (4, 30, and 37°C) and 120 rpm. Cells were harvested by centrifugation at 7,000 ×g, and the culture supernatant was subsequently filtered using 0.2-µm centrifugal filter units (Carl Roth, Karlsruhe, Germany). The cell extracts were prepared from the cell pellet using the Geno/Grinder 2000 (BT&C/OPS Diagnostics, Bridgewater, NJ). The cell pellet was resuspended in 500 µL 50 mM Tris-HCl (pH 8.0), and glass beads (0.1 mm and 2.5 mm) were added prior to mechanical cell disruption for 6 min at 1,300 strokes/min at RT. After centrifugation at 10,000 ×g and 4°C for 25 min, the cell extracts were filtered through 0.2-µm filter units. Cell-free culture supernatants and cell extracts were stored at 4°C until used in the QQ assay. The reporter strains are only able to grow in the top agar when QS-interfering biomolecule is present in the culture supernatant or cell extract, since a lethal gene is under the control of a promoter, which is induced in the presence of the autoinducer (see details of the genetic/strategic design of the reporter strain in Weiland-Brauer, Pinnow, et al. (2015).

3 | RESULTS AND DISCUSSION

3.1 | Cultivated part of jelly-associated bacteria reflects host-specific microbiota

The overall goal of this study was to enrich and isolate bacterial colonizers of the moon jellyfish *A. aurita* and the comb jelly *M. leidyi* to unravel potential host-specific patterns of their microbial community structure based on a cultivation-dependent approach. In the long run, we aim to use these respective isolates in future controlled laboratory experiments to study their function in the metaorganisms in more detail (e.g., by recolonization of germ-free hosts with manipulated microbial communities). Moreover, we aimed to gain insights into interbacterial interactions and evaluate the isolates concerning their ability to interfere with growth of their neighbors and with QS, interactions that might affect the establishment of the host-associated microbiota.

A classical isolation approach was performed using three different solid media at three different incubation temperatures ranging from 4 to 20°C up to 30°C, thus comprising the range of current and expected ocean surface temperatures to ensure high diversity in enriched bacteria. Plate count agar was used for enrichment of the viable bacterial fraction of a sample without any selection, whereas R2A was used for enrichment of heterotrophic, aquatic bacteria, which tend to be slow-growing species and might be suppressed by faster-growing species on a richer culture medium. Marine Bouillon was used to select for marine bacteria preferring high-salt conditions. As expected, enrichment on Marine Bouillon resulted in highest diversity and colony-forming units (cfu) on plates, since the simulation of marine conditions in parallel to rich nutrient supply promoted bacterial growth even for low abundant ones. Only single and less diverse colonies were revealed on R2A agar. Highest cfu were further detected when incubated at 20°C in particular when

TABLE 1 Presence of isolates in different sample types

	Aurelia aurita					*Mnemiopsis leidyi*		Ambient water		
	Native	Husbandry				Native	Husbandry	Native	Artificial	
	Medusa	Medusa	Polyp			Adults	Adults			
	Baltic Sea	Baltic Sea		North Sea	North Atlantic	Baltic Sea	Baltic Sea	Baltic Sea	18 PSU	30 PSU
Acinetobacter	0	0	0	0	0	1	0	0	0	0
Aeromonas	0	0	0	0	0	1	0	0	0	0
Alteromonas	1	0	0	1	0	3	2	0	4	3
Arthrobacter	0	0	3	0	0	0	0	0	0	0
Bacillus	3	1	1	0	0	1	0	0	0	7
Brevibacterium	0	0	0	1	0	0	0	0	0	4
Celeribacter	0	0	0	0	0	0	0	0	4	1
Chryseobacterium	0	0	0	1	0	0	1	0	0	1
Cobetia	0	1	0	0	0	0	0	0	0	2
Colwellia	0	0	0	0	0	1	0	0	0	0
Corynebacterium	0	0	0	0	0	0	0	0	1	0
Enterococcus	0	0	1	2	1	0	0	0	0	0
Exiguobacterium	0	0	0	0	0	1	0	0	0	0
Fictibacillus	0	0	0	0	0	0	0	1	0	1
Gordonia	0	0	1	0	0	0	0	0	0	0
Halomonas	0	0	0	0	0	0	0	0	0	1
Hydrogenophaga	0	0	0	0	0	0	1	0	0	0
Hymenobacter	0	0	0	1	0	0	0	0	0	0
Lacinutrix	0	0	0	0	0	1	0	0	0	0
Leisingera	0	0	0	0	0	1	0	0	0	0
Luteococcus	0	0	0	1	1	0	0	0	1	0
Maribacter	0	1	0	0	0	0	0	0	0	3
Marinobacter	0	0	0	0	0	0	0	0	1	0
Marinomonas	0	0	0	0	0	2	0	0	0	0
Microbacterium	1	0	0	0	0	2	1	0	0	1
Micrococcus	0	0	1	0	1	1	0	0	1	2
Moraxella	0	0	0	0	1	0	0	0	1	0
Ochrobactrum	0	0	0	0	0	0	1	0	0	0
Olleya	0	0	1	1	1	1	0	0	0	0
Pantoea	0	0	0	0	0	1	0	0	0	0
Paracoccus	0	0	1	0	0	0	0	0	0	0
Paraglaciecola	0	0	0	0	1	0	0	0	1	0
Phaeobacter	0	0	0	0	0	0	0	0	1	0
Phaeocystidibacter	0	0	0	0	0	1	0	0	0	0
Pseudoalteromonas	1	2	1	3	2	10	2	3	1	3
Pseudoclavibacter	0	0	0	0	0	2	0	0	11	0
Pseudomonas	7	0	4	0	2	4	1	1	0	3
Psychrobacter	0	0	0	0	0	1	0	0	0	0
Rhodococcus	0	0	0	2	2	1	0	0	1	0
Ruegeria	0	0	2	1	1	0	0	0	0	0
Sagittula	0	0	0	0	0	1	0	0	0	0
Salinibacterium	0	0	0	0	0	0	0	0	1	2
Serratia plymuthica	0	0	0	0	0	0	0	1	0	0
Shewanella	0	0	0	2	0	8	1	0	0	0
Staphylococcus	1	1	2	0	3	1	1	0	8	2
Streptococcus	0	0	0	1	0	0	0	0	0	0
Sulfitobacter	1	2	1	2	2	0	0	0	1	2
Thalassomonas	0	0	0	0	0	0	1	0	0	0
Vibrio	2	0	3	0	0	2	2	0	0	0
Uncultured bacterium	0	0	0	0	0	1	1	0	1	0
TOTAL No. of isolates	17	8	22	19	18	49	15	6	39	38

Presence and abundances (based on total number in percentage per sample, visualized as bars) of isolates in different sample types on genus level.

compared to 4°C best matching ocean surface temperatures in summer. In total, we isolated 84 bacterial strains from *A. aurita* (Table 1 and Table A1; Accession No. MK967003–MK967227). In more detail, 17 bacteria were isolated from the umbrella surface of native Baltic Sea medusae and 8 bacteria from cultured medusa. From the benthic polyps cultured in the laboratory, 22 bacteria were isolated from the Baltic Sea subpopulation, 19 from the North Sea subpopulation, and 18 from the North Atlantic subpopulation (Table 1 and Table A1). The isolation procedure from *M. leidyi* resulted in the identification of 64 bacteria (Table 1 and Table A1), 49 bacteria were enriched from native Baltic Sea individuals and 15 from cultured ones. Moreover, 83 bacteria were isolated from the ambient seawater (Table 1 and Table A1). 16S rRNA gene analyses revealed the identification of eight different bacterial classes (Figure 1), representing 28 families

and 51 genera. In general, distinct differences in the microbial compositions were observed using the cultivation approach between ambient seawater and the two gelatinous zooplankton species (summarized in Figure 1, Table 1 and Table A1). Representatives of the classes Betaproteobacteria, Cytophagia, and unclassified bacteria were shown to be present on the surfaces of the gelatinous zooplankton organisms, but were not isolated from the surrounding seawater samples (Figure 1). Likewise, several bacteria were exclusively isolated from the ambient seawater and assigned to the genera *Celeribacter*, *Corynebacterium*, *Fictibacillus*, *Halomonas*, *Marinobacter*, *Salinibacterium*, and *Serratia* (Table 1 and Table A1). All mentioned bacteria are typically found in the marine environment, some of them also associated with marine eukaryotes (Egerton, Culloty, Whooley, Stanton, & Ross, 2018; Martin et al., 2015; van de Water, Allemand, & Ferrier-Pages, 2018; Weiland-Brauer, Neulinger, et al., 2015). These cultivation-dependent results are in line with several publications demonstrating that the microbiota associated with multicellular eukaryotic host is significantly different to the bacterial communities in the ambient seawater (Egerton et al., 2018; Martin et al., 2015; van de Water et al., 2018; Weiland-Brauer, Neulinger, et al., 2015). This argues for the presence of specific selection mechanisms, both on bacterial and on the host site to establish and maintain such a specific host-associated microbiota (Pietschke et al., 2017; Weiland-Bräuer, Fischer, Pinnow, & Schmitz, 2019). Notable are the frequencies with which the ubiquitous and high abundant occurring bacteria of the genera *Pseudoalteromonas* and *Pseudomonas* were isolated from all samples (Table 1). These occur in open waters, but are also able to colonize animal tissues (Galkiewicz, Pratte, Gray, & Kellogg, 2011; Tarnecki, Patterson, & Arias, 2016). Both genera are well-known marine inhabitants found in symbiotic associations with sponges, corals, and algae and additionally are known for their versatile biotechnological potential with respect to the production of antimicrobials and enzymes of industrial interest (Borchert et al., 2017; Holmström, James, Neilan, White, & Kjelleberg, 1998; Röthig et al., 2016).

Phylogenetic classification revealed that *A. aurita* is colonized by cultivable representatives of genera *Alteromonas*, *Arthrobacter*, *Bacillus*, *Brevibacterium*, *Chryseobacterium*, *Cobetia*, *Enterococcus*, *Gordonia*, *Hymenobacter*, *Luteococcus*, *Maribacter*, *Microbacterium*, *Micrococcus*, *Moraxella*, *Olleya*, *Paracoccus*, *Pseudoalteromonas*, *Pseudomonas*, *Rhodococcus*, *Ruegeria*, *Shewanella*, *Streptococcus Sulfitobacter*, and *Vibrio* (Table 1 and Table A1). In more detail, *Bacillus* was exclusively isolated from Baltic Sea specimens, *Enterococcus* from benthic polyps, and *Luteococcus* from polyps kept under high-salt conditions (30 PSU) (Table 1). Regarding an important function of those bacteria for the host can only be speculated, but the tropodithietic acid-producing genus *Ruegeria* of the Roseobacter clade, which was exclusively isolated from *A. aurita* polyps, is a globally distributed marine bacterial species found primarily in the upper open ocean and has primarily been isolated from marine aquaculture, where *Ruegeria* strains have probiotic potential (Beyersmann et al., 2017; Sonnenschein et al., 2017). Additionally, *Luteococcus* has been isolated from the marine environment and was often found in the intestinal tracts of animals (Fan, Zhang, Li, & Zhang, 2014). A highly specific colonization of *A. aurita* has been previously shown in a 16S rRNA amplicon sequencing approach demonstrating jellyfish-specific microbial patterns, which were even different in different compartments of a medusa, between different subpopulations, and among different life stages (Weiland-Brauer, Neulinger, et al., 2015). The diverse but highly specific colonization of both jellies, *A. aurita* and *M. leidyi*, was recently also demonstrated in a comprehensive microbial community structure analysis (amplicon and metagenomics sequencing) of several metaorganisms (Rausch et al., 2019). In agreement with those reports, all bacteria isolated from *A. aurita* have been found in the respective deposited 16S amplicon data sets (Rausch et al., 2019; Weiland-Brauer, Neulinger, et al., 2015), suggesting that the isolated bacteria indeed reflect the cultivable part of the moon jellyfish microbiota. Besides, our present cultivation-based study likewise indicates host-specific community patterns. Moreover, we were able to cultivate a high proportion of representatives, for *A. aurita* 14 out of 24 genera and for *M. leidyi* 16 out of 19 genera identified by 16S amplicon sequencing (Rausch et al., 2019; Weiland-Brauer, Neulinger, et al., 2015). However, the limitations of the cultivation-dependent approach became apparent for instance on the highly abundant taxon *Mycoplasma*, which was massively detected on the umbrella of *A. aurita* medusa using next-generation sequencing (Weiland-Brauer, Neulinger, et al., 2015), but was not isolated in the present study. The genus *Mycoplasma* is one of the best-known representatives of the bacterial class Mollicutes. *Mycoplasma* often lives in a mutualistic or parasitic lifestyle, but they are also known as commensals in vertebrates and invertebrates (Citti & Blanchard, 2013; Razin, Yogev, & Naot, 1998). Unique characteristics of *Mycoplasma* are the absence of a cell wall, their small cell sizes as well as a reduced genome and a simplified metabolism, which points to an endosymbiotic lifestyle and the requirement of host-specific metabolic compounds for successful growth. So far, *Mycoplasma* was detected in several life stages and subpopulations of *A. aurita* as well as in the sea anemone *Nematostella vectensis* using next-generation sequencing (Daley, Urban-Rich, & Moisander, 2016; Mortzfeld et al.., 2016; Weiland-Brauer, Neulinger, et al., 2015). However, cultivation of the potentially common associate of marine gelatinous zooplankton organisms is extremely challenging due to the mentioned characteristics and novel isolation techniques have to be developed and applied to overcome the bottlenecks in cultivation.

Specific associated bacterial communities can also be proposed for *M. leidyi*, where, likewise, a diverse set of associated colonizers was isolated, which were assigned to the genera *Acinetobacter*, *Aeromonas*, *Alteromonas*, *Bacillus*, *Chryseobacterium*, *Colwellia*, *Exiguobacterium*, *Hydrogenophaga*, *Lacinutrix*, *Leisingeria*, *Marinomonas*, *Microbacterium*, *Micrococcus*, *Ochrobactrum*, *Olleya*, *Pantoea*, *Phaeocystidibacter*, *Pseudoalteromonas*, *Pseudoclavibacter*, *Pseudomonas*, *Psychrobacter*, *Rhodococcus*, *Sagittula*, *Shewanella*, *Staphylococcus*, *Thalassomonas*, and *Vibrio* (Table 1 and Table A1). In addition, bacteria belonging to the genera *Alteromonas*, *Bacillus*, *Chryseobacter*, *Micrococcus*, *Olleya*, *Pseudoalteromonas*, *Pseudomonas*, *Rhodococcus*, *Shewanella*, *Staphylococcus*, and *Vibrio* were isolated from both species, *M. leidyi*

and *A. aurita*, and most of them also from the ambient seawater (Table 1). These bacteria are most likely ubiquitous marine bacteria, whose abundances in the open waters might differ from their abundances on the animals. Several bacteria were exclusively isolated from *M. leidyi*, such as *Acinetobacter*, *Aeromonas*, *Colwellia*, *Exiguobacterium*, *Hydrogenophaga*, *Lacinutrix*, *Marinomonas*, *Ochrobactrum*, *Pantoea*, *Phaeocystidibacter*, *Pseudoclavibacter*, *Psychrobacter*, *Sagittula*, and *Thalassomonas*, which also have been detected in a recent 16S rRNA gene amplification study of the *M. leidyi*-associated microbiota (Jaspers, Weiland-Bräuer, et al., 2019). Several of those bacteria were previously described in association with *M. leidyi* (Daniels & Breitbart, 2012; Hao, Gerdts, Peplies, & Wichels, 2015; Saeedi et al., 2013). For instance, *Aeromonas* was already isolated from *M. leidyi* of the North Sea population (Saeedi et al., 2013), *Marinomonas* was even described as the dominant phylotype of the comb jelly in a 16S amplicon-based study (Hao et al., 2015), and *Colwellia* was isolated from several marine animal and plant tissues (Martin et al., 2015). Besides, *Colwellia* has already been identified on various brown algae and the red alga *Delisea pulchra* using shotgun sequencing, where it was present on diseased thalli and absent from healthy thalli of this red alga (Fernandes, Steinberg, Rusch, Kjelleberg, & Thomas, 2012). However, the hypothesis that those bacteria indeed play crucial roles for the comb jelly, in particular during the invasion process, has still to be proven by functional approaches.

Taken together, our cultivation-dependent approach revealed that the moon jellyfish *A. aurita* and the comb jelly *M. leidyi* harbor a cultivable core microbiota consisting of typically marine and ubiquitous bacteria, which can partly be found in the ambient seawater, but in quite different abundances. These microbes were also found associated with other marine organisms such as brown algae or fish gut (Egerton et al., 2018; Martin et al., 2015; van de Water et al., 2018). In contrast, several bacteria not detected in the ambient water were exclusively isolated from one of the investigated gelatinous zooplankton organisms, suggesting that the animals have their individual host-specific microbial communities, even if they share the same environment. There might be at least three possibilities, why strains were exclusively isolated from the animals, but not from ambient water. The more supposable one is simply based on the abundance of bacteria in ambient water. Bacterial abundancies on the jellies might be much higher than the corresponding colonizer pools in the ambient water, since they might be specifically enriched in the jelly mucus, thus missing them during isolation. Second, there might be a bias during cultivation. Third, bacteria might be vertically transmitted and planula larvae already harbor those bacteria. The metaorganism, as entity of the host and its microbiota, has to control and modulate the microbial colonization of the host tissues to establish and maintain the specific microbiota, which most likely contributes to its overall fitness and health. Ultimately, the established collection of bacterial isolates can now be used for recolonization experiments with artificial (reduced) bacterial communities allowing functional analysis of how the microbes influence the host.

3.2 | Interbacterial interactions control microbial community structure

In nature, bacteria grow in communities, where they are continuously interacting with each other in a cooperative or competitive manner (Geesink et al., 2018). Bacterial community composition and functioning as well as growth and fitness of a single bacterium highly depend on these interactions (Braga, Dourado, & Araújo, 2016; Hibbing, Fuqua, Parsek, & Peterson, 2010; Pande & Kost, 2017), which are often mediated by small molecules secreted by the bacteria. In this respect, the bacterial release of a plethora of primary and secondary metabolites into their environment might play an important role. Particularly, secondary metabolites, which in most cases act as repressing agents, like antibiotics or signaling compounds such as quorum sensing molecules, can have important ecological functions as they can positively or negatively affect the growth of neighboring bacteria (Cornforth & Foster, 2013; Hibbing et al., 2010; Pande & Kost, 2017). For instance, competition between bacteria due to nutritional competition or the production of antimicrobial compounds often leads to exclusion of particular species or strains within a community, consequently often causing community shifts (Sapp et al., 2007). Negative as well as positive bacterial interactions based on competition/cooperation can be monitored with growth inhibition assays as described by Moran *et al.* (Moran et al., 2016). The assay is used to detect growth inhibition and its degree or growth promotion of the neighboring bacteria. Combining such data on bacterial interactions with 16S rRNA community data ultimately

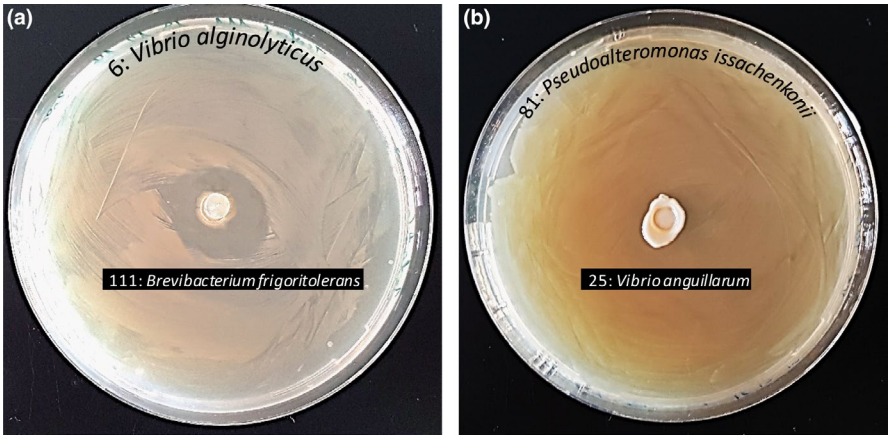

FIGURE 2 Growth inhibition assay. (a) Original photograph shows growth inhibition of isolate 6 (*Vibrio alginolyticus*) in the presence of isolate 111 (*Brevibacterium frigoritolerans*). (b) Original photograph visualizes growth promotion of isolate 25 (*Vibrio anguillarium*) in the presence of isolate 81 (*Pseudoalteromonas issachenkonii*).

TABLE 2 Growth inhibition of neighboring bacteria

Isolate No.	Identified species by 16S rDNA	Inhibition zone [mm]																		
		212	253	122	153	88	188	137	78	125	100	15	126	204	23	6	213	68	70
		Fictibacillus phosphorivorans	*Fictibacillus* sp.	*Paraglaciecola* sp.		*Paracoccus* sp.	*Sulfitobacter pseudonitzschiae*	*Sulfitobacter* sp.								*Vibrio* sp.		*Vibrio gigantis*	
111	*Brevibacterium frigoritolerans*	7 ± 2	3 ± 1	4 ± 1	4 ± 1	6 ± 1	7 ± 2	4 ± 2	3 ± 2	4 ± 1	4 ± 1	2 ± 1	3 ± 2	2 ± 2	2 ± 1	7 ± 3	7 ± 1	6 ± 2	6 ± 3
209		5 ± 1	2 ± 1	4 ± 1	4 ± 2	7 ± 2	7 ± 1	0	0	0	0	6 ± 3	5 ± 1	5 ± 1	0	5 ± 2	8 ± 2	5 ± 2	6 ± 3
210		9 ± 2	3 ± 1	6 ± 1	5 ± 1	6 ± 3	7 ± 1	3 ± 2	3 ± 2	4 ± 1	3 ± 2	2 ± 2	3 ± 2	2 ± 1	0	5 ± 2	9 ± 2	5 ± 1	5 ± 1
113	*Sulfitobacter pontiacus*	6 ± 3	0	3 ± 2	3 ± 1	6 ± 3	6 ± 1	0	0	0	0	0	0	0	0	8 ± 1	6 ± 2	0	0

Note: Isolates 111, 193, 209, and 113 inhibited the growth of the listed bacteria in a growth inhibition assay performed on MB agar plates overnight at 30 °C. The assay was verified with two biological each with two technical replicates. Mean sizes of corrected growth inhibition zones (corrected by 2.5 mm radius of 5-mm agar disk) are listed with respective standard deviations as radius in mm.

enables identifying correlations between microbial community patterns and competitive exclusion (Hibbing et al., 2010; Libberton, Coates, Brockhurst, & Horsburgh, 2014). In the present study, we screened for growth-inhibiting as well as growth-promoting effects of the 231 isolated bacteria (Table A1). Secondary metabolites are already known to play important ecological roles in the interactions with other organisms. For instance, several studies have demonstrated that secondary metabolites produced by bacteria can serve as weapons in microbial warfare or they protect or stimulate the eukaryotic host (Cornforth & Foster, 2013; van Dam, Weinhold, & Garbeva, 2016; Foster & Bell, 2012; Ryu et al., 2003). Therefore, agar disks comprising bacterial lawn of the competing bacteria (feasible for 203 isolates, 28 isolates not used for functional assays are highlighted in Table A1) were placed in prepared cavities of freshly plated agar plates (Figure 2). All isolates were grown on MB-rich medium at 30 °C to make the practical effort appropriate, but being aware of the bias during functional assays. All 203 isolates were tested against each other. Isolates 111, 193, 209 (different *Brevibacterium frigoritolerans* strains), and 113 (*Sulfitobacter pontiacus*) inhibited the growth of 18 isolates belonging to the bacterial families Rhodobacteraceae, Alteromonadaceae, and Vibrionaceae (Table 2) (inhibition zones of 2 to 9 mm). *Brevibacterium* species are strictly aerobic chemo-organotrophic bacteria and *B. frigoritolerans* was already described as isolated from environmental samples, such as different soils (Onraedt, Soetaert, & Vandamme, 2005). Moreover, *Brevibacterium* is known to produce antimicrobial substances, which inhibit the growth of many food poisoning and pathogenic bacteria as well as several yeasts and molds (Bikash, Ghosh, Sienkiewicz, & Krenkel, 2000; Jones & Keddie, 1986; Onraedt et al., 2005; Rattray & Fox, 1999). *Sulfitobacter* widely exists in coastal and open ocean environments and is known for the synthesis of secondary metabolites with antibacterial, antitumor, and antiviral activities (Martins & Carvalho, 2007; Müller, Brümmer, Batel, Müller, & Schröder, 2003). Representatives of the bacterial families inhibited are highly abundant in the marine environment and in particular on gelatinous zooplankton organisms (Elifantz, Horn, Ayon, Cohen, & Minz, 2013; Rausch et al., 2019; Thompson, Iida, & Swings, 2004; Thompson, Randa, et al., 2004; Vergin, Done, Carlson, & Giovannoni, 2013; Weiland-Brauer, Neulinger, et al., 2015), and their colonization and/or abundance might thus be controlled by microbial community members like *Brevibacterium* and *Sulfitobacter*. Moreover, we observed growth-promoting effects of several *Pseudoalteromonas* strains (in total 18) exclusively on *Vibrio* strains (isolates 81, 77, 68, 70, 7, 242, and 213) (Table 3). *Pseudoalteromonas* is a ubiquitous marine bacterium, which often serves as initial bacterial attractant for surrounding bacteria through secretion of chitinases, proteases, or hydrolytic enzymes enabling access to nutrients and thus colonization of biotic surfaces (Everuss, Delpin, & Goodman, 2008). *Pseudoalteromonas* has been identified to support the accumulation of *Vibrio* strains and is consequently often found in aggregates and fouling communities with *Vibrio* (Dang & Lovell, 2002; Long & Azam, 2001; Rao, Webb, & Kjelleberg, 2006), which is in line with our observations on growth-promoting effects of *Pseudoalteromonas* on *Vibrio* strains. Although molecular mechanisms of the identified interactions are so far unknown, the results of this study indicate that neighboring bacteria have competitive and

TABLE 3 Growth promotion by neighboring bacteria

		Growth promoted isolate						
		81	77	68	70	7	242	213
Isolate No.	Identified species by 16S rDNA	*Vibrio anguillarum*		*Vibrio gigantis*		*Vibrio* sp.		
101	*Pseudoalteromonas issachenkonii*	+	+	+	+	+	+	+
25		+	+	-	-	+	+	+
224	*Pseudoalteromonas lipolytica*	+	+	-	-	+	+	+
208	*Pseudoalteromonas prydzensis*	+	+	+	+	+	+	+
91		+	+	+	+	+	+	+
119		+	+	+	+	+	+	+
232	*Pseudoalteromonas* sp.	+	+	-	-	+	+	+
241		+	+	-	-	+	+	+
250		+	+	-	-	+	+	+
4		+	+	-	-	+	+	+
234		+	+	-	-	+	+	+
167		+	+	-	-	+	+	+
65		+	+	-	-	+	+	+
103		+	+	-	-	+	+	+
251	*Pseudoalteromonas tunicata*	+	+	+	+	+	+	+
219		+	+	+	+	+	+	+
243		+	+	+	+	+	+	+
256		+	+	+	+	+	+	+

Note: In total, 18 isolates of genus *Pseudoalteromonas* promoted growth of up to seven gelatinous zooplankton isolates from the genus *Vibrio* in a growth inhibition assay performed on MB agar plates overnight at 30 °C. The assay was verified with two biological each with two technical replicates. Growth promotion is stated as "+", whereas no promoting effect is stated as "-".

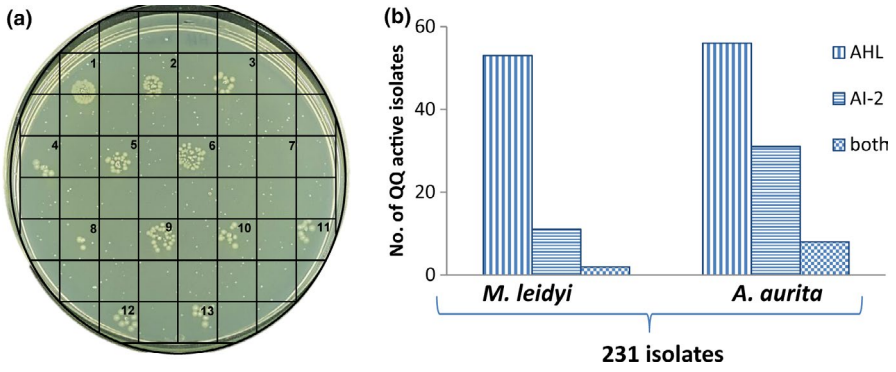

FIGURE 3 Quorum quenching activities of isolates. (a) Original photograph of QQ reporter assay (with AI1-QQ.1) exemplarily showing samples with no (sample 7), low (samples 3, 4, and 8), mid (samples 2, 5, 6, 9, 10, 11, 12, and 13), and high (sample 1) QQ activity of cell-free culture supernatants of selected isolates. (b) Bar plot illustrates QQ activities of bacterial isolates from *Mnemiopsis leidyi* and *Aurelia aurita* against acyl-homoserine lactones (AHL) and autoinducer-2 (AI-2) as well as simultaneous activities.

cooperative relationships, which most likely both affect the bacterial community composition and ultimately impact on a host.

Meanwhile, it is well known that bacterial cell–cell communication, so-called quorum sensing (QS) and its interference (quorum quenching, QQ), has a crucial role in cooperative and competitive microbial interactions, both within a species and between species (Abisado, Benomar, Klaus, Dandekar, & Chandler, 2018). QS is the fundamental system of bacteria regulating cell density-dependent behaviors by the synthesis and detection of small signal molecules (Camilli & Bassler, 2006). Gram-negative bacteria use

N-acetyl-homoserine lactones (AHL) for communication, whereas Gram-positive bacteria use short oligopeptides for QS regulation (Eberl, 1999; Kleerebezem, Quadri, Kuipers, & de Vos, 1997; Miller & Bassler, 2001). Besides this intraspecific communication, AI-2—a furanone-based small molecule—acts as autoinducer in the universal communication among different species (Bassler & Miller, 2013; Bassler, Wright, Showalter, & Silverman, 1993; Chen et al., 2002; Schauder, Shokat, Surette, & Bassler, 2001). QS can be interfered by so-called quorum quenching (QQ) molecules, which, for instance, inactivate autoinducer synthetases, degrade or modify the autoinducers, or interfere with the autoinducer receptors through signal analogs. QQ molecules are synthesized by various bacteria, which ultimately interfere QS-regulated coordinated behaviors like microbial colonization. Thus, QQ activity might represent a crucial mechanism for outcompeting other microbes and might have significant consequences in shaping the structure of polymicrobial communities (Greig & Travisano, 2004; Popat et al., 2015; Rainey & Rainey, 2003; Velicer, Kroos, & Lenski, 2000). Moreover, many bacterial species use QS to control the production of toxins: for example, bacteriocins in *Streptococcus* species (Fontaine et al., 2007; van der Ploeg, 2005) and type VI secretion effectors in *B. thailandensis* (Majerczyk, Schneider, & Greenberg, 2016). Here, QQ activities prevent the increase of potential pathogens and the detrimental altering of community dynamics. QS and its respective interference have meanwhile been evaluated as important to maintain the healthy stability of the microbiota and the metaorganism, and prevent colonization by pathogens (Thompson, Oliveira, & Xavier, 2016; van de Water et al., 2018; Xavier, 2018). Consequently, we evaluated the frequency of QQ activities present in gelatinous zooplankton-associated bacteria. All isolated bacteria were screened for QS-interfering activities using the established reporter strains AI1-QQ.1 and AI2-QQ.1 (Weiland-Brauer, Pinnow, et al., 2015). Screening of cell-free cell extracts and culture supernatants demonstrated that 121 out of the 231 isolated bacteria showed AHL-interfering activities (52%), of which 21 (9%) showed simultaneous interference with AHL and AI-2 (Table A1, Figure 3). In more detail, QQ activities were identified for representatives of Actinobacteria, Bacilli, Flavobacteriia, Alpha-, Beta-, and Gammaproteobacteria, whereas QQ activities were absent for representatives of Actinomycetes and Cytophagia. Notable is the high frequency of QQ activities identified for Gammaproteobacteria mostly represented by *Pseudomonas*, *Pseudoalteromonas*, and *Vibrio*. The high frequency of QS-interfering bacteria strongly argues that QS and the respective interference are important to establish and maintain a healthy and stable microbiota and consequently a healthy metaorganism, for example, by preventing the colonization of pathogens (J. A. Thompson et al., 2016; van de Water et al., 2018; Xavier, 2018). These findings are also in accordance with recent reports on the occurrence of marine bacteria with AHL-QQ activities in pelagic and marine surface-associated communities (Romero, Acuna, & Otero, 2012; Romero, Martin-Cuadrado, Roca-Rivada, Cabello, & Otero, 2011). Remarkably, different isolated strains of bacterial species showed either exclusive interference with AHL or interference with both AHL and AI-2 (Table A1), indicating that different interference mechanisms may have evolved. This is for instance reflected within the *Pseudoalteromonas* species. In summary, the identification of <50% QQ-active bacterial isolates demonstrated a high abundance of QS-interfering bacteria from the marine environment, in particular associated with surfaces of our tested gelatinous zooplankton organisms. We further detected differences in QQ activities on different jellies, which are most likely different not only because of different community patterns, but also because of different QQ expression patterns adapted to ever-changing environmental conditions. Detected QQ activities mainly interfered with Gram-negative AHL communication, which is primarily present in the marine environment (Liu et al., 2018; Rehman & Leiknes, 2018).

Overall, this study provides insights into the cultivable part of the microbiota associated with two gelatinous zooplankton species. In line with deep sequencing approaches, our cultivation-dependent approach revealed that the moon jellyfish *A. aurita* and the comb jelly *M. leidyi* harbor a core microbiota, but both also feature an animal-specific microbiota. A healthy and stable microbiota, which contributes to the overall fitness and health of the metaorganism, has to be established and maintained through attraction and defense mechanisms of the host and its associated microbiota (Bang et al., 2018). We identified interbacterial interactions of those cultivated bacteria in terms of growth-promoting and growth-inhibiting as well as QQ activities. *Brevibacterium frigoritolerans* and *Sulfitobacter* sp. inhibited several bacterial isolates, whereas *Pseudoalteromonas* spp. promoted growth of *Vibrio* strains. Moreover, with over 50% we identified a high frequency of QS-interfering bacteria from the marine environment, which mainly interfere AHL communication primarily present in the marine environment (Liu et al., 2018; Rehman & Leiknes, 2018). Cooperative and competitive interactions, in particular QS and QQ, appear to have an important ecological role in marine environments, particularly in dense microbial communities on biological surfaces. Interbacterial interactions are most likely crucial for maintaining a healthy microbiota of a metaorganism. Thus, identifying and analyzing such attraction or defense mechanisms between microbes as well as between microbes and the host allows gaining insights into the fundamental, but complex interactions within such multi-organismal partnerships and ultimately enables for a better understanding of the establishment and maintenance of a healthy microbiota.

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A former version of this manuscript has been released as a Pre-Print at bioRxiv (The preprint server for biology) under https://www.biorxiv.org/content/10.1101/602268v1 (Prasse, Weiland-Braeuer, Jaspers, Reusch, & Schmitz-Streit, 2019).

CONFLICT OF INTEREST

None declared.

AUTHORS CONTRIBUTION

Nancy Weiland-Bräuer: Conceptualization (equal); Formal analysis (equal); Investigation (lead); Resources (equal); Supervision (equal); Visualization (lead); Writing-original draft (lead); Writing-review & editing (supporting). **Daniela Prasse:** Formal analysis (supporting); Investigation (supporting); Writing-original draft (supporting). **Annika Brauer:** Investigation (supporting). **Cornelia Jaspers:** Resources (supporting); Writing-review & editing (supporting). **Thorsten B. H. Reusch:** Resources (equal); Writing-review & editing (supporting). **Ruth A. Schmitz:** Conceptualization (equal); Funding acquisition (lead); Supervision (equal); Writing-original draft (equal); Writing-review & editing (lead).

ETHICS STATEMENT

None required.

DATA AVAILABILITY STATEMENT

All data generated or analyzed during this study are included in this published article (and its Appendix 1). Sequence data is deposited under GenBank accession numbers MK967003–MK967227.

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APPENDIX 1

TABLE A1 Bacteria isolated from *Aurelia aurita*, *Mnemiopsis leidyi*, and ambient seawater

Isolate	Origin	Best homologue based on 16S full-length rRNA gene (Accession No., identity)	Taxonomic classification				Colony morphology	QQ activity	
			Phylum	Class	Order	Family		AHL	AI-2
14	*A. aurita* medusa Baltic Sea	*Microbacterium* sp. ZV-2-1 (KT597075.1, 99%)	Actinobacteria	Actinobacteria	Actinomycetales	Microbacteriaceae	Light yellow, round	++	-
13	*A. aurita* medusa Baltic Sea	*Bacillus cereus* strain YB1806 (MH633904.1, 99%)	Firmicutes	Bacilli	Bacillales	Bacillaceae	White, oval		
16	*A. aurita* medusa Baltic Sea	*Bacillus* sp. BAM561 (AB330413.1, 98%)	Firmicutes	Bacilli	Bacillales	Bacillaceae	White, round	-	-
17	*A. aurita* medusa Baltic Sea	*Bacillus cereus* (KF624695.1, 98%)	Firmicutes	Bacilli	Bacillales	Bacillaceae	White, roundish	-	-
5	*A. aurita* medusa Baltic Sea	Uncultured *Staphylococcus* sp. (FR690777.1, 93%)	Firmicutes	Bacilli	Bacillales	Staphylococcaceae	White, smeary		
15	*A. aurita* medusa Baltic Sea	*Sulfitobacter* sp. strain B28-5 (MG388121.1, 99%)	Proteobacteria	Alphaproteobacteria	Rhodobacterales	Rhodobacteraceae	White with orange spots, smeary	+++	-
12	*A. aurita* medusa Baltic Sea	*Alteromonas genoviensis* strain PQQ33 (KT730058.1, 99%)	Proteobacteria	Gammaproteobacteria	Alteromonadales	Alteromonadaceae	White, smeary	+++	-
4	*A. aurita* medusa Baltic Sea	*Pseudoalteromonas* sp. DL-6 (CP019770.1, 99%)	Proteobacteria	Gammaproteobacteria	Alteromonadales	Pseudo-alteromonadaceae	White, smeary	-	-
3	*A. aurita* medusa Baltic Sea	*Pseudomonas marincola* strain 002-Na3 (MG456871.1, 94%)	Proteobacteria	Gammaproteobacteria	Pseudomonadales	Pseudomonadaceae	White, round, smeary	-	-
1	*A. aurita* medusa Baltic Sea	*Pseudomonas* sp. JXH-219 (KR012212.1, 100%)	Proteobacteria	Gammaproteobacteria	Pseudomonadales	Pseudomonadaceae	Yellowish-white, smeary	-	-
2	*A. aurita* medusa Baltic Sea	*Pseudomonas* sp. (KR012034.1, 99%)	Proteobacteria	Gammaproteobacteria	Pseudomonadales	Pseudomonadaceae	Orange, round	++	-
8	*A. aurita* medusa Baltic Sea	*Pseudomonas* sp. JXH-340 (KR012328.1, 99%)	Proteobacteria	Gammaproteobacteria	Pseudomonadales	Pseudomonadaceae	Yellow, round	++	-
9	*A. aurita* medusa Baltic Sea	*Pseudomonas* sp. JXH-219 (KR012212.1 99%)	Proteobacteria	Gammaproteobacteria	Pseudomonadales	Pseudomonadaceae	Yellow, roundish	+	-
10	*A. aurita* medusa Baltic Sea	*Pseudomonas* sp. JXH-36 (KR012034.1, 99%)	Proteobacteria	Gammaproteobacteria	Pseudomonadales	Pseudomonadaceae	Yellow, roundish	++	-
11	*A. aurita* medusa Baltic Sea	*Pseudomonas* sp. HN-2 (KJ452338.1, 97%)	Proteobacteria	Gammaproteobacteria	Pseudomonadales	Pseudomonadaceae	Yellow, roundish	++	-

(Continues)

TABLE A1 (Continued)

Isolate	Origin	Best homologue based on 16S full-length rRNA gene (Accession No., identity)	Taxonomic classification				Colony morphology	QQ activity	
			Phylum	Class	Order	Family		AHL	AI-2
6	*A. aurita* medusa Baltic Sea	*Vibrio* sp. Bac180 (KP980718.1, 99%)	Proteobacteria	Gammaproteobacteria	Vibrionales	Vibrionaceae	Light orange in center, round	+++	+
7	*A. aurita* medusa Baltic Sea	*Vibrio* sp. H1309/4.5 (LN871549.1, 97%)	Proteobacteria	Gammaproteobacteria	Vibrionales	Vibrionaceae	White with orange spots, smeary	-	-
24	*A. aurita* medusa Baltic Sea husbandry	*Maribacter* sp. SDRB-Phe2 (MG456900.1, 99%)	Bacteroidetes	Flavobacteriia	Flavobacteriales	Flavobacteriaceae	White-orange, smeary	+	-
22	*A. aurita* medusa Baltic Sea husbandry	*Pseudolateromonas* sp. MACL07 (EF198247.1, 99%)	Bacteroidetes	Flavobacteriia	Flavobacteriales	Flavobacteriaceae	White, smeary		
19	*A. aurita* medusa Baltic Sea husbandry	*Bacillus* sp. strain CL25 (MH605366.1, 99%)	Firmicutes	Bacilli	Bacillales	Bacillaceae	Light orange, round	+	-
18	*A. aurita* medusa Baltic Sea husbandry	*Staphylococcus aureus* subsp. *aureus* JCM 2874 (LC420068.1, 99%)	Firmicutes	Bacilli	Bacillales	Staphylococcaceae	Orange, round	++	-
20	*A. aurita* medusa Baltic Sea husbandry	*Sulfitobacter pontiacus* strain ACBC109 (MK156387.1, 87%)	Proteobacteria	Alphaproteobacteria	Rhodobacterales	Rhodobacteraceae	White, smeary	+	-
23	*A. aurita* medusa Baltic Sea husbandry	*Sulfitobacter* sp. S7-80 (KU999998.1, 99%)	Proteobacteria	Alphaproteobacteria	Rhodobacterales	Rhodobacteraceae	White, round	++	-
21	*A. aurita* medusa Baltic Sea husbandry	*Cobetia amphilecti* (NR_113404.1, 99%)	Proteobacteria	Gammaproteobacteria	Halomonadaceae	Cobetia	White, round	++	-
25	*A. aurita* medusa Baltic Sea husbandry	*Pseudoalteromonas issachenkonii* strain KMM3549 (CP011030.1, 99%)	Proteobacteria	Gammaproteobacteria	Alteromonadales	Pseudo-alteromonadaceae	Yellow, roundish-smeary	++	+
75	*A. aurita* polyp Baltic Sea husbandry	*Arthrobacter* sp. MB182 (JF706644.1, 99%)	Actinobacteria	Actinobacteria	Actinomycetales	Micrococcaceae	White, round		
82	*A. aurita* polyp Baltic Sea husbandry	*Arthrobacter* sp. MB182 (JF706644.1, 99%)	Actinobacteria	Actinobacteria	Actinomycetales	Micrococcaceae	White, round	+	-

(Continues)

TABLE A1 (Continued)

Isolate	Origin	Best homologue based on 16S full-length rRNA gene (Accession No., identity)	Taxonomic classification				Colony morphology	QQ activity	
			Phylum	Class	Order	Family		AHL	AI-2
84	*A. aurita* polyp Baltic Sea husbandry	*Arthrobacter* sp. MB182 (JF706644.1, 100%)	Actinobacteria	Actinobacteria	Actinomycetales	Micrococcaceae	White, round (tiny)	++	-
74	*A. aurita* polyp Baltic Sea husbandry	*Micrococcus luteus* strain BMC2N6_2 (MG996855.1, 99%)	Actinobacteria	Actinobacteria	Actinomycetales	Micrococcaceae	Light yellow, round		
83	*A. aurita* polyp Baltic Sea husbandry	*Gordonia terrae* strain DSO5B42 (KP860547.1, 99%)	Actinobacteria	Actinobacteria	Actinomycetales	Nocardiaceae	Light orange, round		
79	*A. aurita* polyp Baltic Sea husbandry	*Olleya* sp. MOLA 14 (AM990790.1, 99%)	Bacteroidetes	Flavobacteriia	Flavobacteriales	Flavobacteriaceae	Orange, round	+++	+
76	*A. aurita* polyp Baltic Sea husbandry	*Bacillus weihenstephanensis* strain 261ZG8 (KF831379.1, 98%)	Firmicutes	Bacilli	Bacillales	Bacillaceae	White, irregular	-	-
85	*A. aurita* polyp Baltic Sea husbandry	*Staphylococcus warneri* strain D2-1X–27 (MK287635.1, 99%)	Firmicutes	Bacilli	Bacillales	Staphylococcaceae	White-yellow, round	+	-
87	*A. aurita* polyp Baltic Sea husbandry	*Staphylococcus* sp. C34 (JX482523.1, 99%)	Firmicutes	Bacilli	Bacillales	Staphylococcaceae	Brownish, round	+	+
73	*A. aurita* polyp Baltic Sea husbandry	*Enterococcus casseliflavus* strain EC2 (MH376403.1, 99%)	Firmicutes	Bacilli	Lactobacillales	Enterococcaceae	White, roundish-smeary	+	-
88	*A. aurita* polyp Baltic Sea husbandry	*Paracoccus* sp. S1-12 (KP114216.1, 99%)	Proteobacteria	Alphaproteobacteria	Rhodobacterales	Rhodobacteraceae	White, smeary	-	-
86	*A. aurita* polyp Baltic Sea husbandry	*Ruegeria* sp. strain EA372 (KY655473.1, 96%)	Proteobacteria	Alphaproteobacteria	Rhodobacterales	Rhodobacteraceae	White, smeary	-	-
89	*A. aurita* polyp Baltic Sea husbandry	*Ruegeria* sp. strain S5-4-3 (MK743969.1, 99%)	Proteobacteria	Alphaproteobacteria	Rhodobacterales	Rhodobacteraceae	White, round	-	-
78	*A. aurita* polyp Baltic Sea husbandry	*Sulfitobacter* sp. SAG13 (KX268604.1, 99%)	Proteobacteria	Alphaproteobacteria	Rhodobacterales	Rhodobacteraceae	White, smeary	++	-

(Continues)

TABLE A1 (Continued)

Isolate	Origin	Best homologue based on 16S full-length rRNA gene (Accession No., identity)	Taxonomic classification				Colony morphology	QQ activity	
			Phylum	Class	Order	Family		AHL	AI-2
91	*A. aurita* polyp Baltic Sea husbandry	*Pseudoalteromonas prydzensis* strain S2A2 (MH362721.1, 98%)	Proteobacteria	Gammaproteobacteria	Alteromonadales	Pseudo-alteromonadaceae	White-brownish, smeary	+++	+
90	*A. aurita* polyp Baltic Sea husbandry	*Pseudomonas putida* strain KB3 (KU299960.1, 95%)	Proteobacteria	Gammaproteobacteria	Pseudomonadales	Pseudomonadaceae	White-yellow, round	++	++
92	*A. aurita* polyp Baltic Sea husbandry	*Pseudomonas putida* (GU191929.1, 99%)	Proteobacteria	Gammaproteobacteria	Pseudomonadales	Pseudomonadaceae	White, round	++	-
93	*A. aurita* polyp Baltic Sea husbandry	*Pseudomonas* sp. strain AS3-9 (MK193867.1, 99%)	Proteobacteria	Gammaproteobacteria	Pseudomonadales	Pseudomonadaceae	White, round with dent	++	-
94	*A. aurita* polyp Baltic Sea husbandry	*Pseudomonas* sp. RTW2 (LC433924.1, 99%)	Proteobacteria	Gammaproteobacteria	Pseudomonadales	Pseudomonadaceae	Orange, roundish	++	-
77	*A. aurita* polyp Baltic Sea husbandry	*Vibrio anguillarum* strain 12222 (MH036330.1 99%)	Proteobacteria	Gammaproteobacteria	Vibrionales	Vibrionaceae	White-brownish, smeary	++	-
81	*A. aurita* polyp Baltic Sea husbandry	*Vibrio anguillarum* strain 12222 (MH036330.1, 99%)	Proteobacteria	Gammaproteobacteria	Vibrionales	Vibrionaceae	Yellow, round	+++	++
80	*A. aurita* polyp Baltic Sea husbandry	*Vibrio* sp. strain GBPx3 (MK560194.1, 99%)	Proteobacteria	Gammaproteobacteria	Vibrionales	Vibrionaceae	White-brown, smeary	+++	-
111	A. aurita polyp North Sea husbandry	*Brevibacterium frigoritolerans* (JF411310.1, 99%)	Actinobacteria	Actinobacteria	Actinomycetales	Brevibacteriaceae	White, round	+++	-
107	*A. aurita* polyp North Sea husbandry	*Luteococcus japonicas* (NR_119351.1, 99%)	Actinobacteria	Actinobacteria	Actinomycetales	Propioni-bacteriaceae	Orange, round, smeary	+	-
112	*A. aurita* polyp North Sea husbandry	*Rhodococcus degradans* strain OTU62_I (MK547263.1, 99%)	Actinobacteria	Actinobacteria	Actinomycetales	Nocardiaceae	White, smeary	++	+
109	*A. aurita* polyp North Sea husbandry	*Rhodococcus erythropolis* 263AY3 (KF836533.1, 99%)	Actinobacteria	Actinobacteria	Actinomycetales	Nocardiaceae	White, roundish-smeary	-	-

(Continues)

TABLE A1 (Continued)

Isolate	Origin	Best homologue based on 16S full-length rRNA gene (Accession No., identity)	Taxonomic classification				Colony morphology	QQ activity	
			Phylum	Class	Order	Family		AHL	AI–2
106	*A. aurita* polyp North Sea husbandry	*Hymenobacter psychrophilus* (NR_117214.1, 98%)	Bacteroidetes	Cytophagia	Cytophagales	Hymenobacteraceae	Orange-pink, round		
108	*A. aurita* polyp North Sea husbandry	*Chryseobacterium hominis* (JX100820.1, 98-99%)	Bacteroidetes	Flavobacteriia	Flavobacteriales	Flavobacteriaceae	White, round	+	-
98	*A. aurita* polyp North Sea husbandry	*Olleya marilimosa* strain KMM6714 (KC247324.1, 99%)	Bacteroidetes	Flavobacteriia	Flavobacteriales	Flavobacteriaceae	Yellow/ orange, smeary	-	-
110	*A. aurita* polyp North Sea husbandry	*Enterococcus canintestini* strain 0.14 (MK611096.1, 93%)	Firmicutes	Bacilli	Lactobacillales	Enterococcaceae	Translucent, smeary		
96	*A. aurita* polyp North Sea husbandry	*Enterococcus casseliflavus* strain EC2 (MH376403.1, 99%)	Firmicutes	Bacilli	Lactobacillales	Enterococcaceae	White, round	+	-
95	*A. aurita* polyp North Sea husbandry	Uncultured *Streptococcus* sp. (LT697039.1, 99%)	Firmicutes	Bacilli	Lactobacillales	Streptococcaceae	White, round		
104	*A. aurita* polyp North Sea husbandry	*Ruegeria* sp. strain InS–294 (MF359523.1, 99%)	Proteobacteria	Alphaproteobacteria	Rhodobacterales	Rhodobacteraceae	Light, orange, smeary	++	-
113	*A. aurita* polyp North Sea husbandry	*Sulfitobacter pontiacus* strain ACBC109 (MK156387.1, 99%)	Proteobacteria	Alphaproteobacteria	Rhodobacterales	Rhodobacteraceae	White, smeary	-	-
100	*A. aurita* polyp North Sea husbandry	*Sulfitobacter* sp. SAG13 (KX268604.1, 99%)	Proteobacteria	Alphaproteobacteria	Rhodobacterales	Rhodobacteraceae	White-yellow, smeary	+++	-
105	*A. aurita* polyp North Sea husbandry	*Shewanella basaltis* (KC534403.1, 99%)	Proteobacteria	Betaproteobacteria	Alteromonadales	Oxalobacteraceae	White-yellow, smeary	-	-
97	*A. aurita* polyp North Sea husbandry	*Shewanella putrefaciens* strain PF 15 (KY614355.1, 99%)	Proteobacteria	Betaproteobacteria	Alteromonadales	Oxalobacteraceae	Yellowish, smeary	+	+
102	*A. aurita* polyp North Sea husbandry	Uncultured *Alteromonas* sp. clone PD22_850 (HM140647.1, 99%)	Proteobacteria	Gammaproteobacteria	Alteromonadales	Alteromonadaceae	White, brownish in center, round-smeary	+	-

(Continues)

TABLE A1 (Continued)

Isolate	Origin	Best homologue based on 16S full-length rRNA gene (Accession No., identity)	Taxonomic classification				Colony morphology	QQ activity	
			Phylum	Class	Order	Family		AHL	AI-2
99	*A. aurita* polyp North Sea husbandry	*Pseudoalteromonas issachenkonii* strain K-W12 (JQ799065.1, 99%)	Proteobacteria	Gammaproteobacteria	Alteromonadales	Pseudo-alteromonadaceae	Light orange, round	++	+
101	*A. aurita* polyp North Sea husbandry	*Pseudoalteromonas issachenkonii* strain KMM 3549 (CP011030.1, 99%)	Proteobacteria	Gammaproteobacteria	Alteromonadales	Pseudo-alteromonadaceae	Very light orange, smeary	-	-
103	*A. aurita* polyp North Sea husbandry	*Pseudoalteromonas* sp. strain KYW1326 (MH782067.1, 99%)	Proteobacteria	Gammaproteobacteria	Alteromonadales	Pseudo-alteromonadaceae	Brownish, smeary	+++	-
118	*A. aurita* polyp North Atlantic husbandry	*Micrococcus* sp. strain Actino−43 (MH671539.1, 96%)	Actinobacteria	Actinobacteria	Actinomycetales	Micrococcaceae	White, round		
128	*A. aurita* polyp North Atlantic husbandry	*Rhodococcus erythropolis* strain 263AY3 (KF836533.1, 98%)	Actinobacteria	Actinobacteria	Actinomycetales	Nocardiaceae	White, orange, round-smeary	+++	-
131	*A. aurita* polyp North Atlantic husbandry	*Rhodococcus erythropolis* strain 263AY3 (KF836533.1, 99%)	Actinobacteria	Actinobacteria	Actinomycetales	Nocardiaceae	Translucent, round	+++	-
123	*A. aurita* polyp North Atlantic husbandry	*Luteococcus japonicus* (NR_119351.1, 99%)	Actinobacteria	Actinobacteria	Actinomycetales	Propioni-bacteriaceae	White, round	+	-
121	*A. aurita* polyp North Atlantic husbandry	*Olleya* sp. MOLA 14 (AM990790.1, 99%)	Bacteroidetes	Flavobacteriia	Flavobacteriales	Flavobacteriaceae	Light orange, round	++	-
129	*A. aurita* polyp North Atlantic husbandry	*Staphylococcus aureus* strain WMK026R (MK643265.1, 99%)	Firmicutes	Bacilli	Bacillales	Staphylococcaceae	White-yellow, roundish	-	-
124	*A. aurita* polyp North Atlantic husbandry	*Staphylococcus* sp. strain Ursilor/9a (MG948184.1, 97%)	Firmicutes	Bacilli	Bacillales	Staphylococcaceae	White, smeary	-	-
127	*A. aurita* polyp North Atlantic husbandry	*Staphylococcus succinus* subsp. *casei* (NR_037053.1, 99%)	Firmicutes	Bacilli	Bacillales	Staphylococcaceae	Orange, roundish	+++	-
116	*A. aurita* polyp North Atlantic husbandry	*Enterococcus casseliflavus* strain Ta12 (MK517636.1, 99%)	Firmicutes	Bacilli	Lactobacillales	Enterococcaceae	White, round		

(Continues)

TABLE A1 (Continued)

Isolate	Origin	Best homologue based on 16S full-length rRNA gene (Accession No., identity)	Taxonomic classification				Colony morphology	QQ activity	
			Phylum	Class	Order	Family		AHL	AI-2
117	*A. aurita* polyp North Atlantic husbandry	*Ruegeria* sp. strain 1334 - 60 (KY770284.1, 99%)	Proteobacteria	Alphaproteobacteria	Rhodobacterales	Rhodobacteraceae	Pink, smeary	+++	-
125	*A. aurita* polyp North Atlantic husbandry	*Sulfitobacter* sp. SAG13 (KX268604.1, 99%)	Proteobacteria	Alphaproteobacteria	Rhodobacterales	Rhodobacteraceae	White, round	-	-
126	*A. aurita* polyp North Atlantic husbandry	*Sulfitobacter* sp. strain B28-5 (MG388121.1, 99%)	Proteobacteria	Alphaproteobacteria	Rhodobacterales	Rhodobacteraceae	White-orange, round	+++	-
122	*A. aurita* polyp North Atlantic husbandry	*Paraglaciecola* sp. strain M202 (MF443579.1, 99%)	Proteobacteria	Gammaproteobacteria	Alteromonadales	Alteromonadaceae	White, smeary	-	-
119	*A. aurita* polyp North Atlantic husbandry	*Pseudoalteromonas prydzensis* strain S2A2 (MH362721.1, 99%)	Proteobacteria	Gammaproteobacteria	Alteromonadales	Pseudo-alteromonadaceae	Light orange, round	++	-
120	*A. aurita* polyp North Atlantic husbandry	*Pseudoalteromonas* sp. MACL07 (EF198247.1, 99%)	Proteobacteria	Gammaproteobacteria	Alteromonadales	Pseudo-alteromonadaceae	White-brownish, round	++	-
115	*A. aurita* polyp North Atlantic husbandry	*Moraxella osloensis* isolate TID−8 (LN871835.1, 99%)	Proteobacteria	Gammaproteobacteria	Pseudomonadales	Moraxellaceae	White, round	-	-
114	*A. aurita* polyp North Atlantic husbandry	*Pseudomonas* sp. strain THAF187a (MG996698.1, 99%)	Proteobacteria	Gammaproteobacteria	Pseudomonadales	Pseudomonadaceae	White-yellow, round	++	-
130	*A. aurita* polyp North Atlantic husbandry	*Pseudomonas* sp. TKCM64 (LC194999.1, 99%)	Proteobacteria	Gammaproteobacteria	Pseudomonadales	Pseudomonadaceae	White, roundish	+	-
59	*M. leidyi* Baltic Sea	*Microbacterium oxydans* strain DSM 20578(T) (MH321609.1 99%)	Actinobacteria	Actinobacteria	Actinomycetales	Microbacteriaceae	White, round	-	-
63	*M. leidyi* Baltic Sea	*Microbacterium* sp. strain ZMAI−4 (MK178502.1, 99%)	Actinobacteria	Actinobacteria	Actinomycetales	Microbacteriaceae	White, round	-	-
255	*M. leidyi* Baltic Sea	*Pseudoclavibacter* sp. (MK193865.1, 99%)	Actinobacteria	Actinobacteria	Actinomycetales	Microbacteriaceae	Light yellow, round	-	-
52	*M. leidyi* Baltic Sea	*Micrococcus* sp. EF1B-B144 (KC545358.1, 98%)	Actinobacteria	Actinobacteria	Actinomycetales	Micrococcaceae	Light yellow, round	-	-

(Continues)

TABLE A1 (Continued)

Isolate	Origin	Best homologue based on 16S full-length rRNA gene (Accession No., identity)	Taxonomic classification				Colony morphology	QQ activity	
			Phylum	Class	Order	Family		AHL	AI-2
58	*M. leidyi* Baltic Sea	*Rhodococcus* sp. strain GK29 (MK424373.1, 96%)	Actinobacteria	Actinobacteria	Actinomycetales	Nocardiaceae	Orange, roundish-smeary	-	-
61	*M. leidyi* Baltic Sea	*Phaeocystidibacter luteus* strain PG2S01 (NR_132329.1, 99%)	Bacteroidetes	Flavobacteriia	Flavobacteriales	Cryomorphaceae	Dark orange, oval		
54	*M. leidyi* Baltic Sea	*Lacinutrix* sp. strain KMM 6784 (MK587648.1, 99%)	Bacteroidetes	Flavobacteriia	Flavobacteriales	Flavobacteriaceae	White-orange, round	++	-
57	*M. leidyi* Baltic Sea	*Olleya marilimosa* strain KMM6714 (KC247324.1, 99%)	Bacteroidetes	Flavobacteriia	Flavobacteriales	Flavobacteriaceae	Translucent, round	+++	+
270	*M. leidyi* Baltic Sea	*Bacillus aryabhattai* strain MF−90 (MH177254.1, 99%)	Firmicutes	Bacilli	Bacillales	Bacillaceae	Black, round	-	-
264	*M. leidyi* Baltic Sea	*Exiguobacterium acetylicum* (MK478815.1, 99%)	Firmicutes	Bacilli	Bacillales	Bacillaceae	Orange, round		
51	*M. leidyi* Baltic Sea	*Staphylococcus epidermidis* strain C2 (MH304282.1, 92%)	Firmicutes	Bacilli	Bacillales	Staphylococcaceae	Yellow, roundish, smeary	-	-
269	*M. leidyi* Baltic Sea	*Leisingera daeponensis* DSM 23529 strain TF−218 (NR_044026.1, 99%)	Proteobacteria	Alphaproteobacteria	Rhodobacterales	Rhodobacteraceae	Translucent yellow, oval		
62	*M. leidyi* Baltic Sea	*Sagittula* sp. BG−9-E2 (KF560336.1, 89%)	Proteobacteria	Alphaproteobacteria	Rhodobacterales	Rhodobacteraceae	Yellowish, oval	-	-
229	*M. leidyi* Baltic Sea	*Shewanella algicola* (NR_149298.1, 99%)	Proteobacteria	Betaproteobacteria	Alteromonadales	Oxalobacteraceae	Red, round	+++	+
228	*M. leidyi* Baltic Sea	*Shewanella putrefaciens* (MH304323.1, 90%)	Proteobacteria	Betaproteobacteria	Alteromonadales	Oxalobacteraceae	Yellow, round	++	++
248	*M. leidyi* Baltic Sea	*Shewanella putrefaciens* strain NCTC10737 (KF798527.1, 99%)	Proteobacteria	Betaproteobacteria	Alteromonadales	Oxalobacteraceae	White-yellow, round	-	-
237	*M. leidyi* Baltic Sea	*Shewanella* sp. KMM 6721 (KC247331.1, 99%)	Proteobacteria	Betaproteobacteria	Alteromonadales	Oxalobacteraceae	Red, round		
247	*M. leidyi* Baltic Sea	*Shewanella* sp. Man17.1 (LR134321.1, 98%)	Proteobacteria	Betaproteobacteria	Alteromonadales	Oxalobacteraceae	Translucent yellow, round	+++	-
260	*M. leidyi* Baltic Sea	*Shewanella* sp. (KJ922533.1, 89%)	Proteobacteria	Betaproteobacteria	Alteromonadales	Oxalobacteraceae	White-red, round	+++	+
221	*M. leidyi* Baltic Sea	*Aeromonas salmonicida* (HG941669.1, 98%)	Proteobacteria	Gammaproteobacteria	Aeromonadales	Aeromonadaceae	Translucent, round	++	-

(Continues)

TABLE A1 (Continued)

Isolate	Origin	Best homologue based on 16S full-length rRNA gene (Accession No., identity)	Taxonomic classification				Colony morphology	QQ activity	
			Phylum	Class	Order	Family		AHL	AI-2
53	*M. leidyi* Baltic Sea	*Alteromonas naphthalenivorans* strain ACBC117 (MK156421.1, 96%)	Proteobacteria	Gammaproteobacteria	Alteromonadales	Alteromonadaceae	White, roundish-smeary	++	-
60	*M. leidyi* Baltic Sea	*Alteromonas* sp. 2c3 (AJ294361.1, 99%)	Proteobacteria	Gammaproteobacteria	Alteromonadales	Alteromonadaceae	White, round, smeary	++	-
223	*M. leidyi* Baltic Sea	Uncultured *Alteromonas* sp. clone G9UC_PoM_0m_07 (KP076503.1, 98%)	Proteobacteria	Gammaproteobacteria	Alteromonadales	Alteromonadaceae	White with black center, round		
56	*M. leidyi* Baltic Sea	*Colwellia* sp. BSs20120 (EU330346.1, 99%)	Proteobacteria	Gammaproteobacteria	Alteromonadales	Colwelliaceae	Light orange, round	-	-
254	*M. leidyi* Baltic Sea	*Pantoea agglomerans* strain SXAU-S1 (MK875137.1, 96%)	Proteobacteria	Gammaproteobacteria	Enterobacterales	Enterobacteriaceae	Red, round	+++	-
225	*M. leidyi* Baltic Sea	*Acinetobacter* sp. (MH796223.1, 99%)	Proteobacteria	Gammaproteobacteria	Halobacteriales	Moraxellaceae	White, spreading	-	-
261	*M. leidyi* Baltic Sea	*Psychrobacter cryohalolentis* (MH712970.1, 96%)	Proteobacteria	Gammaproteobacteria	Halobacteriales	Moraxellaceae	White, spreading		
222	*M. leidyi* Baltic Sea	*Marinomonas pontica* (MG780341.1, 100%)	Proteobacteria	Gammaproteobacteria	Oceanospirillales	Oceanospirillaceae	Translucent, round	+++	-
55	*M. leidyi* Baltic Sea	*Marinomonas* sp. QHL13 (JQ809718.1, 98%)	Proteobacteria	Gammaproteobacteria	Oceanospirillales	Oceanospirillaceae	Translucent, round	+++	-
262	*M. leidyi* Baltic Sea	Oceanospirillaceae bacterium S−1-3 (AB550533.1, 99%)	Proteobacteria	Gammaproteobacteria	Oceanospirillales	Oceanospirillaceae	Translucent, round	+++	-
224	*M. leidyi* Baltic Sea	*Pseudoalteromonas lipolytica* (MH725436.1, 97%)	Proteobacteria	Gammaproteobacteria	Alteromonadales	Pseudo-alteromonadaceae	White, round	+++	+
232	*M. leidyi* Baltic Sea	*Pseudoalteromonas* sp. (JQ406678.1, 99%)	Proteobacteria	Gammaproteobacteria	Alteromonadales	Pseudo-alteromonadaceae	Orange, round	+	-
234	*M. leidyi* Baltic Sea	*Pseudoalteromonas* sp. 1_2015MBL_MicDiv (CP012738.1, 99%)	Proteobacteria	Gammaproteobacteria	Alteromonadales	Pseudo-alteromonadaceae	Black, round	+++	-
240	*M. leidyi* Baltic Sea	*Pseudoalteromonas* sp. (EU330378.1, 99%)	Proteobacteria	Gammaproteobacteria	Alteromonadales	Pseudo-alteromonadaceae	Yellow, round	+++	-
241	*M. leidyi* Baltic Sea	*Pseudoalteromonas* sp. (MK421604.1, 99%)	Proteobacteria	Gammaproteobacteria	Alteromonadales	Pseudo-alteromonadaceae	White, round	-	-
250	*M. leidyi* Baltic Sea	*Pseudoalteromonas* sp. (FR821214.1, 99%)	Proteobacteria	Gammaproteobacteria	Alteromonadales	Pseudo-alteromonadaceae	Violet, round	+++	-

(Continues)

TABLE A1 (Continued)

Isolate	Origin	Best homologue based on 16S full-length rRNA gene (Accession No., identity)	Taxonomic classification				Colony morphology	QQ activity	
			Phylum	Class	Order	Family		AHL	AI-2
243	*M. leidyi* Baltic Sea	*Pseudoalteromonas tunicata* (KY319053.1, 99%)	Proteobacteria	Gammaproteobacteria	Alteromonadales	Pseudo-alteromonadaceae	Black, round	+	-
251	*M. leidyi* Baltic Sea	*Pseudoalteromonas tunicata* (KY319053.1, 99%)	Proteobacteria	Gammaproteobacteria	Alteromonadales	Pseudo-alteromonadaceae	White, round	-	-
256	*M. leidyi* Baltic Sea	*Pseudoalteromonas tunicata* (KY319053.1, 99%)	Proteobacteria	Gammaproteobacteria	Alteromonadales	Pseudo-alteromonadaceae	Yellow, round	+	-
219	*M. leidyi* Baltic Sea	*Pseudoalteromonas tunicata* (KY319053.1, 100%)	Proteobacteria	Gammaproteobacteria	Alteromonadales	Pseudo-alteromonadaceae	Violet, round	+++	-
235	*M. leidyi* Baltic Sea	*Shewanella baltica* strain 20LCp98 (MK642562.1, 99%)	Proteobacteria	Gammaproteobacteria	Alteromonadales	Shewanellaceae	Yellow, round	++	-
233	*M. leidyi* Baltic Sea	*Shewanella baltica* BA175 (CP002767.1, 97%)	Proteobacteria	Gammaproteobacteria	Alteromonadales	Shewanellaceae	White, round	-	-
265	*M. leidyi* Baltic Sea	*Pseudomonas* sp. (HG738847.1, 94%)	Proteobacteria	Gammaproteobacteria	Pseudomonadales	Pseudomonadaceae	Yellow, round	+	-
249	*M. leidyi* Baltic Sea	*Pseudomonas* sp. P4708 (MK104126.1, 99%)	Proteobacteria	Gammaproteobacteria	Pseudomonadales	Pseudomonadaceae	Black, round	++	-
246	*M. leidyi* Baltic Sea	*Pseudomonas veronii* strain Pvy (CP039631.1, 99%)	Proteobacteria	Gammaproteobacteria	Pseudomonadales	Pseudomonadaceae	White-yellow, spreading	+++	-
213	*M. leidyi* Baltic Sea	*Vibrio* sp. strain 201709CJKOP–94 (MG867544.1, 98%)	Proteobacteria	Gammaproteobacteria	Vibrionales	Vibrionaceae	Yellowish, round	+++	+
242	*M. leidyi* Baltic Sea	*Vibrio* sp. S3SW (KF418795.1, 99%)	Proteobacteria	Gammaproteobacteria	Vibrionales	Vibrionaceae	Translucent, round	-	-
72	*M. leidyi* Baltic Sea husbandry	*Microbacterium* sp. MN2-1 (JQ396523.1, 99%)	Actinobacteria	Actinobacteria	Actinomycetales	Microbacteriaceae	Yellowish-white, round		
257	*M. leidyi* Baltic Sea husbandry	*Chryseobacterium* sp. (HQ911369.1, 99%)	Bacteroidetes	Flavobacteriia	Flavobacteriales	Flavobacteriaceae	Yellow-red, round	++	-
227	*M. leidyi* Baltic Sea husbandry	*Staphylococcus warneri* strain BPB10 (MK203007.1, 99%)	Firmicutes	Bacilli	Bacillales	Staphylococcaceae	Yellow-red, round	-	-
71	*M. leidyi* Baltic Sea husbandry	*Ochrobactrum anthropi* (MK284516.1, 99%)	Proteobacteria	Alphaproteobacteria	Rhizobiales	Brucellaceae	White, round		
69	*M. leidyi* Baltic Sea husbandry	*Falsirhodobacter deserti* strain W402 (KF268394.1, 99%)	Proteobacteria	Alphaproteobacteria	Rhodobacterales	Rhodobacteraceae	Orange, round		
67	*M. leidyi* Baltic Sea husbandry	*Shewanella* sp. KMM 6721 (KC247331.1, 99%)	Proteobacteria	Betaproteobacteria	Alteromonadales	Oxalobacteraceae	Translucent, round	+++	++
217	*M. leidyi* Baltic Sea husbandry	*Hydrogenophaga taeniospiralis* (AB795550.1, 99%)	Proteobacteria	Betaproteobacteria	Burkholderiales	Comamonadaceae	Translucent-red, round	-	-

(Continues)

TABLE A1 (Continued)

Isolate	Origin	Best homologue based on 16S full-length rRNA gene (Accession No., identity)	Taxonomic classification				Colony morphology	QQ activity	
			Phylum	Class	Order	Family		AHL	AI-2
66	*M. leidyi* Baltic Sea husbandry	*Alteromonas genoviensis* strain DB29 (KM609284.1, 99%)	Proteobacteria	Gammaproteobacteria	Alteromonadales	Alteromonadaceae	White, round	++	-
267	*M. leidyi* Baltic Sea husbandry	*Alteromonas macleodii* strain BF−12 (KT428054.1, 98%)	Proteobacteria	Gammaproteobacteria	Alteromonadales	Alteromonadaceae	White, spreading	+	-
244	*M. leidyi* Baltic Sea husbandry	*Thalassomonas* sp. (KC247368.1, 97%)	Proteobacteria	Gammaproteobacteria	Alteromonadales	Colwelliaceae	Translucent-yellow, round	-	-
65	*M. leidyi* Baltic Sea husbandry	*Pseudoalteromonas* sp. Strain B403 (MG388129.1, 99%)	Proteobacteria	Gammaproteobacteria	Alteromonadales	Pseudo-alteromonadaceae	White, smeary	+	+
239	*M. leidyi* Baltic Sea husbandry	*Pseudoalteromonas* sp. (LN871566.1, 99%)	Proteobacteria	Gammaproteobacteria	Alteromonadales	Pseudo-alteromonadaceae	White-yellow, round	+	-
226	*M. leidyi* Baltic Sea husbandry	*Pseudomonas aeruginosa* (HG738847.1, 94%)	Proteobacteria	Gammaproteobacteria	Pseudomonadales	Pseudomonadaceae	Light yellow, round	++	-
68	*M. leidyi* Baltic Sea husbandry	*Vibrio gigantis* strain LPB0246 (MH989593.1, 98%)	Proteobacteria	Gammaproteobacteria	Vibrionales	Vibrionaceae	Light orange, round	+++	+
70	*M. leidyi* Baltic Sea husbandry	*Vibrio gigantis* strain LPB0246 (MH989593.1, 99%)	Proteobacteria	Gammaproteobacteria	Vibrionales	Vibrionaceae	White, orange in center, round	++	-
253	Ambient water Baltic Sea	*Fictibacillus* sp. (MK101065.1, 98%)	Firmicutes	Bacilli	Bacillales	Bacillaceae	Translucent yellow, round	-	-
259	Ambient water Baltic Sea	*Pseudoalteromonas* sp. (KF188488.1, 99%)	Proteobacteria	Gammaproteobacteria	Alteromonadales	Pseudo-alteromonadaceae	Red, round	++	-
230	Ambient water Baltic Sea	*Pseudoalteromonas* sp. P55 (EU935099.1, 98%)	Proteobacteria	Gammaproteobacteria	Alteromonadales	Pseudo-alteromonadaceae	White, round	+++	-
266	Ambient water Baltic Sea	*Pseudoalteromonas tunicata* strain D2 (CP031961.1, 97%)	Proteobacteria	Gammaproteobacteria	Alteromonadales	Pseudo-alteromonadaceae	Translucent yellow, round	+	-
214	Ambient water Baltic Sea	*Serratia plymuthica* (KR611045.1, 99%)	Proteobacteria	Gammaproteobacteria	Enterobacteriales	Yersiniaceae	Red, round	+++	-
231	Ambient water Baltic Sea	*Pseudomonas* sp. (JF766700.1, 99%)	Proteobacteria	Gammaproteobacteria	Pseudomonadales	Pseudomonadaceae	White, spreading	-	-
156	Artificial Seawater 18 PSU	*Micrococcus* sp. strain Actino−43 (MH671539.1, 99%)	Actinobacteria	Actinobacteria	Actinomycetales	Micrococcaceae	Yellow, round		
168	Artificial Seawater 18 PSU	*Salinibacterium* sp. BS−14B (KX000029.1, 99%)	Actinobacteria	Actinobacteria	Actinomycetales	Microbacteriaceae	Yellow, round		

(Continues)

TABLE A1 (Continued)

Isolate	Origin	Best homologue based on 16S full-length rRNA gene (Accession No., identity)	Taxonomic classification				Colony morphology	QQ activity	
			Phylum	Class	Order	Family		AHL	AI-2
143	Artificial Seawater 18 PSU	*Rhodococcus yunnanensis* strain IHBB 9200 (KR085831.1, 99%)	Actinobacteria	Actinobacteria	Actinomycetales	Nocardiaceae	White, round	-	-
169	Artificial Seawater 18 PSU	*Luteococcus japonicus* strain DSM 10546 (NR_119351.1, 99%)	Actinobacteria	Actinobacteria	Propionibacteriales	Propioni-bacteriaceae	Orange, roundish	-	-
157	Artificial Seawater 18 PSU	*Corynebacterium* sp. NML96-0244 (GU238410.1, 99%)	Actinobacteria	Actinomycetales	Corynebacteriaceae	Corynebacterium	White, round		
160	Artificial Seawater 18 PSU	*Staphylococcus aureus* JCM2874 (LC420068.1, 99%)	Firmicutes	Bacilli	Bacillales	Staphylococcaceae	Yellow, round	-	-
162	Artificial Seawater 18 PSU	*Staphylococcus aureus* (CP039759.1, 99%)	Firmicutes	Bacilli	Bacillales	Staphylococcaceae	Orange, smeary	-	-
149	Artificial Seawater 18 PSU	*Staphylococcus saprophyticus* strain AB697718.1 (MH491313.1, 98%)	Firmicutes	Bacilli	Bacillales	Staphylococcaceae	White, smeary	-	-
145	Artificial Seawater 18 PSU	*Staphylococcus* sp. *strain* JLT103 (KX989231.1, 99%)	Firmicutes	Bacilli	Bacillales	Staphylococcaceae	White, round	++	-
150	Artificial Seawater 18 PSU	*Staphylococcus* sp. strain JLT103 (KX989231.1, 99%)	Firmicutes	Bacilli	Bacillales	Staphylococcaceae	White, round	-	-
151	Artificial Seawater 18 PSU	*Staphylococcus* sp. strain GD01 (MG214350.1, 99%)	Firmicutes	Bacilli	Bacillales	Staphylococcaceae	White line, round	-	-
152	Artificial Seawater 18 PSU	*Staphylococcus* sp. DVRSG–2 (KF779128.1, 99%)	Firmicutes	Bacilli	Bacillales	Staphylococcaceae	White line, smeary	-	-
146	Artificial Seawater 18 PSU	Uncultured *Staphylococcus* sp. clone HEM419 (MF148181.1, 99%)	Firmicutes	Bacilli	Bacillales	Staphylococcaceae	White, round		
138	Artificial Seawater 18 PSU	*Celeribacter* sp. R–52665 (KT185135.1, 99%)	Proteobacteria	Alphaproteobacteria	Rhodobacterales	Rhodobacteraceae	White, smeary	-	-
164	Artificial Seawater 18 PSU	*Celeribacter* sp. CY411 (KP201135.1, 99%)	Proteobacteria	Alphaproteobacteria	Rhodobacterales	Rhodobacteraceae	White, round		
165	Artificial Seawater 18 PSU	*Celeribacter* sp. R–52665 (KT185135.1, 99%)	Proteobacteria	Alphaproteobacteria	Rhodobacterales	Rhodobacteraceae	White with light yellow center, smeary	-	-
166	Artificial Seawater 18 PSU	*Celeribacter* sp. R–52665 (KT185135.1, 99%)	Proteobacteria	Alphaproteobacteria	Rhodobacterales	Rhodobacteraceae	White, smeary	-	-
147	Artificial Seawater 18 PSU	*Phaeobacter gallaeciensis* strain P63 (CP010784.1, 97%)	Proteobacteria	Alphaproteobacteria	Rhodobacterales	Rhodobacteraceae	White, round	-	-
137	Artificial Seawater 18 PSU	*Sulfitobacter* sp. SAG13 (KX268604.1, 99%)	Proteobacteria	Alphaproteobacteria	Rhodobacterales	Rhodobacteraceae	White, smeary	+	+

(Continues)

TABLE A1 (Continued)

Isolate	Origin	Best homologue based on 16S full-length rRNA gene (Accession No., identity)	Taxonomic classification				Colony morphology	QQ activity	
			Phylum	Class	Order	Family		AHL	AI-2
163	Artificial Seawater 18 PSU	*Aestuariibacter halophilus* (LC221844.1, 99%)	Proteobacteria	Gammaproteobacteria	Alteromonadales	Alteromonadaceae	Orange, round	+++	-
139	Artificial Seawater 18 PSU	*Alteromonas* sp. JAM-GA15 (AB526338.1, 99%)	Proteobacteria	Gammaproteobacteria	Alteromonadales	Alteromonadaceae	Orange, round	++	-
140	Artificial Seawater 18 PSU	Uncultured *Alteromonas* sp. clone PD22_850 (HM140647.1, 99%)	Proteobacteria	Gammaproteobacteria	Alteromonadales	Alteromonadaceae	White, smeary	++	-
148	Artificial Seawater 18 PSU	Uncultured *Alteromonas* sp. clone PD3_1355 (HM140650.1, 99%)	Proteobacteria	Gammaproteobacteria	Alteromonadales	Alteromonadaceae	White, smeary	+	-
154	Artificial Seawater 18 PSU	Uncultured *Alteromonas* sp. clone C146500156 (JX531176.1, 99%)	Proteobacteria	Gammaproteobacteria	Alteromonadales	Alteromonadaceae	White, smeary	++	-
155	Artificial Seawater 18 PSU	*Marinobacter* sp. Strain AN17_20_3 (MK780031.1, 98%)	Proteobacteria	Gammaproteobacteria	Alteromonadales	Alteromonadaceae	White-yellowish, round	+++	-
153	Artificial Seawater 18 PSU	*Paraglaciecola* sp. strain M202 (MF443579.1, 99%)	Proteobacteria	Gammaproteobacteria	Alteromonadales	Alteromonadaceae	White, round	-	-
167	Artificial Seawater 18 PSU	*Pseudoalteromonas* sp. BSi20316 (DQ492738.1, 93%)	Proteobacteria	Gammaproteobacteria	Alteromonadales	Pseudo-alteromonadaceae	White-yellowish, round	++	-
135	Artificial Seawater 18 PSU	*Moraxella* sp. strain TS14 (MK591880.1, 99%)	Proteobacteria	Gammaproteobacteria	Halobacteriales	Moraxellaceae	White, round	++	-
134	Artificial Seawater 18 PSU	*Pseudomonas anguilliseptica* (JX177685.1, 99%)	Proteobacteria	Gammaproteobacteria	Pseudomonadales	Pseudomonadaceae	Light yellow, round	+++	-
136	Artificial Seawater 18 PSU	*Pseudomonas anguilliseptica* (JX177685.1, 99%)	Proteobacteria	Gammaproteobacteria	Pseudomonadales	Pseudomonadaceae	White-yellowish, round	-	-
141	Artificial Seawater 18 PSU	*Pseudomonas cuatrocienegasensis* (JN644592.1, 98%)	Proteobacteria	Gammaproteobacteria	Pseudomonadales	Pseudomonadaceae	Yellow, round		
132	Artificial Seawater 18 PSU	*Pseudomonas fluorescens* strain G21 (MK874851.1, 98%)	Proteobacteria	Gammaproteobacteria	Pseudomonadales	Pseudomonadaceae	Light orange, smeary	-	-
133	Artificial Seawater 18 PSU	*Pseudomonas* sp. MBEF06 (AB733556.1, 97%)	Proteobacteria	Gammaproteobacteria	Pseudomonadales	Pseudomonadaceae	Light orange, round	-	-
142	Artificial Seawater 18 PSU	*Pseudomonas* sp. Iranica GH10 (KF742672.1, 97%)	Proteobacteria	Gammaproteobacteria	Pseudomonadales	Pseudomonadaceae	Orange, smeary	+	-

(Continues)

TABLE A1 (Continued)

Isolate	Origin	Best homologue based on 16S full-length rRNA gene (Accession No., identity)	Taxonomic classification				Colony morphology	QQ activity	
			Phylum	Class	Order	Family		AHL	AI-2
158	Artificial Seawater 18 PSU	*Pseudomonas* sp. Iranica GH10 (KF742672.1, 96%)	Proteobacteria	Gammaproteobacteria	Pseudomonadales	Pseudomonadaceae	Light yellow, smeary	+	-
159	Artificial Seawater 18 PSU	*Pseudomonas* sp. Iranica GH10 (KF742672.1, 96%)	Proteobacteria	Gammaproteobacteria	Pseudomonadales	Pseudomonadaceae	Light yellow, smeary	+	-
171	Artificial Seawater 18 PSU	*Pseudomonas* sp. Iranica GH10 (KF742672.1, 97%)	Proteobacteria	Gammaproteobacteria	Pseudomonadales	Pseudomonadaceae	Yellowish, round	++	-
170	Artificial Seawater 18 PSU	*Pseudomonas* sp. I-A-R–28 (KT922041.1, 99%)	Proteobacteria	Gammaproteobacteria	Pseudomonadales	Pseudomonadaceae	Yellow, round	+++	-
161	Artificial Seawater 18 PSU	*Pseudomonas zhaodongensis* strain MT325 (MH725487.1, 97%)	Proteobacteria	Gammaproteobacteria	Pseudomonadales	Pseudomonadaceae	Yellow-orange, smeary	-	-
172	Artificial Seawater 30 PSU	*Brevibacterium frigoritolerans* strain MER_TA_42 (KT719448.1, 99%)	Actinobacteria	Actinobacteria	Actinomycetales	Brevibacteriaceae	White, round	-	-
179	Artificial Seawater 30 PSU	*Brevibacterium frigoritolerans* strain MER_TA_133 (KT719536.1, 99%)	Actinobacteria	Actinobacteria	Actinomycetales	Brevibacteriaceae	White, round	-	-
209	Artificial Seawater 30 PSU	*Brevibacterium frigoritolerans* IHB B 6528 (KF475857.1, 99%)	Actinobacteria	Actinobacteria	Actinomycetales	Brevibacteriaceae	White, roundish	-	-
210	Artificial Seawater 30 PSU	*Brevibacterium frigoritolerans* strain DSM 8801 (T) (MK424281.1, 99%)	Actinobacteria	Actinobacteria	Actinomycetales	Brevibacteriaceae	White, smeary	++	-
192	Artificial Seawater 30 PSU	*Microbacterium* sp. JL1103 (DQ985063.1, 99%)	Actinobacteria	Actinobacteria	Actinomycetales	Microbacteriaceae	Light orange, smeary	-	-
182	Artificial Seawater 30 PSU	*Micrococcus* sp. EF1B-B144 (KC545358.1, 99%)	Actinobacteria	Actinobacteria	Actinomycetales	Microbacteriaceae	Pink, round	-	-
173	Artificial Seawater 30 PSU	*Salinibacterium amurskyense* strain BBCC2678 (MK224796.1 95%)	Actinobacteria	Actinobacteria	Actinomycetales	Microbacteriaceae	Light orange-white, round	-	-
178	Artificial Seawater 30 PSU	*Salinibacterium amurskyense* strain BBCC2678 (MK224796.1, 99%)	Actinobacteria	Actinobacteria	Actinomycetales	Microbacteriaceae	Yellowish, round		
175	Artificial Seawater 30 PSU	*Micrococcus* sp. strain Actino–43 (MH671539.1, 99%)	Actinobacteria	Actinobacteria	Actinomycetales	Micrococcaceae	Orange, roundish-smeary	-	-
181	Artificial Seawater 30 PSU	*Chryseobacterium* sp. WW-RP5 (KJ958497.1, 96%)	Bacteroidetes	Flavobacteriia	Flavobacteriales	Flavobacteriaceae	Light orange, smeary	-	-
177	Artificial Seawater 30 PSU	*Maribacter* sp. SDRB-Phe2 (MG456900.1, 98%)	Bacteroidetes	Flavobacteriia	Flavobacteriales	Flavobacteriaceae	Yellowish, smeary	+	-

(Continues)

TABLE A1 (Continued)

Isolate	Origin	Best homologue based on 16S full-length rRNA gene (Accession No., identity)	Taxonomic classification				Colony morphology	QQ activity	
			Phylum	Class	Order	Family		AHL	AI-2
199	Artificial Seawater 30 PSU	*Maribacter* sp. SDRB-Phe2 (MG456900.1, 93%)	Bacteroidetes	Flavobacteriia	Flavobacteriales	Flavobacteriaceae	White, round, smeary in high density	-	-
202	Artificial Seawater 30 PSU	*Maribacter* sp. SDRB-Phe2 (MG456900.1, 99%)	Bacteroidetes	Flavobacteriia	Flavobacteriales	Flavobacteriaceae	White, round, small	-	-
189	Artificial Seawater 30 PSU	*Bacillus* sp. strain KSTI83 (KX989449.1, 97%)	Firmicutes	Bacilli	Bacillales	Bacillaceae	Pink, round	-	-
193	Artificial Seawater 30 PSU	*Bacillus* sp. SG109 (AB425366.1, 99%)	Firmicutes	Bacilli	Bacillales	Bacillaceae	White, roundish	++	-
195	Artificial Seawater 30 PSU	*Bacillus* sp. T1T (AM983464.1, 99%)	Firmicutes	Bacilli	Bacillales	Bacillaceae	Translucent, round	-	-
206	Artificial Seawater 30 PSU	*Bacillus* sp. strain Sf1 (JN975958.1, 99%)	Firmicutes	Bacilli	Bacillales	Bacillaceae	White-orange/ brownish, smeary	-	-
207	Artificial Seawater 30 PSU	*Bacillus* sp. KP067r (KT200468.1, 100%)	Firmicutes	Bacilli	Bacillales	Bacillaceae	White-orange, smeary	-	-
184	Artificial Seawater 30 PSU	*Bacillus thuringiensis* strain 263AG8 (KF836531.1, 99%)	Firmicutes	Bacilli	Bacillales	Bacillaceae	White, brownish center, round	-	-
187	Artificial Seawater 30 PSU	*Bacillus vietnamensis* strain MS2016 (KX683881.1, 99%)	Firmicutes	Bacilli	Bacillales	Bacillaceae	Pink, smeary	-	-
212	Artificial Seawater 30 PSU	*Fictibacillus phosphorivorans* HT5 (MG547923.1, 98%)	Firmicutes	Bacilli	Bacillales	Bacillaceae	Translucent, smeary	-	-
174	Artificial Seawater 30 PSU	*Staphylococcus aureus* strain AR_475 (CP030323.1, 93%)	Firmicutes	Bacilli	Bacillales	Staphylococcaceae	White, round		
180	Artificial Seawater 30 PSU	*Staphylococcus aureus* JCM 2874 (LC420068.1, 99%)	Firmicutes	Bacilli	Bacillales	Staphylococcaceae	White, brownish center, round	+++	-
191	Artificial Seawater 30 PSU	*Celeribacter* sp. CY411 (KP201135.1, 99%)	Proteobacteria	Alphaproteobacteria	Rhodobacterales	Rhodobacteraceae	White, round	-	-
188	Artificial Seawater 30 PSU	*Sulfitobacter pseudonitzschiae* strain H3 (KF006321.2, 95%)	Proteobacteria	Alphaproteobacteria	Rhodobacterales	Rhodobacteraceae	White, smeary	+++	-

(Continues)

TABLE A1 (Continued)

Isolate	Origin	Best homologue based on 16S full-length rRNA gene (Accession No., identity)	Taxonomic classification				Colony morphology	QQ activity	
			Phylum	Class	Order	Family		AHL	AI−2
204	Artificial Seawater 30 PSU	*Sulfitobacter* sp. strain B28-5 (MG388121.1, 99%)	Proteobacteria	Alphaproteobacteria	Rhodobacterales	Rhodobacteraceae	White, round, smeary in high density	-	-
185	Artificial Seawater 30 PSU	*Alteromonas* sp. strain DT074 (MG099550.1, 99%)	Proteobacteria	Gammaproteobacteria	Alteromonadales	Alteromonadaceae	Orange, round	+++	-
186	Artificial Seawater 30 PSU	*Alteromonas* sp. strain DT074 (MG099550.1, 99%)	Proteobacteria	Gammaproteobacteria	Alteromonadales	Alteromonadaceae	Brownish, round	+++	-
190	Artificial Seawater 30 PSU	*Alteromonas* sp. 76-1 (LR136958.1, 99%)	Proteobacteria	Gammaproteobacteria	Alteromonadales	Alteromonadaceae	Light orange, round	-	-
208	Artificial Seawater 30 PSU	*Pseudoalteromonas prydzensis* strain S2A2 (MH362721.1, 99%)	Proteobacteria	Gammaproteobacteria	Alteromonadales	Pseudo-alteromonadaceae	White-yellowish, smeary	+	-
200	Artificial Seawater 30 PSU	*Pseudoalteromonas* sp. ZB23-4 (MG388173.1, 99%)	Proteobacteria	Gammaproteobacteria	Alteromonadales	Pseudo-alteromonadaceae	Grey-white, round	++	-
203	Artificial Seawater 30 PSU	*Pseudoalteromonas* sp. strain SJS4-1 (MG383479.1, 99%)	Proteobacteria	Gammaproteobacteria	Alteromonadales	Pseudo-alteromonadaceae	White, round, smeary in high density	+++	-
201	Artificial Seawater 30 PSU	*Cobetia marina* strain QD34 (KF933690.1, 99%)	Proteobacteria	Gammaproteobacteria	Halomonadaceae	Cobetia	White, round	++	-
194	Artificial Seawater 30 PSU	*Cobetia* sp. S2894 (FJ457279.1, 89%)	Proteobacteria	Gammaproteobacteria	Halomonadaceae	Cobetia	Pink, round	+	-
176	Artificial Seawater 30 PSU	*Halomonas* sp. strain IceBac 363 (KF306352.1, 99%)	Proteobacteria	Gammaproteobacteria	Oceanospirillales	Halomonadaceae	Light orange, round	-	-
197	Artificial Seawater 30 PSU	*Pseudomonas* sp. TKCM64 (LC194999.1, 99%)	Proteobacteria	Gammaproteobacteria	Pseudomonadales	Pseudomonadaceae	White, round	-	-
205	Artificial Seawater 30 PSU	*Pseudomonas* sp. MR3 (JN082728.1, 83%)	Proteobacteria	Gammaproteobacteria	Pseudomonadales	Pseudomonadaceae	White, round	-	-
196	Artificial Seawater 30 PSU	*Pseudomonas syringae pv. atrofaciens* strain GN-In (MK141010.1, 94%)	Proteobacteria	Gammaproteobacteria	Pseudomonadales	Pseudomonadaceae	Yellow, round	+++	+

Bacteria were isolated by classical enrichment on agar plates and taxonomically classified based on partial 16S rRNA gene sequences. QQ activities of isolates are stated in (-) no activity, (+) low, (++) mid, and (+++) high activity against acyl-homoserine lactone (AHL) and autoinducer-2 (AI-2)); light grey highlighted isolates were not used for functional assays.