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Overview and future perspectives of nitrifying bacteria on biofilters for recirculating aquaculture systems

Pamela Ruiz[1,2], José Miguel Vidal[1], Daniela Sepúlveda[1], Claudia Torres[1], Gabriela Villouta[1], Carlos Carrasco[1], Felipe Aguilera[1,3], Nathaly Ruiz-Tagle[1] and Homero Urrutia[1,4]

1 Laboratorio de Biopelículas y Microbiología Ambiental, Centro de Biotecnología, Departamento de Microbiología, Facultad de Ciencias Biológicas, Universidad de Concepción, Concepción, Chile
2 Departamento de Ciencias Biológicas, Facultad de Ciencias de la Vida, Universidad Andres Bello, Concepción, Chile
3 Departamento de Bioquímica y Biología Molecular, Facultad de Ciencias Biológicas, Universidad de Concepción, Concepción, Chile
4 Departamento de Microbiología, Facultad de Ciencias Biológicas, Universidad de Concepción, Concepción, Chile

Correspondence
Homero Urrutia Briones, Laboratorio de Biopelículas y Microbiología Ambiental Centro de Biotecnología, Universidad de Concepción, Casilla 160 C, Concepción. Chile.
Email: hurrutia@udec.cl

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Abstract

Intensive fish culture is a practice in aquaculture systems; however, it can produce negative environmental impacts due to the accumulation of organic nitrogen from feeding procedures, but also from fish wasting products. Recirculating aquaculture systems have emerged as one strategy to reduce these impacts, maintaining a healthy environment for fish. These reduce toxicity level through nitrifying biofilters, which use a microbial consortium to convert ammonia into nitrate. The main component of bacterial consortium is comprised by aerobic ammonia-oxidizing bacteria and aerobic nitrite-oxidizing bacteria, which are part of the whole nitrification process. These nitrifying bacteria grow in suspension or in fixed form, the latter characterized by a biofilm formation where bacteria adhere to a physical substrate in a self-produced polymer matrix. The biofilm formation requires tight communication among bacteria to regulate the transcriptional circuits underlying the production of chemical signal molecules (e.g. N-acetyl-homoserine lactones) that control biofilm formation. This coordination is known as quorum sensing and can be considered as a mechanism that contributes to the coupling and maintenance of nitrification rate among bacteria by regulating expression levels of relevant genes associated with nitrification process. Therefore, the control of this process is crucial in recirculating aquaculture systems and its incorrect manipulation can produce a detriment of water quality. We here present an overview of the nitrification process in recirculating aquaculture systems. Subsequently, we describe nitrifying biofilters and nitrifying bacteria. Finally, we discuss how quorum sensing controls the efficiency of nitrifying bacteria and potential applications of nitrifying biofilters in intensive aquaculture systems.

Key words: bacteria, biofilm, biofilter, N-acetyl-homoserine lactones, nitrifying, quorum sensing.

Introduction

The growing demand for food supply to fulfil human population needs is a pressing concern that claims for alternative sources, particularly because capture fisheries have stagnated in the last years (Ahmed *et al.* 2018). In this regard, aquaculture (i.e. farming of marine organisms) has emerged as an alternative food source for the human population. Indeed, aquaculture not only plays a relevant role in human nutrition and food security but also in terms of people's employment, nation-states exports, and overall socio-economic development (Kobayashi *et al.* 2015). Aquaculture systems range from extensive to intensive depending on the level of inputs of feed and/or fertilizer and stocking density of cultured organisms (Datta 2012). To meet the food demand of a growing world population, many aquafarming industries have adopted an intensive production system where fish are kept at too high a stocking density to obtain significant amounts of feed from their environment to enhance the production of cultured organisms. To do so, fish are dependent on the feed provided and water must be

replenished at a high rate to maintain oxygen levels and remove waste (Badiola *et al.* 2012).

Aquaculture systems are responsible for nutrient enrichment of the water due to fish wastes and uneaten feed inputs. Elements of most concern are nitrogen- and phosphorus-based products that can promote algal growth and affect the availability of high-quality water (Zohar *et al.* 2005; Verdegem 2013; Kawasaki *et al.* 2016). Indeed, serious environmental and ecological concerns have been raised associated with aquaculture production, including water pollution, increased salinity, and destruction of mangrove forests (Arvanitoyannis & Kassaveti 2008; Guimarães *et al.* 2010; Turcios & Papenbrock 2014; Proisy *et al.* 2018). Therefore, sustainable practices are urgently needed in aquaculture systems.

In intensive aquaculture systems, the levels of feed inputs and water management affect the stocking density of the fish that can be cultured. This is, in fact, extremely important because inappropriate practices can provoke alterations in the nitrification process and the accumulation of ammonia-associated products from feeding procedures, but also from fish wasting products (Mommsen & Walsh 1992), generating a detrimental impact on water quality, fish health, and the environment (Nazar *et al.* 2013). This can be observed through the reduction in fish growth or the appearance of chronic diseases such as alteration of ionic balance, hormonal regulation and histopathological changes in the branchial epithelium, as well as in respiratory, cardiovascular, endocrine, and excretory processes (Soderberg 1992; Knoph & Olsen 1994; Tomasso 1994; Wilkie 1997; Cheng *et al.* 2004; Kroupova *et al.* 2005; Svobodova *et al.* 2005). For example, concentrations of nitrite above 5 mg L^{-1} nitrite-nitrogen oxidizes haemoglobin of the blood to methaemoglobin, which does not carry oxygen and can produce death of the fish (Dosdat *et al.* 2003; Lin & Chen 2003; McKenzie *et al.* 2003; Lemarie *et al.* 2004; Timmons & Ebeling 2007; Kumar *et al.* 2013). Therefore, the decomposition of waste products into toxic nitrogenous compounds (i.e. ammonia, nitrite, and to some extent, nitrate) is particularly important in aquaculture systems.

Although intensive aquaculture systems seem to be a promising food source for the human population, it has been shown that these systems may produce negative impacts (Verdegem 2013). However, alternative aquaculture techniques have emerged as ways to manage the negative effects of intensive aquaculture systems and enhance the intensification of fish culture (Dauda *et al.* 2018). One of these alternative techniques is known as Recirculation Aquaculture Systems (RAS). In RAS, water is recycled by recirculating it through biofilters to remove fish waste and food, and then, it is returned to the tanks (i.e. 90–99% of water is reused) (Rosenthal 1986; Verdegem *et al.* 2006; Badiola *et al.* 2012; Nazar *et al.* 2013). By controlling fish waste, uneaten food, the nitrification process, and reducing ammonia toxicity, RAS has appeared as a viable form of intensive fish production (Martins *et al.* 2010; Schneider 2010; Ebeling & Timmons 2012).

The main benefit of RAS is the capacity of reducing the need for fresh, clean water while still maintaining a healthy environment for fish. In this sense, a series of treatment processes are performed to maintain water quality. These steps are often conducted in order or sometimes in tandem and can be cataloged as follows: (i) removal of particles, (ii) biological filtration to remove ammonia and nitrite residues (i.e. biofiltering), (iii) aeration/oxygenation, (iv) buffering of pH, and (v) disinfection (McGee & Cichra 2000) (Fig. 1). From these steps, the most prominent is the removal of ammonia-related residues. This is done by a nitrifying biofilter that uses a microbial consortium to convert ammonia to less toxic nitrate (Crab *et al.* 2007) where the latter is then removed by water exchange (Gutierrez-Wing & Malone 2006; Martins *et al.* 2010). However, the most important disadvantage of the RAS is the deterioration of water quality whether the treatment processes within the system are not adequately controlled (Molleda *et al.* 2008).

In this review, we present an overview of the nitrification process and discuss our current understanding of nitrifying and heterotrophic bacteria present in recirculating aquaculture systems, highlighting examples of microorganisms in RAS. Subsequently, we describe nitrifying biofilters and discuss how quorum sensing controls the efficiency of nitrifying bacteria in RAS. Finally, we discuss the feasibility of using nitrifying biofilters and the potential applications of these biofilters to improve intensive fish farming procedures.

Nitrifying bacteria in recirculating aquaculture systems

Fish produce nitrogen-based waste products as a result of their nutrition and uneaten feed. These products are toxic to captive-reared animals and are environmental stressors that cause reduced appetite, decreases growth rates, and death at high concentrations (Mommsen & Walsh 1992; Kroupova *et al.* 2005; Nazar *et al.* 2013). Therefore, the effective biological filtration of these products is critical to fish production in RAS.

The process by which nitrogenous compounds are aerobically removed by a biological filter or biofilter is called aerobic nitrification (unless otherwise stated, when we refer to nitrifying bacteria, we will allude to aerobic nitrification). This is a two-step process, where ammonium (NH_4^+) is first oxidized to nitrite (NO_2^-) and then nitrite is oxidized to nitrate (NO_3^-) (Fig. 1) (Ebeling & Timmons

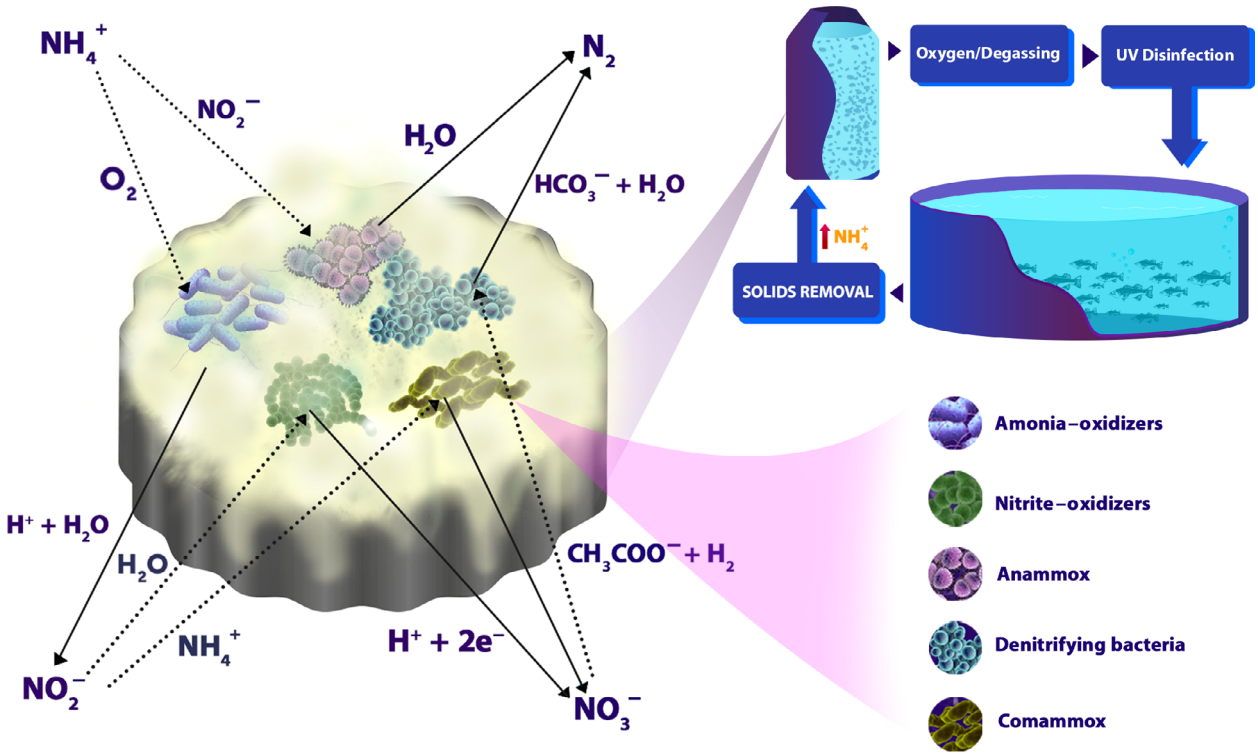

Figure 1 Schematic diagram of a nitrifying biofilter of a recirculation aquaculture system prototype. In a RAS, water flows from a fish tank through a treatment process and is then returned to the tank. The RAS will work effectively if they meet: (i) removal of solids, (ii) nitrifying biofilter, (iii) oxygen/degassing, and (iv) UV disinfection (up-right in the figure). The biofilter is the biological filtration process that allows the elimination of ammonia and nitrite residues. Most RAS biofilters use supports that allow the formation of biofilm from different bacterial consortiums, being responsible for many biogeochemical cycles in aquatic ecosystems, especially in the nitrogen cycle. In the supports (left in the figure),the different bacterial consortiums that participate in the nitrogen cycle are identified: the bacteria ammonia-oxidizer oxidizes the ammonium to nitrite ($NH_4^+ + 1.5O_2 \rightarrow NO_2^- + 2H^+ + H_2O$). Then this nitrite can be used by nitrite oxidizer bacteria, which oxidize it to nitrate ($NO_2^- + H_2O \rightarrow NO_3^- + 2H^+ + 2e^-$). These two processes are the bases of nitrification. However, we can find other bacterial consortia such as anaerobic ammonium oxidizing bacteria (anammox) that oxidize ammonium to nitrite and convert it to N_2 gas ($NH_4^+ + NO_2^- \rightarrow N_2(g) + 2H_2O$). In addition to these two types of nitrifying bacteria, complete ammonia oxidizers (comammox), which possess the full genetic complement for both ammonia and nitrite oxidation ($NH_4^+ \rightarrow NO_2^- \rightarrow NO_3^-$) are present in RAS. Finally, heterotrophic denitrifying bacteria, which use organic matter from uneaten food and fish faeces to metabolize nitrogen oxides (NO_2^-, NO_3^-) to nitrogen gas (N_2) ($5CH_3COO^- + 8NO_3^- + 3H^+ \rightarrow 10HCO_3^- + 4N_2(g) + 4H_2O$), can also be present in RAS (Ebeling & Timmons 2012; Marx Sander *et al.* 2018). The chemical reactions are not balanced.

2012). This process is performed mainly by two different bacterial consortia, which are interdependent aerobic lithoautotrophic microorganisms. These phylogenetically distinct groups of bacteria, known as the ammonia oxidants and nitrite oxidants, perform collectively the nitrification and control ammonia levels (Beman *et al.* 2010). Ammonia-oxidizing bacteria (AOB) obtain their energy by catabolizing un-ionized ammonia to nitrite (Sedlacek *et al.* 2016) and include bacteria from two lineages: β-proteobacteria (e.g. *Nitrosomonas*, *Nitrosovibrio*, *Nitrolobus* and *Nitrospira*) and γ-proteobacteria (e.g. *Nitrosococcus*) (Table 1). In addition to AOB, the presence of ammonia-oxidizing archaea (AOA) has been reported in biofilters (Schreier *et al.* 2010; Sakami *et al.* 2012). These archaea also play an important role in the removal of nitrogen-containing waste and include species of the genera *Nitrosoarchaeum*, *Nitrosopumilus*, *Nitrososphaera*, and *Nitrosotalea* (Phylum: Thaumarchaeota) (Table 1).

It has been documented that AOB and AOA convert ammonium (NH_4^+) to nitrite (NO_2^-) via a single obligate intermediate, hydroxylamine (NH_2OH) (Daims *et al.* 2016; Caranto & Lancaster 2017). This first step in the nitrification process is done by two enzymes: ammonia monooxygenase and hydroxylamine dehydrogenase (Sedlacek *et al.* 2016; Wang *et al.* 2018), where the former oxidizes ammonia to hydroxylamine and the latter oxidizes hydroxylamine to nitrite (Daims *et al.* 2016; Caranto & Lancaster 2017). Within this step, the speed of nitrification is controlled by

Table 1 Diversity of nitrifying bacteria in RAS biofilters

Process	Reaction	Phylum or class	Microorganism	
			Freshwater	Seawater
Nitrification				
Ammonium oxidation	$NH_4^+ + 1.5O_2 \rightarrow NO_2^- + 2H^+ + H_2O$	β-Proteobacteria	*Nitrosomonas* sp. (Lu *et al*. 2016)	*Nitrosomonas* sp. (Paungfoo *et al*. 2007; Foesel *et al*. 2008; Keuter *et al*. 2017)
			Nitrosomonas oligotropha (Pedersen *et al*. 2009; Lu *et al*. 2016)	*Nitrosomona stercoris* (Huang *et al*. 2018)
			Nitrosomonas marina (Lu *et al*. 2016)	*Nitrosomonas marina* (Foesel *et al*. 2008; Sakami *et al*. 2012)
			Nitrosomonas europea (Lu *et al*. 2016)	*Nitrosomonas europaea* (Hovanec & DeLong 1996; Foesel *et al*. 2007; Huang *et al*. 2018)
			Nitrosomonas eutropha (Lu *et al*. 2016)	*Nitrosomonas aestuarii* (Sakami *et al*. 2012; Huang *et al*. 2018)
			Nitrosomonas communis (Lu *et al*. 2016)	*Nitrosomonas cinnybus/nitrosa* (Foesel *et al*. 2008)
			Nitrosomonas nitrosa (Lu *et al*. 2016)	*Nitrosomonas mobilis* (Foesel *et al*. 2008)
			Nirtosomonas ureae (Lu *et al*. 2016)	*Nitrosomonas halophila*
			Nitrosomonas cryotolerans	*Nitrosomonas cryotolerans* (Tal *et al*. 2003; Foesel *et al*. 2008; Huang *et al*. 2018)
				Nitrosomonas eutropha (Huang *et al*. 2018)
			Nitrosospira sp. (Lu *et al*. 2016)	*Nitrosospira* sp. (Foesel *et al*. 2008)
			Nitrosospira briensis (Lu *et al*. 2016)	*Nitrosospira briensis* (Foesel *et al*. 2008)
			Nitrosospira multiformis (Lu *et al*. 2016)	
Ammonium oxidation	$NH_4^+ + 1.5O_2 \rightarrow NO_2^- + 2H^+ + H_2O$	γ-Proteobacteria	*Nitrosococcus oceani* (Lu *et al*. 2016)	
		Thaumarchaeota	*Nitrosoarchaeum limnia* (Lu *et al*. 2016)	*Nitrosopumilus adriaticus* (Huang *et al*. 2018)
			Nitrosopumilus maritimus (Lu *et al*. 2016)	*Nitrosopumilus maritimus* (Sakami *et al*. 2012; Huang *et al*. 2018)
			Nitrososphaera gargensis (Lu *et al*. 2016)	*Nitrosopumilus koreensis* (Huang *et al*. 2018)
			Nitrososphaera viennensis (Lu *et al*. 2016)	*Nitrosopumilus piranensis* (Huang *et al*. 2018)
			Nitrosotalea devanaterra (Lu *et al*. 2016)	
Nitrite oxidation	$NO_2^- + H_2O \rightarrow NO_3^- + 2H^+ + 2e^-$	Nitrospira	*Nitrospira* sp. (Hovanec *et al*. 1998; Itoi *et al*. 2007; Pedersen *et al*. 2009; Santoro 2016)	*Nitrospira* sp. (Keuter *et al*. 2017)
			Nitrospira marina (Hovanec *et al*. 1998)	*Nitrospira marina* (Tal *et al*. 2003; Foesel *et al*. 2008)
			Nitrospira moscoviensis (Hovanec *et al*. 1998; Itoi *et al*. 2007)	*Nitrospira moscoviensis* (Foesel *et al*. 2008)
		α-Proteobacteria	*Nitrobacter* sp. (Hüpeden *et al*. 2016)	

Table 1 (continued)

Process	Reaction	Phylum or class	Microorganism	
			Freshwater	Seawater
				Nitrobacter sp. (Foesel *et al*. 2008; Zhu *et al*. 2016)
		β-Proteobacteria	*Nitrotoga* sp. (Hüpeden *et al*. 2016; Keuter *et al*. 2017) *Nitrotoga arctica* (Hüpeden *et al*. 2016)	
Anammox	$NH_4^+ + NO_2^- \rightarrow N2(g) + 2H_2O$	Planctomycetes	*Candidatus Kuenenia* (van Kessel *et al*. 2011)	*Candidatus Kuenenia* (Tal *et al*. 2006) *Planctomycetes* sp. (Lahav *et al*. 2009) *Candidatus Scalindua* (Tal *et al*. 2006)
		Candidatus Brocadiae	*Candidatus Brocadia* (van Kessel *et al*. 2011)	*Brocadia* sp. (Tal *et al*. 2006)

the ammonia monooxygenase, which is the key enzyme of all known bacterial and archaeal ammonia oxidizers (Daims *et al*. 2016). This enzyme is comprised of three subunits (alpha, beta, and gamma) with putative genes encoding for all three subunits (*amoA*, *amoB*, and *amoC*) (Norton *et al*. 2002). Among them, the α subunit (encoded by the *amoA* gene) is responsible for catalysing the oxidation of ammonia to hydroxylamine and has been used as a functional marker for monitoring ammonia oxidants in diverse environmental samples (Rottthauwe *et al*. 1997; Francis *et al*. 2005). Although it has been suggested that *amoA* gene abundance of AOB may be greater than AOA in estuarine environments, quantitative analyses of the *amoA* gene show that AOAs are ubiquitous and largely outnumber AOB in diverse environments (Leininger *et al*. 2006; Wuchter *et al*. 2006; De Corte *et al*. 2009; Abell *et al*. 2010; Wankel *et al*. 2011; Santoro 2016). This could be explained by a higher AOA/AOB ratio in ecosystems with low-to-intermediate ammonia concentration (Koops & Pommerening-Röser 2001; Verhamme *et al*. 2011).

The second step of nitrification, which corresponds to the oxidation of nitrite to nitrate, is catalysed by nitrite-oxidizing bacteria: NOB. These are phylogenetically, physiologically, and ecologically diverse bacteria belonging to seven genera in four bacterial phyla (i.e. *Nitrobacter*, *Nitrotoga*, *Nitrospira*, *Nitrococcus*, *Nitrospina*, *Nitrolancea*, and ′*Candidatus* Nitromaritima′ (Daims *et al*. 2016). The NOB lineages are unevenly distributed with some representatives inhabiting specific environments, whereas others coexist in particular habitats (Daims *et al*. 2016). For instance, in freshwater and marine environments, the coexistence of species from two or three genera of NOB has been reported (Alawi *et al*. 2007; Attard *et al*. 2010; Daims *et al*. 2016), whereas in RAS, NOB from the genus *Nitrobacter*, *Nitrospira*, and *Nitrotoga* have been reported to coexist (Table 1).

All NOB, independently from their phylogenetic lineage, use the enzyme nitrite oxidoreductase to oxidize nitrite (NO_2^-) to nitrate (NO_3^-) (Dionisi *et al*. 2002; Beman *et al*. 2010). This enzyme belongs to the type II DMSO reductase-like family of molybdopterin-binding enzymes (Lücker *et al*. 2010, 2013), is encoded by two genes (*nxrA* and *nxrB*) (Breuillin-Sessoms *et al*. 2017; Wang *et al*. 2017; Hou *et al*. 2018), is associated with the cytoplasmic membrane (de Almeida *et al*. 2016), and shuttles two electrons per reaction (Table 1). Although nitrite is usually converted to nitrate as quickly as it is produced, lack of biological oxidation of this nitrogen compound results in elevated nitrite levels that can be toxic due to it enters the fish bloodstream, oxidizing the iron in the haemoglobin (Dosdat *et al*. 2003; Lin & Chen 2003; McKenzie *et al*. 2003; Lemarie *et al*. 2004).

In addition to AOB/AOA and NOB, other microorganisms present in a RAS, and which are simultaneously active with AOB/AOA and NOB (van Kessel *et al*. 2011), are anaerobic ammonium-oxidizing (anammox) bacteria (Table 2). These bacteria are a specialized group of planctomycete-like microorganisms and play an important role in the nitrogen cycle because they oxidize ammonium to dinitrogen gas (N_2) using nitrite as the electron acceptor under anoxic conditions (Van Rijn 1996; Hu *et al*. 2011; Table 2; Fig. 1). Therefore, this process does not consume oxygen, it does not need an electron acceptor for the removal of ammonium and does not release toxic intermediaries into the water column (Jetten *et al*. 2009). Indeed, anammox bacteria use 50% less oxygen compared to conventional nitrification–denitrification processes (Jetten *et al*. 2001).

Recently, the surprising discovery of NOB from the genus *Nitrospira* with the capacity of performing complete nitrification by its own has revolutionized research on nitrification and the nitrogen cycle (Daims *et al.* 2015; Gonzalez-Martinez *et al.* 2016; Santoro 2016). These bacteria are known as complete ammonia oxidizers (comammox) and possess the full genetic complement for both ammonia and nitrite oxidation (Fig. 1; Van Kessel *et al.* 2015; Santoro 2016). Like the canonical AOB/AOA and NOB, comammox bacteria utilize the enzymes ammonia monooxygenase and hydroxylamine oxidoreductase for ammonia oxidation even though their forms are phylogenetically distinct from the homologs in AOB and AOA, and nitrite oxidoreductase (NXR), which is highly similar to the NXRs of strictly nitrite-oxidizing *Nitrospira*, for nitrite oxidation (Daims *et al.* 2015; Van Kessel *et al.* 2015). Although these one-step nitrification bacteria were originally identified from a trickling filter connected to an aquaculture system (Van Kessel *et al.* 2015), the identification of comammox has patchily been reported in RAS (Bartelme *et al.* 2017; Huang *et al.* 2018) due to the lack of methods for detecting and quantifying efficiently comammox *Nitrospira* from non-comammox counterparts (Daims *et al.* 2015). Therefore, high-throughput approaches such as meta-(genomics/transcriptomics) should be used to specifically measure the abundance and nitrification activity of comammox (as well as other microbial communities) in order to understand its contribution to nitrification in RAS.

Heterotrophic bacteria in recirculating aquaculture systems

Besides nitrifying bacteria, heterotrophic microorganisms also reside in RAS (Leonard *et al.* 2000; Mahanta *et al.* 2014; Rurangwa & Verdegem 2015). Heterotrophic bacteria are the most abundant and diverse group within RAS and somehow contribute to maintaining suitable water quality by eliminating nitrogenous compounds from the environment through assimilation into microbial biomass in a single-step process called denitrification (Pan *et al.* 2015; Table 2). In this process, heterotrophic denitrifying bacteria use organic matter coming from uneaten food and fish faeces to metabolize nitrogen oxides (NO_2^-, NO_3^-) to nitrogen gas (N_2), producing a large amount of bacterial biomass (Fig. 1; Fdz-Polanco *et al.* 2000; Crab *et al.* 2007). Another heterotrophic microbial community involved in nitrogen cycling and removal in RAS include sulphide-dependent denitrifying bacteria, which are capable of oxidizing organic waste to reduce sulphate to sulphide and ultimately, to produce nitrogen gas. However, they are out of the scope of this review article but see other report for details (Schreier *et al.* 2010; Blancheton *et al.* 2013; Rurangwa & Verdegem 2015). Therefore, sufficient organic carbon concentration or adequate carbon/nitrogen ratio have been demonstrated as a crucial factor in ensuring the desired nitrate concentration in recirculating aquaculture systems (He *et al.* 2018).

Within a RAS, there are full of microniches (e.g. organic carbon dissolved and organic carbon trapped particles) suitable for the growth of heterotrophic bacteria (Michaud *et al.* 2006). Most heterotrophic microorganisms are considered to be neutral and beneficial microbes. For instance, since heterotrophic bacteria are found mainly in the outer layer of a biofilm, it has been proposed that they could protect nitrifying bacteria against detachment (Fdz-Polanco *et al.* 2000). In addition, some heterotrophic bacteria play also a role in the development of fish digestion and morphological changes in larvae, which altogether, protect cultured fish against pathogens (Blancheton *et al.* 2013). Inclusively, it has also been shown that some heterotrophic bacteria increase the expression of proteins related to the ammonium oxidation pathway of AOB, by doing so, promoting nitrification (Sedlacek *et al.* 2016).

Nonetheless, the heterotrophic microbial community in RAS also contains pathogenic and opportunistic bacteria (Leonard *et al.* 2000). In fact, pathogens can accumulate more in RAS than in single-pass systems (Leonard *et al.* 2000), and infections are possible after the release of biofilms and contact with cultured organisms (Michaud *et al.* 2009). Some of the pathogens found in freshwater systems include *Flavobacterium* sp., *Aeromonas salmonicida*, and *Edwardsiella* sp., whereas seawater systems comprise *Aeromonas* sp., *Vibrio* sp., and *Tenacibaculum soleae*, (Itoi *et al.* 2007; Schneider *et al.* 2007; Michaud *et al.* 2009; Martins *et al.* 2013; Ardiansyah & Fotedar 2016) (Table 2).

Most microbiological researchers in RAS have been focused on nitrifying bacteria (Schreier *et al.* 2010; Rurangwa & Verdegem 2015), while heterotrophic bacterial populations have received little attention (Leonard *et al.* 2000; Brailo *et al.* 2019).

Biofilters and recirculating aquaculture systems

As described above, the microbial communities in a RAS comprise a great diversity of nitrifying and heterotrophic bacteria representing unique and complex environments (Fig. 1). Therefore, the development of environmentally sustainable intensive farming of freshwater and marine species using RAS requires the management of nitrifying and heterotrophic bacteria in order to maintain good water quality and health of farmed organisms (Leonard *et al.* 2000; Michaud *et al.* 2009; Mahanta *et al.* 2014). Fortunately, this is done by means of bioreactor assemblies that reduce or eliminate harmful wastes from RAS. Overall, these bioreactors, known as biofilters or nitrifying biofilters, are physical compartments that are distributed in different

Table 2 Heterotrophic bacteria present in RAS biofilters

Process	Reaction	Phylum or Class	Microorganism	
			Freshwater	Seawater
Denitrification	$5;CH_3COO^- + 8NO_3 + 3H^+ \rightarrow 10HCO_3^- + 4N_2(g) + 4H_2O$	α-Proteobacteria		*Paracoccus denitrificans* (Cytryn *et al*. 2003) *Ruegeria* sp. (Michaud *et al*. 2009) *Roseobacter* sp. (Michaud *et al*. 2009)
		β-Proteobacteria	*Comamonas* sp. (Leonard *et al*. 2000; Tal *et al*. 2003; Itoi *et al*. 2007)	*Aquaspirillum* sp. (Schreier *et al*. 2010)
		δ-Proteobacteria	*Pseudomonas* sp. *Pseudomonas mendocina* (Ardiansyah & Fotedar 2016) *Pseudomonas stutzeri* (Ardiansyah & Fotedar 2016) *Azotobacter vinelandii* (Ardiansyah & Fotedar 2016)	*Pseudomonas* sp. (Leonard *et al*. 2000; Tal *et al*. 2003) *Pseudomonas fluorescens* (Borges *et al*. 2008; Michaud *et al*. 2009) *Pseudomonas stutzeri* (Michaud *et al*. 2009)
		Bacilli	*Bacillus licheniformis* (Ardiansyah & Fotedar 2016) *Bacillus subtilis* (Ardiansyah & Fotedar 2016)	*Bacilus licheniformis* (Deng *et al*. 2014) *Bacilus cereus* (Deng *et al*. 2014) *Bacilus methylotrophicus* (Deng *et al*. 2014)
Pathogens	Undetermined	δ-Proteobacteria	*Aeromonas salmonicida* (Ardiansyah & Fotedar 2016) *Edwardsiella* sp. (Schneider *et al*. 2007)	*Aeromonas* sp. (Michaud *et al*. 2009) *Erwinia* sp. (Michaud *et al*. 2009) *Coxiella* spp. (Michaud *et al*. 2009) *Photobacterium damselae* (Martins *et al*. 2013) *Serratia marcescens* (Martins *et al*. 2013) *Vibrio* sp. (Michaud *et al*. 2009)
		Flavobacteriia	*Flavobacterium* sp. (Itoi *et al*. 2007)	*Tenacibaculum soleae* (Martins *et al*. 2013) *Tenacibaculum discolor* (Martins *et al*. 2013)

parts in a RAS and include a medium or system for microbial attachment and growth (Molleda *et al*. 2008; Martins *et al*. 2010; Suhr & Pedersen 2010).

Synthetic polymers (e.g. polypropylene) are increasingly used as material for biofilters in RAS because they provide a uniform surface for the water flow and also are inexpensive and durable (Van Rijn 1996; Timmons & Ebeling 2007). The most important component in a biofilter is the substrate that bacteria (i.e. nitrifying and heterotrophs) use for attachment and colonization (Fig. 1) (Carroza *et al*. 2012). There are many substrates currently used to grow bacteria in a biofilter. These include: (i) emerging substrates (e.g. rotating biological contactors and trickling filters), (ii) submerged substrates (e.g. fixed bed, moving bed, and expandable bead filters), and (iii) fluidized–sand substrates, which provide wide contact surface to support the development of the biofilm and which is suspended by an upward current of water (Ebeling & Michael 2002). Among these substrates, the use of fixed bed filters is the most common choice for both nitrification and denitrification processes in a RAS (Pedersen *et al*. 2015).

Bacteria are able to growth in distinct substrates, and biological treatments (i.e. nitrogen removal conducted by bacteria) in suspension have been successful in filtering

water in tilapia cultures; however, biological treatments in fixed substrates have been more reliable and are used more often to control water quality in RAS (Malone 2013). These fixed-film bioreactors are characterized by the formation of a biofilm (see below), which is defined as a community of microorganisms attached to a physical or liquid substrate that is immersed in a self-produced extracellular matrix (Emparanza 2009; Malone 2013). In this way, nitrifying and heterotrophic bacterial communities compete for space, substrate, organic carbon, and dissolved oxygen to colonize the bioreactor (Schreier *et al.* 2010; Bassin *et al.* 2012; Kumar *et al.* 2013).

The performance of biofilters is conventionally reported as total ammonia nitrogen (TAN) (Wiesmann 1994). This measure is highly influenced by physicochemical factors, such as temperature, pH, dissolved oxygen, and N- and C-loads, but also by the operational management of biofilters, for example, water flow distribution, washing regimes, UV disinfection, and ozonation treatments. Since biofilters are comprised of microbial communities whose structure, dynamics, and activities influence RAS efficiency, it is really complicated to give the best recipe in terms of physicochemical factors and operational management that must have an ideal biofilter. It has been reported that the optimal proliferation of nitrifying bacteria occurs in an environment with a pH between 7 and 9, dissolved oxygen >2.5 mg L^{-1}, and temperature between 8 and 27°C (Wiesmann 1994; Chen *et al.* 2006; He *et al.* 2012; Rodriguez-Sanchez *et al.* 2014). However, the optimal combination of these parameters is difficult to obtain in a highly dynamic system where bacterial metabolisms should be tightly orchestrated to complete the nitrification process (Bentzon-Tilia *et al.* 2016). We can manage some factors, but we could affect the performance of some nitrifying bacteria. For example, NOB have slower growth rates than AOB when the temperature rises to 24°C (Rodriguez-Sanchez *et al.* 2014). Whereas a pH between 7.5 and 8.5 is the most suitable to inhibit NOB activity, it has also been suggested that a pH between 7.5 and 7.8 favours partial nitrification (He *et al.* 2012). In addition, it has been reported that UV disinfection and ozonation treatments disturb considerably the microbial communities in RAS (Sharrer & Summerfelt 2007; Gonçalves & Gagnon 2011; Rose & Rice 2014; Li *et al.* 2017).

Considering the dynamic and adaptive nature of the bacteria in the biofilters, it is unlikely that a biofilter fulfils the above-mentioned criteria, making difficult to compare the nitrification yields from RAS to RAS (Suhr & Pedersen 2010).

Bacterial biofilms, quorum sensing, and recirculating aquaculture systems

Within a biofilter, microorganisms can be found freely floating in the water column in planktonic phase or living in complex aggregations attached to a solid substrate, forming biofilms (Fig. 1) (Sugita *et al.* 2005; Itoi *et al.* 2007; King *et al.* 2008). Biofilms can comprise a single microbial species or multiple microbial species (Tilahun *et al.* 2016). Biofilm formation is a process whereby microorganisms adapt to an aggregate lifestyle on a surface to form microcolonies leading to the production and secretion of extracellular polymeric substances (EPS) (Meyer-Reil 1994; Tilahun *et al.* 2016). This can lead to the formation of multilayered biofilms, which are surrounded by a matrix of EPS (i.e. biofilm maturation). After that, cells can leave the biofilm to colonize new sites (i.e. dispersion) (Decho 1990). The development of biofilms from free-swimming cells involves profound changes in many regulatory processes that result in phenotypic shifts in behaviour (Dickschat 2010; Røder *et al.* 2016).

In a RAS biofilter, it is likely to find the majority of the bacteria organized as biofilms because of the high number of substrates present in a biofilter (Fig. 1). These substrates provide a stable and protective environment for bacteria, which along with RAS conditions, supply enough nutrient and optimal conditions for interactions among bacteria (Prehn *et al.* 2012; Kumar *et al.* 2013; Sánchez-O *et al.* 2016; Zhu *et al.* 2016). Inside a biofilm in a RAS, bacterial distribution is influenced by oxygen and nutrient availability. For instance, the oxic part of the biofilm, which is subjected to high ammonia and nitrite concentrations, is dominated by nitrifying bacteria, while denitrifying organisms are situated in the anoxic layers and heterotrophic bacteria being located in the outermost layer of the biofilm (Fdz-Polanco *et al.* 2000; Leonard *et al.* 2000; Michaud *et al.* 2009).

While biofilm formation and behaviour were originally thought to depend only on environmental factors, we now understand that some bacteria can modify their behaviour in a coordinated fashion, not only in natural environments but also in RAS environments, using a strategy based on cell-to-cell communication that affects gene expression and physiological behaviour of microbial communities. This strategy is known as quorum sensing (QS) (Ng & Bassler 2009; Dickschat 2010). Therefore, RAS biofilter performance critically relies on the interactions of microbial communities within the biofilm. Many bacteria, including nitrifying, denitrifying, and heterotrophic species, coordinate their metabolic activities with respect to changes in cell density through QS signalling systems (Ng & Bassler 2009; Zhu *et al.* 2016).

Although there is no comprehensive knowledge regarding whether nitrifying and heterotrophic bacteria employed in RAS have functional QS systems, it has been found QS molecules in the biofilm maturation process in an Atlantic salmon RAS (Zhu *et al.* 2016).

There are several types of QS signalling systems used by bacteria (Shrout & Nerenberg 2012). To date, the

predominant QS signalling pathway in Gram-negative bacteria corresponds to the LuxI/LuxR system that utilizes acyl-homoserine lactones (AHLs) signal molecules (Mok *et al.* 2003; Liaqat *et al.* 2014). In the LuxI/LuxR system, the AHLs (i.e. autoinducers) are synthesized by LuxI proteins at low cell density, but once bacterial cells grow and only when sufficient AHL signal is present, the autoinducers are bound to LuxR proteins, activating the transcription of *lux* genes which regulates the expression of QS-dependent genes (Fig. 2) (Eberhard *et al.* 1981; Engebrecht *et al.* 1983; Engebrecht & Silverman 1984; Stevens *et al.* 1994; Chen *et al.* 2002). Since the expression of *luxI* is activated by the *luxR* bound to the autoinducer, this self-inducing loop of positive feedback is presumed to enforce synchrony as the cell population changes from low to a high cell density (Fig. 2) (Ng & Bassler 2009). AHL molecules have been detected in an Atlantic salmon RAS (Zhu *et al.* 2016). These molecules were *N*-butyryl-DL-homoserine lactone (C4-HSL), *N*-octanoyl-LD-homoserine lactone (C8-HSL), and *N*-(3-oxooctanoyl)-L-homoserine lactone (3OC8-HSL) and might regulate activities of the biofilm (Zhu *et al.* 2016). For this reason, we strongly believe that QS systems influence RAS biofilms and would like to highlight the different QS systems that might be influencing RAS performance.

Another QS signalling pathway, but predominantly used by Gram-positive bacteria, comprises the use of amino acid peptides as signal molecules (Camilli & Bassler 2006). The QS principle is the same as in AHL-mediated QS system, peptide signals are sensed by a dual-response regulatory cascade and bacterial cells respond to a buildup of the extracellular signal concentrations (Dunny & Leonard

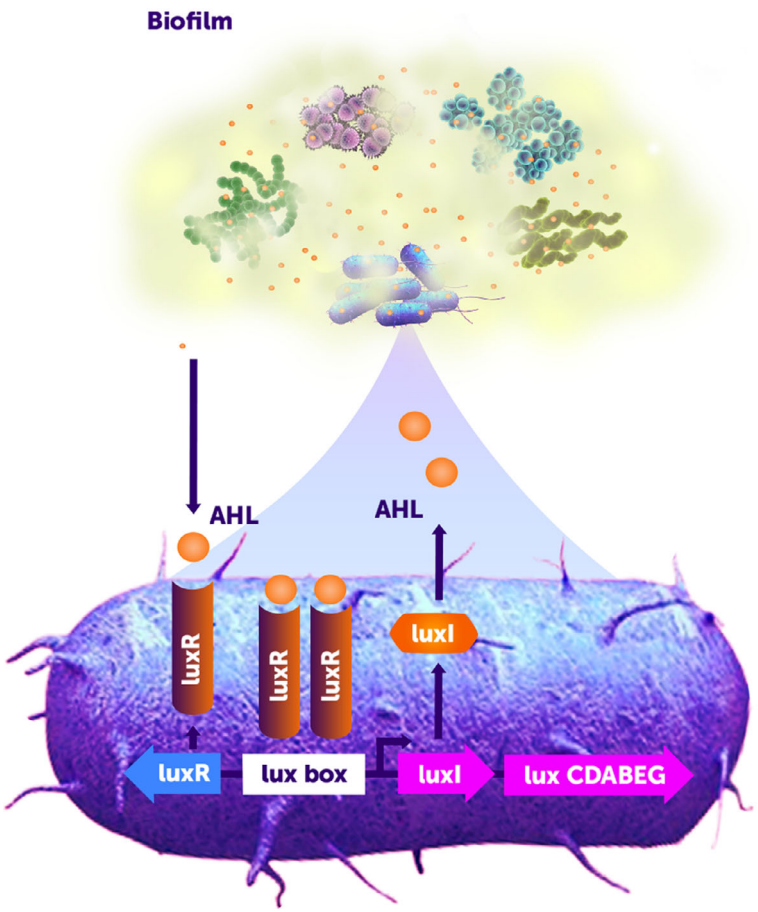

Figure 2 Schematic representation of acyl-homoserine lactone dependent QS system as exemplified by LuxI/R system for *Vibrio fisheri*. Some bacteria can modify their behaviour in a coordinated fashion, using a method of cell-to-cell communication that affects gene expression and physiological behaviour of microbial communities. The QS system works as follows: the gene *luxI* encodes a signal synthase protein that catalyses the synthesis of acylated homoserine lactones AHL (orange circles). In fact, LuxR united to AHL binds a short sequence termed lux box and activate the transcription of the downstream operon *lux CDABEG*, which contains the *luxI* gene that encodes the AHL synthase. The concentration of AHL molecules increases as the bacteria population grow. Many bacteria, including nitrifying, denitrifying, and heterotrophic species, coordinate their metabolic activities with respect to changes in cell density through QS signalling system (Li & Nair 2012; Hmelo 2017).

1997). Transcription of QS-regulated genes occurs by a cascade of responses that involves a sensor kinase protein that phosphorylates a response regulatory protein for then initiates the transcription of a gene, but this cascade is triggered by a sufficient extracellular signal peptide concentration (Shrout & Nerenberg 2012). Another QS system is the AI-2 signalling pathway (Camilli & Bassler 2006). The AI-2 signalling appears to provide the possibility of interspecies communication and quorum sensing, because many bacteria, such as Gram-negative and Gram-positive, have a gene called *luxS* that is required for the synthesis of AI-2 signals (Xavier & Bassler 2003). While many *luxS* genes have been identified in bacteria using genomic techniques (Xavier & Bassler 2003), little is known about the functions of AI-2 signalling pathway. However, it seems reasonable to assume that this QS signalling pathway is important in RAS biofilms with mixed-species, as has been shown in laboratory-scale sequencing batch reactors (Xiong & Liu 2010). Finally, other QS signalling systems involve signals as diverse as natural small molecule (NSM), diffusible signal factor (DSF), and *Pseudomonas* quinone signal (PQS) (Shrout & Nerenberg 2012). None of those QS signalling systems or associated molecules have been found so far in RAS.

Due to QS plays significant roles in controlling cell-to-cell interaction as a means to gauge population density in the biofilm (Dickschat 2010), as well as the detection of AHL molecules in a RAS (Zhu *et al.* 2016) have allowed us to believe that community-signalling aspects of biofilms have the potential to impact design and RAS system operations. For example, by means of controlling the expression of certain genes, we can induce or modify several activities that occur in a RAS biofilter, such as bacteria attachment, biofilm growth, biofilm detachment and bacteria colonization (Zhu *et al.* 2016), but also we can control the physiological behaviour of the biofilm, including resistance to stress, production of toxins and secondary metabolites, and survival and pathogenicity (Horng *et al.* 2002; Lumjiaktase *et al.* 2006; Blackwell & Fuqua 2011; Shrout *et al.* 2011). Particularly in nitrifying bacteria, QS could be considered as a mechanism that contributes to the coupling and maintenance of efficient nitrification among bacteria by inducing and/or increasing the expression levels of genes associated with ammonia oxidation (*amoA*), nitrite oxidation (*Nir*), and the production of exopolysaccharides (*eps*) (Waters & Bassler 2005; Hense *et al.* 2007). Taken together, QS can be seen as a biological control to monitor what is happening in a RAS biofilm.

Another way of regulating biofilm performance is through molecules capable of disrupting QS autoinducers. These molecules are known as QS inhibitors (quorum quenching) and can enzymatically inactivate QS autoinducers, such as AHLs (Dickschat 2010). Over the last few years, a range of QS inhibitors has been identified in various Gram-negative and Gram-positive bacteria (Zhang & Li 2016). Although these QS inhibitors are key molecules for understanding the concept of quorum-quenching (QQ) in regulating quorum-sensing (QS) phenotypes by interrupting bacterial communication (Dong & Zhang 2005; Grandclément *et al.* 2015; Romero *et al.* 2015), not much is known about QS inhibitors in RAS biofilters.

Currently, there are no many reports about QS systems or associated molecules in RAS (Zhu *et al.* 2016), but this information is paramount to fully understand the role of the quorum systems in RAS. Interestingly, studies using genome-wide surveys and domain-based strategies have identified Lux genes (*LuxI, LuxR,* and *LuxS*) in thousands of bacterial genomes (Subramoni *et al.* 2015; Rao *et al.* 2016; Rajput & Kumar 2017).

As the field of genomics and bioinformatics advances, we think that metagenomics approaches, where we will be able to determine bacterial abundance and classification but also assemble bacterial genomes present in a RAS, and bioinformatics surveys for QS and QQ components will gain more attention in the years to come. Consequently, we think that cell signalling and quorum-sensing inducers (and potentially quorum-sensing inhibitors) are essential for biofilm development, as well as for RAS efficiency. Therefore, quorum systems comprise an interesting line of exploration to implement practical applications into the aquaculture.

Biotechnological applications of nitrifying biofilms and recirculating aquaculture systems

The stable and viable nitrifying biofilm is the key component of the intensive RAS. In practice, a biofilm is usually formed by natural colonization of nitrifying bacteria in the water column (Kuhn *et al.* 2010). However, it takes a long time (4–8 weeks) to establish a stable nitrification capacity and a population of nitrifying bacteria in the biofilter, possibly due to the influence of environmental stressors and the balance that must occur between different microbial consortia (Malone & Pfeiffer 2006; Emparanza 2009; Kumar *et al.* 2013). One way of accelerating biofilm maturation is by seeding of a commercial source of nitrifying bacteria followed by the addition of appropriate concentrations of ammonia and nitrite (Brailo *et al.* 2019). Alternatively, the use of water or active media from an already operating system can also accelerate biofilm maturation (Zhu *et al.* 2016). However, these operational managements do not guarantee success in terms of the viability and stability of the RAS biofilm. Thus, the biotechnological improvement of the nitrifying biofilters in RAS draws our attention, since it would allow the development of aquaculture production in an efficient and ecological way (Hüpeden *et al.* 2016).

Next, we will indicate some of the potential biotechnological applications that can be conducted to improve RAS nitrifying biofilters:

(1) A rapid start-up of the nitrifying biofilter is essential to produce a RAS. It has been reported that AHL can activate gene expression and modifies behaviours in microorganisms. In fact, the formation of nitrifying biofilms has been determined using mature biofilm as inoculum to accelerate the process (Valle *et al.* 2004). In RAS, the presence of AHLs in the biofilm maturation, which might be regulating biofilm activities, has been discovered (Zhu *et al.* 2016). As discussed above, nitrifying consortia could be enhanced by means of manipulating the bacteria that affect nitrification, either increasing their abundance or accelerating their settlement capacity in order to form a biofilm in a short period of time.

(2) It has been reported that in order to improve the speed of formation of nitrifying biofilms, it is possible to add extracellular polymeric substances (EPS) produced by heterotrophic bacteria (Tsuneda *et al.* 2001). Furthermore, in the early stages of biofilm formation of nitrifying bacteria, the production of AHL has also closely related to EPS production in the biofilm (Hu *et al.* 2016). Therefore, the use of autoinducers and the appropriate substrate could provide an alternative to rapidly establishing a nitrifying biofilm (Tsuneda *et al.* 2001; Zhu *et al.* 2016).

(3) The use of bacterial biosensors capable of detecting the presence of AHLs of nitrifying bacteria in the RAS biofilter. These bacterial biosensors contain a functional protein of the LuxR family that recognizes exogenous AHLs, at the quorum concentrations, generating a phenotypic change (Steindler & Venturi 2007). Given that there is a large number of AHL-QS systems identified (Camilli & Bassler 2006; Liaqat *et al.* 2014; Grandclément *et al.* 2015), these bacterial biosensors are not biofilm- or nitrifying bacteria-specific. In addition, this technology appears to work only for Gram-negative bacteria where QS is mediated by AHLs. However, the development and improvement of AHL biosensing technology will be fundamental in future studies that involve interaction and communication with eukaryotes, detection of AHLs in environmental samples, interspecies and intergeneric communication, and stage biofilm maturation (Steindler & Venturi 2007).

(4) Pathogenic/opportunistic bacteria may be present in the RAS nitrifying biofilters (Michaud *et al.* 2009; Schreier *et al.* 2010; Martins *et al.* 2013), and it is likely that these bacteria possess a LuxI-LuxR system with species-specific signal molecules (Bzdrenga *et al.* 2017). Therefore, the use of QS inhibitors or quorum quenching (QQ) is an attractive strategy to attenuate bacterial disease by blocking the action of autoinducers (e.g. AHLs, AI-2), and by doing so, QQ-proteins are able to degrade these signal molecules (Defoirdt *et al.* 2004; Gutiérrez-Barranquero *et al.* 2015). This might be possible only whether signal molecules produced by a bacterium are species-specific and pathogenic/opportunistic bacteria have different LuxI-LuxR homologs. If this is the case, QS inhibitors might reduce bacterial infections with a limited possibility that resistance will develop (Defoirdt *et al.* 2004). It should be noted that this potential biotechnological application has not been applied in aquaculture. Therefore, the impact of QS inhibitors on aquaculture systems should be studied in more depth.

Clearly, there are many open questions in this area that can be answered by investigating the importance of QS to nitrifying bacteria in multiple ways. The developments in the field of nitrifying bacteria and QS-regulated behaviours in RAS will undoubtedly bring new insights and surprises to the aquaculture systems, such as intensive fish farming.

Concluding remarks and perspectives

We here reviewed current knowledge on nitrifying bacterial communities, nitrifying biofilters, quorum sensing in biofilms, and recirculating aquaculture systems. From an engineering perspective, in a recirculating aquaculture system, the ideal material for a biofilter should have a high area in terms of volume, but at the same time, it should be inexpensive and durable in the time and should allow a uniform distribution of the water avoiding the obstruction by particles. In addition, an ideal biofilter should remove all nitrogenous compounds of the effluent, produce no nitrite, support dense nitrifying bacterial populations and require low maintenance.

From a biological perspective, nitrifying and heterotrophic bacteria can grow either in suspension or in fixed form. In RAS nitrifying biofilters, different microbes are used to remove toxic ammonia from the water. Although DNA-based molecular techniques have allowed understanding the variation in nitrifying microbial community structure in response to changes in RAS, studies on interactions between nitrifying bacteria and among heterotrophic bacteria are scarce. Therefore, a comprehensive understanding of nitrifying and heterotrophic bacteria composition and activity in a RAS could give us valuable information on the presence/absence of nitrifying and denitrifying bacteria, of potential fish pathogens, and of biocontrol bacteria and their accumulation in the system.

Thanks to the advent of high-throughput sequencing technologies, such as metagenomics and metatranscriptomics, we will be able not only to describe in high-

resolution the bacterial communities in a RAS, but also to know what genes are being expressed at different stages of a RAS and which metabolic pathways are enriched in order to understand the interactions among nitrifying, denitrifying, and heterotrophic bacteria in a biofilm at an unprecedented level.

On the other hand, to obtain a high performance in a RAS, it is necessary to carry out further studies focused on accelerating the growth and adhesion of the bacterial community to the filter. We need to improve the bacterial colonization and start-up of nitrifying biofilters in order to shorten maturation times and improve water quality. In addition, new technologies are necessary to early activate the biofilters with molecules capable of stimulating the expression of key genes in the nitrification process (i.e. QS-mediated starting biofilters). The development and characterization of these molecules have not been defined in the products currently on the market for RAS nitrifying biofilters. By doing so, the aquaculture industry associated with RAS will be benefited, increasing the capacity of intensive fish culture and minimizing the operational and environmental impacts.

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Conflict of interest

The authors declare that they have no conflict of interests.

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