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Salinity Acclimation Strategies in Nitrifying Bioreactors

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Several industries, including aquaculture, produce effluents with high or varying salt concentrations. The treatment of such effluents by the biological nitrification process can be challenging, as the microbes performing this process are sensitive to salinity. In certain cases, such as in recirculating aquaculture systems (RAS), it is essential to maintain high nitrification efficiency during salinity changes to prevent ammonia and nitrite toxicity. Therefore, suitable strategies are required to make nitrifying bioreactors tolerant to salinity variations. Although salinity changes can impact the nitrification performance, it has been shown that nitrifying bioreactors can acclimate to salinity variations over several days. This acclimation can be due to the physiological adaptation of the existing microorganisms or due to selection for microorganisms adapted to that salinity regime. Other factors, such as the biofilm matrix, can also play a role in salinity acclimation. Recent studies have shown that microbial management strategies can be applied to improve the salinity tolerance and reduce the recovery time of nitrifying bioreactors. Here, we discuss the existing knowledge on salinity acclimation in nitrifying systems, and recent advances in strategies to make nitrifying biofilms more tolerant to salinity variations. We also propose directions for future research to improve our understanding of the salinity acclimation mechanisms in nitrifying systems.

Keywords: osmotic stress, osmoregulation, ammonia oxidizing archaea, seawater, halotolerance, compatible solute, osmolyte, wastewater

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INTRODUCTION

Worldwide, more than 5% of effluents are saline or hypersaline (Lefebvre et al., 2007). This will increase in the future as seawater may be utilized to fulfil freshwater shortages. Saline effluents are produced by several industries, such as petroleum refineries, leather, food and aquaculture (Intrasungkha et al., 1999; Lefebvre and Moletta, 2006). Wastewater treatment plants in coastal cities may also receive saline water from seawater flushing (Vyrides, 2015). In many systems, large variations in salinity are common due to process fluctuations, rather than a gradual increase (Lefebvre and Moletta, 2006). Moreover, salinity may change temporally (Vyrides, 2015). High or variable salinity can impact biological water treatment processes such as nitrification, as the osmotic stress can inhibit the activity of the microorganisms (Sleator and Hill, 2002; Madigan et al., 2018).

Nitrification is a two-step microbiological process where ammonia (NH_3) is first oxidized to nitrite (NO_2^-) and subsequently to nitrate (NO_3^-). The two steps are typically performed by two microbial guilds: 1) ammonia oxidizing microorganisms (AOM) that include ammonia oxidizing bacteria (AOB) and archaea (AOA), and 2) nitrite oxidizing bacteria (NOB), respectively (Madigan et al., 2018). Bacteria capable of complete oxidation of ammonia to nitrate (comammox) were recently discovered within the genus *Nitrospira* (Van Kessel et al., 2015). Despite the advantages of more recently discovered processes like anammox, nitrification is still commonly used to convert ammonia in water treatment plants. This is likely because the nitrifying microorganisms grow faster than anammox, and can function efficiently across a wider spectrum of environmental conditions. Nitrification is especially important in recirculating aquaculture systems (RAS). RAS are land-based fish farms with treatment systems to reuse the water. In RAS, nitrification is essential for keeping the concentration of ammonia and nitrite below toxic levels for the fish. Thus, it is vital to maintain high nitrification efficiency during salinity variations.

Although some literature reviews briefly discuss the impact of salinity on nitrification (Lefebvre and Moletta, 2006; Lay et al., 2010; Vyrides and Stuckey, 2017; Zhao et al., 2020), we are not aware of any reviews that describe strategies for salinity acclimation in nitrification processes,. Thus, here we present existing knowledge on the impact of salinity on nitrification and discuss recent advances in salinity acclimation strategies for nitrifying systems.

SALINITY ADAPTION MECHANISMS IN MICROORGANISMS

Salinity changes in the environment of a microbe can disrupt the osmotic balance. This osmotic pressure difference causes an instantaneous efflux or influx of water and/or a cell response to regulate the cellular osmolarity (Csonka, 1989; Sleator and Hill, 2002). The nature of these processes depends on whether the salinity shock is hyper- (salinity increase) or hypoosmotic (salinity decrease). Hypoosmotic shock is less severe as the rigid bacterial cell walls can withstand some increase in pressure caused by water influx (Csonka, 1989; Gonzalez-Silva et al., 2021). In contrast, hyperosmotic shock causes dehydration and plasmolysis (cell shrinkage), which can inhibit nutrient uptake and growth (Csonka, 1989; Madigan et al., 2018).

If the hyperosmotic shock is not severe, the cells can adapt to the higher salinity by increasing the internal osmolarity (Csonka, 1989). To accomplish this without losing water, the cells utilize either (i) the salt-in cytoplasm strategy, or (ii) the organic osmolyte (compatible solute) strategy (Csonka, 1989; Oren, 1999; Sleator and Hill, 2002). The salt-in strategy requires extensive structural adaptations, and is therefore only adopted by obligate halophiles (Sleator and Hill, 2002; Oren, 2011). The osmolyte strategy involves a bi-phasic response with an increase in K^+, followed by an increase of osmolytes in the cytoplasm (Sleator and Hill, 2002). Despite being more energy-intensive than the salt-in strategy, the osmolyte strategy is adapted by most halotolerant microorganisms, as it offers a higher degree of flexibility to combat variations in the external osmolarity (Sleator and Hill, 2002; Oren, 2011). The ability of a microorganism to survive in an environment with high/variable salinity depends on the energy generated during dissimilatory metabolism and the mode of osmotic adaptation (Oren, 2011). Autotrophic nitrifiers generate relatively little energy, and growth at elevated salinities can be challenging (Oren, 2011).

PHYLOGENY AND SALINITY TOLERANCE OF NITRIFYING MICROORGANISMS

Ammonia oxidizing bacteria belong to three genera within β- and γ-*proteobacteria*: *Nitrosomonas*, *Nitrosospira* and *Nitrosococcus* (Prosser et al., 2014). The salt tolerance of the species within *Nitrosomonas* and *Nitrosospira* varies greatly (**Table 1**). For example, whereas *Nitrosomonas oligotropha* has a maximum salt tolerance of ~100 mM (~6‰), other species such as *N. marina, N. aestuarii*, and *N. cryotolerans* are obligate halophiles (Koops et al., 2006). In contrast, *Nitrosococcus* has only been found in marine environments and is reported to be obligately halophilic (Koops et al., 2006).

Ammonia oxidizing archaea are phylogenetically restricted to the phylum *Thaumarchaeota*. AOA are abundant across a wide range of salinities (**Table 1**), both in natural and man-made systems (Francis et al., 2005; Bernhard and Bollmann, 2010; Sauder et al., 2011; Bartelme et al., 2017; Bartelme et al., 2019; Kitzinger et al., 2020). Moreover, AOA have been detected in estuaries, indicating that they can adapt to variable salinity (Bernhard et al., 2010; Santos et al., 2020). AOA are more abundant than AOB in ecosystems with low ammonia concentration (Bernhard et al., 2007; Ward et al., 2007; Bernhard et al., 2010; Nicol et al., 2011; Stieglmeier et al., 2014). Thus, AOA may be an important player in RAS (Sauder et al., 2011), where the ammonium concentration is typically low (<2 mgN L^{-1}). Despite the high relative abundance, the contribution of AOA to the overall nitrification activity is not well understood (Bernhard and Bollmann, 2010; Hatzenpichler, 2012).

The known nitrite oxidizers belong to seven genera within six bacterial phyla. All these genera have been detected in saline environments (**Table 1**), indicating that they contain species that are at least halotolerant, if not halophilic. Members of *Nitrospinae* have only been detected in saline systems, suggesting a halophilic lifestyle (Daims et al., 2016). Comammox *Nitrospira* are mainly found in non-saline to low salinity environments (Daims et al., 2016; Sun et al., 2021a), but were recently detected in estuarine sediments with salinities as high as 55‰ (Liu et al., 2020).

IMPACT OF SALINITY CHANGE ON NITRIFICATION ACTIVITY

Several studies have investigated the impact of salinity on the nitrification process across a wide range of systems – activated

TABLE 1 | Environmental distribution and salinity of environment for genera of ammonia oxidizing bacteria (AOB), ammonia oxidizing archaea (AOA), nitrite oxidizing bacteria (NOB) and comammox bacteria.

Phylogeny	Genus	Detected environment	Salinity of environment	References
Ammonia oxidizing bacteria (AOB)				
β-proteobacteria	*Nitrosomonas*	Freshwater, brackish water, marine/ hypersaline, estuary, engineered	Non-saline to hypersaline	(Norton, 2011) and references within, (Koops and Pommerening-Röser, 2001; Cui et al., 2016)
β-proteobacteria	*Nitrosospira*	Marine water/sediments, estuary, soil, engineered	Non-saline to marine	(Norton, 2011) and references within, (Freitag and Prosser, 2004)
γ-proteobacteria	*Nitrosococcus* Candidatus *Nitrosacidococcus tergens* *Candidatus* Nitrosoglobus terrae	Marine/saline, hypersaline	Typically marine to hypersaline, but may also be present in non-saline systems	(Norton, 2011) and references within, (Koops et al., 1990; Cui et al., 2016; Hayatsu et al., 2017; Picone et al., 2021; Sun et al., 2021b)
Ammonia oxidizing archaea (AOA)				
Candidatus Cenarchaeaceae	*Candidatus* Cenarchaeum	Marine sponges	Marine	(Stieglmeier et al., 2014; Kerou and Schleper, 2017; Polonia and Cleary, 2019)
Candidatus Nitrosocaldaceae	*Candidatus* Nitrosocaldus	Hot springs	Non-saline	(Stieglmeier et al., 2014; Qin et al., 2017; Abby et al., 2018)
Candidatus Nitrosopumilaceae	*Candidatus* Nitrosopumilus	Soil, marine, estuarine sediments	Marine to hypersaline, but may tolerate salinities as low as 3‰	(Stieglmeier et al., 2014; Elling et al., 2015; Ngugi et al., 2015; Qin et al., 2016; Chen et al., 2019)
Candidatus Nitrosopumilaceae	*Candidatus* Nitrosotenuis	Soils, freshwater, hot springs, engineered	Non-saline to low salinity (<3‰)	(Herbold et al., 2016; Sauder et al., 2018)
Candidatus Nitrosotaleaceae	*Candidatus* Nitrosotalea	Soil	Non-saline	(Stieglmeier et al., 2014; Prosser and Nicol, 2016)
Nitrososphaeraceae	*Nitrososphaera*	Soil, hot springs	Non-saline	(Stieglmeier et al., 2014; Kerou and Schleper, 2016)
Nitrososphaeraceae	*Candidatus* Nitrosocosmicus	Soil, sediments, engineered	Non-saline	(Alves et al., 2019)
Nitrosopumilaceae	*Nitrosarchaeum*	Soil, freshwater, estuaries	Non-saline to salinities less than seawater	(Blainey et al., 2011; Stieglmeier et al., 2014; Jung et al., 2018; Tolar et al., 2019)
Nitrite oxidizing bacteria (NOB)				
α-proteobacteria	*Nitrobacter*	Soil, freshwater, marine/hypersaline, subsurface, engineered	Non-saline to hypersaline	(Daims et al., 2016; Ruvindy et al., 2016)
β-proteobacteria	*Nitrotoga*	Soil, freshwater, marine/hypersaline, subsurface, engineered	Non-saline to marine	(Daims et al., 2016; Keuter et al., 2017; Navada, 2021)
γ-proteobacteria	*Nitrococcus*	Soil, marine/hypersaline, engineered	Marine to hypersaline	(Daims et al., 2016)
Nitrospirae	*Nitrospira*	Soil, freshwater, marine, geothermal subsurface, engineered	Non-saline to marine	(Daims et al., 2016; Bayer et al., 2021)
Chloroflexi	*Nitrolancea*	Saline, engineered	Non-saline to hypersaline	(Daims et al., 2016; Zorz et al., 2019; Chen et al., 2020)
Nitrospinae	*Nitrospina*	Marine	Marine (up to 40‰ salinity)	(Daims et al., 2016; Yepsen et al., 2019)
Nitrospinae	*Candidatus* Nitromaritima	Marine/hypersaline	Marine to hypersaline	(Daims et al., 2016; Ngugi et al., 2016)
Complete ammonia oxidizers (comammox)				
Nitrospirae	*Nitrospira*	Soil, freshwater, subsurface, estuaries, sediments, geothermal, engineered	Non-saline to hypersaline	(Daims et al., 2016; Liu et al., 2020)

sludge (Moussa et al., 2006a; Moussa et al., 2006b; Bassin et al., 2012; He et al., 2017), aerobic granular sludge (Bassin et al., 2011; Wang et al., 2017), fixed bed biofilters (Nijhof and Bovendeur, 1990; Sudarno, 2011; Cortes-Lorenzo et al., 2015), and moving bed biofilm reactors (MBBR) (Gonzalez-Silva, 2016). There is consensus that an increase in salinity generally inhibits nitrification. However, a salinity increase from 0 to ~10‰ appears to have a slight positive or no impact on the ammonia oxidation rate (Sudarno, 2011; Aslan and Simsek, 2012; Bassin et al., 2012; Cortes-Lorenzo et al., 2015; Navada et al., 2019), although not without exceptions (Sánchez et al., 2004; Kinyage et al., 2019). This is likely because the energy required for osmoregulation is lowest at salinities close to the isotonic point (~9‰), leaving more energy for growth and metabolism (Oren, 2011; He et al., 2017). A significant difference in microbial community composition and species inventory was observed between fresh- and brackish water (12‰ salinity) biofilms subjected to similar start-up conditions (Navada et al., 2020a). Furthermore, there was no drop in nitrification activity when salinity was increased in brackish water biofilms (12‰) (Navada et al., 2020b). This indicates that 9-12‰ is a critical salinity for adaptation in nitrifiers. This is corroborated by several studies where the nitrification activity dropped significantly at salinities >8-15‰ (Bassin et al., 2011; Bassin et al., 2012; Gonzalez-Silva et al., 2016; Kinyage et al., 2019; Navada et al., 2019; Navada et al., 2020b; Fossmark et al., 2021). Thus, in the present article, salinity adaptation implies salinities >10‰, unless specified otherwise.

Salinity change can impact AOM and NOB to different extents. Some studies found that AOM are more influenced than NOB by a salinity increase (Hunik et al., 1993; Moussa et al., 2006b; Sharrer et al., 2007), whereas others report the opposite (Nijhof and Bovendeur, 1990; Bassin et al., 2011; Sudarno, 2011; Aslan and Simsek, 2012). The discrepancy may be due to differences in experimental conditions, initial microbial community, salinity change method or biofilm history (Navada et al., 2020b). Several studies report nitrite accumulation after a salinity increase (Nijhof and Bovendeur, 1990; Hovanec et al., 1998; Dinçer and Kargi, 1999; Bassin et al., 2011; Cortes-Lorenzo et al., 2015; Gonzalez-Silva, 2016; Navada et al., 2020b). The lower energy yield and slower growth rate of NOB compared to AOM makes them more susceptible to stress, and nitrite oxidation may not generate sufficient energy for osmoregulation at elevated salinities (Oren, 2011). Some studies show that the proportion of NOB is lower than AOB in saline biofilms (Roalkvam et al., 2020; Navada, 2021), whereas others report the opposite (Gonzalez-Silva, 2016; Fossmark et al., 2021). The fragile mutualism between AOM and NOB is likely prone to chaotic instability, where minor perturbations can escalate the instability and lead to nitrite accumulation (Graham et al., 2007). Thus, nitrite concentration should be monitored closely during and after salinity variations.

Many studies report a shift in the microbial community composition after salinity increase (Sudarno, 2011; Bassin et al., 2012; Cortes-Lorenzo et al., 2015; Gonzalez-Silva, 2016; Luo et al., 2016). This community shift likely eliminates microorganisms that cannot survive at higher salinities, and selects for halotolerant or halophilic microorganisms. Shifts in the nitrifying community composition are also reported, with the appearance or disappearance of certain taxa at higher salinities (Moussa et al., 2006b; Bassin et al., 2011; Cortes-Lorenzo et al., 2015). For instance, increasing the salinity to ~33‰ resulted in a loss of *Nitrosomonas oligotropha* (Moussa et al., 2006b). In the same study, *Nitrosomonas europaea* was detected at salinities as high as 66‰. Similarly, the NOB *Nitrospira* disappeared at high salinities, and resulted in nitrite accumulation (Moussa et al., 2006b; Bassin et al., 2011; Rud et al., 2017). In our studies, *Nitrotoga* was the dominant NOB across salinities ranging from freshwater to seawater (Navada, 2021), suggesting that this NOB genus contains species that are highly adaptable to varying salinities.

Salinity changes have more complex effects on biofilms than in monocultures with free-living cells. Extracellular polymeric substances (EPS) in the biofilm matrix can retain water and protect the cells against desiccation (Flemming et al., 2016). Thus, a salinity increase can induce EPS formation as a defense mechanism (Wang et al., 2015; Corsino et al., 2017). Future studies should investigate the role of EPS and the possibility to manipulate it to improve salinity adaptation in biofilms. This requires a better understanding of the interactions between EPS-producing heterotrophs and nitrifying bacteria. Salt can also strengthen the biofilm structure due to better settling characteristics and ionic interactions (Goode and Allen, 2011). As nitrifiers are physiologically diverse, functional redundancy in biofilms may facilitate stable nitrification under osmotic stress. Biofilms can respond to prolonged salinity changes by physiological adaptation of the existing microbes, and through shifts in the microbial community composition by selection of microbes that are more suited to that salinity regime. The adaptation strategy will depend on the intensity and duration of the change (Shade et al., 2012). For example, small salinity increments led to a larger shift in community composition than large increments (Navada et al., 2019).

ACCLIMATION STRATEGIES TO SALINITY CHANGE

Several factors can influence salinity acclimation, and these may be manipulated to develop salinity acclimation strategies (**Table 2**). Not only the salinity, but also the salinity change regime – shock (discrete steps) or gradual – may impact the nitrification performance (Moussa et al., 2006b). Although the nitrification activity can recover after a few days, a large shock change in salinity causes a drastic reduction in activity during the initial days (Nijhof and Bovendeur, 1990; Gonzalez-Silva et al., 2016; Gonzalez-Silva et al., 2021). The salinity can be increased in smaller steps and the system can be acclimated over several days/months with almost no reduction in nitrification activity (Sharrer et al., 2007; Bassin et al., 2011; Bassin et al., 2012). This is a common strategy to adapt the microbes, but the adaptation period can be very long (weeks to months) (Bassin et al., 2012; Vyrides, 2015; Gonzalez-Silva, 2016). Another method is to increase the salinity gradually by increasing the influent salinity. This strategy may be more conducive to the bacteria than shock/step changes in salinity, as it allows the bacteria to

TABLE 2 | Factors influencing salinity acclimation and feasible salinity acclimation strategies for nitrifying bioreactors.

Factors influencing salinity acclimation	References
Native salinity	(Gonzalez-Silva et al., 2016; Navada et al., 2020b)
Whether the salinity change is below or above the isotonic salinity (~9‰)	(Bassin et al., 2012; He et al., 2017; Navada et al., 2019)
Magnitude of salinity change	(Moussa et al., 2006b; Bassin et al., 2012; Gonzalez-Silva, 2016; Navada et al., 2019)
Direction of salinity change (increase or decrease)	(Gonzalez-Silva et al., 2016; Navada et al., 2020b; Gonzalez-Silva et al., 2021)
Shock vs gradual salinity change	(Moussa et al., 2006b; Gonzalez-Silva, 2016; Navada, 2021)
Acclimation time at the given salinity	(Navada et al., 2019; Gonzalez-Silva et al., 2021)
Extracellular polymeric substances (EPS)	(Wan et al., 2014; Wang et al., 2015; Corsino et al., 2017; Campo et al., 2018)
Biofilm structure and ionic interactions	(Goode and Allen, 2011)
Biofilm history (physicochemical environment)	(Cabrol et al., 2016; Saur et al., 2016; Navada et al., 2020b)
Original microbial community composition in the biofilm	(Gonzalez-Silva et al., 2016; Keuter et al., 2017; Navada et al., 2020b)
Functional redundancy in microbial community composition	(Moya and Ferrer, 2016; Ali et al., 2020; Navada et al., 2020b)
Local microbiota in the influent(s)	(Navada et al., 2020a; Roalkvam et al., 2020; Navada et al., 2021)
Local selection pressure	(Nemergut et al., 2013; Gonzalez-Silva et al., 2021)
Physiological adaptation of microbes through *de novo* synthesis of osmolytes	(Wan et al., 2014)
Physiological adaptation of microbes through the uptake of osmolytes from the medium	(Vyrides and Stuckey, 2017)
Salinity acclimation strategies	**References**
Large (gradual) salinity increments (may be more practical than small increments)	(Navada et al., 2019)
Osmotic stress priming (prior exposure to high salinity)	(Navada et al., 2020b)
Start-up in brackish water (>12‰ salinity)	(Navada et al., 2020a)
Seeding with salt-acclimated (>12‰) biofilm	(Bower and Turner, 1981; Li et al., 2019; Roalkvam et al., 2020; Navada et al., 2021)
Inoculation with salt-acclimated nitrifying consortia	(Panswad and Anan, 1999; Sudarno et al., 2010; Shi et al., 2012; Roalkvam et al., 2020)

adapt to the gradually increasing salinity by K^+ uptake or through the synthesis of osmolytes. Indeed, whereas shock transfers from freshwater to seawater caused >95% inhibition (Gonzalez-Silva, 2016; Kinyage et al., 2019), gradual increments in salinity over 2-3 days caused only a 55-75% inhibition (Navada et al., 2019; Navada et al., 2020b; Navada et al., 2021).

One of our studies showed that irrespective of the rate of gradual salinity increment, the ammonia oxidation capacity decreased by 50-90% when the salinity increased from freshwater to seawater (Navada et al., 2019). The nitrification capacity was mainly dependent on the salinity (~2.7% decrease per 1‰ increase) and the recovery time in seawater was independent of the salinity increase regime (~2.1% increase in activity per day). Thus, large salinity increments can be more practical than small increments. Nitrifying bioreactors can adapt to a prolonged exposure to salinity (Sharrer et al., 2007; Bassin et al., 2012). Further, the ammonia oxidation capacity in bioreactors acclimated to seawater was comparable to or higher than those in freshwater (Navada, 2021). These findings contradict the traditional view that the nitrification rate is lower in seawater than in freshwater (Nijhof and Bovendeur, 1990; Chen et al., 2006; Rusten et al., 2006).

Early perturbations in young biofilms are influential in structuring the biofilm and affecting the microbial community composition (Cabrol et al., 2016; Saur et al., 2016). Thus, strategies adopted during the start-up of nitrifying bioreactors can be effective in molding the community composition and the consequent microbial functionality. This strategy was employed by Navada et al. (2020b) to show that osmotic stress priming by seawater exposure could increase the salinity tolerance of freshwater biofilms. We speculate that seawater exposure led either to physiological priming of the nitrifying community, or strengthened the biofilm structure through EPS formation. Both factors could make the biofilms more tolerant to future salinity changes. Future studies should investigate the long-term impacts of seawater priming to reveal whether seawater tolerance is sustained over periods longer than a few weeks. The success of the osmotic priming strategy suggests that newly-started bioreactors are the most susceptible to drastic drops in nitrification due to salinity increase. Thus, suitable start-up strategies should be employed to make bioreactors tolerant to salinity variations.

Brackish water (12-22‰) biofilms can be more tolerant to salinity increase than freshwater biofilms (Gonzalez-Silva et al., 2016; Navada et al., 2020b). Further, although biofilms started up in brackish water had lower nitrification capacity than in freshwater, complete nitrification was established in both bioreactors within 60 days (Navada et al., 2020a). This suggests that start-up in 12‰ brackish water could be a practical strategy. Seeding with brackish biofilm can improve salinity tolerance in bioreactors (Navada et al., 2021). Nitrifying bioreactors seeded with brackish biofilm had only a ~20% reduction in ammonia oxidation capacity compared to 65-75% in bioreactors seeded with freshwater biofilm. Notably, a salinity decrease can also impact nitrification. In our study, a ~50% drop in nitrification capacity was observed when the salinity was reduced from 12 or 32‰ to freshwater, and approximately two weeks were required for acclimation to the new salinity (Navada et al., 2020b).

Inoculation with salt-acclimated biomass or nitrifying consortia can improve salinity adaptation (Panswad and Anan, 1999; Sudarno et al., 2010; Shi et al., 2012; Cui et al., 2016; Vyrides and Stuckey, 2017). However, this strategy may not work during sudden increases in salinity and suitable inocula can be expensive or difficult to procure (Vyrides, 2015). Moreover, the original community composition may be modified through community assembly processes such as dispersal, drift and selection (Nemergut et al., 2013). Thus, the inoculum may be outcompeted by the local microbiota, and the final microbial community will be established primarily based on the local species pool and selection pressure. Although some studies suggest the opposite (Wittebolle et al., 2009; Keuter et al., 2017), this was the case for Navada et al. (2020a). Recent studies show that seeding with local biofilm carriers was more successful than commercial inocula (Roalkvam et al., 2020; Navada et al., 2021). This is likely because the species on biofilm carriers are already adapted to life in a biofilm and the local environment. Thus, local salinity acclimation strategies appear more beneficial than the addition of commercial inocula in nitrifying bioreactors, and should be further investigated.

Halotolerant microorganisms typically utilize the osmolyte strategy to adapt to an increase in salinity (Sleator and Hill, 2002). This strategy can be implemented either by *de novo* synthesis or uptake of osmolyte molecules from the medium (osmoprotectants) (Sleator and Hill, 2002; Oren, 2011). Osmoprotectant uptake is energetically cheaper than *de novo* synthesis (Sleator and Hill, 2002; Oren, 2011), and has been effective for a range of microorganisms (Vyrides and Stuckey, 2017). Thus, the exogenous addition of osmolytes was tested as a feasible strategy for salinity adaptation in nitrifying microorganisms. Contrary to our hypothesis, osmoprotectants did not improve salinity adaptation in nitrifying biofilms, likely due to their uptake by the heterotrophs instead of the nitrifiers (Navada, 2021).

In conclusion, physiological adaptation rather than an alteration in the nitrifying taxa appears to be the dominant mechanism for salinity acclimation in biofilms (Gonzalez-Silva et al., 2016; Navada, 2021). Moreover, several nitrifying taxa have been detected across different salinities, both in man-made and natural ecosystems (Ward et al., 2007; Bernhard and Bollmann, 2010; Gonzalez-Silva, 2016; Santos et al., 2018; Fossmark et al., 2021; Navada, 2021). This suggests that several nitrifiers are halotolerant and can adapt to varying salinities. Future studies should test individual osmolytes at different concentrations, accompanied by metaproteomics. This could further our understanding of transporter genes and facilitate the identification of osmolytes that are preferentially taken up by nitrifiers for salinity acclimation. The effect and contribution of archaea to the overall nitrification performance during salinity variations should be investigated. Estuarine systems should also be studied in combination with engineered systems to advance our understanding of salinity acclimation in nitrifiers.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/supplementary material. Further inquiries can be directed to the corresponding author.

AUTHOR CONTRIBUTIONS

This paper is the result of discussions the authors had during the PhD study of SN. SN wrote the first version of the manuscript and the final version is the result of interactions between the authors. All authors contributed to the article and approved the submitted version.

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The remaining author declares that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.