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REVIEW

Unravelling the potential of halophytes for marine integrated multi-trophic aquaculture (IMTA)—a perspective on performance, opportunities and challenges

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ABSTRACT: The present study critically analyses peer-reviewed literature addressing the potential of halophytes to remediate nutrient-rich effluents from marine and coastal aquaculture, as well as the potential for their economic valorization, from human consumption to an untapped source of valuable secondary metabolites with pharmaceutical potential. The growing body of evidence discussed in this review supports the perspective that halophytes can become a new source of nutrition and other high-value compounds and be easily incorporated into saltwater-based integrated multi-trophic aquaculture (IMTA) systems. In this context, halophytes act as extractors of dissolved inorganic nutrients, primarily nitrogen and phosphate, usually wasted in marine aquaculture farms. Phytoremediation using halophytes has been proven to be an efficient solution, and several ways exist to couple this practice with land-based marine aquaculture systems, namely through constructed wetlands and aquaponics. Focusing research on ecosystem-based approaches to aquaculture production will provide valuable data for producers and policy makers in order to improve decision making towards a sustainable development of this economic sector. Eco-intensification of aquaculture through IMTA will potentially increase the overall productivity and resilience of the sector, and halophytes, in particular, are on the verge of becoming key players for the diversification and promotion of land-based IMTA. This work specifically documents the uncharted potential of *Halimione portulacoides*, an important halophyte in European salt marsh ecosystems, as a new extractive species for IMTA.

KEY WORDS: Sustainable aquaculture · Bioremediation · Dissolved nutrients · Coastal IMTA · Saltwater aquaponics · Blue growth · Circular economy

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INTRODUCTION

Aquaculture has experienced a fast and steady growth over the last decades, achieving a 7.5% annual growth rate between 1990 and 2009, significantly surpassing all other livestock sectors (Troell et al. 2014). Part of such rapid development is explained by the overexploitation of fish stocks that limits the supply of wild marine fish (FAO 2016), leaving aquaculture as the only alternative to meet an ever growing demand for seafood. Nonetheless, the fast development of the industry, which already supplies 50%

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of global seafood, has brought concerns about the extent of its environmental impact (FAO 2016). Organic waste produced in fish farms negatively impacts aquatic ecosystems by modifying water biochemistry and ecological interactions (Troell et al. 2014). Particulate organic matter and dissolved inorganic nutrients, especially nitrogen (N) and phosphorus (P) forms, can promote water eutrophication and dramatically change sediment chemistry and associated benthic biodiversity (Sanz-Lázaro et al. 2011, Sarà et al. 2011, Valdemarsen et al. 2012, Bannister et al. 2014). In this way, new integrative, non-linear production methods are necessary to reduce the ecological impact of fish farms. To promote such measures, the EU (through the Marine Strategy Framework Directive, Water Framework Directive, Circular Economy strategy and the Blue Growth strategy) demands new approaches towards sustainable aquaculture practices and waste management and re-utilization (European Commission 2012, 2015, Science for Environment Policy 2015, European Environment Agency 2016).

Integrated multi-trophic aquaculture (IMTA) systems have been recently studied and endorsed by scientists as a real sustainable solution for the industry (Troell et al. 2009, Barrington et al. 2010, Abreu et al. 2011, Chopin 2015, 2017, Fang et al. 2016, Granada et al. 2016) Conceptually, IMTA is based on an ecosystem approach framework, where nutrients wasted on one trophic level, in particulate and dissolved forms, are redirected to downstream trophic levels to be filtered and/or extracted by capable organisms and utilized for growth. By performing this way, waste is reduced, productivity is increased (Hughes & Black 2016), and the overall resilience of the global food system is improved (Troell et al. 2014). The integration of additional trophic levels greatly depends on the type of aquaculture systems in terms of production intensity and water salinity. Freshwater aquaculture allows for the integration of salt-sensitive extractive species such as vegetables commonly farmed in agriculture, often by coupling fish-rearing systems with hydroponics, an activity known as aquaponics (Graber & Junge 2009, Somerville et al. 2014, dos Santos 2016). However, a major portion (~5/6) of European aquaculture is marine and coastal water-based (FAO 2016), and extractive species need to be salt-tolerant to remediate saline effluents. Important research already exists concerning the use of organisms such as shellfish and seaweeds in marine IMTA (Neori et al. 2004, Troell et al. 2009, Chopin 2015), yet an underrated group of salt-tolerant plants could take IMTA to another level – halophytes.

This paper aims to contextualize the importance of halophytes in a new era of sustainable aquaculture and, particularly, elaborate on the potential of *Halimione portulacoides* (L.) Aellen (Fig. 1), a low C3 shrub from the family Chenopodiaceae (order Caryophyllales), as a bioremediator and valuable co-product for IMTA. This view is supported by both biological and ecological traits, as demonstrated through a critical survey of available peer-reviewed literature. This species was chosen due to its wide geographic distribution, namely in European salt marshes where it colonizes low and mid-marsh areas (Waisel 1972, Castroviejo 1990); it is also a key species characterizing the 'Mediterranean and thermo-Atlantic halophilous scrubs' habitat, classified in the scope of EU Habitats Directive (Council Directive 92/43/EEC; European Commission 1992) and protected in several EU Natura 2000 sites (European Commission

Fig. 1. *Halimione portulacoides*: (A) top view of a specimen and (B) detail of the leaves (edible part), showing their succulence and epidermal bladders. Location: section of the Aveiro Lagoon at Gafanha da Boa-Hora, Aveiro, Portugal (40° 32′ 55.9″ N, 8° 46′ 05.6″ W) (Photos: M. Custódio)

2013). The background knowledge on the species' ecology by some of authors and its ample presence in Portuguese salt marshes (e.g. Sousa et al. 2008, 2010, 2011, Válega et al. 2008a,b), particularly in the Aveiro region, was another reason for selecting this species, as was the fact that it is a perennial and evergreen halophyte, which removes the need for manipulation of the life cycle, as happens with annual plants (e.g. *Salicornia europaea* s.l.). Plus, the species has potential for integration and valorization in the context of the aquaculture sector in regions where it naturally occurs, being suitable for IMTA solutions compatible with marine protected areas (Chopin 2017). Within this context, *H. portulacoides* could diversify the offer of autochthonous halophytes within the market of sea vegetables.

HALOPHYTES — THE NEW PLAYERS IN SUSTAINABLE MARINE AQUACULTURE

Halophytes are salt-tolerant plants that complete their life cycle in saline environments, to which they are highly adapted (Glenn et al. 1999, Flowers & Colmer 2008, Panta et al. 2014). A generally accepted definition for halophytes sets a salt concentration tolerance of at least 200 mM NaCl, as long as the remaining environmental conditions are within the natural environment (Flowers et al. 1986). These unconventional crop plants have been overlooked by the food production sector, which mainly produces salt-sensitive vegetable species, i.e. glycophytes, which depend on freshwater irrigation for optimum yields. Nonetheless, humans in coastal communities within Europe and North America have consumed edible halophytes for centuries. For example, the salty leaves of 'sea purslane' (common name given to plants from the sister genera *Atriplex* and *Halimione*; see Kadereit et al. 2010) have been appreciated in some European countries and are now collected from the wild by professional foragers and sold in specialized online platforms (e.g. online on Farmdrop and Fine Food Specialist, UK), for local restaurants and gourmet cuisine (Barreira et al. 2017). The most recent case of emergent success is *Salicornia* L. spp., which have shown high levels of omega-3 polyunsaturated fatty acids and β-carotene antioxidants, and are already being produced in commercial-scale agriculture operations in the USA and Europe (Boer 2008, Lu et al. 2010, Ventura & Sagi 2013, Panta et al. 2014, Ventura et al. 2015). Moreover, halophytes can also be used as bioenergy sources (Abideen et al. 2011, Ventura et al. 2015, Sharma et al. 2016) and nutraceutical products, such as mineral-rich herbal salts (Kim & Kim 2013).

Halophytic species have developed remarkable physiological traits to succeed in highly saline environments where the majority (>90%) of plant species would perish (Flowers et al. 2010). These adaptations allow for the retention of water, protection of enzymatic machineries and maintenance of homeostasis (Flowers & Colmer 2008, Flowers et al. 2010, Ksouri et al. 2012). A number of metabolites are biosynthesized by these plants (Aquino et al. 2011, Maciel et al. 2016), and many display bioactivity against oxidative stress, microbes, inflammations and tumors (Boughalleb & Denden 2011, Ksouri et al. 2012, Buhmann & Papenbrock 2013a, Rodrigues et al. 2014), which emphasizes their potential to be used by the pharmaceutical industry.

The integration of halophytes with economic potential in marine aquaculture systems to remediate nutrient-rich effluents and process water has received growing attention by research groups interested in sustainable aquaculture, and a developing body of knowledge is already available, indicating promising results (Buhmann & Papenbrock 2013b, de Lange et al. 2013, Shpigel et al. 2013, Waller et al. 2015). Halophytes can be integrated in IMTA systems through modules that allow for sustained plant growth and water (re)circulation, and the 2 main structures used for that purpose are usually constructed wetlands (CWs) and aquaponics systems. CWs have proven to be efficient at removing a wide range of organic and inorganic substances from different wastewater sources (Verhoeven & Meuleman 1999, Imfeld et al. 2009, Vymazal 2010, 2011, Shelef et al. 2013) including aquaculture (de Lange et al. 2013, Turcios & Papenbrock 2014, Carballeira et al. 2016). Aquaponics systems, on the other hand, have been mostly experimented with freshwater setups (Somerville et al. 2014, dos Santos 2016). Both systems have the potential to be used as growth modules for halophytes and support their integration in marine aquaculture activities (Turcios & Papenbrock 2014).

SURVEY OF SCIENTIFIC LITERATURE

A stepwise review of available scientific literature reporting the utilization of halophytes for remediation of marine aquaculture waters was performed, followed by a special focus on *Halimione portulacoides*, with emphasis on its biology, ecology and biochemistry. The different steps of the process carried

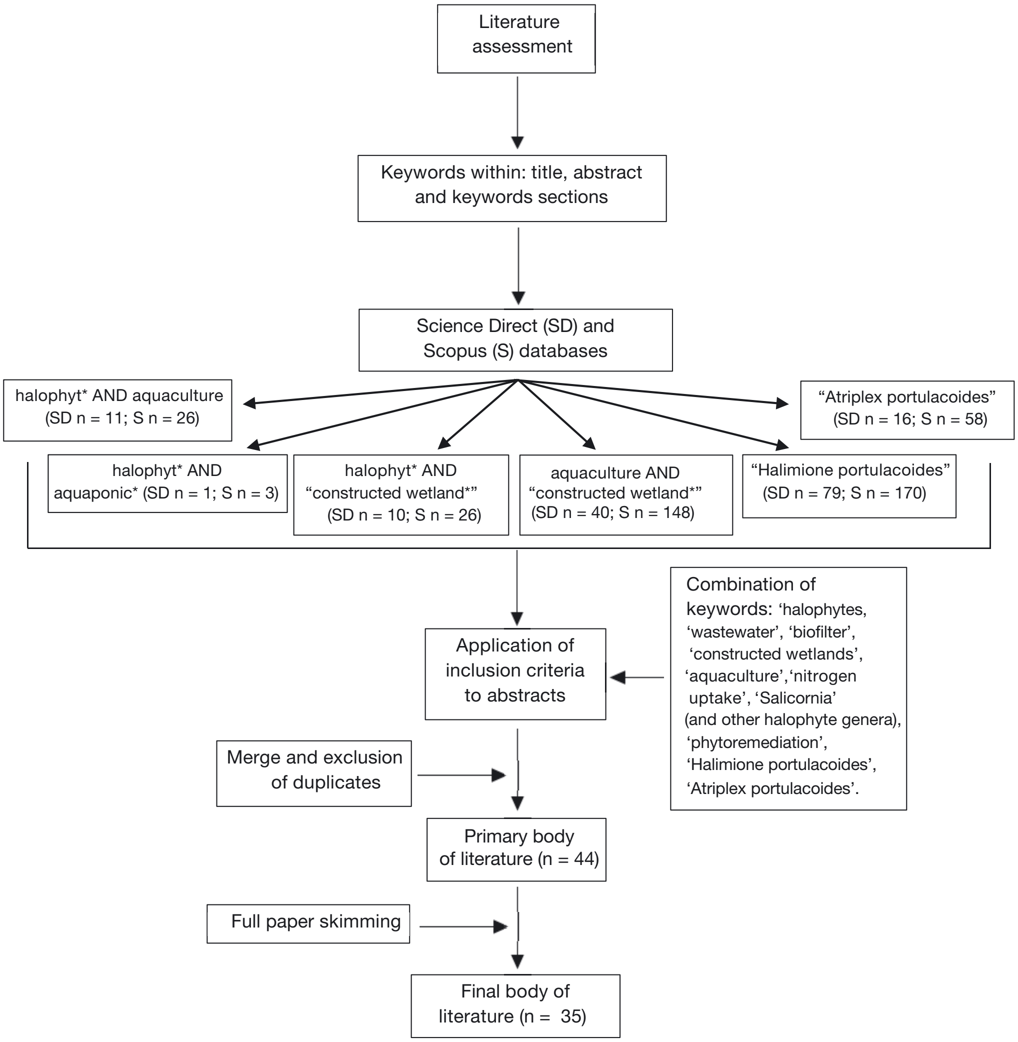

Fig. 2. Process employed for the selection of relevant literature

out for the selection of relevant literature is outlined in Fig. 2. A first assessment was conducted using Science Direct (SD) and Scopus (S) digital databases by searching for specific keywords within the title, abstract and key words sections of papers available online by November 2016. The search term '*Atriplex portulacoides'* was included in the assessment as it is a homotypic synonym of *H. portulacoides*, and some authors opted for that name in their publications. On a subsequent assessment, the abstracts of all publications were surveyed, and the final selection of articles was imported into Mendeley$^{\text{TM}}$ (n = 44). All of these papers were fully read, and from these, 35 peer-reviewed articles were selected as the most relevant for the present review (the complete list of the selected publications is provided in Table S1 in the Supplement at www.int-res.com/articles/suppl/q009p445_supp.pdf). Selected articles had to fulfill the following criteria: (1) include experiments using halophytes as extractive species for saltwater aquaculture effluents and (2) address halophytes growing in CWs and/or aquaponics/hydroponics systems or (3) focus the research on *H. portulacoides* biology, ecology and/or biochemistry.

HALOPHYTES IN AQUACULTURE: FACTS AND FIGURES

Concerning the use of halophytes as biofilters for aquaculture, 15 original research articles and 4 reviews were selected, where the integration and performance of several species were evaluated and discussed. The criteria for species selection, where referred, were based on local availability, salinity tolerance and economic potential. In total, 22 halophyte species (17 genera) were tested, and full species names, number of aquaculture remediation studies per plant species and references are represented in Fig. 3.

The most studied halophyte to date was *Aster tripolium* (5 studies; including the homotypic synonym *Tripolium pannonicum*), followed by *Salicornia europaea* (4 studies), *Phragmites australis* (3 studies) and *S. dolichostachya* (2 studies). All other species have been addressed only once (Fig. 3). The growing modules for halophytes were either hydroponics- or substrate-based, and it appears that the choice of medium depends on the type of intensification being employed for the production of the target fish species (semi-intensive vs. intensive/recirculating aquaculture system [RAS]), as well as halophyte species and biofilter main purpose (wastewater treatment vs. plant biomass production) (Buhmann & Papenbrock 2013b, Buhmann et al. 2015, Chen & Wong 2016). Farmed species from which the effluents originated included different fish and shrimp, and in some studies, artificial solutions mimicking the organic load of aquaculture effluents were used (Buhmann et al. 2015, Quintã et al. 2015a, de Lange & Paulissen 2016). Farmed species included *Chanos chanos* Forssk., 1775 (Lin et al. 2002b), *Dicentrarchus labrax* L., 1758 (Quintã et al. 2015b, Waller et al. 2015), *Oncorhynchus mykiss* Walbaum, 1792 (Lymbery et al. 2006, 2013), *Oreochromis* sp. Günther, 1889 (Brown et al. 1999), *Penaeus vannamei* Boone, 1931 (Lin et al. 2003, 2005, Webb et al. 2012, 2013), *Solea senegalensis* Kaup, 1858 (Webb et al. 2012), *Sparus aurata* L., 1758 (Shpigel et al. 2013) and *Xiphophorus* sp. Heckel, 1848 (Boxman et al. 2017). Effluents originating from the culture of freshwater species were salinized by adding NaCl prior to the irrigation of halophytes. The experiments were performed in diverse geographic regions and climates (Fig. 4): the arid climates of southern Israel (Shpigel et al. 2013) and southwestern USA (Brown et al. 1999), the humid subtropical regions of Taiwan (Lin et al. 2002b, 2003, 2005) and southeastern USA (Boxman et al. 2017), the oceanic climate of northwestern Europe (Webb et al. 2012, 2013, Buhmann et al. 2015, Quintã et al. 2015a, Waller et al. 2015, de Lange & Paulissen 2016) and the Mediterranean climate of southwestern Australia (Lymbery et al. 2006, 2013). Yet, the diversity of studies is still low and additional studies with endemic species in different climate regions are needed. Concerning the economic valorization of plant biomass, researchers referred to the potential of some species to be used as

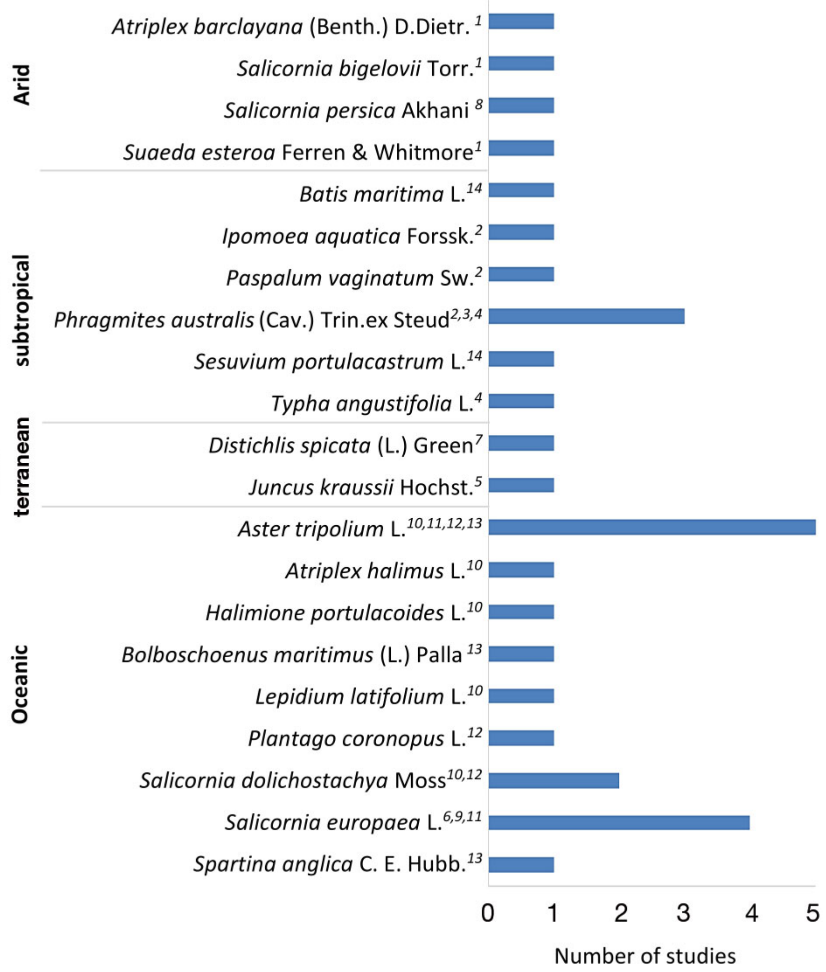

Fig. 3. Number of studies per halophyte species where phytoremediation was tested and growth performances evaluated upon irrigation with saline aquaculture wastewater. The geographic location where each experimental trial took place was ranked following the Köppen climate classification. [1]Brown et al. (1999); [2]Lin et al. (2002b); [3]Lin et al. (2003); [4]Lin et al. (2005); [5]Lymbery et al. (2006); [6]Webb et al. (2012); [7]Lymbery et al. (2013); [8]Shpigel et al. (2013); [9]Webb et al. (2013); [10]Buhmann et al. (2015); [11]Quintã et al. (2015a,b); [12]Waller et al. (2015); [13]De Lange & Paulissen (2016); [14]Boxman et al. (2017). Notes: (i) *Aster tripolium* as *Tripolium pannonicum* (Jacq.) Dobrocz. in Buhmann et al. (2015) and Waller et al. (2015); (ii) *Halimione portulacoides* as *Atriplex portulacoides* L. in Buhmann et al. (2015); (iii) *Bolboschoenus maritimus* as *Scirpus maritimus* L. in De Lange & Paulissen (2016)

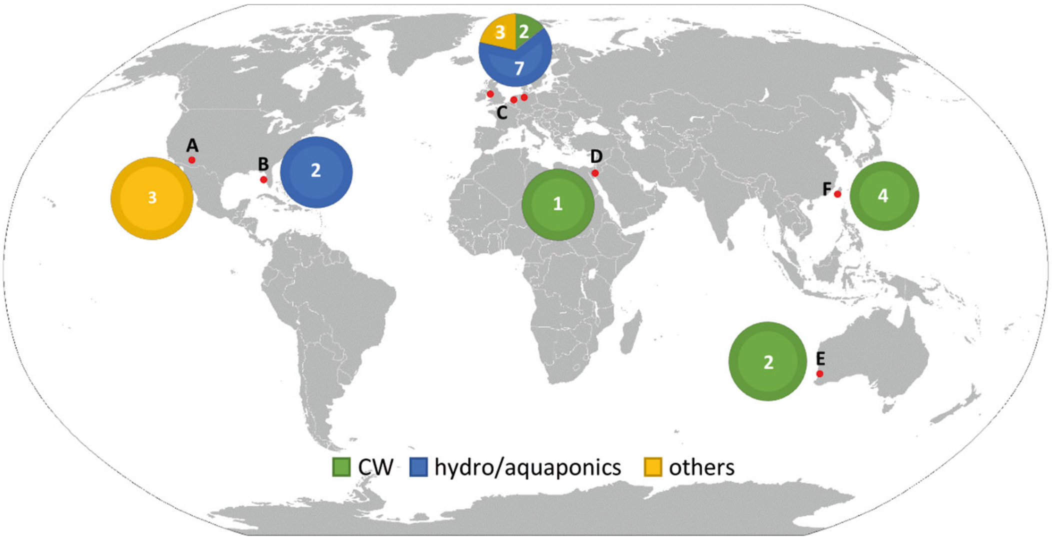

Fig. 4. Geographic locations of previous experiments using halophytes as aquaculture effluent remediators (red dots). Pie charts represent plant-growing systems (CW: constructed wetland; hydro/aquaponics and others [pot-planted or lysimeter]) used in each region in relation to the number of species tested (white numbers). Regions and species (from left to right): (A) South Arizona (USA) – *Atriplex barclayana*; *Salicornia bigelovii* and *Suaeda esteroa*; (B) Florida (USA) – *Batis maritima* and *Sesuvium portulacastrum*; (C) Northern Europe – hydro/aquaponics: *Aster tripolium, Atriplex halimus, Halimione portulacoides, Lepidium latifolium*, *Plantago coronopus, Salicornia dolichostachya* and *Salicornia europaea;* CW: *A. tripolium* and *S. europaea;* others: *A. tripolium*, *Bolboschoenus maritimus* and *Spartina anglica*; (D) Israel – *Salicornia persica*; (E) Southwestern Australia – *Distichlis spicata* and *Juncus kraussii*; (F) Taiwan – *Ipomoea aquatica, Paspalum vaginatum, Phragmites australis* and *Typha angustifolia*. Map editing software: ArcGIS

food for human consumption (e.g. *Salicornia* spp., *A. tripolium* and *Halimione portulacoides*; Lu et al. 2010, Webb et al. 2012, Isca et al. 2014, Buhmann et al. 2015, Quintã et al. 2015a), as forage for livestock (e.g. *Suaeda esteroa* and *Distichlis spicata*; Brown et al. 1999, Lymbery et al. 2013, Panta et al. 2014), as oil sources (e.g. *Salicornia* spp. seeds; Brown et al. 1999, Weber et al. 2007, Sharma et al. 2016) and as sources of extracts with pharmacological applications (Ksouri et al. 2012, Buhmann & Papenbrock 2013a).

In Table 1, data from experiments using CWs is displayed concerning the performance of different halophytes in removing N and P from wastewater. Due to the reduced number of experiments involving hydroponic/aquaponic setups (Buhmann et al. 2015, Quintã et al. 2015a, Waller et al. 2015, Boxman et al. 2017), out of which only 2 included N and P removal efficiencies, and due to several differences in surveyed variables to allow a direct comparison of the data with those reported from CW set ups, studies addressing hydroponic/aquaponic setups were not included in Table 1. For easier comparison between experiments using CWs and whenever possible, values reported on the different studies were converted to a common unit. Due to the variability in environmental and biological factors between experimental conditions (e.g. salinity, substrate, nutrient concentration, water volume, retention time, duration of the experiment, plant density, age of plants and climatic conditions such as temperature and light) results cannot be directly compared. However, despite the existing variability in terms of nutrient removal, which seems to depend on system design, flow regime, nutrient concentration and species (Buhmann & Papenbrock 2013b), not all setups per se are equally effective for nutrient removal, taking into account the specific objectives established for each CW. N removal capacity attained around 90% or more in 4 of the studies that were surveyed (Brown et al. 1999, Lin et al. 2002b, Webb et al. 2012, Lymbery et al. 2013), and only 1 experiment reported a low N removal capacity (11%) (de Lange & Paulissen 2016). While in some of the studies P removal was close to 100% (e.g. Brown et al. 1999), in 1 of the experiments reported, P removal was only 13% (Shpigel et al. 2013). Fig. 5 illustrates the performance of different halophyte species, in terms of N and P removal efficiency attained under different experimental conditions (based on data summarized in Table 1). Although results should not be directly compared, the key point is to highlight the phytoremediation service provided by halophytes in CWs, as most of them fulfilled the objectives under the tested conditions.

Table 1. Performance of constructed wetlands (CWs) using halophytes to remove nitrogen (N) and phosphate (P) from marine aquaculture effluents. TDIN: total dissolved inorganic nitrogen, DIP: dissolved inorganic phosphate, TDN: total dissolved nitrogen, TAN: total ammonium nitrogen, PO_4-P: orthophosphate, TN: total nitrogen, TP: total phosphate, NO_3-N: nitrates. Entries with 2 values indicate separate remediation experiments (different N and P concentrations, system design or plants) within the same study

Species	Effluent origin	Salinity	Substrate	Time (d)	Effluent N concentration (mg l^{-1})	N removal (%)	Effluent P concentration (mg l^{-1})	P removal (%)	Reference
Salicornia europaea	Whiteleg shrimp *Penaeus vannamei*	–	Quarry sand	84	2 g m^{-2} d^{-1} (TDIN)	47	0.81 g m^{-2} d^{-1} (DIP)	67	Webb et al. (2013)
Salicornia europaea	Shrimp, sole and turbot	10–29	Quarry sand + limestone	58	1.5–5.4	98	1.05 to 2.79	36–89	Webb et al. (2012)
Salicornia persica	Gilthead seabream *Sparus aurata*	35	Gravel stone	90	11.1 g m^{-2} d^{-1} (TDN), 10.5 g m^{-2} d^{-1} (TDN)	71, 65	1.6 g m^{-2} d^{-1}, 1.5 g m^{-2} d^{-1}	12 13	Shpigel et al. (2013)
Ipomea aquatica + Paspalum vaginatum + Phragmites australis	Milkfish *Chanos chanos*	5	River gravel +	35	0.6 g m^{-2} d^{-1} (TDIN)	95	0.9 g m^{-2} d^{-1} (PO_4-P)	71	Lin et al. (2002b)
Phragmites australis	Whiteleg shrimp *P. vannamei*	–	Local soil + river gravel	80	0.21 (TAN), 0.41 (NO_3-N)	57, 68	8.45 (PO_4-P)	5.4	Lin et al. (2003)
Salicornia bigelovii *Atriplex barclayana*	Hybrid tilapia	35 (added)	Lysimeter (with soil)	120	77.2 (TN)	95.8, 90.7	25.27 (TP)	99.5 99.7	Brown et al. (1999)
Aster tripolium + Bolboschoenus maritimus + Spartina anglica	Artificial effluent	12.9	Original soil (cores planted on pots)	63	15 (TN)	11	2.5 (TP)	35	de Lange & Paulissen (2016)
Juncus kraussii	Rainbow trout *Onocorhynchus mykiss*	24 (added)	Basalt gravel	38	3.8 (TN)	62	1.27 (TP)	77	Lymbery et al. (2006)
Distichlis spicata	Rainbow trout *O. mykiss*	15 (added)	Washed quartz sand	231	5.0 (TN), 1.0 (TN)	87.7 58.3	1.0 (TP), 0.2 (TP)	91.2 84.5	Lymbery et al. (2013)

CHALLENGES AND OPPORTUNITIES FOR INTEGRATING HALOPHYTES IN IMTA

The eutrophication of water bodies has become a major issue in modern aquaculture due to the intensification and expansion of production and increased use of high-protein pelleted feeds (Edwards 2015). It was estimated that in conventional aquaculture, fish assimilate only 25–40% of the whole N and P available in their diets (Lupatsch & Kissil 1998, Wang et al. 2012), while the rest is wasted into effluent water through feed lixiviation and fish excretion/metabolism. Yet, nutrient-rich wastes could be redirected to trophic levels capable of assimilating these nutrients and convert them into biomass with economic value, while simultaneously reducing water pollution. Given that food waste is an increasing concern in Europe, the potential of this waste redirection can help the implementation of the EU plans for a circular economy, in which the challenge of transition towards reduction of waste and sustainable resource efficiency are key to develop a competitive EU economy (European Commission 2015). Technological improvements and adaptation processes of fish farms could transform aquaculture production, creating new windows of opportunity for a sustainable Blue Growth of European coastal areas (European Commission 2012).

The integration of CWs and aquaponics systems to grow halophytes in IMTA are relatively new concepts that deserve scientific scrutiny in order to evaluate their potential for large-scale application. In the case of CWs, plants function as a solid biological filter where nitrification and denitrification processes occur and nutrients are restrained and extracted from the effluent by the plants, soil microorganisms and substrate (Webb et al. 2012, 2013, Shpigel et al. 2013). In aquaponics, the system necessarily requires an independent upstream biofilter to promote nitrification processes. This is essential in 'free-floating' configurations (e.g. floating rafts [also known as deep-water culture] and nutrient-film technique), while systems using inert growing

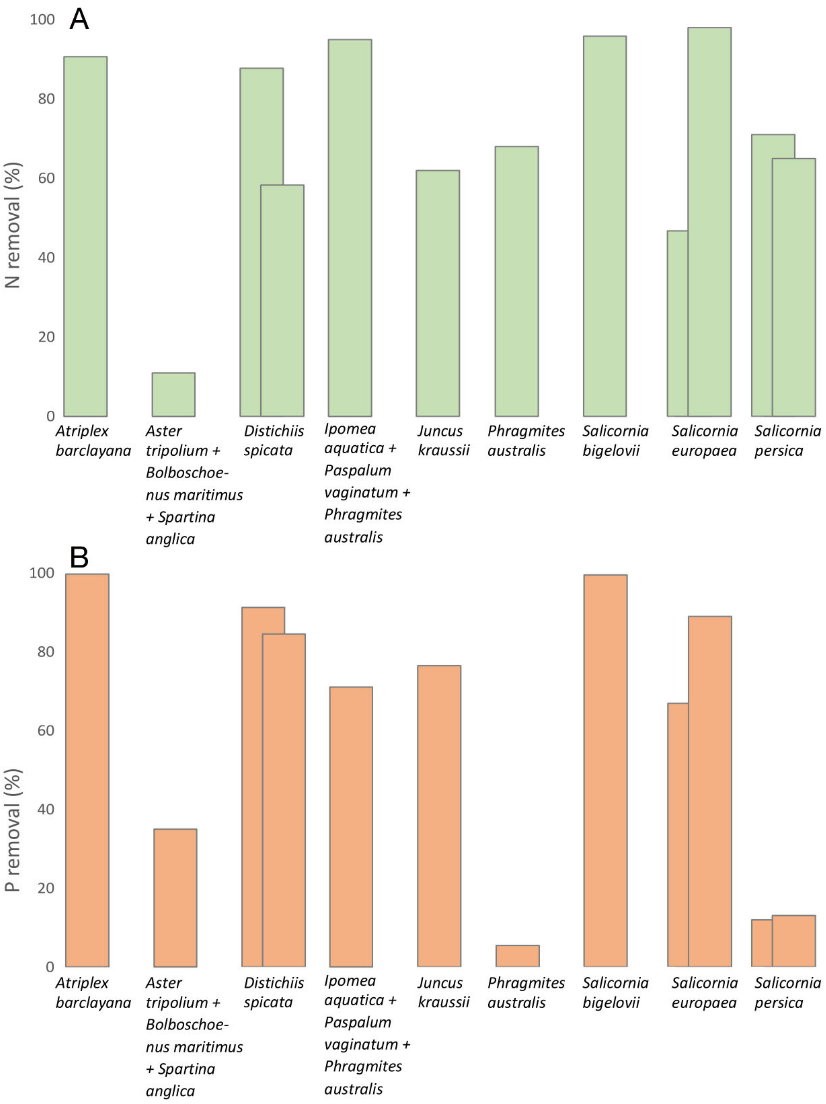

Fig. 5. Average percentage of (A) N removal and (B) P removal from saline aquaculture effluents by halophyte species planted in constructed wetlands (CWs; according to data reported in Table 1). Overlapping bars correspond to different studies using the same species

media, such as expanded clay, allow nitrifying bacteria to establish in the solid surface (Buhmann et al. 2015, Waller et al. 2015, Boxman et al. 2017). Buhmann & Papenbrock (2013b) reviewed some studies that used halophyte CWs as biofilters, showing promising results yet referring to the need for more comprehensive research. To date, the halophytes that received most of the attention, including in agriculture studies, were *Salicornia* and *Sarcocornia* A.J. Scott, which exhibited promising results in terms of growth rates and phytoremediation (Brown et al. 1999, Ventura et al. 2011a,b, Webb et al. 2012, 2013, Katschnig et al. 2013, Ventura & Sagi 2013). Other species, including *Aster tripolium, Plantago coronopus, Lepidium latifolium, Halimione portulacoides* and *Atriplex halimus*, also demonstrated good potential, as already summarized above. Nonetheless, a great variability in results is undeniable and these are most likely due to variable experimental conditions, species-specific traits, system design and the lack of standardized research methods. More data need to be generated under standardized conditions to evaluate which are the most suitable halophytes for IMTA in order to achieve a more cohesive and robust body of knowledge.

The variables that need to be studied concerning the selection of the best halophyte plants for IMTA inlclude salinity tolerance, macro- and micro-nutrient requirements, light and hydraulic regimens, plant density and the potential for economic valorization (Verhoeven & Meuleman 1999, Vymazal 2010, Buhmann & Papenbrock 2013b, Buhmann et al. 2015). For example, in order to investigate the relevance of plant density, *Salicornia europaea* was grown at 10 000 and 200 plants m^{-2} in CWs, with no significant differences in nutrient removal; up to 85% of total dissolved inorganic nitrogen (TDIN) was removed, with a maximum removal rate of 1.5 g N m^{-2} d^{-1} (Webb et al. 2013). Previous observations have shown even higher removal rates (up to 100%) of TDIN (Brown et al. 1999, Webb et al. 2012). Some studies stated that the majority of N removal results from microbial processes and, to a lesser degree, from plant uptake (Lin et al. 2002a, Hadad et al. 2006), but studies with certain species of halophytes advocate otherwise (Webb et al. 2012, 2013). Recently, Quintã et al. (2015b) concluded that hydroponically grown *S. europaea* and *A. tripolium* could assimilate dissolved organic nitrogen (DON, specifically alanine-N and trialanine-N), suggesting that DON removal should also be taken into consideration in phytoremediation of wastewater. Other authors also concluded that some halophytes, namely *Phragmites australis* and *Spartina alterniflora,* seem to directly assimilate both inorganic and organic forms of N (Mozdzer et al. 2010). In terms of dissolved inorganic phosphates (DIP), a CW employing *S. europaea* was able to perform a removal of up to 89%; yet, it is commonly accepted that plants play a small role in phosphate removal, as it is assumed that most of the elimination recorded is achieved through adsorption to the substrate (Lüderitz & Gerlach 2002, Webb et al. 2012, 2013).

While CWs and aquaponics systems can both be used to remediate wastewater and grow halophytic cash crops, they differ in their applicability and purpose. The primary concern of CWs is usually wastewater treatment, where the interplay of many biological and chemical processes results in high removal rates of N and P, but where only a fraction of these nutrients is taken up by plants (Turcios & Papenbrock 2014). On the other hand, the main objective of aquaponics is to maximize plant production (Goddek et al. 2015), which is usually the main source of revenue in freshwater aquaponics. Growing halophytes hydroponically would be a reasonable choice for intensive fish-farming using RAS (Buhmann et al. 2015, Waller et al. 2015). These systems can provide high concentrations of N for plant growth, but parallel nitrifying biofilters are usually necessary to produce the necessary nitrate-N that is more easily absorbed by plants (Stewart et al. 1973, Jensen 1985). To retain most of N in nitrate-N form, anoxic conditions need to be minimized to avoid denitrification, which might occur at very low oxygen concentration (<10%), with the consequent release of N in its atmospheric form (Verhoeven & Meuleman 1999). Since aquaponics systems are typically well aerated and new optimized aquaponics systems are being designed (Kloas et al. 2015, Goddek et al. 2016), this issue may be easily addressed. In CWs, denitrification processes are more likely to happen due to the fundamental characteristics of the system, which create more oxic–anoxic interactions along the sediment profile, enhancing the coupling between nitrification and denitrification. For that reason, if the main goal is water remediation, CWs are the most cost-effective choice and can be used in both open and closed aquaculture systems. Eventually, as highlighted by Chen & Wong (2016), a hybrid approach comprised of both types of growing systems would allow to take advantage of both mechanisms, maximizing nutrient removal and plant biomass production.

Regarding biomass yields in both systems, variability is also evident. Using hydroponics growing systems, Boxman et al. (2017) tested the performance of *Sesuvium portulacastrum* and *Batis maritima* over 30 d (initial density of 24 plants m^{-2}) and obtained average yields of 0.53 and 0.32 kg m^{-2}, respectively. Waller et al. (2015) grew *Salicornia dolichostachya*, *A. tripolium* and *P. coronopus* for 35 d (initial density of 39 plants m^{-2}), with final average yields of 2.70, 1.25 and 0.83 kg m^{-2}, correspondingly. In a CW, Webb et al. (2013) obtained average yields of *Salicornia europaea* after 21 d (initial density of 200 plants m^{-2}) of 2.2 kg m^{-2}. Yield variability might be explained by initial planting densities, availability of physical space for growth and grow-out time to harvest, but species-specific variability is certainly a factor to consider.

The inclusion of halophytes in marine IMTA has been certainly overlooked until recent years due to the lack of a tangible market for its commercialization, when compared with seaweeds, which are commonly studied and used as extractive species in IMTA (Abreu et al. 2011, Chopin 2015, Fang et al. 2016). In fact, global demand for seaweeds is increasing, and the commercial seaweed market is expected to reach US $22.13 billion by 2024 (Grand View Research 2016). Another important factor that makes macroalgae more practical and widely chosen for IMTA is that marine IMTA has been mostly implemented in off-shore settings (Troell et al. 2009, Chopin 2015, Fang et al. 2016). As we move towards the implementation of an increasing number of land-based marine IMTA systems (e.g. saltwater aquaponics, RAS coupled with CWs) which have numerous advantages relative to off-shore settings (Gunning et al. 2016), halophytes can be progressively introduced as an extractive species with commercial and socioecologic interest for those systems. A few localized niche markets already exist for halophytes (e.g. gourmet cuisine), and their distinctive nutritional and biochemical composition can further boost their marketability in the near future (Sharma et al. 2016, Barreira et al. 2017).

THE POTENTIAL OF *HALIMIONE PORTULACOIDES*

To our knowledge, by November 2016, only 1 study had evaluated the potential of *H. portulacoides* as an extractive species for IMTA. Buhmann et al. (2015) used a hydroponics system and an artificial effluent characterized by a salinity of 15, 50 mg NO_3-N l^{-1} and 9.8 mg PO_4–P l^{-1} to investigate the plant's performance. Under the experimental conditions, *H. portulacoides* was able to retain 30% of N and 18% of P in the shoots and roots, and the average decrease of nitrate-N in the effluent was 29 mg l^{-1} and phosphate-P was 5 mg l^{-1}, over a 5 wk period. Moreover, a more recent study by Marques et al. (2017), published after the literature survey was completed, evaluated the capacity of *H. portulacoides* to extract DIN from an intensive RAS farm effluent. Average decrease in DIN was 65%. In both studies, the plant was considered a suitable candidate for the remediation of aquaculture effluents.

A total of 16 studies addressed *H. portulacoides* physiology (n = 4), phytoremediation (n = 8), primary productivity (n = 1) and secondary metabolites (n = 3), which contribute to highlight the potential of this halophyte species for IMTA (Fig. 6). This species is widely distributed throughout salt marsh ecosystems of the Mediterranean, Irano-Turanian and West Euro-Siberian, North American and South African regions (Waisel 1972, Castroviejo 1990). It plays an important role in the ecosystem services provided by coastal wetlands, namely in nutrient cycling and phytoremediation processes (Válega et al. 2008a, Sousa et al. 2010, 2011). Its distribution is correlated with good soil drainage, and it tolerates frequent short inundations as occurs in the intertidal zones where it thrives (Jensen 1985). It can cope and grow within a wide concentration range of dissolved NaCl in the water, from 0 to full strength seawater (~500 mol m^{-3}) and over (up to 1000 mol m^{-3}) (Jensen 1985, Redondo-Gómez et al. 2007). Specialized vacuoles within leaves are responsible for compartmentalizing Na^+ and Cl^- which are further excreted through epidermal bladders, protecting the metabolic machinery from salt-induced stress (Redondo-Gómez et al. 2007, Benzarti et al. 2012, 2015, Shabala et al. 2014). Within the abovementioned spectrum of salinity, optimal growth was found at 85–200 mol m^{-3} NaCl and a gradual depression was observed between 410 and 690 mol m^{-3} NaCl (Jensen 1985, Redondo-Gómez et al. 2007). Nonetheless, growth is stimulated at higher NaCl concentrations with increasing concentrations of dissolved nitrate-N (Jensen 1985). At supra-optimal salinity levels, Cl^- directly competes with NO_3^- uptake (Benzarti et al. 2015), explaining the positive impact of higher nitrate-N concentration at higher salinities. Moreover, decreased stomatal conductance is also observed with increasing Na^+ and Cl^- concentrations (Redondo-Gómez et al. 2007, Flowers & Colmer 2015), a mechanism that prevents water loss and modulates water transport to reduce net uptake of salts to the shoots (Ayala & O'Leary 1995, Khan et al. 2001, Katschnig et al. 2013). In terms of primary production, Neves et al. (2007) conducted field studies in the south of Portugal and determined that mean above-ground biomass production was 598 g m^{-2} yr^{-1}, with maximum values registered in spring, reaching 1077 g m^{-2} yr^{-1}.

In terms of biochemical composition, Vilela et al. (2014) screened for lipophilic and phenolic compounds with potential bioactivity and found that lipophilic fractions of leaves and stems are mainly composed of long chain aliphatic acids and alcohols and smaller quantities of sterols. Also, they identified 13 phenolic compounds with higher concentration in the leaves (4.6 g kg^{-1} dry matter [DM]), from which 3.1 g kg^{-1} DM were sulfated flavonoids. A rare triterpenic ketone with pharmaceutical properties (Hill & Connolly 2015) was found at high concentrations (2.8 g kg^{-1} DM) in the roots, namely the molecule hop-17(21)-en-3-one (Vilela et al. 2014). Rodrigues et al. (2014) looked at the bioactivity of *H. portulacoides* extracts and found high radical scavenging activity (IC50 = 0.9 mg ml^{-1}) against the radical ABTS and a decrease in nitric oxide production after incubation of macrophages with lipopolysaccharide and a chloroform extract

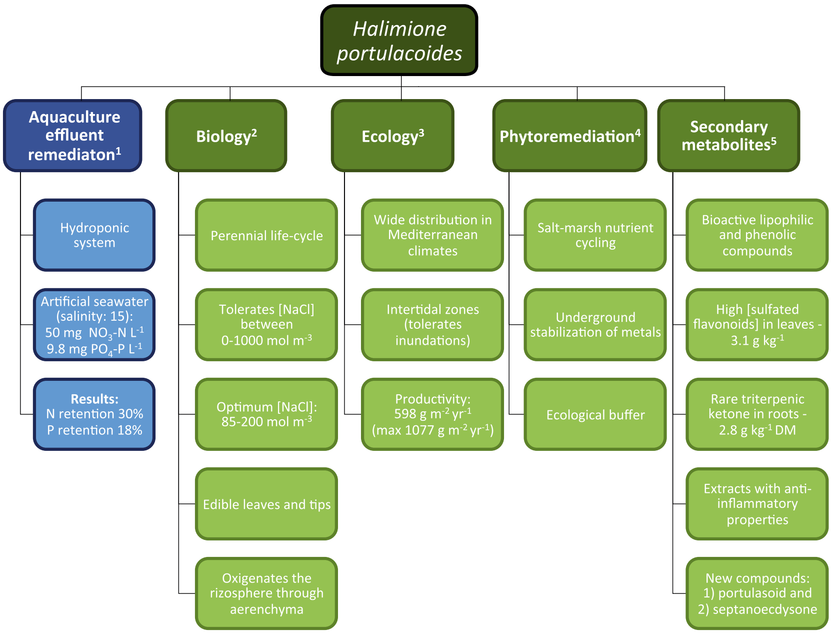

Fig. 6. Summary of *Halimione portulacoides* relevant characteristics found in the scientific literature: [1]Buhmann et al. 2015; [2]Neves et al. 2007, Waisel 1972; [3]Jensen 1985, Redondo-Gómez et al. (2007); [4]Andrades-Moreno et al. (2013), Cambrollé et al. (2012a,b), Sousa et al. (2010, 2011), Válega et al. (2008a); [5]Ben Nejma et al. (2015), Hill & Connolly (2015), Rodrigues et al. (2014), Vilela et al. (2014)

(IC50 = 109 µg ml^{-1}), indicative of anti-inflammatory properties. More recently, 2 new bioactive compounds designated as 'portulasoid' and 'septanoecdysone' were isolated from the plant (Ben Nejma et al. 2015).

This species has also been studied for its high regeneration potential and its remarkable metal phytoremediation capacities, which include stabilization, at the root level, of toxic inorganic substances and extraction and retention of several compounds in above-ground biomass (Sousa et al. 2008, 2010, 2011, Válega et al. 2008a,b, Cambrollé et al. 2012a,b, Andrades-Moreno et al. 2013). These processes occur without compromising key metabolic sites and reinforce its role as an ecological buffer, helping maintain the homeostasis of the salt marsh ecosystem.

The physiological adaptations to salt marsh environments and phytoremediation potential of *H. portulacoides* make this species a good candidate to mitigate potential negative impacts promoted by marine aquaculture effluents, as demonstrated so far. By being exposed to numerous abiotic stresses, these plants are expected to cope with multiple stress-inducing factors that fluctuate on a short-term scale, reinforcing their suitability for IMTA (Walker et al. 2014, Lutts & Lefèvre 2015). Moreover, *H. portulacoides* is widely distributed geographically, with an apparent good productivity (Neves et al. 2007) and can be easily propagated through cuttings, and therefore its use at a large scale is not dependent on wild populations for the harvesting of seeds (Sousa et al. 2010).

Additionally, halophytes have shown a positive correlation between increasing salinity and production of secondary metabolites (Aquino et al. 2011, Benzarti et al. 2012, Buhmann & Papenbrock 2013a) and enhanced production of phenols and flavonoids during the flowering period (Medini et al. 2011, Jallali et al. 2012), allowing for the manipulation of such molecules within the plant. The leaves of *H. portulacoides* have high average levels of sulfated flavonoids (Vilela et al. 2014), therefore being a potential source of these compounds of pharmacological interest (Correia-da-Silva et al. 2014). For instance, *Flaveria bidentis* (L.) Kuntze is recognized as a good source of sulfated flavonoids, namely isorhamnetin 3-sulfate, with about 744 mg kg^{-1} DM (Xie et al. 2012), only 1/4 of the content exhibited by *H. portulacoides*. Moreover, long chain chloroalkanes were also recorded in leaf waxes (Grossi & Raphel 2003) and volatile organic compounds in root exudates (Oliveira et al. 2012). A rare bioactive triterpenic ketone extracted from the roots of this halophyte (Vilela et al. 2014) further elevates the pharmacological interest of this species, and it is likely that future biochemical studies using omics-approaches will reveal new bioactive compounds of interest. Furthermore, by presenting edible leaves and tips, this halophyte may actively contribute to the diversification and expansion of the sea vegetable market.

The potential of *H. portulacoides* to be used as a halophyte biofilter is undeniable, yet little information is available relative to its use and performance. In order to explore its suitability, additional data are required on its planting density, hydraulic regimes, growth medium, nutrient requirements and availability and how these affect growth performance, nutrient uptake, phytoremediation efficiency and biochemical composition. Both CWs and hydroponics modules should be tested in order to find out which growing system is the best for the species.

PRESENT SETBACKS AND FUTURE OPPORTUNITIES

Aquaculture continues to be the fastest-growing industry in the animal food-producing sector, and its sustainability has been a major source of discussion (Troell et al. 2014, FAO 2016). In many regions of the world, including several southern European countries, a significant part of the aquaculture industry is based on semi-intensive farming practices, which are in their essence more sustainable than intensive/super-intensive productions (Bunting 2013, Edwards 2015). Nonetheless, economic issues are a setback to the expansion of those production models, usually related to the price of the end product (which competes in the market with intensively produced ones), the slower capital return and stakeholders' perceptions (FAO 2016). These limit investment and result in the lack of innovation in system design and process optimization. Additionally, promotion of public awareness and political support of these production systems are needed (Feucht & Zander 2015, Bostock et al. 2016).

One of the main challenges faced by these aquaculture practices is how to increase their competitiveness while maintaining their more ecological modes of seafood production. A new focus on product differentiation and certification, highlighting its origin, sustainability, quality and health benefits, will likely be the only pathway to balance economic and environmental tradeoffs of semi-intensive aquaculture and drive investment. In this context, future studies using *Halimione portulacoides* as an aquatic biofilter will generate valuable insights on the integration of halophytes in IMTA, contributing to the diversification of aquaculture and sustainable food production.

Besides the technical and biological features of IMTA, research also needs to address social and economic aspects. For IMTA to attain its true potential, it needs to be socially accepted, and satisfying key stakeholders will be paramount for business success and resilience (Alexander et al. 2016, Chopin 2017). The relatively low number of studies exploring these questions usually addressed consumers' perspectives, and it is now evident that they lack knowledge on aquaculture species and production methods, including IMTA (Shuve et al. 2009, Barrington et al. 2010). Yet, consumers do recognize socio-economic benefits from aquaculture and are concerned with sustainability issues (Whitmarsh & Palmieri 2009, Barrington et al. 2010, Fernandez-Polanco & Luna 2012). Aquaponics, for example, is regarded as the fittest land-based IMTA for sustainable urban farming (Specht et al. 2014), and a European consumer survey about that mode of production found a positive attitude towards local products (Milicic et al. 2017). In the same study, willingness to pay regarding food was mostly based on price and whether the products are free of antibiotics, pesticides and herbicides. This type of study provides valuable guidance concerning marketing efforts that, in this specific case, should be directed towards local shops and restaurants, emphasizing sustainable and organic-based food production (Goddek et al. 2015). A recent study about European stakeholders' perspectives on IMTA, which included industry actors, policy makers, fishermen and other users of the marine environment, found they positively discriminated IMTA in terms of environmental benefits, creation of new income streams and improvement of the overall negative public image of aquaculture (Alexander et al. 2016). Moreover, IMTA systems can incorporate additional sources of profit, including tourism and educational activities. Junge et al. (2017) outlined that a multi-disciplinary approach to aquaponics is essential to its success, and additional actors other than biologists and engineers, such as designers, architects, social and health/nutritional scientists, would be important propellers for the socio-economic valorization of the activity. More multidimensional valuation studies are needed to assess not only the economic potential of IMTA in general and halophytes in particular, but also the ecological and social benefits they can provide in order to fully understand the scope of IMTA in the future of aquaculture.

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