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Potential of Ascidians as Extractive Species and Their Added Value in Marine Integrated Multitrophic Aquaculture Systems–From Pests to Valuable Blue Bioresources

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Ascidians are considered as filter-feeder biofouling pests that negatively affect aquaculture facilities. However, they can also be recognized as a potential co-cultured/extractive species for integrated multi-trophic aquaculture (IMTA) with potential added value as bioresources. A systematic review aiming to understand the ecological importance of ascidians as efficient filter-feeders [What?]; their potential contribution as extractive species [How?]; and to set the benchmark for their nutritional value and potential added value to the aquaculture industry [For what?] is a timely contribution to advance the state of the art on these largely overlooked bioresources. In the last two decades, there has been an overall increase in publications addressing ascidians in aquaculture, namely, their negative impacts through biofouling, as well as their role in IMTA, environmental status, and microbiology. While *Ciona intestinalis*, a solitary ascidian, has been the most studied species, overall, most ascidians present high filtration and fast-growth rates. As ascidians perform well under IMTA, competition for resources and space with other filter-feeders might occur, which may require additional management actions to optimize production. Studies addressing their bioactive products show that ascidians hold great potential as premium ingredients for aquafeed formulations, as well as dietary supplements (e.g., amino acids, fatty acids). Further research on the potential use of ascidians in IMTA frameworks should focus on systems carrying capacity.

Keywords: tunicates, bioresource, IMTA, filtration rate, fatty acids, retention efficiency

INTRODUCTION

Aquaculture is an important source of food, nutrition, income, and livelihoods for hundreds of millions of people worldwide (FAO, 2020). With the continuous increase of the world's population, aquaculture production needs to increase by 21–44 million tons by the year 2050 (Costello et al., 2020). An idealistic scenario, and a major challenge for the aquaculture industry, is to be profitable, product-diversified, socially beneficial, and yet ecologically efficient and environmentally friendly, i.e., to cope with the principles of sustainable development. Integrated multi-trophic aquaculture (IMTA) has the potential to achieve such a goal.

An IMTA framework is a nature-based solution in which the by-products, wastes, uneaten feed, and nutrients from one species are recycled and converted to become fertilizer, feed, and energy for the growth of another (Naylor and Burke, 2005). These systems can be land-based or open-water, use marine, brackish or freshwater, and may include several different combinations of co-cultured species (Neori et al., 2004). IMTA aims at mimicking a natural ecosystem by combining and incorporating complementary species from different trophic or nutritional levels in the same productive environment. In an operational IMTA system, extractive species uptake organic and inorganic matter contributing to reduce costs and comply with environmental regulations (Reid et al., 2020).

In addition, their potential market value (e.g., food, feed, pharma) might provide extra economic benefits to farmers (Barrington et al., 2009; Béné et al., 2015). Selected species should be cultured at densities that optimize nutrient uptake, promote a stable balance between biological and chemical processes improving the ecosystem's health, and should be economically important as aquaculture products (Alexander et al., 2016).

However, implementing a healthful and balanced concept can present multiple challenges to farmers. Nonetheless, an IMTA framework also presents numerous benefits, including the decrease in waste outputs from overall farming activities, the additional production of a marketable product for little or no additional input cost, and more importantly, environmentally sustainable farming operations (Barrington et al., 2009; Troell et al., 2009).

The open key question concerns the optimization of the uptake of particulate and dissolved organic matter from uneaten/undigested feed and feces. Organic nutrients can nitrify the benthic-pelagic community (Albert et al., 2021) and the excess of inorganic nutrients (ammonia, nitrate, nitrite) may ultimately create a bio-deposit and lead to eutrophicated waters (Chopin et al., 2001) and/or represent an economic burden to fish farmers (Fry et al., 2016).

Ascidians, commonly known as sea squirts or tunicates, are found in all marine habitats from shallow water to the deep sea (Shenkar and Swalla, 2011) and there are approximately 3000 described species (Shenkar and Swalla, 2011). Currently classed under Phylum Chordata, ascidians hold a unique evolutionary position as the sister group of vertebrates. These organisms are benthic suspension feeders that filter particulate organic matter from the water column via an oral siphon and expelled filtered water through the atrial siphon (Jørgensen and Goldberg, 1953; Jørgensen, 1954). They present a wide variety of forms (from small colonies to big solitary forms), colors, shapes (from cone-shaped, elongated, globular, or oval), and sizes (generally from 0.5 to 200 mm) (Petersen, 2007; Shenkar and Swalla, 2011).

The body is always covered with a tunic, a protective layer that may be translucid, brightly colored or dull, covered by various kinds of spines, and contain calcareous spicules (Lambert and Lambert, 1987), or even be covered by a dense layer of sand grains (Young, 1989). Most solitary ascidians are hermaphrodites and reproduce by external fertilization (Honegger, 1986). They develop a free-swimming tadpole-like larva that swims during a short period, settles on a wide variety of habitats, and finally matures into a sessile adult (Shenkar and Swalla, 2011). Colonial specimens can reproduce both sexually and asexually (Gasparini et al., 2015). Ascidians often present an invasive behavior, representing the most dominant fouling species worldwide, colonizing natural and artificial substrates (Ordóñez et al., 2013).

While several ascidian species present a preference to settle on natural substrates (Hirose and Sensui, 2021), others settle on artificial structures, such as ship hulls, floating docks (Zvyagintsev et al., 2007), and aquaculture infrastructures (Hodson et al., 2000; Khalaman, 2001; Bullard et al., 2013; Rosa et al., 2013), process known as biofouling. At times some species even grow on other organisms being farmed, such as on the shells of mollusks (Dijkstra and Nolan, 2017; Casso et al., 2018).

Hereupon, these organisms hold great potential as co-cultured/extractive species in IMTA frameworks, with potential to contribute to more efficient, profitable, and sustainable aquaculture systems. Benthic fish contribute to sediment resuspension while searching for food or shelter (Yahel et al., 2008; Carvajalino-Fernández et al., 2020). Although these resuspension events can be brief and localized (Yahel et al., 2002), in an IMTA scenario ascidians, as excellent filter-feeders, can rapidly uptake nutrient recycling and contribute to a positive outcome.

The main objective of this systematic review is to understand how ascidians may no longer be regarded as pest organisms, who's biofouling negatively impacts aquaculture ventures, but rather as important extractive species in IMTA frameworks that yield premium biomass for high-end uses. To this purpose, we surveyed the scientific literature to answer the following three questions: [What do we know?] To better understand the biological and ecological importance of ascidians as filter-feeders in an IMTA framework; [How do ascidians perform in IMTA?] to evaluate which combination of species will contribute the most to enhance the performance of ascidians in IMTA frameworks; and [For what kind of bioactive products?] to recognize ascidians as potential bioresources in different high-end fields, namely, blue biotechnology and human nutrition.

Here, special attention will be given to fatty acids, as both omega-3 (*n*-3) and omega-6 (*n*-6) fatty acids are essential components for food, feed, and pharma industries. The analysis of these three questions will enable us to discuss and conclude on the potential of ascidians as extractive species and their added value in marine IMTA frameworks.

LITERATURE REVIEW

In January 2020, a systematic literature review, with no year restriction, was performed using the databases Thomson Reuters Web of Science (Core Collection) (Topic) and Scopus (Article title, Abstract, Keywords). The strategy used was to search within a combination of specific terms: Filtration AND (tunicate OR ascidian OR "sea squirt*"); Aquaculture AND (tunicate OR ascidian OR "sea squirt*"); Fatty acid* AND (tunicate OR ascidian OR "sea squirt*") to achieve the review's goal.

A schematic representation of the selection process is summarized in **Figure 1**. Overall, a total of 566 publications were retrieved (after excluding duplicates from the two databases), and a spreadsheet with the bibliographic information of each reference was created for further analysis to ascertain their relevance for this study. The review selection consists of two sections.

The first article selection aimed to retain publications with, at least, the abstract in the English language, peer-reviewed academic journals, book chapters, meetings abstracts, short communications, and reports on ascidians within Class Ascidiacea. When studies addressed ascidians in a general way, these were registered as "Ascidiacea." Furthermore, studies addressing the following topics were excluded from the present review: (i) first reports on the occurrence of a new species of ascidian in a given location and their geographic distributions, (ii) embryonic development, (iii) fertilization, reproduction, and associated topics, (iv) invasive behavior of ascidians and mitigation measures.

A total of 148 publications (**Supplementary Table 1**) were considered relevant and selected for further analysis. Ten research categories (aquaculture, biochemistry, biofouling, biology, biotechnology/methods, diseases, environmental, IMTA, microbiology, and review) were created and assigned to each of the 148 publications, with a maximum of four categories being attributed per publication.

The rationale for this procedure is detailed in **Table 1**. Additionally, each publication was also assigned to one of the three questions (occasionally two) initially established: (question 1 [What?]: 75 publications, question 2 [How?]: 31 publications, and question 3 [For what?]: 62 publications). Subsequently, each of the publications assigned to each of the three questions was further screened as detailed in **Figure 1**.

Briefly, concerning question 1, only publications addressing filtration, retention, ingestion, clearance, digestion, and water pumping rates were selected, for a total of 29 publications. Regarding question 2, only publications addressing topics such as aquaculture, IMTA, and growth rates were included, for a total of 19 publications. Finally, for question 3, publications referring to fatty acids and other potential co-products were considered, for a total of 28 publications. Blue biotechnology may focus on a plethora of potentially bioactive compounds (Vieira et al., 2020).

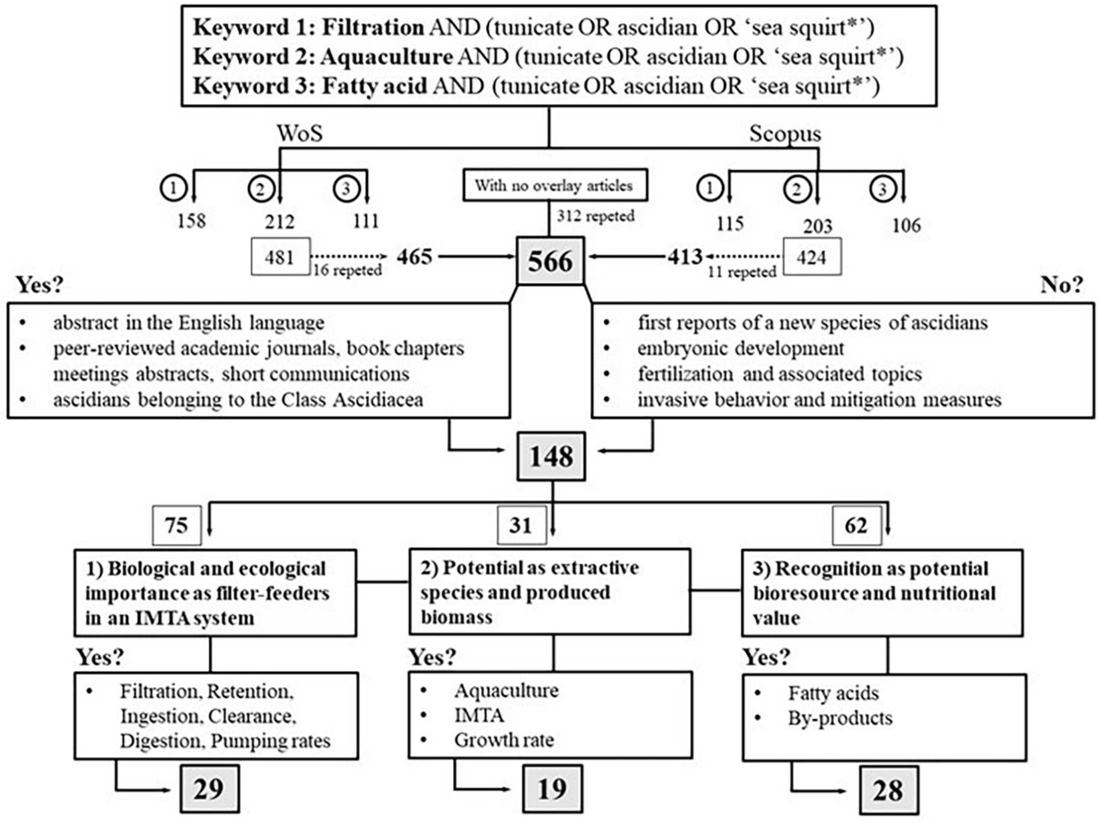

FIGURE 1 | Schematic representation of the process employed for the selection of relevant publications retrieved from each database (Web of Science, WoS; Scopus).

TABLE 1 | Research categories considered and their respective criteria.

Research category	
Aquaculture	Refers to farming of ascidians, impacts that other species may have and economic value
Biochemistry	Refers to proximate composition, lipid composition, fatty acid identification and nutrition information
Biofouling	Refers to biofouling ascidians in aquaculture sites and its impacts on produced species
Biology	Refers to biological and ecological traits such as growth, filtration, clearance, retention rates, natural diets, population interactions, and habitat preferences
Biotechnology/ Methods	Refers to models created and tested, development of technology toward the study of ascidians
Diseases	Refers to diseases associated with ascidians
Environmental	Refers to environmental parameters and their impact on ascidians, pollution, toxicity, and bioremediation
IMTA	Refers to farming ascidians with one or more different trophic groups, along with their interactions and impacts
Microbiology	Refers to the identification, characterization, and isolation of bacteria from ascidians
Review	Refers to any published review on ascidians

As this review targets marine species and they can be seen as sources of the essential omega-3 (*n*-3) and omega-6 (*n*-6) fatty acids, special attention will be given to these bioactive compounds as they can represent an added value for food, feed, and pharma industries.

RESULTS

Out of the 148 publications, 80 fell into the research category "Biology," hence demonstrating the importance of understanding morphology, biology, and anatomy of ascidians in a general manner (**Figure 2**). Since the 21st century, an overall increase in all research categories is noted, but it is worth mentioning a gradual and joint increase of publications in "Aquaculture," "Biofouling," and "IMTA" categories (44, 25, and 7%, respectively) as these are correlated with each other.

In addition, bacteria and associated diseases with ascidians are a growing concern, as seen with the increase in the number of publications within the category "Microbiology." A total of 45 species, belonging to 3 orders and 12 families (**Supplementary Table 2**) were present in this review, in which solitary ascidians represented 72% and merely 28% were colonial ascidians (**Figure 3**).

Despite the high number of ascidians from the marine realm, solely three species dominated the focus of scientists throughout the years. *Ciona intestinalis*, a translucent column-like tunicate, was by far the most studied species, followed by *Halocynthia roretzi* and *Styela clava* (**Figure 3**). A detailed analysis was performed regarding the three questions (**Table 2**). Ascidians *C. intestinalis* and *S. clava* were the two most studied species for their biological and ecological importance as filter-feeders [What?] and on the most effective combination of species for IMTA [How?]; while *H. roretzi* and *Halocynthia aurantium*, were mostly studied for their potential as bioresource [For what?] (26 and 11%, respectively).

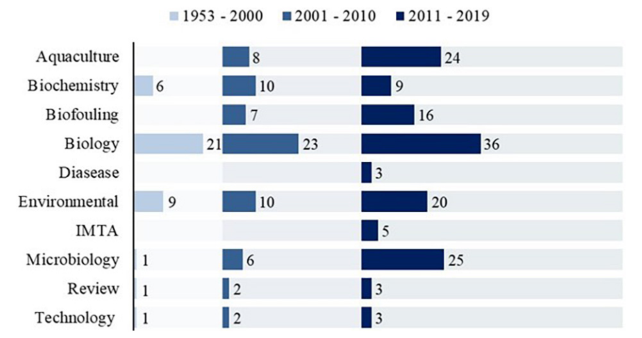

FIGURE 2 | Number of publications (*n* = 148), from 1953 to 2019, assigned to each research category.

[What Do We Know?] (Question 1)

To comprehend the role of ascidians as filter-feeders and their importance, a better understanding of basic biology is needed. Essentially, water filtrations rates were present in most of the 29 publications analyzed (**Figure 1**), with these referring to 31 different species (allocated to 17 different genera). Solitary ascidians, such as *C. intestinalis*, *Phallusia mammillata*, and *Styela plicata*, were the most investigated species accounting for 17.5, 9.5, and 7.9% of the publications, respectively. France is in the leadership both in the number of ascidians species being studied, as well as in the number of studies performed (**Table 3**).

Filtration rates presented a great variability between the different species of ascidians addressed, with intraspecific variability also being recorded, for example, for *C. intestinalis* with values ranging from 3.5 to 11.9 L h^{-1} (Fiala-Médioni, 1974; Petersen and Riisgärd, 1992) and for *P. mammillata* with values ranging from 4.4 to 11.9 L h^{-1} (Fiala-Médioni, 1973; Hily, 1991; **Table 3**). Nakai et al. (2018) demonstrated that water filtration rate increases with size, while Ribes et al. (1998) showed that filtration rates may vary seasonally, displaying an increase with rising water temperatures. Just 30% of publications registered retention rate values. A total of 17 species were investigated, with only two species being colonial ascidians. Particle retention varied from 1.7 to 4.71 μm (mean value).

[How Do Ascidians Perform in Integrated Multi-Trophic Aquaculture?] (Question 2)

Question 2 focused on understanding which combination of species with ascidians contributes the most to enhance the performance of IMTA frameworks, their extractive ability, and their impacts on other cultured species. Only five out of the 19 relevant publications (**Figure 1**) specifically addressed IMTA. These five publications presented similar aspects, as they were all performed in China and addressed *S. clava*.

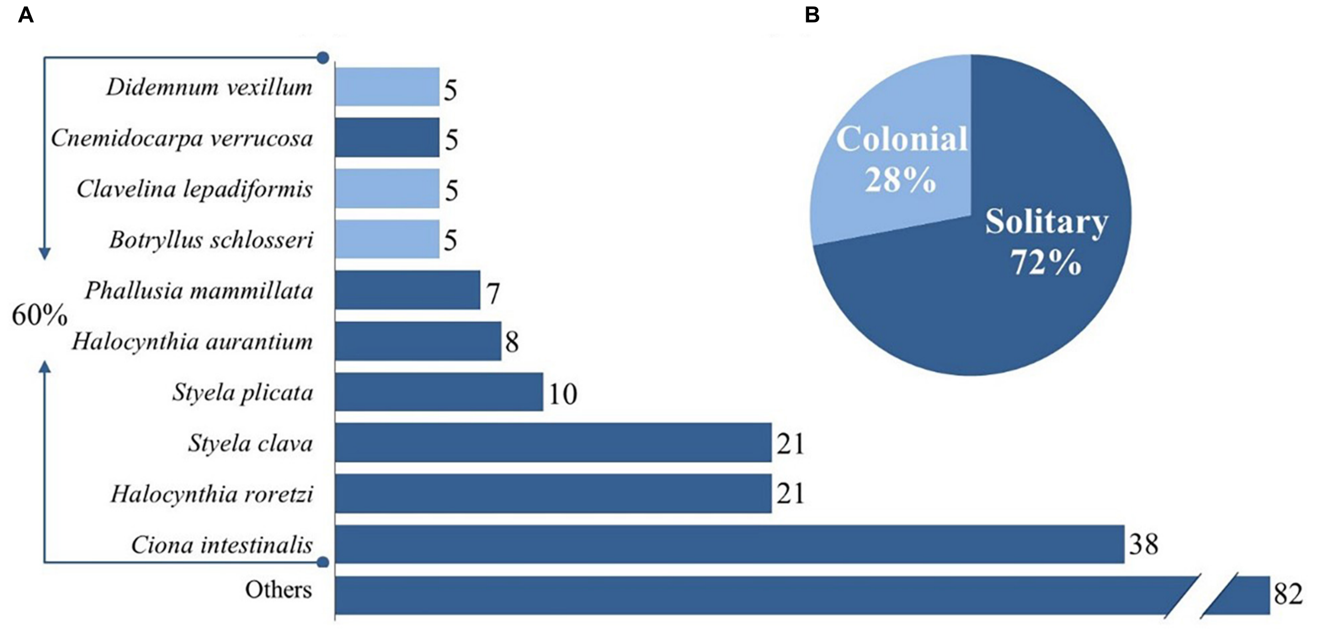

FIGURE 3 | (A) Top ten studied ascidian species and total number of publications addressing them. Light blue represents colonial species, dark blue represents solitary species; **(B)** Percentage of solitary and colonial ascidians addressed in the 148 publications surveyed. See **Supplementary Material** for complete list of studied species (**Supplementary Table 1**).

The main goal of these publications was to optimize the commercial production and growth of the sea cucumber *Apostichopus japonicus* (**Figure 4**). The remaining 14 publications addressed issues associated with the impact of biofouling promoted by ascidians on cultured species, namely, mussels, oysters, and scallops were addressed (**Table 4**). *C. intestinalis* was the most discussed ascidian regarding this topic.

[For What Kind of Bioactive Products?] (Question 3)

The recognition of the nutritional value *sensu lato* of ascidians and their potential as bioresources was considered in 28 publications (**Figure 1**), addressing 25 species belonging to 15 genera.

TABLE 2 | Percentages of the top two research categories, countries, and ascidian species that most contributed to each of the questions [What?], [How?], [For what?], addressed in the 148 publications surveyed.

Questions	Category	Country	Species
(1) [What?]	Biology (52%)	France (18%)	*Ciona intestinalis* (21%)
	Environmental (21%)	Canada (12%)	*Styela clava* (8%)
(2) [How?]	Aquaculture (30%)	Canada (36%)	*Ciona intestinalis* (33%)
	Biology (27%)	China (21%)	*Styela clava* (28%)
(3) [For what?]	Biochemistry (44%)	South Korea (27%)	*Halocynthia roretzi* (26%)
	Microbiology (43%)	Japan (21%)	*Halocyhthia aurantium* (11%)

Ascidians being addressed under this scope mostly originated from Asian countries (China, Japan, South Korea, and North Korea), with a major focus on *C. intestinalis*, *Halocynthia* sp., and *Styela* sp. Amongst the various studies, 16 of them addressed specifically the fatty acid composition of ascidians, including 20 species belonging to 13 genera. From these, few analyzed the tunic and inner body separately (Zhao et al., 2015; Zhao and Li, 2016), with the remaining analyzing the whole body of ascidians.

A wide range of fatty acids was identified with percentages varying from 0.06 to 44% total fatty acid (Jeong et al., 1996; Zlatanos et al., 2009), nonetheless, palmitic acid (16:0), stearic acid (18:0), arachidonic acid [AA-20:4 (*n*-6)], eicosapentaenoic acid (EPA–20:5*n*-3) and docosahexaenoic acid (DHA–22:6*n*-3) were consistently recorded (**Figure 5**), see **Supplementary Table 3** for further detail. Fatty acids 16:0 and 18:0 were constantly higher in all studied ascidians, however, in several species, EPA and DHA presented high values as well (Carballeira et al., 1995; Jeong et al., 1996; Zhao and Li, 2016).

Out of the studies analyzed, biocompounds such as didemnilactones A and B and neodidemnilactone (Niwa et al., 1994), 2,3-dihydroxy fatty acid glycosphingolipids (Aiello et al., 2003), anticancer ecteinascidin 743 (Mendola, 2003), pentylphenols, cyclopropane fatty acid, and cyclopentenones (Rob et al., 2011) were proven to originate from ascidians (**Table 5**). Cytotoxicity against human solid tumor cell lines (Bao et al., 2009), against HCT116 cells (human colon cancer cells), and inhibition of the division of fertilized sea urchin eggs

TABLE 3 | Summary of the main features of filtration, pumping, and retention rate of the studied ascidians addressed in the 29 publications selected regarding question 1 [What?].

Studied species	Country	Filtration rate/Pumping rate	Retention efficiency	References
Ascidiacea	NA	similar in different species suspension feeding is high efficient		Petersen, 2007
Ascidia challengeri	Antarctic	304 ml.h AFDW*	1.2–2 μm	Kowalke, 1999
Ascidia virginea	Sweden	5.2 L.h^{-1}.g^{-1}**		Petersen and Svane, 2002
Ascidiella aspersa	Denmark	5.4 L.h^{-1}.g^{-1}**	2–3 μm completely retained; RE decreased 70% for 1 μm	Randløv and Riisgärd, 1979
Ascidiella aspersa	France	6.28 h^{-1}		Hily, 1991
Ascidiella aspersa	United Kingdom	5.26 L.h^{-1}.g^{-1} at about 10,000 cells ml^{-1}	decrease $>$ 4.5 μm	Pascoe et al., 2007
Ascidiella scabra	United Kingdom	at LPS: 0.71 h^{-1}; decreased with increasing suspension load		Robbins, 1983
Ascidiella scabra	United Kingdom	FE: at HPS unchanged		Robbins, 1984
Boltenia echinata	Sweden	3.8 L.h^{-1}.g^{-1}**		Petersen and Svane, 2002
Ciona intestinalis	United States		1–2 μm	Jørgensen and Goldberg, 1953
Ciona intestinalis	France	3.5 L.h^{-1}.g^{-1}		Fiala-Médioni, 1974
Ciona intestinalis	France	4.3 L.h^{-1}.g^{-1}; FE(mean) = 74% 5.9 L.h^{-1}.g^{-1}*		Fiala-Médioni, 1978a
Ciona intestinalis	Sweden	7.7 L.h^{-1}.g^{-1} **	2–3 μm completely retained; RE decreased 70% for 1 μm	Randløv and Riisgärd, 1979
Ciona intestinalis	United Kingdom	at LPS: 0.21 h^{-1} (mud); 0.11 h^{-1} (*Fucus*); decreased with increasing suspension load		Robbins, 1983
Ciona intestinalis	United Kingdom	FE: at HPS unchanged		Robbins, 1984
Ciona intestinalis	Denmark	11.9 L.h^{-1}.g^{-1} ** 4–21°C increased, >21°C decrease		Petersen and Riisgärd, 1992
Ciona intestinalis	Sweden	8.4 L.h^{-1}.g^{-1}**		Petersen and Svane, 2002
Ciona intestinalis	United Kingdom	4.61 L.h^{-1}.g^{-1} at about 5000 cells ml^{-1}	similar to 2–5.5 μm	Pascoe et al., 2007
Ciona intestinalis	United States	0.07–0.97 L.h^{-1}*		Clos et al., 2017
Ciona intestinalis	France	positively related to food concentration		Hoxha et al., 2018
Ciona robusta	France	positively related to food concentration CR higher than *C. intestinalis*		Hoxha et al., 2018
Ciona savignyi	Japan	0.125 L.h^{-1} ind^{-1} (ind 3.5 cm) 0.359 L.h^{-1} ind^{-1} (ind 5.3 cm) 1.05 L.h^{-1} ind^{-1} (ind 6.4 cm) optimal at 24–25°C		Nakai et al., 2018
Clavelina lepadiformis	France	2.5 L.h^{-1}.g^{-1}		Fiala-Médioni, 1974
Clavelina lepadiformis	Denmark		2–3 μm completely retained; RE decreased 70% for 1 μm	Randløv and Riisgärd, 1979
Clavelina lepadiformis	Sweden	8.9 L^{-1}.g^{-1}**		Petersen and Svane, 2002
Cnemidocarpa verrucosa	Antarctic	348 ml.h AFDW*	1.4–4 μm	Kowalke, 1999
Cnemidocarpa verrucosa	Antarctic		0.2–2 μm	Lesser and Slattery, 2015
Corella eumyota	Antarctic	251 ml.h AFDW*	1.2–5 μm	Kowalke, 1999
Corella parallelogramma	Sweden	7.0 L.h^{-1}.g^{-1}**		Petersen and Svane, 2002
Didemnum sp.	Australia	reduced heterotrophic bacteria		Pile, 2005
Halocynthia papillosa	France	6.3 L.h^{-1}.g^{-1}		Fiala-Médioni, 1974
Halocynthia papillosa	Spain	3.0–3.6 L.h^{-1}.g^{-1}**	0.6–7 μm	Ribes et al., 1998
Halocynthia pyriformis	Canada	136 ml.min^{-1} DW (1 g)	2–5 μm: increased 5–15 μm: decreased	Armsworthy et al., 2001
Halocynthia sp.	Australia	only reduced $<$ 3 μm		Pile, 2005
Halocynthia spinosa	Israel		1 μm at 95% efficiency; 0.3 μm at 50% efficiency	Jacobi, 2018
Herdmania momus	Israel		1 μm at 95% efficiency; 0.3 μm at 50% efficiency	Jacobi, 2018

(Continued)

TABLE 3 | (Continued)

Studied species	Country	Filtration rate/Pumping rate	Retention efficiency	References
Microcosmus sabatieri	France	6.9 L.h^{-1}.g^{-1}		Fiala-Médioni, 1974
Microcosmus exasperatus	Israel		1 μm at 95% efficiency; 0.3 μm at 50% efficiency	Jacobi, 2018
Molgula manhattensis	Denmark	Higher than *C. intestinalis* and *A. aspersa*	2–3 μm completely retained; RE decreased 70% for 1 μm	Randløv and Riisgård, 1979
	Sweden	2.1 L.h^{-1}.g^{-1}**		Petersen and Svane, 2002
Molgula pedunculata	Antarctic	349 ml.h AFDW*	1.2–6.5 μm	Kowalke, 1999
Phallusia julinea	Australia	reduced heterotrophic bacteria		Pile, 2005
Phallusia mammillata	France	4.4 L.h^{-1}.g^{-1} (ind 10–12 cm)		Fiala-Médioni, 1973
Phallusia mammillata	France	4.8 L.h^{-1}.g$^{-1;}$ FE(mean) = 76% 6.3 L.h^{-1}.g^{-1} *		Fiala-Médioni, 1978a
Phallusia mammillata	France	15°C: 4.3 L.h^{-1}.g^{-1}** 20°C: 1.6 L.h^{-1}.g^{-1}** (mean): 10°C: 3.56, 15°C: 5.79, 20°C: 2.63 ml.h^{-1}.g^{-1} DW*		Fiala-Médioni, 1978b
Phallusia mammillata	France	$pO_2 > 119$ mg Hg: decrease $pO_2 > 98$ mg Hg: decrease faster FE: 77–79%		Fiala-Médioni, 1979
Phallusia mammillata	France	11.9 L.h^{-1} g^{-1}		Hily et al., 1992
Phallusia mammillata	NA	825–5100 ml.h (ind 8–128 g WW)		Carlisle, 1966
Phallusia nigra	Israel		1 μm at 95% efficiency; 0.3 μm at 50% efficiency	Jacobi, 2018
Polyandrocarpa zorritensis	Italy	max: 1.745 L.h^{-1}.g^{-1} DW	RE: 41%, removed bacterial biomass of 16.34 + 1.71 μg.C.L^{-1}.g^{-1} DW)	Stabili et al., 2016
Polycarpa mytiligera	Israel		1 μm at 95% efficiency; 0.3 μm at 50% efficiency	Jacobi, 2018
Polycarpa pedunculata	Australia	only reduced < 3 μm		Pile, 2005
Polycarpa sp.	Australia	reduced heterotrophic bacteria		Pile, 2005
Pyura microcosmus	France	1.94 h^{-1}		Hily, 1991
Pyura sp.	Australia	only reduced < 3 μm		Pile, 2005
Pyura tessellata	Sweden	3.0 L.h^{-1}.g^{-1}**		Petersen and Svane, 2002
Styela clava	New Zealand	declined after 3 weeks (sedimentation)		Lohrer et al., 2006
Styela clava	South Korea	0.477 J d^{-1} mean DW (310 mg) at 5–15°C 0.687 J d^{-1} mean DW (310 mg) at 15–25°C		Kang et al., 2015
Styela plicata	France	8.8 L.h^{-1}.g$^{-1;}$ FE(mean) = 80% (mean): 10.7 L.h^{-1}.g^{-1} *		Fiala-Médioni, 1978a
Styela plicata	United States	*Nannochloropsis* sp.: $10^5 + 10^6$ cells: 3158 ml.h^{-1}; *Escherichia coli*: $10^5 + 10^6$ cells: 3475 ml.h^{-1};		Draughon et al., 2010
Styela plicata	United States	<10 μm: decreased (fast and slow flow speeds); >10 μm: decreased (flow speed from 3 to 22 cm.s^{-1}) maximal at intermediate flow speeds 12 cm.s^{-1}		Sumerel and Finelli, 2014
Styela plicata	Italy	max: 1.4 L.h^{-1}.g^{-1} DW	RE: 81% removed bacterial biomass of 32.28 + 2.15 μg C.L^{-1}.g^{-1} DW	Stabili et al., 2016
Styela plicata	Israel		1 μm at 95% efficiency; 0.3 μm at 50% efficiency	Jacobi, 2018

LPS, Low particulate suspension; HPS, High particulate suspension; DR, Digestion rate; RE, Retention efficiency; CR, Clearance rate; FE, Filtration efficiency; IR, Ingestion rate.
**Pumping rate; **Adapted from* Petersen (2007).

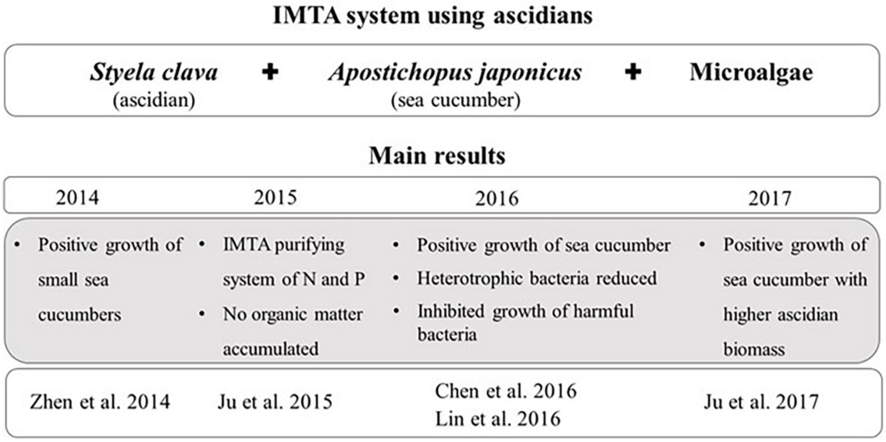

FIGURE 4 | Schematic representation of the main features of integrated multitrophic aquaculture (IMTA) frameworks using ascidians addressed in the 5 of the 19 publications selected regarding question 2 [How?].

(Rob et al., 2011) are just some examples of these compound functionalities.

DISCUSSION

Ascidians as Organic Matter Extractive Species

Over the years, ascidian's biology and functionality have been of growing interest and several studies have addressed water filtration, clearance, retention, pumping, ingestion, and digestion rates. According to Fiala-Médioni (1978a), the definition of filtration rate is the volume of water that has been cleared of particles in a given time frame. Authors have gradually replaced the term "filtration rate" for clearance rate and although this topic has been widely addressed, previous reports have shown considerable variation in the results being reported.

Petersen (2007) complied information on the suspension-feeding of ascidians and concluded that "filtration rates in different species at identical conditions will not vary more than within the same species of different sizes" and also suggests that ascidians are more efficient in non-turbid conditions. Moreover, this present review revealed that since Petersen's (2007) work, there is a generalized lack of studies on this topic. In the last decade, only six new publications have addressed filtration rates, mainly on genus *Styela* and *Ciona* (Draughon et al., 2010; Sumerel and Finelli, 2014; Kang et al., 2015; Stabili et al., 2016; Hoxha et al., 2018; Nakai et al., 2018), and therefore further research is urgently needed.

Testing filtration rates can be very complex in several ways and several variables must be taken into consideration. Robbins (1983) suggested that with an increase in food concentration, the filtration rate would decrease. Randløv and Riisgärd (1979) observed that the presence of a folded pharynx in *Molgula manhattensis* increased the area of the water transporting structure, thus allowing for higher filtration rates. The lag-phase phenomenon was not perceived by Randløv and Riisgärd (1979) leading to lower rates being reported and ultimately to an overall misinterpretation of their findings and not allowing comparison with other studies. Therefore, the need for a lag phase with an appropriate time (20–140 min) is highly recommended (Petersen and Riisgärd, 1992). Moreover, Petersen and Svane (2002) measured the filtration rate of seven ascidians and concluded that the area of the branchial basket and the length of the ciliary band lining the stigmata openings also contributes to higher filtration rates.

Ascidians are very sensitive organisms to any chemical or mechanical disturbance, which can cause them to close their siphons and thereby stop filtration, thus generating unrealistic filtration rates. Several studies in the 1970s (Fiala-Médioni, 1973, 1974, 1978a,b; Randløv and Riisgärd, 1979) concluded that undisturbed ascidians filter water very efficiently and at constant rates, a feature that will unquestionably optimize their performance if these are employed in the IMTA framework.

Most often, it is not easy to evaluate if filtration rates are at their optimal by merely recording the appearance of ascidians (unlike what occurs for some bivalves, such as mussels) (Petersen and Riisgärd, 1992). As environmental variables play an important role in the filtration process, several investigations aimed to elucidate the relationship between filtration rate, body size, temperature, and particle concentration (Fiala-Médioni, 1978b; Petersen and Riisgärd, 1992; Kang et al., 2015). In sum, the standardization of the methodology used to investigate filtration rate is at a high demand to better evaluate and compare data from different research.

Consistent results were observed allowing to affirm that as ascidians increase in size, their filtration rate will also increase, and filtration rate declined with temperatures above 20–21°C, this being true for ascidians from temperate waters. Moreover, the optimal temperature for ascidians' filtration rate may vary with the species being addressed and with the local conditions. Nakai et al. (2018) registered an optimal filtration at temperatures of 24–25°C for *Ciona savignyi*. Several reports focus the deleterious effects of biofouling by ascidians on mussel

TABLE 4 | Summary of the main impacts produced by ascidians in aquaculture scenarios addressed in the 19 publications selected regarding question 2 [How?].

Studied species	Country	Aquaculture species	Main results	References
Ciona intestinalis	Australia	*Mytilus galloprovincialis*	Small mussels: 4% shorter in shell length; 21% reduced flesh weight;	Sievers et al., 2013
			Large mussels: 3.9% shorter in shell length, flesh weights not reduced	
Styela clava			Large mussels: 4.4% shorter in shell length, flesh weights not reduced	
Botrylloides violaceus	Canada	Mussel	*C. intestinalis*: 80% more coverage on unfouled plates	Paetzold et al., 2012
Botryllus schlosseri			*C. intestinalis*: <10% coverage on pre-settled plates	
Ciona intestinalis			Higher individual growth on pre-settled plates than on unfouled plates	
Ciona intestinalis	Canada	*Mytilus edulis*	*C. intestinalis* has a negative impact,	Ramsay et al., 2008a
Styela clava			replacing *S. clava*	
Ciona intestinalis	Canada	*Mytilus edulis*	*C. intestinalis* was marginally higher in August;	Ramsay et al., 2008b
			Mussel loss 50–60% for all treatments	
Ciona intestinalis	Canada	*Mytilus edulis*	*C. intestinalis:* abundance: 98.4–828.6 ind/0.3 m mussel sock;	Lutz-Collins et al., 2009
			Negative effect on epifaunal species, primarily on sessile organisms	
Molgula sp.			*Molgula* sp.: colonized the mussel socks in lower numbers and an opposite spatial pattern of *C. intestinalis*	
Ciona intestinalis	Canada	*Mytilus edulis*	Size and condition decreased with increasing ascidian densities; 50% mussel mortality observed under heavy ascidian fouling	Daigle and Herbinger, 2009
Ciona intestinalis	Canada	*Mytilus edulis*	*C. intestinalis* can dominate mussel biomass and contribute to organic sedimentation	Guyondet et al., 2016
Didemnum sp.	France	*Pinctada margaritifera*	Competition between oysters and ascidians was not a limiting factor,	Lacoste et al., 2016
Herdmania momus			in spite of a diet overlap for nanophytoplankton	
Ascidiella aspersa	Japan	Scallop	*A. aspersa* settle as larvae in early summer, and grows well until winter, resulting in overgrowth on scallops in the harvest season	Kanamori et al., 2017
Ciona savignyi	Japan	*Mizuhopecten yessoensis*	Filtration increased with size increase; *C. savignyi* has the potential to negatively impact the growth of the Japanese scallop through competition for food.	Nakai et al., 2018
Didemnum vexillum	New Zealand	*Perna canaliculus*	Mussels may only be vulnerable to direct *D. vexillum* fouling impacts at early stages of production	Fletcher et al., 2013
Ciona intestinalis	Norway	*Mytilus edulis*	In forced upwelling conditions: positive effect on both species; ascidians would be more efficient at extracting resources due to their lower metabolic cost and higher filtration capacity.	Filgueira et al., 2019
Ciona intestinalis	South Africa	*Mytilus galloprovincialis*	Competitive exclusion of the mussel in dark, sheltered areas and physiological exclusion of the ascidian elsewhere	Rius et al., 2011
Ascidiacea	Spain	Oyster	15 spp. were identified	Casso et al., 2018

farming and their potential competition as filter feeders for trophic resources. One study compared ascidian and mussel filtration rates and highlighted that at 16 and 19°C these are similar (Daigle and Herbinger, 2009).

Conversely, allied with the filtration process is particle retention efficiency. Various approaches have shown that the diet of ascidians mainly comes from smaller particles [particulate organic matter (POM) < 20 µm] (Ju et al., 2015, 2016), picophytoplankton (<2 µm), and phytoplankton biomass (Riisgärd and Larsen, 2016). Moreover, Lacoste et al. (2016) verified an overall lack of food selectivity. The retention efficiency increased for particle sizes 2–5 µm (Armsworthy et al., 2001), in which particles from 2 to 3 µm were completely retained (Randløv and Riisgärd, 1979) and retention efficiency decreased for particles above 4.5 µm (Pascoe et al., 2007).

In general, a threshold of 2–4 µm is observed. In a more recent study, with an *in situ* experiment using 6 different ascidian species, a 95% retention efficiency was registered for 1 µm particles and 50% efficiency for submicron particles (0.3 µm), thus widening ascidians scope (Jacobi, 2018). The ability of *S. plicata* and *Polyandrocarpa zorritensis* to remove *Vibrio alginolyticus* from seawater has also been tested, with *S. plicata* showing a higher efficiency for bioremediation and restoring seawater quality (Stabili et al., 2016). The same authors

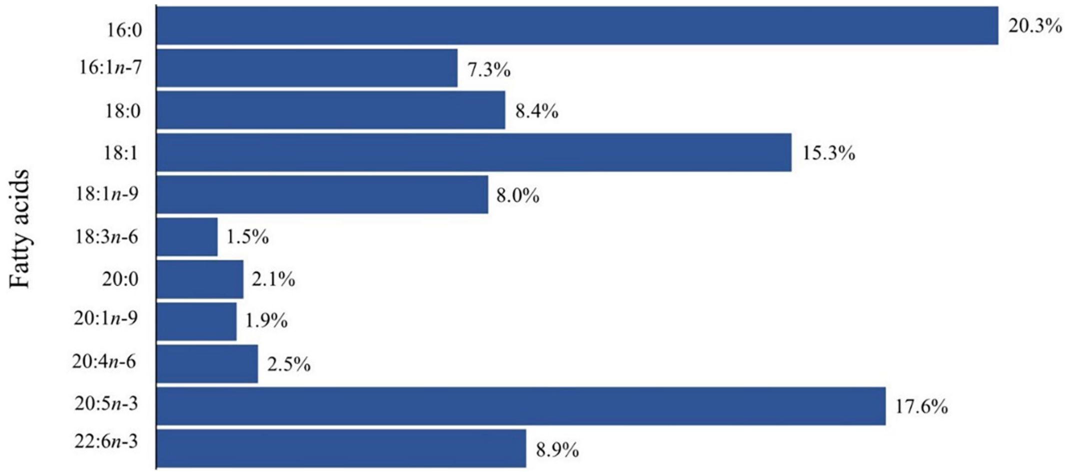

FIGURE 5 | Mean relative percentage values of total fatty acids of the ascidians addressed in this review. See **Supplementary Table 2** for further details.

also demonstrated that retention efficiency was higher in solitary ascidians (81%) than in colonial ones (41%). Lefebvre et al. (2000) used oysters in a land-based fish-farm effluent and confirmed that suspended feeders can improve water quality and add economic value. However, the retention efficiency of filter-feeders in an IMTA scenario must be dealt with caution as many parameters may influence the settling velocity of the suspended particles of organic matter (Reid et al., 2009).

Nonetheless, further research is much needed considering that our systematic review revealed the existence of few publications addressing this topic in colonial ascidians.

Ascidians Incorporated in Integrated Multi-Trophic Aquaculture Frameworks

Despite the increase in interest in IMTA frameworks over the last years, ascidians have rarely been addressed under this scope. Most publications on aquaculture mostly focus on -ascidians as pests due to biofouling features and negative impacts on aquaculture facilities, mainly on shellfish productions (Carver et al., 2003). Cultured shellfish can be negatively affected by ascidian fouling in many ways, with these causing a reduction in mussel growth, flesh weight, and reduced overall size and condition (Daigle and Herbinger, 2009; Sievers et al., 2013; Guyondet et al., 2016; Nakai et al., 2018).

In extreme conditions, this may even lead to mussel mortality (Daigle and Herbinger, 2009). However, this scenario cannot be generalized, as Cordell et al. (2013) did not record any negative effects on mussel growth at four different locations and Sievers et al. (2013) observed no reduction of flesh weight was seen in larger mussels. Moreover, Lacoste et al. (2016) found that food competition between oysters and ascidians was not a limiting factor, which advises caution on making generalized assumptions on the negative impacts of ascidians on the farming of bivalves.

Indeed, several factors such as location, species involved, environmental parameters, sampling, and experiment conditions, among others must also be considered (Fletcher et al., 2013). Furthermore, some ascidians present invasive traits, growing quickly and therefore must be supervised to not overwhelm and overgrow the other culture species.

The solitary ascidian, *C. intestinalis*, was investigated in 60% of publications in this field, given that this is one of the most studied ascidian species. As an example, they present high tolerance to a wide range of salinities and temperatures (Lutzen, 1999; Shenkar and Swalla, 2011), allowing them a worldwide spatial distribution. This biofouling ascidian, with a fast-growing rate (Ramsay et al., 2008b, Lutz-Collins et al., 2009), that contributes to organic sedimentation (Guyondet et al., 2016), and prefers unfouled sites, dark and sheltered areas (Paetzold et al., 2012) does not necessarily have negative impacts on all bivalves or other organisms, further research is needed. Recently, some studies investigated the impacts of the presence of ascidian *S. clava* in an IMTA framework to optimize the growth of the sea cucumber *A. japonicus* (Zhen et al., 2014; Ju et al., 2015, 2016). These studies have shown that an IMTA framework consisting of ascidian-sea cucumbers-microalgae, not only has the potential to reduce organic matter in the surrounding sediment (Ju et al., 2015), it can also reduce harmful bacteria (Lin et al., 2016) and purify the water body from dissolved nutrients such as nitrogen and phosphorus (Ju et al., 2015).

Moreover, this framework can also have a positive impact on the growth performance of these sea cucumber species (Zhen et al., 2014; Chen et al., 2015; Ju et al., 2016). Available literature shows that only one ascidian species (*S. clava*) was addressed in these studies, and yet with very positive results.

How to incorporate and manage ascidians in an IMTA framework is an important issue with many critical factors that must be considered. Growth rate, spawning season, number of generations, settlement locations, and life span are some of these factors. As an example of how contrasting can these factors be for different ascidians, *C. intestinalis* can produce from 12000 to 100000 eggs over different spawning periods, whereas the colonial ascidian *Botryllus schlosseri* can only produce

TABLE 5 | Summary of the main attributes of the bioactive compounds of ascidians and other features addressed in the 28 publications selected regarding question 3 [For what?].

Country	Studied species	Bioactive compounds and others	References
Greece	*Microcosmus sulcatus*	protein 0.8%, moisture: 81.1%, fat: 1.0%, ash: 7.5%;	Zlatanos et al., 2009
		glutamic acid: 1.05 g.100 g freeze-dried	
Italy	*Microcosmus sulcatus*	2,3-dihydroxy fatty acid glycosphingolipids	Aiello et al., 2003
India	*Didemnum psammathodes*	protein: 3.78 μg.ml^{-1}; total carbohydrate: 2.15 μg.ml^{-1};	Sri Kumaran and Bragadeeswaran, 2014
		crude fiber: 9.2 μg.ml^{-1}; total free amino acid: 3.2 μg.ml^{-1};	
		leucine: 540.9 mg.g, arginine: 401.2 mg.g, lysine: 385.4 mg.g	
	Eudistoma viride	protein: 3.62 μg.ml^{-1}; total carbohydrate: 12.2 μg.ml^{-1};	
		crude fiber: 7.9 μg.ml^{-1}; total free amino acid: 3.9 μg.ml^{-1};	
		leucine: 582.3 mg.g, arginine: 365.4 mg.g, lysine: 344.5 mg.g	
Japan	*Didemnum moseleyi*	Didemnilactone and Neodidemnilactone	Niwa et al., 1991
Japan	*Didemnum moseleyi*	Didemnilactones A and B and Neodidemnilactone	Niwa et al., 1994
Japan	*Diplosoma* sp.	Pentylphenols 1 (inhibited the division of fertilized sea urchin eggs) and 2, cyclopropane fatty acid 3, and cyclopentenones 4 (cytotoxity against HCT116 cells) and 5	Rob et al., 2011
Morocco	*Cynthia savignyi*	Cholesterol was the main sterol: 40.8%	Maoufoud et al., 2009
	Cynthia squamulata	Cholesterol was the main sterol: 59.5%	
NA	Ascidiacea	Man-made glue	Pennati and Rothbächer, 2015
NA	Ascidiacea	edible ascidians: raw, cooked, dried, or pickled	Lambert et al., 2016
Norway	*Ciona intestinalis*	Cellulose: 96%;	Hassanzadeh, 2014
		(g.100 g DW): glutamic acid: 5.27; leucine: 2.54; glycine: 2.31	
Norway	*Ciona intestinalis*	Cholestanol: (32.54% tunic,15.81% inner body);	Zhao et al., 2015
		Cholesterol (29.63% tunic, 33.11% inner body)	
South Korea	*Halocynthia roretzi*	Up to 80% of fishmeal could be replaced with tunic meal of sea squirt without retardation in growth. Optimal growth was fishmeal 20 diet	Choi et al., 2018
South Korea	Polyclinidae	1-Aplidic acid A; 2-Aplidic acid B; 3-4Z-Aplidic acid B; 4-Aplidic acid C; 5-4Z-Aplidic acid C; 6-Aplidamide A	Bao et al., 2009
South Korea	*Halocynthia roretzi*	Abalone fed the sea tangle (ST) 400 diet achieved the best growth	Jang et al., 2017
Turkey	*Phallusia* sp.	Cholesterol: 32%; Volatiles: Hydrocarbons: 48.4%	Slantchev et al., 2002
	Styela sp.	Cholesterol: 42.3%; Volatiles: Phenols: 46.2%	
United States	*Styela clava*	US retail price (frozen): ($3.63/kg)	Karney and Rhee, 2009
United States	*Ecteinascidia turbinate*	Anticancer ecteinascidin 743; Commercial-scale in-sea proved cost effective	Mendola, 2003

up to 50 eggs in 3 months (Paetzold et al., 2012). Solitary ascidians *Ascidiella aspersa*, *C. intestinalis* (Millar, 1952), and *Corella willmeriana* (Lambert, 1968) can develop into mature adults in just 3 months reach up to 50, 120, and 12 mm, respectively, with 1 or 2 generations and a life span of 12–18 months (*A. aspersa* and *C. intestinalis*) and 3 months (*C. willmeriana*).

The difficulty arises in the management of these biological and ecological characteristics due to the range of intra and interspecific variability and the potential environmental impacts that using ascidians may bring (e.g., biofouling). The existence of a specific area that may promote the settlement of ascidians, such as longlines or PVC plates, can be a simple solution to foster the production of biomass of these organisms and allow to easily remove their biomass for multiple applications.

Exploring the possibility of using multiple combinations of different ascidian species with other taxa, such as fish, shellfish, or echinoderms (namely, sea cucumbers) is paramount to test innovative IMTA frameworks with enhanced socio-economic and environmental performance.

Ascidians as Bioresources for High-End Uses

Considering the increase of wild-harvested or cultured ascidians for human consumption, mainly in Japan, South Korea, and Chile, knowledge on the proximate composition, biocompounds, food safety issues are of greater relevance.

Over the last decade, an increasing concern on food safety issues associated with ascidians has led prompt several studies on the identification of bacteria associated with edible ascidians such as *H. aurantium* (Chen et al., 2018) and *H. roretzi* (Kumagai et al., 2011). Bacteria associated with ascidians can also be a source of bioactive secondary metabolites and biosurfactants with diverse biotechnology applications in the food-processing industry, among other high-end markets (Achieng et al., 2017).

Several natural products have been isolated from ascidians, for example, the cellulose that is present almost exclusively in the ascidian's tunic and it is rich in carbohydrate contents (Zhao and Li, 2016), whereas the inner body is protein-rich (Berrill and Ray Society, 2005; Hassanzadeh, 2014). Many other compounds, for example, alkaloids, cyclic peptides, and polyketides, collagens, sulfated polysaccharides, glycosaminoglycans, sterols, among others, can be exploited as by-products in the pharmaceutical and chemical industry (Hassanzadeh, 2014; Monmai et al., 2018) due to their antibacterial, antifungal, antitumor and anti-inflammatory activities (Chen et al., 2018). Numerous biocompounds have successfully been retrieved from ascidians, a recent review on this matter describes "about 160 molecules endowed with antimicrobial activity produced by ascidians and/or by their associated microorganisms" (Casertano et al., 2020).

In recent years, the search for new chemical constituents derived from marine invertebrates has increased intensity (Datta et al., 2015). For instance, Pennati and Rothbächer (2015) investigated ascidian's larval bioadhesion properties to develop man-made glues and fouling resistant surfaces from solitary and colonial ascidians. Nowadays, ascidians are used in multiple applications such as fishing bait, health supplement tablets (Lambert et al., 2016), and as ornamental species for marine aquaria, fetching high prices online.[1][2]

Looking at fatty acids in more detail, our review revealed that approximately 70% of publications regarding fatty acids focused on solitary ascidians and once again ascidian *C. intestinalis* was the main focus. Many studies have drawn their attention to establishing ascidians as a new bioresource for *n*-3 fatty acids-rich marine lipids (Hassanzadeh, 2014; Zhao et al., 2015; Zhao and Li, 2016). Nonetheless, the profiling of fatty acids in ascidians, in general, is still poorly explored. Our study retrieved information from 20 species, with 13 ascidian species being addressed only once.

The overall results suggest that ascidians can be a good source of *n*-3 polyunsaturated fatty acids, namely, essential fatty acids such as EPA and DHA, which were detected in most ascidians surveyed (Dagorn et al., 2010; Zhao et al., 2015). Therefore, ascidians present a high nutritional value, they are a healthy seafood choice due to their high protein levels and low calories (Lee et al., 1995; Kang et al., 2011). Hassanzadeh (2014) concluded that the composition profile of ascidian fatty acids seems to be similar to fish oil. Therefore, ascidians biomass may eventually be a good alternative to fish oil and fish meal in formulated aquafeeds.

Moreover, ascidians present amino acid composition similar to egg albumin, suggesting a great potential and capability to be weighed as marine organisms' feed (Hassanzadeh, 2014). Indeed, the replacement of fish meal with ascidian's biomass in aquafeeds has already started being addressed with Jang et al. (2017) and Choi et al. (2018) having partially or fully replaced the fish meal with the tunic of the ascidian *H. roretzi* in aquafeeds for the abalone *Haliotis discus* with compromising its growth performance.

CONCLUSION

In the past two decades, considerable insights have been achieved on ascidians' ecology and biology, including filtration and retention efficiencies. Their nutritional value and potential role in IMTA frameworks are also starting to be thoroughly investigated.

Despite the intra and interspecific variability recorded for ascidians filtration rates, there is a consensus that these organisms do display high filtration rates, that they can retain submicron and picoplankton particles, and they also present a fast-growing rate. As available scientific evidence suggests that these organisms are capable to perform well under an IMTA framework, however, it is important to investigate if competition with other filter-feeders for trophic resources and space can occur, namely, with mussels, scallops, and oysters.

Furthermore, available studies to date suggest that ascidians achieve higher growth performances in IMTA frameworks when in the presence of sea cucumbers and fish. The development of innovative IMTA frameworks is important to maximize the systems carrying capacity.

Finally, among other potentially bioactive compounds, ascidians represent a rich source of EPA and DHA, both being essential fatty acids paramount for human consumption, marine fish, and shrimp nutrition. Despite some cultural barriers in western countries, ascidians are increasingly regarded as a healthy seafood for human consumption, being an interesting source of essential amino and fatty acids. The use of ascidians as an alternative ingredient for the formulation of aquafeeds also looks promising and will certainly deserve further attention in coming years.

AUTHOR CONTRIBUTIONS

LM contributed to the main investigation, writing the original draft, reviewing, and editing the final version. RC provided supervision of the writing, reviewing, editing, and validation. AL contributed to supervision of the writing, reviewing and editing process, validation, and funding acquisition. All authors contributed to the article and approved the submitted version.

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[1] https://www.reefcleaners.org/

[2] https://www.mysaltwaterfishstore.com/

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SUPPLEMENTARY MATERIAL

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