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/or represent an economic burden to fish farmers. 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 \((\text{n}-3)\) and omega-6 \((\text{n}-6)\) 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
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 Asciidiacea. When studies addressed ascidians in a general way, these were registered as “Asciidiacea.” 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).
Halocynthia was by far the most studied species, followed by *H. roretzi* and *Ciona intestinalis*. Solely three species dominated the focus of scientists throughout ascidians (*solitary ascidians represented 72% and merely 28% were colonial* (A total of 45 species, belonging to 3 orders and 12 families)

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,” “Bio fouling,” 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).

[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 Riisgård, 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*. **TABLE 1 |** Research categories considered and their respective criteria.

| Research category | Criteria |
|-------------------|----------|
| 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 |

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

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-20:5n-3) and docosahexaenoic acid (DHA-22:6n-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), antitumor eecteinascidin 743 (Mendola, 2003), pentylenols, 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...
| Studied species | Country | Filtration rate/Pumping rate | Retention efficiency | References |
|----------------|---------|-----------------------------|----------------------|------------|
| Ascidia challengeri | Antarctic | 304 ml*h^{-1} AFDW* | 1.2–2 µm | Kowalewski, 1999 |
| Ascidia virginia | Sweden | 5.2 L*h^{-1} g^{-1} | 2–3 µm completely retained; RE decreased 70% for 1 µm | Petersen and Svane, 2002 |
| Asciidiella aspersa | Denmark | 5.4 L*h^{-1} g^{-1} | 2–3 µm completely retained; RE decreased 70% for 1 µm | Randlov and Riisgård, 1979 |
| Asciidiella aspersa | France | 6.28 h^{-1} | decrease > 4.5 µm | Pascocci et al., 2007 |
| Asciidiella scabra | United Kingdom | 5.26 L*h^{-1} g^{-1} at about 10,000 cells ml^{-1} | | |
| Botryllus echinata | Sweden | 3.8 L*h^{-1} g^{-1} | | |
| Ciona intestinalis | United States | 3.5 L*h^{-1} g^{-1} | similar to 2–5.5 µm | Petersen and Svane, 2002 |
| Ciona intestinalis | France | 4.3 L*h^{-1} g^{-1}; FE(mean) = 74% | | |
| Ciona intestinalis | Sweden | 7.7 L*h^{-1} g^{-1} ** | | |
| Ciona intestinalis | United Kingdom | at LPS: 0.71 h^{-1}; decreased with increasing suspension load | | |
| Ciona intestinalis | United Kingdom | at LPS: 0.21 h^{-1} (mud); 0.11 h^{-1} (Fucus); decreased with increasing suspension load | | |
| Ciona intestinalis | Denmark | 11.9 L*h^{-1} g^{-1} ** | similar to 2–5.5 µm | Petersen and Svane, 2002 |
| Ciona intestinalis | Sweden | 8.4 L*h^{-1} g^{-1} ** | | |
| Ciona intestinalis | United Kingdom | 4.61 L*h^{-1} g^{-1} at about 5000 cells ml^{-1} | 1–2 µm | Petersen and Svane, 2002 |
| Ciona intestinalis | United States | 0.07–0.97 L*h^{-1} | | |
| Ciona intestinalis | France | positively related to food concentration | | |
| Ciona robusta | France | positively related to food concentration | | |
| Ciona savignyi | Japan | 0.125 L*h^{-1} ind^{-1} (ind 3.5 cm) | | |
| Ciona savignyi | Japan | 0.359 L*h^{-1} ind^{-1} (ind 5.3 cm) | | |
| Ciona savignyi | Japan | 1.05 L*h^{-1} ind^{-1} (ind 6.4 cm) | | |
| Cleavelia lepadiformis | France | 2.5 L*h^{-1} g^{-1} | 2–3 µm completely retained; RE decreased 70% for 1 µm | Randlov and Riisgård, 1979 |
| Cleavelia lepadiformis | Denmark | 2.5 L*h^{-1} g^{-1} | 2–3 µm completely retained; RE decreased 70% for 1 µm | Randlov and Riisgård, 1979 |
| Cnemidocarpa verrucosa | Sweden | 8.9 L^{-1} g^{-1} ** | 1.4–4 µm | Petersen and Svane, 2002 |
| Cnemidocarpa verrucosa | Antarctic | 348 ml*h AFDW* | 1.2–5 µm | Kowalewski, 1999 |
| Cnemidocarpa verrucosa | Antarctic | 0.2–2 µm | | Lesser and Slattery, 2015 |
| Corella eumyota | Antarctic | 251 ml*h AFDW* | 0.6–7 µm | Fiala-Médoni, 1974 |
| Corella parallelogramma | Sweden | 7.0 L*h^{-1} g^{-1} ** | 2–5 µm: increased | | |
| Didemnum sp. | Australia | reduced heterotrophic bacteria | 5–15 µm: decreased | | |
| Halocynthia papillosa | France | 6.3 L*h^{-1} g^{-1} | | |
| Halocynthia papillosa | Spain | 3.0–3.6 L*h^{-1} g^{-1} ** | | |
| Halocynthia pyriformis | Canada | 136 ml*min^{-1} DW (1 g) | | |
| Halocynthia sp. | Australia | only reduced < 3 µm | | |
| Halocynthia spinosa | Israel | 1 µm at 95% efficiency; 0.3 µm at 50% efficiency | | |
| Herdmania momus | Israel | 1 µm at 95% efficiency; 0.3 µm at 50% efficiency | | |

(Continued)
| Studied species          | Country         | Filtration rate/Pumping rate           | Retention efficiency                  | References                      |
|-------------------------|-----------------|----------------------------------------|---------------------------------------|---------------------------------|
| *Microcosmus sabatieri* | France          | 6.9 L.h\(^{-1}\).g\(^{-1}\)           | 1 µm at 95% efficiency; 0.3 µm at 50% efficiency | Fiala-Médioni, 1974            |
| *Microcosmus exasperatus* | Israel          | Higher than *C. intestinalis* and *A. aspersa* | 2–3 µm completely retained; RE decreased 70% for 1 µm | Jacobi, 2018                    |
| *Molgula manhattensis*  | Denmark         | 2.1 L.h\(^{-1}\).g\(^{-1}\)**         |                                       | Randlev and Risgård, 1979       |
| *Molgula pedunculata*   | Sweden          | 349 ml.h AFDW*                         | 1.2–6.5 µm                            | Petersen and Svane, 2002        |
| *Phallusia julinea*     | Australia       | reduced heterotrophic bacteria         |                                       | Kowake, 1999                   |
| *Phallusia mammillata*  | France          | 4.4 L.h\(^{-1}\).g\(^{-1}\) (ind 10–12 cm) |                                       | Fiala-Médioni, 1973            |
|                         |                 | 4.8 L.h\(^{-1}\).g\(^{-1}\); FE(mean) = 76% |                                       | Fiala-Médioni, 1978a           |
|                         |                 | (mean): 10°C; 3.56, 15°C; 5.79, 20°C; 2.63 ml.h\(^{-1}\).g\(^{-1}\) DW* |                                       |                                 |
| *Phallusia mammillata*  | France          | pC\(_2\) > 119 mg Hg; decrease         |                                       | Fiala-Médioni, 1979            |
|                         |                 | pC\(_2\) > 98 mg Hg; decrease faster   |                                       |                                 |
|                         |                 | FE: 77–79%                             |                                       |                                 |
| *Phallusia mammillata*  | NA              | 825–5100 ml.h (ind 8–128 g WW)         | 1 µm at 95% efficiency; 0.3 µm at 50% efficiency | Carlisle, 1966                  |
| *Phallusia nigra*       | Israel          | max: 1.745 L.h\(^{-1}\).g\(^{-1}\) DW | 41%, removed bacterial biomass of 16.34 \(\pm\) 1.71 µg.C.L\(^{-1}\).g\(^{-1}\) DW |                                 |
| *Polycarpa mytiligera*  | Israel          | only reduced < 3 µm                    | 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       | 1.94 h\(^{-1}\)                        |                                       | Hily, 1991                     |
| *Pyura microcosmus*     | France          | 3.0 L.h\(^{-1}\).g\(^{-1}\)**         |                                       | Pile, 2005                     |
| *Pyura sp.*             | Australia       | only reduced < 3 µm                    |                                       |                                 |
| *Pyura tessellata*      | Sweden          | 15°C: 4.3 L.h\(^{-1}\).g\(^{-1}\)**   |                                       | Petersen and Svane, 2002       |
|                         |                 | 20°C: 1.6 L.h\(^{-1}\).g\(^{-1}\)**   |                                       |                                 |
| *Styela clava*          | New Zealand     | declined after 3 weeks (sedimentation) |                                       |                                 |
| *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 |                                       |                                 |
| *Styela plicata*        | France          | 8.8 L.h\(^{-1}\).g\(^{-1}\); FE(mean) = 80% |                                       | Fiala-Médioni, 1978a           |
|                         |                 | (mean): 10.7 L.h\(^{-1}\).g\(^{-1}\)** |                                       |                                 |
| *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 | 81% removed bacterial biomass of 32.28 + 2.15 µg.C.L\(^{-1}\).g\(^{-1}\) DW |                                 |
| *Styela plicata*        | Israel          | 1 µm at 95% efficiency; 0.3 µm at 50% efficiency |                                       |                                 |

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).*
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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) compiled 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 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.

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. Randlov and Rijsård (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 Randlov and Rijsård (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 Riisgård, 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; Randlov and Riisgård, 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 Riisgård, 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 Riisgård, 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; Large mussels: 3.9% shorter in shell length, flesh weights not reduced | Severs et al., 2013                |
| Styela clava          | Canada           | Mussel              | C. intestinalis: 80% more coverage on unfouled plates                          | Paetzold et al., 2012              |
| Botryllinae violacea  | Canada           | Mussel              | C. intestinalis: <10% coverage on pre-settled plates                            |                                    |
| Botrylus schlosseri   | Japan            | Mussel              | Higher individual growth on pre-settled plates                                 |                                    |
| Ciona intestinalis    | Canada           | Mytilus edulis      | C. intestinalis: abundance: 98.4–828.6 ind/0.3 m mussel sock;                 | Lutz-Collins et al., 2009          |
| Ciona intestinalis    | Canada           | Mytilus edulis      | Mussel loss 50–60% for all treatments                                          |                                    |
| Molgula sp.           | Greece           | Mussel              | 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       | Norway           | Mussel              | in spite of a diet overlap for nanophytoplankton                               |                                    |
| Ascidella 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. | Figueira 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                  |
| Ascidacea             | Spain            | Oyster              | 15 spp. were identified in which particles from 2 to 3 μm were completely retained (Randlov and Riisgård, 1979) and retention efficiency decreased for particles above 4.5 μm (Pascoe et al., 2007). | 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 (Riisgård 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 (Randlov and Riisgård, 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 Polycandrocarpa 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
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%; glutamic acid: 1.05 g.100 g freeze-dried | Zlatanos et al., 2009 |
| 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; 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; 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 | Sri Kumaran and Bragadeeswaran, 2014 |
| 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. | Pentyphenol 1 (inhibited the division of fertilized sea urchin eggs) and 2, cyclopropane fatty acid 3, and cyclopentenones 4 (cytotoxicity against HCT116 cells) and 5 | Rob et al., 2011 |
| Morocco     | Cynthis savignyi | Cholesterol was the main sterol: 40.8% | Maoufoud et al., 2009 |
| Morocco     | Cynthis squamulata | Cholesterol was the main sterol: 59.5% | |
| NA          | Asciidiacea     | Man-made glue                  | Pennati and Rothbächer, 2015 |
| Norway      | Cliona intestinalis | Cellulose: 96%; (g.100 g DW); glutamic acid: 5.27; leucine: 2.54; glycine: 2.31 | Hassanzadeh, 2014 |
| Norway      | Cliona intestinalis | Cholestanol: (32.54% tunic, 15.81% inner body); Cholesterol (29.63% tunic, 33.11% inner body) | Zhao et al., 2015 |
| 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 |
| Turkey      | 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 turbirae | 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 _Ascidella 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, bio-compounds, 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. auriantium* (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.12

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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1https://www.reefcleaners.org/
2https://www.mysaltwaterfishstore.com/
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SUPPLEMENTARY MATERIAL

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