Aquaculture International
August 2022, Volume 30, Pages 3143-3157
https://doi.org/10.1007/s10499-022-00953-0
https://archimer.ifremer.fr/doc/00788/89980/

Marine ecological aquaculture: a successful Mediterranean integrated multi-trophic aquaculture case study of a fish, oyster and algae assemblage

Roque D'Orbcastel Emmanuelle [1,*], Lutier Mathieu [2,6], Le Floc'h Emilie, Ruelle Francois [3], Triplet Sebastien [3], Le Gall Patrik [4], Hubert Clarisse [5], Fortune Martine [1], Laugier Thierry [1], Geoffroy Thibault [3], Crottier Anaïs [1], Gobet Angélique [1], Fouilland Eric [6]

[1] MARBEC, Univ Montpellier, CNRS, Ifremer, IRD, Sète, France
[2] Ifremer, CNRS, IRD, LEMAR, University of Brest, Plouzané, France
[3] MARBEC, Univ Montpellier, CNRS, Ifremer, IRD, Palavas-les-flots, France
[4] Ifremer, LER Bretagne Nord, CRESCO, Dinard, France
[5] Ifremer, Laboratoire METabolites Des microALGues, Nantes, France
[6] MARBEC, Univ Montpellier, CNRS, Ifremer, IRD, Sète, France

* Corresponding author : Emmanuelle Roque D'Orbcastel, email address : emmanuelle.roque@ifremer.fr

Abstract :

Inspired by agroecology, ecological aquaculture proposes an alternative model that uses ecology as a paradigm to develop innovative, more eco-friendly aquaculture with environmental, economic and social benefits. Integrated multi-trophic aquaculture (IMTA) is one application of this principle. Inspired by the natural trophic chain, it associates primary producers with primary or secondary consumers, providing a new source of biomass without requiring supplementary feed by recycling inorganic and organic wastes. Of these systems, land-based IMTA demonstrate several advantages, especially easier control of nutrient flows, contaminants and/or predators. This study focused on a land-based marine IMTA, combining a recirculating aquaculture system for fish consecutively with a natural marine polyculture of microalgae and oyster cultivation. The objective was to assess the ability of the microalgal polyculture both to bioremediate fish nutrients and to sustain oyster growth. For the first time in a Mediterranean climate, we confirmed the feasibility of developing a microalgae community of interest for oysters maintained by fish effluent. Despite strong variability in microalgae production, this IMTA system resulted in significant oyster growth over the experimental period of 1 month, with growth results of the same order of magnitude as natural juvenile growth. In the conditions tested, this IMTA with reduced human intervention allowed a gain in recoverable biomass of 3.7 g of oyster produced per killogramme of fish feed distributed. By transforming waste into additional biomass, IMTA offer a more promising, ecological avenue for aquaculture, based on a circular economy, which may in turn increase the social acceptability of fish farming.

Keywords : Integrated multi-trophic aquaculture, Nutrient recycling, Oysters, Fish, Microalgae

Abbreviations

ARA Arachidonic acid
EPA Eicosapentaenoic acid
HRAP High-rate algal pond
IMTA Integrated multi-trophic aquaculture
PUFA Polyunsaturated fatty acids
RAS Recirculating aquaculture systems
RE Removal efficiency
SGR Specific growth rate

Introduction

Food system paradigms

Today, the global food system and food security face multiple challenges, with a convergence of population growth and increasing hunger and malnutrition (FAO 2016). Additional pressure, e.g. anthropic activity and environmental pollution, threatens natural resources, while the consequences of climate change are leading to the loss of biodiversity and unbalanced production systems (IPBES 2019). A transition is required towards more sustainable production and consumption.

In recent decades, the general paradigm in animal or vegetal feedstock production, especially in Europe, has been to grow one selected species under conditions of intensive cultivation. This method of production is highly dependent on the species' ability for high and stable growth and resilience to sudden environmental changes. In a context of global change, with extreme climatic events occurring more frequently, in aquaculture systems, high water temperatures potentially increase the risk of some diseases (Karvonen et al. 2010). Monospecific systems are based on species selected for their ability to dedicate their energy to growth and have little adaptability to exogenous pressures; thus, xenobiotics (e.g. antimicrobials) are often needed to maintain productivity in intensive systems (Smith et al. 1999). Of animal production systems, aquaculture is growing 7.8% per year, exceeding all others (Troell et al. 2014). Monospecific aquaculture (especially to raise finfish) is today common worldwide and is often associated with the use of antibiotics (Miranda 2011; Lulijwa et al. 2019), potential chemical contaminants such as heavy metals or dioxins, or hormones (FAO 2003). Another disadvantage is the discharge of large amounts of nutrients (i.e. from organism excretions and unconsumed food), which can cause the eutrophication and deoxygenation of coastal waters when environmental carrying capacity is exceeded (Gowen and Bradbury 1987; Pillay 2004). This can foster the development of pathogens and parasites, which may in turn negatively impact biodiversity, human health and the farmed species (Neori et al. 2004; Jegatheesan et al. 2011), leading to sometimes dramatic environmental concerns due to the presence of potential harmful residues impacting the health of end consumers (Okocha et al. 2018).

From monospecific to multispecies production systems

A major paradigm shift is essential to improve not only aquaculture food safety, but also its social acceptability. In the agricultural sector, research into alternative agriculture applying the principles of ecology emerged in the 1980s (Altieri 1983). The 'agroecology' paradigm is based on several principles: e.g. input reduction, recycling, animal health, biodiversity and synergy (Wezel et al. 2020). It aims to take into account interactions between the plants, animals, humans and the environment within agricultural systems and to imitate the natural processes involved in ecosystem productivity, stability and resilience (Malézieux 2012) in order to develop new production methods (Snapp 2017).

Inspired by this approach, 'ecological aquaculture' has been put forward as an alternative model that uses ecology as a paradigm to develop aquaculture with environmental, economic and social benefits. It maintains that aquaculture should mimic the structure and functions of natural ecosystems and practice nutrient recycling through waste reuse (Costa-Pierce 2015; Aubin et al. 2017). Based on the natural trophic chain, integrated multi-trophic aquaculture (IMTA) is in this sense one of the logical next steps in alternative aquaculture development (Barrington et al. 2009), representing a way to improve existing systems.

Higher diversity in farmed species could help social acceptability

Studies looking into the possibility of IMTA began in the early 1970s (Ryther 1975; Goldman et al. 1974), with research efforts increasing over the last two decades, both in marine ecosystems (Chopin et al. 2001; Hussenot 2003; Barrington et al. 2009 in FAO 2009; Milhazes-Cunha and Otero, 2017; Buck et al. 2018) and freshwater ecosystems (Wongkiew et al. 2017). As mentioned by Chopin (2013), the concept of IMTA can in fact be traced back to the origins of aquaculture (in 2200–2100 BCE, You Hou Bin detailed the integration of fish with aquatic plants). Chopin defines IMTA as '*The farming, in proximity, of species from different trophic levels and with complementary ecosystem functions in a way that allows one species' uneaten feed and wastes, nutrients and by-products to be recaptured and converted into fertilizer, feed and energy for the other crops, and to take advantage of synergistic interactions among species while biomitigation takes place*'.

By integrating species with complementary diets, IMTA reproduce a simplified trophic chain (Fig. 1), in which both primary producers and consumers play a key role. Microalgae or macroalgae nourished by inorganic liquid effluents use photosynthesis to grow, reintroducing energy into the system and acting both to fix CO_2 and to provide O_2 and food for other organisms (Shpigel and Neori 1996; Demetropoulos and Langdon 2004; Barrington et al. 2009). They can serve as a food source for high value-added species, e.g. grazers or filter-feeders such as abalone, urchins, oysters or clams (Tenore 1976; Hugues-Games 1977; Gordin et al. 1981; Borges et al. 2005). Organic compounds released by farmed species or from unused external feed can also be consumed by primary or secondary consumers such as crustaceans, or echinoderms such as holothurians and urchins (Chopin 2013). The resulting reduced environmental impact of IMTA could increase the social acceptability of aquaculture (Alexander et al. 2016; Knowler et al. 2020), representing a perceived improvement over current monoculture practices for the public (Barrington et al. 2010).

In comparison to other systems, IMTA is not only more environmentally friendly, but can also potentially provide more economic stability through product diversification (Granada et al. 2016), although the overall capital gain (via greater degree of productivity) has not yet been demonstrated at an industrial level, apart from in one Asian study (Fang et al. 2019).

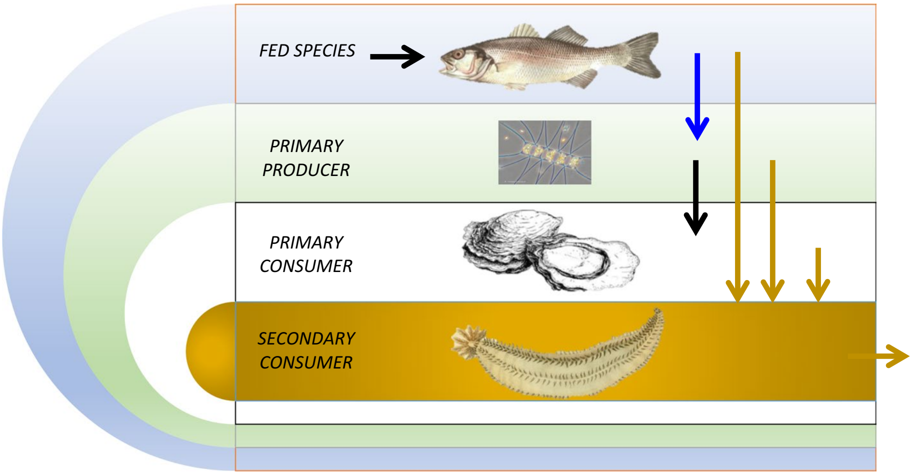

Fig. 1 Theoretical representation of an IMTA assemblage, with triangles representing the different trophic compartments and arrows representing the different flows (blue for inorganic, black for feed, brown for organic)—illustrations from lapecheenligne.com, ©N.Neaud-Masson, shutterstock.com and Manuel d'actinologie ou de zoophytologie Paris; F.G. Levrault, 1834–1836

Current and future challenges of IMTA

IMTA can be developed both in open sea or inland areas (Shpigel and Neori 1996; Neori et al. 1998). Among current IMTA challenges, there are (i) biological challenges with the choice of candidate species adapted to the environmental and societal contexts, (ii) economical challenges to demonstrate their performance and rentability in comparison with conventional systems (Yu et al. 2017) and (iii) zoo-technological challenges to determinate key variables to cultivate candidate species (Buck et al. 2018) and to ensure nutrient fluxes' management (Granada et al. 2016), especially for offshore systems (Buck et al. 2018) where the connectivity between compartments need to be documented. Moreover, new planification of aquaculture area has to be considered, with extensive areas required for species coping with low natural densities, such as holothurian (Tolon et al. 2017; Chary et al. 2019).

Land-based IMTA present several advantages: easier control of flows, less pressure from predators or pathogens and negligible exposure to extreme climatic events (Manzi and Castagna 1989; Neori et al. 2004; Blancheton et al. 2009). Of the systems widely used for land-based fish production, recirculating aquaculture systems (RAS) offer many advantages, such as reduced water consumption based on a bacteria treatment loop (Piedrahita 2003; Martins et al. 2010). Wastewater flow in an RAS is consequently reduced compared to traditional flow-through systems, but carries inorganic compounds such as PO_4^{3-}, NO_3^-, and CO_2. To reduce these compounds, one of the existing treatments proposed by IMTA is to integrate a compartment of primary producers. Macroalgae have frequently been included in these systems as biofilters, e.g. *Ulva* spp. and *Gracilaria* spp. (Neori et al. 2004, 2017; Lopez Figueroa et al. 2012), but microalgae are less frequently used (Milhazes-Cunha and Otero 2017). Like macroalgae, microalgae add value in terms of feeding macro-invertebrates (i.e. filter-feeders), but they could be even more promising because of their higher photosynthesis rate and greater surface-area-to-volume ratio (i.e. higher nutrient uptake) (Milhazes-Cunha and Otero 2017).

One challenge for land-based IMTA systems is ensuring microalgae culture stability to allow both optimal nutrient remediation for the primary culture (e.g. fish) and optimal feeding for the associated culture (e.g. filter species). A monospecific algal culture may be selected in order to meet the needs of the other IMTA species. However, several studies have reported that an algal polyculture consisting of an assemblage of several species presents higher resilience to disturbances and ensures greater efficiency in resource use (Newby et al. 2016). In particular, multispecies algal cultures could better cope with climatic and fish-effluent variability. Some authors have demonstrated that natural plurispecific algal cultures can both grow on finfish effluent and ensure nutrient remediation (Lefebvre et al. 1996, 2004; Neori et al. 2017; Galès et al. 2020). Of course, within the IMTA, microalgae must also fulfil the feeding requirements of filter species. In one study, the addition of silicate in an algal culture initially filled with natural seawater and continuously supplemented with nitrate-enriched RAS wastewater led to a diatom-based algal culture with a remediation capacity equivalent to that of macroalgae (Li et al. 2019). In the microalgae biochemical composition, lipid content as well as essential amino acids and polyunsaturated fatty acids play a major role in the diet energy content, directly controlling oyster assimilation and biomass productivity (Brown et al. 1997 and references therein; Ben Kheder et al. 2010; Anjos et al. 2017). This nutritional value is mainly related to microalgal diversity, with diatoms being the most suitable diet for oyster growth (Brown et al. 1997 and references therein).

The use of a continuous nutrient-enriched multispecies algal culture as an inoculum reservoir, if the culture is well controlled, stabilised and monitored, may help: (i) to reduce the risk of producing undesirable (i.e. toxic) algal species (when using natural coastal seawater inoculum), (ii) to accelerate the time required to reach the maximal microalgal biomass, ensuring optimal inorganic matter remediation and oyster feeding.

This study focused on combining a RAS (for sea bass) with algal polycultures and oyster cultures. We used an inoculum from a year-round algal culture (a high-rate algal pond or HRAP, located close to the IMTA) initially inoculated with natural local seawater. The aim was to assess the algal polyculture's ability to sustain oyster growth from an associated compartment when continuously supplemented with wastewater from a fish-based RAS in an IMTA context.

From IMTA theory to a new way of production

Materials and methods

Land-based marine IMTA system

The experiment ran over 31 days, from 17 April (day 1) to 17 May 2018 (day 32), at the French Institute for Ocean Science (Ifremer) station in Palavas-les-Flots (southern France), which has a Mediterranean climate. The experimental IMTA system (Fig. 2) was adapted following Li et al. (2019), with improved hydrodynamics by including additional recirculation pumps in the outdoor microalgal raceways and oyster tanks.

Three separate units were created to conduct the experiment. An indoor RAS (in triplicate) was dedicated to sea bass (*Dicentrarchus labrax*) ($n = 1380$ fish, split into 460 per tank, initial weight of 425 ± 134 g ind^{-1}), which were reared at a density increasing from 51 (d1) to 56 kg m^{-3} (d32); this unit was considered a nutrient provider. Each was connected

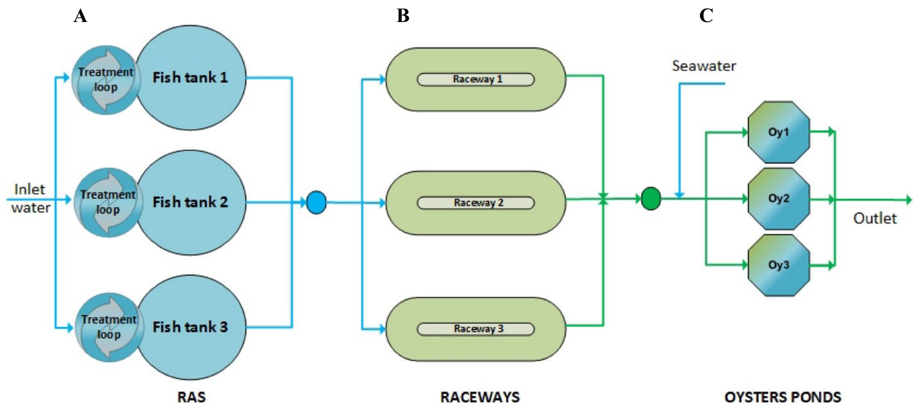

Fig. 2 Experimental land-based IMTA (Ifremer, Palavas) with three compartments: (**A**) fish tanks operating with water recirculation; (**B**) outdoor microalgal raceways receiving fish effluent from A; (**C**) oyster ponds receiving microalgae from lagoons in B. Total surface area = 150 $m.^2$

to an outdoor microalgal raceway (6 m^3, $n=3$), which continuously received RAS wastewater with a fixed flow rate (1 L min^{-1}), ensuring a hydraulic retention time of 4.2 days.

The IMTA microalgal raceways were inoculated with RAS effluent seawater (4:5 of the mix) and a local microalgal reservoir (1:5) containing a consortium dominated by Chlorellales (mainly *Schizochlamydella* sp and *Picochlorum* sp). Silicate (Na_2SiO_3, $5H_2O$) was added to reach a N:Si:P molar ratio of nearly 10:5:1 in order to favour diatom dominance (Lefebvre et al., 1996). Nanostream electronic pumps (Turbelle®) were added in order to limit biodeposition and ensure light access.

The microalgae cultures (chlorophyll a concentration of 6.3 mg L⁻1) were then mixed in a tank with airstones and distributed to 3 outdoor tanks containing juvenile Pacific oysters (*Crassostrea gigas*). The microalgae flow rate of 2.7 L h^{-1} was diluted with 100 L h^{-1} of fresh filtered seawater (dilution factor = 37), in order to approach a daily feeding ration of 6–8% dry weight (DW). This food ration is frequently used to meet the energy requirements of *C. gigas* broodstock in hatcheries (Utting and Millican 1997; Fabioux et al. 2005; Delaporte et al. 2006); and represents a ration 3 times higher than in a previous study (Li et al. 2019). Food distribution was optimised by the inclusion of a homogenisation pump (Turbelle®) and an airlift and by replacing baskets clogged by biofouling with new ones every 2 weeks.

Nutrient remediation and algal biomass production

Throughout the 31-day experiment, the water was sampled 3 times a week to monitor nutrient parameters (inlet and outlet) in the photosynthetic extractive compartment (the 3 outdoor microalgal raceways). Water samples (*n* total = 49) were filtered (GF/F, WhatmanTM) after each sampling and stored (at − 25 °C) for NO_3-N, NO_2-N, NH_4-N and PO_4-P analysis (Alliance® auto-analyser). Nutrient removal efficiency (RE, %) was calculated (see Li et al. 2019).

The microalgal biomass was monitored 3 times a week in the 3 outdoor microalgal raceways; chlorophyll a (Chl*a*) was determined after water sample filtration using GF/F filters (Association 1995), and the pigments were extracted with methanol (Ritchie 2006). Chl*a* concentration was measured using a spectrophotometer and calculated using the Ritchie (2006) equation. The main microalgal species were identified by microscopy with an Olympus IMT2 inverted light microscope, following the protocol of the French Observation and Monitoring Programme for Phytoplankton and Hydrology (REPHY) in coastal waters (Neaud-Masson 2020).

Some environmental parameters (i.e., temperature, salinity, pH) were monitored daily in all tanks (i.e., fish, algae and oyster) using a YSI® probe.

Oyster growth

On d1, 756 8-month juvenile oysters ($n_{total} = 756$) were split into 3 outdoor tanks ($n_{tank} = 252 \pm 3$). The initial fresh weight and length of the juvenile oysters were measured, with values of 1.55 ± 0.33 g ind^{-1} and 22 ± 3 mm ind^{-1}, respectively. The final fresh weight and length were measured after 32 days. The specific growth rate (SGR) was calculated with the equation:

$$SGR\ (in\ \%) = \frac{ln(final\ weight - initial\ weight) * 100}{number\ of\ days}$$

The non-parametric Wilcoxon-Mann–Whitney statistical test was used to assess median differences between experimental conditions.

Results and discussion

An IMTA-microalgae community of interest, but highly variable Chla production

The results confirmed the feasibility of cultivating a microalgae community on fish effluent in a Mediterranean climate.

In all raceways, the Chl*a* pigment concentrations, indicator of algal biomass, showed a similar three-phased pattern (Fig. 3): (1) from d1 to d9, a low initial concentration of around 0.06 mg Chl*a* L^{-1}, with *cyanobacteria* dominance observed in microscopy; (2) from d9 to d16, an increase in production (reaching a maximum of 0.58 mg Chl*a* L^{-1} at d15), with the dominance of *Cylindrotheca closterium* (Ehrenberg) Reimann and Lewin 1964; and finally, (3) after d16, a decline in algal growth, still with *Cylindrotheca closterium* (at d23) as the main algal species, and *Pseudo-nitzschia* and *cyanobacteria* (Fig. 4) at the end of the culture (d28).

Using an inoculum from a local intensive algal culture to start the microalgal culture, we observed that the maximal Chl*a* production was reached after 16 days, twice as fast as in a previous experiment performed during the same seasonal period but using a natural seawater inoculum (Li et al., 2019). The microalgal crash around d24 was probably due to rapid algal CO_2 consumption leading to elevated pH (maximum pH of 10) and CO_2 depletion.

The results also confirmed the feasibility of bioremediating fish nutrients using an inoculum from a local HRAP. The remediation of phosphates was high, $85 \pm 25\%$ (with a maximal value of 97.6%), but was lower for nitrogenous elements, with $49 \pm 21\%$ for NH_4-N (maximal value of 93.5%), and $24.9 \pm 11.1\%$ for NO_3-N (maximal value of 51.3%).

The algal yields—and as a consequence bioremediation efficiency—could be improved, for example, by reusing CO_2 released by the fish in the RAS loop in the algae culture in order to maintain pH at seawater value (*ca* 8) and to avoid CO_2 depletion. Another research

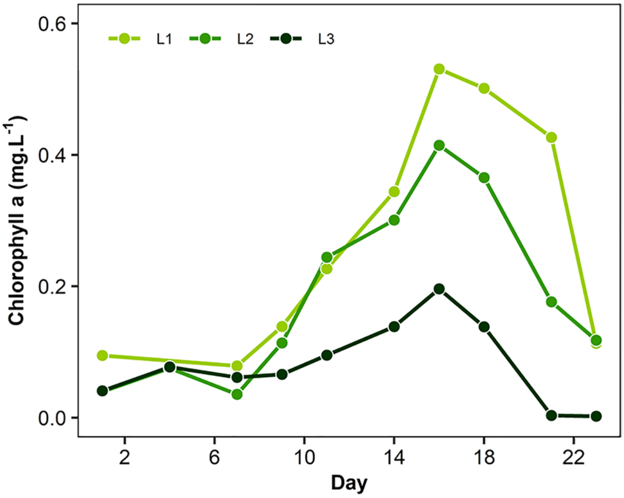

Fig. 3 Temporal Chl*a* concentrations (in mg L.$^{-1}$) during the experiment in the three IMTA-microalgae replicates: L1, L2 and L3

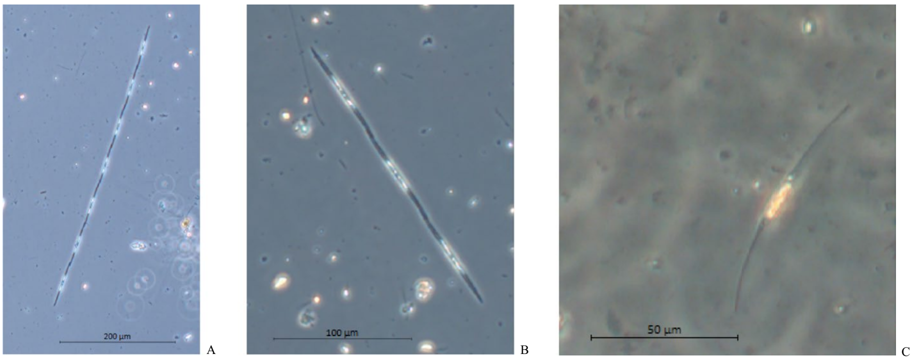

Fig. 4 *Pseudo-nitzschia* (**A** and **B**) and *Cylindrotheca closterium* (**C**) identified in the three IMTA-microalgae replicates (photos © Elise Caillard)

avenue would be to integrate detritivorous organisms (e.g. mullet fish, holothurians, nematodes) with algae cultures, as the former would be able to feed on deposits.

Juvenile oysters more than doubled in weight and length

During the 1-month period, both weight and length gain in the oysters were significant ($p < 0.001$), more than doubling, with a final weight of 3.7 ± 0.9 g ind^{-1} ($n = 754$). No mortality was observed (0.2%). Despite strong variability in algal production within the IMTA-microalgae raceways, the produced biomass allowed significant oyster growth over the experimental period: a very encouraging result. The oyster growth rate of 1.04% was in the same order of magnitude as that of juveniles reared in a nearby natural lagoon (0.97% in Li et al., 2019).

As mentioned by Troell et al. (2009), the integration of bivalves in an IMTA is not straightforward. With the addition of silicates, the phytoplankton that grows with the input of fish nutrients is suitable food for filter-feeders and can have a positive (Lefebvre et al. 2000, 2004) or insignificant (Li et al. 2019) effect on bivalve growth. Those growth results are mainly explained by determining environmental factors, such as ambient concentrations of nutrient availability, particulate organic matter or seston content (Troell and Norberg 1998), but also indirectly by fish-feeding variability (i.e. its duration and quantity).

In our case study, the IMTA microalgal inoculum was mostly composed of Chlorellales—these are not the common microalgae used for juvenile oyster feed, which is usually composed of diatoms or *Prymnesiophyceae* (McCausland et al. 1999; Ponis et al. 2003). Indeed, juvenile oysters are usually not able to retain small particles, e.g. < 4 µm for *C. gigas* when sestonic load is low, < 12 µm when sestonic load is higher (Barillé et al. 1993) and even 20 µm for *Ostrea chilensis* (Dunphy et al. 2006). Chlorellales such as *Schizochlamydella* sp and *Picochlorum* sp are rather small (2–10 microns and 1.5–3 microns, respectively) and consequently not assimilable by juvenile oysters (Korshikov 1953; Tsarenko 2011; Henley et al. 2004). The addition of silicates permitted a shift in the initial algal community towards diatoms of the *Bacillariophyceae* family, whether these were present (but not detectable) in the 1:5 inoculum at the beginning of the period, or in the 4:5 water from the RAS effluent. This shift in the microalgal composition allowed the growth of the juvenile oysters, indicating that the feed composition was both assimilable and resulted in growth gain. *C. closterium*, which grew in the microalgal raceways, are long cells ($>$ to 25 µm; Reimann and Lewin 1964) with a particular shape that could favour its retention on oyster gills and be suitable microalgae for juvenile oyster growth. Its high nutritional value for secondary consumers has previously been described: it has high lipid content and is particularly rich in essential PUFA such as EPA and ARA (Keerthi et al. 2012). Other constituents may also have played a role in the oyster food chain, as ciliates and flagellates from 4 to 72 µm are known to be retained by the oyster (Dupuy et al. 1999). Future experiments on the entire microbial food web are necessary to delve further into the microorganism communities assimilable by oysters in an IMTA oyster-growing context. To reach optimal conditions for bivalve production, these experiments can give rise to improvements in the system—for example, daily uniform fish feeding and therefore, nutrient excretion—to smooth out variations in the microalgae cultures and decrease the risk of crop crashing.

IMTA supplementary biomass production

At a daily feeding rate of 1% of the fish biomass, 5.89 kg of feed day^{-1} was distributed, giving a growth ratio of 2.39 kg of fish day^{-1}. The nutrients excreted by fish and taken in by microalgae fed an oyster biomass of 0.022 kg day^{-1}.

In the experimental conditions tested, the results showed that an IMTA with reduced human intervention allowed a gain in recoverable biomass: i.e. 3.7 g of oyster produced per kg of fish feed distributed. For a production unit of 100 tonnes of fish fed at 1% of the biomass twice a day, an additional production of 2.7 tonnes of oyster could be provided per year. This yield could be even higher if 100% RAS water was used to supplement the microalgal compartment (5% of RAS water was used in this study), as in this case, 20 microalgal raceways could be run. Moreover, only 2% of the microalgae biomass was used to feed the 3 oyster compartments: if 100% was used to feed the oysters, 37 times more oyster biomass would be produced. Further work is needed to investigate the economic viability of such a system in more detail, in order to establish whether there is an overall economic benefit to implementing such a system.

Conclusion

This study demonstrated the feasibility of using an inoculum of a microalgal polyculture (favouring diatoms of interest) from a local intensive basin together with an appropriate oyster–food ratio to feed oyster juveniles in an IMTA community. The experiment resulted in equivalent Chl*a* production in a shorter time frame than a previous published study (15 days less to reach the same production). This IMTA design could still be improved, in particular regarding technical and environmental factors, in order to better control algal culture variability.

By transforming waste into reusable material and additional biomass, IMTA can reduce environmental impact, giving a more positive, ecological image to aquaculture. It could potentially be promoted with a specific 'circular aquaculture' certification. However, despite its promise, in Europe, the development of IMTA still faces various issues. Some of the obstacles could be overcome by pursuing research on biological, economic and social aspects of IMTA and of end consumer perceptions of its products. Innovative zero-waste designs should be studied, with specific attention paid to analysing their effects on the biology and welfare of candidate species and the quality of the end products. Increasing the economic and ecological sustainability of aquaculture should help build the case for its social acceptance.

Acknowledgements The authors would also like to thank colleagues from MARBEC and the French National Research Institute for Agriculture, Food and the Environment (INRAE) for their contribution in the fish biometry: Bastien Sadoul, Eric Gasset, Frédéric Clota, Benjamin Geffroy and the two students Maxime Petit Jean and Baptiste Bal. We also thank Claire Carre for her expertise on phytoplankton, Audrey Mandonnet for her help in the laboratory, Elise Caillard for her photos and Cyrille Przybyla, manager of the VASCO2 project that provided us with the algal inoculum. Finally, many thanks to the editor and referees for their constructive comments on the initial version of this manuscript, and to Elise Bradbury for the English proofreading.

Author contribution ERO and EF designed the study and wrote the manuscript. ML and FR managed the day-to-day experiment. ML, ERO and EF collected the samples. ML, ERO, FR, ST, TL, AC and PLG performed the biometrics. ML, AG, ELF and CH performed the microalgae analyses. TG performed the nutrient analyses. ML performed the statistics. All authors read and approved the final manuscript.

Full names as follows: Emmanuelle ROQUE D'ORBCASTEL (ERO), Eric FOUILLAND (EF), Mathieu LUTIER (ML), François RUELLE (FR), Sébastien TRIPLET (ST), Thierry LAUGIER (TL), Patrik LE GALL (PLG), Clarisse HUBERT (CH), Anaïs CROTTIER (AC), Emilie LE FLOC'H (ELF), Thibault GEOFFROY (TG), Angélique GOBET (AG). All authors approved the manuscript submission.

Funding This study was conducted in the framework of the Cooperation in Fisheries, Aquaculture and Seafood Processing (COFASP) European Research Area Network (ERA-Net) project (IMTA-Effect project) with funding from the French National Research Agency (ANR-15-COFA-0001–06) (for installations, experiments, analyses) and the Marine Biodiversity and Conservation (MARBEC) research group (which funded M. Lutier's Master's degree).

Data availability The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

Declarations

Ethics approval All sampling and animal handling respected good scientific practice and animal welfare rules. The number of fish sampled was limited to that strictly necessary: the reared fish were shared with another ERA-Net project (Animal Health and Welfare – Welfare, Health and Individuality in Farmed Fish, ANIHWA WINFISH, 2015–2018).

Competing interests The authors declare no competing interests.

References

Altieri MA, Letourneau DK, Davis JR (1983) Developing sustainable agroecosystems. BioSci 33(1):45–49

Alexander KA, Freeman S, Potts T (2016) Navigating uncertain waters: European public perceptions of integrated multi trophic aquaculture (IMTA). Env Sci Policy 61:230–237. https://doi.org/10.1016/j.envsci.2016.04.020

Anjos C, Baptista T, Joaquim S, Mendes S, Matias AM, Moura P, Simões T, Matias D (2017) Broodstock conditioning of the Portuguese oyster (*Crassostrea angulata*, Lamarck, 1819): influence of different diets. Aquac Res 48:3859–3878. https://doi.org/10.1111/are.13213

APHA (1995) Standard methods for the examination of water and wastewater, 19th Edition, American Public Health Association Inc., New York

Aubin J, Callier M, Rey-Valette H, Mathé S, Wilfart A, Legendre M, Slembrouck J, Caruso D, Chia E, Masson G, Blancheton JP et al (2017) Implementing ecological intensification in fish farming: definition and principles from contrasting experiences. Rev Aquac 0. https://doi.org/10.1111/raq.12231

Barillé L, Prou J, Heral M, Bougrier S (1993) No influence of food quality, but ration-dependent retention efficiencies in the Japanese oyster *Crassostrea gigas*. J Exp Mar Biol Ecol 171:91–106

Barrington K, Chopin T, Robinson S (2009) Integrated multi-trophic aquaculture (IMTA) in marine temperate waters. In: Soto D (ed.) Integrated mariculture: a global review. FAO Fisheries and Aquaculture Technical Paper. No. 529, 7–46. FAO, Rome

Barrington K, Ridler N, Chopin T, Robinson S, Robinson B (2010) Social aspects of the sustainability of integrated multi-trophic aquaculture. Aquac Int 18–2:201–211. https://doi.org/10.1007/S10499-008-9236-0

Ben Kheder R, Quéré C, Moal J, Robert R (2010) Effect of nutrition on Crassostrea gigas larval development and the evolution of physiological indices. Part A: Quantitative and qualitative diet effects. Aquaculture 305(1–4):165–173. https://doi.org/10.1016/j.aquaculture.2010.04.022

Blancheton JP, Bosc P, Hussenot J, Roque D'Orbcastel E, Romain D (2009) The 'new' European fish culture systems: Recirculating systems, offshore cages, integrated systems. Cah Agric 18(2):227–234. https://doi.org/10.1684/agr.2009.0294

Borges MT, Silva P, Moreira L, Soares R (2005) Integration of consumer-targeted microalgal production with marine fish effluent biofiltration–a strategy for mariculture sustainability. J Appl Phycol 17(3):187–197. https://doi.org/10.1007/s10811-005-4842-y

Brown MR, Jeffrey SW, Volkman JK, Dunstan GA (1997) Nutritional properties of microalgae for mariculture. Aquaculture 151(1–4):315–331. https://doi.org/10.1016/S0044-8486(96)01501-3

Buck B, Troell MF, Krause G, Angel DL, Grote B, Chopin T (2018) State of the art and challenges for offshore integrated multi-trophic aquaculture (IMTA). Review article. Front Mar Sci 5. https://doi.org/10.3389/fmars.2018.00165

Chary K, Fiandrino A, Coves D, Aubin J, Falguiere JC, Callier M (2019) Modeling sea cage outputs for data-scarce areas: application to red drum (*Sciaenops ocellatus*) aquaculture in Mayotte. Indian Ocean Aquac Int 27(3):625–646. https://doi.org/10.1007/s10499-019-00351-z

Chopin T (2013) Aquaculture, Integrated Multi-trophic (IMTA). In: Christou P, Savin R, Costa-Pierce BA, Misztal I, Whitelaw CBA (eds) Sustainable food production. Springer. https://doi.org/10.1007/978-1-4614-5797-8_173

Chopin T, Buschmann AH, Halling C, Troell M, Kautsky N, Neori A, Kraemer GP, Zertuche-González JA, Yarrish C, Neefus C (2001) Integrating seaweeds into marine aquaculture systems: a key toward sustainability. J Phycol 37:975–986. https://doi.org/10.1046/j.1529-8817.2001.01137.x

Costa-Pierce BA (2015) Seven principles of ecological aquaculture: a guide for the blue revolution. Ecological Aquaculture Foundation, Biddeford, Maine, USA. ©2015 Ecological Aquaculture Foundation

Delaporte M, Soudant P, Lambert C, Moal J, Pouvreau S, Samain JF (2006) Impact of food availability on energy storage and defense related hemocyte parameters of the Pacific oyster *Crassostrea gigas* during an experimental reproductive cycle. Aquaculture 254(1–4):571–582. https://doi.org/10.1016/j.aquaculture.2005.10.006

Demetropoulos CL, Langdon CJ (2004) Enhanced production of Pacific dulse (Palmaria mollis) for co-culture with abalone in a land-based system: nitrogen, phosphorus, and trace metal nutrition. Aquaculture 235:433–455. https://doi.org/10.1016/j.aquaculture.2003.09.012

Dunphy BJ, Hall JA, Jeffs AG, Wells RMG (2006) Selective particle feeding by the Chilean oyster Ostrea chilensis implications for nursery culture and broodstock conditioning. Aquaculture 261(2):594–602. https://doi.org/10.1016/j.aquaculture.2006.08.015

Dupuy C, Le Gall S, Hartmann HJ, Bréret M (1999) Retention of ciliates and flagellates by the oyster *Crassostrea gigas* in French Atlantic coastal ponds: protists as a trophic link between bacterioplankton and benthic suspension-feeders. Mar Ecol Prog Ser 177:165–175. https://doi.org/10.1016/j.aquaculture.2017.01.015

FAO (2003). Assessment and management of seafood safety and quality. FAO Fisheries and Aquaculture Technical Paper. No. 444. Rome, FAO. 2003. 230p

FAO (2009). Integrated mariculture: a global review. FAO Fisheries and Aquaculture Technical Paper. No. 529. Rome, FAO. 2009. 183p

FAO (2016). The state of world fisheries and aquaculture 2016. In: Contributing to food security and nutrition for all. Rome, p 200

Fabioux C, Huvet A, Le Souchu P, Le Pennec M, Pouvreau S (2005) Temperature and photoperiod drive *Crassostrea gigas* reproductive internal clock. Aquaculture 250(1–2):458–470. https://doi.org/10.1016/j.aquaculture.2005.02.038

Fang J, Zhang J, Xiao T, Huang D, Liu S (2019) Integrated multi-trophic aquaculture (IMTA) in Sanggou Bay, China. AEI 8:201–205. https://doi.org/10.3354/AEI00179

Galès A, Triplet S, Geoffroy G, Roques C, Carré C, Le Floc'h E, Lanfranchii M, Simier M, Roque D'Orbcastel E, Przybyla C, Fouilland E (2020) Control of the pH for marine microalgae polycultures: a key point for CO_2 fixation improvement in intensive cultures. J CO_2 Util 38:187–193. https://doi.org/10.1016/j.jcou.2020.01.019

Goldman JC, Tenore RK, Ryther HJ, Corwin N (1974) Inorganic nitrogen removal in a combined tertiary treatment-marine aquaculture system. I Removal Effic Water Res 8:45–54

Gordin H, Motzkin F, Huges-Games WL, Porter C (1981) Seawater maricultura pond. An integrated system. European Maric Soc Special Publication 6:1–13

Gowen RJ, Bradbury NB (1987) The ecological impact of salmon farming in coastal waters: a review Oceanogr. Mar Biol 25:563-D575

Granada L, Sousa N, Lopes S, Lemos MFL (2016) Is integrated multitrophic aquaculture the solution to the sectors' major challenges? – a review. Rev Aquac 8:283–300. https://doi.org/10.1111/raq.12093

Henley WJ, Hironaka JL, Guillou L, Buchheim MA, Buchheim JA, Fawley MW, Fawley KP (2004) Phylogenetic analysis of the 'Nannochloris-like' algae and diagnoses of Picochlorum oklahomensis gen. et sp. nov. (Trebouxiophyceae, Chlorophyta). Phycologia 43(6):641–652. https://doi.org/10.2216/i0031-8884-43-6-641.1

Hughes-Games WL (1977) Growing the Japanese oyster (*Crassostrea gigas*) in sub-tropical seawater fishponds. I. Growth rate, survival and quality index. Aquaculture 11:217–229

Hussenot JME (2003) Emerging effluent management strategies in marine fish-culture farms located in European coastal wetlands. Aquaculture 226(1–4):113–128. https://doi.org/10.1016/S0044-8486(03)00472-1

IPBES (2019) Summary for policymakers of the global assessment report on biodiversity and ecosystem services of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services. In: Díaz S, Settele J, Brondízio ES, Ngo HT, Guèze M, Agard J, Arneth A, Balvanera P, Brauman KA, Butchart SHM, Chan KMA, Garibaldi LA, Ichii K, Liu J, Subramanian SM, Midgley GF, Miloslavich P, Molnár Z, Obura D, Pfaff A, Polasky S, Purvis A, Razzaque J, Reyers B, Roy Chowdhury R, Shin YJ, Visseren-Hamakers IJ, Willis KJ, Zayas CN (eds). IPBES secretariat, Bonn, Germany, p 56

Jegatheesan V, Shu L, Visvanathan C (2011) Aquaculture effluent: impacts and remedies for protecting the environment and human health. In: Nriagu J (ed) Encyclopedia of Environmental Health. Elsevier Science, pp 123–135

Karvonen A, Rintamäki P, Jokela J, Valtonen ET (2010) Increasing water temperature and disease risks in aquatic systems: climate change increases the risk of some, but not all, diseases. Int J Parasitol 40(13):1483–1488. https://doi.org/10.1016/j.ijpara.2010.04.015

Keerthi P, Judy J, Yogi K, Katherine A, Geoffrey D, Carmen S (2012) Impact of impurities in biodiesel-derived crude glycerol on the fermentation by *Clostridium pasteurianum* ATCC 6013. Appl Microbiol Biotechnol 93:1325–1335

Knowler D, Chopin T, Martínez-Espiñeira R, Neori A, Nobre A, Noce A, Reid G (2020) The economics of Integrated Multi-Trophic Aquaculture: where are we now and where do we need to go? Rev Aquacult 12:1579–1594. https://doi.org/10.1111/raq.12399

Korshikov AA (1953). Viznachnik prisnovodnihk vodorostey Ukrainsykoi RSR [Vyp] V. Pidklas Protokokovi (Protococcineae). Bakuol'ni (Vacuolales) ta Protokokovi (Protococcales) [The Freshwater Algae of the Ukrainian SSR. V. Sub-Class Protococcineae. Vacuolales and Protococcales]. 1–439. Kyjv [Kiev]: Akad. NAUK URSR

Lefebvre S, Hussenot J, Brossard N (1996) Water treatment of land-based fish farm effluents by outdoor culture of marine diatoms. J Appl Phycol 8(3):193–200. https://doi.org/10.1007/BF02184971

Lefebvre S, Barille L, Clerc M (2000) Pacific oyster (*Crassostrea gigas*) feeding responses to a fish-farm effluent. Aquaculture 187:185–198. https://doi.org/10.1016/S0044-8486(99)00390-7

Lefebvre S, Probert I, Lefrançois C, Hussenot J (2004) Outdoor phytoplankton continuous culture in a marine fish–phytoplankton–bivalve integrated system: combined effects of dilution rate and ambient conditions on growth rate, biomass and nutrient cycling. Aquaculture 240(1–4):211–231. https://doi.org/10.1016/j.aquaculture.2004.06.022

Li M, Callier M, Blancheton JP, Galès A, Nahon S, Triplet S, Geoffroy T, Menniti C, Fouilland E, Roque D'Orbcastel E (2019) Bioremediation of fishpond effluent and production of microalgae for an oyster farm in an innovative recirculating integrated multi-trophic aquaculture system. Aquaculture 504:314–325. https://doi.org/10.1016/j.aquaculture.2019.02.013

Lopez Figueroa F, Korbee N, Abdala Díaz R, Jerez C, Torre M, Güenaga L, Larrubia M, Gomez Pinchetti JL (2012) Biofiltration of fishpond effluents and accumulation of N-compounds (phycobiliproteins and mycosporine-like amino acids) versus C-compounds (polysaccharides) in *Hydropuntia cornea* (*Rhodophyta*). Mar Poll Bull 64:310–318. https://doi.org/10.1016/j.marpolbul.2011.11.012

Lulijwa R, Rupia JE, Alfaro AC (2019). Antibiotic use in aquaculture, policies and regulation, health and environmental risks: a review of the top 15 major producers. Rev Aquac. https://doi.org/10.1111/raq.12344

McCausland MA, Brown MR, Barrett SM, Diemar JA, Heasman MP (1999) Evaluation of live microalgae and microalgal pastes as supplementary food for juvenile Pacific oysters (C*rassostrea gigas*). Aquaculture 174(3–4):323–342. https://doi.org/10.1016/S0044-8486(99)00018-6

Malézieux E (2012) Designing Cropping Systems from Nature. ASD 32:15–29

Martins CIM, Eding EH, Verdegem MCJ, Heinsbroek LTN, Schneider O, Blancheton JP, Roque D'Orbcastel E, Verreth JAJ (2010) New developments in recirculating aquaculture systems in Europe: a perspective on environmental sustainability. Aqua Eng 43(3):83–93. https://doi.org/10.1016/j.aquaeng.2010.09.002

Manzi JJ, Castagna M (1989) Clam culture in North America. Elsevier, Amsterdam, p 461

Milhazes-Cunha H, Otero A (2017) Valorisation of aquaculture effluents with microalgae: the Integrated Multi-Trophic Aquaculture concept. Algal Res 24(B):416–424. https://doi.org/10.1016/J.ALGAL.2016.12.011

Miranda CD (2011). Antimicrobial resistance associated with salmonid farming. Antimicrob Res Environ: 423-451. https://doi.org/10.1002/9781118156247.ch22

Neaud-Masson N (2020). Observation et dénombrement du phytoplancton marin par microscopie optique. Spécifications techniques et méthodologiques appliquées au REPHY. Version 2 – février 2020. ODE/VIGIES/20/03. https://archimer.ifremer.fr/doc/00609/72133/

Neori A, Ragg NLC, Shpigel M (1998) The integrated culture of seaweed, abalone, fish and clams in modular intensive landbased systems: II. Performance and nitrogen partitioning within an abalone (*Haliotis tuberculata*) and macroalgae culture system. Aquac Eng 17:215–239. https://doi.org/10.1016/S0144-8609(98)00017-X

Neori A, Chopin T, Troell M, Buschmann AH, Kraemer GP, Halling C, Shpigel M, Yarish C (2004) Integrated aquaculture: rationale evolution and state of the art emphasizing seaweed biofiltration in modern mariculture. Aquaculture 231(1):361–391. https://doi.org/10.1016/j.aquaculture.2003.11.015

Neori A, Shpigel M, Guttman L, Israel A (2017). Development of polyculture and integrated multi -trophic aquaculture (IMTA) in Israel: a review. The Israeli J Aquac - Bamidgeh, IJA_69.2017.1385 19

Newby DT, Mathews TJ, Pate RC, Huesemann MH, Lane TW, Wahlen BD, Mandal S, Engler RK, Feris KP, Shuri J (2016) Assessing the potential of polyculture to accelerate algal biofuel production. Algal Res 19:264–277. https://doi.org/10.1016/j.algal.2016.09.004

Okocha RC, Olatoye IO, Adedeji OB (2018) Food safety impacts of antimicrobial use and their residues in aquaculture. Public Health Rev 39:21. https://doi.org/10.1186/s40985-018-0099-2

Piedrahita RH (2003) Reducing the potential environmental impact of thank aquaculture effluents through intensification and recirculation. Aquaculture 226:35–44. https://doi.org/10.1016/S0044-8486(03)00465-4

Pillay TVR (2004). Aquaculture and the Environment 2nd edition. Pillay Eds. https://doi.org/10.1002/9780470995730

Ponis E, Robert R, Parisi G (2003) Nutritional value of fresh and concentrated algal diets for larval and juvenile Pacific oysters (*Crassostrea gigas*). Aquaculture 221(1–4):491–505. https://doi.org/10.1016/S0044-8486(03)00075-9

Reimann BEF, Lewin JC (1964) The diatom genus Cylindrotheca Rabenhorst. J Royal Microcopical Soc Ser 3 83(3):283–296

Ritchie RJ (2006) Consistent sets of spectrophotometric chlorophyll equations for acetone, methanol and ethanol solvents. Photosynth Res 89(1):27–41

Ryther JH, Goldman JC, Gifford CE, Huguenin E, Wing AS, Clarner JP, Williams LD, Lapointe BE (1975) Physical models of integrated waste recycling—marine polyculture systems. Aquaculture 5:163–177

Shpigel M, Neori A (1996) The Integrated culture of seaweed, abalone, fish and clams in modular intensive land-based systems: I. Proportions of size and projected revenues. Aquac Eng 15(5):313–326. https://doi.org/10.1016/0144-8609(96)01000-X

Smith DJ, Gingerich WH, Beconi-Barker MG (1999) Use of chemicals in fish management and fish culture past and future. In: Xenobiotics in Fish. Kluwer academic / Plenum publ, 1999. Print.

Snapp (2017). Agroecology: principles and practice, Agricultural Systems 2nd Ed, 33–72

Tenore KR (1976) Food chain dynamics of abalone in a polyculture system. Aquaculture 8:23–27

Tolon T, Emirolu D, Günay D, Hancı B (2017) Effect of stocking density on growth performance of juvenile sea cucumber *Holothuria tubulosa* (Gmelin, 1788). Aquac Res 48:4124–4131. https://doi.org/10.1111/are.13232

Troell M, Joyce A, Chopin T, Neori A, Buschmann AH, Fangh GJ (2009) Ecological engineering in aquaculture — potential for integrated multi-trophic aquaculture (IMTA) in marine offshore systems. Aquaculture 297(1–4):1–9. https://doi.org/10.1016/j.aquaculture.2009.09.010

Troell M, Norberg J (1998) Modelling output and retention of suspended solids in an integrated salmon–mussel culture. Ecol Modell 110:65–77

Troell M, Naylor RL, Metian M et al (2014). Does aquaculture add resilience to the global food system? PNAS 23. https://doi.org/10.1073/pnas.1404067111

Tsarenko PM (2011). Trebouxiophyceae. In: Algae of Ukraine: diversity, nomenclature, taxonomy, ecology and geography. Volume 3: *Chlorophyta*. (Tsarenko, P.M., Wasser, S.P. & Nevo, E. Eds): 61–108. Ruggell: A.R.A. Gantner Verlag K.-G

Utting SD, Millican PF (1997) Techniques for the hatchery conditioning of bivalve broodstocks and the subsequent effect on egg quality and larval viability. Aquaculture 155:45–54

Wezel A, Herren BG, Kerr RB, Barrios E, Gonçalves ALR, Sinclair F (2020) Agroecological principles and elements and their implications for transitioning to sustainable food systems A review. Agronomy for Sustain Dev 40(6):40. https://doi.org/10.1007/s13593-020-00646-z

Wongkiew S, Hu Z, Kartik C, Lee JW, Khanal SK (2017) Nitrogen transformations in aquaponic systems: a review. Aquac Eng 76:9–19

Yu LQJ, Mu Y, Zhao AZ, Lam VWY, Sumaila R (2017) Economic challenges to the generalization of integrated multi-trophic aquaculture: an empirical comparative study on kelp monoculture and kelp-mollusk polyculture in Weihai, China. Aquaculture 471:130–139. https://doi.org/10.1016/j.aquaculture.2017.01.015

Publisher's note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

Authors and Affiliations

Emmanuelle Roque D'Orbcastel[1] · Mathieu Lutier[2] · Emilie Le Floc'h[1] · François Ruelle[3] · Sébastien Triplet[3] · Patrik Le Gall[4] · Clarisse Hubert[5] · Martine Fortune[1] · Thierry Laugier[1] · Thibault Geoffroy[3] · Anaïs Crottier[1] · Angélique Gobet[1] · Eric Fouilland[1]

[1] MARBEC, Univ Montpellier, CNRS, Ifremer, IRD, Sète, France

[2] Ifremer, CNRS, IRD, LEMAR, University of Brest, Plouzané, France

[3] MARBEC, Univ Montpellier, CNRS, Ifremer, IRD, Palavas-les-flots, France

[4] Ifremer, LER Bretagne Nord, CRESCO, Dinard, France

[5] Ifremer, Laboratoire METabolites Des microALGues, Nantes, France