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1 **Integrated multi-trophic aquaculture of red drum (*Sciaenops ocellatus*) and sea cucumber (*Holothuria***
2 ***scabra*): assessing bioremediation and life-cycle impacts**

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11

12 **Abstract**

13 Environmental sustainability of aquaculture is a complex issue involving effects at local (e.g. benthic
14 deterioration), regional (e.g. eutrophication) and global (e.g. catches for feed production) scales as a consequence of
15 farming operations (e.g. waste emissions) and industrial processes involved in the product value chain. Integrating
16 these effects using a holistic and multi-scale framework is essential to assess the environmental sustainability of
17 innovative production systems such as Integrated Multi-Trophic Aquaculture (IMTA), in which organisms of different

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Abbreviations:

AC: Acidification

CC: Climate change

CED: Cumulative energy demand

DEB: Dynamic energy budget

EU: Eutrophication

FCR: Feed conversion ratio

FU: Functional unit

IFF: Ingested fish feces

IMTA: Integrated multi-trophic aquaculture

LCA: Life cycle assessment

LCI: Life cycle inventory

LCIA: Life cycle impact assessment

LU: Land use

N and P: Nitrogen and Phosphorus

NPPU: Net primary production use

ThOD: Theoretical oxygen demand

UFF: Undigested finfish feces

18 trophic levels are co-cultured on the same farm to minimize aquaculture waste. The environmental performances of
19 theoretical production scenarios of red drum (*Sciaenops ocellatus*) sea cage monoculture and an open-water IMTA co-
20 culturing of red drum and sea cucumber (*Holothuria scabra*) were assessed with mathematical models at local and
21 global scales. First, the particulate waste bioremediation potential of sea cucumber production was estimated using an
22 individual-based bioenergetic model. Second, environmental impacts of the monoculture and the IMTA systems were
23 estimated and compared using life cycle assessment (LCA), calculated per kg of edible protein and t of product,
24 including uncertainty analysis. Given the current limits to stocking density observed for sea cucumbers, its co-culture
25 in sea cages suspended beneath finfish nets may decrease slightly (by 0.73%) farm net particulate waste load and
26 benthic impact. The monoculture and IMTA showed little difference in impact because of the large difference in
27 production scales of finfish and sea cucumber species. Removing 100% of finfish feces particulate waste requires
28 cultivating sea cucumber at scale similar to that of finfish (1.3 kg of sea cucumber per kg of finfish). Nonetheless,
29 LCA showed trends in IMTA performance: lower eutrophication impact and net primary production use but higher
30 cumulative energy demand and climate change impacts, generating an impact transfer between categories.
31 Intensification of sea cucumber culture could increase local and global environmental benefits, but further research is
32 necessary to design rearing units that can optimize production and/or bioremediation and that can be practically
33 integrated into existing finfish monoculture units. The methodology defined here can be a powerful tool to predict the
34 magnitude of environmental benefits that can be expected from new and complex production systems and to show
35 potential impact transfer between spatial scales. We recommend applying it to other IMTA systems and species
36 associations and including socio-economic criteria to fully assess the sustainability of future seafood production
37 systems.

38
39 **Keywords:** Integrated Multi-Trophic Aquaculture (IMTA); Life cycle assessment (LCA); Bioremediation; Culture
40 scenario; Sea cucumber
41
42

1 Introduction

Environmental sustainability of aquaculture is a complex and multi-scale issue involving both direct and indirect interactions with the environment (Edwards, 2015). Among the main concerns regarding sustainability of the sector, one can cite its dependence on wild-caught resources and agricultural products for the production of formulated feed, use of natural resources, discharge of chemical contaminants (e.g. medicines, heavy metals), conversion of sensitive areas (e.g. mangroves and wetlands), parasite and disease transfer between farmed and wild species, benthos deterioration and water body eutrophication (Hargrave, 2005; Holmer et al., 2008). From these examples, we can distinguish environmental impacts that are directly related to farm operations (e.g. benthic impact, water eutrophication) and that generally affect the environment at local (farm vicinity) or regional scales (bay, watershed) from those that can be indirectly caused by the successive industrial processes involved in the product value chain (e.g. catches for feed production). Exploring these interactions within a holistic framework is essential to properly address aquaculture sustainability issues and to develop new solutions for minimizing impacts on the environment.

Integrated multi-trophic aquaculture (IMTA) is perceived to be a suitable approach to decrease negative effects of aquaculture waste (Neori et al., 2004; Troell et al., 2003). The main principle of IMTA is to co-culture organisms from different trophic levels, including fed species (e.g. finfish or shrimp) and extractive species that can feed on the solid organic (e.g. bivalves, sea cucumbers, sea urchins) and dissolved inorganic (e.g. macroalgae) waste generated by the fed species. The biomitigation service thus depends on the choice of the extractive organisms, the trophic niche targeted and the associated extractive feeding behavior (e.g. filter feeding, deposit feeding, autotrophic) and its ecological functions.

IMTA can provide both environmental and socio-economic benefits by converting excess nutrients into commercial products. In an open-water IMTA, Reid et al. (2013) estimated that 2.3-4.4 kg of dissolved nitrogen (N) could be removed per kg of kelps (*Alaria esculenta* and *Saccharina latissima*) co-cultured in the proximity of Atlantic salmon (*Salmo salar*) cages. While other aquaculture waste management methods have involved mainly high technology and large operating costs (e.g. water filtering, sediment pumping) (Buschmann et al., 2008), IMTA is a practical bioremediation approach that offers the possibility to generate additional farm revenue (Troell et al., 2009), given that the added species has a market value. A recent study compared the financial performance of an Atlantic salmon monoculture and an IMTA system adding blue mussel (*Mytilus edulis*) and sugar kelp (*Saccharina latissima*) and showed that the IMTA operation was more profitable, with a net present value (NPV) 5.7-38.6% higher (Carras et al., 2019). Additionally, IMTA may also decrease farm economic risk through product diversification, increase the social acceptability of aquaculture due to its better environmental image and may provide differentiation pathways

73 through labeling programs (Alexander et al., 2016; Barrington et al., 2009; Chopin et al., 2012). For example,
74 Barrington et al. (2010) have demonstrated in a survey work, that participants perceived seafood produced in IMTA
75 systems as safe products to eat and showed that 50% of them were willing to pay 10% more for these products if
76 labelled as such.

77 Sea cucumbers (class Holothuroidea) are an interesting candidate as deposit feeder species for IMTA systems due
78 to their ability to consume particulate waste excreted by other cultured organisms (Slater and Carton, 2009;
79 Yokoyama, 2013). This is particularly relevant for fed finfish open-water aquaculture systems, for which reducing the
80 benthic impact is a major ecological challenge (Strain and Hargrave, 2005). The most concentrated sources of
81 nutrients generated by finfish production systems are released as large organic particles (Filgueira et al., 2017),
82 including finfish feces and uneaten finfish feed. Accumulation of this waste on the seabed depends on multiple factors
83 such as farm arrangement (cage layout), production scale (Borja et al., 2009; Giles, 2008), physical characteristics of
84 particles (settling velocity) (Magill et al., 2006; Reid et al., 2009) and hydrodynamics (currents and bathymetry)
85 (Borja et al., 2009; Bravo and Grant, 2018; Keeley et al., 2013). High rates of deposition of organic matter on the
86 sediment can cause organic enrichment, change sediment geochemistry and change benthic community structure near
87 finfish cages (Borja et al., 2009; Karakassis, 2000; Pearson and Rosenberg, 1977). The co-culture of deposit-feeding
88 organisms such as sea cucumber, which can process enriched benthic sediments, thus assimilating bacterial, fungal
89 and detrital organic matter, seems a suitable approach to decrease nutrient enrichment in the sediment and respect the
90 carrying capacity of the ecosystem.

91 Experimental studies have demonstrated sea cucumbers' ability to consume and assimilate aquaculture waste and
92 to reduce its organic and nutrient content, confirming its potential for bioremediation in IMTA (MacDonald et al.,
93 2013; Nelson et al., 2012; Robinson et al., 2019). Previous pilot-scale open water experiments showed overall good
94 growth and survival of sea cucumbers cultured in suspended cages or benthic bottom culture beneath finfish cages
95 under adequate management (Hannah et al., 2013; Yokoyama, 2013; Yokoyama et al., 2013; Yu et al., 2014, 2012),
96 although serious mortality episodes were observed in benthic cultures due to anoxia in the sediment (Yu et al., 2012).

97 Previous studies using mathematical models to examine uptake of solid organic matter or nutrients by sea
98 cucumber species in IMTA systems with finfish resulted in contrasting conclusions (Cubillo et al., 2016; J. S. Ren et
99 al., 2012; Watanabe et al., 2015; Zhang and Kitazawa, 2016). According to MacDonald et al. (2013), three to four
100 *Holothuria forskali* (ca. 400–500 g m⁻²) would process all solid waste produced by a commercial seabass
101 (*Dicentrarchus labrax*) sea-cage production unit. However, the authors assumed a mean solid deposition rate of 8.67 g
102 m⁻² yr⁻¹ citing Magill et al. (2006), while the latter authors actually reported a mean flux under the cage layout of

103 5000-12 000 g m⁻² yr⁻¹. Model simulations by Cubillo et al. (2016) and Ren et al. (2012) predicted that bottom culture
104 of sea cucumbers could remove more than 70% of the benthic particulate organic carbon (C) from Atlantic salmon
105 (*Salmo salar*) farm units. These two studies were mainly exploratory, aiming to maximize production and optimize
106 species combinations to reduce environmental impacts, ignoring technological and rearing constraints for the
107 extractive species. Including such considerations in models can help predict more realistic production design and
108 bioremediation potentials from extractive species and thus better scale and design future IMTA systems. In contrast,
109 Watanabe et al. (2015), who calculated that 4.3% of total particulate nitrogen from milkfish (*Chanos chanos*) culture
110 could be removed by detritivore species, concluded that sea cucumber may not be an effective bioremediator, since an
111 impractical stocking density (ca. 200 times current practices) would be necessary to completely remove particulate N.
112 Overall, two main points limit the ability to compare results of studies. First, the main differences are expected to be
113 due to three factors: i) the sea cucumber species cultured, ii) the production ratio between the main species (i.e.
114 finfish) and the added species (i.e. sea cucumber) and iii) the duration of production cycles. These factors drive system
115 performances and should be clearly stated to improve understanding of system feasibility at pilot and commercial
116 scales. Second, bioremediation potentials are often expressed in relative terms, which are by definition ratios and
117 therefore not directly comparable, and for different fluxes (e.g. C, N, total solids) in the seabed or coming directly
118 from the cages, depending on research objectives. Providing intermediate results and standardizing them using generic
119 performance metrics will facilitate robust comparison of studies and help assess IMTA system performances (Reid et
120 al., 2018).

121 Several indirect environmental impacts caused by producing the additional inputs associated with the added
122 detritivore species and its integration into the finfish monoculture unit are ignored when focusing only on waste
123 bioremediation issues. For instance, environmental impacts of juvenile production, energy use and cage construction
124 should be included in the analysis since they may offset local benefits. To be a sustainable option, IMTA systems
125 should perform environmentally as well as or better than monoculture, considering both direct and indirect impacts.
126 Combined assessment of local impacts and broader global impacts with a life cycle perspective is therefore crucial to
127 properly understand advantages of IMTA over monoculture in terms of environmental sustainability.

128 Life cycle assessment (LCA) is a standardized method (i.e. International Organization for Standardization (ISO)
129 14040) developed to assess environmental impacts of a product by compiling resource use and emissions to the
130 environment at all stages of its life cycle. Each resource used and substance emitted is attributed to one or more impact
131 categories and converted by characterization models into potential environmental impacts (Guinée et al., 2002). The

LCA framework is divided into four steps: goal, scope and system definition; life cycle inventory (LCI) of resource use and emissions; environmental impact assessment and interpretation.

LCA has been extensively applied to aquaculture systems, with 65 studies and 179 aquaculture systems reviewed in a recent meta-analysis (Bohnes et al., 2018). Most studies focused on fed species of high economic value such as salmonids or shrimp (Cao et al., 2013), but a few focused on extractive species, such as two studies of sea cucumber culture (Marín et al., 2019; Wang et al., 2015). LCA has been used mostly to identify problematic stages or components of systems and to compare alternatives such as intensive vs. extensive systems, monoculture vs. polyculture and open water vs. closed recirculating systems. To date, only a few LCA studies have examined the potential of IMTA systems to mitigate aquaculture impacts (Mendoza Beltran et al., 2018; Mendoza Beltrán and Guinée, 2014). In this context, the present study examined environmental benefits and trade-offs for finfish monoculture of shifting to an open-water IMTA system co-culturing suspended sea cucumber culture beneath finfish cages, by assessing the latter's mitigation potential at local and global scales.

2 Materials and methods

2.1 Goal and scope

The main goal of this study was to compare environmental performances of red drum (*Sciaenops ocellatus*) sea cage monoculture to an open-water IMTA co-culturing red drum and sea cucumber (*Holothuria scabra*). Specifically, the objectives were (1) to estimate the net particulate removal of the sea cucumber system and its bioremediation efficiency and (2) to perform an environmental LCA of the monoculture and the IMTA system. This study was an ex-ante analysis of aquaculture farming scenarios in the remote French island of Mayotte, Indian Ocean. The monoculture system was a 299 t farming scenario based on existing red drum farms surveyed on Mayotte and in French Caribbean regions (Guadeloupe and Martinique). Detailed description of the red drum monoculture can be found in Chary et al. (2019). This study focused on describing the extractive sea cucumber system and its integration into the red drum monoculture. *H. scabra* was chosen for co-culture with red drum since it is the most commonly cultured tropical sea cucumber species (Robinson and Lovatelli, 2015) and one of the edible sea cucumbers with a high commercial value (Purcell et al., 2012). It is considered for aquaculture diversification on Mayotte (Cabinet Gressard consultants et al., 2013) and already cultured in the Indian Ocean (Madagascar).

The LCA was performed from the cradle to the farm gate and included multiple stages of finfish monoculture: fingerling production and transport to the farm, feed production and transport to the farm, chemical production, energy production, equipment and infrastructure production, and farm operation (Fig. 1a). Production stages were the same in

161 the monoculture and IMTA systems except for juvenile sea cucumber production, which was added to the IMTA
162 system (Fig. 1b). In the IMTA configuration considered in the present study, sea cucumber production was closely
163 integrated into the monoculture production system (Mendoza Beltrán and Guinée, 2014), i.e. benefitted from the
164 existing infrastructure (e.g. rope lines), equipment (e.g. boats) and operating processes, and required only a few
165 supplementary processes. We assumed that addition of sea cucumbers did not change the productivity of the finfish
166 farm. The IMTA system boundaries included the unchanged monoculture system (same inputs and outputs), juvenile
167 sea cucumber production and transport to the farm and on-farm processes. Farm products from both the monoculture
168 and IMTA were fresh ungutted aquatic products (Fig. 1b).

169 Life cycle impact assessment (LCIA) was expressed simultaneously per kg of edible protein in aquatic products
170 (both finfish and sea cucumbers) (functional unit 1, FU₁) and per t of fresh aquatic product (FU₂). This choice
171 considered the IMTA system as a whole (i.e. no differentiation in the origin of protein or biomass). It assumed that sea
172 cucumber production was an explicit objective of the farm, motivated by finfish waste biomitigation as well as
173 production and revenue diversification. This approach did not require allocation of impacts between co-products as
174 recommended in the ISO guidelines (ISO, 2006a, 2006b) and allowed comparison of farm-level environmental
175 performances of the monoculture and IMTA systems. The primary functional unit was kg of edible protein because
176 protein production is the main function of animal aquaculture production systems. The second functional unit (1 t of
177 product), which is commonly used, allowed for rapid comparison with other studies (Samuel-Fitwi et al., 2012). To
178 maintain homogeneity between products (finfish sold raw and sea cucumber sold processed), and given the unchanged
179 ranking between monoculture and IMTA in sensitivity analyses when adding supplementary life cycle stages, post-
180 harvest processes (i.e. commercialization, transport, use, disposal) were not included in the study.

181
182 < Insert Figure 1 around here >
183

184 **2.2 Inventories**

185 The LCIs of both systems were developed and their environmental impacts were estimated using SimaPro 8.5
186 software and its databases (PRé Consultants, Amersfoort, Netherlands). The ecoinvent 3.0 database was used for all
187 background data except feed ingredients, which were taken from the French EcoAlim v.1.3 database. See the
188 Supplementary Material for detailed LCIs.

189 2.2.1 *Description of the monoculture system and its animal production parameters*

190 The finfish monoculture system described a scenario of a semi-industrial red-drum farm with floating sea cages
191 located on Mayotte Island, Indian Ocean (see Chary et al., 2019). In routine operations, the farm produces 299 t of
192 fresh finfish per year at a low stocking density (max. 20 kg/m³). Culture cycles are 20 months long with progressive
193 harvests from month 13. Harvested products range from portion-size to 3000 g per individual. No chemotherapeutants
194 (e.g. antibiotics) are used during finfish production. Fingerlings (individual weight of 6 g) are produced and
195 transported by truck in plastic bags from a hatchery on Mayotte. Five cohorts of 34 500 fingerlings (950 kg yr⁻¹) are
196 introduced per year. Farm cages are composed of rectangular polyethylene netting arranged in 6 units of 2500 m³ and
197 4 units of 500 m³, yielding a total cage area of 1372 m². Farm productivity per cage area is therefore ca. 218 kg finfish
198 m⁻² yr⁻¹. Land-based facilities consist of one main building for finfish processing and several shipping containers used
199 to stock feed and materials. Feed consists of commercial pressed pellets produced on La Reunion Island and imported
200 to the farm by sea shipping. The feed-conversion ratio (FCR), i.e. the quantity of feed (kg DW) needed per kg of
201 animal weight gain (kg WW), was estimated as 1.91 in the farm scenario, according to the values reported for this
202 species on tropical sea-cage farms (Falguière, 2011).

203 2.2.2 *Assumptions and data sources for the monoculture*

204 LCI data for the finfish system were obtained from data provided by a previous study (Chary et al., 2019) and
205 surveys conducted on Mayotte and La Reunion Islands with managers of existing finfish farms, a hatchery and a feed
206 mill company. LCI data for the finfish hatchery were collected in 2016 through surveys at Eclasia, a hatchery
207 producing red drum fingerlings on La Reunion, since the hatchery on Mayotte closed for economic reasons. The
208 technologies used at Eclasia and their associated yields were representative of those at the hatchery on Mayotte;
209 therefore, we assumed that fingerlings were produced on Mayotte.

210 Data on farm infrastructure and equipment, energy and input consumption were obtained from finfish farm
211 managers in 2016. We had access to the finfish farm' historical datasets, from which detailed data were obtained,
212 allowing the variation in consumption (e.g. fuel, electricity) relative to farm production to be estimated.

213 Annual production data (i.e. feed inputs and finfish harvest volumes) were taken from farm simulations under
214 routine conditions with the FINS farm-scale model (Chary et al., 2019). FINS is a simple model combining farm
215 production and waste emission modules to simulate farm production, feed requirements and waste discharge for
216 finfish sea-cage systems. FINS includes several submodels (e.g. individual growth model, mass balance model),
217 which were parametrized for red drum. The edible protein content in fresh red drum biomass was set to 10.2% based

on a filet yield of 45% and a protein content in filet of 22.6% (Falguière, 2011). Feed intake was calculated for 5 pellet types with relatively similar proximal composition (~50% protein, ~14% lipids, 16% carbohydrate, 10% fiber, 1.5% phosphorus (P)) but differing in diameter (2.2, 3.2, 4.5, 6.0 and 9.0 mm) and ingredient mix. Data on the ingredient mix were provided by a commercial feed-mill manager in La Reunion (data not shown due to confidentiality).

2.2.3 *Sea cucumber system assumptions and data sources*

LCI data for sea cucumbers were taken from model simulations, literature reviews and expert knowledge. LCI data for the sea cucumber hatchery were collected from literature on the *H. scabra* hatchery in southwestern Madagascar (Eeckhaut et al., 2008; Lavitra et al., 2010) and from expert reports of a project for a commercial-scale hatchery on Mayotte (Cabinet Gressard consultants et al., 2013), supplemented with hatchery experience in New Caledonia (Agudo, 2006). Design of the sea cucumber rearing structure is still relatively unknown for suspended co-culture with finfish, particularly for systems at large commercial scales (Zamora et al., 2018). Therefore, data on the rearing structure were based on the current technology used at the pilot scale in previous finfish-sea cucumber IMTA studies (Hannah et al., 2013; Yokoyama, 2013). The sea cucumber rearing system consists of cylindrical cage nets (diameter 2 m, height 40 cm) suspended ~3 m directly below the bottom of the finfish net pens and attached to the existing finfish cage mooring system with ropes (see Fig. 1b in Yokoyama 2013). Sea cucumber cages were composed of metal frames and covered with nylon mesh net. Similarly to the design used by Hannah et al. (2013) and Yokoyama (2013) we did not consider sand substrate in the cages. However, sand can be a necessary material for feeding (Robinson et al., 2013; Watanabe et al., 2012), burrowing, and wellbeing of sea cucumbers (Battaglione and Bell, 2004; Mercier et al., 1999). Due to its direct proximity to the particulate source, we assume that the sea cucumber system retains 100% of finfish feces loads and that they are homogeneously available to the sea cucumbers. The areas of sea cucumber culture and the finfish farm (i.e. total bottom cage area) are identical, i.e. 1372 m², corresponding to 437 cage units adjacent to each other. During the grow-out period, sea cucumbers are assumed to feed exclusively on finfish feces coming from the finfish cages, so no extra feed was considered. Management of sea cucumber culture consists of one cohort of individuals released in cages at a weight of 10 g (Battaglione et al., 1999; Lavitra et al., 2010; Purcell and Simutoga, 2008) and harvested at one time, after a 12 month culture cycle. Juvenile sea cucumbers were assumed to be produced on Mayotte and transported to the farm by truck. A single 12 month culture cycle was chosen instead of several shorter cycles in order to maximize profits, because the retail price of *H. scabra* increases exponentially with its size (Purcell, 2014; Purcell et al., 2018). Annual production and waste emissions data were estimated for sea cucumbers by integrating an individual bioenergetic model into a population dynamics framework (see section 2.2.4).

247 Sea cucumbers must be processed to obtain a dry cooked commercial product called “bêche-de-mer”. The
248 processing yields from fresh animal to bêche-de-mer are assumed to be 7.5% (Lavitra et al., 2008). The protein
249 content in the final product is 51.2% (Average from Ozer et al., 2004) giving an edible protein content in fresh sea
250 cucumbers of 3.8%. Processing stages into bêche-de-mer were not included in the LCA system boundaries.

252 2.2.4 Individual bioenergetic model and population model for the sea cucumber

253 The ecophysiology of sea cucumbers was simulated from seeding to harvest at a daily time step with the Dynamic
254 Energy Budget (DEB) model (Kooijman, 2000). The model’s differential equations were solved with a Runge-Kutta
255 integration method using the deSolve (Soetaert et al., 2010) package in R (R Core Team, 2018). DEB models quantify
256 the rates of energy ingestion, assimilation and use as a function of the organism, temperature and food availability
257 (van der Meer, 2006). DEB parameters for *H. scabra* (version 2017/09/15) were obtained from the “Add my Pet”
258 database (Marques et al., 2018) except for assimilation efficiency, which was calculated specifically for animals fed
259 on finfish feces. The food availability index (f) ranges from 0-1, representing respectively an absence of food and
260 saturated feeding (i.e. *ad libitum*) conditions. We set $f = 1$ and verified that food supply at the cohort level remained
261 non-limiting during sea cucumber grow-out. Maintaining food availability at its maximum causes the model to predict
262 maximum theoretical growth for the farmed animals at a given temperature. This is not likely in practice, due to the
263 many environmental pressures affecting animals’ life cycles (biology), but it allows the maximum mitigation capacity
264 to be predicted, which accords with the goal of this study. Energy from ingested finfish feces (IFF) was converted into
265 mass using gross energy density coefficients of red drum feces (Table A.1).

266 Uptake of solid particulate matter from sea cucumber ingestion and the associated solid and dissolved emissions
267 were estimated using DEB. Sea cucumber fecal emissions (i.e. undigested finfish feces (UFF)) were estimated by
268 DEB using an assimilation efficiency parameter (κ_x), which is the ratio of assimilated energy to ingested energy. In
269 this study, we estimated κ_x for *H. scabra* feeding on finfish feces as 43.65% (Table A.2), since the value of 80% in the
270 “Add my Pet” database was a default value used for a generalized animal and obtained from estimates for a wide
271 variety of species (Kooijman, 2010). See the Appendix A for the method used to estimate κ_x . Dissolved emissions are
272 derived from two distinct mechanisms in DEB. The N:P stoichiometry in the animal is assumed to remain constant
273 over time. Assimilated nutrients that are not retained in biomass gain are therefore excreted to maintain this constant
274 stoichiometry. Thus, N or P are excreted depending on the balance between the stoichiometry of the assimilated feed
275 and that of the animal. The energy used for maintenance, growth and gonad formation can be translated into $N-NH_4^+$

and P-PO₄³⁻ fluxes using conversion factors. See the Appendix A for full details of the equations and parameters used in DEB to estimate dissolved emissions.

On-farm sea cucumber biomass dynamics were calculated by multiplying the number of individuals by the individual weight predicted by DEB. The population dynamics model of sea cucumber represents (i) initial seeding (initial condition), (ii) culture-harvesting strategies, (iii) natural mortality and (iv) culture losses (e.g. poaching, predation). Natural mortality and culture losses were respectively set linearly at 0.055% d⁻¹ (20% per year) and 0.014% d⁻¹ (5% per year) (Robinson and Pascal, 2011; Watanabe et al., 2015), and the harvesting rate equaled 0, except on day 365, when all biomass was harvested. An initial seeding density of 36 g m⁻² (5000 individuals, i.e. 3.6 ind m⁻²) was calculated to achieve a maximum critical stocking density of 2000 g m⁻² during the culture cycle. Since maximum stocking density is reached at the end of the culture cycle, it also corresponds to the system's productivity.

2.2.5 *Grow-out emissions from monoculture and IMTA*

There is direct interaction between finfish and sea cucumber systems in the IMTA system, since sea cucumbers are assumed to feed on finfish feces for growth and thus to retain solid nutrients that would be otherwise released into the marine environment. In this study, on-farm metabolic emissions due to finfish and sea cucumber growth focused on N and P because of their accountability in LCA impact categories such as eutrophication (EU) and their potential to cause environmental damage in aquatic environments. In this case, P emissions are of particular importance because they usually limit primary productivity in tropical oligotrophic environments such as the Mayotte lagoon (Howarth, 1988; Jessen et al., 2015). We also estimated theoretical oxygen demand (ThOD), i.e. the amount of oxygen required to oxidize solid organic waste, since it is also accountable in the EU impact category (Papatryphon et al., 2004). ThOD was calculated based on the chemical oxygen demand of each macronutrient (i.e. protein, carbohydrates, lipids, fiber and ash) in uneaten feed, finfish feces and sea cucumber feces (Kim et al., 2000).

In the finfish monoculture, solid organic particulate waste (i.e. uneaten feed and feces) and dissolved inorganic emissions to the sea were estimated previously for a routine year of production (Chary et al., 2019). The annual solid waste load from the red drum farm was 120 454 kg of feces (including 2867 kg N and 2240 kg P) and 29 474 kg of uneaten feed (including 2428 kg N and 383 kg P). Annual dissolved emissions equaled 33 198 kg N-NH₄ and 2266 kg P-PO₄. ThOD coefficients for uneaten feed and finfish feces were respectively 1.249 and 0.854 kg O₂ per kg.

In the sea cucumber LCI, net N emissions, net P solid and dissolved emissions and net ThOD were calculated as solid and dissolved emissions from sea cucumber growth minus avoided emissions associated with IFF. ThOD coefficients for sea cucumber feces were estimated as 0.764 kg O₂ per kg.

2.2.6 Inputs imported to Mayotte

On Mayotte, most economic inputs used on the farm are imported from La Reunion or France. Therefore, most processes were adapted to include sea transport (1700 km from La Reunion and 9800 km from France) by transoceanic ship from the closest trading ports, and land transport (30 km) by truck from the port to the farm facilities. Fuels were assumed to be imported from Singapore (7000 km).

2.3 Environmental performance assessment

2.3.1 Bioremediation performances

Bioremediation performances of sea cucumber culture were estimated using five indices (Table 1). The solid processing rate ($\text{kg solid m}^{-2} \text{ yr}^{-1}$) represents the ability of sea cucumbers to ingest and process fish feces in time and space. The net solid uptake rate ($\text{kg solid m}^{-2} \text{ yr}^{-1}$) represents the mass balance of net solids of sea cucumbers and equals IFF minus UFF. These two indices assume that finfish and sea cucumber feces have the same impact. Waste extraction efficiency (in %) is the net reduction in solid waste (feces only) of the IMTA system compared to the annual solid waste load of finfish monoculture. The biomass culture ratio (kg:kg) (Reid et al., 2018) is the biomass of co-cultured species required to reach a waste extraction efficiency of 100% (i.e. to retain the annual solid waste load of the finfish unit in sea cucumber biomass). It is important to note that a waste extraction efficiency of 100% does not mean that the IMTA system has zero waste, since the sea cucumber culture also generates solid waste. The culture area ratio ($\text{m}^2:\text{m}^2$) is the sea cucumber culture area necessary to extract 100% of feces released per unit of finfish culture area.

Table 1. Indices used to quantify bioremediation performances of sea cucumbers co-cultured with finfish in an open water integrated multi-trophic aquaculture system. IFF and UFF are respectively cumulative ingested finfish feces and undigested finfish feces by the sea cucumber cohort over the 12-month culture-cycle simulation. WW and DW refer respectively to wet and dry weight.

Index	Equation	Variable description and units
Solid processing rate (SP)	$\frac{IFF}{\text{Sea cucumber culture area}}$	SM: $\text{kg solid m}^{-2} \text{ yr}^{-1}$ IFF: kg DW yr^{-1}
Net solid uptake rate (NSU)	$\frac{IFF - UFF}{\text{Sea cucumber culture area}}$	NSU: $\text{kg solid m}^{-2} \text{ yr}^{-1}$ UFF: kg DW yr^{-1}
Waste extraction efficiency (WEE)	$\frac{IFF - UFF}{\text{Annual fish feces load}} \times 100$	WEE: % Annual finfish feces load: kg DW yr^{-1}
Biomass culture ratio (BC)	$\frac{\text{Annual fish feces load} \times \text{Sea cucumber production}}{(IFF - UFF) \times \text{Fish production}}$	BC: kg:kg Finfish production: kg WW yr^{-1} Sea cucumber production: kg WW yr^{-1}

Culture area ratio (CS)	$BC \times \frac{\text{Fish cage productivity}}{\text{Sea cucumber cage productivity}}$	CS: m ² :m ² Finfish cage productivity: kg m ⁻² yr ⁻¹ Sea cucumber cage productivity: kg m ⁻² yr ⁻¹
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2.3.2 Life cycle impact assessment and uncertainties

Six impact categories were selected for the LCIA: climate change potential (CC), acidification potential (AC), eutrophication potential (EU), cumulative energy demand (CED), land use (LU) and net primary production use (NPPU). These categories were chosen for their relevance to the known principal impacts of aquaculture systems and to enable comparison with previous seafood LCA studies (Bohnes and Laurent, 2019; Pelletier et al., 2007). CC (kg CO₂ eq.) quantifies impact of the production of GHG emissions. AC (g SO₂ eq.) represents damage to ecosystems caused by changes in the acidity of water and soil environments that receive pollutants. EU (g PO₄ eq.) represents impacts on aquatic and terrestrial ecosystems due to over-enrichment in nutrients, resulting in an increase in primary and secondary production, the potential for algal blooms and oxygen depletion in the environment. CED (MJ) includes all energy resources used (e.g. fuel, heating, electricity, gas) in the system and was calculated using the Cumulative Energy Demand method v.1.09 (Frischknecht et al., 2004). LU (m²y) represents the temporary terrestrial ground area used. NPPU (kg C) represents the trophic level estimated from the amount of C from primary production (obtained by photosynthesis) used by the cultured species. Higher NPPU means a higher trophic level. NPPU was quantified according to Papatryphon et al., (2004). For crop-based feed ingredients, NPPU was calculated according to the C content in the harvested part of the crop using its proximate composition and stoichiometric conversion factors for carbohydrate, protein and lipid fractions (Papatryphon et al., 2004). Proximate compositions of crop-based ingredients were taken from Sauvant et al. (2004). For fishery-derived feed ingredients, we used the values calculated by Papatryphon et al. (2004) for Peruvian fisheries products. CC, AP, EP, and LU were calculated according to the CML-2 Baseline 2000 V2.0 method.

It is important to include uncertainty analysis in comparative LCAs, since deterministic results that do not include significance information can lead to oversimplified conclusions (Mendoza Beltran et al., 2018), especially in ex-ante analysis. Uncertainties due to unrepresentativeness (i.e. degree of reliability, completeness, temporal correlation, geographical correlation, technological correlation and sample size) of foreground processes were estimated with the Numerical Unit Spread Assessment Pedigree following the method of Henriksson et al. (2014) and included in the LCI of the monoculture and the IMTA. We simulated 1000 Monte Carlo runs to propagate these uncertainties to the LCIA results per impact category, as commonly done in LCA uncertainty analysis (Avadí and Fréon, 2013). A paired

t-test was used to determine statistical significance of the systems' difference in environmental impacts. The null hypothesis in the t-test was that IMTA and monoculture systems have equal environmental impacts per functional unit.

3 Results

3.1 Sea cucumber: model predictions at individual and system levels

The *H. scabra* DEB model with the fixed f-value of 1 predicted that 10 g juveniles (length = 8 cm) cultured at a water temperature of 25.2-29.6°C (mean = 27.8°C) with ad libitum feeding would grow into 709 g wet weight (WW) (i.e. 103 g DW, 33 cm long) market-size individuals over 365 days. Cumulative ingestion was estimated as 879 g, of which 671 g were not assimilated and egested as feces. FCR was high (8.64). Individual dissolved inorganic excretions were 10.0 g of N-NH₄ and 25.9 g of P-PO₄. These individual results were extrapolated at cohort level to estimate sea cucumber biomass production and emissions in the IMTA system.

Figure 2 shows biomass and waste fluxes in the sea cucumber system and Table 2 summarizes biomass and emission outputs in the monoculture and IMTA. The number of sea cucumber decreased from 5000 to 3894 individuals, providing a potential harvest of ca. 2.8 t (i.e. 106 kg of edible protein) per 12-month cycle for a culture area of 1372 m². The addition of sea cucumber to create the IMTA increased total aquatic production by 0.92% and edible protein production by 0.34% (Table 2). Net on-farm nutrient emissions of sea cucumbers were -30.5 kg N (-72.8 kg solid and 42.3 kg dissolved), -2.8 kg P (-38.8 kg solid and 36.0 kg dissolved).

Figure 2 also presents sea cucumber bioremediation performances when co-cultured with finfish in the IMTA system. IFF by sea cucumbers (3743 kg solid yr⁻¹), represented 3.1% of the annual finfish feces load in monoculture (120 454 kg solid yr⁻¹) and a SP of 2728 kg solid m⁻² yr⁻¹. When including sea cucumber fecal egestion (UFF = 2858 kg solid yr⁻¹), NSU was 0.645 kg solid m⁻² yr⁻¹, and the WEE of the sea cucumber in IMTA was 0.73%. In the IMTA system, the farm solid waste load was reduced by 885 kg solid yr⁻¹ (IFF-UFF), i.e. 320.6 kg solid per t of sea cucumber produced. As a consequence, a 376 t production of sea cucumber is necessary to extract 120 454 kg solid yr⁻¹, i.e. 1.26 times (BC = 1.3:1) the finfish production (298.6 t yr⁻¹). Considering the productivity of sea cucumber (2 kg m⁻² cages yr⁻¹, see section 2.2.4), this sea cucumber production requires a culture surface of ca. 187 860 m² to reach 100% extraction, i.e. 137 times the culture area of the finfish (CS = 137:1).

< Insert Figure 2 around here >

	Unit	Monoculture	IMTA
Production			
Finfish production	t yr ⁻¹	298.578	298.578
Sea cucumber production	t yr ⁻¹	0	2.761
Total production	t yr ⁻¹	298.578	301.339
Total edible protein	t yr ⁻¹	30.455	30.560
On-farm emissions			
Finfish feces	kg yr ⁻¹	120 454	116 711
Sea cucumber feces	kg yr ⁻¹	0	2 858
Uneaten feed	kg yr ⁻¹	29 474	29 474
Net N, solid	kg yr ⁻¹	5 295	5 222
Net N, dissolved	kg yr ⁻¹	33 198	33 240
Net P, solid	kg yr ⁻¹	2 623	2 584
Net P, dissolved	kg yr ⁻¹	2 666	2 702
Theoretical oxygen demand	kg yr ⁻¹	139 721	138 708

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385 **3.2 LCIA results**

386 The monoculture and IMTA systems ranged 863-871 m²y, 9533-9599 kg C, 64 693-64967 MJ, 122.7-124.2 kg PO₄
387 eq., 17.65 kg SO₂ eq., 2 332 kg CO₂ eq. per t of fresh aquatic product respectively for LU, NPPU, CED, EU, AC, CC
388 (Fig. 3). The contribution of the production components to the monoculture and IMTA environmental impacts per kg
389 of edible protein (FU₁) is summarized in Table 3. The same trends were observed in contributions per t of fresh
390 aquatic product (FU₂) (data not shown). The contribution analysis showed few differences in the distribution of
391 impacts between both systems. Feed production was the main contributor, with 73-99% of the impact for all categories
392 except EU. Animal by-products (fish meal and fish oil) contributed most to CC and NPPU, while crop-based products
393 contributed most to AC, CED and LU. Farm operation contributed most (92%) to EU of the monoculture and IMTA
394 systems due to on-farm N and P emissions. In the IMTA system, net emissions from sea cucumbers reduced EU by
395 0.12% due to the emissions avoided by ingesting finfish feces. The ThOD from solid emissions contributed to ca. 9%
396 of EU in both systems. Energy production was the second largest contributor (ca. 12-17%) to CC and AC due mainly
397 to emissions of greenhouse gases (GHGs) and other gases (NO_x, SO₂, NH₃) from petroleum-based electricity
398 production on Mayotte. Fingerling production and juvenile sea cucumber production contributed little (< 4% and <
399 0.5% of total impacts, respectively), regardless of impact category. The contribution of fingerling production to CC,
400 AC and CED were related mainly to energy use in the hatcheries, while its contribution to NPPU and LU were due to
401 the feed used to maintain breeders.

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Table 3. Life cycle impact assessment results per 1 kg of edible protein in a red drum monoculture scenario (Mono) and in an Integrated Multi-Trophic Aquaculture (IMTA) scenario co-culturing red drum and the sea cucumber *H. scabra*. Contribution to the total impact per production component is given in percentage, while mean total impact, calculated from 1000 Monte Carlo runs, is given in absolute value.

Impact	Scenario	Finfish-feed production	Fingerling production	Juvenile sea cucumber production	Equipment and infrastructure	Energy	Chemicals	Farm operation	Mean total per kg of edible protein
Climate change (kg CO ₂ eq.)	Mono	76.2	3.2	-	7.4	12.2	0.0	1.1	22.8
	IMTA	75.4	3.1	0.3	8.3	12.1	0.0	1.1	23.0
Acidification (g SO ₂ eq.)	Mono	74.2	3.2	-	5.2	16.6	0.0	0.9	173.2
	IMTA	73.5	3.2	0.3	5.9	16.5	0.0	0.9	173.9
Eutrophication (g PO ₄ eq.)	Mono	7.0	0.2	-	0.2	0.2	0.0	92.4	1218.5
	IMTA	7.0	0.2	0.0	0.2	0.2	0.0	92.4	1211.2
Cumulative energy demand (MJ)	Mono	97.2	1.5	-	0.9	0.3	0.0	0.1	280.1
	IMTA	97.1	1.5	0.0	1.0	0.3	0.0	0.1	278.8
Net primary production use (kg C)	Mono	98.7	1.3	-	0.0	0.0	0.0	0.0	93.9
	IMTA	98.7	1.3	0.0	0.0	0.0	0.0	0.0	93.7
Land use (m ² y)	Mono	94.4	2.9	-	2.3	0.2	0.0	0.1	8.5
	IMTA	94.3	2.9	0.3	2.5	0.2	0.0	0.1	8.5

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Overall, the uncertainties in the LCIA results were largely higher (3-9% of the mean value, depending on impact category, Fig. 3) than the differences in impact observed between monoculture and IMTA. The IMTA system performed better than the monoculture system for EU, NPPU and LU for both functional units. Differences in impact of aquatic products per kg of edible protein were largest for CC and EU, with a 0.8% increase and 0.6% decrease in IMTA compared to the monoculture system, respectively, while per t of fresh aquatic product, EU decreased by 1.2% in IMTA (Table 4). Despite the high uncertainties, LCA results differed significantly ($p < 0.05$) between the two scenarios, except for LU per kg of edible protein and AC per t of fresh aquatic product.

< Insert Figure 3 around here >

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Table 4. Life Cycle Impact Assessment results of a red drum monoculture (Mono) scenario and an Integrated Multi-Trophic Aquaculture (IMTA) scenario co-culturing red drum and the sea cucumber *H. scabra*, with uncertainty assessed from 1000 Monte Carlo runs. The null hypothesis in the t-test is that both systems have equal environmental impacts per functional unit.

Impact category	Impact per kg of edible protein			Impact per t of harvested product		
	Ranking	Percentage difference	Paired t-test	Ranking	Percentage difference	Paired t test
Climate change	IMTA > Mono	0.8	$p < 0.05$	IMTA > Mono	0.4	$p < 0.05$
Acidification	IMTA > Mono	0.4	$p < 0.05$	IMTA > Mono	0.0	$p > 0.05$
Eutrophication	Mono > IMTA	0.6	$p < 0.05$	Mono > IMTA	1.2	$p < 0.05$
Cumulative energy demand	IMTA > Mono	0.5	$p < 0.05$	IMTA > Mono	0.4	$p < 0.05$
Net primary production use	Mono > IMTA	0.3	$p < 0.05$	Mono > IMTA	0.7	$p < 0.05$
Land use	Mono > IMTA	0.5	$p > 0.05$	Mono > IMTA	0.9	$p < 0.05$

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4 Discussion

We discuss the mitigation potential of the IMTA system in terms of i) the bioremediation efficiency of sea cucumber system co-cultured with finfish and ii) comparison of the impacts of the finfish monoculture and IMTA systems estimated by LCA. Perspectives are then discussed for decreasing the IMTA's benthic impact and overall life-cycle impacts.

4.1 Sea cucumber bioremediation potential

The first important steps to estimate the mitigation potential of organic extractive culture in an IMTA are to quantify its ingestion capacities and estimate the balance between solid uptake and particulate emissions of the extractive species. The individual annual feed energy requirement for *H. scabra* at its maximum growth potential (value = 1 in DEB) was equivalent to the energy contained in 0.879 kg of finfish feces, which is its theoretical ingestion capacity. This ingestion rate is much lower than the range of 9-82 kg sediment yr⁻¹ observed for sea cucumbers feeding in the wild (Purcell et al., 2016) because of the much higher energy content in fish feces. However, our estimates lie within the range of values obtained for sea cucumbers fed with finfish waste, i.e. about 1 kg solids yr⁻¹ for *Holothuria forskalli* and 5 kg solids yr⁻¹ for *Parastichopus californicus* (Cubillo et al., 2016; MacDonald et al., 2013). At the farm scale, the solid processing rate of sea cucumbers appears negligible compared to that of other organic extractive species. For instance, we back-estimated fish feces ingestion rates from mussel lines based on pseudo-feces egestion rates (maximum at 6735 g m⁻² d⁻¹), digestibility of fish feces and seston (respectively 86% and 46%) and their respective percentage in the material ingested by the mussels (maximum 30% of fish feces, and thus 70% of seston) provided by Cranford et al. (2013). The value estimated (793 kg fish feces m⁻² yr⁻¹) is ca. 290 times as high as that calculated for sea cucumbers (Fig. 2). When compared to the net solid uptake, however, conclusions are less straightforward. Mussels also capture suspended ambient seston (non-settling particles) and transform it into pseudo-feces (settling particles), which can lead to no gain in net organic loading (Filgueira et al., 2017). To this extent, sea cucumber showed a low but positive net solid uptake, demonstrating its interest for bioremediation.

The waste extraction efficiency of sea cucumbers was low, and expecting high removal of fish feces may be impractical at a commercial scale. In the conditions simulated, sea cucumber culture can remove 0.73% of the annual finfish farm feces load. Significant change in the production system would be necessary to reach 100% extraction, starting with more balanced production between sea cucumbers and finfish (1.3:1). In such a system, the frontier between primary and secondary species is less clear and would require large changes in the farmer's practices and skill sets, but also in the overall farm design. Given the culture area ratio (137:1) needed to reduce fish feces emissions

451 to zero, the licensed surface area would have to be increased greatly because of limits to stocking density of sea
452 cucumber culture. Stocking density has been mentioned as a limitation of IMTA systems that add sea cucumber
453 (Purcell et al., 2012; Watanabe et al., 2015), mussels (Cranford et al., 2013) and seaweed to existing finfish
454 monoculture for bioremediation. For seaweed, previous studies suggested that 0.07-0.28 ha τ^{-1} of finfish standing stock
455 were necessary to remove all excess dissolved N associated with a commercial finfish farm (see Table 2 in Reid et al.,
456 2013) because of its need to access large amounts of solar radiation at the ocean surface. For the finfish monoculture
457 assessed here (mean = 218 t of finfish biomass stock in routine production), it would represent a culture area ratio of
458 111:1 to 444:1. Thus, sea cucumber may require less area than seaweed to recover nutrients, but since they do not
459 occupy the same trophic niche, comparisons are debatable. Aiming to achieve 100% bioremediation seems unrealistic
460 in open-water IMTA systems regardless of the trophic niche considered and it is not necessarily a relevant goal for the
461 farm; nonetheless, estimating the biomass and culture area of extractive organisms required for this purpose is a way
462 to better design and scale future IMTA systems.

463
464 Compared to previous modeling studies combining finfish and sea cucumber species in an IMTA system, we
465 included the limit to stocking density of sea cucumber when assessing the IMTA's bioremediation potential. Maximum
466 stocking density was limited to 2000 g m^{-2} , according to many experiments that showed a large effect of stocking
467 density on sea cucumber growth (Battaglione et al., 1999; Hannah et al., 2013; T Lavitra et al., 2010; Li and Li, 2010;
468 Pitt and Duy, 2004) and better growth performances at low densities (Slater and Carton, 2007; Yokoyama, 2013; Yu
469 et al., 2014). Setting the maximum stocking density as a function of an organism's characteristics and its rearing
470 constraints offers realistic insight into the bioremediation potential of sea cucumber in co-culture. Studies have
471 demonstrated that beyond a critical density, sea cucumber growth decreased or stopped because of increased
472 competition for resources, such as food and space. Critical density ranged from 200-400 g m^{-2} for *H. scabra* culture in
473 sea cages or pens under natural conditions, i.e. without any added food source (Juinio-Meñez et al., 2014; Namukose
474 et al., 2016; Purcell and Simutoga, 2008). In contrast, *H. scabra* juveniles fed on particulate waste from a commercial
475 land-based abalone aquaculture system grew well at a density of 1000 g m^{-2} with starch-amended effluent (Robinson
476 et al., 2019), confirming that food availability and quality are critical factors regulating sea cucumber growth (Ren et
477 al., 2010; Y. Ren et al., 2012). The higher stocking densities that did not inhibit sea cucumber growth were reported
478 for *Parastichopus californicus* cultivated in suspended cages under sable fish (*Anoplopoma fimbria*), with optimal
479 densities of 1400-2300 g m^{-2} (Hannah et al., 2013). Some authors argued that, in IMTA, optimal densities for sea
480 cucumber growth may not correspond to those that maximize bioremediation (Hannah et al., 2013; Namukose et al.,

2016; Zamora et al., 2018), and that the latter could be higher if particulate bioremediation is the primary aim of the co-culture. This may be true to some extent; nonetheless, given the current state of knowledge, it is difficult to believe that sea cucumber culture can exceed greatly the density limit of a few kg per m². Finding the densities that optimize sea cucumber production or remediation potential is an important area of research for the future. Such practical limits to culture must be acknowledged to consider the degree to which sea cucumber and other species can extract solid waste from commercial finfish aquaculture.

The waste mitigation potential of sea cucumbers may not be sufficient to significantly reduce environmental effects of solid waste deposition on the seabed, and additional analyses are necessary to fully assess local ecological effects of IMTA systems. Compared to the deposition rates usually observed under finfish farms, the net solid uptake of sea cucumber (0.645 kg m⁻² yr⁻¹) is too low to change the ecological status of the sediment in the seabed. On red drum farms (including the monoculture assessed here; see Chary et al. (in preparation)), like on other finfish farms (N. Keeley et al., 2013; Riera et al., 2017), peak deposition rates can range from 15-50 kg solid m⁻² yr⁻¹ at sites of concentration. At these sites, adding sea cucumber under fish nets may not reduce waste fluxes significantly, and the impact, as a detectable change in sediment status, may occur from 0.5 kg solid m⁻² yr⁻¹ (Chamberlain and Stucchi, 2007; Cromey et al., 2012, 2002; Findlay and Watling, 1997; Hargrave, 1994). However, we measured solid uptake of sea cucumbers below finfish cages and not in the seabed. Therefore, several important factors not included in this study will influence dispersion of finfish and sea cucumber solid waste in the water column and the degree of benthic impact. For instance, the spatial arrangement and design of suspended sea cucumber culture may influence local hydrodynamics (Zamora et al., 2018) by decreasing current velocities and reducing waste dispersion. Also, the chemical composition of sea cucumber feces will differ from those of finfish feces by having lower organic content (MacTavish et al., 2012; Neofitou et al., 2019; Paltzat et al., 2008), as will their physical characteristics (density, settling velocities), which are yet to be determined. Although necessary to assess local impacts comprehensively, modeling the benthic effect of the IMTA system, however, lay outside the scope of this study and is a perspective for further research. Also, we did not consider effects of dissolved nutrient waste, which will be higher for farms with sea cucumbers (Purcell, 2004) by ca. 0.1 and 1.4% for dissolved N and P, respectively, according to our results. Upscaling the analysis from local to larger spatial scales is necessary to properly represent their potential eutrophication impact. This is also true to account for other emissions (e.g. GHGs) occurring at the farm and other life-cycle stages and that can have impacts at the global scale. Finally, ending the assessment here would ignore that the IMTA system also produced additional biomass, which is another aim of IMTA systems. Therefore, to compare environmental

performances of monoculture and IMTA systems fully, the analysis must be supplemented with more holistic impact assessment and related to the main functions of both systems, as performed in the LCA.

4.2 LCIA: comparison of monoculture and IMTA

In general, environmental impacts per t of fresh aquatic product were similar to the ranges and main trends of those found in literature. Contribution analysis revealed that feed production was the main driver of environmental impact in all impact categories of both systems, except for EU, for which farm operation (specifically finfish emissions) was the main source of impact, as commonly reported in aquaculture LCA reviews (Aubin, 2013; Bohnes et al., 2018; Parker, 2012). For all impact categories except EU, impacts of the monoculture and IMTA systems lay within the interquartile ranges of the results reviewed from 179 aquaculture systems (Bohnes et al., 2018). Our estimate of 123-124 kg PO₄³⁻ eq. (Fig. 3) largely exceeds the interquartile range of 32-74 kg PO₄³⁻ eq., suggesting that the red drum monoculture and IMTA systems assessed in this study have a higher EU impact than many other seafood systems. Differences in EU were smaller (14-36% higher), however, when compared to other sea-cage systems in Tunisia and Greece (Abdou et al., 2017; Aubin et al., 2009), suggesting that most differences were likely due to the wide variety of systems analyzed and different methodological choices when performing the LCA (Bohnes and Laurent, 2019; Henriksson et al., 2012). Integrating seaweed culture into the IMTA system could address the dissolved nutrient niche (Troell et al., 2003) and reduce the EU impact (Jaeger et al., 2019). Given the domination of feed production in most impact categories, however, most improvement in the environmental performance of both systems studied is expected to come from decreasing the FCR of the finfish culture. Multiple factors influence the FCR, including feed composition and digestibility, rearing technology and practices (e.g. computerized feed-management systems) and the species cultured (Pelletier et al., 2009). These factors offer possibilities for improvements that should be considered to decrease the FCR.

The small differences observed between the monoculture and IMTA were due mainly to the unbalanced scales of the main species (i.e. finfish) and the added species (i.e. sea cucumber). In the IMTA system, the additional 3 t of sea cucumbers (and 109 kg of edible protein) represented a minor increase in annual farm production; therefore, finfish production still drove the impacts. Mendoza Beltran et al. (2018) reported and discussed this issue when comparing impacts of a finfish monoculture (240 t) to those of the same farm in an IMTA system with oysters (244 t of aquatic products). They estimated similar differences between the two systems (0.4-1.8% depending on the impact category) and reported that interpretation of their significance depended on the statistical test used, due to the high uncertainty, mainly in the LCI data. We also observed high uncertainties in our LCIA results. The estimated uncertainties were ca.

541 10 times as high as the differences observed between impacts of the systems, meaning that they cannot be
542 differentiated; thus, both systems had similar impacts. In a recent study, a threshold of 10-30% of difference, based on
543 uncertainties quantified for multiple impact categories (Joliet et al., 2010) was used to differentiate scenarios in LCA
544 (Guérin-Schneider et al., 2018). According to the statistical analysis, some differences were still significant in our
545 study, but they were probably artifacts caused by the large number of runs performed in the Monte Carlo analysis.
546 Nevertheless, the ranking of IMTA compared to monoculture for each impact category can be considered as a general
547 trend and was confirmed for simulations with higher sea cucumber stocking densities (results not shown). In any case,
548 these results confirmed the importance of performing uncertainty analysis in comparative LCAs to avoid overly
549 simplistic conclusions.

550
551 Compared to the monoculture, the IMTA system tended to decrease EU and NPPU impacts but increase CC and
552 CED. Reducing farm nutrient emissions through solid waste extraction by sea cucumbers was one aim of the IMTA;
553 therefore, the decrease in EU was expected. On-farm production of organisms from a lower trophic level that ingested
554 finfish waste for growth increased system productivity without an additional feed cost. This eco-intensification
555 reduced the overall amount of feed used per unit of biomass produced, which explained the decrease in NPPU. IMTA
556 is therefore an interesting way to use feed nutrients better and to mitigate some of the associated environmental
557 impacts. However, ecological intensification of aquaculture (Aubin et al., 2019), through IMTA, shifted
558 environmental burdens to energy-related global impact categories such as CC and CED. Energy use usually increases
559 with system intensity in aquaculture (Aubin et al., 2006; Ayer and Tyedmers, 2009; Dekamin et al., 2015; Samuel-
560 Fitwi et al., 2012) and is associated with increase in GHG emissions when energy originates from fossil sources
561 (Pelletier et al., 2009). Finding such similarities with “classic” intensification is not surprising since finfish and sea
562 cucumbers have similar life cycles, involving a hatchery stage followed by a grow-out stage in sea cages. Therefore,
563 the increase in CC and CED in the IMTA system can be explained by the addition of new energy-demanding
564 components (e.g. juvenile sea cucumber production) and energy inputs (e.g. on-farm fuel and electricity) related to sea
565 cucumber culture. These components were not visible in the contribution analysis because of the large difference in
566 production scales. Further intensification of this IMTA system by increasing sea cucumber production would therefore
567 probably increase energy dependence of the system and the associated GHG emissions, unless it comes with a
568 “greening” of the global energy system at all stages for both species, including hatchery, juvenile transport and farm
569 activities. Close integration of farm activities and infrastructure becomes less likely in IMTA farms with more
570 balanced production between primary and secondary species; therefore, environmental impacts will likely increase if

571 sea cucumber production increases. Impacts will not necessarily transfer from local to global scales for other IMTA
572 systems, particularly for those with species with less similar life cycles (e.g. finfish and seaweed). The same kind of
573 local and global environmental assessment should be encouraged for these systems to select the most sustainable
574 options for future aquaculture development.

575 **4.3 Other perspectives to improve environmental performances**

576 Local and global environmental benefits of the IMTA system were generally low because of the low productivity
577 of sea cucumbers; increasing them will require finding practical methods to intensify sea cucumber production. One
578 option is to investigate the choice and design of rearing structures that can increase the culture surface area and thus
579 the bioremediation potential of the system. An initial approach could be to consider three-dimensional (3D) rearing
580 structures to increase the biomass that can be grown per unit area (Robinson et al., 2011). For example, with a three-
581 level structures, the CS could be ‘virtually’ divided by three, i.e. 45:1 and WEE could increase to 2.20%. However,
582 food availability for sea cucumbers in a 3D structure will be affected by characteristics of the rearing system. The
583 mesh sizes required to contain the sea cucumbers would greatly reduce the amount of farm particles entering the cages
584 (Fortune, 2013; Zamora et al., 2018), with probably a gradual decrease in food availability from the top to the bottom
585 of the rearing structure. Furthermore, accumulation of solids on top of the structure can also be problematic since it
586 may deoxygenate water, which can kill sea cucumbers. Another option is benthic sea ranching of sea cucumbers,
587 which consists of releasing juvenile animals on the seabed, often with minimal or no containment. Local
588 environmental benefits may be increased by sea ranching, since the entire benthic area of the farm becomes available
589 for culture, which means that more biomass can be produced. Chary et al. (in prep) estimated for the monoculture
590 farm assessed here, that the largest benthic area receiving solid deposition rates higher or equal to $2.7 \text{ kg m}^{-2} \text{ yr}^{-1}$
591 (corresponding to the SP of sea cucumbers) can extend up to 15 000 m². For this culture area, and assuming all other
592 hypothesis being equal (except seeding, which becomes 54 500 individuals), 30 t of sea cucumbers could be produced
593 annually, increasing WEE to 8.01%. Moreover, in sea ranching culture sea cucumber feeding and burrowing on the
594 seabed have a bioturbation effect, which can facilitate microbial organic degradation and enhance regeneration and
595 mineralization of surface sediments (MacTavish et al., 2012; Purcell et al., 2016; Slater and Carton, 2009; Yuan et al.,
596 2016). Sea ranching has been suggested to be more practical in IMTA than suspended culture at a large commercial
597 scale because the latter may disrupt normal farming operations (Zamora et al., 2018). Sea ranching has potential major
598 drawbacks, however: little monitoring of cultured animals and difficulties in harvesting, little distinction between
599 cultured and wild animals, risks of benthic predator attacks (Hannah et al., 2013; Robinson and Pascal, 2011; Zamora
600 et al., 2018), the physical characteristics of each site (e.g. depth and bathymetry profile, sediment type) that influence

601 the ability of benthic species to settle, and the need to adapt the location of the animals on the seabed to the farm's
602 organic footprint (Zhang and Kitazawa, 2016). Finding practical farming methods for sea cucumbers to be added to a
603 pre-existing monoculture system thus remains a challenge. Farming structures will have to contain and secure the
604 cultured stocks effectively while optimizing bioremediation, not compromising the normal farm-routine cycle and
605 making the IMTA system at least as profitable as monoculture.

606 **5 Conclusion**

607 We assessed environmental performances of finfish monoculture and sea cucumber-fish IMTA scenarios by i)
608 focusing on the particulate waste bioremediation potential of sea cucumbers and ii) estimating environmental impacts
609 of both systems with LCA per kg of edible protein and t of product. At its maximum ingestion capacity and in tropical
610 water conditions, the sea cucumber *H. scabra* thus has good potential for aquaculture waste bioremediation if
611 cultivated at high densities. However, given the current limits to stocking density observed for this species, its co-
612 culture in sea cages beneath finfish nets may decrease farm net particulate waste load and benthic impact only slightly.
613 Intensification of sea cucumber culture seems possible to increase local environmental benefits, but further research is
614 necessary to design rearing units that can optimize production and/or bioremediation and be practically integrated into
615 existing finfish monoculture units. LCA impacts of the monoculture and IMTA systems differed little because of the
616 large difference in production scales between finfish and sea cucumbers. IMTA showed better performance trends for
617 EU and NPPU but larger impacts for CED and CC, generating an impact transfer between categories. These trends
618 should be confirmed for large commercial IMTA farms with more balanced production scales between co-cultured
619 species when the technology for sea cucumber culture becomes more advanced. Several other important
620 environmental sustainability issues were not addressed in this study, such as potential disease transfer between
621 cultured species or impacts of escaped animals on the local environment; they would need additional research to draw
622 conclusions about broader environmental effects of the studied systems.

623 The use of generic metrics for comparing IMTA waste reduction efficiency and their use along with LCA resulted
624 in a more holistic environmental assessment of the studied systems, addressing impact categories at both local and
625 global scales. Such integrated model-based environmental analysis can be a powerful tool to predict the magnitude of
626 environmental benefits that can be expected from new and complex production systems such as IMTA and to select
627 the best co-culture options from an environmental viewpoint by maximizing resource use and minimizing
628 environmental impacts. Its application to the case study of red drum and sea cucumber co-culture on Mayotte is one of
629 many possibilities combining two or more organisms of different trophic levels and addressing other nutrient niches.
630 Finally, given the differing statuses (trophic level, ecological role and culinary interest) and economic values of the

631 species produced, and the multiple objectives of IMTA systems (biomitigation, production and revenue
632 diversification), we recommend including socio-economic criteria to fully assess the sustainability of future seafood
633 production systems.

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641 **Appendix A**642 **DEB model parameters and assumptions for sea cucumber**

643 Parametrization of the Dynamic Energy Budget (DEB) model integrates data on life-history traits (e.g. age, weight
 644 and length at first feeding or puberty) and longitudinal data on weight, length and reproductive data over time
 645 (Kooijman, 2010). The full list of DEB parameters for *Holothuria scabra* can be retrieved freely from the “Add my
 646 Pet” database (Marques et al., 2018), but this appendix (Table A.1) shows only core parameters used to predict solid
 647 and dissolved waste emissions (Cf. section – “Conversion of DEB energy outputs to N and P fluxes”).

648

649 Table A.1. Dynamic Energy Budget (DEB) parameters used in the present study for the tropical sea cucumber *H.*
 650 *scabra* for the reference temperature of $T = 20$ °C. X corresponds to sea cucumber food resources (fish feces).

Parameter description	Symbol	Value	Unit	Source
Core parameters				
Allocation fraction to soma	κ	0.98	-	(AmP, 2019)
Assimilation efficiency	κ_X	0.44	-	This study
Growth efficiency	κ_G	0.80	-	(AmP, 2019)
Reproduction efficiency	κ_{Go}	0.95	-	(AmP, 2019)
Temperature effect				
Arrhenius temperature	T_A	8000	K	(AmP, 2019)
Reference temperature	T_I	293	K	(AmP, 2019)
Supplementary parameters used to estimate dissolved emissions from DEB outputs				
Feed				
Energy density of feed (fish feces)	ED_{feed}	10 464	J g DW ⁻¹	This study
N to P stoichiometry of feed	NP_X	2.42	mol:mol	This study
Sea cucumber				
N to P stoichiometry of sea cucumber	NP_{SC}	30.05	mol:mol	(Clarke, 2008)
N content in sea cucumber	N_{SC}	6.95	% DW	(Ozer et al., 2004)
P content in sea cucumber	P_{SC}	0.64	% DW	This study
Energy yield of reserve	μ_{EN}	3667	J mmol N ⁻¹	This study
Feces				
Conversion factor of unassimilated food	μ_{NAfeed}	6166	J mmol N ⁻¹	This study
Energy density of sea cucumber feces	ED_{feces}	7 717	J g DW ⁻¹	This study
N content in sea cucumber feces	N_{feces}	0.57	% DW	This study
P content in sea cucumber feces	P_{feces}	1.89	% DW	This study

651

652 This parameter set does not include lower and upper temperature limits, because of the lack of temperature-
 653 dependent data for this species. The default temperature correction factor was therefore used in this study (Marques et
 654 al. 2009) and complied with previous growth data up to 31°C (Thierry Lavitra et al., 2010) and 33°C (Kühnhold et al.,

655 2017). In the present study, the annual sea surface temperature time series in Miangani Bay, Longoni village, for
656 2016-2017 were used as reference for Mayotte lagoon. Water temperature ranged from 25.2 °C on 18 October 2016 to
657 29.6 °C on 6 April 2017.

658 The DEB model used in this study does not include the weight of gonads in total animal weight, because of
659 uncertainties in the reproductive cycle of *H. scabra*. It is known that sexual maturity appears at ca. 180 g (Juinio-
660 Meñez et al., 2013), and depending on the population, an annual, bi-annual or continuous reproductive cycle can be
661 observed (Conand, 1990; Morgan, 2000; Purwati, 2006; Rasolofonirina et al., 2005). In addition, Purwati (2006) and
662 Rasolofonirina et al. (2005) reported gonad indices for *H. scabra* in the Indian Ocean from 0-11% of total body
663 weight, while Penina Tua Rahantoknam (2017) reported values up to 16%.

664

Approach to estimate assimilation efficiency for the DEB model

The DEB model, as well as energy or mass balance approaches, can be used to estimate fluxes of feces and their composition (Bureau et al., 2003; Cho and Bureau, 1998; Papatryphon et al., 2005). In DEB theory, assimilation efficiency (κ_X), which is the ratio of assimilated energy to ingested energy, is used to estimate the percentage of energy from food that is stored in the reserve of the animal. Unassimilated components are assumed to be excreted as feces by the animal. This coefficient is analogous to absorption efficiency in bioenergetics approaches or to apparent digestibility coefficients (ADC) in nutrient mass-balance approaches. In this study, κ_X was estimated with a mass-balance approach using ADC literature values obtained for *H. scabra* or other sea cucumber species (Table A.2). The amount of digested material was estimated by multiplying ADCs for primary nutritional fractions (i.e., protein, lipids, carbohydrates, fiber and ash) by their proximate amounts in sea cucumber feed (finfish feces), by assuming that total dry weight (DW) is the sum of nutritional fractions. Each nutritional fraction has a known gross energy density: respectively 23.6, 39.5, 17.2 and 7.8 kJ g⁻¹ for protein, lipids, carbohydrates (Reid et al., 2018) and fiber (Kraisid Tontisirin. et al., 2003). Gross energy density in feed (ED_{feed}) was estimated by summing the energy in its nutritional fraction: $ED_{feed} = 10\ 464\ \text{J g DW}^{-1}$ (Table A.2). Similarly, gross energy density of sea cucumber feces (ED_{feces}) was subtracted from the sum of energy in indigestible dietary material (5897 kJ for 0.76 g of feces), yielding $ED_{feces} = 7717\ \text{J g DW}^{-1}$ (Table A.2). The energy assimilation efficiency was obtained from the ratio $\kappa_X = \frac{\text{Digested energy}}{ED_{feed}} = 43.65\%$, with digested energy = 4 567 J (Table A.2).

Table A.2. Nutritional mass balance approach for the sea cucumber *H. scabra* feeding on finfish feces in an integrated multi-trophic aquaculture system. Total dry weight (DW) was assumed to be the sum of protein, lipid, carbohydrates, fiber and ash fractions. The N fraction in finfish feces was subtracted from protein content using an N:protein ratio of 16%.

Nutritional fraction	Content in feed (finfish feces ¹)		Sea cucumber digestibility coefficients (%)	Digested material and energy per g of feed ingested		Undigested material and energy per g of feed ingested	
	% DW	J		g g ⁻¹	J g ⁻¹	g g ⁻¹ (%)	J g ⁻¹
Protein	14.85	3 505	86.8 ²	0.12	2 862	0.03 (3.57)	643
from N	2.38	-	-	0.02	-	0.00 (0.57)	-
Lipids	3.75	1 481	23.0 ³	0.01	341	0.03 (3.78)	1 141
Carbohydrates	13.27	2 282	43.2 ²	0.06	985	0.08 (9.87)	1 298
Fiber	27.16	3 196	11.9 ⁴	0.05	380	0.36 (47.24)	2 815
Ash	40.97	0	0.0	0.00	0	0.27 (35.54)	0.00
Phosphorus	1.86	-	55.7 ⁵	0.01	-	0.01 (1.08)	-
Total	100	10 464	-	0.24	4 567	0.76 (100)	5 897

¹Proximate composition of red drum feces calculated for animals fed with commercial Nutrima® diets (Chary et al. 2019)

²Mean coefficient obtained for an animal-ingredient-based diet for *H. scabra* (Orozco et al., 2014)

³Coefficient obtained for a sediment-based diet in the holothurian *Molpadia musculus* (Amaro et al., 2010)

⁴Coefficient obtained for red drum fed commercial diets (Chary et al. 2019). The low fiber digestion observed in this omnivorous finfish species was probably due to intestinal microbiota activity. In the absence of any relevant data on dietary fiber digestibility in holothurian species, we assumed the same partial digestibility for *H. scabra*.

⁵Calculated in this study

688 Conversion of DEB energy outputs to N and P fluxes

689 Several equations are used in the DEB model to estimate N and P emissions in feces and dissolved inorganic
 690 emissions of sea cucumber (Table A.3). As suggested in “Add my Pet”, the life cycle of *H. scabra* was modeled using
 691 a DEB model with metabolic acceleration between birth and metamorphosis (Kooijman, 2014). Description of a
 692 standard DEB model, the full list of equations and DEB nomenclature can be found elsewhere (Kooijman, 2010);
 693 therefore, we present only the methods used to estimate N and P fluxes into food, feces and dissolved emissions from
 694 DEB outputs.

695 Dissolved N and P emissions from sea cucumber were estimated in the DEB model based on the equations of Pete
 696 et al. (2018) (see also Pete et al. in prep) (Table A.3). The conversion factor μ_{UFF} is used to convert the energy from
 697 undigested (unassimilated) finfish feces into N. We calculated μ_{feces} from the equation $\mu_{feces} = \frac{ED_{feed} \cdot M_N}{N_{feed}} = 6\,166\text{ J}$
 698 mmol N^{-1} , with $M_N = 0.014\text{ g mmol}^{-1}$. The N:P stoichiometry in the animal and the feed was respectively taken from
 699 Clarke (2008) for the holothurian *Heterocucumis steineni* and from Chary et al. (2019) for red drum feces. The energy
 700 assimilated from feed is incorporated into reserves and used for maintenance, growth and maturity in juveniles or
 701 reproduction in adults. The energy used for maintenance, growth, and gonad formation can be converted into NH_4^+
 702 and PO_4^{3-} fluxes (in mmol day^{-1}) using the conversion factor μ_{EN} (in J mmol N^{-1}). This conversion factor can be
 703 obtained by dividing the chemical potential in sea cucumber reserves of $550\,000\text{ J mol C}^{-1}$ (Marques et al., 2018) by
 704 the N:C ratio in the organic matter of the reserves, which is $0.15\text{ mol N mol C}^{-1}$ (Marques et al., 2018).

705

706 Table A.3. Equations used in the Dynamic Energy Budget (DEB) model to estimate N and P in food, feces and from
 707 solid and dissolved waste emissions of sea cucumber, modified from Pete et al. (2018) (see also Pete et al. in prep).
 708 Equations describing energy fluxes and variable differential equations in DEB theory can be found elsewhere
 709 (Kooijman, 2010).

Equation	Variable and parameters description	Unit
$IFF = \dot{p}_X \cdot ED_{feed}$	IFF: Ingested finfish feces	g DW d^{-1}
	\dot{p}_X : Ingestion rate	J d^{-1}
	ED_{feed} : Energy density in feed	J g DW^{-1}
$UFF = (1 - \kappa_X) \cdot \dot{p}_X \cdot ED_{feces}$	UFF: Undigested finfish feces	g DW d^{-1}
	κ_X : Assimilation efficiency	%
	ED_{feces} : Energy density in feces	J g DW^{-1}
$F_N = F \cdot N_{feces}$	F_N : N solid emission from feces	g N d^{-1}
	N_{feces} : N content in feces	%
$F_P = F \cdot P_{feces}$	F_P : P solid emission from feces	g P d^{-1}
	P_{feces} : P content in feces	%

$N_{regen} = 0$ because $NP_X < NP_{SC}$	N_{regen} : Regeneration of excess N	mmol N-NH ₄ ⁺ d ⁻¹
$P_{regen} = \frac{\dot{p}_A}{\mu_{UFF}} \cdot \left(\frac{1}{NP_{SC}} - \frac{1}{NP_O} \right)$	P_{regen} : Regeneration of excess N \dot{p}_A : Assimilation rate μ_{UFF} : Conversion factor of undigested finfish feces	mmol P-PO ₄ ³⁻ d ⁻¹ J J mmol N ⁻¹
$CMC = \frac{\dot{p}_{M1} + \dot{p}_J}{\mu_{EN}}$	CMC : Conversion of maintenance cost \dot{p}_{M1} : Structural maintenance rate \dot{p}_J : Maturity maintenance rate μ_{EN} : Energy yield of reserve	mmol N-NH ₄ ⁺ d ⁻¹ J J J
$CGC = \frac{\dot{p}_G \cdot (1 - \kappa_G)}{\mu_{EN}}$	CGC : Conversion of growth cost \dot{p}_G : Structural growth rate κ_G : Growth efficiency	mmol N-NH ₄ ⁺ d ⁻¹ J J
$CCGP = \frac{\dot{p}_{Go} \cdot (1 - \kappa_{Go})}{\mu_{EN}}$	$CCGP$: Conversion of gamete production cost \dot{p}_{Go} : Gonad allocation rate κ_{Go} : Reproduction efficiency	mmol N-NH ₄ ⁺ d ⁻¹ J J
$\frac{dN.NH_4}{dt} = (CMC + CGC + CCGP) \cdot M_{N.NH_4}$	$\frac{dN.NH_4}{dt}$: Total emissions of N-NH ₄ $M_{N.NH_4}$: Molar mass of N	kg N-NH ₄ ⁺ d ⁻¹ kg mmol ⁻¹
$\frac{dP.PO_4}{dt} = \left(P_{regen} + \frac{CMC + CGC + CCGP}{NP_{SC}} \right) \cdot M_{P.PO_4}$	$\frac{dP.PO_4}{dt}$: Total emissions of P-PO ₄ $M_{P.PO_4}$: Molar mass of P	kg P-PO ₄ ³⁻ d ⁻¹ kg mmol ⁻¹

Approach to estimate P digestibility in sea cucumber

No data were found for P digestibility in *H. scabra* or other sea cucumbers; therefore, the fraction of P assimilated from feed (A_{SP}) was back-estimated using a mass-balance approach and was used to calculate P emissions in sea cucumber feces. In the mass-balance approach, the digested nutrient fraction equals the nutrients excreted in dissolved emissions and those retained in biomass gain (Cho and Kaushik, 1990). Dissolved P emissions ($\frac{dP.PO_4}{dt}$) from a 10 g juvenile (age = 88 days) to a final weight of 709 g (age = 453 days) were estimated with the DEB model as 8.46 g in the temperature time series (Cf. section “DEB model parameters and assumptions for sea cucumber”) and using an f -value set to 1. P content (P_{SC}) in sea cucumber, required to calculate the P retained in biomass, was calculated as

$$P_{SC} = \frac{N_{SC} \cdot DW_{SC}}{M_N} \cdot \frac{M_P}{NP_{SC}} = 0.64\% \text{ DW}^{-1},$$

with N content in sea cucumber, $N_{SC} = 6.95\% \text{ DW}^{-1}$ (subtracted from protein content in Ozer et al. 2004); DW ratio in sea cucumber (DW_{SC}) = 14.51% (mean value in Ozer et al. 2004) and P molar mass (M_P) = 31 g mol⁻¹. Using P_{SC} and DW_{SC} , the P retained in biomass was estimated as 0.65 g DW for a biomass gain of 709-10 = 699 g. Following mass-balance principles, the P in feed assimilated by sea cucumbers is therefore the sum of P retained in biomass and P dissolved over the simulated period (i.e. 9.11 g in 365 days). DEB predicted cumulative food ingestion of 879 g finfish feces DW yr⁻¹ per individual in the culture cycle. With a P content in feed (P_{feed}) of 1.86% (Table A.2), cumulative P inputs in feed over the period were thus 16.36 g. Finally, we estimated the percentage of P assimilated from feed (i.e. the ratio of assimilated P to total P input in feed) as $A_{SP} = 55.7\%$. This value was used in the mass-balance calculation to calculate the P content in sea cucumber feces (P_{feces}).

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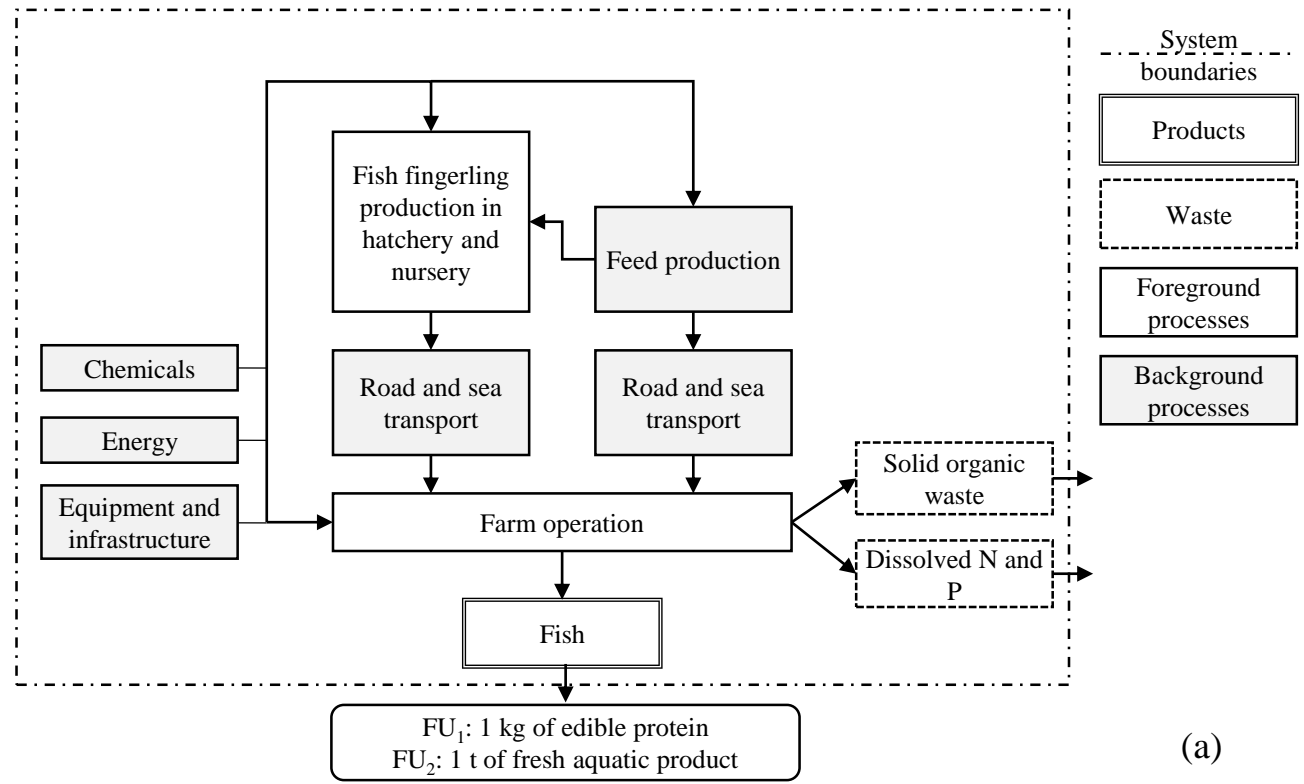
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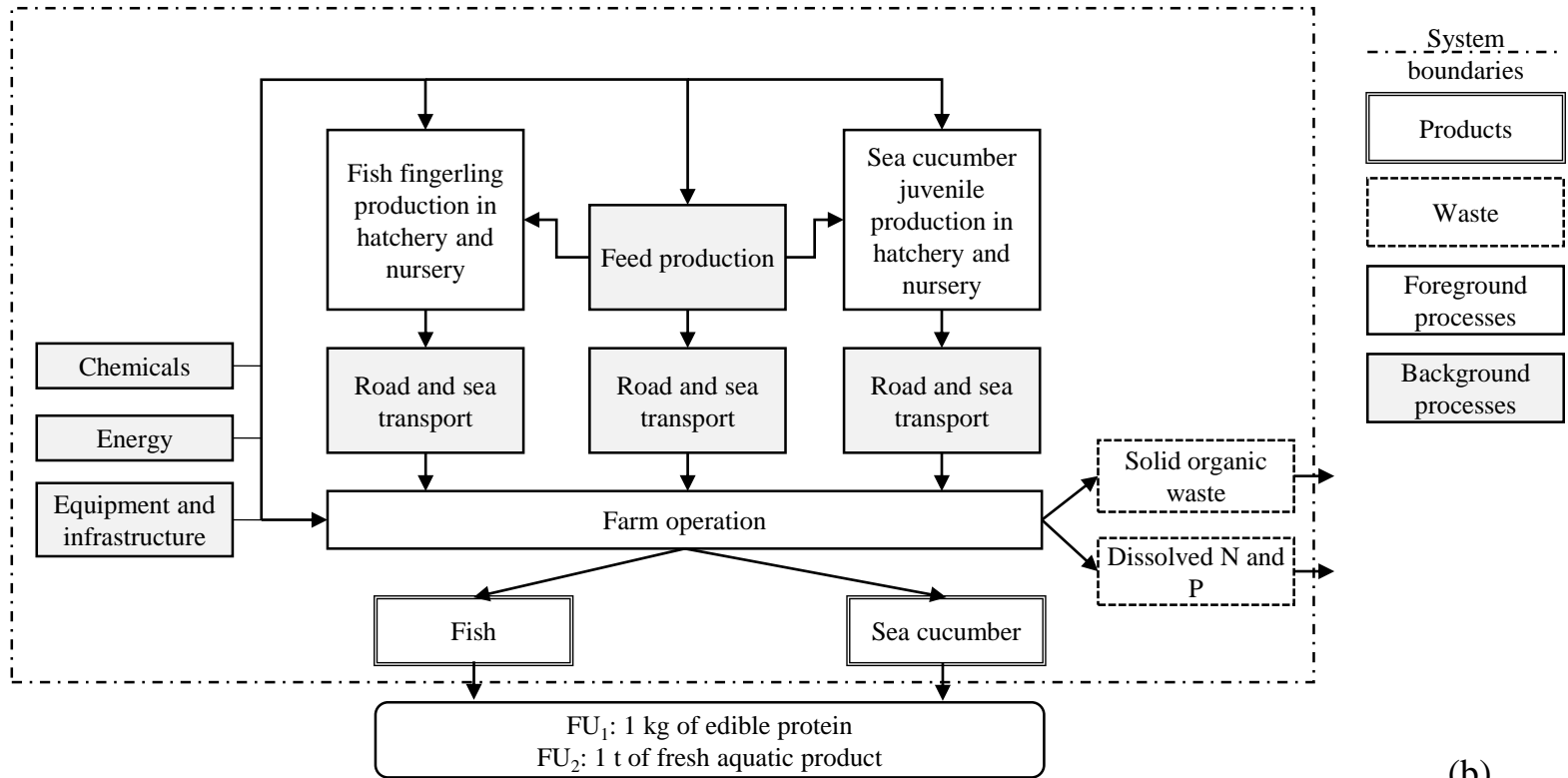
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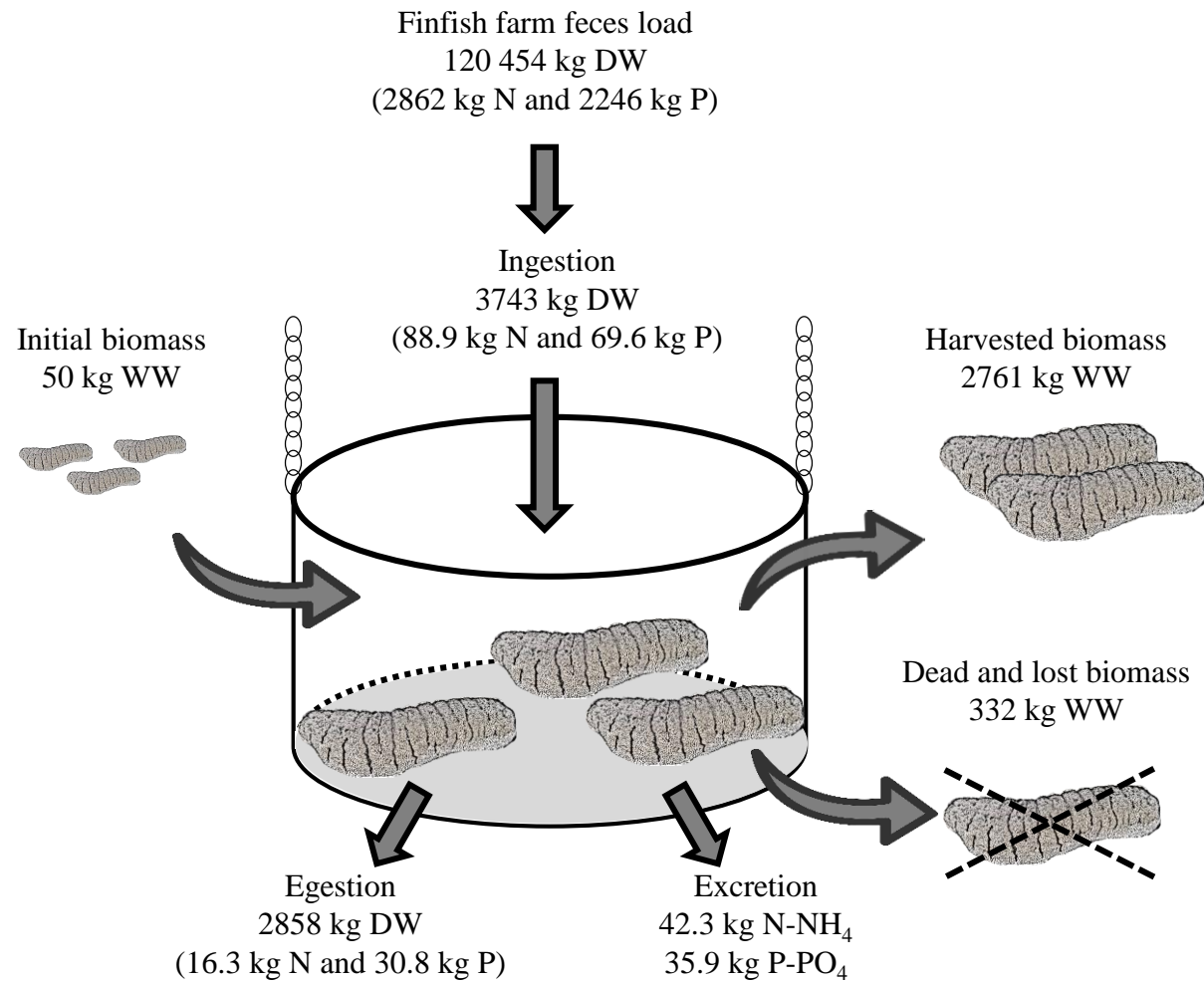
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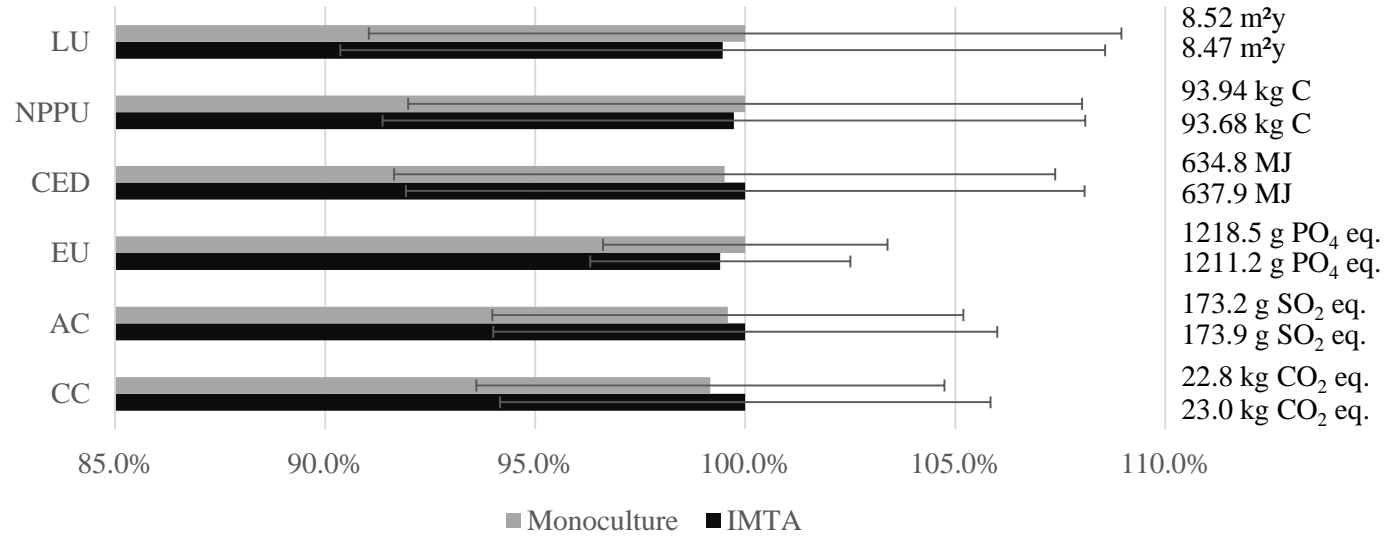


(b)



Index	Value	Unit
Solid processing rate	2.728	kg solids m ⁻² yr ⁻¹
Net solid uptake rate	0.645	kg solids m ⁻² yr ⁻¹
Waste extraction efficiency	0.73	%
Biomass culture ratio	1.3:1	kg sea cucumber:kg finfish
Culture area ratio	137:1	m ² sea cucumber cage: m ² finfish cage

Impact per kg of edible protein



Impact per t of fresh aquatic product

