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REVIEWS IN Aquaculture

REVIEW

Nutrient retention efficiencies in integrated multi-trophic aquaculture

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Abstract

One of the bottlenecks for commercial implementation of integrated multi-trophic aquaculture (IMTA) is the difficulty in quantifying its environmental performance. We reviewed a large body of literature to determine the variability in nutrient dynamics within different IMTA systems (open sea-cages, land-based flow-through and recirculating aquaculture systems), with the aim to provide a generic framework to quantify nutrient retention efficiencies in integrated aquaculture systems. Based on the eco-physiological requirements of the cultured species, as well as the response of "extractive" species to waste from "fed" species, the maximum retention efficiency was defined for a conceptual four-species marine IMTA system (fish–seaweed–bivalve–deposit feeder). This demonstrated that 79%–94% of nitrogen, phosphorus and carbon supplied with fish feed could theoretically be retained. In practice, however, various biological and environmental factors may limit retention efficiencies and thereby influence the bioremediation of IMTA systems. These biological (waste production, stoichiometry in nutrient requirements) and environmental (temporal and spatial connectivity) factors were therefore evaluated against the theoretical reference frame and showed that efficiencies of 45%–75% for closed systems and 40%–50% for open systems are more realistic. This study is thereby the first to provide quantitative estimates for nutrient retention across IMTA systems, demonstrating that a substantial fraction of nutrients released from fish culture units can be retained by extractive species and subsequently harvested. Furthermore, by adapting this framework to the design and the condition prevailing for a specific IMTA system, it becomes a generic tool to analyse the system's bioremediation potential and explore options for further improvement.

KEYWORDS
bioremediation, environmental sustainability, extractive species, IMTA, integrated aquaculture, waste recycling

1 | INTRODUCTION

Aquaculture is the fastest growing food production sector globally.[1] With increasing pressure on freshwater resources and terrestrial space, a substantial expansion of marine aquaculture in particular is foreseen.[2] Rapid development of (marine) aquaculture dependent on formulated feed (i.e. fed species) is associated with various environmental concerns.[3] One of these concerns is the release of fed nutrients, not retained for growth, as organic (i.e. uneaten feed and faeces) and inorganic (i.e. branchial and urinary losses) waste.[4,5] These wastes cause nutrient enrichment, which affects food web functioning, and a loss of valuable resources.[6,7]

The expected growth of (fed) aquaculture requires the development of responsible and sustainable technologies, practices and approaches. Therefore, the integrated multi-trophic aquaculture (IMTA) approach has been developed. In IMTA systems, cultivation of fed species (e.g. fish and shrimp) is linked to cultivation of extractive species (e.g. autotrophs, filter and deposit feeder), in such a way that the waste of fed species becomes a nutrient source for extractive species.[8-11] The idea behind the IMTA approach is that recycling of waste nutrients results in less nutrients being released into the environment, whilst overall productivity of the system increases.[10,12] This approach fits well within the global ambition for circularity in food production, which strives to minimise energy and nutrient losses and maximise resource use efficiency, by closing the nutrient loop.[13]

The general concepts and principles of the IMTA approach are straightforward, easy to visualise and have been well explained in previous reviews.[8,14,15,16] One of the pillars of the IMTA approach is to reduce nutrient losses to the environment, by harvesting nutrients retained in the biomass of extractive species, but it remains unclear under which conditions maximum nutrient retention efficiencies can be achieved. Nutrient removal efficiencies varying between 2% and 100% have been reported for extractive species (e.g. Troell et al.[8]; Schneider et al.[4]), whereby this large scope reflects a broad diversity in cultivation techniques, waste quality, measuring methods, culture intensity and species. In this review we use "system openness" as the main criterium influencing nutrient retention efficiencies in IMTA systems. "System openness" is here defined as the extent to which system functioning is influenced by the surrounding environment and classifies three types of aquaculture production systems: (1) closed systems, where the environment can be controlled (e.g. recirculating aquaculture systems (RAS)); (2) open systems, where control over environmental influences is very limited (e.g. sea cages); and (3) semi-open systems, where environmental influences can partially be controlled (e.g. land-based flow-through systems or ponds).

The concept of integrated aquaculture has its roots in Asia.[17] In Western countries, development of integrated aquaculture is currently moving from a pilot to a commercial scale, but implementation is still limited.[18] Hughes and Black[18] and Hughes[19] reviewed several factors explaining this limited adoption of IMTA in Western countries, with a focus on Europe. One of the bottlenecks is the lack of a quantitative definition of the environmental performance of IMTA, as the benefits of IMTA are mostly conceptually described.[16,19] Know-how on the maximum bioremediation potential of IMTA systems would aid in formulating regulations, policies and certification criteria.[19] Furthermore, where the fraction of waste nutrients harvested via extractive species biomass is relatively small, questions concerning the bioremediation potential of IMTA might arise.[20] To assess the amount of waste nutrients that can be recycled in extractive species biomass, there is thus a strong need to quantify waste flows through IMTA systems and to understand the factors

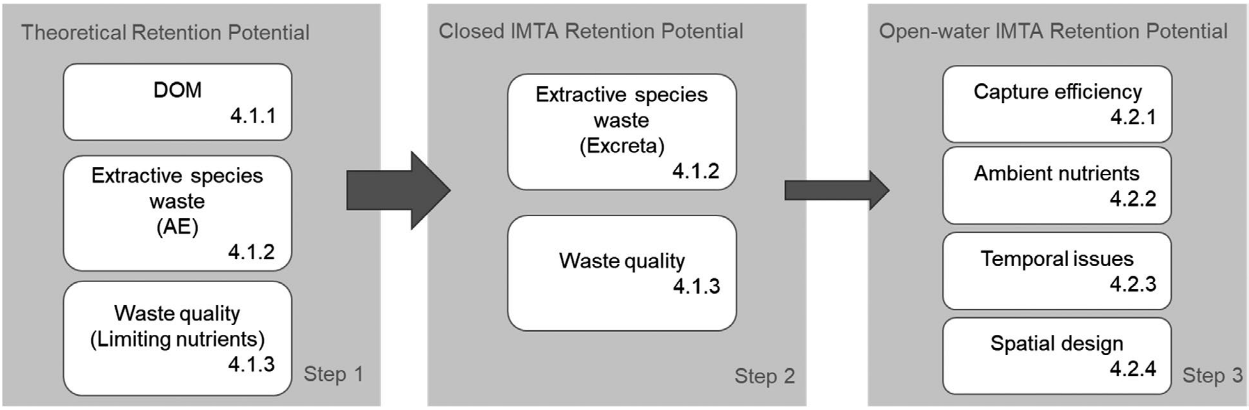

FIGURE 1 Generic framework which can be used to identify factors to consider when quantifying the nutrient retention potential of integrated aquaculture (IMTA) systems according to system openness. The framework consist of three steps. In step 1, the maximum theoretical retention potential of a conceptual IMTA (fish–seaweed–bivalve–deposit feeder) is calculated based on physiological requirements and responses of extractive species fed fish waste and under the assumptions that extractive species perform at their maximum and that ambient nutrients are absent. DOM, dissolved organic matter; AE, assimilation efficiency. Step 1 acts as a reference frame to discuss factors that influence retention potentials under a range of practical conditions. Step 2 considers biological factors, which are the main factors to take into account when calculating the retention potential of closed IMTA systems. Step 3 considers environmental factors, which besides the biological factors have to be taken into account to calculate the retention potential of open water IMTA systems. Factors are described in the section corresponding with the number mentioned in each box. Quantifications per factor are given in Table 2

that influence nutrient retention efficiencies. This will help in identifying options for enhancing bioremediation within IMTA systems.

In this review, we quantify nutrient retention efficiencies in IMTA systems according to system openness, whilst considering several biological and environmental limiting factors (Figure 1). We aim to establish a generic quantitative framework to highlight which factors must be considered when estimating nutrient retention efficiencies. The framework consists of three steps: (i) firstly, a conceptual IMTA system was developed for which we quantified the maximum retention efficiency for the macronutrients nitrogen (N), phosphorus (P) and carbon (C), based on physiological requirements and responses of extractive species fed with fish waste (section 3). These theoretical values were then evaluated against (ii) biological and (iii) environmental factors that place boundaries on the nutrient retention efficiencies that can be expected under practical farming conditions (section 4). The framework presented, when adapted to local conditions and farm design and thus taking into account variability in biological and environmental factors between IMTA systems, can help to identify and optimise the bioremediation potential of integrated systems.

2 | METHOD

This review summarises a large body of peer-reviewed literature on IMTA, with the focus on quantifying nutrient retention by extractive species fed fish waste, under different degrees of system openness. To quantify nutrient retention efficiencies, literature was collated on eco-physiological responses, including nutrient utilization processes, of extractive species fed fish waste. Nutrients retained in extractive species biomass can subsequently be harvested from the system, and these numbers can be used to define the overall bioremediation potential of the system. Peer-reviewed literature was collated from Google Scholar, using the keywords IMTA, integrated aquaculture, integrated mariculture, bioremediation, biomitigation, waste retention and waste removal combined with one of the following keywords: extractive species, seaweed, macro-algae, bivalves, mussel, oyster, deposit feeder, polychaete and sea cucumber. Only studies providing quantitative data were included in the summary, resulting in a total of 25 papers for seaweeds, 17 papers for bivalves and 20 papers for deposit feeders (section 3). These, and additional papers, were used to identify factors that limit nutrient retention efficiencies of extractive species under different farming conditions, which were in turn used to establish a generic quantitative framework (section 4; Figure 1).

3 | MAXIMUM NUTRIENT RETENTION EFFICIENCY BASED ON A CONCEPTUAL IMTA

In this section, we define a conceptual marine IMTA that includes four functional groups, in order to quantify its theoretical maximum nutrient retention potential. The first group, *the fed fish species*, excretes faeces and metabolites that can be used as a nutrient and energy source by extractive species. For the conceptual IMTA, it was chosen to focus on fish as fed species, but it should be noted that invertebrates, like shrimp, are also a major group of fed species.[11] To estimate retention efficiencies, we first qualify and quantify fish waste (section 3.1), and subsequently summarise the eco-physiological responses of extractive species, with a focus on their responses when fed fish waste (section 3.2). Three groups of *extractive species* were chosen, each taking up a different fraction of the waste released by the fed fish: (1) an *autotrophic species*, which takes up inorganic nutrients; (2) a *filter feeder*, which consumes particulate organic matter (POM) suspended in the water column; and (3) a *deposit feeder*, which scavenges on POM that settles on the bottom.[15] Although biofloc technology also focusses on the recycling of waste nutrients into biomass,[21] bioflocs are not included in this review, since the focus is on extractive species that will be harvested from the system for commercial purposes. Data summarised in sections 3.1 and 3.2 are used in step 1 of the framework, where we calculate the theoretical maximum nutrient retention potential of our conceptual IMTA (section 3.3).

3.1 | Fed species

Nutrient retention by the fed species is influenced by species, feeding level and management, diet composition, temperature and fish size.[4,22,23,24,25] Retention efficiencies reported for marine fish species range between 13% and 43% for N, 18% and 36% for P, and 14% and 38% for C (Appendix Table S1). Fed nutrients that are not retained by the fed species become input for the extractive species.

3.1.1 | Waste characteristics

Waste nutrients can be divided into inorganic and organic fractions. Fish excrete inorganic N as NH_3/NH_4^+, inorganic P as PO_4^{3-} and respire inorganic C (CO_2). Under aerobic conditions, NH_4^+ is converted to NO_3^- by nitrifying bacteria, with NO_2^- as an intermediate product. Together, these three forms of N are referred to as dissolved inorganic nitrogen (DIN). Mass balance models indicate that 39–63% N, 18–30% P and 39–70% C in feed are released as inorganic waste (Appendix Table S1).

Faeces and uneaten feed (3–5% of the feed in cage cultures remains uneaten[26,27]) make up the POM waste fraction.[5] In total, 5–45% N, 42–57% P and 6–44% C in feed are released as POM. Breakage and disaggregation of POM results in dissolved organic matter (DOM). The amount of POM that ends up as DOM depends on faecal and feed pellet stability, which is influenced by feed composition, feed processing methods and environmental conditions.[26,27] On average, 1%–7% N, 2%–8% P and 1–6% C in feed become DOM, which indicates that 5%–45% N, 42%–54% P and 5%–44% C remain as POM in the system (Appendix Table S1).

POM can be subdivided into small particles suspended in the water column, that is, suspended solids or suspended particulate matter (SPM), and large particles that sink rapidly to the bottom, that is, settled solids.[28] Wong and Piedrahita[29] estimated that 30% of POM in a commercial rainbow trout farm consisted of suspended solids, whilst the remaining 70% were settled solids. Waste particle size is influenced by fish species and fish size[26]—with bigger fish producing larger particles[30]—and culture systems, as mechanical and hydraulic conditions differ between cages, pond and tank systems.[26]

3.2 | Extractive species

To study the bioremediation potential of extractive species, several methods have been used: (i) *removal rate*: measuring nutrient removal rates (e.g. clearance rate (CR), assimilation efficiency (AE) and feeding rates) (e.g. Lefebvre et al.[31]; Yu et al.[32]; Fang et al.[33]); (ii) *retention*: comparing growth and nutrient retention in biomass measured over time, in and outside IMTA systems (e.g. Sanderson et al.[34]; Jiang et al.[35]; Yu et al.[36]; Tolon et al.[37]); (iii) *balance*: measuring water flows and nutrient concentrations in sediments, inflow and outflow water, of extractive species cultures (e.g. Jones et al.[38]; Al-Hafedh et al.[39]; Marques et al.[40]); (iv) *tracers*: tracing shifts in stable isotope or fatty acid composition (e.g. Handå[41]; Yokoyama[42]; Jiang et al.[35]); and (v) *modelling*: combining growth models with ecological and/or spatial models to simulate the bioremediation potential of extractive species.[43] Below a summary is given on the outcome of the various approaches described to estimate bioremediation potential of the extractive species included in our conceptual IMTA.

3.2.1 | Seaweeds

Data collected on the bioremediation potential of seaweeds in IMTA systems are summarised in Appendix Table S2. The retention method is frequently used to define the bioremediation potential of seaweeds in open water IMTA systems, whilst this method is less common in land-based systems. Several studies reported higher specific growth rates (SGR) and higher N content, some studies reported similar growth rates and N content, and some studies reported lower growth rates and N content for seaweeds cultivated in IMTA compared with seaweeds cultivated away from fish cages. The retention method does not distinguish between nutrients taken up from the environment and those of fish waste origin, but tracer studies do indicate that seaweeds cultivated in open water IMTA take up N derived from fish feed.[44,45]

The balance method was mostly used in semi-open and closed systems to quantify waste extraction efficiency of seaweeds. All studies reporting waste extraction efficiencies looked at inorganic N (as DIN or total ammonia nitrogen (TAN)), whilst few studies looked at inorganic P or C. This main focus on inorganic N can most likely be ascribed to the dominant release of inorganic N by fed species (Appendix Table S1), which plays a crucial role in eutrophication, and nitrogen often being the first limiting nutrient for seaweed growth, in particular in temperate regions.[8] In cases where N loads are low, environmental conditions are close to optimal (in particular light and temperature) and fast growing seaweed genera (e.g. *Ulva* and *Gracilaria*) are cultivated, inorganic N extraction efficiencies of up to 100% have been reported (e.g. Cohen and Neori,[46]; Jiménez del Río et al.[47]; Chow et al.[48]; Jones et al.[49]; Appendix Table S2). Inorganic P extraction efficiencies ranged from 3 to 95% (Jones et al.[49]; Hernández et al.[50]; Appendix Table S2), whilst the only study including C reported extraction efficiencies of 2–5%.[51] The highest N extraction efficiencies were achieved in balance studies (up to 100%; Appendix Table S2), whilst N extraction based on the retention method was at maximum 56%.[52] This suggests that, although often mentioned as negligible processes, nitrification and denitrification may contribute to the high efficiencies reported by balance studies, as removal of TAN and N_2 through nitrification and denitrification is attributed to the seaweed extraction potential when TAN or DIN concentrations are measured in the water. Krom et al.[53] estimated that in their sea bream–seaweed integrated system, approximately 8% of inorganic N entering the seaweed compartment was removed by denitrification. Studies based on TAN/DIN concentrations in the water may therefore overestimate N extraction efficiency of the seaweeds. Lastly, it should be noted that although low nutrient loads result in high extraction efficiencies, as uptake rates of seaweeds follow a Michaelis-Menten saturation curve,[46] the highest growth and tissue content can only be achieved under high nutrient loads.[54]

3.2.2 | Bivalves

In IMTA systems, the role of filter-feeder bivalves (hereafter referred to as bivalves) is to remove POM from the water column (i.e. suspended solids). Bivalves capture fish waste directly by removing feed-derived POM (i.e. fish faeces and feed fines), and also indirectly by removing plankton that has grown on feed-derived inorganic waste.[31] The degree of system openness determines the importance of these two different waste flows. Closed systems, and to a lesser extent semi-open systems, provide opportunities to manage waste flows towards either direct or indirect fractions. For example, microalgae can be cultivated on inorganic waste nutrients in separate cultivation units, before being fed to bivalves.[55,56] In open systems, and the majority of semi-open systems, flows cannot be controlled and direct and indirect mitigation are intertwined. Bivalves prefer plankton to fish feed-derived POM,[31,41] with the different waste flows influencing their bioremediation potential, for example by differences in removal rate (Appendix Table S3). Lefebvre et al.[31] showed that AE of oysters (*Crassostrea gigas*) fed with a phytoplankton diet was higher (66%) than when fed feed-derived POM (56%). Results are less conclusive for mussels; Reid et al.[57] reported comparable AE for *Mytilus edulis* and *M. trossulus* fed salmon feed, salmon faeces or algae diets; whilst based on growth and fatty acid profiles, Handå[41] showed that *M. edulis* assimilated and utilised salmon feed more efficiently than salmon faeces.

Studies using either the retention or the balance method to define the bioremediation potential of bivalves in IMTA are summarised in Appendix Table S4. The majority of these studies used the retention method and show contradictory results. These contradictory results might be explained by differences in ambient food quality and quantity between these studies; in open systems, located in areas or during seasons of low ambient food concentration or quality (i.e. organic content), integration of bivalves with fish cultures can improve growth and bivalve quality (e.g. condition index) (e.g. Peharda et al.[58]; Handå et al.[59]; Appendix Table S4), whilst in areas, or during seasons, of high ambient food concentrations, no enhancement of growth or improved quality was observed (e.g. Peharda et al.[58]; Navarrete-Mier et al.[60]; Handå et al.[59]; Appendix Table S4). In semi-open systems, positive effects on bivalve growth were observed when cultivated on phytoplankton grown on inorganic waste (i.e. fish-microalgae-bivalves), or on a mix of uneaten feed, faeces and phytoplankton (e.g. Shpigel and Blaylock[61]; Jara-Jara et al.[62]; Jones et al.[49]; Appendix Table S4).

The balance method was mostly applied to closed systems, to calculate bivalve waste extraction efficiencies. Bivalves extracted up to 23% organic matter (OM), up to 33% organic N, up to 96% chlorophyll-*a*, up to 88% suspended solids and up to 88% bacteria biomass, when cultivated in effluents of fish or shrimp cultures. In a fish-microalgae-bivalve system, 100% of the microalgae were taken up by the bivalves, whereby the microalgae assimilated 67% of TAN-N and 47% of PO_4-P released by the fish.[55] It can be estimated that by feeding on these microalgae, bivalves retained 58% of TAN-N and 41% of PO_4-P excreted by the fish, if an AE of 87% is assumed for the bivalves (Appendix Table S3).

Tracer studies were applied in open water IMTA systems. Results varied; whilst in some studies aquaculture waste was the main food source, in others food uptake was dominated by ambient plankton (Figure 2). Cultivation area and seasons partially explain these differences.[63,64] For example, in the study of Mazzola and Sarà,[63] phytoplankton made up 5% to 100% of the total diet of *Mytilus galloprovinciales* in an open water IMTA system, the percentage varying according to the season. This indicates that the role of bivalves in organic fish waste bioremediation may vary with the seasons. Most tracer studies showed that uneaten fish feed contributed more to the total diet than fish faeces (Figure 2, Handå[41]). None of the studies in open water IMTA reported if phytoplankton taken up by the bivalves grew on waste or ambient nutrients.

3.2.3 | Sea cucumbers or polychaetes

Deposit feeders, like sea cucumbers and polychaetes, are included in IMTA to remove settled POM. Although often mentioned as candidate species in IMTA systems (e.g. Soto[15]; Chopin et al.[10]), sea cucumbers and polychaetes are not that frequently studied, compared with seaweeds and bivalves.[15] Data collected on the bioremediation potential of sea cucumbers and polychaetes in IMTA are summarised in Appendix Table S3 (removal rate) and Appendix Table S5 (retention and balance studies). These results show that responses of sea cucumbers and polychaetes to aquaculture waste vary between studies. Species, experimental set-up and waste composition contribute to these reported variations.

Removal rate studies for sea cucumbers fed aquaculture waste reported an increase in consumption rate with decreasing substrate OM,[65,66] which reflects compensatory feeding, commonly observed in deposit feeders when (high quality) food is scarce.[67] Low substrate OM is further compensated by more active selection of OM particles.[32,68,69] Both compensatory feeding and active selection result in reworking of surface sediments, affecting sediment ecosystems by reallocation of resources and altering geochemical gradients and nutrient fluxes.[70] This bioturbation by deposit feeders facilitates decomposition of OM in sediments, thereby increasing the net effect on bioremediation of organic waste.[70] The assimilation efficiencies reported for sea cucumbers in integrated systems are highly variable and range from 14% to 88%.

Studies based on the retention method show contrasting results for sea cucumbers in open and semi-open integrated systems. Increased growth was observed for sea cucumbers integrated with fish or bivalves, whilst integration with shrimp was less successful.

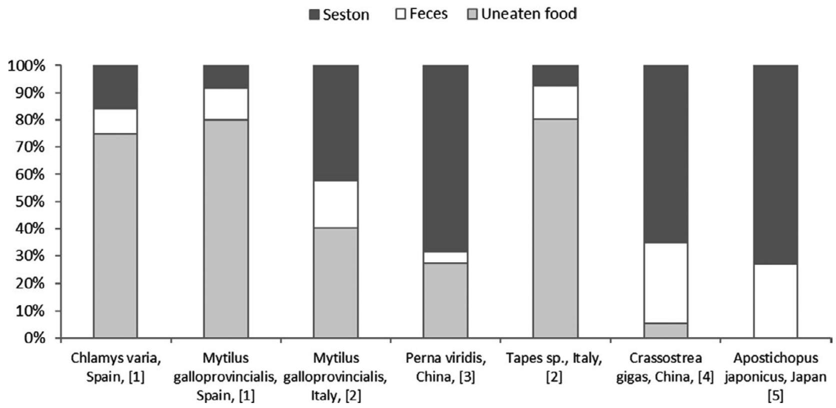

FIGURE 2 Contribution of food sources to the dietary consumption of bivalves and sea cucumbers in open water IMTA systems. Values are based on average stable isotope results from the corresponding papers. 1. Deudero et al.[64]; 2. Mazzola and Sarà[63]; 3. Gao et al.[152]; 4. Jiang et al.[35]; and 5. Yokoyama[42]

Less growth and higher mortality are reported in shrimp-sea cucumber cultures, compared with sea cucumber monocultures, likely due to the high TAN excreted by the shrimp.[71,72] Nevertheless, in a feeding trial, lowest growth was reported when *Stichopus monotuberculatus* was fed only waste from a shrimp farm, compared with a commercial sea cucumber diet or a mixed diet of 50% waste from the shrimp farm and 50% sea mud.[73]

Only a limited number of studies used the balance method to determine waste extraction efficiencies, and they do show that sea cucumbers reduce aquaculture waste. Sea cucumbers can extract 0.1%–20% OM, 3%–10% organic C, 7%–16% organic N and 21%–25% organic P from the aquaculture waste fed directly or from sediments enriched with aquaculture waste. No studies were found quantifying waste extraction efficiencies by sea cucumbers in open systems, but tracer studies indicate that also in open water IMTA, sea cucumbers do assimilate aquaculture waste nutrients.[42,74,75] Yokohama [42] estimated that when cultivated close to fish cages, the diet of *Apostichopus japonicus* consisted for 27% of nutrients from aquaculture origin (Figure 2).

In a similar way to sea cucumbers, AE reported for polychaetes in integrated systems is highly variable, ranging between 24% and 71%. The retention method was mainly used for polychaetes in closed integrated systems. These studies show that polychaetes survive and grow on aquaculture waste, but growth is lower compared with polychaetes fed a commercial worm diet, which contains more protein and energy. There are, however, indications that fish waste can improve fatty acid profiles of polychaetes, making them interesting marine resources.[76-81]

Balance studies reported waste extraction efficiencies for polychaetes, which were higher compared with sea cucumbers; 20%–85% OM, 40%–91% organic C and 30%–91% organic N of the aquaculture waste fed. Also for polychaetes, balance studies in open water IMTA are scarce. Nevertheless, Tsutsumi et al.[82] and Kinoshita et al.[83] showed that mass cultivation of *Capitella* sp. significantly reduced OM levels in sediments underneath fish farms or in fish ponds.

3.3 | Waste retention in IMTA; creating a balance

A key aspect of the bioremediation potential of IMTA is the balance between nutrient input and removal. The latter can be estimated by quantifying the nutrients retained in biomass gain of fed and extractive species. This was done for our conceptual four-species IMTA presented in sections 3.1 and 3.2, assuming that only fed nutrients contribute to biomass gain of IMTA species and species perform at their reported optimum. Salmon was chosen as the fed species, and the starting point was the input of 1 tonne of salmon feed (wet weight), for which the N, P and C waste production was calculated. The solid organic waste fraction was separated into 30% suspended solids consumed by bivalves and 70% settled solids consumed by deposit feeders.[29] For the autotrophic species, kelp and microalgae were chosen and it was assumed that inorganic waste nutrients were incorporated in the tissue, according to the Atkinson ratio for seaweed[84] or the Redfield ratio for microalgae.[85] An additional assumption made was that inorganic C was non-limiting, due to the exchange between the atmosphere and surface water. For the invertebrates, assimilated nutrients were calculated based on AE, with the highest values reported in literature for mussels and polychaetes. Bivalves were included, to directly remove feed-derived POM (i.e. faeces and feed fines); however, as they are also capable of removing microalgae grown on feed-derived inorganic waste nutrients, this scenario (salmon–microalgae and mussel–mussel–polychaete IMTA; Scenario B, Figure 3) was included as an alternative to the salmon–kelp–mussel–polychaete IMTA (Scenario A, Figure 3). It was thereby assumed that all microalgae could be filtered by the bivalves and nutrient assimilation was calculated based on AE.

Data used in the mass balance calculations, with references, are reported in Table 1, whilst the resulting IMTA mass balances for nitrogen, phosphorous and carbon are shown in Figure 3. Under these assumptions, the conceptual salmon–kelp–mussel–polychaete IMTA retains 94% N, 79% P and 94% C provided by the input of fish feed (Scenario A, Figure 3). Scenario B, where seaweeds are replaced with a microalgae–bivalve combination, reduces the maximum retention efficiency to 78% N and 89% C and increases the P retention efficiency to 81% (Scenario B, Figure 3).

4 | FACTORS AFFECTING NUTRIENT RETENTION EFFICIENCIES

The nutrient retention efficiencies calculated for the conceptual IMTA in section 3.3 demonstrate the theoretical retention potential presented in Figure 3 and is referred to as step 1 in the generic framework (Figure 1). In practice, however, various factors limit retention efficiencies of extractive species and thereby influence the bioremediation potential of IMTA systems. Biological limiting factors are grouped under step 2 in the generic framework and reduce the theoretical retention potential to what can be realised in a “closed IMTA system”. Environmental limiting factors are grouped under step 3 in the generic framework and reduce the retention potential further to what can be realised in an “open water IMTA” (Figure 1). How biological and environmental limiting factors restrict the theoretical nutrient retention potential in IMTA is described in more detail below and summarised in Table 2.

4.1 | Biological factors

Biological factors are independent of system openness and are influenced by waste quality and the physiological responses of extractive species feeding on waste nutrients.

4.1.1 | DOM

None of the species included in our conceptual IMTA extracts DOM, resulting in a small non-retained fraction of 3% N, 8% P and 3% C

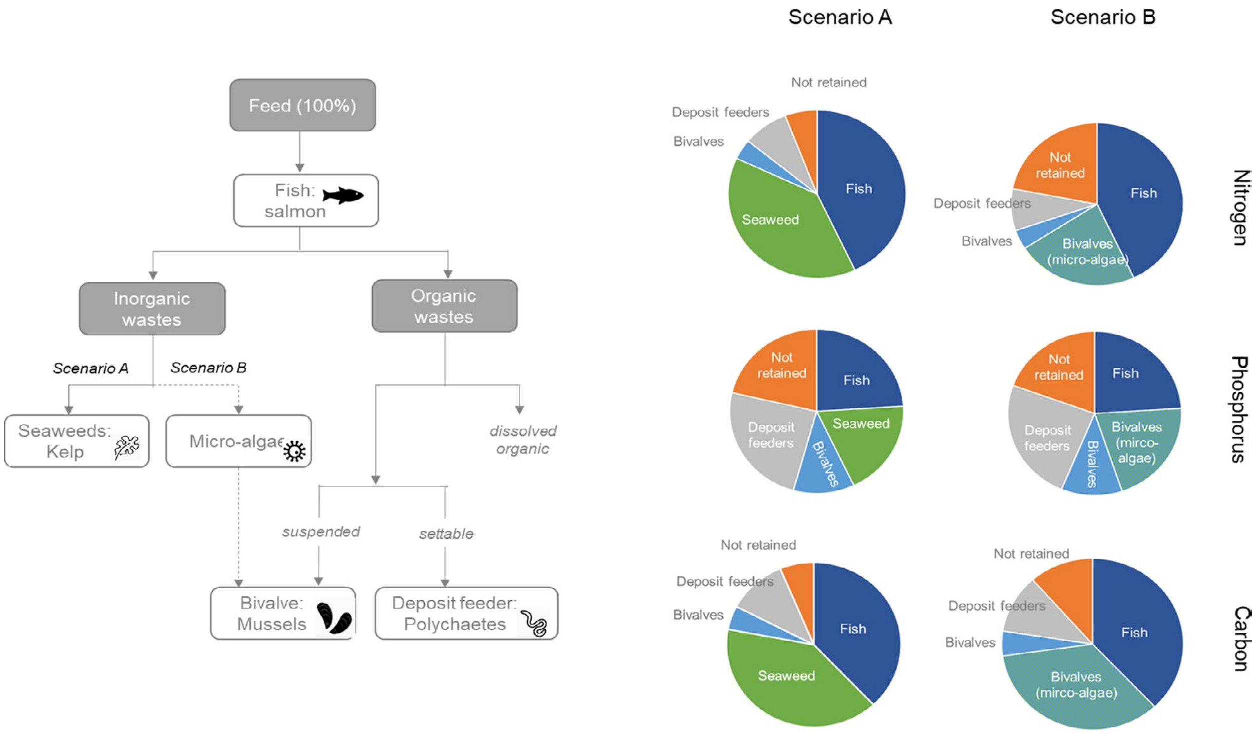

FIGURE 3 Nitrogen, phosphorus and carbon balance of a conceptual four-species IMTA system, indicating the theoretical retention potential (Figure 1). Starting point for the balance was a commercial salmon farm, fed 1 tonne of commercial feed. The following assumptions were made: (1) ambient nutrients are absent, (2) extractive species capture and ingest all of their target waste nutrients and (3) extractive species show optimal performance, that is, highest assimilation efficiencies reported in literature. For *the inorganic waste stream*, two different conversion pathway scenarios were suggested: Scenario A) uptake by seaweeds resulting in a "salmon–kelp–mussel–polychaete" IMTA and Scenario B) uptake by microalgae, which in turn can be assimilated by bivalves, resulting in a "salmon–microalgae and mussel–mussel–polychaete" IMTA. *The organic solid waste stream* was divided in two fractions: 30% was assumed to be suspended and available for bivalves, whilst 70% was assumed to settle on the sediment where they are available for deposit feeders. Pie charts are based on a mass-balance approach (calculations not shown). Data were collected from the literature and referred to in Table 1

(Figure 3, Table 2). Marine DOM represents the largest ocean reservoir of reduced carbon, and due to its key role in the global carbon cycle, the role of DOM in marine ecosystems has been studied extensively.[86-88] Although microbes play a role in the reduction in aquaculture-derived DOM,[89,90] an increase in microbial biomass may contribute to the microbialisation of marine ecosystems.[91,92] Only a few studies, mainly on sponges, looked into DOM removal and use efficiency.[93-95] Analysis of their role in the overall bioremediation potential of IMTA systems is still in its infancy, but all studies indicate that sponges can benefit from cultivation in an IMTA setting.[94,96]

4.1.2 | Extractive species waste production

In our conceptual model, maximum AE data reported for invertebrates were applied to estimate nutrient assimilation. This shows that only a small nutrient fraction was not retained, due to the combined faeces production by bivalves and deposit feeders feeding on organic waste (3%–6% N, 8%–18% P and 3%–5% C; Table 2). In addition, metabolic waste produced by the extractive species should be considered (Table 2). This was estimated as 60%–80% loss of assimilated C as inorganic C through respiration; 10%–75% of assimilated N excreted as inorganic N; and 65% of assimilated P excreted as inorganic P (mussels, Jansen[97] and Filgueira et al.[98]; polychaetes, Honda and Kikuchi[99] and Fang et al.[100]; sea cucumber, Yuan et al.[101]). No study reported a P budget for deposit feeders. The excreted and respired nutrients could serve as an additional nutrient source for autotrophs. In open water systems, it is expected that these inorganic nutrients dilute and disperse quickly or are taken up by autotrophs,[102] whilst in closed systems they will accumulate.

A specific characteristic of bivalves is their pre-ingestive selection of food particles, which occurs above a pseudofaeces threshold concentration of 3–5 mg SPM l^{-1} for the mussel *M. edulis* [103] and 10 mg SPM l^{-1} for the oyster *Crassostrea virginica*.[104] Oysters reject fish faeces as pseudofaeces when a mixed diet of faeces and microalgae is offered, indicating that faeces is not a preferable food source.[31] This has consequences for the bioremediation potential of bivalves in systems with ambient and waste nutrients present, that is, open and semi-open systems (Table 2). In open systems, it will depend on the location if threshold concentrations are reached; SPM concentrations in and around fish cages in Canada and the Mediterranean were occasionally above the threshold level,[105,106] whilst in a study in Norway threshold concentrations were not reached.[106] For semi-open systems,

TABLE 1 Non-retained nutrients (i.e. waste) from salmon culture and maximum responses of extractive species to fish waste, as reported in literature

		Nitrogen		Phosphorus		Carbon	
Parameter	**Unit**	**Value**	**Ref.**	**Value**	**Ref.**	**Value**	**Ref.**
Fed species (salmon)							
Input (feed)							
DM	%	98	138	98	138	98	138
Nutrient composition	% of DM	5.8	138	0.88	138	54	138
Retention (fish biomass)							
Nutrient retention	% of input	43	138	24	138	38	138
Output (waste)							
Inorganic	% of input	39	138	24	138	40	138
Organic_total	% of input	18	138	52	138	21	138
Organic_dissolved	% of input	3	138	8	138	3	138
Organic_solids	% of input	15	138	44	138	18	138
Organic_suspended solids	% of organic_solids	30	29	30	29	30	29
Organic_settled solids	% of organic_solids	70	29	70	29	70	29
Extractive species							
Seaweed							
DM content	%	12	122	12	122	12	122
Nutrient composition	% of DM	5	139	0.51	122	40	51
Bivalves							
Microalgae							
DM content	%	22	140	22	140	22	140
Nutrient composition	% of DM	9	141	1	142	36	141
Bivalves							
DM_mussels	%	25	5	25	5	25	5
DM_oysters	%	13	31	13	31	13	31
Nutrient composition_mussel	% of DM	11	143	1.2	144	37	121
Nutrient composition_oyster	% of DM	8	153	0.8	113	46	113
AE_mussel_phytoplankton	%	87	57	87	57	87	57
AE_oyster_phytoplankton	%	66	31	66	31	66	31
AE_mussel_faeces	%	86	57	86	57	86	57
AE_oyster_faeces	%	56	31	56	31	56	31
Deposit feeders							
DM_sea cucumber	%	8	145	8	145	8	145
DM_polychaete[a]	%	8	145	8	145	8	145
Nutrient composition_sea cucumber	% of DM	7	145	NI		31	146
Nutrient composition_polychaete	% of DM	10	78	NI		49	81
AE_sea cucumber_faeces	%	62	147	60	147	88	148
AE_polychaete_faeces	%	79	99	79[b]	33	79	33

Note: DM, dry matter; AE, assimilation efficiency; NI, No Information.

[a] No info available for polychaetes; therefore, the same data were used as for sea cucumbers.

[b] No data available for phosphorus assimilation efficiency; therefore, the same data were used as for nitrogen and carbon efficiency.

concentrations above the threshold have been reported (e.g. Jones et al.[38]), but threshold concentrations can be avoided by adjusting the water flow.

In our conceptual IMTA, we assumed that inorganic waste nutrients were retained in seaweed biomass, according to the Atkinson ratio. However, seaweeds do also release organic material as metabolic

TABLE 2 Potential limitations influencing the maximum nutrient retention efficiency of IMTA systems varying in openness (open, semi-open and closed systems)

				System			
Factor	**Extractive species**	**Description**	**Nutrient**	**Open**	**Semi-open**	**Closed**	**References**
Biological factors							
4.1.1 Non-retained DOM	None	No DON uptake[a] (*o*)	N	3	3	3	Wang et al.[138]
		No DOP uptake[a] (*o*)	P	8	8	8	Wang et al.[138]
		No DOC uptake[a] (*o*)	C	3	3	3	Wang et al.[138]
4.1.2 Extractive species waste production	Seaweed	PON release (*o*)	N	16–21	16–21	16–21	Zhang et al.[111]
			P	Unknown	Unknown	Unknown	
		POC release (*o*)	C	0.4–24	0.4–24	0.4–24	Wada et al.[110], Zhang et al.[111]
		DOC release (*o*)		7–25	7–25	7–25	Wada et al.[110]
	Bivalves_inorganic	Faeces production[a] (*o*)	N	NA	3–9	3–9	Lefebvre et al.[31], Reid et al.[57]
		Excretion (*i*)			6–8	6–8	Jansen[97]
		Pseudofaeces production (*o*)			Location dependent	NA	
		Faeces production[a] (*o*)	P	NA	3–8	3–8	Lefebvre et al.[31], Reid et al.[57]
		Excretion (*i*)			11–14	11–14	Jansen[97]
		Pseudofaeces production (*o*)			Location dependent	NA	
		Faeces production[a] (*o*)	C	NA	5–14	5–14	Lefebvre et al.[31], Reid et al.[57]
		Respiration (*i*)			21–27	21–27	Jansen[97], Filgueira et al.[98]
		Pseudofaeces production (*o*)			Location dependent	NA	
	Bivalves_organic	Faeces production[a] (*o*)	N	1–2	1–2	1–2	Lefebvre et al.[31], Reid et al.[57]
		Excretion (*i*)		1	1	1	Jansen[97]
		Pseudofaeces production (*o*)		Location dependent	Location dependent	NA	
		Faeces production[a] (*o*)	P	2–6	2–6	2–6	Lefebvre et al.[31], Reid et al.[57]
		Excretion (*i*)		5–8	5–8	5–8	Jansen[97]
		Pseudofaeces production (*o*)		Location dependent	Location dependent	NA	
		Faeces production[a] (*o*)	C	1–2	1–2	1–2	Lefebvre et al.[31], Reid et al.[57]
		Respiration (*i*)		2–4	2–4	2–4	Jansen[97], Filgueira et al.[98]
		Pseudofaeces production (*o*)		Location dependent	Location dependent	NA	
	Deposit feeder	Faeces production[a] (*o*)	N	2–4	2–4	2–4	Honda and Kikuchi[99], Hannah et al.[148]
		Excretion (*i*)		1–5	1–5	1–5	Honda and Kikuchi[99], Yuan et al.[101], Fang et al.[100]
		Faeces production[a] (*o*)	P	6–12	6–12	6–12	Hannah et al.[148], Fang et al.[100]
		Excretion (*i*)		Unknown	Unknown	Unknown	
		Faeces production[a] (*o*)	C	2–3	2–3	2–3	Maxwell et al.[149], Fang et al.[100]
		Respiration (*i*)		6–9	6–9	6–9	Yuan et al.[101], Fang et al.[100]

(Continues)

TABLE 2 (Continued)

Factor	Extractive species	Description	Nutrient	System			References
				Open	Semi-open	Closed	
4.1.3 Waste quality	Seaweed	Stoichiometry[b] (*i*)	P	Location dependent	Location dependent	5	Atkinson and Smith[84]
	Microalgae	Stoichiometry[c] (*i*)	N	NA	Location dependent	13	Redfield et al.[85]
	Bivalves_organic	Stoichiometry[d] (*i*)	P	Location dependent	Location dependent	10–11	Higgins et al.[113], Jansen et al.[150]
			C	Location dependent	Location dependent	3	Higgins et al.[113], Jansen et al.[150]
	Deposit feeder		N, P, C	Location dependent	Location dependent	Unknown	
Environmental factors							
4.2.1 Capture efficiency	Bivalves_organic	Particle size range (*o*)	N	Unknown	0	0	Cripps[119], Brinker and Rösch[120]
		Exposure time[e] (*o*)		1	NA	NA	Cranford et al.[20]
		Particle size range (*o*)	P	Unknown	0	0	Cripps[119], Brinker and Rösch[120]
		Exposure time[e] (*o*)		3	NA	NA	Cranford et al.[20]
		Particle size range (*o*)	C	Unknown	0	0	Cripps[119], Brinker and Rösch[120]
		Exposure time[e] (*o*)		1	NA	NA	Cranford et al.[20]
4.2.2 Ambient nutrients	Bivalves_organic	AE mixed diet[f] (*o*)	N	2	2	NA	Reid et al.[57]
		Food preference (*o*)		Unknown	Unknown	NA	Lefebvre et al.[31], Handå[41]
		AE mixed diet[f] (*o*)	P	6	6	NA	Reid et al.[57]
		Food preference (*o*)		Unknown	Unknown	NA	Lefebvre et al.[31], Handå[41]
		AE mixed diet[f] (*o*)	C	2	2	NA	Reid et al.[57]
		Food preference (*o*)		Unknown	Unknown	NA	Lefebvre et al.[31], Handå[41]
	Deposit feeder	AE mixed diet[f] (*o*)	N	6	6	NA	Fang et al.[33]
		Food preference (*o*)		Unknown	Unknown	NA	
		AE mixed diet[f] (*o*)	P	18	18	NA	Fang et al.[33]
		Food preference (*o*)		Unknown	Unknown	NA	
		AE mixed diet[f] (*o*)	C	8	8	NA	Fang et al.[33]
		Food preference (*o*)		Unknown	Unknown	NA	
4.2.3 Temporal issues	Seaweed	Seasonal mismatch[g] (*i*)	N	18	18	NA	Broch et al.[123]
		Seasonal mismatch[g] (*i*)	P	6	6	NA	Broch et al.[123]
		Seasonal mismatch[g] (*i*)	C	19	19	NA	Broch et al.[123]
	Deposit feeder	Seasonal mismatch[h] (*i*)	N	5	5	NA	Ren et al.[125]
		Seasonal mismatch[h] (*i*)	P	15	15	NA	Ren et al.[125]
		Seasonal mismatch[h] (*i*)	C	6	6	NA	Ren et al.[125]

TABLE 2 (Continued)

Factor	Extractive species	Description	Nutrient	System Open	 Semi-open	 Closed	References
4.2.4 Spatial issues	Seaweed	Spatial arrangement[i] (*i*)	N	20	NA	NA	
		Spatial arrangement[i] (*i*)	P	7	NA	NA	
		Spatial arrangement[i] (*i*)	C	20	NA	NA	
	Bivalves_organic	Spatial arrangement[i] (*o*)	N	2	NA	NA	
		Spatial arrangement[i] (*o*)	P	7	NA	NA	
		Spatial arrangement[i] (*o*)	C	3	NA	NA	

[a] See also Figure 3.

[b] Based on the Atkinson ratio 550:30:1 (C:N:P, molar).

[c] Based on the Redfield ratio 106:16:1 (C:N:P, molar), for microalgae.

[d] Based on an average tissue content for mussels of 161:34:1 (C:N:P, molar) and an average tissue content for oysters of 140:21:1 (C:N:P, molar).

[e] Under the assumption of a current of 8 cm/s, and 100,000 mussels.

[f] Mixed diet; diet composed of fish waste nutrients and low-quality ambient nutrients.

[g] Based on the integration of the kelp species *Saccharina latissima* with salmon in temperate region.

[h] Based on the integration of the sea cucumber *Apostichopus japonicus* with salmon.

[i] Based on an area where tidal currents dominate and extractive species are placed on one side of the fish cage.

products.[107] It is estimated that 18%–62% of their primary production is released as dissolved organic carbon (DOC).[108-110] Additionally, POM is released as a result of three processes: (1) fall-off, whereby a whole individual is lost; (2) break-off, whereby part of the thallus is lost; and (3) distal erosion, whereby leaf tops erode.[111] Estimates on POM release vary; whilst Wada et al.[110] reported that 1%–13% of the primary production of the brown seaweed *Ecklonia cava* is released as particulate organic carbon (POC), Zhang et al.[111] reported that kelp (*Saccharina japonica*) releases 45%–61% and 41%–54% of its primary production as POC and particulate organic nitrogen (PON), respectively. The release of DOC results in a non-retained fraction of 7%–25% C, whilst the release of POM results in a non-retained fraction of 16%–21% N and 0.4%–24% C (Table 2). It should be noted that seaweeds are inorganic extractive species, but their non-retained fraction contributes to the organic nutrient pool in the (eco)system.

4.1.3 | Waste quality

The majority of studies summarised in *section 3* focus on a single element, but organisms require nutrients in balanced amounts (i.e. stoichiometry) to sustain optimal growth and functioning.[112] In our conceptual IMTA, the Atkinson ratio for seaweeds and the Redfield ratio for microalgae were compared with the C:N:P molar ratio of the inorganic waste fraction (264:24:1), indicating P limitation for microalgae and C and N limitation for seaweeds. Assuming a large enough surface area, C limitation is most likely prevented by carbon exchange between the atmosphere and surface water (carbon cycle) and instead N becomes most limiting for seaweeds. The imbalance of inorganic nutrients in fish waste results in an overall non-retained fraction of 5% P by seaweeds, or 13% N by microalgae, in closed systems. In open and semi-open systems, the presence of ambient nutrients plays a role in the stoichiometry of the available nutrients; therefore, the first limiting nutrient will be location dependent (Table 2). The molar ratio of the organic waste fraction in our conceptual IMTA is 65:5:1 (C:N:P), for both the suspended and settled solids. Jansen[97] reported for the mussel *M. edulis* an average tissue C:N:P ratio of 173:35:1, whilst for oysters an average tissue C:N:P ratio of 140:21:1 was reported by.[113] These ratios suggest that for bivalves N is the first limiting nutrient in organic fish waste, resulting in a non-retained fraction of 10%–11% P and 3% C (Table 2). No information was found on tissue C:N:P ratios of sea cucumbers and polychaetes, and it remains unclear to what extent macronutrient composition of organic fish waste is balanced for deposit feeders. For both sea cucumbers and polychaetes, lower growth has been reported when feeding fish faeces, as compared with commercial diets,[73,78,99] suggesting that waste quality is not sufficient to sustain optimal growth. For mussels, it has also been suggested that fish faeces alone is insufficient; integration of *M. edulis* with Atlantic cod in a closed system resulted in nutritionally stressed mussels.[114] The presence of ambient nutrients in open and semi-open systems may overcome these limitations that are potentially faced in closed systems for bivalves and deposit feeders.

4.2 | Environmental factors

Environmental factors influence the connectivity between waste nutrients and the extractive species. For closed systems, it is assumed that this connectivity is optimal, and these factors are therefore more relevant for open and semi-open systems.

4.2.1 | Capture efficiency

The capture efficiency of bivalves depends on particle size and exposure time.[20,115] To be captured, waste particles should fall within a species-specific size range[115]; the mussel *M. edulis* efficiently filters particles between 3 and 1000 µm[116,117]; the oyster *C. gigas* efficiently filters particles between 5 and 541 µm.[118] Little is known about the fraction of waste particles that fall within the bivalve filtering size ranges.[115] Studies on waste particle sizes in land-based fish farms reported ranges between 8–269 µm (salmonid hatchery[119]) and 8–512 µm (trout farm[120]) for the suspended solids. It is therefore suggested that in land-based systems, all waste particles available for bivalves (i.e. suspended solids; 30% of POM, section 3.3) fall within the filtering size ranges of both mussels and oysters and result in 0% non-retained nutrient loss (Table 2). For open water systems, information is lacking on the fraction of waste particles that fall within the filtering size range of bivalves, and it remains unknown to what extent this factor should be taken into account (Table 2).

Capture efficiency is also influenced by exposure time. Whilst in land-based systems exposure time can be controlled, in open water systems this depends on the current. Cranford et al.[20] calculated the capture efficiencies for a cultivation unit of mussels for a range of current speeds and highlighted that exposure time (e.g. current) can seriously limit capture efficiency. In our conceptual model, 5% of carbon supplied with fish feed is retained in mussel biomass (Figure 3). This corresponds to a biomass of 100,000 mussels, with an assumed C content of 37% on a dry weight basis (Smaal & Vonck[121]; Table 1) and an average individual dry weight, without shell, of 0.7 g.[20] Based on Cranford et al.,[20] however, it was estimated that in areas with current speeds of 8 cm s^{-1}, these mussels can only capture 80% of the suspended waste particles. In consequence, 20% of the suspended waste particles will be non-retained. Expressed as percentage of the total fish feed input to the system, this corresponds to a non-retained fraction of 1% N, 3% P and 1% C (Table 2).

4.2.2 | Ambient nutrients

In open and semi-open systems, water exchange imports ambient nutrients into the system, whilst waste nutrients are exported. Ambient nutrients are assumed to affect the bioremediation potential of open and semi-open IMTA systems, as they compete with waste nutrients in concentration and quality. For autotrophs, it can be argued whether or not the presence of ambient nutrients influences their bioremediation capacity, since most likely inorganic N, P and C released by fish do not differ from their ambient counterparts. “Direct uptake” of waste nutrients is therefore not of principal interest for inorganic extractive species, and instead a balance between nutrient inputs and outputs should be created.[122]

Quality differences between waste and ambient POM may influence the bioremediation potential of bivalves and deposit feeders, as low-quality ambient POM can reduce AE. Reid et al.[57] observed that resuspension events and periodic fluxes of low-quality food resulted in a lower AE for mussels cultivated adjacent to salmon cages in the field (54%), compared with mussels fed salmon faeces in the laboratory (86%) (Appendix Table S3). Fang et al.[33] showed that polychaetes fed sediment collected underneath a fish farm had a lower AE (~40%), compared with polychaetes fed deposited material collected from sediment traps deployed in the centre of a fish farm (~60%) (Appendix Table S3). Deposited material consisted mainly of fresh faeces and feed spills, whilst sediment is a mix of fresh and decomposing faeces and microbial communities. The latter is more likely to represent a diet that can be expected in open and semi-open systems. In open and semi-open systems located in areas with (periodically) low-quality ambient nutrients, retention efficiencies of mussels and polychaetes are thus expected to decrease, due to a reduced AE from 86% to 54% for mussels and from 79% to 40% for polychaetes. Mixed diets composed of fish waste nutrients and low-quality ambient nutrients thus increase the total non-retained fraction (Table 2). High-quality ambient POM may also reduce bioremediation potential, as a result of food preferences. Bivalves prefer, for example, plankton over fish feed-derived POM.[31,41] In areas with high-quality ambient food sources, it can therefore be expected that bioremediation potential of bivalves is lower than in our conceptual IMTA; however, exact quantification will depend on local factors, like the ratio and quality difference between ambient and waste POM (Table 2). It should be noted that plankton taken up by bivalves can (partially) be grown on inorganic fish waste, contributing indirectly to the bioremediation capacity of bivalves in open and semi-open systems. For polychaetes and sea cucumbers, no studies were found looking at potential preferences for either ambient food sources encountered at fish farms or fish feed-derived POM, and it remains unknown to what extent this should be taken into account (Table 2).

4.2.3 | Temporal issues

For specific combinations of fed and extractive species, seasonal factors can result in a “mismatch” between nutrient release and uptake. Broch et al.[123] described such a mismatch between integration of the kelp species *Saccharina latissima*, with salmon in an open water system located in a temperate region. Uptake rates of kelp peak during spring, whilst due to the start of distal erosion, kelp is harvested in early to mid-summer.[124] Waste production by salmon fluctuates seasonally, and highest release rates are at the end of the summer, when kelp is already harvested. Based on the model presented by Broch et al.[123] it was estimated that 53% of the waste nutrients are released during the kelp growth cycle, suggesting that nearly half of the inorganic nutrients are non-retained. This results in a non-retained fraction of 18% N, 6% P and 19% C of the total amount fed to the system (Table 2). To survive high and low temperatures, various sea cucumber species undergo aestivation, hibernation or both.[125,126] *Apostichopus japonicus* stops feeding during winter and summer,[125] resulting in a mismatch between the highest waste release by the fed species during summer. Ren et al.[125] indeed observed that in pond systems where *A. japonicus* was integrated with scallops (*Chlamys farreri*), both organic C and total N content of the sediment increased during hibernation and aestivation but decreased during sea cucumber feeding seasons. Based on the salmon waste production cycle presented in Broch et al.,[123] and the aestivation (July–September) and hibernation (October–December) period reported in Ren et al.,[125] it was estimated that only 50% of the waste nutrients are released during the feeding season of *A. japonicus* (Table 2). Both cases demonstrate that temporal issues can limit maximum waste retention in open and semi-open systems, but it should be noted that this is highly species and location specific.

4.2.4 | Spatial design

Integration of extractive species to fish cultures has practical implications, such as a requirement for a greater farm area. Extractive species biomass and corresponding cultivation areas were calculated for our conceptual IMTA and are reported in Table 3. Upscaling to a commercial salmon farm (production of ~1800 tonnes over a 2-year cycle and an average Feed Conversion Ratio (FCR) of 1.1) would in the best case scenario require (i) 47 ha seaweed, (ii) 12 ha bivalves and (iii) 237 ha deposit feeders, assuming that extractive species are harvested yearly. Studies modelling the seaweed and bivalve compartment in open water IMTA already highlighted that large areas are required,[34,122,123,127] which has major implications for the spatial design of IMTA systems. Addition of extractive species to land-based fish farms will increase pressure on space. Whilst closed and semi-open systems can be designed to optimise connectivity between waste and the extractive species, in open systems the spatial arrangement determines connectivity. When tidal currents dominate, and seaweed and bivalve cultivation are placed on one side of the fish cages, they are only exposed to waste nutrients 50% of the time, increasing the non-retained fraction of the overall IMTA system (Table 2). In reality, waste exposure time will probably be higher, as some suspended nutrients will oscillate around the farm. Deposit feeders should be cultivated underneath fish cages, within the farm scale, as their target waste flux settles relatively nearby, resulting in local impacts.[128] In shallow areas (< 20-m depth) farm scale could mean within 30 m from the cages, as this is where most organic waste accumulation is observed,[129,130] whilst for farms located in deeper areas, like fjords, this area is expanded and could reach up to 500 m from the farm.[131] With the trend of moving fish farms to deeper and more exposed locations, it is expected that the affected benthic area becomes larger.[132]

TABLE 3 Scaling of a conceptual four-species IMTA system; biomass (tonnes wet weight) and area (m^2) required per extractive species for maximum retention of waste (salmon farm fed 1 tonne of commercial feed)

Extractive compartment		Biomass (tonnes wet weight)	Area (m^2)
Seaweed	N	4–23	389–23091
	P	3–18	356–15680
	C	4-8	465–7571
Microalgae +bivalves			
Microalgae	N	1–10	4073–36653
	P	1	2852
	C	3–4	9722–14000
Mussels	N	0.7–0.9	96–357
	P	0.6–1	76–381
	C	2	737
Oysters	N	1.3–1.5	268–304
	P	1.3–1.5	263–300
	C	2–3	467–500
Mussels	N	0.08–0.11	11–41
	P	0.3–0.6	42–207
	C	0.3	98
Oysters	N	0.13–0.15	26–30
	P	0.6–0.7	123–140
	C	0.3	54
Sea cucumber	N	0.7–0.9	664–930
	P	ND	ND
	C	2–3	2366–2821
Polychaete	N	0.6–1	1842–3542
	P	ND	ND
	C	1–3	4225–9526

Note: Biomass per extractive species is calculated based on assimilation efficiencies (AE) and tissue contents reported in literature. Data for these calculations can be found in Table 1. Area per extractive species is calculated based on the following stocking densities: 95 tonnes ha^{-1} for seaweeds,[122] 3 tonnes ha^{-1} for microalgae,[142] 76 tonnes ha^{-1} for mussels,[18] 50 tonnes ha^{-1} for oysters,[150] 10 tonnes ha^{-1} for sea cucumbers[151] and 3 tonnes ha^{-1} for polychaetes.[78] ND, not determined.

Dispersal of organic waste particles in open water systems is dominated by a vertical flux, and only a small fraction ends up in the horizontal flux.[115,128,131] The latter is supported by field studies, indicating only minimal and temporal enhancement of suspended particles in the water column around fish farms.[106,133] Given that mussels in open water systems are mostly cultivated in surface waters (up to 13 m), their exposure is only to a minor fraction of the organic waste,[20,128] suggesting that the 30% of POM available as suspended solids for the bivalves in our conceptual IMTA is an overestimation. In addition, due to biodeposition, mussels contribute to the already dominant vertical particle flux, increasing local benthic impact.[20] The bioremediation potential of mussels in

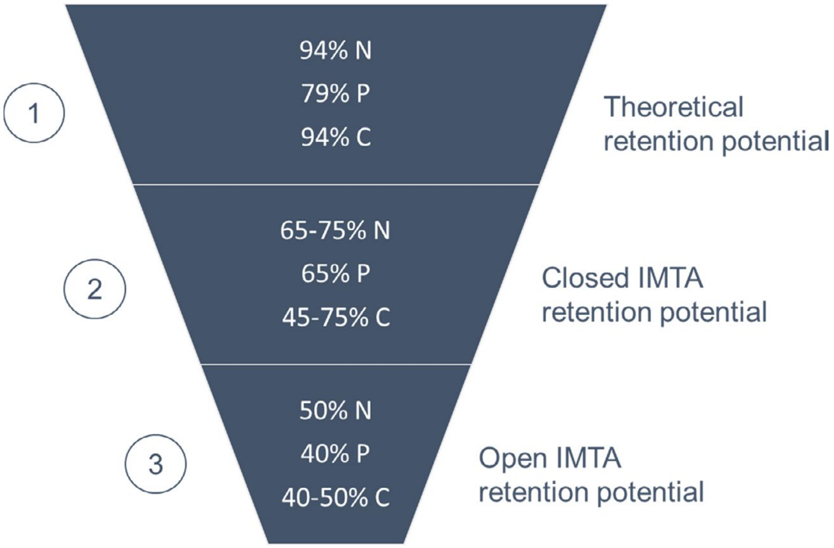

FIGURE 4 Nutrient retention potentials estimated for a conceptual four-species IMTA (salmon–kelp–mussel–polychaete) under different degrees of system openness. The numbers 1, 2 and 3 refer to the different steps of the generic framework, as presented in Figure 1. In step 1, the maximum theoretical retention potential of a conceptual IMTA (fish–seaweed–bivalve–deposit feeder) is calculated. In Step 2, biological factors are considered, resulting in the retention potential of a closed IMTA system. Step 3 considers environmental factors, which besides the biological factors have to be taken into account to calculate the retention potential of an open water IMTA system

open water IMTA has therefore gained critical attention. Cranford et al.[20] estimated that, in open water systems, mussels contribute to a reduced impact of aquaculture on the benthic ecosystem, if their diets consist for a minimum of 15–30% of OM originating from fish faeces. Stable isotope analysis shows that contribution of fish faeces to the overall diet of bivalves is often lower (Figure 2), limiting their role in open water IMTA. Only in areas where seston concentration is low and organic content is high, and if mussels can be cultivated close to cages, might it be possible to reach conditions whereby mussels can play a role in the bioremediation of aquaculture waste.[20,63,128]

In open water fish cage systems, contrary to consensus, extractive species should not be cultured directly alongside the fed species. This is partly because they may hinder the optimal functioning of the system by, for example, making it difficult to access the cages by boat to feed the fish.[18] It is also because inorganic and suspended waste is rapidly dispersed by currents. Therefore, the extractive species in the water column, that is, seaweeds and bivalves, simply need to be located in the area of nutrient dispersion.[102,106,133,134] Hence, in open water IMTA, the bioremediation potential of extractive species could be evaluated at a more regional scale, creating a balance between nutrients excreted by the fed species and nutrients harvested via the extractive species. Such a "balance approach" allows to evaluate "connectivity" between the different functional groups at a larger scale than farm level.[135] Using this approach raises the question of where to establish the boundaries in evaluating IMTA performance. It has been shown that growth of seaweeds and bivalves is only significantly enhanced, compared with reference stations, when cultivated within tens to hundreds of meters from fish cages.[136,137] Using the balance approach for open water IMTA designs, growth enhancement of extractive species (compared with monocultures of seaweeds and bivalves) should therefore not be expected.

5 | RETENTION POTENTIAL OF IMTA SYSTEMS

Based on the highest nutrient use efficiencies reported in literature, we demonstrated that a theoretical maximum nutrient retention potential of 94% for C and N and 79% for P administrated with the fish feed is possible in IMTA systems containing salmon as fed species and kelp, mussel and polychaete as extractive species (Figure 4). These percentages, however, do solely consider the nutrients applied to produce fish, estimate use efficiency of extractive species based only on assimilation efficiencies and assume no ambient nutrients complement waste nutrients from fed fish for extractive species. These percentages also take into account that a small fraction of fish waste is DOM, which extractive species included in our salmon–kelp–mussel–polychaete IMTA cannot use.

The theoretical maximum nutrient retention potential, however, does not account for the feeding metabolism of extractive species. When doing so, the retention efficiencies decrease to 65–75% for N, 65% for P and 45–75% for C with the fish feed still being the only nutrient input to the IMTA, which is the case for an IMTA operated as a closed system (Figure 4).

In semi-open and open systems, limited control over environmental factors, including exposure time to waste nutrients, presence of ambient nutrients influencing food preference and assimilation efficiencies of mixed diets by extractive species, seasonal mismatches between nutrient supply and food requirements, and sub-optimal spatial arrangements reducing nutrient access of extractive species, lessens the retention efficiencies that can be achieved to 50% for N, 40% for P and 40-50% for C, administrated with the feed to the IMTA system (Figure 4).

Concluding, in this study we assumed that 43% N, 24% P and 38% C of the fed nutrients to salmon are retained in fish biomass gain. This means that in closed land-based IMTA system, an additional 22%–32% N, 41% P and 7%–37% C of the fed nutrients can be recycled by extractive species, whilst in an open IMTA system this is 7% for N, 16% for P and 2%–12% for C. In most cases, for open IMTA systems the nutrient retention efficiencies are still overestimated as maximum retention efficiencies reported in literature were used. This makes it attractive to apply a "mass balance approach" over a larger production area, aiming to extract the same amount of nutrients that were fed to fish cages with the nutrients contained in biomass gain of harvested fed and extractive species. An advantage is then that different species can be cultured independently, allowing to optimise production whilst minimising temporal and spatial mismatches. A disadvantage is that fed nutrients and nutrients retained by extractive species are not fully the same, and that local pollution or nutrient shortages may become an issue if the design and local conditions are not carefully investigated.

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