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Into the Wild: Farm-Derived Energy and Nutrients Enter Marine Food Webs With Carrying Capacity Implications for Aquaculture Management

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ABSTRACT

Marine aquaculture is expanding globally, yet its interactions with surrounding ecosystems remain complex and insufficiently understood. This study reviews the fluxes of energy and nutrients from three major aquaculture systems: finfish cages, suspended bivalves, and seaweed farms and considers their implications for ecosystem functioning and management under the ecosystem approach to aquaculture (EAA). Using a focused literature review and expert input from International Council for the Exploration of the Sea (ICES), Working Group on Ecological Carrying Capacity of Aquaculture (ICES WGECCA), we synthesized data on farm-derived fluxes, trophic transfers, and ecological consequences. From this synthesis, we developed three conceptual models illustrating direct and indirect pathways of energy and nutrient exchange between farms and marine food webs. Seven case studies from temperate and subtropical systems were analyzed to exemplify site-specific effects, including organic enrichment, altered benthic-pelagic coupling, and changes in wild species assemblages. Key findings highlight that fed aquaculture (finfish) releases substantial particulate and dissolved waste, influencing benthic geochemistry, while extractive systems (bivalves, seaweeds) modulate nutrient cycling. Integrated multi-trophic aquaculture (IMTA) offers the potential for synergistic flux recycling within the farm system. Wild mobile fauna attracted to farm systems shelter and feed directly on the farmed product, fouling, or particulate wastes and dislodgements from the farm, thereby strengthening farm-environment coupling. These insights underscore the need for adaptive management and carrying capacity (CC) assessments that account for energy-nutrient fluxes to ensure sustainable aquaculture development aligned with EAA principles.

1 | Introduction

World aquaculture production reached a record of 130.9 million tonnes in 2022, comprising 94.4 million tonnes of farmed aquatic animals and 36.4 million tonnes of algae (seaweed and

micro-algae). Of the 94.4 million tonnes of farmed aquatic animals, marine and coastal aquaculture accounted for 33.5% of the production (35.3 million tonnes, with 65.2% of finfish, 13.5% of crustaceans and 20% of molluscs) [1]. Aquaculture can take many forms, encompassing species from all trophic

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levels—from fed animals (e.g., salmon and shrimp) to extractive species (e.g., bivalves and seaweeds). Sustainable aquaculture management requires a comprehensive understanding of the complex ecosystem-level interactions involving the farmed species. Whereas specific interactions such as aquaculture organic loading [2] and the consequences on sediment biogeochemistry and benthic communities have been extensively studied [3], a holistic analysis of how farm-derived energy and nutrients interact with ecosystems remains largely overlooked. Depending on the aquaculture system and scale, these interactions may have consequences on ecosystem functioning and the provision of ecosystem services (ES). A wide variety of interactions between farms and the ecosystems have both net benefits and negative impacts on wild species [2, 3].

In the case of fed species, such as finfish, a large amount of energy and nutrients are released in the form of waste feed and faeces, both of which may attract or deter a variety of wild organisms [4]. Farmed bivalves filter plankton and seston from the water column and release faeces and pseudofaeces, potentially modifying local sedimentation rates and impacting pelagic and infaunal communities. Moreover, the fall-off of bivalves from farm gear may affect the benthos [5]. Farmed seaweeds uptake nutrients from the surrounding environment [6], potentially competing with phytoplankton over this resource [7]. As in the case of farmed bivalves, detachment of seaweeds from cultivation lines may lead to benthic organic enrichment. In all cases, farmed species and physical farm structures (cages, longlines, ropes, trestles, etc.) may act as artificial reefs [8, 9], potentially colonized by biofouling species that may attract or deter primary and secondary consumers and predators. The distribution of motile biota around farms may vary over different spatial dimensions (vertical and horizontal), temporal scales (season, days, hours), and also with respect to farm activities (grow-out duration, harvesting practices, and farmed species) and different farm configurations (floating, suspended, or bottom type farms) [4].

The interdisciplinary concept of carrying capacity (CC) is a framework used to assess the limits of production to avoid causing unacceptable changes to the ecosystem and society [10–12]. From an ecological standpoint, assessing these limits requires understanding farm inputs and outputs and the capacity of the ecosystem to supply inputs and assimilate outputs. While these inputs and outputs can manifest through complex interactions, for example, disease dynamics [13] and gene flow [14], fluxes of energy and nutrients are at the core of these interactions due to cascading effects through food webs [15]. Therefore, mapping and assessing these fluxes underpinning the interactions between aquaculture activities and the surrounding ecosystem is essential for informing and guiding CC assessments, regulatory frameworks and, consequently, for achieving sustainable aquaculture.

The ecosystem approach to aquaculture (EAA) [16] recognizes ecological CC as one of its guiding principles [17–19]. Accordingly, the objectives of this manuscript are to provide an overview of energy and nutrient transfer from aquaculture to the environment and to discuss its implications for ecosystem functioning. This, in turn, can inform CC debates and define what constitutes “unacceptable” changes to a particular

ecosystem exposed to aquaculture. For this purpose, a review of the energy and nutrient fluxes from three marine and coastal aquaculture systems: finfish cages, suspended bivalves, and suspended seaweed farming was completed. Based on this review and expert input from members of the International Council for the Exploration of the Sea (ICES), Working Group on Ecological Carrying Capacity of Aquaculture (ICES WGECCA), we then developed three conceptual models describing the potential fluxes and pathways of energy and nutrients originating from the farm and extending into the surrounding food webs. Then, seven case studies from temperate and subtropical marine aquaculture systems were analyzed to exemplify site-specific effects. Moreover, we evaluated and discussed the potential consequences of these trophic interactions on management, considering interactions with fisheries, ES, nature conservation priorities and aquaculture regulations. This analysis focuses on temperate ocean systems with a few notes on subtropical systems and was not intended to be comprehensive. It rather recognizes that both ecosystem functioning and energy transfer are markedly different between temperate and tropical systems, and provides a future opportunity for an in-depth parallel analysis to be done within tropical systems.

2 | Energy and Nutrient Fluxes From Aquaculture Farms: Three Conceptual Models

In this study, we first synthesized information on farm-derived fluxes, trophic transfers, and ecological consequences. Information was retrieved from a focused literature review and based on expert input from ICES. The literature was retrieved from two search platforms: Web of Science and Google Scholar (with search terms including *aquaculture* AND *finfish* or *bivalve* or *seaweed* AND *marine* AND *nutrient fluxes* or *pathways* or *transfer* AND *effects*), enriched by forward and backward citation tracking, looking for studies addressing specific fluxes described in Table 1. In this focused review, we selected empirical studies that measured nutrients and energy fluxes released by finfish cages, suspended bivalve and seaweed farming and/or that evaluated direct and indirect effects of these fluxes on ecosystems. Pertinent review papers were also included in this work. Our search focused on temperate to subtropical bioregions as it is recognized that tropical systems require their own in-depth analysis due to difference in cultivation species, cultivation practices, and ecosystem dynamics and therefore were excluded from this analysis. A total of 61 studies were retained (including 27 papers on finfish farming, 12 on bivalve farming, and 22 on seaweed farming). During the review process, the following information was extracted: farmed species, type of farm, energy and nutrient fluxes measured or observed, study methodology, observed aquaculture-associated species (from bacteria, fouling organisms, primary, secondary consumers to top predators), and the mechanisms mediating the direct or indirect transfer of nutrients and energy to food webs. This review resulted in a detailed overview of aquaculture-environment interactions (Tables 2a–2c), which formed the basis for developing three conceptual diagrams for different types of aquaculture. These conceptual models represent generalized monoculture systems for finfish (Section 2.1, Figure 1), suspended bivalve (Section 2.2, Figure 2), and suspended seaweed aquaculture (Section 2.3, Figure 3). Farms are inherently variable based on

TABLE 1 | List of fluxes described in the three conceptual aquaculture models (i.e., Figures 1–3).

| Fluxes | Finfish | Bivalve | Seaweed |
|--------------------------------------------------------------------------------------------------------------------------------------|---------|---------|---------|
| Pelagic consumers consuming zooplankton | F1 | B1 | S1 |
| Zooplankton consuming bacterioplankton | F2 | B2 | S2 |
| Zooplankton consuming phytoplankton | F3 | B3 | S3 |
| Farmed bivalve consuming phytoplankton/seston [^] | N/A | B4 | N/A |
| Mortality of planktonic community contributing to OM | F5 | B5 | S5 |
| Bacterioplankton consuming OM | F6 | B6 | S6 |
| Phytoplankton consuming dissolved nutrients | F7 | B7 | S7 |
| Biodeposition (faeces and pseudofaeces [^]) contributing to suspended OM/Seaweed contributing to dissolved organic carbon* | F8 | B8 | S8 |
| Biodeposition (faeces and pseudofaeces [^]) contributing to benthic OM | F9 | B9 | N/A |
| Resuspension contributing to OM | F10 | B10 | S10 |
| Sedimentation contributing to benthic OM | F11 | B11 | S11 |
| Benthic consumers consuming benthic OM | F12 | B12 | S12 |
| Burial removing benthic OM | F13 | B13 | S13 |
| Dislodgements of farmed and fouling species contributing to OM | F14 | B14 | S14 |
| Excretion of farmed species contributing to dissolved nutrients/ Seaweed assimilating dissolved nutrients* | F15 | B15 | S15 |
| Wild species consuming fouling | F16 | B16 | S16 |

(Continues)

TABLE 1 | (Continued)

| Fluxes | Finfish | Bivalve | Seaweed |
|---------------------------------------------------------------------------------------------------------|---------|---------|---------|
| Wild species consuming farmed species (predation) | F17 | B17 | S17 |
| Microphytobenthos consuming dissolved nutrients | F18 | B18 | S18 |
| Mortality of microphytobenthos contributing to benthic OM | F19 | B19 | S19 |
| Remineralization of benthic OM contributing to dissolved nutrients | F20 | B20 | S20 |
| Bacteria consuming benthic OM | F21 | B21 | S21 |
| Respiration of farmed species contributing to CO ₂ /Seaweed contributing to O ₂ * | F22 | B22 | S22 |
| Feed contributing to OM | F23 | N/A | N/A |
| Feed contributing to benthic OM | F24 | N/A | N/A |
| Wild species (bird, fish etc.) consuming feed | F25 | N/A | N/A |
| Fouling consuming dissolved nutrients released by the farm | F26 | B26 | S26 |
| Fouling consuming OM released by the farm/ fouling consuming seaweed* | F27 | B27 | S27 |
| Release of gametes/spores* contributing to OM | F28 | B28 | S28 |
| Escapees/farmed bivalves [^] release into the wild | F29 | B29 | N/A |

Note: ([^]) designates fluxes that are specific to bivalve farming and (*) fluxes that are specific to seaweed farming. Abbreviation: N/A, not applicable.

cultured species, farming practices, scale, water depth, geography, climate, water quality, hydrodynamics and other environmental characteristics. Given this variability, not all of the theorized fluxes shown in the conceptual models are relevant to all farms in practice. Some processes may be stronger or weaker at some farms than at others, and some may not apply. Each flux described inherently affects CC for aquaculture, which is why it is important to characterize these fluxes for an EAA. Avoiding depletion of nutrients and oxygen, and balancing organic loading are imperative for operating within a CC approach.

TABLE 2a | Finfish farming: List of literature identified through the review as described in Section 2 for the conceptual model of finfish farming (cf. Figure 1). Fluxes (numbers) relate to the flows indicated in Figure 1, further described in Table 1.

| References | Farmed species | Type of farm | Fluxes | Farm nutrient 'outputs' | Methodology | Species observed | Transfer of energy and nutrients |
|------------------------------|----------------------|--------------|----------------------------|----------------------------------------------------------------------------|-------------------------------------------------------------------------------------------|----------------------------------------------------------------------------------------------------|----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Angel et al. [20] | <i>Sparus aurata</i> | Net cages | F8, F12, F24 | Uneaten feed, faeces | Fish feed input analysis; sediment sampling to track C, N, P | Foraminifera | Foraminifera sampled along a gradient of organic enrichment produced by the fish farm (abundance, species) Allocation to direct/indirect feeding will depend on the species considered |
| Angel et al. [21] | <i>Sparus aurata</i> | Net cages | F8, F12, F23, F27 | Organically-enriched farm sediments, organically-enriched suspended matter | Fish feed composition; sediment and water column sampling to track C, N | Fish, sea urchins, anemones, crinoids, sponges, bivalves, gastropods, polychaetes, and crustaceans | Predatory fish feeding on schooling fishes. Gastropods, sea urchins feeding on particulate organic matter |
| Arechavala-Lopez et al. [22] | <i>Salmo salar</i> | Net cages | F23, F25 | Uneaten feed | Analyses of fatty acids, total lipids, trace elements comparing farmed feed and wild fish | Saithe <i>Pollachius virens</i> | Farm-aggregated Saithe (<i>Pollachius virens</i>) feeding on excess fish feed |
| Baltadakis et al. [23] | <i>Salmo salar</i> | Net cages | F8, F9, F12, F24 | Particulate matter flux from farm cages | Particle flux via sediment traps, waste dispersion modeling | European lobsters (<i>Homarus gammarus</i>) | Direct consumption of waste feed and faecal material by lobsters or indirect consumption through consumption of fouling organisms by lobsters |
| Bongiorni et al. [24] | <i>Sparus aurata</i> | Net cages | F8, F9, F23, F24 | Uneaten feed, faeces, dissolved excretion | Particle flux via sediment traps, coral growth rates | Fouling organisms (Stony corals, soft corals) | NA |
| Callier et al. [25] | <i>Salmo salar</i> | Net cages | F9, F12, F15, F24, F27 | Uneaten feed, faeces, dissolved excretion | Sediment organic matter, stable isotopes | Benthic and epibenthic invertebrates | Consumption of finfish feed and/or faeces by polychaetes. Consumption of suspended POM by tunicates |
| Colombo et al. [26] | <i>Salmo salar</i> | Net cages | F8, F9, F23, F24, F25, F27 | Uneaten feed, faeces | Stable isotopes; fatty acids | Molluscs (<i>Mytilus edulis</i> , <i>Acmae testudinalis</i>) | Consumption of farm waste (feed/faeces) by molluscs (mussel and limpets) |

(Continues)

TABLE 2a | (Continued)

| References | Farmed species | Type of farm | Fluxes | Farm nutrient 'outputs' | Methodology | Species observed | Transfer of energy and nutrients |
|-----------------------------|-------------------------------------------------------------------------------|--------------|--------------------------------------|-------------------------------------------|--------------------------------------------------------------------------------------------------------------------------------|----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|-----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Cook et al. [27] | <i>Sparus aurata</i> , <i>Dicentrarchus labrax</i> , <i>Salmo salar</i> | Net cages | F8, F9, F12, F15, F23, F24, F26, F27 | Uneaten feed, faeces, dissolved excretion | Epibenthic community analysis | Fouling organisms: Bryozoa, Tunicata, Algae, Mollusca, Porifera | Consumption of waste dissolved nutrients, feed/faeces by epibenthic communities |
| Eden et al. [28] | <i>Sparus aurata</i> | Net cages | F9, F12, F24 | Uneaten feed, faeces | Sediment organic matter, dissolved sulfide, dissolved oxygen Gastropod distribution | Benthic gastropod (<i>Nassarius sinuigerus</i>) | Consumption of organic matter released from the farm by the snail (<i>Nassarius sinuigerus</i>) |
| Elvines et al. [15] | Review | Net cages | F8, F9, F12, F23, F24, F25 | Uneaten feed, faeces | Biochemical tracers: macronutrients, minerals and trace elements, stable isotopes, fatty acids, carotenoid pigments, DNA, CSIA | Many (review) | Review on methods to trace fish farming waste "Fish waste provide a trophic subsidy to many wild farm-associated organisms, either directly through consumption of waste, or indirectly through consumption of other fauna that have consumed fish waste" |
| Fernandez-Jover et al. [29] | <i>Salmo salar</i> , <i>Sparus aurata</i> , <i>Dicentrarchus labrax</i> | Net cages | F12, F23, F25 | Uneaten feed, faeces | Fatty acids | Wild saithe (<i>Pollachius virens</i>), cod (<i>Gadus morhua</i>), Mediterranean horse mackerel (<i>Trachurus mediterraneus</i>), Mediterranean bogue (<i>Boops boops</i>), juvenile mugilid (<i>Liza aurata</i>), juvenile sparid (<i>Oblada melanura</i>), shrimp (<i>Pandalus borealis</i>), sea urchin (<i>Patangus purpureus</i>), sea urchin (<i>Psammechinus miliaris</i>), green-lipped mussels (<i>Perna viridis</i>) | Energy transfer measured as fatty acid signatures relative to control locations in several species. |

(Continues)

TABLE 2a | (Continued)

| References | Farmed species | Type of farm | Fluxes | Farm nutrient 'outputs' | Methodology | Species observed | Transfer of energy and nutrients |
|-----------------------------|----------------------------------------------------------|--------------|-----------------------|-------------------------|-------------------------------------------------------------------------------------------------------------------------------------------------------------------|-----------------------------------------------------------------------------------------------------------------|-----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Ghanawi [30] | <i>Salmo salar</i> , <i>Hippoglossus hippoglossus</i> | Net cages | F9, F24, F25 | Uneaten feed, faeces | Fatty acids | Mackerel (<i>Scomber scombrus</i>) and whiting (<i>Merlangius merlangus</i>) | Mackerel and whiting consumed waste feed |
| Gonzales-Silvera [31] | <i>Sparus aurata</i> , <i>Dicentrarchus labrax</i> | Net cages | F12, F26, F27 | Uneaten feed, faeces | Fatty acids in sediment traps; plankton tows; biofouling on farm gear | Eighteen macroinvertebrate species, and zooplankton, seaweeds | Consumption of organic matter from farms by fouling communities |
| Israel et al. [9] | <i>Gadus morhua</i> | Net cages | F8, F9, F12, F23, F24 | Uneaten feed, faeces | Comparing fouling community at cod farm site to reference site | Diverse community of sessile and motile invertebrates on artificial reefs below cages | Evidence of the uptake of cod farm waste was in the increased fouling community found on the artificial reef below this farm as compared to a nearby reference site |
| Izquierdo-Gomez et al. [32] | <i>Sparus aurata</i> | Net cages | F23, F25 | Uneaten feed | Total lipids and fatty acids feed and commercial wild fish (4 species) | <i>Sardinella aurita</i> , <i>Mullus barbatus</i> , <i>Caranx ronchus</i> , <i>Pomatomus saltatrix</i> | Feeding on excess feed. The work concludes that fish species of different trophic guilds use excess feed either as a direct trophic resource or indirectly via predation on aggregated preys. |
| Izquierdo-Gomez et al. [33] | <i>Sparus aurata</i> , <i>Dicentrarchus labrax</i> | Net cages | F12, F24 | Feed | Stable isotope, size and width of feed waste consumers (prawns) | Penaieid prawn <i>M. kerathurus</i> | Positive effect of feed waste on penaieid prawn growth |
| Katz et al. [34] | <i>Sparus aurata</i> | Net cages | F9, F12, F24 | Uneaten feed, faeces | Sediment dissolved oxygen, sediment sulfides, sediment organic matter, benthic macrofauna | Grey mullets, benthic molluscs | Uptake of organically-enriched sediments by grey mullets and benthic molluscs |
| Laroche et al. [35] | <i>Salmo salar</i> | Net cages | F8, F27 | Uneaten feed, faeces | Deposition rates; Translocation experiment with sponges: gene expression analysis, associated microbial communities, fatty acids, C and N stable isotope analysis | Sponges (<i>Weberella bursa</i>): translocation experiment Microbial associated community | Feeding on organic matter from the farm |

(Continues)

TABLE 2a | (Continued)

| References | Farmed species | Type of farm | Fluxes | Farm nutrient 'outputs' | Methodology | Species observed | Transfer of energy and nutrients |
|----------------------|----------------------|--------------|---------------------------------|--------------------------------------------------------------------------|----------------------------------------------------------------------------------------------------|--------------------------------------------------------------------------------------------------|------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Lojen et al. [36] | <i>Sparus aurata</i> | Net cages | F8, F9, F15, F23, F24, F26, F27 | Uneaten feed, faeces; dissolved excretions, dislodged biofouling | Stable isotope composition of sources and sinks to trace fluxes from farm to surrounding ecosystem | Fouling organisms: sponges, tunicates, polychaetes, algae, sponges, bryozoa | Consumption of particulate nitrogen from fish farm effluents by fouling communities |
| McAllister [37] | <i>Salmo salar</i> | Net cages | F23, F24, F25 | Uneaten feed, faeces (field observations), uneaten feed (lab experiment) | Stable isotopes and fatty acids | <i>Gadus morhua</i> , <i>Sebastes fasciatus</i> | No evidence of finfish farm waste consumption by adults Consumption of feed waste by juvenile Atlantic cod |
| Olsen [38] | <i>Salmo salar</i> | Net cages | F9, F12, F24 | Waste | Fatty acids | Northern shrimp (<i>Pandalus borealis</i>) | Shrimp can incorporate organic fish farm waste into part of their diet, either directly through the consumption of waste feed and faeces or indirectly by feeding on influenced infauna |
| Sardenne et al. [39] | <i>Salmo salar</i> | Net cages | F9, F12, F24 | Uneaten feed, faeces | Fatty acids | Rock crab <i>Cancer irroratus</i> and American lobster <i>Homarus americanus</i> | Consumption of organic wastes from salmon aquaculture by rock crab |
| Tsemel et al. [40] | <i>Sparus aurata</i> | Net cages | F8, F9, F23, F24, F26, F27 | Uneaten feed, faeces | Identification and quantification of invertebrates growing on artificial reefs | Fish, sea urchins, anemones, sponges, bivalves, gastropods, corals, polychaetes, and crustaceans | Focus on the fouling community at the fish farm vs. a reference site to infer that the greater abundance and biofouling community was due to the added nutrients released from the farmed fish |

(Continues)

TABLE 2a | (Continued)

| References | Farmed species | Type of farm | Fluxes | Farm nutrient 'outputs' | Methodology | Species observed | Transfer of energy and nutrients |
|-----------------------|--------------------------------------------------------|--------------|----------------------------------------------|-------------------------|---------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|---------------------------------------------------------------|-----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| White [41] REVIEW | Review | Net cages | F7, F6, F8, F9, F12, F15, F23, F24, F25, F26 | Uneaten feed, faeces | Fatty acids | Several species (review) | Overview of the use of fatty acids to indicate transfer of material from fish farm wastes to benthic and pelagic systems by analyzing vertebrates, invertebrates, sediment and seston |
| White [42] | <i>Salmo salar</i> | Net cages | F8, F9, F23, F24, F12 | Uneaten feed, faeces | Several urchin biometrics (under farm waste vs. control condition). Field and lab experiment to evaluate abundance and effect on reproduction | <i>Gracilechinus acutus</i> (formerly <i>Echinus acutus</i>) | Greater populations of sea urchins adjacent to salmon farms than at reference sites; Indirect: feeding experiments in the lab using salmon feed showed that sea urchins grew more rapidly on this feed than on natural food |
| Woodcock et al. [43] | <i>Salmo salar</i> | Net cages | F9, F12, F24 | Uneaten feed, faeces | Fatty acids and stable isotopes | Brittle stars, urchins and brown crabs | Consumption of aquaculture organic waste by brittle stars, urchins and brown crabs |
| Yoshikawa et al. [44] | <i>Seriola quinqueradiata</i> , <i>Pagrus major</i> | Net cages | F6, F8, F10, F11, F21 | Uneaten feed, faeces | Sediment traps (OM, PON fluxes determination), Bacterial abundance attached to the sinking particles, resuspendable particles, and bottom sediments, Hydrolysis rates of aminopeptidase, chymotrypsin, and glucosidase, mineralization rates of glutamate, glucose, and acetate | Bacteria | Microbial decomposition process of organic matter in sinking particles, resuspendable particles, and bottom sediments |

TABLE 2b | Bivalve farming: List of literature identified through the narrative review as described in Section 2 for the conceptual model of suspended bivalve aquaculture (cf. Figure 2). Fluxes (numbers) relate to the flows indicated in Figure 2, further described in Table 1.

| References | Farmed Species | Type of farm | Fluxes | Farm nutrient 'outputs' | Methods | Species observed | Transfer of energy and nutrients |
|-----------------------|------------------------------------------------------|------------------------------------------------|-------------------------------------------------------------------------------------------|--------------------------------------------------------------------------------------------------------|----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|----------------------------------------------------------------------------------------------------------------------------------|-----------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Brigolin et al. [45] | <i>Mytilus galloprovincialis</i> | Longline | B9, B20, B4 | Faeces and biodeposits quantified on the basis of an individual model upscaled at the population level | Quantification of N loss associated to denitrification process of OM degradation. Quantification of OM burial in deep sediment—methods: biogeochemical modelling, benthic coring, sediment traps data. growth model based on an energy balance; particle tracking model; sediment biogeochemistry model. Chlorophyll an analysis | NA | POC deposition, Mineralisation of total organic carbon, faeces and pseudofaeces dispersal |
| Caldow et al. [46] | <i>Mytilus edulis</i> | Intertidal | B17 | Birds congregating at mussel sites | Observation of birds | <i>Haematropus ostralegus</i> , <i>Numenius arquata</i> , <i>Tringa totanus</i> , <i>Larus ridibundus</i> , <i>L. argentatus</i> | Bird predation. not directly on feeding on farmed mussels, but impacts from shellfish cultivation on bird assemblage. Birds feeding on shellfish was indirectly used. |
| Filgueira et al. [47] | <i>Crassostrea virginica</i> , <i>Mytilus edulis</i> | Numerical model representing suspended culture | B1, B2, B3, B4, B5, B6, B7, B8, B9, B10, B11, B12, B13, B14, B15, B16, B18, B19, B20, B21 | The model tracked egestion but those results are not part of the paper | Spatially explicit hydrodynamic–biogeochemical coupled model, including primary producer and seston sub-models. Chlorophyll-a | NA | NA-The model is NPZ with the addition of seston and bivalves |

(Continues)

TABLE 2b | (Continued)

| References | Farmed Species | Type of farm | Fluxes | Farm nutrient 'outputs' | Methods | Species observed | Transfer of energy and nutrients |
|--------------------------|--------------------------------------------------------------------------------|--------------|----------|----------------------------------------------------------------------------|-----------------------------------------------------------------|--------------------------------------------------------------------------------------------------------------------------------------------------|--------------------------------------------|
| Freire et al. [48] | <i>Mytilus edulis</i> | Raft culture | B12, B16 | Predation; stomach content of swimming crab <i>Liocarcinus arcuatus</i> | Trawls, stomach content analysis of swimming crab | <i>Liocarcinus arcuatus</i> | Crab predation on epifauna |
| Freire et al. [49] | <i>Mytilus galloprovincialis</i> | Raft culture | B12, B16 | Predation; stomach content of the velvet swimming crab <i>Necora puber</i> | Stomach content analysis of the crab | <i>Necora puber</i> | Crab predation on epifauna |
| Richard et al. [50] | Mussels <i>Mytilus galloprovincialis</i> , oysters <i>Crassostrea gigas</i> | Longlines | B17 | Oyster and mussel losses | Acoustic tags on seabream with receivers deployed at farm sites | <i>Sparus aurata</i> | Sea bream predation on mussels and oysters |
| Roycroft et al. [51] | <i>Mytilus edulis</i> | Longlines | B17 | Oyster and mussel losses | Observation with telescope | <i>Phalacrocoracidae, Laridae, Alcidae</i> | Bird predation on mussels |
| Sardenne et al. [52] | American lobster <i>Homarus americanus</i> , rock crab <i>Cancer irroratus</i> | Longlines | B14 | Fallen mussels from farm | Stable isotopes | <i>Homarus americanus</i> | Lobster predation on fallen mussels |
| Šegvić-Bubić et al. [53] | <i>Mytilus galloprovincialis</i> | Longlines | B17 | No information provided | Underwater visual census, rapid visual counts | 16 fish taxa in families: <i>Atherinidae, Belontiidae, Carangidae, Centranchidae, Moronidae, Mugilidae, Pomacentridae, Pomatomidae, Sparidae</i> | Fish predation of farmed mussels |

(Continues)

TABLE 2b | (Continued)

| References | Farmed Species | Type of farm | Fluxes | Farm nutrient 'outputs' | Methods | Species observed | Transfer of energy and nutrients |
|-----------------------|---------------------------------------------------|--------------|----------|------------------------------------------|----------------------------------------------------------------------------------------------------------------|---------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|-------------------------------------------------|
| Underwood et al. [54] | <i>Perna canaliculus</i> | Longlines | B16, B17 | Abundance of fish recruits | SMURFS standard monitoring units for the recruitment of fish, Shannon Biodiversity index | <i>Fosterygion lapillum</i> , <i>F. capito</i> , <i>F. gymnotum</i> , <i>Trachurus</i> spp., <i>Dellichthys trnskii</i> , <i>Parika scaber</i> , <i>Notolabrus celidotus</i> , <i>Pseudophycis barbata</i> , <i>Ericentrus rubrus</i> | Biofouling and fish recruitment to farm |
| Underwood et al. [55] | <i>Perna canaliculus</i> | Longlines | B16, B17 | Mussel losses | eDNA metabarcoding, gut content analysis | <i>Chrysophrys auratus</i> | Snapper feeding on cultured mussels and fouling |
| Zhang et al. [56] | <i>Crassostrea gigas</i> , <i>Chlamys farreri</i> | Longlines | B9 | Biodeposit and pseudofaeces by shellfish | PH, redox potential, color, odor, gas ebullition, of sediment analysis, biodiversity from VanVeen grab samples | 40 macrofauna spp | Biodeposit and pseudofaeces by shellfish |

2.1 | Finfish Farming

Most of marine finfish aquaculture employs floating cages (Figure 1). In intensive finfish farming systems, the primary source of energy comes from finfish feed (pink arrows, Figure 1). Differences in the composition and digestibility of feed offered to finfish will determine the amounts of effluents released from finfish aquaculture. In addition, some of the feed offered to farmed fish is released uneaten from the floating cages (F23, F24). Several authors have quantified feed loss in finfish aquaculture—but since this is influenced by fish species, farm management, season, and water currents, the range of values is quite large [78]. Based on modelling and in situ measurement, the estimated percentage of uneaten feed could range from 1% to ca. 50% [79–81]. Feed pellet sedimentation rates are affected by pellet settling velocity and water current intensity; accordingly, pellets may settle below the cages (F24) or be degraded and dispersed further afield (F23). Feed pellets may also be ingested by wild fish (F25) or benthic organisms (F12). A fraction of the energy contained in ingested feed will be used for metabolism, growth, reproduction, and maintenance. The remaining fraction of the energy will be lost as faeces (F9) or excreted as dissolved nutrients (mainly NH₄⁺, urea, orthophosphate) (F15) and as CO₂ (F22). The fate of fish faeces is affected by their size, texture, and settling velocity, and they will either settle to the seafloor (F9), enter the pool of pelagic organic matter (F8), or be ingested by heterotrophic species (F6, F12). Organic matter that is mineralized by microbes to dissolved inorganic nutrients (F20) will be dispersed in the water column and may be assimilated by primary producers (algae, phytoplankton, plants) (F7).

The energy released from the farm as uneaten feed, faeces and dissolved organic and inorganic nutrients may be used by biofouling biota, such as sponges, tunicates, bryozoa, barnacles, macroalgae, microalgae, corals, hydrozoa, and bacteria which develop on farm structures (F26, F27). Part of the energy assimilated by fouling organisms from farm activities is transferred to the surrounding community through grazing (F16) and predation (F17). Organic matter falling from the cages contributes to the pool of benthic organic matter that may be buried (F13), used by epibenthic consumers and infauna (F12), or remineralised (F20). The release of uneaten feed, faeces and other forms of biomass and nutrients to the surrounding waters and benthos serves as a transfer of energy to a variety of fishes (F12). Different species of birds may feed on both fish feed pellets and farmed fish (F17), and many fish farmers have equipped their cages with nets to prevent such losses.

Additional important fluxes are escapes of farmed fish (F29) from the cages, which may have ecological consequences beyond energy fluxes. The release of gametes and eggs (F28) is another type of flux in certain species, such as farmed cod, which may reproduce within net cages [82]. A variety of marine predators, including orcas, sharks, tuna, seals, and dolphins, have been documented [83] tearing net cages to feed on farmed fish (F17) [84], resulting in the release of farmed fish, energy, and nutrients during the feeding process.

2.2 | Suspended Bivalve Farming

In suspended bivalve cultivation systems (Figure 2) (longlines, fixed pole structures, floating bags and baskets), the main

TABLE 2c | Seaweed farming: List of literature identified through the narrative review as described in Section 2 for the conceptual model of suspended seaweed aquaculture (cf. Figure 3). Fluxes (numbers) relate to the flows indicated in Figure 3, further described in Table 1.

| References | Farmed Species | Type of farm | Fluxes | Farm nutrient 'outputs' | Methods | Species observed | Transfer of energy and nutrients |
|---------------------|-------------------------------------------------------------------------------------------------------------------------------------------------------------------|--------------|--------|-------------------------------|-----------------------------------------------------------------------------------------------|-------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|--------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Anyango et al. [57] | <i>K. alvarezii</i> | Intertidal | S17 | Seaweed biomass eaten by fish | Traps and underwater visual census; stomach analysis using standard taxonomic keys and guides | Of 55 fish belonging to 22 species were observed (caught) at the farmed site, while 122 fish belonging to 25 species were observed (caught) at the unfarmed site. | Herbivorous fishes consume algae. Remnants of <i>K. alvarezii</i> occurred in 24 out of the 33 (73%) fish stomach specimens at the farmed site, and in 60 out of the 79 (76%) fish stomach examined at the unfarmed site |
| Berger et al. [58] | Oarweed (<i>Laminaria digitata</i>) and a diverse range of red algae (including <i>Chondrus crispus</i> , <i>Osmundea pinnatifida</i> , <i>Dilsea carnosa</i>) | Longlines | S27 | NA | Monitoring methods (BRUVs, PAM and visual surveys). | Four types of biofouling organisms (sea fur, bleaching, filamentous algae, and bryozoans). Observation of numerous species associated with seaweed farm, 15 fish and 6 invertebrate species. The two species that are most closely associated with kelp habitats are likely to be the Ballan wrasse (<i>Labrus bergylta</i>) and the Shore crab (<i>Carcinus maenas</i>). | Fouling on seaweed: Visual surveys revealed colonisation of algal, hydroid, and bryozoan species on both the surface and seabed infrastructure, indicating that the farming structures serve as stable substrates for biodiversity accumulation. |

(Continues)

TABLE 2c | (Continued)

| References | Farmed Species | Type of farm | Fluxes | Farm nutrient 'outputs' | Methods | Species observed | Transfer of energy and nutrients |
|----------------------|---------------------------------------------------|------------------------------|---------|---------------------------------------------------------|----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|---------------------------------------------------------------------------------|------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Chen [59] | Wild seaweed in experiment, <i>Ulva prolifera</i> | NA | S10, S6 | DIC, DOC | Measuring degradation of <i>Ulva</i> over 520 days: concentration of DOC, main components of FDOM, molecular fingerprint of DOC, bacterial abundance, bacterial community structure analysis, functional prediction of bacterial communities | NA | Rapid release of DIC from sedimentary macroalgae biomass. Degradation by bacteria. Refractory DOC (RDOC) remained, 1.6% of the biomass. |
| Corrigan et al. [60] | <i>Saccharina Latissima</i> | Longlines | S27 | — | Monthly manual sampling of seaweed. Quantification of epibiont assemblage | Bryozoans, ascidians, algae | Fouling on seaweed: Increases in epibiont abundance and diversity on cultivated kelps over and beyond the growing season, reaching an average abundance of > 6000 individuals per kelp plant, mainly amphipods, molluscs and bryozoans |
| Duarte et al. [61] | Seaweed | 20 different farms and types | S13 | Organic carbon | Combining analyses of organic carbon density with sediment accumulation rate in sediments below seaweed farms relative to reference sediments beyond the farm and/or prior to the farm operation. | NA | Burial: Organic carbon burial rates in the farm sediments averaged 1.87 ± 0.73 ton CO ₂ equivalent ha ⁻¹ year ⁻¹ |
| Førde et al. [62] | <i>Saccharina latissima</i> | Net cages | S27 | Byrzoan fouling, release of bryozoan larvae to plankton | Plankton tows to look for bryozoan larvae. Image analysis for bryozoan fouling on kelp. Rate of fouling analysis | <i>Membranipora membranacea</i> (Linnaeus) and <i>Electra pilosa</i> (Linnaeus) | Bryozoan settle (and feed) on seaweed in mid-June, followed by a rapid colony growth during late June and July. In August and September, the kelp was highly degraded by the bryozoan coverage and highly subjected to breakage of the lamina. |

(Continues)

TABLE 2c | (Continued)

| References | Farmed Species | Type of farm | Fluxes | Farm nutrient 'outputs' | Methods | Species observed | Transfer of energy and nutrients |
|---------------------|--------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|---------------|---------|-----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|-----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|-----------------------------------------------------------------|----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Hall et al. [63] | Wild seaweed in experiment: the perennial habitat forming <i>Fucus vesiculosus</i> and <i>Furcellaria lumbricalis</i> , and the seasonal fast-growing <i>Ulva intestinalis</i> | NA | S6, S8 | DIC, DOC | Bacterial incubation to quantify release rates of DOC by three macroalgae species under both light and dark conditions. The released products were assessed using bacterial incubations whereby radiolabeled leucine was used to evaluate the uptake and lability of these products by marine heterotrophic bacteria. | NA | DOC release at rates of 0.27 mg C·h ⁻¹ under light and 0.13 mg C·h ⁻¹ per unit of dry mass under dark treatments, respectively, other species: negligible. Bacteria consuming DOC. |
| Halling et al. [64] | <i>Eucheuma denticulatum</i> , <i>Kappaphycus alvarezii</i> | Not indicated | S28 | Output of genotypes to wild locations | Genome analysis. Output of genotypes to wild locations | NA | Farmed genotypes on the reefs, not quantified |
| Hehre [65] | Seaweed | NA | S17 | Seaweed biomass eaten by fish | Collected rabbitfish for gut content and stable isotope analyses, quantitative data on the fish assemblages. | 3260 fish were counted representing 138 species and 31 families | Fish consume farmed seaweed (75–87.5%) around farms and consumed will seaweed on sites without farm. |
| Huang [66] | <i>Saccharina japonica</i> | Longlines | S8, S14 | DOM attributes and bacterial community structures within cultivated and non-cultivated kelp areas. Algae detritus contributes to C, N, and S cycling in the sediment environment. | DOM; microbial diversity | NA | significantly higher dissolved organic carbon (DOC) concentrations in the kelp culture area. Indirect: DO affects the marine bacterial community structure and functional genes |

(Continues)

TABLE 2c | (Continued)

| References | Farmed Species | Type of farm | Fluxes | Farm nutrient 'outputs' | Methods | Species observed | Transfer of energy and nutrients |
|-------------------|-----------------------------------------------------------------------------------------|--------------|--------------|-------------------------|--------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|------------------|--------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Jiang et al. [7] | <i>Saccharina japonica</i> | Longlines | S7, S15, S22 | NA | Water transparency, DIN, DIP, and phytoplankton (abundance, diversity) (farming period vs. after kelp removal) | NA | Nutrient uptake by seaweed of 297 t of nitrogen and 42 t of phosphorus, annually. Slightly increased dissolved oxygen from seaweed's photosynthesis. Because of decreased flow velocity, turbulence, and sediment resuspension, kelp farming greatly reduced suspended solids and increased transparency, resulting in increases in phytoplankton chlorophyll a and abundance. |
| Kim et al. [67] | <i>Saccharina Latissima</i> | Longlines | S15 | — | C content in tissue via stable isotopes measurements, C,N,P in algae tissue | NA | Nutrient uptake: C content increased from 20.6% DW in February to 28.5% DW in May. The N content of samples collected in May ranged from 1.0% to 2.6% DW. P concentrations at the 3 sites all differed statistically. |
| Kotta et al. [68] | <i>Saccharina Latissima</i> , <i>Ulva intestinalis</i> , <i>Fucus vesiculosus</i> | Longlines | S15 | — | Growth models and Boosted Regression Trees (BRT) models for the relationship between macroalgal growth yields and surface water temperature, salinity, irradiance, wave height, nitrates (NO ₃ ⁻) and phosphates (PO ₄ ³⁻) values obtained from the Copernicus products (see previous subsection). | NA | Nutrient uptake: different species can remove 0.07%, 0.15% and 0.30% of available N and P from a 1 km ² sea area over a cultivation cycle |

(Continues)

TABLE 2c | (Continued)

| References | Farmed Species | Type of farm | Fluxes | Farm nutrient 'outputs' | Methods | Species observed | Transfer of energy and nutrients |
|------------------------|----------------------------|--------------|----------|----------------------------------------|--------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|------------------|---------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Lowe [69] | Wild seaweed in experiment | NA | S6, S12 | | POM composition measured with multiple methods including visual quantification of living and detrital components, multiple stable isotope (MSI) and fatty acid (FA) analyses. Sampling at multiple temporal and spatial scales | NA | POM from macroalgae consumed by benthic and pelagic consumers. The results of this multi-scale study show that POM composition is highly dynamic and largely driven by phytoplankton abundance, with minor contributions from terrestrial or macrophyte subsidies. |
| Ren et al. [70] | Kelp | Longlines | S11 | Rotten kelp, POC | Sediment traps, ¹³ C and ¹⁵ N | NA | Kelp releases suspended particulate matter (SPM) but contribution rates to the sediments in the IMTA area were very low. |
| Sokolowski et al. [71] | Wild seaweed | NA | S12, S21 | Seaweed OM within the benthic food web | Stable isotope analysis, ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$) of macrobenthic fauna and its potential food sources | NA | Soft-bottom fauna consumes detritus originating from suspended organic matter from macroalgae. Primary consumers feeding on a mixture of plant matter, fecal pellets, decaying animal tissue, bacteria, and protists accounted for the greatest biomass share (62% of the total macrobenthic biomass), followed by secondary consumers (38%). Based on $\delta^{15}\text{N}$ signatures, three trophic levels were detected, corresponding to the following feeding guilds: filter-feeders and feeding generalists (mainly bivalves, crustaceans, polychaetes, and some fish), mixed detritivore-carnivores (polychaetes, priapulids, crustaceans, and ophiuroids) and obligate carnivores (ascidians). |

(Continues)

TABLE 2c | (Continued)

| References | Farmed Species | Type of farm | Fluxes | Farm nutrient 'outputs' | Methods | Species observed | Transfer of energy and nutrients |
|-----------------------|----------------|--------------|--------|---------------------------------|-----------------------------------------------------------------------|---------------------|----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Solidoro [72] | | NA | S7 | — | Dynamic macroalgal growth and water quality model | NA | Nutrient uptake: Results of simulations show that while phytoplankton response to growth factors is more intense and of shorter duration, internal nutrient storage in macroalgae stabilizes the growth process and makes macroalgal communities relatively more independent of variations of chemical and external forcing functions. |
| Stein Fredriksen [73] | Seaweed | NA | SI7 | Carbon and nitrogen | Stable Isotope analysis (Birds, fish, invertebrates and source of OM) | Invertebrates, fish | Two bird species were examined. The $\delta^{13}C$ were -18.32‰ for cormorant and -18.22‰ for eider duck. Their carbon originates from a mixture of kelp (37% for the cormorant and 49% for the eider duck) and phytoplankton, or from red algae. |
| Todd et al. [74] | Wild kelp | NA | SI6 | Habitat and prey for shore crab | Phenotype environment matching | Shore crab | Plain crabs were strongly associated with macroalgae, feeding on a variety of small invertebrates, including barnacles and small crabs, which are abundant in and around the kelp blades. |

(Continues)

TABLE 2c | (Continued)

| References | Farmed Species | Type of farm | Fluxes | Farm nutrient 'outputs' | Methods | Species observed | Transfer of energy and nutrients |
|-------------------|--------------------------------------------------------|--------------|----------|---------------------------------------------------------------------|---------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|------------------|----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Wang et al. [75] | Seaweed, kelp and <i>Gracilariaopsis lemaneiformis</i> | | S13 | Total organic carbon (TOC), total nitrogen (TN), and $\delta^{13}C$ | Burial flux and magnitude of TOC modeled with sediment rate, sediment density estimation. Examined in sediments in a cultivation field of macroalgae (kelp and <i>Gracilariaopsis lemaneiformis</i>) with a three-endmember model | NA | Burial: the burial flux of TOC was $25 \pm 14 \text{ g-C m}^{-2} \text{ year}^{-1}$. Multiplied by the area covered by seawater in Sansha Bay ($3.23 \times 10^8 \text{ m}^2$, Han et al. 2021), the overestimated burial magnitude of TOC reached $(8.2 \pm 4.5) \times 10^3$ tons per year of the macroalgae carbon production in Sansha Bay. |
| Zhang et al. [76] | <i>Saccharina japonica</i> | Longlines | S14, S27 | POM and DOM | Observation, measurements on seaweed in the farm, punch hole method combined with calculations to determine the POC loss; Removal of the entire individual from mariculture ropes (falloff), breakage in sections of the thalli (breakoff), and erosion of distal tissue. | NA | Fall-off rate (16%), positive correlation with kelp length. erosion rate (approximately $10\text{--}15 \text{ g day}^{-1}$). The ratio of total loss of carbon and nitrogen to gross production was 61% and 54%, respectively. Loss from distal erosion, falloff, and breakoff in carbon was 91.5%, 4.2%, and 4.3%, respectively. |
| Zhang et al. [77] | Seaweed | | S6 | POC and DOC | Manual macroalgae and surface water sampling for incubation experiment to analyze POC, DOC and RDOC rates | NA | Indirect: Most of the carbon in the kelp biomass was converted to DIC by bacterial respiration. Only 7.8% of the carbon in the kelp biomass was converted into labile DOC, semi-labile or semi-refractory DOC, and refractory DOC in turn. |

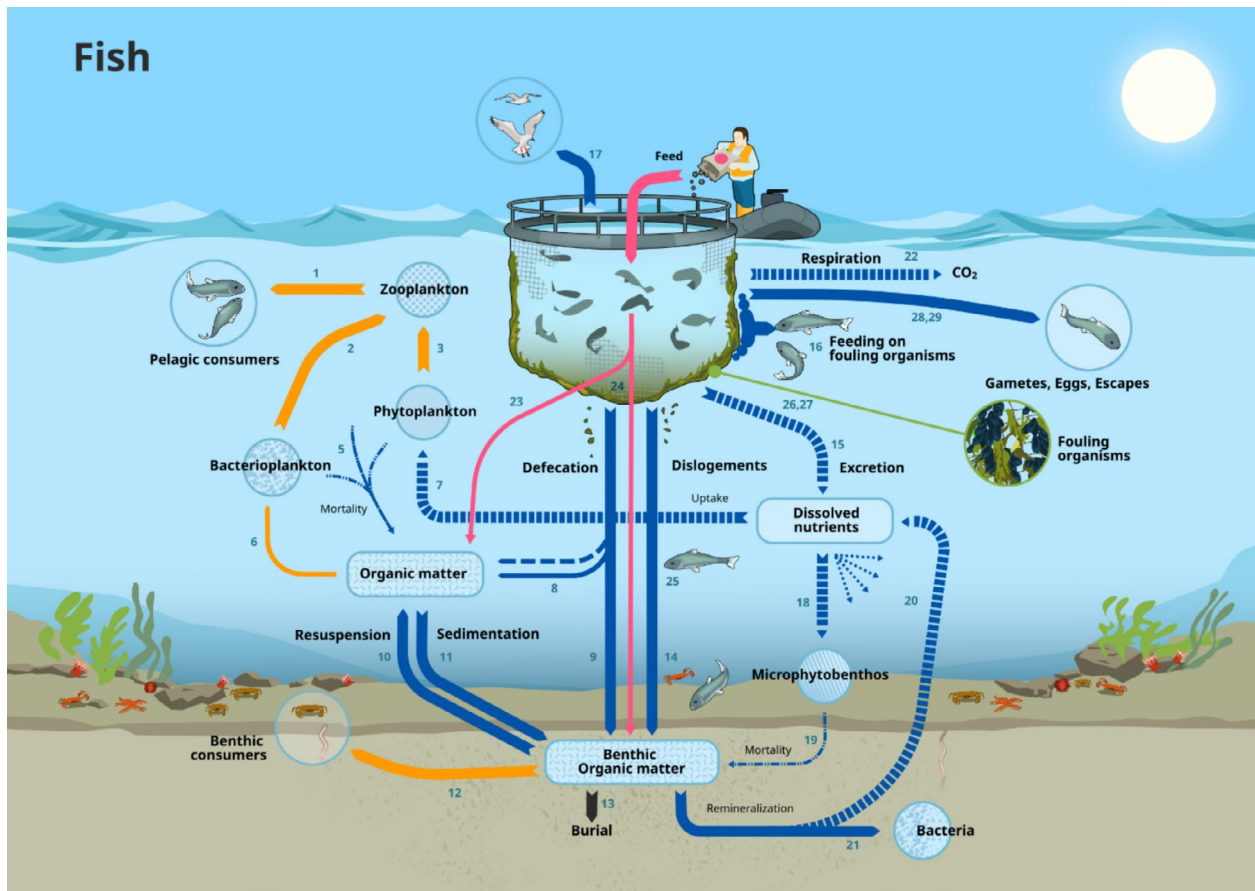


FIGURE 1 | Energy and nutrient fluxes from finfish farming to the environment. Individual flows (and respective numbers) are further explained in Table 1. Arrows describe the flow of energy and nutrients, with the primary source of energy (fish feed, pink), as well as direct (blue), and indirect (orange) fluxes.

energy uptake occurs from the water column to the farmed biomass through the filtration of phytoplankton (B4) and particulate organic matter (POM). In most cases, the primary source of energy for the bivalves is phytoplankton, whose productivity is mainly controlled by the availability of dissolved nutrients (B7). Replenishment of nutrients through advection, upwelling and mixing processes, and freshwater inputs plays a central role in defining the stock of energy available for the farm [47]. Processes of resuspension and sedimentation (B10, B11) are linked to the intensity of benthic-pelagic coupling, which defines the role of the benthic organic matter pool in supplying energy to the farm. Although sedimentation and resuspension processes are primarily controlled by water depth and hydrodynamic conditions at the farm site, they may also be influenced by farm design, types of farm structures, distance between lines, and depth of lines. The pool of suspended energy available to farmed bivalves is further constrained by competing phytoplankton consumers, including grazing by zooplankton and higher trophic levels (B1, B3). The organic matter energy pool is also influenced by the intensity of the microbial loop (B5, B6), which, in turn, is strongly affected by local environmental conditions [85].

Once captured by bivalves, a fraction of the planktonic matter is rapidly released into the water column through the egestion of faeces and the production of pseudofaeces (B8). Faeces and pseudofaeces rapidly sink to the bottom below and near

the farming area (B9), conveying a substantial input of energy to the benthic environment in the form of highly labile POM [45, 56]. This POM may be degraded by bacteria that are present in sediments (B21) and that mediate “early diagenesis” [86–88], converting organic compounds to inorganic nutrients, which eventually diffuse into near-bottom waters (B20). A fraction of the organic matter can be subtracted from this remineralization pathway at different stages, through POM leaching into dissolved organic matter DOM (B8), POM consumption/uptake by benthic consumers (e.g., sea cucumbers, crabs, lobsters) (B12), or POM burial in deep sediments (B13), following sediment redistribution during intense storm events [89] or bioturbation. The excretion (B15) and respiration (B22) by farmed bivalves directly delivers inorganic compounds to the water column, thereby enhancing primary production. In particular, the excretion of nitrogen and phosphorus sustains local energy recycling (B7, B18), a process that is highly dependent on local hydrodynamics.

Most of the energy stored in bivalve tissues and shells is harvested by the farmer, but part may be released into the environment by dislodgement of individuals from the ropes (B14) [52]. Dislodgements may be caused by husbandry practices or by adverse environmental conditions associated with storms or heat waves. Energy is also released from bivalve tissue to the water column during spawning, which may be advected away from

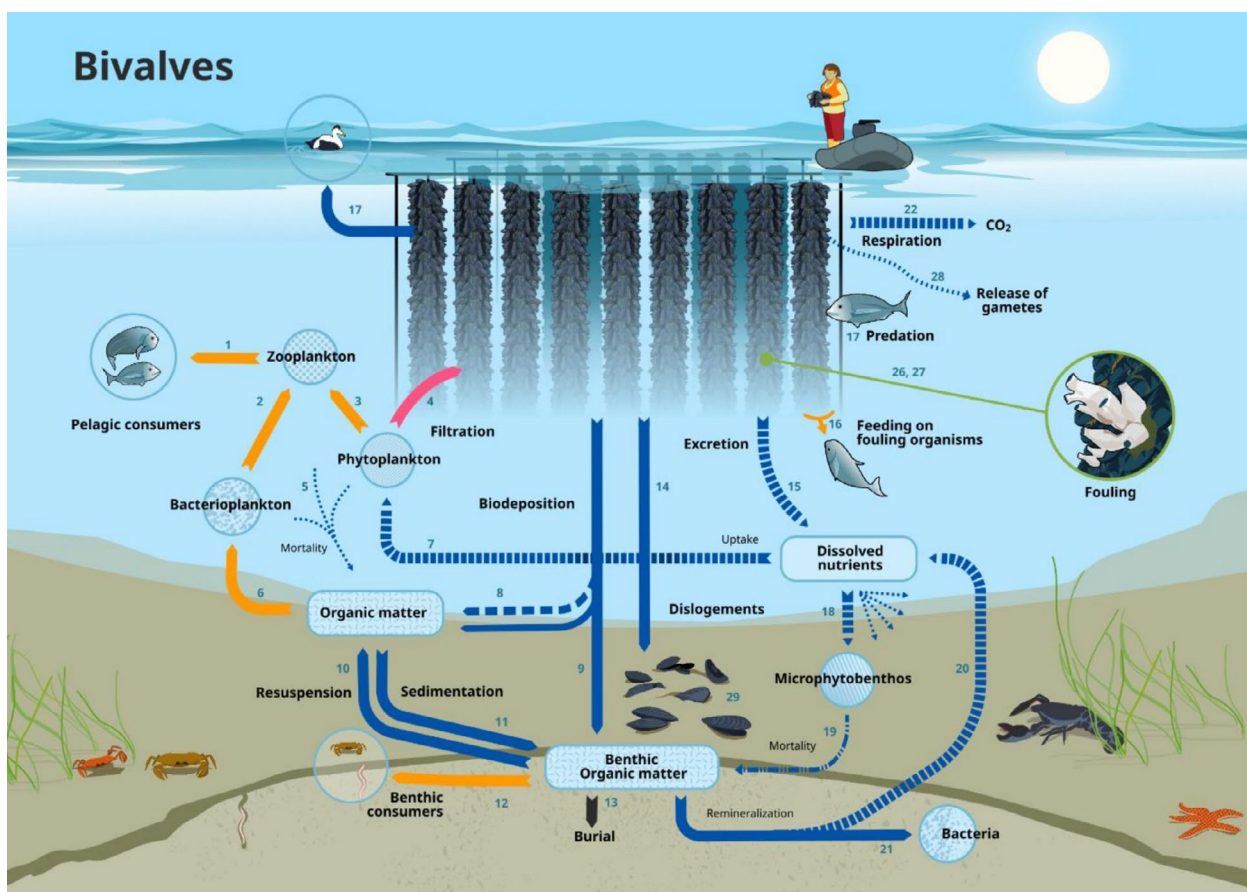


FIGURE 2 | Energy and nutrient fluxes from suspended bivalve farming to the environment. Individual flows (and respective numbers) are further explained in Table 1. Arrows describe the flow of energy and nutrients, with filtration of phytoplankton as the primary source of energy for the bivalves (pink), and subsequent direct (blue), and indirect (orange) fluxes.

the farm site (B28). Predation (B17) by finfish [50] and birds [46, 51, 55] may also represent an important export of energy from bivalve farms. Farms provide physical structures that support the development of diverse fouling communities. In addition to serving as attachment substrata, bivalve farms may also feed fouling organisms through metabolite excretion, thereby transferring to this farm-associated community a fraction of the energy gathered through ingestion of algae and organic matter. Part of this energy is subsequently lost through the grazing of fouling organisms (B16).

2.3 | Suspended Seaweed Farming

In the northern USA and northern Europe, seaweed farming is small-scale, seasonal and consists almost entirely of brown kelps (*Saccharina* spp.) [1, 90]. Similarly, kelp farms in Japan are small, mainly because these are operated manually. Small-scale farms differ greatly from the large-scale intensive and mechanized kelp farms in Korea and China [91]. Brown kelp species are typically farmed by suspension in the water column from a horizontal rope (cf. Figure 3). In contrast, tropical and subtropical seaweeds tend to be grown on ropes in close proximity to the benthos in the intertidal or shallow subtidal zone using fixed off-bottom monoline methods [92] and generally include red seaweeds, for example, *Gracilaria* spp., *Eucheuma* spp., or

Kappaphycus spp. Several different groups of seaweeds, including brown, red and green seaweeds are cultivated in China in a variety of different environments [93].

In all seaweed farms (Figure 3), a proportion of the farmed biomass is released to the surrounding waters via small particles sloughing off of fronds (S8) or entire blades dislodging and sinking to the seafloor (S14), and becoming consumed (S12) or buried (S13). These direct biomass inputs into the environment are analogous to mussel dislodgement from ropes or bivalves spawning. Seaweeds may also release large volumes of dissolved inorganic metabolites and organic compounds, for example, polysaccharides. Episodic release of spores may also occur, thereby exporting energy and nutrients from the farm (S28), though farmers strive to avoid the release of genetic material. Another type of direct nutrient and energy loss is via the consumption of seaweeds or fouling biota by birds (S4). Similarly, pelagic consumers may also feed directly on the seaweeds (S17) and on associated fouling species (S16). The fouling organisms, for example, bryozoa, that develop directly on the seaweeds contribute to the reduction of organic matter in the farm (S27). Some of the fouling biota feed directly on seaweeds, but many simply grow on the available surfaces, without impacting the seaweed biomass (S26). Seaweed holdfasts are often covered by fouling biota, including a variety of small invertebrates that may serve as food for nearby consumers (S16).

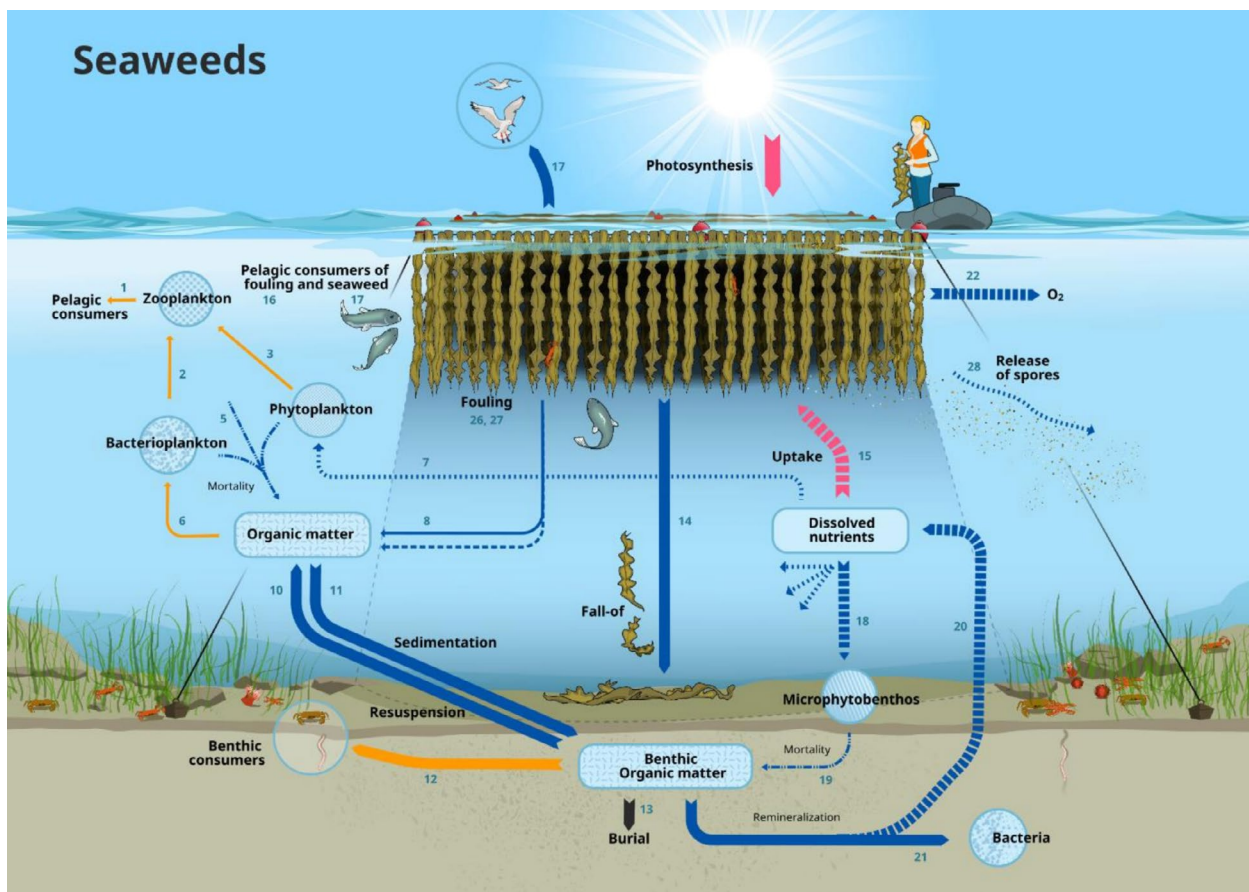


FIGURE 3 | Energy and nutrient fluxes from suspended seaweed farming to the environment. Individual flows (and respective numbers) are further explained in Table 1. Arrows describe the flow of energy and nutrients with principal sources of energy for seaweed (pink), direct (blue) and indirect (orange) fluxes.

Seaweeds are primary producers that release oxygen during photosynthesis (S22), whereas consumers such as finfish and bivalves release carbon dioxide during respiration (F22, B22). Hypoxia in sediment or water column develops when the oxygen demand for organic matter mineralization exceeds the oxygen supply through water renewal. Bivalve farming mitigates eutrophication-driven hypoxia through filtration of seston and acts as a nutrient sink [94]. However, under extreme conditions (e.g., low-oxygen conditions due to summer stratification) and in intensive mariculture, egested and excreted wastes, and the oxygen consumption by shellfish may contribute to oxygen depletion in coastal areas. This has been demonstrated in Rushan Bay (China) where the oxygen consumption associated with an intensive shellfish farm ($554,000 \text{ t year}^{-1}$) has been estimated at 253 Gg year^{-1} , contributing to seasonal oxygen depletion in the bay [94]. Similarly, a finfish-seaweed farm located in a highly sheltered coastal environment (Sansha bay, China) has been shown to contribute to seasonal hypoxia [95]. This study, using DIC isotopic mass balance, determined that in autumn, fish waste decomposition accounted for approximately 88% of DIC accumulation and in spring, macroalgal detritus-derived carbon contributed about 66% to DIC enrichment [95].

As primary producers, seaweeds take up dissolved nutrients (S15), competing with microphytobenthos (S18) and

phytoplankton (S7) over available nutrient resources. Dissolved organic matter released from seaweeds is readily mineralized by microbes (S21) and converted to inorganic nutrients (S20). Seaweed material that breaks off or is sloughed enters POM, which may be further decomposed by detritivores and water column microbes (S6), entering pelagic marine food webs (S1, S2, S3, S6, S7), or it may sink, providing food for benthic consumers (S12). On the seafloor, POM may be buried or resuspended (S10), thereby interacting once more with the pelagic microbial loop.

2.4 | Energy-Nutrient Interaction Mechanism of Mixed Aquaculture Systems

There is a variety of mixed aquaculture systems in operation involving more than one farmed species in a given water body. Integrated multi-trophic aquaculture (IMTA) is one of the most common examples, combining organisms from different trophic levels in the same farm system or area [96]. The practice of IMTA is inherently flexible and only necessitates that more than one species from more than one trophic level be grown in close proximity to each other, or be spatially separated but ecologically linked [97]. Different models of IMTA exist and could integrate fed species (e.g., finfish, shrimp), in combination with one or several extractive species, that typically recycle some of the waste products for a more connected ecosystem management

approach [98, 99]. These extractive species can be filter feeders (e.g., mussels, clams or oysters) or benthic detritivores (e.g., sea cucumbers), which remove POM and plankton, and/or primary producers (e.g., seaweed), which absorb dissolved inorganic nutrients [96].

Fluxes of nutrients and energy presented in the 3 conceptual monoculture models (cf. Figures 1–3) are relevant in an integrated aquaculture approach. In IMTA, some of the food and energy considered lost in monoculture are recaptured and converted into crops of commercial value [96]. Excretion of dissolved nutrients by farmed species (F15, B15) can be assimilated by phytoplankton (B7), which can then be filtered by farmed bivalves (B4). POM released by finfish (F8) can be a source of food for bivalves (B4) and biodeposition from finfish or bivalves farms (F9, B9, F24), a source of OM for detritivorous species (F12). Excreted nutrients or remineralization of POM (F20, B20) could become a source of dissolved inorganic nutrients for farmed seaweed (S15). Overall water quality can be improved when combining extractive species [100]. The energy and nutrients retained by the co-cultured species (in tissue and or shell) will be removed from the ecosystem during harvest.

Several physical and biological factors influence the nutrient retention efficiencies in IMTA [101], including hydrodynamics, biomass ratio among co-farmed species, the synchronicity between nutrient loading and uptake dynamics and the location of extractive species relative to the spatial distribution of nutrient streams [78]. Theoretically, nutrient retention of 79%–94% in a conceptual IMTA (fish–seaweed–bivalve–deposit feeder), decreases to 45%–75% for closed systems and 40%–50% for open systems [101]. In IMTA systems, to determine the optimal biomass ratio among co-farmed species, quantification of the fluxes released by one species and the assimilative capacity of the second species is required, over the overall and respective production cycle. For example, based on modelling approach, a study estimated that 6.7 kg of the kelp *Alaria esculenta* should be harvested to remove the dissolved N excreted by 1 kg of Atlantic salmon over a 2-year production cycle [102]. The collocation of species across different trophic levels can promote and strengthen fluxes that might not otherwise be apparent. Salmon aquaculture can locally enhance primary production and thereby support heightened growth of co-located bivalves [103]. Co-culture experiments conducted in the Tyrrhenian Sea, with mussels suspended at different distances within 1 km from fish cages, reported higher growth (length, weight, and biomass) for the mussels located close to the cages, under the direct influence of organic emissions, with respect to those located far from the farm. This difference was attributed to increased availability of organic matter and chlorophyll-a, indicating that the fish farm waste contributed to local nutrient enrichment and phytoplankton production, which in turn benefited the mussels [104]. In addition, mussels can directly ingest and assimilate fish farm-derived organic waste (e.g., uneaten feed and faeces), which supplements their diet and enhances growth. Additional experiments conducted with Mediterranean mussels grown nearby a seabass/seabream farm, reported that individuals can directly ingest and assimilate fish farm-derived organic waste (e.g., uneaten feed and faeces), which supplements their diet and enhances growth [105]. Contrarily, other studies have shown negligible benefits of bivalve-fish co-culture, with mussel

growth and condition at farms often comparable to those at reference sites, suggesting that waste-derived resources are not always accessible or consumed by extractive species [106–108]. Taken together, these results indicate that the fluxes of matter and nutrients and therefore the potential effects of IMTA can be highly context dependent.

3 | Aquaculture-Environment Interactions

The complexity of ocean structure and functioning, shaped by local physical, chemical, geological, and biological characteristics, hinders the generalization of the effects of aquaculture on energy and nutrient fluxes. In fact, the same farm, in terms of physical structure, stocking biomass, and farming practices, may lead to different ecological dynamics and consequences depending on local variables such as water circulation and depth, nutrient and oxygen availability, and species assemblages. Therefore, extrapolating aquaculture-environment interactions to other farming locations is not straightforward and requires the consideration of local conditions. The following seven case studies illustrate the effects of aquaculture on ecosystems categorized by aquaculture types (finfish, bivalves, seaweed) and farmed species, across a range of environments, from oligotrophic to meso-eutrophic in temperate and subtropical environments.

3.1 | Finfish Farming Case Studies

3.1.1 | Mediterranean and Black Sea (Oligotrophic, Temperate)

Finfish aquaculture in floating cages in the Mediterranean and Black Sea expanded from 5000 to 130,000 t during the 1990s and, despite periods of stagnation, subsequently increased to 520,000 t at the beginning of the 2020s [109]. The main species produced are the Gilthead seabream *Sparus aurata* and the European seabass *Dicentrarchus labrax*, which are farmed in a variety of environmental conditions but share common traits in terms of energy exchanges between the farm and the surrounding ecosystem. The main ecological effects surrounding these fish farms take place in the “zone of effect” [110], which is defined by the flux of organic matter, mainly excess feed and faeces, to the underlying seafloor (F9, F24) [111]. This flux of POM from farmed fish to the sediment organic matter pool showed that benthic impacts were manifested through changes in sediment geochemistry (redox potential, granulometry, organic carbon concentration) and benthic community indicators, indirectly linking the organic matter deposition flux to the energy transferred to benthic consumers (F12) [112]. Consequences of organic matter remineralization on sediment biogeochemistry, associated energy transfer to bacterial communities (F21), and fluxes of nutrients at the sediment–water interface (F20) were explored for different redox conditions in other works [113–116]. Regarding the fraction of energy transferred to wild species through feed loss consumption (F25), it was shown that fish species from different trophic guilds use excess feed either as a direct trophic resource or indirectly via predation on aggregated prey [32]. A follow-up study using stable isotope analysis on prawns targeted by artisanal fisheries, concluded that proximity to fish farms positively affected the body size (larger and heavier) while

no detectable effects on N isotopic values were reported [33]. In studies on the fouling communities (F26-F27) associated with Mediterranean fish cages [31, 117], the focus was zoological and did not quantify the transfer of energy from the farm to the surrounding ecosystem (F16). On the other hand, escapes of farmed fish in the Mediterranean, and their subsequent dispersal (F17) have received attention [118], with emphasis on their ecological interactions with wild stocks. Significant positive correlations were found between seabream escapes and fisheries landings at the Mediterranean level, suggesting that landings of seabream are now driven by aquaculture [119]. The potential role of artisanal fisheries in limiting the impacts of such interactions was also investigated, providing insights on the overall high recapture efficiency (64.7%), on the distance-recapture efficiency relationship, and on the influence of gears used [120].

3.1.2 | Red Sea (Oligotrophic, Subtropical)

Two commercial fish farms produced gilthead seabream at the northern end of the Gulf of Aqaba (Red Sea) from 1990 to 2006. The Gulf of Aqaba is oligotrophic and hosts some of the most diverse coral reefs recorded, though these farms were located at the outflow of the Nachal Arava stream; a sandy area that does not naturally harbor coral reefs. The artificial ecosystem established by the presence of the farms and by the fluxes of energy and nutrients released from them was unique. The sandy seafloor in this area was naturally covered by seagrasses, predominantly *Halophila stipulacea* and associated biota; after the cages were installed and stocked with fish, the seagrass community disappeared, most probably due to shading and the constant sedimentation of organic particles to the seafloor (F9 and F14, F23) [121]. The flux of organic matter from net cages to the seafloor was highest directly beneath the farm and decreased with distance as a function of prevailing east–west currents. As a result of the metabolism of the organic matter, the sediments below the cages became anoxic and sulfidic, triggering the development of a unique microbial community (F21), including the sulfide-oxidizing *Beggiatoa* spp., a suite of *Oscillatoria* spp., and various benthic microalgae and protists [122]. The farming gear in the water column (net cages, floats and buoys, ropes) served as settlement substrata for macroalgae and a variety of invertebrates (bryozoans, hydrozoans, tunicates, sponges, crinoids, barnacles, corals) (F16) and it was possible to trace the flux of nutrients from the farm (uneaten feed, faeces) to the fouling community using stable isotopes [36]. The biofouling community and the organic particles released from net cages served as feed (F16) for a community of foraging finfish that congregated around the cages, and attracted grazers (F16) and predators that prey on the foragers [123]. Planktivorous whale sharks, which visit the northern Gulf of Aqaba on an annual basis, were often seen at the fish farms, emphasizing the fact that these served as a hotspot of productivity. As a result of the congregation of wild finfish at the farms, large predators, including jacks, dolphins and sharks were often observed near the cages.

3.1.3 | Canada (Meso-Eutrophic, Temperate)

Finfish production in Canada is dominated by salmon aquaculture (82,729 t in 2023), accounting for 57% of the total Canadian

aquaculture production [124]. Since the 1990s, numerous studies have evaluated the interactions between salmon aquaculture and wild organisms. Significant changes to infaunal communities and increased abundance of *Beggiatoa* sp. have been observed below salmon cages [125]. Aquaculture induce organic enrichment (F9, F24) and increase sediment microbial activity (F21), potentially altering benthic community structure with enhanced anaerobic activity that may lead to sulfide accumulation with adverse effects on aerobic bacteria, plants and fauna due to progressive oxygen depletion [2]. A review of the effects of Atlantic salmon farms in southwest New Brunswick showed that changes in infaunal community structure and functional changes are mostly near-field effects, limited to the direct farm cage footprint, but also suggested the possibility of more far-field effects resulting from increased organic sedimentation (F11) [126]. Salmon farming in Newfoundland led to rapid changes in epibenthic communities with *Beggiatoa*-like bacterial mats and opportunistic polychaetes appearing when production began, although only in the near-field (100–160 m from the cages) [127].

The effects of salmon aquaculture on American lobster, *Homarus americanus*,—the species with the greatest commercial value in Canada [128]—is controversial. While some authors observed lobsters to be less abundant near salmon farms [129] and lobster catches nearby to be lower [130] (F12), other studies found no changes in lobster abundance below salmon farms [131, 132]. In contrast, rock crabs (*Cancer irroratus*) and green crab (*Carcinus maenas*) were shown to be associated with salmon farms (F12) in Nova Scotia and New Brunswick, respectively [133], with a negative effect on rock crab physiology as a result of including salmon feed in their diet. The association of macroinvertebrates and fish around net pens is a fairly common observation (F12, F16, F25) [134]. The lipid signature of animals in and on salmon net cages differed from those at reference sites, indicating a consumption of organic wastes from coastal salmon aquaculture by wild decapods (Rock crab *Cancer irroratus* and American lobster *Homarus americanus*) and reduction in the diversity of their diet (F25, F16) [39]. Likewise, juvenile Atlantic cod (*Gadus morhua*) may be receiving an energetic subsidy from salmon cages [37]. Salmon farms also attract cormorants, gulls, and other birds, either to the net pens or feeding on fish associated with them (F4) [135].

3.2 | Bivalve Farming Case Studies

3.2.1 | Thau lagoon, France (Oligotrophic, Temperate)

The Thau Lagoon is the main bivalve culture site on the French Mediterranean coast, with a total annual production of ca. 10,000 t (75% Pacific oyster *Magallana gigas*, 25% of Mediterranean mussels *Mytilus galloprovincialis*) [136]. This lagoon is a semi-confined system with inputs from both the surrounding watershed and the Mediterranean Sea. Thau Lagoon has been well studied due to its unique ecological and socio-economic characteristics [137, 138]. Bivalve production is carried out on metal structures called “tables” which employ lines for attachment and harvesting of the bivalves. Since the late 2000s, the operation of strategic wastewater treatment plants has reduced nutrient inputs from the watershed and the lagoon is becoming oligotrophic [139, 140]. Several studies

have evaluated the influence of bivalve farming on the benthos [141–144], the water column and the benthic-pelagic coupling in the lagoon [144, 145]. The farmed oysters have a clear effect (via excretion) on water column nutrient concentrations (B15), with recorded annual increases of 73%, 36%, and 19% for ammonium, phosphates, and silicates, respectively, in a comparison between culture sites and reference sites [146]. The direct and indirect influence of oyster cultures on the regeneration of nutrients in the water column (B15) and in benthos (B20) were quantified [145]. Bivalve filtration (B4) (top-down effect) and excretion of nutrients (B15) (bottom-up effects) have significant influence on phytoplankton turnover [144]. Episodes of mass mortalities in Pacific oysters in the lagoon have been recorded since 2008 [147]. This has led to changes in farming practices; in particular, farmers release more spat into the environment to maintain acceptable levels of production. The mortality of farmed bivalves and subsequent degradation and mineralization of their flesh is a source of nutrients [148, 149] that may affect the local planktonic community (B7) [148, 149]. Biodeposition rates are generally enhanced under oyster farms (B9) and were estimated to reach 300–500 kg ha⁻¹ year⁻¹ nitrogen and 3000 kg ha⁻¹ year⁻¹ carbon [150]. The concentration of nitrogen and phosphorus in bivalve culture sediments was greater than at reference sites [151], with consequences on the structure of the benthic communities [142, 144, 152] and on benthic mineralization rates (B20). Moreover, oxygen demand and nutrient release at the sediment–water interface were greater under adult oyster sites in comparison to reference sites [143, 153]. However, the biodeposition rates and benthic fluxes under juvenile oyster sites were similar to those at reference sites [144]. Predation on oysters by transient fish, particularly gilthead seabream (*Sparus aurata*) represents an export of energy from the bivalve farming area (B17). Gilthead seabream adapt their diets according to food availability [154]. During spring, seabream enter coastal lagoons and feed on bivalves (B17) until the autumn, when they leave [50]. To mitigate these losses, antipredator nets are deployed, but this leads to a reduction in bivalve growth rates due to reduced currents and food availability [50].

3.2.2 | Ireland and the United Kingdom (Meso-Eutrophic, Temperate)

The primary bivalve species cultured in the temperate NW European marine waters are blue mussels (*Mytilus edulis*) and Pacific oysters (*M. gigas*). The primary methods used are either longlines (mussels), bags on trestles (oysters), or on-bottom culturing (mussels, some oysters, and clams) – with numerous variations in the specific structures and methods used at individual sites to suit the needs of that site or location or to evaluate more efficient systems. Longline-grown mussels are suspended on structures from the surface. Seed is generally collected as wild spat (seed) on ropes and then on-grown to market size. Growth generally takes 1.5–2 years. On the trestle system the oyster bags are suspended on metal structures between 0.5 and 1 m off the seabed, in the lower intertidal zone. Growth varies by location and conditions but is generally between 18 and 36 months. Each of these cultivation methods affects energy flows, with some variation throughout the entire cultivation period. The bivalves require phytoplankton and organic carbon (B4); phytoplankton require nutrients from land-based sources (point and diffuse

sources) and form the cycle illustrated (B15, B8, B7, B6, B3, B2). Bottom cultivation requires a certain amount of husbandry, including predator mopping to remove starfish, sea urchins, and crabs (predation equivalent to B16). Farmers, working with fishers, will pot to remove crabs from mussel beds, impacting fluxes (B16, B17) by this practice. Any attraction of species potentially caused by farm structures is, to a varying degree, balanced by the predator control techniques used. Bottom mussel farmers will leave areas of their aquaculture sites fallow after a harvest to allow for substrate recovery. Husbandry requirements are lower on longlines, with fewer predator threats. Key input fluxes to the surrounding environment will be from the production of faeces and pseudofaeces (B8, B9). Poor site husbandry/management or extreme storm events may lead to oysters being released from the pouches which will produce an energy flow similar to dislodged mussels from longlines (B14), escapee fish (F17), or seaweed fall-off (S14). Predation by birds (B17) leads to biomass loss where bottom grown mussels are located in shallow areas [46]. The trestle system keeps the oysters off the seabed, allowing them to feed more efficiently on the plankton in the water (B4) while also protecting them from predators. The trestle structures will influence the local hydrodynamics, slowing down currents and facilitating greater deposition in the area under the trestles. Suspended bivalve culture structures such as buoys and platforms provide perching areas for sea birds. A greater number of species and abundance of birds have been observed in suspended mussel culture sites in Ireland than in a series of control sites [51]. Birds are also attracted by the diverse communities of organisms growing on the farm-associated gear offering a potential food source for a variety of species (B17) [51]. There are reports of farmed Pacific oysters becoming feral and establishing self-sustaining populations in some bays (B29), as a result of aquaculture [155]. This established non-native species population is a significant ongoing addition to the local environment.

3.3 | Seaweed Farming Case Studies

3.3.1 | Gulf of Maine (Meso-Eutrophic, Temperate)

Seaweed cultivation in the northeast USA consists almost entirely of brown kelp, *Saccharina latissima* and *S. angustissima* [90]. Most of these farms are ephemeral and are entirely removed after harvest in the spring to accommodate space for setting lobster traps [90]. In this way, seaweed farming is decoupled from many of the described energy flows during the summer and fall months when mobile fauna are most active [156] and when biogeochemical processes are accelerated [157, 158]. Because of this, seaweed farming in the Gulf of Maine provides temporary sheltering habitat and does not appear to have a substantial impact on biodiversity [156], which contrasts to seaweed farming activity in other regions of the world [159].

3.3.2 | Faroe Islands (Meso-Eutrophic, Temperate)

The Faroe Islands represent a unique environment for seaweed culture. The Gulf Stream provides relatively warm (5°C–11°C) and saline water throughout the year. As the Faroe Islands are located in the middle of the North Atlantic, high waves

and strong currents create exposed open ocean conditions in close proximity to the shore and farm units experience high energy marine conditions. Nutrient levels in the Faroe Islands are fairly high due to year-round upwelling caused by weak water stratification, providing good growth conditions for seaweeds Bak et al., Mols-Mortensen et al. [160, 161]. The natural seaweed community is diverse. The stable water temperatures enable seaweed farming to continue until late summer, even allowing multiple harvests, with growth rates dropping in September due to reduced sunlight, and resuming in March [160, 162]. Furthermore, the strong currents and clear waters allow for unique “vertical seaweed farming” with 10 m deep grow-lines. Seaweed farming structures are generally left in the water for as long as 3 years to enable continuous cultivation, leading to year-round energy flows, such as the release of organic matter from seaweeds (S8, S11, S14), which even increases during the winter months due to high-energy events, that is, storms and high waves. Sedimentation of particulate matter to the seafloor below the seaweed lines is minimal due to the strong currents that disperse the organic residues widely (Grandorf-Bak, unpublished data). Other energy flows, such as pelagic consumers feeding on cultivated seaweed or small invertebrates living within the algae (S16, S17) [159, 163] and fouling of seaweed and farm gear (S26), persist throughout the year, though seaweed biomass is reduced in the winter months, as growth rates drop.

4 | Beyond the Farm: Considerations of Aquaculture-Environment Interactions and Management Implications

The FAO's EAA [16] has the ambition to develop aquaculture while balancing human well-being with the maintenance of ecosystem functions and services; these objectives should be achieved within the context of other sectors and policies. This section will explore how the analysis of energy fluxes related to aquaculture contributes to our understanding of ecosystem functions and services. This is addressed by examining: (i) interactions with fisheries (i.e., the other maritime sector producing food); (ii) ES provided by aquaculture; (iii) interactions with nature conservation priorities and (iv) aquaculture regulations.

4.1 | Potential Effects of Farm-Derived Energy and Nutrient Fluxes on Fisheries

Aquaculture farms serve as sources of energy and nutrients that may stimulate productivity and attract or repel wild species [4], including commercially important species, potentially enhancing or reducing local fisheries [164, 165]. For pelagic species, fisheries enhancement could be particularly relevant in oligotrophic waters where low nutrient levels limit primary production and, subsequently, fisheries landings. For benthic deposit and suspension feeders, the deposition of POM from aquaculture (F14, B14, S14) may increase food availability, potentially leading to increased productivity of fisheries [159, 165].

Farms can also act as a source of dissolved nutrients (F15, B15), which can enhance primary productivity at large spatial scales

in oligotrophic systems [166], which in turn carries the potential to induce a trophic cascade, increasing consumption by wild species at higher trophic levels [32]. The effect fish farms can have on fisheries landings has been corroborated by scientific evidence. For example, the analysis of different auction sites (fish-wharfs) in Greece showed increased fisheries landings in areas with a high density of fish farms compared to areas without or with a low density of farms [167]. The areas with high landings were characterized by an increase in fish biomass in communities without leading to a decrease in diversity, as this increase in biomass was observed not only in species consuming organic waste beneath the cages but also in pelagic and demersal species [167]. These changes suggest that in addition to the direct consumption of excess feed and faeces, nutrient enrichment boosting primary production, and rapid nutrient transfer through the food web contribute to an overall productivity enhancement [167]. A similar study in Spain revealed no benefit in catches, income, or species composition of a small-scale fishery in areas near a fish farm compared to areas away from farms [168]. It is possible that local effects, including the behaviour of the target species, fishing techniques, and access to the farming area for fishing may affect the outcome of such analyses [168]. Similarly, the natural environment may also play a role, as areas with enhanced landings in Greece shared characteristics such as enclosed bays and gulfs with fish farms surrounding the area where the fishing fleet operates [167].

As described in Section 3.1, farms release POM to the environment (F9, B9, S14) that rapidly settles to the ocean floor and may be consumed by detritivores and omnivores, potentially leading to fisheries enhancement. Structures associated with aquaculture farms, including cages, predator exclusion devices, and even the oysters themselves in uncaged (e.g., on-bottom) farms, are well documented as providing habitat for foraging by other species [169–173], including commercially significant Pacific salmon [174] and Dungeness crab [165, 175]. As discussed above, the interaction between salmon farms and lobster fisheries in Canada is debated, with some works suggesting a negative effect of the farms, leading to lower catches in the vicinity of the farms [130, 176], and others describing a lack of effects [131, 177]. Other researchers argue that the two main drivers impacting lobster distribution, hypoxia and therapeutants, should be addressed with existing regulatory compliance, minimizing the potential negative impact on lobsters [178]. Additionally, it has been argued that even if localized lobster displacement exists, the impacts would be negligible when considering the fishery as a whole [179].

While these interactions are better understood at finfish farm sites, sheltering and direct feeding have recently been documented at non-fed bivalve and seaweed farms. For example, higher finfish abundance was observed near oyster and mussel farms than at reference sites, with grow-out gear functioning as an artificial reef [180–182]. Beyond sheltering, the diet of wild snapper caught within mussel farm sites differed from non-farm reference sites, demonstrating direct feeding on mussel crops [55]. It is important to emphasize that these environmental interactions are site-specific and the scientific discourse provides contradictory evidence, ranging from the decrease in fisheries landing with the addition of seaweed farms [183], to negligible effects on landings

due to the mismatch between seaweed farming and finfish migration [156], and to an increase in fisheries landings [6, 159, 163, 184]. Due to the potentially high concentration of wild species around farms, several authors have argued that, where fishing is restricted, farming areas could effectively function as small marine protected areas, potentially contributing to wild stocks through increased feeding and wild fish biomass [123, 185–190].

Beyond the potential effect on fisheries landings, it is important to broaden the view towards ecological and social effects: aquaculture-enhanced fisheries production will likely have positive effects for fishers' income (as long as higher market supply does not reduce prices) and thereby community well-being. This is particularly true for those cases where fishers' livelihoods are intertwined and directly being enriched by aquaculture operations: [191] showed how seaweed aquaculture provided alternative income for small-scale fishers and an increase in social capital, which released pressure and reliance on overfished fisheries resources. At the same time, farm-derived flux effects might negatively affect fishers' operations and incomes when leading to the degradation of habitat that is crucial for fisheries resources. An example for this was presented by Lyimo et al. [192] showing how seaweed aquaculture degraded seagrass beds and by that reduced the income of shellfish collectors.

4.2 | Ecosystem Services Originating From Aquaculture

Farms interact with their surrounding ecosystem and may have a greater or lesser effect depending on the farmed species, gear type, farming intensity, location, and other factors. The ecosystem supports farm production, especially for extractive species that rely on ambient sources of nutrition (i.e., phytoplankton, detritus, nutrients). The farm influences nutrient cycling and energy flows, potentially affecting the delivery of ES. These interactions and outcomes may be positive or negative, depending on the specific local characteristics, the ecosystem service and the normative evaluation of the human community concerned.

Food provisioning is the main ES delivered by aquaculture [193]. Aquaculture-environment interactions expressed through nutrient dynamics may play a role in the delivery of regulating ES. For example, the uptake of carbon and deposition of organic matter in seaweed farming may lead to carbon sequestration (regulating service) [194, 195]. Moreover, direct uptake of (excess) nutrients by seaweeds (S9) and indirect uptake by bivalves can improve water quality (regulating service) [6, 196–197]. The physical presence of farming gear (e.g., seaweed lines) or farmed biomass (e.g., oyster beds), may function as wave barriers and serve as living shorelines, mitigating negative effects of sea level rise (regulating service) [198], serving as a supporting ES. The three-dimensional structure of farm gear provides habitat for wild organisms, enhancing biodiversity (supporting service) [159, 199], which is intrinsically linked to restorative functions and the delivery of ES, potentially contributing to climate resilience [200, 201]. Aquaculture farms are not a replacement for wild habitats but may provide a beneficial “boost” to local biodiversity or biogeochemical cycling (supporting services) [6, 159, 163]. Aquaculture

activities support a cultural lifestyle and sense of place and employment on or near the ocean [202].

EAA principles require aquaculture to be developed in harmony with other activities. Promoting public understanding of ES derived from sustainable aquaculture may enhance social acceptance of the industry [199], especially in highly contested situations, and encourage industry alignment with EAA principles towards improved marine management. Including aquaculture-derived ES in aquaculture regulation, management and practices would further promote EAA principles and would likely ensure that aquaculture continues to contribute to ecosystem service delivery. The interdisciplinary concept of CC defines the limits of unacceptable change [10, 203–205] and could be used as a framework to operationalize the assessment of trade-offs in ES affected by aquaculture.

4.3 | Aquaculture and Ecosystem Functions

The potentially positive impacts of aquaculture, for example, related to ecosystem service provisioning, as discussed above, have recently gained recognition in restoration debates. Multiple protection regimes (e.g., MPAs) are enforced in the sea (see, e.g., IUCN MPA categories)— [206] and aquaculture could potentially be integrated into some of these due to the potential positive outcomes derived from the delivery of ES [207]. Some authors argue for the inclusion of aquaculture in the concept of OECMs (“Other Effective Area-Based Conservation Measures”) [208], potentially contributing to the achievement of international targets on ocean protection [209, 210]. Other works propose to apply IUCN global standards for Nature-based Solutions (NbS) to social-ecological systems and the inclusion of aquaculture in these frameworks [207]. As defined by the Nature Conservancy, “Restorative aquaculture occurs when commercial or subsistence aquaculture provides direct ecological benefits to the environment, with the potential to generate net positive environmental outcomes” [200].

The comprehensive mapping of the pathways of energy and nutrient fluxes from aquaculture to the environment is a key prerequisite for considering an aquaculture farm as a candidate for OECM, restorative aquaculture, or NbS implementation. Knowledge gaps and research needs to advance the understanding of habitat values provided by bivalve and seaweed aquaculture have been identified [159]. This review presents examples of both the contributions and limitations of bivalve and seaweed aquaculture in providing structured habitat, supplying food resources to other species, and supporting the reproduction of wild stocks of native species. In parallel, the study synthesized quantitative evidence on the effects of aquaculture on the abundance and species richness of wild fish and mobile macroinvertebrates. Beyond habitat creation and cascading effects on productivity and biodiversity, bivalves and seaweeds can play a role in ocean restoration via extractive processes, improving water quality through the removal of particulate matter, pollutants, and dissolved nutrients from the water column [193]. These ES align aquaculture with the NbS principles when farming activity is conducted within the ecological CC of the ecosystem. Documenting energy and nutrient fluxes from aquaculture is needed to

evaluate both the NbS performance of farming activities and the ecological CC of the ecosystem. Accordingly, these fluxes help determine the role of aquaculture in ecosystem functioning; however, the relevance of site-specific characteristics, production levels, and aquaculture practices in shaping these fluxes calls for an integrated site-level assessment rather than broad extrapolation [6].

4.4 | Considerations for Aquaculture Regulations

Fluxes of energy and nutrients and subsequent effects on the food web are usually not at the core of aquaculture regulations and constitute a clear example of the complexity of bridging the science-policy interface. While policies require straightforward and unambiguous (scientific) information to set regulations that can be applied to a broad range of farming sites within a jurisdiction, science suggests that the inclusion of local settings and site-specific conditions is essential to understand the potential effects of farm(s) on the environment. This scale-mismatch likely contributes to aquaculture regulations commonly being focused on more pragmatic metrics that do not rely on understanding these local nuances but are grounded on more general and quantifiable effects. This relates, in particular, to fluxes of energy and nutrients that are challenging to monitor and quantify, thereby leading to aquaculture regulations that focus on the consequences of these fluxes rather than on the fluxes themselves. Thus, regulations usually focus on ecosystem compartments for which monitoring is easiest to implement (and potentially enforced), such as the benthic environment. This is evident from the strong bias of ecological indicators of aquaculture effects towards the benthic environment for finfish [211] and bivalves [12]. While some indicators, such as the Shannon Diversity Index or Species Richness, capture to a certain degree the effects on the food web, these are commonly restricted to the benthic community and focus on sessile species, reinforcing this bias.

EAA embraces a multi-scale approach, ranging from the local to the watershed/bay and regional/national scales, and recognizes interactions across scales. Consequently, the focus on the local setting may cause us to miss impacts related to fluxes of energy and nutrients at larger spatial scales. The complexity of integrating these aquaculture environment interactions into regulations calls for rethinking the current regulatory paradigm if the goal is to embrace EAA principles and ultimately achieve sustainable aquaculture. For example, in Atlantic Canada, salmon farming regulations primarily focus on near-field effects, which, together with conflicting scientific findings regarding the interaction of salmon farms with lobster catches [130, 132, 176, 179] have contributed to social opposition among lobster fishers [212]. Regulatory frameworks should meaningfully embrace EAA principles by: (1) enabling adaptive management that accounts for complex interactions across scales and iteratively assesses (and reduces, if necessary) aquaculture impacts, and (2) integrating key stakeholders and their potentially diverging backgrounds, interests, power and affectedness into decision-making processes to promote fair participation and equity among all users of the public commons. The limited adoption of EAA [213] demonstrates the challenges to implementing these principles, yet a transformation towards EAA-guided aquaculture development is urgently needed amidst an ever growing societal need for sustainable seafood production.

5 | Conclusions

Energy and nutrients stemming from aquaculture can alter biogeochemical cycles and modify trophic relationships, potentially affecting ecosystem functioning, the delivery of ES, and human livelihoods depending on aquaculture and other marine-based activities. Consequently, understanding the fluxes of nutrients and energy is essential to estimate the ecological CC of an aquaculture site, a critical tool for developing aquaculture in accordance with EAA principles, and ensuring the long-term sustainability of the industry. Although effects differ among farmed species, particularly between fed and non-fed species, several commonalities emerge across farming systems, from local effects on the benthic environment to interactions with wild species. This study highlights the complexity of quantifying energy and nutrient fluxes, as the characteristics of the farm and local environmental conditions shape ecosystem responses. As demonstrated in the case studies presented here, even within very similar environments, outcomes and conclusions may differ, which adds another layer of complexity to understanding the ecosystem-level and societal implications and externalities of aquaculture. This complexity precludes the extrapolation of effects across farming areas, making each farming site unique regarding its potential impacts on ecosystem structure and functioning. This complexity is evident in the wide range of ecological indicators available to assess the ecological effects of aquaculture, and the lack of a standardized set consistently applied across jurisdictions [12, 211]. While aquaculture management has often avoided this holistic analysis of ecosystem-level interactions in favor of pragmatic regulations that may be realistically implemented, it is important to acknowledge these potential effects. This is particularly relevant when fluxes of energy and nutrients affect other human activities or priorities, such as fishery production and marine conservation, or alter the delivery of ES. Therefore, the main management recommendations stemming from this work reiterate the EAA principles by emphasizing the adoption of adaptive management and the inclusion of key stakeholders and rights-holders in the decision-making process. Adopting adaptive management measures, that is, iterative assessment of fluxes and impacts, is key to promoting sustainable aquaculture in line with the EAA and helps bridge the current science-policy gap for these potential ecosystem-level effects. The meaningful inclusion of key stakeholders into decision-making processes is also critical to ensure that the aquaculture industry not only meets production goals but also maintains the social-ecological integrity of marine systems and is compatible with other ocean uses. Future actionable recommendations for sustainable aquaculture will require a site-specific and holistic assessment of the farming area in the context of the local social-ecological system, that is, considering not only the natural ecosystem, but also the economic, social, and governance dimensions.

Author Contributions

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Disclosure

The authors confirm that during the preparation of this work, no generative AI was used.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

Data sharing not applicable to this article as no datasets were generated or analysed during the current study.

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