

# Farm-scale models in fish aquaculture – An overview of methods and applications

Killian Chary<sup>1</sup>  | Daniele Brigolin<sup>2</sup>  | Myriam D. Callier<sup>3</sup> 

<sup>1</sup>Aquaculture and Fisheries Group, Department of Animal Sciences, Wageningen University and Research, Wageningen, The Netherlands

<sup>2</sup>Department of Architecture and Arts, Università IUAV di Venezia, Venezia, Italy

<sup>3</sup>MARBEC, University of Montpellier, IRD, CNRS, Ifremer, Palavas-les-Flots, France

## Correspondence

Killian Chary, Wageningen University and Research, De Elst 1, Building 122, 6708 WD Wageningen, The Netherlands.

Email: [killian.chary@wur.nl](mailto:killian.chary@wur.nl); [killian.chary@gmail.com](mailto:killian.chary@gmail.com)

## Funding information

French Ministry for Food and Agriculture; French Ministry of the Sea; Institut Français de Recherche pour l'Exploitation de la Mer

## Abstract

Models are important tools to address sustainability challenges associated with developing aquaculture at farm, regional and global scales. Farm-scale models (FSMs), which are integrated mathematical models developed to simulate farm operations, can quantify energy, mass or economic input flows and predict a variety of outputs such as fish biomass, waste and by-products. The variety of farming systems, equations available to build the models, and objectives of applications and intended users has resulted in the publication of wide range of FSMs. We performed a narrative review of 36 fish FSMs published from 1985–2021 to address several questions: Can the main characteristics of these models be defined? How do the farming system studied and the objectives of the study influence model development? What are the main modelling techniques available to simulate the main processes of a fish farm, and what are their advantages and disadvantages? How can FSMs help address sustainability challenges of aquaculture? This review discusses advances, limitations and future lines of research related to FSMs to help select existing models, or develop new ones, that are suitable for their intended use and users. The article is structured according to the main steps of the modelling process: (i) definition of scope and objectives; (ii) process formulation and model selection at individual, cohort and farm levels; (iii) implementation and evaluation; and (iv) applications (e.g. precision fish farming, IMTA modelling, supporting spatial management, life cycle assessment). At each step, recommendations are provided and research needs are stated.

## KEYWORDS

bioeconomic and environmental impacts modelling in aquaculture, decision-support tools, ecosystem approach to aquaculture, farm management, fish farming, individual-level models

## 1 | INTRODUCTION

The increase in the global population, concurrent with an increase in per capita income and an associated shift to diets rich in animal

protein, is increasing demand for seafood products.<sup>1</sup> Considering the current status of wild stocks<sup>2</sup> and the plateauing of<sup>2</sup> or decline in<sup>3</sup> global fisheries production despite improvements in management, aquaculture could provide an increasing and significant proportion of



This article is a Sena De Silva paper.

The Sena De Silva paper is an honorific title dedicated to the memory of Professor Sena De Silva, who was the founding editor of *Reviews in Aquaculture* and a globally renowned aquaculture scholar, pioneer and advocate. The title is awarded to high quality articles that excel in one, or more, of the following qualities: i) Novelty and originality; ii) Likelihood of direct positive impacts for the aquaculture sector, with keen focus on any of, or all three: environmental sustainability, economic viability, and social responsibility iii) Overall quality of scientific reasonings coupled with real-world applicability.

This is an open access article under the terms of the [Creative Commons Attribution](https://creativecommons.org/licenses/by/4.0/) License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

© 2022 The Authors. *Reviews in Aquaculture* published by John Wiley & Sons Australia, Ltd.

animal-protein intake at the global level. Global aquaculture currently produces ca. 114.5 million tonnes of products per year, with a value of over 217 billion euros, representing 52% of the total aquatic food supply for human consumption.<sup>2</sup> The sector is projected to continue growing, with an additional 26 million tonnes of aquatic animals produced in 2030.<sup>2</sup> Aquatic animals (including fish, crustaceans and molluscs), which represented 72% of global aquaculture production by mass in 2018, was dominated by fish.<sup>2</sup>

In 2008, the Food and Agriculture Organisation and international experts developed a strategy to 'better integrate aquaculture activity within its ecosystem in a way that it promotes sustainable development, equity, and resilience of interlinked social and ecological systems' called the 'ecosystem approach to aquaculture' (EAA).<sup>4</sup> The EAA has three main objectives: ensure both (i) human well-being and (ii) ecosystem health (i.e. preserve ecosystem functions and services) and (iii) facilitate the achievement of both in the context of other sectors and policies. To implement EAA, the farm (i.e. from a few tens to hundreds of m<sup>2</sup>, depending on farm size, technology and species), the aquaculture zone or hydrosystem (i.e. waterbody and watershed) and the global scale were identified as the three relevant scales of analysis and action. At the farm scale, major sustainability challenges include mitigating negative impacts of nutrient emissions, decreasing escapes of farmed species, controlling the appearance and spread of diseases, and increasing productivity and ensuring economic viability of individual facilities. Priorities at the aquaculture zone level include mainly the planning and definition of appropriate locations for siting,<sup>5</sup> as well as defining the ecological carrying capacity (i.e. the maximum density of cultured species that does not cause unacceptable ecological impacts<sup>6</sup>) of hosting ecosystems.<sup>7,8</sup> Core issues at the global scale include reducing pressure on wild stocks caused by production of aquaculture feed,<sup>9</sup> decreasing the material and energy footprint of aquaculture, predicting effects of climate change on aquaculture production<sup>10</sup> and developing circular and integrated aquatic food systems.<sup>11</sup>

At each scale, models can play an important role in addressing many of these issues, and developing them is of great relevance to translate EAA principles and recommendations into action.<sup>4,12,13</sup> Models can be used as research tools to describe complex real systems in conceptual objects, reveal system properties, establish research priorities, test scientific hypotheses and help design experiments.<sup>14,15</sup> They can also be used as management and decision-support tools based on scenario analysis, whether the scenarios are predictive (what will happen?), exploratory (what could happen if?) or normative (what should happen?). According to the EAA framework,<sup>4</sup> tools designed at the farm scale should focus on evaluating externalities of inputs and outputs, improving management, facilitating budget calculation (e.g. biomass, nutrients, monetary) and estimation of theoretical maximum farm production (i.e. production carrying capacity<sup>16</sup>) and evaluating the feasibility of integrated multitrophic aquaculture (IMTA). In IMTA systems, species from multiple trophic levels are farmed together at the same site, on the same farm<sup>17</sup> or over a large area<sup>18</sup> to benefit from increased use of nutrient loads and species interactions.<sup>19</sup> According to the EAA, farm-scale tools are also perceived as useful for aquaculture zoning and site selection, area management<sup>20</sup> and more specifically for assessing ecological carrying capacity and compliance with environmental regulations.<sup>12</sup> These objectives require

understanding physical, biological, ecological and economic interactions and processes that occur among the many components of a complex system. This can be facilitated by modelling these processes, as is the case in farm-scale models (FSMs).

The literature regularly uses 'FSM' and similar terms, but these terms may describe a variety of types of models applied in aquaculture. Farm-scale modelling is rarely defined clearly, and its main defining features are rarely specified, suggesting it has not been applied long enough to establish a model-development process or standard terminology. In this review, we define FSMs as integrated dynamic mathematical models developed to simulate farm operations in a given farming system over a defined period (from a few weeks up to an entire farming cycle) to quantify energy, mass or economic inputs flows (e.g. water, feed, fingerlings, money), and use of operations in the system, which produces fish biomass (i.e. harvests and stocks) and other output flows, including waste and by-products (e.g. dead fish, effluents). In this definition, focus is placed on processes that occur within the farm boundaries, thus excluding many of the near- and far-field effects of aquaculture<sup>21</sup> that require considering environmental processes at larger scales. As this review focuses on fish, the acronym 'FSM' will refer hereafter to fish FSMs. Finding an adequate balance of complexity and data requirements and ensuring that the FSM is fit for purpose requires considering several issues during model development. Some of these issues include: what questions the model will address (why?), what type of model is required (how?), what outputs are expected (for what?) and for whom the tools and results are intended. Guidelines for FSM-specific modelling are needed to better understand how these questions should be addressed during the modelling process, and more generally to increase the accuracy, utility and rigour of models that are developed for various uses and users.<sup>22</sup> To our knowledge, no such guidelines are available, and no reviews have attempted to examine critically how the FSMs developed to date have addressed these steps. Furthermore, to our knowledge, no recent review has focused on FSMs applied to fish farming. Although a book chapter on FSMs applied to shellfish systems has been published,<sup>23</sup> these systems differ greatly in the metabolism of the animals farmed, their extractive feeding behaviour and farm management. Reviews of FSMs for fish farming have had a limited scope, focusing on economic aspects<sup>24</sup> or on a single species and specific contexts.<sup>25</sup>

The present study provides a narrative review of the modelling process for fish FSMs based on guidelines developed for ecological/environmental models.<sup>14,15,22,26</sup> This review includes models published from 1985 to January 2021 that cover different species, rearing systems and ecosystems and were developed to explore production, environmental or economic aspects of fish farming. The literature search was conducted in the Web of Science and Google Scholar databases using combinations of the terms 'fish farming', 'aquaculture', 'model', 'modelling', 'farm-scale', 'production' and 'simulation'. The 'snowball' method was then used to expand the search. Only models described in peer-reviewed journal articles and PhD theses in English were included. Table 1 summarises the 36 FSMs considered in our review.

The review is organised according to the main steps of the modelling process, with a particular emphasis given to the model-selection step. In Section 2, we describe how the definition of the context

TABLE 1 Farm-scale models reviewed in this study, ordered by type of aquaculture system

Model name	Area of primary application	Ecosystem	Aquaculture system(s)	Fish species	Highest organisation level	Key modules and processes					Report of model or module validation	Reference (s)
						Individual or population (growth) model category	Biological waste	Waste treatment	Environmental risk or impact	Economic		
N.S.	USA	Freshwater	Earthen pond	<i>Ictalurus punctatus</i>	Rearing unit	Traditional bioenergetic	Egestion	No	No	No	No	27-29
N.S.	Italy	N.S.	Pond	<i>Dicentrarchus labrax</i>	Farm	Simple growth function	-	No	No	Yes	No	30
N.S.	Thailand	Freshwater	Earthen pond	<i>Oreochromis niloticus</i>	Rearing unit	Traditional bioenergetic	-	No	No	No	Yes	31
POND	Thailand, Honduras, Brazil, Poland, USA	Freshwater	Earthen pond	<i>Oreochromis niloticus</i> <i>Colossoma macropomum</i> <i>Piaractus brachipomus</i> <i>Cyprinus carpio</i> <i>Ictalurus punctatus</i>	Farm	Simple growth function	Egestion and excretion	No	Yes	Yes	Yes	32,33
AquaFarm	N.S.	Freshwater Marine	Earthen pond Cages Flow-through Recirculated Hatchery	<i>Oncorhynchus mykiss</i> <i>Oncorhynchus tshawytscha</i> <i>Salmo salar</i> <i>Ictalurus punctatus</i> <i>Oreochromis niloticus</i>	Farm	Simple growth function and traditional bioenergetic	Egestion and excretion	Yes	Yes	Yes	Yes	34
N.S.	Republic of Congo	Freshwater	Earthen pond	<i>Oreochromis niloticus</i> <i>Clarias gariepinus</i> <i>Parachanna obscura</i>	Rearing unit	Simple growth function	-	No	No	No	Yes	35
N.S.	Portugal	Brackish or marine	Earthen pond	<i>Diplodus sargus</i>	Rearing unit	Dynamic Energy Budget	Egestion	No	Yes	No	Yes	36,37
ERA-AQUA	Vietnam	Freshwater	Earthen pond	<i>Pangasionodon hypophthalmus</i>	Rearing unit	Simple growth function	Egestion and excretion	No	Yes	No	No	38
N.S.	Thailand, Vietnam	Freshwater	Earthen pond	<i>Oreochromis niloticus</i> <i>Pangasius bocourti</i>	Rearing unit	Simple growth function	Egestion and excretion	No	Yes	No	Yes	39

TABLE 1 (Continued)

Key modules and processes												
Model name	Area of primary application	Ecosystem	Aquaculture system(s)	Fish species	Highest organisation level	Individual or population (growth) model category	Biological waste	Waste treatment	Environmental risk or impact	Economic validation	Report of model or module validation	Reference (s)
AQUASMAT	Nigeria	Freshwater	Earthen pond Tanks	<i>Clarias gariepinus</i>	Rearing unit	Traditional bioenergetic	Egestion and excretion	No	Yes	Yes	Yes	40,41
N.S.	N.S.	Freshwater	Hatchery	<i>Oncorhynchus mykiss</i> <i>Salmo salar</i>	Farm	Simple growth function	Excretion	Yes	No	No	No	42
N.S.	USA	Freshwater	Flow-through	<i>Oncorhynchus kisutch</i> <i>Oncorhynchus tshawytscha</i>	Farm	Traditional bioenergetic	Egestion and excretion	Yes	No	No	Yes	43
RACEWAY	N.S.	Freshwater	Raceway	<i>Oncorhynchus mykiss</i> <i>Salmo salar</i>	Farm	-	Excretion	No	Yes	No	Yes	44
N.S.	N.S.	Freshwater	Raceway Recirculated	<i>Sparus aurata</i> <i>Salmo salar</i> <i>Oncorhynchus mykiss</i>	Farm	Simple growth function	Excretion	No	Yes	No	Yes	45
RDSS	N.S.	N.S.	Raceway	<i>Oncorhynchus mykiss</i> <i>Salvelinus fontinalis</i> <i>Salmo trutta</i>	Farm	Simple growth function	Excretion	No	Yes	Yes	No	46
N.S.	N.S.	N.S.	Recirculated	<i>Sparus aurata</i>	Farm	Simple growth function	-	No	No	Yes	No	47
N.S.	N.S.	N.S.	Recirculated	<i>Oncorhynchus mykiss</i>	Farm	Simple growth function	Egestion and excretion	Yes	No	No	No	48
N.S.	Israel	N.S.	Recirculated	<i>Sparus aurata</i> <i>Dicentrarchus labrax</i>	Farm	Simple growth function	-	No	No	No	Yes	49,50
N.S.	Netherlands	N.S.	Recirculated	<i>Clarias gariepinus</i>	Farm	Simple growth function	Excretion	Yes	Yes	Yes	No	51
INAPRO	N.S.	Freshwater	Recirculated Aquaponics	<i>Oreochromis niloticus</i>	Farm	Traditional bioenergetic	Egestion and excretion	Yes	Yes	Yes	No	52

(Continues)

TABLE 1 (Continued)

Model name	Area of primary application	Ecosystem	Aquaculture system(s)	Fish species	Highest organisation level	Key modules and processes						Reference (s)
						Individual or population (growth) model category	Biological waste	Waste treatment	Environmental risk or impact	Economic	Report of model or module validation	
FIS-C	USA	Freshwater	Cage	<i>Oncorhynchus tshawytscha</i>	Rearing unit	Traditional bioenergetic	Egestion and excretion	No	No	No	Yes	53
N.S.	Canary Islands - Spain	Marine	Cage	<i>Spanus aurata</i>	Rearing unit	Simple growth model	-	No	No	Yes	Yes	54
MOM	Norway	Marine	Cage	<i>Gadus morhua</i> <i>Hippoglossus hippoglossus</i> <i>Lates calcarifer</i> <i>Spanus macrocephalus</i> <i>Dicentrarchus labrax</i> <i>Spanus aurata</i> <i>Ephiephelus tauvina</i> <i>Ephiephelus malabaricus</i> <i>Lateolabrax japonicus</i> <i>Larimitchys crocea</i> <i>Thunnus thynnus</i> <i>Fugu rubripes</i> <i>Siganus javus</i> <i>Siganus canaliculatus</i> <i>Sciaenops ocellatus</i> <i>Salmo salar</i>	Farm	Traditional bioenergetic	Egestion and excretion	No	Yes	No	No	55,56
FARM	Portugal, Thailand, Norway	Marine Freshwater	Cage Pond	<i>Dicentrarchus labrax</i> <i>Spanus aurata</i> <i>Salmo salar</i> <i>Oncorhynchus mykiss</i> <i>Oreochromis niloticus</i>	Farm	Traditional bioenergetic	Egestion and excretion	No	Yes	Yes	Yes	57-62

TABLE 1 (Continued)

Model name	Area of primary application	Ecosystem	Aquaculture system(s)	Fish species	Highest organisation level	Key modules and processes						Report of model or module validation	Reference (s)
						Individual or population (growth) model category	Biological waste	Waste treatment	Environmental risk or impact	Economic			
RAC	Italy	Marine	Cage	<i>Dicentrarchus labrax</i> <i>Sparus aurata</i>	Rearing unit	Traditional bioenergetic	Egestion and excretion	No	No	No	Yes	63–65	
N.S.	N.S.	Marine	Cage	<i>Spanus aurata</i> <i>Dicentrarchus labrax</i> <i>Thunnus thynnus</i>	Rearing unit	Simple growth function	Excretion	No	No	No	No	66	
N.S.	Israel	Marine	Cage	N.S.	Farm	Simple growth function	-	No	No	No	Yes	67	
N.S.	Canary Islands - Spain	Marine	Cage	<i>Spanus aurata</i>	Farm	Simple growth function	Egestion	No	Yes	Yes	No	68	
N.S.	Mediterranean	Marine	Cage	<i>Dicentrarchus labrax</i>	Farm	Simple growth function	-	No	No	Yes	No	69	
LYCWM	China	Marine	Cage	<i>Larimichthys crocea</i>	Rearing unit	Simple growth function	Egestion	No	No	No	Yes	70	
N.S.	Norway	Marine	Cage	<i>Salmo salar</i>	Rearing unit	Dynamic Energy Budget	-	No	No	No	Yes	71	
N.S.	Mediterranean	Marine	Cage	<i>Spanus aurata</i>	Rearing unit	Simple growth function	-	No	No	Yes	Yes	72	
FINS	Mayotte Islands - France	Marine	Cage	<i>Sciaenops ocellatus</i>	Farm	Simple growth function	Egestion and excretion	No	No	No	Yes	73–75	
Protein and Energy flux model	Portugal	Marine	Cage	<i>Spanus aurata</i>	Rearing unit	Traditional bioenergetic	Egestion	No	No	No	Yes	76	
N.S.	Greece	Marine	Cage	<i>Dicentrarchus labrax</i>	Rearing unit	Dynamic Energy Budget	Egestion and excretion	No	No	No	Yes	77	
ABC	USA	Marine	Cage	<i>Spanus aurata</i> <i>Dicentrarchus labrax</i>	Farm	Traditional bioenergetic	Egestion and excretion	No	Yes	No	No	78	

Note: For each model, key modules and processes considered (yes) or ignored (no) are specified. Abbreviation: N.S.: not specified.

under study and of the objectives can influence FSM construction, and we provide an example of a conceptual model of a marine fish farm. In Section 3, we review how the processes simulated in FSMs can be formulated into equations and discuss model selection as a function of criteria such as complexity, data requirements and generality. In Section 4, we focus on model implementation and evaluation, which include parameter estimation and model validation, along with appropriate sensitivity and uncertainty analyses. In Section 5, we discuss challenges and opportunities in four areas of application of FSMs identified as relevant for implementing the EAA: precision fish farming (PFF), IMTA modelling, supporting spatial management and life cycle assessment (LCA). From these applications, we show how farm-scale modelling is a key step to contribute to challenges highlighted in the EAA, at the farm level and higher levels. Overall, this article discusses advances, limitations and future lines of work related to FSMs to facilitate selection of existing models or development of new tools suitable for their intended use and users.

## 2 | DEFINITION OF SCOPE AND OBJECTIVES

The first step in the development process of FSMs consists of defining the research questions and objectives of the study, conceptualising the system and defining the context under study (i.e. type (s) of farming techniques, fish species and ecosystems).

### 2.1 | Questions and objectives

Modelling a fish farm can be useful to answer a variety of biological, ecological, engineering, management, economic and environmental questions. In FSMs, specific questions are usually translated into estimating or optimising three types of performance: (i) biotechnical (rearing), (ii) economic or (iii) environmental. The most common biological and ecological questions include understanding responses (e.g. growth, survival) and interactions (e.g. eating, breathing, excretion) of the farmed fish populations within their often-variable rearing environment. Engineering questions are related mainly to planning the design of future facilities to reduce risks and guarantee fish welfare and growth. This includes site selection for ponds or open-water systems to predict farm productivity as a function of environmental characteristics (e.g. water quality and quantity, soil conditions, fertility). For highly intensive land-based systems, it is more about designing rearing systems to modify the ambient environment to meet biological requirements. Management questions encompass a broad spectrum of aspects about predicting or optimising daily operations (e.g. determining stocking and feeding rates, predicting dissolved oxygen [DO] levels and examining effects of different management strategies).<sup>79</sup> Economic questions are about finding the most economically efficient scale, technology, resources, schedule and practices (e.g. heating water, feeding rates, maintaining DO at a given level) to minimise production costs, maximise revenue at an acceptable level of risk<sup>80</sup> or, for small-scale farming, free up funds to pay salaries to support a family. Environmental questions are usually related to predicting and

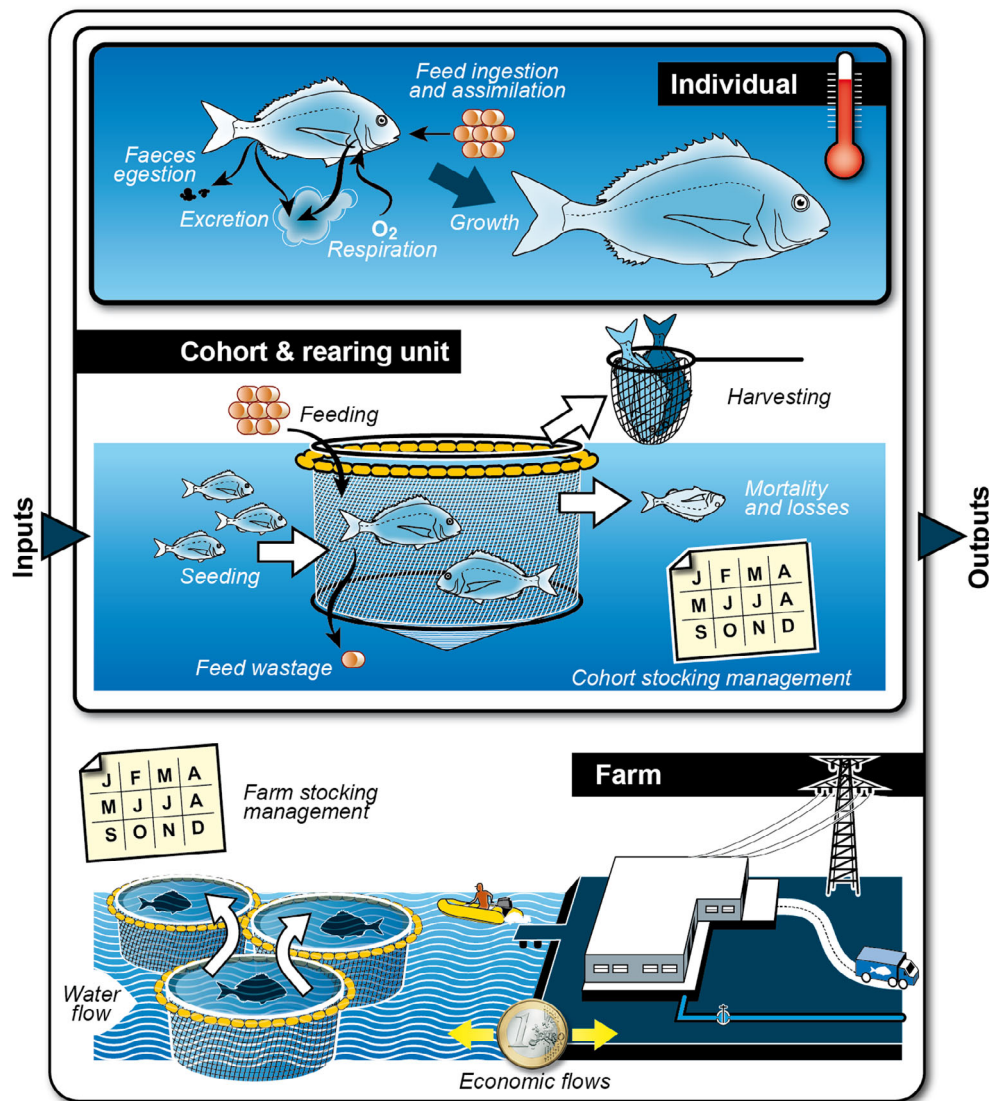
minimising nutrient-related impacts of a given facility or comparing these impacts among scenarios or systems. FSMs can also help estimate resource-use efficiency, in particular for fossil energy and feed inputs, and thus quantify other forms of pressure on the environment. In the studies reviewed, FSM objectives were often not explicitly reported or vaguely stated, such as needing an FSM to 'manage fish production ponds',<sup>36</sup> 'predict outcomes of different management strategies',<sup>27</sup> 'ascertain the temporal pattern of waste loads/discharges'<sup>66</sup> or 'meet fish production targets while maintaining effluent loading compliance'<sup>43</sup>. It is essential to define the question and objectives explicitly, as they serve as a pillar for subsequent modelling steps (e.g. to ensure that models are selected primarily to meet the modelling objectives, to verify the fitness for purpose afterwards).

### 2.2 | Conceptual model of a fish farm

A conceptual model of the system (i.e. a fish farm, in an FSM) is an easy way to visualise and summarise how a system works. Conceptualisation is one of the early steps of the modelling process which shows and summarises key components of the real system, how these components are connected by processes and what data (inputs) are needed to simulate these processes.<sup>14,15</sup> It also helps identify the relevant level of organisation and decide what ecological details need to be included or ignored. Box (e.g. Refs. 54,57,70) or picture (e.g. Ref. 44) models are commonly used as conceptual designs for FSMs. Approximately half of the models reviewed in this study included a conceptual model. Conceptualisation is usually performed after defining the context under study, questions and objectives; an example is presented here (Figure 1) to provide rapid insight into the general structure of FSMs and the processes that they often simulate.

In FSMs, the fish-farm system is usually represented at three levels of organisation: individual fish, the cohort or rearing unit, and the farm (Figure 1). In operational terms, this translates into the integration of different modules (sub-models seen as building blocks) to simulate specific processes at each level, making FSMs integrated models. The lowest level of organisation can either be the individual, which allows the model to produce information at the fish level and potentially to consider properties that differ among individuals in a population (i.e. inter-individual variability, see Section 3.3.3.2), or a population, which provides aggregated outputs for a group of individuals. The lowest organisation level should be chosen based on the amount of detail required and the need to consider inter-individual variability, but it is usually driven mainly by which growth model is chosen, which is the core of FSMs. Indeed, all the FSMs reviewed, except that of Rizzo and Spagnolo<sup>30</sup> and RACEWAY,<sup>44</sup> are based on individual prediction and growth models, although few of these FSMs consider inter-individual variability. At the individual level, the modules simulate fish growth mainly as a function of the physical environment (i.e. temperature and water quality), feed availability and quality, and the status of the individual fish (e.g. size, body weight), which are the main forcing variables and inputs (Table 2). Other important processes simulated at this level are thus feed ingestion and assimilation,





**FIGURE 1** Conceptual model of a marine fish farm that shows the most important processes simulated in farm-scale models at individual, cohort/rearing unit and farm-organisation levels. See Table 2 for the main inputs used to simulate these processes and the associated outputs. [Correction added on 7 June 2022, after first online publication: The captions for Figures 1 and 2 have been transposed.]

respiration and production of metabolic waste (i.e. faeces and dissolved nutrients). The second level of organisation is the cohort (i.e. a population of individuals of the same species and age). Modelling at the cohort level captures effects of farm-management decisions on a fish population and its rearing environment. At this level, effects of other important practices, such as feeding, aeration, fertilisation and water-exchange strategies, on the carrying capacity of the rearing unit and potential growth rate of fish can also be examined. Main inputs at this level are thus the description of rearing practices and production objectives (Table 2). Depending on the amount of detail required, this level can be combined with the rearing-unit level, which is the containment system in which one or more cohorts can be stocked. The third level is the farm level, which represents a group of homogeneous or heterogeneous rearing units. The processes simulated include stocking management on the farm, water flow and quality, waste treatment and economic flows. At this level, the main inputs are the description of farm infrastructure and farming cycles. Outputs

produced at each level are dynamic data, which can be integrated up to the farm level to produce aggregated data about a system's production, environmental (e.g. emissions, resource availability, impacts) and economic performances (Tables 1 and 2).

### 2.3 | Farming systems and hosting ecosystems

The type of farming system and ecosystems studied strongly influence the processes that need to be simulated in the model and the state variables that should be included. Many systems can be used to produce fish in aquaculture. The main types of fish farming systems can be classified along a gradient of rearing intensity, from extensive systems, such as earthen ponds and other open-water systems (e.g. cage or net pen), to more intensive semi-closed or fully closed land-based systems (e.g. tanks, raceways, recirculated aquaculture systems [RAS], hatcheries) (Figure 2). Farm management and operations vary greatly



**TABLE 2** Main inputs used in, and outputs produced by, farm-scale models applied in fish farming

Organisation level	Inputs	Outputs
Individual	<p><b>Species</b></p> <ul style="list-style-type: none"> <li>Individual-growth-model parameters (e.g. assimilation efficiency, body composition)</li> </ul> <p><b>Environment</b></p> <ul style="list-style-type: none"> <li>Water physical (e.g. temperature, salinity, pH) and chemical (e.g. NH<sub>3</sub>, NO<sub>3</sub><sup>-</sup>, O<sub>2</sub>, chlorophyll a) parameters</li> <li>Water current/flow</li> <li>Light availability</li> </ul> <p><b>Rearing practices</b></p> <ul style="list-style-type: none"> <li>Feed availability and composition</li> </ul>	<p><b>Biotechnical</b></p> <ul style="list-style-type: none"> <li>Growth performance</li> </ul> <p><b>Biological</b></p> <ul style="list-style-type: none"> <li>Biological waste emission</li> </ul>
Cohort or rearing unit	<p><b>Rearing practices and cohort characteristics</b></p> <ul style="list-style-type: none"> <li>Production schedule (e.g. stocking/harvesting date)</li> <li>Number and weight of fish stocked in each cohort</li> <li>Feed ration</li> <li>Desired commercial weight</li> <li>Mortality rate</li> <li>Fertilisation rate and composition</li> </ul>	<p><b>Biotechnical</b></p> <ul style="list-style-type: none"> <li>Stocks (harvest, losses)</li> <li>Production efficiency</li> <li>Resource-use efficiency</li> </ul> <p><b>Environmental</b></p> <ul style="list-style-type: none"> <li>Nutrient emissions</li> <li>Impacts on downstream water quality</li> <li>Water use</li> </ul> <p><b>Economic</b></p> <ul style="list-style-type: none"> <li>Income</li> <li>Expenses</li> <li>Profitability</li> </ul>
Farm	<p><b>Farm infrastructure and farming cycle</b></p> <ul style="list-style-type: none"> <li>Technology</li> <li>Number, dimensions and locations of rearing units</li> <li>Production schedule (transfers between rearing units)</li> </ul> <p><b>Market prices</b></p> <ul style="list-style-type: none"> <li>Input and output values</li> <li>Interest and depreciation rates</li> </ul>	

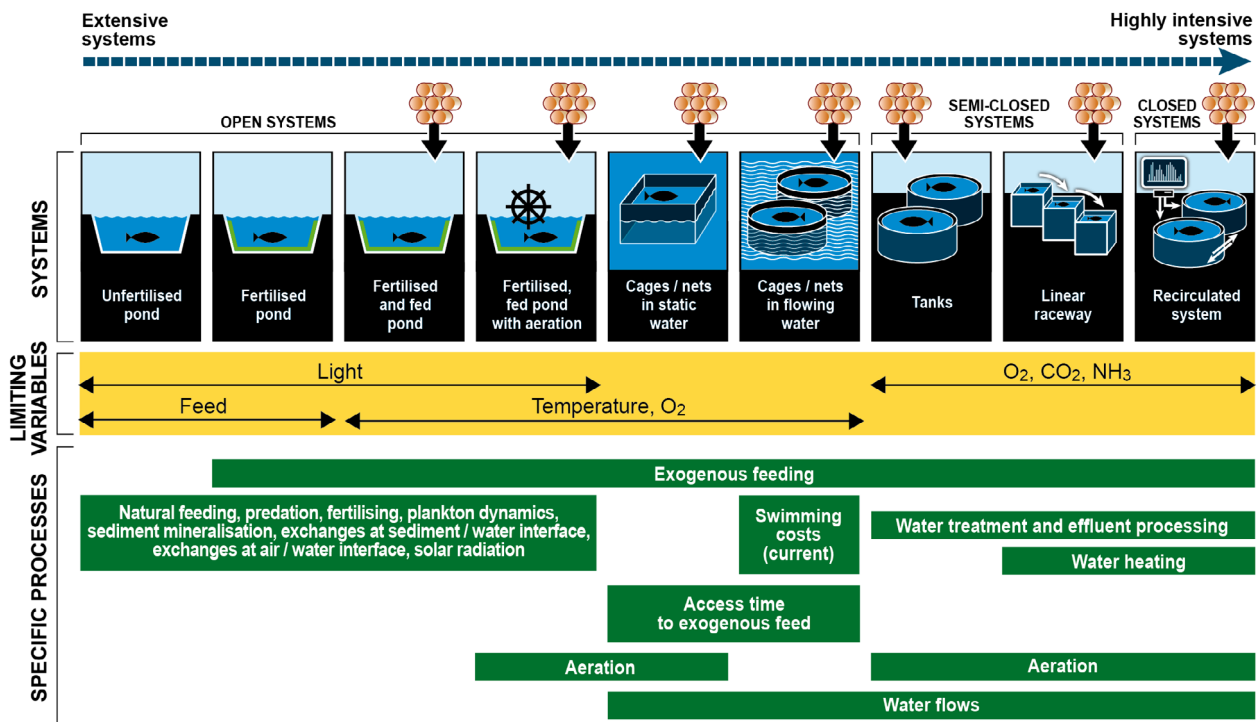
among these farming systems, which requires considering system-specific processes in each model (Figure 2). For instance, in extensive systems, fish yields depend greatly upon pond productivity, especially the natural food web. Modelling plankton dynamics and its interactions with ecological processes in the pond (e.g. sediment biogeochemistry, sediment/water exchanges) and pond-management decisions (e.g. fertilising, liming) is thus necessary. In contrast, in semi-closed or closed systems, natural productivity generally influences farm productivity little, as feed is provided by the farmer and water quality (i.e. plankton dynamics) is monitored. Most FSMs applied to

intensive land-based systems can thus ignore plankton dynamics; however, including water-treatment models (e.g. denitrification, CO<sub>2</sub> stripping and degassing) to simulate dynamics of water quality due to purification processes then becomes necessary. Variables that drive fish growth and thus farm production also vary among farming systems (Figure 2). For instance, water temperature can vary in open-water systems, while water temperature is controlled in some land-based systems and can be adapted to the thermal preference of the farmed species. The same reasoning should be followed according to the type of ecosystem studied, with specific ecological processes that can influence the farm differently depending on salinity (e.g. freshwater, brackish or marine waters), trophic state (e.g. oligotrophic, mesotrophic, eutrophic) or latitudes (e.g. temperate, subtropical, tropical). Knowing which processes are important and which can be ignored for the system under study is essential to reproduce the system's behaviour correctly and keep the model as simple as possible by representing only the most relevant processes and variables (principle of parsimony). As Ford (2010) states, 'the key to a model's usefulness is leaving out the unimportant factors and capturing the interactions between the important factors'.<sup>81</sup>

The more flexible the model is, the more complex it usually becomes. This can explain in part why most of the FSMs reviewed in this study were initially developed for a limited context (i.e. usually one type of farming system, one to three species and one type of ecosystem) (Table 1). Some were refined later to include new species or systems. For instance, FARM was initially developed for marine bivalve farming<sup>57</sup> and was progressively adapted to pond and marine fish farming.<sup>58,59</sup> Similarly, the models developed by Besson et al.<sup>51</sup> and by Halachmi<sup>49,50</sup> were developed for RAS systems and later adapted to sea-cage systems.<sup>67,69</sup>

## 2.4 | Species

Depending on the fish species under study, a varying degree of knowledge and data availability can be expected. The FSMs reviewed referred to species and production areas that are not representative of aquaculture worldwide. In total, 30 species were studied, which is <10% of the 300 fish species farmed globally.<sup>82</sup> FSMs were usually developed and applied for the species most relevant to the researchers' region. Indeed, the species studied most in the FSMs reviewed were seabass (*Dicentrarchus labrax*) and seabream (*Sparus aurata*) (ca. 25% of the FSMs for both species), and most of the models were developed by European research teams. Knowledge of these species is much more advanced than that of other species, which results in greater data availability. For instance, specific reviews of growth models are now available for some of these well-studied species (e.g. seabream<sup>83</sup>). The large choice of individual growth models for these species can facilitate development of new FSMs, allowing one to choose the most appropriate tools to answer the question under study. In contrast, developing FSMs for new species often means modelling in a context of limited knowledge and data scarcity.<sup>73</sup> Parameter estimation requires more effort for these FSMs, as more experiments must be performed to



**FIGURE 2** Important limiting variables and processes to consider to model a variety of fish farming systems [Correction added on 7 June 2022, after first online publication: The captions for Figures 1 and 2 have been transposed.]

obtain parameter values. Using simpler models to build FSMs is often the main approach for limiting data requirements. As highlighted in the EAA, proactive research on new species should be promoted,<sup>4</sup> even if it initially requires developing simpler empirical models. Reviewing the existing information before modelling is thus also a crucial step. Knowledge also determines the amount of detail that can be considered and indicates potential uncertainty in the predictions.

### 3 | PROCESS FORMULATION AND MODEL SELECTION

The second step of FSM development relates to process formulation and model selection, which consider the choice of state variables, the equations available to model relevant processes and the assumptions and constraints associated with each modelling alternative. The reasons for the model chosen should be explicitly stated and will depend on the context under study, the objectives, data availability and the desired complexity or generality, among others. This section presents the types and families of models used in the FSMs reviewed to simulate most important processes at individual, cohort/rearing unit and farm levels.

#### 3.1 | Types of models and criteria for model selection

One essential characteristic that differentiates models is the distinction between empirical and mechanistic models.<sup>84</sup> Choosing an

empirical vs. mechanistic approach in an FSM, especially in models at the individual level, can influence the FSM's properties greatly. Empirical models (also called 'descriptive', 'statistical', 'quantitative' or 'phenomenological') describe observed patterns using equations and parameters that have been fitted statistically, without explicitly describing/formalising the underlying processes. In contrast, mechanistic models (also called 'theoretical') are based on theories about the processes thought to underlie phenomena. The boundary between these model types is sometimes narrow, as it is common to include empirical equations in mechanistic models to improve the fit between observations and simulations (see examples in Section 3.2.1). Empirical models are generally simpler (e.g. fewer input parameters, state variables and forcing variables), easier to calibrate and quicker to run. Their disadvantage is, however, that they have less flexibility (i.e. more difficult to apply to other contexts) and predictive power (i.e. few predictions can be extrapolated out of the range of the data used for calibration<sup>85</sup> and cannot consider changes in the system<sup>14</sup>).<sup>84</sup> Empirical models are, thus, preferred when constructing FSMs when knowledge of the processes is low, such as for new species or environments. Empirical models are thus frequently used as an initial approach.<sup>86</sup> If general applicability is the priority, such as simulating several species using the same set of equations, mechanistic models are more suitable if knowledge and data are sufficient.

When constructing FSMs, other general choices can influence a model's properties and outputs, such as how time (e.g. discrete vs. continuous) and space (e.g. spatially heterogeneous, or not) are modelled and whether random events are allowed (stochastic models)

or not (deterministic models). Dynamics of FSMs are driven by environmental conditions and farmers' decisions, which can vary over space (e.g. practices differ among rearing units) and time (e.g. seasonal change in temperature). FSMs usually use discrete time steps. The time step is based on the most critical processes to consider and the amount of detail. For instance, it can be 1 day for predicting overall growth, or shorter (hour or minute) when metabolic loops that result in fish growth are also simulated. Some FSMs include the spatial dimension, either by making the model grid-based or simply attributing processes clearly to a unit of organisation (e.g. individual, cohort, rearing unit). In FSMs, the choice between deterministic and stochastic models is largely a function of the need to represent variability among individuals at the cohort level and influences mainly model complexity and computing time (see Section 3.3.3.2).<sup>32,80</sup> This general modelling terminology is used and illustrated with examples in the following sections.

## 3.2 | Processes and models at the individual level

### 3.2.1 | Growth

An organism grows due to deposition and accretion of several nutrients from the feed into the body. Nutrient deposition allows tissues and organs to develop and ultimately allows the individual to increase in volume, mass and size. Assimilating and depositing nutrients in an organism for growth, as well as maintaining body components, costs energy. Besides supplying nutrients, feed also meets an animal's energy requirements. For this reason, fish growth models often represent feed quantity and quality, as both strongly influence the amounts of nutrients and energy available to a fish. Because body size and water temperature are key drivers of a fish's ability to ingest and assimilate feed, growth models often include these variables. Many other biotic (e.g. sex, age, genetic pool, parasites, microorganisms, fish stocking density) and abiotic (e.g. light intensity, photoperiod, DO and NH<sub>4</sub> concentrations in water, water salinity, currents) factors are also known to influence fish growth, but they are less often included in growth models.

Individual-level models developed for fish can be classified into four families: (i) simple growth functions (Table 3), (ii) traditional bioenergetic models, (iii) Dynamic Energy Budget (DEB) models and (iv) nutritional models. This distinction is based mainly on model theories and the currency used (mass or energy). It also reflects the chronology of the development of fish growth models and the progressive transition from empirical to mechanistic models. Each family of models, except for a subgroup of nutritional models (metabolic-flux models), was used in at least one of the FSMs reviewed (Table 1). The main concepts, mathematical equations and characteristics of capacity, complexity and data requirements of each model family is presented below and then summarised (Table 4). For more detailed information about individual growth models, refer to previous reviews of models for fish<sup>83,87,88</sup> or for other aquaculture species.<sup>86</sup>

**TABLE 3** Simple functions commonly used to predict fish growth

Model	Variable and parameter	Unit
<b>von Bertalanffy</b>		
$W(t) = W_{\infty} [1 - e^{-k(t-t_0)}]^b$	$W$ : weight	g fresh weight
	$W_{\infty}$ : asymptotic weight	weight
	$k$ : relative growth rate	g fresh weight
	$t$ : age	weight
	$t_0$ : initial age	day <sup>-1</sup>
	$b$ : dimensionless factor	day
<b>Gompertz</b>		
$W(t) = a \cdot e^{b \cdot e^{-ct}}$	$a$ : asymptotic weight	g fresh weight
	$b$ : curve-displacement coefficient	-
	$c$ : growth rate	-
	$t$ : time	day
	<b>Thermal-unit growth coefficient (TGC)</b>	
$W_f = \left( W_0^{1-b} + T \cdot t \cdot \text{TGC} \right)^{\frac{1}{1-b}}$ with $\text{TGC} = \frac{W_f^{1-b} - W_0^{1-b}}{T \cdot t}$	$W_f$ : final weight	g fresh weight
	$W_0$ : initial weight	weight
	$b$ : allometric coefficient	g fresh weight
	$t$ : time	weight
	$T$ : water temperature	-
		day °C

Simple growth functions are semi-empirical models that use regression or polynomial equations to describe the increase in body mass or length over time. Fish growth is often described with three stanzas: exponential, linear and asymptotic growth for early stages (fry), juveniles (fingerlings) and adults, respectively. Depending on the growth stanza examined in the model, the growth function has a different shape (e.g. exponential, bounded, sigmoidal).<sup>88</sup> The main simple growth functions include temperature-independent models such as the von Bertalanffy growth function (VBGF),<sup>89</sup> the Gompertz<sup>90</sup> function, polynomial functions and temperature-dependent models, such as the thermal-unit growth coefficient (TGC) model<sup>91,92</sup> and the function of Lupatsch and Kissil (1998) (Table 3).<sup>93</sup> Some of these models, such as VBGF or TGC, have been applied to many different fish species, demonstrating their general applicability to fish. Parameter estimation requires few data (e.g. time series of body mass and water temperature for temperature-dependent models) and use mathematical fitting methods (e.g. see Refs. 94,95). The use of simple growth functions in FSMs is therefore useful in contexts where few data are available, such as for new aquaculture species or data-poor environments. Due to the functions' empirical nature and few inputs, their parameter values are often site-specific and have limited ability for reuse.

Traditional bioenergetic models (thus excluding DEB models) describe the allocation of feed energy to different metabolic process in an organism, including growth, following a factorial scheme (Figure 3a). These models are based on the principle of energy conservation. All of the energy available to an organism comes from the feed. The organism assimilates a fraction of this energy and then

TABLE 4 Main families of individual-level models applied in the farm-system models reviewed and their characteristics

Model types	Currency (and unit)	Model outputs	Forcing variables	Number of parameters	Simulation time-step	Life cycle stages (and whether parameters change among them)	Generality	Complexity	Use on farmed-fish species	Relevant context of application
Simple growth functions	Independent of temperature	• Growth		< 5	Day	Juvenile, adult (no)	++	+	Wide	Ad libitum feeding Primary
	Temperature-dependant	• Growth	• Temperature	< 5	Day	Juvenile, adult (no)	++	+	Wide	approach and data-scarce context
Bioenergetic models	Energy (J)	• Growth	• Food quantity	> 10	Day	Juvenile, adult (no)	+	++	Wide	Variable environments
		• Energy requirements	• Water temperature							Study of feed requirements
		• Uneaten feed								
DEB	Energy (J)	• Quantity of metabolic waste								
		• O <sub>2</sub> consumption								
		• Growth requirements	• Food quantity	> 10	Hour, day	Embryo, juvenile, adult (yes)	+++	+++	Limited but growing <sup>a</sup>	Variable environments Systems covering multiple life cycle stages (e.g. hatchery, ponds)
Nutritional models	Mass (macro-nutrient)	• Energy requirements	• Water temperature							
		• Uneaten feed								
		• Quantity of metabolic waste								
Mass-balance	Mass	• O <sub>2</sub> consumption								
		• Growth <sup>b</sup>	• Food quality and quantity	5 < x < 10	Static model	Juvenile, adult (no)	+++	+	Wide for estimation of waste <sup>b</sup>	Integrated multitrophic aquaculture systems
Metabolic-flux	Mass (macro-nutrients and substrates)	• Quantity and composition of metabolic waste								
		• Growth	• Food quality and quantity	> 50	Minute, hour	Juvenile, adult (no)	++	+++	Very limited	Variable environments IMTA systems Effect of feed quality on fish
		• Quantity and composition of metabolic waste	• Water temperature							
		• O <sub>2</sub> consumption								

(Continues)

TABLE 4 (Continued)

Model types	Currency (and unit)	Model outputs	Forcing variables	Number of parameters	Simulation time-step	Life cycle stages (and whether parameters change among them)	Generality	Complexity	Use on farmed-fish species	Relevant context of application
		<ul style="list-style-type: none"> <li>Fish body composition</li> </ul>								

Note: Ranking for generality and complexity criteria is based on expert knowledge of the authors.

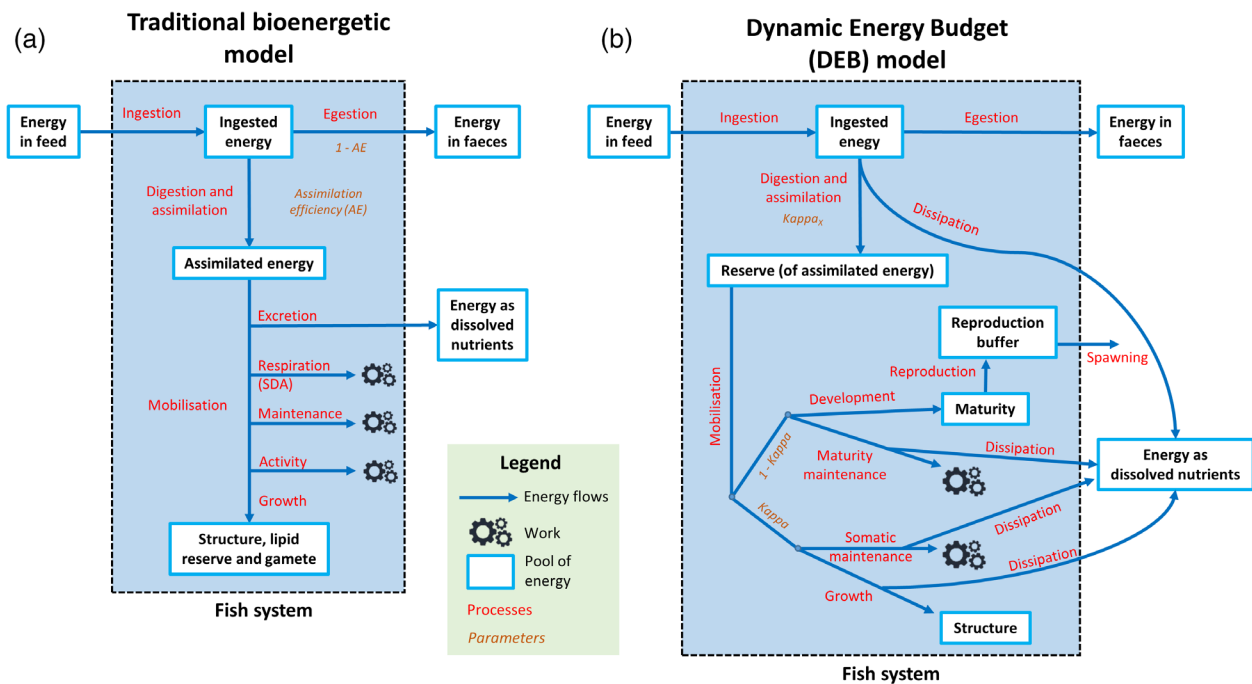
Abbreviations: DEB, Dynamic Energy Budget; IMTA, integrated multi-trophic aquaculture.

<sup>a</sup>DEB models have been widely used for fish but rarely in aquaculture.

<sup>b</sup>Mass-balance models are widely used to predict metabolic-waste emissions but rarely used to predict growth.

egests the remainder as faeces. The assimilated energy can subsequently be used or lost through several pathways (Figure 3a): excretion of dissolved nutrients, respiration associated with feed processing (i.e. 'specific dynamic action' or 'heat increment'), storage of assimilated energy, egestion of waste, maintenance (e.g. basal metabolism, thermal regulation), activities (e.g. swimming) and growth (e.g. somatic growth, gonad formation, synthesis of lipid reserves). In traditional bioenergetic models, these energy fluxes are represented by specific terms of balanced equations with either energy inputs from feed (factorial models) or energy allocated to growth (net-production or net-energy models) which are unknown and subtracted from the other terms. In factorial models, energy allocated to growth must be defined from experimental data or by assuming the genetic growth potential (also called 'desired growth rate'). Growth is thus often expressed using the simple growth functions presented previously (e.g. TGC in the bioenergetic model of Cho and Bureau,<sup>96</sup> exponential functions in those of Lupatsch et al.<sup>98,99</sup> and Glencross<sup>97</sup>). When an individual-level model aims mainly to predict fish growth, factorial models have no advantage over simpler models. In contrast, in net-production models such as scope-for-growth models,<sup>100</sup> the energy available for growth is the state variable. Unlike simple growth functions, net-production models can estimate fish growth under limiting food availability. This can be useful when stocks are not fed ad libitum, such as in unfed pond systems, or when fish do not have full and constant access to the feed distributed.<sup>92</sup> The development and parameter estimation of bioenergetic models is usually performed by estimating each term in the equation using allometric relationships or statistical regressions, based on experiments. These experiments have been described extensively by Strand<sup>101</sup> and Jørgensen et al.<sup>102</sup> More generally, bioenergetic models have the advantage of estimating, within a common conceptual framework, growth potential, solid and dissolved metabolic waste production and oxygen consumption. Traditional bioenergetic models have been criticised for their lack of parsimony<sup>103</sup> and generality.<sup>104,105</sup> They may involve many parameters, which often do not have any biological meaning outside of the species for which they were defined.<sup>103,106,107</sup> Probably for this reason and because of the time required to parameterise models for new species, most traditional bioenergetic models used in aquaculture have been applied to only one or two species (Table 1). A few of them have been applied to more species (suggesting more generality), such as the bioenergetic model in the MOM model,<sup>55,56</sup> or Aquafish, the individual-growth model used in FARM.<sup>58,59</sup> Other models are used in other fish-related research areas. For instance, Fish bioenergetics<sup>108</sup> is a popular model that has been used in ecology for more than 20 years and now includes parameters for more than 73 species. A critical analysis of these models, however, lies beyond the scope of this study.

DEB models are mechanistic bioenergetic models based on a theory founded on physiological principles that are common to all species. DEB theory can be applied to ectothermic or endothermic organisms that are isomorphic (whose body shape does not change over time). Because DEB models can describe the life cycle of an organism through multiple stages (e.g. embryo, juvenile and adult stages in a general model organism), model parameters can change



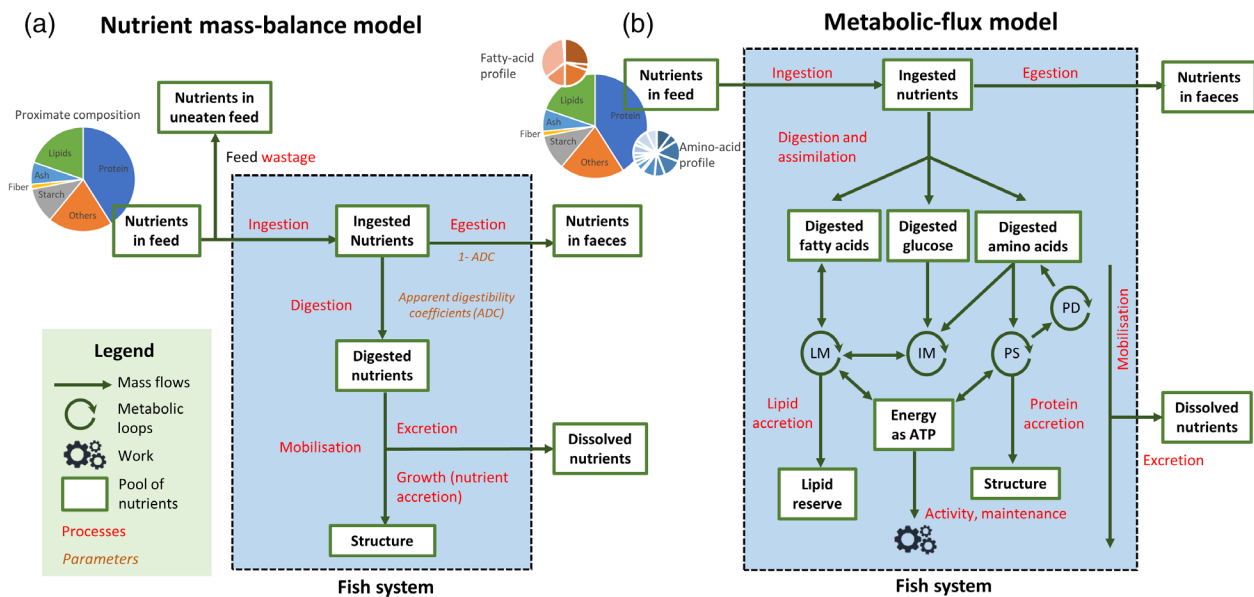
**FIGURE 3** Diagram of individual-level models based on energy, including (a) traditional bioenergetic models and (b) Dynamic Energy Budget models. SDA, specific dynamic activity.

over time. This feature contrasts with traditional bioenergetic models, which do not represent the entire life cycle of individuals<sup>107</sup> and thus ignore effects of metabolic adaptations on energy-balance dynamics.<sup>106</sup> DEB theory uses differential equations to describe flows of assimilation and use of energy from food for an organism's maintenance, reproduction and development (Figure 3b) in response to two forcing variables: temperature and food availability.<sup>109–112</sup> In this theory, after being assimilated, energy is stocked in a reserve compartment (specific to DEB). Part of this energy (determined by the parameter  $Kappa$ ) can be used for structure (i.e. somatic maintenance and growth), and, for embryos and juveniles, the rest ( $1-Kappa$ ) is used for maturity (i.e. complexification of structure) and maintenance of maturity. For adults, who have reached maximum maturity, this remaining energy fraction can be used for maturity maintenance and reproduction (i.e. gonad formation and gamete production). A standard DEB model includes 12 parameters, but depending on the objectives of application, not all of these parameters are necessarily useful.<sup>113</sup> Estimating these parameters requires collecting a large amount of data derived from life-history traits and experiments. These data and the methods to collect them have been described elsewhere.<sup>114</sup> The Add-my-Pet database provides access to parameters for more than 3000 species,<sup>115</sup> including many farmed fish species. Completeness of the data used to calibrate and assess goodness-of-fit of the models is also provided for each species in the database, allowing overall model quality to be assessed. Compared to traditional bioenergetic models, DEB models have greater generality but correspondingly greater complexity. State variables of standard DEBs (i.e. structure, reserve, and maturity or reproduction buffer [sometimes called 'gametes']) are defined in an abstract way, and neither

they nor energy fluxes can be measured directly and operationally, as can be done with traditional bioenergetic models.<sup>107</sup> Moving from model variables to real-world measurements thus requires auxiliary (or conversion) parameters.<sup>116</sup> This high level of abstraction, as well as the expertise required to develop and implement DEB models,<sup>86</sup> may limit its wide applicability, although some 'simpler' variants of general DEB theory also exist.<sup>116</sup> These variants provide a variety of compromises in model capacities and data requirements. The ability of DEB models to represent the entire life cycle of an animal and to quantify reproduction can be useful for modelling farming systems in which reproduction occurs and early stages are important, such as hatcheries, nurseries and extensive pond systems. Moreover, DEB's ability to quantify reproduction also connects individual animals to the population level,<sup>86</sup> which provides the option to simulate population dynamics within the DEB framework.<sup>117,118</sup>

Other families of individual-level models, such as nutritional models, can be used to predict individual fish growth. Nutritional models can estimate fish growth by simulating the fate and accretion of nutrients in the organism, following principles of energy and mass conservation. They include models with two levels of complexity: simple nutrient mass-balance models<sup>96,119,120</sup> and more complex metabolic-flux models.<sup>121–124</sup> Both can simulate fish growth as a function of food nutrients, unlike traditional bioenergetic and DEB models, which often ignore the types of nutrients that provide energy in the food (except some, such as RAC or MOM) and the balance among nutrients required to meet fish requirements. In mass-balance models (Figure 4a), nutrient groups of interest are macronutrients (e.g. protein, lipids), while metabolic-flux models (Figure 4b) also consider the composition of macronutrient substrates (e.g. amino acids,





**FIGURE 4** Individual-level models based on nutrients, including a (a) nutrient mass-balance model and (b) metabolic-flux model (adapted from Johnston et al.<sup>127</sup>). ATP, adenosine triphosphate; IM, intermediary metabolism; LM, lipid metabolism; PD, protein degradation; PS, protein synthesis.

fatty acids). These two types of models, however, ignore micro-nutrients and additives (e.g. vitamins, minerals, trace elements). Because most of the FSMs reviewed include mass-balance modules to estimate farm waste (but not growth), these models are described in more detail in Section 3.2.3. Metabolic-flux models are mechanistic models based on the compartmental approach,<sup>125</sup> which consists of subdividing an organism into multiple compartments (e.g. gut, blood, other organs) through which pools of nutrients with homogeneous kinetics (e.g. protein, lipids, glucose) can circulate. Metabolic loops are used to describe the synthesis and degradation of these nutrient pools (see Zhang et al.<sup>126</sup> for a detailed description of nutrient metabolism in fish). Flows of macronutrients or substrates that circulate between these pools or enter or leave the system are described using differential equations based on the principles of stoichiometry and kinetic saturation. Although mechanistic, these models do not necessarily follow a generic framework, are often parameterised for a single species<sup>102</sup> and have many parameters (e.g. up to 100). Estimating parameters of metabolic-flux models usually requires *in vivo* and *in vitro* experimental data (including digestibility data), but no standard method has been developed to collect them. Metabolic-flux models have been applied to several mammals (see references in Dumas et al.<sup>87</sup>) but only to a few fish species, including Atlantic salmon,<sup>122</sup> rainbow trout<sup>124</sup> and Senegalese sole (*Solea senegalensis*).<sup>123</sup> The outputs of these models include most of those produced with traditional bioenergetic and DEB models (Table 4) and extend to nutrient composition in the fish body and metabolic waste. Only one example of an FSM based on a metabolic flux model was identified during the literature search, but as this commercial model has not been presented in a peer-reviewed article or a PhD thesis, we excluded it from the review. The relatively recent development of metabolic-flux models, their few applications to fish and their high complexity likely explain why no peer-reviewed FSM

based on a metabolic-flux model was identified. The development of such FSM, however, would provide new perspectives for applications, including prediction of fish body composition as a function of feed composition and formulation, or farm production and environmental performances due to new feed formulations (see Section 5.3) and more accurate prediction of production in an IMTA context (see Section 5.2). Development of such models should therefore be encouraged; they may become the next generation of FSMs if developed in the direction of less complexity and more generality.

### 3.2.2 | Food intake

Food is the only source of energy and nutrients that animals have for maintenance, development and reproduction. Fish that feed on plankton, insects, macrophytes, benthic organisms or other fish can obtain food from the environment, as is generally the case in extensive pond systems. In semi-intensive or intensive systems, exogenous feed is provided to fish to meet energy and nutrient requirements and ensure growth objectives (Figure 2). Only FSMs developed for pond aquaculture have included processes related to the availability of natural food from the environment. Some of them (e.g. POND, FARM) can also include exogenous feed supply. The natural food considered in these models is generally limited to phytoplankton or zooplankton. Considering plankton as food requires considering primary productivity dynamics in the FSM, either as a forcing or non-forcing variable (see Section 3.4.3.2). How much natural food or distributed feed is ingested by fish is another important question, as it ultimately determines fish growth potential, as well as nutrient and economic losses due to uneaten feed. Predicting feed intake is particularly complex, however, as it is influenced by many factors, including nutritional



(e.g. proximate composition, dietary preferences, feed attractiveness), environmental (e.g. DO, salinity, temperature, photoperiod), physiological (e.g. genetics, hormonal system) and production-related (e.g. feeding frequency, feeding rate, feeding time) ones.<sup>128</sup>

The modelling approach used to estimate the quantity of feed ingested by fish depends strongly on the family of growth model used in the FSMs. In most FSMs based on simple growth functions, ingested feed equals distributed feed minus a potential fraction of uneaten feed (see Section 3.3.1). In these FSMs, growth is predicted using empirical functions (e.g. von Bertalanffy, TGC models) that do not explicitly include variables for the amount of feed distributed or ingested (Table 3). In FSMs based on simple growth functions, feed supply and feed intake (if calculated as a percentage of feed supply) can still be simulated and vary over time, for instance, using feeding charts or feed conversion rates (FCR, i.e. the number of units of 'dry' aquafeed required to produce 1 unit of 'fresh' fish biomass) (see Section 3.3.1). However, feed supply and feed intake will not influence growth predictions in these FSMs. In contrast, feed supply or availability is a forcing variable of traditional bioenergetic and DEB models. Besides feed availability, the number of variables used to estimate feed intake can vary widely among traditional bioenergetic models. In the FSMs of Yi<sup>31</sup> and Cuenco et al.<sup>27</sup> and in POND,<sup>32,33</sup> the ingestion rate depends on 4–6 physiological or environmental variables, including fish size/weight, temperature, photoperiod, DO concentration, ammonia (NH<sub>3</sub>) concentration and feed availability. Some authors demonstrated greater influence of temperature than other variables on feed intake.<sup>27</sup> In more recent bioenergetic or DEB-based FSMs, feed intake is essentially a function of fish body mass, temperature and feed availability. In the RAC model, for instance, the energy flow from the feed ingested is estimated from maximum ingestion capacity, a temperature-response law and fish body mass. FARM and the FSM of Canale et al.<sup>43</sup> follow the same modelling logic, except that ingestion rate is not function of fish mass but instead of stomach size and fullness (satiety). In these two models, the evacuation rate of the fish's digestive tract thus determines its ability to ingest food again. In DEB theory, feed intake is proportional to animal surface area and varies as a function of feed density and temperature according to the Arrhenius law. Other modelling methods have been developed in the literature to estimate feed intake by fish at the individual or population level (e.g. multiple-regression models, chemical contaminant mass-balance model<sup>128</sup>), but they are used much less often in FSMs than the methods mentioned.

### 3.2.3 | Feed assimilation, egestion and excretion of metabolic wastes

In fish, non-assimilated feed is egested as faeces, and assimilated nutrients that have not been used to produce new tissues or energy are excreted as metabolic end-products with high nitrogen (N) and phosphorus (P) contents. Faeces contains the nutrients already present in the feed, but in percentages that vary with the ability of the fish to digest and assimilate them. Approximately 80%–90% of N is excreted as un-ionised NH<sub>3</sub> through respiration and urine, while

10%–20% of the remaining N is excreted as ammonium (NH<sub>4</sub><sup>+</sup> or ionised ammonia), urea (CH<sub>4</sub>N<sub>2</sub>O), uric acid (C<sub>5</sub>H<sub>4</sub>N<sub>4</sub>O<sub>3</sub>), amino acids (H<sub>2</sub>N–HCR–COOH), creatine (C<sub>4</sub>H<sub>7</sub>N<sub>3</sub>O<sub>2</sub>) and creatinine (C<sub>4</sub>H<sub>7</sub>N<sub>3</sub>O).<sup>129,130</sup> P is excreted mainly as orthophosphates (H<sub>2</sub>PO<sub>4</sub><sup>-</sup>, HPO<sub>4</sub><sup>2-</sup> and PO<sub>4</sub><sup>3-</sup>). Biological waste also includes carbon dioxide (CO<sub>2</sub>) released by respiration.

The method used most to estimate waste emissions, particularly for FSMs based on simple growth functions, is to connect the growth model to a nutrient mass-balance model. In the mass-balance approach (Figure 4a), digested nutrient fluxes are estimated using apparent digestibility coefficients (ADCs) for several macronutrient feed compounds, feed dry weight or feed organic matter. When macronutrient compounds are used, feed is described by its content in primary nutritional categories (i.e. proximate composition: protein, lipids, dietary fibre, ash and N-free extracts [mostly carbohydrates, including starch]). The categories of macronutrient considered in mass-balance models vary among studies but should include at least protein, lipids and starch, which together represent ca. 80% of feed dry weight and nearly 100% of its energy. Undigested nutrients egested as faeces are calculated as a difference (1–ADC). Nutrients retained in the biomass gain (from the growth model or an FCR) are estimated by multiplying the initial and final proximate composition of the fish body by the initial and final body mass, respectively. Finally, dissolved wastes are calculated as the difference between retained and digested nutrients. C and N fluxes can also be calculated from macronutrient fluxes by considering their stoichiometry (e.g. protein is 1/16 N).<sup>131</sup> Simplified element mass balances can also be determined by considering C, N or P ADCs.<sup>45,66</sup> This approach, however, cannot quantify nutrient or energy losses in faeces. For additional information about estimating waste emissions with nutrient mass-balance models, see reviews by Bureau and Hua<sup>129</sup> and Reid et al.<sup>86</sup> Besides mass-balance models, other methods have also been used to estimate fish waste emissions. For instance, Islam<sup>132</sup> developed linear regressions between N and P emissions and FCR. Some statistical models were developed to estimate total N, which was assumed to equal the sum of NH<sub>3</sub> and NH<sub>4</sub><sup>+</sup> emissions, as a proportion of distributed feed, without explicitly considering feed digestibility or assimilation efficiency by fish.<sup>45,46</sup> To be rigorous, however, such empirical models should be used for the same species, range of temperature, feeding regimes and other environmental conditions for which they were initially developed, which probably greatly limits their possible reuse.

In traditional bioenergetic and DEB models, parameters for energy-assimilation efficiency are used to estimate the fraction of ingested energy that can be used for metabolic processes and potentially to estimate the non-assimilated energy egested as faeces. Most models use a single parameter, but some FSMs (e.g. RAC, MOM) specify an assimilation-efficiency parameter depending on the type of macronutrient that provides the energy. FSMs usually assume that parameters for energy-assimilation efficiency and ADCs remain constant over time. Less frequently, ADCs can vary by fish age, as in the INAPRO model. In traditional bioenergetic models, all non-assimilated energy is assumed to be lost as faeces, which differs from DEB models, which can include losses related to digestion.<sup>112</sup> This loss

fraction of dissipated energy, which represents 10% of ingested energy in a standard DEB model, is often assumed to be zero in FSMs.<sup>74,133</sup> The energy fluxes allocated to faeces can then be converted to mass fluxes using energy-density coefficients ( $\text{kJ g}^{-1}$  faeces) in traditional bioenergetic models or using molecular-weight ( $\text{g mol}^{-1}$ ) and chemical-potential ( $\text{J mol}^{-1}$ ) coefficients in DEB models. Bioenergetic models use a variety of methods to estimate dissolved waste. N excretion can be considered proportional to oxygen consumption,<sup>65,86</sup> assimilated energy from protein<sup>43</sup> or ingested N.<sup>40</sup> The same type of approach can be used for P excretion, but this variable is usually estimated from N excretion.<sup>65</sup> The excretion term in standard DEB models is not a single process, as it is in traditional bioenergetic models. In standard DEB models, N emissions can be estimated from energy costs related to assimilation, dissipation (i.e. work that does not produce new biomass, such as maintenance, and overhead costs) and growth<sup>107,112</sup> as done for seabass by Stavrakidis-Zachou et al.<sup>77</sup> Estimating dissolved P emissions is more complex, however, as standard DEB models do not consider P in an organism's biomass components (i.e. structure, reserve and reproduction buffer). Relationships between P and C or N fluxes in an organism must therefore be assumed. For instance, in the FSM of Serpa et al.,<sup>36</sup> dissolved P (and N) emissions of white seabream (*Diplodus sargus*) were estimated as a function of the C emitted by respiration and C:P ratio in the food, assuming that C and P losses must be directly proportional to C and P inputs in food, to ensure that the organism's C: P ratio is maintained.

### 3.2.4 | Respiration

Fish consume oxygen during respiration to produce energy from organic compounds in the feed; this reaction also produces  $\text{CO}_2$  and water. Most FSMs developed for land-based systems estimate oxygen consumption by fish, while only a few FSMs developed for sea cages (e.g. RAC, FARM, FSM of Besson et al.<sup>69</sup>) do. In the open-water systems studied, authors often acknowledge that DO concentration is not a limiting factor.<sup>54,70,73</sup>

Two main approaches are used in FSMs to represent fish oxygen consumption<sup>45</sup>: (i) it is estimated at the individual or population level or (ii) water flows required to make DO concentration non-limiting are calculated. Several linear functions that used distributed feed quantity, fish body mass or temperature as proxies to estimate oxygen consumption at the individual level have been proposed.<sup>45,46</sup> Some of these functions can be connected to simple growth functions or used in traditional bioenergetic models. Fish respiration can also be estimated using indirect calorimetry principles, as in MOM or the FSM of Besson et al.<sup>69</sup> This method assumes that the energy lost through respiration equals that used to oxidise excreted dissolved nutrients. To estimate fish respiration, a nutrient mass-balance model can first be used to estimate digested and non-retained proteins, lipids and carbohydrates; then, these nutrient fluxes are converted to energy fluxes using macronutrient energy densities and converted again to  $\text{O}_2$  fluxes using oxy-caloric coefficients (see Table 2 in Reid et al.<sup>86</sup>).

In FSMs based on traditional bioenergetic models, oxygen consumption by fish is usually estimated by summing the oxygen or energy consumption associated with multiple metabolic costs. Most of these FSMs estimate resting respiration, which corresponds to oxygen consumption for basal metabolism and feed digestion, using temperature-dependent allometric relationships, and ignore metabolic costs of swimming. Similarly, like excretion, oxygen consumption is not a single process in DEB theory,<sup>107</sup> and it can be derived from the energy used for growth and lost through dissipation. The energy expended for swimming and its associated oxygen consumption are probably low for fish reared in environments with slow currents (e.g. ponds, tanks, raceways, cages in protected bays).<sup>134</sup> In rivers or offshore cage systems, however, currents are usually stronger and the energy costs of swimming higher. FSMs developed for high-current systems should probably include swimming costs when estimating fish respiration. FARM can estimate oxygen consumption due to swimming, but it requires current intensity as input data to do so.

## 3.3 | Processes and models at the cohort or rearing-unit level

### 3.3.1 | Feeding and feed wastage

In fed aquaculture, the quantity and quality of feed distributed to a rearing unit depends on several factors. Farmers usually determine a feed ration from a feeding chart that provides theoretical rations (expressed as a percentage of stocking biomass) as a function of fish size and temperature. These theoretical rations are then adapted daily as a function of fish state (e.g. behaviour, health stress), environmental conditions (e.g. current, DO), farming cycle (e.g. starvation before handling) or feed availability on the farm.<sup>135</sup> Because a fish's nutritional requirements and ingestion capacity also vary during its life cycle, pellet composition and size are adapted for a given species over the farming cycle. Optimising feed quality and quantity according to these factors meets fish growth potential and minimises feed losses (i.e. uneaten feed).

In FSMs, the feed ration can be either a forcing variable or an output of the model. The latter approach is generally used in FSMs based on factorial models (e.g. Refs. 31,70,76), which estimate the feed ration from energy or nutrient requirements (see Section 3.2.1). Thus, they can be used to produce a feeding chart or optimise the ration for growth or economic objectives. In the former approach (feed ration as a forcing variable), the user must provide a time series of distributed feed (as in RAC, FARM and FINS, among others) which are used to determine farm performances. Feed ration data can be obtained from farm records, feeding charts or the FCR. Calculating feed ration from a single FCR is easy and common in FSMs<sup>39,42,46,51,66,69</sup>; however, doing so seriously limits model capacities and generality,<sup>43</sup> as feed rations must be assumed to remain constant over time, and FCR is highly farm specific.

Likewise, the quantity of uneaten feed is either a parameter or an output of FSMs (Table 5). In FSMs based on simple growth functions, uneaten feed may be often expressed as a fixed percentage of the feed distributed. In the FSMs reviewed, this percentage ranges from 0%<sup>33</sup> to 41%<sup>70</sup> for pelleted feed and up to 52% for trash-fish feed.<sup>70</sup> In other studies and non-aquaculture FSMs, this percentage generally ranges from 1% to 6% for feed pellets.<sup>119,136–140</sup> However, some FSMs estimate uneaten feed by calculating the difference between the feed ration and the maximum ingestion capacity or energy requirements. When estimated, the percentage of uneaten feed ranges from 1%<sup>70</sup> to ca. 50%.<sup>64</sup> Wastage rate is difficult to measure experimentally at the cohort or farm level, particularly in open-water systems. The wastage rate may vary as a function of feeding strategies, abiotic conditions (e.g. temperature, hydrodynamics) or fish-feeding behaviour, and vary greatly over time on a given farm. For instance, the in situ percentage of uneaten feed was measured as 9%–52% over several experiments on the same farm.<sup>141</sup> Consequently, uncertainty in feed wastage, whether modelled or set as a parameter, is likely to be high. This uncertainty has consequences on estimating waste at rearing-unit and farm levels, given the high percentage of wasted feed in total waste. For instance, feed wastage of 3% represented 12% of total particulate waste of a salmon farm.<sup>142</sup> When feed wastage exceeds 15%–20%, total particulate waste consists mostly of wasted feed.<sup>141</sup> Estimates of waste emissions may thus differ greatly among FSMs depending on whether the percentage of uneaten feed is set by the user or estimated by the model.

### 3.3.2 | Other types of waste in farm effluents

Fish-farm effluents can contain nutrients (e.g. metabolic waste, uneaten feed, fertiliser, dead fish), chemicals (e.g. antibiotics, pesticides, hormones), pathogens and heavy metals.<sup>143</sup> Nutrient waste products were the only waste type considered in most of the FSMs reviewed, but two FSMs also considered the release of chemicals and pathogens. The nutrient waste streams modelled in the reviewed FSMs represent nutrient emissions from metabolic waste, often uneaten feed and fertiliser, but rarely those from decomposition of dead carcasses (e.g. FINS). When mortality is high, these fluxes should also be considered, particularly if farm-management practices do not remove carcasses and process them on land.<sup>144</sup> The release of pathogens (i.e. *Hepatopoietic necrosis virus*, Oyster herpes virus and *Vibrio aestuarianus*) was included in the ABC model, a recent FSM developed from FARM components.<sup>78</sup> In ABC, pathogen loading is a function of the total number of animals at the source (i.e. the primary emission site), proportion of animals infected and a shedding rate per individual. ABC also includes functions for pathogen infection (see Section 3.4.3.4) and transport both within and among farms. Among the FSMs reviewed, only ERA-AQUA, an FSM developed to perform risk assessments of veterinary medicinal products applied in pond aquaculture, incorporated the release of chemicals (i.e. oxytetracycline and benzalkonium chloride).<sup>38</sup> ERA-AQUA represents 15 processes to model drug transfer and dissipation among the sediment, fish, pond water and the watercourse that receives the effluent compartments,

**TABLE 5** Mean percentage of uneaten feed (as a percentage of feed ration) set in or estimated by farm-scale models

Mean uneaten feed	System	Species	Feed type	References
Parameters set by the user				
30%	Pond	African catfish ( <i>Clarias gariepinus</i> )	N.S.	40
1%	Recirculated	African catfish	N.S.	51
52%	Marine cage	Large yellow croaker ( <i>Larimichthys crocea</i> )	Trash fish	70
41%			Pelleted	
5%	Marine cage	Red drum ( <i>Sciaenops ocellatus</i> )	Pelleted	73
5%	Marine cage	Atlantic salmon ( <i>Salmo salar</i> )	N.S.	61
3%	Marine cage	Seabream ( <i>Sparus aurata</i> )	Pelleted	58
7%	Pond	Nile tilapia ( <i>Oreochromis niloticus</i> )	Pelleted	60
3%	Recirculated	Nile tilapia	N.S.	52
10%	Pond	Nile tilapia	N.S.	39
0%	Pond	Nile tilapia	Pelleted	33
Estimated by the model				
ca. 50%	Marine cage	Seabream	N.S.	64
33%	Marine cage	Seabream	Pelleted	65
38%		Seabass ( <i>Dicentrarchus labrax</i> )		
1–7%	Hatchery	Coho salmon ( <i>Oncorhynchus kisutch</i> ) Chinook salmon ( <i>Oncorhynchus tshawytscha</i> )	N.S.	43
15%	Lake cage	Chinook salmon	Pelleted	53

Abbreviation: N.S.: not specified.

using mass-balance equations. None of the FSMs reviewed, however, modelled heavy-metal loads.

### 3.3.3 | Biomass and stocking density

Information about the number of fish alive (cohort size) over time and their weight distribution is necessary to estimate the stocking biomass in a rearing unit; these variables can be simulated in population dynamics models (also called 'biodemographic models') (Figure 5).

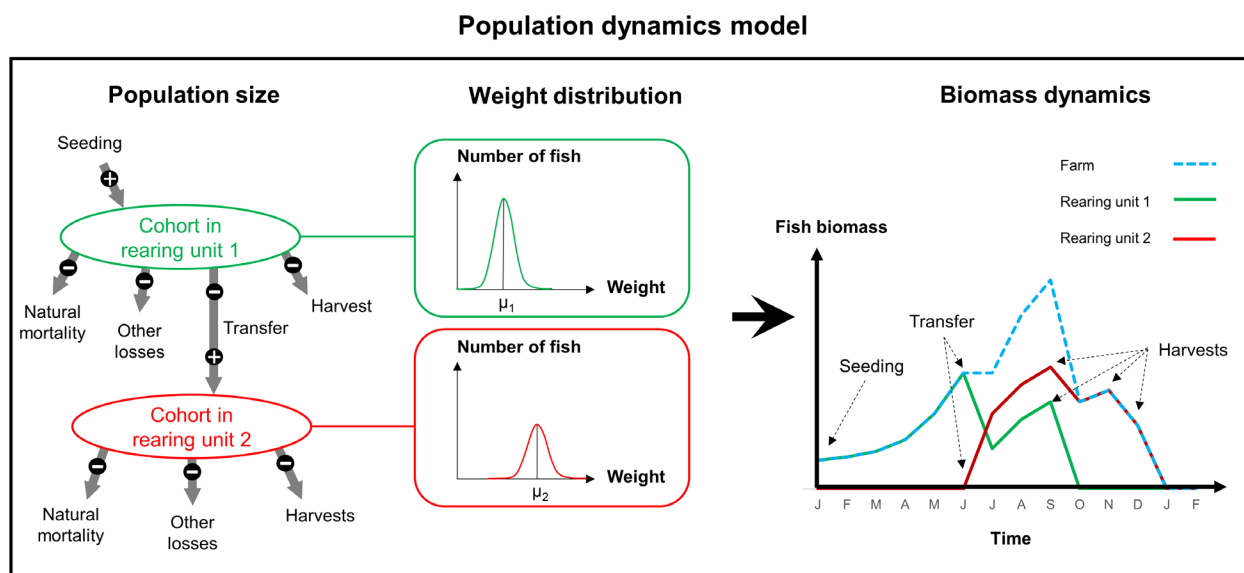
#### Cohort size

Cohort size is determined by several factors. Seeding (i.e. the number of fingerlings introduced into the rearing unit) and natural reproduction increase the number of stocked animals, while natural mortality, other losses, transfer and harvests decrease it. Seeding depends on farm practices: animals can be introduced once, at the beginning of the farming cycle, or continuously during the farming cycle. The seeding rate (i.e. number of fingerlings introduced per unit time) is therefore a model input. Fish do not reproduce in most fish-farming systems (e.g. cages, raceways, RAS) because they are usually harvested before they reach sexual maturity, except for some species such as tilapias, which reach sexual maturity when smaller than market size. Reproduction is therefore almost never modelled, except by certain models applied to pond polyculture systems. Concerning mortality (expressed as the number of dead fish, or percentage of fish in stocks, per unit time), a distinction is made between 'natural' (or 'physiological') mortality, which is theoretically independent of farming practices, and additional mortality or losses, which are related to farm operations (e.g. harvests, transfers between rearing units), diseases, escapes, predation or theft.<sup>25,73</sup> Most FSMs use a fixed mortality (or survival) rate that is expected at the end of a rearing cycle or

based on historical data.<sup>25</sup> A linear (mortality rate remains constant over time) or exponentially decreasing function (mortality rate decreases with fish size/weight) is then fitted to this final mortality rate to determine instantaneous mortality during the farming cycle. This 'survival modelling' method was the one most commonly used in FSMs developed more than 30 years ago.<sup>80</sup> Other methods, such as those used in agent-based models to represent mortality based on foraging and interaction with predators, have thus rarely been incorporated into FSMs to date.<sup>145</sup> Natural mortality is sometimes assumed to be zero due to a lack of information or available relationships (e.g. Refs. 47,71,77). Additional losses can be added to represent the influence of the quality of the rearing environment on fish mortality. For instance, the ABC model considers pathogen interactions with stocking biomass and predicts mortality due to disease.<sup>78</sup> In some pond FSMs, additional losses related to cannibalism or interspecific predation are also simulated using predator-prey relationships in a population dynamics model.<sup>35</sup> In other FSMs, the additional loss rate is essentially used to adjust farm-production efficiency as a function of different rearing practices (e.g. good, average, bad).<sup>30,73</sup> FSMs use a variety of methods to simulate harvest. Harvest rates (expressed as a number or percentage of individuals per unit time) and frequency may form part of input data,<sup>73</sup> or harvesting can be triggered automatically when a targeted market size/weight of the animals is reached.<sup>71,76-78</sup>

#### Inter-individual variability and weight distribution

Most processes simulated at the individual level in FSMs are likely to vary among individuals of a cohort. Studies of inter-individual variability in wild fish populations usually focus on age distributions; in farmed fish cohorts, however, individuals have the same age, so weight distribution due to genetic variability is usually studied. This variability also influences fish ingestion and assimilation capacity, survival and waste emissions. Although nearly all of the FSMs reviewed



**FIGURE 5** General structure of a population dynamics model applied to fish-farming systems. The symbols + and - indicate whether the process increases or decreases population size, respectively.

are based on individual-level models and thus can represent inter-individual variability,<sup>145</sup> they rarely do so; more often, they assume that individual weight predictions are mean values that can be used at the cohort level.<sup>34,43,45,51,66,69,70,73</sup> Different scenarios (e.g. worst-case, average, best-case) are sometimes used to resolve variation in growth among individuals; however, results of these scenarios remain determined by the parameter values and data set beforehand.<sup>34</sup> In some FSMs, variability is represented among individuals or classes of individuals.<sup>30,57,63,72,77</sup> A common method is to use probability distributions, usually Gaussian, for one or more parameters of the growth model (e.g. assimilation efficiency) and to perform as many simulations as there are individuals in the cohort (e.g. Monte Carlo simulations). Models that use random values for model parameters, called stochastic (or probabilistic), are more complex than deterministic models (no random processes) because of the mathematics involved.<sup>80</sup> They also take more time to run because of the large number of simulations required, which greatly increases computing time.<sup>32</sup> One technique to represent inter-individual variability without increasing computing time is to represent the cohort as super-individuals, which are a set (class) of hundreds or thousands of homogenous individuals.<sup>146</sup> This can be done using Markov matrices, such as in the Rizzo and Spagnolo model.<sup>30</sup> Because of these constraints, a few models, such as FARM, provide the ability to choose between inter-individual or inter-class variability. The feasibility of integrating inter-individual variability into an FSM can also differ among families of individual-level models. For instance, DEB theory already considers inter-individual variability due to physiological and environmental factors in a relevant mechanistic way. DEB models can predict biological traits (e.g. food ingestion, growth) of interest in toxicokinetic models, which can be further predicted under dynamic environmental conditions (especially food quality, food availability and temperature) over an animal's life cycle.<sup>147</sup> This can facilitate to some extent the relationship between processes simulated at individual and cohort levels.

Another source of inter-individual variability in fish farming is feed accessibility. Most FSMs consider permanent, equitable and non-competitive access to food resources. Feed is usually assumed to be distributed evenly throughout the entire cage volume and accessible to fish until the population has met its feed requirements or eaten all the feed. Other FSMs, such as that developed by Føre et al.,<sup>71</sup> model the 3D positions of pelleted feed in a cage to represent the amount of time that pellets are available to fish. This time depends on the settling rate of pellets and current intensity. In this model, intake is determined by the stomach volume of fish and their ability to reach the pellets. In the FSM of Serpa et al.,<sup>37</sup> the settling rate of pellets and the height of the tanks (settling distance) are included to represent the access time to the resource. The only FSM reviewed that considers competition for feed was that of Cuenco et al.,<sup>27</sup> which assumes that access to food is positively correlated with fish size (i.e. the largest ones eat first). Better consideration of individual behaviour (e.g. searching for food) and collective behaviour (e.g. competition for resources) in FSMs would probably improve understanding of how feed is wasted, reduce uncertainty surrounding feed wastage and improve estimates of environmental impacts of fed-fish farming.

Protocols and techniques already developed for individual-based and agent-based models<sup>145,148</sup> will help integrate inter-individual variability into FSMs.

#### *Stocking density*

Stocking density (expressed as biomass or number of individuals per unit area or volume) is an important parameter in aquaculture because it can influence growth performance,<sup>149</sup> survival and animal welfare,<sup>150</sup> as well as the quality of the rearing environment. In FSMs, stocking density is often assumed to be unlimited. Some FSMs state this assumption explicitly,<sup>54</sup> but most do not.<sup>53,66,76,77</sup> Some models provide the ability to set or estimate a maximum stocking density.<sup>30,51,67,69,73</sup> In FINS and the FSM of Halachmi,<sup>49,50,67</sup> maximum density is used to back-calculate an initial density, which ensures that the stocking density does not exceed the maximum density. The FSM of Besson et al.<sup>51</sup> follows the same method, except that a second factor also limits the initial density: the ability of a biological filter to process N-NH<sub>3</sub>. This ability also limits the seeding rate in the Seginer and Halachmi model,<sup>47</sup> which can optimise annual stocking density as a function of temperature and market prices or demand for fish. In the adaptation of Besson et al. 's model<sup>51</sup> to marine farms,<sup>69</sup> the DO concentration limits seeding rate. None of the FSMs reviewed except AquaFarm appears to consider minimum stocking density. In AquaFarm, when the density reaches a minimum threshold, fish can be transferred to a smaller rearing volume on the farm. Similarly, when stocking density reaches a maximum threshold, fish can be transferred to larger rearing volumes, or the cohort can be split into sub-cohorts that are transferred to different rearing units.

### **3.4 | Processes and models at the farm level**

#### **3.4.1 | Stocking management**

Halachmi<sup>67</sup> described stock management at the farm level. In the simplest systems, fingerlings are introduced into rearing units, and fish are harvested progressively when they reach a marketable size or all at once at the end of the farming cycle (total harvest). In more complex systems, fish can be transferred between rearing units before harvest to sort them into homogeneous batches or to control stocking density. This kind of stock management requires defining a production plan that includes dates of operations, seeding rate, size at seeding, harvesting rate and market size.<sup>45</sup> This plan is incorporated into the model using a farm-management module, and this information is the main input data. The farm-management module developed by Halachmi<sup>49,50,67</sup> is one of the most complex and sophisticated among those in the FSMs reviewed. It uses queuing theory to optimise rearing unit allocation, seeding rate and density, the number of rearing units and other criteria to increase biomass turnover. The RDSS model has interactive planning to display data entered by the user and track farm operations. INAPRO, FINS, FARM and the FSM of Besson et al.<sup>51,69</sup> have simpler farm-management modules that do not include optimisation functions. Except for INAPRO and FINS, these FSMs



cannot model fish transfers between rearing units. Several of the FSMs reviewed have no farm-management module. Instead, they either simulate each rearing unit and then integrate at the farm level<sup>63,76,77</sup> or represent the farm as a 'black box' that has only one rearing unit. If a study's objective is to estimate the potential production of a farm based on few data and assumptions, a farm-management module is not essential. A 'black box' solution can be suitable and easier to implement. If the objective is to estimate environmental impacts of farm effluents, however, spatially explicit representation of the farm's stocking biomass is important.<sup>151</sup> For instance, to predict the fate of particulate waste from marine cages into the environment, it may be relevant to have time series at a high spatial resolution, as particle transport is driven by currents, which are not necessarily homogeneous at the farm level.

### 3.4.2 | Waste and water treatment

In land-based systems and certain types of semi-enclosed systems at sea,<sup>152,153</sup> different types of filters and treatment systems are used to collect, treat or extract particulate and dissolved wastes.<sup>154-156</sup> The main types of filters used in aquaculture include mechanical filters, clarifiers or settling tanks to collect particulate waste; columns for CO<sub>2</sub> stripping and degassing; and biofilters that contain media seeded with nitrifying bacteria to convert NH<sub>3</sub> into nitrites (NO<sub>2</sub><sup>-</sup>) and then nitrate (NO<sub>3</sub><sup>-</sup>), and denitrification reactors in which bacteria convert NO<sub>3</sub><sup>-</sup> into N<sub>2</sub>. The clean water may return to the fish tank (RAS) or be discharged (flow-through systems). Among the FSMs reviewed, only those applied to land-based aquaculture systems (e.g. RAS<sup>34,48,51</sup>), aquaponic systems<sup>52</sup> or hatcheries<sup>43</sup> consider wastewater treatment. They often use static models of treatment processes, in which the efficiency of each type of filter is set to remove either a fixed percentage (static) or a fixed rate (dynamic). For instance, Besson et al.<sup>51</sup> assume 90% and 100% efficiency for mechanical and biological filters, respectively. Filter efficiency can vary greatly depending on the technology used,<sup>157</sup> and significant differences between theoretical and measured efficiencies have been highlighted.<sup>158</sup> For clarifiers, models that describe sedimentation dynamics of particles in tanks can be used.<sup>52</sup> The capacity of biological filters is usually estimated using dynamic models that simulate dynamics of N transformation by bacteria.<sup>34,52</sup> Models such as AQUASIM, specifically designed to simulate dynamics of N flows in RAS, are also available.<sup>158</sup>

### 3.4.3 | Local environmental impacts

Near- and far-field environmental impacts<sup>21</sup> of fish farming include (i) the use of natural resources and effects of nutrient waste on receiving environments (e.g. effects on water quality, benthic effects, eutrophication),<sup>159</sup> (ii) increased risk of diseases and possible transfer to wild species,<sup>160</sup> (iii) effects of contaminants (e.g. antibiotics, therapeutants, chemicals) on ecosystems and (iv) changes in food webs (e.g. attraction of non-farmed species to farms) caused by the

presence of farmed fish, farm structures and waste emission,<sup>161</sup> (v) risks related to the introduction of non-indigenous species<sup>162</sup> and (vi) genetic pollution.<sup>163</sup> Among them, only some environmental impacts related to the release nutrients, pathogens or contaminants can be modelled at the farm level (i.e. using FSMs alone), because other impacts occur due to or rely on environmental drivers related to larger bay-scale and ecosystem-scale processes. The latter impacts can, however, be modelled by combining FSMs and other types of models, for instance by coupling FSMs with Lagrangian or Eulerian models to simulate benthic effects or pelagic biogeochemistry, respectively (see Section 5.3). Approximately 40% of the FSMs reviewed aimed explicitly to assess local environmental impacts of fish farming. All of them except ABC<sup>78</sup> and ERA-AQUA<sup>38</sup> were limited to water-quality issues or benthic effects of solid waste, which aligns with the general trend over the past few decades for carrying-capacity models to focus on eutrophication.<sup>164</sup>

In aquaculture, water quality can be described using many variables, the most important of which are pH; concentrations of O<sub>2</sub>, NO<sub>2</sub><sup>-</sup>, total dissolved N, P and C, microalgae; and the ratio of NH<sub>3</sub>:NH<sub>4</sub><sup>+</sup> concentrations. In general, nutrient fluxes are simulated using mass-balance approaches in which farm emissions are determined by considering all sources (inputs) and sinks (outputs) for each element or molecule, as well as possible degradation/transformation into other types of substances. Transforming these fluxes into concentrations requires monitoring volumes of water input and water output. Effects of fish farms on water-quality variables are described below, and then methods to estimate these impacts in the FSMs reviewed are presented. Finally, methods used in the FSMs reviewed to estimate other environmental impacts, such as disease spread or negative effects of veterinary medicinal products, are briefly presented.

#### *Dissolved oxygen concentration*

Several physical and biological mechanisms can modify water DO concentration. The maximum DO concentration is determined by water temperature, salinity and pressure. Variation in DO concentration over time depends on the sources and sinks from the farm. DO concentration decreases with fish respiration, so is highly correlated with stocking density. It also decreases with bacterial activity and decomposition by living organisms (e.g. bacteria, plankton) in the system. The amount of particulate matter in the water, including fish faeces, can also decrease the mixing and dispersal of O<sub>2</sub> in the water volume. In contrast, three main mechanisms increase DO concentration: photosynthesis by micro- and macro-algae, aeration systems (e.g. aeration by gravity, O<sub>2</sub> injection, pumps) and gas transfers at the air/water interface (increased by wind). O<sub>2</sub> mass-balance models used in FSMs represent some of these processes. The O<sub>2</sub> mass balance simulated in the AQUASIM model is one of the most detailed. It considers atmospheric exchanges, photosynthesis, instantaneous biochemical demand, respiration of farmed fish and microorganisms (i.e. algae, bacteria), the oxygen used by bacteria for nitrification and oxygen inputs from aeration systems. In FARM, DO concentration is estimated simply from the biological oxygen demand due to primary production, fish respiration and oxygen inputs from aeration systems. FARM considers

effects of DO concentration on fish growth and survival, but the nature of these effects is not detailed.<sup>58</sup> Other FSMs, such as RDSS, RACEWAY or that of Munro,<sup>39</sup> have O<sub>2</sub> mass-balance models with intermediate levels of detail. Stigebrandt<sup>164</sup> argues that fish respiration is the main O<sub>2</sub> sink on fish farms and that a simple mass balance can be used, in which DO concentration equals the input DO concentration minus fish respiration divided by the water-exchange flow. The FSM of Besson et al.<sup>51</sup> calculates the chemical oxygen demand, also called theoretical oxygen demand, necessary to oxidise particulate wastes. These concepts, which are proxies used to estimate DO demand due to bacterial decomposition, can be calculated using stoichiometric coefficients (kg O<sub>2</sub> kg macronutrient<sup>-1</sup>) for each macronutrient in faeces and uneaten feed.<sup>165,166</sup>

#### *Nutrient enrichment, algal growth and eutrophication*

C, N and P are the main elements that limit primary production. Inputs (e.g. feed, fertilisers) and effluents from aquaculture are sources of C, N and P and can therefore stimulate the development of primary production (e.g. bacteria, macrophytes). In extensive and semi-intensive systems, phytoplankton are a direct or indirect source of food for the reared species. However, excessive primary production and its decomposition can consume too much oxygen and lead to hypoxia or anoxia. The risk of eutrophication can be assessed by estimating C, N and P inputs into the environment and predicting the subsequent response of primary production.

In the FSMs reviewed, only models applied to pond systems can simulate primary production as a function of C, N or P inputs. In POND, AquaFarm and the FSM of Yi,<sup>31</sup> microalgae growth is a function of the limiting element (C, N or P). In comparison, in AQUASMAT (application to freshwater ponds in Nigeria) and FARM (application to freshwater ponds in Thailand), N is assumed to be the limiting element and thus the only driver of phytoplankton growth. Effects of nutrient concentration on microalgal growth are usually determined using Michaelis–Menten kinetics.<sup>167</sup> Light intensity, water temperature or pH are other variables used in FSMs to determine microalgal growth. In POND, light intensity is assumed to be the limiting variable when inputs of C, N and P are non-limiting. Other types of models can also be used to simulate trophic interactions in aquatic ecosystems, in particular food-web models such as Ecopath with Ecosim,<sup>168</sup> including in pond systems.<sup>169</sup> FARM includes an ASSETS module<sup>170</sup> to estimate primary production and a eutrophication score. In applications of FARM to offshore systems, however, primary production has been ignored due to the short residence time of the water volume on a farm.<sup>58</sup>

#### *Toxicity of dissolved waste*

Dissolved waste produced by fish metabolism can have direct or indirect toxic effects.<sup>171</sup> NH<sub>3</sub> excreted by fish is toxic to farmed animals but potentially also to other organisms in the environment.<sup>172,173</sup> Depending on water temperature and pH, NH<sub>3</sub> can naturally transform into NH<sub>4</sub><sup>+</sup>, which is much less toxic to fish. NH<sub>3</sub> can also be converted into NO<sub>3</sub><sup>-</sup> by bacteria via a two-step nitrification process. When incomplete, this reaction results in the production of NO<sub>2</sub><sup>-</sup>,

which can also have toxic effects by interfering with oxygen transport and causing respiratory distress in farmed species.<sup>174,175</sup> The CO<sub>2</sub> excreted during respiration via gills can be transformed into different forms (H<sub>2</sub>CO<sub>3</sub>, HCO<sub>3</sub><sup>-</sup>) or remain in the water as dissolved gas. Increased CO<sub>2</sub> concentration can influence fish directly, but also decrease water pH and thus influence NH<sub>3</sub>:NH<sub>4</sub><sup>+</sup> ratios. Several FSMs such as POND, AQUASMAT, AquaFarm, RDSS and the FSM of Gholizadeh<sup>45</sup> can simulate dynamics of NO<sub>2</sub><sup>-</sup> and NH<sub>3</sub> concentrations in the environment, but none of them considers toxic effects of these nutrients on animals. The FSM of Cuenco et al.<sup>27</sup> and Yi<sup>31</sup> simulate a negative feedback of NH<sub>3</sub> concentration on ingestion capacity and a threshold concentration beyond which fish stop eating. These latter processes are of particular interest in systems with little or no water renewal, such as ponds, semi-closed systems, or closed systems. Overall, models are needed that can use a given duration of exposure to a given concentration of toxic substances to predict effects on growth, development and reproduction over time.<sup>176</sup> Bioenergetic models, and specifically DEB, are gaining much attention as a tool to predict these effects on individual animals,<sup>116</sup> suggesting that future DEB-based FSMs could be appropriate tools to better predict the influence of toxic substances on fish farm productivity.

#### *Other local environmental impacts*

Pathogens and therapeutants released by farms or present on or in fish can have negative effects on the environment, fish and human health. In ABC,<sup>78</sup> host-pathogen interactions in a rearing unit are represented using the Susceptible-Exposed-Infected-Recovered (SEIR) model, which is well known in epidemiology to describe disease dynamics within populations. It is based on dynamic ordinary differential equations that consider dynamics of the number of individuals that are susceptible to disease, that become infected and that recover or die after infection. This model can predict impacts of disease spread on farm productivity and is a first and important step to examine subsequent risk of transfer to wild species. In comparison, ERA-AQUA<sup>38</sup> predicts risks of using medicines mixed into feed (i.e. feed treatments) or applied directly to pond water (i.e. bath treatments) to four endpoints: cultured species, non-target aquatic organisms (e.g. algae, invertebrates, fish) in the ecosystem that are exposed to aquaculture effluents, consumer health and trade of the harvested products. It first estimates exposure concentration in the four compartments that it simulates (i.e. sediment, fish, pond water and effluents) and then calculates a risk quotient for each endpoint based on specific safe-exposure concentrations. Other models were developed to assess the emission, fate, exposure and ecotoxicological risks of veterinary medicinal products used in aquaculture (see the review of Rico et al.<sup>177</sup>). Although they are not FSMs, some of these models rely on data provided by FSMs, suggesting the potential for coupling them with FSMs. Although issues such as disease spread and effects of therapeutants can influence ecological carrying capacity strongly,<sup>78</sup> they are still rarely considered when estimating ecological carrying capacity. Modelling these issues is another development pathway for future FSMs or larger modelling systems that include FSMs.



### 3.4.4 | Farm economics

Aquaculture, like any human economic activity, must provide enough profit to live on. Optimising farm production does not necessarily maximise farm profit.<sup>24</sup> Including economic modules in FSMs can thus help select the most profitable options and increase farm efficiency, productivity and competitiveness. In the FSMs reviewed, bioeconomic modules were used mainly to estimate economic profitability of the farming activity under given conditions (e.g. species, location, technology, feed, region) or compare it among a variety of scenarios. In this aim, the models develop a profit-and-loss-account analysis of production. Costs are assigned to all inputs, while prices are assigned to all outputs or products to estimate farm profit. Several costs and revenues can be included in profit-and-loss-account analysis (Table 6). Three cost categories can be analysed: (i) fixed, (ii) depreciable and (iii) variable. Fixed costs are costs disconnected from farm outputs (e.g. insurance, rent). Depreciable costs are related to fixed costs and represent the loss of value of fixed items after some period (e.g. depreciation of equipment). Variable costs are neither fixed nor depreciable, and usually vary as a function of farm production (e.g. feed, fingerlings, energy, labour). Depending on the regulatory context, variable costs may also include environmental taxes such as effluent taxes.<sup>51</sup> Among the FSMs reviewed, only POND and the FSM of Rabassó and Hernández<sup>68</sup> included all three cost categories. Depreciable costs and fixed costs are rarely considered. Simplifying farm economic flows can be justified for analysing comparative scenarios, but models developed to estimate farm profitability in absolute terms should include these costs, as well as all income sources (e.g. public subsidies, closing value), as they usually include only the sale of harvested fish. Aquaculture farms can provide several regulating ecosystem services,<sup>178</sup> such as C and N sequestration in bivalve and seaweed farming, respectively, which can be assigned an economic value<sup>179</sup> and considered in economic analysis when relevant. For instance, in a regulatory-economic environment that rewards reductions in externalities through ‘nutrient credits’ or other economic incentives,<sup>180</sup> this type of revenue should also be considered in profit-and-loss-account analysis, as they can influence farm profitability greatly, particularly for extractive aquaculture or IMTA systems.<sup>181</sup> In fact, the first principle of the EAA explicitly recommends considering the full range of ecosystem functions and services and ensuring a

sustained supply of them to society. FSMs focused on farm economics should therefore progressively include the economic value of other ecosystem services (i.e. provisioning, regulating, supporting and cultural) used and provided by aquaculture systems, as it can foster effective implementation of management options that support development of aquaculture practices in accordance with EAA principles.<sup>179</sup>

Profit-and-loss-account analysis helps measure how well a business is performing, but additional financial statements (e.g. balance sheets, capital account) and economic feasibility analyses (e.g. net present value, internal rate of return, marginal analysis) are required for a comprehensive economic analysis. These are rarely considered in the FSMs reviewed, except for RDSS and the FSMs of Rabassó and Hernández<sup>68</sup> and Hernández et al<sup>54</sup>. Some FSMs also included optimisation methods in the bioeconomic module to help managers make decisions about production strategies, such as seeding and harvest schedules,<sup>47</sup> seeding density<sup>59</sup> and other practices (e.g. feeding rate, water heating).<sup>30</sup> None of the FSMs reviewed used economic analysis for risk assessment or management, although it is another important area for application of bioeconomic models in aquaculture.<sup>24</sup> In addition, none of the FSMs reviewed included social aspects of production, such as income generation, employment opportunities or gender equality. Although these social aspects (human well-being) are fully integrated in EAA principles, FSMs are probably not the most suitable tools to consider them.

## 4 | FARM-SCALE MODEL IMPLEMENTATION AND EVALUATION

The third step of FSM development includes parameter estimation and model evaluation, along with appropriate sensitivity and uncertainty analyses. This process does not have to follow a rigid step-by-step procedure but is rather an iterative operation which can be repeated a few times. Parameter estimation (also called parameterisation) is the process of setting values for each parameter in model equations.<sup>15</sup> Parameter values can be taken directly from the literature, measured in experiments or obtained by calibration. Calibration (also called ‘tuning’) is an iterative process that searches for the best agreement between predicted and observed data for

**TABLE 6** Examples of costs and revenues to consider when applying profit-and-loss-account analysis to aquaculture systems

Costs			Revenue
Fixed	Depreciable	Variable	Variable
Insurance	infrastructure (e.g. cage, tank, building, boats)	Feed	Sales
Rent	Equipment (e.g. pump, filter)	Fingerlings	Closing value
Taxes		Labour	Subsidies
		Energy (e.g. electricity, fuels)	Nutrient credit
		Water	
		Oxygen	
		Chemicals (e.g. fertiliser, therapeutant, disinfectant)	
		Delivery and shipping (e.g. harvest, transport)	
		Maintenance	
		Effluent taxes	

different sets of parameters or different ranges of values. It can be used to estimate parameter values when data are not available, not completely adequate (e.g. values for a different species or ecosystem) or need to be adjusted when value intervals are too wide. Some authors use 'calibration' to describe parameter estimation. Once parameters are obtained and, optionally, calibrated, the model must be evaluated in light of its objectives. This evaluation can be qualitative or quantitative.<sup>26</sup> Qualitative evaluation can aim to understand whether the model meets its objectives, to assess the validity of scientific assumptions or to assess the transparency of the process that produced the model. Quantitative evaluation, often referred to as 'validation' (also called 'corroboration' or 'testing'), consists mainly of objective tests of how well model outputs fit data not used to construct or calibrate the model<sup>14</sup> (i.e. how its outputs fit independent empirical observations). This section presents the concepts and key questions to consider in each phase for FSM implementation and evaluation, as well as a review of how they have been applied to the models analysed in this study.

#### 4.1 | Parameter estimation and model validation

As mentioned, the effort and supporting data required to estimate FSM parameters depends greatly on the species (e.g. well-known vs. new species) and ecosystem under study, the type of individual-level model selected (e.g. empirical vs. mechanistic) and the level of detail required, among other factors. As individual-level models are the core of FSMs, modellers should pay particular attention to how they parameterise it. Using a standard process to estimate individual parameters, as for traditional bioenergetic models, and developing open-access parameter databases (e.g. Add-my-Pet for DEB<sup>115</sup>) can help greatly to reduce the time and resources necessary to develop new FSMs or adapt existing FSMs to new contexts. Simple models, which contain only a few well-defined or directly measured parameters, may not require calibration<sup>14</sup>; therefore, they have not been applied much in simple FSMs. In FSMs based on more complex individual-level models, such as bioenergetic-based FSMs, calibration is a more common practice often used to obtain values for missing parameters rather to refine literature values. This is likely because modellers often struggle with data scarcity and would rather use data for validation than calibration.

Validation is often related to the unresolved and sometimes philosophical debate about its necessity, feasibility and the methods used to perform it.<sup>182</sup> In FSM development, the need to perform validation is determined by the purpose of the model, but validation is certainly possible and often essential for user acceptance. For instance, when FSMs are developed to describe or organise knowledge about a new farming system, validation is unnecessary and irrelevant, but for management and decision-support tools, validation appears necessary. Modellers often want good agreement between model outputs and observations for a few key variables. Depending on the question that the model was developed to answer, certain processes will be prioritised for validation; thus, modellers implicitly accept that some

variables may not be well reproduced. Modellers should explain, however, why lower-priority processes are reproduced less well and draw conclusions about limits of the model's ability to answer the question. Validation results were reported for half of the FSMs reviewed (Table 1). Among them (Table S1), ca. 80% considered weight-/length-at-age observations (e.g. Refs. 64,70) and, more rarely, additional variables for fish performance (e.g. feed intake), water or sediment quality (e.g. Refs. 36,40). From a practical viewpoint, compared to other processes simulated in FSMs, fish weight can be easily measured in any farming system. For instance, in controlled land-based systems, nutrient concentration in water and sediments can be measured on the farm<sup>43</sup> and used to evaluate the fish excretion predicted by the model. In open-water systems, however, it is nearly impossible to measure fish excretion, as the nutrients are immediately dissolved in the water column, flushed with the current, transformed into different compounds, added to background concentrations and assimilated by primary producers. Thus, validation is context dependent. Interestingly, for outputs such as biomass production at the cohort or farm level, only 2 of the 36 FSMs reviewed reported having performed validation.<sup>35,62</sup> One difficulty with validating such aggregated outputs is that when a model performs poorly, modellers do not necessarily know why, particularly if no sensitivity analysis was performed. This outcome suggests that individual processes should be validated before aggregated outputs, which seems reasonable in a context in which new modules are added to adapt models to new applications. Furthermore, additional validation seems necessary when models are applied to a new context, whose values of forcing variables may differ greatly from those explored during the initial validation.

In addition, the FSMs reviewed were often validated without reference to quantitative criteria, leading to subjective conclusions about 'reasonable', 'acceptable' and 'sufficient' model performances (Table S1). For instance, Ernst et al.<sup>34</sup> validated their FSM by comparing many outputs (i.e. water quality, fish growth and mortality, energy and water budgets) to many observed values from the literature but provided only qualitative statements about model performances. Qualitative criteria based on visual assessment were widely used, such as by Canale et al.,<sup>43</sup> who compared measurements and model predictions of P concentration in different compartments of a farm. Other authors used a variety of quantitative goodness-of-fit indicators, especially mean relative error, mean absolute error<sup>76</sup> or root mean square error.<sup>54</sup> Although quantitative, these criteria can still be interpreted subjectively. Another way to evaluate the performance of an FSM (or its modules) is to perform regression analysis between predicted and observed values, as performed in.<sup>33,64,73</sup> This simple parametric test examines the difference from 0, 1 and 1 of the intercept, slope and coefficient of determination ( $R^2$ ), respectively, from which one can obtain useful information about systemic biases of the model and qualify model performances (e.g. Ref. 183). Although some authors state 'there is not, and never will be, a totally objective and accepted approach to model validation',<sup>184</sup> it seems clear that validation based on statistical tests and reporting an associated level of significance will provide more insights into FSM performances to end users.

## 4.2 | Model uncertainty

Assessing uncertainties in integrated modelling may increase trust in model results; thus, from a management viewpoint, knowing the degree of uncertainty in model predictions seems to represent a key prerequisite for interacting with stakeholders.<sup>185</sup> This review found no studies specifically focused on uncertainty analysis of FSMs, although recent studies considered the variability in DEB-simulated growth trajectories due to uncertainty in parameters and initial conditions (e.g. Refs. 77,186). Indeed, assessing uncertainty propagation in integrated mathematical models, such as FSMs, is complex. Here, we provide ideas for future assessment of uncertainty in FSMs by starting from existing examples of uncertainty analysis in integrated models available from other scientific domains, and in particular from the study of Payne et al.,<sup>187</sup> who assessed uncertainties in predictions of climate-change impacts on marine ecosystems. These authors approached uncertainty by breaking it down into (i) structural (model) uncertainty, (ii) initialisation and internal variability uncertainty, (iii) parameter uncertainty and (iv) scenario uncertainty. In FSMs, structural uncertainty can be related to differences in model conceptualisation and underlying hypotheses, and it is present at each level of organisation: individual, cohort and rearing unit. Inventorying the ranges of types and families of individual-level models in the literature for the most common target species (e.g. trout, salmon, seabass, seabream, tilapia) could be useful to assess structural uncertainty in FSMs. To assess uncertainty, model inter-comparison, widely used in other fields (see some examples for marine fisheries and ecosystems,<sup>188</sup> for forestry<sup>189</sup> or for ocean biogeochemistry<sup>190</sup>), could represent the basis for predicting fish growth under common forcing variables (i.e. environmental conditions and feeding regimes). Indeed, this approach could be broadened to higher levels of organisation in FSMs by considering different processes for representing cohort size and inter-individual variability. Uncertainties in model initialisation and parameter values are explored more often. Some of the FSMs reviewed (e.g. Refs. 27,40,49) performed a sensitivity analysis of parameters, which ranks the most influential ones; for instance, Cuenco et al.<sup>27</sup> identified that food-consumption parameters were more influential, and thus critical, than metabolism parameters. Based on the confidence with which parameters were estimated, and their uncertainty, one can obtain a preliminary indication of the potential overall uncertainty in model predictions. For growth models, uncertainty in initial conditions is also often investigated in management applications (e.g. Ref. 186): a straightforward and effective approach is to explore the variability in model predictions as a function of fish size at stocking, which is available to both farm managers and regulators. Although validation experiments often evaluate the response of FSMs under different forcing conditions (see Section 4.1), they rarely assess the uncertainty associated with external forcing. This represents a weakness for two contexts in which models can be applied: (i) simulation in data-scarce conditions and (ii) scenario simulations that address climate-change effects (e.g. Ref. 191). Generalising this concept, and bridging to the following section on model applications, we share the viewpoint of Jakeman et al.,<sup>26</sup> who stated that 'model uncertainty must be considered in the context of the purposes of the model',

with a broad distinction between models used to predict and those used to build scenarios.

## 5 | APPLICATIONS OF INTEREST FOR THE EAA

The fourth step of FSM development is model application. The FSMs reviewed were developed for various purposes, including estimating or comparing production<sup>31,34,76</sup>; socioeconomic outputs<sup>51,69</sup> or environmental impacts<sup>57,68</sup> of scenarios; optimising production, resource use or facilities<sup>30,35,67,72</sup>; verifying compliance with effluent-discharge regulations<sup>43</sup>; and facilitating site selection.<sup>63</sup> In summary, the most frequent applications are assessment of production or ecological carrying capacity (with a focus on eutrophication impacts), as well as economic assessment or optimisation. FSMs can contribute to other key sustainability challenges highlighted in the EAA, at the farm level and higher. We demonstrate this ability by presenting four innovative and relevant applications of FSMs for EAA: (i) PFF, (ii) evaluation of performances and feasibility of IMTA systems, (iii) support for spatial management and (iv) LCA. These applications were also selected to address potential interests of a broad audience, including farm managers, scientists, regulators and policymakers.

### 5.1 | Precision fish farming

The PFF framework<sup>192</sup> was introduced by adapting the Precision Livestock Farming approach to aquaculture.<sup>193</sup> A PFF system consists of a real-time observation component, a dynamic model and a 'control' component, which help farmers make optimal animal-production decisions, thus pursuing some of the EAA objectives. Observation components can include various real-time sensor networks. These may focus on detecting temporal and spatial variability in DO throughout cage farms (see e.g.<sup>194</sup>) and involve telemetry measurements of heart rate and swimming activity, which could provide useful information for assessing the physiological status of farmed fish.<sup>195</sup> In general, monitoring and analysis of fish behaviour is receiving great attention, providing information required to guide daily feeding, schedule making and disease diagnosis.<sup>196</sup> Hydroacoustic systems are increasingly used to support farm operations; for instance, active systems can provide information about fish speed, direction and 3D movements, while passive systems can be adopted to monitor behaviour of certain target species.

In this context in which observation is rapidly developing, the relatively slow development of a new generation of reliable dynamic FSMs that can predict changes in fish variables due to changes in external forcing and control variables seems to be one of the main constraints hindering implementation of the PFF framework. Notably, most FSMs have a temporal resolution that is too coarse for PFF applications. Future FSMs could overcome this limitation by adopting approaches based on control theory (e.g. Ref. 197), as used in other industrial fields. Current FSMs could be combined with data-assimilation and machine-learning techniques, if appropriately

calibrated, to produce short-term predictions of DO concentration dynamics on a farm.<sup>198</sup> As discussed (Section 3.4.3.1), current FSMs represent DO concentration on farms with differing degrees of complexity, so developing specific ‘oxygen-simulation modules’ that can be adapted to different farm settings (i.e. environmental conditions and data availability) could be useful. For monitoring purposes, these short-term oxygen predictions would benefit from acquiring real-time data from current meters to estimate the renewal time of water in cages in marine and freshwater environments.

Examples of ways to improve existing FSMs include improving representation of individual behaviour (e.g. searching for food) and collective behaviour (e.g. competition for resources, use of the water column) to improve representation of the key drivers of feed intake and thus explain how feed is wasted and what causes inter-individual variability in growth. This step could reduce the uncertainty currently associated with parameterising these processes. In parallel, refining the ability of mass-balance and metabolic-flux models to represent digestibility and faeces production as a function of diet composition could increase the ability to represent complex interactions among feeding strategies, water quality and fish welfare on the farm. Assessing the accuracy of these models and using them to make short-term predictions could benefit from a wide range of automatic-recognition methods based on computer vision,<sup>199</sup> including direct (e.g. swimming velocity and acceleration) and indirect (e.g. detection of uneaten pellets) observations of feeding behaviour.

## 5.2 | Feasibility and performances of integrated multitrophic aquaculture systems

IMTA, a direct application of the EAA integration principle integrating the EAA at the farm level, is perceived as a more sustainable practice; however, it requires more research to better assess its feasibility and performance. IMTA systems can include fed species (e.g. fish, shrimp), as well as extractive species such as algae that can feed on dissolved inorganic waste generated by the fed species<sup>200,201</sup> or filter-feeders and detritivores that can feed on organic waste.<sup>202</sup> IMTA can take many forms depending on the associated species (and their subsequent trophic niches), rearing technologies and environment (e.g. land-based vs. open-water IMTA) and the chronology (i.e. simultaneous vs. sequential farming of organisms) and level (i.e. low to high) of integration investigated. The theoretical advantages of IMTA are increased nutrient-use efficiency and production of additional biomass and income.<sup>203</sup> As Reid et al.<sup>86</sup> describe, however, the performances and feasibility of IMTA systems depend on many factors, including (i) an adequate biomass ratio among co-farmed species, (ii) synchronicity between nutrient loading and uptake dynamics and (iii) the location of extractive species relative to the spatial distribution of nutrient streams. These factors can strongly influence the quantity, quality, temporal dynamics and location of nutrient streams in the systems and thus determine the ability of an IMTA to derive added value from these interspecific relationships. The influence of these factors on farm production, profitability and environmental

pressure can be studied by modelling IMTA systems with FSMs, which makes them key tools to promote and develop IMTA under the EAA.

One key challenge when designing a new IMTA system is to find a biomass ratio between the fed and extractive species that reduces nutrient loss to the environment. For instance, if one aims to add seaweed farming to an existing salmon farm, the question becomes how much seaweed biomass is needed to remove a given percentage of the dissolved N excreted by the fish. Answering this question requires quantifying (and qualifying) the waste generated by a given salmon biomass over its farming cycle and the N sequestration potential of the same biomass of seaweed over this period. FSMs that incorporate individual-level models of species from different trophic levels (i.e. IMTA-FSMs) can be used to do this. FSMs can also be used to calculate and optimise the biomass ratio according to a sequestration objective or practical rearing constraints. For instance, Reid et al.<sup>204</sup> estimated that 6.7 ( $\pm 1.5$ ) 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. In another study, Chary et al.<sup>74</sup> estimated that removing 100% of particulate waste from red drum faeces would require growing 1.3 kg of the sea cucumber *Holothuria scabra* per kg of fish but that reaching this biomass ratio on the farm is infeasible in practice due to density constraints on the sea cucumber. Given current stocking-density limits for sea cucumbers, the IMTA system would be able to reduce its net particulate waste load by only 1% compared to that of a fish monoculture. This latter study highlighted the importance of representing rearing constraints. These types of data are usually represented in FSMs but not necessarily in IMTA models (e.g. see Refs. 205,206).

A second important point is to ensure that nutrient emission dynamics from species at higher trophic levels match those of nutrient uptake of extractive species. This is often complex, as the length of the farming cycle and biophysical requirements will vary among co-farmed taxa. Extractive species usually have shorter farming cycles than fed species. For instance, microalgae and ragworm farming cycles last a few days to a few weeks, respectively,<sup>207,208</sup> while fish-farming cycles often range from 6–24 months. Thus, the dynamic character of FSMs and the ability of some of them (e.g. bioenergetic-based FSMs) to represent effects of environmental forcing on the metabolism of farmed species might be able to synchronise or optimise nutrient emission and uptake as a function of environmental forcing.

Third, extractive species in an IMTA system should be placed close to nutrient streams. As most extractive species farmed in IMTA are sessile (e.g. bivalves, seaweed) or move slowly, they will not be able to access waste-nutrient streams if they are not near them. FSMs provide dynamic and sometimes spatially explicit emissions data that can be used as inputs in waste-dispersal (for particulate waste) or -diffusion (for dissolved nutrients) models to estimate the organic footprint and nutrient plume of the farm, respectively. When coupled, these tools can help understand how waste is dispersed with currents, diluted in the water column or deposited on the seabed (see Section 5.3 for further details). Thus, combining FSMs and these site- or bay-scale models can help select the most suitable locations for extractive species.

Some challenges, however, remain to be addressed to develop FSMs for use in an IMTA context. The first challenge is to produce models that represent multiple organisms from different trophic levels. This may be facilitated by broader appropriation of mechanistic modelling methods and theory, such as DEB (e.g. the DEB-based IMTA model of Ren et al.<sup>205</sup>). A second challenge is to consider the issue of waste quality better, as most IMTA models are based on bioenergetic modelling and thus ignore the nutrient profile of waste and its ability to meet requirements of extractive species. Developing FSMs based on bioenergetic models that simulate nutrient fluxes<sup>76</sup> or based on metabolic-flux models, which predict an organism's growth as a function of the nutrient profile of its food (see Section 3.2.1 and Figure 4), would be of interest to improve estimates of the production of IMTA farms. A third and final challenge is to include economic analysis in future IMTA-FSM, as the profitability of IMTA systems is often questioned, particularly when ecosystem services are not internalised (Section 3.4.4). Except for a few applications performed with FARM,<sup>58,61</sup> the profitability of IMTA systems has rarely been analysed as a function of production and environmental performances.

### 5.3 | Supporting spatial management

An ecosystem-based management approach, such as EAA, considers humans as an integral part of the natural ecosystem and, when applied, can show trade-offs and interactions between management goals and goods and services provided by natural ecosystems.<sup>209</sup> Turning an ecosystem-based management approach into practice has become critical in the context of maritime spatial planning (MSP),<sup>210</sup> which is a management tool for maintaining marine ecosystems in a healthy condition while ensuring the sustainable exploitation of ecosystem goods and services.<sup>211</sup> Like maritime uses, aquaculture experiences conflict with other activities and with conservation priorities. In the EU, for instance, where EU Directive 2014/89 provides a legal basis for such an integrated management approach,<sup>212</sup> aquaculture is perceived in many contexts as a 'new player' in the seascape. Science-based zoning and site selection of aquaculture, performed in the framework of implementing MSP, has been acknowledged by researchers<sup>213</sup> and more recently the EU<sup>214</sup> as a priority for sustainable expansion of the sector. Concepts such as Allocated Zones for Aquaculture<sup>215</sup> were introduced to support this approach and models are recognised as useful tools for supporting these tasks,<sup>20</sup> particularly to better understand aquaculture–environment interactions at different levels.

Spatial management of aquaculture involves two of the three scales defined in the EAA, which are addressed by different types of models. FSMs can be coupled with particle-tracking (Lagrangian) models to represent interactions at the local scale (e.g. a specific farm lease) or with Eulerian approaches to represent higher spatial scales (e.g. bay, coastal waterbody). FSMs can also be integrated into wider sustainability assessments using LCA, for instance, by considering total environmental burdens associated with production and transportation of energy and feed used by the farm (see Section 5.4).

For management at a local scale, the ultimate aim of integrating or coupling an FSM with a dispersal model is to estimate pressure (e.g. flows of organic matter or solid waste) or impact (e.g. total sulphide concentration, indicators of benthic community status) on sediments.<sup>216,217</sup> This is associated, implicitly or explicitly, with the concept of assimilative capacity<sup>218</sup> and represents a useful resource for siting farms (i.e. by considering bathymetry and water currents). In a management perspective, this type of model can identify a farm's Allowable Zone of Effect<sup>215</sup> (i.e. where limited impact is permitted). Particle-tracking dispersal models are well established tools for assessing local interactions (e.g. Refs. 136,219). These models can represent farm-level processes with differing degrees of complexity, and the availability of detailed dynamic or cage-specific animal-production input data can improve model accuracy (as mentioned for DEPOMOD<sup>138,140</sup>). One advantage of coupling FSMs with dispersal models is that the FSMs predict dynamics of farm waste at high spatial resolution; this is useful as particle transport is driven by currents, which vary over time and space. Examples of coupling of FSMs and dispersal models are already available (e.g. Refs. 65,66,75). Along with the accuracy with which FSMs represent farm-management processes, a key pre-requisite for integrating FSMs into local management tools seems to be the ability to represent the proportion of uneaten feed lost to the environment. Existing mathematical equations discussed in this review could be improved in the future by considering fish behaviour in cages. In this sense, this is likely a cross-cutting theme between the fields of farm management (see the section on PFF) and spatial management.

A gap seems to exist, however, for aquaculture zones (addressed by Eulerian models), as no FSMs have been specifically developed to feed into the complex biogeochemical models used in operational oceanography.<sup>220</sup> Complex models such as ERSEM<sup>221</sup> and BFM<sup>222</sup> seem to be required to assess potential interactions of multiple farms with coastal biogeochemical processes and lower trophic levels, which is a key step for estimating the nutrient-related ecological carrying capacity of a marine area prioritised for aquaculture. This type of approach was satisfactorily applied in studies that used modified biogeochemical models and quantified fish-farm effluents (e.g. combined use of Delft3D-FLOW and EcoWin,<sup>223</sup> use of POM-ERSEM to predict effects of farm effluents in Greece<sup>224</sup>). In these studies, however, FSMs were not directly coupled with the reaction-transport biogeochemical models. In this sense, developing FSMs specifically designed to feed into operational oceanography models could help greatly to define and manage Allocated Zones for Aquaculture. Promising efforts, which highlight the future potential of these developments, have been made to facilitate online use of biogeochemical models.<sup>225</sup> This idea is supported by results of studies that focused on constraints that have hindered off-the-coast and offshore marine aquaculture expansion,<sup>226</sup> and could help derive future recommendations for implementing MSP that include aquaculture. In this study, stakeholders highlighted the need for informed management plans that could prevent food depletion, disease spread and subsequent decrease/collapse of production. Further development of ecosystem-based models in offshore areas was recommended to optimise the use of space. Indeed,



while at the farm level, the use of sensors (as in PFF) is expected to support future development of spatial management, at the aquaculture-zone level, the ultimate complexity of FSMs will likely depend on the data available. In this respect, interest in applying satellite remote sensing (SRS) in aquaculture<sup>227</sup> to provide data for applying FSMs to site selection has increased in the past decade. Although using SRS to assess aquaculture-zone suitability has focused mainly on surface-water temperatures (e.g. Ref. 228), future FSMs may benefit from development of new algorithms and SRS products (e.g. better characterisation of suspended matter, detection of harmful algal blooms<sup>229,230</sup>), thus providing new opportunities in this area.

## 5.4 | Life cycle assessment

An aquaculture farm can have impacts that are distant from its location due to direct or indirect resource use or pollutant emissions in earlier or later stages of the life cycle of the product system. Assessing the environmental sustainability of aquaculture systems therefore requires extending analysis from the farm level to the entire value chain and using multi-criteria methods. A framework commonly used to assess environmental impacts of a variety of production systems, including aquaculture systems, with a systemic perspective is LCA. LCA is a standardised method that compiles resource use and emissions to the environment ‘from the cradle to the grave’, that is, from extraction of raw materials; through production, transport and use; up to the end-of-life or recycling.<sup>231</sup> The scope of an LCA is therefore much wider than that of an FSM. In LCA, each resource used and substance emitted is attributed to one or more impact categories and converted by characterisation models into potential environmental impacts.<sup>232</sup> Life-cycle impact categories include, among others, climate change, eutrophication, acidification, energy use, biotic and abiotic resource use, aquatic ecotoxicity and ozone depletion. Over the past two decades, LCA has been applied extensively to aquaculture systems. A recent meta-analysis identified 65 studies and 179 aquaculture systems, of which 67% were fish-farming systems.<sup>233</sup> This and other reviews<sup>233–235</sup> have shown that the feed-production stage is the largest source of impact in most of the impact categories usually assessed (including climate change, acidification, cumulative energy use and net primary production use) and that LCA is therefore particularly sensitive to yields (productivity) and input-use efficiency, in particular FCR, which are two characteristics represented by FSM. FSMs can therefore be useful tools to provide detailed inputs for LCA and help assess environmental impacts of aquaculture systems.

With a life-cycle perspective, an initial strategy to decrease total environmental burdens of fed-fish farming is to achieve equal or higher yields while using fewer resources, especially feed, per unit of production. Large room for improvement still exists to increase productivity and decrease environmental impacts of the production of major species such as carp, tilapia and milkfish. Much of this performance gap could be closed by keeping better records, along with monitoring water quality.<sup>236</sup> As mentioned, FSMs can be useful tools

to support daily production management, allowing farmers to keep track of production data; predict body weight; optimise feed management as a function of stocked biomass, environmental conditions and species' energy or nutrient requirements; analyse on-farm performances and report changes. Several examples of commercial user-friendly FSMs dedicated to the sector are already available, but further development of such tools for species produced globally, and for data-scarce contexts will be important. Wider adoption and use of these tools by farmers could help them calculate feed requirements more accurately, thus decreasing feed losses, nutrient losses and the FCR. Furthermore, coupling these FSMs with simple LCA software would allow farmers to predict potential consequences of better management practices on environmental impacts of their products and help them prioritise improvements.

A second strategy to decrease environmental impacts of fed-fish farming systems is to design innovative formulations that incorporate more sustainable ingredients. Ingredients used in aquafeed differ in their nutrient profiles and environmental impacts.<sup>237,238</sup> For instance, fish meal and fish oil are important sources of high-quality proteins, omega-3 fatty acids and micronutrients,<sup>239</sup> but producing them can pressure forage fish stocks and marine food webs.<sup>240</sup> Alternative protein and lipid sources can be obtained from crop-based ingredients, but they have their own strong limitations, typically due to containing carbohydrates with low digestibility for carnivores, containing anti-nutritional elements<sup>239</sup> and having higher overall impacts on eutrophication, land use and human and ecosystem toxicity than fish meal and fish oil.<sup>233,241</sup> Similarly, livestock by-product meals have several advantages, including a high protein content and well-balanced amino acid profile, but can have a high ash content and may carry environmental burdens associated with livestock production.<sup>236</sup> One major challenge for enhancing the sustainability of aquafeed is, thus, to design new eco-efficient aquafeeds based on alternative ingredients that can meet fish nutritional requirements, reduce the overall pressure on marine and land ecosystems and contribute less to climate change. FSMs can influence the design of innovative eco-friendly feed formulations. As Bohnes et al.<sup>233</sup> state, most LCA studies that estimated and compared impacts of conventional and modified diets<sup>166,242–245</sup> did not address the FCR comprehensively, often assuming it to be constant. This is a strong assumption,<sup>239</sup> as a change in ingredients can strongly influence feed digestibility and nutrient use by fish,<sup>246</sup> both of which determine the FCR. Recently, Ghamkhar and Hicks,<sup>247</sup> in a comparative impact assessment of 12 aquafeeds, highlighted the need to consider the FCR of aquafeed with respect to the quantity and quality of fish produced. To do so, the authors performed LCA on previously published results and tested feeds whose FCR had been measured experimentally. A complementary pathway is to develop and use FSMs based on metabolic-flux models to predict fish growth, body composition and nutrient emissions as a function of feed formulation (Section 3.2.1). If sufficient digestibility data for ingredients are available to calibrate these models, developing such FSMs and using them with LCA could serve to simulate formulation scenarios and assess their influence on FCR and impacts on the environment.

## 6 | CONCLUSIONS

To our knowledge, this is the first review of fish FSMs that has covered multiple species, systems and applications. This narrative review considers 36 models published from 1985–2021 applied to freshwater and marine species and a variety of rearing technologies, including ponds, tanks, cages, raceways, RAS and hatcheries. It includes models developed to explore production, environmental or economic aspects of fish farming as well as tools that can support innovative applications, such as PFF, IMTA modelling, spatial management of aquaculture and LCA. Some models that fit our definition of FSMs, particularly commercial ones, were not included because they have not been presented in a peer-reviewed article or Ph.D. thesis. Our review identified important issues at each step of the modelling process, provided recommendations and suggests research needs. We observed limited scoping, characterised by vague objectives rather than explicit questions, and a lack of conceptual models. We encourage future FSM modellers to give greater attention to defining a model's scope and objectives, and more specifically to state the specific management or research question for which the FSM is built. Doing so will help others determine whether these FSMs could be appropriate for reuse in other contexts. This review showed that a variety of FSMs are available to simulate processes at individual, cohort and farm levels, each of which has advantages and disadvantages in terms of complexity, generality and data requirements. This variety can raise questions about the inter-comparability of predictions of different FSM. This kind of comparison has yet to be performed for aquaculture FSMs and remains an area for further research. Data availability is a major constraint in the development of FSMs, particularly for parameter estimation. Developing open-access parameter databases is, therefore, encouraged, as it may greatly decrease the time and resources needed to develop new FSMs and help adapt them to new contexts. Validating FSMs often relies on qualitative assessment, and uncertainty analysis is almost never performed, which may lead to subjective conclusions about model accuracy. We provide recommendations for performing validation and uncertainty analysis in FSMs based on methods used in other scientific domains. Improving these aspects is important to increase model users' confidence in FSMs and will help them use FSMs for management and decision-making.

### AUTHOR CONTRIBUTIONS

**Killian Chary:** Conceptualization; data curation; methodology; project administration; visualization; writing – original draft; writing – review and editing. **Daniele Brigolin:** Conceptualization; methodology; writing – original draft; writing – review and editing. **Myriam D. CALLIER:** Conceptualization; funding acquisition; methodology; writing – original draft; writing – review and editing.

### ACKNOWLEDGEMENTS

The authors thank the French Ministry of Agriculture and Food, the French Ministry of the Sea and IFREMER for financing the MOCAA project (Modelling ecosystem assimilation capacity for sustainable aquaculture 2020–2021), in which this study was performed. We thank the model developers contacted during this study for their time and

valuable information about their models. We thank P. Lopez for editing the figures. We also thank J. Aubin, A. Fiandrino, R. Filgueira, T. Laugier and M. Ubertini for reading and editing the manuscript before submission. We thank M.S. Corson for English copyediting and proofreading.

### FUNDING INFORMATION

French Ministry for Food and Agriculture, French Ministry of the Sea and IFREMER.

### CONFLICT OF INTEREST

All authors agreed to be listed and approved the manuscript for publication. We have no conflict of interest to disclose.

### DATA AVAILABILITY STATEMENT

Data sharing does not apply, as this study did not create or analyse new data.

### ETHICS APPROVAL STATEMENT

This study contains no research with human participants or animals performed by any of the authors.

### PERMISSION TO REPRODUCE MATERIAL FROM OTHER SOURCES

No third-party material taken from other source was used or reproduced in this article.

### ORCID

Killian Chary  <https://orcid.org/0000-0001-9549-9227>

Daniele Brigolin  <https://orcid.org/0000-0002-4590-8616>

Myriam D. Callier  <https://orcid.org/0000-0002-2778-5720>

### REFERENCES

1. Costello C, Cao L, Gelcich S, et al. The future of food from the sea. *Nature*. 2020;588(7836):95–100. doi:[10.1038/s41586-020-2616-y](https://doi.org/10.1038/s41586-020-2616-y)
2. FAO. *The State of World Fisheries and Aquaculture 2020. Sustainability in Actions*; 2020:224. doi:[10.4060/ca9229en](https://doi.org/10.4060/ca9229en)
3. Pauly D, Zeller D. Catch reconstructions reveal that global marine fisheries catches are higher than reported and declining. *Nat Commun*. 2016;7(1):1–9. doi:[10.1038/ncomms10244](https://doi.org/10.1038/ncomms10244)
4. Soto D, Aguilar-Manjarrez J, Brugère C, et al. Applying an ecosystem-based approach to aquaculture: principles, scales and some management measures. In: Soto D, Aguilar-Manjarrez J, Hishamunda N, eds. *Building an Ecosystem Approach to Aquaculture*. FAO/Universitat de Les Illes Balears Expert Workshop. 7–11 May 2007, Palma de Mallorca, Spain. Vol 14. FAO Fisheries and Aquaculture Proceedings; 2008:15–35. doi:[10.1017/S0020818300006160](https://doi.org/10.1017/S0020818300006160)
5. Aguilar-Manjarrez J, Soto D, Brummett R. *Aquaculture Zoning, Site Selection and Area Management under the Ecosystem Approach to Aquaculture*. Report ACS113536. FAO and World Bank Group. 2017: 395. doi:[10.13140/RG.2.2.22893.59369](https://doi.org/10.13140/RG.2.2.22893.59369)
6. McKindsey CW. Carrying capacity for sustainable bivalve aquaculture. In: Christou P, Savin R, Costa-Pierce B, Misztal I, Whitelaw B, eds. *Sustainable Food Production*. Springer; 2013:449–466. doi:[10.1007/978-1-4419-0851-3\\_179](https://doi.org/10.1007/978-1-4419-0851-3_179)
7. McKindsey CW, Thetmeyer H, Landry T, Silvert W. Review of recent carrying capacity models for bivalve culture and recommendations for research and management. *Aquaculture*. 2006;261(2):451–462. doi:[10.1016/j.aquaculture.2006.06.044](https://doi.org/10.1016/j.aquaculture.2006.06.044)



8. Weitzman J, Filgueira R. The evolution and application of carrying capacity in aquaculture: towards a research agenda. *Rev Aquac.* 2019;12(3):1297-1322. doi:10.1111/raq.12383
9. Naylor RL, Goldburg RJ, Primavera JH, et al. Effect of aquaculture on world fish supplies. *Nature.* 2000;405(6790):1017-1024. doi:10.1038/35016500
10. Reid GK, Gurney-Smith HJ, Flaherty M, et al. Climate change and aquaculture: considering adaptation potential. *Aquac Environ Interact.* 2019;11:603-624. doi:10.3354/AEI00333
11. Campanati C, Willer D, Schubert J, Aldridge DC. Sustainable intensification of aquaculture through nutrient recycling and circular economies: more fish, less waste, blue growth. *Rev Fish Sci Aquac.* 2021; 30:1-50. doi:10.1080/23308249.2021.1897520
12. Ferreira JG, Aguilar-Manjarrez J, Bacher C, et al. Progressing aquaculture through virtual technology and decision-support tools for novel management. In: Subasinghe RP, Arthur JR, Bartley DM, et al., eds. *Global Conference on Aquaculture 2010, Phuket, Thailand. 22-25 September 2010.* FAO and NACA; 2012:643-704.
13. Byron CJ, Costa-Pierce BA. Carrying capacity tools for use in the implementation of an ecosystems approach to aquaculture. In: Ross LG, Telfer TC, Falconer L, Soto D, Aguilar-Manjarrez J, eds. *Site Selection and Carrying Capacity for Inland and Coastal Aquaculture. FAO/Institute of Aquaculture, University of Stirling, Expert Workshop, 6-8 December 2010. Stirling, UK.* FAO Fisheries and Aquaculture Proceedings No. 21; 2013:87-101.
14. Jørgensen S, Bendricchio G, eds. *Fundamentals of Ecological Modelling.* 3rd ed. Elsevier; 2001.
15. Jackson LJ, Trebitz AS, Ryn KH, Cottingham L. An introduction to the practice of ecological modeling. *Bioscience.* 2000;50(8):694-706. doi:10.1641/0006-3568(2000)050[0694:AITPO]2.0.CO;2
16. Ross LG, Telfer TC, Falconer L, et al. Carrying capacities and site selection within the ecosystem approach to aquaculture. In: Ross LG, Telfer TC, Falconer L, Soto D, Aguilar-Manjarrez J, eds. *Site Selection and Carrying Capacities for Inland and Coastal Aquaculture. FAO/Institute of Aquaculture, University of Stirling, Expert Workshop, 6-8 December 2010. Stirl;* 2013:19-46.
17. Chopin T, Cooper JA, Reid G, Cross S, Moore C. Open-water integrated multi-trophic aquaculture: environmental biomitigation and economic diversification of fed aquaculture by extractive aquaculture. *Rev Aquac.* 2012;4(4):209-220. doi:10.1111/j.1753-5131.2012.01074.x
18. Sanz-Lazaro C, Sanchez-Jerez P. Regional integrated multi-trophic aquaculture (RIMTA): spatially separated, ecologically linked. *J Environ Manage.* 2020;271:110921. doi:10.1016/j.jenvman.2020.110921
19. Chopin T. Aquaculture, integrated multi-trophic (IMTA) aquaculture integrated multi-trophic (IMTA). In: Christou P, Savin R, Costa-Pierce BA, Misztal I, Whitelaw CBA, eds. *Sustainable Food Production.* Springer; 2013:184-205. doi:10.1007/978-1-4614-5797-8\_173
20. Corner RA, Aguilar-Manjarrez J. Tools and models for aquaculture zoning, site selection and area management. In: Aguilar-Manjarrez J, Soto D, Brummett R, eds. *Aquaculture Zoning, Site Selection and Area Management under the Ecosystem Approach to Aquaculture. Full Document.* 405 p; 2017:99-145. FAO, and World Bank Group.
21. Weitzman J, Steeves L, Bradford J, Filgueira R. Far-field and near-field effects of marine aquaculture. *World Seas: An Environmental Evaluation Volume III: Ecological Issues and Environmental Impacts.* Academic Press; 2018:197-220. doi:10.1016/B978-0-12-805052-1.00011-5
22. Jones HFE, Özkundakci D, Hunt S, Giles H, Jenkins B. Bridging the gap: a strategic framework for implementing best practice guidelines in environmental modelling. *Environ Sci Policy.* 2020;114:533-541. doi:10.1016/j.envsci.2020.09.030
23. Newell CR, Brady DC, Richardson J. *Farm-Scale Production Models. Goods and Services of Marine Bivalves.* Springer International Publishing; 2018:485-506. doi:10.1007/978-3-319-96776-9\_24
24. Llorente I, Luna L. Bioeconomic modelling in aquaculture: an overview of the literature. *Aquac Int.* 2016;24(4):931-948. doi:10.1007/s10499-015-9962-z
25. Anyadike C, Mbajjorgu C, Ajah G. Review of aquacultural production system models. *Niger J Technol.* 2016;35:448-457. doi:10.4314/njt.v35i2.29
26. Jakeman AJ, Letcher RA, Norton JP. Ten iterative steps in development and evaluation of environmental models. *Environ Model Softw.* 2006;21(5):602-614. doi:10.1016/j.envsoft.2006.01.004
27. Cuenco ML, Stickney RR, Grant WE. Fish bioenergetics and growth in aquaculture ponds: I. Individual fish model development. *Ecol Model.* 1985;27(3-4):169-190. doi:10.1016/0304-3800(85)90001-8
28. Cuenco ML, Stickney RR, Grant WE. Fish bioenergetics and growth in aquaculture ponds: II. Effects of interactions among, size, temperature, dissolved oxygen, unionized ammonia and food on growth of individual fish. *Ecol Model.* 1985;27(3-4):191-206. doi:10.1016/0304-3800(85)90002-X
29. Cuenco ML, Stickney RR, Grant WE. Fish bioenergetics and growth in aquaculture ponds: III. Effects of intraspecific competition, stocking rate, stocking size and feeding rate on fish productivity. *Ecol Model.* 1985;28(1-2):73-95. doi:10.1016/0304-3800(85)90014-6
30. Rizzo G, Spagnolo M. A model for the optimal management of sea bass *Dicentrarchus labrax* aquaculture. *Mar Resour Econ.* 1996;11: 267-286. doi:10.1086/mre.11.4.42629170
31. Yi Y. A bioenergetics growth model for Nile tilapia (*Oreochromis niloticus*) based on limiting nutrients and fish standing crop in fertilized ponds. *Aquac Eng.* 1998;18(3):157-173. doi:10.1016/S0144-8609(98)00028-4
32. Bolte J, Nath S, Ernst D. Development of decision support tools for aquaculture: the POND experience. *Aquac Eng.* 2000;23(1-3):103-119. doi:10.1016/S0144-8609(00)00049-2
33. Nath SS. Development of a decision support system for pond aquaculture. Phd thesis, Bioresource Engineering Department, Oregon State University; 1996:293.
34. Ernst DH, Bolte JP, Nath SS. AquaFarm: simulation and decision support for aquaculture facility design and management planning. *Aquac Eng.* 2000;23(1-3):121-179. doi:10.1016/S0144-8609(00)00045-5
35. De Graaf GJ, Dekker PJ, Huisman B, Verreth JAJ. Simulation of Nile tilapia (*Oreochromis niloticus niloticus* L.) culture in ponds, through individual-based modelling, using a population dynamic approach. *Aquac Res.* 2005;36(5):455-471. doi:10.1111/j.1365-2109.2005.01228.x
36. Serpa D, Pousão-Ferreira P, Caetano M, Cancela da Fonseca L, Dinis MT, Duarte P. A coupled biogeochemical-dynamic energy budget model as a tool for managing fish production ponds. *Sci Total Environ.* 2013;463-464:861-874. doi:10.1016/j.scitotenv.2013.06.090
37. Serpa D, Pousão P, Ferreira H, Cancela L, Teresa M, Duarte P. Modelling the growth of white seabream (*Diplodus sargus*) and gilthead seabream (*Sparus aurata*) in semi-intensive earth production ponds using the dynamic energy budget approach. *J Sea Res.* 2013; 76:135-145. doi:10.1016/j.seares.2012.08.003
38. Rico A, Geng Y, Focks A, van den Brink PJ. Modeling environmental and human health risks of veterinary medicinal products applied in pond aquaculture. *Environ Toxicol Chem.* 2013;32(5):1196-1207. doi:10.1002/etc.2153
39. Munro LI. Development and application of dynamic models for environmental management of aquaculture in South East Asia. PhD thesis, University of Stirling; 2014:242.
40. Anyadike CC, Mbajjorgu CC, Ajah GN. Aquacultural engineering aquacultural system management tool (AQUASMAT) I: model development. *Aquac Eng.* 2015;69:60-77. doi:10.1016/j.aquaeng.2015.10.002
41. Anyadike CC, Mbajjorgu CC, Ajah GN. Aquacultural system management tool II: analytical and management capability. *Agric Eng Int.* 2017;19(3):97-104.

42. Colt J, Schuur A, Cryer E, Miles T. Modeling of multiple stocks and programs for master planning and feasibility studies. *Aquac Eng.* 2009;41(3):176-187. doi:10.1016/j.aquaeng.2009.07.005
43. Canale RP, Whelan G, Switzer A, Eisch E. A bioenergetic approach to manage production and control phosphorus discharges from a salmonid hatchery. *Aquaculture.* 2016;451:137-146. doi:10.1016/j.aquaculture.2015.09.008
44. Colt J, Watten B, Rust M. Modeling carbon dioxide, pH, and unionized ammonia relationships in serial reuse systems. *Aquac Eng.* 2009;40(1):28-44. doi:10.1016/j.aquaeng.2008.10.004
45. Gholizadeh M. Development of an integrated model for sustainable aquaculture and optimization of fish production in raceway systems. PhD thesis, School of Graduate Studies, Universiti Putra Malaysia; 2017:148.
46. Wang YH, Turton R, Semmens K, Borisova T. Raceway design and simulation system (RDSS): an event-based program to simulate the day-to-day operations of multiple-tank raceways. *Aquac Eng.* 2008;39(2-3):59-71. doi:10.1016/j.aquaeng.2008.06.002
47. Seginer I, Halachmi I. Optimal stocking in intensive aquaculture under sinusoidal temperature, price and marketing conditions. *Aquac Eng.* 2008;39(2-3):103-112. doi:10.1016/j.aquaeng.2008.09.002
48. Wik TEI, Lindén BT, Wramner PI. Integrated dynamic aquaculture and wastewater treatment modelling for recirculating aquaculture systems. *Aquaculture.* 2009;287(3-4):361-370. doi:10.1016/j.aquaculture.2008.10.056
49. Halachmi I. Aquacultural engineering mathematical principles of production management and robust layout design: part II. Upscaling to a 1000-ton/year recirculating aquaculture system (RAS). *Aquac Eng.* 2012;50:11-19. doi:10.1016/j.aquaeng.2012.03.003
50. Halachmi I. Aquacultural engineering mathematical principles of production management and robust layout design: part I. 250-ton/year recirculating aquaculture system (RAS). *Aquac Eng.* 2012;50:1-10. doi:10.1016/j.aquaeng.2012.03.001
51. Besson M, Komen H, Aubin J, et al. Economic values of growth and feed efficiency for fish farming in recirculating aquaculture system with density and nitrogen output limitations: a case study with African catfish (*Clarias gariepinus*). *J Agric Sci.* 2014;92(12):5394-5405. doi:10.2527/jas2014-8266
52. Karimanzira D, Keesman KJ, Kloas W, Baganz D, Rauschenbach T. Dynamic modeling of the INAPRO aquaponic system. *Aquac Eng.* 2016;75:29-45. doi:10.1016/j.aquaeng.2016.10.004
53. McDonald ME, Tikkanen CA, Axler RP, Larsen CP, Host G. Fish simulation culture model (FIS-C): a bioenergetics based model for aquacultural wasteload application. *Aquac Eng.* 1996;15(4):243-259.
54. Hernández JM, Gasca-leyva E, León CJ, Vergara JM. A growth model for gilthead seabream (*Sparus aurata*). *Ecol Model.* 2003;165:265-283. doi:10.1016/S0304-3800(03)00095-4
55. Ervik A, Hansen PK, Aure J, Stigebrandt A, Johannessen P, Jahnsen T. Regulating the local environmental impact of intensive marine fish farming I. The concept of the MOM system (Modelling-Ongrowing fish farms-Monitoring). *Aquaculture.* 1997;158:85-94. Accessed April 30, 2018. <http://www.ecasa.org.uk/Documents/MOM.I.pdf>
56. Stigebrandt A, Aure J, Ervik A, Hansen PK. Regulating the local environmental impact of intensive marine fish farming: III. A model for estimation of the holding capacity in the Modelling-Ongrowing fish farm-Monitoring system. *Aquaculture.* 2004;234(1-4):239-261. doi:10.1016/j.aquaculture.2003.11.029
57. Ferreira JG, Hawkins AJS, Bricker SB. Management of productivity, environmental effects and profitability of shellfish aquaculture – the Farm Aquaculture Resource Management (FARM) model. *Aquaculture.* 2007;264(1-4):160-174. doi:10.1016/j.aquaculture.2006.12.017
58. Ferreira JG, Saurel C, Ferreira JM. Cultivation of gilthead bream in monoculture and integrated multi-trophic aquaculture. Analysis of production and environmental effects by means of the FARM model. *Aquaculture.* 2012;358-359:23-34. doi:10.1016/j.aquaculture.2012.06.015
59. Ferreira JG, Sequeira A, Hawkins AJS, et al. Analysis of coastal and offshore aquaculture: application of the FARM model to multiple systems and shellfish species. *Aquaculture.* 2009;289(1-2):32-41. doi:10.1016/j.aquaculture.2008.12.017
60. Ferreira JG, Falconer L, Kittiwanih J, et al. Analysis of production and environmental effects of Nile tilapia and white shrimp culture in Thailand. *Aquaculture.* 2015;447:23-36. doi:10.1016/j.aquaculture.2014.08.042
61. Cubillo AM, Ferreira JG, Robinson SMC, Pearce CM, Corner RA, Johansen J. Role of deposit feeders in integrated multi-trophic aquaculture – a model analysis. *Aquaculture.* 2016;453:54-66. doi:10.1016/j.aquaculture.2015.11.031
62. Cubillo AM, Ferreira JG, Lencart-Silva J, et al. Direct effects of climate change on productivity of European aquaculture. *Aquac Int.* 2021;29:1561-1590. doi:10.1007/s10499-021-00694-6
63. Baldan D, Porporato EMD, Pastres R, Brigolin D. An R package for simulating growth and organic wastage in aquaculture farms in response to environmental conditions and husbandry practices. *PLoS One.* 2018;13(5):e0195732. doi:10.1371/journal.pone.0195732
64. Brigolin D, Pastres R, Tomassetti P, Porrello S. Modelling the biomass yield and the impact of seabream mariculture in the Adriatic and Tyrrhenian seas (Italy). *Aquac Int.* 2010;18(2):149-163. doi:10.1007/s10499-008-9232-4
65. Brigolin D, Meccia VL, Venier C, Tomassetti P, Porrello S, Pastres R. Modelling biogeochemical fluxes across a Mediterranean fish cage farm. *Aquac Environ Interact.* 2014;5(1):71-88. doi:10.3354/aei00093
66. Piedecausa MA, Aguado-Giménez F, Cerezo-Valverde J, Hernández-Llorente MD, García-García B. Simulating the temporal pattern of waste production in farmed gilthead seabream (*Sparus aurata*), European seabass (*Dicentrarchus labrax*) and Atlantic bluefin tuna (*Thunnus thynnus*). *Ecol Model.* 2010;221(4):634-640. doi:10.1016/j.ecolmodel.2009.11.011
67. Halachmi I. Aquacultural engineering mathematical principles of production management and robust layout design: part III. 2500-ton/year fish farming in marine net cages. *Aquac Eng.* 2013;54:110-117. doi:10.1016/j.aquaeng.2012.11.001
68. Rabassó M, Hernández JM. Bioeconomic analysis of the environmental impact of a marine fish farm. *J Environ Manage.* 2015;158:24-35. doi:10.1016/j.jenvman.2015.04.034
69. Besson M, Vandeputte M, van Arendonk JAM, et al. Influence of water temperature on the economic value of growth rate in fish farming: the case of sea bass (*Dicentrarchus labrax*) cage farming in the Mediterranean. *Aquaculture.* 2016;462:47-55. doi:10.1016/j.aquaculture.2016.04.030
70. Cai H, Ross LG, Telfer TC, Wu C, Zhu A. Modelling the nitrogen loadings from large yellow croaker (*Larimichthys crocea*) cage aquaculture. *Environ Sci Pollut Res.* 2016;23(1):7529-7542. doi:10.1007/s11356-015-6015-0
71. Føre M, Alver M, Arve J, et al. Modelling growth performance and feeding behaviour of Atlantic salmon (*Salmo salar* L.) in commercial-size aquaculture net pens: model details and validation through full-scale experiments. *Aquaculture.* 2016;464:268-278. doi:10.1016/j.aquaculture.2016.06.045
72. Estruch VD, Mayer P, Roig B, Jover M. Developing a new tool based on a quantile regression mixed-TGC model for optimizing gilthead sea bream (*Sparus aurata* L) farm management. *Aquac Res.* 2017;48(12):5901-5912. doi:10.1111/are.13414
73. Chary C, Fiandrino A, Covès D, Aubin J, Falguière JC, Callier MD. Modeling Sea cage outputs for data-scarce areas: application to red drum (*Sciaenops ocellatus*) aquaculture in Mayotte, Indian Ocean. *Aquac Int.* 2019;27(3):625-646. doi:10.1007/s10499-019-00351-z

74. Chary K, Aubin J, Sadoul B, Fiandrino A, Covès D, Callier MD. Integrated multi-trophic aquaculture of red drum (*Sciaenops ocellatus*) and sea cucumber (*Holothuria scabra*): assessing bioremediation and life-cycle impacts. *Aquaculture*. 2020;516:734621. doi:10.1016/j.aquaculture.2019.734621
75. Chary K, Callier MD, Covès D, Aubin J, Simon J, Fiandrino A. Scenarios of fish waste deposition at the sub-lagoon scale: a modelling approach for aquaculture zoning and site selection. *ICES J Mar Sci*. 2021;78:922-939. doi:10.1093/icesjms/fsaa238
76. Nobre AM, Valente LMP, Conceição L, Severino R, Lupatsch I. A bioenergetic and protein flux model to simulate fish growth in commercial farms: application to the gilthead seabream. *Aquac Eng*. 2019;84:12-22. doi:10.1016/j.aquaeng.2018.11.001
77. Stavrakidis-Zachou O, Papandroulakis N, Lika K. A DEB model for European sea bass (*Dicentrarchus labrax*): parameterisation and application in aquaculture. *J Sea Res*. 2019;143:262-271. doi:10.1016/j.seares.2018.05.008
78. Ferreira JG, Taylor NGH, Cubillo A, et al. An integrated model for aquaculture production, pathogen interaction, and environmental effects. *Aquaculture*. 2021;536:736438. doi:10.1016/j.aquaculture.2021.736438
79. Piedrahita RH. Introduction to computer modeling of aquaculture pond ecosystems. *Aquac Res*. 1988;19(1):1-12. doi:10.1111/j.1365-2109.1988.tb00328.x
80. Cuenco ML. *Aquaculture Systems Modeling: An Introduction with Emphasis on Warmwater Aquaculture*. ICLARM Studies and Reviews 19. 1989:49.
81. Ford A. *Modeling the Environment, Second Edition*. Island Press; 2010:488.
82. FAO. *The State of World Fisheries and Aquaculture 2018 - Meeting the Sustainable Development Goals*. Licence: CC BY-NC-SA 3.0 IGO. FAO; 2018. doi:10.1126/science.aaw5824
83. Seginer I. Growth models of gilthead sea bream (*Sparus aurata* L.) for aquaculture: a review. *Aquac Eng*. 2016;70:15-32. doi:10.1016/j.aquaeng.2015.12.001
84. Kearney MR. What is the status of metabolic theory one century after Pütter invented the von Bertalanffy growth curve? *Biol Rev*. 2021;96(2):557-575. doi:10.1111/brv.12668
85. Weiner J. On the practice of ecology. *J Ecol*. 1995;83(1):153. doi:10.2307/2261159
86. Reid GK, Lefebvre S, Filgueira R, et al. Performance measures and models for open-water integrated multi-trophic aquaculture. *Rev Aquac*. 2020;12(1):47-75. doi:10.1111/raq.12304
87. Dumas A, France J, Bureau D. Modelling growth and body composition in fish nutrition: where have we been and where are we going? *Aquac Res*. 2010;41(2):161-181. doi:10.1111/j.1365-2109.2009.02323.x
88. Lugert V, Thaller G, Tetens J, Schulz C, Krieter J. A review on fish growth calculation: multiple functions in fish production and their specific application. *Rev Aquac*. 2016;8(1):30-42. doi:10.1111/raq.12071
89. von Bertalanffy L. Quantitative laws in metabolism and growth. *Q Rev Biol*. 1957;32(3):217-231. doi:10.1086/401873
90. Gompertz B. On the nature of the function expressive of the law of human mortality, and on a new mode of determining the value of life contingencies. *Philos Trans R Soc Lond*. 1825;115:513-583.
91. Iwama GK, Tautz AF. A simple growth model for salmonids in hatcheries. *Can J Fish Aquat Sci*. 1981;38:649-656. doi:10.1139/f81-087
92. Cho CY. Feeding systems for rainbow trout and other salmonids with reference to current estimates of energy and protein requirements. *Aquaculture*. 1992;100(1-3):107-123. doi:10.1016/0044-8486(92)90353-M
93. Lupatsch I, Kissil GW. Predicting aquaculture waste from gilthead seabream (*Sparus aurata*) culture using a nutritional approach. *Aquat Living Resour*. 1998;11(4):265-268. doi:10.1016/S0990-7440(98)80010-7
94. Katsanevakis S. Modelling fish growth: model selection, multi-model inference and model selection uncertainty. *Fish Res*. 2006;81(2-3):229-235. doi:10.1016/J.FISHRES.2006.07.002
95. Mercier L, Pan J, Paillon C, Awa N, Mouillot D, Darnaude AM. Estuarine, coastal and shelf science otolith reading and multi-model inference for improved estimation of age and growth in the gilthead seabream *Sparus aurata* (L.). *Estuar Coast Shelf Sci*. 2011;92:534-545. doi:10.1016/j.ecss.2011.02.001
96. Cho CY, Bureau DP. Development of bioenergetic models and the fish-PrFEQ software to estimate production, feeding ration and waste output in aquaculture. *Aquat Living Resour*. 1998;11(4):199-210. doi:10.1016/S0990-7440(98)89002-5
97. Glencross BD. A factorial growth and feed utilization model for barrundi, *Lates calcarifer* based on Austratian production conditions. *Aquac Nutr*. 2008;14(4):360-373. doi:10.1111/j.1365-2095.2007.00543.x
98. Lupatsch I, Wm G, Sklan D. Optimization of feeding regimes for European sea bass *Dicentrarchus labrax*: a factorial approach. *Aquaculture*. 2001;202:289-302. doi:10.1016/S0044-8486(01)00779-7
99. Lupatsch I, Kissil GW, Sklan D. Comparison of energy and protein efficiency among three fish species gilthead sea bream (*Sparus aurata*), European sea bass (*Dicentrarchus labrax*) and white grouper (*Epinephelus aeneus*): energy expenditure for protein and lipid deposition. *Aquaculture*. 2003;225:175-189. doi:10.1016/S0044-8486(03)00288-6
100. Bayne BL, ed. *Marine Mussels: Their Ecology and Physiology*. University Printing House; 1976.
101. Strand Å. *Growth- and Bioenergetic Models and Their Application in Aquaculture of Perch (Perca Fluviatilis)*. Vattenbruksinstitutionen Rapport 42 Ume 2005. 2005:63.
102. Jørgensen C, Enberg K, Mangel M. Modelling and interpreting fish bioenergetics: a role for behaviour, life-history traits and survival trade-offs. *J Fish Biol*. 2016;88(1):389-402. doi:10.1111/jfb.12834
103. Ney JJ. Bioenergetics modeling today: growing pains on the cutting edge. *Trans Am Fish Soc*. 1993;122(5):736-748. doi:10.1577/1548-8659(1993)122<0736:BMTGPO>2.3.CO;2
104. van der Veer HW, Cardoso JFJM, Peck MA, Kooijman SALM. Physiological performance of plaice *Pleuronectes platessa* (L.): a comparison of static and dynamic energy budgets. *J Sea Res*. 2009;62(2-3):83-92. doi:10.1016/j.seares.2009.02.001
105. Nisbet RM, Muller EB, Lika K, Kooijman SALM. From molecules to ecosystems through dynamic energy budget models. *J Anim Ecol*. 2008;69(6):913-926. doi:10.1111/j.1365-2656.2000.00448.x
106. Chipps S, Wahl DH. Bioenergetics modeling in the 21st century: reviewing new insights and revisiting old constraints. *Trans Am Fish Soc*. 2008;137:298-313. doi:10.1577/T05-236.1
107. Nisbet RM, Jusup M, Klanjscek T, Pecquerie L. Integrating dynamic energy budget (DEB) theory with traditional bioenergetic models. *J Exp Biol*. 2012;215(6):892-902. doi:10.1242/jeb.059675
108. Deslauriers D, Chipps SR, Breck JE, Rice JA, Madenjian CP. Fish bioenergetics 4.0: an R-based modeling application. *Fisheries*. 2017;42(11):586-596. doi:10.1080/03632415.2017.1377558
109. van der Meer J. An introduction to dynamic energy budget (DEB) models with special emphasis on parameter estimation. *J Sea Res*. 2006;56(2):85-102. doi:10.1016/j.seares.2006.03.001
110. Kooijman SALM. Energy budgets can explain body size relations. *J Theor Biol*. 1986;121(3):269-282. doi:10.1016/S0022-5193(86)80107-2
111. Kooijman SALM. *Dynamic Energy and Mass Budgets in Biological Systems*. Cambridge University Press; 2000. doi:10.1017/CBO9780511565403
112. Kooijman SALM. *Dynamic Energy Budget Theory for Metabolic Organisation*. 3rd ed. Cambridge University Press; 2010. doi:10.1017/CBO9780511805400



113. Lika K, Kearney MR, Freitas V, et al. The “covariation method” for estimating the parameters of the standard dynamic energy budget model I: philosophy and approach. *J Sea Res.* 2011;66(4):270-277. doi:[10.1016/J.SEARES.2011.07.010](https://doi.org/10.1016/J.SEARES.2011.07.010)
114. Kooijman SALM, Sousa T, Pecquerie L, van Der Meer J, Jager T. From food-dependent statistics to metabolic parameters, a practical guide to the use of dynamic energy budget theory. *Biol Rev.* 2008; 83:533-552. doi:[10.1111/j.1469-185X.2008.00053.x](https://doi.org/10.1111/j.1469-185X.2008.00053.x)
115. Marques GM, Augustine S, Lika K, Pecquerie L, Domingos T, Kooijman SALM. The AmP project: comparing species on the basis of dynamic energy budget parameters. *PLoS Comput Biol.* 2018; 14(5):e1006100. doi:[10.1371/journal.pcbi.1006100](https://doi.org/10.1371/journal.pcbi.1006100)
116. Sherborne N, Galic N, Ashauer R. Sublethal effect modelling for environmental risk assessment of chemicals: problem definition, model variants, application and challenges. *Sci Total Environ.* 2020; 745:141027. doi:[10.1016/j.scitotenv.2020.141027](https://doi.org/10.1016/j.scitotenv.2020.141027)
117. Maury O, Poggiale J. From individuals to populations to communities: a dynamic energy budget model of marine ecosystem size-spectrum including life history diversity. *J Theor Biol.* 2013;324:52-71. doi:[10.1016/j.jtbi.2013.01.018](https://doi.org/10.1016/j.jtbi.2013.01.018)
118. Saraiva S, van der Meer J, Kooijman SALM, Ruardij P. Bivalves: from individual to population modelling. *J Sea Res.* 2014;94:71-83. doi:[10.1016/j.seares.2014.06.004](https://doi.org/10.1016/j.seares.2014.06.004)
119. Bureau DP, Gunther SJ, Cho CY. Chemical composition and preliminary theoretical estimates of waste outputs of rainbow trout reared in commercial cage culture operations in Ontario. *N Am J Aquac.* 2003;65(1):33-38. doi:[10.1577/1548-8454\(2003\)065<0033:CCAPTE>2.0.CO;2](https://doi.org/10.1577/1548-8454(2003)065<0033:CCAPTE>2.0.CO;2)
120. Papatryphon E, Petit J, van der Werf HMG, Sadasivam KJ, Claver K. Nutrient-balance modeling as a tool for environmental management in aquaculture: the case of trout farming in France. *Environ Manag.* 2005;35(2):161-174. doi:[10.1007/s00267-004-4020-z](https://doi.org/10.1007/s00267-004-4020-z)
121. Bar NS, Sigholt T, Shearer KD, Krogdahl Å. A dynamic model of nutrient pathways, growth, and body composition in fish. *Can J Fish Aquat Sci.* 2007;64:1669-1682. doi:[10.1139/F07-127](https://doi.org/10.1139/F07-127)
122. Bar NS, Radde N. Long-term prediction of fish growth under varying ambient temperature using a multiscale dynamic model. *BMC Syst Biol.* 2009;3:1-19. doi:[10.1186/1752-0509-3-107](https://doi.org/10.1186/1752-0509-3-107)
123. Rønnestad I, Conceição LEC. Artemia protein is processed very fast in *Solea senegalensis* larvae: a dynamic simulation model. *Aquaculture.* 2012;350-353:154-161. doi:[10.1016/j.aquaculture.2012.04.002](https://doi.org/10.1016/j.aquaculture.2012.04.002)
124. Hua K, Birkett S, De Lange CFM, Bureau DP. Adaptation of a non-ruminant nutrient-based growth model to rainbow trout (*Oncorhynchus mykiss* Walbaum). *J Agric Sci.* 2010;148(1):17-29. doi:[10.1017/S0021859609990037](https://doi.org/10.1017/S0021859609990037)
125. Blaxter KL, Graham NM, Wainman FW. Some observations on the digestibility of food by sheep, and on related problems. *Br J Nutr.* 1956;10(2):69-91. doi:[10.1079/bjn19560015](https://doi.org/10.1079/bjn19560015)
126. Zhang Y, Lu R, Qin C, Nie G. Precision nutritional regulation and aquaculture. *Aquac Rep.* 2020;18:100496. doi:[10.1016/j.aqrep.2020.100496](https://doi.org/10.1016/j.aqrep.2020.100496)
127. Johnston IA, Bower NI, Macquene DJ. Growth and the regulation of myotomal muscle mass in teleost fish. *J Exp Biol.* 2011;214(10):1617-1628. doi:[10.1242/jeb.038620](https://doi.org/10.1242/jeb.038620)
128. Sun M, Hassan SG, Li D. Models for estimating feed intake in aquaculture: a review. *Comput Electron Agric.* 2016;127:425-438. doi:[10.1016/j.compag.2016.06.024](https://doi.org/10.1016/j.compag.2016.06.024)
129. Bureau DP, Hua K. Towards effective nutritional management of waste outputs in aquaculture, with particular reference to salmonid aquaculture operations. *Aquac Res.* 2010;41(5):777-792. doi:[10.1111/j.1365-2109.2009.02431.x](https://doi.org/10.1111/j.1365-2109.2009.02431.x)
130. Jobling M. Energetic models - bioenergetics in aquaculture settings. In: Farrell AP, ed. *Encyclopedia of Fish Physiology.* Vol 3. Academic Press; 2011:1664-1674. doi:[10.1016/B978-0-12-374553-8.00152-0](https://doi.org/10.1016/B978-0-12-374553-8.00152-0)
131. Strain PM, Hargrave BT. Salmon aquaculture, nutrient fluxes and ecosystem processes in southwestern New Brunswick. In: Hargrave B, ed. *Environmental Effects of Marine Finfish Aquaculture, Handbook of Environmental Chemistry.* Vol 5. Springer-Verlag; 2005: 29-57. doi:[10.1007/b136003](https://doi.org/10.1007/b136003)
132. Islam MS. Nitrogen and phosphorus budget in coastal and marine cage aquaculture and impacts of effluent loading on ecosystem: review and analysis towards model development. *Mar Pollut Bull.* 2005;50(1):48-61. doi:[10.1016/j.marpolbul.2004.08.008](https://doi.org/10.1016/j.marpolbul.2004.08.008)
133. Pete R, Guyondet T, Bec B, et al. A box-model of carrying capacity of the Thau lagoon in the context of ecological status regulations and sustainable shellfish cultures. *Ecol Model.* 2020;426:109049. doi:[10.1016/j.ecolmodel.2020.109049](https://doi.org/10.1016/j.ecolmodel.2020.109049)
134. Stigebrandt A. *MOM (Monitoring - On-growing Fish Farms - Modelling). Turnover of Energy and Matter by Fish - a General Model with Application to Salmon.* Institute of Marine Research, Bergen, Norway. 1999:28.
135. Kousoulaki K, Saether B-S, Albrektsen S, Noble C. Review on European sea bass (*Dicentrarchus labrax*, Linnaeus, 1758) nutrition and feed management: a practical guide for optimizing feed formulation and farming protocols. *Aquac Nutr.* 2015;21(2):129-151. doi:[10.1111/anu.12233](https://doi.org/10.1111/anu.12233)
136. Cromey CJ, Nickell TD, Black KD. DEPOMOD—modelling the deposition and biological effects of waste solids from marine cage farms. *Aquaculture.* 2002;214(1-4):211-239. doi:[10.1016/S0044-8486\(02\)00368-X](https://doi.org/10.1016/S0044-8486(02)00368-X)
137. Cromey CJ, Nickell TD, Treasurer J, Black KD, Inall M. Modelling the impact of cod (*Gadus morhua* L.) farming in the marine environment-CODMOD. *Aquaculture.* 2009;289(1-2):42-53. doi:[10.1016/j.aquaculture.2008.12.020](https://doi.org/10.1016/j.aquaculture.2008.12.020)
138. Cromey CJ, Thetmeyer H, Lampadariou N, Black KD, Kögeler J, Karakassis I. MERAMOD: predicting the deposition and benthic impact of aquaculture in the eastern Mediterranean Sea. *Aquac Environ Interact.* 2012;2(2):157-176. doi:[10.3354/aei00034](https://doi.org/10.3354/aei00034)
139. Forrest B, Keeley N, Gillespie P, Hopkins G, Knight B, Govier D. *Review of the Ecological Effects of Marine Finfish Aquaculture: Final Report. Prepared for Ministry of Fisheries. Cawthron Report No. 1285.* Cawthron Institute, Nelson, New Zealand. 2007:71.
140. Chang BD, Page FH, Losier RJ, McCurdy EP. Organic enrichment at salmon farms in the Bay of Fundy, Canada: DEPOMOD predictions versus observed sediment sulfide concentrations. *Aquac Environ Interact.* 2014;5(3):185-208. doi:[10.3354/aei00104](https://doi.org/10.3354/aei00104)
141. Ballester-Moltó M, Sanchez-Jerez P, Cerezo-Valverde J, Aguado-Giménez F. Particulate waste outflow from fish-farming cages. How much is uneaten feed? *Mar Pollut Bull.* 2017;119(1):23-30. doi:[10.1016/j.marpolbul.2017.03.004](https://doi.org/10.1016/j.marpolbul.2017.03.004)
142. Reid GK, Liutkus M, Robinson SMC, et al. A review of the biophysical properties of salmonid faeces: implications for aquaculture waste dispersal models and integrated multi-trophic aquaculture. *Aquac Res.* 2009;40(3):257-273. doi:[10.1111/j.1365-2109.2008.02065.x](https://doi.org/10.1111/j.1365-2109.2008.02065.x)
143. Wang X, Cuthbertson A, Gualtieri C, Shao D. A review on mariculture effluent: characterization and management tools. *Water.* 2020; 12(11):2991. doi:[10.3390/w12112991](https://doi.org/10.3390/w12112991)
144. Olsen LM, Holmer M, Olsen Y. *Perspectives of Nutrient Emission from Fish Aquaculture in Coastal Waters. Literature Review with Evaluated State of Knowledge.* FHF Project No. 542014. The Fishery and Aquaculture Industry Research Fund. 2008:87.
145. Grimm V. Ecological models: individual-based models. *Encyclopedia of Ecology.* Elsevier; 2018:65-73. doi:[10.1016/B978-0-12-409548-9.11144-3](https://doi.org/10.1016/B978-0-12-409548-9.11144-3)
146. Scheffer M, Baveco JM, DeAngelis DL, Rose KA, van Nes EH. Super-individuals a simple solution for modelling large populations on an individual basis. *Ecol Model.* 1995;80(2-3):161-170. doi:[10.1016/0304-3800\(94\)00055-M](https://doi.org/10.1016/0304-3800(94)00055-M)

147. Mounier F, Pecquerie L, Lobry J, et al. Dietary bioaccumulation of persistent organic pollutants in the common sole *Solea solea* in the context of global change. Part 1: revisiting parameterisation and calibration of a DEB model to consider inter-individual variability in experimental and natural conditions. *Ecol Model.* 2020;433:109-224. doi:[10.1016/j.ecolmodel.2020.109224](https://doi.org/10.1016/j.ecolmodel.2020.109224)
148. Grimm V, Berger U, Bastiansen F, et al. A standard protocol for describing individual-based and agent-based models. *Ecol Model.* 2006;198(1-2):115-126. doi:[10.1016/j.ecolmodel.2006.04.023](https://doi.org/10.1016/j.ecolmodel.2006.04.023)
149. Refstie T, Kittelsen A. Effect of density on growth and survival of artificially reared Atlantic salmon. *Aquaculture.* 1976;8(4):319-326. doi:[10.1016/0044-8486\(76\)90114-9](https://doi.org/10.1016/0044-8486(76)90114-9)
150. Lupatsch I, Santos GA, Schrama JW, Verreth JAJ. Effect of stocking density and feeding level on energy expenditure and stress responsiveness in European sea bass *Dicentrarchus labrax*. *Aquaculture.* 2010;298(3-4):245-250. doi:[10.1016/j.aquaculture.2009.11.007](https://doi.org/10.1016/j.aquaculture.2009.11.007)
151. Burić M, Bavčević L, Grgurić S, Vresnik F, Križan J, Antonić O. Modelling the environmental footprint of sea bream cage aquaculture in relation to spatial stocking design. *J Environ Manage.* 2020; 270:110811. doi:[10.1016/j.jenvman.2020.110811](https://doi.org/10.1016/j.jenvman.2020.110811)
152. Chadwick EMP, Parsons GJ, Sayavong B. *Evaluation of Closed-Containment Technologies for Saltwater Salmon Aquaculture.* NRC Research Press; 2010. doi:[10.1139/9780660199689](https://doi.org/10.1139/9780660199689)
153. Nilsen A, Nielsen KV, Biering E, Bergheim A. Effective protection against sea lice during the production of Atlantic salmon in floating enclosures. *Aquaculture.* 2017;466:41-50. doi:[10.1016/J.AQUACULTURE.2016.09.009](https://doi.org/10.1016/J.AQUACULTURE.2016.09.009)
154. Vilbergsson B, Oddsson GV, Unnthorsson R. Taxonomy of means and ends in aquaculture production—part 2: the technical solutions of controlling solids, dissolved gasses and pH. *Water.* 2016;8(9):387. doi:[10.3390/W8090387](https://doi.org/10.3390/W8090387)
155. Vilbergsson B, Oddsson GV, Unnthorsson R. Taxonomy of means and ends in aquaculture production—part 3: the technical solutions of controlling N compounds, organic matter, P compounds, metals, temperature and preventing disease. *Water.* 2016;8(11):506. doi:[10.3390/W8110506](https://doi.org/10.3390/W8110506)
156. Bjornsdottir R, Oddsson GV, Thorarinsdottir RI, Unnthorsson R. Taxonomy of means and ends in aquaculture production-part 1: the functions. *Water.* 2016;8(8):319. doi:[10.3390/w8080319](https://doi.org/10.3390/w8080319)
157. Timmons MB, Michael B, Guerdat T, Vinci BJ. *Recirculating Aquaculture.* 4th ed. Ithaca Publishing Company LLC; 2018.
158. Pedersen LF, Suhr KI, Dalsgaard J, Pedersen PB, Arvin E. Effects of feed loading on nitrogen balances and fish performance in replicated recirculating aquaculture systems. *Aquaculture.* 2012;338-341:237-245. doi:[10.1016/j.aquaculture.2012.01.035](https://doi.org/10.1016/j.aquaculture.2012.01.035)
159. Hargrave BT. *Environmental Effects of Marine Finfish Aquaculture.* Vol 5M. Springer-Verlag; 2005. doi:[10.1007/b12227](https://doi.org/10.1007/b12227)
160. Johansen LH, Jensen I, Mikkelsen H, Bjørn PA, Jansen PA, Bergh O. Disease interaction and pathogens exchange between wild and farmed fish populations with special reference to Norway. *Aquaculture.* 2011;315(3-4):167-186. doi:[10.1016/j.aquaculture.2011.02.014](https://doi.org/10.1016/j.aquaculture.2011.02.014)
161. Callier MD, Byron CJ, Bengtson DA, et al. Attraction and repulsion of mobile wild organisms to finfish and shellfish aquaculture: a review. *Rev Aquac.* 2018;10(4):924-949. doi:[10.1111/raq.12208](https://doi.org/10.1111/raq.12208)
162. Lin Y, Gao Z, Zhan A. Introduction and use of non-native species for aquaculture in China: status, risks and management solutions. *Rev Aquac.* 2015;7(1):28-58. doi:[10.1111/raq.12052](https://doi.org/10.1111/raq.12052)
163. Bradbury IR, Burgetz I, Coulson MW, et al. Beyond hybridization: the genetic impacts of nonreproductive ecological interactions of salmon aquaculture on wild populations. *Aquac Environ Interact.* 2020;12:429-445. doi:[10.3354/AEI00376](https://doi.org/10.3354/AEI00376)
164. Stigebrandt A. Carrying capacity: general principles of model construction. *Aquac Res.* 2011;42:41-50. doi:[10.1111/j.1365-2109.2010.02674.x](https://doi.org/10.1111/j.1365-2109.2010.02674.x)
165. Kim YC, Sasaki S, Yano K, Ikebukuro K, Hashimoto K, Karube I. Relationship between theoretical oxygen demand and photocatalytic chemical oxygen demand for specific classes of organic chemicals. *Analyst.* 2000;125:1915-1918. doi:[10.1039/b007005j](https://doi.org/10.1039/b007005j)
166. Papatryphon E, Petit J, Kaushik SJ, van der Werf HMG. Environmental impact assessment of salmonid feeds using life cycle assessment (LCA). *Ambio.* 2004;33(6):316-323. doi:[10.1579/0044-7447-33.6.316](https://doi.org/10.1579/0044-7447-33.6.316)
167. Roskoski R. Michaelis-Menten kinetics. *Ref Modul Biomed Sci.* 2015. doi:[10.1016/B978-0-12-801238-3.05143-6](https://doi.org/10.1016/B978-0-12-801238-3.05143-6)
168. Christensen V, Walters CJ. Ecopath with Ecosim: methods, capabilities and limitations. *Ecol Model.* 2004;172(2-4):109-139. doi:[10.1016/J.ECOLMODEL.2003.09.003](https://doi.org/10.1016/J.ECOLMODEL.2003.09.003)
169. Aubin J, Baizeau V, Jaeger C, Roucaute M, Gamito S. Modeling trophic webs in freshwater fishpond systems using Ecopath: towards better polyculture management. *Aquac Environ Interact.* 2021;13: 311-322. doi:[10.3354/AEI00406](https://doi.org/10.3354/AEI00406)
170. Bricker SB, Clement CG, Pirhalla DE, Orlando SP, Farrow DRG. *National Estuarine Eutrophication Assessment: Effects of Nutrient Enrichment in the Nation's Estuaries.* NOAA National Ocean Service Special Projects Office and the National Centers for Coastal Ocean Science; 1999:71.
171. Camargo JA, Alonso Á. Ecological and toxicological effects of inorganic nitrogen pollution in aquatic ecosystems: a global assessment. *Environ Int.* 2006;32(6):831-849. doi:[10.1016/j.envint.2006.05.002](https://doi.org/10.1016/j.envint.2006.05.002)
172. Randall DJ, Tsui TKN. Ammonia toxicity in fish. *Mar Pollut Bull.* 2002;45:17-23. doi:[10.1016/S0025-326X\(02\)00227-8](https://doi.org/10.1016/S0025-326X(02)00227-8)
173. Ip YK, Chew SF. Ammonia production, excretion, toxicity, and defense in fish: a review. *Front Physiol.* 2010;1 OCT(1):134. doi:[10.3389/fphys.2010.00134](https://doi.org/10.3389/fphys.2010.00134)
174. Kroupova H, Machova J, Svobodova Z. Nitrite influence on fish: a review. *Vet Med (Praha).* 2005;50(11):461-471. doi:[10.17221/5650-VETMED](https://doi.org/10.17221/5650-VETMED)
175. Lewis WM, Morris DP. Toxicity of nitrite to fish: a review. *Trans Am Fish Soc.* 1986;115(2):183-195. doi:[10.1577/1548-8659\(1986\)115<183:tontf>2.0.co;2](https://doi.org/10.1577/1548-8659(1986)115<183:tontf>2.0.co;2)
176. Ashauer R, Thorbek P, Warinton JS, Wheeler JR, Maund S. A method to predict and understand fish survival under dynamic chemical stress using standard ecotoxicity data. *Environ Toxicol Chem.* 2013;32(4):954-965. doi:[10.1002/etc.2144](https://doi.org/10.1002/etc.2144)
177. Rico A, Vighi M, Van den Brink PJ, et al. Use of models for the environmental risk assessment of veterinary medicines in European aquaculture: current situation and future perspectives. *Rev Aquac.* 2019;11(4):969-988. doi:[10.1111/raq.12274](https://doi.org/10.1111/raq.12274)
178. Weitzman J. Applying the ecosystem services concept to aquaculture: a review of approaches, definitions, and uses. *Ecosyst Serv.* 2019;35:194-206. doi:[10.1016/j.ecoser.2018.12.009](https://doi.org/10.1016/j.ecoser.2018.12.009)
179. Custódio M, Villasante S, Calado R, Lillebø AI. Valuation of ecosystem services to promote sustainable aquaculture practices. *Rev Aquac.* 2020;12(1):392-405. doi:[10.1111/RAQ.12324](https://doi.org/10.1111/RAQ.12324)
180. Knowler D, Chopin T, Martínez-Españeira R, et al. The economics of integrated multi-trophic aquaculture: where are we now and where do we need to go? *Rev Aquac.* 2020;12(3):1579-1594. doi:[10.1111/raq.12399](https://doi.org/10.1111/raq.12399)
181. Nobre AM, Robertson-Andersson D, Neori A, Sankar K. Ecological-economic assessment of aquaculture options: comparison between abalone monoculture and integrated multi-trophic aquaculture of abalone and seaweeds. *Aquaculture.* 2010;306(1-4):116-126. doi:[10.1016/j.aquaculture.2010.06.002](https://doi.org/10.1016/j.aquaculture.2010.06.002)
182. Rykiel EJ. Testing ecological models: the meaning of validation. *Ecol Model.* 1996;90(3):229-244. doi:[10.1016/0304-3800\(95\)00152-2](https://doi.org/10.1016/0304-3800(95)00152-2)
183. Smith EP, Rose KA. Model goodness-of-fit analysis using regression and related techniques. *Ecol Model.* 1995;77(1):49-64. doi:[10.1016/0304-3800\(93\)E0074-D](https://doi.org/10.1016/0304-3800(93)E0074-D)
184. McCarl BA. Model validation: an overview with some emphasis on risk models. *Rev Mark Agric Econ.* 1984;52(3):153-173. doi:[10.22004/AG.ECON.12282](https://doi.org/10.22004/AG.ECON.12282)

185. Kirchner M, Mitter H, Schneider UA, Sommer M, Falkner K, Schmid E. Uncertainty concepts for integrated modeling - review and application for identifying uncertainties and uncertainty propagation pathways. *Environ Model Softw*. 2021;135:104905. doi:10.1016/j.envsoft.2020.104905
186. Giacoletti A, Lucido GD, Mangano MC, Sarà G. Functional trait-based layers - an aquaculture siting tool for the Mediterranean Sea. *Aquaculture*. 2021;532:736081. doi:10.1016/j.aquaculture.2020.736081
187. Payne MR, Barange M, Cheung WWL, et al. Uncertainties in projecting climate-change impacts in marine ecosystems. *ICES J Mar Sci*. 2016;73(5):1272-1282. doi:10.1093/icesjms/fsv231
188. Tittensor DP, Eddy TD, Lotze HK, et al. A protocol for the intercomparison of marine fishery and ecosystem models: fish-MIP v1.0. *Geosci Model Dev*. 2018;11(4):1421-1442. doi:10.5194/GMD-11-1421-2018
189. Erickson A, Strigul N. A forest model intercomparison framework and application at two temperate forests along the East Coast of the United States. *Forests*. 2019;10(2):464-578. doi:10.1101/464578
190. Orr JC, Najjar RG, Aumont O, et al. Biogeochemical protocols and diagnostics for the CMIP6 Ocean Model Intercomparison Project (OMIP). *Geosci Model Dev*. 2017;10(6):2169-2199. doi:10.5194/gmd-10-2169-2017
191. Sarà G, Gouhier TC, Brigolin D, et al. Predicting shifting sustainability trade-offs in marine finfish aquaculture under climate change. *Glob Chang Biol*. 2018;24(8):3654-3665. doi:10.1111/gcb.14296
192. Føre M, Frank K, Norton T, et al. Precision fish farming: a new framework to improve production in aquaculture. *Biosyst Eng*. 2018;173:176-193. doi:10.1016/j.biosystemseng.2017.10.014
193. Berckmans D. General introduction to precision livestock farming. *Anim Front*. 2017;7(1):6-11. doi:10.2527/af.2017.0102
194. Burke M, Grant J, Filgueira R, Stone T. Oceanographic processes control dissolved oxygen variability at a commercial Atlantic salmon farm: application of a real-time sensor network. *Aquaculture*. 2021;533:736143. doi:10.1016/j.aquaculture.2020.736143
195. Svendsen E, Føre M, Økland F, et al. Heart rate and swimming activity as stress indicators for Atlantic salmon (*Salmo salar*). *Aquaculture*. 2021;531:735804. doi:10.1016/j.aquaculture.2020.735804
196. An D, Huang J, Wei Y. A survey of fish behaviour quantification indexes and methods in aquaculture. *Rev Aquac*. 2021;13(4):2169-2189. doi:10.1111/raq.12564
197. Mao JQ, Lee JHW, Choi KW. The extended Kalman filter for forecast of algal bloom dynamics. *Water Res*. 2009;43(17):4214-4224. doi:10.1016/j.watres.2009.06.012
198. Royer E, Faccenda F, Pastres R. Estimating oxygen consumption of rainbow trout (*Oncorhynchus mykiss*) in a raceway: a precision fish farming approach. *Aquac Eng*. 2021;92:102141. doi:10.1016/j.aquaeng.2020.102141
199. Li D, Wang Z, Wu S, Miao Z, Du L, Duan Y. Automatic recognition methods of fish feeding behavior in aquaculture: a review. *Aquaculture*. 2020;528:735508. doi:10.1016/j.aquaculture.2020.735508
200. Abreu MH, Pereira R, Yarish C, Buschmann AH, Sousa-Pinto I. IMTA with *Gracilaria vermiculophylla*: productivity and nutrient removal performance of the seaweed in a land-based pilot scale system. *Aquaculture*. 2011;312(1-4):77-87. doi:10.1016/j.aquaculture.2010.12.036
201. Neori A, Chopin T, Troell M, et al. Integrated aquaculture: rationale, evolution and state of the art emphasizing seaweed biofiltration in modern mariculture. *Aquaculture*. 2004;231(1-4):361-391. doi:10.1016/j.aquaculture.2003.11.015
202. Jiang Z, Wang G, Fang J, Mao Y. Growth and food sources of Pacific oyster *Crassostrea gigas* integrated culture with sea bass *Lateolabrax japonicus* in Ailian Bay, China. *Aquac Int*. 2013;21(1):45-52. doi:10.1007/s10499-012-9531-7
203. Chopin T, Robinson S, Troell M, Neori A, Buschmann A, Fang J. Multitrophic integration for sustainable marine aquaculture. *Ecol*. 2008;3:2463-2475. doi:10.1016/B978-008045405-4.00065-3
204. Reid GK, Chopin T, Robinson SMC, Azevedo P, Quinton M, Belyea E. Weight ratios of the kelps, *Alaria esculenta* and *Saccharina latissima*, required to sequester dissolved inorganic nutrients and supply oxygen for Atlantic salmon, *Salmo salar*, in integrated multi-trophic aquaculture systems. *Aquaculture*. 2013;408-409:34-46. doi:10.1016/j.aquaculture.2013.05.004
205. Ren JS, Stenton-Dozey J, Plew DR, Fang J, Gall M. An ecosystem model for optimising production in integrated multitrophic aquaculture systems. *Ecol Model*. 2012;246:34-46. doi:10.1016/j.ecolmodel.2012.07.020
206. Lamprianidou F, Telfer T, Ross LG. A model for optimization of the productivity and bioremediation efficiency of marine integrated multi-trophic aquaculture. *Estuar Coast Shelf Sci*. 2015;164:253-264. doi:10.1016/j.ecss.2015.07.045
207. Li M, Callier MD, Blancheton JP, et al. Bioremediation of fishpond effluent and production of microalgae for an oyster farm in an innovative recirculating integrated multi-trophic aquaculture system. *Aquaculture*. 2019;504:314-325. doi:10.1016/j.aquaculture.2019.02.013
208. Galasso HL, Lefebvre S, Aliaume C, Sadoul B, Callier MD. Using the dynamic energy budget theory to evaluate the bioremediation potential of the polychaete *Hediste diversicolor* in an integrated multi-trophic aquaculture system. *Ecol Model*. 2020;437:109296. doi:10.1016/j.ecolmodel.2020.109296
209. Levin PS, Fogarty MJ, Murawski SA, Fluharty D. Integrated ecosystem assessments: developing the scientific basis for ecosystem-based management of the ocean. *PLoS Biol*. 2009;7(1):e1000014. doi:10.1371/journal.pbio.1000014
210. UNEP. *Taking Steps toward Marine and Coastal Ecosystem-Based Management*. UNEP Regional Seas Reports and Studies No. 189. 2011:68.
211. Katsanevakis S, Stelzenmüller V, South A, et al. Ecosystem-based marine spatial management: review of concepts, policies, tools, and critical issues. *Ocean Coast Manag*. 2011;54(11):807-820. doi:10.1016/j.ocecoaman.2011.09.002
212. European Commission. *Communication from the Commission to the European Parliament, the Council, the European Economic and Social Committee and the Committee of the Regions. Strategic Guidelines for the Sustainable Development of EU Aquaculture (COM/2013/0229)*. 2013.
213. Sanchez-Jerez P, Karakassis I, Massa F, et al. Aquaculture's struggle for space: the need for coastal spatial planning and the potential benefits of allocated zones for aquaculture (AZAs) to avoid conflict and promote sustainability. *Aquac Environ Interact*. 2016;8(1):41-54. doi:10.3354/aei00161
214. European Commission. *Communication from the Commission to the European Parliament, the Council, the European Economic and Social Committee and the Committee of the Regions. Strategic Guidelines for a More Sustainable and Competitive EU Aquaculture for the Period 2021 to 2030*. 2021.
215. GFCM. *Report of the WGSC-ShoCMed workshop on the definition and environmental monitoring within allowable zone of effect (AZE) of aquaculture activities within the Mediterranean Countries*. 2012.
216. Hargrave BT. Empirical relationships describing benthic impacts of salmon aquaculture. *Aquac Environ Interact*. 2010;1:33-46. doi:10.3354/aei00005
217. Keeley NB, Cromey CJ, Goodwin EO, Gibbs MT, Macleod CM. Predictive depositional modelling (DEPOMOD) of the interactive effect of current flow and resuspension on ecological impacts beneath salmon farms. *Aquac Environ Interact*. 2013;3(3):275-291. doi:10.3354/aei00068
218. Bravo F, Grant J. Modelling sediment assimilative capacity and organic carbon degradation efficiency at marine fish farms. *Aquac Environ Interact*. 2018;10:309-328. doi:10.3354/aei00267
219. Jusup M, Geček S, Legović T. Impact of aquacultures on the marine ecosystem: modelling benthic carbon loading over variable depth.



- Ecol Model.* 2007;200(3–4):459–466. doi:[10.1016/J.ECOLMODEL.2006.08.007](https://doi.org/10.1016/J.ECOLMODEL.2006.08.007)
220. von Schuckmann K, Le Traon PY, Smith N, et al. Copernicus marine service ocean state report, issue 5. *J Oper Oceanogr.* 2021;14(S1):1–185. doi:[10.1080/1755876X.2021.1946240](https://doi.org/10.1080/1755876X.2021.1946240)
221. Butenschön M, Clark J, Aldridge JN, et al. ERSEM 15.06: a generic model for marine biogeochemistry and the ecosystem dynamics of the lower trophic levels. *Geosci Model Dev.* 2016;9(4):1293–1339. doi:[10.5194/gmd-9-1293-2016](https://doi.org/10.5194/gmd-9-1293-2016)
222. Vichi M, Lovato T, Butenschön M, et al. *The Biogeochemical Flux Model (BFM): Equation Description and User Manual. BFM Version 5.2. BFM Report Series N. 1, Release 1.2, June 2020.* 2020.
223. Ferreira JG, Saurel C, JD L e S, Nunes JP, Vazquez F. Modelling of interactions between inshore and offshore aquaculture. *Aquaculture.* 2014;426–427:154–164. doi:[10.1016/j.aquaculture.2014.01.030](https://doi.org/10.1016/j.aquaculture.2014.01.030)
224. Tsagaraki TM, Petihakis G, Tsiaras K, et al. Beyond the cage: ecosystem modelling for impact evaluation in aquaculture. *Ecol Model.* 2011;222(14):2512–2523. doi:[10.1016/j.ecolmodel.2010.11.027](https://doi.org/10.1016/j.ecolmodel.2010.11.027)
225. Bruggeman J, Bolding K. A general framework for aquatic biogeochemical models. *Environ Model Softw.* 2014;61:249–265. doi:[10.1016/J.ENVSOFT.2014.04.002](https://doi.org/10.1016/J.ENVSOFT.2014.04.002)
226. Galparsoro I, Murillas A, Pinarbasi K, et al. Global stakeholder vision for ecosystem-based marine aquaculture expansion from coastal to offshore areas. *Rev Aquac.* 2020;12(4):2061–2079. doi:[10.1111/raq.12422](https://doi.org/10.1111/raq.12422)
227. Saitoh S-I, Mugo R, Radiarta IN, et al. Some operational uses of satellite remote sensing and marine GIS for sustainable fisheries and aquaculture. *ICES J Mar Sci.* 2011;68(4):687–695. doi:[10.1093/icesjms/fsq190](https://doi.org/10.1093/icesjms/fsq190)
228. Porporato EMD, Pastres R, Brigolin D. Site suitability for finfish marine aquaculture in the central Mediterranean Sea. *Front Mar Sci.* 2020;6:772. doi:[10.3389/fmars.2019.00772](https://doi.org/10.3389/fmars.2019.00772)
229. Gernez P, Barillé L, Lerouxel A, Mazeran C, Lucas A, Doxaran D. Remote sensing of suspended particulate matter in turbid oyster-farming ecosystems. *J Geophys Res Ocean.* 2014;119(10):7277–7294. doi:[10.1002/2014JC010055](https://doi.org/10.1002/2014JC010055)
230. Gernez P, Doxaran D, Barillé L. Shellfish aquaculture from space: potential of Sentinel2 to monitor tide-driven changes in turbidity, chlorophyll concentration and oyster physiological response at the scale of an oyster farm. *Front Mar Sci.* 2017;4:137. doi:[10.3389/fmars.2017.00137](https://doi.org/10.3389/fmars.2017.00137)
231. ISO. Environmental management – life cycle assessment – requirements and guidelines. ISO 14044. Published online 2006:46.
232. Guinée JB, Heijungs R, Huppes G, et al. In: Ministry of Housing SP and E (VROM), Centre of Environmental Science (CML), ed. *Handbook on Life Cycle Assessment. An Operational Guide to the ISO Standards.* Kluwer Academic Publishers; 2002.
233. Bohnes FA, Hauschild MZ, Schlundt J, Laurent A. Life cycle assessments of aquaculture systems: a critical review of reported findings with recommendations for policy and system development. *Rev Aquac.* 2019;11(4):1061–1079. doi:[10.1111/raq.12280](https://doi.org/10.1111/raq.12280)
234. Aubin J. Life cycle assessment as applied to environmental choices regarding farmed or wild-caught fish. *CAB Rev Perspect Agric Vet Sci Nutr Nat Resour.* 2013;8:1–10. doi:[10.1079/PAVSNR20138011](https://doi.org/10.1079/PAVSNR20138011)
235. Parker R. *Review of Life Cycle Assessment Research on Products Derived from Fisheries and Aquaculture: A Report for Seafish as Part of the Collective Action to Address Greenhouse Gas Emissions in Seafood. Final Report.* 2012.
236. Henriksson PJG, Troell M, Banks LK, et al. Interventions for improving the productivity and environmental performance of global aquaculture for future food security. *One Earth.* 2021;4(9):1220–1232. doi:[10.1016/j.oneear.2021.08.009](https://doi.org/10.1016/j.oneear.2021.08.009)
237. Henriksson PJG, Mohan CV, Phillips MJ. Evaluation of different aquaculture feed ingredients in Indonesia using life cycle assessment. *Indones J Life Cycle Assess Sustain.* 2016;1(1):13–21. doi:[10.52394/ijolcas.v1i1.4](https://doi.org/10.52394/ijolcas.v1i1.4)
238. Avadí A, Pelletier N, Aubin J, Ralite S, Núñez J, Fréon P. Comparative environmental performance of artisanal and commercial feed use in Peruvian freshwater aquaculture. *Aquaculture.* 2015;435:52–66. doi:[10.1016/j.aquaculture.2014.08.001](https://doi.org/10.1016/j.aquaculture.2014.08.001)
239. Hua K, Cobcroft JM, Cole A, et al. The future of aquatic protein: implications for protein sources in aquaculture diets. *One Earth.* 2019;1(3):316–329. doi:[10.1016/j.oneear.2019.10.018](https://doi.org/10.1016/j.oneear.2019.10.018)
240. Froehlich HE, Jacobsen NS, Essington TE, Clavelle T, Halpern BS. Avoiding the ecological limits of forage fish for fed aquaculture. *Nat Sustain.* 2018;1(6):298–303. doi:[10.1038/s41893-018-0077-1](https://doi.org/10.1038/s41893-018-0077-1)
241. Boissy J, Aubin J, Drissi A, van der Werf HMG, Bell GJ, Kaushik SJ. Environmental impacts of plant-based salmonid diets at feed and farm scales. *Aquaculture.* 2011;321(1–2):61–70. doi:[10.1016/J.AQUACULTURE.2011.08.033](https://doi.org/10.1016/J.AQUACULTURE.2011.08.033)
242. Pelletier N, Tyedmers P. Feeding farmed salmon: is organic better? *Aquaculture.* 2007;272(1–4):399–416. doi:[10.1016/j.aquaculture.2007.06.024](https://doi.org/10.1016/j.aquaculture.2007.06.024)
243. Samuel-Fitwi B, Meyer S, Reckmann K, Schroeder JP, Schulz C. Aspiring for environmentally conscious aquafeed: comparative LCA of aquafeed manufacturing using different protein sources. *J Clean Prod.* 2013;52:225–233. doi:[10.1016/j.jclepro.2013.02.031](https://doi.org/10.1016/j.jclepro.2013.02.031)
244. Nhu TT, Schaubroeck T, Henriksson PJG, Bosma R, Sorgeloos P, Dewulf J. Environmental impact of non-certified versus certified (ASC) intensive *Pangasius* aquaculture in Vietnam, a comparison based on a statistically supported LCA. *Environ Pollut.* 2016;219:156–165. doi:[10.1016/j.envpol.2016.10.006](https://doi.org/10.1016/j.envpol.2016.10.006)
245. Smáráson BÖ, Ögmundarson Ó, Árnason J, Björnsdóttir R, Davíðsdóttir B. Life cycle assessment of Icelandic arctic char fed three different feed types. *Turkish J Fish Aquat Sci.* 2017;17(1):79–90. doi:[10.4194/1303-2712-v17\\_1\\_10](https://doi.org/10.4194/1303-2712-v17_1_10)
246. Glencross BD, Booth M, Allan GL. A feed is only as good as its ingredients - a review of ingredient evaluation strategies for aquaculture feeds. *Aquac Nutr.* 2007;13(1):17–34. doi:[10.1111/j.1365-2095.2007.00450.x](https://doi.org/10.1111/j.1365-2095.2007.00450.x)
247. Ghamkhar R, Hicks A. Comparative environmental impact assessment of aquafeed production: sustainability implications of forage fish meal and oil free diets. *Resour Conserv Recycl.* 2020;161:104849. doi:[10.1016/j.resconrec.2020.104849](https://doi.org/10.1016/j.resconrec.2020.104849)

## SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

**How to cite this article:** Chary K, Brigolin D, Callier MD. Farm-scale models in fish aquaculture – An overview of methods and applications. *Rev Aquac.* 2022;14(4):2122–2157. doi:[10.1111/raq.12695](https://doi.org/10.1111/raq.12695)