Role of deposit feeders in integrated multi-trophic aquaculture — A model analysis

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ABSTRACT

The performance of deposit feeders in integrated multi-trophic aquaculture (IMTA) was analysed through the application of mathematical models. Loading of organic particulates to the benthos as a result of finfish cage culture and shellfish suspended culture was analysed by means of a deposition model (ORGANIX), and an individual model for growth and environmental effects was developed for the California sea cucumber *Parastichopus californicus*. Following validation, the model was combined with existing models for finfish, shellfish, and macroalgae into a framework for simulation of IMTA interactions at the local scale. Several scenarios for different culture combinations and densities were simulated using the Farm Aquaculture Resource Management (FARM) model, using a layout which reflects typical stocking densities and spatial occupation in Europe and North America. The model allows an analysis of the different sources and fate of particulate organic matter associated with distinct culture groups. Our results illustrate the production enhancement for deposit feeders cultivated below both finfish (600%) and shellfish (150%). Furthermore, sea cucumbers are responsible for a significant removal of the particulate organic carbon loading to the bottom, reducing the gross load by up to 86% for finfish culture and 99% for shellfish culture. The role of cultivated seaweeds in reducing the dissolved nitrogen concentration in the farm area was also examined—no significant reduction in ambient nutrient concentration was observed, but the added nitrogen provides a clear stimulus (22% increase) to kelp production. By contrast, shellfish grown in suspended culture in the vicinity of finfish cages show very little change in individual growth or harvestable biomass. This work helps to analyse the ecological and economic potential of various forms of IMTA, and the role of co-cultivation in direct extraction and re-use of materials and energy at both the local (farm) and system (bay, estuary) scales.

Statement of relevance: Analysis of the ecological and economic potential of various forms of IMTA, and the relevance of co-cultivation in direct extraction and re-use of materials and energy at both the local (farm) and system (bay, estuary) scales. FARM model framework applied to understand the roles of suspended bivalve culture and benthic deposit-feeder culture in mitigating the negative externalities of finfish culture.

1. Introduction

Marine finfish aquaculture is expected to increase significantly in the coming decades to help feed a rapidly expanding human population (FAO/NACA, 2012). Many of the production areas in Southeast Asia, China, and South America are already at or approaching carrying capacity (Ross et al., 2013), while a combination of factors including food security, trade balance, and a focus on locally-sourced products drives predicted expansion in Europe and North America. This has stimulated debate on site selection and carrying capacity for development of intensive finfish culture—one of the major issues is the accumulation of wastes. Inorganic waste from fed aquaculture in open water cages tends to disperse over a broad area, but the organic component is deposited relatively near the culture units (Mente et al., 2006).

The accumulation of waste feed and faeces below finfish cages may alter the physical and chemical environment of the water column and seabed, potentially leading to important ecological and economic consequences for both the farmed species and the benthic environment (Brooks et al., 2003; Kalantzi and Karakassis, 2006; Soto, 2009), including decreased yields of cultivated species and reduction of biodiversity (Kinoshita et al., 2008; Sanz-Lázaro and Marín, 2011; Stigebrandt, 2011).

In order to expand, the aquaculture sector needs to develop innovative, responsible, sustainable, and profitable practices which should be ecologically-efficient, environmentally-benign, product-diversified,

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and societally-beneficial (Chopin, 2013). Integrated multi-trophic aquaculture (IMTA) promotes the re-use of materials across different trophic groups and has received increasing attention over the last decade as a tool for improving sustainability of fed aquaculture (Chopin et al., 2012; Costa-Pierce, 2008; Nelson et al., 2012a; Neori et al., 2007; Troell et al., 2009).

IMTA aims to diversify fed aquaculture (e.g. finfish or shrimp) with extractive aquaculture, recapturing the inorganic (e.g. through seaweeds) and organic (through suspension feeders and deposit feeders) nutrients from fed aquaculture for the growth of co-cultured species of commercial value (Chopin et al., 2012; Neori et al., 2007). This has been practised in pond culture in Asia for thousands of years (Moo, undated), but the successful utilization of aquaculture-generated organic particles as a food source for marine bivalves cultured in open-water IMTA systems is limited by the time available to intercept solid wastes contained in the horizontal particle flux and the size range and concentration of these particles (Cheshuk et al., 2003; Cranford et al., 2013; Troell et al., 2011). Physiological model estimates suggest that salmon aquaculture solids would need to comprise at least 10–20% of a mussel's total diet to contribute to a net decrease in the organic loading from an IMTA site (Reid et al., 2013a).

Some data suggest that a correct design of IMTA sites could improve this situation and, indeed, mussels grown very close to fish farms were capable of ingesting at least 20% of their diet from fish-derived sources (Lander et al., 2012, Reid et al., 2013b). But to date, studies addressing the possible synergistic growth effects of IMTA systems on bivalves have yielded contradictory results. Several studies have provided evidence for growth benefits to shellfish or evidence of organic uptake from the farm in open-water IMTA systems (Handå et al., 2012; Jiang et al., 2013; Lander et al., 2012; Peharda et al., 2007), while other studies reported no significant effect (Cheshuk et al., 2003; Irisarri et al., 2013; Navarrete-Mier et al., 2010; Parsons et al., 2002). Because of this variability, the effectiveness of multi-trophic culture has been shown mainly in inland ponds where the food link between both trophic levels is more straightforward (Purcell et al., 2006; Slater and Carton, 2009; Yuan et al., 2013) and, except in the extremely high culture density situations typical of Southeast Asia, it is challenging to establish the benefits of IMTA in open-water or coastal farms (Ferreira et al., 2012).

Moreover, the net ecological benefit from the shellfish component of IMTA for reducing benthic organic enrichment to the benthos has not been clearly demonstrated (Department of Fisheries and Oceans Canada, 2013). Based on available data, it is very unlikely that using only fine-particulate filter feeders in IMTA will significantly reduce organic loading underneath cage operations and subsequent impacts to the benthos (Department of Fisheries and Oceans Canada, 2013). A benthic component of deposit feeders that can utilize the vertical fluxes of organic matter to the seabed from fish and shellfish farms may therefore be an important stage in the development of IMTA systems (Cranford et al., 2013).

Deposit-feeding sea cucumbers have shown promise in recycling the larger particulate waste fraction through their feeding activities when co-cultured with other species, playing a bioremediation role while increasing farm profit (e.g. Paltzat et al., 2008; Slater and Carton, 2007; Yuan et al., 2013). Sea cucumbers are capable of consuming finfish waste, resulting in enhanced growth and survival (Hannah et al., 2013; Nelson et al., 2012a; Orr et al., 2014; Yokoyama, 2013; Yu et al., 2012) and have also been raised successfully in co-culture with shrimps (Martínez-Porchas et al., 2010; Pitt et al., 2004; Yaqing et al., 2004). Co-culture simulations of sea cucumbers with mussel and fish showed that up to 70% of the material that settles on the seafloor could be consumed by these detritus feeders (Ren et al., 2012), with total organic carbon and total nitrogen contents of fish faeces being reduced by an average of 60.3% and 62.3%, respectively (Hannah et al., 2013).

Holothurians also exhibit good growth (Paltzat et al., 2008; Zhou et al., 2006) and low mortality rates (Slater et al., 2009) when cultured in suspended cages or directly on the seabed under cultured bivalves, feeding on bivalve faeces and pseudofaeces (Slater and Carton, 2007, from field measurements; Yuan et al., 2006; Zamora and Jeffs, 2012a, 2012b from laboratory experiments).

Sea cucumbers (known as their commercial product 'bêche-de-mer' or 'trepang') have long been an important fishery resource, with high commercial values in Asia and the Middle East due to their many nutritional and medicinal properties (Bordbar et al., 2011). However, the increasing market demand and prices for bêche-de-mer led to overexploitation of wild stocks worldwide and stimulated the development of commercial aquaculture of sea cucumbers (Purcell et al., 2012; Toral-Granda et al., 2008).

Large-scale commercial aquaculture has only been developed for the most valuable species; notably the Japanese sea cucumber *Apostichopus japonicus* and the sandfish *Holothuria scabra* (see references in Zamora and Jeffs, 2013). But the ongoing market demand for sea cucumbers has increased research efforts focused on other species with commercial aquaculture potential (Nelson et al., 2012a; Paltzat et al., 2008; Zamora and Jeffs, 2013), including the California sea cucumber *P. californicus* and the northern sea cucumber *Cucumaria frondosa* (Nelson et al., 2012a,b).

Previous studies have addressed the performance of sea cucumbers in co-culture with bivalves (e.g. Zhou, 2006), shrimp (e.g. Pitt et al. 2004), salmon (e.g. Ahlgren 1998), and sablefish (Hannah et al., 2013), but to our knowledge only Ferreira et al. (2012), Ren et al. (2012), and Ferreira et al. (2014a) have modelled co-cultivation.

Mathematical models have been applied to predict yield (Ferreira et al., 2008; Gangnery et al., 2004), environmental effects (Cromey et al., 2002; Fabi et al., 2009), and economic optimisation (Ferreira et al., 2009) of finfish and bivalve monoculture (Brigolin et al., 2009; Ferreira et al., 2009) but only a few IMTA combinations have been studied: finfish-shellfish (Ferreira et al., 2012; Reid et al., 2010, 2013a), finfish-sea cucumber or shellfish-sea cucumber (Ren et al., 2012), and finfish-shrimp-seaweed (Ferreira et al., 2014a).

The objective of the present work is to analyse the growth and mitigation potential of deposit-feeding organisms in open water IMTA, in co-cultivation with both finfish and shellfish.

The specific aims are to:

1. Compare the environmental and economic performance of finfish and shellfish monoculture and IMTA with sea cucumbers by means of mathematical models;
2. Explore optimization scenarios in terms of production, environmental sustainability, and economic returns;
3. Discuss the potential role of farm-scale models in supporting the suitability assessment of different IMTA combinations.

2. Methodology

Individual growth and environmental effects models for the species of interest were adapted, extended, or developed. After testing these were integrated into a broader farm-scale framework (Fig. 1). The components of the framework are summarized below.

1. An individual model for finfish (AquaFish; Ferreira et al., 2012), parameterized and validated for Atlantic salmon (*Salmo salar*). The model was applied to calculate finfish production and particulate and dissolved emissions to the environment. An individual model for Pacific oyster *Crassostrea gigas* (AquaShell; Silva et al., 2011) was used in a similar way for the shellfish component. Only changes to parameterization of the finfish model are reported herein—no changes were made to the conceptual framework and computer code of either individual model except the appropriate parameterization of AquaFish for Atlantic salmon. Finally, an individual model for seaweed production (Ferreira et al., 2014a; Saurel et al., 2014) was parameterised for winged kelp (*Alaria esculenta*) to examine the effects on the dissolved emissions from fed and organically extractive aquaculture;
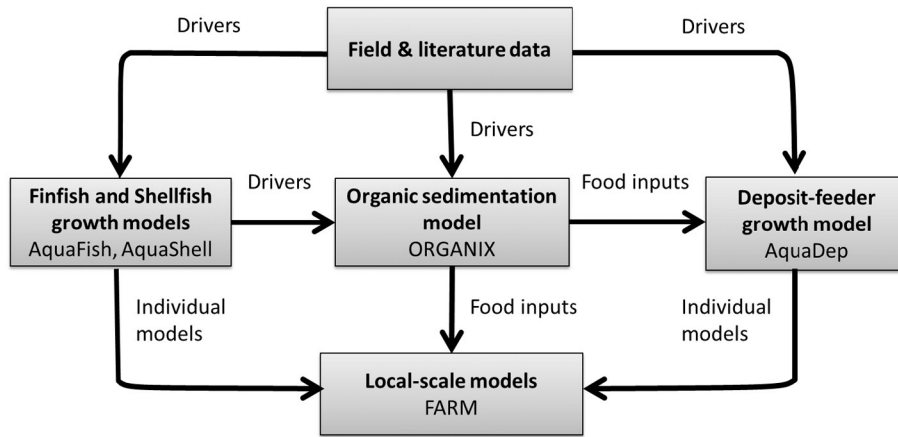
Fig. 1. Modelling framework. Seaweeds not shown since the main emphasis is on the particulate component of IMTA.

2. A model of organic sedimentation (ORGANIX), developed for simulation of waste loading to benthic deposit feeders. This requires a simulation of sedimentation from fish and shellfish farms, and of the spatial distribution of the waste plumes under different culture and physical conditions.
3. An individual model for sea cucumbers (AquaDep), developed and calibrated for physiological simulation of feeding, growth, metabolism, and environmental effects. The combined outputs of models 1 and 2 were used to drive the sea cucumber model.
4. A farm-scale framework (FARM) that includes physical transport of both particulate and dissolved material, integrates individual growth models and adds population dynamics of the species of interest, and IMTA interactions. The model was used to simulate the potential harvest of finfish, shellfish, and deposit feeders; the direct economic value (goods) of different culture combinations; and changes in environmental externalities of finfish monoculture as a result of IMTA (ecosystem services).

2.1. Benthic food supply and distribution

The model was bounded within the benthic area populated by cultivated deposit-feeders, and a mass balance for organic matter within that area was developed. The settlement of particulate organic matter (POM) from salmon cages, shellfish lines, and from the natural water column (background POM) was simulated as an input to the deposit feeder model.

2.1.1. Allochthonous organic supply

There are three components of organic matter supply for deposit-feeders (Fig. 2a). The background loading rate (S_b) was estimated from the background organic particle concentration C_b (g m^{-3}), based on literature data for the settleable fraction α that deposits within the fish cage footprint:

$$S_b = A_f W \alpha C_b \tag{1}$$

where A_f is cage area (m^2) and W is particle fall velocity (m s^{-1}) given by the Stokes equation.

The waste-feed loading rate (S_w) can be estimated from fish farm operational data, and faecal loading rate (S_f) can be estimated from outputs from individual fish. There is no need to calculate concentrations in water and, in a conservative situation, the total input S_i (g d^{-1}) below the cage (where $S_i = S_b + S_w + S_f$) may be seen as a flux that is fully delivered to the benthos.

2.1.2. Shape of the benthic footprint

The benthic footprint area will not be a circle with the diameter of the polar cage (Fig. 2a), but rather a truncated cone, most likely with an elliptical deformation at the base, due to the difference in longitudinal and lateral dispersion (Fig. 2b).

The allochthonous organic loading S_i is conserved, but the mass must be distributed over the wider footprint. Simulation of the food supply from fish or shellfish farms to the deposit-feeder cultivation area was performed using the ORGANIX model, based on the waste
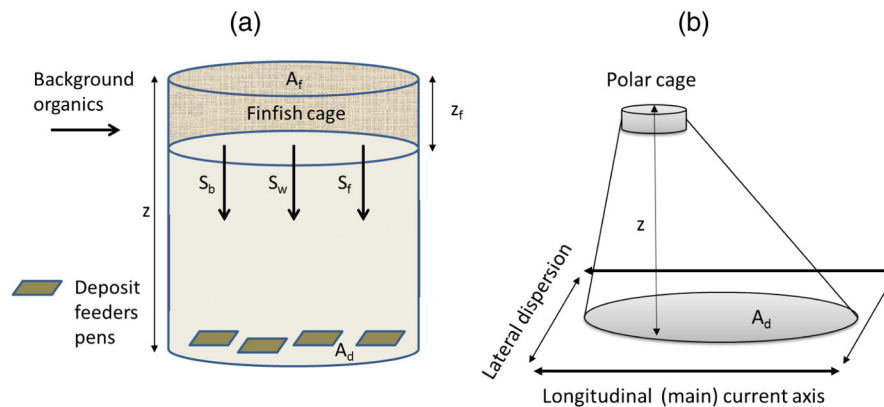

Fig. 2. Model of allochthonous supply of organic material to benthic deposit-feeders under a fish cage (a) without and (b) with advection and dispersion. S_b: background loading (g d^{-1}); S_w: waste feed loading (g d^{-1}); S_f: faecal loading (g d^{-1}); A_f: area of polar cage (m^2); A_d: area of benthic footprint (m^2); z: water column depth (m); Z_f: fish cage depth.

estimates obtained from individual and population models (feed and faeces for finfish, faeces and pseudofaeces for shellfish).

The load distribution of the settling organic particles considers the advective and dispersive components of horizontal movement until the plume reaches the seabed. The time domain is:

$$t = \frac{z}{W} \tag{2}$$

where t is time (s) and z is water-column depth (m).

When $z \gg z_f$ (Fig. 2) the cage can be reduced to a thin surface layer. However, for the values considered in this study, a cage depth of 10 m and a water depth of 30 m, the use of a mean depth (z_f / 2) for the cage, from which particles spread horizontally, was more appropriate.

ORGANIX determines settlement time based on fall velocity, while advection is based on residual circulation and two-dimensional dispersion resolved by means of a Gaussian random walk approach, following various authors (Chapra, 1997; Massel, 1999; Thomann & Mueller, 1987).

Dispersion along the x coordinate can be determined for time t by calculating the probabilities $p_{x,t}$ of particle distribution using Eq. 3:

$$p_{x,t} = \frac{1}{2\sqrt{\pi k_x t}} e^{\frac{x^2}{4k_x t}} \tag{3}$$

where the longitudinal dispersion coefficient k_x is defined as:

$$k_x = \frac{\Delta x^2}{2\Delta t}. \tag{4}$$

Dispersion $p_{y,t}$ along the y coordinate is calculated similarly, and thus dispersion on the x, y plane follows the probability distribution:

$$p_{x,y,t} = p_{x,t} p_{y,t}. \tag{5}$$

The advective component can be simplified by calculating the horizontal components of the residual current velocity $\bar{u}_x$ and $\bar{v}_y$ and using these terms to calculate the displacement in x and y that the particle plume is subject to until it reaches the seabed. Calibration for the Atlantic salmon cage footprint was based on experimental data from Fisheries and Oceans Canada and other literature data (Ferreira et al., 2014b; Reid et al., 2009; Johansen, pers. com.; Robinson, pers. com.)

2.1.3. Full mass balance

A full mass balance can be developed by adding autochthonous source terms and the relevant sink terms.

$$\frac{dC_{org}}{dt} = S_b + S_w + S_f - F_d - G_b - D \tag{6}$$

where C_{org} is mass of organic material; F_d is the net POM uptake rate of deposit feeders (g d^{-1}); G_b is background (other organisms) grazing rate (g d^{-1}) and D is diagenesis (g d^{-1}).[1]

2.1.4. Parameterization of inputs from fish cages

The general mass balance for a cultivated salmon of nominal weight 1 kg is shown in Fig. 3.

Given that feed is represented in dry weight and fish production in wet weight, the Feed Conversion Ratio (FCR) provides limited information, apart from a general indication of efficiency. If we consider the moisture content of *S. salar* muscle to be 73.65% (Atanasoff et al. 2013) then for an FCR of 1.12 (typical value for the Norwegian industry, Johansen unpub. data) the total feed as dry weight used for fish biomass
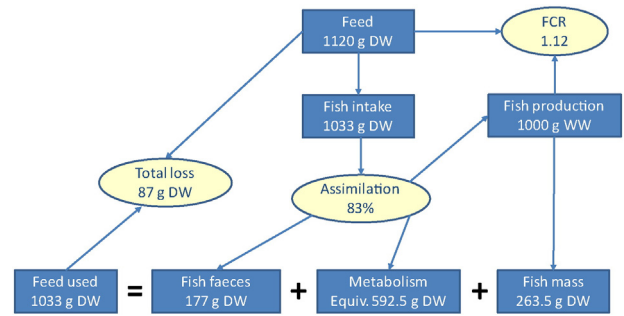

Fig. 3. Mass balance for the production of a 1 kg cultivated Atlantic salmon. A priori unknown terms (fish ration, feed loss, (equivalent) catabolism energy, fish faeces, and fish dry weight) have been determined through the application of the AquaFish individual growth model.

is 1120 g for 263.5 g of fish, with the rest being a sum of wasted feed, faeces and excretion. However, this does not provide any information with respect to the breakdown of that waste into its three components. Since the present modelling analysis focuses on benthic deposition of particulates, we use only the first two terms above, but the inorganic component is of interest in order to verify the mass balance calculations.

Finfish waste feed and faecal loads to drive the sea cucumber model were estimated from the AquaFish individual growth model for Atlantic salmon (Fig. 4; Ferreira et al. 2014b)—these estimates show good correspondence with coefficients taken from the literature (Table 1).

The values for parameterization of background loading (S_b), considering a nominal background concentration C_b of 1 mg L^{-1}, and $\alpha = 0.131$ would provide a S_b of 424.24 g cage^{-1} d^{-1}, i.e. 0.216 g m^{-2} d^{-1} for fine particles with an Equivalent Spherical Diameter of 0.112 mm. When calculated on a per cage basis, this loading is significantly lower than the combined inputs of waste feed and faeces from finfish aquaculture and thus background loading makes little difference to the overall outcome, although it is an important element in the overall mass balance.

The benthic footprint for a salmon cage was simulated with ORGANIX and yielded sedimentation values up to 3280 g C m^{-2} y^{-1}, i.e. 25 g POM m^{-2} d^{-1} (Fig. 5a). We found increased organic enrichment with respect to natural values within a distance of 150 m from the salmon cage. As expected due to their different settling velocities, two separate footprints were observed: one more proximate for the wasted feed and another at a greater distance from the net pens for the faecal material.

Our simulated sedimentation rates (1.4–9.6 g C m^{-2} d^{-1}) were consistent with the range of values (<1 to 15 g C m^{-2} d^{-1}) predicted within 100 m of salmon cages in most of the studies reviewed by Hargrave (2010).

2.2. Individual model for deposit feeders

An individual Net Energy Balance (NEB) model (AquaDep) was developed and tested for sea cucumbers. The model was developed as a generic approach, and applied to simulate the growth and environmental effects for holothurians; its general form is suitable for application to e.g. sea urchins and other deposit-feeders. The literature on sea cucumber physiology focuses mainly on the most important commercial species (e.g. *A. japonicus*, *H. scabra* and *Australostichopus mollis*). In this study the California sea cucumber, *P. californicus*, was selected for parameterization.

The behaviour of the feeding and digestion components of the model was verified by comparison with results obtained experimentally and from literature data. These simulations were validated using field measurements of environmental drivers and sea cucumber growth.

The maximum ingestion rate in dry weight (F_{max}, g DW organic matter ind^{-1} d^{-1}) into the foregut is determined from experimental

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[1] Although G_b and D are presented here for completeness, the FARM model application focuses on the removal of POC by deposit feeders and not on the concentration of sediment organic matter.
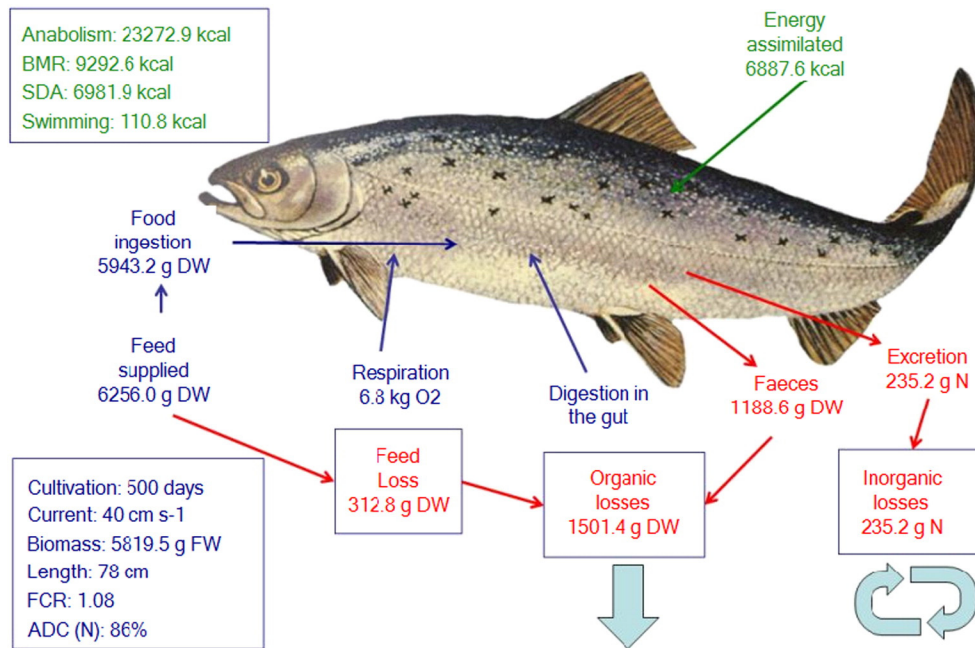
Fig. 4. Mass balance for individual growth of Atlantic salmon, calibrated for a farm in Northern Norway (GIFAS Experimental Station).

data (Yang et al., 2005; Yuan et al., 2009) as a function of allometry and water temperature (Eq. 7).

$$F_{max} = \frac{\left(-6.60T^2 + 191.08T - 938.03\right)\left(1.943W^{0.656}\right)}{E_f} \quad (7)$$

where F_{max} is maximal ingestion (g ind^{-1} d^{-1}); T is seawater temperature (°C); W is sea cucumber wet weight (g); and E_f is energy content in POM (J g^{-1}DW).

The ingestion rate (F, gDW ind^{-1} d^{-1}) is then estimated as a function of food availability and a half-saturation constant for feeding (K_c), through a Michaelis-Menten formulation.

Food entering the gut is either assimilated by the organism or eliminated as faeces. An average assimilation efficiency of 20% is considered (Ahlgren, 1998; Liu et al., 2013; Paltzat, 2006Yu et al., 2014b).

The net energy balance approach, based on the energy available from the assimilated food (anabolism) and the catabolic costs of respiration (RR) and excretion (AER), also allowed the determination of oxygen consumption and excretory loss of ammonia; this has been estimated by Yang et al. (2006) to be a function of allometry and water temperature (Eqs. 8 and 9).

$$AER = \left(0.024T^3 - 1.777T^2 + 41.85T - 222.24\right)\left(0.054W^{0.75}\right) \quad (8)$$

and

$$RR = -0.63e^{(0.11T-0.88)^2}\left(-6.67W^{1.21}\right) \quad (9)$$

Table 1
Comparison between finfish individual model (AquaFish) outputs for growth of a 5 kg salmon (nominal FCR 1.12) and literature values.

Parameter	AquaFish model	Literature (source)
Feed wasted (%)	7.8	12 (Shakouri, 2003)
Ingested feed (%)	92.2	88 (Shakouri, 2003)
Ingested feed lost as faeces (%)	17.1	15 (Reid et al., 2009)
Excretion (%)	57.3	58.3 (Shakouri, 2003; Reid et al., 2009)

where AER is ammonia excretion rate (μg h^{-1}), RR is respiration rate (μg h^{-1}), T is sea water temperature (°C), and W is sea cucumber wet weight (g).

The energy available for growth for a sea cucumber was converted to biomass (B; g wet weight) using a tissue energy content of 23,500 J g DW^{-1} and a 0.10 dry weight to wet weight conversion factor (average value from Dong et al., 2006; Yang et al., 2006; Zamora and Jeffs, 2012a). Sea cucumber contracted length L (cm) was calculated from wet weight biomass, following Hannah et al. (2012):

$$L = 2.5884\,B^{0.3497}. \quad (10)$$

Growth rates were calculated as percentage change in mean whole wet weight (%) from the beginning of the experiment and expressed as absolute growth rate (g d^{-1}) and specific growth rate (% Δd^{-1}).

The model does not include the energy spent for reproduction. Gamete development in *P. californicus* typically occurs in November through June, followed by spawning in the early summer (Cameron, 1980). Cameron and Fankboner (1986) reported gonad indices for *P. californicus* in the British Columbia area ranging from less than 5 to 30% of the body weight, while Benítez-Villalobos et al. (2013) and Santos et al. (2015) reported values from 2 to 15% for *Holothuria fuscocinerea* and *Holothuria forskali*, respectively. However, the energy allocated to gonad production is still unknown in sea cucumbers.

The individual model for sea cucumbers was implemented, calibrated, and validated in the InsightMaker™ visual modelling platform, and subsequently ported to C++. Mass balance outputs were verified to check consistency across both versions.

For performance testing, the model was run for three biodeposition scenarios covering the whole range of loading outputs obtained in ORGANIX (500, 1250, and 3250 g C m^{-2} y^{-1}; i.e. 3.61, 9.01, and 23.44 g POM m^{-2} d^{-1})[2] for low, intermediate and high loading scenarios (Fig. 5a). These values are higher than the 1 g C m^{-2} d^{-1} (2.6 g POM m^{-2} d^{-1}) threshold for POM sedimentation proposed as a threshold for benthic environmental quality by Hargrave et al. (1997). Fig. 5b shows higher growth rates at greater biodeposition loads, and the effect of food limitation on sea cucumber growth at lower POM loading rates.

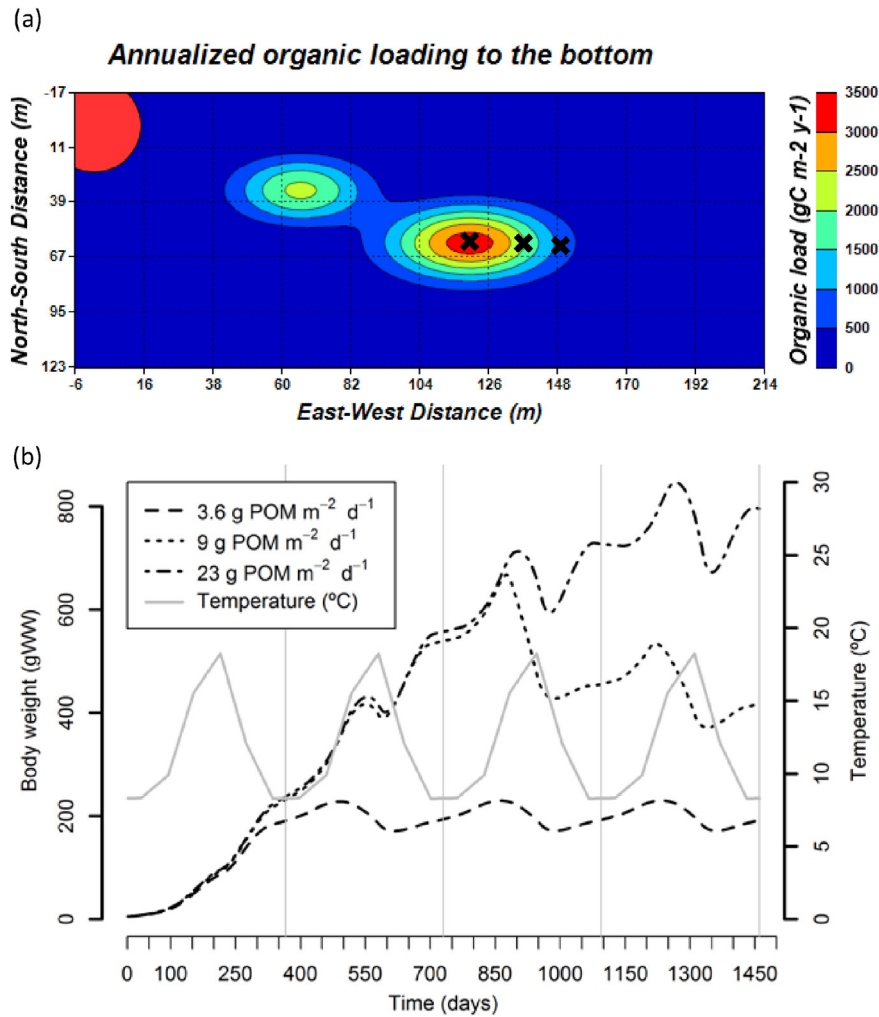[2] A Carbon:POM conversion ratio of 0.38 has been used throughout.

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Fig. 5. (a) ORGANIX results for the benthic footprint of a 10 m depth and 50 m diameter salmon polar cage with 20,000 Atlantic salmon (10.2 ind m^{-2}), considering a 600 day growth cycle to obtain a 5 kg salmon; and (b) simulated growth for a sea cucumber over a 4 year culture period for low, intermediate, and high organic loading scenarios, at the points marked with a cross.

2.3. Finfish individual model

The Atlantic salmon growth model is based on the previously developed generic AquaFish framework for finfish (Ferreira et al., 2012). AquaFish simulates fish growth and physiology through mechanistic representation of feeding and feeding regulation; energy transfers (input and loss) through harvestable products, wastes, and biological processes; oxygen consumption through anabolic and catabolic processes; and mass balance equations to account for the inputs and outputs to the production system. The mechanism for feeding regulation has been adapted from feed tables, which were used to derive equations relating feed intake to allometry and temperature; the finfish model application herein uses data from the GIFAS experimental station in Northern Norway (Johansen, unpub. data), both for individual salmon growth and farm-scale simulations.

The individual salmon mass balance output for a typical culture cycle, validated for the GIFAS case, is shown in Fig. 4. The model shows good correspondence to observed data and therefore this approach was developed for simulating growth of salmon in cage culture using the FARM model.

2.4. Farm-scale implementation

The individual deposit-feeder model was integrated into the well-tested Farm Aquaculture Resource Management (FARM) model

(Ferreira et al. 2007, 2012, 2014b), and a population-dynamics module was added for the California sea cucumber. As reported e.g. in Ferreira et al. (2008) this is a variable amplitude, bi-directional, weight class model driven by scope for growth (including all relevant physiology including reproduction) and mortality, which allows the identification of the harvestable component of the cultured biomass (see e.g. Ferreira et al. (2012) for application to finfish). The FARM model was substantially modified for this work: it is presently capable of simulating the full range of potential trophic groups in IMTA (finfish and/or shrimp, suspension and deposit feeders, and seaweeds). In addition, the simulation of POM throughput in the model no longer considers particulate organics as a bulk parameter, but rather is able to resolve the origin and fate of POM from finfish (both as waste feed and faeces), shellfish (as pseudofaeces and faeces), and background material—this traceability is paramount in establishing the role of different POM components (and therefore different species) in IMTA, and is a potential modelling equivalent of the use of natural isotopes for source apportionment. There are limitations in this approach, e.g. the model cannot explicitly resolve what proportion of POM filtered by shellfish originates in each category, so a pro rata approach is taken in apportioning the sinks based on the relative proportions of the sectorial POM state variables. Conversely, any particulate emissions can be explicitly apportioned.

Another key enhancement to FARM was to further partition the POM components into fine-grain and coarse-grain fractions (doubling the number of state variables), and allowing the user to determine the proportion of suspended to settleable material. Reid et al. (2009) report

values ranging from 13% > 2 mm Ø (87% suspended) to 27% suspended (73% settleable) for salmon culture. While the addition of more user options detracts from the easy-to-use screening model concept that underpins FARM, the reported variability of the two fractions in the literature justifies greater model plasticity.

Fig. 6 illustrates the standard model layout for the farm-scale simulations. A spacing of 50 m between fish cages was used, so that in each 4 ha model section four 50 m diameter polar cages are deployed, each with 200,000 fish. This results in an overall culture density of 20 salmon m^{-2}. Similar calculations were made for Pacific oyster and winged kelp, based on typical culture densities (Table 2).

P. californicus is not currently cultivated commercially, so specific initial (seed) and final (market) sizes are unknown. An initial size in grow-out systems of 3–5 cm in length (≈ 5 g wet weight) was considered (Robinson, pers. com), and a maximum weight of 1.85 Kg (Hannah et al., 2012), corresponding to a maximum length of 61 cm.

Estimated densities for sea cucumber aquaculture vary between 5 and 60 ind m^{-2}, depending on the cultivation technique. For the standard model sea cucumbers were considered to be distributed throughout the entire section, at a density of 20 ind m^{-2}.

An annual temperature time series for British Columbia was taken from sea surface values at Active Pass, Strait of Georgia, during 2007–2011, and other driver data for salinity, chlorophyll, and suspended and dissolved material reflect typical ranges in northern temperate waters. For all drivers, a minimum monthly resolution was used, interpolated by FARM into daily values.

The FARM model was run for a period of 400 days, which was specified as the cultivation period for all IMTA species considered.

3. Results and discussion

An analysis of the individual deposit-feeder model is presented, followed by the results of the full application of finfish, shellfish, seaweed, and deposit-feeder models in an integrated framework.

3.1. Individual sea cucumber modelling

Fig. 7 shows the mass balance for cultivation of a 5 g P. californicus sea cucumber to a market size of 800 g wet weight for the higher loading scenario (23.44 g POM m^{-2} d^{-1}). The AquaDep model estimated a net individual biomass production of 786 g WW for a 1460 day culture cycle, during which each animal had a total oxygen consumption of 0.6 kg O$_2$, excretion of 10.3 g NH$_4$, and a net POM

removal of 3.79 kg DW, or 11.1% of the organic material deposited on the seabed.

In the high loading scenario the model predicted a wet weight of 795.5 g after a four year run (Fig. 5), and a final contracted length of 26.8 cm. The annual percent changes in wet weight were 46.4, 135.0, 30.5 and 9.5% in years 1 to 4 respectively. This is a good match to the findings of Hannah et al. (2013), who reported annual increases for small P. californicus (7–99 g whole wet weight) ranging between 27 and 56%, and up to 164% for 40–120 g individuals.

Despite the economic importance of sea cucumbers, most studies provide growth rates for a short period of time rather than long-term growth patterns. The maximum period analysed was one year for P. californicus (Hannah et al., 2013, 2012; Paltzat et al., 2008) and A. japonicus (Qi et al., 2013), and 9 months for A. mollis (Slater and Jeffs, 2010). Moreover, the few growth rates available are mainly on the temperate Japanese sea cucumber (A. japonicus) and tropical species either in the field (e.g. Yokohama, 2013; Yu et al., 2014a), or reared in land-based tanks (e.g. Battaglene et al., 1999; Liu et al., 2013; Yuan et al., 2014; Zhou et al., 2006), and to our knowledge only a few studies (Hannah et al., 2012, 2013) have reported growth rates for the giant sea cucumber P. californicus.

The individual model reproduced the growth stagnation during the coldest months (Dec–Feb), the weight increase in the spring growing season (Mar–Jun), the negative scope for growth due to aestivation in the summer (Jul–mid. Sep), and the autumn feeding cessation due to seasonal visceral atrophy (mid. Sep.–end Nov).

Water temperature has a major influence on sea cucumber growth. The optimal seawater temperatures are species-specific, with values around 15 °C for A. japonicus and A. mollis (An et al., 2007; Dong and Dong, 2006; Yang et al., 2005; Yuan et al., 2009; Zamora and Jeffs, 2011). In general, sea cucumbers cannot tolerate high temperatures and most adults enter a state of aestivation during summer (Yang et al., 2006). Under aestivation metabolism reduces by 25 to 30% and individuals cease feeding, resulting in gut degeneration and body weight loss (An et al., 2007; Ji et al., 2008; Yang et al., 2006). Threshold temperature for aestivation ranges from 20 to 25 °C, depending on location and body weight (Yang et al., 2005; Yuan et al., 2009). In British Columbia, seawater maximum temperatures are reached in June–July and only occasionally surpass 20 °C. In the first year of simulation we did not observe negative growth during summer, while the high-temperature effect on growth intensified as size increased (Fig. 5b). Many studies already reported that adult sea cucumbers are more affected by seawater temperature than juveniles (Yang et al., 2005; Yuan et al., 2009, 2007) and this seems to be a common trend in marine invertebrates (Peck et al., 2013).

Little quantitative information exists on growth rates of P. californicus and long-term growth trends are still unknown. As with most holothurians, growth of this species is thought to be slow, taking from 4 to 5 years for an adult weight of 500 g to be reached (Department of Fisheries and Oceans Canada, 2013). It is estimated that sea cucumbers grown below oyster farms would require 3 to 4 years to reach market size, i.e. from 218 to 489 g split weight—viscera and internal fluids removed (Paltzat et al., 2008). In a previous study of P. californicus cultured in both suspended and on-bottom cages in British Columbia, positive growth during 2 years indicated that the low end of market size (368 g whole weight or 211 g split weight) could be reached after the third year (Sutherland, 1999). In our study, the 368 g minimum commercial size was reached after 1.4 years, i.e. half of that time. This discrepancy may be due to the fact that our model did not account for the energy lost in reproduction.

Fig. 8 shows the simulated energy allocation for P. californicus during a 4-year growth cycle. In our model the energy lost in faeces was held constant at 80%, due to the use of an average assimilation efficiency—there is, however, more variability in the literature values for the energy lost as faeces, probably related to food quality. Some authors report 30% (An et al., 2007, Yuan et al., 2008b), others 60% (Dong
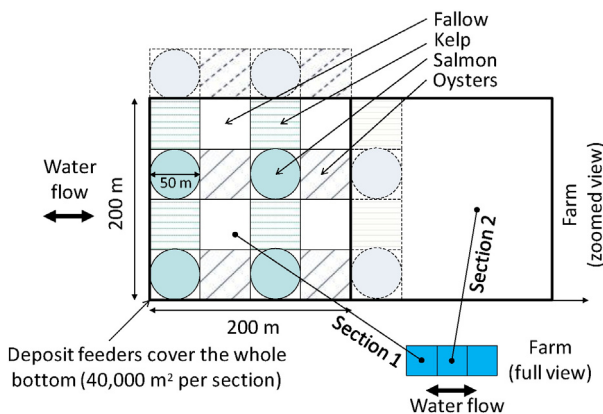

Fig. 6. Layout used for FARM model simulations. The IMTA farm is 600 m long, with three sections of 200 m each. Water flow considers flood and ebb currents, and the various marked (50 × 50 m) monoculture squares are simulated with culture distributed throughout the entire section (4 ha). Culture densities for the standard model are 100 ind m^{-2} (oysters), 20 ind m^{-2} (salmon), 50 ind m^{-2} (kelp), and 20 ind m^{-2} (sea cucumber), for each cultivated area.

Table 2

Summary of FARM outputs for monoculture of sea cucumbers (20 ind m^{-2}) and co-cultured in different IMTA scenarios: IMTA 1: sea cucumbers with finfish (5 ind m^{-2}, i.e. one 50 m Ø cage per model section); IMTA 2: sea cucumbers with finfish (20 ind m^{-2}, i.e. four 50 m Ø cages per section); IMTA 3: sea cucumbers with Pacific oyster longline culture (100 oysters m^{-2}); IMTA 4: sea cucumbers and finfish (IMTA2), with shellfish. IMTA 5 (*standard model*): IMTA 4 with kelp (50 seaweeds m^{-2}). IMTA6: IMTA5 with 4× sea cucumber stocking density, i.e. 80 ind m^{-2}.

	Monoculture	IMTA1	IMTA2	IMTA3	IMTA4	IMTA5	IMTA6
Production							
Deposit feeder (DF) TPP[3] (kg cycle^{-1})	101,859	581,674	602,557	143,630	603,045	603,045	1,847,162
Deposit feeder APP[3]	8.5	48.5	50.2	12.0	50.3	50.3	38.5
Deposit feeder live weight (g)	112.2	299.8	308.9	128.7	309.1	309.1	249.2
Deposit feeder length (cm)	13.5	19.0	19.2	14.2	19.2	19.2	17.8
Deposit feeder yield (g m^{-2} cycle^{-1})	849	4847	5021	1197	5025	5025	15,393
Finfish TPP (t cycle^{-1})	–	2317	9267	–	9267	9267	9267
Finfish FCR	–	1.47	1.47	–	1.47	1.47	1.47
Economics							
Profit deposit feeders (k\$ cycle^{-1})	2182	13,179	13,658	3139	13,669	13,669	41,725
Profit finfish (k\$ cycle^{-1})	–	4707	18,828	–	18,828	18,828	18,828
Profit shellfish (k\$ cycle^{-1})	–	–	–	1203	1214	1214	1214
Profit seaweed (k\$ cycle^{-1})	–	–	–	–	–	170	170
Total profit (k\$ cycle^{-1})	2182	17,886	32,486	4342	33,711	33,881	61,937
Annual profit per unit area (\$ m^{-2} y^{-1})	50	408	741	99	769	773	1413
Environment							
Annual gross POC loading (g C m^{-2} y^{-1})	1048	2846	8242	1196	8394	8394	8394
Annual POC removal by DF (g C m^{-2} y^{-1})	1043	2437	2518	1191	2520	2520	8231
Annual net POC loading (g C m^{-2} y^{-1})	4	409	5724	5	5874	5874	<u>163</u>
P$_{90}$ chlorophyll (µg L^{-1})[4]	4.6	4.6	4.6	4.6	4.6	4.6	<u>4.6</u>
P$_{10}$ dissolved oxygen (mg L^{-1})[4]	7.7	7.4	4.7	7.7	4.7	4.7	4.7
P$_{90}$ DIN(µM)[4]	9.8	10.8	17.2	9.8	17.2	16.8	16.8
Annual cumulative PEQ[5]	5737	13,484	13,930	7243	14,658	18,500	50,066

Underlined value indicates Net loading in IMTA with finfish is below the threshold of 350 g C m^{-2} y^{-1}.

[3] TPP: total physical product, i.e. harvestable biomass; APP: average physical product = output/input.

[4] Percentiles (90 for chlorophyll and dissolved inorganic nitrogen—DIN, 10 for oxygen). These indicators are used for eutrophication assessment as typical extreme values — see Bricker et al. (2003).

[5] PEQ: population-equivalents, an indicator of the ecosystem service provided by all extractive cultures (shellfish, seaweeds, deposit-feeders), as appropriate to each scenario.

et al., 2010; Yuan et al., 2009, Yuan et al., 2008a; Zamora and Jeffs, 2014) although values as high as 95% (Zamora and Jeffs, 2012a) have been registered.

Energy spent in ammonia excretion was negligible, ranging between 0.18 and 1% (mean 0.5%). Various authors agree that ammonia excretion is very low, accounting only for the 2–7% for *A. japonicus* (An et al., 2007, 2009; Dong et al., 2010; Liu et al., 2009; Yuan et al., 2010, 2009) and 0–1.6% for *A. mollis* (Maxwell et al., 2009; Zamora and Jeffs, 2014).

Of the energy consumed, respiratory loss was 1.5–40% (13.5% on average) accounting for the highest proportion of the energy intake.

Most literature suggests respiration accounts for 20–45% of ingested energy, although values up to 90% have been obtained at higher temperatures (An et al., 2007; Maxwell et al., 2009). The upper limit is similar to our results, but we found much lower values at the juvenile stage.

In AquaDep, the energy incorporated as growth diminishes with sea cucumber size and high temperatures, ranging from −20% to 20%. Our values are within the range obtained by other authors (from −80% to 50%) (An et al., 2007; Dong et al., 2010; Maxwell et al., 2009; Yuan et al., 2007, 2006; Zamora and Jeffs, 2014) and our mean value (6.05%) is within the ranges of these studies (4.1–18.1%). However,
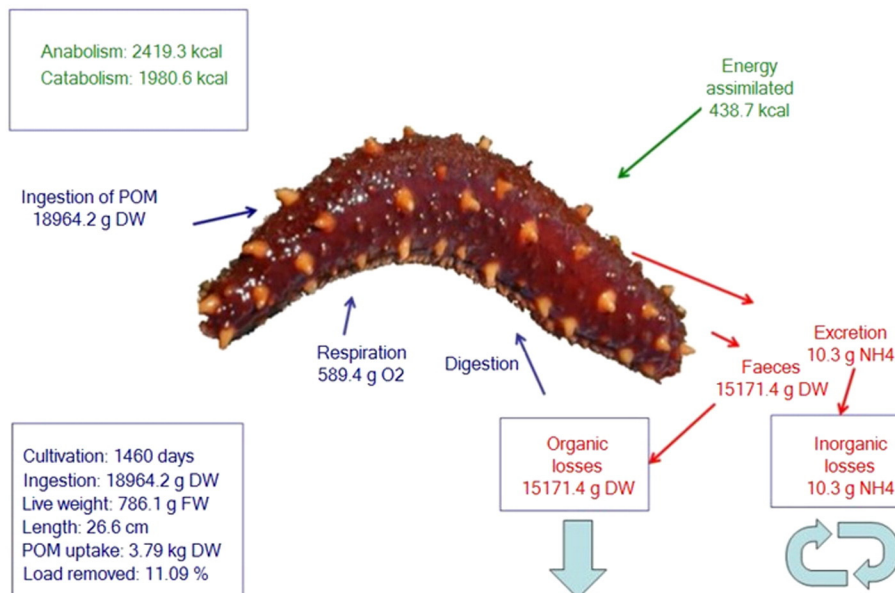

Fig. 7. Mass balance for a four year sea cucumber growth cycle simulated with the AquaDep model.
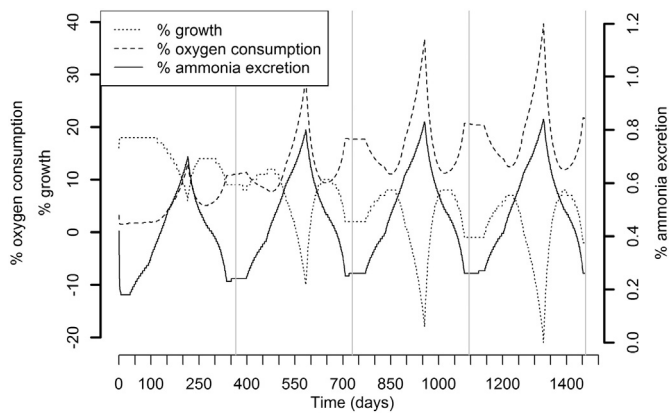
Fig. 8. Energy allocation simulated for *P. californicus* sea cucumber over a 4-year culture period.

the substantial variability in reported data suggests that improved physiological relationships should be developed in order to improve the understanding of underlying factors, and thus the quality of models. We highlight the need for a better understanding of the allocation of resources to gametogenesis, and thus the energy lost in spawning.

3.2. Deposit feeders in IMTA

Table 2 shows the outputs of the FARM model for a range of IMTA combinations (see legend and Fig. 6 for details). For these simulations, the settleable fraction of organic particles from both finfish and shellfish culture was set at 80%, the remainder of the emissions sink much more slowly, at the background rate.

The simulation results are grouped into three blocks, structured on the People-Planet-Profit paradigm. However, the analysis for different scenarios will be made by combining relevant outputs from all three blocks, in order to highlight both the positive and negative aspects of each culture combination.

Deposit feeders grow fairly well in monoculture, providing a potential yield of about 102 tonnes (849 g m^{-2}) per cycle, from the loading of POM due to natural sedimentation of algae and detritus as water moves through the farm. Under natural conditions, practically all the organic load to the sediment is processed by deposit feeders and the net organic enrichment is 4 g Particulate Organic Carbon (POC) m^{-2} y^{-1}, well below the threshold proposed by Hargrave et al. (1997).

With the exception of POM removal by deposit feeders, the results for IMTA1 and IMTA2 correspond to finfish monoculture at two different densities, and IMTA3 to shellfish monoculture. From an environmental perspective, the effect of adding sea cucumbers is quantified in the net POC loading, which accounts for the role of deposit feeders in reducing the gross POC load from finfish and shellfish monoculture.

Both the addition of finfish (IMTA1 and IMTA2) and shellfish (IMTA3) make a significant difference to the harvestable biomass of deposit feeders at the end of the culture cycle; however, the negative environmental externalities of finfish culture are more significant than those of shellfish. In the IMTA1 scenario (lower cultivation density of finfish, equivalent to one 50 m Ø cage in a 200 X 200 m square), the harvestable biomass of sea cucumbers increases sixfold, as does the average physical product (APP); the APP, or ratio of harvestable biomass to seed, is a measure of return on investment, and thus IMTA1 appears to be much more attractive than monoculture from a commercial perspective. This is evident from the annualized farm profit, which increases from 50 to 408 USD m^{-2} y^{-1}, but the loading of POM to the sediment also increases significantly. Nevertheless, in IMTA1 deposit feeders are responsible for a net removal (i.e. accounting for faecal elimination) of 2437 g C m^{-2} y^{-1}, which reduces the net loading to the sediment to 409 g C m^{-2} y^{-1}, only 12% higher than the threshold proposed by Hargrave et al. (1997).

In IMTA2 (four 50 m Ø cages per 200 × 200 m square section, Fig. 6), there is little increase in individual weight or deposit feeder yield, which suggests that although the food (POM) supply triples (the aquaculture component quadruples), other factors are limiting sea cucumber growth, most likely temperature.

The net environmental externalities are substantially greater than in IMTA1, both in terms of net carbon loading to the sediment, because deposit feeders are only capable of removing 30% of the gross load, and with respect to dissolved nitrogen emissions. The typical maximum (percentile 90) of dissolved inorganic nitrogen (DIN) remains almost unchanged for monoculture (9.8 µM), IMTA3 (9.8 µM), and IMTA1 (10.8 µM), but rises sharply to 17.2 µM in IMTA2.

The addition of seaweeds in IMTA5, at a density of 50 ind m^{-2}, has no significant effect on DIN (the P$_{90}$ decreases by 0.4 µM), or on reoxygenation of the water column. This is consistent with simulations by Broch et al. (2013), who determined that an area of 100 ha of kelp (*Saccharina latissima*) was required to offset dissolved emissions from a 6 ha salmon farm. Seaweeds do however provide both an additional crop and substantial ecosystem services—for the standard model (IMTA5) the gross profit increases to 773 USD m^{-2} y^{-1}, and the potential cumulative ecosystem services provided by extractive culture correspond to 18,500 population-equivalents (PEQ), valued at 740,000 USD (see Lindahl et al., 2005; Stephenson et al., 2010), for nitrogen cost calculations.

Co-cultivation of oysters and sea cucumbers (IMTA3) shows that the input of faeces and pseudofaeces from bivalves leads to a 40% increase in harvestable biomass of deposit feeders, and yet adds only 14% more POC (gross load) to the bottom, i.e. is an extremely sustainable combination. This underscores the fact that shellfish are net organic extractors and simultaneously highlights the strong pelagic-benthic coupling between the suspended bivalves and the deposit feeders.

The FARM model was also used to assess interactions among the various pelagic components of the IMTA layout, particularly to investigate (a) how seaweed growth might be enhanced by dissolved nitrogen input from both finfish and shellfish; and (b) to what extent the suspended fraction (i.e. 20% of particles emitted in the standard simulations), which deposits considerably slower than the larger particles, enhances shellfish growth.

With respect to the first question, there is a clear increase in individual growth and total physical product (TPP) for kelp in IMTA. Kelp monoculture results in a final individual weight of 134 g, which increases to 175 g in IMTA5. This is reflected in a 22% increase in TPP for plants of harvestable size from 153 to 214 t cycle^{-1}. By contrast, the individual growth and TPP of shellfish shows no significant increase with the addition of finfish culture. A comparison between bivalve monoculture and IMTA5 shows a trivial enhancement for both indicators: oyster individual weight increases from 60.02 g to 61.65 g, and TPP from 241.9 to 243.9 t cycle^{-1}.

In order to test whether this might be due to the high proportion of settleable solids (80%) defined for both shellfish and finfish in the standard model (IMTA5), a further numerical experiment investigated the inverse situation, i.e. 80% suspended particles. Under these conditions, the difference between monoculture and IMTA5 is slightly greater, but hardly sufficient to justify the positioning of shellfish lines or rafts in the proximity of fish cages: oyster individual weight increases from 60.11 to 65.72 g and TPP from 241.9 to 246.9 t cycle^{-1}. This reinforces the concept that, for direct organic extraction, open water IMTA should focus on benthic bioextractors that can make use of rapidly falling organic particles, rather than arrays of suspended shellfish in the proximity of fish cages (Cranford et al., 2013).

Given the lack of additional harvest potential for deposit feeders at low (IMTA1) and high finfish densities (IMTA5), a final scenario was considered where the stocking density of deposit feeders was increased to 80 ind m^{-2} (IMTA6). The increase shows that sea cucumber growth has a density-dependent response to food supply, with the final weight decreasing by 19% (309 g to 249 g), and a reduction in APP, which drops

from 50.3 to 38.5 (23%). Although the return on investment at the higher density of IMTA6 is decreasing, there is a clear environmental benefit—the net loading from finfish culture is now 163 g C m^{-2} y^{-1}, well within the thresholds for benthic impact.

An analysis using a range of stocking densities can be performed using the FARM model (see e.g. Ferreira et al., 2009), and allows the determination of optimal seeding for profit maximization. This can be combined with the limits for POM loading defined by regulators, to promote environmentally sustainable aquaculture that generates optimal profit while simultaneously protecting the ecosystem.

4. Conclusions

The models developed and tested herein provide a research tool to improve our understanding of the dynamics of IMTA systems and to assist in forecasting productivity and profitability of IMTA farms.

One of the fundamental motivations for this work was to quantify the role of organically extractive aquaculture of filter-feeders suspended in the proximity of fish cages when compared to the role of benthic deposit feeders. By integrating the various components in the FARM model, and discriminating the different sources of POM, as well as the settleable and suspended fractions, we were able to build mass balances for different cultured groups, as shown in Fig. 9.

This approach provides a clearer understanding of mass and energy flow in an IMTA system, and forms the basis for apportioning loads and quantifying the value of the different components. For open water, the model addresses the farm area, and does not extend the analysis to aspects such as diagenesis and dispersion at the broader (ecosystem) scale—this would require a system-scale approach, where the role of the fine particulates which remain in suspension, together with the wider dispersion of dissolved emissions, becomes important at a water-body scale, in the same way as non-point emissions from land may enhance primary production at the bay-scale.

Deposit feeders provide environmental mitigation, offsetting a measureable level of the particulate organic flux from finfish culture, for example, that would otherwise be added to the environment.

The synergistic interactions between finfish and sea cucumbers can be leveraged as a business opportunity within an IMTA system and can contribute to the profitability of a fish farm as secondary cash crop. Sea cucumbers fetch a high market price, with a retail value in China up to US$200 kg^{-1} for some species (Dimock, 1977). There is already a proven Chinese market for *P. californicus*, with a lucrative wild fishery in British Columbia, where a landed value of CAN $3.36 million was generated in 2011 (Fisheries and Oceans Canada, online commercial fisheries statistics). Co-culturing sea cucumbers beneath finfish and shellfish farms will not only provide a profitable added crop, but also reduce the benthic organic loading beneath the farms (MacTavish
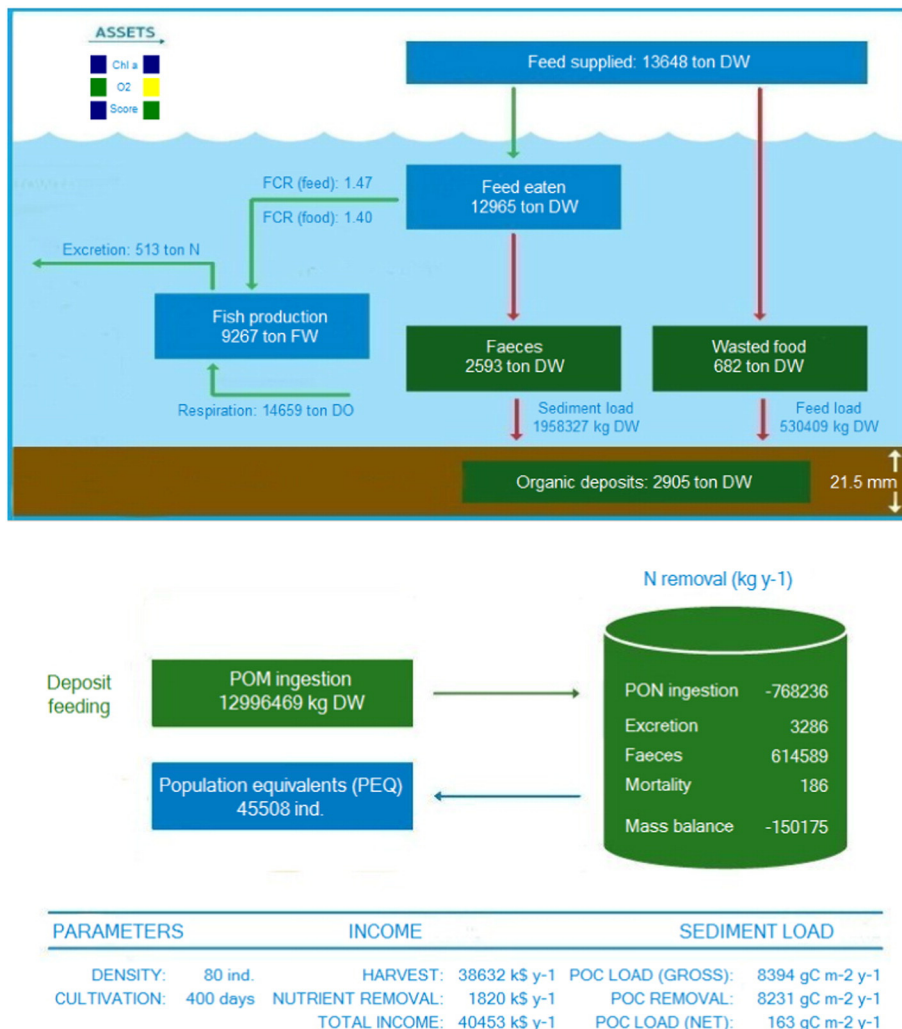

Fig. 9. Mass balance for finfish (top) and deposit feeders (bottom) for the standard IMTA model (IMTA5).

et al., 2012; Slater and Carton, 2009), given the strong link that can be established between settling organic matter and deposit feeders.

This promotion of sustainable aquaculture matches consumer choices for sustainably produced food, especially in developed nations where there is a willingness to pay a premium for more 'environmentally-friendly' products.

Our FARM modelling analysis supports a number of previous results obtained in the field and in situ experiments, and suggests that Western-style (or watershed-scale) IMTA (WIMTA) can play two distinct but complementary roles.

On the one hand, tightly coupled systems where larger particulates from finfish or shellfish culture rapidly reach the bottom may be leveraged for a direct source of extra protein and profit, while providing a meaningful ecosystem service at the local scale. In parallel, since the densities at which fish cages and shellfish longlines or rafts can exist in Europe, the United States, or Canada are determined by rigorous licensing procedures and constrained by social carrying capacity, our results suggest that not all culture structures need to be placed in close proximity, but rather that the environmental advantages of certain types of cultivation occur mainly in the context of integrated catchment management.

Acknowledgements

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