



Cultivation of gilthead bream in monoculture and integrated multi-trophic aquaculture. Analysis of production and environmental effects by means of the FARM model

J.G. Ferreira ^{a,*}, C. Saurel ^a, J.M. Ferreira ^{b,c}

^a New University of Lisbon, Faculty of Sciences and Technology, Centre for Ocean and Environment, DCEA, FCT, Qta Torre, 2829-516 Monte de Caparica, Portugal

^b Departamento de Física, Universidade de Trás-os-Montes e Alto Douro, 5001-801 Vila Real, Portugal

^c Centro de Física Atómica da Universidade de Lisboa, Departamento de Física da Faculdade de Ciências, Av. Prof. Gama Pinto 2, 1649-003 Lisboa, Portugal

ARTICLE INFO

Article history:

Received 3 January 2012

Received in revised form 12 June 2012

Accepted 15 June 2012

Available online 27 June 2012

Keywords:

Gilthead bream

Pond and offshore culture

Finfish and shellfish IMTA

Carrying capacity

Site selection

FARM model

ABSTRACT

The aquaculture growth required to meet increasing protein demand by a growing world population, predicted to reach 9 billion people by 2050, is driving innovation in both siting and culture practice. Limited possibilities for expansion on land and in inshore coastal areas, and technological improvements in farming structures, have led to widespread interest in offshore aquaculture.

A gilthead bream (*Sparus aurata*) model has been developed and integrated with existing shellfish models in the Farm Aquaculture Management System (FARM) model, in order to analyse various aspects of onshore and offshore aquaculture. The FARM model was used to compare the quantitative effects of finfish monoculture with Integrated Multi-Trophic Aquaculture (IMTA) in ponds, in terms of production, environmental externalities, and economic performance. Very clear benefits of IMTA could be seen in the comparison. The same approach was then applied to offshore culture, considering a combination of gilthead in cages and Pacific oyster (*Crassostrea gigas*) suspended from longlines. For offshore culture, the primary production and diagenesis modules of FARM were switched off, since there are no feedbacks from those processes to the farm area. Except in upwelling areas, the concentration of food drivers for filter-feeding shellfish falls markedly with distance from the shore—simulations with FARM suggest that in food-poor areas, co-cultivation of bivalves with fish can significantly improve shellfish production, and that the distribution of finfish can be optimised to reduce shellfish food depletion in the inner parts of the farm. We calculate the environmental benefits of IMTA both in terms of population-equivalents and the potential for nutrient credit trading. The finfish model integrated in FARM deals explicitly with the metabolic energy cost of opposing offshore currents in cage culture, and a model analysis suggests that gilthead cultivation at current speeds in the range of 0.1 to 0.5 m s⁻¹ is optimal. The lower end of that spectrum probably translates into a greater deviation from the fillet quality obtained from wild fish, and above that limit there is a rapid increase of the feed conversion ratio (FCR) and cultivation becomes financially unattractive.

© 2012 Elsevier B.V. All rights reserved.

1. Introduction

Marine finfish aquaculture in Europe is dominated by two major species, Atlantic salmon (*Salmo salar*) in the north, with an annual production of almost 900,000 t (EC Fisheries, 2011), and gilthead bream (*Sparus aurata*) in the south, with an estimated production (2008) of almost 129,000 t y⁻¹ (FEAP, 2009). In both cases, as well as for species such as the European sea bass *Dicentrarchus labrax*, which is cultivated in smaller quantities, the market acceptance of the cultivated product is high (e.g. Verbeke et al., 2007), and wild-captured fish are often

available only at premium prices that are inaccessible to most consumers.

Two important developments are currently occurring in Europe and North America, driven by competition for marine space and by increased environmental awareness (Olesen et al., 2010). The first is an increased interest in offshore aquaculture (Aguilar-Manjarrez et al., 2008), made possible through improvements in culture structures, and the second is the co-cultivation of different trophic groups in Integrated Multi-Trophic Aquaculture (IMTA, e.g. Chopin et al., 2010; Neori et al., 2004; Troell et al., 2009).

In the first case, there are a number of potential benefits in placing culture structures such as sea cages some distance from the shore, reducing visual impacts (Byron and Costa-Pierce, 2010; Byron et al., 2011), and promoting greater dispersion of waste products and uneaten

* Corresponding author.

E-mail address: joao@hoomi.com (J.G. Ferreira).

food, by taking advantage of stronger hydrodynamics and greater water column depth (see Holmer, 2010, for a review). The disadvantages include higher operating costs and potentially lower yields at higher current speeds (Kapetsky et al., 2012).

Allied to the social and environmental carrying capacity advantages of cultivating finfish further out to sea, is the possibility of co-cultivation with bivalve shellfish in longlines or rafts in IMTA (e.g. Ferreira et al., 2010, 2011). The additional food supply to species such as mussels and oysters may to some extent compensate for the more oligotrophic nature of offshore waters, and will reduce the environmental footprint of finfish culture, while providing an extra cash crop for the farmer.

IMTA was documented thousands of years ago in China (Moo, undated), and has been standard practice in SE Asia for hundreds of years (Ferreira et al., in press), but the effectiveness of multi-trophic culture has been shown mainly in inland pond culture, e.g. by combining shrimp or fish with razor clams, together with a primary producer such as water spinach (*Ipomoea aquatica*). It is more difficult to establish the practical consequences of IMTA in open water, due to hydrodynamic effects, except in situations where the cultivation intensity at the whole-bay scale turns embayments or estuaries into the equivalent of a pond. Such high-density culture is widespread in China; for instance in Sanggou Bay (Zhang et al., 2009), an annual production of 150,000 t of kelp, shellfish, and finfish is documented for an area of 140 km² (Ferreira et al., 2008a).

Although the importance of IMTA is increasingly recognised in North America and Europe, it is effectively practised only in a few farms in Canada (Cross, pers. com.), and the cultivation densities are characteristic of aquaculture in the western world, i.e. they are presently too low to allow the environmental benefits to be easily quantified.

Mathematical models have been applied to analyse the production and environmental effects of finfish cultivation (e.g. Corner et al., 2006; Cromey et al., 2002; Skogen et al., 2009; Stigebrandt et al., 2004), and have likewise been used to predict the yield, environmental impact, and economic optimisation of shellfish farming operations (e.g. Brigolin et al., 2009; Chamberlain, 2002; Ferreira et al., 2009; Giles et al., 2009), but the combined production and effects of finfish and shellfish cultivations in IMTA have not to our knowledge been modelled previously, either in ponds or open water farms.

This work aims to develop and test an integrated modelling approach for IMTA of finfish and shellfish, both at the pond scale and in offshore conditions. This combination has been implemented in the FARM model (e.g. Ferreira et al., 2011; Silva et al., 2011), and uses gilthead bream and Pacific oysters (*Crassostrea gigas*) as test species for co-cultivation.

The main objectives are:

1. To examine the production, environmental effects, and economic externalities of monoculture of gilthead bream in ponds, and compare this to IMTA with oysters.
2. To extend this analysis to offshore farms, taking into account both the variation in current speed and the effects of co-cultivation of finfish on oyster growth.
3. To illustrate how models of this nature can assist in supporting site selection, from the standpoints of production, environment, and economic viability.

2. Methodology

The models applied in this work were developed, tested, and combined using a stepwise approach, building on an existing framework. The sequence was:

- development or adaptation of individual models, using the simplest set of formulations that allowed for an analysis of feeding, growth, metabolism, and environmental effects;

- integration of individual growth models into a population dynamics framework (see e.g. Nunes et al., 2011), enabling the models to provide results on the marketable cohorts of finfish and shellfish, in order to focus on the harvestable biomass of interest to producers; population-scale modelling also allowed for food consumption and environmental effects to be simulated at the culture scale;
- simulation of the physical systems where the cultivated species are grown. In the case of pond culture this requires a simulation of sediment diagenesis, whereas in open water the approach previously developed in FARM (e.g. Ferreira et al., 2007) was used, with the additional module for biodeposition described in Silva et al. (2011).

The main methodological innovations were the simulation of growth for gilthead, and the implementation of the diagenesis component. These are described in more detail below.

2.1. Individual model for gilthead bream

Several models already exist for individual growth of gilthead bream (e.g. Brigolin et al., 2010; Hernández et al., 2003; Libralato and Solidoro, 2008); therefore where possible, we drew on formulations already tested by those authors. However, we required an explicit simulation of feeding (see below), and we additionally needed to fraction the various components of metabolism in order to simulate growth at different current speeds.

The individual growth model developed (AquaFish) is based on net energy balance, and uses a similar rationale (i.e. maximum simplicity) to the AquaShell model developed for bivalves (Ferreira et al., 2010; Silva et al., 2011). By contrast to organically extractive shellfish aquaculture, finfish are fed (dry feed pellets in the West but often trash fish in SE Asia)—one of the key indicators of finfish aquaculture is the feed conversion ratio, or FCR, so the feed supplied must be accounted for in the model.

Another key difference in simulating feeding is that a concentration-based approach, as is normally used in shellfish models, is not appropriate, since gilthead (and other fish species such as salmon and bass) eat a 'meal'; this is best thought of by considering that in the wild, gilthead thrive on a diet of discrete prey items such as mussels, crustaceans, and smaller fish.

2.1.1. Feeding and digestion

Elliott and Persson (1978) derived various equations to represent food consumption and gastric evacuation in fish. We have used a similar approach in developing a feeding model, following also from the equations given in Franco et al. (2006).

The maximum food intake (g DW pellets d⁻¹) into the fish stomach is calculated based on allometry (Brigolin et al., 2010), and the temperature effect (f_{θ}) on feeding (Eq. (1)) follows Hernández et al. (2003):

$$f_{\theta} = D \left(e^{\alpha(\theta_m - \theta)} - e^{\beta(\theta_m - \theta)} \right) \quad (1)$$

where (values from Hernández et al., 2003):

θ	water temperature (°C)
θ_m	maximum lethal temperature = 32.9 °C
α	temperature function parameter = -0.12 °C ⁻¹
β	temperature function parameter = -0.15 °C ⁻¹
D	temperature adjustment parameter = 4.93.

Feeding is a function of stomach volume, converted to dry mass of feed pellets, and of stomach 'fullness'; the feeding rate is reduced through the application of a satiation coefficient as the animal's stomach capacity is reached. Fish stomach capacity has been studied by e.g. Knight

and Magraf (1982), and Gosch et al. (2009). In AquaFish, stomach capacity is governed by allometry, after Gosch et al. (2009). Since no data were available for gilthead, an equation for spotted bass (Eq. (2)) was used:

$$S_v = 3.587 \times 10^{-8} L^{3.514} \quad (2)$$

where:

S_v stomach volume (ml)
 L fish length (mm).

S_v was converted to dry mass using the pellet density. Gilthead length (L) was calculated from biomass (W) following Wassef and Shehata (1990):

$$\text{Log } W = -2.1724 + 3.2216 \text{ Log } L. \quad (3)$$

Jobling (1981) provides a detailed review of the different equations for gastric evacuation in fish, of which the first-order decay model (Eq. (4)) appears to be the most realistic. Note that this equation does not include the feeding component described earlier, i.e. it applies for the period when no feeding occurs.

$$\frac{dS_c}{dt} = -\gamma S_c^{0.5} \quad (4)$$

where:

S_c volumetric stomach content (converted to mass, i.e. ρS_c) and therefore using the mass or volume of the stomach content is irrelevant (g DW);
 γ proportionality constant (calibrated to 1.5).

Food entering the gut through gastric evacuation is either assimilated or eliminated as faeces (Eq. (5)):

$$\frac{dG_c}{dt} = \frac{dS_c}{dt} - \varepsilon F_r - \varphi G_c \quad (5)$$

where:

G_c gut content (DW food)
 ε assimilation efficiency (no units)
 F_r feeding rate (g DW d^{-1})
 φ faecal elimination rate (g DW d^{-1}).

Faeces are eliminated when a certain proportion of the gut is filled, but the model can easily accommodate “trickle” faecal elimination if required.

The behaviour of the feeding and digestion components of the model was verified in three ways. Firstly, the dynamics of feeding and gastric evacuation were analysed graphically (Fig. 1) in order to test whether the sequence of events, and their frequencies, appeared appropriate. Secondly, the percentage of body (fresh) weight consumed daily in dry weight of feed was determined for an animal in the 150 g weight range, and compared with the results obtained experimentally by Bavčević et al. (2010). These authors indicate an optimum daily feeding ration of 1.06% body weight for a 155 g gilthead. The feed consumption in AquaFish is 1.61 g DW d^{-1} for a 155.6 g FW gilthead, i.e. 1.04%, which is considered an acceptable result.

Finally, Table 1 shows the closed mass balance for cultivation of one fish to a biomass of approximately 350 g, a typical commercial weight.

The AquaFish model can be used to calculate the Apparent Digestibility Coefficient (ADC, e.g. NRC, 1993; Oliveira et al., 2008), for nitrogen (converted from protein after Breese Jones, 1931) using conversion coefficients for dry feed (Piedecausa et al., 2010), and faeces (Gul et al., 2007). Such derived outputs can be used for additional model validation; the ADC_N for the simulation shown in Table 1 is 81.7%, which compares well with the value of 82.8% calculated by Piedecausa et al. (2010).

2.1.2. Swimming and metabolism

Current speed is a key issue for site selection in offshore finfish aquaculture. Not only does it condition the structural stability and permanence of cages and lines, but it also determines a range of other aspects, including fish growth, product quality, and waste removal. For rapidly swimming fish such as salmon, bass, or bream, cultivation in slow current speeds leads to poorer fillet quality, manifested for instance through higher muscle fat content (Grigorakis, 2007), but swift currents may lead to an excessive metabolic cost.

In order to be of use in offshore aquaculture management, a model must be able to represent the various components of fish metabolism; in AquaFish these are divided into three parts: (a) basal metabolic rate, or BMR; (b) apparent specific dynamic action (SDA), i.e. the metabolic costs of digestion, which may vary between 9 and 26% of the energy of food being processed (Jobling, 1981). The reasons for this energy cost are not fully understood, but are thought to be related e.g. to protein deamination; and (c) locomotion, which includes both fish swimming behaviour and actively opposing an ocean current when cultivated in the open sea.

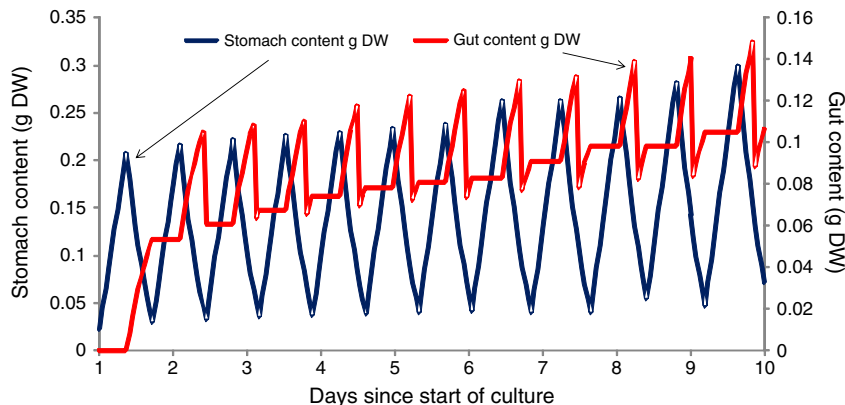


Fig. 1. Simulation of change in stomach content and gut content for a 5 g (fresh weight) gilthead bream fry.

Table 1

Mass balance for feeding and digestion over a 560 day growth cycle in gilthead bream (final biomass: 352 g) simulated with the AquaFish model.

Mass balance term	Value	Units
Total food consumed	645.46	g DW over the culture period
Food in stomach	15.258 ^a	g DW in fish at harvest time
Food in gut	8.031	g DW in fish at harvest time
Food assimilated	441.14	g DW over the culture period
Faeces eliminated	181.03	g DW over the culture period
Total food processed or in digestive tract	645.459	g DW over the culture period
Mass balance	0.001	

^a 77.4% of stomach capacity (19.7 g) of a 350 g gilthead bream.

The net energy balance (E) for a gilthead bream is thus described in AquaFish by Eq. (6):

$$\frac{dE}{dt} = E_i - (E_f + E_b + E_s) \quad (6)$$

where:¹

- E_i energy from assimilated food (gramcal d⁻¹)
- E_f energy cost of feeding (gramcal d⁻¹)
- E_b energy cost of basal metabolism (gramcal d⁻¹)
- E_s energy cost of swimming (gramcal d⁻¹)

$$E_i = \delta \varepsilon g_i \quad (7)$$

where:

- δ energy density of feed (gramcal g⁻¹ DW)
- g_i gut transit (g DW d⁻¹).

BMR, including both temperature and allometric effects, has been simulated following Libralato and Solidoro (2008), and SDA was calibrated as a proportion (C_{SDA}) of energy intake:

$$E_f = C_{SDA} E_i \quad (8)$$

The energy costs of swimming, together with the associated oxygen consumption, are described in detail below.

The power P is related to frictional force F and velocity V as:

$$P = FV \quad (9)$$

For fluids, the frictional force is related to drag coefficient C_d by:

$$F = \frac{1}{2} C_d \rho A V^2 \quad (10)$$

where ρ is the fluid density and A the frontal area or the wetted area. The power P is expressed in W (J s⁻¹) for a force in N and a velocity in m s⁻¹. Since AquaFish uses the day as a time unit (the model timestep may vary but typically 1 h is used), the final equation for the energy cost of swimming (here converted to gramcal d⁻¹) is:

$$E_s = \frac{1}{2} C_d \rho A V^3 \quad (11)$$

Barrett et al. (1999) made detailed measurements of both the minimum drag coefficient for an actively swimming robotic fish and the drag coefficient resulting from towing the robot at the same speed, and found the values of the latter to be significantly higher. This is an example of Gray's paradox (Gray, 1936), who "compared the power required by a rigid model of a dolphin to move at speeds of

around 20 knots with its estimated available muscular power. He estimated that the available muscular power is smaller than the power required to propel the rigid model by a factor of seven, thus concluding that substantial drag reduction must occur in the live dolphin." (Barrett et al., 1999).

C_d can be experimentally correlated with the Reynolds number (Re):

$$Re = \frac{\rho LV}{\eta} \quad (12)$$

where ρ (kg m⁻³) and η (Pas) are seawater density and viscosity, respectively. However, Reynolds numbers for market-size gilthead are up to ten times lower than the range for which a valid correlation is available in the literature, so we opted instead to use a drag coefficient of 0.015 published for rainbow trout by Webb (1975). This is clearly an area where better experimental data are needed; the state of the art has been aptly summarised by Vogel (1994): "For fish... the whole body participates in propulsion, and the situation is catastrophic".

In AquaFish we determine the frontal area (A) through an allometric equation, considering a ratio of 3 between fish length and maximum fish height (Palma et al., 1998) and an elliptical section. The wetted area can be used instead, following Gray (1953) and Niimi (1975).

Oxygen consumption due to metabolism may be represented by:

$$\frac{dO_2}{dt} = -(O_b + O_f + O_s) \quad (13)$$

where:

- O_b oxygen consumption due to basal metabolism (mg O₂ fish⁻¹ d⁻¹)
- O_f oxygen consumption due to feeding (mg O₂ fish⁻¹ d⁻¹)
- O_s oxygen consumption due to swimming (mg O₂ fish⁻¹ d⁻¹).

Oxygen consumption due to BMR was modelled according to Libralato and Solidoro (2008), and for apparent SDA, 1 mg O₂ was consumed for every 13.56 J expended (Elliott and Davidson, 1975). Steinhausen et al. (2010) derived an empirical relationship between swimming speed and oxygen consumption for gilthead:

$$\Delta O_2 = 96.5 + 740 U^{1.47} \quad (14)$$

where:

- ΔO_2 dissolved oxygen consumption (mg kg⁻¹ h⁻¹)
- U swimming speed (body lengths s⁻¹).

Since body length and biomass are known, we can calculate the current velocity equivalent for U, and O₂ consumption rates normalised to fish mass.

2.2. Sediment diagenesis

Organic matter is naturally cycled within an aquaculture pond, regardless of the species cultivated within it, and during fallowing. For the case of a land-based aquaculture, the mass balance of particulate organic matter (POM, mg L⁻¹) is determined using Eq. (15):

$$\frac{dPOM}{dt} = \tau F_w + \sum_{s=1}^{s=n} F_s + S_{pf} + P_m - \sigma POM \quad (15)$$

where:

- τ decomposition rate of excess feed (d⁻¹)
- E excess feed (mg DW L⁻¹)

¹ Energy is actually represented per unit time, i.e. corresponds to power (P=E/t).

S	cultivated species (1 to n)
F _s	faecal contribution of species s (mg DW L ⁻¹ d ⁻¹)
S _{pf}	bivalve shellfish pseudofaeces (mg DW L ⁻¹ d ⁻¹)
P _m	phytoplankton mortality (mg DW L ⁻¹ d ⁻¹)
σ	sedimentation rate of POM (d ⁻¹), determined using Stokes' equation.

The mass balance equation for particulate organic nitrogen (PON) in the sediment is (Di Toro, 2001):

$$\frac{HdPON}{dt} = JPON - k_{PON}HPON - w_{PON}PON \quad (16)$$

where:

H	sediment height (m)
JPON	flux of PON to sediment (mg N m ⁻² d ⁻¹)
k _{PON}	0.03 d ⁻¹ (Cartaxana and Catarino, 1997, 2002)
w _{PON}	loss rate to sediment (burial) (m d ⁻¹).

Sediment diagenesis is calculated following Di Toro (2001) and Simas and Ferreira (2007). Eq. (17) represents the mineralisation of sediment PON to ammonium and the flux of ammonium to the water column.

$$\frac{HdNH_{4(sed)}}{dt} = k_{PON}HPON + kL_{ws} \left(NH_{4(wat)} - NH_{4(sed)} \right) - w_{NH_4}NH_{4(sed)} \quad (17)$$

where:

NH _{4(sed)}	ammonium in sediment (mg N m ⁻³)
NH _{4(water)}	ammonium in water (mg N m ⁻³)
PON	particulate organic nitrogen in sediment (mg N m ⁻³)
kL _{ws}	0.00017 m d ⁻¹
w _{NH₄}	0.0007 m d ⁻¹ .

The ammonium that is returned to the water column, together with that excreted by the cultivated organisms, and nitrogen inflows through water intake, is used to determine primary production. In open water farms, pelagic primary production is neglected, due to the short residence time of water in the farm, and the effects of sediment diagenesis are only considered to establish the benthic footprint of the farm. Incorporation of both these processes in open water farms requires a system-scale modelling approach (e.g. Ferreira et al., 2008b; Nobre et al., 2010).

2.3. Oxygenation

Dissolved oxygen (DO) plays a key role in both the growth and survival of cultivated species, and the water quality in ponds. The mass balance equation for DO contains terms for biological sources (primary production) and sinks (e.g. finfish respiration), together with physical components, which can be divided into natural aeration, artificial aeration, and water exchange.

Natural aeration of ponds is simulated as a function of the DO saturation in the water and atmosphere, and turbulent mixing at the air/water interface, following Chapra (1997) and Nobre et al. (2005), using a Schmidt number of 500. A default wind speed of 2 m s⁻¹ is set, but a climatological time series of wind speeds can be defined by the model user.

Most cultivated ponds are subject to artificial aeration, therefore FARM allows the user to specify three aeration regimes: (i) no artificial aeration; (ii) optimised aeration; and (iii) constant aeration. If the culture pond has oxygen problems, selecting constant aeration will turn on the aerators at dusk (the full photoperiod for any latitude is

simulated in the model) in order to maximise efficiency and minimise energy costs. Aerators will be switched off as soon as 100% saturation is attained. If optimised aeration is preferred, it is triggered whenever DO saturation falls below a user-defined threshold, and turned off when the value in the pond is above the threshold at dawn. The operation of aerators (Eq. (18)) is simulated following Boyd (1998, 2009) and Tucker (2005).

$$OTR = SOTR \frac{C_s - C_p}{9.09} 1.024^{T-20} \omega \quad (18)$$

where:

OTR	oxygen transfer rate in pond water (kg O ₂ h ⁻¹)
SOTR	standard oxygen transfer rate. In FARM this is determined from the relationship between the standard aeration efficiency (SAE) and the horsepower of the aerator.
C _s	DO at 100% saturation (mg L ⁻¹)
C _p	DO in pond (mg L ⁻¹)
T	water temperature (°C)
ω	oxygen transfer coefficient ratio.

In order to determine aquaculture production costs, the model user may specify the unit cost of electricity, or use the default value supplied. DO is considered to affect both growth and mortality, and it is possible to switch off those effects in FARM to examine the sensitivity of the cultivation to this variable. Primary production may also be switched off, to look at the ecosystem service provided by algae in reoxygenating the pond water.

2.4. Model implementation

Component parts of the individual model for gilthead were tested and assembled in PowersimTM, a visual modelling platform. The complete model was then ported to C++, and implemented in object-oriented (OOP) code. Mass balance outputs were verified against the visual platform. Subsequently, the individual model was used to determine the scope for growth for a fish population, using well-tested equations (e.g. Ferreira et al., 2008b). Ten weight classes were used for the population model, ranging from 0 to 460 g. The full model, capable of simulating fish growth and environmental effects both at the individual and population levels, was inserted into FARM, in the context of both land-based and open water cultures. FARM simulates physical and chemical processes in both environments, together with shellfish growth and environmental effects. The combination of the various components into a modelling system was used as a tool for analysis of monoculture versus IMTA, and of the performance of offshore aquaculture.

3. Results and discussion

A brief analysis of the individual finfish model is presented, followed by the results of the full application of finfish and shellfish models in an integrated framework, both for onshore and offshore cultures.

3.1. Individual finfish model

Fig. 2 shows the full mass balance for the growth of a 5 g gilthead fry to a weight of 350 g, over a 414 day culture period, at a temperature range centred around 20 °C. The FCR is 1.3, which is underestimated because the individual AquaFish model does not consider other processes typical of the farm itself (and which are simulated in the final models) such as loss of pellets through deposition. Waste feed in AquaFish is generated only by the animal's incapacity to eat

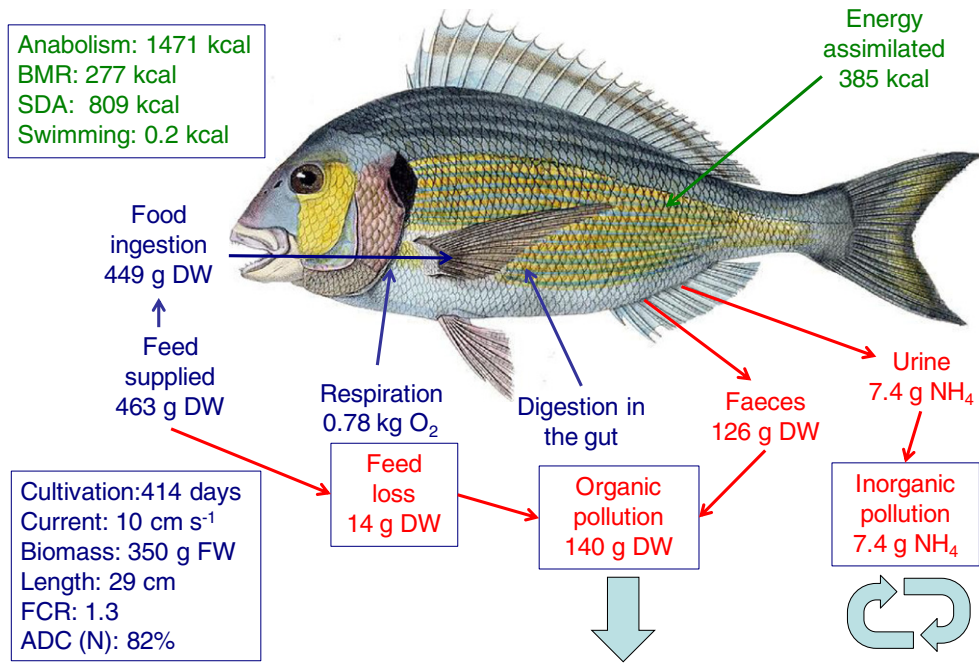


Fig. 2. Mass balance for individual growth of a gilthead bream (350 g final weight). Market sized bream do not normally reach sexual maturity, so the model does not account for reproduction. Gilthead image source: <http://www.archive.org/details/histoirenaturell141255cuvl>.

all the food offered. Complementary cultivation parameters calculated by the model for this example are: specific growth rate (SGR): 1.03% (ln) $g\ d^{-1}$, and a thermal growth coefficient (TGC3, e.g. Jobling, 2003) of $0.37\ g^{1/3}\ ^{\circ}C^{-1}$.

The individual model was validated against measured data from an experimental aquaculture station in southern Portugal (F. Soares, pers. com). Measured biomass after 134 days was 303 (± 69) g, and 367 (± 51) g after 246 days. The model results were 277 g and 396 g, respectively. AquaFish was also tested against growth data from a farm in Turkey (Yilmaz and Arabaci, 2010). The model is able to reproduce the endpoint individual biomass of 337 g, at a mean temperature of 19 $^{\circ}C$, and determines a cultivation period of 338 days. The experimental culture took place between January 1st and December 5th 2006, i.e. 339 days. The farm yields and the model have an identical SGR, and the TGC3 coefficients differ by less than 2%.

For the standard simulation shown in Fig. 2, the AquaFish model gives a total oxygen consumption of 0.057 (50 g biomass), 0.131 (100 g biomass), and 0.773 (endpoint) $kg\ O_2$ during the cultivation cycle of a 350 g bream. The culture periods are 81, 138, and 414 days (end of culture), respectively, and the corresponding mean oxygen consumption is 0.59, 0.40, and 0.22 $mg\ O_2\ g^{-1}\ h^{-1}$. These values compare well with consumption rates of 40–60 $mg\ O_2\ 100\ g^{-1}\ h^{-1}$, i.e. 0.4–0.6 $mg\ O_2\ g^{-1}\ h^{-1}$, for juvenile fish, determined by Requena et al. (1997).

Swimming energy expenditure is low for this simulation, because a 0.1 $m\ s^{-1}$ current speed is considered. However, this changes rapidly when current speed increases (Fig. 3), partly because energy consumption is a function of V^3 (Eqs. (10) and (11)).

Four sections (A–D) are labelled in this figure. In zones C–D, at current speeds above 0.6 $m\ s^{-1}$ the FCR increases exponentially from 1.5 to 10, making profitable cultivation inviable. Zone B is probably the

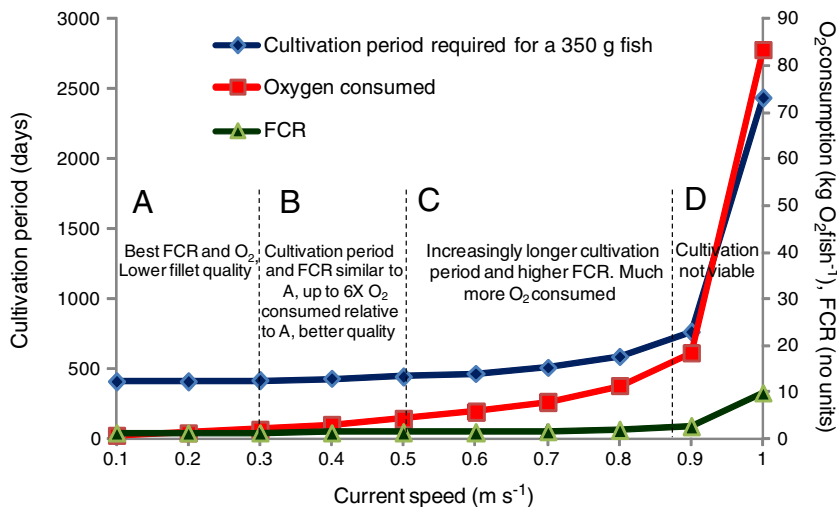


Fig. 3. Effects of different current speeds on (a) cultivation period to grow a 350 g gilthead; (b) FCR; and (c) oxygen consumption. Four different areas (A–D) are identified in the graph. At the far left, the animal grows quickest but the fillet is soft and of lower quality. At the far right, cultivation becomes impossible due to metabolic costs.

most desirable section, where both the cultivation period and FCR are at acceptable levels. Energy costs for aeration will be higher (up to 6× more oxygen is consumed) but the fillet quality will improve. At present there is no price differential for aquaculture products, except on criteria such as organic farming. That in itself is somewhat of a paradox, since the use of species such as the Peruvian anchoveta for fishmeal is simultaneously organic and environmentally unfriendly.

In most markets, there is a discrete and substantial price difference between cultivated and wild fish of the same species, with no intermediate grading based on the quality differential among culture sites. Not only should a premium be placed on the environmental sustainability of the product, but the higher costs associated with better fillets should be compensated by higher prices. This type of gradient is common in other food products, e.g. with cage, cage-free, and free-range eggs.

3.2. IMTA in finfish ponds

The consequences of monoculture versus IMTA are readily observed in onshore aquaculture, which in turn corresponds to a very significant proportion of world aquaculture, due to the role of SE Asia and China in global production (FAO, 2011). Before the advent of electrical aeration devices, pond culture relied on the natural oxygen balance in the culture environment; filter-feeders played a role in removing excess organic material, and autotrophs in removing mineral nutrients and reoxygenating the water. Given the prevalence of pond culture in Asia, perhaps that is one of the historical reasons for IMTA, along with the economic advantages of recycling. The key physical and biogeochemical processes that occur in pond culture were simulated with the FARM model, and results are shown for both monoculture of gilthead and co-cultivation with Pacific oysters (Table 2).

The table shows the model outputs in three blocks, following the People–Planet–Profit approach. A relatively low cultivation density

was used, both for finfish and shellfish, but in a confined environment this is sufficient to quantify substantial benefits when gilthead are cultivated in IMTA. From the production side, the feed required by the finfish is not reduced by IMTA, but if macrobenthic production were included in the model, less feed would be required. In IMTA, 640 kg of market-size oysters are grown in the 420 day cultivation period, providing both goods and services to the farmer. A complementary simulation of oyster monoculture in the same pond (not shown in the table) yields only 1.7 kg of harvestable (60–70 g TFW) oysters for an identical culture period, because the food supply is insufficient to grow market-sized shellfish. A reduction in the threshold harvest weight to 40–50 g TFW yields only 25 kg, i.e. the oysters perform a bioremediation role but the farmer does not get a crop within that cultivation period.

The environmental impact of gilthead culture is substantially reduced in IMTA, for an identical finfish yield. The organic deposition to the bottom of the pond is approximately halved, due to bivalve filtration of POM. The organic material filtered by the oysters is partly detritus from the finfish culture, and partly primary production due to nutrient regeneration. The reduction in organic deposits leads to an equivalent 50% reduction in mineral nitrogen released from the sediment; that reduction, coupled with top-down control of phytoplankton by bivalves, means that net primary production (NPP) in the pond is reduced in IMTA to 20% of the 251 kg N cycle⁻¹ simulated for monoculture.

Other environmental benefits are a 50% reduction in overall accretion of sediments at the bottom of the pond, and a substantial improvement in the ASSETS eutrophication index (Bricker et al., 2003), mainly due to the reduction in chlorophyll (chl) concentration. If an aquaculture pond is renewing water, then the discharge puts pressure on the receiving body, since the nutrients and algae released have an impact on the environment, the cost of which is not internalised by the farmer. A part

Table 2
Key data for gilthead monoculture and IMTA (with bivalves) in onshore ponds, simulated with the FARM model (all results for a complete production cycle).

Parameter	Finfish monoculture	Finfish + shellfish IMTA (all finfish data unchanged)
Model setup		
Cultivation practice	1 ha pond, 2 m depth; fish density: 3 ind.m ⁻² (30,000 fish), 420 day culture period, 10% mortality over cycle; water renewal: 3% pond volume per day, aerators switch on when % saturation D.O. falls below 40%	Pacific oysters added at a density of 5 ind m ⁻² (50,000 oysters), 10% mortality over cycle, 60–70 g harvest weight (total fresh weight, TFW)
Production outputs		
Total feed supplied	15,103 kg dry feed pellets	Feed on organic material in pond
Max individual weight (g)	370	370 (finfish) + 66 (oysters)
Total production (TPP, kg FW)	6272	6272 + 639 = 6911
APP ^a	41.8	41.8 + 6.4
FCR	2.4	–
Environmental impact		
Organic deposits (kg DW)	11,960	5478
Nitrogen regeneration (kg N)	655	315
Primary production (kg N)	251	53
Sediment accretion (mm)	1	0.5
ASSETS eutrophication		
Chlorophyll		
Dissolved oxygen		
ASSETS score ^b		
Externalities		
NH ₄ ⁺ discharge (kg N)	268	407
Algae (kg chlorophyll)	7.40	1.06
Financial data		
Revenue (USD)	15,680	15,680 + 3196 = 18,876
Costs (all in USD)	11,448	11,448 + 123 = 11,571
Feed	3927	3927
Seed	5265	5265 + 100 = 5365
Energy (aeration)	2257	2257 + 23 = 2280
Profit (USD)	4232	4232 + 3073 = 7305

^a APP: average physical product = total production/total fry or seed biomass, a measure of return on investment (ROI).

^b ASSETS score colours: blue (better), green, yellow, orange, and red (worse).

of the price differential between SE Asia and western aquaculture is due to labour costs. Moreover, the lower environmental standards and/or enforcement also increase competitiveness.

The FARM model calculates a substantial difference in environmental externalities between gilthead monoculture and IMTA. The mass balance at the end of the culture (Table 2) shows that the ammonia discharge increases by 52% in IMTA, due to the addition of dissolved nutrients from shellfish excretion, but the particulate waste (whether accounted for as chlorophyll or particulate nitrogen) for IMTA is only 14% of the discharge when compared to gilthead monoculture. The reduction in negative externalities due to the co-cultivation of shellfish corresponds to a waste removal of 9 population-equivalents (PEQ), a substitution cost of 354 USD y^{-1} . The addition of seaweeds to the IMTA system would recapture inorganic nutrients, further reducing the environmental impact of combined culture, and potentially providing an extra crop.

In addition to the ecosystem services provided by IMTA, the overall (goods) revenue increases by 20%, from about 15.5 kUSD to 19 kUSD. However, the profit increase is much more striking, since a large part of the revenue from gilthead culture is spent on feed and energy. Profits rise from 4232 USD per cycle to 7305 USD, i.e. a 70% increase.

3.3. Offshore aquaculture

3.3.1. IMTA in offshore sites

The results for the standard offshore culture model are shown in Table 3, for monoculture of finfish and shellfish, and the two combined in IMTA. There are several important differences when compared to pond culture, due to the dilution effect of offshore waters. Concentrations of nutrients and chlorophyll are much lower in the offshore case, even for finfish monoculture. Contrary to the pond simulations, FARM is not using diagenesis to reintroduce recycled materials into

the offshore farm area, because (i) processing of organic matter in the sediment does not feed back to the farm; and (ii) mixing dilutes the waste products of gilthead culture, even at the relatively high densities of 50 ind. m^{-2} . The percentile 90 (P_{90}) for NH_4^+ over the 420 day culture cycle is about 10 $\mu\text{mol L}^{-1}$, an order of magnitude lower than the value of 192 $\mu\text{mol L}^{-1}$ obtained in IMTA pond culture.

There are no dissolved oxygen problems, and therefore no need for aerators, in either of the three (two monoculture and one IMTA) scenarios. Low values were used for environmental drivers of shellfish growth, since these are typical of offshore areas. The mean value for chlorophyll *a* outside the farm was 0.6 $\mu\text{g L}^{-1}$ (C.V. 24%), with similarly low POM (3.2 mg L^{-1} , C.V. 28%, POM/TPM: 0.19). Values of this order are typical of offshore waters, and the combination of finfish and shellfish culture enhances bivalve production by providing additional organic detritus as a food supplement. Over the entire cycle, IMTA provides a 20% increase in oyster production, corresponding to an additional 41 tTFW of harvestable biomass.

In parallel, the oysters provide a substantial ecosystem benefit by removing a (net) population-equivalent (PEQ) loading equal to 5500 people. The organic deposition is reduced by about 7% in IMTA, although the shellfish also add particulate waste to the culture area due to faeces and pseudofaeces. A full mass balance for the cultivation of shellfish in IMTA is shown in Fig. 4.

The main difference between the mass balance for shellfish monoculture and that shown in Fig. 4 is the removal of organic detritus. Whereas the phytoplankton removed is only 0.5% higher than in monoculture, the removal of detritus increases by 3%. If the concentration of phytoplankton (chl) is increased in the water outside the farm, the differences in shellfish yield from monoculture to IMTA become negligible. This is to be expected given the higher energy content of algae (Platt and Irwin, 1973), and selection for phytoplankton in filter-feeding bivalves (Cranford et al., 2011).

Table 3
Simulation results for gilthead and Pacific oysters in offshore culture using the FARM model (all results for a complete production cycle).

Parameter	Finfish monoculture ^a	Shellfish monoculture ^b	Finfish + shellfish IMTA ^c
Production outputs			
Total feed supplied	2204 t dry feed pellets	Natural organics	Organics
Total production (TPP, tonnes FW)	997	202.9	997 + 243.7 = 1240.7
APP	26.6	6.8	26.6 + 8.1
FCR	2.2	–	–
Environmental impact			
Organic deposits (ton POC y^{-1}) ^d	131.9	103.7	122.1
Organic deposits (kg POC $m^{-2} y^{-1}$)	0.88	0.69	0.81
<i>ASSETS eutrophication</i>			
Chlorophyll			
Dissolved oxygen			
ASSETS score ^e			
<i>Positive externalities</i>			
Population equivalents (PEQ)	–	4692	4830
Nutrient credits (kUSD)	–	188	193
Financial data			
Revenue (all kUSD)	2494	1203	2494 + 1412 = 3906
Farmgate value	2494	1015	2494 + 1219 = 3713
Ecosystem services	–	188	193
Costs (all in kUSD)	1889	30	1889 + 30 = 1919
Feed	573	–	573
Seed	1316	30	1316 + 30 = 1346
Profit (kUSD)	604	1173	604 + 1382 = 1986

^a 200 m (wide) × 750 m (long) farm, 10 m depth, 5 sections (each 150 m long); finfish density: 50 ind. m^{-2} (7.5×10^6 fish), 420 day culture period, 10% mortality over cycle; current speed: bidirectional flow over a semi-diurnal cycle, peak spring tide: 0.2 $m s^{-1}$, and peak neap tide: 0.1 $m s^{-1}$.

^b Pacific oysters at a density of 100 ind. m^{-2} (15×10^6 oysters), 10% mortality over cycle, 90 g harvest weight (TFW). All physical parameters as for finfish.

^c Combination of finfish and shellfish as per the data in the above notes. Financial data combines finfish and shellfish, but shellfish data are better than for oyster monoculture because shellfish production is enhanced in IMTA.

^d Due to cultivation only. Natural sedimentation of particles without any cultivation is determined by the model as 722 tPOC y^{-1} , a background accretion rate of 4.9 $mm y^{-1}$.

^e ASSETS score colours: blue (better), green, yellow, orange, and red (worse).

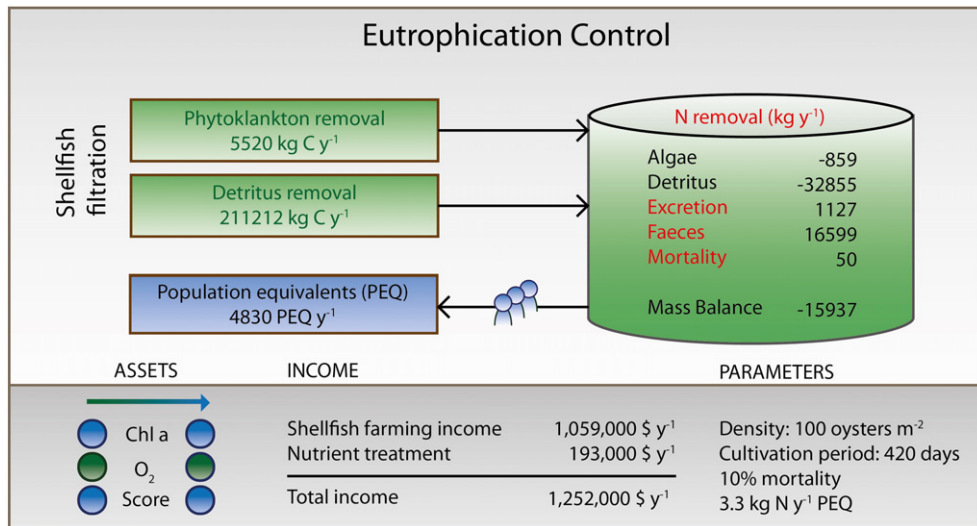


Fig. 4. Mass balance for Pacific oysters cultivated in IMTA with gilthead bream in an offshore farm, determined by means of the FARM model. The ecosystem service provided by the shellfish corresponds to an annual nutrient removal equivalent to almost 5000 PEQ y⁻¹.

The financial outcome of the offshore IMTA scenario is very encouraging, with a proportion of species relatively similar to the pond culture model. However, in ponds, bivalves produce 10% of the fish crop (by weight), and have more of a remedial function, whereas in open water higher densities of fish and shellfish can be cultivated, although much depends on the environmental drivers, including water temperature and the quantity and quality of natural food. The profit from offshore combined culture is over 230% higher than if finfish alone are cultivated, and 68% higher than in shellfish monoculture.

The added value of oysters for nutrient credit trading, due to the role filter-feeding bivalves play in reducing eutrophication symptoms, corresponds to a positive externality supplied by shellfish culture.

The shellfish yield of different sections of the offshore farm is illustrated in Fig. 5. Both the oyster monoculture (dotted) and standard IMTA (dashed) show marked food depletion in the inner section (3)

of the farm, because both chlorophyll and detritus are filtered as water passes through the end sections (1 and 5). An experimental scenario (solid line) is also shown, where the constant finfish density of 50 ind.m⁻² for all sections is changed to 10, 65, 100, 65, 10, for sections 1–5, respectively.

The cultivated fish biomass is unchanged, and the overall finfish harvest (997 tFW) therefore remains the same in this scenario, but the oyster harvest increases to 246.4 tFW, almost 3 t more than the standard IMTA model (Table 3). The extra POM subsidy in the inner sections of the farm provides a more uniform shellfish crop, and eliminates the food depletion effect seen in the other two simulations.

3.3.2. Site selection and current speed

Kapetsky et al. (2012) performed a site selection analysis for offshore aquaculture, using Atlantic salmon and blue mussel (*Mytilus*

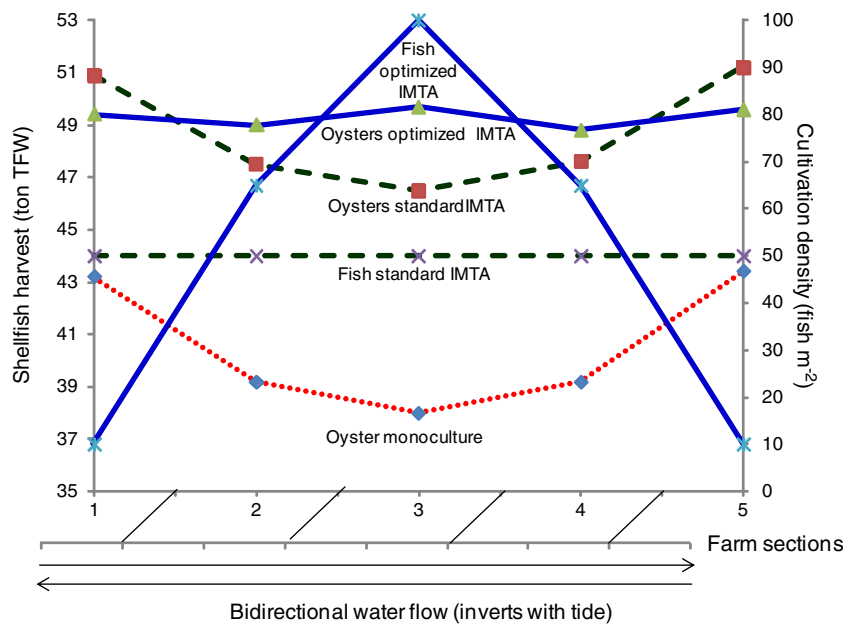


Fig. 5. Optimisation of offshore aquaculture simulated with the FARM model, for a farm split into 5 sections, with the water current alternating in direction between ebb and flood. Three situations are shown (always labelled below each line): (a) dotted line (red) is oyster monoculture; (b) dashed lines (green) are IMTA with the standard model, homogeneous fish density throughout; (c) solid lines (blue) with the same overall fish biomass, but differently distributed to offset shellfish food depletion in the inner part of the farm. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

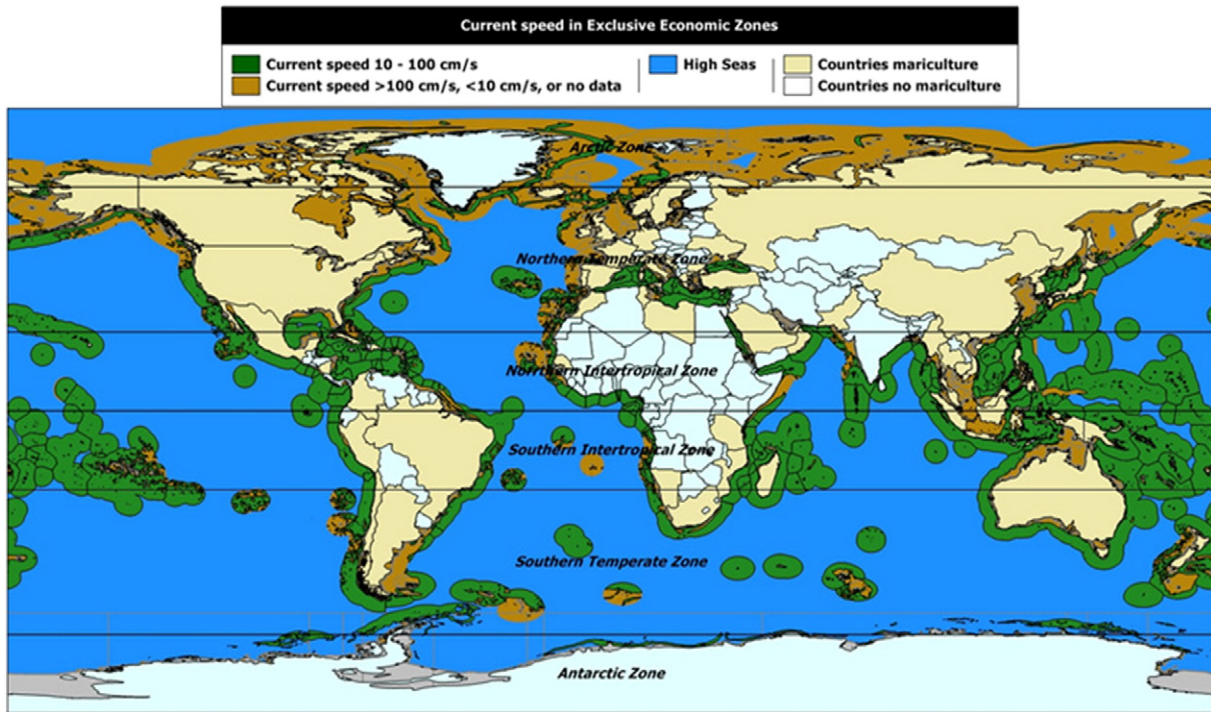


Fig. 6. Marine areas with current speeds suitable for offshore aquaculture, simulated with a Geographical Information System (GIS) for the world ocean. From Kapetsky et al., 2012.

edulis) as indicator species. The biological criteria were sea surface temperature and chlorophyll concentration, both obtained through remote sensing. The water current speed was used as a cut-off point for resistance of culture structures to offshore conditions, with $10\text{--}100\text{ cm s}^{-1}$ defined as an acceptable range (Fig. 6). Although Kapetsky et al. (2012) simulate individual growth of Atlantic salmon by applying the Stigebrandt et al. (2004) model at various locations in the northern and southern hemispheres, no biological effects of current speed were analysed, for lack of a suitable model.

In order to investigate the effects of current speed on finfish aquaculture, we present an analysis of various performance indicators for an offshore gilthead farm (Fig. 7). The farm dimensions and stocking are identical to the previous offshore simulations, but the water current is made to vary (on average) from 0.15 to 1.1 m s^{-1} .

As might be expected on the basis of the results for the individual finfish model (Fig. 3), the farm performs well on all the indicators until the current speed exceeds 0.5 m s^{-1} (the model calculates a sinusoidal oscillation in speed between the peak neap and spring speeds shown). Beyond this point the production (TPP) is severely reduced, and the farm registers a financial loss. This is reflected in the increased FCR, i.e. a higher food supply which is wasted due to the energy consumed by the fish in opposing the higher current speed, and is accompanied by an increase in waste products, exemplified by the ratio of N excreted with respect to harvestable biomass. Contrary to what occurs in the pond culture simulations, there are no noticeable effects on dissolved oxygen due to the higher metabolic costs of cage culture in higher current speed environments. The higher currents provide improved oxygen transport throughout the farm, and

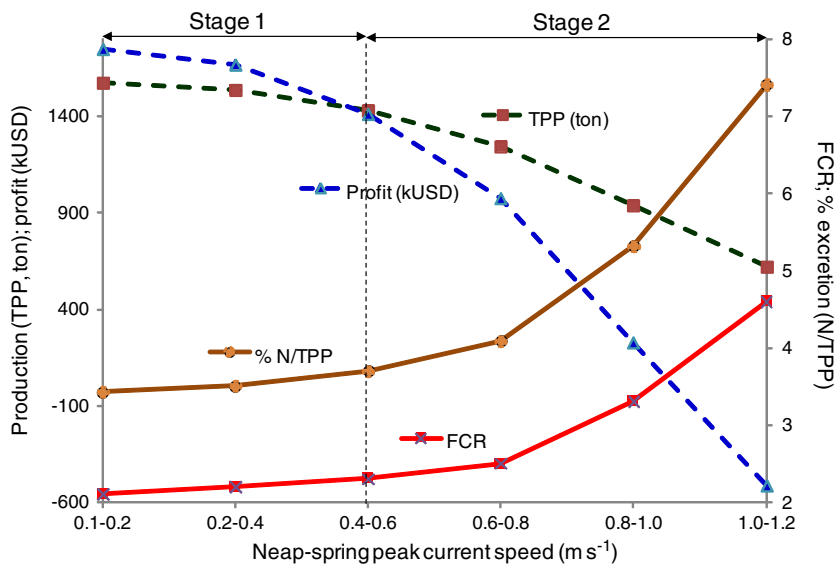


Fig. 7. Effect of current speed on finfish harvestable biomass, FCR, profit, and waste (% nitrogen excreted/biomass produced). Solid lines: left axis; dashed lines: right axis.

the higher consumption becomes an externality imposed on the surrounding environment.

At the population level, it is possible to define two regions (Fig. 7): stage 1 where culture is successful from the production, environmental, and economic perspectives, and stage 2 where this is not the case. One aspect that is not considered in the simulations is the loss of feed from cages due to the higher current speed, which will further degrade performance, shifting the boundary between stages 1 and 2 to the left. Financial calculations in FARM are not considering plant and equipment, leasing, staffing, or transport costs; only the marginal costs of seed, feed, and in onshore culture, aeration, are taken into account.

We suggest that the application of this type of model to offshore culture of salmon, gilthead, bass, and other species such as Cobia (*Rachycentron canadum*), may assist with site selection and improve the zoning obtained with GIS alone by Kapetsky et al. (2012). The combination of GIS and dynamic models such as FARM has previously been described for shellfish culture by Silva et al. (2011), and appears to show promise also on a much broader scale of application.

4. Conclusions

The simulations presented in this work extend the previous application of the FARM model in three ways: firstly, onshore culture in ponds, fully accounting for aeration, water exchange, primary production, and diagenesis is now included; secondly, through the development of a generic finfish individual growth model that accounts for the metabolic cost of growing in a cage under different current speeds in open seawater, we were able to perform a cost–benefit analysis for offshore cultivation; finally, the integration of shellfish and finfish population models in FARM provides a powerful tool for examining the outcomes of IMTA under different environmental conditions.

IMTA began in land-based culture, and in SE Asia it historically developed on land, not just with aquatic species but as part of an agro-aqua economy, variously combining, for instance: rice, tilapia, duck, pigs, shrimp, razor clams, and macroalgae. Although the results from FARM indicate clear benefits of IMTA both on- and offshores, the disadvantages of monoculture are far easier to establish in the simulations for land-based ponds. A fish such as a gilthead bream respire 780 g of oxygen (Fig. 2) in order to reach a market size of 350 g, with obvious consequences on dissolved oxygen in pond water. In offshore culture, environmental impacts of oxygen consumption, ammonia excretion, and waste feed can be simulated only beyond the limits of the farm itself, due to the assimilative capacity of the marine environment (Ferreira et al., in press).

The future integration of aquatic macrophytes in the model framework will extend this analysis to include the value added through the co-cultivation of species that extract inorganic nutrients from the IMTA system. The scale at which such co-cultivation is practised in Asia is possible in part because there is a willing consumer for the different products, including macrophytes. In the west, where different values prevail, it is important to examine the ecological, economic, and social contexts, in order to promote IMTA in the most appropriate way.

One critical aspect of IMTA that has not been addressed in this type of models is biosecurity. A review in Ferreira et al. (in press) discusses ways in which network models of disease spread, based on stochastic approaches of the SIR (susceptible, infected, resistant) type (May and Anderson, 1991), can be used in conjunction with deterministic models such as FARM.

Many problems are ‘solved’ by dealing only with the soluble part of the issue, i.e. changing the boundaries of the problem, and then considering it solved. Simulation models can be very useful within their own bounds of application, but local-scale models are inappropriate for dealing with system-scale carrying capacity for multiple farms, because they cannot account for interactions at that scale. In the same way, issues like biosecurity, and the non-modellable social

component of site selection and carrying capacity, must be fully addressed—they may well correspond to 50% of the problem.

Tools such as FARM, together with a broad range of other models and complementary approaches for carrying capacity and site selection, are essential in order to ensure that the provision of aquacultured food needed for the next generations is not accompanied by systematic environmental damage, often fostered by the legislative and governance divide between the developing and developed world.

Acknowledgements

The authors acknowledge financial support from the EU COEXIST (FP7-KBBE-2009-3-1-2-15) project and the POLIS Litoral FORWARD project. We are grateful to F. Soares for IPIMAR growth data for gilthead bream. J.G. Ferreira is grateful to N. Taylor for insights on biosecurity modelling, and to S.B. Bricker for discussions on the application of the ASSETS eutrophication model to aquaculture. The authors additionally thank three anonymous reviewers for comments on an earlier draft, and R.G. Ferreira for improvements to figures

References

- Aguilar-Manjarrez, J., Kapetsky, J.M., Soto, D., 2008. The potential of spatial planning tools to support the ecosystem approach to aquaculture. *FAO Fisheries and Aquaculture Proceedings*, 17. FAO, Rome.
- Barrett, D.S., Triantafyllou, M.S., Yue, D.K.P., Grosenbaugh, M.A., Wolfgang, M.J., 1999. Drag reduction in fish-like locomotion. *Journal of Fluid Mechanics* 392, 183–212.
- Bavčević, L., Klanjšček, Tin, Karamarko, Vatroslav, Aničić, Ivica, Legović, Tarzan, 2010. Compensatory growth in gilthead sea bream (*Sparus aurata*) compensates weight, but not length. *Aquaculture* 301, 57–63.
- Boyd, C.E., 1998. Pond water aeration systems. *Aquacultural Engineering* 18 (1), 9–40.
- Boyd, C.E., 2009. Advances in technologies and practice for land-based aquaculture systems: ponds for finfish production. In: Burnell, G., Allan, G. (Eds.), *New Technologies in Aquaculture: Improving Production Efficiency, Quality and Environmental Management*. CRC/Woodhead Publishing, Oxford, pp. 984–1009 (Ch. 32).
- Breese Jones, D., 1931. Factors for converting percentages of nitrogen in foods and feeds into percentages of proteins. Circular N° 183. USDA. (August 1931, slightly revised February 1941).
- Bricker, S.B., Ferreira, J.G., Simas, T., 2003. An integrated methodology for assessment of estuarine trophic status. *Ecological Modelling* 169 (1), 39–60.
- Brigolin, D., Dal Maschio, G., Ramapazzo, F., Giani, M., Pastres, R., 2009. An individual-based population dynamic model for estimating biomass yield and nutrient fluxes through an off-shore *Mytilus galloprovincialis* farm. *Estuarine, Coastal and Shelf Science* 82, 365–376.
- Brigolin, D., Pastres, Roberto, Tomassetti, Paolo, Porrello, Salvatore, 2010. Modelling the biomass yield and the impact of seabream mariculture in the Adriatic and Tyrrhenian Seas (Italy). *Aquaculture International* 18, 149–163.
- Byron, C., Costa-Pierce, B.A., 2010. Carrying capacity tools for use in the implementation of an ecosystems approach to aquaculture. *FAO Expert Workshop on Aquaculture Site Selection and Carrying Capacity Estimates for Inland and Coastal Waterbodies*. Institute of Aquaculture, University of Stirling, Stirling, U.K. (6–8 December 2010).
- Byron, C., Bengtson, David, Costa-Pierce, Barry, Calanni, John, 2011. Integrating science into management: ecological carrying capacity of bivalve shellfish aquaculture. *Marine Policy* 35, 363–370.
- Cartaxana, P., Catarino, F., 1997. Allocation of nitrogen and carbon in an estuarine salt marsh in Portugal. *Journal of Coastal Conservation* 3, 27–34.
- Cartaxana, P., Catarino, F., 2002. Nitrogen resorption from senescing leaves of three salt marsh plant species. *Plant Ecology* 159, 95–102.
- Chamberlain, J., 2002. *Modelling the Environmental Impacts of Suspended Mussel (Mytilus edulis) Farming*. Napier University, Edinburgh. (200 pp.).
- Chapra, S.C., 1997. *Surface Water-quality Modelling*. McGraw-Hill, NY.
- Chopin, T., Troell, M., Reid, G.K., Knowler, D., Robinson, S.M.C., Neori, A., Buschmann, A.H., Pang, S.J., Fang, J., 2010. Integrated multi-trophic aquaculture (IMTA)—a responsible practice providing diversified seafood products while rendering biomitigating services through its extractive components. In: Franz, N., Schmidt, C.C. (Eds.), *Proceedings of the Organisation for Economic Co-operation and Development (OECD) Workshop “Advancing the Aquaculture Agenda: Policies to Ensure a Sustainable Aquaculture Sector”*, Paris, France, 15–16 April 2010. Organisation for Economic Co-operation and Development, Paris, pp. 195–217 (426 pp.).
- Corner, R.A., Brooker, A.J., Telfer, T.C., Ross, L.G., 2006. A fully integrated GIS-based model of particulate–waste distribution from marine fish-cage sites. *Aquaculture* 258, 299–311.
- Cranford, P., Ward, J.E., Shumway, S.E., 2011. Bivalve filter feeding: variability and limits of the aquaculture biofilter (Ch. 4) In: Shumway, S. (Ed.), *Molluscan Shellfish Aquaculture and the Environment*. Wiley-Blackwell, pp. 81–124.
- Cromey, C.J., Nickell, T.D., Black, K.D., 2002. DEPOMOD—modelling the deposition and biological effects of waste solids from marine cage farms. *Aquaculture* 214 (1–4), 211–239.
- Di Toro, D., 2001. *Sediment Flux Modelling*. Wiley Interscience. (624 pp.).

- Elliott, J.M., Davidson, W., 1975. Energy equivalents of oxygen consumption in animal energetics. *Oecologia* 19, 195–201.
- Elliott, J.M., Persson, L., 1978. The estimation of daily rates of food consumption for fish. *The Journal of Animal Ecology* 47 (3), 977–991.
- European Commission Fisheries, 2011. Marine species (farmed fish and shellfish) Available: http://ec.europa.eu/fisheries/marine_species/index_en.htm.
- FEAP—Federation of European Aquaculture Producers, 2009. Production and Price Reports of Member Associations of the F.E.A.P. 2001–2008. FEAP Secretariat, Liège, Belgium. (<http://www.aquamedia.org>).
- Ferreira, J.G., Hawkins, A.J.S., Bricker, S.B., 2007. Management of productivity, environmental effects and profitability of shellfish aquaculture—the farm aquaculture resource management (FARM) model. *Aquaculture* 264, 160–174.
- Ferreira, J.G., Anderson, H.C., Corner, R.A., Desmit, X., Fang, Q., de Goede, E.D., Groom, S.B., Gu, H., Gustafsson, B.G., Hawkins, A.J.S., Hutson, R., Jiao, H., Lan, D., Lencart-Silva, J., Li, R., Liu, X., Luo, Q., Musango, J.K., Nobre, A.M., Nunes, J.P., Pascoe, P.L., Smits, J.G.C., Stigebrandt, A., Telfer, T.C., de Wit, M.P., Yan, X., Zhang, X.L., Zhu, M.Y., Zhu, C.B., Bricker, S.B., Xiao, Y., Xu, S., Nauen, C.E., Scalet, M., 2008a. Sustainable options for people, catchment and aquatic resources. In: International Collaboration on Integrated Coastal Zone Management (Ed.), *The SPEAR Project*. IMAR—Institute of Marine Research/European Commission (180 pp. Available: <http://www.biaoqiang.org/documents/SPEAR/book.pdf>).
- Ferreira, J.G., Hawkins, A.J.S., Monteiro, P., Moore, H., Service, M., Pascoe, P.L., Ramos, L., Sequeira, A., 2008b. Integrated assessment of ecosystem-scale carrying capacity in shellfish growing areas. *Aquaculture* 275, 138–151.
- Ferreira, J.G., Sequeira, A., Hawkins, A.J.S., Newton, A., Nickell, T., Pastres, R., Forte, J., Bodoy, A., Bricker, S.B., 2009. Analysis of coastal and offshore aquaculture: application of the FARM model to multiple systems and shellfish species. *Aquaculture* 289, 32–41.
- Ferreira, J.G., Aguilar-Manjarrez, J., Bacher, C., Black, K., Dong, S.L., Grant, J., Hofmann, E., Kapetsky, J., Leung, P.S., Pastres, R., Strand, Ø., Zhu, C.B., 2010. Expert panel presentation V.3. Progressing aquaculture through virtual technology and decision-making tools for novel management. Book of Abstracts, Global Conference on Aquaculture 2010, 22–25 September 2010. FAO/NACA/Thailand Department of Fisheries, Bangkok, Thailand, pp. 91–93.
- Ferreira, J.G., Hawkins, A.J.S., Bricker, S.B., 2011. The role of shellfish farms in provision of ecosystem goods and services (Ch. 1) In: Shumway, S. (Ed.), *Molluscan Shellfish Aquaculture and the Environment*. Wiley-Blackwell, pp. 3–31.
- Ferreira, J.G., Grant, J., Verner-Jeffreys, D., Taylor, N., in press. Modeling frameworks for determination of carrying capacity for aquaculture, in: Meyers, Robert A. (Ed.), *Encyclopedia of Sustainability Science and Technology*. Springer (ISBN: 978-0387894690).
- Food and Agriculture Organization of the United Nations, 2011. Cultured Aquaculture Species Information Programme. <http://www.fao.org/fishery/culturedspecies/search/en>.
- Franco, A.R., Ferreira, J.G., Nobre, A.M., 2006. Development of a growth model for penaeid shrimp. *Aquaculture* 259, 268–277.
- Giles, H., Broekhuizen, N., Bryan, K.R., Pilditch, C.A., 2009. Modelling the dispersal of biodeposits from mussel farms: the importance of simulating biodeposit erosion and decay. *Aquaculture* 291, 168–178.
- Gosch, N.J.C., Pope, Kevin L., Michaletz, Paul H., 2009. Stomach capacities of six freshwater fishes. *Journal of Freshwater Ecology* 24 (4), 645–649.
- Gray, J., 1936. Studies in animal locomotion VI: the propulsive powers of the dolphin. *The Journal of Experimental Biology* 13, 192–199.
- Gray, I.E., 1953. The relation of body weight to body surface area in marine fishes. *The Biological Bulletin* 105, 285–288.
- Grigorakis, K., 2007. Compositional and organoleptic quality of farmed and wild gilthead sea bream (*Sparus aurata*) and sea bass (*Dicentrarchus labrax*) and factors affecting it: a review. *Aquaculture* 272, 55–75.
- Gul, Y., Salim, M., Rabbani, B., 2007. Evaluation of apparent digestibility coefficients of different dietary protein levels with and without fish meal for *Labeo rohita*. *Pakistan Veterinary Journal* 27 (3), 121–125.
- Hernández, J.M., Gasca-Leyva, Eucario, León, Carmelo J., Vergara, J.M., 2003. A growth model for gilthead seabream (*Sparus aurata*). *Ecological Modelling* 165, 265–283.
- Holmer, M., 2010. Environmental issues of fish farming in offshore waters: perspectives, concerns and research needs. *Aquaculture Environment Interactions* 1, 57–70.
- Jobling, M., 1981. Mathematical models of gastric emptying and the estimation of daily rates of food consumption for fish. *Journal of Fish Biology* 19, 245–257.
- Jobling, M., 2003. The thermal growth coefficient (TGC) model of fish growth: a cautionary note. *Aquaculture Research* 34 (7), 581–584.
- Kapetsky, J.M., Aguilar-Manjarrez, J., Jenness, J., 2012. A spatial assessment of potential for offshore mariculture development from a global perspective. FAO Fisheries and Aquaculture Technical Paper. No. 549. FAO, Rome.
- Knight, R.L., Margraf, F. Joseph, 1982. Estimating stomach fullness in fishes. *North American Journal of Fisheries Management* 2 (4), 413–414.
- Libralato, S., Solidoro, C., 2008. A bioenergetic growth model for comparing *Sparus aurata*'s feeding experiments. *Ecological Modelling* 214, 325–337.
- May, R.L., Anderson, R.M., 1991. *Infectious Diseases of Humans: Dynamics and Control*. Oxford University Press, Oxford, U.K. 0-19-854040-X.
- Moo, T.S.Y., undated. Excerpts from Chinese fish culture, by Fan Lee. Contribution No. 459, Chesapeake Biological Laboratory. University of Maryland, Solomons, Maryland, U.S.A.
- National Research Council—NRC, 1993. *Nutrient Requirements of Fish*. National Academy of Science of Washington, Washington, USA.
- Neori, A., Chopin, T., Troell, M., Buschmann, A.H., Kraemer, G.P., Halling, C., Shpigel, M., Yarish, C., 2004. Integrated aquaculture: rationale, evolution and state of the art emphasizing seaweed biofiltration in modern mariculture. *Aquaculture* 231 (1–4), 361–391.
- Niimi, A.J., 1975. Relationship of body surface-area to weight in fishes. *Canadian Journal of Zoology* 53 (8), 1192–1194.
- Nobre, A.M., Ferreira, J.G., Newton, A., Simas, T., Icely, J.D., Neves, R., 2005. Management of coastal eutrophication: integration of field data, ecosystem-scale simulations and screening models. *Journal of Marine Systems* 56, 375–390.
- Nobre, A.M., Ferreira, J.G., Nunes, J.P., Yan, X., Bricker, S., Corner, R., Groom, S., Gu, H., Hawkins, A.J.S., Hutson, R., Lan, D., Lencart e Silva, J.D., Pascoe, P., Telfer, T., Zhang, X., Zhu, M., 2010. Assessment of coastal management options by means of multilayered ecosystem models. *Estuarine, Coastal and Shelf Science* 87, 43–62.
- Nunes, J.P., Ferreira, J.G., Bricker, S.B., O'Loan, B., Dabrowski, T., Dallaghan, B., Hawkins, A.J.S., O'Connor, B., O'Carroll, T., 2011. Towards an ecosystem approach to aquaculture: assessment of sustainable shellfish cultivation at different scales of space, time and complexity. *Aquaculture* 315, 369–383.
- Olesen, I., Myhr, A.I., Rosendal, G.K., 2010. Sustainable aquaculture: are we getting there? Ethical perspectives on salmon farming. *Journal of Agricultural and Environmental Ethics* 24, 381–408.
- Oliveira, A.C.B., Martinelli, L.A., Moreira, M.Z., Cyrino, J.E.P., 2008. Determination of apparent digestibility coefficient in fish by stable carbon isotopes. *Aquaculture Nutrition* 14, 10–13.
- Palma, J., Andrade, J.P., Paspatis, M., Divanach, P., Kentouri, M., 1998. Morphometric characters in gilthead sea bream, *Sparus aurata*, red porgy, *Pagrus pagrus* and their hybrids (*Sparidae*). *Italian Journal of Zoology* 65, 435–439.
- Piedecausa, M.A., Aguado-Giménez, F., Cerezo-Valverde, J., Hernández-Llorente, M.D., García-García, B., 2010. Simulating the temporal pattern of waste production in farmed gilthead seabream (*Sparus aurata*), European seabass (*Dicentrarchus labrax*) and Atlantic bluefin tuna (*Thunnus thynnus*). *Ecological Modelling* 221, 634–640.
- Platt, T., Irwin, B., 1973. Caloric content of phytoplankton. *Limnology and Oceanography* 18 (2), 306–310.
- Requena, A., Fernández-Borrás, J., Planas, J., 1997. The effects of a temperature rise on oxygen consumption and energy budget in gilthead sea bream. *Aquaculture International* 5, 415–426.
- Silva, C., Ferreira, J.G., Bricker, S.B., DelValls, T.A., Martín-Díaz, M.L., Yañez, E., 2011. Site selection for shellfish aquaculture by means of GIS and farm-scale models, with an emphasis on data-poor environments. *Aquaculture* 318, 444–457.
- Simas, T.C., Ferreira, J.G., 2007. Nutrient enrichment and the role of salt marshes in the Tagus estuary (Portugal). *Estuarine, Coastal and Shelf Science* 75, 393–407.
- Skogen, M.D., Eknes, M., Asplin, L.C., Sandvik, A.D., 2009. Modelling the environmental effects of fish farming in a Norwegian fjord. *Aquaculture* 298, 70–75.
- Steinhausen, M.F., Steffensen, J.F., Andersen, N.G., 2010. The effects of swimming pattern on the energy use of gilthead seabream (*Sparus aurata* L.). *Marine and Freshwater Behaviour and Physiology* 43 (4), 227–241.
- Stigebrandt, A., Aure, J., Ervik, A., Hansen, P.K., 2004. 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* 234, 239–261.
- Troell, M., Joyce, Alyssa, Chopin, Thierry, Neori, Amir, Buschmann, Alejandro H., Fang, Jian-Guang, 2009. Ecological engineering in aquaculture—potential for integrated multi-trophic aquaculture (IMTA) in marine offshore systems. *Aquaculture* 297 (1–4), 1–9.
- Tucker, C., 2005. Pond aeration. SRAC Publication No. 3700. Southern Regional Aquaculture Center.
- Verbeke, W., Sioen, I., Brunsø, K., De Henauw, S., Van Camp, J., 2007. Consumer perception versus scientific evidence of farmed and wild fish: exploratory insights from Belgium. *Aquaculture International* 15, 121–136.
- Vogel, S., 1994. *Life in moving fluids, The Physical Biology of Flow* 2nd edition. Princeton University Press, N.J. (467 pp.).
- Wassef, E.A., Shehata, M.B., 1990. Biochemical composition of gilthead bream *Sparus aurata* L. from Lake Bardawil (Egypt). *JKAU Marine Sciences* 1, 55–65.
- Webb, P.W., 1975. Hydrodynamics and energetics of fish propulsion. *Bulletin of the Fisheries Research Board of Canada* 190, 1–158.
- Yilmaz, Y., Arabaci, M., 2010. The influence of stocking density on growth and feed efficiency in gilthead seabream, *Sparus aurata*. *Journal of Animal and Veterinary Advances* 9 (8), 1280–1284.
- Zhang, J., Hansen, P.K., Fang, J., Wang, W., Jiang, Z., 2009. Assessment of the local environmental impact of intensive marine shellfish and seaweed farming—application of the MOM system in the Sunco Bay, China. *Aquaculture* 287, 304–310.