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Abstract: Mollusc culture is one of the most important types of mariculture, with suspension feeding bivalves being among the most cultivated organisms. This is a passive type of culture with bivalves feeding on phytoplankton and detritus. In the last years, there has been a growing concern about carrying capacity (CC) of natural ecosystems for bivalve culture, because of decreases in growth rates and mass mortalities due to overstocking. CC may be evaluated at several spatial scales, ranging from the ecosystem scale to the scale of the cultivation leases and limited by different processes. Several methods have been proposed for CC estimation. The simplest are based on average properties integrated over various time scales, like water renewal rate, phytoplankton primary production and bivalve clearance rate. If the time scale of the former two processes is larger than the time scale for bivalve filtration than, bivalve standing stock is over ecosystem CC. More complex approaches are based on ecosystem box modelling or coupled physical-biogeochemical models. The objective of this work is to evaluate CC for mussel rafts in Galician Rias as a function of mussel loads and current velocities. For this purpose an analytical model was developed and used to find conditions that maximize raft production. Obtained results suggest that CC at the raft scale has not been exceeded by current culture practices. However, it does not seem advisable to increase mussel

loads per raft. Therefore, any possible increase in mussel production should be considered at a higher spatial scale.

MODELLING LOCAL FOOD DEPLETION EFFECTS IN MUSSEL RAFTS OF GALICIAN RIAS

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Abstract

Mollusc culture is one of the most important types of mariculture, with suspension feeding bivalves being among the most cultivated organisms. This is a passive type of culture with bivalves feeding on phytoplankton and detritus. In the last years, there has been a growing concern about carrying capacity (CC) of natural ecosystems for bivalve culture, because of decreases in growth rates and mass mortalities due to overstocking. CC may be evaluated at several spatial scales, ranging from the ecosystem scale to the scale of the cultivation leases and limited by different processes. Several methods have been proposed for CC estimation. The simplest are based on average properties integrated over various time scales, like water renewal rate, phytoplankton primary production and bivalve clearance rate. If the time scale of the former two processes is larger than the time scale for bivalve filtration than, bivalve standing stock is over ecosystem CC. More complex approaches are based on ecosystem box modelling or coupled physical-biogeochemical models. The objective of this work is to evaluate CC for mussel rafts in Galician Rias as a function of mussel loads and current velocities. For this purpose an analytical model was developed and used to find conditions that maximize raft production. Obtained results suggest that CC at the raft scale has not been exceeded by current culture practices. However, it does not seem advisable to increase mussel loads per raft. Therefore, any possible increase in mussel production should be considered at a higher spatial scale.

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Introduction

Carrying capacity (CC) for bivalve cultivation has been the subject of several research projects, stimulated by declines of growth and survival rates in areas where bivalves are abundant. CC estimates for different ecosystems that may be used to regulate aquaculture practices, have been published (Bacher et al., 1998; Ferreira et al. 1998; Duarte et al. 2003). In areas where aquaculture of molluscs is incipient, farmers need to know the maximal densities that may be cultivated in order to obtain maximum economic benefit (Héral, 1993). Overcrowded culture conditions may lead to an increased incidence of shellfish diseases (Dijkema and van Stralen, 1989). Additionally, environmental agencies could benefit with the knowledge of how to regulate bivalve aquaculture in order to prevent ecological impacts. High culture biomass may result in a negative impact on local environment through an increase on organic loading and consequent increased oxygen demand beneath culture leases, phytoplankton biomass reduction and increased nutrient turnovers (Prins et al., 1998; Smaal et al., 2001), compromising the sustainability of culture environments. On the other hand, bivalve growth may assist in eutrophication control through nitrogen and phosphorus removal from the water column (Shpigel, 2005).

CC has been defined, with respect to bivalve culture, as the maximum standing stock that may be kept within a particular ecosystem to maximize production without negatively affecting growth rate (Carver and Mallet, 1990). Alternatively, and more recently, CC has been described as the standing stock at which the annual production of the marketable cohort is maximized (Bacher et al., 1998; Smaal et al. 1998), or the total bivalve biomass supported by a given ecosystem as a function of the water residence time, primary production time and bivalve clearance time (Dame and Prins, 1998). These definitions are focused on target species, despite a growing tendency in Eastern Countries for "ecological aquaculture" that is based on multi-species culture where producers and consumers are grown together in order to facilitate nutrient recycling (e.g. Fang et al., 1996; Grant, 1999). In this approach, the objective is not only to maximize production, but also to optimize species combinations and distributions in such a way as to reduce the environmental impacts of aquaculture. The growing appreciation of multiple ecosystems' services and the need for sustainable management has lead ecologists to model the many interactions between and among species and between species and their environment. A general definition of CC at the ecosystem level could be "the level to which a process or variable may be changed within a particular ecosystem, without driving its structure and function over certain acceptable limits, established in terms of water quality and/or other parameters" (Duarte, 2003).

There are several examples where carrying capacities for bivalve cultivation have been exceeded by non-sustainable practices. These include the bay of Marénnes-Óleron (France), where oyster (*Crassostrea gigas*) growth has been significantly reduced with increased stock densities over the years (Héral, 1993; Raillard and Ménesguen, 1994). Similarly, mussel's (*Mytilus edulis*) growth in the Oosterschelde estuary (Netherlands) has been compromised by increased standing stocks (Smaal et al., 2001).

CC estimates depend on available data and knowledge on bivalve ecophysiology - a field where there were considerable progresses over the last years. Generally, bivalve growth is calculated using scope for growth (*SFG*). *SFG* depends on clearance, filtration, ingestion, absorption, respiration and excretion rates. These rates are computed as a function of food quantity and quality, temperature and physiologic parameters. In the literature it is possible to find equations and parameters describing the ecophysiology of several species - e.g. Barillé et al. (1997) and Ren and Ross (2001) for oyster (*C. gigas*); Hawkins et al. (1998) for clam (*Cerastoderma edule*), oyster (*C. gigas*) and mussel (*Mytilus edulis*); Scholten & Smaal (1998) for mussel (*Mytilus edulis*); Hawkins et al. (1999) for green-lipped mussel (*Perna canaliculus*); Hawkins et al. (2002) for scallop (*Chlamys farreri*); Navarro et al. (1991), Babarro et al. (2000), Figueiras et al. (2002) and Fernandez-Reiriz et al. (2007) for mussel (*Mytilus galloprovincialis*).

The problem of CC may be approached at several spatial scales, ranging from a whole ecosystem, e.g a bay or an estuary, through a particular cultivation area, including several cultivation units, to a cultivation unit, such as a raft. Different processes and variables may limit CC at these different scales. At the ecosystem scale, bivalve production is more likely to be limited by phytoplankton production, whereas at smaller scales, physical mixing is more likely to be the limiting factor. For example, at the scale of a mussel raft, it is expectable that mussels clear the water faster than phytoplankton divides. Therefore, feeding depends upon food input from adjacent water (Duarte et al., 2005).

The methods used for CC estimation may be divided into two main categories: calculation budgets and mathematical models. Models may be divided in box models, coupled physical-biogeochemical models and local depletion models. For a revision on these different approaches see Duarte (2003).

The focus of the present work will be on local depletion models (e.g. Grant et al., 1998). These models are usually applied to the cultivation unit scale, which is divided in several cells, allowing modelling of seston supply decay downstream, as a result of bivalve feeding. Examples may be found in Pilditch et al. (2001), Bacher et al. (2003), Aure et al. (2007) and in Ferreira et al. (2007). Local depletion models are forced by current velocities at the boundaries, solving the transport equation (1), including those boundary conditions and local sources and sinks.

$$\frac{dS}{dt}+\frac{\partial(uS)}{\partial x}+\frac{\partial(vS)}{\partial y}+\frac{\partial(wS)}{\partial z}=A_x\frac{\partial^2 S}{\partial x^2}+A_y\frac{\partial^2 S}{\partial y^2}+A_z\frac{\partial^2 S}{\partial z^2}+Sources-Sinks \quad (1)$$

Where,

u, v and *w* - current speeds in *x*, *y* and *z* directions (m s^{-1}); *A* – Coefficient of eddy diffusivity (m^2 s^{-1}); *S* – A conservative (*Sources* and *Sinks* are null) or a non conservative variable in the respective concentration units.

Local depletion models emphasize the potential importance of altering the geometry of cultivation structures to optimize seston supply. In these models, there is no feedback from the cultivation units to the ecosystem. However, they may be very useful, among other things, to parameterize local depletion effects at larger scale models. Bacher et al (2003) developed a software tool that integrates a local depletion model with a Geographical Information System (GIS) interface for Sungo Bay (People's Republic of China). This tool allows the user to choose a particular area on the GIS and run it using the model to analyze its production potential. A similar approach was further developed by Ferreira et al. (2007) to screen for economically optimal production, using marginal analysis. The same authors also provided a tool to examine interactions between shellfish aquaculture and eutrophication.

Mussel raft culture takes place in Galician Rías since 1946. It started with 125 m^2 rafts and evolved to 500 m^2 rafts (Pérez Camacho and Labarta, 2004). After a period of rapid increase in raft numbers, between 1960 and 1970 (Pérez Camacho et al., 1991), an increase in raft area took place, probably, with the aim of increasing mussel production. Empirical evidence (data presented by Pérez Camacho et al. (1991)), as well as common sense, suggests that larger rafts allow larger yields. However, it is expectable that over a certain raft size, part of the mussels may be food limited, specially, under low current velocities, as water flowing beneath the raft is cleared from food particles by mussels located upstream, with potential negative implications on raft yields. This leads to the need of optimizing raft dimensions and to understand whether it is better to invest in a larger number of smaller rafts or a smaller number of larger rafts. Furthermore, in order to optimize mussel production at the ecosystem scale, it is important to quantify local food depletion effects. Therefore, the objectives of the present work are to:

1) Develop a carrying capacity model (CC) based on local food depletion effects at mussel rafts;
2) Use the model to estimate raft CC as a function of water flow, food concentration, mussel physiology and raft dimensions.

Methodology

Study area

Galician Rias are flooded tectonic valleys on the northwest of the Iberian Peninsula (Fig. 1). They are the ground for the highest mussel production in Europe – 250 X 10^6 kg year^{-1}. This production is based on floating rafts. At present, there are over six thousand mussel rafts in Galician Rias (Table 1), with an area of 500 m^2, with 500 hanging ropes 12 m long (Fig. 2) (Figueiras et al., 2002). The cultivation process may be divided in three stages: (i) obtaining the seed; (ii) growing the seed; (iii) thinning out the juveniles and growing them until commercial (adult) size. The different duration of the commercial cycle (one year) and the cultivation cycle (16 – 18 months) leads to the frequent need of keeping different size mussels in the same rafts.

Conceptuals

The model presented here is a local depletion model and was conceived to estimate carrying capacity (CC) of mussel rafts as a function of water flow, food concentration, mussel physiology and raft dimensions. It was designed to estimate CC at the cultivation leases scale, not accounting for feedbacks between local food depletion effects and ecosystem properties.

Fig. 2 is a simplified scheme of a mussel raft of the type used in Galicean Rias, showing the transport of food in one horizontal dimension. Given the area of mussel rafts (500 m^2) it is assumed that bivalve food supply depends on advection of suspended particles from adjacent waters and that food production within the rafts is negligible. Under this assumption, food concentration changes, as water flows across a mussel raft, may be described by equation 2:

$$Q\frac{dC}{dx} = -CR.C.N\left[ML^{-1}T^{-1}\right] \tag{2}$$

Where,

Q – Water flow [$L^{3}T^{-1}$]; C – Food concentration [ML^{-3}]; x – Distance [L]; CR – Clearance rate of an average mussel [$L^{3}T^{-1}mussel^{-1}$]; N – Mussel number per unit of length [$mussel\ L^{-1}$] (obtained by dividing the total number of mussels in a raft by the distance travelled by the water within the raft).

This equation holds for those situations when water flows perpendicular to the sides of mussel rafts. The solution of equation 2 is:

$$C_x = C_0.\exp\left(-\frac{CR.N.x}{Q}\right) \tag{3}$$

Where C_0 and C_x are food concentrations before water enters the mussel raft and at a distance x within the raft, respectively. Studies of raft culture demonstrate that there is local seston depletion due to suspension feeding, with chlorophyll reduction up to 60% as it passes though the rafts (Pérez Camacho et al., 1991). The same authors state that production on the parts of the raft located upstream, tend to be higher than at the opposite side. This probably holds for those rafts that have only one anchoring system, which allows them to rotate with the tides. Filtration rate (FR) at distance x from water entrance into the mussel raft [$MT^{-1}mussel^{-1}$] may be calculated from the product of *CR* by equation 3, obtaining equation 4:

$$FR_x = CR.C_0.\exp\left(-\frac{CR.N.x}{Q}\right) \qquad (4)$$

Assuming no pseudo faeces production, as is the case in Galicean Rías, due to low suspended matter loads (Figueiras et al., 2002) ingestion rate $IR = FR$. According to (4) *IR* increases asymptotically with *Q* towards $CR.C_0$ and decreases exponentially with *N* towards zero.

An average $\overline{IR}$, integrated over the water path within the raft may be calculated as:

$$\overline{IR} = \frac{CR.C_0.\int_{x0}^{x1}\exp\left(-\frac{CR.N.x}{Q}\right)dx}{\Delta x} \Leftrightarrow \qquad (5)$$
$$\frac{C_0.Q\left[-\exp\left(-\frac{x1.CR.N}{Q}\right)+\exp\left(-\frac{x0.CR.N}{Q}\right)\right]}{N.\Delta x}$$

Mussel scope for growth (*SFG*) may be obtained from 6:

$$SFG = \overline{IR}.AE - R \qquad (6)$$

Where,

AE is absorption efficiency and *R* respiration.

Total scope for growth (*TSFG*) (also referred as production) may be calculated by inserting equation 5 and multiplying the result by *N*:

$$TSFG = \left\{ \frac{C_0 \cdot Q\left[-\exp\left(-\frac{x1.CR.N}{Q} \right) + \exp\left(-\frac{x0.CR.N}{Q} \right) \right]}{N.\Delta x} AE - R \right\} N \qquad (7)$$

The value of *N* that maximizes *TSFG* may be obtained by derivation of *TSFG* with respect to *N*:

$$\frac{dTSFG}{dN} = \frac{\begin{array}{l} C_0 \cdot Q\left[-\exp\left(-\frac{x1.CR.N}{Q} \right)\left(-\frac{x1.CR}{Q} \right) + \exp\left(-\frac{x0.CR.N}{Q} \right)\left(-\frac{x0.CR}{Q} \right) \right] N.\Delta x - \\ C_0 \cdot Q\left[-\exp\left(-\frac{x1.CR.N}{Q} \right) + \exp\left(-\frac{x0.CR.N}{Q} \right) \right] \Delta x \end{array}}{(N.\Delta x)^2} AE.N + \frac{C_0 \cdot Q\left[-\exp\left(-\frac{x1.CR.N}{Q} \right) + \exp\left(-\frac{x0.CR.N}{Q} \right) \right]}{N.\Delta x} AE - R \qquad (8)$$

Assuming $x0 = 0$,

$$\frac{dTSFG}{dN}=\frac{C_0{\cdot}Q\left[-\exp\left(-\frac{x1.CR.N}{Q}\right)\left(-\frac{x1.CR}{Q}\right)\right]N.\Delta x-C_0{\cdot}Q\left[-\exp\left(-\frac{x1.CR.N}{Q}\right)+1\right]\Delta x}{(N.\Delta x)^2}AE.N+\frac{C_0{\cdot}Q\left[-\exp\left(-\frac{x1.CR.N}{Q}\right)+1\right]}{N.\Delta x}AE-R \tag{9}$$

The number of mussels per metre that maximizes production is therefore:

$$N=-\frac{\ln\left(\frac{R.\Delta x}{C_0{\cdot}AE.x1.CR}\right)}{\left(\frac{x1.CR}{Q}\right)} \tag{10}$$

The corresponding total number of mussels within the raft is obtained from (11):

$$N_{total}=N.\Delta x \tag{11}$$

The product of *SFG* by N_{total} is raft production. The relationship between *Production*, flow rate and bivalve abundance is depicted in Figs. 3c, 4c and 4c, showing the parabolic relationship between the former and abundance, described in Bacher et al. (1998), and the asymptotic increase of the former with current speed (a surrogate for flow rate).

The main difference between the models of Grant et al. (1998), Pilditch et al. (2001), Bacher et al. (2003) and Ferreira et al. (2007) and the one presented here if that whereas the former are based on a numerical solution of a transport equation (cf. – Introduction), where the cultivation leases are discretized into boxes, the latter is based on an analytical model. In most situations, it is not possible to find an analytical solution to the CC problem. For example, when bivalve biomass density changes across model domain and over time, as in models that simulate bivalve growth, there are feedbacks between biomass and food consumption that prevent obtaining an analytical solution. However, in the present case, the model was designed for application over short time and spatial scales, when it is reasonable to assume that mussel biomass density does not change significantly. In this situation, it is possible to assume that bivalve feeding is a constant flux and therefore obtain a relatively simple analytical solution. The main advantage of the current approach is the easiness to obtain an estimate of CC, once the necessary parameters are introduced into equation 10, using a simple spreadsheet. To achieve the same goal with a numerical model, it is necessary to perform several simulations under different bivalve densities and to find, iteratively, the value that maximizes *TSFG*. A similar approach to the one described in this work was based on a model by Incze et al. (1981) and applied by Sarà & Mazzola (2004), to calculate the number of rafts that maximise food ingestion by bivalves. In this model, a geometric decrease in food concentration across each raft was assumed, in accordance with the exponential decaying function presented above (equation 2). An analytical solution to the problem was also obtained. This model differed from the one presented herein, not only because it was applied to a different spatial scale (an array of rafts), but also because it did not include a *SFG* maximizing function. The focus of the present work is optimizing mussel production at the raft level.

The main assumptions of the approach developed in this work are: (i) Mussel size homogeneity in the rafts; (ii) Unidirectional flow across the rafts. In spite of the size of the mussel cultivation rafts at Galician Rías (500 m^2) (Figueiras et al., 2002), the assumption of mussel size homogeneity across the rafts does not always holds, because some farmers choose to separate bivalves at different cultivation phases by different rafts, whereas some keep different cultivation phases at the same raft. In the last case, the model may be applied separately to different parts of the raft. Regarding the assumption of a unidirectional flow, it is a common place in local depletion models (e.g. Bacher et al. (2003) and Ferreira et al. (2007)), over spatial scales on the order of hundreds to thousands of meters, therefore it seems more acceptable at the scale of a cultivation raft. This assumption may not hold in cases when strong turbulence develops between mussel ropes. However, assuming that turbulence will be isotropic, the average behaviour across the direction perpendicular to the dominant flow will be similar to that described by equation 2. Some preliminary experimental evidence suggests that lateral flow maybe important in mussel rafts (Blanco et al., 1996) contradicting, at least partially, the above assumption. However, in this case, the model presented here behaves conservatively, leading to an underestimate of CC, since it will not take into account lateral seston fluxes.

Calculations

Several calculations were performed with the above equations, to analyse the dependence of $\overline{IR}$, SFG and raft production on food concentration, current speeds - used as a surrogate for flow rate – and mussel biomass. Equation 10 was used to obtain estimates of the mussel number maximizing raft production for seeds, juveniles and adults and compare these estimates with actual data. In this case, it was assumed only one type of mussels per raft.

Another set of calculations was carried out for hypothetical rafts containing all mussel types in different layouts: seeds, juveniles and adults, (i) along the downstream direction; (ii) along the upstream direction; (iii) parallel to the flow. In these cases, the "normal" (Labarta et al, 2004) number of mussels was assumed (2500, 1000 and 700 mussels per metre of rope for seeds, juveniles and adults, respectively) and several combinations of current speeds and food concentrations tested to compute *SFG* for each mussel type. It was assumed that seeds occupy 14% of raft area, whereas juveniles and adults occupy 43% each. In cases (i) and (ii) food concentration at the upstream limit of the raft area allocated to each mussel class was calculated using equation 3. Equation 7 was used for each class to evaluate production.

Finally, calculations were made after the "best" of the cultivation layouts described in the previous paragraph was achieved in terms of raft production, to analyse the possibility of increasing the number of ropes per raft. Therefore, raft production was calculated as a function of increasing number of ropes with mussels, keeping the number of mussels per rope constant. In these calculations, two approaches were followed: (i) assuming that current speed within the rafts is not affected by rope density; (ii) reducing within raft current speed and flow as a function of drag exerted by mussel ropes. To estimate drag effects, the approach described by Jackson and Winant (1983) for a kelp bed and applied to Saldanha Bay mussel raft culture by Grant et al. (1998), was followed. Drag (D) exerted by individual mussel ropes is described by equation 12:

$$D = C_D \rho u^2 d l ropes \qquad (12)$$

C_D – Drag coefficient (0.5 for flow approaching a cylinder); ρ – seawater density (1.03 g cm^{-3}); u – current velocity (variable); d – diameter of the cluster of mussels surrounding the rope (c.a. 12 cm); l – rope length (12 m); *ropes* – rope number per m^2 (c.a. 0.9).

From equation 12 it is possible to estimate drag per unit area within the raft as $0.75u^2$. Increasing rope density leads to increased drag. Since drag scales as u^2, it is possible to estimate the relative decrease in current velocity as a function of a drag increase.

For all calculations the following conditions were used:

(i) A *CR* of 2.7 L/h/mussel for a standard 0.3 g meat DW individual (Fernandez Reiriz and Labarta, 2004).

(ii) An *AE* of 0.59 was calculated from *AE* = 0.95-0.18/*OCI*. *OCI* stands for organic contents of ingested matter, where a value of 0.5 was assumed (Fernandez Reiriz and Labarta, 2004).

(iii) A respiration rate of 0.21 mL / h / mussel was considered for a standard 0.3 g meat DW mussel (Fernandez Reiriz and Labarta, 2004).

(iv) Allometric coefficients of 0.62 and 0.75 were used for *CR* and respiration, respectively (Fernandez Reiriz and Labarta, 2004).

(v) To convert $\overline{IR}$ and *SFG* from mass to energy units a value of 23500 J / g was assumed for mussel energetic contents (Bayne et al., 1985).

(vi) To convert from mL of oxygen respired to energy units a value of 20.36 J / mL oxygen was used (Bayne et al., 1985).

All values are well within ranges observed in Galician Rias (Fernandez Reiriz and Labarta, 2004).

Results and discussion

In the next paragraphs obtained results will be presented and discussed in the order described above (cf. – Methodology – Calculations).

The solutions of equations 5 – 7, regarding raft average $\overline{IR}$, SFG and raft production, are presented in Figs. 3, 4 and 5 for seed, juvenile and adult mussels, respectively. Results obtained show that $\overline{IR}$ increases asymptotically with current speed and decreases exponentially with biomass (Figs. 2a, 3a and 4a). This decrease is more noticeable for results obtained with juvenile and adult mussels due to their higher clearance rates. Under high current speeds and low mussel stocks, the time scale for filtration (e.g. over 20 minutes for "normal" seed stocks of 2500 mussels per meter of rope (cf. – Methodology – calculations)) is less that the time scale for water renewal (less than 4 minutes for higher current speeds (0.11 m s^{-1})), whereas the opposite is true at low current velocities, leading to possible food limitation. Similar trends are apparent for SFG (Figs. 2b, 3b and 4b), with negative values for juvenile and adult mussels, when low current velocities combine with high mussel biomasses. Mussel production (Figs. 2c, 3c and 4c) exhibits a parabolic response to mussel biomass under low current velocities. This response is nearly linear, in the opposite situations. The parabolic response results from the compromise between mussel individual growth and total growth – when mussel number increases, under food limitation, individual growth reduces but, within certain limits, total production tends to increase due to the larger number of individuals. However, after individual growth is reduced above a threshold, total production decreases (Bacher et al., 1998).

Under current speeds ranging between 0.01 and 0.11 m s^{-1} and *POM* between 0.25 and 1.0 mg/L, the number of mussels that maximizes raft production (equation 10), assuming only one mussel age class per raft, range between near zero till some tens of thousands for seeds, and several thousands for juveniles and adults (Fig. 6). Under a current speed and *POM* concentration representative of "normal" conditions observed near cultivation rafts within the Galician Rias (Perez-Camacho and Labarta, 2004) – up to 2-3 cm s^{-1} and 0.5 mg L^{-1}, respectively – predicted seed, juveniles and adult values per metre of cultivation rope are within the same order of magnitude as those used in the cultivation rafts: a few thousands for seeds and several hundreds for juveniles and adults. Considering that in the model, these mussel abundances are those that maximize total *SFG*, it is apparent that under the mentioned "normal" conditions, raft CC has not been exceeded. It is noteworthy that in these calculations, self-thinning effects at the rope level, related to the multilayer matrices formed by the mussels (Guiñez and Castilla, 1999), were not taken into account. Mussel number was predicted under the assumption that intraspecific competition for food occurs only at the raft level.

Figs. 7, 8 and 9 synthesize results obtained with equation 7 for three different cultivation scenarios as described above (cf. – Methodology – Calculations). It is apparent that under very low food concentrations and current speeds, mussels located downstream may exhibit negative production values. Average production estimates integrated over all food concentrations, current speeds and mussel classes were 0.78, 0.70 and 0.12 kg meat DW h^{-1} for the scenarios represented in Figs 7, 8 and 9, respectively. Therefore, when seed mussels are located upstream, receiving more food, raft production is larger than when adult mussels occupy that position. This may be explained by the fact that adult mussels clear the water very quickly and less food remains for mussels located downstream. When a parallel disposition is used in relation to the flow, with all mussel classes receiving food without prior filtration, production is reduced because each class receives a smaller proportion of inflowing water (proportional to the percentage of the raft they occupy). Therefore, it is apparent that disposing different mussel classes in the seeds, juveniles and adults sequence, within cultivation densities normally used in Galician Rías, it seems a good option in terms of raft production, when the rafts are allowed to rotate with seeds always located at the upstream end.

Considering this mussel sequence, raft production was calculated as a function of increasing number of ropes (cf. – Methodology – Calculations). Results obtained are presented in Fig. 10, where mussel production is plotted as a function of rope density. The choice of plotting adult mussel production together with overall production is justified by the fact that, according to preliminary calculations, adult mussel *SFG* is the most sensitive to increases in raft standing stocks. Increasing rope density from 0.9 (normal value) till 4.7 per m^2, leads to a 5-fold increase in drag and a corresponding $5^{0.5} = 2.2$ decrease in current speed and current flow. When drag is considered, even a 1.5 fold increase in rope density leads to a reduction on adult mussel production (located at the downstream end of the raft). Increasing rope density over 2-times its normal value, may lead to a decrease in overall production. When drag effects are neglected, adult mussel production decreases for rope densities above 1.5 times its normal value. However, overall production may increase until a rope density 3 times its normal value.

From the results obtained in this work, it is apparent that mussel number per raft is close to raft CC. Any increase in rope density may lead to a decrease in adult mussel growth. In fact, the predicted decrease could be even more important if other suspension feeders (epifauna fouling) that may be present on the ropes were considered, such as sponges and barnacles. According to Pérez Camacho et al. (1991), the intensive filtering activity of mussels and their dominance in the raft fauna (95% of total biomass) outcompetes most filter feeders. The importance of these potentially competing organisms was discussed by Grant et al. (1998) in the light of available literature. However, the cited authors did not reach a clear conclusion, suggesting the need for further research. According to the same authors, rope density in culture rafts in Saldanha Bay is c.a. 3 ropes m^{-2}, with average current speeds of 0.075 m s^{-1}- well within the ranges observed in Galician Rias. In Saldanha Bay, raft size is smaller (c.a. 11 X 14 m) than values considered in this work, leading to shorter time scales of water renewal, which may support a large rope density. In fact, rope density reached 4 ropes/m^2 in Galicia, at the beginning of mussel farming activity in 1946, when raft area was solely 125 m^2 (Pérez Camacho and Labarta, 2004).

In order to get some insight into the potential effects of raft size on mussel production, calculations were carried out with equation 10, to estimate the number of mussels optimising overall raft production for rafts with areas from <u>125 till 500</u> m^2 (Pérez Camacho et al., 1991; Pérez Camacho and Labarta, 2004). Equation 7 was then used to estimate raft production. Since production is based on an optimal mussel number, it corresponds to a "potential" maximum yield. These calculations were performed separately for rafts with seed, juvenile and adult mussels, using the same *POM* concentration ranges and current velocities synthesised in Fig. 6. Afterwards, overall averages were calculated for each raft size, pooling together data for seeds, juveniles and adults. Since current velocity and *POM* ranges were not subjected to any probability density function, the calculated averages are not representative of the real system. Nevertheless, they may be used for comparison purposes. Obtained results are shown in Fig. 11, suggesting that an increase in raft size of c.a. 300% (from 125 till 500 m^2), corresponds to an increase in potential raft yield of solely 73%. Separate results for rafts with seeds, juveniles or adults, lead to the same results. The predicted decrease in raft potential yield per unit area (70%), as a result of an increase in raft area, suggests that mussels became more food limited under larger rafts. Therefore, these results suggest that raft area is an important variable to take into account when mussel production is to be optimized at the level of raft parks. Here, a compromise should be achieved between production costs – higher when more rafts are used - and mussel production per raft. Larger scale effects (e.g. at the level of raft parks and at the ecosystem level) should also be investigated prior to any definite recommendation. Furthermore, maximizing production does not necessarily correspond to maximising profit. In fact, according to Ferreira et al. (2007), a producer who bases his decisions on average or total production and revenue principles will earn less profit than one who uses marginal analysis

Conclusions

From the above results, it is apparent that CC at the raft scale in Galician Rías has not been exceeded by current culture practices. In fact, increasing rope density 1.5X does not decline mussel production, suggesting that there is some room for an increase on mussel loads. However, it seems advisable to be conservative about model estimates, especially when the model does not suggest the possibility for a large increase in rope density without affecting the growth of adult mussels. Therefore, any possible increase in mussel production should be considered at a higher spatial scale. Alternatively, changing raft dimensions and the total number of rafts should be considered, for it seems plausible that by reducing raft size, better yields per unit area may be obtained. In any case, larger scale effects of mussel culture – at the scale of the raft parks and at the ecosystem scale - should be considered before any final recommendation is given.

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References

Aure, J., Strohmeier, T., Strand, O., 2007. Modelling current speed and carrying capacity in long-linr blue mussel (Mytilus edulis) farms. Aquaculture Research 38, 304-312.

Babarro, J.M.F., Fernández-Reiriz, M.J., Labarta, U., 2000. Feeding behaviour of seed mussel *Mytilus galloprovincialis* cultivated on the raft: environmental parameters and seed origin. Journal of Shellfish. Research 19, 195-201.

Bacher, C., Duarte, P., Ferreira, J.G., Héral, M., Raillard, O., 1998. Assessment and comparison of the Marennes-Oléron Bay (France) and Carlingford Lough (Ireland) Carrying Capacity with ecosystem models. Aquatic Ecology 31, 379 - 394.

Bacher, C., Grant, J., Hawkins, A.J.S., Fang, J., Zhu, M., Besnard, M., 2003. Modelling the effect of food depletion on scallop growth in Sungo Bay (China). Aquatic Living Resourses 16, 10-24.

Barillé, L., Héral, M. , Barillé-Boyer, A., 1997. Modélisation de l'ecophysiologie de l'huître *Crassostrea gig*as dans un environment estuarien. Aquatic Living Resources 10, 31 – 48.

Bayne, B.L., Brown, D. A., Burns, K., Dixon, D.R., Ivanovici, A., Livingstone, D.R., Lowe, D.M., Moore, M.N., Stebbing, A.R.D., Widdows, J., 1985. The effects of stress and pollution on marine animals. Praeger Publisher, New York, 384 pp.

Blanco, J., Zapata, M., Moroño Á., 1996. Some aspects of the water flow though mussel rafts. Scientia Marina 60, 275 – 282.

Carver, C.E.A., Mallet, A.L., 1990. Estimating carrying capacity of a coastal inlet for mussel culture. Aquaculture 88, 39 – 53.

Dame, R.F., Prins, T.C., 1998. Bivalve carrying capacity in coastal ecosystems. Aquatic Ecology 31, 409 – 421.

Dijkema, R., van Stralen, M., 1989. Mussel cultivation in the Netherlands. World Aquaculture 20, 53-62.

Duarte, P., Meneses, R. , Hawkins, A.J.S., Zhu, M., Fang, J., Grant, J. 2003. Mathematical modelling to assess the carrying capacity for multi-species culture within coastal water. Ecological Modelling 168, 109-143.

Duarte, P., Hawkins, A.J.S, Pereira, A., 2005. How does estimation of environmental carrying capacity for bivalve culture depend upon spatial and temporal scales? In: Dame, R., Olenin, S. (Eds.), The comparative role of suspension feeders in aquatic systems. NATO ARW in Nida, Lithuania, 3-9 October, 2003: 121 - 135. Kluwer Scientific Publishers, Dordrecht, The Netherlands.

Fang, J., Sun, H., Yan, J., Kuang, S., Feng, L., 1996. Polyculture of scallop *Laminaria japonica* in Sungo Bay. Chinese Journal of Oceanology and Limnology 14, 322-329.

Fernandez-Reiriz, M.J., Labarta, U., 2004. Procesos fisiológicos y disponibilidad de alimento del mejillón en las rías gallegas. In Labarta U. (Ed). Bateeiros, mar, mejillón. Una perspectiva bioeconómica. CIEF. Fundación Caixagalicia. Santiago. pp 45-73.

Fernandez-Reiriz, M.J.,Duarte, P., Labarta,U., in press. Modelos de comportamiento alimentario en el mejillón de las Rías de Galicia. In: Biologia y Cultivo del mejillon (*Mytilus galloprovincialis*) en Galicia..Madrid, Biblioteca de Ciencias (CSIC).

Ferreira, J., Duarte, P., Ball, B., 1998. Trophic capacity of Carlingford Lough for aquaculture - analysis by ecological modelling. Aquatic Ecology 31, 361 – 379.

Ferreira, J., Hawkins, A.J.S. and Bricker, S.B.. Management of productivity, environmental effects and profitability of shellfish aquaculture – the Farm Aquaculture Resource Management (FARM) model. Aquaculture (2007), doi: 10.1016/j.aquaculture.2006.12.017.

Figueiras, F.G., Labarta, U., Fernández Reiriz, M.J., 2002. Coastal upwelling, primary production and mussel growth in the Rías Baixas of Galicia. Hydrobiologia 484, 121-131.

Grant, J. S. D., J., Monteiro , P. Pitcher , G., Heasman, K., 1998. Shellfish culture in the Benguela system: A carbon budget of Saldanha Bay for raft culture of *Mytilus galloprovincialis*. Journal ol Wildffish Research 17, 41-49.

Grant, J., 1999. Ecological constraints on the sustainability of bivalve aquaculture. In N. Snennevig, H. Reinertsen and M. New (eds.) Sustainable Aquaculture, food for the future?: 85-96. Balkema.

Guiñez, R., Castilla, J.C., 1999. A tridimensional self-thinning model for multilayered intertidal mussels. The American Naturalist 154, 341-357.

Hawkins, A.J.S., Bayne, B.L., Bougrier, S., Héral, M., Iglesias, J.I.P., Navarro, E., Smith, R.F.M., Urrutia, M.B., 1998. Some general relationships in comparing the feeding physiology of suspension-feeding bivalve molluscs. Journal of Experimental Marine Biology and Ecology 219, 87-103.

Hawkins, A.J.S., James, M.R., Hickman, R.W., Hatton, S., Weatherhead, M., 1999. Modelling of suspension-feeding and growth in the green-lipped *Perna canaliculus* exposed to natural and experimental variations of seston availability in the Marlborough Sounds, New Zealand. Marine Ecology Progress Series 191, 217–232.

Hawkins, A.J.S., Duarte, P., Fang, J.G., Pascoe, P.L., Zhang, J.H., Zhang, X.L., Zhu, M., 2002. A functional model of responsive suspension-feeding and growth in bivalve shellfish, configured and validated for the scallop *Chlamys farreri* during culture in China. Journal of Experimental Marine Biology and Ecology 281, 13-40.

Héral, M., 1993. Why carrying capacity models are useful tools for management of bivalve molluscs culture. In R. Dame (ed.) Bivalve filter-feeders in estuarine and coastal ecosystems: 455-477.. NATO ASI Series.

Incze, L.S., Lutz, R.A., True, E., 1981. Modelling carrying capacity for bivalve molluscs in open, suspended-culture systems. Journal of the World Mariculture Society 12, 135-143.

Jackson, G.A., Winant, C.D., 1983. Effect of a kelp forest on coastal currents. Continental Shelf Research 2, 75-80.

Labarta, U., Fernandez-Reiriz, M.J., Perez-Camacho, A., Perez-Corbacho, E., 2004. Bateeiros, mar, mejillón. Una perspectiva bioeconómica. Centro de Investigaciones Económicas y Financieras (CIEF). Fundación CaixaGalicia. Santiago de Compostela. 274 pp.

Navarro, E., Iglesias, , J.I.P., Pérez-Camacho, A., Labarta, U. Beiras, R., 1991. The physiological energetics of mussels (*Mytilus galloprovincialis*) from different cultivation rafts in the Ria de Arousa. Aquaculture 94: 197-212.

Pérez Camacho, A., Gonzalez, R., Fuentes, J., 1991. Mussel cultura in Galicia (N.W. Spain). Aquaculture 94, 263-278.

Pérez-Camacho, A., Labarta, U., 2004. Rendimientos y producción del mejillón: Bases biológicas para la innovación. In Labarta, U. (Ed). Bateeiros, mar, mejillón. Una perspectiva bioeconómica. CIEF. Fundación Caixagalicia. Santiago. pp 93-121.

Pilditch, C. A., Grant, J., Bryan, K.R., 2001. Seston supply to sea scallops (*Placopecten magellanicus*) in suspended culture. Canadian Journal of Fisheries and Aquatic Science 58, 241-253.

Prins, T.C., Smaal, A., Dame, R., 1998. A review of the feedbacks between bivalve grazing and ecosystem processes. Aquatic Ecology 31, 349 – 359.

Raillard, O., Ménesguen, A., 1994. An ecosystem model for the estimating the carrying capacity of a macrotidal shellfish system. Marine Ecology Progress Series 115, 117 – 130.

Ren, J.S., Ross, A.H., 2001. A dynamic energy budget model of the Pacific oyster *Crassostrea gigas*. Ecological Modelling 142, 105-120.

Sarà, G., Mazzola, A., 2004. The carrying capacity for Mediterranean bivalve suspension feeders: evidence from analysis of food availability and hydrodynamics and their integration into a local model. Ecological Modelling 179, 281-296.

Scholten, H., Smaal, A.C., 1998. Responses of *Mytilus edulis* L. to varying food concentrations: testing EMMY, an ecophysiological model. Journal of Experimental Marine Biology and Ecology 219, 217-239.

Shpigel, M., 2005. Bivalves as biofilters and valuate by-products in land-based aquaculture systems: In: The Comparative Roles of Suspenson-Feeders in Ecosystems, R.F. Dame, S. Olenin (Eds), Kluwer Academic Publishers, Dordrecht, pp 183-198.

Smaal, A.C., Héral., M. (eds) 1998. Modelling bivalve carrying capacity. Aquatic Ecology 4, pp. 439.

Smaal, A. Stralen, M., Schuiling, E., 2001. The interaction between shellfish culture and ecosystem processes. Canadian Journal of Fisheries and Aquatic Science 58, 991 – 1002.

Table 1 – Number of mussel rafts in Galician rías.

Cultivation site	**Number of rafts**
Ría de Ares-Sada	103
Ría Muros-Noia	118
Ría Arousa	2292
Ría Pontevedra	346
Ría de Vigo	478
Galicia	3337
Total	**6674**

Figure captions

Fig. 1 – Location of four Rías Baixas on the NW of the Iberian Peninsula.

Fig. 2 – Scheme of a mussel raft with symbols as described for the model (see text).

Fig. 3 – Ingestion rate (a), mean scope for growth (b) and mussel production (c) for a raft with "seed" mussels solely (0.05 g meat DW) as a function of mussel abundance and current speed, assuming a concentration of *POM* of 0.5 mg L^{-1} and ranges in mussel abundance and current speed within those observed (see text).

Fig. 4 – Ingestion rate (a), mean scope for growth (b) and mussel production (c) for a raft with juvenile mussels solely (1.0 g meat DW) as a function of mussel abundance and current speed, assuming a concentration of *POM* of 0.5 mg L^{-1} and ranges in mussel abundance and current speed within those observed (see text).

Fig. 5 – Ingestion rate (a), mean scope for growth (b) and mussel production (c) for a raft with adult mussels solely (2.25 g meat DW) as a function of mussel abundance and current speed, assuming a concentration of *POM* of 0.5 mg L^{-1} and ranges in mussel abundance and current speed within those observed (see text).

Fig. 6 – Mussel number per metre of rope (obtained from equation 10) that optimizes global *SFG* and production for a raft with "seed" (a), juveniles (b) and adults (c), as a function of current speed and *POM* concentration (see text).

Fig. 7 – Upper left figure: Schematic top view of a mussel raft with seeds, juveniles and adults in the downstream direction, with the former occupying 14% of raft area and the remaining 86% (43% each). The remaining figures show production of each age class calculated with equation 7, for ranges in current speeds (a surrogate for flow) and *POM* concentrations within those observed (see text).

Fig. 8 – Upper left figure: Schematic top view of a mussel raft with seeds, juveniles and adults in the upstream direction, with the former occupying 14% of raft area and the remaining 86% (43% each). The remaining figures show production of each age class calculated with equation 7, for ranges in current speeds (a surrogate for flow) and *POM* concentrations within those observed (see text).

Fig. 9 – Upper left figure: Schematic top view of a mussel raft with seeds, juveniles and adults aligned with the current direction, with the former occupying 14% of raft area and the remaining 86% (43% each). The remaining figures show production of each age class calculated with equation 7, for ranges in current speeds (a surrogate for flow) and *POM* concentrations within those observed (see text).

Fig. 10 – Raft production calculated with equation 7 as a function of rope density (normal density, 1.5X, 2X, 3X, 4X and 5X normal density). Each point corresponds to average production for adults (a) or overall average production for seeds, juveniles and adults (b), integrated for all combinations of three input food concentrations (0.25, 0.50 and 1.00 mg *POM*/ L) and eleven current speeds (0.01 - 0.11 m/s, with a step of 0.01 m/s). The cultivation layout is the same described in Fig. 7, with seed mussels at the

upstream end of the raft. When drag is considered, current speed within the raft is reduced as a function of drag (see text).

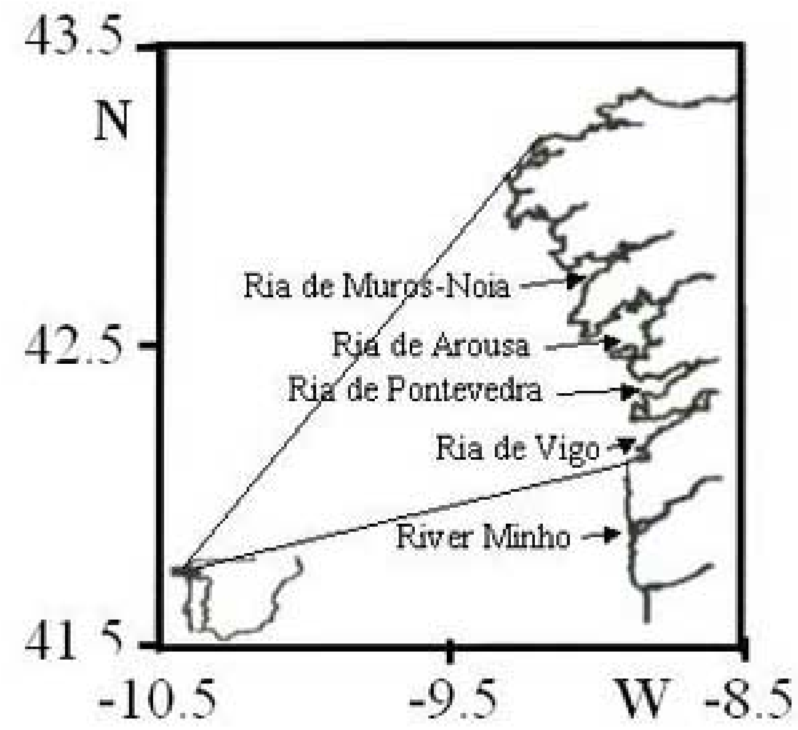
Fig. 11 – Raft production (total and areal) calculated with equation 7, for the number of mussels that maximize overall *SFG*, calculated with equation 10, as a function of raft area (125, 261, 352, 369 and 500 m^2). These production values are average results integrated over ranges in current speeds (a surrogate for flow) and *POM* concentrations within those observed and considering rafts with seed, juveniles and adult mussels (see text).

Dear Dr. Costa-Pierce,

I am submitting the paper “MODELLING LOCAL FOOD DEPLETION EFFECTS IN MUSSEL RAFTS OF GALICIAN RIAS”, by Duarte et al. This paper is original and it was not submitted to any other journal. A previous version of this manuscript was submitted a few weeks ago. However, it was not send out for review, because you considered that this was a contribution very similar to others already printed in Aquaculture. I have sent you an e-mail explaining that this work is different than previously published papers on the carrying capacity subject. On an e-mail message dated 7 February, you asked me to resubmit the manuscript making a note on your decision about the resubmission.

With my best regards,

Pedro Duarte


43.5
N
42.5
41.5
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W
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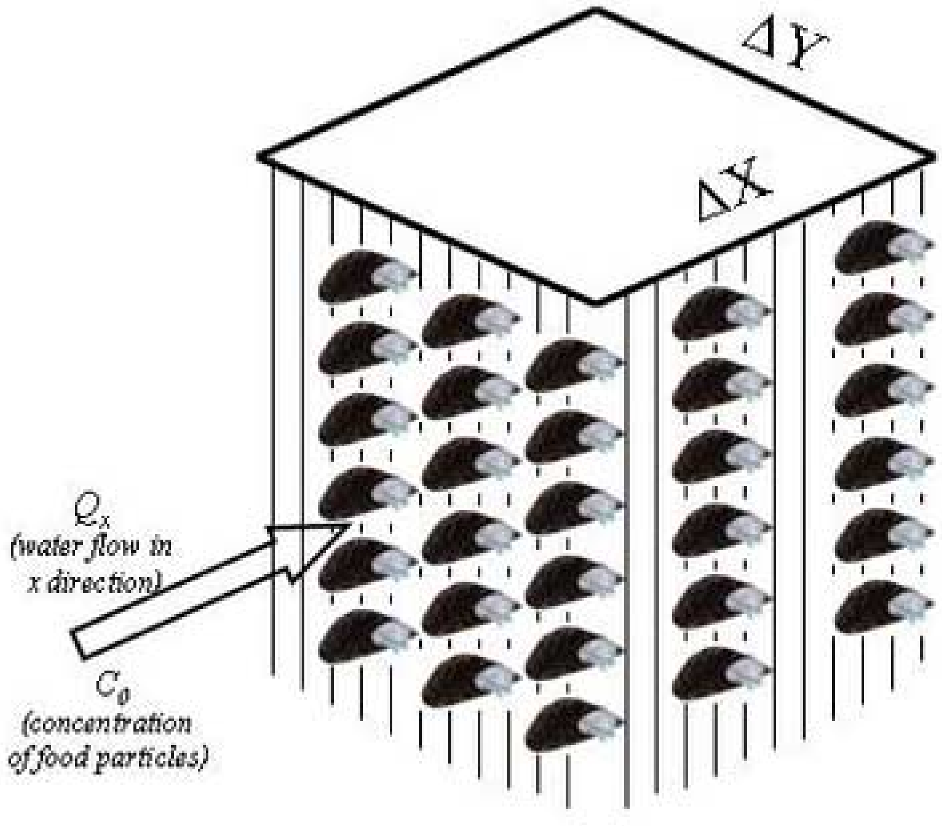
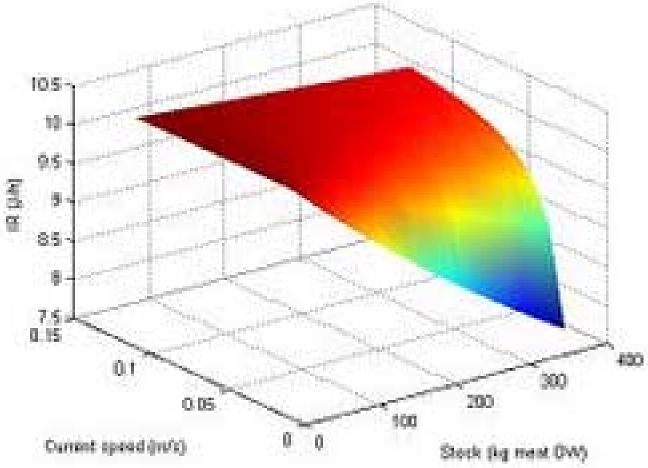
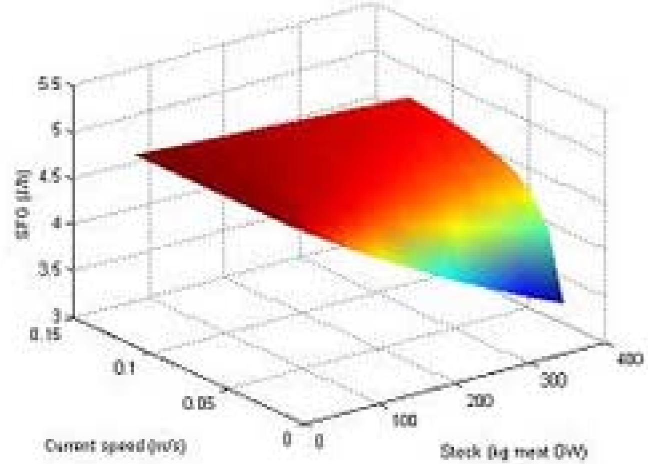
Ria de Pontevedra
Ria de Vigo
River Minho


ΔY
ΔX
Q_x
(water flow in x direction)
C_0
(concentration of food particles)

Figure(s)


10.5
10
9.5
9
8.5
8
7.5
IR (J/h)
0.15
0.1
0.05
0
Current speed (m/s)
0
100
200
300
400
Stock (kg meat DW)

a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5
4.5
4
3.5
3
SFO (J/h)
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0.05
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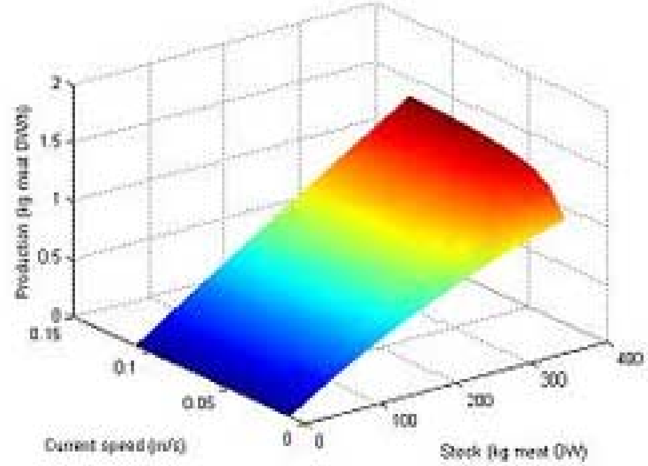
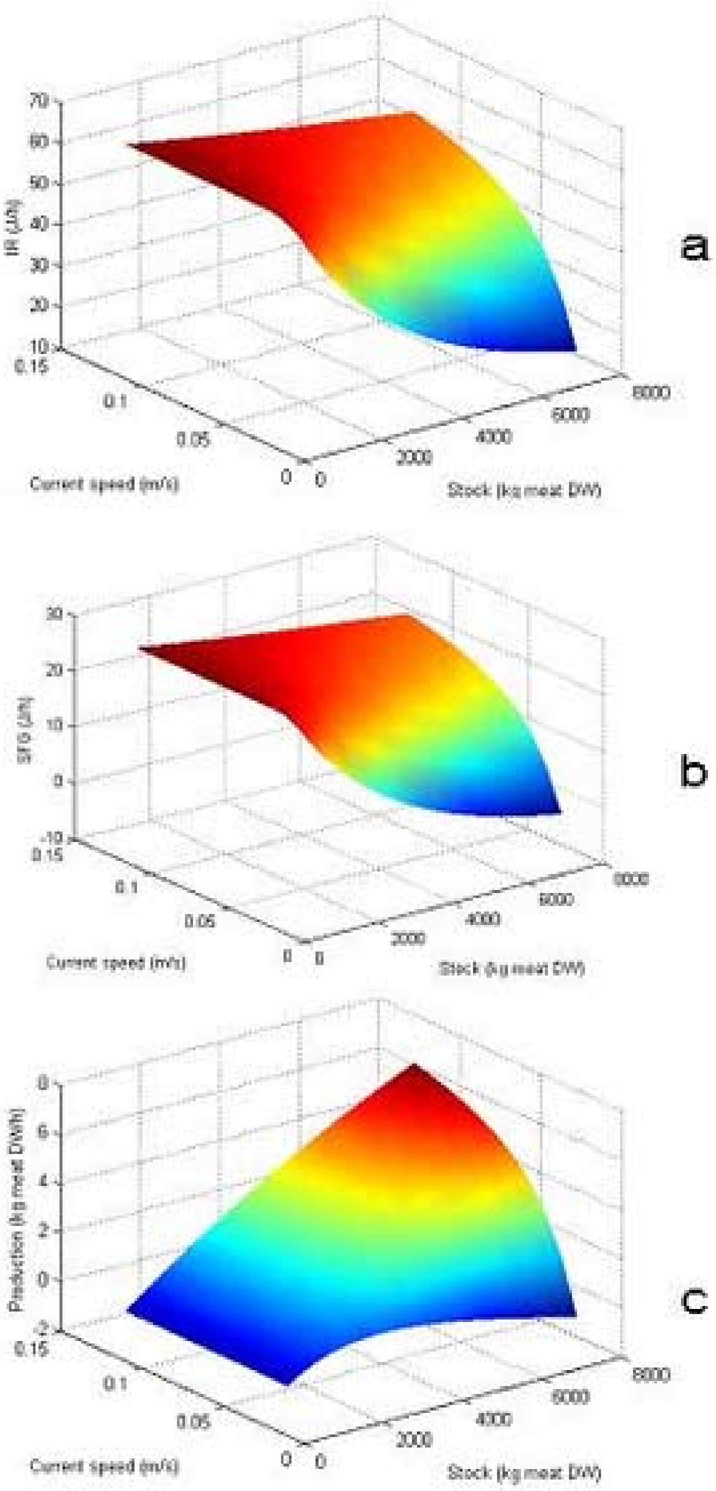
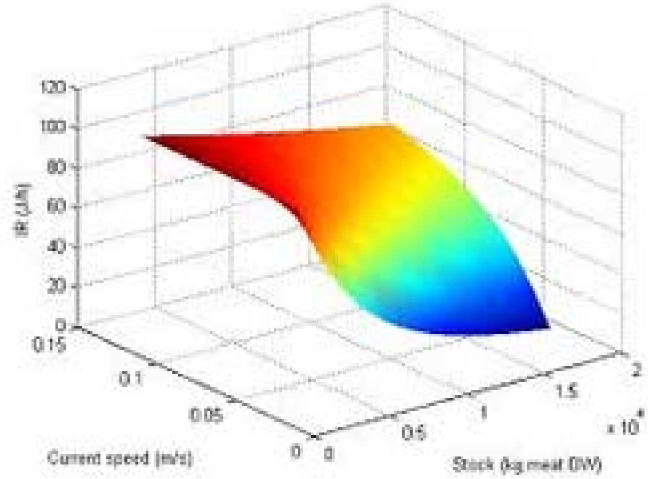
0
100
200
300
400
Stock (kg meat DW)

b

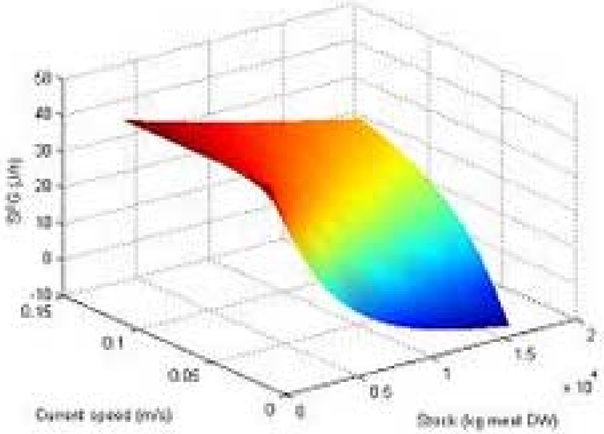

2
1.5
1
0.5
0
Production (kg meat DW/h)
0.15
0.1
0.05
0
Current speed (m/s)
0
100
200
300
400
Stock (kg meat DW)

c

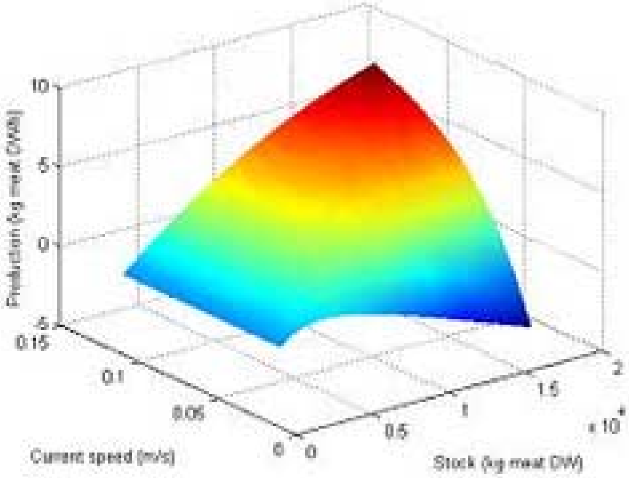

70
60
50
40
30
20
10
IR (J/h)
0.15
0.1
0.05
0
Current speed (m/s)
0
2000
4000
6000
8000
Stock (kg meat DW)
a
30
20
10
0
-10
SFG (J/h)
0.15
0.1
0.05
0
Current speed (m/s)
0
2000
4000
6000
8000
Stock (kg meat DW)
b
8
6
4
2
0
-2
Production (kg meat DW/h)
0.15
0.1
0.05
0
Current speed (m/s)
0
2000
4000
6000
8000
Stock (kg meat DW)
c


120
100
80
60
40
20
0
IR (J/h)
0.15
0.1
0.05
0
Current speed (m/s)
0
0.5
1
1.5
2
x 10⁴
Stock (kg meat DW)

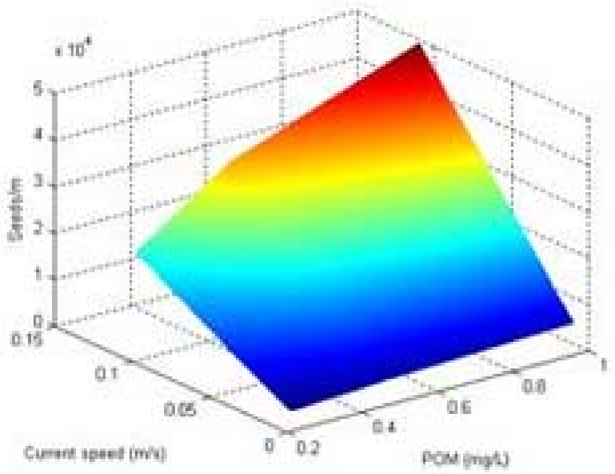
a


50
40
30
20
10
0
-10
SFG (J/h)
0.15
0.1
0.05
0
Current speed (m/s)
0
0.5
1
1.5
2
x 10⁴
Stock (kg meat DW)

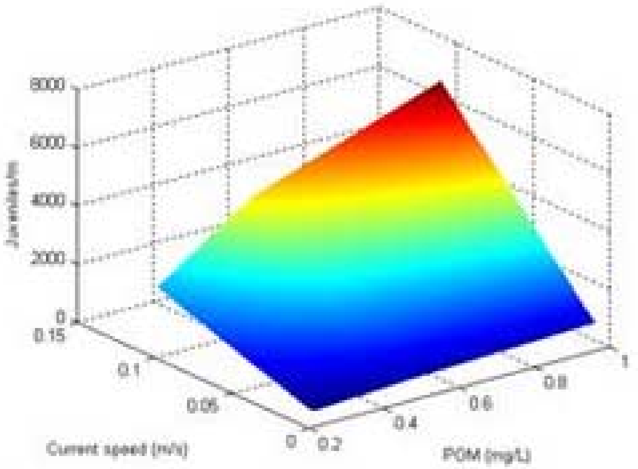
b


10
5
0
-5
Production (kg meat DW/d)
0.15
0.1
0.05
0
Current speed (m/s)
0
0.5
1
1.5
2
x 10⁴
Stock (kg meat DW)

c


x 10^4
5
4
3
2
1
0
Seeds/m
0.15
0.1
0.05
0
Current speed (m/s)
0.2
0.4
0.6
0.8
1
POM (mg/L)

a


8000
6000
4000
2000
0
Juveniles/m
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0.1
0.05
0
Current speed (m/s)
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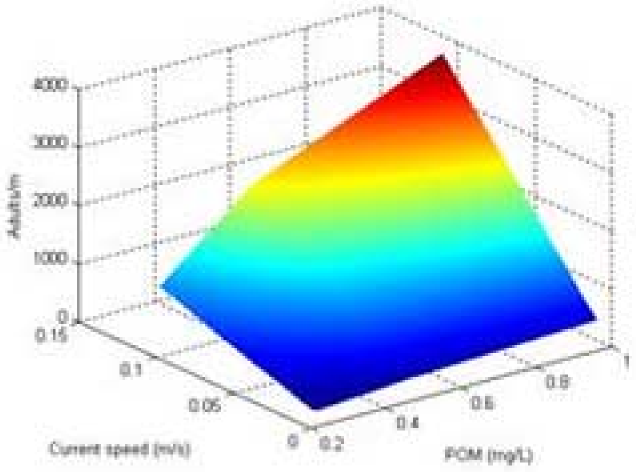
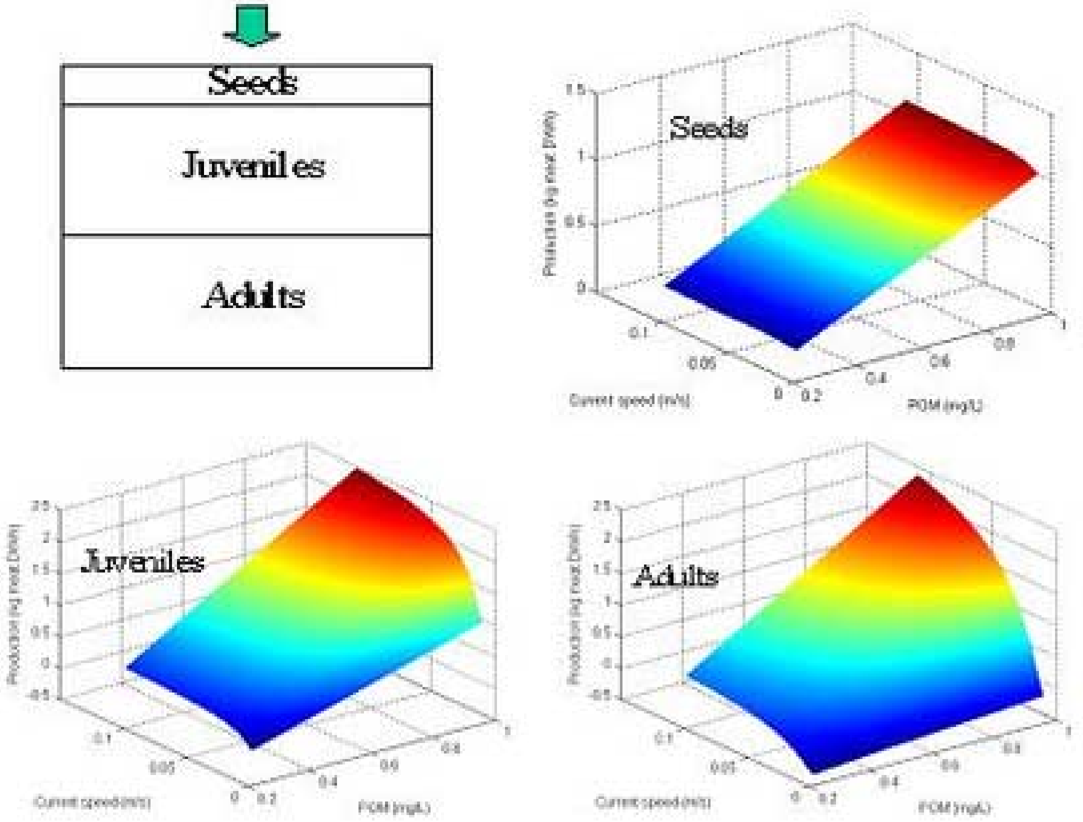
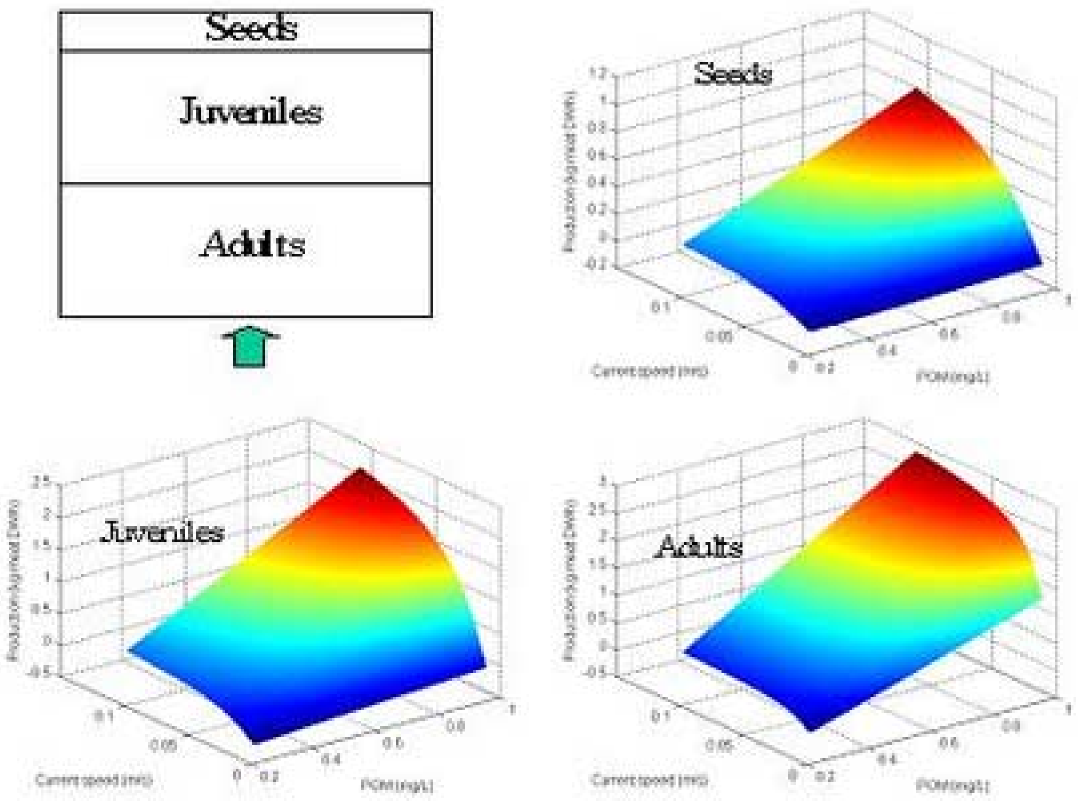
0.4
0.6
0.8
1
POM (mg/L)

b

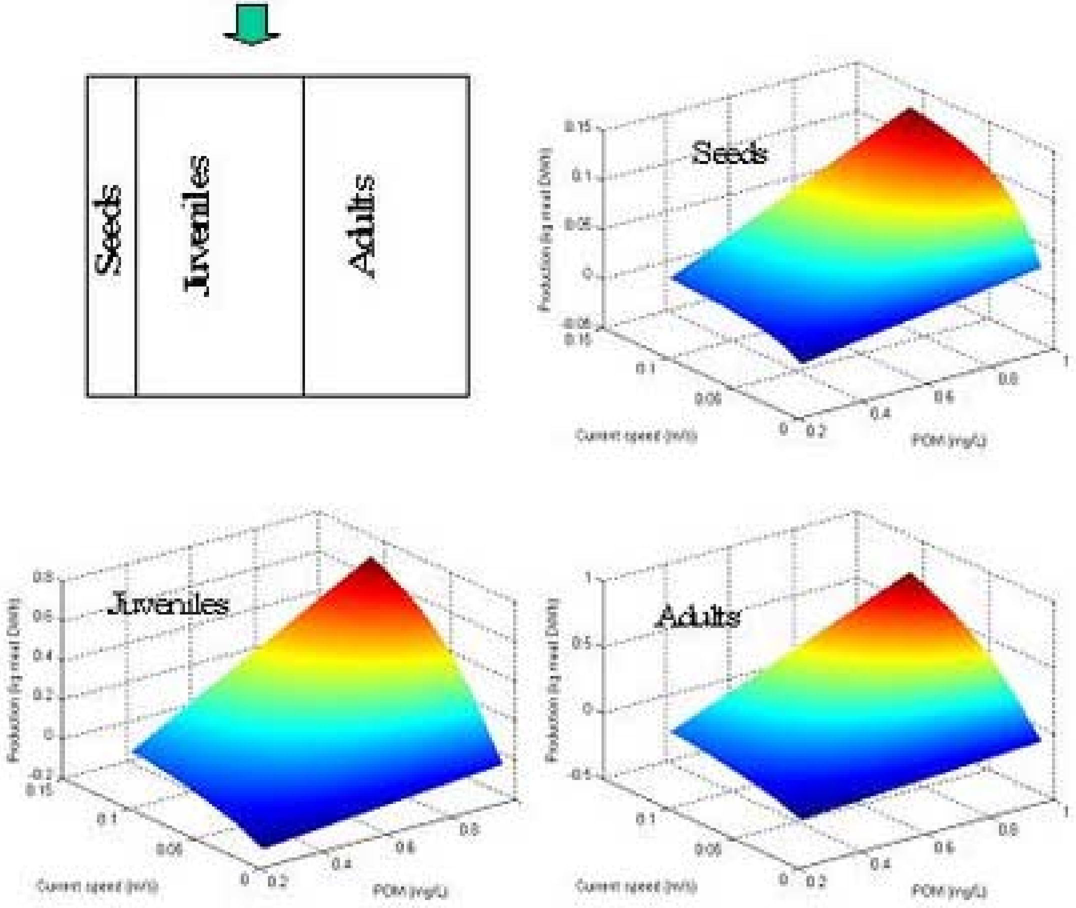

4000
3000
2000
1000
0
Adults/m
0.15
0.1
0.05
0
Current speed (m/s)
0.2
0.4
0.6
0.8
1
POM (mg/L)

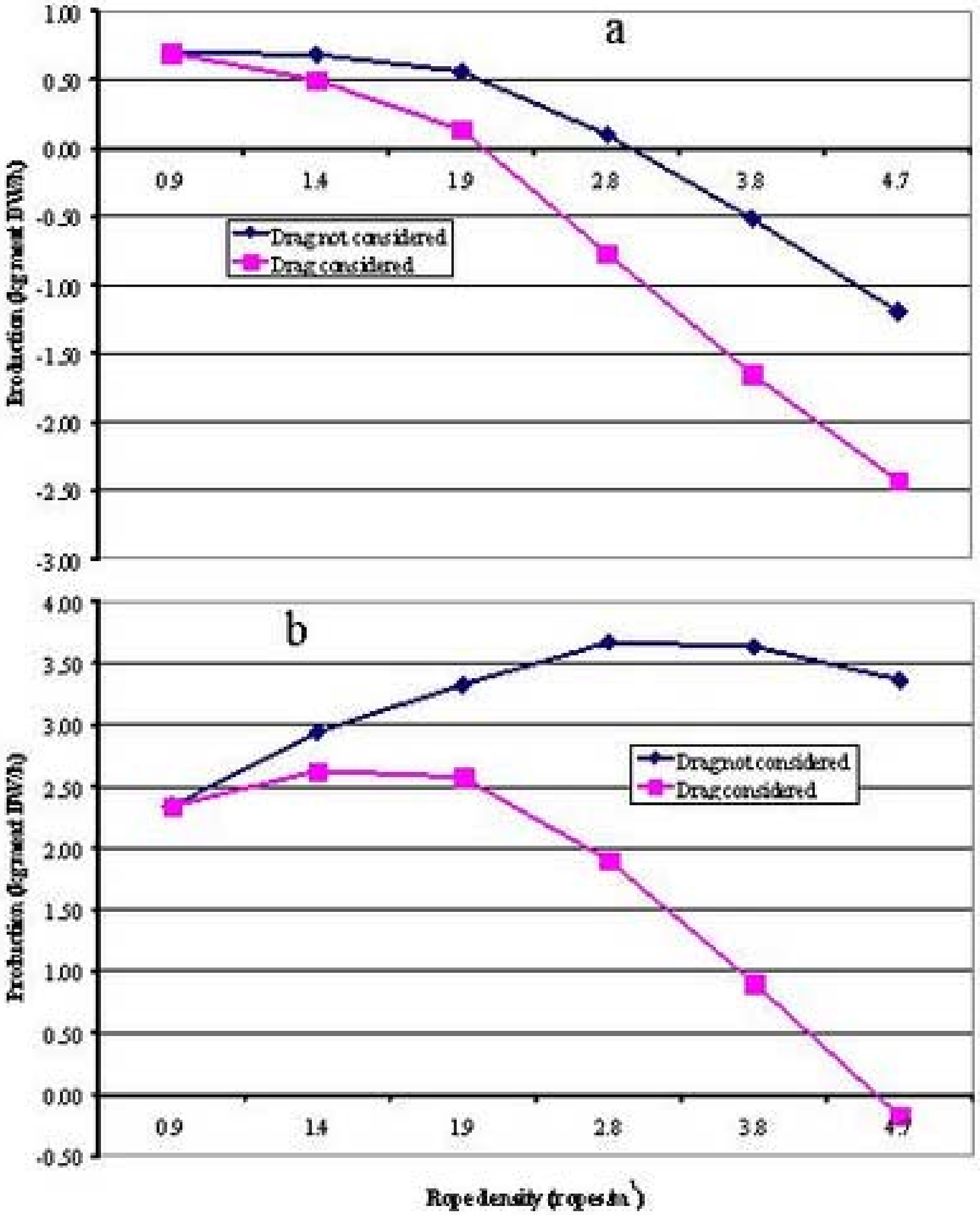
c

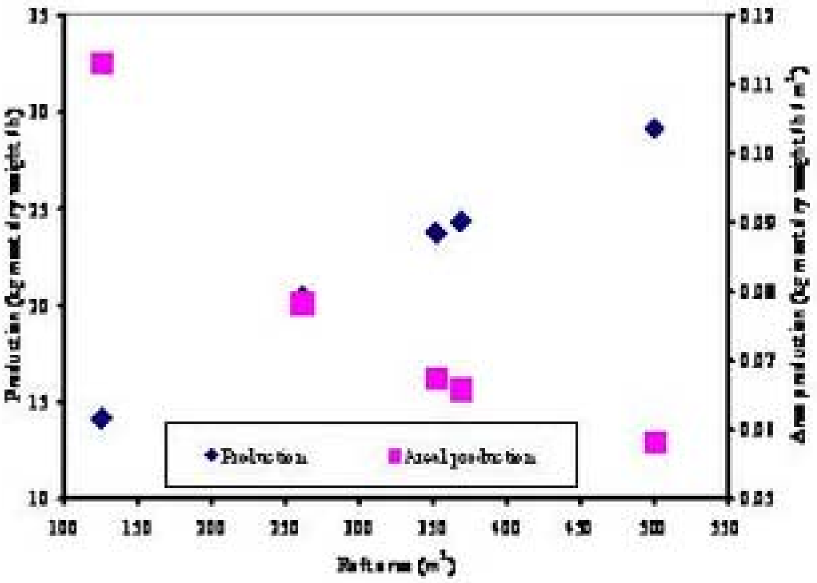

Seeds
Juveniles
Adults
Seeds
Production (kg meat DW/h)
1.5
1
0.5
0
0.1
0.05
0
Current speed (m/s)
0.2
0.4
0.6
0.8
1
POM (mg/L)
Juveniles
Production (kg meat DW/h)
2.5
2
1.5
1
0.5
0
-0.5
0.1
0.05
0
Current speed (m/s)
0.2
0.4
0.6
0.8
1
POM (mg/L)
Adults
Production (kg meat DW/h)
2.5
2
1.5
1
0.5
0
-0.5
0.1
0.05
0
Current speed (m/s)
0.2
0.4
0.6
0.8
1
POM (mg/L)


Seeds
Juveniles
Adults
Seeds
1.2
1
0.8
0.6
0.4
0.2
0
-0.2
0.1
0.05
0
Current speed (m/s)
0.2
0.4
0.6
0.8
1
POM (mg/L)
Juveniles
2.5
2
1.5
1
0.5
0
-0.5
0.1
0.05
0
Current speed (m/s)
0.2
0.4
0.6
0.8
1
POM (mg/L)
Adults
3
2.5
2
1.5
1
0.5
0
-0.5
0.1
0.05
0
Current speed (m/s)
0.2
0.4
0.6
0.8
1
POM (mg/L)

Figure(s)


Seeds
Juveniles
Adults
Seeds
Production (kg meat DW/d)
0.15
0.1
0.05
0
-0.05
Current speed (m/s)
0.15
0.1
0.05
0
POM (mg/L)
0.2
0.4
0.6
0.8
1
Juveniles
Production (kg meat DW/d)
0.8
0.6
0.4
0.2
0
-0.2
Current speed (m/s)
0.15
0.1
0.05
0
POM (mg/L)
0.2
0.4
0.6
0.8
Adults
Production (kg meat DW/d)
1
0.5
0
-0.5
Current speed (m/s)
0.1
0.05
0
POM (mg/L)
0.2
0.4
0.6
0.8
1


a
1.00
0.50
0.00
-0.50
-1.00
-1.50
-2.00
-2.50
-3.00
0.9
1.4
1.9
2.8
3.8
4.7
Drag not considered
Drag considered
Production (kg meat DW/h)
b
4.00
3.50
3.00
2.50
2.00
1.50
1.00
0.50
0.00
-0.50
0.9
1.4
1.9
2.8
3.8
4.7
Drag not considered
Drag considered
Production (kg meat DW/h)
Rope density (ropes ha^{-1})


35
30
25
20
15
10
Production (kg mean dry weight /h)
0.12
0.11
0.10
0.09
0.08
0.07
0.06
0.05
Area production (kg mean dry weight /h m^2)
100
150
200
250
300
350
400
450
500
550
Raft area (m^2)
Production
Areal production