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Weight ratios of the kelps, Alaria esculenta and Saccharina latissima, required to sequester dissolved inorganic nutrients and supply oxygen for Atlantic salmon, Salmo salar, in Integrated Multi-Trophic Aquaculture systems

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ABSTRACT

Estimates of seaweed nutrient sequestration ability in open-water, Integrated Multi-Trophic Aquaculture (IMTA) required to 'balance' nutrients from fish cages have typically assigned a specific nutrient load for a specific fish biomass. The resultant culture area and densities of seaweeds required for full equivalent nutrient sequestration may have meaning only to experienced aquaculturists. Consequently, a novel ratio model is proposed which determines the weight ratio of harvested seaweeds required to sequester an equivalent weight of soluble inorganic nutrients loaded per unit growth of fish. Soluble inorganic nutrient excretion from Atlantic salmon, Salmo salar, was estimated using a semi-stochastic nutritional mass balance approach. Oxygen demand was estimated using respiratory quotients. Nutrient contents of the IMTA kelps, Alaria esculenta and Saccharina latissima, were measured at harvest times, and net oxygen production was estimated using the photosynthetic equation. To quantify uncertainty, input parameters were assigned theoretical distributions (based on empirical or literature data) and the model was run using a stratified sampling approach (Latin Hypercube) over multiple iterations, to generate distributions of weight ratios for the various nutrients. A mathematical simulation of nutrient loading from a salmon farm over a full production cycle was estimated using mean loading values per unit growth, with monthly growth estimated by a thermal growth coefficient (TGC).

Results showed that one kilogramme of Atlantic salmon growth (large fish fed a typical commercial feed, \pm standard deviation) resulted in the excretion of 29.49 \pm 4.20 g nitrogen, 2.26 \pm 2.25 g phosphorus and the respiration of 243.38 \pm 48.28 g carbon. Dissolved oxygen requirements for 1 kg of growth were 455.29 \pm 86.24 g. Salmon smolts placed in cages in spring and harvested 21 months later, load approximately 4 times more nutrients in the second grow-out season. The mean ratios of A. esculenta weight required to sequester nutrients excreted per unit weight of S. salar production were $6.7(\pm 1.5)$:1 for nitrogen, $4.8(\pm 3.0)$:1 for phosphorus, and $5.8(\pm 1.4)$:1 for carbon. Oxygen could be supplied at a weight ratio of $4.1(\pm 1.0)$:1. The mean ratios of S. latissima were $12.9(\pm 2.7)$:1 for nitrogen, $10.5(\pm 6.2)$:1 for phosphorus, and $10.2(\pm 2.2)$:1 for carbon. Oxygen could be supplied at a weight ratio of $7.2(\pm 1.5)$:1. A. esculenta appears to have almost twice the nutrient sequestration capacity per wet weight than S. latissima. However, culture densities of S. latissima are 1.5 times greater than those for A. esculenta and when spatially weighted this difference is reduced to 1–1.5 times.

Numbers of rafts for both kelp species required for full nutrient sequestration from a commercial scale salmon farm exceed the number of rafts which can be practically deployed within a typical site lease area. However, not all inorganic nutrients from cultured fish will be available to IMTA seaweeds, nor should 100% nutrient sequestration need be the only successful endpoint in such systems. These aspects should be considered when assessing the net value of kelps in open-water IMTA systems.

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Integrated Multi-Trophic Aquaculture (IMTA) is a form of food

production, which connects cultures of different organisms, at differ-

ent trophic levels (Chopin et al., 2001; Neori et al., 2007), by nutrient

1. Introduction







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transfer through water (Neori et al., 2004). Nutrient waste from a fed component such as fish, supplies all or partial nutritional inputs for co-cultured species of commercial value. The aim of IMTA is to improve sustainability of fish culture, through nutrient sequestration (Reid et al., 2009), product diversification (Ridler et al., 2007), improved use of coastal 'real estate' (Barrington et al., 2009; Robinson et al., 2011) and there has also been some evidence of pathogen mitigation (Castro et al., 2004; Pang et al., 2006). The IMTA method and its associated variants - such as integrated agriculture-aquaculture (IAA), integrated peri-urban aquaculture (IPUA) and integrated sequential aquaculture (ISA) - and incidental IMTA (not purposely designed cultivation of species of different trophic levels situated in close geographical proximity), have been practised for centuries, mostly in Asia (Chopin, 2012). However, open-water IMTA has only been recently developed in the Western World as a commercial venture (Chopin, 2013).

The fed component of IMTA systems are often referred to as the Fed Trophic Level (FTL). Co-cultured species make up the extractive trophic levels. Nutrient waste from the FTL can be partitioned into three categories and consequently, at least three different extractive species groups or niches are required if all 'nutrient streams' are to be targeted. These nutrient categories and associated niches are as follows:

- Dissolved inorganic nutrients from metabolic and respiration processes, or leached from solid organic waste, including forms such as ammonium (NH⁺₄) and orthophosphates (PO³⁻₄), can be absorbed by inorganic extractive species, such as seaweeds and aquatic plants.
- 2) Small suspended or slow sinking organic particulates generated from feed waste or faeces can be "captured" by organic extractive suspension-feeders, such as shellfish and some grazers.
- 3) Heavier settleable organic solids also generated from feed waste or faeces can be consumed by organic extractive deposit-feeders, such as sea urchins, sea cucumbers, sea worms and deposit-feeding fish (e.g. mullets).

The nutrient recovery efficiency of open-water IMTA will depend on temporal (*e.g.* deployment and grow-out times) and spatial (vertical and horizontal) scales of co-cultured species production, environmental conditions (*e.g.* current flow, temperatures and depth of euphotic zone), husbandry techniques, the number of niches filled, species selection, and the ratio of extractive species to FTL production, as described in this study. Consequently, reporting a single production level for an extractive species, required to sequester a given amount of FTL nutrients, is not possible for all operational scenarios. However, despite these complexities, measures of nutrient mitigation are essential for metrics of sustainability that can be used by environmental managers and these must be developed.

2. Weight ratio approach to quantify dissolved inorganic nutrient sequestration in open-water IMTA

There have been a few reports in the scientific literature on the relative nutrient sequestration potential of seaweeds grown beside fish cages (see Discussion). However, the measures in which this potential has been reported are typically based on site specific data such as production level, stocking densities, peak biomass and area. Arguably, such measures have little intuitive meaning for most stakeholders with the possible exception of highly experienced producers, "coastal managers" and researchers.

One method with the potential to avoid many site-specific operational complexities is to estimate nutrient sequestration values based on weight ratios. For example, given an amount of nutrient released per unit of FTL growth within a site lease area, what extractive species biomass would be required to sequester the equivalent load? This would then be reported as a ratio, such as x: 1 (Eq. (1)). Such a value is conceptually simple and arguably easier to apply for policy and farm management, and enable easier site specific calculations. There is, however, a significant assumption with inorganic extractive species and application of the ratio approach that should be noted. It assumes that we are not concerned with the removal of the actual soluble nutrient molecules excreted directly from the FTL, but only with net equivalents from the surrounding culture area. For example, while portions of excreted ammonium from fish will be directly sequestered by cocultured seaweeds, it is difficult, in the absence of intensive data collection, to determine the amount sequestered directly from the fish versus that from ambient sources. It is unlikely that a molecule of ammonia from the FTL will be any different with respect to availability or function compared to one from the ambient environment. Determining such partitioning requires either the production of the co-cultured species at reference sites, of similar characteristics, for growth comparison with the IMTA site (to determine augmented growth), or the use of tracers such as stable isotopes. It is arguably impractical to collect such data for every site to accommodate the diversity of open-water IMTA production scenarios.

The ratio approach will not be applicable for all co-cultured species niches. In the case of heavier settleable organic solids, the use of nutrient equivalents cannot be used since we are concerned with the actual portions of the organic load settling in a discrete area in close proximity to fish cages. The potential for benthic hydrogen sulphide release is used as a regulatory indicator for impact potential in many jurisdictions (Chang et al., 2011). This is different from the nature of dissolved inorganic nutrients that will 'mix' to manifest a certain area-wide concentration, as the seaweeds will be involved in dissolved nutrient removal, regardless of the original nutrient source and this will be dealt with in the subsequent model.

3. Nutritional mass-balance nutrient loading for Atlantic salmon and sources of variation in estimates

The first step in modelling nutrient recovery in any IMTA system is determining the nutrient load of the FTL (*e.g.* salmon). A simple nutritional mass-balance approach is frequently used for fish to estimate nutrient loading (Papatryphon et al., 2005; Reid and Moccia, 2007) and the basic equations are detailed in the methods (Eq. (2)). This approach typically partitions mass-balance into nutritional categories of proximate composition, such as proteins, lipids, minerals and nitrogen-free extract (NFE). Often, NFE is a "catch-all" term used to describe the remaining category after the fractions of all other categories are subtracted from 1 (or 100, if percentages are used). It is mostly made of carbohydrates and may or may not include fibres depending on the breakdown. Proximate composition of the feed and whole body composition of the fish is required and the mass-balance calculations are done separately for each category.

Despite the relative simplicity of a mass-balance approach, there are many sources of variation in model inputs for nutrient loading estimates. Consequently, a semi-stochastic approach may be more suitable than a deterministic mathematical approach using static input values. We examine several potential sources of variation as a means to quantify uncertainty in model inputs and outputs.

3.1. Fish growth

Application of growth and waste production models for fish are reasonably well developed. The state of fish growth modelling has been recently reviewed by Dumas et al. (2010). For practical application in aquaculture, the amount of feed required to achieve a certain level of production is commonly used to predict growth. This is typically the Feed Conversion Ratio (FCR, feed/growth), although sometimes the reciprocal, Feed Efficiency (FE, growth/feed), is also used. If FCR and growth are known, the amount of feed used and waste estimates can be calculated. Feed wastage will need to be subtracted if it is an economic FCR (feed offered/growth). The FCR is useful for measuring an "end point" such as feed required to meet harvest weight, but is of limited usefulness to provide details on growth rates throughout the production cycle. The FCR is also more of an overall average as it generally increases (*i.e.* decreased feed efficiency) as fish get larger (Azevedo et al., 2004; Reid and Moccia, 2007). Consequently, other modelling approaches may be required to detail growth rates throughout the production cycle. Since fish are poikilothermic, their growth rate is largely influenced by temperature, assuming they are sufficiently fed. A thermal growth coefficient (TGC) model is often used to describe the growth rate of cultured fish based on historical growth performance under a particular temperature regimen and time frame (see Eq. (5)). Both FCR and TGC approaches are used in this study to quantify growth.

3.2. Apparent digestibility coefficients (ADC)

The ADC is the portion of diet, nutritional category or ingredient that is digested or absorbed through the intestinal wall. It is typically reported as a percentage. ADCs can be affected by environmental, metabolic influences, and feed ingredients (National Academies Press, 2011). While proximate composition of nutritional categories are displayed on commercial feed labels (i.e. percentage of proteins, fat, minerals, nitrogen free extract) details of individual ingredients and their quantities in commercial feeds are not always readily available. The approach in this study circumvents this by using ADC distributions of nutritional categories or ingredients commonly used in salmon feeds.

3.3. Whole body composition

Whole body composition is required to supply the retained values in the nutritional mass-balance equation. While it is not required to estimate faecal egestion, it is crucial for estimates of excretion and respiration. Whole body composition is influenced by fish size (Einen and Roem, 1997), life stage (Shearer et al., 1994) and diet (Azevedo et al., 2004; Jobling and Johansen, 2003). While there is good information in the literature on whole body, protein, lipid and dry matter content in salmon, information on mineral content is sparse. This is probably because marine fish also take in non-dietary forms of minerals through drinking, largely to regulate their osmotic balance (National Academies Press, 2011). Consequently, partitioning minerals along nutritional pathways has a much greater degree of uncertainty compared to other nutritional categories and may require individual consideration as we have done with phosphorus (portions are in mineral form) in this study. Minerals other than phosphorus are not directly addressed in this model, but warrant acknowledgement because they contribute to the variability in dry matter.

3.4. Oxygen demand

The difference between what is digested and what is retained in the fish is what is excreted (assuming spawning has not occurred) or respired. Once the post digestion loss of carbon from each nutritional category is known, oxygen demand can be calculated using a respiratory quotient (RQ), which is the amount of oxygen consumed per carbon dioxide produced by catabolism of a nutritional category. Carbon contents of proteins, lipids, fibre/cellulose are 0.50–0.55, 0.80 and 0.42, respectively (Hart et al., 2007; Porter, 1933). RQ values are 1 for carbohydrates, 0.7 for lipids, and 0.95 for protein catabolism that produces ammonia (Jobling, 1994).

4. IMTA kelps

Several salmon sites being converted into IMTA sites are located in the Quoddy Region of the Bay of Fundy, Canada, where kelps and mussels are starting to be commercially cultured adjacent to Atlantic salmon cages. The kelps, *Alaria esculenta* and *Saccharina latissima*, have typically comprised the inorganic extractive component, although several other species of seaweeds are under experimentation. There are several models of kelp growth with a variety of objectives (*e.g.* Broch and Slagstad, 2012). However, in this study's modelling exercise, only the weight and nutrient content at harvest time are considered, as they are indicative of what is ultimately being removed from the IMTA system.

In the present culture configuration, IMTA kelps in the Bay of Fundy are cultured at densities of 13,300 kg fresh weight (FW) for *A. esculenta* and 19,950 kg FW of *S. latissima* per 0.21 hectare raft. This translates into 1.5 times more *S. latissima* produced per unit area than *A. esculenta*. At present, the number of rafts per site may vary from 2 to 6 rafts.

5. Objectives

The objectives of this study were to:

- 1) Apply a stochastic approach to a fish nutritional mass balance model as a means to better quantify uncertainty in nutrient loading
- 2) Use a thermal growth coefficient, calculated from commercial growth data of *S. salar*, to estimate seasonal nutrient loading and oxygen demand from a hypothetical fish farm, for juxtaposition with typical deployment periods of *A. esculenta* and *S. latissima*
- 3) Measure the nutrient content of the kelp species *A. esculenta* and *S. latissima* near harvest times, in an open-water IMTA site in development
- 4) Compare the weight of elemental nitrogen, phosphorus and carbon in the kelps with the inorganic nutrient load excreted or respired per unit *S. salar* growth, as a means to determine nutrient sequestration ratios
- 5) Determine the weight ratios of kelps required for nutrient sequestration on an areal basis to account for different culture densities between the two species examined in this study

To avoid confusion in terminology, herein the term "mass balance" will be used as per convention to describe losses and gains in a system, specifically for the nutritional component of Atlantic salmon. The term "weight ratio" will be used to juxtapose the production related values (*i.e.* kelp to salmon). The term excretion refers to that of soluble inorganic nutrients.

6. Methods

The premise of the ratio model is to report the amount of nutrient (elemental) per unit of fresh kelp weight that is equivalent to the estimated amount of nutrient secreted or respired per unit of salmon growth (Eq. (1)). In the case of dissolved oxygen, the reporting ratio is reversed (*i.e.* kelp supply versus salmon requirement per unit growth). Calculations of salmon faecal and dissolved nutrient production shown in Eq. (2) are based on estimates of nutritional mass balance approach (Papatryphon et al., 2005; Reid and Moccia, 2007; Reid et al., 2009; Strain and Hargrave, 2005). As not all kelp species can be cultured at the same density, Eq. (3) weights weight ratios on an areal basis for comparison between species for application to a culture scenario.

Equation 1: Weight ratio.

$$WtR = \frac{rt_{IE}}{nt_g} \tag{1}$$

where:

- WtR Weight ratio
- *rt_{IE}* Weight of inorganic extractive species which has retained (*rt*) a nutrient weight equal to the weight of nutrient excreted per unit fish growth
- nt_g Weight of dissolved inorganic nutrient (*nt*) excreted per unit fish growth

Table	1	

Input distributions.

Category	Best theoretical distribution fit ^a	Theoretical distribution properties ^b	Data source used to generate theoretical distribution
Atlantic salmon whole Proteins	e body composition (fraction) ^d Triangular, C-S ^a = 2.84	$\label{eq:max} \begin{array}{l} \mu = 0.173 \pm 0.014, min = 0.140, \\ max = 0.190, most \ likely = 0.190 \end{array}$	Azevedo et al. (2004), $n = 1$; Einen and Roem (1997), $n = 10$; Jobling and Johansen (2003), $n = 7$; Karalazos et al. (2011), $n = 4$; Nordrum et al. (2000), $n = 1$; Shearer et al. (1994) ^b $n = 11$;
Lipids	Normal, estimated ^c (see text)	$\label{eq:max} \begin{array}{l} \mu = 0.140 \pm 0.037, min = 0.800, \\ max = 0.200 \end{array}$	Azevedo et al. (2000), $n = 1$; Bicarci et al. (1954), $n = 11$; Azevedo et al. (2004), $n = 1$; Eicarci and Roem (1997), $n = 10$; Jobling and Johansen (2003), $n = 7$; Karalazos et al. (2011), $n = 4$; Nordrum et al. (2000), $n = 1$: Shearer et al. (1994) ^a $n = 11$
DM^{h}	Logistic, $A-D^e = 0.5793$, K-S ^f = 0.1137	$\begin{array}{l} \mu = 0.355 \pm 0.025, \alpha = 0.355, \\ \beta = 0.014, \mbox{min} = 0.280, \mbox{max} = 0.392 \end{array}$	Azevedo et al. (2000), $n = 1$; Sicarci et al. (1504), $n = 11$ Azevedo et al. (2004), $n = 1$; Einen and Roem (1997), $n = 10$; Glover (2009), $n = 1$; Karalazos et al. (2011), $n = 4$; Shearer et al. (1994) $n = 11$
Phosphorus	Normal, $K-S = 0.1852$, A-D = 0.3303	$ \begin{split} \mu &= 4.1 \times 10^{-3} \pm 5.8 \times 10^{-4} \text{,} \\ \text{min} &= 3.0 \times 10^{-3} \text{, max} = 4.8 \times 10^{-3} \end{split} $	Shearer et al. (1994), $n = 11$
Apparent digestibility Proteins Lipids	coefficients $(3)^g$ Weibull, A-D = 0.3698, K-S = 0.0810 Triangular, C-S = 3.68	$\begin{split} \mu &= 86.856 \pm 4.182, \alpha = 3.609, \\ \beta &= 15.072, min = 79.0, \\ max &= 94.5, shift = 73.27 \end{split}$ $\begin{split} \mu &= 90.96 \pm 5.75, min = 76.3 \\ max &= 99.1, most likely = 99.1 \end{split}$	Diets: Aas et al. (2006), $n = 1$; Aksnes et al. (1995), $n = 1$; Arnesen et al. (1995) $n = 2$; Aslaksen et al. (2007), $n = 1$; Azevedo et al. (2004), $n = 4$; Bendiksen et al. (2011), $n = 6$; Bendiksen et al. (2003), $n = 4$; Einen and Roem (1997), $n = 4$; Espe et al. (2000), $n = 1$; Hillestad et al. (1999), $n = 2$; Hillestad et al. (2001), $n = 3$; Karalazos et al.(2011), $n = 2$; Kraugerud et al. (2007), $n = 1$; Olli and Krogdahl (1995), $n = 1$; Krogdahl et al. (2003), $n = 1$; Mundheim et al. (2004), $n = 2$; Nordrum et al. (2000), $n = 1$; Olli and Olsen et al. (2006), $n = 1$; Pratoomyot et al. (2001), $n = 2$; Refstie et al. (2001), $n = 4$; Refstie et al. (2000), $n = 1$; Skrede et al. (2002), $n = 2$; Storebakken et al. (1998), $n = 1$; Diets: Aas et al. (2006), $n = 1$; Aksnes (1995), $n = 1$; Arnesen et al. (2004), $n = 4$; Bendiksen et al. (2007), $n = 2$; Azevedo et al. (2004), $n = 4$; Bendiksen et al. (2007), $n = 2$; Arzevedo et al. (2004), $n = 4$; Bendiksen et al. (2003), $n = 4$; Bierkeng et al. (1999), $n = 6$; Espe et al. (2006), $n = 1$; Hillestad et al. (2007), $n = 1$; Krogdahl et al. (2001), $n = 3$; Kraugerud et al. (2007), $n = 1$; Krogdahl et al. (2003), $n = 1$; Oli and Krogdahl (1995), $n = 1$; Olsen et al. (2000), $n = 1$; Skrede et al. (2002), $n = 2$; Storebakken et al. (2007), $n = 1$; Krogdahl et al. (2000), $n = 1$; Refstie et al. (2007), $n = 1$; Krogdahl et al. (2007), $n = 1$; Refstie et al. (2007), $n = 1$; Olsen et al. (2000), $n = 1$; Skrede et al. (2007), $n = 2$; Nordrum et al. (2000), $n = 1$; Skrede et al. (2002), $n = 2$; Storebakken et al. (2007), $n = 1$; Refstie et al. (2007), $n = 1$; Olsen et al. (2000), $n = 1$; Refstie et al. (2002), $n = 2$; Storebakken et al. (2008), $n = 1$; Refstie et al. (2001), $n = 4$; Refstie et al. (2001
Phosphorus	Beta general, K–S = 0.0429, K–S = 0.2365	$\begin{array}{l} \mu = 59.90 \pm 18.30, \alpha 1 = 3.860, \alpha 2 = 2.136 \\ (min = -5.171, max = 95.915, \\ \text{for theoretical function}), min = 8, max = 94 \end{array}$	Ingredients: Hua and Bureau (2006), $n = 116$, from 22 studies. Supported by National Academies Press (2011) (see Discussion)
Starches Fibres	Weibull, $K-S = 0.1099$, A-D = 0.5843 Normal (see text)	$\begin{split} \mu &= 62.14 \pm 18.70, \alpha = 62.00, \beta = 19.34, \\ min &= 23, max = 93 \\ \mu &= 10.00 \pm 1.89, min = 0, max = 100 \end{split}$	Ingredients: Hua and Bureau (2009), n = 42 from 26 studies Estimated
Nutrient and moisture	e content of kelps (fraction)		
Saccharina latissima Carbon (DM)	Weibull, $A-D = 0.3125$,	$\mu = 0.252 \pm 0.014$, $\alpha = 1.73 \beta = 0.025$, min = 0.221 may = 0.200 shift = 0.220	This study
Nitrogen (DM)	K-S = 0.1228 Weibull, $A-D = 0.3622$, K-S = 0.1268	$\mu = 0.024 \pm 0.004, \alpha = 2.027 \beta = 0.008,$ $\mu = 0.019 \text{ max} = 0.031 \text{ shift} = 0.018$	This study
Phosphorus (DM)	Extreme value, $A-D = 0.2313$, $K-S = 0.0920$	$\mu = 0.0031 \pm 0.0007$, $\alpha = 0.0028$, $\beta = 0.00052$, min = 0.0022, max = 0.0051	This study
Moisture	Logistic, $A-D = 0.57$ 05, $K-S = 0.1315$	$\mu = 0.904 \pm 0.007, \alpha = 0.904,$ $\beta = 0.004, \min = 86.2, \max = 91.3$	This study
Alaria esculenta			This sector
Carbon (DM)	Weibull, $C-S = 0.00$	$\mu = 0.316 \pm 0.012, \alpha = 13.75$ $\beta = 0.134, \text{ shift} = 0.187$	Inis study
Nitrogen (DM)	Normal, $A-D = 0.1655$, K-S = 0.0945	$\mu = 0.033 \pm 0.003$, min = 0.027, max = 0.041	This study
Phosphorus (DM)	Normal, $A-D = 0.2925$, K-S = 0.1231	$\mu = 0.005 \pm 0.001$, min = 0.003, max = 0.006	This study
Moisture	Extreme value, $C-S = 0.80$	$\begin{array}{l} \mu = 0.863 \pm 0.015, \alpha = 0.857, \\ \beta = 0.012, \text{min} = 0.838, \text{max} = 0.890 \end{array}$	This study
Other distributions			
Economic FCR	Normal, estimated	$\mu = 1.2, \sigma = 0.07$	Reid (2007)
vvaste teed Carbon in proteins	Normal, estimated	$\mu = 0.03, \sigma = 0.006$ $\mu = 0.53, \sigma = 0.015$	кею ет аl. (2009) Porter (1933); Hart et al. (2007)
^a Logistic, extreme va	alue, beta general and Weibull	l distributions are relatively similar in shape to th	at of normal distributions, but differ with respect to skewness and prominence

of asymptotic tail regions. For the domains of logistic and extreme values, $-\infty < x < +\infty$; for beta general and Weibull distributions, $0 < x < +\infty$. ^b $\mu = \text{mean}, \pm = \text{one}$ standard deviation about the mean, $\alpha = \text{continuous location parameter}, \beta = \text{continuous scale parameter}, \alpha 1 and <math>\alpha 2$ are continuous shape parameters for a beta general distribution where both $\alpha 1$ and $\alpha 2 > 0$. For triangular distributions, min and max are continuous boundary parameters and "most likely" is the continuous mode parameter. ^c Chi-square statistic. ^d Taken from graphical data showing whole body composition over time, from \geq 500 g fish upwards to spawning; including males and females. ^e Anderson-Darling statistic. ^f Kolmogorov-Smirnov statistic. ^g ADC typically reported as percent. ^h Dry matter

^h Dry matter.

Equation 2: Nutritional mass balance.

where:

IngestedWeight of feed ingestedFeedAmount of salmon feed offered over a period of growthWaste feedFraction of feed offered but not ingestedDigestedFraction digestedADCApparent digestibility coefficientRetainedWeight of nutrient in carcass at harvestExcretedWeight of nutrient excreted

Equation 3: Spatially weighted culture ratio between species of kelps.

$$Ratio_{area} = \frac{[(D_1/D_2) \cdot Nutrient_2]}{Nutrient_1}$$
(3)

where:

*Ratio*_{area} Multiple of species 2 required to equal nutrient sequestration potential of species 1 per unit culture area

*D*₁ Culture density of species 1

*D*₂ Culture density of species 2

- *Nutrient*¹ Nutrient content in species 1 (expressed in DW and adjusted with moisture content of species 1)
- *Nutrient*² Nutrient content in species 2 (expressed in DW and adjusted with moisture content of species 2)

Instead of single static values for model inputs and outputs, distributions were used for the majority of parameters to make the model semi-stochastic. Simulations were run using @Risk software (version 5.0, Palisade Corporation) operating within Microsoft® Excel (2002). Uncertainty in model parameters was represented through the stratified sampling of input distributions. In general, the frequency at which a value from an input distribution is sampled and run is proportional to the frequency at which the value occurs in the distribution. This also enables the generation of output distributions. The specific stratified sampling technique used is Latin Hypercube, which accurately recreates the probability distribution specified by the distribution type, in fewer iterations compared to traditional Monte Carlo sampling. Latin Hypercube accomplishes this by assigning the cumulative distribution equal intervals where sampling is forced to represent values in each interval (while randomly sampling within the interval) which in turn forces a recreation of the probability distribution input (Palisade, 2006) with less data demand.

Theoretical input distributions (Table 1) are used for model execution. The theoretical distributions are either created by assigning the best fitting theoretic distribution to an actual data distribution, or estimated by assigning a specific set of statistical criteria (*e.g.* shape, mean, standard deviation, etc.) which @RISK uses to generate the theoretical distribution. Model simulations were run for 10,000 iterations to ensure good convergence (*i.e.* additional iterations do not markedly change the shape or statistics of the sample distribution).

7. Input distributions

Model inputs with sufficient empirical sample data were fit with @RISK5.0 Professional (the BestFit module), testing 15 different theoretical distribution types, using maximum likelihood estimators to rank the best fits. The highest ranking theoretical fit was determined using the Chi-squared statistic with equal binning. Where best fits of different theoretical distributions were ranked equally by the Chi-square test, or where variability at the outlying tail regions was excessive, Kolmogorov–Smirnov (less sensitive tail discrepancies) and Anderson–Darling tests were used to assess the fit. In a few instances, where a realistic fit was not possible, theoretical distributions were estimated (described below).

Many of the data in this study are proportional (percent or fraction). Consequently, data distributions will not manifest outside 0– 100 (%) or 0.0–1.0 (fraction), which technically violates an assumption of several theoretical distributions where tail asymptotes stretch to infinity (*e.g.* normal distribution). As the primary role of the theoretical distribution in this model is to generate the most accurate representation of data distribution shape and spread, data filters were applied to the theoretical distribution as dictated by the minimal and maximal values of the initial data distribution. This approach was necessary for practical application of the model and also as a means to reduce the number of outliers contributing to output distributions.

Theoretical input distributions and data sources are detailed in Table 1. While most model parameters are stochastic, nutritional categories of proximate composition of commercial salmon feed are entered as static values. This is because proximate composition is typically listed, by law, on feed bags or totes and readily available for stakeholders of a particular operation. Once salmon reach a certain size (*e.g.* 1 kg), the feed type is typically consistent throughout the grow-out season and a data distribution is arguably not required.

7.1. Nutrient loading component

As a simplifying assumption to assist with model parsimony, it was assumed that large fish (\geq 500 g) made up the vast majority of the grow cycle biomass (see TGC model in Results) and no attempt was made to accommodate potentially differing parameters during the relatively small biomass contribution of small fish during the full production cycle. Consequently, FCR, feed type (static values) and body composition distributions were assumed for large fish across the entire mass balance model.

Lipid and protein ADCs drawn from the literature to create data distributions were taken from either commercial feeds, control diets of experimental studies or in some cases experimental diets where there were no significant differences in digestibly with the control diets. There were not enough ADCs in the literature from practical diets (*i.e.* diets with ingredients that are nutritionally sound, cost beneficial and easily sourced in volume necessary for commercial production) to form a representative data distribution for phosphorus and starch so these data distributions were created using ADCs of individual feed ingredients. Fibre is nearly indigestible to all fish species (National Academies Press, 2011) and there also appears little specific data on fibre digestibility for Atlantic salmon. Consequently, this distribution was estimated; normality was assumed in absence of information to the contrary and standard deviation was estimated using the mean coefficient of variation of ADCs from the other nutritional categories.

Data used to create distributions for Atlantic salmon whole body composition were taken from studies with Atlantic salmon with a weight in excess of 500 g and fed practical diets. A realistic distribution could not be fit to the whole body composition for lipids (*i.e.* not enough data for a good fit), so this distribution was assumed normal and standard deviation was estimated so the minimal and maximal values were approximate for the upper and lower 5% delimiters of the theoretical distribution.

Other distributions that required some estimation were assumed normal, including economic FCR, waste feed, and carbon in proteins. Mean economic FCR was estimated based on industry reports throughout the entire grow-out cycle (Reid, 2007) and waste feed was estimated from reported literature values (Reid et al., 2009). It was assumed that mean carbon content of proteins was 0.525 with

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the upper and lower 5% theoretical distribution delimiters at 0.50 and 0.55 (see Introduction).

Salmon oxygen demand was calculated using the reciprocal of the respiratory quotient (RQ) as a function of post-digestive carbon loss (respiration). As an additional simplifying assumption, it was assumed that all protein catabolism produced ammonia (as oppose to urea), as this is the predominant excretory form (approximately 90%) of nitrogen in teleosts (Smith, 1929). In the model, carbon loss is calculated using carbon content from the various proximate compositions, which each have their own individual distributions. Consequently, carbon content is manifested as an intermediate output distribution which is in turn used as in input distribution to determine the output distribution of oxygen consumption.

7.2. Kelp nutrient content and oxygen supply potential

Nitrogen, carbon, phosphorus and moisture content were measured in kelps randomly sampled from rafts adjacent to salmon cages in the Quoddy Region (Bay of Fundy, New Brunswick, Canada) in May 2010, during kelp harvesting period. As some of these kelps were destined for a food-based market, they were typically harvested before any significant frond erosion occurred so this has not been accounted for in the model. Twenty samples each of *S. latissima* and *A. esculenta* were collected for elemental analysis and each sample was divided into three sub-samples. Seaweed tissue samples were ground to a fine powder and dried at 60 °C for 72 h in a forced air oven. A small amount of dry powder (1 to 3 mg) was weighed (Perkin Elmer AD-6 Autobalance) into a tin capsule and analysed using a Perkin Elmer 2400 Series 2 CHNS/O Elemental Analyzer, with results expressed in mg/g dry weight (DW). Total phosphorus content was measured by a colorimetric technique (Murphy and Riley, 1962).

It is well known that autotrophs such as kelps will consume as well as utilize oxygen depending on the phases of the diurnal cycle (day or night) and other influences. Ultimately, however, autotrophs are net oxygen producers. While there is merit to investigate oxygen supply and demand within IMTA systems in the context of season, time of day, hydrodynamics and spatial concentrations, this is beyond the scope of this study. For the purposes of this study, net oxygen production will be juxtaposed with net nutrient sequestration potential as a means to summarise the general net process. It was assumed that the vast majority of carbon in the kelps was from photosynthetic processes and, consequently, the basic photosynthetic equation (Eq. (4)) was used where two moles of oxygen are liberated for every mole of carbon dioxide converted to sugar.

Equation 4: Basic photosynthetic equation.

$$6CO_2 + 6H_2O = C_6H_{12}O_6 + 6O_2 \tag{4}$$

7.3. Temporal nutrient loading at the farm scale during salmon grow-out

Growth rate was calculated using a variant (Cho, 1992; Cho and Bureau, 1998) of the thermal growth coefficient (TGC), initially proposed by Iwama and Tautz (1981), and is shown in Eq. (5). Temperature data used for TGC estimates were previously collected within an area where salmon aquaculture has been and is presently being practised, including areas presently practising IMTA. Monthly mean historical temperature data from a depth of 5 m collected from 25 different stations in the Passamaquoddy Bay area and approaches (Robinson et al., 1996) were pooled (Fig. 1) and historical growth rates under those temperatures (F. Powell, Cooke Aquaculture Inc., pers. comm.) were used to calculate the TGC. A simulation with an initial fish weight of 60 g was assumed, with 300,000 smolts (an approximate mid-sized fish farm in the region) entering the water in spring, with an assumed harvest weight of 6 kg (whole body weight per fish), over a two year grow-out cycle. Mean loading values per unit growth, generated from the nutritional mass balance model, were used for loading estimates and oxygen demand over the growth cycle.

Equation 5: Growth estimate from thermal growth coefficient.

a)
$$TGC = \left[\left(\sqrt[3]{Wt} - \sqrt[3]{Wo} \right) / (T \cdot t) \right] \cdot 100$$
 (5)
b) $Wt = \left\{ \sqrt[3]{Wo} + \left[(TGC/100) \cdot (T \cdot t) \right] \right\}^3$

where:

TGC	Thermal	growth	coefficient
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- Wt End weight
- Wo Initial weight T Temperature (°C)

T Growth duration (days)

The mean amount of nutrients loaded and oxygen demand from a hypothetical 300,000 fish farm is combined with mean nutrient sequestration ratios and raft culture weight during harvest periods to estimate the total number of kelp rafts needed for equivalent nutrient sequestration. Equation 6: Kelp raft number for equivalent nutrient sequestration.

$$n_{raft} = \frac{\left[Wtr * (Wt - Wo) \cdot n_{fish}\right]}{Wt_{raft}}$$
(6)

where:

n _{raf}	Number of kelp rafts
n _{fish}	Number of fish per site
Wo	Initial fish weight (kg)
Wt	Final fish weight (kg)
WtR	Weight ratio
Wt _{raft}	Weight of kelps harvested (kg) per raft

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8. Results

One kilogramme of Atlantic salmon growth (with a typical commercial feed) results in the excretion of 29.49 ± 4.20 g nitrogen, 2.26 ± 2.25 g phosphorus and the respiration of 243.38 ± 48.28 g carbon. Dissolved oxygen requirements for 1 kg of growth are 455.29 ± 86.24 g.

Mean seasonal temperature values in the Passamaquoddy Bay area and approaches, at 5 m deep are depicted in Fig. 1a. The lowest temperatures occurred in February/March at approximately 1 °C, and the highest temperatures occurred in August/September at just under 13 °C. Atlantic salmon TGC calculated from commercial growth data in the area was 0.300. Peak salmon growth and nutrient loading rates occurred from August to September and the least growth occurred from February to March (Fig. 1a). Both species of kelps are deployed from mid-fall to late spring/early summer and are not present during the period of peak nutrient loading. Over a two year production cycle, if salmon smolts are placed in the water at 60 g and harvested 21 months later, approximately 4 times as much nutrient loading occurs in the second grow-out year (Fig. 1b).

Mean nutrient content (\pm standard deviation) of *A. esculenta* upon harvest for nitrogen, phosphorus and carbon were 33.04 \pm 3.41, 4.79 \pm 0.94 and 315.50 \pm 11.95 mg \cdot g DW⁻¹, respectively, with a moisture content of 86.34 \pm 1.43%. The mean ratios of *A. esculenta* weight required to sequester dissolved inorganic nutrients excreted per unit weight of *S. salar* production were 6.7(\pm 1.5):1 for nitrogen, 4.8(\pm 3.0):1 for phosphorus, and 5.8(\pm 1.4):1 for carbon (Fig. 2). Oxygen could be supplied at a weight ratio of 4.1(\pm 1.0):1.

Mean nutrient content of *S. latissima* upon harvest for nitrogen, phosphorus and carbon were 24.47 \pm 3.61, 3.09 \pm 0.75 and 251.96 \pm



Fig. 1. a) Simulation of biomass and growth of 300,000 Atlantic salmon using mean monthly temperatures for growth estimates over a 21 month grow-out cycle. Salmon smolts are typically (but not always) transferred to cages in April and adults are harvested at approximately 6 kg. Monthly mean temperatures in the Passamaquoddy Bay and approaches are derived from temperatures collected at 25 different stations at 5 m deep (Robinson et al., 1996). b) Theoretical loading of soluble nitrogen and carbon, and oxygen demand. Soluble phosphorus loading followed the same seasonal pattern, but at a magnitude more than ten fold less than that of nitrogen (from a low of <0.0 MT to a high of 1.0 MT per month) and was therefore not included on the graph. The maximal deployment duration of kelps is from November to June/July, with peak biomass at the end of the deployment period.

13.64 mg \cdot g DW⁻¹, respectively, with a moisture content of 90.36 \pm 0.08%. The mean ratios of *S. latissima* were 12.9(\pm 2.7):1 for nitrogen, 10.5(\pm 6.2):1 for phosphorus and 10.2(\pm 2.2):1 for carbon (Fig. 3). Oxygen could be supplied at a weight ratio of 7.2(\pm 1.5):1.

On a per weight basis, A. esculenta can sequester nitrogen, phosphorus, carbon, and supply oxygen at 1.9, 2.2, 1.8 and 1.8 times more than S. latissima, respectively. However, since S. latissima can be cultured at densities 1.5 times greater than A. esculenta, this difference is reduced on a spatial basis. If both species are cultured at their maximal practical culture densities, A. esculenta sequesters nitrogen, phosphorus, carbon, and supplies oxygen at 1.3, 1.5, 1.2 and 1.2 times more than S. latissima per culture area, respectively. For a hypothetical 300,000 salmon farm, full equivalent nutrient sequestration by A. esculenta would require approximately (based on the mean weight ratio) 386, 222, 341 and 208 rafts (with present raft designs) for nitrogen, phosphorus and carbon sequestration, and oxygen supply, respectively, over a 2 year grow-out period for Atlantic salmon. Likewise, S. latissima would require approximately 495, 328, 406 and 248 rafts for nitrogen, phosphorus and carbon sequestration, and oxygen supply, respectively. It is important to note that, since the grow-out period for salmon is approximately 2 years, but kelps are harvested annually, two kelp harvests will occur over a typical salmon production period.

9. Discussion

The results from this study suggest that it is impractical to sequester the full equivalent soluble inorganic nutrient load from a typical temperate commercial salmon farm through deployment of proximate kelp rafts, with any of the nutrients investigated or to supply net oxygen requirements. This should not however, be viewed as a failure of the system as even partial nutrient sequestration can be advantageous. The weight ratio model performed reasonably well, but there are several sources of extensive variation, which make reporting mean weight ratios tenuous, without a qualifying error term.

9.1. Nitrogen

Nitrogen it typically the limiting nutrient in marine systems, and is therefore of greatest concern for the potential to promote eutrophication. Consequently, this nutrient has also been of most interest in marine IMTA systems. While the weight ratios for nitrogen are highly variable, even the best performing kelp species in this study (*A. esculenta*) at the lower 5% delimiter of the nitrogen weight ratio distribution, suggests culture requirements of 4.7 times the weight of salmon for equivalent nutrient sequestration. This is roughly 30% less of the mean nitrogen weight ratio (6.7). Translated into the number of rafts, over 250 rafts would still be required. Even this best case scenario suggests practical limitations for culturing the amount of kelps required for full sequestration.

The commonly used weight conversion factor of 6.25 from nitrogen to proteins (i.e. nitrogen * 6.25 = total proteins) was used in this study. However, there are some limitations to this approach, which relate mainly to the fact that there are nitrogen containing compounds other than amino acids, and this is discussed in detail in National Academies Press (2011). Variation of nitrogen related values in this study may therefore be larger than reported. While it may be



Fig. 2. Weight ratios of the kelp, Alaria esculenta, required to sequester nutrients and supply dissolved oxygen per unit growth of Atlantic salmon (Salmo salar). Delimiters indicate upper and lower 5% of values. Mean ratios are the values reported in the upper right corner of the sub-figures.



Fig. 3. Weight ratios of the kelp, *Saccharina latissima*, required to sequester nutrients and supply dissolved oxygen per unit growth of Atlantic salmon (*Salmo salar*). Delimiters indicate upper and lower 5% of values. Mean ratios are the values reported in the upper right corner of the sub-figures.

theoretically possible to produce such distributions, it is non-trivial and of a scope necessitating a separate study. Nevertheless, our nitrogen excretion values were similar to those found in the literature (Azevedo et al., 2002; Storebakken et al., 2000) and the weight ratio distribution shape (normal) was as expected.

9.2. Carbon

In this study we also explored carbon sequestration. Inorganic carbon such as carbon dioxide in the world's waters has not traditionally been considered an environmental concern to the same degree as eutrophication. However, recent developments with ocean acidification due to increased atmospheric carbon dioxide levels (Denman et al., 2011) have warranted serious concern. There also have been some suggestions that the world's seaweed biomass may act as a considerable carbon sink for anthropogenic CO₂ emissions (Chung et al., 2011). However, these discussions are still in their infancy. In order to supply information for such considerations, appropriate data must be made available and it may be important to consider the carbon removal from the localized marine environment upon harvest of cultured kelps. The carbon in CO₂ from respiring cultured fish will originate from the feed and varying portions of this will be of terrestrial origin. If one of the objectives of IMTA is to remove the inputs associated with aquaculture, soluble carbon may further warrant inclusion. This is obviously a complex issue and the significance of aquaculture as a contributor of carbon dioxide into the world's oceans is presently not well estimated, nor understood. Nevertheless, there may be a roll for carbon sequestration by seaweeds and this potential should be explored. Weight ratios for inorganic carbon were similar to those for nitrogen for both species and, consequently, similar issues of culture space requirements exist.

9.3. Oxygen

Our estimates of oxygen requirement per kg growth were within the ranges reported for salmonids (National Academies Press, 2011). Oxygen supply potential by kelps was investigated in this study as it is a logical extension to potential environmental benefits of nutrient sequestration. While most salmon farms are located in areas with good oxygen supply, addition of large biomass of co-cultured organic extractive species (e.g. shellfish, deposit feeders) will result in additional oxygen demand. Consequently, any benefit to net oxygen supply from IMTA kelps warrants acknowledgement. Given light–dark respiration cycles, and current direction of bi-modal tidal cycles, spatial and temporal oxygen delivery from kelps to co-cultured species (invertebrates and fish) will have to be considered in term of equivalents for the surrounding area (see Introduction).

9.4. Phosphorus

Phosphorus is typically the limiting nutrient in fresh water, so this is also of interest since IMTA is not limited to marine systems. Extensive variation in weight ratios was particularly acute with phosphorus, where highly variable phosphorus loading values contributed to the denominator of the weight ratio for phosphorus. Nevertheless, the variation of phosphorus loading from salmon in this study (2.3 \pm 2.2 g P kg⁻¹) is not dissimilar to that found in the literature with ranges such as 0.0 g P kg⁻¹ (Azevedo et al., 2002) to 10.5 g P kg⁻¹ (Storebakken et al., 2000), depending on the diet. The reliance on phosphorus ADCs of ingredients in the absence of commercial diet ADCs may have contributed some additional variation. Phosphorus ADC values of ingredients for salmonids (mostly studies with rainbow trout) from Hua and Bureau (2006) include a wide range of values including those from experimental diets. Their values were compared with National Academies Press (2011) phosphorus ADCs which included more practical ingredients consumed by rainbow trout. The mean ADC was fairly close with those of Hua and Bureau (2006), where the theoretical distribution produced a mean ADC of 59.9 \pm 18.0%, compared to a distribution generated from National Academies Press (2011) of 61.0 \pm 22.0%. However, data from Hua and Bureau (2006) were chosen for the model because they included most of the meta analysis values from National Academies Press (2011) in addition to others, which resulted in the generation of a better theoretical fit. It should be noted that the shape of the model's phosphorus ADC distribution is beta general (see Table 1), with a stretched asymptotic tail at the lower values, reflective of the handful of low ADC values, presumably from some experimental diets. Consequently, this distribution shape minimally represents these low values with only 10% of iterations that used ADCs lower than 35% for the model simulation. Ideally, an ADC for the specific diet used will reduce this variation substantially, and, in the case of phosphorus, this can be calculated with detailed knowledge of feed ingredients (Hua et al., 2008). It should also be noted that the maximal phosphorus content is twice the minimal phosphorus content for both kelp species, and this wide range will have also contributed to the large variation to the numerator of the phosphorus sequestration ratio. A similar rational was used for the estimation of theoretical distribution of dietary starch ADC, based on a data distribution of starch ingredient ADCs.

The phosphorus weight ratio distribution is cut off at zero just beyond the lower 5% delimiter. This may initiatively seem a result of error propagation but this result is not unexpected. Unlike nitrogen excretion which is "spent fuel" as a result of protein catabolism, phosphorus is excreted when it is present in excess of metabolic requirements that manifests once phosphorus concentration in the blood exceeds a certain threshold (Bureau and Cho, 1999). Consequently, if an optimal amount of phosphorus is being metabolized, there will be little or no phosphorus excretion and the weight of kelps needed to sequester the equivalent amount is zero. However, fish feed with low phosphorus will be more commonly used in freshwater systems to reduce additional loading of the typical limiting nutrient in that environment.

9.5. Thermal growth coefficient

There are a number of limitations in the use of TGCs that should be noted. The TGC assumes growth increases in a steady and predictable manner with increasing temperature, and growth in length at all temperatures increases linearly over time (Jobling, 2003). We know that this is not entirely true for fish growth under all conditions (Björnsson et al., 2001; Dumas et al., 2007; Jobling et al., 1994; Koskela et al., 1997). Nevertheless, TGC has proven its effectiveness for accurately predicting long term growth (Thorarensen and Farrell, 2011) which is the context for which it is applied in this study. It is also understood that TGC typically works well within the range of a specie's optimal growth temperatures, but may not generate accurate results outside of those ranges (Jobling, 2003). Maximal temperatures used to calculate TGCs in this study were just under 13 °C, and it has been reported that TGC is a good predictor of Atlantic salmon growth for temperatures at least as high as 14 °C (Thorarensen and Farrell, 2011). However, the lower range of growth rate in our study, at approximately 1 °C, is probably outside of the lower thermal range required for accurate prediction. Almost no growth occurs in the model while those temperatures are experienced by the fish. Since the calculation of historical TGC was done using growth data from the same conditions, growth, or lack of, during low temperature periods will already be embodied in this particular TGC and this will be reflected in long term growth predictions. Consequently, we believe the application of TGC for the prediction of commercial salmon grow-out over a production cycle for this study is appropriate.

Application of a TGC to estimate monthly biomass and inorganic nutrient loading form a salmon farm, illustrated potential management related challenges for nutrient sequestration. The single year-class requirements per site (required in New Brunswick, Canada) result in a 4 times greater nutrient load in year 2. Equivalent nutrient sequestration by kelps would also require similar scale up the second year, if full sequestration was desired. Consequently, if the number of rafts is fixed, the proportion of nutrient sequestered will be substantially less in year 2.

9.6. Moisture content of kelps

From the predictions in this study, *A. esculenta* appears to have approximately twice the dissolved inorganic nutrient sequestration potential of *S. latissima*. This is based in part on the moisture content of *A. esculenta* which is 4% less than that of *S. latissima*. This may not seem like a large difference but sequestration potential is highly sensitive to moisture content. A difference in moisture content from 90 to 80% will double the dry matter content and, consequently, the nutrient sequestration potential. It should be noted that the differences between these two kelps are based on data at spring harvest times. Moisture content in wild kelps, particularly in *S. latissima*, are known to vary widely, ranging from 75% to 92% depending on the season, part of the organism analysed and shore exposure (Black, 1950). Although in a practical culture scenario, when production densities are considered, the difference in sequestration potential is, however, reduced to 1–1.5.

9.7. Kelps in open-water IMTA systems

Net values of nutrient sequestration and oxygen supply of kelps are intended to be equivalency parameters and not intended to provide insight into the spatial and temporal manifestation of nutrient sequestration and oxygen supply. This model in its present form does not directly address the nuances of kelp placement to maximize nutrient interception, matters of practical production, nor augmented growth or grow-out periods. However, some general observations and inferences can be made. Obviously there will be no sequestration for periods during which the kelps are not deployed. Research is presently conducted on developing cultivation techniques for a few seaweed candidate species which will have their peak biomass production during summer and early fall, hence contributing to an increased year-long biomitigating efficiency of the inorganic extractive component of IMTA systems. It is also clear that it will be easier to sequester a larger proportion of nutrients from year one of the salmon production cycle when fish are smaller and the nutrient load is far less (assuming only one year class at a time is carried through the production area as in southwestern New Brunswick, where the Bay of Fundy is divided into bay management areas).

Seaweed weight ratios necessary for full sequestration from fish farms cannot readily be estimated from most previous studies. However, seaweed culture area required per unit fish production can be estimated from a few studies. These values range between 0.067 and 0.276 ha of seaweed cultivation per metric tonne of annual fish production, required to achieve full equivalent sequestration of nitrogen, depending on the species of seaweed and fish (see Table 2). Applying the same metric to this study, mean nitrogen sequestration can be achieved in A. esculenta and S. latissima, at 0.100 and 0.129 haper metric tonne of S. salar produced per year, respectively (Table 2). It is difficult to directly compare these studies due to parameters such as different spacing between rafts, different environments and different grow-out cycles of fish cohorts. For example, in our study a single fish cohort per site will be produced throughout a two year grow-out cycle, resulting in approximately 4 times more loading in the second year and 2 seaweed harvests per raft will occur during that time. Nevertheless, upon calculating a yearly average for comparison purposes, our results fall within the ranges of seaweed culture area reported for nitrogen sequestration from other studies, despite some system differences. This may suggest that such practical culture limitations exist in general for the use of seaweeds to completely sequester equivalents of soluble inorganic nutrients from commercial fish aquaculture. However, it is interesting to note that while studies in Norway (Broch and Slagstad, 2012), Chile (Troell et al., 1997) and Canada (Petrell et al., 1993) have concluded that the use of seaweeds for complete nutrient sequestration from fish farms is either inconclusive or impractical, Jiang et al. (2010) reported that in Nansha Bay, China, IMTA seaweeds are an effective method to reduce nutrient pollution, despite seaweed culture area per fish production (from their study) at the higher end of estimated ranges (see Table 2). This interpretation may reflect the fact that the scale of seaweed culture in China is magnitudes beyond that which occurs in the western world and that such large scales already exist there in IMTA settings and are also economically viable and socially acceptable.

It should be noted that IMTA kelps are not the only autotrophs to factor into the nutrient dynamics of aquaculture. Other primary producers are also present, such as phytoplanktonic species in the water column and natural seaweed beds in the vicinity, on the bottom and the tidal zone (which is considerable in the Bay of Fundy with abundant coverage by seaweeds). Consequently, not all the dissolved inorganic nutrient loading from fish cages will be available to IMTA kelps, and this may be something to consider in discussions on the effectiveness of nutrient sequestration. Where conditions are favourable, direct increases of primary productivity have been reported near fish cages (Sarà, 2007) and recent evidence suggests IMTA shellfish have increased growth rates due to this process (Sarà et al., 2012). However, there has been no evidence of increased phytoplanktonic biomass at fish cages in the highly hydrodynamic environment of the Bay of Fundy (Harrison et al., 2005).

9.8. Management implications for IMTA

The term "balance" has often been associated with IMTA design (e.g. Barrington et al., 2009), as it intuitively seems a logical and easy to understand endpoint for environmental mitigation, to remove from a system what has been put in. However, "balance" in a general sense may also refer to other aspects of environmental sustainability, economic stability and societal acceptability and this may require further consideration. Interpretation of balance is also a function of spatial scale. The "I" in IMTA (Integrated) should be understood as cultivation in proximity, not considering absolute distances but connectivity in terms of ecosystemic functionalities (Chopin et al., 2010). If the scale is expanded to the bay or regional level, this gives much more freedom for culture placement. This could facilitate kelp raft placement in areas beyond the site lease area of a fish farm, thereby enabling increases in nutrient sequestration at that scale. Further extrapolation to a global scale, shows that annual mariculture (aquaculture in seawater) production is split between 18.1 million tonnes (48.8%) of animal production and 19 million tonnes (51.2%) of seaweed production (FAO, 2012), although the weight ratio approach we present would still need to be applied to account for the various species to determine what culture outcomes would result in a balance of the global mariculture nutrient load. Moreover, if aquaculture is to make a major contribution to the efficient and responsible food production systems of the future, fed and extractive aquacultures will have to be geographically more evenly distributed (presently, 98.9% of seaweed aquaculture takes place in Asia).

While equilibrium is the basis for the weight ratios in this study as a means to provide a metric for effectiveness, the authors suggest that complete dissolved inorganic nutrient balance (100% sequestration) is not necessarily an end point for IMTA systems, as long as the assimilative capacity of the ecosystem is not exceeded. Not all nutrient loading is detrimental and it is in part a function of the assimilative capacity of the receiving environment (Chopin et al., 2012). Nutrients are essential for life and only act as a pollutant when present in excess. Even some portion of nutrient recovery may have positive effects on performance based standards of fish farms and in the broader context of integrated coastal zone management (ICZM).

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Table	2

Nutrient sequestration estimates of seaweeds grown near fish cages in open waters.

Species	Inorganic soluble nutrient	Metric	Seaweed area per fish biomass, for equivalent nitrogen sequestration ^a	Study
Saccharina latissima	Nitrogen	80,000 \times 5 m ropes (80 ha) to remove 10 MT loading from 1000 MT salmon during a 120 day kelp deployment	0.080 ha MT ⁻¹ 120 day ⁻¹ (or 0.240 ha MT ⁻¹ year ⁻¹) ^b	Broch and Slagstad (2012)
Gracilaria chilensis	Nitrogen, phosphorus	1 ha (0.5 kg m ^{-2}) would remove 6.5% of nitrogen and 27% of phosphorus from 227 MT of salmon production	$0.068 \text{ ha } \text{MT}^{-1} \text{ year}^{-1}$	Troell et al. (1997)
G. chilensis	Nitrogen	100 ha required to sequester the load from 1500 MT of salmon production	$0.067 \text{ ha } \text{MT}^{-1} \text{ year}^{-1}$	Abreu et al. (2009)
S. latissima	Nitrogen ^c	10, 60 m ropes at peak kelp biomass would consume between 9–10% of ammonium produced from 12, 10 kg m ⁻³ , salmon cages	-	Petrell et al. (1993)
Undaria pinnatifida, Saccharina japonica, Ulva pertusa	Nitrogen ^c , oxygen	Nitrogen sequestration required for Japanese amberjack, by <i>U. pinnatifida, Saccharina japonica</i> and <i>U. pertusa</i> is 27, 105 and 7.6 kg \cdot m ⁻² of fish farm, respectively. To meet the oxygen demand for Japanese amberjack, from <i>U. pinnatifida, S. japonica</i> and <i>U. pertusa</i> is 0.83, 1.17, and 6.39 (kg wet \cdot fish ⁻¹) ^d , respectively.	-	Kitadai and Kadowaki (2007)
Saccharina, Gracilaria	Nitrogen	To balance output of sea bass, <i>Lateolabra japonicus</i> (75% of fish), and large yellow croaker, <i>Pseudosciaena</i> <i>crocea</i> (25% of fish), 450 m ^b of <i>Saccharina</i> (for the winter–spring load) and 690 m ^b of <i>Gracilaria</i> (for the summer–fall load) are required per cage ^e	0.180 ha MT ⁻¹ for winter-spring (<i>Saccharina</i>), 0.276 ha MT ⁻¹ for summer-fall (<i>Gracilaria</i>)	Jiang et al. (2010)
Alaria esculenta, S. latissima	Nitrogen	0.21 ha rafts producing 13,300 kg FW on ropes and being harvested each year, 0,21 ha rafts producing 19,950 kg FW on ropes and being harvested each year ^f	0.100 ha MT ⁻¹ year ⁻¹ 0.129 ha MT ⁻¹ year ⁻¹	This study This study

^a Estimated from studies in which data were available.

^b Data extrapolated to a full year equivalent including periods in which kelps are not deployed, for comparison purposes.

^c Phosphorus uptake was also measured but not juxtaposed with fish cages.

^d Biomass of fish not reported.

^e 250 kg of fish per cage.

^f Includes periods when kelps are not deployed.

This is the basis for some bioeconomic management approaches, where the removal of some "pollutant" allows greater freedom to expand production of a commodity while still remaining within a sustainable loading threshold (e.g. Roan and Martin, 1996).

10. Conclusion

This study presents a novel semi-stochastic modification to a salmon nutrient loading model and a nutrient sequestration metric for kelps in open-water IMTA system. This approach should provide an easily understood metric for aquaculture stakeholders, to form a basis for practical interpretation of nutrient sequestration potential of various seaweeds during harvesting periods. While study results suggest that it is impractical to sequester the full soluble inorganic nutrient load from a typical temperate commercial salmon farm through kelp culture, a weight ratio approach will still provide useful metrics for farm management and discussions of sustainability. Full sequestration of IMTA nutrients need not be viewed as the only successful endpoint for IMTA as any degree of nutrient sequestration and oxygen supply can have environmental, economic and societal value.

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