Impacts of harmful algal blooms on marine aquaculture in a low-carbon future

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Abstract – The IPCC Special Report on Global Warming of 1.5°C highlights the potential for dietary shifts to reduce greenhouse gas emissions from livestock. Reductions in the consumption of terrestrial animal protein require increases in the consumption of other food categories, to maintain food security, balanced dietary patterns, and protein intake. Aquaculture has long been suggested as one way to meet future food security needs, and marine and estuarine aquaculture in particular is associated with comparatively low greenhouse gas emissions. However, marine and freshwater aquaculture is affected by factors including harmful algal blooms (HABs), which have been increasingly documented around the world, correlated to increases in worldwide aquaculture. In this study, we applied a global multi-region input-output model to capture the direct effects as well as the indirect and induced effects HABs might pose to a global dietary transition from terrestrial livestock to increased seafood consumption from marine and estuarine aquaculture sources. We found that marine and estuarine aquaculture has a substantial potential to replace meat consumption from terrestrial livestock sources, as increases in CO_2 emissions from aquaculture were more than offset by reductions in emissions from mainly cattle grazing and associated land clearing. HABs were found to have a minor monetary impact, but the impact on protein supply was found to be potentially sizeable. For example, in a future setting where 40% of terrestrial protein sources were replaced by aquaculture, a HAB-caused global loss of 5% would set in motion numerous supply-chain cascades, affecting industries auxiliary to aquaculture, indirectly and ultimately reducing protein intake by 10-20%. Such reductions have the potential for pushing parts of Sub-Saharan populations into protein-energy malnutrition. Nevertheless, there remains a significant potential for a dietary transition to increased aquaculture seafood to contribute to reductions in GHG.

Introduction

The Special Report on Global Warming of 1.5°C (IPCC, 2018) highlights the need to reduce greenhouse gas (GHG) emissions from food production (Rogelj et al., 2018). Consuming less meat is seen as the most effective amongst dietary transition options and has human-health co-benefits (Bajželj et al., 2014; Erb et al., 2016; Godfray et al., 2018; IGES et al., 2019; McMichael et al., 2007; Stehfest et al., 2009; Tilman and Clark, 2014). Ambitious shifts to alternative diets have the potential to halve projected increases in food system emissions (Springmann et al., 2018), and contribute one fifth of the reductions needed to keep global warming below 2°C (Griscom et al., 2017). Reductions in meat consumption requires increases in the consumption of other foods, to maintain food security (FAO, 2018a), balanced dietary patterns (Willett et al., 2019), and protein intake (Raubenheimer and Simpson, 2016; Simpson and Raubenheimer, 2005; Willett et al., 2019).

The potential for aquaculture and fisheries as a protein source to ensure future food security has been indicated in many reviews (Gephart et al., 2021; Klinger and Naylor, 2012). Aquaculture is a vector for potentially maintaining sustainable seafood production (FAO, 2018a) given that globally, wild catches have stabilised or decreased (FAO 2018, 2020). Since 1990, aquaculture has grown 527%, the most rapidly growing food production sector (FAO, 2018a). Global aquaculture operations now provide more than half of the world's seafood (inland: 51 Mt, marine: 30 Mt; (FAO, 2018a), see Fig. 2 panel b).

Aquaculture and fisheries generally emit significantly less GHG per kg of food product or protein than most terrestrial livestock (*SI* 1). Of all aquaculture, marine and estuarine aquaculture, which makes up around a third of production, has amongst the lowest GHG emissions per kg. To provide one kg of food product, marine and estuarine aquaculture, excluding macroalgal aquaculture, has been estimated to emit 0.5-7.5 kg of CO_2-equivalents, which is less than or comparable to fisheries (0.9-20.8), poultry (1.5-7) and pork (3-8), but significantly lower than beef (16-40) and lamb (12-28) (Ainsworth and Cowx, 2018; Hilborn et al., 2018; Parker et al., 2018; Parker et al., 2015; Scarborough et al., 2014; Tilman and Clark, 2014). Marine and estuarine aquaculture consists mostly of bivalve molluscs, finfish, and crustaceans, which are grown in coastal ponds or tanks, and floating cages, bags and rafts in estuarine or coastal locations (Klinger and Naylor 2021, Ray et al. 2019; Hasan and Soto 2017; Willer and Aldridge 2020, Hilborn et al. 2018; MacLeod et al. 2020). Life Cycle Assessment (LCA) studies have been used to estimate the GHG/kg edible product of bivalves at 0.5 – 4.0 kg CO_2 equiv/kg product, with a mean among studies of ~2.3 kg CO_2 equiv/kg product, which indicates that it is generally lower than that of finfish production (*SI* 1). Bivalves constitute about half of non-macroalgae marine/estuarine aquaculture production, with finfish and crustaceans constituting the remaining amount (FAO 2020).

Currently, land-based aquaculture supplies more product than marine aquaculture (FAO 2020). However, some countries are constrained in their ability to expand land-based aquaculture, due to land and freshwater scarcity, environmental regulation and other environmental factors (Abate et al., 2016; Costello et al., 2020a). For example, in China, the world's largest aquaculture producer, the amount of land and public waters available for aquaculture has plateaued or even decreased in recent years (Wang et al., 2020). In European and North American countries however, the expansion of marine aquaculture may be restricted by regulations on the use of coastal areas (Silva et al., 2011), and technology can be more difficult for some forms of marine aquaculture. As marine aquaculture may have fewer barriers to expansion in China and many developing countries (Froehlich et al., 2018; Klinger et al., 2017), generally has lower GHG emissions than land based aquaculture, and less requirement for freshwater (Yuan et al., 2019), an expansion of marine aquaculture to compensate for a reduction in livestock-based animal protein is a potential policy option (Costello et al., 2020b).

Climate change is predicted to impact aquaculture, due to ocean acidification, temperature and precipitation changes, biosecurity risks of disease and parasites, and harmful algal blooms (Barange et al., 2018; Froehlich et al., 2018). Ocean temperature, rainfall and ocean acidification changes are expected to occur over the long term, allowing for specific adaptation and mitigation strategies to assist in reducing their impact on aquaculture. However, of the short term impacts on aquaculture, an increased incidence and impact of harmful algal blooms is already being reported (Trainer et al., 2020b).

Harmful algal blooms (HABs) occur when certain species of marine microalgae proliferate in large concentrations and produce highly potent biotoxins that accumulate in seafood, either causing deaths of fish or shellfish or substantially delaying harvest until the toxins can be depurated. Aquaculture is significantly more impacted by HABs than wild capture fisheries (Trainer et al., 2020a), as cultivated species cannot move away from areas where HABs are occurring and may die through water deoxygenation or toxins, and because HABs commonly occur in estuarine or coastal waters where aquaculture is also conducted. Increasing incidences of harmful algal blooms has been found to be highly correlated with increasing aquaculture around the world (Hallegraeff et al., 2021).

Estimates of the cost of HABs to the aquaculture industry have been conducted for the United States (Anderson et al., 2000; Hoagland et al., 2002), Chile (Díaz et al., 2019), Australia (Campbell et al., 2012), European countries (Sanseverino et al., 2016b), Canada, China, Korea and Russia (Trainer et al., 2020a). For example, a HAB event in Chile in 2016 in the Patagonian Fjords led to the deaths of 40,000 t of fish and an estimated economic loss of ~ $US 800 M (Díaz et al., 2019). In China, a bloom of the HAB species *Karenia mikimotoi* in 2012 led to a loss of $US 330 M (Guo et al., 2014). Current global impacts have been estimated at $US 8 B annually (Brown et al., 2020), representing 3.2% of the annual revenue of $US 250 B (FAO, 2020b). These losses comprise the costs of precautionary harvest area closures if suspected biotoxins are present, human health costs (Kouakou and Poder, 2019), costs associated with seafood safety monitoring, and a minor impact due to tourism losses (Sanseverino et al., 2016a). Locally, such as in Chile and Japan, losses can be significantly higher, for example up to 20% of revenue (Díaz et al., 2019; Itakura and Imai, 2014). (Adams et al., 2018) review the literature on the economic consequences of HABs, distinguishing methodologies, data sources, spatial and temporal scopes, as well as species and impact types (Adams et al., 2018).

In this work, we assess how significantly expanded future marine aquaculture could be impacted by HABs. To do this, we proceed in three steps, focusing on defining what we understand by "significantly expanded future marine aquaculture". First, we define desired reductions of red meat consumption, and projected decline of global wild capture fisheries. We then establish the dietary energy and macronutrient loss associated with these meat and wild capture fish reductions. Second, we determine the level of aquaculture expansion that is required to offset these dietary energy and macronutrient losses.

Third, we subject this post-transition food system (less red meat and wild-capture fish, more marine aquaculture) to losses caused by HABs. Here, using a global multi-region input-output model, we are able to capture not only the direct effects of the blooms (termed "*direct output impacts*" by (Adams et al., 2018), but also the indirect and induced effects (Shumway et al., 1988). A number of authors (Athearn, 2008; Dyson and Huppert, 2010; Evans and Jones, 2001) use an input-output model (IMPLAN) for the USA to evaluate the economic consequences of HABs, but do so by using multipliers from a static model. Here, we apply an improved input-output-based disaster modelling method utilising mathematical optimisation to determine the post-HAB economic constellation with minimum output losses.

We report the monetary loss as well as loss of protein inputs as a consequence of potential future HABs. We also report reduced GHG emissions and land requirements as a result of a dietary transition from red meat and wild-capture fish to marine aquaculture, because these environmental benefits would be forgone if HABs limited the expansion of marine aquaculture, and therefore the substitution potential for meat.

Materials and methods

Assessments of effects resulting from changes in the food system require the use of tools that capture entire supply-chain networks, such as life-cycle assessment (Poore and Nemecek, 2018). Here we use a state-of-art life-cycle tool from the Industrial Ecology repertoire – input-output analysis (Malik et al., 2018; Suh, 2009) – and couple this with a technique from the field of disaster analysis (Okuyama, 2007; Okuyama and Santos, 2014).

Input-output analysis

Input-output (IO) databases have enjoyed lasting popularity within Industrial Ecology (Dietzenbacher et al., 2013; Malik et al., 2018; Rose and Miernyk, 1989; Suh, 2009; Suh and Nakamura, 2007). The foundations of input-output analysis have been described in detail elsewhere (Leontief, 1966; Miller and Blair, 2010), and therefore will be reiterated here only inasmuch is required to explain the procedures followed in this work.

Since our assessment covers the entire world, we use a global multi-region input-output (MRIO) database (Isard, 1951; Leontief and Strout, 1963), consisting – as with any IO system – of matrices describing intermediate demand **T** ($N \times N$), final demand **y** ($N \times M$), primary inputs **v** ($K \times N$) expressed in monetary units, and so-called satellite accounts **Q** ($L \times N$) in physical units, for example greenhouse gas emissions in tonnes, and land use in hectares. The global production recipe **A** can be derived from intermediate demand as $\mathbf{A} = \mathbf{T}\left(\widehat{\mathbf{T}\mathbf{1}^{\mathbf{T}} + \mathbf{y}\mathbf{1}^{\mathbf{y}}}\right)^{-1} =$

$:\mathbf{T}(\hat{\mathbf{x}})^{-1}$, where $\mathbf{x} \coloneqq \mathbf{T}\mathbf{1}^{\mathbf{T}} + \mathbf{y}\mathbf{1}^{\mathbf{y}}$ is called total output (N×1), $\mathbf{1}^{\mathbf{T}} = \left\{\underbrace{\mathbf{1},\mathbf{1},\dots,\mathbf{1}}_{N}\right\}$ and $\mathbf{1}^{\mathbf{y}} = \{\underbrace{\mathbf{1},\mathbf{1},\dots,\mathbf{1}}_{M}\}$ are summation operators fitting **T** and **y**, and where the hat symbol (^) denotes vector diagonalization. The fundamental IO accounting identity is readily derived from product and industry balances, and reads $\mathbf{x} = (\mathbf{I} - \mathbf{A})^{-1}\mathbf{y} =: \mathbf{L}\mathbf{y}$, where **L** is the famous Leontief inverse, covering the entire – in our case global – supply-chain network. The monetary formulation can be extended to reflect quantities of pollution and resource use (Leontief and Ford, 1970, 1971) as $\mathbf{F} = \mathbf{Q}(\hat{\mathbf{x}})^{-1}\mathbf{L}\mathbf{y} =: \mathbf{q}\mathbf{L}\mathbf{y} =: \mathbf{m}\mathbf{y}$, where **F** ($L$×$M$) holds – in our case – greenhouse gas emissions and land use embodied in final demand **y**, **q** describes the environmental and resource intensity of production, and where **m** are environmental and resource multipliers. In contrast to intensities **q**, multipliers **m** include impacts across the entire supply-chain underpinning a final demand bundle **y**.

Data for **T**, **y**, **v**, and **Q** were taken from a tailored data build in the Global MRIO Lab (Lenzen et al., 2017); the dimensions of the matrices used in this work are N = 52 regions × 53 products = 2756 intermediate sectors[1] (*SI* 4), M = 52 regions × 6 final demand actors[2] = 312 final demand destinations, K = 52 regions × 6 primary input sources[3] = 312 primary input origins, and L = 2 physical satellites (greenhouse gas emissions and land use – *SI* 5).[4] Primary data for greenhouse gas emissions and land use are from EDGAR v5.0 Global Greenhouse Gas Emissions (Crippa et al., 2020) and FAOSTAT database (FAO, 2018b), respectively.

Given the importance of food categories for this study, and considering that monetary data sources on food consumption are not comprehensive for all countries, we undertook additional data curation after the table build in the MRIO Lab. We first replaced all MRIO entries on wild fisheries and aquaculture with values from FAO's FishStat repository (FAO, 2020a). Second, we adjusted all MRIO entries so that they adhere to the World Bank's compilation of global household expenditure surveys (World Bank, 2017). We finally calibrated monetary consumption data in the MRIO's final consumption block (first column in **y**) against food balances on dietary energy and macronutrient intake (FAOSTAT, 2019a). Because these data are cast in monetary and energy units, respectively, bridging information on dietary energy and macronutrient content and on commodity prices is required. The former is readily available from the USDA National Nutrient Database for Standard Reference (USDA, 2019) as energy coefficients (in kJ/100 g) and coefficients for protein, fat and carbohydrate (in g/100 g). Macronutrient coefficients are converted into energy units using mass-specific energy contents (17 kJ/g for protein, 27 kJ/g for fat, and 17 kJ/g for

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[1] Throughout the presentation of results, we distinguish between "aquaculture" and "aquaculture products", in accordance with National Accounts conventions, which delineate sectors of the economy into primary (extraction), secondary (manufacturing) and tertiary (services) producers. When primary and secondary producers offer similar commodities, such as fish (raw) and fish (processed), National Accounts distinguish the two by calling the secondary (manufactured) output "product".

[2] Household final consumption, Non-profit institutions serving households, Government final consumption, Gross fixed capital formation, Changes in inventories, Acquisitions less disposals of valuables.

[3] Compensation of employees, Taxes on production, Subsidies on production, Net operating surplus, Net mixed income, Consumption of fixed capital.

[4] The 2756 sectors constitute 52×53 region-product pairs that are arranged linearly across the 2756 rows and columns of input-output matrices and the $\boldsymbol{\Gamma}$ matrix. For example, element 53 is product 1 made in region 2.

carbohydrates). Since there exists no globally comprehensive source for commodity prices, data were generated first by comparing monetary and mass values for international commodity trade by country (UNSD, 2019b), and then complemented with producer price data on crops, livestock and food items (FAOSTAT, 2019b). The resulting global prices π_i^r for commodities *i* produced in regions *r* must satisfy equivalence between a) food consumption $\sum_{i,r} y_{i1}^{rs}$ as stated in the MRIO table, and b) measured per-capita energy and macronutrient balances n^s in consuming regions *s*, as follows:

$$n^s = \sum_{i,r} \frac{v_i y_{i1}^{rs}}{P^s} \pi_i^{r\,-1} =: \sum_{i,r} G_i^{rs} \pi_i^{r\,-1} , \tag{1}$$

where y_{i1}^{rs} is the MRIO entry describing the consumption in region *s* of commodity *i* produced in region *r*, v_i is the energy and macronutrient content of commodity *i* re-classified from data in (USDA, 2019) into MRIO products by means of a binary concordance matrix, and P^s is the population in region *s* (UNSD, 2019a). Taking the price set generated from Comtrade and FAOSTAT as an initial estimate $\pi_{i,0}^{r\,-1}$, food-balance-compliant prices π_i^r are determined via quadratic minimisation of $\sum_{i,r}\left(\pi_i^{r\,-1} - \pi_{i,0}^{r\,-1}\right)^2$, subject to eq. 1. For further details see *SI* 9.

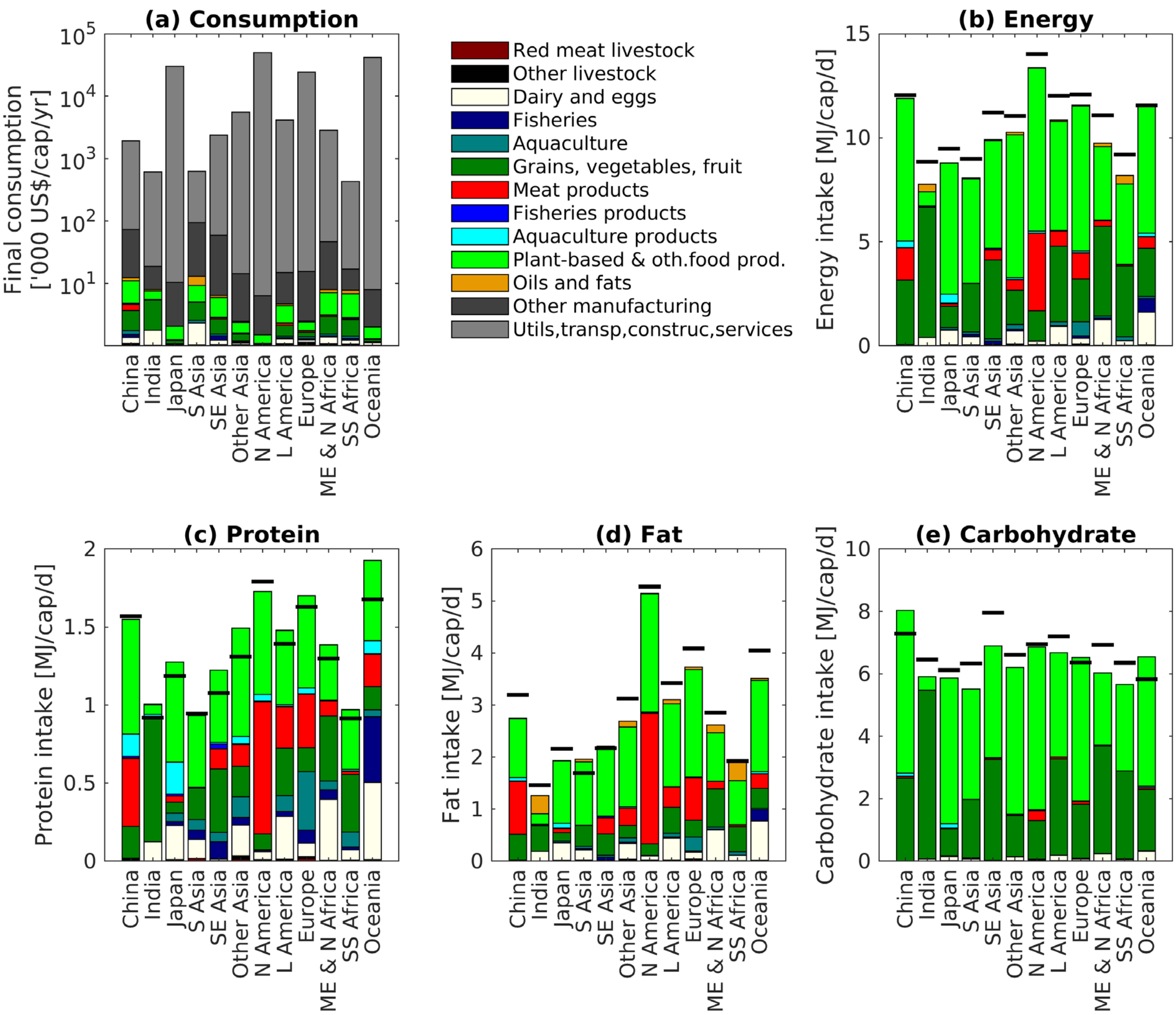

Fig. 1: Food system features by commodity and region. a) Expenditure, b) dietary energy (see also *SI* 3), c) protein intake, d) fat intake, and e) carbohydrate intake. Black horizontal lines in panels b) – e) represent reported food balances (FAOSTAT, 2019a).

Disaster analysis

Since our study concerns food systems, and food is primarily destined for final consumers (households), we focus on the effects of declines in production of final consumption possibilities, and accordingly use the disaster analysis by (Steenge and Bočkarjova, 2007). Here, pre-disaster total output $\mathbf{x}_0$ (N×1) is subjected to fractional changes assembled in the so-called events matrix $\mathbf{\Gamma}$ (N×N), so that immediate post-disaster output is $(\mathbf{I}-\mathbf{\Gamma})\mathbf{x}_0$. Steenge and Bočkarjova's original method leads to negative final demand (Faturay et al., 2020), especially for large shocks. Whilst in a national setting, negative final demand can be interpreted as reliance on assistance from other countries, such an interpretation does not make sense in a global application (Dietzenbacher et al., 2019). We therefore use a modified analysis variant (Faturay et al., 2020), formulated as a quadratic optimisation problem in which we minimise the departure $(\tilde{\mathbf{x}}-\mathbf{x}_0)^2$ of post-disaster output $\tilde{\mathbf{x}}$ from pre-disaster output $\mathbf{x}_0$, subject to two conditions: i) post-disaster output is limited to $\tilde{\mathbf{x}} \leq (\mathbf{I}-\mathbf{\Gamma})\mathbf{x}_0$, and ii) post-disaster final demand net of existing stocks must be strictly non-negative: $\tilde{\mathbf{y}} = (\mathbf{I}-\mathbf{A})\tilde{\mathbf{x}} \geq \min(\mathbf{0}, \mathbf{y}_{\mathrm{St}})$. Existing stocks $\mathbf{y}_{\mathrm{St}} < 0$ allow industries to continue sales for a limited time, despite their production downturn. The vector $\tilde{\mathbf{y}}$ holds post-disaster consumption possibilities, the quantity of interest in this work. Because of the involvement of **A** and **L**, these consumption possibilities capture effects throughput the global supply-chain network, and include spill-over effects into regions and economic sectors that are not directly hit by the disaster. Environmental and resource impacts d**F** of the disaster can be estimated from the difference of pre- and post-disaster consumption as $\mathrm{d}\mathbf{F} = \mathbf{m}(\tilde{\mathbf{y}}-\mathbf{y}_0)$. This disaster method has been used in prior work, for example on severe space weather events (Schulte in den Bäumen et al., 2014), floods (Schulte in den Bäumen et al., 2015), tropical cyclones (Lenzen et al., 2018), earthquakes (Faturay et al., 2020), the coronavirus pandemic (Lenzen et al., 2020), and the effects of climate change on local food supply (Malik et al., 2020).

Three-step procedure

First, we define desired reductions of red meat consumption, and projected decline of global wild capture fisheries. Second, we determine the level of aquaculture expansion that is required to offset these dietary energy and macronutrient losses. Third, we subject this post-transition food system (less red meat and wild-capture fish, more marine aquaculture) to losses caused by HABs. Within this procedure, we refrain from choosing specific levels of reductions, but instead investigate the effects of 1% declines in global red meat output and wild-caught seafood harvest. This is because i) the IPCC itself offers a wide range of possible mitigation pathways (IPCC, 2019a), all based on human preferences, ii) methods for analysing the effects of economic interventions work best for marginal changes, and cannot represent well the likely non-linearities resulting from large shocks, and iii) our results for 1% declines can be extrapolated to provide an indication for the possible effects of more severe changes to the food system. For example, the IPCC lists a "no animal-source food" option amongst its pathways, and 2½-fold increases in the consumption of seafood have been suggested (Springmann et al., 2018; Willett et al., 2019).

The first step – a dietary transition involving a 1% reduction of red meat consumption, and a 1% decline of global wild fisheries – is therefore defined by setting $\Gamma_{ii}^{(1)} = 0.01$ for i ∈ {lamb, beef, wild-caught seafood}, and $\Gamma_{ii}^{(1)} = ½ \times 0.01$ for i ∈ {meat products}, assuming that 50% of meat products derive from lamb or beef (there exist no globally complete IO data to distinguish the origin of processed meat products).

Second, we determine the level of aquaculture expansion that is required to compensate the dietary energy and macronutrient loss $-\Delta n^s$ from the first step by solving

$$-\Delta n^s = \sum_{i,r} \frac{\nu_i \Delta y_{i1}^{rs}}{P^s} \pi_i^{r-1} = \sum_{i,r} \frac{\nu_i}{P^s \pi_i^r} y_{i1}^{rs} \gamma_i^{rs} =: \sum_{i,r} H_i^{rs} \gamma_i^{rs} \quad (2)$$

for γ_i^{rs}, with i ∈ {aquaculture} and r not land-locked. Again, this is done via quadratic minimisation, this time of additional expenditure on aquaculture products $(\Delta y_{i1}^{rs})^2$. The γ_i^{rs} (< 0, because this is an expansion) are then used to populate the $\Gamma_{ii}^{(2)}$, and the whole scenario is defined by $\mathbf{\Gamma}^{(1)} + \mathbf{\Gamma}^{(2)}$.

Third, we subject the post-transition food system to aquaculture losses caused by harmful algal blooms, by setting $\Gamma_{ii}^{(3)} = 0.032$ for i ∈ {aquaculture} (current losses; (Brown et al., 2020), and defining the whole scenario by $\mathbf{I} - \left[\mathbf{I} - \left(\mathbf{\Gamma}^{(1)} + \mathbf{\Gamma}^{(2)}\right)\right] \otimes \left[\mathbf{I} - \mathbf{\Gamma}^{(3)}\right]$.

Results

Steps 1 and 2: Substitution of red meat and wild-caught seafood with aquaculture-derived seafood

We determined the expansion of global aquaculture production required to meet the dietary energy and macronutrient shortfalls brought about by reductions in red meat and wild-caught seafood consumption, by solving eq. 2 for minimum additional expenditure on aquaculture products, subject to adherence to food balances, and excluding land-locked countries (Fig. 2).

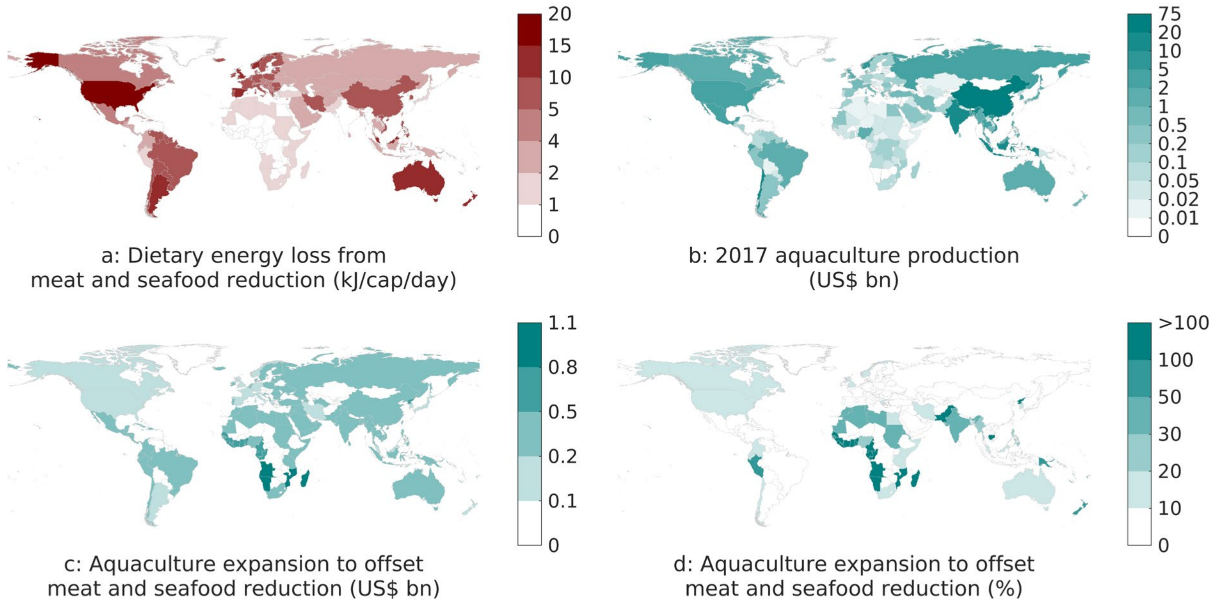

Fig. 2: Reduction in dietary energy intake resulting from a 1% reduction in meat and wild-caught seafood consumption (scenario 1, in kJ/cap/day panel a); world aquaculture production (in US$bn panel b); and aquaculture expansion that is required to compensate the dietary energy and macronutrient loss from meat reduction (scenario 2, in US$bn panel c, and in % panel d).

Dietary energy loss (mostly from protein and fat) is highest in affluent countries across Europe, North America, Argentina, Australia and New Zealand (Fig. 2 panel a; compare with dietary patterns in Fig. 1). Current aquaculture operations are concentrated around South, East and South-East Asia, Chile, Norway and Oceania (panel b). Guided by minimising overall cost, our optimisation algorithm places additional aquaculture output into low-cost developing countries (see Fig. *SI* 2.1), notably in coastal Africa (panel c). Preference is given to domestic markets, because again, domestic sources of seafood tended to be less expensive than imports in many countries. As a result, for established producers such as China, Japan, Vietnam, Indonesia, Chile and Norway, the upscaling is relatively small, also because suitable coastal land areas are often already occupied, and expansions are costly. In contrast, for other countries, such as Angola, Namibia, Mozambique, Madagascar, Peru, Pakistan, Cambodia and Papua New Guinea, these expansions would mean establishing entirely new aquaculture capacity (panel d). The potential for this in terms of the suitability of conditions is discussed in the Discussion section. Exceptions are New Zealand and to a lesser degree Australia, which despite established aquaculture industries are allocated further significant increases. This is because New Zealand mussels and Australian salmon are farmed at a lower cost compared to other developed countries, such as Japan, Norway or Canada (Fig. *SI* 2.1). Globally, an up to 10% increase in aquaculture is needed to compensate for a 1% reduction in meat and wild-caught seafood consumption, which is understandable given that the global turnover of the latter two industries exceeds 1 trillion US$.

Step 3: Impacts of a dietary transition, and of harmful algal blooms on a post-transition aquaculture industry

Here, we present results for a 1% decline in meat and wild-caught fish consumption (step 1), compensated by an energy- and nutrient-neutral scale-up of aquaculture (step 2), and followed by a HAB-caused 3.2% loss of aquaculture (step 3). As explained in the Introduction, in addition to the monetary loss and loss of protein input as a consequence of potential future HABs, we also report reduced GHG emissions and land requirements as a result of a dietary transition from meat to marine aquaculture. Whilst the former are direct losses, the latter can be regarded as environmental benefits forgone if HABs limited the expansion of marine aquaculture, and therefore the substitution potential for meat.

Clearly, a dietary transition (scenarios 1 and 2) leads to net reduced GHG emissions and land use, in our case of –0.2% and –0.8%, respectively (Fig. 3, columns 1 and 2). Increases in CO_2 emissions from aquaculture are more than offset by reductions in emissions from mainly cattle grazing and associated land clearing (Gasser et al., 2020; Houghton et al., 2012; IPCC, 2019b), as well as reductions in CH_4 emissions from enteric fermentation and manure, and reductions in CO_2 emissions from fishing fleets and meat processing. These reductions far exceed emissions from aquaculture operations, including processing (see SI 1). More specifically, the magnitude of the net effects can be understood by considering that i) land clearing for grazing and livestock are responsible for about 12% of global emissions, 1% of which is 0.12% as shown by the livestock and fisheries column segments in Fig. 2; and ii) land use for grazing represents 60% of agricultural land, 1% of which is 0.6%, as in the column segments. Emissions and land use effects play out in a major way in Latin America, mainly Brazil, where rainforest land is cleared at high rates for establishing cattle ranches (Cederberg et al., 2011; Karstensen et al., 2013; Lenzen et al., 2013).

The increases in land use due to aquaculture are exclusively indirect, and due to land requirements of industries providing operating inputs for aquaculture (compare with an analysis by (Froehlich et al., 2018); for further details, see *SI* 6). These are land-intensive livestock by-products (eg beef meat and bone meals (Hua et al., 2019), beef tallow for shrimp (Nates, 2017), vegetable proteins and cereal grains (eg soybeans, barley, rice, peas, canola, lupine, wheat gluten, corn gluten (Naylor, 2016)) for fish feed pellets, or wood and other materials for marine structures such as fish pens, mussel rafts and oyster racks. Plant proteins and oils are increasingly used as alternative feeds because of the unsustainability of fishmeal production (Rust et al., 2011).

It is interesting to see that the effects of a transition spill over into non-animal sectors, such as grains growing, plant-based products and other manufacturing, which can be explained by inter-industry transactions, for example of grains for feedlots, meat and fish contained in food products classified as 'other', or reductions in machinery sales to livestock farms. In addition, a significant part of landings of global marine fisheries are directed towards non-food purposes (Cashion et al., 2017).

As expected from the relatively small size of the aquaculture industry turnover, current global impacts of HABs (8 US$bn or 3.2% annually; (Brown et al., 2020) have a minor impact on monetary consumption levels, but the impact on protein supply is sizeable (Fig. 3, columns 3 and 4). The magnitude of the net effects can be understood by considering that i) even after compensating for a loss in meat and fish consumption, global aquaculture still only represents about 1% of global turnover, on which HABs would then impose a 3.2% or 15.4 US$bn decline;

and ii) seafood supplies about 15% of global protein intake (WHO, 2020), 3.2% of which is about 0.6%, as in the column segments. Whist these global percentages appear small, local impacts in aquaculture industries might be considerably large. In addition, loss of protein availability would not just affect regions hosting aquaculture operations, but also spill over into other regions, because of international trade.

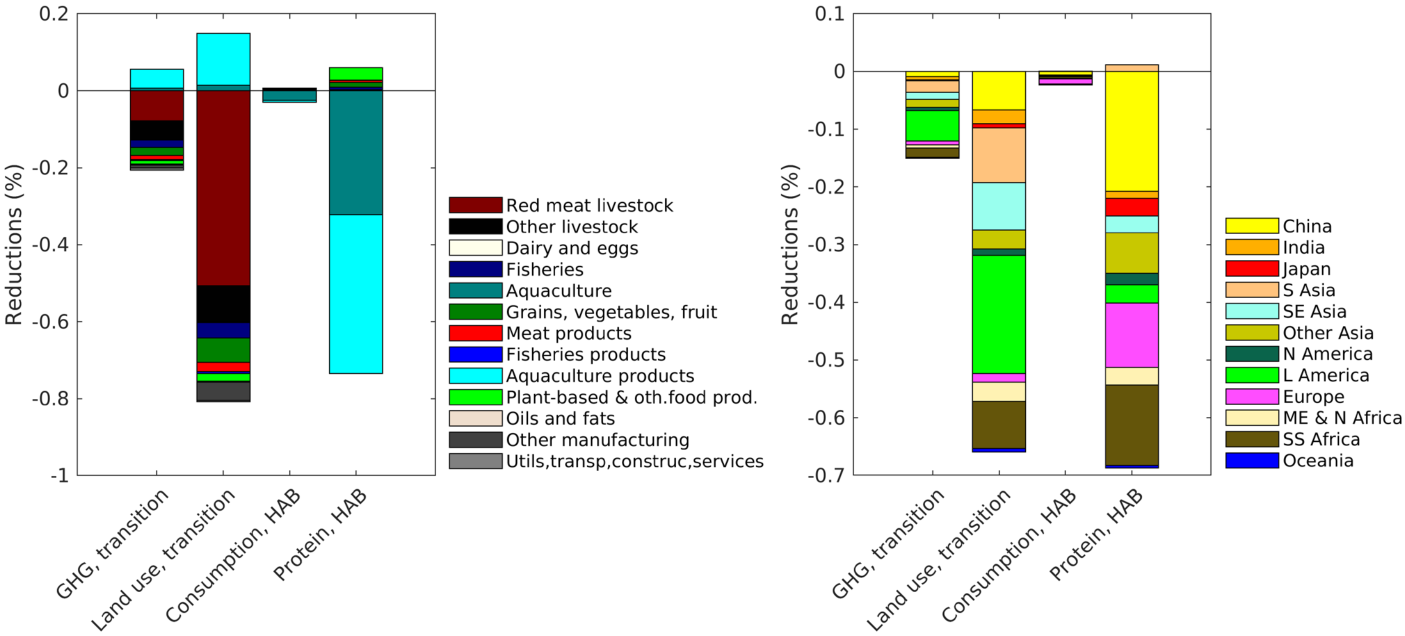

Fig. 3: Impacts on GHG emissions and land use resulting from a 1% reduction in meat and wild-caught fish consumption (scenarios 1 and 2, columns 1 and 2); and impacts on consumption possibilities and protein availability in a post-transition world, resulting from a HAB-caused 3.2% reduction in aquaculture (scenario 3, columns 3 and 4). Impacts are shown as percentage of world totals, by commodity (left panel) and region (right panel). For reference, total GHG emissions are 53 Gt CO_2-e, total land use is 10.4 billion hectares, and total household consumption is 48 US$tn.

Interestingly, grains and plant-based products experience a small increase in consumption possibilities and protein supply. This is a particular feature of the method initially devised by Steenge and Bočkarjova, where increases in consumption possibilities in a post-disaster world arise out of industries not having to supply to customers affected by a disaster, and thus their output becomes available for consumption by others. In our case, these increases are the grain- and plant-by-products used in aquaculture for fish feed (Rust et al., 2011). It is therefore questionable whether these increased consumption opportunities would be taken up by households.

Sensitivity analyses indicating impacts of larger reductions and HABs

The analysis described in the previous section is based on values for 1% meat and seafood reductions, and 3.2% aquaculture losses due to HABs. We now extend the range of possible outcomes, up to 50% relative reductions and losses (Fig. 4).

For 10% meat and seafood reductions, and 10% HAB-related losses, our model yields losses of consumption possibilities of up to 130 US$bn. These are mainly caused by the reduction in red meat and wild-caught seafood. HAB-related aquaculture losses are less than 30 US$bn, mainly because even after replacing 10% of red meat and wild-caught seafood, aquaculture would still represent a (globally) relatively small industry, with 10% of losses representing an even smaller part. This of course changes once dietary transitions become significant, because then aquaculture would become a globally significant industry, and HABs would be of major concern (Fig.4, panels a-c). The same reasoning holds for HAB-related protein loss (panel f), which only becomes significant in scenarios where global aquaculture becomes sizeable after replacing around 40% of terrestrial livestock. Larger-scale transitions (eg 10%) would be accompanied by significant reductions of greenhouse gas emissions (–1.4%) and land use (–4.5%; panels d and e). Relative land use reductions exceed relative emissions reductions, because cattle grazing occupies the largest land areas globally, whereas aquaculture's land requirements are negligible in comparison.

All scenarios show increasing non-linearity for reductions and losses above 10% (all panels, especially panel c), leading to protein losses exceeding HAB-related direct damages when dietary transitions approach 45% (panels a and f). These non-linearities – eventually becoming instabilities beyond 50% transition – are a direct consequence of damages spilling over from final demand into intermediate demand as disaster events (the Γ-matrix entries) scale up, setting in motion unmitigated supply-chain cascades. For example, ongoing and large HAB events and related aquaculture facility shutdowns would lead to reduced demand for all kinds of aquaculture inputs, such as electricity, diesel, chemicals, equipment and plastic consumables, and thus indirectly cause shutdowns in other parts of the global economy. These in turn will affect secondary auxiliary industries, such as fossil fuel extraction, ore mining, refining, and fabricated metal manufacturing. These knock-on effects will eventually loop back on the aquaculture industry itself, causing losses additional to the initial, HAB-induced losses. These supply-chain ripples are the key mechanisms at work in the disaster methods by (Steenge and Bočkarjova, 2007) and (Faturay et al., 2020).

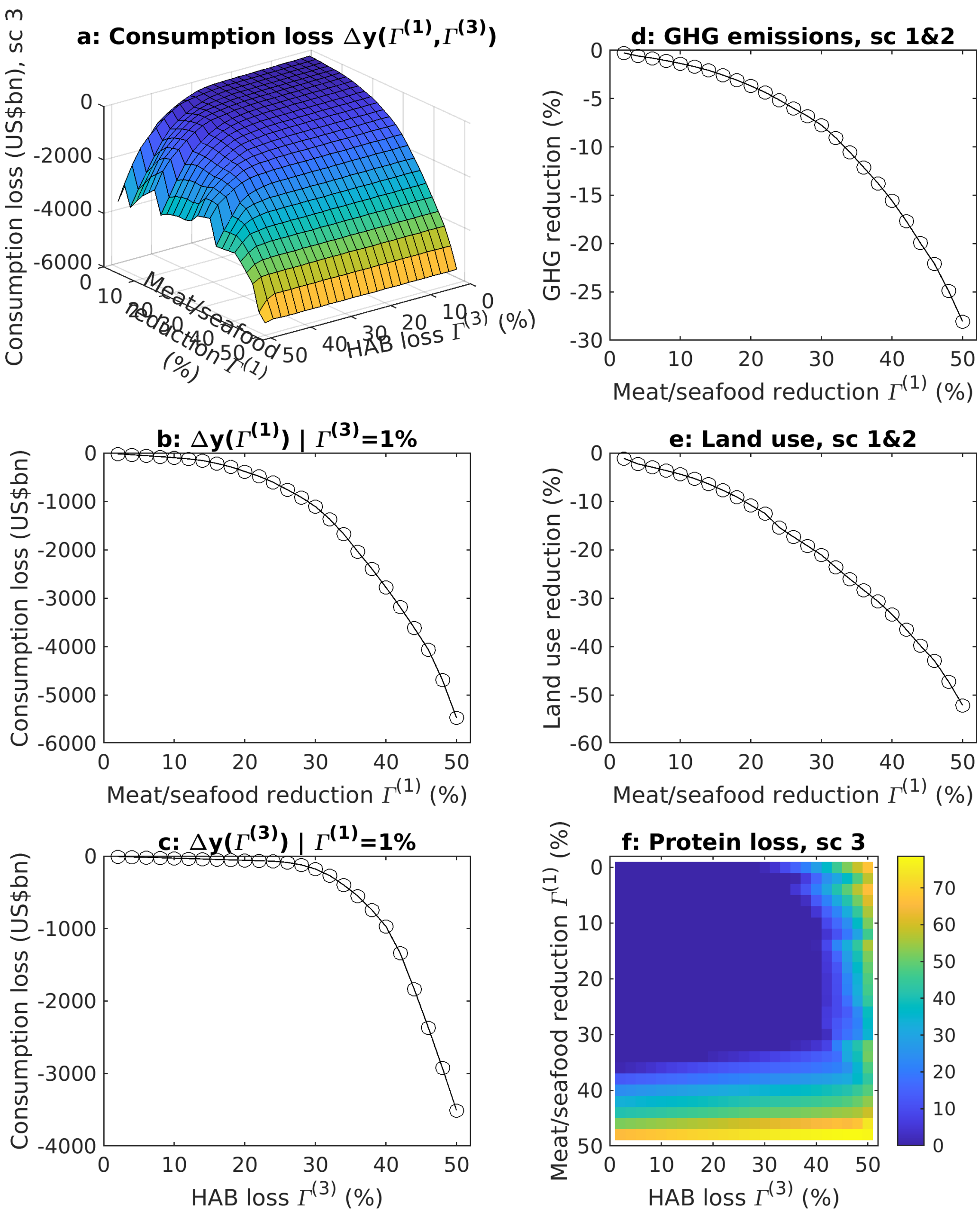

Fig. 4: Sensitivity analysis of consumption losses, and greenhouse gas emission and land use changes, for meat and seafood reductions (scenario 1), and HAB-related losses (scenario 3), of up to 50%. Panel a: Consumption loss as a function of meat/seafood reduction and HAB loss; panels b and c: marginal slices of the 2-D function in panel a, for 1% meat/seafood reduction and HAB loss; panels d and e: reductions in greenhouse gas emissions and land use as a function of meat/seafood reduction (independent of HAB losses – see Fig. *SI* 7.3); panel f: protein loss as a function of meat/seafood reduction and HAB loss. Individual graphs are reproduced in *SI* 7.

Discussion

Methodological qualifications

The results of this analysis are affected by a number of sources of uncertainty. First, entries in (MR)IO tables are affected by measurement errors (Bullard and Sebald, 1977). Whilst these can be large for small industries, and range beyond 100% relative standard deviation, the results reported here are the outcome of significant aggregation, for example in the matrix sums ($\mathbf{T1^T} + \mathbf{y1^y}$) and products ($\mathbf{qL}(\tilde{\mathbf{y}} - \mathbf{y}_0)$). Quantitative simulations have shown that – facilitated by so-called error propagation – relative standard deviations of such aggregate quantities are usually below 10% (Heijungs and Lenzen, 2014). In this work, we have ensured maximum accuracy for important entries, by calibration of the MRIO table against FishStat (FAO, 2020a), global household expenditure surveys (World Bank, 2017), and food balances (FAOSTAT, 2019a). Second, in static-IO theory, the inference of changes in greenhouse gas emissions and land requirements from changes in economic output assumes strict linearity, and does not consider for example elastic demand responses to price signals or slack production capacity. As such, impacts tend to be over-estimated for larger economic shocks. Third, the disaster method by Steenge and Bočkarjova leads to negative final demand, which again is a result of the strict linearity of the static IO system, and its inability to include slackness (Faturay et al., 2020). Prior work has sought to dampen the "explosion" of impacts for large shocks (see Fig. 4), by preventing shortfalls of minor, non-essential inputs from transmitting ripple effects from the initial shock (Schulte in den Bäumen et al., 2014). However, the threshold for excluding non-essential inputs is largely arbitrary, and addressing these issues is the aim of future work. Fourth, pinning down global commodity prices (as described in the Methods section) is fraught with uncertainty, because reported monetary trade and consumption data do not conform with measured physical data from food balances, thus necessitating adjustment of prices. Misreporting of international trade shipments between supplier and recipient (see Fig. 2 in (Lenzen et al., 2012) leads to price outliers of up to 1000 US$/kg and 1 US¢/kg (Fig. *SI* 3.1). However, these outliers are associated with small transactions, and do not distort our overall results. Fifth, estimating the magnitude of future fish stock collapses due to overfishing, and future dietary changes is uncertain and/or based on assumptions about human behaviour. Instead of settling on particular scenarios, we have chosen to offer a sensitivity analysis instead. Sixth, exactly solving eq. 2 to determine the level of aquaculture expansion that is required to compensate the dietary energy and macronutrient loss from read meat and wild-caught seafood reductions is not always possible. Scaling up the output of a particular supplying region affects all receiving regions, and in some regions more than necessary dietary energy and macronutrients will be available. These inaccuracies play out in the future protein scenarios in panel f of Fig. 4, but their effect on overall results is small.

The findings for large-scale transitions and HAB events (Fig. 4) need to be qualified. On one hand, large-scale economic upheaval is likely to spill deep into supply-chain areas initially untouched by HABs, and affect an increasing range of directly or remotely auxiliary industries. However, on the other hand, economic interdependency is not rigid, and producers can – especially in the long term – adjust operating inputs, thus avoiding some of the transmission of exogenous shocks throughout the economy. An example for such an adjustment are aquafeeds based on microalgae (Shah et al., 2018; Shields and Lupatsch, 2012; Tibbetts, 2018), which can replace unsustainable fishmeal, fish-oil, and plant-based feeds.

Expansion of marine and estuarine aquaculture

In recent years, research has increasingly indicated that globally, aquaculture can continue to expand and play an important role in replacing wild capture fisheries and ensuring future food security (Costello et al., 2020a; Gephart et al., 2021; Klinger and Naylor, 2012; Kobayashi et al., 2015; Willer and Aldridge, 2020). While freshwater aquaculture forms the bulk of current production, our study has focused on marine and estuarine aquaculture, as: 1) it is generally associated with lower GHG emissions per kg of protein than freshwater aquaculture, due to the more frequent use of recirculation systems, and the production of nitrous oxide and methane emissions (MacLeod et al., 2020; Yuan et al., 2019), 2) it has a lower requirement for potentially scarce freshwater resources (Yuan et al., 2019); 3) land scarcity and environmental regulation may impede the expansion of land based aquaculture (Abate et al., 2016; Costello et al., 2020a; Wang et al., 2020). Marine and estuarine aquaculture has been acknowledged as an area for sustainable growth of food resources; for example, an international panel on the ocean economy (Costello et al., 2019) found that a combination of sustainable development of marine aquaculture and improved fisheries management could supply >6× more food product than it does today with comparatively low environmental impacts.

The scope for regional expansion of aquaculture in particular countries depends on ocean use constraints such as zoning restrictions on coastal waters, amongst other factors. This issue has been reviewed in recent years (Garlock et al., 2020). In terms of specifically marine aquaculture, an expansion in offshore cobia (*Rachycentron canadum*), Atlantic salmon (*Salmo salar*) and blue mussel (*Mytilus edulis*) aquaculture has been modelled (Kapetsky et al., 2013). In that study, Brazil, India, Taiwan, Indonesia, Australia, Venezuela and the USA were nations with amongst the greatest area to expand their industries, based on an analysis of cost and the availability of suitable oceanic conditions (temperature, currents, etc) for species' growth in national marine Exclusive Economic Zones (Kapetsky et al., 2013). Similar to this study, they found that coastal African nations had substantial potential to expand their marine and estuarine aquaculture industries or develop new industries, in particular, Madagascar, Libya, Mozambique, South Africa, Nigeria, Algeria, and Angola (Kapetsky et al., 2013), as well as countries in Asia and Latin America. A study analysing countries with suitable conditions for expanded bivalve aquaculture found that substantial additional capacity was available in China, Venezuela, Senegal, Sierra Leone, India and Myanmar (Willer and Aldridge, 2020). These authors found that some areas of West Africa, South Asia and South America showed particularly potential for the expansion of bivalve aquaculture, due to their high mean annual chlorophyll a concentrations and additional nutrient sources (Willer and Aldridge 2020). In our study, factors such as suitable oceanic conditions were not included in the scenarios, and the fact that similar regions were identified in our study (countries of West Africa, South Asia, west coast of South America, Australia and New Zealand) as having the potential for the expansion based on economic factors indicates that these regions may be particularly suitable for expansion.

In terms of GHG, fed aquaculture species such as fish generally have higher GHG than non-fed species such as bivalves (MacLeod et al., 2020; Willer and Aldridge, 2020), which have amongst the lowest GHG of any animal protein source. The need to reduce the environmental impact of aquaculture feeds in GHG emissions and other environmental impacts has been discussed (Klinger and Naylor, 2012), and potential solutions to replacing products in fish meal so as to lower GHG is an important consideration that may impact future scenarios.

In this study, we have modelled aquaculture seafood as a replacement for meat from terrestrial livestock based on its protein (macronutrient) content. It is important to note that seafood also contain substantial micronutrients, generally not as readily available in terrestrial food sources, that may assist in reducing micronutrient deficiencies in populations in many areas of the world, and that an expansion of seafood in diets has been advocated for that purpose (Hicks et al., 2019; Willer and Aldridge, 2020). These include calcium, iron, omega-3, zinc, vitamin A and vitamin B12 (Hicks et al., 2019).

Impact of HABs on future expansion of marine aquaculture

While the expansion of marine and estuarine aquaculture has advantages in terms of its comparatively lower GHG emissions (Ainsworth and Cowx, 2018; Hilborn et al., 2018; Parker et al., 2018; Parker et al., 2015; Scarborough et al., 2014; Tilman and Clark, 2014), its growth has the potential to be limited by incidences of HABs. An increase in reports of HABs around the world has been reported, related to regional factors including climate-change driven increases in seawater temperature, leading to range expansions of HAB species and increases in their seasonal growth windows, increases in species growth rates, and other oceanic changes such as increased ocean stratification and changes to coastal current velocities (Ajani et al., 2017; Hallegraeff, 2010; Jardine et al., 2020; Murray et al., 2016). The expansion of aquaculture itself was found to be strongly correlated with reported increases in HABs (Hallegraeff et al., 2021), which may be related to increased water quality monitoring and surveillance, as well as the retention of fish in small areas, where they may be more susceptible to HAB toxins.

While our study uses data from across the marine aquaculture sector, some commercially grown fish and invertebrate species are likely to be more susceptible to certain types of HABs than others, and therefore, the choice of species is important. Certain bivalve molluscs can accumulate HAB toxins at substantially faster rates (up to 100-fold) than other species, and are therefore likely to require more frequent and longer harvest area closures (Bricelj and Shumway, 1998; Farrell et al., 2015; Reizopoulou et al., 2008; Rourke et al., 2021). For example, mussels and scallops have been found to take up marine biotoxins at faster rates than oyster species (Bricelj and Shumway, 1998; Farrell et al., 2015; Rourke et al., 2021), thus impacting their susceptibility to the economic impacts of HABs. Farmed fish are generally not susceptible to marine biotoxin accumulation, and are instead impacted by 'fish-killing' HABs that may occur less frequently. However, these impacts are potentially large scale and may result in the mass deaths of fish (Díaz et al., 2019), which could have a much larger economic impact than temporary harvesting area closures impacting bivalve aquaculture.

A further consideration is that some countries expanding their marine and estuarine aquaculture seafood production for export markets rather than domestic consumption, as modelled in this study, would likely require assistance to improve their HAB and other water quality monitoring programs to ensure seafood safety as part of quality assurance programs.

They may require assistance from international agencies in order to obtain training and infrastructure for these programs.

Conclusions and outlook

By applying a global multi-region input-output model capturing direct, indirect and induced effects, we have confirmed that marine and estuarine aquaculture has a substantial potential to replace meat consumption from terrestrial livestock sources. We found that increases in CO_2 emissions from aquaculture were more than offset by reductions in emissions from mainly cattle grazing and associated land clearing. HABs were found to have a minor monetary impact on marine and estuarine aquaculture, but the impact on protein supply was found to be potentially sizeable. For example, in a future setting where 40% of terrestrial animal protein sources were replaced by aquaculture, a HAB-caused global loss of 5% would set in motion numerous supply-chain cascades, affecting industries auxiliary to aquaculture, indirectly and ultimately reducing protein intake by 10-20%.

WHO and FAO guidelines (FAO, 2001; WHO, 2002) recommend safe protein and energy intakes around 0.6-1 g/day/kg body mass, and 160-200 kJ/day/kg body mass. Given the protein energy content of 17 MJ/g, these values translate into minimum protein requirements of 6-8% of dietary energy. Fig. 1 shows that in India and Sub-Saharan Africa, about 12.5% and 11% of energy intake, respectively, comes from protein. Given that these are regional averages, the unequal distribution of protein intake means that protein-energy malnutrition occurs in certain countries and low-income segments of populations, amounting to a global rate of about 2,000 cases per 100,000 people, and causing more than 200,000 deaths in 2019 (IHME, 2021). In addition, animal experiments (Hernández et al., 2008) have shown mild protein malnutrition setting in below 7.2% of dietary energy. For those world regions where protein intake is above 15% (Fig. 1 panel c), intensified HABs would likely not shift diets below the recommended protein range. However, in regions such as Sub-Saharan Africa and India, HABs causing 10-20% protein loss could push parts of populations into protein-energy undernutrition. This is especially the case for Sub-Saharan Africa, where our analysis has identified potential for new aquaculture expansion (Fig. 2 panel d).

Nevertheless, there remains a significant potential for a dietary transition to increased aquaculture seafood to contribute to reductions in GHG despite the occurrence of HABs. These results will be of benefit for policy development by organisations of global governance, such as the FAO and the IPCC, and can contribute to FAO's mandate in assisting stakeholders in the implementation of sustainable fisheries and aquaculture development while reducing GHG emissions. An expansion in marine aquaculture species associated with the lowest GHG emissions such as marine bivalves, would likely maximise these benefits relative to an expansion of species with higher impacts, as long as such expansion was undertaken in regions of world with lower potential HAB problems. Future studies should model these differences among aquaculture species and regions in greater detail.

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