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Sustainable integration of aquaculture into existing food production sectors

A dissertation submitted in partial satisfaction of the
requirements for the degree Doctor of Philosophy in
Environmental Science and Management

by

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Abstract

Sustainable integration of aquaculture into existing food production sectors

by

Jessica L. Couture

As the global human population grows and the middle class widens, resources are becoming increasingly scarce and today's highly interconnected food systems require complex solutions. Freshwater supplies and land to expand agriculture is limited, as is the capacity to assimilate pollution from excess nutrients and greenhouse gas emissions. Since the 1970s fisheries catches have stagnated. Meanwhile, aquaculture has rushed to meet growing seafood demand and has become one of the world's fastest growing food sectors. In order to avoid competition for land and water resources, aquaculture is increasingly moving offshore, where it is encountering new conflicts with capture fisheries. Maintaining healthy wild capture fisheries while sustainably expanding aquaculture offshore will be important to ensuring diverse and robust seafood supply into the future, so understanding the interactions between these coupled sectors will be important to their responsible co-management. This work seeks to understand ways to sustainably develop aquaculture into an increasingly resource scarce and uncertain future. The work here highlights some of the most pressing issues is aquaculture development and identifies pathways to more efficient food production and co-management.

A primary environmental burden of aquaculture comes from their feed, which are comprised of capture fisheries products and crops that could be used directly for human

consumption and can have high environmental footprints associated with them. Novel feed ingredients have been developed to reduce reliance on these human-food inputs, namely, single cell proteins (SCPs), and may also decrease the environmental impacts of aquaculture feeds. SCPs are protein-rich non-human food inputs that can reproduce quickly and efficiently. My first chapter considers SCP ingredients in compound aquaculture feeds and compares the environmental footprint of replacing conventional ingredients with these emerging inputs. This work focuses on salmon feeds produced in Norway, the world's largest producer of farmed salmon and leader in aquaculture development, to be able to more fully investigate the tradeoffs and nuances of the feed production system. The second chapter places these ingredients in the context of global feeds by considering the potential role of these ingredients in animal production more broadly. Specifically, I project meat consumption into the future and compare the relative importance of shifting human versus animal diets in the overall greenhouse gas impacts of meat production.

By placing aquaculture in marine environments, farms initiate additional interactions with wild species and capture fisheries. Chapter three simulates several impacts of ocean farms on wild capture fisheries. I use a theoretical bioeconomic model to predict how changes to movement and access to wild species at a farm might affect population and fishing dynamics in order to inform siting and co-management of these highly connected systems. This dissertation incorporates multi- and interdisciplinary approaches to address some of today's biggest food production challenges, calling upon industrial and population ecology, economics, and statistical and theoretical modeling methods.

This work finds that novel feed inputs -- particularly single cell protein meals -- can decrease environmental impacts of aquaculture feeds, of particular note are single cell yeast

protein meals. While bacteria meals can decrease demands for land and impacts on eutrophication, their potential for further environmental benefits are less certain. In the larger context of global livestock production, yeast protein meals can decrease impacts of meat production, and both human diets and inputs to feeds can help decrease impacts of meat production into the future. In the third chapter I conclude that ocean farms can benefit wild populations and fisheries catches when stocks are overfished by allowing populations to recover through de facto protection within the boundaries of the farm. Smaller farms can provide more benefits to fisheries compared to large contiguous farms of the same size due to increased access to protected and recovered stocks, although strong farm-level management is important to ensure neutral or positive direct impacts to wild populations to optimize benefits from farms. These results are geared to inform strategic planning and management of aquaculture and some of the key industries with which it interacts to guide more sustainable food systems into the future.

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Chapter 1: Environmental benefits of novel non-human food inputs to salmon feeds

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1.1 Introduction

More efficient food systems are needed to feed a rapidly growing human population in environmentally sustainable ways. How to feed >9 billion people by the year 2050 (FAO 2016) is a major question, but doing so without further degrading or destroying natural ecosystems and their capacity to support food production adds a significant degree of difficulty. Our challenge is exacerbated by a clear trend indicating that as a country develops economically, and per capita income rises, there follows a shift in human behavior towards greater consumption of animal-based products, specifically meat-eating (Tilman and Clark 2014; He et al. 2018). The FAO estimates that from 2010 to 2050 food production must increase by 70% and meat production in particular must increase ~100% to meet increased demand (FAO 2009; Alexandratos and Bruinsma, n.d.). But animals must be fed to produce meat, and today most animal feeds are comprised of crop-based cereals, legumes, and seeds that require large tracts of land to grow. These crop-based feeds are also composed mainly of the same food stocks that much of the world's human population, located in the least developed countries, depend upon for their nutrition (Solomons 2000; Darnton-Hill and

Coyne 1998). Clearly there is need to develop new sources of animal feeds that do not reduce our overall capacity to feed humans, and that minimize further demand on strained resources.

Seafood is an important source of protein that can help alleviate some of the major challenges facing food production systems. Wild fisheries have historically provided most of our seafood but recently aquaculture, which includes both freshwater and ocean-based mariculture, has overtaken wild caught fisheries in seafood-based protein production (FAO 2018). An important player in these trends is Atlantic Salmon (*Salmo salar*), whose farmed production has recently overtaken total wild production of the major salmon species, statistics that continue to diverge (FAO 2018). In terms of revenue produced by mariculture, Atlantic Salmon is the highest valued fish species (FAO 2018). A top carnivore, salmon are initially bred and reared in land-based freshwater facilities but the majority of growth occurs in the coastal ocean pens. Salmon grow very rapidly to large sizes thereby requiring large amounts of protein-rich food. Rapid expansion of salmon farming has generated great demand for salmon feeds, which now represent the highest cost in salmon production and comprise the majority of the environmental impacts of salmon farming (Pelletier et al. 2009; Ellingsen, Olaussen, and Utne 2009). As such, developing low cost, environmentally less-impactful feeds is one of the biggest obstacles to aquaculture sustainability.

Globally, the aquaculture industry used ~40 million tonnes of feed in 2012, an amount that has grown at an average annual rate of 10.3% per year since 2000 and is expected to reach over 65 million tonnes by 2020 (Tacon and Metian 2015). For carnivorous species such as salmon, fish-based feed ingredients (i.e., fishmeal and fish oil) enhance growth rate mainly by providing essential amino acids and lipids (Tacon and Metian 2015). Through innovations, the conversion rate of 4 kg of fish-based ingredients in feeds to 1kg of

salmon biomass has decreased to <1:1, due mainly to the emergence and use of alternative, mostly plant-based ingredients. The alternatives have been developed primarily because of the rising cost of fishmeal and oil, as well as a growing concern about overfishing vulnerable wild fish stocks (Tacon and Metian 2008; Naylor et al. 2009). In response, fish nutritionists and health scientists have produced an impressive array of alternative salmon feed ingredients to replace fish-based inputs while maintaining rapid growth and survivorship rates in salmon (Tacon and Metian 2008; Papatryphon et al. 2004).

Replacements for fish-based ingredients are usually plant based, with soy inputs making up most heavily used substitutes (Tacon, Hasan, and Metian 2011). Soy has high protein and lipid content and other important essential nutrients, which make them great substitutes for nutritious fishmeal and oil ingredients. As a result, soy is now found in almost all aquaculture feeds (Tacon, Hasan, and Metian 2011; Storebakken, Shearer, and Roem 1998; Gatlin et al. 2007; Kissil et al. 2000; P D Adelizi et al. 1998). Impacts on wild fisheries and overall costs associated with predominantly fish-based feeds have declined by integrating soybean and other crops (e.g., wheat, corn, rapeseed) but other environmental costs have apparently increased. Recent studies indicate that intensified crop production, and soy in particular, has increased land conversion and use in farming (Willaarts, Niemeyer, and Garrido 2011; Gutzler et al. 2015; Pellegrini and Fernández 2018). Saponins in soybean meal can cause enteritis in salmon which leads to slower growth (van den Ingh, Olli, and Krogdahl 1996; Knudsen et al. 2008; Krogdahl et al. 2015; Heikkinen et al. 2006; Marjara et al. 2012), a limitation that can be overcome by condensing the soy product further into soy protein concentrate. Condensing soy, however, requires a greater total input of soy per unit of salmon, which in turn requires additional land use, energy and other limited resources

(Dalgaard et al. 2008). Finally, and perhaps most importantly for human welfare, using soy and other products as alternatives in salmon feed reduces their availability for direct human consumption, particularly for the least food-secure people living in less developed countries which depend primarily on crop-based foods (Solomons 2000; Darnton-Hill and Coyne 1998). Use of these important protein-rich crops to produce high value products such as salmon diverts these important and accessible resources away from those who most need them. Further exacerbating the issue, feeding crops to livestock is inefficient energetically because energy conversion rates between trophic levels is low (Pauly and V. Christiansen 1995). To address these inefficiencies and inequalities, the livestock feed industry is working to develop feeds that minimize human-food ingredients, with the intended outcomes being increased supply of human-food resources and reduced environmental impacts (Tacon and Metian 2015; Schader et al. 2015; Ytrestøyl, Aas, and Åsgård 2015; Tallentire, Mackenzie, and Kyriazakis 2018).

Emerging single cell proteins (SCP) make up a diverse group of promising feed ingredients (Tallentire, Mackenzie, and Kyriazakis 2018). SCPs, which include methanotrophic bacteria, *Methylococcus capsulatus* (Bath), and a common yeast, *Saccharomyces cerevisiae*, are fast growing, protein-rich organisms that are produced at relatively low cost in closed, controlled environments. SCP-derived nutrients are naturally high in protein but can also be manipulated to meet different nutritional requirements, including salmon diets (Tacon, Albert G. J. 1987). Methanotrophic bacteria oxidize methane into carbon dioxide, which would generate climate change benefits if the methane was to be otherwise released into the environment (Cumberlage, Blenkinsopp, and Clark 2016). Salmon fed *M. capsulatus* diets resulted in increased growth compared to salmon fed soy-

based diets. Bacteria-inclusive feeds may also produce healthier fish through bioactive components that enhance gut health in Atlantic salmon (Øverland et al. 2010; Romarheim et al. 2011). For centuries, *S. cerevisiae* yeast have been used for centuries for human consumption in foods like beer and bread and were traditionally grown on simple sugar media. In order to conserve resources yeast producers, particularly those producing yeast for animal feeds, have used byproducts from other industrial processes to feed the yeast cells, such as wheat grains from biofuels production (Tallentire, Mackenzie, and Kyriazakis 2018). These low resource methods are being further improved upon by sourcing more non-human food inputs, such as algae and lumber byproducts, to feed cell propagation (Department of Animal and Aquacultural Sciences at the Norwegian University of Life Sciences, 2016). Whether the replacement of human-food ingredients with SCP ingredients in salmon feeds could decrease the overall environmental impacts of salmon farming has yet to be determined.

High environmental impacts of feeds in aquaculture production are well documented (Pelletier et al. 2009; Ellingsen, Olaussen, and Utne 2009; Boissy et al. 2011) and further studies indicate that fish-based ingredients in salmon feeds have higher impacts than soy-based feeds (Papatryphon et al. 2004; Boissy et al. 2011). Still, nutritionists and fish farmers understand the importance of fish ingredients in feeds for carnivorous fish (Papatryphon et al. 2004; Boissy et al. 2011), therefore, salmon feeds today minimize fish inclusion while maintaining nutritious diets. With fish ingredients at a minimum, focus has turned to increasing sustainability of feeds through other highly demanded ingredients, particularly soy (Dalgaard et al. 2008). Here we test whether the replacement of soy-based ingredients in salmon feed with protein-rich bacteria and yeast can further reduce the environmental

impacts of Atlantic salmon production. The use of life cycle assessments to measure the environmental impacts of seafood products is becoming more common, and provides a way to compare disparate production methods (fishing versus aquaculture, different feeds, etc.) side-by-side (Ziegler et al. 2016). We use attributional life cycle assessment (ALCA) to compare the impacts of soy protein concentrate against bacteria meal and yeast protein concentrate directly, then also compare feeds in which soy ingredients are replaced with either bacteria- or yeast-based ingredients. Environmental performance was assessed based on seven resource use and emissions metrics. Results are intended to inform feed producers, salmon industry, researchers, consumers and consumer awareness campaigns of the tradeoffs between current and emerging feeds and feed inputs. There are many different ways to assess environmental impacts from food production; while the use of LCA is growing in popularity, it is important to remember that LCA does not measure all environmental impacts equally well and should be complemented with other types of assessments.

1.2 Methods

ISO-compliant ALCA was used to assess the environmental impacts of replacing soy ingredients with novel single cell protein (SCP) meals, focusing on resource use and emissions to the natural environment (ISO 2006). We first compared these ingredients directly by assessing the impacts of soy protein concentrate compared to bacteria meal and yeast protein concentrate. Bacteria meal is produced through fermentation of methanotrophic bacteria, harvest of bacteria cells, which are condensed and dried into a meal. Yeast Protein concentrate production uses the wheat byproduct of biofuels production, which is fed to yeast cells, which are similarly harvested, condensed and dried into a meal. The wheat must also be treated with enzymes to make the sugars available to the yeast cells. These meals were

compared on an equal protein basis: 660g of protein, which is the protein content of 1kg of soy protein concentrate. Two feed analyses were also conducted. One assessed how total feed impacts change when soy protein concentrate is replaced by the SCP meals on an equal protein basis, with all other ingredients held constant (Feeds Analysis 1, FA1). FA1 allows for comparison of the different protein meals in a whole feed context without conflating the meal impact differences with impact changes due to varying the non-target ingredients. In the second analysis, soy protein concentrate is replaced by the SCP meals on an equal mass basis and non-target ingredients were adjusted to meet the nutrient requirements of salmon, they were formulated to have equal protein and lipid levels (Feeds Analysis 2, FA2). FA2 is believed to be a more realistic scenario in commercial feed formulations. All products were assessed from cradle-to-factory-gate at the industrial scale. System boundaries for the three analyses are defined in Figure 1. In each analysis, each of the three treatments were assessed based on the following seven midpoint impact categories: climate change impacts, acidification, aquatic eutrophication (freshwater and marine separately), land occupation, water consumption, and primary production requirement (Table S1).

ReCiPe (Goedkoop et al. 2009; Huijbregts et al. 2016) methods (v.1.11) were used to calculate environmental impact indicators for all impact categories except land occupation and primary production requirements (PPR) (Table S1). Climate change impacts quantify all emitted greenhouse gases converted to kilograms of CO₂-equivalent (Huijbregts et al. 2016). We excluded biogenic carbon from this analysis since any uptake of carbon in crop material will quickly be digested and respired through consumption of the food items by salmon and human consumers in a relatively short timespan so no true sequestration is achieved (BSI 2011). Acidification impacts measure the emissions of acidifying compounds from the

process (SO_x, NO_x, NH₃). Aquatic eutrophication (freshwater and marine) impacts were considered separately since each system is limited by different nutrients (kilograms of phosphorous and nitrogen, respectively). Land occupation measures the total area of land occupation (m²) per portion of a year (a) from agriculture, urban and transformation activities (Goedkoop et al. 2009). Freshwater consumption was measured in meters cubed of water removed from the local watershed (Huijbregts et al. 2016). For simplicity of analysis and interpretation the land occupation and water consumption indicators used here are accounting metrics and lack characterization factor calculations. PPR is quickly becoming an important impact indicator in food and aquaculture LCAs with developments still emerging (Table S1). The calculations used here employed the methods of Cashion et al. (2016), which uses Pauly and Christiansen's (1995) equation for primary production requirement with updated trophic level and trophic efficiency data (Pauly and V. Christiansen 1995; Cashion et al. 2016; Libralato et al. 2008; FAO 2018). PPR was calculated for each feed ingredient and weighted sums were used to assess the total PPR for each feed. Impacts from fish-based ingredients were calculated using species specific data for transfer efficiencies (Libralato et al. 2008) and trophic level (FAO 2018) while standard values were used for carbon content (Pauly and V. Christiansen 1995) and inclusion in fishmeal and fish oil for all input fish species. PPR values for plant-based ingredients were sourced from the literature (Pelletier et al. 2009) and weighted based on their inclusion in each feed.

These three analyses compare how impacts will change with replacement of soy ingredients with novel SCP meals. The meal analysis compares soy protein concentrate, bacteria meal and yeast protein concentrate at equal protein levels (660g protein). Since the meals have different protein concentrations, the masses of meals differ for this analysis: 1kg

soy protein concentrate, 0.94kg bacteria meal, 1.07 kg yeast protein concentrate. The FA1 analysis is based on a standard industrial salmon feed use in Norway which uses 25% soy ingredients. These ingredients are directly replaced with one each of bacteria meal and yeast protein concentrate at masses that maintain equal protein levels for the entire feed (Table 1). The FA2 analysis similarly replaces the soy ingredients with the novel feeds, while also maintaining consistent lipid levels by varying the other ingredients in the feed. Total feed masses as well as inclusion of fish ingredients, fishmeal and fish oil, were held constant in the FA2 feeds (Table 1). Full product inventories are documented in the supporting information file: “customProcessesLCI.xlsx” for review and reuse (Kuczenski 2018).

Since the feed commodities market fluctuates widely, and therefore commercial feed compositions as well, the standard feed used in this study was formulated based on the relative amounts of feed ingredients imported by the Norwegian fish feed industry in 2016 (Norwegian Agricultural Agency and Statistics Norway 2017) and balanced to meet the nutritional needs of salmon. This feed includes fishmeal and soy protein concentrate as the main protein ingredients. Mineral and vitamin mixes were included at a consistent rate in all feeds but comprised only 2% of the total feeds so were excluded from this analysis. Globally, Norway is the largest producer of farmed salmon, so we assumed production of all three feeds occurs in Oslo, Norway and transportation (Searates 2018) of feed ingredients to Norway were based on the sourcing and imports data from the Norwegian government (Norwegian Agricultural Agency and Statistics Norway 2017).

Data for our analyses were gathered from a variety of sources. Feed formulations were designed with the goal of achieving nutritional balance between the feeds. Through close collaborations with industry we understand that feed formulations change often and

quickly, so we use Norwegian imports data combined with nutritional requirements to guide the formulation of the standard feed and design the novel feeds to match this nutritionally (Table 1). Data for the novel meals were more difficult to acquire. Bacteria meal data were obtained directly from a company producing bacteria meal at an industrial scale. Yeast protein concentrate production data were sourced from Tallentire et al. (2018). Data for input ingredients to these feeds were mainly sourced from the Thinkstep Professional Extension and EcoInvent databases (EcoInvent 2016; “Professional Database 2018: GaBi Software” 2018). Additional data were gathered from the scientific literature (Table S2).

Economic-based allocation was used for the many inputs that are co-produced in this analysis. Price allocation was employed for all input ingredients since production and use of input resources is driven by the more valuable product. Also, no common nutritional allocation (calories, protein content, etc.) exists for the co-produced pairs. A sensitivity analysis of allocation choice compared results from economic versus mass allocations. To test sensitivity of results to our assumption that production occurs in Norway, we also model production of the FA1 in high salmon producing (farming) and geographically disparate locations: Chile and British Columbia, Canada. Data for these analyses used imports data from each country to determine the sources of feed ingredients and calculate transportation distances from the source locations (Government of Canada 2018; Data Chile 2018; Searates 2018).

Life cycle assessments come with large uncertainty in data and methods, but unfortunately uncertainty for this analysis was hindered by lack of actual uncertainty measures and use of uniform distributions would not add to the results.

1.3 Results & Discussion

Based on the data used here, the novel meals are able to decrease environmental impacts of protein meals and feeds compared to human food, soy-based ingredients and feeds. These benefits are realized at varying degrees due to trade-offs between environmental performance and nutritional quality of the SCP meals (Figure 2). For all of the impact indicators tested, yeast protein concentrate had much lower impacts than soy protein concentrate. Bacteria meal was also able to decrease impacts for most indicators compared to soy protein concentrate with two exceptions: climate change impacts and freshwater consumption, for which bacteria meal and soy protein concentrate had similar impacts. Low impacts of the yeast protein concentrate give the yeast-based feed lower overall impacts in the FA1 feed compared to the standard feed. The bacteria-based feed showed similar impacts to soy protein concentrate for five of the seven indicators and lower impacts in the remaining two, with impacts matching the yeast-based feed. Despite yeast protein concentrate having lower environmental impacts at the protein level, higher protein and lipid levels in the bacteria meal result in equal impacts in five of the seven indicators from their respective FA2. Low climate change and water consumption impacts of the yeast feed relative to the other two feeds make it the overall lowest impact feed for the FA2 analysis (Figures 2C and 3). Sensitivity analyses of the geographic location and allocation methods show that these assumptions only modestly affect the results and did not change the overall findings.

1.3.1 Meals

For all seven environmental indicators assessed, soy protein concentrate had or was among the highest impacts of the three meals. Yeast protein concentrate showed the lowest impacts for all indicators except primary production requirements (PPR), and had the lowest

impacts overall. Both SCP meals performed better than soy protein concentrate in five of the seven impact indicators tested. Of these five, yeast and bacteria both had considerably lower impacts than soy protein concentrate in marine eutrophication and land, with bacteria meal showing intermediate freshwater eutrophication impacts; between the yeast and soy protein concentrates. These impact indicators are associated with farming, which is necessary for soy production. While yeast protein concentrate also uses crop-based inputs, allocation with valuable biofuels, makes these impacts low for the yeast product. PPR impacts for yeast protein concentrate (0.582 kg C) are therefore intermediate between bacteria meal, which does not depend on primary production at all (0.00 kg C), and soy protein concentrate (1.06 kg C). While soy protein concentrate impacts are also allocated with soybean oil co-production, soy protein concentrate receives a higher percent of the impacts than yeast protein concentrate. In a similar trend as we saw with the freshwater eutrophication impacts, bacteria meal and yeast protein concentrate both had lower acidification impacts than soy protein concentrate, yeast protein concentrate causing significantly lower impacts, and bacteria meal only marginally lower. Many of the differences in relative impacts are likely due to the low allocation of yeast impacts in the biofuels production (both economically and mass-based). Climate change impacts and water consumption were remarkably similar for bacteria meal and soy protein concentrate production. Bacteria meal produces 8.26 kg CO₂ eq. per 660 grams of protein and soy protein concentrate produces 8.55 kg CO₂ eq. High climate change impacts in bacteria meal production are expected, given the use of methane to feed the bacteria and carbon dioxide release from the cells during the fermentation phase. Comparable climate change impacts in soy protein concentrate production are caused, in large part, by land use changes for soy farming (64%). Water consumption was also similar

for bacteria meal ($1.03 \times 10^{-1} \text{ m}^3$) and soy protein concentrate ($9.56 \times 10^{-2} \text{ m}^3$), with bacteria meal requiring slightly more water to produce 660g of protein. Yeast protein concentrate, in contrast, had considerably lower climate change and water consumption impacts ($0.21 \text{ kg CO}_2 \text{ eq.}$ and $5.90 \times 10^{-3} \text{ m}^3$). Fermentation of the methanotrophic bacteria requires aqueous chemical inputs, which increase the water requirements for this process (particularly calcium chloride (41%) and ammonia (35%)), despite attempts by the producer to recycle water internally. Higher acidification in bacteria meals is likely the result of greenhouse gas emissions from the fermentation process as well, although, they are below the acidifying emissions of soy protein concentrate production.

Requirements for cell growth are already being addressed by the feeds industry, although innovations are still in development. Yeast protein concentrate producers are learning to extract lignocellulose from non-human food sources such as lumber by-products to be used as a growing medium for yeast cells and also testing yeast growth on sugars from fast-growing macroalgae. Similarly, labs that produce methanotrophic bacteria are investigating ways to efficiently sequester methane from existing sources, to create a net reduction of greenhouse gases during this fermentation phase. These innovations could help further decrease the environmental impacts of these SCP inputs. Since these meals would likely not be used in isolation, the impacts may change when these meals are incorporated into compound salmon feeds.

1.3.2 Feeds Analysis 1 (FA1)

Benefits of the novel SCP salmon feeds are significantly muted in the FA1 feed results since the impacts of the target meals are low compared to impacts from the other feed ingredients. Since Feed Analysis 1 holds all other ingredients constant and allows the meals

to vary to meet consistent protein levels, it is predictable that the soy-based standard feed would maintain the highest impacts, as we saw in the meals analysis. Differences in target meal inclusion in the FA1 feeds were insufficient to alter which treatments had the lowest and highest impacts. In fact, many of the same trends described for the meals analysis are maintained, with the notable exception that PPR impacts are so dampened by the high (and equal) fishmeal and fish oil inclusion in the FA1 feeds, that differences in PPR impacts between treatments are lost (standard: 22.62 kg C, bacteria: 22.54 kg C, yeast: 22.55 kg C). Relatively low impacts of yeast protein concentrate production lead to overall lower impacts in the yeast feeds, despite lower protein content in this meal. Particularly for climate change impacts bacteria (3.25 kg CO₂ eq.) and standard (3.23 kg CO₂ eq.) feeds remain about equal, and the yeast feed (1.05 kg CO₂ eq.) results in much lower impacts. The other five impact indicators track similarly to the meals results, again, with muted impacts relative benefits of the SCP feeds (Figure 2B). Yeast again, has the lowest impacts for acidification, freshwater eutrophication, and water consumption.

In contrast to the meals results, bacteria had only two indicators that are considerably lower than the standard feed, the remaining five are about equal to the standard feed. The bacteria feed did show slightly lower acidification (1.28×10^{-2} kg SO₂ eq.) and freshwater eutrophication (2.91×10^{-4} kg P eq.) compared to the standard feed (1.34×10^{-2} kg SO₂ eq., 3.31×10^{-4} kg P eq.), but the relative benefits of the SCP ingredient for these metrics were diminished when included in the FA2 feed. Marine eutrophication and land occupation impacts for bacteria (1.78×10^{-3} kg N eq., 1.90 m²a) and yeast (1.97×10^{-3} kg N eq., 1.85 m²a) FA1 feeds were about equal to each other and lower than the standard feed (2.55×10^{-3} kg N eq., 2.68 m²a), although less significantly than in the meals analysis.

When feeds are compared on an equal protein basis, the yeast feed results in the lowest environmental impacts overall, with lower impacts than the standard feed for all indicators and lower impacts than the bacteria feed for four indicators and similar results for three. The bacteria-based feed also improves environmental performance compared to the standard feed for marine eutrophication and land occupation, and shows similar results for the remaining five indicators. Since this feeds analysis uses an equal base of non-target ingredients the results closely mirror the results of the meals analysis, but show that when incorporated into a whole feed, the impacts of non-target feed ingredients reduce the differences in impact. The FA1 results highlight that impacts from the non-target ingredients are large compared to those of the target meals, leading to relatively similar impacts across treatment feeds.

1.3.3 Feeds Analysis 2 (FA2)

To learn more about how the non-target feeds might impact the environmental impacts of salmon feeds with the SCP meals, FA2 substitutes the meals on an equal mass basis and then varies the other ingredients to produce feeds with equivalent protein and lipid concentrations. In FA2, the impacts of the novel SCP feeds became even more similar to each other, with about equal impacts for four of the seven indicators, and maintained similar or lower impacts compared to the standard feed for all indicators except water consumption, for which the bacteria feed exceeded the standard feed (Figure 2C). Impacts from the FA2 SCP feeds converged for acidification and marine eutrophication impacts. Bi-directional shifts in acidification impacts led to about equal impacts for the SCP feeds, with the FA2 bacteria feed (1.06×10^{-3} kg SO₂ eq.) causing lower impacts than its FA1 counterpart and the FA2 yeast feed (1.04×10^{-3} kg SO₂ eq.) causing higher impacts than in FA1. Both feeds had

lower acidification impacts than the standard feed. Both novel SCP-based feeds saw increases in marine eutrophication impacts compared to the FA1 feeds. Increases were greater for the bacteria-based FA2 feed (1.93×10^{-3} kg N eq.), which led to equal impacts (yeast: 1.98×10^{-3} kg N eq.) between the novel feeds. Water consumption was also marginally higher for both SCP feed than in the previous analysis, increasing the disparity between the standard and bacteria feed. It should be noted, that in the FA2 analysis, bacteria meal (which has relatively high water consumption impacts) inclusion was higher than in FA1, whereas yeast protein concentrate inclusion was decreased compared to FA1 (Table1). Climate change impacts, PPR, freshwater eutrophication and land occupation did not change compared to FA1 for any of the treatments.

Compared to the FA1 feeds, the FA2 feeds held the mass of target meals constant which resulted in higher bacteria meal and lower yeast protein concentrate inclusion than the FA1 feed compositions. Overall, the FA2 yeast feed remains the lowest impact feed due to significantly lower impacts for the climate change and water consumption indicators. Based on these data, these novel SCP meals are both strong alternatives to soy protein concentrate in salmon feeds and improvements in these technologies could help make them even more beneficial.

1.4 Sensitivity analyses

Our analysis required a number of assumptions. We assumed that each of the feeds were produced in Norway, which is the largest producer of farmed salmon (FAO 2016), and therefore accounted for transportation from source locations to Oslo, Norway. Fish oil and fishmeal species compositions were based on weighted combinations of species caught in each source country. Importantly, yeast was produced domestically in Norway, whereas both

soy protein concentrate and bacteria meal were produced in the Americas and therefore required much further shipping. Bacteria meal was produced in the United States in this study since this is the location of a plant set to open this year. Ingredient sourcing was based on recent Norwegian imports data for feed production. To test the sensitivity of our results to the feed production location, we also modeled the same FA1 feeds produced in Chile and British Columbia, Canada. Results from this sensitivity analysis show that this model is not sensitive to the location of production (Figure S1). Allocation was based on price for all co-produced ingredients. A second sensitivity analysis tested the impacts of our allocation method by comparing results from an economically allocated model to mass allocated results. While results varied slightly between the methods, relative results between the treatments were consistent, suggesting our model is robust with regard to allocation methods (Figure S2).

Future studies should incorporate ongoing developments in bacteria and yeast meals production to assess whether these changes can further reduce the environmental footprint of SCP feeds. Bacteria cells could potentially be grown using diverted methane rather than newly extracted natural gas, but realized efficiencies and proof of concept have not yet been tested. Similarly, work continues developing industry byproducts for yeast production rather than human-food wheat inputs (Øverland and Skrede 2017), which could further decrease land use and primary production requirements as well as outputs from farming. This analysis stops at the feed factory gate due to lack of information on the effects of these novel feeds on salmon growth and waste production. Following a series of robust feeding trials, a more inclusive study from cradle to grave would provide a more complete picture of the impacts of these feeds.

1.5 Conclusions

The presented life cycle assessment suggests that replacing soy protein concentrate with bacteria meal or yeast protein concentrate in salmon feeds has the potential to decrease the environmental impacts of salmon farming in addition to easing stress on human-food resources. Tallentire et al. (2018) suggest that the climate change impacts of bacteria meal could be even lower than was estimated here. These SCP meals are still being developed with a focus on improving efficiency and reducing impacts of these novel ingredients, particularly through feeding cells byproducts from other industries. Additional single celled proteins such as microalgae could prove environmentally beneficial or supplement these benefits as well (Kousoulaki et al. 2015; Sarker et al. 2016). Many of these SCPs are still in the developmental stages but feed companies are rapidly developing industrial scale production lines for these feed ingredients. Developments such as these are essential for moving aquaculture towards the food security solution our planet needs.

1.6 Figures

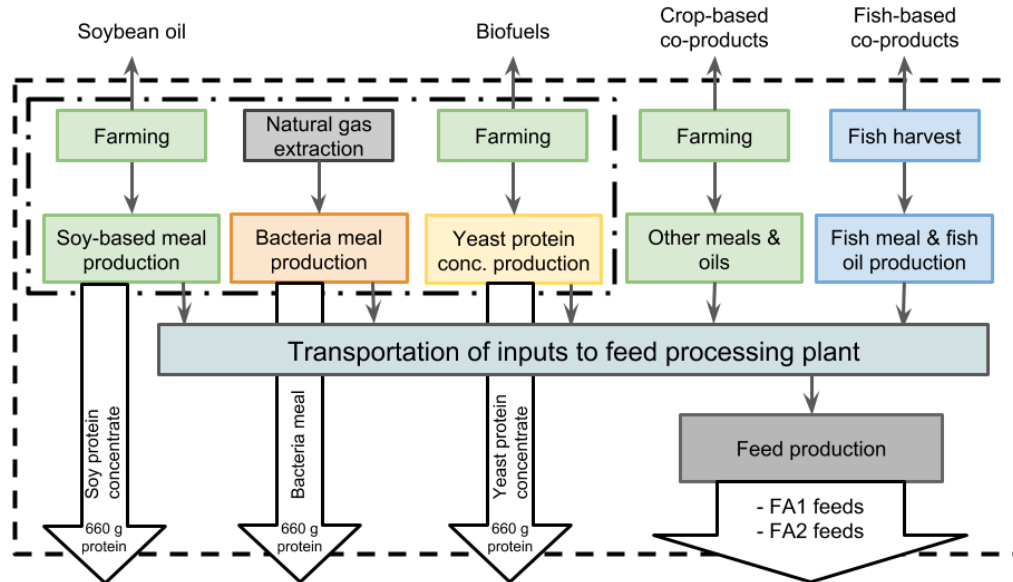


Figure 1: System boundary. These analyses assess the processes of novel single cell protein meals and salmon feeds production from cradle to factory gate. Boundaries for the meals analysis are represented by the dot-dashed line, and each of the FA1 (380g of protein equivalent) and FA2 feeds (1 kg of feed) by the black dashed line.

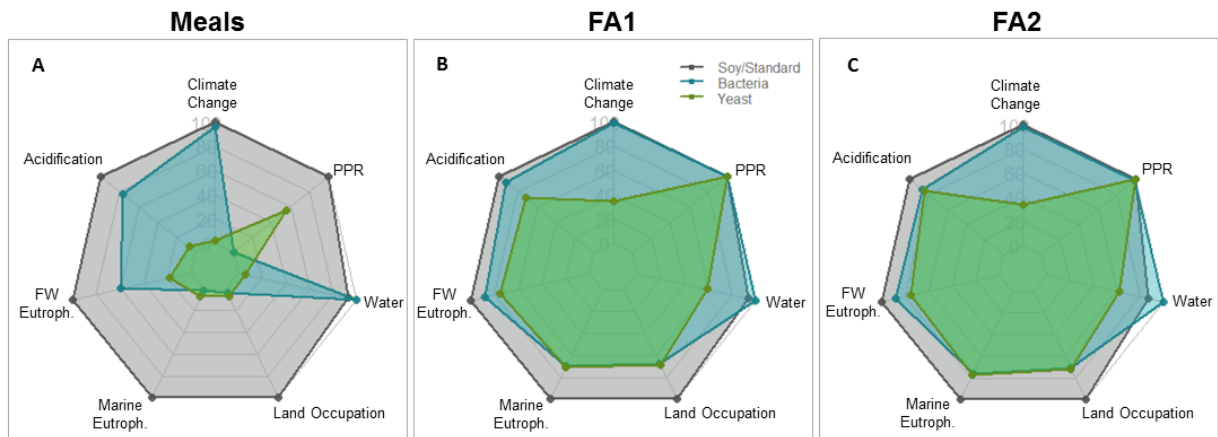


Figure 2: Radar charts comparing the three meals (A) and feeds (B, C) based on seven impact indicators. Axes for each of the impact indicators: (from the top counter clockwise) climate change, acidification, freshwater eutrophication, marine eutrophication, land occupation, water consumption, primary production requirement (PPR). Results are scaled to the highest value for each indicator.

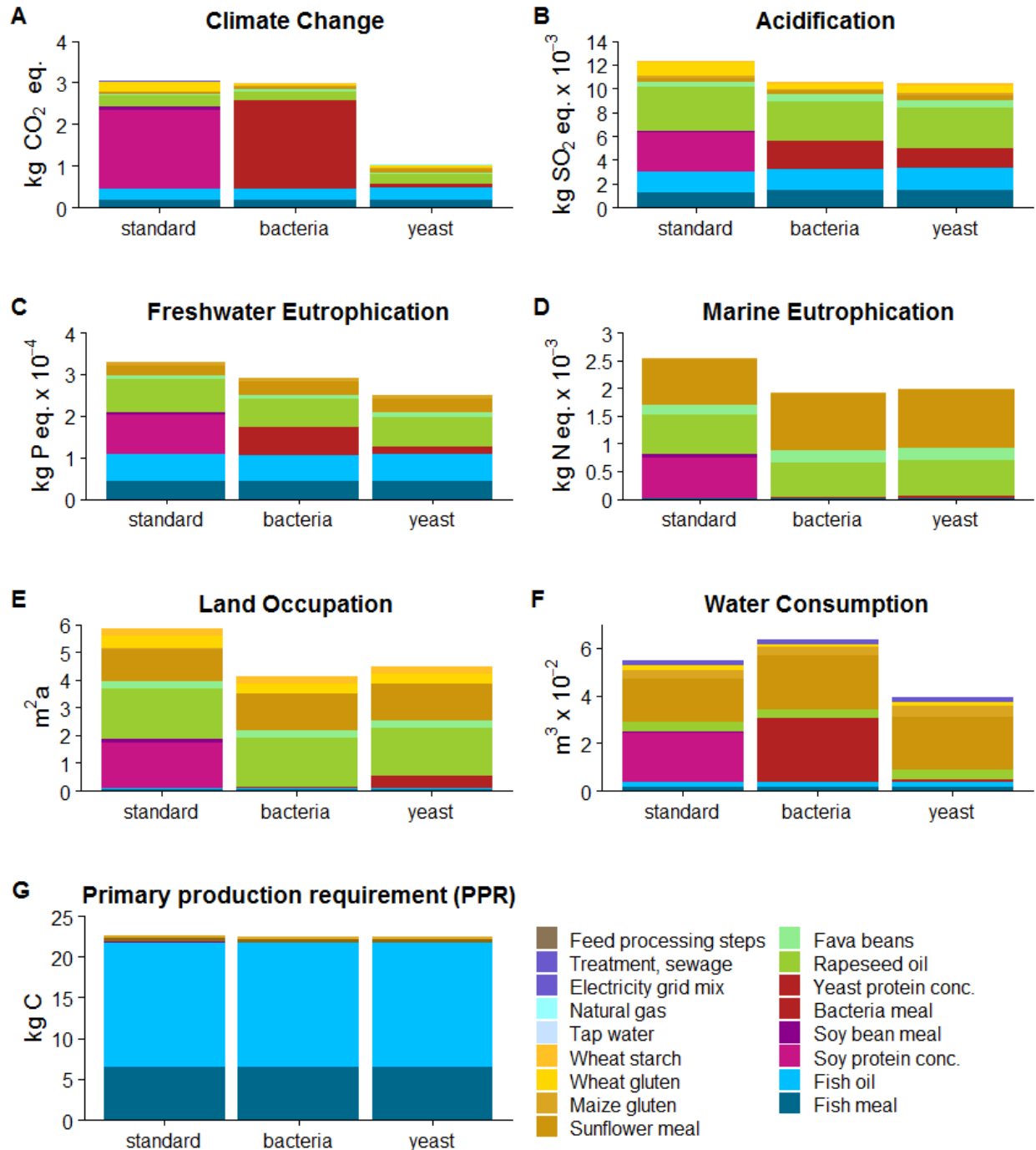


Figure 3: Results of environmental indicators for the FA2 feeds. Single cell protein feeds were formulated to match the standard feed for protein and lipid content, fish inclusion, and total feed mass. (A) Climate change impacts, (B) acidification potential, (C) freshwater eutrophication, (D) marine eutrophication, (E) land occupation, (F) freshwater consumption, (G) primary production requirement.

Table 1: Formulations for each feed analyzed. Values are in grams, FA1 feeds may not sum to 1kg. Mineral and vitamin mix was excluded from analysis.

	Standard	FA1		FA2	
		Bacteria	Yeast	Bacteria	Yeast
Meals					
Soy protein concentrate	220.0	0.0	0.0	0.0	0.0
Bacteria meal	0.0	227.1	0.0	250.0	0.0
Yeast protein concentrate	0.0	0.0	257.3	0.0	250.0
Soybean meal	30.0	0.0	0.0	0.0	0.0
Non-target ingredients					
Wheat starch	90.0	90.0	90.0	122.6	92.8
Wheat gluten	90.0	90.0	90.0	55.6	86.2
Corn gluten	20.0	20.0	20.0	19.5	23.1
Sunflower meal	40.0	40.0	40.0	51.7	49.6
Fava/field beans	40.0	40.0	40.0	48.5	47.8
Rapeseed oil	180.0	180.0	180.0	162.2	160.5
Fishmeal	160.0	160.0	160.0	160.0	160.0
Fish oil	110.0	110.0	110.0	110.0	110.0
Mineral & vitamin mix	20.0	20.0	20.0	20.0	20.0
Nutrients					
Protein	381.3	381.3	381.3	381.3	381.3
Lipid	314.5	331.4	317.8	314.5	314.5
Starch	83.2	82.6	82.6	109.6	90.0

Table S1: Definitions, units, and data sources for the impact indicators used in the analysis.

Impact inventory	Units	Definition	Source
Climate change	kg CO ₂ eq. – to air	Greenhouse gas emissions reported in kilograms of carbon dioxide equivalent	ReCiPe 1.11
Terrestrial Acidification	kg SO ₂ eq. – to air	Emission of acidifying compounds into the air expressed in kilograms of sulfur dioxide (includes NO _x , NH ₃ , SO ₂)	ReCiPe 1.11
Freshwater eutrophication	kg P eq.	Emissions of phosphorous compounds to freshwater (Phosphate, phosphoric acid, total phosphorous)	ReCiPe 1.11
Marine eutrophication	kg N eq.	Emissions of nitrogen compounds to marine waterways (Ammonia, ammonium ion, nitrate, nitrite, nitrogen dioxide, nitrogen monoxide, nitrogen total)	ReCiPe 1.11
Land occupation and transformation	m ² a	The amount of agricultural area occupied and the time of occupation in years (a, annual)	Inventory data
Water consumption	m ³	Water consumption is the amount of water that the watershed of origin loses to the product, through evaporation, evapotranspiration, or loss to other water body (sea or other watershed)	ReCiPe 1.11
Primary production requirement	kg C/kg feed	Estimate of the net primary production required to yield the amount of biomass used in the feeds. Measured in kilograms of carbon per kilogram of feed	Cashion 2016

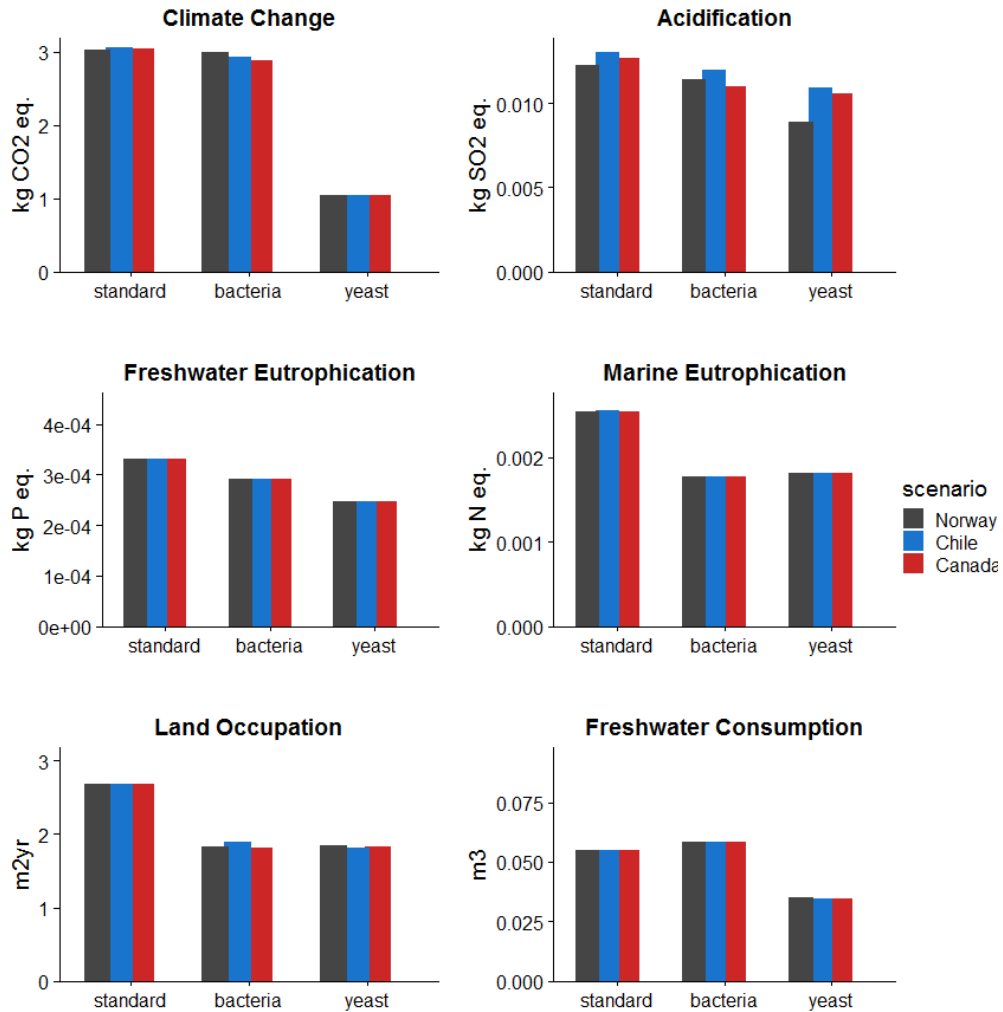


Figure S1: Sensitivity analysis of location of salmon feed production. To test the sensitivity of these results to the assumption that production occurred in Oslo, Norway, we collected data for feed ingredient sources for two additional countries that are leaders in salmon farming: Chile and Canada (British Columbia). Feed production location scenarios replaced transportation distances with country specific import distances using sourcing data for each feed ingredient.⁸⁻¹⁰ Marginal differences in results by production country suggest our models were not sensitive to production location. Acidification impacts are the most impacted, but relative impacts between treatments remain about constant.

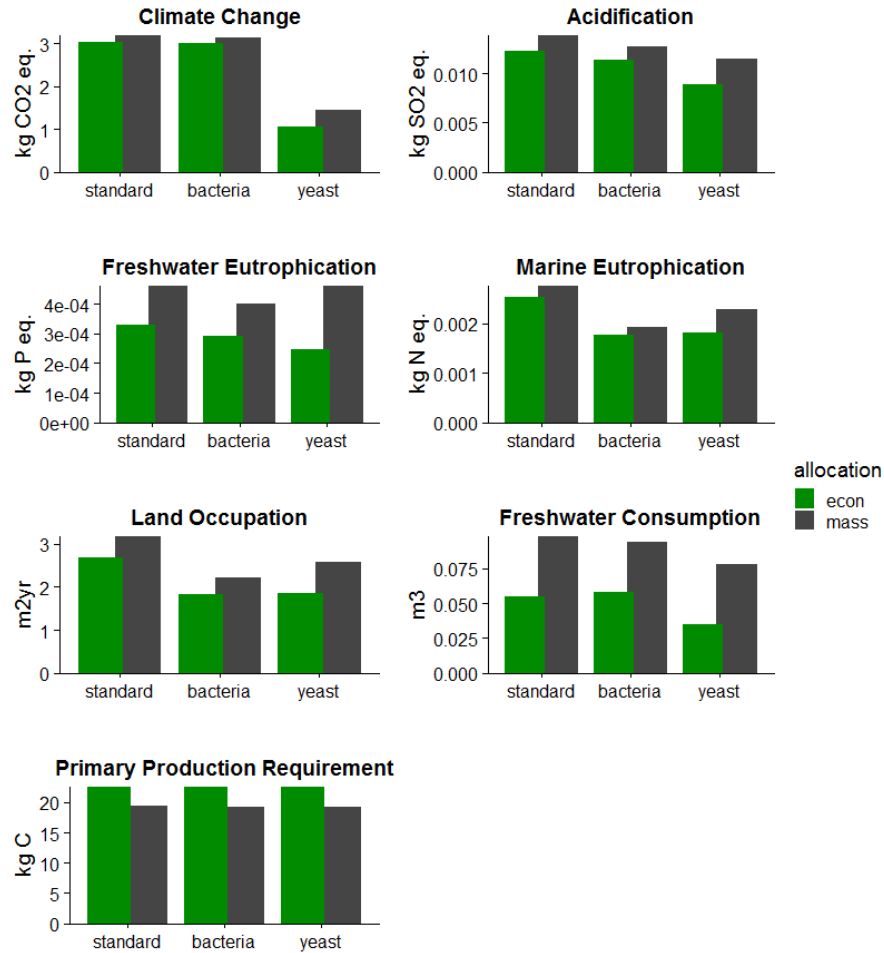


Figure S2: Sensitivity analysis of allocation method. Economic allocation was used for all analyses in this study. To test the sensitivity of our results to this assumption, we compare the study results to results using mass-based allocation. Results suggest that our results are sensitive to allocation method, particularly for the yeast feed. Yeast feed land occupation and freshwater and marine eutrophication impacts were considerably higher using mass-based allocation than economic-based, and actually shift the yeast feed from lowest impacts to intermediate or similar to the standard feed. All feeds had about double the water consumption impacts with mass-based allocation, but relative impacts between the treatments remain about the same. Despite these impacts, economic allocation is important for product production, particularly for yeast, since the higher priced item will drive production and therefore also the resource use and emission impacts.

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Chapter 2: Replacing crop inputs to feeds can also decrease greenhouse gas emissions in animal production

This chapter is in preparation for submission to a peer-reviewed journal with authorship as follows: Jessica L. Couture, Roland Geyer, Darcy Bradley, Benjamin Halpern, Steven Gaines

2.1 Introduction

As the global human population and per capita demand for animal based protein continue to rise, concerns are growing about how to efficiently and sustainably feed the world (World Economic Forum 2017; Searchinger et al. 2018). While resources essential to food production, such as water and land, are limited, food production is also a major contributor of greenhouse gas emissions. Livestock production is particularly resource intensive, requiring large amounts of land, water and feeds, and is a dominant source of greenhouse gas (GHG) emissions (Tilman and Clark 2014; Herrero et al. 2013). Today's global markets create highly interconnected food systems, due to variability in consumption and production of meat products, resource use and dependencies, and imports and exports of resources and products. High protein plant ingredients, for example, are consumed by humans as well as used in animal feeds, are highly traded in the global market, and are often co-produced with other valuable products. Meanwhile, animal feed compositions shift quickly based on competing prices and availability of crop-based inputs. Given the high environmental impacts of animal protein production, much work has focused on quantifying these impacts to climate change with messages directing demand away from animal products generally (Tilman and Clark 2014; Berners-Lee et al. 2018; Di Paola, Rulli, and Santini 2017; Rööß et al. 2017), while other research has focused on decreasing impacts of animal feeds

specifically (Froehlich et al. 2018; Pikaar et al. 2018; Couture et al. 2019; Kim et al. 2019), stopping short of how changes to feeds can impact the larger impacts of meat production.

This work aims to assess the greenhouse gas mitigation potential of replacement of existing feed ingredients with novel protein inputs in different livestock feeds, to understand how to best decrease climate change impacts of meat production more broadly.

The sources of greenhouse gas emissions from animal production vary greatly based on product, which makes the solutions to this issue complex, but also creates several avenues for improvement. Ruminants produce the potent GHG methane through enteric fermentation and manure outputs (Opio et al. 2013; Caro et al. 2014). While ruminant production releases the highest rates of GHGs, only 10% of these emissions come from production of their feeds. In contrast, pigs and chickens are considered more efficient products, chickens more so than pigs, for which emissions come predominantly from manure production and feed inputs, each making up about half of the GHG emissions (Caro et al. 2014; M. MacLeod, Gerber, and Mottet 2013). Aquaculture is often considered an efficient alternative to land-based animal production, with feed production making up the majority (60-95%) of GHGs emissions from production (M. J. MacLeod et al. 2020; Pelletier et al. 2009). Therefore, the relative importance of feeds to emissions is also highly dependent on human diets and demand for these products. Despite the variation in emissions sources, all of these products use similar feed inputs, dominated by major crops including grains such as wheat and corn, grasses, oilseeds and legumes (Mottet, Opio, et al. 2017), with 35% of global crop production dedicated to feeding livestock (Mottet, de Haan, et al. 2017).

Relieving our reliance on crop-based feed inputs might be important to meeting increasing needs for both human food and animal feeds. While the FAO confirms that by mass 86% of

the crops that go into animal feeds are inedible to humans, limitations on land and water will make it difficult to expand crop production for livestock or humans (Froehlich et al. 2018; Tilman et al. 2011). Meanwhile, crop markets are becoming more volatile with increased crop failures, price fluctuations and escalating climate related uncertainties (Cottrell et al. 2019; Erokhin and Gao 2020). Increasing temperatures are compromising crop yields (Zhao et al. 2017) as agriculture researchers are looking to improvements in growing efficiencies to fill increasing demands (Tilman et al. 2011; Garnett et al. 2013). Expansion of land for farming brings additional impacts to climate change by releasing GHGs (Iversen, Lee, and Rocha 2014) and also threatens biodiversity, especially in developing countries (Zabel et al. 2019). As consumers, animal-based protein products are automatically a less efficient use of resources (due to losses through respiration and conversion of food into energy, for example) than autotrophic plant-based protein for human consumption. How much less efficient depends on feed conversion ratios (FCRs), nutrient requirements of the animal, and direct impacts of the specific feed crop. For example, the low GHG-intensity of some cattle feeds are outweighed by their low nutrient levels and the high FCR of cattle production. Several alternatives to plant-based feed inputs have been developed and studied as a way to mitigate some of these sustainability issues, including single cell proteins (SCPs), insect meals, animal byproducts and algae. Limitations on fish supplies for fishmeal led to dedicated efforts to decrease fishmeal inclusion in both land-based and aquaculture livestock feeds with great success. Where fishmeal used to be a main ingredient in pig and chicken feeds, now only traces are used, and fish feeds have also drastically decreased their contribution of fish inputs (Tacon and Metian 2015). Similar efforts are being directed towards decreasing human food and other plant-based inputs to animal feeds (Couture et al.

2019; Øverland et al. 2010). Of the major feed alternatives to fish and crop inputs, SCPs are an ideal case study, because they are protein rich, not consumed by humans, require minimal land and reproduce quickly and efficiently. Addition of these non-plant inputs to feeds helps to diversify feed ingredient portfolios to buffer against agricultural risks. Other alternatives should also be considered in the feed portfolio such as animal byproducts, algae and insect meals, but we limited this analysis to SCP inputs since their inclusion in animal feeds have proven beneficial, their production is considered efficient and is not dependent on other production systems.

This work first assesses the current status of animal feeds across land-based and aquaculture products assessing production rates, trends in product demand, feed compositions, dietary requirements and the GHG emissions of feed inputs. Projections of animal production are estimated to 2050 based on current trends in meat consumption, as well as the GHG emissions of the feeds needed to produce such livestock. To assess the mitigation potential of different feed compositions, four feed scenarios are developed based on protein equivalence: business as usual (BAU feeds) maintains current feed compositions constant to 2050, a soybean meal dominated growth (soy growth) assumes current feeds remain the same but any growth in livestock production is fed soy for protein requirements. Methanotrophic bacteria meal dominated growth (bacteria growth), and yeast meal dominated growth (yeast growth) are modeled as the soy growth scenarios with bacteria and yeast as the sole protein ingredients for growth in livestock production, respectively. We also developed three scenarios for human diets for our projections of livestock production and thus feed demands to 2050: constant diets (CD diets) assumes current (2018) meat consumption levels remain constant through 2050 and are scaled by projected total meat demand; continued current

trends in consumption shifts (shifting diets, SD diets) assumes that shifts in demand for meat products continue on current trajectories; accelerated diet shifts (ADS) doubles (cuts in half for those declining) current trends in diet shifts. Shifting diets scenarios focus on changes among meat consumption and do not consider shifts to no-meat diets (vegetarianism or veganism). Investigating the interactions between changes in human diets and animal feed compositions helps us to better understand how these changes might make food systems more or less sustainable into the future and therefore where resources and efforts might be best allocated.

2.2 Results & discussion

2.2.1 Current trends

Total livestock meat production for cattle, pigs, chicken, small ruminants (which includes sheep and goats), and aquaculture was tracked from 1960-2018. Percent contributions by mass of each of these five product groups were calculated as the total production for each group for a given year divided by the total livestock production that year. Trends over the last 20 years (1998-2018) show that total production of all meat products are increasing, but relative compositions differed significantly (Figure 1). Already trends are shifting away from animals whose production emits the largest amounts of GHGs towards more efficient products (Tilman and Clark 2014; Herrero et al. 2013). Cattle, pig, and small ruminant production emit the most GHGs of the livestock groups assessed, and their production is increasing relatively slowly, leading to steady declines in their contributions to total animal meat production (Figure 1B). The percent contribution of pigs is declining by 0.32% per year, cattle contribution is declining by 0.28% per year, and production of small ruminants (sheep and goats), which contribute less than 1% of global meat production, is also declining

by 0.024% annually. In contrast, chicken and aquaculture production are increasing rapidly both in absolute amounts and relative contributions, 0.35% increase per year for aquaculture and 0.27% for chicken (Figure 1B). As the diet scenarios demonstrate, although the annual production of all animal products are currently increasing, if current shifts in diets continue, high emission products will be rare by 2050 (Figure S3).

2.2.2 Projections to 2050

We projected total animal meat consumption to 2050 based on population growth and three diet scenarios. These production projections were combined with each of the four feed composition scenarios, resulting in 12 total feed projections. Shifting human diets helps to mitigate GHG emissions from livestock feeds to 2050. Continuing current trends in diet shifts (shifting diets, SD) will lead to greater mitigation of emissions from feeds compared to constant diets (CD) and additional acceleration of diet shifts (ADS) can provide additional benefits over the standard shifts (SD). Replacing conventional crop-based protein ingredients with yeast protein further mitigates emissions from feeds (Figure 2 A, B, C). The relative benefit of shifting human diets compared to replacing proteins with yeast in feeds depends on relative diet compositions. For example, GHG emissions decrease by approximately 2200 mt CO₂-eq by 2050 when continuing to shift diets (SD) compared to maintaining constant diets (CD), whereas replacement of BAU feeds with yeast in either the CD or SD scenarios only decreases emissions by about 1100 mt CO₂-eq. By contrast, when diets are shifted even further (ADS), there is only a 537 mt CO₂-eq. decrease in GHG emissions compared to the SD scenario, but replacement of BAU feeds with yeast mitigates approximately 1200 mt CO₂-eq. of GHG emissions. Ruminants have lower protein requirements than the other livestock groups, so as the contributions of these products take up less of the total meat

production, efficiency of protein inputs to feeds becomes more important to total feed emissions. Since human diets are currently moving away from ruminant products, feed development should emphasize low impact, high protein feed ingredients such as yeast meals at industrial scales and competitive prices.

GHG emissions from land use change required to increase crop production for livestock feeds into the future, under both the BAU feed and soy dominant feed scenarios result in high feed impacts. Since the methanotrophic bacteria are fossil-based, release of carbon dioxide during its production leads to high GHG emissions as well. Increasing benefits of BAU feeds over the soy growth and bacteria growth feed scenarios reflects the high impacts of bacteria meal production and particularly high land use change impacts of soy compared to other crop ingredients. For all diet scenarios the BAU, soy growth and bacteria growth scenarios resulted in similarly high GHG emissions. Bacteria growth consistently resulted in the highest emissions, with the BAU feeds emitting the fewest GHGs of the three. Given similar emissions rates, bacteria can still be favorable to plant-based ingredients to avoid the competition for and risks of agricultural crops into the future. Yeast is conventionally fed plant-derived sugars so can also be vulnerable to climate change impacts on agriculture and market fluctuations, although several innovations in sugar sources are helping to break this dependency (Øverland and Skrede 2017; Sharma et al. 2018).

High costs and environmental impacts of the feed industry have motivated several innovations in the production of feed inputs. For crop-based inputs, no till farming can help decrease GHG emissions by sequestering carbon in soils, compared to conventional tillage farming. We found that this approach to farming can significantly decrease GHG emissions making plant-based feeds more comparable to yeast feeds (Figure S4). There are several

caveats to these farming benefits though with results varying by soil type and duration of application (Six et al. 2004). Negative impacts of climate change on farming coupled with contributions of GHG emissions from farming to climate change create a positive feedback loop in which increasing farming creates additional threats to agriculture futures. Yeast can also be produced in several ways, decreasing its burden on agricultural demands. Wheat based production of biofuels produces both distiller's dried grains with solubles and yeast by-products, which can be used in animal feeds (Tallentire, Mackenzie, and Kyriazakis 2018). This process decreases the overall impacts of feeds (Figure S4) but is limited by biofuels demand and production (Couture et al. 2019). Similarly, novel feed sources for yeast are being developed and tested including macroalgae and lignocellulose from lumber industries (Øverland and Skrede 2017; Sharma et al. 2018). As these methods develop, future work should also consider the limitations and emissions of these alternative yeast production pathways in the complete profile of protein alternatives. Methanotrophic bacteria shows the highest GHG emissions due to dependence on fossil methane inputs, but bacteria producers are actively investigating the potential to use diverted methane or biogas to feed bacteria cultures, with the goal of mitigating existing emissions sources. The decreased dependence on agricultural products and potential benefits to global emissions make this a promising alternative.

2.2.3 Limitations & opportunities

Willingness to incorporate novel SCP meals into the different livestock feeds is as yet unknown. Our analysis reflects relatively low expected use in cattle and small ruminant feeds, since these feeds tend to be low in protein and use fewer compound feeds. Relatively high protein requirements in pigs and chickens means they still consume large amounts of

fishmeal and soy, although proportionately fishmeal makes up a small fraction of their feeds so fishmeal was not included in these feeds for this analysis. SCP use in these feeds is more likely and could provide greater benefits to reducing emissions than SCPs in the cattle industry. In fact, as diets shift towards products with lower total production emissions, GHG impacts from feeds make up a larger contribution of the total impacts of animal production (Figure S5), so using lower impact feed ingredients will play an increasingly significant role in total impacts from meat production. Therefore, given increasing demands for chicken and high, though declining, demands for pig, replacement of crop inputs with SCP in chicken and pig feeds could have significant impacts on GHG emissions.

Fishmeal, soybean meal, and rapeseed meals are used in animal feeds in high quantities.

They are also co-produced with valuable oils and can be considered byproducts of the oil counterparts. A consequential analysis of the key meals and oils used in animal feeds would give more insight into the relative drivers of demand and expected availability of these products into the future. Microalgae oil is another efficiently produced single cell product quickly becoming a viable lipid-rich alternative to fish oil, soybean oil and other vegetable oils (Sarker et al. 2020; Shah et al. 2018). Microalgae oil brings healthy omega-3 and other amino acids to animal feeds and could play an important role in food and feeds, likely further decreasing our overall dependence on land-based crop and limited fish supply inputs given meal-oil co-production.

Prices and scale of production of SCPs continue to be prohibitive to broad adoption, but, as with many new technologies, prices start high but can decrease through technological innovation and efficiencies of scale. Greenhouse gas emissions from yeast meal production (0.58 kg CO₂-eq./kg meal) are considerably lower than soybean meal production (5.75 kg

CO₂-eq./kg meal, with land-use change), while yeast meal prices (\$300-800/tonne; Alibaba Group 2021) are only moderately higher (soybean meals: \$300-\$550/tonne; Index Mundi 2021b), so a small carbon tax (~\$20/tonne CO₂; below the OECD low-end carbon tax benchmark of <\$30/tonne CO₂; OECD 2019) could make yeast more cost effective than soy. Although yeast production is still limited by production volume, broader inclusion in animal feeds could motivate investment in improving production efficiency and technology. Alternatively, subsidies to farming could be redirected towards the necessary research and development in yeast meals to make these products more even more environmentally and cost efficient.

Bacteria meal is priced similar to fishmeal (\$1,500/tonne; Index Mundi 2021a), so can already act as a replacement for fishmeal, but remains prohibitively higher than soybean meal. With similar greenhouse gas emissions to soybean meals, a carbon tax would not be able to narrow the price gap between bacteria and soybean meals. Replacement of natural gas feed media with biogas or diverted methane from existing sources could decrease the greenhouse gas emissions of bacteria meal production enough to make a carbon tax benefit the economic viability of bacteria meal as a replacement for soybean meal. Additional research is needed to develop the technology for methane capture and assess the tradeoffs and benefits of replacement in bacteria production. Several studies have begun to confirm the benefits of SCPs to animals, and further support for this research could help move these promising inputs from feed innovations to established feed ingredients (Øverland et al. 2010; Romarheim et al. 2011; Agboola et al. 2020; Ma et al. 2019). Additional studies such as the one conducted here can help to understand which other feed alternatives can help diversify animal feed portfolios and also mitigate the climate impacts of our food systems.

2.3 Conclusions

Shifting human meat diets is important to decreasing the overall impacts of animal protein production. Current trends show decreases in the relative contributions of high emitting animal products and increases in more efficient meats such as chicken and aquaculture products. Continuing or accelerating these trends will help make our food systems more sustainable into the future. Shifts in demand for meat products are increasing the contribution of feeds to total production emissions, making lower impact feeds more significant to GHG mitigation in animal production. Continuing current trends of shifting human diets towards lower emission products (i.e., more aquaculture and chicken) as well as increasing use of lower impacts feed inputs can together support needed growth in animal production, while decreasing GHG emissions below current levels. Increasing inclusion of protein rich yeast ingredients in feeds can bring down the impacts of animal production overall and further innovations in SCPs and other feed alternatives can help to further mitigate GHG emissions of food production. These results should motivate the dedication of additional resources and attention towards these actions.

2.4 Methods

To estimate the greenhouse gas emissions of animal feeds for our three human diet scenarios and four animal feed scenarios we built a model that estimates animal production to 2050, applies feed scenarios to animal production rates, and calculates greenhouse gas emissions for feeds and total animal production for each of the 12 scenarios. Total animal production and relative diets were estimated based on current rates of total meat production and relative consumption rates, respectively. Feed requirements were calculated by first converting meat

amounts to total carcass biomass using data on edible portions and feed conversion ratios (FCRs). Feed compositions were determined using the FAO GLEAM model (Mottet, Opio, et al. 2017) for land-based livestock and aggregated feeds based data in the literature for aquaculture (Tacon and Metian 2015; Troell et al. 2014). Feed substitutions were calculated on a protein equivalent basis and amounts of substitutes were then estimated based on protein content. All modeling and analysis was conducted in R (R Core Team 2021) and all data and code are available here github.com/couture322/globalFeeds-GHG.

2.4.1 Meat production, trends, and diet scenarios

Meat production from 1960 - 2018 was plotted using FAO data for land-based meat production and aquaculture production (FAO 2019). Data were limited to livestock animals that represent over 2% of global livestock production. Sheep and goats were combined into a “small ruminants” grouping since diets and production methods are similar between these products. Aquaculture data were limited to fed species, since feeds are the focus here.

Aquaculture production was combined into one “aquaculture” group, although there is known heterogeneity in culture and feeds of aquaculture species, data limitations to feed compositions of smaller taxonomic groups, discussed below, limited more specific classification of aquaculture products. Absolute production quantities and relative contributions were calculated for each year in the time series.

Current total production and percent contribution trends were calculated using the most recent 20 years of data (1998-2018). These trends were then used to project total production of animal meat from 2018-2050 (Figure S2) using a linear regression.

Human diet scenarios were projected based on current consumption rates and trends in consumption rates. The “constant diets” (CD) scenario held the relative meat compositions

from 2018 constant and scaled these proportions to meet the increasing total meat demand. The “shifting diets” (SD) diet scenario assumes that the 20 year trends in changes in diet continue to 2050, so percent contributions are also projected to shift along with increasing production. For “accelerated diet shifts” (ADS) trends from the SD scenario are doubled for which regression slopes were doubled for positive trends or halved for negative trends (Figure S3). Contributions from the five livestock groups sum to one for every year for all diet scenarios. In the ADS scenarios, cattle contributions reach zero before 2050, in such cases remaining contributions are evenly distributed among the remaining animal production groups (ie. aquaculture, chicken, pigs, small ruminants). Production quantities for each livestock grouping were calculated by multiplying the projected annual diet contribution shares by the projected total meat production.

2.4.2 Animal feeds & feed input scenarios

Livestock feed compositions were calculated using data from the FAO GLEAM model, which includes data for each animal product for different production levels from different geographic regions. Our model uses industrial scale feeds only and weights compositions based on relative production by region. Ingredients contributing to 5% or more of these global feeds were included in this analysis.

Data about the composition of feeds for aquaculture products are not as available as for land-based livestock. In part these data gaps arise because aquaculture products are highly variable in species cultured, culture methods, and feed compositions. The most recent data for fishmeal inclusion in feeds came from Tacon & Metian (2015); and data for crop-based ingredients to make up rest of the feeds were based on proportions reported in Troell et al. (2014). A cutoff of 5% inclusion was applied to these feed compositions.

Feed quantities for each unit of animal product was calculated from meat production data by scaling by edible portion values and FCRs (Fry et al. 2018a; 2018b; 2016) for each product grouping. Feed input demands were calculated from projected feed requirements based on feed compositions for each group and protein demand is calculated based on protein content of each feed ingredient, weighted by inclusion rates. Protein requirements were then used to calculate feed input projection scenarios.

Feed replacement scenarios (soy growth, bacteria growth, yeast growth) are applied to future projections and assume current feed production continues as usual, but protein requirements for growth of any animal product group uses the alternative meals. Only ingredients with protein content greater than 20% were replaced to represent realistic replacement of higher protein ingredients with protein meals. Inclusion rates of lower protein ingredients were held constant. In projections where absolute production of a product decreased below current levels (due to diet shifts) all production of that product is assumed to use current feed formulations. The “business as usual” feed scenario assumes that feed compositions remain constant at 2018 compositions for all growth. The “soy growth” case assumes that all protein requirements for growth in livestock production after 2018 are met with soybean meal. The soy scenario reflects the strong move towards soy use as an efficient and low cost feed ingredient, especially after limitations to fishmeal began to be realized. For “bacteria growth” scenarios all growth in production is fed methanotrophic bacteria meal for protein. Similarly, for “yeast scenarios” yeast is the sole ingredient to meet protein needs of production expansion. For all replacement scenarios, production up to 2018 levels are fed the same feeds as in 2018.

2.4.3 Greenhouse gas emissions

Emissions data from the Intergovernmental Panel on Climate Change (Intergovernmental Panel on Climate Change 2014) models were used for per unit production of feed inputs and excludes biogenic carbon. For all projections, 2018 feed input use amounts were assumed to continue to 2050, and any growth in demand for crop inputs to feeds (above 2018 amounts) would require land use changes to expand crop production. Emissions from land use change for crop inputs are from the FAO LEAP model (FAO 2017) which uses PAS2050 methodology. Bacteria protein meal is produced through fermentation and drying of methanotrophic bacteria that consume fossil methane and release carbon dioxide (Couture et al. 2019). Yeast are modeled using conventional production methods with sugar cane molasses as a growth medium, the life cycle inventory for this process is from the Thinkstep database (Thinkstep 2018).

2.5 Figures

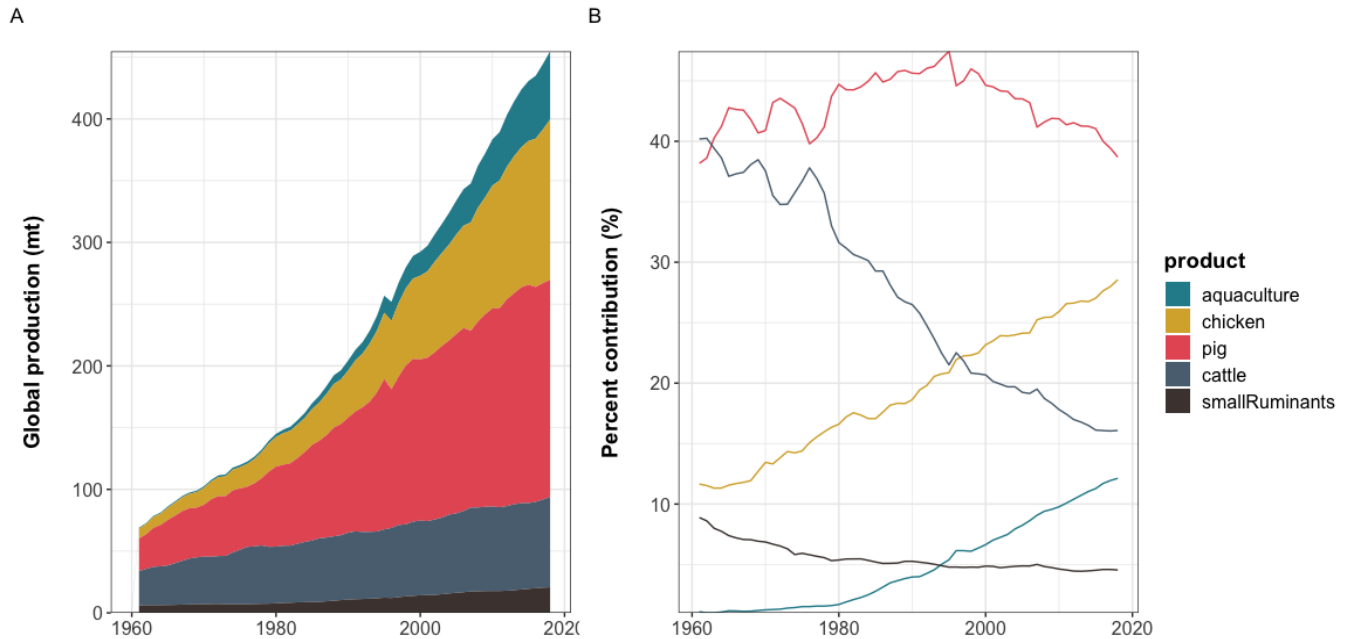


Figure 1: Trends in livestock production by product groups. (A) Total production of meats by weight, and (B) annual percent contributions of product groups to total animal meat production.

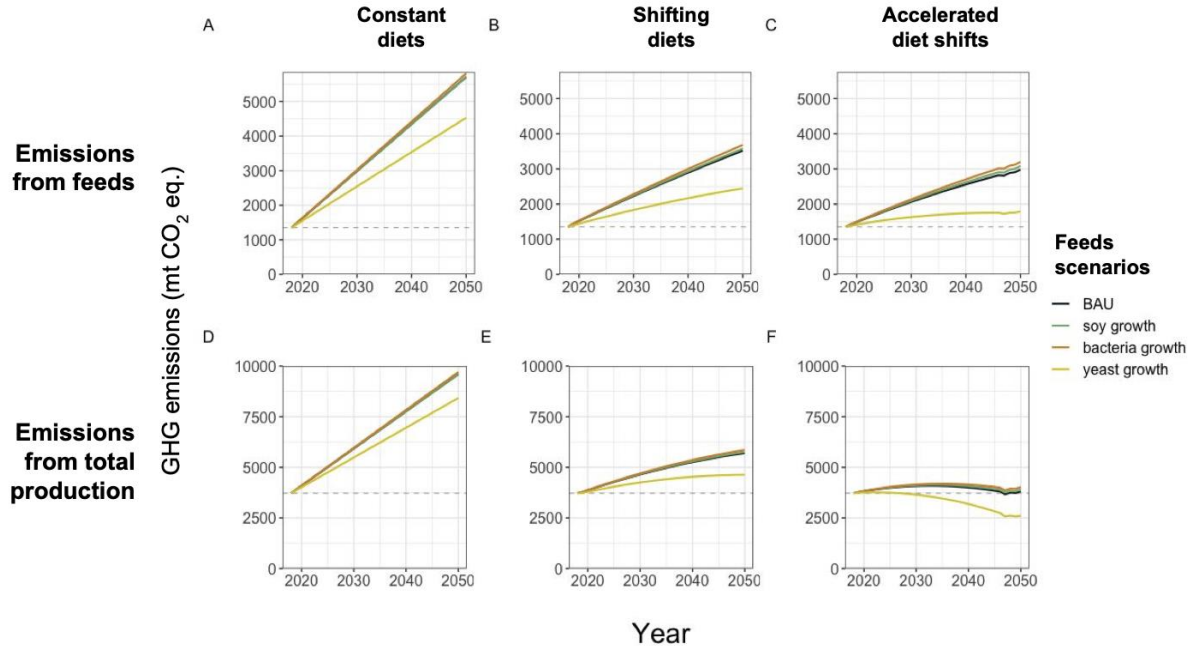


Figure 2: Projected greenhouse gas emissions from feed production (A, B, C) and total livestock production (D, E, F) for three animal consumption (human diet) scenarios: constant diets, (A, D); shifting diets (B, E); accelerated diet shifts, ADS (C, F).

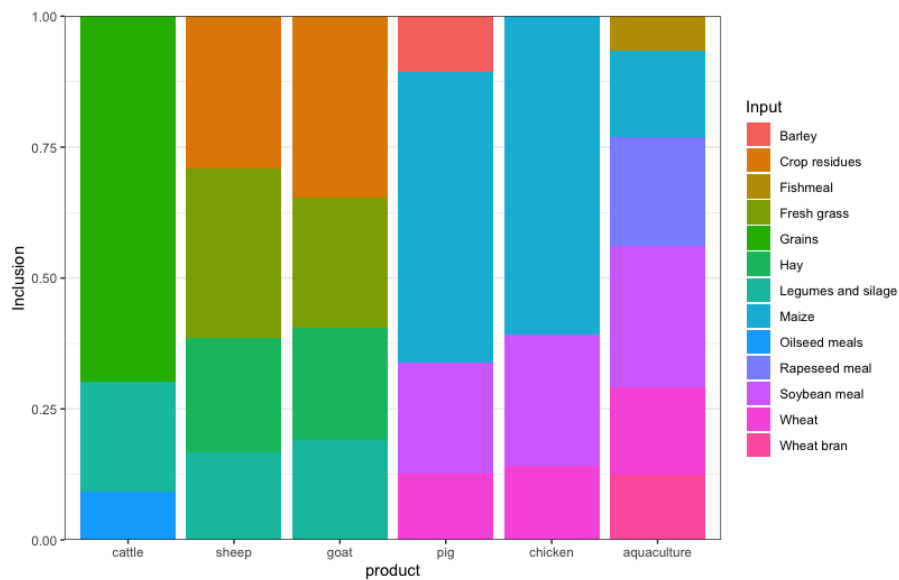


Figure S1: Feed compositions used in feed impacts model

Table S1: Protein content of inputs to livestock and aquaculture feeds. Bolded ingredients (those with protein content greater than 20%) are replaced in growth projection scenarios, non-bolded are kept at constant inclusion rates to 2050.

input	proteinContent	source
Fishmeal	68.00	Couture et al. 2018
Soybean meal	49.50	Encyclopedia of Animal Science, Chiba 2011
Oilseed meals	44.78	Encyclopedia of Animal Science
Rapeseed meal	40.00	Encyclopedia of Animal Science
Fresh grass	19.00	Soder & Muller 2007
Barley	12.50	Arendt & Zannini 2013
Wheat	12.00	Arendt & Zannini 2013
Hay	11.00	University of Minnisota
Maize	10.00	Klopfenstein 1996
Wheat bran	9.00	Arendt & Zannini 2013
Grains	8.50	Encyclopedia of Animal Science
Legumes and silage	7.50	Koliver et al. 2001
Crop residues	3.25	Chen et al. 2017

Table S2: Calorific content of feeds scenarios. "Growth" scenario feeds replace ingredients indicated in table S1 only for growth in feeds above 2018 levels. Values are in kcal/kg of feed and averaged across multiple sources.

product	bauFeed	soyGrowth	bacteriaGrowth	yeastGrowth
cattle	4095.677	4532.869	4420.578	4489.481
pig	3539.175	4655.498	4368.775	4544.713
chicken	3373.113	4689.298	4351.241	4558.679
aquaculture	2048.816	4805.211	4097.243	4531.665
sheep	3339.222	3339.222	3339.222	3339.222
goat	3366.119	3366.119	3366.119	3366.119

Table S3: Data sources for calorific content data used in Table S2.

input	ref
Fishmeal	USDA national animal nutrition program database
soybean meal	USDA national animal nutrition program database
oilseed meals	USDA national animal nutrition program database
cottonseed meal	USDA national animal nutrition program database
rapeseed meal	USDA national animal nutrition program database
Fresh grass	Stergiadis et al. 2015
Barley	USDA national animal nutrition program database
Wheat	USDA national animal nutrition program database
Hay	U. Minn website: 760-1100kcal/lb
Wheat bran	USDA national animal nutrition program database
Grains	Ave of DE from USDA grains: wheat, barley, oat, rice, rye, sorghum, triticale, millete, corn
Maize	USDA national animal nutrition program database
Legumes and silage	USDA national animal nutrition program database
Crop residues	ave from USDA
Yeast	Rumsey et al. 1991
Bacteria	Hellwing 2005

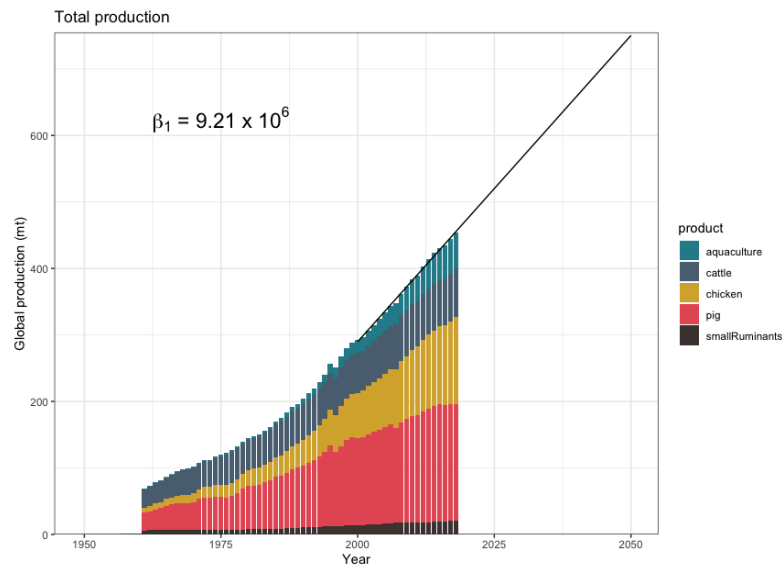


Figure S2: Projection of production to 2050 based on current and recent trends in growth. Calculated based on total meat production from 1998-2018.

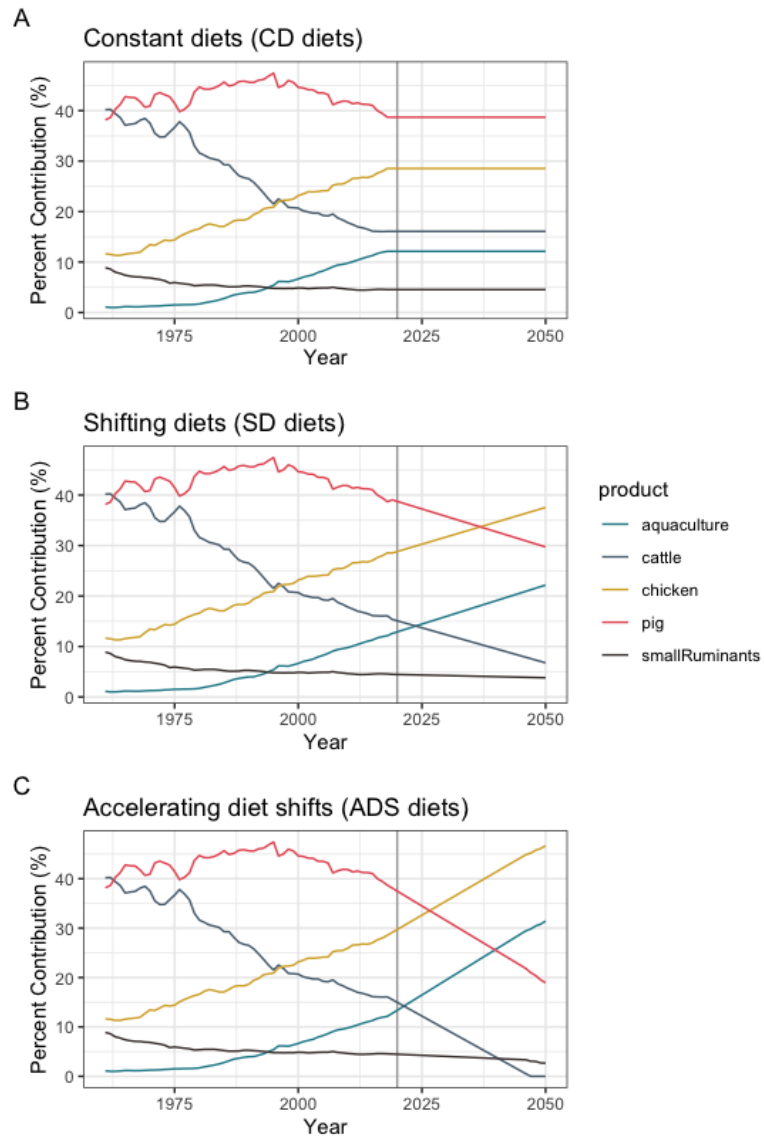


Figure S3: Diet scenarios were calculated based on the below composition scenarios applied to total production levels projected above (Figure S1).

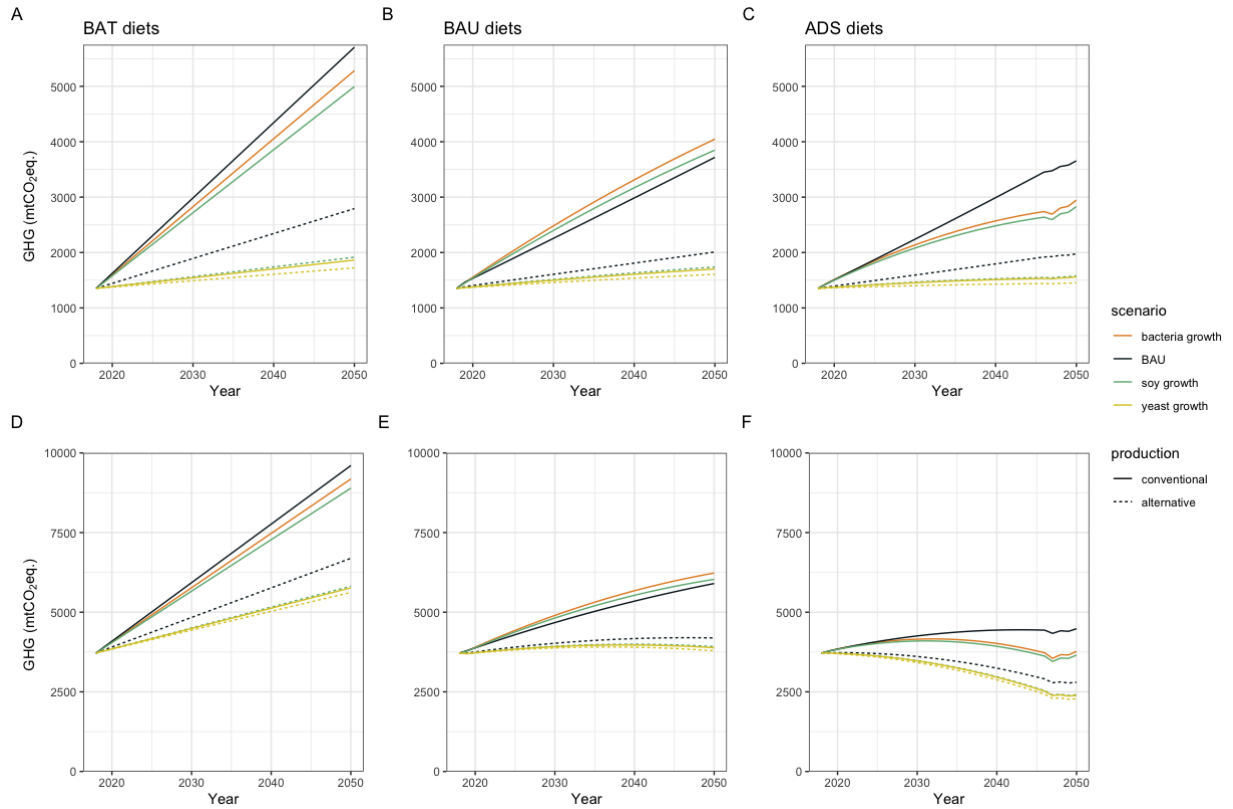


Figure S4: Projected greenhouse gas emissions of conventional versus alternative production methods for feed inputs. Alternative methods (dotted lines) refer to no till farming for crop inputs and yeast byproduct from biodiesel production from wheat. Real benefits of no-till farming vary by soil-type, location and over time, so these results are likely optimistic.

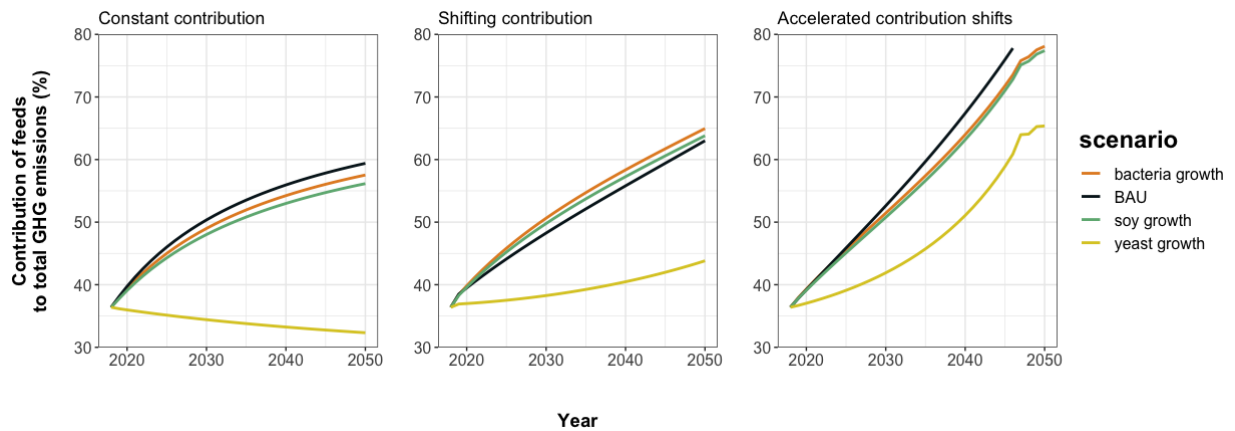


Figure S5: Contribution of feeds to total production emissions for projected years

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Chapter 3: Fish aggregation at ocean aquaculture can augment wild populations and local fishing

This chapter is in preparation for submission to a peer-reviewed journal with authorship as follows: Jessica L. Couture, Darcy Bradley, Benjamin Halpern, Steven Gaines

3.1 Introduction

Seafood is an efficient way to provide nutrition for the growing human population in an increasingly resource constrained world (Delgado, International Food Policy Research Institute, and WorldFish Center 2003; The World Bank 2013; Froehlich et al. 2020). While fisheries management is generally improving around the world, wild seafood catch has remained largely stagnant for several decades (Free et al. 2020; Hilborn et al. 2020).

Meanwhile, aquaculture is the fastest growing food sector in the world, and ocean spaces are considered the next frontier for aquaculture expansion (Gentry et al. 2017; Froehlich et al. 2017). As the aquaculture industry further develops in marine environments, simultaneously maintaining the health of wild fisheries is critical, both as a backstop for biodiversity and as a food security and livelihood source for millions of people around the world (FAO 2020). Given the social and economic importance of wild fisheries, understanding how potentially competing seafood production methods interact will be important to optimize co-management of these closely connected sectors (Clavelle et al. 2019).

Marine aquaculture may impact the population dynamics of local wild species through a myriad of mechanisms, which vary by farm type and farmed species, environment, and wild species characteristics, among other factors. First, farm structure may provide habitat for wild species, and case studies have documented attraction of wild organisms to farm areas (Fernandez-Jover et al. 2009; Oakes and Pondella 2009; Drouin et al. 2015)-and increased biomass at and around farms (Oakes and Pondella 2009; Karakassis 2000; Uglem

et al. 2009). Second, excess feed from finfish farms, fouling on aquaculture infrastructure, and wastes from cultured organisms can also provide nutritional supplements to the surrounding ecosystem (DeAlteris, Kilpatrick, and Rheault 2004; Marengi and Ozbay 2010; Arechavala-Lopez et al. 2011). These food subsidies, if moderate in scope, can benefit local wild populations, while excessive waste and parasite and disease transmission can cause harm (Costello 2009; Lafferty et al. 2015), leading to positive or negative impacts to fitness (e.g., alterations to natural mortality and growth rates) of wild populations (Talijančić et al. 2019; Akyol and Ertosluk 2010; Bagdonas, Humborstad, and Løkkeborg 2012; Taranger et al. 2015). Third, farming operations often restrict other ocean uses, including wild capture fisheries, which may impact the population dynamics of target species and the economics of the fisheries depending on the patterns of redistribution of fishing effort following farm installation (Kathrin Bacher and Gordo 2016; Bagdonas, Humborstad, and Løkkeborg 2012; Akyol and Ertosluk 2010) (Figure 1).

In this way, marine aquaculture can act both as something akin to a fish aggregating device (FAD), with fish attracted to and accumulating around its structure, and as a mini-marine protected area (MPA), since farms effectively provide refuge from fishing even though they tend to be small ($<1 \text{ km}^2$) (NOAA 2020) compared to MPAs (10^6 km^2) (Protected Planet 2021). Just as FADs are man-made structures used to concentrate naturally dispersed fish populations to increase fishing efficiency, aquaculture installations may provide a similar service to capture fisheries despite prohibiting fishing at the farm itself, because fishers can fish the edge of the farm. FADs are especially effective for pelagic species that tend to be broadly distributed (Girard, Benhamou, and Dagorn 2004; Wilson et al. 2020). The growth of ocean farms offshore will likely increase interactions with pelagic

fishes in ways that make them more predictably accessible. In overfished or weakly regulated fisheries, the protection conferred by aquaculture farms could also serve a stock rebuilding function (Gaines et al. 2010; Halpern, Lester, and Kellner 2009), potentially providing spillover benefits to surrounding fisheries for some stocks (Buxton et al. 2014; Goñi et al. 2010). However, farming is unique in that it often results in added nutrient input to the surrounding environment, which may augment or undermine these purported fisheries benefits depending on the context and quantity of inputs.

Here, we use spatially explicit population models to forecast how marine aquaculture might impact wild populations of harvested species and the fisheries they support. Specifically, we explore how a farms impact total population abundance and catch (i.e., biomass), assessing the influence of farm design (i.e., the size and spacing of installations) and species-specific movement rates (i.e., the likelihood that a species' will aggregate at a farm). We simulate movement of wild fish populations around farms, varying levels of attraction to farm structure, protection from fishing at farms given various installation designs, and direct impacts from farming operations to assess net effects on total biomass and catches. Our results are intended to inform strategic marine aquaculture design and planning to promote productive marine aquaculture growth, sustainable fisheries, and healthy marine ecosystems simultaneously into the future.

3.2 Results & Discussion

3.2.1 Simulating Ocean Aquaculture

To understand how wild fish and fisheries might respond to ocean farms, we built a spatially explicit age-structured population and fishing model and tracked total biomass and fishery catch (catch biomass; Ovando, Dougherty, and Wilson 2016) for several farm

scenarios compared to a business as usual control (i.e., no farms). Building on existing bioeconomic models used to understand the effects of MPAs on wild populations and fishing, this model represents the effects of aquaculture farms by considering how attraction to a farm interacts with variable farm design and impacts on the survival of wild populations at farms. Attraction, although not unique to ocean farms, has not yet been considered in these spatially explicit bioeconomic models. Farm design brings in the single-large or several-small (SLOSS) protected area considerations (Halpern and Warner 2003; Tjørve 2010) to test how attraction will affect these dynamics. Since farms are rarely inert, we also consider the role of positive and negative impacts to wild populations among these other axes of influences.

Species level population dynamics are modeled to simulate survival, aging, movement, and reproduction of a single-species within its natural range. Fishery management for all scenarios is modeled in two ways: strong or weak, with strong management modeled as fishing with constant effort set at the rate that generates maximum sustainable yield (MSY) and poor management as a high effort open access fishery. Farm results are compared to a control with no farm but under the corresponding fishery management scheme to calculate relative benefits or losses to population biomass and fishing due to ocean farms.

Farm scenarios simulate three variables: aggregation at a farm, farm designs, and impacts of aquaculture on wild fish survival. Aggregation was modeled as a combination of attraction to a farm and increased carrying capacity at a farm. Attraction to a farm was modelled as the likelihood of moving to patches containing farms when fish are within a defined distance from the farm. Given the uncertainty in this parameter, we simulate various

levels of attraction: none, low, moderate, high. Maximum aggregation at the farm was set by the patch-level carrying capacity at farms. The aggregation effect of increasing carrying capacity at a farm is uniform for all farm scenarios and acts on the growth rates of individuals in farm patches. Fishing was excluded at farms, and the effect of spatial fishing bans were tested under several farm designs by varying farm size and spacing. We simulated impacts of aquaculture operations on fitness of wild populations by adjusting the natural mortality parameter at farms. Benefits from food supplements at farms, for example, increase growth and decrease natural mortality whereas stress or damage from parasites increase natural mortality rates.

Below we first discuss the effects of aggregation to spaces where fishing is prohibited by comparing a scenario with no aggregation to increasing levels of aggregation: low, moderate, high. We then vary farm design to assess how total farm area and size of individual farms affect the impacts of attraction to farms. Since attraction acts on fish movement patterns, we also consider how species with different movement rates could be differentially affected by these parameters, and end by considering how positive or negative impacts of a farm on survival might affect attracted populations and fishery results.

3.2.2 Aggregation at farms

Across most scenarios, total catch increased due to the aggregation effect of farms for both strong and poor fishery management scenarios, with benefits eroding as farm sizes grow (Figures 2, S3). However, increasing the attraction effect led to relatively lower total catch in well-managed fisheries (i.e., those fished at MSY – Figure 2), because the combined impact of higher carrying capacity at the farm and higher attraction to the farm resulted in fewer fish available in the fished areas. At low levels of attraction, catches increased 6-18% relative to

the control in well-managed fisheries, while also increasing total biomass (15-20% increase over controls, figure S3). Higher levels of attraction, however, caused losses to total catches (20-75% losses depending on total farm area), but still increased total biomass of the population by 10-21% through protection in the farms.

Under weak fishery management, fisheries benefits from farms were even greater, with yields increasing up to 35% over controls. The benefits of farms when fisheries were weakly managed occur only after a period of significant initial fisheries losses, since the benefits require time for populations in farms to grow. Time to recovery was delayed and losses were deeper with increasing attraction due to greater initial removal of biomass from fishable areas soon after farm establishment. Accordingly, benefits to total biomass accumulated more quickly with higher levels of attraction (Figure S1), because more fish were more immediately protected from fishing. For scenarios with strong management, timing of benefits and losses were similar for biomass and catches across all levels of attraction (Figure S2).

While attraction itself is a difficult parameter to measure empirically, understanding which species aggregate around marine farms and to what extent they are attracted can help understand where they might lie along the spectrum of attraction, and how the combination of attraction and ability to sustain greater biomass together contribute to observed aggregations. As marine aquaculture grows in many countries, total farm areas remain small compared to species ranges, particularly as farms move offshore where species movement tends to be higher. Therefore, we can expect to see benefits to total biomass from aggregation at a farm, as long as farms are well managed at the farm level, so as to avoid pollution, disease transmission, or proliferation of parasites to wild populations. While tradeoffs were

found between level of attraction and benefits to catches for well managed fisheries, where losses are felt, increases in population biomass can help create a buffer to management uncertainty. Where management is strong, the resources and local knowledge are likely available to effectively adapt management to the new setting to minimize losses to the fishery. A better understanding of how fish behave around marine aquaculture farms will help to better model interactions with marine farms and inform strategic planning of ocean farms to maximize benefits to the wild populations and local fishing.

3.2.3 *Farm design*

Farm design was simulated in several configurations to test how siting and planning might affect the outcomes of other farm impacts tested here. Total farm area modeled as one large contiguous farm and divided up into smaller farms, the size of each based on total area and number of farms: $farm\ size = \frac{total\ farm\ area}{number\ of\ farms}$. Dividing up total farm area into networks of smaller farms increases benefits of aggregation to fishing catches both when fishery management is weak (Figure 2, S1 & 2) and at low levels of attraction with strong management (Figure 2). Breaking up total farm area into smaller farms increases access to farms via an increased edge to area ratio, which attracts wild individuals more quickly, leading to more rapid benefits from increased carrying capacity and protection from fishing. Smaller farms also accelerated the time to recovery of fishing yields after farm introduction in the weak management scenarios, and initial losses were less severe than with large contiguous farms (Figure S1) due to the effects of increased edges.

Interactions between aggregation at farms and smaller farm areas can provide synergistic benefits to local fishing especially for smaller to moderate total farm areas (up to 35% over the control), although at low levels of attraction benefits to fisheries were seen for

even large total farm areas (>60% total species range). Given the small fraction of species ranges that are currently occupied by marine aquaculture, these results suggest there is substantial scope for well designed and executed farms to create fisheries benefits. Increases in carrying capacity benefit growth of individuals, benefits which can then spill over to predictable nearby fishable areas. When farm areas take up less than 50% of the total range of the wild species, which is most realistic particularly for offshore farms, fishing yields are higher than when attraction acts on contiguous farms of the same total area. Smaller farm designs that include attraction reach benefits over control scenarios that with no attraction would require much larger total farm areas (Figure 2D).

Aquaculture farms designed as individual smaller farms can increase benefits to both wild populations and fishing. With this configuration, farm-level management at each site is important to ensuring benefits rather than increasing exposure to harm. In addition to dispersing environmental impacts of a farm, smaller farms can amplify benefits to fishing from modifications to the distributions of wild species. Given the interactions between aggregation and farm design, understanding the movement patterns of the stock of interest, and how such patterns will be modified by ocean aquaculture, is important to determining ideal sizing and spacing of new ocean farms.

3.2.4 Species movement

To understand how results might change for different species, we varied average adult movement from sessile (movement = 0) to highly mobile pelagics (movement = 60% of the total simulated space). When fishery management was weak, benefits to catches were highest for moderate and highly mobile species across farm areas. When movement is low, benefits are also realized, although less so, for total farm areas less than 50% of species

ranges. For sessile species under weak management, fishery losses were felt for all farm sizes (Figure S6). As movement slows, benefits from the farm to growth and survival (from protection from fishing) are less efficiently distributed into fishable areas, with benefits to sessile species remaining inside the farm area. Biomass increases for all movement rates under weak management (Figures S5 & S6). Similarly, when fishing is well managed, catches only increased for highly mobile species, with losses for sessile and less mobile species, again likely due to removal of fishable areas causing more losses than any benefits from the farm.

Movement patterns around farms play a dominant role in our forecasts of outcomes of wild species fisheries with aquaculture. Unfortunately, our empirical understanding of behavioral responses such as their scales of attraction and their propensity to move from a farm across multiple fished species and farm types remains relatively limited. As ocean farms move further offshore (Froehlich et al. 2020; Gentry et al. 2017), the species they interact with will likely be more highly mobile and migratory. As a result, farms will likely increasingly fill the FAD role of attracting fish to a known location, which can enhance the predictability of high fishing yield locations. Further empirical research is needed to characterize if and how ocean farms might cause interruptions to migrations and longer distance movement. While data are lacking to properly quantify attraction to a farm, there is less information still on the retention of wild species once they arrive at ocean farms, which is an important factor in species aggregation at a farm.

Although we have included several species behaviors in our model forecasts, there are other behaviors that require further exploration. One is the potential consequences of movement between farms. For example, *Pollachius virens* is an important fishery species

with variable movement patterns – at times remaining relatively sedentary, but also embarking on longer migrations (Jakobsen and Olsen 1987; Homrum et al. 2013). These fish have been documented spending significant time at salmonid farms in Norway (Uglem et al. 2009; 2014). In this particular case, *P. virens* were found to move long distances between farms, thereby increasing connectivity between aquaculture sites and potentially transporting parasites or diseases between farms. This well-studied case of specific changes in behaviors around farms demonstrates the need for further investigation into how ocean aquaculture uniquely affects different species, in order to better incorporate potentially novel interactions into planning and management of regional aquaculture as well as to fully understand risks to cultured and wild species.

3.2.5 *Impacts to fitness from ocean farms*

Farm activities can provide benefits or damage to wild populations nearby by providing protection and/or food subsidies, or creating unhealthy conditions, respectively. Effects of ocean farms on the fitness of wild populations were simulated by modifying natural mortality rates for individuals that came into contact with farm spaces. Negative impacts (e.g., from pollution) increased natural mortality, and positive impacts (e.g., from food supplements) decreased local natural mortality. Such contrasting impacts to the survival of wild organisms at aquaculture sites predictably intensified or dulled benefits from farms in weak fishery management scenarios but caused unexpected impacts to catches when fishing was well managed (Figure 3). At high levels of damage, causing significant mortality to wild populations (greater than fishing mortality), both total biomass and fishing yields see substantial losses (Figure S3), as expected. Low to moderate harm to wild populations,

however, can still result in benefits to both wild populations and fishing, especially with smaller farm sizes.

Counterintuitively, fishing yields can have the opposite reactions when fisheries are well managed. Losses to fishing are felt when farms provide positive impacts to fitness across mobile species and catches increase for species with high mobility when farms produce negative impacts (Figure 3). Benefits to fishing in the negative impacts scenarios are due to increased mortality controlling biomass within the farm, so that carrying capacity benefits to growth rates can produce larger fish spilling over outside the farms, whereas where mortality is decreased, more crowded farm areas further limit individual growth rates (Figure 3). These confounding impacts on individual versus population growth rates in well managed fisheries could create complex outcomes to fishing yields highlighting the need for a better understanding of these individual impacts on species of interest.

These results indicate that while benefits can be realized from changes to movement and protection from fishing at ocean farms, negative impacts need to be minimized to support a healthy ecosystem. Still, trade-offs between different farm designs, modification to movement and direct impacts can lead to surprising results, such as benefits to wild populations despite increased stress to individuals (Figure 3B-D). Designing ocean farms as networks of small to moderate sized farms, rather than very large contiguous farms, can increase benefits in settings with weakly managed fisheries even if the fitness impacts are unknown.

3.2.6 *Real world applications*

The complex interactions demonstrated here help to highlight potential consequences of ocean farms on wild populations and fishing but also indicate that a stronger

understanding of the various impacts of ocean farms will be needed to predict how wild populations and fishing will be impacted in a given setting. Variation in responses across parameters suggests that location and species specific data will be needed. Quantifying aggregation is likely the trickiest of the parameters tested here to determine for a given farm and species, but a before-after-control-impact (BACI) designed study of a farm site tracking species of interest would help to understand the extent to which fish are attracted to farms and how much carrying capacity is affected at a farm. With these BACI data, the model described here can be used with more commonly accessible parameters, such as fishery management and species-specific ranges and movement rates, to predict population and fishery responses.

In reality, farms greater than 50% of a species' range are highly unlikely, and in fact existing ocean farms would rarely exceed 20% of species ranges. The “smaller farms” designs divided total farm areas into farms taking up only 5% of species ranges, which can still be a considerable size depending on the species considered. High variability in movement rates between species is common. Species with moderate to high movement might interact with offshore pelagic farms, such as finfish pens and mussel lines, whereas sessile and low movement species might be found at farms nearer to shore seaweed or oyster farms, particularly when considering species targeted for fishing. That being said, crabs and lobsters have relatively low movement rates and interact with deeper off-shore farms (Milewski, Smith, and Lotze 2021), and sessile species such as seaweeds and mussels recruit to novel farm structures.

Often considered a nuisance to farmers, fouled individuals can attract and feed predatory fish species (Callier et al. 2017). Larger predatory fish are also attracted to ocean

farms to prey on aggregated wild species (K Bacher, Gordo, and Sagué 2012) or the biomass of the farmed product itself (Sanchez-Jerez et al. 2008). In many locations ocean farms create more of a dynamic system than was tested here. Incorporation of these interactions into this already complex system will add another layer of intricacy. Multi-species and ecosystem level interactions at an ocean farm could change the outcomes found here, but are important to understanding the real impacts of ocean farms on fishery and conservation goals.

3.3 Conclusions

This work is the first to simulate how changes in movement of wild species and protection from fishing at marine aquaculture sites can impact wild populations and local fisheries. Attraction to aquaculture farms can augment protection from fishing at a farm, providing greater benefits to overfished populations and surrounding fisheries. Smaller farms can further amplify these benefits by increasing edges for both enhanced access to farms and facilitating spillover of fish back to fishable areas. Movement patterns and interactions of farm impacts to targeted species can result in highly variable outcomes including increases in fishing when natural mortality is increased and losses to fisheries when farms decrease mortality. Understanding how movement patterns might be further modified by ocean farms (e.g. which species will be more resident or transient at farms and seasonality of farm use and migrations) will help to optimize farm design in support of fisheries objectives. These relationships can be highly nuanced and variable by farm, location, and wild species, so understanding the local communities, fisheries management, and aquaculture goals, will be essential to the application of these findings. More empirical research is needed to further classify interactions between different species groups and the various types of marine

aquaculture to better inform planning and siting of marine aquaculture. Both wild fisheries and marine aquaculture are predicted to be increasingly significant food sources into the future, so understanding how to best plan for and manage these coexisting industries will allow us to efficiently produce diverse seafood products while also supporting robust coastal economies into the future.

3.4 Methods

To test the responses of wild populations and capture fisheries to marine aquaculture, we built a spatially explicit age-structured population and fishing dynamics model to simulate movement of wild fish and fishers around ocean farms. Our model allows farms to affect wild populations by 1) attracting fish to the farm area with increasing carrying capacity at the farm sites, 2) protecting individuals from fishing, and 3) altering mortality rates. The base model simulates movement, reproduction, and mortality (natural and fishing) of wild fish and fishery yields. When farms are added, we modify fish movement to include attraction to farm spaces in addition to the random density dependent movement in the base model. Carrying capacity is also applied spatially affecting individual growth rates at a given patch, with a higher carrying capacity at farms to represent the ability of farms to support higher densities of attracted individuals. Several farm sizes are tested to understand the effects of different planning and siting designs on outcome variables. Impacts are also tested across a range of adult movement values to test how different species types might be affected by marine aquaculture. Natural mortality is adjusted for individuals at farms to simulate direct impacts of the farms on the fitness of wild populations and test the effects of attraction to these positive and negative influences. Total biomass and fishing biomass are tracked for each scenario and compared to a control with no farms present (using the base model). All

modeling and analysis was conducted in R (R Core Team 2021) and all data and code are available here: github.com/couture322/oceanFarms.

3.4.1 The base model

3.4.1.1 Population model

The model is a single-species deterministic model that represents the range of a theoretical species divided into spatial patches (Ovando, Dougherty, and Wilson 2016). All scenarios are run on a 1-dimensional closed system of 100 patches of identical size, with no immigration or emigration out of the system. Patches are connected via larval dispersal and adult movement. Larval supply is high to emphasize the impacts of adult movement and spillover, and larval dispersal is uniform across all patches with density dependent survival by patch (Babcock and MacCall 2011). Patch-level carrying capacity is uniform across all patches and acts on individual growth rates in a given patch. Carrying capacity is determined based on equilibrium biomass per patch without either farms or fishing. Fishing is modeled in two ways: weak fishery management and strong fishery management.

Adult movement is calculated for each time step using a Gaussian movement kernel to calculate the probability of moving from one patch to another. Probabilities are based on the distance between patches, and a static movement parameter that scales movement to specified species mobility. The probability of movement from patch i to patch j is

$$p_{i,j} = e^{\frac{-d_{i,j}^2}{2\sigma_m^2}}$$

where d is the distance between i and j in number of patches and σ_m scales movement for a species based on a species range parameter. The sum of movement probabilities from a given

patch, p_i , to all other patches is 1. Edges are wrapped to avoid edge effects in movement (Ovando, Dougherty, and Wilson 2016).

Carrying capacity is calculated as the equilibrium biomass per patch with no fishing and no farms, and is applied uniformly across all patches. Fish length is calculated using the von Bertalanffy growth equation for each age group and adjusted based on the patch carrying capacity. Average weight-at-age, w_{age} , is thus density dependent and calculated as:

$$w_{age+1} = w_{age} + (b_2 L_{age+1}^{b_1} - b_2 L_{age}^{b_1}) \left(1 - \frac{bm_{patch}}{K_{patch}} \right)$$

where b_1 and b_2 are weight-at-age constants and L is length. bm_{patch} is the total biomass currently occupying the patch, and K_{patch} is the carrying capacity for total biomass in a patch.

Fishing dynamics

Impacts of ocean farms on capture fisheries resources are considered under weak and strong fishery management regimes as in Ovando et al. (2016). Weak fishery management is represented by a high value fishery under open access management. Strong fishery management is represented by constant effort at maximum sustainable yield. In both scenarios, fishing effort is tracked rather than individual fishers or boats in order to simplify the fishing models. Fishers are assumed to be knowledgeable about where fish biomass is highest and so gravitate to more profitable fishing patches, therefore effort in a patch is scaled based on fishable biomass available in a given patch. Catch biomass, $C_{i,t}$, is tracked by patch, i , and time-step, t , as

$$C_{i,t} = \sum_a \frac{F_{i,t} v_a}{F_{i,t} v_a + M} N_{i,a,t} (1 - e^{-M - F_{i,t} v_a}) w_a$$

where F is fishing mortality, M is natural mortality, and v_a is selectivity at age. Fishing mortality is removed from the total population biomass.

3.4.2 *The aquaculture farms model*

To test the impacts of ocean farms on wild populations and fisheries we modified the base model to incorporate farm impacts identified in the literature, particularly: 1) protection from fishing, 2) aggregation modeled as attraction to farms and increased capacity at farms, and 3) impacts on population fitness (Figure 1). These three elements are varied across parameter spaces to assess how each affects population biomass and fishery catches. Farm design is also changed by varying the number of farms in order to understand the role that farm siting could play in these results. Particular patches in the 100 patch array were indicated as farm patches based on total farm size and the size of each farm and these farm patches experienced the modifications described below.

3.4.2.1 *Protection from fishing*

To represent physical and regulatory limitations to fishing at farms, fishing was prohibited at farm sites for the farm scenarios and effort was redistributed to non-farm fishable spaces. Redistribution of fishing, $F_{i,t}$, for a given patch, i , and time-step, t , was calculated as:

$$F_{i,t} = F_{i,base} \frac{1}{1 - P_{farm}} \bar{B}_{i,t}$$

where $F_{i, base}$ is the fishing mortality for the given patch before farms were introduced, P_{farm} is the proportion of patches in the farm, and $\bar{B}_{i,j}$ is total fishable biomass (biomass of legal size in non-farm patches) (Halpern, Gaines, and Warner 2004).

Farm design was tested by dividing up total farm areas into different size groups of farm patches. Total farm area is set manually as a percent of the total system, $N_{patches}$, and is divided up into farms of a designated size: *total farm area* = $N_{patches} \times \textit{proportion farm area}$. Farm size is a separate parameter which divides up the total farm area into individual farms so the number of farms depends on total farm area and farm size.

$$N_{farms} = \frac{\textit{total farm area}}{\textit{farm size}}$$

3.4.2.2 Aggregation at farms

Aggregation was modeled as both attraction to farm spaces and increased carrying capacity at farms. Attraction to the farm modified movement from density dependent random movement to increase the likelihood of directional movement towards the farm when within an indicated vicinity, or zone of influence (ZOI). Attraction, A , to a farm patch is simulated by increasing the likelihood of movement to farm patches, j_{farm} from patches within a designated distance from the farm, i_{ZOI} , relative to movement to other patches, $j_{non-farm}$, where A is a scalar multiplier greater than one:

$$p_{i_{ZOI},j_{farm}} = e^{\frac{-d_{ij}^2}{A^2\sigma_m^2}}$$

Since attraction is difficult to quantify, the attraction parameter was varied over a range of values from 1 (no attraction) to 15. Case studies report densities of up to 20 times that found away from the farms, which represents a combination of attraction and ability to retain individuals, so we thought 15x attraction was conservative. Carrying capacity, K , was also increased at a constant rate, $K_{farm} = 10^2 K_{patch}$, at farms to allow for the buildup of

attracted biomass at farms. K acts to limit growth of individuals as indicated in equation 2. Density dependent movement was still applied as in the base model to realize spillover benefits from the farms, but growth rate limitations were relieved at the farm with the increased carrying capacity.

3.4.2.3 Impacts to fitness

Direct impacts from marine aquaculture on the fitness of wild populations are tested as decreases and increases to natural mortality, to represent benefits and damage to wild populations, respectively. Carrying capacities were held constant for all farm scenarios, so impacts to natural mortality act in addition to changes in growth rate from carrying capacity at farms. Positive impacts were represented as a 20% decrease in base natural mortality, and negative impacts to the population were simulated as a 20% increase in natural mortality.

3.5 Figures

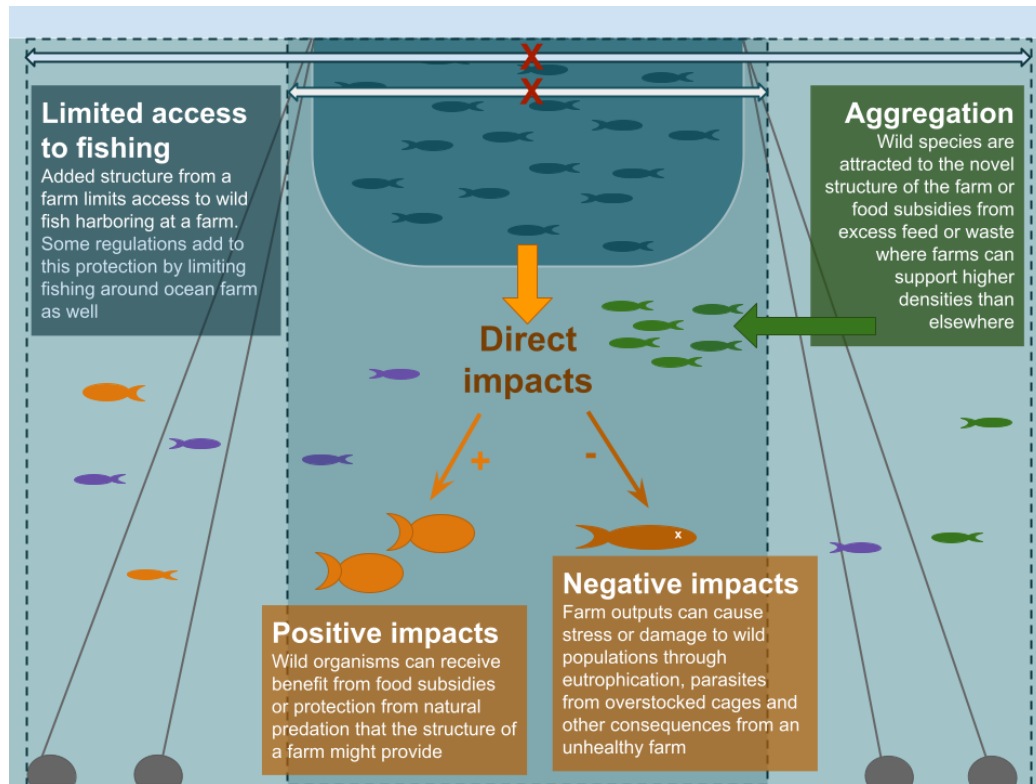


Figure 1: Diagram of marine aquaculture interactions with wild populations and capture fisheries.

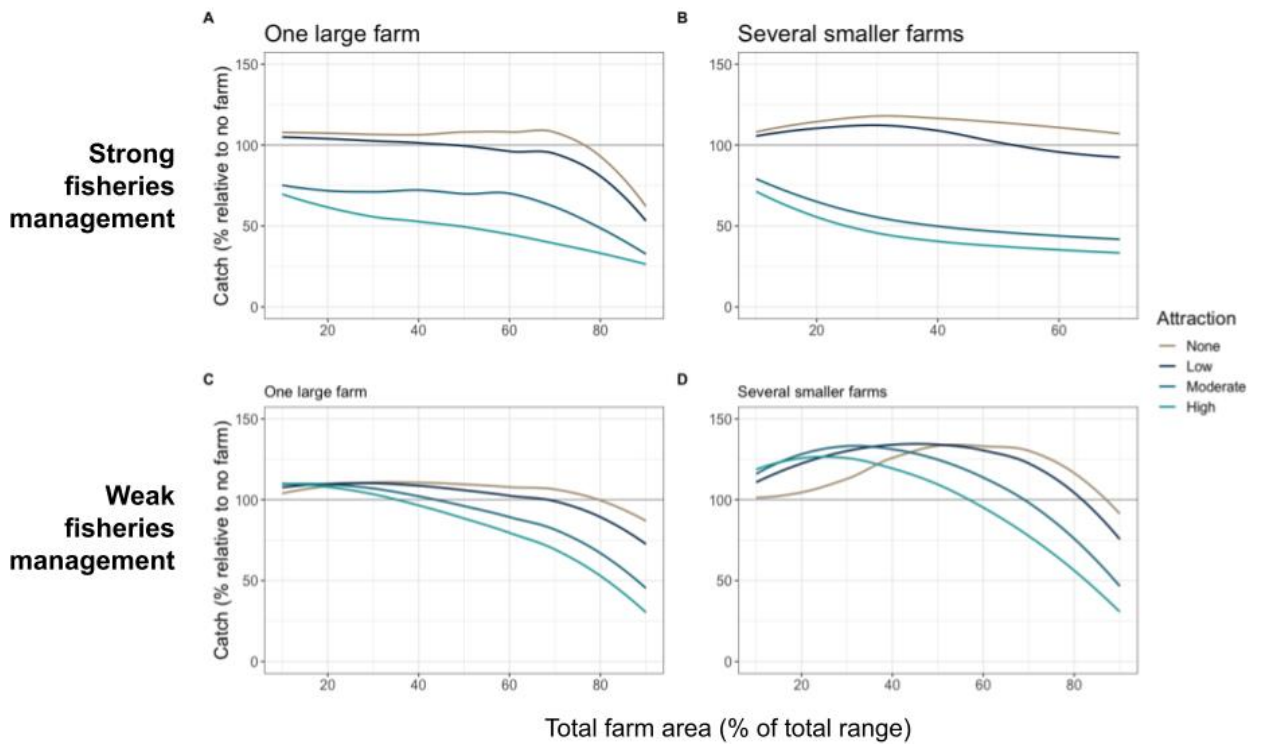


Figure 2: Differences in equilibrium catch biomass relative to catches with no farm, given different levels of attraction to farms with farms of varying total area coverage for (A, C) one large contiguous farm and (B, D) total farm area broken up into smaller separate farms. Top plots (A, B) are run under strong fisheries management, bottom plots (C, D) are under poor management. Catch biomass difference is calculated as the difference between catch biomass with the farm scenario and a scenario with no farm.

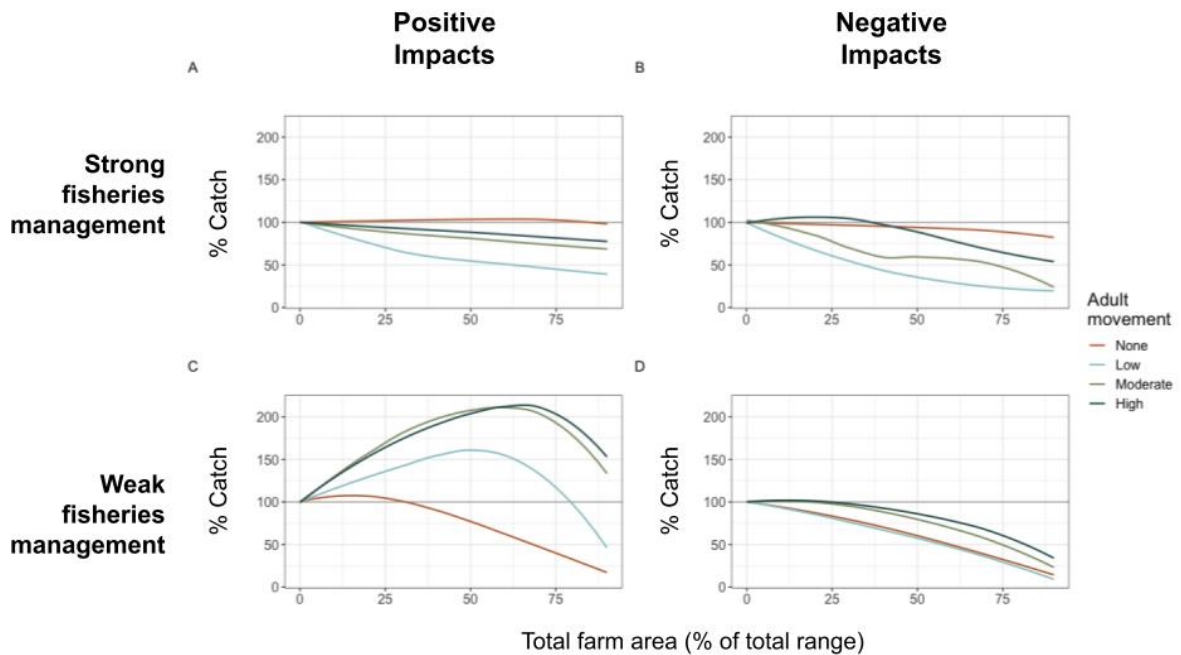


Figure 3: Relative differences in catch biomass compared to no farm over a range of total farm areas. Farms are all divided into several smaller farms. Farm scenarios with positive (A, C) and negative impacts to the wild population (C, D), under strong (A, B) and weak (B, D) fishery management.

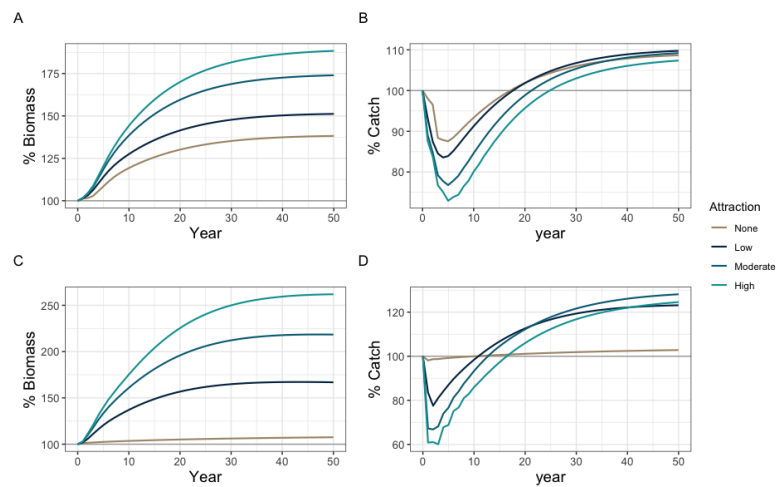


Figure S1: Farm impacts over time for a high value open access fishery. In each plot the level of attraction is varied. Top plots represent one large farm at 20% total coverage (A, B), and the bottom plots represent the 20% farm area broken into several smaller farms (C, D). Biomass and catches are relative to the base scenario with no farm (farm scenario/no farm scenario).

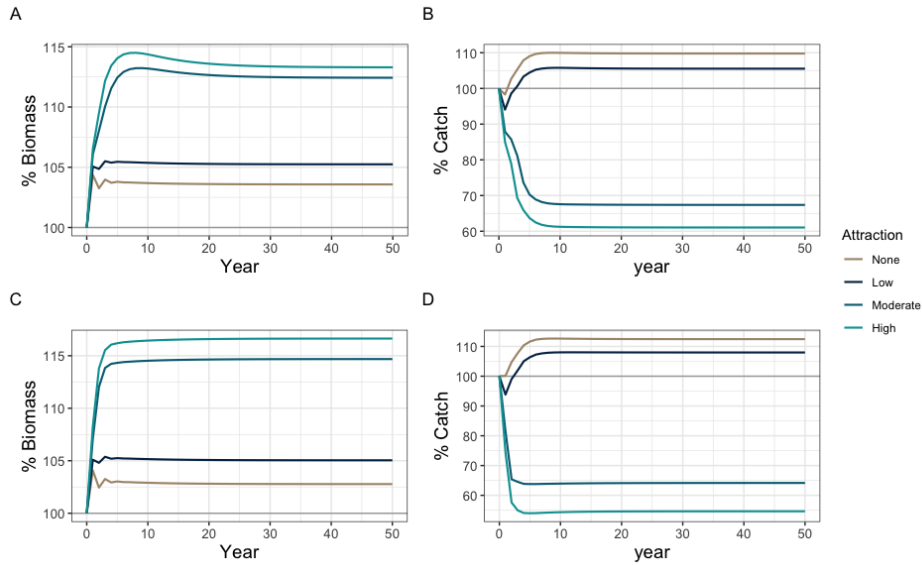


Figure S2: Farm impacts over time for a fishery fished at constant effort at maximum sustainable yield. In each plot the level of attraction is varied. Top plots represent one large farm at 20% total coverage (A, B), and the bottom plots represent the 20% farm area broken into several smaller farms (C, D). Biomass and catches are relative to the base scenario with no farm (farm scenario/no farm scenario).

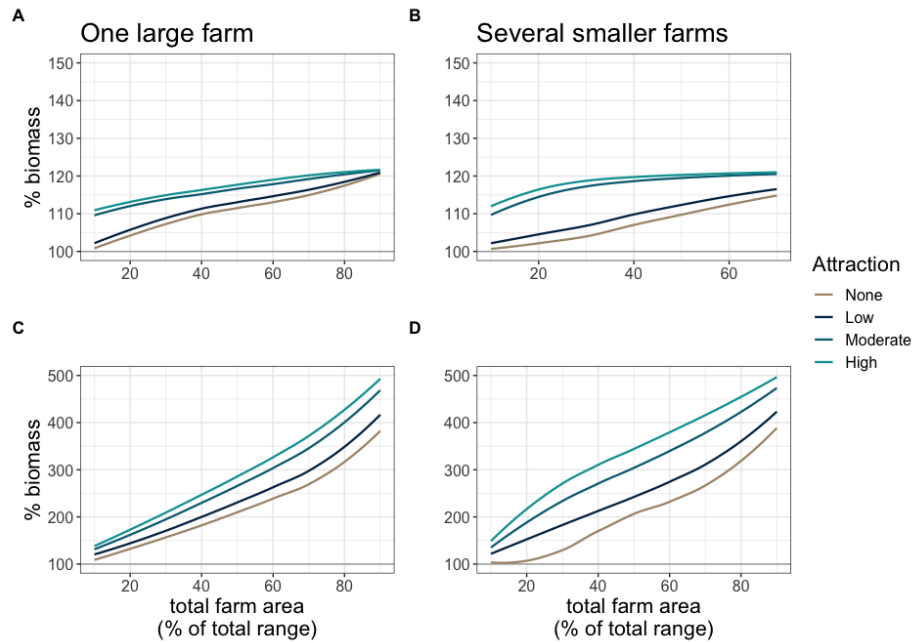


Figure S3: Equilibrium biomass differences given different levels of attraction to farms with farms of varying total area coverage for (A) one large contiguous farm and (B) total farm area broken up into smaller separate farms. Catch biomass difference is calculated as the difference between catch biomass with the farm scenario and a scenario with no farm.

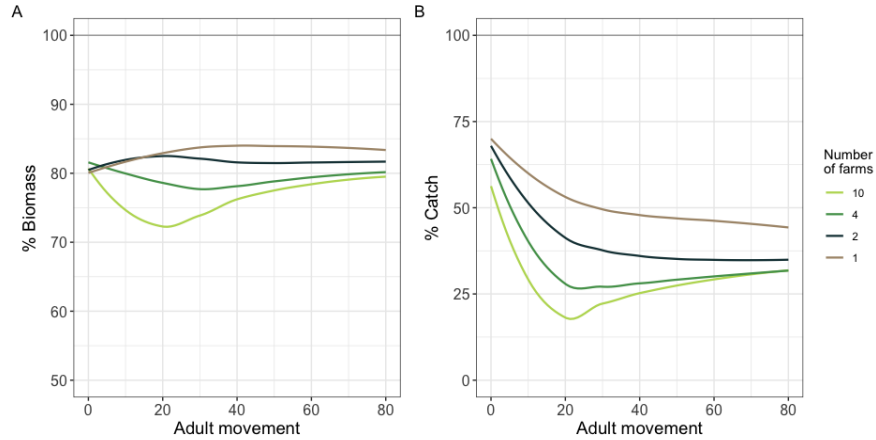


Figure S4: Equilibrium differences in total biomass and catch biomass for different species based on adult movement for farm scenarios with very damaging effects on the wild population (damage > fishing mortality). Different farm designs are tested by farm size resulting in the indicated number of farms.

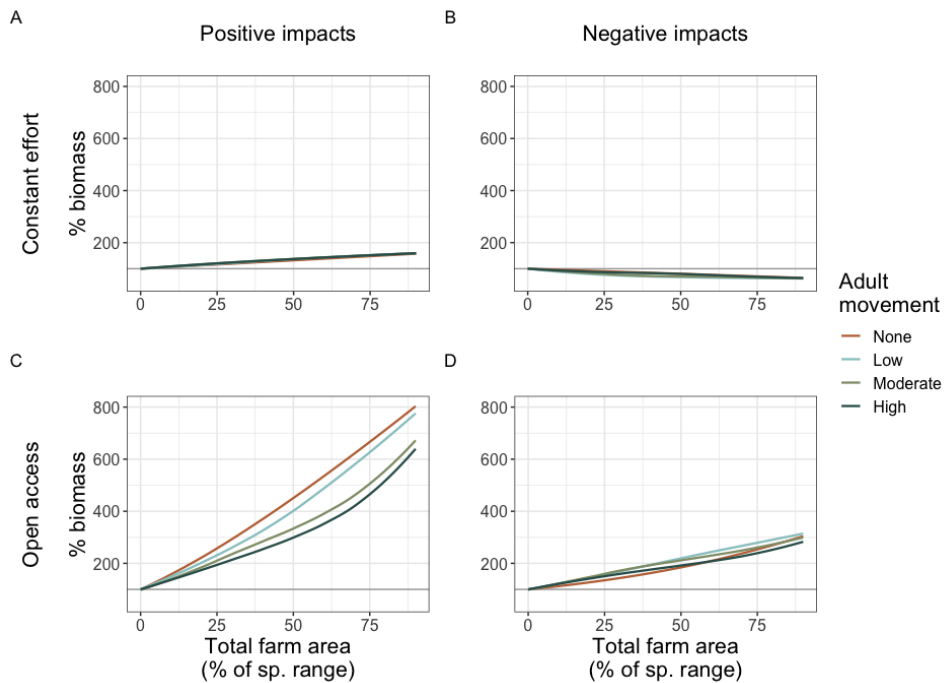


Figure S5: Relative differences in total biomass compared to no farm over a range of total farm areas. Farms are all divided into several smaller farms. Farm scenarios with positive (A, C) and negative impacts to the wild population (C, D), under strong (A, B) and weak (B, D) fishery management.

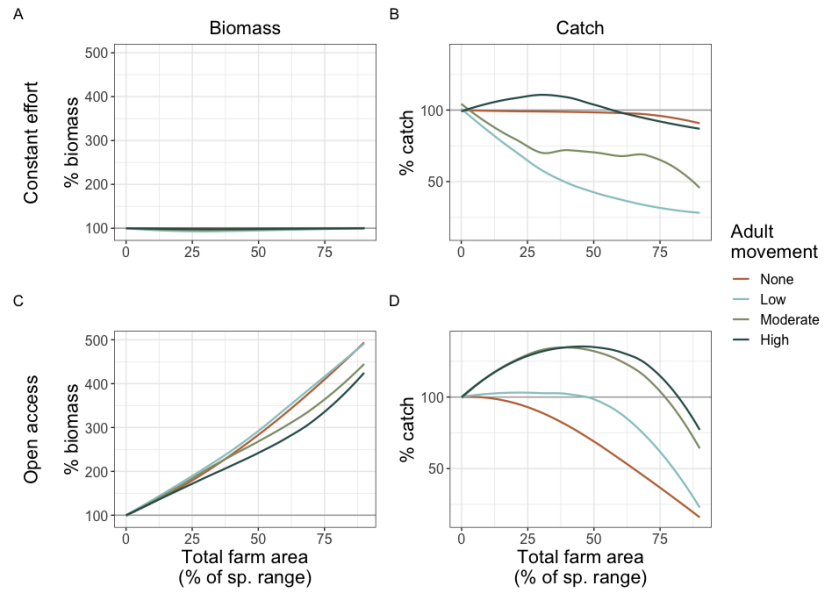


Figure S6: Relative differences in total biomass and catches compared to no farm over a range of total farm areas. Farms are all divided into several smaller farms. Here farms have no impact on wild population natural mortality rates.

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