

1 **Agriculture can help aquaculture become greener**

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24 **Abstract**

25 Aquaculture, the farming of fish and seafood, is recognised as a highly efficient system to produce
26 protein for human consumption. In contrast, many terrestrial animal protein production systems are
27 inefficient, impacting on land use and exacerbating climate change. Humankind needs to adopt a more
28 plant-centric diet, the only exception being fish consumed as both a source of protein and essential
29 dietary nutrients such as omega-3 fatty acids. Here, we consider the implications of such a transition,
30 and the challenges that aquaculture must overcome to increase productivity within planetary
31 boundaries. We consider how agriculture, especially crops, can provide solutions for aquaculture,
32 especially the sectors that are dependent on marine ingredients. For example, agriculture can provide
33 experience of managing monocultures and new technologies such as genetically modified crops
34 tailored specifically for use in aquaculture. We propose that a closer connection between agriculture
35 and aquaculture will create a resilient food system capable of meeting increasing dietary and
36 nutritional demands without exhausting planetary resources.

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46 **Main**

47 Never before has the impact of humanity on the planet and its ecosystems been so obvious and so
48 deleterious. Efforts have been made to define the maximum potential of a system to operate under
49 different scenarios – such methodologies have helped define “planetary boundaries” (PBs) within
50 which food production must operate to avoid impact on natural capital and the environment¹. The
51 EAT-Lancet Commission report proposed a “planetary health diet”, where adults consumed 2500
52 calories/day and the majority of these foodstuffs are derived from plants¹. Specifically, animal-derived
53 protein was targeted for significant reduction, on the basis that terrestrial animal production systems
54 are not only inefficient in terms of protein input:output ratios, but also contribute to climate change
55 both directly (methane emission) and indirectly (deforestation). Production of animal protein for
56 human consumption is undergoing a radical reconfiguration². This Perspective highlights how
57 agriculture and aquaculture can work synergistically to deliver a sustainable future, with a focus on
58 the salmon industry since this represents the primary nexus for omega-3 fish oils between the oceans
59 and our mouths.

60 *A Future for Fish on the Planetary Plate*

61 The EAT-Lancet Commission and the recommended “Planetary Health Plate”¹ proposed fish as the
62 only form of animal protein recommended for increased production and consumption but it made no
63 distinction between wild capture and aquaculture, nor marine and freshwater species. Distinction
64 between these two niches is critical in terms of the presence/absence of the nutritionally important
65 omega-3 long-chain polyunsaturated fatty acids (LC-PUFAs); lipids that play a vital role in neonatal and
66 infant development as well as cardiovascular health and metabolic pathologies such as type-2
67 diabetes³, but of which human have a very low capacity to synthesise⁴.

68 Demand for aquatic species as a key source of protein for human consumption and omega-3 LC-PUFAs
69 has continued to grow⁵. Since 2015, the majority (currently 52%) of all fish and seafood consumed is

70 produced by aquaculture⁵. The two production systems are quite different in terms of impact on the
71 environment, as deduced from Life Cycle Analysis⁶ – only aquaculture has the potential to meet the
72 needs of 10bn people in 2050 whilst remaining within PBs. However, to achieve that will require a
73 significant reconfiguration of current aquaculture food systems (Fig. 1), and to some extent, the path
74 will need to be like that proposed for humans – a predominantly plant-based diet^{1,6}.

75 However, the paradigm of aquaculture overcoming the limited supply of fish and seafood from our
76 oceans is problematic, since aquaculture feeds, especially for salmonids and marine fish, are based on
77 fishmeal (FM) and fish oil (FO), both extracted from wild capture marine fisheries⁴. Dating back to the
78 1970s, this was a logical practice for the farming of carnivorous fish species since FM and FO reflected
79 their natural diets, providing balanced nutrients that were readily available and cheap. However, the
80 subsequent global expansion of aquaculture, growing at an annual rate averaging around 10 % in the
81 1980s and 1990s, and almost 6 % over the last 20 years, has meant that this practice has become
82 unsustainable worldwide⁵. While aquaculture production of fish and seafood has increased from
83 around 10 million tonnes in 1990 to 81 million tonnes in 2016, global reduction (feed-grade) fisheries
84 have been static over this period with catches plateauing around ~20-25 million tonnes, producing
85 around 5-6 million tonnes of FM and 0.8 – 1.2 million tonnes of FO annually⁷. Thus, while demand
86 from aquaculture has increased, supply has remained relatively constant, and so other protein and oil
87 sources were required to replace FM and FO in feed formulations^{8,9}. While terrestrial animal by-
88 products such as poultry meals, blood meal and tallow have been used in some parts of the world, the
89 predominant alternative ingredients have been derived from plants seed meals and vegetable oils¹⁰.
90 Thus, it was hoped that plant-based products could deliver to the needs of aquaculture, using a small
91 percentage of global agricultural acreage to satiate the oil and protein requirements of aquafeed diets.

92 *The Impact of Evolving Fish Feed Formulations*

93 The change in feed formulations from a traditionally marine-derived to a terrestrial agriculture-
94 derived raw material base has been successful in supporting the growth of aquaculture. In addition,

95 aquaculture feeds and feeding strategies are now significantly more sustainable than in the past ¹¹.
96 FM and FO are not inherently unsustainable products, as they are often portrayed. The reduction
97 fisheries from which FM and FO are derived are no different to all other fisheries on the planet in that
98 they must be properly managed and regulated to ensure catches are sustainable⁴. In addition,
99 although a significant proportion of FM and, to a lesser extent, FO is produced from recycling the by-
100 products of food (capture) fisheries and aquaculture⁴, the fundamental issue with marine ingredients
101 is that they are finite on an annual basis, and thus limiting as demand increases from direct human
102 consumption and aquaculture^{7,12}. Thus, formulating feeds with large proportions of marine
103 ingredients became unsustainable¹³. Consequently, as demand for FM and, especially FO, increased,
104 availability declined and prices rose, feed manufacturers chose to increasingly replace FM and FO with
105 plant seed protein meals and vegetable oils that were readily available and cheaper. The finite amount
106 of FM and FO, constrained by the PB of what the oceans could produce, was spread thinner across the
107 ever-increasing volume of demands¹⁴.

108 The changing raw material base of aquaculture feed also has consequences for human nutrition as the
109 nutrient composition of the farmed fish is altered¹². This includes potential reductions in minerals e.g.
110 iodine and selenium, and vitamins such as vitamin D, that are traditionally associated with fish and
111 seafood. Lower levels of essential nutrients in raw material feed ingredients has consequently
112 impacted their levels in farmed fish. However, the most important impact has been on the fatty acid
113 composition of farmed fish. In oily species such as salmon and trout, fish produced on predominantly
114 vegetarian feeds have significantly reduced levels of the omega-3 LC-PUFA, EPA (eicosapentaenoic
115 acid) and DHA (docosahexaenoic acid)¹². In 1990, around 90 % of the feed formulation for salmon was
116 FM and FO, whereas by 2016, marine ingredients had reduced to around 25 %, with 75 % coming from
117 terrestrial plant sources¹¹. Consequently, the large-scale adoption of this vegetarian replacement
118 strategy lowered EPA and DHA levels in salmon feeds, resulting in 2016 in a decline of omega-3 LC-
119 PUFA in farmed salmon to around 50 % of those farmed a decade earlier¹⁵. Sprague et al.^{15,16} also
120 indicated that this replacement strategy, substituting marine FM and FO with terrestrial plant-derived

121 ingredients devoid of omega-3 LC-PUFA, had reached a point whereby further substitution would
122 seriously impact the quality of salmon and farmed fish in general. In addition, omega-3 LC-PUFA have
123 the same essential roles in fish as they do in humans^{17,18}, they are equally important for the health of
124 fish, this could be compromised in farmed animals by further reductions in the levels of EPA and DHA
125 in feeds^{19,20}.

126 Expanding production of aquaculture while simultaneously increasing sustainability is only possible
127 through the extensive use of plant meals and vegetable oils. Therefore, agriculture has a vital role to
128 play in helping to further transform aquaculture. Some of this is already underway, with the
129 application of data-driven approaches to many aspects of industrial-scale aquaculture. Equally,
130 selective breeding approaches established for terrestrial animals and plants, such as genomic
131 selection and genome wide association studies (GWAS), are now also used routinely in genetic
132 improvement for some commercial fish species²¹. However, it is the unrivalled potential of agriculture
133 to expand that has the greatest potential to help aquaculture – twinning the continued growth of the
134 latter with the former can help aquaculture to become greener and create a truly sustainable solution.

135 Crop-based agriculture plays a central role in global nutrition and food security. The global production
136 of vegetable oils has increased from 148 million tonnes in 2010 to 198 million tonnes in 2017. Thus,
137 the total outputs of the reduction fisheries look rather insignificant, which indicate that crop-based
138 agriculture has the capacity to contribute to the relief of current bottlenecks in the aquaculture sector.
139 In the long term, significantly less land will be needed to produce feed ingredients for terrestrial animal
140 protein production^{2,23}.

141 *Approaches to Increase the Synergy between Agriculture and Aquaculture*

142 One focus to increase this synergy would be to use crops to produce some of the specialised feed
143 ingredients that aquaculture is dependent on, namely omega-3 LC-PUFA and high-quality protein²².
144 There is also strong demand for the antioxidant pigments like astaxanthin for skin and flesh

145 colouration in many farmed species. Such new contributions would be in addition to the already
146 significant contribution plant products make to aquafeeds but, in some cases, provide a better tailored
147 composition (in terms of nutrition) or provide a *de novo*, scalable source of a previously rate-limiting
148 component – examples are listed below:

149 *Plant-derived omega-3 LC-PUFA replacements:*

150 Although this concept has been mooted for well over a decade²⁴, in the last few years, major progress
151 has been made with the development of different crop species capable of accumulating EPA and/or
152 DHA. We have recently reviewed the different emerging alternative sources of omega-3 LC-PUFA
153 (plants, algae) as sustainable solutions to the current supply gap²⁵ but will briefly focus here on the
154 role of transgenic plants. Progress has been achieved by genetic modification, introducing genes from
155 marine microalgae to the oilseed crops *Brassica napus* (Canola) and *Camelina sativa* (Camelina). Both
156 have now been brought to an advanced stage of technology-readiness. In the case of Canola²⁶,
157 recently granted deregulated status in the USA means that the crop is approved for commercial
158 cultivation and can be grown at any scale. Concomitant to the progress in Canola, a platform for the
159 synthesis of both EPA and DHA in transgenic Camelina has also been developed. The accumulation of
160 EPA and DHA in Camelina seed oil has been established as a viable prototype^{27,28}, subject to approved
161 experimental environmental release in the UK, USA and Canada, providing significant data as to the
162 stability of this trait²⁸, as well as providing sufficient oil for the evaluation of the material as a drop-in
163 replacement for FO. All studies to date confirm the promise of using GM plants to provide a terrestrial
164 source of FO, in both aquaculture^{27,29,30} and direct human nutrition³¹.

165 *Plant-based sources of astaxanthin and other ketocarotenoids:*

166 Compared with omega-3 LC-PUFA, the requirement by aquaculture for the pigment astaxanthin, a
167 ketocarotenoid that gives the flesh of salmonids its distinctive pinkish hue, is relatively modest (~500
168 metric tonnes/annum). Currently, most astaxanthin in aquafeed formulation is produced by chemical

169 synthesis or via fermentation of microorganisms which accumulate ketocarotenoids, though both
170 processes have a significant environmental footprint and a lack of flexibility³². Several recent attempts
171 to use transgenic plants to produce ketocarotenoids and validate their bioequivalence to other
172 industrial sources have proved successful. For example, it was shown that ketocarotenoids made in
173 transgenic maize were efficiently taken up by trout and improved the pigmentation of the flesh³³.
174 Similar studies in trout and longfin yellowtail demonstrated the efficacy of astaxanthin produced in
175 transgenic soybean³⁴. More recently, transgenic tomato fruit was used to accumulate astaxanthin for
176 evaluation in aquafeed trials of trout³⁵. Based on these studies, it was estimated that 1 hectare of
177 transgenic tomatoes could produce 34Kg of ketocarotenoids³⁵, meaning that the total current
178 requirements of aquaculture could be produced in less than 15,000 hectares of greenhouses.

179 *Improved protein composition and designer crops tailored for aquafeed:*

180 Many marine carnivorous species do not perform well on diets lacking FM, and possible reasons may
181 include: (1) a sub-optimal amino acid balance for fish, specifically a relative deficiency of methionine,
182 lysine, cysteine and the non-protein amino acid L-taurine³⁴; (2) the presence of anti-nutritional factors
183 such as plant-specific secondary metabolites; and (3) an abundance of oligosaccharide species that
184 are nutritionally inadequate and/or impede digestibility. When these are combined with a general lack
185 of palatability, fish very often do not thrive on diets rich in plant protein despite the latter's
186 environmental credentials. Therefore, efforts are underway to tailor the composition of plant seeds
187 for aquaculture, including the reduction of seed glucosinolates that can act as feeding deterrents to
188 the fish. A more speculative advance would be the transgenic co-production of vaccines to some of
189 the diseases that are problematic in aquaculture³⁶.

190

191 *Learning from Agriculture*

192 One of aquaculture's main advantages is that it produces fish over a three-dimensional space and can
193 thus deliver exceptionally high yields over a relatively small surface area. For example, a sea-pen
194 holding 200,000 Atlantic salmon (1 million Kg of slaughter-ready biomass), only has a surface diameter
195 of ~50m. Given the relentless pressure on land for terrestrial meat production, it is not surprising that
196 there has been a global drive towards aquaculture production, even before the constraints of
197 operating within PBs was fully articulated. For example, in Norway (a major aquaculture-intensive
198 country), the government has set a goal to increase salmon production five-fold to over 5 million tons
199 by 2050.

200 Increased growth in production volumes, however, produces similar problems to those encountered
201 by agriculture during the mid-20th Century expansion. Firstly, large concentrations of animals are a
202 breeding ground for many pathogens. In open sea-pens for Atlantic salmon there has been a massive
203 increase in sea lice infestations. These parasitic copepods attach to the skin and, as they mature,
204 produce wounds that can eventually kill the fish. The short life cycle of sea lice ensures a relatively fast
205 evolution of resistance to chemical treatments and, in that respect, this is a similar problem that
206 industrialised agriculture has faced since the 1960s, i.e. reliance on artificial pesticides in a
207 monoculture³⁷. Similar to agroecological methods used in some agricultural systems, other
208 management measures can be adopted to reduce this pressure including the use of "cleaner fish"
209 (such as ballan wrasse and lumpfish) that prey on salmon lice³⁸. However, while the use of cleaner fish
210 has expanded over the past decade, high mortality rates and inherent disease still cause major fish
211 welfare issues³⁸. It is possible that in general, aquaculture practices may also be stressful for the fish,
212 making them susceptible to many other opportunistic diseases. This may be mitigated via functional
213 feeds with ingredients such as omega-3 LC-PUFAs, which are known to be precursors of anti-
214 inflammatory and stress modulating compounds.

215 *Sourcing and developing improved nutrition*

216 In view of the predicted increase in aquaculture production volumes, it is expected that dietary
217 macronutrients like proteins and lipids in aquaculture feeds will come from a wide variety of sources.
218 These could include processed meals and oils from poultry, swine and cattle, by-products from capture
219 and farmed fish, and fishery discards. It's likely that lower trophic levels from the marine environment
220 including algae, krill and mesopelagic fish will increasingly be incorporated, particularly as n-3 LC-PUFA
221 sources. Single cell proteins (SCP)³⁹ such as yeast, microalgae or bacteria, as well as insects⁴⁰ are also
222 being increasingly positioned as novel protein sources for animal feeds, due to their generally high
223 protein contents and favourable amino acid profiles.

224 These variations in nutrient sources will have a major impact on the gastrointestinal microbiota of
225 farmed fish⁴¹, which is a potential major health and welfare issue in fish. To maintain optimum fish
226 health and welfare in intensive monoculture systems, future aquaculture might depend on a stable
227 and controlled gut microbiota to prevent pathogen entry and eliminate establishment of harmful
228 bacteria. This balance can, to some extent, be controlled by a probiotic approach⁴², common in Asian
229 aquaculture. Most of these bacteria, however, will not establish themselves in the intestines, and need
230 fibres or other "prebiotic" components to stabilize. Alternatively, both can be fed simultaneously to
231 the fish, in a "synbiotic" approach^{41,43}. Many of these components are of plant origin and it is expected
232 that agriculture will have a key role in optimising these products specifically for aquaculture in the
233 future. In addition to fibre, other plant-derived components, such as terpenoid oils, which have been
234 reported as antimicrobial, antioxidants, immune stimulators and stress-reducing agents and will
235 contribute significantly to improved health and welfare of farmed fish⁴⁴.

236 *Conclusions and Future Prospects*

237 Aquaculture already plays a central role in feeding us, but with the shifts in multiple factors described
238 above, that role will expand and become more critical. Aquaculture has previously been portrayed by
239 some in a negative light, with a focus on the environmental impact of fish farms and examples of poor
240 animal health. However, further growth in the industry will come with increased public awareness, so

241 aquaculture needs to adopt a new approach to scrutiny. In that case, they can learn from the lessons
242 of the plant biotechnology industry⁴⁵. Much benefit can be derived from establishing public dialogues
243 between industry and the consumer, helping to develop a more co-operative model of food
244 production within the aquaculture sector. It is also important to recognise that aquaculture is a highly
245 innovative industry, being adaptive and welcoming to new technologies and approaches. Ultimately,
246 the two systems, aquaculture and agriculture, need to work in tandem to meet the challenges of
247 operating resiliently within PBs and delivering optimal nutrition for a growing population. It is our
248 hope that the ideas outlined in this article are just the starting point for a more integrated approach
249 to sustainable aquaculture, one in which the major role of agriculture is fully incorporated.

250

251 **Acknowledgements**

252 Rothamsted Research receives grant-aided support from BBSRC. JAN and RPH were partially
253 supported by BBSRC ISPG *Tailoring Plant Metabolism* (BBS/E/C/00010420). JAN, DRT and MBB were
254 partly supported by BBSRC IPA, *Evaluating novel plant oilseeds enriched in omega-3 long-chain*
255 *polyunsaturated fatty acids to support sustainable development of aquaculture* (BB/J001252/1), and
256 BBSRC IPA *Novel omega-3 sources in feeds and impacts on salmon health* (BB/S005919/1). REO, JAN,
257 DRT & MBB were also partly supported by Research Council of Norway HAVBRUK Program *Transgenic*
258 *oilseed crops as novel, safe, sustainable and cost-effective sources of EPA and DHA for salmon feed*
259 (245327).

260

261 **Competing Interests**

262

263 The authors declare the following competing interests: Johnathan Napier is listed as an inventor on
264 patents (granted and pending) relating to the production of omega-3 long chain polyunsaturated
265 fatty acids in transgenic plants.

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387 **Figure Legend**

388 **Figure 1.** *Salmon Farming in Shetland.* The pristine environment and clean waters around the
389 Shetland Islands make it a desirable location for aquaculture. However, such activities come not only
390 with a responsibility to maintain the beautiful surroundings, but also not to degrade the natural
391 capital. Such farms also face logistical challenges, operating in remote locations with extended supply
392 chains. The challenge is to provide an economic return for the business, be excellent stewards of the
393 environment and deliver safe and healthy fish for ever-increasing human consumption.



Figure 1. *Salmon Farm in Shetland.* The pristine nature of the environment around the Shetland Islands makes it a desirable location for aquaculture activities. However, such activities come not only with a responsibility to maintain the beautiful surroundings, but also not to over-exploit the natural capital. Such farms also face logistical challenges, operating in remote locations with extended supply chains. The challenge is to provide an economic return for the business, be excellent stewards of the environment and deliver safe and healthy fish for ever-increasing human consumption.