

Agriculture can help aquaculture become greener

Johnathan A. Napier^{1*}, Richard P. Haslam¹, Rolf-Erik Olsen², Douglas R. Tocher³ and Mónica B. Betancor³

1. Rothamsted Research, Harpenden, Herts AL5 2JQ, UK

2. Norwegian University of Science and Technology, Department of Biology, 7491 Trondheim, Norway

3. Institute of Aquaculture, Faculty of Natural Sciences, University of Stirling, Stirling FK9 4LA, Scotland, UK

*for correspondence: johnathan.napier@rothamsted.ac.uk

ORCID iDs

JAN <https://orcid.org/0000-0003-3580-3607>

RPH <https://orcid.org/0000-0001-6226-5643>

REO <https://orcid.org/0000-0001-7523-3165>

DRT <https://orcid.org/0000-0002-8603-9410>

MBB <https://orcid.org/0000-0003-1626-7458>

Abstract

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

Main

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

A Future for Fish on the Planetary Plate

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

Demand for aquatic species as a key source of protein for human consumption and omega-3 LC-PUFAs 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,

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

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

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

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

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

Approaches to Increase the Synergy between Agriculture and Aquaculture

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

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

Plant-derived omega-3 LC-PUFA replacements:

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

Plant-based sources of astaxanthin and other ketocarotenoids:

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

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

Improved protein composition and designer crops tailored for aquafeed:

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

Learning from Agriculture

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

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

Sourcing and developing improved nutrition

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

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

Conclusions and Future Prospects

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

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

Acknowledgements

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

Competing Interests

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

References

1. Willett, W., Rockström, J., Loken, B., Springmann, M., Lang, T., Vermeulen, S., ... & Jonell, M. Food in the Anthropocene: the EAT–Lancet Commission on healthy diets from sustainable food systems. *The Lancet*, **393**, 447–492 (2019).
2. Tubb, C., and Seba, T. Rethinking food and agriculture 2020–2030. <https://www.rethinkx.com/food-and-agriculture> (2019).
3. Calder, P.C. Very long-chain n-3 fatty acids and human health: fact, fiction and the future. *Proc. Nutr. Soc.* **77**, 52–72 (2018).
4. Hamilton, H.A., Newton, R., Auchterlonie, N.A. & Müller, D.B. Systems approach to quantify the global omega-3 fatty acid cycle. *Nat. Food* **1**, 59–62 (2020).
5. Food and Agriculture Organisation (FAO). Food and Agriculture Organisation (FAO). The State of World Fisheries and Aquaculture 2020 Food: Sustainability in action. 206 pp. (FAO, 2020).
6. Troell, M., Jonell, M. & Crona, B. The Role of Aquatic Food in Sustainable Healthy Diets: The EAT–Lancet Commission report through a blue lens (2020) https://eatforum.org/content/uploads/2019/11/Seafood_Scoping_Report_EAT-Lancet.pdf
7. IFFO, The Marine Ingredients Organisation (2018) The continuing importance of fishmeal and fish oil in aquafeeds. <http://www.iffonet/system/files/AquaFarm%20Feb18%20NA.pdf> Accessed May 2020.
8. Gatlin, D.M., Barrows, F.T., Brown, P., Dabrowski, K., Gibson, G.T., Hardy, R.W., Elliot, H., Hu, G., Kroghdahl, A., Nelson, R., Overturf, K., Rust, M., Sealey, W., Skonberg, D., Souza, E.J., Stone, D., Wilson, R. & Wurtele, E. Expanding the utilization of sustainable plant products in aquafeeds: a review. *Aquacult. Res.* **38**, 551–579 (2007).
9. Turchini, G.M., Ng, W.K. & Tocher, D.R. (Eds.). *Fish Oil Replacement and Alternative Lipid Sources in Aquaculture Feeds* 533 pp. (Taylor & Francis, CRC Press, 2011).
10. Shepherd, C.J., Monroig, O. & Tocher, D.R. Future availability of raw materials for salmon feeds and supply chain implications: The case of Scottish farmed salmon. *Aquaculture* **467**, 49–62 (2017).
11. Aas, T.S., Ytrestøyl, T. & Åsgård, T. Utilization of feed resources in the production of Atlantic salmon (*Salmo salar*) in Norway: An update for 2016. *Aquacult. Rep.* **15**, 100216 (2019). <https://doi.org/10.1016/j.aqrep.2019.100216>
12. Tocher, D.R. Omega-3 long-chain polyunsaturated fatty acids and aquaculture in perspective. Feeding aquaculture in an era of finite resources. *Aquaculture* **449**, 94–107 (2015).
13. Naylor, R.L., Hardy, R.W., Bureau, D.P., Chiu, A., Elliot, M., Farrell, A.P., Forster, I., Gatlin, D.M., Goldburg, R.J., Hua, K., Nichols, P.D. *Proc. Natl. Acad. Sci. USA* **106**, 15103–15110 (2009).
14. Ytrestøyl, T., Aas, T.S. & Åsgård, T. Utilisation of feed resources in production of Atlantic salmon (*Salmo salar*). *Aquaculture* **448**, 365–374 (2015).

- 301 15. Sprague, M., Dick, J.R. & Tocher, D.R. Impact of sustainable feeds on omega-3 long-chain fatty acid
302 levels in farmed Atlantic salmon, 2006–2015. *Sci. Rep.* **6**, 21892 (2016).
- 303 16. Sprague, M., Betancor, M.B., Dick, J.R. & Tocher, D.R. Nutritional evaluation of seafood, with
304 respect to long-chain omega-3 fatty acids, available to UK consumers. *Proc. Nutr. Soc.* **76** (OCE2), E38
305 (2017).
- 306 17. Tocher, D.R. Metabolism and functions of lipids and fatty acids in teleost fish. *Rev. Fisheries Sci.*
307 **11**, 107-184 (2003).
- 308 18. Tocher, D.R. Fatty acid requirements in ontogeny of marine and freshwater fish. *Aquacult. Res.* **41**,
309 717-732 (2010).
- 310 19. Montero, D. & Izquierdo, M. “Welfare and health of fish fed vegetable oils as alternative lipid
311 sources to fish oil”. In *Fish Oil Replacement and Alternative Lipid Sources in Aquaculture Feeds* (eds
312 Turchini, G.M., Ng, W.-K. & Tocher, D.R.) 439-485 (Taylor & Francis, CRC Press, 2011).
- 313 20. Tocher, D.R. & Glencross, B.D. “Lipids and fatty acids”. In *Dietary Nutrients, Additives, and Fish*
314 *Health*. (eds Lee, C.-S., Lim, C., Webster, C. & Gatlin III, D.M.) 47-94 (Wiley-Blackwell, 2015).
- 315 21. Houston, R.D., Bean, T.P., Macqueen, D.J., Gundappa, M.K., Jin, Y.H., Jenkins, T.L., Selly, S.L.C.,
316 Martin, S.A., Stevens, J.R., Santos, E.M. Davie, A. & Robledo, D. Harnessing genomics to fast-track
317 genetic improvement in aquaculture. *Nat. Rev. Genet.*, (2020) [https://doi.org/10.1038/s41576-020-](https://doi.org/10.1038/s41576-020-0227-y)
318 [0227-y](https://doi.org/10.1038/s41576-020-0227-y)
- 319 22. Herman, E.M. & Schmidt, M.A. The potential for engineering enhanced functional-feed soybeans
320 for sustainable aquaculture feed. *Front. Plant Sci.* **7**, 440 (2016).
- 321 23. Mehrabi, Z., Gill, M., Wijk, M., Herrero, M. & Ramankutty, Livestock policy for sustainable
322 development. *N. Nat. Food* **1**, 160–165 (2020).
- 323 24. Domergue, F., Abbadi, A. & Heinz, E. Relief for fish stocks: oceanic fatty acids in transgenic oilseeds.
324 *Trends Plant Sci.* **10**, 112-116 (2005).
- 325 25. Tocher, D.R., Betancor, M.B., Sprague, M., Olsen, R.E. & Napier, J.A. Omega-3 long-chain
326 polyunsaturated fatty acids, EPA and DHA: Bridging the gap between supply and demand. *Nutrients*
327 **11**, 89 (2019)
- 328 26. Petrie, J.R., Zhou, X.R., Leonforte, A., McAllister, J., Shrestha, P., Kennedy, Y., Belide, S., Buzza, G.,
329 Gororo, N., Gao, W., Lester, G., Mansour, M.P., Mulder, R.J., Liu, Q., Tian, L., Silva, C., Cogan, N.O.I.,
330 Nichols, P.D., Green, A.G., de Feyter, R., Devine, M.D., Singh, S.P. Development of a *Brassica napus*
331 (Canola) crop containing fish oil-like levels of DHA in the seed oil. *Front Plant Sci.* **11**, 727. (2020).
- 332 27. Betancor, M.B., Sprague, M., Usher, S., Sayanova, O., Campbell, P.J., Napier, J.A. & Tocher, D.R. A
333 nutritionally-enhanced oil from transgenic *Camelina sativa* effectively replaced marine fish oil as a
334 source of eicosapentaenoic acid for farmed Atlantic salmon (*Salmo salar*). *Sci. Rep.* **5**, 8104 (2015).

335 28. Han, L., Usher, S., Sandgrind, S., Hassall, K., Sayanova, O., Michaelson, L.V., Haslam, R.P., Napier,
336 J.A. High level accumulation of EPA and DHA in field-grown transgenic *Camelina* - a multi-territory
337 evaluation of TAG accumulation and heterogeneity. *Plant Biotechnol J.* doi: 10.1111/pbi.13385 (2020).

338 29. Betancor, M.B., Li, K., Bucerzan, V.S., Sprague, M., Sayanova, O., Usher, S., Han, L., Norambuena,
339 F., Torrissen, O., Napier, J.A., Tocher, D.R. & Olsen, R.E. Oil from transgenic *Camelina sativa* containing
340 over 25 % n-3 long-chain polyunsaturated fatty acids as the major lipid source in feed for Atlantic
341 salmon (*Salmo salar*). *Br. J. Nutr.* **119**, 1378-1392 (2018).

342 30. Ruyter, B., Sissener, N.H., Østbye, T.K., Simon, C.J., Krasnov, A., Bou, M., Sanden, M., Nichols, P.D.,
343 Lutfi, E., Berge. n-3 Canola oil effectively replaces fish oil as a new safe dietary source of DHA in feed
344 for juvenile Atlantic salmon. *Br J Nutr.* **122**, 1329-1345. (2019).

345 31. West, A.L., Miles, E.A., Lillycrop, K.A., Han, L., Sayanova, O., Napier, J.A., Calder, P.C. & Burdge, G.C.
346 Postprandial incorporation of EPA and DHA from transgenic *Camelina sativa* oil into blood lipids is
347 equivalent to that from fish oil in healthy humans. *Br. J. Nutr.* **121**, 1235–1246 (2019).

348 32. Lim, K.C., Yusoff, F.M., Shariff, M. & Kamarudin, M.S. Astaxanthin as feed supplement in aquatic
349 animals. *Rev. Aquacult.* **10**, 738-773 (2018).

350 33. Breitenbach, J., Nogueira, M., Farré, G., Zhu, C., Capell, T., Christou, P., Fleck, G., Focken, U., Fraser,
351 P.D. & Sandmann, G. Engineered maize as a source of astaxanthin: processing and application as fish
352 feed. *Transgenic Res.* **25**, 785-793 (2016).

353 34. Park, H., Weier, S., Razvi, F., Peña, P.A., Sims, N.A., Lowell, J., Hungate, C., Kissinger, K., Key, G.,
354 Fraser, P., Napier, J.A., Cahoon, E.B. & Clemente, T.E. Towards the development of a sustainable soya
355 bean-based feedstock for aquaculture. *Plant Biotechnol J.* **15**, 227-236 (2017).

356 35. Nogueira, M., Enfissi, E.M., Valenzuela, M.E.M., Menard, G.N., Driller, R.L., Eastmond, P.J., Schuch,
357 W., Sandmann, G. & Fraser, P.D. Engineering of tomato for the sustainable production of
358 ketocarotenoids and its evaluation in aquaculture feed. *Proc. Natl. Acad. Sci. USA* **114**, 10876-10881
359 (2017).

360 36. Clarke, J.L., Waheed, M.T., Lössl, A.G., Martinussen, I. & Daniell, H. How can plant genetic
361 engineering contribute to cost-effective fish vaccine development for promoting sustainable
362 aquaculture? *Plant Mol. Biol.* **83**, 33-40 (2013).

363 37. Simon, J. C. & Peccoud, J. Rapid evolution of aphid pests in agricultural environments. *Curr. Op.*
364 *Insect Sci.* **26**, 17-24 (2018).

365 38. Barrett, L.T., Overton, K., Stien, L.H., Oppedal, F. & Dempster, T. Sea lice removal by cleaner fish in
366 salmon aquaculture: a review of the evidence base. *Internatl. J. Parasitol.*, in press
367 <https://doi.org/10.1016/j.ijpara.2019.12.005>

368 39. Jones, S.W., Karpol, A., Friedman, S., Maru, B.T. & Tracy, B.P. Recent advances in single cell
369 protein use as a feed ingredient in aquaculture. *Curr. Op. Biotechnol.* **61**, 189-197 (2020).
370

371 40. Arru, B., Furesi, R., Gasco, L., Madau, F.A. & Pulina, P. The introduction of insect meal into fish diet:
372 the first economic analysis on European sea bass farming. *Sustainability* **11**, 1697 (2019).

- 373 41. Ringø, E., Zhou, Z., Vecino, J.L.G., Wadsworth, S., Romero, J., Krogh, A., Olsen, R.E., Dimitroglou,
374 A., Foey, A., Davies, S., Owen, M., Lauzon, H.L., Martinsen, L.L., de Schryver, P., Bossier, P., Sperstad,
375 S. & Merrifield, D.L. Effect of dietary components on the gut microbiota of aquatic animals. A never-
376 ending story? *Aquacult. Nutr.* **22**, 219-282 (2016).
- 377 42. European Food Safety Authority. Scientific Opinion on the efficacy of Bactocell (*Pediococcus*
378 *acidilactici*) when used as a feed additive for fish. *EFSA Journal* **10**, 2886 (2012).
- 379 43. Ringø, E., Olsen, R.E., Gonzalez Vecino, J.L., Wadsworth, S. & Song, S.K. Use of immunostimulants
380 and nucleotides in aquaculture: a review. *J. Mar. Sci. Res. Development* **1**, 104 (2012).
- 381 44. de Freitas Souza, C., Baldissera, M.D., Baldisserotto, B., Heinzmann, B.M., Martos-Sittha, J.A. &
382 Mancera, J.M. Essential oils as stress-reducing agents for fish aquaculture: a review. *Front. Physiol.* **10**,
383 785 (2019).
- 384 45. Napier, J. A., Haslam, R. P., Tsalavouta, M., & Sayanova, O. The challenges of delivering
385 genetically modified crops with nutritional enhancement traits. *Nature Plants*, **5**, 563-567. (2019).
- 386

Figure Legend

Figure 1. *Salmon Farming in Shetland.* The pristine environment and clean waters around the Shetland Islands make it a desirable location for aquaculture. However, such activities come not only with a responsibility to maintain the beautiful surroundings, but also not to degrade 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.



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.