

1 **Harvesting the benefits of nutritional research to address global challenges in** 2 **the 21st century**

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7 **Abstract**

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9
10 Substantial progress has been made over the past twenty years in improving feeds and feeding for
11 most aquaculture species. There have been notable improvements in feed efficiency (through a better
12 understanding of requirements and improved feed management) and ingredient sustainability
13 (through increased capability to use a wider range of ingredients). While advances have been made
14 in understanding the requirements of many of the main aquaculture species, there is still much to be
15 done on defining requirements, especially for many of the species being farmed in the developing
16 world. Gains in the efficiency of feeds is slowing for developed species, but such gains are still
17 appreciable for less developed species. There is a growing need to more precisely prescribe the
18 required levels of essential nutrients and various additives in the diet based on age, genotype,
19 environment, and immune status to deliver a "precision nutrition" approach to farming aquaculture
20 species. Plant resources remain the dominant ingredient used in compound feeds across the world.
21 Whereas marine resources remain an important inclusion in many feeds, they are increasingly seen
22 as a low-volume high-value resource with strategic applications. As a source of omega-3, marine
23 resources still dominate supply, though microalgal and genetically modified crop options are
24 emerging. There is still further need to diversify our ingredient options to provide greater resilience,
25 as the sustainability of different feed ingredient sources, including possible climate change impacts, is
26 becoming a growing issue. There is an increased demand for biocircularity in our feed ingredient
27 supply chains. Fundamentally what is needed to sustain future feed ingredient needs are sustainable
28 sources of cost-effective protein, some essential amino acid additives, some omega-3 resources, plus
29 various minerals, and vitamin additives. The increasing use of new and varied resources will ensure
30 that food safety remains an important issue throughout the world. Feed manufacturing has evolved
31 from a simplistic exercise to a highly complex science with state-of-the-art engineering. However, the
32 application of such advanced feed manufacturing is not consistent across all sectors and further
33 support is needed, as there is still widespread use of pelleting, mash, and trash-fish feeding in the
34 developing world. Similarly, feed management has also dichotomised between the developed and
35 developing world, with a high reliance on manual skilled labour in the developing world, whereas more
36 advanced aquaculture systems are becoming increasingly reliant on automated computer-controlled
37 feeding systems.

38 39 **Key Messages**

- 40
- 41 • There has been substantial progress in improving feeds and feeding for most aquaculture
42 species, with notable improvements in feed efficiency (through a better understanding of
43 requirements and improved feed management) and ingredient sustainability (through
44 increased capability to use a wider range of ingredients).
 - 45 • While advances have been made in understanding the requirements of some of the main
46 aquaculture species, there is still much to be done on defining requirements, especially for
47 many of the species being farmed in the developing world.
 - 48 • Gains in the efficiency of feeds is slowing for developed species, but such gains are still
49 appreciable for less developed species.

- 50 • There is an emerging need to adopt a "precision nutrition" approach to the supply of essential
51 nutrients and various additives in the diet based on age, genotype, environment, and immune
52 status.
- 53 • Plant resources have become the dominant ingredient used in feeds across the world.
54 Although marine resources remain an important inclusion in many feeds, they are increasingly
55 seen as a low-volume high-value resource with strategic applications. Marine sources of
56 omega-3 still dominate supply, though microalgal and genetically modified crop options are
57 emerging.
- 58 • There remains a need to diversify our ingredient options to increase resilience, as the
59 sustainability of different feed ingredient sources, including possible climate change impacts,
60 is becoming a growing issue. There is an increased demand for biocircularity in our feed
61 ingredient supply chains. The increasing use of new and varied resources will ensure that food
62 safety remains an important issue throughout the world.
- 63 • Feed manufacturing has evolved from a simplistic exercise to a highly complex science with
64 state-of-the-art engineering. However, the application of such advanced feed manufacturing
65 is not consistent across all sectors and further support is needed, as there is still widespread
66 use of pelleting, mash, and trash-fish feeding in the developing world.
- 67 • Feed management has also dichotomised between the developed and developing world, with
68 a high reliance on manual skilled labour in the developing world, contrasting advanced
69 aquaculture systems that are increasingly reliant on automated computer-controlled feeding
70 systems in the developed world.
- 71 • Improved feed design, manufacturing and management systems are supporting better feeds
72 and feeding, resulting in faster growing fish (through better specifications and higher intakes)
73 and lower FCRs (through more efficient feeds and less wastage), but declining employment in
74 the sector as automation increases.

75 76 **Introduction**

77
78 With any science-based prediction of the future and of which path to follow (essentially a navigation
79 exercise) we need to understand where we are and where we have been. It is only once we understand
80 this context of our situation that we can then begin to make some rational prediction about where we
81 are heading. As such, in this paper we examine the three key themes that underpin the feeds and
82 feeding process (requirements /ingredients /management) and have framed our review of this
83 journey in terms of the past-present-future. Additionally, it needs to be noted that the top seven
84 species groups (carps, tilapia, catfish, shrimp, freshwater spp., salmonids, and marine spp.),
85 collectively comprise close to 90% of all aquaculture production and as such form the focus on the
86 paper. While increasingly, each of these species' groups are being produced intensively and are reliant
87 on compounded feed for their sole nutritional inputs, this is not equally the case among all seven
88 groups. Substantial production, particularly of carps, which comprise almost 50% of global aquaculture
89 production, are still produced in small-scale extensive, semi-intensive and integrated polyculture
90 systems. Notably, feed specifications, ingredient use and feeding practices also vary regionally across
91 the world. As such, in this paper we have attempted to generalise on those issues that affect the three
92 key themes that underpin the feeds and feeding process across the world.

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98 **Requirements**

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100 **Past (before 2010)**

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102 The terms nutrient “requirement” and “specification” have frequently been used interchangeably.
103 While “specification” is the detailing of the design instructions for something (e.g., a diet containing
104 40% protein), the actual nutrient requirement of an animal is more based around the need for a
105 particular nutrient required by the animal on a certain body weight basis per defined duration (e.g.,
106 mg protein / kg^{0.7}/ d), and for defined physiological functions such as maintenance, maximal growth,
107 or optimal health. The process of establishing these nutritional requirements (optimum dietary levels)
108 for aquaculture species has been a big challenge not only because of the difficulties associated with
109 feeding an aquatic animal, but also considering the increasing number of species of commercial
110 importance (Hua et al., 2019; Boyd et al., 2020). This contrasts with what has happened with terrestrial
111 domestic species, such as poultry and pigs, where the definition of nutritional requirements is
112 generally focused on a single species (NRC, 1981). Additionally, finfish and shellfish requirements vary
113 not only among species, but can also depend on their developmental stage and in some cases different
114 environmental constraints (NRC, 2011). Moreover, requirements may further depend on the farming
115 system used and regionality. In many cases production of key aquaculture species was undertaken in
116 extensive, semi-intensive and integrated polyculture systems meaning that a holistic systems
117 approach to nutrition had to be used rather than a monoculture approach. Aquaculture was notable
118 in being much more varied in the nutritional requirements of its species than in livestock production.
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121 Traditionally the definition of requirements for essential nutrients (energy, protein, lipid, amino acids,
122 fatty acids, vitamins, and minerals) for most species was undertaken on a gross nutrient basis only
123 (Cowey, 1992; Boonyaratpalin, 1997; NRC, 2011). Requirements were typically defined based on
124 empirical experiments and limited to small animal sizes and laboratory environments. This served well
125 in terms of defining the distinct differences among many of the species and between aquatic and
126 terrestrial animals (NRC, 2011).

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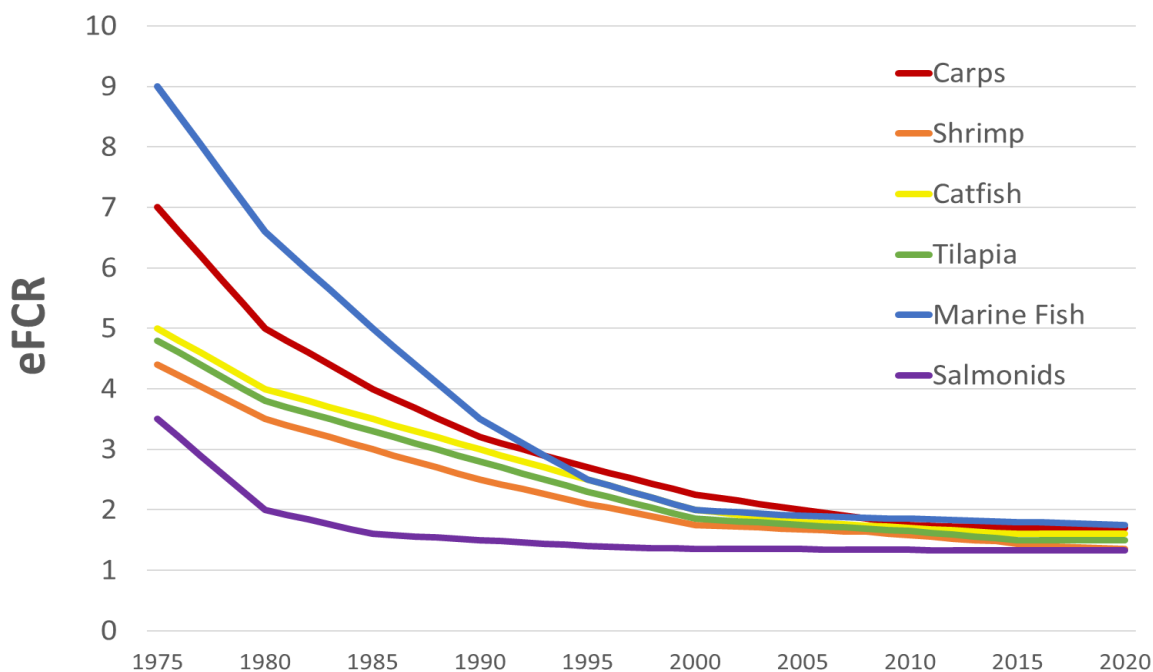
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148 Initially, the definition of nutrient requirements for many species led to big gains being made in feed
 149 efficiency, with improvements in FCR values from 1.8 - 3 to 1.2 – 1.8 being achieved for many species.
 150 However, as time has passed there have been diminishing returns on any improvements in the
 151 definition of nutrient requirements across most species' groups (Figure 1).
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 157 *Figure 1. Changes in economic feed conversion ratios (eFCR) of major aquaculture species groups over*
 158 *the past forty-five years.*
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160
 161 Prior to 2010, there was also an introduction in the use of various modelling systems to define
 162 requirements for energy and some macronutrients and explore various physiological processes
 163 (Shearer, 1995; Dumas et al., 2010). These models were largely derived from similar approaches used
 164 for terrestrial species but had to include various empirically derived features to account for the
 165 differences between poikilotherms and endotherms (Cho & Bureau, 1998; Lupatsch et al., 2001).
 166 Different iterations of either nutrient flow or nutrient demand models were developed, that were
 167 largely based around factorial bioenergetic processes (Cho & Bureau, 1998; Glencross, 2008).
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169 **Present (2010 – 2020)**
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171 Since 2010, smaller improvements in feed efficiency have been made, with typical changes from FCR's
 172 of 1.5 - 2 to 1 – 1.5 for some species (Figure 1). Such gains were mainly due to the increasing knowledge
 173 about nutritional requirements but also due to better management practices following the
 174 intensification of growing systems (NRC, 2011). An increasing level of replacement of fish meal with
 175 plant proteins as the main ingredients in commercial feeds demanded a better knowledge of amino
 176 acid requirements. Although fish meal has an amino acid balance close to that of many fish
 177 requirements most plant protein do not, thus meeting fish demands for growth with plant proteins
 178 required a deeper knowledge about amino acid requirements in terms of amounts and balance
 179 (Kaushik & Seiliez, 2010).

180 This was especially important for carnivorous species which have higher demand for amino acids, but
181 it was also important for omnivores such as tilapia and shrimp, where the high cost of fish meal limited
182 its use in commercial feeds. A deeper knowledge about the requirement of other nutrients such as
183 taurine, n-3 fatty acids, and various vitamins and minerals also became important with increasing
184 levels of fish meal replacement, since these nutrients are less available or even absent in plant sources
185 (Gatlin et al., 2007; Dominguez et al., 2020a, 2020b).

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188 During the 2010-2020 decade, after the NRC publication (NRC 2011), there was an increasing level of
189 definition of requirements for animals of different sizes and in some cases different environmental
190 constraints (e.g., hypoxia, temperature, salinity, etc). Both, age, and environmental conditions may
191 markedly affect fish physiology and modulate the expression of key genes, affecting nutrient
192 utilization and nutritional requirements (Izquierdo & Koven, 2011; Fernández-Palacios et al., 2011;
193 Hamre et al., 2013; Lund et al., 2019; Torno et al., 2019). However, such information is still scattered
194 and absent for some species (e.g., *Seriola*, *Sole*) (Sicuro and Luzzana, 2016; Valente et al., 2019).
195 Industrial breeding programs are rapidly progressing, based in the recently developed customized
196 genomic tools for marker-assisted selection, and are producing fast growing animals with improved
197 FCR that may have different requirements for specific nutrients (Glencross et al., 2013; Janssen et al.,
198 2017; De Verdal et al., 2018; Ferosekhan et al., 2021). Moreover, nutritional history (protonutrition)
199 and nutritional programming affect the utilization of dietary nutrients and therefore could affect fish
200 requirements (Turkmen et al., 2019). The main drivers for such development were the high cost of
201 aquafeed, that typically represents 50% of the variable production cost of intensive aquaculture,
202 together with the increasing pressure for producing more sustainable diets able to address the
203 Sustainable Development Goals established by UN. This implies knowing more about the
204 requirements of the various species to sustain optimal growth and produce high quality and healthy
205 animals. In many of those species already produced at large scale, requirements for macro-nutrients
206 and most micro-nutrients are now well established for early/larval, juvenile, grower, and broodstock
207 stages of the production cycle. But most non-mainstream species still need clearer definition of many
208 of the basic nutrient requirements and their response to environmental constraints remains largely
209 unknown. Modern aquaculture today uses diets that rely on a variety of alternative raw materials that
210 need to be balanced with additives including certain amino acids, minerals, and vitamins to ensure the
211 optimal use of the feed. However, to face various growing environmental and production challenges,
212 the currently established requirements of many amino acids and other micronutrients may need to
213 be revisited to assure fish growth and robustness into the future (Prabhu et al. 2014; Kousoulaki et al.
214 2021; Hamre et al. 2016; Aas, Ytrestøyl, and Åsgård 2019; Berntssen et al. 2018).

215

216 The last comprehensive compilation of nutritional requirements of fish and shrimp was published on
217 2011 (NRC 2011). This publication included the requirements of various freshwater and marine fish as
218 well as shrimp of commercial importance. Despite organizing and facilitating the access to nutritional
219 requirement information for various important aquaculture species, it also made clear several
220 unknowns not only on micronutrient (vitamins and minerals) but also on amino acid requirements.
221 Notably, the compiled requirement specifications were largely defined from animals in juvenile stages
222 and based on using highly digestible diets and animals maintained in optimal growing conditions. In
223 most cases, requirements were presented as a single recommendation for each species and did not
224 consider changes in requirements throughout the various production stages. Therefore, despite the
225 increasing use of farming system environments to undertake research and provide industrially
226 relevant information for some species such as salmon, this is not so for many other species (Ng &
227 Romano 2013).

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231 Most feeds in the world are still formulated on a crude composition basis, though there is increasing
232 formulation of feeds on a digestible nutrient basis in the developed world for some species, like
233 Atlantic salmon. The quality of the formulation depends on various knowledge sets, including the
234 accurate understanding of the nutrient requirements, the nutritional composition of the ingredient
235 being used and their nutrient digestibility and/or bioavailability, and the processes being used to form
236 the feed into a physical pellet. The feed of salmon is highly efficient. However, the feed efficiency of
237 most other cultured fishes or shrimp lags that of salmon.

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240 This is mainly due to the rapid development of aquaculture with high diversity and complexity of
241 cultured species and feed ingredients used in developing countries, and the lack of comprehensive
242 knowledge of essential nutrient requirements of so many cultured animals and of the digestibility or
243 the bioavailability of non-traditional ingredients or their nutrients. For example, nutritional studies
244 published in China have been conducted on more than 200 species representing a wide geographic
245 distribution, different feeding habits (herbivorous, carnivorous, omnivorous, and filter feeders), and
246 different culture modes. It is evident from the information provided in the NRC (2011) that the tables
247 listing the nutritional requirements of salmonids are mostly complete, while those for many other
248 important marine or freshwater species are either incomplete or mostly blank (Hardy et al., 2021).
249 Despite the already high number of species produced in aquaculture, increasing pressure in the last
250 decade for further species diversification has brought attention to several either low trophic species
251 or very fast growing or endangered species (Naylor et al. 2021; Boyd et al. 2020; Cottrell et al. 2021;
252 Newton et al. 2021).

253

254 Over the past decade, there has been a growing use of factorial and nutrient-flow (or demand)
255 modelling systems to define requirements for energy and macronutrients for an increasing number of
256 species. Such models are now being widely used to iteratively define nutritional requirements for
257 various species across their production size ranges and within varying environmental conditions
258 (Glencross & Bermudes, 2012; Chowdhury et al., 2013). There has been increasing levels of adoption
259 of modelling by the commercial aquaculture sector as a means of refining feed design and improving
260 feed management. Furthermore, the development of mechanistic models has further advanced our
261 understanding of the interrelationships between different metabolic pathways and nutrient use and
262 how this influences growth and body composition (Bar et al., 2007; Bar & Radde, 2009).

263

264 A growing understanding of the role of the microbiome in nutrient supply/utilisation has emerged.
265 Brought about by low-cost methods to evaluate microbial diversity using 16S ribosomal RNA
266 sequencing technologies. This has enabled an increased understanding of the physiological interaction
267 between the microbiome and its host. However, its potential to mediate how organisms respond to
268 multiple environmental factors remains poorly understood. For example, most aquafeeds contain
269 carbohydrate-based binders (e.g., starches) which do not exist in the aquatic environment. These
270 complex carbohydrates are influential in the development of a particular microbiomes. Differences in
271 microbiome structures have been observed between fish fed either extruded or non-extruded pellets
272 containing starch (Barreto-Curiel et al., 2018). So, it is apparent that the gelatinization process is
273 influential to the structure of the different microbial communities. Understanding the impacts of such
274 dietary changes on the resulting microbial communities will be helpful to identify those strategies that
275 are beneficial or not (Fuentes et al., 2020). Another important aspect is the differences in microbiome
276 structures in organisms subjected to stress, whether due to effects of system intensity, environmental
277 contamination, temperature, and/or nutritional deficiencies. Studies have shown that stress,
278 particularly chronic stress, and microbial manipulation (probiotics or prebiotics) influences the
279 microbiome structure of the fish gut (Serradell et al. 2020; Rimoldi et al. 2020; Anker-Ladefoged et al.,
280 2021).

281 However, there is still insufficient information on the influence of nutritional or environmental factors
282 on the microbiome on fish growth and health to assess the economic benefits of adding probiotics in
283 the feed or water.

284
285 The growing need for immune enhancing diets comes back to issues of poor definition of micro-
286 nutrient supply under prevailing conditions linked to large-scale marine ingredient replacement
287 without tacking all the requirement issues comprehensively. Consequently, functional feeds are being
288 developed to enhance animal health. Such functional feeds must have optimized nutrient composition
289 and are supplemented with some functional additives, allowing the farmer to not only to meet the
290 needs for better growth, but also improve the immunity, stress resistance and health status of
291 aquaculture animals, whilst ensuring the quality and safety of the products.

292 The most common functional additives used in aquafeeds include preservatives (antioxidant),
293 nutritional supplements (amino acids, vitamins, trace elements), enzymes, pigments (carotenoids),
294 palatants, and immunomodulators (probiotics, prebiotics, plant extracts, and nucleotides). The
295 mechanistic action of such functional additives is multi-dimensional. They can act directly and/or
296 indirectly on the animal, such as antioxidation, modification of gut microbe profiles, improvement of
297 digestive tract morphology, elevation of digestive enzyme activities and nutrient absorption, and
298 enhancement of immunity and disease resistance (Tacchi et al., 2011; Aguirre-Guzmán et al., 2012;
299 Torrecillas et al., 2014; Hoseinifar et al., 2017; Hayatgheib et al., 2020). In the future, further studies
300 are needed on the functional mechanisms of individual additives and also their interactions, especially
301 their synergistic effects. Usage of many such additives is however under strict regulations that vary
302 widely among countries, though there are levels of regulation exerted on their use through global
303 efforts such as Codex Alimentarius (<http://www.fao.org/fao-who-codexalimentarius/home/it/>).

304

305 ***Future (2020 and beyond)***

306

307 Analysis of the changes in the FCR values for most mainstream species demonstrates that
308 improvements have been plateauing for some time and only smaller gains are now being made,
309 leading to a point of diminishing returns for many species (Figure 1) (Naylor et al., 2009; Ytrestøyl et
310 al., 2015; Tacon, 2020). Any future work on defining requirements needs to focus more precisely on
311 refining estimates with further consideration of nutrient interactions and the use of new and more
312 stable delivery forms, that help reduce nutrient wastage and increase efficiency. In the coming
313 decades, aquaculture sustainability will remain a major concern. Water quality remains vital for
314 aquaculture production and inadequate nutrition and feeding practices are known to deteriorate
315 water quality. Thus, designing more efficient feeds through better knowledge of nutrient
316 requirements, their appropriated balance and effective delivery forms, will improve nutrient stability
317 and absorption and minimize nutrient waste. Likewise, refining feeding management practices to
318 avoid excess nutrient load in the water will limit (or reduce) the increased oxygen demand following
319 eutrophication which can compromise fish health, welfare, and growth.

320

321 There is a growing need to prescribe the required levels of essential nutrients in the diet more
322 precisely based on age, genotype, nutritional history, environment, farming system, and immune
323 status to deliver a "precision nutrition" approach to farming animals. This will necessitate the use of
324 various modelling (using big data), internet-of-things (IoT), and artificial intelligence (AI) approaches
325 to support aquaculture production and feed specification management. An integration between
326 traditional models with more mechanistic approaches will lead to better prescription of nutrient and
327 energy requirements based on an increasing number of input parameters. Advances in such modelling
328 systems are now already accommodating demands for amino acids and net energy demands for
329 various species (Hua & Bureau, 2019; Glencross, 2021).

330

331 The improved definition of requirements for key nutrients (energy, amino acids, fatty acids) on a
332 digestible and net basis is still required for most species and especially those in the developing world.
333 The future of aquaculture nutrition will increasingly be based on precision and smart farming that will
334 require a clear definition of nutrient requirements on a digestible and a net basis. This is particularly
335 important in the context of encouraging the utilisation of locally sourced ingredients. The shift towards
336 increasing use of alternative ingredients in recent years has made it even more important to formulate
337 diets on a digestible nutrient basis, not only due to the presence of antinutritional factors that can
338 interfere with nutrient utilization, but also due to the variability in the bioavailability of the nutrients
339 required to formulate balanced diets (Boyd et al. 2020).

340 Some of these new ingredients have complex matrices that limit digestion and/or absorption of
341 nutrients (e.g., algae) (Valente et al., 2021), highlighting the relevance of formulating on a digestible
342 basis as is already done in many other species.

343
344 Tailoring fish diets to produce valued-added products able to respond consumer's expectation will
345 also gain importance in the future. This will include nutrient fortification of fish via their diet for
346 children, pregnant women, and elderly people, by enrichments in omega-3 (especially EPA and DHA),
347 selenium, vitamin D and iodine. The capacity of farmed fish to not only increasingly supply protein for
348 the world, but to also do so in a way that enhances the nutrition of the young and at risk will become
349 increasingly important (Thilsted, 2012; Tacon & Metian, 2013). This food fortification/enhancement
350 combined with a growing focus on food safety will enhance the role of nutrition as a critical control
351 point in aquaculture.

352
353 Functional diets for challenging production periods and conditions will gain increasing prominence.
354 Climate change and growing levels of intensification and the use of recirculating aquaculture systems
355 (RAS) will increase the susceptibility of fish to alterations in environmental conditions that will increase
356 stress which will need to be mitigated. Functional diets that contain ingredients or additives that
357 affect animal robustness and health will become increasingly important. Because production system
358 environmental changes are expected with the growing intensification of aquaculture, it will be
359 necessary to further investigate what positive effects functional diets will have, by identifying the most
360 adequate ingredients and/or additives that result in improved animal performance and health. The
361 formulation of diets for challenging times in the fish production process will be increasingly required.
362 The use of various feed additives to help or mitigate the effects of stress through the year or seasonally
363 will become increasingly common. Although the potential for formulating marine ingredient free diets
364 already exists for a vast majority of species, it is usually not cost-effective in most cases for carnivorous
365 species. Such diets are also often associated with chronic health issues and poor animal robustness,
366 so formulating based on nutrients (amino acids and fatty acids) will further require the search for
367 additives that can be used to improve the general health status and robustness of different
368 aquaculture species in a future with constraints on marine ingredient use.

369
370 Over the past 40 years, the rapid development and increasing intensification of aquaculture across a
371 broad range of species and geographies have led to problems arising in some cases. Issues such as
372 environmental deterioration and stress, sometimes leading to disease outbreaks and then subsequent
373 abuses of antimicrobials and other chemical drugs have been reported in various sectors. These issues
374 threaten food safety and sustainability of aquaculture. Misuse of antimicrobials not only leads to drug
375 residues, affects food safety, but also potentially leads to drug-resistant pathogens, that can then lead
376 to public health issues. Many countries have legislated to prohibit the use of antimicrobials as growth
377 promoters in animal feed (since 2006 in EU), and many are gradually restricting its use for medical
378 purposes to tackle the emergence of bacteria and other microbes resistant to antimicrobials. In
379 addition, due to constraints on further growth in the production of fish meal, fish oil and other marine-
380 derived ingredients, many non-traditional ingredients have been used to replace fish meal and fish oil
381 in aquafeeds.

382 In many cases, this has resulted in growth retardation and impaired health of fish and shrimp as the
383 changes were often not supported by science or backed up with required alternatives to bring a
384 positive outcome. Hence, in the future, we must look for new technologies or nutritional approaches
385 (e.g., functional feeds) to mitigate the negative aspects of substitutions of marine-derived ingredients
386 and the reduction in the use and overall stewardship of antibiotics to ensure the good growth, health,
387 product safety of aquaculture animals and to enable the sustainable development of aquaculture. In
388 parallel, there is also an opportunity to tailor flesh quality to increasing consumer's demand for
389 healthier products.

390 The fortification of aquafeeds with omega-3 (especially EPA and DHA), vitamin D and minerals (e.g.,
391 selenium and iodine) can help providing adequate nutrition for vulnerable population groups (Thilsted
392 et al., 2014; Kwasek et al., 2020).

393
394 Having defined the nutritional requirements of the various aquaculture species, there is additionally
395 a need to find the appropriate raw materials (ingredients) from which to provide these nutrients and
396 energy. This supply of raw materials also needs to develop sustainable supply chains to enable the
397 aquaculture sector to continue to grow amongst the various sustainability challenges that production
398 of aquaculture feeds faces (MacLeod et al., 2020; Naylor et al., 2021).

399

400 **Ingredients**

401

402 There have been marked shifts in ingredient use for aquaculture feeds over the past several decades.
403 In this section we review the practices of the past and the present to predict future trends and needs.
404 While not all aquaculture uses industrially produced compounded feeds, this is the fastest growing
405 feed sector in the world and indicators suggest that more and more aquaculture production is
406 becoming increasingly intensified and reliant on the provision of external feed inputs.

407

408 ***Past (before 2010)***

409

410 From the late 20th century to 2010, global aquafeed production grew from <5Mtonnes in 1990 to
411 ~30Mtonnes in 2010. Fish meal and fish oil were considered critical ingredients in feeds for many
412 carnivorous fish and crustacean species, and their global production averaged ~6Mtonnes and
413 1MTonnes per annum respectively over this period. Fish meal use in aquaculture feeds peaked during
414 2005 – 2010 at ~3.6 Mtonnes per annum (Figure 2). Fish oil use peaked a bit before this at around
415 0.9Mtonnes per annum. Recognition that such marine ingredients were limited in supply led to a
416 global effort to move towards more use of alternative ingredients in aquafeeds. Early fish meal
417 alternatives were primarily of animal origin due to availability, cost, and protein content. Since then,
418 the perceived risks associated with inclusion of rendered animal by-products in aquafeeds have seen
419 their restriction in several geographic regions (primarily within European countries) due to concerns
420 of pathogens and zoonotic disease transmission (Glencross et al., 2020). Plant proteins were initially
421 only a minor contributor to aquaculture feed protein and lipids for most carnivorous species, but by
422 2010 inclusion levels reached about 28% of the total feed inputs for salmon feeds globally, up from
423 12% in 2000. At the same time fish meal reduced from up to 45% in 2000 to 23% of the diet in 2010
424 (Ytrestøyl et al., 2015). This switch was initiated by several El Nino events, which reduced the
425 availability of fish meal and forced the prices up. The feed production sector responded primarily by
426 increasing use of soy and some (wheat and corn) gluten meals. While much of the use of fish meal and
427 fish oil prior to 2010 was driven by economy of nutrients, plant proteins were seen to have significant
428 limitations, often containing lower protein content, antinutritional factors, and imbalanced nutrient
429 profiles (Gatlin et al., 2007).

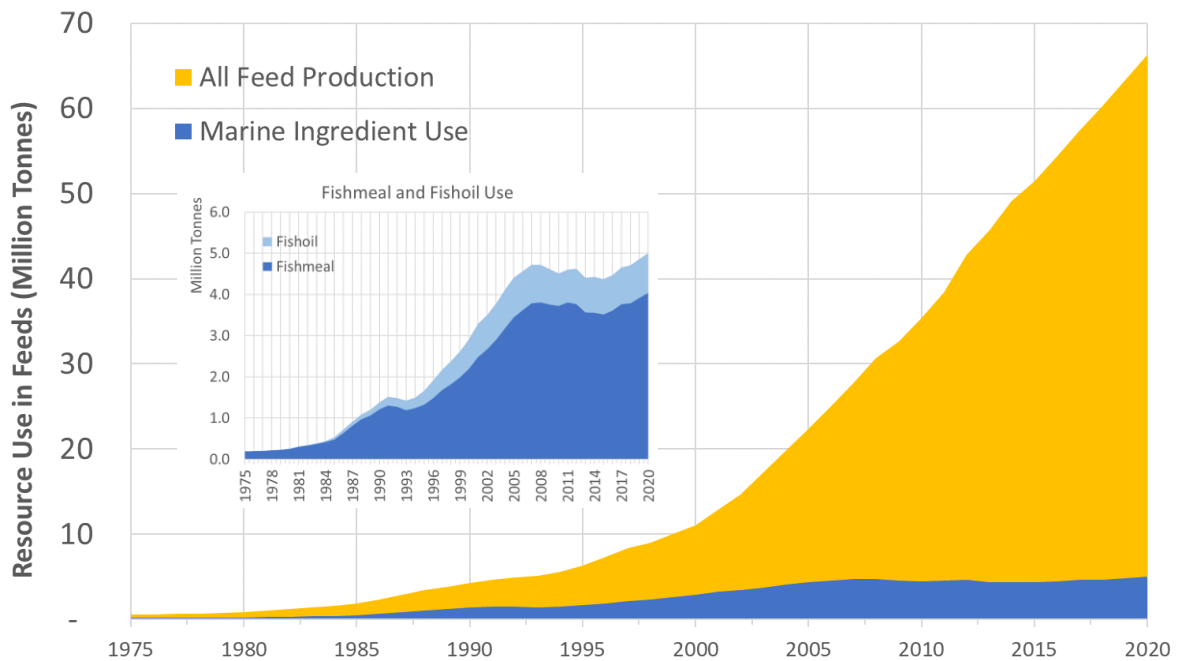
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433 Although these constraints still existed for plant ingredients, reduced fish meal supplies, and increased
 434 costs drove the demand for alternative protein sources. Terrestrial plant ingredients were generally
 435 considered as being more sustainable and gained a more significant position in aquafeeds with new
 436 processing technologies leading to the creation of a variety of plant protein concentrates that could
 437 compete with the higher price and protein content of fish meal. Although still not widely used in feeds
 438 for carnivorous species, plant proteins and oils were already by this time the major contributor to
 439 aquaculture feed protein and lipids for omnivorous and herbivorous species. Soybean meal was
 440 already a widely used ingredient in feeds for omnivorous and herbivorous species, with other grains
 441 being used included a range of cereal, oilseed, pulse, and various grain legume seed products. Typical
 442 inclusion levels of soybean meal in feeds for such omnivorous and herbivorous species ranged from
 443 15% to 45% (Tacon et al. 2011).

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Figure 2. Estimated feed production for all fed aquaculture species sector from 1975 to 2020, with concurrent marine ingredient use across the aquaculture sector. Shown in the inset is a magnified set of the marine ingredient (fish meals + fish oils) use data across the same time. Data derived from FishStat 2020 and IFFO 2021.

454 **Present (2010 – 2020)**

455

456 Presently there is ~60Mtonnes of aquafeed production globally, of which fish meal is now only ~4MT,
457 fish oil is ~1MT and the rest (~55MT) is mostly plant derived resources (IFFO, 2021). Use of marine
458 ingredients (proteins and oils) in aquafeeds has stabilised since 2010 and they are now seen more as
459 strategic ingredients, with a growing use of by-product fish meal now contributing to >30% of all
460 marine ingredient use in manufactured feeds (Hamilton et al., 2020; IFFO, 2021).

461

462 Plant proteins continue to be the main contributor to aquaculture feed protein and lipids for most
463 aquaculture species, but their use is also seen as contentious in some circumstances (e.g., soybean
464 use and associated deforestation concerns). Notably, feeds for carnivorous species are now
465 predominantly composed of plant proteins and oils (Ytrestøyl et al., 2015). The increasing use of
466 processing to produce protein concentrates from soy, peas, and other legumes as well as cereal
467 glutens has occurred. This processing maximises the protein concentration, quality and suitability for
468 use in feeds, whilst minimising the non-nutritive factors (Drew et al., 2007). To balance the amino
469 acids, the use of plant proteins and the concurrent reduction in fish meal has led to a much more
470 complicated formulation, now involving a greater number of protein sources with addition of some
471 crystalline essential amino acids to create a balanced diet to support high growth performance and
472 healthy fish. This broader raw material array brings some advantages to the feed sector, in that it is
473 not reliant on any one ingredient – so there is more resilience to supply chain threats (such as poor
474 harvests). But plant proteins also bring some sustainability challenges to address (Malcorps et al.,
475 2019).

476

477 The focus on soy and deforestation is probably foremost, which has led the feed industry to work with
478 their soy suppliers in Brazil to set deforestation and conversion free cut-off dates in 2020 for their
479 entire supply chain. Plant proteins also typically have a much higher carbon footprint than fish meal,
480 which has pushed the overall footprint of the feed up over the last 20 years (MacLeod et al., 2020).
481 Carbon footprint is increasingly of interest, as the carbon impact of food systems has been publicly
482 highlighted. Here aquaculture is in a very good position, being a typically low greenhouse gas (GHG)
483 emitter compared to other food systems, but it also has a great opportunity to improve. It has been
484 suggested that replacing 20-30% of fish meal in shrimp feeds with plant protein ingredients could
485 result in a 63% increased demand for freshwater, 81% increase in land requirements, and a need for
486 83% more phosphorus (Malcorps et al., 2019).

487

488 Across a broader range of life cycle assessment impact factors, it has been argued that there is
489 insufficient land for the expansion of animal feed crop production (Popp et al., 2017), as it currently
490 occupies roughly one-third of global croplands (Robinson et al., 2018). Furthermore, there are
491 additional pressures on land use due to population growth, climate change, and demands for food
492 and biofuels (Spiertz & Ewert, 2009; Godfray et al., 2010). In their discussion, Malcorps et al. (2019)
493 remind us that Sustainable Development Goals of the United Nations include food security, hunger
494 reduction, and protection of life on land and in the sea. They emphasize that minor price changes to
495 crops resulting from increased pressure on land-based food production systems could have dire
496 consequences in developing countries, where 50% of the household income is spent on food (Spiertz
497 & Ewert, 2009).

498

499 The current focus is not only on the reduced reliance on fish meal and fish oil derived from capture
500 fisheries, but also increasingly on the overall sustainable supply of terrestrial and plant feed
501 ingredients. Some of the raw materials used in aquaculture feeds can be consumed by humans,
502 resulting in food-feed competition. There is also a consideration of whether raw materials which could
503 be consumed directly by humans should be used for animal feeds.

504 The shift towards plant-based ingredients in aquaculture feed also faces competition from livestock
505 and agriculture sectors as well as biofuel production. Marine and terrestrial ingredient sources are
506 both vulnerable to climate change, which may cause disruption and decrease in supply and higher
507 costs for aquaculture feeds (FAO, 2018). There is thus a trend towards increased use of by-products
508 as feedstuffs in aquaculture and livestock feeds with a growing focus on bio-circularity of resources.
509 However, consumer concerns have been raised in some markets around the use of by-products, in
510 particular animal by-products which could bring a good nutritional input but are blocked from use in
511 some supply chains due to perceived health risks and social objections (Glencross et al., 2020). In
512 parallel, circular proteins such as insects and microbial biomass are being increasingly advocated as
513 sustainable alternatives, as they can convert various waste streams such as food waste, household
514 waste, plant by-products, sludge into high-quality nutrients. High production and processing costs still
515 limits their large-scale production, and a range of regulations still limit their application in certain
516 markets.

517
518 Both microalgal and genetically modified crops have been commercialised that produce long-chain
519 omega-3 in industrial volumes (>1000 tonnes). Due to an urgent need for fish oil alternatives, a range
520 of omega-3 rich ingredients are emerging, e.g., microbial ingredients (microalgae), oil seeds with high
521 level of LC-PUFAs (rapeseed and camelina), and increased use of fish by-products, and lower-tropic
522 marine species (e.g., krill, mesopelagic fish) (Hamilton et al., 2020). Up to eight relatively new sources
523 of EPA and DHA with industrial potential for aquafeeds have been recently described (Tocher et al.
524 2019). These products included five microalgal sources, two genetically modified seed crop oils, and
525 one yeast biomass. Identification of cost-effective, alternative lipids high in the LC-PUFAs EPA and DHA
526 remains a substantial hurdle for the future of aquaculture. Both microalgal and genetically modified
527 crops will undoubtedly play an increasingly important role in aquafeeds for those species requiring LC-
528 PUFAs. Perhaps equally important is the need to fortify fish feeds toward the improvement of human
529 health.

530
531 Food safety is a considerably overlooked aspect of much fish nutrition research but is increasingly
532 highlighted socially and politically (Glencross et al., 2020a). As an example, perceptions over the use
533 of food waste for livestock and fish feeding has limited efforts in this area, particularly in developed
534 countries, and yet there is an estimated 1.3 billion tons of human food lost and wasted each year
535 (Gustavsson et al., 2011). Concerns over genetically modified feed ingredients also limit options in
536 certain parts of the world, but others are readily adopting this technology. Food safety risks are
537 associated with the possible chemical contaminants and biological hazardous materials present in
538 ingredients and feeds, which might be passed to humans who consume aquaculture products.
539 Concerns have been raised about antimicrobial residues, persistent organic pollutants, heavy metals,
540 mycotoxins, and industrial contaminants (Tacon et al. 2008; Glencross et al., 2020). Additional
541 concerns over microplastics in fish meal have been raised recently (Hanachi et al. 2019; Gündoğdu et
542 al. 2021; Thiele et al. 2021).

543 544 **Future (after 2020)**

545
546 It has been suggested that by the year 2050 that aquaculture production is going to double and
547 intensify. Fundamentally what it will need to feed that production is sustainably sourced, economic,
548 good quality protein, some essential amino acid (EAA) additives, some omega-3 options, various
549 mineral and vitamin additives, and cost-effective energy sources. To do that will mean we need
550 another 50MT of resources that we currently do not have or are presently being used in other sectors.
551 Although gains in crop productivity have kept pace with demand through most of the 20th century,
552 they are not keeping up with demands more recently (Grassini et al., 2013; Schauburger et al., 2018).
553 Notably, most currently used plant protein resources are also used in pig and poultry feeds (so a
554 competition issue exists).

555 There is additionally the concern that many of these plant protein resources can be used directly to
556 feed humans rather than animals. Add into the equation that there is a declining availability of
557 freshwater, phosphates, and arable land, and it is obvious that terrestrial crop products are not the
558 only solution going forward. Further competition for ingredients of plant origin is also occurring for
559 human food and non-food products such as biofuels. While many plant source ingredients are
560 considered economically sustainable, questions have been raised about their social and
561 environmental sustainability, notably products from soy and palm oil production (Hospes 2014;
562 Okereke and Stacewicz 2018). These constraints provide a strong argument for the development of
563 non-traditional protein and oil sources.

564

565 Fish meal and fish oil are still considered among the most nutritious ingredients as they are rich
566 sources of essential nutrients and have a high level of palatability in virtually all aquaculture species.
567 Increasingly fish meal and oil production will come from by-product resources from fish caught for
568 direct human consumption (e.g., Alaskan pollock) or aquaculture by-product. By 2030 more than one
569 third of all fish meal and oil will come from by-product sources (IFFO, 2021). The continued reduction
570 in the reliance on fish meal and fish oil, combined with the concurrent increased use of alternative
571 raw materials in aquaculture feeds highlights the need for an approach based on complementarity of
572 ingredients (Turchini et al., 2019). The increasing use of alternatives brings about the need for a range
573 of feed additives to supplement specific essential nutrients including essential amino acids, essential
574 fatty acids, and trace elements. We may also see greater usage of bioactive compounds, prebiotics,
575 probiotics and other immunostimulants (Boyd et al., 2020). It is critical to find additional, cost-
576 effective ingredient sources to meet the growing nutrient demand. This burgeoning demand, growing
577 ingredient competition, and heightened sustainability awareness provide a strong argument for the
578 development of non-traditional protein and oil sources, especially those part of the circular
579 bioeconomy like such as insects, microalgae, microbial biomass, and food waste.

580

581 Technologies that produce protein, amino acids, and omega-3 using non-competitive processes based
582 on non-food grade resources (e.g., bacteria, yeasts, and algae; single-cell ingredients [SCI]) perhaps
583 offer the most potential to generate the additional resources needed (Glencross et al., 2020b). As
584 biotechnology advances, a broader range of substrates from various waste streams will be used in the
585 fermentation process to reduce costs and increase profitability of SCI production. This will include the
586 downstream processing to enhance the nutritional value of the microbial ingredients. As the
587 competition for natural resources increases and the technology advances, production of microbial
588 ingredients will shift from being dependent on photosynthesis and products from this process as
589 substrates, towards use of cheaper input factors (e.g., organic acids, CH₄, H₂ and CO₂ gas) from
590 industrial waste or other renewable sources.

591

592 Additionally, there will be increasing pressure to source ingredients locally for feed production and
593 reduce dependence upon imported sources. This will demand more effort be given to use of local
594 ingredients, the adoption of nutrient recycling and use of innovative raw material processing
595 techniques. This will probably be coupled with the use of renewable energies as the type of fuel used
596 for processing has a remarkable life cycle impact on such ingredients (Campos et al. 2020). In the
597 future there is likely to be more competition for natural resources; driven by factors such as
598 population growth, development of the bioeconomy, and climate change. Aquaculture production will
599 play an increasing role in meeting the global protein supply and the need for feed to sustain this
600 production will clearly increase.

601

602 Sustainability of different feed ingredient sources, including possible climate change impacts, is
603 becoming a growing issue. For the global aquaculture sector to grow sustainably, it must have a
604 sustainable supply of the nutrients to make the feeds.

605 The key sustainability issues vary from ingredient to ingredient and the historical approach was to
606 focus just on one feed ingredient at a time – such as fishmeal or soy. Sustainability of different feed
607 ingredient combinations will become a key defining characteristic of their utility, with increasing use
608 of independent certification systems to verify claims. Going forwards, we will see an increasing focus
609 on the sustainability of the feed ingredient supply chains. The discussion should move beyond
610 whether an individual ingredient is sustainable or not, to one of whether that supply chain is. For
611 example, fishmeal can be supplied sustainably – from sustainably managed fisheries. Soy can be
612 farmed sustainably, on land which was not recently converted from native vegetation. Independent
613 certification schemes have been established to provide verification of claims. There are a broad range
614 of schemes with different levels of value and credibility, but all add cost to the overall supply chain.
615 However, the expectation is that the use of certification to verify sustainability claims will continue to
616 grow. As the topics covered by sustainability increase, the number of schemes is likely to continue to
617 grow. For example, through moving beyond fisheries and deforestation issues to addressing issues of
618 human rights, carbon footprint, land, and water use. The level of complexity to be managed will
619 increase, but the information to do this has to keep pace, so good decisions are made on the latest
620 reliable data. This can only be supported by a full value chain commitment to change – led from the
621 consumer and retail end to support the upstream supply side’s transformation. Without commitment
622 from the market, changes will be harder to implement and value. Assessment of the sustainability of
623 feed ingredients varies depending on the type of ingredients as their social, economic, and
624 environmental impacts all differ considerably. There is a need for harmonisation of various
625 aquaculture related sustainability certification standards to ensure consistency (Kok et al., 2020). The
626 adoption of certification schemes will continue to reduce or eliminate ingredients from unsustainable
627 sources.

628

629 Food safety will become an increasingly important issue in the future. Driven by consumer perception,
630 politics and some level of science, consumers will gravitate toward those products that align with their
631 attitudes, preferences, and expectations. Food safety will continue to be important for feed
632 manufacturers and fish producers to meet consumer demand for disclosure of credence attributes.
633 In addition to safety, these include origin, sustainability, and nutritional content. As such, both
634 mandatory and voluntary labelling will continue to be strong drivers of the seafood market.

635

636 **Feed Management and Manufacturing**

637

638 ***Past (before 2010)***

639

640 Feed rationing systems and management of how much and when feed was delivered to the animal
641 were largely based on prior experience or demand based, relying on the animal providing feedback to
642 the person feeding them. Most feeding was manual, using hand, blower, or other simple delivery
643 systems. As such feeding was a labour-intensive process (Ibrahim & Sultana, 2006). Traditional feeding
644 regimes were based on experience of the operators, considering factors such as weather, water
645 colour, season, and animal behaviour among other things. The diet was selected based on price and/or
646 feed manufacturer recommendations. The focus was on fish growth. Traditional end points for manual
647 feeding were judged by farmers making decisions based on their experience and skills. This primarily
648 entailed deciding what feed, when, and how much was delivered to the animal (Jobling et al., 1995;
649 Paspatis & Boujard et al., 1996). Assessments of animal behaviours and interactions with feeds and
650 the feeding process were somewhat subjective, though for certain species some simple tools, like feed
651 trays, were used to assist the process (Tacon, 2002). For technologically advanced sectors, sensor-
652 based feeding systems were emerging (Kadri et al., 1998).

653

654

655 Historically, many feeds were based on the use of trash-fish and/or made on-farm by the farmers.
656 These may have initially been fed as intact trash-fish or made into a moist mash with the use of other
657 materials and binders or made into dried pellets using simple pelleting manufacturing systems (Hasan
658 & New, 2013). With the growth and increasing technical demands on the sector, specialist feed
659 compounders emerged and brought advancements in the various processes used in feed
660 manufacturing. Additionally, the feed manufacturing sector played an important role in helping
661 farmers, not only in the provision of feed inputs, but more importantly in the management of the feed
662 on the farm and in the use of appropriate environmentally sound husbandry practices. In many
663 countries the feed manufacturers were the closest contact in the value-chain between the farmer and
664 the government legislature (Tacon et al., 1995). Notable among the manufacturing introductions
665 during this period was that of expansion extrusion, which was introduced into some sectors from
666 1980's onwards and by the 2000's became widely used across the developed world for most fish
667 species, and increasingly was being applied in the developing world.

668

669 ***Present (2010 – 2020)***

670

671 In the present day, feed management systems in technologically advanced sectors are becoming
672 increasingly computerised in modern developed-world aquaculture. Automated centralised
673 pneumatic feeding systems using in-cage cameras and computer-based decision-making tools are
674 widespread resulting in a reduced level of labour (Aas et al., 2011; Waagbo et al., 2013). However, in
675 the developing world where the majority of aquaculture still occurs, feeding is still largely a manually
676 controlled and managed process with important labour demands and continues to be a significant
677 rural employer (El-Sayed, 2013; Hung & Quy, 2013; Ng & Romano, 2013). Feeding end points are still
678 largely judged by farmer decisions in combination with computerised algorithms. The interpretation
679 of the fish responses is experience-based and depends on the experience and skills of the individual
680 farmer.

681

682 The use of growth and energetics models are increasingly being applied for the evaluation and
683 management of feeding regimes for various species (Cho & Bureau, 1998; Zhou et al., 2005; Glencross
684 & Bermudes, 2012; Liu et al., 2018). The application of modelling helps reduce both the feed cost and
685 the waste being discharged (Bueno et al., 2017). Historically, modelling focused only on evaluating the
686 feeding rate, but increasingly, diet formulation, environmental factors, feeding frequency, feeding
687 rhythm and even animal behaviour are all being taken into consideration.

688

689 Manufacturing of feeds in the developed world is now mostly based on modern extrusion technologies
690 (Barrows et al., 2007). There has been considerable development of engineering technological
691 capabilities in this area, allowing considerable control over the forming, cooking and densification
692 attributes of the feeds. Such engineering systems are highly complex but offer a substantial level of
693 control on the pellet forming process, enabling the user significant control on pellet density, durability,
694 and oil infusion capacities (Sørensen, 2012). Despite these advancements, and the increasing level of
695 industrialisation of feed manufacturing, some sectors (e.g., shrimp farming), have still tended to stay
696 with manufacturing approaches like pelleting, while other sectors in the developing world, particularly
697 small-scale aquaculture operations, have continued to use an on-farm mash feed manufacturing
698 approach. Shrimp feeds, despite being still predominantly pelleted, are beginning to emerge as
699 extruded products through some companies (Obaldo et al., 2000; Soares et al., 2021). In the
700 developing world there is still widespread use of pelleting, mash, and trash-fish feeding, especially on-
701 farm, although extrusion is increasingly being used by commercial feed suppliers in these parts of the
702 world (Edwards et al., 2004; Xu et al., 2007; Tacon & Metian, 2009; Merican, 2021).

703

704

705

706 **Future (after 2020)**

707

708 To increase sustainability of fish production and optimise fish product quality and animal welfare, it is
709 becoming even more important to monitor and control the animal production process (Antonucci &
710 Costa, 2020). By reducing the feed conversion ratio, farmers will have less waste and loss of nutrients
711 to the water they farm in, and they will tend to reduce their overall carbon footprint. To achieve this,
712 we need a better understanding of feed intake and its physiological points of regulation and how this
713 is affected by production system (e.g., RAS, pond, or cage) and a range of other abiotic factors. In the
714 future we will see increasing use of mechanised and automated feeding in the developing world,
715 matching that already being undertaken in much of the developed world. This use of mechanised and
716 automated feeding will aid in improving production efficiencies (through less wastage) and animal
717 growth rates (through higher intakes), by allowing for the better alignment of feeding with the needs
718 of the animals being farmed, but it will correspondingly reduce labour demands and employment in
719 the sector. Already there are signs of increasing use of autonomous feeding systems in the developing
720 world, occurring through the development of a variety of low-cost automatic feeding systems (e.g.,
721 <https://www.efishery.com/>).

722

723 The use of artificial intelligence (AI) in feeding systems is emerging. AI is going to impact businesses
724 of all shapes and sizes across all industries (Marr, 2020). The increasing use of centralised computer-
725 controlled feeding systems and in-cage / in-pond sensors and cameras will increasingly make an
726 internet-of-things system of control more feasible for feeding aquaculture species (Martos-Sittha et
727 al., 2019; Måløy et al., 2019; Mustapha et al., 2021). The development of complex algorithms and AI
728 that monitors feeding behaviour will be used to help make decisions about feeding management
729 (Jones et al., 2012; Zhou et al., 2018). Coupled with more precisely defined energy and nutrient
730 demands over various size classes, environments, genotypes and in situ bio-loggers, the inclusion of a
731 precision nutrition approach will complement completely automated feeding (Hvas et al., 2020; Zhang
732 et al., 2020).

733

734 The use of automation and AI will lead to precision and smart farming increasingly becoming a focus.
735 The use of big data applications may play a major role in improving the efficiency of the entire supply
736 chain, with focus on food security, safety, and sustainability (Gilpin, 2015). These will provide an
737 increasing focus on the application of principles of precision fish farming (PFF) to shift feeding
738 management from comprising largely experience-driven processes to become a more knowledge-
739 driven procedure (Føre et al., 2018). PFF feeding regimes based on animal demands and farm targets,
740 including specialised diet formulations, considerations of environmental factors, animal health and/or
741 quality and/or water quality will be included into the AI system to provide precise decisions for
742 management of computer-controlled systems. Biological and system informatics will become
743 combined to increase the precision control of fish farming. The use of intelligent sensors and
744 monitoring, will support the application of predictive models and simulation systems, leading to
745 improved decision management and integration of operations that will enhance the overall precision
746 control of fish farming operation (Fore et al., 2018). The use of models to predict environmental
747 fluctuations and adjust feed distribution accordingly and autonomously to minimise feed waste and
748 improve efficiency should be a primary goal for improved production efficiency in aquaculture. The
749 optimal solution should be the use of real-time techniques that can determine the actual feeding
750 behaviour of the fish. Therefore, to ensure efficient feeding in aquaculture, it is necessary to develop
751 a smart feeding regime system that can analyse the appetite status of farmed fish (Adegboye et al.
752 2020).

753

754 There will continue to be increasing use of extrusion feed production with greater uptake in the
755 developing world and development of novel extrusion applications for non-traditional species based
756 on improved feed technical qualities and flexibility of the manufacturing systems used.

757 This increasing shift to manufactured feeds across the developing world will result in an overall
758 improvement in feed quality and resource utilisation by the sector, further aiding a move away from
759 the use of trash-fish and farm-made feeds. Additionally, because of the increased use of automatic
760 feeders, there will be increased demand for the use of high-physical quality non-clogging extruded
761 feeds in these feeding systems. The increasing demand for functional feeds with specialist additives
762 will see the emergence of nanotechnology to precision deliver certain high-valued compounds to the
763 fish, by preventing them to be digested or metabolised at certain stages of the absorption process,
764 allowing for targeted nutrient and nutraceutical delivery. Such novel encapsulation methods will
765 enable the protection of certain labile functional ingredients from the damaging forces involved in
766 extrusion.

767

768 **END NOTE**

769

770 Many of the advances in nutritional understanding of aquaculture species over the past twenty years
771 has come from an intense focus on a few species. However, it should be clearly acknowledged that
772 part of the challenge of aquaculture nutrition is the diversity of species involved and that their
773 requirements can be just as diverse. There is an urgent need to bring our understanding of many of
774 the non-focus species into the same level of understanding. Additionally, although marine derived
775 ingredients are still widely used in feeds, even salmon farming has now become a net producer of
776 seafood. Globally around 4 MT of fishmeal and 1MT of fish oil is contributing to the production of
777 more than 40MT of farmed fish and shrimp, an almost ten times multiplier effect. The widespread use
778 of plant proteins and oils has underpinned the growth of aquaculture over the past twenty years. The
779 capacity for aquaculture to achieve this has been the result of decades of nutrition research (Naylor
780 et al., 2020). The future will require further work in developing the potential of a range of sustainable
781 feed protein and oil options, particularly those from the circular bioeconomy.

782

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