ENVIRONMENTAL RESEARCH
LETTERS

PURPOSE-LED PUBLISHING™

Part of the
ENVIRONMENTAL RESEARCH
SERIES

LETTER • OPEN ACCESS

Feed conversion efficiency in aquaculture: do we measure it correctly?

To cite this article: Jillian P Fry *et al* 2018 *Environ. Res. Lett.* **13** 024017

Environmental Research Letters

OPEN ACCESS

RECEIVED
9 August 2017

REVISED
13 December 2017

ACCEPTED FOR PUBLICATION
18 December 2017

PUBLISHED
6 February 2018

LETTER

Feed conversion efficiency in aquaculture: do we measure it correctly?

Jillian P Fry[1,2,3,6], Nicholas A Mailloux[1], David C Love[1,2], Michael C Milli[1] and Ling Cao[4,5]

1 Johns Hopkins Center for a Livable Future, Johns Hopkins University, 615 N Wolfe Street, Baltimore, MD, United States of America
2 Department of Environmental Health and Engineering, Bloomberg School of Public Health, Johns Hopkins University, 615 N Wolfe Street, Baltimore, MD, United States of America
3 Department of Health, Behavior and Society, Bloomberg School of Public Health, Johns Hopkins University, 624 N Broadway, Baltimore, MD, United States of America
4 Center on Food Security and the Environment, Stanford University, 616 Serra St, Stanford, CA, United States of America
5 Institute of Oceanography, Shanghai Jiao Tong University, Shanghai, People's Republic of China
6 Author to whom any correspondence should be addressed.

E-mail: jfry3@jhu.edu

Keywords: aquaculture, agriculture, food security, animal production efficiency

Supplementary material for this article is available online

Abstract

Globally, demand for food animal products is rising. At the same time, we face mounting, related pressures including limited natural resources, negative environmental externalities, climate disruption, and population growth. Governments and other stakeholders are seeking strategies to boost food production efficiency and food system resiliency, and aquaculture (farmed seafood) is commonly viewed as having a major role in improving global food security based on longstanding measures of animal production efficiency. The most widely used measurement is called the 'feed conversion ratio' (FCR), which is the weight of feed administered over the lifetime of an animal divided by weight gained. By this measure, fed aquaculture and chickens are similarly efficient at converting feed into animal biomass, and both are more efficient compared to pigs and cattle. FCR does not account for differences in feed content, edible portion of an animal, or nutritional quality of the final product. Given these limitations, we searched the literature for alternative efficiency measures and identified 'nutrient retention', which can be used to compare protein and calories in feed (inputs) and edible portions of animals (outputs). Protein and calorie retention have not been calculated for most aquaculture species. Focusing on commercial production, we collected data on feed composition, feed conversion ratios, edible portions (i.e. yield), and nutritional content of edible flesh for nine aquatic and three terrestrial farmed animal species. We estimate that 19% of protein and 10% of calories in feed for aquatic species are ultimately made available in the human food supply, with significant variation between species. Comparing all terrestrial and aquatic animals in the study, chickens are most efficient using these measures, followed by Atlantic salmon. Despite lower FCRs in aquaculture, protein and calorie retention for aquaculture production is comparable to livestock production. This is, in part, due to farmed fish and shrimp requiring higher levels of protein and calories in feed compared to chickens, pigs, and cattle. Strategies to address global food security should consider these alternative efficiency measures.

1. Introduction

The global food system is a major force driving humanity towards bypassing multiple planetary boundaries, including freshwater use, land use change, biodiversity loss, climate change, and water quality degradation [1, 2]. This is, in part, because an increasingly affluent and growing global human population is consuming more meat and dairy products [3–6]. Food animal products provide a concentrated source of calories, protein, and some micronutrients. There are, however, well-documented inefficiencies in terrestrial livestock

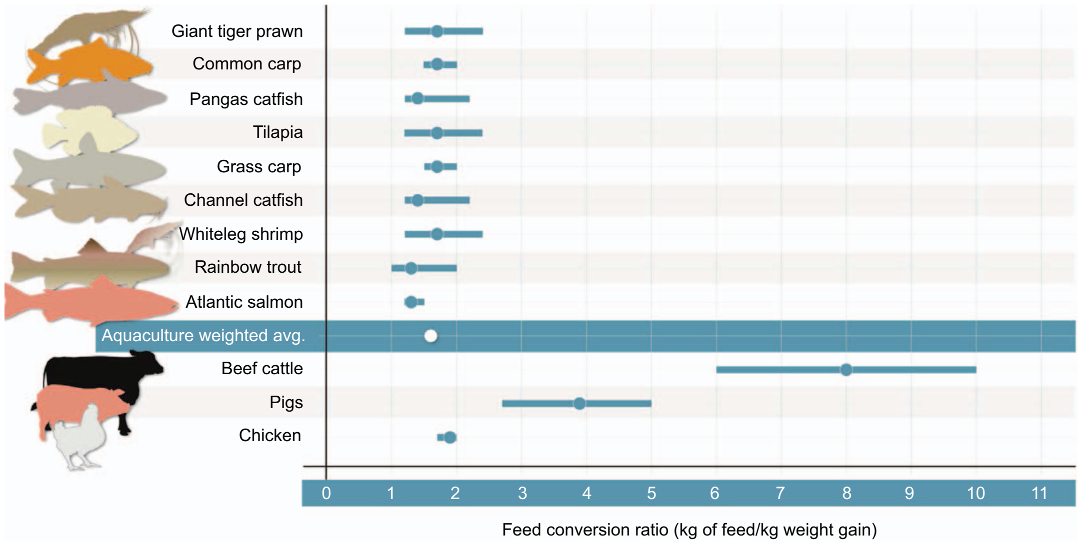

Figure 1. Feed conversion ratios for selected aquatic and terrestrial farmed animal species. Dots represent means and bars indicate range. Lower values signify higher efficiency. Sources: Tacon and Metian (2008) [12], Smil (2013) [13], Shike (2013) [14], Zuidhof *et al* (2014) [15], and Rabobank Research (2015) [16].

production. Approximately 36% of global crop-based calories (3.41×10^{15} kcal) are fed to livestock, and of those, just 12% enter the human food supply [7].

Aquaculture, or farmed seafood, is the fastest growing food animal sector and now contributes more to the human food supply (by weight) than wild-caught seafood (adjusting for wild-caught fish not eaten by people) or beef [8, 9]. (We use the term, seafood, to refer to aquatic animals caught or farmed for human consumption in marine and freshwater settings.) Seafood, from farmed and wild sources, provides 17% of global animal protein, and accounts for over half of animal protein supplies in some developing countries [8]. Aquaculture is heterogeneous in terms of farmed species and production methods. Fed aquaculture, including both intensive and semi-intensive systems, involves relatively high stocking densities and either farm-made feeds or commercial compound feeds formulated to meet nutritional requirements. Unfed aquaculture includes filter-feeding molluscan shellfish (e.g. oysters, clams, mussels) and aquatic plants (e.g. microalgae, seaweed). Globally, aquaculture production continues to expand and intensify. About 70% of global aquaculture (excluding aquatic plants) relies on commercial compound feed, and demand for commercial feed is growing faster than the industry as a whole. A significant proportion of aquaculture feed contains ingredients made from wild-caught fish [10]. To reduce pressure on depleted wild fisheries, the industry is increasingly relying on alternative feed ingredients including crop-based ingredients (e.g. soy, rapeseed, wheat, groundnuts, and corn) and terrestrial animal byproducts as substitutes for fishmeal and fish oil [11].

The efficiency with which animals turn feed into meat and other food products, such as eggs or milk, varies by species and production method. A common measure of this efficiency is the feed conversion ratio (FCR), calculated as the ratio of feed intake to weight gain. Typical FCRs for animals raised using commercial feeds and intensive production methods (i.e. not extensive production like grazing) are as follows: beef cattle: 6.0–10.0, pigs: 2.7–5.0, chickens: 1.7–2.0, and farmed fish and shrimp: 1.0–2.4 (figure 1) [12–16]. Aquatic animals have lower (more efficient) FCRs than large terrestrial animals in part because they expend less energy to move, stay upright, and regulate their body temperatures due to buoyancy and because most are ectothermic [17, 18]. Expanding aquaculture is thus widely viewed as an opportunity to meet rising demand for animal products using less feed, especially compared to pigs and cattle [19, 20]. FCR is a limited measure of efficiency, however, because it only accounts for the weight of feed inputs and not the nutritional content of the feed, the portion of the animal that is inedible, or the nutritional quality of the final product. Using FCRs relies on an implicit assumption that various species are similar across these areas, making FCR a potentially flawed tool for cross-species comparisons.

We reviewed the literature and identified 13 different approaches to measure aquatic animal production efficiency beyond FCR (supplementary table S1 available at stacks.iop.org/ERL/13/024017/mmedia). Based on our review, a more precise measure than FCR is the efficiency with which an animal converts nutrients in feed into nutrients for the human food supply, specific examples of 'nutrient retention' measures are sometimes called a 'protein/calorie efficiency ratio' or 'protein/calorie retention'. These have been calculated for major livestock products [7, 21] and for two aquaculture species (for example, see [22, 23]), but more work is needed. Ytrestøyl *et al* calculated protein and calorie efficiency for farmed salmon in Norway [22].

Table 1. Data used to calculate protein and calorie retention for selected aquatic and terrestrial farmed animal species.

Species	FCR[a]	Edible portion of animal[b]	Feed content[c] (g or kcal per 100 g of feed)		Human nutrition[d] (g or kcal per 100 g serving)	
			Protein	Calories	Protein	Calories
Carps	1.5–2.0					
Common carp	–	0.36–0.54	17–45	175.8–554.2	18	109–127
Grass carp	–	0.36–0.54	25	326.0–345.5	17–18	112–127
Catfishes	1.2–2.2					
Channel catfish	–	0.35–0.63	28–32	345–390	15–17	117–119
Pangas catfish	–	0.35–0.63	26–32	339–388	15	97
Salmonids	–					
Atlantic salmon	1.2–1.5	0.58–0.88	35.5–44	372–554.5	20	208
Rainbow trout	1.0–2.0	0.40–0.82	40–47	383–454	20	141
Shrimps	1.2–2.4					
Giant tiger prawn	–	0.40	25–45	225–433	20	85
Whiteleg shrimp	–	0.62–0.65	25–45	277–417	20	85
Tilapias	1.4–2.4	0.37–0.45	20–32	216–404.4	20	96
Cattle	6.0–10	0.52–0.64	7–15.4	188–339	15–20	214–276
Chicken	1.7–2.0	0.70–0.78	18–23	320	18.6	215
Pigs	2.7–5.0	0.68–0.76	13.2–20.9	326.5–335.1	15–18.2	211–304

[a] Data sources: Tacon and Metian (2008) (aquatic species) [12]; Smil (2013) (livestock species) [13]; Shike (2013) (cattle) [14]; Zuidhof *et al* (2014) (chicken) [15]; Rabobank Research (2015) (pigs) [16].

[b] Data sources: see table S4.

[c] Data sources: see table S5.

[d] Data sources: USDA National Nutrient Database for Standard Reference [27]; Shauhua Zahn, Nanyang Technical University (personal communication); Seafood Health Facts [28]; USDA National Nutrient Database terms used for beef: 'composite of trimmed retail cuts, separable lean and fat, trimmed to 1/8″ fat, all grades, raw' and 'variety meats and by-products, mechanically separated beef, raw'; USDA National Nutrient Database term used for chicken: 'meat and skin, raw'; USDA National Nutrient Database terms used for pork: 'composite of trimmed leg, loin, shoulder, and spareribs, separable lean and fat, raw' and 'fresh, variety meats and by-products, mechanically separated, raw'.

Smil [23] (also cited in [20, 24]) provided protein and calorie efficiency for farmed carp, however, Smil does not provide methods or reference source data, making it impossible to independently reproduce the calculations or update estimates as newer data becomes available. Given the pressing challenges of limited resources and rising global demand for animal products, it is critical to know which aquaculture species most efficiently retain protein and calories in feed, and how aquatic species compare to livestock. Our study fills this critical research gap.

2. Methods

For this study, we calculated the protein and calorie retention typical of commercial production for several farmed aquatic and terrestrial animals by developing equations and collecting data necessary for filling in each variable. We included nine major aquaculture species: common carp (*Cyprinus carpio*), grass carp (*Ctenopharyngodon idella*), channel catfish (*Ictalurus punctatus*), pangas catfish (*Pangasius pangasius*), Atlantic salmon (*Salmo salar*), rainbow trout (*Oncorhynchus mykiss*), giant tiger prawn (*Penaeus monodon*), whiteleg shrimp (*Litopenaeus vannamei*), tilapia (*Oreochromis niloticus* and other cichlids); and three livestock groups (cattle raised for beef, pigs, and chickens raised for meat). The aquaculture species included in the study comprised over half (57%) of global production of fed aquaculture in 2012 [10, 25], and the livestock are the top land animals produced for meat in the US and globally [9, 26].

We collected data from numerous sources on FCRs, feed composition, yield/edible portion, and nutritional profiles of edible flesh (table 1), and using these data we calculated protein and calorie retention using equations 1 and 2. (See the supplementary material for additional details regarding species selection, data extraction, and development of the retention equations.) The equations we developed are comparable to the 'Nutrient retention' measure in table S1, but no specific equation was supplied in the paper that described the measure [22] or other studies that calculated protein and calorie retention for livestock. We focused on collecting data that reflects intensive/commercial production, and focused on top-producing countries where possible. For example, we searched for feed content information for complete, commercially available feeds and not supplementary feeds used in extensive or semi-intensive production settings. Mean retention values and standard deviations were calculated using Excel (Microsoft Corp., Redmond, WA) and Crystal Ball (Oracle Corp., Redwood Shores, CA). For each species, two types of simulations were run: protein retention and calorie retention. The retention equation and values collected for each variable were entered into the software. A Monte Carlo simulation was run for each retention/species combination using custom fit distribution settings, meaning the values were not expected to fit a specific probability distribution. Each Monte Carlo simulation ran 5000 trials; each trial randomly sampled the values entered. Calculating the retention means and standard deviations in this way allowed for inclusion of multiple values and provided a range of likely retention values based on all of the data we collected.

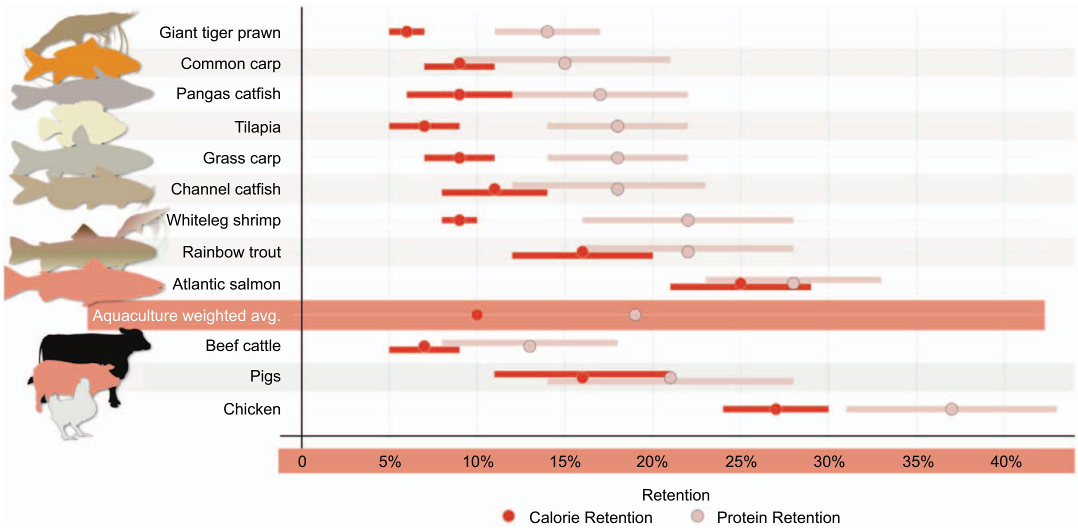

Figure 2. Protein and calorie retention for selected aquatic and terrestrial farmed animal species. Dots represent sample means and bars represent standard deviations. Higher values indicate more efficient retention.

Equation (1). Protein retention of selected aquatic and terrestrial animals.

$$\text{Protein retention} = \frac{(\text{g protein in edible portion})}{(\text{g protein in feed})}$$

$$= \frac{(\text{edible portion})\,(\text{g protein per 100 g of edible portion})}{(\text{FCR})\,(\text{g protein per 100 g feed})}$$

Equation (2). Calorie retention of selected aquatic and terrestrial animals.

$$\text{Calorie retention} = \frac{(\text{calories in edible portion})}{(\text{calories in feed})}$$

$$= \frac{(\text{edible portion})\,(\text{calories per 100g edible portion})}{(\text{FCR})\,(\text{calories per 100 g feed})}$$

3. Results

Based on global production levels for each aquatic species (i.e. a weighted average), we estimate that for every 100 g of protein in aquaculture feed for these nine species/species groups, 19 g are available in the human food supply (19% retention), and for every 100 kcal in aquaculture feed, 10 kcal enter the human food supply (10% retention) (figure 2). Protein and calorie retention values for aquatic and terrestrial species were similar. Protein retention means ranged from 14%–28% for the nine aquatic species, and 13%–37% for livestock. Calorie retention means ranged from 6%–25% for the aquatic species, and 7%–27% for livestock. Chickens performed best for both protein and calorie retention, followed by Atlantic salmon.

The factors that drive protein retention are the FCR, concentration of protein in feed, and edible portion. There is little variation in protein levels in edible flesh among aquatic and terrestrial species. Aquatic species have FCRs similar to chickens and lower than pigs and cattle, but require higher levels of protein in their feed compared to livestock. For example, the relatively high mean protein retention for Atlantic salmon (28%) is due to a low FCR (1.2–1.5) and high edible portion (0.58–0.88); these factors offset the high levels of protein in Atlantic salmon feed (35.5%–44%). Chicken has the highest mean protein retention (37%), due to a low FCR (1.9), low feed protein level (18%–23%), and high edible portion (0.70–.78) (table 1).

For calorie retention, there is more variation in calories in edible flesh (compared to the above-described variation in protein in flesh) and less variation in feed calories by species compared to feed protein levels. Similar to above, chicken and Atlantic salmon have the highest mean calorie retention: 27 and 25%, respectively. Pigs have an FCR (3.9) that is less efficient than chicken and aquatic species, but high calories in edible flesh (211–304 kcal per 100 g) and the high edible portion (0.68–0.76) improves pig calorie retention (16%). Giant tiger prawn and tilapia have the lowest mean calorie retention for aquaculture, 6% and 7%, respectively. These values are driven by low calorie content in edible flesh and low edible portions.

4. Discussion and conclusions

A limitation of relying solely on FCRs to assess efficiency becomes apparent when comparing FCRs and retention values (figures 1 and 2). If FCRs are a good predictor of nutrients retained in outputs, calorie and protein retention for aquatic species would be similar to, or higher than, chicken. Instead, when using the protein and calorie retention measures as derived above, the values for aquatic species are, with the exception of Atlantic salmon, more similar to retention values for pigs and cattle. Therefore, aquatic species, taken together, have little or no efficiency benefit over livestock when assessed on the basis of these alternative

Table 2. Mean FCR and retention values in the current study and past research.[a]

	Current study				Cassidy *et al* (2013)				Shepon *et al* (2016)			
	FCR[b]	Feed/edible weight	Protein retention	Calorie retention	FCR	Feed/edible weight	Protein retention	Calorie retention	FCR	Feed/edible weight	Protein retention	Calorie retention
Common carp	1.7	3.78	0.15	0.09								
Grass carp	1.7	3.78	0.18	0.09								
Channel catfish	1.4	2.87	0.18	0.11								
Pangas catfish	1.4	3.02	0.17	0.09								
Atlantic salmon	1.3	1.77	0.28	0.25								
Rainbow trout	1.3	2.14	0.22	0.16								
Giant tiger prawn	1.7	4.25	0.14	0.06								
Whiteleg shrimp	1.7	2.68	0.22	0.09								
Tilapia	1.7	4.17	0.18	0.07								
Aquatic weighted average	1.6	3.08	0.19	0.10								
Beef cattle	8.0	14.0	0.13	0.07	12.7	21.2	0.05	0.03	14	36	0.03	0.03
Pigs	3.9	5.34	0.21	0.16	6.5	9.3	0.10	0.10	3.1	6.0	0.09	0.09
Chicken	1.9	2.57	0.37	0.27	2.5	3.3	0.40	0.12	1.9	4.2	0.21	0.13
Eggs							0.35	0.22			0.31	0.17
Dairy							0.43	0.40			0.14	0.17

[a] Sources: Cassidy *et al* (2013) [7] and Shepon *et al* (2016) [21].

[b] FCRs are average values based on Tacon and Metian (2008) (aquatic species) [12]; Smil (2013) (livestock species) [13]; Shike (2013) (cattle) [14]; Zuidhof *et al* (2014) (chicken) [15]; and Rabobank Research (2015) (pigs) [16].

measures, which is the opposite of the result when comparing FCRs.

Animal production involves complex biological, social, and economic systems that vary by producer, region, and within particular breeds or sub-species of animals. Identifying differences by geography or climate was not possible in the current study. A strength of this study is identifying the range of likely protein and calorie efficiencies using existing commercial farming practices. Large standard deviations for some species may reflect higher uncertainty due to data variance and/or more data availability for certain species. Our aquaculture results are consistent with a previous Atlantic salmon estimate (27% protein and 24% calorie retention in Ytresoyl *et al* [22]) and lower than a protein retention estimate for carps (30% in Smil [23]; we calculated 15% for common carp and 18% for grass carp). Importantly, we found that Atlantic salmon performs much better than, and is therefore not representative of, other aquatic species.

We calculated retention values for livestock instead of using values from existing sources to ensure standardized methods were used across aquatic and terrestrial species. The work of Cassidy *et al* and Shepon *et al* use overall feed use and production data, therefore taking breeding animals and early mortalities into account [7, 21]. These data were not consistently available for aquaculture, so our results are based on estimated inputs fed directly to meat-producing animals to produce a unit of edible flesh, and does not account for breeding animals, wasted feed, or mortalities. Therefore, our results may overestimate retention. Not surprisingly, given the data used, our livestock retention results are generally higher than previous studies (table 2). The data used in this study for meat-producing animals was more robust compared to previous studies due to inclusion of multiple sources of data for many variables and use of Monte Carlo simulations for each retention/species combination to provide likely values based on all data collected.

Another reason our protein and calorie retention results may overestimate retention for aquaculture and livestock is due to our exclusion of feed and nutrient composition data for the earliest life stages. Detailed information on feed content across lifestage was not available for all species in the study. The final lifestage (i.e. growout) involves the majority of feed consumption and weight gain. Feed used in the earliest lifestages are higher in protein (this is true for aquatic and terrestrial animals), but smaller amounts of feed are used. Future research could refine retention calculations by using feed information across multiple lifestages.

Adequate protein and calories, as well as micronutrient intake, are critical for avoiding malnutrition in humans. Aquaculture expansion has been promoted as part of a solution to provide animal protein more efficiently, but in the case of fed aquaculture, the implications of consuming farmed aquatic animals that have higher requirements for protein in their diet compared to terrestrial animals (including humans) and relatively low retention of protein and calories must be considered. Fed aquaculture requires more highly nutrient-dense feed than livestock production (i.e. higher in protein and calories), and results in a loss of most protein (81%) and calories (90%) during production. Animal products' contribution to calories in the human food supply is less critical compared to protein and some micronutrients, but understanding retention of calories in animal feed is important due to the massive reduction during animal production and the resulting impact on the overall supply of calories. In addition, relationships between feed requirements and affordability of final products should be explored. Feed costs make up more than 50% of production costs in aquaculture [29], and requirements for highly nutrient-dense feeds likely influence prices of some farmed seafood even though FCRs are low. Unfed aquaculture, including aquatic plants and certain shellfish, represents a critical opportunity to expand production of highly nutritious human food with no feed inputs.

Animal agriculture, including fed aquaculture, relies on increasing amounts of grains, cereals, oilcakes, and other staple crops for feed inputs as production expands [11, 30]. Arable land used to grow feed crops can compete with alternative land uses such as growing crops directly for human consumption, which provides a more efficient transfer of calories and protein [2, 31, 32]. While food security advocates may wish for a shift in land use towards edible crops, the financial calculus for farmers' crop planting decisions are tied to complex social, political, and economic forces that may be difficult to change. It is important to note that animals' diets can include human-indigestible forages or by-products not considered to be human-edible (e.g. distillers grains, bloodmeal), depending on the species and production method, which reduces competition for food between animal agriculture and humans. Efforts are underway to develop and scale-up production of insects as animal feed (and for human consumption), but insects are not presently a major component of feed.

Future research should explore potential implications and tradeoffs of increasing demand for aquaculture feed that is higher in protein and calories, as compared to livestock feed that is higher in starches. For example, crops that are high in starch have higher yields per hectare than crops high in protein due, in part, to the energy cost of nitrogen fixing for legumes [33]; average yields in tonnes per hectare for 2010–2014 were: maize 5.27, wheat 3.15, soy 2.50, and groundnuts 1.66 [34]. Soy and groundnuts are a significant source of protein in aquaculture feeds and demand for these ingredients is growing [11]. Therefore, global land requirements for feed production could expand more rapidly than current trends indicate and demand for nitrogen fertilizer could grow more slowly. Other topics for additional investigation include protein and calorie

retention in non-intensive production settings, strategies aquaculture producers can employ to improve protein and calorie retention, and retention of marine omega-3 fatty acids and micronutrients (e.g. iron) in farmed seafood. Current efforts to reduce FCRs in aquaculture and livestock production focus on genetic improvements through breeding and genetic engineering, development of nutritionally superior feeds and supplements, identification and implementation of improved husbandry practices including ideal environmental conditions for faster animal growth, and overcoming cost and other barriers to increase producer access to all of these developments. In addition to FCR, researchers should explore the impact of these changes on protein and calorie retention. For example, it is possible that providing feed higher in protein could result in a more efficient FCR but less efficient protein retention.

Our results reveal a different ranking in terms of efficiency of farmed animal species when measured by FCR versus protein and calorie retention. We do not argue, however, that retention measures should replace FCR as the major indicator of feed efficiency. Instead, the best path forward is to use multiple measures to compare efficiency of various types of food production, including animals and plants. Discussions of sustainable food systems should be informed by a combination of factors including FCRs and nutrient retention, and also environmental footprint measures including resource use (e.g. land, water, fertilizer), greenhouse gas emissions, and negative externalities including biodiversity loss and water pollution. To facilitate uptake of retention measures by researchers and other stakeholders, we provide our data sources and equations, which can be refined and applied to additional species, settings, and nutrients.

Growing evidence supports dietary shifts toward more efficient types of animal protein and plant-based foods [2, 4, 6, 7, 21]. In order to inform policy change and other interventions, there is a need to better understand the flow and loss of nutrients in the global food system, especially for fed aquaculture, and the implications for resource use and global food security. Our results show that protein and calorie retention in aquaculture varies by species, is lower than chickens, and similar to pig and cattle production, despite lower FCRs. This research demonstrates the importance of assessing animal production efficiency using multiple measures.

Acknowledgments

Support for J P F, N A M, D C L, and M C M was provided by the Johns Hopkins Center for a Livable Future (CLF) with a gift from the GRACE Communications Foundation. The authors thank Brent Kim, Roni Neff, Shawn McKenzie, Jim Yager, and Leo Horrigan at CLF for providing helpful feedback on the manuscript.

ORCID iDs

Jillian P Fry https://orcid.org/0000-0002-5836-9076
Nicholas A Mailloux https://orcid.org/0000-0002-4041-3665
David C Love https://orcid.org/0000-0002-2606-8623

References

[1] Rockström J *et al* 2009 A safe operating space for humanity *Nature* **461** 472–5
[2] Foley J A *et al* 2011 Solutions for a cultivated planet *Nature* **478** 337–42
[3] Tilman D *et al* 2011 Global food demand and the sustainable intensification of agriculture *Proc. Natl Acad. Sci. USA* **108** 20260–4
[4] Wirsenius S, Azar C and Berndes G 2010 How much land is needed for global food production under scenarios of dietary changes and livestock productivity increases in 2030? *Agric. Syst.* **103** 621–38
[5] Ran Y *et al* 2016 Assessing water resource use in livestock production: a review of methods *Livest. Sci.* **187** 68–79
[6] Tilman D and Clark M 2014 Global diets link environmental sustainability and human health *Nature* **515** 518–22
[7] Cassidy E S *et al* 2013 Redefining agricultural yields: from tonnes to people nourished per hectare *Environ. Res. Lett.* **8** 034015
[8] UN Food and Agriculture Organization 2016 *The State of World Fisheries and Aquaculture* (Rome: FAO) (Accessed: 9 November 2017) (www.fao.org/3/a-i5555e.pdf)
[9] United States Department of Agriculture 2017 *Livestock and Poultry: World Markets and Trade* (Accessed: 9 November 2017) (https://apps.fas.usda.gov/psdonline/circulars/livestock_poultry.pdf)
[10] Tacon A G J and Metian M 2015 Feed matters: satisfying the feed demand of aquaculture *Rev. Fish. Sci. Aquac.* **23** 1–10
[11] Fry J P *et al* 2016 Environmental health impacts of feeding crops to farmed fish *Environ. Int.* **91** 201–14
[12] Tacon A G J and Metian M 2008 Global overview on the use of fish meal and fish oil in industrially compounded aquafeeds: trends and future prospects *Aquaculture* **285** 146–58
[13] Smil V 2013 Should we eat meat? *Evolution and Consequences of Modern Carnivory* (Chichester: Wiley-Blackwell)
[14] Shike D W 2013 *Beef Cattle Feed Efficiency* (Accessed: 2 November 2017) (http://lib.dr.iastate.edu/cgi/viewcontent.cgi?article=1027&context=driftlessconference)
[15] Zuidhof M J *et al* 2014 Growth, efficiency, and yield of commercial broilers from 1957, 1978, and 2005 *Poult. Sci.* **93** 2970–82
[16] Rabobank Food and Agribusiness Research 2015 *Pigs Might Fly: Peak Pork Production Potential* (Accessed: 2 November 2017) (https://research.rabobank.com/far/en/sectors/farm-inputs/Pigs_Might_Fly.html)
[17] Naylor R L *et al* 2009 Feeding aquaculture in an era of finite resources *Proc. Natl Acad. Sci. USA* **106** 15103–10
[18] Torrissen O *et al* 2011 Atlantic Salmon (*Salmo salar*): the 'super-chicken' of the Sea? *Rev. Fish. Sci.* **19** 257–78
[19] Béné C *et al* 2005 Feeding 9 billion by 2050—putting fish back on the menu *Food Secur.* **7** 261–74
[20] High Level Panel of Experts (HLPE) on Food Security and Nutrition 2014 *Sustainable Fisheries and Aquaculture for Food Security and Nutrition* (Rome: FAO) (Accessed: 24 January 2017) (www.fao.org/3/a-i3844e.pdf)
[21] Shepon A *et al* 2016 Energy and protein feed-to-food conversion efficiencies in the US and potential food security gains from dietary changes *Environ. Res. Lett.* **11** 105002

[22] Ytrestøyl T, Aas T S and Åsgård T 2015 Utilisation of feed resources in production of Atlantic salmon (*Salmo salar*) in Norway *Aquaculture* **448** 365–74

[23] Smil V 2002 Nitrogen and food production: proteins for human diets *Ambio* **31** 126–31

[24] Hall S *et al* 2011 *Blue Frontiers: Managing the Environmental Costs of Aquaculture* (Penang: FAO) (Accessed: 3 February 2017) (www.conservation.org/publications/documents/BlueFrontiers_aquaculture_report.pdf)

[25] FAO, 2017 Fishery Statistical Collections 2017 (www.fao.org/fishery/statistics/global-production/en)

[26] US Department of Agriculture Economic Research Service 2016 Livestock and Meat Domestic Data (Accessed: 25 January 2017) (www.ers.usda.gov/data-products/livestock-meat-domestic-data/livestockmeat-domestic-data/#All-meat-statistics)

[27] USDA National Agricultural Library 2016 National Nutrient Database for Standard Reference Release 28 (https://ndb.nal.usda.gov)

[28] Seafood Health Facts Pangasius (www.seafoodhealthfacts.org/description-top-commercial-seafood-items/pangasius)

[29] Rana K J, Siriwardena S and Hasan M R 2009 *Impact of Rising Feed Ingredient Prices on Aquafeeds and Aquaculture Production* (Rome: FAO) (Accessed: 25 May 2017) (www.fao.org/docrep/012/i1143e/i1143e00.htm)

[30] Alexandratos N and Bruinsma J 2012 *World agriculture towards 2030/2050: The 2012 revision 12-3* (Rome: FAO) (Accessed: 29 June 2016) (www.fao.org/economic/esa)

[31] Gephart J A *et al* 2016 The environmental cost of subsistence: optimizing diets to minimize footprints *Sci. Total Environ.* **553** 120–7

[32] Davis K *et al* 2016 Meeting future food demand with current agricultural resources *Glob. Environ. Change* **39** 125–32

[33] Bues A *et al* 2013 *The Environmental Role of Protein Crops in the New Common Agricultural Policy* (Brussels: European Union) (Accessed: 17 May 2017) (www.europarl.europa.eu/RegData/etudes/etudes/join/2013/495856/IPOL-AGRI_ET(2013)495856_EN.pdf)

[34] OECD-FAO 2016 *Agricultural Outlook 2016–2025* (Paris: OECD Publishing) (http://stats.oecd.org/index.aspx?queryid=71240)