Aquaculture will continue to depend more on land than sea

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Aquaculture is a major producer of aquatic foods, contributing substantially to global food and nutrition security, and is likely to expand further in response to increasing demand from an increasingly populous and affluent world[1,2]. Projections by Costello and colleagues suggest high growth potential for marine aquaculture (mariculture), alongside a relatively marginal increase in freshwater aquaculture[3]. We contend that these projections inflate the growth potential of mariculture and undervalue the present and future roles of freshwater aquaculture[1,2,4,5](Fig. 1, Supplementary Figs. 1-3). Balanced approaches to science, policy, and investment that prioritize freshwater aquaculture development in addition to mariculture can contribute more to global food security than those favouring mariculture alone.

Costello et al. (2020) overestimate current mariculture production and future production potential, while underestimating freshwater aquaculture production and potential in six ways. These include: (1) defining brackishwater aquaculture as part of mariculture; (2) excluding crustaceans from their model; (3) conflating freshwater capture fisheries and freshwater aquaculture production; (4) making projections of marine bivalve production that are inconsistent with historical trends; (5) making over-optimistic assumptions about marine finfish farming technologies; and (6) not accounting for high potential to raise freshwater aquaculture yields through intensification (see Supplementary Information Section 1 for full details).

Costello et al. (2020) and a rapidly growing body of high-profile science and policy literature overemphasize the importance and potential of mariculture[4]. Mariculture dominates peer-reviewed publications related to aquaculture policy (Fig. 1), whereas freshwater aquaculture currently accounts for 77% of edible aquaculture production globally (excluding aquatic plants). Freshwater aquaculture has provided 80% of total fed finfish (finfish raised using external feed inputs) production since 2000 (Supplementary Fig. 5). Production of extractive freshwater species (filter-feeding finfish) is much greater than production of extractive marine species (bivalves) in terms of quantities of edible food produced (Supplementary Fig. 6). Crustaceans are farmed in brackishwater and, increasingly, in freshwater, but very rarely in seawater (Supplementary Fig. 7).

Perceptions of high growth potential for mariculture are based on the assumption that the oceans offer vast areas for farm expansion while potential for freshwater aquaculture growth is heavily constrained by the availability of land and freshwater[3,7]. In fact, land and freshwater limitations constitute a challenge for both fed mariculture and freshwater aquaculture as both depend on land and freshwater resources for production of feed inputs[8].

The land and freshwater footprints of feed production are greater than direct land and freshwater use in finfish grow-out, including for freshwater pond farms[9–11]. Agricultural products such as soy are increasingly incorporated into the diets of fed mariculture species to reduce reliance on wild fish; this has resulted in many fed mariculture species having similar land and water footprints to freshwater species[11,12]. For example, the area of land used for agriculture to supply feed ingredients for the Norwegian salmon industry was 0.36 ha tonne^{-1} salmon or 0.44 million ha in total in 2016, which is 10 times greater than the area used by salmon farms at sea (Supplementary Table 2). Fed mariculture and freshwater aquaculture often have similar impacts on climate, land use, nutrient discharge, and biodiversity, as feed use is the leading driver behind these impacts[8,12]. Increased connections between sea-based production and land are not inherently negative, but need to be accounted for in sustainability analysis[8].

Aquaculture development is driven by both intensification and horizontal expansion. Potential to expand freshwater aquaculture by converting agricultural land to fish ponds, and to raise freshwater pond yields by intensification are substantial[5]. Moreover, most freshwater aquaculture occurs in major river basins in Asia where freshwater is comparatively abundant, so generalized models of global water availability can be misleading (Supplementary Fig. 8).

Freshwater finfish culture dominates global aquaculture production partly because the major species farmed (carps, catfish, and tilapias) are omnivorous or herbivorous (Fig. 2) and require relatively low levels of protein and expensive fishmeal/fish oil in feeds. The major farmed freshwater finfish species are simple to breed, and their high tolerance of low dissolved oxygen levels and accumulation of nutrients makes them easy to farm using relatively low-cost basic technologies. Consequently, much farmed freshwater finfish is mass-produced, available and accessible to low- and middle-income consumers, and makes an important but underappreciated contribution to global food and nutrition security[13]. Aquatic food consumption per capita in the Global South grew substantially from 5.2 kg in 1961 to 19.4 kg in 2017[2]. Since the 1990s, this growth has been mainly driven by freshwater aquaculture. It is projected that the highest future growth of aquatic food consumption will be seen in Global South countries experiencing the highest rates of population growth (especially in Africa), rapid aquaculture expansion (especially in Asia), rapid urbanization, and economic development[2]. Thus, developing low-cost freshwater aquaculture could better match future demand for aquatic foods at the global scale.

In contrast, only a small number of high-income countries and China are major producers of marine finfish, the most important of which are salmonids[2]. Most farmed marine finfish are expensive carnivorous species and, apart from salmon, are produced at low volumes relative to major farmed freshwater finfish. These fish are more reliant on quality protein and fishmeal/fish oil in feeds, or are fed on unprocessed low-value “trash fish”[14]. Farmed marine fish often have high concentrations of polyunsaturated fatty acids resulting from high-quality fish diets, but high feed costs and large fixed costs associated with infrastructure investments, especially for off-shore farms, make them unaffordable for most consumers worldwide[4]. Meanwhile, per capita aquatic food consumption has plateaued at around 25kg capita^{-1} in high-income countries in the Global North since 2000, with a heavy dependence on aquatic food imports from the Global South, including farmed freshwater species such as tilapia and pangasius[2,6].

Availability of space for farming is often not the primary determinant of aquaculture development potential[9,15]. Realizing the apparently high potential of mariculture inferred from available ocean space will be challenging due to biological, economic, environmental, and social constraints[4]. Finfish mariculture produces high-value food mainly to meet diversified demand from wealthier consumers globally, and has potential to grow further as the global middle class expands. Marine bivalves and seaweeds are attractive from environmental, resource use and nutritional perspectives, but they have far more limited markets than finfish. Conversely, freshwater aquaculture already makes major contributions to global food security, providing an affordable, accessible, and stable supply of aquatic food to vast numbers of consumers, particularly in the Global South. Freshwater aquaculture is no more resource-constrained than fed mariculture, and can continue to grow through horizontal expansion, intensification, and more efficient resource use. Greater investment in research on key freshwater species and farming systems is necessary to deliver much-needed increases in global aquatic food production and nutrition security, benefiting a broad set of producers and consumers.

Data availability

Secondary data were obtained from several sources: FAO statistics (www.fao.org/fishery/statistics/software/fishstatj/en), Fishbase (www.fishbase.org), and Web of Science (www.webofscience.com/). All data analysed in this study are either included in the Supplementary Information or available on GitHub (https://github.com/AquacultureFuture/LandAndSea).

References

1. Edwards, P., Zhang, W., Belton, B. & Little, D. C. Misunderstandings, myths and mantras in aquaculture: Its contribution to world food supplies has been systematically over reported. *Mar. Policy* **106**, 1–9 (2019).
2. FAO. *The State of World Fisheries and Aquaculture 2020. Sustainability in action.* (2020).
3. Costello, C. *et al.* The future of food from the sea. *Nature* (2020). doi:10.1038/s41586-020-2616-y
4. Belton, B. *et al.* Farming fish in the sea will not nourish the world. *Nat. Commun.* **11**, 1–28 (2020).
5. Edwards, P. Aquaculture environment interactions: Past, present and likely future trends. *Aquaculture* **447**, 2–14 (2015).
6. FAO. Fishery and Aquaculture Statistics. (2021).
7. Gentry, R. R. *et al.* Mapping the global potential for marine aquaculture. *Nat. Ecol. Evol.* **1**, 1317–1324 (2017).
8. Cottrell, R. S. *et al.* Considering land–sea interactions and trade-offs for food and biodiversity. *Glob. Chang. Biol.* **24**, 580–596 (2018).
9. Troell, M., Jonell, M. & Henriksson, P. J. G. Ocean space for seafood. *Nat. Ecol. Evol.* **1**, 1224–1225 (2017).
10. Pahlow, M., van Oel, P. R., Mekonnen, M. M. & Hoekstra, A. Y. Increasing pressure on freshwater resources due to terrestrial feed ingredients for aquaculture production. *Sci. Total Environ.* **536**, 847–857 (2015).
11. Gephart, J. A. *et al.* The 'seafood gap' in the food-water nexus literature—issues surrounding freshwater use in seafood production chains. *Adv. Water Resour.* **110**, 505–514 (2017).
12. Gephart, J. A. *et al.* Environmental performance of blue foods. *Nature* **597**, 360–365 (2021).
13. Belton, B., Bush, S. R. & Little, D. C. Not just for the wealthy: Rethinking farmed fish consumption in the Global South. *Glob. Food Sec.* **16**, 85–92 (2018).
14. Zhang, W. *et al.* Fishing for feed in China: Facts, impacts and implications. *Fish Fish.* **21**, 47–62 (2020).
15. Oyinlola, M. A., Reygondeau, G., Wabnitz, C. C. C., Troell, M. & Cheung, W. W. L. Global estimation of areas with suitable environmental conditions for mariculture species. *PLoS One* 1–19 (2018). doi:10.1371/journal.pone.0191086

Fig. 1: Aquaculture and capture fisheries production, and publications related to aquaculture policy. (a) Live-weight production (1950-2019). **(b)** Edible weight production (1950-2019). **(c)** Number of publications on aquaculture policy recorded in the Web of Science database (1990-2020). Conversion factors from live-weight to edible food equivalent production can be found in ref.[1] and ref.[3]. Data source: ref.[6]. Aquatic plants, mammals and 18% marine capture production used for non-food purposes[3] were excluded from analysis. See Supplementary Table 1 for search query sets used for publications related to aquaculture policy and Supplementary Fig. 4 for countries of origin of authors and funding.

Fig. 2: Production, price, natural trophic level (TL), and the correlation between TL and $\log_{10}$-transformed price of the top 20 brackishwater, marine, and freshwater finfish species. (a) Production. **(b)** Price. **(c)** TL. **(d)** Correlation between TL and $\log_{10}$-transformed price. Blue represents freshwater species, yellow brackishwater species, and red marine species. For the boxplots, the centre line indicates the median, "x" indicates the mean, the box limits indicate the first and third quartiles, and the whiskers indicate the data range. The bubble size of each data point in **d** represents the production volume. The dashed blue line in **d** is a linear fitted line. Natural TL are from Fishbase and reflect species' diets in nature. See Supplementary Table 3 for a detailed dataset.

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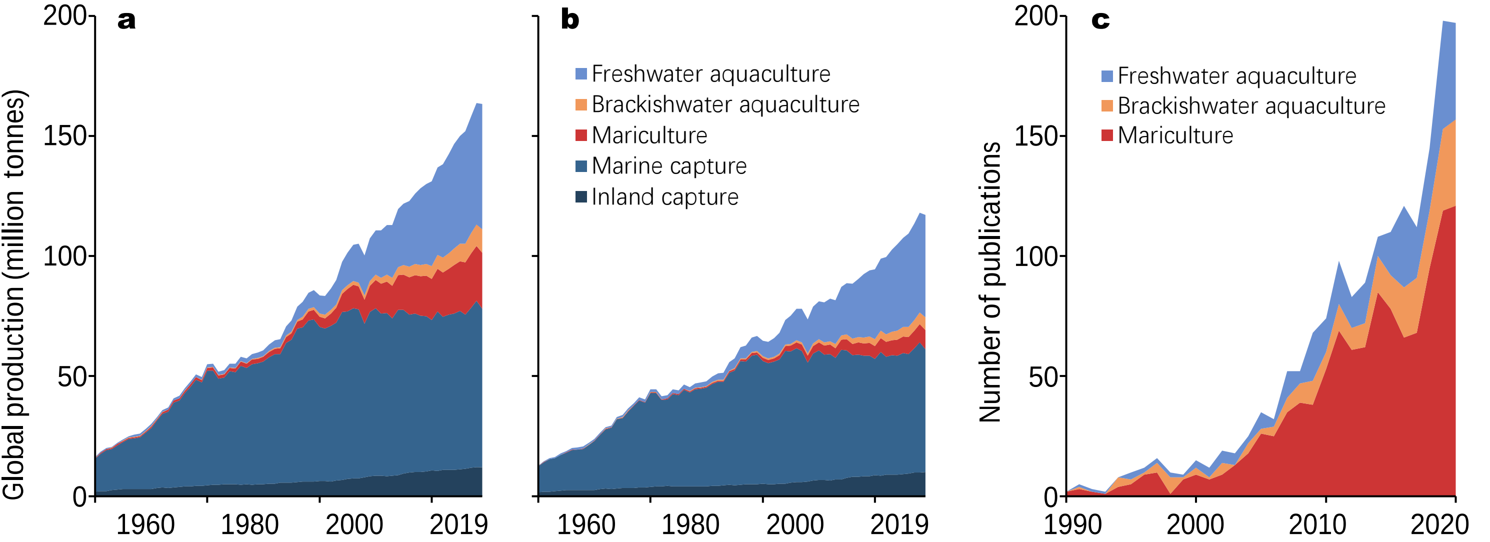
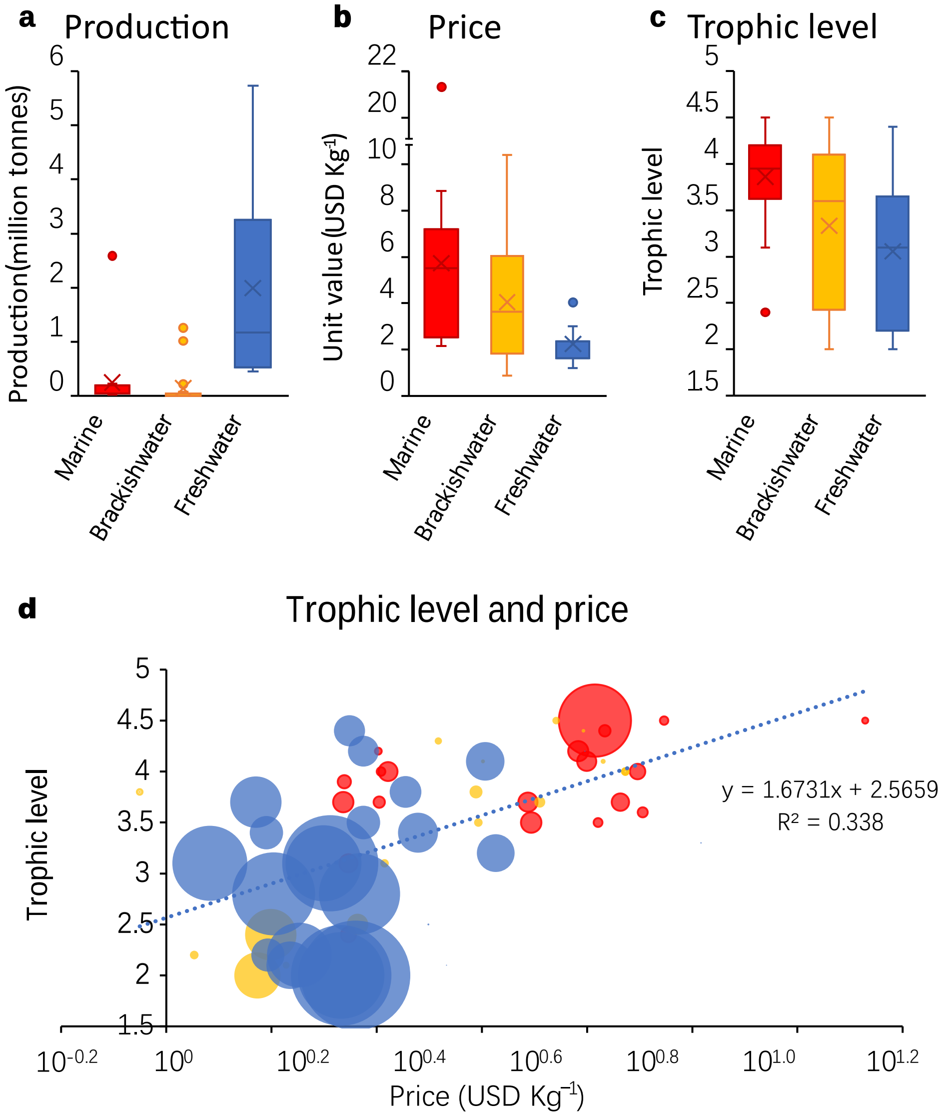
Competing interests: W.Z. is a member of the BAP Committee on Climate Action. He has no affiliation with any for-profit company. B.B. has no competing interests. P.E. is an Emeritus Professor with no commercial interests. P.J.G.H. is a member of the BAP Committee on Climate Action and scientific advisor for SeaBOS. D.C.L. has received in-kind and financial support from a wide range of commercial and non-commercial entities, serves as a committee member for standards organizations and is a director of a commercial tilapia hatchery in Thailand. R.N. is the Chair of the BAP Committee on Climate Action. M.T. is a member of the Program Committee for The Marine and Coastal Science for Management (WIOMSA/MASMA), member of Action Areas and Solution Clusters Working Groups – Blue foods, United Nations Forum on Sustainability Standards (UNFSS), scientific lead for SeaBOS, and a Review Editor for Aquaculture Environment Interactions.


a
b
c
Global production (million tonnes)
Number of publications
Freshwater aquaculture
Brackishwater aquaculture
Mariculture
Marine capture
Inland capture
0
50
100
150
200
1960
1980
2000
2019
1990
2010
2020



a
Production
Production(million tonnes)
0
1
2
3
4
5
6
Marine
Brackishwater
Freshwater
b
Price
Unit value(USD Kg-1)
0
2
4
6
8
10
20
22
Marine
Brackishwater
Freshwater
c
Trophic level
Trophic level
1.5
2
2.5
3
3.5
4
4.5
5
Marine
Brackishwater
Freshwater
d
Trophic level and price
Trophic level
1.5
2
2.5
3
3.5
4
4.5
5
y = 1.6731x + 2.5659
R² = 0.338
10-0.2
100
100.2
100.4
100.6
100.8
101.0
101.2
Price (USD Kg-1)

Supplementary Information for

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This document contains Section 1, Fig. S1-S12, and Table S1-S3

Section 1: We contend that the model used by Costello et al. (2020)[1] overestimated current mariculture production and future production potential, and underestimated freshwater aquaculture production and potential in six ways.

1. Brackishwater aquaculture defined as mariculture

The Food and Agriculture Organization of the United Nations (FAO) categorizes aquaculture according to farming environment as marine (mariculture), brackishwater, and freshwater. Mariculture is defined as '*conducted in the sea, in a marine water environment*'; brackishwater aquaculture, or coastal aquaculture, as '*practiced in completely or partially artificial structures in areas adjacent to the sea, such as coastal ponds and gated lagoons*'; while freshwater aquaculture, or inland aquaculture, is aquaculture that '*produces most farmed aquatic animals, mainly in freshwater*'[2].

In the present study, we followed FAO's definitions and data, as reported in the FAO FishstatJ database (Aquaculture Production (Quantities and values) 1950-2019, Release date: March 2021), which categorizes aquaculture as mariculture, brackishwater aquaculture, or freshwater aquaculture. Excluding aquatic plants, mariculture accounts for 14% of farmed edible aquatic food from aquaculture in 2019, brackishwater aquaculture accounts for 9%, and freshwater aquaculture accounts for 77% (Fig. 1 in the main text).

In Costello et al. (2020), mariculture and brackishwater aquaculture were aggregated as mariculture. Thus, mariculture production and potential were overestimated. Moreover, Costello et al. (2020) selected Atlantic salmon (*Salmo salar*), milkfish (*Chanos chanos*), and barramundi (*Lates calcarifer*) to represent mariculture finfish in their model, but salmon, milkfish, and barramundi are all euryhaline species, and milkfish and barramundi are farmed mainly in land-based brackishwater ponds (Fig. S9).

2. Crustacean farming not included in the model

Crustacean farming was excluded from the model developed by Costello et al. (2020). This is an important omission. Crustacean production is one of the fastest-growing sub-sectors of aquaculture globally. Farmed crustaceans account for 11% of global aquaculture production (live weight), about 7% edible weight in 2019[3]. Almost all global crustacean aquaculture production occurs in brackishwater and freshwater pond systems. Mariculture contributed less than 0.01% of farmed crustacean production in 2019 (Fig. S7). Crustacean production from freshwater has grown faster than production in brackishwater in recent two decades, due mainly to the rapid expansion of crawfish (*Procambarus clarkii*), mitten crab (*Eriocheir sinensis*), and whiteleg shrimp (*Litopenaeus vannamei*) farming in freshwater in China[3]. Excluding crustaceans from the model biases the apparent current and projected contribution of mariculture to global aquatic food supply upward.

3. Aggregated reporting of freshwater capture fisheries and freshwater aquaculture

Projections by Costello et al. (2020) combine production from freshwater aquaculture and freshwater capture fisheries under the category 'freshwater fisheries'. However, freshwater aquaculture dominates freshwater aquatic food production and holds far greater potential to expand in future than freshwater capture fisheries. The share of freshwater aquaculture in 'freshwater fisheries' increased from 11.8% in 1950 to 68.3% in 2000 and then to 81.2% in 2019. This trend is likely to continue (Fig. S10). Analysis of global household consumption surveys has shown that freshwater capture fisheries landings may be underreported by 65%[4]. However, after correcting for possible underreporting, freshwater aquaculture would have supplied 72.4% of freshwater fisheries production in 2019. Because freshwater capture fisheries are growing much more slowly than freshwater aquaculture and have much less scope to expand, aggregating them under the heading 'freshwater fisheries' lowers the growth rate of freshwater aquatic food production as compared to freshwater aquaculture alone.

4. Projections of marine bivalve production inconsistent with historical trends

Marine bivalves are filter feeders, deriving nutrients from plankton and organic matter in the water column. Their production was seen by Costello et al. (2020) as unconstrained by feed or space limitations, thus having the greatest potential for increased production and contributions to the future supply of food from the sea[1]. The projected share of bivalve mariculture in marine food production increased from the current 5% (2.86 million tonnes (Mt) in 2017) to 6% (3.85 Mt, current demand scenario), 11% (9.07 Mt, future demand scenario), and 17% (17.61 Mt, extreme demand scenario) by 2050[1].

However, FAO statistics show that the share of non-fed aquaculture (excluding aquatic plants but including both marine molluscs and freshwater filter-feeding finfish) in total aquaculture production (live-weight) declined from 43.9% in 2000 to 30.5% in 2018[2], because growth of aquatic food production has been driven predominantly by intensification of the fed-aquaculture[2,5–7]. Molluscs production (98% of which is comprised of filter-feeding bivalves) has grown in absolute terms, but the share of molluscs in global aquaculture (excluding aquatic plants) has declined steadily, from 46.5% by live-weight production (14.5% by edible-food production) in 1950 to 30% live-weight (8.1% edible-food) in 2000, and 20.6% live-weight (5.3% edible-food) in 2019 (Fig. S2). The share of molluscs in mariculture production (excluding aquatic plants) has also fallen consistently, from 90.1% by live-weight production (65.1% by edible-food production) in 1980 to 82.0% live-weight (48.1% edible-food) in 2000, and 74.1% live-weight (36.9% edible-food) in 2019[3].

There is potential for mollusc farming to grow, but the activity also faces challenges that are overlooked by Costello et al. (2020). Limited demand for bivalves in most markets, poor water quality linked to coastal pollution, and future ocean acidification may constraint sectoral expansion[8–10]. Although there are ongoing efforts to expand mussel farming to the open sea in Europe (e.g., https://offshoreshellfish.com/) and New Zealand, production costs are still relatively high, and output is limited and mainly supplies niche premium markets.

Filter-feeding freshwater finfish such as silver carp (*Hypophthalmichthys molitrix*) and bighead carp (*Hypophthalmichthys nobilis*) are produced mainly without external feed inputs. Rohu (*Labeo rohita*) and catla (*Gibelion catla*) are also filter feeders mostly raised in fertilized ponds but also consume supplementary feeds. These species make a much larger contribution to total aquatic production than marine molluscs, as measured in terms of edible food (Fig. S6). Freshwater filter-feeding finfish are among the most affordable and popular aquatic food items in China[11] and some other Asian countries such as India and Myanmar. Moreover, freshwater finfish (mainly filter-feeding silver carp) is increasingly used as a raw material to produce surimi and other processed fish products, as a substitute for fish sourced from marine capture fisheries. Silver carp-based surimi production in China increased from 15,000 mt in 2011 to over 100,000 mt in 2018[12–14]. The amount produced in 2018 would have required 400,000 mt of farmed silver carp as raw material, equivalent to more than 10% of China's total silver carp production.

5. Optimistic assumptions about marine finfish farming technology

The share of fed finfish production originating from freshwater aquaculture has been stable at around 80% of total fed finfish production since the late 1990s, while the share of fed finfish production originating from mariculture has been stable at around 13% since 2000 (Fig. S5). However, Costello et al. (2020) projected finfish mariculture production to increase from 6.77 Mt in 2017 to 7.67 Mt (current demand scenario), 13.98 Mt (future demand scenario), or 27.94 Mt (extreme demand scenario) by 2050. The latter two scenarios equate to the share of finfish mariculture in total aquaculture increasing by 3% and 6%, respectively (total aquaculture production used here was calculated as finfish marine + bivalve marine + inland fisheries using data in Table S13 in Costello et al. (2020)). The latter two growth scenarios are underpinned by several optimistic supply-side assumptions about marine finfish aquaculture technology.

The type of marine finfish farming depicted in Costello's analysis was based on large circular fish cages of 9,000 m^3 volume per cage that are 80 m in circumference, 25.5 m in diameter, and 17.7 m in depth. Such large-sized marine cages require very high levels of investment and operating costs and are suitable for production in more exposed marine environments. They are used mainly for farming high-value marine finfish species such as Atlantic salmon in the Global North and increasingly being adopted by finfish mariculture in China for high-value species such as large yellow croaker (*Larimichthys crocea*) and pompano (*Trachinotus blochii*).

Costello et al. (2020) suggested that seas with waters ≤200 m deep were suitable for mariculture and assumed that all marine finfish culture would occur in large-sized marine finfish cages in exposed marine environments. However, even when equipped with large-sized marine cages, most existing mariculture operations in the open sea area are located in shallow subtidal zones close to land (11-100 m, 71% farms ≤30 m) to minimize operating costs[15] and limit exposure to harsh weather conditions and high waves[16]. Marine cages are best suited for deployment in deep fjords and lochs that offer a balance between providing shelter from extreme weather and using tidal flows to flush the systems and maintain water quality. Such locations are quite scarce globally. Climate change is expected to result in rising sea levels, water temperature increases, higher ocean acidity, changes in salinity, and increase of frequency and strength of severe weather[17], making site selection of marine cages increasingly difficult.

In the Global South, traditional small square cages are much more widely used in finfish mariculture than large cages of the type described above. For example, in China, the largest mariculture producing country, small nearshore cages produced 0.55 Mt finfish in 2019, while large-sized cages produced 0.21 Mt[18]. Traditional small-sized square cages have three dimensions between 3-8 m with 27-512 m^3 volume per cage, and are mainly constructed by farmers using low-cost locally sourced materials[19]. Cages of this type cannot withstand strong water currents and are mostly located in shallow inshore waters and sheltered sites. Replacing small cages with large ones and expanding to deeper and more exposed waters would require higher investment in infrastructure and better management skills, which are unlikely to be economically viable or technically feasible for most small-scale farmers in the Global South.

Costello et al. (2020) used Atlantic salmon farming as a success story to demonstrate the feasibility of reducing the dependence of marine finfish culture on fish-based ingredients to overcome feed limitations. However, Atlantic salmon farming has received massive investment in selective breeding and research on fish nutrition. Moreover, salmon are cold-water finfish with a low metabolic rate. These factors make salmon uniquely efficient compared with other farmed species[9,20]. Atlantic salmon is the most important mariculture finfish species, accounting for 46% of finfish mariculture production. In contrast, warmwater mariculture and freshwater aquaculture in the Global South are highly diversified, with hundreds of species and varied farming systems. Most of these species and production systems have received little R&D investment, and utilize fish- and crop-based feed resources less efficiently than Atlantic salmon. For example, many common mariculture species such as large yellow croaker and groupers are still fed mainly on low-value/trash fish[21,22], making it challenging to scale up production, and posing serious sustainability problems. Selective breeding programmes for GIFT strain tilapia in freshwater and selective breeding and nutritional research on whiteleg shrimp in brackishwater have delivered significant performance gains that partly explain the massive growth of these species compared to many others that have yet to receive such basic R&D.

Fishmeal and fish oil are considered to be the most nutritious and digestible ingredients for farmed fish, and their availability is a major constraint for both marine and freshwater fed aquaculture growth[2,9,23]. Replacement of fishmeal with crop-based alternatives is much easier to achieve with major freshwater aquaculture species than marine aquaculture species[24,25]. We anticipate that this factor will favour faster production growth for farmed freshwater finfish species than marine finfish, if fishmeal availability decreases globally while global aquaculture continues to expand[2].

Technological advances in feeds and utilization of novel feed ingredients [24] such as aquatic food processing wastes, microbial ingredients, insects, algae, and genetically modified plants are often cited as having potential to improve the performance of mariculture. However, if realized, these advances could also benefit freshwater aquaculture, so they cannot necessarily be expected to confer a comparative advantage only to marine finfish farming.

Costello et al. (2020) contend that developing land-based aquaculture may “exacerbate climate change and biodiversity loss, and compromise the delivery of other ecosystem services”. However, Life Cycle Assessment (LCA) studies show that fed species raised in mariculture and freshwater aquaculture often have similar impacts on climate change and delivery of ecosystem services such as the release of Greenhouse Gas and nutrients, acidification, biotic depletion, and energy use[26–30]. This is because fed freshwater and marine aquaculture both depend on feeds, which account for more than 90% of the environmental impacts of fed aquaculture production[25,30].

Aquaculture can cause biodiversity loss in several ways, including resource consumption, land modification, and waste generation, introduction of invasive species, habitat loss, pollution, and overfishing to produce fishmeal[31–33]. One of the most important impacts of aquaculture on biodiversity is using low-value/trash fish from non-targeted fisheries for feed, which is also closely linked to overfishing and seabed damage[25,34]. For example, around one-third of the Chinese domestic marine capture fisheries production was low-value fish, of which 89% juveniles, used mainly in aquaculture feeds[21,22,25]. Major mariculture finfish species have higher natural trophic levels on average than freshwater aquaculture finfish species and thus require inclusion of marine ingredients in diets[35], or are fed mainly on trash fish[21,22], causing more impact on wild fish populations and marine ecosystems than freshwater aquaculture.

Use of plant-based ingredients in aquaculture feed can also impact biodiversity. Agricultural products such as soy are increasingly incorporated into the diets of fed mariculture species to reduce reliance on wild fish as a protein source. Demand for soy has resulted in land clearance and tropical deforestation, especially in the Amazon, and an increasing trend in ecotoxicity from fertilizer and pesticide use[25]. Freshwater aquaculture species such as carp, catfish and tilapia use more plant-based ingredients in the feed than mariculture species, but mariculture species require higher crude protein levels in feed and usually need high-quality plant-based protein ingredients. In contrast, plant-based ingredients for freshwater aquaculture species are more diversified, mainly agricultural by-products such as brans and oil cakes[8,36,37]. Moreover, there are widely reported impacts on biodiversity by both mariculture and freshwater aquaculture through fish escapes, disease and parasite transmission[38–42].

Although further studies are needed for quantitative comparisons of the impact on biodiversity between mariculture and freshwater aquaculture, current evidence shows that fed species from mariculture do not perform better than fed freshwater aquaculture on climate, biodiversity, and other ecosystem services.

6. Potential for intensification and spatial expansion of freshwater aquaculture

It has been suggested that the most successful mariculture countries such as Chile, China, and Norway are not among the countries with the highest biological growth potential and most suitable sea areas to develop mariculture[43,44]. However, there has been no reduction in freshwater aquaculture's contribution to total production among most of the top ten aquaculture producing countries since 2000 (Fig. S11), including in countries deemed highly biophysically suited for mariculture such as Indonesia[1,43].

Freshwater aquaculture takes place in natural lakes and rivers, reservoirs and irrigation canals, and in diverse culture facilities including ponds, rice fields, cages, tanks, Recirculating Aquaculture Systems (RAS), split-ponds, and in-pond raceways. Freshwater aquaculture growth is made possible by both horizontal expansion and intensification. Converting rice fields to fishponds is often attractive to farmers because the potential financial returns are generally higher than those from most terrestrial plant crops.

Intensification is now the major driver of increases in aquaculture production. The real production cost and retail value of the key freshwater aquaculture species have declined steadily over the last two decades in response to efficiency gains and intense competition. For example, average pond aquaculture yields in China increased from less than 1 mt ha^{-1} in 1980 to 4.9 mt ha^{-1} in 2000 and then to 8.3 mt ha^{-1} in 2018[18,45], and still have much potential to increase further. Some farming systems and areas have much higher yields than others. For example, in southern China, yields of farmed snakehead (*Channa argus*) and largemouth black bass (*Micropterus salmoides*) average around 150 mt ha^{-1} and 60 mt ha^{-1}, respectively, whereas in middle and eastern China, yields for these species average 30-50 mt ha^{-1} and 15 mt ha^{-1} [46]. These yield gaps are mainly due to differences in farming techniques and climate, but improved techniques such as low-cost plastic-covered tunnels could greatly increase productivity in middle and eastern China.

Extremely high land-use efficiencies are possible. For example, in Vietnam 1 Mt of pangasius (*Pangasianodon hypophthalmus*) is produced in 6,000 ha of ponds (166 mt ha^{-1}), equivalent to only 0.08% of the total national area of 7.4 million ha of rice fields. In Bangladesh, 0.3 Mt of pangasius is produced from 7,400 ha of ponds (41 mt ha^{-1}), equivalent to 0.06% of the total national area of 12 million ha of rice fields. Conversion of rice fields to fish ponds thus appears to be a 'non-issue' in both cases, as massive fish production is obtained from less than 0.1% of the national rice fields area in both countries[6]. Even in the largest aquaculture producing country, China, aquaculture ponds only occupy 2% of national arable land. These ponds generate a higher average yield and value of edible biomass per hectare than terrestrial plant crops[18,47].

Large yield gaps in freshwater aquaculture within China, and between China and most other countries (Fig. S12), indicate great potential to further increase freshwater aquaculture output from existing farm areas in those countries.

There is a recent shift towards constructing large-scale, closed, indoor, super-intensive, land-based RAS[6]. For example, Atlantic salmon, the most important finfish mariculture species, is increasingly farmed in land-based RAS in Europe and the USA[6,48,49]. This reduces environmental impacts on coastal waters and also reduce other potential negative effects e.g. sea lice infestations. However, salmon RAS have high energy demands, and are dependent on high-quality feeds in the same way as cage farming. RAS provide additional potential for land-based aquaculture production growth, including production of marine fish species, though the high infrastructure and operating costs currently limit widespread uptake[9,48,49].

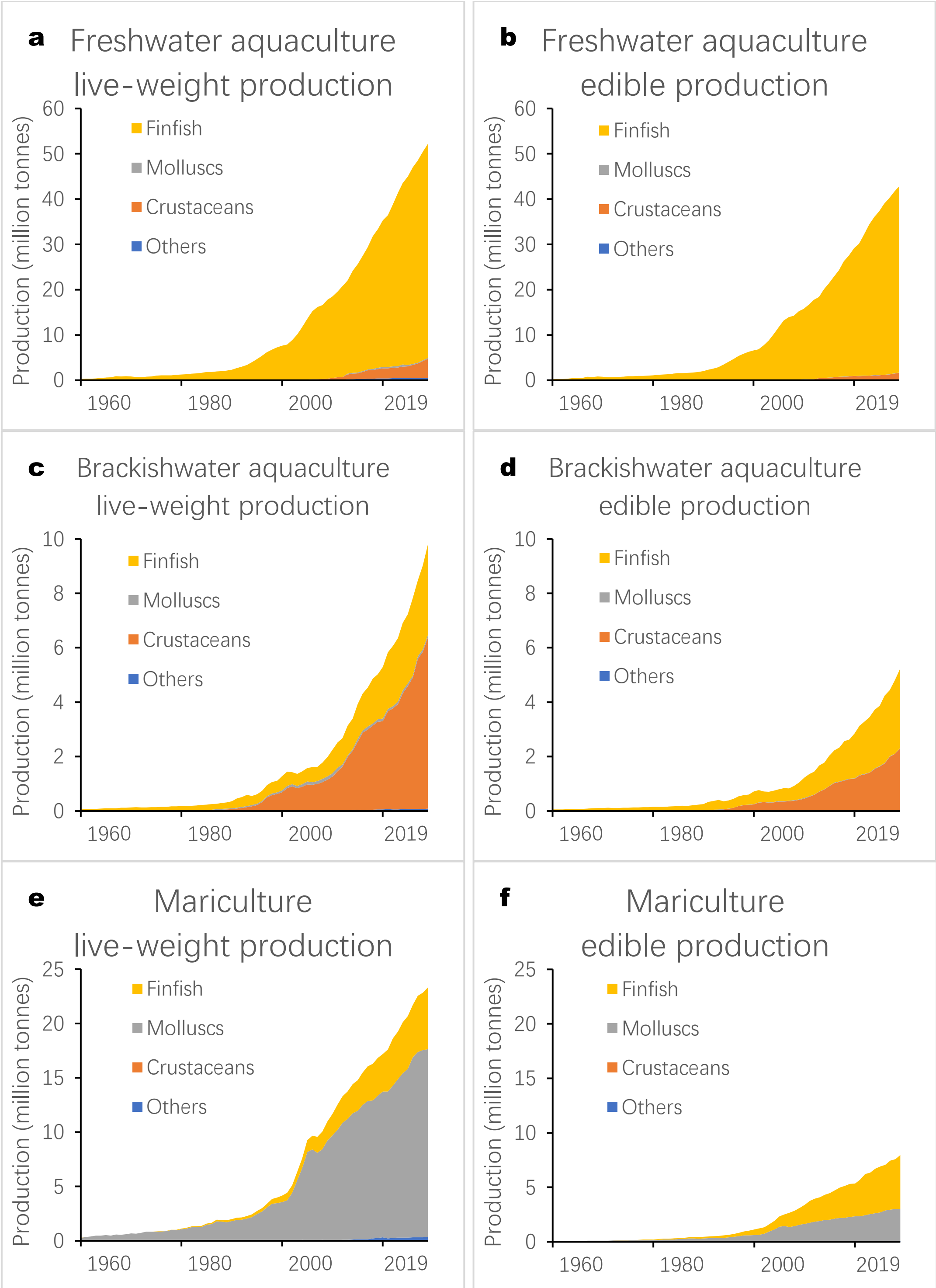

Fig. S1: Live weight and edible production from freshwater aquaculture, brackishwater aquaculture and mariculture. (a) Live-weight production from freshwater aquaculture. **(b)** Edible production from freshwater aquaculture. **(c)** Live-weight production from brackishwater aquaculture. **(d)** Edible production from brackishwater aquaculture. **(e)** Live-weight production from mariculture. **(f)** Edible production from mariculture. Conversion factors from live weight to edible food can be found in ref.[1,50]. Aquatic plants were excluded from analysis. Data source: ref.[3].

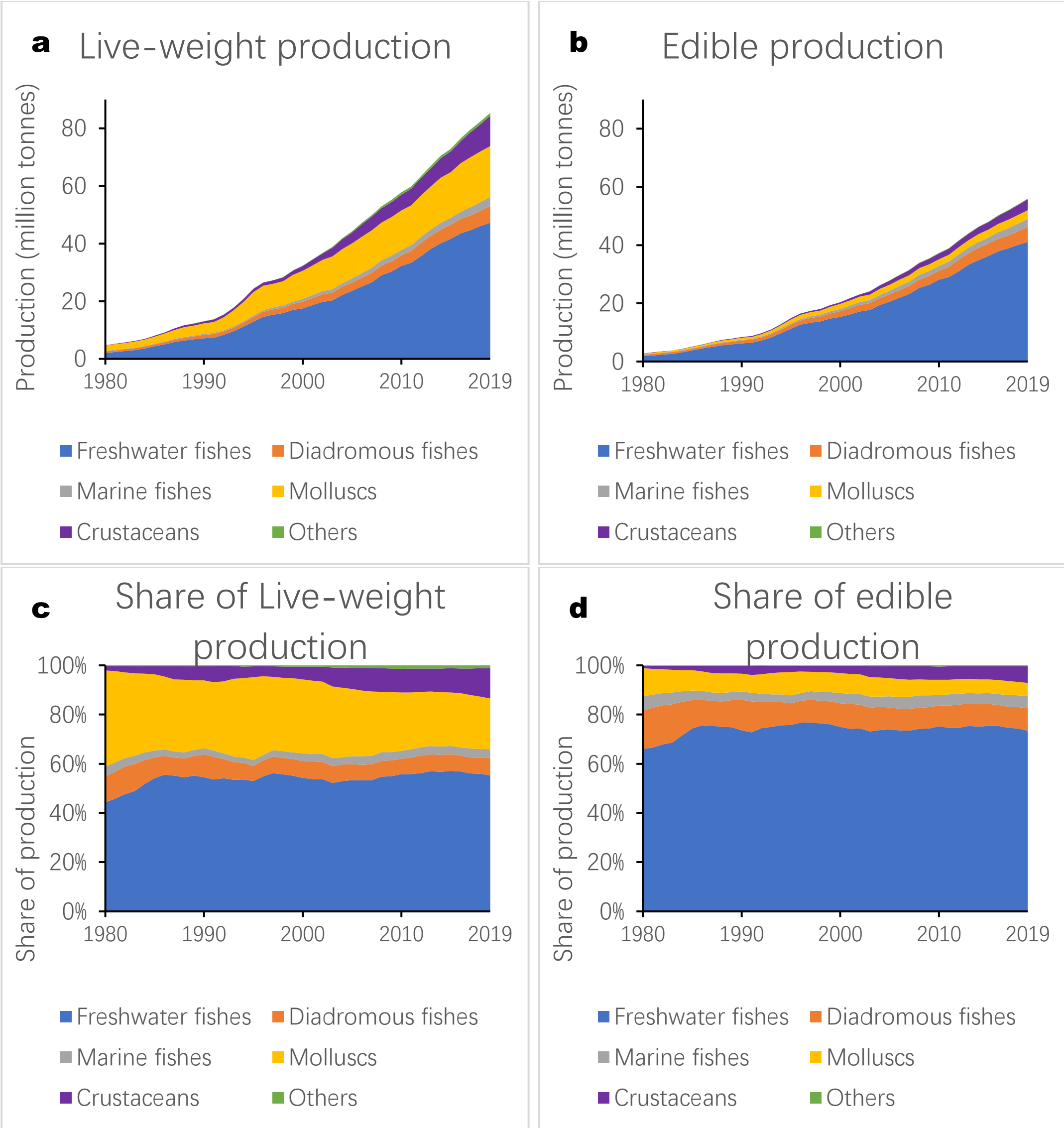

Fig. S2: Aquaculture production and share of production by different species groups. (a) Live-weight aquaculture production by species group. **(b)** Edible equivalent production by species group. **(c)** Share of live-weight aquaculture production by species group. **(d)** Share of edible equivalent production by species group. Conversion factors from live weight to edible food can be found in ref.[1,50]. Data source: ref.[3].

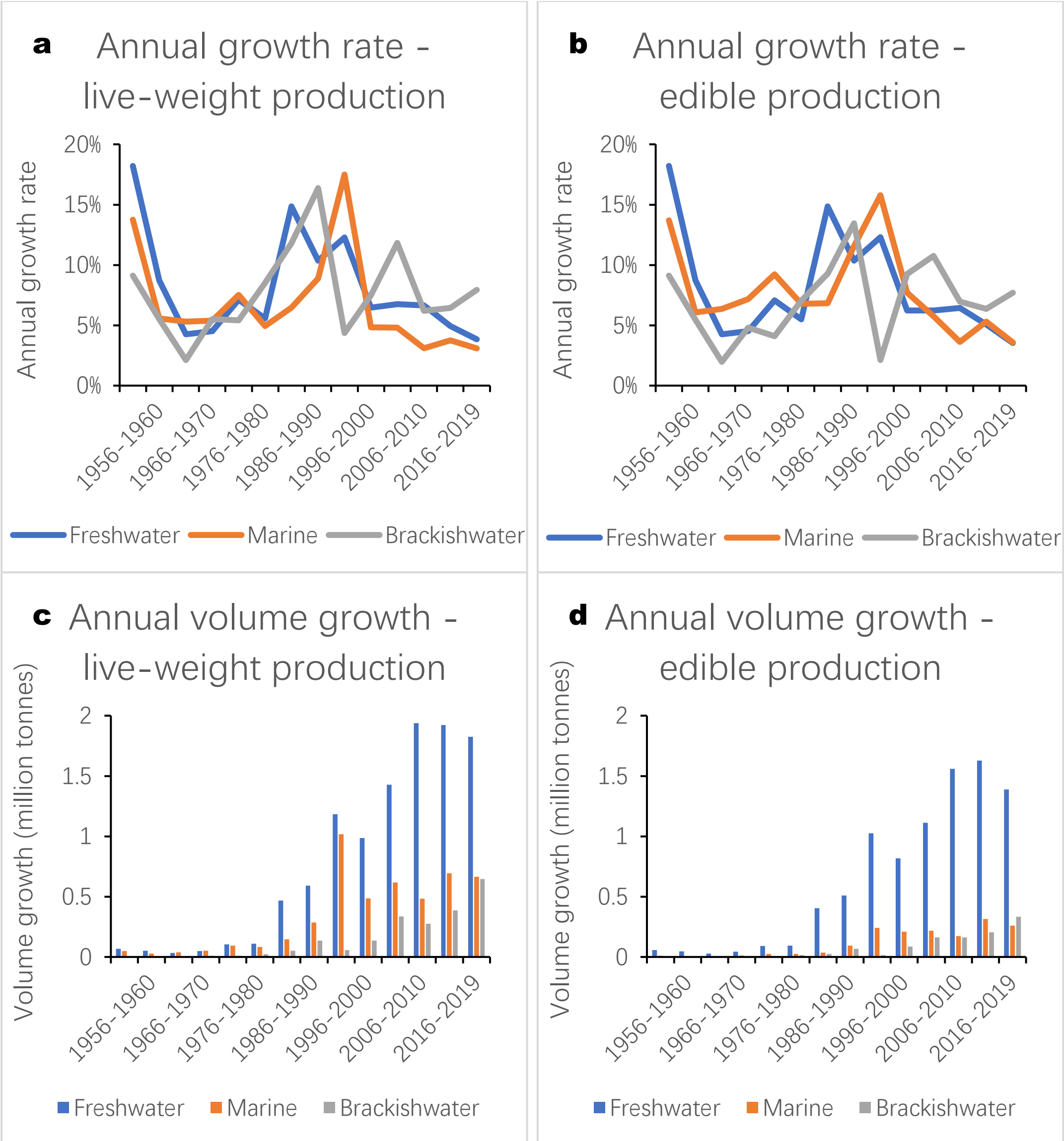

Fig. S3: 5-year average annual growth rates and net annual volume growth of aquaculture production. (a) 5-year average annual growth rates by live-weight aquaculture production. **(b)** 5-year average annual growth rates by edible equivalent production. **(c)** 5-year average net annual volume growth by live-weight aquaculture production. **(d)** 5-year average net annual volume growth by edible equivalent production. Conversion factors from live weight to edible food can be found in ref.[1,50]. Data source: ref.[3].

Figure Note: Freshwater aquaculture produces much more aquatic food than mariculture and brackishwater aquaculture. Even with similar growth rates, freshwater aquaculture has much higher net annual volume growth due to the larger production base value[50].

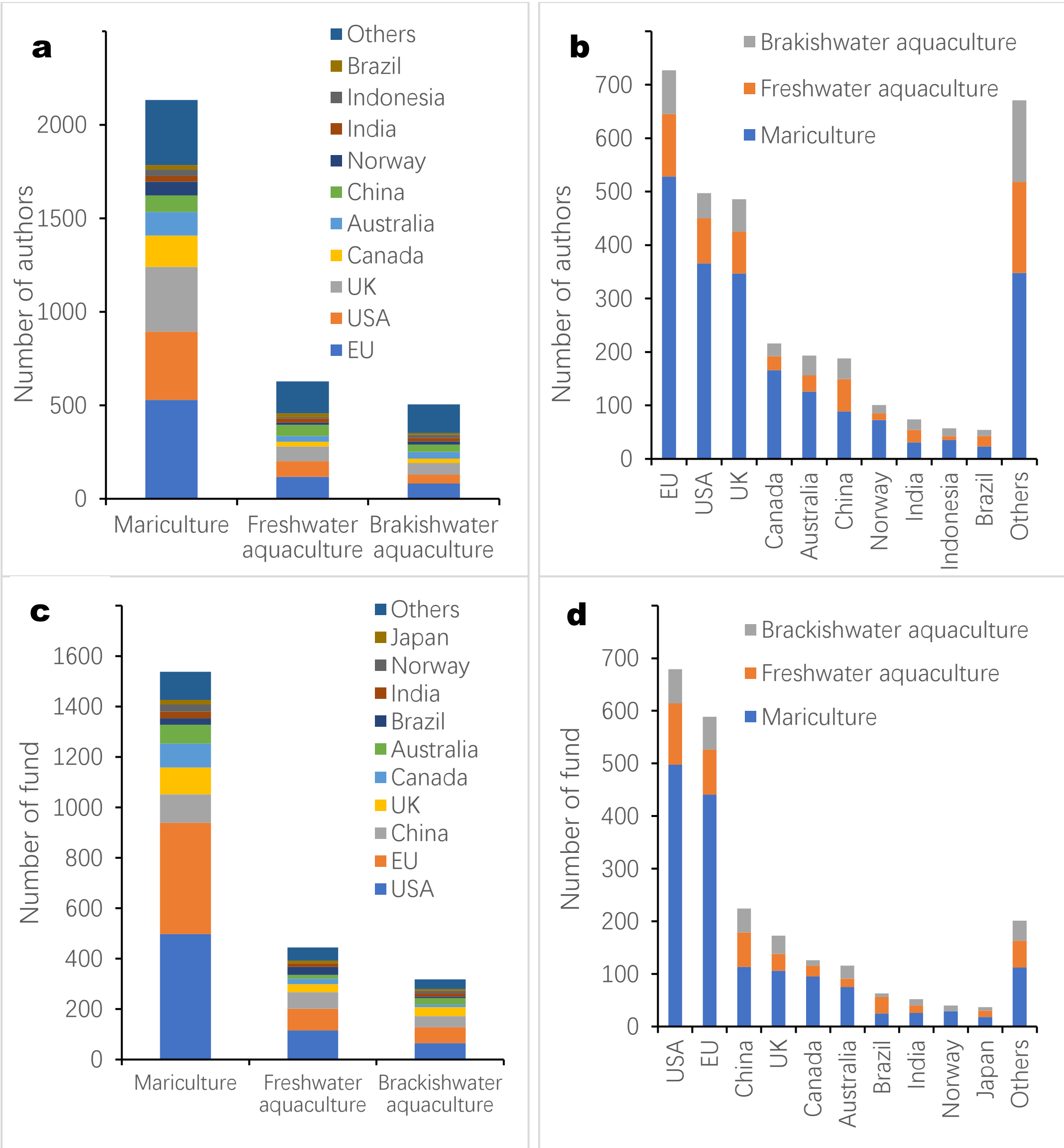

Fig. S4: Countries of origin of authors and funding of peer-reviewed publications on aquaculture policy. (a) Number of authors by country and aquaculture environment in peer-reviewed publications related to aquaculture policy, Web of Science database, 1990-2020. **(b)** Number of authors by aquaculture environment and country in peer-reviewed publications related to aquaculture policy, Web of Science database, 1990-2020. **(c)** Number of funders by country and by aquaculture environment in peer-reviewed publications related to aquaculture policy, Web of Science database, 1990-2020. **(d)** Number of funders by aquaculture environment and country in peer-reviewed publications related to aquaculture policy, Web of Science database, 1990-2020. See Table S1 for search query sets used for publications related to aquaculture policy. EU refers to European Union and individual EU countries. The EU countries are: Austria, Belgium, Bulgaria, Croatia, Cyprus, Czechia, Denmark, Estonia, Finland, France, Germany, Greece, Hungary, Ireland, Italy, Latvia, Lithuania, Luxembourg, Malta, Netherlands, Poland, Portugal, Romania, Slovakia, Slovenia, Spain and Sweden.

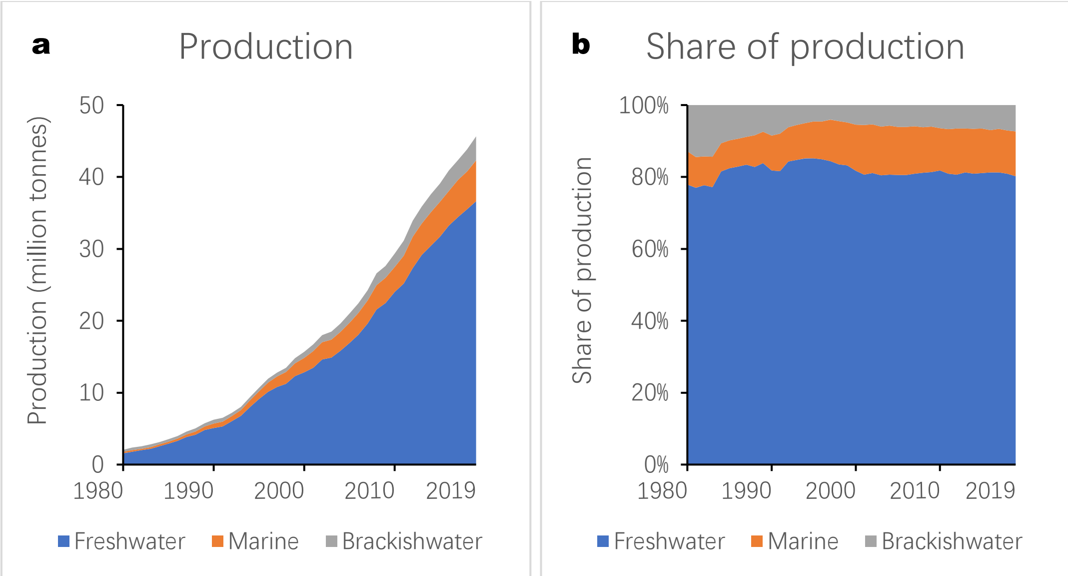

Fig. S5: Production and share of production of fed finfish from mariculture, brackishwater aquaculture, and freshwater aquaculture in 1980-2019. **(a)** Production of fed finfish from mariculture, brackishwater aquaculture, and freshwater aquaculture in 1980-2019 (excluding freshwater filter feeder finfish). **(b)** Share of production of fed finfish from mariculture, brackishwater aquaculture, and freshwater aquaculture in 1980-2019 (excluding filter feeder finfish). Freshwater filter feeder finfish are silver carp, bighead carp, calta, and rohu (Both Indian major carps rohu and catla are mostly raised in fertilized ponds and fed with supplementary rice bran and oil cakes, we estimate half of the nutrition of catla and rohu comes from filter-feeding in the absence of data). Data source: ref.[3].

Figure Note: For fed finfish aquaculture, production from freshwater is 4.5 times more than from marine and brackish waters together, and the growth of freshwater and marine/brackish water is kept at the same pace.

Fig. S6: Production and share of marine extractive species (filter feeder mollusc, mainly bivalves) and freshwater extractive species (filter feeder finfish). (a) Live-weight production of marine extractive species (filter feeder molluscs, mainly bivalves) and freshwater extractive species (filter feeder finfish). **(b)** Edible equivalent production of marine extractive species and freshwater extractive species. **(c)** Share of live-weight production of marine extractive species and freshwater extractive species. **(d)** Share of edible equivalent production of marine extractive species and freshwater extractive species. Freshwater filter feeder finfish are silver carp, bighead carp, catla, and rohu (Both Indian major carps rohu and catla are mostly raised in fertilized ponds and fed with supplementary rice bran and oil cakes, we estimated that half of the nutrition of catla and rohu comes from filter-feeding in the absence of data). Non-filter feeder marine molluscs such as abalone, winkles, and conchs, and squids, cuttlefishes, and octopuses are excluded from the analysis. Conversion factors from live weight to edible food can be found in ref.[1,50]. Data source: ref.[3].

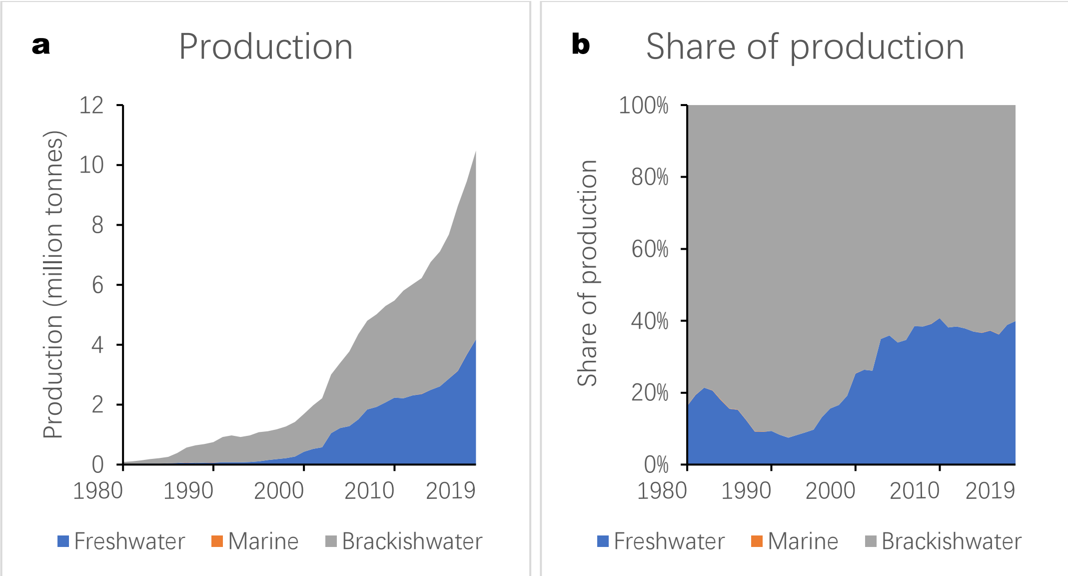

Fig. S7: Production and share of production of crustaceans from mariculture, brackishwater aquaculture, and freshwater aquaculture in 1980-2019. (a) Production of crustaceans from mariculture, brackishwater aquaculture, and freshwater aquaculture in 1980-2019. **(b)** Share of production of crustaceans from mariculture, brackishwater aquaculture, and freshwater aquaculture in 1980-2019. Data source: ref.[3].

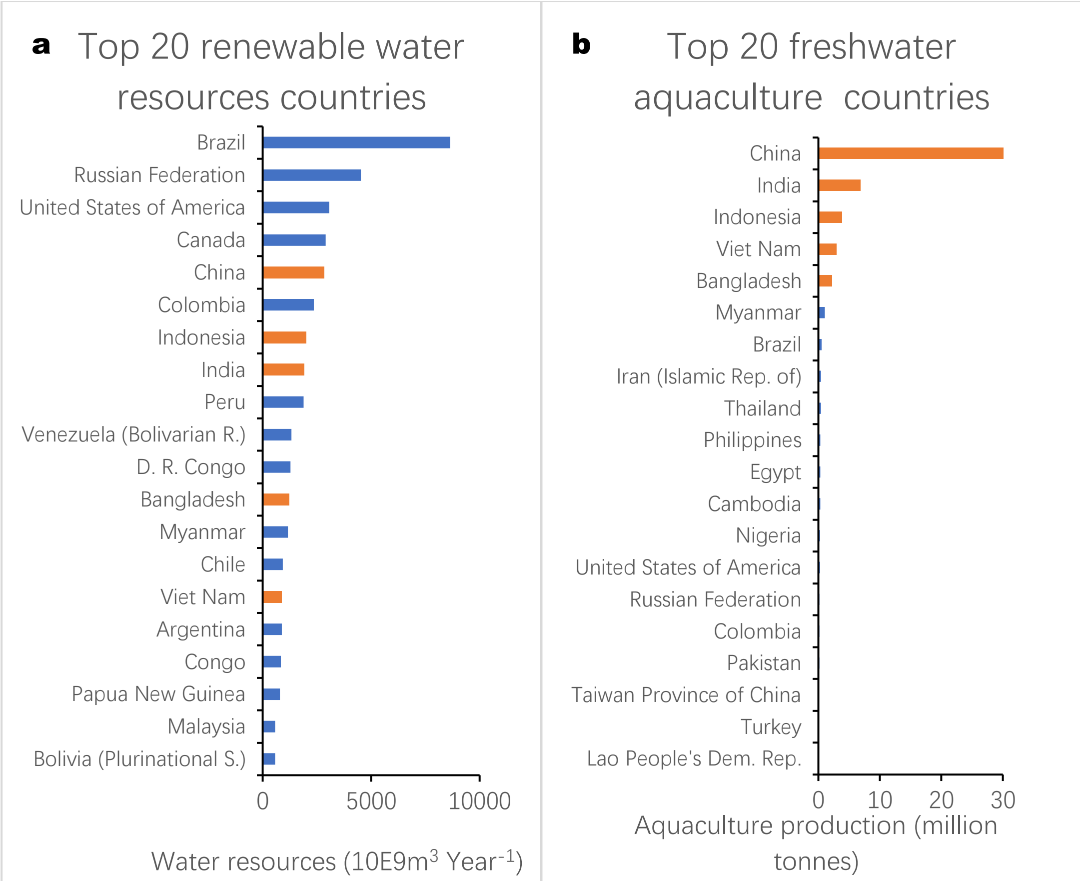

Fig. S8: Top 20 countries for freshwater aquaculture production and top 20 countries for total renewable water resources. (a) Top 20 countries for freshwater aquaculture production in 2019. **(b)** Top 20 countries for total renewable water resources. Yellow-coloured bars are for the top five freshwater aquaculture producing countries, and all of them are in Asia with rich water resources. Data source: ref.[3,51].

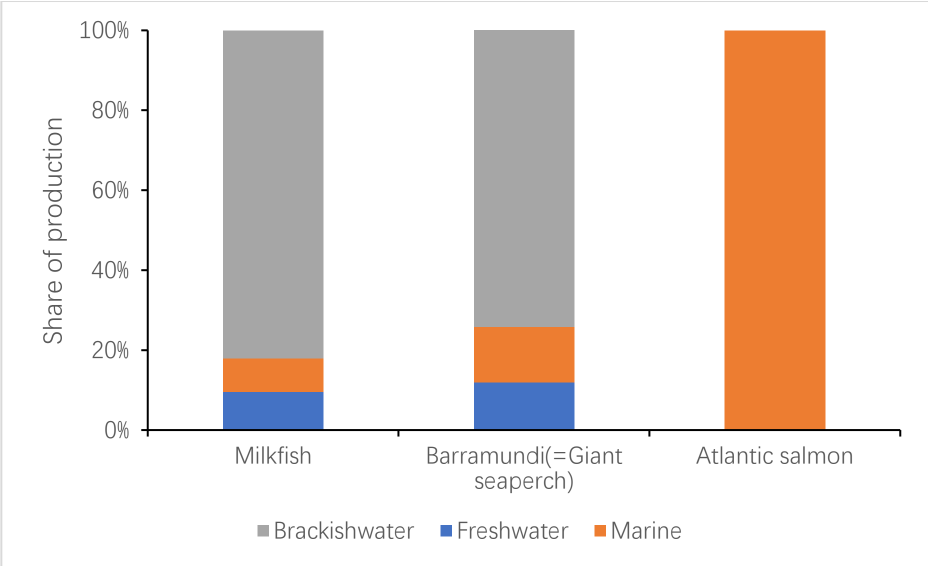

Fig. S9: Share of the aquaculture production of milkfish, barramundi, and Atlantic salmon from different environments in 2019. Data source: ref.[3].

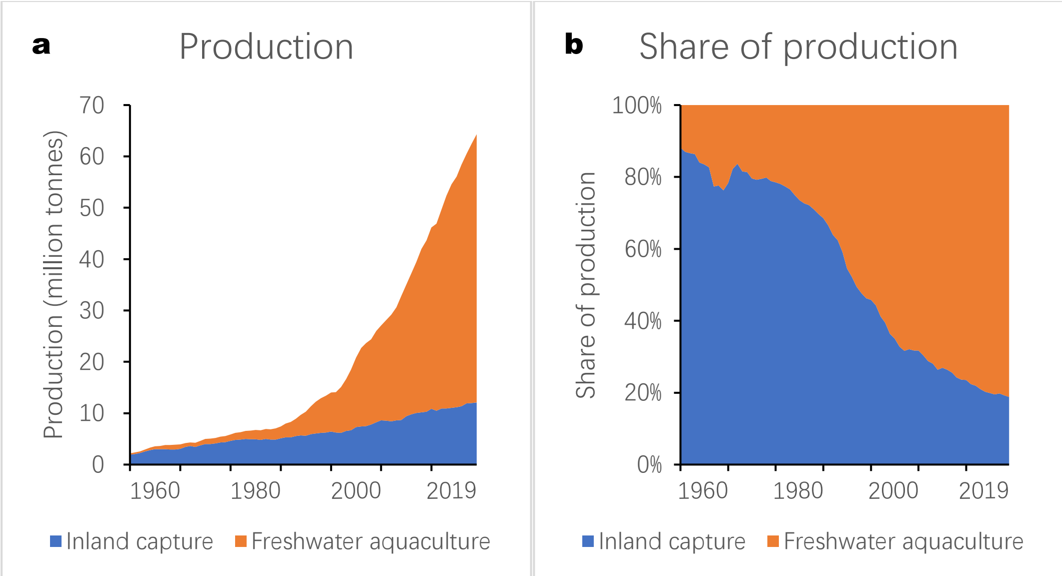

Fig. S10: Production and share of freshwater aquaculture and freshwater capture fisheries in total freshwater fisheries production. (a) Production of freshwater aquaculture and freshwater capture fisheries. (**b)** Share of freshwater aquaculture and freshwater capture fisheries in total freshwater fisheries production. Aquatic plants excluded. Data source: ref.[3].

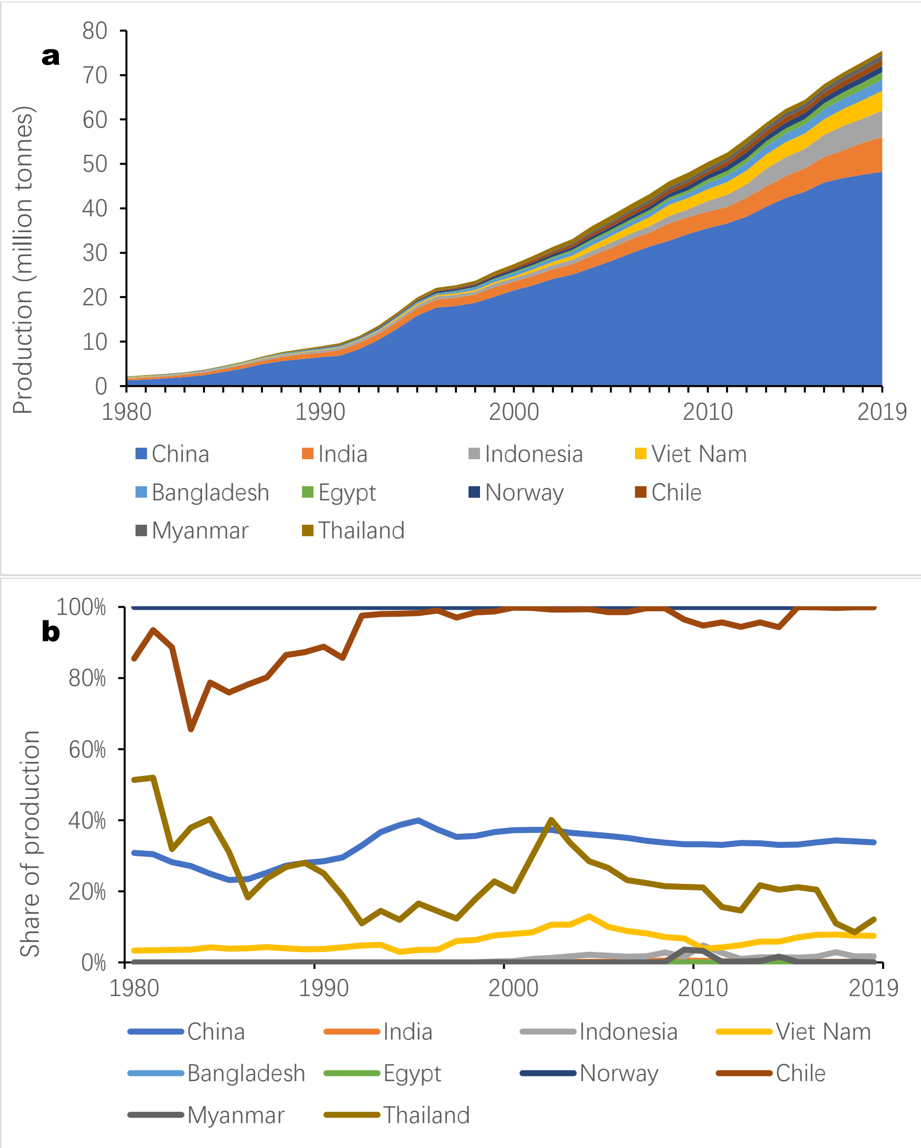

Fig. S11: Total aquaculture production and share of mariculture in total aquaculture production in the top ten aquaculture producing countries. (a) Total aquaculture production in the top ten aquaculture producing countries (aquatic plants excluded). **(b)** Share of mariculture in total aquaculture production in the top ten aquaculture producing countries (aquatic plants excluded). Data source: ref.[3].

Figure note: All the top five aquaculture producing countries are Global South countries in Asia (China, India, Indonesia, Vietnam, and Bangladesh, in order of production volume), for which the majority of their production is produced in freshwater.

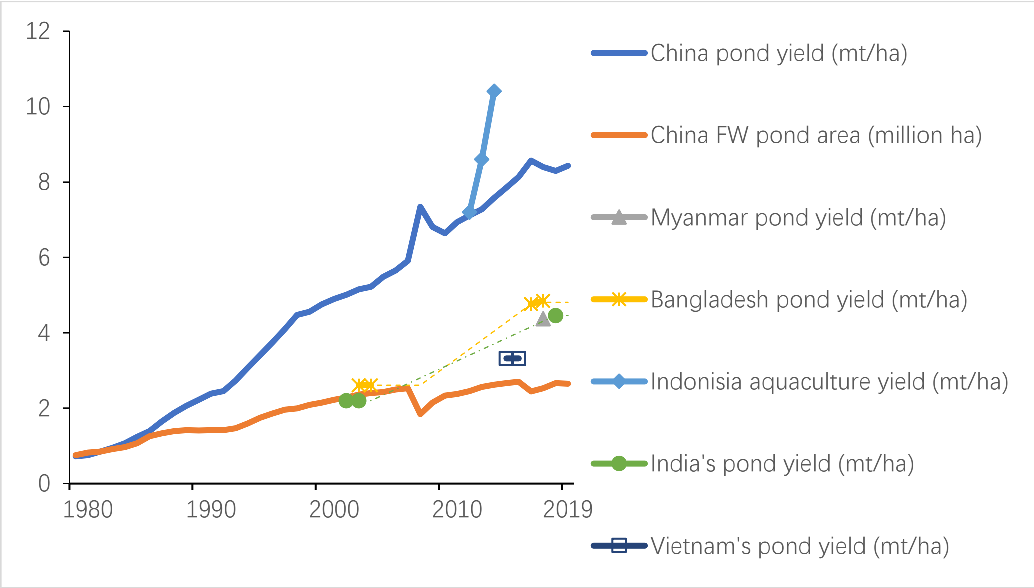

Fig. S12: Freshwater pond aquaculture yield and freshwater pond area in China and aquaculture yield in other major aquaculture producing countries. The fluctuation of China's freshwater aquaculture pond area and yield around 2007 and 2016 resulted from data adjustments after two national agriculture censuses[18,45]. Dashed lines are moving averages. Data source: ref.[18,52–58]

Table S1 Search query sets used in the Web of Science (WOS) database for policy-related studies in mariculture, brackishwater aquaculture, and freshwater aquaculture

Environments	Searching query sets
Freshwater aquaculture	TS=("policy" OR "policies") AND TS=("aquaculture" OR "aqua culture" OR "aqua-culture" OR "fish farm" OR "fish farming") AND TS=("freshwater" OR "fresh water" OR "fresh-water" OR "inland" OR "in land" OR "land based" OR "land-based" OR "landbased") NOT TS=("brackishwater" OR "brackish-water" OR "brackish water" OR "coastal" OR "marine" OR "seawater" OR "sea water" OR "sea-water" OR "ocean" OR "offshore" OR "off shore" OR "off-shore")
Mariculture	TS=("policy" OR "policies") AND (TS=("mariculture" OR "mari culture" OR "mari-culture") OR (TS=("aquaculture" OR "aqua culture" OR "aqua-culture" OR "fish farm" OR "fish farming") AND TS=("marine" OR "seawater" OR "sea water" OR "sea-water" OR "ocean" OR "offshore" OR "off shore" OR "off-shore"))) NOT TS=("freshwater" OR "fresh water" OR "fresh-water" OR "inland" OR "in land" OR "land based" OR "land-based" OR "landbased" OR "brackishwater" OR "brackish-water" OR "brackish water" OR "coastal")
Brackishwater aquaculture	TS=("policy" OR "policies") AND TS=("aquaculture" OR "aqua culture" OR "aqua-culture" OR "fish farm" OR "fish farming") AND TS=("brackishwater" OR "brackish-water" OR "brackish water" OR "coastal") NOT TS=("freshwater" OR "fresh water" OR "fresh-water" OR "inland" OR "in land" OR "land based" OR "land-based" OR "landbased" OR "marine" OR "seawater" OR "sea water" OR "sea-water" OR "ocean" OR "offshore" OR "off shore" OR "off-shore")

Note: We conducted extensive literature searches in Jan. 2021 and Aug. 2021 using the advanced search function of the Web of Science database. OR, AND, NOT are Boolean operators. TS: Topic. Other searching sets are: Databases= WOS (Core Collections: SCI-EXPANDED, SSCI, CPCI-S, CPCI-SSH, A&HCI, BKCI-SSH, BKCI-S), BIOSIS, KJD, MEDLINE, RSCI, SCIELO; Timespan=1990-2020; Search language=Auto. Data source: ref.[59].

A total of 1,740 literature records were found in 1990-2020, including freshwater aquaculture 333, mariculture 1140, and brackishwater aquaculture 267. Mariculture publications have more citations per publication (18.7 citations) than freshwater aquaculture (14.3) and brackishwater aquaculture (12.8).

Scientometric research based on the Web of Science (WOS) database has shortcomings, including but not limited to:

1) missing of important grey literature from key organizations, such as standards, guidelines, and technical reports from the United Nations Food and Agriculture Organization (FAO), the WorldFish Centre, and the International Food Policy Research Institute (IFPRI)[60–62];

2) the majority of literature collected in the Web of Science database is published in English in international journals[61,62], while an extensive and highly relevant literature on aquaculture exists in non-English language journals[25]. As a result, 97.6% of all literature records collected by the present study are in English;

3) underrepresentation of certain social sciences and humanities research[61,62], although Social Sciences Citation Index (SSCI) was one of the Web of Science database core collections used by the present study; and

4) in aquaculture, the published literature is biased towards export-oriented species such as salmon, shrimp, and catfish consumed mainly in the Global North and biased against aquaculture production and consumption in the Global South[63].

However, the Web of Science database has been widely used for scientometric studies in fisheries and other research fields[61,62]. The majority of literature collected by the Web of Science database was peer-reviewed[61], and thus was the most appropriate source of data for the purpose of the present study.

Table S2 Land footprint (LF) and water footprint (WFP) of Atlantic salmon cage farming in Norway in 2016

Feed raw material (FRM)	Proportion in feed	Yield t ha^{-1} yr^{-1}	LF, ha t^{-1} salmon	Green WFP m^3 t^{-1} FRM	Blue WFP m^3 t^{-1} FRM	Water footprint, m^3 t^{-1} salmon	
						Green	Blue
Fishmeal/oil	27%						
Soy, Brazil	13%	3.39	0.05	2037	70	274.6	9.4
Soy, Canada	7%	2.86	0.03	2037	70	145.0	5.0
Rapeseed oil, global	20%	2	0.13	1703	231	340.6	46.2
Wheat, EU	18%	4	0.06	1277	342	229.9	61.6
Beans/peas, EU	8%	1.9	0.06	1453	33	116.2	2.6
Other	6%	3	0.03	947	81	60.6	5.2
Sum	**100%**		0.36			**1166.9**	**130.0**
Total salmon farming in Norway			**444,482**			**1,438,824,690**	**160,294,932**

Note: Total salmon farming production in Norway was 1.233 million tonnes in 2016, and FCR (feed conversion ratio) was at 1.32. Thus, total land footprint was 444,482 ha, which was 10 times larger than the directly used sea area by the salmon farming industry in Norway. The fish farming area including moorings occupying 418 km^2 or 41,800 ha in Norway in 2016. Data source: ref.[64–69].

Table S3 Production, price, and trophic level (TL) of top 20 finfish species from mariculture, brackishwater aquaculture, and freshwater aquaculture

Environments	Species (ASFIS Name[70])	Production in 2019 (000 mt)	Price (USD/kg)	Trophic level (TL) (mean±se)	Average TL	Fishbase species ID, or Latin name, or note
Fresh-water	Grass carp(=White amur)	5728.38	2.29	2.0±0.00	2	ID=79
	Silver carp	4827.72	2.15	2.0±0.00	2	ID=274
	Common carp	4411.90	2.05	3.1±0.0;	3.1	ID=1450
	Nile tilapia	3572.59	2.15	2.0±0.00	2	ID=2
	Catla	3286.27	1.60	2.8±0.22	2.8	ID=4439
	Bighead carp	3145.90	2.33	2.8±0.33	2.8	ID=275
	[Carassius spp]	2755.69	1.99	3.1±0.24	3.1	ID=270
	Striped catfish	2682.25	1.21	3.1±0.46	3.1	ID=14154
	Roho labeo	1992.88	1.79	2.2±0.12	2.2	ID=82
	Torpedo-shaped catfishes nei	1260.11	1.48	3.7±0.59	3.7	*Clarias fuscus*
	Tilapias nei	1076.95	1.72	2.1±0.0	2.1	Note: Blue tilapia is referenced, ID=1387
	Wuchang bream	762.86	3.01	3.4±0.5	3.4	ID=285
	Rainbow trout	708.49	4.04	4.1±0.3	4.1	ID=239
	Black carp	680.45	4.23	3.2±0.44	3.2	ID=4602
	Yellow catfish	536.96	2.37	3.5±0.1	3.5	ID=28052
	Pangas catfishes nei	531.00	1.55	3.4±0.51	3.4	ID=292
	Mrigal carp	523.89	1.56	2.2±0.2	2.2	ID=66743
	Largemouth black bass	480.14	2.85	3.8±0.4	3.8	ID=3385
	Snakehead	462.18	2.23	4.4±0.3	4.4	ID=4799
	Channel catfish	453.51	2.37	4.2 ±0.3	4.2	ID=290
Brackish water	Milkfish	1261.26	1.58	2.4±0.20	2.4	ID=80
	Nile tilapia	1017.70	1.49	2.0±0.00	2	ID=2
	Mullets nei	219.59	2.31	2.5±0.17	2.5	ID=785
	Barramundi(Asian seabass)	80.04	3.88	3.8±0.60	3.8	ID=346
	Gilthead seabream	57.25	5.13	3.7±0.0	3.7	ID=1164
	Mozambique tilapia	35.50	1.13	2.2±0.0	2.2	ID=3
	European seabass	35.09	3.92	3.5±0.50	3.5	ID=63
	Groupers nei	32.00	7.46	4.4±0.7;3.7 ±0.3;3.6±0. 55;4.0±0.0; 4.0±0.60;4. 1±0.72	4	Note: Average of *Plectropomus leopardus; Epinephelus areolatus; Epinephelus awoara; Epinephelus coioides;* ID=6468; *Epinephelus fuscoguttatus*
	Atlantic salmon	26.96	5.51	4.5±0.3	4.5	ID=236
	Meagre	25.35	3.29	4.3±0.75	4.3	ID=418
	Tilapias nei	22.91	1.69	2.1±0.0	2.1	Note: Blue tilapia is referenced, ID=1387
	Fourfinger threadfin	11.71	6.77	4.1±0.5	4.1	ID=340
	Rainbow trout	7.25	4.00	4.1±0.3	4.1	ID=239
	Arctic char	6.32	6.21	4.4±0.5	4.4	ID=247
	North African catfish	2.45	0.89	3.8±0.4	3.8	ID=1934
	Flathead grey mullet	1.71	3.15	2.5±0.17	2.5	ID=785
	Japanese seabass	0.99	2.60	3.1±0.3	3.1	ID=4589
	Senegalese sole	0.91	10.39	3.3 ±0.46	3.3	ID=8852
	Amberjacks nei	0.68	6.25	4.0 ±0.65;4 .2±0.1;4.5± 0.0	4.2	Note: Average of *Seriola quinqueradiata; Seriola lalandi; Seriola dumerili*
	Blue tilapia	0.50	3.41	2.1±0.0	2.1	ID=1387
Marine water	Atlantic salmon	2586.89	6.53	4.5±0.3	4.5	ID=236
	European seabass	228.13	4.94	3.5±0.50	3.5	ID=63
	Large yellow croaker	225.55	2.17	3.7±0.56	3.7	ID=428
	Coho(=Silver) salmon	221.11	6.07	4.2±0.70	4.2	ID=245
	Gilthead seabream	201.50	4.87	3.7±0.0	3.7	ID=1164
	Rainbow trout	200.80	6.30	4.1±0.3	4.1	ID=239
	Groupers nei	197.37	2.64	4.4±0.7;3.7 ±0.3;3.6±0. 55;4.0±0.0; 4.0±0.60;4. 1±0.72	4	Note: Average of *Plectropomus leopardus; Epinephelus areolatus; Epinephelus awoara; Epinephelus coioides;* ID=6468; *Epinephelus fuscoguttatus*
	Japanese seabass	180.95	2.22	3.1±0.3	3.1	ID=4589
	Pompano	168.00	7.30	3.7±0.46;	3.7	ID=1963
	Japanese amberjack	135.60	7.87	4.0±0.65	4	ID=381
	Milkfish	128.80	2.22	2.4±0.20	2.4	ID=80
	Porgies, seabreams nei	101.36	2.18	3.8±0.43;3. 2±0.45;4.5 ±0.7;4.5±0. 7;3.3±0.47	3.9	Note: Average of *Acanthopagrus latus;* ID=6531; *Pagrus major; Lutjanus erythropterus; Rhabdosargus sarba*

	Turbot	77.61	6.82	4.4±0.0	4.4	ID=1348
	Red drum	76.81	2.54	3.7±0.57	3.7	ID=1191
	Silver seabream	62.00	8.05	3.6±0.2	3.6	ID=6426
	Lefteye flounders nei	49.81	6.62	3.5±0.37	3.5	ID=8901
	Cobia	47.71	2.56	4.0±0.0	4	ID=3542
	Bastard halibut	45.32	8.84	4.5±0.8	4.5	ID=1351
	Amberjacks nei	31.77	2.53	4.0 ±0.65;4 .2±0.1;4.5± 0.0	4.2	Note: Average of *Seriola quinqueradiata; Seriola lalandi; Seriola dumerili*
	Pacific bluefin tuna	26.06	21.32	4.5±0.3	4.5	ID=14290

Note: Prices were calculated using aquaculture production volume and value data from FAO FishstatJ database. Trophic levels are from Fishbase and reflect species' diets in nature, although the trophic levels of farmed finfish mainly depend on artificial feed types. For example, carnivorous species like salmon can be farmed on complete vegetarian diets, and species like carps can be farmed with inclusion of animal resources to speed up growth[71]. The important difference between these species relates to their ability to tolerate and digest different crops and fibre resources[25]. The top 20 freshwater finfish species have significantly lower trophic levels than the top 20 mariculture species (P=0.004). The top 20 mariculture finfish species are also significantly more expensive than freshwater finfish species (P=0.000), with price significantly correlated with trophic level (P=0.000). Independent-samples nonparametric Kruskal-Wallis test was used for significance test, and Spearman correlation test (two-tailed) was used for correlation test using IBM SPSS 22 statistic software. Aggregated species categories such as “freshwater fishes nei”, “marine fishes nei”, and “cyprinids nei” were excluded from the analysis. nei: not elsewhere included or unidentified species[72]. Data source: ref.[45,73].

References

1. Costello, C. *et al.* The future of food from the sea. *Nature* (2020). doi:10.1038/s41586-020-2616-y
2. FAO. *The State of World Fisheries and Aquaculture 2020. Sustainability in action.* (2020).
3. FAO. Fishery and Aquaculture Statistics. (2021).
4. Fluet-chouinard, E., Funge-smith, S. & Mcintyre, P. B. Global hidden harvest of freshwater fish revealed by household surveys. *Proc. Natl. Acad. Sci.* **115**, 7623–7628 (2018).
5. Little, D. C. *et al.* Sustainable intensification of aquaculture value chains between Asia and Europe: A framework for understanding impacts and challenges. *Aquaculture* **493**, 338–354 (2018).
6. Edwards, P. Aquaculture environment interactions: Past, present and likely future trends. *Aquaculture* **447**, 2–14 (2015).
7. Edwards, P. The Changing Face of Pond Aquaculture in China. *Glob. Aquac. Advocate* 77–80 (2008).
8. Pahlow, M., van Oel, P. R., Mekonnen, M. M. & Hoekstra, A. Y. Increasing pressure on freshwater resources due to terrestrial feed ingredients for aquaculture production. *Sci. Total Environ.* **536**, 847–857 (2015).
9. Belton, B. *et al.* Farming fish in the sea will not nourish the world. *Nat. Commun.* **11**, 1–28 (2020).
10. Willett, W. *et al.* Food in the Anthropocene: the EAT–Lancet Commission on healthy diets from sustainable food systems. *Lancet* **393**, 447–492 (2019).
11. Newton, R., Zhang, W., Xian, Z., McAdam, B. & Little, D. C. Intensification, regulation and diversification; the changing face of inland aquaculture in China. *Amibo* (2021).
12. Xu, S. *et al.* Current situation and development strategies of freshwater fish processing industry in Hunan Province (in Chinese). *Food Mach.* **33**, 213–216 (2017).
13. Chen, J. Development Status of Frozen Surimi Industry in China (in Chinese). *China Food News* 1 (2013).
14. Zhu, Y. *et al.* Research on the quality and efficiency improvement of bulk freshwater fish processing (in Chinese). *Sci. Fish Farming* 70–72 (2020).
15. Froehlich, H. E., Smith, A., Gentry, R. R. & Halpern, B. S. Offshore aquaculture: I know it when I see it. *Front. Mar. Sci.* **4**, 154 (2017).
16. Benetti, D. D., Benetti, G. I., Rivera, J. A., Sardenberg, B. & O'Hanlon, B. Site selection criteria for open ocean aquaculture. *Mar. Technol. Soc. J.* **44**, 22–35 (2010).
17. Oyinlola, M. A., Reygondeau, G., Wabnitz, C. C. C. & Cheung, W. W. L. Projecting global mariculture diversity under climate change. *Glob. Chang. Biol.* **26**, 2134–2148 (2020).
18. MOA. *China Fishery Statistical Yearbook 2020*. (China Agriculture Press, 2020).
19. Chen, J. *et al.* A review of cage and pen aquaculture: China. in *Cage aquaculture – Regional reviews and global overview* (eds. Halwart, M., Soto, D. & Arthur, J. R.) 50–68 (FAO Fisheries Technical Paper. No. 498, 2007).
20. Torrissen, O. *et al.* Atlantic Salmon (Salmo salar): The "Super-Chicken" of the Sea? *Rev. Fish. Sci.* **19**, 257–278 (2011).
21. Greenpeace. *An investigation report into China's marine trash fish fisheries*. (2017).
22. Zhang, W. *et al.* Fishing for feed in China: Facts, impacts and implications. *Fish Fish.* **21**, 47–62 (2020).
23. Troell, M. *et al.* Does aquaculture add resilience to the global food system? *Proc. Natl. Acad. Sci.* **111**, 13257–13263 (2014).
24. Cottrell, R. S., Blanchard, J. L., Halpern, B. S., Metian, M. & Froehlich, H. E. Global adoption of novel aquaculture feeds could substantially reduce forage fish demand by 2030. *Nat. Food* **1**, 301–308 (2020).
25. Naylor, R. L. *et al.* A 20-year retrospective review of global aquaculture. *Nature* **591**, 551–563 (2021).
26. Hall, S. J., Delaporte, A., Phillips, M. J., Beveridge, M. & O'Keefe, M. *Blue Frontiers: Managing the environmental costs of aquaculture*. *The WorldFish Center* (2011).
27. Hilborn, R., Banobi, J., Hall, S. J., Pucylowski, T. & Walsworth, T. E. The environmental cost of animal source foods. *Front. Ecol. Environ.* **16**, 329–335 (2018).
28. MacLeod, M., Hasan, M. & Robb, D. *Quantifying and mitigating greenhouse gas emissions*

from global aquaculture. (FAO Fisheries and Aquaculture Technical Paper No. 626, 2018).
29. MacLeod, M. J., Hasan, M. R., Robb, D. H. F. & Mamun-Ur-Rashid, M. Quantifying greenhouse gas emissions from global aquaculture. *Sci. Rep.* **10**, 1–8 (2020).
30. Gephart, J. A. *et al.* Environmental performance of blue foods. *Nature* **597**, 360–365 (2021).
31. Diana, J. S. Aquaculture production and biodiversity conservation. *Bioscience* **59**, 27–38 (2009).
32. Cao, L., Diana, J. S. & Keoleian, G. a. Role of life cycle assessment in sustainable aquaculture. *Rev. Aquac.* **5**, 61–71 (2013).
33. De Silva, S. S. Aquaculture: a newly emergent food production sector—and perspectives of its impacts on biodiversity and conservation. *Biodivers. Conserv.* **21**, 3187–3220 (2012).
34. Ruiz-Salmón, I. *et al.* Life cycle assessment of fish and seafood processed products – A review of methodologies and new challenges. *Sci. Total Environ.* **761**, 144094 (2021).
35. Hua, K. *et al.* The Future of Aquatic Protein: Implications for Protein Sources in Aquaculture Diets. *One Earth* **1**, 316–329 (2019).
36. Rana, K. J., Siriwardena, S. & Hasan, M. R. *Impact of rising feed ingredient prices on aquafeeds and aquaculture production*. *FAO Fisheries and Aquaculture Technical Paper* **541**, (2009).
37. Chatvijitkul, S., Boyd, C. E., Davis, D. A. & McNevin, A. A. Embodied Resources in Fish and Shrimp Feeds. *J. World Aquac. Soc.* **48**, 7–19 (2017).
38. Adarsha, H. S., Prabhudeva, K. N. & Rajanna, K. B. A Review on Translocation and Management of Genetic Resources of Commercially Important Aquaculture Finfishes. *Univers. J. Environ. Res. Technol.* **1**, 115–123 (2011).
39. Clavelle, T., Lester, S. E., Gentry, R. & Froehlich, H. E. Interactions and management for the future of marine aquaculture and capture fisheries. *Fish Fish.* **20**, 1–21 (2019).
40. Asche, F. & Khatun, F. *Aquaculture: issues and opportunities for sustainable production and trade*. *ICTSD Natural Resources, International Trade and Sustainable Development Series Issue Paper No. 5* (International Centre for Trade and Sustainable Development (ICTSD), 2006).
41. Barrett, L. T., Swearer, S. E. & Dempster, T. Impacts of marine and freshwater aquaculture on wildlife: a global meta-analysis. *Rev. Aquac.* **11**, 1022–1044 (2019).
42. Bouwmeester, M. M., Goedknegt, M. A., Poulin, R. & Thieltges, D. W. Collateral diseases: Aquaculture impacts on wildlife infections. *J. Appl. Ecol.* **58**, 453–464 (2021).
43. Gentry, R. R. *et al.* Mapping the global potential for marine aquaculture. *Nat. Ecol. Evol.* **1**, 1317–1324 (2017).
44. Davies, I. P. *et al.* Governance of marine aquaculture: Pitfalls, potential, and pathways forward. *Mar. Policy* **104**, 29–36 (2019).
45. FAO. Fishery and Aquaculture Statistics. Global aquaculture production 1950-2018 (FishstatJ). (2020).
46. Zhang, W. & Ma, X. China's aquaculture development trends since 2000 and future directions (in Chinese). *J. Shanghai Ocean Univ.* 1–10 (2019).
47. National Bureau of Statistics of China. *China Statistical Yearbook 2019*. (China Statistics Press, 2019).
48. Roberts, C. A. *et al. A Risk Benefit Analysis of Mariculture as a means to Reduce the Impacts of Terrestrial Production of Food and Energy*. *Scottish Aquaculture Research Forum* (2015).
49. Murray, F., Bostock, J. & Fletcher, D. *Review of Recirculation Aquaculture System Technologies and their Commercial Application Prepared for Highlands and Islands Enterprise*. (2014).
50. Edwards, P., Zhang, W., Belton, B. & Little, D. C. Misunderstandings, myths and mantras in aquaculture: Its contribution to world food supplies has been systematically over reported. *Mar. Policy* **106**, 1–9 (2019).
51. FAO. AQUASTAT Main Database, Food and Ag riculture Organization of the United Nations (FAO). (2016). Available at: http://www.fao.org/aquastat/en/. (Accessed: 22nd November 2020)
52. MOA. *China Fishery Statistical Yearbook 2019*. (China Agriculture Press, 2019).
53. Informa Markets. Vietnam Aquaculture Overview. *Informa Markets* (2017). Available at: https://www.aquafisheriesexpo.com/vietnam/en-us/news-updates/vietnam-aquaculture-overview. (Accessed: 10th January 2021)
54. Ministry of Fisheries Animal Husbandry & Dairying. *Handbook on FISHERIES STATISTICS 2018*. *Govt. of India* **7**, (2019).
55. Fisheries India. Fisheries statistics and resources of the world and India-2018-19. *Fisheries*

India (2019). Available at: https://www.fisheriesindia.com/2019/12/fisheries-statistics-of-world-and-india.html. (Accessed: 10th January 2021)
56. Department of Fisheries. *Fisheries statistics of Bangladesh 2017-2018. Fisheries Resources Survey System (FRSS), Department of Fisheries. Bangladesh: Ministry of Fisheries.* **35**, (2018).
57. Beijnen, J. van. The future of fish farming in Myanmar. *The Fish Site* 1 (2018). Available at: https://thefishsite.com/articles/the-future-of-fish-farming-in-myanmar. (Accessed: 10th January 2021)
58. FAO. National Aquaculture Sector Overview. (2005). Available at: http://www.fao.org/fishery/countrysector. (Accessed: 20th December 2020)
59. Clarivate. Web of Science online database. *Web of Science* (2020). Available at: https://apps.webofknowledge.com. (Accessed: 5th January 2021)
60. FAO. Contribution of fisheries to food security. *Fish. andAquaculture Dep. Food Agric. Organ. United Nations* 4 (2016).
61. Smith, H. & Basurto, X. Defining Small-Scale Fisheries and Examining the Role of Science in Shaping Perceptions of Who and What Counts: A Systematic Review. *Front. Mar. Sci.* **6**, (2019).
62. Moed, H. F. Citation Analysis in Research Evaluation. *Angew. Chemie Int. Ed.* **45**, 2831–2832 (2006).
63. Belton, B. & Bush, S. R. Beyond net deficits: new priorities for an aquacultural geography. *Geogr. J.* **180**, 3–14 (2014).
64. Aas, T. S., Ytrestøyl, T. & Åsgård, T. Utilization of feed resources in the production of Atlantic salmon (Salmo salar) in Norway: An update for 2016. *Aquac. Reports* **15**, 100216 (2019).
65. FAO. FAOSTAT. (2017). Available at: http://www.fao.org/faostat/en/. (Accessed: 1st February 2018)
66. Mekonnen, M. M. & Hoekstra, A. Y. The green , blue and grey water footprint of crops and derived crop products. 1577–1600 (2011). doi:10.5194/hess-15-1577-2011
67. Winther, U., Hognes, E. S., Jafarzadeh, S. & Ziegler, F. *Greenhouse gas emissions of Norwegian seafood products in 2017*. (2020).
68. IDH & IUCN NL. *European soy monitor*. (2017).
69. BarentsWatch. Area use: A marine production plant requires acreage. (2017). Available at: https://www.barentswatch.no/havbruk/areal-use. (Accessed: 1st August 2021)
70. FAO. ASFIS List of Species for Fishery Statistics Purposes. *FAO Fisheries and Aquaculture Department* 1 (2013).
71. Cottrell, R. S. *et al.* Time to rethink trophic levels in aquaculture policy. *Rev. Aquac.* 1–11 (2021). doi:10.1111/raq.12535
72. Cao, L. *et al.* China's Aquaculture and the World's Wild Fisheries. *Science (80-.).* **347**, 133–135 (2015).
73. Froese, R. & Pauly, D. FishBase. *World Wide Web electronic publication* (2019). Available at: www.fishbase.org. (Accessed: 10th November 2020)