


The future of food from the sea




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Global food demand is rising, and serious questions remain about whether supply can increase sustainably¹. Land-based expansion is possible but may exacerbate climate change and biodiversity loss, and compromise the delivery of other ecosystem services^{2–6}. As food from the sea represents only 17% of the current production of edible meat, we ask how much food we can expect the ocean to sustainably produce by 2050. Here we examine the main food-producing sectors in the ocean—wild fisheries, finfish mariculture and bivalve mariculture—to estimate ‘sustainable supply curves’ that account for ecological, economic, regulatory and technological constraints. We overlay these supply curves with demand scenarios to estimate future seafood production. We find that under our estimated demand shifts and supply scenarios (which account for policy reform and technology improvements), edible food from the sea could increase by 21–44 million tonnes by 2050, a 36–74% increase compared to current yields. This represents 12–25% of the estimated increase in all meat needed to feed 9.8 billion people by 2050. Increases in all three sectors are likely, but are most pronounced for mariculture. Whether these production potentials are realized sustainably will depend on factors such as policy reforms, technological innovation and the extent of future shifts in demand.

Human population growth, rising incomes and preference shifts will considerably increase global demand for nutritious food in the coming decades. Malnutrition and hunger still plague many countries^{1,7}, and projections of population and income by 2050 suggest a future need for more than 500 megatonnes (Mt) of meat per year for human consumption (Supplementary Information section I.1.6). Scaling up the production of land-derived food crops is challenging, because of declining yield rates and competition for scarce land and water resources². Land-derived seafood (freshwater aquaculture and inland capture fisheries; we use seafood to denote any aquatic food resource, and food from the sea for marine resources specifically) has an important role in food security and global supply, but its expansion is also constrained. Similar to other land-based production, the expansion of land-based aquaculture has resulted in substantial environmental externalities that affect water, soil, biodiversity and climate, and which compromise the ability of the environment to produce food^{3–6}. Despite the importance of terrestrial aquaculture in seafood production

(Supplementary Fig. 3), many countries—notably China, the largest inland-aquaculture producer—have restricted the use of land and public waters for this purpose, which constrains expansion⁸. Although inland capture fisheries are important for food security, their contribution to total global seafood production is limited (Supplementary Table 1) and expansion is hampered by ecosystem constraints. Thus, to meet future needs (and recognizing that land-based sources of fish and other foods are also part of the solution), we ask whether the sustainable production of food from the sea has an important role in future supply.

Food from the sea is produced from wild fisheries and species farmed in the ocean (mariculture), and currently accounts for 17% of the global production of edible meat^{9–12} (Supplementary Information section I.1, Supplementary Tables 1–3). In addition to protein, food from the sea contains bioavailable micronutrients and essential fatty acids that are not easily found in land-based foods, and is thus uniquely poised to contribute to global food and nutrition security^{13–16}.

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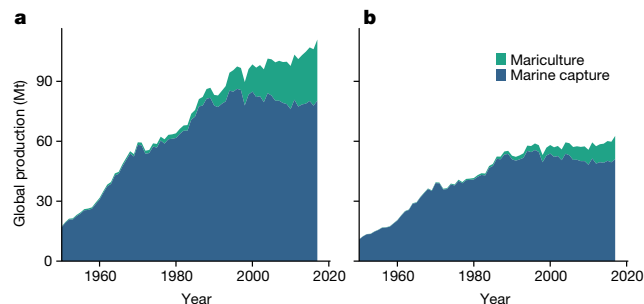


Fig. 1 | Marine harvest and food from the sea over time (excluding aquatic plants). Data are from ref. ⁹. **a, b.** Harvests (live-weight production) (**a**) are converted to food equivalents (edible production)¹⁰ (**b**). In **b**, there is also an assumption that 18% of the annual landings of marine wild fisheries are directed towards non-food purposes⁴⁷.

Widely publicized reports about climate change, overfishing, pollution and unsustainable mariculture give the impression that sustainably increasing the supply of food from the sea is impossible. On the other hand, unsustainable practices, regulatory barriers, perverse incentives and other constraints may be limiting seafood production, and shifts in policies and practices could support both food provisioning and conservation goals^{17,18}. In this study, we investigate the potential of expanding the economically and environmentally sustainable production of food from the sea for meeting global food demand in 2050. We do so by estimating the extent to which food from the sea could plausibly increase under a range of scenarios, including demand scenarios under which land-based fish act as market substitutes.

The future contribution of food from the sea to global food supply will depend on a range of ecological, economic, policy and technological factors. Estimates based solely on ecological capacity are useful, but do not capture the responses of producers to incentives and do not account for changes in demand, input costs or technology^{19,20}. To account for these realities, we construct global supply curves of food from the sea that explicitly account for economic feasibility and feed constraints. We first derive the conceptual pathways through which food could be increased in wild fisheries and in mariculture sectors. We then empirically derive the magnitudes of these pathways to estimate the sustainable supply of food from each seafood sector at any given price²¹. Finally, we match these supply curves with future demand scenarios to estimate the likely future production of sustainable seafood at the global level.

Sustainably increasing food from the sea

We describe four main pathways by which food supply from the ocean could increase: (1) improving the management of wild fisheries; (2) implementing policy reforms of mariculture; (3) advancing feed technologies for fed mariculture; and (4) shifting demand, which affects the quantity supplied from all three production sectors.

Although mariculture production has grown steadily over the past 60 years (Fig. 1) and provides an important contribution to food security²², the vast majority (over 80%) of edible meat from the sea comes from wild fisheries⁹ (Fig. 1b). Over the past 30 years, supply from this wild food source has stabilized globally despite growing demand worldwide, which has raised concerns about our ability to sustainably increase production. Of nearly 400 fish stocks around the world that have been monitored since the 1970s by the UN Food and Agriculture Organization (FAO), approximately one third are currently not fished within sustainable limits¹. Indeed, overfishing occurs often in poorly managed ('open access') fisheries. This is disproportionately true in regions with food and nutrition security concerns¹. In open-access

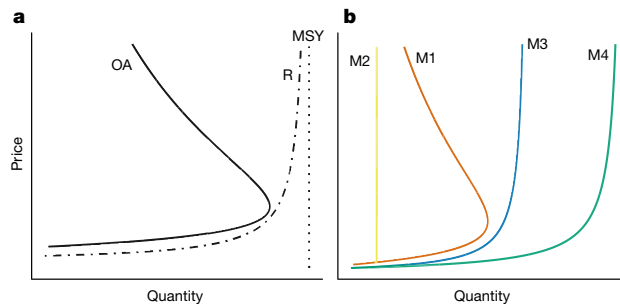


Fig. 2 | Hypothetical supply curves for wild fisheries and mariculture, showing the influence of price on production quantity. **a.** Wild fisheries. Curves represent poorly managed (open access) fisheries (OA); management reform for all fisheries (MSY); and economically rational management reform (R). **b.** Mariculture. Curves represent weak regulations that allow for ecologically unsustainable production (M1); overly restrictive policies (M2); policies that allow for sustainable expansion (M3); and a reduced dependence on limited feed ingredients for fed-mariculture production (M4).

fisheries, fishing pressure increases as the price rises: this can result in a 'backward-bending' supply curve^{23,24} (the OA curve in Fig. 2a), in which higher prices result in the depletion of fish stocks and reduced productivity—and thus reduced equilibrium food provision.

Fishery management allows overexploited stocks to rebuild, which can increase long-term food production from wild fisheries^{25,26}. We present two hypothetical pathways by which wild fisheries could adopt improved management (Fig. 2a). First, independent of economic conditions, governments can impose reforms in fishery management. The resulting production in 2050 from this pathway—assuming that fisheries are managed for maximum sustainable yield (MSY)—is represented by the MSY curve in Fig. 2a, and is independent of price. The second pathway explicitly recognizes that wild fisheries are expensive to monitor (for example, via stock assessments) and manage (for example, via quotas)—management reforms are adopted only by fisheries for which future profits outweigh the associated costs of improved management. When management entities respond to economic incentives, the number of fisheries for which the benefits of improved management outweigh the costs increases as demand (and thus price) increases. This economically rational management endogenously determines which fisheries are well-managed, and thus how much food production they deliver, resulting in supply curve designated R in Fig. 2a.

Although the production of wild fisheries is approaching its ecological limits, current mariculture production is far below its ecological limits and could be increased through policy reforms, technological advancements and increased demand^{19,27}. We present explanations for why food production from mariculture is currently limited, and describe how the relaxation of these constraints gives rise to distinct pathways for expansion (Fig. 2b). The first pathway recognizes that ineffective policies have limited the supply^{28,29}. Lax regulations in some regions have resulted in poor environmental stewardship, disease and even collapse, which have compromised the viability of food production in the long run (curve M1 in Fig. 2b). In other regions, regulations are overly restrictive, convoluted and poorly defined^{30,31}, and thus limit production (curve M2 in Fig. 2b). In both cases, improved policies and implementation can increase food production by preventing and ending environmentally damaging mariculture practices (the shift from M1 to M3 in Fig. 2b) and allowing for environmentally sustainable expansion (the shift from M2 to M3 in Fig. 2b).

The second pathway to sustainably increase mariculture production is through further technological advances in finfish feeds. Currently, most mariculture production (75%) requires some feed input (such as fishmeal and fish oil) that is largely derived from wild forage fisheries¹.

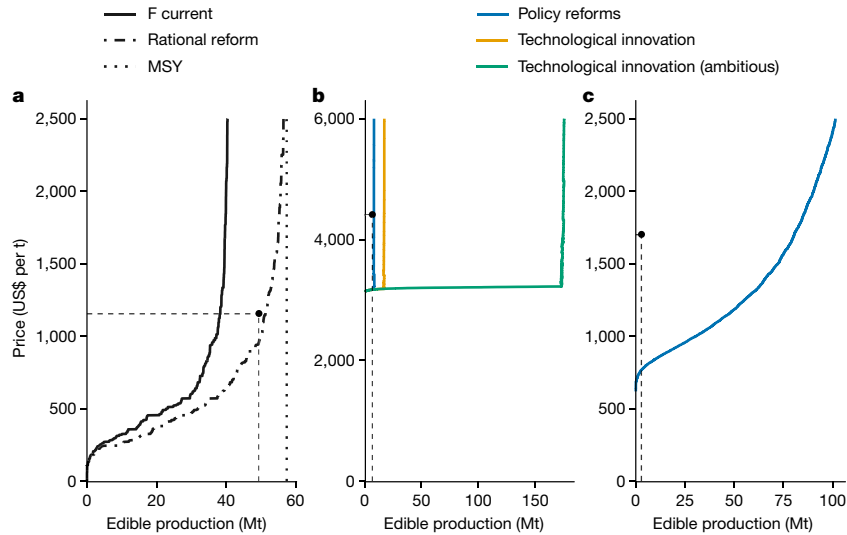


Fig. 3 | Estimated sustainable supply curves for wild fisheries, finfish mariculture and bivalve mariculture. **a–c**, Points represent current production and average price in each sector: marine wild fisheries (**a**), finfish mariculture (**b**) and bivalve mariculture (**c**). In **a**, supply curves for annual steady-state edible production from wild fisheries are shown under three different management scenarios: production in 2050 under current fishing effort assuming that fishing only occurs in fisheries that are profitable (*F* current); the economically rational supply curve aimed at maximizing profitability (rational reform); and a reform policy aimed at maximizing food production, regardless of the economic

considerations (MSY). In **b**, supply curves for finfish (fed) mariculture show: future steady-state production under current feed assumptions and policy reform (policy reform); sustainable production assuming policy reform and a 50% reduction in fishmeal and fish oil feed requirements (technological innovation); and sustainable production assuming policy reform and a 95% reduction in fishmeal and fish oil feed requirements (technological innovation (ambitious)). In all cases, feed ingredients are from the economically rational reform of wild fisheries.

If fed mariculture continues using fishmeal and fish oil at the current rate, its growth will be constrained by the ecological limits of these wild fisheries³². Alternative feed ingredients—including terrestrial plant- or animal-based proteins, seafood processing waste, microbial ingredients, insects, algae and genetically modified plants—are rapidly being developed and are increasingly used in mariculture feeds^{33–36}. These innovations could decouple fed mariculture from wild fisheries (but may refocus pressure on terrestrial ecosystems) and could catalyse considerable expansion in some regions^{37,38}. This has already begun for many fed species, such as Atlantic salmon—for which fish-based ingredient use has been reduced from 90% in the 1990s to just 25% at present³⁹. A reduced reliance on fishmeal and fish oil is expected to shift the supply curve of fed mariculture to the right (curve M4 in Fig. 2b).

The final pathway is a shift in demand (aggregated across all global fish consumers), which affects all three production sectors. When the sustainable supply curve is upward-sloping, an increase in demand (rightward shift; for example, from rising population, income or preferences) increases food production.

Estimated sustainable supply curves

We estimate supply curves of food from the sea in 2050 for the three largest food sectors in the ocean: wild fisheries, finfish mariculture and bivalve mariculture. We construct global supply curves for marine wild fisheries using projected future production for 4,702 fisheries under alternative management scenarios (Fig. 3a). We model future production with a bioeconomic model based on ref. 17, which tracks annual biomass, harvest and profit, and accounts for costs associated with extraction and management (see Methods and Supplementary Information for details). Managing all fisheries to maximize food production (MSY) would result in 57.4 Mt of food in 2050 (derived from 89.3 Mt of total harvest, hereafter noted as live-weight equivalent), representing a 16% increase compared to the current food production (Fig. 3a). Under a scenario of economically rational reform (in which

the management approach and exploitation rate of fisheries depend on profitability), the price influences production (Fig. 3a). At current mean global prices, this scenario would result in 51.3 Mt of food (77.4 Mt live-weight equivalent)—a 4% increase compared to current food production. These management-induced shifts in supply are ultimately limited by the carrying capacity of the ecosystem. If current fishing pressure is maintained for each fish stock when profitable (*F* current, referring to the current fishing mortality rate), food production from wild fisheries is lower for most prices than under the two reform scenarios (owing to fishing too intensively on some stocks, and too conservatively on others)²⁵: this supply curve is not backward-bending, as it reflects constant fishing pressures.

We estimate the production potential of mariculture at a resolution of 0.217° around the world for finfish and bivalves. Ecological conditions—sea surface temperature, dissolved oxygen and primary productivity—determine the suitability of each pixel for mariculture production. We build on previous models¹⁹ by including economic considerations (including the capital costs of vessels and equipment, and the operating costs of wages, fuel, feed, insurance and maintenance; Supplementary Tables 5–7) to determine whether farming an ecologically suitable area is economically profitable at any given price. Summing economically viable production for each sector at the global level for different prices produces two mariculture supply curves. This approach assumes that the most profitable sites will be developed first, but does not explicitly include challenges such as the cost of public regulation and the delineation of property rights. Farm design is based on best practice for sustainable production, and we therefore interpret the results as an environmentally sustainable supply. We examine a range of assumptions regarding production costs, and explore different technological assumptions with respect to the species type farmed for finfish mariculture (Methods, Supplementary Information section 1.3, Supplementary Table 9). The supply curve for finfish mariculture differs substantially among future feed-technology scenarios, although all of these scenarios foretell a substantial increase in annual food supply in

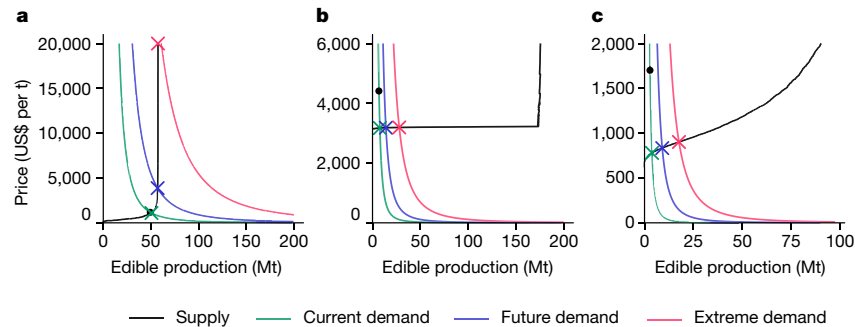


Fig. 4 | Supply and demand curves of food from the sea for the three sectors. **a–c.** Supply and demand curves for marine wild fisheries (**a**), finfish mariculture (**b**) and bivalve mariculture (**c**). In each panel, the solid black line is the supply curve from Fig. 3: for wild fisheries, the rational reform scenario is shown, and for finfish mariculture the technological innovation (ambitious)

scenario is shown. Future demand refers to estimated demand in 2050; extreme demand represents a doubling of the estimated demand in 2050. The intersections of demand and sustainable supply curve (indicated with crosses) provide an estimate of the future food from the sea. Points represent current production and average price in each sector.

the future compared to the current production of the sector (6.8 Mt of food) (Fig. 3b). However, the policy reform scenario—which assumes mariculture policies are neither too restrictive nor lax (curve M3 in Fig. 2b), but that fishmeal and fish oil requirements match present-day conditions—produces a modest additional 1.4 Mt of food at current prices. In this scenario, marine-based feed inputs limit mariculture expansion even as the price increases considerably.

Two feed-innovation scenarios—representing policy reform plus a 50% or 95% reduction in fishmeal and fish oil requirements, which we refer to as ‘technological innovation’ and ‘technological innovation (ambitious)’, respectively—can substantially shift the supply curve.

At current prices, future supply under these scenarios is predicted to increase substantially to 17.2 Mt and 174.5 Mt of food for technological innovation and technological innovation (ambitious) scenarios, respectively (Fig. 3b). Bivalve mariculture is constrained by current policy but not by feed limitations, and is poised to expand substantially under policy reform scenarios. At current prices, economically rational production could lead to an increase from 2.9 Mt to 80.5 Mt of food (Fig. 3c). Even if our model underestimates costs by 50%, policy reforms would increase the production potential of both fed and unfed mariculture at current prices. For fed mariculture, this remains true even when evaluating mariculture species with different feed demands (Atlantic salmon, milkfish and barramundi).

Estimates of future food from the sea

Our supply curves suggest that all three sectors of ocean food production are capable of sustainably producing much more food than they do at present. The quantity of seafood demanded will also respond to price. We present three demand-curve estimates, shown in Fig. 4 (Methods, Supplementary Information). The intersections of future demand and sustainable supply curves provide an estimate of future food production from the sea. Because it is a substantial contributor to fish supply and—in some instances—acts as a market substitute for seafood, we also account for land-based aquatic food production (from freshwater aquaculture and inland capture fisheries; Supplementary Information section 1.4, Supplementary Tables 10–12). Estimates of future production from this fourth sector (‘inland fisheries’) are shown side-by-side in Supplementary Fig. 3 and Supplementary Tables 13, 14 (for quantities of food) and in Supplementary Tables 15, 16 (for live-weight equivalents), and are discussed with the results on food from the sea.

Even under current demand curves (green curves in Fig. 4), the economically rational reform of marine wild fisheries and sustainable mariculture policies (stocking densities consistent with European organic standards⁴⁰) under the technological innovation (ambitious) scenario could result in a combined total of 62 Mt of food from the

sea per year, 5% more than the current levels (59 Mt). But we know that demand will increase as incomes rise and populations expand. Under the ‘future demand’ scenario (purple curves in Fig. 4), total food from the sea is projected to increase to 80 Mt. If demand shifts even more (as represented by our ‘extreme demand’ scenario; red curves in Fig. 4), the intersection of supply and demand is expected to increase to 103 Mt of food. Using the approach used by the FAO to estimate future needs, the world will require an additional 177 Mt of meat by 2050 (Supplementary Information section 1.1.6)—our results suggest that additional food from the sea alone could plausibly contribute 12–25% of this need. Another possibility we consider is that future consumers will not distinguish between fish-producing sectors, such that all sources of fish (including land-based) would be substitutes for each other. Adopting that assumption alters the supply-and-demand equilibrium, and implies that the increase among all sources of fish (sea and land) relative to the present could be between 90–212 Mt of food; under this scenario, expansion of aquatic foods alone could possibly exceed the 177-Mt benchmark.

Our results also suggest that the future composition of food from the sea will differ substantially from the present (Fig. 5). Although wild fisheries dominate edible marine production at present, we project that by 2050 up to 44% of edible marine production could come from mariculture (rising to 76% when all fish are substitutes and land-based fish are included under extreme demand scenarios (Supplementary Fig. 3, Supplementary Table 14)), although all sectors could increase production. Although even more substantial increases are technically possible (for example, fed mariculture alone is capable of generating at least the benchmark 177 Mt of additional meat), actually realizing these gains would require enormous shifts in demand.

Our models rely on a number of assumptions and parameters that are uncertain, and which may interact in nonlinear ways. To test the robustness of our main conclusions, we examine a range of scenarios and run an extensive sensitivity analysis (Supplementary Information). Across a wide range of cost, technology and demand scenarios, we find that sustainably harvested food from the sea: (1) has the potential to increase considerably in the coming decades; (2) will change in composition, with a greater future share coming from mariculture; and (3), in aggregate, could have an outsized role in meeting future meat demands around the world (Supplementary Figs. 1–4, Supplementary Tables 13–17).

Conclusions

Global food demand is rising, and expanding land-based production is fraught with environmental and health concerns. Because seafood is nutritionally diverse and avoids or lessens many of the environmental

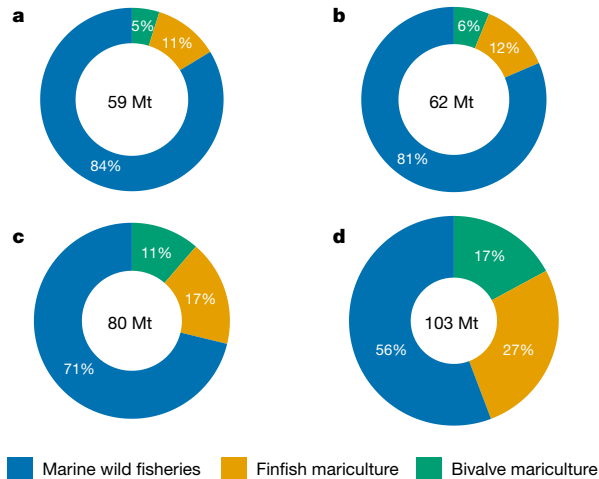


Fig. 5 | Composition of current and future food from the sea under three alternative demand scenarios. **a**, Composition of current (initial production) food from the sea. **b–d**, Composition of future (2050) food from the sea under scenarios of current (**b**), future (**c**) and extreme (**d**) demand. The sustainable supply curves assumed for these predictions are: rational reform for wild fisheries; technological innovation (ambitious) for finfish mariculture; and policy reform for bivalve mariculture, as shown in Fig. 3. The total production of food from the sea per year is shown in the centre in each panel.

burdens of terrestrial food production, it is uniquely positioned to contribute to both food provision and future global food and nutrition security. Our estimated sustainable supply curves of food from the sea suggest substantial possibilities for future expansion in both wild fisheries and mariculture. The potential for increased global production from wild fisheries hinges on maintaining fish populations near their most-productive levels. For underutilized stocks, this will require expanding existing markets. For overfished stocks, this will require adopting or improving management practices that prevent overfishing and allow depleted stocks to rebuild. Effective management practices commonly involve setting and enforcing science-based limits on catch or fishing effort, but appropriate interventions will depend on the biological, socioeconomic, cultural and governance contexts of individual fisheries. Effective management will be further challenged by climate change, species composition changes in marine ecosystems and illegal fishing. Directing resources away from subsidies that enhance fishing capacity towards building institutional and technical capacity for fisheries research, management and enforcement will help to meet these challenges. Increased mariculture production will require management practices and policies that allow for environmentally sustainable expansion, while balancing the associated trade-offs to the greatest extent possible; this principle underpins the entire analysis. We find that substantial expansion is realistic, given the costs of production and the likely future increase in demand.

We have identified a variety of ways that sustainable supply curves can shift outward. These shifts interact with future demand to determine the plausible future equilibrium quantity of food produced from the sea. We find that although supply could increase to more than six times the current level (primarily via expanded mariculture), the demand shift required to engage this level of supply is unlikely. Under more realistic demand scenarios and appropriate reforms of the supply, we find that food from the sea could increase in all three sectors (wild fisheries, finfish mariculture and bivalve mariculture) to a total of 80–103 Mt of food in 2050 versus 59 Mt at present (in live-weight equivalents, 159–227 Mt compared to 102 Mt at present). When combined with projected inland production, this represents an 18–44% per decade increase in live-weight production, which is

somewhat higher than the 14% increase that the Organisation for Economic Co-operation and Development (OECD) and the FAO project for total fish production during the next decade⁴¹. Under some scenarios, future production could represent a disproportionate fraction of the estimated total increase in global food production that will be required to feed 9.8 billion people by 2050. Substantial growth in mariculture will rely partly on public perceptions. Although there is some evidence of a negative public perception of aquaculture, it is highly variable by region and by context^{42,43}, and certifications and the provision of other information can help to alleviate concerns and expand demand⁴⁴.

These global projections will not have uniform implications around the world. For example, improved policies that shift the supply curve outward will decrease prices, but income-induced demand shifts will increase prices. Both effects increase production, but have vastly different consequences for low-income consumers. Bivalves may contribute substantially to food security by providing relatively low-cost and thus accessible food, because they have a high production potential at low costs compared to finfish production (Fig. 3). If all seafood is perfectly substitutable, bivalves could contribute 43% and 34% of future aquatic food under future and extreme demand scenarios, respectively (Supplementary Fig. 3)—which suggests potential large increases in production, provided demand is high enough. Trade also has an important role in distributing seafood from high-production to low-production regions, and in overcoming regional mismatches in price. The rate of international trade of seafood products has increased over past decades, and 27% of seafood products were traded in 2016¹, although major economic disruptions—such as the COVID-19 pandemic—can jointly reduce both supply and demand of traded seafood. On the other hand, trade may become increasingly relied upon as climate change alters regional productivity.

Substantially expanding the production of food from the sea will bring co-benefits and trade-offs, and will require national and inter-regional governance, as well as local capacity to ensure equity and sustainability. The improved management of wild fisheries can not only increase fish biomass, but also brings the co-benefit of improved livelihoods of fishers. However, there will be some short-term costs as overfished stocks rebuild to levels that support greater food provision. As mariculture expands, interactions with wild fisheries and other ecosystem services (via spatial overlaps, pollution and so on) must be constantly addressed. Ambitious technical innovation (that is, the substitution of marine ingredients with terrestrial-sourced proteins) can help to decouple fed mariculture from wild fisheries, but will probably refocus some pressure on terrestrial ecosystems. Climate change will further challenge food security. Estimates suggest that active adaptation to climate-induced changes will be crucial in both wild fisheries⁴⁵ and mariculture⁴⁶. Climate-adaptive management of wild fisheries and decisions regarding mariculture production (for example, the type of feed used, species produced and farm siting) could improve food provision from the sea under conditions of climate change.

We have shown that the sea can be a much larger contributor to sustainable food production than is currently the case, and that this comes about by implementing a range of plausible and actionable mechanisms. The price mechanism—when it motivates improved fishery management and the sustainable expansion of mariculture into new areas—arises from change in demand, and acts on its own without any explicit intervention. The feed technology mechanism is driven by incentives to innovate, and thus acquire intellectual property rights to new technologies. When intellectual property is not ensured, or to achieve other social goals, there may be a role for public subsidies or other investments in these technologies. The policy mechanism pervades all three production sectors, and could make—or break—the ability of food from the sea to sustainably, equitably and efficiently expand in the future.

Online content

Any methods, additional references, Nature Research reporting summaries, source data, extended data, supplementary information, acknowledgements, peer review information; details of author contributions and competing interests; and statements of data and code availability are available at <https://doi.org/10.1038/s41586-020-2616-y>.

1. FAO. *The State of World Fisheries and Aquaculture* (FAO, 2018).
2. Olsen, Y. Resources for fish feed in future mariculture. *Aquacult. Environ. Interact.* **1**, 187–200 (2011).
3. Foley, J. A. et al. Solutions for a cultivated planet. *Nature* **478**, 337–342 (2011).
4. Foley, J. A. et al. Global consequences of land use. *Science* **309**, 570–574 (2005).
5. Mbow, C. et al. in *Climate Change and Land (IPCC Special Report)* (eds Shukla, P. R. et al.) Ch. 5 (IPCC, 2019).
6. Amundson, R. et al. Soil and human security in the 21st century. *Science* **348**, 1261071 (2015).
7. UNDP. Sustainable Development Goal 2, *Sustainable Development Goals*. <https://sustainabledevelopment.un.org/sdg2> (accessed 27 July 2020).
8. De Silva, S. & Davy, F. *Success Stories in Asian Aquaculture* (Springer 2010).
9. FAO Fisheries and Aquaculture Department. *FishStatJ – Software for Fishery and Aquaculture Statistical Time Series*. <http://www.fao.org/fishery/statistics/software/fishstatj/en> (2019).
10. 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**, 103547 (2019).
11. FAO. *FAOSTAT*. <http://www.fao.org/faostat/en/#home> (2020).
12. Nijdam, D., Rood, T. & Westhoek, H. The price of protein: review of land use and carbon footprints from life cycle assessments of animal food products and their substitutes. *Food Policy* **37**, 760–770 (2012).
13. Kawarazuka, N. & Béné, C. Linking small-scale fisheries and aquaculture to household nutritional security: an overview. *Food Secur.* **2**, 343–357 (2010).
14. Allison, E. H. *Aquaculture, Fisheries, Poverty and Food Security (Working Paper 2011–65)* (WorldFish Center, 2011).
15. Golden, C. D. et al. Fall in fish catch threatens human health. *Nature* **534**, 317–320 (2016).
16. Hicks, C. C. et al. Harnessing global fisheries to tackle micronutrient deficiencies. *Nature* **574**, 95–98 (2019).
17. Costello, C. et al. Global fishery prospects under contrasting management regimes. *Proc. Natl Acad. Sci. USA* **113**, 5125–5129 (2016).
18. Ye, Y. & Gutierrez, N. L. Ending fishery overexploitation by expanding from local successes to globalized solutions. *Nat. Ecol. Evol.* **1**, 0179 (2017).
19. Gentry, R. R. et al. Mapping the global potential for marine aquaculture. *Nat. Ecol. Evol.* **1**, 1317–1324 (2017).
20. Troell, M., Jonell, M. & Henriksson, P. J. G. Ocean space for seafood. *Nat. Ecol. Evol.* **1**, 1224–1225 (2017).
21. Costello, C. et al. *The Future of Food from the Sea* <http://oceanpanel.org/future-food-sea> (World Resources Institute, 2019).
22. Belton, B., Bush, S. R. & Little, D. C. Not just for the wealthy: rethinking farmed fish consumption in the Global South. *Glob. Food Secur.* **16**, 85–92 (2018).
23. Copes, P. The backward-bending supply curve of the fishing industry. *Scott. J. Polit. Econ.* **17**, 69–77 (1970).
24. Nielsen, M. Trade liberalisation, resource sustainability and welfare: the case of East Baltic cod. *Ecol. Econ.* **58**, 650–664 (2006).
25. Hilborn, R. & Costello, C. The potential for blue growth in marine fish yield, profit and abundance of fish in the ocean. *Mar. Policy* **87**, 350–355 (2018).
26. Hilborn, R. et al. Effective fisheries management instrumental in improving fish stock status. *Proc. Natl Acad. Sci. USA* **117**, 2218–2224 (2020).
27. Joffre, O. M., Klerkx, L., Dickson, M. & Verdegem, M. How is innovation in aquaculture conceptualized and managed? A systematic literature review and reflection framework to inform analysis and action. *Aquaculture* **470**, 129–148 (2017).
28. Abate, T. G., Nielsen, R. & Tveterås, R. Stringency of environmental regulation and aquaculture growth: a cross-country analysis. *Aquac. Econ. Manag.* **20**, 201–221 (2016).
29. Gentry, R. R., Ruff, E. O. & Lester, S. E. Temporal patterns of adoption of mariculture innovation globally. *Nat. Sustain.* **2**, 949–956 (2019).
30. The Sea Grant Law Center. *Overcoming Impediments to Shellfish Aquaculture Through Legal Research and Outreach: Case Studies* (NOAA, 2019).
31. Davies, I. P. et al. Governance of marine aquaculture: pitfalls, potential, and pathways forward. *Mar. Policy* **104**, 29–36 (2019).
32. Froehlich, H. E., Jacobsen, N. S., Essington, T. E., Clavelle, T. & Halpern, B. S. Avoiding the ecological limits of forage fish for fed aquaculture. *Nat. Sustain.* **1**, 298–303 (2018).
33. Klinger, D. & Naylor, R. Searching for solutions in aquaculture: charting a sustainable course. *Annu. Rev. Environ. Resour.* **37**, 247–276 (2012).
34. Cao, L. et al. China's aquaculture and the world's wild fisheries. *Science* **347**, 133–135 (2015).
35. Little, D. C., Newton, R. W. & Beveridge, M. C. M. Aquaculture: a rapidly growing and significant source of sustainable food? Status, transitions and potential. *Proc. Nutr. Soc.* **75**, 274–286 (2016).
36. Shah, M. R. et al. Microalgae in aquafeeds for a sustainable aquaculture industry. *J. Appl. Phycol.* **30**, 197–213 (2018).
37. Troell, M. et al. Does aquaculture add resilience to the global food system? *Proc. Natl Acad. Sci. USA* **111**, 13257–13263 (2014).
38. Froehlich, H. E., Runge, C. A., Gentry, R. R., Gaines, S. D. & Halpern, B. S. Comparative terrestrial feed and land use of an aquaculture-dominant world. *Proc. Natl Acad. Sci. USA* **115**, 5295–5300 (2018).
39. Aas, T. S., Ytrestøyl, T. & Åsgård, T. Utilization of feed resources in the production of Atlantic salmon (*Salmo salar*) in Norway: An update for 2016. *Aquacult. Rep.* **15**, 100216 (2019).
40. European Union. Commission Regulation (EC) No 889/2008 of 5 September 2008 laying down detailed rules for the implementation of Council Regulation (EC) No 834/2007 on organic production and labelling of organic products with regard to organic production, labelling and control. *Offic. J. EU* **L250**, 1–84 (2008).
41. OECD & Food and Agriculture Organization of the United Nations. *OECD-FAO Agricultural Outlook 2019–2028* (OECD, 2019).
42. Froehlich, H. E., Gentry, R. R., Rust, M. B., Grimm, D. & Halpern, B. S. Public perceptions of aquaculture: evaluating spatiotemporal patterns of sentiment around the world. *PLoS ONE* **12**, e0169281 (2017).
43. Bacher, K. *Perceptions and Misconceptions of Aquaculture: A Global Overview* (GLOBEFISH, 2015).
44. Bronnmann, J. & Asche, F. Sustainable seafood from aquaculture and wild fisheries: insights from a discrete choice experiment in Germany. *Ecol. Econ.* **142**, 113–119 (2017).
45. Gaines, S. D. et al. Improved fisheries management could offset many negative effects of climate change. *Sci. Adv.* **4**, eaao1378 (2018).
46. Froehlich, H. E., Gentry, R. R. & Halpern, B. S. Global change in marine aquaculture production potential under climate change. *Nat. Ecol. Evol.* **2**, 1745–1750 (2018).
47. Cashin, T., Tyedmers, P. & Parker, R. W. R. Global reduction fisheries and their products in the context of sustainable limits. *Fish Fish.* **18**, 1026–1037 (2017).

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Methods

Sample size was a census of all available fisheries data. No experiments were conducted.

Here we describe our methods in brief: detailed methods, sensitivity analyses and robustness checks are provided in the Supplementary Information.

Sustainable supply curves

The supply of food from marine wild fisheries is jointly determined by ecosystem constraints, fishery policy and prevailing economic conditions. Estimated supply curves show the projected 2050 production quantity at a given price, incorporating harvesting costs, management costs and fishery-specific engagement decisions for individual fisheries. Current management of the 4,702 marine fisheries included in our study range from open access to strong target-based management¹⁷. Using data from the RAM Legacy Stock Assessment Database⁴⁸, the FAO⁹ and refs.^{17,49,50}, we calculate three supply curves that represent summed global production from established wild fisheries for a range of prices (Fig. 3). The first (F_{current}) assumes that all fisheries in the world maintain their current fishing mortality rate if profitable (that is, fisheries for which current fishing pressure would result in steady-state profit < 0 are not fished). The second (rational reform) assumes that fisheries are reformed to maximize long-term food production (that is, adopt F_{MSY} , the fishing mortality rate that results in maximum sustainable yield (MSY)), but only at prices for which reform results in greater future profit than that of current management. Importantly, adopting reform is associated with greater management costs for fisheries that are currently weakly managed. If a fishery is managed, its production changes, which alters the supply curve. Production occurs in a given fishery only if future profit > 0 . The third supply curve (MSY) assumes that all fisheries are managed to maximize sustainable yield, regardless of the cost or benefit of doing so (Fig. 3). Supply curves under alternative cost assumptions yield results similar to those presented in Fig. 3 (Supplementary Fig. 1).

To construct supply curves for finfish and bivalve mariculture (which account for 83% of current production of edible animal products from mariculture¹¹), we use a previously published¹⁹ global suitability dataset at a resolution of 0.217°. Ecological conditions (that is, surface temperature, dissolved oxygen and primary productivity (bivalves only)) determine the suitability of different areas for production. We build on ref.¹⁹ by including economic considerations (for example, the capital costs of vessels and equipment and operating costs of wages, fuel, feed, insurance and maintenance; see Supplementary Information section 1.3, Supplementary Tables 5–7 for more details) to determine whether an ecologically suitable area is also economically profitable to farm at a given price. For any given price, we estimate the potential production and profitability of each pixel, and determine the global set of economically viable pixels for mariculture production of finfish and bivalves; we allow for production of both kinds of mariculture in the same pixel, provided the pixel is economically suitable for both. Summing production in this manner at the global level provides a point on the supply curve, at which farm design (Supplementary Table 4) is based on best practices for sustainable production (that is, stocking densities consistent with European organic standards⁴⁰). We then derive supply curves under different assumptions regarding mariculture policy and technological innovation, which affect the parameters of the supply model.

We estimate supply curves for finfish mariculture under three scenarios, all of which assume that wild fisheries are rationally managed; this pins down the potential supply of wild fish that can be used as feed in mariculture (Supplementary Table 8). We display three supply curves for fed mariculture (Fig. 3). The policy reforms scenario represents a future in which regulatory barriers are removed, unsustainable production is prevented and mariculture continues to use feed ingredients

from wild fisheries at the current rate (that is, feed conversion ratios remain static, fishmeal and fish oil inclusion rates in feed remain the same, and feed availability depends on production from wild fisheries). This scenario represents the economically rational sustainable production given the current feed context. Two technological innovation scenarios represent policy reform plus a 50% and (a more ambitious) 95% reduction in fishmeal and fish oil requirements for fed mariculture production. The supply curve for bivalve (unfed) mariculture (Fig. 3) reflects production in the set of pixels for which unfed mariculture can be profitably produced at any given price.

Supply meets demand

To estimate how food from the sea might help to meet future increases in demand at the global level, we require estimates of the current and future demand curves of food from the sea. The intersection of future demand curves and our estimated sustainable supply curves provides an estimate of food from the sea in 2050. As a benchmark, we assume that the three sectors are independent, but that increases in demand are parametric, so each of the three sectors experiences a proportional increase in future demand—for example, as global population and per capita incomes rise (see Supplementary Information for detailed results, assuming all aquatic foods are perfect substitutes). We assume a straightforward structure in which each sector faces an isoelastic demand (for example, see ref.⁵¹, with own price elasticity = -0.382 ; ref.⁵²; and sector-specific income elasticities estimated from ref.⁵¹). Using these elasticities, the coefficient on current-demand curve in each sector (current, in Fig. 4) is tuned so the demand curve passes through the current price of seafood in that sector (averaged across fish from that sector) given the current global gross domestic product and population. Effectively, this approach assumes that all fish within a sector are substitutes. We do not explicitly estimate a current supply curve because it is not required to perform our calculations and—for reasons stated in the Article—we do not necessarily regard the current supply as sustainable.

To project future demand at the global level, we develop two scenarios that we term future and extreme (Fig. 4). The future demand represents the demand curve for food from the sea in each sector given exogenous estimates of future population size and global income in 2050^{53,54}, which are entered as parameters in the demand curve (Supplementary Information). The extreme scenario doubles the quantity demanded at any given price in 2050, relative to the future scenario; we regard demand shifts larger than this amount as unlikely.

The Supplementary Information contains an extensive set of robustness checks and sensitivity analyses. One important alternative to the model in the Article is to allow all fish to be perfect substitutes in the future. Under that model, land-based fish production (aquaculture and capture) must be accounted for because those fish act as substitutes for food from the sea. Although this tends to increase the final estimates of food production from the sea, our qualitative findings are robust to this assumption and the Supplementary Information reports how this changes the model results described in the Article.

Reporting summary

Further information on research design is available in the Nature Research Reporting Summary linked to this paper.

Data availability

All datasets analysed during the current study are available in a Dryad repository at <https://datadryad.org/stash/dataset/doi:10.25349/D96G6H>.

Code availability

All code used to conduct the study are available in a GitHub repository: https://github.com/emlab-ucsb/future_food_from_sea.

Article

48. Ricard, D., Minto, C., Jensen, O. P. & Baum, J. K. Examining the knowledge base and status of commercially exploited marine species with the RAM Legacy Stock Assessment Database. *Fish Fish.* **13**, 380–398 (2012).
49. Melnychuk, M. C., Clavelle, T., Owashi, B. & Strauss, K. Reconstruction of global ex-vessel prices of fished species. *ICES J. Mar. Sci.* **74**, 121–133 (2017).
50. Mangin, T. et al. Are fishery management upgrades worth the cost? *PLoS ONE* **13**, e0204258 (2018).
51. Cai, J. & Leung, P. *Short-term Projection of Global Fish Demand and Supply Gaps* (FAO, 2017).
52. Muhammad, A., Seale, J. L. Jr, Meade, B. & Regmi, A. *International Evidence on Food Consumption Patterns: An Update Using 2005 International Comparison Program Data*. Technical Bulletin No. TB-1929 (United States Department of Agriculture, 2011).
53. PwC. *The Long View: How will the global economic order change by 2050?* <https://www.pwc.com/gx/en/world-2050/assets/pwc-the-world-in-2050-full-report-feb-2017.pdf> (2017).
54. United Nations. World population projected to reach 9.8 billion in 2050, and 11.2 billion in 2100. *World population projected to reach 9.8 billion in 2050, and 11.2 billion in 2100* <https://www.un.org/development/desa/en/news/population/world-population-prospects-2017.html> (2017).

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Competing interests C.C. serves as trustee for Environmental Defense Fund and Global Fishing Watch. H.E.F. serves as a scientific advisor on the Technical Advisory Group for the Aquaculture Stewardship Council. R.N. serves on the scientific advisory board for Oceana and *Nature Food*. C.L.d.M. has undertaken work funded by government agencies, fishery industry organizations and regional fisheries management organizations. C.D.G. serves on the scientific advisory board for Oceana.

Additional information

Supplementary information is available for this paper at <https://doi.org/10.1038/s41586-020-2616-y>.

Correspondence and requests for materials should be addressed to C.C., L.C. or S.G.

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Study description	Analysis of existing data to derive supply of seafood.
Research sample	Publicly available data sources used: FAO Fishery and Aquaculture Statistics (FishstatJ); FAOSTAT; Costello, C., Ovando, D., Clavelle, T., Strauss, C.K., Hilborn, R., Melnychuk, M.C., Branch, T.A., Gaines, S.D., Szuwalski, C.S., Cabral, R.B. and Rader, D.N., 2016. Global fishery prospects under contrasting management regimes. <i>Proceedings of the National Academy of Sciences</i> , 113(18), pp.5125-5129; Mangin, T., Costello, C., Anderson, J., Arnason, R., Elliott, M., Gaines, S.D., Hilborn, R., Peterson, E. and Sumaila, R., 2018. Are fishery management upgrades worth the cost?. <i>PLOS One</i> , 13(9); Cai, J. & Leung, P. Short-term projection of global fish demand and supply gaps. Food and Agriculture Organization of the United Nations, 2017; Gentry, R.R., Froehlich, H.E., Grimm, D., Kareiva, P., Parke, M., Rust, M., Gaines, S.D., Halpern, B.S. (2017) Mapping the global potential for marine aquaculture. <i>Nature Ecology & Evolution</i> 1(9) 1317-1324.
Sampling strategy	Sample is a census of all available fisheries data.
Data collection	Only pre-existing data was used in the analysis.
Timing and spatial scale	FAO Fishstat-J: 1950-2017; global scale Costello et al. 2016: historical 1950-2012; projections 2013-2050; global scale Mangin et al. 2018: 2012; global scale Cai et al. 2017: mean values based on mid-2010s to early 2020s; global scale Gentry et al. 2017: no temporal aspect; global scale
Data exclusions	No data were excluded from the analysis.
Reproducibility	Experimental replication was not attempted, as no experiment was performed.
Randomization	The study did not involve group allocation.
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