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Strategic planning could reduce farm-scale mariculture impacts on marine biodiversity while expanding seafood production

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Mariculture is one of the fastest growing global markets. Although it has potential to improve livelihoods and facilitate economic growth, it can negatively impact marine biodiversity. Here we estimate local cumulative environmental impacts from current and future (2050) mariculture production on marine biodiversity (20,013 marine fauna), while accounting for species range shifts under climate change. With strategic planning, the 1.82-fold increase in finfish and 2.36-fold increase in bivalve production needed to meet expected global mariculture demand in 2050 could be achieved with up to a 30.5% decrease in cumulative impact to global marine biodiversity. This is because all future mariculture farms are strategically placed in sea areas with the lowest cumulative impact. Our results reveal where and how much mariculture impacts could change in the coming decades and identify pathways for countries to minimize risks under expansion of mariculture and climate change through strategic planning.

Seafood is an essential source of protein and nutrition for humanity¹, and cultivated seafood production has been steadily increasing over the past few decades²⁻⁴. Mariculture has been gaining attention as a potential means to meet increased global seafood demand and improve livelihoods and facilitate economic growth⁵⁻⁷. These potential benefits, combined with rapid advances in technology, portend a sustained expansion of mariculture and associated infrastructure in the coming century^{5,6,8}. Whereas valuable for economies and human nutrition, mariculture can have negative consequences for marine environments and biodiversity^{9,10}. For instance, some forms of mariculture, particularly shrimp farming, have resulted in substantial losses or modifications of marine habitats, including mangroves and seagrasses^{11,12}. In

nearshore finfish farms, nitrogen or phosphorus emissions can cause local eutrophication, resulting in water pollution, harmful algal blooms or even hypoxic dead zones^{13,14}. By contrast, shellfish farming (for example, oysters, mussels) can remove nutrients and carbon from the water through bivalve feeding and growth¹⁵. Yet the extent to which mariculture impacts biodiversity remains an important knowledge gap.

Quantifying how and where mariculture may impact marine biodiversity requires understanding the extent to which mariculture activities and marine species distributions overlap in space. Looking ahead, strategic mariculture planning requires understanding how this overlap may change in the future, which in turn requires accounting for climate-change-associated shifts in both the distributions of marine

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Here we quantified the current (2020) and future (2050) negative impact of environmental pressures from mariculture on 20,013 marine fauna across ten taxa (bony fish, cephalopods, corals, echinoderms, elasmobranchs, marine arthropods, marine mammals, marine reptiles, molluscs and sponges) in the global oceans, accounting for alternative emissions scenarios (we report the results for Representative Concentration Pathway (RCP) 8.5 in the main text, but those for RCP 4.5 are presented in the Supplementary Information). We quantified an index of the cumulative impact from mariculture (CIM) on marine biodiversity that estimates how each species in a given local community would be impacted by mariculture pressures in that specific area. To do this, we synthesized publicly available datasets on current and future mariculture farms and production, the intensity of mariculture pressures and species' vulnerability to these pressures to quantify the potential negative impact on marine species from two ubiquitous local-scale stressors associated with the whole animal (bivalve, finfish and shrimp) farming industry at a 0.5° cell resolution: (1) eutrophication from on-farm nitrogen (N) and phosphorus (P) emissions and (2) habitat degradation from current and future mariculture. Specifically, we integrated: (1) the intensity of mariculture pressures based on the type of mariculture farm and farm density^{20,21}, (2) the vulnerability of each species to each of the pressures (based on Butt et al.²²) and (3) the probability of species occurrence in the locations where mariculture occurs, ranging from 0.5 to 1 (based on Kaschner et al.²³) (Supplementary Fig. 1 and Methods).

To forecast future CIM in 2050, we projected the quantity of additional farms that would be needed to meet future global demand for mariculture seafood in 2050 where future finfish and bivalve production would undergo 1.82- and 2.36-fold increases beyond their current production levels, respectively⁵, while holding shrimp production constant at 2020 levels²⁴. We further made the assumption that existing shrimp farms will remain in their current locations for the following reasons: (1) data on future distributions of shrimp farms and future demand for shrimp products are not available; (2) shrimp farms can persist in the same location for decades under some management regimes²⁵; (3) abandoned shrimp farms can be reutilized through recovery efforts²⁵ and (4) the placement of shrimp farms in new areas by replacement of coastal wetlands has been largely prohibited through legislation across the world²⁶⁻²⁹, which means that abandoning existing shrimp farms and developing new farms in coastal wetlands is less likely than in the past. We assumed that future mariculture pressures and production per farm remain constant at 2020 levels for each farm type. We then assessed how strategic planning for the expansion of mariculture to meet future global production demand could change global CIM by 2050 by estimating best-case and worst-case scenarios based on minimum and maximum projected global CIM values in 2050, respectively. To do this, we calculated CIM per farm for each type of mariculture in every ocean cell that is predicted to be suitable for developing bivalve and finfish mariculture in 2050. We chose the CIM per farm as a metric to allocate future bivalve and finfish farms



Fig. 1 | **Distribution of CIM on marine biodiversity in 2020. a**–**c**, Global scale (**a**), Europe (**b**) and Southeast Asia (**c**). Their distributions were divided into five categories using quintiles.

because CIM was calculated for each cell based on the number of farms within it. The information on CIM per farm enables us to identify cells with the lowest or highest impacts. Using these estimates, we selected optimal and suboptimal mariculture locations to quantify the best-case (minimizing global CIM) and worst-case (maximizing global CIM) scenarios, respectively. These analyses were conducted (1) at a global-scale by allowing increases in bivalve and finfish farms to occur anywhere deemed suitable in 2050 across exclusive economic zones (EEZs) and (2) at the country level by allocating increases in bivalve and finfish farms to each country currently engaged in mariculture in proportion to the projected feasibility of mariculture areas for bivalve and finfish farming within the EEZ of those countries in 2050. These best- and worst-case scenarios were compared to the current (2020) CIM and future (2050) CIMs associated with each of 10,000 randomized mariculture scenarios simulated by randomly allocating a sufficient number of bivalve and finfish farms to meet global demands in 2050 across all feasible bivalve and finfish mariculture areas available in 2050. Our analysis for allocating future mariculture farms excluded sea areas currently occupied by other marine activities and accounted for the anticipated expansion of marine activities in the future (Methods).

Results

Environmental impacts of current mariculture

We found strong spatial heterogeneity in the global distribution of current (2020) CIM on marine biodiversity (Fig. 1). Impacts from nitrogen and phosphorus emissions accounted for the majority (78.9%) of total CIM globally (Supplementary Table 1). Generally, Southeast and East Asian countries such as China, Vietnam, Indonesia and the Philippines have the largest concentrations of current mariculture (Supplementary Fig. 2a; 55% of top quintile farms) and thus the greatest impact on marine biodiversity (CIM). Indeed, most (70%) areas within the top quintile of CIM in 2020 are located in Southeast and East Asian countries (Fig. 1), matching areas of very high species richness (72% of the top quintile of marine species richness) (Supplementary Fig. 2b).



Fig. 2| Changes in nitrogen and phosphorus emissions and CIM between 2020 and 2050. a, N and P emissions from current and future mariculture, with future estimates based on future global demand for finfish and bivalve production. b, The range of changes in impacts from each pressure and resulting local CIM in 2050 under the best-case (bottom points) and worst-case (top points) scenarios compared to 2020. H refers to marine habitat degradation. Total nitrogen and phosphorus emissions in 2050 are the same for all mariculture expansion scenarios, including the best-case and worst-case scenarios and climate change scenarios (Methods). The horizontal dashed line at 0 indicates a scenario in which future CIM is equal to current CIM. Points below/above the dashed line indicate lower/higher future CIM compared to the current CIM. Blue and orange points represent future CIM estimated at the country level and at the global scale, respectively.

Importantly, CIM does not simply increase proportionally with total mariculture production. Instead, it is driven by the nature and extent of pressures from different mariculture production types and the relative vulnerability and diversity of species concentrating in specific locations (Methods). For example, 90% of mariculture farms in China are bivalve farms, which have generally lower environmental impacts than finfish and shrimp farms, whereas the proportion of bivalve farms in Indonesia is only 5.9%. As a result, although China has a far greater number of farms than Indonesia, its aggregated CIM is considerably lower (Supplementary Table 2). This difference also results from the fact that Indonesia has a much higher species richness (measured as the sum of probability of species occurrence across all species within its EEZ), resulting in a greater number of species exposed to mariculture than China (Supplementary Fig. 2b and Supplementary Table 2).

Environmental impacts of future mariculture

To meet the global future demand for bivalve and finfish production in 2050, we estimate that the current (2020) area globally dedicated to mariculture will need to increase by 40.5% from 108,729 hato 152,785 ha. The expanded mariculture footprints will further degrade marine habitats. Despite this expansion, total on-farm nitrogen and phosphorus emissions from mariculture in 2050 are projected to decrease by 57.9% and 11% compared to 2020 estimates, respectively (Fig. 2a). These decreases arise because bivalve farms absorb nitrogen and phosphorus and thus expanded bivalve production will compensate for increased emissions of nitrogen and phosphorus from expanded finfish production. Total emissions of N and P of global mariculture are determined by the total global production, whereas the impacts of on-farm N and P emissions on marine species vary depending on the location of mariculture farms. As the combined effects of absorption of nutrients by bivalve farms and the emissions of nutrients from finfish and shrimp farms could vary in locations and in ways that are difficult to quantify at the spatial resolution of our global data, we simplified the calculation of the impacts of N and P emissions by using the net emissions of N and P from all mariculture farms in each ocean cell.

In the best-case scenario, total CIM is projected to decrease by 27.5% in the country-level analysis and by 30.5% in the global-scale analysis, relative to 2020 estimates. Impacts of nutrient emissions will decrease by 32.6% in the country-level analysis and by 34.7% in the global-scale analysis. Similarly, impacts of habitat degradation will also decrease by 8.5% in the country-level analysis and by 14.9% in the global-scale analysis (Fig. 2b). The placement of farms based on the best-case scenario will result in a CIM that is on average 37.7% lower than that of the randomized scenarios (randomly locating future farms globally) (Extended Data Fig. 1a). This finding is, in part, because of the opportunity under the best-case scenario to strategically relocate 88.5% of existing bivalve and finfish farms to areas that will result in the lowest CIM. This large fraction of existing farms are expected to be unsuitable for their currently cultivated species in 2050, according to existing projections due to changing temperature, oxygenation, pH and productivity⁶, when overlaying the map of current mariculture farms²⁴ on the map of suitable bivalve and finfish farming areas in 2050⁶. In addition, the best-case scenario also benefits from the strategic placement of all expanded farms required to meet global bivalve and finfish food demand in 2050 in areas with the lowest CIM. As a result, the placement of new bivalve and finfish farms under the best-case scenario would see their associated CIM reduced by 87.7% (country-level analysis) and 92.2% (global-scale analysis) compared to the level in 2020.

Conversely, the worst-case scenario-maximizing future CIM by placing all new farms required to meet global demand by 2050 in areas with the highest CIM-suggests that CIM would increase by 270.3% at the country level and by 420.5% at the global scale relative to current CIM (Fig. 2b); and by 366.6% on average compared to the randomized scenarios (Extended Data Fig. 1b). Because mariculture productivity per farm is likely to increase in the future owing to advances in technology, we conducted a sensitivity analysis to estimate CIM changes when each farm increased production by 10%, 20% and 30% and found similar predicted CIM in 2050 (Supplementary Table 3). This finding suggests that future CIM under the best-case and worst-case scenarios is not sensitive to the rate of increase in production per farm, because all future farms are also strategically placed in sea areas with the lowest impacts or largest impacts.

Nonetheless, the impacts of nitrogen and phosphorus emissions contributed more to the future CIM than habitat degradation in 2050, accounting for 74.2% and 93.1% of global CIM under the best-case and worst-case scenarios, respectively (Supplementary Table 1). Because a quantitative comparison of the extent to which habitat degradation differs among bivalve, finfish and shrimp farms is lacking, we conducted a sensitivity analysis to examine how different weighting values for each type of mariculture affect Global CIM. It reveals that future CIM is not sensitive to the choice of weightings (Supplementary Table 4).

Although outcomes for our study under RCP 4.5 and 8.5 are largely similar, future CIM under RCP 8.5 is surprisingly slightly lower than that under RCP 4.5. This unexpected result arises from differences in the projected range expansions and contractions of marine species under both scenarios²³, resulting in a higher overlap of marine species and mariculture farms under RCP 4.5 (Fig. 3 and Extended Data Fig. 2) and an overall decrease in species richness of 7% across all potential mariculture areas under RCP 8.5 compared to RCP 4.5.

Mariculture impacts by taxonomic groups

The proportion of species experiencing an increase in the amount of their spatial distribution affected by mariculture in 2050 under bestand worst-case scenarios is much more variable at the global scale than the country level (Fig. 4a). This discrepancy is due to the differences in assumptions for these two analyses. The country-level approach



Fig. 3 | Global distribution of CIM in 2050 under the best-case and worst-case scenarios. a, Best-case scenario estimated at the global scale. b, Worst-case scenario estimated at the global scale. c, Best-case scenario estimated at the country level. d, Worst-case scenario estimated at the country level. The distribution of CIM was divided into five categories using quintiles.

imposes the limitation that future farms can only be distributed on a country-by-country basis within their respective EEZs; therefore, mariculture farms are not necessarily placed in the lowest-impact areas across the oceans. By contrast, the global-scale analysis allows for an unrestricted expansion of mariculture across all EEZs, which can then be concentrated in all areas with the lowest impacts (Methods). Nonetheless, our results show that under the best-case scenario, future total CIMs (that is, across all species by taxonomic group) estimated at the country level and global scale could be smaller than current CIM for all taxonomic groups except for marine mammals (Fig. 4b). However, non-optimal placement scenarios (worst-case scenario and randomized scenarios) are predicted to result in increases in CIM over current levels for all taxonomic groups (Supplementary Table 5). This is because new farms are randomly located in either high-impact areas or low-impact areas under the randomized scenarios. An important finding is that marine mammals will experience the largest increases in the impacts in the future. For example, the average CIM for marine mammals will increase -2.87 times, which is much larger than all other groups (range: 1.01 for marine reptiles and molluscs to 1.45 for cephalopods; Supplementary Table 5). This finding emerges because marine mammals are highly vulnerable to habitat damage²² and have the largest proportion of their range overlapped with mariculture farms.

Mariculture impacts relative to production

Strategic planning of mariculture should take into consideration countries in which increases in production can occur without proportional increases in CIM. Future CIM will change based on the changes in the number of mariculture farms and the types of mariculture and the number and identity of species present in a location. Estimated at the global scale, mariculture will expand to 103 countries under the best-case scenario and to 93 countries under the worst-case scenario (Fig. 3a,b). For countries that currently have mariculture and are predicted to have mariculture in the future (n = 60 under both scenarios for the country-level analysis; n = 62 under the best-case scenario and 57 under the worst-case scenario for the global-scale analysis), their future CIM typically does not increase proportionally with mariculture production. In the country-level analysis, countries with larger proportions of feasible bivalve and finfish mariculture areas in 2050, such as the USA and Pacific Island countries, are expected to experience greater expansions of mariculture. This is because these countries will receive more mariculture production, following the principle used to allocate global mariculture production among existing mariculture countries in 2050. Under the best-case scenario, most countries (86.7% at the country-level analysis and 88.7% at the global-scale analysis), including India, the Philippines and Malaysia, will fall below the 1:1 line change (less than directly proportional), although 18 countries including Brazil and France (both at the country level and global scale) do see an increase in total CIM (log ratio >0) (Fig. 5a,c). By contrast, under the worst-case scenario, the proportion of these countries that fall below the 1:1 line change decreases to 46.7% at the country-level estimation and 75.4% at the global-scale estimation, respectively (Fig. 5b,d). These findings suggest that strategic planning can reduce the number of countries with increases in CIM exceeding increases in production.

Discussion

Our study addressed important knowledge gaps in understanding how animal mariculture impacts marine biodiversity currently and how these impacts could change under climate change if animal mariculture scales up to meet global seafood by 2050. Our findings show that strategic planning in the placement of future mariculture can substantially reduce impacts on marine biodiversity in the face of expected large expansion of mariculture and the shifting species distributions under climate change. Specifically, despite large increases in total production, best-case scenarios would reduce CIM by 27.5% (country-level analysis) and 30.5% (global-scale analysis) compared to 2020 and by 37.7% relative to random distributions of farms. Given that both climate change and expansion of mariculture are probably unavoidable, the need for strategic planning is clear.

We identified existing areas where cumulative impacts of current mariculture activities on marine biodiversity are very high, for example, southeast China (Fig. 1). These areas should be prioritized for replanning to minimize environmental impacts on marine biodiversity whenever possible. This is particularly important for marine mammals, which are expected to experience the largest increases in impacts from the expanded mariculture in the future. Although replanning may not be possible in all contexts, examples do exist where countries are both adjusting current operations and planning for the future. For example, China^{30,31} and many European countries^{32,33} have been updating their existing marine spatial planning to manage current marine activities



Fig. 4 | Changes in impacts of mariculture by taxonomic groups between 2020 and 2050. a, The proportion of species within each taxonomic group experiencing increases in the proportion of the range affected by mariculture in 2050 under the best-case (bottom points) and worst-case (top points) planning scenarios compared to 2020. b, The range of changes in CIM by taxa in 2050 under the best-case and worst-case planning scenarios, compared to CIM in 2020. These results are shown for the baseline scenario in which production per farm does not change. The horizontal dashed line at 0 indicates a scenario in which future CIM is equal to current CIM. Taxonomic groups were ranked in order of decreasing impacts under the best-case scenario estimated at the global scale.

including mariculture and to plan future marine activities. The available mariculture areas with the lowest CIM per farm within each country's EEZ (Extended Data Figs. 3 and 4) could be integrated into the implementation of the Marine Spatial Planning Global 2030 initiative³⁴ and help guide coastal countries to plan future mariculture in sea areas with minimal biodiversity impacts.

Strategic mariculture planning, however, should not neglect local communities, as doing so could create or exacerbate social inequities and environmental injustices³⁵. In particular, if mariculture displaces local fisheries, mariculture expansion can negatively impact local food security, given that most mariculture production is traded and not consumed locally. Mariculture can compete for space and market share with small-scale fisheries, particularly when target species overlap^{36,37}. In any case, interactions between the two sectors are highly context specific and include both positive and negative outcomes³⁸. Nevertheless, where conflicts are anticipated, several measures could be adopted by governments to avoid these negative outcomes, such as financially compensating local fishing communities for costs of changing to mariculture production, providing income diversification through new employment opportunities for affected stakeholders and ensuring benefits from new mariculture production are equitably distributed to local communities. Additionally, engaging local communities and stakeholders in the decision process of whether or not to pursue mariculture in their waters, where to locate it and which species to farm is an important way to include local voices and values in decision making³⁹.

Our results could be refined with several areas of research. For example, incorporating the effects of changes in temperature or other environmental factors on the metabolism, growth rate and harvest size of cultivated species would refine future estimates of production per farm. Research on how changes in temperature contribute to metabolic stress in marine species and how that stress may interactively affect species vulnerability to anthropogenic stressors would refine future estimates of cumulative impacts to marine species. Likewise, incorporating the regulatory and logistic constraints (for example, feasibility of moving operations to distant areas) to developing mariculture in new areas, such as those identified in our models, would help generate more realistic future scenarios. Furthermore, insights on how technological advances in mariculture practices could reduce nutrient loading and habitat degradation may alter model outputs. However, our sensitivity analysis on the increase in production per farm indicated that the improvement of production efficiencies due to technological progress would not demonstrably change the magnitude of future CIM and the potential of strategic planning in reducing CIM (Supplementary Table 3).

The scale of expansion of mariculture will vary among coastal countries given varying demands and capacities for developing mariculture. Although local or regional demands for seafood could impact the expansion of small-scale mariculture, such factors are unlikely to affect the large-scale expansion of mariculture in the future. This is because large-scale mariculture food in many mariculture countries is mainly exported to countries with high demand for seafood, such as the USA and China, rather than being consumed by local communities⁴⁰. For example, countries such as Norway and Vietnam have developed large-scale mariculture mainly for exporting seafood, rather than for meeting local seafood demand⁴⁰. Given this, in addition to the global-scale estimation that mariculture can expand to any country, we conducted another estimation of future CIM at the country level by considering the demand for developing mariculture industry in each current mariculture country. The country-level analysis only focused on the expansion of mariculture among existing mariculture countries, because these countries have larger potential for expanding mariculture compared to those countries without current mariculture activities. However, regardless of the extent to which mariculture expands in each country, as long as each country places new farms in areas with the lowest impacts through strategic planning, the total CIM will decrease dramatically compared to mariculture scenarios without strategic planning, as suggested by our country-level and global-scale analyses and the randomization analyses.

Although our work accounted for several major mariculture farm types and pressures, we were unable to account for all of them due to data limitations. We did not, for example, account for seaweed farms due to data gaps in the current distribution of seaweed farms, which also limits a robust estimation of future seaweed production in 2050 and the average emissions of N and P from seaweed farms. Likewise, we lack global datasets for other pressures, such as genetic pollution of local wild stocks from escaped cultivated species⁹, marine macroand microplastic pollution⁴¹, oceanic noise⁴² and light pollution⁴³ and entanglement of marine life in mariculture equipment⁴⁴. As such, our estimates of the cumulative impacts of bivalve, finfish and shrimp mariculture are probably underestimated.

Compared to finfish and shrimp farms, bivalve farms can generate positive environmental benefits, such as habitat creation ¹⁵. However, we were unable to quantify the benefits of habitat creation using the model we developed to assess the negative environmental impacts of mariculture. This is because the negative impacts were assessed based on the vulnerability of species to mariculture pressures, which specifically refers to negative responses of species to these pressures²². In addition, the negative impacts of habitat degradation caused by bivalve farms are not comparable to the positive impacts of habitat creation from these farms. Evaluating these benefits on marine biodiversity thus requires new approaches. By contrast, we accounted for the nutrient reductions from bivalve farms for the purpose of calculating the net emissions of N and P from all farms in each cell.

Our work highlights the potential for strategic planning to overcome one of the key sustainability challenges our world faces: balancing the growing demand for mariculture with biodiversity impacts in the dynamic context of climate change. Far from hopeless, our results show that despite increasing pressures from human demand and increasingly



log-scaled production ratio (2050/2020)

Fig. 5 | Relationship between changes in CIM and changes in factors including total mariculture production and marine species richness for each country. a,b, Best-case (a) and worst-case (b) scenario estimated at the global scale. c,d, Best-case (c) and worst-case (d) scenario estimated at the country level. Species richness was calculated as the sum of species probability occurrence value across all mariculture areas. The dashed line refers to a line with a slope equal to 1. If the point (each country) is below the dashed line, it indicates that the change in CIM is smaller than the change in mariculture production. Countries listed in each panel are all countries that have both current and future mariculture farms. We log-transformed each variable in each panel because the range of each variable among countries was very large.

impactful climate change, strategic planning can dramatically reduce the impacts of mariculture on biodiversity to below the current impact level. Irrespective of the magnitude of reduction in CIM, our study provides strong evidence that combining predictions of CIM with models of extinction risk for marine species^{45,46} can provide a useful roadmap to guide future management of mariculture that can help bridge the important compromise between meeting the world's nutritional needs and protecting the ocean's biodiversity.

Methods

Intensity of environmental pressures from mariculture

We assessed the impact of mariculture on 20,013 marine species spanning ten taxonomic groups (Supplementary Table 6). We focused on three pressures for which data were available: nitrogen (N) and phosphorus (P) emissions and marine habitat degradation from four mariculture categories of bivalve molluscs, general marine fish, Salmonidae and shrimps.

We measured the intensities of nitrogen and phosphorus pressures based on their emissions from mariculture at a 0.5° resolution. As the vulnerabilities of species to nitrogen and phosphorus pressures were measured by the vulnerability of species to eutrophication, we summed nitrogen and phosphorus emissions into a single potential eutrophication pressure to avoid double counting of the impacts of nitrogen and phosphorus emissions (described below). Although nitrogen and phosphorus emissions vary spatially and have different consequences depending on the local oceanography, we were unable to evaluate their impacts separately because we only have measures of species vulnerability for eutrophication. Instead, we measured the

potential impacts of eutrophication on marine biodiversity as a proxy for the impacts of nitrogen and phosphorus emissions. Although nutrient pollution does not necessarily lead to eutrophication (whether a system becomes eutrophic depends on its initial status and hydrodynamics and other abiotic and biotic factors), the increase of nitrogen and phosphorus emissions from mariculture will increase the risk and severity of eutrophication. Therefore, we used the intensity of total nitrogen and phosphorus emissions in each cell to measure the risk and severity of the potential eutrophication pressure on marine species. Because we focused on local impacts of nitrogen and phosphorus emissions on marine species, we only included on-farm emissions of nitrogen and phosphorus. We did not account for the impacts of off-farm emissions of nitrogen and phosphorus, which refer to feed-associated emissions²⁰. Such land-sourced nitrogen and phosphorus emissions do not directly impact marine species surrounding mariculture farms. Instead, they affect species in estuaries by contributing to the overall pool of land-sourced nitrogen and phosphorus in the watersheds⁴⁷. In addition, off-farm nitrogen and phosphorus emissions are much smaller than on-farm emission²⁰ (Supplementary Table 7).

Data for the on-farm emissions (kg per tonne of live weight produced) of N and P were sourced from Gephart et al.²⁰. The on-farm N and P emissions are the differences between N and P contents of feed components and N and P contents of the production of cultured species²⁰. We used the median values of on-farm N and P emissions per tonne of live weight of cultured species created by Gephart et al.²⁰ to calculate the intensity of each of these pressures caused by each type of mariculture farm. Gephart et al.²⁰ data for salmon and miscellaneous marine fishes were used as the proxy for Salmonidae fish and general marine fish, respectively (Supplementary Table 7).

Point data for spatial locations of global mariculture farms in 2020 were derived from the global distribution of aquaculture farms published by Clawson et al.²⁴. We excluded 30 aquaculture farms (<0.001% of all farms) located in the cells that were entirely on land by overlapping the map of cells with aquaculture farms on the map of global land areas. Data on global land areas were downloaded from ArcGIS Hub (https://hub.arcgis.com/datasets/esri::world-continents/ explore). We used the average surface area per farm of 11,561 m² (ref. 21) to quantify the physical footprint of each farm both at present and in the future. Clawson et al.²⁴ mapped mariculture in six production categories: general marine fish, shrimps, bivalve molluscs, Salmonidae fish, bluefin tuna and non-shrimp crustaceans. Given unavailable data for intensities of environmental pressures caused by bluefin tuna and non-shrimp crustaceans farms²⁰ (following section), we excluded these farms (1,365 of 95,413; 1.43% of total) from our analysis. Regarding general marine fish, shrimps, bivalve molluscs and Salmonidae, their global average production of live-weights per farm (2017) was 865.7 tonnes, 336.6 tonnes, 283.4 tonnes and 866.4 tonnes, respectively²⁴.

We calculated the total emission (TE) of a given emitting mariculture pressure *k* (that is, N or P) from farms of type *f* in any given cell *j* as follows:

$$\mathsf{TE}_{k,f,j} = E_{k,f,j} \times P_f \times N_{f,j} \tag{1}$$

where $E_{k,f,j}$ is the value of the pressure k load per tonne of live weight emitted by a farm of type f (Supplementary Table 7), P_f is the production of a farm of type f and N_f is the total number of farms of type f within that cell in 2020 (current emission estimate) or projected for 2050 (future emission estimate). The intensity of the potential eutrophication pressure caused by nitrogen and phosphorus emissions was measured as the sum of the total emissions of nitrogen and phosphorus in each ocean cell. Data on the distribution of current farms and the production of per farm were provided by Clawson et al.²⁴.

The risks of different mariculture farms on marine habitat degradation can differ substantially^{12,48,49}. For instance, certain farms, such as salmon farms, result in relatively minor habitat degradation⁴⁸, whereas shrimp farms can result in substantial damage to marine habitats including mangroves¹². By contrast, the effects of bivalve farms on habitat modification are the smallest, mainly involving modifications of benthic habitats⁴⁹ and, in many cases, can help create habitat¹⁵. Therefore, the degree of habitat degradation caused by bivalve farms, finfish farms (general marine fish and Salmonidae fish) and shrimp farms can be classified as low, median and high. On the basis of this, and owing to the lack of available data for accurately quantifying impacts on marine habitat by each mariculture farm, we used a simple weight scheme to distinguish the magnitude of habitat degradation across the four categories of mariculture farms (Supplementary Table 8). The intensity of marine habitat degradation (*H*) in cell*j* was then calculated as a weighted area of mariculture farms in 2020 within cell*j* based on the average surface area per reported farm location of 11,561 m² (ref. 21):

$$H_{j} = \sum_{f=1}^{4} (A_{f,j} \times W_{f})$$
(2)

where $A_{f,j}$ is the total area of mariculture farm f in cell j and W_f is the weighted value for mariculture farm f (Supplementary Table 8). As the weights associated with the pressure of marine habitat degradation among different mariculture farms were determined subjectively, we conducted a sensitivity analysis to assess the effects of this weighting approach on mariculture impacts using two different weight schemes (Sensitivity analysis section).

Index of cumulative environmental impacts of mariculture on marine biodiversity

We used a modified version of Maxwell et al. index of cumulative risks of human pressures on marine predators⁴⁵ to calculate our local (cell-wise) index of cumulative environmental impacts from mariculture pressures (CIM) in each 0.5° cell globally within coastal (EEZ) waters, including eutrophication induced by nitrogen and phosphorus emissions and marine habitat degradation (Supplementary Fig. 1). The CIM is the sum of the impacts (for example, risks) of each mariculture pressure *k* (*n* = 2) on marine biodiversity, calculated as follows:

$$CIM = \sum_{k=1}^{2} CIM_k$$
(3)

The cumulative environmental impact of pressure k (CIM_k) was calculated as:

$$\operatorname{CIM}_{k} = \sum_{i=1}^{n} S_{j} \times O_{i,j} \times V_{i}$$
(4)

where *n* is the number of marine species occupying any given cell *j*, *S* is the relative intensity of each mariculture-induced pressure *k* from all the farms within a given cell *j*, *V* is the vulnerability of each marine species *i* present in cell *j* to these pressures (next section) and *O* is the probability of species occurrence, where the value of *O* is at least 0.5 (that is, cells with a probability of species occurrence below 0.5 were excluded) (Supplementary Fig. 1).

The relative intensity of each pressure of eutrophication (nitrogen and phosphorus emissions) and marine habitat degradation in each cell j (S_j) at present and in 2050 was calculated by dividing the total intensity value in cell j, estimated by equations (1) (nitrogen and phosphorus emissions, TE_j) and (2) (marine habitat degradation, H_j), by the maximum intensity value across all ocean cells between 2020 and 2050 under all mariculture development scenarios under both RCPs 4.5 and 8.5. This transformation enables us to make comparisons between the current and future cumulative environmental pressures from mariculture. All mariculture development scenarios include the best-case impact scenario and the worst-case impact scenarios (following sections). Given the negative emissions of N and P from bivalve farms, the total nitrogen and phosphorus emissions from all mariculture farms We did not use the normalization method (<u>Original value – minimum value</u>) to

normalize the intensity values of mariculture pressures in 2020 and 2050 to the range from zero to 1, because this would transform the minimum intensity value of each pressure into zero and downscale the actual magnitude of the range of the pressure intensities. We also did not log-transform the intensity value of each pressure to avoid down-scaling the actual magnitude of the increase in mariculture intensity in the future.

Following Maxwell et al.⁴⁵, we used the probability of species occurrence to measure spatial variation in species presence, rather than using a binary variable (absent or present)⁴⁶. In addition, the probability of occurrence can be regarded as a habitat suitability index, which can be used as a proxy of species abundance⁵⁰.

Data for the probability of species occurrence at present and in 2050 under RCPs 4.5 and 8.5 in 0.5° cells were derived from AquaMaps (version 7/2019)²³. The AquaMaps model simulates species probability of occurrence on a 0–1 scale in 0.5° cells using a set of environmental parameters including depth, temperature, salinity, primary production, sea ice concentration and the distance to land from 2000 to 2014, based on the distribution of species' occurrence records²³. The AquaMaps datasets excluded all marine species with less than ten documented 'presence cells' (that is, cells with at least one presence record), which may exclude a few highly endemic species. Because AquaMaps' data includes very few species (<5% of named species) for marine birds (nine species) and polychaetes (608 species), we excluded these groups. Therefore, we focused on mariculture impacts on 20,013 marine species with available vulnerability data spanning ten taxonomic groups (Supplementary Table 6).

Cumulative environmental impacts of future potential mariculture in 2050 at the global scale

The distribution of potential farming areas that could be developed based on expected positive economic benefits in mid-century (2051-2060, referred to as '2050' throughout the text for simplicity) under RCP 4.5 and RCP 8.5 scenarios were obtained from Free et al.⁶ at 10-km resolution. These potential mariculture areas exclude current marine protected areas and areas where other physical marine activities such as shipping lanes exist. Free et al. created the global map of potential mariculture areas using a combination of habitat suitability estimates for 122 finfish species and 22 bivalve species and economic profits calculated by the estimated revenues and costs⁶. Habitat suitability for each species was determined based on temperature, salinity, oxygen availability, primary productivity and ocean acidification⁶. As our study did not include current tuna farms owing to unavailable data for pressure emissions, we excluded potential tuna farming areas from global potential mariculture areas in 2050. Therefore, the potential mariculture areas in each pixel we used for analysis refer to at least species that can be cultivated in each pixel.

The habitat suitability for each cultivated species was simulated based on environmental parameters from the earth system model GFDL-ESM2G, without considering the geographical distributions of cultivated species⁶. This is because mariculture could introduce non-native species to sea areas that are suitable for the growth of non-native species. In comparison, the AquaMaps projected future distributions of marine species using climatic parameters from the MPIM-ESM-MR model. Although these two datasets were projected using different earth system models, Free et al.⁶ demonstrated that their results were robust to the choice of earth system models. This is because suitable sea areas for cultivating species were determined by the profits of cultivation and habitat suitability, with the profits in each cell based on production 6 .

Cumulative environmental impacts from future potential mariculture on marine biodiversity in 2050 were calculated as the sum of risks of future potential bivalve, finfish (general marine fish and Salmonidae fish) mariculture in 2050 plus the risks from current shrimp farms. We assumed that the existing shrimp farms at present will remain in 2050. This is based somewhat on the lack of available data on projected distributions of shrimp farms, but also because shrimp farms are less likely to relocate because: (1) shrimp farms can operate sustainably for decades with proper management²⁵; (2) abandoned shrimp farms can still be reutilized through appropriate recovery efforts²⁵; (3) placing new shrimp farms in new areas that would damage coastal wetlands has been largely prohibited through the enforcement of legislation across the world^{26–29}. We included shrimp farms for analysis to avoid underestimation of mariculture pressures on marine species.

To estimate future intensity of pressures caused by potential mariculture farms in 2050, first we remapped the global distributions of potential farming areas for each of bivalve, Salmonidae fish and general marine fish farms based on the maps created by Free et al.⁶. We did not consider future expansions of shrimp farms in 2050 because Free et al.⁶ datasets did not include shrimp species. Second, we calculated the total area of potential bivalve, Salmonidae fish, and general marine fish farms in each cell in 2050. Then we calculated cumulative environmental impacts of all potential farming areas for each type of mariculture farm in each cell in 2050 following the same procedure described above (equations (1)–(4)).

Given our present and future estimations of cumulative mariculture impacts are not directly comparable, the former being based on current farm locations while the latter refers to potential future suitable areas for mariculture, we conducted a simulation to test for the potential scope for mariculture planning to reduce future biodiversity risks of expanded mariculture while meeting projected future demands for the sector. Our exercise started from the assumption that future mariculture expansion will meet seafood production levels (live weight) of 16.08 million tonnes for finfish mariculture and 54.44 million tonnes for bivalve mariculture by 2050⁵, which represents an increase of 1.82- and 2.36-folds of current demand levels (8.82 million tonnes for finfish and 23.09 million tonnes for bivalve)⁵. In our study, finfish mariculture was divided into general marine fish and Salmonidae fish farms, according to the varying N and P emissions (Supplementary Table 7) and the varying production per farm. We then estimated demands for 9.67 million tonnes of general marine fish and 6.41 million tonnes of Salmonidae fish in 2050. This estimation was based on the proportions of the current yields of general marine fish (60.15%) and Salmonidae fish (39.85%) in relation to the current yields of finfish.

Given the expected expansions of other marine activities, such as offshore structures (that is, wind farms) and shipping routes^{51,52}, the entire ocean cell is unlikely to be used for developing mariculture in the future. Therefore, we assumed that only a small proportion of the ocean cell where sea areas are suitable for mariculture development can be utilized for mariculture in 2050. To estimate this proportion, we calculated the average proportion of each ocean cell occupied by current mariculture farms (0.02%). We then used this value as the maximum proportion of each ocean cell that can be occupied by mariculture farms in 2050.

We generated two extreme scenarios corresponding to the configurations of bivalve and finfish mariculture development that meet these production targets will lead to maximum and minimum associated risks. This was done by ordering all potentially suitable mariculture cells in either increasing (best-case scenario) or decreasing (worst-case scenario) CIM value per unit farm and then sequentially incorporating potentially suitable cells for mariculture development until production targets were met. The reason to select potentially mariculture cells based on CIM value per unit farm is that many potentially mariculture cells are suitable for both finish and bivalve mariculture development. For cells that are suitable for multiple mariculture farms, the type of mariculture farm with the least risks per unit farm was selected to calculate the minimum cumulative environmental impacts of future mariculture farms, whereas the type of mariculture farm with the largest risks per unit farm was selected to calculate the maximum cumulative environmental impacts from future mariculture farms. Finally, to compare these extreme scenarios against the range of possible combinations of risks associated with future mariculture development at production targets, we randomly bootstrapped (10,000 repetitions) the selection of suitable cells for development until the production target for bivalve and finfish mariculture was met.

As shrimp farms can occupy physical space in sea areas that are suitable for developing bivalve and finfish mariculture in 2050, these sea areas are not available for placing bivalve and finfish farms. Therefore, when allocating future bivalve and finfish farms in 2050, we only considered suitable sea areas for bivalve and finfish mariculture in each cell in 2050 that are not occupied by existing shrimp farms within the same cell. For bivalve mariculture, the number of cells (N_b) required under both mariculture development scenarios was calculated by solving the following equilibrium equation:

$$D_{b,2050} = \sum_{j=1}^{N_b} \left(\frac{A_{j,b}}{A_{per}} - N_{shrimp,j} \right) \times Y_b$$
(5)

where $D_{b,2050}$ is the demand for the targeted bivalve mariculture food in 2050; $A_{j,b}$ is the projected potential suitable area for mariculture development of bivalve type in cell *j*; A_{per} is the average surface area per farm of 11,561 m² (ref. 21); $N_{shrimp,j}$ is the number of shrimp farms within the projected potential mariculture areas in cell *j*; and Y_b is the live-weight production per bivalve farm, derived from Clawson et al.²⁴.

For finfish mariculture, the required number of cells (N_f) was calculated by solving the following equilibrium equation:

I

$$D_{\rm f,2050} = \sum_{j=1}^{N} \left[\left(\frac{A_{j,\rm g}}{A_{\rm per}} - N_{\rm shrimp,j} \right) \times Y_{\rm g} + \left(\frac{A_{j,\rm s}}{A_{\rm per}} - N_{\rm shrimp,j} \right) \times Y_{\rm s} \right]$$
(6)

where $D_{f,2050}$ is the demand for finfish mariculture food in 2050; $A_{j,g}$ is the area of all potential general marine fish farming areas in cell *j*; $A_{j,s}$ is the area of all potential Salmonidae fish farming areas in cell *j*; Y_g and Y_s are the production of live-weights per general marine fish farm and the production of live-weights per Salmonidae fish farm, respectively, derived from Clawson et al.²⁴. The number of bivalve and finfish farms in each cell calculated by equations (5) and (6) includes the new farms established in 2050 and the existing farms at present that are still available in 2050.

Cumulative environmental impacts of future potential mariculture in 2050 at the country level

In addition to the global-scale analysis where future mariculture is allowed to expand to countries with no documented current mariculture, we also estimated future total CIM at the country level. The estimation of future CIM at the country level was based on the consideration of the demand for developing mariculture. We assessed future CIM for each of the current mariculture countries that will have suitable mariculture areas based on each country's available mariculture areas in 2050. In consideration of a proportion of existing bivalve and finfish (general fish and salmonid) farms that will still be available in 2050, we allocated the additional needed bivalve and finfish production to each current mariculture country proportionally, according to the proportion of potential mariculture areas for each type of mariculture within each country' EEZ. This will allow all countries have sufficient future suitable sea areas for bivalve and finfish mariculture to meet future country-level bivalve and finfish production demands. Then we estimated the future CIM for each country under the best-case

and worst-case scenarios using the same approach as we did for the global analysis.

Vulnerability of marine species to mariculture pressures

Data on the vulnerability of each species to each mariculture pressure were derived from Butt et al.²². For 377 AquaMap species that were not assessed by Butt et al.²², we assumed their vulnerability scores to be equal to those of other assessed species within the same genus, where each of these assessed species has identical vulnerability scores. We excluded the unassessed AquaMap species where all assessed species within the same genus have varying vulnerability scores. Therefore, our analysis included 20,013 marine species across ten taxa. We did not include marine plants as the species' vulnerability data did not include marine plants. Regarding N and P emissions, given that nutrient pollution causes eutrophication¹³, we used the vulnerability value of each species to eutrophication as proxies for the combined N and P emissions.

Given that the vulnerability scores of all species to all three mariculture pressures are all non-negative, our analysis assumed that each of three pressures would generate varying negative impacts to marine species. Although eutrophication caused by N and P emissions can benefit some marine species, such benefits are very limited⁵³. By contrast, eutrophication has substantial detrimental effects on ocean systems, leading to the creation of dead zones^{53,54}. Therefore, our assessment did not account for these limited benefits.

Sensitivity analysis

Scenarios of advances in mariculture technology. The production per farm is expected to increase owing to advances in mariculture technologies. Therefore, we made a conservative assessment by assuming that the live-weight production per farm in 2050 would remain at the current level, considering this as a baseline scenario. We then conducted three different scenario analyses to investigate how future CIM would change with a 10%, 20% and 30% increase in the production per farm for bivalve and finfish fisheries. We did not consider shrimp to ensure the global production mariculture food in 2050 was equal to the baseline scenario with no increase in the production per farm. This makes the sensitivity analysis comparable to the baseline scenario.

Probability of occurrence scenario analysis. We assumed species to be present in a cell whenever their probability of occurrence was equal to or higher than 0.5. This is a common threshold used by other studies using the AquaMaps data to determine marine species distributions^{46,55-57}. Nonetheless, given the subjectivity of threshold selection, we conducted a sensitivity analysis on the choice of threshold by repeating our analysis using the alternative thresholds of 0.25 and 0.75.

Weighted values for pressure of marine habitat degradation. Given the subjectivity of the weighted values assigned to each mariculture farm, we conducted a sensitivity analysis on the selection of the weighted values using two different weight schemes. For the weight scheme 1, we assumed that the intensity of marine habitat degradation caused by bivalve farms was larger than the baseline metric and the intensity of marine habitat degradation caused by shrimp farms was smaller than the baseline metric. By contrast, for the weight scheme 2 we assigned a smaller value to bivalve farms and a larger value to shrimp farms, relative to the baseline metric (Supplementary Table 8). Results also remained invariant to the choice of weighting values (Supplementary Table 4).

Reporting summary

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

Data availability

Data on the distribution of current mariculture farms were obtained from ref. 24. Data on the distribution of potential mariculture areas in 2050 were obtained from ref. 6. Data on the current and future distributions of marine species were obtained from AquaMaps²³. Species vulnerability data were obtained from ref. 22. Source data are provided with this paper.

Code availability

The code used to conduct the analysis are archived via Figshare at https://doi.org/10.6084/m9.figshare.27132759 (ref. 58).

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Author contributions

D.M., B.S.H. and N.H.C. conceived this study. D.M., B.S.H., C.M.F., J.G.M., M.F. designed the methods, with input from B.A., J.A., B.C.W. and N.H.C. D.M. collected data, performed the analysis and drafted the initial manuscript. D.M., B.S.H., B.A., J.A., J.G.M., C.M.F., B.C.W., M.F., K.K. and N.H.C. edited the manuscript. N.H.C., B.A., J.A. and B.C.W. acquired the funding.

Competing interests

The authors declare no competing interests.

Additional information

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Extended Data Fig. 1| Distribution of changes in CIM between the best-case and worst-case scenarios and each randomized mariculture scenario. (a and b): RCP 8.5 scenario; (c and d): RCP 4.5 scenario.



Extended Data Fig. 2 | Global distribution of CIM in 2050 under the best-case and worst-case scenarios under RCP 4.5. (a) best-case scenario estimated at the global scale, (b) worst-case scenario estimated at the global scale, (c) best-case

scenario estimated at the country level, (**d**) worst-case scenario estimated at the country level. The distribution of CIM was divided into five categories using quintiles.



Extended Data Fig. 3 | Global distribution of CIM per unit farm across all potential mariculture areas in 2050 under RCP 8.5. (a) general marine fish. (b) Salmonidae fish. (c) bivalve. The distribution of CIM per unit farm was divided into five categories using quintiles.



Extended Data Fig. 4 | **Global distribution of CIM per unit farm across all potential mariculture areas in 2050 under RCP 4.5.** (a) general marine fish. (b) Salmonidae fish. (c) bivalve. The distribution of CIM per unit farm was divided into five categories using quintiles.

nature portfolio

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Reporting Summary

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For	all st	atistical analyses, confirm that the following items are present in the figure legend, table legend, main text, or Methods section.
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\boxtimes		For null hypothesis testing, the test statistic (e.g. F, t, r) with confidence intervals, effect sizes, degrees of freedom and P value noted Give P values as exact values whenever suitable.
\boxtimes		For Bayesian analysis, information on the choice of priors and Markov chain Monte Carlo settings
\boxtimes		For hierarchical and complex designs, identification of the appropriate level for tests and full reporting of outcomes
\boxtimes		Estimates of effect sizes (e.g. Cohen's d, Pearson's r), indicating how they were calculated
		Our web collection on <u>statistics for biologists</u> contains articles on many of the points above.

Software and code

Policy information about <u>availability of computer code</u>									
Data collection	This study did not involve any code to collect the datasets.)							
Data analysis	The code used to conduct the analysis are archived in Figshare (https://doi.org/10.6084/m9.figshare.27132759).								

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Reporting on sex and gender	N/A
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Population characteristics	N/A
Recruitment	N/A
Ethics oversight	N/A

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Ecological, evolutionary & environmental sciences study design

All studies must disclose on these points even when the disclosure is negative.

Study description	We developed an index of cumulative environmental impacts of mariculture on marine biodiversity by considering the vulnerability of species to mariculture pressures (nitrogen and phosphorus emissions and habitat degradation), the intensity of these pressures, and the probability of species occurrence. Using this index, we quantified the current and future (2050) cumulative impacts of mariculture on 20,013 marine species.			
Research sample	This study did not involve sampling.			
Sampling strategy	N/A			
Data collection	All datasets used in this study are publicly available or can be accessed by request from the data owner.			
Timing and spatial scale	N/A			
Data exclusions	N/A			
Reproducibility	This study did not involve any experimental procedures.			
Randomization	We conducted 10,000 randomization analyses to place future bivalve and finfish farms randomly across all potential mariculture areas in 2050.			
Blinding	This study did not involve any blinding procedures.			
Did the study involve field	d work? Yes X No			

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\ge	Palaeontology and archaeology	\boxtimes	MRI-based neuroimaging	
\times	Animals and other organisms			
\boxtimes	Clinical data			
\boxtimes	Dual use research of concern			
\boxtimes	Plants			

Plants

Seed stocks	N/A
Novel plant genotypes	N/A
Authentication	N/A