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Aquaculture carrying capacity estimates show that major African lakes and marine waters could sustainably produce 10–11 Mt of fish per year

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Aquaculture carrying capacity (CC) can be used to guide sustainable aquaculture development over the long term through the regenerative power of the environment. In this study, a model has been developed to estimate CC by combining marine spatial planning for physical CC, management criteria for production CC, eutrophication and pathogen risk for ecological CC, and social acceptance based on legislative and management criteria. The estimates of CC for major African freshwater lakes and the marine exclusive economic zones of Africa indicate that 10–11 Mt of fish could be produced annually while preserving ecosystem goods and services, potentially increasing fish consumption by the population of the African continent by 7 kg per capita per year (an increase of 70%). Supply-side forecasts and demand-side estimates can support policymakers in defining targets for aquaculture expansion that avoid ecological, economic and social tipping points.

Aquatic food security is increasingly dependent on farming and accounts for 60% of all finfish and shellfish consumed worldwide[1]. The overwhelming majority of aquaculture takes place in emerging economies (>90% of the 80 Mt annual production in 2020[1]), which are largely responsible for the consistent 6–8% annual increase in production. This growth rate, fuelled by the twin pressures of human population expansion and the need to increase per capita consumption of fish, and stimulated by the decrease in the wild capture of key species, is having an impact on both the environment and society[2].

To ensure the sustainable growth of aquaculture, given limited resources such as space and water quality and the need to balance competing uses and the equilibrium of ecological, economic and social factors, it is essential to determine the carrying capacity (CC) in an integrated manner[3].

CC is presently defined through four pillars: physical, production, ecological and social[4,5]. Together, these correspond to the Food and Agricultural Organization (FAO) definition of the ecosystem approach to aquaculture, predicated on the optimization and preservation of human capital, ecosystem services and multiple system uses[6].

Different approaches have been applied to evaluate CC, but in general this has been done only for each pillar per se.

The evaluation of physical CC typically relies on marine spatial planning (MSP), resulting in a suitability analysis[7,8], that is, it evaluates the effect of the environment on aquaculture but not the effect of aquaculture on the environment. MSP often includes factors such as buffer zones near cities or designated tourism areas when dealing with land-based aspects, as well as nature conservation areas, breeding grounds and other designated zones within the water body. The physical pillar thus includes an important social and multi-use component, but as a single criterion of suitability it will almost certainly result in severe damage to the ecosystem because ecological CC is not considered as a constraint.

Production CC has mainly been assessed through mathematical models of individual and population growth; as bivalves are organic extractors, there has been more emphasis on species such as mussels and oysters[9–11]. Complex modelling frameworks have been developed to extend this assessment to the system scale for bays and estuaries by combining simulations of catchment loading,

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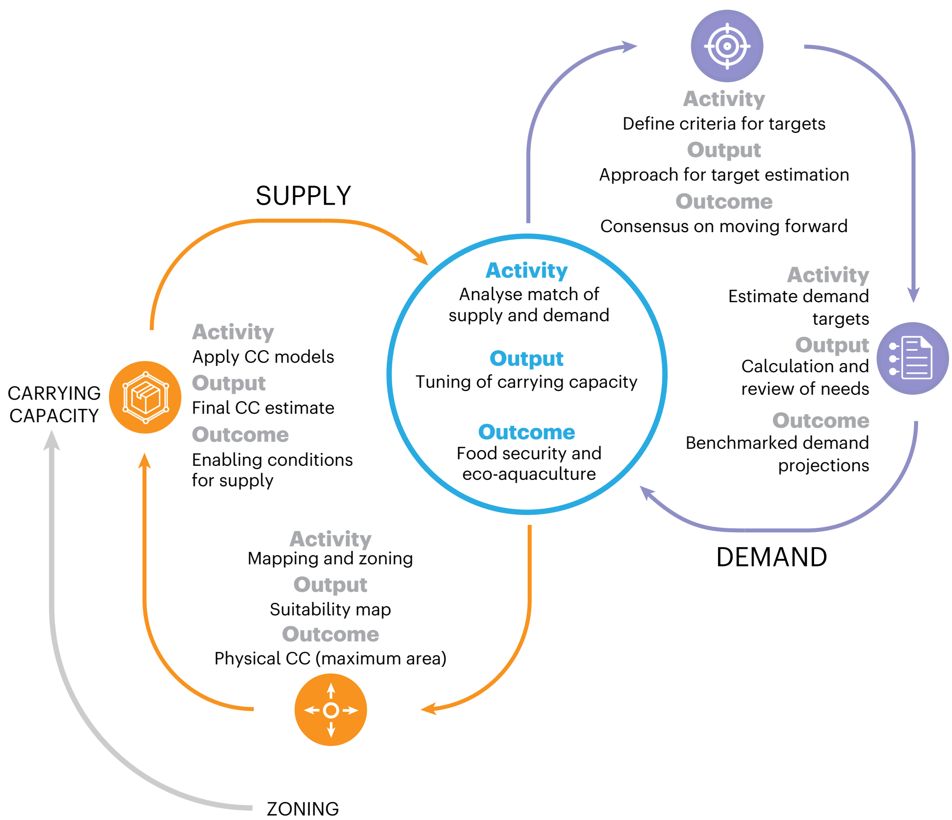

Fig. 1 | AQRATE framework for integrated assessment of CC. The AQRATE framework integrates the physical, production, ecological and social pillars of CC. The left side of the diagram corresponds to the zoning and CC components (supply) and the right side addresses the demand for aquaculture products. Credit: A. Fernandes, Longline Environment Ltd.

circulation, biogeochemistry and ecology[12,13]. Frameworks of this kind address food depletion—a natural limitation on the production CC of filter feeders—and also ecological CC, as thresholds for eutrophication indicators such as chlorophyll and dissolved oxygen can be simulated[14], as well as resource partitioning between cultivated and wild species[15].

The production CC for finfish has focused mainly on the cage or farm scale, with an emphasis on physiological modelling[16,17]. Such models can be extended to deal with environmental emissions[18] and usually consider loss of particulate organic carbon from faeces and uneaten feed. A natural development of this has been the local-scale simulation of particulate organic carbon loading to the sediment through models such as DEPOMOD[19] and ORGANIX[18], which provide information on ecological CC and can incorporate metrics such as sulfide and redox potential[20].

Such metrics have been used by regulators in Norway, Scotland, Canada and elsewhere for both licensing and monitoring, but the broader-scale effects of fish farms on system-scale eutrophication due to dissolved emissions, which are two to three times greater than particulate losses, are not usually considered.

The relationship between ecological CC and pathogens[21–23] is another component that is usually considered separately from other aspects and rarely integrated[24].

Finally, social CC, which is less amenable to mathematical modelling, has been addressed through a variety of methodologies[25], some of which use indicators from both ecological and social CC[26].

Although these pillars are accepted as the basis for quantifying sustainable CC, and different approaches have been proposed to evaluate each component, the pillars need to be combined to provide a single recommendation for policymakers with respect to the stocking density of cultivated species in a particular area.

To address this need, the Aquaculture Rating Thresholds for Ecosustainability (AQRATE) framework has been developed, which brings together the physical, production, ecological and social pillars of CC to provide a precautionary estimate of where, what and how much stock can be cultivated in a given area. The model focuses on open water bodies (inshore or offshore, marine or freshwater) as these present the greatest challenges with respect to connectivity, competing uses and ecological balance, but a subset of this approach could be applied to pond-based systems.

This work used established indicators and well-tested mathematical models to estimate CC using an integrated approach by combining (1) MSP for physical CC, (2) management criteria for production CC, (3) eutrophication and pathogen risk for ecological CC, and (4) social licence based on legislative and management criteria.

The model outputs an overall range of areal occupation and stocking density that can be used for policy and management; the framework was tested in different ecosystems to make real-world predictions and assess the comparative role of each pillar. The CC estimates can be further refined if necessary with appropriate local-scale models for production, economic viability and benthic impact.

AQRATE provides policymakers and managers with a framework that is simple to use and suitable for data-poor ecosystems to meet the needs of aquaculture development in different parts of the world.

The resulting supply-side precautionary forecast can be compared with realistic demand-side estimates to support the definition of targets for expansion that avoid ecological, economic and social tipping points.

Results

The AQRATE framework (Fig. 1) was tested in two case studies to illustrate its application in fresh and marine waters. The Kenyan part

Table 1 | Values for parameters used for application of the AQRATE framework in the Kenyan EEZ of Lake Victoria

Parameter	Value	Notes
Farmed species	Nile tilapia	Only species already cultivated in all of Lake Victoria
Number of production cycles	Two cycles per year	Conservative estimate
Inshore cage depth	3 m	Net depth
Inshore stocking density	15 kg m^{-3}	At harvest
Offshore cage depth	10 m	Net depth
Offshore stocking density	30 kg m^{-3}	At harvest
Edible proportion of fish	70%	Offcuts include head, gut, bones and skin
Target per capita fish consumption	15 kg cap^{-1} yr^{-1}	Triple the present-day value of 5 kg cap^{-1} yr^{-1}
Catchment nitrogen (N) load	85 mg N m^{-2} d^{-1}	Determined from the SWAT model[52]
Catchment phosphorus (P) load	8 mg P m^{-2} d^{-1}	Determined from the SWAT model[52]
DIN threshold for a zone	42 μg N l^{-1}	Precautionary for eutrophication assessment
PO_4 threshold for a zone	6 μg P l^{-1}	Precautionary for eutrophication assessment

The values were obtained from detailed mathematical models, published work or by consultation with local stakeholders.

of Lake Victoria was used as an example of an application for Nile tilapia (*Oreochromis niloticus*) in freshwater and an offshore coastal area of the Arabian Sea was used to analyse the CC for barramundi (*Lates calcarifer*).

Application to the Kenyan exclusive economic zone of Lake Victoria

To apply the framework, a number of assumptions were made with respect to model parameters (Table 1). These assumptions were derived from more detailed models, stakeholder consultation or the use of heuristics, but the final values of these and other parameters for the various CC pillars should be determined by local policymakers and other relevant actors.

The Kenyan exclusive economic zone (EEZ) of Lake Victoria was divided into two parts, an inshore area and an offshore area, based on the type of cage culture that currently exists in each. The offshore component was further subdivided into an area with a maximum depth of 45 m and a deeper area, termed the high-investment offshore zone (HIOZ), allocated to operators capable of managing aquaculture with deeper moorings, cages appropriate for high energy conditions and suitable service vessels.

A geographic information system (GIS) suitability analysis (Supplementary Section III and Extended Data Figs. 1–4) yielded the areas shown in Extended Data Table 1. Four suitability categories were used: highly suitable, suitable, moderately suitable and unsuitable. When unsuitable areas were excluded from further analysis, 1,936 km^2 remained available for aquaculture (Extended Data Fig. 5) out of a total area of 3,836 km^2 (50%).

If all of this area were used for aquaculture, based on the stocking densities given in Table 1 and two production cycles per year, the total production would be in excess of 1 Gt yr^{-1}, and the results would be catastrophic. A possible approach to refine this number would be to apply a heuristic coefficient in an attempt to capture the reduction imposed by the other three CC pillars, for example, by considering 0.1% of this area (or some other value). However, the application of AQRATE allows CC to be scientifically quantified, therefore providing an evidence-based, spatially discretized estimate of the potential for sustainable aquaculture (Fig. 2 and Methods).

The results obtained with this application are summarized in Table 2. The different zones shown for the Kenyan EEZ of Lake Victoria in Extended Data Table 1 were aggregated by region (anonymized as A–E) and divided into inshore, offshore and HIOZ areas.

Table 2 shows the area of cages and corresponding tonnage that could be allocated for each pillar, that is, the respective CC, for each region. The total area and tonnage per pillar are also shown; the values in bold show different limiting pillars for different zones, and thus the limitations of a bulk assessment, which may overestimate CC.

The current population of Kenya is 53.8 million. The estimated CC is 258,279 t yr^{-1} live weight based on the data used in this case study (Fig. 3), yielding 180,795 t yr^{-1} of tilapia fillet after deducting 30% for offcuts such as head, bones and frame, which would increase fish consumption by 3.4 kg per capita per year (3.4 kg cap^{-1} yr^{-1}). In an alternative calculation, a target to increase the current consumption of 5 kg cap^{-1} yr^{-1} by 10 kg could be met for about 18 million people, that is, ~30% of the present population. Based on current market prices, the annual gross income corresponding to the CC estimated with AQRATE would be about US$270 million.

As aquaculture develops in the Kenyan Lake Victoria EEZ over the next decade, the CC estimates from AQRATE should be reviewed to determine whether social, environmental or economic indicators show major alterations.

Supply and demand. On the demand side (Fig. 1), an extra 10 kg of fish per capita per year corresponds to an overall demand of 538,000 t yr^{-1}, which, after factoring in a 30% loss for offcuts, represents a production of about 769,000 t yr^{-1}. The CC range determined for this example would satisfy about one-third of this requirement. Although setting higher CC targets would enhance demand satisfaction, it increases risk with respect to sustainability and potentially creates 'boom-and-bust' conditions with the associated socio-economic and environmental consequences. These are in the first instance disastrous for local populations, but can have far-reaching effects on public attitudes and policy options at the regional level.

Application to the offshore coastal area of Pakistan

AQRATE was also applied to the two coastal provinces of Pakistan, that is, Baluchistan and Sindh, both of which border the Arabian Sea. No data were available on nutrient loading from land, so conservative estimates of dissolved inorganic nitrogen (DIN) of 70 mg m^{-2} d^{-1} and phosphate (PO_4) of 4 mg m^{-2} d^{-1} were used. As for the Lake Victoria case study, these and other parameter choices were determined heuristically and through consultation, as stakeholder engagement and local decision-making are critical.

Asian sea bass (barramundi) have a longer culture cycle than tilapia and a period of 455 days was selected. As this analysis was performed for offshore culture in the open sea, the spacing between farms was increased to 20 farm units.

The offshore area of each province, labelled A and B in Extended Data Table 2, was divided into four zones, corresponding to the four physical suitability classes, but the MSP analysis indicated that there were no areas that were unsuitable or highly suitable for barramundi culture. MSP determined a very large available area of 18,825 km^2, about five times greater than the area for Kenya, and once again the result of occupying the whole area to grow fish would be catastrophic. The application of the AQRATE framework greatly reduces the available space (Table 3). As expected, for large open-ocean areas eutrophication is not a major concern, and if only this component of the ecology pillar were used, the potential production would be almost 30 Mt. This is 1% of the physical CC, but disease—the other component of the pillar—greatly reduces this number.

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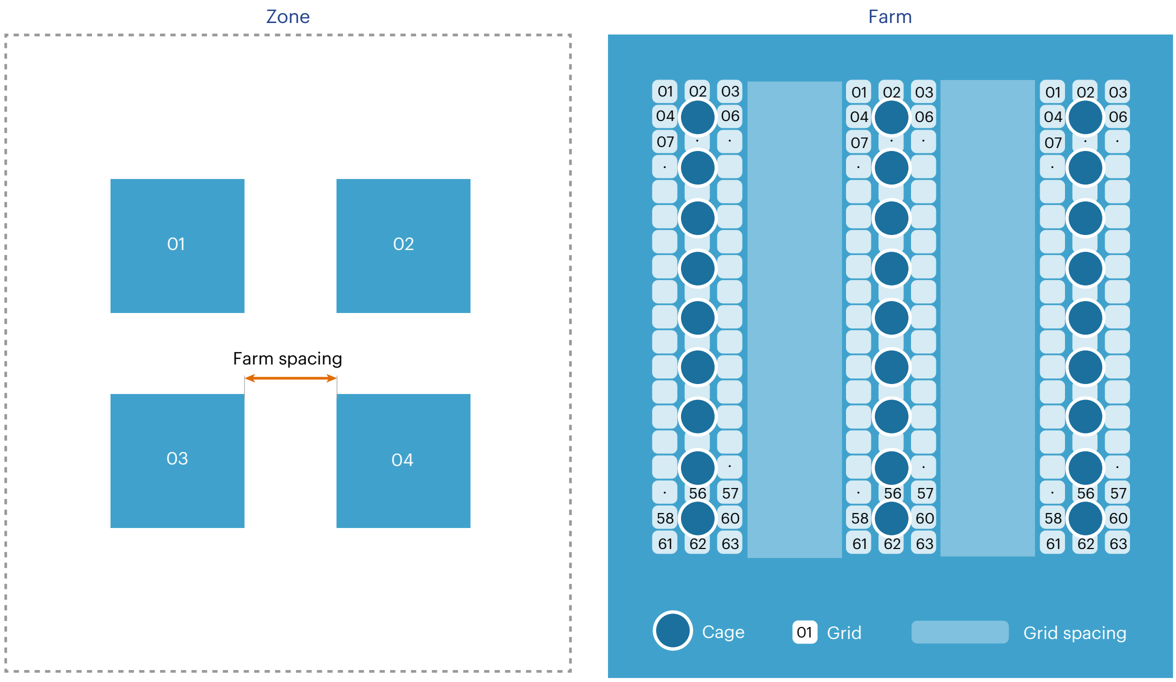

Fig. 2 | Application of AQRATE to the Kenyan EEZ of Lake Victoria. Production and social CC (policy and licensing) for an example with four farms in a zone, with each farm having three grids with nine cages each. See Supplementary Information for the equations used for the calculations. Credit: A. Fernandes, Longline Environment Ltd.

Table 2 | CC estimated by AQRATE for different zones A–E in the Kenyan EEZ of Lake Victoria

	Kenyan EEZ, Lake Victoria					
Zone name	**Production and social CC area (km^2)**	**Production and social CC tonnage (t)**	**Eutrophication CC area (km^2)**	**Eutrophication CC tonnage (t)**	**Disease CC area (km^2)**	**Disease CC tonnage (t)**
Zone A inshore	0.033	3,004	0.174	15,626	**0.005**	**449**
Zone A offshore	**0.000**	**0**	0.162	97,485	0.029	17,515
Zone A HIOZ	0.000	0	0.000	0	0.000	0
Zone B inshore	0.185	16,611	**0.012**	**1,036**	0.025	2,291
Zone B offshore	**0.170**	**101,788**	0.173	103,595	0.225	134,743
Zone B HIOZ	**0.021**	**12,723**	0.157	94,004	0.033	19,675
Zone C inshore	0.128	11,486	0.105	9,480	**0.018**	**1,583**
Zone C offshore	**0.021**	**12,723**	0.096	57,364	0.025	15,097
Zone C HIOZ	0.000	0	0.000	0	0.000	0
Zone D inshore	0.308	27,744	**0.029**	**2,566**	0.042	3,800
Zone D offshore	**0.127**	**76,341**	0.193	115,638	0.195	116,798
Zone D HIOZ	**0.085**	**50,894**	0.144	86,192	0.122	73,202
Zone E inshore	0.008	707	0.113	10,179	**0.001**	**114**
Zone E offshore	**0.042**	**25,447**	0.207	124,436	0.086	51,336
Zone E HIOZ	**0.021**	**12,723**	0.108	64,912	0.052	31,249
Total	1.149	352,193	1.671	782,511	0.858	467,851

CC estimates, aggregated by region (A–E), are divided into inshore, offshore, and HIOZ. The area and tonnage for each CC pillar are shown, together with the respective totals. The area and tonnage values shown in bold show that different CC pillars may be limiting in different zones, justifying a granular zone-by-zone approach.

The social pillar is also much lower (0.01% of the physical CC) as a more conservative farm spacing is used. If the zonal approach is applied, the final area available for cage culture is 1.73 km^2, corresponding to a potential annual production of 276,699 t (see also Discussion and Methods). If the less precautionary bulk approach is used, disease is the limiting pillar, but the overall change is small: a total cage area of 1.75 km^2 and a production of 279,473 t yr^{-1}.

Supply and demand. Per capita fish consumption in Pakistan is the lowest in the world[1], estimated at 1.9 kg cap^{-1} yr^{-1}. A barramundi production of between 276,699 and 1,221,451 t yr^{-1} could potentially enhance domestic consumption by 1–5 kg cap^{-1} yr^{-1}, considering a population of 231.4 million. At the lower end of the range, per capita consumption would increase by a half, at the higher end it would more than double. However, this is an oversimplification because the low consumption of aquatic products in Pakistan[27] is attributed to (1) the high proportion of the country that has poor access to the sea, (2) the low income per capita, and (3) cultural reasons and social acceptance.

An alternative is to estimate the potential income from the cultivated barramundi crop: at a farmgate price of around US$5 kg^{-1}, the gross annual income would range between US$1,383 and 6,107 million.

Discussion

The limiting pillar for CC can vary between zones (for example, in some zones eutrophication may limit CC, in others social CC or disease risk may be limiting, Table 2); a bulk approach can more than double the estimate of CC, particularly when a simulation considers offshore areas with larger cages and inshore areas with artisanal grids of small cages. In the Kenyan EEZ of Lake Victoria, the use of a bulk approach for CC would select disease risk as the limiting pillar, allowing a total area A_{cc} of 0.86 km^2, 5,744 cages and a production of 467,851 t yr^{-1}. However, for a more granular zone-by-zone analysis, these numbers change to 0.46 km^2, 2,402 cages and a production of 258,279 t yr^{-1} (Fig. 3), that is, the carrying capacity is roughly halved.

Note that there are nonlinearities in these estimates as the overall zonal/bulk ratios are 0.53, 0.42 and 0.55 for area, number of cages and production, respectively. While the area is reduced to 53% using the zonal approach and the production is 55% of the bulk estimate for CC, there are only 42% of the cages because this case study considers both inshore and offshore (including HIOZ) areas, which have different parameterization for, for example, cage areas and net depths.

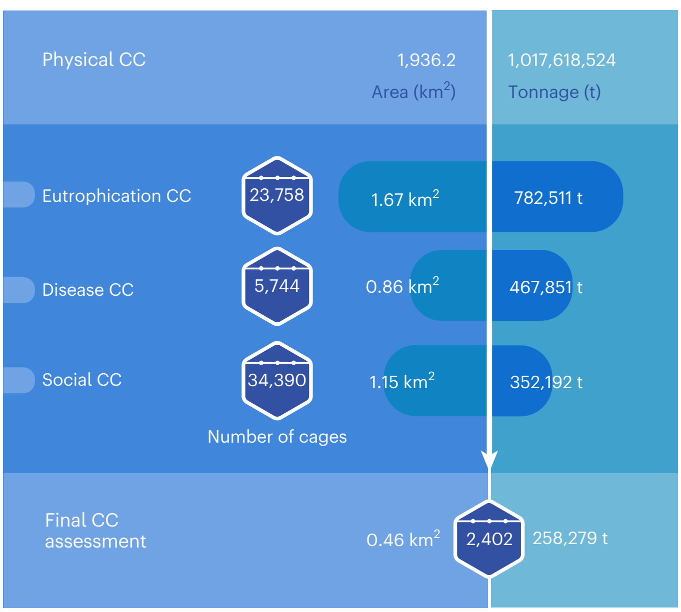

Fig. 3 | The final results of AQRATE application to the Lake Victoria case study. Physical CC is greatly reduced by other CC pillars and the smallest bulk estimate (Social CC) is about 36% higher than the final granular CC estimate of 258 kt. Credit: A. Fernandes, Longline Environment Ltd.

A subset of pillars can be used to calculate CC by excluding the disease component, which is equivalent (see Methods) to setting the risk tolerance factor (R_p) to 1. If this is applied to the Kenyan Lake Victoria case study, the cage area increases to 0.58 km^2, corresponding to 8,652 cages and a production of 269,324 t yr^{-1}. Food security increases in terms of population served as almost 20 million people would have access to an additional 10 kg fish per capita per year. Extended Data Table 3 shows the response of the AQRATE framework to small changes (~10%) in some model parameters. The default settings used for the Lake Victoria case study identify 15 suitable zones (grouped suitability classes) from the MSP analysis. The limiting pillar for CC differs (Table 2) between inshore zones, where two zones are limited by eutrophication and three zones by pathogens, and offshore zones, all of which are limited by social CC. This is consistent with the fact that inshore zones would, as a rule, be more susceptible to nutrient enrichment and disease risk due to both direct loading from land and smaller dilution volume.

Small changes in model parameterization allow more scope for development and annual tonnage increases to 363,241 t yr^{-1}. There is a 41% increase in both area and production and a 55% increase in the number of cages (Extended Data Table 3), adding almost 5 kg cap^{-1} yr^{-1} to the fish supply for the Kenyan population or providing improved food security (an additional 10 kg of aquatic products per capita per year) to 25 million people.

This underscores the importance of environmental measurements and stakeholder participation to identify perceived risk, improve data quality and focus scarce resources on parameter estimation.

For marine waters, a similar sensitivity analysis shows that if the disease component is not considered and a more business-oriented social policy is applied by defining ten farm units as adequate spacing, the final estimate of CC is 1,221,451 t yr^{-1}, that is, a roughly threefold increase. This is still well below the threshold of the eutrophication pillar, so AQRATE does not flag this as a concern, but disease outbreaks are boom-and-bust events, so omitting this indicator from the analysis is always problematic.

Coefficients derived from these case studies may be used to scale CC to wider areas as a potential indicator of production; these values were used to estimate the contribution that aquaculture can make to food security in Africa, one of the most critical parts of the world with respect to population growth, protein supply and micronutrients[28].

Figure 4 shows the potential CC of (1) Lake Victoria, the largest lake in Africa, (2) the African Great Lakes, that is, ranked by size, Victoria, Tanganyika, Malawi, Turkana, Albert, Kivu and Edward[29], (3) other large lakes and reservoirs in Africa, and (4) the summed marine area of the EEZ of African nations[30].

The suitable area in Lake Victoria was calculated by MSP using depth as a criterion and the same ranges were applied to the Kenyan EEZ. The ratio between the suitable and total area was 0.40, which compares well with the value of 0.39 calculated for the Kenyan EEZ using AQRATE (Δ = 3.3%) and lends credence to the scaling exercise. For freshwater systems, factors of 2.38 × 10^{-4} for CC area and 2.54 × 10^{-4} for CC annual production were used, based on the Kenya case study, while for the marine EEZ, 9.19 × 10^{-5} was used for both the CC area and

Table 3 | CC estimated by AQRATE for coastal waters in the Arabian Sea

Pakistan marine EEZ, Arabian Sea						
Zone name	Production and social CC area (km^2)	Production and social CC tonnage (t)	Eutrophication CC area (km^2)	Eutrophication CC tonnage (t)	Disease CC area (km^2)	Disease CC tonnage (t)
Zone A offshore	0.933	149,288	103.754	16,600,649	0.835	133,665
Zone B offshore	1.039	166,253	81.520	13,043,183	0.911	145,808
Total	1.972	315,542	185.274	29,643,833	1.747	279,473

CC estimates are aggregated by region (A and B). The area and tonnage for each CC pillar are shown, together with the respective totals.

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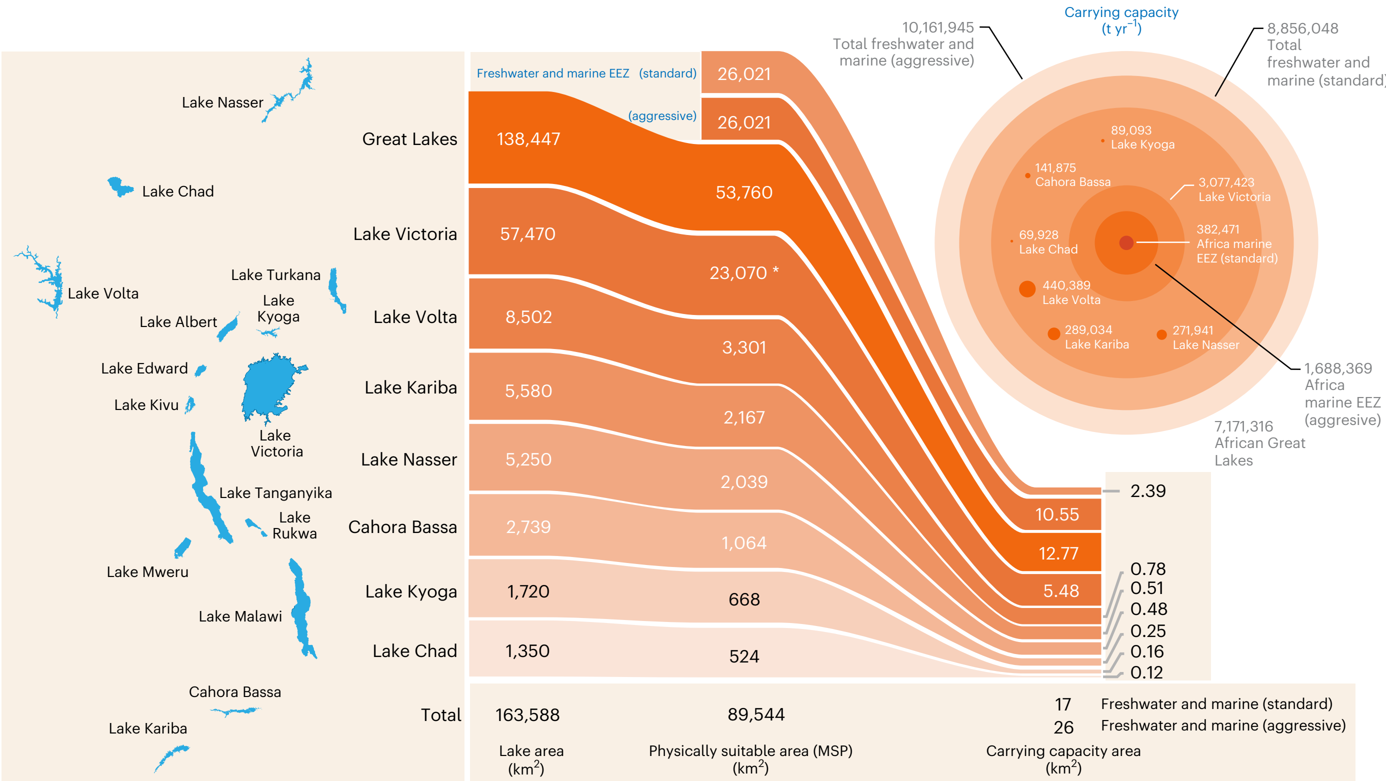

Fig. 4 | Results for AQRATE upscaling to the whole of Africa. CCs estimated for major freshwater areas of Africa, including the seven great lakes of Africa (Victoria, Tanganyika, Malawi, Turkana, Albert, Kivu and Edward, which constitute 85% of the total area), other large lakes and the African EEZ. *Suitable inshore area: 3,224 km^2; suitable offshore area: 19,846 km^2. Total suitable area calculated bottom-up from MSP, all others calculated top-down using the proportion of total area of the system(s). Credit: A. Fernandes, Longline Environment Ltd.

the annual production, based on the standard Pakistan case study, and 4.05×10^{-4} for the CC area and tonnage in the aggressive (no disease and increased social acceptance) scenario.

A CC of 3 Mt yr^{-1} of tilapia was estimated for Lake Victoria, scaling to 7.2 Mt yr^{-1} for the African Great Lakes. A further 1.3 Mt yr^{-1} aggregate production was calculated for Cahora Bassa (Mozambique), Lake Kariba (Zimbabwe and Zambia), Lake Kyoga (Uganda), Lake Volta (Ghana), Lake Chad (Nigeria, Niger, Chad and Cameroon) and Lake Nasser (Egypt).

The total available area estimated by MSP for cobia (*Rachycentron canadum*) production in the African marine EEZ is about 26,000 km^2, one of the limiting factors being suitable access to port facilities[29]; the application of the AQRATE CC model reduces the available area to 2.4 and 10.6 km^2 for the standard and aggressive scenarios, respectively. The corresponding yields are 382,471 and 1,688,369 t yr^{-1}, respectively, based on the AQRATE coefficients for barramundi.

Overall, the projection for sustainable aquaculture production in Africa is between 8.8 and 10.2 Mt yr^{-1}, bearing in mind that only a subset of the freshwater area is used. This compares well with estimates of 11 Mt yr^{-1} in 2030 in the HIGH scenario calculated by Chan et al. using the International Model for Policy Analysis of Agricultural Commodities and Trade (IMPACT) model[31,32], particularly considering that the AQRATE estimate does not include land-based ponds: Egypt alone produces around 1.6 Mt yr^{-1} (ref. 1), of which 86% is pond culture[33].

The IMPACT model uses socio-economic variables to predict aquaculture production and estimates an annual aquaculture production of 18.8 Mt for the HIGH scenario in 2050.

Based on the present study, it seems unlikely that the forecast of 10–11 Mt can be doubled without major environmental consequences.

As the current population of Africa is about 1.3 billion, an annual aquaculture production of 11.5 Mt (including Egyptian pond production) would increase the average per capita consumption by 7 kg yr^{-1}, assuming that the harvested fish would be for the domestic market.

This increase would potentially boost the current average consumption based on the predicted supply by 70%, but Chan et al.[31] predict that consumption in Africa will show weak growth under a HIGH scenario, reaching only 14 kg cap^{-1} yr^{-1} in 2050, partly dependent on the predicted increase in gross domestic product, but also on demographics, as the population is expected to grow from 1.7 billion in 2030 to 2.5 billion in 2050[34]. Demand satisfaction for blue protein calculated by AQRATE under those demographic shifts would lower the average consumption increase to 5.4 kg cap^{-1} yr^{-1} in 2030 (54%) and 3.7 kg cap^{-1} yr^{-1} in 2050 (37%).

The HIGH scenario analysed with IMPACT, which predicts aquaculture yields in line with the AQRATE model, would lead to the direct and indirect creation of 1.9 million jobs[30]. This supports a development strategy focused on the sustainable use of water resources, aimed simultaneously at contributing to food security and preserving ecosystem services. This strategy also creates the conditions for progressively better governance, a key component for the stable growth of the industry.

For Africa, the model predicts that about 80% of cultivated fish will originate from freshwater and 20% from marine waters. There has been some debate regarding the relative roles of freshwater and marine waters in aquatic food production worldwide[35,36]. In the present study, although freshwater is dominant, both ecosystems emerge as important contributors to protein supply from aquaculture. Four factors may increase the proportion from marine waters: (1) inland systems have a higher environmental susceptibility due to longer water residence time and shallower depth, (2) technological developments in offshore aquaculture will be an enabling factor for expansion in marine waters in the coming decades, (3) climate change will increase pressure on freshwater resources and (4) the trend to farm lower down the food chain favours marine organisms such as bivalves[37] and seaweeds[29,38,39], particularly in light of climate change.

The rapid worldwide expansion of aquaculture that has occurred in the past decades has led to an important discussion on CC. While the definition of zones[6,40] has been very useful for area management, the question of determining what and how much can be grown sustainably within such zones has been addressed in a more fragmented manner.

As in other areas of food production, and in particular its relationship with both the natural and social environments, a number of tools have been developed on the basis of well-established concepts. By providing a framework to integrate these concepts and developing simple quantitative methods for their practical application, this work contributes to the sustainable development of a fundamental sector for human food security.

Methods

Overview

The general approach used to estimate CC is shown in Fig. 1. The supply-side steps (left) address both the MSP process and the determination of CC. The final value or range for CC corresponds to what can be sustainably produced. In most parts of the world, inshore aquaculture is prevalent, whether in lakes and reservoirs or in coastal embayments. The AQRATE framework deals with both inshore and offshore conditions. The definition of offshore is complex[41]; in this work, depth is used as a criterion. The main part of this work concerned the development of the supply-side framework, and therefore the focus was on environmental and social CC. However, from a policy perspective, it is important to understand the potential demand for what can be supplied to avoid creating unrealistic expectations that can result in negative social and economic consequences. The final part of the methodology described here addresses these aspects in a simplified manner. The full set of equations used for the various parts of the framework is provided in Supplementary Section I.

CC assessment

Zoning. The output of MSP is the zoning of a particular water body using a classification scheme normally based on multi-criteria evaluation implemented by means of a GIS (Extended Data Figs. 1–3). This classification usually defines various suitability categories (Extended Data Table 4 and Extended Data Fig. 4); AQRATE can accommodate a range of methodologies, from binary schemes (suitable/unsuitable) to five-category schemes (highly suitable/suitable/moderately suitable/moderately unsuitable/unsuitable; Extended Data Table 5).

MSP has been extensively used as a policy-support tool[29,42–45]. In 2014, European Union directive 2014/89/EU placed a legal requirement on Member States to develop and implement maritime spatial plans by 2021. MSP yields a set of areas A_m (one per zone) corresponding to the zoning of the water body of interest. A suitability class is assigned to each area A_m (Extended Data Fig. 5); therefore, although the sum of the zone areas equals the area of the water body, the sum of suitable zone areas will in general be less than the area of the water body.

For any suitable zone, given the available area A_m determined by MSP, the next step is to determine a precautionary factor α to be applied, resulting in a new, smaller area A_{cc} available for cultivation considering the production, ecological and social pillars, where $A_{cc} = \alpha A_m$. The precautionary factor α is determined heuristically, taking into account a number of key factors (equation (1)):

$$\alpha = \min(\alpha_\rho, \alpha_\varepsilon, \alpha_\delta, \alpha_\sigma, \ldots) \quad (1)$$

where α_ρ is the production-based maximization of harvestable biomass[4,46,47] or profit[48], α_ε is the eutrophication potential based on overall dissolved emissions from an area, α_δ is the pathogen risk and connectivity, and α_σ is the acceptable social impact of structures. The final value of α is the minimum calculated for all pillars.

Simple zone-scale models are used to quantify the various components of α, including (1) a model for space allocation constraints, such as typical grid layouts and spacing, how many grids should constitute a typical farm and how far apart farms should be spaced, (2) a mass balance model for the emissions of dissolved nutrients, allowing water quality thresholds to be tested to optimize aquaculture stocking density, and (3) a pathogen model addressing stocking density, connectivity and risk, providing information on both stocking density and spatial distribution within an (MSP) suitable area.

These zone-scale models are briefly described below (for details and equations, see Supplementary Information).

Production and social CC. At its most basic, the production CC is the total yield of the suitable area determined by a GIS if it were all used for fish farming. However, it must take into account other constraints, for instance, typical grid layouts and spacing, how many grids should constitute a typical farm and how far apart farms should be spaced. The physical zone determined to be suitable through MSP would, as a rule, already exclude non-compatible areas such as navigation channels and protected areas.

These criteria overlap to a considerable degree with the social CC. The social pillar can also include other stakeholder-derived information, such as viewsheds or noise, but here the social pillar is limited to the policy choices made for licensing and restrictions derived from the physical CC classification. By definition, this is the social element of the system.

Within the area classified as suitable by GIS multi-criteria evaluation, there will be a number of policy-driven spatial constraints. These are related to the way managers plan the distribution of cages, grids and farms. Such decisions should be informed by ecological CC indicators such as eutrophication and disease risk and should also be supported by stakeholder consultation, that is, the social licence.

The aquaculture infrastructure for a zone consists of primary structures and supporting elements such as vessels and onshore facilities. The focus of this section is the primary component: farms that contain grids, which in turn contain cages (Fig. 2).

Ecological CC. Ecological CC is considered to have two components: eutrophication potential and disease risk. These are reviewed in turn.

Eutrophication potential. Two aquaculture-derived sources should be considered to contribute to eutrophication in the water column. The first is the direct input of nutrients into the water column due to fish excretion and the second is the indirect input of nutrients into the water column due to sediment diagenesis of organic particulates from fish farming, that is, uneaten feed and undigested food. Only the first component (direct emissions) is used to calculate α_ε. The second component can be addressed through local-scale deposition models such as ORGANIX (ref. 18) and will not constrain the overall area but the allowable production within an area through stocking density restrictions.

A simple mass balance model (Supplementary Equation (9) and Supplementary Section I) can be used to determine the direct eutrophication potential of aquaculture in a particular zone classified as suitable, and the formulation is generic for any dissolved nutrient.

The total load M_{in} is divided into three components: the background load M_b, the loading from land M_l, and the load from existing and/or planned aquaculture M_a. The load from finfish aquaculture is determined from the number of cages, stocking density and emissions of PO_4 or DIN from an individual fish. Seven species are included in AQRATE: Atlantic salmon, rainbow trout, gilthead bream, European seabass, barramundi, amberjack and Nile tilapia. Together, these correspond to a large percentage of world finfish aquaculture, and the emissions of DIN and PO_4 are calculated by means of the AquaFish physiological model[49].

A key question with respect to eutrophication potential is the choice of thresholds to use. A comprehensive set of values was compiled by El-Serehy et al.[50] on the basis of a range of international standards from different sources.

Eutrophication thresholds should be set on the basis of existing standards for eutrophication; for example, for phosphate, a value of 30 µg l^{-1} might be considered as a maximum as it is in the upper range of the trophic scale. A precautionary approach might set a value of 50% of that threshold, which is on the border of mesotrophic and eutrophic, to avoid tipping points and provide a buffer for climate change and any extreme environmental events.

The thresholds defined by different nations and organizations are somewhat variable, but an upper threshold of 10–15 µg l^{-1} of PO_4 is often considered to be the distinction between mesotrophic and eutrophic water bodies.

AQRATE determines the concentration of the nutrient of interest for a particular zone based on the mass balance (for all equations and details, see Supplementary Information) and calculates what capacity (if any) exists for additional aquaculture. This is expressed in terms of space, number of cages and annual tonnage.

Disease risk. A disease event[51] that occurs within a farm will originate within a cage (the index case), but will not be containable at the level of a grid of cages. It may be containable by avoiding transmission among grids, but that too is unlikely. It will be contained if the distance between farms is sufficient and biosecurity measures are promptly taken.

Waterborne pathogens released by exposed or infected host organisms decay through physical processes (dilution in the water column) and natural mortality. As a result, connectivity between farms is a key concern and the pathogen risk coefficient α_6 can be parameterized on that basis.

This can be achieved with complex models[23], but AQRATE aims to minimize both data needs and cost, so a simpler approach can be applied on the basis of local current speeds and on the relevant pathogens.

Slower currents will decrease connectivity and lower stocking densities will reduce the pathogen concentration at the adjacent farming area. Decay rates have been determined for some pathogens, but data tend to be sparse.

In the AQRATE framework, policymakers can specify the risk tolerance factor R_p within the range $0.01 \le R_p \le 1.00$, where the maximum risk tolerance implies that disease is not included in the analysis. The critical R_p may differ from species to species due to different host–pathogen profiles, which may be an important criterion for optimizing species selection.

The coefficient α_6 can be adjusted on the basis of the probability of disease occurrence; for example, if the area has no reported pathogen events, a higher tolerance may be used. However, poor husbandry, including ineffective or non-existent biosecurity, and weak governance, including poor reporting and enforcement, are major causes of disease propagation and therefore choices for spacing should follow the precautionary principle.

Final CC assessment. The final value or range of CC for each zone is determined by a stepwise procedure whereby the lowest estimate for CC, which corresponds to the lowest value of α, is taken to be the recommended value based on the results obtained from the physical, production, ecological and social pillars.

Estimation of demand for aquaculture products

Various approaches may be used to estimate demand, including complex economic methodologies such as the willingness to pay. Such approaches require surveys and other bespoke tools and may be economically impracticable in many parts of the world. There are, however, some general principles that can be applied to allow demand to be calculated (Fig. 1, right), leaving aside price-based calculations and aspects such as the substitute goods principle.

The uncertainties in demand estimates, associated for instance with market fluctuations, mean that for the purpose of matching supply and demand an order of magnitude calculation is probably sufficient as a first approach. In addition, policymakers should aim for a range rather than a specific number. This fits well with the proposed methodology for aquaculture CC, which is by definition a range conditioned by a set of underlying assumptions.

A primary consideration is whether demand for aquaculture products is predicated on exports, internal consumption or both. In many emerging economies, the primary reason for developing aquaculture is to satisfy internal demand, with the twin objectives of increasing the per capita consumption of fish and addressing expected population growth, but this approach can be easily adapted to include an export component.

A simple approach for estimating the demand is to compare the per capita consumption of fish with a target value and scale that to the present and projected population, taking into account the various sources of aquatic products, that is, national fisheries, national aquaculture production and imports.

Demand may be calculated using equation (2):

$$D_f = \frac{P_{t+\Delta t}}{1,000}(C_t - C_p) \tag{2}$$

where D_f is the demand for fish (t yr^{-1}), $P_{t+\Delta t}$ is the population (for the current year, $t = y_0$ and $\Delta t = 0$, and for a future year, $t = y_t$ and $\Delta t = y_t - y_0$), C_t is the target per capita fish consumption (kg cap^{-1} yr^{-1}) and C_p is the present-day per capita fish consumption (kg cap^{-1} yr^{-1}).

The demand for fish D_f can be satisfied from both national sources and imports, and the product origin can be cultivation and/or capture fisheries.

A key underlying assumption is that there is a willingness by the population to eat more fish, that is, that consumption is not limited by factors other than potential supply. Further assumptions must be considered in this calculation, such as changes in fisheries and the potential role of exports.

A range can be determined simply by considering (1) the demand at the present time (population = P_t) to meet the objective function set in C_t, which might, for instance, be based on the current world average calculated by FAO, and (2) the demand at a future point, for example, in 25 years (2050), that is, at population P_{t+25} ($= P_{2050}$).

More realistic approaches might consider a shift in the world average consumption by 2050 (based for instance on FAO projections) and use that number as C_t. There is, however, some uncertainty in such estimates because an increase in population worldwide might decrease per capita consumption by 2050, bucking the trend observed in recent years of an increase in global per capita consumption. Furthermore, externalities such as the recent substantial increases in cereal prices (grains are used as energy sources and binding agents in fish feed) due to war might also affect both supply and demand.

Synthesis of supply and demand

The evaluation of CC using the methodology described above will provide a robust general indicator of sustainable production. A comparison of these numbers with demand-side policy for improving food security will allow policymakers to assess to what extent aquaculture development can help to meet the needs of the population. If sustainable aquaculture production at CC exceeds demand requirements, precautionary adjustments can be made to, for example, nutrient thresholds, disease risk or social acceptance factors. However, if it is necessary to increase production beyond the supply-side estimates of CC, managers can iteratively adjust thresholds, bearing in mind that in doing so they may be pushing environmental and social systems nearer to the tipping point.

Reporting summary

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

Data availability

All data used for the carrying capacity calculations are provided in the Supplementary Information and the spreadsheet model available at https://gitlab.com/nature-food/aqrate-calculation/-/blob/b77243d83cee8c8841b01865e439c2541736e499/AQRATE_calculation_template.xlsx.

Code availability

The equations used to determine carrying capacity can be implemented in simple spreadsheets, making the approach a good alternative to the development of complex computer code. A full spreadsheet model illustrating the application of AQRATE to one of the case studies is available at https://gitlab.com/nature-food/aqrate-calculation/-/blob/b77243d83cee8c8841b01865e439c2541736e499/AQRATE_calculation_template.xlsx.

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Author contributions

J.G.F. conceptualized the AQRATE integrated carrying capacity framework and respective model equations, performed the calculations, developed the spreadsheet model and wrote the paper.

Competing interests

The authors declare no competing interests.

Additional information

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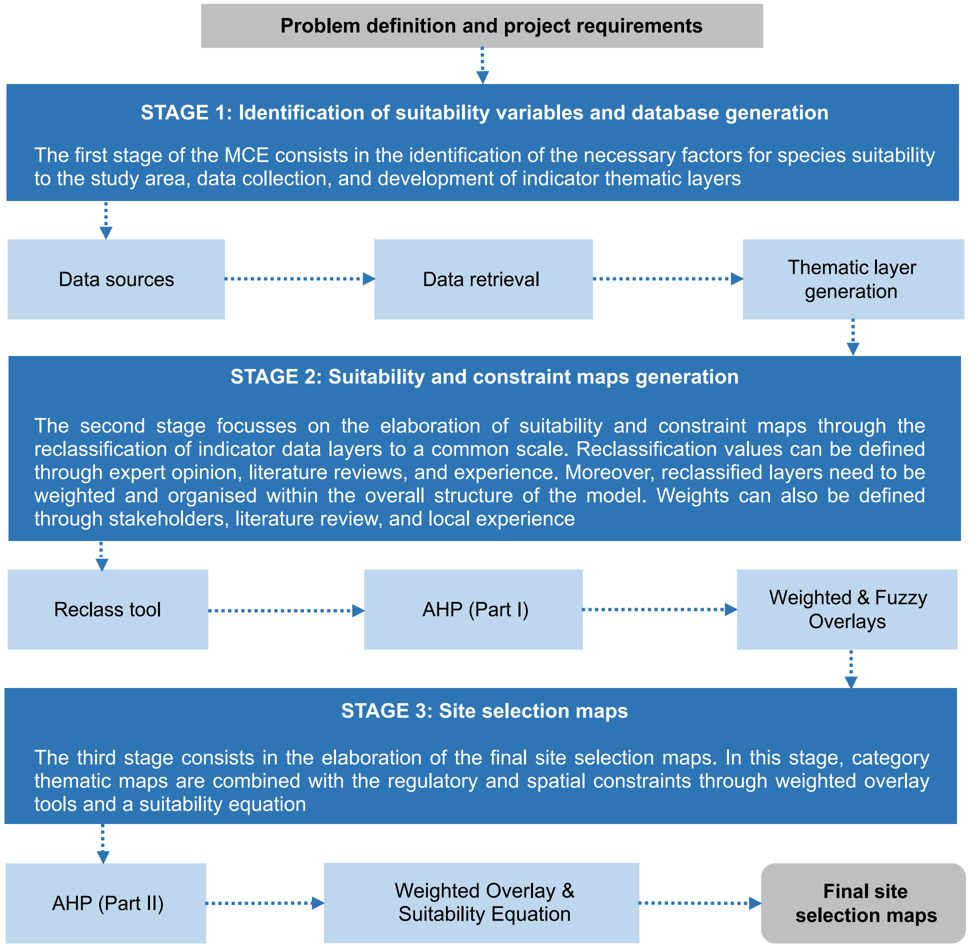
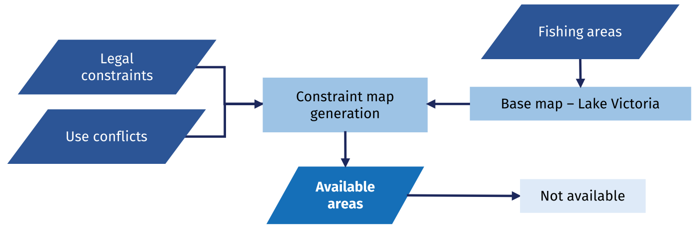


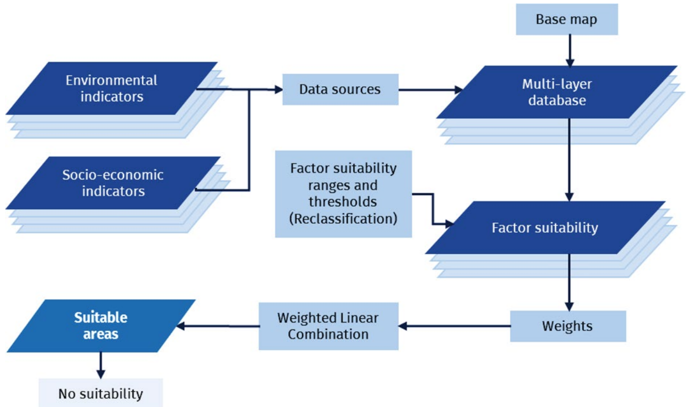
Extended Data Fig. 1 | Mapping methodology Lake Victoria. Methodology for mapping suitable areas for aquaculture in Lake Victoria.

https://doi.org/10.1038/s43016-025-01114-1



Extended Data Fig. 2 | Constraint map methodology. Methodology for the generation of the constraint maps.

https://doi.org/10.1038/s43016-025-01114-1



Extended Data Fig. 3 | Zoning methodology. Methodology for zoning of environmental and socio-economic factors.

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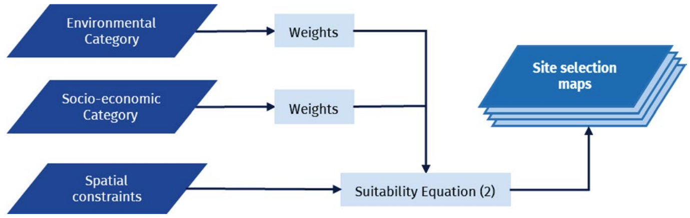

Extended Data Fig. 4 | Site selection methodology. Methodology for site selection maps in Lake Victoria.

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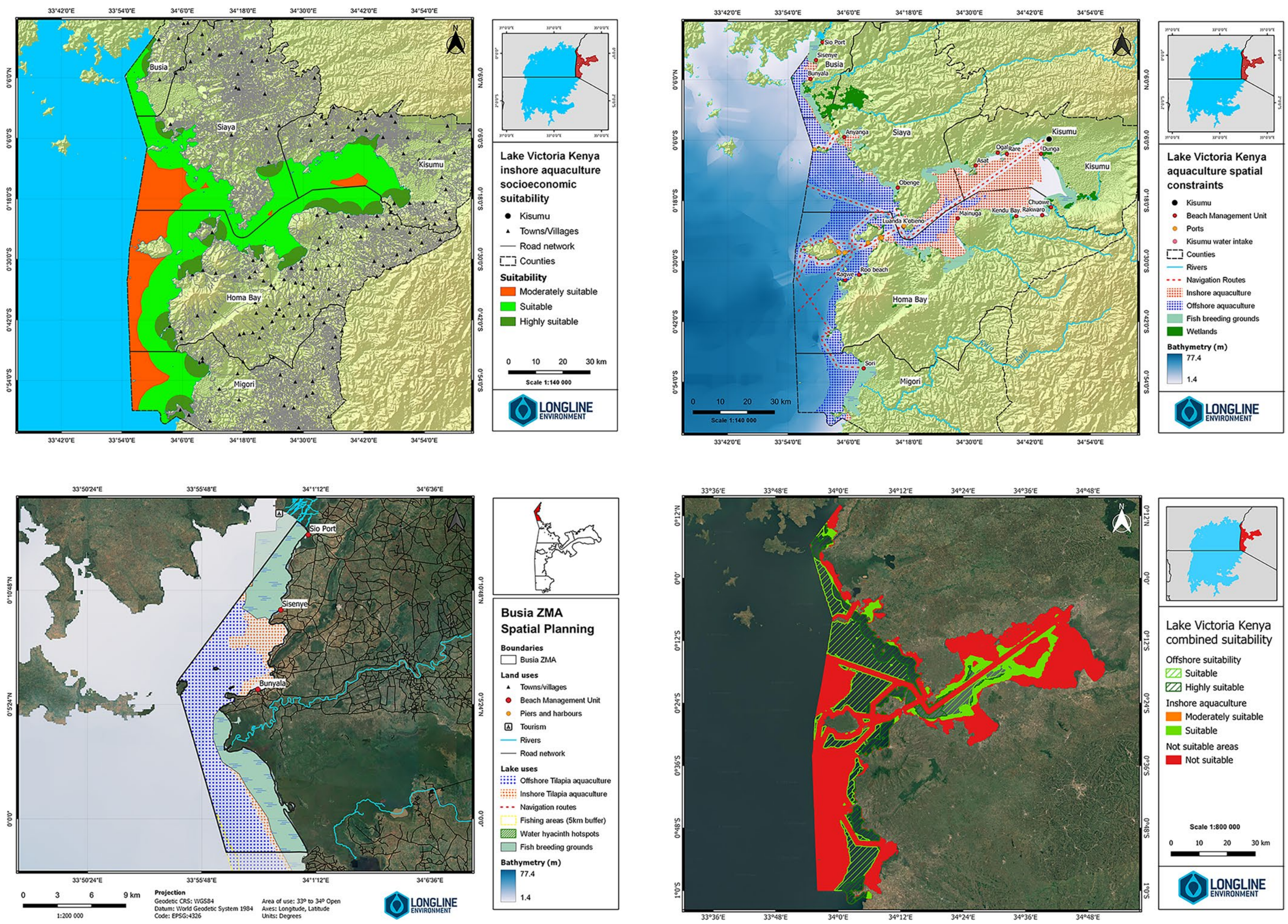

Extended Data Fig. 5 | MSP results Lake Victoria. Results for physical carrying capacity in Lake Victoria: top left: socioeconomic suitability for Nile Tilapia offshore aquaculture; top right: spatial constraints to Tilapia cage aquaculture in Lake Victoria; bottom left: spatial mapping of activities and infrastructure in Busia county, Lake Victoria; bottom right: final map of MSP, or Physical CC, for the Kenyan EEZ of Lake Victoria.

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Extended Data Table 1 | GIS MSP Lake Victoria areas and suitability

Zone name	Zone area (km^2)	Stocking density (kg m^{-3})	Cage depth (m)	Suitability (no units)
Zone A inshore	15.39	15	3	3
Zone A offshore	32.85	30	10	3
Zone A offshore	30.17	30	10	4
Zone B inshore	78.58	15	3	3
Zone B offshore	339.19	30	10	3
Zone B offshore	145.60	30	10	4
Zone B HIOZ	56.92	30	10	2
Zone B HIOZ	13.86	30	10	3
Zone C inshore	54.32	15	3	3
Zone C offshore	54.32	30	10	3
Zone D inshore	0.19	15	3	2
Zone D inshore	130.17	15	3	3
Zone D offshore	272.94	30	10	3
Zone D offshore	147.29	30	10	4
Zone D HIOZ	10.53	30	10	2
Zone D HIOZ	252.84	30	10	3
Zone E inshore	3.90	15	3	3
Zone E offshore	122.35	30	10	3
Zone E offshore	62.35	30	10	4
Zone E HIOZ	112.43	30	10	3

Zones, respective areas, and suitability obtained through GIS and MSP for the Kenyan EEZ of Lake Victoria; High Investment Offshore Zones (HIOZ) have a depth greater than 45 m and require deeper moorings, cages appropriate for high energy conditions, and suitable service vessels. Stocking density and cage depth are model assumptions. The total EEZ area covered is 3,836 km^2, of which 1,936 km^2 are suitable to some degree. Unsuitable zones not shown.

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Extended Data Table 2 | GIS MSP Arabian Sea areas and suitability

Zone name	Zone area (km^2)	Stocking density ($kg\ m^{-3}$)	Cage depth (m)	Suitability (no units)
Zone A offshore	7782.1	20	10	2
Zone A offshore	1221.4	20	10	3
Zone B offshore	9713.2	20	10	2
Zone B offshore	108.2	20	10	3

Zones, respective areas, and suitability obtained through GIS and MSP for the offshore Arabian Sea area of Pakistan. Stocking density and cage depth are model assumptions. The total EEZ area covered is 18,825 km^2, all of which is suitable to some degree. Unsuitable zones not shown.

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Extended Data Table 3 | AQRATE sensitivity analysis

Parameter/result	Default setup	Sensitivity analysis	Percentage change
Gap between farms (inshore)	6	6	0.0
Gap between farms (offshore)	8	7	-12.5
N load (mg N m^{-2} d^{-1})	85	77	-9.4
P load (mg P m^{-2} d^{-1})	8	7	-12.5
Pathogen die-off constant (d^{-1})	0.40	0.45	12.5
Pathogen dilution constant (d^{-1})	0.40	0.45	12.5
Area (km^2)	0.46	0.65	41.3
Number of cages	2,402	3,719	54.8
Production (t y^{-1})	258,279	363,241	40.6

Sensitivity analysis to changes in some AQRATE parameters. A change of about 10% was applied to nutrient loading from land (eutrophication assessment), to two of the pathogen risk parameters (disease assessment) and to the production and social pillar (offshore farm spacing).

Extended Data Table 4 | Suitability scores MSP

Category/Parameter		Units	Data range	Not suitable (1)	Moderately suitable (2)	Suitable (3)	Highly suitable (4)	Data Source*
Water quality								
Water temperature		°C	23.6-27.3	<22	22-25, 30+	25-28	28-30	7, 8, 9, 10, 11, 12, 13
Dissolved oxygen		mg L^{-1}	4.1-8.7	<4	4-5	5-6	>6	
pH		-	5.9-8.7	<4	4-6.5	8-9	6.5-8	
Nitrite (N-NO_2)		mg L^{-1}	0.003-6.9	>5	1-5	0.1-1	<0.1	
Nitrates (N-NO_3)		mg L^{-1}	0.009-21.7	>50	20-50	10-20	<10	
Ammonium		mg L^{-1}	0.04-0.43	>1	0.5-1	0.2-0.5	<0.2	
Total dissolved solids (TDS)		mg L^{-1}	53.8-225.4	>500 & <30	300-500	70-300	30-70	
Water hyacinth hotspots		-	-	Areas containing potential hotspots of water hyacinths are classified as 'moderately suitable' (score 2)				7, 14
Hydrodynamics								
Wind speed		m s^{-1}	*For estimation of wave height and fetch*					8, 9, 15
Wind direction		degrees						
Current velocity		cm s^{-1}	<1	2-3<	3-5>	5<	<1	
Wave height	Inshore	>0.5		0.4-0.5	0.2-0.4	<0.2	>0.5	
	Offshore	m						
Socioeconomic								
Distance to roads	Inshore	km		>9	6-9>	3-6>	<3	8, 15, 16
	Offshore			>9	6-9>	3-6>	<3	
Distance to urban areas	Inshore	km		>30	15-30	5-15	<5	
	Offshore			>30	20-30	10-20	<10	
Spatial constraints (Boolean constraints)				**Not suitable (0)**		**Suitable (1)**		
Bathymetry	Inshore	m	-	<6 and >10		6-10		7
	Offshore		-	<10 and >45		10-45		8
Distance to ferry boat lanes		km	-	<1		>1		7, 8
Distance to wastewater sources		km	-	<0.5		>0.5		15
Distance to water intake station		km	-	<0.5		>0.5		15
Distance to piers/harbours		km	-	<1		>1		7
Distance to agriculture runoff		km	-	<0.5		>0.5		15
Distance to fish landing sites		km	-	<0.5		>0.5		15
Distance to industry			-	<0.5		>0.5		15, 17
Fish breeding areas		km	-	Excluded				7
Protected areas		-	-					18

Reclassification and suitability scores for Nile Tilapia considered for physical carrying capacity. *All references given in the Supplementary Information.

https://doi.org/10.1038/s43016-025-01114-1

Extended Data Table 5 | Reclassification MSP

Site suitability	Score	Description
Not suitable	**1**	Data whose values are above or under the specified thresholds for fish growth and survival. It also represents socio-economic factors which require considerable cost and time in aquaculture operations and, therefore, worthless for siting.
Moderately suitable	**2**	Values are between the threshold limits, however, far from optimal for fish growth, production.
Suitable	**3**	Provides good conditions for fish aquaculture, whose values are between a scale considered good for fish growth, production.
Highly suitable	**4**	Represents optimal values for fish aquaculture. Describes environmental values that enhance fish growth and favourable proximity to places that provide appropriate conditions for farm operations.

Reclassification values for the user-defined reclassification.

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Reporting Summary

Nature Portfolio wishes to improve the reproducibility of the work that we publish. This form provides structure for consistency and transparency in reporting. For further information on Nature Portfolio policies, see our Editorial Policies and the Editorial Policy Checklist.

Statistics

For all statistical analyses, confirm that the following items are present in the figure legend, table legend, main text, or Methods section.

n/a	Confirmed	
☒	☐	The exact sample size (*n*) for each experimental group/condition, given as a discrete number and unit of measurement
☒	☐	A statement on whether measurements were taken from distinct samples or whether the same sample was measured repeatedly
☒	☐	The statistical test(s) used AND whether they are one- or two-sided *Only common tests should be described solely by name; describe more complex techniques in the Methods section.*
☒	☐	A description of all covariates tested
☒	☐	A description of any assumptions or corrections, such as tests of normality and adjustment for multiple comparisons
☒	☐	A full description of the statistical parameters including central tendency (e.g. means) or other basic estimates (e.g. regression coefficient) AND variation (e.g. standard deviation) or associated estimates of uncertainty (e.g. confidence intervals)
☒	☐	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.*
☒	☐	For Bayesian analysis, information on the choice of priors and Markov chain Monte Carlo settings
☒	☐	For hierarchical and complex designs, identification of the appropriate level for tests and full reporting of outcomes
☒	☐	Estimates of effect sizes (e.g. Cohen's *d*, Pearson's *r*), indicating how they were calculated

Our web collection on statistics for biologists contains articles on many of the points above.

Software and code

Policy information about availability of computer code

Data collection	No software was used
Data analysis	Microsoft Excel 365; QGIS V. 3 for the GIS component in Part IV of the supplementary information

For manuscripts utilizing custom algorithms or software that are central to the research but not yet described in published literature, software must be made available to editors and reviewers. We strongly encourage code deposition in a community repository (e.g. GitHub). See the Nature Portfolio guidelines for submitting code & software for further information.

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All manuscripts must include a data availability statement. This statement should provide the following information, where applicable:

- Accession codes, unique identifiers, or web links for publicly available datasets
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All data used for carrying capacity calculations are given in the Supplementary Information section and in the spreadsheet model available at https://gitlab.com/nature-food/aqrate-calculation/-/blob/b77243d83cee8c8841b01865e439c2541736e499/AQRATE_calculation_template.xlsx

Research involving human participants, their data, or biological material

Policy information about studies with human participants or human data. See also policy information about sex, gender (identity/presentation), and sexual orientation and race, ethnicity and racism.

Reporting on sex and gender	*Use the terms sex (biological attribute) and gender (shaped by social and cultural circumstances) carefully in order to avoid confusing both terms. Indicate if findings apply to only one sex or gender; describe whether sex and gender were considered in study design; whether sex and/or gender was determined based on self-reporting or assigned and methods used. Provide in the source data disaggregated sex and gender data, where this information has been collected, and if consent has been obtained for sharing of individual-level data; provide overall numbers in this Reporting Summary. Please state if this information has not been collected. Report sex- and gender-based analyses where performed, justify reasons for lack of sex- and gender-based analysis.*
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Population characteristics	*Describe the covariate-relevant population characteristics of the human research participants (e.g. age, genotypic information, past and current diagnosis and treatment categories). If you filled out the behavioural & social sciences study design questions and have nothing to add here, write "See above."*
Recruitment	*Describe how participants were recruited. Outline any potential self-selection bias or other biases that may be present and how these are likely to impact results.*
Ethics oversight	*Identify the organization(s) that approved the study protocol.*

Note that full information on the approval of the study protocol must also be provided in the manuscript.

Field-specific reporting

Please select the one below that is the best fit for your research. If you are not sure, read the appropriate sections before making your selection.

☐ Life sciences ☐ Behavioural & social sciences ☒ Ecological, evolutionary & environmental sciences

For a reference copy of the document with all sections, see nature.com/documents/nr-reporting-summary-flat.pdf

Ecological, evolutionary & environmental sciences study design

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

Study description	Development of a mathematical model for determining carrying capacity in aquaculture by combining physical, production, ecological and social pillars
Research sample	Datasets used for the carrying capacity physical pillar were obtained through GIS analysis for (i) Lake Victoria and the Arabian Sea (Longline Environment Ltd) and (ii) FAO (African coastal area)
Sampling strategy	No samples taken
Data collection	Data obtained from sources indicated in the 'Research sample' section
Timing and spatial scale	No data collection over time and space
Data exclusions	No exclusions
Reproducibility	All calculations were reproducible, see Excel sheet on gitlab link as an example
Randomization	This is not relevant to the study, which was the development and application of a mathematical model to existing datasets
Blinding	This is not relevant to the study, which was the development and application of a mathematical model to existing datasets

Did the study involve field work? ☐ Yes ☒ No

Reporting for specific materials, systems and methods

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Materials & experimental systems

n/a	Involved in the study
☒	☐ Antibodies
☒	☐ Eukaryotic cell lines
☒	☐ Palaeontology and archaeology
☒	☐ Animals and other organisms
☒	☐ Clinical data
☒	☐ Dual use research of concern
☒	☐ Plants

Methods

n/a	Involved in the study
☒	☐ ChIP-seq
☒	☐ Flow cytometry
☒	☐ MRI-based neuroimaging

Plants

Seed stocks	Not used
Novel plant genotypes	Not used
Authentication	Not used