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Supplementary information

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Marine aquaculture can deliver 40% lower carbon footprints than freshwater aquaculture based on feed, energy and biogeochemical cycles

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Global area suitable for mariculture

Figure S1. Global area suitable for offshore marine aquaculture. Following Gentry et al.¹, we constrain suitable farming areas at ~ 10 km resolution for each mariculture species to regions with moderate sea surface temperature ranges, high dissolved oxygen levels, and low shipping traffic (see Methods). The map used in this figure is from the 'maps' package in the open-source software R.

Figure S2. **The diagram of particle export algorithm and validation with previous studies**. The particle export algorithm is based on Dunne et al.^{2,3} and Martin et al.⁴, using satellite-constrained NPP and chlorophyll as the initial inputs. More details are presented in Eq. 3-5. We also compare key parameters (global total POC fluxes at the base of the euphotic zone, *pe* and *Rf*) calculated in this work with previous studies, including Xie et al.⁵, Henson et al.⁶, Devries et al.⁷, Nowicki et al.⁸, Laws et al.⁹, and Dunne et al.^{2,3}.

Text S1. Methane (CH4) formation in offshore mariculture areas

Net primary productivity (NPP) is the primary fuel of the carbon cycle in the ocean, and CH4 is a byproduct of this cycle. According to Moderate Resolution Imaging Spectroradiometer (MODIS) retrievals¹⁰, the annual mean oceanic NPP is estimated to be 48 Tg C a^{-1} from 2010-2019, a few orders of magnitude larger than other sources (e.g., river inputs)¹¹.

Methanogenesis in the anoxic environment is the primary pathway to produce CH4, using hydrogen, carbon dioxide and acetate as substrates¹². The primary substrate of this process is the particulate organic matter (mainly produced by NPP) that sinks to the sediment¹¹. However, this process is suppressed in marine waters by another group of anaerobic microorganisms, sulfate-reducing bacteria (SRB), which use sulfate as a terminal electron acceptor to degrade organic compounds 13 . The SRBs are ubiquitous in the environment, especially in marine sediment. In the presence of an excess of sulfate, SRBs compete with methanogens for the common substrates, including hydrogen and acetate ^{13,14}. Importantly, the hydrogen-utilizing SRBs can easily out-compete hydrogenutilizing methanogens¹³. Thus, high sulfate concentrations in marine waters can significantly suppress the gross CH_4 formation 12,13,15 .

Methanogenic reactions 13 $4H_2 + HCO_3^- + H^+ \rightarrow CH_4 + 3H_2O$ $\text{Acetate}^- + \text{H}_2\text{O} \rightarrow \text{CH}_4 + \text{HCO}_3^-$

Sulphate-reducing reactions¹³ $4H_2 + SO_4^{2-} + H^+ \rightarrow HS^- + 4H_2O$ $\text{Acetate}^- + \text{SO}_4^{2-} \rightarrow \text{HS}^- + 2\text{HCO}_3^-$ Other oranigc acids + SO_4^{2-} \rightarrow Acetate⁻ + HS⁻ + 2HCO₃

CH4 produced from bottom waters and sediments will be ventilated into the atmosphere through gas ebullition and diffusion. A large fraction of methane (>50%) will be oxidized and dissolved in the waters along the path to the atmosphere, and this fraction increases with water depths $16-18$.

Text S2. Nitrous oxide (N2O) formation in offshore mariculture areas

N₂O can be produced through microbial nitrification and denitrification. Although there is no consensus about the oxygen threshold defining the extent of denitrification, the denitrification process is only expected to occur in an environment with very low oxygen concentrations of <10- 22 μmol L^{-1} ¹⁹, an order of magnitude lower than the sub-lethal oxygen limit for finfish (138 μmol L^{-1} or 4.41 mg L^{-1})²⁰. This implies nitrification should be the primary pathway of N₂O formation in mariculture waters 2^{1-23} . This assumption is supported by Battaglia and Joos²⁴, who estimated that 95.5% of oceanic N_2O emissions are from nitrification as constrained by a global surface ocean partial pressure N₂O observation dataset. We also test this hypothesis by estimating the N₂O production from the nitrification yield 24 and dissolved oxygen concentrations 25 at seafloors, and the results are highly correlated $(R=0.78)$ with these N₂O fluxes measurements in the surface ocean (Fig. S3-S4), strongly supporting our assumption here.

Given the much lower yield of N_2O at high oxygen concentrations and the inhibitory effects of light ¹¹ on nitrification in the surface ocean, N₂O production mainly occurs below the euphotic zone¹¹. Thus, organic matters from NPP that sink to the bottom ocean should be the primary fuel driving the nitrification processes in mariculture areas. These organic matters are remineralized to form ammonium ($NH₄⁺$). The ($NH₄⁺$) can be oxidized to nitrite ($NO₂⁻$) by ammonia-oxidizing bacteria (AOB) and subsequently to nitrates ($NO₃⁻$) by nitrite-oxidizing bacteria (NOB)¹¹. N₂O is an intermediate product of such processes.

The effects of salinity on N_2O emissions are complicated and vary across studies. Theoretically, the low-level salinity can slightly suppress the activity of AOB but strongly inhibits the activity of NOB, thus likely leading to accumulated nitrite $(NO₂)$ and higher N₂O emissions^{26,27}. However, lower salinity (<10-15 ppt) has been reported to enhance N_2O emissions only in a fraction but not all of previous studies^{26–29}. But the suppressive effect on N_2O emissions is a ubiquitous feature due to the strong suppressive effects on the activities of both AOB and NOB. Thus, N_2O production efficiency from marine waters is likely to be much lower than that of freshwater systems. Besides suppressive effects of salinity, lower N_2O fluxes in mariculture can also be related to the toxicity of multiple organic carbon pounds and ions (chloride, hydrosulfide, etc.)¹¹, and decreasing microbe's abundance and activities $30-32$.

Figure S3. **The sea-air N2O flux in potentially suitable areas for mariculture**. The data shown here is from Yang et al³³. The bottom panel shows N₂O fluxes in these coastal upwelling regions³³. The map used in this figure is from the 'maps' package in the open-source software R.

Figure S4. N₂O yield from nitrification conditioned on dissolved O₂ concentrations in waters 24, as determined by Eq. 1.

Figure S5. Predicted vs. observed N₂O flux in mariculture waters. The predicted N₂O emissions are obtained from nitrification N2O yield (Fig. S3) and dissolved oxygen levels in the aphotic zone. The correlation coefficient is shown inset.

Figure S6. **Aquafeed transformation pathways in aquaculture**. (a) Flow of nitrogen in the aquaculture system, as synthesized by Hu et al.³⁴ from a variety of studies. (b) Flow of carbon in the aquaculture system, as summarized by Olsen et al.³⁵.

Algorithm

$$
NPP_{solid} = Q \times F_c \times C_{solid} \qquad NPP_{new} = Q \times F_N \times N_{am} \times \frac{1}{s}
$$

Step 3: Calculate the lower and upper bounds of emission intensity emitted by the aquatic environment.

 δ_{N-C}

Figure S7. The algorithm to calculate GHG emission intensity arising from mariculture's **aquatic environment**. More details can be found in Methods. For the lower bound in Step 3, we assume that all NPP_e resembles the behaviors of NPP, which means \sim 26% of NPP_e is exported into aphotic zones and participates in the biochemical production of CH₄ and N₂O (Fig. S6a). For the upper bound, we assume all NPP_{solid} can quickly sink to the seafloor, and all NPP_{new} can enter the aphotic zone (Fig. S6b). a
V \overline{N} .
ei

Figure S8. **Aquafeed transformation pathways with different particle export efficiencies**. (a) assumes both NPP_{solid} and NPP_{new} resemble the behavior of ocean NPP, which means on average 26% is exported to the aphotic zone; (b) assumes all NPP_{solid} will quickly sink to the seafloor and all NPP_{new} is exported to the aphotic zone. The lower (or higher) export efficiency corresponds to lower (or higher) GHG emission intensity (EI).

 $CH₄$ and N₂O production efficiencies in offshore mariculture waters

Figure S9. **CH4 and N2O production efficiencies in offshore mariculture areas**. (a) Spatial distribution of annual mean CH4 production efficiencies, calculated as the fraction of carbon released into the atmosphere in the form of CH4 relative to organic carbon inputs into the waters by the oceanic net primary productivity (NPP). (b) Same as (a), except that the production efficiencies are binned to ocean areas with different seafloor depths. (c-d) Same as (a-b) but for the production efficiency of N_2O in terms of nitrogen. White areas in (a) and (c) denote the areas not suitable for marine aquaculture. For (c) and (d), the hinges in each boxplot refer to the 10^{th} , 25^{th} , 50^{th} , 75^{th} , and 90th quantiles. The maps used in this figure are from the 'maps' package in the open-source software R.

 $N₂O$ production efficiency in potential mariculture areas and in these coastal upwelling regions

Figure S10. **The N2O production efficiency, which is defined as the fraction nitrogen emitted into the atmosphere in the form N2O from NPP, in global potential mariculture areas.** The bottom panel shows N_2O fluxes in these coastal upwelling regions³³. The maps used in this figure are from the 'maps' package in the open-source software R.

Figure S11. Future projections of global fish protein demand relative to the 2012 level in different socio-economic scenarios (toward sustainability, business as usual, and stratified societies). The data is obtained from FAO 36 .

Figure S12. **Validation of our LCA results**. (a) Comparison of EI from feed and energy (not including the emissions from the aquatic environment) derived in this study with results in Gephart et al37. The correlation coefficient is shown inset. (b) Predicted EI using FCR, edible portion, and total protein content in feed, with a linear regression model. The coefficient of determination (R^2) is 94%.

Table S1. **Global area, production, and GHG emissions in different freshwater aquaculture systems**. GHG production is calculated by multiplying the area or production by the emission factor collected in this work (Source Data Fig. 3).

 \ddagger Data is from Yuan et al.³⁸ for the year 2014.

[†] The emission factors can be found in Source Data Fig. 3.

Table S2. Comparison of the GHG inventory of freshwater aquaculture compiled in this study with previous studies.

Table S3. Calculate the emission intensity (EI) arising from the aquatic environment of

freshwater aquaculture.

Table S4. Life-cycle assessment of GHG emissions for key aquaculture species.

		GHG emissions arising from different sectors ($kgCO_2e$ kg ⁻¹ CW)					
Species	Total Feed Aquatic environment Energy				FCR	Type	
Fish-general [†]	15.22	5.21	0.6	9.41	1.62	Freshwater	
Shrimp	20.37	7.09	3.87	9.41	1.33	Freshwater	
Bivalves	1.24	θ	1.24	θ	$\mathbf{0}$	Freshwater	
Aquatic plants	0.11	θ	0.11	θ	θ	Freshwater	
Catfish	15.27	5.76	0.11	9.41	1.65	Freshwater	
Cyprinid	14.29	4.37	0.51	9.41 1.64		Freshwater	
Tilapia	18.94	8.48	1.05	9.41	1.67	Freshwater	
Diadromous fishes [‡]	16.60	5.19	2.00	9.41	1.23	Freshwater	
Fish-general [†]	9.00	6.72	2.1	0.18	1.59	Mariculture	
Shrimp	10.51	7.26	3.08	0.17	1.49	Mariculture	
B ivalves	1.23	$\mathbf{0}$	1.23	Ω	θ	Mariculture	
Seaweeds	0.11	$\mathbf{0}$	0.11	θ	Ω	Mariculture	
High-EI fishes $\frac{8}{3}$	14.88	11.77	2.76	0.36	2.68	Mariculture	
Low-EI fishes ^{&}	7.43	5.39	1.89	0.14	1.33	Mariculture	

† Here fish-general doesn't include crustaceans and molluscs.

‡ Here refers to salmon and trout.

 $\frac{1}{2}$ Here refers to fish species with EI from feed and energy exceeding 10 kgCO₂e kg⁻¹CW, including cobia, mullet (low edible portion),

pompano, red drum, seabream, tuna (very high FCR), and turbot.
[&] Here refers to fish species with EI from feed and energy less than 10 kgCO₂e kg⁻¹CW, including amberjack, barramundi, grouper, meagre, milkfish, salmon (highest global production), seabass, trout, and yellow croaker.

Table S5. Key input data and results for key species in marine and freshwater aquaculture.

§ Here we assume all freshwater fishes have the same GHG EI arising from the aquatic environment.

[‡] The FCR for tuna is the average value from four references (9.73, 18.2, 24.8, and 15.3).

Table S6. Projection of 2012-2050 GHG emissions in three socioeconomic scenarios (towards sustainability, business as usual, and stratified societies) **if only relying on freshwater aquaculture to meet fish protein needs.**

Projected fish protein needs $(g \, day^{-1}person^{-1})$ and future population (in million) (a)														
Scenarios	2012	2015	2020	2025	2030	3035	2040	2045	2050					
Towards sustainability ³⁶	5.41	5.3	5.39	5.33	5.28	5.14	4.95	4.72	4.5					
Business as usual ³⁶	5.41	5.26	5.31	5.22	5.16	5.06	4.93	4.77	4.62					
Stratified societies ³⁶	5.41	5.21	5.15	4.94	4.78	4.68	4.62	4.57	4.52					
Population (million) ³⁶	7097.5	7349.8	7758.2	8141.7	8500.8	8838.9	9157.2	9453.9	9725.2					
(b) Global fish protein needed (Tg protein a^{-1}) [†]														
Towards sustainability	14.0	14.2	15.3	15.8	16.4	16.6	16.5	16.3	16.0					
Business as usual	14.0	14.1	15.0	15.5	16.0	16.3	16.5	16.5	16.4					
Stratified societies	14.0	14.0	14.6	14.7	14.8	15.1	15.4	15.8	16.0					
(c) Global fish protein needed from freshwater aquaculture (Tg protein a^{-1}) ^{\ddagger}														
Towards sustainability	4.27	4.47	5.52	6.09	6.64	6.84	6.80	6.54	6.23					
Business as usual	4.27	4.36	5.29	5.76	6.26	6.58	6.73	6.71	6.65					
Stratified societies	4.27	4.23	4.84	4.93	5.08	5.35	5.69	6.02	6.30					
(d) Fish protein from marine aquaculture (assumed to be kept at the 2012 level) (Tg protein a^{-1})														
All scenarios	1.42	1.42	1.42	1.42	1.42	1.42	1.42	1.42	1.42					
(e) CO_{2e} from freshwater aquaculture (TgCO ₂ e a ⁻¹) [§]														
Towards sustainability	377	394	486	537	585	603	599	577	549					
Business as usual	377	385	466	508	552	580	593	592	586					
Stratified societies	377	373	426	435	448	472	502	531	555					
(f) CO_{2e} from freshwater and marine aquaculture (TgCO ₂ e a ⁻¹) [#]														
Towards sustainability	408	425	517	568	616	634	630	608	580					
Business as usual	408	416	497	539	583	611	624	623	617					
Stratified societies	408	404	457	466	479	503	533	562	586					

[†] Calculated by multiplying fish protein needs per person with the total population.

‡ It assumes the newly increased fish protein will be met by freshwater aquaculture.

 $\frac{1}{2}$ Here we calculate the climate impacts (in the form of CO₂e) of freshwater aquaculture in order to produce the needed fish protein in (c). The average protein content in edible fish flesh is 18% , taken from FAO^{40} .

[#] The GHG emissions from marine aquaculture is assumed to be at the 2012 level, which is estimated to be 31 Tg a⁻¹ CO_{2e} (26 Tg a⁻¹) ¹ for finfish and 5 Tg a^{-1} for bivalves).

Text S3. Calculating needed mariculture areas to meet target protein needs

We follow the method proposed by Gentry et al.¹ to calculate the biomass production per unit area in offshore mariculture farming. It is noted that mariculture is still at the nascent stage, and its farming density is quite variable across regions and species. Thus, the numbers reported here are subject to large uncertainty and do not necessarily match regional statistics.

For finfish, using the farm designs of Gentry et al.¹, the calculated stocking density at the harvest time is 11 kg $m³$, which is comparable to the European organic standard maximum density of 15 kg m^{-3 41}. After considering the growth potential of 120 finfish species across global suitable mariculture areas, the mean wet biomass production per unit area is estimated to be 1.43 ± 0.24 kg m^2 , compared to a global mean of 1.2 kg m⁻² reported by Free et al.⁴². For bivalve, we calculate the global mean biomass production per unit area from 40 species to be 1.18 ± 0.38 kg m⁻², in which the large uncertainty partly arising from the high variability of the relationship between length and weights⁴³. For reference, the areal biomass production is 0.6 kg m⁻² at the global scale by Free et al. ⁴², 1.24 kg m⁻² in China⁴⁴, and up to 3 kg m⁻² for some bivalve species⁴⁵.

Table S7. GHG emissions and farming areas in 2050 associated different mariculture developing strategies. The numbers shown in the table are the average of three socioeconomic scenarios (towards sustainability, business as usual, and stratified societies).

† Strategy 1 is consistent with the scenario in Table S6.

‡ In 2012, about 18.8 million tons of aquaculture is produced in marine waters, including 14.0 million tons of bivalves and 4.8 million tons of finfish. The produced protein is 0.84 Tg a⁻¹ for bivalves and 0.58 Tg a⁻¹ for finfish.

[§] Because the carbon footprint of finfish (9.0 kgCO₂e kg⁻¹CW) and bivalve (1.2 kgCO₂e kg⁻¹CW) differ by a factor of 7.5, we propose two extreme scenarios here to estimate the range of emitted GHG. For example, in the finfish-only scenario, we assume all proteins in mariculture are provided by finfish farming.

 $*$ The farming area here is calculated using the method described in Text S3. The global potential area is 11.4 and 1.5 million km² for finfish and bivalves¹, respectively.

Table S8. Uncertainty of key parameters used in this study.

† If the number reported includes % in this column, it means relative one standard deviation (1σ). Otherwise, it refers to the absolute value.

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