

Displacing fishmeal with protein derived from stranded methane

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Methane emitted and flared from industrial sources across the United States is a major contributor to global climate change. Methanotrophic bacteria can transform this methane into useful protein-rich biomass, already approved for inclusion into animal feed. In the rapidly growing aquaculture industry, methanotrophic additives have a favourable amino acid profile and can offset ocean-caught fishmeal, reducing demands on over-harvested fisheries. Here we analyse the economic potential of producing methanotrophic microbial protein from stranded methane produced at wastewater treatment plants, landfills, and oil and gas facilities. Our results show that current technology can enable production, in the United States alone, equivalent to 14% of the global fishmeal market at prices at or below the current cost of fishmeal (roughly US\$1,600 per metric ton). A sensitivity analysis highlights technically and economically feasible cost reductions (such as reduced cooling or labour requirements), which could allow stranded methane from the United States alone to satisfy global fishmeal demand.

umanity must address the challenge of meeting growing food demand in the face of global climate change. Current food systems directly emit greenhouse gases but also contribute indirectly to climate change (for example, through land use change¹). One important global source of protein and micronutrients is seafood, the production of which increased from 40 to 180 million metric tons per year between 1960 and 2015². Farming aquatic animals now accounts for almost half of all animal-source seafood³, with 90% of the world's marine fisheries fully fished or overfished4. While practices vary greatly worldwide, fed aquaculture relies on fishmeal for protein, consuming 70% of global fishmeal production and increasing pressures on marine resources^{5,6}. Overfishing marine environments leads to long-term loss in biodiversity and irreversible damage to marine ecosystems7. Many plant proteins are a promising substitute for fishmeal but require additional inputs of land, freshwater and fertilizer8.

Methane has at least 25 times the global warming potential of CO_2 over a 100-year period⁹. The total annual methane emissions in the United States for 2014–2018 exceeded 630 million metric tons of CO_2 equivalents per year. In 2018, oil and gas systems accounted for nearly 30% of total emissions, with landfills and wastewater treatment accounting for another 17% and 2%, respectively ¹⁰. Unlike other major methane emitters, these sources also flare methane, releasing large amounts of CO_2 to the atmosphere. Taken together, methane emissions and flaring in the United States release nearly 14 billion m³ per year. Because these sources are geographically dispersed and small scale, increasing unit capital and labour costs, methane is emitted or flared rather than captured, cleaned and used ¹¹.

Methanotrophic bacteria transform methane into protein-rich biomass, which can be used as an animal feed and has a similar amino acid profile to fishmeal. Methanotrophic feed, referred to as single cell protein (SCP), is approved for salmon feed in the European Union at rates of up to 33%¹². Because methanotrophs do not require light, dense cultures are grown in bioreactors with low spatial footprints not feasible with terrestrial agriculture¹³.

Companies in the United States and the European Union (such as Calysta¹⁴ and Unibio¹⁵) are commercializing the production of methanotrophic SCP from natural gas.

Industrial production of methanotrophic SCP is depicted in Fig. 1. Methanotrophic growth requires methane, oxygen, nitrogen, phosphorus and trace metal micronutrients. Compressors separately deliver pressurized methane and oxygen to the bioreactor and provide mixing. Methanotrophs grow in pressurized, top-fed airlift bioreactors equipped with cooling jackets and coils to remove metabolic heat produced during growth, maintaining biologically viable temperatures 16. Biomass is then dewatered and dried for storage and shipping.

Using methane currently emitted or flared to produce methanotrophic SCP can incentivize the capture of stranded resources with the dual benefit of reducing greenhouse gas emissions and generating a sustainable protein substitute for fishmeal. Stranded methane has also been proposed as a feedstock for future biomanufacturing, potentially enabling a paradigm shift from large-scale mega-facilities to smaller-scale, widespread, mobile production¹¹. Recent studies have evaluated potential environmental benefits of methanotrophic SCP and indicate promising economics^{17–19}. This analysis evaluates the market potential of methanotrophic SCP across existing sources of stranded methane. While we focus on the United States, the same approach can be applied elsewhere.

Here we investigate the capacity to convert stranded methane into methanotrophic SCP at a cost competitive with fishmeal. We evaluate the market potential and cost sensitivities by modelling the production process outlined in Fig. 1. Our analysis assumes mature methanotrophic SCP production facilities using current technology. We consider different scenarios for production, in which methane is derived from different sources of stranded methane in the United States: wastewater treatment plants, landfills, and oil and gas facilities. We compare a fourth scenario in which natural gas is purchased from the grid. We conclude with an analysis of the stranded methane market potential and the cost of scaling SCP production.

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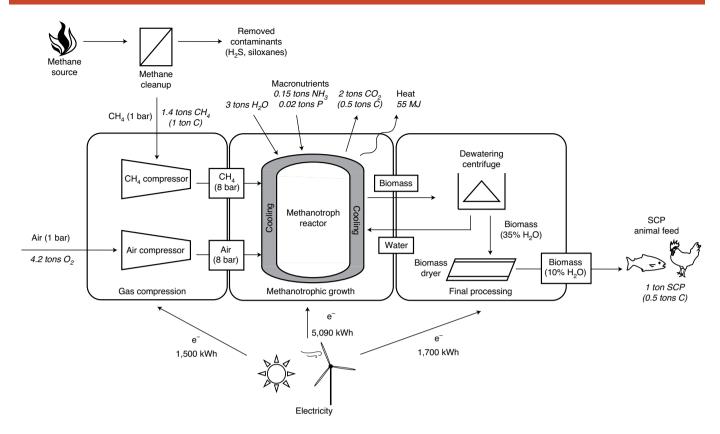


Fig. 1 | Process model for methanotrophic biomass production. Methane is cleaned to remove contaminants, then compressed and delivered to the growth bioreactor along with compressed air, which is the source of oxygen. Methanotrophic growth occurs in pressurized bioreactors equipped with cooling jackets and coils to remove the metabolic heat produced. Exhaust CO_2 is released from the growth bioreactors, and biomass is processed in dewatering centrifuges and dryers, after which it can serve as SCP feed for agriculture or aquaculture. The labels on the figure in italics represent the mass or energy flow associated with the production of one ton of methanotrophic SCP.

Results

Our analysis indicates that the production of methanotrophic protein from stranded methane in the United States is economically competitive with fishmeal, when considering both potential cost and volume of production.

Stranded methane in the United States. Stranded methane produced from industrial sources is either directly emitted to the atmosphere as methane or combusted in flares and emitted as CO₂. In this study, we analyse methane emitted and flared from landfills²⁰ and from oil and gas facilities^{21,22}. We also consider methane from wastewater treatment plants with operational anaerobic digesters that lack biogas utilization technology on-site^{23–25}, indicating that the methane is probably flared²⁶. The geographic distribution of the included methane sources and their respective sizes are depicted in Fig. 2a for the contiguous United States. The methane sources are distributed across the country, with landfills and wastewater treatment plants concentrated near population centres.

We compare methane emitted and flared from the sources in question in Fig. 2b–d (see Supplementary Table 1 for the summary statistics). Mean methane production is the lowest for wastewater treatment plants (less than 1 ton CH_4 per day) and the highest for landfill flaring (31 tons CH_4 per day) and oil and gas flaring (10 tons CH_4 per day). The maximum reported values range from 148 tons CH_4 per day for wastewater treatment plants to 420 tons CH_4 per day directly emitted from oil and gas facilities. The low mean and median values compared with the maximum reported source sizes as well as the heavy tail distributions are indicative of the high

number of smaller methane sources and the small number of high emission point sources, evident in Fig. 2b-d.

Fully utilizing stranded methane resources and reducing their climate change impact will require harnessing sources that correspond to smaller-than-conventional bioreactors (depicted by the vertical line in Fig. 2b–d). We also compare methanotrophic SCP production potential with the current global fishmeal market. High-quality fishmeal is 60–72% crude protein²⁷, and methanotrophic biomass is 67–81% crude protein¹². This analysis thus defines the SCP product as the organic biomass of the dried cell (commonly referred to as volatile suspended solids), which we compare directly with fishmeal. Should smaller methane sources become economically competitive and technologically viable for methanotrophic SCP production, the resulting biomass could readily exceed the current size of the global fishmeal market using US-based stranded methane alone.

Protein production economics. We establish four baseline scenarios, in which methane is sourced from wastewater treatment plants, landfills, oil and gas facilities, and natural gas purchased from the grid (Table 1). The wastewater treatment plants, landfills, and oil and gas facilities are sized on the basis of the largest methane sources in our dataset, when considering both emissions and flaring. These large methane sources are likely to be the most cost-effective locations for methanotrophic SCP production due to their potential to benefit from economies of scale. The grid scenario is sized to match the landfill scenario, where physically proximate population centres make labour and electricity more readily available and therefore more representative of early production locations.

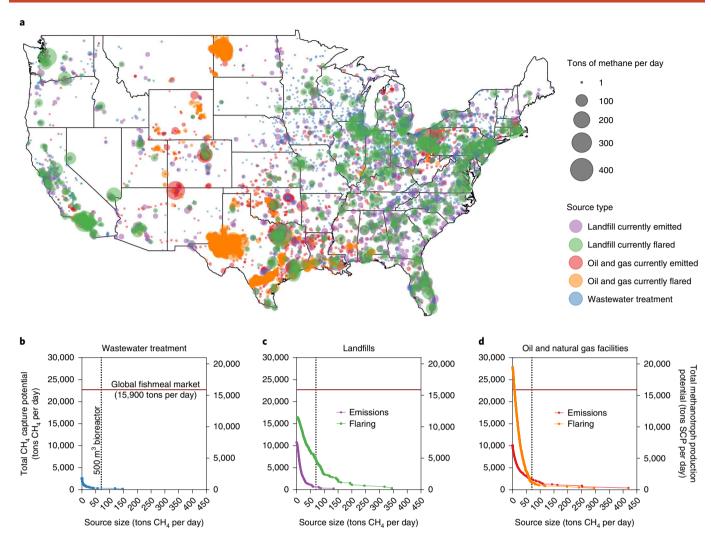


Fig. 2 | Methane sources and capture potential. a, Unused methane generation in the contiguous United States. Point sources indicate methane currently emitted and flared from landfills^{20,21} and from oil and gas facilities^{21,22} and methane production from wastewater treatment plants currently not utilized^{23,25}. **b-d**, Cumulative methane capture potential for different source types (wastewater treatment (**b**), landfills (**c**) and oil and natural gas facilities (**d**) is depicted on the left y axis (tons CH₄ per day). The right y axis depicts the corresponding total methanotrophic production potential in tons of SCP per day, calculated assuming a yield of 0.7 tons SCP per ton CH₄ (refs. ^{13,64}). The horizontal line indicates production equivalent to the total global fishmeal market (15,900 tons per day). The vertical line at a source size of 86 tons CH₄ per day corresponds to a 500 m³ bioreactor, a typical size for an industrial-scale reactor²⁸. Bioreactor size is calculated assuming a yield of 0.7 tons SCP per ton CH₄ (ref. ¹³), a cell growth rate of 4 per day¹³ and a cell density of 30 g SCP l⁻¹ (ref. ¹⁶).

We find that production costs for methanotrophic SCP are lower than the market price for fishmeal in the landfill and oil and gas scenarios when using the ten-year average market price of fishmeal (US\$1,600 per ton) as a benchmark for comparison (Fig. 3). For the wastewater treatment scenario, the production cost is slightly higher (US\$1,645 per ton), largely due to increased labour cost. The grid scenario is the most expensive (US\$1,783 per ton), attributable to the cost of purchasing natural gas. All scenarios except for wastewater treatment are individually capable of producing over 159 tons SCP per day, which represents 1% of the global fishmeal market (15,900 tons SCP per day)² and a meaningful market share for emerging technologies.

Electricity costs make up over 45% of the total levelized cost in all scenarios. Over 60% of the power needed is required for removing metabolic heat from the bioreactor (Fig. 3 and Supplementary Table 2), an amount in line with previous studies of methanotrophs¹⁶. We thus depict cooling costs separately from electricity costs associated with powering other equipment in Fig. 3. Considering electricity alone, cooling requires US\$509 per ton SCP, dewatering and

drying combined require US\$177 per ton SCP, and air compression requires US\$136 per ton SCP (Supplementary Tables 2 and 3). Capital costs make up less than 15% of the total levelized cost in all scenarios but remain one of the leading costs in the breakdown. Methane cleanup (where required), nutrient media (N, P, $\rm H_2O$), and operations and maintenance each make up 5–10% of total levelized cost across all scenarios. In the grid scenario, the cost of purchasing natural gas is 18% of the total cost.

Despite having an SCP production rate over 50% lower than the other baseline scenarios, the wastewater treatment plant scenario is only 6% more costly than the landfill and oil and gas scenarios. This is because our model implements a conservative approach to capital cost scaling whereby large bioreactors do not benefit from economies of scale. Specifically, we assume that industrial bioreactors will not exceed 500 m³ in volume²⁸, so for methane sources requiring total reactor volumes exceeding this cut-off, we maintain a constant unit capital cost. This is representative of multiple reactors operating in parallel, as opposed to an increasingly large single bioreactor (see Methods for more details). As all four scenarios

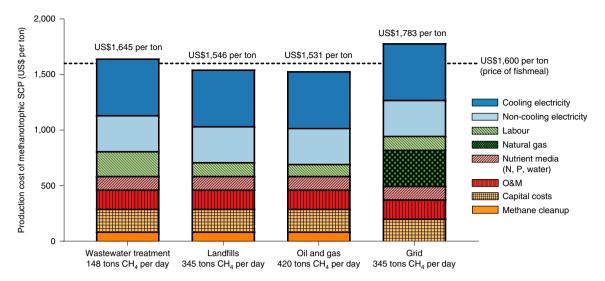


Fig. 3 | Levelized cost of methanotrophic microbial protein across baseline scenarios in which methane comes from wastewater treatment, landfills, oil and gas facilities, and the natural gas grid. The baseline scenarios represent the largest feasible sources of stranded methane by source type. The grid baseline is sized to match the landfill baseline. In all cases, the largest cost is electricity. The power needed for heat removal is separated from other electricity costs to illustrate its impact. The grid scenario sees an increase in cost due to the purchase of natural gas, which is slightly offset by the removal of the methane cleanup requirement. The baseline scenarios for landfill and oil and gas are lower than the average ten-year market price of fishmeal (US\$1,600 per ton). Further opportunities for cost reduction are present at wastewater treatment plants, through locally sourced nutrients and cooling water. O&M, operations and maintenance.

have a total bioreactor volume greater than 500 m³, they do not gain additional benefit from economies of scale, and all have the same capital cost contribution to total levelized cost. However, labour costs also increase with decreasing production rate, resulting in the increased cost at wastewater treatment plants. For the grid scenario, the additional cost of natural gas (US\$326 per ton SCP) increases the total levelized cost, which is only somewhat offset by removing the requirement for methane cleanup (US\$89 per ton SCP).

Figure 4 depicts a supply curve for the production of methanotrophic SCP from the stranded methane sources in Fig. 2. The cost of production is calculated using the baseline assumptions and scaling relationship described in the Methods. Keeping prices at or below the benchmark price of fishmeal (US\$1,600 per ton), these sources are able to produce nearly 2,200 tons SCP per day, or 14% of the global fishmeal market. Including sources that produce methane at costs of up to US\$2,050 would enable production at a level greater than the current global fishmeal market of 15,900 tons SCP per day.

We identify key cost sensitivities in Fig. 5, which depicts a sensitivity analysis that begins with the cost of producing methanotrophic protein in the landfill scenario. Here the levelized cost of methanotrophic SCP production under baseline assumptions is US\$1,546 per ton. We use the landfill scenario for the sensitivity analysis because these facilities are typically located close to population centres, meaning that labour and electricity are probably readily available (see Supplementary Fig. 1 for sensitivity analyses of the wastewater treatment, oil and gas, and grid scenarios). The input variables included in Fig. 5 are those that result in a change of 5% or greater in the calculated levelized cost. The high cost of cooling is reflected in the sensitivity to the coefficient of performance (COP) for the assumed refrigeration system¹⁶; doubling the COP reduces the levelized cost by over 15%, whereas decreasing the COP from 3 to 2 increases the cost by over 15%. The high sensitivity to electricity also aligns with the large contributions of cooling, gas compression and biomass drying to the total cost. Decreasing the cost of electricity to US\$0.06 kWh⁻¹, in line with industrial rates in the lowest-cost parts of the United States (Mississippi and Texas²⁹), reduces the levelized cost by 22% to US\$1,214 per ton SCP, whereas increasing the

Table 1 Characterizing four methane source scenarios				
Scenario	Source size (tons CH ₄ per day)	Total reactor volume (m³)	Methanotroph production (tons SCP per day)	
Wastewater treatment	148	860	83	
Landfills	345	2,010	193	
Oil and gas	420	2,450	235	
Grid	3/15	2.010	102	

Methane source sizes represent the largest point sources from emissions or flaring in each location type. The total reactor volume and methanotroph SCP production rate are calculated on the basis of a methane utilization rate of 0.14 tons ${\rm CH_4\,per\,m^3\,per}$ day and a microbial yield of 0.7 tons volatile suspended solids (SCP) per ton ${\rm CH_4}$. Methanotroph production potential assumes the same microbial yield and applies a utilization factor of 80% to allow for the time needed for maintenance and repairs.

price to that available to residential consumers, US $\$0.14\,kWh^{-1}$ (as in Pennsylvania and Illinois²⁹), increases the levelized cost by 22% to US\$1,881 per ton.

The model is also sensitive to labour, unit capital cost and microbial yield. We increase labour by 350% to 4.5 worker-hours per ton SCP, reflecting a 90% smaller facility at a size that our model suggests would be necessary to fully offset the fishmeal market using the current supply of stranded methane from the sources analysed. This increase in the labour requirement introduces a 28% increase in cost to nearly US\$1,985 per ton. Increasing the unit capital cost by 156% to the high value reported in the literature (US\$1.3M per ton per day¹⁷) increases the total levelized cost by 21%. Increasing the microbial yield by 29% to the high value reported in the literature decreases the price by 1.8% to US\$1,520, indicating the potential of selecting for higher-yield organisms to introduce additional marginal cost savings.

The input parameters that introduce changes in levelized cost less than 5% are summarized in Supplementary Table 4. The costs of non-methane substrates (ammonia and phosphorus) have

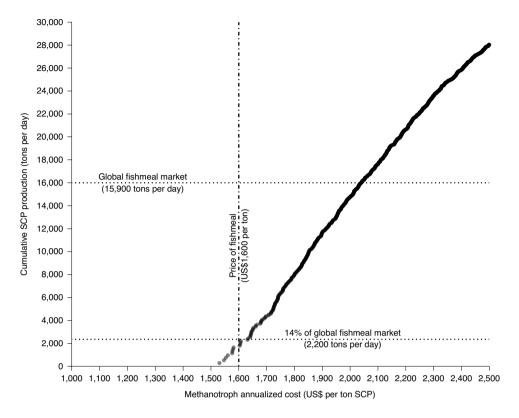


Fig. 4 | Supply curve for methanotrophic production using stranded methane. Each point represents a point source of methane, and the x axis indicates the corresponding levelized cost of protein that can be produced from that facility. The y axis indicates the cumulative amount of protein that can be produced with each additional facility. When the cost of methanotrophic protein is kept below that of fishmeal, methanotrophic production potential is equivalent to 14% of the global fishmeal market. Allowing costs to reach US\$2,050 could enable fully offsetting the global fishmeal market. We include only methane that is not currently being used elsewhere—the full market potential for SCP production from methane is even higher if we consider displacing other applications.

minimal impacts (less than 3%) on the levelized cost within the price ranges observed for these compounds over the past ten years. Infrastructure lifetime, weighted average cost of capital, scaling factor and utilization factor also introduce changes of less than 5%.

Discussion

We find that methanotrophic biomass is cost competitive with fishmeal when produced with current technology. Stranded methane in the United States can serve as a growth substrate capable of supporting methanotrophic SCP production that can offset 14% of the global fishmeal market. Companies are already commercializing the production of methanotrophic SCP using natural gas, which we find to be nearly economically competitive with fishmeal. Our model indicates that replacing purchased grid natural gas with stranded methane is competitive at a large scale, lowering costs to below the ten-year average price of fishmeal. The largest sources of stranded methane can serve as a starting point for industrial SCP production, enabling technological advances and cost reductions that can further expand production to include smaller sources of methane at more remote locations. Using smaller methane sources will enable protein production to exceed the current global fishmeal market. Reaching such production levels will require meaningful cost reductions for smaller-scale facilities, potentially through increased electrical efficiency and reduced labour requirements.

We identify a number of priority areas for cost reduction to enable the commercialization and expansion of methanotroph SCP production. Across all scenarios considered, cooling costs are dominant. Reactors may be designed to facilitate surface area for heat transfer³⁰, while culturing thermophilic methanotrophs can

enable higher-temperature operation, thus reducing heat removal requirements¹⁶. Electricity costs may be further reduced by switching electric-powered applications to gas, which can also reduce reliance on grid electricity for remote locations. Future analysis should evaluate the trade-off associated with using stranded methane for methanotrophic feedstock versus meeting the energy demand for production, as well as opportunities for on-site renewable energy generation.

As methanotrophic production scales to capture smaller sources of methane, the labour cost per ton of protein increases³¹. Research and development priorities would thus benefit from focusing on automating processes to reduce labour requirements at small-scale facilities. Automation will also enable utilizing stranded methane from remote oil and gas facilities not readily accessible by population centres, where labour is at a premium. As technology advances, smaller methane point sources are also likely to benefit from economies of unit number, whereby the production of many smaller units enables greater capital cost savings than the production of larger-scale facilities¹¹.

This analysis makes the generous assumption that currently vented methane emissions can be captured and concentrated at minimal additional capital cost. While this is the case for methane flares, vented sources of methane may be diffuse and require capital investment for capture. For landfills, a number of existing capping techniques can be used to reduce and collect diffuse emissions³², many of which are currently used in the United States for capturing landfill gas²⁰. This analysis also considers methane emissions and flaring as separate sources. However, for landfills and oil and gas facilities, both types of point source may occur in close proximity or

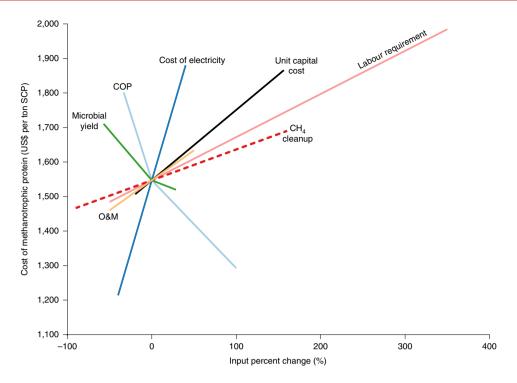


Fig. 5 | Sensitivity analysis for baseline methanotroph production at landfills, individually varying the parameters to low and high values. The *x* axis represents the resulting percent change of each parameter input, and the *y* axis represents the corresponding levelized cost of production US\$ per ton SCP (note: to show differences more clearly, the *y* axis does not end at zero). We include all input parameters that result in a change of 5% or greater in calculated levelized cost of methanotrophic SCP (US\$ per ton). Production is highly sensitive to cost of electricity, cooling COP, and labour. Levelized cost is also sensitive to unit capital cost and microbial yield. Changes in slope for microbial yield and COP are reflective of nonlinearities in these inputs.

even at the same facility. Further opportunities for large-scale production may thus be available by collecting methane from physically proximate sources and using pooled gas to feed a larger bioreactor than would be feasible from the individual sources on their own. Furthermore, in this analysis, we only consider methane that is not currently being used elsewhere. Considering the displacement of other applications will increase the full market potential for methanotrophic SCP. Our analysis is focused on the United States due to the availability of high-quality data; however, stranded methane around the world could be used with similar systems. This analysis also does not consider policies (such as carbon credits or tax) that may increase the economic favourability of methanotrophic SCP.

The methane production rate and economic prospects of current stranded methane sources are expected to change with the transforming energy landscape. Fossil methane is currently the largest source of stranded methane in the United States, the production of which will decrease with the transition to renewable energy. As conventional natural gas is phased out, approaches such as the bio-electrolytic production of methane from carbon dioxide and hydrogen may be used as future renewable substrates for growth³³.

While we find methane from wastewater treatment plants to be currently not competitive with the price of fishmeal, these facilities present a number of opportunities for cost reduction. Labour and electricity will be readily accessible for facilities such as wastewater treatment plants and landfills, typically located near population centres, whereas meeting these requirements will be more costly at remote oil and gas facilities. Nitrogen and phosphorous may be locally sourced from effluent, potentially through the use of precipitated struvite³⁴, although future analysis must determine the economic impacts of additional treatment processes needed. Wastewater effluent could replace refrigerant for cooling should thermophilic production be adopted¹⁶. Future research should further investigate the cost-saving opportunities presented by

co-located wastewater treatment plants through different cooling and nutrient recovery technology configurations.

Methanotrophic SCP may also economically benefit from increasing cost and environmental limitations on fishmeal production. Fishmeal prices have nearly tripled in real terms since 2000 (Supplementary Fig. 2)³⁵, while total production has decreased³⁶. Yet fishmeal currently accounts for nearly 20% of capture fishery production, despite decreasing inclusion rates of fishmeal in aquaculture feed (discussed in Supplementary Note 1)². Methanotrophs can also confer health benefits to fish and shrimp, which may further increase their value (discussed in Supplementary Note 2)¹³. In addition to serving as a component of aquaculture feed, methanotrophs are promising for use in agricultural animal and pet feeds¹².

Any protein under consideration as a fishmeal replacement will require holistic economic, environmental and nutritional evaluation³⁷. While we do not include a life-cycle assessment, incentivizing the capture of methane provides a beneficial end-use for gas that is currently emitted or flared. Substantial reductions in climate change impact can be achieved through the use of renewable methane rather than the current industry approach of using grid-supplied natural gas³⁸. This can be readily achieved for methane currently flared or emitted at point sources or diffuse sources that can be readily capped (discussed above).

Further environmental benefits may be derived by providing an alternative to wild-caught fishmeal, when not harvested sustainably through improved management practices (see Supplementary Note 1 for further details)^{39,40}. However, because fishmeal provides vitamins, minerals and lipids essential for fish growth, in addition to protein⁴¹, fully replacing fishmeal will require the development of feed blends that meet life-stage-specific and species-specific nutritional requirements, potentially through combining diverse species of methanotrophs with other feed ingredients. Additional uses for forage fish, such as fish oil, may also drive future demand.

One potential replacement for fish oil is microalgae, which is not yet economically competitive with fish oil, largely due to the high costs of fermentation⁴² and the energy requirements for collection and drying⁵. However, technological advances accompanying the widespread production of methanotrophic SCP could improve the economic prospects for microalgae cultivation, potentially through innovative approaches that involve co-culturing methanotrophs with algae^{43,44}. Additional environmental benefits could be achieved if methanotrophic SCP were to replace soybean in animal feeds, but this would require further cost reductions¹⁷ (Supplementary Note 1).

Our analysis demonstrates the market potential for methanotrophic SCP grown on stranded methane to serve as a replacement for fishmeal in animal feed. At current market prices, we find that a 20% decrease in methanotrophic SCP production costs could supply the total global demand for fishmeal. A reduction in demand for fishmeal would probably lower prices, potentially increasing the demand for fishmeal in other sectors (namely, pet food or agricultural feeds)³⁶. However, methanotrophs are also a promising replacement for fishmeal in other such sectors¹² and may also see a corresponding price reduction as technologies mature. As some producers may prefer to pay a premium for fishmeal, market acceptability studies are a key area of future research. Furthermore, expanding methanotrophic production to secondary markets such as bioplastic production could serve to further incentivize methane capture. Overall, reducing methane emissions and the over-harvesting of marine resources are highly complex problems, but methanotrophic SCP is promising as one part of a suite of necessary interventions for sustainable food production.

Methods

Here we describe the methods used for the two key components of our study: analysis of stranded methane in the United States and evaluation of protein production economics through techno-economic modelling. Additional details on methodology are included in the Supplementary Information.

Data. Wastewater treatment data. We used data from the US Environmental Protection Agency (EPA)'s publicly available Clean Watersheds Needs Survey to identify wastewater treatment facilities with anaerobic digestion and their corresponding geographic location (latitude and longitude), average daily treatment rate and presence of biogas utilization unit processes. Using previously described methods⁴⁵, we merged the 2004, 2008 and 2012 data to generate a dataset for all wastewater treatment facilities with anaerobic digestion that do not have on-site biogas utilization facilities, as well as their reported wastewater flow rates and geographic coordinates. Biogas production corresponding to a given flow rate was calculated by using the conversion 1.5 standard cubic feet of biogas produced per 100 gallons of wastewater processed⁴⁶ and assuming 60% methane content in biogas, a conservative estimate for anaerobic digestors⁴⁷. See Supplementary Methods for further details.

Landfill data. For the landfill direct emissions data, we used the EPA's publicly available Facilities Level Information on GreenHouse Gases Tool²¹ for 2019 methane emissions from the following sectors: municipal landfills, industrial landfills and solid waste combustion. For the flaring data, we used the EPA's Landfill Methane Outreach Program from August 2020²⁰. See Supplementary Methods for further details.

Natural gas and petroleum data. For the natural gas and petroleum direct emissions data, we also used the EPA's Facilities Level Information on GreenHouse Gases Tool²¹, downloading all 2019 methane emissions for the Petroleum and Natural Gas Systems sector, including all sub-headings. For the flaring data, we used Visible Infrared Imaging Radiometer Suite data from 2019²² (discussed further in Supplementary Methods).

Techno-economic model. This analysis models a methanotroph production system consisting of the following cost components: annualized capital costs, annualized operations and maintenance, methanotroph nutrient requirements (ammonia and phosphorus), water, labour and electricity demand for all equipment and processes. We included the cost of methane cleanup (US\$ per ton CH_4) as well. While additional micronutrients are required for microbial growth (for example, trace metals), we consider these to be minor costs and did not include them in the scope of the current analysis (Supplementary Note 3). We established baseline values for each input to determine the levelized cost in four

different scenarios for sourcing methane: co-location with wastewater treatment plants, landfills, natural gas facilities and a facility with a paid connection to the natural gas grid.

Methanotrophic properties. For the purposes of this analysis, we defined the final SCP product as the organic biomass of the dried cell (also referred to as volatile suspended solids). Microbial properties of yield (tons SCP produced per ton substrate consumed), cell density (grams SCP per litre) and specific growth rate (per day) determine how much biomass can be produced in a reactor in a given period of time (see Supplementary equations (1) and (2) in Supplementary Methods). We used these parameters to determine methanotroph production rate for our baseline levelized cost calculations. Using the stoichiometry in equation (1) to describe methanotrophic growth¹³, we calculated the baseline microbial yields for each compound required for growth: methane, oxygen and nitrogen (in units of N as ammonia). For phosphorus, we assumed 2% of biomass by weight (Supplementary Table 8)⁶:

$$CH_4 + 1.5 \ O_2 + 0.10 \ NH_3 \rightarrow 0.10 \ C_5 H_7 O_2 N$$

$$+0.5 \ CO_2 + 1.8 \ H_2 O + 643 \ kJ \ heat \eqno(1)$$

For cell density in the bioreactor, microbial growth rate (per day) and heat production (kJ per g SCP), we surveyed the literature to identify representative values for industrial methanotrophic growth (Supplementary Tables 7 and 8). From these values, we calculated the methane utilization rate (0.14 tons $\mathrm{CH_4}$ per m³ per day) and the size of the bioreactor needed for a given source size. See Supplementary Methods for further details.

Capital costs. We modelled a methanotroph production system with the following equipment: methane and air compressors, growth bioreactor, dewatering centrifuge and biomass dryer (Fig. 1). We first determined a literature baseline unit capital cost value on the basis of reported costs and capacity. For the bioreactor, this literature baseline value was then scaled to the size established for each methane source scenario described in Table 1. We assumed that all equipment costs except the bioreactor have a constant unit capital cost, to represent the increasing unit number of the equipment operating in parallel. We used 500 m³ as a benchmark for the largest bioreactor size feasible in our model. This is representative of the largest industrial aerated, stirred-tank bioreactors in operation28. For bioreactors smaller than 500 m³, we applied a scaling relationship based on the total bioreactor volume described in equation (2). For bioreactors 500 m³ or greater, we used the unit capital cost of a 500 m³ reactor as a model for multiple reactors operating in parallel. For the bioreactor scaling factor n, we used 0.7, a mid-value of the reported and calculated scaling factors in the literature^{28,48} (see Supplementary Methods for additional details):

$$Cost_2 = Cost_1 \left(\frac{Size_2}{Size_1} \right)^n \tag{2}$$

Gases are pressurized from 1 bar to 8 bar before delivery to the methanotrophic bioreactor ^{16,49}. For air and methane compression, we used the continuous centrifugal air compressor described in Levett et al. ¹⁹. For air compression, we calculated the unit capital cost using the reported air flow rate, capital costs and electricity usage for a 52.8 MW compressor (Supplementary Table 3). To establish the literature baseline unit capital cost for methane compression, we used the same compressor specifications but scaled the capital cost for the reduced methane flow rate reported in Levett et al. using the size scaling exponent for air compression $(n=0.34)^{19}$. We assumed a power rating of 3.6 MW for the reported methane flow rate, on the basis of modelling in Aspen Plus V11 37.0.0.

Pressurized gases and media enter the continuous airlift methanotrophic bioreactor. Heat is removed via a cooling jacket and coils included in the bioreactor capital cost. Biomass from the bioreactor is dewatered in a biomass centrifuge, reducing the water content to 35% (ref. ¹⁶). Biomass is then dried in a continuous rotary drum dryer that further reduces the moisture content to 10% (ref. ¹⁶).

All costs were adjusted to 2020 US dollars using the annual average Consumer Price Index for all urban consumers as reported by the US Bureau of Labor Statistics³¹. To calculate the levelized capital cost, we used a weighted average cost of capital of 10%, representative of a new technology⁵². We assumed an infrastructure lifetime of 20 years¹⁶ (the calculations are shown in the Supplementary Methods). The cost of operations and maintenance of equipment was set at 10% of the total capital cost per year¹⁶.

Electricity costs. To calculate electricity costs, we considered the power demand of individual equipment needed for each stage of methanotrophic biomass production: gas compression (methane and air), growth reactor, dewatering and drying. We used the reported power demand in Levett et al. 16 and the equipment capacity for each unit process to determine the electricity cost in US\$ $_{2020}$ per ton SCP. The electricity needed for heat removal from the growth reactor was calculated using the heat production rate for methanotrophs (see equation (3)) 13 divided by the COP (heat energy removed per electricity input):

$$\mbox{Heat production rate} = \Delta_c H_{met} \times \frac{1}{Y} \times \mu \times \rho \times V \eqno(3)$$

where $\Delta_c H_{\rm met}$ is metabolic heat production (kJ per g CH₄), Y is cell yield (g SCP per g CH₄), μ is growth rate (per day), ρ is cell density (g SCP per l) and V is reactor size (l).

For the price of electricity, we used U\$\$0.10 kWh⁻¹, representative of US commercial prices⁵³. This is a conservative assumption, as landfills and wastewater treatment plants may have access to industrial prices for electricity (averaging around U\$\$0.07 kWh⁻¹ in the United States⁵³). However, some facilities may not be able to reach the same scale as large industrial customers and thus may pay closer to commercial rates. Note that remote oil and gas facilities may not have an electric grid connection, potentially increasing electricity costs at these locations.

Methane cleanup. We assumed that all stranded methane in this analysis requires cleaning to remove contaminants before use as a methanotroph feedstock. As methanotrophs metabolize and assimilate CO₂ into their biomass⁵⁴, cleanup costs will be lower than those required for injected biomethane into the natural gas grid⁵⁵. Because of the different levels of treatment required to clean and upgrade biogas, landfill gas and natural gas, we calculated the cost of methane cleanup separately from the equipment costs associated with methanotrophic biomass production (bioreactor, gas compression systems and post-processing). We surveyed the literature to calculate the cost of methane cleanup per ton CH4 and considered systems designed for desulfurization and siloxane removal⁵⁶⁻⁵⁸, and we included the annualized capital cost, variable costs and/or electricity costs (additional details are provided in the Supplementary Methods). Depending on the extent of contaminant removal, cleanup costs reported in the literature ranged from US\$5 per ton CH₄ to US\$128 per ton CH₄. We used a mid-value of US\$50 per ton CH₄ as our baseline value, representative of the cost of upgrading a wastewater treatment facility to include an adsorption unit for biogas cleanup⁵⁷. For the grid baseline scenario, we removed the cost of methane cleanup.

Macronutrient costs. Microorganisms require substrates that serve as sources of macro- and micronutrients necessary for growth. Macronutrient requirements are provided in equation (1). For methanotrophs, methane is the source of energy and carbon. For facilities located at wastewater treatment plants, landfills, and oil and gas facilities, we assumed that methane is readily available at no additional capital cost aside from cleanup. While reasonable for flared methane, we recognize that this is a generous assumption for methane currently directly emitted. For the grid scenario, we used the US Energy Information Administration industrial price for US natural gas averaged over the past ten years (US\$234 per ton CH_4)⁵⁹.

We used urea and diammonium phosphate as sources of nitrogen and phosphorus. We calculated baseline substrate costs using yield values (mol SCP per mol substrate) and assumed a phosphorus content in biomass of 2% (Supplementary Table 8)⁴⁷. For baseline prices, we used the ten-year average from 2010 to 2020 reported by the World Bank Commodity Price Index, converted to US\$₂₀₂₀ for urea (CH₄N₂O) and diammonium phosphate ((NH₄)₂HPO₄)³⁵. This resulted in baseline costs of US\$550 per ton NH₃ and US\$1,790 per ton phosphorus, or US\$83 per ton SCP for NH₃ and US\$36 per ton SCP for phosphorus, using the yield assumptions in Supplementary Table 8. For oxygen supply, we used the delivery of compressed air to the bioreactor. The cost of oxygen is thus accounted for in the capital cost of the air compressor and the associated electricity cost (described above), rather than a direct input to our substrate cost calculation. In the Supplementary Methods, we compare compressed air delivery with the cost of an air separation unit and purchasing commercial O₂.

Labour costs. To determine the labour demand in worker-hours per ton SCP for a given plant size, we used values reported in the literature for bioplastic production of polyhydroxybutyrate (PHB) using methanotrophs. Specific strains of methanotrophic bacteria can accumulate PHB when subjected to imbalanced growth conditions in a process that is similar to methanotrophic SCP production, albeit with additional processing steps⁶⁰ (Supplementary Note 3 discusses the differences between PHB and SCP cultivation). Criddle et al. 31 report the number of personnel needed for the three stages of production (fermentation, extraction and packaging) for plant capacities ranging from 500 tons PHB per year to 100,000 tons PHB per year. We used the number of personnel required for fermentation and packaging (PHB biopolymer extraction is not necessary for SCP production) and the total reported hours of operation per year to determine worker-hours needed per ton of PHB produced in a given plant size. We directly used these values as the worker-hours needed to produce an equivalent mass of methanotrophic biomass. This is a conservative assumption, as fermentation bioreactors that can support a fixed rate of PHB production can probably produce twice as much methanotrophic biomass: PHB can make up 50% of cell biomass when methanotrophs are subjected to the required multi-stage fermentation process described by Criddle et al.³¹. The labour calculations are discussed more fully in the Supplementary Methods.

Water and land requirements. We determined a water requirement of 33.3 tons $\rm H_2O$ per ton SCP using the cell density of $\rm 30\,g\,l^{-1}$. For our system, we assumed

that 90% of the water requirement is met by capturing water from dewatering centrifuges and recycling it to the main growth reactor(s) 16 . The remaining water requirement is met through purchasing water at US\$1 m $^{-3}$, a relatively high value. This could be representative of the cost of desalinated water 61 or building a pipeline to transport water to a remote location. Due to the comparatively low cost of water in our results, we combined this cost with that of the macronutrients nitrogen and phosphorus, referring to the cost of all three as 'nutrient media'.

In our analysis, we did not add additional costs for the purchase of land. For the scenarios under consideration, the methanotrophic SCP production equipment is being added to an existing facility, which we assume has sufficient vacant space.

Utilization factor. We applied a utilization factor of 80% to our baseline scenario to account for plant downtime for maintenance and repair. This means that the facility produces 80% as much SCP as it could over the whole year if it operated at full capacity all the time. The average utilization of oil refinery capacity over the past ten years is 90% (ref. ⁽²⁾). To account for the potentially variable quantity and quality of gas production across our different scenarios, we chose 80%. When methane is sourced from wastewater treatment or the natural gas grid, we anticipate this value to be conservative.

We applied the utilization factor to all inputs that vary with the final SCP production rate: annualized capital cost, annualized operations and maintenance, worker hours needed and total annualized methane cleanup. While total annualized methane cleanup includes variable costs that are fixed per ton of CH₄ treated, we assumed that costs are dominated by capital.

Total levelized cost. We calculated the total levelized cost of producing methanotrophic protein including all techno-economic parameters described above using equation (4) (for additional details on the full formulation, see Supplementary Methods):

$$Total\ levelized\ cost\ =\ annualized\ capital\ cost\ +\ annualized\ O\&M \\ +electricity\ cost\ +\ substrate\ cost\ +\ labour\ cost \eqno(4)$$

We calculated facility size (tons $\mathrm{CH_4}$ per day) for each methane source scenario (wastewater treatment, landfills, oil and gas, and grid) using the largest point sources in our database, with the grid case at the same scale as the landfill case. We compared the methanotroph production cost with the price of fishmeal, represented by the average price over the past ten years, US\$1,612 per ton (the ten-year low and high are US\$1,351 per ton and US\$1,944 per ton) 35 .

Supply curve. To make the supply curve depicted in Fig. 4, we generated a master dataset with the total annualized cost of methanotroph production, under the baseline assumptions, for each methane source included in Fig. 2. We sorted the methane sources in order of increasing production cost and calculated the cumulative SCP production rate (tons per day) as higher-cost locations were incrementally added to the total production. We used the ten-year average price of fishmeal (US\$1,600) for comparison, although see Supplementary Fig. 2 for historical fishmeal prices from the past four decades³⁵. The fishmeal production rate of 15,900 tons per day is from 2018³.

Sensitivity analysis. The sensitivity analysis individually varied each input parameter from its baseline to low and high values, representing the feasible range of current values reflected in the existing literature, and calculated the resulting total annualized cost of methanotrophic biomass.

We surveyed the literature to determine low and high unit capital costs for methanotrophic biomass production, included in Supplementary Table 14. We considered techno-economic analyses where methanotrophic biomass itself was the final product as well as those where methanotrophs were being used for polyhydroxyalkanoate production. In the latter scenario, capital costs were adjusted to include only the processes necessary for methanotrophic biomass production (Supplementary Methods). For the weighted average cost of capital, used in converting capital cost into levelized cost, we used a low value of 8% and a high value of 12%, representing modest variation in potential investor confidence in this emerging technology⁵². We varied the COP from a baseline of 3 (ref. ¹⁶) to a low value of 2 and a high value of 6. The low and high endpoints for microbial yield were based on experimentally reported values in the scientific literature⁶³.

For ammonia and phosphorus, we maintained the baseline described above, using the average ten-year price. We used the lowest and highest annual average prices during this period as the low and high values. For the cost of electricity, we used a low value of US\$0.06 kWh⁻¹, which is a low-end price for industrial consumers in the United States⁵³. For the high value, we used US\$0.14 kWh⁻¹, just above the average residential prices in the United States⁵³ (one-year average industrial, residential and commercial electricity costs are reported in the Supplementary Methods).

Our baseline value for the labour requirement (one worker-hour per ton) is based on literature for PHB production. For the low value, we reduced this requirement by 50%. This was chosen to reflect the fact that an SCP production facility should be able to produce twice as much final product as a PHB facility, because PHB will reach only 50% of the total cell dry mass (that is, bioreactors

producing 500 tons of PHB per year can produce 1,000 tons of SCP per year) and the high value input, we calculated the plant size needed to completely meet the market demand for fishmeal on the basis of the supply curve in Fig. 4, applying the labour cost scaling relationship described in the Supplementary Methods to determine the associated labour requirement. This high input value of six worker-hours per ton SCP corresponds to a source size of 24 tons CH_4 per day and produces methanotrophic biomass at US\$1,972 per ton under the baseline assumptions at a landfill or oil and gas facility.

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

Data availability

The data used in the analysis and figures are publicly available. The data on flaring from oil and gas facilities are available through the Earth Observation Group (https://eogdata.mines.edu/download_global_flare.html). All data on methane emissions from oil and gas facilities and landfills, flaring from landfills, and unit processes at wastewater treatment plants are available from the US EPA through the following programmes: Facilities Level Information on GreenHouse gases Tool (https://ghgdata.epa.gov/ghgp/main.do), Landfill Methane Outreach Program (https://www.epa.gov/lmop/lmop-landfill-and-project-database) and Clean Watersheds Needs Survey for 2004 (https://www.epa.gov/cwns/clean-watersheds-needs-survey-cwns-2004-report-and-data), 2008 (https://www.epa.gov/cwns/clean-watersheds-needs-survey-cwns-2012-report-and-data).

Code availability

Code supporting the current study is available at https://github.com/sahar-elabbadi/methane-to-protein.

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Author contributions

S.H.E. and E.D.S. conceptualized the project. S.H.E. and E.D.S. devised the methodology with feedback from A.R.B., C.S.C. and S.P.L. S.H.E. and E.D.S. validated the methodology, conducted the investigation and wrote the original draft of the paper. S.H.E., E.D.S., A.R.B., S.P.L. and C.S.C. reviewed and edited the paper. E.D.S., A.R.B. and C.S.C. supervised the project S.H.E. and E.D.S. conducted the project administration. S.H.E., E.D.S., A.R.B., S.P.L. and C.S.C. acquired the funding.

Competing interests

The authors declare no competing interests.

Additional information

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Data used in analysis and figures are publicly available. Data on flaring from oil and gas facilities are available through the Earth Observation Group (https://eogdata.mines.edu/download_global_flare.html). All data on methane emissions from oil and gas facilities and landfills, flaring from landfills, and unit processes at wastewater treatment plants are available from the US Environmental Protection Agency through the following programs: Facilities Level Information on Greenhouse Gases Tool (https://ghgdata.epa.gov/ghgp/main.do){https://ghgdata.epa.gov/ghgp/main.do), Landfill Methane Outreach Program (https://www.epa.gov/lmop/lmop-landfill-and-project-databas), and Clean Watersheds Needs Survey for 2004 (https://www.epa.gov/cwns/clean-watersheds-needs-survey-

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All studies must disclose	on these points even when the disclosure is negative.	
Study description	We conducted a quantitative analysis of stranded methane sources in the United States from landfills, oil and gas facilities and wastewater treatment plants. Our techno-economic model evaluates the cost of producing methanotrophic protein from point sources of methane, and compares price and production volume with that of the global fishmeal market.	
Research sample	We use existing publicly datasets for our analysis of methane emissions and flaring in the United States. Data on flaring from oil and gas facilities are available through the Earth Observation Group at the Colorado School of Mines (https://eogdata.mines.edu/download_global_flare.html). All data on methane emissions from oil and gas facilities and landfills, flaring from landfills, and unit processes at wastewater treatment plants are available from the US Environmental Protection Agency through the following programs: Facilities Level Information on Greenhouse Gases Tool (https://ghgdata.epa.gov/ghgp/main.do), Landfill Methane Outreach Program (https://www.epa.gov/lmop/lmop/landfill-and-project-database), and Clean Watersheds Needs Survey for 2004 (https://www.epa.gov/cwns/clean-watersheds-needs-survey-cwns-2004-report-and-data), 2008 (https://www.epa.gov/cwns/clean-watersheds-needs-survey-cwns-2012-report-and-data).	
Sampling strategy	We use all reported data in our datasets, and did not sub-sample.	
Data collection	Not applicable	
Timing	Not applicable, we did not generate new datasets but used publicly available datasets.	
Data exclusions	Not applicable, we did not generate new datasets but used publicly available datasets.	
Non-participation	Not applicable	
	Not applicable	

Ma	terials & experimental systems	Me	thods
n/a	Involved in the study	n/a	Involved in the study
\boxtimes	Antibodies	\boxtimes	ChIP-seq
\boxtimes	Eukaryotic cell lines	\boxtimes	Flow cytometry
	Palaeontology and archaeology	\boxtimes	MRI-based neuroimaging
\boxtimes	Animals and other organisms		
\boxtimes	Human research participants		
\boxtimes	Clinical data		
\boxtimes	Dual use research of concern		