# Displacing fishmeal with protein derived from stranded methane

Sahar H. El Abbadi<sup>1</sup>, Evan D. Sherwin<sup>2</sup>, Adam R. Brandt<sup>2</sup>, Stephen P. Luby<sup>3</sup>, and Craig S. Criddle<sup>1\*</sup>

# **ABSTRACT**

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 for animal feed. In the rapidly growing aquaculture industry, this can replace ocean-caught fishmeal, reducing demands on over-harvested fisheries. Here, we analyze 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 equivalent to 14% of the global fishmeal market at prices at or below the current cost of fishmeal of roughly \$1,600 per metric ton. A sensitivity analysis highlights technically and economically feasible cost reductions, e.g. reduced cooling or labor requirements, which could allow stranded methane from the US alone to satisfy global fishmeal demand.

# Introduction

11

12

13

15

16

17

18

20

21

22

23

24

26

28

Humanity 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, e.g., through land use change<sup>1</sup>. One important global source of protein and micronutrients is seafood, production of which increased from 40 to 180 million metric tons/year between 1960 and 2015<sup>2</sup>. Farming aquatic animals now accounts for almost half of all animal-source seafood<sup>3</sup>, with 90% of the world's marine fisheries fully fished or overfished<sup>4</sup>. Fed aquaculture relies upon fishmeal for protein, consuming 70% of global fishmeal production, increasing pressures on marine resources<sup>5–7</sup>. Over-fishing marine environments leads to long-term loss in biodiversity and irreversible damage to marine ecosystems<sup>8</sup>. Many plant proteins are a promising substitute for fishmeal, but require additional inputs of land, freshwater and fertilizer<sup>9</sup>.

Methane has at least 25 times the global warming potential of CO<sub>2</sub> over a 100-year time period <sup>10</sup>. Total annual methane emissions in the US for 2014-2018 exceeded 630 million metric tons of CO<sub>2</sub> 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 <sup>11</sup>. Unlike other major methane emitters, these sources also flare methane, releasing large amounts of CO<sub>2</sub> to the atmosphere. Taken together, methane emissions and flaring in the US release nearly 14 billion m³/year. Because these sources are geographically dispersed and small-scale, increasing unit capital and labor costs, methane is emitted or flared rather than captured, cleaned and used <sup>12</sup>.

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 (EU), at rates of up to 33%<sup>13</sup>. Because methanotrophs do not require light, dense cultures are grown in bioreactors with low spatial footprints not feasible with terrestrial agriculture<sup>14</sup>. Companies in the US and EU (Calysta<sup>15</sup>, Unibio<sup>16</sup>) are commercializing production of methanotrophic SCP from natural gas.

Industrial production of methanotrophic SCP is depicted in Figure 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 jacket and coils to remove metabolic heat produced during growth, maintaining biologically viable temperatures<sup>17</sup>. Biomass is then de-watered and dried for storage and shipping.

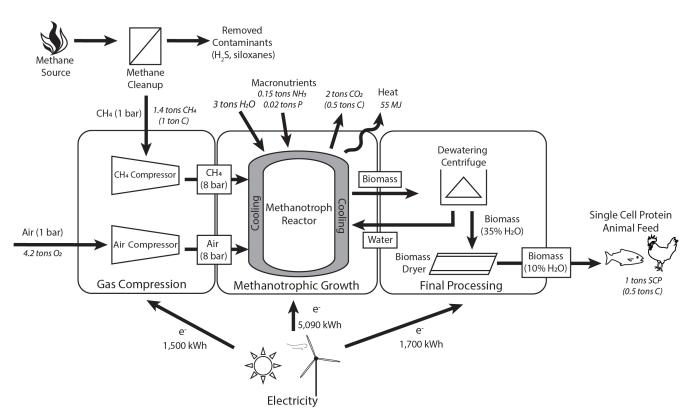
Using methane currently emitted or flared to produce methanotrophic SCP can incentivize capture of stranded resources with the dual benefit of reducing greenhouse gas emissions and generating a sustainable protein substitute for fishmeal. Stranded methane has also been proposed as a feedstock for future biomanufacturing, potentially enabling a paradigm shift from large-scale mega-facilities to smaller-scale, widespread, mobile production<sup>12</sup>. Recent studies have evaluated potential

<sup>&</sup>lt;sup>1</sup>Stanford University, Department of Civil & Environmental Engineering, Stanford, 94305, USA

<sup>&</sup>lt;sup>2</sup>Stanford University, Department of Energy Resources Engineering, Stanford, 94305, USA

<sup>&</sup>lt;sup>3</sup>Stanford University, Division of Infectious Diseases and Geographic Medicine, Stanford, 94305, USA

<sup>\*</sup>criddle@stanford.edu



**Figure 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 for removal of metabolic heat produced. Exhaust CO<sub>2</sub> is released from growth bioreactors, and biomass is processed in dewatering centrifuges and dryers, after which it can serve as single cell protein (SCP) feed for agriculture or aquaculture. The labels on the figure in italics represent the mass or energy flow associated with the production of 1 ton of methanotrophic SCP.

environmental benefits of methanotrophic SCP, and indicate promising economics<sup>18–20</sup>. To the best of our knowledge, this analysis is the first to evaluate the market potential of methanotrophic SCP across existing sources of stranded methane. While we focus on the US, 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 modeling of the production process outlined in Figure 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 US: 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 cost of scaling SCP production.

#### 39 Results

30

31

32

33

34

35

36

37

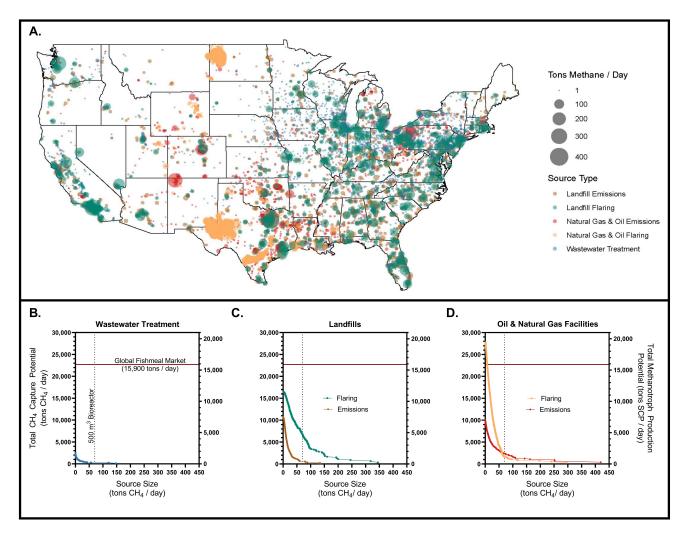
38

47

#### 40 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 CO<sub>2</sub>. In this study, we analyze methane emitted and flared from landfills<sup>22</sup>, and oil and gas facilities<sup>21,23</sup>. We also consider methane from wastewater treatment plants with operational anaerobic digesters that lack biogas utilization technology on-site<sup>24–26</sup>, indicative that the methane is likely flared<sup>29</sup>. The geographic distribution of included methane sources and their respective sizes are depicted in Figure 2a for the contiguous US. Methane sources are geographically distributed across the country, with landfills and wastewater treatment plants concentrated near population centers.

We compare methane emitted and flared from the sources in question in Figures 2b-d. Mean methane production is lowest for wastewater treatment plants (less than 1 ton  $CH_4/day$ ) and highest for landfill flaring (31 tons  $CH_4/day$ ) and oil and gas



**Figure 2.** A. Unused methane generation in the United States. Point sources indicate methane currently emitted and flared from landfills<sup>21,22</sup>, oil & gas facilities<sup>21,23</sup>, and methane production from wastewater treatment plants currently not utilized<sup>24–26</sup>. B-D. Cumulative methane capture potential for different source types is depicted on the left y-axis (tons  $CH_4/day$ ). The right y-axis depicts the corresponding total methanotrophic production potential in tons of single cell protein (SCP) per day, calculated assuming a yield of 0.7 tons SCP/ton  $CH_4^{14,27}$ . Horizontal line indicates production equivalent to the total global fishmeal market, 15,900 tons/day. The vertical line at source size of 86 tons  $CH_4/day$  corresponds to a 500 m<sup>3</sup> bioreactor, a typical size for an industrial-scale reactor<sup>28</sup>. Bioreactor size is calculated assuming a yield of 0.7 tons SCP/ton  $CH_4^{14}$ , a cell growth rate of 4 d<sup>-114</sup>, and a cell density of 30 g  $SCP/L^{17}$ .

flaring (10 tons CH<sub>4</sub>/day). Maximum reported values range from 148 tons CH<sub>4</sub>/day for wastewater treatment plants to 420 tons CH<sub>4</sub>/day directly emitted from oil and gas facilities. Low mean and median values compared with maximum reported sources sizes (see Supplementary Table S1 for summary statistics) as well as the heavy tail distribution are indicative of the high number of smaller methane sources and a small number of high emission point sources, evident in Figures 2b-d.

50

52

53

54

56

57

58

Fully utilizing stranded methane resources and reducing their climate change impact will require harnessing sources that correspond to smaller-than-conventional bioreactors (depicted through the vertical line in Figures 2b-d). We also compare methanotrophic SCP production potential to the current global fishmeal market. High quality fishmeal is 60-72% crude protein<sup>30</sup>, and methanotrophic biomass is 67%-81% crude protein<sup>13</sup>. Thus, this analysis 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 based on 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 centers make labor and electricity more readily available, and therefore more representative of early production locations.

**Table 1.** Characterizing four methane source scenarios. Methane source sizes represent the largest point sources from emissions or flaring in each location type. Total reactor volume and methanotroph SCP production rate are calculated based on a methane utilization rate of 0.14 tons  $CH_4/m^3$ -day and a microbial yield of 0.7 tons volatile suspended solids (SCP)/ton  $CH_4$ . Methanotroph production potential assumes the same microbial yield, and also applies a utilization factor of 80% to allow for time needed for maintenance and repairs.

Scenario	Source Size (tons CH <sub>4</sub> /day)	Total Reactor Volume (m <sup>3</sup> )	Methanotroph Production (tons SCP/day)
Wastewater Treatment	148	860	83
Landfills	345	2,010	193
Oil & Gas	420	2,450	235
Grid	345	2,010	193

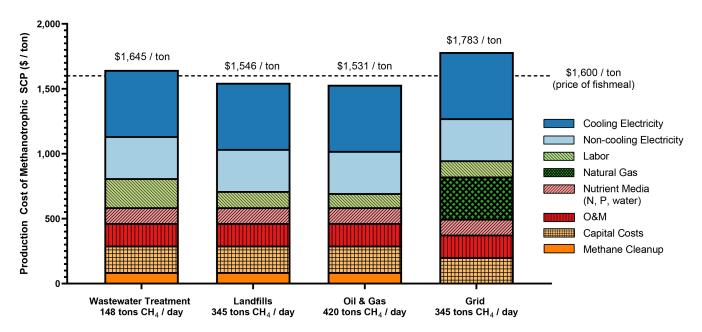
We find production costs for methanotrophic SCP are lower than the market price for fishmeal in the landfill and oil and gas scenarios when using the 10-year average market price of fishmeal (\$1,600/ton) as a benchmark for comparison (Figure 3). For the wastewater treatment scenario, production cost is slightly higher (\$1,645/ton), largely due to increased labor cost. The grid scenario is the most expensive (\$1,783/ton), attributable to the cost of purchasing natural gas. All scenarios except for wastewater treatment are individually capable of producing over 159 tons SCP/day, which represents 1% of the global fishmeal market (15,900 tons SCP/day)<sup>2</sup> and a meaningful market share for emerging technologies.

Electricity costs make up over 45% of total levelized cost in all scenarios. Over 60% of power needed is required for removing metabolic heat from the bioreactor (Figure 3 and Supplementary Table S2), an amount inline with previous studies of methanotrophs<sup>17</sup>. We thus depict cooling costs separately from electricity costs associated with powering other equipment in Figure 3. Considering electricity alone, cooling requires \$509/ton SCP, dewatering and drying combined require \$177/ton SCP, and air compression requires \$136/ton SCP (see Supplementary Tables S2 and S3). Capital costs make up below 15% of total levelized cost in all scenarios, but remains one of the leading costs in the breakdown. Methane cleanup (where required), nutrient media (N, P, H<sub>2</sub>O), 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 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 industrial bioreactors will not exceed 500 m³ in volume²8, so for methane sources requiring total reactor volumes exceeding this cut-off, we maintain 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 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, labor 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 (\$326/ton SCP) increases the total levelized cost, which is only somewhat offset by removing the requirement for methane cleanup (\$89/ton SCP).

Figure 4 depicts a supply curve for production of methanotrophic SCP from the stranded methane sources in Figure 2. Cost of production is calculated using the baseline assumptions and scaling relationship described in Methods. Keeping prices at or below the benchmark price of fishmeal (\$1,600/ton), these sources are able to produce nearly 2,200 tons SCP/day, or 14% of the global fishmeal market. Including sources that produce methane at costs of up to \$2,040 would enable production at a level greater than the current global fishmeal market of 15,900 tons SCP/day.

We identify key cost sensitivities in Figure 5, which depicts a sensitivity analysis that begins with the cost of producing methanotrophic protein in the landfill scenario. Here, levelized cost of methanotrophic SCP production under baseline assumptions is \$1,546 /ton. We use the landfill scenario for the sensitivity analysis, as these facilities are typically located in



**Figure 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. 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 cooling costs to illustrate its impact. The grid scenario sees an increase in cost due to purchase of natural gas, which is slightly offset by the removal of the methane cleanup requirement. Baseline scenarios for landfill and oil and gas are lower than the average 10-year market price of fishmeal, \$1,600/ton. Further opportunities for cost reduction are present at wastewater treatment plants, through locally sourced nutrients and cooling water.

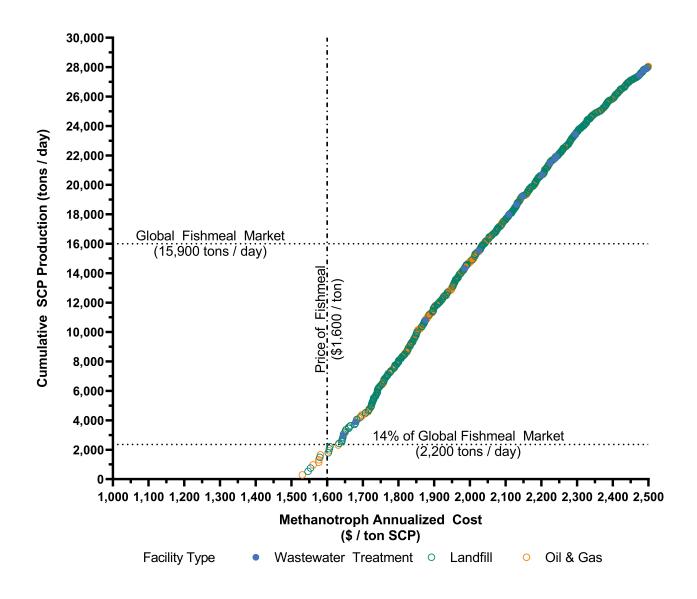
close proximity to population centers, meaning labor and electricity are likely readily available (see Supplementary Figure S1 for sensitivity analysis of wastewater treatment, oil and gas, and grid scenarios). Input variables included in Figure 5 are those that result in a change of 5% or greater in calculated levelized cost. The high cost of cooling is reflected in the sensitivity to coefficient of performance (COP) for the assumed refrigeration system <sup>17</sup>; doubling COP reduces levelized cost by over 15%, whereas decreasing COP from 3 to 2 increases cost by over 15%. The high sensitivity to electricity also aligns with the large contribution of cooling, gas compression and biomass drying to total cost. Decreasing cost of electricity to \$0.06/kWh, in line with industrial rates in the lowest-cost parts of the US (Mississippi, Texas<sup>31</sup>), reduces levelized cost by 22% to \$1,214/ton SCP, whereas increasing the price to that available to available to residential consumers, \$0.14/kWh (as in Pennsylvania, Illinois<sup>31</sup>), increases levelized cost by 22% to \$1,881/ton.

The model is also sensitive to labor, unit capital cost and microbial yield. We increase labor by 350% to 4.5 worker-hrs/ton SCP, reflecting a 90% smaller facility at a size our model suggests would be necessary to fully offset the fishmeal market using the current supply of stranded methane from the sources analyzed. This increase in labor requirement introduces a 28% increase in cost to nearly \$1,985/ton. Increasing unit capital cost by 156% to the high value reported in literature, \$1.3M/ton/day<sup>18</sup>, increases total levelized cost by 21%. Increasing microbial yield by 29% to the high value reported in the literature decreases price by 1.8% to \$1,520, indicative of the potential of selecting for higher yield organisms to introduce additional marginal cost savings.

Input parameters that introduce changes in levelized cost less than 5% are summarized in Supplementary Table S4. The costs of non-methane substrates (ammonia and phosphorus) have minimal impact (less than 3%) on levelized cost within the price ranges observed for these compounds over the past 10 years. Infrastructure lifetime, weighted average cost of capital (WACC), scaling factor (n), 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 production of methanotrophic SCP using



**Figure 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. Maintaining the cost of methanotrophic protein at below that of fishmeal can potentially produce over 14% of the global fishmeal market. Allowing costs to reach \$2,050 could enable fully offsetting the global fishmeal market. We only include methane from facilities that are not currently being used elsewhere: the full market potential for SCP production from methane is even higher if we consider displacing other applications.

natural gas, which we find to be nearly economically competitive with fishmeal. Our model indicates replacing purchased grid natural gas with stranded methane is competitive at large scale, lowering costs to below the 10-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 exceeding 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 labor requirement.

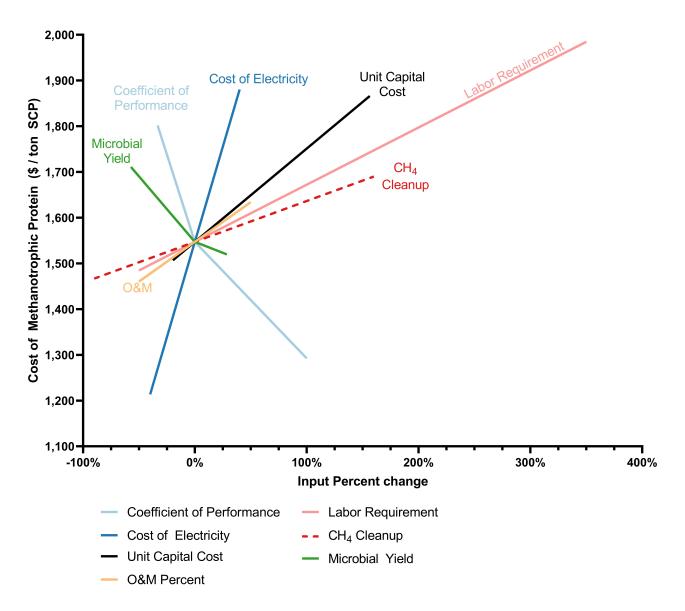
123

124

126

127

128



**Figure 5.** Sensitivity analysis for baseline methanotroph production at landfills, individually varying 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 \$/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 (\$/ton). Production is highly sensitive to cost of electricity, cooling coefficient of performance (COP), and labor. Levelized cost is also sensitive to unit capital cost and microbial yield. Changes in slope for microbial yield and coefficienct of performance are reflective of non-linearities in these inputs.

We identify a number of priority areas for cost reduction to enable 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 transfer<sup>32</sup>, while culturing thermophilic methanotrophs can enable higher temperature operation, thus reducing heat removal requirements<sup>17</sup>. 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 energy demand for production, and opportunities for on-site renewable energy generation.

As methanotrophic production scales to capture smaller sources of methane, labor cost per ton of protein increases<sup>33</sup>. Thus, research and development priorities would benefit from focusing on automating processes to reduce labor requirements at

small-scale facilities. Automation will also enable utilizing stranded methane from remote oil and gas facilities not readily accessible by population centers, where labor is at a premium. As technology advances, smaller methane point sources are also likely to benefit from economies of unit number, whereby production of many smaller units enables greater capital cost savings than production of larger-scale facilities 12.

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 emissions<sup>34</sup>. 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 even at the same facility. Thus, further opportunities for large scale production may 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 displacement of other applications will increase the full market potential for methanotrophic SCP. Our analysis is focused on the US 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 favorability 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 US, 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 growth<sup>35</sup>.

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. Labor and electricity will be readily accessible for facilities such as wastewater treatment plants and landfills, typically located near population centers, 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 use of precipitated struvite<sup>36</sup>, although future analysis must determine the economic impacts of additional treatment processes needed. Wastewater effluent could replace refrigerant for cooling should thermophilic production be adopted<sup>17</sup>. 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 (see Supplementary Figure S2)<sup>37</sup>, while total production has decreased<sup>38</sup>. 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)<sup>2</sup>. Methanotrophs can also confer health benefits to fish and shrimp, which may further increase their value (discussed in Supplementary Note 2)<sup>14</sup>. In addition to serving as a component of aquaculture feed, methanotrophs are also promising for use in agricultural animal and pet feeds<sup>13</sup>.

Any novel protein under consideration as a fishmeal replacement will require holistic economic, environmental and nutritional evaluation<sup>39</sup>. While we do not include a life-cycle assessment, incentivizing 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 use of renewable methane rather than the current industry approach of using grid-supplied natural gas<sup>40</sup>. Further environmental benefits can be derived from reducing pressure on over-harvested marine ecosystems by replacing fishmeal derived from forage fish. However, because fishmeal provides vitamins, minerals, and lipids essential for fish growth, in addition to protein<sup>41</sup>, fully replacing fishmeal will require development of feed blends that meet life-stage 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 fermentation<sup>42</sup>. However, technological advances accompanying widespread production of methanotrophic SCP could improve economic prospects for microalgae cultivation, potentially through innovative approaches that involve co-culturing methanotrophs with algae<sup>43,44</sup>. Additional environmental benefits can be achieved if methanotrophic SCP were to replace soybean in animal feeds, but this would require further cost reductions<sup>18</sup>.

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 total global demand for fishmeal. A reduction in demand for fishmeal would likely lower prices, potentially increasing the demand for fishmeal in other sectors, namely pet food or agricultural feeds<sup>38</sup>. However, methanotrophs are also a promising replacement for fishmeal in other such sectors<sup>13</sup>, and may also see a corresponding price reduction as technologies mature. Furthermore, expanding methanotrophic production to secondary markets such as bioplastic production could serve to further incentivize methane capture. Overall, reducing methane emissions and over-harvesting of marine resources are highly

complex problems, but methanotrophic SCP are promising as one part of a suite of necessary interventions for sustainable food production.

# Methods

#### Data

Wastewater Treatment Data We use data from the US Environmental Protection Agency (EPA)'s publicly available Clean Watershed Needs Survey (CWNS) 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 methods<sup>45</sup>, 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 sfc of biogas produced per 100 gallons of wastewater processed<sup>46</sup> and assuming 60% methane content in biogas, a conservative estimate for anaerobic digestors<sup>47</sup>. See Supplementary Methods for further detail.

**Landfill Data** For landfill direct emissions data, we use EPA's publicly available Facilities Level Information on GreenHouse gases Tool (FLIGHT)<sup>21</sup> for 2019 methane emissions from the following sectors: municipal landfills, industrial landfills and solid waste combustion. For flaring data, we used EPA's Landfill Methane Outreach Program (LMOP) from August 2020<sup>22</sup>. See Supplementary Methods for further detail.

Natural Gas and Petroleum Data For natural gas and petroleum direct emissions data we also used the EPA FLIGHT database<sup>21</sup>, downloading all 2019 methane emissions for the Petroleum and Natural Gas Systems sector, including all subheadings. For flaring data, we used Visible Infrared Imaging Radiometer Suite (VIIRS) data from 2019<sup>23</sup>. See Supplementary Methods for further detail.

#### Techno-economic Model

This analysis models a methanotroph production system consisting of the following costs components: annualized capital costs, annualized operations and maintenance, methanotroph nutrient requirements (ammonia, phosphorus), water, labor, and electricity demand for all equipment and processes. We include the cost of methane cleanup (\$/ton CH4) as well. While additional micronutrients are required for microbial growth (e.g. trace metals), we consider these to be minor costs and are not included in the scope of the current analysis (see Supplementary Note 3). We establish 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 (ton SCP produced/ton substrate consumed), cell density (grams SCP/L), and specific growth rate (day<sup>-1</sup>) determine how much biomass can be produced in a reactor for a given period of time (see Supplementary Equations (S1) and (S2)). We use these parameters to determine methanotroph production rate for our baseline levelized cost calculations. Using the stoichiometry in Equation (1) to describe methanotrophic growth<sup>14</sup>, we calculate baseline microbial yields for each compound required for growth: methane, oxygen and nitrogen (in units of N as ammonia). For phosphorus, we assume 2% of biomass by weight (Table 2)<sup>47</sup>.

$$CH_4 + 1.5O_2 + 0.10NH_3 \rightarrow 0.10C_5H_7O_2N + 0.5CO_2 + 1.8H_2O + 643kJHeat$$
 (1)

For cell density in the bioreactor, microbial growth rate (day<sup>-1</sup>) and heat production (kJ/g SCP), we surveyed the literature to identify representative values for industrial methanotrhopic growth (Table 2). From these, we calculate methane utilization rate and the size of the bioreactor needed for a given source size. See Supplementary Methods for further detail.

#### Capital Costs

We model a methanotroph production system with the following equipment: methane and air compressors, growth bioreactor, dewatering centrifuge, and biomass dryer (see Figure 1). We first determine a literature baseline unit capital cost value based on reported costs and capacity. For the bioreactor, this literature baseline value is then scaled to the size established for each methane source scenario described in Table 1. We assume all equipment costs except the bioreactor have constant unit capital cost, to represent increasing unit number of the equipment operating in parallel. We use 500 m<sup>3</sup> as a benchmark for the largest bioreactor size feasible in our model. This is representative of the largest industrial aerated, stirred-tank bioreactors in operation<sup>28</sup>. For bioreactors smaller than 500 m<sup>3</sup>, we apply a scaling relationship based on total bioreactor volume described in Equation (2). For bioreactors 500 m<sup>3</sup> or greater, we used the unit capital cost of a 500 m<sup>3</sup> reactor as a model for multiple

**Table 2.** Baseline methanotroph properties: growth rate, substrate yields, bioreactor cell density, calculated methane utilization rate and heat production. Yield is the amount of methanotrophic SCP produced per input of a given substrate, and here unless a different input is specified, refers to the yield on methane. Oxygen and ammonia yields are derived from stoichiometry in Equation (1) and phosphorus yield is based on an assumption of 2% phosphorus in cell biomass<sup>47</sup>. Yield and growth rate vary across different methanotrophic species<sup>48</sup>. Baseline values in this analysis are representative values from methanotrophic industrial production<sup>14,17</sup>, but species selection may further optimize production rates. Units for methane utilization rate are in terms of tons CH<sub>4</sub> per m<sup>3</sup> of reactor volume per day.

Parameter	Units	Baseline Value
Growth Rate	g SCP/g SCP - day	4 <sup>14,27</sup>
Yield	g SCP/g CH <sub>4</sub>	$0.7^{14}$
Oxygen yield	g SCP/g O <sub>2</sub>	$0.2^{14}$
Ammonia yield	g SCP/g NH <sub>3</sub>	$6.6^{14}$
Phosphorus yield	g SCP/ g P	153 <sup>47</sup>
Cell Density	g/L	$30^{17}$
Methane Utilization Rate	tons $CH_4/m^3$ - d	0.14
Heat Production	kJ/g SCP	5514

reactor operating in parallel. For the bioreactor scaling factor n, we use 0.7, a mid-value of reported and calculated scaling factors in the literature<sup>28,49</sup>. 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  $^{17,50}$ . For air and methane compression, we use continuous centrifugal air compressor described in Levett  $^{17}$ . For air compression, we calculate unit capital cost using reported air flow rate, capital costs and electricity usage for a 52.8 MW compressor (Table S3). To establish the literature baseline unit capital cost for methane compression, we use the same compressor specifications but scaled capital cost for the reduced methane flow rate reported in Levett et al. using the size scaling exponent for air compression (n = 0.34) $^{51}$ . We assume a power rating of 3.6 MW for the reported methane flow rate, based on modeling in Aspen Plus.

Pressurized gases and media enter the continuous airlift methanotrophic bioreactor. Heat is removed via cooling jacket and coils included in bioreactor capital cost. Biomass from the bioreactor is dewatered in a biomass centrifuge, reducing the water content to 35%<sup>17</sup>. Biomass is then dried in a continuous rotary drum dryer that further reduces moisture content to 10%<sup>17</sup>.

All costs were adjusted to 2020 US dollars using annual average Consumer Price Index for all urban consumers as reported by the US Bureau of Labor Statistics<sup>52</sup>. To calculate levelized capital cost, we use a weighted average cost of capital (WACC) of 10%, representative of a new technology<sup>53</sup>. We assume infrastructure lifetime of 20 years<sup>17</sup> (calculations in Supplementary Methods). Cost of operations and maintenance of equipment was set at 10% of total capital cost per year<sup>17</sup>.

#### Electricity Costs

To calculate electricity costs, we consider the power demand of individual equipment needed for each stage methanotrophic biomass production: gas compression (methane and air), growth reactor, dewatering and drying. We used reported power demand in Levett<sup>17</sup> and equipment capacity for each unit process to determine electricity cost in \$2020 per ton SCP. The electricity needed for heat removal from the growth reactor is calculated using the heat production rate for methanotrophs (see Equation (3))<sup>14</sup> divided by coefficient of performance, or COP (heat energy removed per electricity input). For price of electricity, we use \$0.10/kWh, representative of commercial prices<sup>54</sup>. This is a conservative assumption, as landfills and wastewater treatment plants may have access to industrial prices for electricity (averaging around \$0.07/kWh in the US<sup>54</sup>). 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.

$$Heat Production Rate = \Delta_c H_{MET} * \frac{1}{Y} * \mu * \rho * V$$
(3)

```
268 Where
269 \Delta_c H_{met} is metabolic heat production (kJ/g CH<sub>4</sub>)
270 Y is cell yield (g SCP/g CH<sub>4</sub>)
271 \mu is growth rate (day<sup>-1</sup>)
272 \rho is cell density (g SCP/L)
273 V is reactor size (liters)
```

#### Methane Cleanup

We assume all stranded methane in this analysis requires cleaning to remove contaminants before use as a methanotroph feedstock. As methanotrophs metabolize and assimilate CO<sub>2</sub> into their biomass<sup>55</sup>, cleanup costs will be lower than those required for injected biomethane into the natural gas grid<sup>56</sup>. Because of the different levels of treatment required to clean and upgrade bio/landfill/natural gas, we calculate the cost of methane cleanup separately from the equipment costs associated with methanotrophic biomass production (bioreactor, gas compression systems, post-processing). We surveyed the literature to calculate the cost of methane cleanup per ton CH<sub>4</sub>, and considered systems designed for desulfurization and siloxane removal<sup>57–59</sup>, and included the annualized capital cost, variable and/or electricity costs (additional detail in Supplementary Methods). Depending on the extent of contaminant removal, cleanup costs reported in the literature ranged from \$5/ton CH<sub>4</sub> to \$128/ton CH<sub>4</sub>. We use a mid value of \$50/ton CH<sub>4</sub> as our baseline value, representative of the cost of upgrading a wastewater treatment facility to include an adsorption unit for biogas cleanup<sup>58</sup>. For the grid baseline scenario, we remove the cost of methane cleanup.

#### **Macronutrient Costs**

Microorganisms require substrates that serve as sources of macro- and micro- nutrients 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 assume 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 US Energy Information Administration industrial price for US natural gas averaged over the last 10 years (\$234/ton CH<sub>4</sub>)<sup>60</sup>.

We use urea and diammonium phosphate as sources for nitrogen and phosphorus. We calculate baseline substrate costs using yield values (mol SCP/mol substrate) and assume a phosphorus content in biomass of 2% (Table 2)<sup>47</sup>. For baseline prices we use the 10-year average from 2010 to 2020 reported by the World Bank Commodity Price Index, converted to \$2020 for urea ( $CH_4N_2O$ ) and diammonium phosphate ( $(NH_4)_2HPO_4$ ), respectively<sup>37</sup>. This results in baseline costs of \$550/ton NH<sub>3</sub> and \$1,790/ton phosphorus, or \$83/ton SCP for ammonia and \$36/ton SCP for phosphorus, using yield assumptions in Table 2. For oxygen supply, we use delivery of compressed air to the bioreactor. Thus, the cost of oxygen is accounted for in the capital cost of the air compressor and associated electricity cost (described above), rather than a direct input to our substrate cost calculation. In Supplementary methods, we compare compressed air delivery with the cost of an air separation unit and purchasing commercial O<sub>2</sub>.

#### Labor Costs

To determine the labor demand in worker-hrs/ton SCP for a given plant size, we used values reported in the literature for bioplastic production of polyhydroxybutyrate (PHB) using methanotrophs. Specific stains 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 steps<sup>61</sup> (Supplementary Note 3 discusses the differences between PHB and SCP cultivation). Criddle et al. (2014) report the number of personnel needed for the three stages of production (fermentation, extraction and packaging) for plant capacities ranging from 500 tons PHB/year to 100,000 tons PHB/year<sup>33</sup>. 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-hrs needed per ton of PHB produced in a given plant size. We directly used these values as the worker-hrs 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 likely 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 and colleagues<sup>33,62</sup>. Labor calculations are discussed more fully in Supplementary Methods.

# Water and Land Requirements

We determine a water requirement of 33.3 tons H<sub>2</sub>O/ton SCP using the cell density of 30 g/L. For our system, we assume that 90% of the water requirement is met by capturing water from dewatering centrifuges and recycling it to the main growth reactor(s)<sup>17</sup>. The remaining water requirement is met through purchasing water at \$1/m<sup>3</sup>, a relatively high value. This could be representative of the cost of desalinated water<sup>63</sup> or building a pipeline to transport water to a remote location. Due to the

comparatively low cost of water in our results, we combine this cost with that of macro-nutrients nitrogen and phosphorus, referring to the cost of all three as "nutrient media."

In our analysis, we do not add additional costs for purchase of land. For 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 apply a utilization factor of 80% to our baseline scenario to account for plant downtime for maintenance and repair. This means 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 last 10 years is 90%<sup>64</sup>. To account for 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 single cell protein 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 which are fixed per ton of CH<sub>4</sub> treated, we assumed 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 full formulation, see Supplementary Methods.

Total Levelized Cost = Annualized Capital Cost + Annualized O&M + Electricity Cost + Substrate Cost + Labor Cost (4)

We calculated facility size (tons  $CH_4/day$ ) 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 compare methanotroph production cost to the price of fishmeal, represented by the average price over the last ten years, \$1,612/ton (10-year low and high are \$1,351/ton and \$1,944/ton, respectively)<sup>37</sup>.

# Supply Curve

To make the supply curve depicted in Figure 4, we generated a master dataset with the total annualized cost of methanotroph production, under baseline assumptions, for each methane source included in Figure 2. We sorted methane sources in order of increasing production cost, and calculated the cumulative SCP production rate (tons/day) as higher cost locations are incrementally added to total production. We use the 10-year average price of fishmeal (\$1,600) for comparison, although see Supplementary Figure S2 for historical fishmeal prices from the last four decades<sup>37</sup>. Fishmeal production rate of 15,900 tons/day is from 2018<sup>2</sup>.

#### Sensitivity Analysis

The sensitivity analysis individually varies each input parameter from its baseline to low and high values, representing the feasible range of current values reflected in the existing literature, and calculates 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 Table 3. We considered techno-economic analyses where methanotrophic biomass itself was the final product as well as those where methanotrophs were being for polyhydroxyalkanoate production. In the latter scenario, capital costs were adjusted to include only the processes necessary for methanotrophic biomass production (See Supplementary Methods). For weighted average cost of capital (WACC), used in converting capital cost into levelized cost, we use a low value of 8% and high value of 12%, representing modest variation in potential investor confidence in this emerging technology<sup>53</sup>. We vary COP from baseline of 3<sup>17</sup> to a low of 2 and a high value of 6. Microbial yield low and high endpoints are based on experimentally reported values in the scientific literature<sup>48</sup>.

For ammonia and phosphorus, we maintained the baseline described above, using the average 10-year price. We use the lowest and highest annual average price during this period as low and high values, respectively. For cost of electricity, we use a low value of \$0.06/kWh, which is a low-end price for industrial consumers in the United States<sup>54</sup>. For the high value, we used \$0.14/kWh, just above average residential prices in the US<sup>54</sup> (1-year average industrial, residential and commercial electricity costs are reported in Supplementary Methods).

Our baseline value for labor requirement (1 worker-hr/ton) is based literature for polyhydroxybutyrate (PHB) production. For the low value, we reduce 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 only reach 50% of the total cell dry mass (i.e. bioreactors producing 500 tons/year of PHB can produce 1,000 tons/year of SCP)<sup>62</sup>. For the high value input,

we calculated the plant size needed in order to completely meet market demand for fishmeal based on the supply curve in Figure 4, applying the labor cost scaling relationship described in the Supplementary Methods to determine the associated labor requirement. This high input value of 6 worker-hrs/ton SCP corresponds to a source size of 24 tons CH<sub>4</sub>/ day, and produces methanotrophic biomass at \$1,972/ton under baseline assumptions at a landfill or oil and gas facility.

**Table 3.** Baseline, low and high inputs for sensitivity analysis. Baseline scenario is used in the main analysis. Low and high values represent the range reported in the literature for current technology or prices. Substrate cost baseline values reflect the 10-year price average. Low and high substrate costs are the annual average low and high values within the same time period<sup>37</sup>. Baseline electricity costs reflect typical commercial prices, low value and high value represent industrial and residential prices, respectively<sup>54</sup>. Unit capital cost, labor requirements, methane clean, microbial yield, and scaling factor reflect mid, high and low values reported in the literature. Unit capital cost baseline value is the result of this analysis.

Input Parameter	Units	Low	Baseline	High
Ammonia price <sup>37</sup>	\$/ton NH <sub>3</sub>	400	550	810
Phosphorus price <sup>37</sup>	\$/ton P	1,315	1,790	2,300
COP	kW/kW(e)	2	3 <sup>17</sup>	6
Unit capital cost	\$/ton SCP/day	407,000 <sup>65</sup>	507,000	$1,300,000^{18}$
Cost of electricity <sup>54</sup>	\$/kWh	0.06	0.10	0.14
WACC (discount rate)	%	8%	10%	12%
Labor requirement	worker-hrs/ton SCP	0.5	$1^{17,33}$	4.5
CH <sub>4</sub> cleanup	\$/ton CH <sub>4</sub>	5 <sup>57</sup>	50 <sup>58</sup>	130 <sup>59</sup>
Microbial yield	tons SCP/ton CH <sub>4</sub>	$0.3^{48}$	$0.7^{14,17}$	$0.9^{48}$
Scaling Factor (n)		$0.6^{49}$	0.7	$0.8^{28}$
O&M percent	%	5	$10^{17,65}$	$15^{18}$
Utilization Factor	%	0.7	0.8	0.9

# Data availability

376

378

379

380

382

370

371

372

373

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), 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

<sup>384</sup> Code supporting the current study is available at: https://github.com/sahar-elabbadi/methane-to-protein

# 385 Acknowledgements

This study was funded by the Stanford Center for Innovation in Global Health, and the Stanford Natural Gas Initiative, an industry consortium that supports independent research at Stanford University. We thank Bob Hickey for input on industrial bioreactor scaling.

# 389 References

- 1. Mbow, C. et al. Food Security. In Climate Change and Land: an IPCC special report on climate change, desertification, land degradation, sustainable land management, food security, and greenhouse gas fluxes in terrestrial ecosystems, 437–550 (Intergovernmental Panel on Climate Change, 2019).
- 2. FAO. GLOBEFISH Highlights January 2020 ISSUE, with Jan. Sep. 2019 Statistics (FAO, 2020).
- 3. Edwards, P., Zhang, W., Belton, B. & Little, D. C. Misunderstandings, myths and mantras in aquaculture: Its contribution to world food supplies has been systematically over reported. *Mar. Policy* **106**, 103547, DOI: 10.1016/j.marpol.2019.103547 (2019).
- 4. Willett, W. *et al.* Food in the anthropocene: The EAT–Lancet commission on healthy diets from sustainable food systems. The Lancet 393, 447–492, DOI: 10.1016/S0140-6736(18)31788-4 (2019). Publisher: Elsevier.
- 5. Naylor, R. L. *et al.* Feeding aquaculture in an era of finite resources. *Proc. Natl. Acad. Sci.* **106**, 15103–15110, DOI: 10.1073/pnas.0905235106 (2009).
- 6. Shah, M. R. *et al.* Microalgae in aquafeeds for a sustainable aquaculture industry. *J. Appl. Phycol.* **30**, 197–213, DOI: 10.1007/s10811-017-1234-z (2018).
- 7. Naylor, R. L. *et al.* A 20-year retrospective review of global aquaculture. *Nature* **591**, 551–563, DOI: 10.1038/s41586-021-03308-6 (2021).
- 8. Ortuño Crespo, G. & Dunn, D. C. A review of the impacts of fisheries on open-ocean ecosystems. *ICES J. Mar. Sci.* **74**, 2283–2297, DOI: 10.1093/icesjms/fsx084 (2017).
- Malcorps, W. *et al.* The sustainability conundrum of fishmeal substitution by plant ingredients in shrimp feeds. *Sustainability* 11, 1212, DOI: 10.3390/su11041212 (2019).
- 10. Boucher, O., Friedlingstein, P., Collins, B. & Shine, K. P. The indirect global warming potential and global temperature change potential due to methane oxidation. *Environ. Res. Lett.* **4**, 044007, DOI: 10.1088/1748-9326/4/4/044007 (2009).
- 11. US Environmental Protection Agency. Inventory of U.S. Greenhouse Gas Emissions and Sinks: 1990-2018. Tech. Rep. 430-R-20-002, United States Environmental Protection Agency (2020).
- 12. Clomburg, J. M., Crumbley, A. M. & Gonzalez, R. Industrial biomanufacturing: The future of chemical production. Science 355, eaag0804, DOI: 10.1126/science.aag0804 (2017).
- 415 **13.** Øverland, M., Tauson, A.-H., Shearer, K. & Skrede, A. Evaluation of methane-utilising bacteria products as feed ingredients for monogastric animals. *Arch. Animal Nutr.* **64**, 171–189, DOI: 10.1080/17450391003691534 (2010).
- 14. El Abbadi, S. H. & Criddle, C. S. Engineering the dark food chain. *Environ. Sci. & Technol.* 53, 2273–2287, DOI: 10.1021/acs.est.8b04038 (2019).
- 15. Calysta. Our Products. Date Accessed: 2021-06-26.
- **16.** Unibio. Protein. Date Accessed: 2021-06-26.
- 17. Levett, I. *et al.* Techno-economic assessment of poly-3-hydroxybutyrate (PHB) production from methane—the case for thermophilic bioprocessing. *J. Environ. Chem. Eng.* **4**, 3724–3733, DOI: 10.1016/j.jece.2016.07.033 (2016).
- 18. Pikaar, I. *et al.* Decoupling livestock from land use through industrial feed production pathways. *Environ. Sci. & Technol.* 52, 7351–7359, DOI: 10.1021/acs.est.8b00216 (2018).
- Matassa, S. *et al.* Upcycling of biowaste carbon and nutrients in line with consumer confidence: the "full gas" route to single cell protein. *Green Chem.* 22, 4912–4929, DOI: 10.1039/D0GC01382J (2020). Publisher: The Royal Society of Chemistry.
- Verbeeck, K., Vrieze, J. D., Pikaar, I., Verstraete, W. & Rabaey, K. Assessing the potential for up-cycling recovered resources from anaerobic digestion through microbial protein production. *Microb. Biotechnol.* DOI: https://doi.org/10.1111/1751-7915.13600 (2020). \_eprint: https://onlinelibrary.wiley.com/doi/pdf/10.1111/1751-7915.13600.
- 21. Environmental Protection Agency. Facilities Level Information on GreenHouse gases Tool (2019). Date Accessed: 2020-12-20.
- **22.** Environmental Protection Agency. Landfill Gas Energy Project Data and Landfill Technical Data (2020). Date Accessed: 2020-11-04.
- 495 **23.** Earth Observation Group. Global Gas Flaring Observed From Space (2019). Date Accessed: 2020-11-25.

- 496 24. Environmental Protection Agency. Clean Watershed Needs Survey (CWNS) 2004 Report and Data (2004). Date Accessed: 2020-12-23.
- 438 **25.** Environmental Protection Agency. Clean Watershed Needs Survey (CWNS) 2008 Report and Data (2008). Date Accessed: 2020-12-23.
- **26.** Environmental Protection Agency. Clean Watershed Needs Survey (CWNS) 2012 Report and Data (2012). Date Accessed: 2020-12-23.
- 27. Xiao, J. & VanBriesen, J. M. Expanded thermodynamic true yield prediction model: adjustments and limitations. Biodegradation 19, 99–127, DOI: 10.1007/s10532-007-9119-5 (2008).
- **28.** Humbird, D., Davis, R. & McMillan, J. Aeration costs in stirred-tank and bubble column bioreactors. *Biochem. Eng. J.* **127**, 161–166, DOI: 10.1016/j.bej.2017.08.006 (2017).
- Shen, Y., Linville, J. L., Urgun-Demirtas, M., Mintz, M. M. & Snyder, S. W. An overview of biogas production and utilization at full-scale wastewater treatment plants (WWTPs) in the United States: Challenges and opportunities towards energy-neutral WWTPs. *Renew. Sustain. Energy Rev.* **50**, 346–362, DOI: 10.1016/j.rser.2015.04.129 (2015).
- 30. Cho, J. H. & Kim, I. H. Fish meal nutritive value. *J. Animal Physiol. Animal Nutr.* 95, 685–692, DOI: https://doi.org/10.1111/j.1439-0396.2010.01109.x (2011).
- 451 **31.** US Energy Information Administration. Electric Power Monthly U.S. Energy Information Administration (EIA) (2021).
  452 Date Accessed: 2021-07-05.
- <sup>453</sup> **32.** Petersen, L. A., Villadsen, J., Jørgensen, S. B. & Gernaey, K. V. Mixing and mass transfer in a pilot scale U-loop bioreactor. <sup>454</sup> *Biotechnol. Bioeng.* **114**, 344–354, DOI: 10.1002/bit.26084 (2017).
- 455
   456
   456
   457
   458
   459
   450
   450
   451
   452
   453
   454
   455
   456
   457
   457
   458
   459
   450
   450
   451
   452
   453
   454
   455
   457
   457
   458
   459
   450
   450
   451
   452
   453
   454
   457
   457
   458
   459
   450
   450
   451
   452
   453
   454
   457
   450
   450
   451
   452
   453
   454
   457
   450
   451
   452
   453
   454
   454
   457
   450
   451
   452
   452
   453
   454
   452
   453
   454
   454
   455
   454
   454
   455
   456
   457
   457
   458
   450
   450
   450
   450
   450
   450
   450
   450
   450
   450
   450
   450
   450
   450
   450
   450
   450
   450
   450
   450
   450
   450
   450
   450
   450
   450
   450
   450
   450
   450
   450
   450
   450
   450
   450
   450
   450
   450
   450
   450
   450
   450
- Cusworth, D. H. *et al.* Using remote sensing to detect, validate, and quantify methane emissions from California solid waste operations. *Environ. Res. Lett.* **15**, 054012, DOI: 10.1088/1748-9326/ab7b99 (2020).
- 35. Siegert, M. *et al.* Comparison of Nonprecious Metal Cathode Materials for Methane Production by Electromethanogenesis. *ACS Sustain. Chem. & Eng.* **2**, 910–917, DOI: 10.1021/sc400520x (2014).
- **36.** Kim, A. H. *et al.* More than a fertilizer: wastewater-derived struvite as a high value, sustainable fire retardant. *Green Chem.* **23**, 4510–4523, DOI: 10.1039/D1GC00826A (2021).
- 464 **37.** The World Bank. Commodity Prices Annual prices. Tech. Rep., The World Bank (2021).
- Jannathulla, R. *et al.* Fishmeal availability in the scenarios of climate change: Inevitability of fishmeal replacement in aquafeeds and approaches for the utilization of plant protein sources. *Aquac. Res.* **50**, 3493–3506, DOI: https://doi.org/10.1111/are.14324 (2019).
- 39. Pelletier, N., Klinger, D. H., Sims, N. A., Yoshioka, J.-R. & Kittinger, J. N. Nutritional Attributes, Substitutability,
   Scalability, and Environmental Intensity of an Illustrative Subset of Current and Future Protein Sources for Aquaculture
   Feeds: Joint Consideration of Potential Synergies and Trade-offs. *Environ. Sci. & Technol.* 52, 5532–5544, DOI:
   10.1021/acs.est.7b05468 (2018).
- 472 **40.** Cumberlege, T., Blenkinsopp, T. & Clark, J. Assessment of environmental footprint of FeedKind protein. Tech. Rep., The Carbon Trust (2016). Date Accessed: 2021-06-26.
- 41. Kok, B. *et al.* Fish as feed: Using economic allocation to quantify the Fish In: Fish Out ratio of major fed aquaculture species. *Aquaculture* **528**, 735474, DOI: 10.1016/j.aquaculture.2020.735474 (2020).
- 476 **42.** Klinger, D. & Naylor, R. Searching for Solutions in Aquaculture: Charting a Sustainable Course. *Annu. Rev. Environ.*477 *Resour.* **37**, 247–276, DOI: 10.1146/annurev-environ-021111-161531 (2012).
- 43. van der Ha, D., Bundervoet, B., Verstraete, W. & Boon, N. A sustainable, carbon neutral methane oxidation by a partnership of methane oxidizing communities and microalgae. *Water Res.* 45, 2845–2854, DOI: 10.1016/j.watres.2011.03.005 (2011).
- 480 44. Rasouli, Z., Valverde-Pérez, B., D'Este, M., De Francisci, D. & Angelidaki, I. Nutrient recovery from industrial wastewater as single cell protein by a co-culture of green microalgae and methanotrophs. *Biochem. Eng. J.* 134, 129–135, DOI: 10.1016/j.bej.2018.03.010 (2018).
- 483 **45.** Gingerich, D. B. & Mauter, M. S. Air emission reduction benefits of biogas electricity generation at municipal wastewater treatment plants. *Environ. Sci. & Technol.* **52**, 1633–1643, DOI: 10.1021/acs.est.7b04649 (2018).

- 46. Parker, N., Williams, R., Dominguez-Faus, R. & Scheitrum, D. Renewable natural gas in California: An assessment of the technical and economic potential. *Energy Policy* **111**, 235–245, DOI: 10.1016/j.enpol.2017.09.034 (2017).
- 487 **47.** Rittmann, B. E. & McCarty, P. L. *Environmental Biotechnology: Principles and Applications* (McGraw-Hill Education, 2020), 2 edn.
- 48. Meraz, J. L., Dubrawski, K. L., El Abbadi, S. H., Choo, K.-H. & Criddle, C. S. Membrane and fluid contactors for safe and efficient methane delivery in methanotrophic bioreactors. *J. Environ. Eng.* **146**, 03120006, DOI: 10.1061/(ASCE)EE. 1943-7870.0001703 (2020).
- 492 **49.** Vo, T. T. Q., Wall, D. M., Ring, D., Rajendran, K. & Murphy, J. D. Techno-economic analysis of biogas upgrading via amine scrubber, carbon capture and ex-situ methanation. *Appl. Energy* **212**, 1191–1202, DOI: 10.1016/j.apenergy.2017.12.099 (2018).
- 495 50. Wendlandt, K.-D., Jechorek, M., Helm, J. & Stottmeister, U. Producing poly-3-hydroxybutyrate with a high molecular mass from methane. J. Biotechnol. 86, 127–133, DOI: 10.1016/S0168-1656(00)00408-9 (2001).
- <sup>497</sup> **51.** Garrett, D. E. Chemical Engineering Economics (Van Nostrand Reinhold, New York, 1989).
- <sup>498</sup> **52.** U.S. Bureau of Labor Statistics. CPI for all urban consumers (CPI-U). Tech. Rep., U.S. Bureau of Labor Statistics (2020).
- 499 53. New Constructs. Weighted average cost of capital (WACC): explanation and examples. Tech. Rep. (2016).
- 500 **54.** U.S. Energy Information Administration. Retail sales of electricity to ultimate customers (Annual). Tech. Rep., U.S. Energy Information Administration (2020).
- 55. Yang, S. *et al.* Global molecular analyses of methane metabolism in methanotrophic Alphaproteobacterium, *Methylosinus trichosporium* OB3b. Part II. Metabolomics and 13C-labeling study. *Front. Microbiol.* **4**, DOI: 10.3389/fmicb.2013.00070 (2013).
- 56. Czyrnek-Delêtre, M. M., Ahern, E. P. & Murphy, J. D. Is small-scale upgrading of landfill gas to biomethane for use as a cellulosic transport biofuel economically viable? *Biofuels, Bioprod. Biorefining* **10**, 139–149, DOI: 10.1002/bbb.1627 (2016).
- 508 **57.** Tansel, B. & Surita, S. C. Managing siloxanes in biogas-to-energy facilities: Economic comparison of pre- vs post-combustion practices. *Waste Manag.* **96**, 121–127, DOI: 10.1016/j.wasman.2019.07.019 (2019).
- 58. Aguilera, P. G. & Gutiérrez Ortiz, F. J. Techno-economic assessment of biogas plant upgrading by adsorption of hydrogen sulfide on treated sewage–sludge. *Energy Convers. Manag.* **126**, 411–420, DOI: 10.1016/j.enconman.2016.08.005 (2016).
- 59. Pipatmanomai, S., Kaewluan, S. & Vitidsant, T. Economic assessment of biogas-to-electricity generation system with H<sub>2</sub>S removal by activated carbon in small pig farm. *Appl. Energy* **86**, 669–674, DOI: 10.1016/j.apenergy.2008.07.007 (2009).
- 60. US Energy Information Administration. United States Natural Gas Industrial Price (Dollars per Thousand Cubic Feet)
   (2020). Date Accessed: 2021-07-05.
- 61. Pieja, A. J., Rostkowski, K. H. & Criddle, C. S. Distribution and selection of Poly-3-hydroxybutyrate production capacity in methanotrophic proteobacteria. *Microb. Ecol.* 62, 564–573, DOI: 10.1007/s00248-011-9873-0 (2011).
- 62. Rostkowski, K. H., Pfluger, A. R. & Criddle, C. S. Stoichiometry and kinetics of the PHB-producing Type II methanotrophs

  Methylosinus trichosporium OB3b and Methylocystis parvus OBBP. Bioresour. Technol. 132, 71–77, DOI: 10.1016/j.

  biortech.2012.12.129 (2013).
- 63. Ghaffour, N., Missimer, T. M. & Amy, G. L. Technical review and evaluation of the economics of water desalination:

  Current and future challenges for better water supply sustainability. *Desalination* 309, 197–207, DOI: 10.1016/j.desal. 2012.10.015 (2013).
- 64. US Energy Information Administration. U.S. refinery utilization and capacity (2019). Date Accessed: 2021-02-22.
- 65. Listewnik, H.-F., Wendlandt, K.-D., Jechorek, M. & Mirschel, G. Process design for the microbial synthesis of poly-β-hydroxybutyrate (PHB) from natural gas. *Eng. Life Sci.* **7**, 278–282, DOI: 10.1002/elsc.200620193 (2007).