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Uses and benefits of algae as a nutritional supplement for honey bees

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Honey bees are essential agricultural pollinators that are threatened by various interacting stressors, posing risks to beekeeping industries and human food security. Malnutrition is a major factor underlying managed bee colony losses that can be countered by feeding artificial diets, which aim to deliver essential macro- and micronutrients. Current bee nutritional supplements show room for improvement and require resources that compete with human food production. Algae and microalgae in particular have been gaining traction in the literature as alternative feed sources and nutritional supplements for livestock, including honey bees. Herein, we review the current literature and categorize the effects of algae supplementation on honey bee colony productivity as well as effects on individual bee physiology and health. In general, we conclude that algae biomass appears to be suitable for use as a bee feed additive and as a source of health-stimulating natural products. Additionally, we suggest research areas that could improve the development of sustainable algae-based nutrition supplements for honey bees.

KEYWORDS

microalgae, *Apis mellifera*, spirulina, *Chlorella*, pollen substitute, biomass, sustainable diet, pathogen resistance

Introduction

Honey bees (*Apis mellifera*) play a major economic role in the modern world and are a vital aspect of human food security (Khalifa et al., 2021). Managed bee colonies contribute to 35% of global food production, while their services and products are a multibillion-dollar global industry, providing economic benefits to agricultural, food production, and medicinal sectors (Klein et al., 2006; van der Sluijs and Vaage, 2016). However, honey bees are currently facing high colony mortality rates, habitat loss, and climate change, which threaten their populations and the services they provide to humans (Potts et al., 2010). As such, modern beekeeping is challenged to overcome factors such as changing weather patterns, lack of forage, reduced forage nutritional diversity, parasites, pathogens, and pesticides (Potts et al., 2010; Vaudo et al., 2015; Dolezal and Toth, 2018). Managed bee colonies require constant human inputs in the form of disease control and supplemental nutrition. Artificial diets and feed supplements from a variety of plant and animal products show mixed results in their capacity to support colony growth and productivity (Noordyke and Ellis, 2021; Paray et al., 2021; Tsuruda et al., 2021). The current research focused on artificial diets indicates that there are opportunities for improving bee feed to serve the growing demands of beekeepers who have become increasingly reliant on supplemental nutrition (Ricigliano et al., 2022b). Importantly, given the challenges of feeding the world's human population, sustainable ingredients that do not compete with human food production are excellent candidates to address this crucial need of modern beekeeping. Algae biomass shows promise as an alternative feed source as well as a source of health-modulating natural products for honey bees (Ricigliano and Simone-Finstrom, 2020). Due to their nutrition content, sustainability, and amenability to trait manipulation, algae could potentially be developed into novel nutritional supplements that can bolster bee populations in the face of current stressors (Oswald et al., 1967; Stengel et al., 2011; Vigani et al., 2015; Piwowar and Harasym, 2020; Ricigliano, 2020; Xing et al., 2021). This review first provides an overview of honey bee nutrition and nutritional supplementation, then examines current literature concerning the effects of algae and associated products on honey bee colony productivity and bee physiology.

Honey bees' nutritional requirements and artificial diets

Honey bees' nutritional requirements

Nutritional needs for honey bees are provided primarily by floral nectar and pollen. Nectar acts as the main carbohydrate source for bees (Wright et al., 2018; Tsuruda et al., 2021). Pollen is the primary source of macronutrients for honey bees, providing protein, essential amino acids, and lipids (Brodschneider and Crailsheim, 2010; Wright et al., 2018; Tsuruda et al., 2021). At the colony level, pollen consumption is dependent on the size of the colony, with some estimates of pollen consumption approaching 57 kg per year to provide sufficient protein for a colony of 20,000 individuals (Tsuruda et al., 2021). Honey bee colonies function as a "common stomach" in which nutritional deficiencies stimulate foraging workers to gather nectar and pollen (Schmickl and Karsai, 2017; Wright et al., 2018; Tsuruda et al., 2021). Once stored in the hive, pollen is consumed by nurse bees who digest and assimilate nutrition, producing a protein- and lipid-rich glandular secretions (i.e., jelly proteins) that are used to rear larvae and feed other bees (Crailsheim et al., 1992). Since honey bees cannot synthesize arginine, histidine, lysine, tryptophan, phenylalanine, methionine, threonine, leucine, isoleucine, and valine, these amino acids must be present in the diet (De Groot, 1953). Amino acids supplied in free form appear to shorten bee lifespan and are therefore best delivered in the form of crude protein from pollen or feed with an amino acid profile that recapitulates jelly proteins (Wright et al., 2018). Lipids can comprise as little as 2% to as much as 60% of the weight of the pollen (Roulston and Cane, 2000; Roulston et al., 2000). Essential fatty acids, such as linoleic acid, γ-linoleic α-linoleic acid, and palmitic acid, are important lipid constituents that can comprise up to 80% of the lipid content (Wright et al., 2018). Phytosterols from pollen are also essential for physiological functions in bees (Chakrabarti et al., 2020). The health benefits of dietary lipids are impacted by the ratios in which they occur relative to other nutrients. While typically balanced in pollen, a 10:1 protein to lipid content ratio and a low linoleic acid: α-linoleic acid ratio is optimal for bee health, with higher ratios and concentrations of certain fatty acids causing increased mortality (Ma et al., 2015; Wright et al., 2018; Tsuruda et al., 2021). Honey bees must maintain proper nutrition due to interacting stressors, notably parasites and pathogens (Dolezal and Toth, 2018). This complex of nutritional and pathogenic stressors can impair immune function, retard development, and reduce bee lifespans, which can quickly destroy entire colonies (Dolezal and Toth, 2018; Ramsey et al., 2019). Nutritional stresses can also lower disease resistance by impacting the diversity and function of essential gut microbiota (Castelli et al., 2020). Five species clusters of bacteria consisting of *Snodgrassella alvi*, *Gilliamella apicola*, two species of *Lactobacillus sp*., and *Bifidobacterium sp*. are considered core to the honey bee gut microbiota (Raymann and Moran, 2018). These bacteria influence honey bee nutrient utilization, immunity, development, hormone signaling, and behavior (Engel et al., 2012; Moran, 2015; Raymann and Moran, 2018). While some physiological effects in correlation with microbiota populations have been reported, the complex interplay among other environmental factors necessitates further studies to understand the full impact of nutrition on bee gut microbiota (Engel et al., 2016; Raymann and Moran, 2018).

Current artificial diets for honey bees

Beekeepers feed managed colonies artificial "pollen substitute" diets to compensate for periods of inadequate pollen forage and to increase the size of colonies before their use in pollination services (Johansson and Johansson, 1977; Ricigliano et al., 2022b). A variety of commercial feed products and diet formulations employ different components as partial or full replacement for natural pollen. Artificial diets incorporate protein-rich ingredients such as soy, yeast, pea, milk proteins, or eggs (Paray et al., 2021). Some diets may also include a fraction of bee-collected pollen, which can increase consumption and brood rearing (Ricigliano et al., 2022a). Generally, bees have a strong preference for natural pollen from diverse sources and will consume pollen before consuming artificial diets (Herbert et al., 1980; Requier et al., 2015; Wright et al., 2018). Therefore, feed is typically given during dearth periods such as during winter (Manning, 2018; Tsuruda et al., 2021). Soy tends to be used the most often due to the availability and cheap cost of the product, however, soy contains anti-nutritional factors such as protease inhibitors and toxic sugars (Ricigliano, 2020; Noordyke and Ellis, 2021; Paray et al., 2021). Additionally, soy-based products may be unpalatable having been reported as being consumed at lower levels than soy-free substitutes and accumulating at higher levels among hive debris compared to natural pollen diets (Ellis and Hayes, 2009; Saffari et al., 2010; Noordyke and Ellis, 2021). Common animal products such as egg and whey proteins have shown some benefits as a protein substitute; however, their efficiency varies and there are environmental concerns with these protein sources (Eshel et al., 2014; Paray et al., 2021). The impact of feed ingredients varies due to factors such as environment, season, laboratory vs. field conditions, and formulation (Manning, 2018; Tsuruda et al., 2021). As such, an all-encompassing artificial diet that meets the nutritional requirements of bees under diverse management conditions has yet to be developed (Manning, 2018; Wright et al., 2018; Noordyke and Ellis, 2021).

Algae as an animal feed source

Algae are a rich source of carbohydrates, proteins, lipids, vitamins, minerals, and amino acids (Yaakob et al., 2014; Singh et al., 2017; Khan et al., 2018). Macroalgae can be seen with the naked eye, whereas microalgae require the use of an optical device to see individual organisms (Suganya et al., 2016; Pereira, 2021). There are over 40,000 algae species from two domains that are broadly divided into prokaryotic unicellular cyanobacteria microalgae (blue-green algae), and eukaryotic unicellular/multicellular algae (green algae, red algae, and brown algae) (Yaakob et al., 2014; Suganya et al., 2016; Khan et al., 2018; Pereira, 2021; Ullmann and Grimm, 2021). Microalgae are particularly efficient at producing large quantities of complete proteins, polyunsaturated fatty acids (PUFAS), and other important nutritional biomolecules (Yaakob et al., 2014; Singh et al., 2017; Ullmann and Grimm, 2021). Delivered either as a whole cell powder or as extracts, algae and algae products are welldocumented to have multiple beneficial effects on livestock, which are evident in mammals, birds, and fish (Yaakob et al., 2014; Suganya et al., 2016; Andrade et al., 2018; Khan et al., 2018; Araújo et al., 2021). Nutrition is also important to the ability of an organism to resist pathogens and their associated diseases. A wide variety of biomolecules occurring in algae have shown promise for supporting disease resistance in animals (Yaakob et al., 2014; Suganya et al., 2016; Singh et al., 2017; Andrade et al., 2018; Khan et al., 2018). Algae are a rich source of carotenoids such as astaxanthin as well as polyunsaturated fatty acids such as docosahexaenoic acid, both of which modulate animal stress responses (Yaakob et al., 2014; Suganya et al., 2016; Singh et al., 2017; Khan et al., 2018). In general, research indicates that algal biomass and extracts can bolster immune function, general stress resistance, and survival in livestock and aquaculture stocks (Madeira et al., 2017; Saadaoui et al., 2021; Valente et al., 2021). Though the benefits of microalgae to insects are understudied compared to other livestock, the available literature indicates benefits to insect health, production, growth, and reproduction (Truzzi et al., 2020). In recent decades, microalgae production techniques have been developed to allow for the efficient production of different species (Singh and Sharma, 2012; Araújo et al., 2021; Ullmann and Grimm, 2021). Today the most commonly produced microalgae are the green algae in the division Chlorophyta, and blue-green cyanobacteria in the genus *Arthrospira*, commonly called spirulina (Andrade et al., 2018; Araújo et al., 2021). Modern technologies enable the mass culturing of microalgae under a variety of conditions for biomass production and wastewater treatment, thus enabling different industries to use algae as a sustainable resource (Singh and Sharma, 2012; Suganya et al., 2016; Khan et al., 2018; Wollmann et al., 2019; Piwowar and Harasym, 2020; Araújo et al., 2021).

Literature review: Effects of algae on honey bees

Literature review methodology and overall results

Literature related to the effects of algae on honey bees was obtained *via* database searches between May 2019 and August 2022. Databases used included Google Scholar, EBSCOhost, Scopus, and the University of Nebraska Lincoln's database search engine. Key terms used in the searches included "algae", "bees", "honey bees", "apis", "*chlorella*", and "spirulina". Search results were characterized based on bee colony productivity and health, individual bee physiology, and disease resistance, algae species used, and delivery methods (Supplementary Table 1). A total of 35 pieces of literature were identified, which comprised journal articles, agricultural publications, university publications, patents, and consortiums. A total of 24 literature pieces were used in this review. The earliest publications relating to algae and honey bees were published in 1976 and 1977. There were no publications in the 1980s, one publication in the 1990s, and three publications in the 2000s. There were sixteen publications in the 2010s and 13 publications between January 2020 and August 2022. Most of the literature was published in Eastern Europe with eleven publications from Moldova, four from Russia, three from the Czech Republic, and two from Ukraine. Five publications were from the United States, two from China, and one each from France, India, Turkey, Saudi Arabia, Egypt, Sweden, Germany, and Italy. A total of 24 different algae varieties were reported. Algae species varied across microalgae and macroalgae; however, most of the literature is focused on microalgae. The algae spanned different genera with the majority belonging to *Arthrospira* (spirulina) and *Chlorella*. The green microalgae *Oocystis borgei*

Snow and *Scenedesmus quadricauda* each were reported twice in the literature. All other named species were reported only once. The remaining literature did not provide species names and only provided the genus (Supplementary Table 1). The cyanobacterium *Arthrospira platensis* (spirulina) was used in most publications followed by green microalgae belonging to the genus *Chlorella*. Algae delivery methods varied in the reviewed literature and were administered to colonies or caged bees as whole-cell powders or extracts. Formulations included pastes, powders, patties, candies, or liquid supplements (Supplementary Table 1).

Honey bee colony performance and productivity

The available literature indicates that when fed with algae products, honey bees appear to benefit at the colony level in their fecundity, brood rearing, colony population size, and production of honey and wax. This was reflected across multiple countries and environments.

Queen fecundity

The addition of microalgae biomass or supplements in nutritional sources increased egg-laying rates in honey bee queens. The egg laying rate increased in hives supplemented with *Oocystis borgei Snow* when compared to controls fed sugar paste. Queens from hives supplemented with *Oocystis borgei Snow* experienced an 8.3% increase in 24-h egg laying rate compared to controls, and a 6.6% increase relative to hives fed sugar paste with added spirulina (Cebatori et al., 2017). Queens from hives fed sugar paste containing *Scenedesmus quadricauda* exhibited a 7.8% increase in egg laying compared to controls fed sugar paste, and a 6.2% increase relative to hives fed spirulina paste (Cebatori et al., 2016). Hives fed sugar syrup supplemented with *Chlorella vulgaris* had an increase in queen egg laying rates when compared to controls fed honey or sugar syrup. Experimental hives showed a 6.4% increase in 24-h egg laying rate relative to unfed controls, and a 12.7% increase compared to controls fed sugar syrup (Eremia et al., 2013). Queens from hives fed sugar syrup with spirulina extracts had a 44.7% higher 24-h egg laying rate relative to hives fed only sugar (Toderaş et al., 2014). Queens from hives fed algae pastes containing *Scenedesmus quadricauda*, *Scenedesmus apiculatus*, and *Oocystis borgei Snow* expressed an increased 24-h egg laying rate by 8.8% compared to controls fed honey and powdered sugar and an increase of 7.1% relative to hives fed pastes containing spirulina (Toderaş et al., 2017). The reported increases in queen fecundity are in agreement with reports of increased capped brood and adult bee populations (Brood production and viability and Colony population sizes sections). Queens from algae-fed hives fed algae-produced mated queens that were 7.3% heavier than control hives fed honey. Interestingly, bees-fed algae suspensions produced significantly larger queen cells compared to controls (Eremia et al., 2012).

Brood production and viability

Algae supplementation has been shown to increase honey bee colony brood production. The five articles reporting increased queen fecundity in hives supplemented with algae (Queen fecundity section) reported correlations in increased capped brood numbers and brood viability. Hives fed with sugar paste containing *Oocystis borgei Snow* exhibited increased capped brood and brood viability compared to hives fed sugar paste or sugar paste supplemented with spirulina. Experimental hives showed a significant increase of 8% in capped brood and an increase of 1.5% in brood viability relative to controls. Experimental hives also experienced an in an increase of 6.5% in capped brood compared to hives-fed paste containing spirulina (Cebatori et al., 2017). Colonies fed a paste of *Scenedesmus quadricauda* experienced a significant increase in capped brood and brood viability. *Scenedesmus*-fed hives exhibited an increase of 7.7% in capped brood and 1.1% in brood viability compared to controls (Cebatori et al., 2016). Hives fed sugar syrup containing *Chlorella vulgaris* showed a significant increase in capped brood compared to unfed hives and controls fed sugar syrup (Eremia et al., 2013). Hives fed sugar syrup containing spirulina extracts were observed to have 44.9% more brood than control hives fed sugar, and brood was on average 14% more viable than brood from control hives (Toderaş et al., 2014). Hives fed sugar pastes supplemented with *Scenedesmus quadricauda, Scenedesmus apiculatus,* and *Oocystis borgei Snow* had significantly more brood, averaging at 8.3% more than control and averaging 6.8% more brood than control hives fed sugar paste with spirulina. The same study reported that hives supplemented with *Spirulina platensis*, *Scenedesmus quadricauda*, and *Scenedesmus apiculatus* had a significant increase in brood viability, averaging 1.4% higher than control hives (Toderaş et al., 2017). This increase in total brood and brood viability correlated with increased colony sizes in hives-fed algae supplements (Colony population sizes section). Similar increases in brood production in algae-fed hives were reported in other studies. Hives fed a paste of *Chlorella sorokiniana* showed a significant increase in spring brood rearing when compared to controls fed sugar. Algae-supplemented hives experienced a two-fold increase in capped brood area when compared to control hives. *Chlorella* spp. applied directly as a paste led to a 44.4% increase in brood area compared to hives fed with *Chlorella*-supplemented candies (Jehlík et al., 2019). Colonies fed during dearth periods with patties or honey-containing spirulina were observed to have a 54.2% increase in total brood area relative to unfed controls (Kumar et al., 2013). Bee colonies infested with Varroa destructor mites and treated with algae filtrates had higher levels of capped brood compared to controls. Colonies treated with filtrates of *Chroococcus minutus*, *Calothrix parietina*, and *Gloeocapsa giganteus* featured an average increase of 45.3% more brood compared to untreated controls. Colonies treated with filtrates of *Chroococcus minutus* and *Gloeocapsa giganteus* had an 8.6% and 3.8% respective increase in brood area compared to controls treated with oxalic acid (Hassan and Mahmoud, 2006).

Colony population sizes

In agreement with increased queen fecundity (Queen fecundity section) and brood production (Brood production and viability section), honey bee colonies treated with algae-based supplements had increased colony population sizes. Colonies fed paste of *Oocystis borgei Snow* exhibited a 7.1 and 8.1% increase in population size relative to controls fed sugar paste or paste supplemented with spirulina, respectively (Cebatori et al., 2017). Colonies fed paste containing *Scenedesmus quadricauda* had a 9.3 and 8.3% increase in colony population size compared to hives fed sugar paste or supplemented with spirulina, respectively (Cebatori et al., 2016). Hives supplemented with *Chlorella vulgaris* exhibited a 10.7% increase in population size relative to unfed controls and hives fed sugar syrup (Eremia et al., 2013). Hives fed spirulina extracts featured on average 17.5% larger populations than control hives (Toderaş et al., 2014). Hives-fed paste containing *Scenedesmus quadricauda*, *Scenedesmus apiculatus*, and *Oocystis borgei Snow* featured an average population increase of 8.2% compared to controls, and a 7.2% increase compared to hives fed spirulina paste (Toderaş et al., 2017).

Honey and wax production

Overall, the reviewed literature reported increased honey production in hives supplemented with algae products. Hives-fed paste containing *Oocystis borgei Snow* featured a 38.7% increase in honey production compared to controls (Cebatori et al., 2017). Similarly, hives fed extracts of *Scenedesmus quadricauda* showed a 27.6% increase in honey production relative to controls (Cebatori et al., 2016). Hives fed pastes of *Spirulina plantensis*, *Scenedesmus quadricauda*, *Scenedesmus apiculatus*, and *Oocystis borgei Snow* increased in honey production by up to 28.8% compared to controls fed honey and powdered sugar (Toderaş et al., 2017). Hives supplemented with *Chlorella vulgaris* exhibited a 17.2% increase in honey production relative to control hives (Eremia et al., 2013). Honey production increased by up to 69.1% in hives supplemented with suspensions of *Chroococcus minutus*, *Calothrix parietina*, and *Gloeocapsa giganteus* relative to controls (Hassan and Mahmoud, 2006). Honey production increased by 12.1% in hives fed *Chlorella* in sugar syrup suspension (Eremia et al., 2021). Hives fed a 10% spirulina solution featured increased antioxidant activities and fatty acid content in the honey produced compared to honey from control hives (Guldas et al., 2022). While this is a promising finding with implications for human nutrition, further studies are necessary to ensure that honey produced under these conditions is suitable for human consumption. Nevertheless, spirulina is typically produced for use in human food products and supplements. Wax production was also observed to increase when hives were supplemented with algae biomass. Hives-fed sugar syrup containing spirulina extracts featured 39.7% higher wax production compared to controls fed sugar (Toderaş et al., 2014). Total wax production increased on average by 20.8% when hives were fed algae pastes of *Spirulina plantensis*, *Scenedesmus quadricauda*, *Scenedesmus apiculatus*, and *Oocystis borgei Snow* compared to controls (Toderaş et al., 2017). Colonies fed pastes of *Oocystis borgei Snow* exhibited a 27.9% increase in wax production compared to controls (Cebatori et al., 2017). Experimental hives supplemented with sugar paste containing *Scenedesmus quadricauda* increased wax production by 11.5% compared to control hives (Cebatori et al., 2016).

Disease resistance and hygenic behavior

The literature indicates that algae-based feed supplements and extracts applied either directly to colonies or to pathogens and pests have the potential to inhibit disease growth or infestations when compared to different controls. Experimental hives supplemented with *Oocystis borgei Snow* exhibited increased hygienic behavior, an indicator of disease resistance potential, when compared to the control hives (Cebatori et al., 2017). Similarly, hives fed extracts of *Scenedesmus quadricauda* showed increased hygienic behavior when compared to controls (Cebatori et al., 2016). Experimental hives supplemented with *Spirulina platensis*, *Scenedesmus quadricauda*, *Scenedesmus apiculatus*, and *Oocystis borgei Snow* had a 2.7% increase in hygienic behavior to the control hives fed with honey and powdered sugar (Toderaş et al., 2017). Four studies reported similar observations of disease resistance when pathogens or their honey bee hosts were directly or indirectly exposed to algae products. Hives infested with *Varroa destructor* mites and fed algae had lower infestation rates compared to untreated control hives and hives treated with oxalic acid. The average mite infestation rate was 2.7% when fed isolates of *Chroococcus minutus*, *Calothrix parietina*, and *Gloeocapsa giganteus* compared to untreated control hives with an infestation rate of 26.26% and oxalic acid-treated hives with an infestation rate of 2.9% (Hassan and Mahmoud, 2006). Honey bees infected with *Nosema ceranae* and fed *Porphyridium marinum* and *Porphyridium purpureum* extracts had lower parasite loads compared to controls. Experimental bees expressed up to a 30% decrease in *Nosema* loads relative to unfed controls and at half the *Nosema* load of the individuals treated with fumagillin (Roussel et al., 2015). Extracts of

Chlorella sorokiniana had anti-microbial effects on plate cultures of *Paeniebacillius larvae* bacteria (Vránová, 2017), and similar antimicrobial effects were observed when applying *Chlorella vulgaris* extracts to spores and vegetative state cultures of *Paenibacillus larvae* bacteria (Dostálková et al., 2021).

Impacts of algae supplementation on honey bee physiology

The literature reports a number of different physiological impacts on individual bees fed algae-based nutritional supplements. Thorax and fat body masses of bees fed spirulina paste matched that of pollen-fed bees (Ricigliano and Simone-Finstrom, 2020). Similarly, bees fed spirulina had head protein concentrations that matched pollen-fed bees but were lower than bees fed a commercial pollen substitute (Ricigliano and Simone-Finstrom, 2020). In a different study, spirulina-fed workers met or exceed the body masses of pollen-fed workers across two different genetic lines of honey bees. Furthermore, bees supplemented with spirulina had a significant increase in mRNA expression levels of the nutritional storage lipoprotein Vitellogenin (Ricigliano et al., 2021). In another study, bees fed sugar pastes of *Chlorella vulgaris* or spirulina exhibited similar growth characteristics as bees fed natural pollen (Ricigliano et al., 2022a). Bees fed algae expressed higher mRNA levels of *Vitellogenin* compared to sugar-fed controls, whereas *Chlorella* fed-bees featured *Vitellogenin* mRNA levels trending higher, but not statistically different than pollen-fed bees. Furthermore, bees fed both algae types featured higher levels of antioxidant gene transcripts and spirulina-fed bees expressed higher transcript levels of *shock protein 90* (Ricigliano et al., 2022a). Increased body and tissue masses and nutrient levels were observed in bees fed *Chlorella sorokiniana* relative to bees from control hives fed sugar. Average midgut mass increased 1.5-fold in bees from algae-fed hives relative to control hives and bees had larger hypopharyngeal glands when fed *Chlorella sorokiniana*. In the same study adult bees fed *Chlorella sorokiniana* featured a 1.7-fold higher fat body lipid content and a 5.6-fold increase in larval fat body lipids. Furthermore, bees fed *Chlorella sorokiniana* showed increased concentrations of lineic acid relative to control bees whereas fat body glycogen concentrations decreased 3.8- and 1.5-fold in workers and larvae, respectively. Finally, bees fed *Chlorella sorokiniana* had significantly higher levels of Vitellogenin mRNA transcripts and lower levels of TOR and InR2 mRNA transcripts relative to controls (Jehlík et al., 2019). This study is in agreement with a similar study that tested the impacts of *Chlorella sorokiniana.* Bees fed diets supplemented with 0.5–10% *Chlorella sorokiniana* exhibited increased hypopharyngeal gland development, higher amino acid content, and higher levels of Vitellogenin mRNA expression (Jang et al., 2022).

Effects of algae on honey bee microbiota

Gut microbiota changes were observed in honey bee colonies sprayed with a commercial supplement containing seaweed extracts. Bees sprayed with a mixture of sugar syrup and seaweed extracts showed a 13% increase in gut abundance of *Bartonella spp*. after 1 month. Furthermore, the product containing seaweed extracts also led to a 6.8% decrease in gut *Bombilactobacillus spp.* which was correlated with a significant decrease in the species *Bombilactobacillus mellis*. In the same study, bees supplemented with a commercial probiotic exhibited a significantly higher abundance of total *Lactobacillaceae spp*. when compared with bees sprayed with the seaweed supplement (Alberoni et al., 2021). Bees fed spirulina were observed to have comparable levels of beneficial gut bacteria to bees fed natural pollen diets. Spirulina-fed bees had similar abundances of *Lactobacillus* as bees fed natural pollen and had higher abundances of *Lactobacillus* relative to bees fed commercial pollen substitute or sugar. Furthermore, bees fed spirulina had higher abundances of *Bifidobacterium* than bees fed pollen substitute or sugar. However, average *Bifidobacterium* abundance was higher in bees fed natural pollen relative to bees fed spirulina. Bees fed spirulina also had on average higher abundances of *Snodgrassella* relative to bees fed sugar, pollen substitute, or pollen (Ricigliano and Simone-Finstrom, 2020). Interestingly, *Cyanobacteria spp.* were observed to compromise 1.83% of the total gut microbiome of foraging bees collected during the beginning of the overwintering period (Liu et al., 2021). While not core constituents of the gut microbiome, cyanobacteria are present in “dirty” or turbid water sources that are attractive to foraging honey bees (Butler, 1940). Population changes in gut microbiota and other associated variables are still a relatively new field of study (Zheng et al., 2018). More research is necessary to understand the impacts of algae products on honey bee gut microbiota.

Mortality and toxic effects of algae on honey bees

The literature contains mixed reports pertaining to the effects of different algae species on bee mortality. Bees fed with water containing *Anabaena flos-aquae* were observed to have no difference in mortality rates compared to the controls provided distilled water (Barker, 1977). Mortality rates of bees fed *Chlorella sorokiniana* was observed to be no different from mortality rates of controls fed sugar (Jehlík et al., 2019). Bees fed spirulina were observed to have negligible mortality rates compared to pollen- and sugar-fed controls after 10 days of feeding (Ricigliano et al., 2021). In another study, bees fed spirulina had a negligible difference in mortality rates compared to controls fed sugar, pollen, or pollen substitute

(Ricigliano and Simone-Finstrom, 2020). In some instances, algae supplementation increased survival. Honey bees infected with the gut pathogen *Nosema ceranae* had increased survival rates when fed polysaccharides extracted from the algae *Porphyridium marinum* relative to untreated and fumagillin-treated controls (Roussel et al., 2015). Colonies fed sugar syrup containing *Chlorella* in the fall had a 20.8% increase in overwinter survival relative to controls, and a 5.7% increase in survival compared relative to controls fed a commercial feed additive (Eremia et al., 2021). Caged bees fed sugar syrup with different concentrations of *Chlorella vulgaris* suspension had significantly lower mortality rates than bees fed only sugar syrup (Yefimenko and Odnosum, 2020). Bees fed pollen patties containing 2 or 5% *Chlorella* had the lowest mortality rate compared to other tested diets (Jang et al., 2022). Some literature indicates that algae consumption increases mortality rates and could cause detrimental physiological effects. Bees fed pollen, pollen substitute, and date paste were observed to have higher mortality rates when different concentrations of spirulina were added to the diets (Khan and Ghramh, 2022). Honey bee larvae reared under laboratory conditions and directly fed a diet containing *Chlorella vulgaris* extracts showed a significant increase in mortality relative to controls fed a standard larval diet. In the study, larvae fed *Chlorella vulgaris* extracts had an average mortality rate that was 31.3% higher than controls. Here, the authors argue that this may be due to the direct feeding of the algae to larvae instead of prior digestion from nurse bees (Dostálková et al., 2021). Bees fed sugar water containing the cyanobacterial toxin, beta-N-methylamino-L-alanine (BMAA) showed a significant increase in mortality relative to controls. In the same study, bees exposed to BMAA retained the toxins 72 h after ingestion and spread toxins *via* trophallaxis. Furthermore, the brains of bees exposed to BMAA showed a 1.8-fold increase in reactive oxygen species, had significantly higher levels of intracellular Ca^{2+} ions within the neuron cells, and had higher levels of spontaneous activity. Finally, bees exposed to BMAA also expressed a significant decrease in operant conditioning learning to odor stimuli after 5 days (Okle et al., 2013).

Conclusion

Overall, current research indicates that algae biomass and extracts can provide numerous benefits to honey bees. Incorporating algae feeds and supplements into existing beekeeping practices have the potential to sustainably improve honey bee colony productivity and health. Additional studies and reproduction of previous results are necessary to build a complete profile of the ideal parameters for feed composition and delivery to bee colonies. Future research should focus on large-scale colony-feeding experiments using feed compositions that showed promise in laboratory and or small-scale field experiments. Characterization of diverse algae species for their nutritional value may help identify species candidates for honey bee diet development. Fractionization and metabolomic characterization of algae extracts combined with laboratory bioassays may identify natural products and structural leads for bee therapeutic development. Genetic engineering techniques may enable algae strain development that could address the specific health requirements of honey bees in a changing global climate. Among the literature reviewed, all but one study focused on *Apis mellifera*. Further research could be expanded to the development of nutrition supplements for other bee species of commercial importance such as *Apis cerana* and the genus *Bombus*.

Author contributions

All authors listed have made a substantial, direct, and intellectual contribution to the work and approved it for publication.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fsufs.2022.1005058/full#supplementary-material

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