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Potential applications of lipid droplets from marine plants and microalgae in food and health

Buntora Pasaribu [a,c,d,*], Alifannursin M. Atsarak [b,c,d], Lantun P. Dewanti [e], Yuniarti MS. [a], Syawaludin A. Harahap [a], Pringgo D.K.N.Y. Putra [e], Lady A. Sriwijayanti [e], Arif S.W. Kusuma [f], Rizky Abdulah [g], Alvita Karina Putri [c], Jogi R.N. Panggabean [c,d], Yeni Mulyani [a], Neng T. Sofyana [a], Tonni A. Kurniawan [h], Yunita E. Puspitasari [i]

[a] Department of Marine Science, Faculty of Fisheries and Marine Science, Universitas Padjadjaran, Bandung, Indonesia
[b] Master of Marine Conservation Study Program, Faculty of Fisheries and Marine Science, Universitas Padjadjaran, Bandung, Indonesia
[c] Torgas Laboratory, Jatinangor 45363, Indonesia
[d] Shallow Coastal and Aquatic Research Forensic (SCARF) Laboratory, Faculty of Fishery and Marine Science, Universitas Padjadjaran, Jl. Raya Bandung-Sumedang Km. 21, Bandung, Indonesia
[e] Department of Fisheries, Faculty of Fisheries and Marine Science, Universitas Padjadjaran, Bandung, Indonesia
[f] Department of Biological Pharmacy, Faculty of Pharmacy, Universitas Padjadjaran, Bandung, Indonesia
[g] Department of Pharmacology and Clinical Pharmacy, Faculty of Pharmacy, Universitas Padjadjaran, Bandung, Indonesia
[h] Collage of Environmental and Ecology, Xiamen University, Xiamen 361102, Fujian Province, China
[i] Department of Fish Product Technology, Faculty of Fisheries and Marine Science, Universitas Brawijaya, Malang, Indonesia

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ABSTRACT

Lipid droplets serve as an essential storage energy, well known to exist in plants. Lipid droplets have been observed in seagrass, diatoms, and microalgae. The potential of lipid droplets as a food source derived from marine sources demonstrated a promising candidate for blue food sources for future applications. Moreover, there is limited information on droplet protein from marine plants, which is crucial for exploration in the food industry. We summarized the advantages of using lipid droplets and identified lipid droplets in marine plants and microalgae as alternative potential food sources for application in industry. The challenge and future direction of lipid droplet protein in the emerging food application and health benefits are discussed. The integral proteins play a crucial role in enhancing the rate of successful encapsulation and delivery. This strategy provides an interesting perspective for the implementation of lipid droplets in the food and pharmaceutical industries. Recent advances in hydrogel-based encapsulation matrices have further demonstrated the potential to stabilize lipid droplet structures within cellulose nanofiber networks and hydrocolloid scaffolds, broadening the functional scope of lipid droplet-based delivery systems.

1. Introduction

A lipid droplet is an organelle composed mainly of triacylglycerols and sterol esters surrounded by phospholipids embedded with specific proteins (Vence and Huang, 1987). As a storage energy source, lipid droplets have been found in diverse organisms and are commonly preserved in the form of carbohydrates and lipids (Murphy, 2001). Lipid droplets are unique organelles due to their hydrophobic feature and stability, which result from proteins providing steric hindrance and electronegative repulsion on their surface phospholipids. It has been reported that lipid droplets are present in primitive plant fungi, as well as in higher plants in seeds, flowers, and pollen (Murphy et al., 2001; Walther & Farese, 2009).

Lipid droplets are also widely identified in microalgae and marine plant species (Pasaribu et al., 2017b; Xu & Shanklin, 2016). The lipid droplets from diverse marine plants and microalgae were successfully identified and isolated, providing an opportunity to investigate their major integral proteins, as well as their functions and applications. Lipid droplets in microalgae are isolated from oil-rich cells that accumulate under stress conditions (Pasaribu et al., 2024). In contrast, in marine

* Corresponding author.
E-mail address: buntora.pasaribu@unpad.ac.id (B. Pasaribu).

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plants, lipid droplets are typically isolated from seeds (Pasaribu et al., 2017b). It has been reported that lipid droplets play a crucial role in storing energy to support the growth and development of microalgae (Ischebeck et al., 2020).

Lipid droplets have been extensively utilized in various food and nutraceutical products (Calahorra et al., 2018). The unique structure of lipid droplets has demonstrated potential as a component with emulsifying functions, making them suitable for use as delivery vehicles (Zheng et al., 2019). The interaction between protein materials and the phospholipid structure on the surface of lipid droplets facilitates intercellular communication, crucial for cargo delivery and signaling mechanisms (Wei et al., 2024).

Studies have shown that the membrane structure of lipid droplets offers significant advantages in stabilizing emulsions and maintaining physicochemical stability under elevated heat conditions (Nikiforidis et al., 2013). The amphipathic nature of lipid droplets and the presence of phospholipids may enhance steric and electrostatic repulsion between the oil and water phases, thereby preserving emulsion stability during food processing (Sun et al., 2023). Additionally, the size and surface structure of lipid droplets play a critical role in lipid digestion (Pan et al., 2024). It has been reported that variations in lipid droplet size impact lipid digestion, potentially leading to inefficient fat utilization (Yuan et al., 2025).

The structural stability of lipid droplets provides enhanced protection of bioactive components during storage and transport, which in turn influences the digestibility and absorption of specific nutrients (Şen et al., 2024). Efforts to harness lipid droplets have extended their application from food products to therapeutic technologies. However, a significant challenge in the development of effective therapeutic agents is their insolubility in water, alongside issues related to toxicity and low efficacy (Acevedo-Fani et al., 2020). The chemical structure of hydrophobic therapeutic agents often degrades upon exposure to human body fluids due to the presence of metals and enzymes, reducing their biological function (Kharat & McClements, 2019). Lipid-based carriers have been reported to be necessary to enhance the functional delivery and efficacy of therapeutic agents (Zheng et al., 2019).

The native lipid droplets that consist of central hydrophobic domains limit the wide application of food and delivery cargos (Vardar et al., 2024). The development of lipid droplets inspired researchers to fabricate engineered lipid droplets with synergistic effects and improved control of drug release and loading for food nutrients (Vardar et al., 2024). The integration of intact lipid droplets into hydrogel-forming matrices, including cellulose nanofiber networks and hydrocolloid polymer coatings, has been shown to yield structured oleogel systems with measurable rheological and thermal properties (Mert & Vilgis, 2021).

Lipid droplets in marine plants and microalgae have been extensively studied over the past decade. The diverse applications have been widely explored in biotechnology and the food sector, including use as feedstock, food supplements, biofuels, and drug delivery. In this review, we explore recent advances in lipid droplet research from marine plants and microalgae, with a particular focus on structure, composition, and potential applications. Another important aspect is the current progress in the identification of lipid droplet-associated proteins in marine plants and microalgae. In addition, the key challenges and future research perspectives of lipid droplet in marine plants and microalgae are discussed.

2. The structural composition and biogenesis of lipid droplets

Lipid droplet protein serves as an energy storage system found in a diverse range of organisms, including plants, animals, microalgae, and microbes (Huang, 2018). The size of lipid droplets in microalgae is influenced by nutritional status and environmental factors, with an average diameter ranging from 0.5 to 2.5 μm (Pasaribu et al., 2017a; Pasaribu et al., 2014) (Fig. 1). Briefly, lipid droplets are relatively simple organelles composed mainly of triacylglycerols and sterol esters surrounded by phospholipids with embedded proteins such as oleosin, caleosin, and steroleosin (Hanano et al., 2023; Pasaribu et al., 2016) (Fig. 2A).

Lipid droplet biogenesis is proposed to involve the initiation of TAG synthesis at the endoplasmic reticulum (ER), where two leaflets of ER membranes form a lens-like structure (Chapman et al., 2019; Guzha et al., 2023) (Fig. 3). Consequently, the mature lipid droplet (LD) detaches from the ER membrane and is released into the cytosol. It has been reported that TAG synthesis is initiated with the conversion of glycerol-3-phosphate (G3P) to phosphatidic acid (PA) via esterification with two acyl-CoA molecules through the enzymes glycerol-3-phosphate acyltransferase (GPAT) and lysophosphatidic acid acyltransferase (LPAT). Phosphatidic acid (PA) is then dephosphorylated by phosphatidic acid phosphatase (PAP) to produce diacylglycerol (DAG). Finally, DAG is catalyzed by diacylglycerol acyltransferase (DGAT) to generate TAG.

2.1. Triacylglycerols (TAGs)

A lipid droplet is mainly composed of triacylglycerols and sterol esters, with the exception of the jojoba plant, which stores wax esters (Huang, 2018). As a major component of lipid droplets, TAGs represent an important source of functionally valuable compounds in the food and pharmaceutical industries. In addition to TAGs, other minor neutral lipid components such as diacylglycerides and free fatty acids are involved in lipid homeostasis and cellular energy balance, and serve as an energy source during unfavorable conditions (Abdullah et al., 2020; Xu & Shanklin, 2016; Yang & Benning, 2018). However, analytical analysis of lipid droplets using the GC–MS approach indicated that TAGs

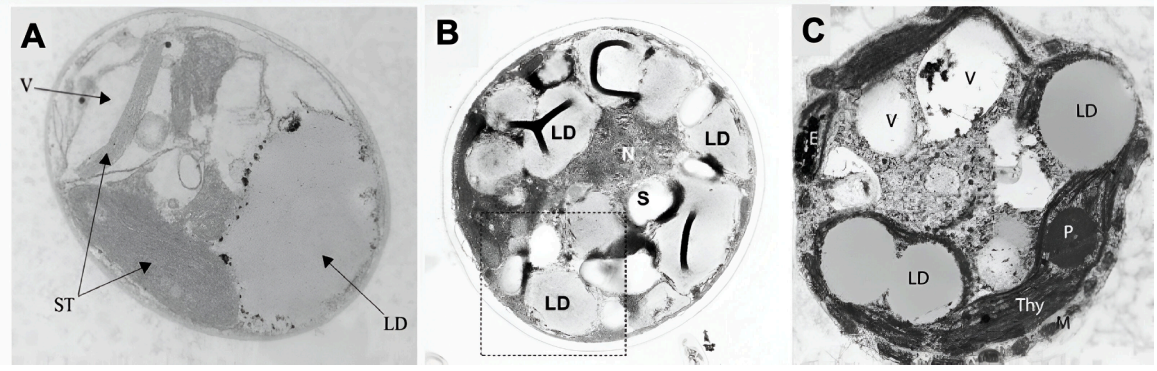

Fig. 1. Electron micrograph of lipid droplets in Microalgae.(A) Induction of lipid droplets in *Nannochloropsis spp.* cells (Dong et al., 2013) (B) Lipid droplets accumulated in intracellular of *Symbiodiniceae* clade B treated with Nitrogen deprivation (Pasaribu et al., 2016). (C) Lipid droplet located close to chloroplast in *Chlamydomonas reinhardtii* (Fan et al., 2011) LD; Lipid Droplet, ST: Stacks of thylakoids, Thy: Thylakoid membranes, S: Starch, V: Vacuole, N: Nucleus, E: Eye spot.

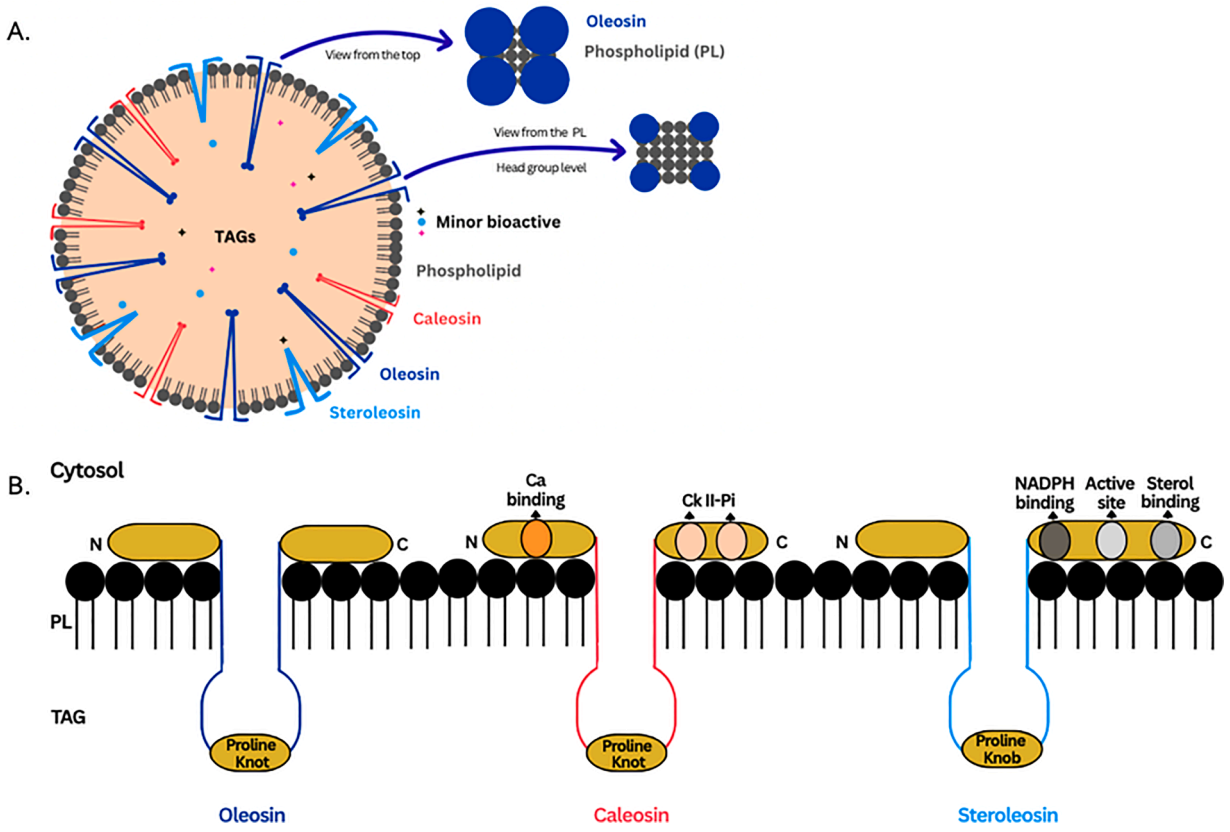

Fig. 2. Morphology and structure of lipid droplet Protein. (A) A structural model of lipid droplet morphology. (B) A structural model of lipid droplet-associated proteins located on the surface of lipid droplet. TAG: Triacylglycerol, PL: Phospholipid.

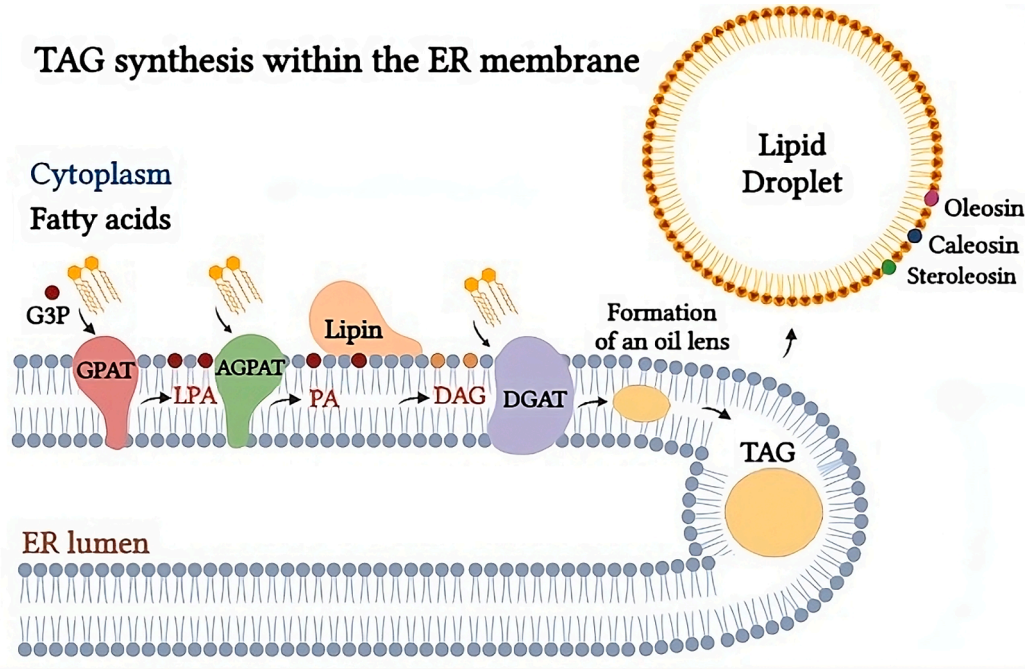

Fig. 3. Model of lipid droplet proteins formation in Plants.

are present in higher quantities, with fatty acids mainly including palmitic acid, stearic acid, and linoleic acid in angiosperm and gymnosperm seeds (Pasaribu et al., 2014; Zaaboul et al., 2018).

2.2. Proteins

Lipid droplets isolated from plants and microalgae demonstrate protein contents ranging from 0.5–8% (Xu & Shanklin, 2016). Among these proteins, oleosin is a major protein identified in seed plant lipid

droplets and has a major influence on lipid droplet size while maintaining the structural integrity of lipid droplets during desiccation (Cai et al., 2015). Three classes of lipid droplet proteins, oleosin, caleosin, and steroleosin, have been identified in plants (Pasaribu et al., 2014; Pasaribu et al., 2016; Tzen et al., 1998).

2.2.1. Oleosin

Oleosin is a class of alkaline proteins with relatively low molecular weight (10–24 kDa) that accumulate on the surface of lipid droplets in desiccation-tolerant seeds (Khanam et al., 2023). The structure of oleosin has been described as consisting of three distinct structural domains: an N-terminal amphipathic domain, a central anti-parallel β-strand domain, and a C-terminal amphipathic α-helical domain (Huang, 2018; Pasaribu et al., 2020). As a hydrophobic protein, oleosin structure is relatively conserved among plants and contains a characteristic motif known as the "proline knot" (Abell et al., 1997; Zhang et al., 2023) (Fig. 2B).

The function of the proline knot likely plays a key role in oleosin structure and targeting to lipid droplets. Two oleosin isoforms, oleosin-H and oleosin-L, have been identified and were reported to contribute to structural stability in sesame seeds (Pasaribu et al., 2014). In addition, P-oleosin is found in pollen grains (Jiang et al., 2007; Pasaribu et al., 2017), and a distinct class of oleosin-like proteins termed oleo-pollenin has been identified in the tapetum and external surfaces of pollen grains (Pasaribu et al., 2020).

To date, oleosin has been shown to play a crucial role in seed stability during germination and post-germination stages (Shao et al., 2019) and is involved in lipid droplet biogenesis. Double mutations in ole1 and ole2 resulted in defective seed germination in Arabidopsis, demonstrating the importance of oleosin in the germination process (Shimada et al., 2018). Oleosin also contributes to maintaining the stability of lipid droplet size and diameter (D'Andrea, 2016). Knockdown of oleosin results in the fusion of lipid droplets in rice and soybean (Schmidt & Herman, 2008; Wu et al., 2010). Similarly, single mutations of ole1 or ole2 produce larger lipid droplets in mutant Arabidopsis compared with wild-type plants (Shimada et al., 2018).

2.2.2. Caleosin

Caleosin is a lipid droplet-associated protein that coexists with the more abundant oleosin in seed and pollen lipid droplets. It has been identified not only in higher plants such as *Cycas revoluta* seeds but also in evolutionarily earlier organisms including algae and fungi, suggesting a conserved biological role across taxa (Lin et al., 2012; Pasaribu et al., 2020). Structurally, caleosin consists of an N-terminal hydrophilic region containing a Ca^{2+}-binding EF-hand motif, proline knot, a central hydrophobic domain, and a C-terminal hydrophilic region (Frandsen et al., 1996; Saadat, 2023; Yamaguchi-Shinozaki et al., 1992) (Fig. 2B).

Compared with oleosin, the hydrophobic region of caleosin is shorter, a feature proposed to influence its targeting and anchoring to lipid droplets (Shen et al., 2016). These structural characteristics are closely linked to its biological functions, as caleosin has been associated with intracellular signaling pathways and the regulation of lipid droplet assembly and mobilization through phosphorylation-dependent mechanisms (Hanano et al., 2006; Poxleitner et al., 2006).

Beyond its structural and regulatory roles, emerging evidence highlights the involvement of caleosin in environmental adaptation and stress responses. For example, the expression of a novel caleosin/peroxygenase isoform (PdPXG4) was shown to facilitate adaptation to environmental contaminants, including dioxins, in date palm seedlings (Hanano et al., 2023). Similarly, the stress-responsive calcium-binding protein RD20/CLO3 interacts with the α-subunit of the heterotrimeric G-protein complex and has been implicated in regulating etiolation and leaf morphology in *Arabidopsis* (Brunetti et al., 2022). Caleosin-like proteins contribute to fungal disease-related processes, as deletion of the caleosin PXG motif was found to increase endogenous polyunsaturated fatty acid hydroperoxide accumulation and antioxidant activity while suppressing fungal development (Hanano et al., 2015).

2.2.3. Steroleosin

Steroleosin is a minor integral protein that was first identified in sesame seeds (Lin et al., 2002). Unlike oleosin and caleosin, which are anchored to lipid droplets through their central hydrophobic domains, steroleosin possesses a unique structural organization consisting of an N-terminal lipid-anchoring domain, proline knob, and a soluble sterol-binding dehydrogenase domain. This configuration enables steroleosin to localize a soluble dehydrogenase enzyme to the lipid droplet surface through its N-terminal segment (Pasaribu et al., 2016)

Steroleosin is composed of three functional regions in C terminal domain: an NADPH-binding subdomain, an active site region, and a sterol-binding subdomain (Pasaribu et al., 2016) (Fig. 2B). In addition, its N-terminal hydrophobic segment contains a proline-rich region and is organized into two amphipathic α-helices connected by an intervening hydrophobic region (Lin et al., 2002). This structural arrangement is considered essential for maintaining lipid droplet association while preserving the enzymatic activity and sterol-binding capacity of the protein. The structural diversity of steroleosin has also been demonstrated through the identification of multiple isoforms across plant species. In sesame oil bodies, two steroleosin isoforms, Steroleosin A and Steroleosin B, have been identified and shown to possess distinct sterol-binding sites (Lin & Tzen, 2004). Similarly, steroleosin proteins have been characterized in Arabidopsis, where molecular weight-based classification revealed eight distinct isoforms, including acidic H-steroleosins and alkaline L-steroleosins (Aziz et al., 2020).

Functionally, steroleosin has been associated with sterol-mediated signaling pathways through its sterol-binding dehydrogenase domain (Saleem et al., 2023). Through its enzymatic activity, steroleosin contributes to the regulation of plant growth and development by catalyzing the conversion of sterol substrates into brassinosteroids, which serve as essential hormones controlling diverse physiological processes in plants (Lin et al., 2002). Recent findings identified Steroleosin B as a direct sesamin-binding protein, uncovering a previously unrecognized function of steroleosin in lignan-mediated signaling pathways involved in the regulation of growth and developmental processes in *Arabidopsis thaliana* (Tera et al., 2019).

2.3. Phospholipids

Phospholipids form a single-layer membrane located on the surface of lipid droplets along with membrane proteins (Nikiforidis et al., 2013). These phospholipid monolayers are densely packed with hydrophobic acyl chains facing the TAG matrix and hydrophilic head groups exposed to the external environment (Abdullah et al., 2020). Phosphatidylcholine has been identified as the major phospholipid, while minor components include phosphatidylserine, phosphatidylethanolamine, and phosphatidylinositol (Zhou et al., 2019).

In sesame-derived lipid droplets, phospholipids consist of approximately 41.2% phosphatidylcholine, 15.8% phosphatidylethanolamine, 20.9% phosphatidylinositol, and 22.1% phosphatidylserine (Şen et al., 2024). Similarly, phospholipids in peanut-derived lipid droplets consist of approximately 60.8% phosphatidylcholine, 25.5% phosphatidylserine, 8.6% phosphatidylethanolamine, and 5.1% phosphatidylinositol (Zhou et al., 2019).

3. Compositional characteristics of LDs in marine plants and algae

The identification of a major integral protein is important to understand the physiological function of lipid droplets as a storage energy during the fourth metabolism. Here, we summarized the current lipid droplet proteins that have been successfully identified through complete gene-encoded lipid droplet proteins and isolated from marine plants and microalgae as a future application for sustainable and potentially

biocompatible material of lipid droplets from marine sources (Table 1). Although marine plants and microalgae represent phylogenetically diverse groups, comparative studies reveal several conserved features in their lipid droplet systems. Across these taxa, triacylglycerols (TAGs) are consistently identified as the predominant neutral lipid storage component, indicating a conserved mechanism for intracellular energy reserve. At the protein level, caleosin- and oleosin-related proteins primarily contribute to lipid droplet structure and stabilization in marine plant systems, whereas microalgae exhibit more diverse lipid droplet-associated proteins, including Stramenopile Lipid Droplet Protein (StLDP), Lipid Droplet Surface Protein (LDSP), and Seipin-mediated regulatory pathways involved in lipid droplet biogenesis and size control. In addition, lipid accumulation in microalgae is frequently stimulated under environmental stress conditions, particularly nutrient limitation, suggesting an adaptive and evolutionarily conserved response for maintaining cellular energy balance. This foundation information provides a broader understanding of lipid droplet biology in marine organisms and emphasize the considerable potential of marine plants and microalgae for applications in biotechnology, food systems, pharmaceuticals, and sustainable bioresource development.

3.1. *Symbiodiniaceae spp.*

The isolation of lipid droplets in endosymbiotic Symbiodiniaceae was conducted through complex purification techniques. First, the endosymbiotic Symbiodiniaceae were purified from the tentacles of coral example *Euphylia glabaerscens* (Pasaribu et al., 2017). The purification aimed to isolate pure endosymbiotic Symbiodiniaceae without any contamination from Host cells. The purified Endosymbiotic Symbiodiniaceae underwent the breakage process to extract the LDs from the intracellular cells. The breakage consisting of LDs was purified by using Triton x-100 detergent methods for the removal of nonspecifically associated proteins from the LDs' surface (Pasaribu et al., 2017). It was reported that the Symbiodiniaceae lipid droplet protein identified is related to Caleosin known as Symbidinium lipid droplet Protein (SLDP) (Pasaribu et al., 2017). The lipid profile of pure LDs in Endosymbiotic Symbiodiniaceae demonstrated a higher content of TAGs (triacylglycerols). The confirmation of major neutral lipid contents in LDs in Symbiodiniaceae was consistent with major LDs observed in the Land Plants, Marine Plants, and Algae (Hanano et al., 2023; Huang, 2018; Pasaribu et al., 2014; Pasaribu et al., 2017).

Table 1
Advantages and disadvantages of utilizing lipid droplet protein in drug and food delivery.

Advantages	Disadvantages	References
Bioavailability, bioaccessibility, and biocompatibility	Health concerns related to allergenic compounds in some oleosomes (e.g., peanut and hazelnut)	Chen et al., 2005; Chang, 2013; Cho et al., 2018; Gallier and Singh, 2012; Gallier et al., 2013; Ponds et al., 2002; White et al., 2006; Zuidmeer-Jongejan et al., 2014
Easy to manipulate for encapsulation	Risk of leakage and aggregation	Ashique et al., 2026; Chen et al., 2004, 2005; Mert and Vilgis, 2021; Yuan et al., 2025
Easy handling and isolation	—	Abdullah et al., 2020
Large capacity	—	Karefyllakis et al., 2017
Stability in physical and chemical conditions against external environmental stress, such as temperature and oxidation	The off-flavors associated with volatile compounds	Fisk et al., 2006; Musakhanian et al., 2022; Nikofiridis et al., 2013; Tai, Chen, Peng and Tzen, 2002

3.2. *Seagrass*

Seagrass is a submerged flowering plant that resides in shallow coastal areas. It plays a crucial role in maintaining the marine ecosystem stability, such as for carbon storage, crucial nurseries for the fish, and a source of sustenance for various marine creatures (Papenbrock & Teichberg, 2023). The identification of lipid droplet protein in Seagrass seed *T. hemprichii* was isolated through detergent Triton x-100 methods. The challenge of isolating Seagrass seed *T. hemprichii* was the lack of lipid droplets observed in the intracellular cells. However, the isolation of seagrass seed showed the triacylglycerols (TAGs) were mainly neutral lipids, which is similar to those in sesame seed lipid droplets (Pasaribu et al., 2014). The molecular biology approach to investigate the lipid droplet protein identified in Seagrass seed T. hemprichii demonstrated a full-length cDNA fragment encoding this putative oleosin, comprises 163 amino acid residues with a molecular mass of 17 kDa and was homologous to oleosin from diverse species, particularly in the central hydrophobic domain that is responsible for protein anchoring on the surface of lipid droplets (Pasaribu et al., 2017). To date, lipid droplet proteins in seagrass have not been extensively investigated, potentially due to the strong dependence of seagrass seed development and germination on environmental conditions (Soong et al., 2013). Lipid droplets appear to be present in low abundance and exhibit a dispersed distribution within seagrass seeds. Combined with the predominance of starch granules in seagrass tissues, these characteristics demonstrated substantial technical challenges for efficient lipid droplet isolation, purification, and subsequent protein characterization and downstream proteomic analyses (Pasaribu et al., 2017b). Therefore, future research should prioritize the development and optimization of methodologies to overcome these technical limitations, which may facilitate a more comprehensive understanding of lipid droplet-associated proteins and advance knowledge of lipid droplet biology in seagrass.

3.3. *Diatom*

Diatom is a unique single-cell marine algae composed of the siliceous skeleton (frustale). Diatoms are mostly found in the ocean and freshwater environments. The lipid droplets of the diatom have been successfully isolated by sucrose density centrifugation. However, the lack of neutral lipid presence in Diatom intracellular cells required the modification of environmental stress conditions. Nitrogen deprivation treatment could have a severe impact on lipid droplet accumulation in *Phaeodactylum tricornutum*. The isolation of lipid droplet fraction identified the Stramenopile Lipid Droplet Protein (StLDP) as a main surface protein on *Phaeodactylum tricornutum* lipid droplets. The confirmation of StLDP was confirmed by proteomic analysis with a short sequence in the N-terminal region ranging from 16 to 197 amino acid residues (Yoneda et al., 2018).

A mechanistically significant advance in understanding diatom lipid droplet biogenesis was recently provided by the functional characterization of Seipin in *P. tricornutum*. Le Moigne et al. (2025) demonstrated that the *P. tricornutum* Seipin homolog (PtSeipin) localizes specifically to the chloroplast endoplasmic reticulum membrane (cERM), a membrane system unique to secondary endosymbiont-derived plastids, where it co-localizes with cERM-resident DGAT enzymes responsible for the final step of TAG biosynthesis (Le Moigne et al., 2025). Knockout of PtSeipin by CRISPR/Cas9-mediated gene disruption resulted in up to a 6-fold increase in TAG content relative to wild-type under standard growth conditions, with TAG reaching up to 64% of total glycerolipid, while overexpression of PtSeipin increased lipid droplet number with smaller individual LD size. These findings establish PtSeipin as a key regulator of LD size distribution and TAG partitioning in diatoms, operating from the cERM rather than the cortical ER as in yeast and mammalian systems, an evolutionary divergence directly attributable to the secondary plastid membrane architecture unique to stramenopiles. The PtSeipin knockout

lines have been recognized as promising candidates for biofuel applications given their substantially elevated TAG content (Le Moigne et al., 2025).

3.4. *Chlorella sp*

Chlorella sp. is a unicellular photosynthetic green microalga widely distributed across marine, freshwater, and terrestrial environments (Kotrbáček et al., 2015). Due to its high protein content and abundance of essential nutrients, Chlorella biomass has attracted considerable attention as a valuable nutritional resource (Mendes et al., 2024). Among Chlorella related taxa, the marine microalga Auxenochlorella protothecoides has been shown to enhance lipid accumulation under nutrient-limited conditions, resulting in the formation of lipid droplets. Proteomic analysis of isolated lipid droplets identified a 29 kDa caleosin protein associated with the lipid droplet surface. This caleosin exhibited sequence similarity to caleosin proteins previously reported in lipid droplets of various plant species, suggesting a potentially conserved role in lipid droplet formation and stabilization across photosynthetic organisms (Lin et al., 2012; Pasaribu et al., 2014).

3.5. *Nannochloropsis sp*

Nannochloropsis is a marine microalga recognized for its high capacity to accumulate triacylglycerols (TAGs), making it an important model for lipid metabolism studies. TAG accumulation can be enhanced under environmental stress conditions, including altered light intensity, increased salinity, and nitrogen deprivation. These neutral lipids are predominantly stored within cytosolic lipid droplets. The composition and dynamics of lipid droplet-associated proteins in *Nannochloropsis* sp. have been investigated using lipid droplet isolation through homogenization and centrifugation (Vieler et al., 2012). Among the identified proteins, lipid droplet surface protein (LDSP) was proposed to contribute to lipid droplet organization. Functional evidence obtained through complementation experiments using an Arabidopsis OLEOSIN-1 mutant indicated that LDSP may influence lipid droplet morphology and size regulation (Vieler et al., 2012).

4. Potential applications of marine lipid droplets

The lipid droplet application as a natural carrier of food bioactive constituents and drug delivery has been extensively investigated in recent years, including cancer therapy, skin cream, and food emulsion from marine plants and microalgae (Fig. 4). The main advantages of utilizing lipid droplet as a carrier of food bioactive or drug delivery include: (i) size stability of lipid droplet protein as a cargo delivery of target materials, (ii) higher bioavailability, (iii) a simple self-assembled and equipped with targeting motif without required a chemical modification, (iv) better biocompatibility, (v) tolerance against various environmental stresses such as higher temperature and low pH (Deckers et al., 2003; Hou et al., 2003; Chen et al., 2005; Chiang et al., 2011; Peng et al., 2004) (Table 2).

4.1. *Applications of LDs for targeted cancer therapy*

The development of lipid droplets for targeted therapy has been extensively exploited for cancer treatment. In contrast to conventional drugs, lipid droplet technology has specific advantages for drug delivery, such as bioavailability, stability, and solubility (Maurer et al., 2013). Given the practicality of lipid droplet physical properties, a simple and effective construction by purifying the recombinant protein fused with a drug encapsulated in artificial lipid droplets could be developed for targeted therapy in cancer treatment. Chiang et al. (2018) developed an artificial lipid droplet system incorporating an anti-EGFR targeting strategy for the delivery of camptothecin (CPT). The study demonstrated strong antitumor activity in both *in vitro* and *in vivo* models, highlighting the ability of lipid droplet-based carriers to enhance targeted drug accumulation and improve therapeutic efficacy. In this case, the oleosin was carried out by fusion with the Epidermal growth factor receptor (EGFR). The Lipid droplet was constituted with matrix oils, phospholipids, and Ole-ZEGFR2. The lipid droplets were encapsulated with the hydrophobic anticancer drug, camptothecin (CPT). The formulation of designated CPT on Lipid droplet Protein showed a satisfactory antitumor effect with an efficiency exceeding 90% in treating lung cancer. These engineered lipid droplet systems improved the delivery efficiency of lipophilic anticancer agents and resulted in enhanced tumor suppression in both cellular and animal studies. The formulation demonstrated the potential of lipid droplet-based systems for integrating multifunctional components to enable controlled and targeted drug release. Therefore, this finding highlights the potential of lipid droplet-based delivery platforms as a promising strategy for next-generation cancer therapeutics.

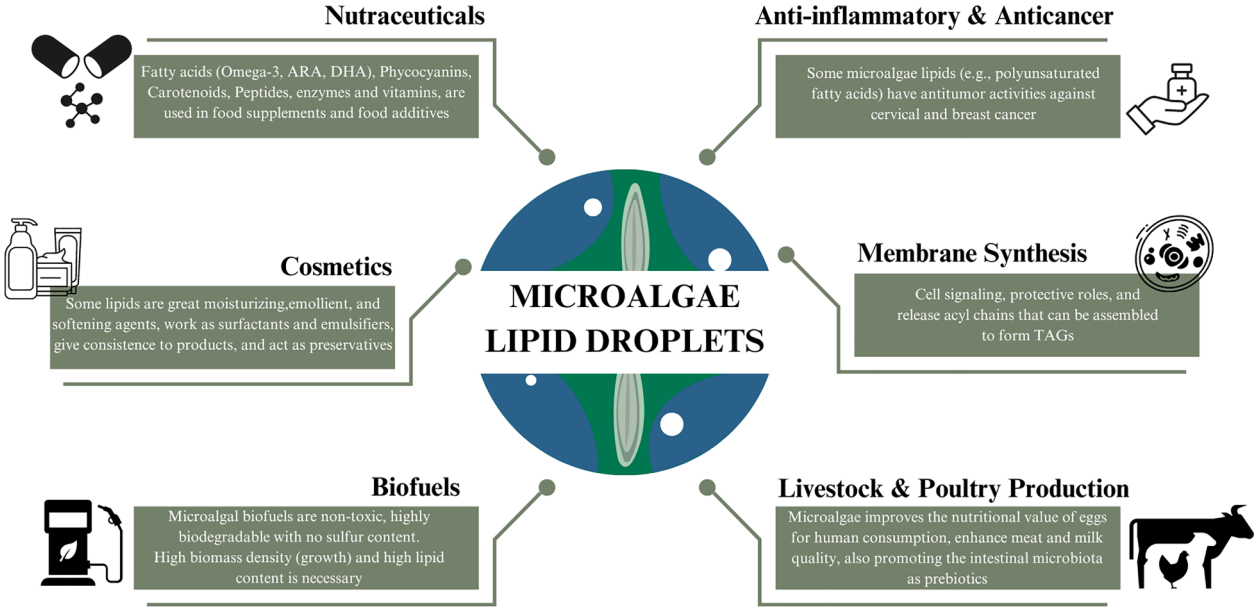

Fig. 4. Applications of Microalgae Lipid droplets.

Table 2
Summary of lipid droplet proteins applications from microalgal species.

Species	Lipid droplet (LD) proteins	Applications	References
Closterium acerosum	Oleosin	LD stability and lipid storage.	Huang et al., 2013
Auxenochlorella protothecoides	Caleosin	Biofuel production, dietary supplement, and dairy products	Patel et al., 2018; Ribeiro et al., 2017
Chlorella vulgaris		Used as a raw material for profitable biodiesel production and yoghurt.	Adepoju and Selezneva, 2024; Charuchinda et al., 2015; Zhang et al., 2014
Chlamydomonas reinhardtii	Major Lipid Droplet Protein (MLDP)	Biofuels' production	Devadasu & Subramanyam, 2021
Dunaiella salina		Nutraceutical, cosmeceutical, biodiesel	Monte et al., 2020; Weldy & Huesemann, 2007
Scenedesmus quadricauda		Grow as waste water sources, along with high biomass and lipid content make as suitable choice as biofuel feedstock	Anand & Arumugam, 2015
Chromochloris zofingiensis		Biodiesel and an alternative promising source of natural astaxanthin	Zhang et al., 2021
Lobosphaera incisa		Biotechnological platform for the production of high value pharmaceutical and nutraceutical compounds by genetic and metabolic engineer	Kugler et al., 2019
Haematococcus pluvialis	Haematococcus oil globule protein (HOGP)	Animal feed, food coloration, pharmaceutical industry, cosmetic industry.	Pujithaa et al., 2023
Nannochloropsis oceanica	Lipid Droplet Surface Protein (LDSP)	Anti-inflammatory, biodiesel	Conde et al., 2023;Ma et al., 2016
Phaeodactylum tricornutum	LD-associated protein (PtLDP1)	Food industry, anticancer, antioxidant, anti-inflammatory, neuroprotective, hepatoprotective, and hypocholesterolemic properties.	Uzlaşır et al., 2024
Fistulifera solaris	A homolog of oleosome-associated-protein 1 (DOAP1)	Biodiesel and food supplement	Liang et al., 2015
Symbiodiniceae clade C	Symbiodiniaceae lipid droplet protein (SLDP)	Energy storage	Pasaribu et al., 2024

In a parallel study, Steiner-Zitzenbacher et al. (2026) developed a DHA-rich algae oil nanoemulsion (AOE1) varied across tumor models and demonstrated distinct therapeutic profiles. The metastatic clear cell sarcoma model exhibited rapid and sustained reductions in cell viability following treatment with the algae oil nanoemulsion, where 0.08% AOE1 reduced cell viability to below 10% within 24 h, and this suppressive effect persisted throughout the 72 h observation period. In contrast, the greatest therapeutic benefit in combination treatment was identified in esophageal adenocarcinoma, where the algae oil nano-emulsion synergistically enhanced the efficacy of cisplatin, suggesting that the DHA-based nano-formulation may sensitize tumor cells to chemotherapy (Steiner-Zitzenbacher et al., 2026). Additional enhancement of chemotherapeutic responses was also observed in the breast cancer model, whereas the lung and colon cancer models exhibited more moderate or predominantly additive responses. DHA from microalgae has been reported for plays a role in preventing and suppressing cancer cell growth, including prostate, colon, lung, and breast cancers (El-Hack et al., 2019). The algal oil nanoemulsion demonstrated the efficient biocompatibility, stability, and formulation flexibility, supporting its potential application as a nanocarrier for future cancer therapy.

4.2. Application of LDs in skin cream formulations

The skin cream is applied to human skin to protect it from external substances and maintain the skin hydrated and soft. The skin cream formulations, particularly obtained from plants and biotechnology, originated, making products in which the development of an oilseed crop extraction method was necessary (Bonnet, 2018). Lipid droplets are a unique organelle with a neutral lipid reservoir and are embedded with some protein, potentially a future encapsulation system in skin products. The size of lipid droplets, topology, stability, and time-release delivery are the benefits of using lipid droplets as skin emulsion cream (Tang & Guth, 2006). Furthermore, the skin cream lipid droplet product significantly augmented the Sun Protector Factor (SPF) boosting of traditional sunscreen products (Gruber et al., 2018). *In vivo* clinical testing showed lipid droplet protein technology formulation has minimal sun filter of octylmethoxycinnamate and butylmethoxydibenzoylmethane, but high SPF values are consistent and stable over time (Bowe & Kircik, 2014).

A new type of oil-in-water emulsion was tested by using a lipid droplet designed as a carrier for sphingolipids (Marcoux et al., 2004). In this system, lipid droplet proteins are 250 nm oil globules encapsulated with a lamellar liquid crystal phase, which enables penetration of lipophilic compounds through the SC and their release within the epidermis. The result shows that the dryness of skin has a higher percentage improvement with lipid droplet protein sphingolipid compared with the water-in-oil emulsion. It appears that the designated lipid droplet sphingolipid technology offers a powerful and efficient option to replace a water-in-oil emulsion of skin cream (Marcoux et al., 2004). Lipid droplets were shown to be promising delivery agents for treating skin disease. Acidic fibroblast growth factor (FGF1) was efficiently fused with lipid droplet protein, which beneficially affected wound healing (Guo et al., 2022). 100 ng/mL Acidic fibroblast growth factor fused lipid droplet protein (OLAF) was demonstrated to increase the healing effect on the proliferation, vascular integrity, angiogenesis, and inflammation on the wound sites of rats (Guo et al., 2022).

Microalgal lipids have been reported to exhibit anti-inflammatory and antioxidant activities in addition to UV-filtering properties (Dhotre, 2026). Moreover, bioactive compounds, particularly carotenoids and tocopherols derived from algal oils, have shown the ability to neutralize UV-induced reactive oxygen species. Algal oils formulated with 6% TiO_2 (SPF 15–20) demonstrated enhanced photoprotective effects by reducing erythema and supporting post-exposure skin repair (Galani et al., 2023). Therefore, lipid droplets derived from algae might offer a promising alternative formulation for the treatment of skin diseases.

4.3. Plant-based dairy products

Lipid droplets demonstrated a potential food carrier and nutritional value that consisted of various unsaturated fatty acids and beneficial properties, in which can be substituted dairy products in food application. Lipid droplets extracted from plants and microalgae have shown potential as substitutes for milk fat globules in yogurt formulations, resulting in products with comparable lipid content (~3% w/w) while

increasing polyunsaturated fatty acid levels (Mantzouridou et al., 2019). The texture and stability of lipid droplets have widely applied in various dairy products, such as yogurt, milk, and whipping cream (Fu et al., 2020; Mishra and Mishra, 2013; Wang et al., 2022). Lipid droplets have been successfully integrated into more complex food systems. Soybean lipid droplets combined with fructooligosaccharides and probiotic strains such as Lactobacillus acidophilus and Lactobacillus plantarum have been shown to improve flavor development and textural properties during soymilk fermentation (Mishra & Mishra, 2013). Similarly, yogurt-based fermentation systems incorporating *Chlorella* spp. have been reported without significant alterations to the physicochemical properties of yogurt (Adepoju & Selezneva, 2024). A further application of pistachio lipid droplets used in plant-based milk formulations, optimized with 5 wt% sugar and 0.02 wt% vanilla to enhance sensory quality (Shakerardekani et al., 2013). Lipid droplets also contribute to the stability of foam and emulsion systems in plant-based dairy products, serving as essential structural and functional ingredients. The production of milk-based microalgae *Chlorella protothecoides* have been reported to provide high levels of antioxidants and essential fatty acids, including eicosapentaenoic acid (EPA) (Ribeiro et al., 2017). Furthermore, microalgae are recognized as important sources of long-chain polyunsaturated fatty acids, particularly EPA and docosahexaenoic acid (DHA) (Jain et al., 2023; Zhao et al., 2022). In a recent study, DHA can be effectively encapsulated within artificial lipid droplets to mimic milk fat globule structures (Tang et al., 2026). This lipid droplet–based encapsulation strategy significantly enhances the thermal protection and functional stability of DHA in dairy systems during processing. Therefore, the lipid droplet might offer significant potential for the development of dairy-mimicking and nutrient-enriched functional foods in the future.

4.4. Dietary and nutritional supplements

The nutritional properties of microalgae demonstrate excellent sources of various natural compounds (Ahmad et al., 2025). Fatty acid contents in lipid droplets of *Auxechlorella* species comprised 10% of docosahexaenoic acid (DHA), and eicosapentaenoic acid (EPA) (Pasaribu et al., 2014). Globally, the application of the product has been widely used for healthy supplement purposes, prepared in powder, pills, or pastilles. The methods were conducted for the drying of microalgae, including spray drying, drum drying, freeze-drying, solar drying, and convective drying (Neves et al., 2019). There are several algal lipid-based products that have been commercially distributed in the market, including RawRX Vegan Omega-3 capsules, Swisslife Forever Vegan Omega, Vegan Omega DHA Supplement (Ominibiotics), and Microalgae DHA Algae Oil (Green Magic by SVA) (Ahmad et al., 2025). The development of lipid droplets and algal lipid systems has been increasingly explored for applications in dietary supplements. It has been reported that algae-derived lipids containing EPA and DHA can reduce blood triglyceride levels by up to 26% (Remize et al., 2021). In addition, lipids from *Odontella aurita*, which are rich in polyunsaturated fatty acids (PUFAs) including EPA, have shown significant effects in supporting the treatment of cardiovascular diseases (Haimeur et al., 2012; Mimouni et al., 2015). These findings highlight the importance of microalgae-derived PUFAs in food and dietary supplements for health maintenance. Moreover, the consumption of dietary diacylglycerol (DAG)-enriched oils in mice has been shown to significantly improve lipid metabolism and influence both body and kidney weight (Lu et al., 2020). Algae contain a wide range of bioactive molecules that are essential for health maintenance and have been extensively used in nutraceutical applications. One of the most well-known bioactive compounds is astaxanthin, a carotenoid with strong antioxidant properties that has been reported to gastroprotective, neuroprotective, ocular-protective, anticancer, hepatoprotective effects, and to support kidney function (Yuan et al., 2011). Ota et al. (2018) reported rapid astaxanthin accumulation within lipid droplets in *Haematococcus pluvialis* within approximately 10 minutes of light exposure, highlighting its dynamic intracellular behavior under stress conditions. In pararell study, astaxanthin extracted from *Haematococcus* has been evaluated in human studies, where no toxicity was observed during an 8-week administration period (Satoh et al., 2009). This highlights the effectiveness of lipid droplets as promising strategy for nutraceutical and health supplement applications.

4.5. Hydrogel-based applications

A structurally distinct application of lipid droplets has emerged through their integration into hydrogel-forming matrices, yielding composite materials referred to as oleogels. In these systems, intact lipid droplets are embedded within a three-dimensional network formed by hydrocolloid polymers or cellulose nanofibers, which provide mechanical integrity while the lipid droplet cores retain their native TAG payload and surface protein architecture (Mert & Vilgis, 2021). The cellulose nanofiber network physically immobilizes the lipid droplets, and Fourier-transform infrared spectroscopy (FTIR) analysis has confirmed hydrogen-bonding interactions between the cellulose hydroxyl groups and the phospholipid head groups of the lipid droplet surface monolayer. Rheological analysis of such oleogel systems reveals gel-like behavior in which storage modulus G' exceeds loss modulus G'', confirming stable network formation, with thermal stability maintained up to 80°C, a property directly relevant to food processing and heat-stable delivery applications (Mert & Vilgis, 2021). An alternative approach involves the surface coating of individual lipid droplets with hydrocolloid polymers before their assembly into gel networks; this modification alters the interfacial rheology and surface charge of the lipid droplets, enabling denser gel formation at lower concentrations and providing nanoscale structural organization confirmed by small-angle neutron scattering (SANS) (Mert & Vilgis, 2021). The application of these oleogel concepts to marine microalgal lipid droplets represents a largely unexplored direction in which the unique surface proteins of marine species (StLDP, SLDP, caleosin-like proteins) could be harnessed within hydrogel scaffolds to produce delivery systems with tunable release kinetics and enhanced structural stability.

5. Challenge and future directions

The development of lipid droplet protein technology has been extensively developed in recent years. The use of lipid-droplet proteins as cargo for delivering bioactive constituents and drug compounds could facilitate an alternative paradigm in the future of the food and pharmaceutical industries. Despite substantial progress in understanding lipid droplet (LD) proteins and their emerging applications, several critical barriers continue to limit their broader applications. Future advances should prioritize challenges according to their impact on feasibility and implementation, particularly in terms of mechanistic, molecular design, stability, and scalable engineering. The most fundamental challenge is the limited mechanistic understanding of LD biogenesis, compartmentalization, and protein lipid interactions in marine plants and microalgae. Lipid droplets are dynamic organelles primarily composed of triacylglycerols and sterol esters embedded by a phospholipid monolayer and associated proteins, including oleosin, caleosin, and steroleosin. Although substantial progress has been achieved in identifying LD-associated proteins in plants and microalgae, the molecular mechanisms governing LD assembly, membrane remodeling, and environmental responsiveness are still limited. Moreover, the presence of conserved structural motifs, such as the proline knot domain among LD-associated proteins, suggests broader biological functions that may differ across eukaryotic systems. Addressing these knowledge gaps will require higher-resolution approaches capable of linking structure to function of LD in marine plants and microalgae. Advanced technologies such as cryogenic electron microscopy (Cryo-EM), integrative structural biology, and AI-assisted protein modeling platforms

including AlphaFold may provide opportunities to elucidate LD architecture and protein interactions at molecular resolution.

Current strategies rely on integrating recombinant LD-associated proteins with functional cargos to generate artificial, magnetic, or tunable LD platforms. While oleosin-based systems have demonstrated in land plants strong stabilizing capacity due to their structural characteristics, long-term physicochemical stability, thermal tolerance, storage performance, and reproducibility under manufacturing conditions remain insufficiently validated in marine plants and microalgae. These limitations become particularly important for food and pharmaceutical applications, where industrial-scale production requires robust formulation consistency. In addition, many currently explored LD platforms rely on plant-derived ingredients that may introduce allergen-related concerns, including components originating from peanut, sesame, and hazelnut sources. Consequently, identifying alternative LD proteins from marine plants and microalgae may represent a promising direction to improve stability while reducing potential safety concerns. Although LD-based encapsulation systems have demonstrated promising performance in laboratory settings, their broader implementation requires standardized evaluation of safety, biocompatibility, toxicity, storage conditions, and manufacturing reproducibility. Regulatory acceptance will likely depend not only on therapeutic performance but also on quality control, scalability, and long-term environmental and human safety assessments. Establishing standardized characterization frameworks for engineered LD formulations therefore represents an essential step toward commercialization.

Beyond food and pharmaceutical applications, marine lipid droplets also offer a promising opportunity for sustainable bioenergy development. The high triacylglycerol accumulation of marine microalgae highlights as attractive feedstocks for biodiesel and integrated biorefinery platforms. Species such as *Chlorella vulgaris, Nannochloropsis oceanica*, and *Phaeodactylum tricornutum* have demonstrated efficient conversion of inorganic carbon into neutral lipids under nutrient limitation. Recent advances further suggest that targeted engineering of LD regulatory pathways may improve lipid productivity without causing major metabolic imbalance. For example, disruption of LD biogenesis regulators has been proposed as a strategy to enhance TAG accumulation and expand biofuel feasibility. However, industrial implementation will require maintaining LD surface protein functionality throughout biomass processing, extraction, and downstream conversion. Improving protein thermostability and mechanical robustness therefore remains an important engineering target. Moreover, coupling lipid production with recovery of high-value co-products, including carotenoids and polyunsaturated fatty acids, may strengthen the economic feasibility of marine LD-based biorefinery systems. Future progress in LD research will depend not only on improving biological understanding but also on addressing engineering scalability and formulation stability. Integrating these priorities may accelerate the translation of lipid droplet technologies across food, pharmaceutical, and energy applications.

6. Conclusions

The use of lipid-droplet proteins as vehicles for delivering bioactive constituents and drug compounds could facilitate an alternative paradigm in the future of the food and pharmaceutical industries. Lipid droplet protein technology may represent a more advanced method in carrying bioactive constituents and drugs, bioactive delivery as an alternative solution to improve on existing challenges, including membrane penetrating capability, the digestive system, and bioavailability. Furthermore, the integration of lipid droplets into hydrogel-based matrices, including cellulose nanofiber networks and hydrocolloid scaffolds, provides a structural dimension that extends their utility from passive carriers into functional biomaterials with engineerable rheological properties and controlled release behavior (Mert & Vilgis, 2021). The genetic tractability of marine microalgal lipid droplet biogenesis as exemplified by the Seipin-mediated TAG amplification demonstrated in *Phaeodactylum tricornutum* positions marine lipid droplet research at the intersection of food science, pharmaceutical delivery, and bioenergy, suggesting that marine-derived engineered lipid droplet systems will play an increasingly central role in next-generation blue bioeconomy applications (Le Moigne et al., 2025).

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Declarations

Ethics approval and consent to participate

Not applicable. This study did not involve any experiments on human participants, human data or tissue, animals, or plants.

Consent for publication

Not applicable. This manuscript does not contain any individual person's data in any form.

Abbreviations

The following abbreviations are used in this manuscript:

LD	Lipid Droplet
TAG	Triacylglycerol
ER	Endoplasmic Reticulum
DGAT	Diacylglycerol Acyltransferase
SLDP	Symbiodiniaceae Lipid Droplet Protein
LDSP	Lipid Droplet Surface Protein
EGFR	Epidermal Growth Factor Receptor
CPT	Camptothecin
SPF	Sun Protector Factor

CRediT authorship contribution statement

Buntora Pasaribu: Writing – review & editing, Writing – original draft, Supervision, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Alifannursin M. Atsarak:** Writing – original draft, Formal analysis, Data curation. **Lantun P. Dewanti:** Formal analysis, Data curation. **Yuniarti MS.:** Formal analysis. **Syawaludin A. Harahap:** Writing – review & editing. **Pringgo D.K.N.Y. Putra:** Visualization. **Lady A. Sriwijayanti:** Data curation. **Arif S.W. Kusuma:** Investigation. **Rizky Abdulah:** Supervision, Writing – review & editing. **Alvita Karina Putri:** Visualization, Validation. **Jogi R.N. Panggabean:** Validation, Methodology. **Yeni Mulyani:** Writing – review & editing. **Neng T. Sofyana:** Formal analysis. **Tonni A. Kurniawan:** Writing – review & editing. **Yunita E. Puspitasari:** Writing – review & editing, Supervision.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Data availability

Data will be made available on request.

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