Current Research in Food Science 9 (2024) 100860

Contents lists available at ScienceDirect

Current Research in Food Science

journal homepage: www.sciencedirect.com/journal/current-research-in-food-science

Review Article

Plant-based seafood alternatives: Current insights on the nutrition, protein-flavour interactions, and the processing of these foods

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ARTICLE INFO

Handling Editor: Professor Aiqian Ye

ABSTRACT

Fish are an important food source; however, the sustainability of current seafood supplies is a major concern for key stakeholders. The development of plant-based seafood alternatives may be suitable products to alleviate some of the pressures on aquatic ecosystems and help support environmental sustainability. However, the widespread adoption of these products weighs heavily on the ingredients used in the formulations which should not only satisfy nutritional and sustainability targets but must also meet consumer approval and functionality. In this review, we highlight recent advances in our understanding of the nutritional quality and sensory challenges in particular flavour (which includes taste and aroma), that have so far proven difficult to overcome in the development of plant-based seafood alternatives. Protein interactions that contribute to flavour development in plant-based seafood alternatives and the factors that impact these interactions are also discussed. We also review the recent advances in the innovative technologies used to improve the texture of products in this emerging food category. Finally, we highlight key areas for targeted research to advance the development of this growing segment of food products.

1. Introduction

Seafood in particular fish, fulfill an important role in human nutrition as a source of biologically valuable protein, fatty acids and micronutrients (Potter et al., 2020; Koehn et al., 2022). Although demand for seafood is rising (total production of seafood by capture fisheries and aquaculture was estimated at 179 million tonnes in 2018), and it has become increasingly apparent that the current global seafood practices are unsustainable (FAO, 2022; Koehn et al., 2022). Indeed, almost 30% of global fish stocks are overfished whereas 60% of the remaining supplies are being fished at maximum capacity (FAO, 2022; Chuah et al., 2024). Moreover, the effects of climate change and overfishing have contributed in part to the decline in some marine populations (Potter et al., 2020).

Traditionally, aquaculture (the farming of fish, shellfish and aquatic plants) has been used to supplement seafood supplies and support livelihoods (Ahmed et al., 2019). Unfortunately, aquaculture has not solved the problems associated with the fishing industry, instead, the sector has been criticized for not reducing the fishing of wild seafood to sustainable levels because many aquaculture species rely on wild fisheries (in particular small pelagic fish) for fish meal or oil production, which creates other issues related to food insecurity in some regions (Froehlich et al., 2023; Chuah et al., 2024). In addition to the dependency of aquaculture on captured fish, inputs from fertilizers and the presence of toxins can result in poor water quality and generate environmental conditions that promote parasitic growth and disease in fish (Ahmed et al., 2019). For example, effective sea lice control is still one of the biggest threats to salmon farming (Powell et al., 2018).

Moreover, marine pollutants such as harmful chemicals, heavy metals (for e.g., cadmium, copper, lead, and zinc), oil, algal blooms, and plastics are harmful to marine environments and aquatic species (Elgendy et al., 2023). Although some policies on ocean governance exist (United Nations Convention on the Law of the Sea, UNCLOS; Global Sustainable Development Goal 14 #, Life below water) (Sarwar et al., 2021), compliance to these principles varies across different jurisdictions, in part due to limited quantitative indicators and limitations on evaluating the effectiveness of operational controls (da Costa et al., 2020; Cormier and Elliott, 2017). Thus, the reported incidents of pollutants have been increasing; for example, plastics account for approximately 85% of total marine litter (Auta et al., 2017). Microplastics

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https://doi.org/10.1016/j.crfs.2024.100860
Received 21 June 2024; Received in revised form 9 September 2024; Accepted 15 September 2024

(small fragments, < 5 nm) of plastic materials, can also be ingested, often through passive water filtration or confounded with prey, and accumulate in seafood tissue which has negative consequences on their physiology and nutrient quality (Barboza et al., 2018). Moreover, microplastics can absorb harmful chemicals and heavy metals, which can subsequently find their way into the food chain (Barboza et al., 2018). The present challenges in the seafood and aquaculture industries have unveiled the need to effectively manage marine pollution and conventional utilization of fishery resources to responsibly meet global seafood demands. This leaves us with the urgent question of what opportunities exist to help address the sustainability concerns of the seafood industry.

Recent discussions on sustainable foods encourage increased consumption of plant and plant foods to improve human health and promote sustainability (Vermeir et al., 2020; Alae-Carew et al., 2022). The development of plant-based seafood alternatives is an underexplored path that could partially alleviate some of the pressures on aquatic ecosystems. Plant-based seafood alternatives are food products that are formulated using plant ingredients, and they are designed to mimic the texture, taste and flavour of seafood (Zhong et al., 2023). Recent market reports also indicate that opportunities for new alternative seafood niche markets are steadily increasing (Good Food Institute, 2019**)**.

Several companies in North American and Europe (including New School Inc., The Plant-based Seafood Co. and Hooked, respectively) are at the forefront of innovation in this area and Table 1 highlights some of the commercial plant-based seafood alternatives currently in the marketplace (Ran et al., 2022). However, for plant-based seafood alternatives to be more widely adopted by consumers, some technological challenges that have, so far, proven difficult to overcome need to be addressed. Among these challenges, nutritional quality, flavour and texture appear to be more pressing (Good Food Institute, 2019; Kim et al., 2023). Moreover, these challenges must be addressed in the face of growing concerns about the environment and the responsible use of resources (Caparorgno and Mathys, 2018).

A recent consumer choice study by Kim et al. (2023) and current reviews on ingredient selection and processing which have improved our understanding of consumer acceptance of these foods, are discussed in other articles on this subject (Lanz et al., 2024; Appiani et al., 2023; Zhong et al., 2023). However, the evaluation of flavour interactions in plant-based seafood alternatives and how these interactions impact product quality has not been fully explored (Wang et al., 2024). Equally important is the nutritional quality of these foods and although some work has been done to identify novel protein sources (Mahmud et al., 2024; Li et al., 2024a,b) more rigorous efforts are needed to improve limitations in the essential amino acid and omega-3 fatty acid compositions. Here we highlight recent studies that focus on the nutritional and sensory challenges as well as the key flavour interactions that occur in plant-based foods with a focus on proteins and seafood alternatives which is a new contribution to the field. A fundamental understanding of these interactions is necessary for consumer adoption of these food products and their success in the marketplace. Recent advances in the technologies used to improve the texture of products in this emerging food category are also highlighted. Finding innovative approaches to improve the texture of plant-based seafood alternatives will also help to improve the quality and overall acceptability of these products.

2. Addressing the nutritional challenge of plant-based seafood alternatives

Traditional seafood are rich sources of protein, fatty acids, water and micronutrients (Zhong et al., 2023). Thus, it can be easily appreciated that the ingredients used in plant-based seafood analogues are selected in most cases to meet these nutrient requirements. Here we highlight the general nutritional profiles of commercial PBSA and then we focus on proteins, as key nutrients that are needed to improve the nutritional properties of plant-based seafood analogues.

2.1. Overview of the nutritional values of current commercial plant-based seafood alternative

Besides the ethical and environmental sustainability concerns, the growing popularity of plant-based products is fueled by the supposed nutritional merits compared to the animal-based products (Boukid, 2021). However, a deeper assessment may reveal critical concerns: whether plant-based foods can truly measure up to the nutritional values of animal-based products due to the lack or insufficiency of certain important nutrients (e.g., as ω-3 fatty acids, vitamin A, vitamin B12, zinc, and calcium) in the plant sources used to formulate these alternatives (Murphy and Allen, 2003; Allès et al., 2017). The prevailing concerns surrounding plant-based analogues including seafood alternatives continue to cast doubts on their viability as functional foods capable of fulfilling customers' nutritional needs.

Seafood products are excellent sources of high-quality protein, essential nutrients (vitamins A, B1, B2, and D), and minerals (iron, iodine, phosphorus, and zinc) (Benjamin et al., 2018; Reksten et al., 2020). They are also the major source of ω-3 fatty acids (alpha-linolenic acid (ALA), eicosapentaenoic (EPA), and docosahexaenoic (DHA) acids) that provide anti-inflammatory, antithrombotic, and other beneficial physical and cognitive health functions (Calder, 2018; Mozaffari et al., 2020). Comparatively, many plant-based products, including seafood alternatives, have been shown to have lower quantities of these essential nutrients (Boukid et al., 2022; Curtain and Grafenauer, 2019). The recent study conducted by Boukid et al. (2022) highlighted the differences in the nutritional composition between plant-based seafood analogues and their respective conventional types. The authors compared the nutritional information of a range of seafood alternatives (i.e., tuna, shrimp, calamari, fish fingers, fish sticks, salmon, caviar, and fillet) with conventional products and observed relatively lower protein contents in seafood alternatives. Some of the alternatives showed higher calories and fats (finger and sticks), while others, such as tuna, fingers, sticks, salmon, and fillet alternatives, contained more salt than their corresponding counterparts (Boukid et al., 2022). The blending of proteins from various sources as well as biofortification of seafood alternative with omega-3 fatty acids and micronutrients (vitamins, minerals) are believed to be effective solutions for achieving nutritional equivalence with conventional products (Boukid et al., 2022; Kazir and Livney, 2021).

Plant-based analog formulations use high levels of starches as ingredients to enhance the structural, textural, and binding properties of products (Curtain and Grafenauer, 2019). However, these are usually digestible starches, which have been implicated in the risk of obesity and diabetes due to their ability to cause a spike in the blood sugar level (Miao and Hamaker, 2021). Utilizing dietary fibers, slowly digestible starches, or resistant starches instead of rapidly digestible starches improves the nutritional profile of seafood alternatives (McClements and Grossmann, 2024). Companies have also found a way to meet the necessary omega-3 level by adding plant or microbial oils with omega-3 fatty acids to PBSA foods. These oils include flaxseed oil (ALA) or algal oil (EPA and DHA) (McClements and Grossmann, 2021). Good Catch plant-based tuna and Gardein (2023) plant-based fish fillets and crab cakes are fortified with algal oil. They're among the few brands with added algal oil and have product information including omega-3 on the labels. Several of these food manufacturers are also fortifying their products with micronutrients such as vitamin B12, calcium, zinc, iodine, and iron (Alcorta et al., 2021; Key et al., 2022), although there is still little information about the bioavailability of these vitamins and minerals in a PBSA matrix.

The safety of plant-based products is also key to their wholesomeness and acceptability. Carcinogenic and/or mutagenic compounds such as heterocyclic aromatic amines can be formed in protein-rich foods via high-temperature processing (e.g., grilling, roasting, baking, and frying) (Barzegar et al., 2019; Hou et al., 2017); as well as antinutritive factors such as tannins, saponins, phytic acid, protease inhibitors, α-amylase

Table 1
Some commercially available plant-based (PB) seafood analogues present in the marketplace.

Name of Company	Type of Product	Main Protein type	Non-proteins Ingredients	Nutrition	References
Current Food	Salmon (Classic smoked slices)	Pea protein	Water, High-Oleic Sunflower Oil, Natural Flavors, Bamboo Fiber, Gelifier, Potato Starch, Sea Salt, Algae Oil, Lycopene, Iron, Vitamin B12	Energy: 130 kcal, Total Carbohydrate: 10 g, *Fiber: 5 g,* Protein: 6 g, Fat: 8 g, *-Saturated fat*: 1 g, Salt: 0.84 g, Vit.B12: 3.49 mcg	Current Foods (2023)
Current Food	Tuna (cubes & fillet)	Pea protein	Water, high-oleic sunflower oil, natural flavors, bamboo fiber, gelifier, potato starch, sea salt, vegetable juice, algae oil, lycopene, citric acid, iron, vitamin b12	Energy: 225 kcal, Total Carbohydrate:22.5 g, *fiber*: 9 g, Protein: 9 g, Total Fat: 11.25 g, *saturated fat*: 0 g, Salt: 1 g, Vit.B12: 0.36 mcg	Current Foods (2023)
Omni Foods	Tuna in oil	Soy Protein Concentrate, Soy Protein Isolate, Wheat Gluten	Water, canola oil, yeast extract salt, potato starch, wheat starch, algal oil, artificial flavours, carrot juice concentrate, vegetable extract (soybean, carrot, natural flavours)	Energy: 170 kcal Total Carbohydrates: 3.8 g Total Fat:11.0 g *Saturated Fat*: 1.2 g Protein: 13.0 g Salt:1.2 g	Mighty Plants (2024)
Sophie's Kitchen	Fish fillets	Textured vegetable protein (pea protein, pea starch)	Canola oil, rice flakes (from brown rice), konjac powder, seaweed powder, potato starch, powdered cellulose, organic agave nectar, turmeric, white pepper, sea salt, ginger	Energy: 180 kcal Total Carbohydrates: 20 g fiber: 4.6 g Total Fat:8 g Saturated Fat: 1 g Protein: 8 g Salt:0.4 g	Future Farm Co. (2022)
Gardein	mini crab cakes	Chickpea flour, soy flour	Bell peppers, green onion, potato starch, distilled vinegar, methylcellulose, salt, sugar, lemon juice concentrate, garlic powder, tapioca starch, yeast, natural flavors, yeast extract, degerminated yellow corn flour, titanium dioxide (color), spices, leavening, sodium acid pyrophosphate, sodium bicarbonate, monocalcium phosphate, onion powder, DHA algal oil, autolyzed yeast extract, gum Arabic, dextrose, malic acid, xanthan gum	Energy: 490 kJ/140 kcal, Total Carbohydrate: 13 g *fiber: 0 g* Total Fat: 6 g, *saturated fat: 0.5 g,* Protein: 9 g, Salt: 0.33 g	Gardein (2023)
Century Pacific Food Inc.	Unmeat Tuna, canned in water	Wheat and Non-GMO Soy Proteins	Water, Natural Flavors, Salt, Vegetable Broth, Seasonings, Citric Acid (Acidulant), Thickeners (Corn Starch, Xanthan Gum), Sugar, and Yeast Extract	Energy: 60 kcal Total Carbohydrate: 5 g fiber:2 g Total Fat: 0 g Saturated Fat: 0 g Protein: 9 g Salt:0.8 g	Century Pacific Food Inc. (2024)
Ademi Foods Inc	Shrimp	Pea Protein, Konjac,	Water, Natural Flavors, Contains Less Than 2% Of The Following: Curdlan Gum, Sea Salt, Titanium Dioxide For Color, Calcium Hydroxide, Vegetable Juice (Color), And Monk Fruit Extract.	Energy: 70 k cal, Total carbohydrate: 7 g, *fiber: 7 g,* Total Fat: 0 g, *saturated fat: 0. g,* Protein: 7 g, Salt: 0.45 g	Ademi Foods (2024)
Good Catch Foods	Salmon burgers classic style	Good catch 6-plant protein blend (pea protein isolate, soy protein concentrate, chickpea flour, faba protein, lentil protein, soy protein isolate, navy bean powder)	Water, coconut oil, natural vegan flavors, sunflower oil, methylcellulose, yeast extract, corn starch, onion powder, salt, lemon juice, lemon, orange, shallot, spice, sugar, garlic powder, annatto extract, vegetable juice	Energy: 740 kJ/177 kcal, Total Carbohydrate: 8.8 g, *fiber: 1.8 g* Total Fat: 9.3 g, *saturated fat: 6.2 g*, Protein: 14.2 g, Salt: 0.5 g	Good Catch (2023)
Fish Peas	Tuna (flakes in brine)	Wheat Protein	Water, Acidity Regulator: (E450v, E500i), Antioxidant: E306), Sunflower Oil, Water, Flavouring, Salt, Citrus Fibre, Sugar, Acidity Regulators: Citric Acid, Acetic Acid, Caramel (Sugar, Water).	Energy: 910/219 kcal, Total Carbohydrate: 5.3 g, *fiber: 1.3 g,* Total Fat: 15.4 g, *saturated fat: 1.5 g,* Protein: 14.1 g, salt: 1.5 g	Fish Peas (2023)
Good Catch Foods	Crab cake	Good catch 6-plant protein blend (pea protein isolate, soy protein concentrate, chickpea flour, faba protein, lentil protein, soy protein isolate, navy bean powder)	Water, sunflower oil, wheat flour, red bell pepper, corn starch, green onion, parsley, natural flavors, salt, lemon juice, methylcellulose, corn maltodextrin, organic cane sugar, onion powder, spices, paprika, yeast extracts, garlic powder, yeast, corn flour, xanthan gum, annatto extract, acetic acid	Energy: 320 kJ/160 kcal, Total Carbohydrate: 9 g *fiber: 1 g* Total Fat: 5 g, *saturated fat: 0.5 g,* Protein: 20 g, salt: 0.58 g	Good Catch (2023)

inhibitors, and lectins (phytohemagglutinin) found in pulses can pose potential risks to consumers (Samtiya et al., 2020). Researchers have promoted the use of natural plant extracts containing antioxidants, such as phenolic compounds, in the formulation of PBSA products as a strategy to mitigate the formation of these toxicants (Tsen and Smith, 2006; Lu et al., 2018; Gibis and Weiss, 2010). When consumed in high quantities, antinutrient factors can limit nutrient utilization and impair gastrointestinal functions; therefore, they must be eliminated from the protein ingredient through cooking (Torres et al., 2016), soaking and germination (Handa et al., 2017), or fermentation (Nduti et al., 2016). There is, however, a need for more research specifically to ascertain the existence or generation of such harmful substances in PBSA and the extent of their risks to consumers.

The primary aim is to develop PBSA that mimics the nutritional and sensory properties of conventional products; as such, a right balance should be established such that efforts to improve the nutritional profile or preserve safety do not compromise other essential characteristics such as flavor and texture. Consumers should also be provided with clear nutritional information so they can make informed choices about their dietary needs. This nutritional deficit, along with the underwhelming sensory and flavor characteristics, is limiting the widespread adoption of plant-based products, including plant-based seafood alternatives. There is, however, little work done to ascertain the nutritional variations between current plant-based seafood alternatives and their conventional counterparts on the marketplace. Information that highlights the disparity between seafood products and alternatives will be useful for the formulation of products with an improved nutritional profile that meet the health needs of consumers.

2.2. Proteins in plant-based seafood alternatives

Proteins are macro molecules that play important roles in diet and nutrition (Duluins and Baret, 2024). Plant protein ingredients can be found as concentrates or isolates, containing over 80% and over 90% protein concentration, respectively (Ma et al., 2022). However, in terms of the nutritional benefits they provide, not all sources of proteins are considered equal. Compared to animal protein sources, there are several notable differences in: (1) protein quality, (2) protein structure, and (3) protein solubility. Each component will be discussed separately below.

The current standard used to evaluate protein quality depends on the efficiency with which a host extracts amino acids from the food matrix and utilizes them in functions such as growth and or maintenance (Marinangeli and House, 2017). Two main approaches used to evaluate protein quality are: (1) Protein Digestibility-Corrected Amino Acid Score (PDCAAS) and (2) Digestible Indispensable Amino Acid Score (DIAAS). Both methods are used to determine the quality of single protein sources, however, PDCAAS is being replaced by the DIASS because the latter is not truncated at 1, which allows for differentiation between higher quality protein foods (Forester et al., 2023). A study by Herreman et al. (2020) compared the quality of animal and plant-based protein sources and highlighted that the blending of the appropriate sources of protein is an important step to achieve adequate DIASS scores. As shown in Table 1, pulse protein sources from pea, faba bean and chickpeas are common choices for plant-based seafood alternatives. Pulses are also good examples of sustainable ingredients because they require less water and fertilizers and help fix nitrogen in the soil (Good Food Institute, 2019).

Plant sources of protein provide less complete protein nutrition due to lower digestibility and a few missing essential amino acids (EAA) (Day et al., 2022). These limitations can be overcome by removing anti-nutritional factors (for e.g., phytates, lectins and tannins) or dietary fibres that reduce protein digestibility (Thakur et al., 2019), or by complementation. Protein complementation refers to the blending or pairing of different sources of plant proteins that are rich in the deficient amino acids, which together build a complete profile of amino acids resulting in improved protein quality (Nowacka et al., 2023). A well-known example is combining cereal and pulses sources such as beans. This combination works because pulses are rich in lysine but have low amounts of the sulfur-containing amino acids methionine and cysteine whereas the opposite is true for cereal-derived proteins (NIZO, 2022).

Unfortunately, complementation strategies do not address the inherent structure of plant proteins, which compared to animal proteins, have a greater abundance of β-sheet structures that can promote protein aggregation and reduce digestibility (Sim et al., 2021; Carbonaro et al., 2012). In addition, some protein blends can also result in decreased protein solubility (NIZO, 2022).

Protein quality is an important factor to consider when selecting ingredients for formulating plant-based seafood alternatives since protein digestion and absorption kinetics are important components of protein quality. In contrast to the well-characterized animal proteins, plant proteins are just beginning to be understood (Carbonaro et al., 2012). Thus, more work needs to be done to better understand how to select protein combinations that do not negatively impact protein functionality, sustainability and consumer acceptability of the proteins as well as the plant-based seafood alternative products to which they will be applied (Nowacka et al., 20223; McClements and Grossmann, 2024).

3. Addressing the sensory challenge of plant-based seafood alternatives

3.1. Seafood flavours for the development of plant-based seafood alternatives

The unsatisfactory sensory characteristics, including the flavour of plant-based alternatives, remain a major obstacle to wider market acceptability (Kim et al., 2023). For seafood alternatives, identification of the primary contributors to the characteristic seafood flavours is a crucial stage in the formulation process. The characteristic aroma of seafoods is derived from a combination of different odor-active volatiles, including alcohols, aldehydes, ketones, amines, and sulfur compounds, which are produced through the hydrolysis and oxidation of polyunsaturated fatty acids and the breakdown of sulfur amino acids (Jones et al., 2022; Nieva-Echevarría et al., 2017).

Polyunsaturated fatty acids and other flavour precursors are usually constituents of marine biota, for instance omega-3 fatty acids in sea weeds are absorbed when consumed by marine organisms (Luo et al., 2024). Other molecules with physiological functions in marine organisms, including osmolytes like trimethylamine oxide (TMAO), Betaine (N,N-trimethyl glycine), also play a role in the distinct seafood flavour (Yancey et al., 2002; Luo et al., 2024). Polyunsaturated fatty acids (PUFAs) undergo lipoxygenase activity or autoxidation (Kitabayashi et al., 2019; Bai et al., 2019), generating odor-active volatiles such as aldehydes (e.g. 4-heptenal, hexanal, nonanal, and (E,E)-2,4-heptadienal), alcohols (e.g., 1-penten-3-ol and 1-octen-3-ol), and ketones (e.g., 1-octen-3-one, (Z)-1,5-octadien-3-one) (Table 2), which impart the fresh fish with green, plant-like, metallic, and fishy aromas (An et al., 2020; Morita et al., 2003; Nogueira et al., 2019).

Sulfur compounds such as dimethyl sulfide, dimethyl disulfide, and methanethiol have been identified as key contributors to the characteristic smell of fresh and cooked seafood. Heating can induce the degradation of sulfur-containing compounds such as dimethylsulfoniopropionate, methionine, and taurine, resulting in these odor-active sulfur compounds (Franczuk and Danikiewicz, 2018; Yu et al., 2012; Varlet and Fernandez, 2010). Trimethylamine (TMA) also contributes to the seafood aroma through enzymatic and bacterial degradation of the nitrogen-containing compound trimethylamine oxide (TMAO) (Alasalvar et al., 2005). Trimethylamine (TMA) gives off pungent ammonia-like odors and is often used as an indicator of seafood microbial spoilage (Alasalvar et al., 2005).

Freshly harvested saltwater fish typically have subtle green and

Table 2
A list of some major seafood flavor compounds and their odor descriptions.

Compound	Odor description	References
Aldehyde		
Hexanal	Fishy, grass	Giri et al. (2010)
(Z)-4-Heptenal	cooked vegetable/fishy	Varlet et al. (2006)
(E,E)-2,4-heptadienal	Deep fried, fatty, fishy	Giri et al. (2010)
Octanal	fatty, soap, lemon	Varlet et al. (2007)
2-Octenal	Aromatic, oxidized oil-like	Giri et al. (2010)
Benzene acetaldehyde	Sweet, fruity	Varlet et al. (2006)
Nonanal	Gravy, green, fruity, sweet, melon, soapy, fatty	Giri et al. (2010)
4-ethyl- Benzaldehyde	Almond, fruity, nutty, creamy bean flavor.	Tanchotikul and Hsieh (1989)
Alcohols		
1-Penten-3-ol	Burnt, meaty	Giri et al. (2010)
1-Octen-3-ol	Fishy, grassy	Giri et al. (2010)
1-Octanol	Fatty, green	Giri et al. (2010)
(E)-2-penten-1-ol	Green, plastic	Giri et al. (2010)
3-Methyl-1-butanol	Rancid, pungent, balsamic	Giri et al. (2010)
2-Methyl-1-butanol	Fusel oil, ripe onion, malty	Giri et al. (2010)
Ketones and esters		
1-Penten-3-one	Pungent, fish-like, rotten, fruity, plastic, leather	Giri et al. (2010)
3-Octen-2-one	Fatty, spicy	Jones et al. (2022)
2-butanone	Ethereal, cheese, chemical	Giri et al. (2010)
2-heptanone	Fruity, spicy	Joffraud et al. (2001)
2,3- Octanedione	metallic feel	Yajima et al. (1983)
3-Methylbutyl acetate	Fruit, sweet, banana, ripe	Joffraud et al. (2001)
Ethyl octanoate	fruit, fat	Parlapani et al. (2017)
Acids		
Acetic acid	Sour, vinegar, pungent	Joffraud et al. (2001)
Propanoic acid	Pungent, rancid, soy, fruity, cheesy	Giri et al. (2010)
Pentanoic acid	Sweaty, pungent, sour, cheesy, beefy	Pham et al. (2008)
Hexanoic acid	Sweaty, pungent, rancid	Pham et al. (2008)
Tetradecanoic acid	marine, fatty, cheese-vfrs	Varlet et al. (2007)
3-Methyl butanoic acid	Over ripe fruit, sweaty	Giri et al. (2010)
2-Methyl butanoic acid	Sweet, cheese, rancid	Giri et al. (2010)
Furans		
2-Pentyl furan	Buttery, green bean-like	Giri et al. (2010)
2-acetylfuran	cooked vegetable, potato valet	Varlet et al. (2007)
2-Ethylfuran	Rubber, pungent	Giri et al. (2010)
Sulfur compounds		
Hydrogen sulfide	Rotten eggs	Dalgaard (1995)
Methanethiol	Sulfur, gasoline, garlic	Dalgaard (1995)
Dimethyl sulfide	Cabbage, sulfur, gasoline	Dalgaard (1995)
Dimethyl disulfide	Onion, cabbage, putrid	Dalgaard (1995)
Dimethyl trisulfide	Sulfur, fish, cabbage	Dalgaard (1995)
Nitrogen containing compounds		
Methylpyrazine	Fishy, nutty, ammonical	Giri et al. (2010)
2-Ethyl-3-methyl pyrazine	Nutty, earthy, roasted, potato	Giri et al. (2010)
2,6-Dimethyl pyrazine	Baked potato, nutty, fruity	Giri et al. (2010)
Tetramethylpyrazine	Fermented soy	Giri et al. (2010)
Trimethylpyrazine	Burnt, bread	Giri et al. (2010)
Ammonia	Ammoniacal	Karpas et al. (2002)
Trimethylamine	Fishy, oily, rancid, sweaty	Karpas et al. (2002)
2-Acetyl pyrrole	Nutty, anisic	Giri et al. (2010)
Others		
8-heptadecene	animal, roasty, chemical	Varlet et al. (2006)
2,6-dimethylphenol	chemical, burnt, spicy	Varlet et al. (2006)
4-methylguaiacol	candy, spicy, smoked	Varlet et al. (2006)
Benzothiazole	green, plastic, fruity	Varlet et al. (2006)
Limonene	pine/chemical, floral/fresh	Varlet et al. (2006)

seaweed-like aromas. However, during storage, the seaweed aroma begins to change as neutral-to-acid odors such as heptenal, (Z)−1,5−octadien−3−one, and methional begin to emerge resulting in undesirable off-flavours (Triqui and Bouchriti, 2003). In addition, heat processing techniques like steaming and roasting trigger chemical reactions between dicarbonyl compounds such as reducing sugars and lipid degradation by-products, and amino acids through Strecker and Maillard reactions. These reactions produce a wide variety of odor-active compounds in seafoods, including 2-petyl furan methional, 3-methylbutanal, 3,4-dihydro-2H-pyrrole, 2-acetylthiazole and alkyl-pyrazine compounds (Xu et al., 2013; Yaylayan and Keyhani, 1990; Varlet and Fernandez, 2010).

It is also important to note that, flavour profiles of seafoods generally exhibit certain common volatile components such as (Z)-1,5-octadien-3-one, dimethyl trisulphide, 2-acetyl-2-thiazoline, furaneol, 1-octen-3-ol which collectively create the foundation of seafood flavour. The presence of additional distinct volatiles determines the unique flavour attributes of respective seafood types (Luo et al., 2024). Findings by Luo et al. (2024) indicate that cooked seafoods have a more uniform flavour profile due to the presence of identical compounds formed by thermal processes. In contrast, raw seafoods typically possess more distinct volatile compounds that vary between different species.

A recent report by Luo et al. (2024) highlighted the molecules responsible for the distinctive flavour attributes of specific seafood species as well as the different molecules that induce the disparate flavour characteristics between fresh and cooked seafood. According to the authors, thermally induced Maillard reaction products such as 2-ethylpyrazine, 2-acetyl-2-thiazoline, and 2-acetylpyrazine impart marked nutty flavours in cooked Mollusca such as mussels and clams, while 3-methylbutanoic acid, acetic acid, and decanoic acid, together with sotolone and indole, shape the distinct flavour of crustaceans. Some other seafood types, such as oily fish and white fish, display comparable volatile profiles. However, once they are cooked, oily fish exhibit an earthy and sweet aroma due to the presence of 1-octen-3-one, heptanal along with 2,3-pentanedione and benzaldehyde, while (E)-2-nonenal, 1-hexanol, nonanal, and octanal impart typical “fish-like” notes in cooked white fish (Jones et al., 2022).

3.2. Taste, an important attribute of plant-based seafood alternatives

The flavour of food is an essential quality attribute that largely determines consumer acceptability. The consumer relies on a multisensory mechanism influenced by sensory (vision, audition, smell, and touch) cues as well as emotional experiences, environmental and personal variables (e.g., age and health status) that potentially help shape the flavour experience (Rai et al., 2023; Spence, 2015). Basically, when food is consumed, non-volatile chemical constituents (e.g., salt, sugar) are dissolved in the saliva and detected by the taste receptors in the mouth. The coupling of this mechanism with trigeminal sensations in the mouth and the detection of aroma volatiles by olfactory receptors in the nasal epithelium underpin flavour perception (Spence, 2015; Spence et al., 2017). As such, the flavour appeal which is highly dependent on the olfactory and gustatory characteristics (taste and trigeminal sensations) of novel foods including plant-based seafood alternatives, are key determining factors that will foster customer allegiance and encourage individuals to include these seafood alternatives into their daily eating habits (Forde and de Graaf, 2022; Spence, 2015). Plant based seafood alternatives mimic the taste and sensory characteristics of traditional seafood by blending pulse proteins (such as soy, pea, chickpea, etc.) with water, flavouring, fat, binding, and coloring additives (Kyriakopoulou et al., 2019). Kazir and Livney (2021) assert most commercially available plant-based seafood alternatives are specifically formulated to imitate popular saltwater species like salmon, tuna, and prawn.

Formulations incorporate seafood flavourings to impart unique umami flavours with savory and brothlike sensations to the products (Ninomiya, 2002). These flavourings can be produced using ingredients such as soy sauce, mushrooms, or mushroom sauce to imitate an umami taste which is also a key characteristic of seafood flavour. The umami taste is generated from non-volatiles such as free glutamic acid and 5′-nucleotides (guanosine monophosphate, inosine monophosphate) (Sarower et al., 2012). Free amino acids such as glycine, alanine, and aspartate, as well as organic acids including lactic and succinic acids, are found to enhance the umami taste and impart a sweet taste (Shi et al., 2022; Ninomiya, 2002). Peptides also act as Maillard reaction reactants that generate seafood aroma volatiles, in addition to contributing to seafood taste properties (Hessel, 1999; Yang et al., 2019; Zou et al., 2018). A study has shown that peptides such as Ala-Ala and Ala-Leu impart a sweet and kokumi taste to anaerobically steamed salmon (Dong et al., 2024). Park et al. (2002) observed in their study on fish sauce that Asp-Met-Pro imparted umami taste, Val-Pro produced a sweet taste while sour taste perception was attributed to Asp-Glu, Tyr-Pro, and Val-Pro-Glu peptides present in the product. Other peptides such as Tyr-Pro-Orn, Val-Pro-Orn, Ala-Pro, Gly-Phe, Gly-Tyr, and Phe-Pro were also responsible for the bitter tastes in fish sauce product (Park et al., 2002).

Seaweed species are currently being utilized to create seafood flavourings that mimic the distinct tastes of various fish and shellfish species, owing to their inherent oceanic flavour (Kazir and Livney, 2021). In a recent study, Coleman et al. (2022), demonstrated the potential of microalgae as a viable ingredient for creating plant-based seafood alternatives with desirable taste. The microalgae *Rhodomonas salina, Tetraselmis chui, and Phaeodactylum tricornutum* possess significant amounts of essential seafood aroma compounds (dimethylsulfide, fatty acid-derived compounds, and trimethylamine) as well as taste compounds (glutamic acid, alanine, arginine, and 5-ribonucleotides). This abundance of compounds contributes to a more pronounced seafood odor and taste in these microalgae compared to seaweeds (Coleman et al., 2022).

It is also worth noting that constituents in seafood alternatives, especially the protein, influences the product's flavour quality not only because of their potential interaction with added flavour compounds, but also because they may generate some typical protein off-flavour. To improve the overall flavour perception, there is a need to remove from the plant protein any precursors and molecules that are associated with off-flavours such as beany, green, and pea aromas (volatiles), as well as the bitter, astringency, and metallic taste (non-volatiles) (Wang et al., 2022a). These unpleasant flavours in pulses are typically produced by heat-induced Maillard reactions, oxidation of unsaturated fatty acids, and lipid hydrolysis (Sharan et al., 2022; Jelen, 2011). These off-flavours bind to proteins and diffuse into protein-rich fractions, imparting unwanted flavours into the product thereby reducing acceptability (Zhang et al., 2021a; Mittermeier-Kleßinger et al., 2021). Pulses can be sprouted/germinated (Eum et al., 2020; Akkad et al., 2021) and fermented (Wang et al., 2022b; Tao et al., 2022) to trigger the breakdown of off-flavor precursors or generate fruity/floral flavours such as ethyl acetate and 2-methylbutyl acetate that can mask these off-flavours (Hirst and Richter, 2016; Fischer et al., 2022). Heat treatment (Frohlich et al., 2021; Zhang et al., 2012) and high-pressure processing (Ueno et al., 2019), as well as the selection of an optimal storage condition and packaging materials are among the strategies that have been utilized to mitigate off-flavor generation in pulse proteins (Yang et al., 2023; Liang et al., 2020).

Ideally, the added flavour compounds are expected to be compatible with the protein, (irrespective of the source), be able to withstand processing, and beyond that, be sufficiently released into the mouth during consumption. The inability to accurately reproduce the taste and sensory attributes of conventional seafood hinders the widespread adoption of seafood alternatives (Nowacka et al., 2023). Typically, we prepare conventional seafoods through smoking, roasting, and frying, all of which require heat treatment. These processes trigger chemical reactions like lipid oxidation, protein denaturation, nucleotide degradation and transformation, and the Maillard reaction, which amplifies the production and release of certain odorants (Madruga et al., 2010). The development of delicious plant-based seafood alternatives that provide consumers with the same sensory experience as conventional products requires insights into the interactions between the major ingredients (i.e., protein) and flavour compounds, as well as factors that influence the release or perception of these seafood flavours.

3.3. Factors that impact protein-flavour interactions and plant-based seafood flavour delivery

Generally, interactions between food ingredients such as protein and flavor compounds directly influence the amount of the volatiles that are released, which alters the resulting flavor perception (Chen et al., 2019). The reactivity of the flavour compound which is based on the partition coefficient (Log P), functional group, and chain length as well as the protein structure play significant roles in this process (Weerawatanakorn et al., 2015; Wang and Arntfield, 2015b). A number of authors (Table 3) have shown that various classes of flavour volatile compounds (alcohols, aldehydes, ketones, esters, and sulfides) can bind to pulse proteins, such as peas, soy, chickpeas, yellow eyes, and faba beans via interactions with the hydrophobic areas of the 11 S protein, the primary seed storage unit of pulses (Semenova et al., 2002; Guo et al., 2019, 2024; Bi et al., 2022). Reversible non-covalent interactions, such as hydrophobic and electrostatic contacts, hydrogen bonds, van der Waals forces, and covalent interactions, are the primary forces that induce protein and flavour binding (Wang and Arntfield, 2014; Suppavorasatit and Cadwallader, 2012). Covalent bonds are irreversibly formed between compounds and specific residues on the protein chain (e.g., -NH2, -SS-, and -SH); stronger bindings occur but there is limited release of the flavours during mastication (Anantharamkrishnan and Reineccius, 2020).

Aside from the nature of the protein and flavour compounds, environmental factors such as pH, temperature, ionic strength conditions, pressure, oxidation conditions, and other small molecules all play an important role in manipulating protein-flavour interaction and flavour release (Weerawatanakorn et al., 2015). A few authors have explored the binding of flavour compounds to proteins (Barallat-Pérez et al., 2023b; Wang and Arntfield, 2014; Guo et al., 2023, 2024; Anantharamkrishnan et al., 2020; Bi et al., 2022). Other reports also highlighted the impact of environmental factors such as the effects of heat treatment (Wang and Arntfield, 2015b; Guo et al., 2019; Anantharamkrishnan and Reineccius, 2020; Wongprasert et al., 2024), salts and pH (Wang and Arntfield, 2015a; Anantharamkrishnan and Reineccius, 2020) and chemical and enzymatic approaches (Wang and Arntfield, 2016a; Okagu et al., 2021; Suppavorasatit and Cadwallader, 2012) on protein-flavour interaction.

The protein-flavour interactions in these studies were investigated using analytical techniques such as mass spectrometry, circular dichroism, ultraviolet spectroscopy, and fluorescence spectroscopy. (Wongprasert et al., 2024; Guo et al., 2024; Bi et al., 2022). These analytical tools have demonstrated their effectiveness in measuring the changes in protein conformation caused by flavour binding. Thermodynamic models, such as the Klotz model, the Hill equation, and the Stern-Volmer equation, are commonly employed to determine the number of non-covalent binding sites and the strength of the forces that mediate the interaction between proteins and ligands (Condict and Kasapis, 2022). Several authors have applied Scatchard plots and/or the Klotz equation using data from head space analysis to derive binding parameters; the Klotz model (1) has been widely accepted as a reliable method for analyzing the binding characteristics of flavour compounds and proteins (Bi et al., 2022; Wongprasert et al., 2024; Kühn et al., 2007).

$$\frac{1}{v} = \frac{1}{n} + \frac{1}{nK[L]} \tag{1}$$

where v is the number of moles of the flavour compound bound per mole of protein.

n is the number of binding sites on the protein,
K is the binding constant and
L is the concentration of the incoming ligand.

Table 3
Recent research on the interactions between plant-based proteins and flavor compounds.

Protein type	Flavor compounds	Influencing factors	Investigation techniques	Major findings	References
Soybean protein isolate (SPI)	2-acetylfuran Furfural 5-methylfurfural	Position and number of methyl groups on the flavor compounds	SPME-GC/MS, PSD/Zeta potential, UV–Visible absorption spectrum, Fluorescence spectrum, FRET, TIC, DC, Time resolved fluorescence, Three Dimension fluorescence spectrum, Molecular docking.	• The flavor binding affinity to the protein follows the order: 2-acetylfuran > furfural>5-methylfurfural. • Presence of methyl side chain on acetyl group of the2-acetylfuran allows higher molecular flexibility of compound enhancing binding capacity to proteins. • Fluorescence quenching of the SPI by the compounds occurs via both static and dynamic quenching with static quenching being the primary method.	Li et al. (2024)
Pea protein isolate (PPI)	Pyrazines (2,3,5-trimethyl-pyrazine (TRP), 2,5-dimethyl pyrazine (DP), 2-methylpyrazine (MP))	Number of alkyl group and Concentration of flavor compound.	SPME-GC/MS, UV–Visible absorption spectrum. Fluorescence and synchronous fluorescence spectra. PSD/Zeta potential. Protein surface hydrophobicity. CD, DSC, 3-dimensional fluorescence spectroscopy. Molecular docking.	• Increase in number of alkyl group increased binding ability of PPI to pyrazines in the order:2-methylpyrazine <2,5-dimethyl pyrazine <2,3,5-trimethyl-pyrazine. • Increase in concentration of pyrazines (0.08 mM–0.4 mM) increased the adsorption capacity of PPI. • MP and DP exhibited static quenching whiles TRP was subjected to dynamic quenching.	Guo et al. (2024)
Pea protein isolate	**Strawberry esters** (ethyl butanoate, ethyl isopentanoate, ethyl hexanoate, and methyl anthranilate)	Temperature	GC-MS, Equilibration time, Molecular docking	• Binding affinity of PPI to esters decreased for each compound as temperature increased from 5 °C to 25 °C. • Long chain esters had higher overall binding affinity than short chain esters • The binding force between PPI and esters were van der Waals forces and hydrogen bonding	Wongprasert et al. (2024).
Pea protein	(Z)-2-penten-1-ol, hexanal, and (E)-2-octenal	Chain length and functional group of flavour compound	GC-MS, Fluorescence spectrum, Time resolved fluorescence, Protein surface hydrophobicity, CD, Molecular docking, Addition of bond disrupting/bond enhancing agents	• Molecular structure influences the flavor binding of PPI with (E)-2-octenal exhibiting highest binding, followed by hexanal and (Z)-2-penten-1-ol. • Hydrophobic interaction was the major force between (Z)-2-penten-1-ol, (E)-2-octenal and pea protein whiles hydrogen bonding was dominant between hexanal and pea protein.	Bi et al. (2022)
Yellow pea, soy, fava bean, and chickpea, with whey as a reference	Esters and ketones with different chain lengths (C4, C6, C8, and C10)	Protein type and concentration	APCI-TOF-MS	• Increase in concentration of protein led to stronger binding with flavor compounds. • Hydrophobic interactions between compounds and proteins decreased among proteins in the order chickpea > pea > fava bean > whey > soy. • The retention of esters and ketones is mostly determined by the flavor compounds, with the protein type playing a secondary role.	Snel et al. (2023)
Soy, pea and lupin protein	Hexanal, heptanal, trans-2-heptenal, cis-4-heptenal, octanal, 2-octanol, 2-heptanone, 2-octanone, 2-nonanone, and 2-decanone	Position of carbonyl group, degree of unsaturation of flavor compound	HS GC-MS, Protein surface hydrophobicity, Protein sulfhydryl groups measurement.	• Positioning of the carbonyl group (towards) the edge of the compound promoted binding. • The increase in degree of unsaturation increased flavor binding. • Heat treatment led to a slight increase in the hexanal-protein binding 5 °C–90 °C.	Barallat-Pérez et al. (2023b)

Abbreviations: SPME-GC–MS, solid-phase microextraction coupled with gas chromatography–mass spectrometry; CD, circular dichroism spectroscopy; APCI-TOF-MS, Atmospheric pressure chemical ionization time-of-flight mass spectroscopy; DSC, differential scanning calorimetry; PSD, Particle size distributions; FRET, Fluorescence resonance energy transfer measurement; TIC, Isothermal titration calorimetry.

Molecular docking is another approach used to predict interactions between proteins and small molecules. This technique uses computer simulations that can provide insights into important factors involved in flavour binding, such as protein binding sites (Zhao et al., 2020). Molecular docking also helps to demonstrate the effects of flavour binding or changes in physiological conditions on the protein structure (Guo et al., 2024; Wongprasert et al., 2024; Zhang et al., 2022a; Dinu et al., 2022; Bi et al., 2022; Zhang et al., 2023). There are limited studies that specifically assess the interactions of plant-based protein with key seafood flavours. As such, much of the publications cited in this section are intended to provide an overview of the progress made thus far in the efforts to better comprehend the mechanism of protein-flavour interactions in these foods. Understanding the binding phenomena between seafood flavours and proteins is therefore key to finding the right balance between flavour retention and release which will help improve the overall sensory profile (texture, and flavour (taste and aroma)) as well as the nutritional quality of seafood alternatives.

3.3.1. *Impact of protein structure*

Many recent studies have shown evidence of structural alterations in proteins caused by the adsorption of flavour compounds (Bi et al., 2022; Zhang et al., 2023; Wongprasert et al., 2024; Barallat-Pérez et al., 2023b). The extent of these modifications is dependent on the chemistry and concentration of the flavour compound as well as the isolation process used to extract protein from the food matrix (Barallat Pérez et al., 2023a). Nevertheless, the accessibility of protein binding sites for reactions with ligand molecules is controlled by the configuration and state of the protein (Dinu et al., 2022). In other words, the protein possesses binding pockets generated by the various functional groups present on its surface, which allow for interactions with specific compounds depending on how well they fit into the cavity (Barallat Pérez et al., 2023a). Consequently, flavour compounds with low binding constants and rigid structures will not bind well to the protein's surface due to the inability to fit into the protein's hydrophobic pockets (Guo et al., 2019).

Generally, flavour compounds interact with carboxyl (−COOH), sulfhydryl (−SH), or hydroxyl (−OH) groups of the proteins via electrostatic attractions and form hydrogen bonds, whereas amine (−NH2) or hydroxyl (−OH) groups form stronger ionic bonds and electrostatic linkages with flavours (Wang et al., 2022a; Wang and Arntfield, 2015a, 2015b; Reineccius, 2005). The irreversible covalent interaction between aldehyde-lysine and amines-carbonyl group demonstrates the possibility of interaction between flavour compounds and the side chains of proteins (Zhang et al., 2021a). Unlike non-covalent bonding, covalent bonds are invariably stable, and induce higher binding affinity when flavour compounds are combined with proteins, particularly those with a higher level of lysine, arginine and cysteine content (Wang & Arntfield, 2015a, 2016a, 2016b; Vatansever et al., 2024).

It is important to note that pulse proteins possess notably high concentrations of lysine (-NH_2 source), and this makes them susceptible to binding with unwanted flavour compounds (i.e., volatile or non-volatile) via both reversible and irreversible interactions. This could potentially interfere with the desirable flavour perception in the final product (Vatansever et al., 2024). The type of bonding, either covalent or noncovalent has a marked effect on the eventual flavour quality of the product. In contrast to the covalent bonds, non-covalent bonding occurs more rapidly and has been linked to food flavour deterioration and short shelf life (Anantharamkrishnan et al., 2020). Moreover, Gu et al. (2020) and Ma et al. (2019) argue that the various forms of bonding can be effectively harnessed to enhance the overall flavour characteristics of a product. Furthermore, the reversible interaction can help in finding balance between retention and release of the flavour whereas nonreversible interactions can help in eliminating off-flavours from foods (Gu et al., 2020; Ma et al., 2019).

Different protein fractions have been shown to have varied binding affinities to different flavours (Barallat Pérez et al., 2023a). Semenova et al. (2002) proved that the interior pockets of legumin is only compatible with short chain flavour molecules such as butyl acetate and amyl acetate. The study conducted by Heng et al. (2004) on pea proteins found a significant affinity of vicilin (7 S) for aldehydes, specifically octanal and pentanal, with binding percentages of 88% and 75% respectively whereas a weak interaction with ketone, 2-octanone was reported. Legumins (11s) on the other hand could only establish stable covalent hydrogen bonds with aldehydes via the sulfhydryl and amine groups on the protein (Heng et al., 2004; Guo et al., 2023).

An increase in protein concentration has also been associated with an increase in the binding percentage of flavour volatiles (Dinu et al., 2022). In a recent study, Snel et al. (2023) used atmospheric pressure chemical ionization time-of-flight mass spectroscopy (APCI-TOF-MS) to assess the binding of series of esters and ketones with different chain lengths (C4, C6, C8, and C10) with protein isolates of yellow pea, soy, fava bean, and chickpea, with whey as a control. The authors observed that an increase in protein concentration (5, 10, 20, 30 and 50 gkg−1) enhanced the retention of the volatiles which in turn decreased the concentration of the flavour compounds in the headspace. In a recent study, Zhang et al. (2023) observed the differences in the mechanisms involved in the adsorption of pentylfuran by different protein types (soy protein, peanut protein, and wheat protein). The authors concluded that the variation in conformation of the protein dictated the degree of binding to the compound and this occurred via hydrophobic interactions. Hence, the source of protein influences its binding behavior to flavour compounds.

The type of method used to isolate pulse proteins from flour generated from the dried seeds also influences their binding affinities to flavour compounds (Zhang et al., 2021a). In their work on pea protein isolates, Wang and Arntfield (2014) demonstrated that isolates generated via the alkaline-extraction -isoelectric precipitation method expressed higher binding affinities to homologous aldehydes (octanal, heptanol, and hexanal) compared to salt-extracted pea protein isolates. In another study, Xu et al. (2020) observed that beany odorants (i.e., hexanal and (*E*,*Z*)-2,6-nonadienal) found in pea proteins showed lower binding affinity in alkaline-extracted pea protein isolates compared to the raw pea flours.

3.3.2. *Impact of the chemistry of flavour compounds*

Food flavourings usually consist of several flavour compounds with specific functional groups and distinct notes that collectively produce the final aroma of the product. Differences in the structure or the stereochemistry of each flavour compound affects its interaction with the protein thus, perception of the flavour (Weerawatanakorn et al., 2015; Barallat Pérez et al., 2023a).

The location of the functional group of the molecule influences the binding to the protein as such, molecules that are structurally similar for instance nonanone and 2-nonanal would still exhibit varied binding capacities to proteins, with the aldehyde having a higher retention (Viry et al., 2018). Few recent studies have reported that aldehydes exhibit the highest binding affinity to protein followed by the alcohols, ketones, and esters (Zhang et al., 2022b; Guo et al., 2023). Damodaran and Kinella (1981) also attributed the superior binding capacity of aldehydes to the location of the keto functional group at the very end of the structure. This location enabled more adequate contact between the aldehyde chain and the protein via hydrogen interactions. However, positioning the functional group in the middle of the carbonyls as seen in ketones restricts this maneuver (Kühn et al., 2008).

In addition, Zhang et al. (2022b) postulated that alcohols in pulses bind more strongly to proteins than the ketones and esters due to their hydroxyl groups which acts as neutrophiles and electrophiles; conversely, the carbonyl group in ketones or esters is less electrophilic and exhibit less affinity to the protein. Moreover, Barallat Pérez et al. (2023a) also stated that the molecular spatial configuration of flavour compounds modulates protein-flavour interactions. Spherical structures are less favorable in binding with proteins due to the induced steric hindrance, which limits access to the protein's hydrophobic pockets required for hydrophobic interactions (Zhou and Cadwallader, 2006).

Within the same functional group, increasing the length of the aliphatic chain has been shown to elevate the flavour binding constant or degree of flavour retention degree (Viry et al., 2018; Wang and Arntfield, 2014). Wang and Arntfield (2014) observed higher binding capacities for long-chain aldehydes compared to short-chain ones irrespective of the protein type (pea, canola, or wheat protein) and protein isolation methods (alkaline- or salt-extracted). In addition, Guo et al. (2023) concluded that four types of protein-flavour interactions namely competitive, noncompetitive, anticompetitive and salting out emerge in a system with multiple flavours. At low flavour concentrations

(0.04–0.16 mM), the authors observed a competitive binding between two long chain compounds, ethyl caprylate and undecanal due to their compatibility to the same binding site on the soy protein surface. However, when undecanal was mixed with carvone which has a compact structure, a non-competitive binding occurred possibly because of the preference for different and independent binding sites on the protein.

Compounds having double bonds have a greater negatively charged surface area due to the presence of π electrons (Zhou and Cadwallader, 2006). This property, in addition to the structural rigidity imposed by the double bonds enhance binding capacity and retention to proteins (Ayed et al., 2014; Barallat Pérez et al., 2023a). Furthermore, the Michael addition between the double bonds (electrophiles) of the unsaturated carbonyl and the lysine or histidine residues (enolates or neutrophiles) of the protein, in tandem with the hydrophobic bonds, introduces new binding sites for interaction with the flavour compounds (Kühn et al., 2008; Leonard et al., 2022). In a study with soy protein, Leonard et al. (2022) showed that unsaturated aldehydes have higher retention with the protein than saturated ones. In addition, Barallat-Pérez et al. (2023b) also investigated the molecular interactions between commercial whey- or plant-based protein isolates such as pea, soy, and lupin, with carbonyl and alcohol flavour compounds by static headspace (HS) GC-MS. It was concluded that the degree of unsaturation of the flavour compound and the positioning of the carbonyl groups towards the edge of structure rather the middle improved the retention by 4.65% and 52.76% respectively.

Moreover, the increase of the concentration of flavour compound has been shown to enhance the adsorption ability of protein to flavour compounds (Guo et al., 2020a, 2024). In a recent study, Guo et al. (2024) assessed the mechanism of the binding between pea proteins and 3 pyrazines of different numbers of alkyl groups (*2*-methylpyrazine, 2, 5-dimethyl pyrazine, 2,3,5-trimethyl-pyrazine). The results showed stronger binding force with pea protein as the number of alkyl group increased protein (PPI). The retention of the pyrazines also increased as the concentration was increased from 0.08 mM to 0.4 mM (Guo et al., 2024).

3.3.3. *Impact of heat treatment*

During processing or preparation, seafood alternatives will possibly be subjected to some level of heat, which is likely to cause denaturation of the protein constituent. The ensuing conformational change will alter the distribution of bindings sites which affects the flavour binding capabilities of the protein (Wang and Arntfield, 2017; Anantharamkrishnan and Reineccius, 2020). Studies over the years have however demonstrated that the effect of heat on flavour binding is not one sided as both an increase (Xu et al., 2019; Viry et al., 2018) and a decrease (Xu et al., 2019; Wang and Arntfield, 2015b) has been reported. Thermal denaturation is known to induce the unfolding of the protein structure, exposing several interior hydrophobic cores or hidden binding sites thereby promoting flavour binding (Chen et al., 2023).

On the other hand, heat treatments (indirect effect) can cause the unfolding of proteins, followed by the aggregation of protein molecules and this facilitates the release of bound flavours (Xu et al., 2019; Zhang et al., 2021a). The elevation of the activity coefficient of the flavour compounds which is referred to as the direct temperature effect also contributes to the decline in binding and promotes release (Zhang et al., 2021a; Chen et al., 2023). As Chen et al. (2023) concluded, an interplay of the effects of protein structural changes and the coefficient of the flavour compounds during heat treatment account for the retention or the release of the flavour compounds from foods matrices.

Some authors have also speculated that the type of heating method; conventional heating or novel approaches such as low-temperature vacuum heating and microwave could possibly affect proteins' binding affinity of favor compounds (Chen et al., 2023; Han et al., 2019). Although, there is little literature on the impact of these different techniques on plant-based protein, Han et al. (2019) observed a stronger binding affinity of ketones to myofibrillar proteins due to a stronger structural change to the α-helix induced by microwave heating as compared to conventional water bath heating.

Guo et al. (2019) also demonstrated the variation in the binding capacities to flavour compounds due to the preheating of the protein solely, prior to mixing with the flavour compound, using headspace solid-phase microextraction gas chromatography–mass spectrometry (HS–SPME/GC–MS) technology. The authors observed that the binding affinities of preheated soybean protein isolate to hexyl acetate and heptyl acetate decreased with increasing temperature, while the proteins' bindings to geraniol, linalool, linalyl acetate, and linalyl formate were increased. The preheating treatment possibly caused an increase in the number of binding sites with lower affinity on the protein's secondary structure and the decline in the high affinity primary binding sites on the hydrophobic surface (Guo et al., 2019). There is however a limited number of investigations done to understand the impact of heating processing on the interactions between plant-based protein with seafood flavours and this work should be further explored. Globular proteins such as pea proteins have their maximum structural stability within the temperature range of 10–20 °C (Damodaran and Parkin, 2018; Dias et al., 2010; Liu et al., 2022). Besides high temperatures, proteins can also undergo structural changes at low temperatures, below −20 °C, through a process called cold denaturation (Damodaran and Parkin, 2018; Dias et al., 2010). Nevertheless, there is limited knowledge regarding the cold denaturation mechanism in plant proteins, its impact on their functionalities, and its significance for product development (Helmick et al., 2021). If systematic research can confirm the advantages of cold denaturation, it could introduce a new method of processing to modify proteins and enhance their suitability in product development, including innovative dietary options like plant-based seafood substitutes.

3.3.4. *Impact of ionic strength/salt*

Changes in pH of the matrix solution induces structural and functional changes to the protein which affects flavour-protein binding affinity and hence flavour perception. Wang and Arntfield (2015a) studied the impact of pH change (3, 5, 9, 11) on the binding affinity of pea protein isolate to 3 ketones (2-octanone, 2-heptanone, and 2-hexanone). The authors observed that the overall binding effect to the ketones followed the order $3 < 11 < 9 < 7 < 5$. Plant proteins typically have an isoelectric point between 4 and 5. Near the isoelectric point, proteins denature partially, enhancing hydrophobic interactions with flavour compounds. At acidic pH (3), the protein denaturation alters the conformation of protein which results in the loss of hydrophobic pockets available for flavour binding. As the pH rises to basic levels (9–11), the solubility of the proteins is increased which however lessens the hydrophobic binding sites available for interactions (Wang and Arntfield, 2015a; Gao et al., 2020). Guo et al. (2020a) who also observed a positive correlation between the binding of flavour compounds (heptyl acetate, hexyl acetate, linalyl acetate, linalyl formate, geraniol, linalool) to soy protein isolates as pH increased from 3 to 9. The authors explained that increase in pH enhanced the flexibility of the protein structure as the protein denatures and unfolds, revealing sulfhydryl and hydrophobic regions in their structure and allowing new protein-flavour interactions to develop (Guo et al., 2020a).

Addition of ionizable salts (ions), including their specific type and concentration can alter the state of charged groups on the protein, thus affecting interactions and solubility (Zhang et al., 2021a; Wang and Arntfield, 2017). Anions and cations that have the capacity to trigger protein precipitation generally lead to the unfolding of protein peptides, which in turn exposes hydrophobic areas, allowing unrestricted access to flavour compounds (Zhou et al., 2019). Salts can be classified as either chaotropic or non-chaotropic based on their impact on the interactions between proteins and ligands. The introduction of bond disrupting chemicals or chaotropic salts, such as guanidine hydrochloride, $NaClO_4$, and NaSCN, causes protein denaturation, leading to the breakdown of intra-molecular forces such as hydrogen bonding and hydrophobic interactions (Wang and Arntfield, 2015a; Zhang et al., 2021a). On the other hand, Na_2SO_4, KCl, and NaCl are non-chaotropic salts that have the tendency to enhance the hydrophobic interactions between protein and flavour compounds, thus leading to improved flavour bindings (Wang and Arntfield, 2015a; Zhang et al., 2021a).

Wang and Arntfield (2015a) also reported an increase in flavour binding abilities of salt-extracted pea protein to ketones (2-hexanone, 2-heptanone and 2-octanone) on addition of high concentration of NaCl (from 0.25 M to 1 M) whereas the addition of chaotropic salt (NaSCN) reduced the flavour binding. In a subsequent study with different type of chaotropic ($Cl_3CCOONa$) and non-chaotropic salts (Na_2SO_4), the authors concluded that $Cl_3CCOONa$ reduced the binding capacity of the salt-extracted pea protein for benzaldehyde, 2-octanone and hexyl acetate, while the Na_2SO_4 improved the flavour binding effect of the protein (Wang and Arntfield, 2016b).

Understanding the effect of pH and ionic conditions in the food system will enable us to modify the flavour-protein interaction, which leads to better flavour perception. Nonetheless, it is important to be aware of the limitations of these treatments, as excessive measures may result in unpleasant alterations to other sensory characteristics such as texture and mouthfeel. There is however a need to find a good balance to develop the most acceptable products. Currently, there is insufficient research to provide enough insight into the impact of pH and ionic strength on interactions between plant proteins and seafood flavour compounds.

3.3.5. *Impact of small molecules (water and sugar)*

Food is a complex system consisting of macromolecules such as proteins, lipids, and carbohydrates and small molecules like flavour compounds that participate in reactions with significant effects on the quality and functional characteristics of the food. A few studies have provided insight on the interaction between these macromolecules and flavour compounds; and how these interactions affect flavour delivery (Guo et al., 2020a, 2024; Barallat-Pérez et al., 2023b; Liang et al., 2020; Shao et al., 2021). Guichard (2011) highlighted that fat has the greatest impact on flavour partitioning in comparison to proteins and carbohydrates. Nevertheless, there is a scarcity of data regarding the significant influence that small molecules such as sugar and water have on protein-flavour interactions. Further instrumental and sensory assessments are necessary to gain a deeper understanding of how low-molecular-weight sugars impact the flavour binding of plant-based proteins, as some authors have suggested that sugars may enhance the thermal and conformational stability of globular proteins in an aqueous medium (Kulmyrzaev et al., 2000; Baier and McClements, 2001; Khan and Shabnum, 2001).

Sugars can protect the protein molecules, stabilize the structure, and limit protein aggregation, which can have an impact on the protein-flavour interaction (Olsson and Swenson, 2019; Olgenblum et al., 2023). Some investigations conducted on beverages attempted to provide insights on the influence of sugars on flavour delivery. It was explained that the interaction between the sugar and water molecules in the system cause the flavour compounds to concentrate in the residual water in the system; this modifies the flavour partitioning and facilitates their release (Hansson et al., 2001; King et al., 2006; Tsitlakidou et al., 2019).

Interactions with water molecules in the system influence the physicochemical behavior of the food constituents including strength of interactions between macromolecules and ligands (Zhang et al., 2021a). Zhou and Cadwallader (2006) found that polar flavour compounds interact with soy proteins through both specific (hydrogen-bonding, dipole forces) and non-specific (van der Waals forces) interactions. Adsorption of water at low humidity (e.g., 0% RH) has been shown to facilitate these interactions. At higher humidity (30–50%), the effect of water on binding to polar compounds were non-existent, although an adverse effect on binding with alcohols were observed. Nonpolar flavours, such as hydrocarbons, remained unaffected by environmental relative humidity due to non-specific protein interactions. Seuvre et al. (2001) demonstrated the effect of water on the conformation of b-lactoglobulin and the aroma retention capacity. According to the authors, low water content (less than 6%) showed minimal modification to the binding of four flavour compounds (2-nonanone, d-linalool, Isoamylacetate and benzaldehyde) to the protein. However, hydration (in solution) of the protein spiked the flavour retention up to 40 folds higher than at low water levels, with the greatest effect observed on the 2-nonanone. Seuvre et al. (2001) attributed this observation to the unfolding of the protein by water, leading to an increase in accessibility to binding sites, and the potential dissociation of compounds before binding to the proteins. Since water generally serves as the solvent, it is essential to respect the influence of other factors in the matrices, such as pH and the properties of the flavour compounds under study, as these also affect the protein, thereby influencing its flavour binding abilities.

3.3.6. *Protein modification*

The state of a protein's native conformation, including their active residues regulates its behavior in an environment with other compounds (Saffarionpour, 2024). Enzymatic and non-enzymatic modification (Acylation) methods can alter the protein structure and hence are commonly used to modify the protein's functionality including flavour binding ability (Dent and Maleky, 2022; Wang and Arntfield, 2016a). Acetylation and succinylation are the most used acylation approaches which have shown to be detrimental to the flavour binding capacity of proteins, hence the flavour perception (Saffarionpour, 2024). Acylation at high levels trigger protein subunit separation by concealing lysine residues and exposing key hydrophobic regions on the protein surface. This alteration hinders the binding of volatiles, such as aldehydes, to the ε-amino groups of lysine residues (Wang and Arntfield, 2016a; Shen et al., 2022; Shah et al., 2019).

During acetylation and succinylation, a positively charged lysine residue in a protein molecule is replaced with hydrophobic acetyl groups and succinyl groups, respectively. This increases the negative charge of the protein, thus weakening the protein's characteristics especially the flavour binding abilities (Shen et al., 2022; Shah et al., 2019). Okagu et al. (2021) also successfully applied succinylation to reduce the retention of hydrophobic off-flavours in pea proteins. The authors explained that adding succinic groups to the protein made the surface less hydrophobic and raised the negative charges on the protein thus affecting the binding affinity.

Proteins may be modified enzymatically via enzymatic hydrolysis using protease enzymes such as Alcalase, Papain, Bromelain, Trypsin, or Chymotrypsin (García Arteaga et al., 2020; Samaei et al., 2020; Zhou et al., 2021). These enzymes initiate the dissociation of the peptide bonds and reduction of protein's molecular weight; the proteins tertiary structure is destabilized as a result, weakening the hydrophobicity thus affecting the flavour-protein interactions (Chen et al., 2023; Wang and Arntfield, 2017). Wang and Arntfield (2016a) found that when pea protein was treated with the endopeptidase alcalase, it caused the protein peptides to be broken down, reduced the hydrophobicity on the surface, and decreased the ability to bind with esters and ketones. However, a relatively higher retention of aldehydes and disulfides occurred (Wang and Arntfield, 2016a).

Enzymatic deamidation is another approach used by Temthawee et al. (2020) in a study where protein glutaminase was shown to minimize the overall binding capacity of modified coconut protein to vanillin. Suppavorasatit and Cadwallader (2012) also subjected soy proteins to enzymatic deamidation by glutaminase and observed a decrease in the binding affinity for vanillin and maltol at 25 °C. Essentially, enzymatic deamidation impairs protein–flavour interaction. Although this is not in the scope of the review, it's crucial to acknowledge that plant proteins often exhibit off-flavours such as grassy, fruity, or roasted notes. These off-flavours can hinder their use in food formulation. Chen et al. (2023) have proposed the application of these techniques to eliminate these off-flavours or address flavour fade issues in food products.

4. Emerging technologies to mimic the texture of plant-based seafood alternatives

The texture of seafood is determined by its elasticity and the tactile/mouthfeel sensation it produces during mastication (Ran et al., 2022). The differences in physicochemical characteristics between animal and plant proteins make it difficult to replicate the tender, chewy texture of meat and seafood in their alternatives (Zhong et al., 2023). Wheat, gluten, soy, and pea proteins are the most used protein sources due to their lower costs and superior functional qualities such as high oil absorbency, gelation, emulsification, and more; hence, they are capable of effectively imitating the fibrous textures seen in meat (Guo et al., 2020b) (see Fig. 1).

Extrusion, a complex thermo-mechanical process, has been extensively employed by the industry to create meat alternatives that closely resemble the texture of traditional meat (Samard and Ryu, 2019; Vatansever et al., 2024) and alternative seafood products (Table 4). This technique involves subjecting the formulation to a continuous process of churning, shearing, heating, and cooling in a heated barrel to solidify the fiber or strand. Subsequently, the cooked mass is then extruded through a nozzle (Singh et al., 2021). The extrusion processes can be categorized as either high-moisture or low-moisture, depending on the quantity of water introduced into the extruder to produce meat-like slices (Singh et al., 2021). Scientists have devised further innovative methods, such as electrospinning, shear-cell, and 3D printing, as alternatives to extrusion (Fig. 2), for applications in plant-based meat and seafood alternatives with a more refined texture (Cornet et al., 2022).

4.1. Electrospinning

Electrospinning is a robust, economical, and rapid technique that has been applied for the structuring of polymer solutions into micro and nanoscale fibers using high voltage (Nieuwland et al., 2014). For plant-based analogues, the procedure entails propelling the protein solution through a hollow needle or a spinneret by generating an electric force between the spinneret and the ground surface (Nieuwland et al., 2014). A key requirement for electrospinning is for proteins to be highly soluble and behave as random coils (Dekkers et al., 2018). However, plant proteins commonly used for plant-based formulations alternatives (such as soy protein) are generally in their native globular conformation, which can impede fiber couplings and entanglements, hence complicating the process of electrospinning (Nieuwland et al., 2014). The proteins must therefore be unfolded and denatured prior to electrospinning. This can be achieved by subjecting them to a mix of alkaline and heat treatment at a pH over 4.5, which helps in unfolding and solubilizing the proteins (Vega-Lugo and Lim, 2008). Using higher concentrations of the solution for the process has also been recommendation as long as the proteins remain dissolved in the solution (Moreira et al., 2019). An alternative approach involves integrating the proteins with other functional components, such as the biopolymers cellulose and maltodextrin to optimize the spinning procedure (Kutzli et al., 2020). The addition of other proteins, plasticizers and cross-linkers can increase the intermolecular interactions between the proteins and copolymers which in turn improves water resistant capacity, thermal resistance and the mechanical strength of the fibres (Federici et al., 2020). In a recent study, Ozturk et al. (2023) demonstrated the potential of the prolamin

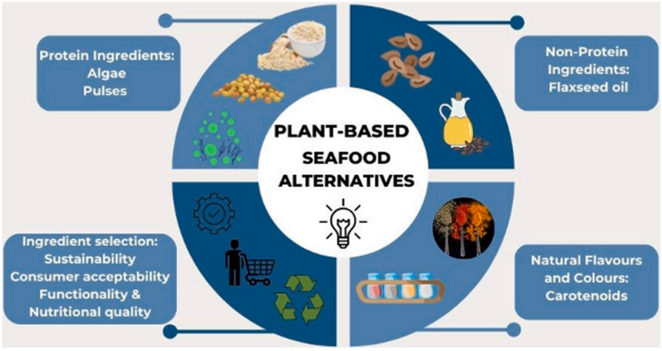

Fig. 1. Key ingredients that have been used in the development of plant-based seafood products. The ingredients used in these formulations should exhibit high nutritional quality and functional properties and have reduced contributions to greenhouse gas emissions. Using these high-quality ingredients is a first step in formulating products with improved consumer acceptability.

Table 4
Technologies to produce seafood alternatives, respective products developed, and their associated advantages and limitations.

Techniques	Raw materials	Products Developed	Advantages	Limitations	References
Wet spinning	Soy protein isolate, algae and pea proteins	Plant-based shrimp and crab sticks, algal-based fish fillets	Production of defined fibrous protein products	Generate large amount of chemical waste	(Dekkers et al., 2018; Mu et al., 2019; Zhang et al., 2021b)
Electrospinning	Soy protein isolate and alginate	Plant-based fish fillets and crab meat, algal-based shrimp	Scalable approach, cost effectiveness, production of very thin fibrils	Proteins must be in an unfolded confirmation, rather that globular nature	(Mattice and Marangoni, 2020; Moreira et al., 2019)
Extrusion	Pea protein	Plant-based fish sticks and shrimp nuggets	Energy efficient, low cost, highly versatile and productive, enhancing protein digestibility, and destruction of anti-nutritional factors	Presence of too many insoluble components can disturb cross-linking of proteins	(Lima et al., 2022; Sha and Xiong, 2020; Zhang et al., 2021b)
3D Printing	Soy protein isolate and xanthan gum	Plant-based fish fillets and crab meat	Reduce energy and waste in the food industry, customizing nutritional content of the product, designing products with similar texture to muscle fibers	Printed protein solution needs to be homogeneous and have adequate printability	(Chen et al., 2019; Godoi et al., 2016; Sha and Xiong, 2020)
Freeze structuring	Plant proteins	Plant-based shrimp nuggets and crab cakes	Modulation of textural properties of plant proteins	Proteins should show relatively more solubility before freezing, during the freezing process these proteins get insoluble	(Dekkers et al., 2018; Lima et al., 2022)
Shear cell technology	Plant proteins and algae	Plant-based scallops and lobster tails, algal-based fish cakes	Cost effective and Production of defined fibrous protein structures	Limited scalability and process optimizing challenge	(Dekkers et al., 2016; Grabowska et al., 2014)
Mixture of proteins and hydrocolloids	Soy, rice, corn and lupine	Plant-based fish cakes and shrimp paste, algal-based seafood sticks	Development of fiber frameworks that can be modifiable	Texture limitation and flavor masking	(Dekkers et al., 2018; Singh and Sit, 2022)

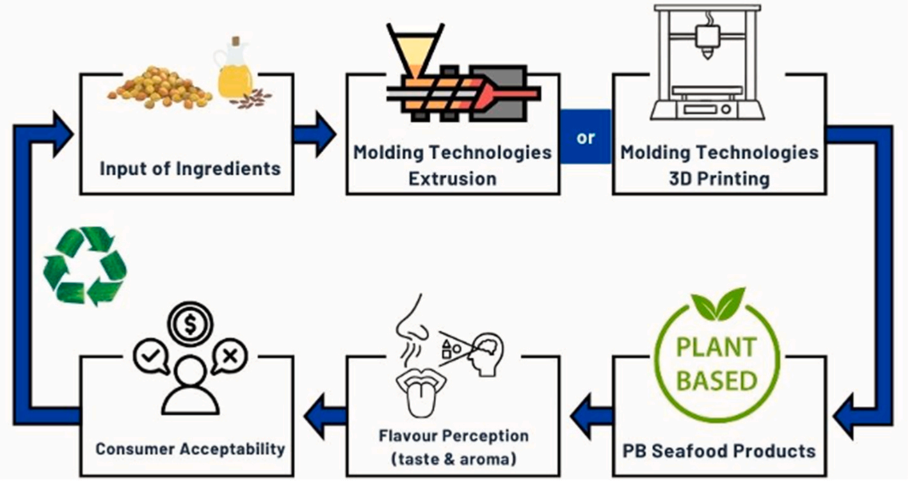

Fig. 2. The main steps involved in the development of plant-based seafood alternatives. Selected ingredients are usually extruded or molded using other technologies such as 3D printing or electrospinning to form structures resembling conventional seafoods. The resulting plant-based seafood alternatives are prepared to match the flavour and aroma of traditional seafood products, which are important to increase consumer adoption of these foods. A big challenge is to ensure that the sustainability advantage is not lost in any steps of the production and consumption chain.

protein zein, to create a dispersed viscoelastic network within a pea protein-based structure, which has encouraging implications for plant-based formulations.

4.2. *Wet spinning*

Another approach that can be used in industrial applications for the production of seafood analogues is wet spinning (Kyriakopoulou et al., 2019). In 1954, Boyer obtained a patent for applying the wet spinning technique in the development of meat analogues (Dekkers et al., 2018). In this approach, the protein solution (ideally $\geq$20%) is driven into a coagulation bath containing a solvent which can limit the solubility of the protein solution, or facilitate cross-linking and fiber formation (Kazir and Livney, 2021; Nowacka et al., 2023). This solvent can also cause protein precipitation, and with the high shear forces of the bath nozzle, proteins get aligned forming stretched filaments (Dekkers et al., 2018). To enhance the production of protein cross-linking, binding agents, such as Ca^{2+} must be added to the solvent. Changing the acidity of the solution, can also facilitate the formation of inter- and intra-molecular bonds between the protein chains (Chen et al., 2023). The fibres ($\sim$20 μm thickness) formed from the process are physically or chemically treated then washed and purified from the solvent (Kazir and Livney, 2021; Nowacka et al., 2023). The treatment helps to improve fibre properties such as mechanical strength and molecular orientation (Chen et al., 2023). The structure of the fibres formed is mainly dependent on the solidification mechanism, which means there can be three types of products. Fiber products can be collected upon solidification of the dispersed phase while removing the continuous phase, capillary filled gels can be received when the continuous phase is hardened while the dispersed phase remain as a liquid, and fiber filled gels can be attained when both the continuous and dispersed phases get solidified (Dekkers et al., 2018).

Although wet spinning has a long history in making fibrous protein products, there are several factors that must be considered (Boukid, 2021). First, the procedure requires the use of pure proteins, low pH, high concentrations of salt and chemical additives (Boukid, 2021). Second, the use of large amounts of chemical reagents and the generated waste can lead to sustainability issues (Kołodziejczak et al., 2021). Third, on a large scale, the structural modification of plant proteins using wet spinning does not alter substantially after the chemical or physical treatment due to the complexity of the secondary and tertiary structures. As a result, the application of this method can be limited when producing fish alternatives with satisfactory textural properties (Zhong et al., 2023).

4.3. *3D printing*

3D printing, which is also known as additive manufacturing (AM), is a principal food processing technique which includes stereolithographic and photographic methods (Severini et al., 2018). This strategy has been developing rapidly over the last decade with various techniques, but the most common method is based on syringe injection. In this method, a protein solution is extruded through a moving fine syringe nozzle together with a very high viscosity nature. Then layer by layer is moved to form a 3D product, e.g., muscle-shaped structure (Sha and Xiong, 2020). This print is based on a pre-engineered digital model and the printed protein template must have appropriate printability (the ease with which the material can be controlled and deposited by a 3D printer (Wang et al., 2022c), and should be homogeneous (Dick et al., 2019; Wang et al., 2018). This printability is based on chemical and physical nature of the protein, the flowability through the nozzle, and the quickness of solidifying the 3D framework. For example, in the presence of wheat flour, molecular interactions between proteins and carbohydrates can promote the formation of the fibrous product, and the mixing of gelatin to the 3D printed soy proteins can increase the chewiness as well as the hardness of the final print (Chen et al., 2019; Godoi et al., 2016). For fish and meat products, the 3D printed model must be durable and resistant to thermal cooking processes, because of the need for heat processing of printed products before consuming (Kazir and Livney, 2021).

Not only animal proteins, but also several plant-based materials such as pea protein, soy protein and wheat protein have been examined for 3D printing (Ramachandraiah, 2021). Multiple achievements were accomplished when using soy proteins to synthesize a range of seafood analogues, e.g., fish fillet analogues and protein rich snacks (Chen et al., 2019; Shahbazi et al., 2021). Particularly, the presence of salt can decrease the viscosity of the mixture of soy protein and xanthan gum which can improve the printability of the solution (Phuhongsung et al., 2020). Although various studies have been completed on 3D printing, still there are some challenges when using plant-based proteins, to obtain acceptable mouthfeel and texture. It was also found that, pretreatment of plant proteins without using additives can reduce the capability of forming a suitable 3D structure (Godoi et al., 2016).

Three types of approaches have been presented to adjust the 3D structure as well as viscoelastic behavior of 3D-printed plant-based alternatives: process control, co-printing with other biopolymers, and the use of enzymes (Chen et al., 2019). Among these strategies, process control is the most straightforward method used to tune rheological and structural aspects of plant proteins. For an instance, heating-cooling procedures have improved the accuracy and printing quality of soy products (Chen et al., 2019). With respect to co-printing with other biopolymers, surface active polymers (e.g., esterification of starch with dicarboxylic acid – OSA modified starch), gelatin, xanthan gum, sodium chloride and sodium alginate were reported to strengthen the 3D printed structure of soy protein, yet more mechanical understanding are still required (Phuhongsung et al., 2020). Also, these biopolymers can significantly enhance the shear-thinning behavior. Increase in biosurfactants concentration can also result with boosting viscosity recovery, elastic modulus, and yield stress (Shahbazi et al., 2021). Transglutaminase (TGase) is an important cold-set binder which is commonly used in enzymatic treatments for modifying plant-based proteins during the printing process. TGase can restructure the plant-based materials such as, soy, pea and wheat proteins, by helping the binding of various meat analogues cohesively (Dong et al., 2020; Shand et al., 2008).

Optimizing printing parameters are carried out based on the structural and physical properties of the desired product. To produce fine fibrous structures with small diameters, which are found in fish-meat materials, small diameter nozzles are preferred (Nachal et al., 2019). However, this small nozzle height and high printing speed can hinder the settling of printed protein solution, therefore, printing precision and mechanical strength of the final product can be reduced (Nachal et al., 2019). In addition, another study has shown that, in low moving speeds, less accurate prints can be formed due to the instability of the flow, and the printed fibers get thicker when a high nozzle height is used (Wang et al., 2018).

The main challenges of 3D printing are scalability process, maintenance services, production cost, complexity of spatial structure, and regulatory frameworks such as labelling and adulteration. Business level operation of 3D technology depend on the availability of material and labor supply, cost competition, consumer demand as well as government policies (Godoi et al., 2016).

4.4. Shear cell technology

This novel technology, which is based on the concept of flow-induced structuring, has been successfully used to structure plant proteins (Manski et al., 2007a, 2007b). The procedure can be carried out in either a conical shear cell or a cylindrical Couette cell, where high shear forces is applied to a protein-rich material under high temperatures to produce anisotropic fiber-like structures that mimics those found in meat (Cornet et al., 2022). The Couette shear cell was also designed using the concept of shear-induced structuring and has been successfully used to develop meat analogues at elevated temperatures while maintaining the structural integrity. Unlike typical extrusion techniques, shear cell technology imparts a more well-defined and constant deformation of plant-based proteins, enabling the production of fibrous meat analogues that remain stable and structurally consistent even after cooling (Manski et al., 2008).

Several studies have investigated how adding ingredients like l-cysteine, ascorbic acid, and xanthan could improve the texture and functionality of meat substitutes in the shear-cell device (Taghian et al., 2023a; Taghian et al., 2023b; Wehrmaker et al., 2022). The study conducted by Taghian et al. (2023b) showed that the addition of xanthan to the protein matrices in the shear cell device enhanced the juiciness and anisotropy of the meat alternatives they developed. However, scaling the technology necessary for mass production of these protein structures appears to be a challenge (McClements and Grossmann, 2021).

4.5. Other emerging techniques

Fibrous structures can also be formed using a technique designed and patented by Mehran et al. (2013). This technology involves creating a stable emulsion in a colloidal solution by mixing water, hydrocolloids (e.g., sodium alginate and methylcellulose), and plant proteins. The homogeneous mixture is then mixed with a solution of a metal cation, such as calcium, to coagulate the protein and form a fibrous product (Mehran et al., 2013).

In their study, Kobata et al. (2023) explored the application of emulsion gel technology to create a substitute for sea foie gras, a popular Asian delicacy usually obtained from the liver of monkfish. The scientists combined RuBisCO protein isolates extracted from duckweed, with flaxseed oil to create concentrated oil-in-water emulsions. The mixture was then heated to induce protein coagulation. The resulting emulsion gel can be utilized to create an alternative that possess the same textural characteristics as authentic foie gras (Kobata et al., 2023). However, additional research is required to compare the sensory and nutritional qualities of alternatives with the conventional sea foie gras products.

Of the current technologies discussed in this paper, extrusion is the leading processing technique used for developing plant-based seafood analogues. However, several bottom-up approaches such as electrospinning and 3D-printing, which can assemble individual elements into a more textured structure, have revealed the capability of mimicking the unique W-shaped muscle structures of fish (Nowacka et al., 2023; Zhong et al., 2023). Wet spinning is also an emerging technology which has the potential of developing seafood alternatives with their characteristic texture and appearance, but these novel technologies are still being used at the research level and may be too expensive for large-scale production (Zhong et al., 2023).

4.6. Impact of processing technologies on the quality of PBSA

As previously discussed, processing technologies play an important role in advancing the development of plant-based foods including seafood alternatives (Lanz et al., 2024). However, in recent years, high moisture extrusion (>40%) has emerged as one of the predominant texturing methods for producing plant-based foods (Sun et al., 2021). Although there are not many specific examples of PBSA, the effects reported generally for plant-based foods may apply in this context.

The reported beneficial effects of extrusion include improving product texture as well as inactivation of hydrolytic enzymes (e.g., lipoxygenases) and anti-nutritional factors such as trypsin inhibitors that limit protein digestibility (Boukid, 2021). Extrusion also facilitates the digestion of dietary fibers by disrupting glycosidic bonds in insoluble polysaccharides and converting them to small soluble components (Yu et al., 2023). Other benefits of extrusion include, enhanced soluble dietary fibres changes reduced lipid oxidation and improved starch gelatinization (Nikmaram et al., 2017). Although starch gelatinization can have a positive effect on texture formation, the presence of fewer starch particles can result in reduced viscosity which requires high screw speed, which in turn can affect the functionality of the plant proteins (Rong et al., 2023). Extrusion can also induce the disruption of hydrogen and valence bonds between starch molecules, which can increase the interactions with amylase, hence improving starch digestibility (Huang et al., 2022).

However, the high temperatures used (140–180 °C) in extrusion can have negative consequences on the protein used (Leonard et al., 2020). For example, during extrusion, hydrophobic residues in proteins get exposed to high shear and temperature environments, which cause unfolding of proteins and changes in their arrangement to match the direction of the flow in the extruder (Yu et al., 2023). Due to this heat instability, proteins can be denatured during the extrusion process (Zhao et al., 2022). In addition, new intermolecular interactions and aggregations among the proteins can occur, which results in changes in the protein content and functional properties (Yu et al., 2023). The high temperatures (140–180 °C) encountered during extrusion processing can also facilitate the Maillard reaction, which can generate alterations in protein structure, functional characteristics, and nutritional properties (Yu et al., 2023; Zhao et al., 2022).

Proteins also play an important role in contributing to the flavour of plant-based foods. When hydrolyzed to amino acids, they act as flavour precursors in the Maillard reaction which result in desirable product attributes (brown color formation and flavour development) (Wang and Arntfield, 2017). The breakdown of proteins to peptides can also contributes to flavour development (Wang and Arntfield, 2017). However, during extrusion, the high temperature processing of protein products can lead to harmful byproducts such as heterocyclic aromatic amines and advanced glycation end products (Nowacka et al., 2023).

In the extrusion process, lipids can cause emulsification and plasticization, delivering desirable viscosity and texture to the extruded products. As a result, the texture, sensory attributes, and nutritional quality of the final plant-based product is impacted (Lampi et al., 2015). During this processing technique, lipids can make complexes with starch, and interact with proteins via hydrogen and covalent bonds and electrostatic interactions (Kyriakopoulou et al., 2021). Furthermore, high temperature and pressure conditions can induce lipid oxidation and degradation, forming volatile compounds such as alcohols, ketones, aldehydes, and esters. These by-products often linked to undesirable odors and can negatively impact the flavour profiles and acceptability of plant-based seafood products (Guo et al., 2020a; Kyriakopoulou et al., 2021).

During extrusion, physical parameters such as the screw speed, barrel temperature, die diameter, as well as the moisture content of raw materials in the extrusion process, can influence the vitamin retention in plant-based seafood products. Micronutrients such as vitamins B2, B6, B12, biotin, niacin, and pantothenic acid are stable during the process whereas thiamine has poor stability, and vitamins A, B1, C, E, and folate can be lost (Brennan et al., 2011; Riaz et al., 2009).

When determining the quality of 3D printed foods, the properties of the materials, as well as the processing and post-processing factors (for e.g., baking and steaming) should be considered (Wang et al., 2021). The application of 3D printing in the food industry (especially for PBSA) is still in its infancy and more work needs to be done to better understand the impact of this processing method on the quality of plant-based foods (Lanz et al., 2024). In general, nutrient quality may decrease over time due to slow degradation, oxidation or interactions between materials or other components in the food matrix Among the limited literature available on plant-based foods developed with 3D printing technology, the majority have focused on texture design (Fahmy et al., 2021). Conversely, others have evaluated the color and appearance of 3D printed vegetables and found no difference when compared to their conventional counterparts (Bhat et al., 2021). In one study, (Tay et al., 2023) used 3D printing to develop plant-based salmon fillets and transglutaminase was used to promote aggregate binding. Inspite of these advances, the technology still faces many challenges including slow consumer acceptability and concerns about the microbial quality and the safety of 3D printed foods which need to be addressed in a timely manner (Abedini et al., 2024). Little is also known about protein flavour interactions in 3D produced food matrices and how these interactions contribute to flavour profiles. Thus, more work needs to be done to increase consumer understanding about 3D technology and the regulations that guide the safe processing of these foods. Research with the goal to better understand food matrix interactions in these food systems, would also contribute to improving product quality.

5. Future directions and conclusions

The acceptability of plant-based seafood is heavily dependent on the sensory characteristics (texture and flavour quality), as well as the nutritional quality of the products. Over the years, a few studies have revealed that flavour perception in plant-based seafood productions is possible because of interactions between the proteins and the sea flavours. However, various factors affect these interactions, including the intrinsic physicochemical properties of the protein and the chemical properties of the flavour compounds, such as structure and functional class. In addition, extrinsic or environmental factors such as temperature, pH, ionic strength, and other ingredients in food systems can affect protein-flavour interactions, thus influencing flavour retention and release.

Scientists have utilized a combination of multi-spectroscopic methods (GC/MS, fluorescence measurement, circular dichroism, and differential scanning calorimetry) and computational techniques (molecular docking) to study the interactions between plant proteins and flavour compounds. They have examined the binding forces involved, which can be either covalent or non-covalent, and have also investigated the changes in the protein's conformational dynamics after the flavours are adsorbed. While there are existing studies on the interactions between proteins and flavours, there is a dearth of information regarding the binding mechanisms between plant-based proteins and seafood flavours. Further research should explore protein-flavour binding phenomena in complex solid matrices that accurately replicate the conditions of a real seafood alternative systems. Gaining insight into the mechanism that modulate the interactions between proteins and seafood flavour, as well as the elements that affect these interactions, is an essential process in discovering possible approaches to control and enhance flavour delivery, and overall flavour quality of plant-based seafood alternatives.

Currently, manufacturers are formulating plant-based seafood alternatives using commercial flavouring agents with diverse volatile compositions These product developers expect that these flavour compounds will effectively adhere to the food matrix, withstand any extrinsic conditions from production to the consumer's plate, and thereafter be released adequately during consumption. However, there is a lack of research regarding the adsorption process or the binding behavior of plant proteins in complex flavour systems that contain a wide variety of seafood flavour compounds. Furthermore, besides these theoretical studies, dynamic in vivo techniques such as Atmospheric Pressure Chemical Ionization-Mass Spectrometry (APCI/MS) as well as sensory evaluations should be utilized to gain a more comprehensive understanding of the compounds that contribute to seafood flavour perception. These techniques can also help determine the effect of external conditions on the stability of protein-flavour binding and how this translates into flavour delivery during mastication, both in vivo and in vitro.

Although PBSA is often promoted as a viable substitute for traditional seafood, however, there are some limiting factors, including lower protein quality, the absence of omega 3 and other micronutrients, that need to be addressed for PBSAs to effectively fulfill consumers' nutritional requirements. Blends of protein isolates or concentrates (cereals, pulses) have been used to improve the quality of protein and enhance the nutritional value of PBSA relative to conventional products. Extrusion processing is currently the method of choice for texture design, and 3D-printing and electrospinning are promising technologies, however, the applicability of these processing methods for large-scale production and concerns about microbial safety needs to be further investigated. Furthermore, it may even be worth assessing whether combining one of more these techniques could be more successful at achieving more comparable product structures. More comprehensive assessments of the gastrointestinal behavior of PBSA are necessary to enhance our understanding of the digestibility, accessibility, and bioavailability of nutrients in these foods. Overall, PBSAs that effectively replicate the sensory characteristics as well as the nutritional qualities of their conventional counterparts can be viable means of fostering consumers' willingness to incorporate these foods in their diets.

CRediT authorship contribution statement

Enoch Enorkplim Abotsi: Conceptualization, writing and reviewing. **Yashodha Panagodage:** writing and reviewing, All authors contributed to the article and approved the submitted version. **Marcia English:** Conceptualization, writing, reviewing, editing, Funding acquisition, Supervision, project administration.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

Marcia English reports was provided by Nothing to declare. Marcia English reports a relationship with Nothing to declare that includes:. Marcia English has patent pending to Nothing to declare. Nothing to declare, ME. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

No data was used for the research described in the article.

Acknowledgments

The research program of ME is supported by the Natural Sciences and Engineering Research Council of Canada (NSERC) Research Chairs, NSERC Discovery Grant RGPIN-2021-03195 and a Field Catalyst grant from the Good Food Institute. EA is a recipient of a Memorial University of Newfoundland Doctoral Scholarship and YP is a recipient of a Nova Scotia graduate scholarship.

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