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Review Article

Sustainable processing of seafood byproducts through enzymatic technologies: A comprehensive review

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Abstract

Commercial fishing operations often discard up to half of their raw catch, including scales, shells, frames, viscera, and other less desirable parts. This discarded biomass, coupled with low-value by-catch, poses significant environmental challenges due to its rapid decomposition. However, these materials represent an underutilized source of valuable compounds such as proteins, enzymes, carotenoids, fats, and minerals. This review consolidates recent advances in enzymatic technologies for the sustainable processing of seafood byproducts. It highlights the role of fishery-derived enzymes such as proteases, lipases, chitinases, alkaline phosphatases, transglutaminases, and hyaluronidases in the extraction, modification and valorization of marine biomolecules. Particular attention is given to enzymes from cold-adapted species, which offer high catalytic efficiency at low temperatures, enabling energy-efficient processing while maintaining product quality. The review identifies outstanding research gaps, including large-scale enzyme stabilization, recovery efficiency, and integration of biocatalytic systems with green extraction technologies. By summarizing these innovations and challenges, this work provides a framework for developing sustainable, enzyme-driven seafood waste valorization strategies that align with circular bioeconomy principles.

Key words: Bioactive peptides, Fishes, Lipases, Proteases, Seafood

Introduction

In 2022, global seafood production reached 223.2 million tons (MT), with 185.4 MT derived from capture fisheries and 37.8 MT from aquaculture. Of this, 157 MT were utilized for human consumption, resulting in an average *per capita* consumption of 20.2 kilograms. The global demand for seafood is projected to increase by 60% by 2050, driven by the growing population expected to reach 9.8 billion (FAO, 2014). Sea bass and tilapia are among the major aquaculture species contributing significantly to global seafood output. Both species generate substantial quantities of by-products during processing. For instance, the global market value for sea bass reached USD 4,039.9 million, and tilapia production reached 4,407.2 thousand tons in 2021 (Pathinathan *et al.*, 2024a, b, c). The processing of approximately 160 million tons of fish and seafood from both wild and cultured sources produces large volumes of waste, including scales, shells, skeletal frames, viscera, heads, livers, skins, roe, and other discarded parts. These by-products, if not effectively managed, pose serious environmental threats.

Nevertheless, fishery waste represents a rich

repository of value-added compounds such as proteins, enzymes, bioactive peptides, lipids, carotenoids, minerals, hydroxyapatite, and chitin. Efficient utilization of these resources contributes not only to environmental protection but also to the development of a sustainable blue bioeconomy (Arvanitoyannis and Kassaveti, 2008; Rustad *et al.*, 2011; Sachindra and Mahendrakar, 2015). Enzymes derived from fishery by-products—including proteases, lipases, and transglutaminases (TGases)—have attracted increasing interest for their roles in food processing, quality control, and product development. Particularly, enzymes from cold-adapted marine species demonstrate unique biochemical features such as high catalytic efficiency at low temperatures, low activation energy, and high substrate specificity (Venugopal, 2009; Trincone, 2011). For example, pepsin from the stomach of polar cod remains active in cold environments, and certain fish trypsins exhibit remarkable stability in high-salt conditions. Despite growing interest in enzymatic valorization, systematic analyses of enzyme sources, their biotechnological applications, and integration into sustainable processing frameworks still remain limited.

Therefore, the objectives of this review are to:

I) Summarize current knowledge on enzymatic

technologies applied to seafood byproducts;

II) Highlight the biochemical properties and industrial potential of enzymes derived from marine and cold-adapted species;

III) Identify technological challenges and research gaps hindering large-scale enzyme utilization; and Propose strategies for advancing sustainable seafood byproduct processing through enzyme-driven innovations.

This review seeks to provide a comprehensive overview of recent developments and future perspectives in enzymatic valorization, thereby contributing to the advancement of sustainable seafood processing and supporting circular bioeconomy initiatives.

Methodology

This review was conducted in accordance with the Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA) guidelines to ensure a transparent, systematic, and reproducible approach to literature identification, screening, eligibility assessment, and inclusion of relevant studies (PRISMA).

Fish proteases

Fish proteases include both endopeptidases, which break down protein molecules internally, and exopeptidases, which cleave the side chains of these molecules (Song *et al.*, 2023). These proteases, which originate from fish and aquatic invertebrates, are classified into four distinct groups. Proteases containing aspartic acid within their active center are referred to as acidic or aspartic proteases. Examples include pepsin and cathepsin D. Proteases are classified based on the amino acid residue present in their active site. Serine proteases, such as trypsin and chymotrypsin, contain a serine residue at their active site. In contrast, cysteine proteases, including calpain and cathepsins B, H, and L, possess a cysteine residue that plays a crucial role in catalysis. Fish and shellfish-derived trypsin are known for their potent enzyme activities and are capable of functioning effectively across a wide range of pH and temperature conditions. Enzymes extracted from fish viscera, such as alkaline proteases, exhibit peak performance at a pH of 10. Carp and seal chymosin, also referred to as rennin, are acidic proteases renowned for their impressive capacity to initiate milk coagulation. Notably, chymotrypsin, a proteolytic enzyme produced by fish pancreas, shows higher specific enzymatic activity than its bovine equivalent (Shahidi and Kamil, 2001; Sriket, 2014). Extensive studies have been conducted on novel acidic proteases isolated from sardines, significantly enriching the repertoire of enzymatic tools available in the field. Isolation of fish lysosomal cathepsins from various fishery products has been achieved, underscoring their importance in industrial settings. Cathepsin K is recognized as the most potent mammalian collagenase, capable of breaking down collagen type I in acidic conditions. Other collagenolytic enzymes belong to the group of metalloproteinases, which function optimally at

neutral pH. These enzymes differ from the serine protease family of collagenases in their catalytic mechanisms. Metalloproteinases typically hydrolyze types I, II, and III tropocollagens (Daboor *et al.*, 2010). In fish tissues, collagenase activity -particularly that of cathepsin B- is a major contributor to quality deterioration. This observation suggests that fish muscle waste, which is highly prone to rapid degradation, could serve as a valuable source for collagenase extraction (Sovik and Rustad, 2006). Additionally, cathepsin L, with an optimal pH of 5.5 and temperature of 55°C, has been purified from the skeletal muscle of blue scad (*Decapterus maruadsi*) (Zhong *et al.*, 2012).

Collagenases, abundant in epithelial, cartilaginous, and bony tissues, as well as in the digestive systems of fish and shellfish, play crucial roles in numerous biological and industrial processes. Biologically, they participate in tissue remodeling, wound healing, embryonic development, and the degradation of extracellular matrix proteins. Industrially, collagenases are employed in leather processing, food and cosmetic industries, pharmaceutical formulations, and biomedical applications such as cell culture and tissue dissociation. In addition, an acidic serine carboxypeptidase has been isolated from the hepatopancreas of squid, further highlighting the diversity of proteolytic enzymes derived from marine organisms (Bougatef, 2013; Khandagale *et al.*, 2015; Khangembam and Chakrabarti, 2015; Zamani and Benjakul, 2016) (Table 1). Proteases derived from fishery products, some relevant properties and applications.

The proteolytic functions of enzymes within fish muscle tissue at the point of expiry

In postmortem fish tissues, muscle proteases initiate crucial degradation processes in both myofibrillar proteins and collagen (Felberg *et al.*, 2010). The enzymatic reactions result in several undesirable effects such as texture degradation, gaping fillets, softening of crustaceans, flavour changes, and the occurrence of belly bursting in deep-sea fish (Sriket, 2014). A particular serine protease plays a crucial role in the activation of the polyphenol oxidase (PPO) zymogen, which is responsible for the formation of black spots in crustaceans (Klomklao *et al.*, 2012). Proteases play a substantial role in the biochemical changes that occur in postmortem fish and seafood products due to their enzymatic activity (Yang *et al.*, 2015). Furthermore, the proteases found in surimi and washed fish meat cause a condition known as "modori," characterized by a softening effect (Felberg *et al.*, 2010; Klomklao *et al.*, 2012).

Lipases

A diverse group of enzymes known as lipases catalyze the hydrolysis of ester bonds in a wide range of substrates, including triglycerides, phospholipids, cholesteryl esters, and fat-soluble vitamin esters (Kapoor and Gupta, 2012). These enzymes exhibit specific characteristics with respect to fatty acid chain length, the

nature of the alcohol moiety, and stereospecificity (Kamal *et al.*, 2015). Research on lipases in aquatic organisms is focused on their distribution, biochemical properties, and physiological roles. In seafood and food processing, lipases are utilized for flavor modification through reactions such as hydrolysis, esterification, and transesterification, which influence the development of

desirable aroma compounds and lipid restructuring (Kamal *et al.*, 2015). They can also be applied for the selective modification of fatty acids, including the enrichment or alteration of polyunsaturated fatty acid (PUFA) content in fish oils, depending on the enzyme's specificity and reaction conditions.

Table 1: Proteases derived from fishery products, some relevant properties and applications

Enzyme	Fish/Shellfish	Some outstanding properties	References	Applications
Pepsin	Sardine, capelin, cod, salmon, shark, mackerel, orange roughy, tuna, trout, carp, harp seals	Generally low activation energy, low temperature is optimal	Haard and Simpson (2006); Sriket (2014)	Cheese manufacturing fish sauce and fermented products
Trypsin	Sardine, capelin, salmon, cod, bluefish, anchovy, Atlantic croaker, carp, aquacultured tilapia, ray fish, cuttlefish, mackerel, threadfin hakeling, red snapper, shrimp, Antarctic krill peel and exudate, smooth hound	Molecular weights about 25 kDa, optimal pH 8-9, and temperature 50-60°C. Threadfin hakeling trypsin has lower optimal temperature and lower thermostability than mammalian trypsin. Smooth hound trypsin has high salt tolerance	Bustos <i>et al.</i> (1999); Balti <i>et al.</i> (2009); Kishimura <i>et al.</i> (2010); Klomklao <i>et al.</i> (2012); Bougatef (2013); Sriket (2014); Zamani and Benjakul (2016)	Meat tenderization, digestibility improvement, wound healing and anti-inflammatory formulations
Gastricin	Hake, Atlantic cod	Optimal activity at pH 3	Haard and Simpson (2006)	Production of bioactive peptides, Cold-active enzyme systems bioconversion of proteinaceous waste
Alkaline proteinase	White croaker, chum salmon, tilapia, aquacultured tilapia, viscera of Monterey sardine, goby	Extremely stable in the pH range of 5-12 and relatively stable towards oxidizing agents	Sila <i>et al.</i> (2012)	Protein hydrolysis and peptide production, meat tenderization, fish sauce fermentation
Acidic protease	Sardine, orange roughy	Acidic protease, pH optima 2.5, temperature optima 37-45°C	Castillo-Yanez <i>et al.</i> (2004); Khaled <i>et al.</i> (2011)	Flavor development, meat tenderization, collagen and gelatin modification
Calpain	Freshwater prawn and fish muscle	Optimal pH 5-7.5, temperature 50°C to 60°C	Chere <i>et al.</i> (2007); Sriket (2014)	Fish and seafood processing, protein hydrolysis, drug discovery and enzyme therapy research
Chymotrypsin	Carp, capelin, herring, Atlantic cod, rainbow trout, scallop, spiny dogfish, prawn, sardine	Milk clotting activity at alkaline pH	Sila <i>et al.</i> (2012); Sriket (2014)	Ophthalmic surgery wound healing protein sequencing and structural studies
Lysosomal cathepsins type B, H, L	Atlantic white croaker, carp, tilapia, herring, dogfish, rainbow trout, crustaceans, mollusks, squid, prawn muscle	Optimal pH 5-7.5, Catalytic activity is possible at low temperatures	Shahidi and Kamil (2001); Sriket (2014)	Disease Biomarkers drug targeting and therapeutics
Cathepsin D and other lysosomal cathepsins	Capelin, carp, tilapia, chum salmon, squid, white croaker, tilapia, cod, Pacific rockfish	Except cathepsin D, an aspartic protease, others are serine or cysteine proteases. Degrade fish myofibrils	Aoki <i>et al.</i> (2004), Chere <i>et al.</i> (2007); Sriket (2014)	Disease Biomarkers, enzyme replacement therapy (ERT)
Collagenases	Carp, catfish, cod, crab species, pacific rockfish, marine bivalves	Comparable to mammalian metalloproteinases	Shahidi and Kamil (2001); Arneesen and Gildberg (2006); Daboer <i>et al.</i> (2012)	Cell and tissue dissociation treatment of fibrosis tissue engineering
Elastase	Herring, sardine	Causes belly bursting	Felberg <i>et al.</i> (2010)	Drug development and screening cell culture studies
Chymosin (rennin)	Carp, seal	Optimal pH 2.0-3.5, possesses high milk clotting activity	Shahidi and Kamil (2001)	Milk coagulation, milk protein and peptide research
Alkaline peptidase	Silver mojarra	Optimum activity at pH 8.5, temperature 50 and 55°C	Silva <i>et al.</i> (2011)	Bioactive peptides production leather and textile industry

Table 2: Transglutaminases derived from fishery products, some relevant properties and applications

Enzyme	Fish/Shellfish source	Some outstanding properties	References	Applications
Transglutaminase (TGase)	Cod (<i>Gadus morhua</i>)	Calcium-dependent enzyme; stable at low temperatures; cross-links myofibrillar proteins	Ando <i>et al.</i> (1989)	Used in fish sausage, surimi, and gel-based seafood products to improve texture and water-holding capacity
Transglutaminase (TGase)	Red sea bream (<i>Pagrus major</i>)	Exhibits high activity at moderate temperatures (25-35°C); maintains stability in brackish and marine environments	Khiari (2024)	Enhances gel strength in fish paste and improves cohesiveness in restructured seafood
Transglutaminase (TGase)	Crab (<i>Portunus trituberculatus</i>)	Salt-tolerant enzyme; functions well in high ionic strength environments; promotes strong gel networks	Muzzarelli and Muzzarelli (2005)	Used in binding fragmented crab meat and forming structured crab analogs

Table 3: Carbohydrases derived from fishery products, some relevant properties and applications

Enzyme	Fish/Shellfish source	Some outstanding properties	References	Applications
Amylase	Sardine (<i>Sardinella longiceps</i>), Rainbow trout (<i>Oncorhynchus mykiss</i>), Mullet (<i>Mugil cephalus</i>)	Optimum activity at pH 7-8 and 45-55°C; calcium-dependent stability	Klomklao <i>et al.</i> (2012)	Used in starch hydrolysis, production of maltose syrups, and improving digestibility in fish feed formulations
β -Amylase	Catfish (<i>Clarias gariepinus</i>)	Active in slightly acidic to neutral pH; contributes to maltose release	Sriket (2014)	Used in maltose syrup production and carbohydrate modification in aquaculture feeds
Chitinase	Shrimp (<i>Penaeus monodon</i>), Crab (<i>Portunus pelagicus</i>)	Thermostable; active at pH 6-8; capable of degrading α - and β -chitin	Le and Yang (2019)	Converts chitin waste into chito-oligosaccharides and glucosamine for biomedical and agricultural uses
Chitosanase	Squid (<i>Todarodes pacificus</i>)	High specificity toward partially deacetylated chitosan; active at pH 6.5	Kim <i>et al.</i> (2003)	Used to produce low-molecular-weight chitosan and bioactive oligosaccharides
Cellulase	Fish gut microflora (e.g., <i>Tilapia</i> , <i>Mugil cephalus</i>)	Endoglucanase activity; stable at pH 7-8 and 37-45°C	Ray <i>et al.</i> (2012)	Applied in the conversion of cellulose-based feed material and bioconversion of fish waste
Lysozyme	Salmon (<i>Salmo salar</i>), Shrimp (<i>Penaeus japonicus</i>)	Antibacterial enzyme hydrolyzing peptidoglycan; stable at a wide pH range	Kamal <i>et al.</i> (2018)	Used as a natural preservative and antimicrobial in seafood storage and processing

Carbohydrases

Carbohydrases obtained from fish and seafood include a range of enzymes such as chitinases (Proespraiwong *et al.*, 2010), abalone-derived amylase (Hsieh *et al.*, 2014), β -1,3-glucanase sourced from the sea cucumber (Zhu *et al.*, 2008) and β -galactosidase extracted from tilapia (Taniguchi and Takano, 2004). Chitinases display both endo-chitinase and exo-chitinase activities. Enzymes known as endochitinases break down chitin, a main polysaccharide found in crustaceans, by randomly cleaving internal β -1,4-N-acetyl-D-glucosaminide bonds, resulting in soluble N-Acetylglucosamine oligomers. Exochitinases, specifically chitobiosidases, split dimers such as GlcNAc2 and higher chitin polymers like GlcNAc3 and GlcNAc4 into GlcNAc monomers, whereas N-acetyl glucosaminidases target the final, nonreducing N-acetyl glucosamine residues of chitin. Lysozyme, a bacterium-killing enzyme capable of breaking down GlcNAc3-5, is discovered in the digestive tracts and pyloric caeca of both shellfish and finfish (Dahiya *et al.*, 2006). Carbohydrases derived from fishery products, some relevant properties and applications are listed in the Table 3.

Transglutaminases

Transglutaminases, also known as TGases, are crucial enzymes involved in numerous cellular processes, including growth regulation, cell differentiation, blood clotting, skin cell maturation, and the strengthening of red blood cell membranes. These enzymes facilitate acyl-transfer reactions, specifically by catalyzing the bonding of the gamma-carboxamide group of peptide-bound glutamine residues with the epsilon-amino group of lysine residues and other amines present in proteins. This process leads to cross-linking, primarily the creation of (γ -glutamyl)-lysine linkages between proteins, where the lysine ϵ -amino group acts as the acceptor (Shahidi and Kamil, 2001; Binsi and Shamasundar, 2012). As indicated in Table 2, TGases are isolated from various fish species.

Other enzymes

Enzymes that play a significant role in the assessment of seafood quality include alkaline phosphatase, urease, 5'-nucleotidase, nucleoside phosphorylase, xanthine oxidase, trimethylamine oxide (TMAO) reductase and TMAO-demethylase (Zhu *et al.*, 2008; Benjakul *et al.*, 2009; Klomklao *et al.*, 2012). Hyaluronidase, a naturally occurring component found in animal tissues, increases tissue permeability through the enzymatic breakdown of hyaluronic acid. Natural sources of hyaluronidase have

been identified in several marine organisms, including the shells of shrimp, Norway lobsters, and stonefish that reside in shallow tropical waters.

Utilization of enzymes from seafood waste in seafood processing

Fishery discards represent a valuable reservoir of diverse enzymes such as proteases, chitinase, alkaline phosphatase, and hyaluronidase, predominantly found in the intestines, pyloric ceca, pancreatic tissues, hepatopancreas, shell, and other waste components (Sriket, 2014). However, due to their high perishability, large quantities of fresh waste materials must be consistently available to ensure efficient enzyme recovery and to prevent enzymatic degradation prior to processing.

Several commercially feasible methods for isolating enzymes from crude fish waste extracts have been developed, including precipitation techniques using salts and polyacrylic acids, isoelectric solubilization/precipitation, ultrafiltration, pH adjustment, flocculation, membrane filtration, and overcooled acetone extraction (Benjakul *et al.*, 2009; Murado *et al.*, 2009; Penven *et al.*, 2013). Each of these techniques exhibits distinct advantages and limitations. For instance, salt and solvent precipitation are inexpensive and relatively simple, providing high recovery yields but often resulting in partial enzyme denaturation. Isoelectric solubilization/precipitation enables selective recovery of enzymes with minimal chemical interference, though the method requires precise pH control and is limited by scalability. Ultrafiltration and membrane filtration are gentle, scalable, and suitable for industrial use, yet they demand high initial investment and continuous membrane maintenance. Overcooled acetone extraction is shown to be particularly effective for recovering collagenases from ray fish (Murado *et al.*, 2009), allows rapid protein precipitation with good yield and stability but involves safety concerns and solvent recovery issues that may hinder large-scale operations.

More recently, glycation-based separation techniques have emerged as a promising alternative, enabling selective modification and isolation of specific protein fractions without extensive purification steps. This method may offer better enzyme stability and yield but remains at the experimental stage for large-scale applications. Similarly, various reviews on lipase purification from fisheries highlight the growing efforts to optimize recovery efficiency and product purity (Kurtovic *et al.*, 2009).

Applications of fishery-derived enzymes for seafood processing

Enzyme use in industrial processing, including fishery-derived enzymes, offers several advantages over traditional chemical methods. Benefits include improved process control, increased safety in environmental and toxicological terms, decreased energy usage, and lower operational costs.

A- Proteases

Protein extraction from fish processing effluent byproducts

Fishery byproducts are rich in various proteins, such as myofibrillar and sarcoplasmic proteins, along with collagen. Collagen obtained from various fish components such as fins, scales, skins, bones, heads, and swim bladders of bighead carp has been extracted through the use of enzymes including collagenases, pepsin sourced from tuna, or trypsin sourced from cod or tuna pyloric caeca. Pepsin-solubilized collagen serves as a promising substitute for mammalian-derived collagen. Pepsin-solubilized collagen and its hydrolyzed derivative, gelatin, have a variety of applications across the food, pharmaceutical, and photographic industries (Guillen *et al.*, 2011).

Fish protein hydrolysates

Fish protein hydrolysate (FPH) is a product resulting from the breakdown of fish proteins, which consists of smaller peptides and amino acids. Fish protein hydrolysate is produced by treating fish meat with enzymes such as trypsin, alcalase, chymotrypsin, pepsin, and others, under strict conditions of pH and temperature control. FPHs are usually found in the form of an amorphous powder with the ability to absorb moisture. They consist of approximately 81-93% protein, less than 5% fat, 3-8% ash, and 1-8% moisture content. Lean fish species or their processing by-products serve as ideal raw materials for producing FPH, which in turn has applications in the form of food binders, emulsifiers, gelling agents, and nutritional supplements. FPH can be used as a cryoprotectant and a nutritional supplement in liquid fertilizer and aquafeed formulations. Proteases derived from seafood, including those obtained from Atlantic salmon, and trypsin isolated from fish pyloric ceca, have been employed in the manufacturing of FPH (Venugopal, 2009; Chalamaiah *et al.*, 2012; Zamani and Benjakul, 2016).

Research has identified a potential solution to reduce the bitterness often linked with FPHs, specifically an acidic serine carboxypeptidase derived from squid hepatopancreas. This enzyme effectively eliminates bitterness by selectively removing specific amino acids located at the carboxy-terminal end as demonstrated by Komai *et al.* (2007).

Fish protein hydrolysate (FPH) functions as a rich source of bioactive peptides, exhibiting a broad range of functionalities that encompass antioxidant, antimicrobial, antihypertensive, anti-amnesic, mineral-binding, immunomodulatory and antithrombotic properties (Vercruysse *et al.*, 2005; Ktari *et al.*, 2013; Hayes *et al.*, 2019; Zhang *et al.*, 2015). Crude alkaline protease extracts from cuttlefish and sardinelle were used to hydrolyze cuttlefish by-products, yielding protein hydrolysates with significant antioxidant activity (Ktari *et al.*, 2013). Moreover, fish intestinal protease has been applied to produce a phosphopeptide with calcium-binding properties from fish bone, as documented by

Jung *et al.* (2005). Additionally, peptides with hyaluronidase and elastase inhibitory properties have been developed from clam sources, according to Sutthiwanjampa and Kim (2015).

Fish sauce

The condiment known as fish sauce is highly regarded for its unique taste, and its production involves the breakdown of fish through the action of enzymes that are naturally present. The production process can be accelerated by including external enzymes such as proteases (Lopetcharat *et al.*, 2001). The inclusion of squid hepatopancreas has been found to speed up sauce production from capelin.

The ripening of fermented fish commodities

The process of ripening is vital in developing the unique flavour and delicate texture of fermented fishery products over a period of time. The natural process of storage maturation can be accelerated through the addition of external proteases, as noted in research by Bekhit (2011).

Meat tenderization

The post-mortem hardening of meat is a major issue as it influences consumer acceptance of the final product. Preliminary research by Aoki *et al.* (2004) indicates that shrimp protease is capable of effectively tenderizing beef. Furthermore, protease treatment has been shown to reduce the rigid texture of squid rings, especially after the removal of the resilient outer layer of proteoglycans.

Control of curd formation in canned fish products

Effective control of curd formation in canned salmon can be achieved using protease treatment, as documented by Five *et al.* (2024).

Fish sizing and measurement

Whole finfish scales can weigh up to 5% of their total weight. Manual or mechanical scrubbing of scales off the fish can be damaging, particularly for species with large scales such as haddock, salmon, perch, ocean bream, and silver carp. Dipping the fish in a slightly acidic water solution that includes an appropriate enzyme for breaking down proteins makes it simpler to remove the scales. Collagenase derived from crab hepatopancreas has been effectively used for de-skilling squid according to Plekhova *et al.* (2024).

Production of caviar

Caviar is a cured product made from the eggs of fish species such as the white sturgeon, salmon, and trout, among others. Manually extracting roe sacks for caviar production often requires a lot of labor, but the use of proteases, such as collagenases, can facilitate this process by making it easier to remove the supportive tissue surrounding the eggs (Bekhit, 2022).

Chitin extraction

Discarded shrimp shells are primarily composed of chitin, a substance also found in the shells of crustaceans and cephalopods. Chitosan, which is produced by partially deacetylating chitin, is a valuable type of sugar known for its numerous beneficial properties, such as antimicrobial, antitumor, cholesterol-lowering, immune-stimulating effects among others (Venugopal, 2009, 2011). Conventional chitin extraction techniques involve the use of demineralization and deproteinization processes, typically employing strong acids or bases. The employment of alkaline proteases sourced from fish viscera facilitates the gentle extraction of proteins under less harsh conditions. Chitosan, which possesses antimicrobial and antioxidant properties, can function as a stabilizer in seafood-based products (Alishahi and Aider, 2012).

Extraction of carotenoids

Carotenoids can be extracted from shrimp and crab shell waste, which usually contain around 150 milligrams of carotenoids per kilogram of dry weight. Astaxanthin, the main carotenoid, can be extracted from shrimp waste through the process of trypsin hydrolysis. Astaxanthin is highly valued in aquafeed formulations and for its ability to enhance the coloration of various salmonid and crustacean species (Armenta-Lopez *et al.*, 2002).

Extraction of chondroitin sulfate and hyaluronic acid

Glycosaminoglycans such as chondroitin sulfate (CS) and hyaluronic acid (HA) have a wide range of biomedical applications. The fins of Elasmobranchs are a primary source of chondroitin sulfate, and skate pancreas proteases has been used to extract chondroitin sulfate from skate cartilage (Venugopal, 2016). Protease treatment has also been used to isolate HA from fish eyeballs, as described by Vazquez *et al.* (2013).

Production of flavor enhancers for seafood products

The demand for seafood-flavoured products is increasing, with growing interest in enhancing the sensory characteristics of surimi-based products, such as imitation crab meat and fish sausages. Crustacean shells and also other sources are rich in natural flavor compounds, including nucleotides, amino acids, and volatile aldehydes, which are extracted and developed with the aid of proteases (Imm and Lee, 1999). Furthermore, FPHs can act as effective flavor enhancers, providing a means to incorporate fish oil and other bioactive ingredients into seafood-based products (Peinado *et al.*, 2016).

Muscle enzymes, including cathepsins, calpains, peptidases, and aminopeptidases, work in conjunction with lipases to release specific flavor-active compounds such as short-chain peptides, free amino acids (e.g., glutamic acid and glycine), and volatile fatty acids responsible for umami, sweet, and savory notes (Toldra,

2007; Bekhit, 2011). The interaction of these hydrolytic enzymes leads to the breakdown of muscle proteins and lipids into smaller molecules that contribute to the characteristic aroma and taste of processed seafoods. These enzymatic reactions are particularly important in improving the sensory properties of restructured or heat-treated products, providing desirable flavors reminiscent of fresh marine fish and shellfish.

Reducing the viscosity of sticky water

A by-product of fishmeal production, stick water, presents viscosity challenges during concentration by evaporation. When the dissolved protein content exceeds 25%, viscosity increases, leading to evaporator blockage and reduced evaporation efficiency. Protease treatment can help mitigate this problem (Venugopal *et al.*, 2000).

Control of enzymatic discoloration

Enzymatic browning presents a substantial obstacle to the shellfish, fruit and vegetable industries. Proteolytic

enzymes obtained from crustaceans like crayfish, which lack a stomach, have shown the ability to inactivate PPO enzymes responsible for browning, providing a promising substitute for sulfites (Benjakul *et al.*, 2009). Furthermore, hypotaurine and other sulfinic acid derivatives found in blue mussels have been found to be inhibitors of PPO enzymes (Schulbach *et al.*, 2013).

Manufacture of feed for aquaculture

Essential omega-3 fatty acids, including docosahexaenoic acid (DHA) and eicosapentaenoic acid (EPA), which are vital for aquafeed nutrition, were obtained via enzymatic degradation of eye or brain matter sourced from dusky rockfish and salmon (Reppond *et al.*, 2009).

B- Transglutaminase

Change in surface quality

Table 4: Processing approaches and applications of transglutaminase (TGase) in processed fishery and seafood products

Process	Uses	References
Protein recovery from filleting waste, mollusk shells, frames of fish such as Pollock, etc.	Waste utilization, cleaner fish frames, and shells as calcium source	Arnesen and Gildberg (2006); Jeya Shakila and Jeyasekaran (2015)
Extraction of chondroitin sulfate and hyaluronic acid	Lower cost, important bioactive compounds	Vazquez <i>et al.</i> (2013)
Extraction of collagen and gelatin	Enhances protein cross-linking, gel strength, texture, and structural stability of processed fishery and seafood products	Arnesen and Gildberg (2006); Nalinanon <i>et al.</i> (2008); Ahmad and Benjakul (2010)
Preparation of hydrolyzates from fish and shellfish	Nutritional additives, flavor enhancers, use in aquafeed	Benjakul <i>et al.</i> (2009); Venugopal (2009); Chalamaiah <i>et al.</i> (2012); Venugopal Menon and Lele (2015)
Preparation of antioxidant, antimicrobial peptides	Preservation of seafood at chilled temperatures	Kristiansson and Rasco (2000); Kim and Mendis (2006); Chalamaiah <i>et al.</i> (2012); Hayes and Flower (2013); Ktari <i>et al.</i> (2013)
Removal of fish roe sacks for caviar production	More convenient compared to cumbersome manual process	Gildberg (1993)
Ripening of fermented roe	Less time, higher yield	Bekhit (2011)
Debitting of protein hydrolyzates	Better acceptance	Stefansson (1998); Komai <i>et al.</i> (2007)
Control of blackening in shellfish	Better marketing	Benjakul <i>et al.</i> (2009)
Membrane removal from cod liver	Cleaner liver for oil extraction	Gildberg (1993)
Peeling and deveining of shrimp	Simplification of traditional hand peeling	Venugopal (2006, 2009); Husain (2010)
Control of "curd" formation in canned salmon	Better product appearance	Yadav <i>et al.</i> (2025)
Recovery of chitin from shellfish waste for the preparation of chitosan (deacetylated chitin) and chitosan oligosaccharides	Improved, less costly process, energy savings. Chitosan and chitosan oligosaccharides can stabilize seafood-based products. Composite film of chitosan-squid collagen is a good bio packaging	Kim and Rajapakse (2005); Lin <i>et al.</i> (2009); Venugopal (2009, 2011); Alishahi and Aider (2012); Thiago <i>et al.</i> (2012); Vazquez <i>et al.</i> (2013)
Seafood flavor extraction	Recovery of fish flavor from shrimp shell, low-cost fish	Imm and Lee (1999); He <i>et al.</i> (2004); Toldra (2007); Peinado <i>et al.</i> (2016)
Reduction of viscosity of fish meal stick water	Better water evaporation, cost reduction	Venugopal <i>et al.</i> (2000)
Scaling of fish	Efficient process	Stefansson (1998); Tschersich and Choudhury (1998)
Ripening of salted fish	Better flavor	Toldra (2007)
Control of enzymatic browning	Inactivation of polyphenol oxidase, better color	Benjakul <i>et al.</i> (2009); Schulbach <i>et al.</i> (2013)

The texture of processed fishery products has a significant influence on consumer satisfaction. Traditionally, additives such as starches and other carbohydrates have been used to modify texture. In contrast, transglutaminase (TGase) offers an alternative approach by catalyzing protein cross-linking, thereby modification of textural properties (Table 4). Processing approaches and applications of transglutaminase (TGase) in processed fishery and seafood products (An *et al.*, 2021).

C- Lipases

Production of polyunsaturated fatty acids (PUFAs)

Polyunsaturated fatty acids (PUFAs), particularly EPA and DHA, are products of lipases and have gained significant attention for their unique nutritional advantages. Researchers are currently exploring alternative lipid sources due to the distinct benefits associated with EPA and DHA. The technique involves using lipases to enhance fish oils with EPA and DHA. This process incorporates either acidolysis, which involves the exchange of fatty acids within triglycerides or mixed triglycerides, or transesterification, where fatty acids are exchanged between different triglycerides or monoesters. (Klinkesorn *et al.*, 2004; Venugopal, 2009).

Flavor enhancement

Muscle enzymes, including cathepsins, calpains, peptidases, and aminopeptidases, work in conjunction with lipases to release flavor compounds such as free amino acids, peptides, and volatile fatty acids that contribute to umami, savory, and characteristic seafood aromas. For instance, the proteolytic breakdown of muscle proteins by cathepsins and calpains generates short-chain peptides responsible for umami taste, while lipase activity releases free fatty acids that undergo oxidation to produce aldehydes, ketones, and alcohols associated with desirable cooked or fresh fish flavors (Toldra, 2007; Bekhit 2011).

D- Carbohydrases

The conversion of chitin to chitosan

Using traditional methods to convert chitin to chitosan, such as treating with concentrated sodium hydroxide at high temperatures, is known to be time-consuming. On the other hand, employing chitinase for deacetylation offers a more affordable and environmentally friendly solution (Venugopal 2009, 2011).

Increasing the shelf life of fishery products

Prolonging the shelf life of fishery products can be attained via multiple approaches, one of which includes soaking fresh shrimp in lysozyme solution at levels of up to 150 micrograms per milliliter. This process effectively reduces the spread of spoilage microorganisms through

lysozyme's action on the mucopeptide structure within microbial cell walls. Notably, enzymes derived from clam and Arctic scallops have shown significant antibacterial properties, even when exposed to lower temperatures. Enhancing the quality of fish was achieved by combining lysozyme with glucose oxidase and catalase, resulting in a synergistic effect that preserves freshness (Wu and Wang, 2025). Previous studies of Vaishnav *et al.* (2025) have shown that using antibacterial and antioxidant peptides derived from fishery waste offers a promising approach to preserving seafood.

Removing the shells and veins from shrimp

The process of peeling and deveining shrimp, along with removing the internal organs in clams, involves submerging headless shrimp in a circulating water solution that includes amylase and sodium bicarbonate. Following this, the shellfish are subjected to a washing process using water jets and air to efficiently remove both the shell and the gills (Hannan *et al.*, 2022).

Keeping the good appearance of cooked and frozen shrimp

To preserve the characteristic yellow color of precooked frozen shrimp or crab, which frequently loses its hue due to oxidation, a process involves immersing the cooked shrimp in glucose oxidase. Generation of gluconic acid through this process reduces the surface pH and subsequently slows down bacterial spoilage (Hannan *et al.*, 2022).

Other applications of carbohydrases

Beta-galactosidase has a significant place in the food industry, where it is used to improve sweetness, solubility, flavor, and digestibility (Husain, 2010). Its multi-faceted use in numerous food products highlights its adaptability and efficiency.

Incorporating carbohydrases into aquafeed formulations may offer a viable approach to reduce the adverse effects of non-starch polysaccharides present in the feed (Sinha *et al.*, 2011). This targeted adjustment not only improves the nutritional profile of aquafeed but also boosts its digestibility, leading to healthier growth in aquatic species.

Enzymatic biosensors for seafood quality assessment

Quality control

Enzymes such as 5'-nucleotidase, nucleoside phosphorylase, xanthine oxidase, and trimethylamine N-oxide (TMAO) reductase are employed either directly or as integral components in biosensors designed to detect a range of seafood-related metabolites and contaminants. For instance, 5'-nucleotidase catalyzes the hydrolysis of nucleotide monophosphates to nucleosides, allowing for the identification of adenosine and inosine, which are freshness indicators in fish muscle. Nucleoside phosphorylase aids in detecting hypoxanthine, another important metabolite associated with postmortem

degradation and quality loss. Xanthine oxidase is commonly used to measure xanthine and uric acid, key markers of nucleotide catabolism that reflect the freshness and biochemical state of fish. Similarly, TMAO reductase detects trimethylamine (TMA) generated from the reduction of TMAO, a compound directly linked to spoilage and off-odors in marine fish (Waffo *et al.*, 2021). Biosensors that use these enzyme systems have proven to be valuable analytical tools for monitoring seafood freshness, detecting toxins, and identifying contaminants. They combine a biological recognition element (such as enzymes, antibodies, receptors, or microbial cells) with a physical or chemical transducer to produce measurable signals. Recent advances in nanomaterial-based biosensors and microfluidic platforms have further improved detection sensitivity, selectivity, and real-time monitoring capabilities (Chen *et al.*, 2022, Prabhakar *et al.*, 2023).

Applications of cold-adapted enzymes

Cold-adapted enzymes also play vital roles in seafood processing. Cold-active proteases enable low-temperature operations such as meat tenderization, caviar production, carotenoprotein extraction, and surface flavor enhancement of marine fish and shrimp during chilled storage (Alishahi and Aider 2012; Sidhu *et al.*, 2020; Zhang *et al.*, 2015). These enzymes provide energy-efficient and sustainable alternatives while maintaining the delicate sensory attributes of seafood products.

Cold-active lipases contribute to flavor development due to their efficacy at low temperatures (Birschbach *et al.*, 2004). Transglutaminase (TGase) sourced from polar fishes enable texture modification at low temperatures (Bougatef *et al.*, 2010; Sriket, 2014). Carbohydrases, along with proteases and lipases, make up a major part of the global market for food and beverage additives, which is expected to reach around US \$2300 million by 2018. Among the commercially available enzymes derived from marine sources are fish trypsin, chymotrypsin, and cold-active chlamysin (lysozyme) obtained from a marine bivalve, as noted by Shahidi and Kamil (2001). Furthermore, there are various commercial products available, including a cold-tolerant protease from North Atlantic cod called Penzim, Neptune Aquatein, krill extract, heat-sensitive shrimp alkaline phosphatase, cod uracil-DNA glycosylase from Atlantic cod, oyster peptide and protein mixtures from Central Institute of Fisheries Technology in Kochi, India, as well as a range of seafood protein extracts. Furthermore, there is potential for protein engineering endeavors aimed at introducing innovative and precise sequence specificity into marine enzymes, paving the way for intriguing applications. Pepsin-extracted collagens and gelatins, particularly from fish sources like cod bone gelatin, have gained attention as valuable food ingredients, Karim and Bhat (2009) and Guillen Gomez *et al.* (2011). Despite their recognized health benefits, FPHs remain limited in availability (He *et al.*, 2013). Countries like Norway have embraced enzymatic fish processing techniques, as

outlined by Chen *et al.* (2025). However, on a global scale, there is a notable scarcity of commercial facilities dedicated to isolating fishery enzymes and other value-added products, despite the abundance of discarded fishery byproducts, as discussed by Rigueto *et al.* (2023). As highlighted by Olsen *et al.* (2014), the limited market presence of fishery by-products, including enzymes, can be attributed to several factors. These include the challenge of securing a consistent supply of high-quality waste for secondary processing and the considerable costs associated with isolating ingredients. However, despite these challenges, there is hope regarding the potential of fishery waste to serve as a valuable source of enzymes for biotechnological applications in seafood processing.

Conclusion

The strategic implementation of innovative secondary processing techniques to effectively utilize fishery waste serves as a pivotal approach to confronting both environmental and economic challenges. Converting fishery by-products into value-added compounds such as enzymes, proteins, lipids, and minerals not only minimizes environmental pollution but also enhances resource efficiency within the seafood processing chain. From an industrial perspective, enzymes extracted from cold-water fish species have shown immense potential for application in food preservation, flavor enhancement, pharmaceutical formulations, leather processing, and biodegradable detergent production. These bio-based alternatives offer energy-efficient and sustainable options that align with the global shift toward circular bioeconomy models. Overall, embracing such eco-innovative approaches strengthens waste management practices, supports sustainable industrial growth, and promotes a more environmentally friendly, more profitable future for the fisheries and allied sectors.

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Conflict of interest

The authors declare no conflict of interest.

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Use of generative AI and AI-assisted technologies statement

The authors declare that no generative AI or AI-

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