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The sea walnut *Mnemiopsis leidyi*: from ecological nuisance to potential biological resource

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This review synthesizes current knowledge on the sea walnut *Mnemiopsis leidyi*, focusing on its potential as an emerging source of bioactive compounds rather than solely as a marine invader. The Ponto–Mediterranean expansion of the species and its ecological impacts are briefly outlined to provide context on the origin and magnitude of available biomass. Particular emphasis is placed on biological traits, physiological plasticity, and environmental tolerance that enable recurrent production of large gelatinous stocks. Recent evidence indicates substantial biochemical diversity, including antibiofilm and antimicrobial peptides, photoproteins, and a largely unexplored immune-associated molecular space with potential biotechnological and pharmaceutical relevance. These characteristics position *M. leidyi* as a promising candidate for biorefinery approaches aimed at extracting high-value molecules from low-cost marine biomass. However, pronounced spatial and temporal variability, together with the inherent unpredictability of natural blooms, represents a major bottleneck for reliable biomass supply and industrial exploitation. Addressing this constraint will require complementary strategies to stabilize production and improve process scalability. By integrating ecological context with biochemical and applied perspectives, this review identifies key challenges, knowledge gaps, and future directions for the sustainable valorization of gelatinous marine biomass and its derived biomolecular resources.

KEYWORDS
bioactive compounds, Black Sea, marine bio-refinery, Mnemiopsis leidyi, Ponto-Mediterranean region

1 Introduction

Gelatinous zooplankton blooms are increasingly recognized as major pulses of organic matter in coastal systems (Boero et al., 2008; Condon et al., 2010; Wright et al., 2021). The so-called "sea walnut", *Mnemiopsis leidyi* (Ctenophora, Lobata) is among the most studied bloom-forming gelatinous taxa due to its invasive spread across Eurasian seas and recurrent seasonal outbreaks (Shiganova et al., 2019 and references herein). Blooms represent a threat to fisheries and planktonic food webs (Knowler, 2005; Finenko et al., 2006; Oguz et al., 2008; Piccardi et al., 2025), while bloom biomass releases substantial amounts of dissolved organic carbon, stimulating microbial activity and altering nutrient cycling in coastal waters (Ciglenečki et al., 2021; Paliaga et al., 2021). At the same time, blooms may represent both a management challenge and an opportunity, as they generate large amounts of biomass that could serve as a source of bioactive components or high-value molecules.

Within a circular economy framework, this bloom biomass can be reframed from ecological liability to underutilized biological resource. Periodic mass occurrences generate concentrated, and often locally accessible, organic material that is otherwise left to decompose, contributing to biogeochemical imbalances. Valorizing this biomass through biorefinery approaches could simultaneously mitigate disposal costs, reduce environmental impacts associated with bloom decay, and create added value from a currently unmanaged input stream. In this perspective, the sustainable exploitation of invasive species aligns ecological management with resource recovery, transforming control efforts into opportunities for innovation.

Historically, bioprospecting has emphasized organisms rich in secondary metabolites, such as sponges, cnidarians, tunicates (Genta-Jouve and Thomas, 2012; Rudovica et al., 2021; Liu et al., 2024). Ctenophores are mostly water and have been underexplored chemically. Yet "lack of classic secondary metabolites" does not imply lack of value: many current biomedical materials and nutraceutical ingredients are macromolecular, such as collagen/gelatin peptides and glycosaminoglycans (Zhong et al., 2005; Larue et al., 2024). Moreover, functional screening approaches can bypass the need for high natural abundance by discovering sequences and producing them recombinantly from expression libraries (Ladewig et al., 2023).

This study provides a brief overview of the invasion history of *Mnemiopsis leidyi* in the Ponto-Mediterranean basin, highlights the species' biological characteristics and the traits that make it a successful invader, and subsequently explores its potential as a source of bioactive compounds. Figure 1 summarizes the main concepts and thematic structure of this review and serves as a graphical abstract.

2 The Ponto-Mediterranean invasion of the sea walnut

The lobate ctenophore *Mnemiopsis leidyi* Agassiz, 1865, is widely recognized in the invasion biology literature as one of the world's most impactful invasive alien species and has been included among the "100 of the world's worst invasive alien species" compiled from the IUCN's Global Invasive Species Database (Lowe et al., 2000; ISSG, 2004). Its native range encompasses estuarine and coastal environments along the western Atlantic, extending from Chesapeake Bay on the eastern coast of the United States through the Gulf of Mexico and southward to Argentine waters (GESAMP, 1997). Over the past four decades, *M. leidyi* has expanded across Eurasian waters via two principal invasion routes (Ghabooli et al., 2011, 2013; Bayha et al., 2015). One pathway involved transport from the Gulf of Mexico to the Black Sea, where the species was first recorded in 1982 (Pereladov, 1988, in Shiganova et al., 2019), followed by a rapid spread to the Azov (Studenikina et al., 1991) and Caspian Sea (Ivanov et al., 2000), and multiple regions of the Mediterranean basin (Boero et al., 2008; Fuentes et al., 2009; Shiganova et al., 2019). A second invasion corridor connected populations from the eastern United States to

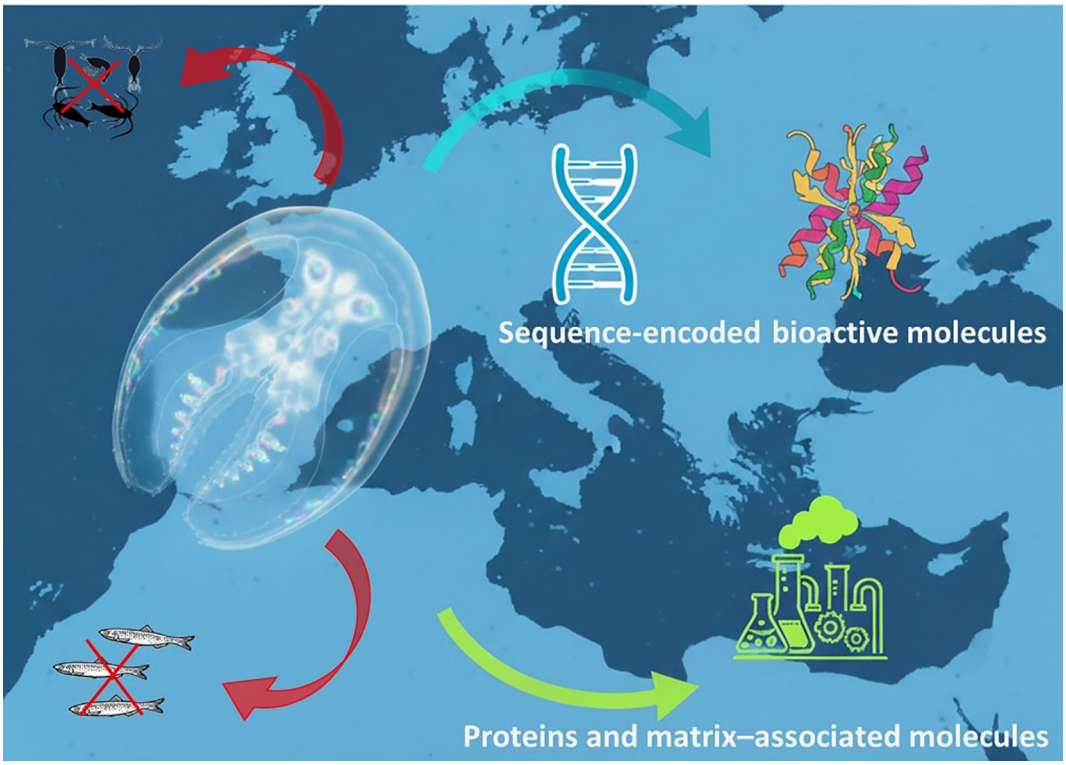

FIGURE 1
Conceptual diagram of jellyfish biomass valorization. Schematic showing the transition from European jellyfish blooms (impacting fish and plankton stocks) to the extraction of sequence-encoded bioactive molecules, proteins, and matrix-associated molecules through laboratory processing and DNA sequencing.

northern European waters, including the North Sea and the Baltic Sea (Faasse et al., 2006; Javidpour et al., 2006; Oliveira, 2007; Van Ginderdeuren et al., 2012; Antajan et al., 2014).

M. leidyi was first recorded in the Mediterranean Sea during the spring–summer period of 1990, when it was observed in the Gulfs of Saronikos and Elefsis in the western Aegean Sea (Shiganova et al., 2001a, 2004). Subsequent sightings followed in 1992 in the Marmara Sea (Shiganova et al., 1995), in the Bay of Mersin along the Turkish Mediterranean coast, in 1993 near Kuşadası on the Turkish Aegean coast (Uysal and Mutlu, 1993; Kideys and Niermann, 1994), and later offshore of Syria (Shiganova, 1997). Because these observations were largely restricted to port-adjacent areas and did not result in long-lasting populations, the introduction of *M. leidyi* was attributed to transport via ballast water (Shiganova et al., 2001b). *M. leidyi* was observed several times in the Berre Lagoon near Marseille (Delpy et al., 2016) and in the Bay of Piran, in the northern Adriatic Sea (Shiganova and Malej, 2009). Within the Mediterranean, the Adriatic Sea, particularly its northern sector, has become a recurring hotspot for *M. leidyi* blooms: after initial detection in 2005, a major bloom occurred in 2016, followed by repeated warm-season events in subsequent years (Malej et al., 2017; Putelli et al., 2025). Field and molecular studies indicate that *M. leidyi* populations in the Adriatic are maintained through local reproduction rather than repeated transient introductions (Putelli et al., 2025). Table 1 summarizes the chronology of *M. leidyi* first discoveries and spread in the Ponto-Mediterranean basin, including Baltic and North Seas.

3 Biological traits and environmental tolerance of the sea walnut

Mnemiopsis leidyi is characterized by rapid growth, early sexual maturity, and exceptionally high reproductive output (Baker and Reeve, 1974; Reeve et al., 1989). These biological traits underpin both its success as an invasive species and its capacity to generate large, episodic biomass in invaded aquatic systems (Purcell et al., 2007; Fuentes et al., 2010; Shiganova et al., 2019). The life cycle of *M. leidyi* is marked by rapid physiological transitions and high nutritional demands that shift significantly from the larval to adult stages (Sullivan and Gifford, 2004; Rapoza et al., 2005). As simultaneous hermaphrodites, adults release gametes for external fertilization, leading to the hatching of a tentaculate cydippid larva within 24 hours (Presnell et al., 2022; Rapoza et al., 2005). These early larvae (<5 mm) are primarily micro-planktivorous, relying on a diet of protists, including dinoflagellates and ciliates, to sustain high initial growth rates (Sullivan and Gifford, 2004; Rapoza et al., 2005). As the organism enters the transition stage (approximately 5 mm), it begins to develop oral lobes while resorbing its tentacles, shifting its dietary focus toward mesozooplankton such as copepod nauplii and small copepodites (Rapoza et al., 2005; Waggett and Sullivan, 2006). Upon reaching the lobate stage (>15 mm), the animal becomes a voracious generalist predator, utilizing its large oral lobes and cilia-generated feeding currents to capture larger crustaceans and even fish larvae (Colin et al., 2015; Purcell, 2009).

TABLE 1 Chronology of *Mnemiopsis leidyi* first discoveries and spread in Europe.

Region / Basin	First detection	Subsequent establishment / spread highlights	References
Black Sea	1982 (introduced via ballast water)	Became widespread and caused major ecological changes; numerous follow-up studies document its dominance and ecosystem impacts in the 1990s	Pereladov, 1988, in Shiganova et al., 2019; Shiganova, 1997; 1998
Azov Sea	1988	Presence increasing over next years	Studenikina et al., 1991
Aegean Sea (Eastern Mediterranean)	1990	Continued sightings in the early 1990s and confirmed presence in Greek and Turkish coastal waters	Uysal and Mutlu, 1993; Kideys and Niermann, 1994; Shiganova et al., 2001a;
Marmara Sea	1995	Presence increasing over next years	Shiganova et al., 1995
Caspian Sea	1999	Spread throughout the basin after initial detection	Ivanov et al., 2000
French NW Mediterranean	2005	Distribution expanded in subsequent years; blooms reported in surveillance programs from Berre Lagoon and other French coastal waters	Delpy et al., 2016
North Sea	2006	Low-density records; evidence of presence increasing over next years	Boersma et al., 2007
Baltic Sea (Kiel Bight / Western Baltic)	2006	Overwintering and seasonal persistence recorded; eastward extension to central Baltic in following years	Javidpour et al., 2006; Kube et al., 2007
Levantine Sea (Israel)	2009	Swarms observed throughout 2009; suggests local reproduction and seasonal blooms	Galil et al., 2009
Spanish NW Mediterranean	2009	Large swarms persisted through summer 2009; also recorded in Balearic Islands	Fuentes et al., 2009
Italian NW Mediterranean	2009	Continuous presence during summer 2009; swarms in Ligurian Sea and other sectors	Boero et al., 2009
Western Mediterranean (Sardinia Lagoons)	2015	First massive bloom in S'Ena Arrubia Lagoon, Sardinia	Diciotti et al., 2016
Northern Adriatic Sea	2016	Distribution expanded in subsequent years; suggests local reproduction and seasonal blooms	Shiganova and Malej, 2009

In the Black Sea, the reproductive peaks of *M. leidyi* are concentrated in the summer and early autumn, a timing dictated by the intersection of optimal water temperatures and zooplankton availability (Shiganova et al., 2014). Over the last decade, a shift toward earlier reproduction in May and June has been observed (Shiganova et al., 2018); this phenological change is attributed to rising spring temperatures and the subsequent early emergence of warm-water prey species (Shiganova et al., 2014, 2018). The reproductive strategy shifts in the Mediterranean. In areas such as the Aegean and Levantine Seas, as well as along the Ligurian coast, population increases and spawning events occur during the spring, autumn, and occasionally winter, aligning with local zooplankton pulses (Shiganova et al., 2004). Interestingly, extreme summer heat in these regions can cause *M. leidyi* to vanish from the upper water column, with a diminished new generation persisting in deeper thermal refugia (Shiganova et al., 2004). In contrast, the nutrient-rich Northern Adriatic Sea supports massive abundances and high reproductive rates specifically during the late summer and autumn (Malej et al., 2017; Putelli et al., 2025).

The invasiveness of *M. leidyi* is largely rooted in its extreme physiological tolerance and r-selected (Pianka, 1970) life history traits, which allow it to exploit disturbed or fluctuating ecosystems (Shiganova et al., 2001). Within contemporary life-history theory, the classical r/K framework is now interpreted along a broader fast–slow (pace-of-life) continuum describing trade-offs between rapid development, early reproduction and high fecundity versus delayed maturation and competitive persistence (Stearns, 1992; Healy et al., 2019), positioning *M. leidyi* toward the fast end of this spectrum. Temperature serves as the primary "on-off" switch for its invasive potential; although individuals can survive near-freezing temperatures in a state of reduced metabolic activity, rapid population expansion typically occurs once water temperatures exceed 15–20 °C (Sullivan et al., 2001). During these warm periods, a single adult can produce up to 10,000 eggs per day, quickly overwhelming the grazing capacity of local predators and outcompeting native zooplanktivorous predators (Jaspers et al., 2015). Moreover, individuals in invaded habitats have been observed to initiate reproduction at body masses two orders of magnitude lower than those of native populations, indicating selection based on standing genetic variation during the invasion process (Jaspers et al., 2018). Furthermore, the species' ability to tolerate a wide salinity gradient enables it to colonize diverse environments ranging from the high-salinity Mediterranean to the brackish Baltic and Caspian Seas (Lehtiniemi et al., 2012). While low salinity (<10 PSU) can act as a stressor that limits maximum body size and egg viability (Jaspers et al., 2011), the lack of natural specialized predators in these newly colonized areas often compensates for lower reproductive rates (Jaspers et al., 2015). This resilience is capped by its unique survival mechanism: during periods of prey depletion or environmental instability, *M. leidyi* can undergo reverse development back to the cydippid stage, essentially "recycling" its body plan to survive until favorable conditions return (Soto-Angel and Burkhardt, 2024). Table 2 shows the invasive mechanisms and environmental facilitators for the sea walnut.

4 Impacts of the sea walnut on marine biodiversity

Where introduced, *Mnemiopsis leidyi* has repeatedly formed high-biomass blooms capable of restructuring pelagic food webs (Kideys et al., 2005; Finenko et al., 2006; Marchessaux et al., 2021; Piccardi et al., 2025). Its ecological significance stems from the combination of its biological traits (broad tolerance to temperature and salinity, rapid reproduction, including self-fertilization) and non-selective predation on zooplankton and early life stages of fish and invertebrates, which together enable abrupt increases in abundance and strong top-down impacts on plankton communities, with cascading consequences for biodiversity and ecosystem functioning. The best-studied example is the Black Sea, where *M. leidyi* blooms coincided with sharp declines in mesozooplankton and ichthyoplankton diversity and abundance, as well as major fishery collapses and regime shifts (Shiganova, 1998; Finenko et al., 2006; Marchessaux et al., 2021; Piccardi et al., 2025). Importantly, biodiversity impacts are not uniform across invaded regions; rather, they depend on recipient ecosystem structure (e.g., degree of enclosure and stratification), background stressors (eutrophication, overfishing), climatic constraints, and the presence or arrival of effective predators such as *Beroe ovata* (Kideys, 2002; Kideys et al., 2005; Purcell et al., 2007).

4.1 Pathways of biodiversity impact: mechanisms and ecological "pressure points"

M. leidyi is a generalized predator that consumes a wide size spectrum of zooplankton, including copepods and cladocerans, as well as meroplankton such as bivalve veligers and other larval stages

TABLE 2 Invasive mechanisms and environmental facilitators.

Factor	Role in invasiveness	Impact on native ecosystem
Eurythermy	Survival from 0 °C to 32 °C; rapid blooming in summer.	Seasonal dominance and competition with fish larvae (Shiganova et al., 2001)
Euryhalinity	Tolerance of 3 to 39 PSU.	Ability to bridge oceanic and estuarine habitats (Lehtiniemi et al., 2012)
High Fecundity	Daily release of thousands of eggs in optimal conditions.	Rapid depletion of zooplankton stocks (Jaspers et al., 2011)
Phenotypic Plasticity	Reverse development during nutrient/salinity stress.	Persistence in habitats where other species would perish (Soto-Angel and Burkhardt, 2024)

(Colin et al., 2010). This predation can reduce zooplankton abundance and simplify community composition, effectively lowering functional diversity within the grazing guild and weakening top-down control on phytoplankton (Shiganova, 1998; Tiselius and Møller, 2017). Recent work focusing on meroplankton highlights an additional biodiversity-relevant pathway: predation on larvae of ecologically and economically important taxa can suppress recruitment and alter benthic–pelagic coupling (Schroeder et al., 2023). In invaded systems, *M. leidyi* can directly reduce ichthyoplankton (fish eggs and larvae) through predation and indirectly through competition with planktivorous fish for shared zooplankton prey (Finenko et al., 2006; Marchessaux et al., 2021; Piccardi et al., 2025). In the Black Sea, field assessments linked higher *M. leidyi* abundance with declines in fish eggs and larvae and mesozooplankton, alongside reduced fish catches and lower diversity in pelagic communities (Shiganova, 1998). When *M. leidyi* suppresses copepod grazers, phytoplankton biomass may increase due to release from grazing pressure, representing a classic trophic cascade. Long-term analyses of the Black Sea describe regime shifts in which overfishing and other stressors set the stage for ecosystem-scale cascades involving *M. leidyi* blooms (Tiselius and Møller, 2017). Sustained monitoring in invaded coastal waters has similarly documented reductions in grazing copepods and concomitant increases in primary producers during periods of *M. leidyi* dominance.

4.2 Case study: Black Sea—biodiversity loss, regime shifts, and partial recovery

The Black Sea is widely considered the flagship case for *M. leidyi* impacts. Analyses of 1992–1997 data indicate that increases in *M. leidyi* were associated with declines in abundance and species diversity of mesozooplankton and ichthyoplankton, with some taxa reported to virtually disappear during peak invasion years (Shiganova, 1998). These changes were not solely a consequence of invasion but occurred in a system already stressed by eutrophication and fisheries pressure. However, the *M. leidyi* outbreak amplified top-down control, pushing the pelagic community toward lower biodiversity and a gelatinous-dominated, trophically simplified food web structure (Shiganova, 1998). Declines in Black Sea pelagic fisheries, particularly of zooplanktivorous fish, have been repeatedly linked to the combined effects of *M. leidyi* predation on early fish stages and competition for zooplankton prey (Kideys et al., 2005). This case is frequently cited as a central example of how an invader can shift community composition and reduce biodiversity at higher trophic levels (Shiganova, 1997, 1998). A broader synthesis (Kideys, 2002) emphasized the fall and rise of the ecosystem, attributing severe degradation in the late 1980s to early 1990s to eutrophication and the arrival of the sea walnut, with subsequent improvement linked to reduced nutrient inputs and the later arrival of the natural predator *Beroe ovata* (Kideys, 2002; Kideys et al., 2005). The arrival of *B. ovata* in the Black Sea was associated with reduced *M. leidyi* biomass and signs of recovery in zooplankton performance (species richness, abundance, and biomass) during the transitional period following predator establishment (Kamburska, 2004). Importantly, recovery does not necessarily imply a full return to pre-invasion biodiversity states; food webs may remain altered and interannual variability can persist. Nonetheless, this predator–prey coupling represents one of the clearest examples of biotic resistance, or delayed natural control, mitigating the biodiversity impacts of an invasive gelatinous predator (Kamburska, 2004).

4.3 Beyond the Black Sea: spread and biodiversity impacts in other regions

In Northern Europe, *M. leidyi* was first recorded in the western Baltic (Kiel Bight) in October 2006 (Javidpour et al., 2006). Subsequent observations documented distribution patterns and evidence consistent with overwintering and broader basin spread, which represents an important prerequisite for persistent biodiversity impacts (Kube et al., 2007). Quantitative assessments in Kiel Fjord evaluated seasonal diet composition and predation impact soon after invasion and explicitly framed the phenomenon as a matter of concern, reflecting potential ecosystem-level consequences of sustained predation pressure on zooplankton functional groups (Javidpour et al., 2009). In parallel, studies of food-web responses in invaded coastal plankton systems have demonstrated strong trophic cascades (reduced grazers and increased primary producers) linked to the presence of the sea walnut, mechanistically consistent with biodiversity and functional shifts in planktonic communities (Tiselius and Møller, 2017). Reports of first occurrence and rapid spread in the North Sea emphasized ecosystem sensitivity and uncertainty about future impacts, underscoring the need for continued monitoring (Boersma et al., 2007). These early warning studies are biodiversity-relevant because they capture invasion stages during which management and surveillance may still influence outcomes, for example by detecting establishment, identifying hotspots, or linking blooms with plankton shifts. In the Mediterranean, records from the Levant stress that *M. leidyi* blooms raise concern due to documented impacts elsewhere, notably on fisheries, and because dense swarms can interfere with coastal infrastructure through clogging of seawater intake systems—an economic impact often co-occurring with ecological disruption (Galil et al., 2009). In other enclosed or semi-enclosed systems, such as the Caspian Sea, recent analyses continue to document major changes in abundance and diversity across trophic levels following *M. leidyi* invasion, consistent with the Black Sea pattern of combined top-down and bottom-up forcing (Roohi et al., 2024).

4.4 Biodiversity dimensions affected by Mnemiopsis leidyi

The most consistently reported biodiversity effect is a reduction in the taxonomic diversity of zooplankton and ichthyoplankton communities during or following outbreak periods, particularly in heavily stressed, semi-enclosed seas (Shiganova, 1997, 1998). Even when taxonomic losses are partial or reversible, functional consequences can be substantial. By selectively or broadly removing grazers and larval stages, *M. leidyi* alters energy

pathways, shifts energy flow toward microbial loops and phytoplankton-dominated systems, and may reduce food-web resilience to environmental variability. Long-term trophic-cascade analyses provide a mechanistic link between predation pressure and large-scale community reorganization (Daskalov et al., 2007; Tiselius and Møller, 2017). Predation on meroplankton and early fish life stages can create recruitment bottlenecks that propagate into altered adult community composition and reduced biodiversity at higher trophic levels. This is particularly concerning in nursery areas, where larval stages of multiple species co-occur and remain highly vulnerable within the plankton (Schroeder et al., 2023).

4.5 Interactions with other stressors and implications for management

A recurring theme is that *M. leidyi* impacts are magnified when ecosystems are already destabilized, particularly by overfishing and eutrophication (Purcell et al., 2007). Black Sea analyses explicitly link intense fishing pressure to regime shifts and trophic cascades in which sea walnut outbreaks become pivotal drivers of altered ecosystem states (Daskalov et al., 2007). This suggests that mitigating invasion impacts is not only a matter of invasive-species control but also of reducing background pressures that weaken ecosystem resistance, for example by restoring predator populations and controlling nutrient loads. The documented partial recovery following reduced nutrient inputs and the arrival of *B. ovata* underscores the importance of both abiotic and biotic controls (Kideys, 2002; Kideys et al., 2005).

5 Exploring the potential valorization of the sea walnut

5.1 Towards Mnemiopsis leidyi bio-refinery

Unlike many benthic marine invertebrates traditionally targeted for natural product discovery, *Mnemiopsis leidyi* is a gelatinous organism composed predominantly of water, with organic matter concentrated in proteins and extracellular matrix components (Yousefian and Kideys, 2003). Biochemical analyses of *M. leidyi* biomass consistently show that proteins constitute the dominant fraction of dry mass, followed by smaller contributions from lipids, polysaccharides, and low-molecular-weight nitrogenous compounds (Yousefian and Kideys, 2003; Anninsky et al., 2005; Rečnik et al., 2024). From a chemical standpoint, these characteristics indicate that the primary exploitable molecular space of *M. leidyi* lies in proteins and extracellular matrix–associated macromolecules rather than in classical low-molecular-weight secondary metabolites, as typically reported for other marine invertebrates (Genta-Jouve and Thomas, 2012; Rudovica et al., 2021; Liu et al., 2024).

The internal organization of *M. leidyi* also has direct implications for biomass chemistry. The body plan consists of ectoderm and endoderm separated by a thick mesoglea, a gelatinous extracellular matrix (ECM) described in zoological literature as rich in poorly characterized polysaccharides and sparsely populated by cells (Brusca et al., 2022). Classical ultrastructural studies reported an apparent absence of fibrillar collagen and elastin fibers in ctenophore connective tissue (Harrison and Westfall, 1991). However, modern genomic analyses reveal that *M. leidyi* possesses multiple collagen IV–like genes, consistent with a basement-membrane-type extracellular matrix rather than a fibrillar collagen scaffold (Ryan et al., 2013). This apparent discrepancy highlights the need to distinguish between structural fiber visibility and molecular presence. It also underscores the importance of modern proteomic and glycomic approaches for characterizing ctenophore ECM chemistry (Draper et al., 2019).

The sea walnut occupies a pivotal phylogenetic position as one of the earliest-branching metazoan lineages (Brusca et al., 2022). The publication of its genome revealed unexpected complexity in cell signaling, adhesion, and immune-related gene families, with important implications for the evolution of cell types and defense mechanisms (Pett et al., 2011; Ryan et al., 2013). These genomic features provide a strong biological rationale for exploring *M. leidyi* as a source of sequence-encoded bioactive molecules. Marine bioprospecting has traditionally focused on benthic invertebrates such as sponges, corals, and tunicates that produce abundant low-molecular-weight secondary metabolites (Genta-Jouve and Thomas, 2012; Rudovica et al., 2021; Liu et al., 2024). In contrast, gelatinous zooplankton, particularly ctenophores, have long been considered chemically unpromising because of their high water content and the apparent absence of classical secondary metabolites (Clarke et al., 1992). Emerging literature on *M. leidyi* suggests that its relevance for marine bioactive compound discovery lies not in bulk extract chemistry but in its sequence-encoded bioactive space, especially peptides and immune-associated macromolecules (Ladewig et al., 2023). In this framework, *M. leidyi* should be regarded primarily as a source of biological information rather than as a reservoir of extractable small molecules (Ryan et al., 2013; Koutsouveli et al., 2025). This perspective represents a conceptual shift in marine bioprospecting, aligning ctenophores with modern discovery strategies based on genomics, functional screening, and recombinant production (Moutinho Cabral et al., 2024). Table 3 summarizes candidate active principles identified in *M. leidyi* biomass.

5.2 Antibiofilm peptides

The strongest experimental support for pharmaceutical-relevant bioactivity in *M. leidyi* derives from the identification of antimicrobial and antibiofilm peptides through functional screening of expression libraries. Ladewig et al. (2023) generated *Escherichia coli* expression libraries from *M. leidyi* cDNA and identified short peptide sequences capable of inhibiting biofilm formation by opportunistic pathogens. Notably, the antibiofilm activity was retained following chemical synthesis of the peptides, indicating that bioactivity is intrinsic to the encoded sequences rather than dependent on the heterologous expression host (Ladewig et al., 2023). This observation is particularly relevant given the persistent clinical burden of biofilm-associated

TABLE 3 Candidate active principles in *Mnemiopsis leidyi* biomass.

Candidate class	Representative molecules / fraction	Primary evidence type	Application space	Most realistic production route	Evidence strength (today)
Antibiofilm peptides (AMP-like)	short peptides validated by chemical synthesis after clone screening	expression library → biofilm assay → peptide synthesis validation	anti-infective coatings; topical antibiofilm agents	synthetic peptide / recombinant	High (functional)
Photoproteins	mnemiopsin (coelenterazine-dependent, Ca^{2+}-regulated)	biochemistry/structure-function; genomics; recombinant expression	diagnostics, reporters, biosensors	recombinant protein	High (tool candidate)
Immune-related protein space	expanded immune-related domains; ETosis-like behavior	chromosome-level genome immune repertoire; immune cell assays	upstream discovery rationale for effectors	discovery → recombinant	Medium (rationale)
Mesoglea polysaccharides	"uncharacterized glucopolysaccharides" (gel-like ECM)	anatomical/overview descriptions	hydrogels/scaffolds (conditional)	extraction + purification after chemical validation	Low–Medium (composition unknown)
ECM proteins (collagen-related)	collagen IV gene duplications reported in portal integration paper	genomic/database evidence	biomaterials/ECM biology tools	recombinant or targeted extraction	Medium (genomic)
Bulk protein + NPS/ hydrolysates	protein-rich dry-matter fraction; NPS	biochemical composition study	nutraceutical peptides (requires assays)	extraction + enzymatic hydrolysis	Medium (substrate)
Lipids/fatty acids	low total FA; "lipid-poor" characterization	comparative FA analyses	minor lipids (speculative)	solvent/SFE (targeted)	Low (yield constraint)

infections (Costerton et al., 1999; Hall-Stoodley et al., 2004; Percival et al., 2015) and the increasing recognition of marine-derived peptides as structurally diverse antibiofilm agents with distinct modes of action (Sukmarini et al., 2023; Behzadnia et al., 2024; Wang et al., 2025; Carroll et al., 2025). In this context, the sequence-based discovery strategy applied to *M. leidyi* avoids reliance on bulk biomass extraction and thereby circumvents practical limitations associated with gelatinous organisms, including rapid post-mortem degradation and logistical constraints (Clarke et al., 1992; Guy-Haim et al., 2020). Instead, *M. leidyi* can be conceptualized as a genomic source of bioactive sequences, enabling scalable production through peptide synthesis or recombinant expression. Such an approach aligns with current marine drug discovery paradigms that increasingly emphasize sequence-defined actives and rational optimization over complex natural extract mixtures (Wang et al., 2025; Carroll et al., 2025).

5.3 Immune-associated molecular space

Recent genomic analyses indicate that ctenophores possess a more complex innate immune repertoire than previously assumed (Bolte et al., 2013; Koutsouveli et al., 2025). Chromosome-level genomes reveal expanded and unique immune-related domain architectures in *M. leidyi* (Koutsouveli et al., 2025), and reviews of ctenophore immune repertoires emphasize the potential for divergent molecular components (Traylor-Knowles et al., 2019). Functional studies have demonstrated that immune cells of *M. leidyi* can form extracellular DNA traps in response to microbial exposure and chemical stimulation, providing direct evidence of active immune defense mechanisms (Vandepas et al., 2024). Although specific antimicrobial effector molecules have not yet been isolated from this system, these findings provide a biological rationale for targeted proteomic and peptidomic investigation of immune-challenged specimens. Such systematic approaches represent a promising strategy for identifying structurally and functionally novel marine bioactive compounds.

5.4 Photoproteins and bioluminescence-related proteins

Photoproteins constitute a second well-characterized class of *M. leidyi*–derived biomolecules (Schnitzler et al., 2012). The Ca^{2+}-regulated mnemiopsin has been studied in detail with respect to its luminescent reaction mechanism and structural features (Burakova and Vysotski, 2019; Soares et al., 2025). Photoproteins are primarily positioned as biotechnological tools; however, within the context of marine bioactive compound research, their relevance lies in their functional novelty and evolutionary distinctiveness (Giardi and Pace, 2005; Eglen and Reisine, 2008). Although native photoproteins can be isolated from fresh biomass for analytical purposes, recombinant expression of *M. leidyi* photoproteins in *E. coli* has been successfully demonstrated, enabling purification and functional characterization independent of biomass availability (Schnitzler et al., 2012). These proteins therefore exemplify how ctenophores can contribute structurally distinct molecular scaffolds and novel functionalities to the broader marine bioactive repertoire.

5.5 Mesoglea polymers

The ctenophore mesoglea has often been described as a gelatinous extracellular matrix rich in uncharacterized polysaccharides (Brusca et al., 2022), prompting interest in potential biomaterial applications. Classical ultrastructural studies describe ctenophore connective tissue as unusual and lacking the fibrillar collagen and elastin fibers typical of other metazoan ECMs (Hernandez-Nicaise et al., 1989; Draper et al., 2019). However,

genomic and chromosome-level analyses indicate that *M. leidyi* nonetheless encodes basement-membrane-type components (e.g., collagen IV–like sequences and conserved ECM domains), implying a mesogleal ECM organization distinct from canonical fibrillar matrices (Ryan et al., 2013; Koutsouveli et al., 2025). Recent evo-devo and ECM biology work further highlights that such divergent ECM architectures can harbor lineage-specific domain combinations and bioactive motifs relevant to development and host–microbe interactions (Draper et al., 2019; Hynes, 2009). While these molecules may ultimately be exploitable as bioactive scaffolds or delivery matrices, their immediate relevance for drug discovery remains secondary to peptide- and immune-derived actives isolated via genomic and functional screening approaches.

5.6 Bulk proteins and hydrolysates

Protein-rich biomass fractions of *M. leidyi* support the feasibility of producing protein concentrates and enzymatic hydrolysates (McNamara et al., 2013; Vansteenbrugge et al., 2016). Biochemical composition studies consistently identify protein as the dominant organic fraction of *M. leidyi* dry matter (Anninsky et al., 2005; Yousefian and Kideys, 2003), further supporting the feasibility of producing protein concentrates and enzymatic hydrolysates from bloom biomass. Validation of hydrolysate-derived actives requires nutraceutical-oriented assays, such as antioxidant or enzyme-inhibitory activity, together with cytotoxicity and stability testing to ensure safety and regulatory compliance. Table 4 shows comparative biochemical composition profiles of the sea walnut and other ctenophores, such as *Beroe ovata* and *Pleurobranchia pileus*. All three species exhibit a protein-dominated biochemical composition, with proteins accounting for the majority of organic matter, whereas lipids and carbohydrates represent comparatively smaller fractions; however, *Beroe* and *Pleurobrachia* generally display higher absolute organic and protein concentrations than *M.s leidyi*, consistent with the latter's more gelatinous body structure.

5.7 Lipids

Recent advances in high-resolution lipidomics and optimized extraction/analysis workflows have begun to unveil species- and tissue-specific lipidome signatures in jellyfish, and pointing to gelatinous organisms as an under-explored source of potentially bioactive marine lipids with pharmaceutical relevance (Waqas et al., 2025; Nautiyal et al., 2025). Comparative biochemical and trophic studies consistently describe *M. leidyi* as relatively lipid-poor compared with other ctenophore species (Yousefian and Kideys, 2003; Vansteenbrugge et al., 2016). This characteristic constrains the feasibility of lipid-based bioactive compound discovery from this organism. Table 4 shows comparative fatty-acid profiles of the sea walnut and *B. ovata* and *P. pileus*. The first published fatty acid characterization of *M. leidyi* (Vansteenbrugge et al., 2016) reported that total fatty acids (FA) in dry biomass averaged approximately 2.15 mg g^{-1} dry weight (DW), with high variance (± 2.05 mg g^{-1}), indicating both low overall lipid content and pronounced seasonal or spatial variability. *M. leidyi* exhibited three- to four-fold lower total FA concentrations compared to some native ctenophores, such as *Beroe* (≈ 9.44 mg g^{-1} DW) and *P. pileus* (≈ 7.00 mg g^{-1} DW).

TABLE 4 Comparative biochemical composition and fatty-acid profiles of *Mnemiopsis leidyi, Beroe ovata* and *Pleurobranchia pileus* (WW, wet weight; DW, dry weight; OM, organic matter).

Component	*Mnemiopsis leidyi*	*Beroe ovata*	*Pleurobrachia pileus*	References
Dry matter	2.0–4.1 % WW	3.5–6.0 % WW	3.0–5.5 % WW	Anninsky et al., 2005; Rečnik et al., 2024
Total organic matter	84 mg g^{-1} DW	95–120 mg g^{-1} DW	90–110 mg g^{-1} DW	Anninsky et al., 2005; Yousefian and Kideys, 2003
Elemental C	34–38 % DW	—	35–40 % DW (reported range)	Rečnik et al., 2024
Elemental N	8–10 % DW	—	8–11 % DW	Rečnik et al., 2024
Protein	0.92 ± 0.14 mg g^{-1} WW	1.93 ± 0.42 mg g^{-1} WW	1.4–1.6 mg g^{-1} WW	Anninsky et al., 2005; Yousefian and Kideys, 2003
Protein	80.6 ± 3.3 % OM	76.9 ± 3.4 % OM	75–82 %	Anninsky et al., 2005; Yousefian and Kideys, 2003
Lipids	0.10 ± 0.03 mg g^{-1} WW	0.31 ± 0.13 mg g^{-1} WW	0.15–0.25 mg g^{-1} WW	Anninsky et al., 2005
Lipids	9.0 ± 2.3 % OM	12.2 ± 3.6 % OM	10–15 % OM	Anninsky et al., 2005
Carbohydrates	0.07 ± 0.02 mg g^{-1} WW	0.14 ± 0.03 mg g^{-1} WW	0.10–0.15 mg g^{-1} WW	Anninsky et al., 2005
Σ Fatty acids (total)	0.1–4.2 mg g^{-1} DW	6.5–12.0 mg g^{-1} DW	5.0–9.0 mg g^{-1} DW	Vansteenbrugge et al., 2016
Total SFA	30–40 % ΣFA	25–32 % ΣFA	28–35 % ΣFA	Vansteenbrugge et al., 2016
Palmitic acid (16:0)	18–25 % ΣFA	15–20 % ΣFA	16–22 % ΣFA	Vansteenbrugge et al., 2016
Stearic acid (18:0)	6–10 % ΣFA	4–7 % ΣFA	5–8 % ΣFA	Vansteenbrugge et al., 2016
Total MUFA	18–30 % ΣFA	20–30 % ΣFA	18–25 % ΣFA	Vansteenbrugge et al., 2016
Oleic acid (18:1 ω9)	8–15 % ΣFA	10–18 % ΣFA	9–14 % ΣFA	Vansteenbrugge et al., 2016
Total PUFA	18–30 % ΣFA	30–45 % ΣFA	28–40 % ΣFA	Vansteenbrugge et al., 2016
EPA (20:5 ω3)	6–12 % ΣFA	10–18 % ΣFA	8–15 % ΣFA	Vansteenbrugge et al., 2016
DHA (22:6 ω3)	5–10 % ΣFA	8–15 % ΣFA	7–12 % ΣFA	Vansteenbrugge et al., 2016
PUFA/SFA ratio	0.5–0.9	1.0–1.6	0.9–1.4	Vansteenbrugge et al., 2016

TABLE 5 Technical parameters for sea walnut cultivation.

Parameter	Optimal range	Significance
Temperature	22 °C – 26 °C	Maximizes metabolic rate and egg production (Gambill et al., 2015)
Salinity	15–25 PSU	Balances osmotic stress and reproductive success (Jaspers et al., 2015)
Flow Velocity	0.5 – 1.5 cm/s	Prevents sedimentation without causing tissue shear (Presnell et al., 2022; Soto-Angel et al., 2024)
Feeding Frequency	2–4 times daily	Necessary to maintain the high carbon demand of rapid growth (Baker and Reeve, 1974; Sullivan and Gifford, 2004)

TABLE 6 Nutritional and dietary shifts by stage.

Stage	Size	Primary diet	Key nutrient info
Cydippid	<5 mm	Microplankton (Dinoflagellates, ciliates)	Require microprotists for growth; low retention of large prey (Sullivan and Gifford, 2004)
Transition	5–15 mm	Mixed (Protists and small copepods)	Metamorphosis phase; growth rate may temporarily dip during lobe formation (Rapoza et al., 2005)
Lobate	>15 mm	Mesozooplankton (Copepods, fish eggs)	High clearance rates; microprotists become insufficient for maintenance (Baker and Reeve, 1974)
Reverse	Variable	Autophagy / Tissue Reorganization	Drastic reduction in carbon/ nitrogen biomass to survive starvation (Soto-Angel and Burkhardt, 2024)

Major saturated fatty acids (SFA) included palmitic acid (16:0) and stearic acid (18:0), consistent with general marine invertebrate lipid patterns (Imbs et al., 2021). Monounsaturated fatty acids (MUFA), such as oleic acid (18:1ω9) and palmitoleic acid (16:1ω7), were present and varied with size class, though at lower relative proportions than in some native ctenophore species. Polyunsaturated fatty acids (PUFA) were dominated by the canonical marine n-3 PUFAs EPA (20:5ω3) and DHA (22:6ω3), along with minor amounts of linoleic (18:2ω6), arachidonic (20:4ω6), and alpha-linolenic (18:3ω3) acids. These long-chain n-3 PUFAs are typical biomarkers of marine trophic transfer to higher consumers and reflect dietary integration (Dalsgaard et al., 2003). PUFA/SFA ratios in *M. leidyi* were lower than in *Beroe*, indicating a relatively lipid-poor profile and potential trophic differences.

5.8 Feasibility and perspectives of sea walnut cultivation

Blooms of ctenophores, including *M. leidyi*, remain difficult to predict, as the relationships between life-history strategies, bloom formation, and environmental variability are not yet fully understood (Schnedler-Meyer et al., 2018). Environmental fluctuations may lead to irregular and episodic increases in abundance, resulting in blooms that vary considerably in timing and intensity across coastal and semi-enclosed ecosystems (Purcell, 2005; Condon et al., 2013). It is therefore evident that reliance on such an unpredictable resource is not feasible. The transition of *M. leidyi* from a marine ecological threat to a potential feedstock for biorefineries requires a paradigm shift in cultivation techniques. Historically, ctenophores were considered difficult to culture due to their extreme fragility; however, recent advancements in gelatinous zooplankton husbandry have made high-density, controlled biomass production possible. The current gold standard for stable culture involves the use of plankton kreisels and pseudo-kreisels, which utilize laminar water flow to maintain individuals in constant suspension (Presnell et al., 2022; Soto-Angel et al., 2024). Table 5 summarizes the technical parameters for sea walnut cultivation.

M. leidyi is characterized by remarkably high growth potential and has been reported to double its body mass in less than 24 hours under favorable conditions (Baker and Reeve, 1974), suggesting

TABLE 7 Evidence levels for candidate bioactive principles in *Mnemiopsis leidyi*.

Molecular class	Evidence type	Validation status	Key references	Developmental stage
Antibiofilm peptides (cDNA library-derived)	Functional screening + synthetic validation	Experimentally validated bioactivity (*in vitro* antibiofilm assays; activity retained after synthesis)	Ladewig et al., 2023	Lead-level (preclinical *in vitro*)
Immune-associated peptides / effectors	Genomic expansion + ETosis functional evidence	Biological plausibility; no isolated effector molecules yet	Ryan et al., 2013; Traylor-Knowles et al., 2019; Vandepas et al., 2024; Koutsouveli et al., 2025	Hypothesis-driven discovery phase
Extracellular matrix polymers (collagen IV-like, mesoglea polysaccharides)	Genomic + ultrastructural + evo-devo inference	Structural presence demonstrated; no direct pharmacological validation	Draper et al., 2019; Ryan et al., 2013; Koutsouveli et al., 2025	Speculative biomaterial potential
Photoproteins (mnemiopsin)	Biochemical + recombinant expression	Functionally validated (biotechnological use); limited therapeutic testing	Schnitzler et al., 2012; Burakova and Vysotski, 2019	Validated molecular scaffold
Bulk protein hydrolysates	Biomass compositional studies	Feasible production; bioactivity requires targeted assays	Yousefian and Kideys, 2003; McNamara et al., 2013	Nutraceutical exploration
Lipids / fatty acids	Biochemical profiling + lipidomics	Chemical presence documented; no demonstrated pharmacological leads	Vansteenbrugge et al., 2016; Waqas et al., 2025	Exploratory stage

potential advantages for biomass production. During the early larval (cydippid) stage, successful rearing appears to depend on microplankton-based diets composed of rotifers (Brachionus plicatilis) and ciliates during the first 5–7 days of development (Sullivan and Gifford, 2004). At later (lobate) stages, enriched *Artemia salina* nauplii or frozen copepod biomass are commonly employed (Baker and Reeve, 1974); however, their cost may limit large-scale implementation. Consequently, ongoing research increasingly considers artificial microencapsulated diets as a potential alternative to live feeds, which could improve the economic feasibility of *M. leidyi* cultivation for biorefinery-oriented production (Jaspers et al., 2015). Table 6 summarizes nutritional and dietary shifts across developmental stages. A distinctive feature of *M. leidyi* cultivation for biotechnological purposes is its metabolic plasticity: reverse development, involving size reduction while maintaining tissue integrity (Soto-Angel and Burkhardt, 2024), could allow biorefineries to maintain live biomass during supply chain interruptions without complete culture loss. Furthermore, the high water content (>95%) of ctenophores facilitates low-energy extraction of water-soluble proteins and collagen, although it necessitates efficient dewatering technologies to concentrate the organic fraction for downstream processing.

From a techno-economic perspective, several constraints must be carefully evaluated before industrial-scale production can be considered. Capital expenditures would include specialized recirculating aquaculture systems equipped with kreisels, fine filtration units, temperature control, and continuous monitoring to prevent mechanical damage to organisms (Malone and Pfeiffer, 2006; Badiola et al., 2012). Operational costs are likely to be dominated by energy demand for water circulation and climate control, as well as by the production or procurement of live feed (rotifers, ciliates, *Artemia*), which can represent a substantial fraction of total rearing expenses (Lubzens et al., 2001; Conceição et al., 2010). Given the extremely high water content of *M. leidyi* biomass (>95%; Lucas et al., 2011), downstream processing poses additional economic challenges, as large volumes must be handled to recover relatively small amounts of dry organic matter. This makes dewatering, concentration, and stabilization steps critical cost drivers (Hsieh et al., 2001; Leone et al., 2015). Consequently, the economic viability of cultivation will depend on achieving high volumetric productivity, reducing feed costs (e.g., through formulated or microencapsulated diets), optimizing energy efficiency, and targeting high-value bioproducts capable of offsetting production and processing expenditures (Klinger and Naylor, 2012; FAO, 2020).

6 Conclusions

The sea walnut *Mnemiopsis leidyi* exemplifies how a species traditionally regarded as an ecological problem can also be reconsidered as a source of biological and biotechnological opportunities. Its biological traits and broad environmental tolerance underpin both its ecological impacts and its capacity to generate large biomasses, characteristics that may also support its potential valorization. Emerging evidence highlights a diverse repertoire of bioactive molecules, including antibiofilm peptides, photoproteins, and immune-associated compounds, positioning *M. leidyi* as a promising candidate for marine biorefinery approaches. At present, antibiofilm peptides represent the only experimentally validated pharmaceutical leads identified from *M. leidyi*, whereas immune-derived sequences, ECM-associated polymers, lipids, and bulk protein fractions define a broader theoretical molecular space that warrants systematic proteomic, peptidomic, and functional investigation (Table 7). However, pronounced spatial and temporal variability of natural blooms limits the reliability of biomass supply and currently constrains industrial exploitation. Addressing this challenge will require integrated research efforts combining ecological, biochemical, and applied perspectives, together with the development of controlled production strategies. By linking impact assessment with sustainable valorization frameworks, future research may help reposition the sea walnut from an unmanaged ecological pressure to a regulated marine bioresource within the emerging blue bioeconomy.

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