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Review

Emerging Marine Nematodes as Model Organisms: Which Species for Which Question?

Federica Semprucci [1,†], Eleonora Grassi [1,†], Adele Cocozza di Montanara [2,*], Roberto Sandulli [2,*] and Elisa Baldrighi [3]

[1] Department of Biomolecular Sciences (DiSB), University of Urbino 'Carlo Bo', Loc. Crocicchia, 61029 Urbino, Italy; federica.semprucci@uniurb.it (F.S.); e.grassi5@campus.uniurb.it (E.G.)
[2] Department of Sciences and Technologies (DiST), Parthenope University of Naples, ULR CoNISMa, Centro Direzionale Isola C4, 80143 Naples, Italy
[3] Department of Biology, University of Nevada-Reno, Mailstop 314, Reno, NV 89557, USA; ebaldrighi@unr.edu
* Correspondence: adele.cocozzadm@gmail.com (A.C.d.M.); roberto.sandulli@uniparthenope.it (R.S.)
† These authors contributed equally to this work.

Abstract: Marine nematodes possess all the prerequisites to serve as "simpler models" for investigating biological phenomena and are gaining attention as emerging model organisms. This review evaluates their potential to address diverse biological questions regarding ecosystem functioning, climate change adaptation, host–microbe interactions, ecotoxicology, and biotechnological applications. Among the reviewed taxa, *Litoditis marina* and select Monhysteridae species, such as *Diplolaimella dievengatensis*, *Halomonhystera disjuncta*, and *Diplolaimelloides* spp., emerge as leading candidates due to their manageable life cycles, adaptability to laboratory conditions, and available genomic resources. These tiny organisms provide valuable insights into phenomena such as developmental plasticity, epigenetic regulation, and adaptive responses to environmental stress. Symbiotic relationships in Stilbonematinae and Astomonematinae, alongside the antimicrobial properties of the Oncholaimidae species, offer unique opportunities to explore mutualistic evolution and resilience in extreme environments. Despite challenges in culturing these species, recent advances in culturing other meiofaunal organisms with chemosynthetic symbionts have opened up promising opportunities. The roles of marine nematodes as ethical and versatile models position them to address pressing challenges in biological and biomedical research, highlighting their significant potential for future studies.

Keywords: Nematoda; marine ecosystems; eco-evo-devo; non-human species

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1. Introduction

A model organism can be a non-human species (e.g., microbe, plant, or animal) with extensive genomic research data. These organisms are used to study and understand specific biological phenomena, with the expectation that discoveries made in these models will provide new insights into "big biological questions" [1]. Model organisms are widely employed to explore potential causes and treatments for human diseases when direct experimentation on humans is unfeasible or ethically problematic [2]. This approach is supported by the common descent of all living organisms, as well as the conservation of metabolic and developmental pathways and genetic material over the course of evolution [3].

The use of model organisms is not confined to biomedical research. Significant advancements in developmental biology, eco-toxicology, fertilization processes, speciation, symbiosis, and sexual selection have been achieved using these models [3]. Furthermore, emerging animal models—species with less neurological complexity than those protected by legislation—are increasingly recognized as a valid application of the Three Rs principle (Replacement, Reduction, and Refinement). To support this approach, databases of invertebrate species currently used or with potential applications in biomedical research are continually being developed and updated.

Meiofauna, an unconventional and often overlooked group of invertebrates (body size: 30–500 µm), inhabit aquatic environments across a range of habitats, from polar regions to tropical zones, including some of the most extreme conditions [4–7]. Their biodiversity is remarkable, with new species frequently described [8]. Among meiofauna, free-living nematodes represent the most abundant taxon in all types of environmental matrices and play key roles in ecosystem processes such as biomineralization, bioturbation, and oxygen and nutrient cycling [5,9–11]. These traits have led to a growing interest in their use for ecological assessments of anthropogenic disturbances [12–14] (Supplementary Materials, Table S1).

Can marine nematodes truly be considered model organisms? As shown in Table S1, nematodes possess all the prerequisites to serve as "simpler models" in which biological phenomena can be investigated and later validated in more complex ecological contexts. Moreover, nematodes are the most successful meiobenthic phylum for use under laboratory-controlled conditions [9].

The terrestrial free-living nematode *Caenorhabditis elegans* (Rhabditidae) has been one of the most significant model organisms since 1963, especially in eukaryotic genetics and developmental biology, partly due to its invariant number of somatic cells, which facilitated the mapping of its complete cell lineage. *C. elegans* was the first multicellular organism to have its genome fully sequenced (*Caenorhabditis elegans* Sequencing Consortium, 1998) and embryonic cell lineage mapped [15,16]. Additionally, many key genes involved in developmental and cellular processes, such as apoptosis, have been identified in this species. Similarly, *Pristionchus pacificus* (Diplogasteridae), a nematode species described in 1996, has provided valuable insights into how environmental conditions during development can shape phenotypes, demonstrating surprising phenotypic plasticity [17,18].

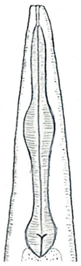
In this review, we critically summarize the progress made so far on marine nematodes as model organisms. A shortlist of marine and estuarine species suitable for addressing specific biological questions is presented. For each candidate, we evaluate feasibility of rearing under controlled conditions, generation time, potential for manipulation of eggs/embryos and adults, and the current state of genome sequencing knowledge. Two central questions guide this review: (1) Which marine nematodes are the most promising candidates as model organisms? (2) For which biological questions can specific nematode candidates serve as models? Ultimately, this paper aims to provide a compelling overview of marine nematodes as viable alternatives to the well-established model *C. elegans* and as an exemplary application of the Three Rs (Replacement, Refinement, and Reduction) principle. Indeed, animal experimentation for scientific purposes is regulated at an international level and primarily concerns the use and protection of vertebrates and cephalopods. The use of emerging animal models—species that are recognized to have less neurological complexity compared to those protected by regulations—is steadily increasing. Indeed, this trend is increasingly regarded as a valid example of 'replacement', one of the 3R principles aimed at replacing the use of animals with higher neurological complexity in research.

2. Snapshot of Model Organisms Within Marine Nematodes

The family Monhysteridae includes numerous bacterivorous nematodes recognized as cosmopolitan species and widely used as marine model organisms (Figure 1 and Table 1).

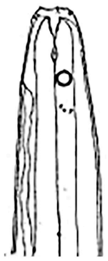
Model organism identikit

Litoditis marina



Dioecious
Generation time: 4–5 days
Rearing: healthy worms were cultured on SW-NGM agar plates (prepared with seawater with a salinity of 3ppt) seeded with *E. coli* OP50, maintained and propagated at 20°C

Halomonhystera disjuncta

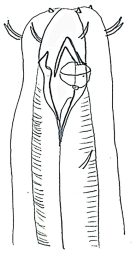


Dioecious
Generation time: 4–5 days
Rearing: cryptic species GD1 were cultivated at 16°C on petri dishes filled with 0.8% nutrient:bacto agar in a ratio of 1:7 prepared in artificial seawater with a salinity of 25ppt. *E. coli* K12 can be added as a food source

Metoncholaimus pristiurus

Dioecious
Generation time: n/a
Rearing: specimens selected in 80% of a biosubstrate made from the endoskeleton of *Sepia officinalis*, fed on *Porcellio Scaber* (different concentrations). Temperature of 18°C/12°C and light/dark photoperiod cycle of 8.5/15.5 h

Oncholaimus campylocercoides

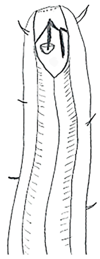


Dioecious
Generation time: n/a
Rearing: to achieve the mono-species level, a grain size magnification was applied by gradually adding a biosubstrate made from either the crushed shells of *Mytilus galloprovincialis* or minced leaves of *Posidonia oceanica*. After selection, this model was cultured and fed with earthworm powder (560 mg.l-1)

Metoncholaimus albidus

Dioecious
Generation time: n/a
Rearing: individuals of *M. albidus* were maintained in glass petri dishes (H 25 mm, diam. 150 mm) containing sterilized oxygenated seawater (Instant Ocean at a salinity of 33ppt), at 18°C and with natural light. The worms were fed weekly with 0.5 g of a ground commercial dried baby crop (HiPP Biologique, France)

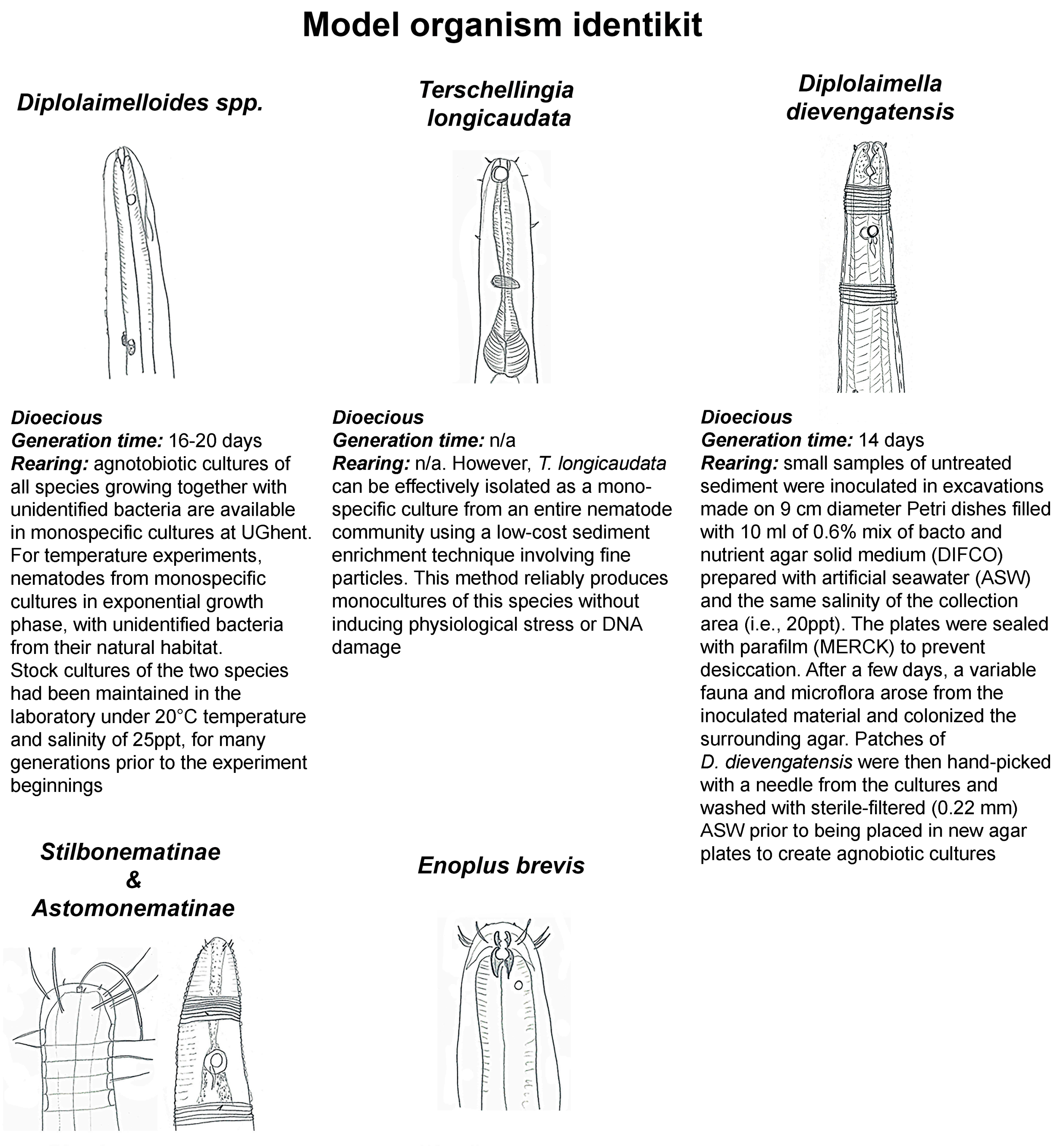
Oncholaimus dyvae



Dioecious
Generation time: n/a
Rearing: n/a

(**a**)

Figure 1. *Cont.*



Model organism identikit

Diplolaimelloides spp.

Dioecious
Generation time: 16-20 days
Rearing: agnotobiotic cultures of all species growing together with unidentified bacteria are available in monospecific cultures at UGhent. For temperature experiments, nematodes from monospecific cultures in exponential growth phase, with unidentified bacteria from their natural habitat. Stock cultures of the two species had been maintained in the laboratory under 20°C temperature and salinity of 25ppt, for many generations prior to the experiment beginnings

Terschellingia longicaudata

Dioecious
Generation time: n/a
Rearing: n/a. However, *T. longicaudata* can be effectively isolated as a monospecific culture from an entire nematode community using a low-cost sediment enrichment technique involving fine particles. This method reliably produces monocultures of this species without inducing physiological stress or DNA damage

Diplolaimella dievengatensis

Dioecious
Generation time: 14 days
Rearing: small samples of untreated sediment were inoculated in excavations made on 9 cm diameter Petri dishes filled with 10 ml of 0.6% mix of bacto and nutrient agar solid medium (DIFCO) prepared with artificial seawater (ASW) and the same salinity of the collection area (i.e., 20ppt). The plates were sealed with parafilm (MERCK) to prevent desiccation. After a few days, a variable fauna and microflora arose from the inoculated material and colonized the surrounding agar. Patches of *D. dievengatensis* were then hand-picked with a needle from the cultures and washed with sterile-filtered (0.22 mm) ASW prior to being placed in new agar plates to create agnobiotic cultures

Stilbonematinae & Astomonematinae

Dioecious
Generation time: n/a
Rearing: n/a

Enoplus brevis

Dioecious
Generation time: n/a
Rearing: n/a

(**b**)

Figure 1. Identikit of some free-living marine nematodes considered suitable model organism candidates. (**a**) *L. marina, H. disgiunta, M. pristiurus, O. campylocercoides, M. albidus, O. dyvae.* (**b**) *Diplolaimelloides* spp. *T. longicaudata, D. dieverngatensis,* Stilbonematinae and Astomonematinae, *E. brevis.*

Table 1. List and main characteristics of some free-living marine nematodes considered suitable model organism candidates.

Free-Living Marine Nematodes	Relevant Available Information	Source
Litoditis marina		
Distribution	Cosmopolitan	[19–31]
Typical habitat	Littoral zone of coast and estuaries, macrophytes washed ashore and holdfasts of living macroalgae	
Feeding	Bacterial biofilms that grow on the algal talli	
Cryptic species occurrence	Occurrence of 10 cryptic species with different functions (e.g., feeding habits)	
Brood size and mating system	Up to 600 eggs; internal fertilization	
Living mode	High dispersal rate via seawater circulation and aerial transport, short generation time, euryhaline and eurythermal, presence of the Dauer stage under harsh conditions	
Promising characteristics	Successfully cultivated in laboratory, well-defined embryonic cell lineage, short generation time, clear genetic background and sequenced genome, CRISPR/Cas9 genome editing. *L. marina* PmIII cryptic species is the most suitable model. Distinguished intraspecific microbiome among *L. marina* cryptic species	
Possible application mode	Molecular biology, cell biology, physiology and behaviour regulation, identification of the key genes and genetic pathways involved in the osmoregulation, sympatry speciation phenomena, role in the ecosystem functioning control (distinct influence on algae decomposition processes and microbial assemblages), ecotoxicology, sensitivity to heavy metals and climate change effects	
Halomonhystera disjuncta		
Distribution	Cool waters of temperate and subpolar zones	[21,32–36]
Typical habitat	Both shallow-water and deep-sea; macroalgal holdfasts and wrack deposits; organically enriched substrata	
Feeding	bacterivorous	
Cryptic species occurrence	Occurrence of five cryptic species	
Brood size and mating system	Greatest at 16 °C: up to 600 eggs; internal fertilization	
Living mode	tolerance to temperature changes and high concentrations of heavy metals; ovoviviparous females observed in unfavourable conditions	
Promising characteristics	It is successfully cultivated in laboratory. In particular, the cryptic species Gd1 is successful used in thermal stress experiments because it has a wide geographic distribution and can tolerate a wide temperature range	
Possible application mode	Previsions of climate change effects, interspecific interactions between cryptic species, response to different environmental conditions (i.e., S; T; sulphides)	
Metoncholaimus pristiurus		
Distribution	Cosmopolitan	[37–42]
Typical habitat	Widely distributed, common in stagnant marine waters with black muddy sediments and organic detritus	

Table 1. *Cont.*

Free-Living Marine Nematodes	Relevant Available Information	Source
Metoncholaimus pristiurus		
Feeding	Facultative predator	[37–42]
Cryptic species occurrence	NONE	
Brood size and mating system	Up to 40 eggs; internal fertilization	
Living mode	Opportunistic lifestyle	
Promising characteristics	Rearing in laboratory conditions, large sized nematode, good for developing ecotoxicological methods/tests not expensive and simple; high tolerance in changing sediment grain size	
Possible application mode	Biomarker approach applicable (discernible oxidative stress responses are valid for catalase and glutathione S-transferase), ecotoxicology applications	
Oncholaimus campylocercoides		
Distribution	Cosmopolitan	[43–45]
Typical habitat	Lagoons and marine waters; shallow water hydrothermal vents; brackish water	
Feeding	Facultative predators	
Cryptic species occurrence	NONE	
Brood size and mating system	ca. 12; internal fertilization	
Living mode	Tolerant to sulfidic conditions. Association with thiosymbion bacteria are not documented in the literature but cannot be excluded. They can survive at elevated temperatures (25 to 30 °C), in pH ranging from 6.5 to 7, salinities ranging from 39 to 46 ppt,	
Promising characteristics	Abundant in lagoonal and marine waters; big sized nematode; rapidly reproducing species; adaptation to sulfidic conditions in form of viscous inclusions in the epidermis	
Possible application mode	Suggested a model of sulphide metabolism; large application in ecotoxicology assay	
Metoncholaimus albidus		
Distribution	Cosmopolitan	[46,47]
Typical habitat	Among small stones and sand in tide pools; coarse sediment Shallow waters; hydrothermal vents also in deep sea	
Feeding	Facultative predator	
Cryptic species occurrence	NONE	
Brood size and mating system	Up to 3 eggs; internal fertilization	
Living mode	Tolerant to sulfidic conditions thanks to the symbiosis with thiosymbion bacteria	
Promising characteristics	Big sized worm, abundant and in high biomass within the sediments. It has never been reared, but specimens can be maintained alive in laboratory conditions. Distinct microbiome (Campylobacterota and Gammaproteobacteria)	
Possible application mode	Interaction between nematodes and bacteria, evolution of symbiosis, transmission mode of symbionts, microbiome role against pathogenic infections characterization; AMPs extraction	

Table 1. *Cont.*

Free-Living Marine Nematodes	Relevant Available Information	Source
Oncholaimus dyvae		
Distribution	Associated with the *Bathymodiolus byssus* (MAR)	[48,49]
Typical habitat	Lucky Strike vent field on the Mid-Atlantic Ridge (MAR) at 1700 m water depth	
Feeding	Detritivore/bacterivore, which partly relies on free-living chemoautotroph microbes	
Cryptic species occurrence	NONE	
Brood size and mating system	Gravid female with 2 fertilized eggs	
Living mode	Able to adapt and be very abundant in active vent areas due to their association with chemosynthetic microorganisms (Epsilonproteobacteria and Gammaproteobacteria)	
Promising characteristics	Large sized nematode, abundant and with high biomass in vent bottoms, interesting symbiotic association with Epsilonproteobacteria and Gammaproteobacteria	
Possible application mode	Interaction between nematodes and bacteria, evolution of host-symbiont dependence, transmission mode of symbionts, symbiont's role in the prevention of pathogens	
***Diplolaimelloides* spp.**		
Distribution	Cosmopolitan	[50–56]
Typical habitat	Commonly found on decaying cordgrass leaves, organically enriched substrata, mainly associated with macrophytes, cyanophytes	
Feeding	Bacterivorous—selective and non-selective	
Cryptic species occurrence	NONE	
Brood size and mating system	Up to 47 eggs; internal fertilization	
Living mode	*Diplolaimelloides* spp. generally dominate the nematode community on decaying phytodetritus in salt marshes	
Promising characteristics	*Diplolaimelloides* spp. are easily maintained in culture, easy measurements of the population growth, generation time, fecundity and respiration of this species in relation to different environmental parameters	
Possible application mode	Role in the ecosystem functioning control (species-specific influence on the decomposition process of macrophytes, bacterial communities, inhibition and stimulation of nutrient mineralization, bio-stabilization of sediments), effects of global climate change on benthic system, model for study of interspecific interactions and effects of food availability on population development	
Terschellingia longicaudata		
Distribution	Cosmopolitan	[57,58]
Typical habitat	Intertidal and shallow subtidal sediments; rich in organic matter	
Feeding	Chemoautotrophic bacteria	
Cryptic species occurrence	YES	

Table 1. *Cont.*

Free-Living Marine Nematodes	Relevant Available Information	Source
Terschellingia longicaudata		
Brood size and mating system	N/A; internal fertilization	[57,58]
Living mode	Endobenthic	
Promising characteristics	Abundant benthic nematode species	
Diplolaimella dievegantesis		
Distribution	Cosmopolitan	[59–61]
Typical habitat	Intertidal estuarine sand bank	
Feeding	bacterivorous	
Cryptic species occurrence	Possible occurrence	
Brood size and mating system	Uterine cells with mostly one thin-shelled (0.5 pm thick) egg at a time; internal fertilization	
Living mode	Opportunistic, it can take advantage in disturbed or pollutant environments	
Promising characteristics	It is successfully cultivated for assay experiments in laboratory, high hatching rate. Populations from distinct climate regions (tropical vs. temperate) exhibit similar life-cycle characteristics under standardized conditions	
Possible application mode	Phylogeny, ecotoxicology, role in the ecosystem functioning control (differential influence on the decomposition process of macrophytes), mechanism of food selection	
Stilbonematinae (mainly *Laxus oneistus*) and Astomonematinae		
Distribution	Low oxygen and hydrogen sulphide enrich sediments	[62–65]
Typical habitat	Both the members of Stilbonematinae and Astomonematinae live between oxidized and reduced sediment layers from intertidal to deep sea habitats	
Feeding	Both Stilbonematinae and Astomonematinae are associated with Gammaproteobacteria. The cuticle of the Stilbonematinae is almost entirely covered by bacteria that are both used to survive in sulphur conditions and grazed by host Astomonematines are mouthless and their esophagus is vestigial. They depend entirely on their bacterial symbionts for their nutrition, even if the exact mechanism of transfer is unknown	
Cryptic species occurrence	NONE	
Brood size and mating system	N/A; internal fertilization	
Living mode	Tolerant to sulphidic conditions. They carry sulphur-oxidizing bacteria (SOB) within their body as endosymbionts or on their surface as ectosymbionts	
Promising characteristics	Stilbonematids may be useful to understand symbiosis establishment, due to their accessibility, abundance and relative simplicity of this association. In Stilbonematinae, host and ectosymbiont coat can be easily separated from each other and both host-secreted and microbe-associated molecular patterns (MAMPs) identified through 'omics' can be expressed in vitro and directly tested	
Possible application mode	Interaction between nematodes and bacteria, evolution of host-symbiont dependence, transmission mode of symbionts, symbiont's role in the prevention of viral bacteria human infections	

Table 1. *Cont.*

Free-Living Marine Nematodes	Relevant Available Information	Source
Enoplus brevis		
Distribution	Baltic, Mediterranean, North Sea, and North Atlantic Ocean	[66,67]
Typical habitat	Sandy littoral; marine, brackish; sea intertidal zone	
Feeding	Predator	
Cryptic species occurrence	NONE	
Brood size and mating system	16–20 days at 20 °C; internal fertilization	
Living mode	*E. brevis* can live in sediments with low oxygen partial pressure	
Promising characteristics	*E. brevis*, along with *E. communis*, are the only free-living nematodes with hemoglobin	
Possible application mode	Study of enoplidan development in comparison with *C. elegans* could elucidate the role of cell lineage in nematode development and evolution	

Laboratory studies on *Diplolaimella dievengatensis* have investigated the effects of heavy metal and surfactant on its life cycle [68], its mechanisms of food selection [69], and its role in the decomposition of macrophytes [70] (Supplementary Materials, Table S2). Interestingly, redundancy among *Diplolaimella dievengatensis*, *Diplolaimelloides meyli*, and *Diplolaimelloides oschei* appears unlikely, as they exhibit species-specific effects on the decomposition rates of *Spartina anglica* detritus (common cordgrass) and the associated microbial community [70]. These Monhysteridae representatives are successfully cultivated in laboratory settings for experimental assay [61], allowing detailed studies of their distinct behaviours. For example, monhysterids exhibit "random walk" behaviour in the absence of attractive stimuli but migrate directionally toward food patches when accessible [69].

Available data suggest that *Diplolaimella dievengatensis* populations demonstrate similar life cycles across distinct climate regions (tropical vs. temperate) and their life-cycle characteristics remain consistent under standardized cultured conditions. This consistency makes *Diplolaimella dievengatensis* a promising cosmopolitan model organism due to its methodological advantages [60]. Moreover, recent molecular analyses suggest that *Diplolaimella dievengatensis* may represent a cryptic species complex [59,61].

Diplolaimelloides meyli and *Diplolaimelloides oschei* are opportunistic colonizers of decaying organic matter, used to evaluate the top-down effects of metazoans on the bacterial community structure. These species influence *Spartina anglica* decomposition by altering bacterial activity, either stimulatory or inhibitory, thereby impacting nutrient mineralization and marine ecosystem functioning [52,53]. Furthermore, these species play a significant role in stabilizing intertidal sediments, increasing sediment cohesion by stimulating microbial extracellular polymeric substance (EPS) production [55](Supplementary Materials, Table S2).

Given the increasing frequency and intensity of extreme temperatures and diurnal temperature fluctuations, *Diplolaimelloides meyli* and *Diplolaimelloides oschei* have been employed to assess the effects of global climate change on marine systems [56]. Studies revealed that fluctuating daily temperatures significantly influence individual species and interspecific interactions, altering dynamics from symmetrical to asymmetrical inhibitory effects, as seen with *D. meyli* over *D. oschei*. These findings underscore the crucial role of temperature fluctuations in shaping species assemblages and the entire ecosystem functioning [56] (Supplementary Materials, Table S2).

Diplolaimelloides bruciei was first reported from fungal-degraded *Spartina alterniflora* marsh grass. Laboratory studies measured its population growth, generation time, fecundity, and respiration under varying temperature and salinity conditions [50]. It is hypothesized that *Diplolaimelloides bruciei* persists as a reserve population—either as resting eggs or at low adult densities—poised to exploit temporary food sources when available [50]. Warwick [50] underlined its high and relatively stable production efficiency over the temperature ranges, emphasizing its high efficiency in food sources utilization.

Halomonhystera disjuncta (Figure 1) is a cryptic species complex comprising five distinct species [21], exhibiting widespread distribution and the ability to thrive in harsh environments. The unusual trait of retaining eggs, so that they hatch within the female body, may enhance its adaptability to toxic environments [34] (Table 1).

The cryptic species Gd1 of *Halomonhystera disjuncta* is often used to study thermal fluctuations due to its broad temperature tolerance [35]. Short-term daily exposure to stressful temperatures has been shown to enhance its fitness, likely due to thermal tolerance plasticity, whereas prolonged exposure to high temperatures negatively impacts fitness, egg mortality, and development and behaviour such as reduced motility and diminished taxis towards food [36]. Temperature also alters bacterial stimulus perception, potentially due to changes in the production or diffusion of attractive compounds by bacteria [69]. Moreover, competition exacerbates negative effects on *Halomonhystera disjuncta* fitness and food-finding behaviour across temperature regimes, with pronounced impacts at extreme temperatures. These findings suggest that thermal stress impacts species fitness and interactions, diminishing intrinsic tolerance to environmental perturbations and potentially disrupting species coexistence (Supplementary Materials, Table S2).

Among the **Rhabditidae** (which includes *C. elegans*), *Litoditis marina* (Figure 1) presents several cryptic species, forming the *L. marina* complex, that display distinct dispersal rates and varying responses to temperature and salinity gradients [71–74]. Sympatry among these cryptic species is common [22]. Indeed, in saltmarsh habitats, niche partitioning mechanisms and seasonal fluctuations enable their stable coexistence, preventing the exclusion of even the less abundant populations [75]. A key factor in maintaining their coexistence appears to be the distinct intraspecific microbiomes associated with each sibling species [26–28]. Moreover, each species within the *L. marina* complex plays a unique functional role in the ecosystem, influencing algal decomposition processes and microbial assemblages in different ways [75,76] (Table 1), similar to the effects observed in *Diplolaimelloides meyli* and *Diplolaimelloides oschei*.

As an intertidal species, *Litoditis marina* is physiologically adapted to wide variations in salinity, temperature, and desiccation stress. The ability to perceive and respond to salinity fluctuations is particularly notable, allowing survival in salinities up to 60 ppt. Recent studies have provided a baseline for identifying the key genes and genetic pathways involved in its osmoregulation, offering valuable insights into the mechanisms underlying euryhalinity in marine invertebrates [25,77]. Zhao et al. [30] assessed the tolerance of *Litoditis marina* to acidic pH stress, revealing that the species fails to develop into adulthood under such conditions. Moreover, a reduction in the expression of genes within the cytochrome P450 pathway makes *Litoditis marina* more vulnerable to acidic stress, potentially rendering it more susceptible to future global climate changes compared to *C. elegans*.

The successful application of CRISPR/Cas9 genome editing in *L. marina* marks a significant advancement, enabling functional analyses of additional genes (Supplementary Materials, Table S2). As *Caenorhabditis elegans*, *L. marina* undergoes four larval stages, including an alternative Dauer stage that is triggered under unfavourable conditions. This development strengthens its potential as a satellite marine model organism alongside the well-established biomedical model nematode, *C. elegans*.

Several species among the **Oncholaimidae** family (Figure 1) could be considered model organisms. One notable example is *Metoncholaimus albidus*, which, to the best of our knowledge, has not been reared under laboratory conditions. However, specimens can be kept alive for studies on symbiotic relationships [46,47]. This species harbours a distinct microbiome compared to the microbial communities found in the surrounding water and sediment [46,47]. On its cuticle, *M. albidus* hosts Campylobacterota (rod-shaped ectosymbiotic bacteria) and Gammaproteobacteria (filamentous bacteria), which are also found in other invertebrates from hydrothermal vents. Gene sequence analysis of *aprA* suggests that *M. albidus* symbionts are capable of both reduction and oxidation pathways, providing a potential adaptive advantage that allows the nematode to migrate between sulfidic and oxygenated sediment layers, utilizing both metabolic strategies [46] (Table 1). The high similarity between bacteria associated with nematodes from shallow vents and those from deep-sea vents indicates that nematode-bacterial associations may be shaped more by environmental factors than by co-evolutionary processes [78]. Many nematode species, such as *Caenorhabditis elegans* and *Ascaris suum*, produce antimicrobial peptides (AMPs) as a natural defence against attacks [79]. Bruno et al. [47] isolated antibacterial substances from *M. albidus* and two undescribed *Oncholaimus* species (Supplementary Materials, Table S2). Members of Oncholaimidae exhibit significant biomass advantageous for bioassay-guided purification protocols aimed at exploring antibacterial activities [47]. The microbiome within the digestive system of *Oncholaimus* species also differs markedly from the surrounding habitat, suggesting potential symbiotic relationships, as observed in *Oncholaimus dyvae* [48]. Preliminary findings showed promising antibacterial activity only in *Oncholaimus* species, with bioactivity (possibly AMPs) observed against *Escherichia coli*, *Aeromonas hydrophila* (Gram-negative), and *Micrococcus luteus* (Gram-positive), warranting further investigation [47].

Metoncholaimus pristiurus was described by Cobb [80] as a cost-effective model for live studies. Today, *Metoncholaimus pristiurus* seems to be a very promising model organism to investigate the impact and bioaccumulation effects of many pollutants such as heavy-metals, permethrin, anthracene, polybrominated diphenyl ether, and PVC microplastic polymers [38–40,42]. Also, many pharmaceutical compounds detectable in aquatic habitats have been investigated on *Metoncholaimus pristiurus* revealing a different sensitivity spectrum [38,40,41] (Supplementary Materials, Table S2).

Oncholaimus campylocercoides has been used to study the effects of oxygen depletion. Under sulfidic conditions, it develops oily, viscous inclusions in its epidermis, composed of elemental sulphur [44]. The longer the exposure to sulfidic conditions, the more sulphur accumulates, but these deposits disappear upon reintroduction to normoxic conditions. Such accumulations are common in sulphur-oxidizing bacteria symbiotic with invertebrates, suggesting a similar association may exist for *O. campylocercoides*. This species has been widely used in ecotoxicological studies [38,39,41,45,81] and was proposed as model for assessing the toxicity of benzo(a)pyrene (BaP), revealing early gender-specific responses that might lead to a revaluation of the BaP thresholds in the environmental regulations [81]. The results obtained so far indicate that *Oncholaimus campylocercoides* could be regarded as bioindicator of beta-blockers (Supplementary Materials, Table S2). Conversely, *O. campylocercoides* is not reliable to detect the effects of hydroxychloroquine drug or microplastic contamination since this species appears to be tolerant to both pollutants [41].

Oncholaimus dyvae is a recently described species found at a depth of 1700 m, associated with the *Bathymodiolus byssus* [49]. This nematode thrives in high temperatures environments and inhabits sediments near hydrothermal vent emissions. Stable nitrogen isotope ratios, along with a lack of potential prey in its habitat, suggest that *O. dyvae* is a detritivore/bacterivore relying partially on free-living chemoautotrophic microbes [49]

(Table 1). Epsilonproteobacteria and Gammaproteobacteria (sulphur-oxidizing bacteria) were found in its cuticle, digestive cavity, and intestine, and they are recognized as potential symbionts. These bacteria likely provide nutritional benefits, assist with detoxification, or protect against pathogens, as observed in other nematodes [48].

All the species in the **Stilbonematinae** (Figure 1) sub-family (Desmodoridae) are completely covered by sulphur-oxidizing bacteria. In the *Stilbonema* and *Leptonemella* genera (Table 1), the bacterial coat is multi-layered, with bacteria embedded in a mucous matrix; in contrast, *Laxus*, *Catanema*, and *Robbea* are covered by mono-layered bacterial coats [65]. These symbionts are typically rod-shaped bacteria and attached with one pole to the cuticle of the worm, except for the tail tip and the anterior body region. However, filamentous bacterial coats are observed in genera such as *Eubostrichus* and *Adelphus* [82,83]. A distinctive feature exclusive to the Stilbonematinae is the presence of epidermal complexes consisting of at least two gland cells and sensory neurons, known as glandular sense organs (GSOs) [84]. These GSOs play a key role in ectosymbiosis by expressing a mannose-binding lectin (Mermaid, C-type), which mediates both symbiont–symbiont aggregation and symbiont–host attachment [63]. Molecular analysis has revealed that the symbionts of Stilbonematinae belong to the Gammaproteobacteria, a group also shared with mouthless oligochaetes and the nematode *Astomonema* [65]. This supports the hypothesis that these taxa acquire symbionts from their shared habitat.

Laxus oneistus is the most studied species in this subfamily. Like other members of the subfamily, it lives a few centimetres below the surface of sandy bottoms and thrives in environments where oxygen availability and exposure to hydrogen sulphide often limit many other metazoans [82,83,85]. The association between *Laxus oneistus* and its symbionts is highly species-specific; this nematode hosts only the *Candidatus* genus Thiosymbion [65]. The mode of ectosymbiont transmission from adults to offspring in the Stilbonematinae is not fully understood. It is unclear whether the bacteria are acquired through horizontal transmission from the environment or are passed vertically from mother to offspring, but a mixed mode of transmission is most likely [65]. While *Laxus oneistus* has never been reared in the laboratory, interesting information has been obtained from studying early juvenile development in specimens isolated from back-reef lagoon substrates [86]. The data demonstrated that symbionts are acquired early in development, as bacteria were present even in the earliest juvenile stages (J1/2), with the bacterial phylotype matching the monolayer coat observed in adults. In juveniles, symbiont traces were detectable from the pharynx to the anus, suggesting a trophic interaction between the host and its ectosymbionts. Stable carbon isotope incorporation experiments indicated that the ectosymbionts are a major component of the Stilbonematinae diet [87]. The occurrence of filamentous microorganisms associated with the GSOs of the juveniles created a complex named Glandular Sense Organ Associated Microbe (GAM). These GAMs appeared to penetrate the setae, suggesting a nutritional interaction with *Laxus* juveniles. The mucus secreted by the GSOs is rich in proteins attracting high bacterial abundances. *Laxus oneistus* feeds on the microorganisms colonizing the mucus in a mutualistic relationship (e.g., mucus-trap hypothesis) [86]. Further investigations into bacterial cell division revealed that host factors can influence bacterial cell division, modifying canonical cell division mechanisms seen in model bacteria like *Escherichia coli* to integrate host cues [88]. Thus, the molecular and cellular processes involved in animal–microbe symbioses are likely conserved but may be modified as the host and symbionts coevolve.

Despite current limitations in rearing Stilbonematinae species, a significant advantage is that they can be easily separated from their ectosymbionts. Both host-secreted and microbe-associated molecular patterns can be identified using microarray, transcriptomic, and proteomic studies and expressed in vitro for direct testing [63]. The accessibility, abundance, and relative simplicity of this association in *Laxus oneistus* make it a potentially suitable model to study mutualistic associations (Supplementary Materials, Table S2). The C-type lectin expressed in this nematode shares structural and functional similarities with a human HIV-1 receptor and could potentially block viral infection in human immune cells [89]. *Laxus oneistus* encodes 117 C-type lectin domain-containing proteins as well as various antimicrobial peptides (AMPs), including saposin-like, thaumatin-like, and macin-like proteins [65].

Astomonematinae, Enoplidae, and Linhomoeidae remain relatively understudied as model organisms, yet some members of these taxa exhibit intriguing features.

Astomonematinae (Siphonolaimidae) (Figure 1) are extremely long and slender nematodes. Unlike stilbonematines, however, they harbour symbiotic bacteria that fill the cells of the reduced intestine [82,83]. The reliance of Astomonematinae on their prokaryotic symbionts (Gammaproteobacteria) is particularly evident as these nematodes lack a functional mouth opening, a normal intestine, and possess a vestigial pharynx [90]. Current evidence strongly suggests that this is an obligatory mutualistic relationship [88]. Nevertheless, the mechanism of nutrient transfer remains unresolved as no evidence of phagocytic digestion has been observed [65]. Astomonematinae are typically found in environments with reduced conditions, such as intertidal subsurface sulphide-enriched sediment layers or sublittoral methane seepages. More recently, they have also been reported in deep-sea habitats [64,65,82,83] (Table 1).

Clarification of their phylogenetic relationships and the detection of the aprA gene—characteristic of sulphur-oxidizing bacteria—indicate that the symbionts of *Astomonema* species utilize reduced sulphur compounds as an energy source for their hosts [91]. Furthermore, the frequent loss of the hind body and subsequent wound healing observed in *Astomonema southwardorum* represents a phenomenon with potential significance for regenerative medicine. This warrants further investigation at histological, ultrastructural, and molecular levels [64].

Enoplus brevis (**Enoplidae**) (Figure 1) is one of the least known marine nematodes as a model organism. However, it is notable for its known cell lineage [67] and the presence of hemoglobin—a rare trait among nematodes [66]. Atkinson noticed that the high concentration of this protein in the pharynx allows *E. brevis* to feed in muddy sediments with low oxygen partial pressure. This represents an example of respiratory homeostasis, enabling the species to survive in potentially anoxic substrates (Table 1). Furthermore, physiological experiments on heavy metal uptake have demonstrated that *E. brevis* can serve as an early indicator of contamination by copper, lead, and mercury, as these metals exhibit lethal toxicity to its populations [92,93] (Supplementary Materials, Table S2).

Among **Linhomoeidae**, *Terschellingia longicaudata* (Figure 1 and Table 1) is recognized as a complex of multiple cryptic species [57]. Laboratory experiments on this species have primarily focused on its role in ecotoxicology [58] (Supplementary Materials, Table S2). Indeed, *T. longicaudata* can be effectively isolated as a mono-specific culture from an entire nematode community using a low-cost sediment enrichment technique involving fine particles. This method reliably produces monocultures of *T. longicaudata* without inducing physiological stress or DNA damage, which are critical prerequisites for applying biomarkers in sediment contamination studies [94].

3. Discussion

3.1. Which Marine Nematodes Are the Best Candidates as Model Organisms?

To date, when strictly considering the requirements for a model organism (see Table S1), only Rhabditidae (e.g., *Litoditis marina*) and Monhysteridae (e.g., *Diplolaimella dievengatensis*, *Diplolaimelloides bruciei*, *Diplolaimelloides meyli*, *Diplolaimelloides oschei*, *Halomonhystera* *disjuncta*) can be regarded as viable alternatives to *Caenorhabditis elegans*. Other families, such as Oncholaimidae, Desmodoridae, and Linhomoeidae, possess intriguing attributes and distinctive biological traits. However, their potential as model organisms is currently constrained by challenges in rearing them under controlled conditions, limited ease of manipulation, and insufficient genomic data. Addressing these practical obstacles would be a valuable endeavour.

For example, research on *Metoncholaimus pristiurus* and *Oncholaimium campylocercoides* (species of Oncholaimidae) shows promising potential. Conversely, the reproductive biology of species such as *Metoncholaimus albidus*, Astomonematinae, and Stilbonematinae is poorly understood, and these organisms are rarely maintained in laboratory settings across multiple generations—a significant drawback for their establishment as model organisms [65]. This limitation is likely tied to their obligate symbiotic relationships with Campylobacterota and Gammaproteobacteria, which necessitate specific environmental conditions that are challenging to replicate in the laboratory. Nonetheless, recent advances in culturing other meiofaunal organisms with chemosynthetic symbionts, such as the flatworm *Paracatenula* and gutless oligochaetes, provide promising opportunities for these marine nematodes as well. These symbioses, ranging from ectosymbionts to intracellular partnerships, offer rare opportunities to investigate mutualistic evolution and resilience in extreme environments. However, challenges remain, particularly in culturing Stilbonematinae, Astomonematinae, and Oncholaimidae species, as well as in obtaining comprehensive genomic data. Addressing these limitations will be essential to fully unlock their potential as model organisms.

Among the marine nematodes cited above, *Litoditis marina* stands out as a particularly promising model organism. It shares morphological similarities with the terrestrial counterpart *C. elegans* and fulfils the highest number of prerequisites for model organisms. These include a well-defined embryonic cell lineage and a sequenced genome, which facilitate its use in studies on molecular biology, cell biology, physiology, and behavioural regulation. For these reasons, *Litoditis marina* emerges as the most promising marine nematode model.

3.2. Which Nematode Candidate Can Be a Model Organism for Which Question?

3.2.1. Functional Redundancy and Ecosystem Dynamics

Litoditis marina, *Diplolaimella dievengatensis*, *Diplolaimelloides meyli*, and *Diplolaimelloides oschei* are suitable model organisms for understanding how biodiversity loss affects ecosystem functioning and for the study of ecological roles in sibling species with possible overlapping among them. Previous studies have demonstrated species-specific effects of Monhysteridae and Rhabditidae nematodes on decomposition rates, microbial community structures, and sediment stabilization, challenging the concept of functional redundancy [52,53,55,70,75,76] (see Supplementary Materials, Table S2). This makes these nematodes ideal for testing hypotheses about biodiversity and ecosystem stability, further highlighting the difficulty of predicting the effects of biodiversity loss in aquatic systems [95,96].

3.2.2. Climate Change and Adaptations to Its Escalating Environmental Effects

Litoditis marina, *Halomonhystera disjuncta* (Gd1), *Diplolaimelloides meyli* and *Diplolaimelloides oschei* are suitable model organisms for several key questions related to climate change. For example, how do daily temperature fluctuations affect species interactions and ecosystem processes? Which mechanisms underline thermal tolerance plasticity? How do marine nematodes adapt to extreme environmental changes like salinity and desiccation? What genes are involved in osmoregulation and stress responses? The species mentioned above have been used to study the effects of environmental parameter fluctuations (e.g., temperature, pH, and salinity) on fitness, competition, and food-finding behaviour, offering valuable insights into the impact of global climate change on marine ecosystems. Monhysteridae nematodes are increasingly used to assess the effects of climate change on marine benthos, revealing that temperature changes affect population fitness, foraging behaviour, and competition with significant consequences for species coexistence and ecosystem functioning [36,56,69,97]. With a sequenced genome and successful CRISPR/Cas9 applications, *Litoditis marina* is a promising model for understanding the genetic mechanisms that enable marine invertebrates to resist environmental stressors [25,30,77] (see Supplementary Materials, Table S2).

3.2.3. Host–Microbe Interactions and Symbiosis

Stilbonematinae (e.g., *Laxus oneistus*), Astomonematinae, *Metoncholaimus albidus*, and *Litoditis marina* are suitable model organisms for the study of evolution and adaptation of host–microbe associations in environmental extreme conditions, the coevolutionary mechanisms involved, and the molecular mechanisms underlying mutualism and symbiosis. Moreover, microbiomes may contribute to the resilience of nematode species to environmental perturbations. *Laxus oneistus* and Astomonematinae rely on sulphur-oxidizing bacterial symbionts to thrive in low-oxygen environments. Their unique adaptations provide insight into the evolution of mutualistic relationships. There is variability in the dependence on symbiosis in marine nematodes, ranging from facultative to obligate mutualists. Some nematodes form exclusive partnerships with a single symbiont, while others host diverse symbiotic communities, like the human gut microbiome. Symbiont location also varies from endosymbionts within (intracellular) nematode cells (e.g., Astomonematinae) to ectosymbionts on the nematode surface (e.g., Stilbonematinae or some Oncholamidae). Although Stilbonematinae and Astomonematinae are not closely related, their sulphur-oxidizing bacterial symbionts enable them to occupy similar ecological niches, representing a case of convergent evolution. These nematodes provide a model for understanding how bacteria adapt to form symbioses with animal hosts (see Supplementary Materials, Table S2). Future research could focus on how nematodes and their symbionts communicate, adapt, and manage their nutritional status, as well as on inter-symbiont competition and cooperation, the role of symbiont communities in nutrition and immunity, and other related processes. As noted by Heppert et al. [88], studying animal-bacterial symbioses through these tiny yet powerful organisms will undoubtedly lead to valuable discoveries, which could even help clarify the functioning of the human microbiome. *Litoditis marina* and *Metoncholaimus albidus*, with their intraspecific microbiome associations and distinctive roles in ecosystems, particularly their adaptations to extreme and polluted environments, are also promising models for studying the resilience of these animals [46,47,98].

3.2.4. Ecotoxicology and Pollution Monitoring

Litoditis marina, *Metoncholaimus pristiurus*, *Oncholaimus campylocercoides*, and *Terschellingia longicaudata* are suitable model organisms and possible sentinels for environmental contamination, useful for the study of the effects of pollutants such as heavy metals, microplastics, and hydrocarbons. These species have proven useful in assessing the impacts of various pollutants, including heavy metals, polycyclic aromatic hydrocarbons, and microplastics (see Supplementary Materials, Table S2 for further details). The Oncholaimidae and Linhomoeidae species have been successfully cultured for biomarker development, enhancing their role as pollution sentinels [37,58]. Their biomarker responses and sensitivity to contamination make them effective models for ecotoxicological studies.

3.2.5. Biotechnological and Biomedical Applications

Laxus oneistus (Stilbonematinae) and *Oncholaimus dyvae* are suitable model organisms for biomedical and biotechnological studies. *Laxus oneistus* produces lectins like human immunoreceptors, which may block pathogen transmission [89]. This nematode encodes 117 C-type lectin domain-containing proteins, as well as various antimicrobial peptides (AMPs), including saposin-like, thaumatin-like, and macin-like proteins [65]. Additionally, Oncholaimus species produce AMPs, and studying these two families holds enormous potential for discovering new AMPs, with possible applications in combating antibiotic resistance [46,47].

4. Conclusions

While the terrestrial nematode *Caenorhabditis elegans* remains one of the "big six" standard model organisms in genetics and developmental biology, certain marine nematodes are emerging as promising candidates to complement and expand biological research.

Among the taxa reviewed, *Litoditis marina* and select Monhysteridae species, such as *Diplolaimella dievengatensis*, *Halomonhystera disjuncta*, and *Diplolaimelloides* spp., demonstrate significant potential as model organisms. Their controllable life cycles, adaptability to laboratory conditions, and available genomic resources make them highly suitable for research. Recent advances in molecular tools, such as CRISPR/Cas9 genome editing and transcriptomics, have already begun to bridge some gaps that in the past occurred.

Studies on these nematodes provide valuable insights into biological phenomena such as developmental plasticity, epigenetic gene regulation, niche construction, adaptive responses to environmental changes, and defence strategies. Moreover, the high tolerance and survival rate under stressful conditions of Monhysteridae and Rhabditidae can be useful to understand the physiological mechanisms underpinning the resistance and resilience of the phylum Nematoda.

Ultimately, marine nematodes not only align with the principles of the 3Rs (Replacement, Reduction, and Refinement), but also offer practical and ethical solutions to pressing biological and biomedical challenges, underscoring their immense promise for future research.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/d17010059/s1, Table S1: Prerequisites required for a model organism and advantages associated with the use of nematodes as bioindicators; Table S2: Different uses 'tool for which job' of free-living marine nematodes as valuable model organisms [99–101].

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