CHAPTER 2
BIOLOGICAL CHARACTERISTICS, ECOLOGICAL ROLES, AND CULTURE POTENTIAL OF NEREIDIDAE (POLYCHAETA) FROM INDONESIAN COASTAL WATERS

Edy YUWONO[1]
Junardi[2]
Eko Setio WIBOWO[3]

[1]Graduate Program of Biology, Faculty of Biology and Agriculture, National University, Jl. Harsono RM Block Kenanga No.11 Ragunan, South Jakarta 12520, Indonesia, edyyuwono@gmail.com, ORCID ID: 0009-0002-6421-4449
[2]Biology Department, Faculty of Mathematics and Science, Tanjungpura University, Pontianak, West Kalimantan 78124, Indonesia, ORCID ID: 0000-0001-6054-2758
[3]Faculty of Biology, Jenderal Soedirman University, Jl. Dr. Soeparno No.63, Purwokerto 53122, Indonesia, ORCID ID: 0000-0002-1938-6260.

INTRODUCTION

The diversity of marine worms, particularly Polychaeta, in Indonesian waters is substantial. Within this tropical archipelago, members of the family *Nereididae* comprise 22 genera and 85 species (Pamungkas & Glasby, 2015). Species belonging to Nereididae are characterized by an eversible pharynx bearing paragnaths, a pair of cirriform antennae, four pairs of elongated tentacular cirri, and four distinct eyes located on the head. Each body segment bears parapodia, which support locomotion and respiration (Wilson et al, 2023). These errant polychaetes typically inhabit mucous-lined burrows and are widely distributed across Indonesian coastal and marine ecosystems, particularly in muddy and sandy substrates (Siregar & Yuwono, 2005; Asnawi et al., 2018; Wibowo et al., 2022). They are frequently reported as dominant taxa in benthic assemblages collected from estuaries and marine environments throughout Java, Sumatera, Sulawesi, and several other regions of the country (Sawestri, 2013; Glasby et al., 2007; Pamungkas, 2020; Ramses et al., 2020).

Members of the Nereididae are also regarded as economically important organisms due to their potential use as bait for recreational fisheries and as a valuable nutritional resource for aquaculture species. Their tissues contain essential proteins, lipids, amino acids, and vitamins, and they have been proposed as an alternative to fishmeal and fish oil in aquaculture feeds (Yuwono et al., 2001; Hadiyanto, 2013; Herawati et al., 2020).

In shrimp aquaculture, nereidid worms are commonly administered to broodstock diets, either singly or in combination with other natural feeds (Yuwono, 2005; Wibowo et al., 2020). They are widely recognized for their effectiveness in stimulating ovarian maturation and spawning (Subaidah et al., 2017), and diets containing Nereididae have been shown to enhance reproductive performance in *Litopenaeus vannamei* broodstock (Yang et al., 2022). This response is associated with the relatively high lipid content of nereidid tissues, which supports final gamete maturation in shrimp that exhibit limited capacity for *de novo* cholesterol synthesis (Nguyen et al., 2012; Palmer et al., 2014; Wang et al., 2019; Wibowo et al., 2020).

Several nereidid species, including *Perinereis* sp. (Meunpol et al., 2005), *Nereis diversicolor* (Wang et al., 2020), and *Namalycastis rhodochorde* (Junardi et al., 2022), have also been reported to contain progesterone, which is thought to contribute to broodstock sexual maturation (Nguyen et al., 2012). In addition, broodstock fed live Nereididae have been shown to produce juveniles with improved survival rates (Muli et al., 2016).

Nereididae, particularly the giant nypa worm, are predominantly harvested from natural habitats through manual digging, as documented among marine worm collectors in Situbondo, Banyuwangi, and Tuban (Rasidi, 2013). Similar harvesting activities occur in the Kapuas River estuary, Kalimantan, where the worms are collected for use as bait in both local and international markets (Junardi, 2021). However, intensive harvesting poses potential ecological risks. Excessive excavation may threaten population sustainability and disrupt ecosystem functioning, as nereidid burrowing activity plays a critical role in sediment reworking, bioturbation, and nutrient cycling in coastal environments (Rodrigues-Filho et al., 2023). For this reason, detailed studies of the ecology and broader biological attributes of Nereididae are urgently required.

A considerable number of research outputs concerning the biology of Indonesian Nereididae have been disseminated in national and international scientific publications. A synthesis of these studies is needed to evaluate the current state of knowledge and to identify research gaps that remain to be addressed. In particular, recent molecular phylogenetic work has revealed fundamental implications for nereidid classification. Pamungkas et al. (2025) demonstrated that traditional subfamily groupings within Nereididae, such as *Dendronereidinae*, are not uniformly supported by genetic data, prompting the establishment of a new subfamily, *Tylorrhynchinae* subfam. nov., and the description of previously unrecognized species from Indonesian waters. These findings underscore how molecular systematics can refine our understanding of nereidid diversity and evolutionary relationships, with direct relevance to biodiversity assessment and conservation planning. This chapter, therefore, provides an overview of the progress of research on the biological characteristics of Nereididae inhabiting Indonesian waters, integrating both classical morphological studies and contemporary molecular insights.

1. HISTORICAL AND CONTEMPORARY TAXONOMIC STUDIES OF INDONESIAN NEREIDIDAE

Taxonomy plays a crucial role in documenting biodiversity and supports both conservation initiatives and the sustainable use of biological resources (Sekar et al., 2021). Taxonomic investigations traditionally rely on morphological characters to distinguish among taxa (Jost, 2017). In Polychaeta, species are typically characterized by the presence of parapodia - paired appendages with dorsal and ventral lobes bearing bundles of chaetae - which function primarily in locomotion and respiration (Read & Fauchald, 2023). More than 80 families are currently recognized within the class, each defined by distinctive body forms and chaetal structures. Members of the family Nereididae are characterized by a prostomium fused with the peristomium around the mouth region, a pair of lateral antennae positioned between two palps, two pairs of tentacular cirri, and two pairs of well-developed eyes (Wilson et al., 2023). The eversible pharynx consists of a proximal oral ring and a distal maxillary ring bearing two jaws and, in some taxa, paragnath groups. The peristomium lacks parapodia but carries four pairs of tentacular cirri; parapodia are uniramous in the first two setigers and biramous thereafter, each equipped with a dorsal and a ventral cirrus. Setae are generally compound in both notopodia and neuropodia, although simple falcigers occur in some genera, and branched gills may arise on the mid-anterior segments in certain species. The pygidium terminates in a pair of cirri, and body length ranges from a few centimeters to over one meter in the largest species (Glasby et al., 2007).

Historical and contemporary research indicates that studies of Indonesian marine polychaetes have been conducted for more than two and a half centuries. The earliest documented description was Amphinome rostrata (Amphinomidae), described by Pallas in 1766 from material collected in Ambon (Pamungkas & Glasby, 2019). More recent assessments by the same authors recorded 713 species representing 55 families within Indonesian waters. Subsequent work by Villalobos-Guerrero and Idris (2021) included the redescription of several nereidid species listed in the World Polychaeta Database (Read & Fauchald, 2018), including *Neanthes gisserana* from eastern Seram Island, *Neanthes vandersandei* from East Flores, and *Neanthes thysanota* from Pulo Damar Besar, Jakarta Bay.

Comparative examinations of historical museum collections alongside recently acquired specimens have further demonstrated the exceptionally high diversity of Polychaeta in Indonesia's marine and coastal ecosystems. Nevertheless, the true richness of these taxa is likely underestimated due to gaps in systematic sampling and dedicated taxonomic research. Although Indonesia is believed to harbor polychaete diversity exceeding that of many neighboring regions, only a fraction has been formally documented - approximately 11,500 examined specimens representing 85 families (Pamungkas et al., 2019). Mass-spawning nereidid worms observed in Ambon were shown to consist of four species - *Ceratonereis singularis australis, Composetia marmorata, Nereis gisserana,* and *Perinereis nigropunctata* - identified for the first time from preserved epitoke specimens collected from the Banda Sea (Pamungkas & Glasby, 2015). These findings highlight the importance of continued taxonomic investigation of nereidid populations across diverse Indonesian habitats.

Recent molecular phylogenetic work has further advanced nereidid systematics. Using mitochondrial and nuclear genetic markers, Pamungkas et al. (2025) reassessed relationships within the subfamily Dendronereidinae and showed that several traditional subfamily boundaries are not consistently supported by molecular phylogenetic evidence. Their analyses indicated that only the type genus, *Dendronereis*, forms a coherent clade, whereas other genera previously assigned to Dendronereidinae are more appropriately classified elsewhere. To accommodate these distinct evolutionary lineages, the authors erected a new subfamily, Tylorrhynchinae subfam. nov., to include clades comprising *Dendronereides* and *Tylorrhynchus*. The study also described two new Indonesian species, underscoring the continuing discovery of nereidid diversity even within relatively well-studied regions.

Additional taxonomic contributions have emerged in recent years. Pamungkas (2020) noted that comprehensive studies on Nereididae in Indonesia have only recently gained significant momentum. A new species, Namalycastis rhodochorde, was described from mangrove habitats in the Kakap Estuary near Pontianak, West Kalimantan (Glasby et al., 2007), while Perinereis aff. arabica was reported from Gunungkidul, Yogyakarta (Hadiyanto, 2013).

Pamungkas and Glasby (2015) also conducted a taxonomic revision of Nereididae from Ambon, based on specimens collected in 1866 alongside samples obtained in 2009 and 2014. Their work documented the presence of multiple species, including *Ceratonereis sp. cf. C. perkinsi, Ceratonereis singularis australis, Composetia marmorata, Neanthes pachychaeta, Neanthes unifasciata, Neanthes sp. cf. N. gisserana, Neanthes sp. cf. N. masalacensis, Nereis sp., Perinereis helleri, Perinereis nigropunctata*, *Solomononereis marauensis*, and *Websterinereis foli*. These findings challenge earlier assumptions that the mass-spawning "wawo" or "laor" in Ambon represented a single species and further emphasize the significance of taxonomic research in elucidating nereidid diversity in Indonesia. Despite these advances, specialized taxonomic studies on Polychaeta remain limited, as many investigations have been embedded within broader ecological research frameworks — including studies in Jakarta Bay (Abdurrahman et al., 1990), the Mahakam Delta, East Kalimantan (Finishia et al., 2014), mangrove forests of North Sumatra (Rabiah et al., 2017), the Prawean Coast of Jepara, Central Java (Apriyanti & Tumiran, 2018), Tahura Ngurah Rai, Bali (Priyandayani et al., 2018), and Gresik, East Java (Madyowati & Kusyairi, 2020). Dedicated, integrative taxonomic research on Polychaeta — particularly Nereididae — is therefore essential as a scientific foundation for biodiversity assessment, sustainable utilization, and conservation planning. At the same time, expansion of comprehensive ecological investigations is urgently needed to deepen understanding of nereidid biodiversity, functional roles, and potential applications

2. ECOLOGY

2.1 Distribution, Community Structure, and Functional Roles

Ecological studies on the family Nereididae (Polychaeta, Annelida) in Indonesia have been conducted across a variety of coastal settings, gradually building a broader understanding of their habitat preferences and ecological significance. Early work along the northern coast of Java (Siregar & Yuwono, 2005) and in the mangrove forests of West Kalimantan (Junardi & Wardoyo, 2008) first highlighted the prominence of nereidid worms in intertidal benthic communities.

Subsequent research expanded this geographical scope to the southern coast of Central Java (Wibowo et al., 2017) and Manado Bay in Sulawesi (Lumingas et al., 2022), thereby encompassing regions with contrasting hydrodynamic conditions, sediment characteristics, and levels of human influence.

Collectively, these investigations demonstrate that nereidid polychaetes inhabit a broad range of coastal environments, including mudflats, sandy shores, estuarine channels, and mangrove sediments. In many of these habitats they occur at relatively high densities and often represent a dominant component of the benthic macrofauna, contributing to processes such as sediment turnover and organic matter transformation. Their distribution and abundance are strongly shaped by environmental gradients—particularly sediment composition, salinity, organic enrichment, and tidal exposure—indicating a close ecological association with local habitat conditions.

This pronounced sensitivity to environmental variation has important implications for coastal research and management. Patterns emerging from existing studies suggest that members of the Nereididae possess considerable potential as biological indicators for assessing habitat quality and detecting anthropogenic disturbance within Indonesian coastal ecosystems.

More broadly, ecological research on Indonesian nereidids has focused primarily on species diversity, community composition, and abundance in relation to environmental and habitat characteristics (Yusron, 1985; Finishia et al., 2014; Rabiah et al., 2017; Priyandayani et al., 2018; Madyowati & Kusyairi, 2020). These studies have sought to characterise spatial and temporal variability in nereidid assemblages, revealing fluctuations in population density and community structure in response to seasonal cycles, hydrological dynamics, and substrate stability. This body of work has provided valuable insight into the factors shaping the distribution and persistence of nereidid populations across Indonesian coastal habitats.

Beyond patterns of diversity and community structure, several studies have also highlighted the functional roles of nereidids in benthic ecosystems. Through activities such as sediment bioturbation, nutrient recycling, and participation in trophic interactions, these worms influence the organisation and productivity of benthic food webs.

However, these functional and mechanistic dimensions have received comparatively less attention than taxonomic and community-level surveys, leaving important questions regarding the behavioural, physiological, and ecosystem-level drivers of their ecological roles largely unresolved.

Taken together, the available literature emphasises both the ecological importance of nereidid polychaetes and the need for more integrative approaches. Future research would benefit from combining detailed taxonomic surveys—using both morphological and molecular techniques—with studies of life-history traits, reproductive strategies, and behavioural ecology to better understand population dynamics and responses to environmental variability. Equally important are investigations that explicitly link nereidid activity to ecosystem-level processes such as bioturbation, nutrient fluxes, and trophic pathways, supported by long-term monitoring across seasons and habitat types. Such multidisciplinary efforts are essential for fully elucidating the ecological significance of nereidids and for informing management and conservation strategies aimed at sustaining the resilience of Indonesian coastal ecosystems.

2.2 Substrate Productivity and Its Role in Supporting Nereidid Diversity

The diversity of Polychaeta in Indonesian coastal and mangrove ecosystems is closely linked to environmental characteristics, particularly sediment composition and the availability of organic matter. Sediment conditions influence not only the physical stability of the benthic habitat but also the quantity and quality of trophic resources that sustain detritivorous and deposit-feeding taxa, such as nereidid worms. Evidence from the Peniti mangrove forest in West Kalimantan exemplifies this relationship, where high polychaete diversity has been recorded in clay-mud substrates enriched with organic carbon (Junardi & Wardoyo, 2008). Within this habitat, species richness was higher in stands dominated by *Sonneratia alba* compared with those dominated by *Rhizophora mucronata*, a pattern attributed to the greater organic-carbon content of *Sonneratia* sediments, which supports enhanced microbial activity and detrital food production for benthic invertebrates.

Comparable ecological trends have been documented in other regions; for example, Sweetman et al. (2010) reported that elevated substrate organic-carbon levels increase resource availability and promote the development of structurally complex benthic communities. Differences in litter quality further reinforce habitat suitability patterns. Leaves of *Sonneratia alba* possess higher nutritional value and a lower C/N ratio compared with *Rizhophora mucronata,* resulting in faster decomposition and more efficient transfer of organic matter into the benthic food web (Pendleton et al., 2012). In combination with favorable physicochemical conditions and the stabilizing influence of mangrove root structures, these factors create productive and ecologically supportive environments for the settlement, growth, and persistence of nereidid worms. Consequently, the interaction between sediment geochemistry, detrital resource pathways, and habitat structure plays a pivotal role in shaping the diversity, distribution, and ecological success of Polychaeta in Indonesian mangrove ecosystems.

Despite these insights, several knowledge gaps remain. Current studies are largely descriptive and site-specific, leaving a limited understanding of the broader spatial and temporal dynamics of polychaete communities across Indonesia's diverse mangrove and coastal systems. In particular, the functional roles of nereidid worms in nutrient cycling, sediment reworking, and energy transfer within benthic food webs remain poorly quantified. Moreover, the influence of environmental stressors—including pollution, habitat alteration, and climate-related changes—on polychaete diversity and ecosystem functioning is insufficiently understood.

To address these gaps, future research should adopt integrative and multidisciplinary approaches. Priority areas include: (i) broad-scale surveys combining morphological and molecular taxonomy to capture species diversity and biogeographic patterns; (ii) experimental and observational studies quantifying the functional contributions of nereidids to sediment biogeochemistry, organic matter processing, and trophic dynamics; (iii) assessments of the effects of environmental gradients and anthropogenic disturbances on polychaete community structure; and (iv) long-term monitoring to understand temporal variability and resilience of benthic assemblages.

Such research would not only advance ecological theory regarding benthic invertebrates in mangrove and coastal ecosystems but also inform sustainable management and conservation strategies, highlighting the critical roles of Polychaeta in maintaining ecosystem health and productivity.

2.3 Influence of Sediment Composition and Organic Matter on Polychaete Diversity

Members of the family Nereididae exhibit a remarkably broad ecological distribution, inhabiting a wide spectrum of marine environments that range from soft muddy and sandy bottoms to rocky coastal substrates (Siregar & Yuwono, 2005; Finishia et al., 2014; Jumars et al., 2015; Asnawi et al., 2018; Balakrishnan & Tudu, 2021). In Indonesia, tropical coastal systems across Java, Sumatra, Sulawesi, and Kalimantan represent major centres of nereidid occurrence, where these polychaetes form integral components of benthic communities spanning estuarine channels, intertidal flats, and mangrove forests (Yuwono et al., 1994; Siregar & Yuwono, 2005; Junardi, 2008; Sawestri, 2013; Apriyanti & Tumiran, 2018; Junardi, 2018; Lumingas et al., 2022; Sari et al., 2022; Wibowo et al., 2022). Their widespread presence across diverse habitat types highlights their adaptability to environmental variability, including differences in sediment composition, salinity gradients, tidal regimes, and hydrodynamic exposure.

Within these habitats, nereidid polychaetes frequently dominate soft-muddy and sandy-mud substrates, environments that are particularly suitable for their burrowing lifestyle and deposit-feeding behaviour (Asnawi et al., 2018; Hajializadeh et al., 2020). Fine-grained sediments provide structural stability essential for tube-building, burrow excavation, and maintenance, while the upper layers of sediment are typically enriched in labile organic matter that can be readily ingested and assimilated to support growth and metabolism (Jumars et al., 2015). The combination of favourable substrate properties, abundant food resources, and stable hydrological conditions in coastal and mangrove ecosystems creates optimal conditions for the settlement, development, and long-term persistence of nereidid populations.

This broad ecological tolerance and habitat flexibility not only underpins the high abundance and widespread distribution of nereidids in tropical coastal systems but also allows them to perform important ecological roles, including sediment reworking, nutrient cycling, and energy transfer within benthic food webs. By thriving in habitats that vary in sediment type, organic content, and tidal influence, nereidid polychaetes exemplify the complex interactions between benthic fauna and their physical and chemical environment, making them valuable model organisms for studies of tropical coastal ecology.

The ecological significance of the family Nereididae extends far beyond their numerical abundance and spatial distribution. Through their continuous burrowing and foraging activities, nereidid polychaetes exert profound influences on sediment structure, physical stability, and benthic biogeochemical processes. Species such as *Nereis virens*, *Nereis diversicolor*, *Nereis falsa*, and *Nereis pelagica* act as principal agents of bioturbation, actively reworking sediments through processes that include ventilation, selective feeding, and burrow construction and maintenance (Mustajärvi et al., 2019; He et al., 2022). By ingesting organic-rich deposits and recycling particulate matter within the substrate (Asnawi et al., 2018; Kanaya, 2023), these worms play a crucial role in mitigating excessive organic accumulation, enhancing sediment aeration, and promoting the overall quality and stability of benthic habitats (Bergström et al., 2019).

In addition to their roles as sediment engineers, many nereidid species function as omnivorous or opportunistic predators, feeding on a variety of small crustaceans, diatoms, detritus, and other benthic invertebrates (Belfetmi et al., 2021). Through these trophic interactions, nereidid polychaetes occupy a central position within coastal food webs, linking primary producers and detrital resources to higher trophic levels such as fishes and crustaceans. Their dual function as both ecosystem engineers and trophic mediators underscores the integral role, they play in maintaining ecological balance and supporting the productivity of tropical coastal ecosystems.

The combination of wide habitat tolerance, functional versatility, and strong interactions with both biotic and abiotic components of their environment has established nereidid polychaetes as valuable model organisms for ecological research.

Their high abundance, distinct habitat preferences, and sensitivity to environmental change further highlight their utility as bioindicators, capable of reflecting the condition of coastal ecosystems and signalling the impacts of anthropogenic disturbances such as pollution, habitat modification, and hydrological alteration.

Despite extensive ecological documentation, several knowledge gaps remain. Most studies in Indonesia have been descriptive and limited to specific sites, leaving the spatial and temporal dynamics of nereidid populations across diverse habitats poorly understood. Functional roles in sediment biogeochemistry, nutrient fluxes, and ecosystem productivity remain only partially quantified, particularly under variable environmental and anthropogenic stressors. Additionally, the interactions between nereidid worms and other benthic fauna, as well as their responses to climate-related changes such as sea-level rise, temperature fluctuations, and salinity shifts, are still poorly explored

2.4 Trophic Interactions, Host–Pathogen Relationships, and Bioindicator Roles

Polychaetes of the family Nereididae interact with a broad spectrum of organisms within their habitats and frequently occupy dual ecological roles as both predators and prey. Several studies have identified nereidid worms as an important natural food source for shrimp (Rajuansah et al., 2021; Herawati et al., 2022). However, their consumption may also facilitate the transmission of marine pathogens. For example, outbreaks of White Spot Syndrome Virus (WSSV) in *Litopenaeus vannamei* have been linked to the ingestion of infected nereidid worms collected from natural habitats such as the Mahakam Delta (Kalimantan) and the coastal waters of Semarang, Central Java. Individuals of *Dendronereis* spp. were shown to harbor active WSSV infections, with viral replication occurring in the intestinal tissues and transmission to shrimp occurring through oral exposure (Desrina et al., 2014). Beyond pathogen dynamics, nereidid polychaetes form a key component of estuarine and marine food webs (Balakrishnan et al., 2019).

They represent a major dietary resource for numerous demersal fish and shorebird species (Wibowo et al., 2022), while themselves functioning primarily as deposit feeders that process organic material within sediments (Bergström et al., 2019). The life histories of some species, such as *Namalycastis rhodochorde*, include a planktonic larval stage followed by a transition to a sedentary benthic phase, rendering them particularly sensitive to long-term environmental fluctuations (Junardi et al., 2020). At the same time, many nereidids exhibit notable physiological tolerance and adaptive capacity (Alter et al., 2021). For instance, *Namalycastis abiuma* from coastal regions of Java and Sumatra is capable of surviving under low dissolved-oxygen conditions, yet displays morphological abnormalities when exposed to mercury contamination (Sawestri, 2013).

These biological responses, together with their strong association with substrate conditions and organic enrichment, have contributed to the widespread use of nereidid worms as bioindicators of environmental change in coastal and marine ecosystems (Sabha et al., 2022). Accordingly, many coastal monitoring programs employ quantitative assessments of macroinvertebrate assemblages -including Nereididae - in relation to physicochemical and habitat variables (Abdullah et al., 2022; Sahidin et al., 2018), thereby reinforcing their value as indicator taxa for evaluating anthropogenic disturbance and overall environmental quality.

According to Schmeller et al. (2018), a bioindicator is defined as a species or taxonomic group that exhibits measurable biological responses to anthropogenic stressors, including industrial and chemical pollution. Macrozoobenthic organisms such as nereidid polychaetes are particularly responsive to shifts in environmental conditions because they inhabit the sediment–water interface, where contaminant accumulation and physicochemical fluctuations are most pronounced (De Marchi et al., 2018; Ramses et al., 2020). Their relatively short life cycles and rapid generation turnover enable timely detection of environmental disturbance (Sanchis et al., 2021), making them suitable indicators for assessing ecosystem integrity in marine and coastal habitats (Dean, 2008; Sawestri, 2013; Wardiatno et al., 2017; Sahidin et al., 2018; Ramses et al., 2020; Abdullah et al., 2022; Sabha et al., 2022).

Correspondingly, nereidid assemblages have been widely incorporated into coastal monitoring programs and pollution assessments (Wibowo et al., 2017). Industrial and urban pollution can modify both the physicochemical properties of sediments and the community structure of nereidid populations, as documented in coastal environments such as Sayung District, Demak, Indonesia (Iqbal et al., 2020). Because nereidid worms are largely sedentary and inhabit burrows or attach to hard substrates, they experience prolonged exposure to contaminants and can reflect the historical accumulation of pollutants in benthic habitats (Dsikowitzky et al., 2011). Consequently, the bioaccumulation of heavy metals—including cadmium (Cd), lead (Pb), and mercury (Hg) - in nereidid tissues has been widely applied as an indicator of environmental contamination (Liline & Rumahlatu, 2019). Similar applications have been reported internationally, where members of Nereididae have been used to evaluate exposure to Cd, Zn, and Cu in coastal ecosystems (Dean, 2008).

Beyond metal accumulation, several studies have examined physiological and biochemical biomarkers in nereidid species. For instance, oxidative stress responses - including glutathione, glutamate cysteine ligase, and glutathione-S-transferase activity - have been evaluated in *Perinereis gualpensis* as indicators of contaminant-induced cellular stress (Díaz-Jaramillo et al., 2011). Such biomarker approaches complement abundance- and distribution-based assessments, providing mechanistic insight into how pollutants influence organismal health and population dynamics.

Taken together, the abundance, spatial distribution, contaminant burden, and physiological status of nereidid polychaetes collectively provide robust indicators of environmental quality in coastal and estuarine ecosystems (Sahidin et al., 2014; Wardiatno et al., 2017; Sahidin et al., 2018). Their widespread use—both in Indonesia and globally—reflects their ecological importance, broad habitat representation, and rapid yet measurable responses to environmental disturbance.

3. REPRODUCTION

3.1 Reproductive Biology, Developmental Stages, and Epitoky Variation

Species of Nereididae inhabiting Indonesian coastal and estuarine environments generally exhibit gonochoristic reproduction, with males and females occurring as separate individuals that release sperm and oocytes into the surrounding water, where fertilization takes place externally during synchronized spawning events (Yuwono et al., 1994; Junardi et al., 2010; Pamungkas & Glasby, 2015). Such reproductive behavior is typical of broadcast-spawning polychaetes and is closely linked to tidal cycles, lunar periodicity, and local hydrodynamic conditions that enhance fertilization success and larval dispersal. Observations of sea worms previously identified as *Nereis* sp. (Yuwono et al., 1994) and *Dendronereis javaensis* (Yuwono, 2008), and more recently described as *Dendronereis javaensis* by Pamungkas et al. (2025) - the name adopted in this manuscript - show that spawning occurs year-round, peaking in February–March, after which adults die, indicating a semelparous life-history strategy. Comparable spawning periodicity and post-reproductive mortality have also been documented in nereidid populations from the southern coast of Lombok (Bachtiar & Bachtiar, 2019), suggesting that semelparity may be a prevalent reproductive trait among several Indonesian taxa. Following external fertilization, embryos develop into planktonic trochophore larvae, which form the earliest free-swimming developmental stage (Fig. 1). In *Dendronereis javaensis*, the trochophore stage persists for approximately one to two days before transitioning into a three-setiger benthic larva (Yuwono et al., 1994). During subsequent ontogenetic progression, the head becomes fully differentiated, parapodia develop on successive segments, and anal cirri form at the posterior end, marking the establishment of key morphological features associated with benthic life. Within roughly ten weeks, larvae metamorphose into juveniles capable of burrowing and sediment feeding, and these individuals typically attain reproductive maturity within one to two years, depending on environmental conditions and resource availability.

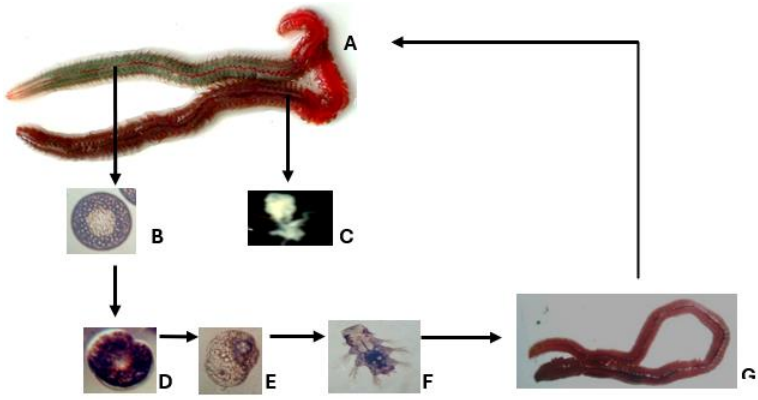


Figure 1. Life Cycle of *Dendronereis Javaensis* (Polychaeta, Nereididae). Adult Worms (A) Produce Oocytes (B) That Are Fertilized by Spermatozoa (C). The Fertilized Oocyte (D) Undergoes Division and Spirally Cleaving Embryos Developing into Planktonic Trochophore (E), Which Then Develops into Benthic Larvae With 3 Setigers (F) and Further Develops into an Immature Worm (G).

In many nereidid species, reproductive maturation is accompanied by epitoky, a metamorphic transition in which benthic, non-reproductive atoke forms transform into pelagic epitokes specialized for spawning (Fischer, 1999). This process often involves enlargement of the eyes, reconfiguration of parapodia for swimming, and alterations in body pigmentation and musculature. For example, *Perinereis cultrifera* from Maluku waters exhibits pronounced epitokous modification of parapodia and enhanced swimming capacity during the reproductive phase (Rettob, 2012). However, epitoky expression is not universal among Indonesian nereidids. Several species - such as *Dendronereis javaensis* from northern Java (Yuwono et al., 1994), *Nereis* sp. from Ambon (Pamungkas, 2009), and *Namalycastis abiuma* from Kalimantan (Junardi et al., 2014) - display minimal or no conspicuous epitokous transformation, indicating variability in reproductive strategies within the family.

In *Namalycastis rhodochorde*, maturation is instead characterized by distinctive physiological and chromatic changes, including a shift in body coloration (pink-to-reddish in females and greenish in males) and softening of the body wall, which subsequently ruptures during gamete release (Junardi et al., 2014).

These contrasting reproductive modes underscore the diversity of life-history strategies among Indonesian Nereididae and highlight the influence of evolutionary lineage, habitat characteristics, and reproductive ecology on the expression of epitoky and spawning behavior.

3.2 Reproductive Strategy and Life-History Patterns

The reproductive biology of nereidid polychaetes represents a distinctive life-history strategy shaped by physiological specialization and environmental adaptation. In *Dendronereis javaensis*, as in many members of Nereididae, reproduction encompasses several sequential processes, beginning with gametogenesis (oogenesis in females and spermatogenesis in males), followed by gamete maturation, spawning, and the subsequent development of larvae and juveniles into fully formed adults (Yuwono, 2008). Field observations across multiple coastal and estuarine habitats in Indonesia indicate that reproductive activity can occur throughout the year, although pronounced spawning peaks are typically recorded during specific months, notably February, March, and June (Yuwono et al., 1994; Junardi et al., 2010, 2014; Bachtiar & Bachtiar, 2019). These temporal patterns suggest that local environmental conditions—such as temperature, salinity, tidal cycles, and organic-matter availability—may act as reproductive cues that synchronize spawning within populations.

Consistent with earlier accounts, nereidid polychaetes are dioecious and exhibit semelparous reproduction, meaning that individuals reproduce only once before death. Species such as *Dendronereis javaensis, Nereis sp., Namalycastis abiuma,* and *Namalycastis rhodochorde* undergo a terminal reproductive event in which adults allocate substantial physiological resources to gamete production during gametogenesis. Upon release of mature gametes during spawning, somatic degeneration ensues and the adults die shortly thereafter (Yuwono et al., 1994; Pamungkas, 2009; Junardi et al., 2014, 2021). This strategy reflects a trade-off between survival and reproductive investment, maximizing reproductive output at the expense of post-spawning survival. The completion of the life cycle is thus transferred to the next generation, with larval development and recruitment playing a pivotal role in sustaining population continuity within nereidid communities

3.3 Gametogenesis, Spawning Regulation, and Reproductive Cycles

The reproductive system of nereidid polychaetes displays remarkable diversity in gamete origin and developmental pathways, reflecting both phylogenetic differentiation and adaptation to environmental conditions. Gametes may arise within discrete gonadal structures, originate from proliferative cells that differentiate freely within the coelomic cavity, or develop through a combination of these mechanisms (Eckelbarger, 2005). Several tropical Indo-Pacific taxa, including *Dendronereis javaensis* (Yuwono et al., 1994) and *Namalycastis rhodochorde* (Junardi, 2021), lack true gonads; instead, their gametes develop extra-gonadally within the coelom, where differentiation proceeds in association with coelomic tissues and nutrient-transporting cells.

Male gametogenesis (spermatogenesis) in nereidids follows a conserved morphological sequence. Spermatogonial clusters proliferate during the premeiotic phase and subsequently segregate during meiotic prophase to form characteristic spermatid tetrads. These tetrads differentiate into fully developed spermatozoa as maturation progresses (Yuwono et al., 1994). In *Namalycastis rhodochorde*, immature males contain undifferentiated spermatocytes dispersed within the coelomic fluid (Fig. 2A, 2B). These develop into spermatid tetrads during the submature phase (Fig. 2C) and eventually transform into motile spermatozoa at sexual maturity (Fig. 2D) (Junardi et al., 2022). Morphologically, the spermatozoa are characterized by a cone-shaped acrosome enclosing the nucleus and an elongated posterior flagellum, structural features that enhance motility and facilitate fertilization of free-spawning oocytes (Yuwono, 1992). Consistent with semelparous life histories, males typically die following gamete release during spawning (Yuwono et al., 1994).

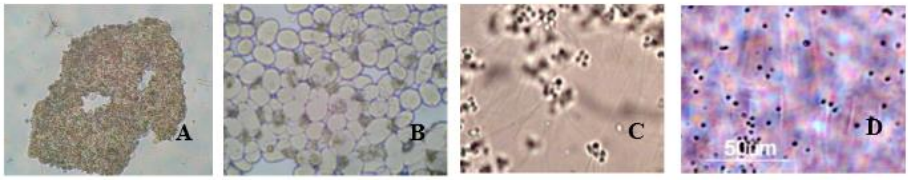


Figure 2. Spermatogenesis in *Namalycastis rhodochorde* (Polychaeta, Nereididae). (A) Undifferentiated spermatocytes in immature male coelom; (B) Spermatocyte clusters in immature stage; (C) Spermatid tetrads at submature stage; (D) Mature spermatozoa in coelomic fluid, exhibiting cone-shaped acrosome and posterior flagellum. Adapted from Junardi et al. (2022).

Female gametogenesis (oogenesis) in nereidids occurs via either intraovarian or extraovarian pathways (Eckelbarger, 2005). In *Dendronereis javaensis*, oogenesis is extraovarian: early oocytes are released into the coelom, where they proliferate, increase in size, and undergo sequential differentiation (Yuwono et al., 1994). Oocyte development progresses through proliferative, previtellogenic, vitellogenic, and corticogenic stages. Vitellogenesis—marked by the accumulation of yolk proteins—initiates when oocytes reach diameters of approximately 50–60 µm, followed by cortical alveoli formation during corticogenesis. Fully mature oocytes attain uniform sizes ranging from 140–160 µm. Notably, tropical nereidids tend to produce smaller mature oocytes compared with temperate representatives such as *Perinereis cultrifera,* whose oocytes may reach 280–320 µm (Bharathidasan et al., 2017), suggesting ecological or energetic trade-offs in reproductive allocation. Immature female individuals typically contain oogonia and developing oocytes of varying sizes within the coelom. The previtellogenic stage concludes when oocytes detach from cluster arrangements and disperse individually. During vitellogenesis, yolk deposition is facilitated by eleocytes present in the coelomic fluid (Eckelbarger, 2005), after which corticogenesis produces submature oocytes of relatively uniform maximum size (Lawrence & Soame, 2009; Yuwono et al., 1994). In mature females, lipid droplets frequently appear prior to spawning, a pattern documented in N. rhodochorde (Junardi et al., 2014). Overall, female gametogenesis follows a well-ordered trajectory from undifferentiated to immature, submature, and finally mature oocyte stages (Fig. 3).

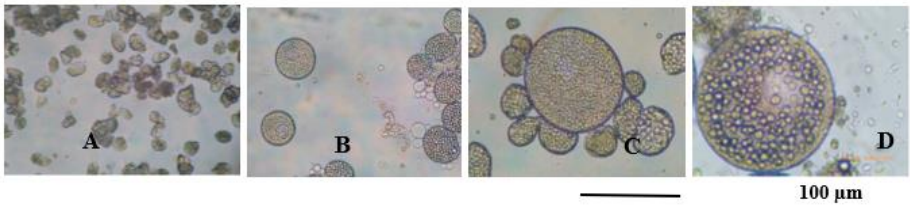


Figure 3. Oogenesis in Nereididae (Polychaeta). Stages of female gametogenesis (A). Undifferentiated oocyte; (B). Immature oocyte during previtellogenesis; (C). Submature oocyte during corticogenesis; (D). Mature oocytewith yolk accumulation and lipid droplets prior to spawning. Adapted from Yuwono et al. (1994) and Junardi et al. (2014)

Spawning in nereidids occurs through the synchronized release of mature gametes into the surrounding water column, a process governed by the interaction of environmental cues and internal regulatory mechanisms. Exogenous drivers include tidal, lunar, and seasonal temperature cycles, which collectively modulate reproductive timing and larval survival prospects (Bachtiar & Odani, 2021). In many tropical systems, seasonal temperature peaks—particularly during March—are associated with enhanced plankton availability, thereby increasing post-spawning recruitment success (Mulyadi & Saputra, 2019). Fecundity appears to be influenced more strongly by environmental conditions and food resources than by body size in some species, including *P. erinereis cultrifera* (Rettob, 2012).

Endogenous regulation involves neuroendocrine and hormonal controls that mediate gamete maturation and reproductive readiness (Ram et al., 1999; Andries, 2001). Additional environmental signals include photoperiod (Fischer, 1999), short-term light–dark cycles (Hardege et al., 1998; Zantke et al., 2013), water temperature (Hardege et al., 1994), salinity (Fong, 1993), climate variability (Lawrence & Soame, 2004), and tidal rhythms (Wilcockson & Zhang, 2008). Temperature acts as a particularly strong trigger: in cultivated Nereis diversicolor, spawning is initiated either by rising temperatures from 6°C to 12°C or by declining temperatures from 12°C to 6°C (Bartels-Hardege & Zeeck, 1990).

In natural habitats, spawning thresholds vary geographically; for instance, Nereis falsa in tropical East Algeria spawns at 20–23°C (Daas et al., 2011). Lunar periodicity functions as a key zeitgeber in many nereidids, influencing tidal regimes and synchronizing reproductive events within populations (Bentley et al., 1999). In West Kalimantan estuaries, N. rhodochorde displays a distinct spawning window from May to July, with maximum oocyte diameters observed in June (Junardi et al., 2014), paralleling reproductive peaks in Perinereis nuntia brevicirris in Malaysian waters (Ong, 1996). By contrast, N. abiuma exhibits year-round reproduction with pronounced peaks in March and July (Junardi et al., 2014), a pattern reminiscent of the 28-day spawning cycle documented in Platynereis dumerilii (Olive et al., 2005).

Spawning duration varies considerably among species and appears to reflect differences in maturation synchrony within populations. In N. rhodochorde, mature individuals persist for approximately nine weeks, whereas *Ceratonereis limnetica* and *Hediste atoka* exhibit far shorter reproductive windows of only 3–5 days (Glasby, 1986; Kikuchi & Yasuda, 2006). Extended spawning periods, such as the 13-week duration reported in P. nuntia brevicirris, are typically associated with asynchronous maturation across individuals (Hardege et al., 1994). Taken together, these observations indicate that annual reproductive cycles in nereidids are shaped by a combination of genetic regulatory mechanisms, fecundity, body size, and the interplay of environmental drivers (Tessmar-Raible et al., 2011).

3.4 Early Embryogenesis and Larval Development

Artificial fertilization has provided an important experimental approach for elucidating the early developmental processes of nereidid polychaetes, particularly in tropical species (Table 1). In *Dendronereis javaensis*, mature oocytes and spermatozoa have been successfully fertilized in vitro using seawater media of 15–17 ppt salinity at room temperature (Yuwono et al., 2002). Fertilized eggs of both *Dendronereis javaensis* and *Namalycastis rhodochorde* have also been obtained from mature individuals collected directly from their natural habitats, allowing comparative observation of laboratory-induced and naturally spawned embryos.

Successful fertilization is indicated by the rapid formation of a fertilization membrane (Sawada, 1984), which in *Dendronereis javaensis* appears within 2–3 minutes following exposure to spermatozoa (Yuwono et al., 2002). This developmental response is notably faster than that documented for the temperate species *Perinereis cultrifera*, in which membrane formation requires 10–20 minutes (Bharathidasan et al., 2017), suggesting that tropical nereidids may possess accelerated early cellular activation mechanisms. Following fertilization, the zygote undergoes rapid cleavage divisions.

In *Dendronereis javaensis*, the 2-cell stage is reached approximately 40 minutes post-fertilization, and rotating larvae develop within 2.5–3 hours (Yuwono et al., 2002). A similar pattern is observed in *N. rhodochorde*, where rotating larvae also appear within 2.5–3 hours (Junardi et al., 2020). These developmental rates are substantially faster than those of *P. cultrifera*, in which the 2-cell stage occurs 1.5–2 hours after fertilization and trochophore larvae do not appear until 60–63 hours post-fertilization (Bharathidasan et al., 2017). The comparison highlights a consistent trend: tropical nereidid species exhibit markedly accelerated embryogenesis and larval formation relative to temperate taxa.

Table 1. Comparative Developmental Stages of Fertilized Mature Oocytes in *Dendronereis Javaensis* (Previously Referred to As *Nereis* Sp.; Yuwono Et Al., 2002) And *Namalycastis Rhodochorde* (Junardi et al., 2020)

Development of the fertilized egg	Age	
	Dendronereis javaensis	*Namalycastis rhodochorde*
Formation of fertilization membrane	2 minutes	-
Beginning of cell division	20 minutes	-
2-cell stage	40 minutes	36 minutes
4-cell stage	50 minutes	42 minutes
8-cell stage	1 hour	1 hour
16-cell stage	1.5 – 2 hours	1.5 – 2 hours
32-cell stage	2 – 2.5 hours	2 – 2.5 hours

Broader interspecific comparisons further support this latitudinal pattern. In the temperate polychaete *Nereis diversicolor*, fertilization membrane formation takes approximately 30 minutes, the 8-cell stage is achieved only after 16 hours, and trochophore larvae emerge around five days post-fertilization (Wang et al., 2020). By contrast, the developmental sequence of *N. rhodochorde* more closely parallels that of *Dendronereis javaensis* and, to a lesser extent, *P. cultrifera*: fertilized eggs progress rapidly through the 2-, 4-, 8-, 16-, and 32-cell stages, followed by rotating embryos, trochophore larvae with paired eyes, metatrochophore stages, and three-setiger early nectochaeta Following fertilization, the zygote undergoes rapid cleavage divisions. In *Dendronereis javaensis*, the 2-cell stage is reached approximately 40 minutes post-fertilization, and rotating larvae develop within 2.5–3 hours (Yuwono et al., 2002). A similar pattern is observed in *N. rhodochorde*, where rotating larvae also appear within 2.5–3 hours (Junardi et al., 2020). These developmental rates are substantially faster than those of *P. cultrifera*, in which the 2-cell stage occurs 1.5–2 hours after fertilization and trochophore larvae do not appear until 60–63 hours post-fertilization (Bharathidasan et al., 2017). The comparison highlights a consistent trend: tropical nereidid species exhibit markedly accelerated embryogenesis and larval formation relative to temperate taxa.

Broader interspecific comparisons further support this latitudinal pattern. In the temperate polychaete *Nereis diversicolor*, fertilization membrane formation takes approximately 30 minutes, the 8-cell stage is achieved only after 16 hours, and trochophore larvae emerge around five days post-fertilization (Wang et al., 2020). By contrast, the developmental sequence of *N. rhodochorde* more closely parallels that of *Dendronereis javaensis* and, to a lesser extent, *P. cultrifera*: fertilized eggs progress rapidly through the 2-, 4-, 8-, 16-, and 32-cell stages, followed by rotating embryos, trochophore larvae with paired eyes, metatrochophore stages, and three-setiger early nectochaeta within approximately three days (Fig. 4) (Junardi et al., 2020; Yuwono et al., 1994; Bharathidasan et al., 2017). Collectively, these findings indicate that tropical nereidid worms possess accelerated early life-history trajectories, likely reflecting adaptive responses to warm-water environments characterized by higher metabolic rates and more dynamic ecological conditions.

The use of artificial fertilization techniques has thus been instrumental in revealing fine-scale developmental differences across species and climatic regions, while providing baseline data for future studies on larval ecology, reproductive biology, and potential aquaculture applications.

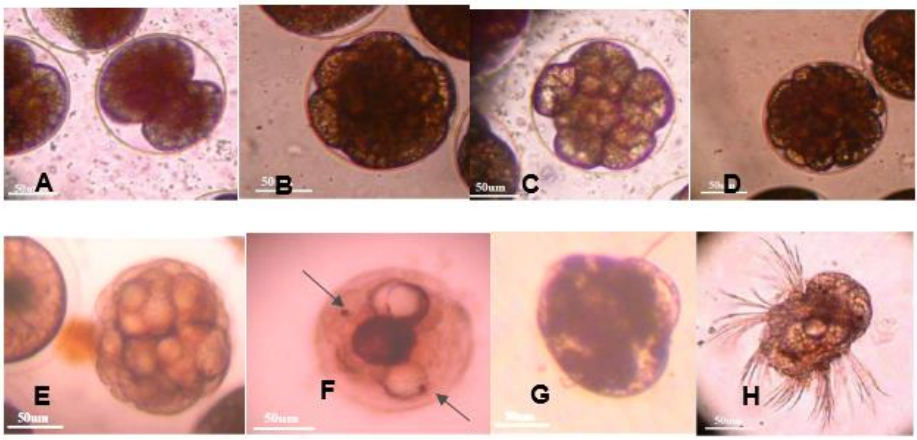


Figure 4. Embryonic development of *Namalycastis rhodochorde* (Junardi et al, 2020): A. 2-cell division (36 minutes); B. 4-cell division (42 minutes); C. 8-cell division (53 minutes); D. 16-cell division (120 minutes); E. 32-cell division (150 minutes, rotating larvae); F. trochophore larvae with two eyes (240 minutes, free-swimming larvae, black arrows indicated eyes); G. metatrochophore (22 hours); H. 3-setiger early nectochaeta (3 days).

3.5 Endocrine Regulation of Reproduction

Endocrinological research on nereidid polychaetes has played a pivotal role in advancing understanding of reproductive regulation and has provided a physiological basis for managing maturation and spawning in aquaculture contexts (Olive, 1999). Early investigations into nereidid neuroendocrinology began with Scharer's pioneering work in 1936, which identified neurosecretory cells in the cerebral ganglia of *Nereis virens*, a temperate-zone species (Baskin, 1976). Subsequent studies demonstrated that hormones produced in the brain exert regulatory control over both gametogenesis and the transition to reproductive metamorphosis (Durchon & Hauenschild, as cited in Pfannenstiel, 1978), thereby establishing the conceptual foundation for a neuroendocrine model of reproduction in the group.

Experimental studies on tropical nereidids have since expanded this framework. In *Dendronereis javaensis* from the Brebes coast of Central Java, surgical removal of the cerebral ganglia accelerates sexual maturation while simultaneously suppressing posterior segment regeneration, indicating that brain hormonal activity diminishes as worms transition from submaturity to full maturity (Yuwono et al., 1994). Comparable findings have been reported in *Nereis diversicolor*, where brain hormone concentrations are elevated in immature individuals but progressively decline during maturation, eventually ceasing upon attainment of full reproductive condition (Golding, 1983; Yuwono, 1992; Golding & Yuwono, 1994).

Implantation experiments—where cerebral ganglia from immature worms are transplanted into sexually mature individuals—reverse the maturation process, lending strong support to a single-hormone model in which the brain-derived factor nereidin inhibits sexual maturation while maintaining gametogenic processes (Andries, 2001; Schenk et al., 2016). The regulatory influence of nereidin on oocyte development has been confirmed through histological and experimental analyses. In decerebrated *Dendronereis javaensis*, oocyte growth proceeds rapidly, but this acceleration is halted when cerebral ganglia are re-implanted, demonstrating the inhibitory role of the hormone in controlling vitellogenesis and maturation timing (Yuwono et al., 1994, 1998). In addition to endocrine control, reproductive synchronization in nereidids is mediated by chemical communication.

Female-derived sex pheromones—such as 5-methyl-3-heptanone in *Platynereis dumerilii* and *Nereis succinea*—induce male spawning responses, while bioactive peptides such as “nereithione” facilitate mate recognition and coordinated gamete release (Zeeck et al., 1990; Ram et al., 1999; Hardege et al., 2004). These findings underscore the integration of endocrine and pheromonal signaling in reproductive behavior. More recent research, however, has challenged the sufficiency of the classical single-hormone nereidin model and points toward a more complex, multi-hormonal regulatory system.

In *N. virens*, the steroid hormone 17β-estradiol has been shown to promote vitellogenesis (Garcia-Alonso et al., 2006), while additional hormones including oxytocin, serotonin, progesterone, and testosterone have been detected in both temperate and tropical nereidids such as *Perinereis* sp., *N. diversicolor*, and *N. rhodochorde* (Durou & Mouneyrac, 2007; Meunpol et al., 2007; Junardi et al., 2014, 2022). These discoveries suggest that nereidid reproduction is governed not by a single inhibitory neurohormone alone, but through a coordinated network of interacting endocrine pathways that respond to both internal physiological status and external environmental cues.

Accordingly, contemporary perspectives increasingly favor a multi-hormone framework that integrates neurosecretory control, steroidal modulation, and environmentally driven endocrine signaling (Lawrence & Soame, 2009). Despite these advances, detailed mechanistic studies—particularly on tropical nereidid taxa—remain limited. Further research combining endocrinology, molecular biology, and experimental ecology will therefore be essential to validate and refine this emerging model of reproductive regulation in Nereididae.

CONCLUSION

Nereidid polychaetes are widely distributed and ecologically important in Indonesian waters, and research over recent decades has generated valuable knowledge on their ecology, reproduction, endocrinology, and taxonomy. These insights underpin their growing relevance in aquaculture, particularly as fishing bait and as a nutritious feed source for shrimp and fish, while emerging evidence also indicates potential roles in bioremediation, cosmetic applications, and human nutrition.

Despite this progress, taxonomic understanding of Indonesian Nereididae remains limited and warrants greater research attention, alongside integrative studies of reproductive mechanisms, endocrine regulation, and ecological functioning. By synthesising current knowledge of the biology and ecology of nereidid worms, this chapter highlights both their ecological significance and applied potential, while identifying key research priorities to support future scientific development, conservation, and sustainable utilisation.

Acknowledgments

The authors would like to express their sincere gratitude to the reviewers for their valuable comments, suggestions, and constructive feedback, which greatly contributed to improving the quality and clarity of this book chapter. The preparation and writing of this manuscript were carried out independently and were not funded by any institution or funding agency.