The First Records of Pelagic Gastropods Species from the Celebes Sea, North Sulawesi, Indonesia

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ABSTRACT

Despite their weak swimming abilities, which prevent them from swimming against general ocean currents, gastropod larvae can still achieve widespread dispersal. This study aimed to identify pelagic gastropod species, both holoplanktonic and meroplanktonic, and to analyze their distribution in the Celebes Sea. Gastropods were sampled using an Isaacs-Kidd Midwater Trawl (IKMT) during the EWIN 2018 Cruise aboard the R.V. Baruna Jaya VIII LIPI. Species identification relied on morphology and DNA barcoding. Eight holoplanktonic gastropod species were identified: *Atlanta inclinata* (Atlantidae, Subclass Caenogastropoda), *Creseis acicula, Creseis virgula, Boasia chierchiae, Styliola subula* (Creseidae), *Cavolinia labiata*, *Telodiacria* sp. (Cavoliniidae), and *Clio convexa* (Cliidae), all belonging to Subclass Heterobranchia. The meroplanktonic species identified, all Caenogastropoda, included *Reticutriton pfeifferianus* (Cymatiidae), *Dulcerana granularis* (Bursidae), and *Lampasopsis rhodostoma* (Bursidae). Most species were found distributed across stations in the eastern and western parts of the Celebes Sea. With the exception of *Creseis acicula, Styliola subula,* and *Reticutriton pfeifferianus*, all identified species represent first records for the Celebes Sea. This study marks the first research in the Celebes Sea utilizing morphology and DNA barcoding for identifying pelagic gastropod species, providing a foundational dataset for future investigations.

Keywords: DNA barcoding, Holoplankton, Meroplankton, Pteropod, Teleplanic larvae

INTRODUCTION

Most benthic marine invertebrates have planktonic, usually feeding larval stages (Strathmann, 1993; Strathmann and Grünbaum, 2006; Marshall *et al*., 2012). These planktonic stages, which vary in duration, are collectively categorized as meroplankton. At certain times and in specific areas, meroplankton can constitute a considerable proportion of the zooplankton, which is otherwise dominated by holoplanktonic species that spend their entire life cycle in the water column (Jitchum and Duangdee, 2015). The duration of meroplanktonic stages ranges from a few days to several months (Sawatpeera *et al*., 2001; Scheltema, 2001; Zhao *et al*., 2003; Ompi *et al*., 2023). For some gastropod larvae with planktonic stages lasting several months (teleplanic larvae), dispersal across oceanic barriers has been demonstrated (Scheltema, 1998; Swearer *et al*., 2019). However, many larvae settle relatively close to their parental populations (Levin, 2006; Kim *et al*., 2022).

The phylum Mollusca includes both holoplanktonic and benthic species with planktonic larvae. Holoplanktonic species are primarily

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gastropods, whereas meroplanktonic larvae originate from all mollusc classes. Many holoplanktonic gastropods have worldwide distributions (Lalli and Gilmer, 1989), but they often exhibit marked genetic differences among biogeographic regions (Jennings *et al*., 2010; Wall-Palmer *et al*., 2018). Recently, holoplanktonic gastropods have become important for studying ocean acidification due to their thin, fragile aragonitic shells that are easily dissolved (Bednaršek *et al*., 2012; Bednaršek and Ohman, 2015; Janssen *et al*., 2019). Therefore, gathering information about their distribution and abundance is crucial.

The Celebes Sea, also known as the Sulawesi Sea, is part of the Coral Triangle, renowned as a biodiversity hotspot (Hoeksema, 2007). The sea reaches depths of up to 6,200 m (Amri *et al*., 2015) and features an active submarine volcano located at depths of 1,000–2,000 m in the West Kawio, west of the Sangihe Islands (Amri *et al*., 2015). This unique geological feature may significantly influence the presence and distribution of marine species. The interaction between the deep-sea environment and the volcanic activity can create unique ecological niches, influencing the distribution and diversity of marine life. Volcanic activity can alter water chemistry and temperature, impacting the survival and development of marine species.

The Celebes Sea houses a large number of benthic mollusks, mostly bivalves and gastropods (Burghardt *et al*., 2006; Ompi, 2010; Ompi *et al*., 2019). Approximately 300 gastropod species have been identified from the Celebes Sea (e.g., Boneka and Mamangkey, 2013; Kaligis *et al*., 2018; Ompi *et al*., 2019; Aulina *et al*., 2023), accounting for 15% of gastropod species from Indonesian marine waters (Dharma, 2005). Many of these benthic species seasonally produce planktonic larvae. Currently, more than 300 species of planktonic gastropods have been identified from the Indo-Pacific (e.g., Strong *et al*., 2019), with 15% described solely from the Celebes Sea (e.g., Ompi, 2010; Puspasari *et al*., 2018; Simbolon *et al*., 2021). This study aimed to identify gastropod pelagic species and determine their distribution. The origin of these pelagic species in relation to currents, the distribution of parent benthic species, and various environmental factors are discussed. This information is crucial for the future management of climate change and sustainable fisheries.

MATERIALS AND METHODS

Sampling and morphological observation

Zooplankton was collected during the EWIN 2018 Cruise aboard the RV Baruna Jaya VIII LIPI from October 6 to October 22, 2018, using an Isaacs-Kidd Midwater Trawl (IKMT) with a 5 m² mouth opening and 0.5 mm mesh. The depth at the various stations ranged from 863 m at station 24 to 4,828 m at station 21. The distance between stations was 30 to 50 nautical miles, measured using a SIMRAD EM 1002 multibeam echo sounder. The first sampling trip covered stations 1 to 17, and the second trip covered stations 18 to 34 (Figure 1). Samples were taken both during the day and night.

Samples were sorted into subsamples of 50 mL under a dissecting microscope. For this study, gastropods were separated and placed in glass Petri dishes before being photographed. The length of specimens was measured to the nearest µm using an eyepiece micrometer (Ompi and Svane, 2018). A total of 368 specimens were found, but not all could be identified morphologically. Preliminary identification, based on shell presence and shape, structure, color, and sizes including foot and parapodia, was carried out under a compound microscope using available literature (Bandel *et al*., 1997; Young *et al*., 2002; Garilli *et al*., 2017; Hall *et al*., 2017; Wall-Palmer *et al*., 2018; Janssen *et al*., 2019). Names were verified using WoRMS (World Register of Marine Species) for nomenclatural accuracy.

After morphological identification, samples were placed in separate glass vials for individual larvae, labeled, and preserved in 99.9% ethanol in preparation for DNA analysis at the Genetic Laboratory, LON, Ancol. DNA was extracted from the tissue of individual larvae using the Qiagen DNeasy Blood and Tissue Kit, following the standard protocol (Catalog No. / ID 69506).

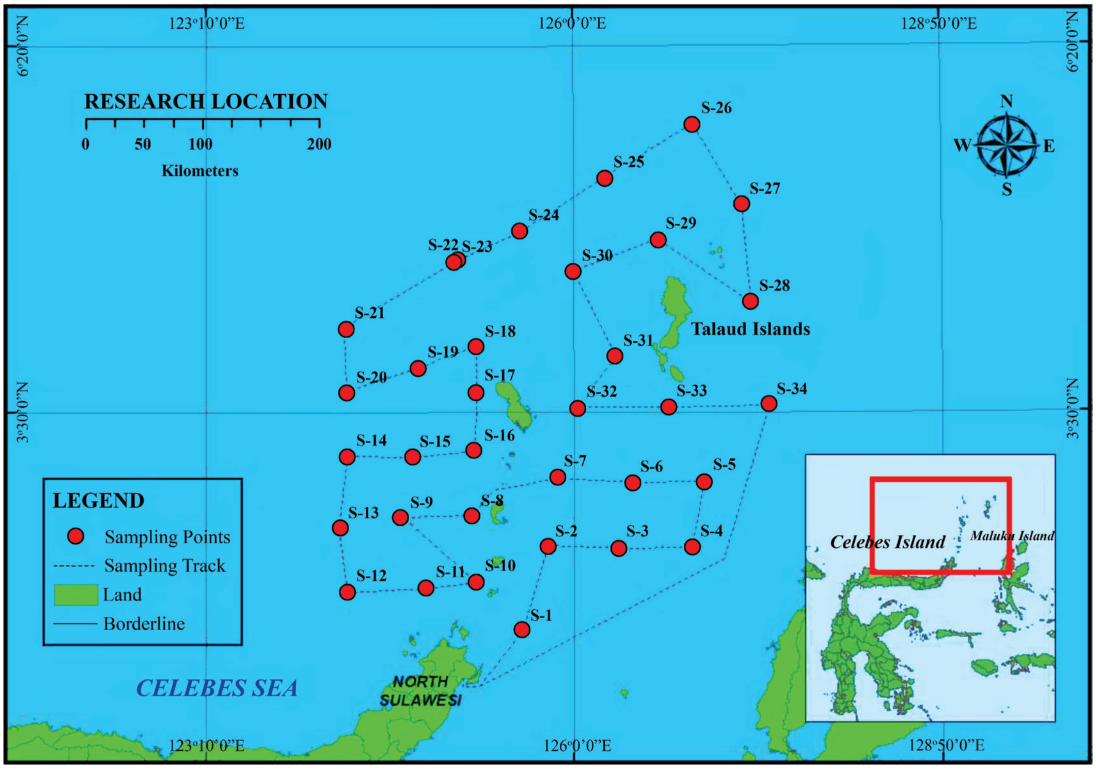

Figure 1. Location of study areas: Large map: the Celebes Sea with dashed lines indicating sampling track and sampling sites with red circle; insert: Close up of the Celebes Island and Sea.

Genetic analyses

The details of DNA extraction have been described by Simbolon *et al*. (2021). Molecular analysis was applied to confirm the morphological identification at the species level. The COI gene segment of the mitochondrial genome was amplified using DNA-specific universal barcoding primer pairs: forward primer LCO 1490 (5'-GGTCAACA AATCATAAAGATATTGG-3') and reverse primer HCO 2198 (5'-TAAACTTCAGGGTGACCAAAA AATCA-3') (Folmer *et al*., 1994). DNA quality was assessed using an IMPLEN Nanophotometer.

PCR was performed in a 30 µL reaction volume with the following reagents: 19.7 µL ddH$_2$O, 3 µL Taq buffer, 3 µL MgCl$_2$, 0.6 µL dNTP mix, 0.5 µL BSA, 1 µL each of the reverse and forward primers, 0.2 µL Taq DNA polymerase, and 1 µL DNA template (approximately 100 ng). The reactions were cycled under the following conditions: initial denaturation at 95 °C for five minutes; 35 cycles of denaturation at 95 °C for one minute, annealing at 40 °C for one minute, and extension at 72 °C for 90 s; followed by a final extension at 72 °C for five minutes. PCR results were visualized using electrophoresis on 2% agarose gel under a UV transilluminator. Successful PCR products were sequenced by Macrogen Ltd. (Singapore).

Sequences were edited and aligned using Geneious Prime software (https://www.geneious.com). The edited sequences were then compared with those in the Nucleotide GenBank NCBI database using the Basic Local Alignment Search Tool (BLAST). A similarity of $\geq 97.37\%$ for species validation was considered acceptable, as this confidence level is used in other studies (e.g., Stahlhut *et al*., 2013; Sani *et al*., 2021). Slightly lower similarity levels (90–97%) were accepted for identification at the genus level.

RESULTS AND DISCUSSION

Seven holoplanktonic and three meroplanktonic gastropods were identified to the species level, while one holoplanktonic specimen was identified only to the genus level. Species identity was verified using both morphological and molecular barcode analysis (NCBI accession numbers listed in Table 1). Each species is briefly described below, with information on distribution and comments on taxonomy. Pictures of eight species are presented, while images of the remaining three species are not displayed due to poor image quality.

Holoplanktonic species

From the present material, one species belonging to the subclass Caenogastropoda, order Littorinimorpha, and six species (plus one identified only to genus) from the subclass Heterobranchia, suborder Euthecosomata, were identified.

Subclass Caenogastropoda

Order Littorinimorpha

Family Atlantidae

Atlanta inclinata J.E. Gray, 1850

This holoplanktonic gastropod from the family Atlantidae features large eyes, a swimming fin, snout, foot, and operculum (Figure 2a). The shell is smooth with a broadly oval aperture and a spire with a short apex. It is transparent for about half of its diameter, while the rest has a yellowish-violet color. A brown line is visible along the keel of the shell (Figure 2a). The shell can reach a diameter of up to 6 mm. The species, *A. inclinata*, was recorded at 5 out of 34 stations in the Celebes Sea (Table 1).

Atlanta inclinata exhibits a wide distribution and has been documented in the Atlantic, Pacific, and Indian oceans (Wall-Palmer *et al*., 2018) (see records on GBIF at https://www.gbif.org/species/2301383). The specimens collected in this study represent the first record of *A. inclinata* from the Celebes Sea. Previously, the species was collected during the Siboga Expedition (1899–1900) at six stations in the Indonesian Archipelago (Tesch, 1906), but none were recorded in the Celebes Sea.

Wall-Palmer *et al*. (2018) documented 18 species of *Atlanta* across the entire Indo-Pacific Region, including the Red Sea. Among these, they distinguished two closely related species, *A. inclinata* and *Atlanta tokiokai* van der Spoel and Troost, 1972, which have partially overlapping distributions. *A. tokiokai* is characterized by specimens with a colored (golden) keel base, whereas *A. inclinata* tends to be slightly larger in shell size (Wall-Palmer *et al*., 2018). The specimens examined in this study exhibited a colored keel, similar to *A. tokiokai*, but were near the maximum size known for this species, making size alone insufficient for species identification. However, BLAST alignment confirmed the specimens as *A. inclinata* (accession number FJ876841), matching sequences from specimens found in the North-east Atlantic Ocean (Jennings *et al*., 2010). Recent molecular analyses have indicated a low genetic distance between the two species and some geographic structuring within both (Wall-Palmer *et al*., 2018).

Subclass Heterobranchia

Order Pteropoda

Suborder Euthecosomata

Family Creseidae

This study documented four pteropod species from the family Creseidae in the Celebes Sea. These species are characterized by narrow tube or needle-shaped shells. Most of them exhibit broad biogeographic ranges, with two species previously recorded in the Celebes Sea or nearby waters during old expeditions such as Siboga (Tesch, 1906) and Dana (Tesch, 1948). Specimens collected during these expeditions have been utilized in several modern studies (Corse *et al*., 2013; Burridge *et al*., 2015).

Table 1. Species identification based on DNA barcode BLAST results and sampling sites in the Celebes Sea revealed matches with a similarity percentage of ≥97%. Except for sites 1 (1 sample), 8 and 9 (2 samples each), and 12 (3 samples), the remaining sites had sample sizes ranging from 5 to 35.

Family	DNA Code	Identity of the nearest sequence of BLAST result	E-value Level	% Similarity (97.37–100)	GenBank Accession	Species Justification	Stations	Sizes Length (mm)
Creseidae	ML161	*Creseis acicula*	0.00	97.72	FJ876888	*Creseis acicula* (Rang, 1828)	19	7
	ML149	*Boasia chierchiae*	0.00	98.44	KC774044	*Boasia chierchiae* (Boas, 1886)	18	3
	ML174	*Styliola subula*	0.00	98.49	KF200174	*Styliola subula* (Quoy and Gaimard, 1827)	21	6
	ML 96	*Creseis virgula*	0.00	99.37	KC774047	*Creseis virgula* (Rang, 1828)	10	7
	ML139	*Creseis virgula*	0.00	99.06	KC774047	*Creseis virgula* (Rang, 1828)	18	–
	ML161	*Creseis virgula*	0.00	97.72	KC774047	*Creseis virgula* (Rang, 1828)	19	–
	ML112	*Creseis virgula*	0.00	98. 6	KC774047	*Creseis virgula* (Rang, 1828)	12	7
Cavoliniidae	ML101	*Cavolinia labiata*	0.00	98.91	KC774038	*Cavolinia labiata* (d'Orbigny, 1835)	11, 5	7
	ML 7	*Telodiacria danae*	0.00	90.37	KC774075	*Telodiacria* sp.	2	4
Cliidae	ML 51	*Clio convexa*	0.00	98.03	KC774069	*Clio convexa* (Boas, 1886)	5	6
Atlantidae	ML 12	*Atlanta inclinata*	0.00	97.34	FJ876841	*Atlanta inclinata* J.E., Gray, 1850	2	6
	ML 76	*Atlanta inclinata*	0.00	97.64	FJ876841	*Atlanta inclinata* J.E., Gray, 1850	6	6
	ML108	*Atlanta inclinata*	0.00	97.34	FJ876841	*Atlanta inclinata* J.E., Gray, 1850	11	6
	ML158	*Atlanta inclinata*	0.00	97.81	FJ876841	*Atlanta inclinata* J.E., Gray, 1850	19	6
	ML172	*Atlanta inclinata*	0.00	97.98	FJ876841	*Atlanta inclinata* J.E., Gray, 1850	21	–
Cymatiidae	–	*Reticutriton pfeifferianus* (Reeve, 1844)	–	–	–	–	1,2,3,4,5,7, 8,9,15,18,19 22,23,28, 32	5
Bursidae	ML143	*Dulcerana granularis*	0.00	99.69	MF124228	*Dulcerana granularis* (Röding, 1798)	18	3
	ML155	*Dulcerana granularis*	0.00	98.90	MF124228	*Dulcerana granularis* (Röding, 1798)	19	3
	ML123	*Dulcerana granularis*	0.00	98.46	MF124228	*Dulcerana granularis* (Röding, 1798)	14	3
	ML 43	*Lampasopsis rhodostoma*	0.00	99.82	JX 241373	*Lampasopsis rhodostoma* (G.B. Sowerby II, 1835)	4	3
	ML 75	*Lampasopsis rhodostoma*	0.00	99.65	JX 241373	*Lampasopsis rhodostoma* (G.B. Sowerby II, 1835)	6	3

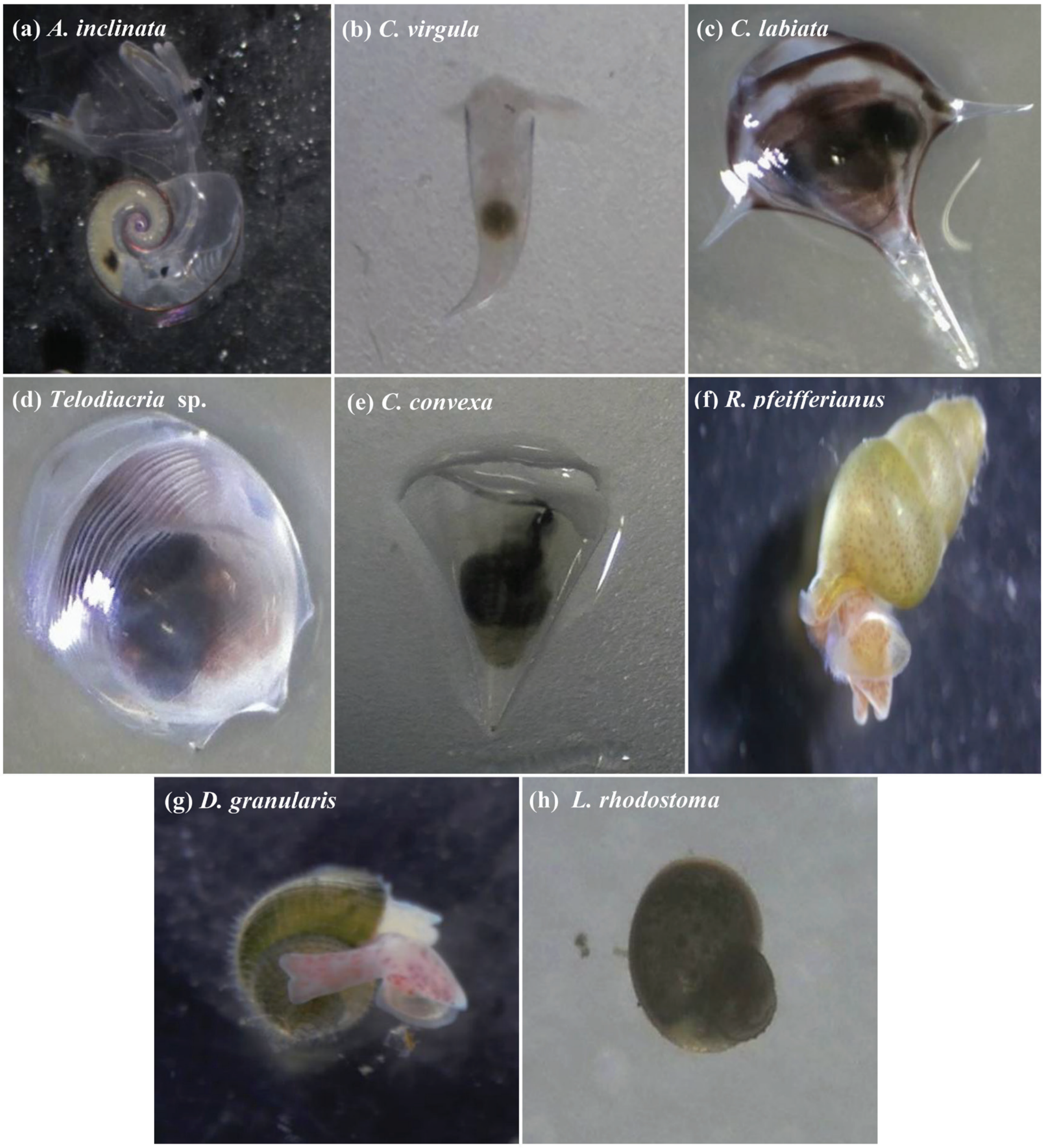

Figure 2. Morphology and coloration of specimens:
(a) *Atlanta inclinata* J.E., Gray, 1850;
(b) *Creseis virgula* (Rang, 1828);
(c) *Cavolinia labiata* (d'Orbigny, 1835);
(d) *Telodiacria* sp.;
(e) *Clio convexa* (Boas, 1886);
(f) *Reticutriton pfeifferianus* (Reeve, 1844);
(g) *Dulcerana granularis* (Röding, 1798) or *D. affinis* (Broderip, 1833);
(h) *Lampasopsis rhodostoma* (G.B. Sowerby II, 1835).

Creseis acicula (Rang, 1828)

This species has a smooth shell with slight irregularities. The shells are transparent and tube-shaped, with a pair of transparent wings, appearing straight and needle-shaped. BLAST alignment identified these characteristics as matching *Creseis acicula* (Rang, 1828) with accession number FJ876888.1 (Table 1), corresponding to a specimen collected from the Indian Ocean northwest of Australia (Jennings *et al*., 2010). This species was recorded exclusively at station 19 (Table 1; Figure 1).

Creseis acicula is among the most commonly found pteropod species in the Indo-Pacific Region (see records on GBIF at https://www.gbif.org/species/2293883). It was first documented in the Celebes Sea by the Siboga Expedition (Tesch, 1904) and has been observed in high abundance in the Aegean Sea (Tunçer *et al*., 2021), as well as in the Indian Ocean (Panchang *et al*., 2007; Jennings *et al*., 2010). Janssen *et al*. (2019) reported occurrences of this species in the Northeast Pacific Sea.

Creseis virgula (Rang, 1828)

This species possesses a transparent, smooth, and uncoiled shell (Figure 2b). The shell is elongated and narrow, tube-shaped, and curves posteriorly. Growth lines are visible just below the rounded aperture. Identification of the specimens in this study relied on DNA data and BLAST analysis with Accession number KC774047.1 (Table 1). The sequence from the present specimens (Accession number KC774047.1) matched that obtained from specimens collected by the Tara Expedition in the northern Indian Ocean near the Maldives (Corse *et al*., 2013), identified as *Creseis virgula*.

Creseis virgula was recorded at stations 10, 12, 18, and 19 in this study (Table 1). This species was previously documented in the Makassar Strait by the Siboga Expedition (Tesch, 1904) and the Dana Expedition (Tesch, 1948). However, prior to this study, it had not been recorded in the Celebes Sea. *C. virgula* exhibits a global distribution across tropical and warm temperate waters (see records on GBIF at https://www.gbif.org/species/2293881), including the Philippines, Japanese, and northern and eastern Australian waters.

Boasia chierchiae (Boas, 1886)

This species features a short, tube-shaped, transparent, and uncoiled shell with a transverse ring (Figure 2c). The BLAST identification confirmed its identity as *Boasia chierchiae* (Boas, 1886) (KC774044.1) (Table 1), matching a specimen from the Gulf of Aden (Corse *et al*., 2013). Currently, this species is recognized as *Boasia chierchiae* (Boas, 1886) according to WoRMS (2024).

Boasia chierchiae was exclusively recorded at station 18 in this study (Table 1; Figure 1). This marks the first record of the species in the Celebes Sea. Previously, it had been documented in the Andaman Sea of the Indian Ocean (Panchang *et al*., 2007; Corse *et al*., 2013), and subsequently in the Pacific coast of Mexico (see records as *Creseis chierchiae* on GBIF at https://www.gbif.org/species/2293884).

Styliola subula (Quoy and Gaimard, 1827)

This species has a transparent, tube-shaped shell resembling a sharp needle, with visible growth lines on the shell surface. BLAST alignment of the specimens in this study, with accession number KF200174.1 (Table 1), matched the sequence of a specimen collected from the East of Madagascar Sea in the Indian Ocean (Corse *et al*., 2013), confirming its identity as *Styliola subula* (Quoy and Gaimard, 1827).

Styliola subula was exclusively found at station 21 in this study (Table 1). Previous studies, such as those by the Siboga Expedition (Tesch, 1904) and the Dana Expedition (Tesch, 1948), also recorded this species in the Celebes Sea. This species is widely distributed throughout warm temperate and tropical waters globally (see data on GBIF at https://www.gbif.org/species/5190445). It has been documented along most of the western Pacific rim, including waters around the Philippines and China, south of Japan, and further south in Australian waters.

Family Cavoliniidae

One species from the family Cavoliniidae was identified with a similarity level ≥ 97% (Sani *et al*., 2021) in the specimens collected from the Celebes Sea (Table 1). Species of this family exhibit shells that are globose in outline, with the dorsal surface extending above the ventral surface, forming a hood-like structure. A short spine was observed posteriorly on the species. Additionally, another specimen from the same family was identified at the genus level due to a similarity level < 97% (Table 1).

Cavolinia labiata (d'Orbigny, 1835)

The species has a broad shell, with the width comprising 80% of its length (Figure 2c). Both the dorsal and ventral sides are convex, though not globose. It features a long and thick caudal spine, along with distinct lateral spines. The shell sculpture shows faint growth lines. Identification of the present specimen relied on DNA data and BLAST analysis with accession number KC774038.1 (Table 1). The DNA sequence of this specimen matched with a sample collected by the Tara expedition from waters near Madagascar in the Indian Ocean (Corse *et al*., 2013), identified as *Cavolinia labiata* (de'Orbigny, 1835).

This species was found at stations 5 and 11 in this study (Table 1), marking its first record from the Celebes Sea. Information on the distribution of this species is scarce (see data on GBIF at https://www.gbif.org/species/5724505). Previously, it had been recorded from waters around Madagascar in the Indian Ocean and in South African waters of the South Atlantic Ocean (Corse *et al*., 2013).

Telodiacria sp.

The specimen features a globose shell with very short caudal and lateral spines (Figure 2d). Growth lines on the dorsal shell surface are clearly visible. BLAST analysis of the present specimen identified it as *Teliodiacria danae* (van Leyen and van der Spoel, 1982) with accession number KC 774075.1. However, the similarity level was only 90.37% (Table 1), leading to its identification only to the genus level, *Telodiacria*. The original DNA sequence identifying it as *T. danae* was sampled from the Caribbean (Corse *et al*., 2013). In the present study, *Telodiacria* sp. was exclusively recorded at station 2 (Table 1; Figure 1).

Family Cliidae

Species in this family has shells that are roughly triangular or pyramidal in outline. Only one species from this family was identified in the present material.

Clio convexa (Boas, 1886)

The specimen in this study exhibits a pyramidal shape with a smooth and translucent shell, revealing internal structures (Figure 2e). Dorsally, the shell is convex. BLAST analysis identified the present specimen as *Clio convexa* (Boas, 1886) with accession number KC774069.1 (Table 1). The molecular sequence matching the present specimen was originally sampled from the east of Madagascar in the Indian Ocean (Corse *et al*., 2013).

This species was exclusively found at station 5, marking its first record from the Celebes Sea (Table 1, Figure 1). *Clio convexa* has been previously recorded in surrounding waters, such as Papua New Guinea, the waters northeast of Australia, Madagascar, and the Red Sea in the Indian Ocean (Corse *et al*., 2013) (see records on GBIF at https://www.gbif.org/species/4359332).

For many years, *Clio convexa* was considered a morphological variety of the widely distributed species *Clio pyramidata* L., 1767 (Van der Spoel, 1973). However, a more recent molecular study confirmed *Clio convexa* and *Clio pyramidata* as distinct species, with six species of the family Cliidae identified east of Madagascar in the Indian Ocean (Corse *et al*., 2013). Previously, specimens from the Pacific Ocean were described as a separate species, *Clio teschi*, in an unpublished thesis, but this classification is not considered valid, and the accepted name is *C. convexa* (WoRMS, 2024). These species share similar morphology, such as pyramidal shells, but variations in the curvature of the ventral and dorsal shells distinguish them.

Meroplanktonic spp.

Benthic gastropods from the family Cymatiidae are fairly common in Indonesian waters. In a recent study by Simbolon *et al*. (2021), larvae of eight species from the family Cymatiidae were identified by DNA barcoding in the Celebes Sea. Among these species, *Reticutriton pfeifferianus* (Reeve, 1844) was included in their study. However, detailed descriptions of its morphology and distribution are provided in the present study.

Family Cymatiidae

Reticutriton pfeifferianus (Reeve, 1844)

The larva of this gastropod exhibits a smooth, pale-yellow shell adorned with brown dots throughout (Figure 2f). The shell is spirally coiled with four whorls, and the aperture features a short siphonal canal. Reddish-brown dots are scattered on the foot, and when swimming, four long, narrow, white velar lobes are visible, each approximately the same length as the shell. The shell measures 5 mm in length and 3 mm in width. Adult benthic gastropods from this region can typically be identified to the species level based on morphological characteristics (Tucker and Dance, 2000; Dharma, 2005).

The larva of *R. pfeifferianus* was identified at 15 of 34 stations in the Celebes Sea (Table 1; Figure 1). In a recent phylogenetic revision of the superfamily Tonnoidea, the COI sequence (MH581362.1) of a specimen collected in the Mozambique Channel, Madagascar, matched the present specimens (Simbolon *et al*., 2021). The species has also been recorded to the east of Borneo, southeast of Papua New Guinea, northeast and northwest of Australia (Kirkendale *et al*., 2019), and northward in the Celebes Sea, including Philippine waters, as reported by GBIF (https://www.gbif.org/species/6488776). Recent records of adult *R. pfeifferianus* include Sarawak, Malaysia (Morni *et al*., 2017), the Andaman Islands (Rao and Dey, 2000), and Thailand (Gulf and Andaman coasts) (Tantanasiriwong, 1978; Wells *et al*., 2021).

Species of family Cymatiidae are known to have long-lived (teleplanic) larvae that may disperse over long distances. Given the presence of four whorls, the present specimens likely spent a significant time in the water column. However, there remains the possibility that these specimens belong to a previously undocumented species of family Cymatiidae or one that has not been subjected to DNA sequencing, as most specimens could only be identified at the genus level (Simbolon *et al*., 2021). If confirmed by subsequent identifications (Simbolon *et al*., 2021), this finding represents the first record of *R. pfeifferianus* from the Celebes Sea.

Family Bursidae

Fifteen species of the family Bursidae from the Indo-Pacific Ocean were included in the study (Castelin *et al*., 2012), but larvae of only two species were identified from the Celebes Sea in the present study. These species are *Dulcerana granularis* (Röding, 1798) or *D. affinis* (Broderip, 1833), and *Lampasopsis rhodostoma* (G.B. Sowerby II, 1835).

Dulcerana granularis (Röding, 1798) *or D. affinis* (Broderip, 1833)

This larva exhibits a yellow-green and brown coloration, with a spirally coiled shell comprising three whorls adorned with a rectangular periostracal pattern (Figure 2g). Tiny hairs are arranged in spiral lines on the whorls. The white foot displays reddish-brown dots across its surface, with a well-developed propodium and an identified operculum. A white velum is visible during swimming. The specimen in the photograph appears to have visible eyes through the shell, though these may also be pigment spots of the partly retracted head. This larva measures 2.5 mm in height and 1.5 mm in width (Table 1).

BLAST identification identified the specimen as *Bursa granularis* (Röding, 1798) (MF124228.1), which is currently recognized as *Dulcerana granularis* (Roding, 1798) according to the World Register of Marine Species (WoRMS). However, supplementary material from Sanders *et al*. (2021) suggests that this GenBank number corresponds to *D. affinis* (Broderip, 1833) from Papua New Guinea. Morphologically, larval shells of most *Dulcerana* species, as well as other genera in this family, are very similar in size and shape. According to voucher numbers provided by Sanders *et al*. (2021), the specimen matching the present material is now identified as *Dulcerana affinis*, known for its distribution in the western and central Pacific (Sanders *et al*., 2017).

Periostracal hairs have not been previously described for *Dulcerana* species, potentially due to their absence from the protoconch of adult snails (Bandel *et al*., 1994). However, such hairs have been documented in larval shells of various Bursidae species from the Red Sea (Bandel *et al*., 1994). Given the overlapping distributions of *D. granularis* and *D. affinis*, the present specimens could pertain to either species, suggesting the need for further collection and analysis to confirm their identity.

In this study, larvae were recorded at stations 14, 18, and 19 (Table 1; Figure 1), marking the first record of this species in the Celebes Sea. The species exhibits a broad geographical distribution across the Indo-Pacific, including the Malacca Sea, Papua New Guinea, Philippines, and the Indian Ocean (Sanders *et al*., 2017) (see records in GBIF at https://www.gbif.org/species/11155573 and https://www.gbif.org/species/11171205).

Lampasopsis rhodostoma (G.B. Sowerby II, 1835)

This larva features a yellow and brown coloration in its spirally coiled shell, comprising three whorls (Figure 2h). Reddish-brown dots are scattered across the surface of the shell. A small rib around the spire is expected, although the photo of the present specimen is unfortunately not available due to a blurry image.

In BLAST analysis, the present specimen was identified as *Bursa rhodostoma* (G.B. Sowerby II, 1835) (accession number JX241373.1) (Table 1). However, according to the World Register of Marine Species (WoRMS), it is currently recognized as *Lampasopsis rhodostoma* (G.B. Sowerby II, 1835) (WoRMS, 2024). The COI sequences of the present specimen matched with an original specimen collected in Philippine waters in the Indo-West Pacific Ocean (Castelin *et al*., 2012).

This species was identified at two stations, stations 4 and 6 (Table 1; Figure 1), in this study, marking its first record in the Celebes Sea. *Lampasopsis rhodostoma* is known for its wide geographical distribution across the Indian and Indo-Pacific Oceans (Castelin *et al*., 2012) (see records in GBIF at https://www.gbif.org/species/11114460).

Distribution

This study emphasizes both the advantages and drawbacks of using single-gene barcode analysis for zooplankton species identification. Barcoding from bulk zooplankton samples has been proposed for biodiversity surveys (Machida *et al*., 2009; Bucklin *et al*., 2021). However, it underscores the critical need for taxonomic expertise, especially in regions where only a fraction of species have been sequenced and a significant proportion remain unnamed and undescribed (Pappalardo *et al*., 2021). The use of COI barcode sequences offers the advantage of access to a large database like GenBank, containing sequences from diverse species worldwide. However, a drawback is the potential for inaccuracies in species identification and the challenge of keeping identifications current as new information emerges. This necessitates checking specific accession numbers against the latest literature, especially in cases where the original specimen in the database may have been misidentified (Collins and Cruickshank, 2013).

Indonesian seas harbor one of the world's most complex current systems, complicating the estimation of likely pathways for planktonic larvae from hatching to settlement. The Indonesian Throughflow directs water from the Pacific Ocean northwestward to southeastward across the Celebes Sea, with occasional incursions of South China Sea water entering from the north via the Sulu Sea (Feng *et al*., 2018; Taufiqurrahman *et al*., 2020). Zooplankton, including gastropods, observed in the Celebes Sea are therefore likely sourced from the northwest Pacific or the South China Sea.

However, the present results indicate otherwise. While holoplanktonic species exhibit wide distributions across the Pacific, Indian, and even Atlantic Oceans (Sanders *et al*., 2017; Wall-Palmer *et al*., 2018), the six Thecosomata species identified in this study matched specimens from the Indian Ocean, and one heteropod matched a specimen from the Atlantic Ocean off western Africa. Among the meroplanktonic species, the benthic adults appear to predominantly occur south and east of the Celebes Sea, with one matching a specimen from Madagascar, another from Papua New Guinea, and only one from Philippine waters. However, current distributional records of adult populations may be incomplete. Genetic differentiation among populations of other marine invertebrates with planktonic larvae has been documented in this region (Benzie, 1999; Barber *et al*., 2000; Kochzius and Nuryanto, 2008). To ascertain the origin of larvae found in the plankton of the Celebes Sea, additional samples should be collected and more genes sequenced. This data should be compared with genetics of local adult populations as well as those from the western Pacific and Indian Ocean.

In addition to currents, abiotic factors such as temperature and salinity, and biotic factors such as food availability and predator avoidance, may influence the distribution of planktonic gastropods. While these gastropods cannot swim against currents, they can adjust their vertical position in the water column to potentially change their direction of movement between different water masses (Wall-Palmer *et al*., 2018). By retracting into their shells and sinking passively towards the bottom, they may move away from unfavorable positions in the water column. Active swimming is required to move upwards.

The number of pelagic gastropod species identified in this study is insufficient to draw conclusions about their distribution patterns within the Celebes Sea. The highest species richness (five species) was observed at station 19, followed by four species at station 18, three species at stations 2 and 5, and two species each at stations 4, 6, 11, and 21. Thirteen stations had only one identifiable species, and another 13 stations had no identifiable species at all (Figure 3).

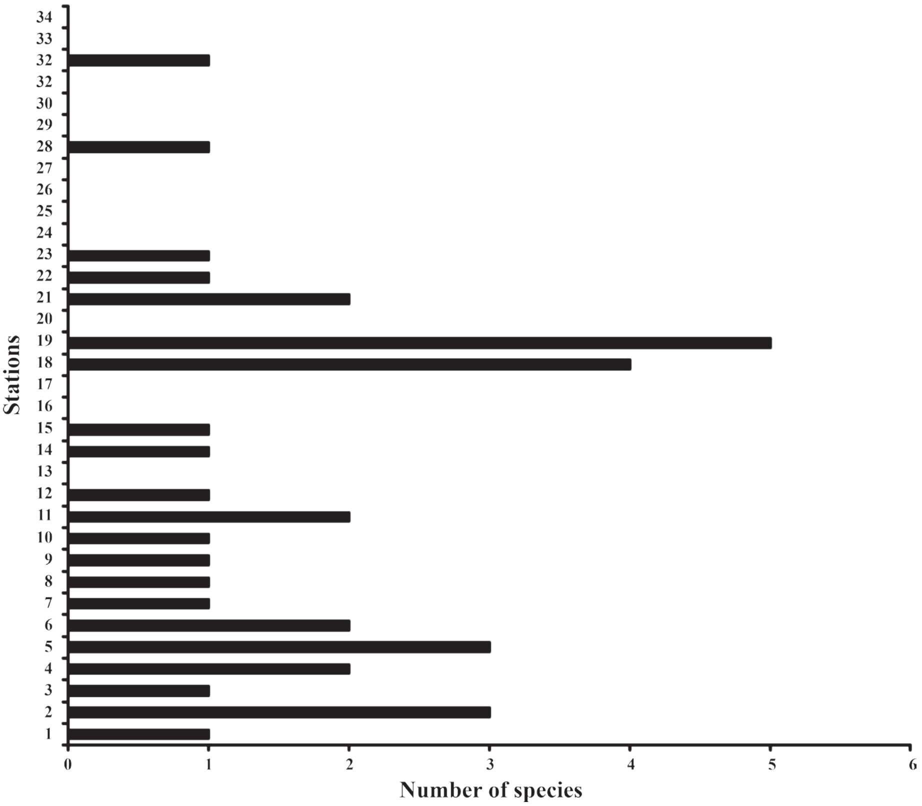

Figure 3. Number of species recorded at each site in the Celebes Sea, north Sulawesi, Indonesia.

Salinity and temperature are frequently cited as key factors influencing the distribution of marine invertebrates (e.g., Kim *et al*., 2022). In the Celebes Sea, these variables show minimal variation and primarily indicate the inflow of oceanic water to the east, freshwater outflow to the south near Sulawesi's mainland, and the presence of submarine volcanoes in the western part of the sampling area (Amri *et al*., 2015; Rozirwan *et al*., 2021). It is noteworthy that the holoplanktonic species *Creseis virgula* was observed at stations 10, 12, 18, 19, and *D. granularis/affinis* was found at stations 14, 18, and 19, particularly in waters surrounding the seamount and near Sangihe Island (Table 1, Figure 1). Salinity in the Celebes Sea ranged from 33.54 to 34.31‰, while seawater temperatures ranged from 28.64 to 30.24 °C (Wijayanti *et al*., 2020; Rozirwan *et al*., 2021). Salinity and surface seawater temperatures at stations 14–20, close to seamount volcanoes, were slightly higher (salinity 34.20–34.25‰, seawater temperature≥30 °C) compared to other stations (Rozirwan *et al*., 2021). Planktonic gastropods have been observed around seamounts in various regions (Kim *et al*., 2022; Çağlar and Öztürk, 2022). However, the distribution of *Atlanta inclinata*, which was found at 5 stations (Table 1), did not correlate with salinity or temperature. This species exhibits tolerance to a wide range of environmental conditions, from cold to warm tropical waters (e.g., Jennings *et al*., 2010; Wall-Palmer *et al*., 2018).

In this study, ten species and one genus of pelagic snails were identified. A recent study identified four additional meroplanktonic larvae and three larvae that could only be identified to the genus level from the caenogastropod family Cymatiidae, collected at the same stations (Simbolon *et al*., 2021). Despite identifying approximately 20 species, this represents only a fraction of the potential biodiversity of pelagic gastropods. Strong *et al*. (2019) documented 17 species of the family Bursidae and 30 species of Cymatiidae from Indo-Pacific regions. Nonetheless, this study represents the first investigation of its kind in the Celebes Sea utilizing DNA barcoding for species identification, establishing a foundational baseline for future research endeavors.

CONCLUSIONS

This study identified seven pteropod species: *Creseis acicula, C. virgula, Boasia chierchiae, Styliola subula, Cavolinia labiata, Teliodiacria* sp., and *Clio convexa*, along with one heteropod species, *Atlanta inclinata*. Additionally, three species—*Reticutriton pfeifferianus, Dulcerana granularis/ D. affinis,* and *Lampasopsis rhodostoma*—were identified as meroplanktonic species. Among these, eight species (*C. virgula, B. chierchiae, C. labiata, Teliodiacria* sp., *C. convexa, D. granularis/D. affinis*, and *L. rhodostoma*) represent new records for the Celebes Sea. The distribution of these species was observed to be more prominent to the east and west of Sangihe Island, with slightly higher salinity and seawater temperatures noted in the western part of the Celebes Sea compared to the east. Future studies should focus on investigating seasonal variations, larval dispersal patterns, and responses to environmental fluctuations, particularly in the vicinity of Sangihe Island and its surroundings, to provide valuable insights into the ecological roles and adaptations of these species in the Celebes Sea.

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