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Exploring diel vertical migration and spatiotemporal variation of zooplankton backscattering strength using an acoustic Doppler current profiler instrument in the Halmahera Sea, Indonesia

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Abstract: Given its critical role in marine ecosystems, this study comprehensively examined zooplankton distribution and behavior in the Halmahera Sea. The temporal and spatial dynamics of zooplankton acoustic backscatter values were analyzed using a 153.6 kHz vessel-mounted acoustic Doppler current profiler (ADCP). Analysis was supplemented by biological sampling with a bongo plankton net. Further evaluation included the analysis of oceanographic and bathymetric data. The acoustic, oceanographic, and biological sampling data were obtained from the Jala Citra I "Aurora" survey expedition in 2021, while the bathymetry data were obtained from the General Bathymetric Charts of the Ocean (GEBCO). The raw ADCP data, represented as digital counts, were transformed into mean volume backscattering strength (MVBS) expressed in decibels (dB) using sonar equations to yield a measure proportional to zooplankton biomass. Temporal observations revealed a diel vertical migration (DVM) pattern in zooplankton aggregation, characterized by movements responding to the daily solar cycle. Spatial observations indicated a higher zooplankton density in semi-enclosed waters than in open water. The high values of acoustic backscatter are not attributed to a single species of zooplankton. Biological sampling identified that *Oncaea* spp. and *Oithona* spp., a species from the Cyclopoida order, exhibit the highest abundance. The study concludes that the ADCP, based on acoustic backscatter measurements and data sampling, is an effective tool for detecting the presence and behavior of zooplankton.

Keywords: acoustic backscatter; acoustic Doppler current profiler; diel vertical migration; Halmahera Sea; zooplankton

Abbreviations: Acoustic Doppler Current Profiler (ADCP); diel vertical migration (DVM); mean volume backscattering strength (MVBS); sound scattering layer (SSL)

INTRODUCTION

Comprehensive analysis of zooplankton distribution characteristics is paramount to the multifaceted roles of zooplankton in marine ecosystems. These organisms are primary consumers, thereby determining the secondary productivity of aquatic environments, which influences the establishment of fishing grounds [1]. They are integral to material cycling processes and energy flows within the ecosystem [2] and are bioindicators of aquatic productivity and fertility [3]. Furthermore, zooplankton facilitates the biological pump mechanism by translocating carbon and nitrogen molecules to deeper water strata. They also contribute to the mixing and stratification of seawater masses through their active transport during DVM [4-5]. This research underscores the necessity of its study in marine biological research.

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Several studies investigating zooplankton in Indonesian seas have been undertaken, with the majority employing biological sampling methodologies. While this approach is considered the gold standard in zooplankton research [6], it has limitations in delineating the zooplankton spatial and temporal distribution scales, particularly in deep-sea environments. This issue underscores the need for complementary methodologies to comprehensively understand zooplankton dynamics across various spatial and temporal scales [7]. Continuous monitoring on a large spatial scale is required to examine the distribution pattern and abundance of zooplankton in the water column. Hydroacoustic technology is a sophisticated method for quantifying the abundance and discerning the distribution patterns of zooplankton within the water column [6-7]. The ADCP is a hydroacoustic equipment that can be used to study spatially and temporally zooplankton in the water column. An ADCP operates based on the Doppler effect, emitting a sound pulse signal that reflects off scatterers in the water column. The echo reflected by the target is then processed to obtain more information. The ADCP can also calculate the speed and direction of an object in the water column [8-9]. Data processing can be used to determine the distribution of zooplankton abundance by converting the results of acoustic scattering measurements into mean volume backscattering strength (MVBS) in decibels (dB) [6].

The DVM of zooplankton, a key ecological process, has been extensively studied using ADCP instruments. Previous research found significant spatiotemporal variation in zooplankton backscattering strength, identified a strong signal in the sound scattering layer [10], and seasonal variability of the zooplankton [11]. The accuracy of biomass estimates based on net samples was also highlighted [11,12]. Another study demonstrated the use of ADCP measurements for monitoring zooplankton distributions, showing a strong correlation between backscatter estimates and zooplankton concentration [13] and detailed measurements of zooplankton swimming speeds and migration patterns [14]. These studies underscore the importance of ADCP instruments in understanding the complex dynamics of zooplankton in marine ecosystems.

ADCP-sounding data is typically used for qualitative research, providing rough estimations [8]. However, ADCP can continuously measure object velocities across a large detection area because it contains numerous transducers in one instrument at a specific angle. As a result, ADCP facilitates the observation of migratory biota [2,15]. So far, the ADCP instrument has been used primarily for oceanographic observations such as current direction and velocity and suspended sediment concentrations in Indonesian waters, resulting in a lack of attention to zooplankton organisms [10]. The ADCP has a twofold function: to measure the speed and direction of objects in the water column and to gather detailed acoustic backscatter data, which is then used for zooplankton biomass analysis. Thus, the procedure is crucial for current measurement and biomass assessment. Therefore, the primary objective of this research was to optimize the application of ADCP data in the Indonesian Sea for a comprehensive understanding of zooplankton distribution patterns. This study examined the temporal and spatial characteristics of the acoustic backscattering of zooplankton from the ADCP instrument in the Halmahera Sea, accompanied by the results of biological sampling. Moreover, the study aimed to elucidate the vertical migration patterns of zooplankton, extending to the deep-sea regions to facilitate a temporal analysis of zooplankton stratification, thereby providing novel insights into the dynamics of marine ecosystems over time.

MATERIALS AND METHODS

Study area

The acoustic data were collected in the Halmahera Sea, Indonesia, from August 14-18, 2021, with predefined tracks (Supplementary Fig. S1). The Halmahera Sea is a regional sea located in the central-eastern part of the Australasian Mediterranean Sea. It is centered at about 1°S and 129°E and is bordered by the Pacific Ocean to the north, Halmahera Island to the west, Waigeo Island and West Papua Province to the east, and the Seram Sea to the south [16]. The Halmahera Sea is a significant entry point for the Indonesian throughflow (ITF) current, which is the mass exchange of seawater between the Pacific Ocean and the Indian Ocean [17]. Despite the Halmahera Sea's significant role in the ITF, there is a noticeable lack of comprehensive research in this area, particularly concerning zooplankton dynamics and acoustic studies.

A previous acoustic survey was conducted in the Halmahera Sea, primarily focusing on seabed mapping and seamount exploration. An expedition in the Halmahera Sea in 2021 utilized a multibeam survey, surface-towed magnetic survey, and seafloor sampling to confirm the presence of underwater hazards [18]. Another study was conducted in Buli Bay, East Halmahera's coastal area, using a conventional sampling method to analyze the composition and abundance of zooplankton [19].

In this research, three acoustic acquisition lanes consisted of one lane on semi-enclosed water and two on open water. Oceanographic data were obtained from three separate stations, one of which was also used to collect biological samples. The raw data of ADCP was recorded as echo intensity, with a maximum depth of 240 m. This research used primary data from the Jala Citra I "Aurora" survey expedition commemorating the 100th World Hydrography Day. The survey was a collaboration between the Hydro-Oceanographic Center of the Indonesian Navy and researchers from government research agencies, universities, and other private parties using the KRI Spica-934 ship.

Environmental data acquisition

Oceanographic data represented by temperature and salinity parameters were collected using MIDAS SVX2 CTD three times during the survey, with varying depth circumstances dependent on pressure at specific depths. This type of CTD combines the sound velocity profile (SVP) components with CTD in general so that the data obtained consists of sound speed, temperature, and salinity. MIDAS SVX2 uses a distributed processing concept; each sensor has a processor that controls sampling and calibrates readings. Each sensor is then controlled by a central processor, meaning all data is sampled at the same time, providing good-quality profile data. The oceanographic data measurements, marked with a square icon on the research location map, were carried out on September 2-8, 2021 (Supplementary Fig. S1). The water column was measured both during the day and at night. When carrying out the measures, the ship was stationary at one spot for 24 h, utilizing the dynamic positioning mode [20]. During the survey, the CTD sampling rate was 8 Hz (recording eight data samples per second) with a continuous 60-s sample interval. Grid obtained from the Halmahera Sea – GeoTIFF bathymetry data downloaded from the open-source GEBCO. The boundaries of the study area were set at coordinates 1°48'13" N – 128°31'58" S and 1°3'10" S – 131°13'41" E. Bathymetry data were downloaded in 2021 to adjust for the period when the ADCP, CTD, and biology sampling data were obtained.

Acoustic data acquisition

The ADCP is an instrument that uses sound waves at a fixed frequency to measure the speed and direction of object movement in the water column based on the Doppler effect [21]. The ability of ADCP to measure reflected acoustic signals from the object can be used to study the migration patterns and temporal evolution of zooplankton biomass.

A 153.6 kHz broadband ADCP was installed on the bottom hull to measure the acoustic backscatter of zooplankton in the Halmahera Sea. The speed of the research vessel was set at 4 knots with a sampling interval of 1 s. The slope of the transducer's emitted beam against the vertical axis is 30°. The instrument was set to record 60 depth cells with bin sizes of 4 m each for a total depth of 240 m, with the first bin at 8.29 m. The threshold range used for visualization in predicting the presence of zooplankton organisms was between -90 dB and -65 dB [7,22-24]. Acoustic data in the first bin was not included in data processing to ensure good data quality near the surface because it is contaminated with sea surface reflections and side-lobe interference [2]. The individual MVBS measurements from each ADCP beam result in a similar pattern, with minor changes in detail and offset. This problem can be avoided by removing data with a percent-good value of less than 70% [25].

Data analysis

The raw acoustic data derived from the ADCP are represented as echo intensity (EI) values. These EI values, which are linear data, serve as received signal strength indicators (RSSI) and are quantified using a unit count that ranges from 0 to 255 [26]. The EI data were transformed into MVBS in decibels (dB) for subsequent analysis, rendering the value absolute and proportionate to the zooplankton biomass [27]. The MVBS calculation was processed using the Deines and

Mullison equation with the correction of sound attenuation and transmission losses [28-29]. Raw acoustics data was extracted using the WinADCP software. The acoustic backscattering strength and vertical distribution of zooplankton were visualized in the echogram using MATLAB 2016a (Mathwork, Inc.). The computation of the MVBS value adheres to the sonar equations method, with the configuration of data acquisition and data processing delineated in Supplementary Table S1.

DVM pattern was quantitatively measured based on the averaged MVBS around the detection zooplankton area [30]. The dimensions of the SSL in the DVM movement can fluctuate based on the distribution of acoustic backscattering. For instance, the range at midnight might differ from that at twilight due to the movement of zooplankton. The daily pattern was established by calculating the average within the identified SSL range over time.

Biology sample collection

Biological samples, marked with a black dot icon on the research location map, were taken in the ADCP track at around 20:00 to 21:00 local time (UTC +9) with coordinate 0.9936 N – 129.423 E (Supplementary Fig. S1). Biological samples were obtained by towing a twin plankton net (bongo net), with a mesh size of Ø 300 μm, that was lowered to a depth of 150 m. Samples were preserved with 1% Lugol solution. The biology samples were brought to the Marine Microbe and Plankton Laboratory, National Research and Innovation Agency (BRIN) for further investigation.

The analysis of species identification, taxa number, and abundance was performed using the Sedgewick-Rafter counting cell. Zooplankton abundance was calculated as ind m^{-3}. Zooplankton was identified morphologically and observed using stereomicroscopes equipped with a camera. The standard length (L) was measured for 30 specimens and was then converted into wet weight (W) based on the empirical W-L relationship proposed by Satapoomin (1999) for *Oncaea* spp. [31] and by Kiørboe and Sabatini (1994) for *Oithona* spp. [32]. The results of the towing plankton net were analyzed further to determine the diversity index using the Shannon-Wiener equation, the uniformity index using the evenness equation, and the dominance index using the Simpson equation [33].

RESULTS

Environment condition

The vertical profile of oceanographic data is characterized by three distinct depth layers: the surface mixed layer, the thermocline layer (temperature profile), the halocline layer (salinity profile), and the deep-sea layer (Supplementary Fig. S2). As depth increases, the primary high-temperature parameter in the surface layer decreases. The distribution pattern of salinity is inversely and vertically related to the temperature. The salinity profile exhibited homogeneity across the vertical profiles of each station, with variations in salinity concentration dependent on depth strata.

Empirical formulas were employed to calculate the temperature, salinity, depth, and pH, yielding the characteristics of sound velocity and the absorption coefficient of the propagating acoustic wave signal in the water column (Supplementary Fig. S3) [34,35]. The vertical profile of sound velocity mirrors the temperature profile, with values decreasing with increasing depth. However, the vertical profile of the absorption coefficient in the surface layer significantly decreased to 96 m, after which it stabilized at 240 m.

The study encompassed research sites in semi-enclosed and open water areas (Supplementary Fig. S4). The bathymetric contour in the semi-enclosed water site, known as the Sagawin Strait, features a narrow bottom flanked by cliffs with a maximum depth of 450 m. The bathymetric contour steepens, reaching a maximum depth of 800 m as one moves away from the strait, with significant elevation drops over short distances. The bathymetric contours of the open-water site, located in the northern Halmahera Sea, deepen towards the Pacific Ocean shelf. The open-water bathymetric contour exhibits a more gradual slope than the semi-enclosed water and is characterized by elevation changes over extended distances. High elevation areas are indicated by light blue to white colors, signifying features such as sandbars or shoal morphology.

Temporal distribution of zooplankton

The echogram representation of the results from the ADCP instrument's sounding in a water column cross-section delineates the varying properties of an object's

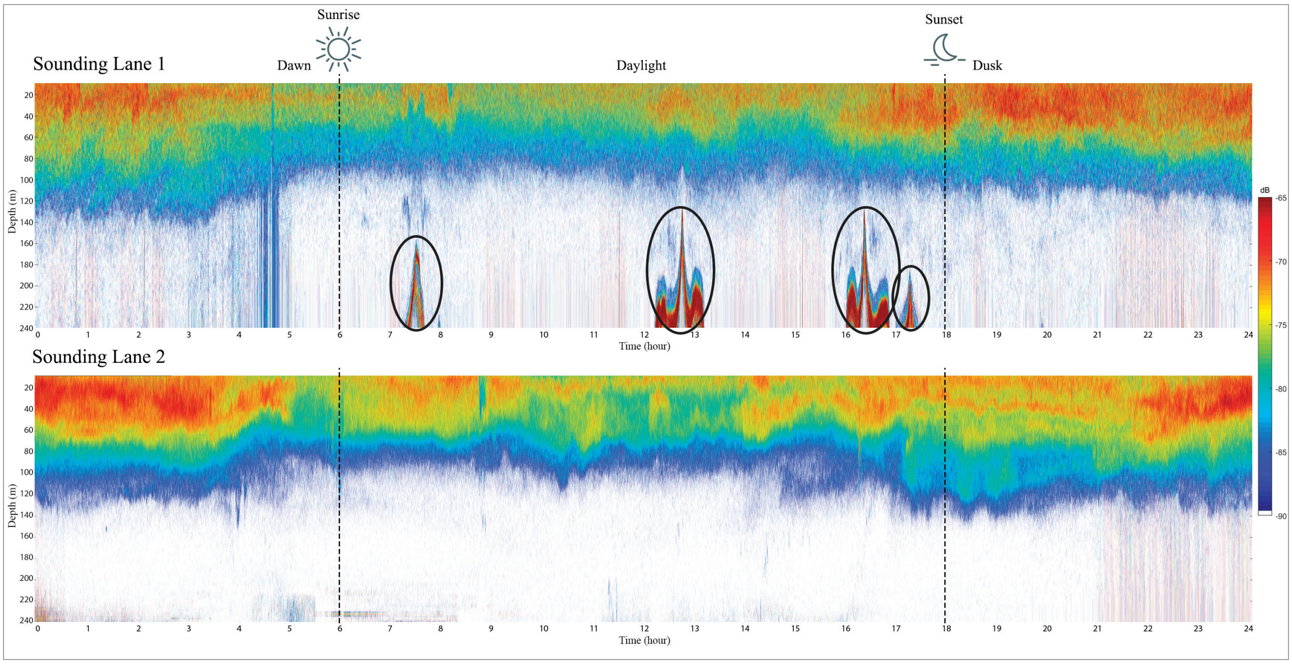

Fig 1. Full-day ADCP sounding results in open-water sounding lanes 1 and 2. There is a transformation in the strength of the acoustic backscatter signal and the thickness of the scattering layer, which indicates the occurrence of the zooplankton migration phenomena. During the day, the MVBS value is lower, accompanied by a thin SSL thickness. At night, the MVBS value is higher, accompanied by a large SSL thickness.

backscattered reflection. Strong signals are shown in red, while weaker signals are in blue. By measuring the MVBS value, the echogram was utilized to show the presence and density of zooplankton in the water column. A strong acoustic backscatter signal indicates a high zooplankton density, whereas a weak signal indicates a low zooplankton density [36,37].

Both echograms (Fig. 1) depict the schooling of zooplankton aggregations in the water column, displayed in hues ranging from light blue and yellow to orange [38]. An SSL is formed by a horizontally linked group of zooplankton patches on a spatial scale. An SSL is a condition in which a contrasting MVBS value is found and has a higher pixel value than background pixels outside of the SSL, which have a lower value [7]. Due to the limited range of acoustic signals, the movement of zooplankton from the deep layer to the surface and vice versa is less discernible. This study's observations focused on the signal strength and thickness of the zooplankton SSL [39]. Repeated objects with inverted patterns are observed at the maximum sounding depth in the full-day echogram of acoustic transect 1. The circled objects exhibit inverted forms because the acoustic transects operated in parallel through the exact study location. The object has a maximum acoustic backscatter value of -65 dB, hypothesized to be caused by fish schooling. The strong acoustic backscatter was identified at night at 8 to 60 m depth, averaging -68 dB. During the day, a weaker acoustic backscatter value was observed within this depth range, averaging -75 dB.

The echogram depicted a low zooplankton density in the surface layer, represented by yellow and light blue colors between 07.00 and 12.00 local time. The thickness of the SSL tends to be low as the maximum depth of the acoustic signal backscattering layer is confined to 100 m. The graph of daytime MVBS data (Fig. 2) similarly showed the low density of zooplankton patches. MVBS exhibited a wide range in the surface layer, with low values ranging from -81.08 dB to -66.43 dB. These MVBS magnitude circumstances persist until the maximum depth, where low MVBS values dominate the value distribution.

In contrast to daytime conditions, between 19.00 and 24.00 local time, there was a high zooplankton density in the surface layer shown by the echogram, which is dominated by orange and yellow colors. As the

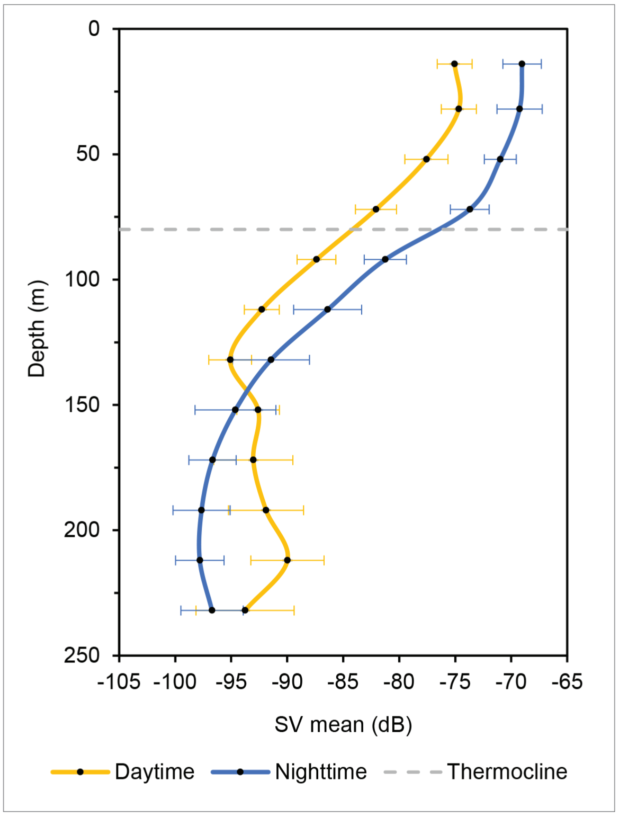

Fig 2. The scatter plot showcases the vertical distribution of the mean scattering volume (SV) during both daytime and nighttime at different depths. The spread of points at each depth represents the standard deviation, indicating the variability of SV.

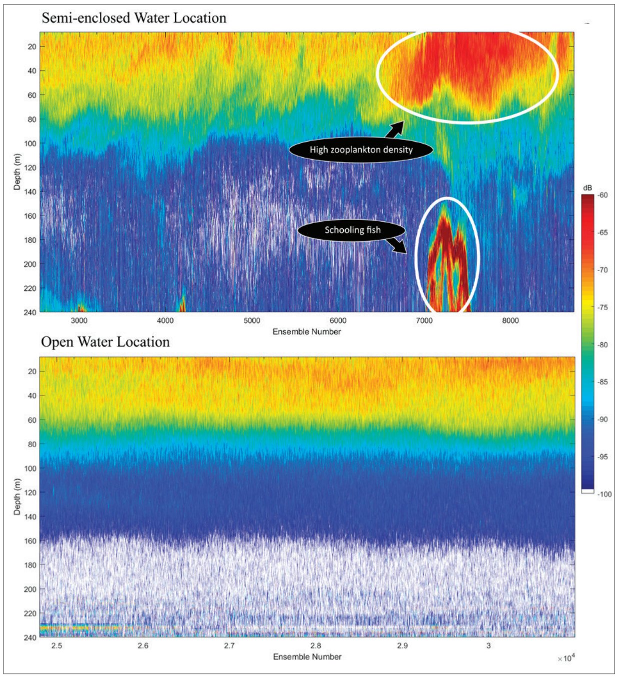

Fig. 3. Acoustic backscatter echogram of zooplankton in semi-enclosed water and open-water locations. Based on the differences in the characteristics of the two waters, the semi-enclosed water has a higher zooplankton density than the open-water location.

maximum depth of the acoustic signal backscattering layer was limited to 140 m, the thickness of the SSL tends to be high. The graph of nighttime MVBS data (Fig. 2) likewise showed a high density of zooplankton patches. MVBS exhibited a narrow range in the surface layer, with high values ranging from -75.76 dB to -63.88 dB. These MVBS magnitude circumstances persist until the maximum depth, where high MVBS values dominate the value distribution. Fig. 2 also shows the vertical distribution of the mean SV during both daytime and nighttime at different depths. The mean SV is higher at night compared to the daytime from the surface until 140 m of depth. On the other hand, during the day, the mean SV value tends to be greater than at night at depths ranging from 150 m up to the maximum depth that can be detected by the ADCP, which is 240 m. This demonstrates that the mean SV varies with depth and is related to the time of day, indicating the occurrence of daily vertical migration of zooplankton.

Spatial distribution of zooplankton

Fig. 3. illustrates that the zooplankton SSL pattern on the open-water echogram was more constant and stable than on the semi-enclosed water echogram. The open-water echogram can only reach a depth of 100 m based on the zooplankton SSL maximum depth range. However, the semi-enclosed water echogram can reach up to 120 m. The high MVBS value is distributed more evenly along the near-surface water column in the open-water echogram than in the semi-enclosed water echogram. Predation phenomena in the water column food chain were captured on the semi-enclosed water echogram and can be detected between 7000-8000 ensembles at 150-240 m.

The density levels of zooplankton schooling varied in the sounding lane (Fig. 4). The strength and weakness of the zooplankton acoustic backscatter signal are influenced by the level of schooling density, the zooplankton species, as well as the physical characteristics of zooplankton (size, shape, orientation, constituent materials, density, and surface roughness)

Computation of all ADCP sounding lanes in both open and semi-enclosed water sites illustrates the mean outcome per 36 m, or equivalently, ten depth layers (Fig. 5). As the depth increased, the MVBS value

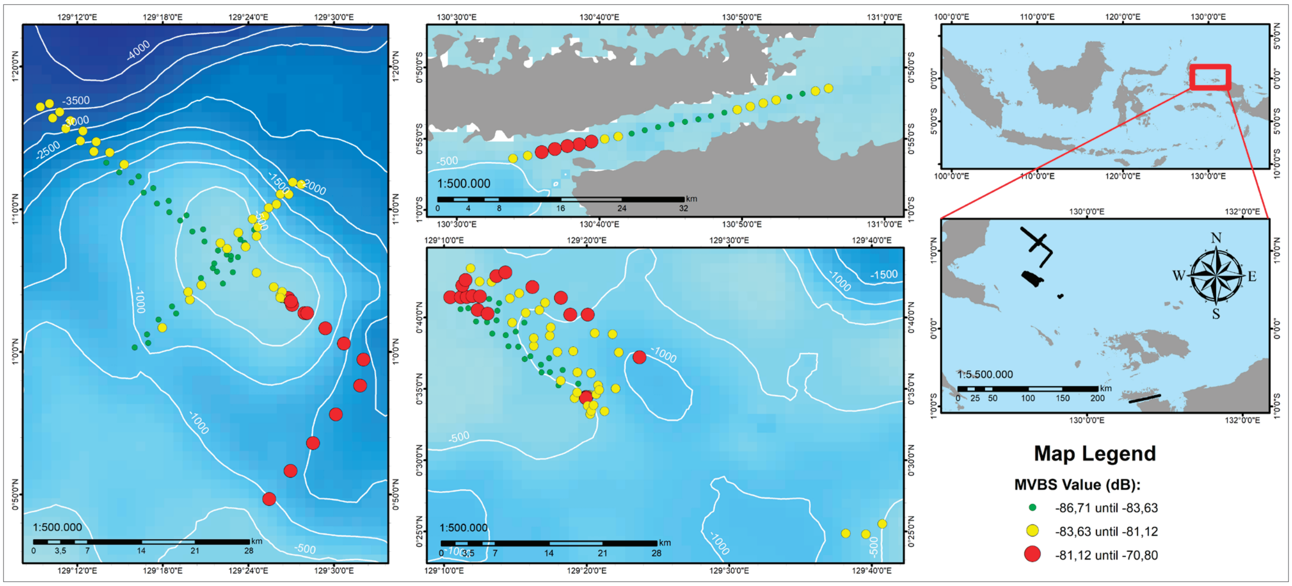

Fig. 4 Spatial visualization of the horizontal zooplankton MVBS average in the Halmahera Sea, Indonesia.

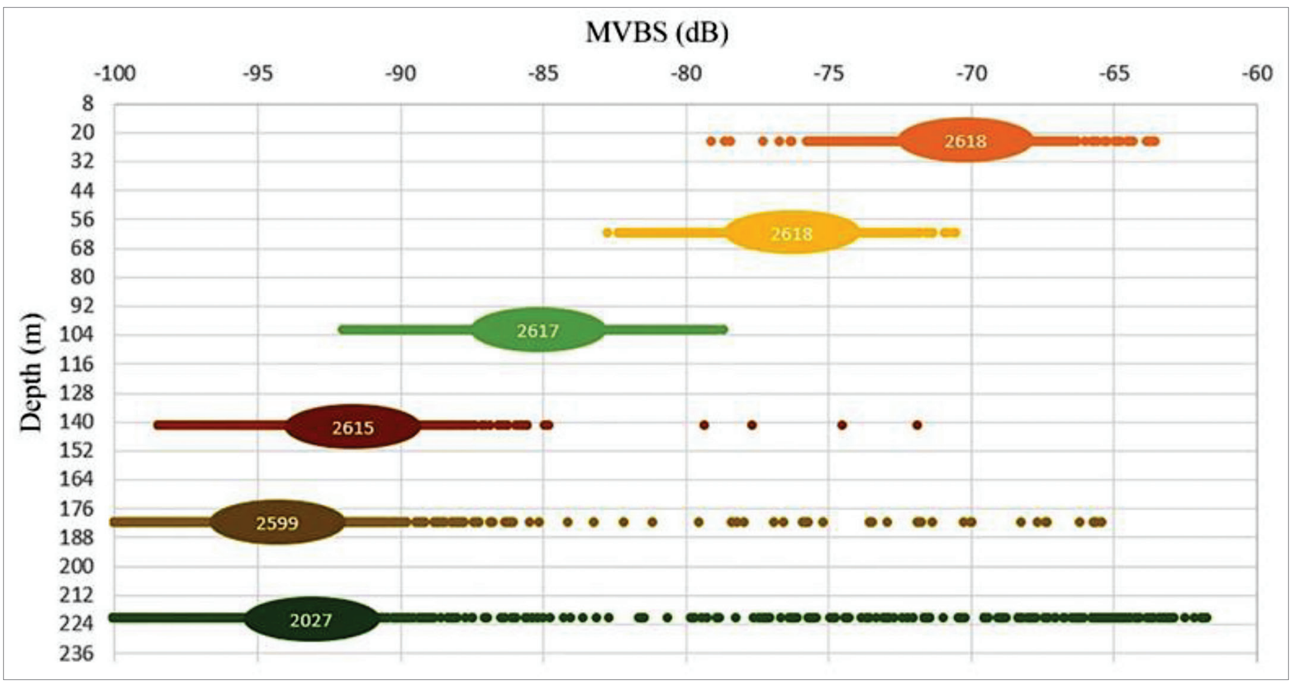

Fig. 5 Spatial visualization of the vertical zooplankton MVBS average at the three sounding lanes in the Halmahera Sea, Indonesia. The dominant MVBS value is found most often near the surface layer with a value of 2618. The number of MVBS values that are found in the layers of depth decreases with increasing depth, ending with a minimum value of 2027.

exhibited a decreasing trend. Near the surface, MVBS values tended to cluster, falling within a narrow range; however, in the middle layer, the range of MVBS values expanded. Upon reaching the instrument's maximum sounding depth, the MVBS values were uniformly distributed across the threshold range.

Analysis of zooplankton characteristics

Biological sampling results revealed the presence of 16 zooplankton taxa at the research site, with a total abundance of 274 individuals per cubic meter (ind m^{-3}) (Table 1). The sampling process also filtered larvae of

Table 1. The result of biological sampling in the Halmahera Sea, Indonesia

NO.	ORGANISM	ABUNDANCE (ind m^{-3})	Composition (%)	*L-W Relationship*
1.	Calanoida (order)			
	Acartia (genus)	23.86	8.71	
	Pontella (genus)	20.39	7.44	
	Euchaeta (genus)	9.32	3.40	
	Clausocalanus (genus)	9.97	3.64	
2.	Cyclopoida (order)			
	Oncaea (genus)	88.32	32.23	$2.51 \times 10^{-8} L^{2.9}$ [31]
	Corycaeus (genus)	16.14	5.89	
	Oithona (genus)	36.21	13.22	$9.47 \times 10^{-7} L^{2.16}$ [32]
	Farranula (genus)	5.45	1.99	
3.	Copelata (order)			
	Oikopleura (genus)	0.40	0.15	
4.	Aphragmophora (order)			
	Sagitta (genus)	1.01	0.37	
5.	Harpacticoida (order)			
	Microsetella (genus)	7.00	2.55	
6.	Polychaeta (class)	0.12	0.04	
7.	Gastropoda larvae (class)	55.00	20.07	
8.	Brittle stars larvae (class)	0.18	0.12	
9.	Fish larvae	0.33	0.07	
10.	Siphonophorae (order)	0.00	0.11	
11.	*Evadne* (genus)	0.30	3.41	
The number of Taxa		16		
Abundance Total (ind m^{-3})		274.00		
Diversity Index		1.99		
Uniformity Index		0.72		
Dominance Index		0.18		
Sampling Coordinate		0.9936, 129.423		

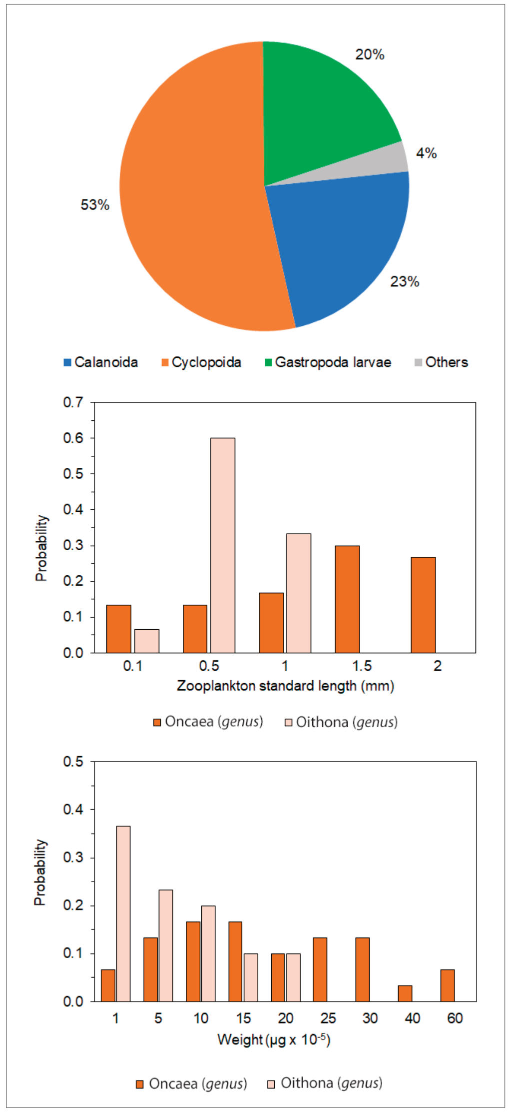

Fig. 6 The composition, histogram of standard length (L), and (c) wet weight (W) distribution derived from the most abundant zooplankton species, i.e., *Oncaea* spp. and *Oithona* spp.

various marine organisms, including fish, gastropods, and brittle stars (ophiopluteus). The genera *Oncaea* spp. and *Oithona* spp., belonging to Cyclopoida, dominated with an abundance of 88.32 ind m^{-3} and 36.21 m^{-3}, respectively, while Polychaeta exhibited the lowest abundance at 0.12 ind m^{-3}. These findings underscore the diverse zooplankton community structure within the study area. The study also revealed high species diversity within the zooplankton community based on the diversity index (1.99), suggesting the presence of different species in the ecosystem that contributed to its overall biodiversity. The distribution of individuals among the different species was even but not entirely uniform based on the measured uniformity index, indicating a balanced ecosystem where no single species significantly outnumbers the others. Lastly, the dominance index was measured at 0.18, which is relatively low and suggests that no single species dominated the community, further supporting the notion of a balanced and diverse ecosystem.

This study comprehensively analyzes the most abundant zooplankton species, namely *Oncaea* spp. and *Oithona* spp. The composition and distribution of these species were examined using a histogram of standard length (L), and the wet weight (W) of zooplankton was derived using the W-L conversion (Fig. 6). It was observed that larger individuals, ranging from 1.5-2 mm, were predominantly *Oncaea* spp., while *Oithona* spp. were primarily found to be 0.5 mm in length. The weight analysis revealed that *Oithona* spp. are lighter than *Oncaea* spp., which exhibits a diverse weight range.

DISCUSSION

An organism's existence cannot be separated from the environmental conditions that allow it to survive. Optimal conditions for zooplankton development are typically within a temperature range of 20-30°C and a salinity range exceeding 20 practical salinity units (PSU) [19]. These parameters, critical for the metabolic activities of marine biota, are frequently investigated to understand their distribution and movement. The temperature differential is attributed to significant sunlight penetration in the surface layer [40]. The continuous renewal of seawater shapes the salinity distribution pattern due to the mass circulation pattern of water at one of the ITF's transport gates, which facilitates exchange between the Pacific and the Indian Ocean [41]. These factors influence the presence of marine organisms and the pattern of sound wave propagation in the water column during hydroacoustic sounding [37]. The parameters of sound velocity and the absorption coefficient at each depth layer impact the noise level and transmission losses [42].

The Halmahera Sea, characterized by diverse bathymetric contours and bordered by several large and small islands, exhibits variable morphology in its bathymetry. It is filled with thin but deep sediments and numerous forms that describe a transition zone, with depths ranging from 0-2000 m [20]. The Sagawin Strait, a 5-km body of water, separates Batanta Island from Salawati Island [43].

The MVBS value of the zooplankton target varies from -86.50 dB to -68 dB at depths of approximately 5-200 m [23,37]. The diel vertical migration scattering layer of zooplankton is represented with a maximum MVBS fluctuating between depths of 40 m and 120 m [44-46]. Schooling of mesopelagic fish at depths of 200-240 m can be correlated to fish larvae [47], decapods such as shrimp [48], jellyfish [26], or zooplankton species such as krill [48,49].

Both full-day echograms revealed a transformation in the strength of the acoustic signal backscattering and the thickness of the SSL based on the characteristics of the zooplankton temporal distribution observed through the SSL pattern. This indicates the phenomenon of zooplankton DVM before sunrise and after sunset. DVM, a phenomenon driven by zooplankton movement over 24 h [8], results in variations in the biomass, abundance, and composition of zooplankton species in the surface layer between day and night [46].

The acoustic backscatter signal decreased during the full-day echogram sounding in lanes 1 and 2, from 03:35-04:46 and 03:31-05:11 local time. This decrease was evidenced by a color change from orange to a mixture of yellow and light blue and a weakening of the scattering layer. The maximum depth of the signal layer with a strong acoustic backscattering intensity was reduced from 140 m to 100 m. These observations suggest a movement of aggregation towards deeper waters, with the characteristics of the zooplankton patch changing from high to low density at the surface layer.

Between 15:27-18:30 and 14:41-21:25 local time, the acoustic backscattering signal strengthened, as indicated by the color change from yellow to orange and a thickening of the scattering layer. The maximum depth of the signal layer with high acoustic backscattering power increased from 100 m to 140 m, pointing to the migration of aggregation towards the surface, with the characteristics of the zooplankton patch changing from low to high density.

The duration of zooplankton migration before sunrise is significantly shorter than that of zooplankton movement after sunset. The DVM patterns in both echograms are characterized as nocturnal migration. The most common migration pattern for zooplankton organisms is nocturnal migration, where organisms swim upward into the near-surface (euphotic) layer after sunset and downward towards the deep ocean layer at sunrise. The two full-day echograms indicated slightly different timings and durations of zooplankton movement. However, the migratory pattern of the two remains similar, occurring when light penetration is high at sunrise and low at sunset. Endogenous and exogenous factors influence the characteristics and patterns of the DVM phenomenon, for example, the size of the zooplankton, light intensity, food availability, and predation [8,50]. The underlying factor is thought to be a strategy for evading predators. By minimizing the risk of visually focused predators during the day, zooplankton might feed in the epipelagic zone at night [51].

The density of zooplankton was higher in the semi-enclosed water site than in the open-water site. The semi-enclosed water location, with river estuaries and mangrove forests along the Sagawin Strait, supports water fertility [37,52]. Sufficient light intensity and abundant nutrients can enhance phytoplankton's primary productivity, contributing to the high density of zooplankton [53].

The object captured in the semi-enclosed water echogram is presumed to be a mesopelagic schooling fish hunting for zooplankton in the near-surface layer. Several sounding results from previous research have indicated that numerous mesopelagic fish approach the surface from morning to noon. In the Halmahera Sea, these mesopelagic fish species might include *Lampanyctus turneri*, *Argyropelecus affinis*, and *Vinciguerria lucetia* [22,54].

The high density of zooplankton in the semi-enclosed water location is associated with the influx of nitrogen from terrestrial sources, which correlates with the abundance of phytoplankton, a primary factor contributing to the large population of zooplankton [53]. Conversely, the characteristics of zooplankton density in the open-water site are contingent upon the timing of the ADCP sounding, which is linked to the DVM phenomena of zooplankton. The density of zooplankton was low during ADCP sounding from morning to noon, as indicated by the predominance of the green circle. However, during ADCP sounding from afternoon to evening, the density of zooplankton was high, as evidenced by the predominance of the yellow and red circles. The MVBS values in the semi-enclosed waters sounding lane and the two open-water sounding lanes yield vertical scatter graphs that reveal high zooplankton density near the surface layer, which gradually diminishes as depth increases. This is also evident in the echogram display, which shows orange dominating the top layer and yellow and light blue dominating the layer below. While zooplankton is distributed evenly across the ocean, the signal strength of the significant acoustic backscatter in the upper layer suggests a high density of zooplankton near the surface [55].

Each acoustic target possesses a unique impedance and characteristics that can alter an object's acoustic backscattering value. Therefore, understanding the characteristics of an object used as an acoustic target is crucial. Endogenous factors, such as the characteristics of zooplankton species, influence the characteristics and distribution patterns of zooplankton in the water column, in addition to external influences [50].

According to previous research employing traditional field sampling techniques in the Halmahera Sea, the primary zooplankton organisms discovered, in terms of their abundance and dispersion in the water column, were Copepods [19]. Other zooplankton families identified in the study's observation sites included Polychaeta, Bivalvia, Gastropoda larvae, Brittle stars larvae (class), Siphonophorae, Aphragmophora, and Harpacticoida (order). Zooplankton from the genera *Evadne*, *Creseis*, and *Oikopleura* were also found in the research [19]. It should be noted that most of these zooplankton species were at least 1 cm in length. ADCP instruments can detect zooplankton organisms with a minimum length of 1 cm at a frequency of 153.6 kHz [14,22,54]. The zooplankton community in the study area exhibits a high level of species diversity, as indicated by the diversity index. This diversity is reflected in the ADCP acoustic data, which shows strong backscatter values [56]. Importantly, these strong acoustic backscatter values are not dominated by a single species of zooplankton [7]. Instead, they represent the collective acoustic signatures of a diverse zooplankton species, suggesting a rich and varied zooplankton community where no single species dominates. The zooplankton community's high diversity contributes to the ecosystem's robustness and resilience, allowing it to maintain its function and structure under varying environmental conditions. This high level of biodiversity is a key characteristic of a healthy and balanced marine ecosystem.

The presence of zooplankton in the research area is not influenced by temperature and salinity changes due to the minimal temperature variability in these regions [12]. The DVM of zooplankton is primarily driven by sunlight due to its location in the tropical area, like previous research in the northern Gulf of Mexico shelf, which can occur at dawn and dusk [57]. In this region, the DVM mechanism of zooplankton is a strategy to evade predators. One limitation of this study is the absence of additional acoustic instruments operating at different frequencies, which could have facilitated the identification of zooplankton based on frequency differentiation techniques [22]. It is important to note that this study did not carry out an acoustic estimation of zooplankton abundance due to the use of a single frequency of ADCP. Furthermore, the diversity of zooplankton types found in the study area adds a layer of complexity to the estimation of zooplankton abundance, as it could potentially lead to overestimation. For future research, comparing the ADCP results with data from other scientific echosounders would be beneficial. This approach could enhance the accuracy of zooplankton detection and provide a more precise understanding of their behavior.

CONCLUSIONS

The MVBS values converted from ADCP raw data ranged from -86.50 dB to -68 dB. The DVM phenomenon was observed in temporal measurements of zooplankton aggregations that moved downward before sunrise and upward after sunset. Biological sampling revealed the presence of 16 taxa, dominated by *Oncaea* spp. and *Oithona* spp. from the order of Cyclopoida, that participate in this migratory activity. Spatial observations indicate that zooplankton density is significantly higher in semi-enclosed waters than in open-water locations. This could be attributed to the higher nutrient availability and lower predation risk in semi-enclosed waters. The characteristics of zooplankton acoustic backscattering in the open-water site correlate with the ADCP sounding time, which aligns with the DVM phenomena. The MVBS of zooplankton is more pronounced in the surface layer and decreases with increasing depth in the vertical distribution. This pattern is consistent with the known behavior of zooplankton, which often migrate to deeper waters during the day to avoid predators and return to the surface at night to feed. The study provides valuable insights into the behavior and distribution of zooplankton, contributing to our understanding of marine ecosystems and the factors that influence their structure and function. The key findings underscore the pivotal role of zooplankton as the first consumer in food webs and their significant contribution to fisheries catches in the Halmahera Sea. These findings enhance our understanding of zooplankton dynamics and their implications for ecosystem functioning, particularly in association with the Indonesian throughflow current. This research also underscores the need for a comprehensive, long-term approach to marine conservation in the Halmahera Sea, emphasizing the importance of scientific research in informing effective ecosystem management and conservation strategies.

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Author contributions: GRM: conceptualization, data handling and analysis, visualization, writing, editing; SP: supervision, conceptualization, review; AD: data sampling and acquisition, supervision, conceptualization, editing, review; SS: data sampling and acquisition, review; IJ: review; DA: data sampling & acquisition, review; and DSM: data sampling and acquisition. All authors have read and agreed to the published version of the manuscript. GRM and AD are the main contributors, SP, SS, IJ, DA, DSM are member contributors.

Conflict of interest disclosure: The authors declare no conflict of interest.

Data availability: Data underlying the reported findings have been provided as a raw dataset, which is available here: https://www.serbiosoc.org.rs/NewUploads/Uploads/Maharani%20et%20al_Raw.Dataset.xlsx All data sets are courtesy of Pushidrosal. Access to each data set is available by request to pusdalops@pushidrosal.id.

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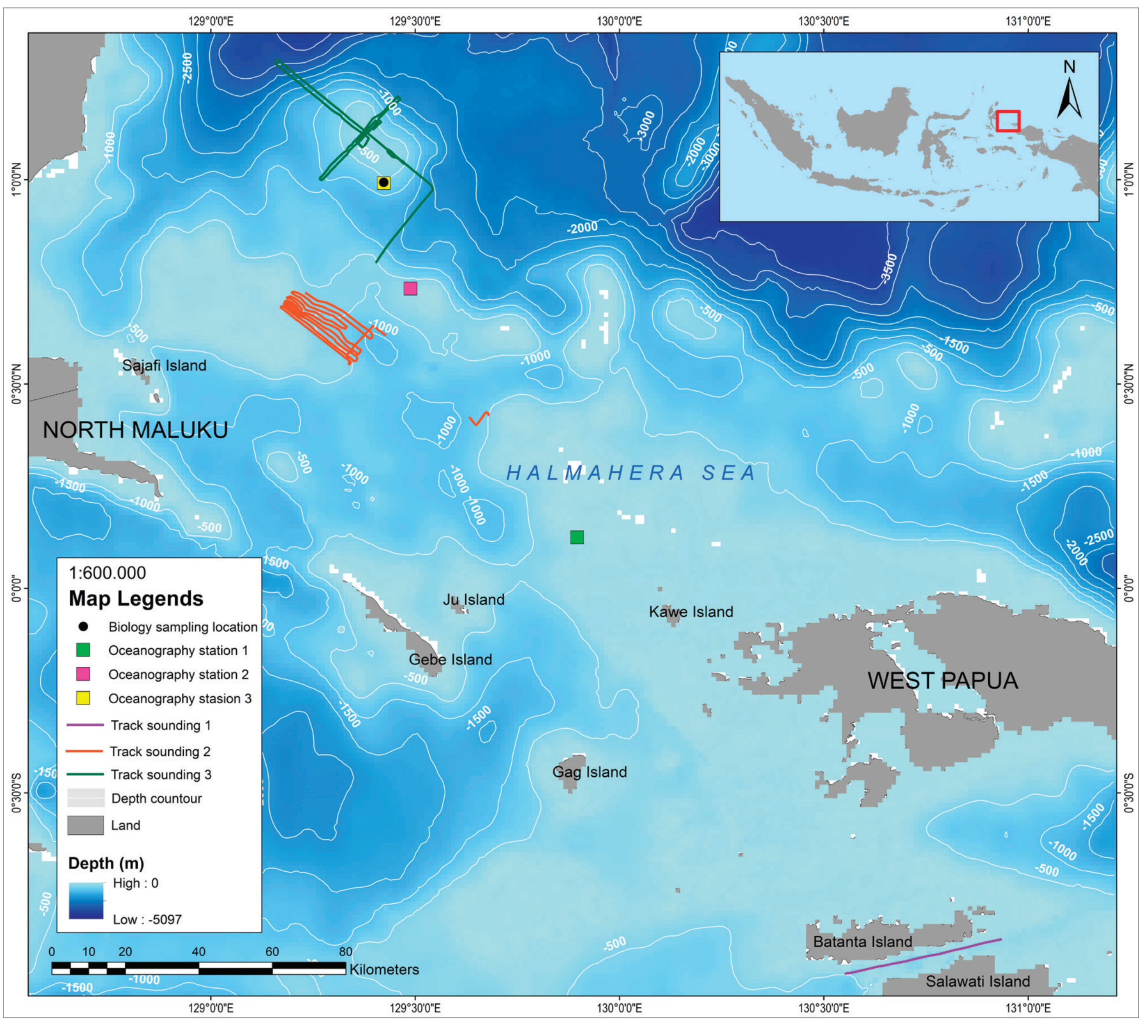
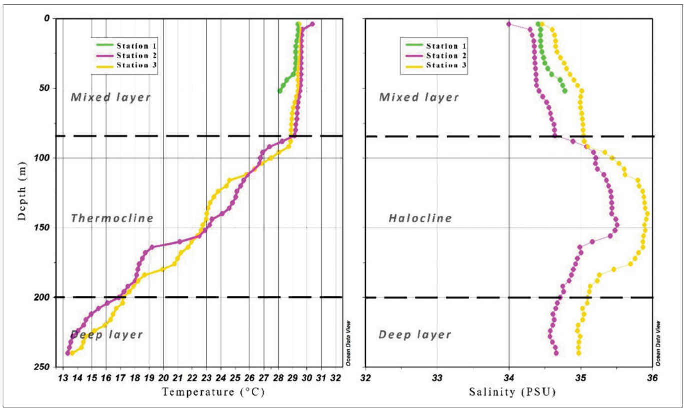
SUPPLEMENTARY MATERIAL

Supplementary Table S1. ADCP instrument parameter configuration for data processing

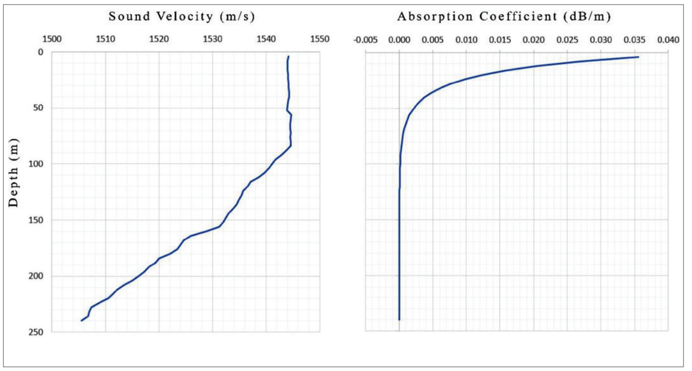
Parameters	Values	Source
K_2, noise factor	4.3	[58]
K_S, system frequency constant	4.17×10^5	[58-59]
T_X, transducer temperature (°C)	20	On-site measurement
B, blanking zone (m)	4	Instrument calibration
D, bin size (m)	4	User-defined
n, the number of bins	60	User-defined
θ, beam angle (°)	30	Instrument calibration
C_1, sound velocity calibration (m s^{-1})	1475	[2,8]
R_0, Rayleigh distance (m)	1.88	[29, 60]
H, distance of instrument to the surface (m)	3.5	Instrument calibration
L, pulse wavelength (m)	4	Instrument calibration
K_1, output power calibration (Watt)	3.3	[58]
C, system constant (dB)	-153.3	[29, 60]
L_{DBM}, logarithmic pulse (dB)	0.60206	Instrument calibration
P_{DBM}, logarithmic power (dB)	21	[29, 60]



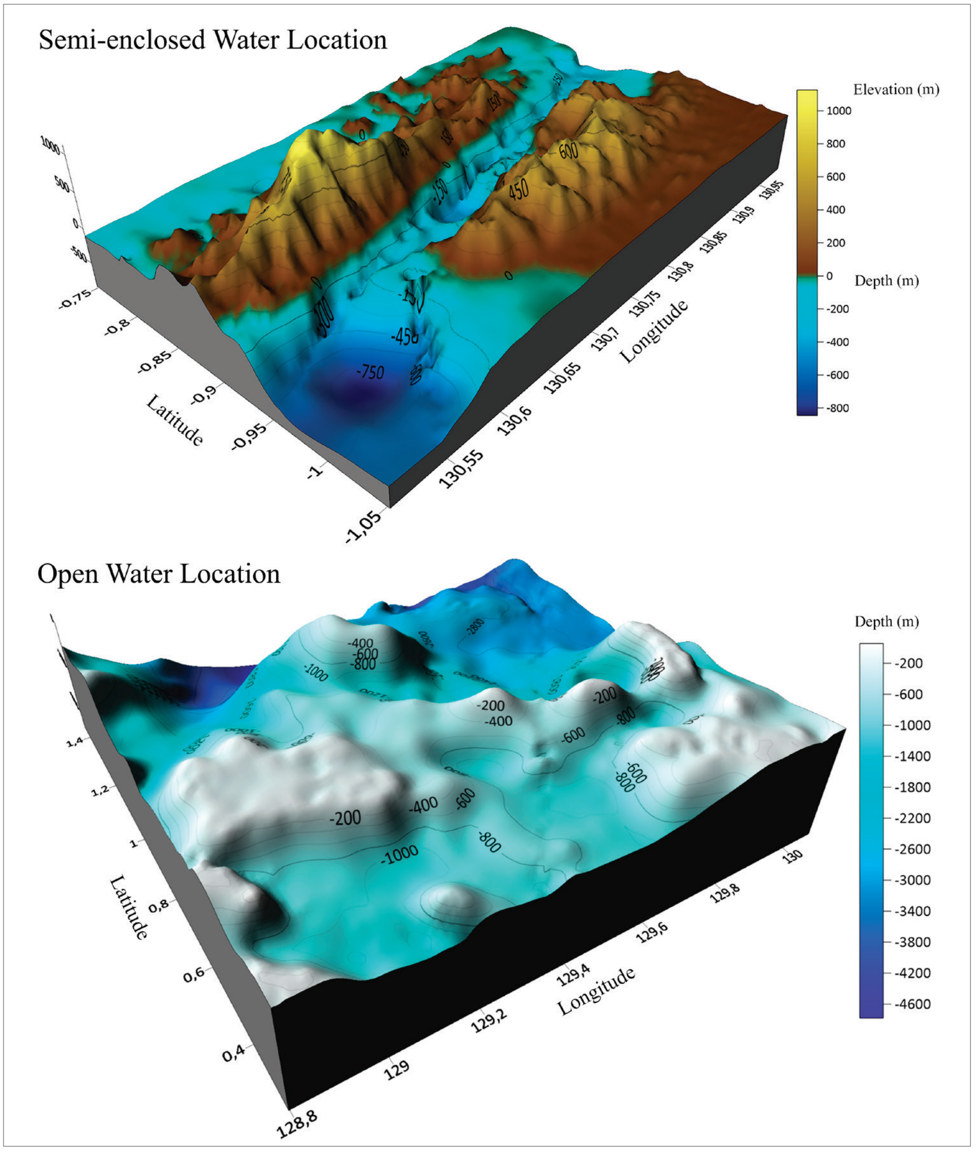
Supplementary Fig. S1. Locations of research in the Halmahera Sea, Indonesia.



Supplementary Fig. S2. Vertical profiles of temperature and salinity at three CTD measurement stations in the Halmahera Sea, Indonesia.



Supplementary Fig. S3. Vertical profile of sound velocity and absorption coefficient in the Halmahera Sea, Indonesia.



Supplementary Fig. S4. Visualization of seabed characteristics in the semi-enclosed water and open-water location.