

Biomass, vertical distribution and community structure of mesozooplankton in the Sulu Sea and its adjacent waters

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Abstract

The Sulu Sea is a semi-isolated basin in which of the mesopelagic layer and below ($>ca. 600\text{ m}$) are homogeneous with high temperature ($ca. 10^\circ\text{C}$). The biomass, abundance, vertical distribution, and community structure of mesozooplankton in the upper 1000 m in the Sulu Sea and its adjacent Celebes and South China seas were investigated in February 2000 and November–December 2002. The total mesozooplankton biomass in the 0–1000 m water column was higher in the Sulu (19.6 g m^{-2}) and the Celebes seas (19.7 g m^{-2}) than in the South China Sea (15.0 g m^{-2}). The total biomass in the mesopelagic layer (400–1000 m) was fairly constant in these seas, ranging $4.48\text{--}4.99\text{ g m}^{-2}$, and did not show significant variation. Likewise, there was no significant deviation from an exponential decrease in biomass and abundance with depth. The vertical distribution patterns of higher taxonomic groups also did not show specific patterns in the Sulu Sea compared to the other areas. Cluster analysis based on the Bray–Curtis dissimilarity indices applied to higher mesozooplankton taxa indicates several distinct communities between different depth layers, rather than between stations or sea areas. These results suggest that warm and homogeneous mesopelagic water in the Sulu Sea does not drastically influence the total mesozooplankton standing stocks, vertical distribution patterns, and the community structure at the higher taxonomic levels compared with those in its adjacent seas. However, the composition of copepods from the 2000 cruise indicates marked differences in the composition of calanoid families between the Sulu and Celebes seas, with dominance of Eucalanidae, Metridinidae, and Lucicutiidae in the layer of lower dissolved oxygen in the Sulu Sea, suggesting difference in community structure at lower taxonomic levels (genera and/or species) between these areas.

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1. Introduction

Semi-isolated marine habitats often exhibit characteristic faunal compositions reflecting to their

characteristic hydrographic features. For example, in the Red Sea and the Mediterranean Sea, which are partially landlocked and have unique warm waters in the meso- and bathypelagic layers, the degree of decrease in zooplankton biomass with depth is greater than those in more typical open-ocean conditions, and true bathypelagic species are

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often replaced by submerging mesopelagic species (Weikert, 1982; Scotto di Carlo et al., 1984; Weikert and Koppelman, 1993, 1996). These observations imply that the process controlling the vertical distributions of zooplankton in these specialized environments differ from those in more-typical open oceans (Wishner, 1980; Weikert and Trinkaus, 1990).

The Sulu Sea is a marginal sea in the western tropical Pacific, rimmed by islands and sills mostly shallower than 200 m (Exon et al., 1981). The sea has a homogeneous and warm (ca. 10 °C) water from the mesopelagic zone to the bottom at ca. 5000 m (Frische and Quadfasel, 1990). Salinity and dissolved oxygen are also almost constant in the mesopelagic and deeper layers. While the near-surface circulation is governed mainly by the seasonally reversing monsoon winds, the deep circulation is considered to be forced by the inflow of intermediate water from the South China Sea through a single 420-m deep channel in the Mindoro Strait, which supplies the only source of deep waters to the Sulu Sea basin (Wyrski, 1961; Frische and Quadfasel, 1990). While the Sulu Sea exhibits characteristic hydrographic features, the adjacent South China Sea and the Celebes Sea have more typical open-ocean conditions (Wyrski, 1961). Together, these areas provide an excellent setting to examine responses of pelagic communities and the mechanisms of organic matter transport and recycling to different water-column structures.

There have been several biological studies on the Sulu Sea, but most of them focused on taxonomy and/or ecology of benthic foraminifers (e.g., Rathburn et al., 1996, and references therein) and descriptions of new species, such as copepods (Suarez-Morales, 2000; Ohtsuka et al., 2005), mysids (Murano and Bravo, 1998), and decapods (Kensley, 1996). In contrast to the accumulated information on benthos, the knowledge on the pelagic communities in the Sulu Sea is limited to chlorophyll distribution and primary production at selected sites and seasons (San Diego-McGlone et al., 1999; Jones, 2002; Wang et al., 2006). Few studies have been made of zooplankton in the Sulu Sea, the Celebes Sea or the southern, deep areas of the South China Sea; even basic data on biomass, abundance and vertical distributions of zooplankton in the oceanic area of these seas are lacking, except for studies on microzooplankton in the Celebes Sea (Taniguchi, 1977), larval fishes (Campos and Estremadura, 2003), chaetognaths (Johnson et al.,

2006), and selected groups of copepods (Zalkina, 1977; Kuriyama, 2005; Matsuura, 2005).

The present study examines the vertical patterns of biomass, abundance and community structure of mesozooplankton in the upper 1000 m of the Sulu Sea and the adjacent Celebes and South China seas on the basis of finely stratified day–night samplings. The results are compared with other tropical–subtropical oceans to examine the effects of the specific hydrographic conditions of the Sulu Sea on mesozooplankton community structure and distribution.

2. Materials and methods

2.1. Sampling and sample processing

Investigations were made at five stations (Fig. 1, Table 1) during cruises of the R/V *Hakuho Maru* in February 2000 and November–December 2002: two stations of the same location in the Sulu Sea (stns 4 and 26), two stations in the Celebes Sea (stns 2 and 23), and one station in the South China Sea (stn 16). At each station, plankton samples were collected using a MOCNESS-1 (Multiple Opening-Closing Net and Environmental Sensing System; mouth

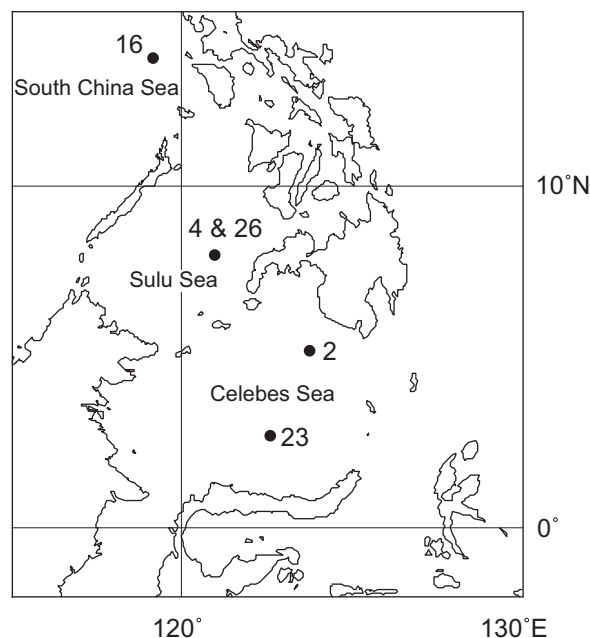


Fig. 1. Location of sampling stations during the KH-00-1 (stns 23 and 26) and KH-02-4 (stn 2, 4 and 16) cruises of R/V *Hakuho Maru*.

Table 1

Sampling records of MOCNESS in the Celebes (CS), Sulu (SS) and South China seas (SCS)

Cruise	Area	Stn	Date	Time	Sampling depth (m)	Total water depth (m)	Geographic position	
							Latitude (N)	Longitude (E)
KH-00-1	CS	23	19 Feb. 2000	D	200–1000	5388	2° 25.8'	122° 28.2'
			19 Feb. 2000	D	0–200	5398	2° 25.1'	122° 28.1'
			19 Feb. 2000	N	200–1000	5397	2° 28.3'	122° 28.8'
			19 Feb. 2000	N	0–200	5376	2° 31.7'	122° 30.0'
	SS	26	24 Feb. 2000	N	200–1000	4890	7° 33.7'	121° 29.1'
			25 Feb. 2000	N	0–200	4887	7° 33.3'	121° 28.2'
			25 Feb. 2000	D	200–1000	4889	7° 38.0'	121° 29.4'
			25 Feb. 2000	D	0–200	4878	7° 33.5'	121° 25.9'
KH-02-4	CS	2	15 Nov. 2002	D	0–200	5149	5° 08.0'	124° 07.9'
			15 Nov. 2002	D	200–1000	5144	5° 10.5'	124° 07.1'
			15 Nov. 2002	N	200–1000	5134	5° 09.9'	124° 07.1'
			15 Nov. 2002	N	0–200	5134	5° 07.9'	124° 08.1'
	SS	4	20 Nov. 2002	D	0–200	4479	7° 26.3'	121° 13.2'
			20 Nov. 2002	D	200–1000	4474	7° 28.2'	121° 14.7'
			20 Nov. 2002	N	200–1000	4491	7° 27.2'	121° 14.8'
			20 Nov. 2002	N	0–200	4478	7° 27.6'	121° 15.7'
	SCS	16	9 Dec. 2002	N	200–1000	5005	13° 33.6'	119° 29.4'
			10 Dec. 2002	N	0–200	3855	13° 39.4'	119° 32.3'
			10 Dec. 2002	D	0–200	5004	13° 31.6'	119° 30.0'
			10 Dec. 2002	D	200–1000	4789	13° 34.2'	119° 33.5'

Time: D, day; N, night.

area, 1 m²; mesh size, 0.33 mm; Wiebe et al., 1976) from 16 discrete depth layers in the upper 1000 m both day and night. The sequence of depth intervals was every 25 m from 0 to 200 m, and every 100 m from 200 to 1000 m. The samples were immediately fixed and preserved in 4% formaldehyde/seawater solution buffered with sodium tetraborate.

Zooplankton were sorted from the original samples into the following 22 higher taxonomic groups: Foraminifera, Nemertinea, Nematoda, Siphonophora, Cnidaria except for Siphonophora (indicated as “other Cnidaria” in this study), Ctenophora, Chaetognatha, Polychaeta, Copepoda, Amphipoda, Ostracoda, Cladocera, Mysidacea, Luciferidae, Euphausiacea, Decapoda, crustacean larvae, Pteropoda, Heteropoda, Cephalopoda, Thaliacea, and Appendicularia. The numbers of animals in each taxon were counted, and wet weight was measured on an electronic balance (Chyo Electronic Balance JP-300WP), after removing the interstitial water on through filter paper. Animals larger than 20 mm in longest dimension, except chaetognath, and the exoskeletons of crustaceans (mostly copepods) that lacked recognizable inner tissues, which assumed to be dead carcasses or molts, were

excluded from the analysis. Each sample was examined in its entirety except for those from some shallow-layer tows containing very large numbers of animals; in such cases an aliquot ($\frac{1}{16}$ or larger) was examined. The biomass and abundance values were expressed in numbers per m³ of water filtered. The daytime sample in the 600–700 m layer at stn 2 was lost, hence the interpolated values from the upper and lower layers were applied for this depth interval in the calculation of the water-column biomass and abundance. For a more detailed taxonomic examination of the pattern of vertical distribution, the copepods from the 2000 cruise (stns 26 and 23) were further identified to order and calanoid copepods were enumerated at the family level.

At each station, water temperature and salinity were measured with a CTD-system (SBE 9 plus with SBE 32 Carousel water sampler, SEA-BIRD Electronics, INC.) and simultaneous water samples for the measurement of dissolved oxygen and chlorophyll pigments were collected. Dissolved oxygen was measured with an automatic Winkler titrating machine (Hirama ART-3), while the concentration of chlorophyll *a* was measured by the fluorometric method (Strickland and Parsons, 1972) using an

on-board fluorometer (Nishimura and Ohwada, 2003; Nishida and Gamo, 2004).

2.2. Data analysis

To examine the difference in biomass between locations, a Kruskal–Wallis test was applied to the biomass values in and below the mesopelagic layers (400 m) of the three study areas. To test whether the degree of decrease in biomass and abundance with depth differs between the study areas, a linear regression analysis was applied to the vertical profiles of \log_{10} -transformed biomass and abundance data from the daytime series; then an ANCOVA (analysis of covariance) was performed to test for the differences in slope (i.e. the degree of exponential decrease in biomass or abundance with depth) and y -intercepts of the regression lines.

Differences in mesozooplankton community structure with time of day, station and depths down the water column were explored using the Bray–Curtis dissimilarity index on the basis of \log_{10} -transformed abundance data of higher taxonomic groups (see Section 2.1). Clustering by the UPGMA method (Unweighted Pair Group Method with Arithmetic Mean; [Sneath and Snokal, 1973](#)) was performed to classify the samples on the basis of the between-sample dissimilarity matrix.

3. Results

3.1. Hydrography

A steep thermocline was common to three areas, but temperatures decreased more gradually below 200 m in the Sulu Sea than in the Celebes and South

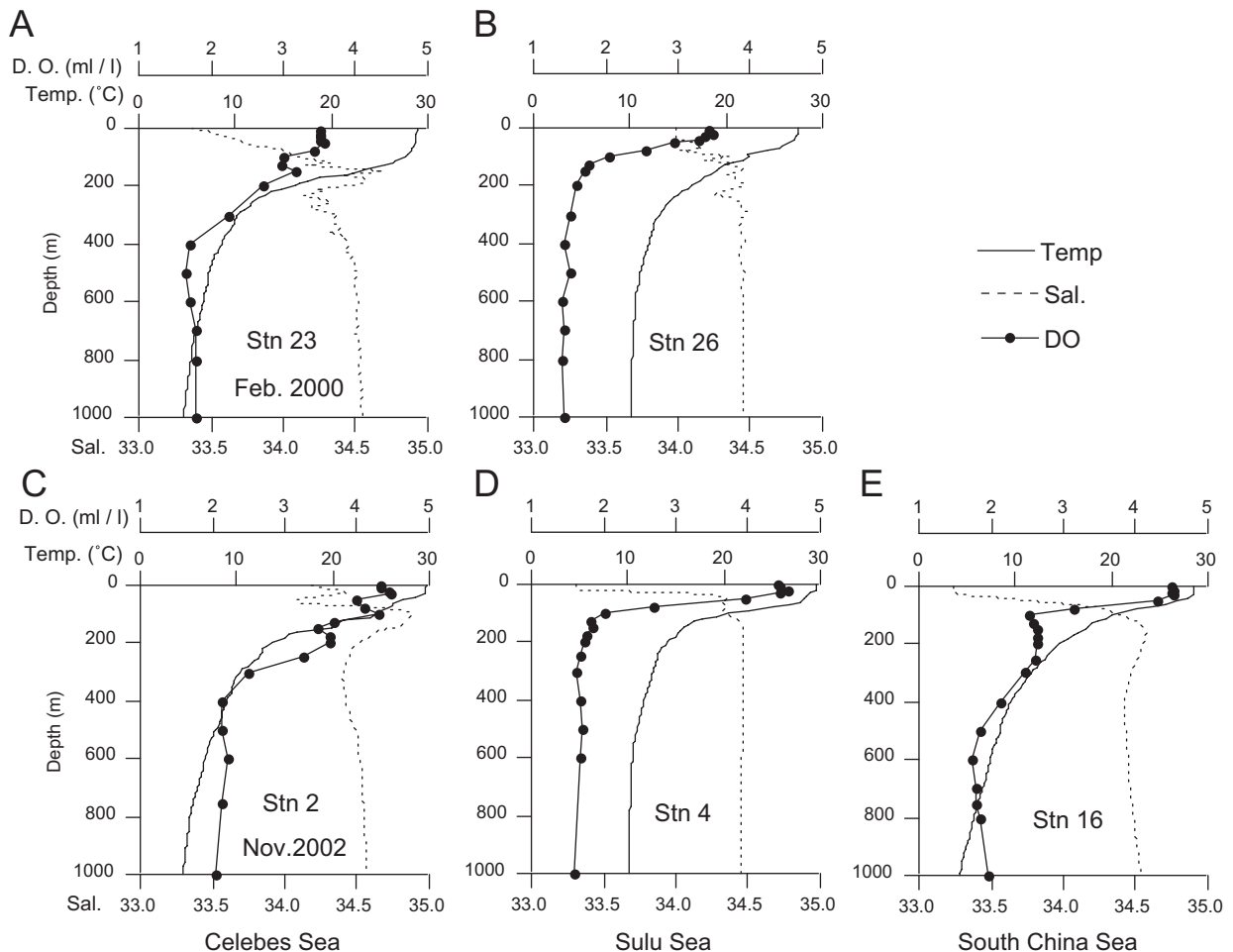


Fig. 2. Vertical profiles of water temperature, salinity and dissolved oxygen at stations in the Celebes (A, C), Sulu (B, D), and South China seas (E).

China seas (Fig. 2). Below 600 m, the temperature became fairly constant at ca. 10 °C in the Sulu Sea, while it continued to decrease to ca. 4 °C at 1000 m in the Celebes and South China seas. The salinity fluctuated considerably near surface according to the season and stations. From 400 to 1000 m in the Sulu Sea, salinity was nearly constant at ca. 34.4–34.5 (Fig. 2B, D), while in the Celebes and South China seas there was a subsurface maximum in 100–200 m and a minimum in 200–400 m (Fig. 2A, C, E). Dissolved oxygen content in the Sulu Sea sharply decreased from near-surface ($>3 \text{ ml l}^{-1}$) to ca. 100 m (ca. 2.0 ml l^{-1}), followed by a more gradual decrease to ca. 1.5 ml l^{-1} at 1000 m (Fig. 2B, D). In the Celebes Sea, there were oxyclines at 200–400 m and the waters in the upper 300–400 m were more oxygenated ($>2 \text{ ml l}^{-1}$) than in the Sulu Sea, followed by relatively constant values ($2.0\text{--}2.5 \text{ ml l}^{-1}$) in 400–1000 m (Fig. 2A, C). The dissolved oxygen in the South China Sea showed a similar pattern, but with a marked near-surface oxycline, a moderate minimum (ca. 1.5 ml l^{-1}) at ca. 600 m, and gradual increase to ca. 2.0 ml l^{-1} at 1000 m (Fig. 2E). In summary, the lower oxygen waters in the subsurface layers (ca. 150–300 m) of the Sulu Sea showed a clear contrast with those in the Celebes and South China seas.

The concentration of chlorophyll *a* at all stations showed a subsurface maximum in the 50–75 m layer, except for that in the Sulu Sea in February 2000 (stn 26), with a near-surface maximum of $0.50 \mu\text{g l}^{-1}$ (Fig. 3). The maximum values were higher in the Sulu Sea (0.50 and $0.68 \mu\text{g l}^{-1}$) than in the Celebes

Sea (0.27 and $0.45 \mu\text{g l}^{-1}$) and South China Sea ($0.31 \mu\text{g l}^{-1}$). The depth-integrated values in the 0–200 m in all three seas ranged from 25.9 to 33.1 mg m^{-2} (see Fig. 3), being greatest at stn 2 in the Celebes Sea and least in the South China Sea.

3.2. Total biomass and abundance

In the Celebes Sea, the 0–1000 m biomass ranged from 12.4 to 28.5 g m^{-2} , and was higher in November 2002 (stn 2) than in February 2000 (stn 23) (Table 2). In the Sulu Sea, similar values were obtained in the two periods, ranging from 17.0 to 22.4 g m^{-2} . The average overall values were quite similar between the Celebes Sea (19.7 g m^{-2}) and the Sulu Sea (19.6 g m^{-2}), but a lower value (15.0 g m^{-2}) was obtained in the South China Sea. While the biomass values in the 0–1000 m water column showed some degree of regional and seasonal differences, the biomass below 400 m was fairly constant in all the seas, ranging between 4.48 and 4.99 g m^{-2} on average. There were no significant differences in biomass values in the 400–1000 m range between the areas (Kruskal–Wallis test, $p > 0.1$). The percentages of 400–1000 m biomass to the total biomass were lower in the Sulu Sea (24.1%) and the Celebes Sea (25.4%) than in the South China Sea (29.9%), indicating that the biomass in the epipelagic layers varied and affected the fluctuation in the 0–1000 m biomass (see Table 3 also).

The total mesozooplankton biomass decreased with depth by three orders of magnitude in all the

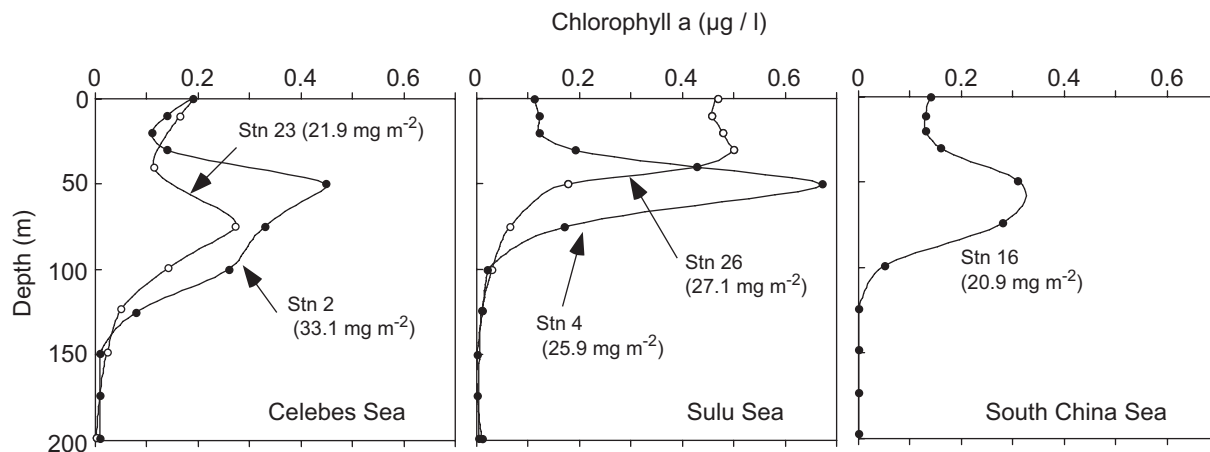


Fig. 3. Vertical profiles of chlorophyll *a* concentration in the Celebes, Sulu, and South China seas. Depth-integrated chlorophyll values (0–200 m) are indicated in parentheses.

Table 2

Mesozooplankton biomass (g m^{-2} WW) in the 0–1000 m water column, the biomass below 400 m, and the percentage of them to the total biomass in the Celebes, Sulu, and South China seas

Sea area	Day	Night	Average	% of 400–1000 m
Celebes (stn 23)	12.5 (3.73)	12.4 (4.39)	12.5 (4.06)	
Celebes (stn 2)	28.5 (8.62)	25.0 (3.19)	26.8 (5.91)	
Celebes (overall)			19.7 (4.99)	25.4
Sulu (stn 26)	21.1 (4.22)	17.9 (2.32)	19.5 (3.27)	
Sulu (stn 4)	17.0 (5.00)	22.4 (7.34)	19.7 (6.17)	
Sulu (overall)			19.6 (4.72)	24.1
S. China (stn 16)	14.4 (4.63)	15.5 (4.32)	15.0 (4.48)	29.9

Biomass below 400 m are shown in parenthesis. Biomass in the 400–1000 m showed no areal differences (Kruskal–Wallis test, $p > 0.1$, see Section 3.2).

Table 3

Total biomass of mesozooplankton in wet weight in the Celebes, Sulu, and South China seas

Station	Celebes Sea				Sulu Sea				S. China Sea	
	Feb. 2000		Nov. 2002		Feb. 2000		Nov. 2002		Nov. 2002	
	23D	23N	2D	2N	26D	26N	4D	4N	16D	16N
<i>Biomass (g m^{-2})</i>										
0–100 m	4.2	6.2	10.4	11.5	7.4	8.3	8.0	8.9	5.0	8.1
100–200 m	2.9	1.0	5.4	5.0	4.4	4.6	1.3	2.5	1.7	1.8
200–400 m	1.5	0.9	4.1	5.3	5.1	2.7	2.7	3.7	3.1	1.3
400–600 m	2.0	1.0	5.5	1.5	2.5	1.3	4.0	5.6	2.7	2.6
600–800 m	1.5	1.0	2.5	1.4	1.0	0.4	0.5	1.0	1.2	1.1
800–1000 m	0.5	2.4	0.6	0.4	0.8	0.6	0.4	0.8	0.7	0.6
Total (0–1000 m)	12.5	12.4	28.5	25.0	21.1	17.9	17.0	22.4	14.4	15.5
<i>Biomass (% of 0–1000 m)</i>										
0–100 m	34.0	49.4	36.5	46.0	35.0	46.4	47.1	39.7	34.7	52.3
100–200 m	23.6	7.7	18.9	20.0	21.0	25.8	7.9	11.2	11.8	11.6
200–400 m	12.4	7.5	14.4	21.2	24.0	14.9	15.9	16.5	21.5	8.4
400–600 m	16.3	8.2	19.3	6.0	11.9	7.4	23.5	25.0	18.8	16.8
600–800 m	10.0	7.7	8.8	5.6	4.5	2.2	2.9	4.5	8.3	7.1
800–1000 m	3.6	19.4	2.1	1.6	3.6	3.4	2.4	3.6	4.9	3.9

seas, ranging between 1.5 mg m^{-3} (stn 2, night, 900–1000 m) and 169 mg m^{-3} (stn 2, day, 25–50 m) (Fig. 4A). The overall average of 0–100 m biomass was 7.8 g m^{-2} (range, 4.2–11.5), and that of 800–1000 m biomass was 0.8 g m^{-2} (0.4–2.4) (Table 3). The 0–100 m biomass was higher at night than in the daytime at all stations, with average values of 8.6 and 7.0 g m^{-2} , respectively, and a night/day ratio of 1.23.

In February 2000, the vertical profiles showed similar patterns between the Celebes Sea (stn 23) and the Sulu Sea (stn 26), with peak biomasses occurring in the upper 100 m and larger daytime

values than those at night at 400–800 m. There were secondary daytime peaks at 150–250 m and a nighttime increase in the near-surface layers, suggesting diel vertical migrations of constituent animals passing through the thermoclines and oxyclines in the subsurface layers. Below 200 m the biomass decreased steadily in the Sulu Sea but fluctuated considerably in the Celebes Sea, reflecting the patchy occurrence of cnidarians (see next section).

In November 2002 the daytime bimodal peaks and gaps in the subsurface layer were less apparent at all stations than in February 2000. There were

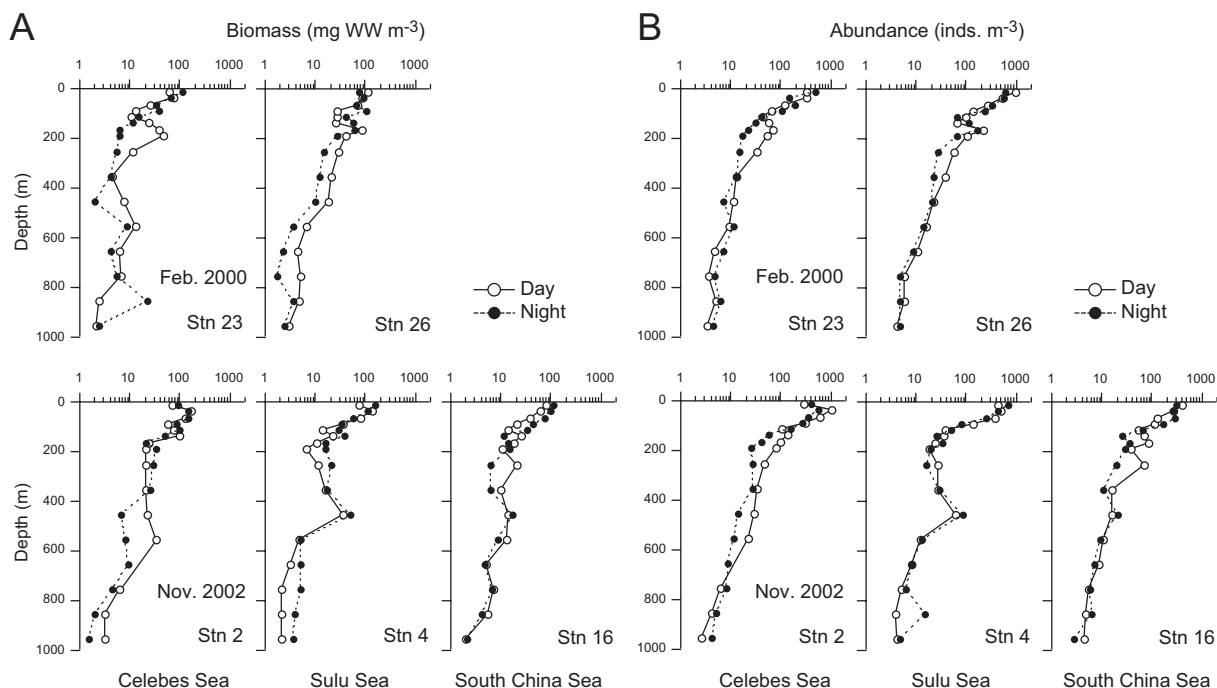


Fig. 4. Vertical distribution of total mesozooplankton biomass (A) and abundance (B) in the Celebes, Sulu, and South China seas.

peaks in the Sulu Sea in the 400–500 m layer both day and night, which were dominated by copepods.

The total mesozooplankton abundance (Fig. 4B) showed similar patterns to the biomass, with much of the zooplankton (68–83% of 0–1000 m abundance) being concentrated in the upper 200 m and showing secondary daytime peaks at the similar depth layers with those of biomasses. The abundance values below 400 m decreased more steadily with increasing depth.

While significant linear regressions between the depth and either \log_{10} -transformed biomass or abundance in the 0–1000 m were obtained at all daytime stations ($p < 0.05$, r^2 values ranged 0.70–0.88 for biomass and 0.72–0.90 for abundance), the vertical profiles of biomass and abundance showed a steeper decrease in the 0–200 m than below at most stations (Fig. 4). Thus, the regression analysis using the data from 200 to 1000 m depths also were performed. A significant correlation was found in all the cases ($p < 0.05$, r^2 values ranged 0.50–0.90 for biomass and 0.70–0.88 for abundance). The ANCOVA indicated there were no significant differences ($p > 0.5$) in the slopes of these depth-biomass or depth-abundance regressions for both 0–1000 and 200–1000 m water column

Table 4

Analysis of covariance for the linear regressions of biomass and abundance versus depth

Depth layers	N	df	F	p	SQ
Biomass					
0–1000 m					
Slope	79	4	0.91	0.46	0.23
y-intercept	79	4	4.78	<0.01	1.20
200–1000 m					
Slope	39	4	0.83	0.51	0.15
y-intercept	39	4	2.57	0.06	0.46
Abundance					
0–1000 m					
Slope	79	4	0.79	0.54	0.23
y-intercept	79	4	3.52	0.01	1.03
200–1000 m					
Slope	39	4	0.88	0.49	0.08
y-intercept	39	4	3.1	0.03	0.28

N, number of samples; df, degree of freedom; SQ, critical sum of squares.

(Table 4). For the y-intercepts, significant differences ($p < 0.05$) were detected in biomass and abundance in both depth ranges, except for the regression for the 200–1000 m biomass.

Table 5

Total biomass (0–1000 m, wet weight) of major mesozooplankton and their relative compositions to the total biomass (%) in the Celebes, Sulu, and South China seas

Station	Celebes Sea				Sulu Sea				S. China Sea		Average
	Feb. 2000		Nov. 2002		Feb. 2000		Nov. 2002		Nov. 2002		
	23D	23N	2D	2N	26D	26N	4D	4N	16D	16N	
Biomass (g m ⁻²)											
Copepoda	4.5	3.7	12.9	9.4	10.8	9.8	9.6	13.3	7.7	7.5	8.9
Chaetognatha	1.7	1.1	2.6	2.5	1.5	1.4	0.9	0.9	1.3	1.4	1.5
Siphonophora	1.4	1.8	3.3	2.7	1.1	1.4	1.1	1.7	1.3	1.3	1.7
Euphausiacea	0.9	0.9	1.0	1.7	1.1	1.3	1.6	1.3	0.8	1.6	1.2
Decapoda	1.3	0.7	0.9	1.2	1.3	0.8	0.6	1.3	0.7	0.6	0.9
Other Cnidaria ^a	0.6	2.7	2.1	3.6	0.9	0.7	1.0	1.3	0.6	0.7	1.4
Pteropoda	0.9	0.2	3.6	2.2	1.8	1.3	0.5	0.8	0.4	0.7	1.2
Ostracoda	0.4	0.9	0.6	0.5	0.9	0.7	1.1	1.1	0.3	0.4	0.7
Thaliacea	0.1	0.1	0.4	0.3	0.1	0.0	0.1	0.1	0.6	0.7	0.2
Others	0.6	0.5	1.1	1.0	1.7	0.5	0.5	0.6	0.7	0.7	0.8
Total	12.5	12.4	28.5	25.0	21.1	17.9	17.0	22.4	14.4	15.5	18.7
Biomass (%)											
Copepoda	36.1	29.5	45.3	37.4	51.0	55.0	56.7	59.5	53.7	48.4	47.8
Chaetognatha	13.7	8.5	9.1	10.1	7.2	7.6	5.5	4.0	9.1	9.0	8.2
Siphonophora	11.4	14.3	11.4	10.7	5.0	7.5	6.5	7.6	8.9	8.5	9.1
Euphausiacea	7.4	7.3	3.5	6.6	5.0	7.2	9.4	6.0	5.7	10.2	6.5
Decapoda	10.3	5.4	3.2	4.9	6.2	4.3	3.5	5.7	4.7	3.6	5.0
Other Cnidaria ^a	5.0	22.0	7.4	14.2	4.2	4.0	6.1	5.8	3.9	4.6	7.6
Pteropoda	7.1	1.3	12.6	8.8	8.5	7.5	2.8	3.4	3.0	4.3	6.6
Ostracoda	2.8	7.3	2.1	1.9	4.4	3.7	6.2	4.9	2.0	2.4	3.6
Thaliacea	1.0	0.6	1.5	1.1	0.4	0.2	0.6	0.5	4.2	4.2	1.3
Others	5.1	3.7	3.8	4.2	8.1	3.0	2.8	2.5	4.8	4.8	4.3

^aCnidaria except for Siphonophora.

3.3. Higher-taxon composition and vertical distribution

Among the major zooplankton taxa (Table 5), copepods dominated at all stations, contributing 47% on average (range, 30–60%) to the total mesozooplankton biomass, while other taxa contributed less than 15%, with the exception of cnidarians (siphonophores excluded) which comprised ca. 22% of the total biomass at stn 23 (Celebes Sea, February 2000). The contribution of copepods was slightly higher in the Sulu Sea (51–60%) than in the Celebes Sea (30–45%) and South China Sea (48–54%), and values larger than 10% were observed at some Celebes Sea stations in the chaetognaths, siphonophores, other cnidarians and pteropods.

Copepods (Fig. 5A) have a similar vertical distribution to the total mesozooplankton biomass, with much of the biomass in the upper 200 m at all

stations. In the Sulu Sea in November 2002 (stn 4) there were marked biomass peaks in the 400–500 m layer. Chaetognaths (Fig. 5B) were also distributed mainly in the upper 200 m in all three areas, with a consistent pattern of diel migration mostly within the upper 100 m. The ostracods (Fig. 5C), siphonophores (Fig. 5D), and pteropods (Fig. 6A) were also distributed mainly in the upper 200 m, but considerable biomass was extended to deeper layers (200–600 m) at some stations. The euphausiids (Fig. 6B) and decapods (Fig. 6C) exhibited marked day–night shift of biomass between the meso- and epipelagic layers, with deeper biomass peaks, both day and night, in the decapods than in the euphausiids. The cnidarians other than siphonophores (Fig. 6D) showed quite different patterns between stations, which may be attributed to the relatively sparse and patchy occurrence of the group, rather than to regional/temporal differences.

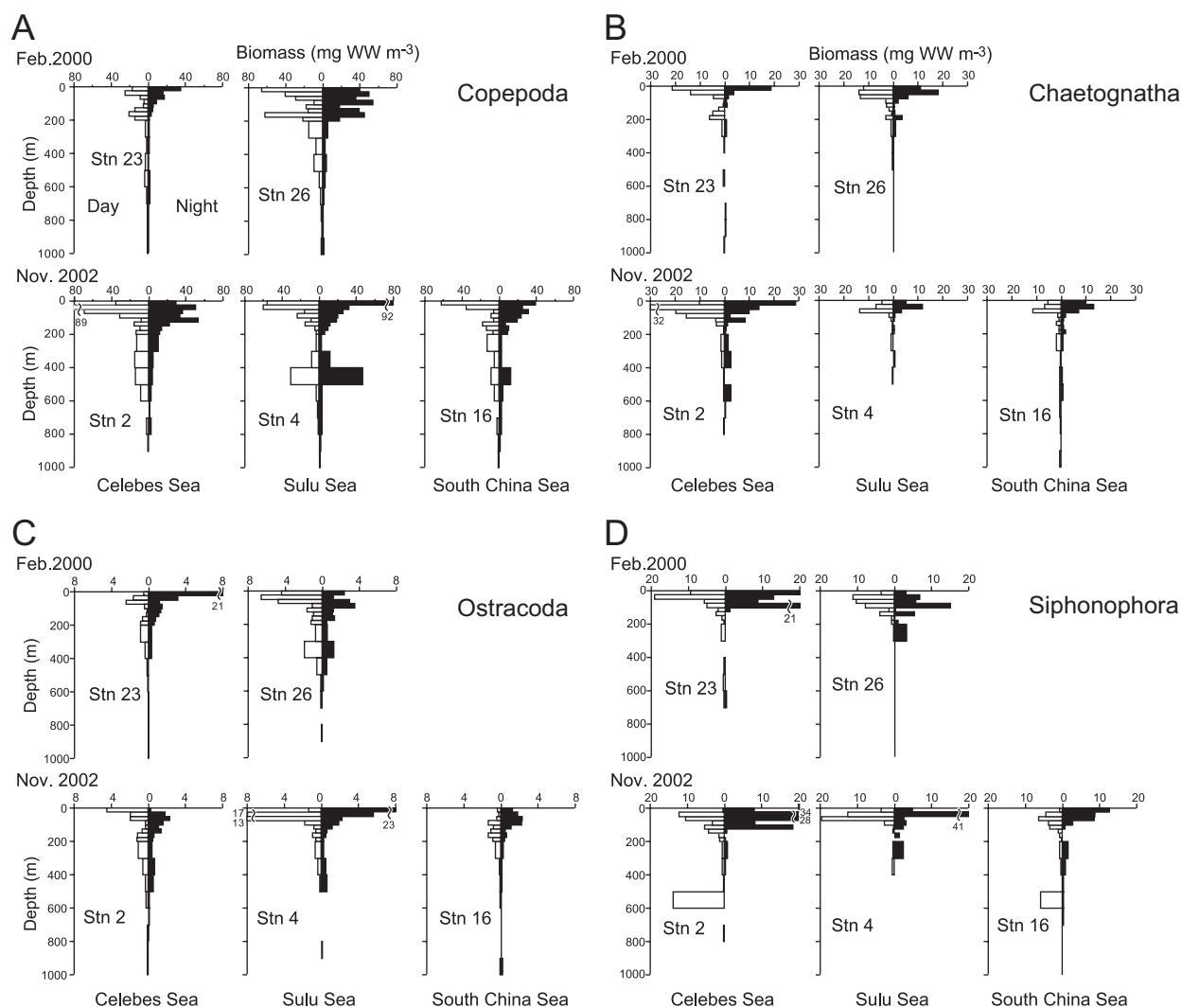


Fig. 5. Day/night vertical distributions of biomass of mesozooplankton in the Celebes, Sulu, and South China seas. A, Copepoda; B, Chaetognatha; C, Ostracoda; D, Siphonophora.

3.4. Community structure

In February 2000, there were four distinct clusters, based on higher taxa, that approximately coincided with the sampling depths of 0–75, 25–300, 125–700, and 700–1000 m at the dissimilarity level of 0.35 (Fig. 7). Each cluster contained samples from both the Sulu and Celebes seas, day and night, and have low dissimilarities (mostly <0.2). In November 2002, three clusters were recognized at the dissimilarity level of 0.4, corresponding to the sampling depths of 0–150, 150–500, and 300–1000 m (Fig. 8). Again, all clusters comprised samples from the Sulu, Celebes, and South China seas and have low dissimilarities (mostly <0.2) within the clusters.

3.5. Composition and vertical distribution patterns of copepods

A comparison of Sulu Sea (stn 26) and Celebes Sea (stn 23) in February 2000 showed that Calanoida predominated throughout the upper 1000 m contributing 43–96% (water column average: 75%) to the total copepod abundance, followed by Poecilostomatoida (20%) and, to a much lesser extent, Cyclopoida (3.4%), Mormonilloida (0.9%), Harpacticoida (0.6%), and Siphonostomatoida (0.2%) (Fig. 9A). Mormonilloida were mostly restricted in the deeper layers (>300 m) and were five times more abundant in the Celebes Sea than in the Sulu Sea.

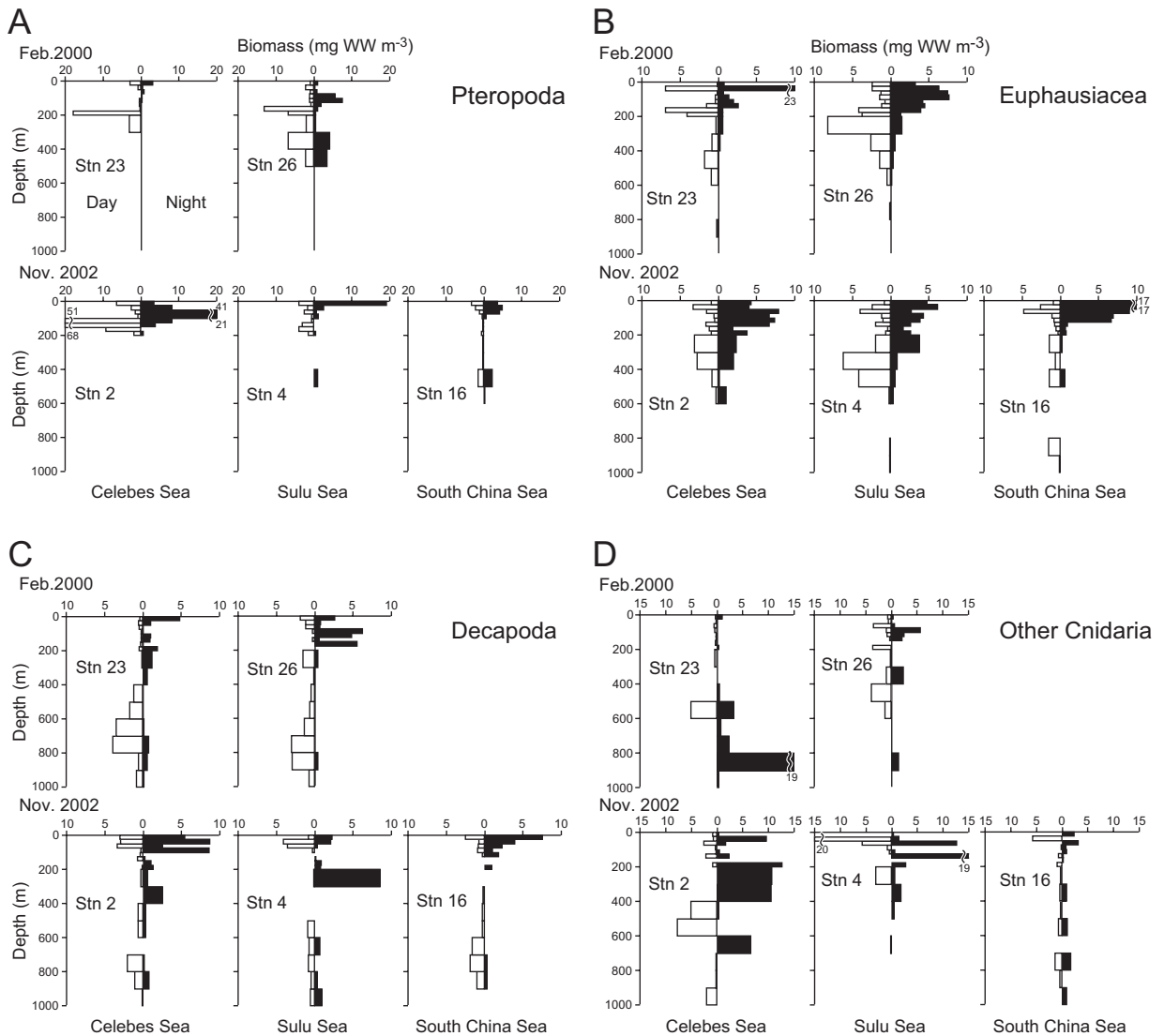


Fig. 6. Day/night vertical distributions of biomass of mesozooplankton in the Celebes, Sulu, and South China seas. A, Pteropoda; B, Euphausiacea; C, Decapoda; D, Cnidaria (other than Siphonophora).

Among the calanoid copepods (Fig. 9B), the families Calanidae, Clausocalanidae, Paracalanidae, and Acartiidae dominated in the upper layers (0–100 m) in both the Sulu and Celebes seas. In the Celebes Sea, Calanidae and Scolecitrichidae were dominant in 100–400 m. In contrast, in the Sulu Sea Eucalanidae and Metridinidae were abundant in 100–200 and 200–400 m, respectively. Below 400 m, in the both seas, Metridinidae, Lucicutiidae, and Scolecitrichidae were major constituents. There were marked differences in the relative integrated abundance of the major families between the Sulu and Celebes seas.

4. Discussion

4.1. Mesozooplankton biomass and chlorophyll *a* concentrations

The present investigations were conducted in February 2000 and November 2002 during the winter northeast monsoon season in southeast Asia, which induces coastal upwelling, mesoscale eddies, and other local features (Wyrski, 1961), which in turn result in complex patterns of biological production in this region (Ning et al., 2004). It is also known, however, that the Sulu Sea is a

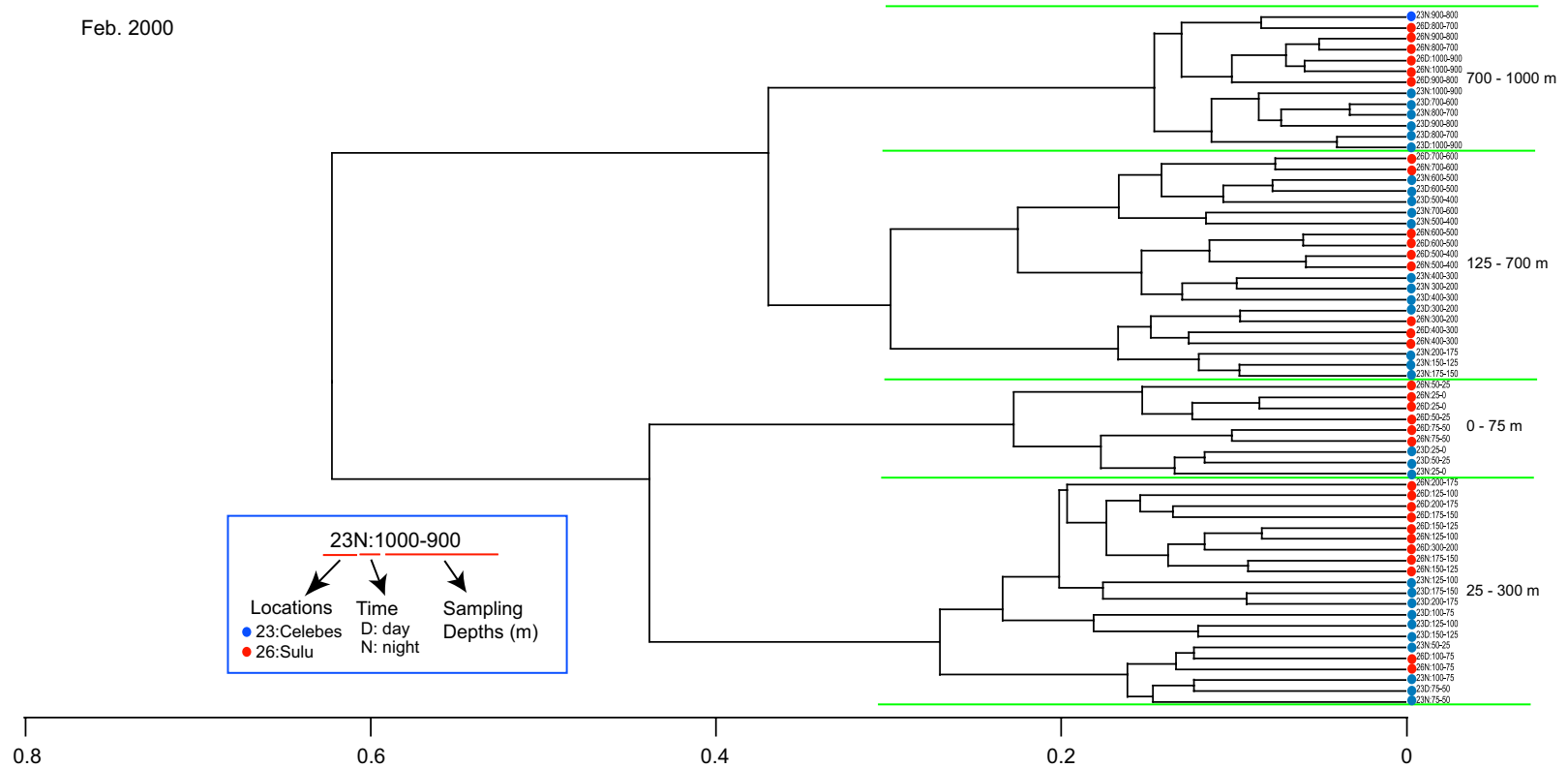


Fig. 7. Mesozooplankton faunal groups in February 2000: a comparison of two seas based on a cluster analysis using \log_{10} -transformed higher taxa abundance data and the Bray–Curtis dissimilarity index. Clustering by UPGMA was applied to the between-sample dissimilarity matrix. Stations were classified into four groups at the 0.35 linkage level. Blue and red dots indicate samples collected in the Celebes and Sulu seas, respectively.

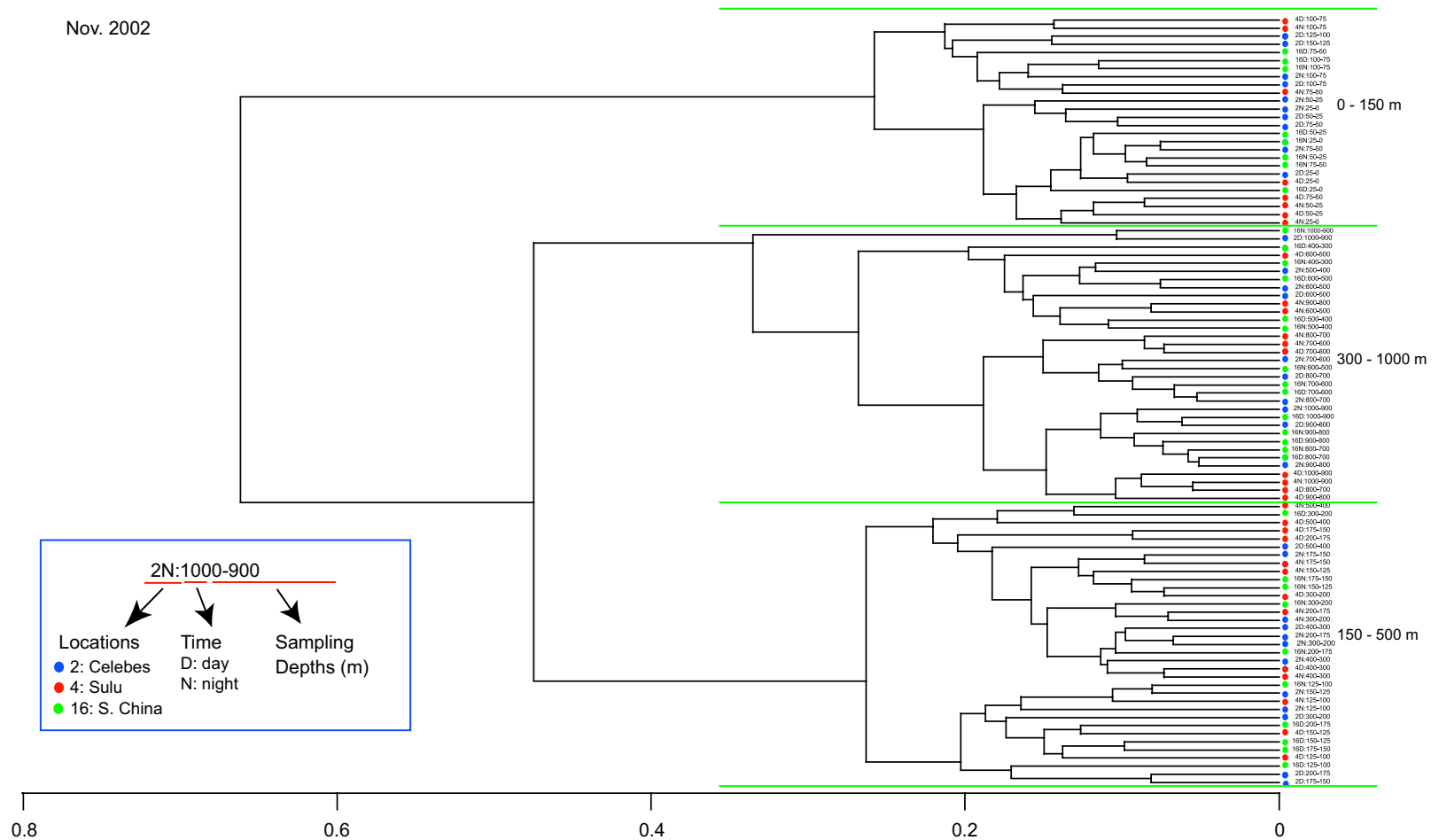


Fig. 8. Mesozooplankton faunal groups in November 2002: a comparison of three seas based on a cluster analysis using \log_{10} -transformed higher taxa abundance data and the Bray–Curtis dissimilarity index. Clustering by UPGMA was applied to the between-sample dissimilarity matrix. Samples were classified into three groups at the 0.4 linkage level. Blue, red, and green dots indicate samples collected in the Celebes, Sulu, and South China seas, respectively.

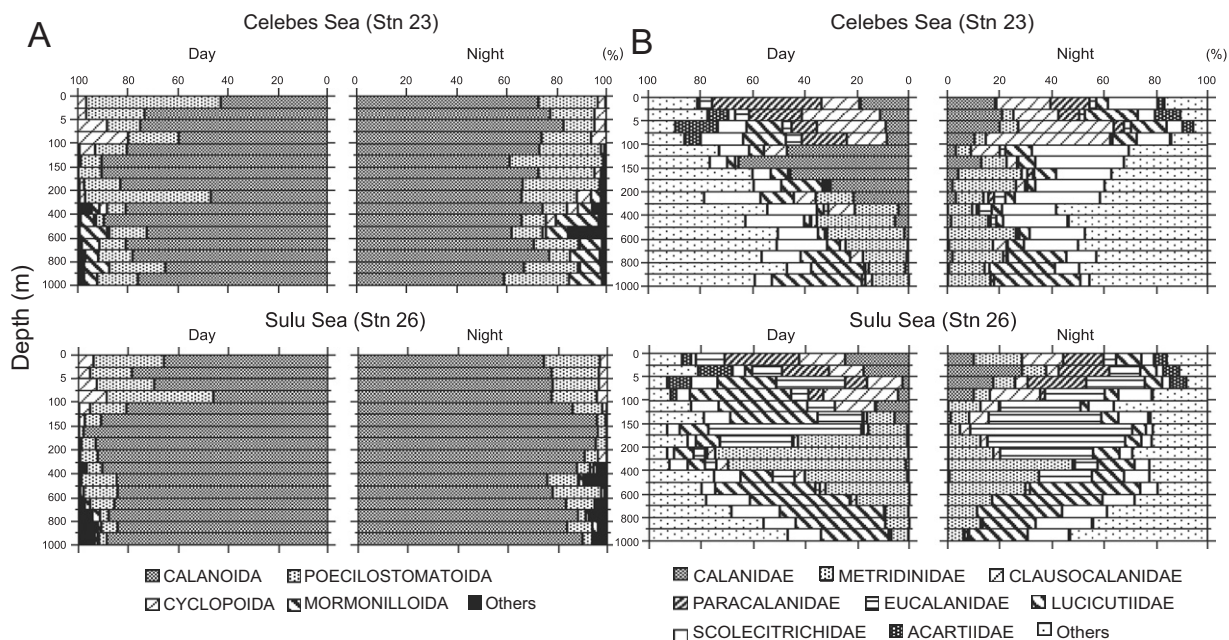


Fig. 9. Vertical patterns of composition of copepod orders (A: percentage abundance of adults and immature copepodids) and families of calanoid copepods (B: percentage abundance of adults) in the Sulu and Celebes seas in February 2000.

relatively quiet and self-contained hydrographic basin with little flow occurring through it and with little change in its mixed-layer depths between the two monsoon seasons (Wyrtki, 1961; Longhurst, 1998). While the present observations are limited in their spacio-temporal coverage, the results may be compared with available literature information to characterize the oceanographic conditions and biological productivities of the study sites.

The observed standing stocks of chlorophyll *a* and its maximum values in the water column were comparable to those reported from the South China Sea off Mindoro Strait in winter (75 m , $0.23 \pm 0.12\text{ }\mu\text{g l}^{-1}$; Ning et al., 2004), the South China Sea (21 mg m^{-2}) and the Sulu Sea (24 mg m^{-2}) off Palawan in May (San Diego-McGlone et al., 1999). Jones (2002) analyzed satellite images and estimated the surface chlorophyll levels through the winter in the central region of the Sulu Sea and off Palawan in the South China Sea to be generally less than $0.2\text{ }\mu\text{g l}^{-1}$, which correspond with the present observation (Fig. 3), but with occasional blooms approaching 1 mg m^{-2} in the Sulu Sea. San Diego-McGlone et al. (1999) also reported higher primary production rates in May ($195\text{ g C m}^{-2}\text{ yr}^{-1}$) in the oceanic region of the Sulu Sea than in the South China Sea ($147\text{ g C m}^{-2}\text{ yr}^{-1}$). These observations suggest that the levels of energy sources for

mesozooplankton are higher in the offshore deep areas of the Sulu and Celebes seas than those in the southern South China Sea during the study periods. There is significant positive correlation between the integrated chlorophyll *a* concentrations and the average integrated biomass of mesozooplankton in the 0–1000 m water column for all sampling stations ($p < 0.01$, $n = 5$, $r = 0.97$), but not for those in the 400–1000 m ($p > 0.05$, data not shown) (Fig. 10). This correlation suggests that the observed variations in the water-column biomass were mainly due to the epipelagic mesozooplankton that are assumed to respond to changes in algal biomass or primary productivity over a relatively short time period.

4.2. Biomass, abundance and vertical distribution patterns of mesozooplankton

The present biomass values, as represented by the average of the 0–400 and 400–1000 m layers, are comparable to those reported from the tropical to subtropical areas of the Indian Ocean, North and South Pacific, and Arabian Sea (Table 6), but are lower compared with the seamount area in the eastern tropical Pacific (Saltzman and Wishner, 1997a).

It is noteworthy that no marked difference was observed between the biomass, abundance, and

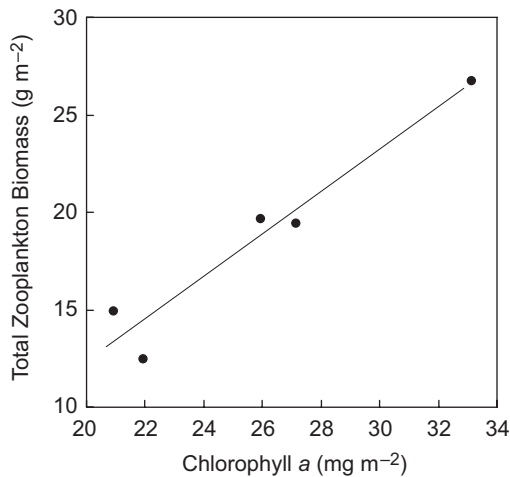


Fig. 10. Relationship between the total mesozooplankton biomass in the 0–1000m water column and the integrated concentrations of chlorophyll *a* during the research periods. Mesozooplankton biomass values are average of day and nighttime samplings at the station. See also Table 2 and Fig. 2.

degree of exponential decrease to mesopelagic depths even though the temperature was 5 °C higher in the mesopelagic zone of the Sulu Sea relative to the Celebes and South China seas. These observations differ from those made in the semi-isolated Levantine Basin of eastern Mediterranean Sea or Red Sea, where the degree of decline in zooplankton abundance with depth was significantly higher than that observed in the open Atlantic and Pacific oceans, using the same regression analysis (Weikert, 1982; Weikert and Trinkaus, 1990). This might be due to the more extreme conditions (i.e. much higher temperatures and salinities) of the water below mesopelagic layers observed in these seas than in the Sulu Sea. However, it is also interesting to discuss the reason for similar standing stocks and degree of their decline with depth between the mesopelagic layers of the Sulu Sea and its adjacent waters, in spite of their clearly different hydrographic characteristics more or less.

Table 6
Literature records of mesozooplankton biomass in the tropical–subtropical oceans

Area	Layer (m)	Biomass (mg m ⁻³)		Reference	Mesh size (mm)
		Average (<i>n</i>)	Range		
Indian Ocean	0–500	16.8 (12)	6.5–39	Vinogradov (1968)	0.38
	500–1000	5.8 (13)	3.3–15.1		0.38
North Pacific	0–500	17.1 (7)	4.6–52	Vinogradov (1968)	0.38
	500–1000	3.3 (9)	1.6–9.4		0.38
E. tropical Pacific ^a	0–600	132		Saltzman and Wishner (1997a)	0.34
	600–1000	52.3			0.34
South Pacific	0–500	15.3 (5)	5.4–38	Vinogradov (1968)	0.38
	500–1000	4.4 (5)	1.9–9.4		0.38
Arabian Sea	0–500	31.0 (4)	21–60	Vinogradov (1968)	0.38
	500–1000	7.5 (4)	4.1–12.1		0.38
Arabian Sea	0–150	112 (6) ^b	33–229 ^b	Koppelman et al. (2003)	0.33
	150–1050	8.2 (6) ^b	4.0–13.1 ^b		0.33
Red Sea	0–600		2–39 ^c	Weikert (1982)	0.38
	600–1050		0.1–2.5 ^c		0.38
E. Mediterranean Sea	0–450	10.12 ^d (2)	8.8–11 ^d	Weikert and Trinkaus (1990)	0.33
	450–750	6.07 ^d (2)	5.3–6.9 ^d		0.33
Sulu Sea	0–400	37 (4)	30–42	This study	0.33
	400–1000	7.9 (4)	3.9–12.2		0.33
Celebes Sea	0–400	37 (4)	20–55	This study	0.33
	400–1000	8.3 (4)	5.3–14.4		0.33
South China Sea	0–400	26 (2)	24–28	This study	0.33
	400–1000	7.5 (2)	7.2–7.7		0.33

^aSeamount area.

^bRecalculated from standing stock (WW m⁻²), and treated 0.5–5 mm fraction only.

^cReadings from the plots of figure.

^dRecalculated from standing stock (WW m⁻²).

Generally, higher temperature enhances the decomposition cycles of sinking particles, which may affect the resource availabilities for mesozooplankton in the mesopelagic layers. During the research periods, however, bacterial communities in the Sulu Sea and its adjacent water were basically depth-dependant, and the effect of warm water in the Sulu Sea was not clear (Yoshida et al., 2007). This suggests that the decomposition process or the amount of particle flux in the mesopelagic water in the Sulu Sea may not be greatly different from other seas at least in the upper 1000 m, and this may reflect the similar mesopelagic biomass of mesozooplankton in the Sulu Sea to its adjacent waters. To clarify these points, comparative studies to investigate the export flux in these seas, vertical profiles of sinking particles, and mesozooplankton biomass below bathy-pelagic layers are essential.

4.3. Community structure of mesozooplankton and taxonomic composition of copepods

Mesozooplankton clusters based on higher taxa abundance in the study area are separated by depths layers, rather than the sea areas, suggesting that the different mesopelagic conditions in the Sulu and other seas are similarly favorable to the major animal groups in the upper 1000 m.

In contrast to the similarities in both vertical patterns of the higher taxa composition and group structure in all three seas, the composition of copepod communities at the order and family levels showed several differences between the Sulu and Celebes seas, as represented by the reduced abundance of Mormonilloidea in the Sulu Sea and the differing vertical distribution of major families in the Celebes and Sulu seas.

Low abundance of Mormonilloidea has been reported from the Red Sea (Beckmann, 1984) but not from the eastern Mediterranean (Böttger-Schnack, 1994) and the NE Atlantic (Weikert and Koppelman, 1993) where they were common in the meso- and bathypelagic depths. The absence of marked oxygen minimum zone (OMZ) in the latter areas ($>3.8 \text{ ml O}_2 \text{ l}^{-1}$ in the Levantine Sea: e.g., Manca et al., 2004; $>4.0 \text{ ml O}_2 \text{ l}^{-1}$ in the NE Atlantic: e.g., Sverdrup et al., 1942) as compared with the Red Sea (Böttger-Schnack, 1994) may be a factor for this discrepancy. However, the oxygen levels in the latter ($>0.9 \text{ ml O}_2 \text{ l}^{-1}$), as well as in the Sulu Sea ($>1.5 \text{ ml O}_2 \text{ l}^{-1}$) are higher than areas with more extreme OMZ ($<0.1 \text{ ml O}_2 \text{ l}^{-1}$) such as in the

Arabian Sea and the eastern tropical Pacific, where Mormonilloidea are of abundance comparable to other areas without marked OMZ. In these areas the Mormonilloidea appeared to avoid the layer of extreme OMZ by vertical shift of populations to the upper or lower layers (Böttger-Schnack, 1996; Saltzman and Wishner, 1997b). Hence, the lower oxygen levels throughout the mesopelagic depths in the Sulu Sea relative to the Celebes and South China seas, if with any effect, may not be a single factor that is responsible for the scarcity of Mormonilloids in the Sulu Sea, necessitating further analysis on synergistic effect of temperature, oxygen content, and ecological characteristics of these copepods.

The characteristic dominance of Augaptilidae, Eucalanidae, and Lucicutiidae in the Levantine Sea (eastern Mediterranean) and that of Augaptilidae, Lucicutiidae, and Scolecitrichidae in the central Red Sea, as compared with the oceanic NE Atlantic, have been reported, along with the depth-related sequence of zonal dominance by one single-species of each family (Scotto di Carlo et al., 1984; Weikert and Trinka, 1990; Weikert and Koppelman, 1993). The abundance and depth distributions of these species are governed by the hydrographic features of the environment that are considerably different between these seas. For example, the mass occurrence of *Eucalanus monachus* in the Levantine Sea was related to the meso-scale gyres (Weikert and Koppelman, 1993), while the depth distributions of the dominant inter-zonal species of *Haloptilus*, *Pleuromamma*, and *Lucicutia* were related to the presence of moderate OMZ in the central Red Sea (Weikert, 1982), in addition to the homogenous waters of high temperature and salinity in the both seas. In the present study the elevated dominance of Eucalanidae, Metridinidae, and Lucicutiidae with depth-related sequence in the Sulu Sea relative to the Celebes Sea appears to coincide with the reduced oxygen content in the subsurface layer and the higher temperature in the mesopelagic zone in the Sulu Sea relative to the Celebes Sea, suggesting possible effect of these hydrographic conditions on the observed faunal differences, while further discussion will awaits species-specific information.

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