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Diversity and community structure of pelagic cnidarians in the Celebes and Sulu Seas, southeast Asian tropical marginal seas



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ABSTRACT

The Sulu Sea is a semi-isolated, marginal basin surrounded by high sills that greatly reduce water inflow at mesopelagic depths. For this reason, the entire water column below 400 m is stable and homogeneous with respect to salinity (ca. 34.00) and temperature (ca. 10 °C). The neighbouring Celebes Sea is more open, and highly influenced by Pacific waters at comparable depths. The abundance, diversity, and community structure of pelagic cnidarians was investigated in both seas in February 2000. Cnidarian abundance was similar in both sampling locations, but species diversity was lower in the Sulu Sea, especially at mesopelagic depths. At the surface, the cnidarian community was similar in both marginal seas, but, at depth, community structure was dependent first on sampling location and then on depth within each Sea. Cnidarians showed different patterns of dominance at the two sampling locations, with Sulu Sea communities often dominated by species that are rare elsewhere in the Indo-Pacific. Mesopelagic and bathypelagic species recorded in the Sulu Sea did not have significantly different vertical distributions in the Celebes Sea. However, some deep mesopelagic genera were absent from the Sulu Sea in the sampled depth range. These results suggest that a combination of environmental and physiological parameters determine the distribution and dominance of pelagic cnidarians.

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1. Introduction

The Sulu Sea is a semi-isolated, marginal sea in southeast Asia, separated from adjacent basins by high sills, usually less than 200 m below the surface (Fig. 1). The deepest passage, a narrow trough extending to 400 m depth, the Mindoro Strait, links the Sulu Sea with the East China Sea, and another passage, about 270 m deep, the Sibutu Passage, communicates with the Celebes Sea to the South (Exon et al., 1981). However, due to the hydrography of the area, the main water exchanges with the Sulu Sea are surface flows, no deeper than 200 m on average (Lukas et al., 1991; Metzger and Hurlburt, 1996; Spintall et al., 2012), that usually flow from North to South. This leads to sharp stratification of the water column. Temperatures throughout the entire water column are high, with temperatures of ~10 °C to a depth of 5000 m, accompanied by low oxygen values (Exon et al., 1981; Quadfasel et al., 1990). Rainfall and terrestrial freshwater discharge create a low salinity zone near the surface (Exon et al., 1981; Nishikawa et al.,

2007), and it has been proposed that the low salinity-high temperature combination at depth is due to turbidity currents from such discharges, with high densities due to the particle load, flowing downslope and mixing with the basin waters over geological time periods (Quadfasel et al., 1990).

The Celebes Sea is also a semi-closed marginal sea, but deep channels communicate with the Java, Molucca, and Philippine Seas. Hydrographic conditions in the mesopelagic zone of the Celebes Sea are oceanic, and highly influenced by Pacific waters (Toole, 1987; Lukas et al., 1991).

Due to the limited exchange with surrounding oceans, semi-isolated marginal seas are highly vulnerable to anthropogenic influences such as global warming, expansion of low oxygen zones and heightened rainwater runoff (McKinnon et al., 2014), but they are ideal areas to study dispersal and distribution mechanisms of pelagic species, and especially of deep-water bathypelagic species. High temperatures at depth, such as those observed in the Mediterranean, Red, and Sulu Seas may also play a crucial role in determining species composition at depth, as many pelagic species tolerate only relatively narrow temperature ranges (Sameoto, 1984; Chen, 1986; Stensholt et al., 2002). However, unlike many pelagic invertebrates, jellyfish appear to be quite resilient to changes in temperature and other

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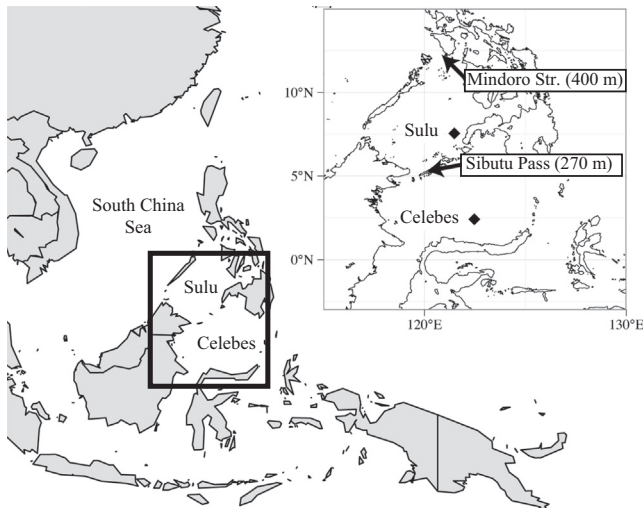


Fig. 1. Map of the sampling locations.

Table 1
Characteristics of MOCNESS sampling during this study.

Location	Date	Time	Sampling depth (m)	Latitude (N)	Longitude (E)
Celebes	19 Feb. 2000	Day	200–1000	2°25.8'	122°28.2'
	19 Feb. 2000	Day	0–200	2°25.1'	122°28.1'
	19 Feb. 2000	Night	200–1000	2°28.3'	122°28.8'
	20 Feb. 2000	Night	0–200	2°31.7'	122°30.0'
Sulu	24 Feb. 2000	Night	200–1000	7°33.7'	121°29.1'
	25 Feb. 2000	Night	0–200	7°33.3'	121°28.2'
	25 Feb. 2000	Day	200–1000	7°38.0'	121°29.4'
	25 Feb. 2000	Day	0–200	7°33.5'	121°25.9'

hydrographical variations (Richardson, 2009). The apparent absence of some cnidarians from certain areas is thought to reflect sampling problems more than a true absence of the species (Pugh, 1999a; Mapstone, 2009; Nishida and Nishikawa, 2011).

Geological characteristics and benthic communities are relatively well studied in the Sulu and Celebes Seas (e.g. Billard, 1913; Exon et al., 1981; Ohtsuka et al., 2005), but pelagic communities are still quite under-studied. While the diversity of medusae in the South China Sea has been studied some detail (e.g. Gao et al., 2002; Zhang, 2005), most knowledge about the pelagic medusae of other southeast Asian Seas comes from the late 19th century oceanographic expeditions of the *Albatross*, *Challenger*, *Galathea*, *Sibogoa*, or *Discovery* (Maas, 1905; Lens and van Riemsdijk, 1908; Bigelow, 1919), and few studies have been performed since (e.g. Musaeva, 1976; Acabado et al., 2010). Information on the siphonophore communities is scarcer still.

In February 2000, a sampling program was performed in the Sulu and Celebes Seas, using stratified plankton net tows, in order to study the diversity, vertical distribution, and community structure of mesoplankton from the surface down to 1000 m (Nishikawa et al., 2007). The present study examines the community structure and vertical distributions of pelagic cnidarians in both seas. These results not only document the cnidarian fauna of a little-studied geographic zone, but also shed light on the effect that hydrographic characteristics of the Sulu Sea may have on the distribution of these animals. This work complements studies of mesoplankton distributions at higher taxonomic levels (Nishikawa et al., 2007), and those of chaetognaths and *Euaugaptilus* copepods (Johnson et al., 2006; Matsuura et al., 2010), previously reported.

2. Material and methods

Sampling was performed during the cruise KH-00-1 of the R/V *Hakuho Maru* both day and night in the Celebes Sea (2°25'N, 122°28'E) and in the Sulu Sea (7°33'N, 121°29'E) on the 19th and 25th of February 2000, respectively (Table 1). Water temperature and salinity were measured using an SBE 9+ CTD system on an SBE 32 Carousel (Sea-Bird Electronics, Inc.). Water samples were collected simultaneously, and dissolved oxygen concentrations were measured using a Winkler titration machine (Hirama ART-3). Plankton samples were collected using a MOCNESS-1 (Multiple Opening-Closing Net and Environmental Sensing System: 1 m² mouth opening, 330 μm/mesh; Wiebe et al., 1985) net, in 25 m intervals in the upper 200 m of the water column, and in 100 m intervals between 200 and 1000 m. The filtered volume was 370 m³ on average per net in the upper 200 m and 1050 m³ for the other nets. A single tow was performed for each depth interval, time and station. Bulk plankton was preserved in 4% seawater-buffered formalin, and cnidarians were hand-sorted out of the bulk sample. All cnidarians ('Siphonophora' and 'other Cnidaria' in Nishikawa et al., 2007) were counted and identified to the lowest taxonomic level possible using the most recent taxonomic guides to each group (Sears, 1953; Kramp, 1961; Totton, 1965; Pugh, 1998, 1999a, 1999b, 2006; Bouillon et al., 2004; Mapstone, 2009; Grossmann et al., 2014a) and/or the original descriptions. Classification follows that established in the *World Register of Marine Species* (2014). The maximum number of zooids comprising a single siphonophore colony followed Grossmann and Lindsay (2013); one *Melophysa melo* colony was considered to have a single functional nectophore and up to 9 bracts (Totton, 1965; personal observations). For siphonophore species of the Abylidae, Amphicaryoninae, Clausophyidae, Diphyidae and Nectopyramidinae, presenting several independently-living life stages, the sexual eudoxid and asexual polygastric stages, each stage was counted separately, and these stages were called "forms". Abundance of each species and form was estimated in number of individuals/m³, the filtered volume being estimated by a flow-meter situated just above the mouth of the net. Shannon's diversity (H') and Pielou's evenness (J') indices were calculated in natural logarithm base on untransformed form abundance using the R package *BiodiversityR* (Kindt, 2013). ANOVA tests were used to test for differences in abundance, richness and diversity between sampling locations and times. Statistical significance was determined at $\alpha=1\%$, under the null hypothesis of non-different distributions.

After removing all forms comprising less than 2% of the total abundance of a given net sample, a hierarchical cluster analysis was performed on square-root transformed form abundance data using the software PRIMER v.6 (Clarke and Warwick, 2001) with an average linkage and Bray–Curtis similarity index. A Similarity Percentage (SIMPER) routine was carried out on the groups obtained in order to determine the forms contributing most to the Bray–Curtis dissimilarity between clusters.

3. Results

3.1. Hydrography

Sampling was performed in a pelagic part of each Sea, with bottom depths of around 5000 m (Fig. 1). In the Sulu Sea, the surface mixed layer extended down to around 65 m (Fig. 2), with near-constant temperature (24.8 °C), salinity (34.00) and dissolved oxygen (4.35 mL/L). Below that, salinity increased and dissolved oxygen decreased rapidly to 34.50 and 1.9 mL/L, respectively, at 150 m and remained constant throughout the rest of the water column. Below 150 m, temperature decreased gradually to ~10 °C at around 400 m and then remained constant down to 1000 m. In the Celebes Sea, a marked thermocline was present between 75 and 200 m, followed

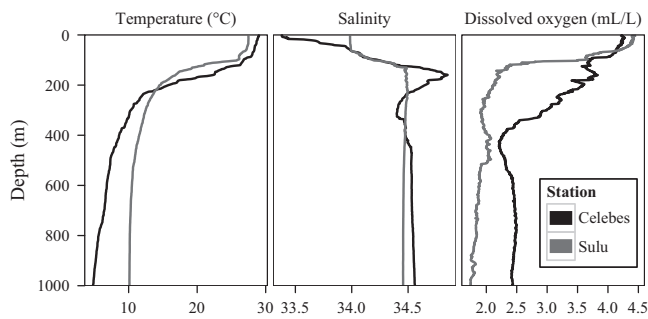


Fig. 2. Vertical profiles of temperature ($^{\circ}\text{C}$), salinity, and dissolved oxygen (mL/L) in the Celebes and Sulu Seas during February 2000.

by a gradual decrease in temperature from 15.7°C at 200 m to 4.8°C at 1000 m. Salinity was very low (33.38) at the surface, increasing to 34.85 at 222 m. A small decrease in salinity was found at 315 m. Salinity then remained constant at around 34.55 from 420 m down to 1000 m. The dissolved oxygen profile in the Celebes Sea showed the presence of two low oxygen zones, the first around 150 m (oxygen ~ 3.6 mL/L) and the second at 400 m (oxygen ~ 2.2 mL/L).

3.2. Cnidarian abundance, diversity and vertical distribution

A total of 105 cnidarian species were identified in the MOCNESS net samples: 4 scyphozoan, 6 anthozoan, 6 leptomedusan, 4 narcomedusan, 11 trachymedusan and 74 siphonophore species (Table 2). Siphonophores were represented by 11 physonect species and 63 calyophoran species, totalling 84 distinct siphonophore forms. These records have been added to the Ocean Biogeographic Information System via the Biological Information System for Marine Life (BISMaL) (Grossmann et al., 2014b). A total of 89 cnidarian forms (74 species) were collected in the Sulu Sea, which was significantly fewer than the 113 forms (97 species) found in the Celebes Sea (Table 3). About 56% of the forms were found at both sampling locations. In both Seas, form richness was highest between 25 and 150 m, decreasing sharply at around 175 m depth before increasing again in deeper layers (Fig. 3). At neither station was there a significant change in form richness between day and night samples (Table 3).

Siphonophores represented 90% of the form richness of each net sample, on average. Calyophorae were represented by 24 different genera, and 8 genera of Physonectae were present: *Agalma*, *Apolemia*, *Bargmannia*, *Frillagalma*, *Halistemma*, *Melophysa*, *Nanomia* and *Resomia*. Noteworthy was the complete absence from both seas of the cosmopolitan, epipelagic species *Muggiaea atlantica* and of the calyophoran Family Sphaeronectidae. Diel vertical migration (DVM), when present (e.g. the calyophoran siphonophores *Abylopsis tetragona*, *Diphyes* spp. and *Vogtia glabra*, the physonect siphonophores *Halistemma* sp. and *Nanomia bijuga*, and the hydromedusa *Liriope tetraphylla*), was performed in both the Sulu and Celebes Seas (Fig. 4). Because of the high sills surrounding most of the Sulu Sea (≥ 250 m), many of the deep mesopelagic cnidarian species found in the Celebes Sea (e.g. *Botrynema brucei*, *Crystallophyses amygdalina*, *Gilia reticulata*, *Lensia havock*, *Lensia quadriculata*) were absent from the Sulu Sea (Table 2) in the sampled depth range. However, when present (e.g. *Dimophyses arctica*, *Haliscera conica*, *Lensia achilles*, *Lensia lelouveteau*), the mean depth of abundance was similar in the Sulu and Celebes Seas at a given sampling time (100 m difference on average) (Fig. 4). Apart from eudoxid stages of the Genus *Chuniphyes*, no clausophyid siphonophores were present in the Sulu Sea.

At both stations, abundance was highest in the upper 200 m of the water column and during the day (Fig. 3). Maximum abundance was found between 25 and 50 m, with 10.13 ind./ m^3 in the Celebes Sea and 8.68 ind./ m^3 in the Sulu Sea. At night, maximum abundance was found between 25 and 50 m in the Sulu Sea

(4.7 ind./ m^3), but two peaks of abundance were present at night in the Celebes Sea: between the surface and 25 m (2.7 ind./ m^3) and between 50 and 75 m (3.16 ind./ m^3). Below 200 m, abundance decreased to about 0.056 and 0.043 ind./ m^3 in the Celebes and Sulu Seas, respectively.

Despite similar profiles of total cnidarian abundance and of vertical species distributions (Fig. 4), community composition was different at the two sampling locations (Table 4). In the Sulu Sea, the dominant forms in the top 50 m, both day and night, were polygastric stages of *Lensia subtiloides*, and indeed, this was the most abundant form collected in the Sulu Sea, even when all depths were combined (7.7 ind./ m^3). In the Celebes Sea, the most abundant forms, when all depths were combined, were *Abylopsis eschscholtzi* eudoxid stages and *Chelophyes contorta* polygastric stages (4.0 ind./ m^3). Down to 200 m, calyophoran abylyds and non-*Lensia* diphyids tended to dominate in the Celebes Sea, with occasional high abundances of upper-mesopelagic and closely related five-ridged *Lensia* species (*Lensia leloupi* between 125 and 150 m during the day, *Lensia panikkari* between 150 and 175 m at night) (Grossmann et al., 2014a). In the Sulu Sea, the calyophoran, *Diphyes dispar*, the physonect, *Melophysa melo*, and the hydromedusan jellyfish, *L. tetraphylla*, were the most abundant taxa between 50 and 200 m. In the Celebes Sea and during the day in the Sulu Sea, the majority of the *D. dispar* polygastric stages were large (anterior nectophores 2 to 3 cm in length), but a second, rarer, cohort was also present in the upper 50 m of the water column (anterior nectophores of polygastric stages ≤ 1 cm in length). At night in the Sulu Sea, the cohort of smaller animals extended from the surface down to 100 m and represented the majority of the *D. dispar* polygastric stages present. Two distinct generations of *C. contorta* and *Diphyes bojani* polygastric stages were also present in the surface waters of the Celebes Sea during the sampling period, the former in the upper 50 m of the water column, the latter between 50 and 75 m, both day and night.

In the mesopelagic zone in the Celebes Sea, the most abundant taxa included the cosmopolitan calyophoran siphonophore *D. arctica*, and multistriate *Lensia* species, such as *Lensia ajax* and *L. lelouveteau*. In the Sulu Sea, most of the mesopelagic zone was dominated by polygastric and eudoxid stages of the possibly polyphyletic *L. achilles* (Grossmann et al., 2014a) and by the multistriate, *L. ajax*.

Shannon's diversity index (Fig. 5) was high at both stations both day and night in the upper 100 m of the water column ($H' = 2.75$ on average), but was significantly lower below 100 m (Table 5) in the Sulu Sea ($H' = 1.6$ on average) than in the Celebes Sea ($H' = 2.3$ on average). Pielou's evenness index was high ($J' = 0.85$ on average) for all net samples except that collected at night between 150 and 175 m in the Sulu Sea. This could be directly correlated to the high abundance of *M. melo* physonect colonies, representing 62% of the total cnidarian abundance of that sample. The daytime sample collected between 900 and 1000 m in the Sulu Sea contained a single form, *L. achilles* eudoxid stages; therefore, Shannon's diversity index was null, and Pielou's evenness index could not be calculated.

3.3. Community structure analysis

A multivariate cluster analysis performed on square-root transformed abundance data showed first a separation of the net samples based on depth and then, for the deeper samples, on sampling location (Fig. 6). Two sub-groups were found within the surface cluster. The first, cluster A, containing all net samples collected above 125 m during day and night in the Sulu Sea and at night in the Celebes Sea, and those collected above 300 m in the Celebes Sea during the day. The second, cluster B, contained the net samples collected in the Sulu Sea between 125 and 200 m at night and between 125 and 300 m during the day. Abylyds and

Table 2

List of Cnidaria collected during the present study, with depth range (m) and mean depth (weighted by abundance) at each station during day and night. p, polygastric stage; e, eudoxid stage; l, larval stage.

Class Hydrozoa Owen, 1843			Celebes Sea			Sulu Sea					
			Day		Night	Day		Night			
Order SIPHONOPHORAE Eschscholtz, 1829											
Family Abylidae Agassiz, 1862	<i>Abyla haeckeli</i>	p.			100–125	112.5		125–500	193.64		
	<i>Abyla tottoni</i>	p.			75–100	87.5					
	<i>Abyla trigona</i>	p.	75–175	127.18	25–50	37.5					
	<i>Abyla</i> sp.	e.	0–175	104.7	0–100	22.67	75–100	87.5			
	<i>Abylopsis eschscholtzii</i>	p.	25–125	59.78	0–125	55.1	0–100	26.23	0–900	40.34	
		e.	0–400	35.46	0–300	43.83	0–150	38.13	0–125	29.71	
	<i>Abylopsis tetragona</i>	p.	25–300	87.62	0–300	70.33	0–300	72.27	0–125	55.72	
		e.	25–700	130.45	25–1000	65.03	0–300	82.22	0–200	47.2	
	<i>Bassia bassensis</i>	p.	0–125	42.74	0–175	41.63	0–75	29.74	0–75	33.33	
		e.	0–150	34.38	0–150	44.37	0–100	44.58	0–100	30.11	
	<i>Ceratocymba dentata</i>	e.			200–300	250					
	<i>Ceratocymba leuckartii</i>	p.	100–150	131.66	0–150	42.86					
		e.	100–300	156.29	75–400	111.61			0–50	29.02	
	<i>Enneagonum hyalinum</i>	p.	100–400	166.26	50–300	111.29	50–600	86.71	75–500	115.72	
		e.	100–300	143.09	50–200	88.21	25–150	80.93	50–500	86.18	
	Family Diphyidae Quoy & Gaimard, 1827	<i>Chelophyes contorta</i>	p.	0–300	30.66	0–300	33.13	0–100	27.94	0–100	53.74
		<i>Chelophyes</i> spp.	e.	0–50	16.64	0–175	32.42			50–75	62.5
		<i>Dimophyes arctica</i>	p.	200–900	355.75	175–500	273.52	175–700	199.15	150–175	162.5
			e.	150–800	313.76	200–800	334.09			400–500	450
<i>Diphyes bojani</i>		p.	0–150	54.03	0–100	46.52	25–900	64.34	0–100	35.35	
		e.	25–175	71.78	0–100	42.97	25–125	46.93	0–125	32.44	
<i>Diphyes chamissonis</i>		p.	0–900	28.22	0–50	16.04	0–150	36.65	0–100	33	
		e.	0–75	29.52	0–75	25.5	0–125	28.26	0–100	35.37	
<i>Diphyes dispar</i>		p.	0–125	45.27	0–500	28.49	0–700	47	0–1000	57.11	
		e.	0–125	66.89	0–100	38.42	0–600	72.26	0–100	55.3	
<i>Eudoxoides mitra</i>		p.	50–300	97.71	25–100	64.62	0–900	69.38	0–125	63.6	
		e.	25–300	110.2	25–500	67.19	0–175	61.8	0–1000	61.4	
<i>Eudoxoides spiralis</i>		p.					0–100	33.59	50–75	62.5	
<i>Gilia reticulata</i>		p.	900–1000	950	900–1000	950					
<i>Lensia achilles</i>		p.	500–900	680	300–900	503.85	400–800	568.82	300–900	536.67	
		e.	300–1000	464.67	300–600	455.26	500–1000	671.38	500–1000	677.83	
<i>Lensia ajax</i>		p.									
<i>Lensia asymmetrica</i>		p.	300–700	452.94	300–700	414.95	500–600	550			
<i>Lensia campanella</i>		p.	0–300	33.95	0–200	41.19	0–125	52.49	50–100	72.01	
<i>Lensia conoidea</i>		p.	300–400	350	200–400	299.12	125–300	165.85	100–175	145.83	
		e.			100–125	112.5					
<i>Lensia cordata</i>		p.	600–700	650							
<i>Lensia cossack</i>		p.	25–50	37.5			0–25	12.5	75–100	87.5	
		e.	25–175	100.21	0–300	45.8	25–100	60.48	0–400	74.21	
<i>Lensia exeter</i>		p.	400–500	450	300–500	371.28					
<i>Lensia fowleri</i>		p.			175–200	187.5	100–125	112.5	100–125	112.5	
<i>Lensia grimaldii</i>		p.	300–400	350	700–800	750					
<i>Lensia havock</i>		p.	600–700	650	600–800	697.62					
<i>Lensia hotspur</i>		p.	25–300	52.29	0–500	67.93	75–125	99.3	50–125	89.83	
<i>Lensia leloupi</i>		p.	125–300	145.8	75–150	103.65	50–150	67.42	50–175	99.14	
<i>Lensia lelouveteau</i>		p.	300–1000	587.85	300–1000	503.57	500–600	550			
<i>Lensia meteori</i>		p.	100–125	112.5	50–300	85.37	125–175	150.46	100–125	112.5	
<i>Lensia multicristata</i>	p.	200–700	431.45	200–700	417.3	175–200	187.5	175–300	203.58		
<i>Lensia panikkari</i>	p.	300–500	404.36	100–400	214.01	0–125	27.29	175–200	187.5		
<i>Lensia quadriculata</i>	p.	700–800	750	700–800	750						
<i>Lensia subtilis</i>	p.	100–125	112.5	50–75	62.5	50–175	123.85	75–100	87.5		
<i>Lensia subtiloides</i>	p.	0–125	40.43	50–150	80.35	0–125	26.58	0–200	33.59		
	e.					0–50	35.75	0–25	12.5		

Table 2 (continued)

Class Hydrozoa Owen, 1843			Celebes Sea			Sulu Sea				
Order SIPHONOPHORAE Eschscholtz, 1829			Day		Night		Day	Night		
	<i>Lensia</i> sp. A	p.			125–150	137.5				
	<i>Lensia</i> sp. B	p.	75–100	87.5						
	<i>Muggiaea delsmanni</i>	p.			200–300	250	0–200	58.34		
	<i>Sulculeolaria angusta</i>	p.					50–75	62.5		
	<i>Sulculeolaria biloba</i>	p.	125–150	137.5						
	<i>Sulculeolaria chumi</i>	p.	0–300	55.02	0–150	20.15	75–900	111	50–1000	91.15
	<i>Sulculeolaria monoica</i>	p.							75–100	87.5
	<i>Sulculeolaria quadrivalvis</i>	p.	0–175	69.48			25–50	37.5	75–100	87.5
	<i>Sulculeolaria turgida</i>	p.	75–300	141.52	0–150	16.08				
aff. Diphyidae	<i>Eudoxia galathea</i>	e.					100–125	112.5	75–125	91.19
Family Clausophyidae Totton, 1965	<i>Chuniphyes moserae</i>	p.	600–1000	780.65						
	<i>Chuniphyes multidentata</i>	p.	100–600	322.01	300–1000	589.34				
	<i>Chuniphyes</i> spp.	e.	300–900	530	300–1000	493.52	400–900	644.12		
	<i>Clausophyes moserae</i>	p.	500–900	675.25	600–1000	775.68				
	<i>Crystallophyes amygdalina</i>	p.			700–1000	891.18				
	<i>Heteropyramis crystallina</i>	e.	800–900	850						
	<i>Heteropyramis maculata</i>	p.	500–600	550						
		e.	500–600	550						
	<i>Kephyes</i> sp. A	p.			900–1000	950				
	<i>Kephyes</i> spp.	e.	800–1000	876.47	900–1000	950				
Family Hippopodiidae Kolliker, 1853	<i>Hippopodius hippopus</i>	p.	25–300	68.33	25–200	73.44	0–150	38.05	0–300	55.22
	<i>Vogtia glabra</i>	p.	75–100	87.5	25–200	62.13	25–200	71.56	25–300	51.64
	<i>Vogtia pentacantha</i>	p.	200–300	250					200–300	250
	<i>Vogtia serrata</i>	p.	300–400	350						
Family Prayidae Kolliker, 1853	<i>Amphicaryon acaule</i>	p.	50–200	100.69	25–100	49.42			50–125	73.71
	<i>Amphicaryon ernesti</i>	p.					100–125	112.5	125–150	137.5
	<i>Amphicaryon peltifera</i>	p.	75–100	87.5	50–75	62.5				
	<i>Amphicaryon</i> spp.	e.	50–150	72.65	25–125	62.08	50–125	81.72	50–100	72.01
	<i>Nectopyramis natans</i>	p.			500–600	550				
	<i>Nectopyramis thetis</i>	e.	500–600	550						
	<i>Rosacea plicata</i>	p.	75–100	87.5	200–500	300	50–500	147.98	125–500	239.56
Suborder PHYSONECTAE Haeckel, 1888	<i>Agalma elegans</i>		0–100	26.82	25–75	47.73	25–50	37.5	50–175	84.92
	<i>Agalma okeni</i>		600–700	650	50–100	76.32			75–100	87.5
	<i>Agalmatidae</i> spp.	l.	25–300	79.28	50–175	95.7				
	<i>Apolemia</i> sp.						500–600	550		
	<i>Bargmannia amoena</i>				500–600	550	500–600	550	200–500	293.09
	<i>Bargmannia elongata</i>						300–700	414.49		
	<i>Frillagalma</i> sp. A		25–150	41.67	0–100	18.95				
	<i>Frillagalma vityazi</i>				900–1000	950				
	<i>Halistemma</i> sp.		150–600	200.24	75–100	87.5	100–600	253.22	100–700	179.42
	<i>Melophysa melo</i>		25–50	37.5			100–200	155.23	100–200	153.3
	<i>Nanomia bijuga</i>		25–300	43.9	0–125	34.25	50–400	83.82	0–300	46.74
	<i>Resomia ornicephala</i>								100–150	131.74
Order TRACHYMEDUSAE Haeckel, 1866	<i>Aglaura hemistoma</i>		0–900	30.34	0–800	27.13	0–125	33.57	0–150	63.12
	<i>Amphogona apicata</i>		200–300	250						
	<i>Arctapodema</i> sp.				200–400	315.52			300–400	350
	<i>Botrynema brucei</i>		800–1000	890.91	900–1000	950				
	<i>Colobonema sericeum</i>				500–600	550			300–400	350
	<i>Halicreas minimum</i>		600–800	680.77	500–1000	730.17	400–500	450	175–200	187.5
	<i>Haliscera conica</i>		600–900	733.87	400–1000	702.38	800–900	850	800–900	850
	<i>Liriope tetraphylla</i>		0–175	54.99	0–125	35.08	0–150	62.48	0–100	36.58
	<i>Pantachogon haeckeli</i>						100–500	207.79		
	<i>Rhopalonema velatum</i>		25–50	37.5						
	<i>Rhopalonematidae</i> sp. A		800–900	850						

Table 4
Most abundant form per net sample. In parentheses, abundance as ind./m³.

Depth range (m)	Celebes		Sulu	
	Day	Night	Day	Night
0–25	<i>Chelophyes contorta</i> p. (1.60)	<i>Lensia subtiloides</i> p. (2.18)	<i>Lensia subtiloides</i> p. (2.18)	<i>Chelophyes contorta</i> p. (0.42)
25–50	<i>Chelophyes contorta</i> p. (1.37)	<i>Lensia subtiloides</i> p. (2.76)	<i>Lensia subtiloides</i> p. (2.76)	<i>Chel. contorta</i> p.; <i>Diphyes bojani</i> e. (0.14)
50–75	<i>Abylopsis eschscholtzi</i> e. (0.68)	<i>Diphyes dispar</i> p. (0.52)	<i>Diphyes dispar</i> p. (0.52)	<i>Abylopsis eschscholtzi</i> e. (0.42)
75–100	<i>Bassia bassensis</i> e. (0.26)	<i>Liriopse tetraphylla</i> (0.50)	<i>Liriopse tetraphylla</i> (0.50)	<i>Abylopsis tetragona</i> p. (0.32)
100–125	<i>Lensia subtiloides</i> p. (0.13)	<i>Liriopse tetraphylla</i> (0.09)	<i>Liriopse tetraphylla</i> (0.09)	<i>Abylopsis tetragona</i> p. (0.03)
125–150	<i>Lensia leloupi</i> p. (0.12)	<i>Melophysa melo</i> (0.16)	<i>Melophysa melo</i> (0.16)	<i>Abylopsis eschscholtzi</i> e.; <i>Eudoxoides mitra</i> e.; <i>Lensia</i> sp. A (0.004)
150–175	<i>Eudoxoides mitra</i> e. (0.06)	<i>Melophysa melo</i> (0.24)	<i>Melophysa melo</i> (0.24)	<i>Lensia panikkari</i> p. (0.01)
175–200	<i>Abylopsis tetragona</i> e. (0.07)	<i>Vogtia glabra</i> <i>Melophysa melo</i> (0.05)	<i>Vogtia glabra</i> <i>Melophysa melo</i> (0.05)	<i>Chelophyes contorta</i> p. (0.01)
200–300	<i>Amphogona apicata</i> (0.02)	<i>Halistemma</i> sp. (0.06)	<i>Halistemma</i> sp. (0.06)	<i>Dimophyes arctica</i> e. (0.02)
300–400	<i>Dimophyes arctica</i> e. (0.03)	<i>Lensia ajax</i> p. (0.02)	<i>Lensia ajax</i> p. (0.02)	<i>Dimophyes arctica</i> e. (0.03)
400–500	<i>Lensia panikkari</i> p. (0.01)	<i>Bargmannia elongata</i> (0.01)	<i>Bargmannia elongata</i> (0.01)	<i>Lensia ajax</i> p. (0.01)
500–600	<i>Lensia lelouveteau</i> p. (0.01)	<i>Lensia achilles</i> e. <i>L. achilles</i> p. (0.01)	<i>Lensia achilles</i> e. <i>L. achilles</i> p. (0.01)	<i>Lensia multicristata</i> p. <i>Heteropyramis maculata</i> e.; <i>Halicreas minimum</i> (0.004)
600–700	<i>Clausophyes moserae</i> p. (0.005)	<i>Lensia achilles</i> e. (0.01)	<i>Lensia achilles</i> e. (0.01)	<i>Clausophyes moserae</i> p. (0.003)
700–800	<i>Lensia lelouveteau</i> p. (0.003)	<i>Lensia achilles</i> p. (0.004)	<i>Lensia achilles</i> p. (0.004)	<i>Lensia ajax</i> p. (0.004)
800–900	<i>Dimophyes arctica</i> p.; <i>Chuniphyes</i> e. <i>Kephyes</i> e.; <i>Aglaura hemistoma</i> (0.003)	<i>Chuniphyes</i> e. (0.003)	<i>Chuniphyes</i> e. (0.003)	<i>Halicreas minimum</i> (0.005)
900–1000	<i>Chuniphyes moserae</i> p. (0.003)	<i>Lensia achilles</i> e. (0.003)	<i>Lensia achilles</i> e. (0.003)	<i>Frillagalma vityazi</i> (0.01)

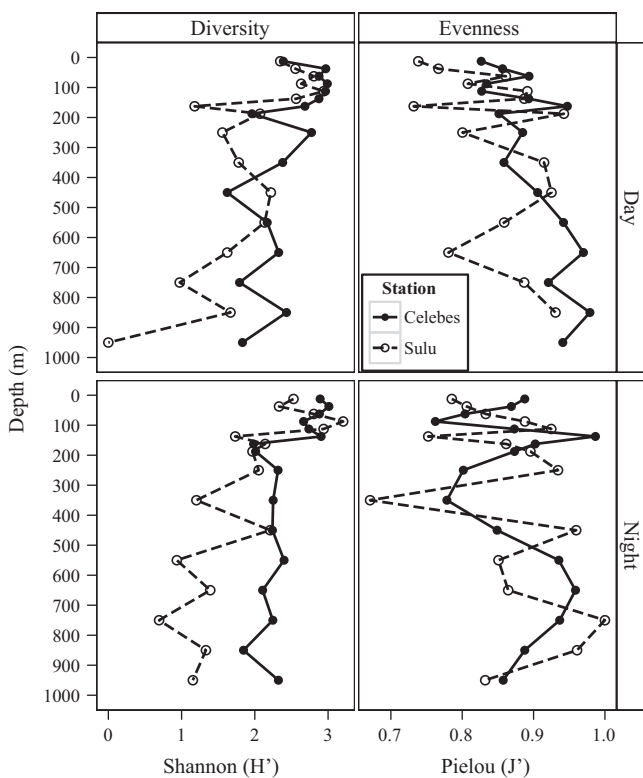


Fig. 5. Shannon's diversity (H') and Pielou's evenness (J') indices over depth at each station during each sampling time.

Table 5
Statistical results of ANOVA tests on the effect of sampling location (Station) and time on Shannon's diversity index (H') in the upper 100 m of the water column, and in the deeper layers. *df*, degrees of freedom; *MS*, mean square.

ANOVA	<i>df</i>	<i>MS</i>	<i>F</i> -value	<i>p</i> -Value	
Sampling depth < 100 m	Shannon (H') ~ station	1	0.134	2.058	0.175
	~Time	1	0.036	0.548	0.472
Sampling depth ≥ 100 m	Shannon (H') ~ station	1	4.514	14.148	< 0.001
	~Time	1	0.041	0.129	0.721

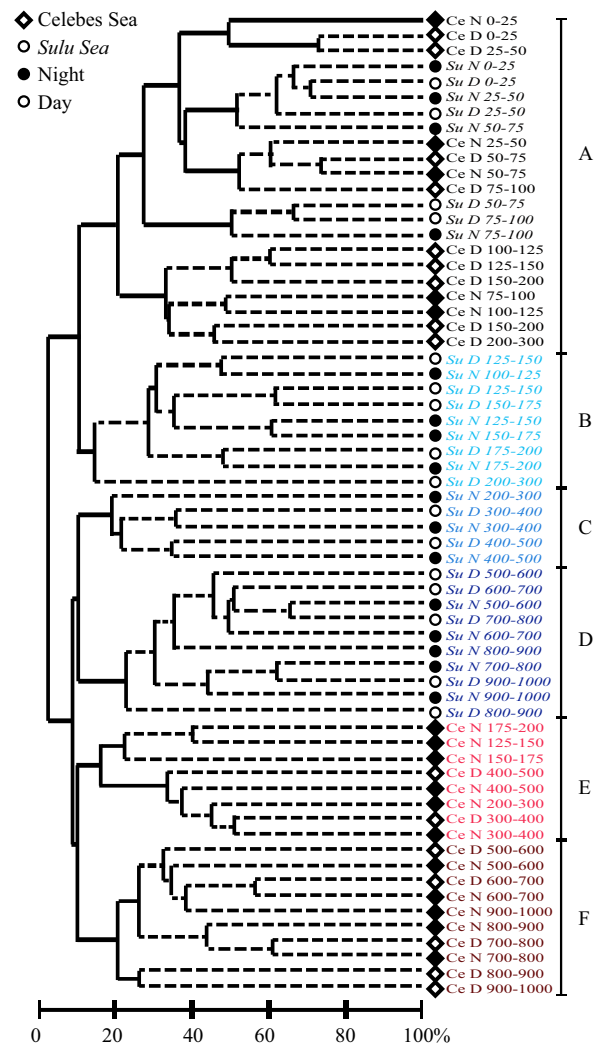


Fig. 6. Community structure analysis dendrogram (clustering performed on square-root-transformed form abundance data, with an average linkage and Bray–Curtis similarity). Letters to the right represent clusters of distinct cnidarian communities. Ce, Celebes Sea; Su, Sulu Sea; D, Day; N, Night.

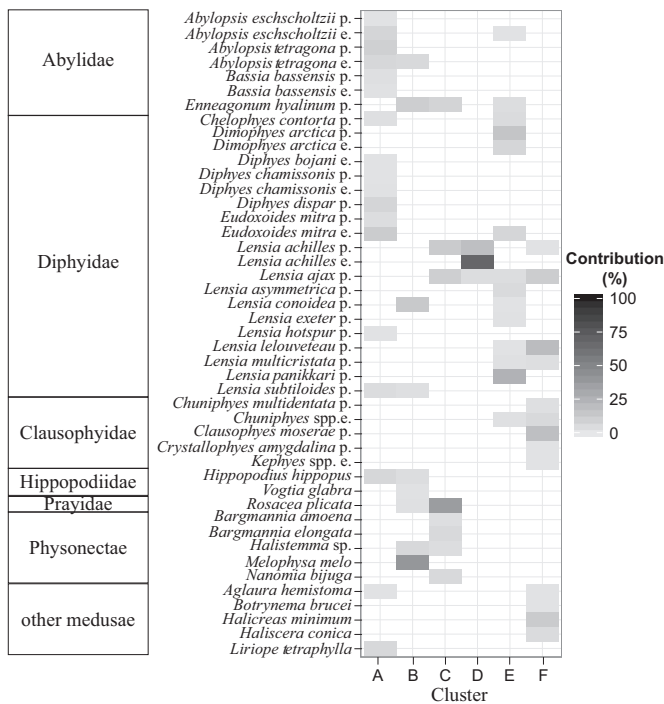


Fig. 7. Forms contributing to dissimilarity between clusters. e, eudoxid stage; p, polygastric stage.

collected between 500 and 1000 m, while another (C in Sulu, E in Celebes) grouped the net samples collected between 300 and 500 m during the day, and between 200 and 500 m at night in the Sulu Sea, or between 125 and 500 m at night in the Celebes Sea. In the Celebes Sea, the little-known, *L. panikkari*, contributed most to the upper-mesopelagic cluster E (25.4%), followed by *D. arctica* eudoxids (15.9%). In the deeper cluster (cluster F), dominant species included *L. lelouveteau*, *Clausophyes moserae*, *Halicreas minimum* and *L. ajax*. In the Sulu Sea, *L. achilles* contributed most to the deep cluster D (68.6% for eudoxids, 18.7% for polygastric stages), with *Rosacea plicata* and *L. ajax*, contributing most to the upper-mesopelagic cluster C.

4. Discussion

This study provides some of the most detailed information on mesopelagic cnidarian diversity and vertical distribution in this region to date by means of using a multiple opening-closing net system. A diverse community of pelagic cnidarians was found in both the Celebes and Sulu Seas in February 2000, during the winter monsoon season. Pelagic cnidarians collected in both Seas were typical of the tropical and subtropical Indo-Pacific (Daniel, 1985; Zhang, 1979; 2005; Gao et al., 2002, Hsieh et al., 2013). However, due to the limited knowledge of this area, this represents the first record from these tropical marginal seas for many species, especially in the mesopelagic zone.

The surface cnidarian communities showed similar abundances and species diversities in the two seas, both being dominated by calyphoran abyliids, non-*Lensia* diphyids, and the hydromedusa, *L. tetraphylla*. With a mean abundance of 2.1 ind./m³ (Fig. 3), the density of cnidarians in the Sulu Sea in February 2000 was twice that recorded in the eastern central Sulu Sea and more than ten-fold that found at coastal stations of the Sulu Sea in December 2007 using a similar MOCNESS sampling system (Acabado et al., 2010). No previous density estimates exist for the Celebes Sea, but during the present sampling effort, siphonophores and other

pelagic cnidarians were found to be one of the most important groups contributing to the total mesozooplankton biomass in the Celebes Sea in terms of wet weight, being surpassed only by copepods and chaetognaths (Nishikawa et al., 2007). Surface siphonophore abundance and community composition in the Celebes and Sulu Seas in February were similar to those previously recorded from the South and East China Seas in winter (November to March) (Zhang and Lin, 2001; Zhang, 2005). Similar siphonophore species were found to dominate surface waters during the summer monsoon season in the Sulu and South China Seas (Musaeva, 1976; Li et al., 2012). However, in the East and South China Seas, the abundance of siphonophores and their proportion relative to other medusae changed depending on season (Xu et al., 2008; Li et al., 2012). Further studies are therefore necessary to quantify the seasonal variation of cnidarian abundance and community structure over the entire water column in the Celebes and Sulu Seas.

At depth, the cnidarian community found in the Celebes Sea was primarily composed of mesopelagic species common throughout the northwest Pacific and China Seas (Alvaríño, 1974; Zhang, 1984; Gao et al., 2002; Grossmann and Lindsay, 2013). However, the high abundance of some species, such as *L. panikkari*, also pointed to an important influx of tropical Indian Ocean waters. Indeed, while patchy reports exist from both the Atlantic and Pacific Oceans (Pugh, 1990; Gibbons and Thibault-Botha, 2002; Grossmann and Lindsay, 2013), this species appears to be predominantly found in the tropical Indian Ocean (Daniel, 1974, 1985). Several presently undescribed species were collected in the mesopelagic zone of the Celebes Sea, but this is believed to reflect more the previous lack of sampling performed in this area than a fauna peculiar to this Sea, as these species have also been collected at other locations in the Pacific (Lindsay, unpublished data). In the Sulu Sea, the cnidarian community was characterized by the absence, in the sampled depth range, of deep mesopelagic cold-water species, such as the siphonophores, *G. reticulata*, *L. havock*, *L. grimaldii*, *L. quadriculata*, and the halicreatid trachymedusa, *B. brucei*. Additionally, except for several *Chuniphyes* spp. eudoxid stages collected at depth in the Sulu Sea, the siphonophore Family Clausophyidae was completely absent from this basin, while all five clausophyid genera were found in the mesopelagic zone of the neighbouring Celebes Sea, and are common in the South China Sea and surrounding tropical and temperate areas (Alvaríño, 1974; Zhang, 1984; Gao et al., 2002). The lack of polygastric stages seems to indicate the absence of a viable standing stock of these animals in the Sulu Sea, the observed eudoxid stages possibly having been released by polygastric stages in neighbouring seas and transported into the Sulu Sea via communicating troughs. The larvae of these species could develop in shallower waters and ontogenetically migrate into deeper, colder waters, allowing lateral transport of larvae at shallower-than-sill depths in the Sulu Sea. Moreover, during the winter monsoon season (December–March), intermediate waters from the South China Sea, notably Subtropical Lower Water and the upper layers of the North Pacific Intermediate Water enter the Sulu Sea through the Mindoro Strait (Quadfasel et al., 1990; Chen et al., 2006; Spintall et al., 2012). These colder waters rapidly mix with warmer, more saline waters in the shallow eastern edge of the Sulu Sea; there have been no records of unaltered Pacific water masses in the Sulu Sea (Tessler et al., 2010; Spintall et al., 2012). The presence of other deep mesopelagic species in the Sulu Sea (e.g. *L. lelouveteau*, *Bargmannia amoena*, *Colobonema sericeum*) confirm the presence of fauna associated with Pacific intermediate waters, and suggests that high temperatures throughout the water column limit the establishment of some deep-water species, rather than the limiting factor being the presence of sills. Indeed, in other seas where temperatures at depth stay relatively high (e.g. Mediterranean Sea, Red Sea), non-*Kephyes* Clausophyidae, *G. reticulata*, *L. havock*, *B. brucei* and other deep-water halicreatids are also rare or absent (Alvaríño, 1974; Gamulin and

Kršinić, 2000; Lučić et al., 2011; Gravili et al., 2013), while other mesopelagic species (e.g. *Kephyes ovata*; *Lensia multicristata*; *Haliscera* spp.) have well-established populations (Gamulin and Kršinić, 2000; Lučić et al., 2011; Gravili et al., 2013). Further studies focussing on differences in the physiology of these animals and vertical distribution patterns of their different life stages would be necessary to explain the absence of some deep-sea taxa in warm marginal seas.

Evenness was high at both sampling locations (Fig. 5), except in the Sulu Sea between 150 and 175 m during both day and night. Low evenness in this layer was correlated with an increase in abundance of the physonect siphonophore, *M. melo* (Table 4). This species has been recorded in the upper 200 m of the water column throughout the tropical and sub-tropical regions of the Atlantic, Indian, and Pacific Oceans, as well as the Mediterranean Sea (Totton, 1954; Alvaríño, 1974). However, it is usually rare (Alvaríño, 1974; Daniel, 1985), and has never been recorded as a dominant siphonophore species, while in the present study, it was the most abundant species throughout the thermocline layer (125–200 m) in the Sulu Sea, with up to 0.24 colonies/m³ between 150 and 175 m during the day. In the Celebes Sea, this species was collected only once, between 25 and 50 m during the day, while common surface species, such as *C. contorta*, *A. eschscholtzi*, and *A. tetragona*, which dominate in the Celebes Sea between 100 and 200 m (Fig. 4, Table 4), were less abundant in the Sulu Sea, perhaps allowing the rarer *M. melo* to flourish in that community.

The absence of 'normal' Indo-Pacific fauna might also explain the high abundance of *L. achilles* in the mesopelagic layers of the Sulu Sea (Table 4). Indeed, in the Celebes Sea, as in many other areas of the Indo-Pacific, *D. arctica* tends to be the dominant siphonophore between 250 and 500 m, followed by members of the Clausophyidae and deep mesopelagic species (*G. reticulata*, *L. havock*, *L. lelouveteau*) below 800 m (Totton, 1954; Daniel, 1985; Zhang, 2005; Mapstone, 2009). Since these species are absent or very rare, possibly lacking breeding populations in the Sulu Sea, this might allow mesopelagic species that are typically less abundant, such as *L. achilles*, to become dominant. However, sampling for molecular studies on cryptic speciation within *L. achilles* and other genera, should be a high priority when considering drivers behind the observed community composition and comparative ecology of these basins. Unlike chaetognaths and copepods (Johnson et al., 2006; Matsuura et al., 2010), cnidarian species collected in the Sulu Sea did not have significantly different depth distributions compared to the Celebes Sea or other areas of the Indo-Pacific (Alvaríño, 1971; Zhang, 2005; Grossmann and Lindsay, 2013), but in mesopelagic layers, the overall diversity of pelagic cnidarians was lower in the Sulu Sea. Diel vertical migration of pelagic cnidarians, when present, was found in both Celebes and Sulu Seas (Fig. 4), while chaetognaths in the Sulu Sea had limited DVM, possibly impaired by the sharp oxycline (Johnson et al., 2006). This result supports the hypothesis of higher resilience to environmental conditions of cnidarians compared to other marine invertebrates.

In the Sulu Sea, while a peak in cnidarian abundance was found between 25 and 50 m during both day and night (Fig. 3), and the community structure was similar during these two sampling periods, an estimate of siphonophore biomass in the Sulu Sea showed a clear decrease in total biomass during the night relative to that found during the day (Nishikawa et al., 2007, Fig. 5 D:122). This observation could be directly linked to the presence of several distinct cohorts of the abundant epipelagic species *D. dispar*. Indeed, during the day, most of the *D. dispar* polygastric stages were large, with anterior nectophores measuring 2–3 cm. Only in the top 50 m of the water column could a second cohort be found, with anterior nectophores measuring 1 cm or less. At night, however, this second cohort of smaller animals extended from the surface to 100 m depth, often representing the majority of the *D. dispar* polygastric stages present. For a similar abundance, the biomass measured at night in the

surface waters of the Sulu Sea was therefore less than that measured during the day. Similarly, the large increase in biomass of 'other cnidarians' in the mesopelagic layers of the Celebes Sea (Nishikawa et al., 2007) was not correlated with a large increase in total cnidarian abundance (Fig. 3), but rather with an increase in abundance of a few larger animals, such as the halicreatid, *H. minimum* and clausophyid siphonophores.

At a species and life stage level, cnidarian community structure observed in February 2000 in the Celebes and Sulu Seas was highly dependent on sampling location, with only the surface community being similar in both seas (Fig. 6). This is quite different from the community structure of the mesoplankton observed at order level (Nishikawa et al., 2007), where depth, rather than sampling location, was found to be the determining factor in community segregation. As with copepods and chaetognaths (Johnson et al., 2006; Nishikawa et al., 2007; Matsuura et al., 2010), this study underlines how choice of different higher taxa as proxies of species diversity (Gaston and Williams, 1993; Gladstone and Alexander, 2005; Kallimanis et al., 2013) can give very different results.

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