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Community structure and vertical distribution of chaetognaths in the Celebes and Sulu Seas

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Abstract—Chaetognath community structure, vertical distribution and migration patterns were investigated in two marginal basins—the Celebes and Sulu Seas. The two seas are part of an island arc located in the southeastern Asia region of the western equatorial Pacific Ocean. The Sulu Sea had higher species diversity (Shannon Index, H') and higher overall chaetognath abundance than the Celebes Sea. Twenty-two species from 4 genera were collected from the Sulu Sea and 19 species from 4 genera were collected from the Celebes Sea. Three species were collected exclusively in the Sulu Sea: *Sagitta bipunctata*, *Sagitta nagae* and an unidentified *Sagitta* species. *Sagitta enflata* was the numerically dominant species at both locations. Species diversity in the Celebes Sea was fairly even between the surface and 1000 m. However, in the Sulu Sea substantial drops in diversity occurred at 175–200 m—below the oxycline, thermocline and halocline—as well as at 900–1000 m. The drop at 175–200 m and 900–1000 m was largely due to the numerical dominance of the species *Sagitta decipiens* and *Sagitta macrocephala*, respectively. In the Celebes Sea only, a large portion of the overall chaetognath population migrated downwards during the day into the 125–200 m layer. Cluster analysis using Ward's method, along with weighted mean depth values, revealed that this migration was largely attributable to the species *Sagitta pacifica*, *Sagitta ferox-robusta*, *Sagitta neglecta* and *Pterosagitta draco*. A similar migration of the overall population was blocked in the Sulu Sea—apparently by the oxycline. It seems the group of migrating chaetognaths in the Celebes Sea prevented the numerical dominance of *S. decipiens* at the lower edge of the epipelagic region, possibly through competition, and consequently prevented the same drop in diversity (H') at 175–200 m as was recorded in the Sulu Sea.

Key words: Celebes Sea, Sulu Sea, chaetognatha, species diversity, diel migration

Introduction

The Celebes and Sulu Seas are marginal basins in the southeastern Asia region of the western equatorial Pacific Ocean. Though close in proximity, they are believed to have formed independently from very different origins (Leg124-scientific-party 1989) and are presently separated by a sill with only ~250 m of clearance above it. The two seas are part of an island arc with 2 contrasting zones (Arief 1998). The Sulu Sea is located in the western zone and is subject to heavy rainfall and subsequent high freshwater discharge, while the Celebes Sea is in the eastern zone, receives about one-half the rainfall of the Sulu and is filled mainly by Pacific Ocean water masses (Toole 1987).

Extensive research has been conducted to elucidate the physical structure and flow of water through the Celebes Sea, Sulu Sea and surrounding regions (Wyrtki 1961, Murauchi et al. 1973, Quadfasel et al. 1990, Hautala et al. 1996, Morey et al. 1999). In general, the pathway of the Indonesian Throughflow is such that North Pacific water moves into the Sulu Sea via the South China Sea, while the Celebes Sea is fed by North Pacific water from the east that passes to the south of Mindanao Island. The Sulu Sea is a semi-isolated basin and most channels connecting it to surrounding seas are less than 200 m deep. The deepest channel is 420 m in depth and is located in Mindoro Strait where it connects the Sulu Sea to the South China Sea. It is through this single sill that deep water in the Sulu Sea is replenished by dense thermocline water from the South China Sea. The next deepest sill (~250 m) is the one separating the Sulu Sea from the Celebes Sea, and water mainly moves out of the Sulu Sea through this channel.

Both seas are recognized as generally having surface waters of high temperature and low salinity. Water temperatures in the two seas are quite similar above ~250 m—the portion of water above the sill separating the seas. However, below this sill (>250 m) the characters of each region become more apparent. While the Celebes Sea steadily decreases in temperature to about 4°C or less at the ocean floor, the Sulu Sea is characterized by unusually warm and homogenous mesopelagic water—a constant of ~10°C (Ocean Research Institute 1975).

Though physical oceanography and geophysical research has been prolific in this region, biological and ecological research is lacking in published literature, especially with respect to chaetognaths. Quantitative data regarding the chaetognath community in the Celebes and Sulu Seas appears to be non-existent. Chaetognaths are an important component of zooplankton communities as they are highly abundant predators of copepods and have the potential to make a significant impact on copepod populations (Sameoto 1972, Feigenbaum and Maris 1984, Pakhomov et al. 1999) as well as contribute to ocean flux (Dilling and Alldredge 1993, Terazaki 1995). In addition, they have been historically used as biological indicators of water masses (Bieri 1959, Alvariño 1965, Stone 1969). Because chaetognaths possess distinct species-specific affinities for certain temperatures and salinities (Grant 1991), the unique features of the Celebes and Sulu Seas—origin, source water, atmospheric influence—and the subsequent hydrographic conditions make it very likely that the two seas harbor different chaetognath communities; especially with respect to the mesopelagic region.

This study provides an introductory comparative report on the structure and composition of the chaetognath community in the Celebes and Sulu Seas, along with details regarding vertical distribution and migration patterns. This is an integral step for further clarifying the nature of the zooplankton community in the region.

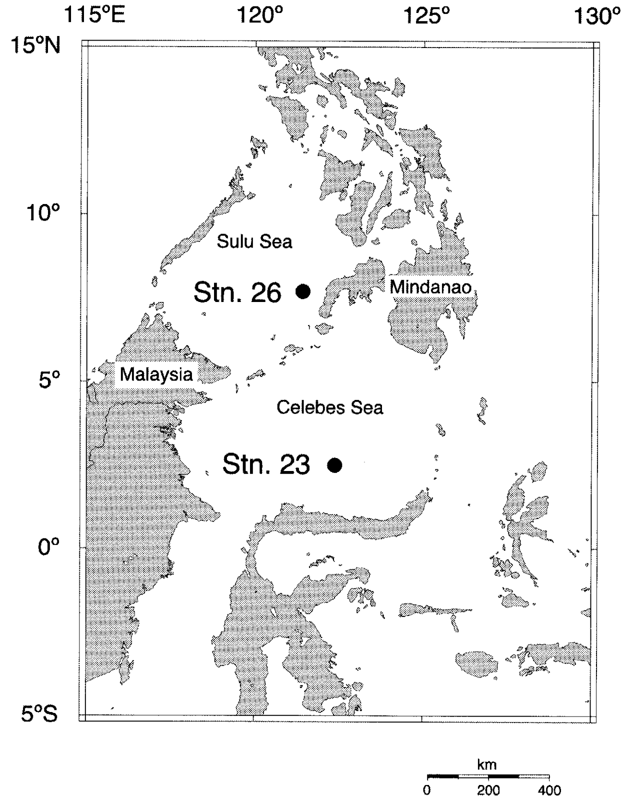

Fig. 1. Map of study site and sampling locations—Celebes and Sulu Seas in the western equatorial Pacific.

Method

Sampling

Zooplankton samples were collected from the Celebes Sea and Sulu Sea during the KH-00-1 cruise conducted by the R/V 'Hakuho Maru' of the Ocean Research Institute, University of Tokyo, using a MOCNESS [Multiple Opening/Closing Net and Environmental Sampling System, with a mouth area of 1 m^2 and 0.33 mm mesh; (Wiebe et al. 1976, Wiebe et al. 1985)]. Two consecutive daytime tows and nighttime tows were made at station 23 (2°30′N, 122°24′E, 5386 m water depth) in the Celebes Sea on February 19, 2000 and at station 26 (7°39′N, 121°22′E, 4892 m water depth) in the Sulu Sea on February 24 and 25, 2000 (Fig. 1).

Two deployments of the MOCNESS sampled 16 discrete layers from 1000 m depth to the surface: 100 m intervals below 200 m and 25 m intervals above 200 m. The net was retrieved at such a speed so as to maintain a 45° angle, in general this meant the line speed was between 0.2–0.4 m s^{-1} and the boat was traveling between 1–3 knots. The average volume of water filtered was 1285.8 and 1288.2 m^3 per hundred-meter layer at the Celebes Sea and Sulu Sea, respectively. Nets were rinsed down into the cod end and the samples were fixed with a 10% buffered formalin and seawater solution. Temperature, salinity and dissolved oxygen data was collected by CTD during sampling.

Laboratory analysis

Chaetognaths were separated out from the rest of the samples, sorted by species and enumerated to calculate the abundance density (ind. m^{-3}). A statistical t-test on the Shannon Index (H') was used to compare species diversity between the two seas (Magurran 1988, Fowler et al. 1998). The formula for calculating H' is:

$$H' = -\Sigma p_i \ln p_i$$

where p_i is the proportional abundance (n_i/N) of the ith species.

To explore differences and similarities in community structure with respect to depth at both locations, cluster analysis using Ward's method was conducted based on the abundance (ind. m^{-3}) of each species at every depth layer sampled. Cluster analysis was ordered on the first principal component collected from a Principal Component Analysis (PCA) on the multivariate correlations of the abundance data. The multivariate, PCA and subsequent cluster analyses plus heat maps were done with JMP statistical software, Version 5, SAS Institute Inc., Cary, NC, 1989–2002.

The weighted mean depth was calculated for the species *Sagitta pacifica*, *Sagitta ferox-robusta*, *Sagitta neglecta* and *Pterosagitta draco* to further clarify vertical migration patterns. The formula for calculating WMD is:

$$\mathrm{WMD} = (\Sigma n_i d_i)/(\Sigma n_i)$$

where n_i is the abundance of individuals (ind. m^{-3}) in depth stratum i and d_i is the midpoint of the stratum.

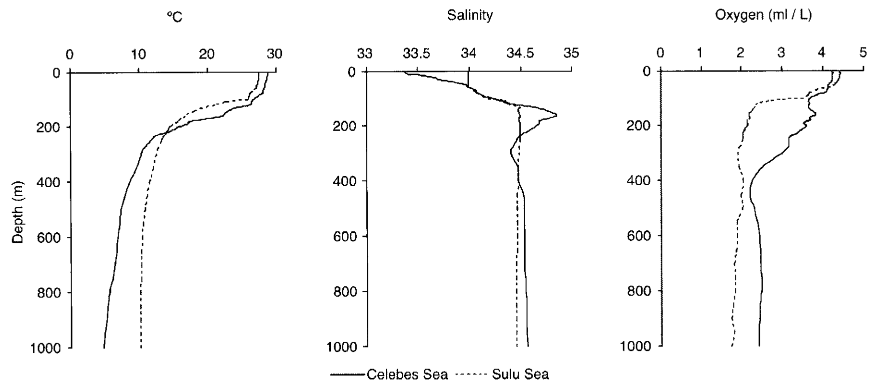

Fig. 2. Temperature, salinity and oxygen profiles for the Celebes and Sulu Seas in the western equatorial Pacific at the time of sampling.

Results

Hydrographic profile

At the time of sampling, the thermocline in the Celebes Sea was between about 150–250 m and in the Sulu Sea it was located at about 100 m (Fig. 2). Temperatures continued to decline in the Celebes Sea approaching 5°C at 1000 m. In the Sulu Sea, temperature stabilized below ~400 m and remained at just over 10°C.

A distinct halocline was present in the Sulu Sea at about 100 m with a sharp increase in salinity (Fig. 2). Salinity increased in the Celebes Sea as well, however the halocline stretched between the surface and about 160 m. Below 160 m, salinity in the Celebes Sea dropped about one-half point and finally stabilized at around 350 m. Dissolved oxygen in the Sulu Sea decreased sharply between 50–150 m forming a strong oxycline, below which oxygen levels stabilized. In the Celebes Sea there was a gradual decrease in oxygen from the surface to about 400 m where it stabilized.

Species composition

The Sulu Sea had higher species diversity (H') and higher overall chaetognath abundance than the Celebes Sea. Twenty-two species from 4 genera were collected at the Sulu Sea and 19 species from 4 genera were collected at the Celebes Sea (Table 1). *Sagitta enflata* was the numerically dominant species at both locations comprising 39.5% of the total identifiable chaetognaths in the Sulu Sea and 38.6% in the Celebes (Fig. 3). Other numerous species included *S. pacifica*, *P. draco*, *Krohnitta pacifica*, *Sagitta decipiens* and *Eukrohnia hamata* which comprised 11.8%, 6.7%, 12.1%, 8.4% and 2.6% respectively of the total identifiable chaetognaths in the Sulu Sea and 22.2%, 17.1%, 2.2%, 1.9% and 2.4% respectively of the total identifiable chaetognaths in the Celebes Sea (Fig. 3). Three species were collected exclusively in the Sulu Sea: *Sagitta bipunctata*, *Sagitta nagae* and a *Sagitta* species that was not readily identifiable by modern chaetognath keys.

The Shannon Index (H') value for the Sulu Sea overall was 2.11, and 1.87 for the Celebes Sea overall. A *t*-test found the difference between the two H' values to be highly significant ($P<0.001$). Comparing species diversity (H') of chaetognaths with respect to depth at each location, the Celebes Sea appeared to have fairly similar levels of diversity between the surface and 1000 m, though slightly elevated nearer to the surface (Fig. 4). However, in the Sulu Sea substantial drops in diversity occurred at 175–200 m—below the oxycline, thermocline and halocline—as well as at 900–1000 m (Fig. 4). Furthermore, these drops were coupled with noticeable peaks in H' at 50–75 m and 500–600 m. In general, the number of species per depth layer seemed to correlate fairly well with diversity in both seas (Fig. 4), but a notable exception was found in the Sulu Sea from 900 to 1000 m at night—species number was fairly high while diversity was fairly low.

Abundance and vertical distribution

Total chaetognath abundance was higher in the Sulu Sea than the Celebes Sea however the overall distribution pattern was quite similar—the bulk of the population was in the upper 75 m (Fig. 5). In the Celebes Sea, a portion of the population migrated downwards during the day into the 125–200 m layer. There was no such migration in the Sulu Sea. The total chaetognath abundance integrated over each haul was 4.71 individuals (ind.) m^{-3} in the Sulu Sea during the day and 5.22 ind. m^{-3} at night. In the Celebes Sea there were 3.05 ind. m^{-3} during the day and 2.97 ind. m^{-3} at night.

The most abundant species, *S. enflata*, was found in excess of 10 ind. m^{-3} in the upper 50 m of both seas (Fig. 6). *Sagitta pacifica* had abundance peaks of over 5 ind. m^{-3} in the upper 50 m at night in both seas but during the day abundance values dropped to less than 5 ind. m^{-3} and they were found deeper in the water column suggesting vertical migration by this species (Fig. 6). Similarly, *P. draco* seemed to engage in vertical migration at both regions. In the Celebes Sea, *P. draco* abundance peaked in the upper 25 m at 6.8 ind. m^{-3} during the night while during the day they peaked be-

Table 1. The species collected and their per cent of the total number of chaetognaths in the Celebes and Sulu Seas in the western equatorial Pacific.

Region	Species	Per cent of total	Water Mass
Celebes Sea	*Sagitta enflata*	25.98	Warm
(n=3638)	*Sagitta* spp. juveniles[A]	24.21	—
	Sagitta pacifica	14.93	Warm
	Pterosagitta draco	11.52	Warm
	Aidano group	8.43	Warm
	Sagitta neglecta	2.72	Warm
	Sagitta ferox-robusta	1.89	Warm
	Sagitta hexaptera	1.88	Warm
	Eukrohnia hamata	1.63	Meso
	Krohnitta pacifica	1.49	Warm
	Sagitta decipiens	1.30	Meso
	Sagitta bedoti	1.15	Warm
	Sagitta macrocephala	0.96	Meso
	Sagitta brunni	0.50	Warm
	Sagitta pulchra	0.38	Warm
	Eukrohnia bathypelagica	0.24	Meso
	Eukrohnia fowleri	0.21	Meso
	Sagitta lyra-scrippsae	0.19	Mix
	Sagitta septata	0.16	Warm
	Sagitta sp. A[A]	0.12	—
	Sagitta zetesios	0.11	Meso
	Eukrohnia spp. juveniles[A]	0.02	Meso
Sulu Sea	*Sagitta* spp. juveniles[A]	34.50	—
(n=4155)	*Sagitta enflata*	23.51	Warm
	Krohnitta pacifica	7.20	Warm
	Sagitta pacifica	7.01	Warm
	Aidano group	6.04	Warm
	Sagitta decipiens	5.00	Meso
	Pterosagitta draco	3.99	Warm
	Sagitta macrocephala	1.95	Meso
	Sagitta pulchra	1.53	Warm
	Eukrohnia hamata	1.53	Meso
	Sagitta ferox-robusta	1.33	Warm
	Sagitta neglecta	1.30	Warm
	Sagitta brunni	1.26	Warm
	Sagitta hexaptera	1.19	Warm
	Sagitta bedoti	0.84	Warm
	Sagitta nagae	0.75	Mix
	Eukrohnia bathypelagica	0.55	Meso
	Sagitta zetesios	0.21	Meso
	Sagitta lyra-scrippsae	0.11	Mix
	Sagitta sp. B[A]	0.06	—
	Sagitta septata	0.05	Warm
	Sagitta bipunctata	0.05	Warm
	Sagitta sp. A[A]	0.03	—
	Eukrohnia fowleri	0.01	Meso
	Eukrohnia spp. juveniles[A]	<0.01	Meso

[A]Unidentified.

Aidano Group: *Sagitta* species often referred to as *Aidanosagitta*. *Sagitta neglecta* was identified to species level, the other Aidanos just to genus level due to very small body size (~4–7 mm) and time constraints.

The water masses that each species is typically associated with are shown: Meso, mesopelagic water; Mix, mixed epipelagic water; Cold, cold epipelagic water; Warm, warm epipelagic water.

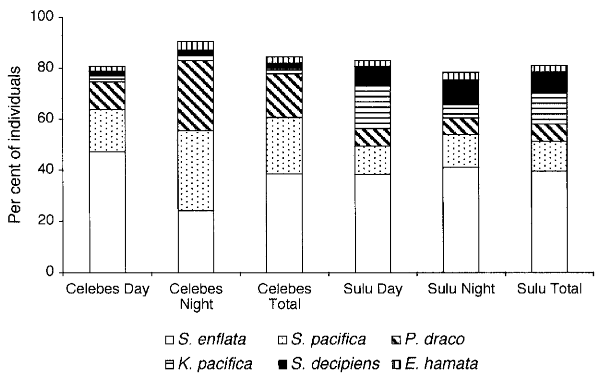

Fig. 3. Relative abundance of the major identifiable species in the Celebes Sea and the Sulu Sea in the western equatorial Pacific.

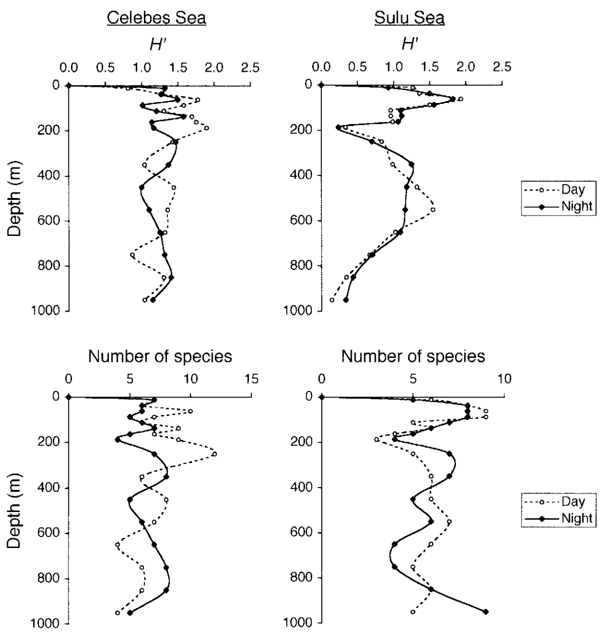

Fig. 4. Species diversity as measured by the Shannon Index (*H'*) (top) and the number of species (bottom) in the Celebes and Sulu Seas in the western equatorial Pacific. Data points correspond to the middle of each sampling layer.

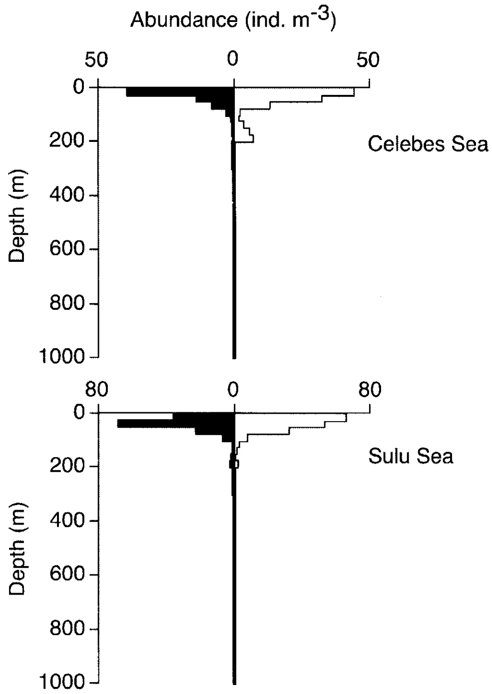

Fig. 5. Overall abundance and vertical distribution of chaetognaths in the Celebes and Sulu Seas in the western equatorial Pacific. Nighttime is in black.

tween 25–50 m at 4.3 ind. m^{-3} (Fig. 6). In the Sulu Sea, *P. draco* peaked between 25–50 m at 1.8 ind. m^{-3} during the night and during the day they peaked between 50–75 m at 4.1 ind. m^{-3}. Both *S. neglecta* and *S. ferox-robusta* showed signs of vertical migration in the Celebes Sea, yet no evidence of such movement in the Sulu Sea. In the Celebes Sea, maximum abundance of *S. neglecta* in the day was 1.3 ind. m^{-3} at 175–200 m, while at night it was 0.25 ind. m^{-3} at 0–25 m (Fig. 6). Similarly, the maximum abundance of *S. ferox-robusta* in the Celebes Sea was 0.8 ind. m^{-3} at 175–200 m in the day and 0.34 ind. m^{-3} at 50–75 m in the night. In the Sulu Sea, both species remained concentrated in the upper 75 m during day and night.

Though vertical migration was not as clear with *K. pacifica*, the species was obviously more abundant during the daytime at both locations and tended to concentrate in the upper 100 m (Fig. 6). Furthermore, *K. pacifica* was considerably more abundant in the Sulu Sea (max. abund. 8.1 ind. m^{-3}) than the Celebes Sea (max. abund. 0.63 ind. m^{-3}) and a few individuals were able to exploit the warm mesopelagic water of the Sulu Sea by distributing to 500–600 m. *Sagitta decipiens* was also much more abundant in the Sulu Sea, where they were highly concentrated between 175–200 m. The maximum abundance was 2.1 ind. m^{-3} in the Sulu Sea compared to only 0.18 ind. m^{-3} in the Celebes (Fig. 7). The other 5 mesopelagic species *E. hamata*, *Eukrohnia bathypelagica*, *Eukrohnia fowleri*, *Sagitta macrocephala* and *Sagitta zetesios* were all slightly more abundant in the Sulu Sea compared to the Celebes Sea, however their vertical distribution patterns were essentially unchanged (Fig. 7). *Eukrohnia hamata* had surprisingly similar vertical distribution patterns in both seas. Peak abundance was consistently found at 300–400 m for all four hauls and tapered off in the depths below this.

Cluster analysis of the Celebes Sea data revealed a clearly demarcated epipelagic group (0–200 m) and mesopelagic group (200–1000 m) of chaetognaths during the day (Fig. 8). At night, the split was a little shallower: an upper epipelagic group (0–25 m) and a lower epi-mesopelagic group (Fig. 9). *Pterosagitta draco* could be seen to associate strongly with 0–50 m depth at night and 25–75 m at day-further evidence of vertical migration by this species. Likewise, *S. pacifica* was strongly associated with 0–25 m depth at night and 50–75 m during the day. *Eukrohnia*

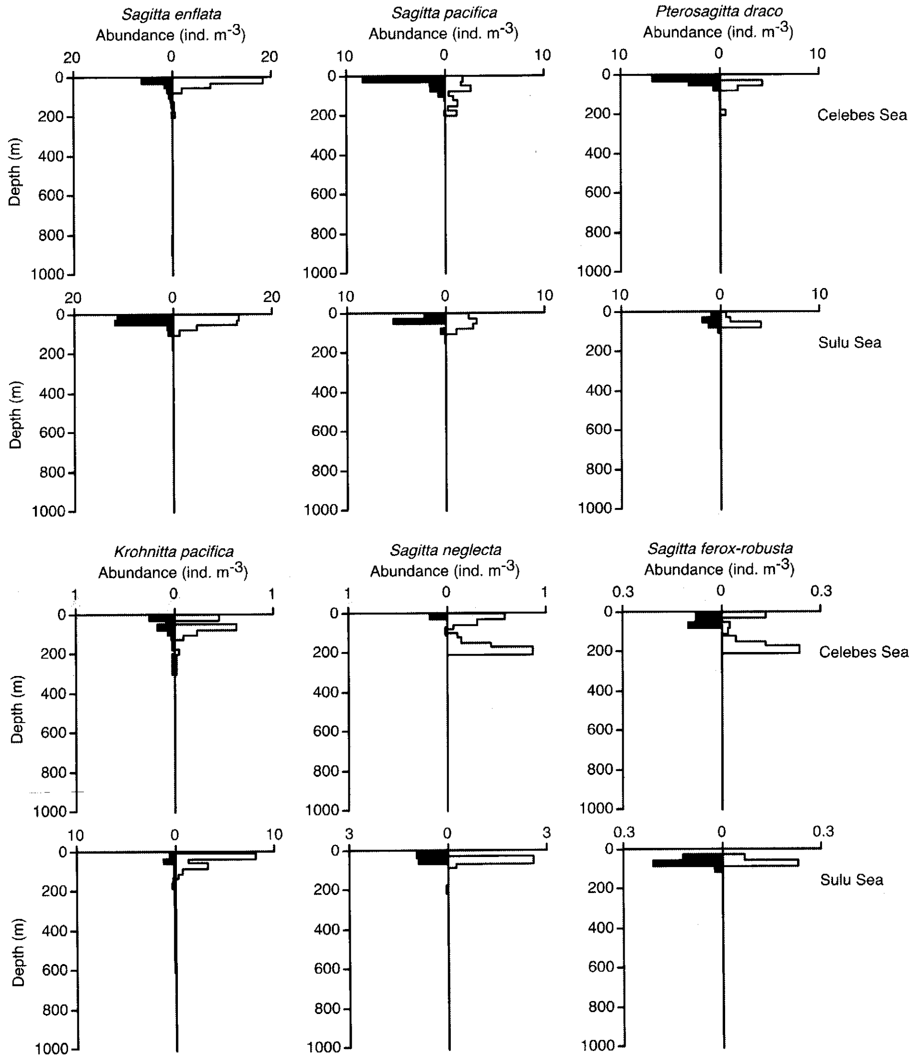

Fig. 6. Abundance and vertical distribution of *Sagitta enflata, Sagitta pacifica, Pterosagitta draco, Krohnitta pacifica, Sagitta neglecta* and *Sagitta ferox-robusta* in the Celebes and Sulu Seas in the western equatorial Pacific. Nighttime is in black.

hamata and *S. zetesios* were consistently associated with 300–400 m depth. The cluster analysis also revealed that the vertical migration and daytime peak at 125–200 m in the Celebes Sea chaetognath population was largely attributable to the species *S. pacifica*, *S. ferox-robusta*, *S. neglecta* and *P. draco*. These species did not associate with 125–200 m at night, but associated strongly with that region during the day (Figs. 8 and 9). Calculated weighted mean depth values (WMD) indicated migration to deeper water during the day and a return to shallower water at night in the Celebes Sea (Table 2); vertical distribution plots further indicated this (Fig. 6).

In the Sulu Sea, cluster analysis revealed upper epipelagic (0–75 m) and lower epi- mesopelagic (75–1000 m) groups similar to the Celebes Sea during day and night (Figs. 10 and 11). Again, evidence was found for the vertical migration of *P. draco* (associated strongest with 50–75 m at day, and 25–50 m at night) and *S. pacifica* (associated strongest with 25–75 m at day, and 0–50 m at night). However, WMD values did not show a very strong shift of population center for these species between day and night (Table 2). Like the Celebes Sea, *E. hamata* and *S. zetesios* were associated strongly and consistently with 300–400 m depth. Finally, *S. decipiens* maintained a strong association with 175–200 m depth at both night and day.

Discussion

The chaetognath species collected from both the Sulu Sea and Celebes Sea were typical for equatorial waters and showed little or no deviation from previous reports on equatorial studies in the Pacific Ocean, the South China Sea and near the Philippines (Alvariño 1967, Jumao-as and von Westernhagen 1975, Rottman 1978). Composition of the community as well, in terms of proportional abundance, was not unusual; *S. enflata* has been well studied and is frequently the numerically dominant species in lower latitudes and equato-

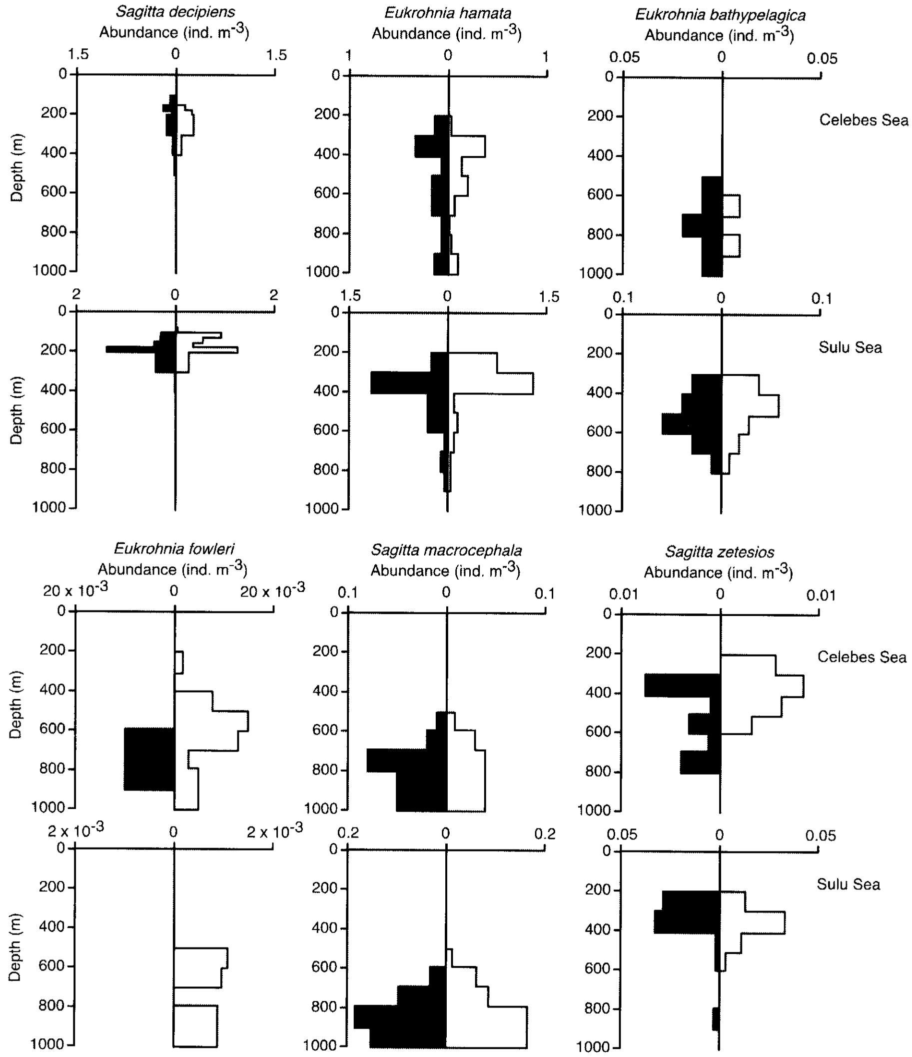

Fig. 7. Abundance and vertical distribution of *Sagitta decipiens*, *Eukrohnia hamata*, *Eukrohnia bathypelagica*, *Eukrohnia fowleri*, *Sagitta macrocephala* and *Sagitta zetesios* in the Celebes and Sulu Seas in the western equatorial Pacific. Nighttime is in black.

rial waters (Tokioka 1962, Kehayias et al. 1996, Terazaki 1996, Kehayias 2003, Giesecke and Gonzalez 2004). The overall number and variety of species in both seas was quite similar—only 3 species were collected in the Sulu Sea that were not found in the Celebes Sea: *S. nagae*, *S. bipunctata* and an unidentified *Sagitta* species. *Sagitta nagae* is a mixed-water species common in the seas around Japan (Chihara and Murano 1997) and *S. bipunctata* is a temperate-warm-water species with a cosmopolitan distribution (Alvariño 1965). Both of these species have been reported from the South China Sea (Alvariño 1967, Rottman 1978) and it is quite probable that they were carried into the Sulu Sea by water flowing from that region. *Sagitta nagae* is believed to keep a slightly northern distribution, appearing only in the South China Sea with seasonal southward current flow (Alvariño 1967); thus it would seem they could reach the Sulu Sea periodically, but be effectively absent from the Celebes Sea. In regards to *S. bipunctata*, Alvariño (1965) describes their distributional range to include the equatorial western Pacific Ocean region, including the Celebes Sea, so it is very unlikely that *S. bipunctata* is a species exclusive to the Sulu Sea even though they were absent from Celebes Sea collections.

The vastly different hydrographic conditions found in the mesopelagic layer of the 2 seas had little influence on the bulk of the chaetognath population, as most chaetognaths were concentrated in the upper epipelagic region. Surprisingly, the same deep-water species were collected from the mesopelagic layer of both seas, and the warm, homogenous mesopelagic water of the Sulu Sea had only a limited effect on these species: increased abundance and success was noted; yet vertical distribution was basically unaltered. It would seem the homogeny of the hydrographic conditions, through the mesopelagic layer to the sea floor, offered little incentive for mesopelagic species to modify distribution patterns in the Sulu Sea, as there were no alternate conditions to descend in to. The vertical distribution of the mesopelagic species *E. bathypelagica*, *E. fowleri*, *S. macrocephala* and *S. zetesios* was not unusual in either sea when compared to pre-

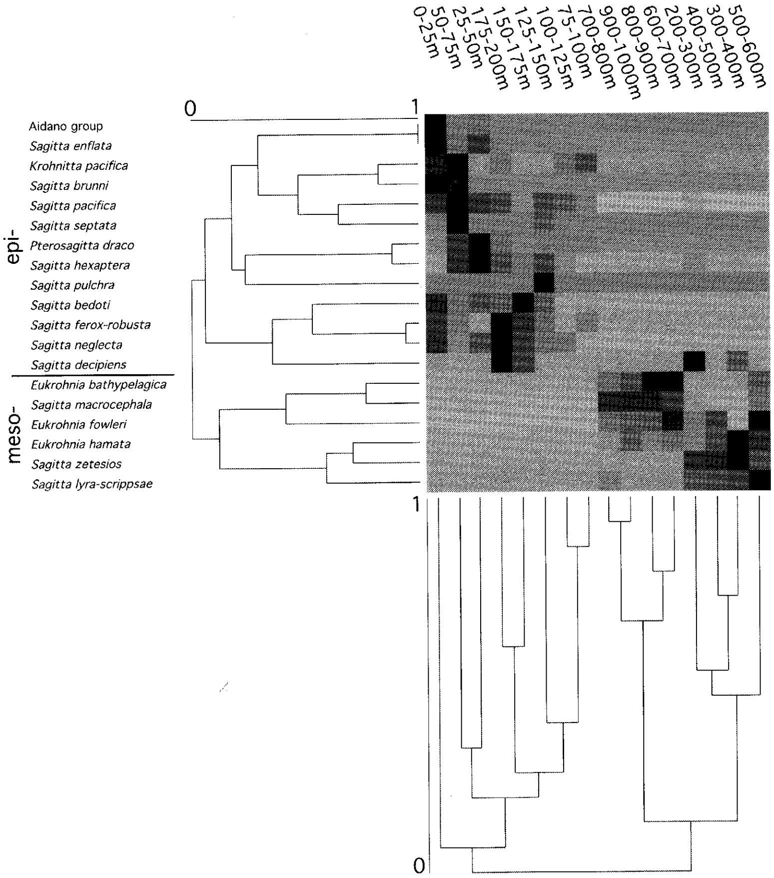

Fig. 8. Celebes Sea, daytime. Two-way clustering dendrogram based on species abundance (ind. m^{-3}) at each depth layer. Dendrogram is scaled from 0 to 1 with 0 showing the least similarity (least information remaining) and 1 showing the most similarity (most information remaining). Shading shows the relative degree of affiliation between each species and depth layer: dark=strong affiliation, light=weak affiliation.

vious studies (Terazaki and Marumo 1982, Terazaki and Miller 1982, Cheney 1985). However, it was a little unusual for the maximum concentration of *E. hamata* in both seas to be consistently at 300–400 m depth. *Eukrohnia hamata* is a species easily influenced by warm temperature and will shift vertically to distribute in cooler waters (Cheney 1985, Johnson and Terazaki 2003). However, the fact that they did not concentrate deeper in the Celebes Sea where colder water temperatures were available, suggests there was an overriding factor keeping the maximum abundance in the 300–400 m depth range. One possibility is that salinity may be influencing *E. hamata* distribution, more so than temperature, since salinity was equal at both sampling stations between 350–400 m.

A single epipelagic species, the well-known warm-water species *K. pacifica*, was able to exploit the Sulu Sea's warm mesopelagic layer with a few individuals distributing to 500–600 m compared to only 200–300 m in the Celebes Sea. Surprisingly, other warm-water epipelagic species did not do the same. However, the fact that only a very small fraction of the *K. pacifica* population moved into those depths implies that the movement had little to do with the species capability as a whole—rather it was a matter of resiliency of a few individuals.

The chaetognath population in the Sulu Sea was much more abundant, and the cause of the increased success and abundance of the Sulu Sea chaetognaths was most likely linked to higher productivity in that region. Chlorophyll *a* concentrations are much higher in the Sulu Sea where diatoms are major contributors, while smaller-sized producers such as prochlorophytes and haptophytes are dominant in the Celebes Sea (K. Furuya and N. Ramaiah, University of Tokyo, pers. comm.). Total mesozooplankton biomass was also higher in the Sulu Sea during the KH-00-1 cruise (J. Nishikawa, University of Tokyo, in prep.). Additionally, higher levels of rainfall in the Sulu Sea region creates elevated runoff compared to the Celebes Sea, which could boost productivity by injecting greater amounts of nutrients into the Sulu Sea.

Along with being more abundant, the Sulu Sea chaetognath population was more diverse than the Celebes Sea population. This may at first seem somewhat anomalous considering that studies have found high abundance to be generally linked with high productivity, and diversity is generally con-

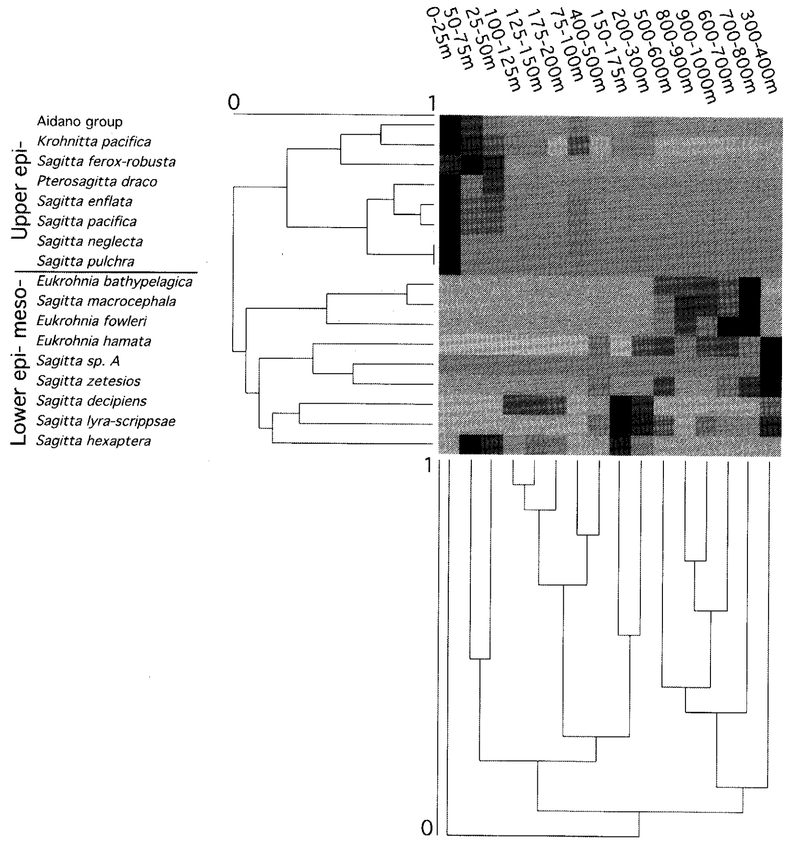

Fig. 9. Celebes Sea, nighttime. Two-way clustering dendrogram based on species abundance (ind. m^{-3}) at each depth layer. Dendrogram is scaled from 0 to 1 with 0 showing the least similarity (least information remaining) and 1 showing the most similarity (most information remaining). Shading shows the relative degree of affiliation between each species and depth layer: dark=strong affiliation, light=weak affiliation.

sidered to be lower in regions of high productivity (Angel 1991, 1993, 1997, Pierrot-Bults 1997). However, those previous studies also noted a drop in species number along with diversity, which was not the situation in this study—essentially the same number of species was found in both seas. Species diversity as measured by H' rises when many species are present in comparable abundances and falls when a few species are present in numbers far greater than the other species. So, within this study, the difference in diversity between the seas simply reflects a greater number of species enjoying comparable success and thus comprising more similar proportions of the community in the Sulu Sea compared to the Celebes Sea. This is visible in Fig. 3.

In addition to higher overall species diversity in the Sulu Sea, there were also marked dips and peaks in diversity through the water column that were not seen in the Celebes Sea (Fig. 4). The large drop in diversity between 175 and 200 m depth was partially the result of a decrease in the number of species at that depth, but it was largely caused by the very high abundance of *S. decipiens* compared to other species present. The lowest sampled depth (900–1000 m) in the Sulu Sea had an even better example of the influence of individual species abundance on diversity—though nighttime species number was high, diversity was low due to the numerical dominance of the zone by *S. macrocephala*. The high diversity at 50–75 m depth was the result of high species number and comparable levels of abundance for all species present. Likewise, from 500 to 600 m depth, though overall abundance was very low, there were several species at similar levels of abundance so H' was high.

Compared to the Sulu Sea, the Celebes Sea had much less fluctuation in H' with depth. This demonstrates that no single species was ever overwhelmingly dominant in abundance at any layer sampled, thus no drop in H'. Furthermore, the species present at any one layer were never all at comparable levels of abundance, thus no spike in H'. The important question is: what caused the large difference between the chaetognath communities when they are essentially composed of the same species in both seas? The answer could be linked to hydrography or food conditions.

Though *S. decipiens* is generally regarded as a mesopelagic species (Sund 1961, Alvariño 1965, Vucetic 1969), they distributed across the transition zone of the upper mesopelagic and lower epipelagic in both the Celebes and Sulu Seas. Cheney (1985) reported a similar situation in the North Atlantic. *Sagitta decipiens* was much more successful

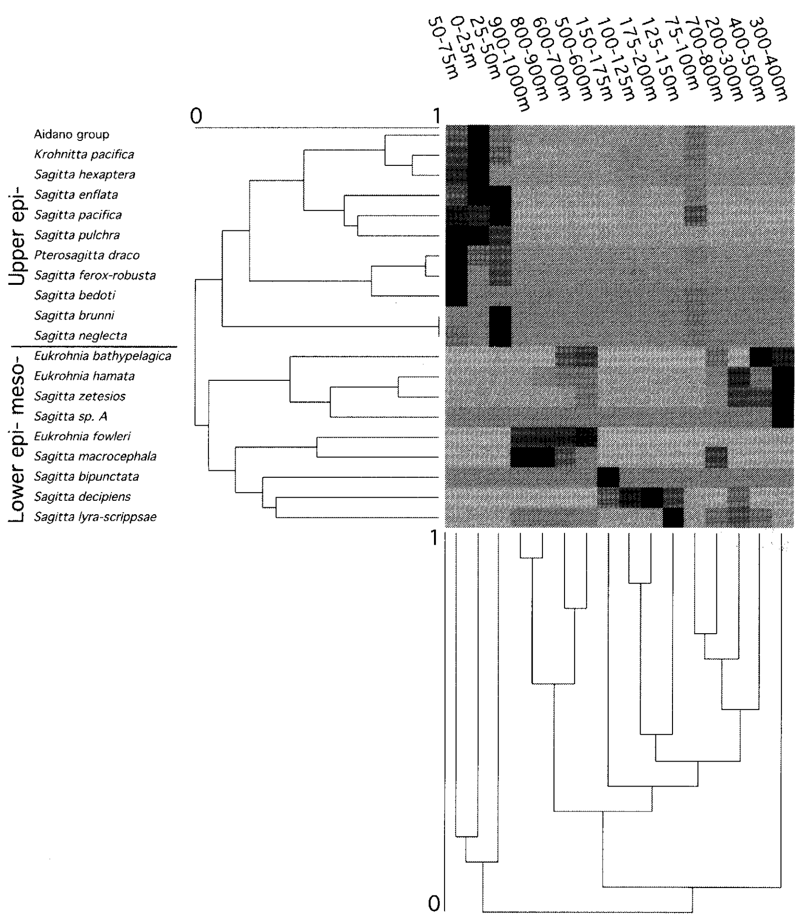

Fig. 10. Sulu Sea, daytime. Two-way clustering dendrogram based on species abundance (ind. m^{-3}) at each depth layer. Dendrogram is scaled from 0 to 1 with 0 showing the least similarity (least information remaining) and 1 showing the most similarity (most information remaining). Shading shows the relative degree of affiliation between each species and depth layer: dark=strong affiliation, light=weak affiliation.

in the Sulu Sea compared to the Celebes Sea; the overall abundance was on average 6 times higher in the Sulu Sea. This success and abundance, precluding other species, lowered H' considerably at the bottom edge of the epipelagic zone (175–200 m) in the Sulu Sea. *Sagitta decipiens* was able to maintain a nearly unchallenged dominant presence during the day and night in a small niche at 175–200 m in the Sulu Sea; examination of the dendrograms revealed that they were the only species strongly associated with that layer (Figs. 10 and 11). However, within the Celebes Sea *S. decipiens* was not very abundant and was weakly associated with the 175–200 m depth layer. Furthermore, 4 other chaetognath species were able to migrate downwards and associate with that depth layer during the day (Fig. 6 and 8). It seems the presence of this group of migrating chaetognaths prevented the numerical dominance of *S. decipiens* at the lower edge of the epipelagic region, possibly through competition, and consequently prevented the same drop in diversity (H') at 175–200 m as was recorded in the Sulu Sea. A similar migration of competitors was blocked in the Sulu Sea—apparently by oxygen levels. Examining the hydrographic conditions of the two regions, it is likely that the oxycline in the Sulu Sea, and to a lesser degree the thermocline, formed a barrier to vertical movement of chaetognath species into the 175–200 m layer, effectively leaving *S. decipiens* unperturbed and dominant. In the Celebes Sea there was no such barrier preventing movement into that depth. *Sagitta decipiens* has been reported to inhabit low oxygen environments (Srinivasan 1947, Sund 1961) and in this study it is clear they thrive in the low oxygen waters of the Sulu Sea below the oxycline where epipelagic species are unable to migrate into.

Like *S. decipiens*, *S. macrocephala* was also more successful in terms of abundance in the Sulu Sea compared to the Celebes Sea, however the lack of any hydrographic boundaries and the overall homogenous conditions of the 900–1000 m layer in both seas suggests their success was based on other factors, such as prey/food. However, detailed feeding investigations were beyond the scope of this project. *Sagitta macrocephala* is very deeply distributed and because of this, ecological information is rather limited—their bioluminescent capabilities were not even discovered until 1994 (Haddock and Case 1994). Naturally, further study will be

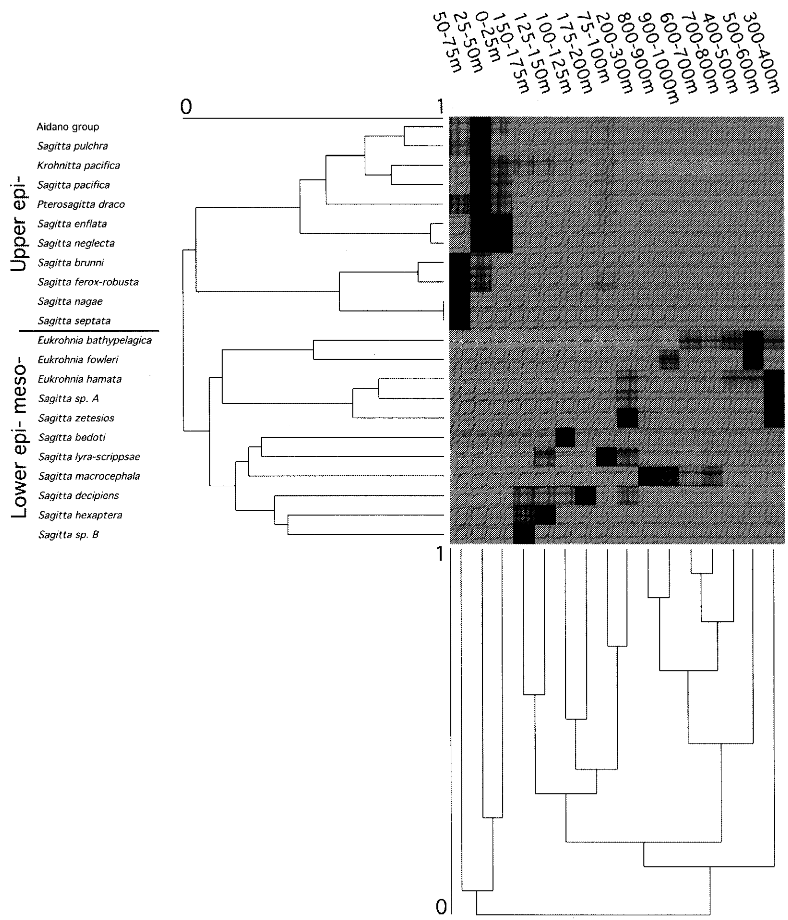

Fig. 11. Sulu Sea, nighttime. Two-way clustering dendrogram based on species abundance (ind. m^{-3}) at each depth layer. Dendrogram is scaled from 0 to 1 with 0 showing the least similarity (least information remaining) and 1 showing the most similarity (most information remaining). Shading shows the relative degree of affiliation between each species and depth layer: dark=strong affiliation, light=weak affiliation.

Table 2. Weighted mean depth (WMD) values in meters for select species in the Celebes and Sulu Seas in the western equatorial Pacific.

	Celebes Sea		Sulu Sea	
	Day	Night	Day	Night
Sagitta pacifica	85	27	45	34
Pterosagitta draco	60	23	53	42
Sagitta ferox-robusta	130	41	57	56
Sagitta neglecta	115	17	41	28

necessary to uncover the particular mechanism of their success in the Sulu Sea.

The cluster analysis revealed 2 vertically demarcated groups of chaetognaths in both seas during day and night. In the Sulu Sea, the split occurred consistently both night and day near 75 m depth and was most likely governed by the hydrographic conditions—thermocline, halocline and oxycline—that it coincided with. In the Celebes Sea, the depth of the split shifted between day (200 m) and night (25 m) and was most likely influenced by the vertical migration made possible by a deeper thermocline and by the absence of a strong oxycline. Previous research has revealed vertical migration in many chaetognath species (Terazaki 1992, Duró et al. 1994, Terazaki 1996, Nishihama 1998). Of the 4 migrating species recorded here, only *P. draco* could be confirmed as a migrator from previous work by other researchers (Pierrot-Bults 1982, Duró et al. 1994). The other species—*S. pacifica*, *S. ferox-robusta*, *S. neglecta*—have not been clearly reported. Terazaki (1996) published data that showed possible migration of *S. pacifica* but nothing conclusive, and no evidence for *S. ferox-robusta* or *S. neglecta*. The lack of data for these 3 species in published literature is probably because they are not dominant and usually comprise only a small portion of the chaetognath population; therefore they do not receive much attention. Migration in this study seemed to be very much influenced by hydrographic conditions, as the degree of vertical movement was quite large in the Celebes Sea and minimal or non-existent in the Sulu Sea (Fig. 6 and Table 2). This concept has important ramifications in the study of vertical migration among chaetognaths—just because a species migrates in one location doesn't necessarily mean it will migrate in another. Kehayias et al. (1994) made a similar observation in the Eastern Mediterranean, where they found no evidence of vertical migration among several species that had been previously reported as migrators by other researchers.

This initial report on the chaetognaths of the Sulu and Celebes Seas is a good starting point for chaetognath research in the region. Future study should expand on this work with analysis of the predator-prey relationships between chaetognaths and copepods to tease out potential species selectivity and further explain the relative success and distribution among chaetognath species in the two seas.

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References

Alvariño, A. 1965. Chaetognaths. Oceanogr. Mar. Biol. Ann. Rev. 3: 115–194.

Alvariño, A. 1967. The Chaetognatha of the NAGA Expedition (1959–1961) in the South China Sea and the Gulf of Thailand. Part 1-Systematics. Scripps NAGA, 4–2, La Jolla.

Angel, M. V. 1991. Variations in time and space: Is biogeography relevant to studies of long-time scale change? J. mar. biol. Ass. U.K. 71: 191–206.

Angel, M. V. 1993. Biodiversity of the Pelagic Ocean. Conserv. Biol. 7: 760–772.

Angel, M. V. 1997. Pelagic Biodiversity. *In* Marine biodiversity: patterns and processes. Angel, M. V. (ed.), pp. 35–68, Cambridge University Press, Cambridge, UK.

Arief, D. 1998. Outer Southeast Asia: A region of deep straits, including the Banda Sea coastal segment (13°). *In* The Sea. Robinson, A. R. and Brink, K. H. (eds.), pp. 507–522, John Wiley and Sons.

Bieri, R. 1959. The distribution of the planktonic Chaetognatha in the Pacific and their relationship to the water masses. Limnol. Oceanogr. 4: 1–28.

Cheney, J. 1985. Spatial and temporal abundance patterns of oceanic chaetognaths in the western North Atlantic—II. Vertical distributions and migrations. Deep-Sea Res. 32: 1041–1059.

Chihara, M. and Murano, M. (eds.) 1997. An illustrated guide to marine plankton in Japan. Tokai University Press, Tokyo.

Dilling, L. and Alldredge, A. L. 1993. Can chaetognath fecal pellets contribute significantly to carbon flux? Mar. Ecol. Prog. Ser. 92: 51–58.

Duró, A., Gili, J.-M. and Andréu, P. 1994. Influence of the pycnocline on the vertical migration of the chaetognaths in the northern Benguela. J. Plankton Res. 16: 1149–1165.

Feigenbaum, D. and Maris, R. C. 1984. Feeding in the Chaetognatha. Oceanogr. Mar. Biol. Annu. Rev. 22: 343–392.

Fowler, J., Cohen, L. and Jarvis, P. 1998. Practical Statistics for Field Biology. John Wiley & Sons Ltd., Chichester.

Giesecke, R. and Gonzalez, H. E. 2004. Feeding of *Sagitta enflata* and vertical distribution of chaetognaths in relation to low oxygen concentrations. J. Plankton Res. 26: 475–486.

Grant, G. C. 1991. Chaetognatha from the central and southern middle Atlantic Bight: species composition, temperature-salinity relationships, and interspecific associations. Fish. Bull. 89: 33–40.

Haddock, S. H. D. and Case, J. F. 1994. A bioluminescent chaetognath. Nature 367: 225–226.

Hautala, S. L., Reid, J. L. and Bray, N. 1996. The distribution and mixing of Pacific water masses in the Indonesian Seas. J. Geophys. Res. 101: 12,375–312,389.

Johnson, T. B. and Terazaki, M. 2003. Species composition and depth distribution of chaetognaths in a Kuroshio warm-core ring and Oyashio water. J. Plankton Res. 25: 1279–1289.

Jumao-as, M. D. B. and von Westernhagen, H. 1975. Vertical distribution of epiplanktonic chaetognaths in the upper 100 m of the Hilutangan Channel, Cebu, The Philippines. Mar. Biol. 29: 201–210.

Kehayias, G., Fragopoulu, N. and Lykakis, J. 1994. Vertical community structure and ontogenetic distribution of chaetognaths in upper pelagic waters of the Eastern Mediterranean. Marine Biology 119: 647–653.

Kehayias, G., Lykakis, J. and Fragopoulu, N. 1996. The diets of the chaetognaths *Sagitta enflata*, *S. serratodentata atlantica*, and *S. bipunctata* at different seasons in Eastern Mediterranean coastal waters. ICES J. Mar. Sci. 53: 837–846.

Kehayias, G. 2003. Quantitative aspects of feeding of chaetognaths in the eastern Mediterranean pelagic waters. J. Mar. Biol. Ass. U.K. 83: 559–569.

Leg124-scientific-party 1989. Origins of marginal basins. Nature 338: 380–381.

Magurran, A. 1988. Ecological Diversity and its Measurement. University Press, New Jersey.

Morey, S. L., Shriver, J. F. and O'Brien, J. J. 1999. The effects of Halmahera on the Indonesian Throughflow. J. Geophys. Res. 104: 23281–23296.

Murauchi, S., Ludwig, W. J., Den, N., Hotta, H., Asanuma, T., Yoshii, T., Kubotera, A. and Hagiwara, K. 1973. Structure of the Sulu Sea and the Celebes Sea. J. Geophys. Res. 78: 3437–3447.

Nishihama, S. 1998. Diel vertical migration of chaetognaths in the Tsushima Current area of the Japan Sea. Bull. Jpn. Sea Natl. Fish. Res. Inst. 48: 71–83.

Ocean Research Institute, U. o. T. 1975. Preliminary report of the R/V Hakuho Maru Cruise KH-72-1 (The Seas of Southeast Asia). Ocean Research Institute, University of Tokyo.

Pakhomov, E. A., Perissinotto, R. and Froneman, P. W. 1999. Predation impact of carnivorous macrozooplankton and micronekton in the Atlantic sector of the Southern Ocean. J. Mar. Sys. 19: 47–64.

Pierrot-Bults, A. C. 1982. Vertical distribution of chaetognatha in the Central Northwest Atlantic near Bermuda. Biological Oceanography 2: 31–61.

Pierrot-Bults, A. C. 1997. Biological diversity in oceanic macrozooplankton: More than counting species. *In* Marine biodiversity: patterns and processes. Ormond, R. F. G., Gage, J. D. and Angel, M. V. (eds.), pp. 69–93, Cambridge University Press, Cambridge, UK.

Quadfasel, D., Kudrass, H. and Frische, A. 1990. Deep-water renewal by turbidity currents in the Sulu Sea. Nature 348: 320–322.

Rottman, M. L. 1978. Ecology of recurrent groups of pteropods, euphausiids, and chaetognaths in the Gulf of Thailand and the South China Sea. Mar. Biol. 48: 63–78.

Sameoto, D. D. 1972. Yearly respiration rate and estimated energy budget for Sagitta elegans. J. Fish. Res. Bd. Canada 29: 987–996.

Srinivasan, M. 1947. Distribution of chaetognaths, with special reference to *Sagitta decipiens* as an indicator of upwelling along the West coast of India. J. mar. biol. Ass. India 16: 126–142.

Stone, J. H. 1969. The Chaetognatha community of the Agulhas Current: its structure and related properties. Ecol. Monogr. 39: 433–463.

Sund, P. N. 1961. Some features of the autoecology and distributions of Chaetognatha in the eastern tropical Pacific. Bull. Inter-Am. Trop. Tuna Comm. 5: 305–340.

Terazaki, M. and Marumo, R. 1982. Feeding habits of meso- and bathypelagic chaetognatha, *Sagitta zetesios* Fowler. Oceanologica Acta 5: 461–464.

Terazaki, M. and Miller, C. B. 1982. Reproduction of Meso- and Bathypelagic chaetognaths in the Genus *Eukrohnia*. Mar. Biol. 71: 193–196.

Terazaki, M. 1992. Horizontal and vertical distribution of chaetognaths in a Kuroshio warm-core ring. Deep-Sea Res. 39: S231–S245.

Terazaki, M. 1995. The role of carnivorous zooplankton, particularly chaetognaths in ocean flux. *In* Biogeochemical Processes and Ocean Flux in the Western Pacific. Sakai, H. and Nozaki, Y. (eds.), pp. 319–330, Terra Scientific Publishing Co., Tokyo.

Terazaki, M. 1996. Vertical distribution of pelagic chaetognaths and feeding of *Sagitta enflata* in the Central Equatorial Pacific. J. Plankton Res. 18: 673–682.

Tokioka, T. 1962. The outline of the investigations made on chaetognaths in the Indian Ocean. Inform. Bull. Planktol. Japan 8: 5–11.

Toole, J. M. 1987. WOCE, interbasin exchanges, and marginal sea overflows. Eos. Trans. Amer. Geophys. Union 68: 2–3.

Vucetic, T. 1969. Distribution of *Sagitta decipiens* and identification of Mediterranean water masses circulation. Bull. Inst. Oceanogr. Monaco 69: 1398.

Wiebe, P. H., Burt, K. H., Boyd, S. H. and Morton, A. W. 1976. A multiple opening/closing net and environmental system for sampling zooplankton. J. Mar. Res. 34: 313–326.

Wiebe, P. H., Morton, A. W., Bradley, A. M., Backus, R. H., Craddock, J. E., Barber, V., Cowles, T. J. and Flierl, G. R. 1985. New developments in the MOCNESS, an apparatus for sampling zooplankton and micronekton. Mar. Biol. 87: 313–323.

Wyrtki, K. 1961. Scientific results of marine investigations of the South China Sea and the Gulf of Thailand, physical oceanography of the Southeast Asian waters. Scripps Inst. NAGA, La Jolla.