Spatial distribution of chaetognaths off the northern Bicol Shelf, Philippines (Pacific coast)

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The composition, abundance, and distribution of chaetognaths off the northern Bicol Shelf, Philippines (Pacific coast), from 31 stations along transects perpendicular to the coast were analysed. Samples were collected in April, 2001. In all, 26 species belonging to 14 genera were identified. *Flaccisagitta enflata* was the most abundant and frequently captured species at all stations, and constituted 41.9% of the total specimens. Most of the smallest diversity values were observed from areas affected by upwelling, although the greatest densities were observed at stations located within the upwelling zones. The occurrence of mesopelagic and bathypelagic species (*Decipisagitta decipiens*, *Caecosagitta macrocephala*, and *Eukrohnia fowleri*), in samples collected from upper water layers, could be explained by vertical transport caused by upwelling.

Keywords: bathypelagic, benthic, chaetognath, epipelagic, mesopelagic, northern Bicol Shelf, upwelling.

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Introduction

The northern Bicol Shelf (NBS), with a surface area of ∼11 600 km^2, is the second widest shelf area in the Philippines after the northern Palawan Shelf (Amedo *et al*., 2002). Hydrographically, the NBS is one of the most complex regions of the Philippines. It is bounded on the east by the Philippine Sea and is part of the western boundary of the world's largest ocean, the Pacific (Amedo *et al*., 2002; Udarbe-Walker *et al*., 2002).

Several ocean currents affect the Philippine coast (Udarbe-Walker *et al*., 2002), including the North Equatorial Current (NEC), Kuroshio Current (KC), Mindanao Current (MC), Luzon Undercurrent (LU), and the Mindanao Undercurrent (MU; Qu *et al*., 1998; Figure 1). These currents are involved in the transport and exchange of water masses between the northern and southern hemispheres of the Pacific (Fine *et al*., 1994; Udarbe-Walker *et al*., 2002). They also exhibit interannual fluctuations linked to climatic variability (Lukas, 1988, 1998; Lukas *et al*., 1991; Qui and Lukas, 1996; Udarbe-Walker *et al*., 2002).

Although oceanographic characterization of the region has been extensive, the results of biological and ecological research, especially of zooplankton communities, are lacking in the scientific literature. Zooplankton presence and abundance depend essentially on oceanographic characteristics such as currents and water masses. The present study site is located within an upwelling region. Although upwelling is known to enhance the nutrient distribution and primary production (Amedo *et al*., 2002; Primavera *et al*., 2002), the importance of upwelling in relation to zooplankton production and distribution is not well understood.

Chaetognaths occupy a prominent place among the total zooplankton (Reeve, 1971). Often, they belong with the top five most abundant zooplankton groups in the oceans, and their distribution and abundance can serve to corroborate variations in hydrographic conditions (Alvariño, 1964). Their close relationships with certain environmental variables (e.g. salinity, temperature, and dissolved oxygen) and their species-specific horizontal and vertical distribution make them excellent indicators of water masses (Bieri, 1959). The distribution patterns of some species have also been associated with hydrographic phenomena such as upwelling events. Certain species descend at convergence sites to depths greater than where they usually live, and species living at moderate depths rise towards the surface in regions of upwelling (Vinogradov, 1970). Mesopelagic and bathypelagic species like *Decipisagitta decipiens*, *Caecosagitta macrocephala*, and *Eukrohnia fowleri* are occasionally found in surface waters. These species normally do not reach these layers during their vertical migrations, so their presence has been considered an indicator of coastal upwelling events (Alvariño, 1964, 1965; Nair and Rao, 1973; Nair, 1977).

As active carnivores, chaetognaths form an important link in the marine food chain (Reeve, 1971). They feed mostly on copepods, crustacean larvae, and other chaetognaths, but occasionally on foraminiferans and fish larvae (Gray, 1961). Under conditions of low productivity, chaetognaths may strongly influence their prey populations (Øresland, 1990). Their roles as predators and competitors of larval fish have been evaluated in recent years (Baier and Purcell, 1997; Brodeur and Terazaki, 1999). Feigenbaum (1991) reports that the impact of chaetognath predation on fish larvae could be extensive because of the scarcity of fish

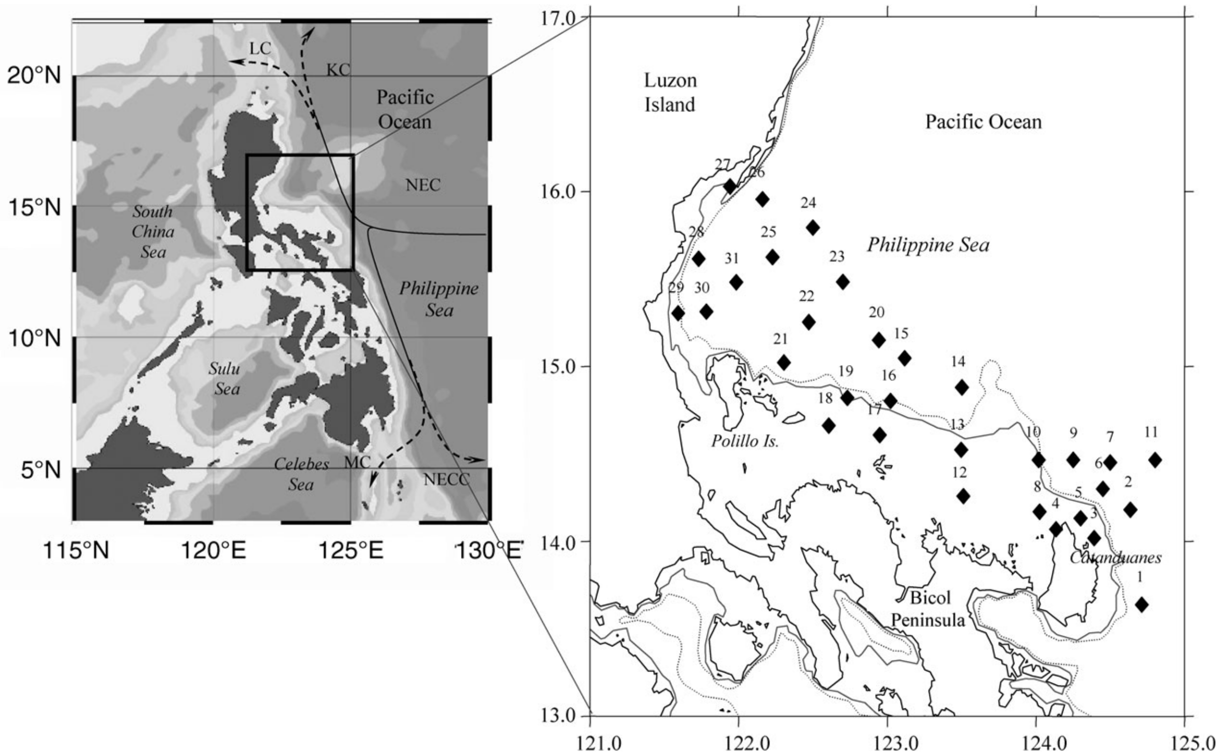

Figure 1. Map of the Philippines region, a schematic representation of large-scale circulation east of the Philippines, and locations of stations in northern Bicol Shelf (April 2001). Acronyms denote the Luzon Current (LC), KC, NEC, MC, and North Equatorial Counter Current (NECC). The 200 m isobath is shown as a thick line surrounding the major islands, and the lighter line represents the 500 m isobath.

larvae in the plankton, and could contribute to reductions of larval abundance during periods of fish production (Casanova, 1999).

Although the distribution and systematics of chaetognaths have been studied comprehensively in various parts of the world, relatively few studies have been conducted in the Philippines. Among these, Michael (1919), Bieri (1959), Alvariño (1967), and Rottman (1978) tackled taxonomic descriptions and distributional records. Others include Jumao-as and von Westernhagen (1975), Johnson (2005), and Cordero (2006), all of which are limited to specific basins, focusing on the western side and inland basins of the Philippines. The present study examined the species composition, abundance, and distribution of chaetognaths in relation to oceanographic conditions and processes along the Pacific coast of the Philippines, over the NBS.

Material and methods

Study area hydrography

The hydrographic features of the area during the survey are described by Amedo *et al.* (2002). The NEC bifurcates offshore of the NBS and gives rise to the north-flowing KC and the south-flowing MC (Figure 1). The bifurcation of the NEC occurs between 11°N and 14.5°N, and tends to shift to the north with increasing depth (Qui and Lukas, 1996). Numerical models indicate that the bifurcation may occur as far as 20°N for water of intermediate depths (Toole *et al.*, 1990; Qu *et al.*, 1998). The effects of these processes on the shelf areas are still unknown, but these energetic current systems can potentially impinge on the continental shelf and may give rise to secondary features such as upwelling (Amedo *et al.*, 2002).

Distinct upwelling signals from temperature (colder areas) and large chlorophyll concentrations were observed off the NBS during the survey (Amedo *et al.*, 2002). The upwelling area was detectable at a depth of 50 m at the shelf break between 14.75–15.0°N and 122.5–123.0°E (Figure 2), which is driven by a combination of prevailing alongshore winds that set up the Ekman layer transport offshore and a horizontal pressure gradient that sustains a borclinic jet. The strength of the upwelling varies with shifts in the bifurcation latitude. The bifurcation of the NEC occurs at a higher latitude during *El Niño*–Southern Oscillation years and at a lower latitude during *La Niña* years. Seasonally, the NEC bifurcates at the northernmost position in October and in the southernmost position in February (Qui and Lukas, 1996). Based on this, strong upwelling is likely during *La Niña* and the northeast monsoon season.

Oceanographic sampling

An oceanographic cruise was conducted in the NBS between 1 and 11 April 2001 on the MV "DA-BFAR". The area investigated extended from 124.80–122.41°E and 11.25–15.79°N, covering 31 stations (Figure 1).

Zooplankton and ichthyoplankton were sampled using double oblique tows of a 60-cm bongo net with a 335-μm mesh to a maximum depth of 100 m (close to the thermocline depth) at deep stations or to 5 m above the bottom at shallow stations. A flowmeter was mounted at the mouth of the net to measure the volume of water filtered. The dates, station locations, bottom depth, and volume of water filtered are presented in Table 1. For each haul, the length of wire paid out was adjusted using the angle of declination to maintain the standard depth of sampling.

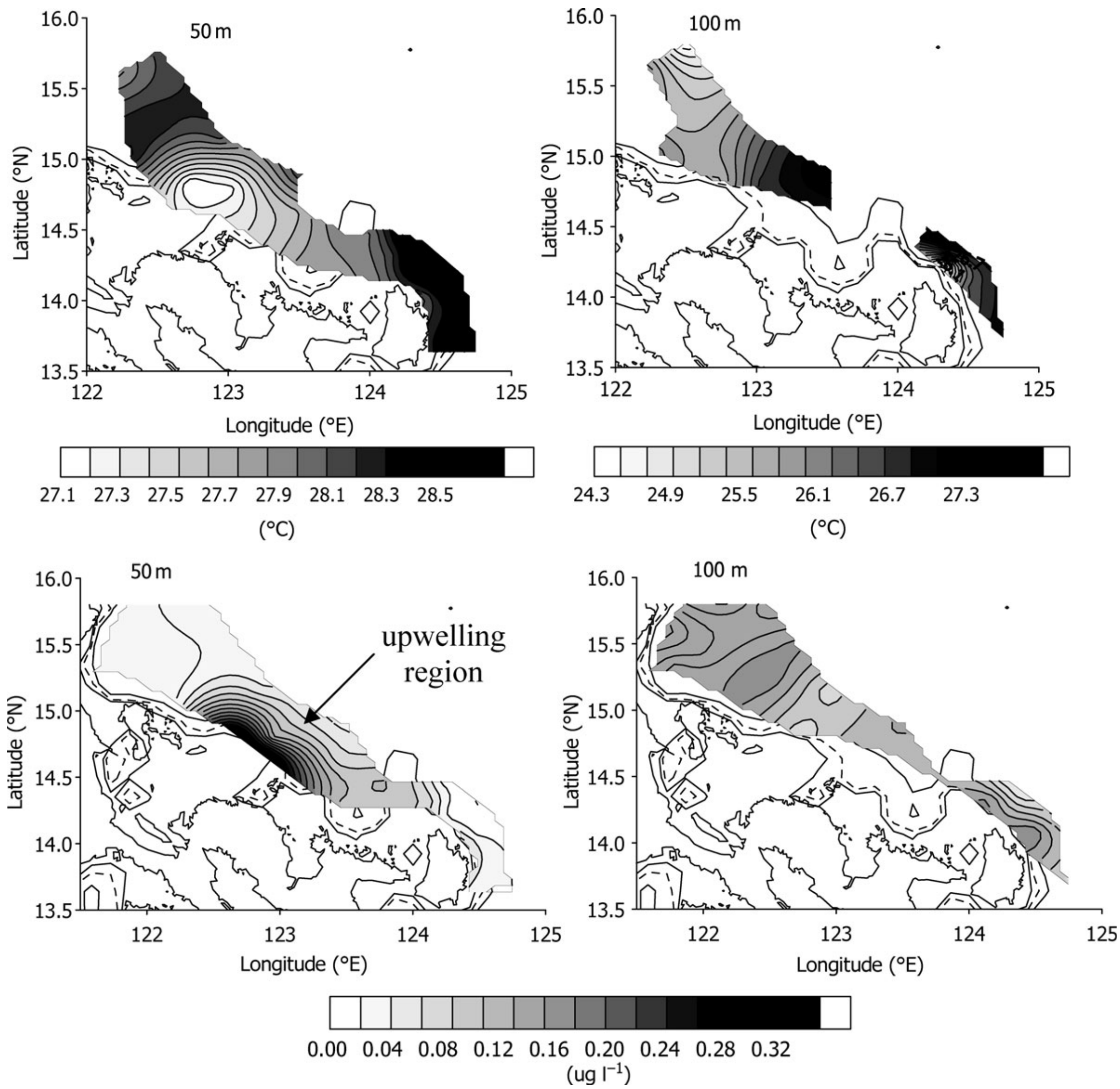

Figure 2. Horizontal temperature and chlorophyll *a* concentrations on the Northern Bicol Shelf during April 2001. The dashed line represents the 200 m isobath, and the thick line represents the 500 m isobath. The figures are taken from Amedo *et al.* (2002).

Sample processing

Samples were preserved in 10% buffered formalin solution. Zooplankton biomass at each station was determined by measuring the displaced volume of each sample, and is expressed in ml m^{-3}. Chaetognaths were sorted and identified to species level. Densities were calculated as the number of individuals 100 m^{-3}. Identification was done under compound and dissecting microscopes, using the keys of Michael (1911), Alvariño (1967), Michel (1984), Pierrot-Bults and Chidgey (1988), Bieri (1991), and Casanova (1999).

Data analysis

The Shannon diversity index (*H*'; Shannon, 1948) was computed to compare species diversity among stations, as was species richness (*S*, total number of species recorded in each of the stations), where

$$H' - \sum (P_i) \ln P_i,$$

where P_i is the proportional abundance of the *i*th species (n_i/N). Cluster analyses (Q and R) were performed to examine the distributional similarities of the different species, based on their relative abundance. The Q-mode cluster analysis was performed to form station clusters and the R-mode analysis to form assemblages of species showing similar relative abundances at the same stations. Cluster analysis was done using the program COMM (Piepenburg and Piatkovski, 1992).

Results

Species composition, spatial distribution, and abundances

In all, 9029 specimens were examined, and 26 species from 14 genera were identified. Table 2 lists the species recorded, their mean densities, and relative abundance. *Flaccisagitta enflata* was the dominant species and made up 41.9% of all chaetognaths recorded. Among the top ten species were *Aidanosagitta neglecta*

Table 1. Station locations, date of sampling, volume of water filtered, and bottom depth of the area surveyed during the April 2001 cruise.

Station	Location		Date	Volume filtered (ml)	Depth of water (m)
	°N	°E			
1	13.64	124.71	2 April 2001	245.1	125
2	14.18	124.64	3 April 2001	89.7	150
3	14.07	124.14	3 April 2001	100.3	115
4	14.02	124.39	3 April 2001	44.7	88
5	14.13	124.30	3 April 2001	64.4	48
6	14.30	124.45	3 April 2001	110.5	223
7	14.45	124.50	3 April 2001	196.1	1000
8	14.17	124.02	4 April 2001	56.2	53
9	14.47	124.25	4 April 2001	118.9	1000
10	14.47	124.02	4 April 2001	167.5	1000
11	14.46	124.80	4 April 2001	72.6	300
12	14.26	123.51	4 April 2001	114.6	65
13	14.52	123.50	4 April 2001	107.9	90
14	14.88	123.50	4 April 2001	177.0	500
15	15.05	123.12	4 April 2001	154.1	1000
16	14.80	123.02	5 April 2001	103.7	500
17	14.61	122.95	5 April 2001	109.5	150
18	14.66	122.61	5 April 2001	18.0	40
19	14.82	122.73	6 April 2001	93.2	39
20	15.15	122.94	6 April 2001	181.9	1000
21	15.02	122.31	6 April 2001	71.1	1000
22	15.25	122.47	6 April 2001	155.1	2 000
23	15.48	122.70	7 April 2001	223.6	2100
24	15.79	122.50	7 April 2001	172.6	1000
25	15.63	122.23	7 April 2001	126.8	1000
26	15.96	122.16	7 April 2001	106.4	1000
27	16.03	121.94	7 April 2001	201.0	140
28	15.62	121.73	7 April 2001	108.7	1000
29	15.30	121.59	7 April 2001	51.9	400
30	15.31	121.78	7 April 2001	61.1	2000
31	15.48	121.98	8 April 2001	198.3	1830

(12.5%), *Serratosagitta serratodentata* (10.2%), *Sagitta bipunctata* (7.3%), *Ferosagitta ferox* (5.7%), *Zonosagitta bedoti* (4.7%), *Aidanosagitta oceanica* (3.2%), *Ferosagitta robusta* (3.2%), *Mesosagitta minima* (2.3%), and *Serratosagitta pacifica* (1.7%). Together, these ten species constitute 92.7% of all chaetognaths recorded.

The highest chaetognath abundances (3089 ind. 100 m^{-3}) were recorded at stations located close to the shelf break, particularly in the central portion of the shelf (Figure 3). High overall abundance in this area is primarily attributed to large overall concentrations at two stations, 17 (1137 ind. 100 m^{-3}) and 19 (3089 ind. 100 m^{-3}), which are both located near the upwelling zone. Abundances then gradually decrease towards the east. However, chaetognath abundances were moderately large in the westernmost portion of the shelf. Overall density ranged from 2.8 to 3089 ind. 100 m^{-3}, with a mean of 435 ind. 100 m^{-3}.

The average Shannon diversity index (*H'*) value was 4.07 (Table 3). In general, the NBS appeared to have fairly similar

Table 2. Mean densities and relative abundance of chaetognaths collected on the northern Bicol Shelf in April 2001.

Species	Mean (ind. 100 m^{-3})	s.d.	Percentage
Flaccisagitta enflata	182.5	269.9	41.9
Aidanosagitta neglecta	54.5	60.6	12.5
Serratosagitta serratodentata	44.5	46.7	10.2
Sagitta bipunctata	31.9	81.7	7.3
Ferrosagitta ferox	24.7	47.5	5.7
Zonosagitta bedoti	20.6	46.5	4.7
Aidanosagitta oceanica	14.2	40.5	3.2
Ferrosagitta robusta	14.0	33.7	3.2
Sagitta juvenile	10.0	9.2	2.3
Mesosagitta minima	10.0	16.5	2.3
Serratosagitta pacifica	7.3	22.5	1.7
Decipisagitta decipiens	7.2	14.4	1.6
Flaccisagitta hexaptera	4.3	20.5	1.0
Aidanosagitta johorensis	4.1	8.9	1.0
Caecosagitta macrocephala	2.1	3.9	0.5
Aidanosagitta regularis	1.1	2.4	0.3
Serratosagitta tasmanica	0.7	1.7	0.2
Zonosagitta nagae	0.6	1.3	0.1
Pterosagitta draco	0.6	1.3	0.1
Zonosagitta pulchra	0.3	0.9	0.1
Aidanosagitta bedfordii	0.2	1.2	>0.1
Sagitta sp.	0.2	0.9	>0.1
Krohnitta pacifica	0.07	0.3	>0.1
Krohnitta subtilis	0.05	0.3	>0.1
Eukrohnia fowleri	0.04	0.2	>0.1
Aidanosagitta septata	0.04	0.2	>0.1
Paraagitta setosa	0.02	0.1	>0.1
Spadella sp.	0.01	0.1	>0.1
			100.000
Total number of species	26		
Total number of individuals	9029		
Total number of genera	14		
Mean	435.8		

levels of diversity among stations, though species richness demonstrates a gradual change just east of the upwelling zone (Table 3). However, a substantial decrease in diversity and number of species occurred at station 11.

The Q-mode cluster analysis revealed two major station clusters: the eastern and the western station clusters (Figure 4), formed primarily because of differences in densities. Many species were at all stations, but in varying abundances from one station cluster to another, resulting in station clusters that are not delineated by rigid boundaries. The assemblages characterizing the station clusters are therefore differentiated more by abundance and relative densities than by the presence or absence of any particular species. The R-mode cluster analysis defined two major species assemblages: one ubiquitous and the other with much smaller overall abundances, but also occurring much less

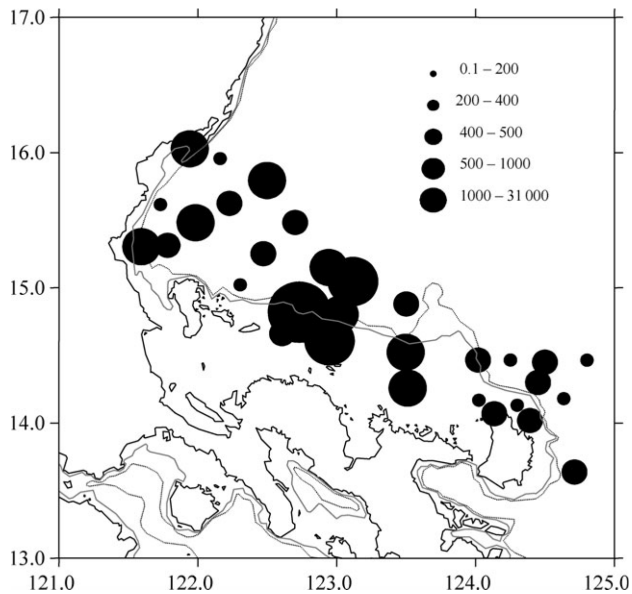

Figure 3. Spatial distribution of chaetognath densities (ind. 100 m^{-3}) in the area surveyed during the April 2001 cruise.

frequently on the eastern half of the shelf, particularly near Catanduanes.

The first cluster was made up of species of moderate to great overall abundance that occurred frequently in both western and eastern portions of the NBS. These included *F. enflata*, *A. neglecta*, *S. serratodentata*, *F. ferox*, and *S. bipunctata*, which displayed the largest concentrations in the central NBS region (Figure 5a–e). *Ferosagitta robusta* and *Z. bedoti* did not display marked spatial differences in abundance distribution, although *Z. bedoti* was frequently absent at the inner shelf stations (Figure 5f and g). *Ferosagitta robusta* displayed small abundances at the extreme western part of the study area (Figure 5g), whereas various unidentifiable juvenile chaetognaths were distributed rather evenly along the shelf (Figure 5h).

The second species assemblage consisted of species that demonstrated moderate to small overall abundances, but occurred more frequently in the western portion of the shelf, and species having

Table 3. Shannon diversity index (*H′*) and species richness (*S*) in the area surveyed during the April 2001 cruise.

Station	Shannon diversity index (*H′*)	Species richness (*S*)
1	3.765	15
2	4.214	6
3	4.467	10
4	3.765	6
5	4.348	5
6	4.453	12
7	4.473	12
8	4.323	8
9	3.995	8
10	3.734	13
11	0.120	3
12	3.881	14
13	4.308	16
14	3.583	15
15	4.255	14
16	4.472	18
17	4.291	12
18	4.380	7
19	4.264	12
20	4.414	15
21	4.400	6
22	4.426	13
23	4.473	17
24	4.350	13
25	3.852	11
26	4.097	11
27	4.438	14
28	4.473	9
29	3.460	14
30	4.154	15
31	4.471	19

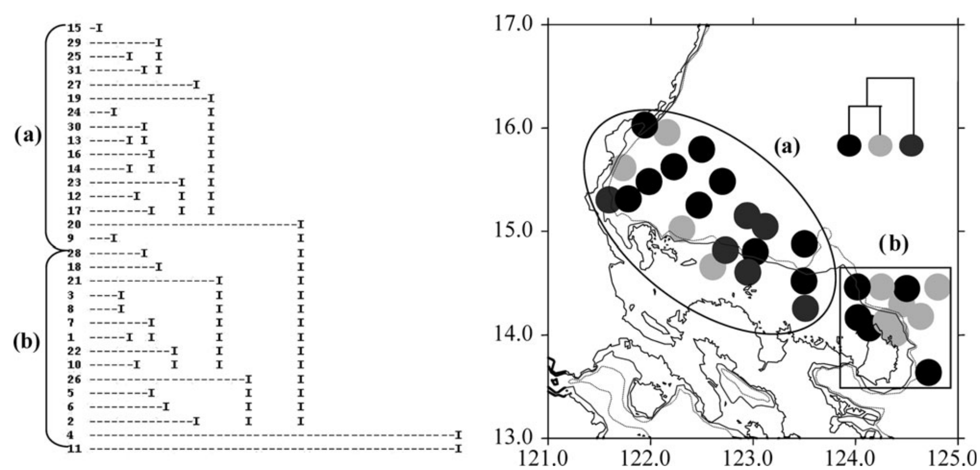

Figure 4. Dendrogram of chaetognath station clusters based on results of cluster analysis and map of the geographical location of station clusters: (a) western cluster and (b) eastern cluster.

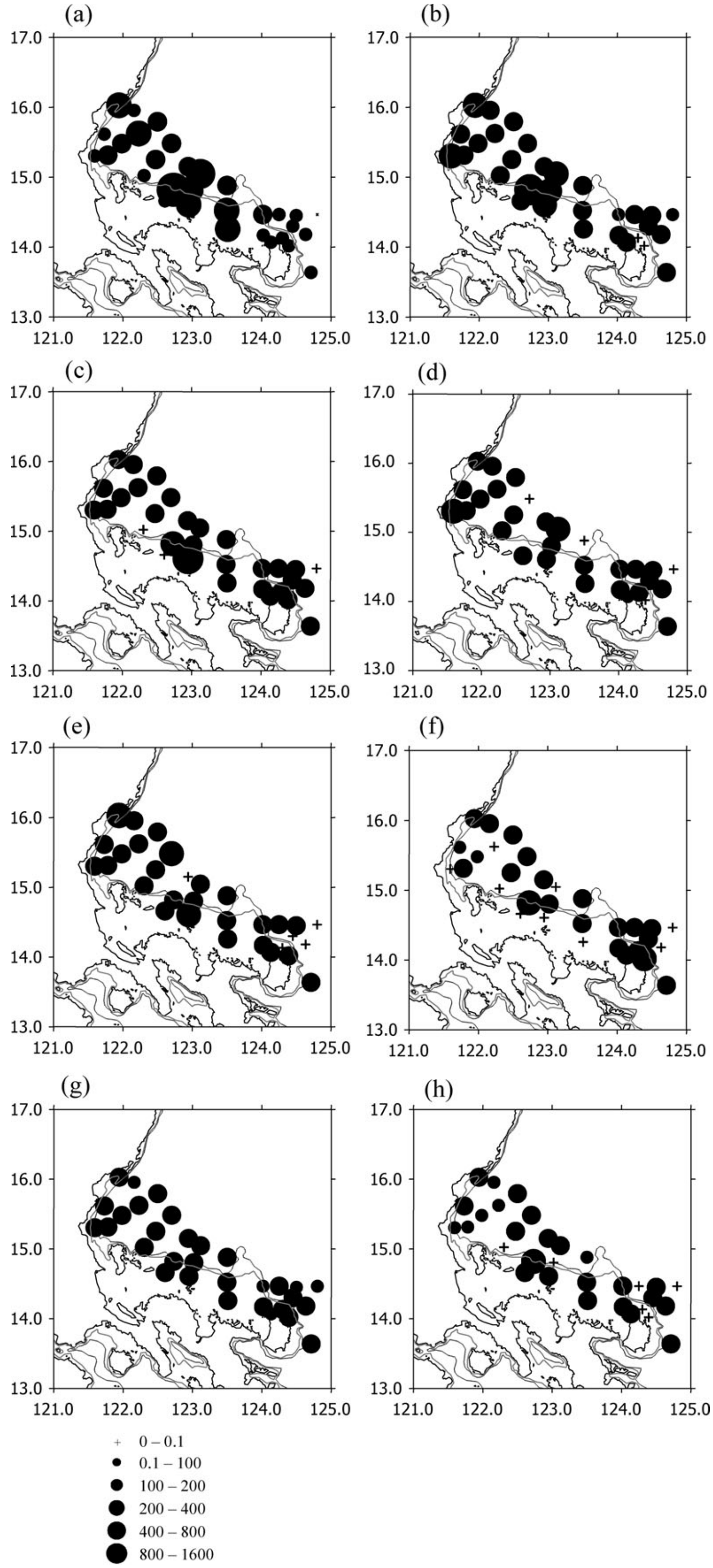

Figure 5. Horizontal distribution of assemblage 1: (a) *F. enflata*, (b) *A. neglecta*, (c) *F. ferox*, (d) *S. bipuntata*, (e) *S. serratodentata*, (f) *Z. bedoti*, (g) *Sagitta juvenile*, and (h) *F. robusta*.

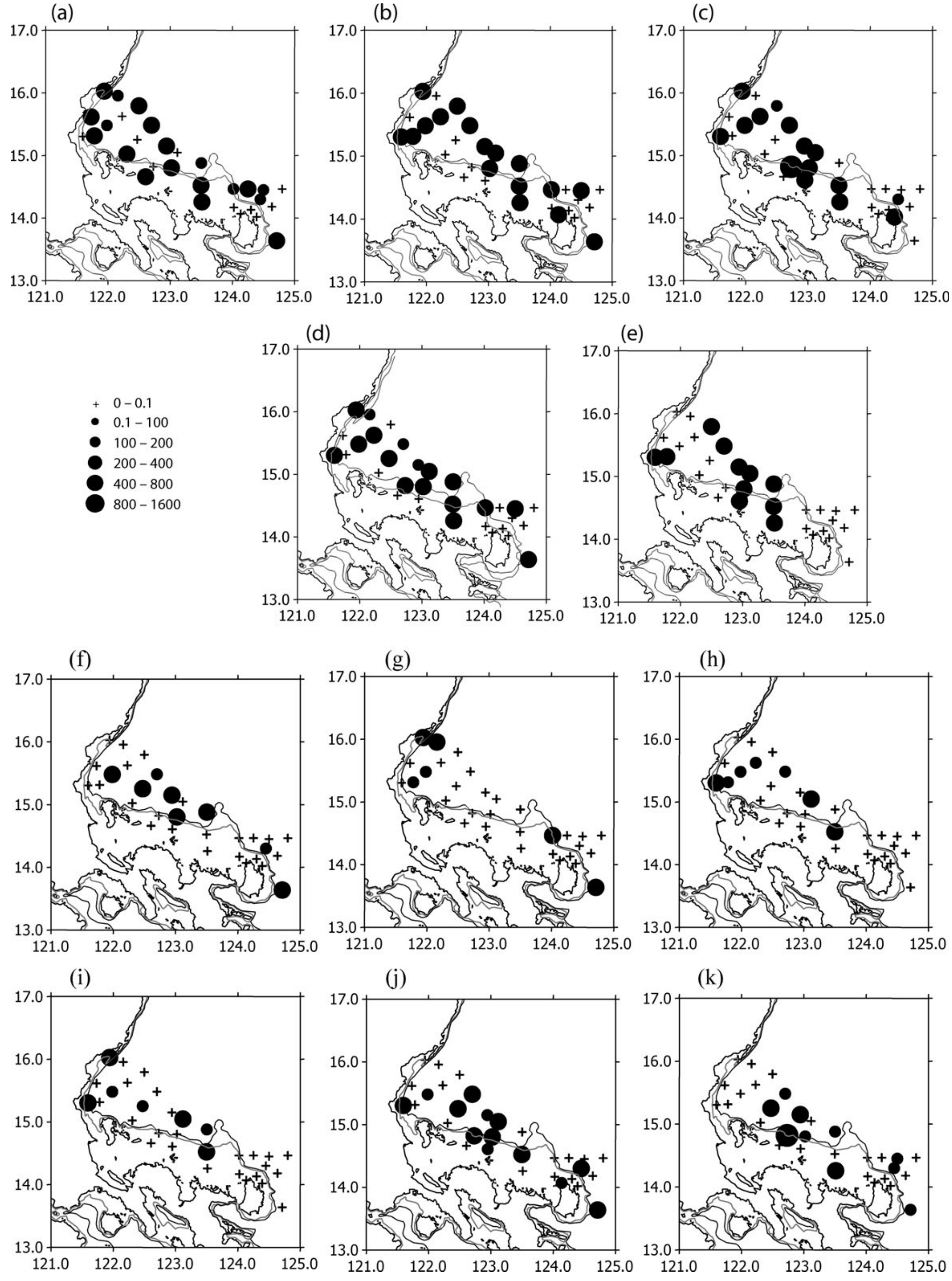

Figure 6. Horizontal distribution of assemblage 2: (a) *M. minima*, (b) *S. oceanica*, (c) *D. decipiens*, (d) *S. pacifica*, (e) *A. johorensis*, (f) *A. regularis*, (g) *S. tasmanica*, (h) *Pterosagitta draco*, (i) *Z. nagae*, (j) *C. macrocephala*, and (k) *F. hexaptera*.

low overall frequency of occurrence and did not reveal recognizable or similar distribution patterns. Both *A. oceanica* and *S. pacifica* had high abundance in the central NBS region (Figure 6a and b). *Mesosagitta minima* and *D. decipiens* had rather evenly distributed densities (Figure 6c and d). Similarly, *Aidanosagitta johorensis* occurred only in moderate abundances, but was conspicuously absent around Catanduanes (Figure 6e). *Aidanosagitta regularis*, *Serratosagitta tasmanica*, *Pterosagitta draco*, and *Zonosagitta nagae* were not recorded at the inner shelf stations, and the latter two species were absent from the waters

Table 4. Comparison of Shannon diversity index (*H'*) with previous studies.

Location	*H'* values/ranges	Reference
Sulu Sea	2.11	Johnson (2005)
Sulu Sea	2.07–3.17	Cordero (2006)
Celebes Sea	1.87	Johnson (2005)
Bicol Shelf	0.12–4.47	Present study

around Catanduanes, east on the NBS (Figure 6f–i). *Caecosagitta macrocephala* and *Flaccisagitta hexaptera*, on the other hand, were recorded at a few inner shelf stations, particularly in the central portion of the NBS (Figure 6j and k).

The remaining rare species (*Aidanosagitta bedfordii*, *Zonosagitta pulchra*, *Aidanosagitta septata*, *Parasagitta setosa*, *Spadella* spp., *Krohnitta pacifica*, *Krohnitta subtilis*, and *E. fowleri*) occurred in patches of low densities solely in the central portion of the shelf and are not included in any of the major assemblages formed by the cluster analysis.

Discussion

The overall species composition from the samples is consistent with the species reported in previous investigations in various areas in the region (Alvariño, 1967; Jumao-as and von Westernhagen, 1975; Rottman, 1978; Johnson, 2005). In the Hilutungan Channel, Jumao-as and von Westernhagen (1975) reported 13 species of chaetognaths, all of which have also been recorded in the present study. They also found *F. enflata* to be the most common and abundant species. Of the 13 species, 12 were described as epiplanktonic, and the only mesopelagic species was *D. decipiens*. Similarly, 22 species were recently reported from the Sulu Sea and Celebes Sea (Johnson, 2005), where *F. enflata* also dominated the chaetognath assemblages and contributed ~39% of all chaetognaths recorded. All 22 species reported by Johnson (2005) have been found in previous investigations (Alvariño, 1967; Jumao-as and von Westernhagen, 1975; Rottman, 1978; Cordero, 2006). In this study, all previously reported species from the Philippines were found. The overall range of abundances observed in the study area is within the upper range of values reported in previous studies in other areas of the country (Alvariño, 1967; Jumao-as and von Westernhagen, 1975; Rottman, 1978; Johnson, 2005; Cordero, 2006).

The NBS is divided into two regions: the eastern and the western regions do not appear to correspond strictly to the regions defined by the cluster analyses. The assemblages were generally similar because the diversity and number of species did not vary significantly. All *H'* values were relatively large compared with previous studies in the Philippines (Table 4), although there are some instances when diversity is inversely related to species number. Species diversity reveals peaks with greater species richness, regardless of dominance by any particular species. However, a slight variation in species richness was observed in the eastern portion of the NBS. Such a scenario seems to agree with the observed upwelling events in the region. In this case, the gradual change in species richness just east of the upwelling region can be related to this phenomenon.

The vertical distribution of chaetognaths varies with latitude and in different regions because of the differences in temperature, salinity, dissolved oxygen, and other local hydrological conditions, as well as time of sampling. Consequently, it is not uncommon to see inconsistent and even conflicting results from previous studies. For instance, in the present study, *S. serratodentata*, *S. tasmanica*, *F. hexaptera*, *K. subtilis*, and *K. pacifica* are well represented in the epipelagic layer, but these species have been reported previously as mesopelagic species in the South Atlantic (Casanova, 1999), in the Caribbean Sea (Michel, 1984), and in the Philippines (Michael, 1919). Similarly, Johnson (2005) noted the occurrence of *K. pacifica* in mesopelagic waters of the Sulu and Celebes seas, and linked such occurrences with the resilience of a few individuals. Nevertheless, others have suggested that the presence of epipelagic species at great depths and of meso- and bathypelagic species at the surface are a result of downwelling and upwelling events. For instance, Stepien (1980) reported finding shallow-living zooplankton (including chaetognaths) at great depth in the Straits of Florida as a result of downwelling events. Alvariño (1964), on the other hand, attributed the presence of mesopelagic species of chaetognaths in the upper 100 m off San Diego, California, to upwelling.

Species reported as prevalent in certain regions may be categorized as exclusive to tropical, subtropical, temperate, and subtemperate regions or to the Pacific or Atlantic oceans. For example, *S. serratodentata* has been reported as common and typical of tropical and temperate Atlantic waters and, reportedly, does not occur in Philippine waters (Bieri, 1959). However, this species has been reported from the Pacific Ocean, Mediterranean Sea, and Indian Ocean (Grant, 1967), as well as in other seas (Pierrot-Bults and Chidgey, 1988). Michael (1919), Jumao-as and von Westernhagen (1975), and Cordero (2006) report this species in the western part and inland waters of the Philippines. Michael (1919) considered this species to be unusually variable, but might have been referring to the closely related *S. pseudoserratodentata*, which was not yet described at the time but has since been reported in the Pacific (Bieri, 1959).

Serratosagitta serratodentata is commonly misidentified as *S. pacifica* or, as in the case of Jumao-as and von Westernhagen (1975), *S. tasmanica* or *S. pseudoserratodentata*. In this study, the difficulty of distinguishing this species from *S. pacifica* was encountered, making thorough examination necessary. The following diagnostic features were verified in specimens examined: 9–10 (mostly 10) anterior teeth; 19–20 posterior teeth; 10–10.5 mm maximum body length; 6–7 hooks; 23–24% relative tail length; and seminal vesicles with a conspicuous trunk and a large knob with two horn-like prominences (Krohn, 1853). Although the condition of some specimens collected in this study had disintegrated with time, sufficient structures and characteristics remained intact to verify that they were indeed *S. serratodentata*. Some taxonomists, however, have considered *S. pacifica* to be a variety of *S. serratodentata* (Tokioka, 1940) because of similarities, and the specimens found on the NBS may be incorrectly identified.

Hyman (1959) argued that the majority of chaetognaths are epipelagic, whereas others are migratory species with a wide range of vertical movement in the water column (Bieri, 1959; Cheney, 1985). Many species display ontogenetic differences in vertical distribution, wherein young individuals live closer to the surface, and larger and mature individuals in deeper water. In general, diel vertical migrations cover distances of <50 m and are primarily within the upper 100 m (Cheney, 1985). Casanova (1999) describes diel migrations in *F. enflata*, *S. serratodentata*, and *K. pacifica*. *Flaccisagitta enflata* and

S. serratodentata descend to deeper waters at noon, whereas *K. pacifica* does so during daylight in general. The diel migration might be attributed to feeding behaviour. In the Indian Ocean, the number of *F. enflata* with food in their guts increases towards noon (Øresland, 2000). The vast majority of the previous studies provide evidence of ontogenetic vertical migrations of mesopelagic and bathypelagic chaetognaths (Russell, 1931; David, 1955; Alvariño, 1964; Pearre, 1973; Pierrot-Bults, 1982). For example, in the Antarctic species *S. gazellae*, mature individuals reproduce below 750 m, whereas their young rise to the surface layer (David, 1955).

In practice, chaetognaths have been categorized by the area of their greatest concentration on a regular basis and over a large scale. In this study, of the 26 species recorded in the epipelagic zone of NBS, 22 have been previously described as epipelagic. The ocean, however, is a dynamic environment, so species can be moved around and displaced to areas where they are otherwise uncommon. The occurrence, though rare, of mesopelagic, bathypelagic, and benthic species (*D. decipiens*, *C. macrocephala*, *E. fowleri*, and *Spadella* spp.) in samples collected from upper layers, particularly near the upwelling zone, is one of the most interesting findings of this study. *Decipisagitta decipiens* and *C. macrocephala* have been previously reported to undergo ontogenetic migrations (Alvariño, 1964; Vinogradov, 1970; Kehayias *et al.*, 1994; Kehayias, 2003). Most of the specimens collected in this study were of immature stages and found shallower, consistent with known ontogenetic vertical migration patterns. On the other hand, the bathypelagic species *E. fowleri* rarely or never reaches the epipelagic layer (Alvariño, 1964; Vinogradov, 1970). Its occurrence in the near-surface (∼100 m) water sample at station 16, with a depth of 500 m, can only be attributed to vertical transport. The benthic species *Spadella* spp. was collected at an adjacent station (17) located farther inshore on the shelf, with a depth of 150 m. Although spadellid chaetognaths are occasionally caught with plankton nets, this usually happens when the net strikes the seabed (e.g. Bieri, 1974; Bieri *et al.*, 1987). This was not possible at this station (150 m bottom depth), because the depth of double oblique tows at any time during the survey did not reach >100 m. It is not known whether this spadellid species moves vertically in the water column. However, assuming that it is truly benthic, its occurrence in the plankton sample must be attributed to some means of vertical transport off the bottom, such as upwelling.

Stations 16 and 17 are located just inshore of the weak upwelling area reported by Amedo *et al.* (2002). Although indicators of upwelled water at this location are only evident 50–100 m below the surface, this is enough to transport deep-water organisms to depths sampled by the double oblique tows used in the survey.

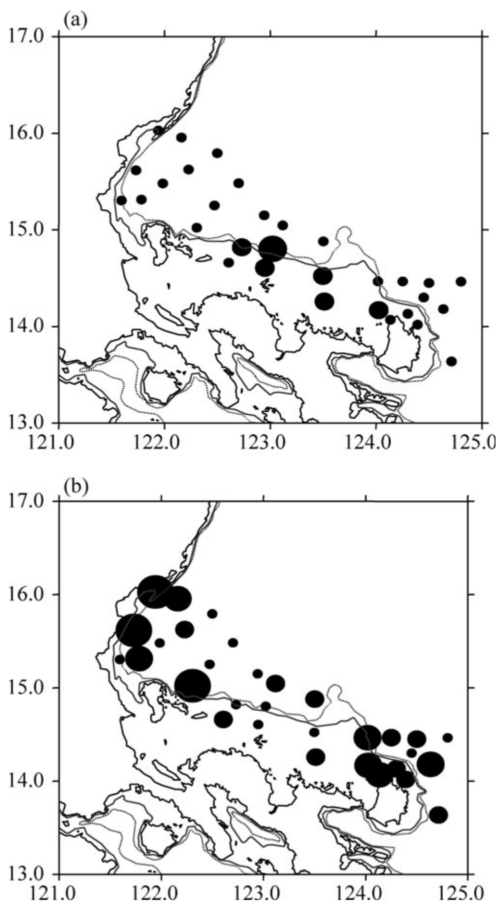

Figure 7. Spatial distribution of (a) fish eggs and (b) fish larvae in the area surveyed during the cruise and adjacent internal basins in April 2001 (Campos *et al.*, unpublished data).

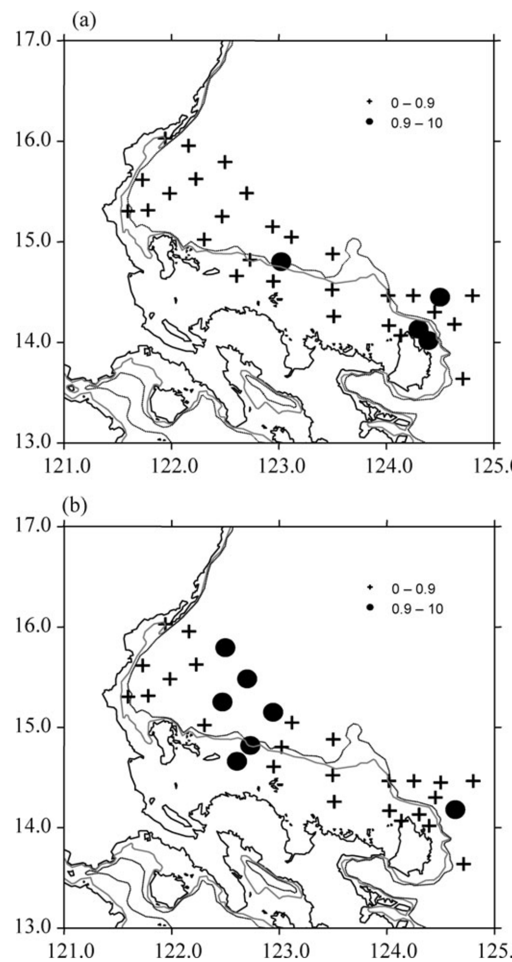

Figure 8. Spatial distribution of (a) fish eggs and (b) fish larvae found in the gut of the chaetognath species *S. enflata* in the area surveyed during the April 2001 cruise.

It is not known whether the processes bringing about the upwelling at this location extend to the shallower portions of the shelf, but the occurrences of *E. fowleri* and *Spadella* spp. recorded in this study are consistent with such an event. Similarly, chaetognath species assemblages, as measured by species richness and relative abundance, also reveal a gradual change just east of the upwelling area.

Fish eggs (Figure 7a) on the NBS in April 2001 were located away from the central portion of the shelf, where both chaetognath and larval fish concentrations (Figure 7b) were largest (Campos *et al.*, unpublished data). Egg predation in *F. enflata* (Figure 8a) was greatest where fish egg concentrations were also largest, whereas predation on fish larvae (Figure 8b) closely followed the distribution of larval fish abundance as well. The reason for the distributions of fish eggs and larvae on the shelf is not clear. However, if we assume that fish stocks would benefit if their spawning sites were located upstream of food-rich areas where larvae will eventually be concentrated, the importance of the upwelling area in the central portion of the shelf becomes more apparent. Chaetognaths prey heavily on zooplankton, but rarely feed on fish eggs and larvae (Øresland, 1990; Feigenbaum, 1991; Baier and Purcell, 1997; Brodeur and Terazaki, 1999). Both eggs and larvae were found in the guts of *F. enflata*, the most abundant species recorded during the survey. Reeve (1971) stated that chaetognaths are mechano-receptive predators and feed only on living, moving prey. However, immobile or less mobile plankton like fish eggs, gastrula larvae, and radiolarians in chaetognath guts have been reported in several studies (Gray, 1961; Jumao-as and von Westernhagen, 1975; Cordero, 2006). The heads of chaetognaths possess structures that have been putatively described as chemoreceptors (Thuesen and Bieri, 1987; Thuesen *et al.*, 1988), and these could play a role in choosing to ingest fish eggs, especially at high egg density. It is known that chaetognaths ingest prey once captured in the net (Sullivan, 1980), and more work is needed to determine the prevalence of chaetognath predation on fish eggs.

The overall results of the study are consistent with the area of upwelling being a major hydrographic feature of the NBS, at least from the shelf break and farther offshore. This specific area is also where relatively large chlorophyll concentrations (Primavera *et al.*, 2002), together with the largest values of total zooplankton and pelagic fish biomass (Tanay, 2002), and total larval fish concentrations (unpublished data) were also observed within the same period (April 2001). Upwelled water is generally associated with high production capacity and is the likely reason that this specific area is able to support large consumer concentrations. How this key feature affects the dynamics of productivity on and off the NBS merits further study. The present knowledge of the extent of geographical and vertical distribution of chaetognaths is not definitive, and many unexplored waters, particularly in high-diversity areas such as the Indo-West Pacific, remain to be fully characterized. It is hoped that this study will provide some useful data and will serve as a basis of comparison with future works in the Philippines and elsewhere.

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