Siphonophora

Introduction

In 1971, Alvariño reviewed the world-wide distribution of the Siphonophora, and Björnberg, the occurrence of species in the Caribbean. Previous work in the southwestern North Atlantic and the Caribbean was also cited by Owre & Foyo (1972) when they reported the collection of nine species in the area. The same nine are listed here, with Porpita umbella included for convenience. Some specialists classify P. umbella in Order Chondrophora (Hand, 1972), while others (e.g., Pugh, 1974) continue to include it in Order Siphonophora, Sub-order Cystonectae.

Recently, Alvariño (1974) recorded the occurrence of 20 species in various oblique and horizontal tows from the western Caribbean: Abyla haeckeli, Agalma okeni, Amphicaryon acaule, Chelophyes contorta, Enneagonum hyalinum, Lensia challengeri, L. fowleri, L. hotspur, L. subtilis, Muggiaea atlantica, M. kochi, Stephanomia bijuga and Sulculeolaria chuni, in addition to seven of those reported here, Abylopsis eschscholtzii, A. tetragona, Chelophyes appendiculata, Diphyes bojani, D. dispar, Eudoxoides mitra and E. spiralis. Our most uncommon forms, Bassia bassensis and Ceratocymba leuckartii, were not found in Alvariño's Caribbean collections. Owre & Foyo (1972) reported B. bassensis from the surface at one station in the eastern Caribbean, and in the present study, it was collected from the surface and at 103 m at a station south of Jamaica (P 6606, Sta. 4), the only siphonophore species found there at that time. C. leuckartii was collected once, at 25 m in the south central Caribbean (P 6811, Sta. 5).

Based on the total estimated numbers collected at all stations, the seven more common species rank in the following declining order of

abundance: A. tetragona, D. bojani, A. eschscholtzii, C. appendiculata, E. mitra and D. dispar almost equally numerous, and E. spiralis (Table 22).

Porpita umbella was caught only once, in a surface tow from the central Caribbean (P 6811, Sta. 4, seven juveniles).

Distribution

Pugh (1974) published an important study on the vertical distribution of siphonophores in the upper 1000 m off Fuerteventura, Canary Islands. In horizontal and oblique hauls with a 10-foot IKMT and horizontal tows with a 1 m^2 ring net, 64 species were collected. Few were common. The list did not include Ceratocymba leuckartii. In his discussion of each species, Pugh cited previous observations on vertical distribution, of which the following are pertinent to our work: Bigelow & Sears (1937), Leloup (1933, 1934), Leloup & Hentschel (1935), Moore (1949, 1953), Moore & Corwin (1956), Patriti (1970), Stepanyants (1967), and Totton (1954, 1965).

The vertical distribution of the seven more numerous species collected in the Caribbean is summarized in Table 22; Tables 25-31 contain the raw data. Although all are primarily epipelagic, each species except for Diphyes dispar was collected well below 200 m at least once. Pugh (1974) collected D. dispar at 780 m. The record of 2500 m for Chelophyes appendiculata and Eudoxoides spiralis is particularly unusual (Table 22). However, the maximum number of each species, i.e., over 90 percent of the total catch, was collected over a comparatively narrow range of depth. D. dispar appears to be essentially restricted to surface waters in the Caribbean, Abylopsis eschscholtzii to the upper 50 m, A. tetragona, C. appendiculata, D. bojani and E. spiralis to the upper 100 m, and

E. mitra may be common at various depths from the surface to 250 m. Primarily, they are organisms of the highly variable Tropical Surface Water and the Subtropical Underwater, as shown in the T-S-P diagrams (Figs. 11-13). These data suggest that A. eschscholtzii (Fig. 13A) and D. dispar (Fig. 13B) may be more tolerant of low salinities than the other species and also stenothermal in comparison with them. A. tetragona (Fig. 11A) was numerous in both warm layers and also was collected in the boundary layers between warm and cold water spheres. The distribution of D. bojani (Fig. 12A) appeared linked to the warm water sphere, with one record from Subantarctic Intermediate Water. Similarly, E. spiralis (Fig. 13C) was most frequently collected in the warm water sphere, and there were isolated records from the SAIW and the NADW. C. appendiculata (Fig. 11B) and E. mitra (Fig. 12B) were the only species found to be relatively common over a broad range of temperature. The hydrographic and biological data reported by Owre & Foyo (1972) are in agreement with these observations.

Although Pugh's (1974) material was collected differently, his conclusions regarding these few species are similar to ours. He caught Abylopsis tetragona at 615 m but found that it mainly lives quite near the surface. The few specimens of A. eschscholtzii came from depths of 50 to 410 m whereas in the Caribbean it was numerous in the upper 50 m. Pugh found most specimens of Bassia bassensis, which is rare in the Caribbean, in the upper 100 m, usually close to the surface. It has been reported by many authors that Chelophyes appendiculata, described by Pugh as "probably the commonest and most widely distributed species of siphonophore," has a broad vertical distribution as well. Sources have found it most numerous in the upper 100 m, as we did, or 200 m, and

Leloup & Hentschel (1935), who caught it as deep as 1000 m, reported a second peak at 400-600 m. Pugh commented that the main concentration of C. appendiculata occurred just below the depth of the 15°C isotherm, at 14.4-14.5°C, and that Moore (1953) had reported a significant correlation between the depth of the 15°C isotherm and the distribution of siphonophores, including C. appendiculata. However, the present data indicate that this species has a broad distribution with regard to temperature in the Caribbean. The majority of specimens of Diphyes dispar were collected from the upper 50 m by Pugh as they were in the Caribbean, but D. bojani, which has found somewhat deeper than D. dispar in the latter area and was the second most numerous form, was caught only once by Pugh, at 800 m. Pugh also noted that Eudoxoides mitra, although mainly an inhabitant of the upper 150 m, resembles C. appendiculata in its relatively broad vertical range. Authors generally agree that E. spiralis is found most frequently in the upper 100 m (Pugh, 1974).

TABLE 22

Relative abundance and vertical distribution of siphonophores collected in the Caribbean Sea and adjacent areas.

Species	Depth Range (m)	Range (m) of Maximum Nos.	Number of Samples	Total Estimated Numbers Collected
A. eschscholtzii	0-1272	0-50	79	13,040
A. tetragona	0-1665	0-100	110	15,608
C. appendiculata	0-2500	0-100	85	7,482
D. bojani	0-996	0-100	86	14,667
D. dispar	0-50	0	35	4,213
E. mitra	0-822	0-250	47	4,250
E. spiralis	0-2500	0-100	31	1,700

TABLE 23

Relative abundance of five groups of organisms collected at stations selected to compare distribution in major Caribbean areas

Region	Station	Siphonophora	Copepoda	Euphausiacea	Chaetognatha	Salpidae	Total
Yucatan Channel	P6701, Sta. 2	215	39,874	569	2,544	20	43,222
	P6805, " 2	800	63,720	790	1,531	0	66,841
	P6811, " 20	230	46,400	40	947	0	47,617
	P6904, " 2	1,550	117,780	70	736	1,250	121,386
Western Caribbean	P6805, " 3	1,100	184,323	330	5,658	100	191,511
	" , " 4	700	74,928	150	838	800	77,416
	P6811, " 14	300	50,866	0	3,521	0	54,687
	" , " 15	120	40,752	100	1,865	350	43,187
	" , " 16	150	61,616	392	1,216	0	63,374
	" , " 17	170	81,372	20	918	0	82,480
	" , " 18	150	107,330	400	1,261	150	109,291
	" , " 19	300	50,188	465	1,266	0	52,219
Central Caribbean	P6606, " 4	400	72,970	1,160	855	300	75,685
	P6805, " 5	250	62,430	498	4,143	50	67,371
	" , " 7	1,550	88,298	360	9,257	55	99,520
	P6811, " 2	60	47,156	550	1,257	30	49,053
	" , " 3	600	124,259	170	1,314	200	126,543
	" , " 4	590	198,608	240	3,872	150	203,460
Eastern Caribbean	P6805, " 9	450	35,339	1,572	2,978	300	40,639
	" , " 10	1,350	25,193	811	2,619	350	30,323
	" , " 11	240	17,108	954	2,636	0	20,938
	P6911, " 1	1,540	77,672	150	586	1,550	81,498
	" , " 2	1,504	63,003	584	2,180	650	67,921
	" , " 3	150	99,664	720	1,926	150	102,610
	" , " 4	210	33,342	400	1,545	620	36,117
	" , " 5	570	52,164	302	1,598	30	54,664
	" , " 6	930	59,293	0	1,292	220	61,735
	" , " 7	124	35,861	600	728	312	37,625
	" , " 8	250	54,345	100	924	2,120	57,739
	" , " 9	1,150	106,718	357	5,293	1,650	115,168

TABLE 23 (Continued)

Region	Station	Siphonophora	Copepoda	Euphausiacea	Chaetognatha	Salpidae	Total
	P6911, Sta. 10	650	97,726	796	3,622	1,850	104,644
	" , " 11	1,210	66,921	112	6,276	550	75,069
Areas of Upwelling	P6606, " 11	0	29,724	0	910	0	30,634
	" , " 12	50	121,957	75	8,600	25	130,707
	" , " 13	50	52,133	270	980	25	53,458
	" , " 14	100	77,500	540	4,000	150	82,290
	P6811, " 5	2,650	112,029	800	7,595	1,000	124,074
	" , " 6	750	85,782	670	1,373	600	89,175
	" , " 7	1,254	94,730	690	3,128	0	99,802
	" , " 8	3,145	25,824	280	1,174	40	30,463
	" , " 9	1,300	129,204	3,350	3,225	105	137,184
	" , " 10	1,450	110,583	1,380	7,847	500	121,760
	" , " 11	625	177,904	2,750	4,617	650	186,546
	" , " 12	670	78,885	84	2,490	200	82,329
Windward Passage	" , " 1	100	90,261	450	2,019	100	92,930
Mona Passage	P6911, " 12	403	74,607	380	2,010	0	77,400
Grenada Passage	G6722, " 15	120	7,966	6	831	64	8,987
	" , " 17	370	33,639	230	1,042	10	35,291

The seven more common species were broadly distributed across the Caribbean and all were collected in the Gulf of Mexico (P 6803, Sta. 4-11). With the exception of E. mitra, they also occurred in collections from the Antilles Current (e.g., P 6904, Sta. 15-22). Siphonophores were present at all but one of 48 stations selected to compare abundance of five groups of organisms in the major oceanic areas of the Caribbean (Table 23, Fig. 14). Four of these stations were occupied in the dry season, the two in the Grenada passage and two of the four in the Yucatan Channel. All of the samples used to compare numbers in the western, central and eastern Caribbean and the areas of upwelling were collected during the wet season, presumably the period of greatest productivity.

Absence and very low numbers of siphonophores are a consequence of the phenomenon of swarming as well as patchiness caused by physical and chemical factors. The data summarized in Table 24 suggest that they are most abundant in the eastern Caribbean and the areas influenced by upwelling off Central America between Colombia and Honduras, compared with the central and western Caribbean. The relatively large numbers collected in the Gulf of Darien and the Gulf of Mosquitoes may, however, reflect physical aggregation caused by the general westward drift in combination with the cyclonic circulation in the area, rather than higher productivity associated with upwelling. The abundance recorded for the Yucatan Channel probably did result from the massing of plankton as the Caribbean waters flowed into the strait.

TABLE 24

Data on horizontal distribution of siphonophores summarized from Table 23.

Location	No. of Stations	Range in No. Siphonophores Collected	Avg. of Total No. Collected per Station
Yucatan Channel	4	215-1550	699
Western Caribbean	8	120-1100	374
Central Caribbean	6	60-1550	575
Eastern Caribbean	14	124-1540	738
Areas of upwelling	12	0-3145	1003
Passages	4	100-403	248

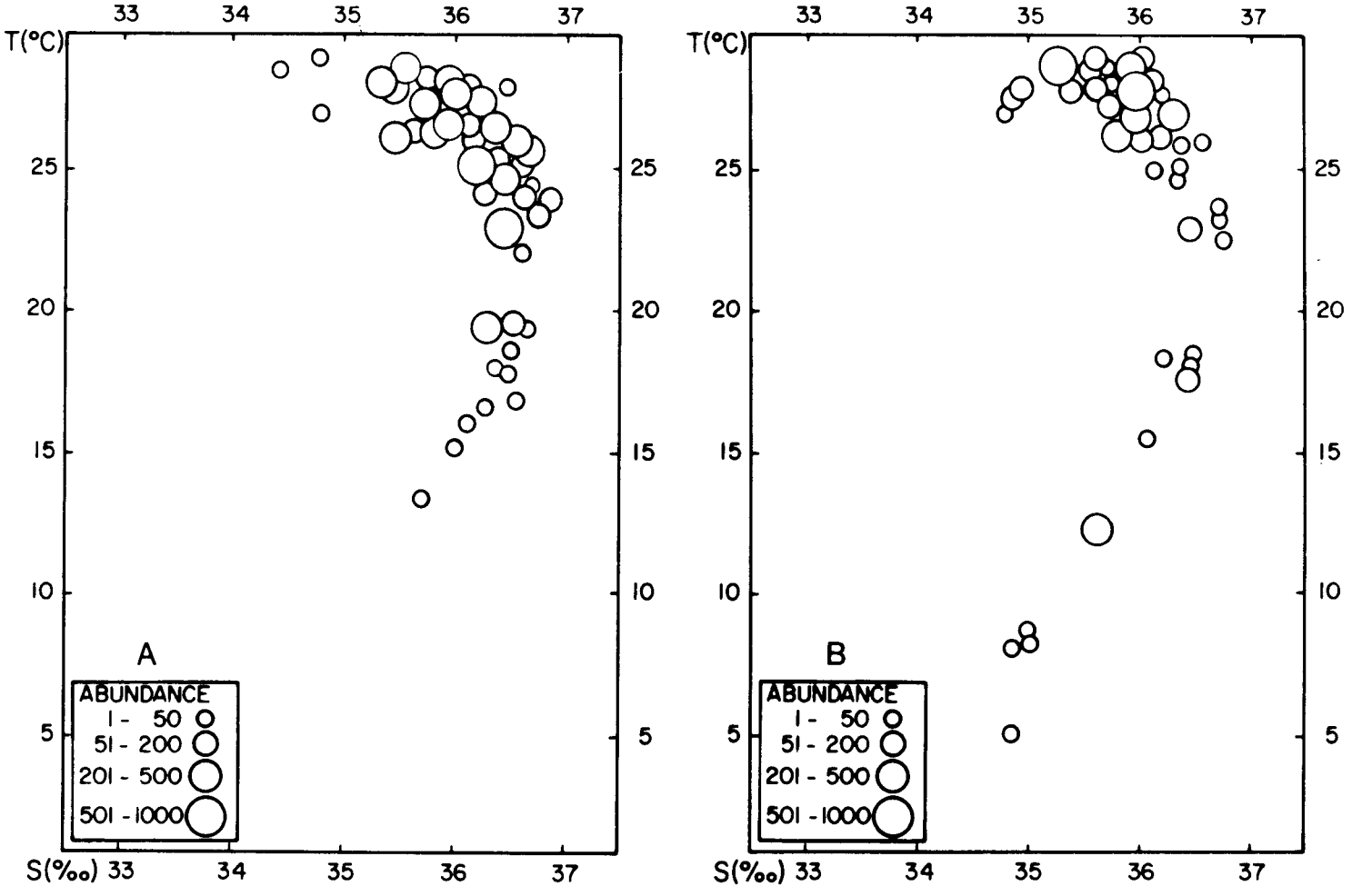

Figure 11. T-S-P diagrams, (A) Abylopsis tetragona and (B) Chelophyes appendiculata

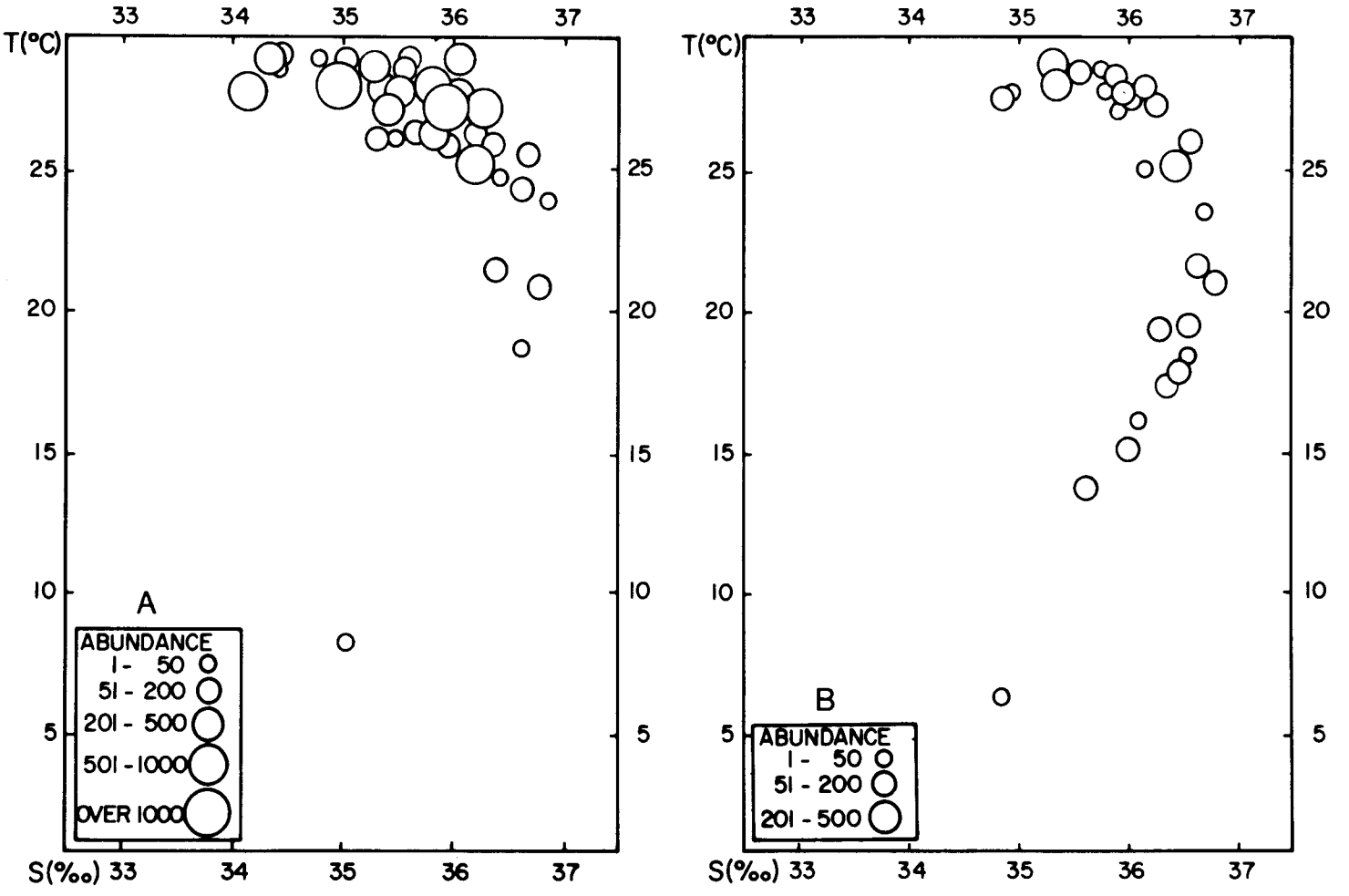

Figure 12. T-S-P diagrams, (A) Diphyes bojani and (B) Eudoxoides mitra

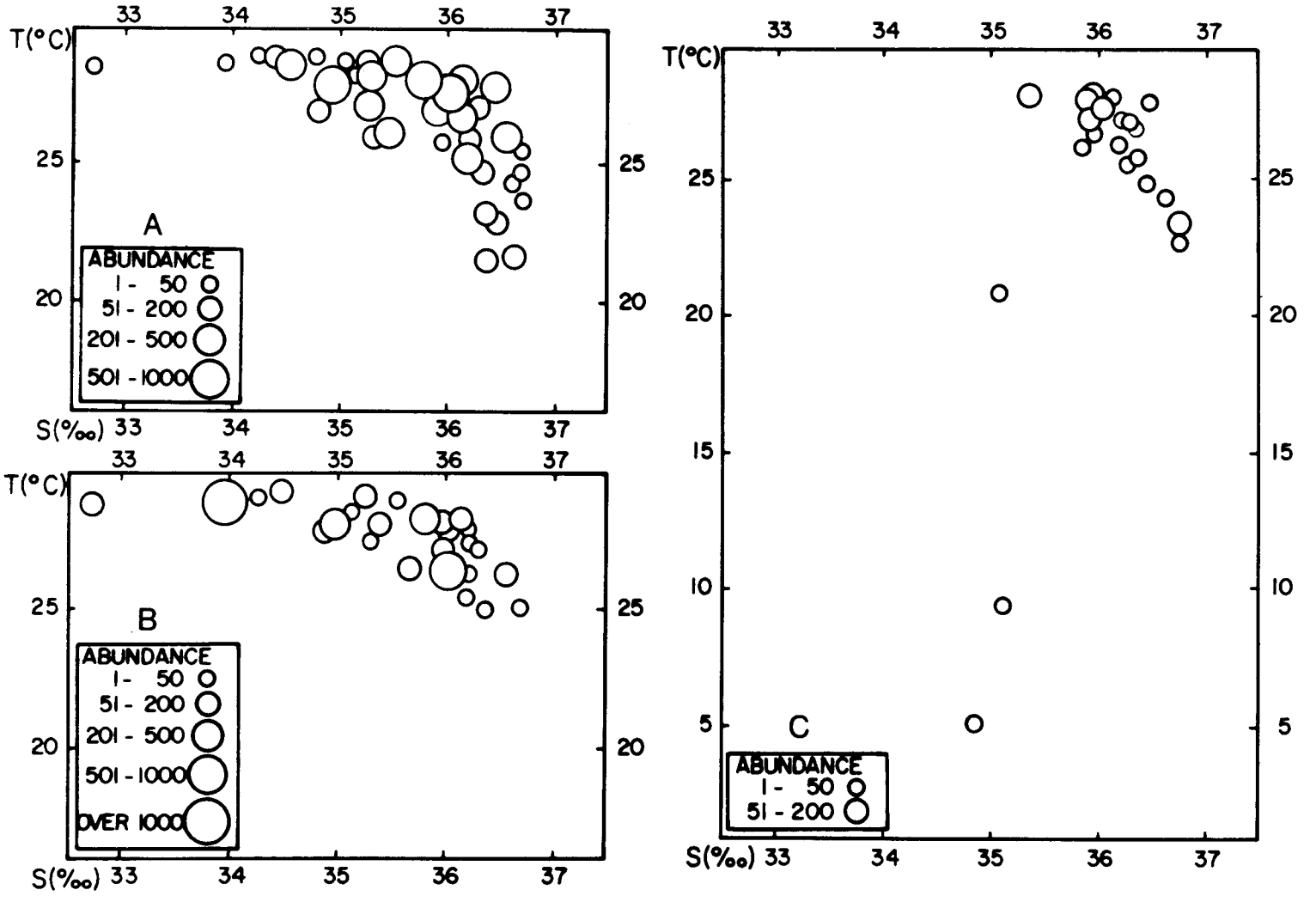

Figure 13. T-S-P diagrams, (A) Abylopsis eschscholtzii, (B) Diphyes dispar and (C) Eudoxoides spiralis

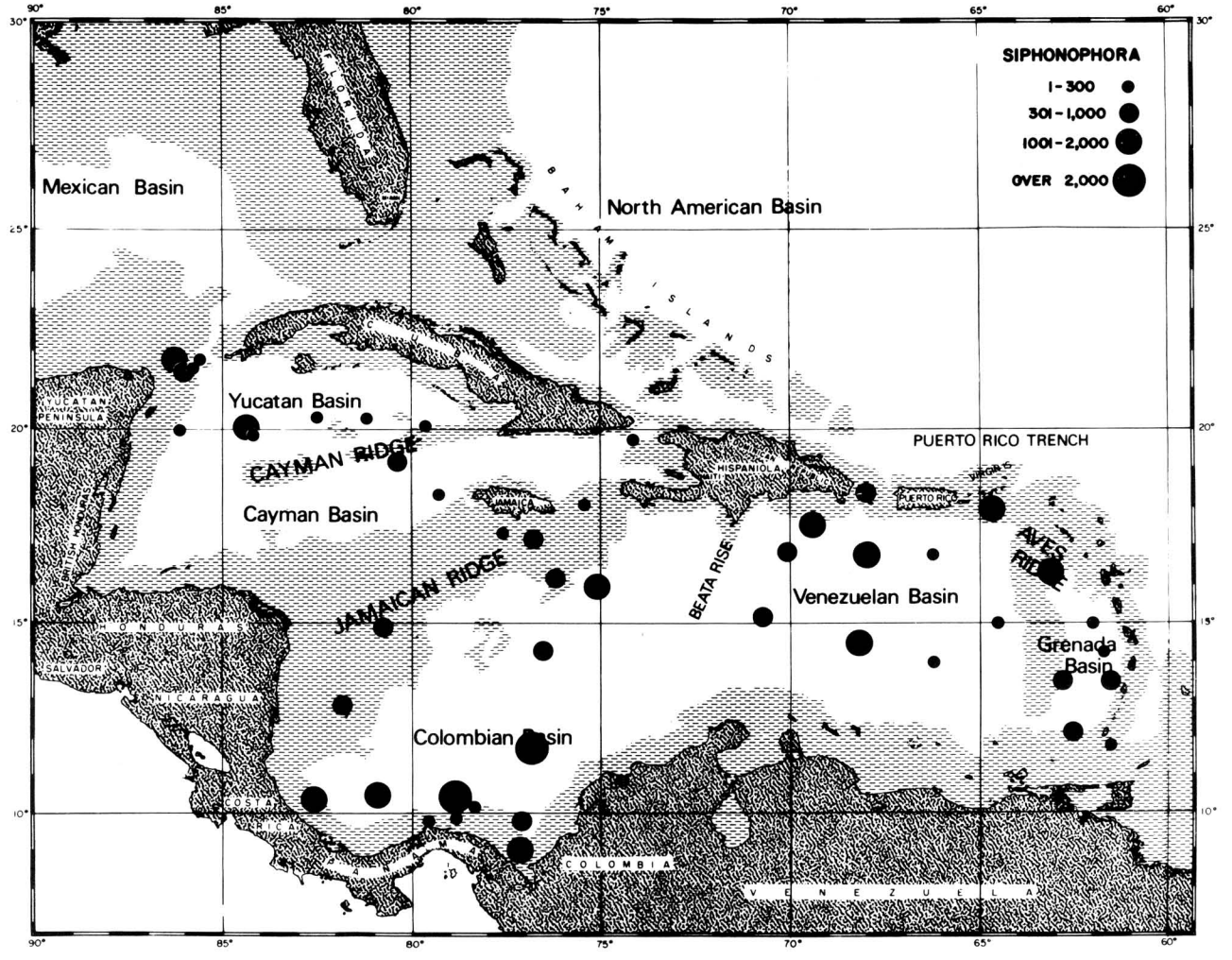

Figure 14. Total numbers of Siphonophora collected at 48 stations selected to compare abundance in major Caribbean areas (see Table 23)

TABLE 25

Vertical Distribution of *Abylopsis eschscholtzii*

CRUISE	STATION	DEPTH (m)	ESTIMATED NUMBER
P-6701	3	0	20
	12	0	120
		100	50
	13	0	350
	14	0	100
	18	0	100
	22	0	20
G-6722	9	0	300
	10	0	150
	17	0	320
P-6803	4	30	100
	11	0	80
		30	150
	15	0	160
	18	0	300
	20	0	85
	22	0	10
P-6805	2	0	250
	3	0	450
	4	0	200
	5	0	50
	7	0	450
		50	250
	10	0	100
P-6811	2	0	10
	3	0	300
	5	0	650
	6	0	250
	7	0	30
	8	0	990
		27	30
	9	0	250
		50	150

TABLE 25 (continued)

Vertical Distribution of *Abylopsis eschscholtzii*

CRUISE	STATION	DEPTH (m)	ESTIMATED NUMBER
	10	0	150
		25	350
	12	35	100
	14	0	50
	15	0	100
	16	52	50
	18	0	100
	19	0	150
	20	0	150
P-6904	1	0	100
		38	250
	2	0	900
		14	400
	3	0	200
		30	100
	4	0	90
	6	0	250
		31	160
	9	0	10
	10	0	85
		30	180
	11	0	200
		45	350
	12	0	120
	13	0	50
	16	0	58
		59	40
	18	0	40
		62	40
	20	0	140
	21	0	75
P-6911	1	0	120
	2	53	150
		1272	4
	4	0	20

TABLE 25 (continued)

Vertical Distribution of *Abylopsis eschscholtzii*

CRUISE	STATION	DEPTH (m)	ESTIMATED NUMBER
	5	0	265
	6	0	20
	7	0	20
	9	0	100
	10	56	50
	11	0	100
	12	0	18
	13	0	50
	14	0	30
	16	0	30
		51	200

TABLE 26

Vertical Distribution of *Abylopsis tetragona*

CRUISE	STATION	DEPTH (m)	ESTIMATED NUMBER
P-6606	8	100	100
	12	100	50
P-6701	1	0	10
	2	90	150
		220	5
	3	0	70
		115	25
	4	0	10
	5	0	350
		90	300
	8	0	150
		250	20
	10	0	9
	11	110	150
	12	0	60
		100	450
	13	100	50
	14	100	100
	16	0	60
	20	250	30
G-6722	4	55	200
	9	40	100
	10	45	20
		225	10
	12	0	100
	15	30	20
P-6803	4	0	120
		30	600
	8	40	250
	15	100	50
		200	20
	16	100	80
	17	0	50
		100	50

TABLE 26 (continued)

Vertical Distribution of *Abylopsis tetragona*

CRUISE	STATION	DEPTH (m)	ESTIMATED NUMBER
	18	0	120
		100	120
	20	0	55
		75	120
	25	0	20
	26	100	40
P-6805	2	0	50
	3	0	200
	4	90	50
	5	0	100
	7	0	50
		50	350
	9	0	300
	10	0	250
		55	50
P-6811	3	225	180
	4	0	350
		270	20
	5	25	700
	6	25	150
	7	90	4
		125	40
		225	50
	8	27	10
	12	35	100
		160	50
	14	0	50
	17	0	60
		85	50
		237	30
	19	0	100
P-6904	1	38	750
	2	0	250
	3	30	300

TABLE 26 (continued)

Vertical Distribution of *Abylopsis tetragona*

CRUISE	STATION	DEPTH (m)	ESTIMATED NUMBER
		265	30
	4	30	390
		230	50
		470	25
	6	31	400
	7	25	500
	9	0	15
		70	100
	10	0	19
		30	60
		1665	1
	12	30	500
	13	48	200
	14	37	20
		239	30
	15	52	150
	16	59	120
	18	0	30
		62	60
	19	30	250
	20	0	120
		10	200
	22	0	8
		40	100
		252	30
P-6911	1	65	300
	2	53	350
	3	60	100
	4	81	100
	5	59	60
	6	50	350
	7	0	20
		60	20
	8	60	150
	9	60	400
	10	56	300

TABLE 26 (continued)

Vertical Distribution of *Abylopsis tetragona*

CRUISE	STATION	DEPTH (m)	ESTIMATED NUMBER
	12	36	10
		200	2
	13	65	500
	15	0	30
		53	320
	17	54	250

TABLE 27

Vertical Distribution of *Chelophyes appendiculata*

CRUISE	STATION	DEPTH (m)	ESTIMATED NUMBER
P-6606	13	100	25
	14	10	50
P-6701	1	530	5
	2	0	5
		220	5
	3	0	60
		350	20
	4	0	10
		505	16
	5	0	50
	8	0	200
		505	10
G-6722	10	45	10
		225	45
P-6803	4	30	200
	8	95	50
	11	2500	4
	15	0	40
	16	0	20
		100	20
	17	0	250
		490	20
	20	0	30
	22	0	110
		100	50
	25	0	20
	26	100	40
P-6805	2	0	200
	3	0	450
	4	0	100
	5	0	100
	7	50	50
	9	65	50

TABLE 27 (continued)

Vertical Distribution of *Chelophyes appendiculata*

CRUISE	STATION	DEPTH (m)	ESTIMATED NUMBER
	10	0	650
P-6811	1	0	50
	2	0	10
	4	0	50
	5	0	50
	6	25	50
	8	0	60
		1000	5
	9	0	100
	10	0	150
	11	0	150
		590	25
	12	35	50
		160	20
	14	0	200
	15	55	20
	17	237	30
	18	0	50
	20	0	30
		75	50
P-6904	1	0	150
	3	30	250
	4	30	90
	6	31	80
	7	25	50
	9	0	65
		676	20
	10	0	6
		30	60
		233	10
		1892	2
	11	0	50
		45	50
	12	30	450
	13	0	300

TABLE 27 (continued)

Vertical Distribution of *Chelophyes appendiculata*

CRUISE	STATION	DEPTH (m)	ESTIMATED NUMBER
		48	50
	15	52	50
	16	0	4
	17	0	50
	18	0	210
		62	20
	19	0	10
	20	0	30
	21	0	20
P-6911	1	0	570
	9	60	100
	11	58	100
		234	60
	12	344	40
	14	0	60
		34	400
	16	0	60

TABLE 28

Vertical Distribution of *Diphyes bojani*

CRUISE	STATION	DEPTH (m)	ESTIMATED NUMBER
P-6701	3	0	60
	4	0	10
	5	0	50
	8	0	150
	10	0	9
	11	110	50
	12	0	10
		100	150
	14	0	200
		100	50
	24	100	100
G-6722	4	0	750
	9	0	500
		40	100
	10	45	10
	12	0	50
		181	10
	15	0	100
	17	250	10
P-6803	11	30	100
	16	0	40
	17	0	250
	20	0	40
		75	40
	22	0	70
	25	0	60
P-6805	2	0	50
	11	0	240
P-6811	2	0	20
	4	50	150
	5	0	750
		25	100
	6	0	50

TABLE 28 (continued)

Vertical Distribution of *Diphyes bojani*

CRUISE	STATION	DEPTH (m)	ESTIMATED NUMBER
		25	50
	8	0	1740
		27	10
	9	0	400
	10	0	450
	11	0	250
	12	35	300
	19	0	50
P-6904	1	0	900
	3	30	100
	4	30	90
	6	31	40
	7	0	50
	9	676	20
	10	0	1
		30	60
	11	0	50
		45	550
	12	30	1200
	13	0	350
	14	37	60
	16	0	2
		59	80
	17	0	90
	18	0	60
	19	30	50
	20	0	40
		10	50
	21	0	10
	22	40	50
P-6911	1	0	390
	2	0	450
		53	550
	4	0	40
		81	50

TABLE 28 (continued)

Vertical Distribution of *Diphyes bojani*

CRUISE	STATION	DEPTH (m)	ESTIMATED NUMBER
	5	59	240
		996	5
	7	0	24
		60	20
	8	60	50
	9	0	150
		60	100
	10	0	200
		56	50
	11	0	50
		58	400
	12	0	6
		36	10
	13	0	100
		65	50
	14	0	180
	15	0	30
		53	40

TABLE 29

Vertical Distribution of *Diphyes dispar*

CRUISE	STATION	DEPTH (m)	ESTIMATED NUMBER
P-6701	3	0	20
	8	0	200
	22	0	20
G-6722	17	0	40
P-6803	8	0	40
	15	0	80
	20	0	10
	22	0	10
P-6805	2	0	100
	7	50	150
	9	0	100
	10	0	150
P-6811	2	0	10
	5	0	300
	6	0	50
	7	0	1080
	8	0	270
	9	0	150
	10	0	200
		25	50
P-6904	1	0	600
		38	50
	4	30	30
	9	0	10
	11	0	50
	13	0	100
	17	0	50
	18	0	20
	20	0	10
	21	0	10
P-6911	1	0	60

TABLE 29 (continued)

Vertical Distribution of Diphyes dispar

CRUISE	STATION	DEPTH (m)	ESTIMATED NUMBER
	6	0	60
	9	0	100
	12	0	3
	15	0	30

TABLE 30

Vertical Distribution of Eudoxoides mitra

CRUISE	STATION	DEPTH	ESTIMATED
P-6606	14	10	50
P-6701	2	220	20
	3	115	5
	8	505	10
	20	250	90
	24	100	50
G-6722	4	55	50
	10	225	110
	12	80	50
		181	10
P-6803	8	40	100
		175	30
	16	225	1
	22	100	50
P-6805	2	0	100
	4	90	350
	7	50	200
	10	0	150
P-6811	1	0	50
	2	822	10
	3	225	120
	4	270	20
	6	0	50
		25	150
	7	225	50
	8	0	30
	9	0	100
		50	150
	10	0	50
	11	45	200
	12	160	50
	16	52	100

TABLE 30 (continued)

Vertical Distribution of *Eudoxoides mitra*

CRUISE	STATION	DEPTH (m)	ESTIMATED NUMBER
P-6904	1	38	50
	5	250	80
	7	25	100
	10	233	30
	11	45	50
	14	239	30
P-6911	1	65	100
	6	50	400
	7	60	20
	9	60	200
	10	56	50
	11	58	500
	12	78	20
		153	60
		200	4

TABLE 31

Vertical Distribution of Eudoxoides spiralis

CRUISE	STATION	DEPTH (m)	ESTIMATED NUMBER
P-6606	13	100	25
P-6701	2	90	30
	4	0	5
P-6803	8	0	20
	11	30	50
		2500	4
	17	0	50
	20	0	35
		75	20
P-6805	2	0	50
	7	0	50
P-6811	5	25	50
	10	25	50
P-6904	4	30	30
	11	0	150
		45	150
	12	30	100
	13	0	150
		48	50
	14	37	40
	15	52	100
	16	0	26
		59	40
	18	0	35
	20	0	40
		10	50
	22	554	20
P-6911	3	60	50
	6	50	100
	8	60	50
	15	53	80