DISTRIBUTION AND ABUNDANCE OF *PHYSALIA* IN FLORIDA WATERS

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ABSTRACT

Distribution, abundance and size of the Portuguese man-of-war (*Physalia physalis*) were monitored in the western Caribbean, Gulf of Mexico and coastal waters of Florida by aerial surveys from April 1969 through February 1971. The Florida Keys were more closely monitored by field surveys. *Physalia* occurred beyond the continental shelf throughout the study area. Movement and dispersion is controlled by surface currents; winds are the controlling factor for *Physalia* strandings along shorelines. A seasonal cycle of distribution was observed for *Physalia*. In fall, they occur mostly in the Caribbean. In winter, they occur in all areas studied, but in spring and summer they appear mostly in the Florida Straits. Maximum abundance is from December through February and minimum abundance is from June through July. *Physalia* float length varies from a minimum average of 6.39 cm (2.55 inches) from December through January to a maximum average of 21.92 cm (8.63 inches) from April through July. *Physalia* four or five inches in float length are probably capable of spawning. Spawning, based on recruitment of small *Physalia*, first occurs in the Caribbean in August. The spawning area then spreads, until by December it includes all the Caribbean and Gulf of Mexico. It then decreases in the Caribbean and increases in the Florida Straits until February. Spawning ceases within the study area by May.

Physalia are dioecious and fertilization appears successful only when animals are abundant. The most mature germ cells found were oogonia during vitellogenesis, and spermatids.

Laboratory studies of survival and growth of *Physalia* were attempted. Several live gonodendra were maintained for possible fertilization and identification of larval forms. None of these attempts were successful.

INTRODUCTION

One of the best known warm water Siphonophores, the Portuguese man-of-war, *Physalia physalis* (L.) invades the Gulf Stream along the Keys and east coast of Florida every winter and spring. They frequently appear close to shore in such abundance as to become hazardous to the public. *Physalia* are capable of paralyzing swimmers with their nematocyst laden tentacles, and even after *Physalia* have been washed ashore they are able to inflict painful stings. When they become so plentiful they cannot be avoided, the beaches are closed, inconveniencing both Florida residents and tourists.

This study was funded in part by the United States Department of the Interior, Bureau of Commercial Fisheries Jellyfish Act (PL 89-720), passed to " . . . provide assistance to the States . . . in controlling and eliminating jellyfish and other such pests in such coastal waters." Before control or elimination of *Physalia* can be considered, its life history must be known. Very little is known of the distribution of *Physalia* within the coastal waters of the eastern United States even though circumtropical distribution is established by records of capture in the Pacific Ocean (Mackie, 1960; Southcott, 1967), Atlantic Ocean (Wilson, 1947; Totton, 1960; Lane and Dodge, 1958), Indian Ocean (Ganapati and Subba Rao, 1961), Caribbean Sea (Fontaine, 1954) and Gulf of Mexico (Woodcock, 1944; Larimer and Ashby, 1962).

Considerable work has been completed on morphology and developmental biology, the most recent and comprehensive being that of Totton (1960) and Mackie (1960). Unfortunately, little is known concerning details of seasonal abundance, growth rates or reproduction.

PROCEDURES AND RATIONALE

The man-of-war is a colony of individuals, each performing a specific function of survival, but none are capable of active propulsion. The

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float and its sail or crest utilizes the wind for movement. Since appendages and part of the float are submerged, movement is also affected by currents. Numerous investigations (e.g., Sims and Ingle, 1967) have shown that many larval and adult marine organisms are transported from the Caribbean to the coasts of Florida by currents. The proposed study area, therefore, included the western Caribbean as far as Grand Cayman, the Yucatan Straits, the northcentral Gulf of Mexico and the coasts of Florida from shore to 30 to 50 nautical miles (48-80 km) out.

FIELD STUDIES

Offshore surveys

Lane (1960) reports that *Physalia* are numerous and small in early winter, becoming larger and less numerous until April when they disappear from waters of the Gulf Stream near Miami, Florida. Information obtained from fishermen suggests that this is also true along the Florida Keys. Monthly sampling would detect these changes in abundance and size but other areas surveyed might not follow this pattern. The study area was therefore divided into sections which in final analysis could be compared.

Two vehicles were available for these monthly surveys, aircraft, and research vessel. Aerial surveys were chosen based on the following factors. Aircraft were able to survey the areas in one fourth the time at $400 less per month. Visibility, as related to the areas in which *Physalia* could be counted and measured, was essentially the same by either method. However, areas of converging surface currents could possibly trap *Physalia* much as they do *Sargassum* and trash. These disturbances were visible many miles from the aircraft, but had to be more closely approached for accurate counts and measurements. Considerable information on pelagic fishes, sharks, porpoises, turtles, rays and many other marine animals could also be obtained. The commercial fishing industry has shown that aircraft can spot such animals much better than can fishing vessels.

Once aircraft were selected, transects were plotted within each section to best utilize time, fuel stops and radio navigational aids. Figure 1 shows these transects, division of the study area into sections and basic winter current patterns. These surveys were conducted monthly from April 1969 through February 1971 with single or twin engine overhead, fixed wing aircraft at altitudes of 300 to 450 meters. Lower altitudes were occasionally used to verify sightings and counts. Only the surface water directly below the aircraft, about 55 m wide, had conditions necessary for accurate determinations of size and frequency of *Physalia*. They appeared opaque white with an occasional bluish cast by reflected sunlight. Position and approximate float length were recorded for all *Physalia*. Position, approximate size, weight, and numbers were recorded for other marine animals.

An inexperienced observer has great difficulty detecting objects even as large as turtles and sharks. For this reason we were fortunate to have as primary pilot William P. Richardson, a professional fish spotter. For the past twenty-five years he has been using aircraft to search out schooling fishes of commercial importance and to guide their quick and efficient capture. Years of experience enable him to sight schools of fish from altitudes over 900 m and to determine species and approximate total weight. Size estimates were based on experience and comparison with regularly encountered objects of known dimensions. Furthermore, any possible error was more or less standardized since the same two observers made nearly all surveys.

Occasional observations were also made from the FDNR R/V *Hernan Cortez* and other research vessels whenever possible. Due to other obligations, these vessels were unable to sample regularly; therefore, the data are used only to support the accuracy of aerial survey results.

All aerial survey float length approximations and distances were recorded in English units since the pilot was not experienced in visual determinations of metric units. Subsequent conversion from English to metric units would have been time consuming and unnecessary. Metric units were used for laboratory analyses. All statistical analyses were calculated in original units and converted to metric for comparison.

Inshore surveys

Concurrent with aerial surveys, the Marine Research Laboratory maintained a field station at Key West. From November 1969 through September 1971, daily to twice weekly obser-

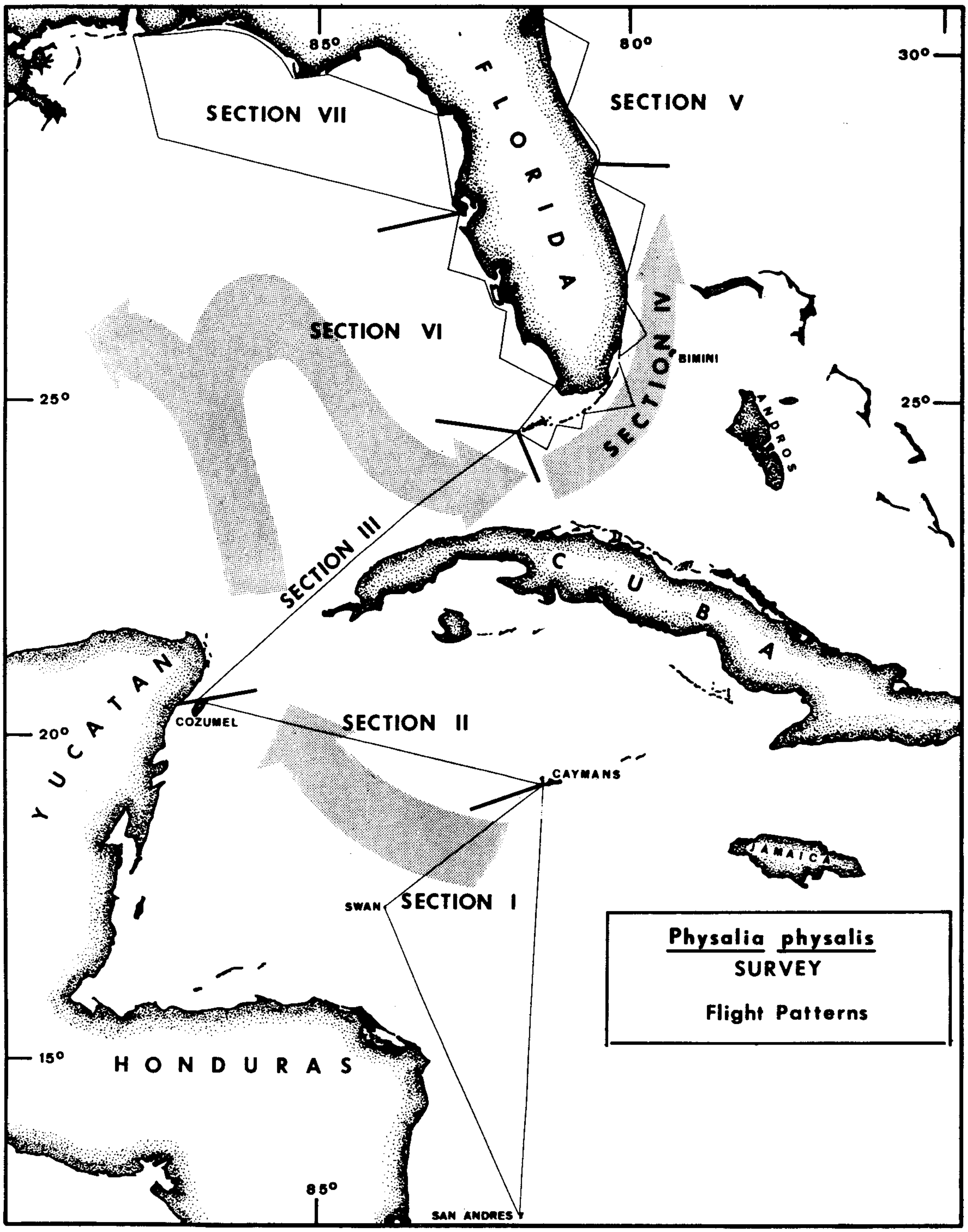

Figure 1. Division of study area into sections showing areas surveyed and winter current patterns.

vations were made from beaches, piers and bridges along the Florida Keys. Location and approximate float length were recorded during these surveys and numerous beached specimens were returned to the laboratory for experimentation.

LABORATORY STUDIES

To supplement distribution and abundance data, facilities were prepared for live maintenance of *Physalia* to determine growth rates and methods of reproduction, and to identify larval stages if possible. Previous records (Bigelow, 1891; Totton, 1960) of attempts to maintain live *Physalia* revealed that death occurred within a few days to two weeks of captivity. Initial attempts to maintain *Physalia* substantiated this difficulty. Appendages, especially gastrozoids, sever from the colony, muscle tissues of the float become flexed in spots and the outer tissues dessicate, leading to collapse. The sequence of events may be different for each individual, but the results are the same. Although these difficulties in survival had not been overcome previously, it was hoped that some results on growth and reproduction would be obtained.

Survival and growth

Studies on survival and growth of *Physalia* were conducted seasonally at St. Petersburg and Key West from April 1970 through September 1971. Live specimens used for Key West experiments were obtained during surveys of the Florida Keys. Most came directly from southern Key West beaches and were either recently stranded or were scooped up by bucket before stranding. Live specimens were also collected from Key West in the above manner and returned to St. Petersburg during aerial surveys. Additional specimens were collected from the Gulf Stream east of Palm Beach. Gulf Stream specimens were collected by bucket, put in aerated water in 75 liter plastic trash cans, and immediately returned to St. Petersburg to insure their freshest possible condition.

During experiments on survival and growth numerous tanks of different sizes and shapes were tried. These included styrofoam chests, 38, 110 and 190 liter glass aquaria, rectangular wooden tanks and polyethylene circular tanks. For most of the experiment, however, polyethlyene tanks were used. These were continually modified and changed throughout the study program as results determined factors necessary for survival.

Only the tank system thought best suited for survival is described (Figure 2). This was basically a 1900 liter conical bottom polyethylene tank (1.32 m diameter x 1.63 m deep). It drained from the center bottom by a 3.8 cm PVC pipe also serving as the intake for the recirculating water system. This system filtered the water, maintained oxygen levels, produced a current across the surface of the tank and provided a bathing system to keep the float of *Physalia* moist. High volume, low pressure air from a blower was ducted around the tank just above the water surface to keep the animals from touching the tank sides and to produce a surface wind opposing water current. In this way *Physalia* were continually sailing as if in their natural environment.

Large *Physalia* could be fed by placing small live fish and crustacea directly in the tentacles. Small *Physalia* could not hold fish in their tentacles or within the gastrozoids. Thus, a small glass tank (30.5 cm square x 61 cm deep) was designed to sufficiently concentrate the available supply of *Artemia* and plankton to allow *Physalia* to capture them.

Previous works (Bigelow, 1891; Totton, 1960 and others) have shown that *Physalia* can alter the shape and length of the float, ("somersaulting behavior") so drastically that measurements of increased float size (growth) could not be accurately determined. Diameter of the gas gland, visible in nearly all live *Physalia*, was not altered. This dimension was best suited for growth rate measurements. Representative samples of various sizes from collections at Key West were returned to that laboratory for accurate float length measurements and preservation. These were then sent to St. Petersburg to be measured again for float length and gas gland diameter.

Reproduction

Preserved *Physalia* collected in Key West were also used for studies of reproduction. Gonodendra were removed, sectioned and stained for determination of developmental stages and sex. Representative gonophores and germ cells were measured for indications

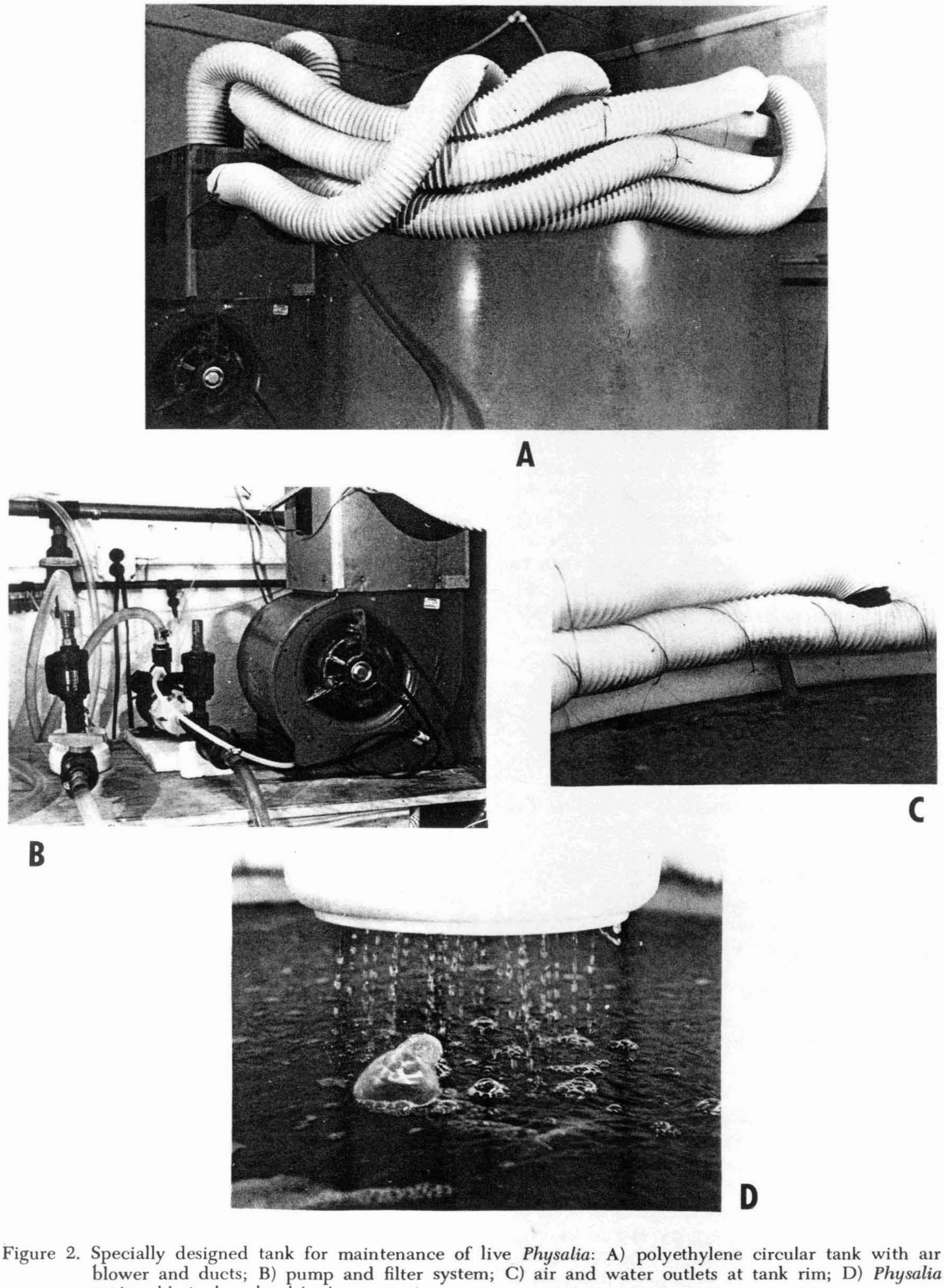

Figure 2. Specially designed tank for maintenance of live *Physalia*: A) polyethylene circular tank with air blower and ducts; B) pump and filter system; C) air and water outlets at tank rim; D) *Physalia* centered in tank under dripping sea water.

of maturity. Hematoxylin/eosin-y stain was used for all slide preparations.

Live gonodendra of both sexes were kept in 4000 ml beakers and other containers in an effort to obtain larval stages. Gonodendra were collected as they dropped naturally from the float or in some cases were cut from the colony. The attempts involved aeration and non-aeration of water and introduction of food. The water was changed daily in all experiments. These experiments were conducted at Key West and St. Petersburg.

RESULTS AND DISCUSSION

PRELIMINARY INVESTIGATIONS

A basic understanding of current and wind patterns is necessary to evaluate the overall movement of *Physalia* within the study area.

Currents

General patterns of sea surface currents within the study area are described by Leipper (1954), Salsman and Tolbert (1963), Nowlin (1971) and others. Based on these reports the central axis of the currents flows eastward through the Caribbean, turns north through the Yucatan Straits and continues into the Gulf of Mexico forming the Loop Current. The northern limit of the Loop Current is seasonally variable, extending further north during summer than winter. It then circulates clockwise returning on a southerly course to form the Gulf Stream flowing through the Florida Straits and eventually into the Atlantic. As described by Nowlin (1971), the Loop Current is influenced by water depth in the Gulf of Mexico, especially along Florida's west coast where a large continental shelf exists. This shelf causes friction with the massive flow of water thereby confining the Loop Current to deeper areas offshore. Bathymetry of the Caribbean and Florida Straits shows two other broad continental shelves within the study area, one along eastern Florida north of Cape Canaveral and the other along northeastern Honduras and Nicaragua. The currents are also confined to offshore areas by these shelves.

Current patterns as related to the transects flown within each section show that surveys were conducted over the main currents in sections I, II, and the western portion of section III. Section VI surveys were made far inshore of the Loop Current as it flows from section III. During summer the northern extent of the Loop Current was surveyed in section VII; during winter it was not. Turning south and passing by section VI again, the Loop Current was still not surveyed. Once reaching the eastern part of section III the currents become the Gulf Stream and were surveyed from here through all of section IV. Finally, the Gulf Stream flows 28 to 37 km farther offshore than those areas surveyed in section V. Current velocities vary seasonally; however, they average yearly approximately 2 km/hr in the Caribbean to nearly 6 km/hr in the Florida Straits.

Winds

In the study area winds are generally from the east to south averaging 20-30 km/hr, but may be altered by storm fronts and hurricanes. Wind affects movement of *Physalia* directly and by altering surface currents. As reported by Woodcock (1944) and others, winds of sustained direction and velocity produce vortices of circulating surface water parallel to the wind. Conversely, strong currents change relative direction and velocity of wind. These interactions also affect the movements of *Physalia*.

Induced motion of Physalia *in the study area*

Physalia occur dimorphically in left and righthanded forms (sinistral and dextral). Basic physics applied to these two forms dictate that *Physalia* will travel at some velocity directly proportional to wind velocity. The imbalance of wind force and water drag due to the oral orientation of appendages causes lefthanded *Physalia* to move at some angle to the right of parallel wind direction and righthanded *Physalia* to move in an opposite fashion (Figure 3). It is also apparent that at some increased wind velocity *Physalia* can no longer maintain this angle and are driven more parallel to wind direction. Wilson (1947) suggested that *Physalia* are probably driven more directly before the wind during a storm. Results of experiments by Totton (1960) show that 180 mm *Physalia* travel approximately 20 m/min (0.65 knots), 34-42° from parallel wind direction in a wind velocity of "rather less than 19 knots". Woodcock (1944) suggests that the angle from parallel wind direction is about 45°. Woodcock (1956) as reported by Totton (1960) shows 0.51 knots for 170 mm *Physalia* in a 13 knot wind.

To show probable effects of normal currents and winds on *Physalia* in the study area, vector diagrams of these forces and the resultant effect of left and righthanded *Physalia* are drawn for most sections (Figure 4). The hypothetical animals are approximately 180 mm float length to allow use of Totton's results on wind induced motion of *Physalia*. The various interactions of wind and currents, although not considered here, would produce a change in direction away from current and more parallel to wind.

In sections I and II (Figure 4-A) winds are from the east and surface currents are from the southeast. Righthanded *Physalia* move with the currents at increased velocity and lefthanded *Physalia* move to the south of current direction. In the Yucatan Straits, in section V and in part of section IV (Figure 4-B), wind and surface currents are at right angles, causing *Physalia* to veer slightly to the west of current direction. In parts of sections III and IV (Figure 4-C), the winds and currents nearly oppose each other, thus righthanded *Physalia* move with the current at decreased velocity and lefthanded move slightly to the north of current direction. In section VI (Figure 4-D) two currents are encountered, one moving south-southeast near the continental shelf and the other moving north-northwest farther offshore. *Physalia* move northwest in the northbound current

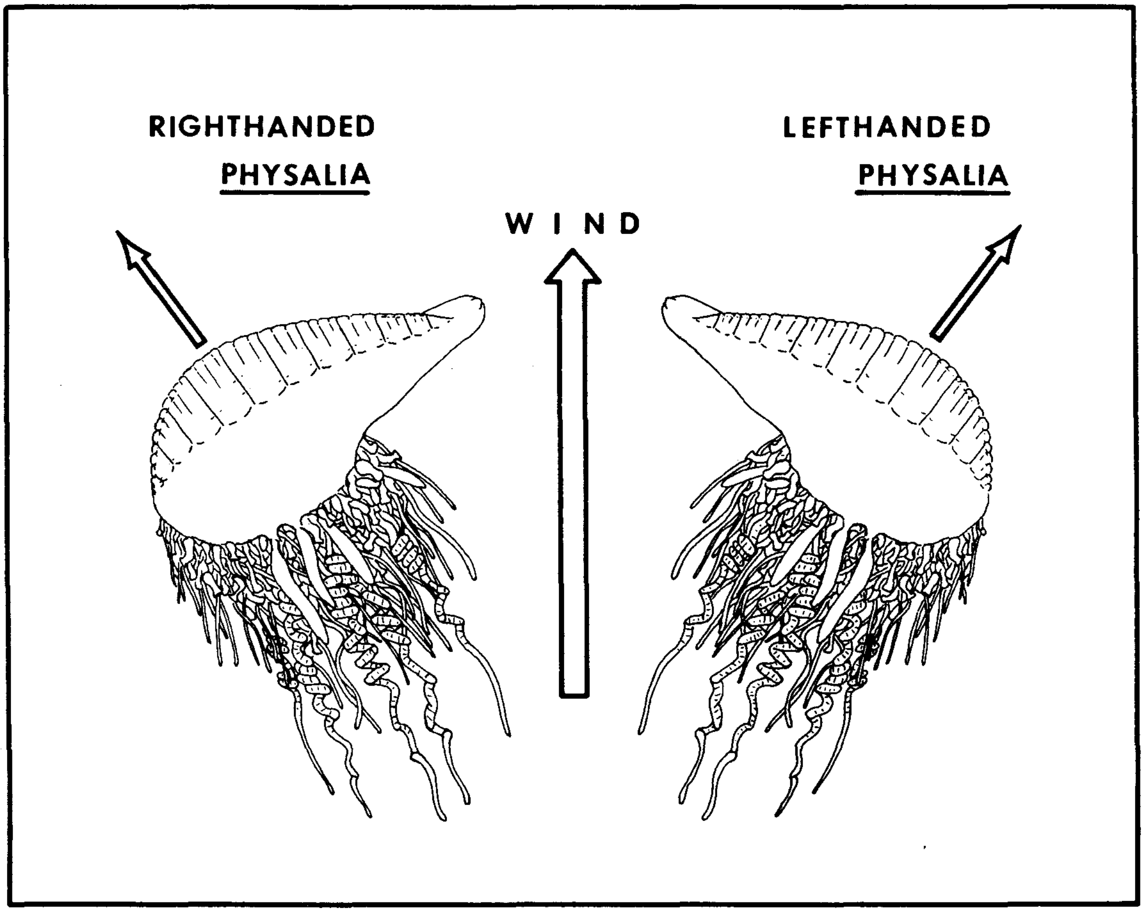

Figure 3. Sailing direction of left and righthanded *Physalia*.

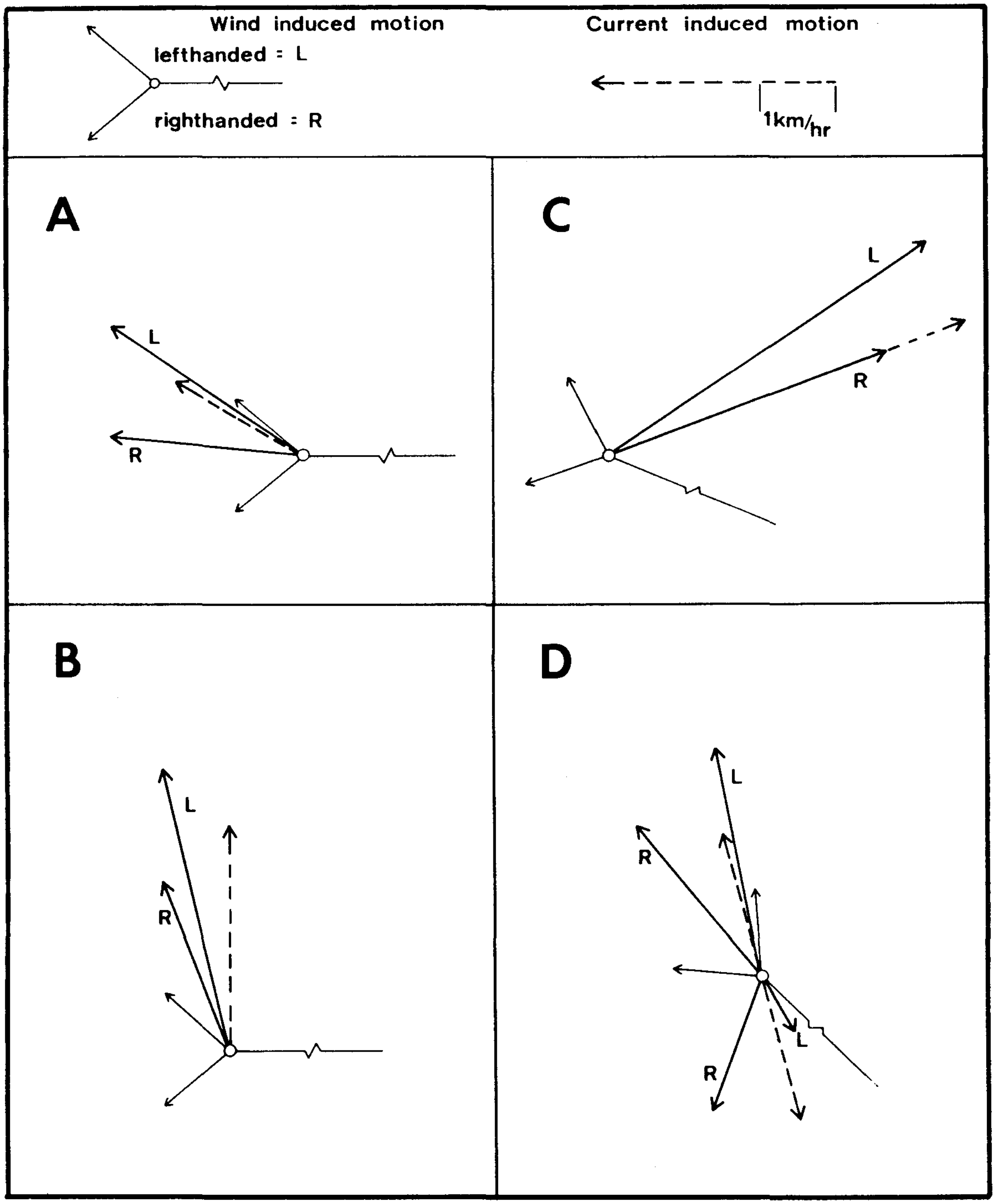

Figure 4. Wind and current induced motion of *Physalia* within the study area. A) Caribbean; B) Yucatan Straits and Florida's east coast; C) Florida's southeast coast; D) Florida's west coast.

and southwest or southeast in the southbound current.

Based on these vector diagrams, *Physalia* are moved mostly by currents. Winds, however, produce components of velocity away from current direction causing *Physalia* to be moved into countercurrents and eddies close to shore or to be stranded. Under normal conditions, *Physalia* can be expected to move through sections in the following order: section I, section II, the western portion of section III, sections VI, VII, VI, the eastern portion of section III, section IV and finally section V (Figure 1).

Small *Physalia* show less float surface area, reduced crest, fewer tentacles and less oral orientation of appendages than do large animals. These differences indicate that smaller animals sail more closely parallel to wind direction and probably at reduced speed under the same wind velocity.

If sailing directions relative to left or righthandedness diverge with increasing size, small animals, having less divergent sailing direction, should be found stranded in approximately equal numbers in the Keys while large lefthanded animals should occur far more frequently than righthanded ones.

During Florida Keys surveys 146 *Physalia* were collected from November 1970 through May 1971, examined for left or right orientation, and measured for float length (Table 1). Of these, one hundred-seven were lefthanded and 39 were righthanded. Mean float length of lefthanded individuals (71.17 mm) was significantly larger than mean float length of righthanded invididuals (29.56 mm) ($t' = 5.6^{**}$, d.f. = 106 and 38).

Similarly, *Physalia* collected by the R/V *Hernan Cortez* on 24 November 1968, at 23°50'N, 83°59'W were examined for size and left or right orientation. This time 43 were righthanded and 17 were lefthanded. Mean float length was 32.71 mm for righthanded and 29.88 mm for lefthanded, an insignificant difference. The location of this capture (shown in Figure 7) puts these *Physalia* near the southern edge of the Loop Current as described by Leipper (1954) and Nowlin (1971). Once past the Yucatan Straits the two forms of *Physalia* would tend to become separated, large lefthanded to the north, and small of both forms and large righthanded to the center and southern sections of the current. These results agree with the hypothesized spatial separation of the two forms.

TABLE 1. STATISTICAL PARAMETERS OF *PHYSALIA* CAPTURED ALONG THE FLORIDA KEYS

	Lefthanded	Righthanded
N	107	38
Mode	15 mm	15 mm
$\bar{x}$ (mean)	71.168 mm	27.56 mm
S^2	3789.89	935.36
$S\bar{x}$	5.951	4.90
95% CI	±11.84 mm	±9.903 mm

DISTRIBUTION

Distribution of *Physalia*, as observed from aerial surveys, shows variation among sections, within sections and among months. To illustrate these distributional variations, the results are presented in two forms: 1) monthly maps (Figures 5-16) depicting the approximate location and concentration of all *Physalia* observed, and 2) total monthly abundance and average float lengths per section (Table 2).

Physalia are nearly always absent from sections V, VI and the coastals areas of section VII (Figures 5-16). This distribution depends directly on the relationship of currents and the areas surveyed within each section. In section VI, for example, the currents are considerably farther offshore than the areas surveyed, and under normal conditions of current and wind, *Physalia* do not reach these areas. The surveys made in section V, although not extending over the major currents, are much closer, and as a result, *Physalia* do occasionally appear. Had surveys been made farther offshore in sections V and VI, *Physalia* abundance would no doubt have been similar to that of neighboring sections.

The observed relationship between currents and *Physalia* distribution is further substantiated by results from section VII where nearly all *Physalia* sightings occurred well offshore. The Loop Current normally sets up large countercurrents within this area during winter. Figure 4-D shows how *Physalia* within the Loop Current could be

Figure 5. Surveys conducted and approximate location and concentration of all *Physalia* observed during September.

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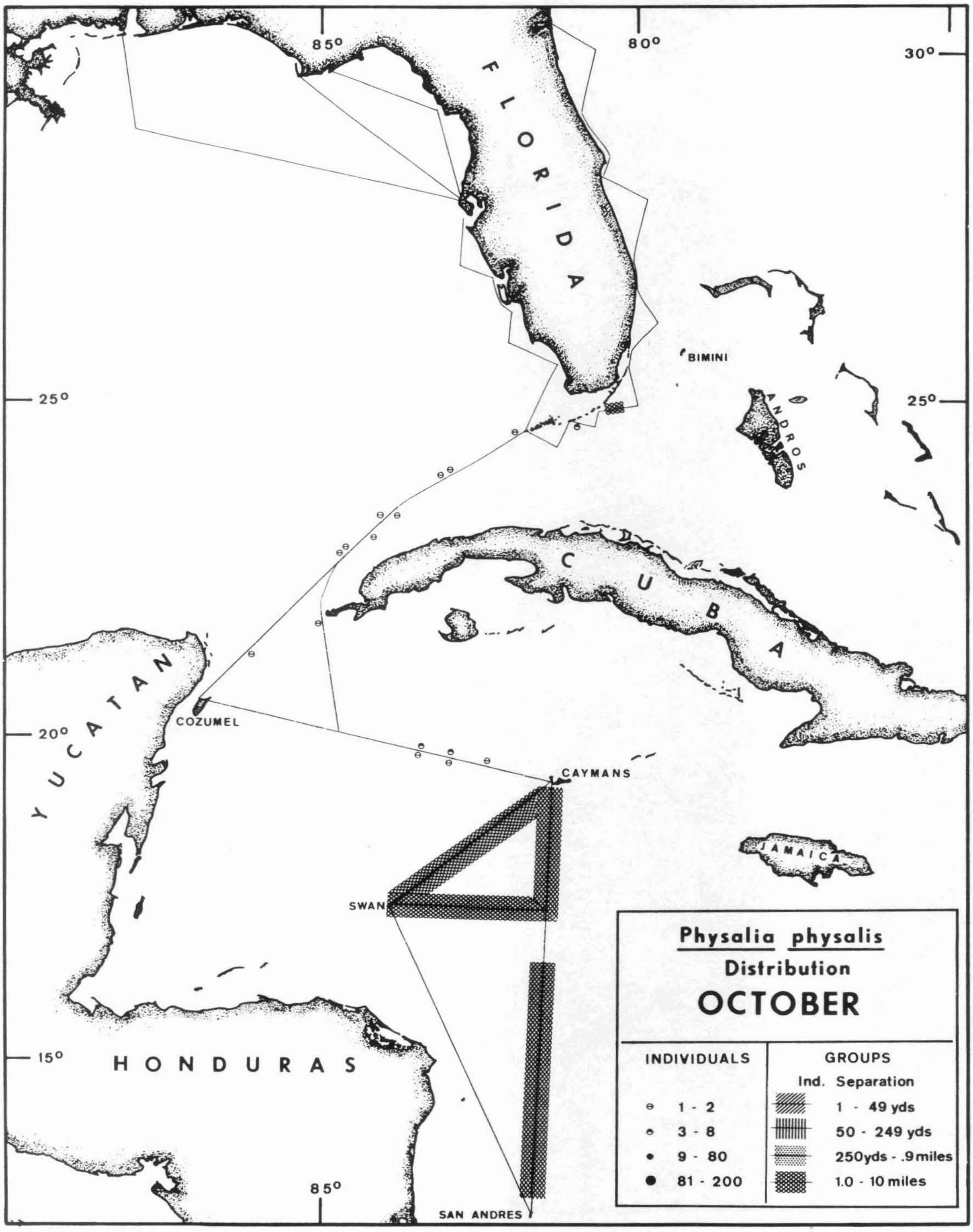

Figure 6. Surveys conducted and approximate location and concentration of all *Physalia* observed during October.

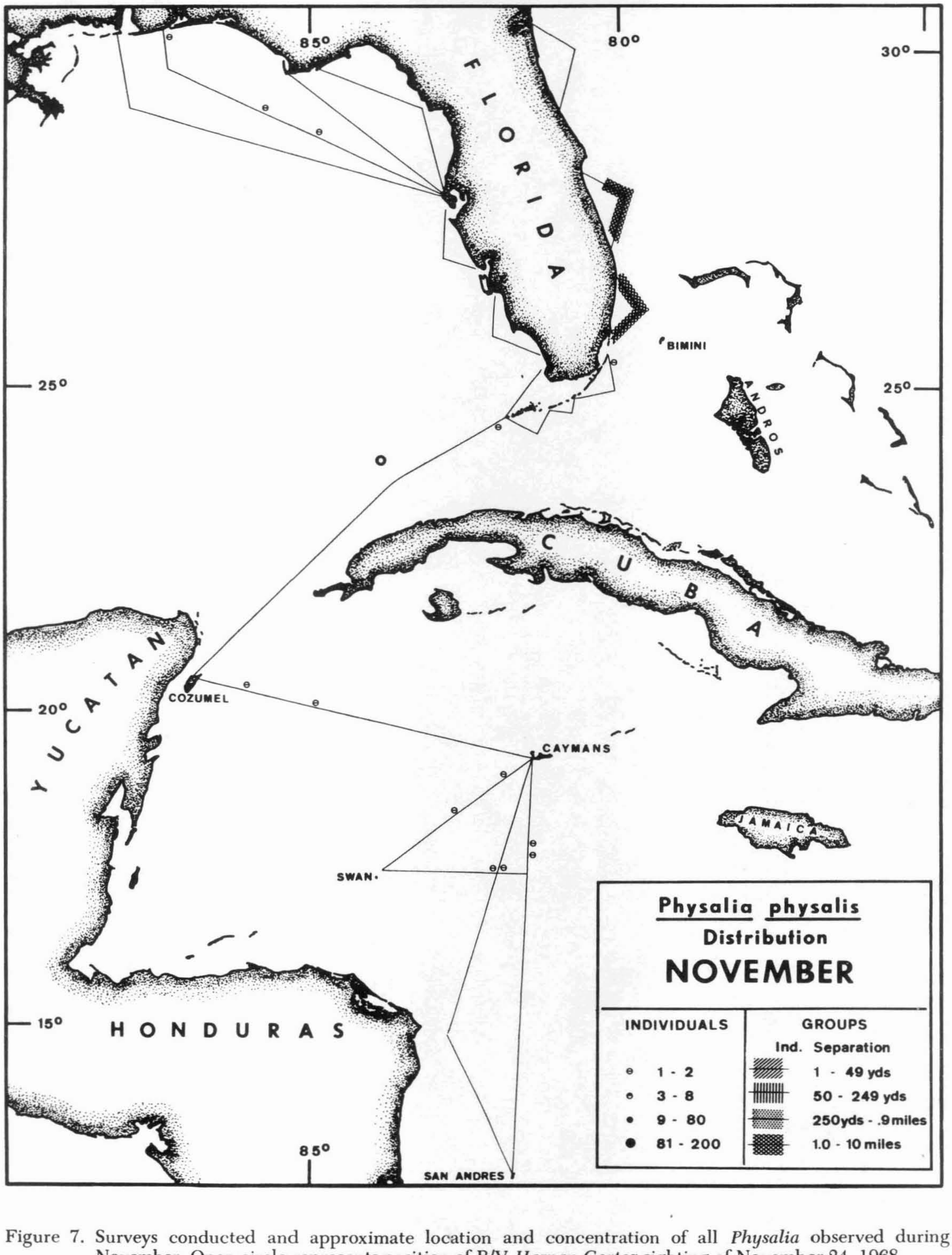

Figure 7. Surveys conducted and approximate location and concentration of all *Physalia* observed during November. Open circle represents position of R/V *Hernan Cortez* sighting of November 24, 1968.

Figure 8. Surveys conducted and approximate location and concentration of all *Physalia* observed during December.

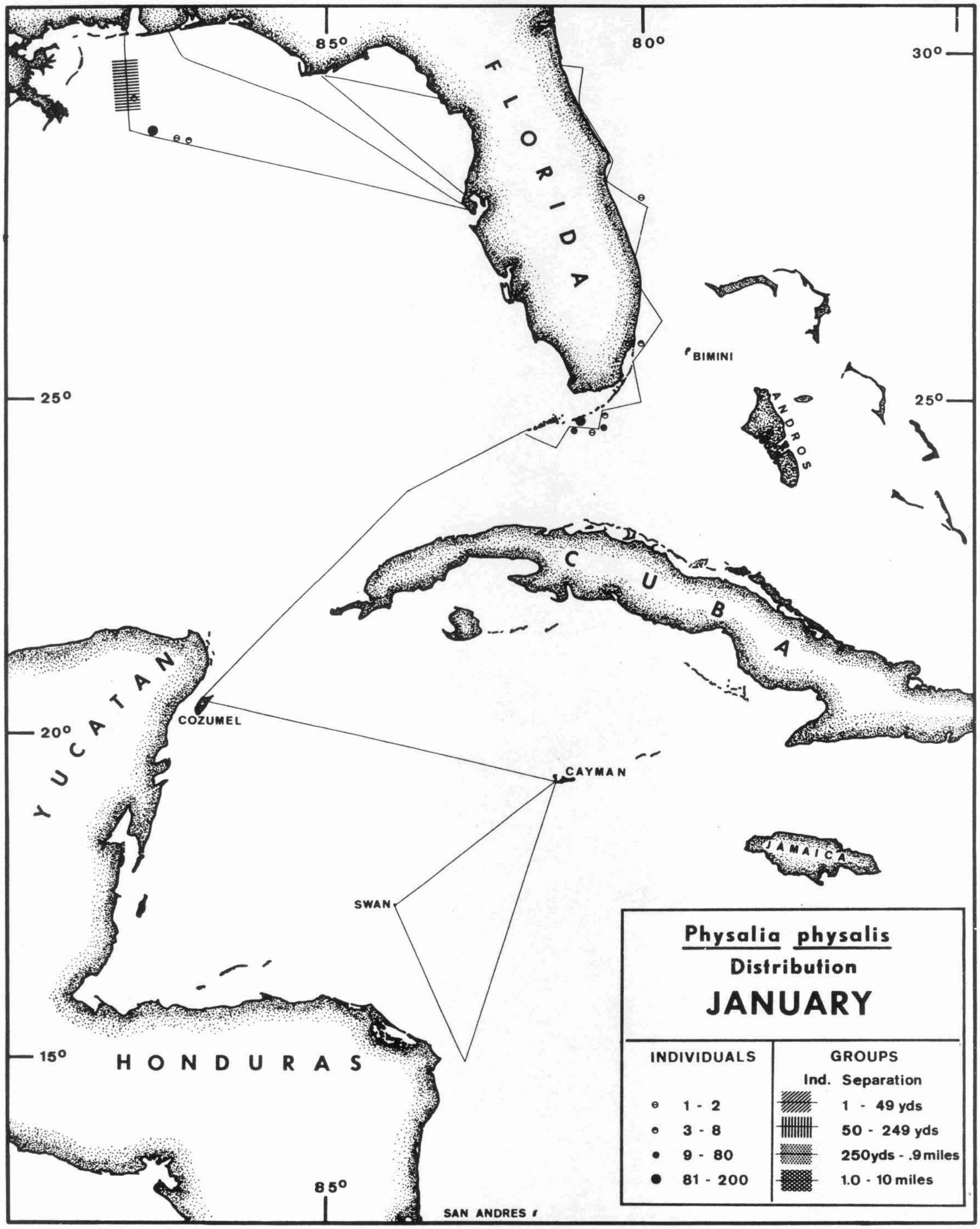

Figure 9. Surveys conducted and approximate location and concentration of all *Physalia* observed during January.

Figure 10. Surveys conducted and approximate location and concentration of all *Physalia* observed during February.

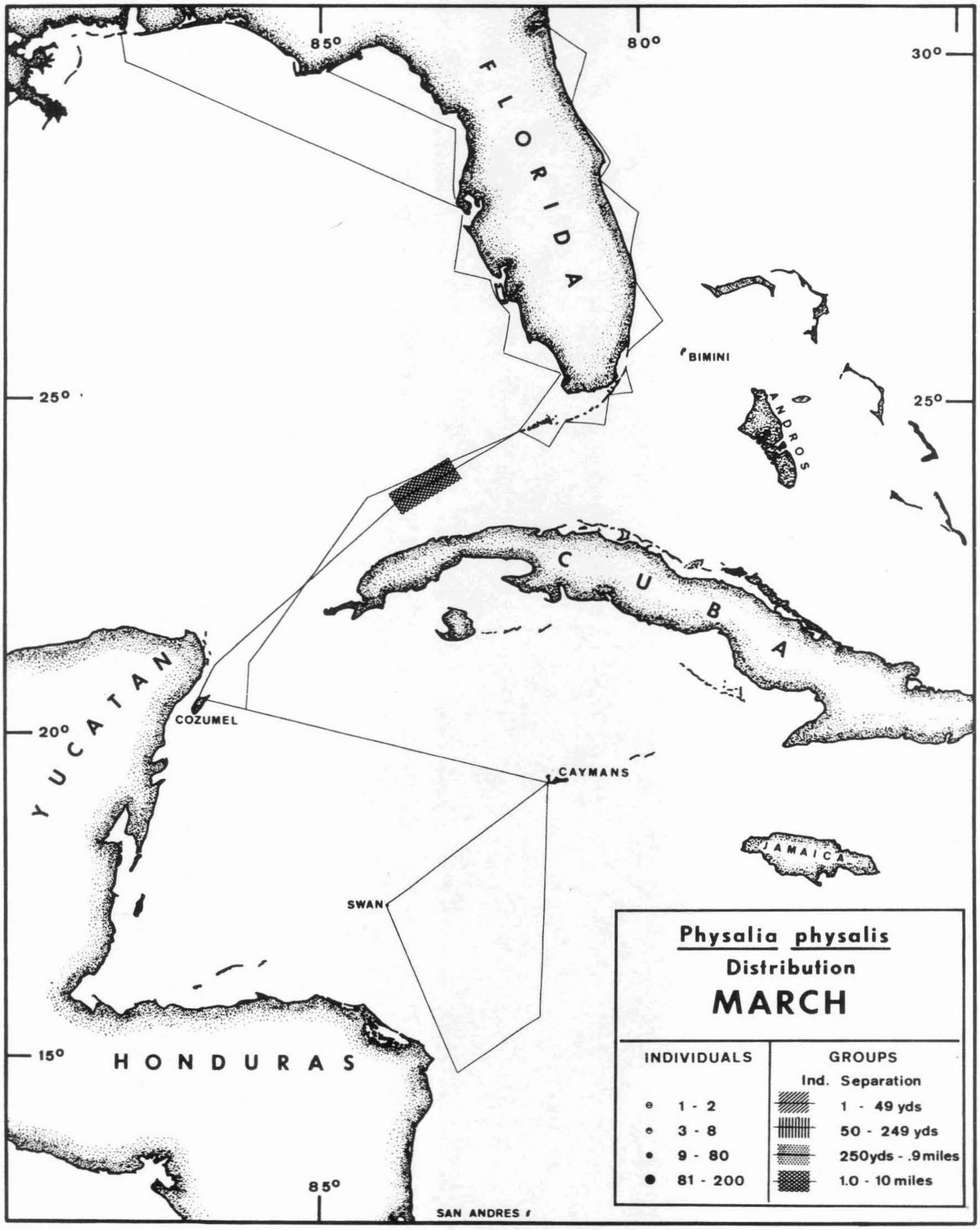

Figure 11. Surveys conducted and approximate location and concentration of all *Physalia* observed during March.

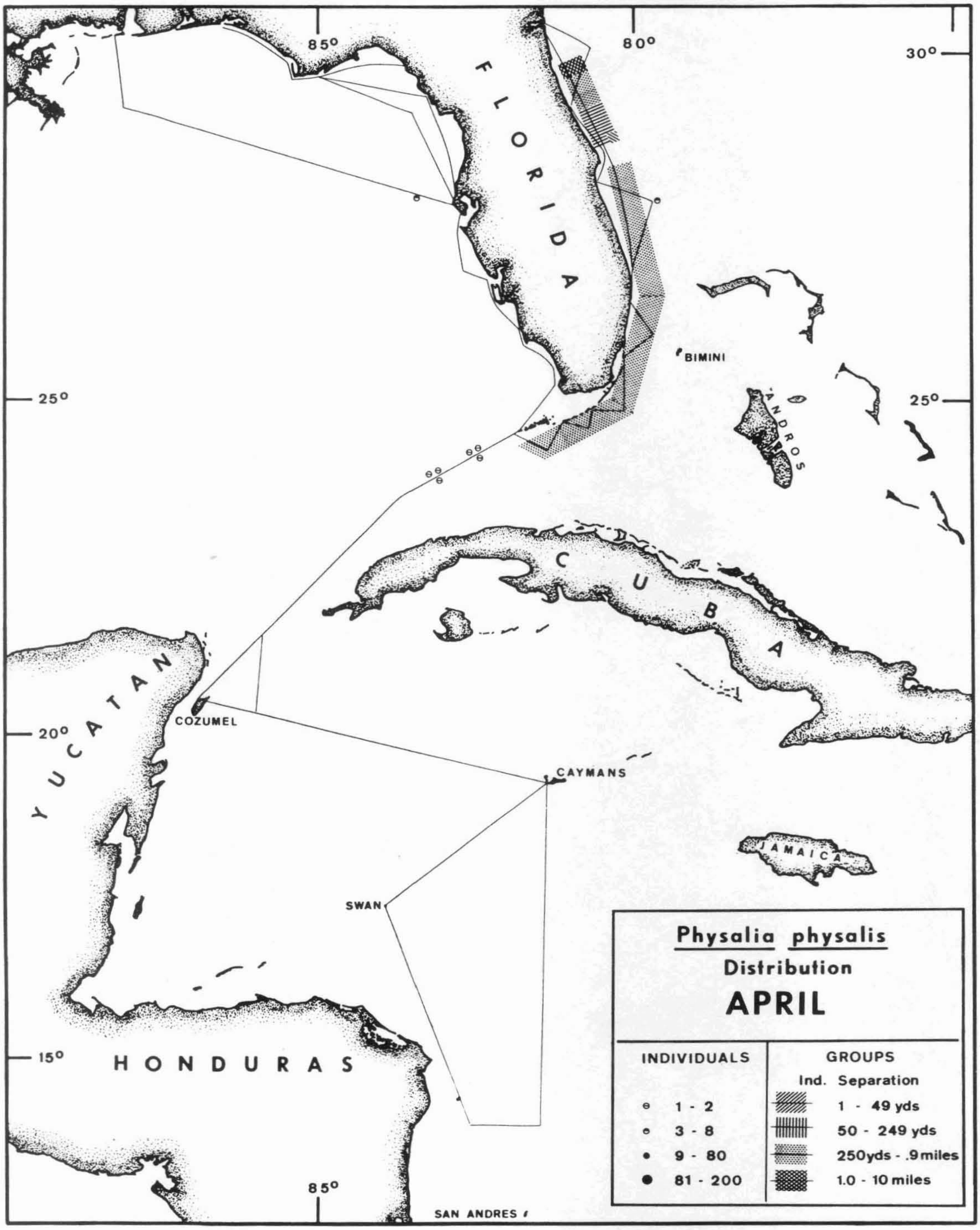

Figure 12. Surveys conducted and approximate location and concentration of all *Physalia* observed during April.

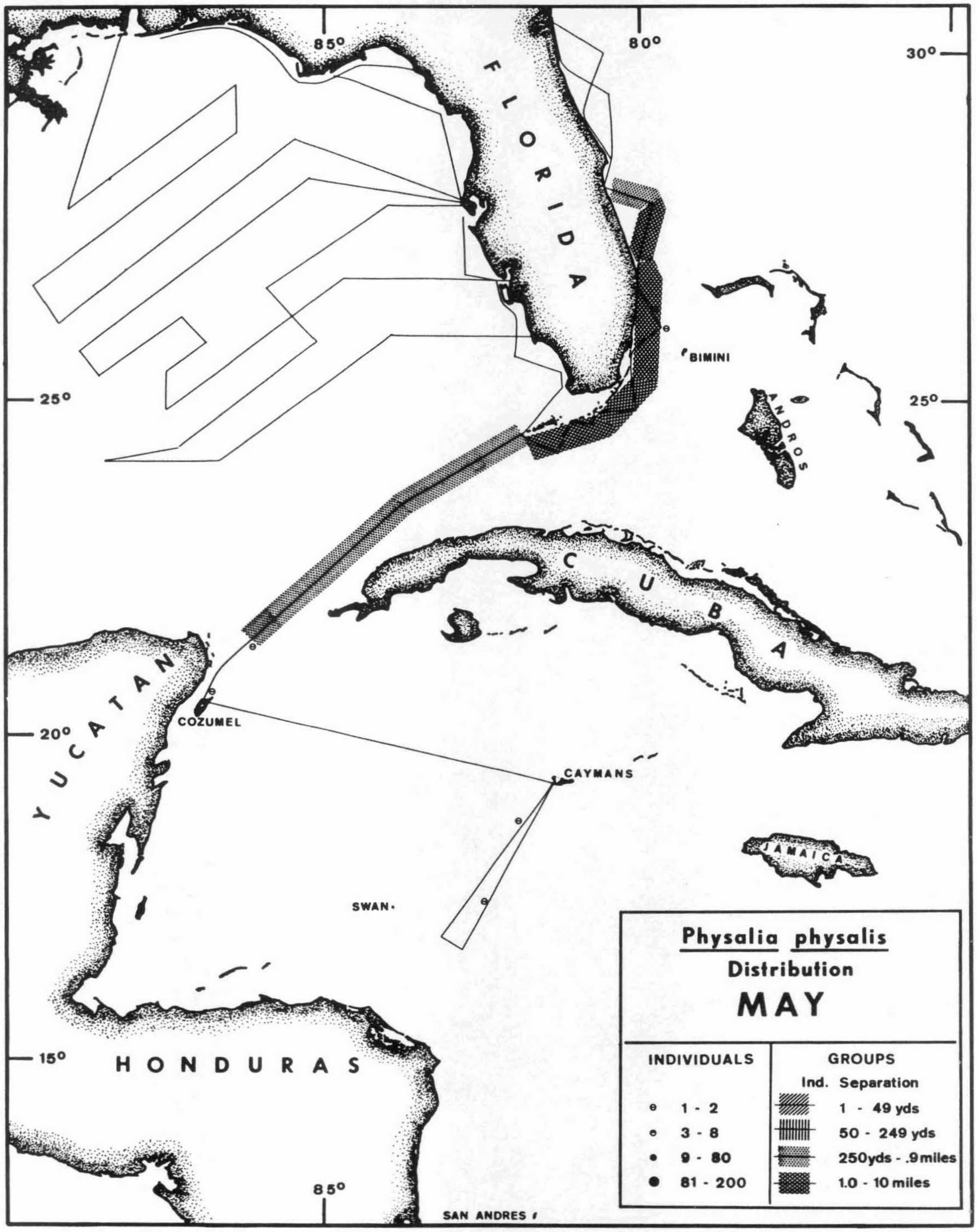

Figure 13. Surveys conducted and approximate location and concentration of all *Physalia* observed during May.

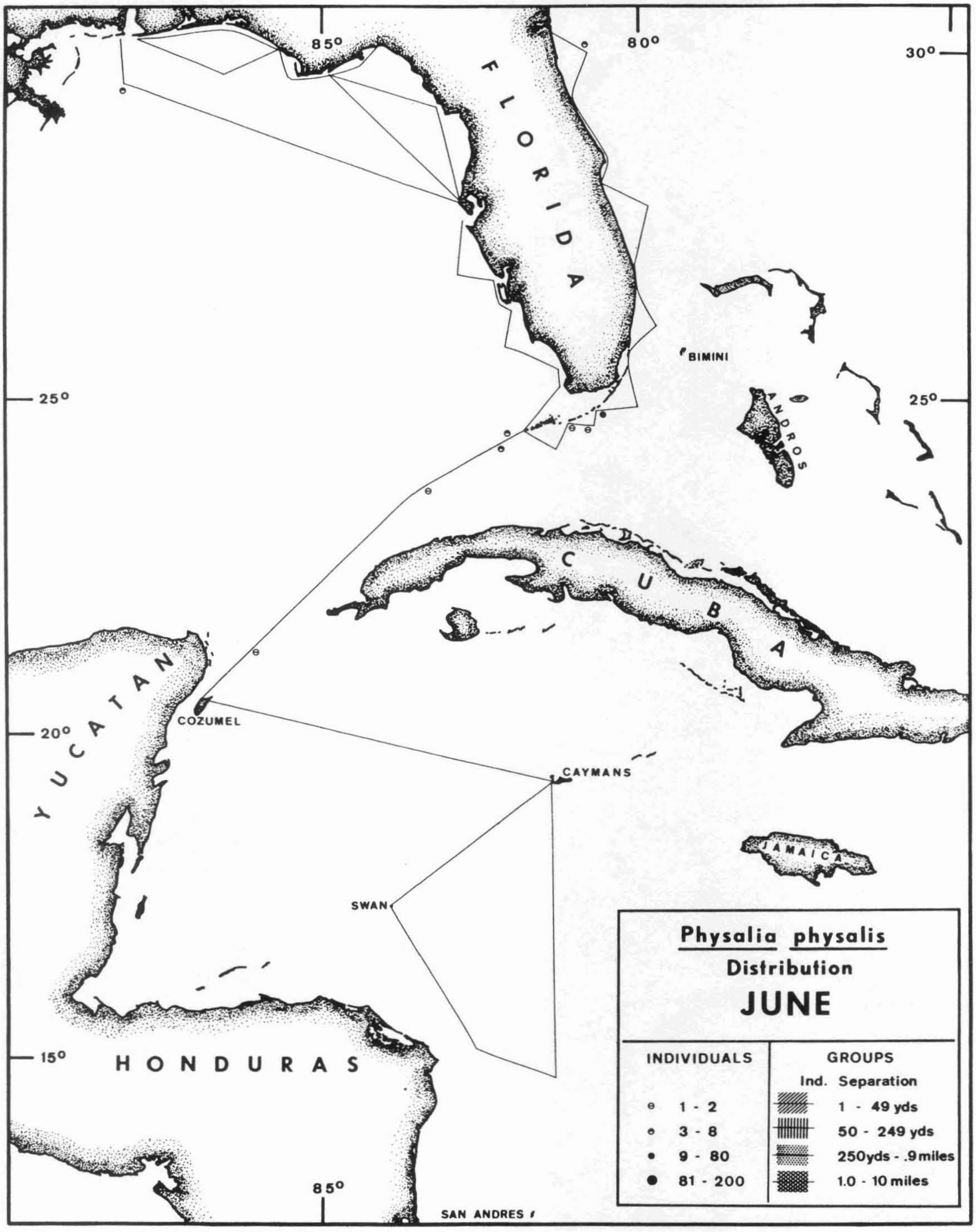

Figure 14. Surveys conducted and approximate location and concentration of all *Physalia* observed during June.

Figure 15. Surveys conducted and approximate location and concentration of all *Physalia* observed during July.

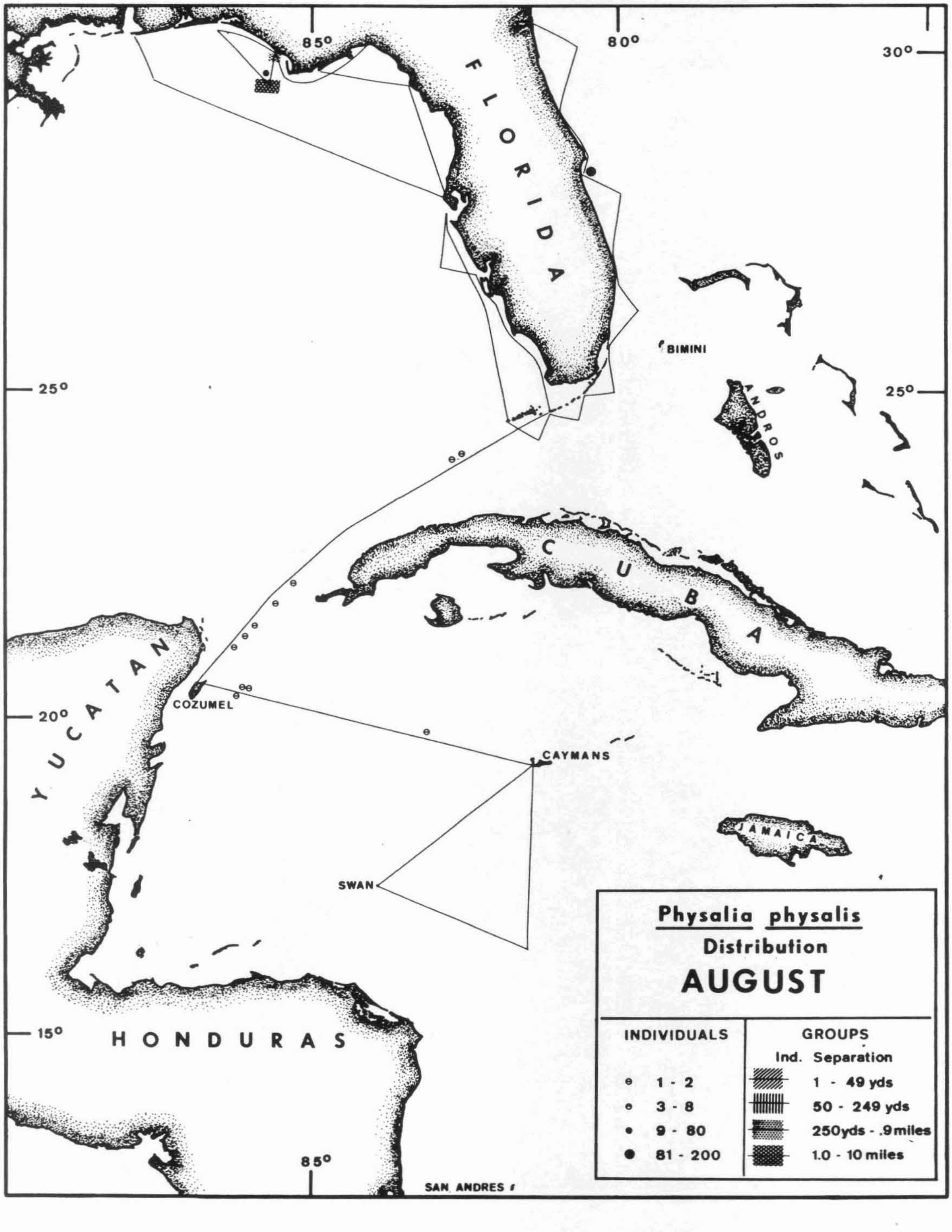

Figure 16. Surveys conducted and approximate location and concentration of all *Physalia* observed during August.

pushed north and into this countercurrent. This combination of wind and current was probably responsible for the large concentrations of *Physalia* during December 1969 and February 1970, as shown by total monthly abundance in Table 2. Section I also has a broad continental shelf but was surveyed infrequently.

Physalia appear throughout sections II, III, and IV. Distributional characteristics of *Physalia* as related to currents and winds could be rather closely examined in section IV where a barrier reef occurs 4 to 20 km offshore with the Gulf Stream adjacent.

Physalia occurred inshore in the Florida Keys only during those months (October through June) when they were known from aerial surveys to be present offshore. Further,

TABLE 2. AVERAGE SIZE AND TOTAL ABUNDANCE OF *PHYSALIA* BY MONTH BY SECTION AS RECORDED BY AERIAL SURVEYS. (No *Physalia* were observed in Section VI)

Section	I		II		III		IV		V		VII	
	No.	Size in. (cm)	No.	Size in. (cm)	No.	Size in. (cm)	No.	Size in. (cm)	No.	Size in. (cm)	No.	Size in. (cm)
J	•0		•0		•0		177	3.25 (8.26)	•0		1,293	2.52 (6.40)
F	58	3.67 (9.32)	8	7.00 (18.00)	26	6.62 (16.81)	29	4.24 (10.77)	0		91,658	4.99 (12.67)
M	•0		•0		•5	6.00 (15.00)	•0		•0		•0	
A	•0		•0		•7	6.00 (15.00)	799	9.00 (23.00)	508	9.00 (23.00)	6	5.00 (13.00)
M	•2	8.00 (20.00)	0		264	8.98 (22.81)	83	7.97 (20.24)	0		0	
J	•0		0		14	9.00 (23.00)	13	8.69 (22.07)	3	5.33 (13.50)	8	6.00 (15.00)
J	NS		•1	9.00 (23.00)	8	8.50 (21.60)	12	8.83 (22.43)	2	8.00 (20.00)	2	8.00 (20.00)
A	•0		•8	5.50 (14.00)	8	8.50 (21.60)	110	7.00 (18.00)	0		44	7.00 (18.00)
S	•0		•0		•1	5.00 (13.00)	10	5.35 (13.59)	•0		3	5.50 (14.00)
O	117	3.99 (10.13)	14	3.36 (8.53)	11	3.95 (10.00)	13	3.46 (8.79)	0		0	
N	8	5.25 (13.34)	3	4.00 (10.00)	1	2.00 (5.10)	26	3.52 (8.94)	•0		3	4.67 (12.00)
D	187	2.57 (6.52)	267	2.51 (6.38)	449	2.51 (6.38)	22	4.45 (11.30)	1	5.00 (13.00)	37,895	2.50 (6.35)

• = sampled only once
NS = not sampled

their appearance inshore was much less frequent. Only 64 of 212 inshore surveys were positive for *Physalia* and only 4 of 13 positive aerial surveys showed *Physalia* inshore.

Physalia are almost certainly present year round in varying abundances over the deeper waters adjacent to Florida. Sections III and IV yielded *Physalia* throughout the year, except for March which was sampled only once and under poor conditions. In the Caribbean *Physalia* appeared primarily from october through February.

During the year *Physalia* show three phases of distribution: 1) September through November — sparse in the Gulf and Gulf Stream and increasing density in the Caribbean, 2) December through May — well distributed throughout the Gulf and Gulf Stream and beginning to decrease in the Caribbean and 3) June through August — decreasing in the Gulf and Gulf stream and absent in the Caribbean. Maximum density in the study area occurs from December through February.

ABUNDANCE

Aerial surveys

Physalia reach maximum abundance from December through February and then gradually decline to a minimum in September (Figure 17-B).

Inasmuch as distribution is a function of abundance, variations by section are similar (Figure 18). Sections I and II have very few *Physalia* in spring and summer but show signs of increasing abundance in the fall, peaking in December. Two abundance peaks occur in section III (December and May), one in section IV (April) and one in section VII (December through February). Figure 18 indicates that *Physalia* are present along the coasts of Florida year round, but may disappear in the Caribbean during summer.

Analysis of variance and related tests were used to determine the significance of abundance results from aerial surveys. The data compiled by average monthly abundance per section formed a Poisson distribution requiring logarithmic transformation. Steel and Torrie (1960) and Sokal and Rohlf (1969) discuss basic logarithmic transformations. Due to the extremely large range of values, including zeros, it was necessary to use an altered form of a double logarithmic transformation $\{\ln[\ln(x+1)]+1\}$. Naperian logarithms were used because the Wang Electronic Calculator was programmed to do them automatically.

The great abundance of *Physalia* during December and February in section VII was caused by converging surface currents and winds. Had such phenomena taken place in other sections, recorded *Physalia* abundance might have been considerably greater. By using the double logarithmic transformation, tremendous variations in abundance do not appear as prominently in the graphic presentations, and are probably a more meaningful representation of true variation in abundance.

Average monthly abundance showed significant differences among treatments (monthly mean abundance) when computed by analysis of variance in Randomized Complete Block Design (RCB ANOVA; $F = 2.37^*$, d.f. = 10). Procedures for these and all other statistical tests were obtained from Steel and Torrie (1960) and Sokal and Rohlf (1969). Transformed data was coded by +10 to remove zeros. Bartlett's Chi Square ($\chi^2 = 10.86$; $P = 0.05$) showed normal distribution and equal variance, two requirements for ANOVA computation. Duncan's new multiple range test (Table 3-A) showed that mean abundance of *Physalia* in December is significantly greater than mean abundance in all months but February and August. Likewise, mean abundance in February is significantly larger than mean abundance in September and June. The RCB ANOVA computed above also showed significant differences among blocks (sectional mean abundance; $F = 3.70^*$, d.f. = 4). Yearly mean abundance of *Physalia* in section IV is significantly greater than in sections I and II (Table 3-B).

These tests show that *Physalia* are being recruited into the study area from fall through winter. Those occurring in section I must be recruited from the east and must in turn progress through all other sections. Decreasing abundance in the Caribbean after December indicates a great reduction or cessation of recruitment from the east. Abundance in section VII remains high through February and in section IV remains high through April, demonstrating the time lag between sections.

Numbers of *Physalia* observed in the Caribbean are insufficient to explain the consider-

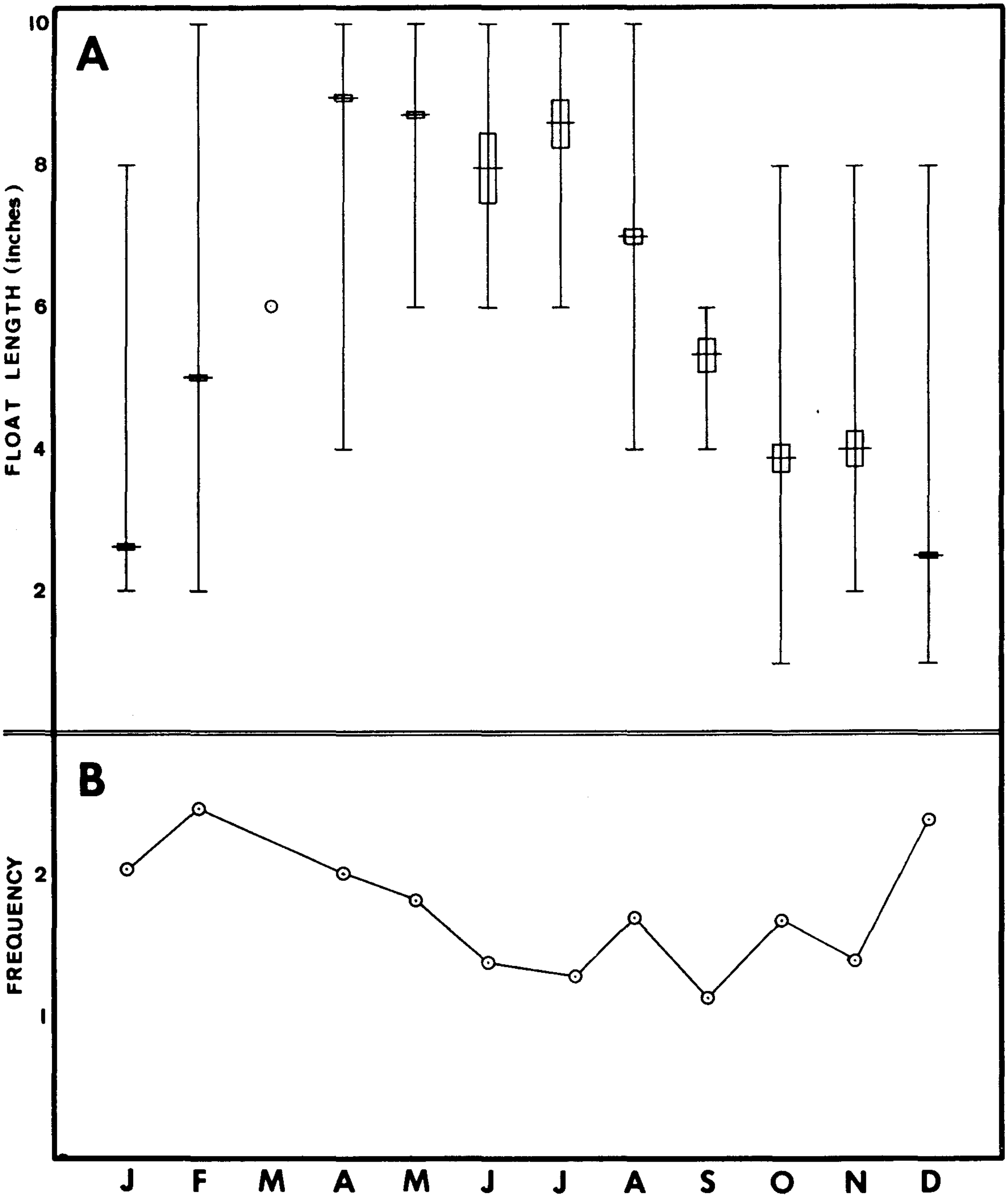

Figure 17. Size and abundance of *Physalia* as observed by aerial surveys: A) monthly mean float lengths; B) monthly abundance transformed by $\{\ln[\ln(x + 1)] + 1\}$.

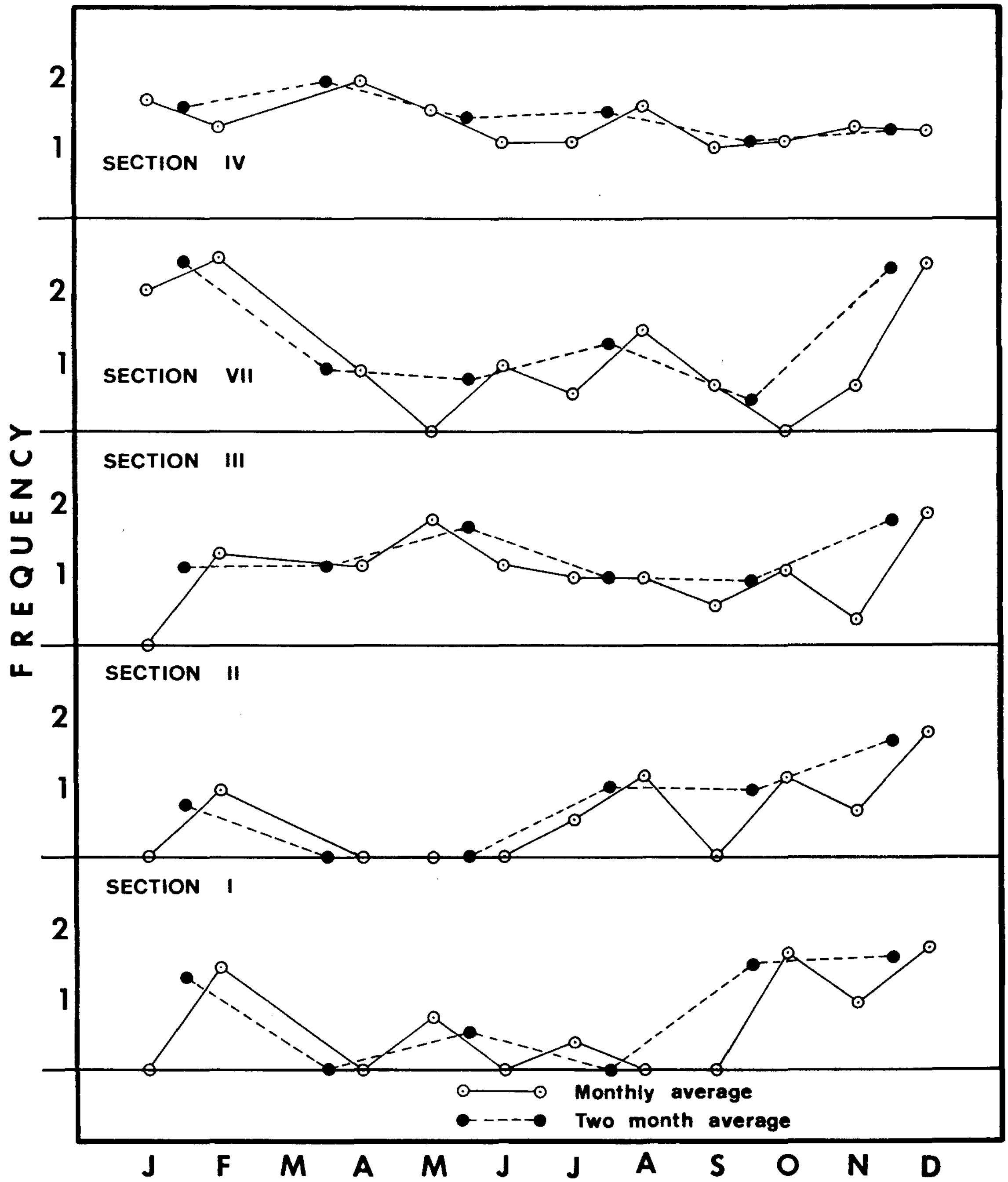

Figure 18. *Physalia* abundance by section as observed by aerial surveys. All values transformed by $\{\ln [\ln (x + 1)] + 1\}$.

ably greater numbers occurring later in the Gulf of Mexico and Florida Straits. Thus, *Physalia* must have been too small to be seen as they moved through the Caribbean or there was additional recruitment from north of the Caribbean. After February, recruitment into the Gulf stops, and after April it stops in the Florida Straits. Thus the remaining *Physalia* progressively leave the study area. The currents do not remove them from the Gulf quickly because of numerous countercurrents and eddies. Consequently, the remnants of one season's *Physalia* are still present when the next season's influx begins.

Florida Keys surveys

These surveys (Figure 19-B) generally show the same seasonal abundance variations as do aerial surveys for section IV. Maximum abundance was during December and April; none occurred during summer.

Although techniques of aerial and ground surveys differed and the results were not strictly equivalent, ground surveys in the Florida Keys show that the winter crop of *Physalia* is greater than that indicated by aerial survey, a fact substantiated by the foregoing statistical analysis. Peak abundance in the Florida Keys may equal or exceed that recorded in the Gulf; thus, the fluctuations in abundance in section IV should more closely resemble those of section VII (Figure 18).

SIZE

Aerial surveys

Float lengths of *Physalia* recorded during aerial surveys ranged from 1-10 inches (2.5-25.4 cm) with monthly means ranging from 2.50-8.94 inches (6.35-22.71 cm) (Figure 17-A).

Variations in monthly mean float lengths are inversely proportional to variations in abundance. *Physalia* increase in float length from February through April, remain fairly constant through July and then decline from August through January.

Table 2, showing average monthly float lengths by section, provides a basis for integrating the various aspects of *Physalia* dynamics within the study area. In July only a few uniformly large residual animals (8-9 inches) (20-22 cm) were observed with

TABLE 3. DUNCAN'S NEW MULTIPLE RANGE TESTS FOR SIGNIFICANT DIFFERENCES IN *PHYSALIA* ABUNDANCE BY MONTH AND BY SECTION AS RECORDED FROM AERIAL SURVEYS. Nonsignificantly different means are underlined. $\bar{x}$ represents abundance values transformed by $\{\ln[\ln(x+1)]+1\}$ and coded by $+10$.

A. Order of increasing mean abundance by month

	Sept.	June	July	Jan.	Nov.	Apr.	May	Oct.	Aug.	Feb.	Dec.
$\bar{x}$	10.44	10.64	10.70	10.74	10.78	10.79	10.81	10.98	11.03	11.50	11.79

B. Order of increasing mean abundance by section

	II	I	III	VII	IV
$\bar{x}$	10.56	10.63	11.00	11.08	11.36

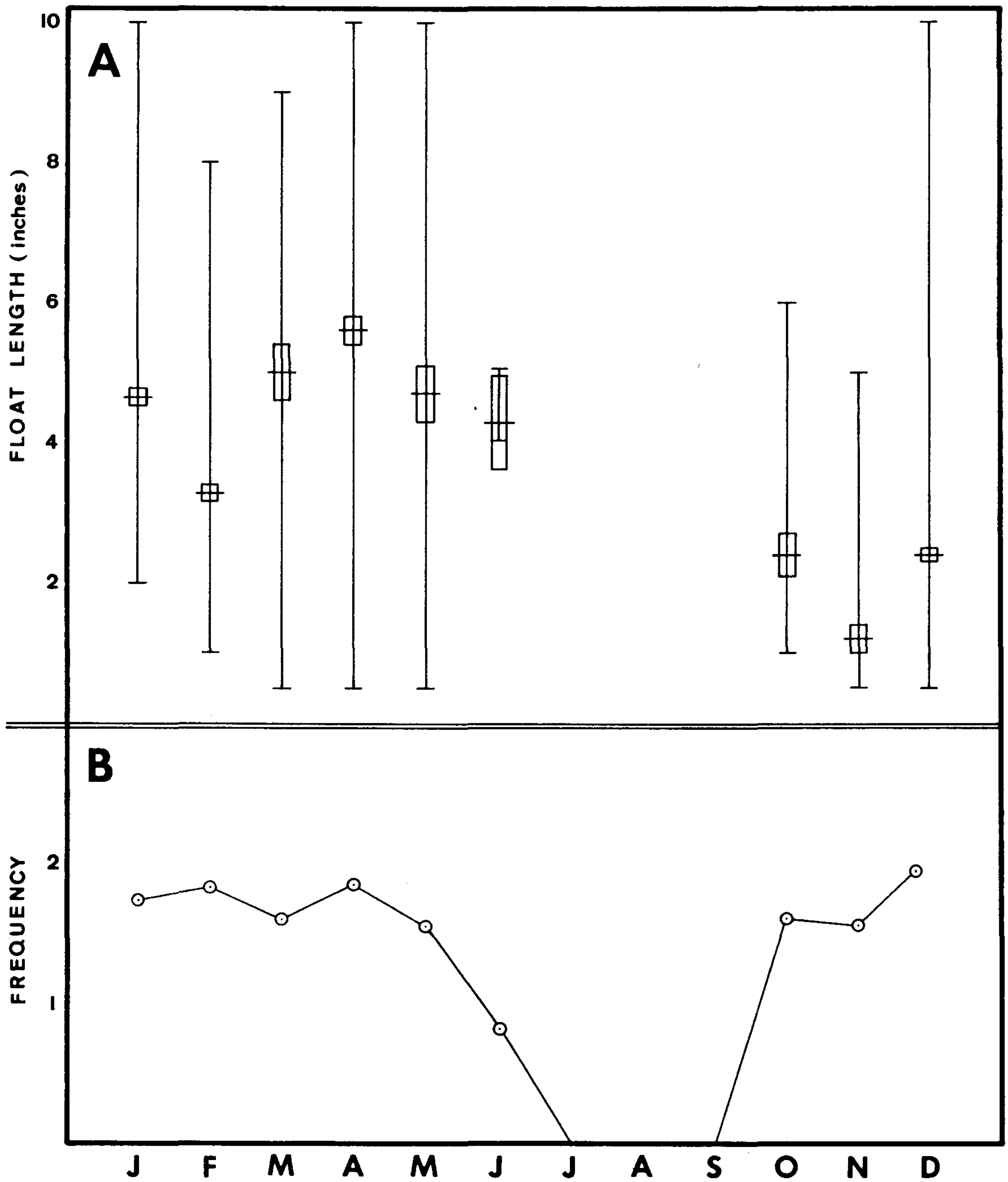

Figure 19. Size and abundance of *Physalia* as observed from Florida Keys surveys: A) monthly mean float lengths; B) monthly abundance transformed by $\{\ln [\ln (x + 1)] - 1\}$.

no small animals present in the study area. An influx of smaller animals resulting in a decrease of mean size to 5.5 inches (14 cm) first occurred in section II during August. From September through December, centers of production moved progressively downcurrent giving rise to increasing numbers of successively smaller animals. Details of this progression are treated following discussions of growth and reproduction.

Completely random design analyses of variance (CRD ANOVA) were computed for monthly mean float lengths and sectional mean float lengths. Since average float lengths by month by section were used, the computed means from the CRD ANOVA are independent of abundance. The CRD ANOVA with unequal sample size was necessary because not all months and sections had *Physalia* size approximations.

Bartlett's Chi Square ($\chi^2 = 18.17$; $P = 0.05$) indicated normal distribution and equal variance for monthly mean float lengths without transformations. The CRD ANOVA ($F = 13.00^{**}$, d.f. = 10) showed a highly significant difference among treatments (monthly mean float lengths). Two tests were used (Table 4 A-B) to determine where these significant differences occur: 1) Kramer's proposed procedure for use of Duncan's new multiple range test with unequal sample size, and 2) the least significant difference procedure (lsd). The validity of Kramer's procedure has not been verified (Steel and Torrie, 1960), whereas the lsd procedure has been verified but may err slightly. Both tests show that

TABLE 4. SIGNIFICANT DIFFERENCES IN MEAN *PHYSALIA* FLOAT LENGTHS AS RECORDED BY AERIAL SURVEY. Nonsignificantly different means are underlined. $\bar{x}$ represents mean float length in inches.

A. Kramer's procedure (order of increasing mean float lengths by month)

	Jan.	Dec.	Oct.	Nov.	Sep.	Feb.	Apr.	Aug.	June	May	July
$\bar{x}$	2.88	2.91	3.69	3.89	5.28	5.31	6.66	7.00	7.90	8.32	8.58

B. LSD procedure (order of increasing mean float lengths by month)

	Jan.	Dec.	Oct.	Nov.	Sep.	Feb.	Apr.	Aug.	June	May	July
$\bar{x}$	2.88	2.91	3.69	3.89	5.28	5.31	6.66	7.00	7.90	8.32	8.58

C. Order of increasing mean float lengths by section

	I	VII	II	IV	III
$\bar{x}$	4.70	5.13	5.23	5.98	6.11

significantly larger *Physalia* occur from May through August than from October through January. Although the tests diverge slightly both are judged reliable for these data.

Bartlett's Chi Square (χ^2 = 1.30; P = 0.05) for sectional mean float lengths again indicated normal distribution with equal variance. The CRD ANOVA (F = 0.51, d.f. = 4) showed no significant differences among mean float lengths by section. Accordingly, recruitment of small *Physalia* apparently occurs in all sections. Had recruitment occurred from a particular area such as the Caribbean or farther east then significantly greater yearly mean float lengths should have been recorded along the coasts of Florida than in the Caribbean, especially if, as Totton suggests, *Physalia* growth is rapid.

Florida Keys surveys

Physalia float lengths ranged from 0.5-10 inches (1.3-25.4 cm) with monthly means ranging from 1.2-5.6 inches (3.0-14.2 cm) (Figure 19-A). Maximum float length was recorded during April and minimum length during November. The same inverse relationship of size to abundance occurred but several important variations are apparent. Very small *Physalia* could not be detected by aerial survey. Minimum length observed by aerial survey was approximately 1" (25 mm) whereas by ground surveys *Physalia* as small as 9 mm were recorded. Of those measured in the laboratory the modal length was 15 mm. Smallest specimens collected by the R/V *Hernan Cortez* (23°50'N, 83°59'W) were 8 mm.

Very small animals were almost continuously present from October through May in the Florida Keys even though average length increased from December through April. Frequency of smallest animals begins to diminish by February consistent with aerial survey results but does not cease until May. Therefore, recruitment into the Gulf and Florida Straits is a combination of the two aforementioned factors: 1) In fall very small animals are being transported from the Caribbean to the Gulf and Florida Straits, and 2) during winter very small *Physalia* originate within the Gulf and Florida Straits.

SURVIVAL AND GROWTH

Laboratory studies

Preliminary experiments on *Physalia* survival were conducted in Key West from January through March 1970. Six *Physalia* (6-20 cm) were kept individually in 190 liter aquaria and wooden tanks 1.2 x 2.4 x .15 m deep. During these trials water temperature ranged from 16-25° C and salinity from 33.4-35.0°/₀₀. Greatest daily variation in temperature was 3° C. Longest survival was six days for one 21 cm specimen. As with the other specimens it began to show signs of stress by the second day of capitivity. From these experiments, two conditions were found necessary for survival in addition to the basic requirements of water quality, temperature, salinity and oxygen: 1) *Physalia* must be handled no more than absolutely necessary, and 2) the surface tissues of the float must be kept moist. Dessication of float tissues was an especially severe problem and was compounded by the tendency of the animals to adhere to tank sides, preventing them from somersaulting. Changing sea surface conditions apparently cause somersaulting with sufficient regularity to insure adequate float moistness.

Six *Physalia* were captured in Key West in March 1970 and brought to St. Petersburg for tests of various equipment designed to keep them from adhering to the tank sides. These animals were placed in a 200 liter polyethylene tank to test effects of various water currents and directions. *Physalia* could be forced to remain in the center of the tank using water currents but the technique debilitated the animals.

Later experiments tested the use of air currents for this purpose in specially designed tanks. Unfortunately, they could not be installed until February 1971. From December 1970 through January 1971, 33 *Physalia* (20-140 mm) were kept in other aquaria, tanks and styrofoam ice chests. Of seven animals (44-66 mm), two survived ten days in an aerated ice chest with only bits of frozen shrimp for food. Discounting deaths caused by equipment failures, average survival of the 33 specimens was seven days.

Experiments with the large, partially completed polyethylene tank systems were conducted from February through June 1971 with 18 *Physalia* (32-210 mm). Maximum survival was six days but the average was only three days. Water temperature ranged from 22-28° C, and salinity from 36-38 °/oo. Specimens were kept in groups no larger than three. Several air systems were tried but none proved to be successful.

Four *Physalia* were brought from Palm Beach to St. Petersburg in April 1971, and placed in tanks with inadequate air systems similar to those in Key West. Although maximum survival was only three days, they fed well, one consuming six anchovies daily. This animal became stuck to the tank and died, but appeared in excellent condition until that time.

During the third winter (1971-72), the tanks were subsequently modified to include a coordinated system of air and current to more closely control the movement of *Physalia* within the tank. Unfortunately, suitable animals thus far could not be obtained but future work with these modified tanks is foreseen. In anticipation of using this modified system, a ratio was derived to relate the gas gland to float length. This ratio, based on measurements of 144 preserved *Physalia*, was G = 0.22 F where G = gas gland and F = float length (Figure 20). Linearity, checked by regression of G/F on G, showed a slope of $\beta = 0.004$ with 95% confidence limits of $+ 0.009$ and $- 0.002$. The relationship of gas gland diameter and float length from data reported by Totton shows nearly the same ratio, G = 0.21 F.

Field studies

Although no growth rates were obtained in the laboratory, some indication of growth could be inferred from aerial surveys. In section VII large numbers of *Physalia* were observed during December 1969 and February 1970. At least part of this population of *Physalia* was probably being maintained within the Gulf. These animals increased in mean size from 2.5 to 5 inches during that period, a growth of 1.25 inches (32 mm) per month. The largest *Physalia* collected was 251 mm, and at this growth rate it would be a minimum of 8 months old. Since this rate was determined from young animals having rapid growth, a period of one year is a more plausible estimate.

REPRODUCTION

Reproductive zooids (gonodendra) consist of palpons, nectophores, jelly polyps and gonophores. Gonophores appear as small egg shaped capsules on the end branches of the gonodendron and are the only reproductive members. Each gonophore has a central spadix of multinucleate endodermal cells separating the coelenteron from a layer of germ cells. Covering the germ cells is a layer of ectoderm. Totton (1960) gives a more complete and detailed account of the development of gonodendra.

Preserved specimen studies

One hundred forty-six gonodendra from 45 *Physalia* were sectioned and stained to study development and maturity of germ cells. Most were from preserved specimens; however, several were collected as they dropped from captive *Physalia*. From 6 to 17 gonodendra were removed from each of 6 preserved specimens. Of the remaining *Physalia*, (live and preserved) only the largest two or three gonodendra were taken from each.

Within the gonophores two distinct types of germ cell development are readily distinguishable in all but very early stages. When gonophores first bud, the germ layer is a cap of cells on top of the endodermal spadix. As gonophores mature, germ cells develop into a layer covering the spadix. Spermatogonia form a thick layer (Figure 22-A) while oogonia form a convoluted band several cells wide but only one cell thick (Figure 23-A). All gonophores examined from one gonodendron were of the same sex and appeared to be in approximately the same stage of development. All gonodendra from one *Physalia* were of the same sex but in various stages of development. Seventeen *Physalia* were female and 28 were male.

After review of all slides it appeared that germ cells in larger gonophores were more advanced than those of small gonophores. To verify this relationship, the surface area of sagittal sections of three representative gonophores (Figure 22-A) from each gonodendron were measured and averaged. Germ cell diameter within each of these gonophores was also measured. Only the largest gonodendron (largest gonophore size) from each of the

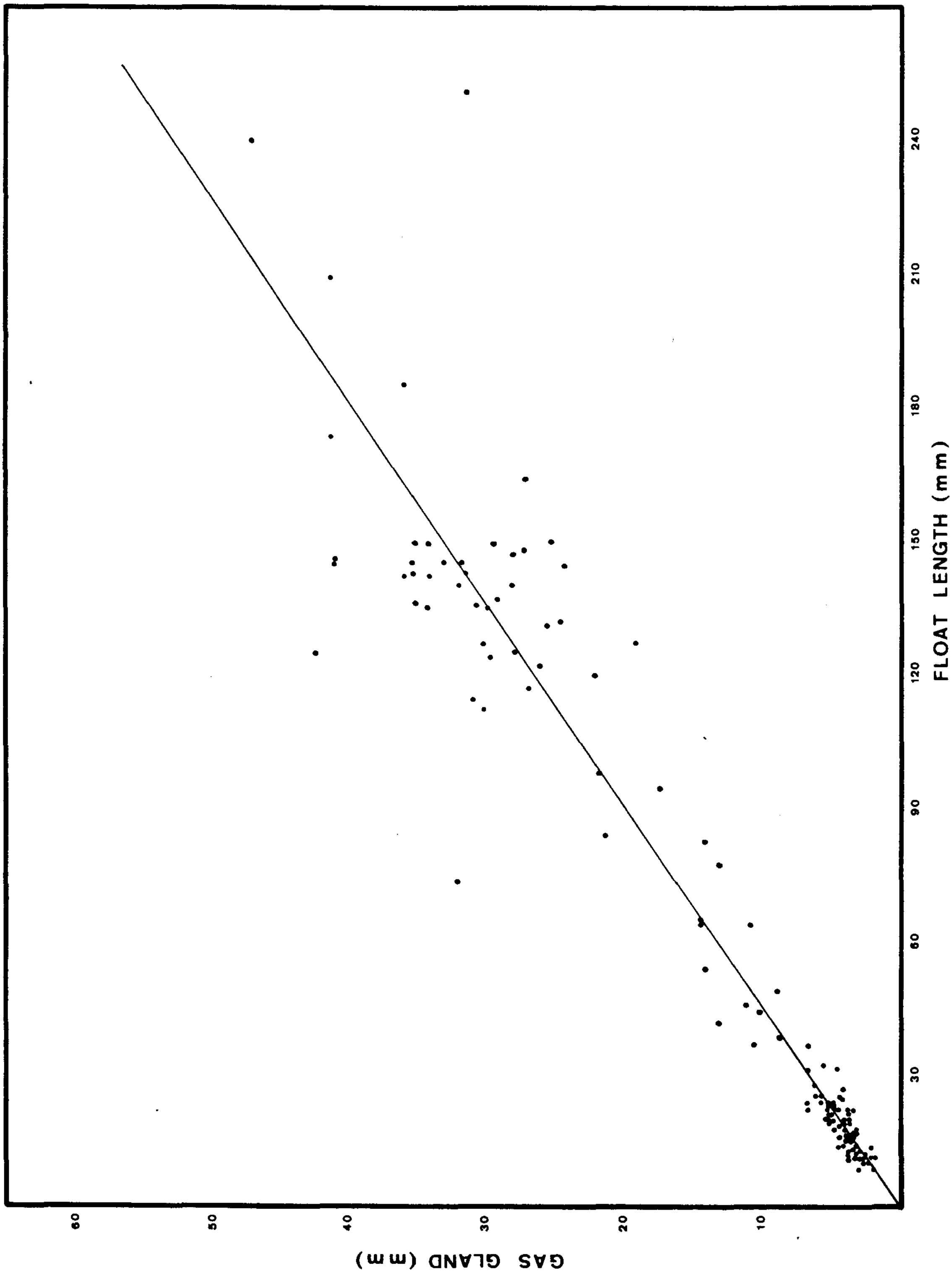

Figure 20. Relationship of float length to gas gland diameter.

45 *Physalia* were selected for determination of germ cell developmental stages (Figure 21).

Spermatogonia in gonophores with sagittal section areas of 0.1 to 0.35 mm^2 were in a densely packed layer around the spadix (Figure 22-A). Nonspherical spermatogonia varied in size among and within gonophores. There appeared to be very little cytoplasm in these cells except during those rare instances when cell division was encountered. Accelerated division of spermatogonia occurred in gonophores with areas of 0.35 to 0.81 mm^2. Many appeared to be in early stages of meiotic division and the cells were densely packed and varied in size (Figure 22-B). In the three most advanced gonophores, germ cells (apparently spermatids) had become spherical, 6.5 to 7.0 μ with nuclei approximately 5.0 μ (Figure 22-D). Two of three gonophores showed no germ cell division. Spadix cells had disappeared in some of the gonophores, leaving only a membrane connected to the coelenteron (Figure 22-C). According to Totton (1965) the physonect, *Halistemma rubrum*, produces spermatozoa. It is possible that *Physalia* do also, but none were found.

Oogonia begin development at approximately the same size as spermatogonia but grow considerably larger. No signs of division were found. All oogonia are apparently formed at an early stage of gonophore development before enlargement occurs. The largest oogonia represented by the graph are 14 μ in diameter, most of which is the nucleus (Figure 23-B). One gonodendron not represented in Figure 21 was found in a tank at Key West several days after capture of the *Physalia*. It had broken into parts and only a few end branches could be found. The gonophores measured 1.725 mm^2 and the oogonia were from 14 to over 70 μ in diameter. There appeared to be yolk globules within the cytoplasm of most oogonia (Figure 23-C). Since Totton (1965) and Kaestner (1970) reported yolk rich eggs from 0.3 to 0.7 mm diameter in physonects and calycophores, these *Physalia* eggs may represent stages of vitellogenesis prior to meiotic division and formation of polar bodies.

Since spermatids were found in gonophores still attached to preserved specimens, fertilization may take place closer to the surface than previously suggested by Hyman (1940) and Totton (1960). Gonodendra are probably released from the colony and end branches subsequently break off, as Totton suggests; however, it seems that this should take place at or very near germ cell maturity. Release of gonodendra may be a chemical response occurring when large groups of *Physalia* are present in one area.

All preserved *Physalia* were examined but only those specimens over 9 cm had well developed gonodendra. The most mature gonodendron from each of these was examined for gonophore size and germ cell diameter (Figure 21). Among the specimens upon which the figure is based, no correlation exists between animal size and gonodendron maturity. Thus it is probable that both male and female *Physalia* are capable of reproduction at 9 to 15 cm float length.

Live gonodendra studies

Occasionally when large *Physalia* were collected, gonodendra were released into the collecting bucket or the laboratory tanks. Gonodendra immediately sank to the bottom of their containers. They appeared physically good and were active for the first 24 hours, then disintegrated rapidly. One gonodendron, surviving over 90 hours was checked after three days. It appeared more transparent, and no fluids circulated in the coelenteron, but it was still active.

SPAWNING

Based on integration of the various aspects of *Physalia* dynamics, the season and location of spawning within the study area can be described. In the Caribbean in August, effects of spawning (recruitment) are first observed as increased abundance and decreased size. By December these effects have modified the stocks of *Physalia* in the Gulf and Florida Straits. The production (spawning) center moves progressively from the Caribbean into the Gulf and Florida Straits and, by May, into the Atlantic.

Since *Physalia* are dioecious, some critical density is probably required for successful fertilization. Increasing numbers of mature *Physalia* in the Caribbean in fall are responsible for the considerably greater abundance of small animals in the Gulf during winter. Some of

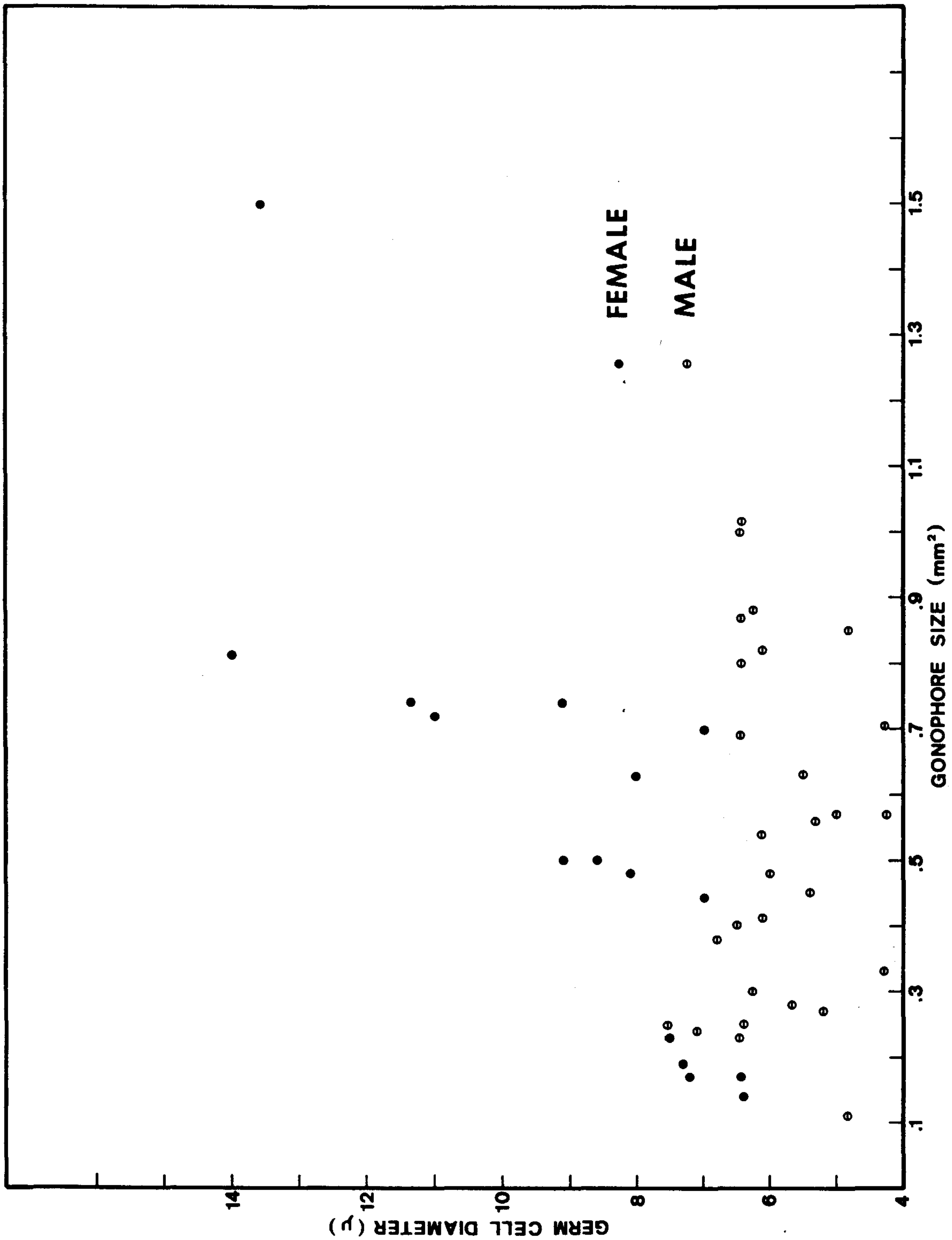

Figure 21. Relationship of gonophore size to germ cell diameter in 16 female and 28 male gonodendra.

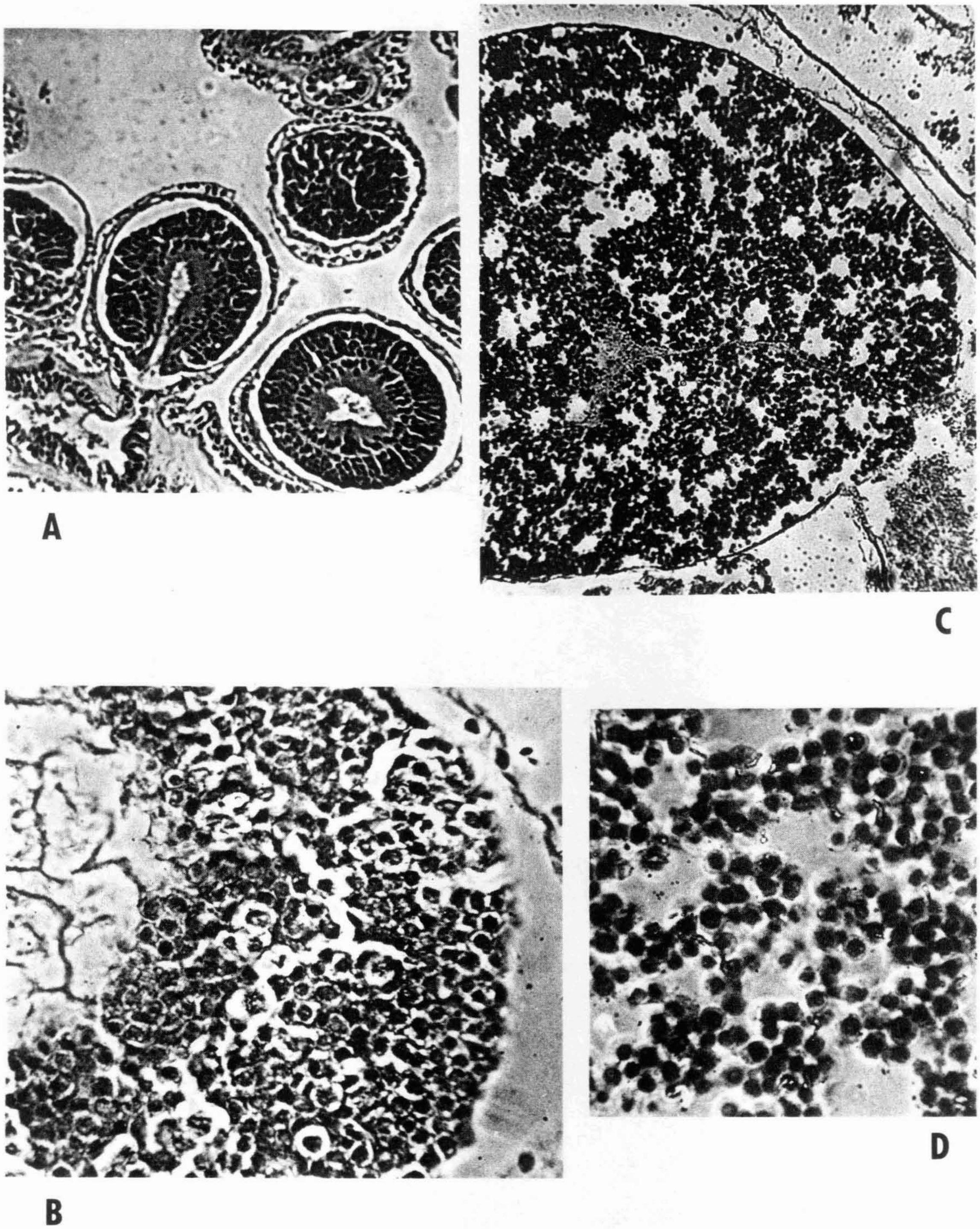

Figure 22. Stages of spermatogenesis: A) spermatogonia in young gonophore (x 183); B) meiotic division of spermatogonia (x 430); C) gonophore with spermatids and vestige of original spadix (x 150); D) spermatids from above gonophore (x 615).

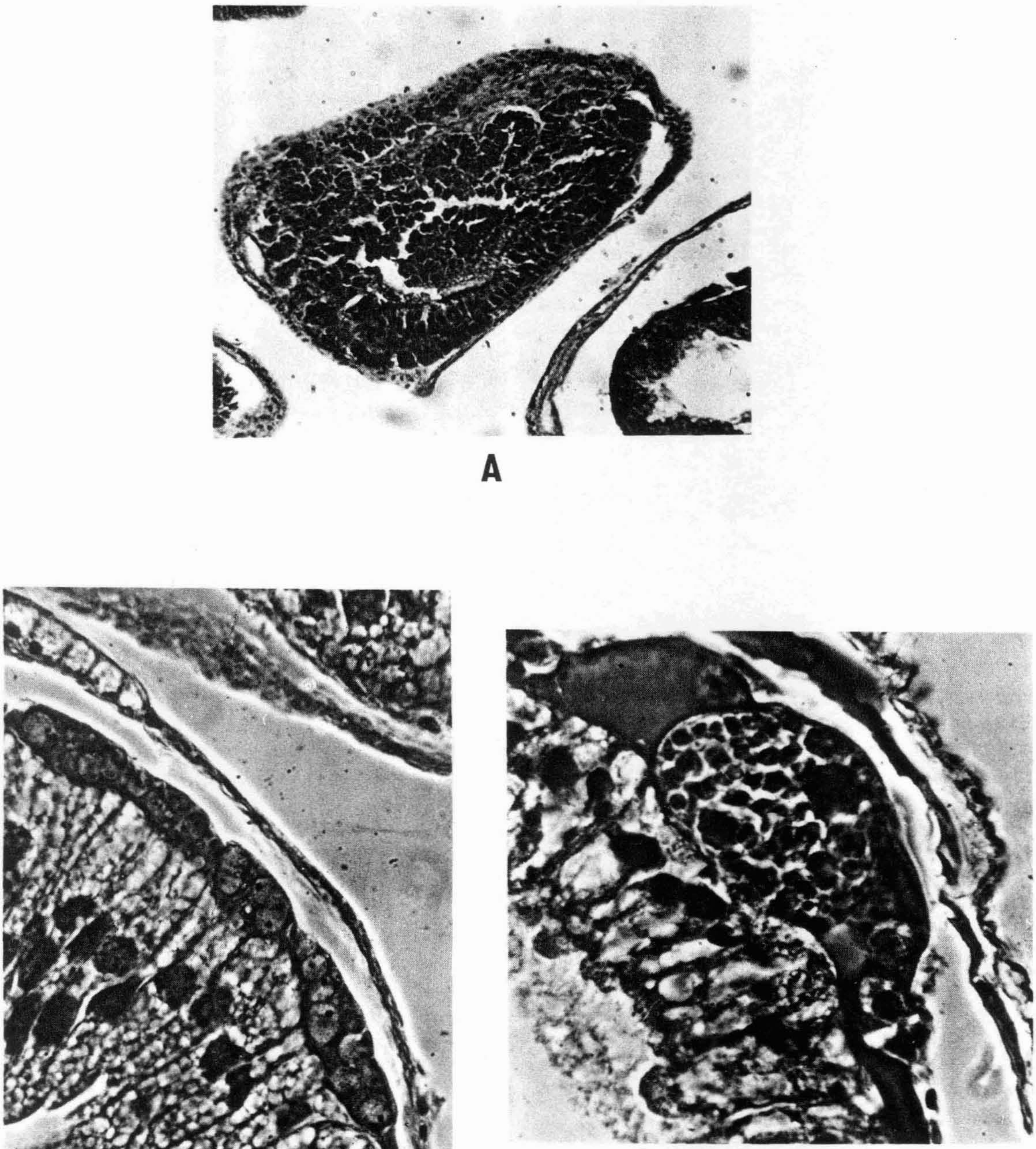

Figure 23. Stages of oogenesis; A) convoluted band of oogonia; B) single layer of oogonia on outer edge of spadix (x 285); C) oogonia during vitellogenesis (x 667).

these, plus the remaining adults entering from the Caribbean, are in turn responsible for increasing abundance in the Florida Straits. Russell (1938) showed that a larval calycophore, *Muggiaea atlantica*, develops a larval nectophore within 48 hours. Totton (1965) suggests that larval physonects develop more slowly, possibly taking a week. If larval *Physalia* develop at a similar rate, sufficient density for successful reproduction is maintained in the Florida Straits until May.

Initiation and cessation of the spawning cycle are probably influenced by seasonal events occurring in the Atlantic. Influx of *Physalia* into the Atlantic in spring from the Florida Straits may be the reason for increased productivity. They might be the same animals appearing in the Caribbean in August, but if they grow as fast as postulated, it is doubtful. *Physalia* spawned along Florida's coast would be several inches long before reaching currents that could carry them back into the Caribbean. Eldred (1971) shows that the common eel larvae (*Anguilla rostrata*) are five or six months old before they reach the Yucatan Straits from their spawning grounds in the Atlantic, the Sargasso Sea, according to Schmidt (1925). Photoperiod or temperature may also influence the spawning cycle of *Physalia;* however, spawning occurs from October through May in the Florida Keys, a very wide range of temperatures and photoperiods.

A full understanding of the complex pattern of *Physalia* dynamics must await further information, particularly from the Atlantic, on seasonal distribution, abundance, size, and spawning.

SUMMARY

1. Aerial surveys were conducted over the western Caribbean, Gulf of Mexico and coastal waters of Florida from April 1969 through February 1971. The approximate size and location of all visible *Physalia* were recorded.
2. Field surveys were conducted along bridges, piers and beaches in the Florida Keys. Approximate size of all *Physalia* were recorded. One hundred forty-six *Physalia* were collected for measurements of float length and gas gland diameter and for determinations of sex and maturity.
3. Sixty-seven *Physalia* were maintained in laboratory tanks to obtain data on survival and growth. Attempts to maintain live, severed gonodendra in laboratory tanks to obtain mature gametes were unsuccessful.
4. *Physalia* are moved primarily by the major currents flowing west through the Caribbean, the Yucatan Straits, into the Gulf of Mexico, then east and north through the Florida Straits. *Physalia* are driven ashore by winds mostly in areas where major currents are close to land.
5. Distribution shows a definite yearly cycle. *Physalia* appear mostly in the Caribbean in fall, throughout the study area in winter, and only along the coasts of Florida during spring and summer. This yearly cycle begins in late summer with recruitment of *Physalia* into the Caribbean from the Atlantic.
6. Abundance of *Physalia* from December through February in the study area was significantly greater than during June and July. Observed abundance was also significantly greater in the Gulf of Mexico and Florida Straits than in the Caribbean. The total population of *Physalia* in the Florida Straits, at least during winter, is considerably greater than indicated by aerial surveys, *Physalia* may disappear from the Caribbean during summer but appear to be present all year in the Gulf and Florida Straits.
7. Winter abundance levels are caused by recruitment of small *Physalia* from within the Caribbean, Gulf of Mexico and Florida Straits. Monthly average *Physalia* float lengths are smallest when abundance is highest. *Physalia* have minimum average float lengths 6-10 cm during fall and winter and maximum average float lengths 21-24 cm during spring and summer. Smaller *Physalia* occur first in the Caribbean, then in the Gulf and Florida Straits, demonstrating the time lag between occurrences in these areas and the progression of the center of production through the study area.
8. Possible growth rate of *Physalia* was determined from several aerial survey sightings. They appeared to grow approximately 32 mm per month. Estimated

age of the largest *Physalia* seen or collected (251 mm or 10 inches) is approximately one year.

9. Recognition of male and female germ cells is possible in all but the very smallest gonophores. All gonophores of one gonodendron appeared to be in the same stage of development whereas various gonodendra from one *Physalia* were in different stages of development. *Physalia* are dioecious; the most mature germ cells found were oogonia during vitellogenesis, and spermatids. Based on 45 specimens, *Physalia* with 9 to 15 cm floats are capable of spawning.
10. Spawning begins in the Caribbean in fall. *Physalia* larvae probably develop to small floating forms very rapidly and it appears that at least some animals produced in the Caribbean are capable of spawning by the time they reach the Gulf and Gulf Stream. Numbers of reproducing *Physalia* are increased, in turn producing the great abundance of young seen during winter. It is not known what triggers this spawning cycle but it probably begins in the Atlantic.

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