Epipelagic Amphipods of the Family Hyperiidae from the International Indian Ocean Expedition, 1959–1965

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and

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SMITHSONIAN CONTRIBUTIONS TO ZOOLOGY • NUMBER 359

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ABSTRACT

Bowman, Thomas E., and Maura McManus McGuinness. Epipelagic Amphipods of the Family Hyperiidae from the International Indian Ocean Expedition, 1959–1965. *Smithsonian Contributions to Zoology*, number 359, 53 pages, 87 figures, 5 tables, 1982.—About 1300 samples of Hyperiidae from almost all parts of the Indian Ocean, collected by vertical tows from a depth of 200 m to the surface, were examined. Fifteen species, including 8 not previously known from the Indian Ocean, were identified and enumerated, and their distributions mapped. Most species were more or less randomly scattered over the entire Indian Ocean. *Themisto gaudichaudii* was confined to cool water, mostly south of 30°S, but penetrated farther north to the west of Australia. The most abundant and widespread species were *Hyperioides sibaginis* and *Lestrigonus schizogeneios*, each of which occurred at more than one-half of all the stations; together they made up 41 percent of the total number of specimens of Hyperiidae. There were no apparent differences in numbers of specimens between day and night samples. Nine species occurred more frequently in the Arabian Sea during the NE monsoon than during the SW monsoon. It is suggested that the swifter anticyclonic gyre of the SW monsoon causes greater spatial separation. Species confined to definite biotic provinces in the Pacific Ocean show no provincialism in the Indian Ocean, and physiological races may have evolved in the 2 oceans.

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Epipelagic Amphipods of the Family Hyperiidae from the International Indian Ocean Expedition, 1959–1965

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Introduction

From 1959 to 1965 nine nations participated in a cooperative scientific investigation of the Indian Ocean. They were Australia, India, Japan, Pakistan, South Africa, the United Kingdom, the United States, the USSR, and West Germany. This investigation, known as the International Indian Ocean Expedition (IIOE), carried out many projects, one of which was a survey of the zooplankton of the upper 200 m. Since 18 research vessels were cooperating in this survey, steps were taken to increase the comparability of the samples collected. The "Indian Ocean standard net" was designed by R.I. Currie for use on all ships (Currie, 1963; Motoda, 1962). This net had a mouth opening of 1 m^2 (diameter 113 cm) and was 500 cm in length, excluding the bucket. The upper 200 cm were cylindrical, the lower 300 cm conical. Mesh openings in the filtering parts were 0.33 mm. Each of the 18 participating ships was requested to make a vertical tow at about 2000 hrs at each station from 200–0 m, retrieving the net at 1 m per second using 4 mm diameter wire cable. The use of a flow-meter was recommended since vertical net hauls are rarely absolutely vertical, but this recommendation was not followed by any of the participants. According to Tranter and Smith (1968), the standard net has an initial filtration efficiency of about 0.96; hence a vertical tow from 200 m would filter about 192 m^3 of water.

Further details on the IIOE zooplankton program can be found in IOBC (1969), Rao (1973), and Sakthivel and Rao (1973).

The standard vertical samples (a total of 1548) were sent to the Indian Ocean Biological Centre (IOBC), established at Cochin, Kerala State, India, in 1962 (Hansen, 1966). There the samples were sorted and the sorted material was sent to specialists throughout the world for study. The amphipods were sorted into 9 groups, mostly families, by K.K. Chandrasekharan Nair. About 2000 of Nair's sorted samples were checked by Hans-Eckard Gruner and the senior author during a 2-month visit to the IOBC in October–November 1968.

The family Hyperiidae, which comprises about 45% of the Amphipoda collected, was assigned to the senior author for study, and the present re-

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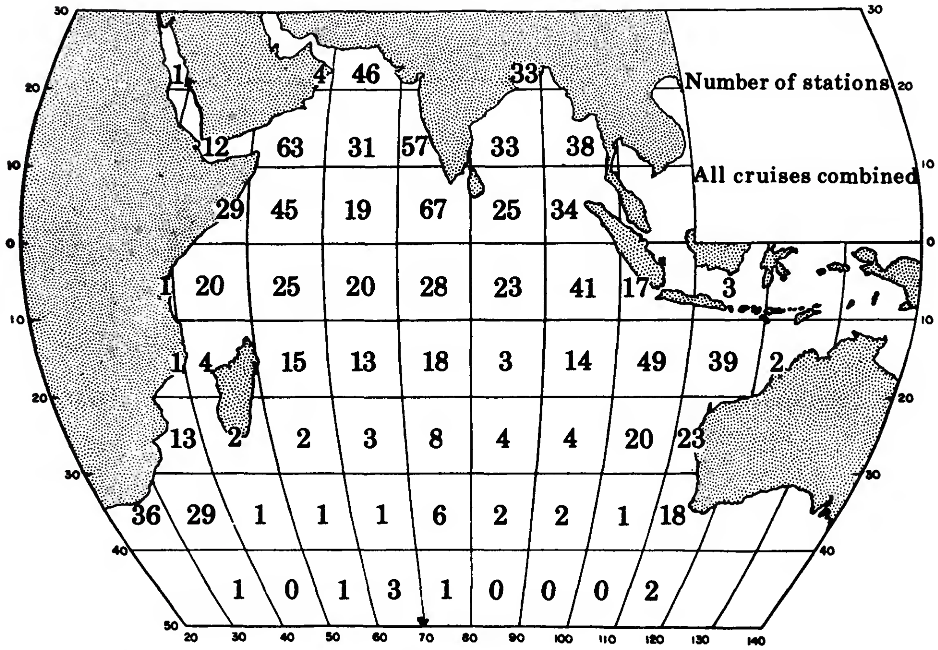

FIGURE 1.—Numbers of IIOE samples containing Hyperiidae for each 10° square.

port is concerned with the distribution of members of this family in the Indian Ocean. About 1300 samples were received and their contents enumerated according to species. The geographic distribution of these samples is shown in Figure 1.

Despite use of a standard net and efforts to have all research vessels follow a uniform procedure, the comparability of the samples is limited. Some vessels paid out exactly 200 m of wire; others used more wire to compensate for the wire angle, and in some instances wire angles were not recorded. In shallow waters many samples were taken with less than 200 m of wire. Other limiting factors are the patchiness of the zooplankton and the fact that hyperiid amphipods are associated with gelatinous zooplankters during part of their life histories (Harbison, Biggs, and Madin, 1977; Laval, 1980). The number of hyperiid amphipods in a sample must be strongly influenced by the number of gelatinous zooplankton hosts captured.

Considering these factors, the standard samples give, at best, semiquantitative information on the distribution of hyperiid amphipods in the Indian Ocean. They do, however, provide valuable information on overall distribution and relative abundance of the individual species.

ACKNOWLEDGMENTS.—For helpful reviews of the manuscript we thank Frank D. Ferrari and Anne C. Cohen. Mrs. Cohen also prepared several of the illustrations. For gracious hospitality and many courtesies received by the senior author during his visit to the IOBC, thanks go to David J. and Helen A. Tranter, to K.K. Chandrasekharan Nair, and to the Director of the IOBC, T.S.S. Rao. Allocation of the IIOE collection of Hyperiidae to the senior author was made possible by H.-E. Gruner, of the Zoologisches Museum der Humboldt Universität zu Berlin, who was Senior Specialist for the Amphipoda on this project.

The Species of Hyperiidae in the Indian Ocean

Past records of Hyperiidae from the Indian Ocean, surprisingly few in number, are listed below:

Hyperia galba (Montagu)
Walker (1904), Ceylon.
Spandl (1924), Red Sea.
Lestrigonus bengalensis Giles
Giles (1887), Bay of Bengal.
Walker (1904), Ceylon.
Walker (1909), north of Chagos Island (4°16′S, 71°53′E), Mauritius Island, Cargos Carajas Shoals, Desroches Atoll.
Spandl (1924), Red Sea (as *Hyperia dysschistus* Stebbing).
Nayar (1959), Coast of Madras.
Bowman (1973), Gulf of Camby, Arabian Sea.
Lestrigonus crucipes (Bovallius)
Walker (1904), Ceylon.
Barnard (1937), Gulf of Oman, Central Arabian Sea.
Bowman (1973), Arabian Sea.
Lestrigonus schizogeneios (Stebbing)
Pirlot (1930), southern coast of Lomblen Island, Savu Sea.
Barnard (1937), northern Arabian Sea.
Tranter (1977), eastern Indian Ocean (110°E).
Hyperietta vosseleri (Stebbing)
Spandl (1924), Red Sea (as *Hyperia fabrei* Milne Edwards).
Tranter (1977), eastern Indian Ocean (110°E).
Hyperioides longipes Chevreux
Barnard (1937), Gulf of Aden.
Pillai (1966), Arabian Sea.
Tranter (1977), E Indian Ocean (10°E).
Hyperoides sibaginis (Stebbing)
Nair (1972), southwestern coast of India.
Phronimopsis spinifer Claus
Walker (1909), north of Chagos Island (4°16′S, 71°53′E).
Spandl (1924), Red Sea.
Tranter (1977), eastern Indian Ocean (110°E).

As previously pointed out (Bowman, 1973), the 2 records of *Hyperia galba* must be considered misidentifications. The remaining 7 species in the list occurred in the IIOE collections; the following 8 additional species bring the total of Hyperiidae species to 15: *Hyperietta luzoni* (Stebbing), *Hyperietta stebbingi* Bowman, *Hyperietta stephenseni* Bowman, *Hyperoche* species (undescribed), *Hyperionyx macrodactylus* (Stephensen), *Lestrigonus macrophthalmus* (Vosseler), *Themistella fusca* (Dana), and *Themisto gaudichaudii* Guérin-Méneville.

Representative specimens of the IIOE species of Hyperiidae have been deposited in the Indian Ocean Biological Centre, Cochin, Indian (now incorporated into the National Institute of Oceanography Regional Centre, Cochin). The rest of the collections are deposited in the Division of Crustacea, Smithsonian Institution.

Descriptions of all Indian Ocean species of Hyperiidae except *Hyperoche* species and *Themisto gaudichaudii* are given by Bowman (1973). To facilitate rapid identification of Indian Ocean Hyperiidae we have provided 2 pictoral keys, one to females with rudimentary antenna 2 (Figure 2), and the other to females in which antenna 2 is not rudimentary (Figure 3). For identification of the more difficult males, refer to Bowman (1973).

Relative Abundance of Species

In Rao's (1973) Table 5, which shows the numerical abundance in percentage of 12 categories of zooplankters in the standard samples, copepods are by far the most numerous, making up an average of 75.53% of the total samples, and the amphipods rank twelfth, averaging only 0.23%. The overwhelmingly dominant copepods are followed by Ostracoda (6.44%), Chaetognatha (6.41%), and Euphausiacea (2.3%). Each of the other taxa comprises less than 2% of the total.

Of the Amphipoda families, the Hyperiidae was by far the most abundant, making up 45.18% of the total specimens (Nair, Jacob, and Kumaran, 1973). Next came the Phrosinidae (15.93%), the Pronoidae and Lycaeidae combined (10.89%), the Platyscelidae and Parascelidae combined (7.71%), and the Phronimidae (6.88%). Thus the amphipods, which were a minor constituent of the standard samples, were dominantly Hyperiidae.

The distributions of the species are shown in a series of maps (Figures 4–77). On these maps positive stations are indicated by open circles, other stations by dots. In addition to showing the distributions obtained from all the samples, we show the day versus night distributions and the distributions during the 2 monsoon seasons, northeast (16 October–15 April) and southwest (16 April–15 October). These distributions were plotted to examine possible diel vertical migrations and the effect of the semiannual reversal of circulation north of 10°S.

Figures 78 and 79 show the relative abundance and frequency of occurrence of the species. Two species, *Lestrigonus schizogeneios* and *Hyperioides sibaginis*, occurred in more than half the samples examined and together comprised 41% of all the

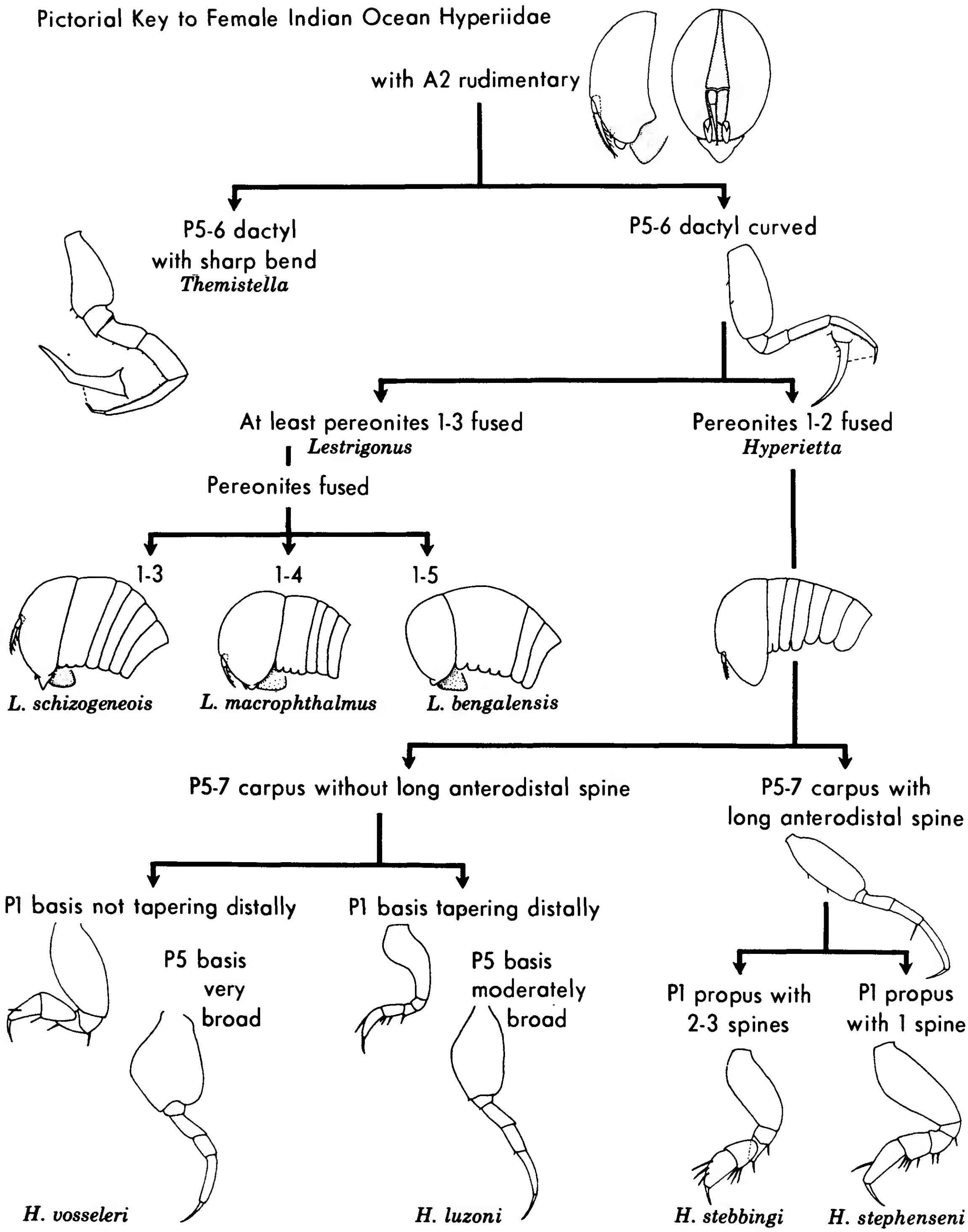

FIGURE 2.—Pictorial key to females of species of Indian Ocean Hyperiidae with antenna 2 rudimentary.

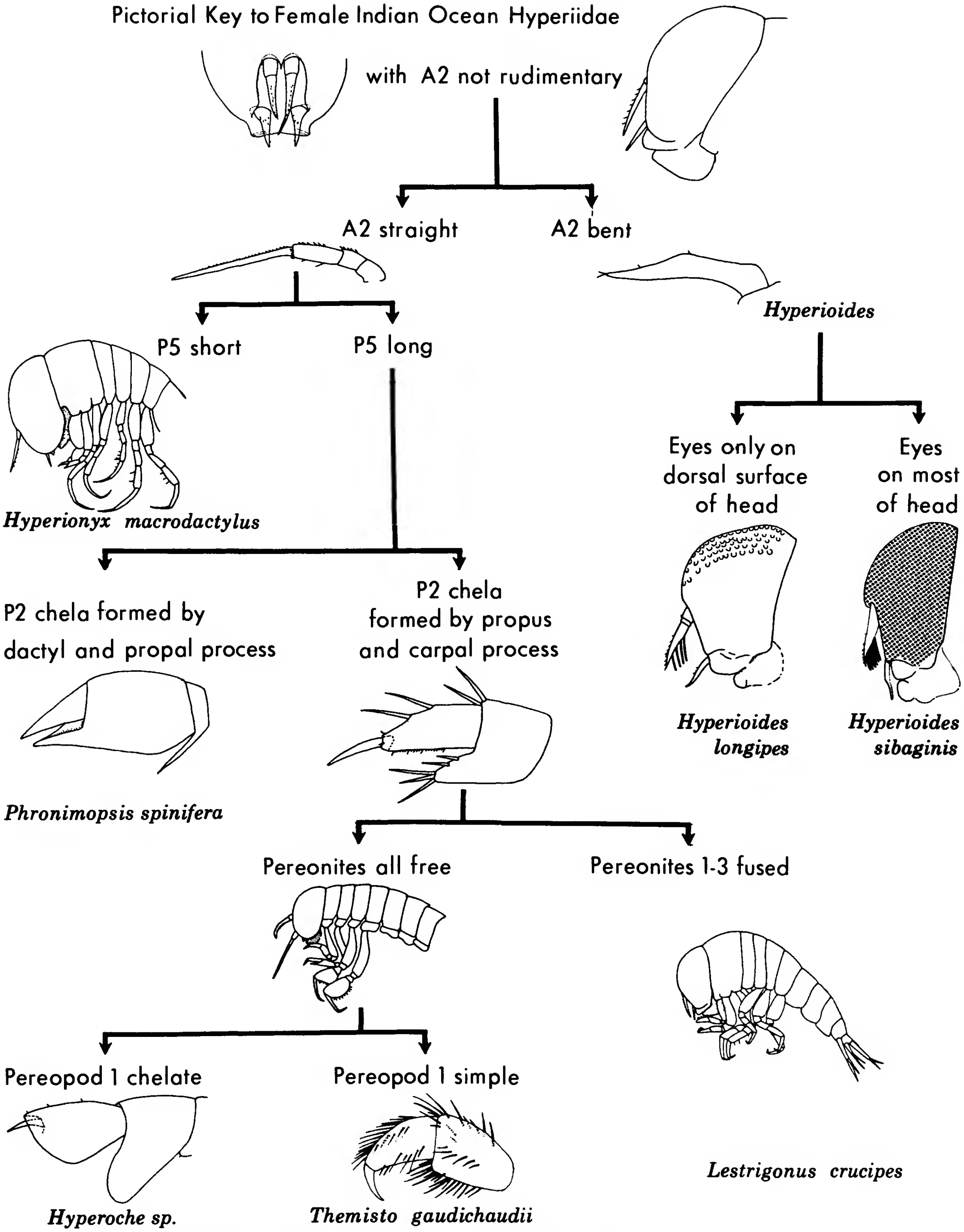

FIGURE 3.—Pictorial key to females of species of Indian Ocean Hyperiidae with antenna 2 not rudimentary.

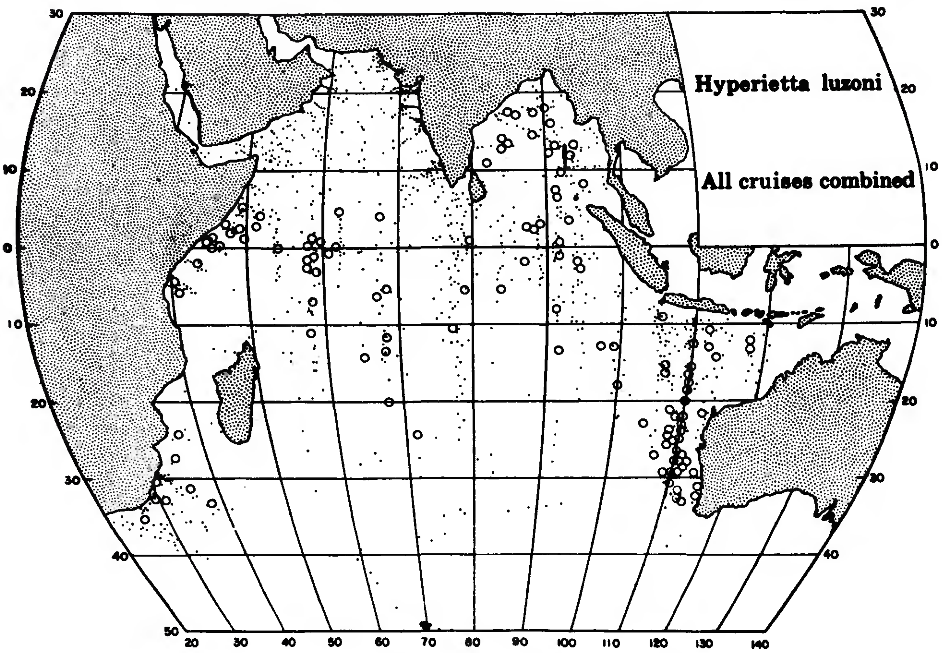

FIGURE 4.—*Hyperietta luzoni*, all IIOE samples.

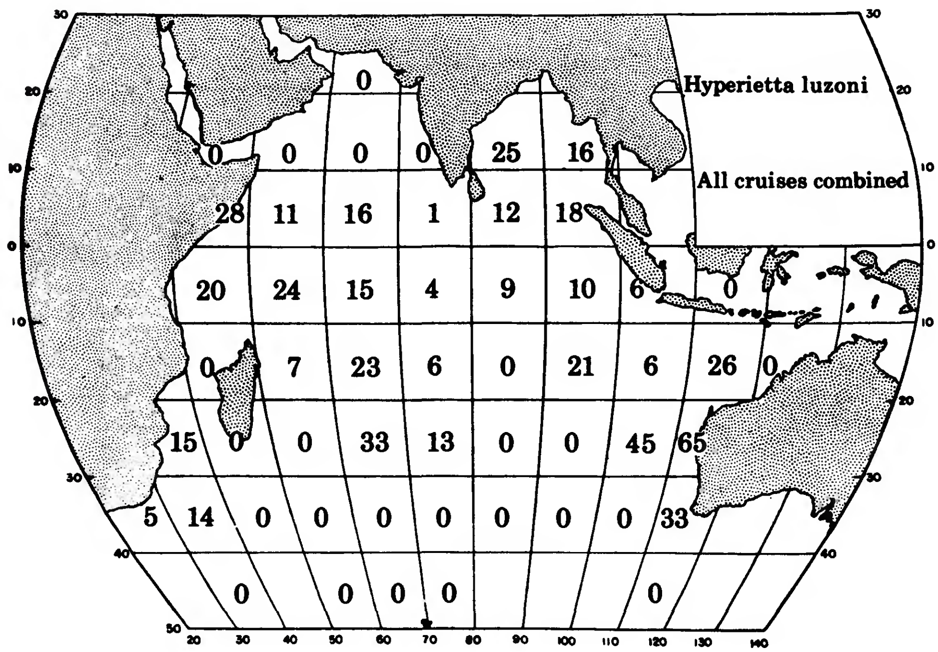

FIGURE 5.—*Hyperietta luzoni*, percent occurrence for each 10° square.

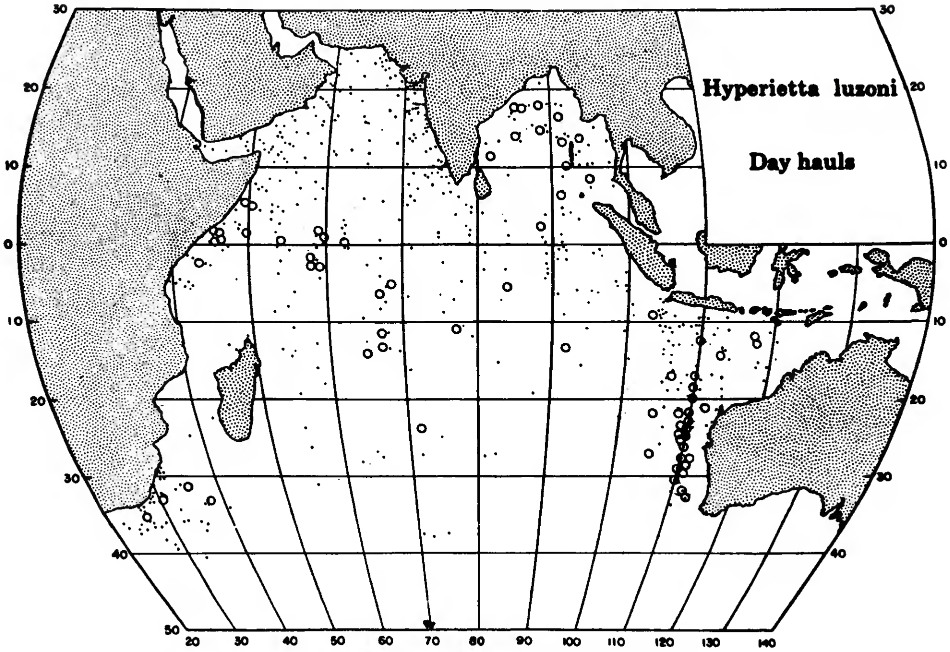

FIGURE 6.—*Hyperietta luzoni*, day stations.

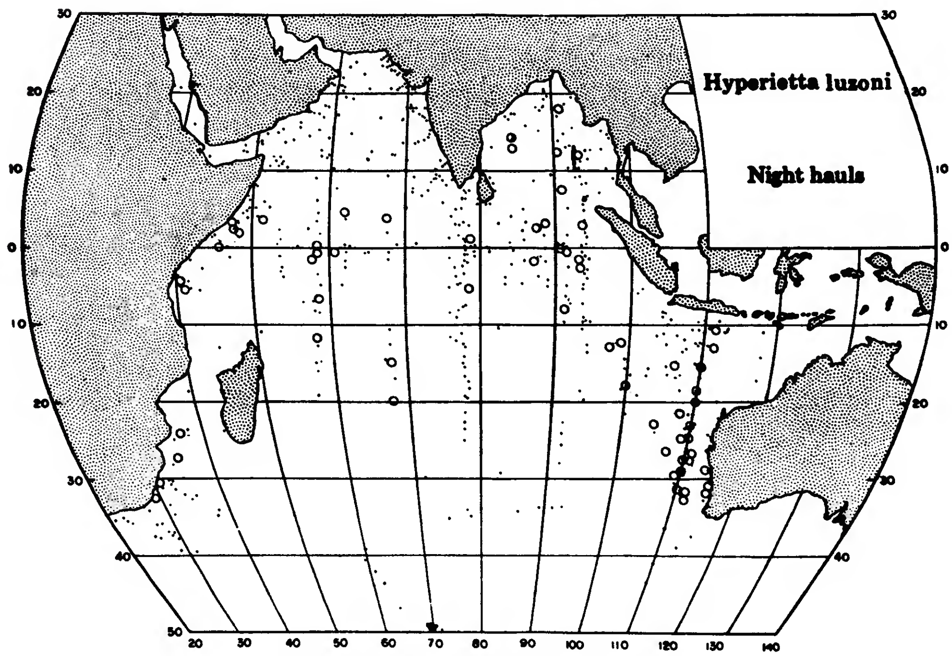

FIGURE 7.—*Hyperietta luzoni*, night stations.

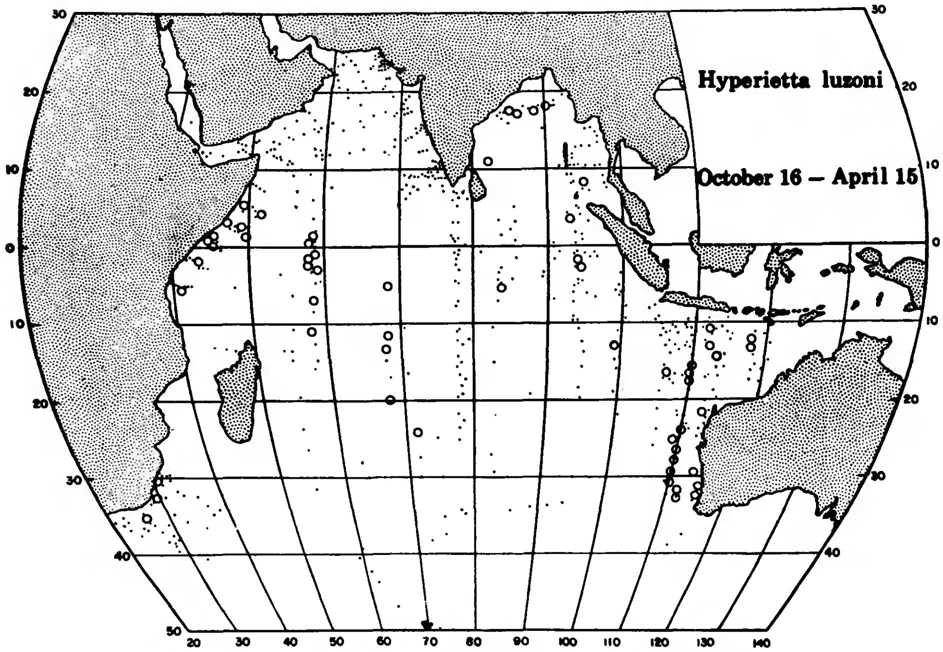

FIGURE 8.—*Hyperietta luzoni*, NE monsoon.

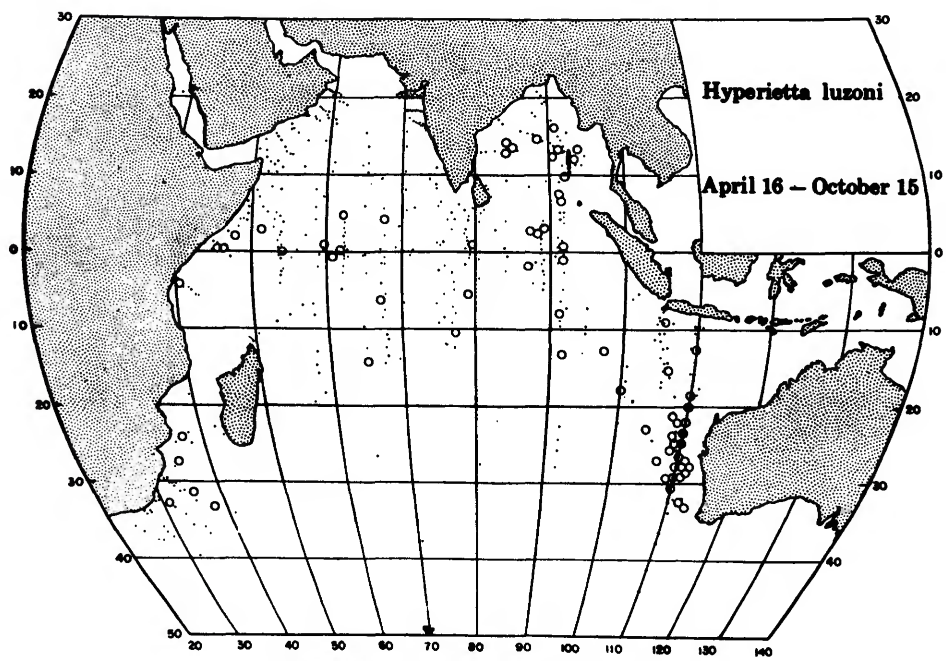

FIGURE 9.—*Hyperietta luzoni*, SW monsoon.

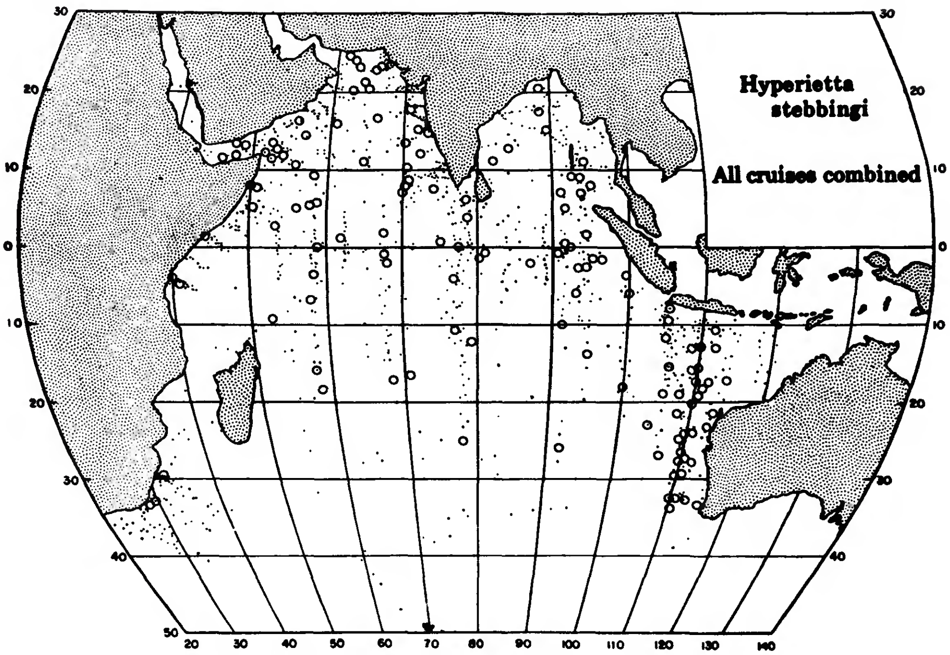

FIGURE 10.—*Hyperietta stebbingi*, all IIOE samples.

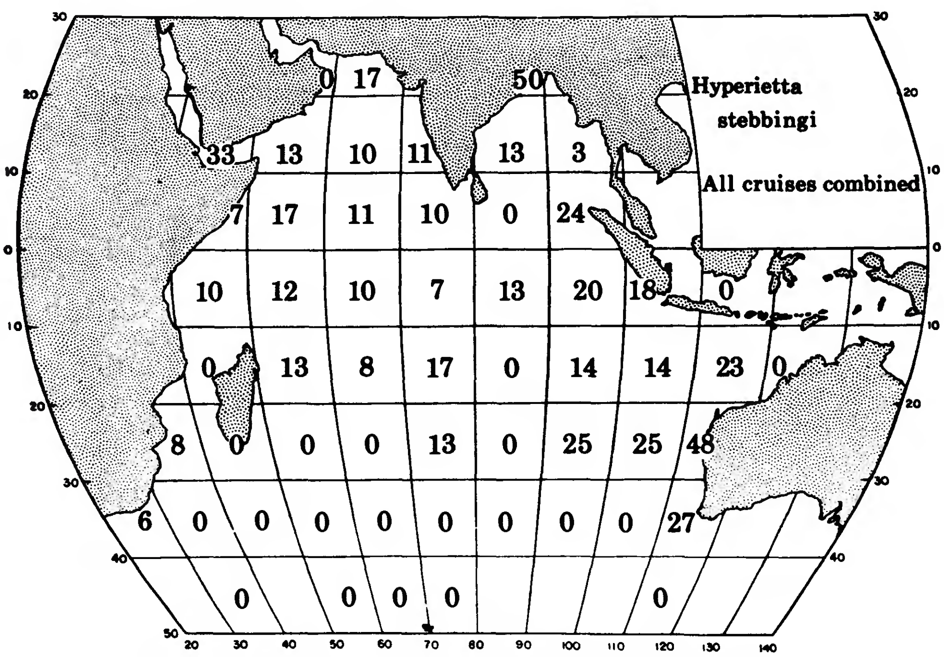

FIGURE 11.—*Hyperietta stebbingi*, percent occurrence for each 10° square.

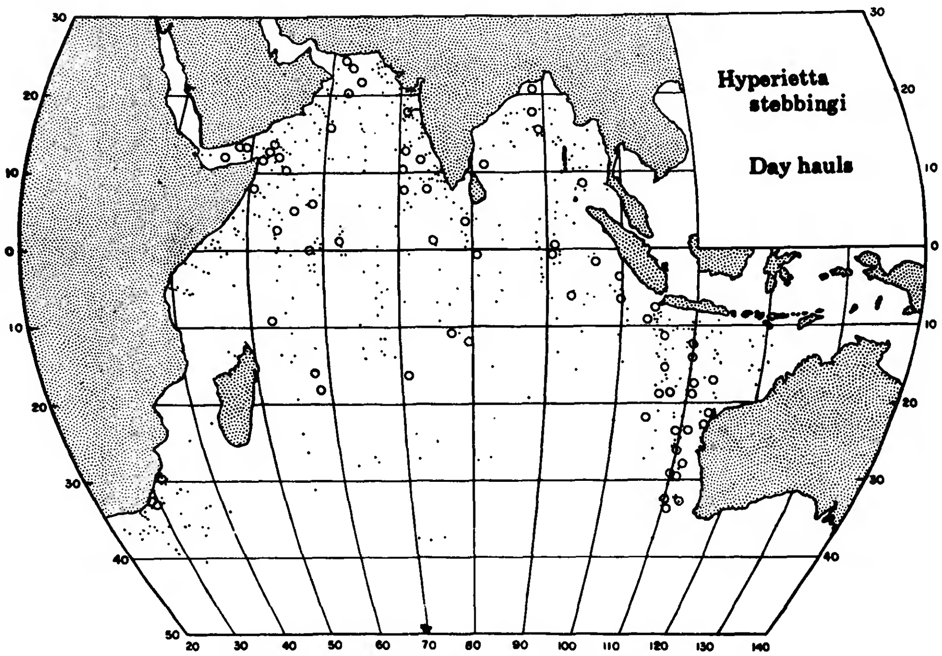

FIGURE 12.—*Hyperietta stebbingi*, day stations.

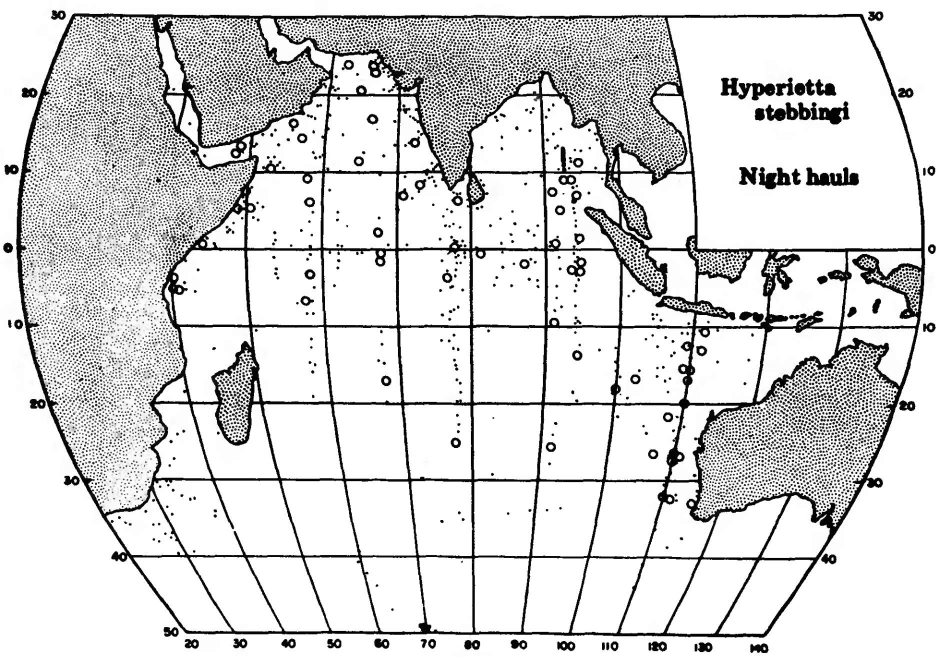

FIGURE 13.—*Hyperietta stebbingi*, night stations.

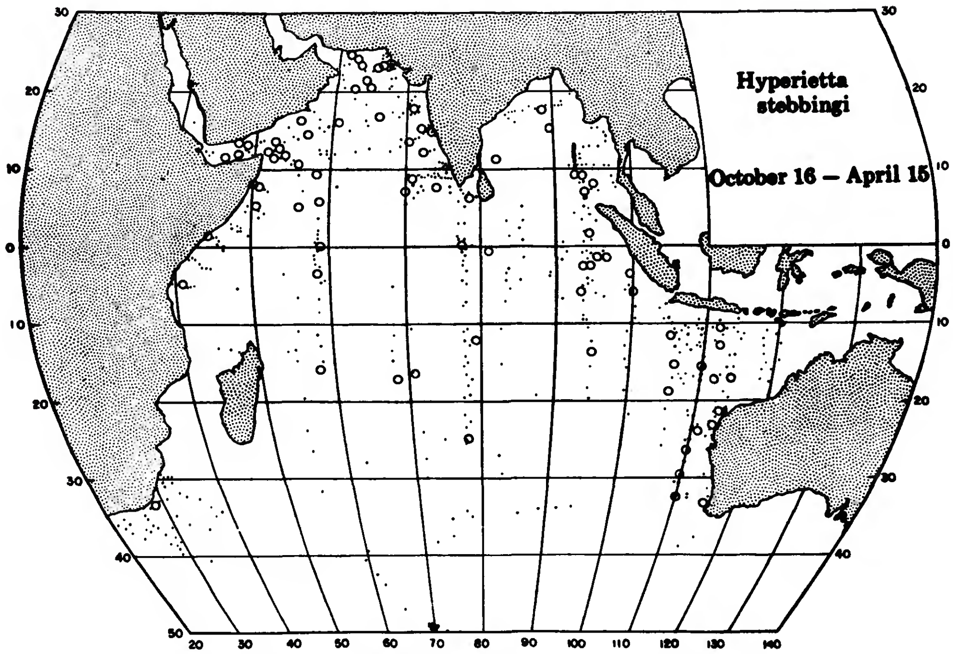

FIGURE 14.—*Hyperietta stebbingi*, NE monsoon.

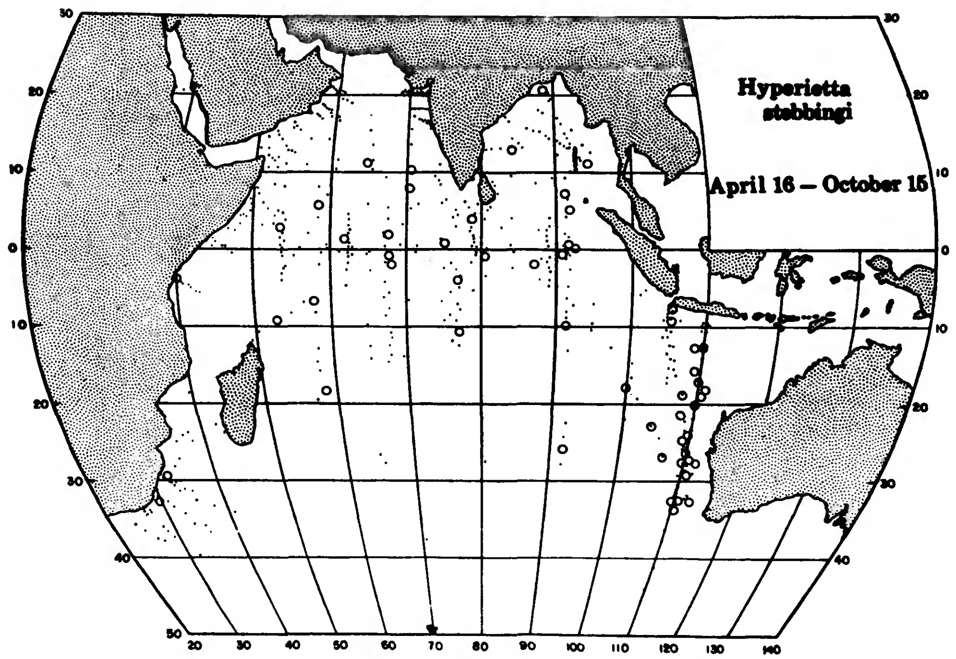

FIGURE 15.—*Hyperietta stebbingi*, SW monsoon.

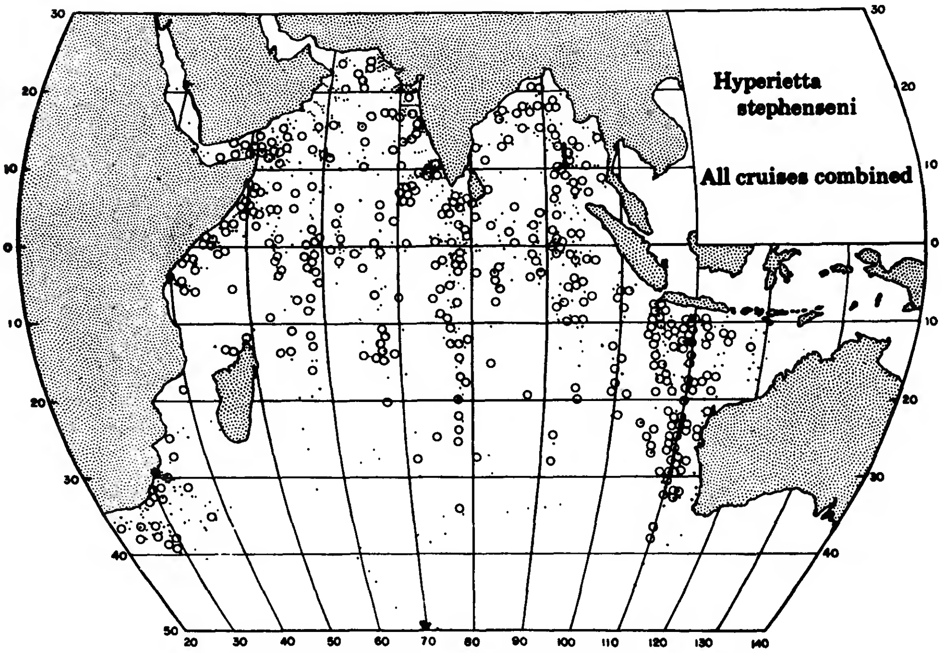

FIGURE 16.—*Hyperietta stephenseni*, all IIOE samples.

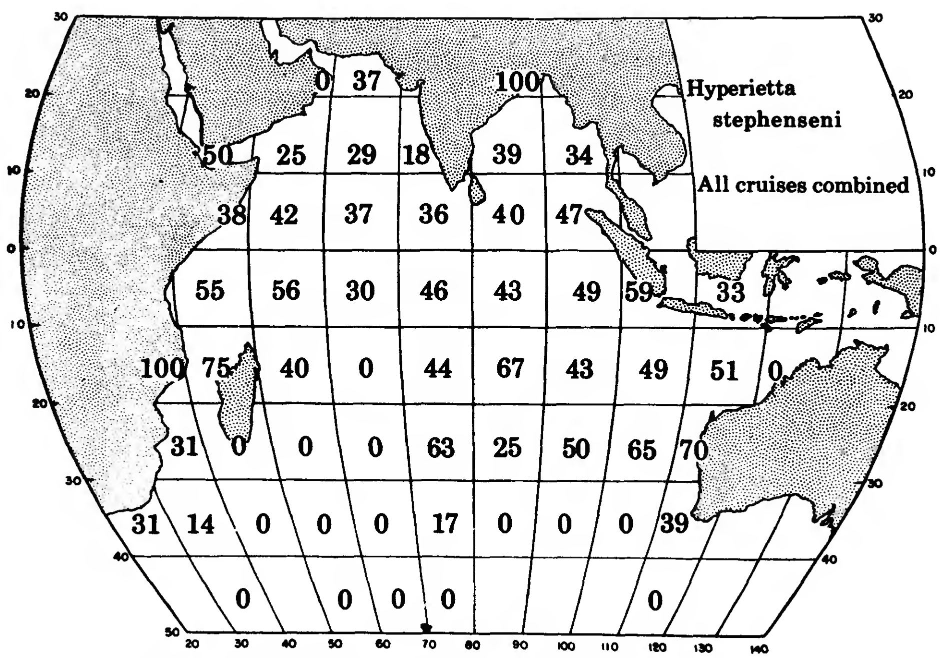

FIGURE 17.—*Hyperietta stephenseni*, percent occurrence for each 10° square.

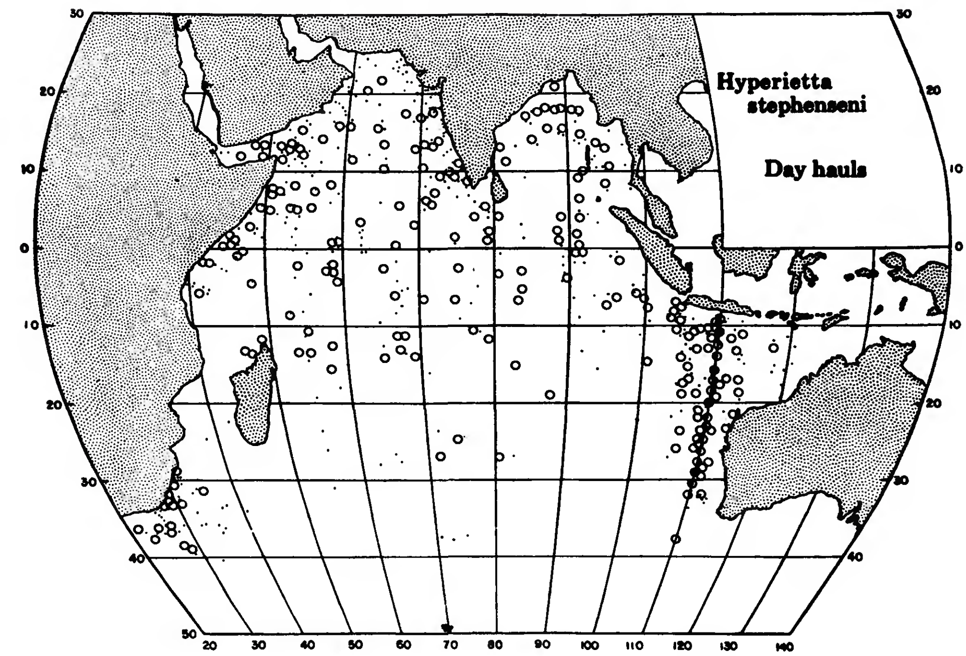

FIGURE 18.—*Hyperietta stephenseni*, day stations.

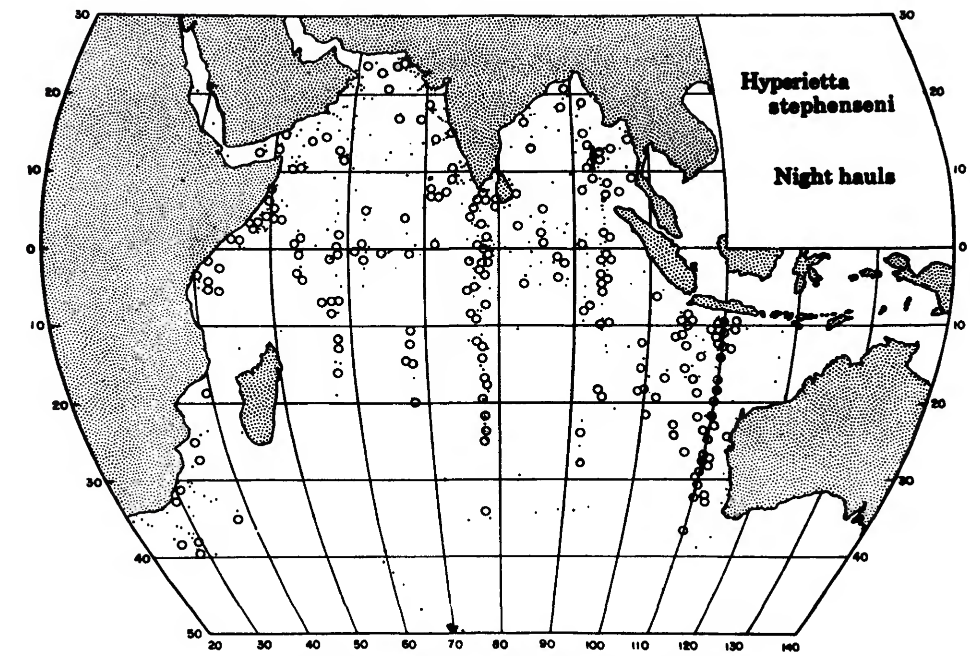

FIGURE 19.—*Hyperietta stephenseni*, night stations.

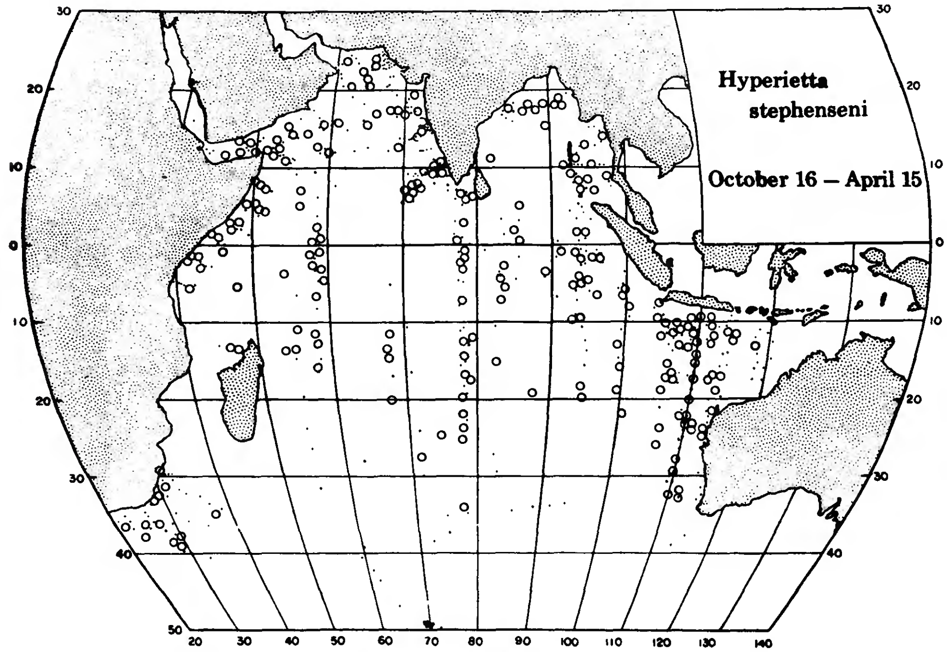

FIGURE 20.—*Hyperietta stephenseni*, NE monsoon.

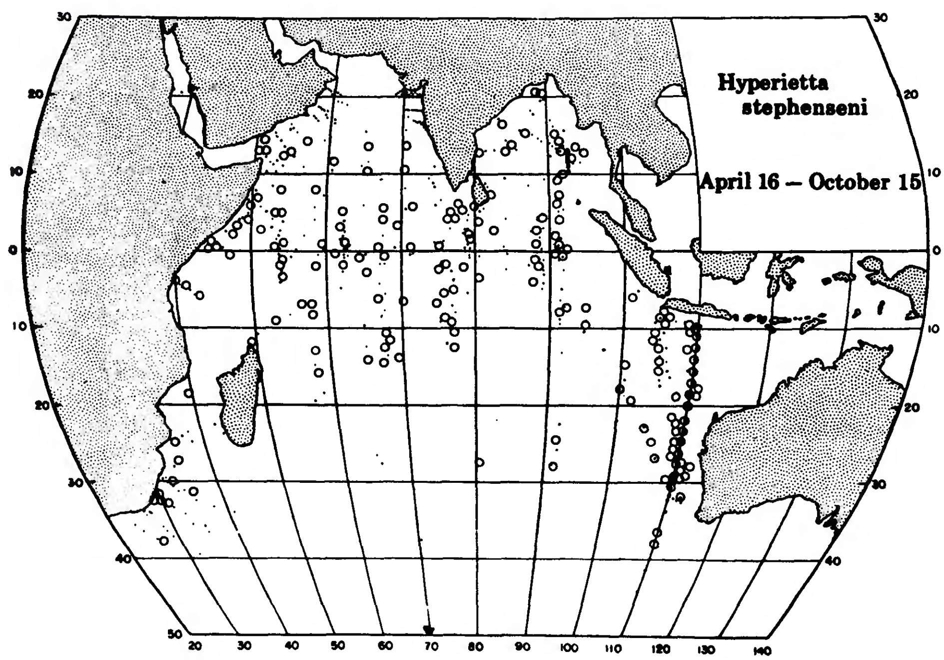

FIGURE 21.—*Hyperietta stephenseni*, SW monsoon.

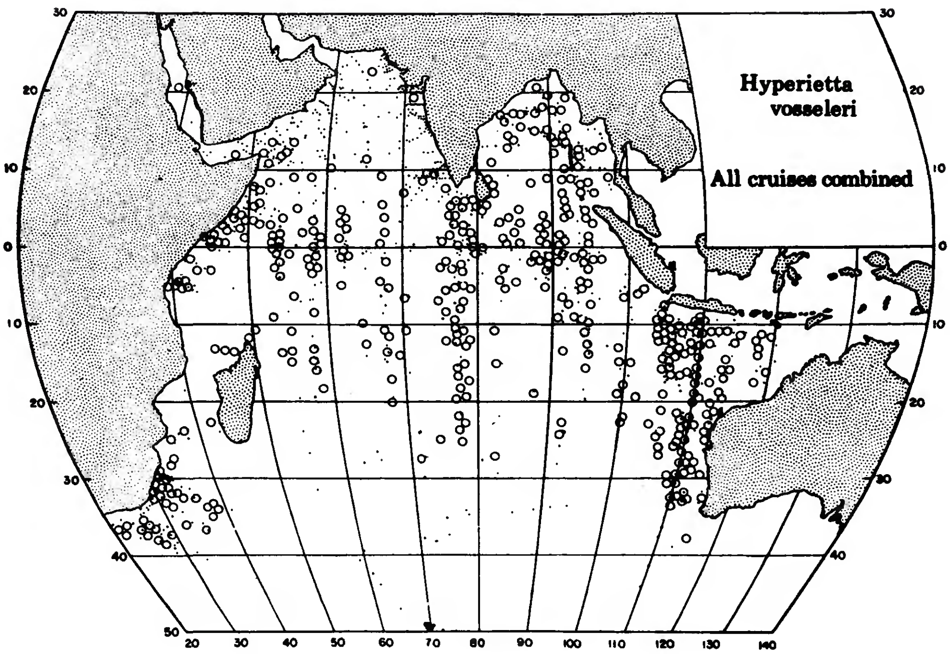

FIGURE 22.—*Hyperietta vosseleri*, all IIOE samples.

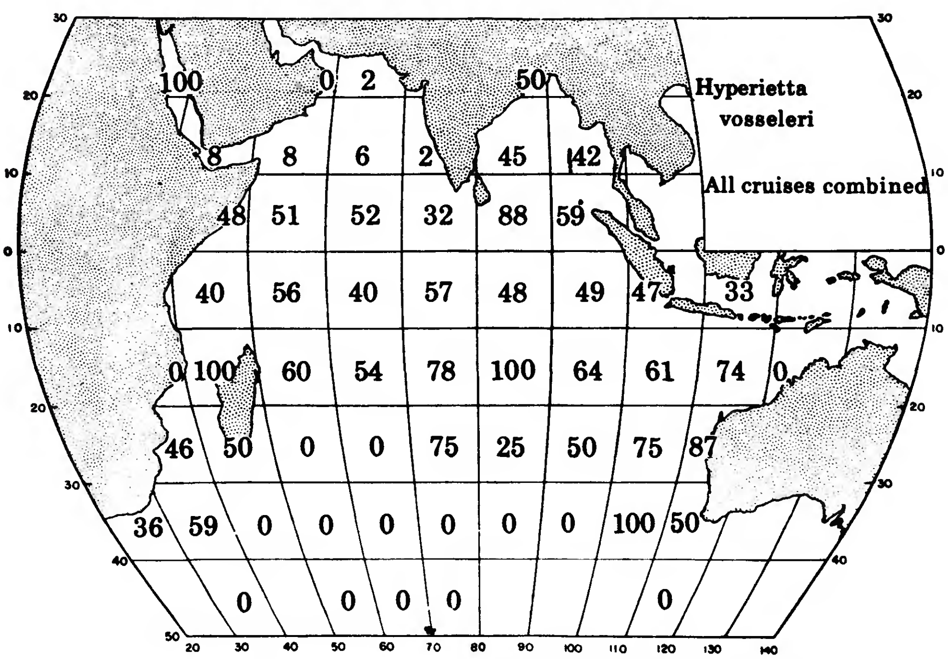

FIGURE 23.—*Hyperietta vosseleri*, percent occurrence for each 10° square.

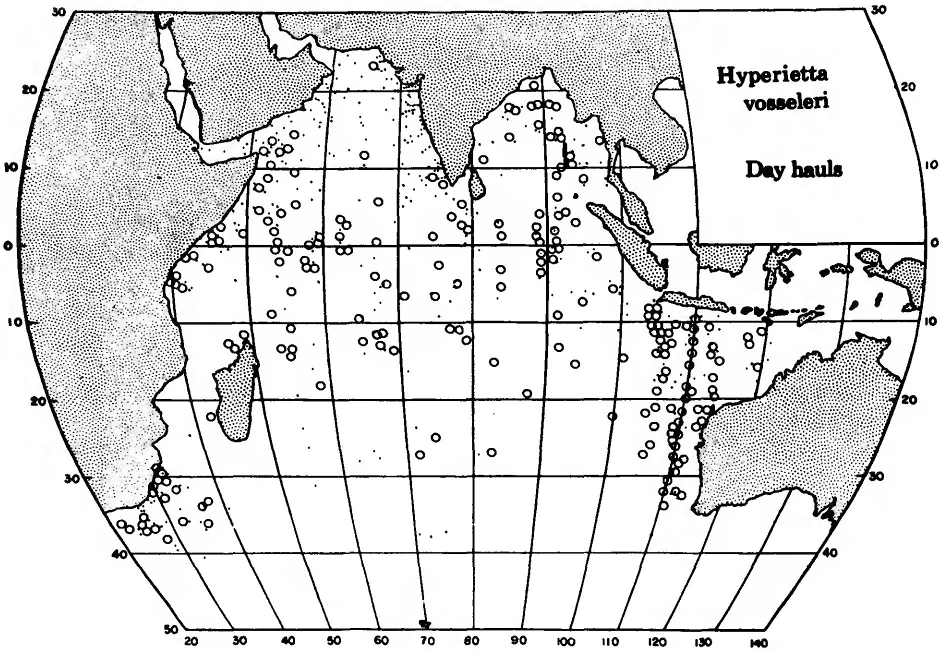

FIGURE 24.—*Hyperietta vosseleri*, day stations.

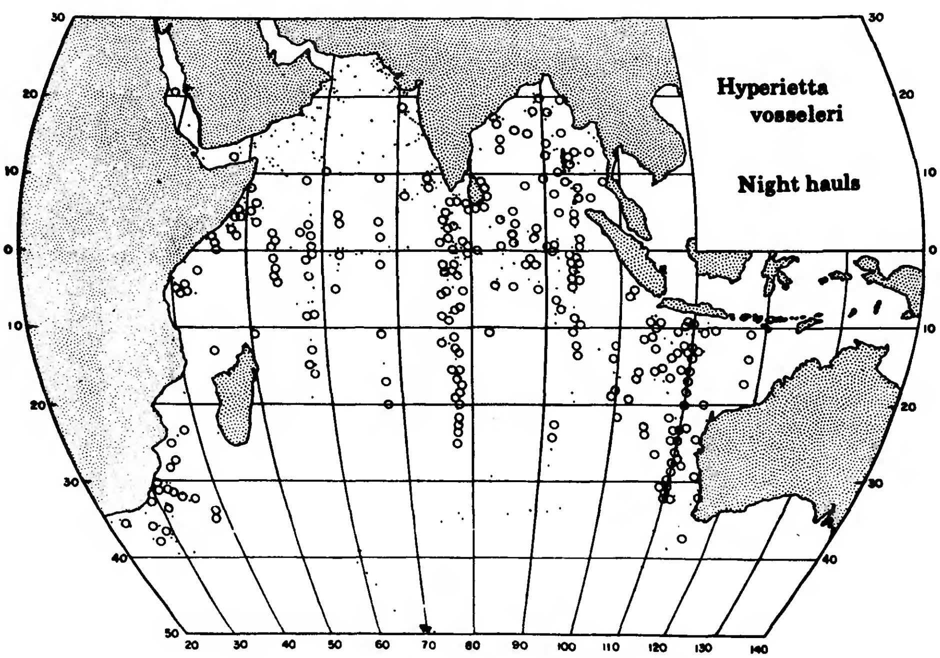

FIGURE 25.—*Hyperietta vosseleri*, night stations.

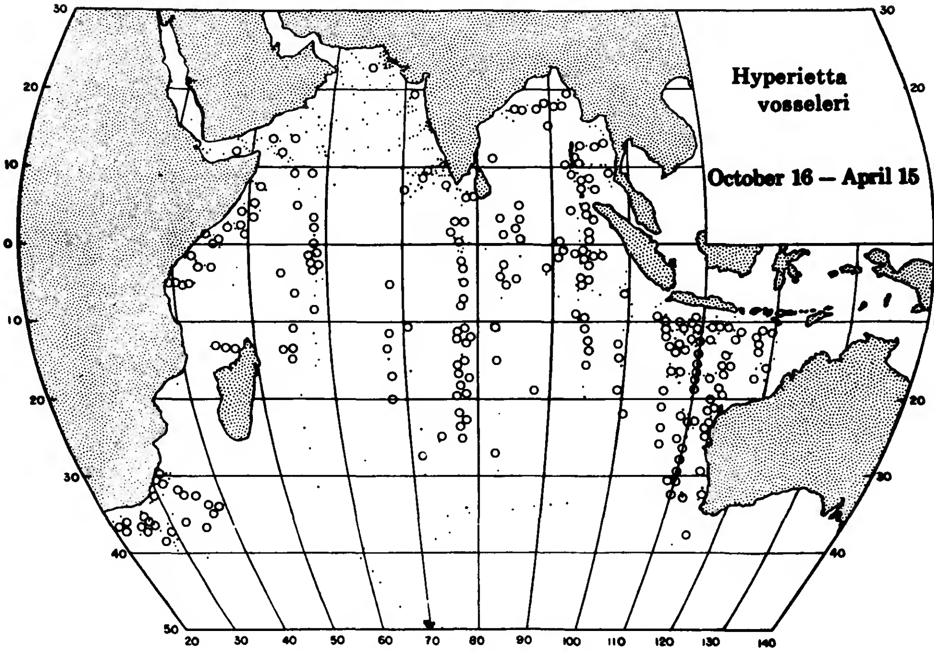

FIGURE 26.—*Hyperietta vosseleri*, NE monsoon.

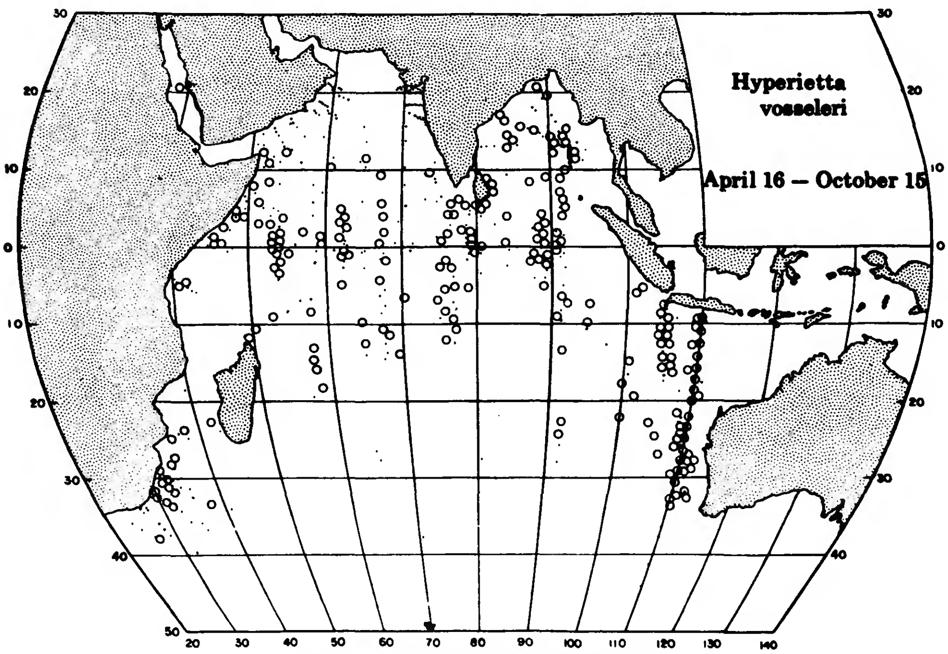

FIGURE 27.—*Hyperietta vosseleri*, SW monsoon.

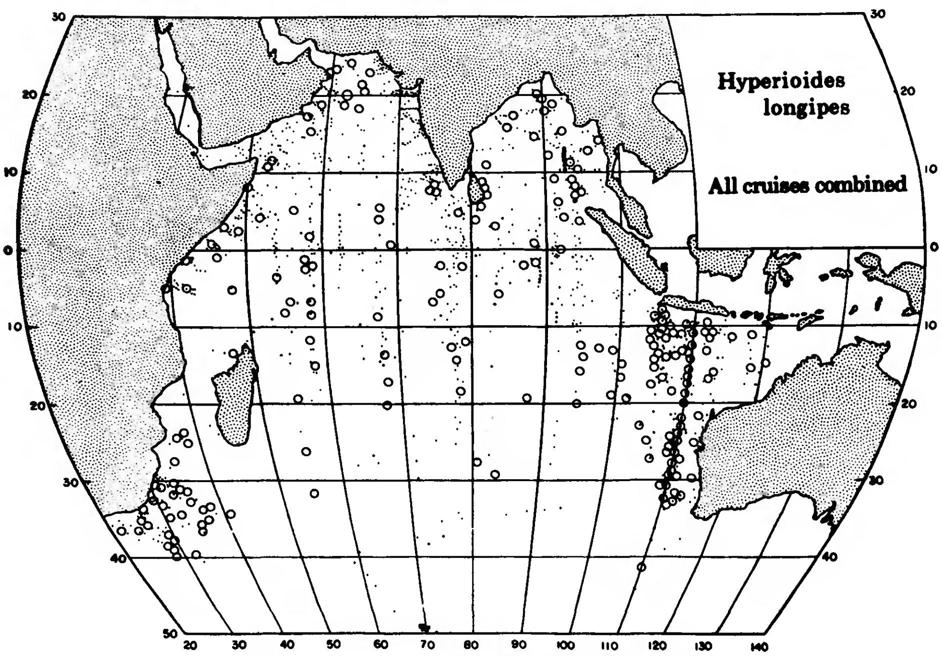

FIGURE 28.—*Hyperioides longipes*, all IIOE samples.

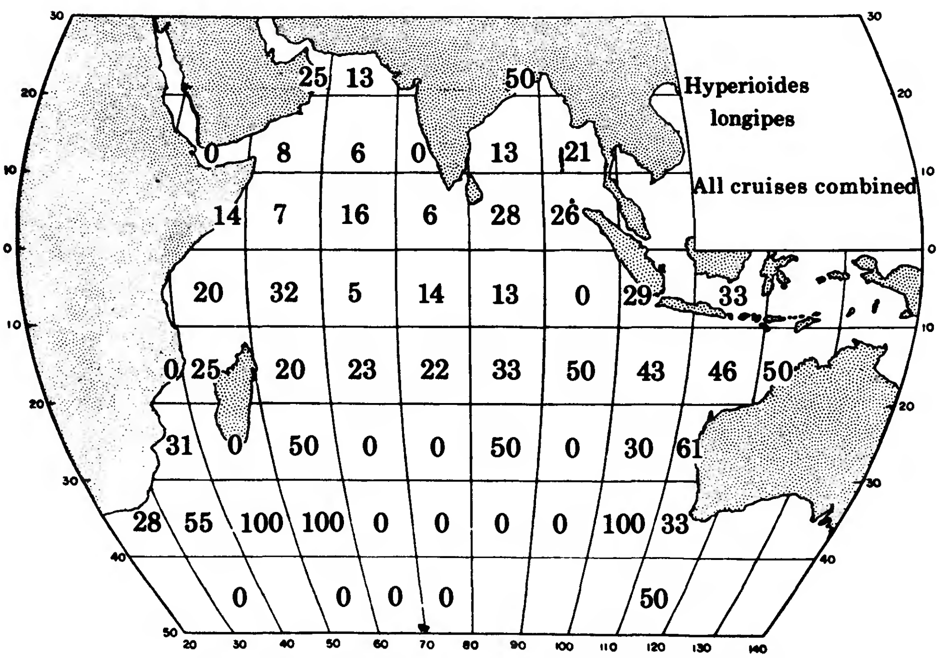

FIGURE 29.—*Hyperioides longipes*, percent occurrence for each 10° square.

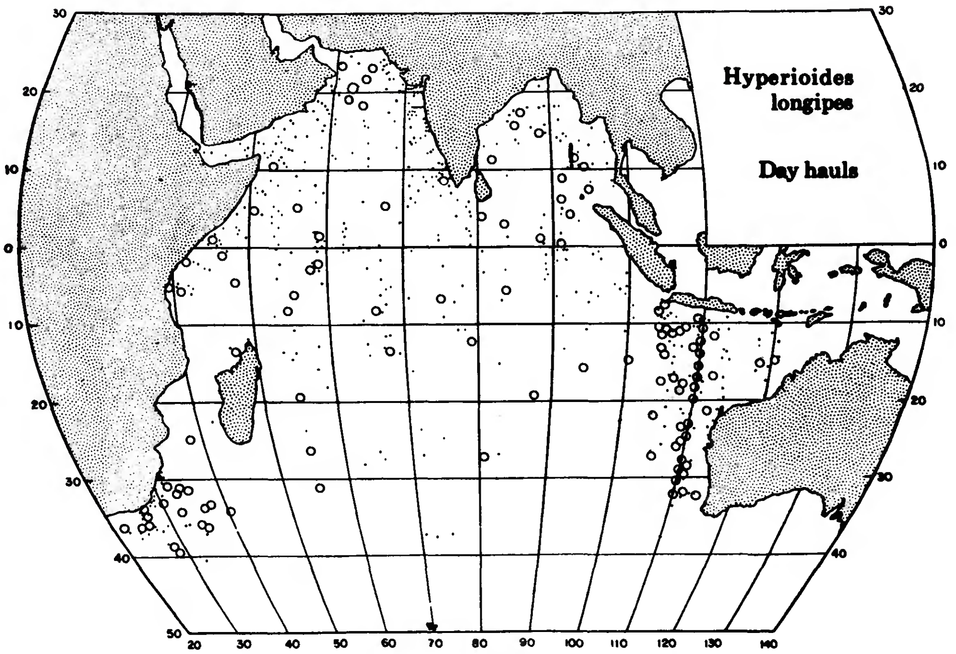

FIGURE 30.—*Hyperioides longipes*, day stations.

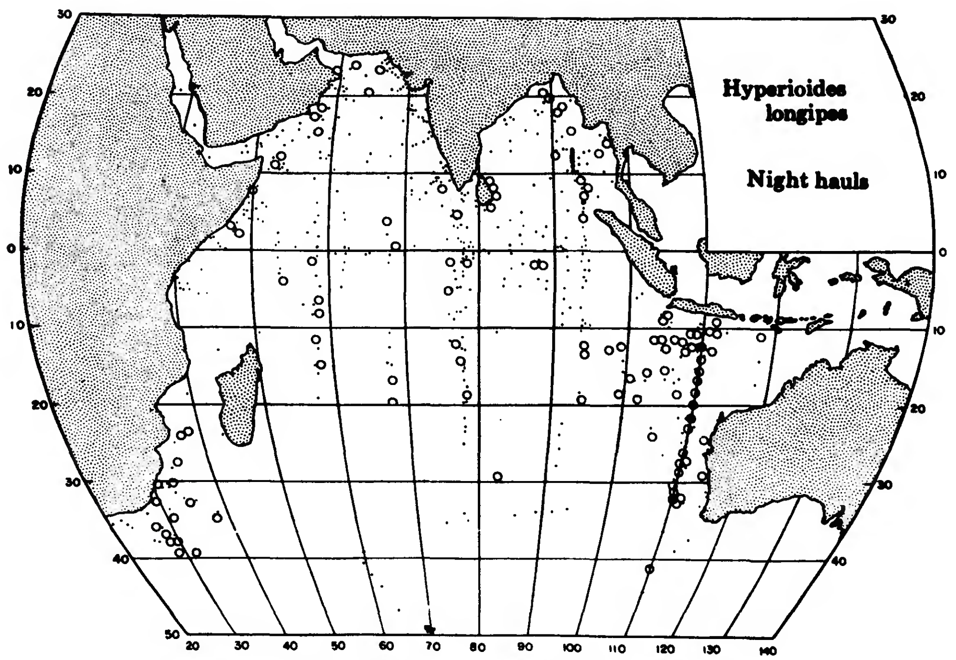

FIGURE 31.—*Hyperioides longipes*, night stations.

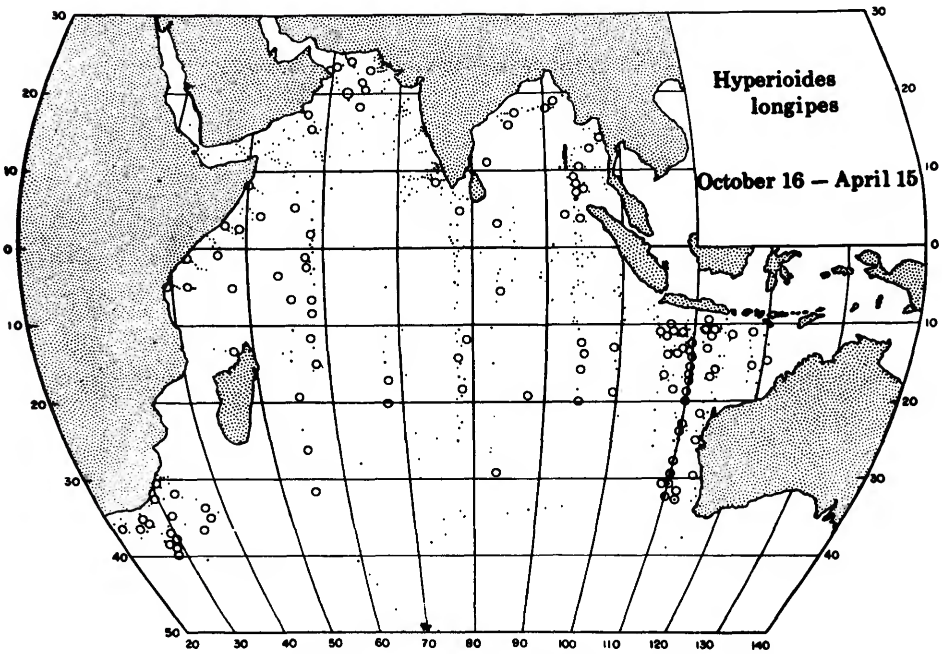

FIGURE 32.—*Hyperioides longipes*, NE monsoon.

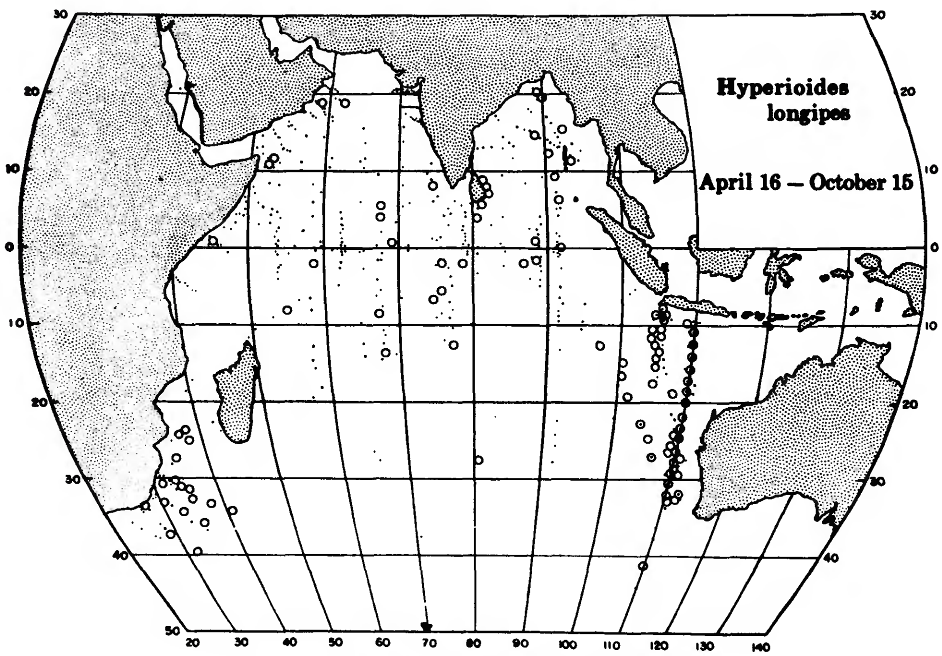

FIGURE 33.—*Hyperioides longipes*, SW monsoon.

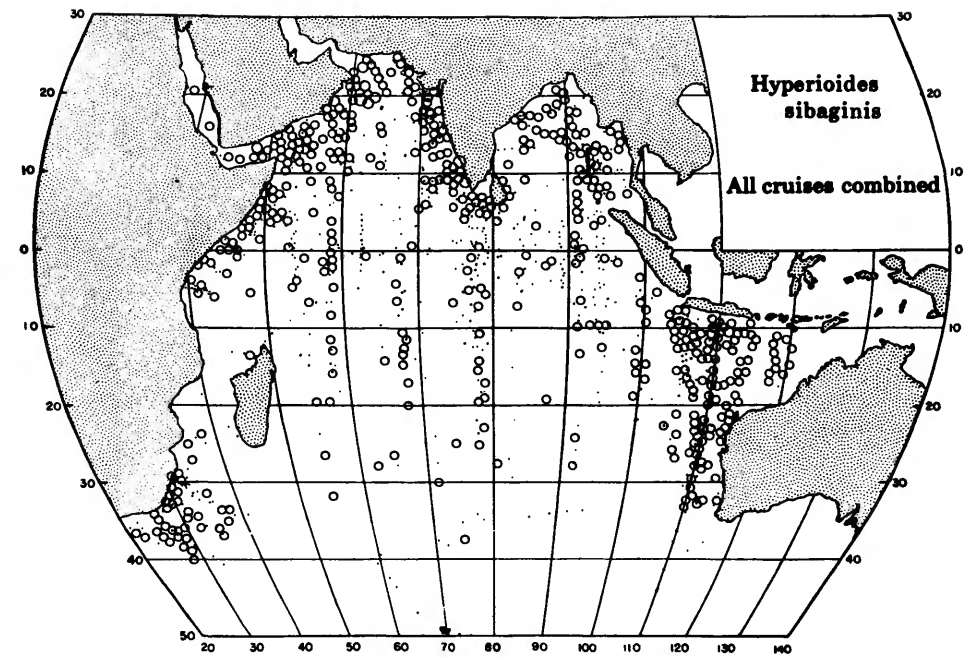

FIGURE 34.—*Hyperioides sibaginis*, all IIOE samples.

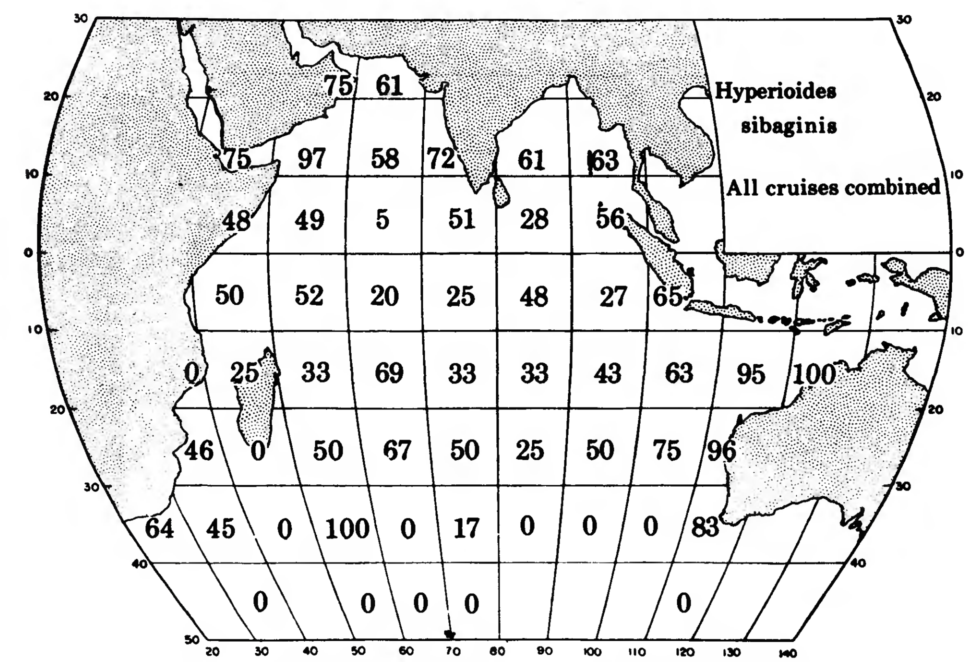

FIGURE 35.—*Hyperioides sibaginis*, percent occurrence for each 10° square.

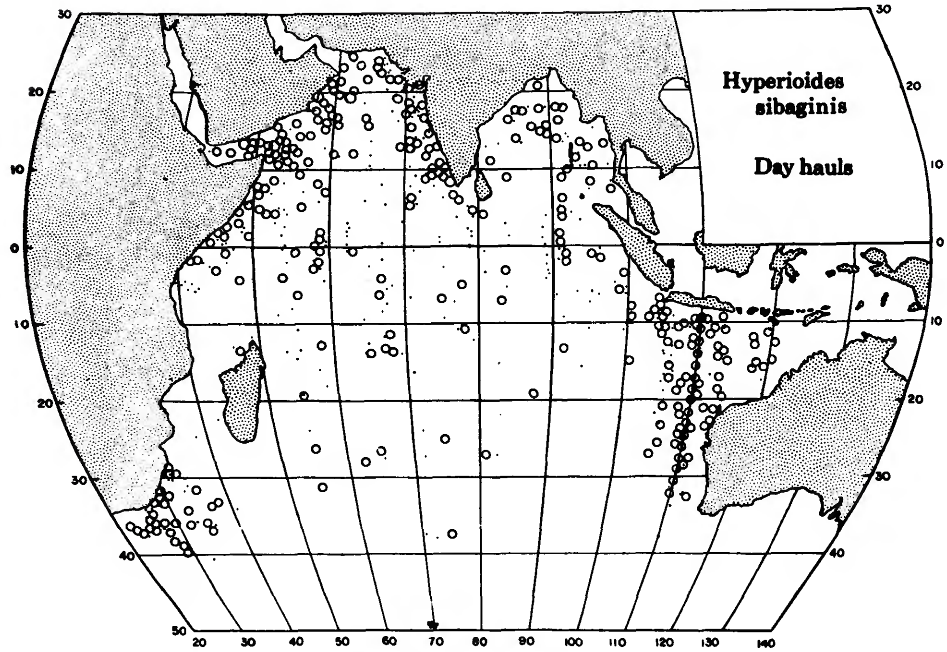

FIGURE 36.—*Hyperioides sibaginis*, day stations.

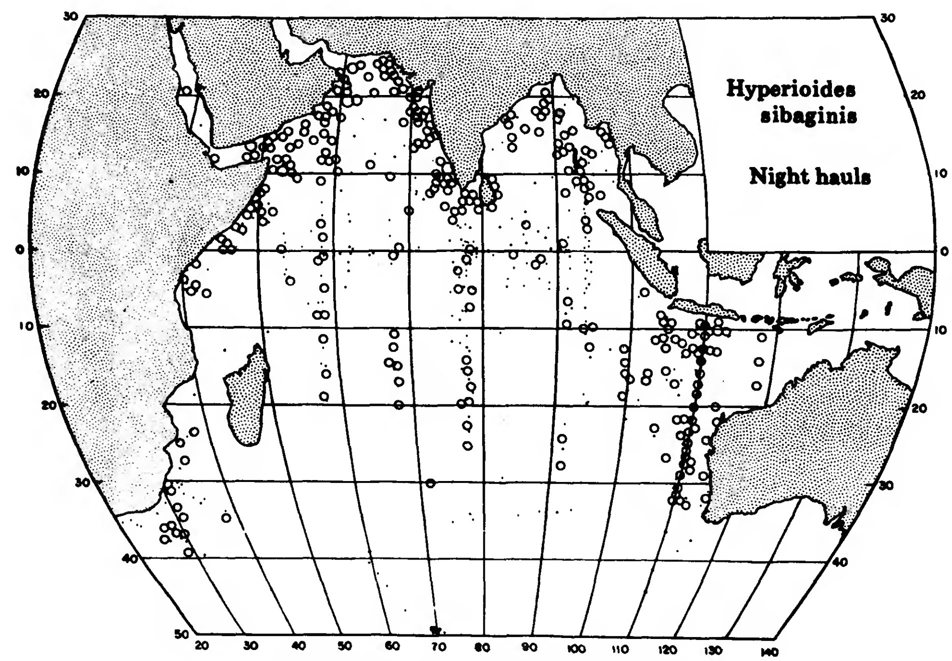

FIGURE 37.—*Hyperioides sibaginis*, night stations.

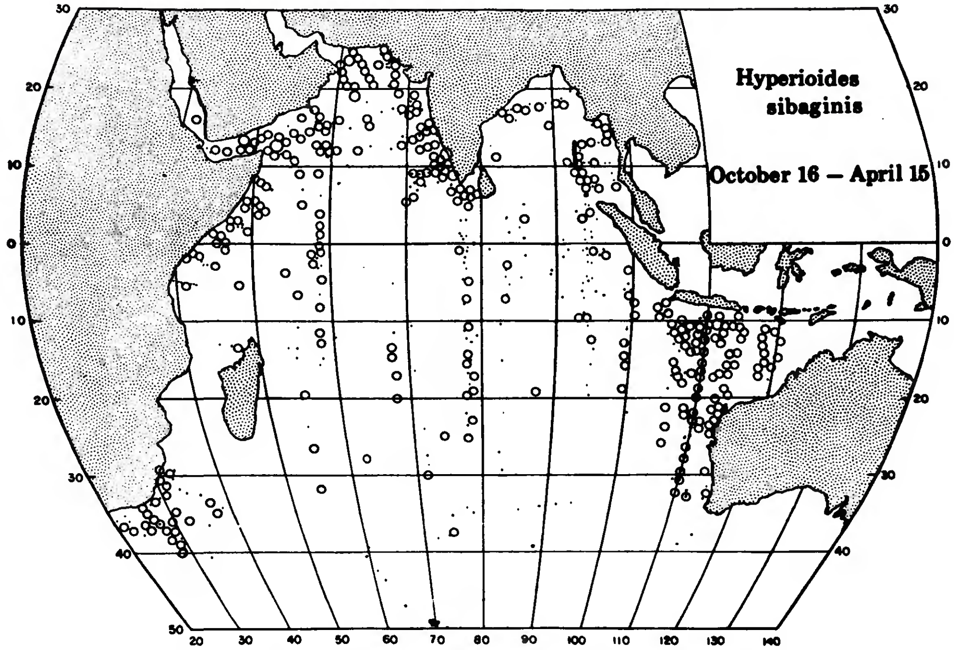

FIGURE 38.—*Hyperioides sibaginis*, NE monsoon.

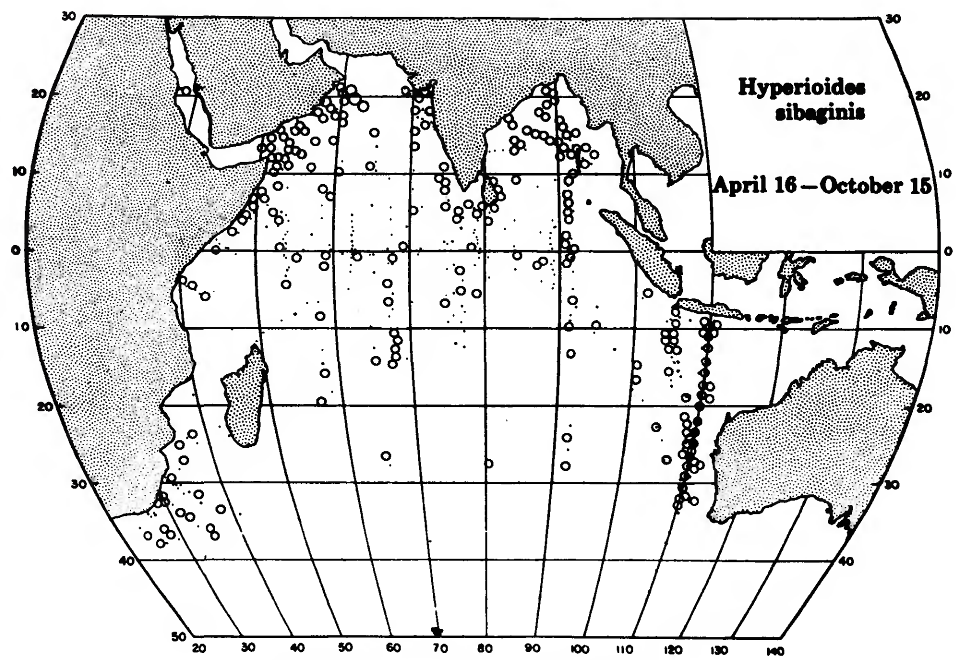

FIGURE 39.—*Hyperioides sibaginis*, SW monsoon.

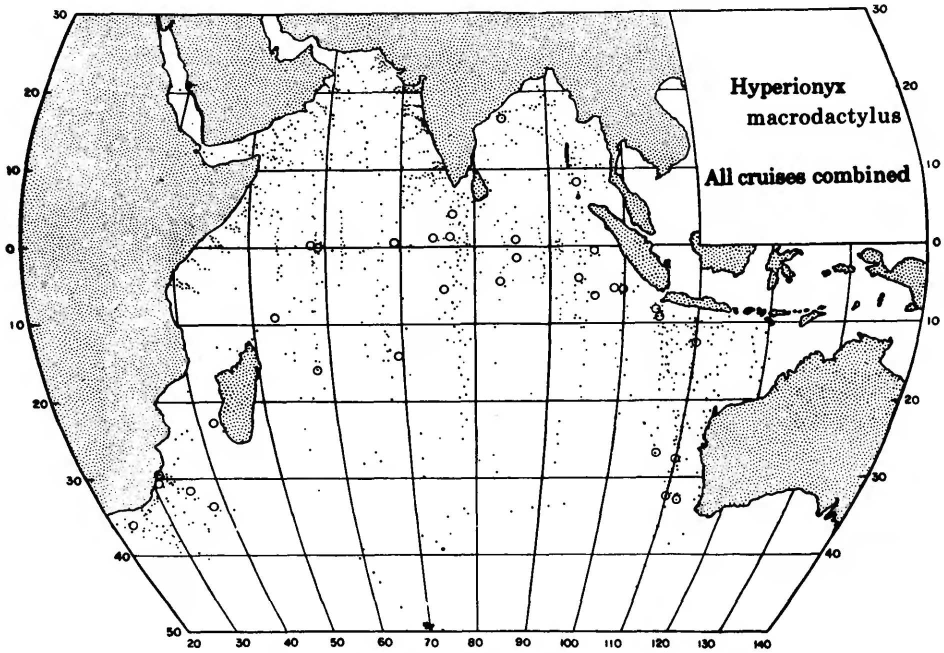

FIGURE 40.—*Hyperionyx macrodactylus*, all IIOE samples.

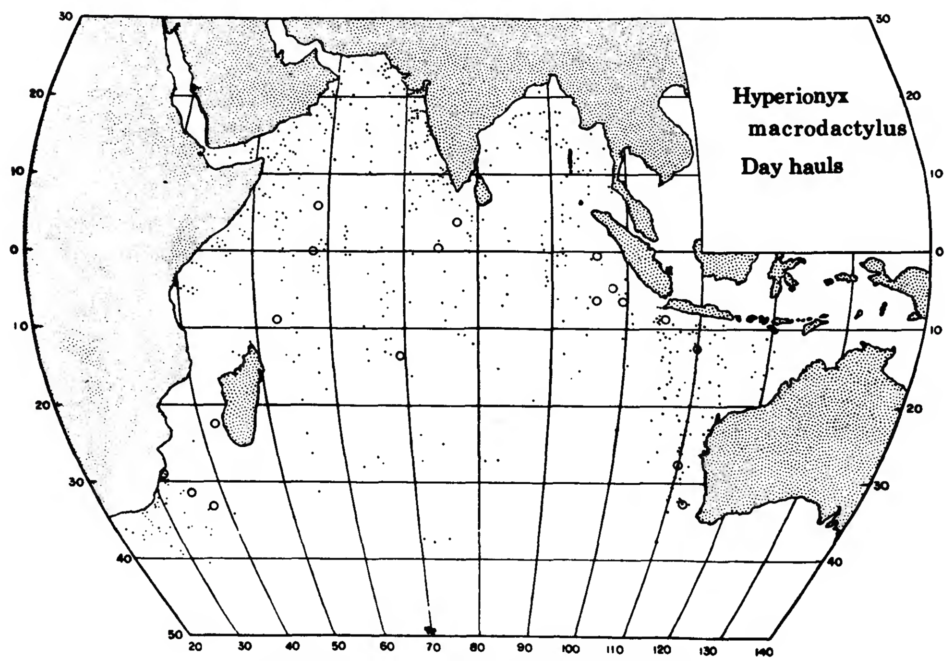

FIGURE 41.—*Hyperionyx macrodactylus*, day stations.

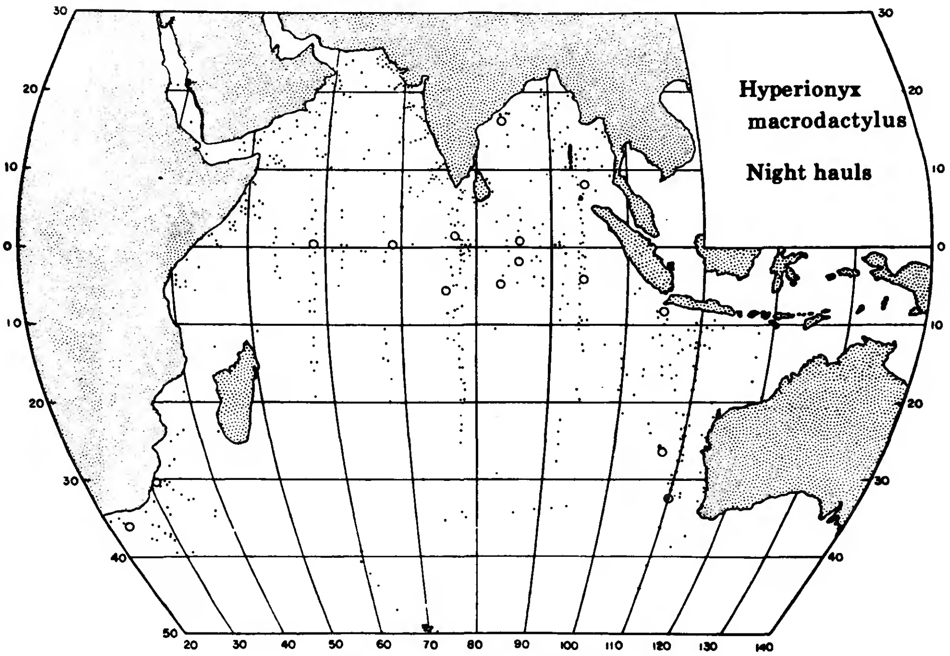

FIGURE 42.—*Hyperionyx macrodactylus*, night stations.

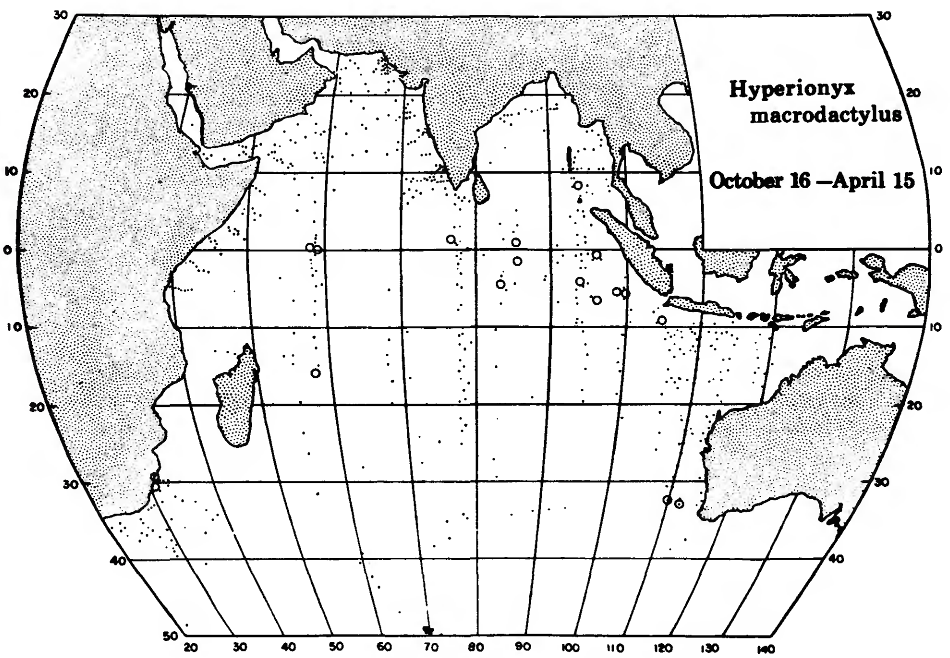

FIGURE 43.—*Hyperionyx macrodactylus*, NE monsoon.

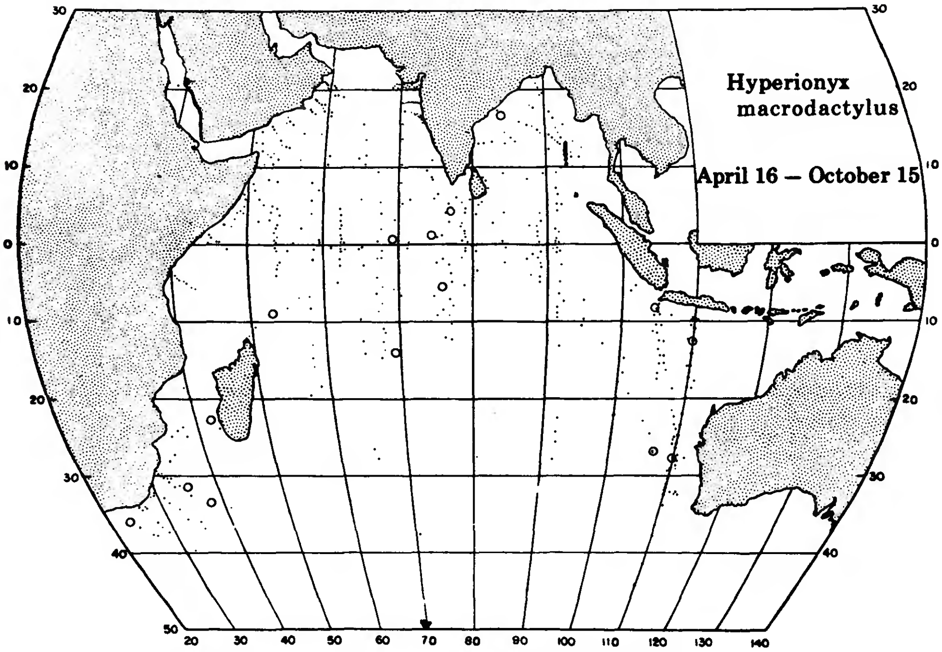

FIGURE 44.—*Hyperionyx macrodactylus*, SW monsoon.

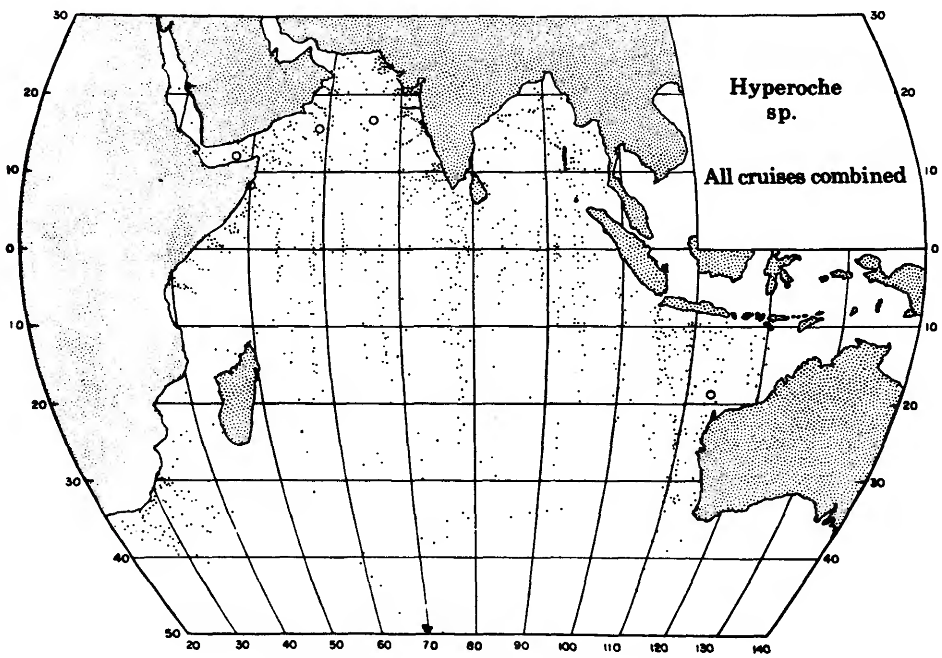

FIGURE 45.—*Hyperoche* sp., all IIOE samples.

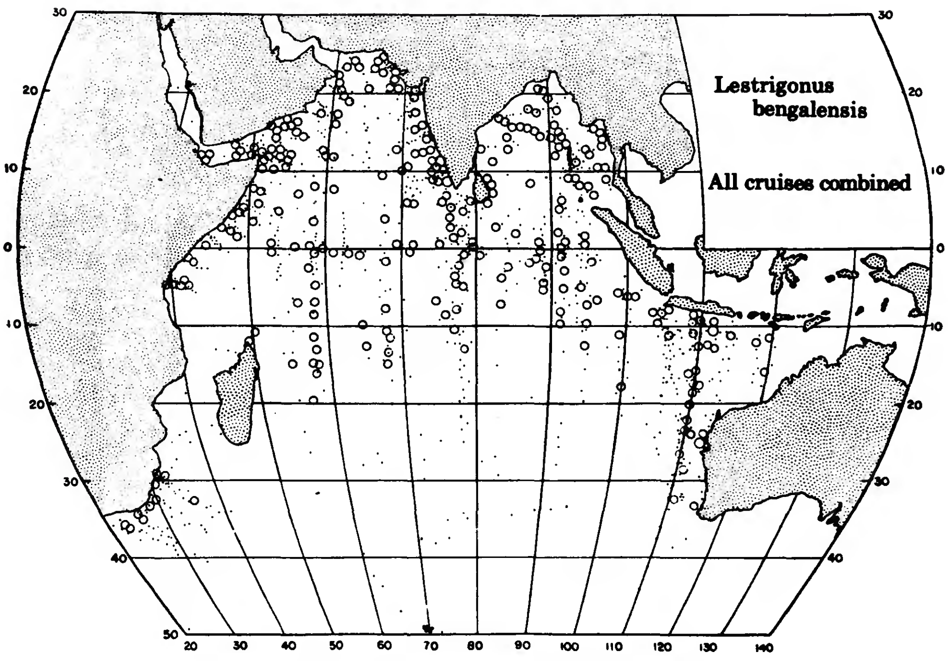

FIGURE 46.—*Lestrigonus bengalensis*, all IIOE samples.

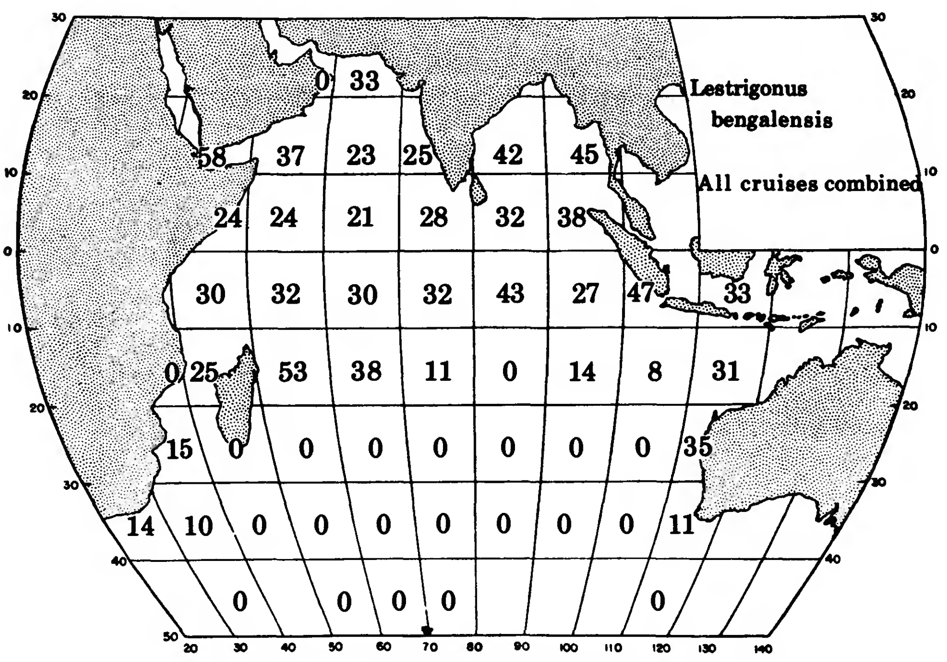

FIGURE 47.—*Lestrigonus bengalensis*, percent occurrence for each 10° square.

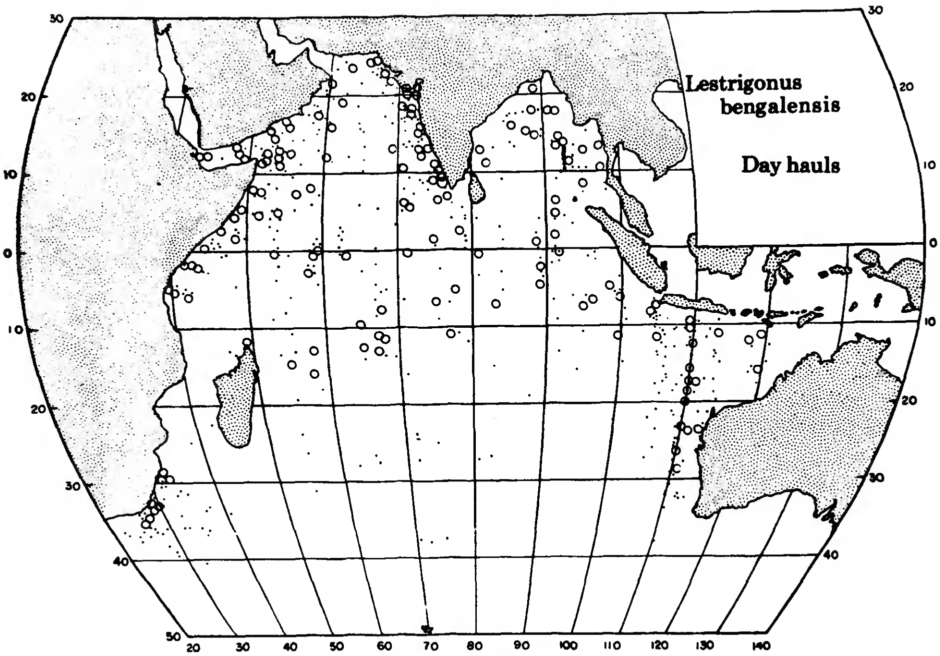

FIGURE 48.—*Lestrigonus bengalensis*, day stations.

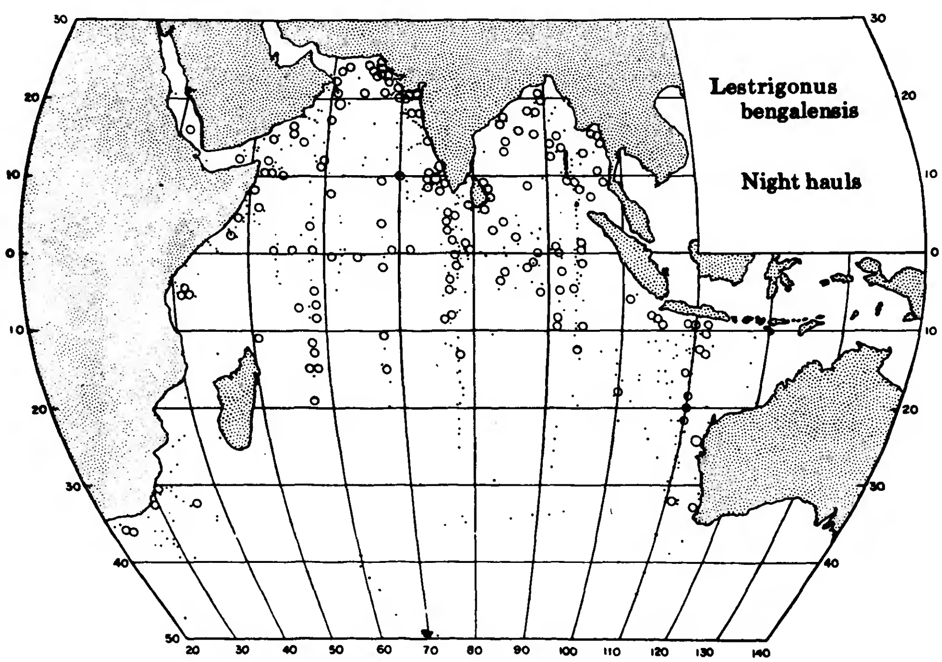

FIGURE 49.—*Lestrigonus bengalensis*, night stations.

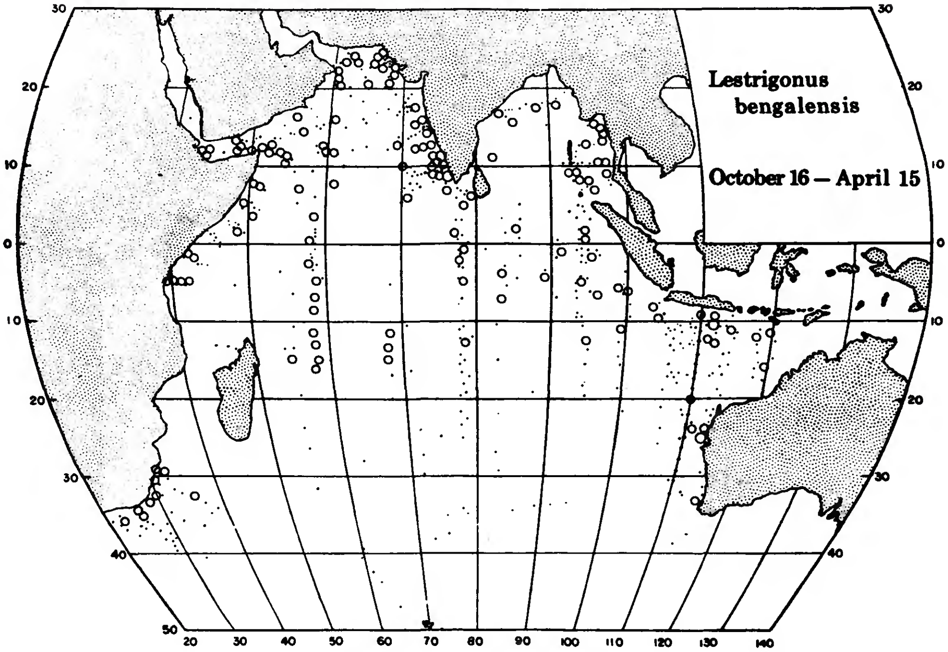

FIGURE 50.—*Lestrigonus bengalensis*, NE monsoon.

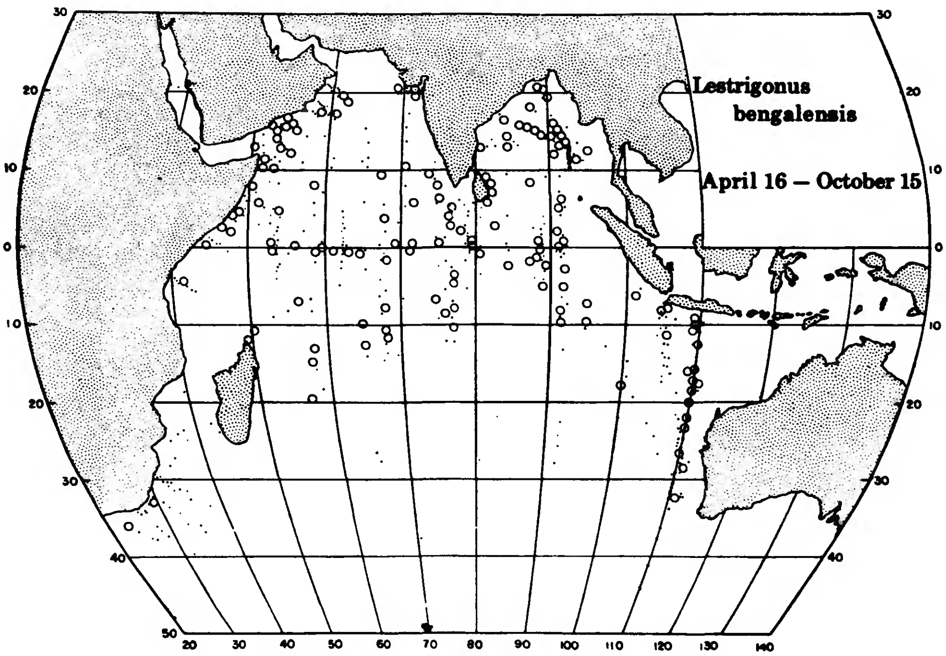

FIGURE 51.—*Lestrigonus bengalensis*, SW monsoon.

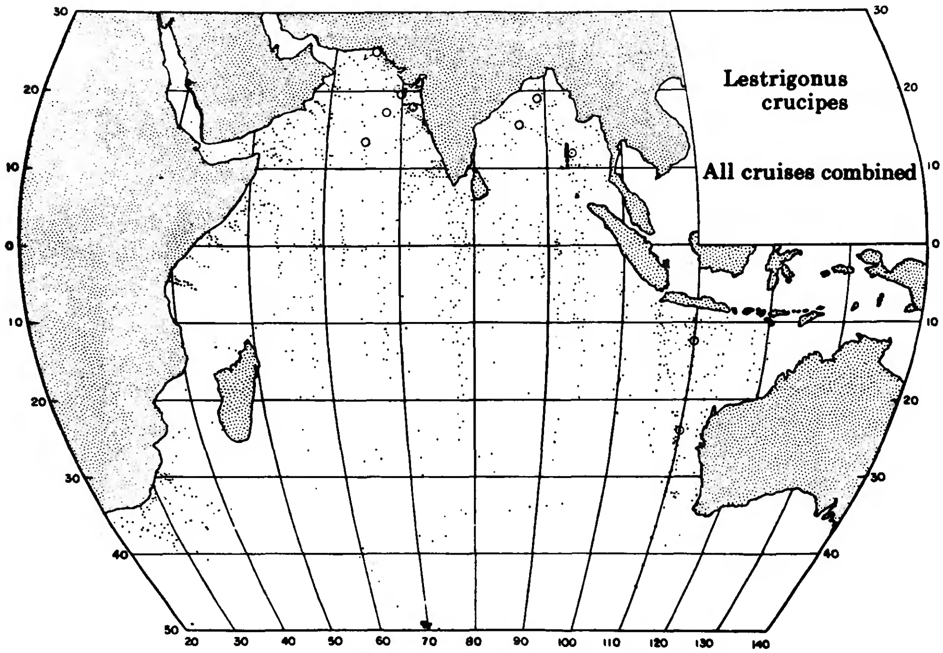

FIGURE 52.—*Lestrigonus crucipes*, all IIOE samples.

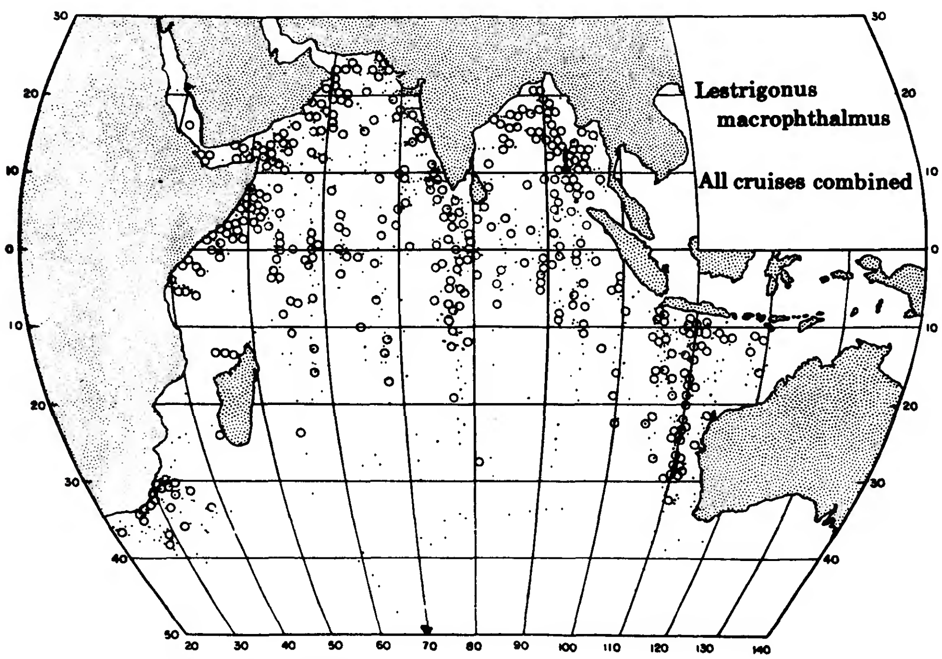

FIGURE 53.—*Lestrigonus macrophthalmus*, all IIOE samples.

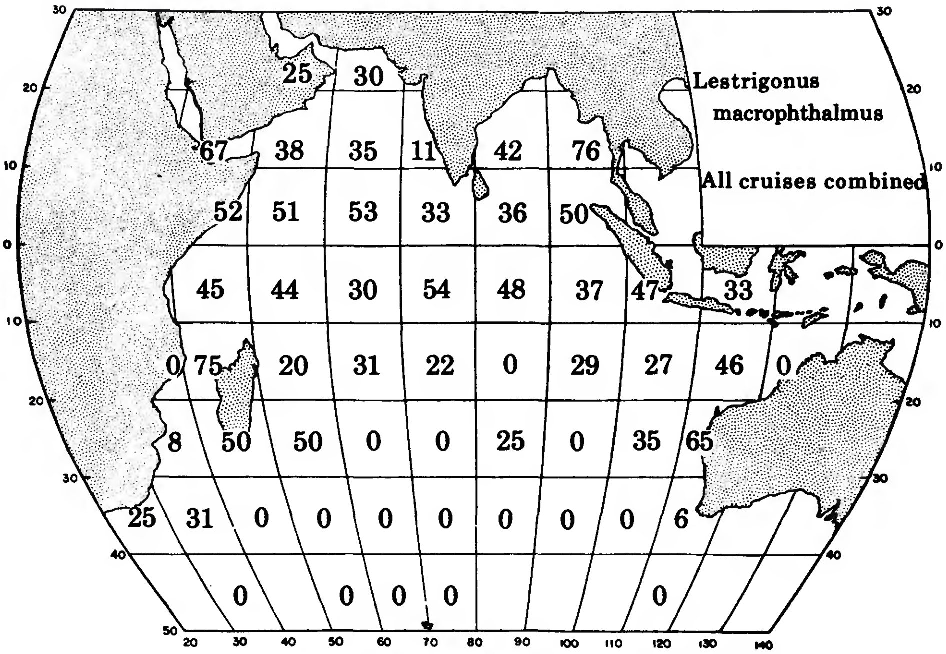

FIGURE 54.—*Lestrigonus macrophthalmus*, percent occurrence for each 10° square.

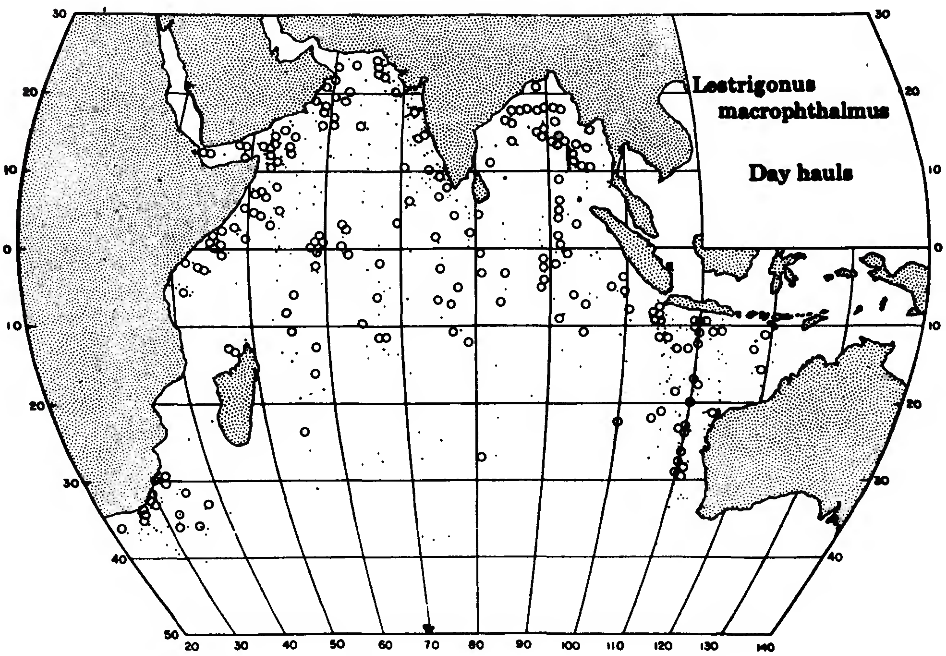

FIGURE 55.—*Lestrigonus macrophthalmus*, day stations.

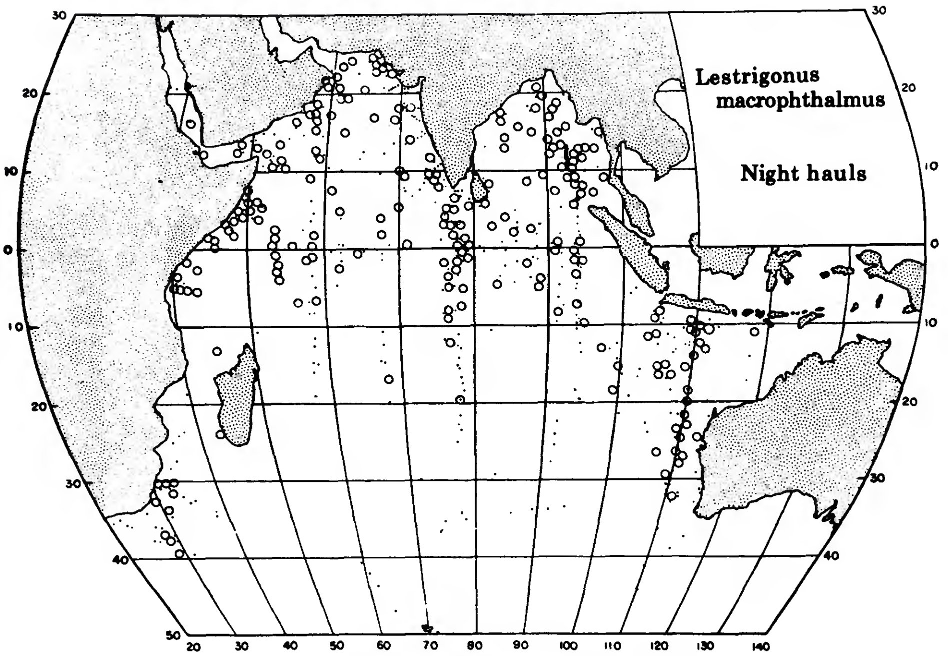

FIGURE 56.—*Lestrigonus macrophthalmus*, night stations.

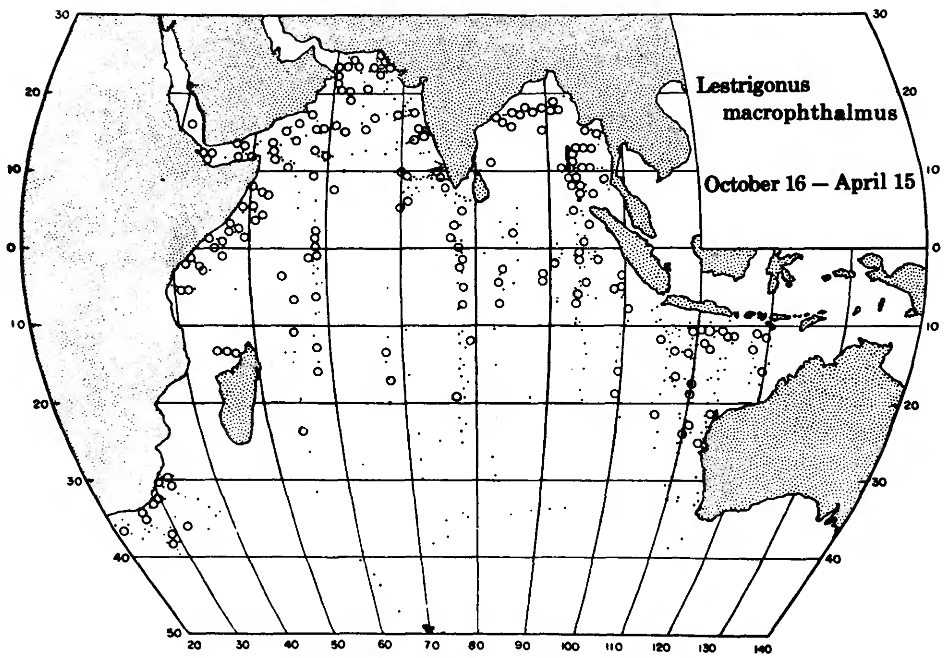

FIGURE 57.—*Lestrigonus macrophthalmus*, NE monsoon.

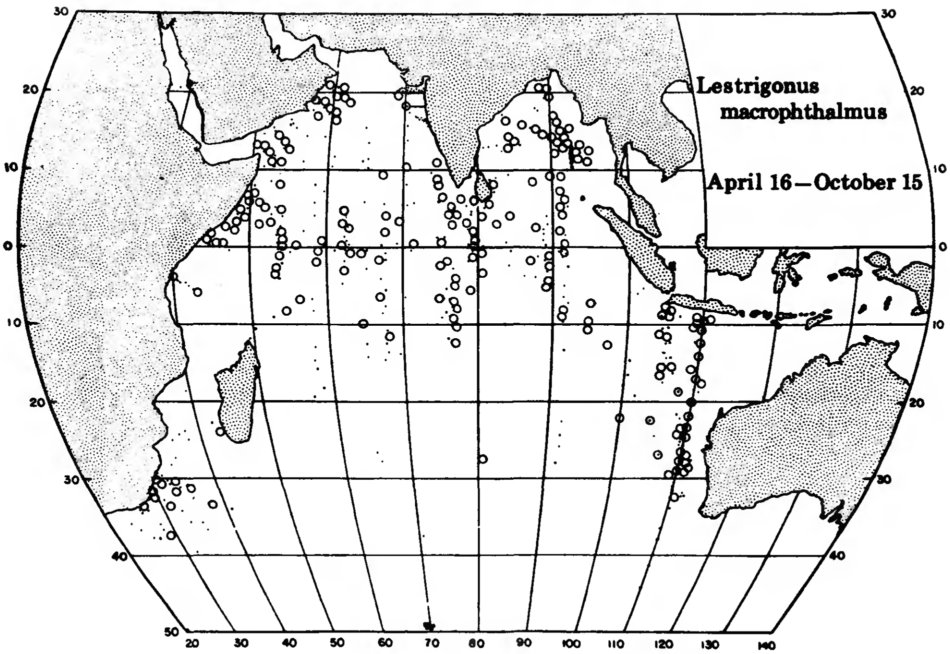

FIGURE 58.—*Lestrigonus macrophthalmus*, SW monsoon.

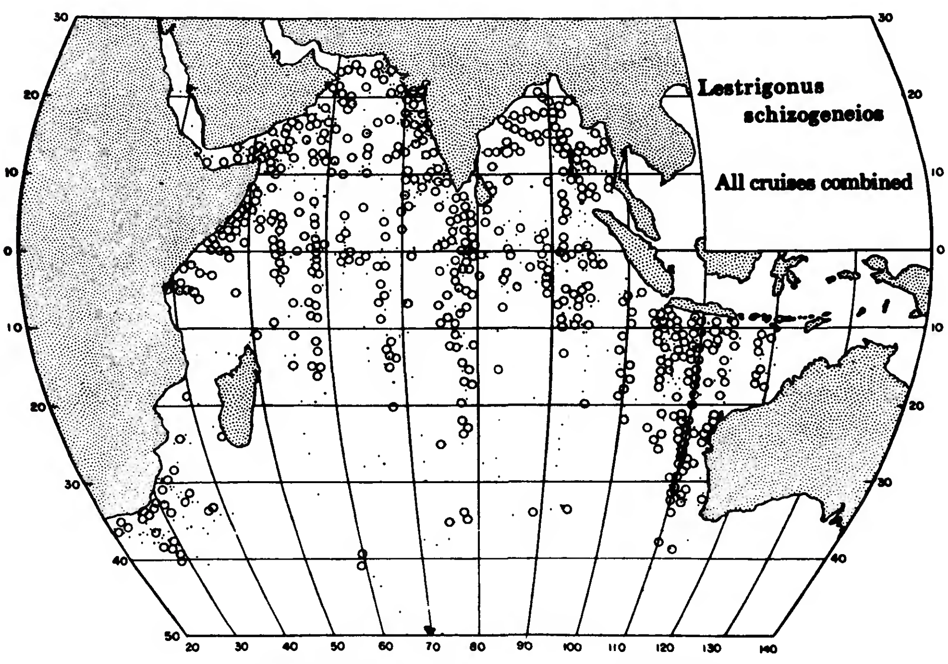

FIGURE 59.—*Lestrigonus schizogeneios*, all IIOE samples.

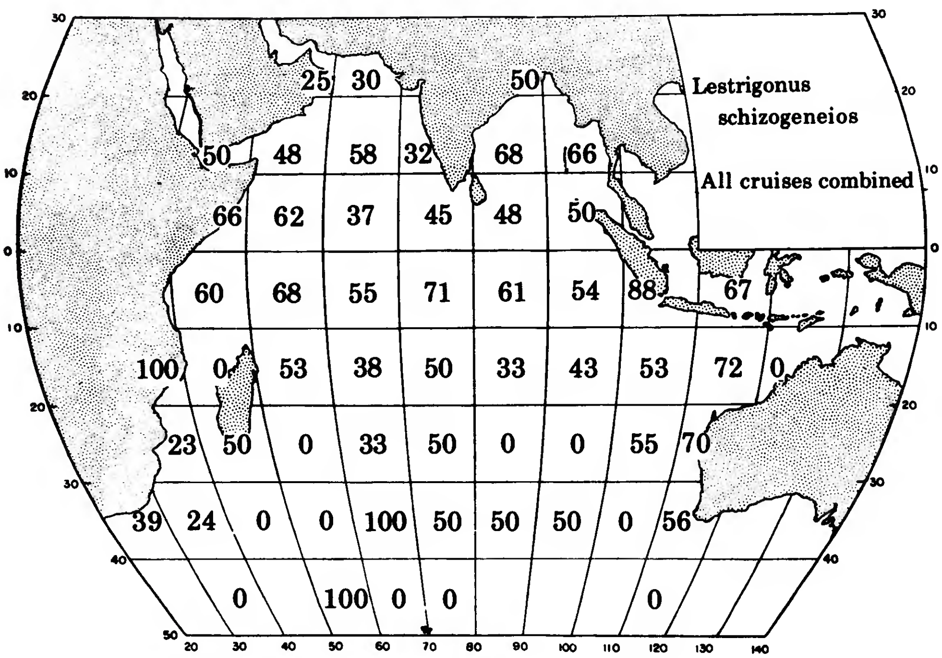

FIGURE 60.—*Lestrigonus schizogeneios*, percent occurrence for each 10° square.

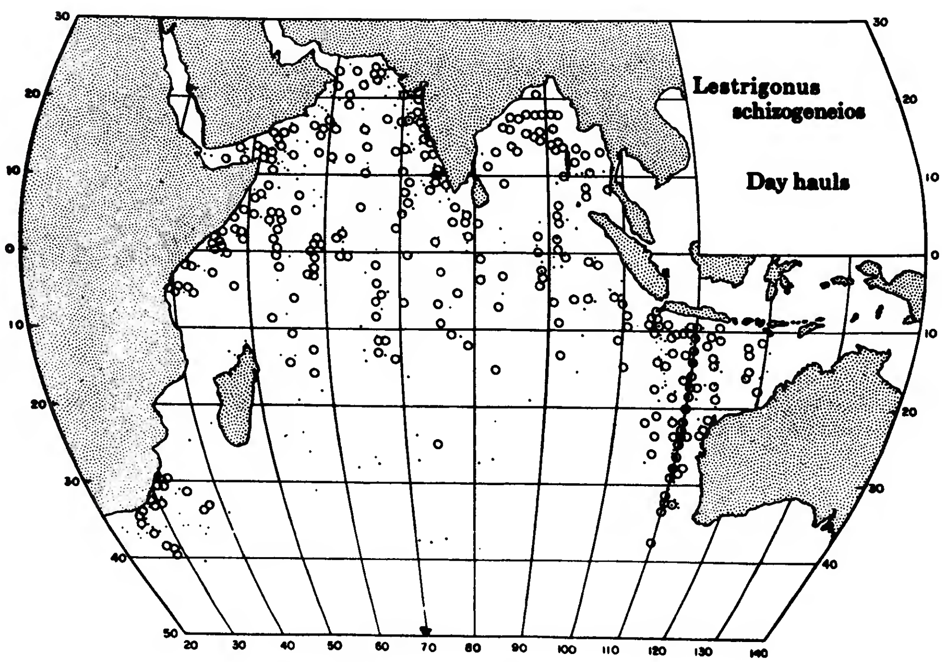

FIGURE 61.—*Lestrigonus schizogeneios*, day stations.

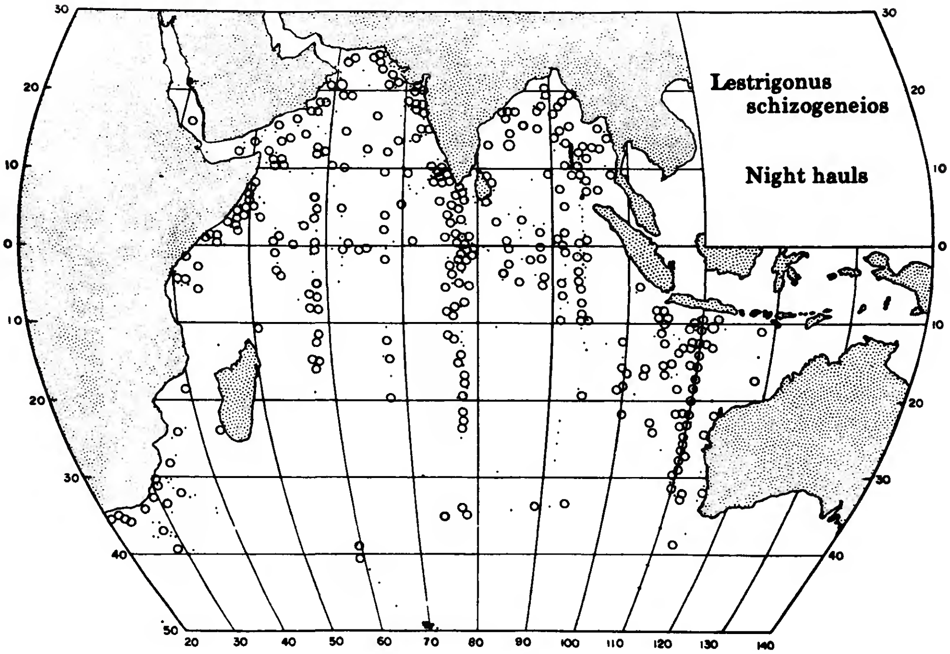

FIGURE 62.—*Lestrigonus schizogeneios*, night stations.

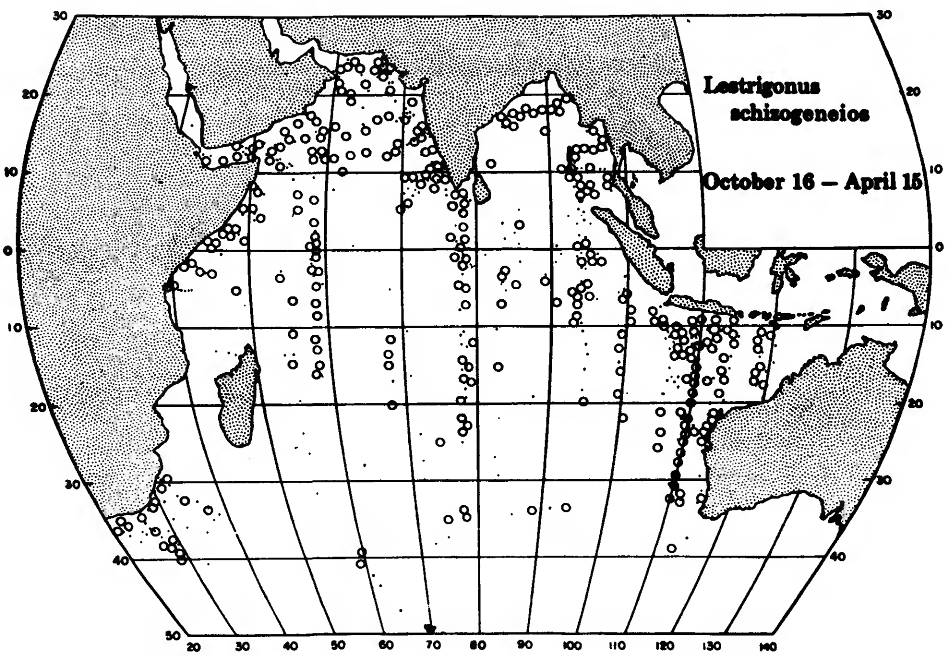

FIGURE 63.—*Lestrigonus schizogeneios*, NE monsoon.

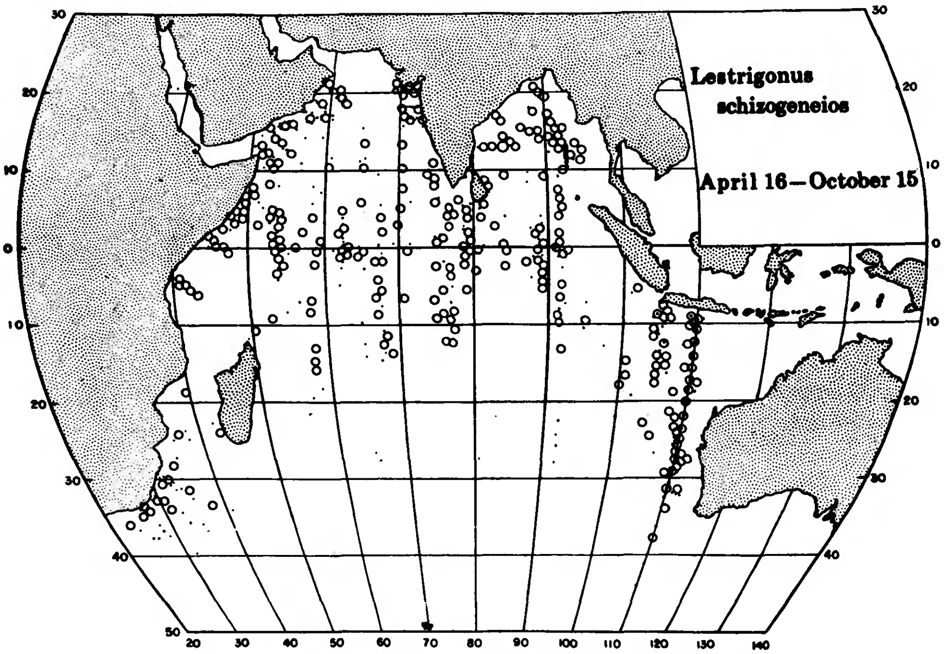

FIGURE 64.—*Lestrigonus schizogeneios*, SW monsoon.

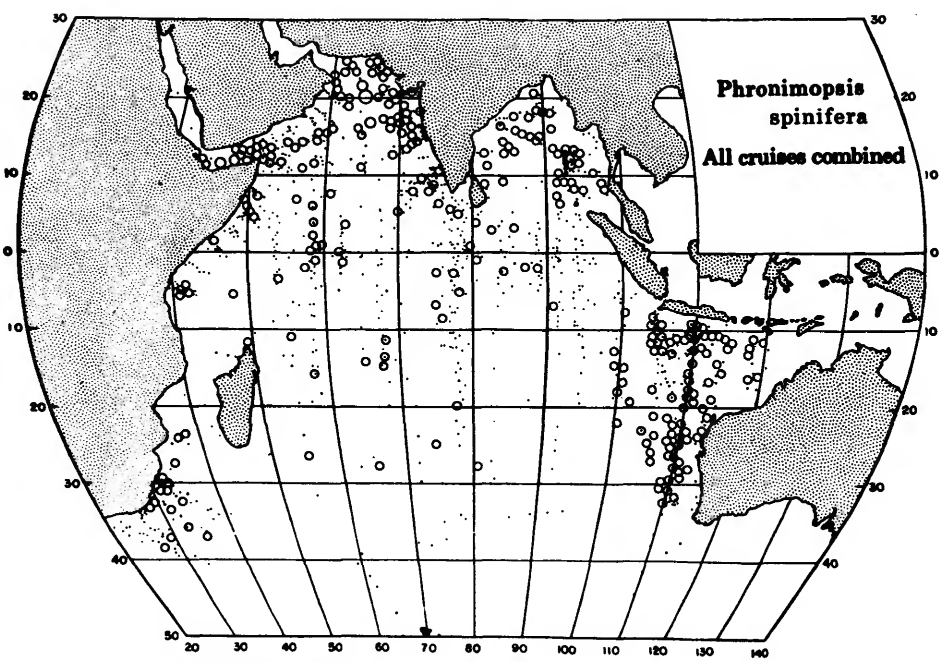

FIGURE 65.—*Phronimopsis spinifer*, all IIOE samples.

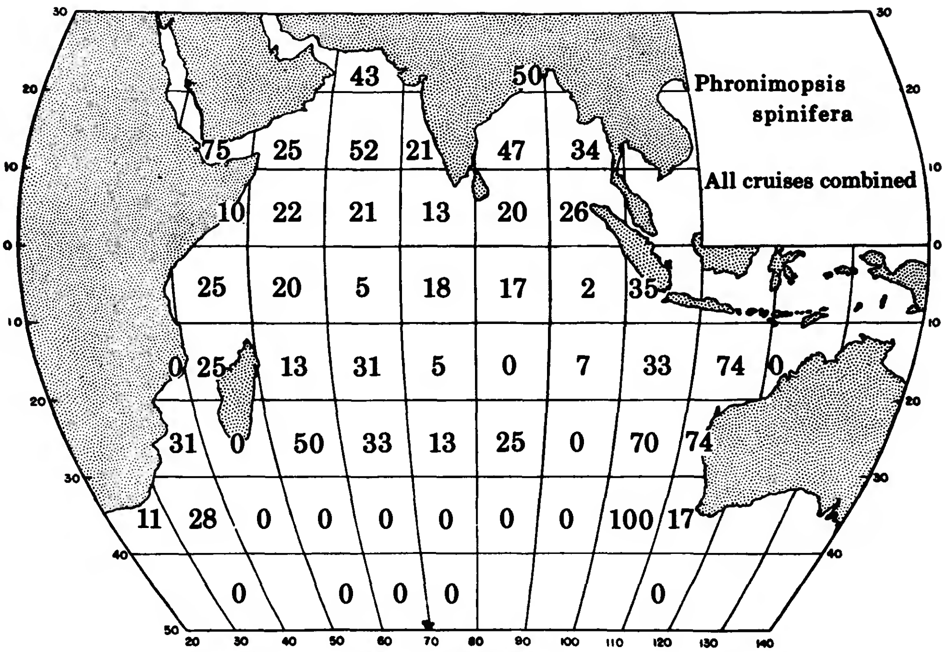

FIGURE 66.—*Phronimopsis spinifer*, percent occurrence for each 10° square.

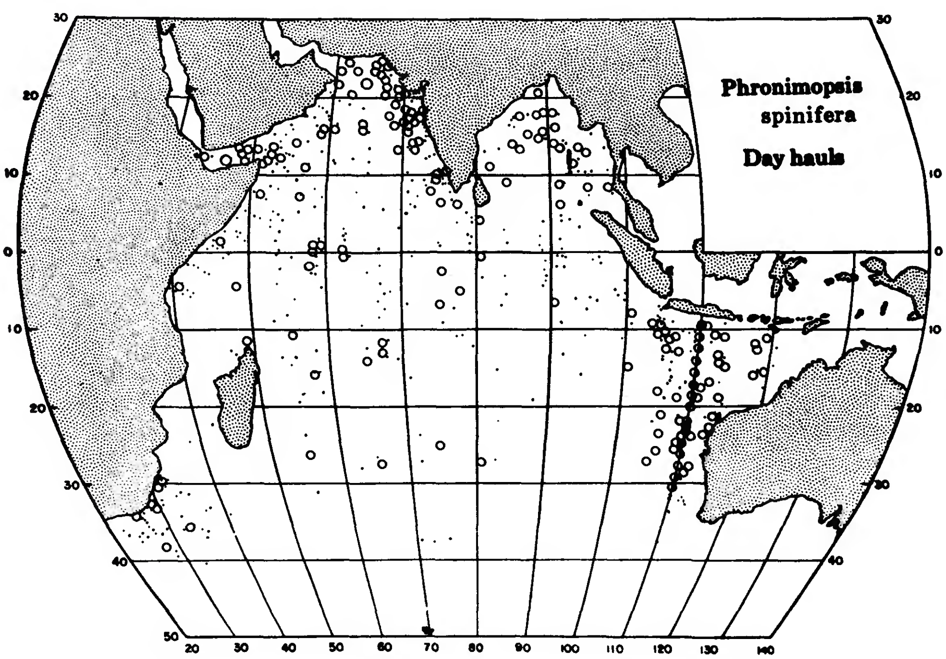

FIGURE 67.—*Phronimopsis spinifer*, day stations.

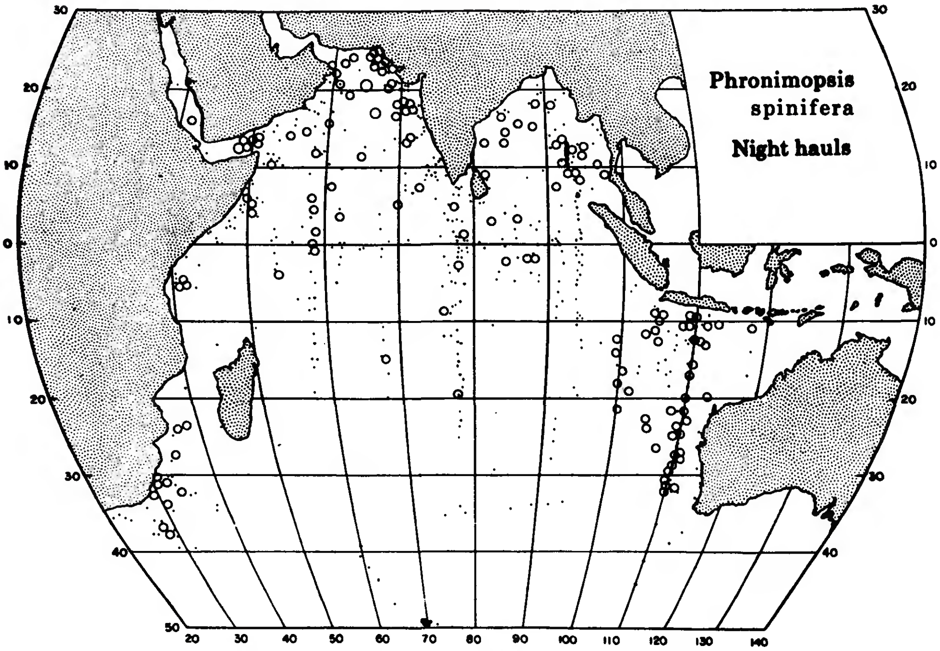

FIGURE 68.—*Phronimopsis spinifer*, night stations.

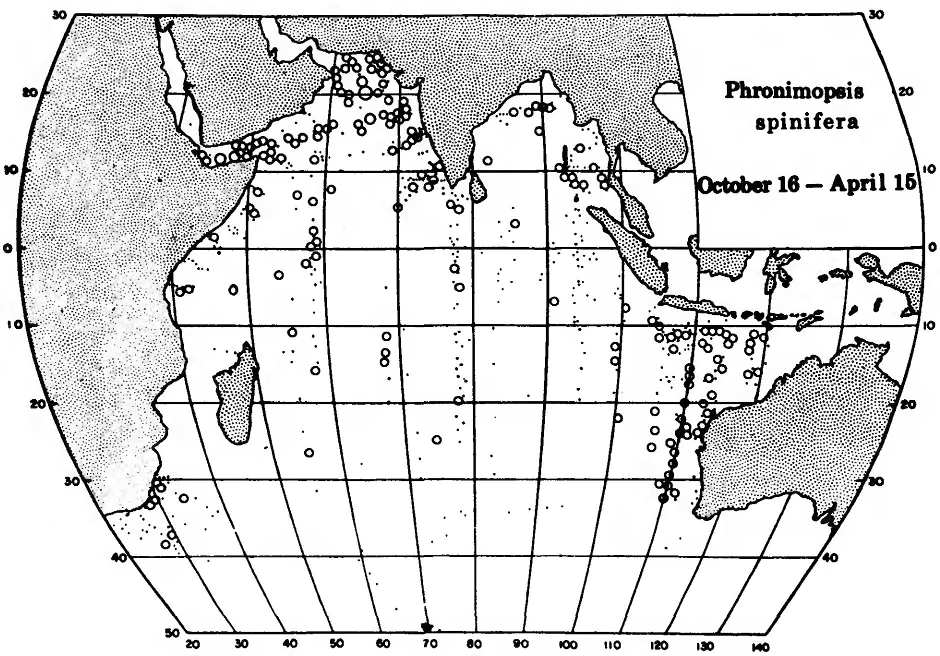

FIGURE 69.—*Phronimopsis spinifer*, NE monsoon.

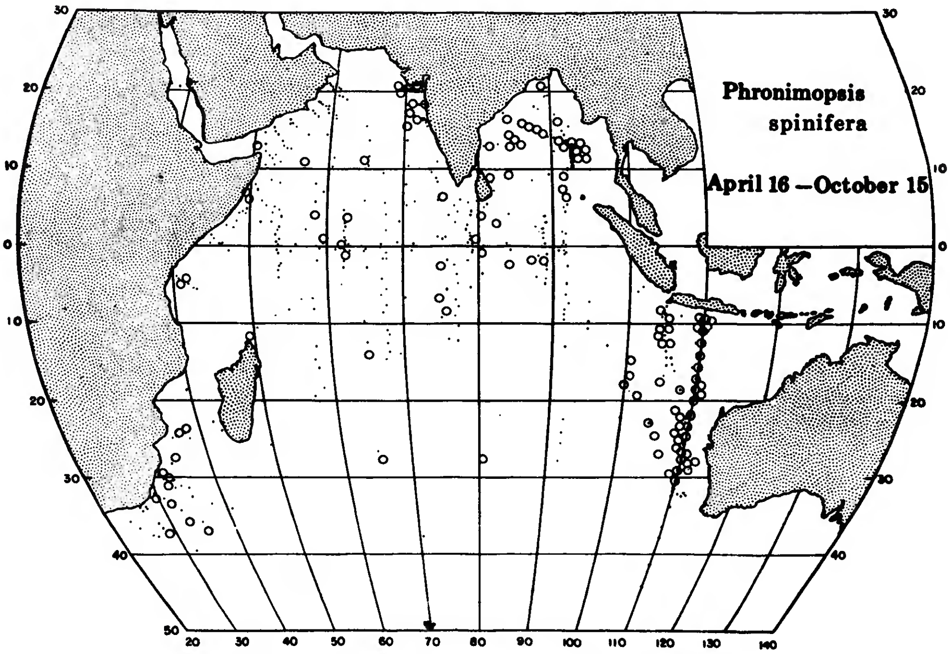

FIGURE 70.—*Phronimopsis spinifer*, SW monsoon.

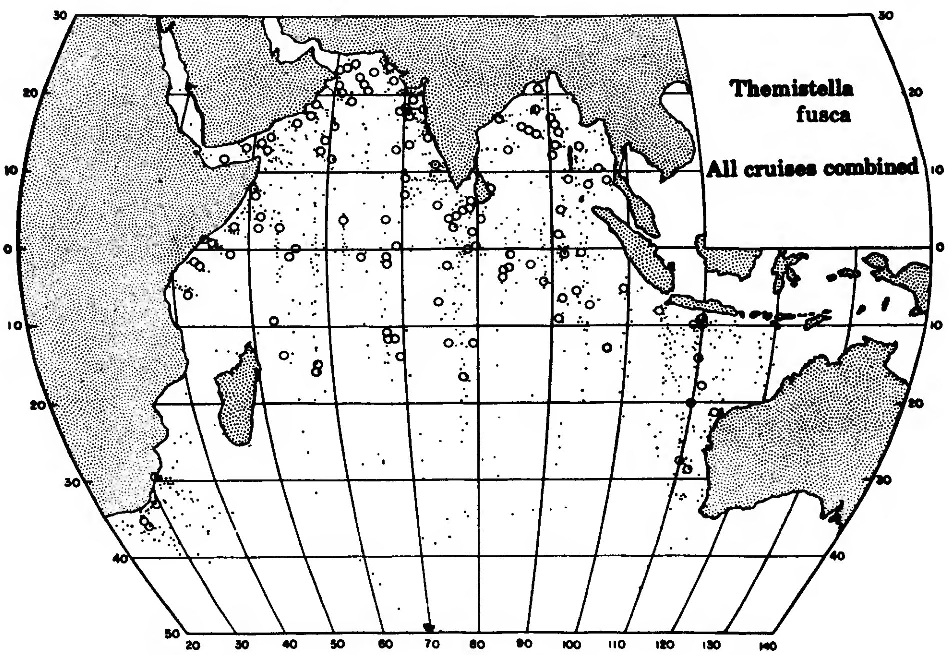

FIGURE 71.—*Themistella fusca*, all IIOE samples.

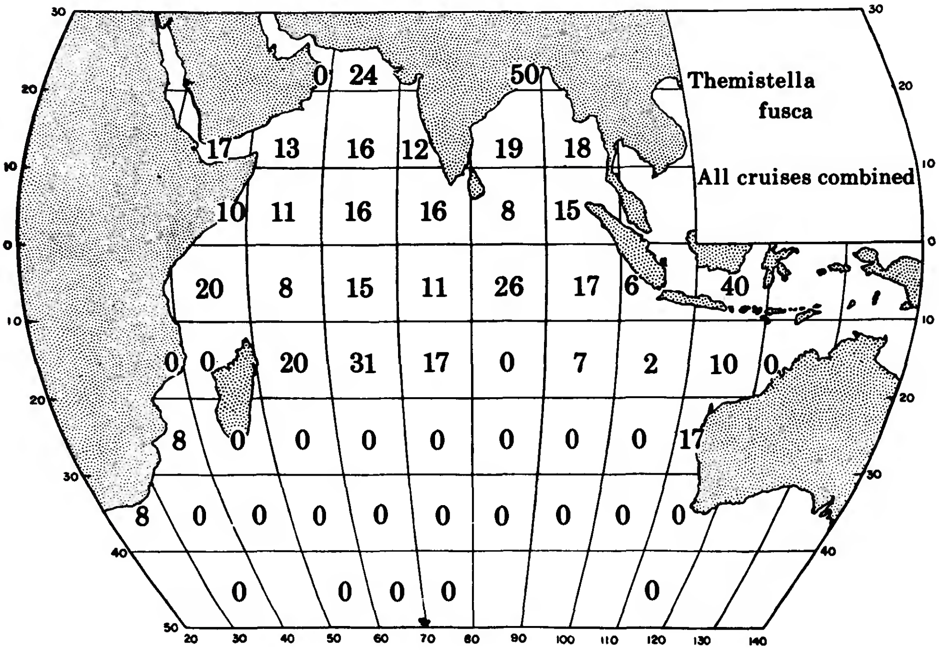

FIGURE 72.—*Themistella fusca*, percent occurrence for each 10° square.

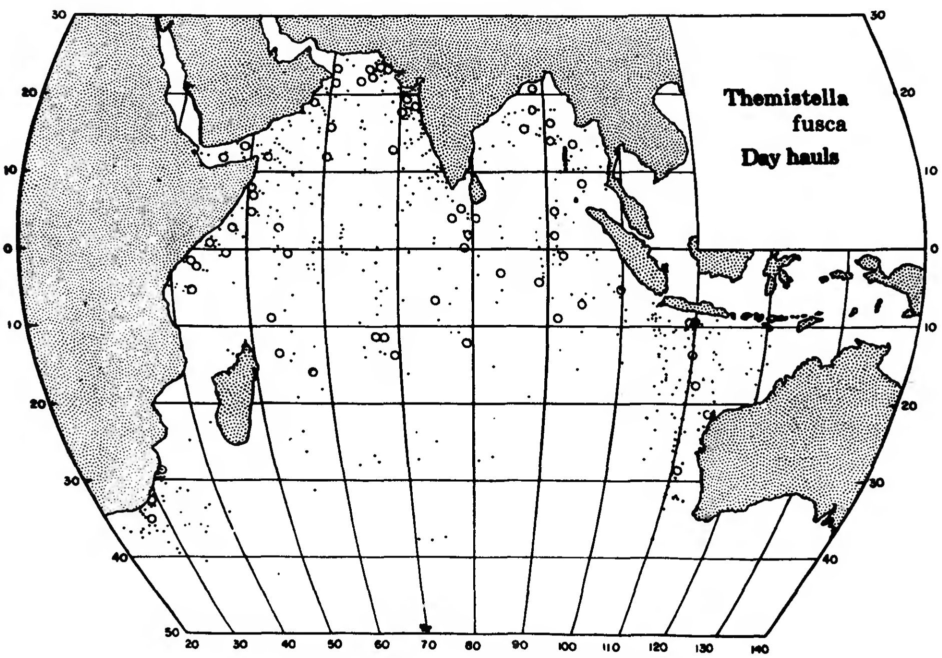

FIGURE 73.—*Themistella fusca*, day stations.

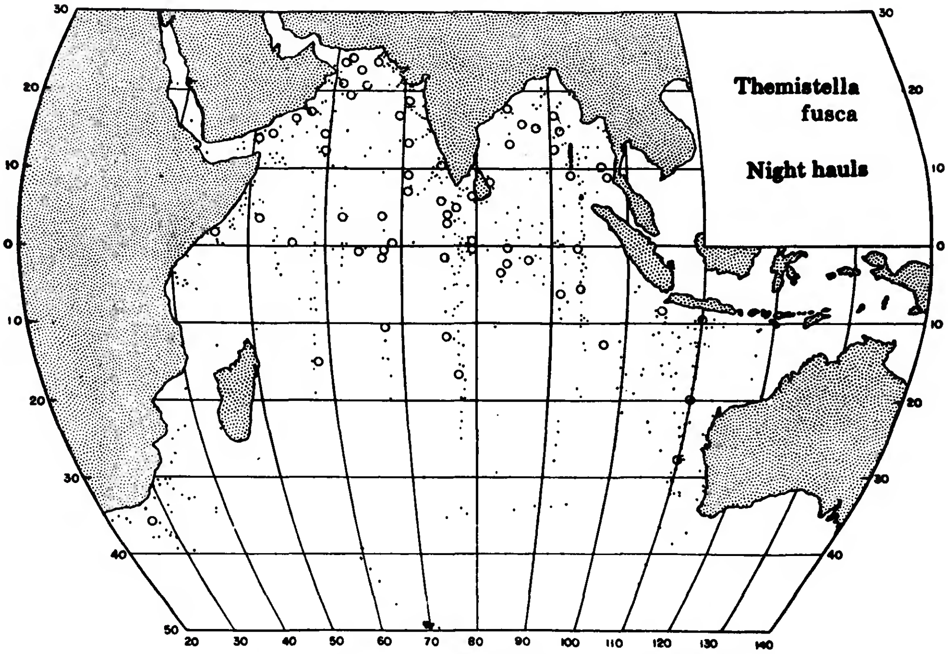

FIGURE 74.—*Themistella fusca*, night stations.

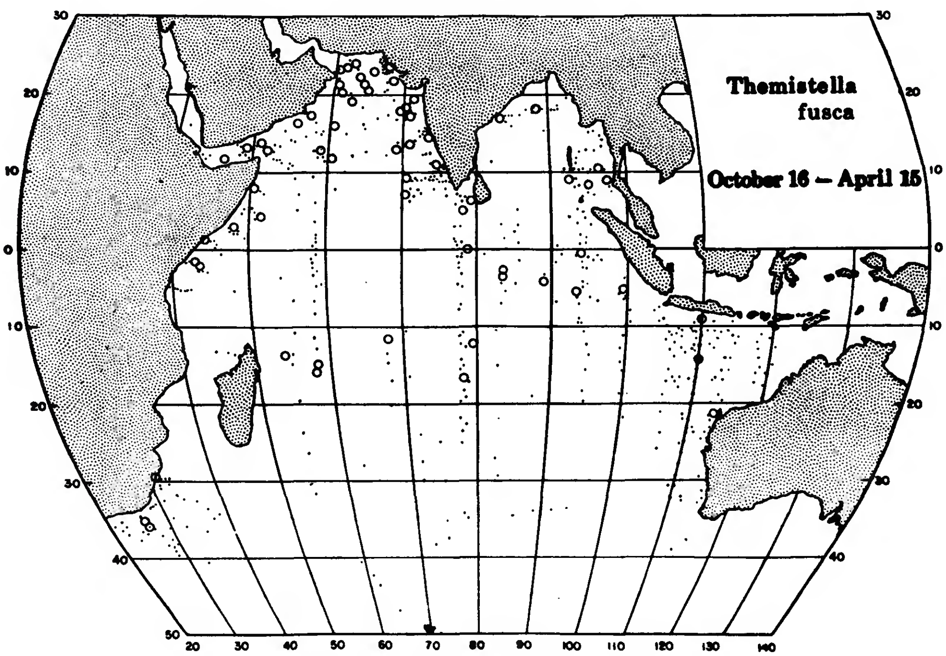

FIGURE 75.—*Themistella fusca*, NE monsoon.

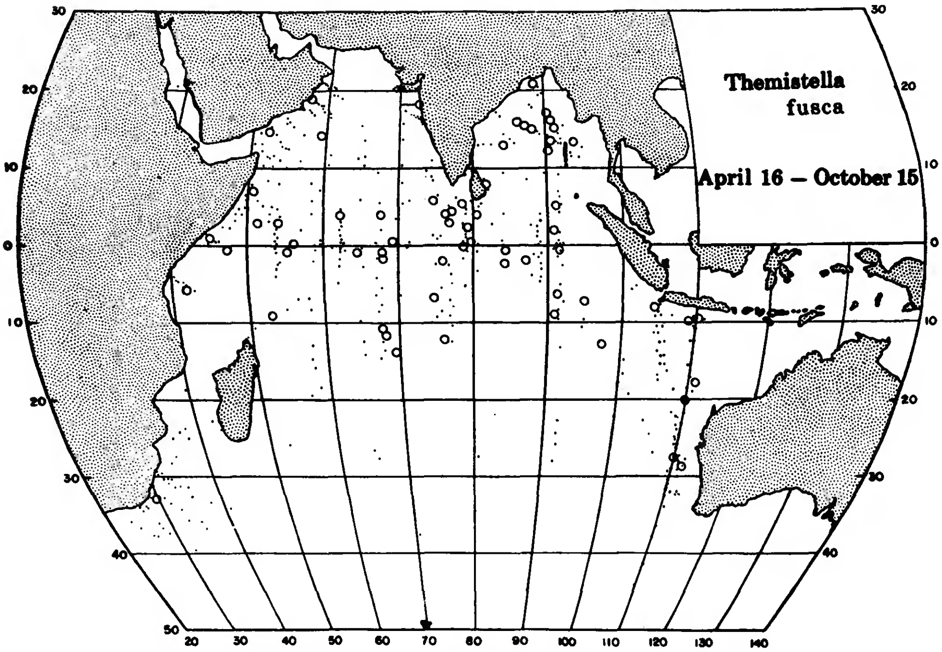

FIGURE 76.—*Themistella fusca*, SW monsoon.

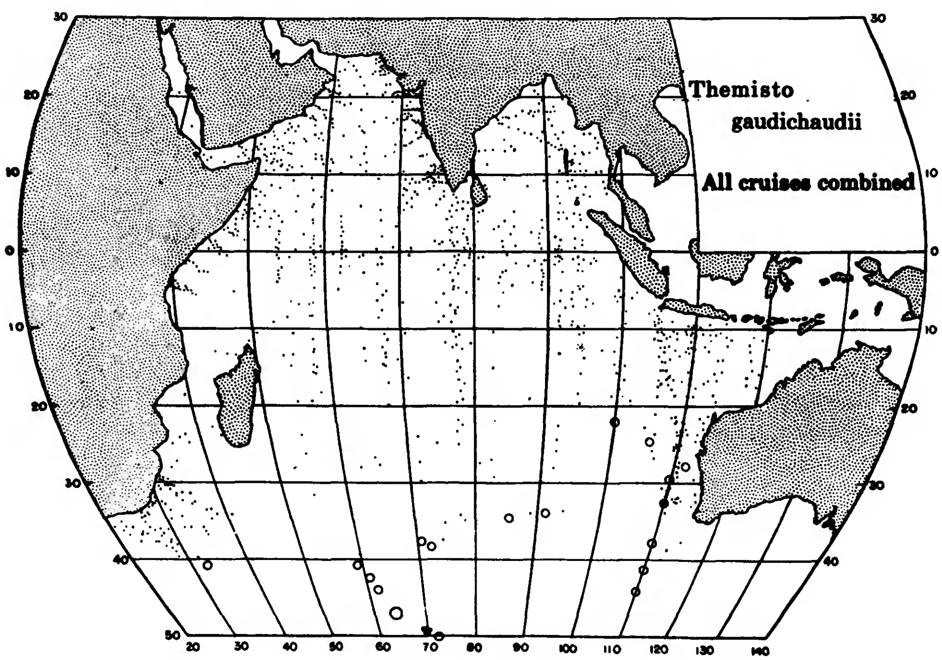

FIGURE 77.—*Themisto gaudichaudii*, all IIOE samples.

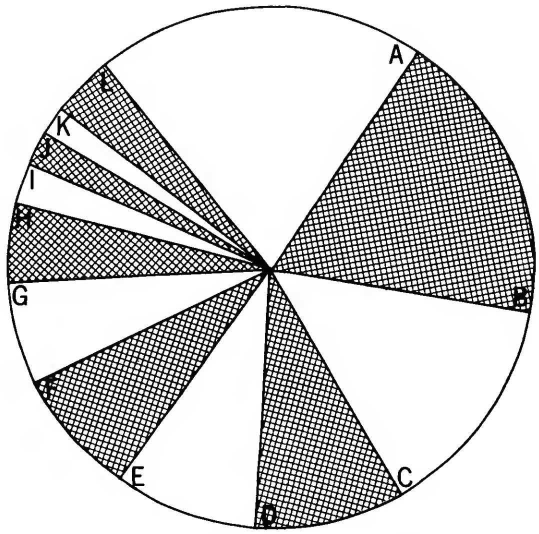

FIGURE 78.—Relative abundance of species of Hyperiidae, percent total specimens, all IIOE samples combined. A, *Hyperioides sibaginis*, 22.3%; B, *Lestrigonus schizogeneios*, 18.7%; C, *Phronimopsis spinifer*, 13.3%; D, *Lestrigonus macrophthalmus*, 9.4%; E, *Hyperietta vosseleri*, 9.2%; F, *Lestrigonus bengalensis*, 7.9%; G, *Hyperietta stephenseni*, 7.0%; H, *Hyperioides longipes*, 4.7%; I, *Themistella fusca*, 2.0%; J, *Themisto gaudichaudii*, 1.8%; K, *Hyperietta luzoni*, 1.7%; L, other species (*Hyperietta stebbingi*, *Hyperionyx macrodactylus*, *Lestrigonus bengalensis*, *Lestrigonus crucipes*, *Hyperoche* species), 2.0%.

specimens. Less abundant but still widespread were the species *Hyperietta vosseleri*, *H. stephenseni*, *Lestrigonus macrophthalmus*, *L. bengalensis*, *Phronimopsis spinifer*, and *Hyperioides longipes*. The remaining species were few in number, but also widely distributed. In general, as would be expected, the more abundant species occurred at more stations and appeared to be more widely distributed. Less abundant species were more likely to be absent from parts of the Indian Ocean. The fact that *Hyperietta luzoni* and *Hyperionyx macrodactylus* were not collected from the Arabian Sea does not prove that they do not occur there.

The number of specimens per sample varied greatly, from 1 to 350 (~ 1.75/m^3). Bar graphs of 7 size-classes of specimens per sample, given for 4 cruises (Figure 80), show a predominance of small samples, with the 1–10 class the largest.

None of the samples contained all 15 species of Hyperiidae, and it was unusual to find as many as 10 species. Figure 81 shows the number of species per sample for 6 cruises, excluding samples lacking Hyperiidae. Most samples contained 1–7 species.

Species groups were not detected. Co-occurrence of species (except *Hyperoche* species, was calculated according to the affinity index of Fager and McGowan (1963), and from the affinity indices a dendrogram (Figure 82) was constructed using Mountford's (1962) method. The dendrogram shows only that the more abundant a species, the greater the probability that it will occur with other species. As Laval (1980) observed, statistically derived associations between species of hyperiids are biologically meaningless because hyperiids are associated with their gelatinous hosts and not with other hyperiids. Associations between hyperiid species would be found only if they shared the same host. The known hosts of hyperiids are summarized by Laval (1980) except for the genus *Hyperia*, for which they are listed by Thurston (1977). A good beginning has been made in identifying hosts, mostly in the Atlantic Ocean, but most of the hosts and the degree of host specificity remain unknown. Of the Indian Ocean Hyperiidae, species of *Lestrigonus* are asso-

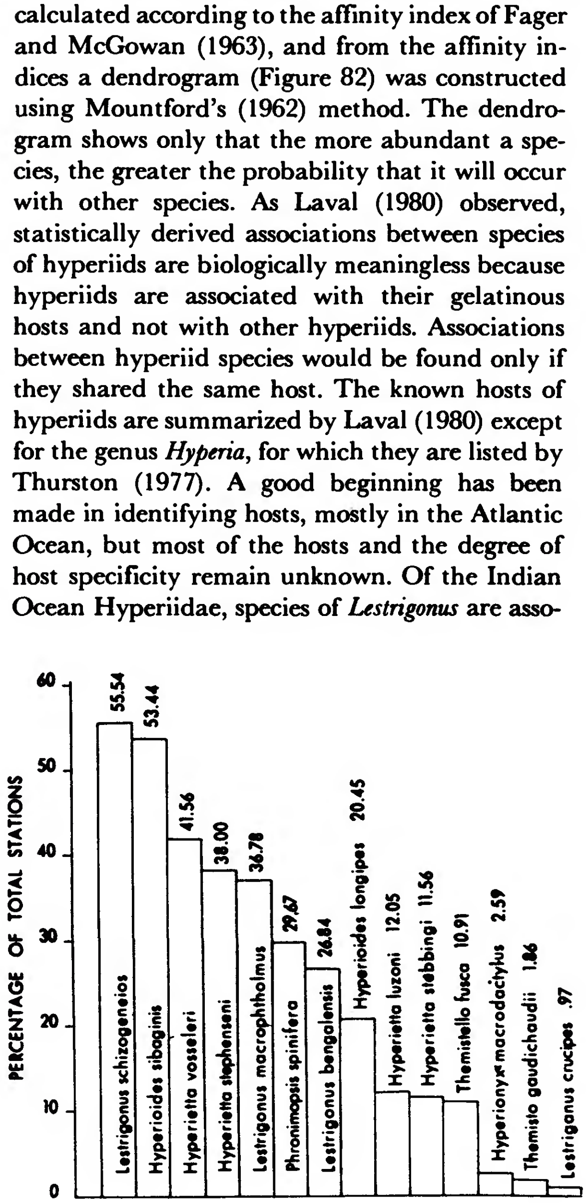

FIGURE 79.—Frequency of occurrence of species of Hyperiidae (percent of total IIOE stations at which each species occurred).

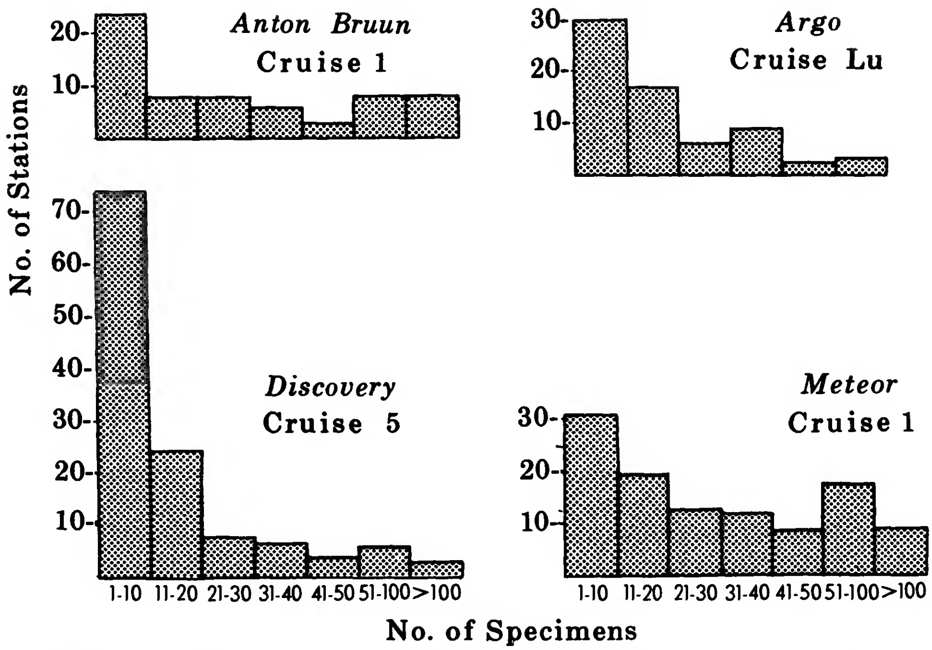

FIGURE 80.—Distribution of number of specimens of Hyperiidae per station (~2 × number of specimens per 100 m³) for 4 IIOE cruises.

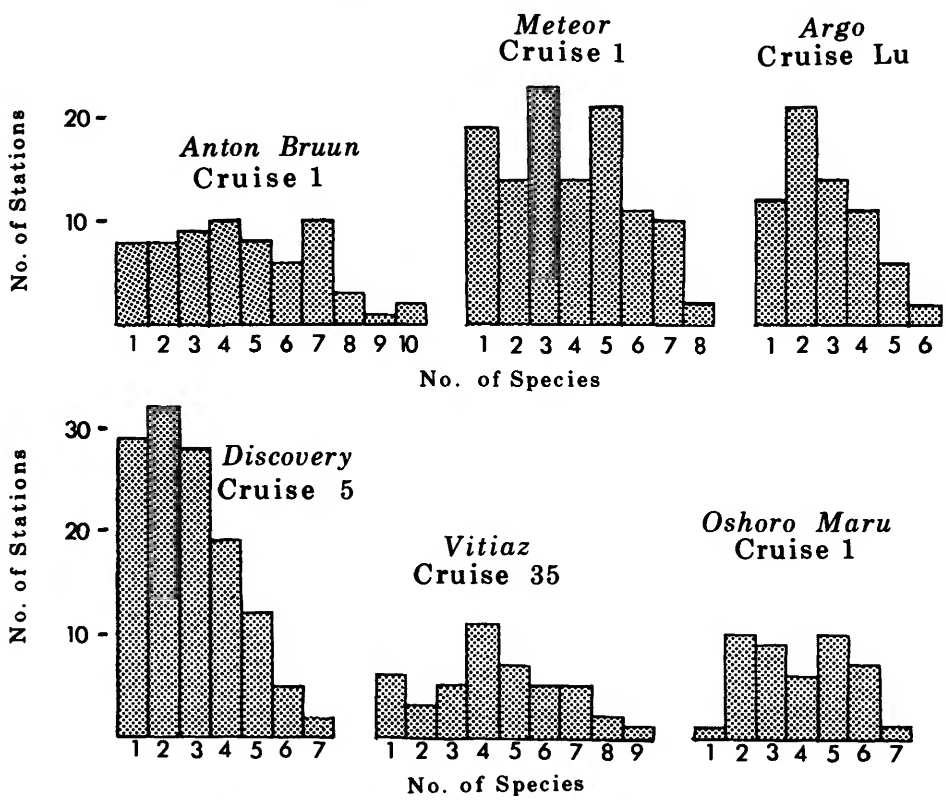

FIGURE 81.—Species diversity of Hyperiidae for 6 IIOE cruises.

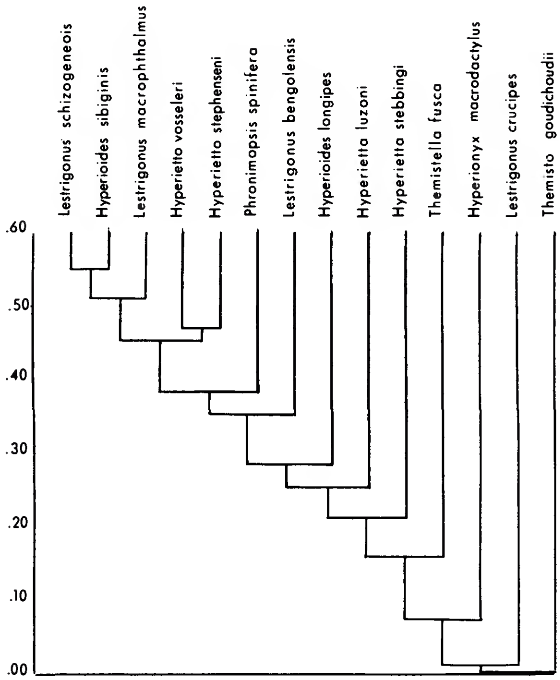

FIGURE 82.—Dendrograms from affinity indices for all IIOE samples.

ciated with medusae, species of *Hyperietta* with colonial radiolarians, and *Hyperioides longipes* with siphonophores. Juvenile *Themisto gaudichaudii* are associates of salps. The hosts of *Hyperionyx*, *Phronimopsis*, and *Themistella* are not yet known; neither has that of the widespread and abundant *Hyperioides sibaginis* been discovered. We suspect that the last will prove to be a siphonophore that is widespread and common in the Indian Ocean.

Comparison of Day and Night Samples

Figures 6, 12, 18, 24, 30, 36, 41, 48, 55, 61, 67, and 73 show the distributions of 12 of the species during the day. Distributions of these species during the night are shown in Figures 7, 13, 19, 25, 31, 37, 42, 49, 56, 62, 68, and 74. Stations are classified as day or night stations following IOBC (1969), which makes allowances for local variations in the onset of dawn and dusk. The samples of Hyperiidae came from 545 day stations and 550 night stations. Comparison of day and night distributions does not reveal obvious differences for any of the 12 species. Table 1 shows the percentage of day and night stations at which each of 11 species was collected. Seven of the 11 species occurred at a higher percentage of day stations, but the differences were slight and probably not significant. The IIOE standard samples do not provide evidence for diel vertical migrations in the Hyperiidae.

Effects of the Monsoon Seasons on Distributions

Circulation in the northern Indian Ocean is unusual in that the direction of flow is reversed twice a year, owing to seasonal changes in the prevailing winds or monsoons. From about November to March when the northeast monsoon prevails, the monsoon gyre flows counterclockwise, and from about April to October the southwest monsoon results in a clockwise-flowing monsoon gyre. A detailed discussion summarizing the pattern of circulation in the Indian Ocean is given by Wyrtki (1973). To examine the effect of the monsoon seasons, we have plotted distributions of 12 of the species of Hyperiidae from 16 April to 15 October (SW monsoon) (Figures 9, 15, 21, 27, 33, 39, 44, 51, 58, 64, 70, and 76), and from 16 October to 15 April (NE monsoon) (Figures 8, 14, 20, 26, 32, 38, 43, 50, 57, 63, 69, and

TABLE 1.—Frequency of occurrence (%) at 545 day and 550 night stations, all cruises combined

Species	*Day stations*	*Night stations*
Lestrigonus schizogeneios	57	62
Hyperioides sibaginis	59	55
Hyperietta vosseleri	44	48
Hyperietta stephenseni	44	39
Lestrigonus macrophthalmus	36	42
Phronimopsis spinifer	35	29
Lestrigonus bengalensis	28	30
Hyperioides longipes	23	22
Hyperietta luzoni	14	12
Hyperietta stebbingi	13	12
Themistella fusca	12	11

75). The most noticeable seasonal differences in distribution are seen in the Arabian Sea, where 9 species occurred more frequently during the NE monsoon. The remaining species occurred rarely (*Hyperietta vosseleri*) or not at all (*Hyperietta luzoni*, *Hyperionyx macrodactylus*) in the Arabian Sea. Frequencies of occurrence in the Arabian Sea (north of 10°N) are shown in Table 2. Within the Arabian Sea the differences are noticeable both along the west coast of India and in the northern part of the Sea, but did not appear to be significant off the Arabian Peninsula.

The reasons for the greater frequency of occurrence during the NE monsoon are not apparent. Oceanic circulation is much stronger during the SW monsoon, and causes intense upwelling in several places (Wyrtki, 1973). Primary production in the Arabian Sea is 5 times greater during the SW monsoon than during the NE monsoon. Secondary production is only slightly higher, but measurements of secondary production during the NE monsoon were inadequate (Cushing, 1973).

Perhaps the current pattern during the NE monsoon leads to the accumulation of Hyperiidae in the Arabian Sea. The NE monsoon current, usually strongest (1 knot) south of Sri Lanka and in the southern Arabian Sea, sends a strong branch north along the west coast of India from November to January, carrying low-salinity water from the Bay of Bengal. Perhaps hyperiids and their gelatinous hosts are entrained in this branch and accumulate in the slowly moving cyclonic gyre within the Arabian Sea. The swifter anticyclonic gyre of the SW monsoon would cause greater spatial separation of hyperiids and would tend to carry them out of the Arabian Sea.

TABLE 2.—Frequency of occurrence (%) of Hyperiidae in the Arabian Sea north of 10°N at 120 stations during the NE monsoon and 100 stations during the SW monsoon

Species	*NE monsoon*	*SW monsoon*
Lestrigonus schizogeneios	65	46
Hyperioides sibaginis	109	51
Hyperietta vosseleri	5	5
Hyperietta stephenseni	37	11
Lestrigonus macrophthalmus	47	30
Phronimopsis spinifer	64	21
Lestrigonus bengalensis	49	31
Hyperioides longipes	11	4
Hyperietta luzoni	0	0
Hyperietta stebbingi	23	2
Themistella fusca	30	4

Distribution Patterns of Indian Ocean Hyperiidae

Excluding *Themisto*, which is limited to colder waters in the southern part of the ocean, the Indian Ocean species of Hyperiidae fall into 3 groups when separated by patterns of global distribution: 1) Indo-Pacific (*Hyperioides sibaginis*, *Hyperoche* species); 2) Atlantic-Indo-West Pacific (*Lestrigonus crucipes*, *L. macrophthalmus*); and 3) circumglobal (the remaining 10 species).

Fleminger and Hulsemann (1973) have shown that warm-water epiplanktonic copepods have 2 general patterns of distribution. Species that occur up to the latitudes of subtropical convergences (about 40°) or beyond tend to be circumglobal, whereas species that are limited to lower latitudes (usually not beyond 20° or 30°) tend to show regional provincialism. If these 2 patterns were valid for the Hyperiidae, we would expect the Indo-Pacific species to be confined to lower latitudes than the circumglobal species. But Figures 83–85, which show the approximate southern boundaries of 10 species of Hyperiidae in the Indian Ocean, indicate that this is not the case. *Hyperioides sibaginis* (Figure 85) extends as far or farther south than any species except *Themisto gaudichaudii* and *Lestrigonus schizogeneios* (Figure 83). Too much reliance should not be placed on the boundaries in Figures 83–85, since they reflect in part differences in frequency of occurrence, especially in the central Indian Ocean south of 20°S, where the density of sampling was low.

In the eastern Pacific, from which much larger samples have been available, 20 of these same species can be assigned to biotic provinces (McGowan, 1974), as previously noted (Bowman, 1973):

Transition province, *Hyperietta stephenseni*, *H.*

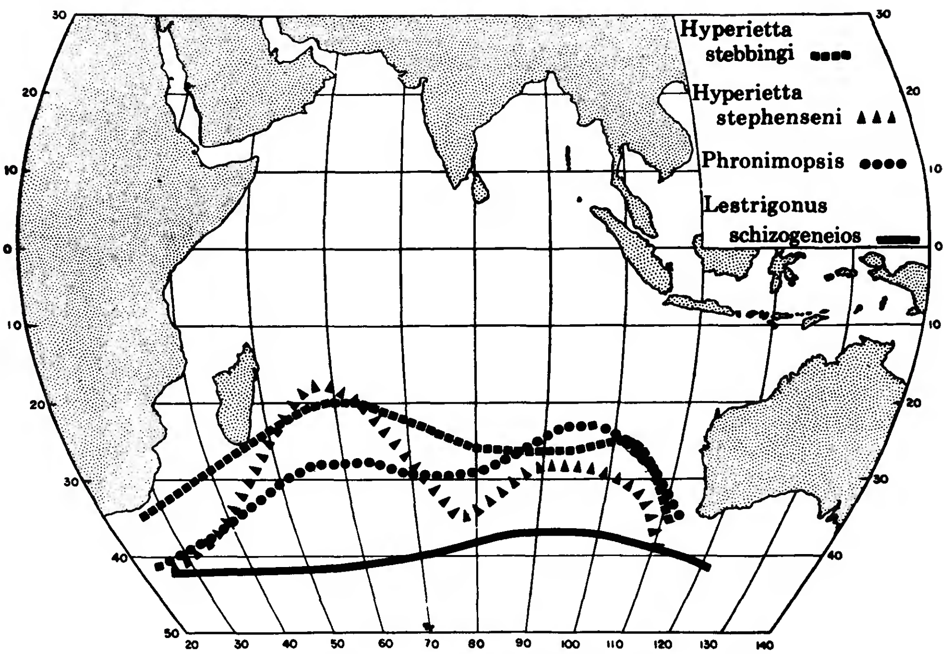

FIGURE 83.—Approximate southern boundaries of Transition species of Hyperiidae in the Indian Ocean.

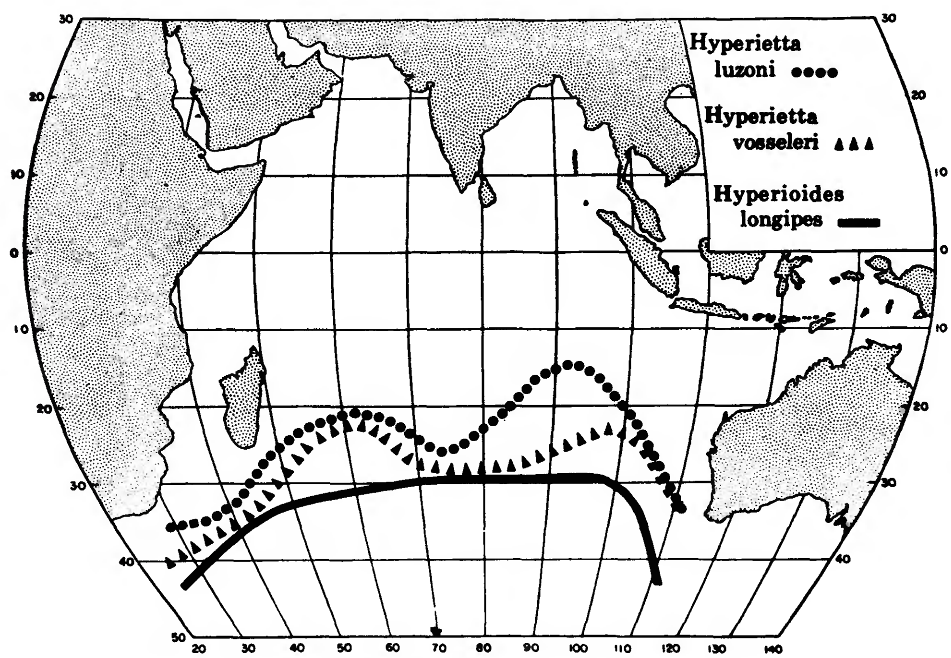

FIGURE 84.—Approximate southern boundaries of Central species of Hyperiidae in the Indian Ocean.

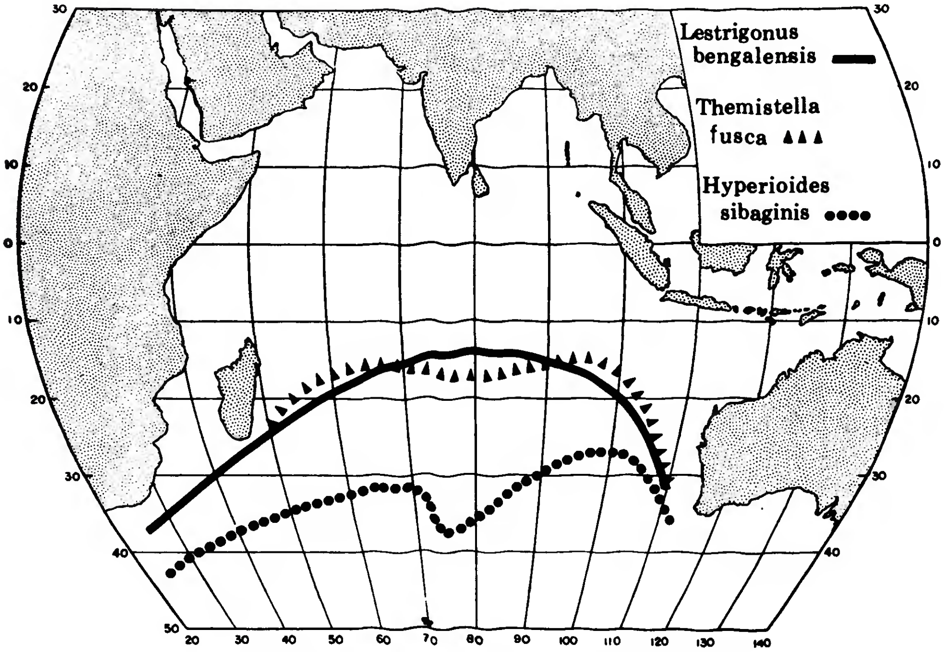

FIGURE 85.—Approximate southern boundaries of Warm-Water Cosmopolitan species of Hyperiidae in the Indian Ocean.

stebbingi, *Lestrigonus schizogeneios*, *Phronimopsis spinifer*;

Central province, *Hyperietta luzoni*, *H. vosseleri*, *Hyperioides longipes*; and

Warm-Water Cosmopolitan province, *Hyperioides sibaginis* (not known from the Atlantic), *Lestrigonus bengalensis*, *Themistella fusca*.

Phronimopsis was not included in Bowman's (1973) study; hence a map showing its distribution in the northeastern Pacific is given here (Figure 86) to support its classification as a Transition species.

The approximate boundaries of the Transition and Central provinces in the Pacific are shown in Figure 87, sketched by hand from McGowan's (1974) figures 2 and 3. The overlap of the provinces appears extensive, but is much less when boundaries are adjusted to include only high percentages of the faunas (McGowan, 1974, figs. 8, 9).

Both Transition and Central species of Pacific Hyperiidae, especially the former, are absent from large areas on either side of the equator. In the Indian Ocean these same species are scattered throughout the area sampled, including the regions of highest surface temperature, i.e., 28–30°C—higher than the maximum temperatures encountered, at least by the Transition species, in the Pacific. Distributional patterns in the Indian Ocean are similar for both groups of species, as well as for the Warm-Water Cosmopolitan species. The approximate southern boundaries (Figures 83–85) are similar for the 3 groups of species, with the more abundant species generally occurring farther south. A possible exception is *Lestrigonus bengalensis*.

To further illustrate the lack of spatial separation of Transition, Central, and Warm-Water Cosmopolitan species in the Indian Ocean, Table 3 shows the numbers of species of each group taken on Cruise 23 of R/V *Umitaka Maru*, which occupied a series of 20 stations along the 78th meridian, from 7°39′N to 24°57′S. Hyperiids were collected at 18 of the 20 stations. Species of all 3 groups were present at 10 stations, of only 2 groups at 7 stations, and of only 1 group at 1 station. During Cruise 3 R/V *Kagoshima Maru* also occupied a series of 23 stations along the 78th meridian, from 6°23′N to 24°38′S, and Hyperiidae were collected at 18 of those stations. Species of all 3 groups were present at 5 stations, of only 2 groups at 8 stations, and of only 1 group at 5 stations (Table 4).

Thus the 10 species of Hyperiidae listed above have 3 distinct patterns of distribution in the Pacific, but such differences are not evident for the same 10 species in the Indian Ocean. Whether or not such patterns existed in the past is an interesting question. During the last glacial maximum, which occurred 18,000 years ago, the average surface temperature of the entire Indian Ocean was 1.4°C cooler during February and 1.5°C cooler in August (Prell and Hutson, 1979) than it is today.

No morphological differences have been noted between Pacific and Indian specimens of any nominal species of Hyperiidae, but physiological adaptations that enable populations of Transition and Central species to tolerate lower temperatures in the Pacific and higher temperatures in the Indian Ocean must have evolved. Whether the populations represent either physiological races or cryptic species is unknown.

TABLE 3.—Numbers of specimens for each species group of Hyperiidae collected on *Umitaka Maru* Cruise 23 (dash = no data)

Station	Species group			Position
	Transition	*Central*	*Warm-Water Cosmopolitan*	
1-1	2	–	–	04°57′S, 77°59′E
1-2	4	1	1	06°04′N, 77°46′E
1-4	–	1	2	03°05′N, 77°51′E
1-5	1	2	3	01°57′N, 77°47′E
1-6	1	–	–	01°00′N, 78°03′E
1-7	3	3	3	00°08′N, 78°02′E
1-8	6	–	5	00°52′S, 78°03′E
1-9	3	2	5	01°59′S, 78°01′E
1-10	8	1	2	02°49′S, 78°01′E
1-11	2	5	12	05°00′S, 78°10′E
1-12	4	9	7	07°15′S, 78°13′E
1-14	–	3	1	10°51′S, 78°07′E
1-15	–	1	1	12°54′S, 78°01′E
1-16	2	2	–	15°06′S, 77°55′E
1-17	5	2	4	17°30′S, 78°04′E
1-18	1	1	–	19°53′S, 77°49′E
1-19	1	1	2	22°17′S, 78°00′E
1-20	5	1	10	24°57′S, 77°52′E

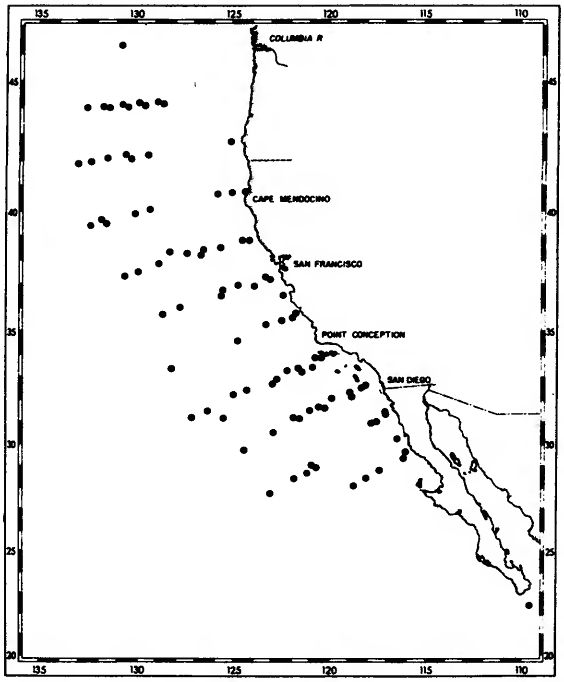

FIGURE 86.—Distribution of *Phronimopsis spinifer* in the northeastern Pacific, CalCOFI cruises 1, 5, 9, and 20 combined.

Distributions of the Individual Species

Lengthy accounts of the distributions of the IIOE species of Hyperiidae would be of little value, and we limit our discussion to the brief summaries that follow.

Hyperietta luzoni (Figures 4–9).—Most common off Australia; sparsely scattered elsewhere, but not found in the Arabian Sea.

Hyperietta stebbingi (Figures 10–15).—Scattered throughout the Indian Ocean; most common off Australia; uncommon off South Africa.

Hyperietta stephenseni (Figures 16–21).—Common and rather uniformly distributed.

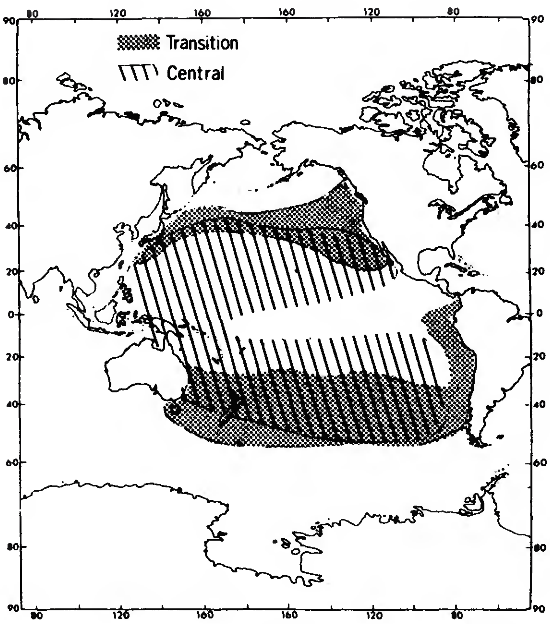

FIGURE 87.—Approximate boundaries of Transition and Central provinces in the Pacific (from McGowan, 1974).

Hyperietta vosseleri (Figures 22–27).—Common throughout the Indian Ocean except in the Arabian Sea, where it rarely occurs.

Hyperioides longipes (Figures 28–33).—Most common off Australia and South Africa; absent off the west coast of India and from most of the Arabian Sea except the northern part; not common off Somalia.

Hyperioides sibaginis (Figures 34–39).—Very common and rather uniformly distributed.

Hyperionyx macrodactylus (Figures 40–44).—Scarce, in a band along the equator, with a few occurrences off Australia and South Africa and 1 in the Bay of Bengal.

Hyperoche species (Figure 45).—A few occurrences in the Arabian Sea, Gulf of Aden, Somalia, and off Australia.

Lestrigonus bengalensis (Figures 46–51).—Widespread, with tendency to be more common in coastal waters, at least in the Arabian Sea.

Lestrigonus crucipes (Figure 52).—A few occurrences in the Bay of Bengal and the Arabian Sea, and 2 along 110°E.

Lestrigonus macrophthalmus (Figures 53–58).—Common and rather uniformly distributed.

Lestrigonus schizogeneios (Figures 59–64).—Very common and rather uniformly distributed; greater penetration to south in central Indian Ocean than most species.

Phronimopsis spinifer (Figures 65–70).—Common and rather uniformly distributed, but infrequent off Somalia and in the central Indian Ocean.

Themistella fusca (Figures 71–76).—Sparsely and rather uniformly scattered.

Themisto gaudichaudii (Figure 77).—Confined to cold water. Kane's (1966, text-figure 4) map of its world distribution shows that it is limited to latitudes greater than 40°S in the Indian Ocean; hence it was surprising to find it at a few stations between 30°S and 20°S to the west of Australia. In her samples from the 110°E meridian Tranter (1977:647) found *Themisto* only "south of 33°S, on the September cruise, in the deep subtropical water mass." Most of the northward flow from the west wind drift occurs between 95°E and 105°E, which is about where the northernmost IIOE samples of *Themisto* were collected.

Comparison with Other Studies

Three recent studies of the Hyperiidae in a circumscribed region can be compared to the results obtained from the IIOE collections. Tranter (1977) studied samples from the eastern Indian Ocean along a north-south section (9–32°S, 110°E). Her samples were from the upper 200 m, and most were taken with the Indian Ocean standard net; hence they are comparable to ours.

TABLE 4.—Numbers of specimens for each species group of Hyperiidae collected on *Kagoshima Maru* Cruise 3 (dash = no data)

Station	*Species group*			*Position*
	Transition	*Central*	*Warm-Water Cosmopolitan*	
11	1	–	–	04°57′S, 77°59′E
12	1	3	–	03°24′S, 78°02′E
14	2	–	1	00°57′S, 78°03′E
15	3	–	1	00°01′S, 78°06′E
16	1	–	–	01°06′N, 78°03′E
18	2	2	–	03°29′N, 77°54′E
19	4	2	7	05°04′N, 77°46′E
20	4	2	3	06°23′N, 78°01′E
21	–	1	–	08°00′S, 77°52′E
23	–	1	–	11°03′S, 77°57′E
24	1	1	–	12°30′S, 77°58′E
25	2	5	1	14°03′S, 77°58′E
26	–	2	1	15°27′S, 77°57′E
27	2	1	2	16°53′S, 77°55′E
28	–	2	–	18°24′S, 78°06′E
29	12	2	2	19°44′S, 77°57′E
30	3	2	–	21°32′S, 77°58′E
31	2	2	–	23°02′S, 77°52′E

TABLE 5.—Percent of total Hyperiidae collected by expedition or researcher (dash = no data)

Species	*IIOE*	*Shulen-berger*	*Thurston*	*Tranter*
Hyperietta luzoni	1.7	2.6	-	4.2
Hyperietta stebbingi	1.5	0.3	-	1.0
Hyperietta stephenseni	7.0	5.1	14.6	7.8
Hyperietta vosseleri	9.2	52.6	2.1	12.1
Hyperioides longipes	4.7	6.4	73.5	42.9
Hyperioides sibaginis	22.3	14.7	-	-
Lestrigonus bengalensis	7.9	9.7	-	-
Lestrigonus macrophthalmus	9.4	0.1	0.6	-
Lestrigonus schizogeneios	18.7	2.4	7.2	12.6
Phronimopsis spinifer	13.3	3.9	0.2	17.0
Themistella fusca	2.0	0.8	0.8	-

Thurston (1976) analyzed collections made SE of Fuerteventura, Canary Islands (~28°N, 14°W), during the SOND cruise, 1965. The SOND samples encompassed greater depths (to 950 m), but the Hyperiidae were taken mostly at shallow depths; therefore the relative abundance of the species can be compared to that of the IIOE species.

Shulenberger's (1977, 1978) collections came from the North Pacific central gyre (28°N, 155°W). Depth-stratified tows made with opening-closing Bongo nets sampled 6 intervals from 0–600 m. Most of the Hyperiidae occurred in the upper 100 m.

In Table 5 the percent of total Hyperiidae collected in the above studies is listed for 11 IIOE species. Thurston's and Tranter's collections contained only 7 of these 11 species, but each author listed a species not in the IIOE collections: *Lestrigonus latissimus* was named by Thurston, *Iulopis loveni* by Tranter. Shulenberger lists 5 non-IIOE species: *Hyperietta parviceps*, *Lestrigonus shoemakeri*, *L. latissimus*, *Pegohyperia princeps*, and *Iulopis loveni*.

The most striking regional differences shown in Table 5 are the dominance of *Hyperietta vosseleri* in the North Pacific central gyre and of *Hyperioides longipes* in the eastern Indian Ocean and Canary Islands collections. *Hyperioides sibaginis*, which was nearly 5 times as abundant as *H. longipes* in the IIOE collections and more than twice as abundant in the central Pacific collections, did not occur in the other collections. Shulenberger (1978) found nearly perfectly reciprocal depth distributions of the 2 species, with *Hyperioides sibaginis* living mainly above 75 m and *H. longipes* almost entirely below 75 m. Perhaps when *H. sibaginis* is absent, *H. longipes* can extend its vertical range into the upper layer and expand its population.

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