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Euthecosomatous Pteropods (Mollusca) in the Gulf of Thailand and the South China Sea: Seasonal Distribution and Species Associations

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Euthecosomatous Pteropods (Mollusca) in the Gulf of Thailand and the South China Sea: Seasonal Distribution and Species Associations

By

Marcia Rottman

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ERRATA NAGA REPORT

Volume 4, Part 6

EUTHECOSOMATOUS PTEROPODS (MOLLUSCA) IN THE GULF OF THAILAND AND THE SOUTH CHINA SEA: SEASONAL DISTRIBUTION AND SPECIES ASSOCIATIONS

By

Marcia Rottman

page 12, 3rd paragraph, line 10, S-3 should read S-8

page 26, 1st paragraph, line 2, clava (fig. 26a)., should read (Fig. 27).

page 60-61, Figure 26 a, b was inadvertently included. The pteropod identified as *Creseis virgula clava* was subsequently recognized which is combined with that of *Creseis chierchiaie* in Figure 25 a, b.

**EUTHECOSOMATOUS PTEROPODS (MOLLUSCA) IN THE GULF
OF THAILAND AND THE SOUTH CHINA SEA: SEASONAL
DISTRIBUTION AND SPECIES ASSOCIATIONS**

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ABSTRACT

The Gulf of Thailand and the South China Sea were each sampled during five cruises of the Naga Expedition, 1959-1961. The following twenty species were present: *Cavolina gibbosa*, *C. globulosa*, *C. inflexa*, *C. longirostris*, *C. uncinata*, *Clio recurva*, *C. cuspidata*, *C. pyramidata*, *Creseis acicula*, *C. chierchiae*, *C. virgula*, *C. bulgia*, *Cuvierina columnella*, *Diacria quadridentata*, *D. trispinosa*, *Hyalocylis striata*, *Limacina bulimoides*, *L. inflata*, *L. trochiformis*, and *Styliola subula*. Distribution maps are presented for each species and variations in distribution are related to climatic and hydrographic parameters. Statistical treatment of the data helped to establish recurrent species groups among ten selected species and to relate the distribution of these groups to environmental configurations.

Broadly speaking, there are two recurrent species groups. The first is restricted to the deeper-water areas of the South China Sea, while the second occurs in both the Gulf of Thailand (a shallow, estuarine environment) and all of the South China Sea. The members of the first group, Group A, are *Clio pyramidata*, *Creseis virgula virgula* + *C. virgula conica*, *Limacina bulimoides*, *L. inflata*, and *Styliola subula*. This group has the narrowest environmental tolerances. It does not occur in the low salinity, high temperature, low oxygen environment of the Gulf of Thailand and the extent of its penetration of the Sunda Shelf area of the southern South China Sea varies with season. Because of their relative rarity in the samples *Cavolina gibbosa*, *C. globulosa*, *C. inflexa*, *C. uncinata*, *Clio recurva*, *C. cuspidata*, *Cuvierina columnella*, and *Diacria trispinosa* were not included in the statistical treatment, but their distribution patterns place them with Group A.

The second broad group has been divided into two, based on the extent of tolerance for the most extreme conditions in the Gulf of Thailand. Group B, consisting of *Diacria quadridentata*, *Hyalocylis striata*, and *Limacina trochiformis*, is less tolerant of extreme Gulf conditions than the following Group, C, and tends to be concentrated in the central, deeper area of the Gulf of Thailand. *H. striata* was absent from the Gulf during January-May, 1960 (Cruises S-3 and S-5), and *D. quadridentata* was absent during April-May (S-5). The members of Group C, *Creseis acicula* and *Cavolina longirostris*, have the broadest environmental tolerances and were present and abundant even at nearshore stations in the Gulf of Thailand where salinities were below 29 ‰. Group C tended to be most abundant around the margins of the Gulf. The members of both Groups B and C were widely distributed in the South China Sea as well.

INTRODUCTION AND ACKNOWLEDGEMENTS

The Naga Expedition was sponsored by the governments of Thailand, South Viet Nam, and the United States to conduct a study of the marine resources in the area of the Gulf of Thailand and the South China Sea. The field activities of the expedition were carried out by R/V *Stranger* during the years 1959-1961. This paper presents the results of a study of the euthecosomatous pteropods found in the Naga plankton samples. There have been three main topics of inquiry: identification of 1) the species present in the samples, 2) recurrent species associations, and 3) the relation of species distribution to the physical features of the environment.

Table 1 gives the numerical designation, dates, monsoon season, and area sampled for each cruise studied in the preparation of this paper. All subsequent references to cruise numbers refer to those given in Table 1. Figures 1 and 2 show the bottom topography of the Gulf of Thailand and the South China Sea respectively. Figure 3 gives the geographical locations of places and cruise track line numbers referred to in the text.

In acknowledgement, I express gratitude to Edward Brinton, who introduced me to the world of plankton and put me to work on the Naga pteropods, and whose advice and aid made preparation of this paper possible. I thank Cadet Hand, Bodega Marine Laboratory, for encouragement and J. Wyatt Durham, Department of Paleontology, University of California at Berkeley, for advice and for the use of photographic equipment. John McGowan read an early version of the manuscript and made a number of valuable suggestions. To Don L. Eicher I owe a great debt for his careful reading and constructive criticism of the wording of the manuscript in its final stages and for advice concerning preparation of the plates. Norman Nielsen exercised great care in printing my photos of pteropods and photographed one specimen.

Table 1 NAGA EXPEDITION CRUISE DESIGNATIONS, DATES, SEASONS
AND LOCALITIES

Cruise	Date	Monsoon Season	Locality
S1	Oct. 19-31, 1959	SW to NE	Gulf of Thailand
S2	Nov. 30-Dec. 13, 1959	NE	South China Sea
S3	Jan. 19-30, 1960	NE	Gulf of Thailand
S4	Feb. 27-March 19, 1960	NE	South China Sea
S5	April 21-May 2, 1960	NE to SW	Gulf of Thailand
S6	May 21-June 24, 1960	SW	South China Sea
S7	Aug. 2-14, 1960	SW	Gulf of Thailand
S8	Sept. 8-Oct. 6, 1960	SW to NE	South China Sea
S9	Nov. 9-24, 1960	NE	Gulf of Thailand
S10	Jan. 10-Feb. 13, 1961	NE	Gulf of Thailand

SECTION I. METHODS

COLLECTION AND DATA PREPARATION

The Naga pteropod material was obtained by the use of two plankton nets (Faughn, 1974). The 1-meter diameter net with a mesh of 0.64 mm carried a flow meter which indicated the distance traveled by the net during the tow. From this the number of cubic meters of water filtered was calculated, assuming 100% efficiency. McGowan (1971) has reviewed the reliability of net sampling, concluding that there may be fairly large discrepancies between replicate tows and with varying net size and volume of water sampled. Certainly some pteropods actively avoid the net, and some pteropods, especially juveniles, may pass through the net. In any case, all samples were obtained in the same manner with a standard net.

Four hundred thirty-five 1-meter net samples were examined. These consist of all samples from cruises S-1 through S-9 plus those samples collected in the Gulf of Thailand during S-10. (Not included are a few samples lost or spoiled and, with the exception of S-10, those samples from the Gulf of Thailand which were obtained enroute between Bangkok and the South China Sea cruises.) The estimated number of individuals per 1000 m³ for each species and each cruise are presented in Appendix 1.

Some samples were too large to be convenient for counting. These were divided into aliquots. The most common fractions were 1/5, 1/4, and 1/2. The number of individuals counted in the fraction was multiplied by the appropriate number to obtain an estimated number of individuals in the entire sample. Aliquots for S-1 through S-8 were obtained by agitating the zooplankton together with a suitable amount of the fluid preservative, pouring the suspension into a graduated cylinder, and pouring off the desired amount. For counting samples from cruises S-9 and S-10 a Folsom plankton splitter was available, and this device was used for obtaining the aliquot.

Several of the samples from the first two cruises, particularly S-1, were partially spoiled, and reliable counts of the pteropods in them could not be made. The pteropods were picked out of the unspoiled samples from S-1; some specimens are inevitably destroyed in the picking process. For these reasons, I have chosen to omit the first two cruises from the statistical portion of this study. The pteropods in samples from the other cruises were counted directly in the plankton samples.

One source of uncontrolled variation in the records of pteropod and zooplankton volume densities is related to the fact that plankton tows were taken without regard for the time of day. In the Gulf of Thailand (maximum depth slightly over 80 m) and the shallow shelf area of the South China Sea, this is probably not a significant factor. In oceanic areas of the South China Sea significant vertical migrations probably do take place, but little has been done to ascertain their effect on the results of Naga plankton sampling.

A second type of net used for plankton tows was the 2-meter diameter stramin net (mesh size 1.0 mm). This net did not carry a flowmeter, making possible only qualitative studies of the material collected. Nineteen 2-m net samples were studied. These samples were collected during S-4, S-6, and S-8. The species found in these samples are given in Appendix 2. In general the 2-m net samples contained mostly the larger pteropods, such as the adults of the genera *Cavolina*,¹ *Clio*, *Cuvierina*, *Styliola*, *Hyalocylis*,¹ *Diacria*, and *Creseis*. However, smaller species and young of some of these genera were occasionally found. The 2-m net samples were sorted without the use of a microscope, and therefore some of those very small organisms which did not go

¹ *Cavolina* Abildgaard 1791 and *Hyalocylis* Fol 1875 are the original spellings of the names of these genera. Some modern authors have followed Pelseneer (1888), who altered the original spelling to what he considered to be more correct forms: *Cavolinia* and *Hyalocylis*. However, under the rules of the International Code of Zoological Nomenclature (1964) his emendations appear not to be justified.

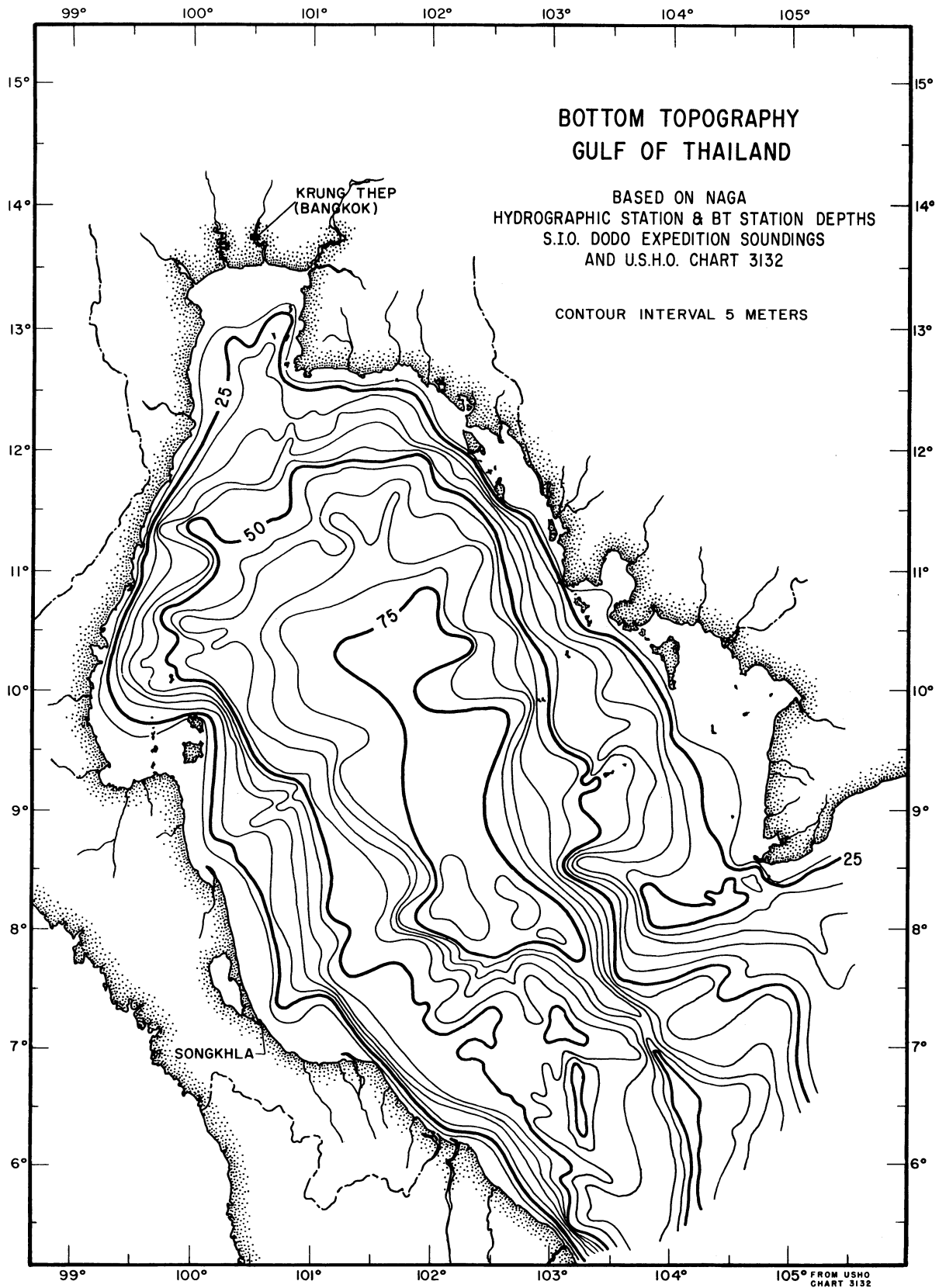


Figure 1. Bottom Topography, Gulf of Thailand (reproduced from Robinson, 1974).

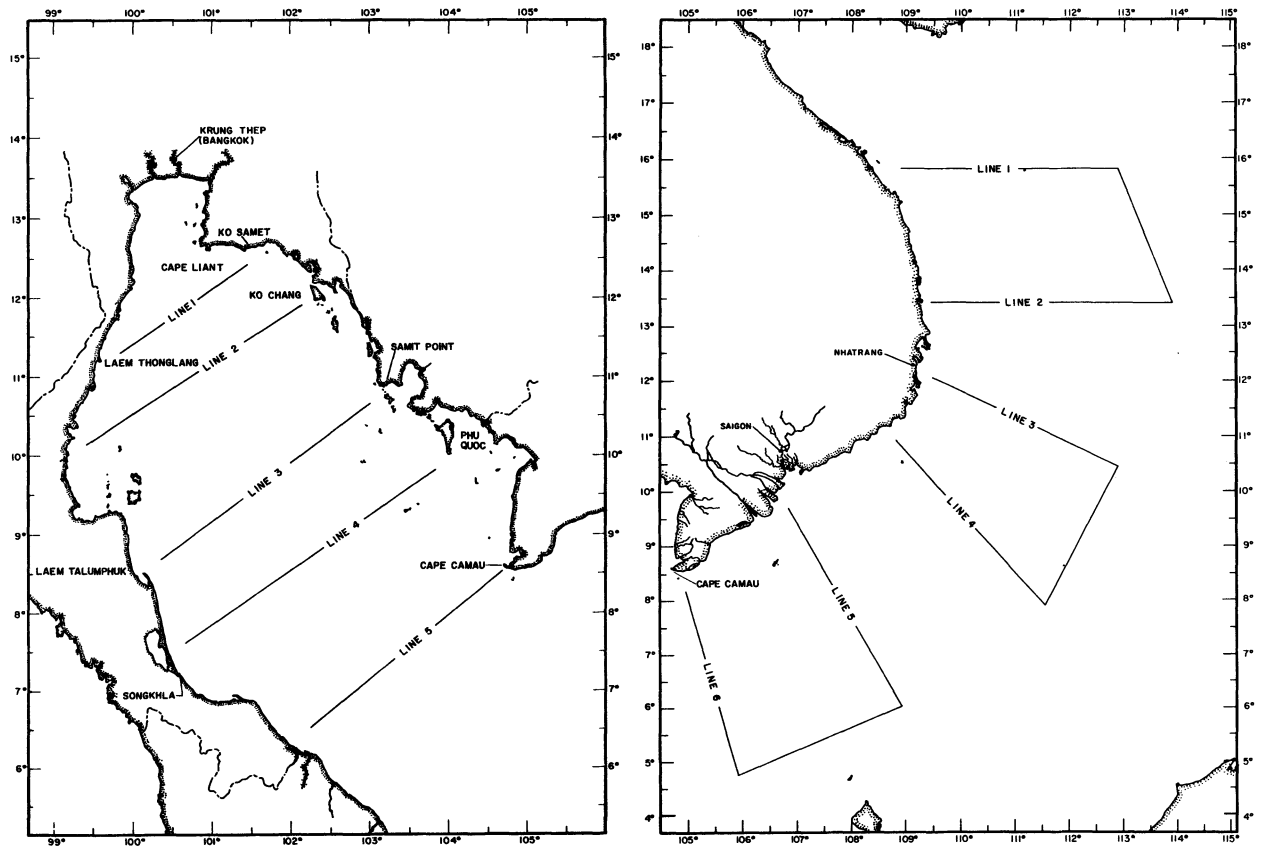


Figure 3. Gulf of Thailand and the South China Sea: geographical locations of place names and cruise track line numbers.

through the net could have been overlooked.

In addition, a number of samples were collected during the trans-Pacific cruise of the R/V *Stranger* enroute to Southeast Asia. Both the 1-m and 2-m nets were used to collect these samples, but in this case the 1-m net, as well as the 2-m net, did not carry a flow meter. Thus no quantitative comparisons among these samples are possible. The species found in the trans-Pacific samples, as well as the position of each station, are given in Appendix 3.

STATISTICAL PROCEDURES

The distributions of the ten most common pteropod species found in the Naga samples were selected for statistical analysis. The remaining species are all relatively rare. In order to satisfy the 200-case limitation of the Spearman's (1904) rank correlation computer program used, 197 stations were chosen from cruises S-3 through S-8, allotting an equal number of stations to the following three seasons: northeast monsoon, southwest monsoon, and intermonsoon. Within the seasons the stations selected were chosen with the aid of a table of random numbers.

Determining Species Association.

Recurrent species groups were established on the basis of presence and absence using the same index of affinity employed by Fager and McGowan (1963). When only species presence and absence are considered, inherent differences in magnitude in the underlying distributions of the species do not prevent each species from playing an equal role in the determination of the recurrent groups. Species which show affinities are a relatively common part of each other's environment. Neither two widespread species nor one widespread and one very rare species having a small overlap in their distributions in which they are always found together will show affinity with this method. Fager's (1957) method was used to group species on the basis of their index of affinity.

Concordance.

The Friedman (1937) rank test was used to study the relationship between abundances of members of the groups established using the index of affinity. This is almost identical with the method associated with Kendall's (1955) coefficient of concordance. The Friedman rank test was used to measure the degree of consistency with which the members of a group rank the favorability of the environment at each station in terms of their abundance. (It is assumed that greater abundance indicates a more favorable environment.)

Determining Associations with Physical Environment.

Spearman's (1904) rank correlations were calculated between individual species abundances and the following parameters: salinity, temperature, and dissolved oxygen content at 10 m and depth of water.

SECTION II. DISTRIBUTION

GENERAL

Twenty species of euthecosomatous pteropods were found in the plankton samples studied. Distribution maps are presented for each species, except *Clio cuspidata* which occurred only once. *Creseis chierchiae* was unfortunately not distinguished from *Creseis bulgia* until the counting was completed (see page 87) and distribution charts combining these two species are given. *Creseis acicula*, *Creseis chierchiae*, *Creseis bulgia*, *Cavolina longirostris*, *Limacina trochiformis*, *Hyalocylis striata*, and *Diacria quadridentata* occurred in both the Gulf of Thailand and the South China Sea. However, though *Hyalocylis striata* and *Diacria quadridentata* were present in the South China Sea at all times, they were absent from the Gulf of Thailand during at least part of the period of the northeast monsoon. Judging by population density, all of the above species are

more tolerant of the broad, shallow shelf area in the southern one-third of the South China Sea than are the remaining thirteen species recorded. The species which inhabit the Gulf of Thailand are not all equally tolerant of the environmental conditions there. As a general rule, *H. striata*, *D. quadridentata* and *L. trochiformis* are concentrated in the lower and middle parts of the central Gulf, where salinity conditions are generally less extreme than near shore, and at the head of the Gulf. *Cavolina longirostris* and *Creseis acicula*, on the other hand, are much more tolerant of coastal conditions and tend to be more abundant around the margins and in the upper parts of the Gulf.

Except for three questionable records, the remaining thirteen species were not found in the Gulf of Thailand. These species are *Cavolina gibbosa*, *C. globulosa*, *C. inflexa*, *C. uncinata*, *Clio recurva* (= *Clio balantium*, see p. 85), *C. cuspidata* (which occurred only once), *C. pyramidata*, *Creseis virgula virgula* + *C. virgula conica*, *Cuvierina columnella*, *Diacria trispinosa*, *Limacina bulimoides*, *L. inflata*, and *Styliola subula*. Many of these were present in only very low concentrations and at only a few stations per cruise. In general, the above species are more widely distributed in the off-shelf area of the northern two-thirds of the South China Sea study area. When they do occur in the southern third of the area (lines 5 and 6), they are found along the offshore halves of the lines (see Fig. 3), the most frequent occurrences being at the outer end of line 5.

There is also a seasonal dimension to the general distribution pattern in the South China Sea. During the northeast monsoon the southern limit of the distributions of many of these species extends farther southward, well into the deeper off-shelf parts of the area traversed by line 5 and 6. During the southwest monsoon the distributions contract northward. Figures 4, 5, 6, and 7 show the limit of the distributions of four off-shore species (*Limacina inflata*, *L. bulimoides*, *Styliola subula*, and *Creseis virgula virgula* + *C. virgula conica*) during each South China Sea cruise. Cruise S-2 took place during the early part of the northeast monsoon. S-4 was conducted at the end of the same season. Maximum penetration of the southern area covered by lines 5 and 6 occurred during these two cruises. The next cruise, S-6, took place during the height of the southwest monsoon, and S-3 was conducted at the very end of that season and into the transition period. It is quite clear from Figures 4 through 7 that the southern limits of the distributions of these four species were shifted northward during the southwest monsoon. Only one of the four species, *L. inflata*, was present in the line 5-6 area during the southwest monsoon season. It was found only at the two outermost stations of line 5 and had retreated considerably from its positions during the northeast monsoon (S-2 and S-4). Is this seasonal change a purely mechanical response to changing wind directions or are other environmental factors involved? Perhaps surface shelf waters are transported from the south into the outer line 5 and 6 area during the southwest monsoon, making this area less favorable for these species, while the northeast monsoon may extend the southern range of favorable oceanic waters into this same area.

The Gulf of Thailand distribution patterns of some species show striking continuity with those in the South China Sea, despite the disparity of time between cruises. For example, during October 1959 (S-1) *Diacria quadridentata* was present along the southernmost line in the Gulf of Thailand with adults concentrated along the western half of that line (see Fig. 28a). In the South China Sea in November-December 1959 (S-2) this species was present at all stations online 6 except the one nearest shore. Adults were concentrated near the outer end of line 6, while some juveniles were present nearer shore, close to Cape Camau, contiguous to where juveniles were found in the Gulf during S-1. As *D. quadridentata* subsequently moved up the Gulf and away from the Cape Camau area (January 1960, S-3), its South China Sea distribution (February-March 1960, S-4) moved farther offshore and away from Cape Camau (Fig. 28b).

The southernmost area of the Gulf of Thailand (line 5) was sampled early in August, 1960 (S-7), and it was late September before the southernmost area of the South China Sea (line 6) was sampled during S-8. In spite of the nearly two-month time lapse between sampling of these adjacent areas, the continuity between the S-7 and S-8 distributions of *Limacina trochiformis*, *Hyalocylis striata*, and *Creseis acicula*, as well as *D. quadridentata*, is obvious (see Figs. 33b, 30b,

24b, and 28d). Evidently, pteropod distribution patterns in this area are sometimes maintained over a period of several months.

Three species of the genus *Limacina* were present throughout the year in the South China Sea. *Limacina bulimoides* and *L. inflata* had generally similar distributions, as they apparently do throughout the North Pacific (McGowan, 1960). There are some indications, however, that *L. inflata* is slightly more tolerant of conditions in the southern shelf area than *L. bulimoides*. During the northeast monsoon, the ranges of both species extended further southward than during the southwest monsoon (Figs. 4 and 5). Together, these two species seem to complement the distribution of *L. trochiformis*, which was generally most abundant in the southern and coastal areas of the South China Sea and which occurred in the Gulf of Thailand. While the areal distributions of *L. inflata* and *L. bulimoides* tend to be similar and complementary to *L. trochiformis*, *L. bulimoides* reached its maximum abundance during the same period as *L. trochiformis* (northeast monsoon, S-4) and the average concentration of both *L. bulimoides* and *L. trochiformis* dropped between S-4 and S-6 (southwest monsoon), just at the time when *L. inflata* rose to its peak abundance (Fig. 8).

Five members of the genus *Cavolina* were found in the Naga plankton samples: *Cavolina longirostris*, *C. gibbosa*, *C. inflexa*, *C. globulosa*, and *C. uncinata*. (In addition, *C. tridentata* was found in the trans-Pacific samples; see Appendix 3.) Of these five, only *C. longirostris* occurred in the Gulf of Thailand and in significant numbers. The rest are mostly restricted to the northern two-thirds of the survey area in the South China Sea and were found only in very low abundances. The distributions of most of these species, especially adult specimens, were patchy. Records of juveniles (see distribution maps) include only those specimens which were definitely assignable to a species.

Species of the genus *Clio* were restricted to the northern areas of the South China Sea. *C. pyramidata* was not found south of line 4 at any time during the four cruises studied. Its invasion of the area covered by lines 3 and 4 was the most widespread during cruises S-4 and S-8, corresponding to its two periods of highest concentrations: late in the northeast monsoon in 1960 and the period of transition from the southwest to the northeast monsoon in 1960.

McGowan (1960) described a number of distributional groups of pteropods in the North Pacific. Not surprisingly, most of the species found in the Naga samples from the South China Sea are members of one of McGowan's equatorial groups (III, Equatorial and Central; IV, Equatorial and West Central; VI, Equatorial). However, three of McGowan's Central (Group V) species, *Clio pyramidata*, *Cavolina inflexa*, and *Styliola subula*, were consistently present in the South China Sea during the Naga cruises. McGowan's distributional records show all three species present at stations on the Pacific side of the Philippines opposite the South China Sea. Of the three species, the distribution of *Cavolina inflexa* is most nearly restricted to the Central environment. Nevertheless, I have found it as far south as 5° N in the South China Sea, and of the large species of *Cavolina*, *C. inflexa* was the one most consistently present in the Naga survey area. *S. subula* was not only regularly present but was relatively abundant (up to 683/1000 m³).

The large species *Clio recurva* was found only in 2-m net samples and was not captured during November-December 1959 (S-2) or May-June 1960 (S-6). It was present in eight samples taken during February-March 1960 (S-4) and in one during September-October 1960 (S-8). It was spread out over the eastern (off-shelf) part of the northern two-thirds of the area late in the northeast monsoon, 1959 (S-2), while the one record from S-8 (transition to northeast monsoon, 1960) was located midway between the outer ends of lines 3 and 4.

McGowan (1960) raised some doubt about the presence of *Clio recurva* (= *Clio balantium*) in the waters of the Indo-Australian Archipelago. He said, "Tesch [1946, 1948], in addition to reporting the occurrence of 14 specimens at three different stations in the North Pacific listed 13 more specimens that were taken at eight stations in equatorial latitudes of the Indian Ocean and the waters of the Indo-Australian Archipelago. But in spite of its apparent tropicality in these areas it did not occur in the [Scripps] or Dana samples from the equatorial Pacific. All Pacific records with the exception of the one of Meisenheimer [1905], are between latitudes 35°N to

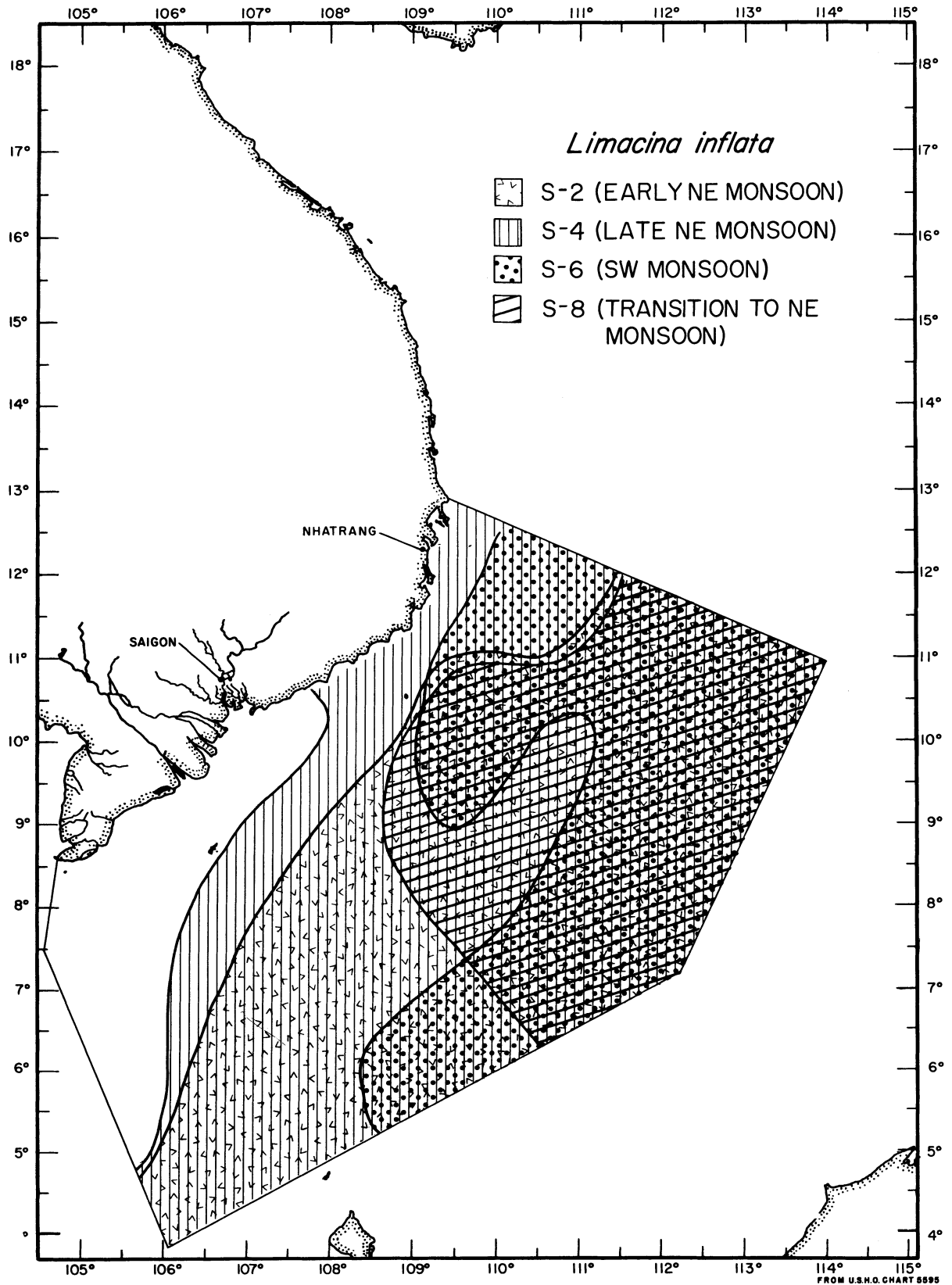


Figure 4. Southwestern limit of the distribution of *Limacina inflata* during cruises S-2 through S-8.

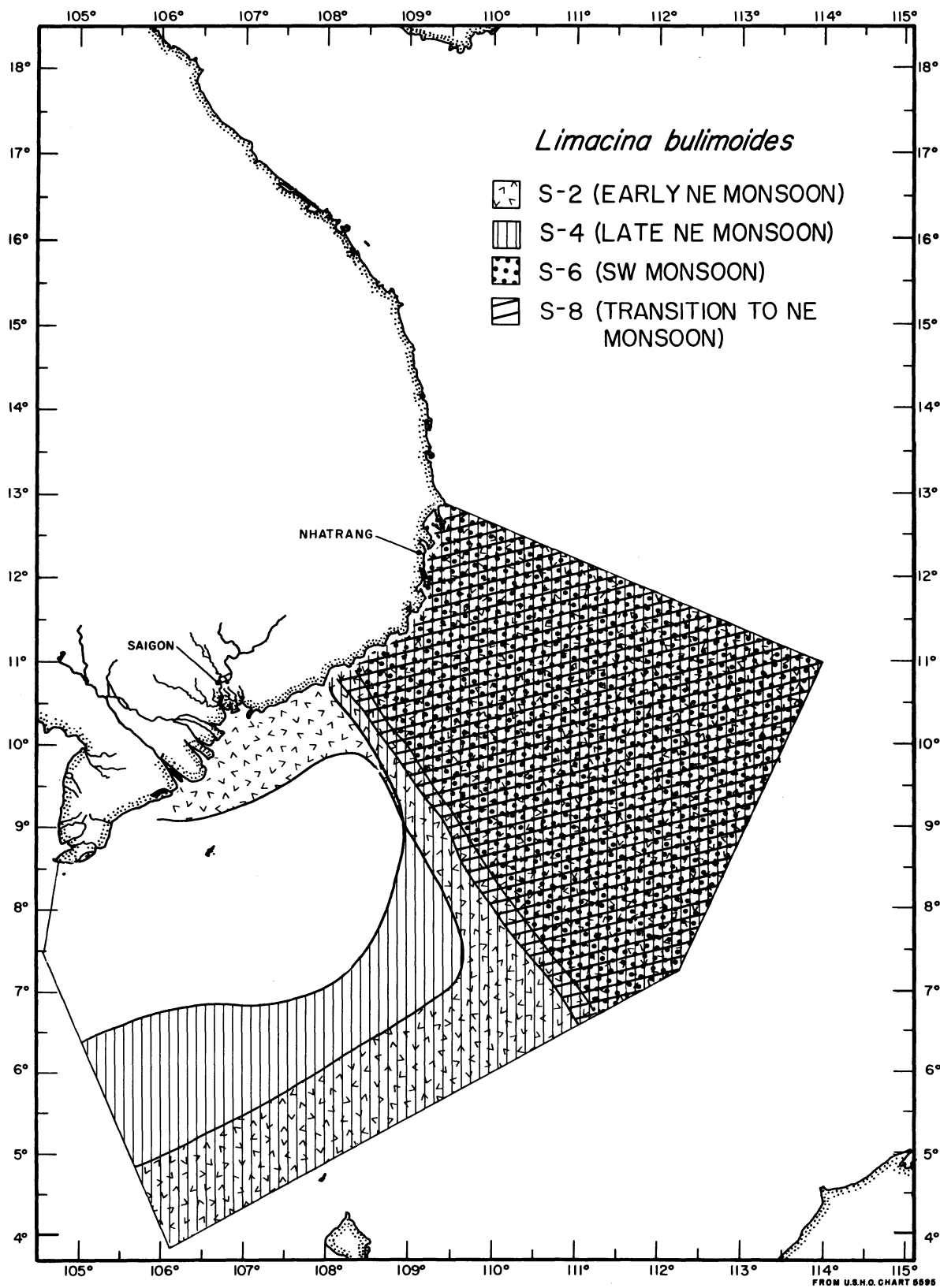


Figure 5. Southwestern limit of the distribution of *Limacina bulimoides* during cruises S-2 through S-8.

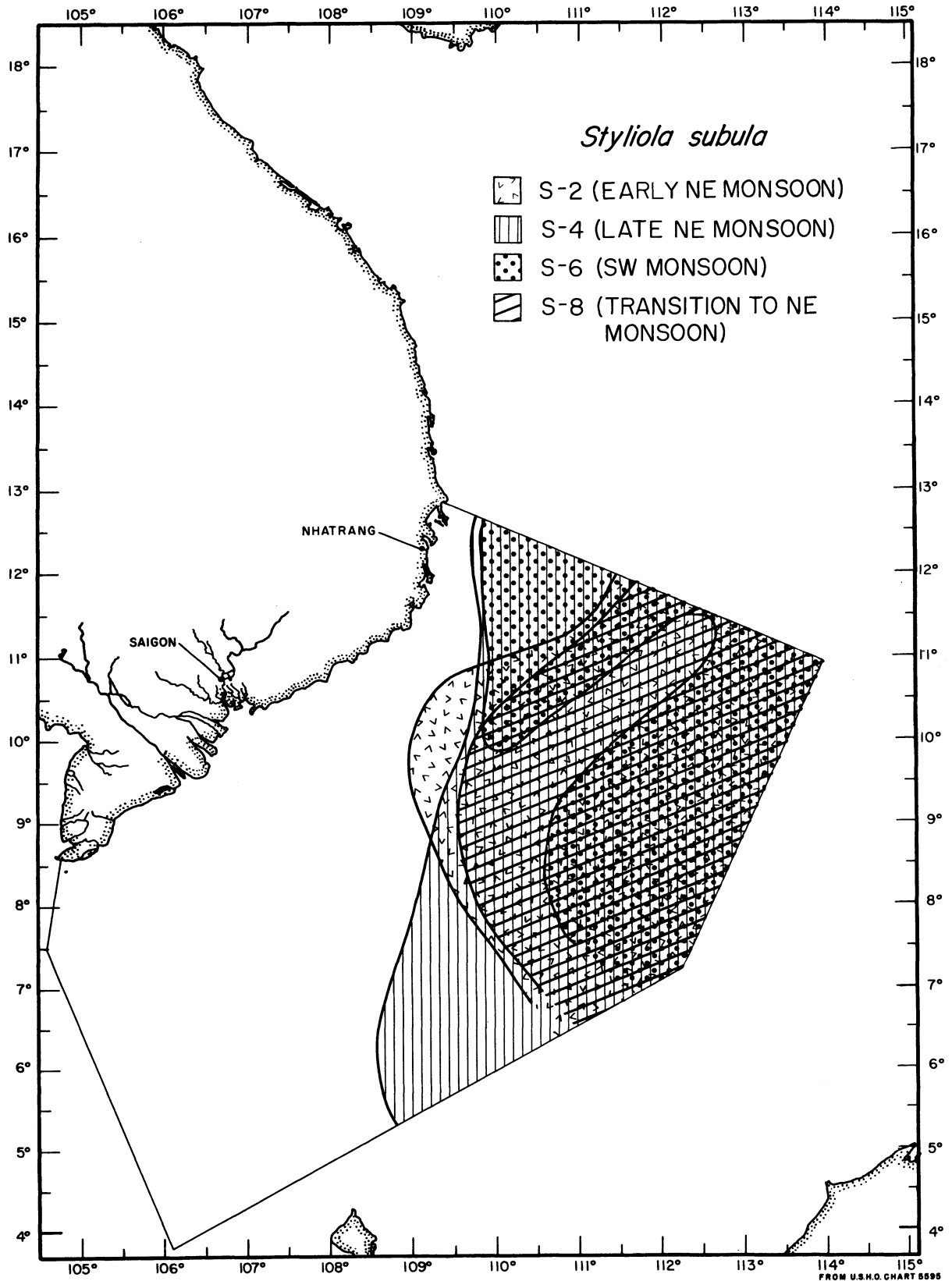


Figure 6. Southwestern limit of the distribution of *Styliola subula* during cruises S-2 through S-8.

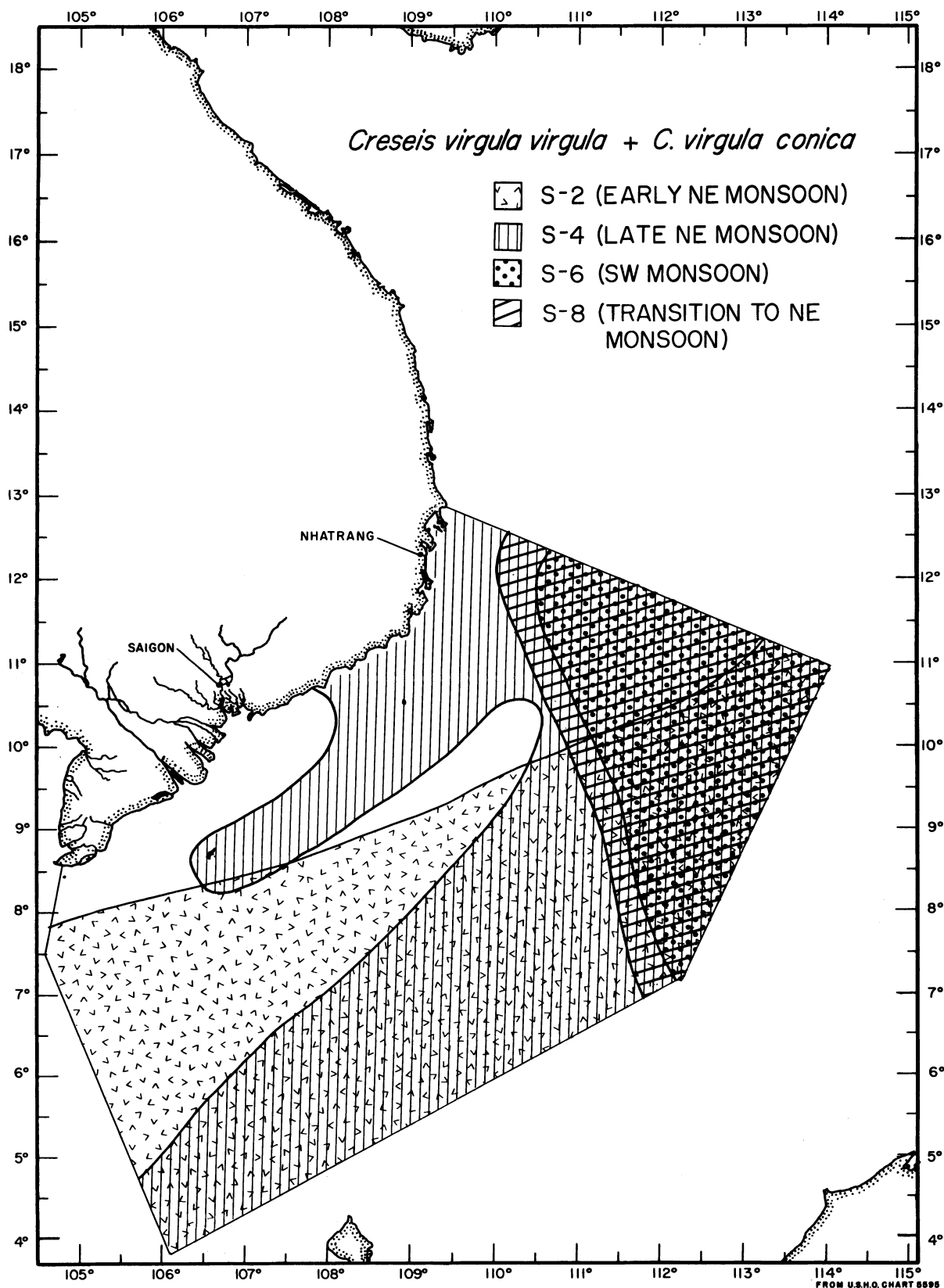


Figure 7. Southwestern limit of the distribution of *Creseis virgula* during cruises S-2 through S-8.

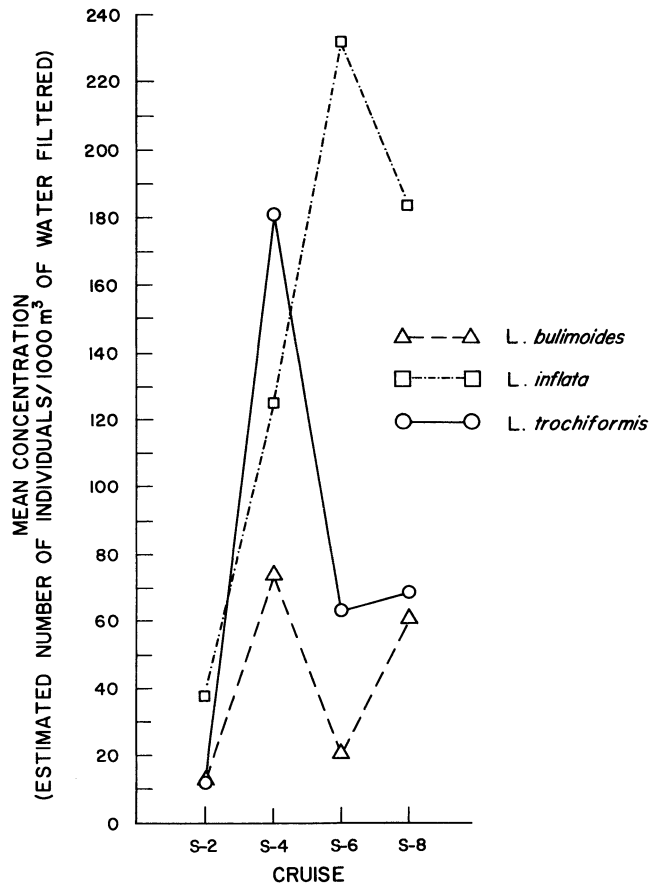


Figure 8. Mean concentrations of three species of *Limacina* in the South China Sea.

46° N, or in the cooler parts of the California Current. Because the equatorial waters of the Indian Ocean and the Pacific intercommunicate through the Indo-Australian Archipelago it is strange that *C. [recurva]* has not been found in the equatorial Pacific.

“In addition to this peculiar distribution pattern Tesch noted a further eccentricity of the species; he pointed out that the ‘young’ specimens collected by the Dana in the Indo-Australian region had ‘cusped, not obtuse embryonic shells,’ a feature also noted by Meisenheimer of his one Pacific specimen taken north of New Guinea near the equator . . . However, an explanation of these inconsistencies may be possible . . . *Clio* [sp., informally described in this thesis] bears some resemblance to *C. [recurva]* . . . In addition *Clio* [sp.] has a sharply cusped larval shell and is, in the Pacific, an equatorial species. If it may be assumed that both Tesch and Meisenheimer were dealing with adult *Clio* [sp.] which they believed to be young *C. [recurva]*, then the distributional and morphological problems mentioned above would be resolved. But more data are necessary.”

However, *Clio recurva* was found in the South China Sea. Thus the additional data provided by Naga have not given support to an easy resolution of the problems of (1) the relationships of Meisenheimer’s (1905) New Guinea specimen and Tesch’s (1946) “young” Indo-Australian specimens, called *Clio [recurva]*, to McGowan’s *Clio* [sp.] and to *Clio recurva* as designated by Spoel (1967) (see p. 85, below), and (2) the apparent absence of *Clio recurva* from the equatorial Pacific east of the Naga area but not from the equatorial Indian Ocean. There can be no doubt about the identity of the specimens of *C. recurva* from the Naga material. The larval shell is rounded, not cusped, the lateral edges are produced into distinct “gutters,” not just truncate as

in *Clio* [sp.], and several rather large specimens were found, one measuring 20 mm in length. In addition, the shell is curved dorsally, and there are three longitudinal dorsal ridges. These characters do not fit McGowan's description of *Clio* [sp.], but they do fit *C. recurva*. Thus, it would seem that some further explanation of the apparent distribution of *C. recurva* is necessary.

The distribution pattern of *Diacria quadridentata* in the Gulf of Thailand suggests that populations are transported into the Gulf from the South China Sea area and are maintained there as long as conditions are favorable. The results of the first Naga cruise (S-1) indicated that such an influx was taking place during the October 1959 transition to the northeast monsoon. At that time adult *D. quadridentata* were present at the three westernmost stations of line 5 (at the mouth of the Gulf) and at one station along the western part of line 4, as well as at one station farther up the Gulf, just off Ko Chang (Fig. 29a). This last occurrence may have been the residual survivor from a previous influx. Juveniles were present at two of the stations where adults were found at the southern end of the Gulf and reached their maximum abundance at the same station as the adults. In general, where they occurred together, juvenile population densities were much lower than adult concentrations. Juveniles were also present at two stations on line 5 and at one station on line 4 where there were no adults. During January 1963 (S-3) none of this species was found along line 5 and the distribution lies in a wide band across the central Gulf, narrowing at the coasts. Juveniles were present at only one station during S-3, the station at which adults were at their maximum. Juvenile abundance at this station was low (9/1000 m³). This pattern suggests an influx of a population from outside the Gulf as the northeast monsoon developed (S-1). As the dry season progressed the population moved up into the Gulf and spread out, at the same time losing juveniles.

Redfield (1939) studied the history of a population of *Limacina retroversa* as it entered and drifted across the Gulf of Maine, spreading out as it progressed. On the basis of size distributions, he concluded that *L. retroversa* probably reproduced during its drift. In the case of *Diacria quadridentata* in the Gulf of Thailand, the evidence suggests that reproduction does not take place since the juvenile population was reduced as the population progressed up the Gulf. *D. quadridentata* was completely absent from the Gulf of Thailand during the next cruise in April-May 1960 (S-5) when surface temperatures were above 30°C. Between April-May and August (S-7) temperatures cooled and *D. quadridentata* re-entered the Gulf in approximately the same area as it did prior to S-1. Line 5 was omitted on the November 1960 cruise (S-9) so the extent of the *D. quadridentata* distribution at the mouth of the Gulf is unknown. However, the known November 1960 distribution suggests that between August (S-7) and November (S-9) *D. quadridentata* moved somewhat further up the Gulf and decreased significantly in abundance.

Spoel (1967) gives temperature and salinity ranges for most pteropod species. The lower limits of the salinity ranges given by Spoel appear to be too high for all species found in the Naga samples. Except in coastal areas affected by runoff (where salinities are even lower), the salinity at 10 m in the South China Sea is generally between 33 and 34 ‰. Even at 50 m, salinities greater than 34 ‰ do not dominate. Therefore, all twenty species recorded here tolerate salinities between 33 and 34 ‰. Further, those species which inhabit the Gulf of Thailand can withstand much lower salinities. The lowest salinity at which each of the five Gulf species was found is as follows (salinities are given as ranges because they were taken from contoured salinity maps in Robinson, 1974): *Cavolina longirostris*, 27.5-28.0 ‰; *Creseis acicula*, 27.5-28.0 ‰; *Limacina trochiformis*, 29.5-30.0 ‰; *Hyalocylis striatay*, 30.5-31.0 ‰; *Diacria quadridentata*, 31.0-31.5 ‰. Spoel noted Tampi's (1959) report of a salinity range of 25-45 ‰ and a temperature range of 26-33° C. for *Creseis acicula* as an exception, but these ranges are certainly more in keeping with the Naga results than those given by Spoel (10.0-27.9°C and 35.5-36.7 ‰). In the Naga samples *C. acicula* reached its maximum abundance of 27,300/1000 m³ at a station where the salinity was slightly less than 31.0 ‰ at the surface and about 32 ‰ near the bottom. It might be supposed that the salinity limits suggested here represent isolated catches of a few specimens. However, this is not the general case though *H. striata* and *D. quadridentata* were not really abundant at the lower limit observed. *H. striata* generally preferred salinities greater than 32 ‰ and reached its peak abundance of 14,200/1000 m³ at a station where the surface salinity was

between 32.5 and 33.0%. Spoel, on the other hand, states that with respect to *H. striata* “the salinity is always near 36.2‰.”

The upper limits of the temperature ranges given by Spoel (1967) appear to be too low. All species were present at stations where the temperature exceeded 29°C. *Creseis acicula*, *Limacina trochiformis*, and *Cavolina longirostris* were all present in the Gulf of Thailand during S-5 when all surface temperatures were greater than 30°C, but *Hyalocylis striata* and *Diacria quadridentata* were then completely absent. It may be significant that *Creseis acicula* and *Limacina trochiformis* were at the lowest mean concentrations for the Gulf of Thailand and during this period of high temperatures. Though *H. striata* and *D. quadridentata* were absent from the Gulf during the warm inter-monsoon period (S-5), both species were present at several stations occupied in the South China Sea during September-October 1960 (S-8) where the temperature exceeded 30°C. Perhaps the generally lower salinities of the Gulf of Thailand make it more difficult for these species to withstand high temperatures.

Some general effects of the presence of other organisms on the abundance of pteropods were noted. Large concentrations of salps and echinoderm larvae seemed to be accompanied by a lower abundance of pteropods. This inverse relationship is true to an even greater extent with heavy phytoplankton concentrations. At most stations where phytoplankton occurred in unusually heavy concentrations pteropods were rare.

The following discussion treats the cruises individually in terms of seasonal and hydrographic parameters and their relation to the distributions of pteropod species. The climatic and oceanographic information used here was taken from Robinson (1974). South China Sea temperature and upwelling information is found in LaFond (1963). Table 2 presents the mean zooplankton volumes for each cruise. In the South China Sea nearly all pteropod species had their lowest mean population densities during November-December 1959 (S-2). This was also the period of lowest mean zooplankton volume (Fig. 9). The cruise having the greatest number of species (7) with highest mean concentrations was during September-October 1960 (S-8) (Table 3), the period of highest mean zooplankton volume. In the Gulf of Thailand the situation was rather different (Fig. 10). While October 1959 (S-1) was the period of lowest mean zooplankton volume, only *Cavolina longirostris* then had its lowest mean population density. The inter-monsoon period of April-May 1960 (S-5) was by far the period of highest mean zooplankton volume in the Gulf but it was also the period when all the other Gulf pteropods (except *C. longirostris*) were at their lowest mean concentrations (Table 4). During the southwest monsoon, 1960 (S-7), the period of third highest mean zooplankton volume, all Gulf species except *Limacina trochiformis* were found at their highest mean concentrations.

Table 2 MEAN ZOOPLANKTON VOLUMES

Cruise	Total (cc/1000 m ³)	No. of Stations	Mean (cc/1000 m ³)
S-1	6,550	33	199
S-2	1,150	26	44
S-3	8,440	33	256
S-4	3,470	41	85
S-5	39,300	67	587
S-6	4,190	50	84
S-7	24,400	62	393
S-8	4,270	43	99
S-9	23,300	58	401

Table 3 Highest and Lowest Mean Concentration of Each Species in the South China Sea

SPECIES	MEAN CONCENTRATION (No. of individuals/1000 m ²)	CRUISE DURING WHICH LOWEST MEAN CONCENTRATION OCCURRED			
		S-2	S-4	S-6	S-8
<i>Cavolina gibbosa</i>	0.00	X	X		
<i>Cavolina globulosa</i>	1.17			X	
<i>Cavolina inflexa</i>	1.11	X			
<i>Cavolina longirostris</i>	1.31	X			
<i>Cavolina uncinata</i>	0.00	X			
<i>Clio pyramidata</i>	0.807	X			
<i>Creseis acicula</i>	51.50	X			
<i>Creseis virgula</i>	2.35				X
<i>virgula + C.</i>					
<i>virgula conica</i>					
<i>Cuvierina columnella</i>	0.00		X		
<i>Diacria quadridentata</i>	13.80	X			
<i>Diacria trispinosa</i>	0.846	X			
<i>Hyalocylis striata</i>	4.92	X			
<i>Limacina bulimoides</i>	12.00	X			
<i>Limacina inflata</i>	37.40	X			
<i>Limacina trochiformis</i>	11.50	X			
<i>Styliola subula</i>	10.50	X			
SPECIES	MEAN CONCENTRATION (No. of individuals/1000 m ³)	CRUISE DURING WHICH HIGHEST MEAN CONCENTRATION OCCURRED			
		S-2	S-4	S-6	S-8
<i>Cavolina gibbosa</i>	0.869				X
<i>Cavolina globulosa</i>	8.49		X		
<i>Cavolina inflexa</i>	4.78			X	
<i>Cavolina longirostris</i>	19.40				X
<i>Cavolina uncinata</i>	0.452			X	
<i>Clio pyramidata</i>	7.73		X		
<i>Creseis acicula</i>	22600				X
<i>Creseis virgula</i>	11.30			X	
<i>virgula + C.</i>					
<i>virgula conica</i>					
<i>Cuvierina columnella</i>	0.804				X
<i>Diacria quadridentata</i>	67.20				X
<i>Diacria trispinosa</i>	8.87				X
<i>Hyalocylis striata</i>	24100				X
<i>Limacina bulimoides</i>	73.50		X		
<i>Limacina inflata</i>	23200			X	
<i>Limacina trochiformis</i>	18100		X		
<i>Styliola subula</i>	46.20			X	

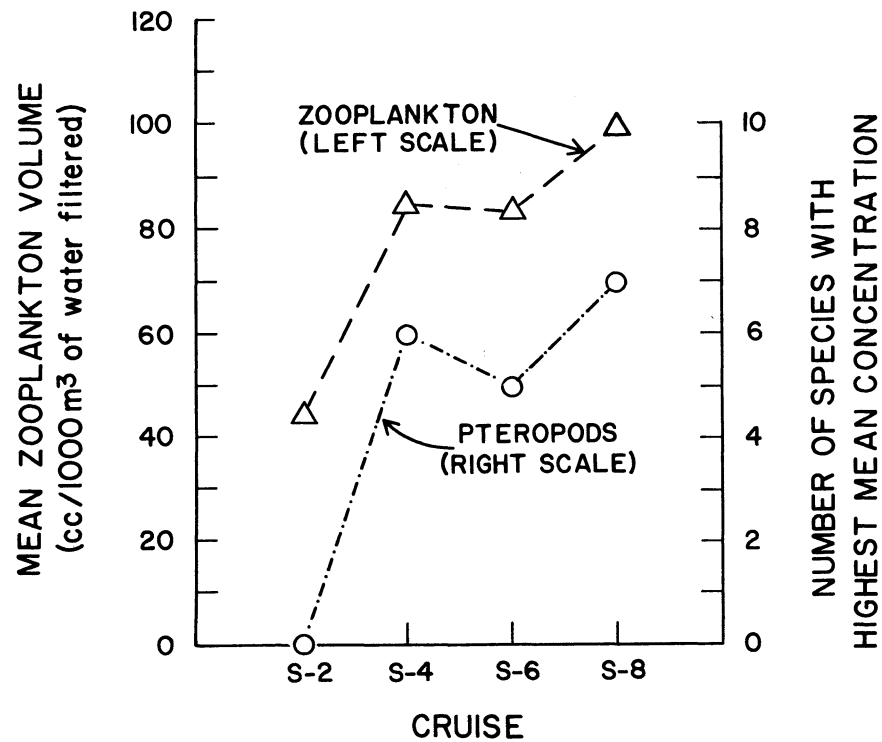


Figure 9. South China Sea. Mean zooplankton volume and number of species with highest mean concentration for each cruise.

Table 4 HIGHEST AND LOWEST MEAN CONCENTRATION OF EACH SPECIES IN THE GULF OF THAILAND

Species	Mean Concentration (No. of individuals/1000 m ³)	Cruise During Which Lowest Mean Concentration Occurred				
		S-1	S-3	S-5	S-7	S-9
<i>Cavolina longirostris</i>	30.8	X				
<i>Creseis acicula</i>	91.9			X		
<i>Diacria quadridentata</i>	0			X		
<i>Hyalocylis striata</i>	0		X	X		
<i>Limacina trochiformis</i>	23.9			X		
Species	Mean Concentration (No. of individuals/1000 m ³)	Cruise During Which Highest Mean Concentration Occurred				
		S-1	S-3	S-5	S-7	S-9
<i>Cavolina longirostris</i>	333				X	
<i>Creseis acicula</i>	1120				X	
<i>Diacria quadridentata</i>	19.6				X	
<i>Hyalocylis striata</i>	503				X	
<i>Limacina trochiformis</i>	118		X			

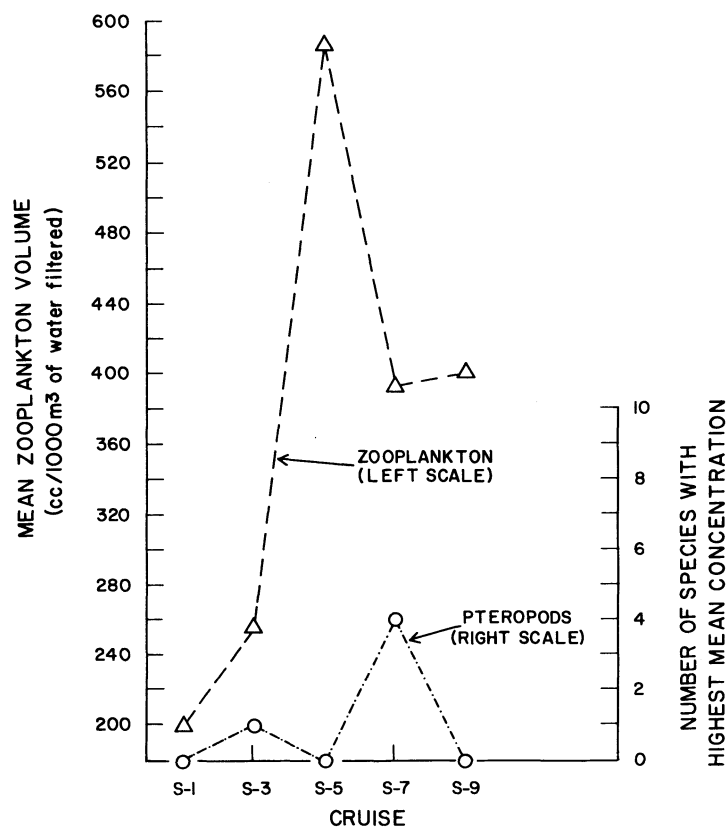


Figure 10. Gulf of Thailand. Mean zooplankton volume and number of species with highest mean concentration for each cruise.

GULF OF THAILAND

October 19-31, 1959 (Cruise S-1). This cruise was conducted during the transition from the southwest to northeast monsoon season. The area from Samit Point to Cape Camau was one of relative abundance for *Creseis acicula* (Fig. 24a) and *Cavolina longirostris* (Fig. 20a). This was associated with the period of maximum river flow and runoff. The greatest abundance of *C. longirostris* (one which was more than twice that found at any other S-1 station) occurred just off Phu Quoc Island, where the salinity was very low (less than 28 ‰). High population densities also occurred at several other stations in the same general area. *Creseis acicula* was the only species that was widely distributed in the Gulf during S-1. There were three areas in which it was most abundant: off Songkhla, at mid-Gulf on line 4, and along the east coast from Samit Point to Cape Camau. An area of high population density, similarly centered around the middle of line 4, occurred during S-5, which was conducted during the other inter-monsoon period (April-May).

January 19-30, 1960 (Cruise S-3). During this period, all Gulf species were widespread and fairly abundant, except *Hyalocylis striata* which was absent (Fig. 31a). Along the northwest coast of the Gulf there was a concentration of surface water having relatively low salinity (30.0-30.9 ‰) and low temperature (27.0-27.9°C). This water extended (with slightly higher salinities) south-

eastward. In this area both *Limacina trochiformis* (Fig. 34a) and *Cavolina longirostris* (Fig. 20b) achieved their highest concentrations for this cruise. *Limacina trochiformis* (Fig. 34a) was absent in the area of influx and exit of a body of cold, high-salinity water around Cape Camau and along line 5, while *Creseis acicula* was relatively abundant there (Fig. 24a). Both *C. acicula* and *C. longirostris* were particularly abundant in the Samit Point to Phu Quoc Island area, as they were during October 1959 (S-1), but population densities for both species in this area were higher in January than in October.

April 21-May 2, 1960 (Cruise S-5). This cruise took place during the transition month between the southwest and northeast monsoon seasons. Rainfall was slightly below average on the surrounding land areas and river discharge was low. During this period surface temperatures were everywhere above 30°C and were the highest observed on any of the cruises. Mean zooplankton volume was also at its maximum, nearly one and one-half times that observed during any other Gulf cruise (Fig. 10). In contrast all pteropod species, except *Cavolina longirostris*, then had their lowest mean densities for the Gulf of Thailand (Table 4), and two species, *Hyalocylis striata* (Fig. 31a) and *Diacria quadridentata* (Fig. 29c) were absent.

Cavolina longirostris (Fig. 20c) and *Creseis acicula* (Fig. 24a) were, as usual, abundant in the Samit Point to Cape Camau area, even during this period of low river discharge. These two species were widespread in the coastal areas of the Gulf and absent farther offshore. *C. acicula* was also relatively abundant in a large patch centered on line 4. *Limacina trochiformis*, on the other hand, was concentrated over the central trough in a tongue extending as far north as line 2 (Fig. 34a). This difference in distributions is a clear example of the general pattern of pteropod distributions in the Gulf of Thailand: *C. acicula* and *C. longirostris* thrive in the rigorous environment of the Gulf coastal areas while the remaining three species *L. trochiformis*, *H. striata*, and *D. quadridentata*, when present, prefer the central area of the Gulf. Of these latter three species, *L. trochiformis* is the most tolerant of coastal conditions.

Creseis virgula conica and *C. virgula virgula* were found, each at only one station and at very low concentrations, in the Gulf during this cruise (Fig. 27). This was the only instance in which either one occurred in a Gulf sample and suggests the possibility that this sample was accidentally contaminated with plankton from another region. However, preliminary results of a study by this author of bottom samples from the Gulf show that *C. virgula conica*, at least, is present at times in the Gulf.

August 2-14, 1960 (Cruise S-7). Cruise S-7 was conducted during the height of the southwest monsoon. Surface temperatures had cooled considerably since April-May (S-5); no surface temperatures exceeded 30°C and most were less than 29°C. All Gulf pteropod species, except *Limacina trochiformis*, achieved their maximum mean densities during this cruise (Table 4), while the mean zooplankton volume was only about two-thirds the S-5 value (Fig. 10).

Surface salinities were relatively low along the east coast (less than 32.0 ‰), probably as a result of the higher than average rainfall there. Rainfall was lower than normal along much of the west coast and surface salinities were higher (greater than 32.0 ‰). *Diacria quadridentata* (Fig. 29d), *Hyalocylis striata* (Fig. 31b) and *Limacina trochiformis* (Fig. 34b) were concentrated in the central Gulf. Where present at coastal stations, they were mostly limited to the west coast along which salinities were higher. *Cavolina longirostris* (Fig. 20d), and *Creseis acicula* (Fig. 24b), on the other hand, were generally more abundant around the margins of the Gulf and were widely present in the low salinity area.

After being absent from the Gulf during the April-May 1960 (S-5) period of high temperatures, both *Diacria quadridentata* (Fig. 29d) and *Hyalocylis striata* (Fig. 31b) had returned to the Gulf by August (S-7). Both species were distributed in a tongue-like pattern in the central Gulf, reaching as far north as line 3, but *H. striata* had a wider distribution and was far more abundant (mean, 503/1000 m³; maximum, 14,200/1000 m³) than *D. quadridentata* (mean, 19.6/1000 m³; maximum, 417/1000 m³).

Three cruises sampled the Bight of Bangkok at the head of the Gulf: S-5, S-7, and S-9, – all just before or during the southwest monsoon season. Only *Cavolina longirostris* (Fig. 20d,e) and *Creseis acicula* (Fig. 24a,b) were found within the Bight. During S-5 only *C. acicula* was present in the Bight, where it reached its second highest abundance for that cruise (660/1000 m³) at the northernmost station.

Despite the August 1960 rainfall at Bangkok being higher than normal for this season (Robinson, 1974) and the river discharge much increased over previous months, surface salinities were 33.0-33.9‰ at the head of the Gulf and in the Bight – the highest recorded for this area by the Naga expedition. *Creseis acicula* was present at all six stations in the Bight, but it was more abundant at the eastern stations where it reached a density of 18,500/1000 m³, about eight times the maximum abundance observed outside the Bight during this cruise and about four times the density achieved at any other Bight station. *Cavolina longirostris*, on the other hand, was found at only the three eastern stations in the Bight and was quite abundant at two of these (467 and 635/1000 m³).

November 8-24, 1960 (Cruise S-9). Though the northeast monsoon is normally well developed in November, winds were highly variable during S-9 (Robinson, 1974) and the maximum rainfall for the year fell along the southwest coast of the Gulf. All Gulf species were present. *Diacria quadridentata* was found at only three stations; juveniles were present at two of these and population densities for both adults and juveniles were extremely low at the two northern stations. The distribution pattern of *D. quadridentata* (Fig. 29e) is strikingly similar to that of well oxygenated water at 50 m. There was a large body of high salinity (greater than 33.0‰) water in the central Gulf and this area was relatively unfavorable for all species.

The distribution of *Hyalocylis striata* (Fig. 31b) suggests that the population which entered the Gulf during May-July (between S-5 and S-7) moved northward and decreased in numbers during September-October (between S-7 and S-9). While this species was still comparatively abundant at a few stations, neither the maximum (3,000/1000 m³) nor the mean (96.1/1000 m³) population density was comparable to S-7 values (14,200/1000 m³ and 503/1000 m³ respectively).

Cavolina longirostris (Fig. 20e) and *Creseis acicula* (Fig. 24b) were again observed in the Bight of Bangkok, where *C. acicula* was relatively abundant (600/1000 m³), while *C. longirostris* occurred in much smaller numbers (70/1000 m³). Two other species, *Hyalocylis striata* (Fig. 31b) and *Limacina trochiformis* (Fig. 34b) occurred, though in low concentrations (13/1000 m³), at station 39 just south of the “neck” of the Bight. This was the northernmost occurrence of these two species recorded in the Gulf of Thailand during the Naga cruises.

The low salinity area along the west coast of the Gulf was probably the result of the high rainfall on the adjacent land. Within this low salinity area, south of Songkhla, *Creseis acicula* occurred in the highest concentration recorded for any pteropod species during the Naga cruises: 27,300/1000 m³.

SOUTH CHINA SEA

November 26 - December 13, 1959 (Cruise S-2). The northernmost lines (1 and 2) were omitted during this first South China Sea cruise, which took place during the early part of the northeast monsoon season. Flow in the Mekong River had peaked two months earlier (in September) but there was still some dilution of nearshore waters.

All but three species were at their lowest observed mean concentrations during this cruise. Of the three exceptions, two are large species of *Cavolina* (*C. globulosa*, Fig. 18a, and *C. inflexa*, Fig. 19a) whose occurrence in the samples was so infrequent and irregular that comparisons of

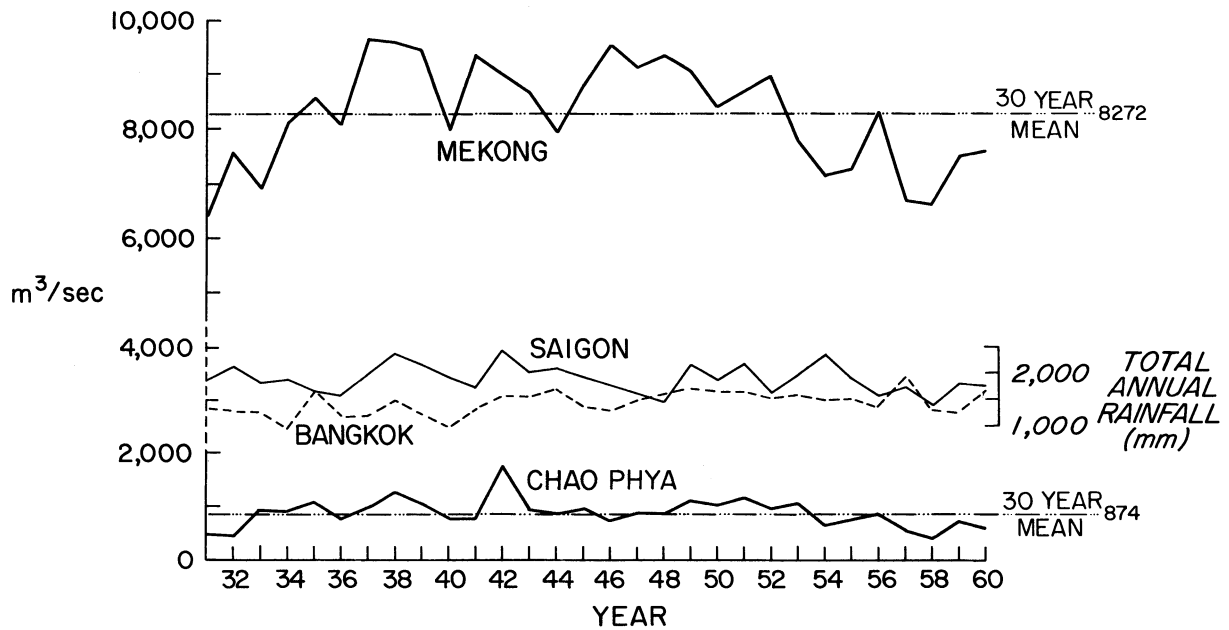


Figure 11. Comparison of total annual rainfall with mean annual river flow (reproduced from Robinson, 1974).

mean concentration between cruises are not meaningful. The third species was *Creseis virgula clava* (Fig. 26a). Why did the first Naga cruises, October 1959 in the Gulf of Thailand (S-1), and November-December 1959 in the South China Sea (S-2) find such low concentrations of pteropods? No decisive answer can be provided, but it may be significant that the 1957 and 1958 mean annual flow rates of the Mekong River were farther below the 30-year mean than at any time since 1931 (Fig. 11). The same situation prevailed in the Gulf of Thailand, where the mean annual flow of the Chao Phya River had not been as far below the 30-year mean since 1932. In fact Figure 12 shows that the 1956-1960 five-year mean monthly flow during peak flow months was nearly 1200 m³/sec, i.e., more than one-third, below the 1931-1950 20-year mean. Can these low flow years have seriously affected the supply of nutrients and organic matter to the Gulf of Thailand and the South China Sea?

During October 1960 (S-2) all pteropod species except *Creseis acicula* (Fig. 24a) and *Limacina bulimoides* (Fig. 32) were absent from the nearshore stations on lines 5 and 6 where the influence of the Mekong River is most pronounced. *C. acicula* was always present at these stations and its abundance at coastal stations in the Gulf of Thailand is an indication of its tolerance for nearshore, high runoff conditions. On the other hand, *L. bulimoides* is a member of the offshore, oceanic group of pteropods, and it is surprising to find it at the nearshore station just opposite the mouth of the Mekong River. It is not surprising that it occurred in low numbers in this sample (4/1000 m³).

During this early part of the northeast monsoon all species which are also found in the Gulf of Thailand were present at most line 5 and line 6 stations, southwest of the Indochinese peninsula (except *Hyalocylis striata*, Figure 31a, which was, nevertheless, present at some stations). The following oceanic species were also present at some of the more offshore stations on lines 5 and 6: *Cavolina globulosa* (Fig. 18a), *C. inflexa* (Fig. 19a), *Limacina bulimoides* (Fig. 32), and *L. inflata* (Fig. 33).

February 27-March 19, 1960 (Cruise S-4). This cruise took place near the end of the dry season (northeast monsoon) and salinities were nowhere less than 33 ‰. *Creseis acicula* (Fig. 24a)

and *Limacina trochiformis* (Fig. 34a) were the only species present at the nearshore stations of the southern lines (5 and 6), despite the fact that there was no evidence of dilution by the Mekong. *Diacria quadridentata*, *Hyalocylis striata*, and *Limacina bulimoides*, as well as the more characteristically oceanic species *Creseis virgula virgula* + *C. virgula conica*, *Cavolina inflexa*, *C. globulosa*, *C. uncinata*, *Styliola subula*, and *L. inflata*, were each present somewhere along the outer half of line 5 and/or 6. This period at the end of the northeast monsoon saw the maximum southward penetration of oceanic group species. At the same time the distribution of *Cavolina longirostris* (Fig. 20b) was shifted southward in the northern part of the South China Sea and this species was completely absent from the northernmost line (1) and from all but two stations of line 2.

Upwelling occurred along the shoreward ends of lines 2, 3, and 4 (LaFond, 1963) and may have contributed to relatively great abundances of *Creseis acicula* (Fig. 24a) and *Limacina trochiformis* (Fig. 34a) in that area. *Limacina inflata* (Fig. 33) was present at all stations except the nearshore stations of lines 1 and 5 and all but the outermost line 6 station but it did not reach its maximum mean concentration until the following cruise. On the other hand, *L. trochiformis* and *L. bulimoides* were at their peak mean concentrations during this cruise (S-4) (Fig. 8).

May 21-June 24, 1960 (Cruise S-6). The southwest monsoon was fully developed during this period. Since maximum flow in the Mekong River was not reached for another two months (August), only slight dilution of nearshore waters was recorded. Upwelling occurred on line 4 and may have contributed to the relative abundance of *Limacina trochiformis* there (Fig. 34a).

During this period of well developed southwest winds, the distributions of the oceanic group of species (i.e., those which do not occur in the Gulf of Thailand) were shifted northward and did not penetrate as far south as line 5. There were three exceptions: *Cavolina uncinata*, present

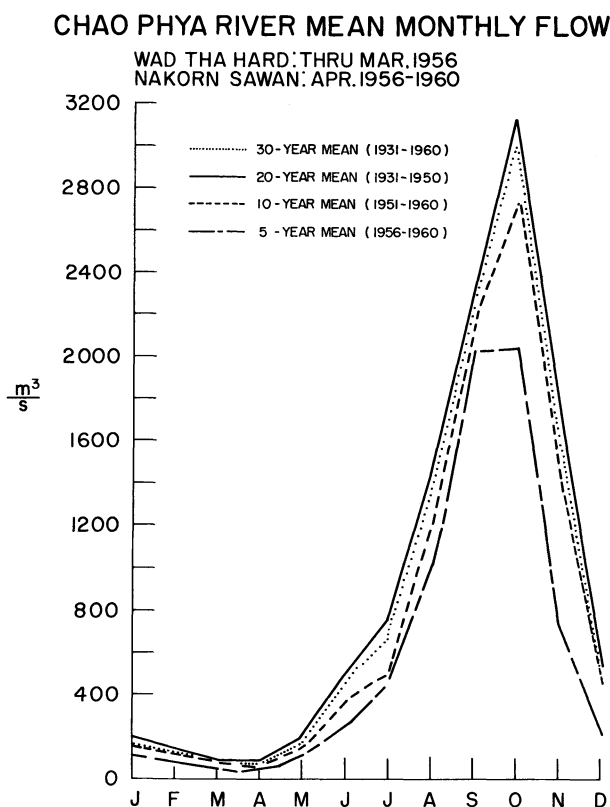


Figure 12. Five-, ten-, twenty-, and thirty-year mean monthly flow of the Chao Phya River (reproduced from Robinson, 1974).

at one station between lines 5 and 6 (Fig. 21); *C. inflexa* juveniles, present at two stations of line 6 and at two on the track between lines 5 and 6 (Fig. 19b); and *Limacina inflata* at one station at the offshore end of line 5 (Fig. 33). At the same time that the southern limit of oceanic species distributions was shifted northward, *Cavolina longirostris* moved northward to occupy the area of lines 1 and 2 (Fig. 20c). This was the only cruise during which this species was consistently present this far north.

While other species were concentrated to the north during the southwest monsoon season, the distribution of *Creseis acicula* indicated a reverse pattern with a drop in abundance along lines 1 through 4. Mean abundance (for total cruise area) of *C. acicula* rose between March and May (between S-4 and S-6) but this was largely the result of high concentrations at about five stations in the shallow southern shelf part of the South China Sea, lines 5 and 6 (Fig. 24a). Between S-4 and S-6 the number of stations in the northern two-thirds of the area (lines 1 through 4) that had abundances of *C. acicula* greater than 50/1000 m³ dropped to one-half the S-4 number (14 down to 6).

Limacina inflata reached its maximum mean concentration during May-June (S-6), while the mean concentrations of both *L. trochiformis* and *L. bulimoides* dropped from their February-March (S-4) values (Fig. 8). In addition to *L. inflata*, two other species reached their peak abundances during S-6: *Creseis virgula virgula* + *C. virgula conica* and *Styliola subula*. *S. subula* reached relatively high densities at some stations (up to 683/1000 m³).

September 6-October 8, 1960 (Cruise S-8). This cruise took place during the transition period from southwest to northeast monsoon. Nevertheless, rainfall was still high and the Mekong River flow was higher than the 30-year mean for the months of September and October. Lowering of salinities to less than 33 ‰ was evident at the nearshore stations on lines 2 through 6 and extended past the second station from shore on lines 3 and 5. At the nearshore station on line 5, just off the mouth of the Mekong, the salinity had fallen to 30.66 ‰. At Cape Camau the salinity was down to 31.59 ‰. Only *Cavolina longirostris* (Fig. 20d) and *Creseis acicula* (Fig. 24b) were present at the nearshore stations of lines 5 and 6, where maximum dilution occurred. *C. acicula* was particularly abundant (in terms of this cruise) at these stations. With the seasonal shift toward northeast winds, *Cavolina longirostris* was present at only four scattered stations in the area covered by lines 1 and 2.

Four of the five Gulf species had their highest mean concentrations during September-October: *Cavolina longirostris*, *Creseis acicula*, *Diacria quadridentata* and *Hyalocylis striata*. The only other species then reaching its peak mean concentration was *Diacria trispinosa*. *Creseis virgula virgula* + *C. virgula conica* was the only species which had its lowest mean abundance during S-8. *L. inflata* was still quite abundant, though its maximum (2140/1000 m³) and its mean (184/1000 m³) were considerably below the May-June (S-6) highs (232/1000 m³ and 4010/1000 m³ respectively).

Hyalocylis striata was very abundant to the south (Fig. 31b), along line 6. The distribution of stations at which it was abundant suggests that there was a relationship between these large concentrations and the presence of large numbers of *H. striata* in the Gulf of Thailand during the preceding August (S-7). The S-8 distributions of several other species suggest similar relationships with S-7 species patterns, for example, *Creseis acicula* (Fig. 24b), *Diacria quadridentata* (Fig. 29b), and *Limacina trochiformis* (Fig. 34b).

SECTION III. ENVIRONMENTAL RELATIONSHIPS AND SPECIES GROUPINGS

The impressions gained by visual study of distribution maps have been supplemented by a statistical study of pteropod distributions. The statistical study has concentrated on two major questions: (1) are there two basic groups of pteropods in the survey area, as the distribution maps suggest (see page 11), and (2) are there significant associations between hydrographic parameters and species-abundance?

SPECIES ASSOCIATIONS

Table 5 presents the index of affinity calculated for each species pair. Figure 13 is a diagrammatic representation of the recurrent groups found using all indices of affinity greater than or equal to 0.500 (indicating that the species considered were part of each other's environment somewhat more than half the time). Species having affinity only with some but not all members of an established group are called associate species.

Two, *Creseis acicula* and *Limacina trochiformis*, of the three species in Group I (Fig. 13) are found in the Gulf of Thailand at all seasons. The third, *Diacria quadridentata*, was not present in the Gulf during the northeast to southwest intermonsoon period when all surface temperatures exceeded 30°C. The two Group I associate species, *Hyalocylis striata* and *Cavolina longirostris*, also occur in the Gulf of Thailand. Group II consists of four species not found in the Gulf: *Limacina inflata*, *L. bulimoides*, *Clio pyramidata*, and *Styliola subula*. Group II's single associate, *Creseis virgula virgula* + *C. virgula conica*, was also not found in the Gulf. These results confirm the intuitive conclusion that there are two recurrent groups of species. One group (Group I),

Table 5 INDEX OF AFFINITY

	TOTAL NUMBER OF OCCUR- RENCES	<i>Creseis</i> <i>acicula</i>	<i>Creseis</i> <i>virgula</i> + <i>C.</i> <i>virgula</i> <i>conica</i>	<i>Cavolina</i> <i>lon-</i> <i>girostris</i>	<i>Limacina</i> <i>inflata</i>	<i>Limacina</i> <i>trochi-</i> <i>formis</i>	<i>Limacina</i> <i>bu-</i> <i>limoides</i>	<i>Hyalocylis</i> <i>striata</i>	<i>Diacria</i> <i>quadri-</i> <i>dentata</i>	<i>Styliola</i> <i>subula</i>
<i>Creseis</i> <i>acicula</i>	356									
<i>Creseis</i> <i>virgule</i> <i>virgule</i> + <i>C.</i> <i>virgule</i> <i>conica</i>	58	.3662								
<i>Cavolina</i> <i>lon-</i> <i>girostris</i>	227	.6942	.2407							
<i>Limacina</i> <i>inflata</i>	97	.4468	.5415	.2496						
<i>Limacina</i> <i>trochi-</i> <i>formis</i>	221	.7076	.4206	.4888	.5398					
<i>Limacina</i> <i>bu-</i> <i>limoides</i>	103	.4639	.5514	.3520	.7807	.4761				
<i>Hyalocylis</i> <i>striata</i>	109	.5006	.1964	.4426	.3602	.4228	.4230			
<i>Diacria</i> <i>quadri-</i> <i>dentata</i>	153	.5924	.4842	.4038	.5913	.6105	.6438	.5623		
<i>Styliola</i> <i>subula</i>	70	.3679	.4491	.2228	.7656	.4268	.7312	.3101	.5516	
<i>Clio pyra-</i> <i>midata</i>	55	.3198	.4383	.1947	.6128	.3606	.6478	.2681	.4661	.7213

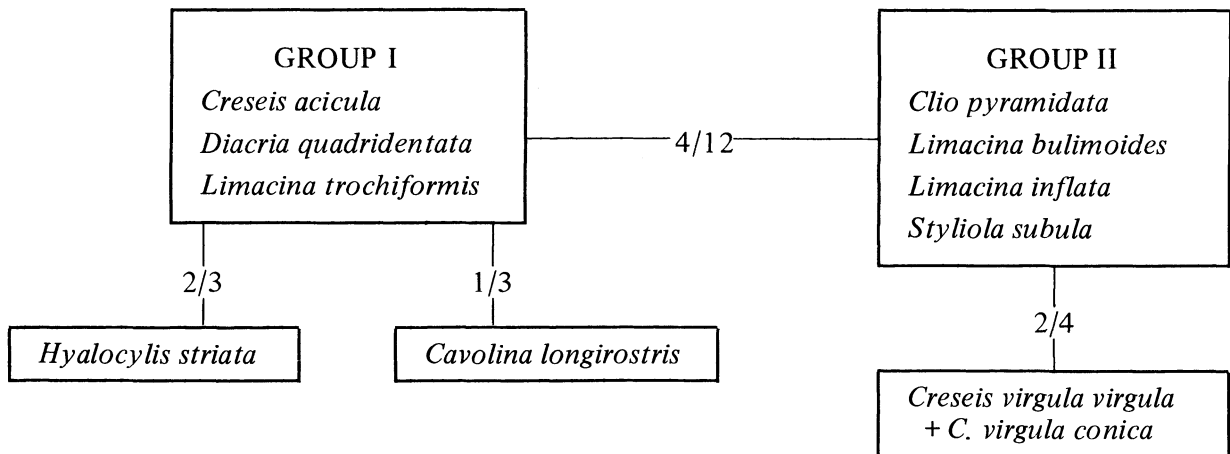


Figure 13. Diagrammatic representation of recurrent species groups formed using indices of affinity greater than or equal to 0.500. (Fractions appearing on linkage lines represent number of connections over total possible.

along with its associates, occurs in the Gulf of Thailand and over the shallow Sunda Shelf. The members of this group are also found in the oceanic areas of the South China Sea. Members of the other group (Group II), however, are not present in the Gulf of Thailand, and within the South China Sea they are generally found only in the oceanic (deep water) areas.

Recurrent species groups were established on the basis of simple presence and absence. Do the species of each group consistently rank the stations similarly in terms of their abundance? The results of the Friedman rank test provide an answer to this question. Table 6 gives the χ^2 values obtained for the Friedman statistic for several combinations of species (χ^2 values greater than 228.55 are significant at the 0.05 level, and χ^2 values greater than 242.1 are required for significance at the 0.01 level). Data from 197 stations were used for each concordance test. All species groupings given in Table 6 show significant agreement of abundance rankings at the 0.05 level and all but Group I are also significant at the 0.01 level.

The addition of its two associate species (*Hyalocylis striata* and *Limacina trochiformis*) to Group I (*Creseis acicula*, *Cavolina longirostris*, and *Diacria quadridentata*) increases the χ^2 value of the group to 340.14 ($p \ll 10^{-7}$). Thus the Gulf of Thailand group in the broad sense (all five species found in the Gulf) has highly significant agreement on abundance rankings.

The χ^2 value for Group II (*Limacina bulimoides*, *L. inflata*, *Clio pyramidata*, and *Styliola subula*) is 648.32. The addition of the group's associate species, *Creseis virgula virgula* + *C. virgula conica*, raises the χ^2 value for the total group of five species to more than twice the value for the Gulf of Thailand group in its broadest sense (Group I + 2 associates). Thus the members of the oceanic species group (Group II + associate) have extremely significant agreement on what constitutes a favorable habitat. The physical conditions of their environment are considerably less variable than those in the Gulf of Thailand. The agreement among the Gulf species is less significant and the Gulf habitat itself is more variable. These results probably reflect differing degrees of tolerance for varying environmental conditions between the groups. The oceanic group and its associate have a relatively narrow range of tolerance of environmental conditions and are thereby limited in their distribution. The Gulf species form a group because their tolerance of a wide range of environmental conditions allows them to inhabit the Gulf and shallow Sunda Shelf areas, but the responses of individual member species to particular environmental conditions are apparently not so consistently similar.

Table 6 RESULTS OF FRIEDMAN RANK TEST (CONCORDANCE)

Species Combination	Friedman Statistic $\sim\chi^2$ (196)
Group I (Gulf of Thailand)	
<i>Creseis acicula</i>	
<i>Diacria quadridentata</i>	
<i>Limacina trochiformis</i>	237.51
Group I + 1 Associate (<i>Hyalocylis striata</i>)	313.13
Group I + Both Associates (<i>H. striata</i> and <i>Cavolina longirostris</i>)	340.14
Group II (South China Sea)	
<i>Clio pyramidata</i>	
<i>Styliola subula</i>	
<i>Limacina inflata</i>	
<i>Limacina bulimoides</i>	648.32
Group II + Associate (<i>Creseis virgula virgula</i> + <i>C. virgula conica</i>)	728.62
Gulf of Thailand shallow water species pair	
<i>Creseis acicula</i>	
<i>Cavolina longirostris</i>	289.44
Gulf shallow water pair + <i>Limacina trochiformis</i>	265.15
Gulf of Thailand deeper water pair	
<i>Diacria quadridentata</i>	
<i>Hyalocylis striata</i>	316.09
Gulf deeper water pair + <i>Limacina trochiformis</i>	356.82
All 10 species used in the statistical analysis	555.66

PHYSICAL ENVIRONMENT

What physical conditions are associated with abundance of particular pteropod species? Table 7 gives Spearman's (1904) rank correlations between individual species abundances and temperature, salinity, and oxygen at 10 m and depth of water. The following species exhibit relatively high positive rank correlations (greater than 0.500) with depth of water: *Clio pyramidata*, *Creseis virgula virgula* + *C. virgula conica*, *Diacria quadridentata*, *Limacina bulimoides*, *L. inflata*, and *Styliola subula*. All but one of these (*D. quadridentata*, whose rank correlation of 0.545 with depth of water is next to lowest of the above species) belong to the oceanic group of species (Group II and associate). These same species, without *D. quadridentata*, also have relatively high rank correlations (greater than 0.400) with salinity. *Cavolina longirostris*, *Creseis acicula*, and *Limacina trochiformis* are not significantly correlated with salinity. The only species having significant negative rank correlation with depth is *Creseis acicula*, the most abundant pteropod species in the shallow parts of the Gulf of Thailand. *C. longirostris*, which was also

Table 7 SPEARMAN'S RANK CORRELATION COEFFICIENTS

	Depth of Water	Temperature at 10 m	Salinity at 10 m	Oxygen at 10 m
<i>Cavolina longirostris</i>	-.150	.104	-.228	-.267
	-2.118	1.451	-3.261	-3.866
<i>Clio pyramidata</i>	.611	-.188	.428	.184
	<u>10.740</u>	-2.665	<u>6.604</u>	2.605
<i>Creseis acicula</i>	-.388	-.006	-.214	-.294
	<u>-5.864</u>	-.085	-3.053	-4.280
<i>Creseis virgula</i> <i>virgula</i> + <i>C.</i> <i>virgula conica</i>	.514	-.202	.471	.239
	<u>8.351</u>	-2.878	7.445	<u>3.435</u>
<i>Diacria quadridentata</i>	.545	-.231	.357	.220
	9.046	-3.303	<u>5.331</u>	3.138
<i>Hyalicylis striata</i>	.393	-.083	.284	.092
	<u>5.948</u>	-1.166	<u>4.126</u>	1.293
<i>Limacina bulimoides</i>	.766	-.317	.545	.244
	<u>16.601</u>	-4.655	<u>9.056</u>	<u>3.504</u>
<i>Limacina inflata</i>	.730	-.335	.582	.297
	<u>14.893</u>	-4.960	<u>9.974</u>	<u>4.329</u>
<i>Limacina trochiformis</i>	.323	-.360	.188	.134
	<u>4.759</u>	-5.382	2.660	1.885
<i>Styliola subula</i>	.703	-.260	.499	.262
	<u>13.767</u>	-3.752	<u>8.012</u>	<u>3.787</u>

(Note: t-values appear beneath each coefficient; underlined values are significant at the 0,05 level)

common in the shallow areas of the Gulf, was the only species which showed no significant correlation with depth. These same two species (*C. acicula* and *C. longirostris*) were the only ones which had negative rank correlations with salinity, but those correlations were not statistically significant at the 0.05 level. The other three species which occur in the Gulf of Thailand, *Limacina trochiformis*, *Hyalocylys striata*, and *Diacria quadridentata*, had low positive rank correlations with salinity, but that of *Limacina trochiformis* is not statistically significant. These three Gulf species tend to be concentrated in the central Gulf where conditions are less extreme.

Creseis acicula and *Cavolina longirostris* are negatively correlated with dissolved oxygen content. This is consistent with their abundance in the coastal areas of the Gulf of Thailand, where two

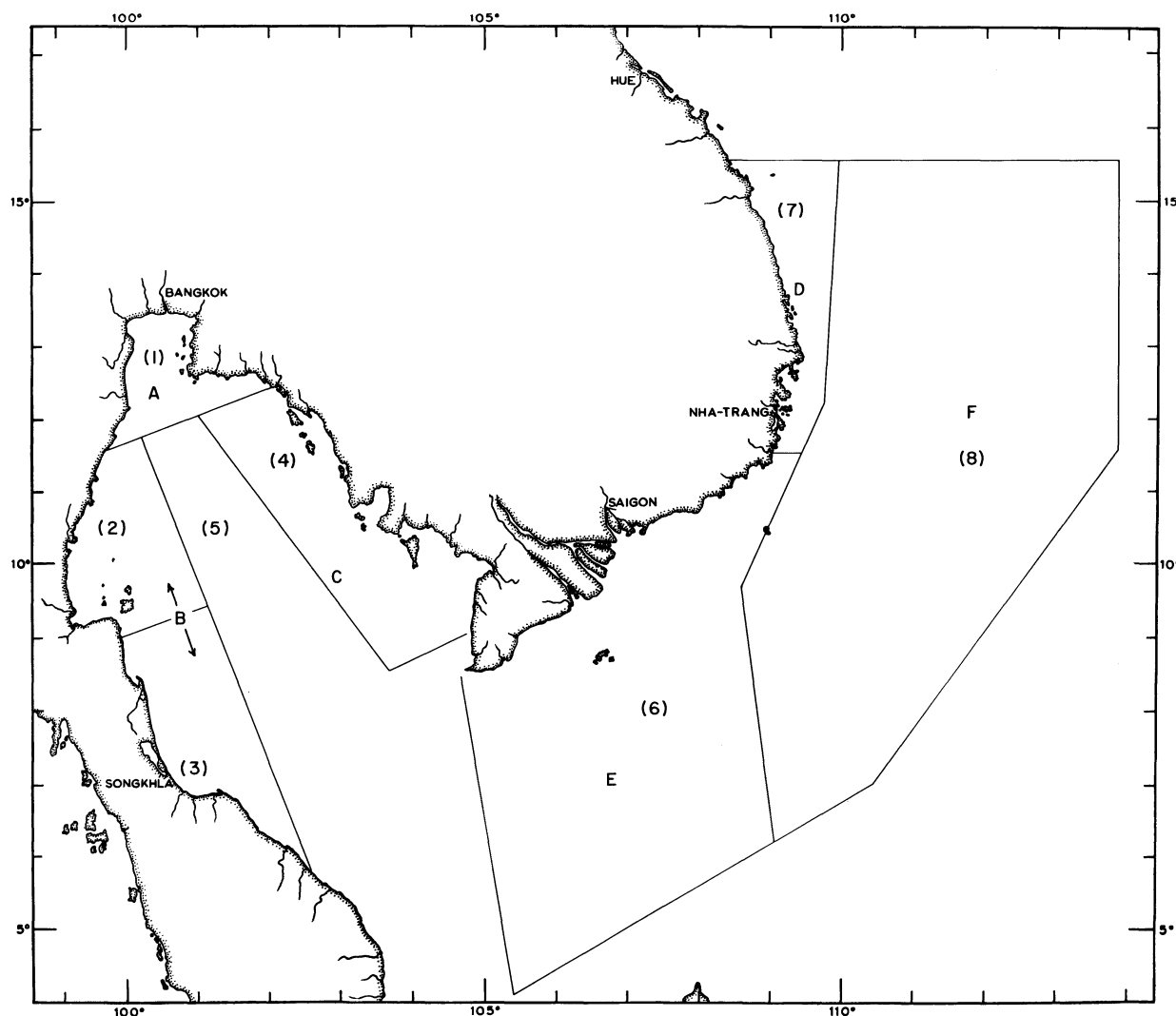


Figure 14. Areal divisions of the Gulf of Thailand and the South China Sea (modified from Brinton, 1975).

factors contribute to lowering of oxygen values: (1) higher temperatures are most common here, and (2) these areas are the scene of upwelling of water relatively low in oxygen. The other three Gulf species, *D. quadridentata*, *H. striata*, and *L. trochiformis*, show no significant rank correlation with oxygen. All oceanic group species are positively correlated with oxygen content at the 0.05 level, except *Clio pyramidata*, which is not significantly correlated with oxygen.

All significant rank correlations with temperature are negative. The three species of the genus *Limacina* have the three highest (negative) rank correlations with temperature. Of the five species which occur in the Gulf of Thailand, only *L. trochiformis* is significantly correlated with temperature.

In order to investigate general species abundances within smaller areas with similar environmental characteristics the survey area was divided into eight areas. These areas were chosen to correspond with those of Brinton (1975). Figure 14 outlines the eight areas on a map of the

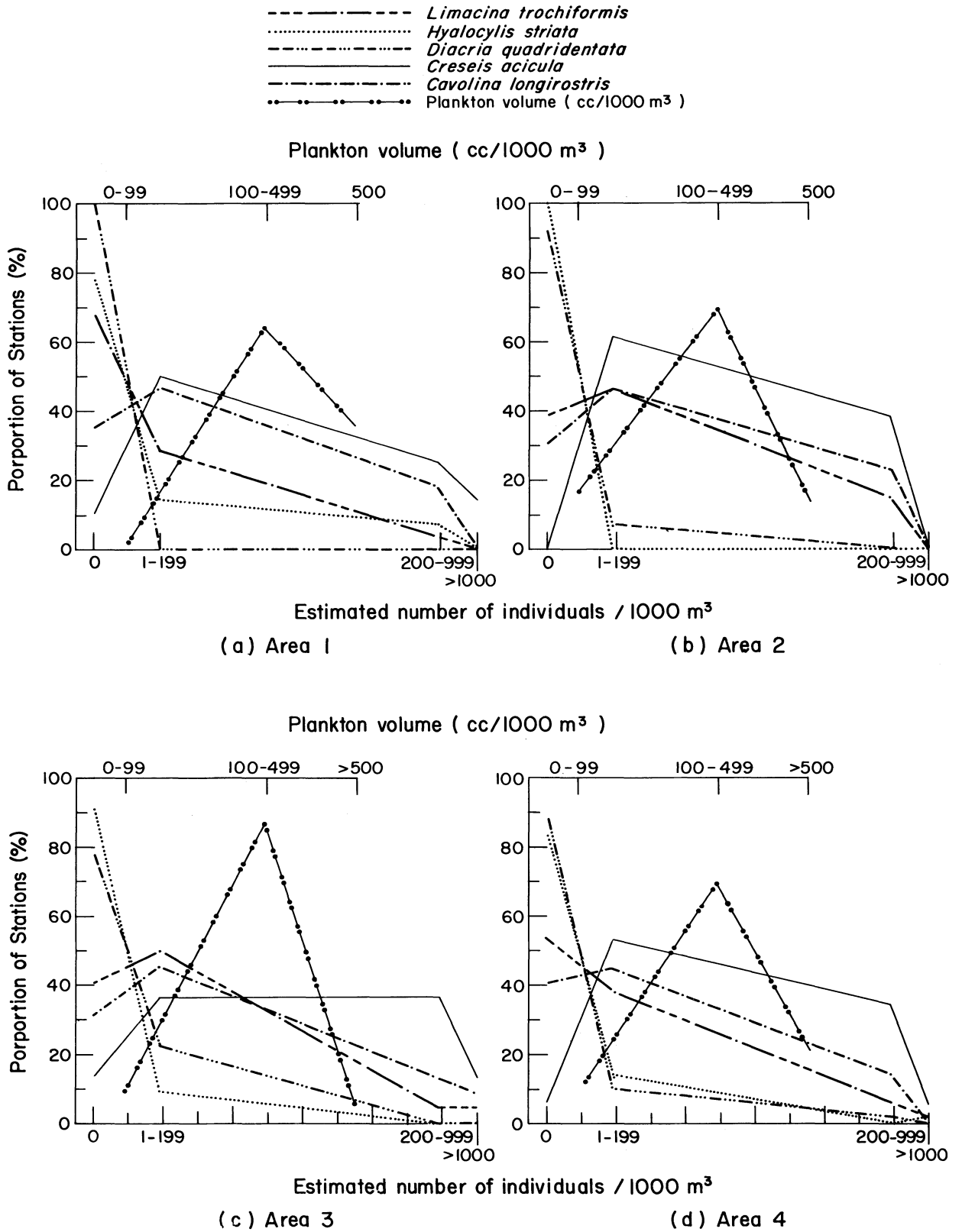


Figure 15a-d. Percentages of pteropod and zooplankton volume concentrations in various areas of the Gulf of Thailand and the South China Sea (for locations of areas, see Figure 14).

Gulf of Thailand and the South China Sea. Population densities were grouped into four ranges: 0, 1-199, 200-999, and greater than or equal to 1,000 individuals per 1,000 m³ of water filtered. For each area the percentage of stations at which the abundance of each species fell within each of the four ranges was calculated (Fig. 15).

In the Gulf of Thailand *D. quadridentata* and *H. striata* were absent from a high percentage of stations (they were completely absent during cruise S-5 and *H. striata* was also absent during cruise S-3). The percentage of stations at which their population densities were in the 1-199/ 1000 m³ range was relatively low and their abundances fell within the higher ranges at even fewer stations. *D. quadridentata* was not found in Area 1 during any of the cruises, nor was *H. striata* present in any samples from Area 2. *C. acicula* and *C. longirostris* were generally more abundant than *D. quadridentata* and *H. striata* throughout most of the Gulf. In Areas 2, 3, and 5, which are along the west coast and in the central Gulf, *L. trochiformis* had population densities very similar to *C. acicula* and *C. longirostris*. In Areas 1 and 4, however, *L. trochiformis* was less abundant and its population densities were more like those of *D. quadridentata* and *H. striata*. Areas 1 and 4 are the ones in which the higher temperatures, lower salinities, and lower oxygen concentrations which distinguish the Gulf of Thailand from the oceanic areas of the South China Sea are most strongly developed.

Most of Area 6 is part of the relatively shallow Sunda Shelf. Group I (Fig. 13) and its associate species are generally much more abundant in Area 6 than is Group II. In fact one species, *Clio pyramidata*, was not found within this area, and another, *Styliola subula*, occurred at only one station.

Area 7 is the area of the narrow northern continental shelf. It is a shallow area, but there is nothing comparable to the Mekong delta of the southern shelf. The typical conditions of the other shallow areas are not so well developed here. Nevertheless, this shelf area is a relatively more favorable environment for the Gulf species than for most of the oceanic group.

In Area 8 all species except *H. striata* have a similar abundance pattern. Surprisingly, the Gulf species are not only present in Area 8 (the deep water oceanic part of the South China Sea), but they are not particularly less abundant than the species limited to this area.

Stations were grouped on the basis of three ranges of water depth: 0-50 m, 51-200 m, and greater than 200 m. The mean abundance of each species (and zooplankton volume) was calculated for each depth range. Figure 16 presents these means graphically. All sites where depth exceeds 200 m are located in the South China Sea, and all Group II members, as well as Group II associate *Creseis virgula virgula* + *C. virgula conica*, were most abundant in this depth range. Most sites which fall within the intermediate depth range (51-200 m) are located over the Sunda Shelf in the southern South China Sea. Three species, *Diacria quadridentata*, *Hyalocylis striata*, and *Limacina trochiformis* had their maximum mean abundance in this area. *Creseis acicula* and *Cavolina longirostris* were most abundant in the shallow (0-50 m) depth range in the Gulf of Thailand. The stations where water depths are between 51 and 200 m have zooplankton volumes that, though only half those found in the shallower areas, are still twice those found in the areas exceeding 200 m in depth. Likewise, the maximum mean population densities of those pteropod species which achieve their greatest abundance in water 51-200 m in depth are generally higher than those species which prefer the deeper water areas and lower than those which are most abundant in the shallower areas.

SUBDIVIDING THE GULF OF THAILAND GROUP

Several lines of evidence suggest that the Gulf of Thailand species group (in its broadest sense) is not as homogeneous as the South China Sea (oceanic) group, and that it might reasonably be divided into two subgroups. The Friedman statistic for the Gulf group of five species is less than half that for the South China Sea group of five species, indicating less agreement among the Gulf species on which stations are favorable.

C. acicula and *C. longirostris* were present in the Gulf of Thailand during the entire sampling period. They were present and abundant in the shallow areas of the Gulf and achieved their

maximum mean abundances in shallow waters (less than 50 m) of the Gulf. The minimum salinity at which they occurred was the lowest of all the pteropod species found in the Naga samples: 28.5-29.0 ‰).

Diacria quadridentata and *Hyalocylis striata*, on the other hand, were absent from the Gulf during part of the survey period. The lowest salinity at which they occurred was 3 ‰ higher than for *C. acicula* and *C. longirostris*. Both *D. quadridentata* and *H. striata* reached their maximum mean abundance outside the Gulf on the Sunda Shelf (in the 50-200 m depth range).

One other species occurs in the Gulf of Thailand: *Limacina trochiformis*. The evidence suggests that it belongs in the subgroup with *D. quadridentata* and *H. striata*. *L. trochiformis* was present in the Gulf throughout the survey period and in Areas 2, 3, and 5 (Fig. 14) its population densities were similar to those of *C. acicula* and *C. longirostris*. However, in Areas 1 and 4, where the most extreme Gulf conditions are developed, *L. trochiformis* is less abundant, as are *D. quadridentata* and *H. striata*. *L. trochiformis* reached its maximum mean abundance outside the Gulf in the 50-200 m depth range on the Sunda Shelf, as did *D. quadridentata* and *H. striata*. The Friedman statistic values indicate that the abundance of *L. trochiformis* is more consistently in agreement with *D. quadridentata* and *H. striata* than with the other two Gulf species (Table 6). When *L. trochiformis* is included with *C. acicula* and *C. longirostris*, the Friedman statistic for the resulting group of three species is lower than for just *C. acicula* + *C. longirostris*. On the other hand, the addition of *L. trochiformis* to form a group of three with *D. quadridentata* and *H. striata* raises the value of the Friedman statistic. Finally, the minimum salinity at which *L. trochiformis* was found is somewhat less than that for *D. quadridentata* and *H. striata*, but it is still 2‰ greater than for *C. acicula* and *C. longirostris*, indicating that it, like *D. quadridentata* and *H. striata*, is not as tolerant of the more extreme Gulf conditions. Thus *L. trochiformis* appears to be properly grouped with *D. quadridentata* and *H. striata* in subdividing the Gulf of Thailand group.

DISCUSSION

All the pteropod species found in the Naga samples are widespread and relatively common in oceanic areas. However, they do not all show equal tolerance for the wide range of salinities, temperatures, and oxygen concentrations characteristic of the Gulf of Thailand. Those species which can best tolerate the estuarine aspects of the Gulf achieve much greater population densities. Those species which can only withstand the more uniform areas of the Gulf generally find it a less favorable environment than the waters over the continental shelf in the southern South China Sea, where they reach their maximum mean population densities.

From an environmental point of view the species studied appear to fall into three recurrent groups. The three groups represent progressively broader ranges of environmental tolerance. Group A, consisting of *Clio pyramidata*, *Creseis virgula virgula* + *C. virgula conica*, *Limacina inflata*, *L. bulimoides*, and *Styliola subula* (and intuitively including all other South China Sea pteropod species not found in the Gulf of Thailand) has a relatively narrow range of environmental tolerance. The species in Group A do not occur in the Gulf of Thailand and are seldom found over the Sunda Shelf. When they are there, it is at the northernmost, outermost stations (in deeper water), usually during the northeast monsoon. These species have highly significant positive rank correlations with salinity and depth. The agreement among these species as to what constitutes a favorable environment is the greatest of the three groups.

Group B consists of *Diacria quadridentata*, *Hyalocylis striata*, and *Limacina trochiformis*. These species are able to withstand the Gulf of Thailand environment some of the time. This represents a broadening of environmental tolerance over Group A. Several lines of evidence support the placement of *L. trochiformis* in Group B with *D. quadridentata* and *H. striata* despite the fact that it was present in the Gulf during the entire sampling period. Within the Gulf, the species of Group B generally prefer Areas 2, 3, and 5. The shallow estuarine environment of the Gulf is not as favorable for these three species as the areas of somewhat greater depths (50-200 m) and higher salinities which are mostly found in the southern third of the South China Sea. It is

there that their maximum mean population densities are achieved. The members of this group have low positive rank correlations with salinity and depth. In terms of environmental preferences, *D. quadridentata* shows the greatest similarity with Group A. Group B has less agreement among its member species as to what constitutes a favorable environment than Group A, but the agreement is still highly significant.

Group C, consisting of *Creseis acicula* and *Cavolina longirostris*, has the broadest environmental tolerance of the three groups. Both species—but especially *C. acicula*—do well in the Gulf of Thailand, including Areas 1 and 4. They both achieve their maximum mean population densities in the shallow waters of the Gulf. The members of this group are not significantly correlated with temperature or salinity and they have low negative rank correlations with oxygen content. *C. longirostris* has no significant rank correlation with depth, while *C. acicula* is negatively correlated with depth. The negative rank correlations with oxygen do not necessarily indicate that these specimens prefer low oxygen conditions. Rather, it seems much more likely that the lower oxygen content at some Gulf stations is well within their range of tolerance and that large population densities in such environments are a result of abundant food supply.

Creseis bulgia and *C. chierchiaie* were both present in the Gulf of Thailand (see p. 90), but because they were combined in the counting (see p. 87), the affinity of either species with Group B or C could not be determined.

Fager and McGowan (1963) found recurrent groups of zooplankton species in the North Pacific. Their data came from 201 samples taken in the summer months. Eleven species of pteropods were included in their groupings. Nine of the eleven have been found in the Naga samples. How well do the more local and detailed groupings presented here compare with Fager and McGowan's recurrent groups derived from less detailed sampling of a much larger area? In a general way the results of the two studies compare fairly well. Fager and McGowan's Groups I and III are closely tied to each other and together these two groups contain all the members of the South China Sea oceanic group (Group A).

Chen and Bé (1964) studied the pteropods at five stations in the western North Atlantic (north of Bermuda). Samples were collected at weekly or bi-weekly intervals throughout a 31/2-year period and 235 samples were studied. Fourteen species found in the Naga samples also occurred in their samples. All fourteen belong to their subtropical group, which they divided into two categories as follows: (Letters following species names

Category III		Category IV	
<i>Clio pyramidata</i>	A	<i>Creseis virgula virgula</i>	A
<i>C. polita</i>		<i>C. virgula conica</i>	A
<i>Cuvierina columnella</i>	A	<i>C. acicula</i>	C
<i>Limacina bulimoides</i>	A	<i>Hyalocylis striata</i>	B
<i>L. inflata</i>	A	<i>Limacina trochiformis</i>	B
<i>L. lesueurii</i>		<i>Cavolina longirostris</i>	C
<i>Creseis virgula constricta</i>		<i>C. inflexa</i>	A
<i>C. virgula clava</i>		<i>C. gibbosa</i>	A
<i>Diacria trispinosa</i>	A		
<i>D. quadridentata</i>	B		
<i>Styliola subula</i>	A		

indicate the group to which each of the species found in the Naga samples belongs.)

All species which occur both in the Naga samples and in Category III are members of the South China Sea oceanic group in its broadest sense (Group A), except *Diacria quadridentata*, which is the Gulf of Thailand species most closely allied to Group A. All Gulf of Thailand group members (Groups B and C), except *D. quadridentata*, are included in Category IV, but Category IV includes three species which, in my samples, would be placed among the Category III species. These three species are *Creseis virgula virgula* + *C. virgula conica*, *Cavolina inflexa*, and *Cavolina gibbosa*. Thus, my results are in general agreement with those of Chen and Bé, though there are some clear differences which may be the result of sampling different latitudinal zones.

SECTION IV. CHARTS OF THE DISTRIBUTIONS OF THE SPECIES

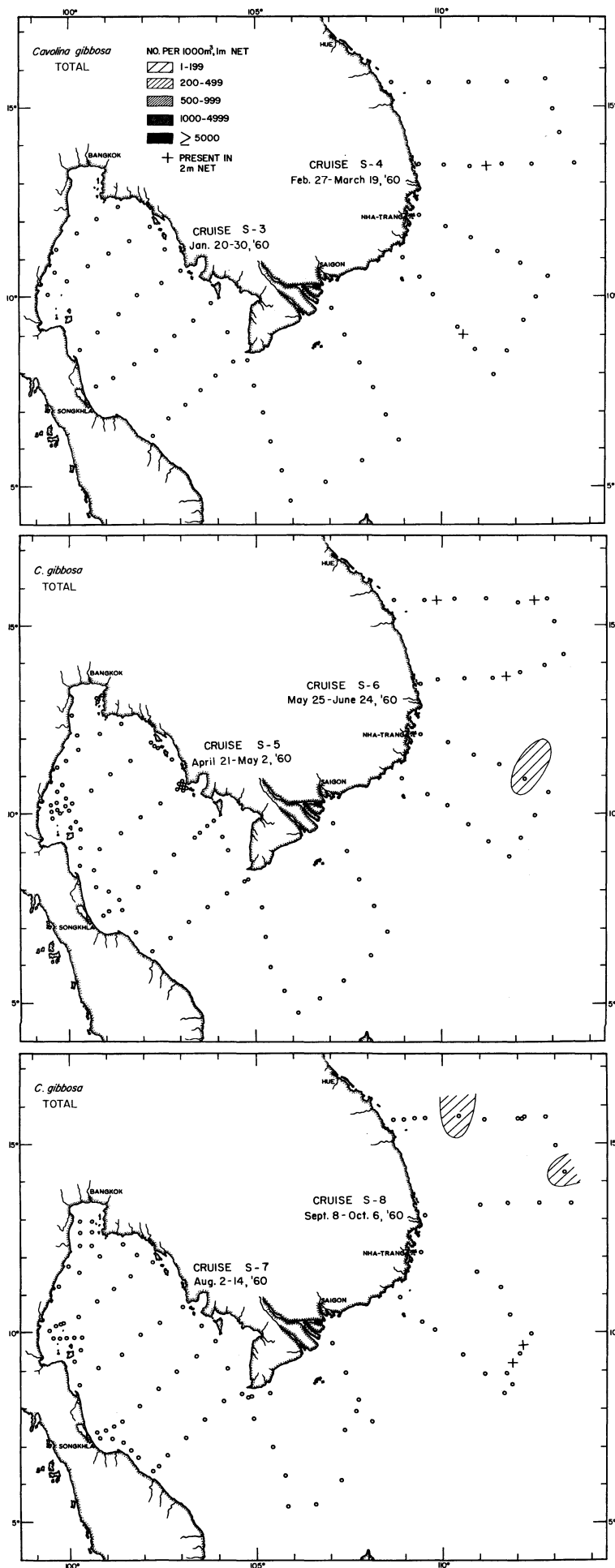


Figure 17

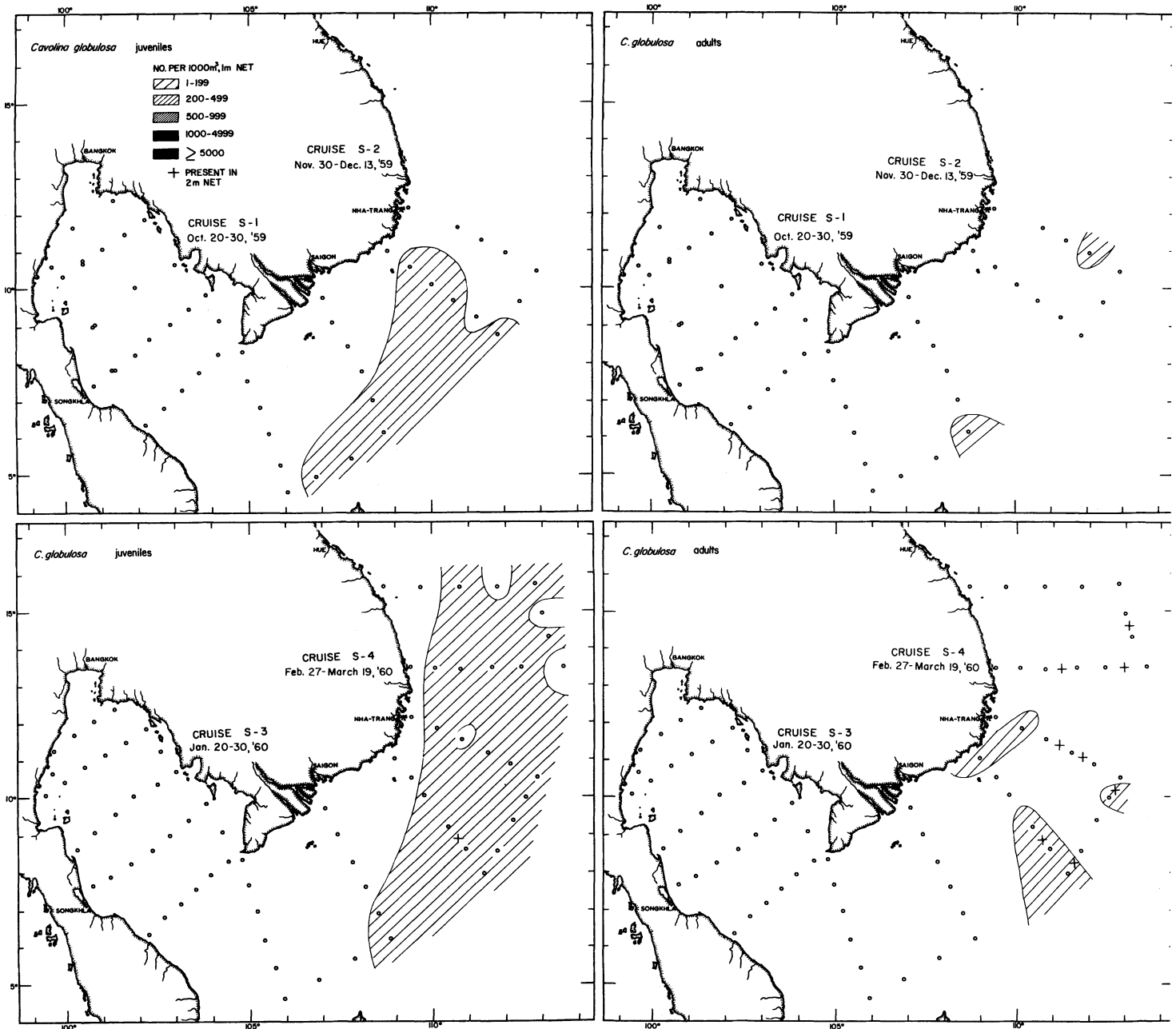


Figure 18a

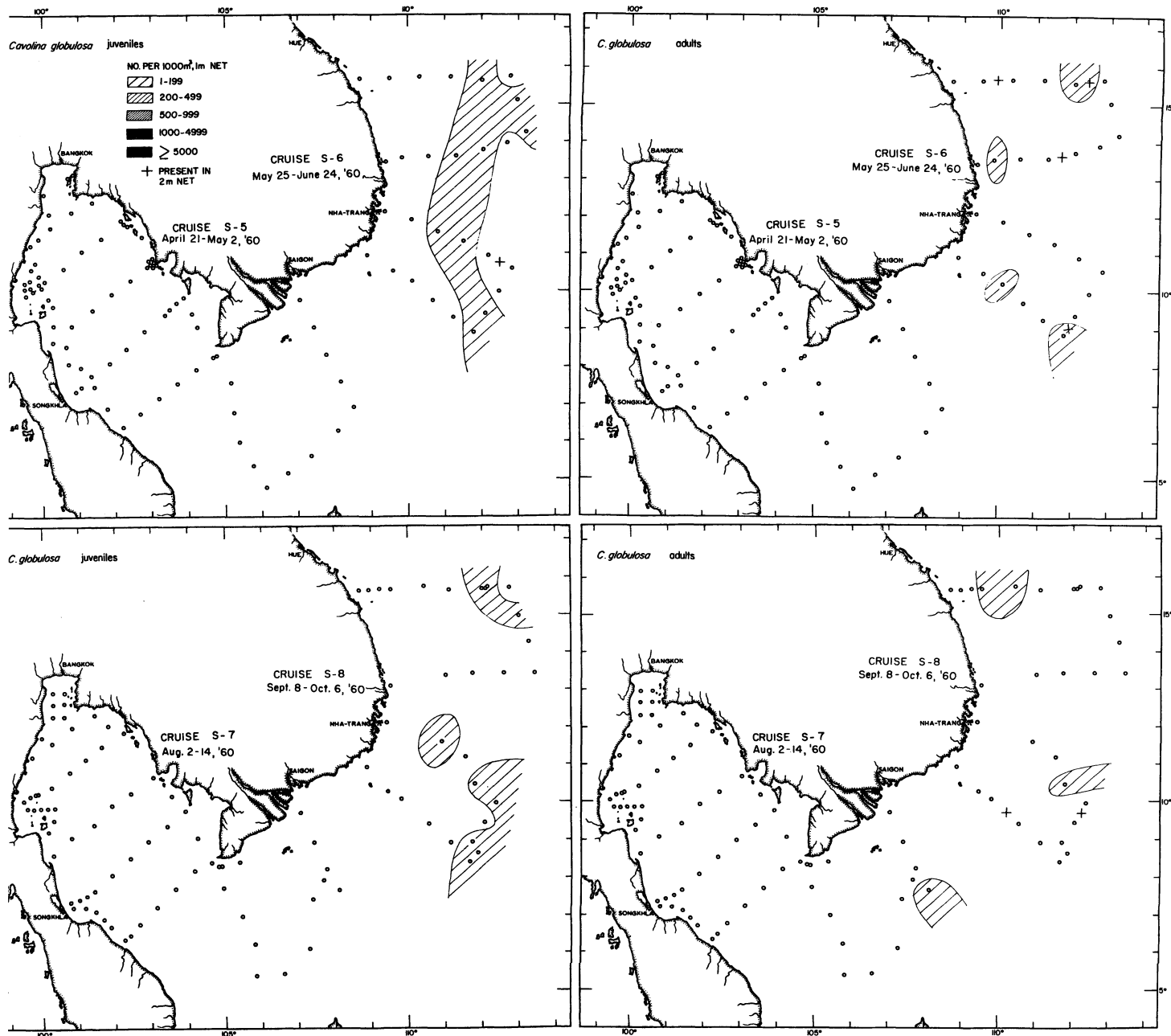


Figure 18b

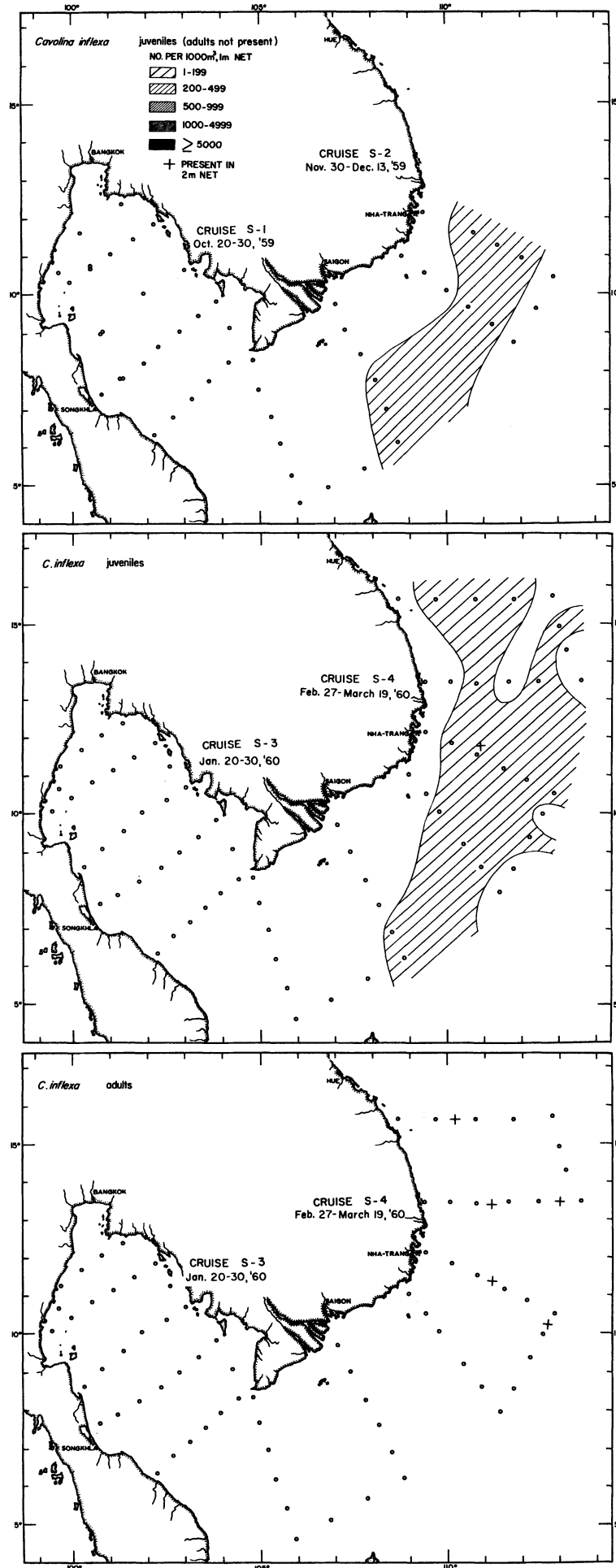


Figure 19a

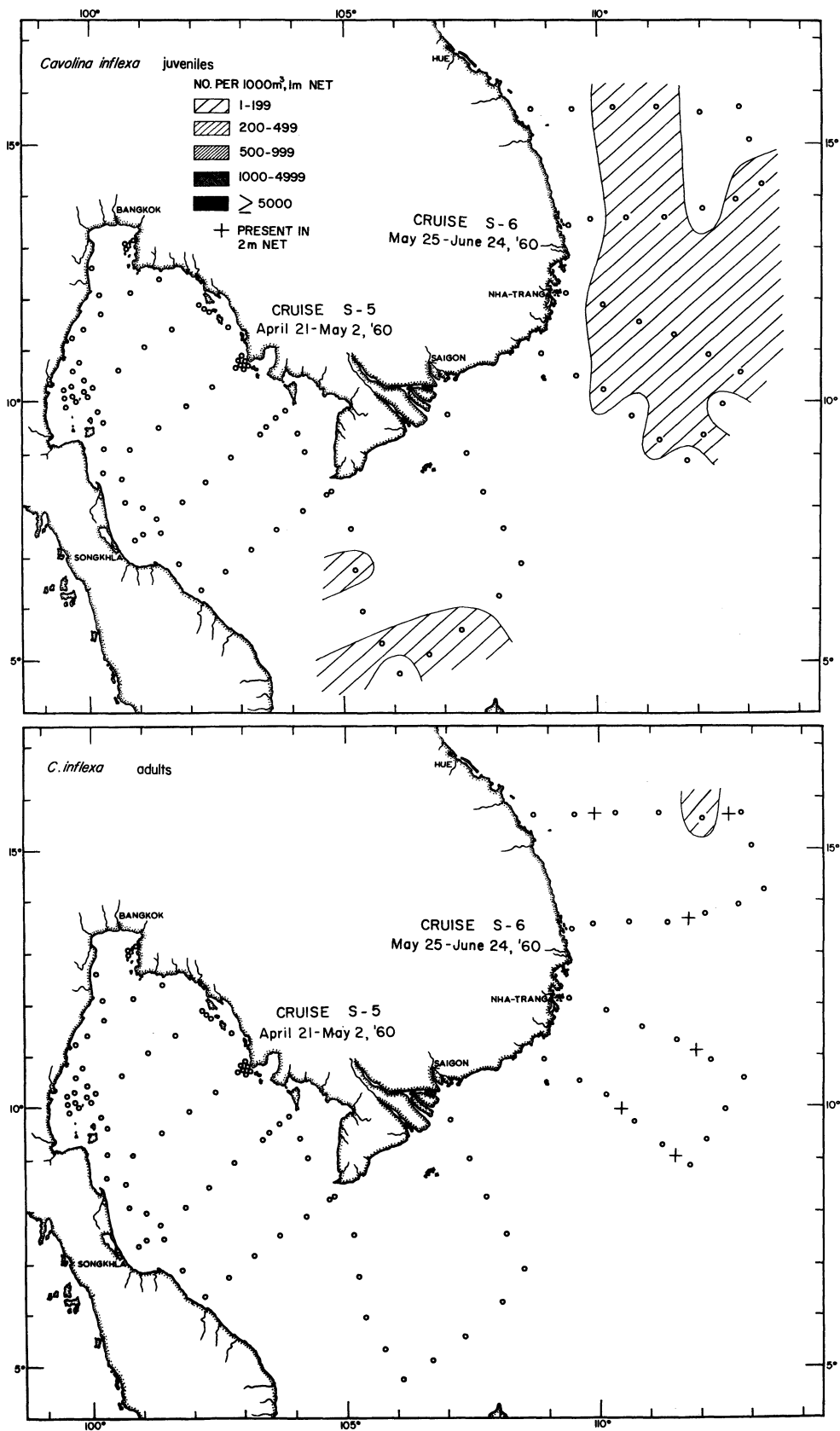


Figure 19b

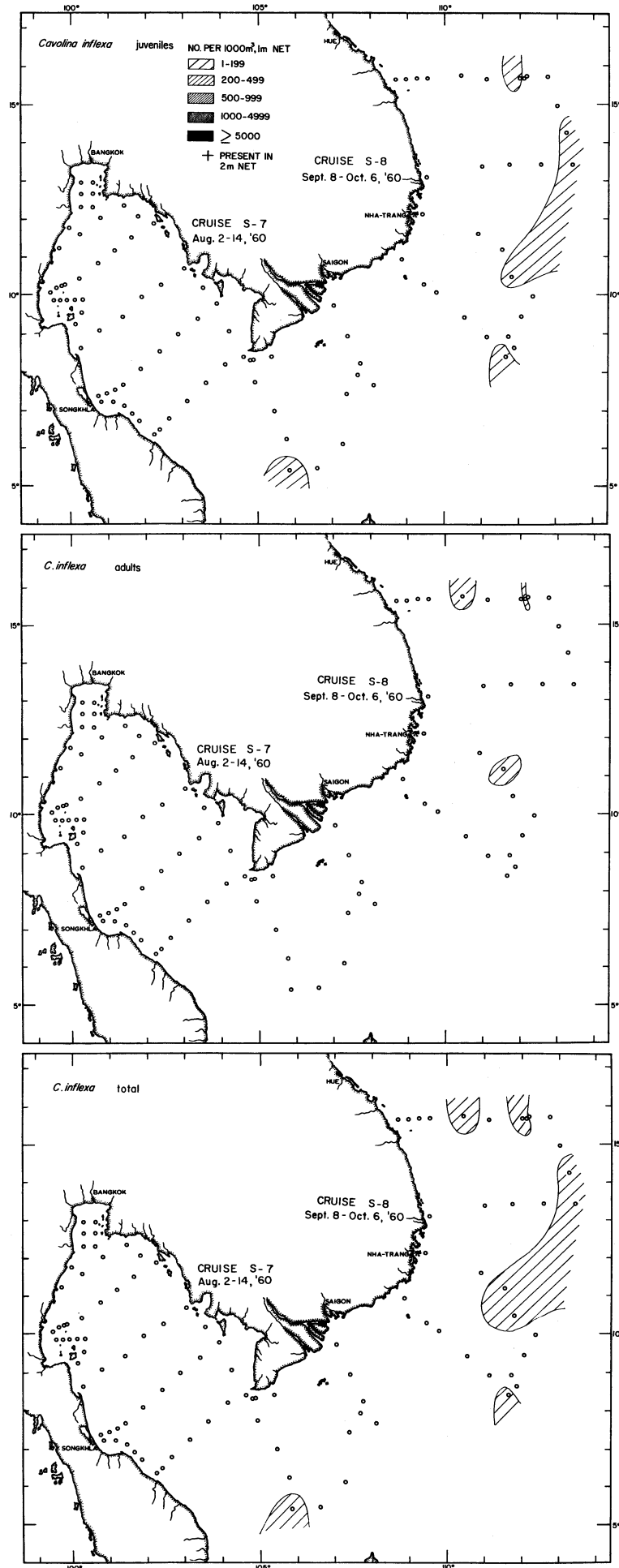


Figure 19c

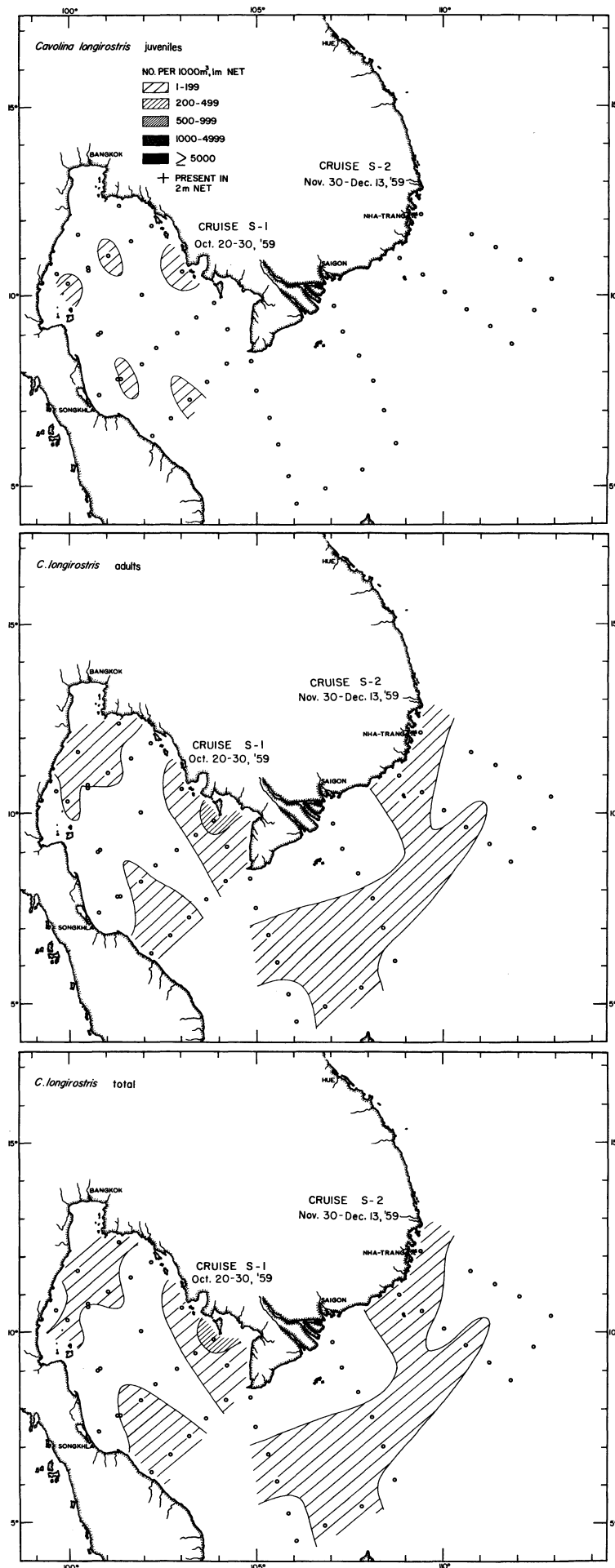


Figure 20a

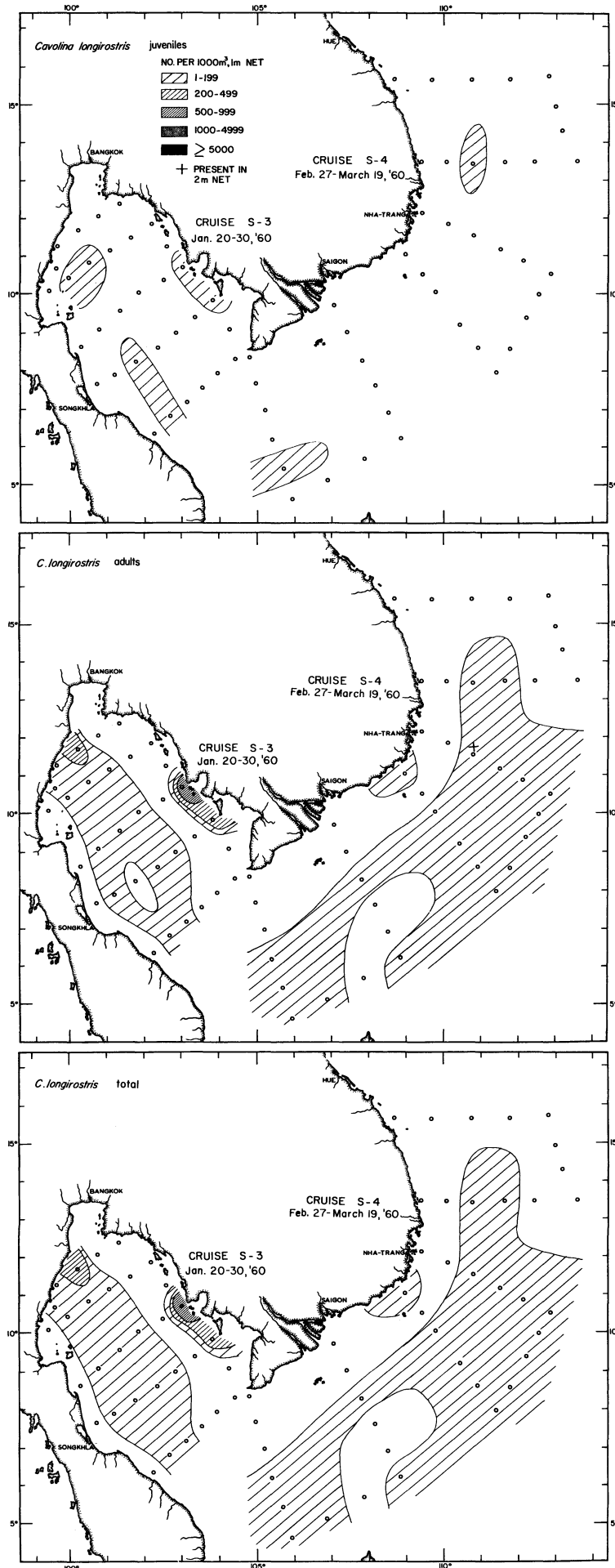


Figure 20b

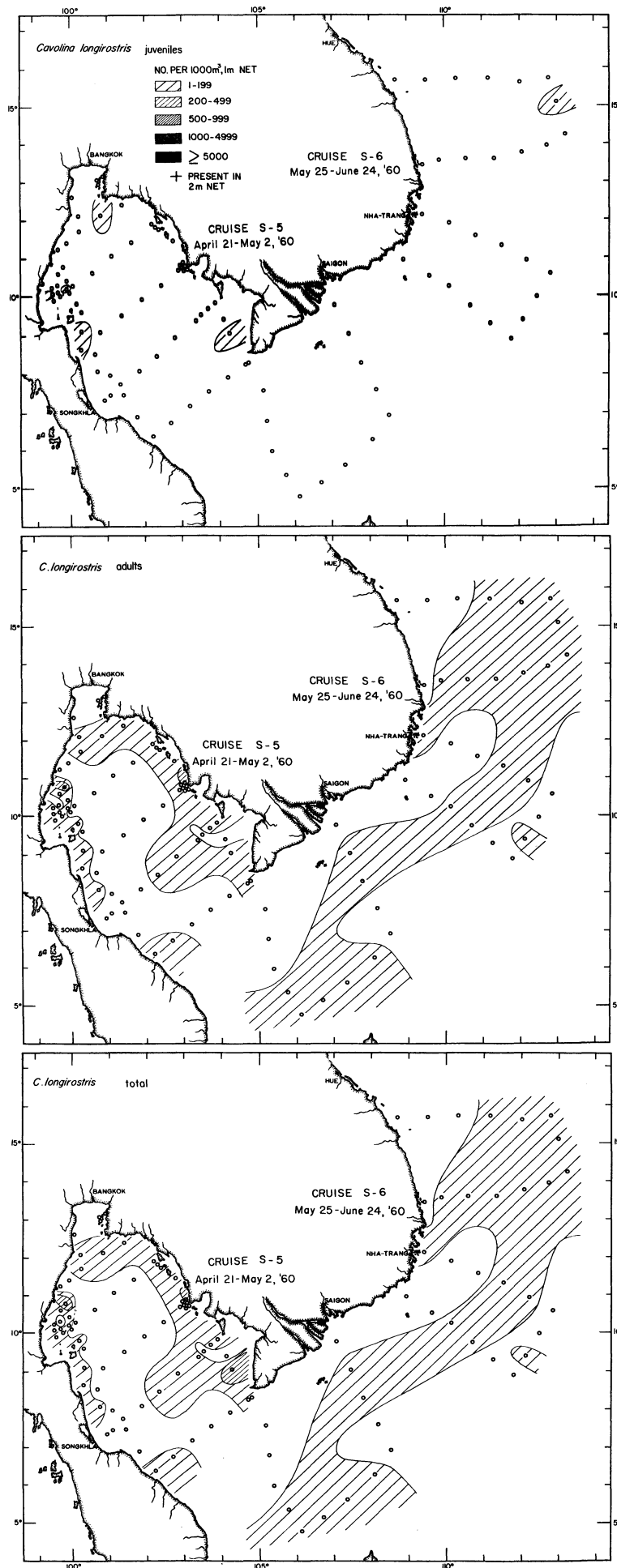


Figure 20c

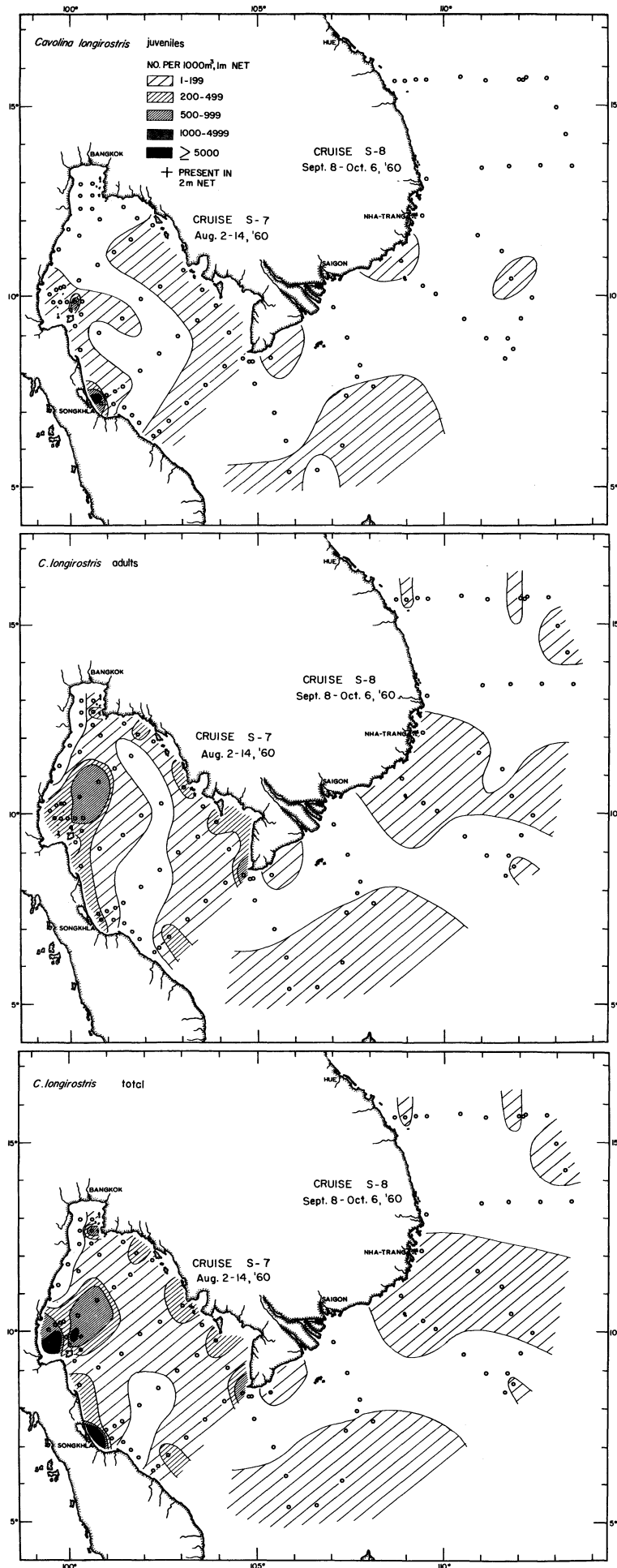


Figure 20d

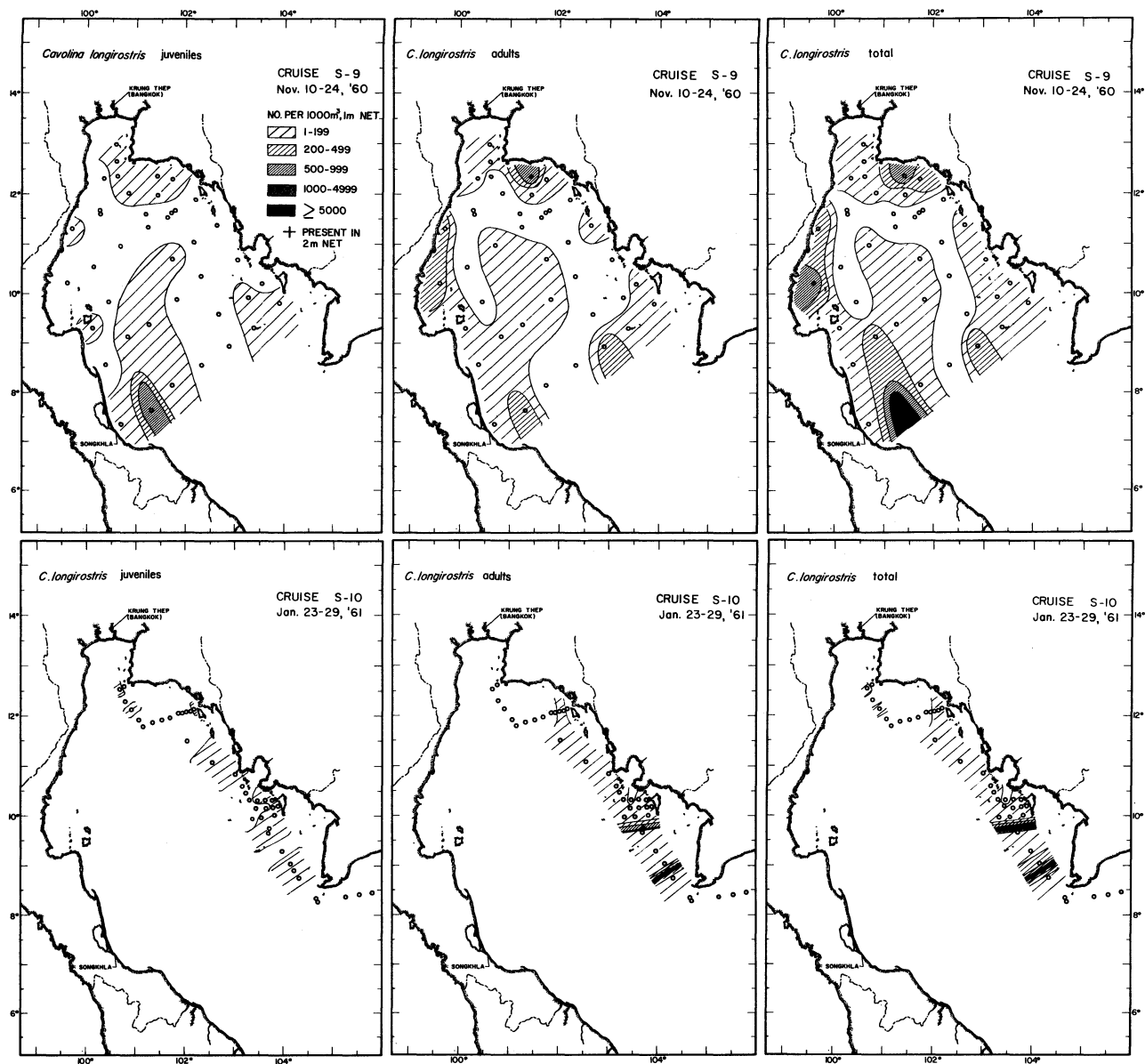


Figure 20e

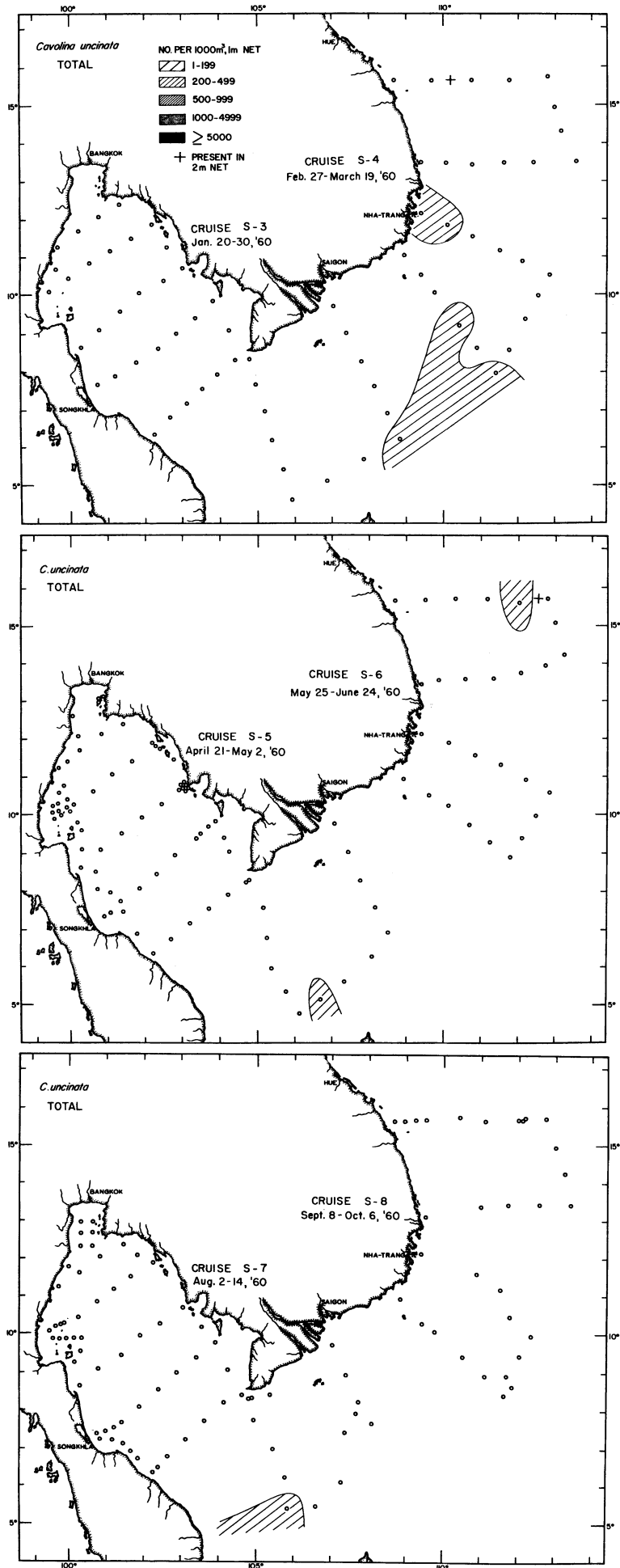


Figure 21

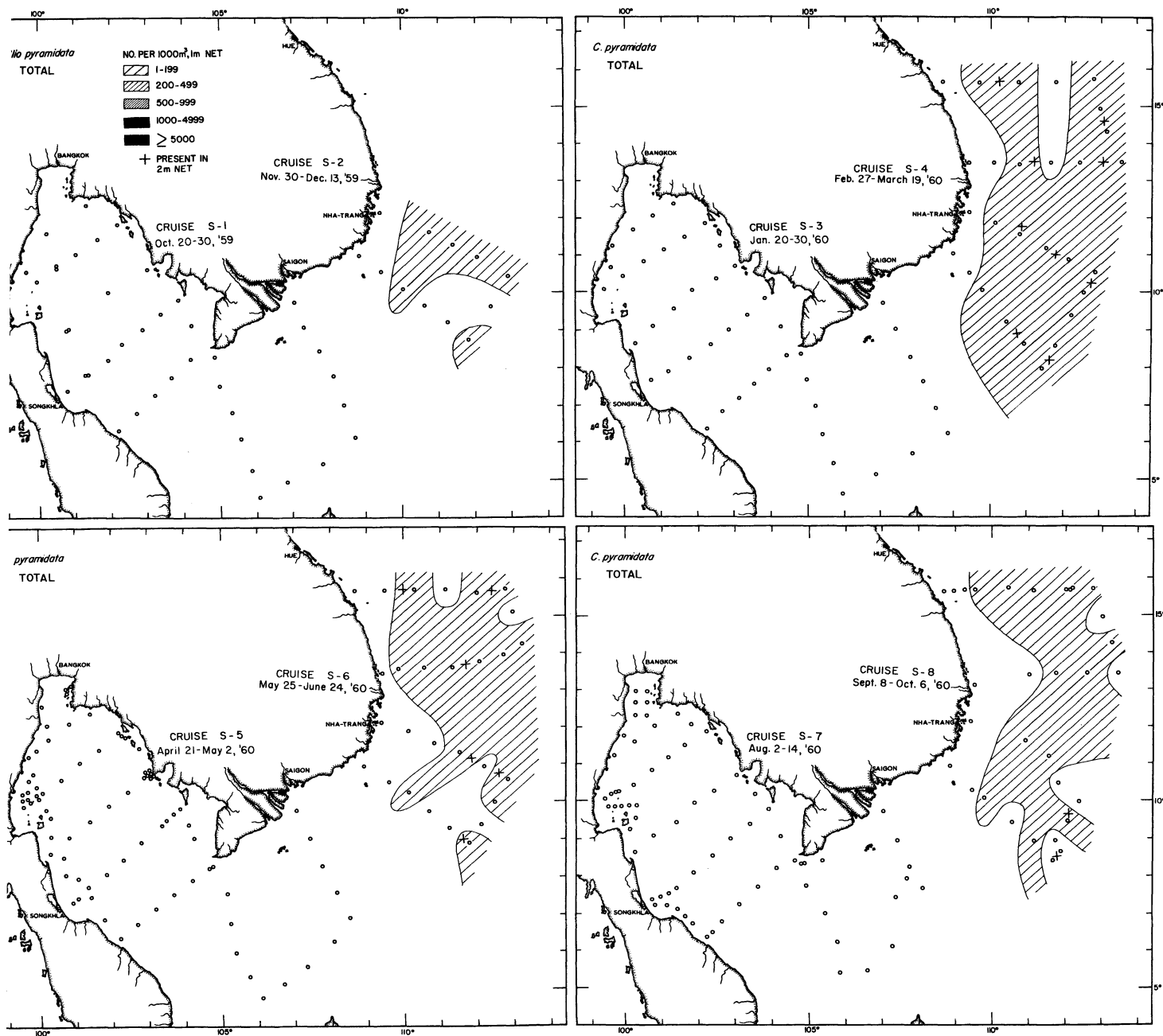


Figure 22

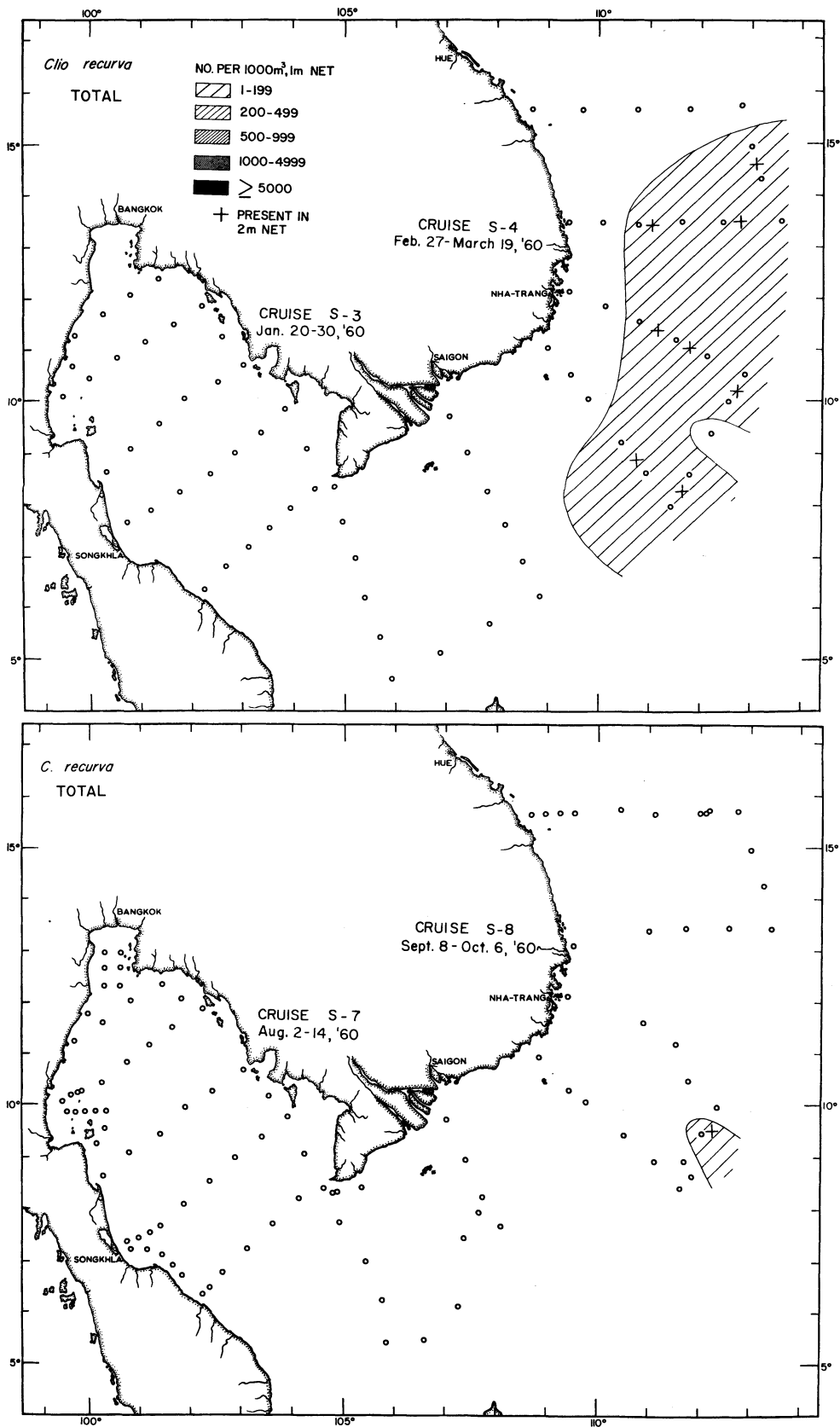


Figure 23

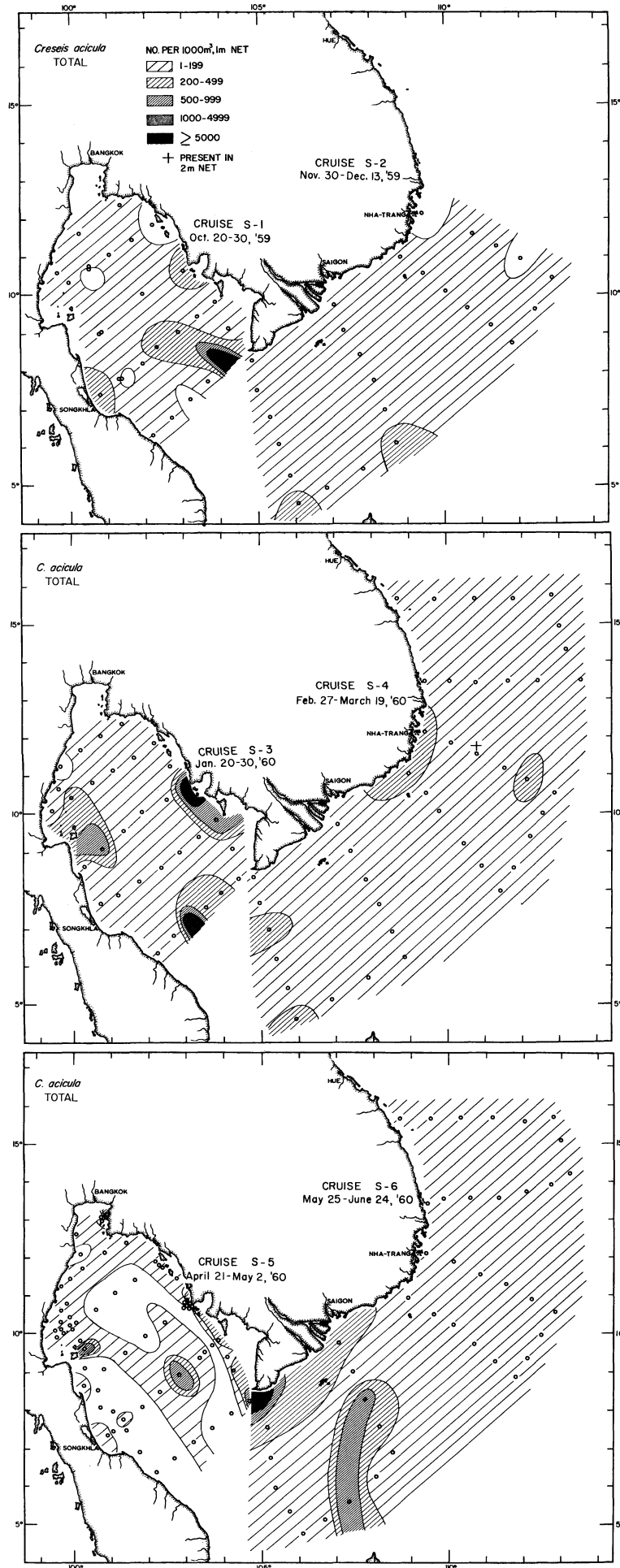


Figure 24a

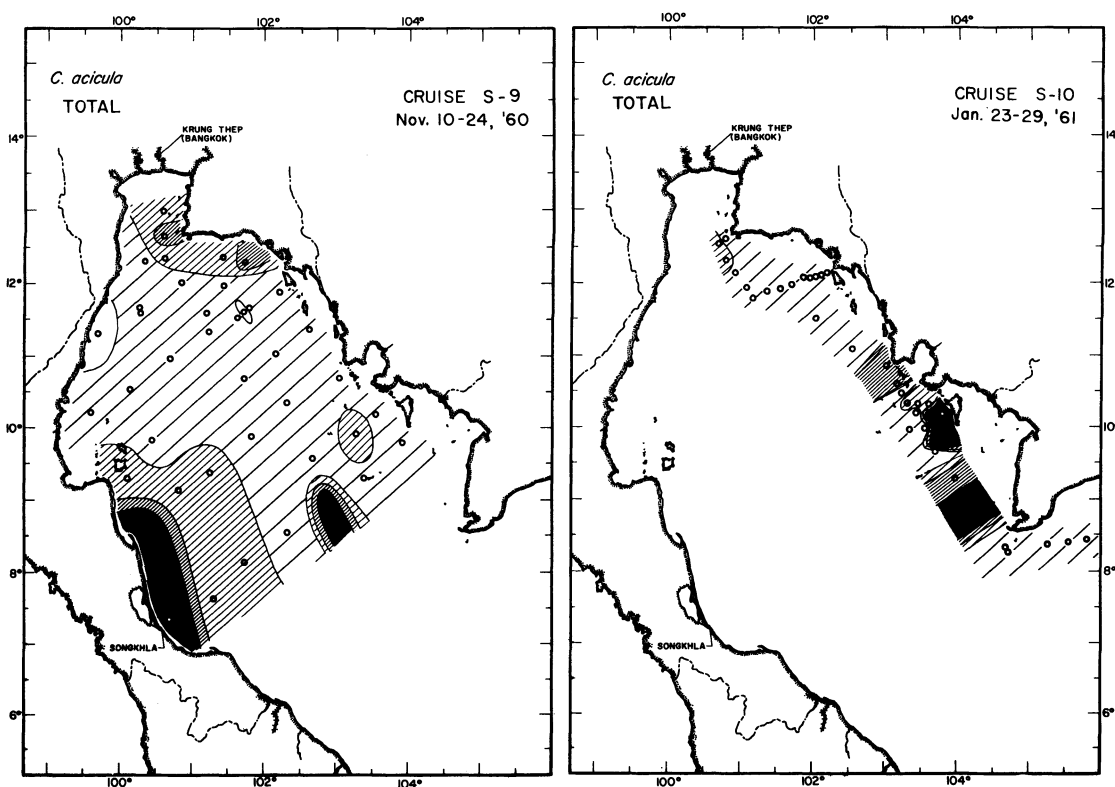
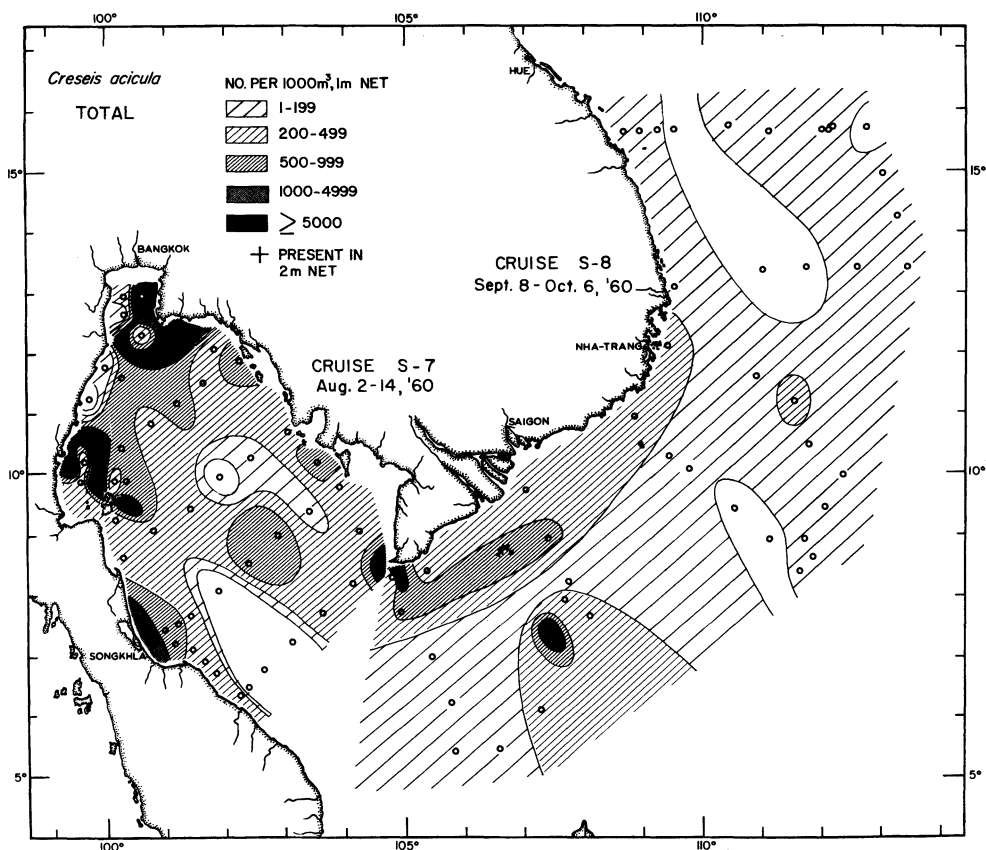


Figure 24b

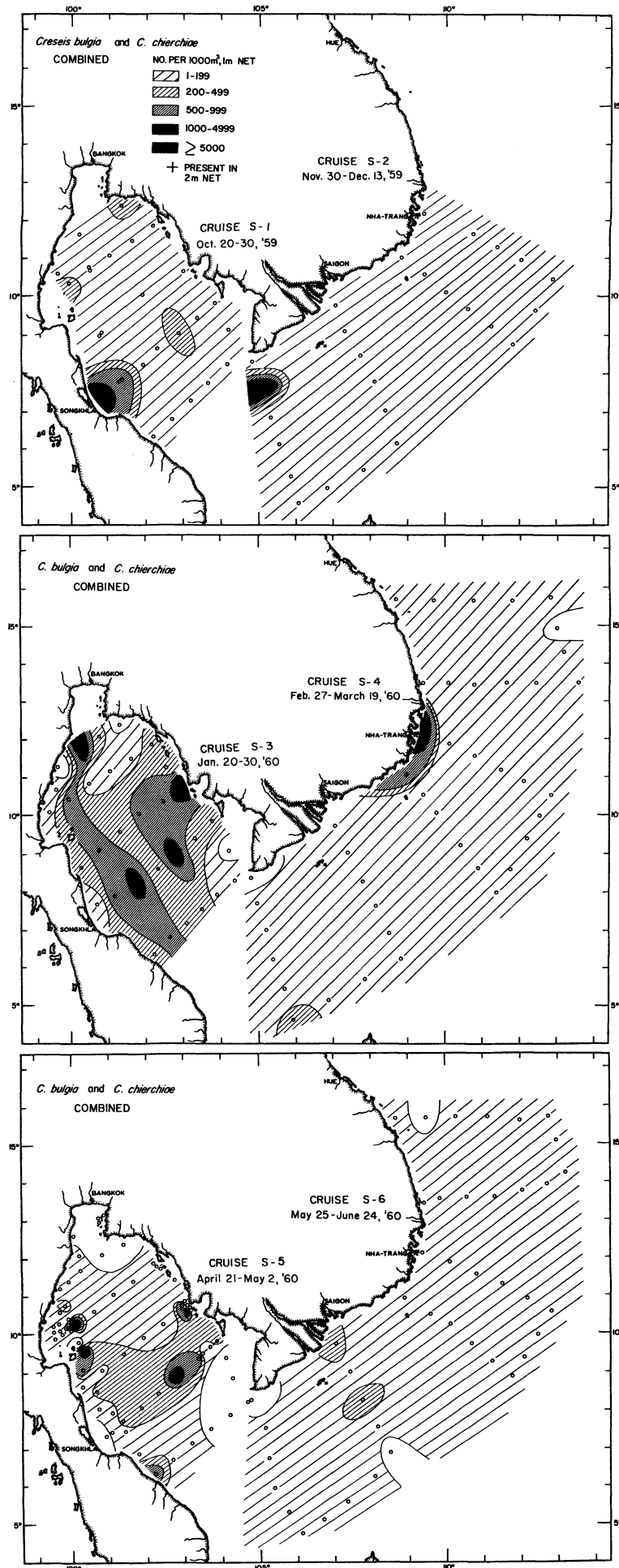


Figure 25a

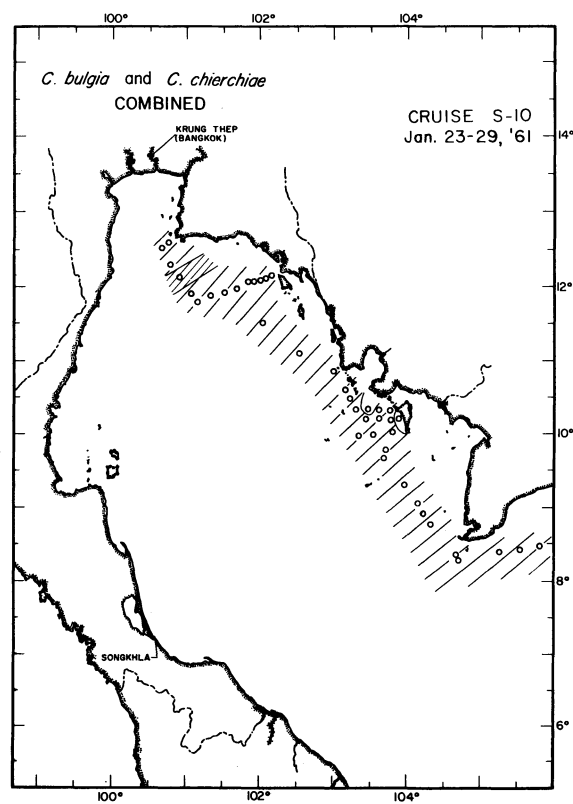
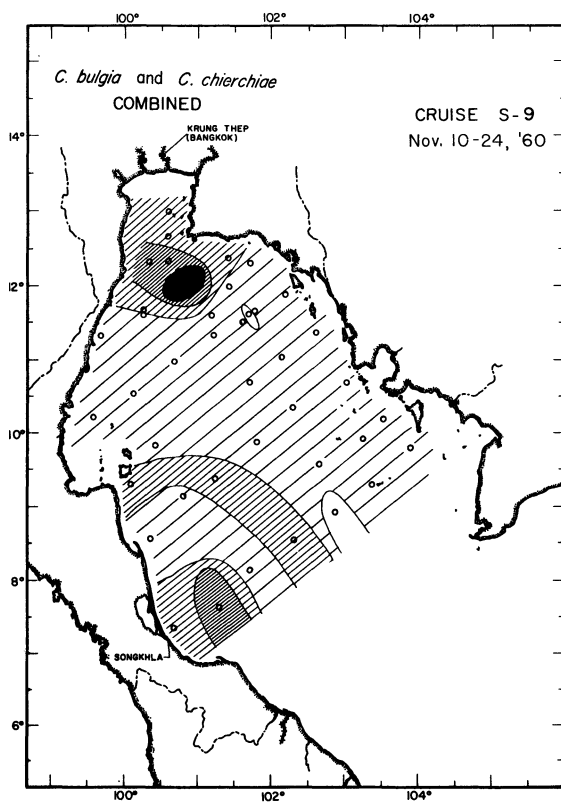
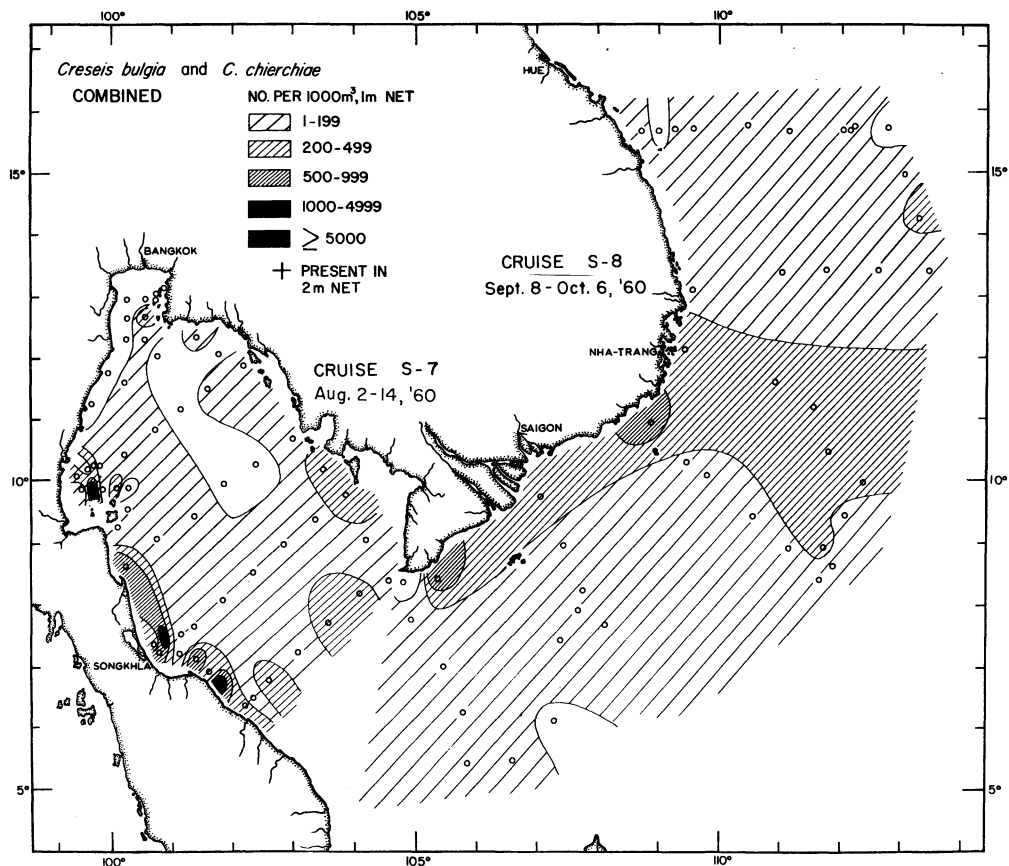


Figure 25b

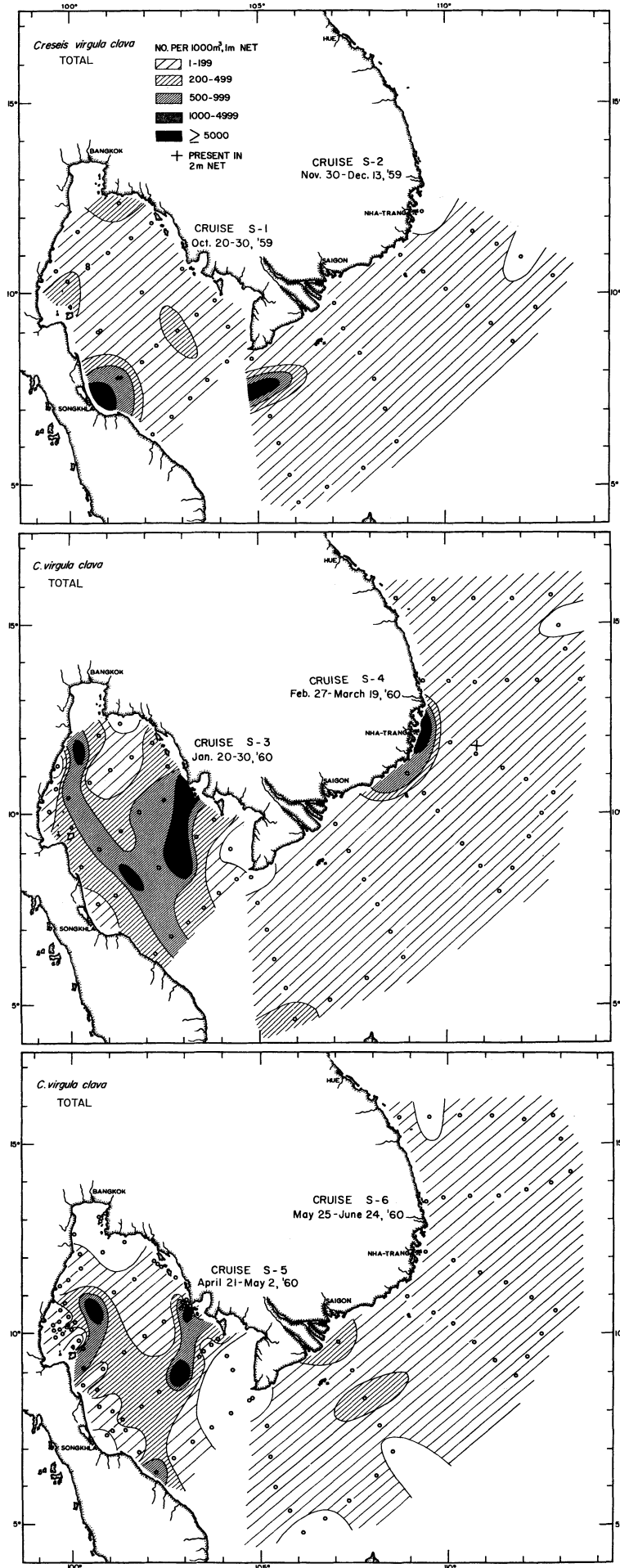


Figure 26a

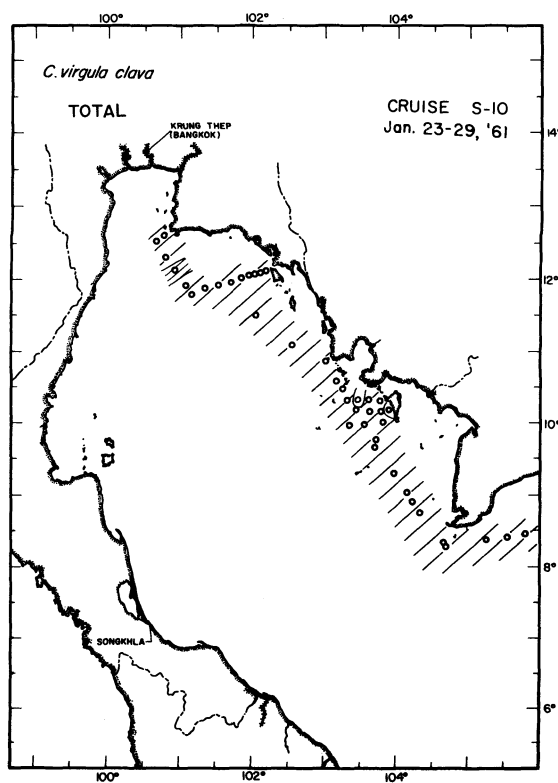
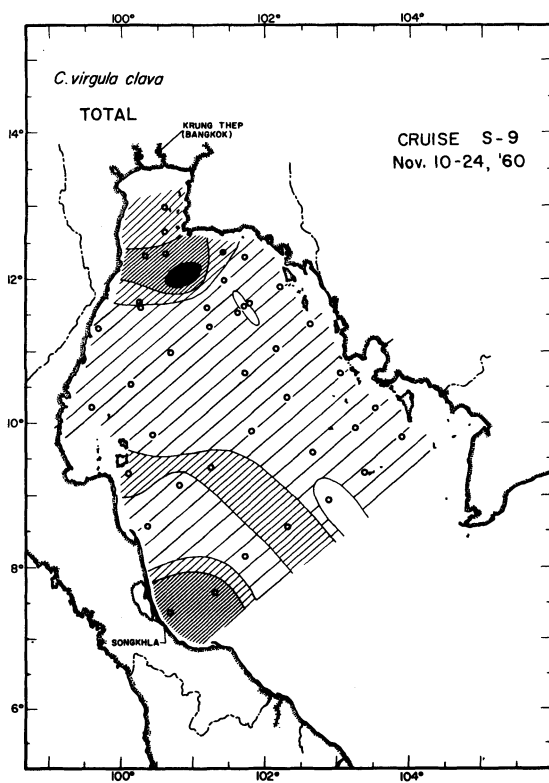
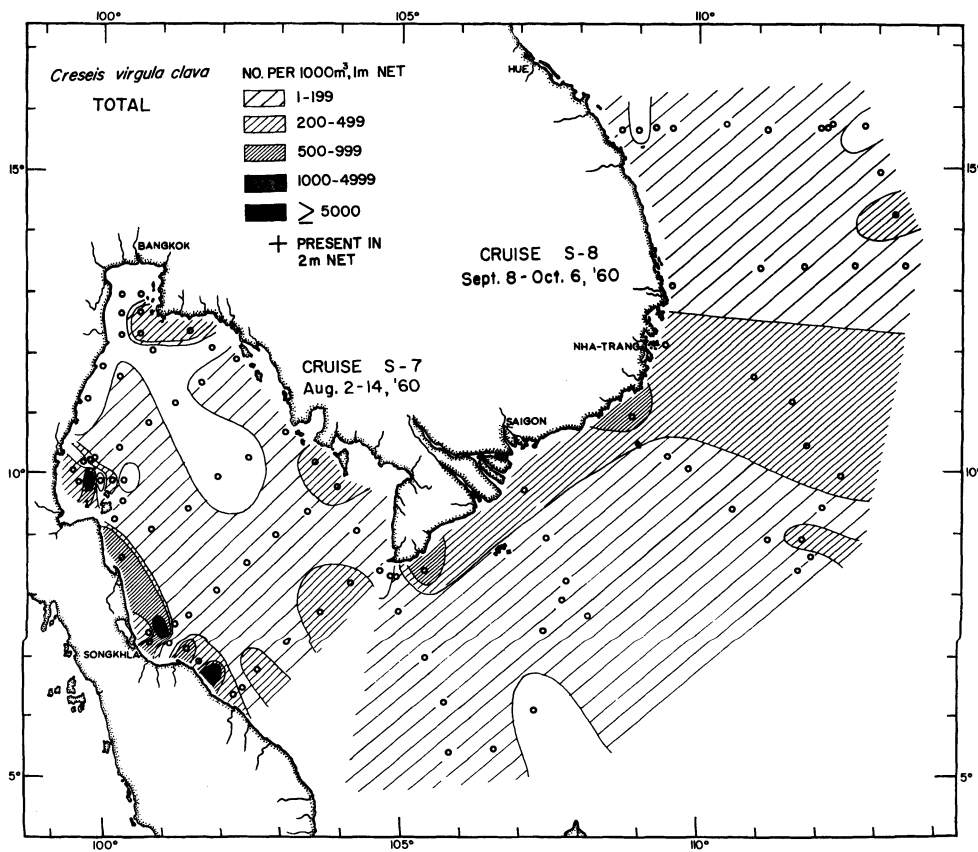


Figure 26b

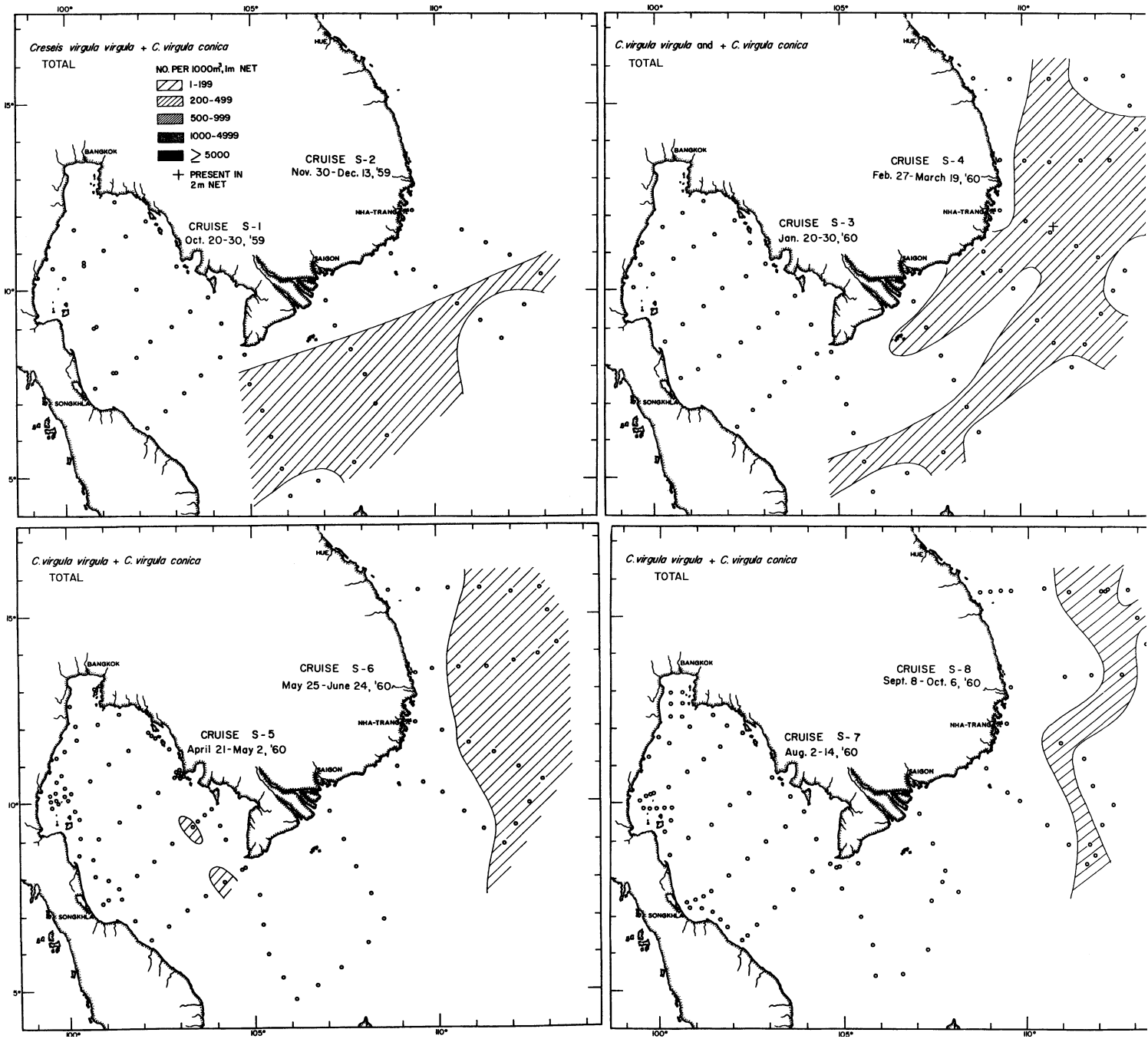


Figure 27

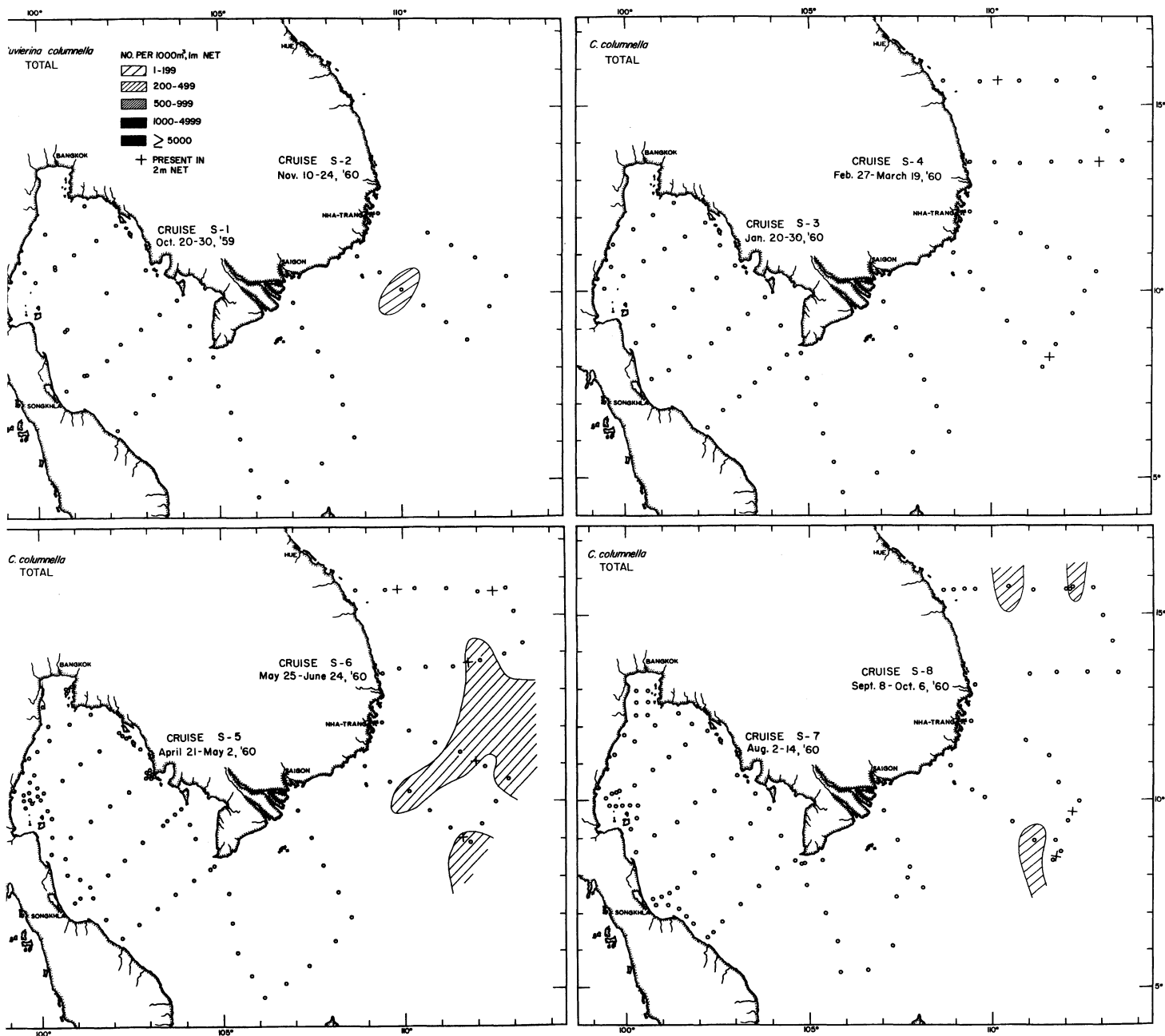


Figure 28

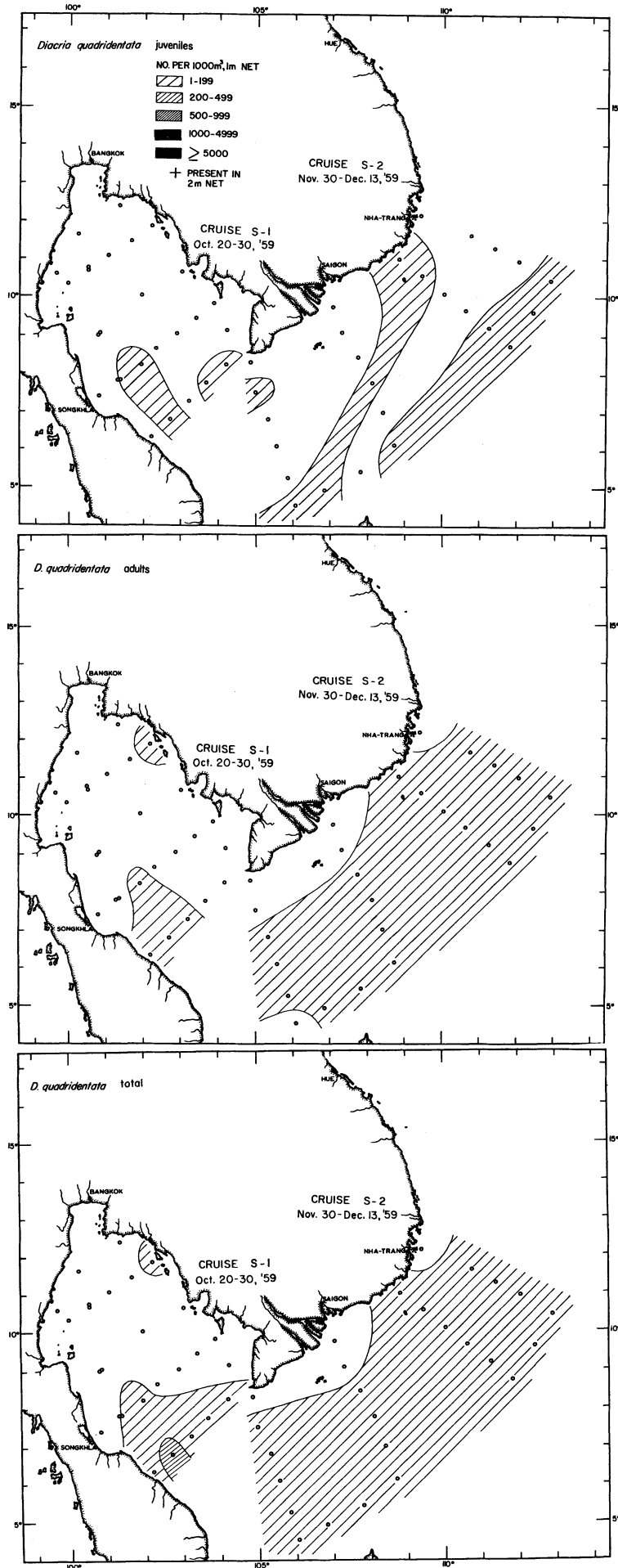


Figure 29a

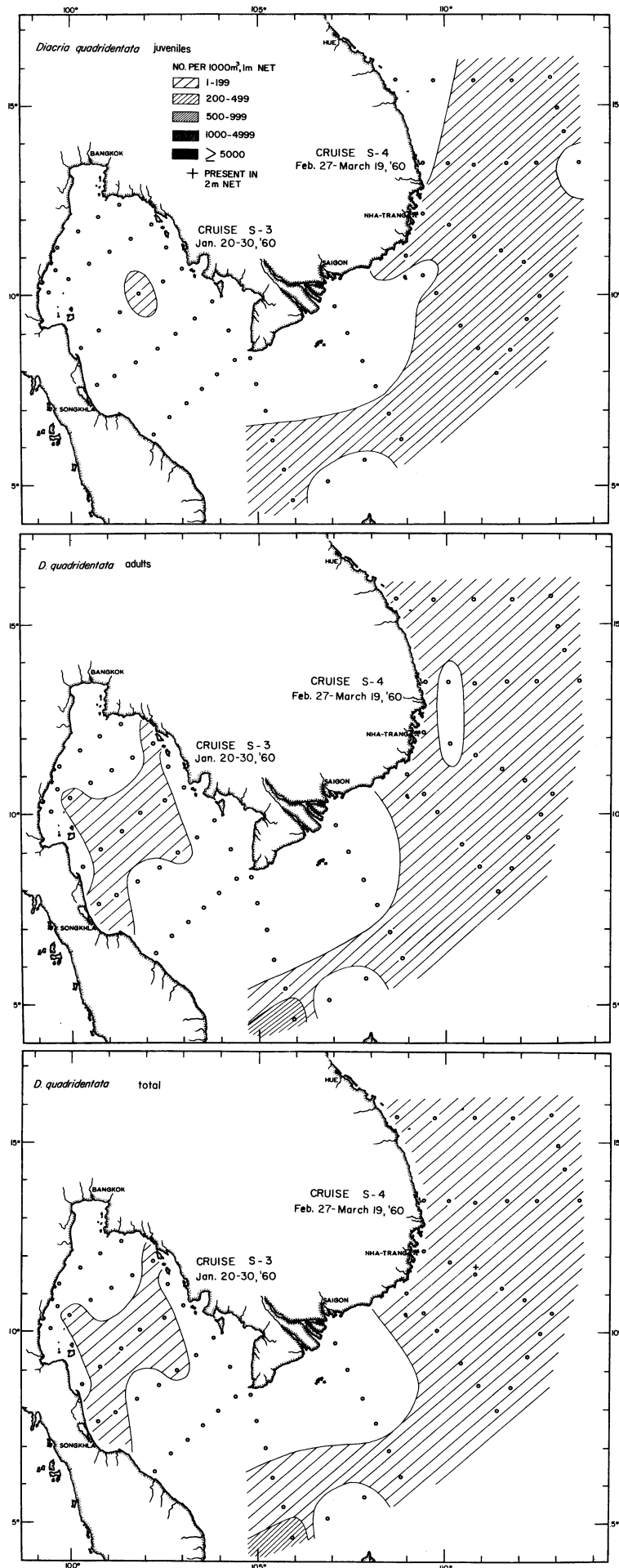


Figure 29b

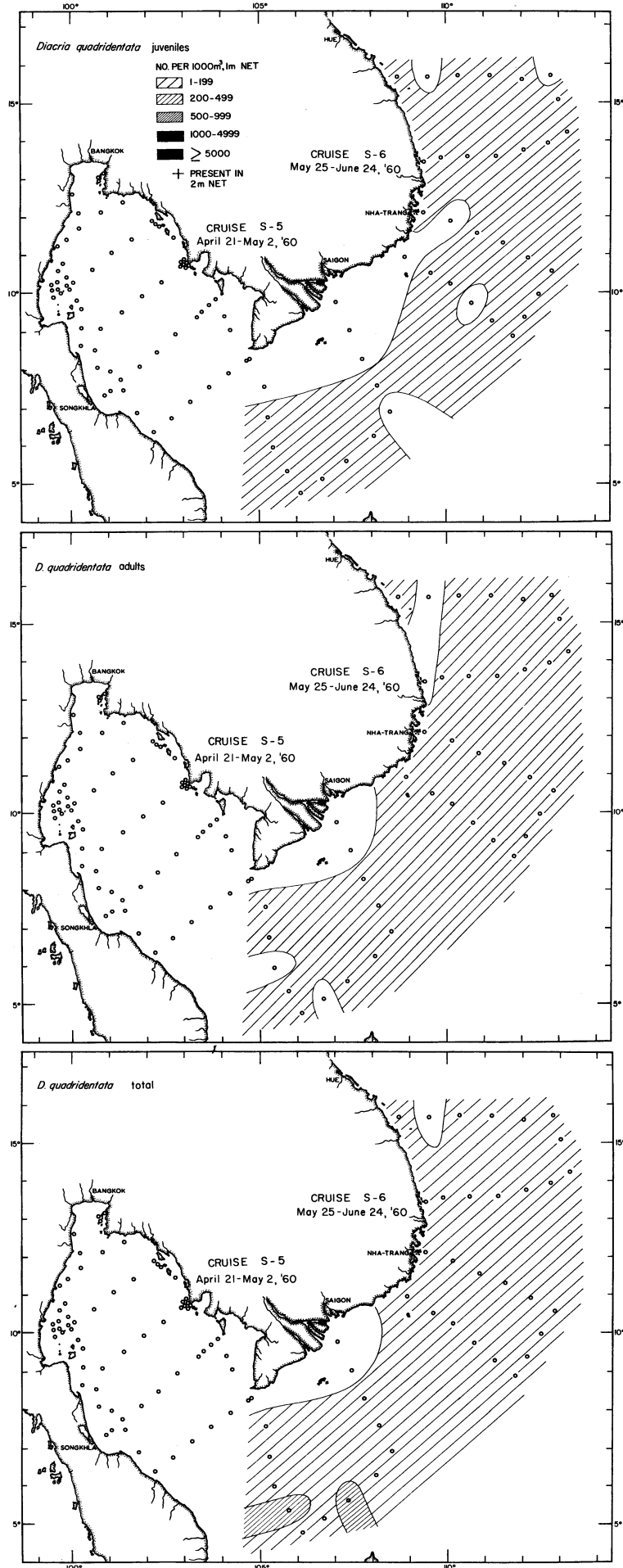


Figure 29c

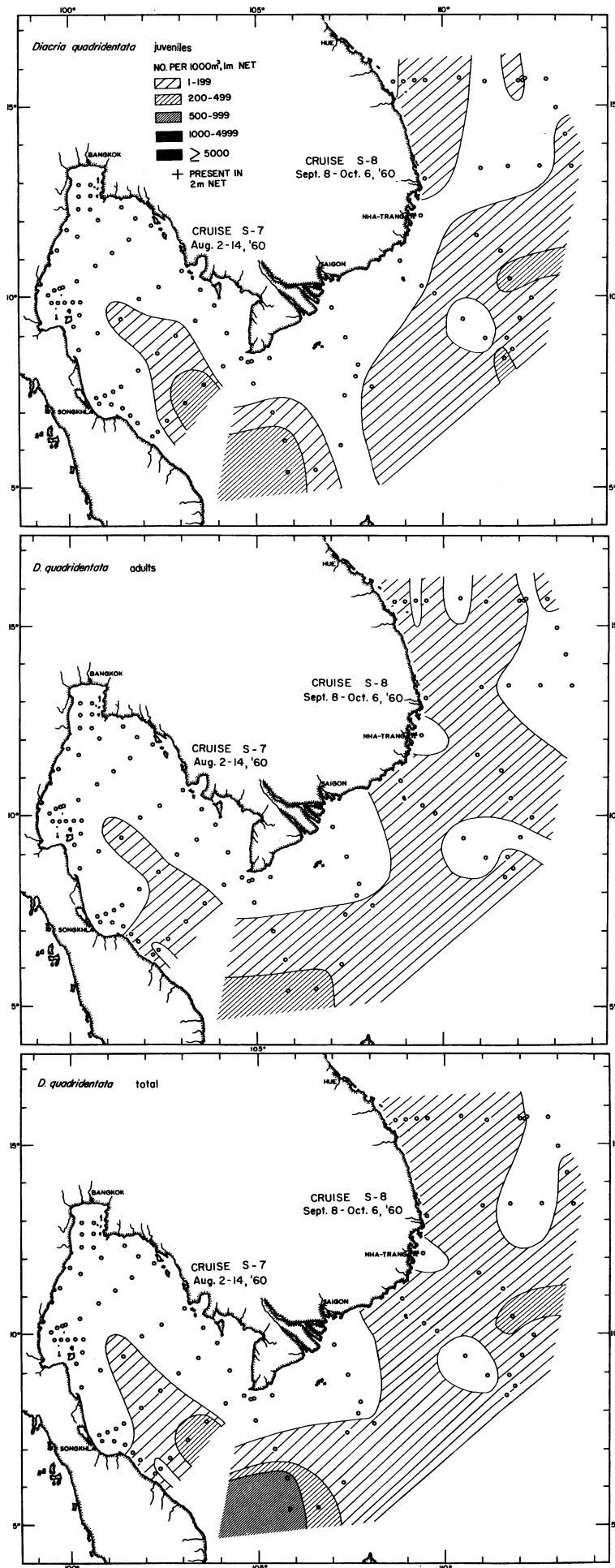


Figure 29d

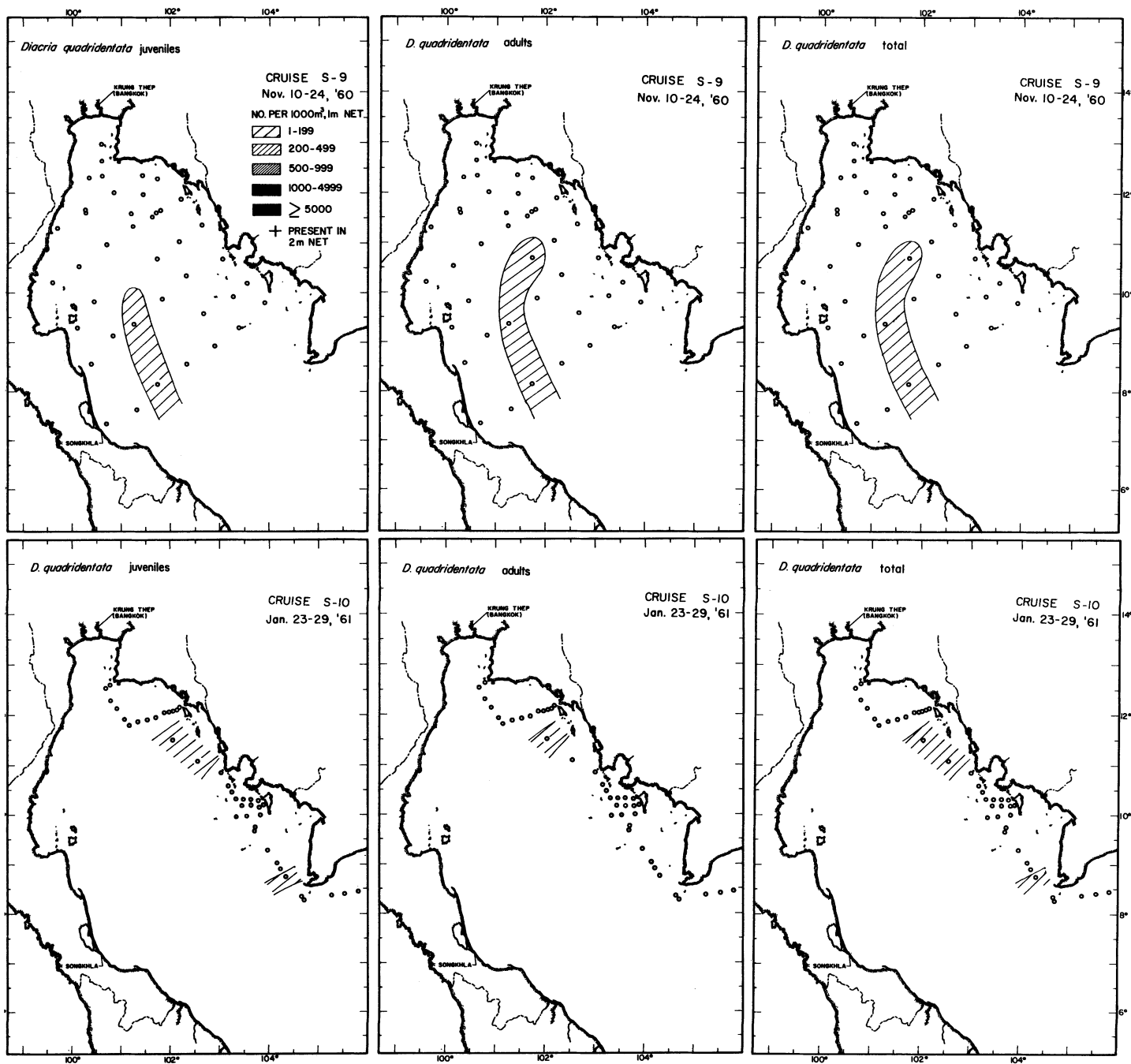


Figure 29e

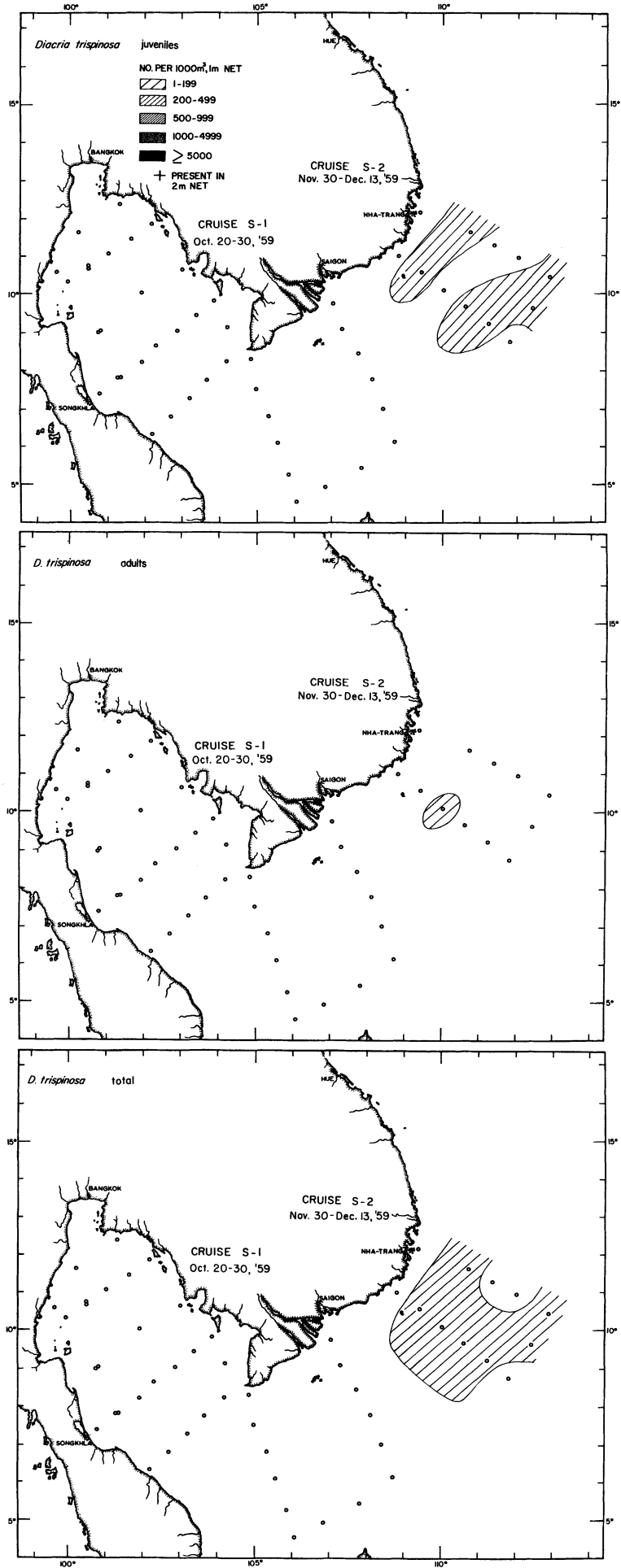


Figure 30a

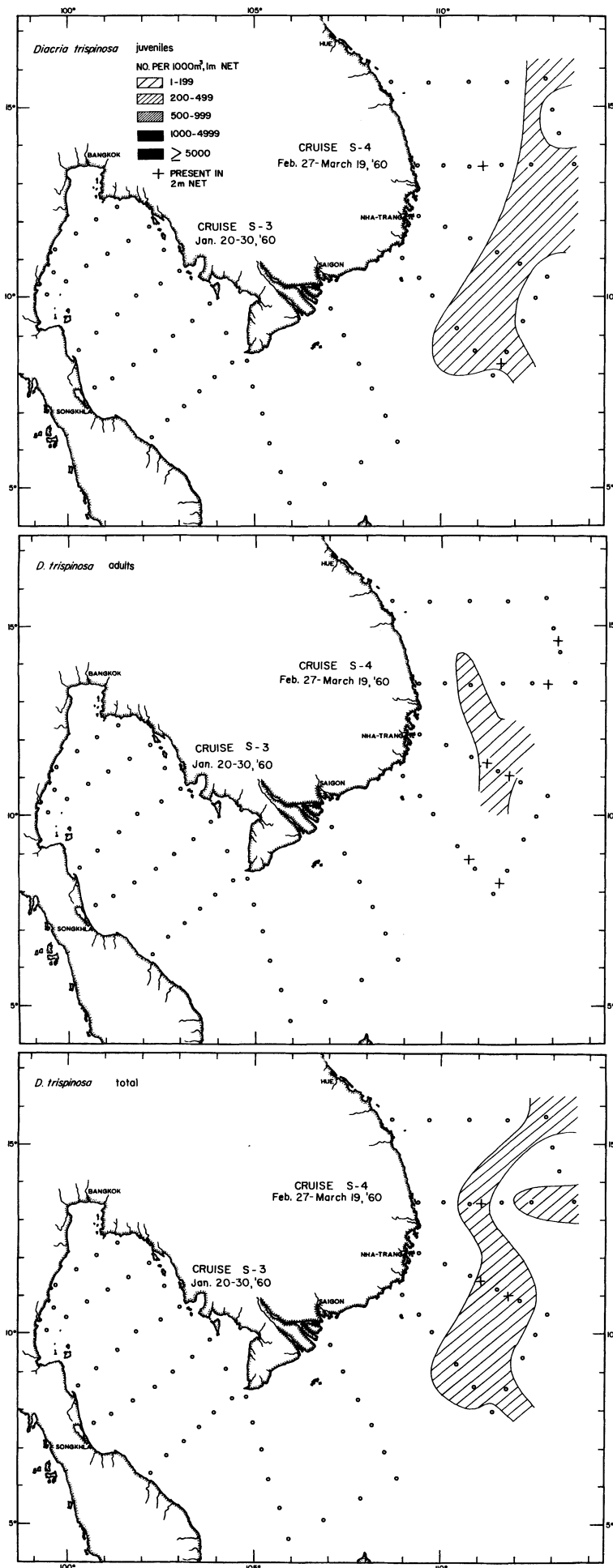


Figure 30b

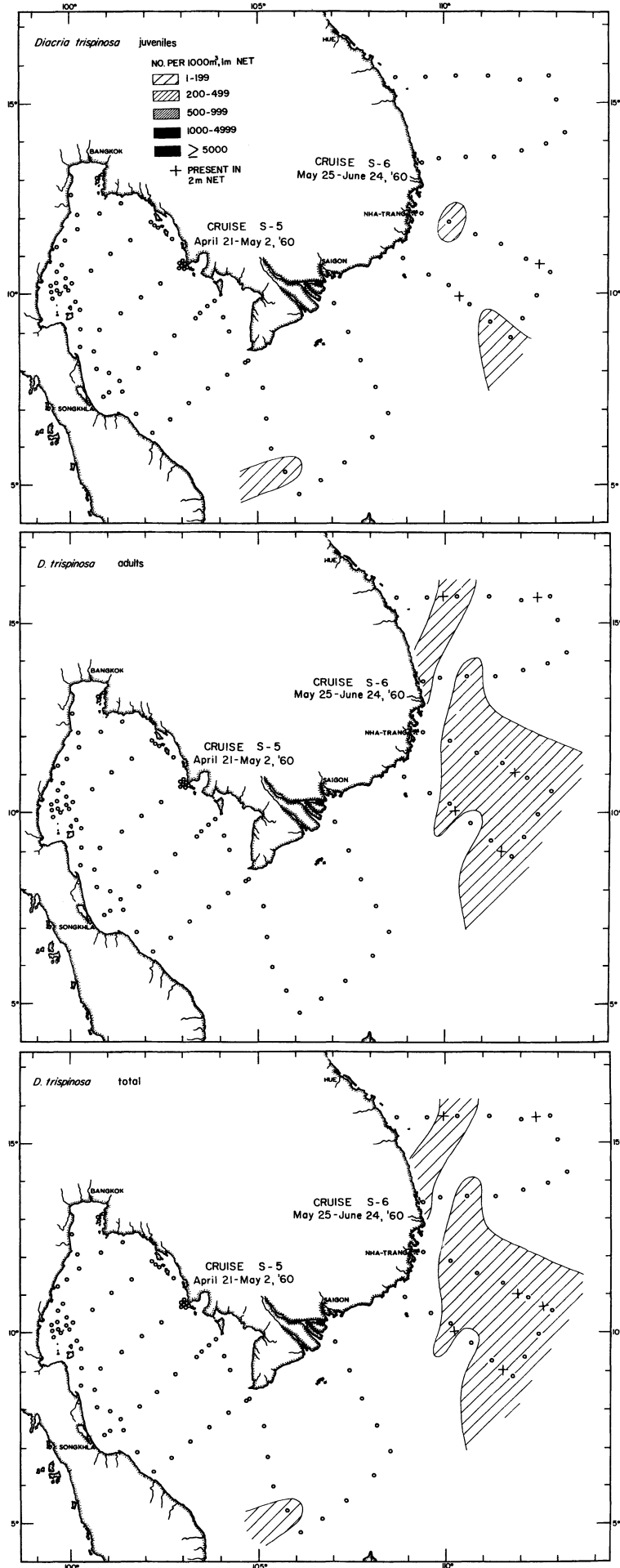


Figure 30c

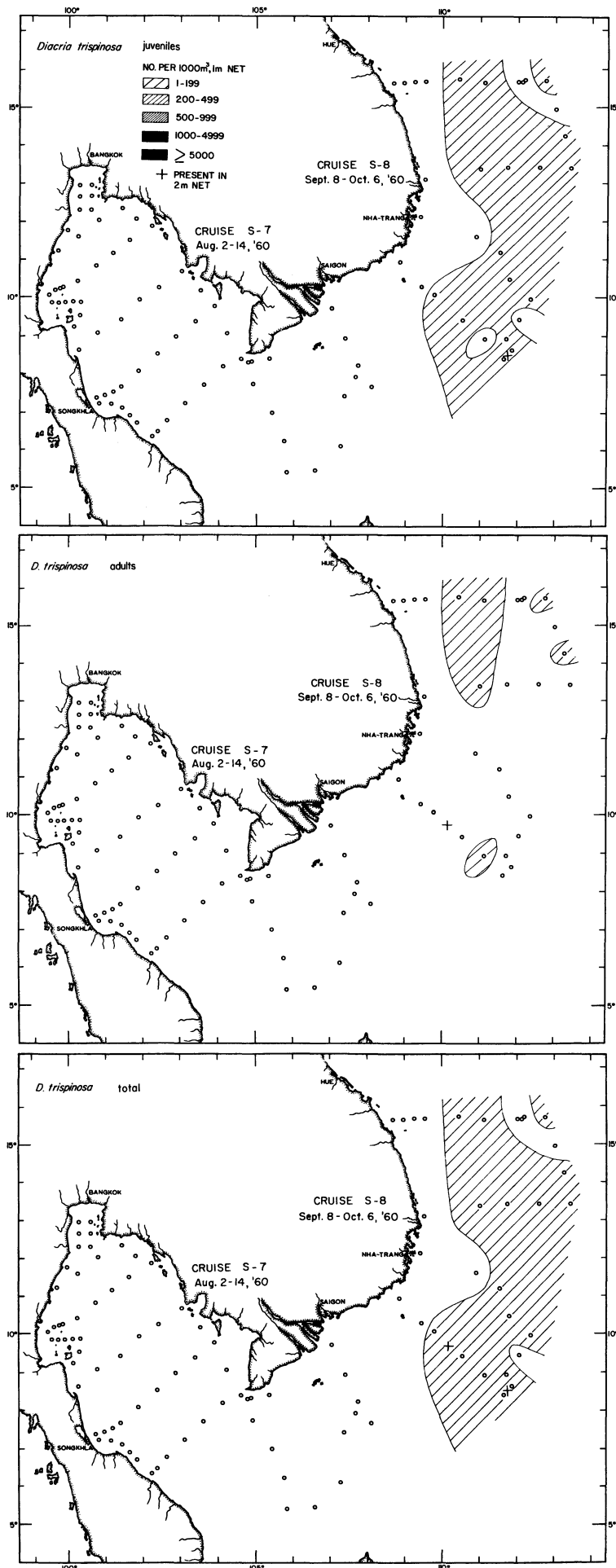


Figure 30d

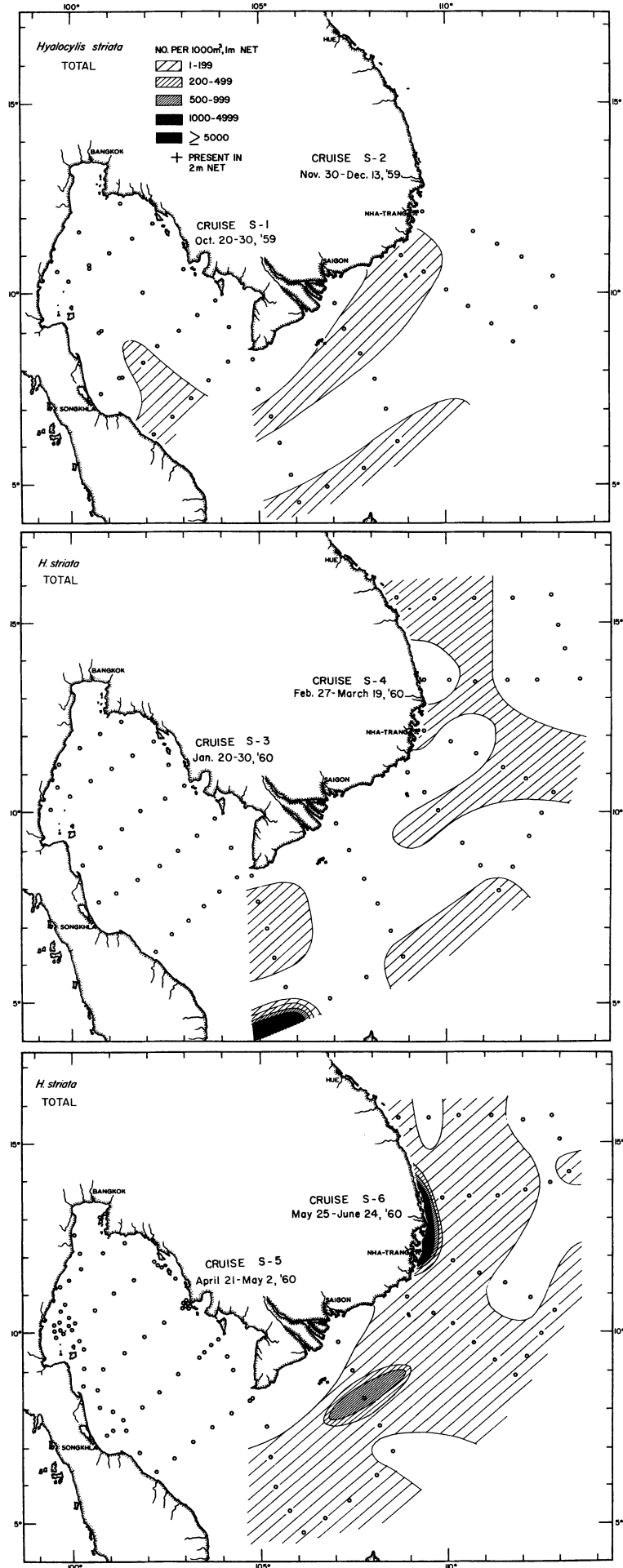


Figure 31a

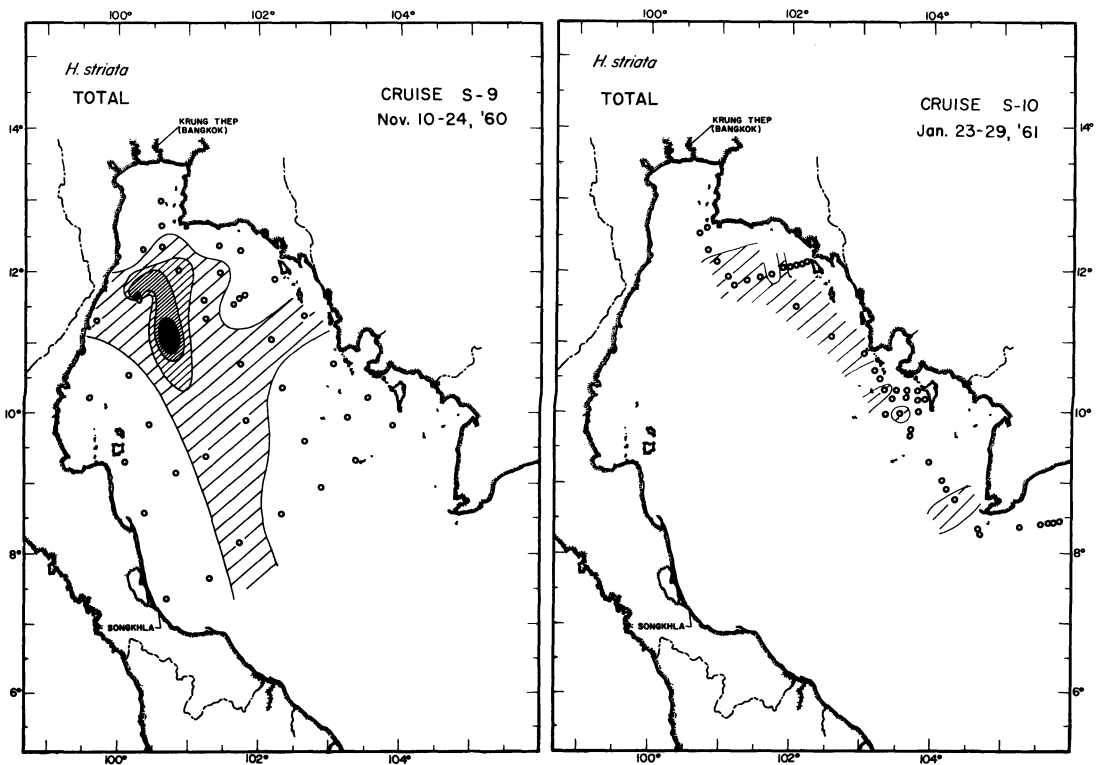
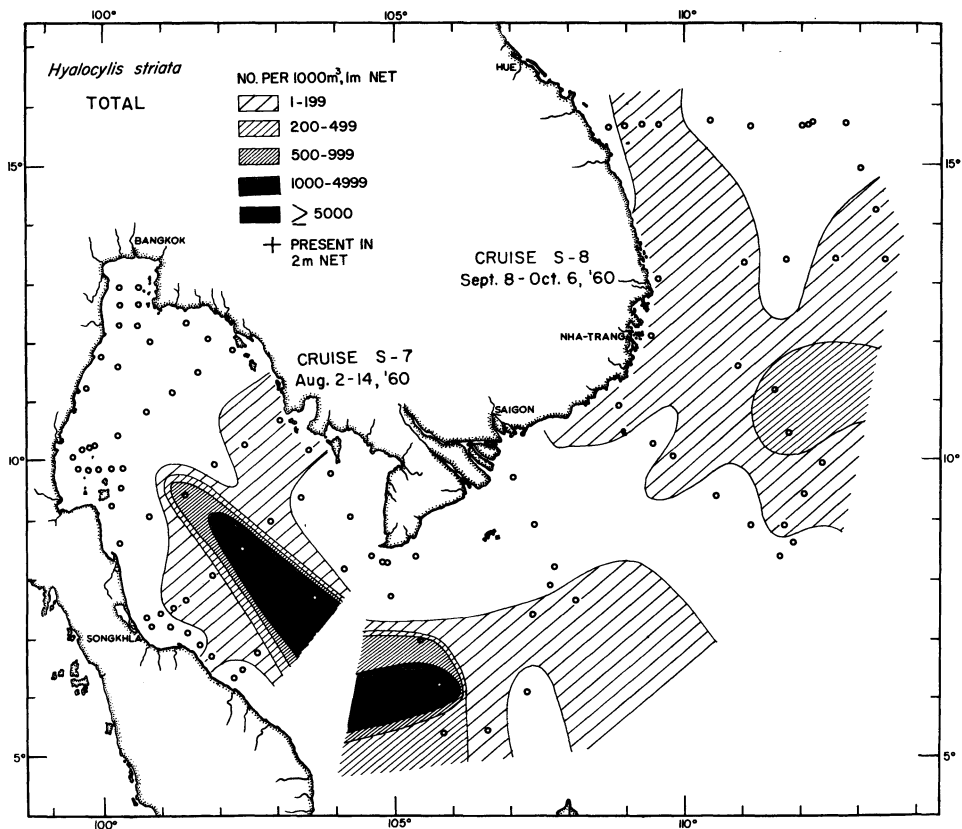


Figure 31b

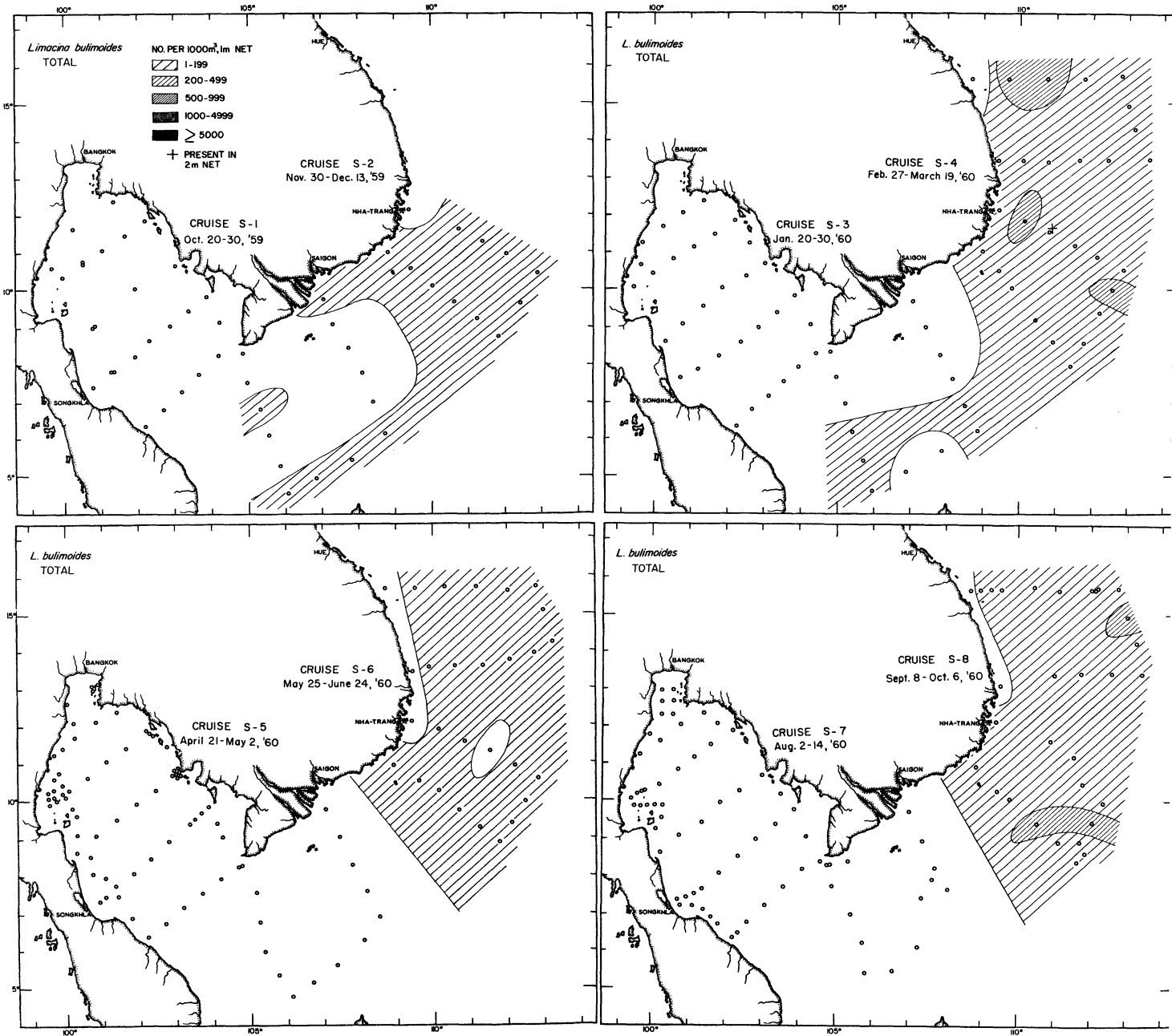


Figure 32

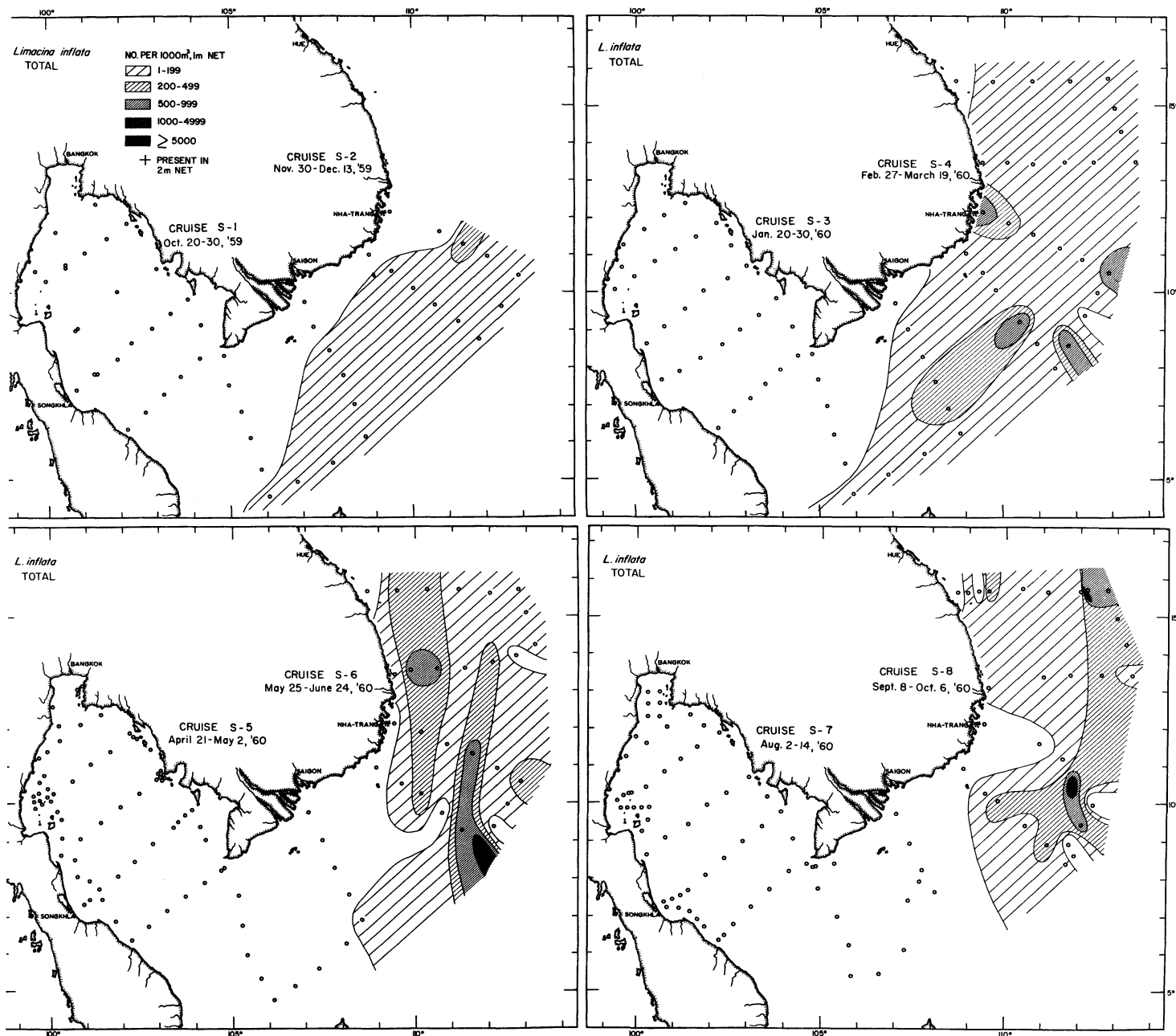


Figure 33

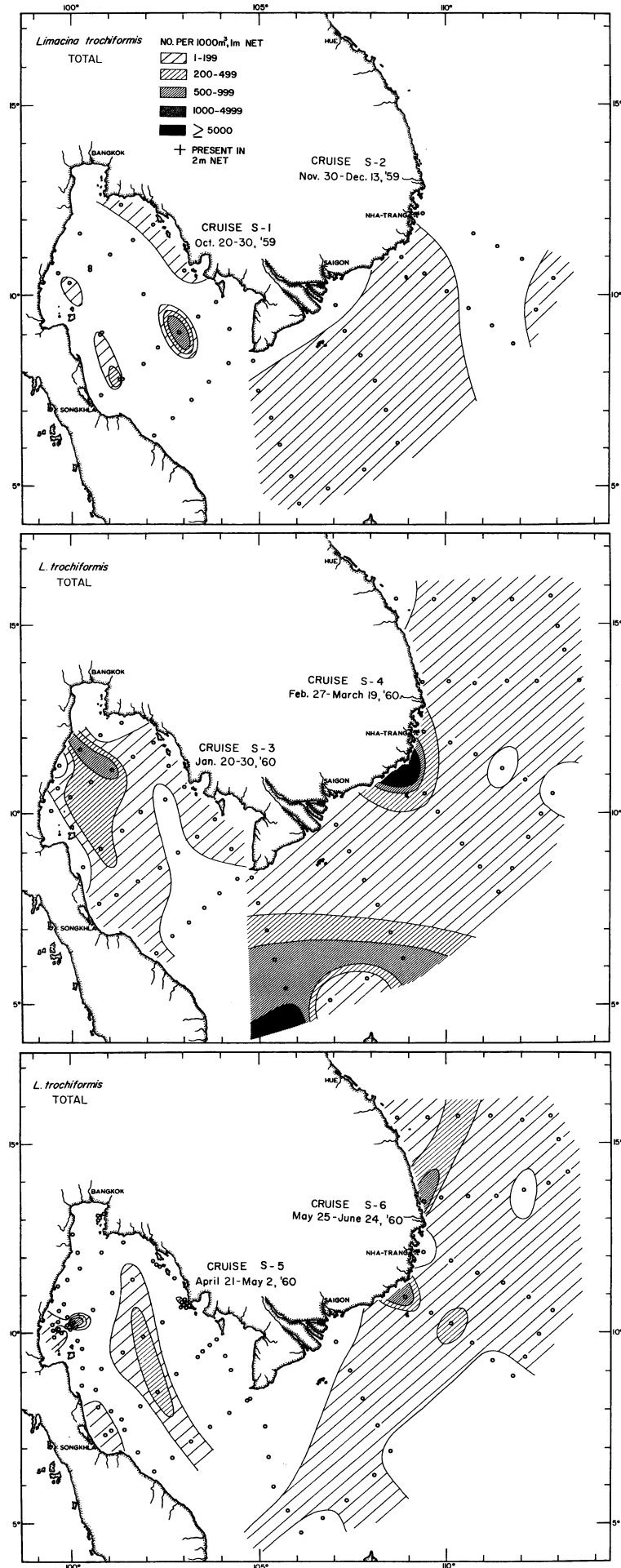


Figure 34a

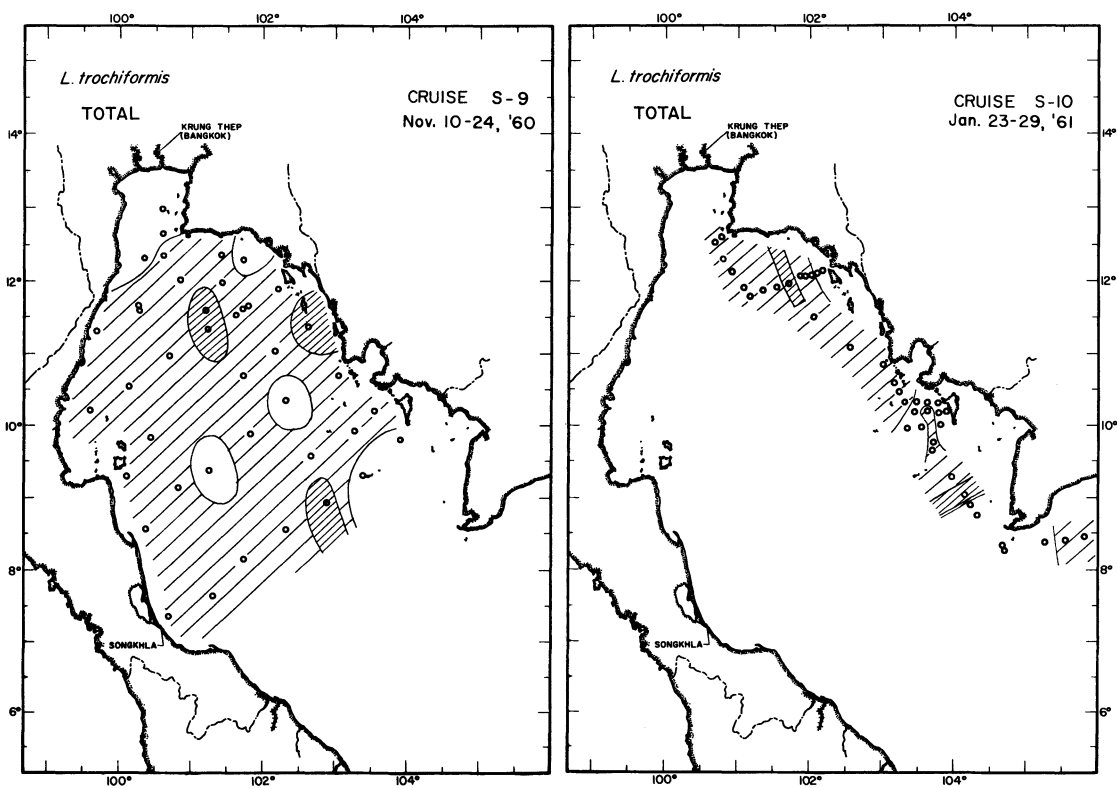
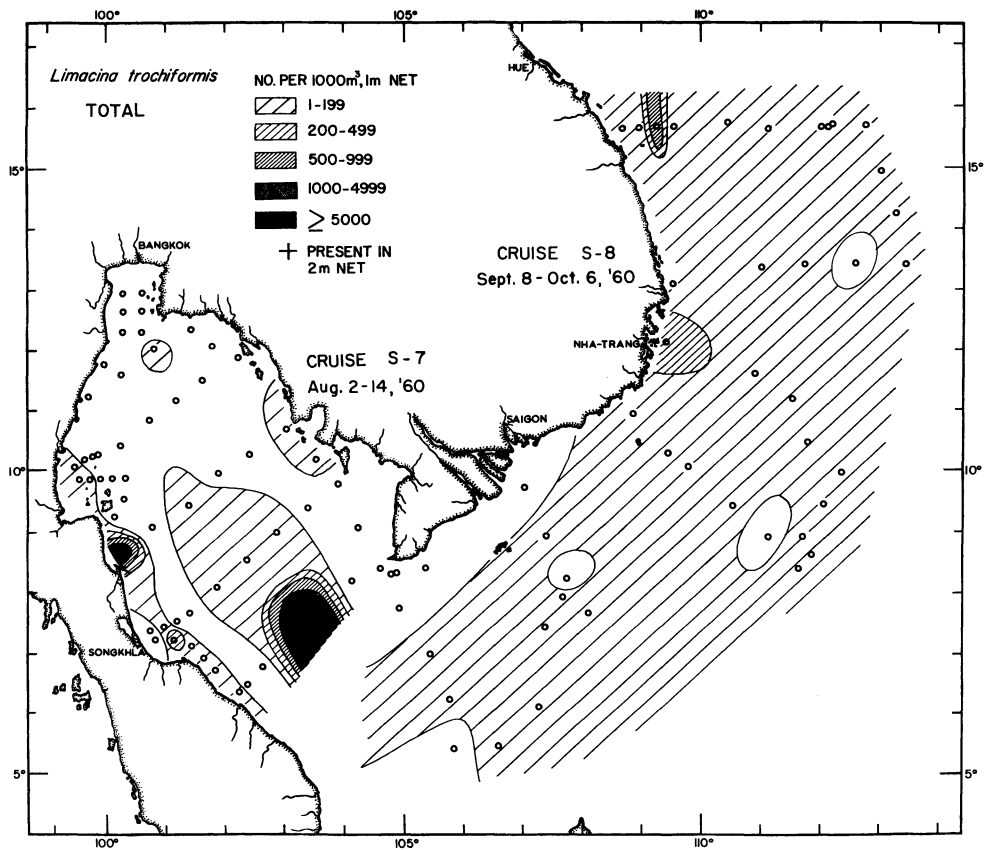


Figure 34b

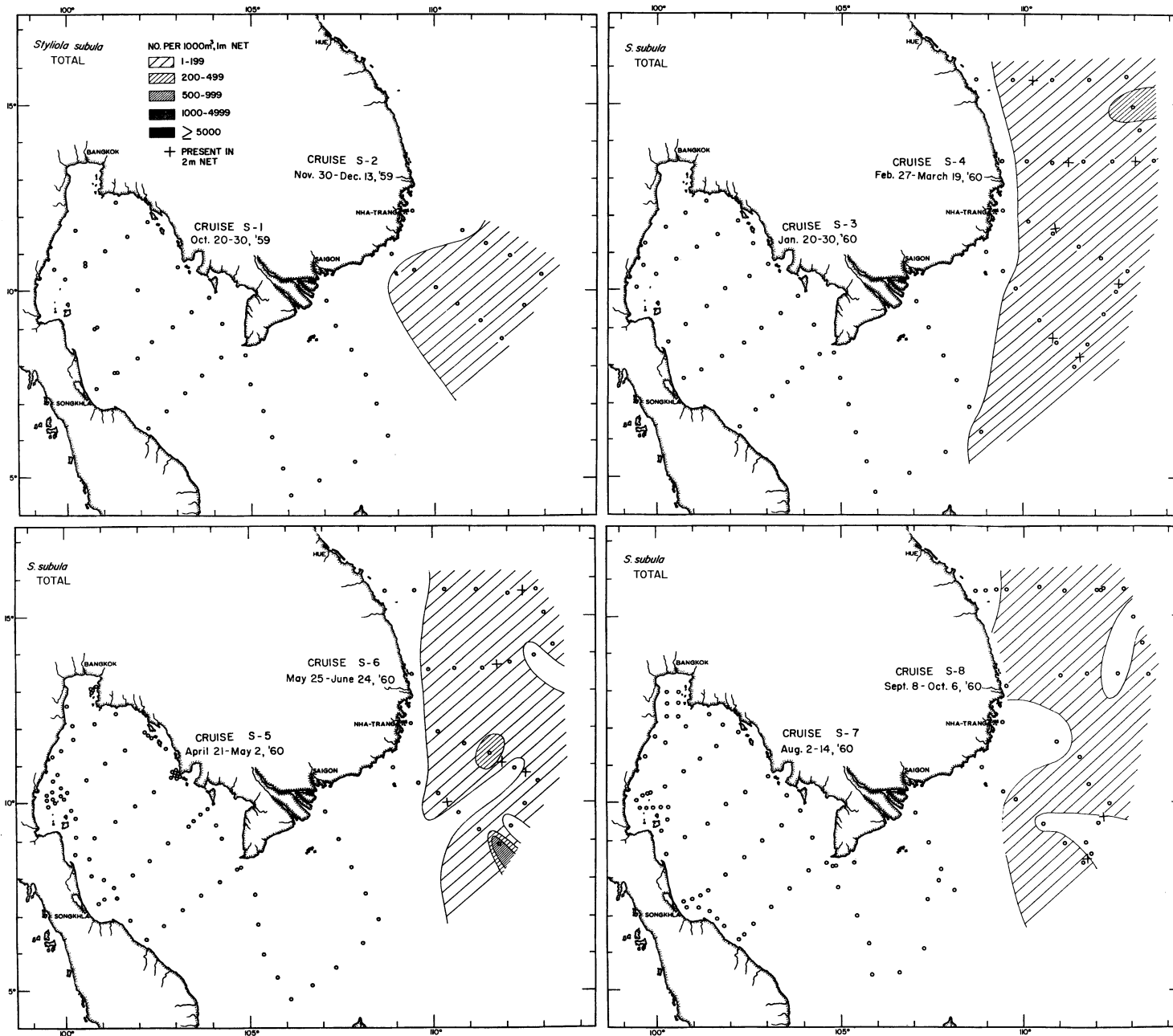


Figure 35

SECTION V. IDENTIFICATION OF THE SPECIES

This section presents photographs of each species found in the Naga material, accompanied by comments on distinguishing characteristics. In addition, the juvenile development of the shell of *Cavolina longirostris* and the taxonomic status of *Creseis virgula constricta* are discussed. To facilitate reference, the genera are listed alphabetically with species also in alphabetical order under each genus.

Since I have not studied the soft parts of pteropods in detail, the presentation will be limited to the shells except where a few comments on the identification of individuals which have lost their shells might be helpful. The systematic presentation will be that of Tesch (1946 and 1948), although Spoel's (1967) use of the name *Clio recurva* (= *Clio balantium*) is accepted. A more thorough account of the anatomy and the systematics of the species included here can be found in Tesch and Spoel.

Genus *Cavolina* Abildgaard 1791

Cavolina gibbosa (MS Rang, *In* d'Orbigny, 1836)

Plate II, 2a-b.

Of the species of *Cavolina* found in the Naga samples, this is one of the largest (ca. 10 mm total length). Its general shape is somewhat more flattened dorso-ventrally than other members of the genus, with the exception of *C. inflexa* which is so different that there is little likelihood of a mistake in distinguishing between the two.

Cavolina globulosa (MS Rang, *In* Gray, 1850)

Plate II, 1a-b.

Cavolina globulosa occurs in the South China Sea, together with other members of this genus, rendering it impossible to distinguish young forms of this species with as great a certainty as was possible with *C. longirostris* in the Gulf of Thailand. Some juveniles of *C. globulosa* are illustrated in Figure 36.

Cavolina inflexa (Lesueur, 1813)

Plate I, 2a-b.

Some young stages of this species also seem distinguishable, although again, as with *C. globulosa*, there was no place in the Naga area where this species was the only one of the genus present (Fig. 37). There should be no difficulty in distinguishing the fairly large, rather triangular youngest form shown from the smaller, more slender *C. longirostris* and from the squarer *C. globulosa*.

Cavolina longirostris (MS Lesueur, *In* Blainville, 1821)

Plate I, 1a-c.

This species has a shape typical of the genus *Cavolina*, except that the adults do not have the curved "tail" found on the other members of this genus. The lateral spines vary in shape from simply triangular to a more elaborate notched form. The dorsal surface of the shell at the rostrum

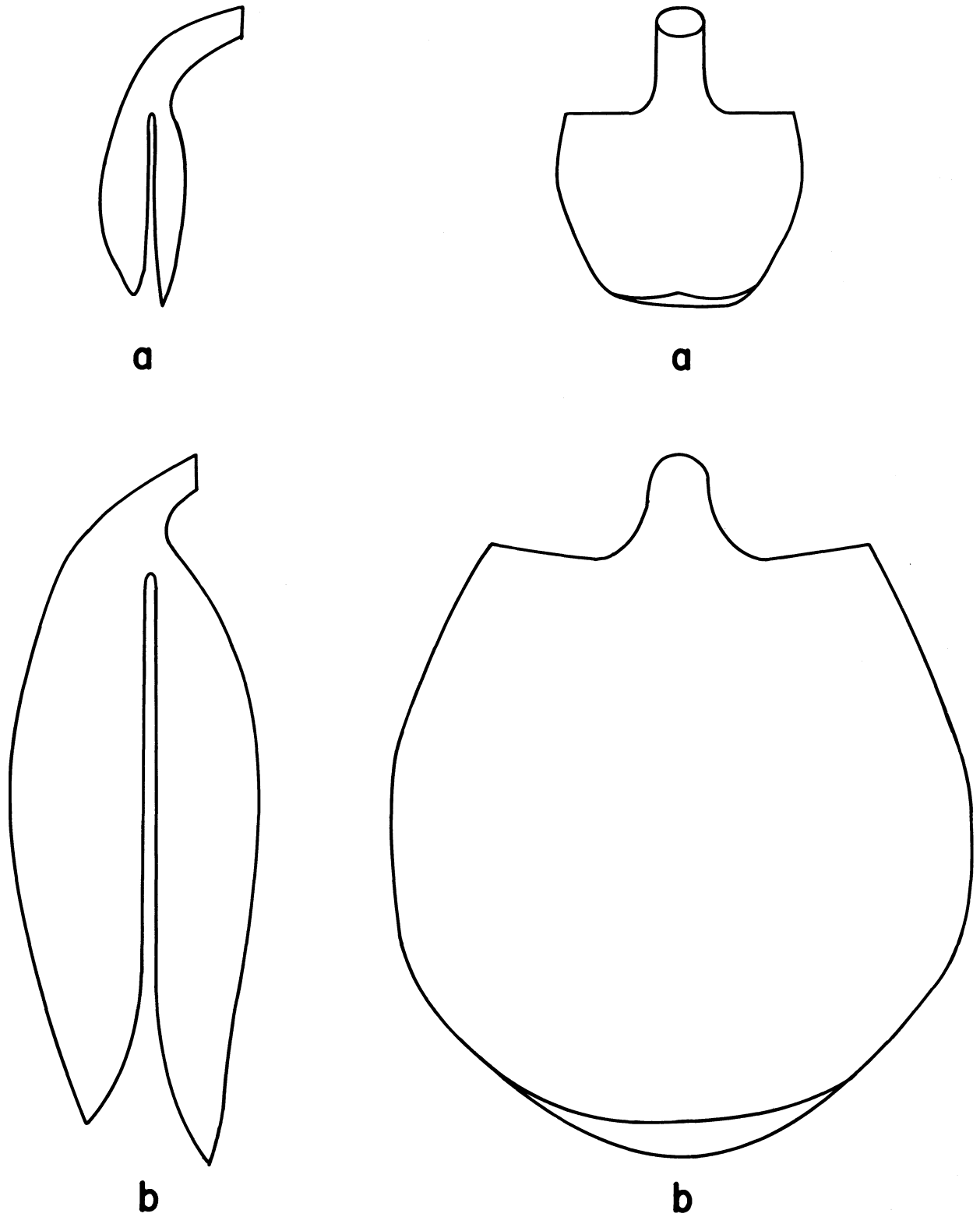


Figure 36. Juvenile *Cavolina globulosa*. Length of figured specimens: a. 1.5 mm; b. 3.5 mm.

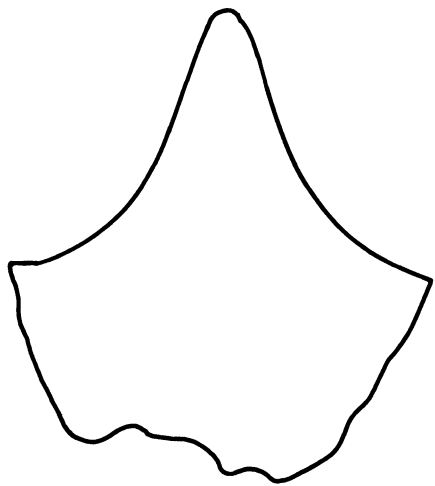
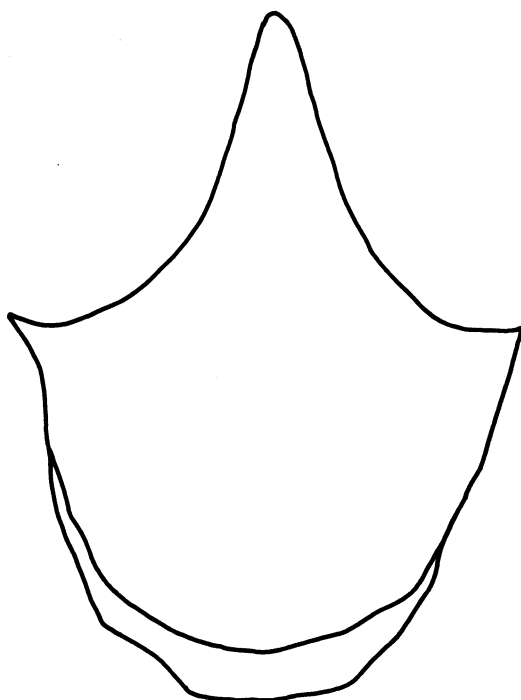
**a****a****b**

Figure 37. Juvenile *Cavolina inflexa*. Length of figured specimens: a. 2.5 mm; b. 3.7 mm.

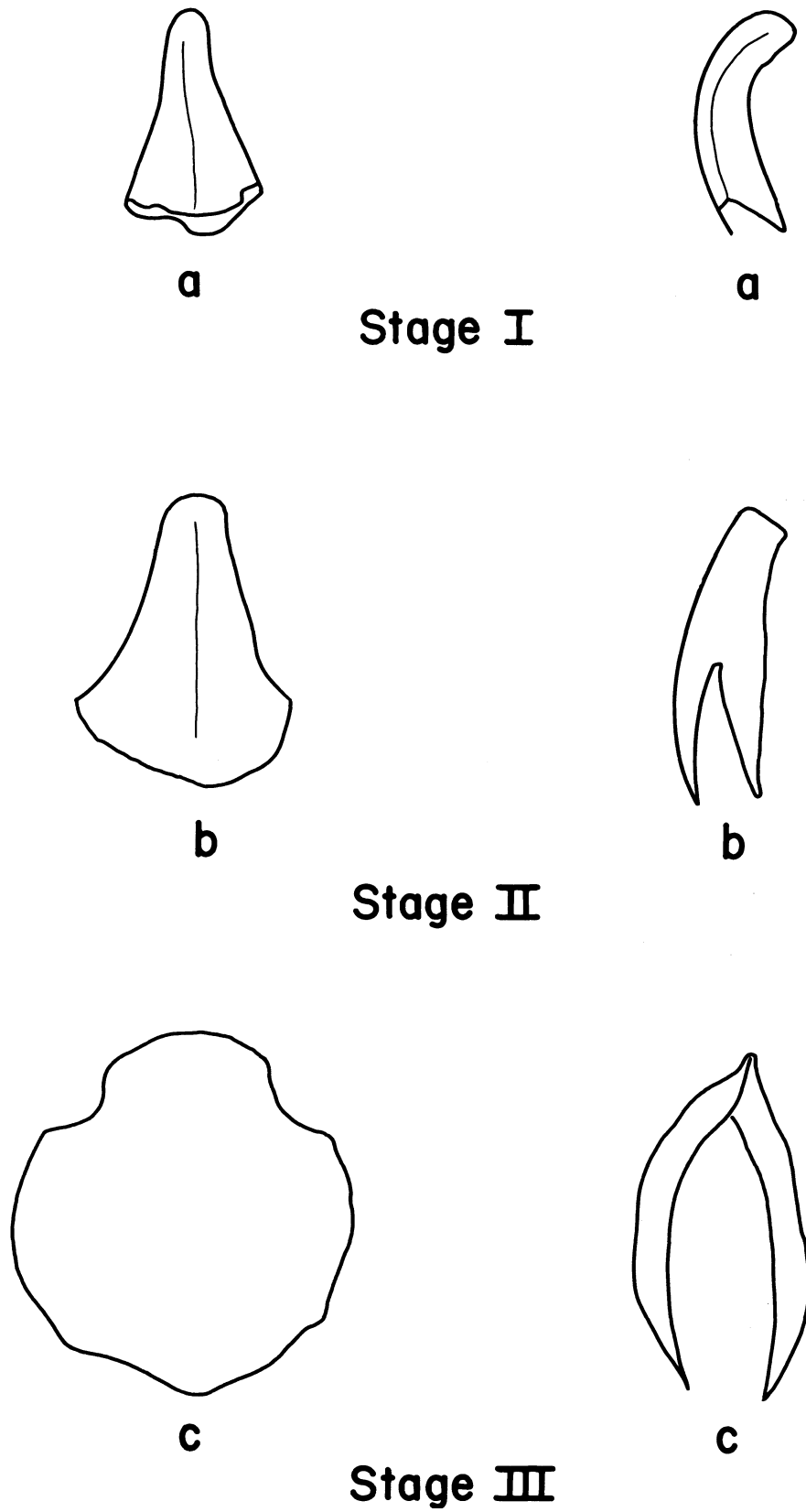


Figure 38. Juvenile *Cavolina longirostris*. Length of figured specimens: a. 0.63 mm; b. 0.81 mm; c. 1.0 mm.

may be formed into a transverse wall (variety *angulata* Souleyet) or it may gradually curve ventrally as in the variety *longirostris*.

The soft parts of this species and those of *Diacria quadridentata* are quite similar. *C. longirostris*, however, has a single-lobed liver, appearing as a single dark spot in the main visceral mass, while *D. quadridentata* has a bilobed liver.

Development of *Cavolina longirostris*. The Gulf of Thailand has provided a unique situation for the study of the development of the shell of the young of this species, since this is the only adult member of the genus *Cavolina* which occurs here. In fact, as mentioned in the section on distribution, the other species of this genus belong to the offshore group and were not found in the shallow shelf area southwest of the outer stations of lines 5 and 6 in the South China Sea, nor were there identifiable juvenile stages of these other species found in the shallow shelf area. Thus, it seems reasonable to assume that the young stages found in the Gulf of Thailand do not belong to any other species of *Cavolina*. This assumption is supported by the fact that these young forms seem to fall, without exception, into a graded series from the youngest stage to the adult *C. longirostris*.

The youngest stage, called Stage I for the purposes of labeling distribution maps and counting, is of a triangular shape in dorsal and ventral view. The apex is not extremely pointed, and the lateral edges curve slightly outward from the apex. The base of the triangle is rounded and is often a broken, jagged edge. A lateral view shows a thin shell curved dorsally and a slight inverted-v-shaped opening at the sides of the opening of the shell. At this stage there is a very low, wide raised portion on the dorsal surface in the place where the prominent central longitudinal ridge develops in the older stages. The general shape of the shell of *C. longirostris* at this stage is quite reminiscent of the dorsally curved tails of other members of this genus (Fig. 38a—the overall length of the specimen figured is 0.63 mm).

The second stage, II, is quite similar to Stage I except that the area around the aperture has become more flaring, and the pointed tip has broken off. The broken section is sometimes open, but often it has been closed off by a rounded septum. Also, the lateral inverted-v-shaped opening, which will eventually be the slit between the dorsal and ventral surfaces, is much longer (Fig. 38b—the specimen shown is 0.81 mm long). The next stage, III, has an outline similar to that of the adult, the posterior “neck” having become a relatively smaller proportion of the total shell. The opening between the dorsal and ventral surfaces has narrowed to a thin slit, but the closure point has not yet formed. At this stage the rostrum has begun to extend significantly beyond the ventral side of the shell. The central longitudinal ridge on the dorsal surface has become more prominent (Fig. 38c—the overall length of the figured specimen is 1.0 mm).

Cavolina uncinata (Rang, 1829)

Plate I, 3a-b.

This species is similar to *C. globulosa*. It can be distinguished from *C. globulosa* by its prominent posteriorly directed lateral spines and larger size. Where it curves dorsally, the anterior portion of the ventral surface of the shell is more rounded than that of *C. globulosa* which makes a sharper bend and then has a flat portion which slants posteriorly. In addition, *C. uncinata* has five ridges on the dorsal surface, while *C. globulosa* has only three. *C. uncinata* is commonly amber in color, while *C. globulosa* is generally clear with an amber area on the posteriorly slanting surface mentioned above.

Genus *Clio* Linné 1767*Clio cuspidata* (Bosc, 1802)

Plate III, 4.

The shell is triangular and curved dorsally. There are numerous conspicuous transverse folds. In the adult there are long lateral spines which Tesch (1946) says are often broken off. There is also a median dorsal rib in the adults, but this is not well developed in young individuals. The young do not yet have the long lateral spines but can be distinguished from the young of *C. pyramidata* by the dorsal curvature of the shell and by the shape of the larval shell, which is more rounded with a small sharp cusp.

Clio pyramidata Linné 1767

Plate III, 6.

There are three longitudinal ridges on the dorsal surface of the shell, the median one extending to the acute end. The shell lacks transverse folds and does not curve dorsally as in most of the other species of this genus. The lateral margin of the shell forms a sharp edge. The present specimens agree with Spoel's (1967) description of *Clio pyramidata* forma *lanceolata* (Lesueur, 1813).

Clio recurva (Children, 1823)

Plate III, 5.

This species attains the large size of 20 mm in length and larger. As with several other members of the genus *Clio*, both the dorsal and ventral surfaces of *C. recurva* have numerous transverse ridges. The lateral margin of the shell is doubled, with a flat depressed area between the dorsal and ventral portions. This forms a margin having the appearance of a gutter, which is deepest toward the aperture and disappears toward the apex.

There is a discussion above (p. 13) of McGowan's (1960) observations on the distribution of *Clio recurva* and of *Clio* [sp.] which was informally described in McGowan's dissertation. Reference was made to specimens reported as *Clio [recurva]* by Meisenheimer (1905) and some of the (smaller) specimens included under *Euclio balantium* (= *Clio recurva*) by Tesch (1946, 1948). These records were included in Spoel's (1967) synonymy of *Clio recurva*.

Genus *Creseis* Rang, 1828*Creseis acicula* Rang, 1828

Plate IV, 3.

The slender shell of *Creseis acicula* attains rather great lengths (25 mm in a very long specimen, 15 to 20 mm being more common). It is usually straight, though there are specimens which are slightly bent in as many as two directions. This bending seems to occur at random, no two shells being bent in exactly the same way. The larval shell is slender, having no prominent inflation near its base. In this respect this species (Plate IV, 3) resembles *C. virgula* (Plate IV, 2b-d).

The soft parts of *C. acicula* appear superficially similar to those of *Hyalocyclus striata*. *C.*

acicula may be correctly identified by the presence of a tentacular lobe on each anterior fin margin. These tentacular lobes are smaller and less prominent than those of *C. virgula*. Another helpful circumstance is that *C. acicula* does not usually die with its fins spread widely apart as does *Hyalocylis striata*.

Creseis bulgia Sakthivel, 1974

Plate IV, 5a-b, Fig. 39a.

The Naga samples contain a species of *Creseis* recently described by Sakthivel (1974). This species is similar to *Creseis virgula constricta* and to *Creseis chierchiaie*. Comparison with specimens of *C. virgula constricta* kindly sent to me by Dr. Allan Bé reveals some differences. Specimens of *Creseis bulgia* are much shorter, less than half the length, and the shape of the adult shell is somewhat different. The shape of the adult portion of Bé's specimens, just beyond the juvenile shell, is quite similar to *Creseis virgula conica*. It is narrower and does not expand in diameter as rapidly as in *Creseis bulgia*. This might be a difference between specimens from different oceans except that in the Sulu Sea specimens with inflated juvenile shells and the same shape as Bé's specimens are common as well as those with the shape characteristic of *Creseis bulgia*. Specimens of *Creseis bulgia* are, in many ways, much more similar to *Creseis chierchiaie*, though they do not have the transverse ridges characteristic of *C. chierchiaie*. *Creseis bulgia* also superficially resembles *Creseis calciformis* Meisenheimer, which is the juvenile of *Cuvierina columnella*.

Creseis chierchiaie Boas, 1886

Plate IV, 4a-b, 5, Figs. 39a, 40a.

This species is rather small and stubby, its proportions resembling those of *C. virgula* more closely than those of *C. acicula*. It has a larval shell which is inflated near the base. Unlike any other described member of the genus *Creseis*, the shell of this species is not smooth but possesses transverse ridges, much like *Hyalocylis striata*, except on a much smaller scale. The tentacular lobe on the anterior fin margin is small (Fig. 40a), resembling that of *Creseis acicula*.

This species was found by Boas (1886) in the Caroline Islands and in abundance in the Gulf of Panama, and by Dall (in McGowan, 1960) near Florida. Tesch (1946), however, states that he did not find it even though "both of these regions [Gulf of Panama and Florida] have been thoroughly explored by the 'Dana'." It has also been reported from the Caroline Islands by Tokioka (in McGowan, 1960), and McGowan (1960) found it at a few stations in the western tropical Pacific. *C. chierchiaie* was present in Naga Expedition samples from both the Gulf of Thailand and the South China Sea.

Creseis chierchiaie and *Creseis bulgia* share a number of morphological characteristics. They have similar shapes, sizes, and proportions. (Tables 8 and 9 give measurements of a number of specimens of *Creseis bulgia* and *C. chierchiaie* respectively.) The larval shells of both forms are somewhat inflated and have a constriction at their bases (Fig. 39). The tentacular lobes on the fin margins are small and not prominent in both forms (Fig. 40a). The tentacular lobes on the fin margins of *Creseis virgula virgula*, on the other hand, are quite prominent and distinctive (Fig. 40b).

Unfortunately, no separate data on the quantitative distribution of *Creseis chierchiaie*, *Creseis bulgia*, and *Creseis virgula constricta* are available because their separate existence was not discovered before the counting was completed. This is due to the following factors. Neither *Creseis virgula constricta* nor *C. bulgia* had been described at the time the counting was done and *C. virgula constricta* forms a very small proportion of the specimens counted (probably less than 1%). The microscope power used for counting was not sufficient to display the ridges characteristic of *C. chierchiaie*, and higher power was not used because presence of this species was not

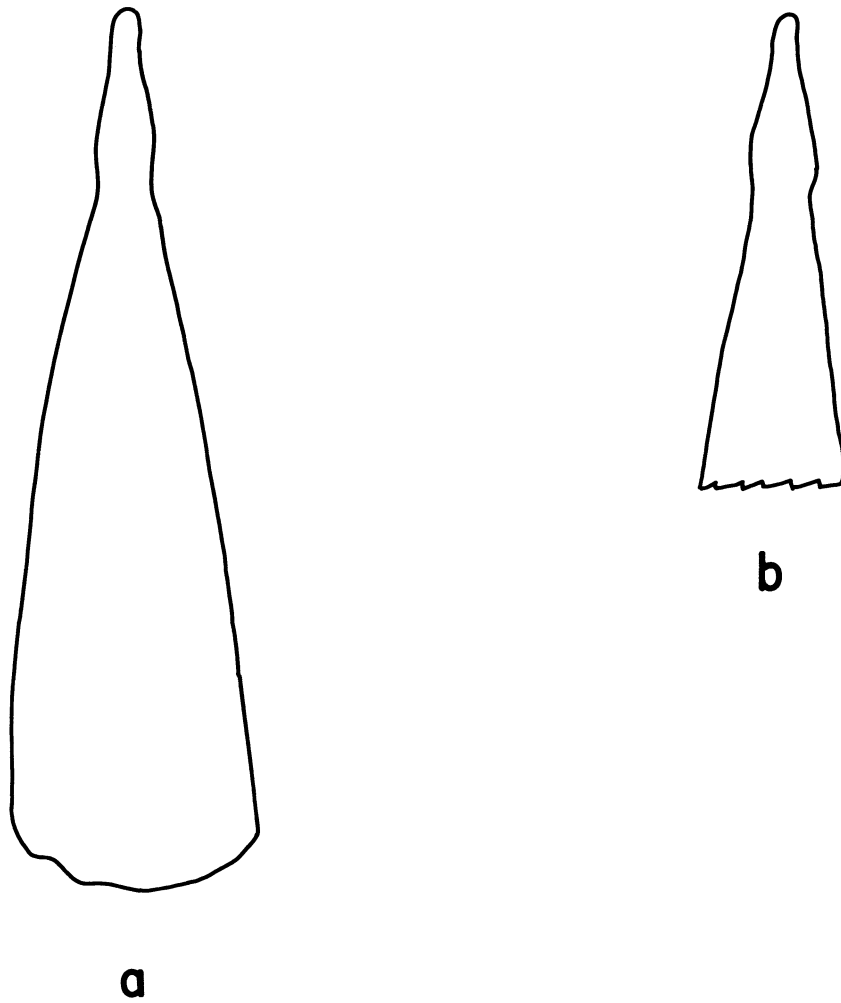


Figure 39. a. *Creseis bulgia*. Length of figured specimen: 2.0 mm. b. *Creseis chierchia*, same magnification as (a). NOTE: transverse ridges and part of shell omitted.

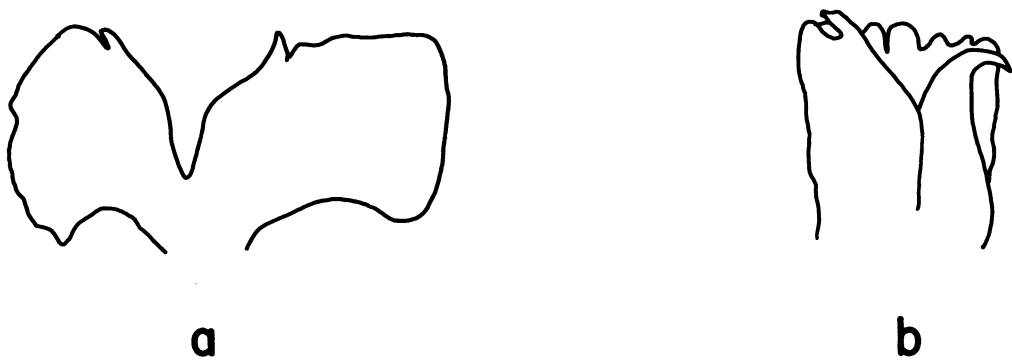


Figure 40. Anterior foot lobes: a. *Creseis chierchia*, X57; b. *Creseis virgula virgula*, contracted individual, X28.75.

Table 8 MEASUREMENTS, in mm, of *Creseis bulgia*

TOTAL LENGTH	LARVAL SHELL LENGTH	WIDTH AT INFLATION	WIDTH AT BASE OF LARVAL SHELL	WIDTH AT APERTURE
0.68	0.40	*	*	*
0.84	0.40	*	*	*
1.0	0.40	0.14	0.12	0.28
1.0	0.46	0.14	*	*
1.5	0.40	0.16	*	*
1.6	0.42	0.16	*	*
1.7	0.42	0.14	0.12	0.46
1.7	0.44	0.14	*	*
1.8	0.42	0.14	0.12	0.48
1.9	0.44	0.14	0.13	0.44
1.9	0.44	0.13	0.12	0.44
1.9	0.40	0.13	0.12	0.48
1.9	0.42	0.14	*	*
1.9	0.44	0.16	*	*
2.0	0.44	0.14	*	*
2.0	0.46	0.16	0.14	0.44
2.0	0.44	0.13	0.12	0.50
2.0	0.46	0.13	0.10	0.41
2.0	0.43	0.15	0.13	0.41
2.1	0.44	0.14	0.12	0.48
2.2	0.44	0.16	0.14	0.50
2.2	0.40	*	*	*
2.6	0.48	*	*	*

Table 9 MEASUREMENTS, in mm, of *Creseis chierchiaie*

TOTAL LENGTH	LARVAL SHELL LENGTH	WIDTH AT INFLATION	WIDTH AT BASE OF LARVAL SHELL	WIDTH AT APERTURE
0.84	0.42	0.16	*	*
0.88	0.40	0.16	*	*
0.96	0.40	0.14	*	*
0.96	0.42	0.14	*	*
1.8	0.46	0.14	0.14	0.44
1.9	0.44	0.14	*	*
1.9	0.46	0.16	0.14	0.46
2.0	0.44	0.14	0.13	0.44
2.1	0.48	0.14	0.13	0.49
2.4	0.44	0.14	0.13	0.52

expected. The lack of expectation was due to the casual manner in which Tesch (1946) mentions *C. chierchiaie*, apparently because he did not find it, and because the descriptions of it (Boas, 1886; Tokioka, 1951) were not available in Bangkok, where most of the counting was performed.

Table 10 summarizes the results of subsequent examination of twenty selected samples for the presence of *Creseis chierchiaie* and *Creseis bulgia*. On the basis of the data presented in Table 10 the following statements can be made:

1. Both species are found in both the Gulf of Thailand and the South China Sea.
2. Each may occur singly or with the other in both the Gulf of Thailand and the South China Sea.
3. *Creseis bulgia* was found in 1.67 times as many of the samples examined as *Creseis chierchiaie*.

Generally, when both species are present in a sample, one is considerably more abundant than the other, and either species may be the more abundant one. Figure 25a,b presents distribution maps of the combined distributions of *Creseis bulgia* and *Creseis chierchiaie* (a few specimens of *Creseis virgula constricta* and *C. virgula conica* are undoubtedly also included). Examination of the data from the 20 selected samples points up one important aspect of the distribution of *Creseis bulgia*: it clearly belongs with the shallow-water recurrent species group, since it occurs in the Gulf of Thailand. This is also true of *Creseis chierchiaie*. Whether these species should be placed in Group B or Group C (p. 39) cannot be established with the present data.

Table 10 OCCURRENCE OF *Creseis chierchiaie* AND *C. bulgia* IN SELECTED SAMPLES

a) By Area		
	South China Sea	Gulf of Thailand
No. of Samples Examined	7	13
Both Species Together	3	3
<i>C. chierchiaie</i> Only	4	5
<i>C. bulgia</i> Only	5	10

b) By Cruise							
	S-1	S-3	S-4	S-5	S-6	S-7	S-8
<i>C. chierchiaie</i> Only	0	1	0	0	1	1	0
<i>C. bulgia</i> Only	2	3	1	1	0	1	1
Both Species Together	1	0	0	1	0	1	3

Creseis virgula (Rang, 1828)

Plate IV, 2a-e.

This species exhibits considerable variation, ranging from relatively short, with the curved part of the shell comprising a large portion of its length, as in the conspicuously curved subspecies *Creseis virgula virgula*, through the slightly curved subspecies *C. virgula conica*, to the almost entirely straight subspecies *C. virgula clava* (the three subspecies distinguished by Tesch, 1913). There is little or no constriction where the juvenile shell joins the adult shell, except in the subspecies *C. virgula constricta*. The tentacular lobes on the fin margins are prominent and distinctive (Fig. 40b). *Creseis virgula virgula* was by far the most common of the subspecies in the Naga plankton samples.

Genus Cuvierina Boas, 1886

Cuvierina columnella (Rang, 1827)

Plate II, 3a-b.

This species has a smooth, bottle-shaped shell, usually broken off at the small end in adults. There is a rounded convex septum closing off the shell a short distance anterior to the broken edge.

The young have a smooth conical shell with a larval shell similar to that of *Creseis chierchiaie*. The conical shell usually breaks off after the formation of the adult shell, leaving the jagged broken edge projecting somewhat beyond the closing septum. However, the juvenile shell is occasionally retained in the adult (Plate II, 3b). The tip of the larval shell is usually broken off in those cases where the juvenile shell remains attached to the adult. The juvenile shell may be distinguished from *Creseis chierchiaie* and *C. virgula constricta* by its larger size, straighter sides, and greater diameter for a given length.

Genus Diacria Gray, 1847

Diacria quadridentata Lesueur (MS In Blainville, 1821)

Plate V, 2a-d.

The shells of the adult individuals of this species of the genus *Diacria* do not bear notable similarities to those of the other species of the genus, *D. trispinosa*. The general form of the shell of *D. quadridentata* is much more suggestive of the genus *Cavolina*. However, the young of the two species of *Diacria* are quite similar. The Naga material contains a fairly good series of developmental stages between the young of this species and the adult form which differs greatly from the young and which, unlike *D. trispinosa*, is never found with the juvenile shell attached. The posterior end of the adult indicates the original presence of the flat juvenile shell which is so similar to that of *D. trispinosa*. There is a rounded convex septum closing off the shell surrounded by a straight "wall." This wall is broken off and does not extend beyond the septum. This is similar to the situation commonly found in *Cuvierina columnella*.

The young of this species resemble young of *D. trispinosa*, and the reader is referred to that description, below. The two distinguishing features of *D. quadridentata* are the larger apical angle and the more oval larval shell (Plate V, 5 a).

The soft parts of the adult of this species are similar in general appearance to those of *Cavolina longirostris*. The two species may be distinguished by the presence in *D. quadridentata* of a bilobed liver, which appears as a dark bilobed mass in the viscera, while *C. longirostris* has a single-lobed liver.

Diacria trispinosa (MS Lesueur, In Blainville, 1821) Plate V, 3a-c.

The Naga material contains both of the varieties of *Diacria trispinosa* designated by Boas (1886): *D. trispinosa* var. major with backward pointing lateral projections and *D. trispinosa* var. minor with the lateral spines pointing straight outwards. Tesch (1946) says of the variety minor that it "is by far the more numerous," but this is not particularly the case with the Naga specimens.

The shell of young individuals is flat, diverging slightly from the base of the larval shell. The margins are formed into slightly thickened ridges of a yellowish-brown color. In later stages the apertural end begins to flare outwards. In the Naga material a fairly continuous series from this young form to the adult was present. The juvenile shell is often broken off of the adult, leaving a short posterior projection with an irregular or jagged edge. The young individuals of *D. trispinosa* can be distinguished from the very similar young of *D. quadridentata* by the more rounded larval shell (Plate V, 3a-b) and by the smaller apical angle.

Genus Hyalocylis Fol 1875

Hyalocylis striata (Rang, 1828)

Plate IV, 1a-b.

This species has a conical shell which does not have a point at the apex. There is a rounded

closure at the small end of the shell, but this is frequently broken off in preserved material. No individuals were found with a juvenile shell still attached. The adult shell curves slightly dorsally. A prominent characteristic of the species is the presence of pronounced transverse ridges encircling the shell. The aperture is oval, but the cross-sectional shape gradually becomes circular toward the apex. The soft parts are very similar to *Creseis acicula*, but *H. striata* regularly dies with its foot lobes extended, while *C. acicula* does not, and this feature can be helpful for identifying specimens which have lost their shells.

It has been suggested that *Creseis chierchiaie* is merely the young of *H. striata* (Spoel, 1967). Neither the specimen of *C. chierchiaie* shown in Plate IV, 4, nor the one shown in Figure 39b, can be the young of *H. striata*, since they possess tentacular lobes on the fin margins, which *H. striata* does not. The specimen in Plate IV, 5, tentatively identified as *C. chierchiaie*, does not possess the inflated larval shell found in *C. chierchiaie* and its size and shape are somewhat different. Menzies (1958) figured a specimen from the Mediterranean which he had identified as *C. chierchiaie*. McGowan (1960) noted that the specimen illustrated by Menzies differed from those illustrated by Boas (1886), Tesch (1913), and Tokioka (1951). He said, "Perhaps the most significant of these differences is in the shape of the larval shell. Menzies indicates that it is rather bluntly rounded and not separated off from the adult shell by any sort of a constriction. The illustrations of *C. chierchiaie* in Boas (1886) and Tokioka (1951) both show this larval tip to be much more pointed and set off from the adult shell by a gentle but broad constricted area. The horizontal striations shown by Menzies differ in kind and number from those of the other authors, and further, his shell proportions are clearly different." Menzies' illustration more closely approximates the specimen in Plate IV, 5. Could these both be the young of *Hyalocyclus striata*?

Genus *Limacina* Bosc, 1817

Limacina bulimoides (d'Orbigny, 1836)

Plate III, 3.

Of the two spire-bearing species of *Limacina* found in the Naga material, *L. bulimoides* has the higher spire; an individual selected at random had a ratio of the spire height to the diameter of the largest whorl of 2.0, while a randomly selected individual of *L. trochiformis*, the other spired species, had a corresponding ratio of 1.3. Also, the aperture of *L. bulimoides* has a straight columnellar margin, producing a kind of triangular tip projecting down the umbilicus.

Limacina inflata (d'Orbigny, 1836)

Plate III, 1a-c.

This species of *Limacina* is planispiral. The aperture may have a narrow projection curving on around the shell a short distance in the direction of the last whorl. This is produced by a thickened portion of the shell, which is stronger and thus less prone to breakage than the rest of the shell on either side.

Limacina trochiformis (d'Orbigny, 1836)

Plate III, 2.

Of the two spire-bearing species of *Limacina* found in the Naga material, *L. trochiformis* has the lower spire (see the above section on *Limacina bulimoides* for a comparison of spire heights). In addition, the columnellar margin is rounded, producing a more rounded aperture than is found on *L. bulimoides*.

Genus *Styliola* Gray, 1850

Styliola subula (Quoy and Gaimard, 1827) Plate V, 1a-b.

The shell of this species is conical and has a round aperture like that of *Creseis acicula*. In contrast to *C. acicula*, however, it has a groove running obliquely from the mid-dorsal portion of the aperture to the apex.

The young can be distinguished from similar forms by the sharply pointed larval shell and by the presence of the longitudinal groove.

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PLATE 1

1. *Cavolina longirostris* (Lesueur)
 - a. *C. l. angulata*, lateral view; b. *C. l. longirostris*, lateral view; c. *C. l. longirostris*, ventral view; X15.
2. *Cavolina inflexa* (Rang)
 - a. lateral view; b. ventral view; XI5.
3. *Cavolina uncinata* (Rang)
 - a. lateral view; b. dorsal view; X10.

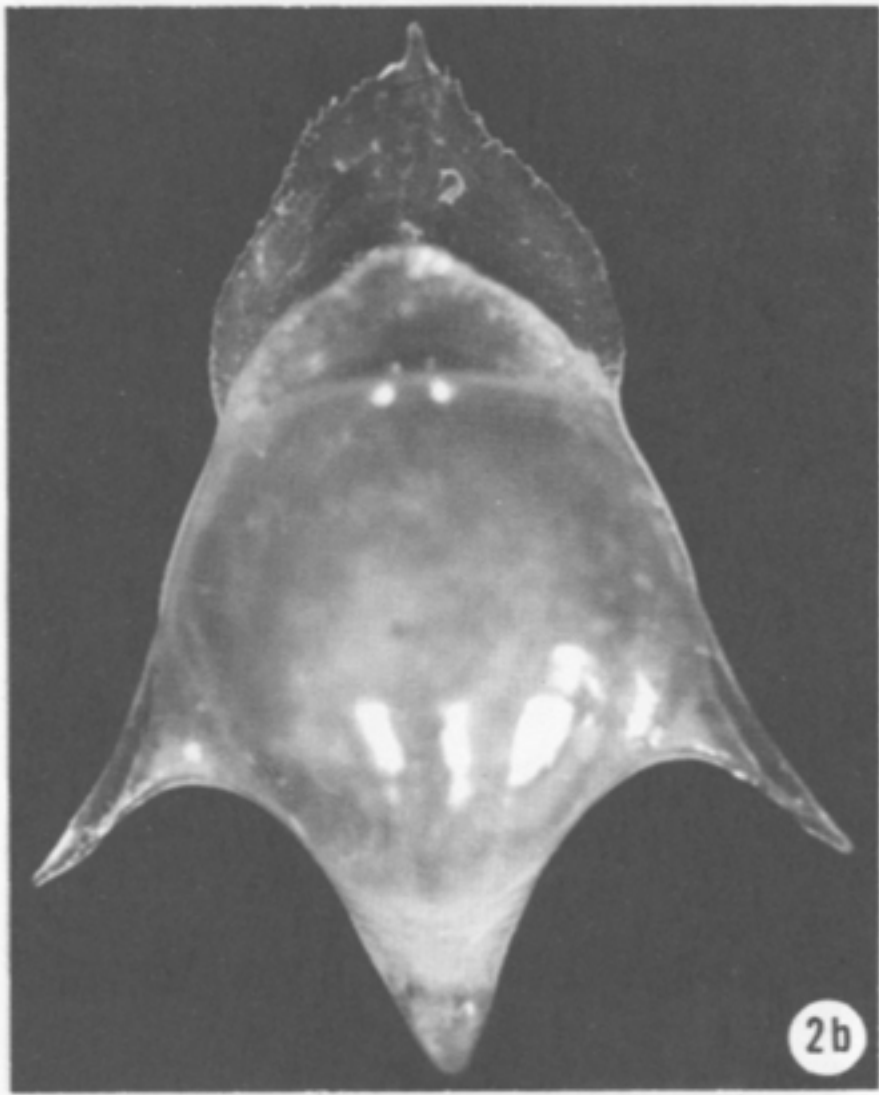
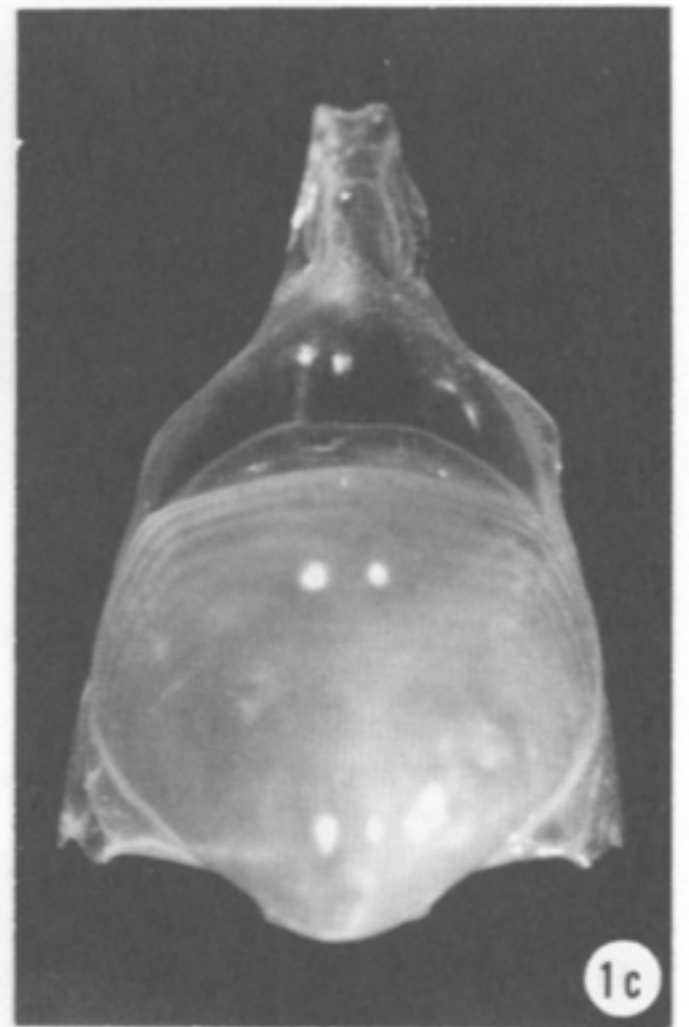
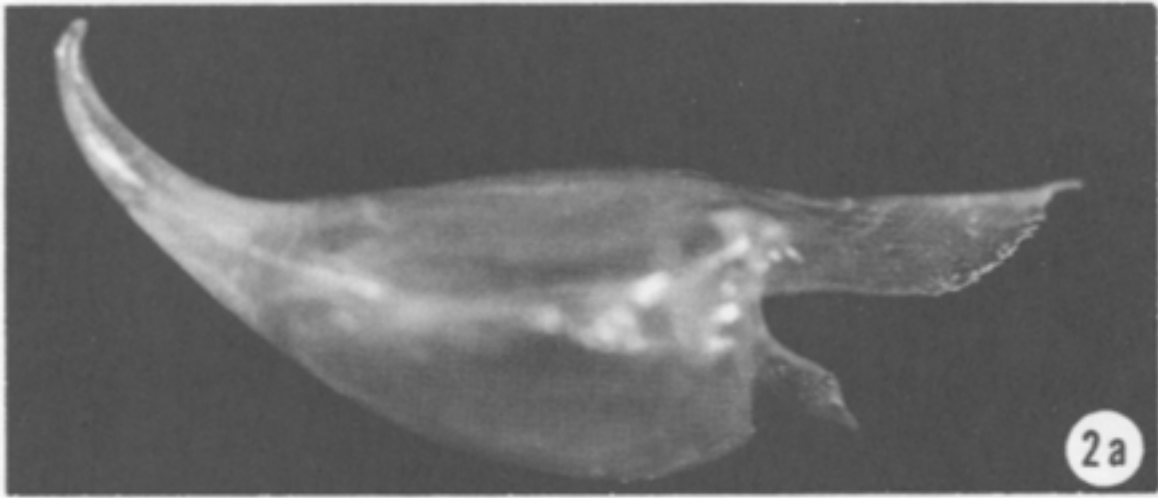
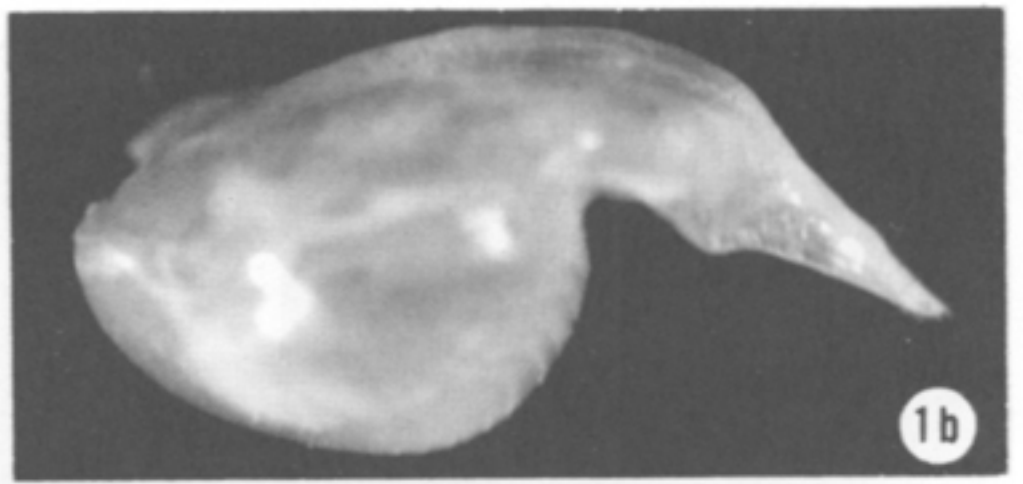
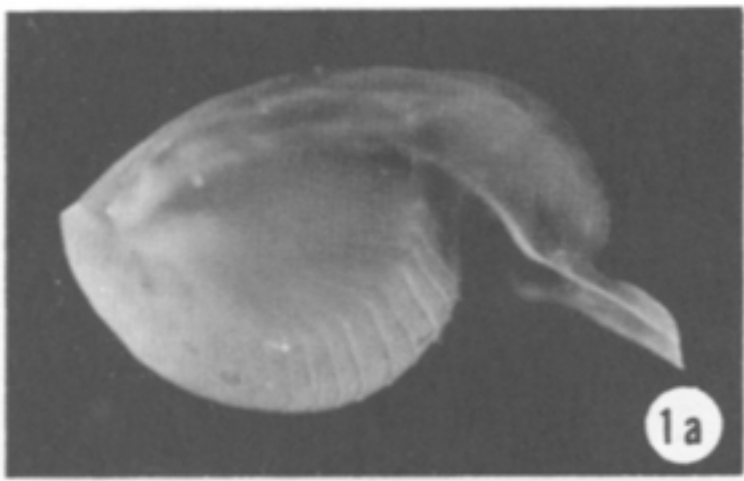


PLATE 2

1. *Cavolina globulosa* (Rang)
a. lateral view; b. ventral view; X15.
2. *Cavolina gibbosa* (Rang)
a. lateral view; b. ventral view; X10.
3. *Cuvierina columella* (Rang)
a. adult; b. juvenile still attached to adult; X15.

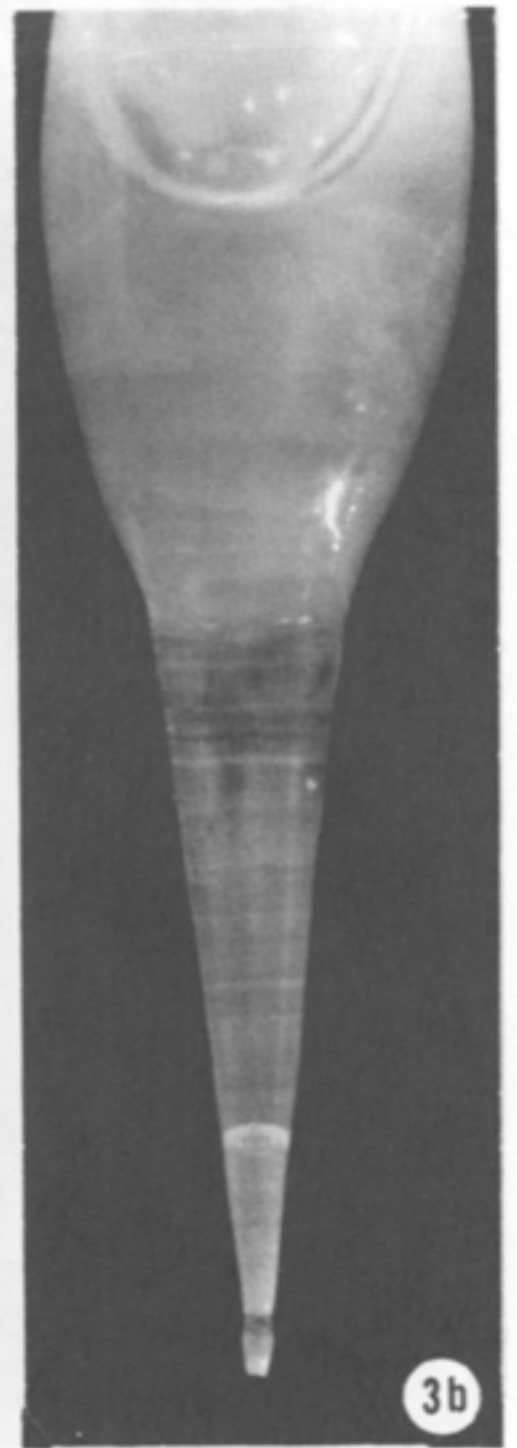
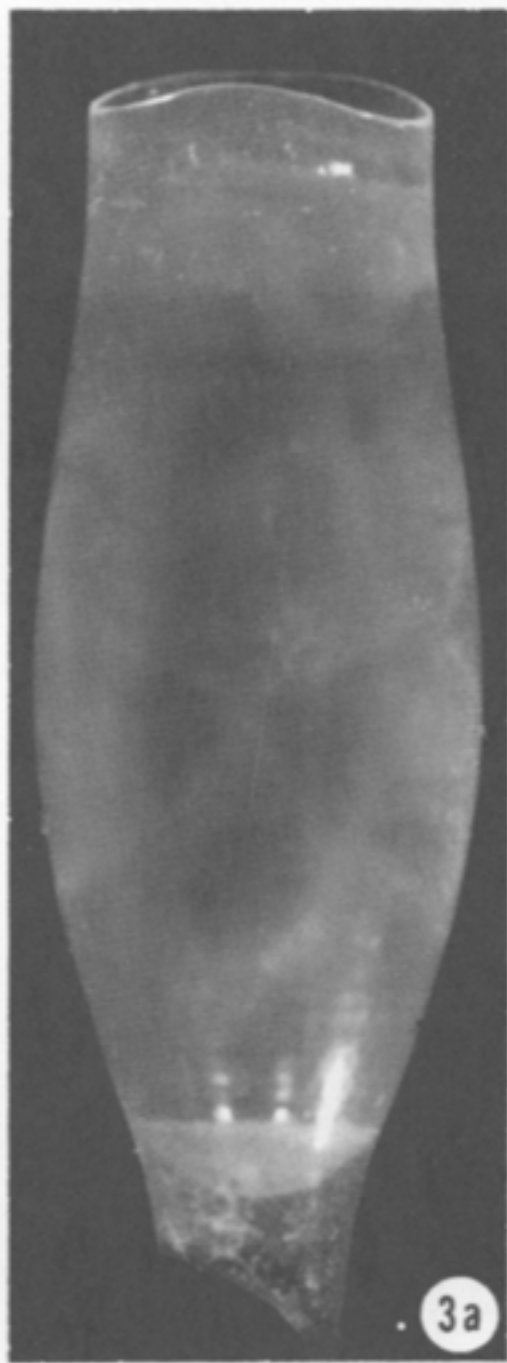
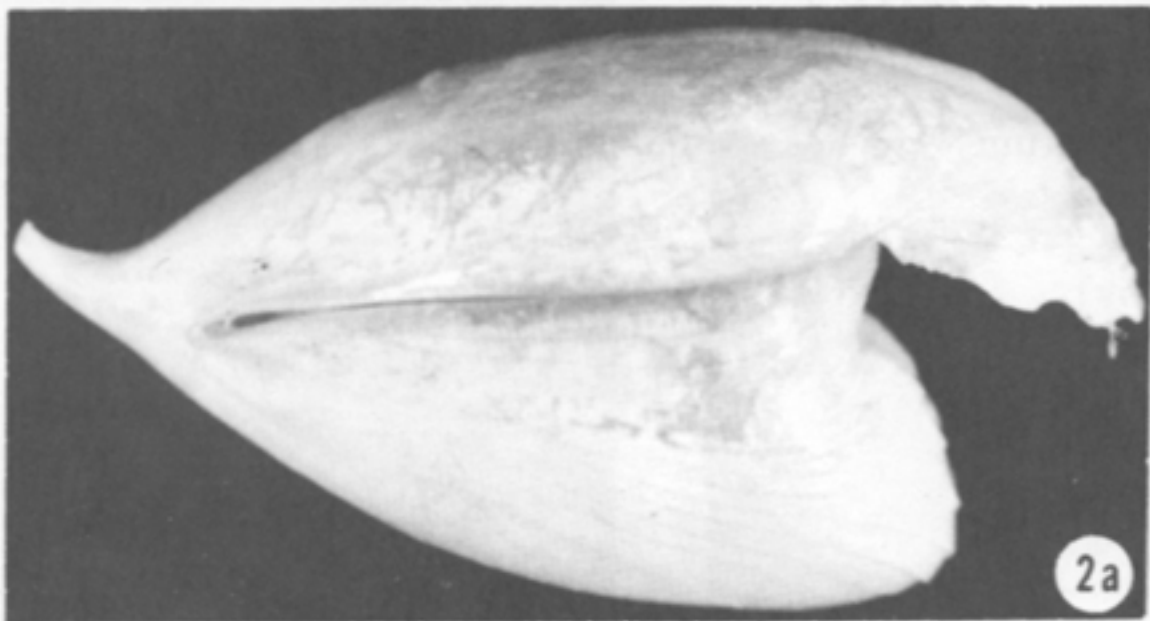
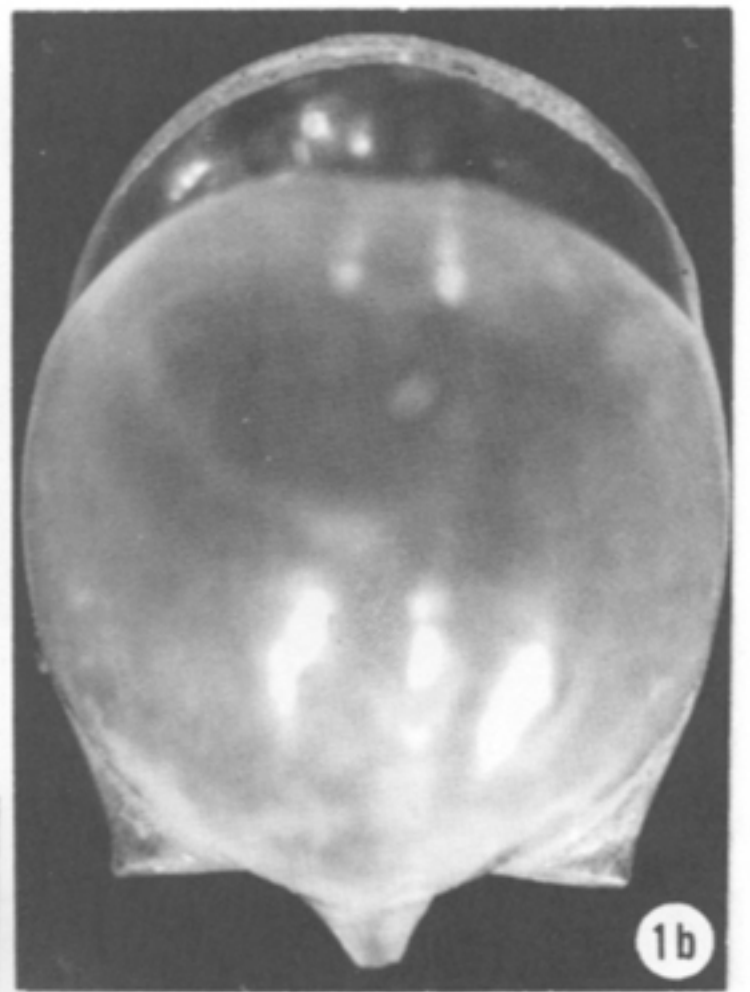
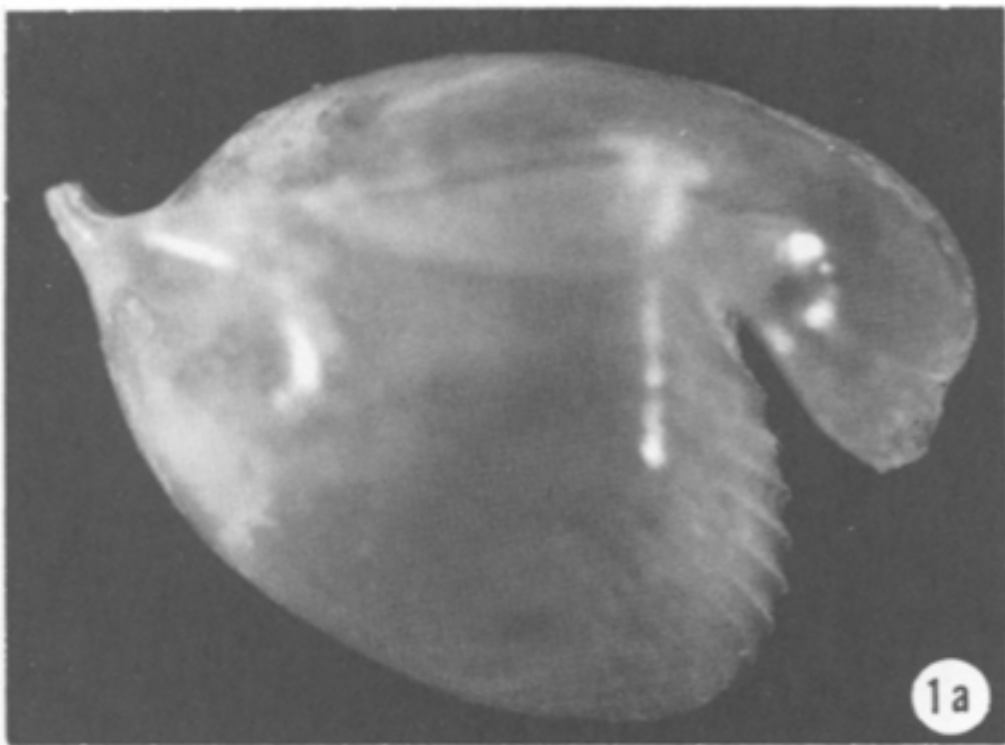


PLATE 3

1. *Limacina inflata* (d'Orbigny)
 - a. spiral view, note pronounced rostrum and ridge around aperture;
 - b. spiral view;
 - c. apertural view; X50.
2. *Limacina trochiformis* (d'Orbigny) Apertural view, X50.
3. *Limacina bulimoides* (d'Orbigny) Apertural view, X50.
4. *Clio cuspidata* (Bosc)
Dorsal view of a young individual, X10.
5. *Clio recurva* (Children) (= *Clio balantium*) Dorsal view, X5.
6. *Clio pyramidata* Linné Dorsal view, X8.

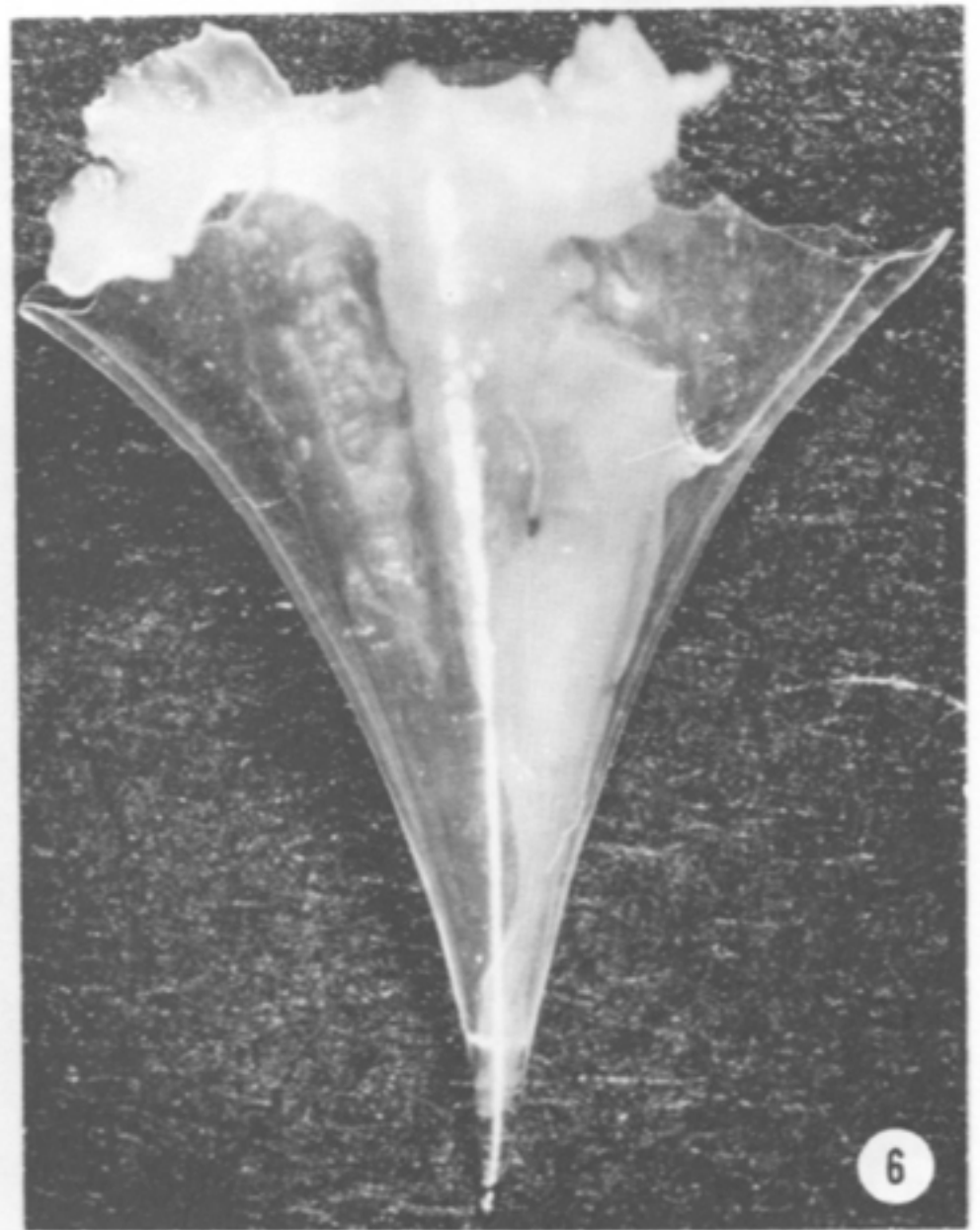
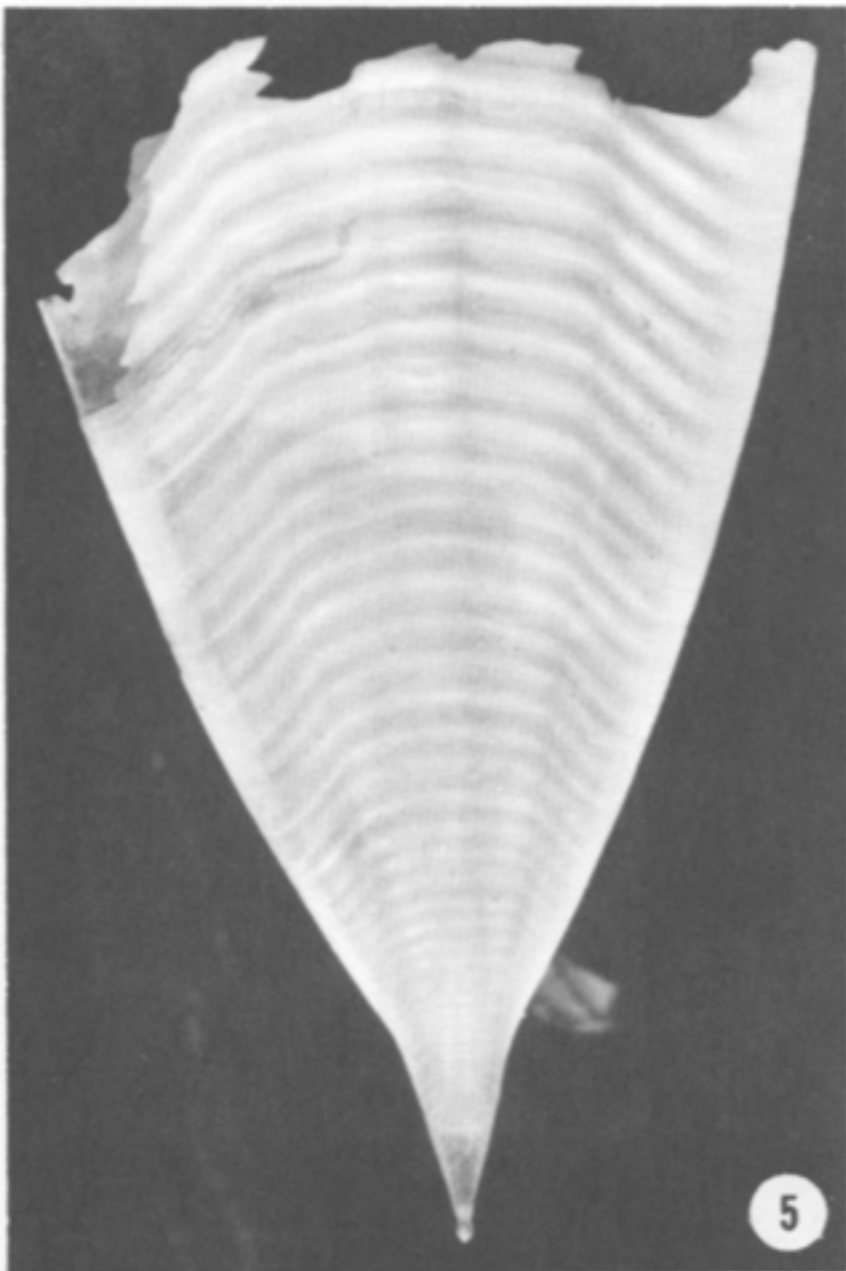
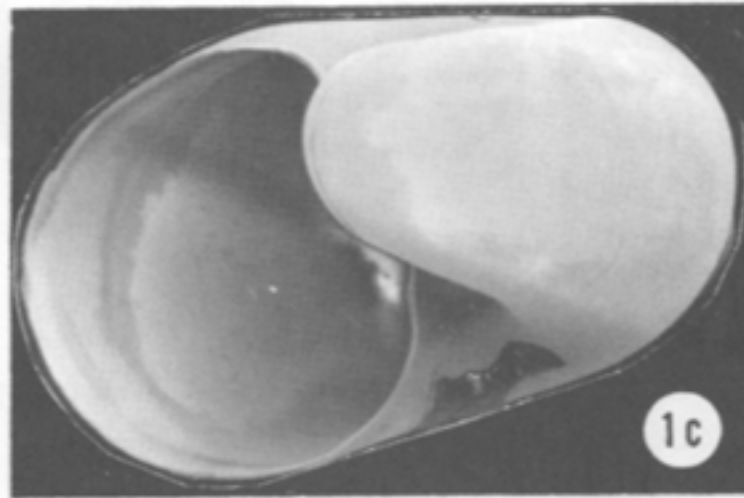
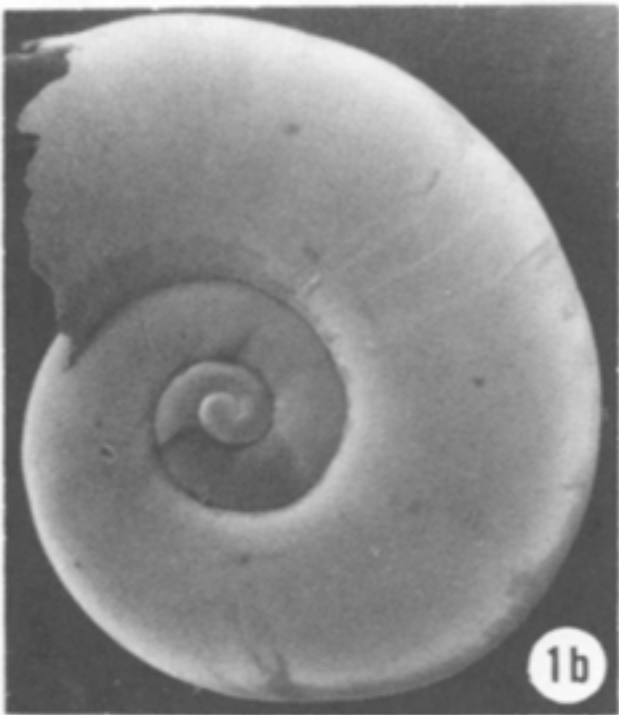
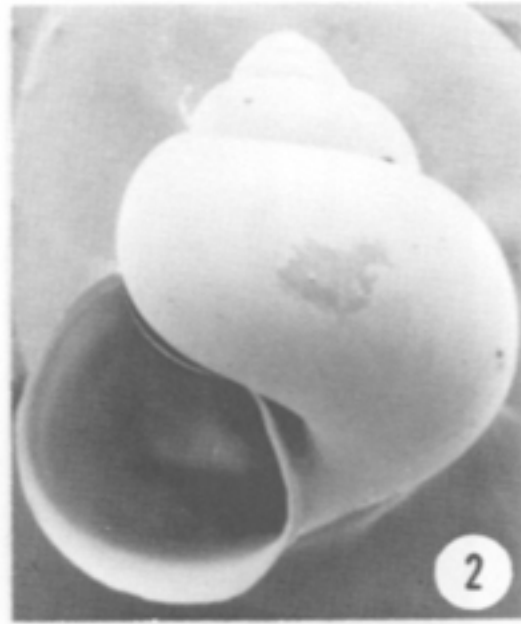
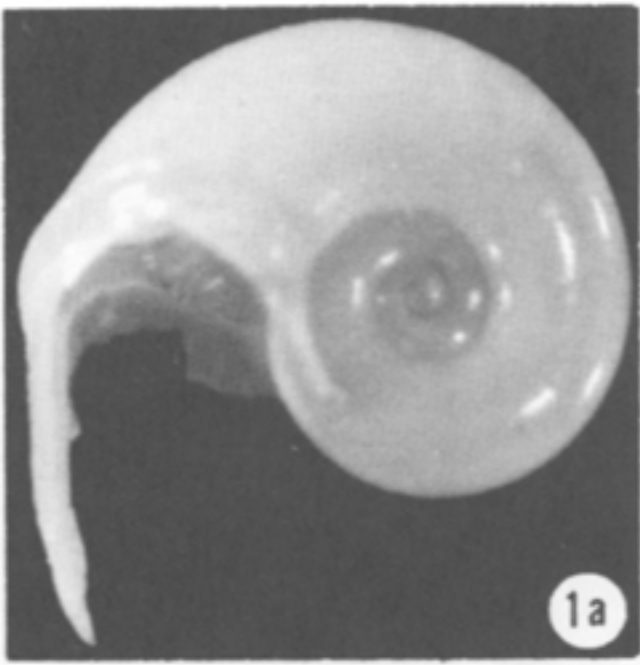
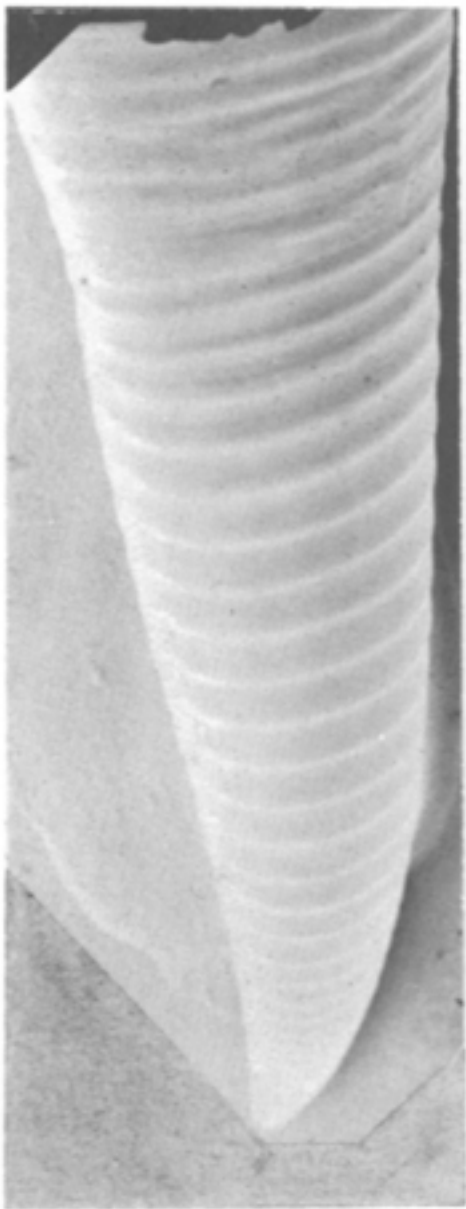


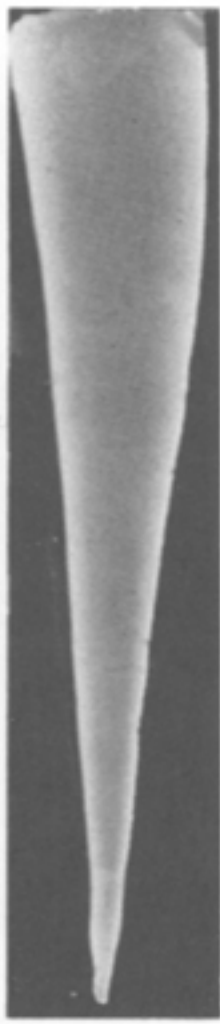
PLATE 4

1. *Hyalocylis striata* (Rang)
 - a. oblique view, emphasizing transverse ridges, shape distorted; b. normal view; X10.
2. *Creseis virgula* Rang
 - a. *C. v. constricta*, X30; b. *C. v. constricta*, larval shell, X100; c. *C. v. conica*, XI5; d. *C. v. conica*, larval shell, XI00; e. *C. v. virgula*, X20.
3. *Creseis acicula* Rang Part of a small specimen, X50.
4. *Creseis chierchiae* Boas
 - a. entire specimen, note transverse ridges and inflated juvenile shell, soft parts of this specimen had tentacular lobes on fin margins, X40; b. larval shell, XI00.
5. *Creseis bulgia* Sakthivel
 - a. X30; b. larval shell, XI00.
6. *Creseis chierchiae* Boas?

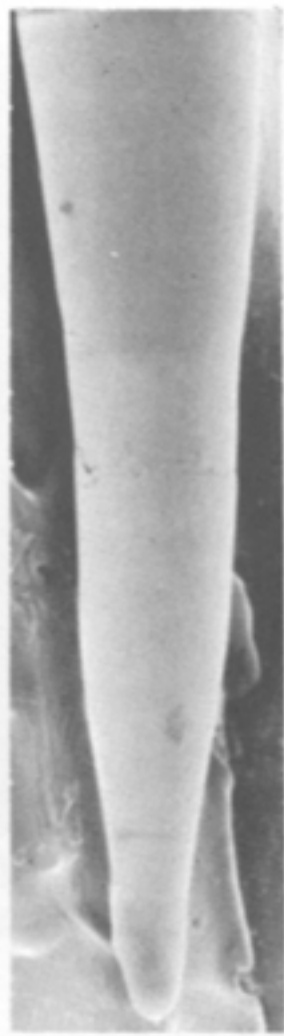
Note large size, more prominent transverse ridges, and uninflated larval shell. Possibly the young of *Hyalocylis striata*.



1a



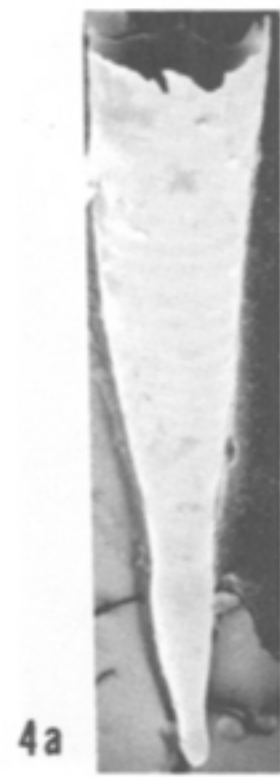
2a



2b



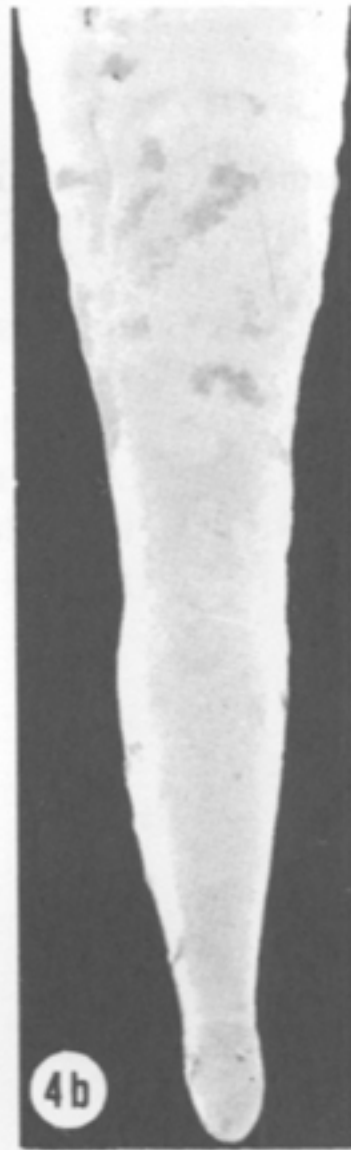
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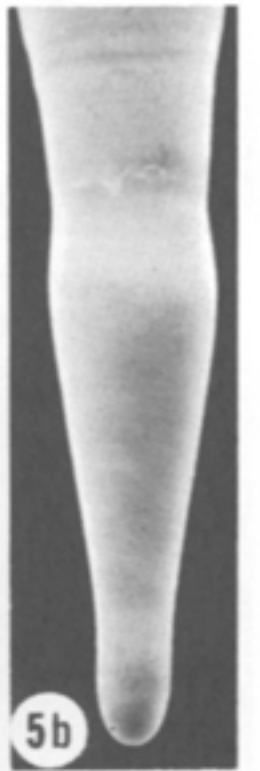
4a



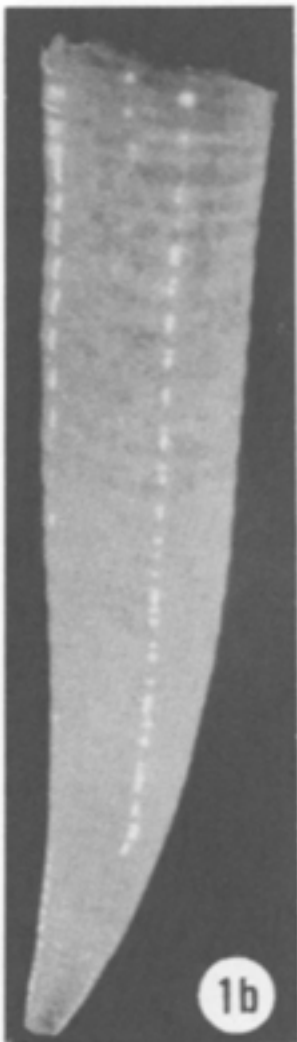
5a



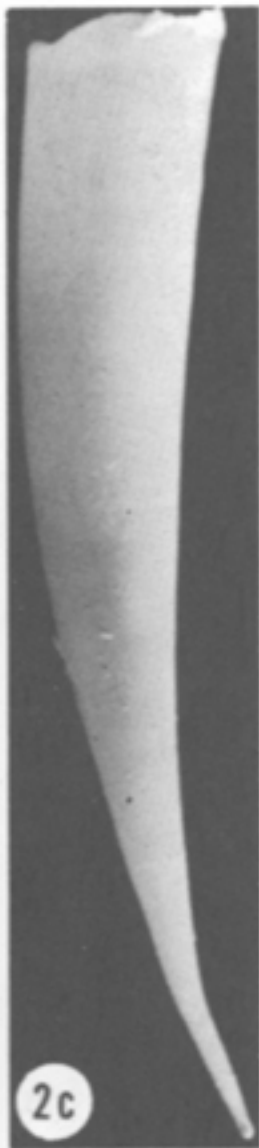
4b



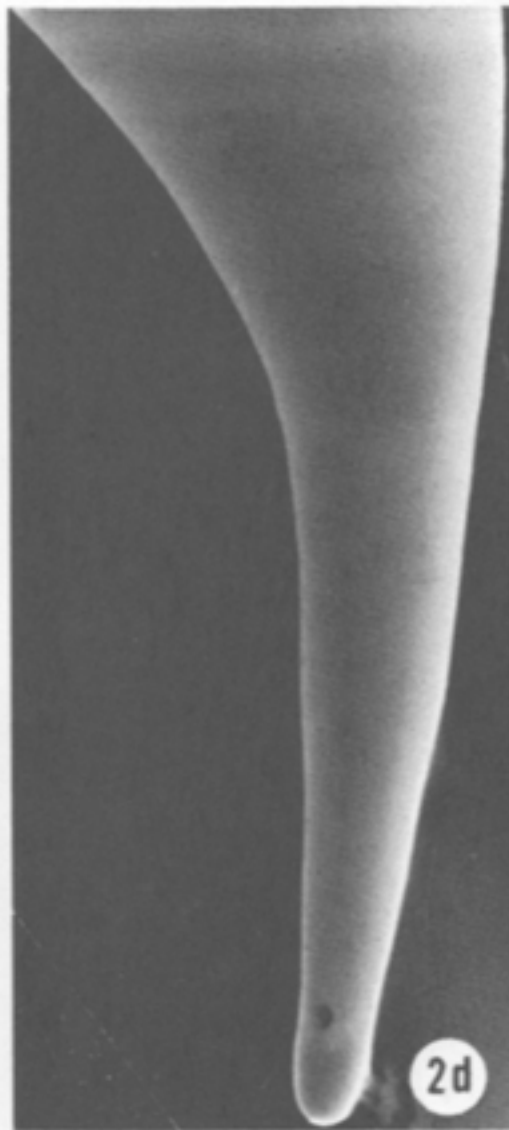
5b



1b



2c



2d



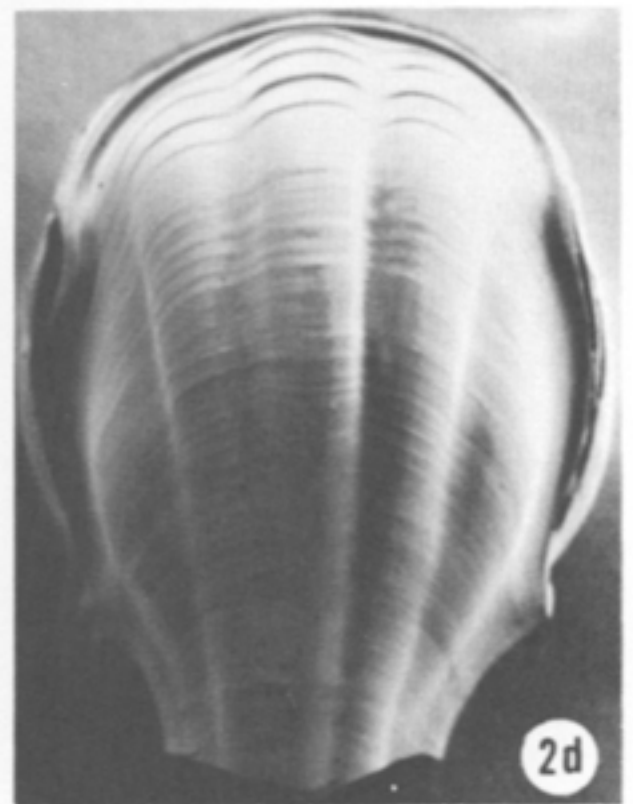
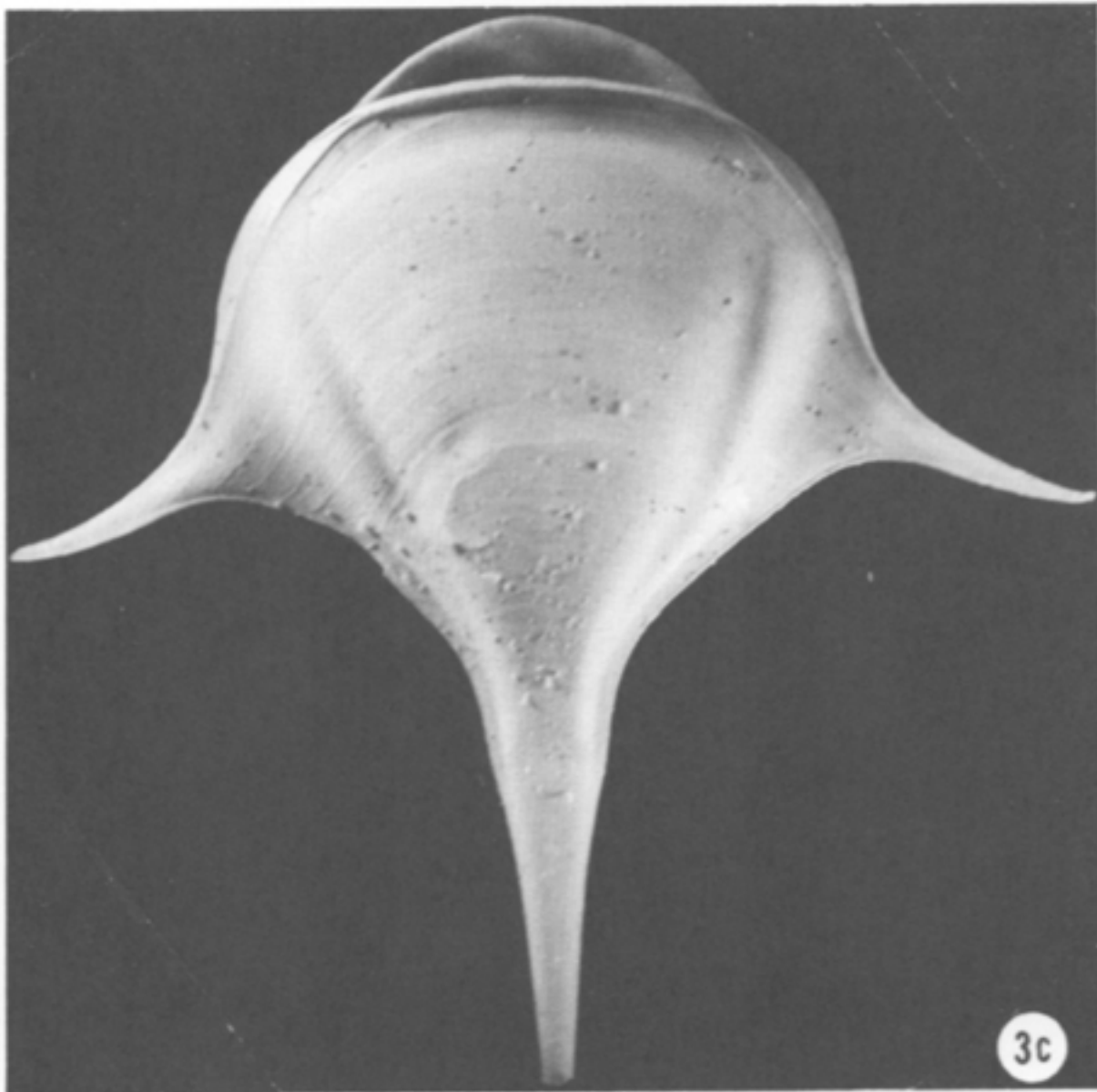
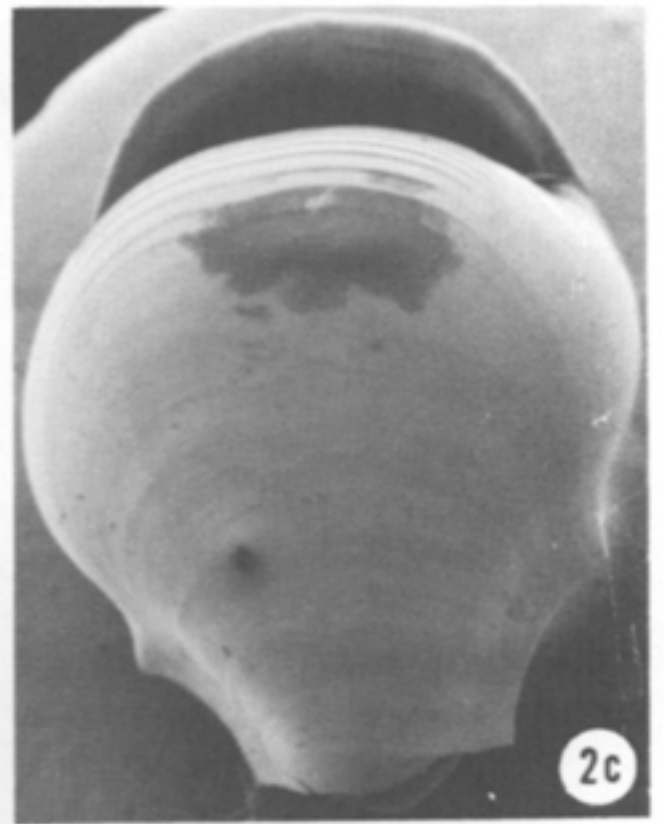
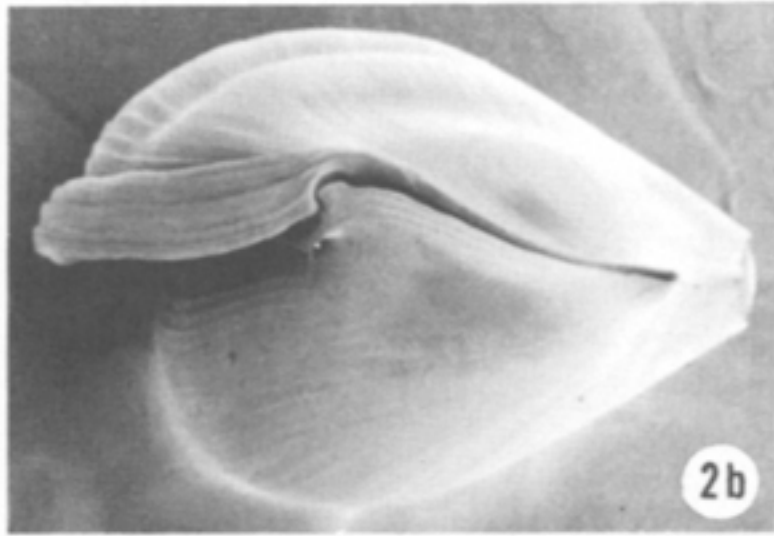
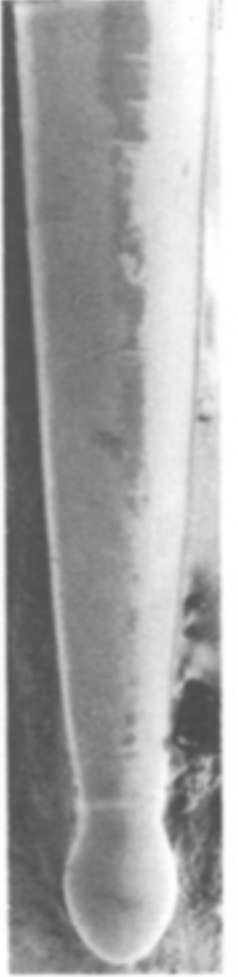
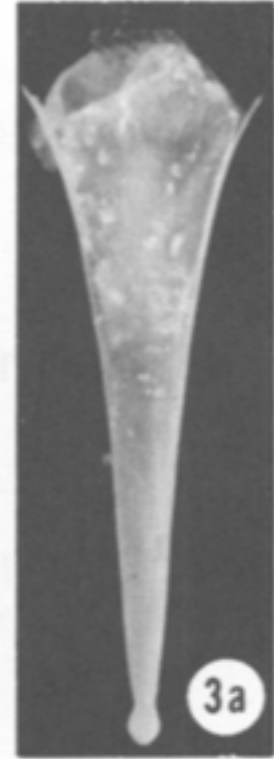
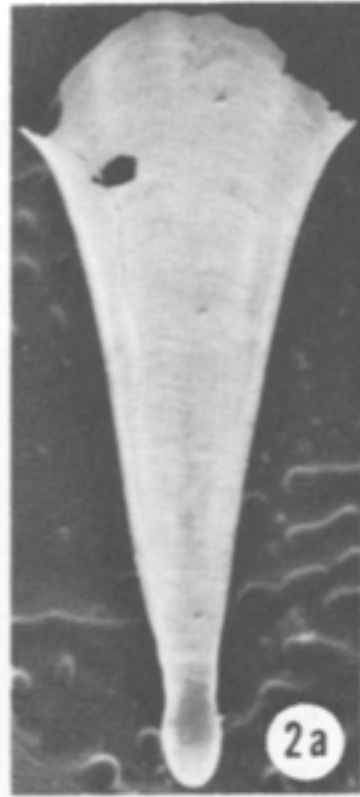
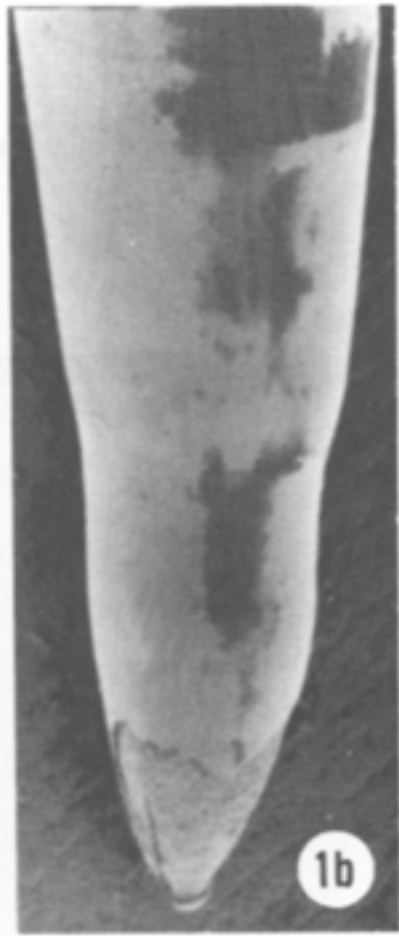
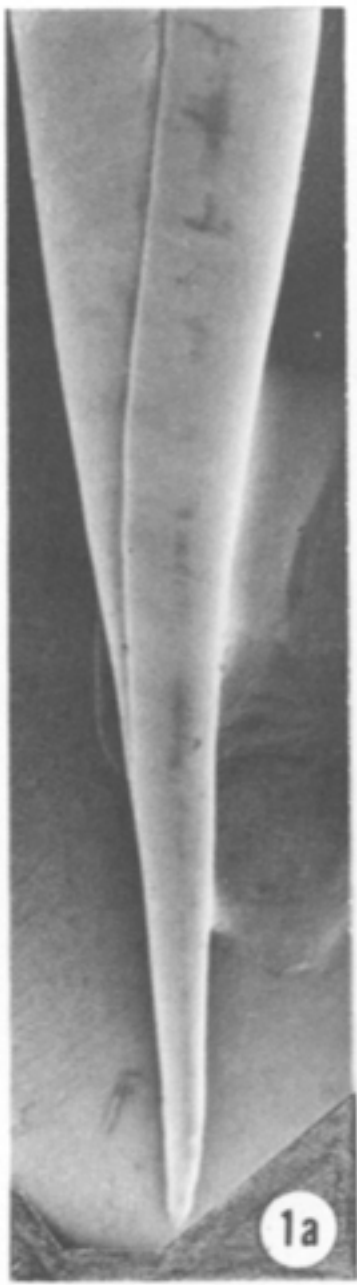
2e



6

PLATE 5

1. *Styliola subula* Quoy et Gaimard
a. X20; b. juvenile shell, X200.
2. *Diacria quadridentata* (Lesueur)
a. juvenile, X30; b. lateral view, X30; c. ventral view, X30; d. dorsal view, X30.
3. *Diacria trispinosa* (Lesueur)
a. juvenile, X15; b. juvenile, X50; c. ventral view, X5.



IDENTIFICATION NUMBERS USED IN PLACE OF SPECIES NAMES
IN APPENDIX LISTS

<i>Cavolina</i>	<i>gibbosa</i>	1
<i>C.</i>	<i>globulosa</i>	2
<i>C.</i>	<i>inflexa</i>	3
<i>C.</i>	<i>longirostris</i>	4
<i>C.</i>	<i>uncinata</i>	5
<i>Clio</i>	<i>recurva</i>	6
<i>C.</i>	<i>pyramidata</i>	7
<i>Creseis</i>	<i>acicula</i>	8
<i>C.</i>	<i>virgula virgula</i> and <i>C. v. conica</i>	9
<i>Cuvierina</i>	<i>columnella</i>	10
<i>Diacria</i>	<i>quadridentata</i>	11
<i>D.</i>	<i>trispinosa</i>	12
<i>Hyalocylis</i>	<i>striata</i>	13
<i>Limacina</i>	<i>bulimoides</i>	14
<i>L.</i>	<i>inflata</i>	15
<i>L.</i>	<i>trochiformis</i>	16
<i>Styliola</i>	<i>subula</i>	17

APPENDIX I

ESTIMATED NUMBER OF INDIVIDUALS PER 1000 m³ OF WATER FILTERED

Cruise S-1

Species Stations	4		8	11		13	16
	A	J		A	J		
2	3		14				
3			19				
4							
5	10		8	13		18	
6	33		74	115	91	156	
7	3	3		68		3	
8			22		4		
9	15		1469		15		
10	133		50				
11	314		113				
12	21		3				
13			362				985
14			212				
15	2		36	7	9	16	
16		12	196		12		427
17			235				
18	*	*	*	*	*	*	*
19			28				3
20	*	*	*	*	*	*	*
21			33				
22	*	*	*	*	*	*	*
23	98	3	215				28
24	*	*	*	*	*	*	*
25				3			6
26			6				
27	50	25	123				
28							
29	3	9	17				9
30	*	*	*	*	*	*	*
31			4				
32	*	*	*	*	*	*	*
33	21		25				
34	*	*	*	*	*	*	*
35	74		39				4

Cruise S-3

1			163				93
2	126		58				
3	136	15	2136				
4			221				
5			224				
6			43				
7			188				62
8	407	23	790				136
9			54				108
10	12		46	12			
11	14		57				156
12		11	87				120
13	16		196	16			98
14			30	15			30
15			120				
16	47		711	32			237
17	9		109	9			109
18	9		44	80	9		169
19			39	20			
20	540	112	1890				112
21			104				125
22			84	34			34
23			139				60
24	18		52				525
25	84	9	47				353
26	104	13	339	13			235
27			28				
28	16		32				63
29	180						
30	220		128				954
31			16				
32			69				

*Sample spoiled. Pteropods not counted.

Appendix 1, contd.

Estimated Number of Individuals per 1000 m³ of Water Filtered

Cruise S-2

Species	1	2		3		4		5	6	7	8
		A	J	A	J	A	J				
Stations											
6						4					
7	NET, WITH SAMPLE LOST										
8					2					4	2
9					2					2	2
10					7					3	
11		3								6	6
12											2
13			2							2	10
14					2						27
15			3		3	1					13
16			2							4	4
17			2			2					34
18						4					60
19											27
20											1
21											30
22					2	2					45
23			7		4	2					28
24		1	4		7						328
25			5			5					51
26			2			2					100
27											264
28											27
29						5					90
30						7					36
31											81
32											76

Species	9	10	11		12		13	14	15	16	17
			A	J	A	J					
Stations											
6											
7											
8			2			2		2			
9			3					90	228		72
10			2					20	26		3
11	1		1	3		3		52	156	1	48
12			2	4		2		7	145	7	42
13			4	2				25	40		8
14			4	7		7		16	31		20
15	13		1			1		13	4		1
16		2	4		2			27	126		68
17			14	41		5	2	22	49	14	10
18			18	4				11	4	35	
19								4			
20							1				1
21	4						11				19
22	6		4						26		18
23	18		60	2					43		4
24	4		28						4		4
25	4		24	7			1	1	3		11
26	27		24				3	5	85		75
27			36	20			72	7	2		20
28	3			8			3	15	5		20
29	8		14								5
30	5		11								11
31	3		2				24	2			10
32				3							44

Appendix 1, contd.

Estimated Number of Individuals per 1000 m³ of Water Filtered

Cruise S-4

Species	1		2		3		4		5	6	7	8
	A	J	A	J	A	J	A	J				
Stations												
1												89
2					9						19	28
3			11		11						5	32
4					4							4
5			4								4	26
6					8						8	23
7			11								11	23
8											11	8
9			4		4						16	27
10			5				20					46
11			6		6		11	6			6	50
12			4									8
13												12
14									2			263
15			2	7					2			13
16					7		+				33	+
17			9		9		9				17	+
18			30		4		4				7	263
19			7		7		7				22	59
20			2	6			17				23	86
21				7			7				7	52
22				6		7					6	94
23			4	43			16			2	16	17
24			2	24		4	16			2	36	115
25			10	29		6	23			2	63	98
26				7		7	30				7	133
27												54
28			3				14					240
29												22
30												11
31							10					52
32												10
33				63		27						90
34				42		6	36			2		30
35												90
36							11					110
37							77					454
38							2	30				120
39							172					192
40												208
41												48
42												61

Species	9	10	11		12		13	14	15	16	17
			A	J	A	J					
Stations											
1			188				49				
2			9				9	282	141	19	
3	21		21	11			16	486	11	27	19
4			17	4				25	4	17	71
5			58	7			4	33	7	29	18
6			135	23				75	143	30	233
7	11		69	11				69	114	57	57
8	4		15				11	15	57	4	30
9	4		19	8			8	23	140	23	47
10	5		5	10				46	10	5	26
11	17		39	11	2		17	132	160	11	50
12	4			4				47	4	4	8
13			25	25				25	37	100	
14			44	11			142	131	936	427	
15	7			7				264	317	59	53
16	+		+	+				+	+	+	+
17	9		17	29	9	17	34	111	154		120
18	11		11	7		11	78	52	30	37	7
19			15	7			7	184	280		81
20			23	11				201	183	29	29
21	14		22	15				141		22	22
22	18		18	6		6		112	745	53	118
23			43	16			16	96	101	80	91
24	12		24	24		4		32	16	67	4
25	6		46	34				126	545	86	40
26			22	15		15	7	104	67	96	30
27	15		5					36	15	444	
28	70		28	14				70	85	1140	
29										43	
30	44								23	11	
31									10	21	
32									255	29	
33	18		81	72				27	396	324	
34			67	55			6	6	55	667	6
35	18								9	45	
36									33	11	
37			232	68			2620	10	19	1220	
38	4		4	2				8		640	
39				38				115	38	959	
40								42		499	
41								12		36	
42										61	

Appendix 1, contd.

Estimated Number of Individuals per 1000 m³ of Water Filtered

Cruise S-5

Species	4		8	11		13	16
	A	J		A	J		
Stations							
U-1			7				
U-2	87		348				
U-3			12				
U-4	363		25				
U-5	3		13				
U-6			16				
U-7	13		733				
U-8							
U-9	31	11					
U-10							
U-11							
U-12							
U-13							
1	3						
2	3						
3			15				15
4							
5	SEE NOTE A						
6	3		831				
7	196	166	357				
8			151				
9	16		251				
9A	49						
9B			56				
10	27	NOTE B	163				
11	15		543				
12	5		54				
13							295
14			4				
14B							6
15			126				8
16	19						4
17	10	3	174				
18							
19			5				15
20							259
21			82				
22	39						
22A	15		169				15
22B	28		39				
22C	34		203				3
22D	11						
22E	52		156				39
22F	373		224				
23	27		15				
23A	26		59				
23B	20		3				
24	15		2				
25							28
26							
27							
28			3				822
28A	48	3	127				10
28B	2		9				
29	107	30	26				40
29A	14	5	82				28
29B	133		111				4
29C	101		31				3
29D			12				4
30	13		23				
31			3				
32	54		36				
33	38	4	45				
34	3		3				
34A							
34B			153				
34C			660				

NOTES: A. Also present at this station: *Cresets virgula virgula* at a concentration of 4/1000 m³ (= 1 specimen in sample).
 B. Also present at this station: *Cresets virgula conica* at a concentration of 3/1000 m³ (= 1 specimen in sample).

Appendix 1, contd.

Estimated Number of Individuals per 1000 m³ of Water Filtered

Cruise S-6

Species	1	2		3		4		5	6	7	8
		A	J	A	J	A	J				
Stations											
1											89
2											2
3X					21					10	10
4					10	2					4
5		4	2	16		24		16		2	57
6						4				4	16
7			2			4	10				4
8			4		8	2				10	30
9					2	5				4	14
10			2			6				2	2
11X			2		2	2				2	20
12X					10	4				6	26
13		4				2				35	4
14											3
15						3					5
16			11		4						23
17			2		6						11
18					13	6				2	52
19	2				2	6					70
20					53					30	60
21			2							15	65
22		2	10		7	6					15
23										10	10
24					7						7
25AX		2				2					8
26					10	2				5	30
27											7
28											126
29											403
30						2					40
31						46					617
32											216
33											117
34						5					38
35					9	9					632
36					3	19		3			38
37						4					32
38					15	2					83
39											137
40					3						119
41											383
42											2740

Species	9	10	11		12		13	14	15	16	17
			A	J	A	J					
Stations											
1			9	36			9			27	
2			2	10				2	232	45	
3X			2	10	2		10	73	374	353	52
4	4		29	10			4	29	10	10	4
5	12		16	16				16	82	8	10
6	56		2					40	164	24	7
7	6		32	20				20	62	10	20
8	2		15	45			2	8	66	15	47
9	7		14	21				21		7	
10	22	4	7	22			4	89	325		104
11X	27		6	4			10	8	8	6	8
12X	21		26	26	5		31	31	732	26	88
13			14	44			149	8	554	68	27
14				54	18		1560		72	664	
15			48	72			2160				
16			2		2	2	45	4	238	34	23
17	34		2	2	6		2	25	110	8	34
18	39	4	26	13	13				842	52	402
19	34		44	18	18			26	52	26	
20	46	16	39	7	30		16	53	454	39	152
21	65		58	15	33		8	8	96	25	50
22	98		30	15	9		7	30		2	
23	2	2	81	18	4	10	18	182	4010		683
24			7	2	2	7	4	7	843		71
25AX			8				22	61		168	
25		2	10	10	20		80	100	391	210	160
27			145	2			110	4	7	71	
28			26				65	13		617	
29							2			4	
30							596			24	
31			46				2				
32			89	25							
33			2						10	30	
34			135	38			5			10	
35			106	140			53			31	
36				14			14				
37			4	11			4			27	
38			122	95		15	2				
39				121			15				
40			3	132			13				
41			66								
42											

Appendix 1, contd.

Estimated Number of Individuals per 1000 m³ of Water Filtered

Cruise S-7

Species	4		8	11		13	16
	A	J		A	J		
Stations							
1	167		18500				
2			350				
3			98				
4	635		4780				
5	40		387				
6			1910				
7			149				
8	SEE NOTE A						
9	169		506				
10	66		1450				13
11	84		1260				
12	497		355				
13	110	47	880				
14		14	306				
15	137	30	624				
16	564		439				
17	667		638				
17A	431	48	1360				
17B	352	SEE NOTE B 1280					
18	585	13	266				
18A	666	SEE NOTE B 1220					93
18B	1270	41	422				82
18C	3650	154	6910				96
18D	218	54	2270				
18E	523	720	443				
18F	558	61	863				
18G	325	51	1730				
19	61	15	410				
20	208	95	510				1260
21	18		442				
22	25	38	265	13	25	550	25
23	22						
24		26	119			26	
25	236	129	365			8	15
26	44	66	765			22	22
27	359	19	453				
28	95	24	96				
29	13		653		13	51	13
30			777	11	11	14200	178
31			121			130	19
32		24	212			94	
32A	23	104	933			104	
32B	33	16	642				99
33	398	1163	1200				
33A	211	878	1000				
33B	34	34	581				376
33C			242				174
33D			310	14			14
34			253	35		52	13
35		45	227	15			15
35A	7	3	13				
36	251	11	55	153	22	350	
37	40	67	107	80	307	3840	1490
38	21	42	250	42	375	9250	1770
39	19	19	921				
40	836	100	2430				
41	105	35	332				

- NOTES: A. Extremely high concentration of phytoplankton. Few, if any pteropods.
 B. The only size distinction made in *Cavolina longirostris* was between Stage I and the other 3 stages as a group, whose count appears under adult.

Appendix 1, contd.

Estimated Number of Individuals per 1000 m³ of Water Filtered

Cruise S-8

Species	1	2	3	4	5	6	7	8
	A	J	A	J	A	J		
Stations								
U-1								1090
U-2					35	18		405
1								40
1A					40			27
1B								10
2		4					39	
3	2	4	2				10	51
4							49	20
5			10	20	10		10	41
5A ₁			20	10			40	70
5A ₂			20				31	153
6							10	
7			10		31			31
8	2			21	21		21	52
9				11				56
10							34	23
11							2C	
12								
14								74
15					97			327
17					10		20	101
18			10			10	10	214
19		13	53	13	13			132
20			45		18			118
21							19	9
22			71					30
22B			8		4			65
23			8					47
24				8				
25							9	
26					6		28	34
27					10			40
28					29	14		348
29								200
30								790
31								56
32								355
33					159	40		3340
34		2			63	32		315
37					14	14		226
38					42			126
39				10	10		10	120
40					118	34		51
41								70
42								972
43								219

Species	9	10	11	12	13	14	15	16	17
	A	J	A	J					
Stations									
U-1									
U-2			40					20	
1			67	13		27	13	174	
1A				10		10		788	
1B			10	48		29	136	291	48
2		8		10	20	20	51	123	31
3	20				20	58	29	10	39
4	10		10	10			72	10	62
5		10	10	10			30	1900	90
5A ₁	20	10					61	551	82
5A ₂			10		10		31	759	125
6							388	265	163
7	10				2	21	104	425	104
8			21	2	21	52	108	32	11
9			11		11	22	12	287	11
10	12					12	10	10	10
11						12	11	11	32
12			11	11		32	11	137	11
14			21	21		22	32	278	
15						145	24	71	
17	10		71	10		61	50	71	
18			41	51	20	245	82	113	41
19			211	211	26	304	132	2140	119
20			54	72	45	45	72	18	9
21				9		9	356	945	19
22	10		40	71	40	10	111	30	30
22B	12		4	11	8		31	11	11
23	4		4	23	4		19	4	4
24							199	298	9
25		9			2	9	438	45	27
26			6	34	28	6	108	222	86
27			30				69	10	20
28			14			44	14		130
29									
30									50
31									
32									44
33			146			13			93
34			32	21		10			10
37			14						14
38			266	14		14			28
39			310	240		420			
40			84	472		8970			51
41			94	47		609			70
42									
43									

Appendix 1, contd.

Estimated Number of Individuals per 1000 m³ of Water Filtered

Cruise S-9

Species	4		8	11		13	16
	A	J		A	J		
Stations							
1			40			8	177
2			130				3
3			3				3
4	151		2550				7
5	122	87	464				6
6	25	5	365	5	5	5	
7	23		129			9	18
8			18				
9		12	175				128
10	19		99	SEE NOTE A			12
11		56	272				12
12			135				28
13	41	24	125				
14	12	25	91				
15	230		1030				345
16			120				6
17		2	404	91	73	21	13
18	NOTE B 1887	162	284				66
19	NOTE B 127		27300				64
20	NOTE B 156		248				16
21	NOTE B 867		48				21
22	5		75			3000	194
23			102			96	216
24			20				10
25			36				82
26			15				15
27	21		10			62	489
28			33			11	122
29	5	2	38	2		2	30
30			57			130	209
31	42	21	110			17	59
32	67	134	959				
33							
34	NOTE B 610		357				51
35		3	65			437	43
36			77			575	148
37	244	45				7	67
38	30		8				
39		26	291			13	13
40	13	26	600				
41	56	14	367				

- NOTES: A. Also present at this station: *Limacina bulimoides*, *L. inflata*, and *Styliola subula* each at a concentration 6/1000 m³ (= 1 specimen of each in sample).
- B. Preservation of material did not permit a distinction between the stages of *Cavolina longirostris*. Number given is the combined count of all stages.

Cruise S-10

U-1			74				31
U-2	6		25	3	3	103	81
U-3	3	8	47		3	164	68
U-4	188		159				20
U-5	950	155	2310				142
U-6	1500	153	1070				
U-7			55				
U-32			10				14
U-35			14				4
U-36			56				
U-37			113				
U-38	103	8	1850		8	8	424
U-39	215		1240				27
U-40	5	5	641				38
U-41	27	16	49				11
U-42	23	11	2480				
U-43	80		102			11	
U-44	128		89				
U-45	82		27				
U-46	77	15	1100				46
U-47	196	3	5270				
U-49	141	13	3560				
U-50	126	11	1380				
U-51	103	23	251				
U-52			225				
U-53	4		243			4	11
U-54	7	13	584				20
U-55	108	21	637			2	32
U-59			127				
U-60	3		79				
U-61	3		32				19
U-62			3				8
U-63			15			9	64
U-64			6				313
U-65			18			16	132
U-66			20			36	55
U-67			3			7	53
U-68			7			28	49
U-71		15	51			66	90
U-74			240				8
U-77		2	372				12

Appendix 2

Species Found in 2-m. Net Samples

Cruise S-4

Species	1	2	3	4	5	6	7	8	10	12	13	17
	A	J							A	J		
Stations												
60-215			X		X		X	X	X			X
60-222		X				X	X			X		
60-226		X	X	X		X	X		X			X
60-229	X	X	X	X		X	X	X			X	X
60-241		X	X			X				X		
60-244		X		X		X	X			X		
60-248		X	X			X	X					X
60-253		X		X		X	X	X	X		X	X
60-258	X	X	X	X		X	X	X	X			X

Cruise S-6

60-441	X	X		X	X		X		X	X		X
60-452	X	X	X	X	X	X	X		X	X		X
60-462	X	X		X	X		X		X			X
60-508				X	X		X		X	X		X
60-512	X		X	X			X		X		X	X
60-518		X		X	X		X	X	X		X	X
60-527				X	X			X	X	X	X	X

Cruise S-8

60-787	X	X		X		X	X	X	X			X	X
60-793		X					X		X		X		X
60-802		X		X			X		X	X			X

Appendix 3

Species Found in the Trans-Pacific Samples

Species	1	2	3	4	7	8	9	10	11	12	13	14	15	17
	A	J	A	J					A	J	A	J		
Stations														
(HG) 27			X		X	X					X			
(HG) 30					X			X	X		X			
(HG) 31		X	X	X	X	X	X	X	X		X	X		X
(HG) 32	X	X	X	X	X	X		X			X	X		X
(HG) 33	X			X	X	X		X			X			
(HG) 35				X	X	X	X	X			X	X		X
(HG) 36	X	X	X	X	X	X	X	X	X	X	X	X	X	X
(HG) 36		X	X	X	X	X		X			X	X	X	X
(GM) 38			X	X	X	X		X			X	X	X	X
(MN) 44			X	X	X	X	X	X	X			X		X

Cavolina tridentata present at stations: (HG) 32, 35, 36 and (GM) 38.