

THOMAS E. BOWMAN

*The Distribution of  
Calanoid Copepods off  
the Southeastern  
United States Between  
Cape Hatteras and  
Southern Florida*

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## ABSTRACT

Bowman, Thomas E. The Distribution of Calanoid Copepods off the Southeastern United States Between Cape Hatteras and Southern Florida. *Smithsonian Contributions to Zoology*, number 96, 58 pages, 1971.—About 100 species of epipelagic calanoid copepods occur in waters off the southeastern coast of the United States. From inshore waters seaward the species diversity increases from less than 10 species/station in coastal waters to more than 40 species/station in some oceanic stations. The species composition changes concomitantly, and, using the Fager-McGowan index of association, coastal, shelf, and oceanic associations have been identified, each with characteristic indicator species. The seaward gradient in diversity is explained by Sanders' stability-time hypothesis. The calanoid fauna south of Cape Hatteras is compared with the fauna north of Cape Hatteras.

Two species of *Paracalanus*, *P. quasimodo*, new species, and *P. indicus*, new rank (= *P. parvus* var. *indicus*), both formerly referred to *P. parvus*, are described and compared with the more northern *P. parvus*. Taxonomic remarks are given concerning *Rhincalanus cornutus*, *Pleuromamma gracilis* and *P. piseki*, and *Heterorhabdus papilliger*.

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Thomas E. Bowman

# The Distribution of Calanoid Copepods off the Southeastern United States Between Cape Hatteras and Southern Florida

## Introduction

In Atlantic waters along the east coast of the United States much less attention has been given to the plankton in the region south of Cape Hatteras than to that in the region north of Cape Hatteras. South of Cape Hatteras the species of chaetognaths and their distribution have been discussed by Bumpus and Pierce (1955) and Pierce and Wass (1962), and the association of pteropod species with the three water masses off Cape Hatteras has been analyzed by Chen and Hillman (1970). Investigations of planktonic copepods have been for the most part taxonomic studies, especially of Florida Current species (summarized in Owre and Foyo 1967) or analyses of vertical movements (e.g., Moore and O'Berry 1957). An overall survey of the patterns of copepod distribution was not possible until an adequate program of plankton sampling could be carried out.

Owing to interests in the relatively unexplored area south of Cape Hatteras by the U. S. Fish and Wildlife Service, the Navy Hydrographic Office, and the Office of Naval Research, a program to investigate these waters was developed in the early 1950s. A pattern of 16 transects forty miles apart, each transect containing 3–6 stations twenty miles apart, was established (Figure 1). The lines extended seaward beyond the axis of the Gulf Stream, and 9 special stations were set up farther offshore. The 97-foot vessel *Theodore N. Gill*, with accom-

modations for eight scientists and ten crew, made a series of nine cruises over the station grid between January 1953 and December 1954, making oceanographic measurements and plankton collections at each station.

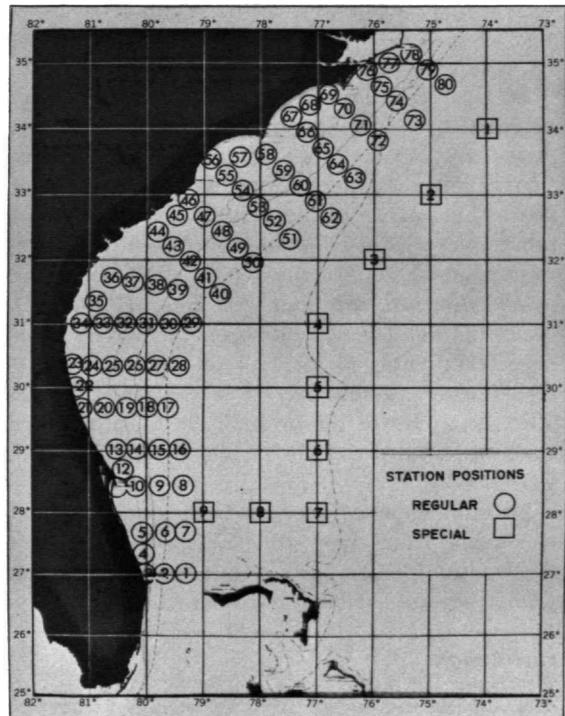


FIGURE 1.—Basic station plan.

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## Methods

The basic physical biological and chemical data, together with procedures and methods, have been published for each cruise. This paper is limited to Cruises 1-4 (February-November 1953), for which the relevant information is given by Anderson, Gehringer, and Cohen (1956a, 1956b), and Anderson and Gehringer (1957a, 1957b).

Plankton tows were made during Cruises 1 and 2 with a standard half-meter no. 1 silk net with an Atlas-type current meter suspended in the mouth to measure the amount of water filtered. During Cruises 3 and 4 (and later cruises) tows were made with the all-metal, half-meter Gulf III sampler (Arnold and Gehringer 1952), except when adverse sea conditions made it unsafe to tow the Gulf III and the silk net was substituted. Nets were towed obliquely starting at 70 m (100 m of cable out), or less in shallow water, and retrieved at the rate necessary to bring them to the surface in about 20 minutes. The silk net was towed at 1-2 knots, the Gulf III at 5-6 knots. Plankton samples were preserved in 5 percent buffered formalin.

Aliquots of 40 ml, comprising 10 percent of the total sample, were sent to me by William W. Anderson, Director of the Bureau of Commercial Fisheries, South Atlantic Fisheries Investigations, Brunswick, Georgia. Subsamples of the aliquots were removed with a 2 ml Stempel pipet and placed in a plastic, rectangular counting chamber for enumeration of the calanoid copepod species. Depending on the abundance of the plankters, from 1-3 2 ml subsamples (0.5 to 1.5 percent of the entire sample) were enumerated. Usually 100 or more, sometimes several hundred, copepods were counted and identified, the number depending on the species diversity. The number of each species counted was corrected to the number per 100 m<sup>3</sup> of water strained. The remainder of the original 40 ml aliquot was examined and species not present in the subsample were noted.

Both the 40 ml aliquots and the counts of calanoids made from them are permanently stored in the Division of Crustacea, Smithsonian Institution, where they are available to interested investigators.

## Circulation

The circulation in the area surveyed by the *Gill* has been discussed by Bumpus (1955), Bumpus and

Pierce (1955), Pierce and Wass (1962), and Gray and Cerame-Vivas (1963), hence only a brief summary is given here.

The dominant offshore feature is the Gulf Stream (Florida Current), which has an average velocity greater than 150 cm/sec. West of this lies the Carolinian Coastal water, composed of Florida Current water plus river-runoff water, which extends from Cape Hatteras to off Daytona Beach or at times to off Cape Kennedy. Carolinian Coastal water is more saline than most coastal water, because (1) there is less runoff, (2) the runoff enters from sounds rather than from river mouths, and (3) the Florida Current frequently makes broad excursions over the shelf.

Between Cape Hatteras and Cape Cod the shelf water is known as Virginian Coastal water and is colder and less saline than Carolinian Coastal water. It drifts slowly southward along the coast at about 3-20 miles/day, due to a dynamic current induced by the addition of fresh water from river runoff. Such a south-flowing dynamic current is very transient in Carolinian Coastal water; it is restricted to a very narrow portion of the shelf and develops only during periods of substantial runoff. There is usually little motion, mostly a drift to the northeast.

There is no regular communication between the two coastal waters, but Virginian water may be driven around Cape Hatteras by the northeast winds which are common from November to May.

Between the Gulf Stream and the Virginian Coastal water is a slowly revolving (about 10 cm/sec) gyre of slope water. This water has essentially the same characteristics as Gulf Stream water but has a slightly lower salinity, due to admixture with coastal water. No slope water intervenes between the Gulf Stream and Carolinian Coastal water.

The eastern border of the Florida Current merges with the Sargasso Sea, without any sharp boundary. T-S curves are not distinctive enough to separate the two water masses in the boundary zone, but they can be distinguished by plotting dissolved O<sub>2</sub> against sigma-t. The special stations show intrusion of Sargasso Sea water, while the regular stations near the axis of the Gulf Stream do not. In the upper 100 meters the two water masses cannot be distinguished on any basis, and analysis of the *Gill* samples has not brought to light any consistent differences in the calanoid fauna.

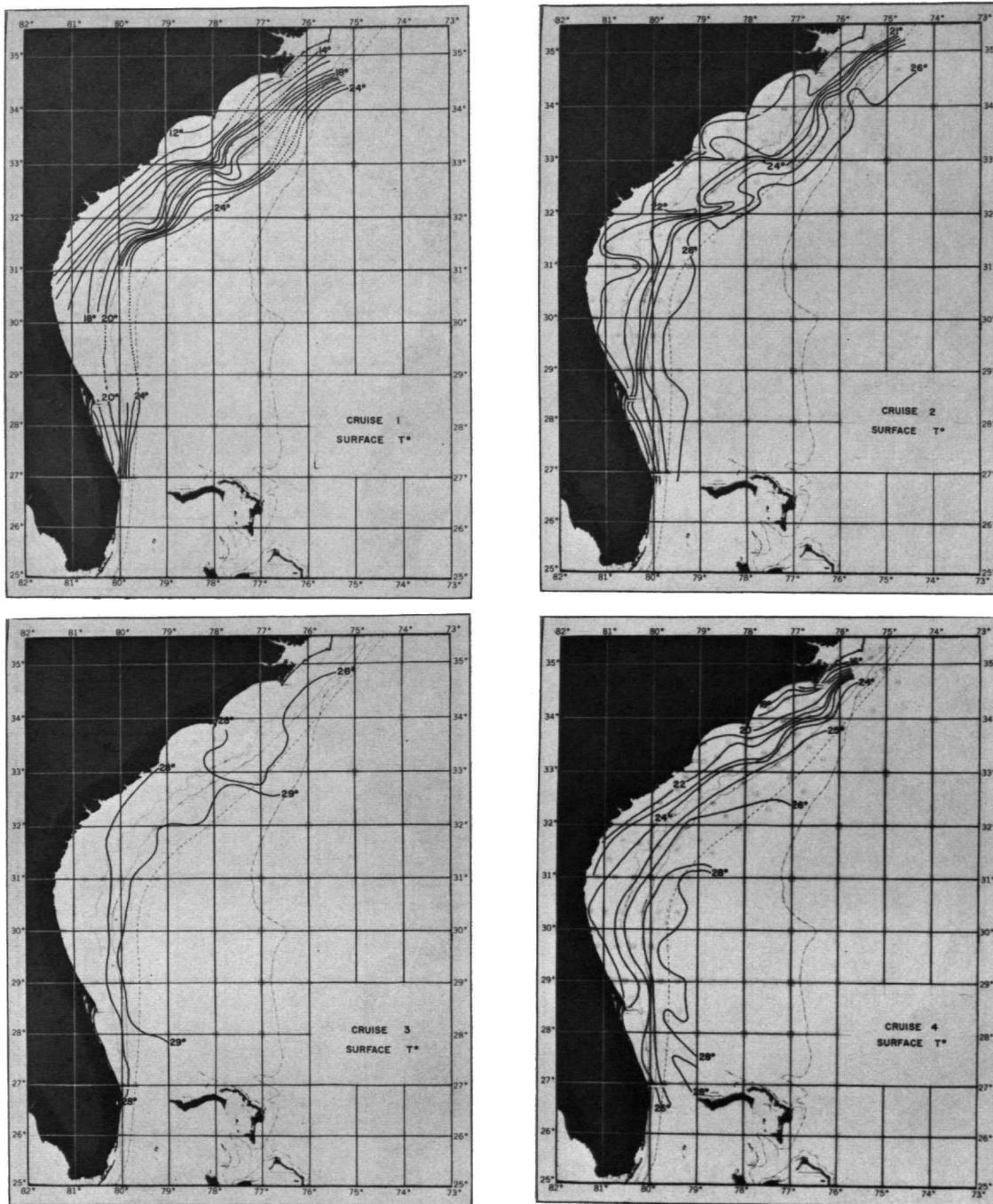


FIGURE 2.—Surface temperatures ( $^{\circ}\text{C}$ ), Cruise 1 (10 February–10 March 1953; Cruise 2 (16 April–15 May 1953); Cruise 3 (16 July–12 August 1953); Cruise 4 (5 October–14 November 1953).

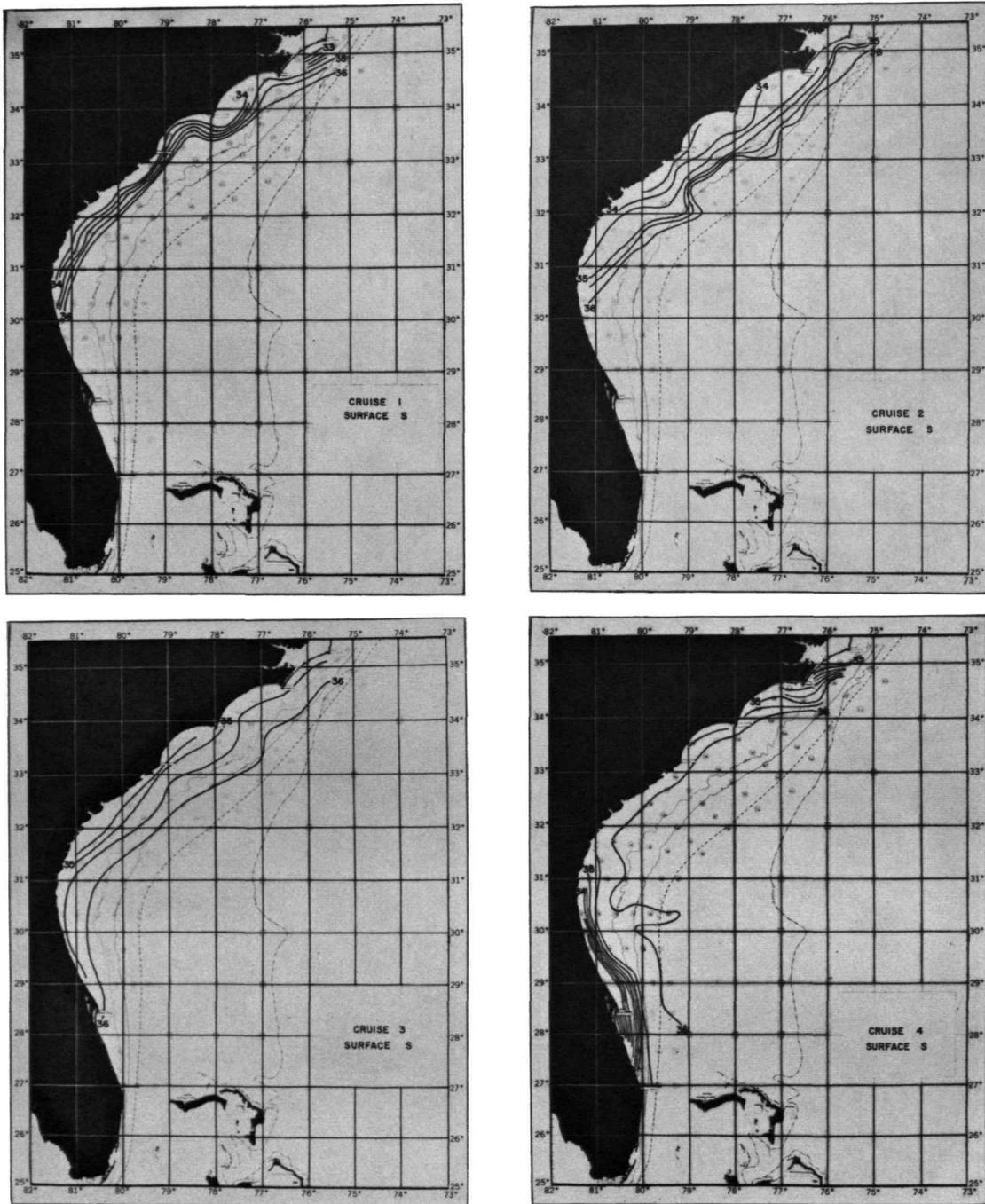


FIGURE 3.—Surface salinities (‰), Cruises 1-4.

### Seasonal Changes in Temperature and Salinity

Figures 2 and 3 show the distribution of surface temperature and surface salinity during the four cruises. In February–March strong gradients of both temperature and salinity were present, roughly parallel to the coastline. Temperatures ranged from 12°C near the coast to over 24°C in the Gulf Stream, and the 36‰ isohaline was well inside the 20-fathom line. By April–May the inshore surface water was warmer and the 36‰ isohaline had moved offshore. The surface temperature range over the area was now from about 20°C to 26°C. The salinity range was about the same as in February–March, but a layer of water of reduced salinity extended out to about the 100-fathom line northward from the Savannah section. In July–August the surface waters reached their greatest uniformity in temperature. Salinity distribution was similar to that in the spring, except that it was higher at the most shoreward stations. In the fall the temperature and salinity gradients were again well formed. An especially strong salinity gradient off the Florida coast presumably resulted from heavy runoff in the area, reported in the U. S. Weather Bureau's *Climatological Data—National Summary* for September 1953 as follows:

The heavy rains over the peninsular portion of Florida during August and September caused high stages on several streams. The St. Johns River experienced record flooding. Pasture and farm lands along the banks of the Kissimmee River were flooded and heavy discharge from the river caused Lake Okeechobee to rise to 0.6 feet above desirable level. Lake Istokpoga overflowed and inundated farm roads. Localized flooding was reported in low-lying sections of Miami and other cities on the coastal ridge.

Flood conditions still existed in Florida when Hurricane Hazel crossed the Florida Peninsula from Charlotte Harbor on the west coast to near Vero Beach on the east coast on 9 October. The effects of the rains that fell during Hazel are reported in *Climatological Data—National Summary* for October 1953:

As a result of the above-normal rainfall in this area since May, the soil was saturated, lakes were full, and some streams, particularly the St. Johns and Kissimmee Rivers, were already overflowing at the end of September. The 3- to 5-inch rains which fell during the passage of this storm augmented these flood conditions, and the resulting damage which included the total loss of some plantings, and damage to roads,

sewers, and drainage systems was estimated to be at least \$9,000,000.

The stations of Cruise 4 off the Florida coast were occupied between 12 October and 22 October, shortly after the passage of Hurricane Hazel, and the effects of the flood conditions are evident in the salinity chart. As we shall see, the lowered salinity had a marked effect on the distribution of copepods in this region.

### The Species of Calanoid Copepods

About one hundred species were identified in the samples. They are listed below in taxonomic order.

#### Calanidae

- Calanus gracilis* Dana
- Calanus minor* (Claus)
- Calanus robustior* Giesbrecht
- Calanus tenuicornis* Dana
- Undinula vulgaris* (Dana)

#### Eucalanidae

- Eucalanus attenuatus* (Dana)
- Eucalanus crassus* Giesbrecht
- Eucalanus elongatus* (Dana)
- Eucalanus monachus* (Giesbrecht)
- Eucalanus pileatus* Giesbrecht
- Eucalanus subtennis* Giesbrecht
- Mecynocera clausi* Thompson
- Rhincalanus cornutus* (Dana)

#### Paracalanidae

- Acrocalanus andersoni* Bowman
- Acrocalanus longicornis* Giesbrecht
- Calocalanus contractus* Farran
- Calocalanus gracilis* Tanaka
- Calocalanus pavo* (Dana)
- Calocalanus pavoninus* Farran
- Calocalanus plumulosus* (Claus)
- Calocalanus styliremis* Giesbrecht
- Paracalanus aculeatus* Giesbrecht
- Paracalanus crassirostris* Dahl
- Paracalanus indicus* Wolfenden
- Paracalanus pygmaeus* (Claus)
- Paracalanus quasimodo*, new species

#### Pseudocalanidae

- Clausocalanus furcatus* (Brady)
- Clausocalanus species*<sup>1</sup>
- Ctenocalanus vanus* Giesbrecht

#### Aetideidae

- Euaetidius giesbrechti* (Cleve)
- Euchirella amoena* Giesbrecht

<sup>1</sup> Frost and Fleminger's (1968) monograph on *Clausocalanus* had not appeared at the time the copepods were being enumerated, and only the distinctive *C. furcatus* can be considered to have been reliably identified.

*Euchirella curticauda* Giesbrecht  
*Euchirella messinensis* (Claus)  
*Euchirella pulchra* (Lubbock)  
*Euchirella rostrata* (Claus)  
*Undeuchaeta major* Giesbrecht  
*Undeuchaeta plumosa* (Lubbock)

**Euchaetidae**  
*Euchaeta marina* (Prestandrea)

**Phaennidae**  
*Phaenna spinifera* Claus  
*Xanthocalanus agilis* Giesbrecht

**Scolecithricidae**  
*Lophothrix latipes* (T. Scott)  
*Scaphocalanus curtus* (Farran)  
*Scaphocalanus echinatus* (Farran)  
*Scolecithricella ctenopus* (Giesbrecht)  
*Scolecithricella dentata* (Giesbrecht)  
*Scolecithricella tenuiserrata* (Giesbrecht)  
*Scolecithrix bradyi* Giesbrecht  
*Scolecithrix danae* (Lubbock)  
*Scottocalanus securifrons* (T. Scott)

**Temoridae**  
*Temora stylifera* (Dana)  
*Temora turbinata* (Dana)  
*Temoropia mayumbaensis* T. Scott

**Metridiidae**  
*Pleuromamma abdominalis* (Lubbock)  
*Pleuromamma gracilis* (Claus)  
*Pleuromamma piseki* Farran  
*Pleuromamma xiphias* (Giesbrecht)

**Centropagidae**  
*Centropages furcatus* (Dana)  
*Centropages hamatus* (Lilljeborg)  
*Centropages typicus* Krøyer  
*Centropages violaceus* (Claus)

**Pseudodiaptomidae**  
*Pseudodiaptomus coronatus* Williams

**Lucicutiidae**  
*Lucicutia flavicornis* (Claus)  
*Lucicutia gaussae* Grice

**Heterorhabdidae**  
*Heterorhabdus papilliger* (Claus)

**Augaptilidae**  
*Haloptilus longicornis* (Claus)  
*Haloptilus oxycephalus* (Giesbrecht)  
*Haloptilus spiniceps* (Giesbrecht)

**Arietellidae**  
*Arietellus setosus* Giesbrecht

**Candaciidae**  
*Candacia armata* (Boeck)  
*Candacia bipinnata* (Giesbrecht)  
*Candacia curta* (Dana)  
*Candacia ethiopica* (Dana)  
*Candacia longimana* (Claus)  
*Candacia pachydactyla* (Dana)  
*Canadacia paenelongimana* Fleming & Bowman  
*Paracandacia bispinosa* (Claus)  
*Paracandacia simplex* (Giesbrecht)

**Pontellidae**  
*Anomalocera ornata* Sutcliffe  
*Calanopia americana* F. Dahl  
*Labidocera acutifrons* (Dana)  
*Labidocera aestiva* Wheeler  
*Labidocera nerii* (Krøyer)  
*Labidocera scotti* Giesbrecht  
*Pontella meadi* Wheeler  
*Pontella securifer* Brady  
*Pontella spinipes* Giesbrecht  
*Pontellina plumata* (Dana)  
*Pontellopsis perspicax* (Dana)  
*Pontellopsis regalis* (Dana)  
*Pontellopsis villosa* Brady

**Acartiidae**  
*Acartia danae* Giesbrecht  
*Acartia negligens* Dana  
*Acartia tonsa* Giesbrecht

All but about a dozen of the above species may be identified with the aid of Rose (1933) or Owe and Foyo (1967). Taxonomic considerations are not the principal objective of the present paper, and they are dealt with only when problems were encountered, namely in the genera *Paracalanus*, *Pleuromamma*, and *Heterorhabdus*.

### Zonation and Species Associations

The most striking aspect of the distribution of the copepods was the marked inshore-offshore zonation. Certain species were restricted to coastal waters; others were found only in oceanic waters. Along with the change in species composition in samples collected at progressively greater distances from shore was an increase in the number of species in a sample. The extremes were a station where only *Acartia tonsa* was collected (Cruise 1, Station 23) and one which yielded 42 species of calanoids (Cruise 3, Station 48). The maps in Figure 4 show clearly the inshore-offshore zonation in numbers of species.

It was evident that the species associations in coastal and shelf waters differed from those in oceanic waters. To identify these associations, I have used the affinity index of Fager and McGowan (1963):

$$\frac{C}{AB} - \frac{1}{2B}$$

where C is the number of joint occurrences of a pair of species; A is the total number of occurrences

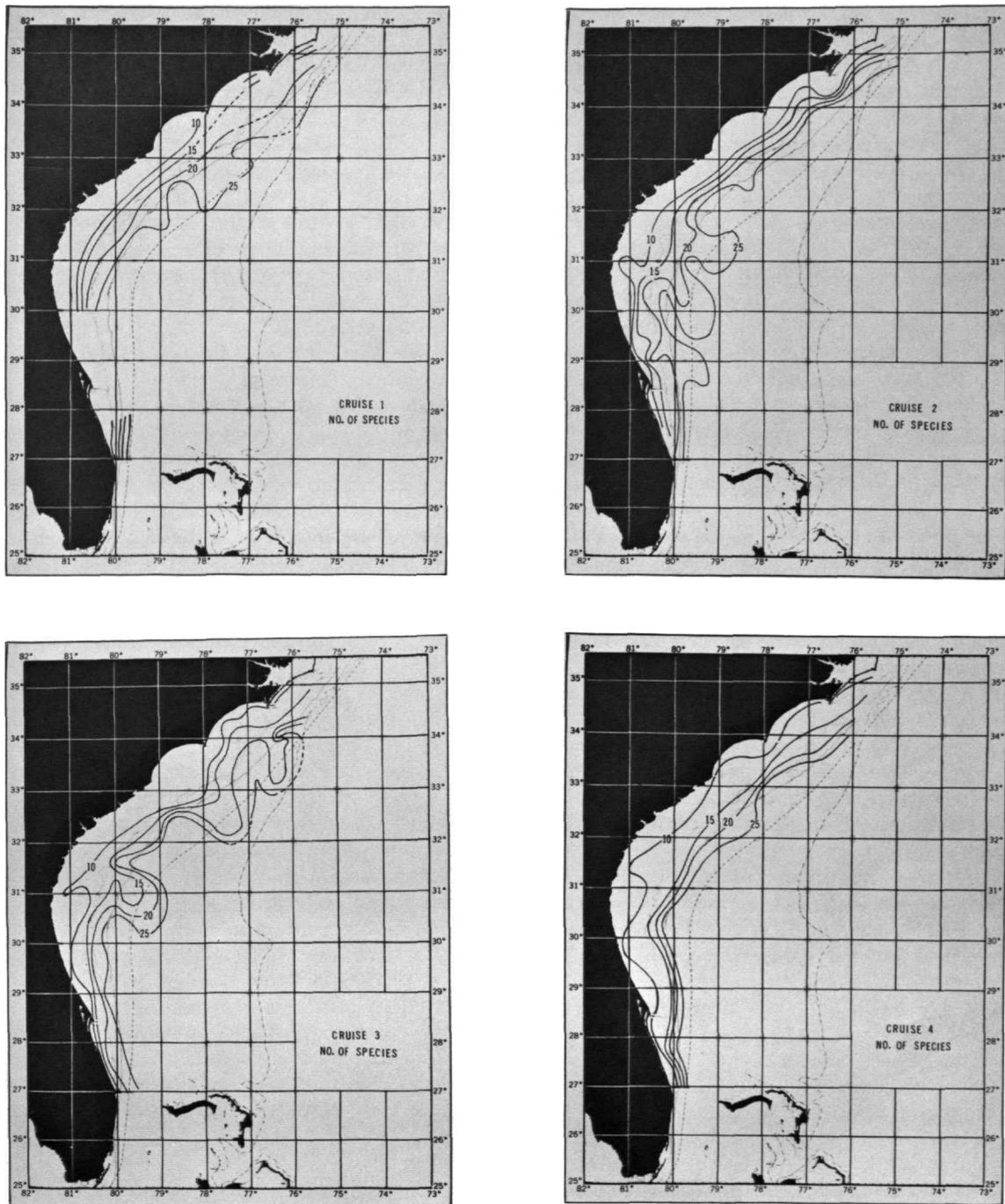


FIGURE 4.—Number of species of calanoid copepods, Cruises 1-4.

of species A; B is the total number of occurrences of species B and  $A \leq B$ .

It was not practical to compute affinity indexes between all possible pairs of the 94 species, and I therefore restricted my analysis to 13 species which were consistently present in the samples in significant numbers. From the 78 affinity indices computed from the 13 species for each cruise, dendrograms were constructed by the methods of Mountford (1962). The results, shown in Figures 5-6, are remarkably consistent in that almost identical groupings of species were obtained in the separate analyses made for each of the four cruises. This consistency confirms the validity of the method used. From the shore outward the following calanoid associations can be identified.

1. A coastal association of two species, *Acartia tonsa* and *Labidocera aestiva*. *Acartia tonsa* is a widely distributed estuarine species tolerant of wide ranges in salinity. *Labidocera aestiva* is less euryhaline but well known as a coastal species. The association of the two species is not high (affinity indices 0.56, 0.33, 0.56, and 0.51 for Cruises 1-4) and is not statistically significant on Cruise 2. One might argue for separating the coastal assemblage into the estuarine *A. tonsa* and the coastal *L. aestiva*.

2. A shelf association of four species: *Paracalanus parvus*, *Centropages furcatus*, *Eucalanus pileatus*, and *Temora turbinata*. On Cruise 2, *Labidocera aestiva* joins this association, and on Cruise 4, *T. turbinata* leaves it to join the oceanic association. The remaining three species are consistently associated.

3. An oceanic association of the other seven species. These species branch in various ways in the four dendrograms but occur together consistently. They form a rather tightly knit group, with the exception of *Lucicutia flavicornis*, which has the lowest association with the other species of any member of the oceanic association.

Of the 81 species for which affinity indices were not computed, almost all of them could be placed in the oceanic association by their distribution patterns. The higher number of species in offshore stations has already been mentioned. The distribution of selected genera and species will be considered later in this paper.

A calanoid association is a reliable indicator of the presence of coastal, shelf, and oceanic water at

a given locality. This is shown diagrammatically in Figure 7. For simplicity the lines of stations are arranged in parallel rows as though the coastline were vertical, and stations between the main lines are omitted. Each station is represented by a pie diagram that shows the percentage of coastal (black), shelf (stippled), and oceanic (white) indicator species. Nine of the thirteen species represented in the dendrograms (Figures 5-6) were used in constructing the pie diagrams, as follows:

Coastal: *Acartia tonsa*, *Labidocera aestiva*.

Shelf: *Centropages furcatus*, *Eucalanus pileatus*, *Paracalanus parvus*.

Oceanic: *Calanus minor*, *Undinula vulgaris*, *Euchaeta marina*, *Clausocalanus furcatus*.

In calculations of percentages, the combined number of those of the nine species present at any station was considered 100 percent.

The pie diagrams show, as expected, a shift from coastal to shelf to oceanic indicator species as we move away from the coast (to the right in the diagrams). They indicate the extent to which Carolinian Coastal water, the habitat of the shelf species, has received incursions of Florida Current water, the habitat of the oceanic species, or brackish water from the sounds and river mouths, in which the coastal species thrive. Rarely does a station have only shelf species; usually there is an admixture of oceanic and/or coastal species. Pure oceanic stations, however, are common. Stations dominated by coastal species are few and in general close to shore. The two stations most frequently dominated by coastal species were Station 11, at Cape Kennedy, and Station 23, at Jacksonville Beach near the mouth of the St. Johns River.

Figure 8 shows for each of the four cruises a vertical section through the line of stations 40-44, lying off Charleston, South Carolina, with temperature profiles plotted. As in Figure 7, pie diagrams illustrate the seaward changes in the percentages of coastal, shelf, and oceanic species.

Seasonal changes in distribution will be discussed in the section on distribution of the individual species.

### Species Diversity

I have already pointed out the greater numbers of calanoid species at the oceanic stations compared

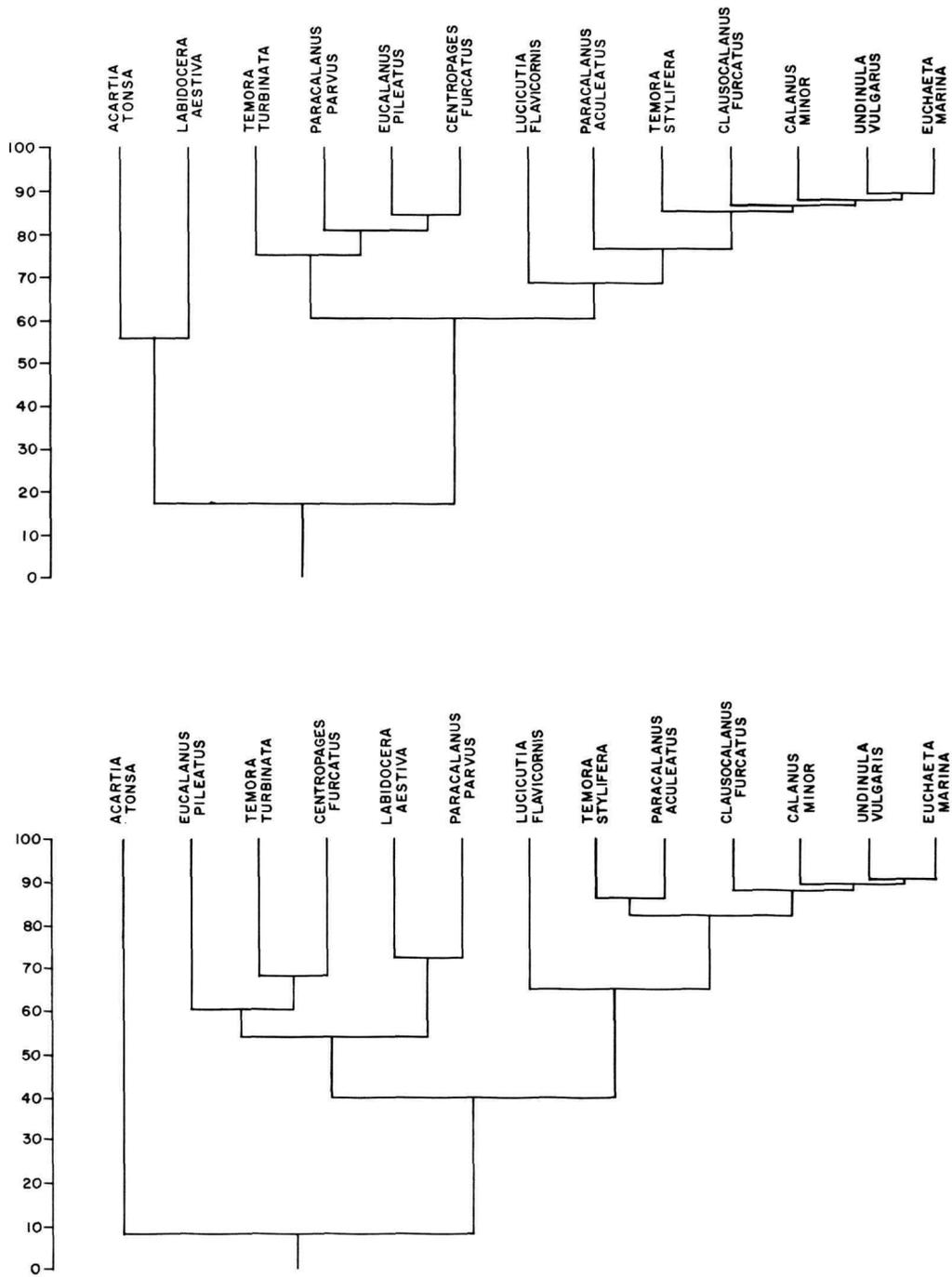


FIGURE 5.—Dendrograms from affinity indices (vertical scale) among 13 common calanoids, Cruises 1 (above) and 2 (below).

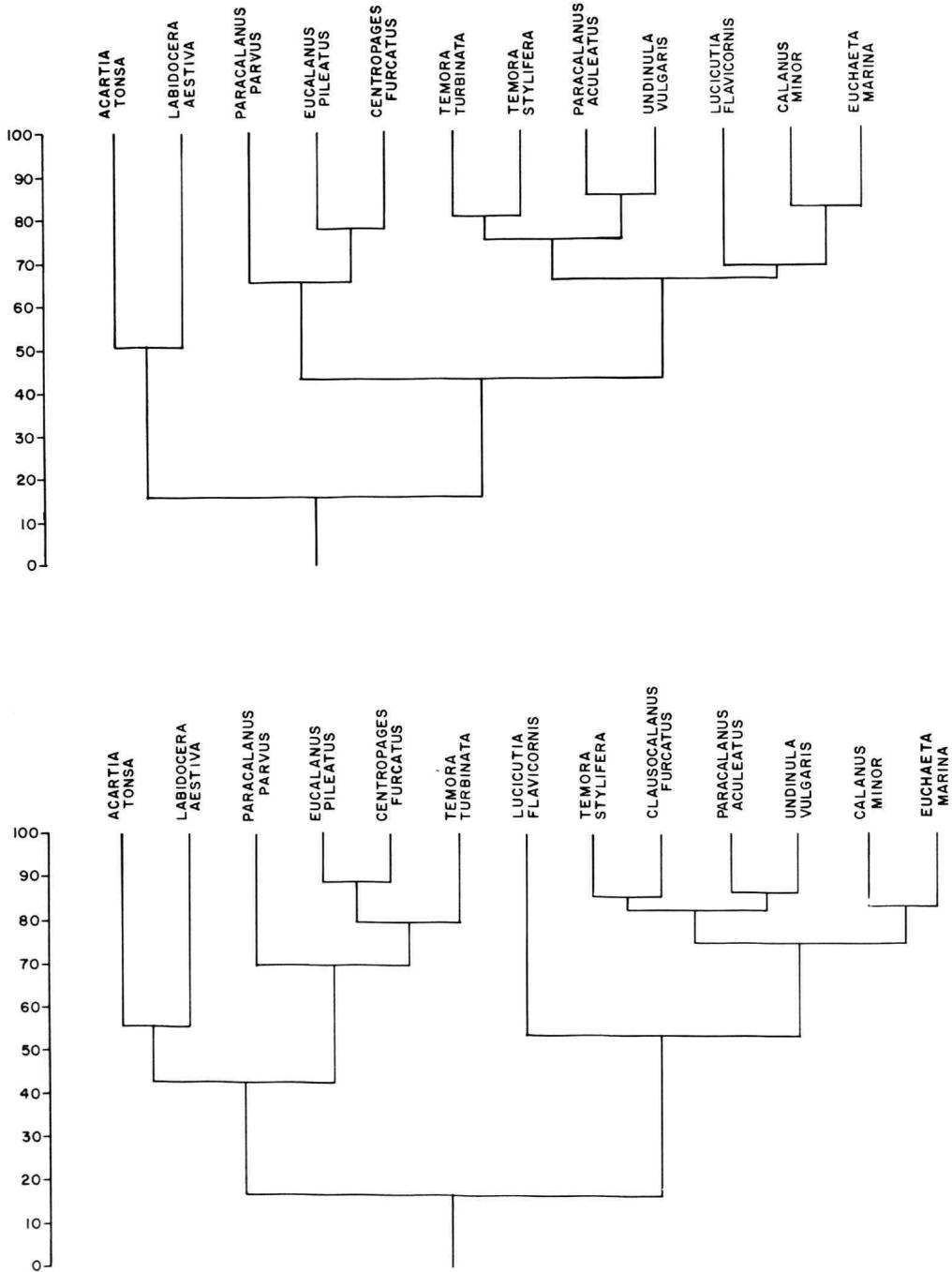


FIGURE 6.—Dendrograms from affinity indices (vertical scale) among 13 common calanoids, Cruises 3 (above) and 4 (below).

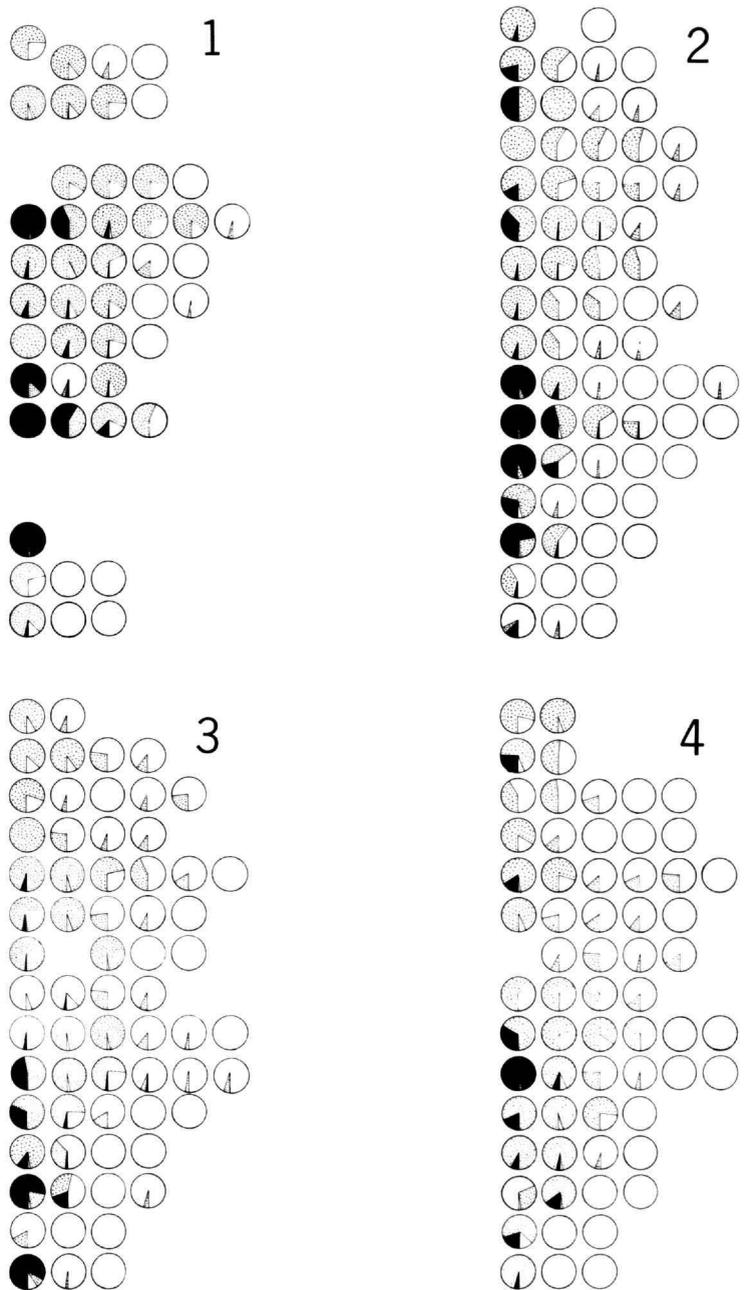


FIGURE 7.—Percentages of coastal (black), shelf (stippled), and oceanic (white) indicator species, Cruises 1-4. For explanation see text.

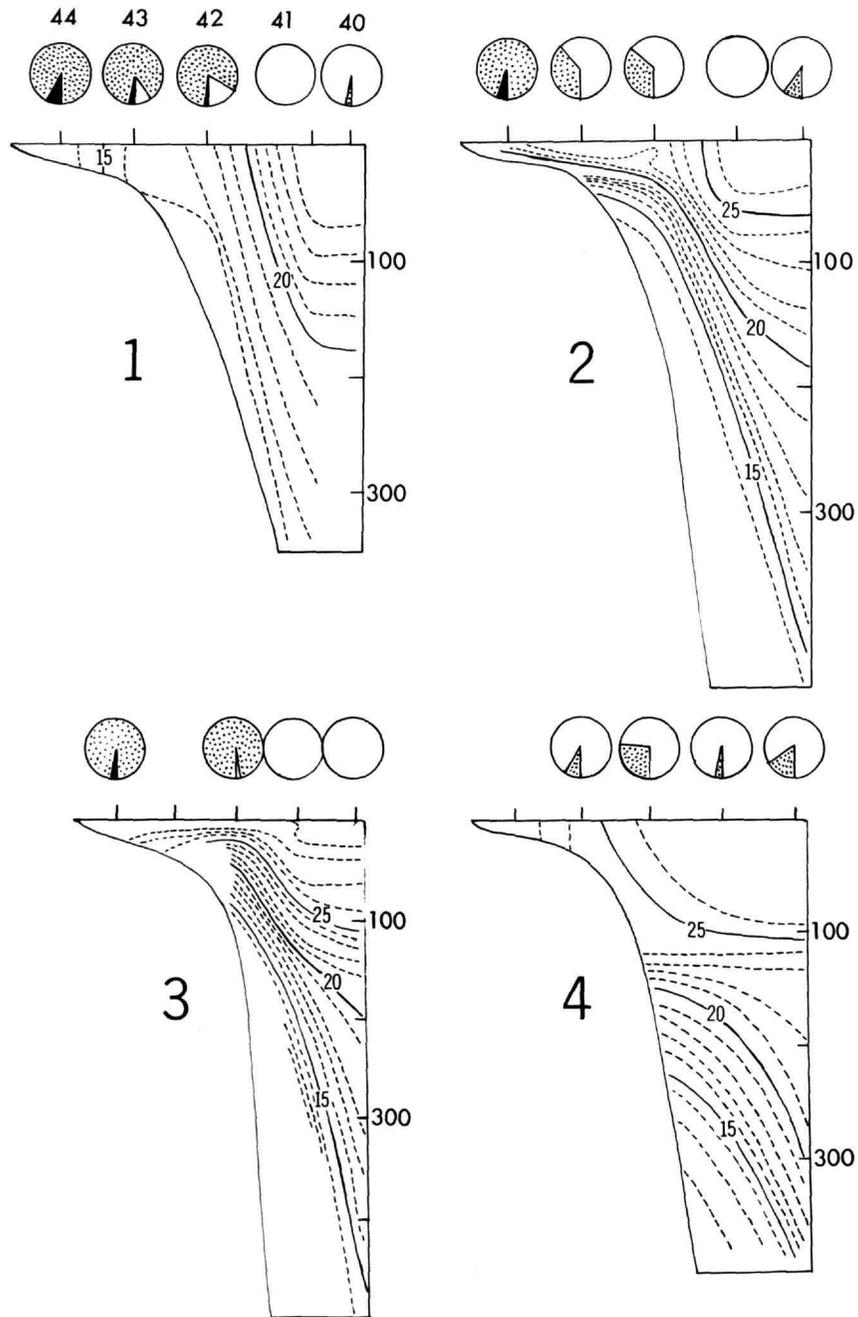


FIGURE 8.—Vertical sections for Cruises 1-4 through Stations 40-44, off Charleston, South Carolina, with temperature profiles in degrees centigrade and depths in meters. Pie diagrams show percentages of coastal (black), shelf (stippled), and oceanic (white) indicator species.

with the smaller numbers in shelf waters and the very small numbers along the coast. In other words, the species diversity, i.e., the absolute number of species present, is greatest in oceanic waters and least in coastal water.

Under many conditions, diversity is directly correlated with sample size, especially in small samples. This effect led Sanders (1968) to devise his rarefaction method, which allows comparison of diversity in samples of different sizes. Fortunately it is not necessary here to resort to Sanders' technique or the other mathematical stratagems discussed in his paper. The net tows made during the *Gill* cruises commonly filtered between 100 and 200 cubic meters of water, sometimes much more, and the numbers of calanoids collected were very great, amounting to several hundred thousand in some samples. Although the size of the samples varied greatly, it is safe to say that all but an insignificant number of the calanoid species at each station were collected and enumerated. The simplest and most direct expression of diversity, the number of species, is not affected by sample size in the *Gill* collections. The charts in Figure 4 may be considered as charts of species diversity.

### Dominance Diversity or Equitability

A second concept of diversity is the extent to which the species in a sample are equally abundant. This dominance diversity or equitability is greatest when the species of a sample occur in equal numbers and minimal when the specimens of a sample are most unequally divided among the species. Most of the commonly used measurements of diversity take into account the equitability as well as the number of species. Lloyd and Ghelardi (1964) presented a method for calculating the equitability component ( $\epsilon$ ) of diversity measured by the Shannon-Wiener information function. Sanders (1968) demonstrated that  $\epsilon$  is not independent of sample size but decreases with increasing sample size. He also found only a weak correlation between the rank in dominance diversity (judged from cumulative frequency curves) and the rank in species diversity. Moreover, species diversity faithfully reflected the type of environment, but dominance diversity did not.

A rough estimate of equitability is the percent of all the calanoid species in a sample that together comprises half the total number of calanoid specimens in that sample. In Figure 9 this measure-

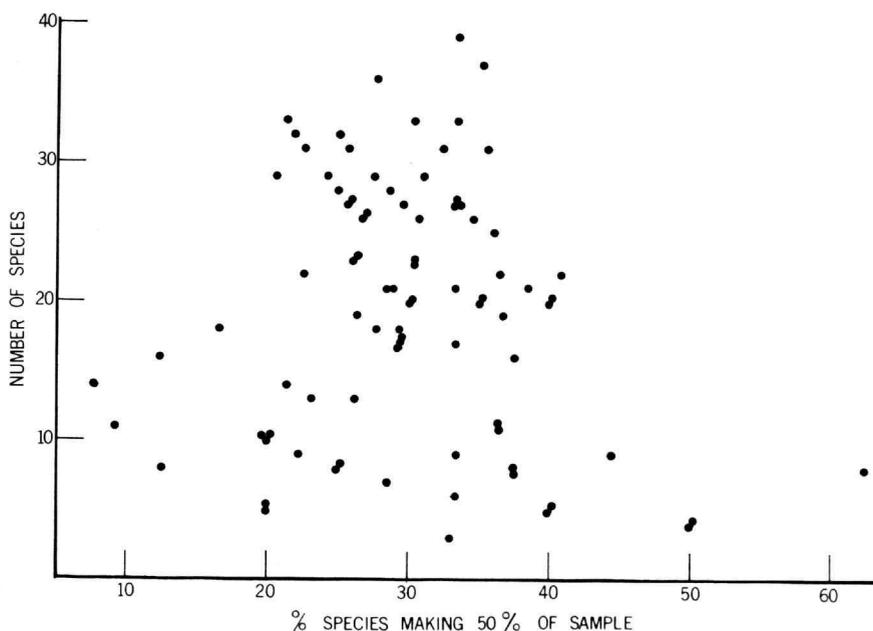


FIGURE 9.—Relationship between equitability and species diversity. Each dot represents 1 station of Cruise 2.

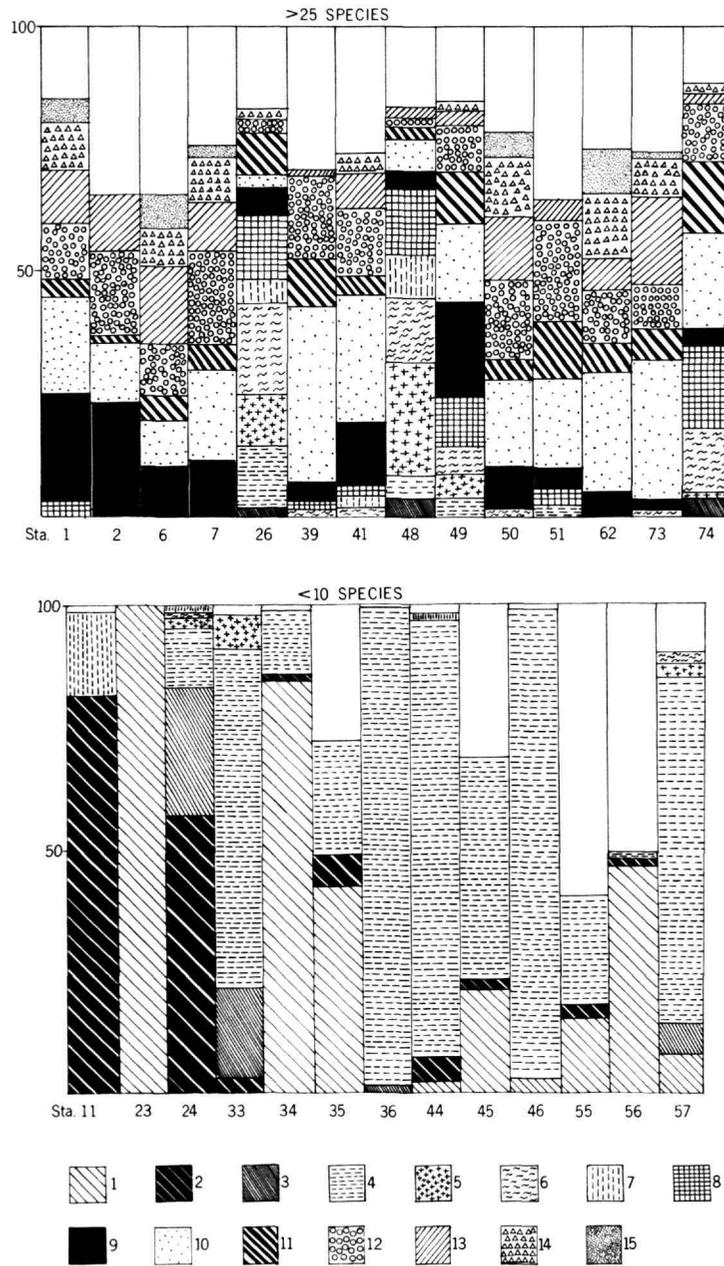


FIGURE 10.—Relative percentage of 15 species of calanoids at two groups of stations from Cruise 1. Above: stations with > 25 calanoid species. Below: stations with < 10 calanoid species. 1, *Acartia tonsa*; 2, *Labidocera aestiva*; 3, *Centropages furcatus*; 4, *Paracalanus* "parvus"; 5, *Eucalanus pileatus*; 6, *Temora stylifera*; 7, *Temora turbinata*; 8, *Paracalanus aculeatus*; 9, *Clausocalanus furcatus*; 10, *Calanus minor*; 11, *Undinula vulgaris*; 12, *Euchaeta marina*; 13, *Lucicutia flavicornis*; 14, *Pleuromamma gracilis*; 15, *Pleuromamma adbominalis*.

ment is plotted against the number of species for the stations of Cruise 2. It can be seen that equitability measured in this way is much more variable in the samples with few species (coastal and shelf samples), than in the oceanic samples. In the latter samples 20-40 percent of the species commonly make up half the sample, so the specimens in the samples are far from being equally divided among the component species.

A way of showing visually the degree of equitability is by a series of bar graphs indicating the percentage composition by species of samples from different stations. In Figure 10, bar graphs are given for two groups of stations from Cruise 1: (1) stations with less than 10 species of calanoids (coastal and shelf stations); (2) stations with 25 or more species (oceanic stations). The rather low equitability at both groups of stations is evident. Despite the high species diversity at the oceanic stations, a few species tend to dominate the samples numerically. Commonly these are the seven species used to construct the affinity diagrams (Figures 5-6) plus *Pleuromamma gracilis* and *P. abdominalis*.

The 9 Special Stations, on the eastern Gulf Stream edge of the western Sargasso Sea, are farthest removed from the influence of coastal water. Even these purely oceanic stations were usually dominated by a few species as shown below for Cruise 2:

Percent of sample	Special Stations								
	1	2	3	4	5	6	7	8	9
<i>Calanus minor</i>	28	14	26	33	8	32	5	10	10
<i>Clausocalanus furcatus</i>	15	31	11	22	4	13	3	2	2
<i>Lucicutia flavicornis</i>	16	1	—	5	21	2	17	29	13

Grice and Hart (1962) reported that *C. furcatus* was the most abundant calanoid in their Gulf Stream and Sargasso Sea samples. *Lucicutia flavicornis* was also numerically significant, but the importance of *C. minor* was less than in the *Gill* samples.

A number of theories have been proposed to explain the sort of dominance diversity found in the *Gill* samples. Most of these are highly mathematical and are based on simplified assumptions that are not yet fully proved. New and revised theories appear at a greater rate than the observations and

experiments needed to supply a firm factual basis for them. It is impossible for a mathematical amateur to evaluate the merits of these theories, and I retreat to the company of those who hold ". . . the conviction that synecological and ecosystem approaches are too complicated for meaningful results as long as we do not understand enough about the individual species and factors in nature." (Hedgpeth 1967b.)

### The Stability-Time Hypothesis and the *Gill* Samples

To explain the increase in species diversity from coastal to oceanic waters, Sanders' (1968) stability-time hypothesis, proposed to account for variations in benthic diversity, may be applied to the pelagic realm. Sanders defined two contrasting types of communities:

1. The physically controlled community, where physical conditions fluctuate widely and the animals are exposed to severe physiological stress. Adaptations are primarily to the physical environment. The species forming such communities are few in number and eurytopic.

2. The biologically accommodated community, where physical conditions are stable for long periods of time. Stress is from biological rather than physical forces. Such communities are composed of many species, which are stenotopic.

Neither type of community exists in pure form; all communities in nature fall somewhere between the two extreme types. Applied to the pelagic realm, the inhabitants of coastal waters constitute essentially a physically controlled community, whereas those of oceanic waters compose a biologically accommodated community.

Figures 11-12 show the ranges in surface temperature and salinity during *Gill* Cruises 1-4, and indicate that stress from these factors increases toward the coast. Nearshore surface-living copepods must endure an annual temperature range of about 15°C and a salinity change of more than 2‰. Along the axis of the Florida Current they are subjected to annual variations of only about 5°C and less than 0.5‰.

We know little about the ability of copepods to withstand salinity changes, and nothing about the

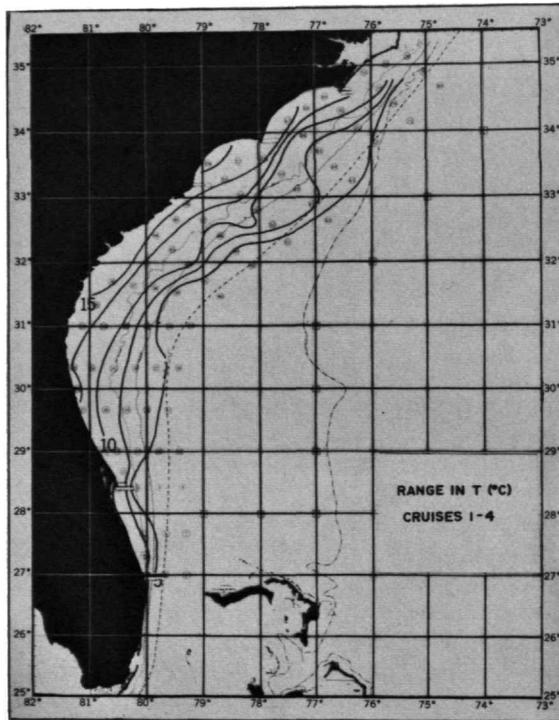


FIGURE 11.—Variation in surface temperature during Cruises 1-4.

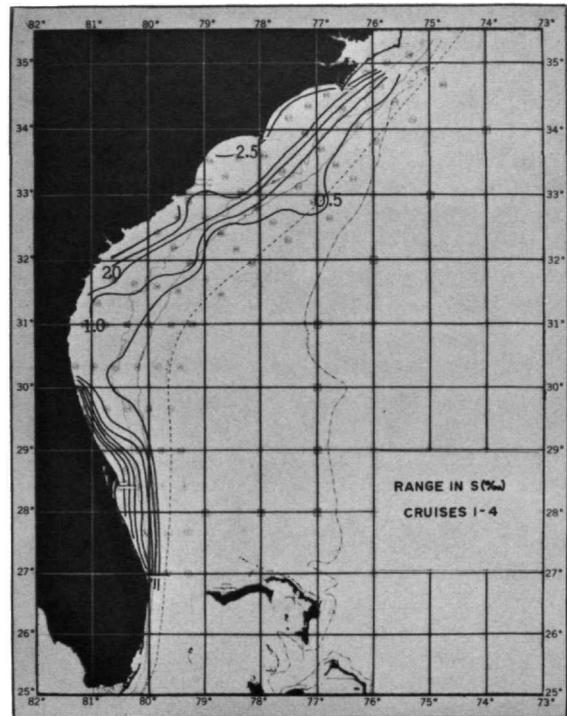


FIGURE 12.—Variation in surface salinity during Cruises 1-4.

mechanisms involved. Some preliminary experiments were carried out by Hopper (1960). Working aboard ship in the Caribbean and South Atlantic, he subjected eight species of oceanic calanoids, including *Undinula vulgaris*, to reduced salinities. He found that diluting sea water by up to about 7%, or decreasing the salinity to 33.50‰, had no effect on survival. This dilution amounts to a reduction in salinity of 2.52‰, greater than that endured by species of the *Gill* oceanic association and most members of the shelf association. The salinity tolerance of Hopper's copepods was greater than would be expected from distributional data, but his experiments were necessarily too limited in duration and in number of specimens to warrant definite conclusions as to the role of salinity as a limiting factor in distribution.

More extensive experiments on tolerance to salinity reductions have been performed with coastal species. Lance (1963) found the order of salinity tolerance in three species of *Acartia* from South-

ampton Water to be *A. tonsa* > *A. bifilosa* > *A. discaudata*, and later (1964) added more copepod species to give an expanded order (for adult females) *A. tonsa* > *A. bifilosa* > *A. discaudata* > *A. clausi* > *Centropages hamatus* > *Temora longicornis*. Tundisi and Tundisi (1968) carried out experiments on tolerance to reduced salinity in planktonic crustaceans in the vicinity of Cananea, Brazil (about 25°S). The order of tolerance of the four calanoid species was *Pseudodiaptomus acutus* > *Acartia lilljeborgii* > *Centropages furcatus* > *Temora stylifera*.

Information on relative tolerance to reduced salinity is available from distributional as well as experimental data. Cronin, Daiber, and Hulbert (1962) analyzed the distribution of calanoids along the axis of the Delaware River estuary with salinities decreasing from about 30‰ at the mouth to fresh-water conditions upstream. The order of tolerance indicated by their analysis was *Eurytemora* spp. > *Acartia tonsa* > *Pseudodiaptomus coronatus* > *Centropages hamatus* + *typicus* (not distin-

guished) = *Labidocera aestiva* > *Temora longicornis* ? = *Paracalanus parvus*.

From studies of the copepods in bays and coastal waters outside of the bays of Puerto Rico by Coker and González (1960) and González and Bowman (1965), the order of tolerance of calanoids to bay water (not necessarily to low salinity) is approximately *Acartia tonsa* > *Paracalanus crassirostris* > *Paracalanus "parvus"* > *Temora turbinata* > *Centropages furcatus*.

Applying the above experimental and distributional data to the *Gill* calanoids, we would expect to find an order of tolerance about as follows: *Acartia tonsa* > *Pseudodiaptomus coronatus* = *Paracalanus crassirostris* > *Labidocera aestiva* > *Paracalanus "parvus"* > *Temora turbinata* > *Centropages furcatus* > *Temora stylifera*. This order fits reasonably well the distributional patterns of these species on the four *Gill* cruises.

*Acartia tonsa* thrives under hypersaline conditions as well as in estuaries. In the Laguna Madre of Texas, a hypersaline lagoon, it is the most abundant zooplankton and occurs at salinities as high as 80‰ (Simmons 1957; Hedgpeth 1967a). Carpelin (1967) emphasized the fact that organisms capable of tolerating increases in salinity can also tolerate reductions in salinity relative to marine water and points out that this was observed and commented upon by Ferronnière (1901) many years ago. Coastal and estuarine copepods should not be looked upon simply as animals adapted to withstand reductions in salinity, but, from a broader viewpoint, as eurytopic animals adapted to withstand fluctuations in various physical conditions, including but not necessarily limited to temperature and salinity. Eurytopic species must maintain a high degree of genetic variability and cannot be closely adapted to narrow ecological niches. Physiological efficiency must be sacrificed for adaptability.

In contrast, oceanic copepods are stenotopic and can tolerate only limited fluctuations in environmental conditions. If the relatively stable conditions of the environment persist long enough, interspecific competition leads to greater specialization and increased efficiency. The niches occupied become narrower and more numerous. The end result is Sanders' (1968) biologically accommodated community. That a seemingly uniform layer of the

ocean can support as many as 40 species of calanoids, each with a distinct niche, challenges the imagination, especially when it is realized that all samples contained also a number of noncalanoid zooplankton species. A high degree of specialization in feeding habits of oceanic calanoids would not be a surprising find. Until now investigations of feeding and nutrition in calanoids have been carried out largely with the more accessible coastal and shelf species, and it will be interesting to see whether oceanic species have more restricted diets. A greater efficiency in feeding compared with inshore species is also to be expected. There is evidence that *Acartia* is a relatively inefficient feeder compared to more oceanic copepods (Conover 1956).

In addition to feeding specializations, coexistence could be achieved by vertical segregation and seasonal separation. To what extent these factors operate in marine calanoids is poorly known (Mullin 1967), but all three mechanisms have been shown to function in enabling several species of *Diaptomus* to coexist in a Canadian lake (Sandercock 1967).

**Distribution of the Individual Species of Calanoids**

The quantitative distributions of the individual species are shown on a series of maps on which the number/100 m<sup>3</sup> at each station is indicated by one of a series of the symbols in Figure 13.

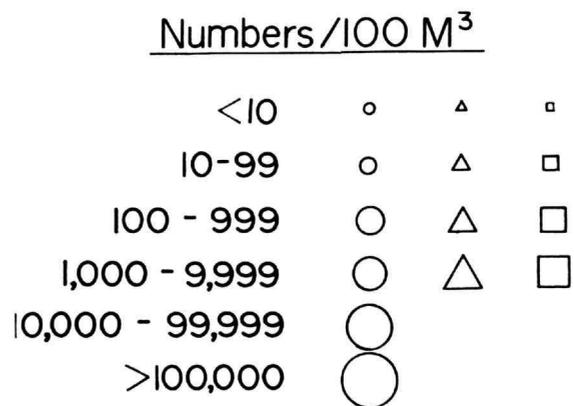


FIGURE 13.—Symbols used on maps (Figures 14–50) to indicate presence and numerical abundance of calanoids on *Gill* cruises.

For some species that occurred rarely or in small numbers, only the qualitative distribution is shown, and in some cases the distribution on all four cruises is combined on one map.

### Calanidae

*Undinula vulgaris* and *Calanus minor* were among the most abundant and widespread of the oceanic calanoids (Figures 14–15). The large species, *Calanus gracilis* and *Calanus robustior*, occurred in many of the samples collected at night in oceanic waters but were absent from most of the samples collected during the day. *Calanus tenuicornis* occurred in small numbers at some oceanic stations and appeared to be more restricted to oceanic waters than the other Calanidae.

### Eucalanidae

*Eucalanus pileatus* was a widespread and abundant member of the shelf association (Figure 16). The other species of *Eucalanus* (*attenuatus*, *crassus*, *elongatus*, *monachus*, *subtenuis*) occurred less frequently and in much smaller numbers, in oceanic waters (Figures 16–17), as did *Rhincalanus cornutus*. *Mecynocera clausi* was strictly limited to oceanic waters (Figure 18).

The specimens of *Rhincalanus* all belonged to forma *atlantica* Schmaus (1917), distinguished from Schmaus' forma *typica* by the female 5th legs (Figures 19a,c). Schmaus' forma have been ignored by most authors, and some confusion could arise from the fact that the leading monographs on western Atlantic calanoids (Wilson 1932; Owre and Foyo 1967) illustrate their accounts of *R. cornutus* with figures copied from Giesbrecht (1892). Giesbrecht's illustrations are of f. *typica*, which occurs in the Indopacific but not in the Atlantic.

A further complication is Schmaus' decision to designate as f. *typica* the Indopacific variety, although the type-locality for *R. cornutus* given by Dana (1852) is in the Atlantic (1°N, 18°W). Schmaus was aware that on the same page and preceding the original diagnosis of *R. cornutus* was Dana's diagnosis of a very similar species, *Rhincalanus rostrifrons*, from the Sulu Sea. The two species were combined by Giesbrecht (1892), since

the only differences between them could be explained by the fact that *R. cornutus* was based on adult females and *R. rostrifrons* on immature males.

Although the differences between them are slight, I believe the two forms merit recognition as full species. In addition to the differences between the female 5th legs, the Indopacific form has relatively longer 1st antennae, about 1.5 times as long as the body (only 1.3 times as long in the Atlantic form). Figures 19b,d show the distal segments of the 1st antennae of specimens of the two forms with nearly identical body lengths. The longer segments of the Indopacific form are evident.

A detailed comparison of the appendages and a study of body proportions, which I have not attempted, might reveal other differences. The two forms appear to be completely separated geographically, and no intergrades have been reported. Hence I propose to recognize an Indopacific species, *R. rostrifrons* Dana (= *R. cornutus* f. *typica* Schmaus), and an Atlantic species, *R. cornutus* Dana (= *R. cornutus* f. *atlantica* Schmaus).

### Paracalanidae

*Acrocalanus andersoni* and *A. longicornis*, as reported previously (Bowman 1958), are both limited to oceanic waters. Neither species occurs in large numbers, although *A. longicornis* was collected much more commonly than *A. andersoni*.

In the genus *Paracalanus* the most common species presented unexpected taxonomic problems, and it is necessary to discuss its systematics in detail.

Sewell (1929) divided the species of *Paracalanus* into two groups, the *Parvus* group and the *Aculeatus* group. Characters that Sewell used to distinguish the two groups were the form of the spermatheca, the armature of the swimming legs, the length and segmentation of antenna 1, and the proportionate lengths of the prosome and urosome. Sewell included *P. crassirostris* in the *Parvus* group, but this species and its close relatives (summarized by Wellershaus 1969) form a third distinct and coherent group. The characteristics of the *Crassirostris* group include the small size, thick and blunt rostral setae, and short terminal setae of the 5th legs.

In the Gill samples there are two species of the *Parvus* group, one a prominent member of the shelf

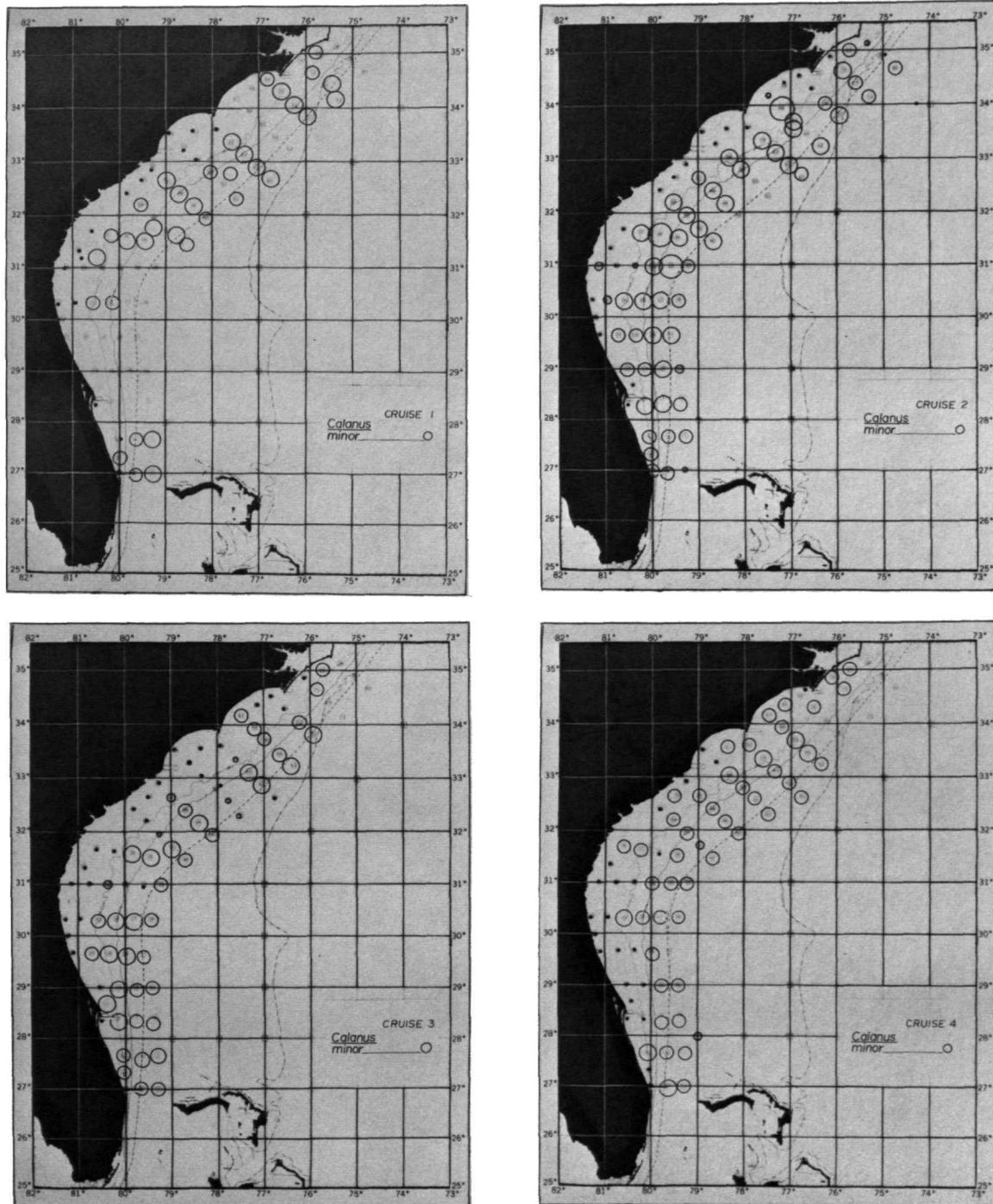
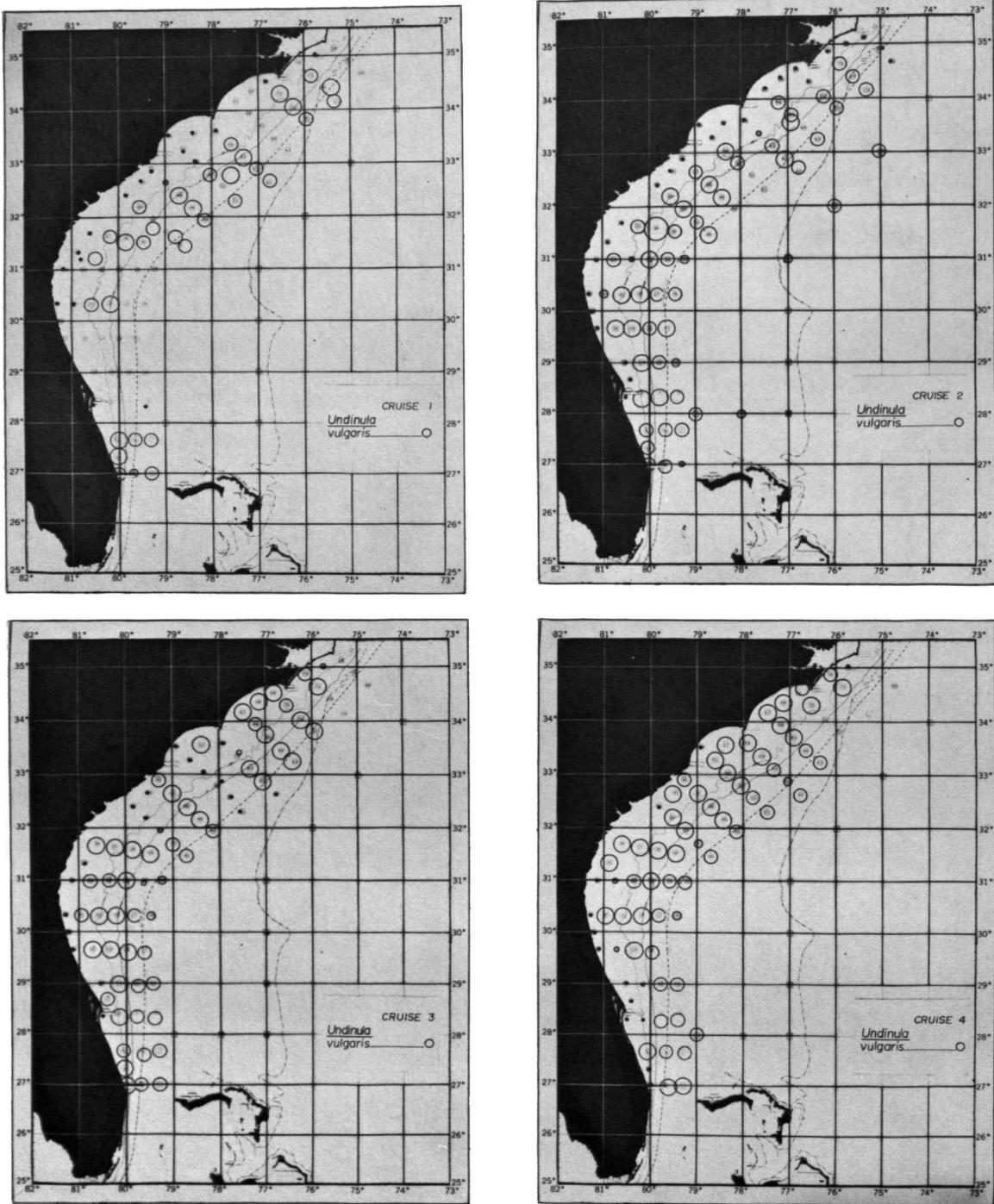


FIGURE 14.—Distribution of *Calanus minor*, Cruises 1-4.

FIGURE 15.—Distribution of *Undinula vulgaris*, Cruises 1-4.

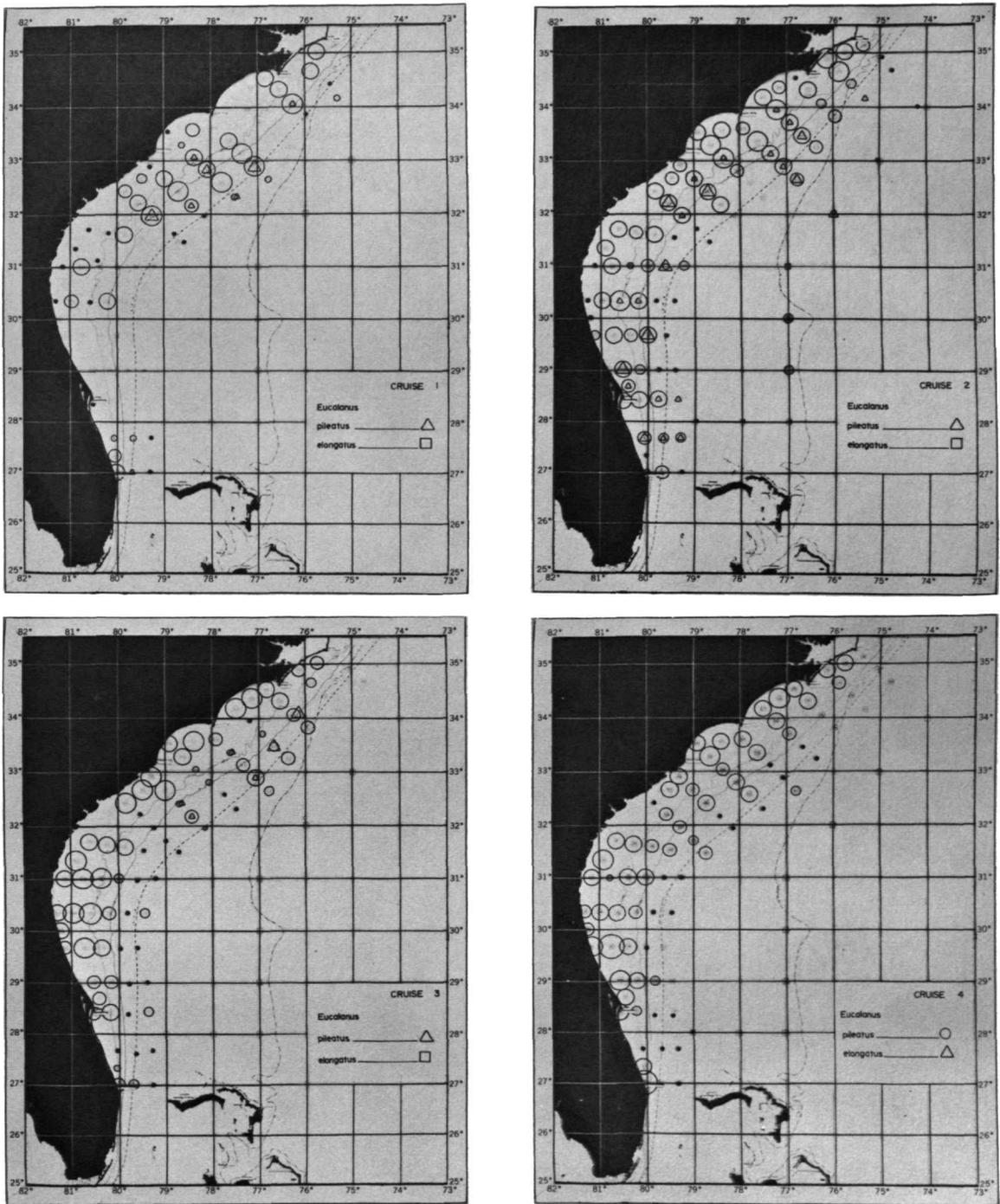


FIGURE 16.—Distribution of *Eucalanus pileatus* and *E. elongatus*, Cruises 1–4.

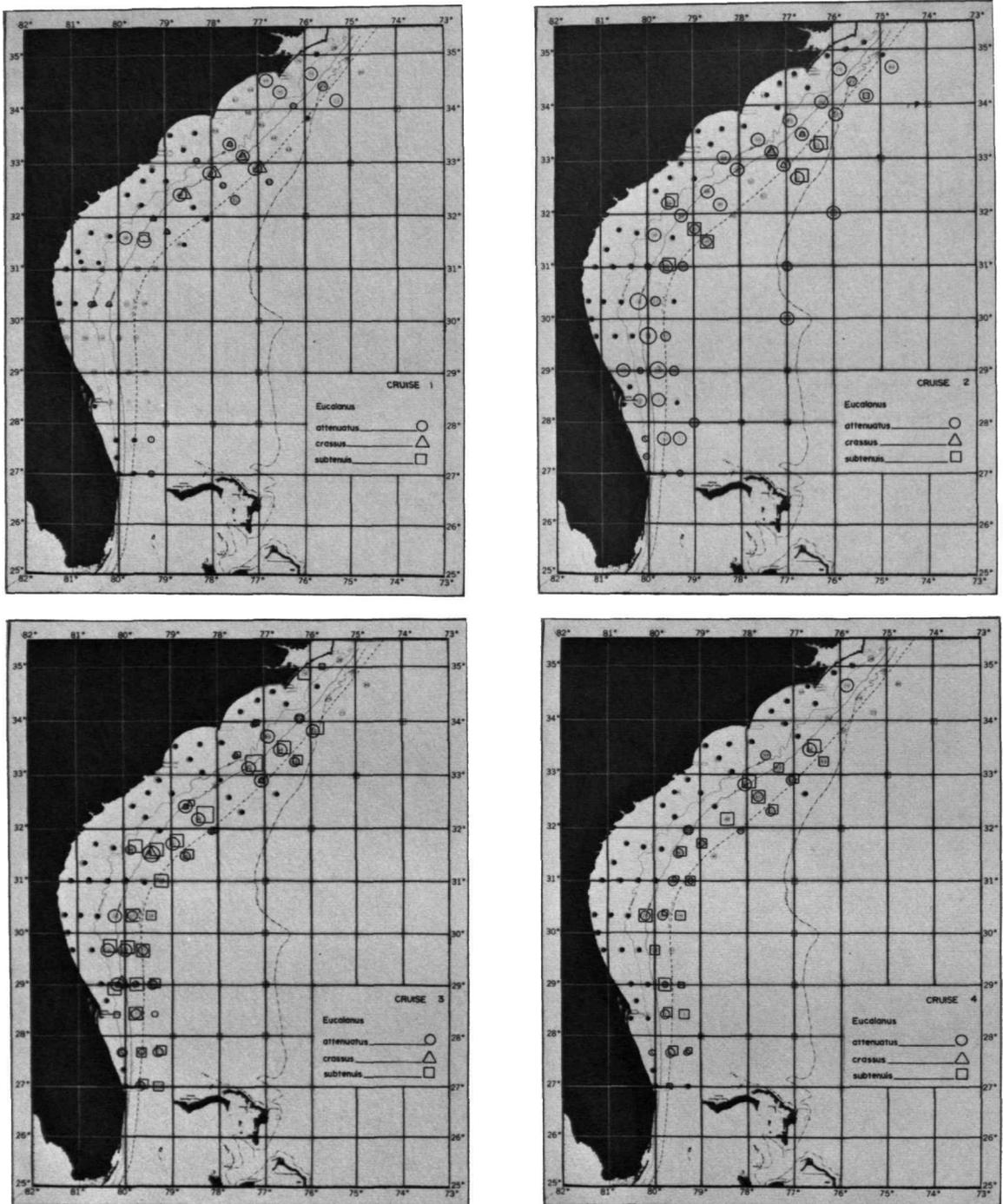


FIGURE 17.—Distribution of *Eucalanus attenuatus*, *E. crassus*, and *E. subtenius*, Cruises 1–4.

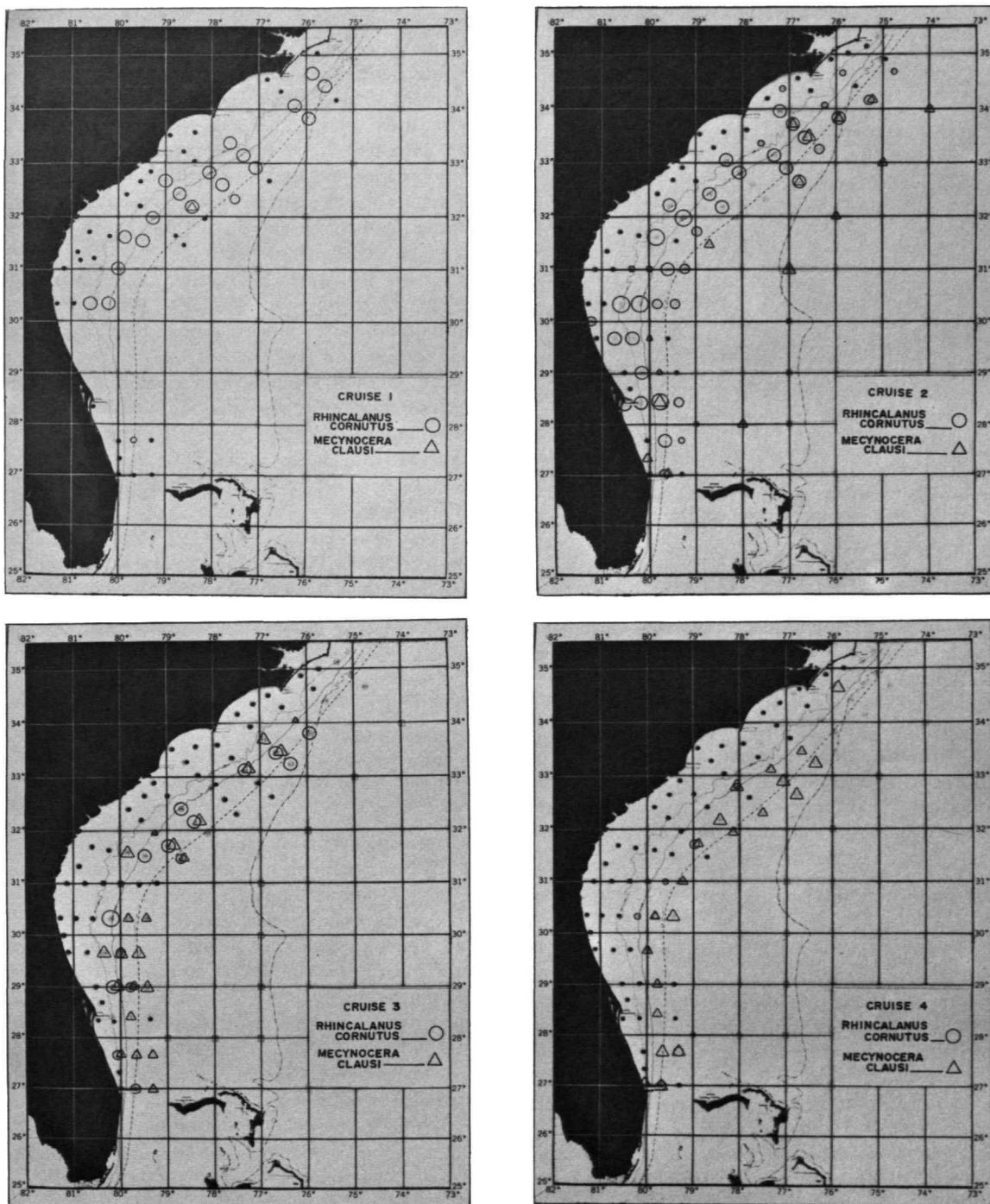


FIGURE 18.—Distribution of *Rhincalanus cornutus* and *Mecynocera clausi*, Cruises 1-4.

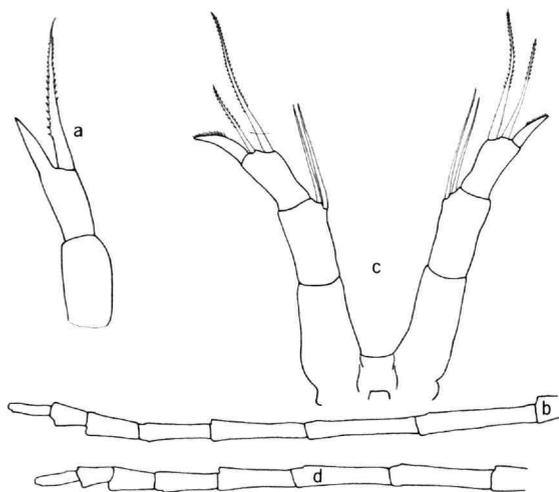


FIGURE 19.—*Rhincalanus rostrifrons*, ♀: a, 5th leg; b, distal segments of 1st antenna, dorsal. *Rhincalanus cornutus*, ♀: c, 5th legs; d, distal segments of 1st antenna, dorsal.

association, the other also a constituent of the shelf association but much less common. The two species were not distinguished at first, and both were enumerated as *P. parvus* in the counts of Cruises 1-3. When I realized that I was lumping two species I examined them in detail and concluded that the less common species is identical with the *P. parvus* of Giesbrecht, which I consider to be *P. indicus* Wolfenden (see under *P. indicus*) and the common species is an undescribed species which I propose to name *Paracalanus quasimodo*.

#### *Paracalanus quasimodo*, new species

FIGURES 20-21, 22a

SYNONYMY.—Probably many references to western Atlantic specimens of "*Paracalanus parvus*," summarized by González and Bowman (1965), are attributable to *P. quasimodo*.

DIAGNOSIS.—Female. In *Parvus* group. Body rather stocky for a *Paracalanus*, about 1.0 mm in length. Prosome about 3 times as long as urosome, with characteristic dorsal hump similar to those in some species of *Acrocalanus* but less strongly developed. Forehead not vaulted. Head fused with 1st pedigerous somite; 4th and 5th pedigerous somites separated by indistinct suture. Genital segment rather

broad in relation to length; lateral part of posterior margin sometimes armed with row of minute spinules; lateral surface with cluster of spinules on either side, anterior and dorsal to spermatheca. Spermatheca obovate, distal half often narrower than proximal half. Remaining urosomites relatively broader and shorter than those of *P. indicus*.

Antenna 1, 25-merous, often broken at suture between segments 8 and 9, reaching to about posterior margin of caudal ramus.

Legs 1-4 with surface armature as shown in Figures 20h-k; pattern very similar to that of *P. indicus*; basipod conspicuously spinose. Leg 5, terminal spine longer than 2nd segment.

Male. Genital segment with cluster of spinules on either side, otherwise identical with *P. indicus*.

The name is derived from the protagonist of Victor Hugo's classic novel, *The Hunchback of Notre Dame*, and alludes to the distinctive shape of the prosome.

TYPES.—Holotype ♀ (USNM 134484) and allotype ♂ (USNM 134485) from Cruise 4, Station 57, 27 October 1953, off Florida, 33°34'N, 78°24'W.

#### *Paracalanus indicus* Wolfenden, new rank

FIGURES 22b-m, 23a

*Paracalanus parvus* (Claus).—Giesbrecht, 1892:164-199, pls. 1, 6, 9.—Sewell, 1929:68-71, figs. 24-25.

*Paracalanus parvus* var. *indicus* Wolfenden, 1905:998, pl. 96: figs. 7, 9-11.

DIAGNOSIS.—Female. Body more slender and slightly shorter than *P. quasimodo*, length about 0.9 mm. Prosome about 3.2 times as long as urosome; dorsal hump only slightly or not at all developed, hence prosome not so high in relation to its length as in *P. indicus*. Forehead not vaulted. Genital segment, viewed dorsally, narrower than in *P. quasimodo*, lateral parts of posterior margin with row of minute spinules, without cluster of spinules above spermatheca. Spermatheca subelliptical, not narrowing distally.

Antenna 1 reaching about to posterior margin of anal segment. Armature of legs very similar to that of *P. quasimodo* but slightly less strongly developed.

Male. Identical to *P. quasimodo* except for the lack of spinules on the genital segment.

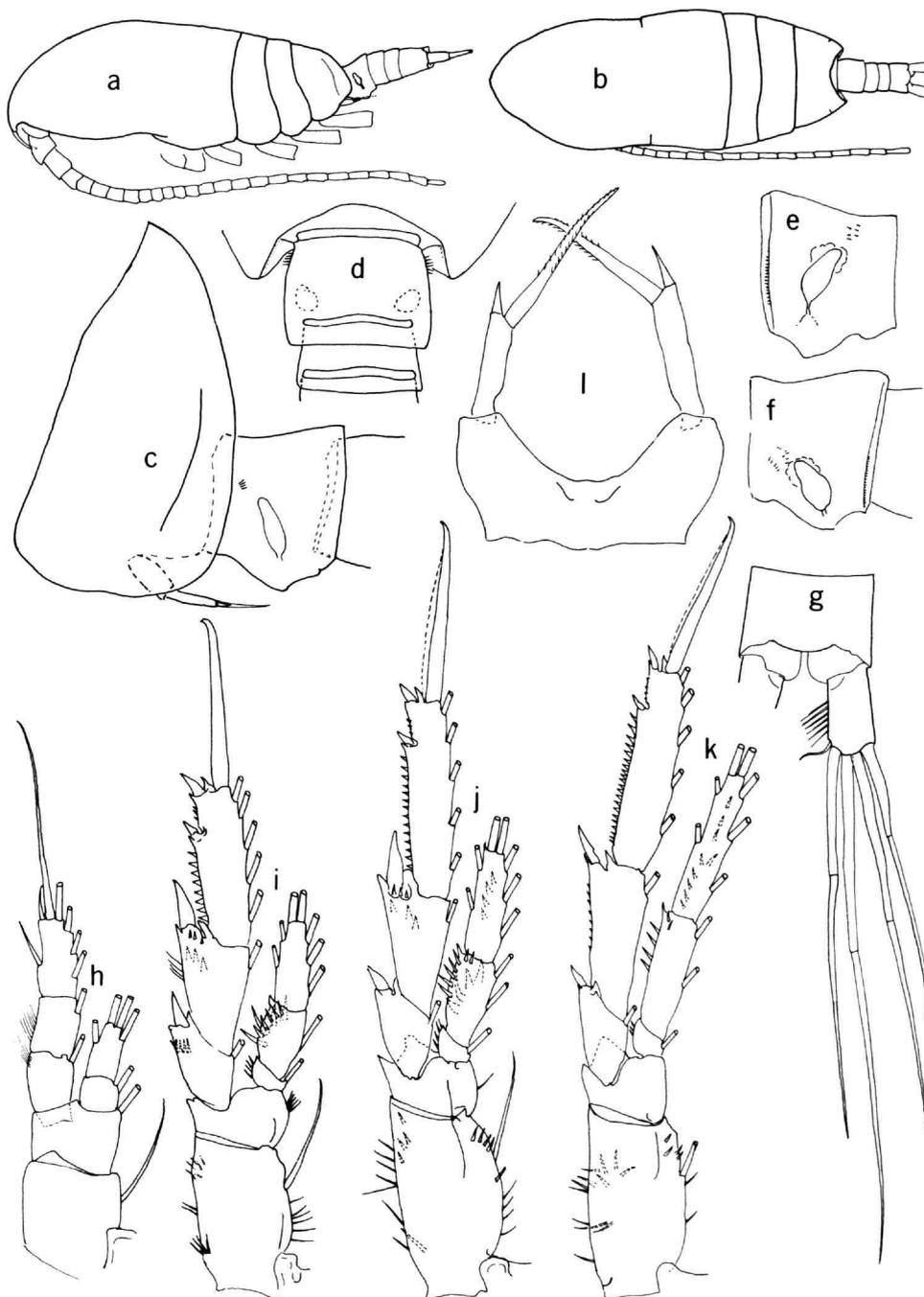


FIGURE 20.—*Paracalanus quasimodo*, new species, ♀: *a*, lateral view; *b*, dorsal view; *c*, 5th pedigerous and genital segments, lateral; *d*, same, dorsal; *e-f*, right and left sides of genital segment; *g*, anal segment and caudal rami, dorsal; *h-k*, legs 1-4.

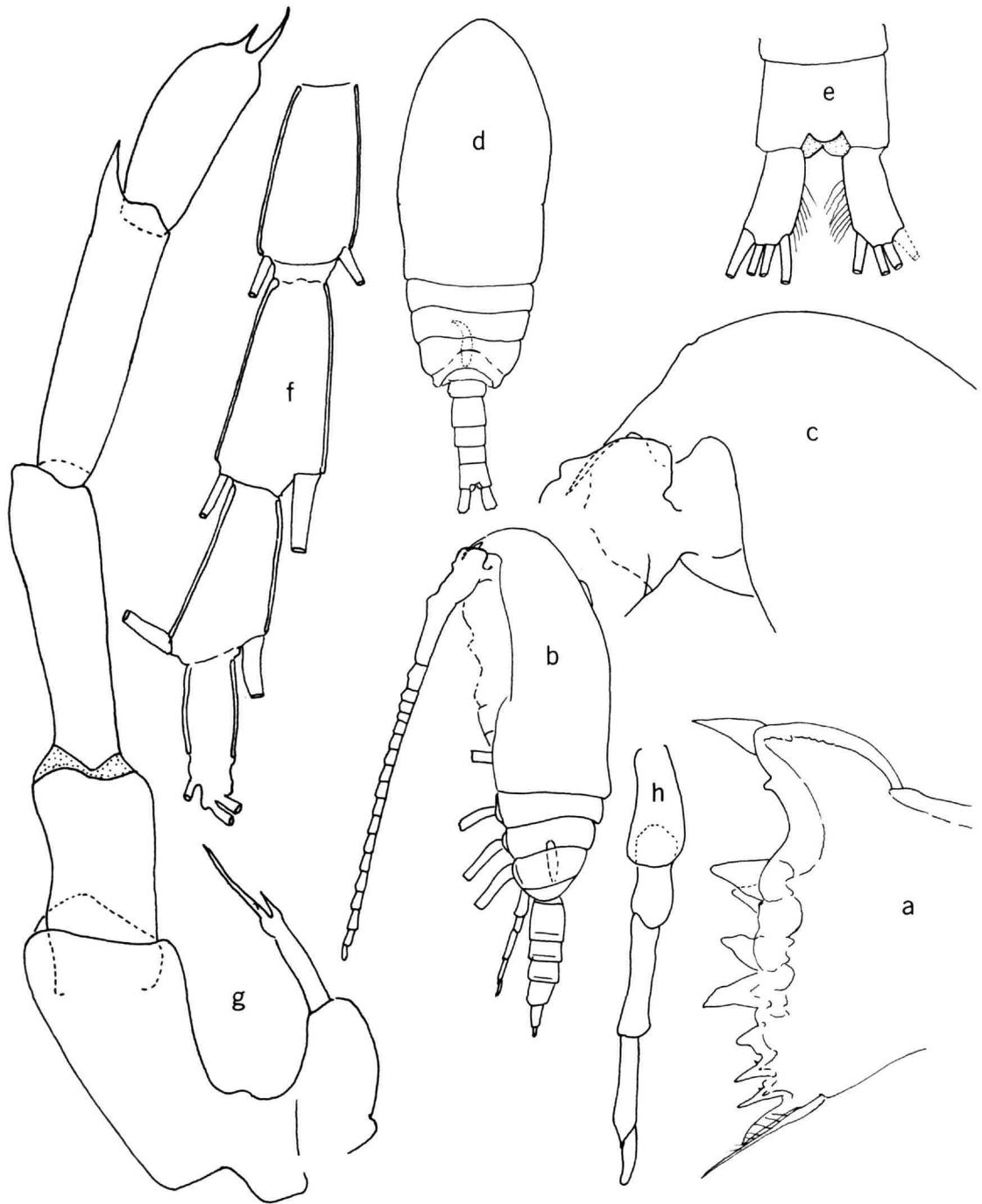


FIGURE 21.—*Paracalanus quasimodo*, new species: *a*, mandibular blade, ♀; *b–h*, ♂: *b*, lateral view; *c*, head and base of antenna 1, lateral; *d*, dorsal view; *e*, anal segment and caudal rami, dorsal; *f*, distal segments of antenna 1; *g*, leg 5, anterior; *h*, left leg 5, lateral.

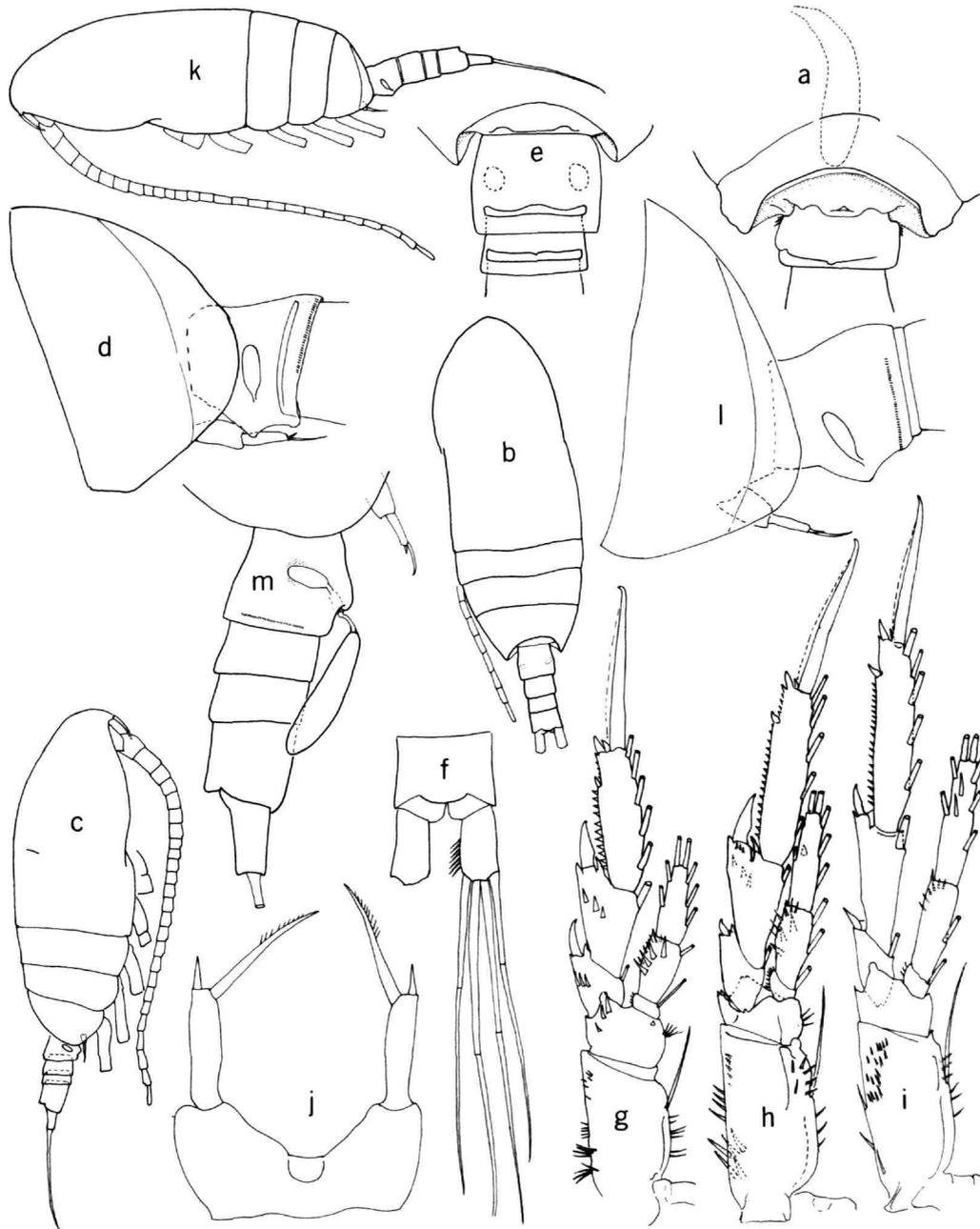


FIGURE 22.—*Paracalanus quasimodo*, new species, ♂: a, posterior prosome and genital segment, dorsal. *Paracalanus indicus*, ♀: b–j, from Gill Cruise 4, Station 35: b, dorsal view; c, lateral view; d, posterior prosome and genital segment, lateral; e, same, dorsal; f, anal segment and caudal rami, dorsal; g–j, legs 2–5. k–l, from Gulf of Naples: k, lateral; l, posterior prosome and genital segment, lateral. m, from Martinique, West Indies; urosome and spermatophore, lateral.

The *Gill* specimens are very similar to and perhaps conspecific with specimens from the Gulf of Naples collected for the Smithsonian Institution by Dr. L. S. Kornicker; a few illustrations of Dr. Kornicker's specimens are given for comparison (Figures 22*k-l*).

Wolfenden (1905) proposed his varieties *borealis* and *indicus* after comparing specimens from the Indian Ocean (Maldiva Archipelago) and the Faroe Channel with each other and with the descriptions and illustrations of Sars (1901, Norwegian specimens) and those of Giesbrecht (1892) and Scott (1894) from the Gulf of Naples and Gulf of Guinea respectively. If further study should show that the Indian Ocean and Mediterranean-Atlantic forms that Wolfenden considered identical are specifically distinct, the specific name *indicus* must be restricted to the Indian Ocean form. My use of the name *indicus* for the *Gill* species is tentative.

#### *Paracalanus parvus* (Claus)

FIGURES 23*b-p*

*Calanus parvus* Claus 1963:173, pl. 26: figs. 10-14; pl. 27: figs. 1-4.

*Paracalanus parvus* (Claus).—Boeck 1865:233q.—Sars 1901: 17-18, pls. 8-9.

In a plankton sample from the Gulf of Maine (Station 20056, south of Mt. Desert Island, 3 March 1920) are *P. parvus* group specimens that closely resemble those described by Sars. I have compared the Gulf of Maine specimens with specimens collected from the type-locality, Helgoland, kindly sent to me by Dr. Erik Hagmeir of the Meeresstation Helgoland, and there is close agreement. A few illustrations of the Helgoland specimens are given (Figures 23*n-p*) to show the similarity with Gulf of Maine *P. parvus*. This species was not found in the *Gill* collections, but for comparative purposes a brief diagnosis and some illustrations are given herein. It would be of considerable interest to know how far south its range extends before it is replaced by the two other *Parvus* group species.

DIAGNOSIS.—Female. Body slender, length 0.85-0.90 mm. Prosoma about 3.3-3.4 times as long as urosome, without dorsal hump. Forehead distinctly vaulted. Genital segment without spinules. Antenna 1 reaching to midlength of caudal ramus. Surface

armature of legs rather sparse, absent from 1st basal segment.

Male. Distinguished from the other two western Atlantic males in the *Parvus* group by the absence of spinules on the basal segments of the legs.

DISTRIBUTION OF *Gill Paracalanus* SPECIES.—*Paracalanus quasimodo* and *P. indicus* were not enumerated separately for Cruises 1-3 but were counted together as *Paracalanus parvus*. On Cruise 4 separate counts were made of the two species, and the result is shown in Figure 24. Although there is a slight indication that *P. indicus* is more likely to be found in the more oceanic stations, it is obvious that the two species usually occur together. The Fager-McGowan index of affinity for Cruise 4 is 0.821, higher than that of the combined species, *Paracalanus "parvus"* with any other species. The relative abundance of the two species varied markedly from station to station, but over the whole cruise area *P. quasimodo* was on the average about 3 times as numerous as *P. indicus*.

In view of the close association of the two species, I did not feel that the possible refinement of results justified my spending the considerable time that would be required to separate the species in Cruises 1-3 counts and to recalculate the affinity indices and to reconstruct the trellis diagrams.

*Paracalanus "parvus"* is a prominent member of the shelf association. In the cruise area it did not show much seasonal variation either in the extent of distribution or in abundance (Figure 24).

*Paracalanus aculeatus* is a common and abundant constituent of the oceanic association, but appears to be rather tolerant of shelf waters, for it may be found at all but the innermost stations of any cruise (Figure 25).

*Paracalanus crassirostris* is uncommon in the *Gill* samples, occurring at only a few inshore stations of each cruise (Figure 25). Its rarity may be due in part to its passing through the net because of its small size, but the distribution is in keeping with its known abundance in estuaries (references in González and Bowman 1965). Its abundance off the Florida coast during Cruise 3 and especially during Cruise 4 reflects the reduced salinity caused there by high runoff.

The species of *Calocalanus* are all oceanic. *C. pavo* is relatively common but never very abundant. *C. pavoninus* is much less common; it occurred at

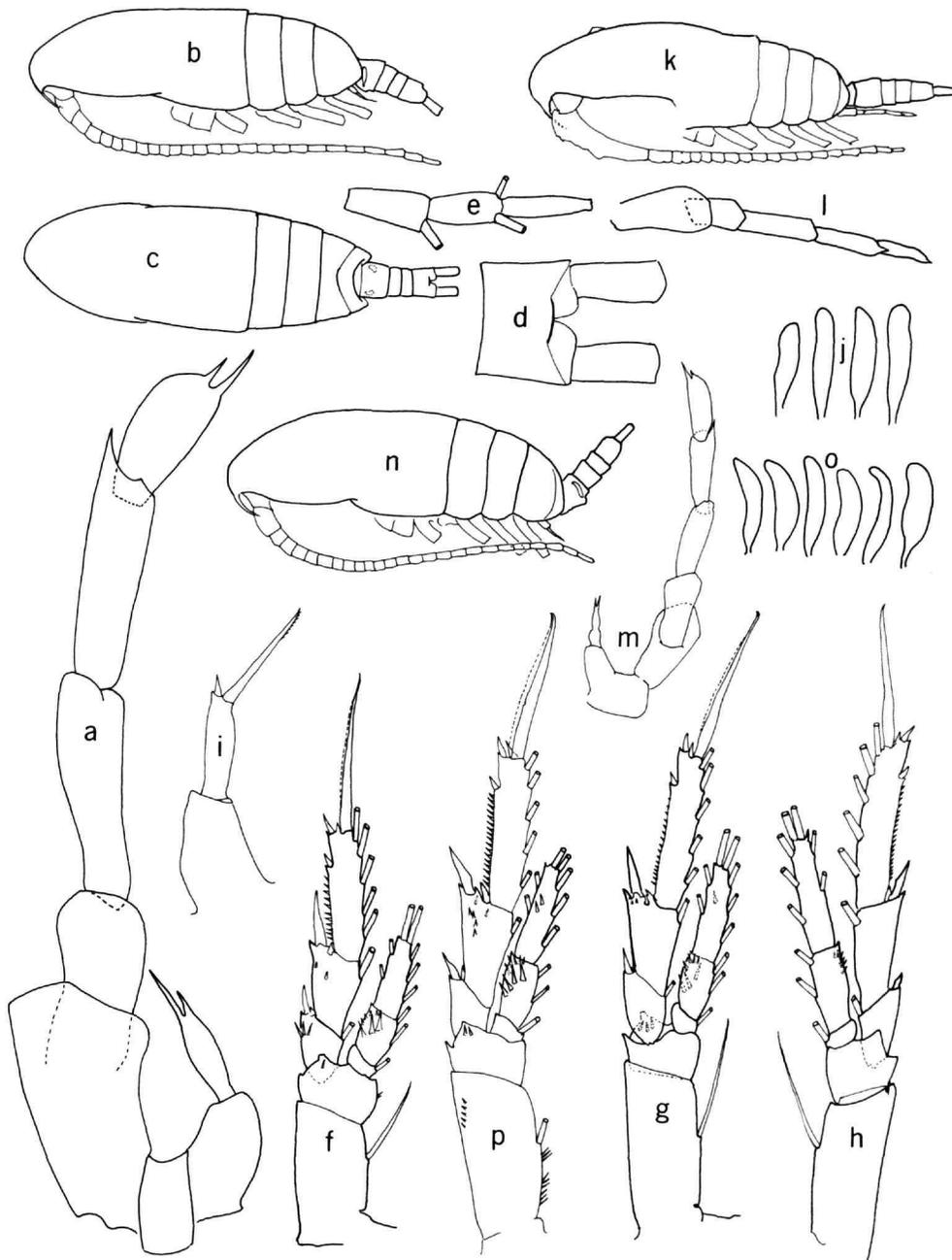


FIGURE 23.—*Paracalanus indicus*, ♂: a, leg 5. *Paracalanus parvus*, from Gulf of Maine, ♀: b, lateral view; c, dorsal view; d, anal segment and caudal rami, dorsal; e, distal segments of antenna 1; f-i, legs 2-5; j, spermathecae from different specimens; k-m; ♂: k, lateral view; l, left leg 5, lateral; m, leg 5. *Paracalanus parvus* from Helgoland, ♀: n, lateral view; o, spermathecae from different specimens; p, leg 3.

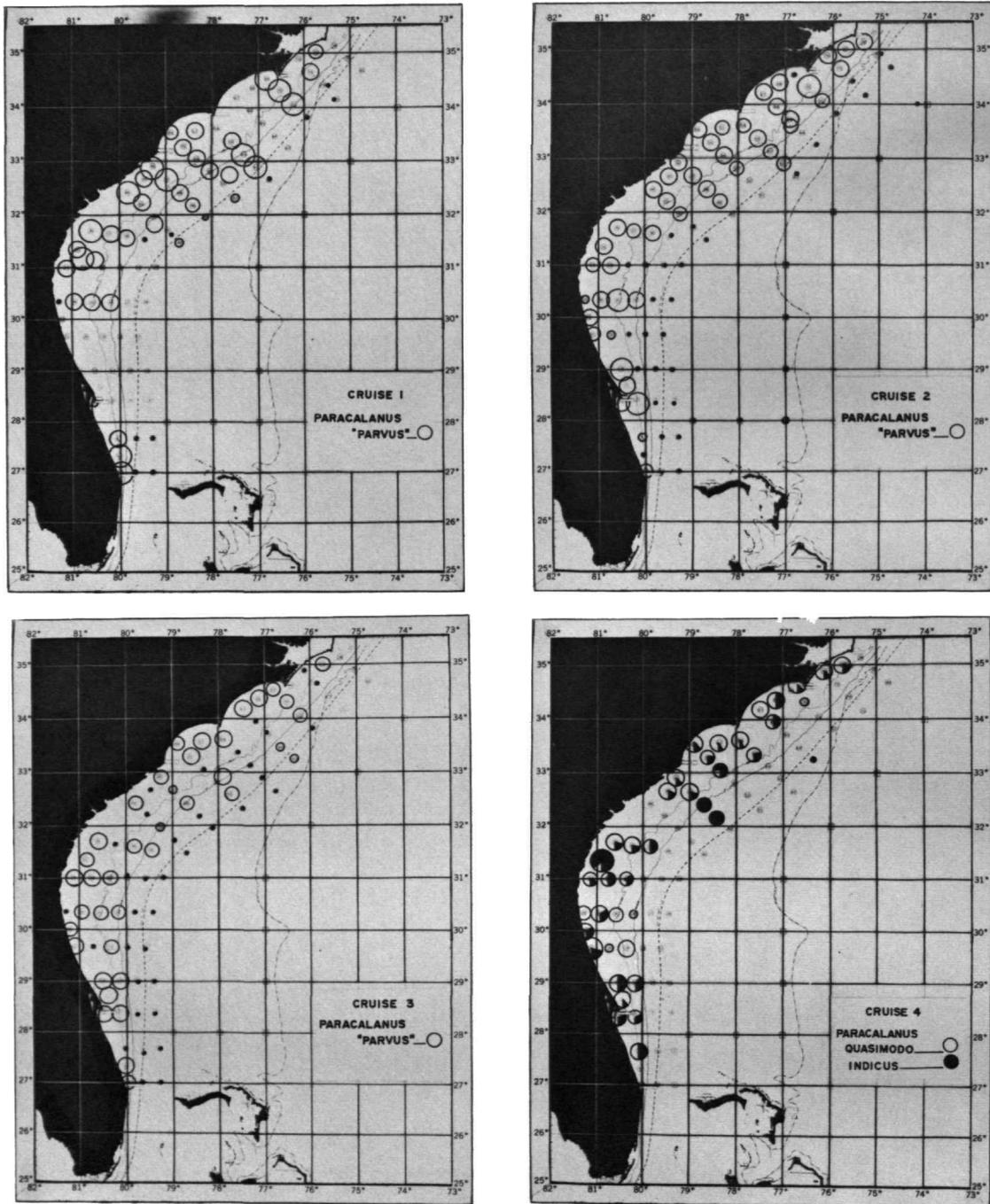


FIGURE 24.—Distribution of *Paracalanus* "parvus" (*P. quasimodo* + *P. indicus*), Cruises 1-4. Counts of the two species are combined on Cruises 1-3, separated on Cruise 4.

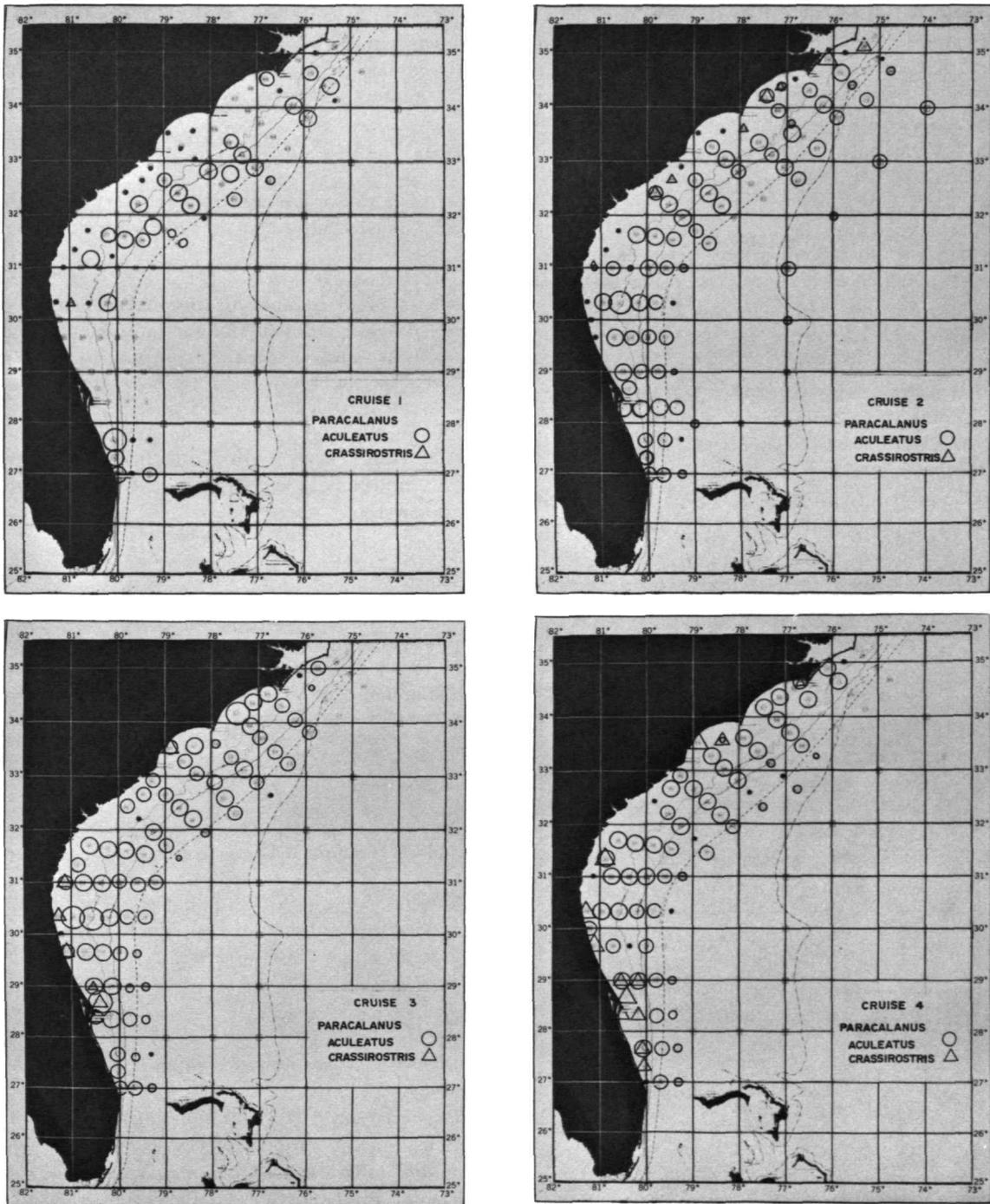


FIGURE 25.—Distribution of *Paracalanus aculeatus* and *P. crassirostris*, Cruises 1-4.

only slightly more than half as many stations and the average number per station was less than half that of *C. pavo*. The other four species were only rarely encountered. The distribution of all six species during Cruise 4 is shown in Figure 26 (qualitative only).

### Pseudocalanidae

When the *Gill* calanoids were being enumerated, Frost and Fleminger's (1968) revision of *Clausocalanus* had not appeared, and I was unable to identify with confidence any species of this genus except the distinctive *C. furcatus*. The following other species could occur in the *Gill* region, according to Frost and Fleminger: *C. arcuicornis*, *C. jobei*, *C. lividus*, *C. mastigophorus*, *C. parapergens*, *C. paululus*, and *C. pergens*.

*Clausocalanus furcatus* is one of the dominant species in the oceanic plankton. It occurs in large

numbers in oceanic waters and is found not infrequently in shelf waters (Figure 27).

*Ctenocalanus vanus* occurred sporadically in small numbers, generally in oceanic waters.

### Aetidae

*Euaetidius giesbrechti* occurred occasionally and in small numbers, always in oceanic waters (Figure 28).

The large-sized species of *Euchirella* and *Undeuchaeta* occur mainly at depths greater than those sampled by the *Gill* nets and are uncommon in the samples. As shown in Figure 29, the most frequently collected species of *Euchirella* was *E. amoena*, which was recorded from 16 stations in Cruises 1-4. Each of the other species of *Euchirella* and the two species of *Undeuchaeta* were found in only one to three samples. Both genera were strictly limited to oceanic waters.

### Euchaetidae

*Euchaeta marina* occurred in moderate to large numbers at most oceanic stations of all four cruises (Figure 30) and, because of its common occurrence and abundance, was selected as one of four indicator species for oceanic waters.

### Phaennidae

*Phaenna spinifera* occurred in small numbers at a few of the oceanic stations of each cruise (Figure 31).

*Xanthocalanus agilis* was found twice, at Station 27 of Cruise 2 and Station 7 of Cruise 4, both oceanic stations.

### Scolecithridae

*Lophothrix latipes* was found once, at Station 27 of Cruise 4.

*Scaphocalanus curtus* was found at three oceanic stations: Special Station 1 of Cruise 2 and Stations 52 and 53 of Cruise 4. *Scaphocalanus echinatus* did not occur in the Cruise 3 samples but was present at a total of 11 stations, all oceanic, during the other three cruises.

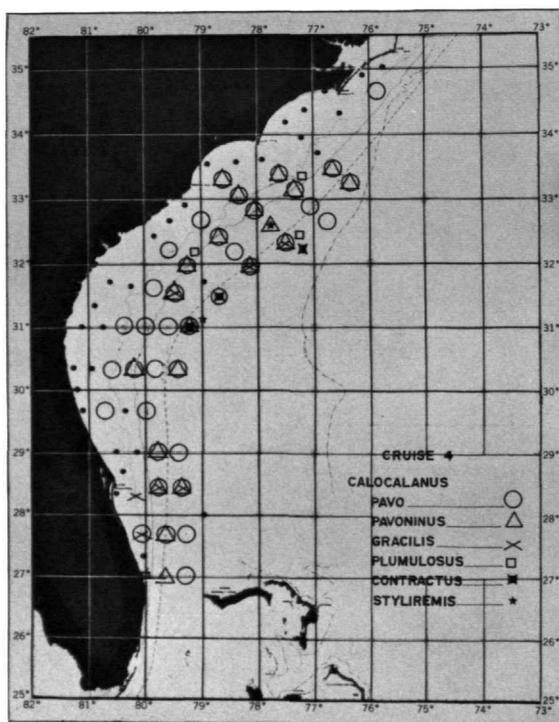


FIGURE 26.—Distribution of *Calocalanus* species, Cruise 4 (nonquantitative).

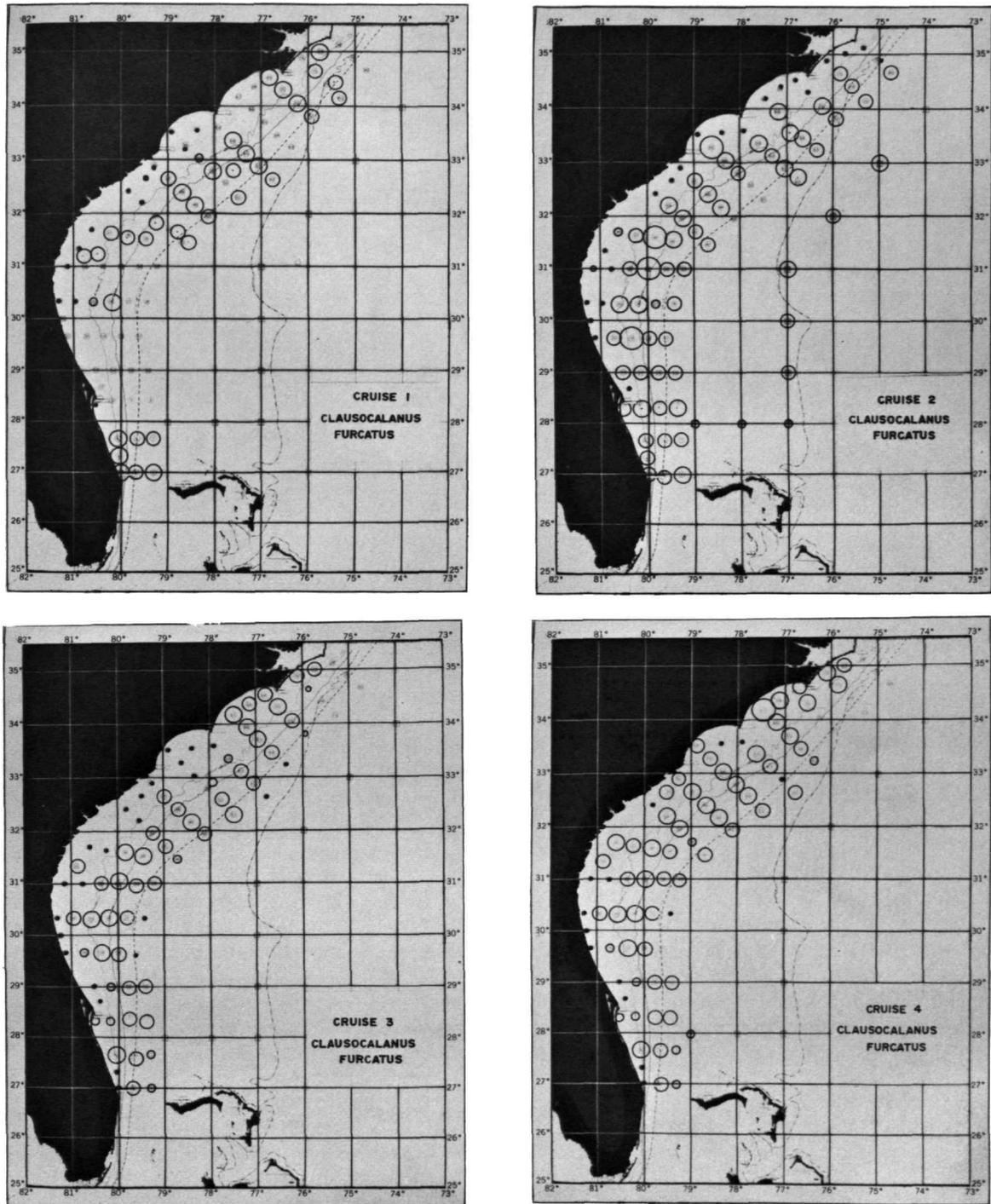


FIGURE 27.—Distribution of *Clausocalanus furcatus*, Cruises 1-4.

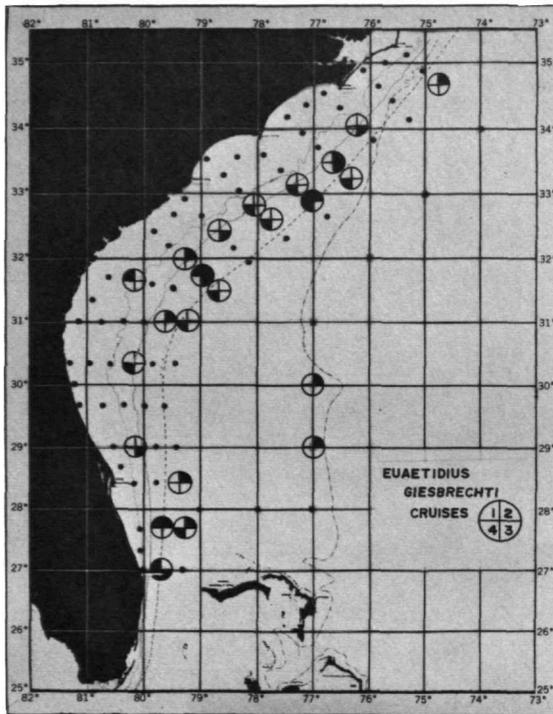


FIGURE 28.—Distribution of *Euaetidius giesbrechti*, Cruises 1-4 (nonquantitative).

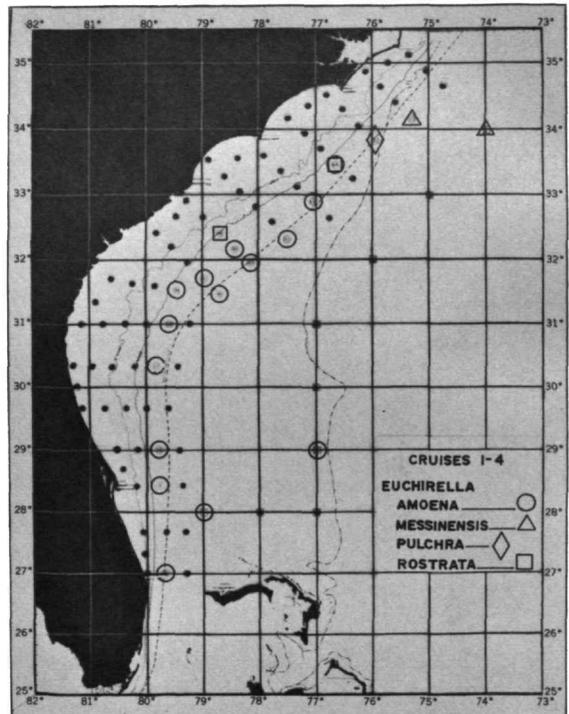


FIGURE 29.—Distribution of *Euchirella* species, Cruises 1-4 combined (nonquantitative).

*Scolecithrix danae* was a common and sometimes fairly abundant constituent of the oceanic plankton on all cruises. *Scolecithrix bradyi* was a much rarer and less abundant oceanic species (Figure 32).

The three species of *Scolecithricella* occurred sporadically and in small numbers, always at oceanic stations. *S. ctenopus* was the rarest of the three; it was not present in the Cruise 2 samples and was present at only four stations on each of the other cruises. *S. dentata* was somewhat more common and was taken on all four cruises. *S. tenuiserrata* occurred much more frequently than *S. dentata*. The occurrence of the three species on Cruise 4 is shown in Figure 33.

*Scottocalanus securifrons* was found once, on Special Station 5 of Cruise 2.

#### Temoridae

*Temora stylifera* and *T. turbinata* were widespread and abundant on all cruises (Figure 34). As shown

in the dendrograms and distribution charts, *T. turbinata* usually was more prevalent at inshore stations, whereas *T. stylifera* was more commonly found at the oceanic stations. *T. turbinata* might be classified as a shelf species that frequently occurs in oceanic waters, and *T. stylifera* as an oceanic species that frequently occurs in shelf waters. The two species differ in their seasonal abundance (Figure 35): *T. stylifera* occurred in greatest numbers in the winter and spring (Cruises 1 and 2); whereas *T. turbinata* was most abundant in the summer and fall (Cruises 3 and 4).

*Temoropia mayumbaensis* occurred at a very few stations, all in oceanic waters.

#### Metridiidae

Members of the genus *Pleuromamma* are noted for their vertical diurnal migrations (Moore and O'Berry 1957) and are usually found in samples collected at night. The occurrence of the four spe-

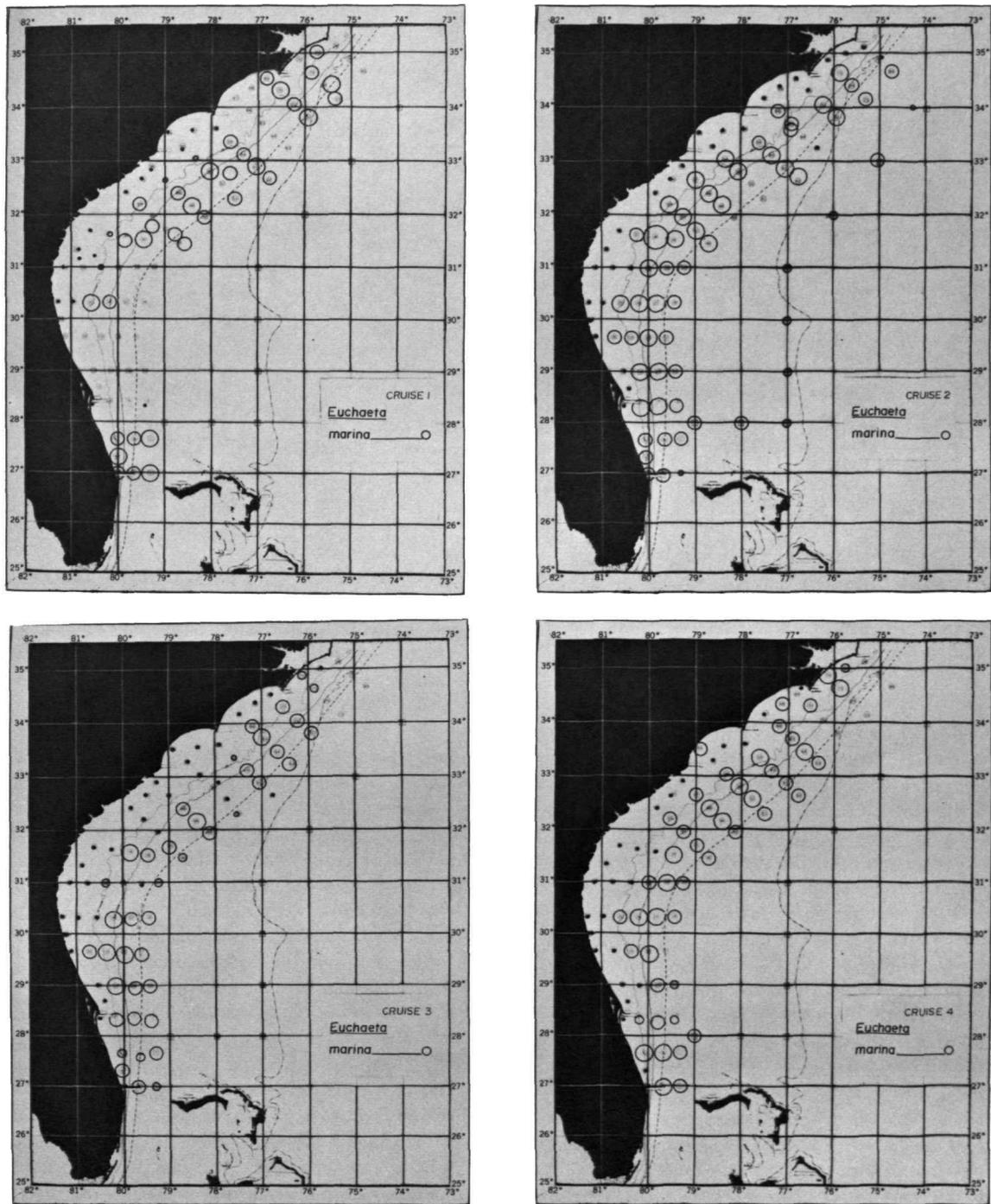


FIGURE 30.—Distribution of *Euchaeta marina*, Cruises 1-4.

TABLE 1.—Comparative abundance and sex ratios of *Pleuromamma gracilis* and *P. piseki*

Cruise	Station	No. of		
		<i>P. piseki</i>	<i>P. gracilis</i>	Females/males
I	1	4.3	5.0	2.5
	6	3.5	6.0	1.0
	7	2.8	4.5	1.7
	48	1.5	5.0	1.0
	50	2.3	3.5	3.0
	62	11.7	4.0	2.0
II	18	2.8	7.5	2.0
	27	2.0	5.0	5.0
	Spec. 1	1.5	7.0	1.1
	Spec. 5	3.6	3.5	1.5
III	5	3.0	5.0	5.0
	16	2.4	11.0	1.5
	17	3.3	No ♂	2.3
	50	5.5	33.0	No ♂
IV	6	3.6	3.8	0.7
	6	2.7	5.0	8.0
	7	6.3	1.0	0.4
	27	6.3	5.3	2.0
	40	2.9	5.7	2.5
	60	5.0	2.9	1.3
	61	4.6	2.3	4.0

FIGURE 31.—Distribution of *Phaenna spinifera*, Cruises 1-4 (nonquantitative).

cies during Cruises 1-4 in relation to time of day and the percent of oceanic indicator species is shown graphically in Figure 36. It is apparent that most of the occurrences were at oceanic stations, largely between 6 P.M. and 9 A.M. The few scattered occurrences during the day and at nonoceanic stations were *P. Abdominalis* and *P. gracilis*. Of the two large species, *P. abdominalis* occurred much more frequently and in larger numbers than *P. xiphias* (Figure 37).

*Pleuromamma gracilis* was much more common than the closely related *P. piseki*. The two species showed a marked difference in the proportion of males and females. In *P. gracilis* the females were always much more abundant than the males, whereas in *P. piseki* the sexes were much more nearly equal in number, with the females usually slightly more numerous (Table 1). The reason for the difference in sex ratio is not obvious. Owre and Foyo's (1967) data indicate that the two species live at similar depths, so that Mednikov's (1961)

evidence that the prevalence of females increases with the depth at which a calanoid species dwells cannot easily be applied. It is possible that in *P. gracilis* the sex ratio is similar to that of *P. piseki*, but most of the males remain below the upper 70 m sampled by the Gill. Moore and O'Berry's (1957) data show that the majority of the *P. gracilis* population is always below the Gill sampling depth, but provides no information on the proportion of males and females at different depths.

Difference in the male 1st antennae in the two species might be related to the difference in sex ratios. In *P. gracilis*, which has relatively fewer males, the esthetes are noticeably larger, perhaps because the *P. gracilis* males must do more searching for females than the *P. piseki* males. Other noteworthy differences in the geniculate 1st antennae are the more robust spines on fused segments 19-21, the coarser teeth in the spine-row of segments 18 and 19-21, and the much broader segments 14, 15, and 16 in *P. piseki* (Figure 38).

Because the two species have not always been distinguished by plankton workers, illustrations are given here of some of the structures that are useful in separating *P. gracilis* and *P. piseki*. In the male, in addition to the characters of the grasping antennae, the larger spermatophore in *P. piseki* is

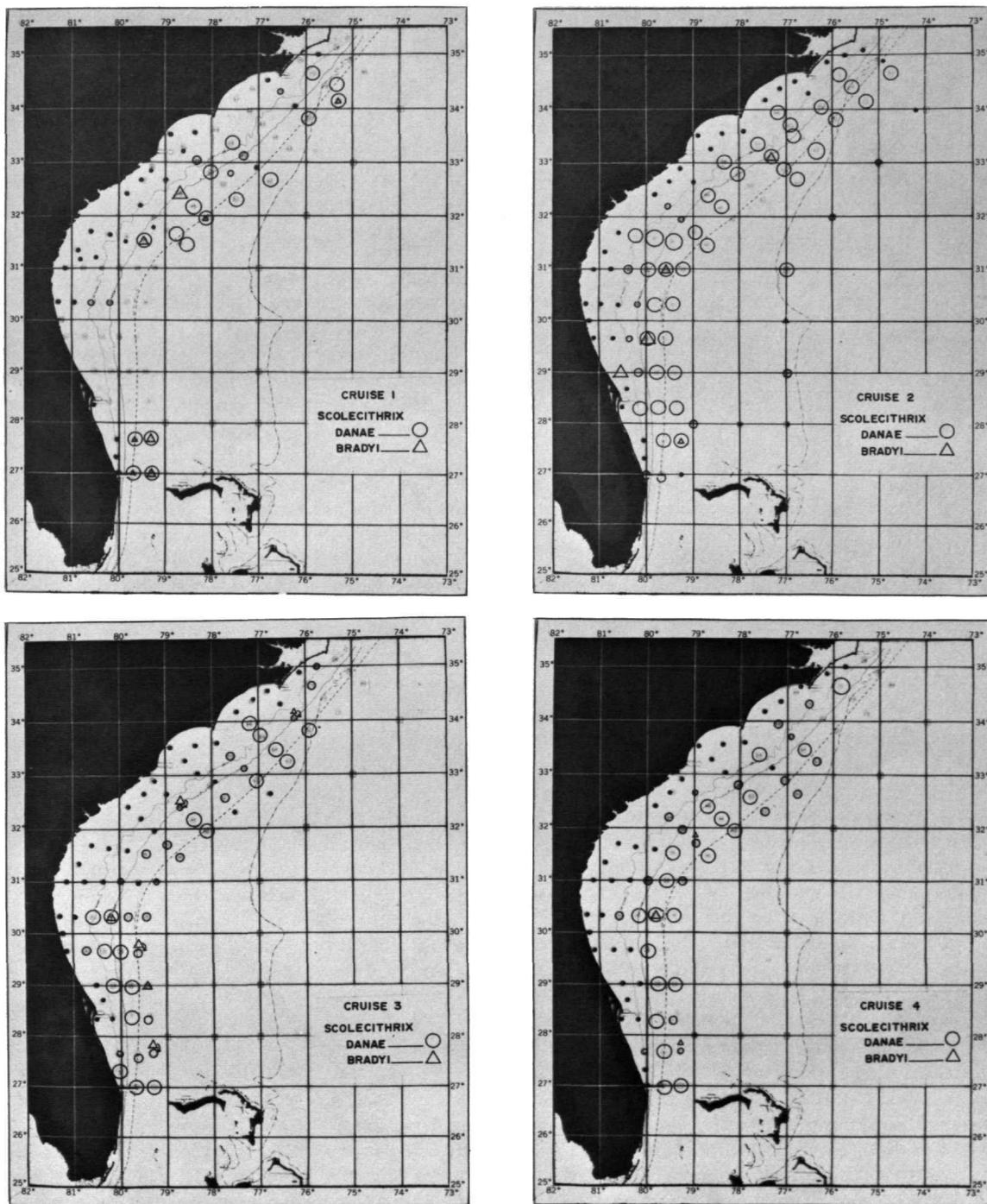


FIGURE 32.—Distribution of *Scolecithrix danae* and *S. bradyi*, Cruises 1-4.

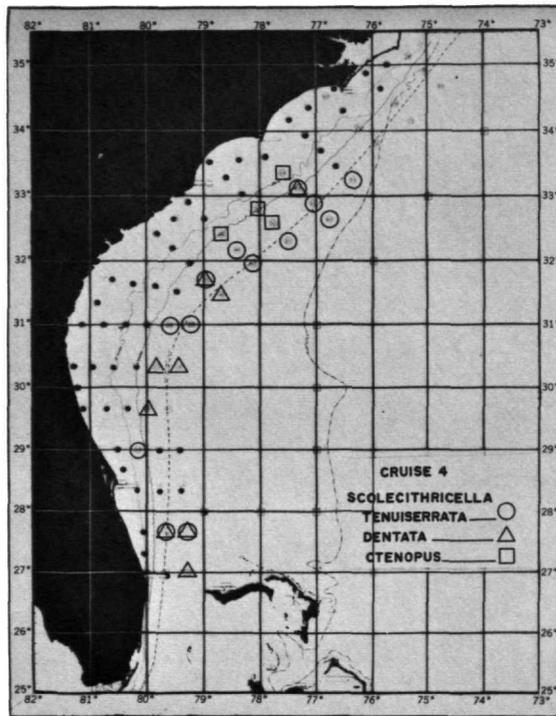


FIGURE 33.—Distribution of *Scolecithricella* species, Cruise 4 (nonquantitative).

helpful (Figures 38c,g). In *P. piseki* the spermatophore extends anteriorly beyond the anterior margin of the 3rd pedigerous somite, whereas in *P. gracilis* the spermatophore does not quite reach this margin. In the female the more divergent lateral margins of the anal somite in *P. gracilis* are usually emphasized. Males exhibit a similar but smaller difference (Figures 38d,h). The female 5th legs of the two species are similar, but differ in the relative lengths of the 3 terminal spines (Figures 39d,h). In *P. gracilis* the central spine extends beyond the others; in *P. piseki* the medial spine is the longest. Most useful for quick identification of the female is the genital somite. In *P. piseki* the dark pigment knob is usually apparent, and in profile the posterior margin of the genital swelling is more vertical. Viewed dorsally or ventrally, the shape of the spermatheca differs in the two species. In *P. gracilis* it is kidney-shaped (Figure 39e); in *P. piseki* it is asymmetrical, with a broad lobe on the right side in the posterior half (Figure 39b).

As Steuer (1932) clearly showed, the numerical dominance of *P. gracilis* over *P. piseki* in the area sampled by the *Gill* does not hold in all regions where the two species occur together. For example, Deevey (1964), in her study of variations in length of calanoids sampled near Bermuda, used *P. piseki*, but not *P. gracilis*.

### Centropagidae

*Centropages typicus* occurred at a few of the northernmost stations, near Cape Hatteras, in Cruises 1, 2, and 4 (Figure 40). It is not a normal inhabitant of Carolinian Coastal water, but is one of the dominant species of Virginian Coastal water, especially during the winter and spring (Bigelow and Sears 1939; Van Engel and Tan 1965). Its presence is an indication of the movement of coastal water from the north around Cape Hatteras, which normally serves as a natural barrier between the two coastal plankton faunas.

*Centropages hamatus* occurred only at ten inshore stations of Cruise 1. The calanoid fauna at these stations was dominated by *Paracalanus "parvus"* or *Acartia tonsa*, or both. As pointed out by Deevey (1960), *Centropages hamatus* has an unusually wide latitudinal range, and its seasonal occurrence varies with latitude. In the Gulf of Maine it occurs primarily from late summer to winter (Bigelow 1926), but south of Cape Cod it is a winter-spring species (Deevey 1960; Van Engel and Tan 1965; Grice 1956; Jacobs 1969), and in the *Gill* samples it was not found at other seasons.

*Centropages furcatus* was one of the most common and abundant shelf species.

*Centropages violaceus* was limited to oceanic water. It was fairly common but always occurred in small numbers.

### Pseudodiaptomidae

*Pseudodiaptomus coronatus* was found only once, at Station 56 of Cruise 1, a station close to shore in Long Bay, South Carolina, occupied just after midnight. *P. coronatus* is a typical estuarine species (Cronin et al. 1962; Jacobs 1961, 1969) and is not fully planktonic, since it is capable of clinging firmly to the substrate and often does in laboratory culture (Jacobs 1961). It tends to remain near or

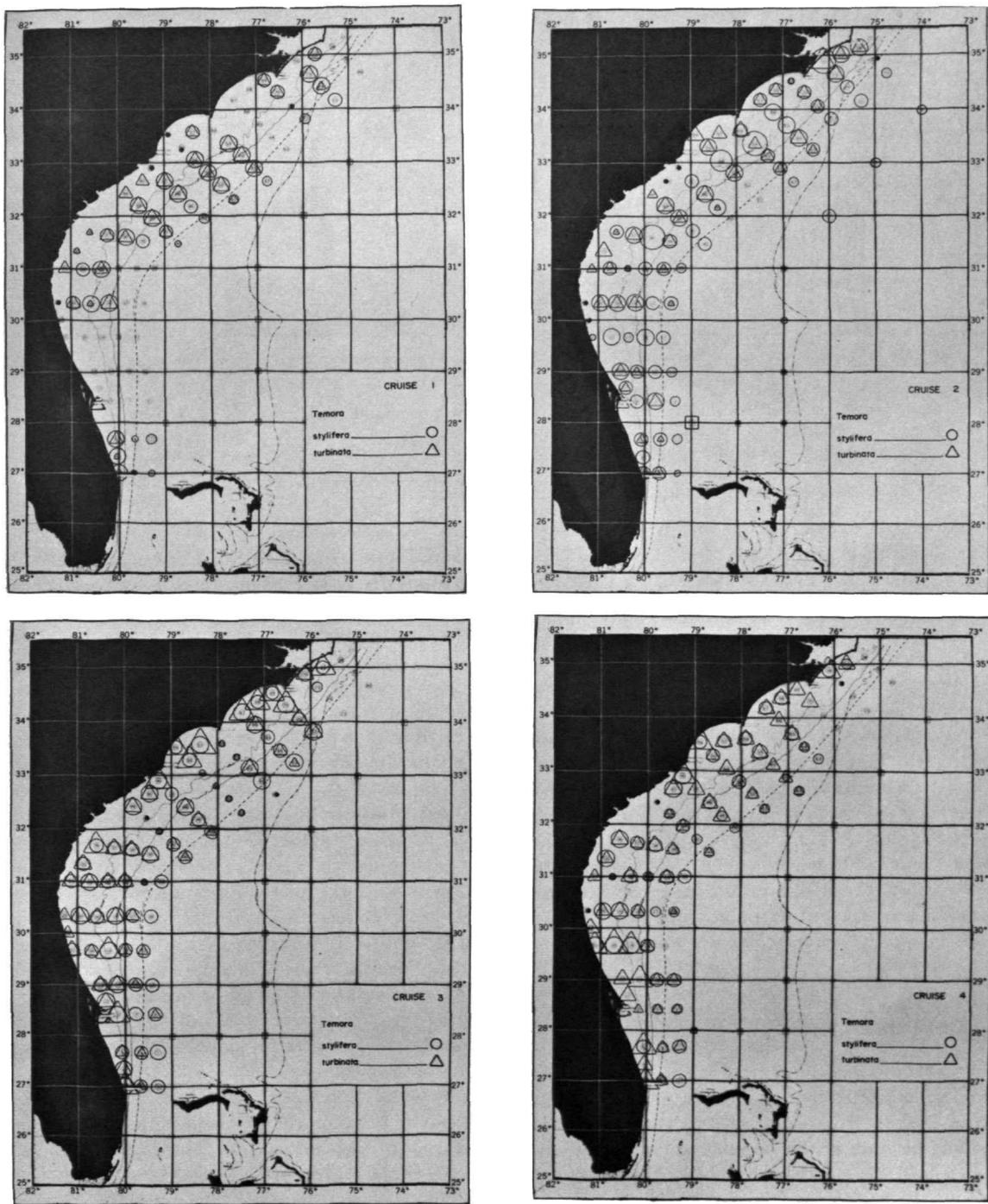


FIGURE 34.—Distribution of *Temora stylifera* and *T. turbinata*, Cruises 1-4.

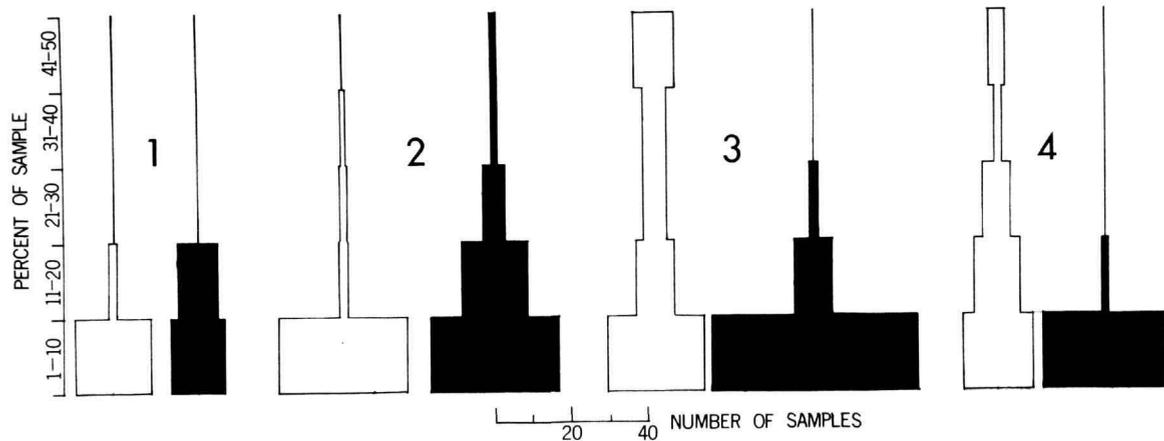


FIGURE 35.—Relative abundance of *Tempora stylifera* (black) and *T. turbinata* (white), Cruises 1-4. Width of bar represent number of samples in which a species formed a particular percentage, in steps of 10% of the sample.

on the bottom during the day and is taken in surface collections mainly at night.

#### Lucicutiidae

Both species of *Lucicutia* encountered had oceanic distributions, but *L. flavicornis* was far more abundant than *L. gausae* and occurred at many more stations (Figure 41). Because of its abundance *L. flavicornis* was one of the species for which affinity indices were computed. It was clearly a member of the oceanic association but, as can be seen in the trellis diagrams (Figures 5-6), consistently had the lowest affinity indices with other oceanic species of any member of the association. A rather striking suctorian was attached to the urosome of a number of specimens of *L. gausae* but was found only once on *L. flavicornis*.

#### Heterorhabdidae

*Heterorhabdus papilliger* was fairly common but never abundant at the oceanic stations of all four cruises (Figure 42). As suggested by Owre and Foyo (1967), the bulk of the population of this species lives below the depth sampled by the Gill and moves toward the surface at night.

Owre and Foyo (1967) found that *H. spinifrons* (Claus) was about as abundant as *H. papilliger* at

their "40 mile station" (about 40 miles east of Miami, Florida, in the Florida Current), but I have not found *H. spinifrons* in the Gill samples. Specimens that I originally thought were *H. spinifrons* proved upon close examination to be specimens of *H. papilliger* in which the rostrum was sharply pointed rather than bluntly rounded. Specimens with blunt rostrums and with sharp rostrums occurred together in the same sample and agreed in all characters except the rostrum. (Figure 43b shows the exopod of the right 5th leg of a male with pointed rostrum; this leg is typical for *H. papilliger*). This is a rather disturbing discovery, since the keys to the species of *Heterorhabdus* in many widely used works on calanoids are so constructed that the sharp-rostrum individuals of *H. papilliger* will key out to *H. spinifrons*. Hence persons making routine identifications of planktonic copepods and using such keys could easily be misled. Works containing such keys are those of Giesbrecht and Schmeil (1898), Esterly (1905), Wilson (1932), Rose (1933), Brodsky (1950), and Owre and Foyo (1967). A more reliable separation of the two species can be based on the relative lengths of the setae on the distal segments of the 2nd maxillae. In *H. papilliger* the 2 large setae of the penultimate lobe are subequal, and the more distal seta, like that of the terminal segment, is armed with rather coarse spinules. In *H. spinifrons* the distal seta of the

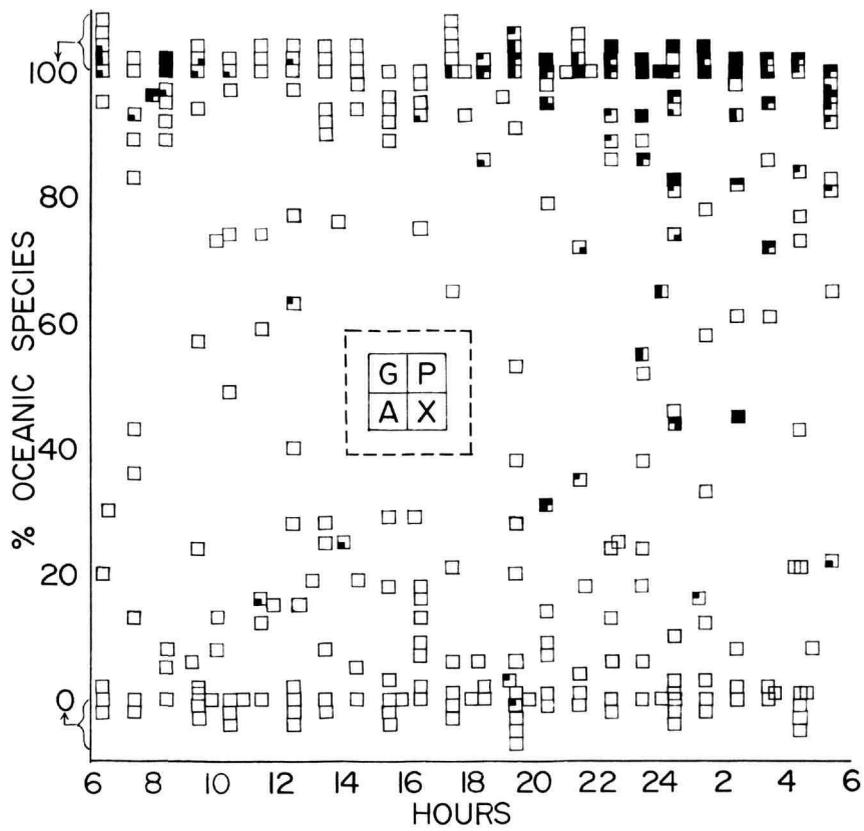


FIGURE 36.—Occurrence of *Pleuromamma* species, Cruises 1-4, in relation to time of day and percent of oceanic indicator species. Each square represents a station; occurrence of a species at a station is shown by solid black in its fourth of the square. G = *P. gracilis*, P = *P. piseki*, X = *P. xiphias*, A = *P. abdominalis*.

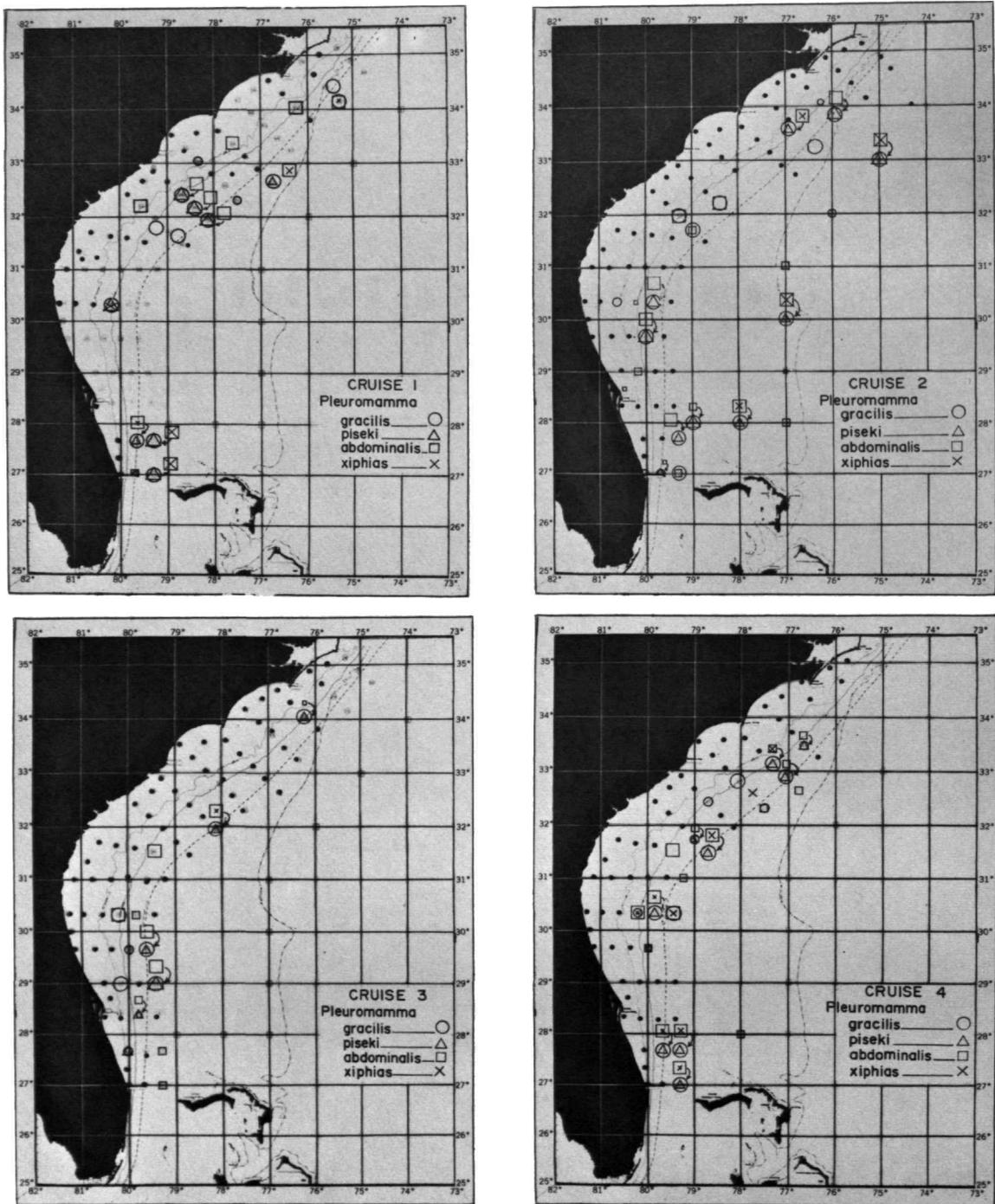


FIGURE 37.—Distribution of *Pleuromamma* species, Cruises 1-4.

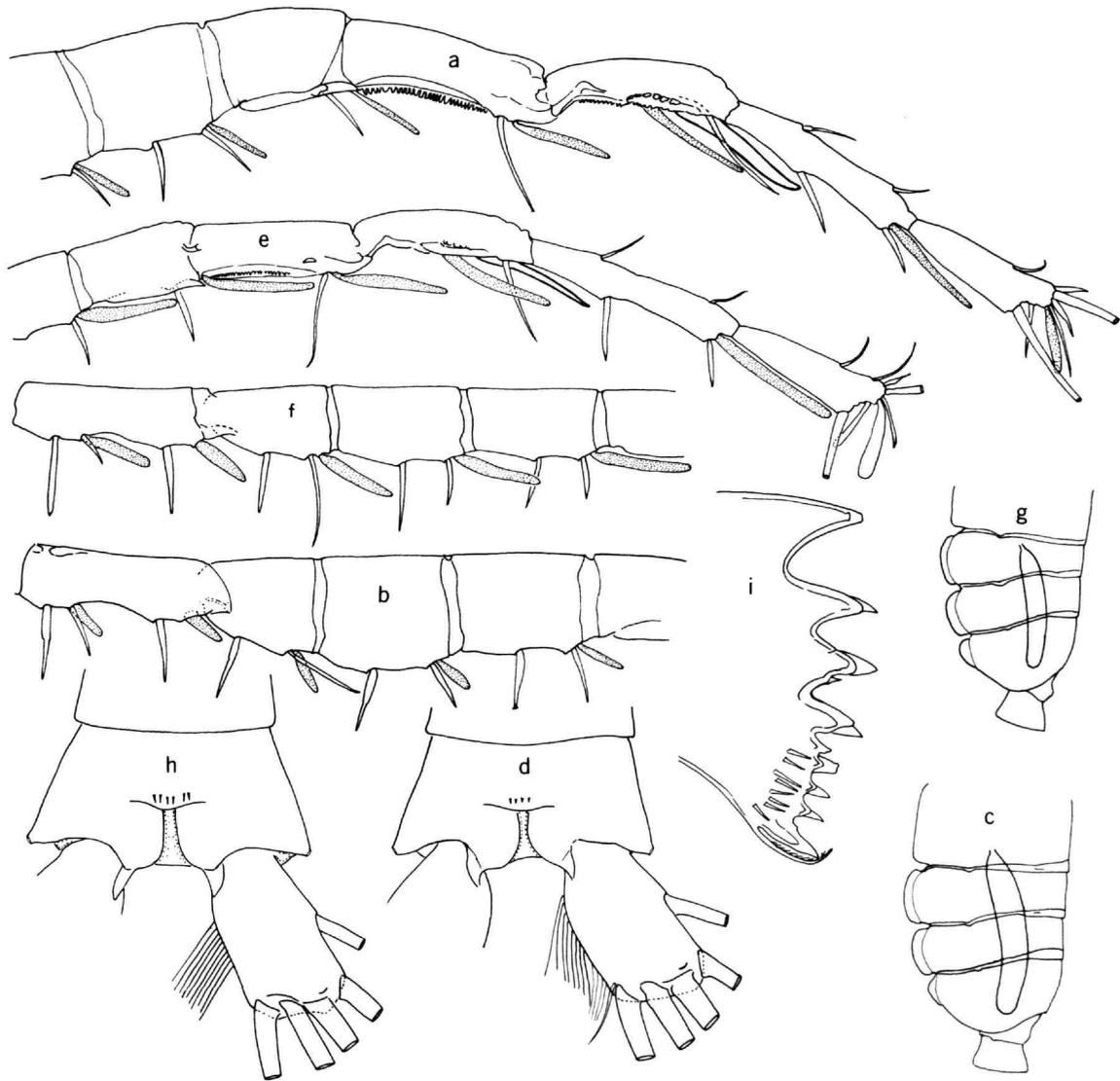


FIGURE 38.—*Pleuromamma piseki*, ♂: *a*, distal segments of left antenna 1; *b*, segments 13–16 of left antenna 1; *c*, posterior segments of prosome, lateral, showing position of spermatophore; *d*, anal segment and caudal ramus, dorsal. *Pleuromamma gracilis*, ♂: *e*, distal segments of left antenna 1; *f*, segments 13–16 of left antenna 1; *g*, posterior segments of prosome, lateral, showing position of spermatophore; *h*, anal segment and caudal ramus, dorsal; *i*, mandibular blade.

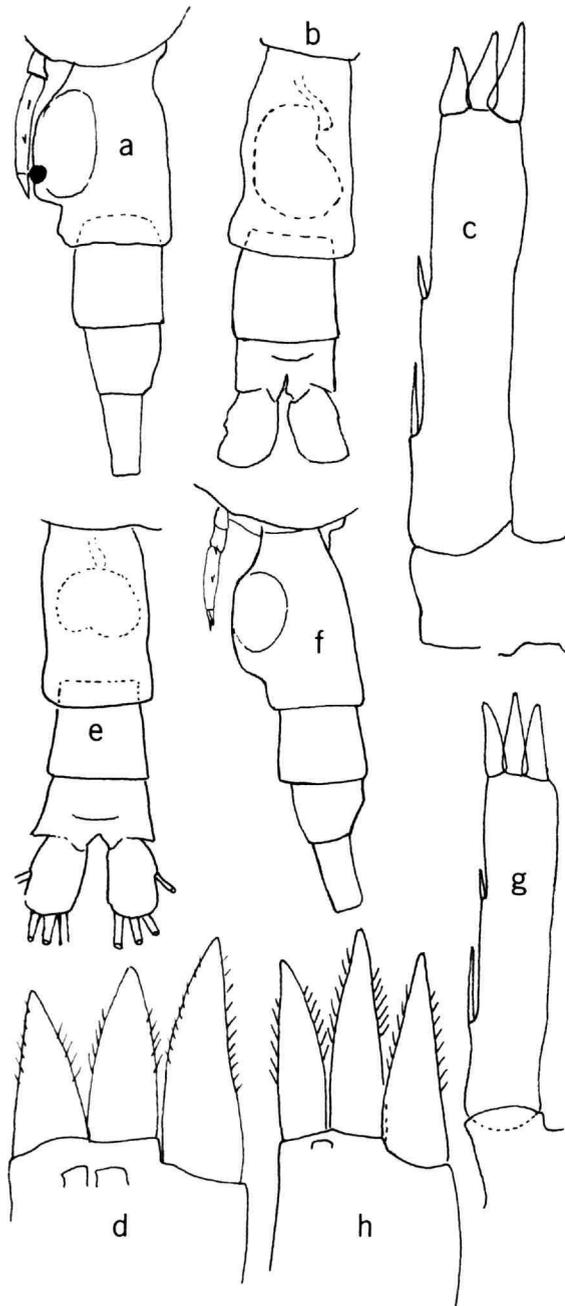


FIGURE 39.—*Pleuromamma piseki*, ♀: a, urosome, lateral; b, urosome, dorsal; c, leg 5; d, leg 5, terminal spines. *Pleuromamma gracilis*, ♀: e, urosome, dorsal; f, urosome, lateral; g, leg 5; h, leg 5, terminal spines.

penultimate lobe is noticeably longer than the proximal seta, and it is armed with much finer and more closely set spinules than the seta of the terminal segment. On the antepenultimate lobe the medial seta is more than half as long as the other two setae in *H. papilliger*, but much less than a fourth as long in *H. spinifrons*. These features are shown in Figures 43c–d in which the setae are drawn more widely separated than in their natural position so that their relative sizes can be easily compared.

Park's (1970) *Heterorhabdus spinifer* appears to be identical with the pointed rostrum form of *H. papilliger*. Park states that, in addition to the pointed rostrum, *H. spinifer* is distinguished by the absence of an inner seta on the 1st segment of the endopod of the female 5th leg, and by the "characteristic internal projection on the second exopodal segment of the [male] right leg." A comparison of Giesbrecht's (1892) Plate 20: figures 33–35 of *H. papilliger* and Park's (1970) Figure 237 of *H. spinifer* does not reveal any significant difference in the male 5th legs, and the absence of a single seta on the female 5th leg is of questionable significance at the species level. Despite my respect for Park's accuracy and taxonomic judgment I must question the validity of *H. spinifer* until more convincing evidence can be presented.

#### Augaptilidae

Three species of *Haloptilus* occurred in the *Gill* samples, all strictly limited to oceanic water (Figure 44). *H. longicornis*, the most common, was found in small numbers at a moderate number of stations on each cruise. The bulk of the population probably lives below the depth sampled by the *Gill* (Roehr and Moore 1965). *H. spiniceps* occurred at a few stations of Cruises 2, 3, and 4 but was not found in the Cruise 1 samples. Only a single specimen of *H. oxycephalus* was identified, from Cruise 2, Station 8.

#### Arietellidae

One specimen of *Arietellus setosus* was found, at Station 7 of Cruise 2.

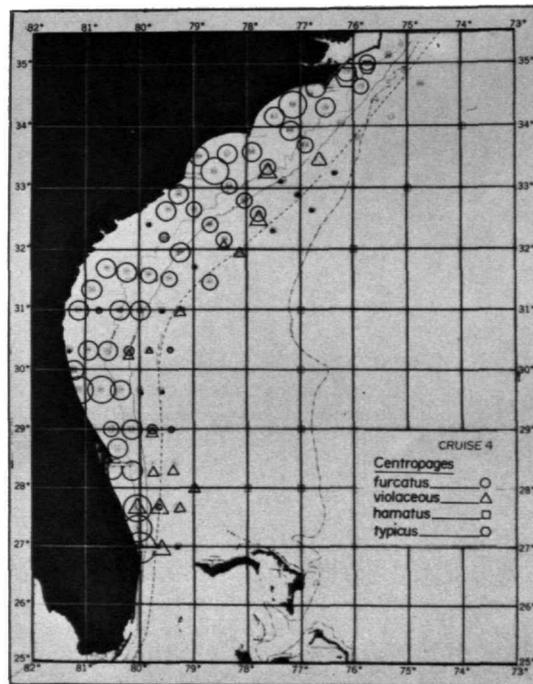
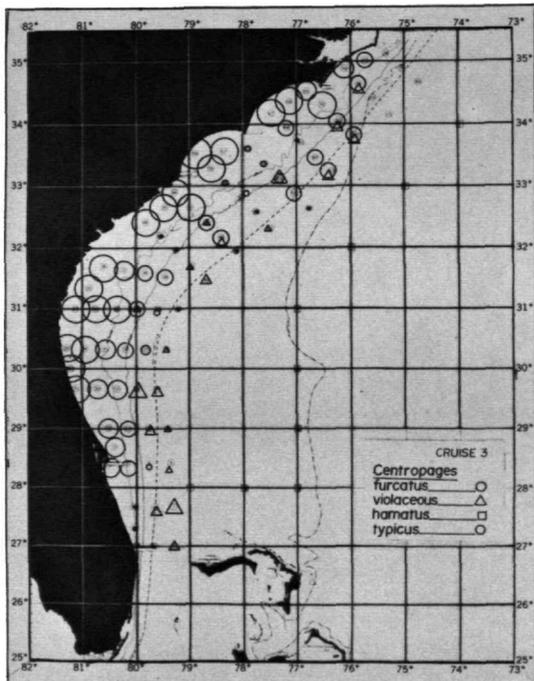
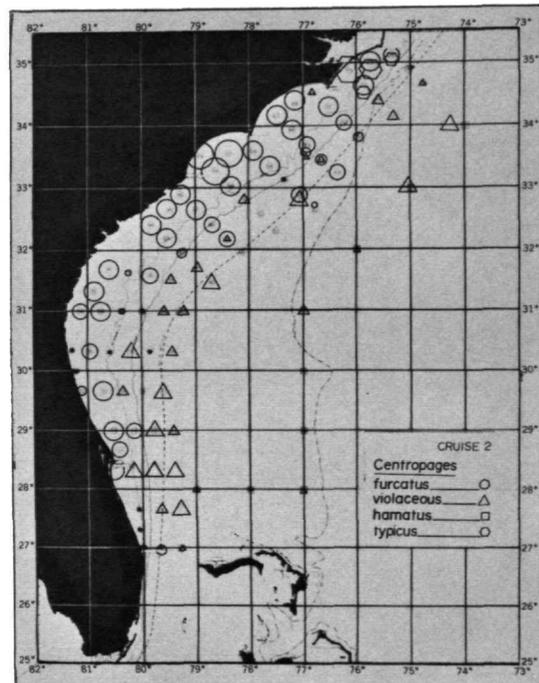
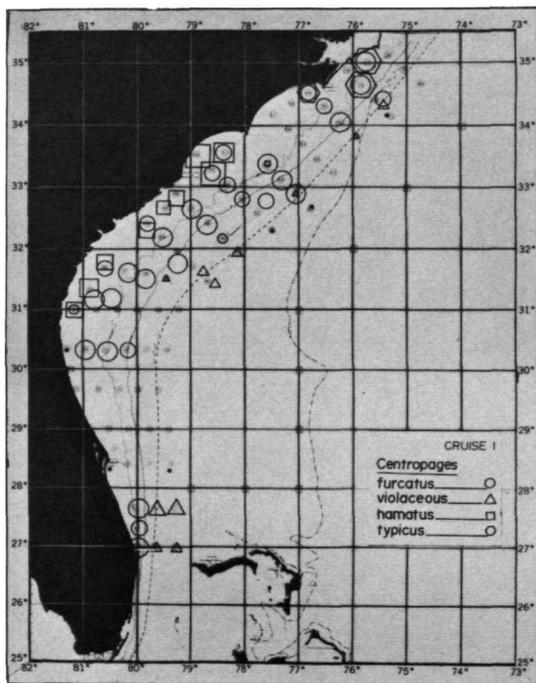
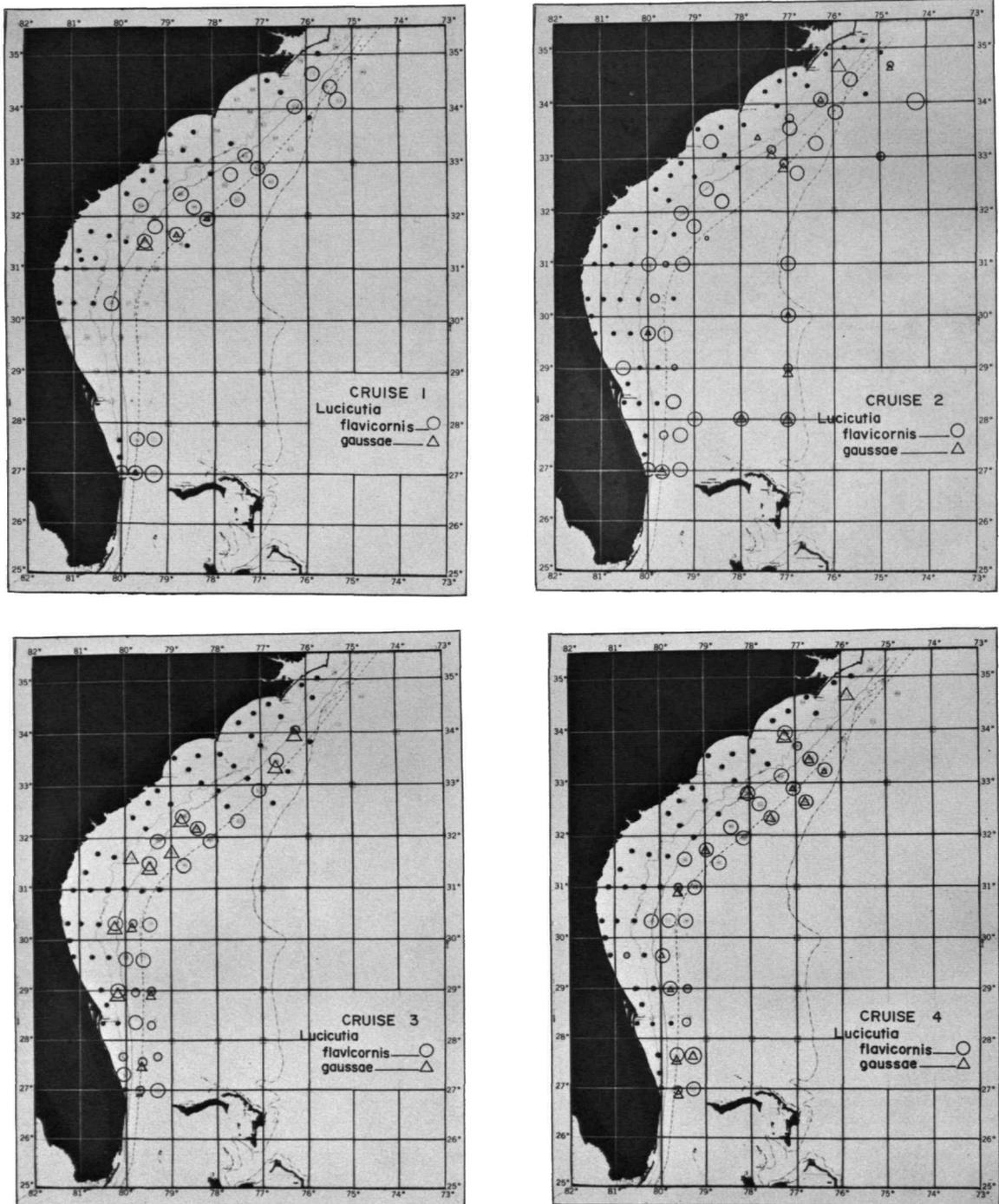


FIGURE 40.—Distribution of *Centropages* species, Cruises 1-4.

FIGURE 41.—Distribution of *Lucicutia flavicornis* and *L. gausae*, Cruises 1-4.

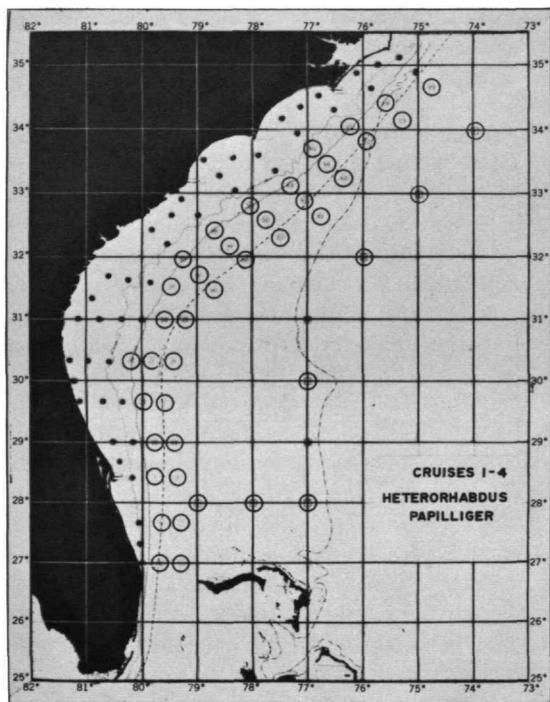


FIGURE 42.—Distribution of *Heterorhabdus papilliger*, Cruises 1-4 combined (nonquantitative).

### Candaciidae

A brief discussion of species of *Candacia* in the area sampled by the *Gill* is given by Fleminger and Bowman (1956), but these remarks were based on only Cruise 1.

All seven of the species of *Candacia* in the *Gill* samples were limited to oceanic water (Figure 45). *C. curta* and *C. pachyactyla* were encountered fairly frequently, always in small numbers; the other species were usually found at not more than three stations of any cruise.

Both species of *Paracandacia* also were found only at the oceanic stations (Figure 46); *P. bispinosa* occurred slightly more frequently than *P. simplex*, but the difference may not be significant, since I did not distinguish the very similar immature stages of the two species.

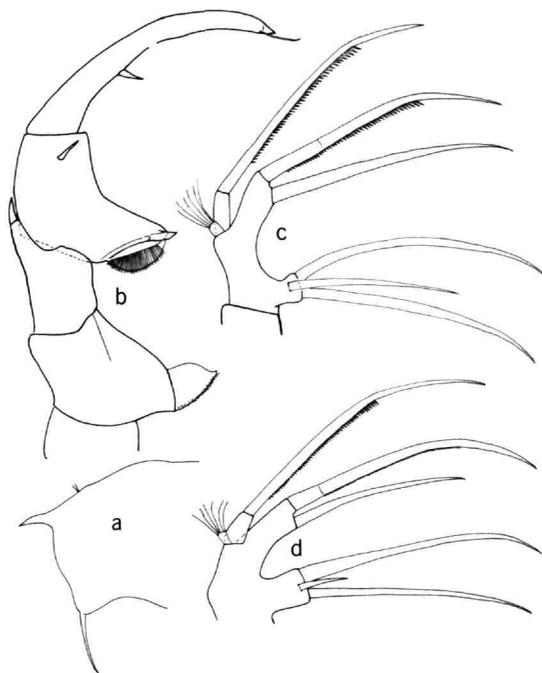


FIGURE 43.—*Heterorhabdus papilliger*: a, head of ♂ with pointed rostrum, lateral; b, exopod of right leg 5 from same specimen; c, distal end of ♀ maxilla 2. *Heterorhabdus spinifrons*, ♀, from Bache Station 10209 (near *Gill* special Station 8): d, distal end of maxilla 2.

### Pontellidae

*Anomalocera ornata* was collected at six stations of Cruise 1 and three stations of Cruise 3, all of them coastal stations with bottom depths not greater than 36 m (Figure 47). It is probably more abundant and widespread than is apparent from the *Gill* collections, since *A. ornata* presumably lives close to the surface like its northern relative, *A. patersoni* (Bigelow 1926), and is not adequately sampled by oblique tows.

*Calanopia americana* had a rather unusual distribution (Figure 47). In the summer and fall (Cruises 3 and 4) the largest populations were at inshore stations, with smaller numbers farther out on the shelf and even at some of the oceanic stations. In the winter and spring (Cruises 1 and 2) it was less common overall and occurred mainly well out on the shelf. The overall distribution of

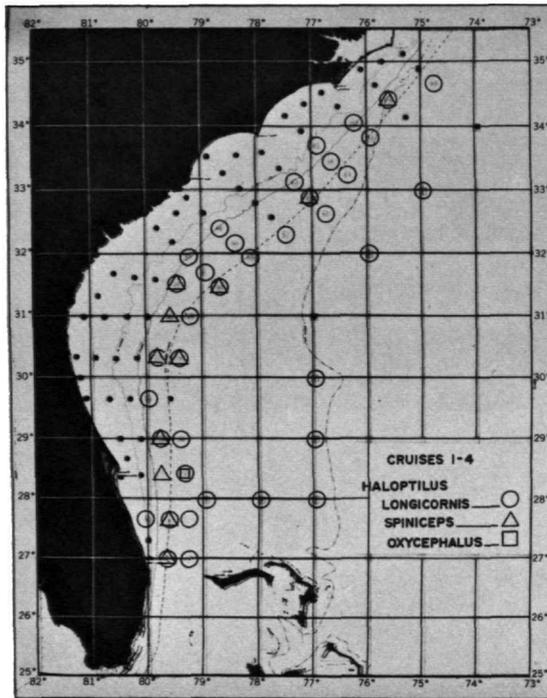


FIGURE 44.—Distribution of *Haloptilus* species, Cruises 1-4 combined (nonquantitative).

*C. americana*, summarized by González and Bowman (1965) and by Owre and Foyo (1967), shows it to be a tropical and subtropical species, ranging from Cape Hatteras to southern Brazil, principally in coastal waters but sometimes offshore. It could be postulated that along the United States coast south of Cape Hatteras it moves offshore into warmer water as the temperature drops seasonally. Such a migration by a planktonic copepod only about 1.5 mm long and supposedly at the mercy of ocean currents is not very likely. In St. George's Harbor, Bermuda, *C. americana* stays on the bottom during the day and probably burrows into the mud (Clarke 1934). Just before sunset it begins an upward migration and occurs in the plankton throughout the night. In Puerto Rico and the Lesser Antilles, González and Bowman (1965) reported that *C. americana* was collected in nets towed at night but not during the day.

Figure 48 shows the distribution of stations at which *C. americana* was found in relation to the

time of day when the stations were occupied. In this graph the data of Cruises 1-4 are combined and the day is divided into 2-hour intervals. In general, *C. americana* occurred most frequently around the middle of the night but, in contrast to its behavior at Bermuda, was present in the plankton at all hours. Owre and Foyo (1967) also found it in their Florida Current, 40-mile station during the day, although in smaller numbers than at night. No explanation for the difference in behavior is offered here, but I might point out that the energy required for *Calanopia* to swim to the bottom and back daily at the Gill stations and the 40-mile station (depth at the latter about 738 m) is much greater than in St. George's Harbor (12.5-14 m) and at the West Indian localities reported by González and Bowman (1965).

*Labidocera aestiva* was abundant at many inshore stations (Figure 49) and, as stated earlier, was one of two species that formed the "coastal association." Of the common calanoids, only *Acartia tonsa*, the other member of the coastal association, was more severely restricted to coastal waters. *L. aestiva* was most widespread in the winter and spring, when it occurred at a number of the stations on the shelf, although the greatest numbers were at coastal stations. In the summer and fall (Cruises 3 and 4) its distribution was more restricted to the coast. Large numbers along the coast of Florida during Cruise 4 resulted from the flood conditions discussed earlier in this paper.

The other species of *Labidocera* were quite uncommon. *Labidocera acutifrons* occurred at a few oceanic stations. Fleminger (1957) has already documented the oceanic distribution of this species in the Gulf of Mexico, and Sherman and Schaner (1968) associated its presence over George's Bank with an incursion of Gulf Stream water. *L. nerii* was found at two oceanic stations (Cruise 1, Station 49; Cruise 3, Station 31). Finally, *L. scotti* was collected at Cruise 1, Station 49, and Cruise 4, Station 5.

*Pontella meadi* (including *P. pennata* Wilson, considered by Fleminger [1957] to be synonymous) occurred at six stations of Cruise 2 and three stations of Cruise 3, all in coastal and shelf waters. This distribution agrees with the findings of Fleminger (1957) and Sherman and Schaner (1968), who characterized *P. meadii* as a coastal species.

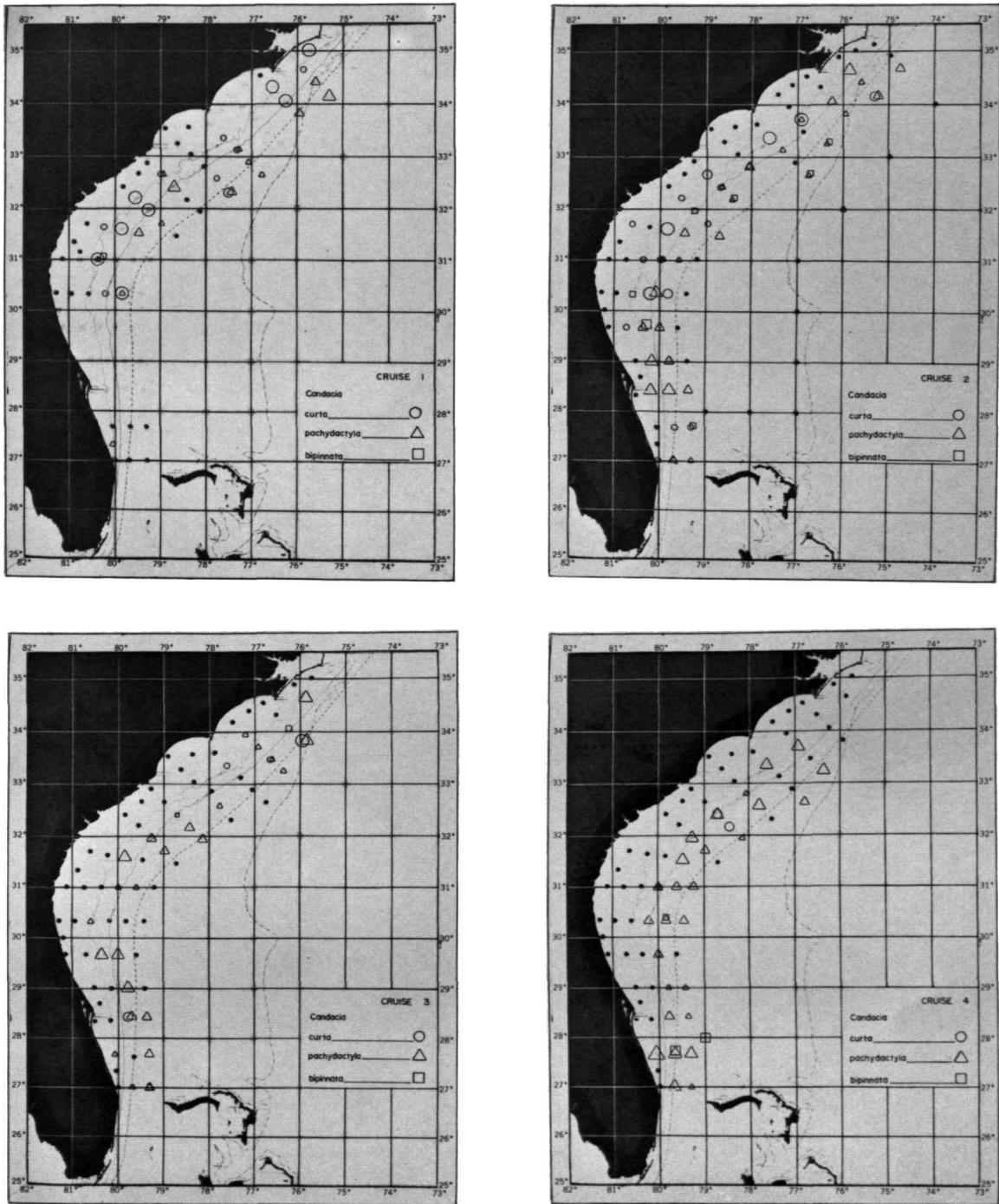


FIGURE 45.—Distribution of *Candacia* species, Cruises 1-4.

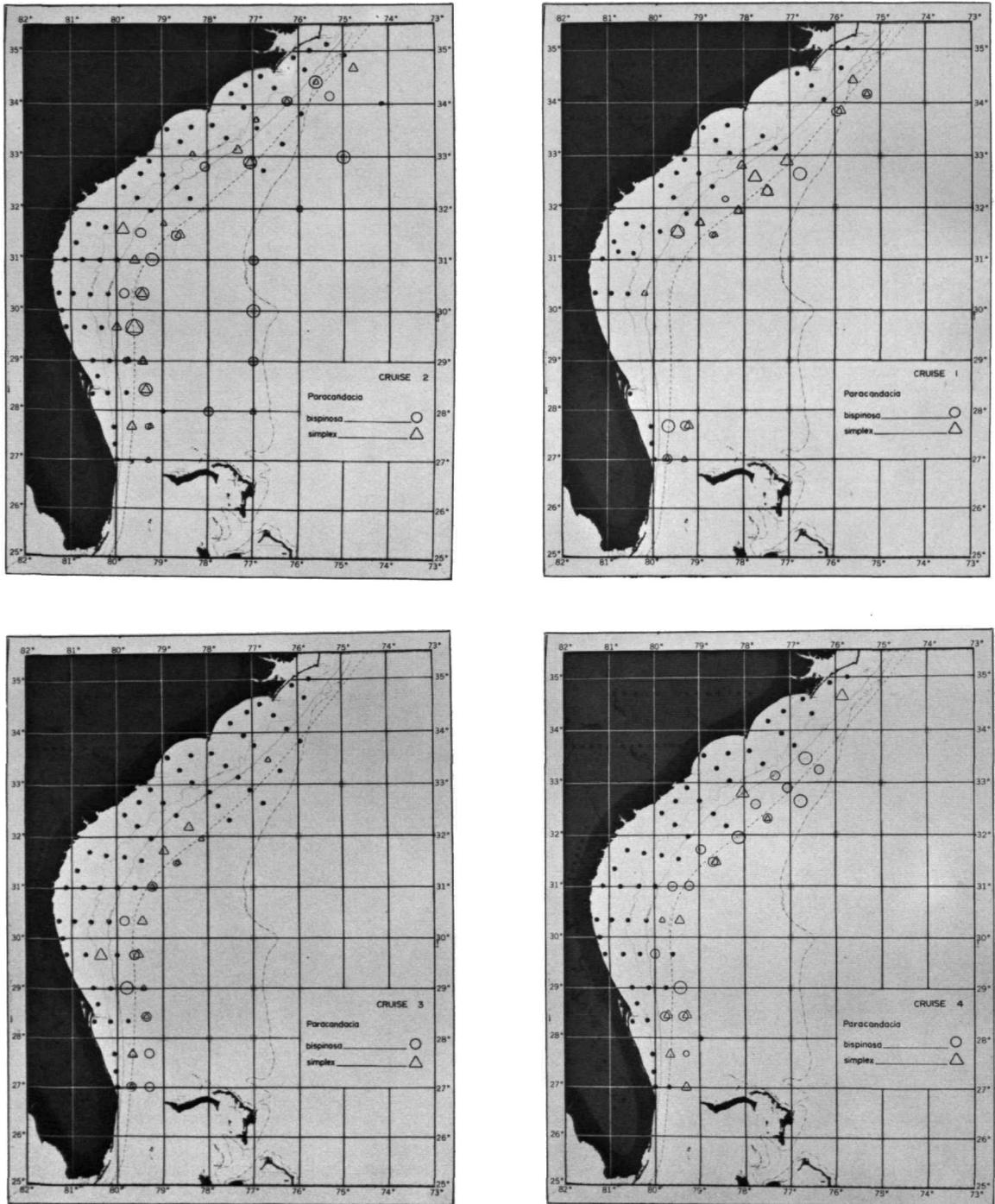


FIGURE 46.—Distribution of *Paracandacia bispinosa* and *P. simplex*, Cruises 1-4.

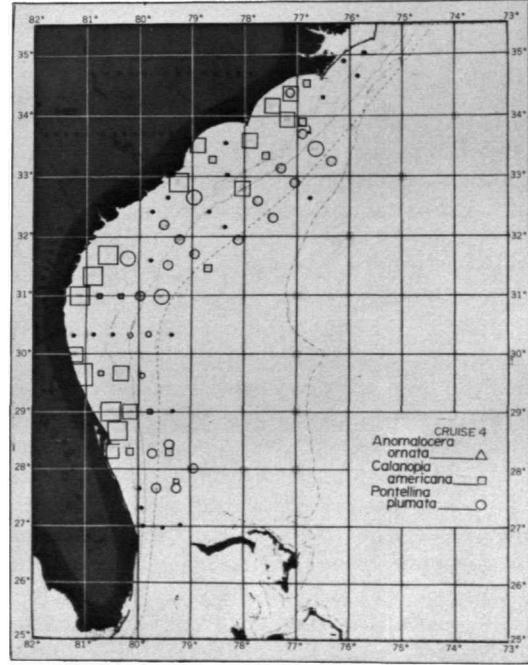
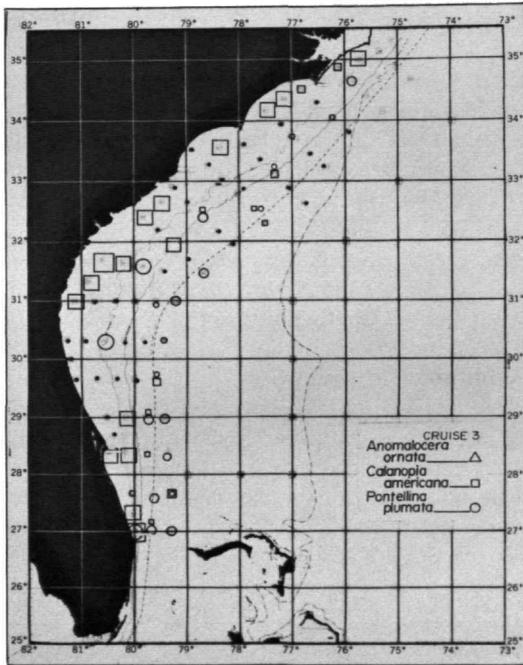
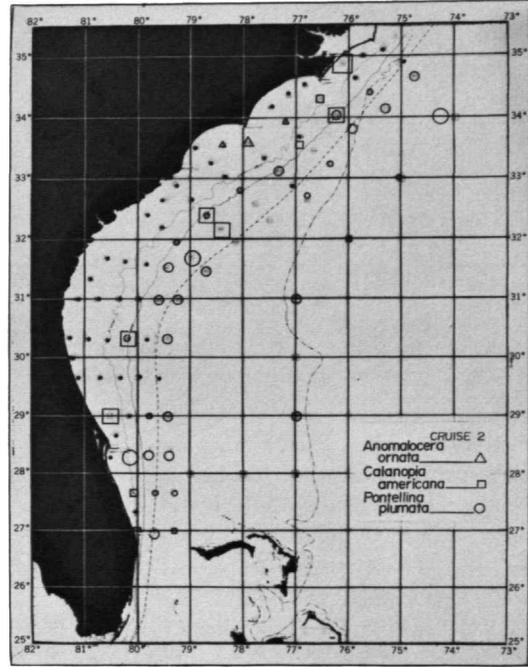
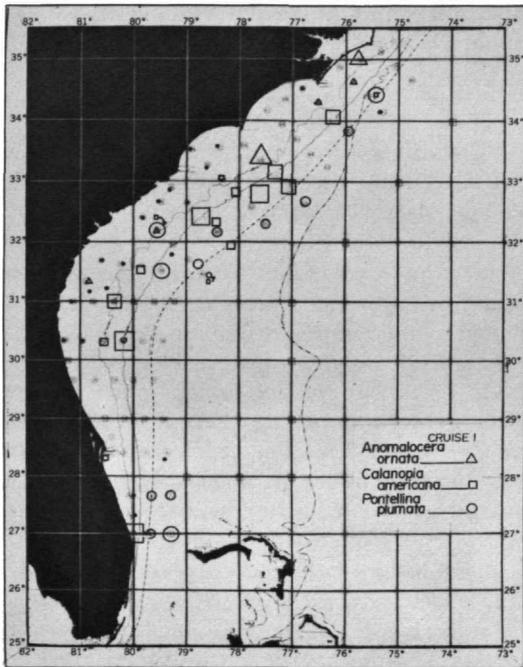


FIGURE 47.—Distribution of *Anomalocera ornata*, *Calanopia americana*, and *Pontellina plumata*, Cruises 1-4.

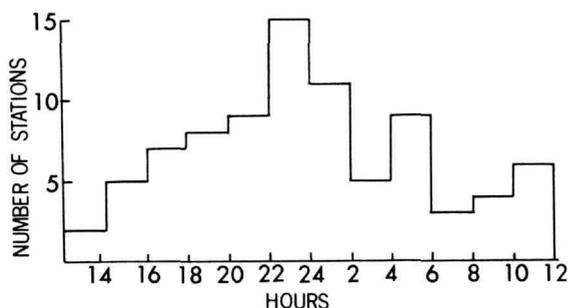


FIGURE 48.—Occurrence of *Calanopia americana*, Cruises 1-4 combined, in relation to time of day.

*Pontella securifer*, on the other hand, was found at six oceanic stations of Cruise 3. In the Gulf of Mexico, Fleminger (1957) found *P. securifer* in slope and oceanic waters; other authors (summarized by Sherman and Schaner 1968) have shown it to be associated with high oceanic waters.

*Pontella plumata* occurred at a moderate number of oceanic stations on all four cruises.

The three species of *Pontellopsis* were taken at only one or two oceanic stations each.

#### Acartiidae

*Acartia tonsa* was strictly limited to coastal waters, as is to be expected of a copepod known to be a typical estuarine species (Figure 50). During the winter (Cruise 1) it was abundant at stations along the coast of South Carolina, but at other seasons it was confined mainly to the coasts of Georgia and Florida, where more stations were close to shore than to the north. Its abundance at the Florida stations in the fall (Cruise 4) is associated with the strong salinity gradient along the coast that resulted from the flood conditions discussed previously.

*Acartia danae* and *A. negligens* are both characteristic of oceanic water. *Acartia danae* was the more common of the two species and was somewhat less restricted to oceanic water. It occurred occasionally in shelf water, whereas *A. negligens* never did. Figure 51, a T-S-P diagram (Bary 1959) for Cruise 4, with occurrences of the two species plotted on a surface temperature-salinity graph, shows the narrower range of conditions under which *A. negligens* exists.

#### Comparison of Carolinian and Virginian Calanoid Faunas

It is instructive to compare the calanoid fauna south of Cape Hatteras, sampled by the *Gill*, with that north of Cape Hatteras, sampled by Bigelow and Sears (1939), Deevey (1952a, 1952b, 1960), Grice and Hart (1962), and Van Engel and Tan (1965).

**THE SHELF ASSOCIATION.**—During the warmer months Van Engel found that the coastal waters off the mouth of Chesapeake Bay are dominated by *Labidocera aestiva*, *Centropages furcatus*, and *Eucalanus pileatus*. *Candacia armata* and *Temora stylifera* were less important. Except for *Candacia armata*, these are important species in Carolinian water. Conspicuous for its absence was the other dominant member of the shelf association south of Cape Hatteras, *Paracalanus "parvus."*

Farther north, off the mouth of Delaware Bay, Deevey (1960) recorded the year-round presence of *Paracalanus parvus*, with minimal numbers in the spring. It is not known which of the three East Coast species of the *Paracalanus parvus* group Deevey had. *Eucalanus pileatus* appeared in the Delaware Bay samples from July–December, and Deevey lists it as one of the most consistent warm water or southern forms. *Centropages furcatus* was much less in evidence; during the sampling period (May 1929–July 1933) it was collected only during September–November 1930.

Neither *Centropages furcatus* nor *Eucalanus pileatus* occurs in Block Island Sound, but Deevey (1952a, 1952b) reports the presence of *Paracalanus parvus*, with maximum numbers in August. Again, it is not known whether this is the true *P. parvus* or one of the species of the *Parvus* group that occurred in the *Gill* samples.

Whereas the species composition of the calanoid shelf association south of Cape Hatteras remains rather constant throughout the year, seasonal changes take place north of Cape Hatteras. *Pseudocalanus minutus* and *Centropages typicus* are the dominant species during the colder months off Chesapeake Bay (Van Engel and Tan 1965), Delaware Bay (Deevey 1960), and Block Island Sound (Deevey 1952a, 1952b).

In summary, the species that throughout the year dominate the shelf association south of Cape Hat-

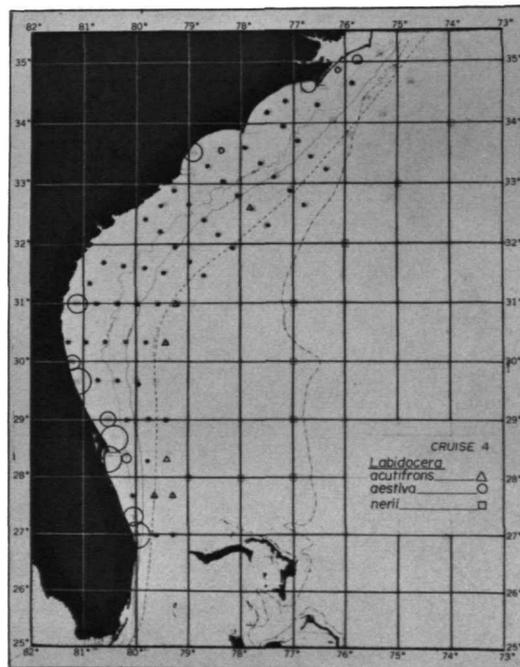
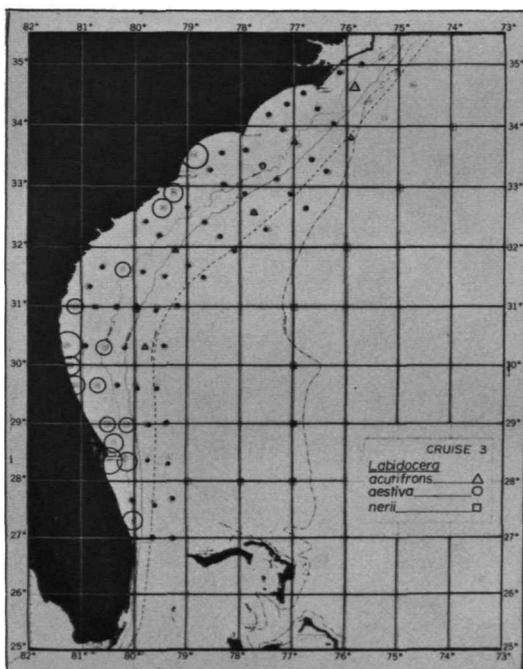
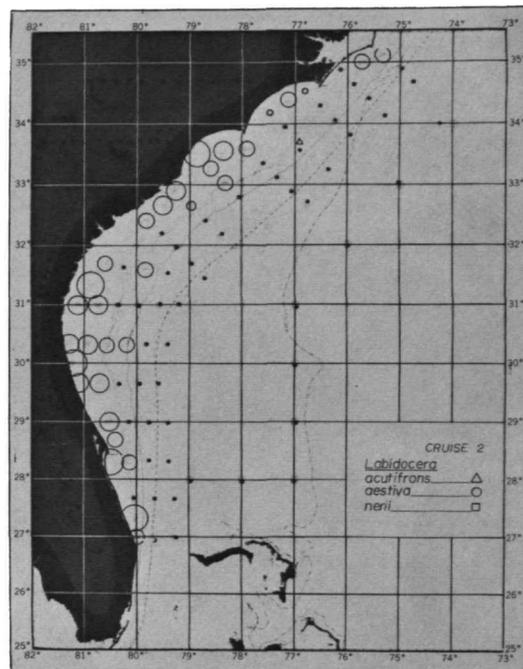
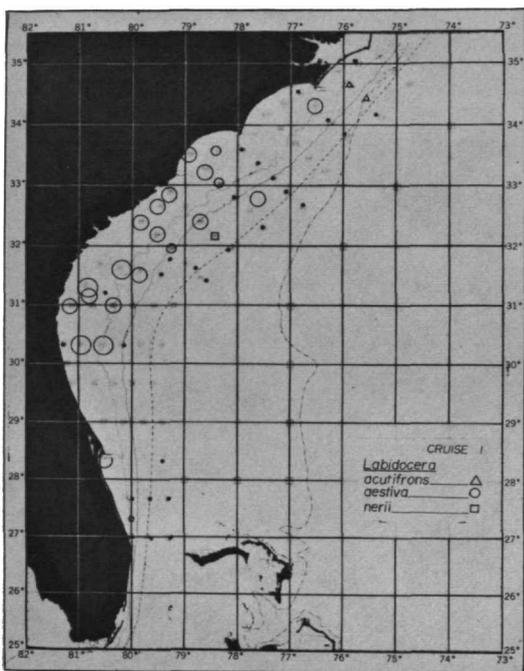


FIGURE 49.—Distribution of *Labidocera* species, Cruises 1-4.

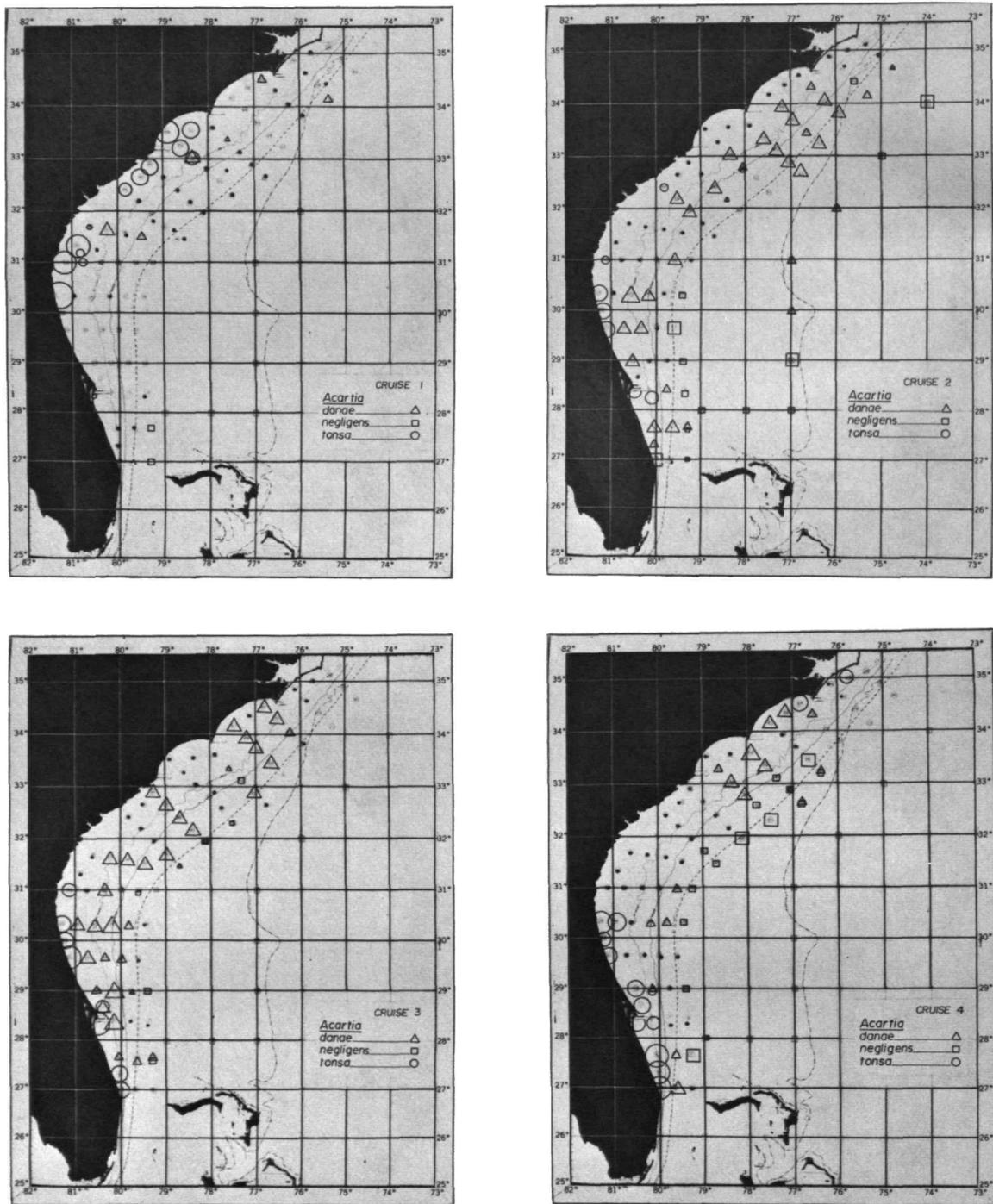


FIGURE 50.—Distribution of *Acartia* species, Cruises 1-4.

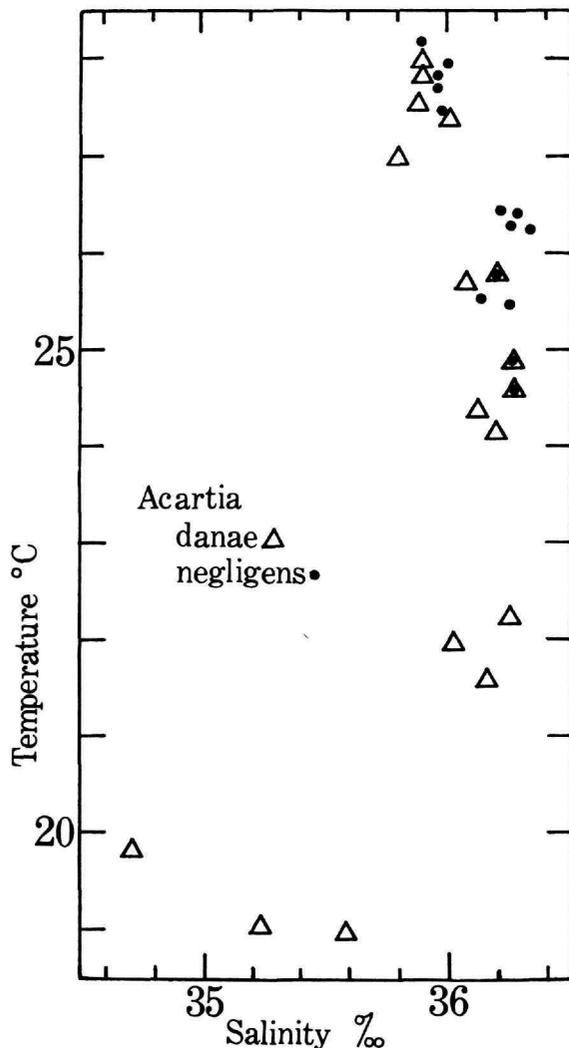


FIGURE 51.—Temperature-Salinity-Plankton diagram for *Acartia danae* and *Acartia negligens*.

teras appear in significant numbers north of Cape Hatteras only during the warmer months. As we go farther north they tend to diminish in numbers and to disappear, at first during the colder months, later year-round, and to be replaced by northern species, especially *Pseudocalanus minutus* and *Centropages typicus*.

**THE OCEANIC ASSOCIATION.**—The calanoid species forming the oceanic association are essentially the

same on both sides of Cape Hatteras. To the north this association moves farther offshore, since its western boundary follows the Gulf Stream and a region of slope water, consisting of mixed oceanic and coastal water is present, containing, as might be expected, a mixture of shelf and oceanic calanoid species. This slope water is not present south of Cape Hatteras.

In Grice and Hart's (1962) study of the zooplankton from stations in a New York-Bermuda transect, the calanoid species in their stations II (Gulf Stream) and JJ, KK, LL, and NN (Sargasso Sea) are by and large those that occurred at the oceanic stations sampled by the Gill. Grice and Hart's oceanic samples were collected from a depth of 200 m, hence they contained a few more species than the Gill samples, collected from about 70 m.

**THE COASTAL ASSOCIATION.**—Both *Acartia tonsa* and *Labidocera aestiva* occur in coastal waters abundantly as far north as Cape Cod. Going north from Cape Hatteras the seasonal occurrence of *Acartia tonsa* becomes increasingly more limited to the warmer months, and it is gradually replaced by its northern relative, *Acartia clausi*. North of Cape Hatteras *Labidocera aestiva* occurs from early summer to early winter, in contrast to its year-round occurrence in the Gill samples.

*Paracalanus crassirostris* and *Pseudodiaptomus coronatus*, coastal species that were inadequately sampled by the Gill, are abundant in coastal waters north of Cape Hatteras, but the northern extent of their occurrence in significant numbers is uncertain, since ordinary net tows do not collect representative numbers of either the tiny *P. crassirostris* or the nocturnally benthic *P. coronatus*.

The fact that oceanic and coastal calanoid species of the Gill collections occur both north and south of Cape Hatteras, whereas the shelf species are replaced by other species, requires an explanation. The conditions of temperature and salinity for the oceanic species do not change significantly in the oceanic water of the Florida Current as it passes Cape Hatteras and heads away from the continent. Oceanic species will enjoy stable conditions of high temperatures and salinities, regardless of whether they are in the Florida Current, the Gulf Stream, or the Sargasso Sea. In contrast, coastal species must be able to withstand severe fluctuations in temperature and salinity. The acquisition of a high degree

of tolerance in the coastal species enables them to thrive over a considerable latitudinal range.

The shelf species have neither the tolerance to environmental changes of the coastal species nor the constant conditions surrounding the oceanic species. Hence they cannot survive in environmental changes as great as those occurring north of Cape Hatteras in the colder months and are replaced by species with similar tolerances but adapted to lower temperatures.

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