

Vertical Distribution  
of *Themisto gaudichaudii*  
(Amphipoda: Hyperiidea)  
in Deepwater Dumpsite 106  
off the Mouth of Delaware Bay

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SMITHSONIAN CONTRIBUTIONS TO ZOOLOGY • NUMBER 351

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SMITHSONIAN INSTITUTION PRESS

City of Washington

1982

## ABSTRACT

Bowman, Thomas E., Anne C. Cohen, and Maura McManus McGuiness. Vertical Distribution of *Themisto gaudichaudii* (Amphipoda: Hyperiidea) in Deepwater Dumpsite 106 off the Mouth of Delaware Bay. *Smithsonian Contributions to Zoology*, number 351, 24 pages, 16 figures, 1982.—*Themisto gaudichaudii*, a bipolar hyperiid amphipod, was collected in discrete-depth samples taken between the surface and 1800 m in a warm core eddy as it passed through Deepwater Dumpsite 106, a site off the mouth of Delaware Bay where industrial wastes are dumped in the Atlantic Ocean. The species was most abundant in the upper strata (1–125 m) but was found in all depth intervals sampled during the day (1–25 to 1425–1800 m) and at night in depth intervals from 1–25 to 700–800 m. Night catches exceeded day catches, probably because of greater net avoidance during the day. The data do not show whether or not vertical migration occurred, probably because sampling did not partition finely enough the upper layers, where previous studies have shown that diel vertical migrations of *Themisto* occur. Abundance was greater in the warmest, shallow, central part of the eddy than in the deeper and peripheral parts of the eddy.

OFFICIAL PUBLICATION DATE is handstamped in a limited number of initial copies and is recorded in the Institution's annual report, *Smithsonian Year*. SERIES COVER DESIGN: The coral *Montastrea cavernosa* (Linnaeus).

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### Library of Congress Cataloging in Publication Data

Bowman, Thomas E.

Vertical distribution of *Themisto gaudichaudii* (Amphipoda—Hyperiidea) in Deepwater Dumpsite 106 off the mouth of Delaware Bay.

(Smithsonian contributions to zoology ; no. 351)

Bibliography: p.

1. *Themisto gaudichaudii*—Vertical distribution.
  2. Waste disposal in the ocean—Environmental aspects—Delaware Bay (Del. and N.J.)
  3. Crustacea—Vertical distribution.
  4. Crustacea—Delaware Bay (Del. and N.J.)—Vertical distribution.
- I. Cohen, Anne C. II. McGuiness, Maura McM. III. Title. IV. Title: Deepwater Dumpsite 106 off the mouth of Delaware Bay. V. Series.

QL1.S54 no. 351 [QL444.M315] 591s [595.3'71] 81-18442 AACR2

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# Vertical Distribution of *Themisto gaudichaudii* (Amphipoda: Hyperiidea) in Deepwater Dumpsite 106 off the Mouth of Delaware Bay

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## Introduction

The name "Deepwater Dumpsite 106" (DWD-106) is applied to a rectangular area 90 miles east of the mouth of Delaware Bay (Figures 1, 2) where acid waste, industrial chemicals, and radioactive wastes are dumped, principally in liquid form either in solution or in suspension. Evaluation of the effects of this waste disposal upon the environment is the responsibility of NOAA, which in 1972 established a program to examine the physical and biological characteristics of DWD-106. This program included the Nektonic Sampling Program, consisting of 4 cruises that sampled the nekton with 10-foot Isaacs-Kidd midwater trawls (IKMT). Samples from one of these cruises (cruise 2, 23 Jul–3 Aug 1975) offered the opportunity of examining the depth distribution of the most abundant pelagic amphipod in DWD-106, *Themisto gaudichaudii* Guérin-Méneville, 1825, and the study reported herein was therefore undertaken.

**ACKNOWLEDGMENTS.**—We are most grateful to Robert H. Gibbs for the collections used in our study, for analyzing our data with his computer

program, for responding patiently to our inquiries concerning data and collection methods, and for reviewing the manuscript. Lee-Ann Hayek gave useful advice on statistical treatment of our data. Frank D. Ferrari and Edward J. Zillioux also reviewed the manuscript.

## Nomenclature

The amphipod genus *Themisto* Guérin-Méneville, 1825, was replaced with *Euthemisto* by Bovallius (1887) because it was a junior homonym of the nudibranch *Themisto* Oken (1815). *Parathemisto* Boeck (1870) and *Themisto* Guérin-Méneville were combined under *Themisto* by Stephensen (1924), corrected by Barnard (1930) to *Parathemisto*, the name currently used by most zoologists. Volume 3 of *Oken's Lehrbuch der Naturgeschichte* (1815) was placed, however, on the Official List of Rejected Works by Opinion 417 of the International Commission of Zoological Nomenclature (1956), which ruled that no name published in Oken's volume 3 acquired the status of availability by reason of having been so published. Consequently the name *Themisto*, first made available by Guérin-Méneville and a senior synonym of *Parathemisto*, is the valid name of the amphipod genus.

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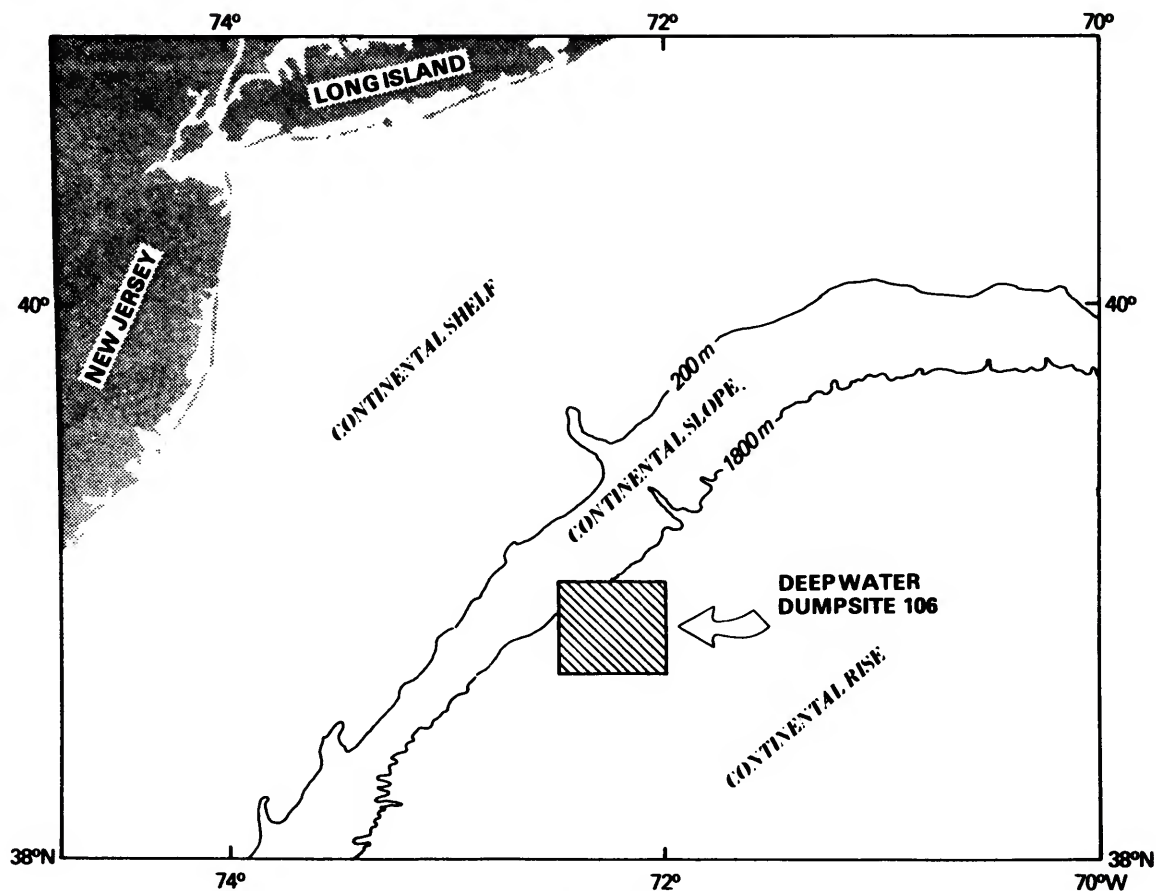


FIGURE 1.—Location of Deepwater Dumpsite 106 (from Ingham et al., 1977).

### Geographic Distribution

*Themisto gaudichaudii* is an abundant and widely distributed hyperiid amphipod, inhabiting sub-polar and temperate seas of both hemispheres. Its worldwide distribution, especially in the Southern Ocean, is summarized by Kane (1966). It is one of a few truly bipolar pelagic animals (Dunbar, 1979), but is known in the North Pacific only from the Yellow Sea, East China Sea, and Korea Strait (Yamada, 1933; Bowman, 1960). A few scattered records from the tropical Atlantic (Voseler, 1901) are incompatible with the distribution pattern of *T. gaudichaudii* and require confirmation before they can be accepted. Similarly, Ev-

ans' (1961) records of *Themisto* species in the tropical Atlantic at temperatures of about 25°–27°C are questionable.

*Themisto gaudichaudii* is a variable species, occurring in several forms previously accorded specific status. Recently Shearer and Evans (1974) demonstrated that the characters used to separate *T. gaudichaudii* and *T. gracilipes* (Norman) depend on body size and undetermined conditions affecting development. They therefore reduced *T. gracilipes* to a junior synonym of *T. gaudichaudii*. This merging expands the global distribution of *T. gaudichaudii* given by Kane (1966) to include the Mediterranean Sea (Stephensen, 1924), Tristan da Cunha (doubtfully — Stephensen, 1924), the



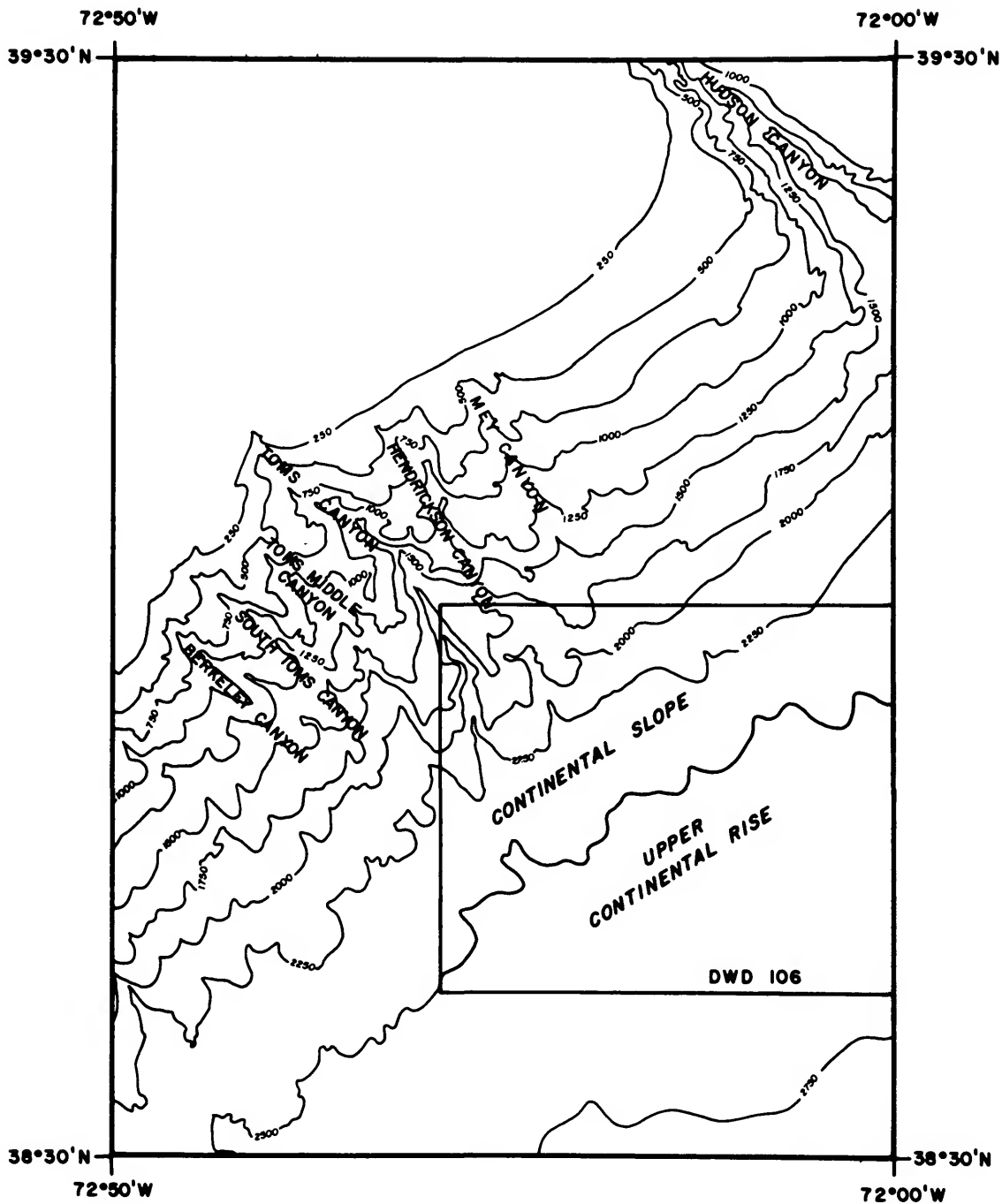


FIGURE 2.—Bathymetry in vicinity of Deepwater Dumpsite 106 (from Bisagni, 1977).

Juan Fernandez Islands, and the Yellow and East China seas (Bowman, 1960).

The southern limits of *T. gaudichaudii* along the North American Atlantic coast have not been determined, but it is known to penetrate Virginian coastal water to the latitude of the mouth of Chesapeake Bay, about 37°N (Bigelow and Sears, 1939; Grant, 1979; Short, 1980). At present the zooplankton composition of shelf waters between Cape Henry and Cape Hatteras is largely unexplored, but Virginian coastal water overlies the shelf south to Cape Hatteras (about 35°20'N), and *T. gaudichaudii* probably will be found to reach Cape Hatteras also. *Themisto gaudichaudii* does not occur south of Cape Hatteras. It was not present in numerous plankton samples collected between mid-Florida and Cape Hatteras and examined for calanoid copepods (Bowman, 1971).

#### Previous Studies of Vertical Distribution

From past studies of vertical distribution in *T. gaudichaudii*, 4 general statements can be made.

1. The vertical range appears to be considerable, from the surface to depths sampled by nets towed at the end of 1000 meters of wire (Stephensen, 1924), or about 500 meters actual depth (Schmidt, 1912). The latter, stations of the Danish Oceanographical Expeditions 1908–1910, were mainly sampled by non-closing nets, Petersen's young fish trawl (Schmidt, 1912). Despite Schmidt's confidence that the catches of these trawls reflected with reasonable accuracy the pelagic biota present at depths at which the trawls were towed horizontally, confirmation with closing net samples has been desirable. The present study presents such confirmation for the first time.

2. Most of the population occurs in the upper 100–300 meters.

3. Within the upper 100–200 meters a marked diurnal vertical migration takes place, toward the surface at night and away from the surface during daylight (Hardy and Gunther, 1935; Bary, 1959; Kane, 1966; Everson and Ward, 1980).

4. Juveniles tend to be more restricted than

adults to shallow depths (Bigelow, 1926; Bousfield, 1951).

#### *Themisto gaudichaudii* in Deepwater Dumpsite 106

LOCATION AND WATER TYPES.—DWD-106 is located at 38°40'N to 39°00'N and 72°00'W to 72°30'W, over the continental slope and rise, where water depths range from 1550 m in the northwest corner to 2750 m in the southeast corner (Figures 1, 2). It lies within "one of the most variable and complex oceanographic regions of the entire western North Atlantic" (Ingham et al., 1977). The surface layer is normally occupied by slope water, which lies between fresher shelf water to the west and more saline gulf water to the east. Occasional intrusions of the cool, low salinity shelf water occur into the upper layers of the dumpsite, and anticyclonic warm core eddies spun off from the Gulf Stream pass through the dumpsite at irregular intervals, about 3 times a year, at least partly covering the dumpsite about 20% of the time. Such an eddy occupied the dumpsite throughout cruise 2, with its center just northeast of the dumpsite (about 39°45'N, 71°55'W). Its presence was clearly shown by the depression of the 15°C isotherm to depths of up to more than 500 m, resulting in a nearly isothermal pool of 15°–16°C North Atlantic central water below about 50 m, surrounded by slope water (Figure 3). Above 50 m the temperature rose sharply to 24°–26°C at the surface (Figure 4). Eddy water in the dumpsite was arbitrarily divided into an eastern area in the core of the eddy and a western area in the periphery of the eddy (Figure 5).

We have not been able to obtain from our sample analyses any correlation between the depth distribution of *Themisto gaudichaudii* and physical oceanographic conditions. For further details of the latter consult Goulet and Hausknecht (1977).

SAMPLING.—Samples were collected with a 10-foot IKMT lined with 3/8 inch (0.95 cm) stretch mesh. At the cod end was a 1-m plankton net of

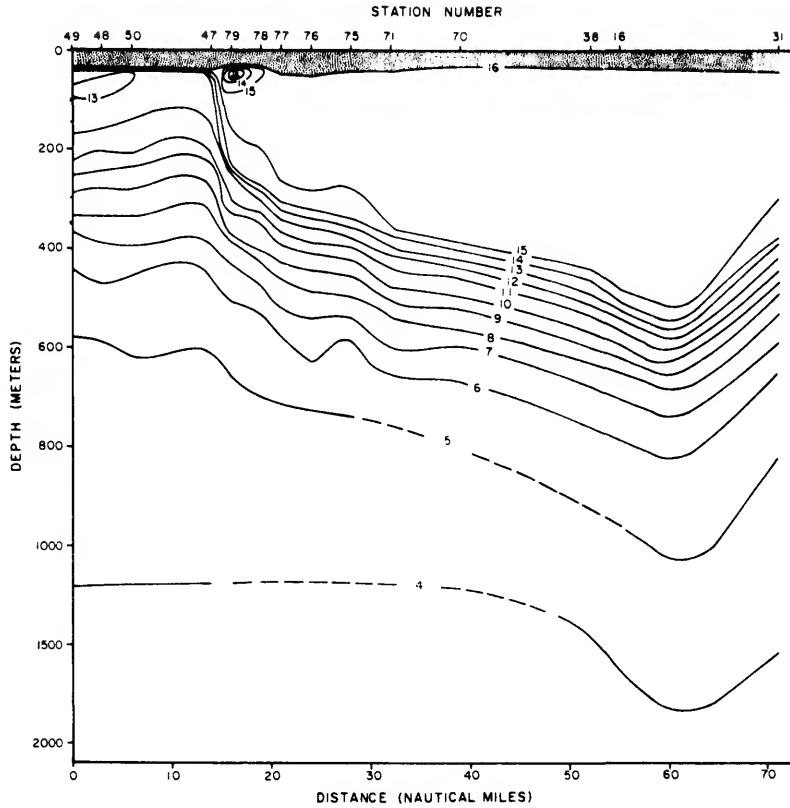


FIGURE 3.—East-west vertical section through Deepwater Dumpsite 106 in July 1975 showing temperature structure ( $^{\circ}\text{C}$ ) in upper 2000 m. (from Goulet and Hausknecht, 1977).

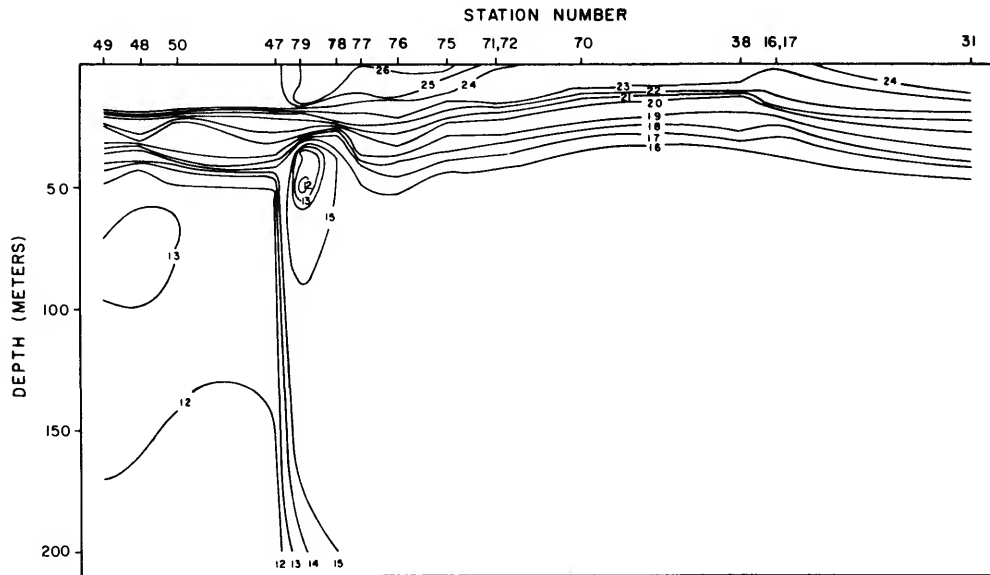


FIGURE 4.—East-west vertical section through Deepwater Dumpsite 106 in July 1975 showing temperature structure in upper 200 m (from Goulet and Hausknecht, 1977).

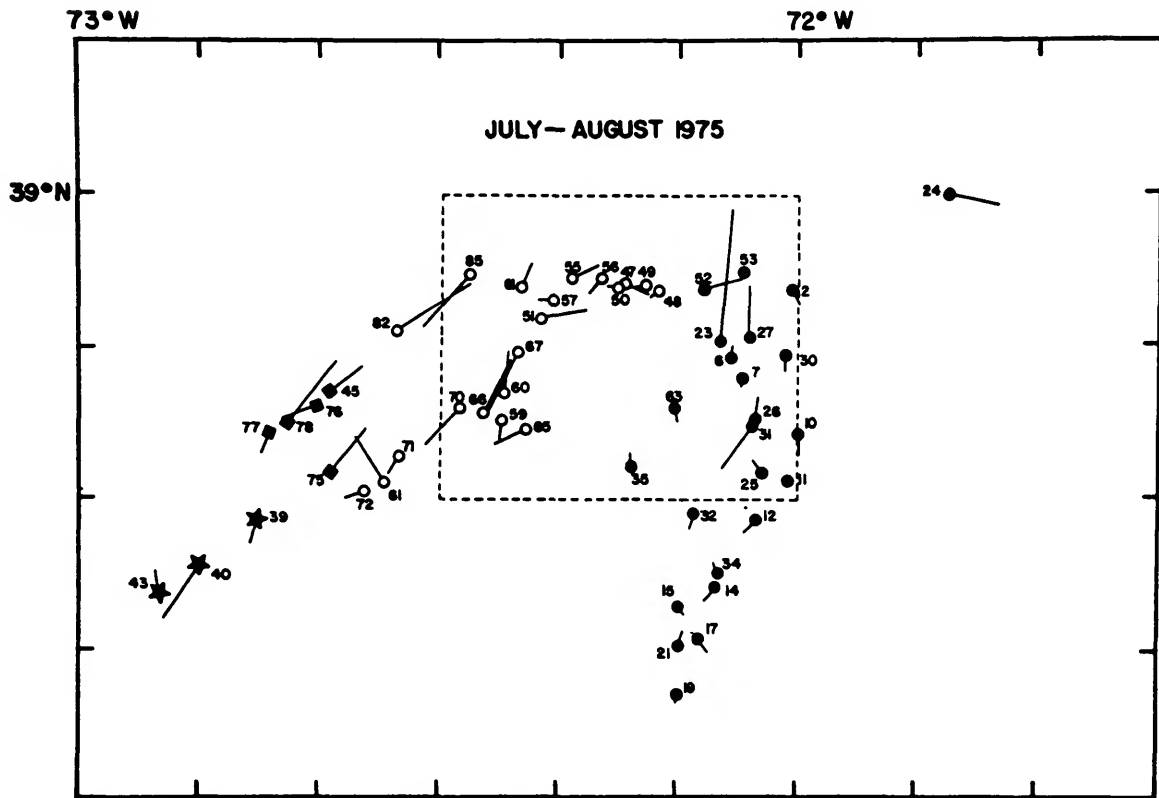


FIGURE 5.—Trawl positions, cruise 2 (symbols indicate beginning position of tow; Stars = trawls made in slope water; squares = transitional water; open circles = western eddy; closed circles = eastern eddy; dashed line = DWD-106; from Krueger, et al., 1977).

no. 00 (0.752 mm) mesh equipped with a 4-chambered, cod-end sampler designed after Aron et al. (1964). Four samples, 3 closed, 1 open, were taken during each fully successful haul. Fishing depth was monitored electronically aboard ship, allowing selection of depths at which chambers were closed. A flow meter was not used and specimens will be reported as numbers per hour of towsing time rather than as numbers per volume of water filtered.

The main trawling program consisted of oblique tows. In each tow the net was sent to the desired depth with all chambers and the cod end open; then the net was retrieved slowly and the chambers were closed at selected intervals of decreasing depth. These discrete-depth samples

were taken from the surface to 800 m, with a few samples as deep as 1800 m. Sampling intervals at night in the upper 200 m were narrow in order to determine more precisely the upper levels reached by vertical migrators. Because this stratum normally is sparsely inhabited during the day by midwater nekton, the principal target of the program, sampling of shallow strata was often curtailed in the daytime in favor of sampling the deeper strata more effectively.

Because a flow meter was not used, quantitative comparisons of samples are not reliable. The quantity of water strained per unit of time may have varied considerably because of fluctuations in ship speed and in the amount of clogging of the net. The most serious offenders in net-clogging

were salps, which were abundant at DWD-106. All 3 of the 25–1 m night tows and 2 of the 3 50–26 m night tows in the western eddy collected large numbers of salps. One to 4 quarts of salps were discarded from each of these samples at the time of collection. Unfortunately some *Themisto* may have been thrown out with the salps, since juvenile *Themisto gaudichaudii* have been observed clinging to salps in large numbers (Madin and Harbison, 1977).

Another factor affecting the quantitative reliability of the cruise 2 samples is the patchy distribution of *T. gaudichaudii* due to the formation of swarms (Hardy and Gunther, 1935; Bary, 1959; Nemoto, 1959; Gray and McHardy, 1967; Everson and Ward, 1980), which appear to be limited to near-surface waters; at greater depths swarms disperse (Kane, 1966). Thus patchiness may not be a significant factor except in shallow strata.

Some samples, collected by oblique tows that extended over 2 or more strata, were not used because samples of the included smaller strata were available.

Night samples are those taken from after sunset to before sunrise; day samples are those from after sunrise to before sunset. Only 2 samples were collected less than 2 hours from sunrise or sunset: 1 hour 59 minutes, and 1 hour 54 minutes. Thus, in effect day began 2 hours after sunrise and ended 2 hours before sunset; night began 2 hours after sunset and ended 2 hours before sunrise.

**ANALYSIS OF DATA.**—Both “compressa” and “bispinosa” forms (Stephensen, 1924; Hurley, 1955) of *T. gaudichaudii* were present in the cruise 2 samples, but of the total of 937 specimens caught, only 4 (0.43%) were “bispinosa.” This agrees with reports that “compressa” is more abundant in inshore waters and at lower latitudes, whereas “bispinosa” predominates in offshore waters and at higher latitudes (Bigelow, 1926; Barnard, 1932; Kane, 1966). Our analysis is concerned with the “compressa” form only.

The average number of specimens/hour for each stratum in both eddy regions was derived by calculating the number/hour for each sample

in that stratum, summing the numbers/hour for all samples of the stratum, and dividing by the number of samples collected in the stratum, including samples that did not contain *Themisto*:

$$\frac{\sum \frac{N_s}{T_s}}{\sum s} = \text{Av. no. of specimens} \\ \text{/hour (for any stratum)}$$

where  $N_s$  = number of specimens in a sample,  $T_s$  = number of hours of tow in collecting that sample, and  $s$  = an individual sample from the same stratum. This method gives equal weight to all the individual samples and was chosen in preference to calculating the sum of all specimens in a stratum divided by the number of hours towed in the stratum:

$$\frac{\sum N_s}{\sum T_s}$$

because the former is an average of the number/hour of the replicate samples rather than an average of the total catch in the stratum. Averaging the replicates weights for patchiness. Unless all replicate numbers/hour are equal, averaging the total catch discards the information derived from replicates.

The sex, length, and state of maturity were determined for all specimens of *Themisto*. The stages, listed below, are based on the state of development of the oostegites in females, and of the second antenna in males, as in Kane (1963).

Stage	Oostegites (♀)	Segment of ant. 2 flagellum (♂)
1	Absent	1–4, short
2	Up to 1/2 length of gills	~8, short
3	Subequal to gills	~13, short
4 (adult)	Longer than gills	~21, elongate

Conclusions offered herein concerning the vertical distribution of *T. gaudichaudii* are drawn from inspection of graphs that summarize virtually all of our data (Figures 6–15). Each graph has right and left components. The left component shows the numbers of amphipods/hour of towing. The base of each triangle, on the depth ordinate, encompasses the depth interval sampled; the apex

of the triangle indicates the mean number of amphipods/hour for all tows sampling that depth interval and is read from the abscissa (in Figures 8-15 solid lines = ♀, dashed lines = ♂). The number/hour for individual samples is indicated by a circle in Figures 6 and 7; and by a circle (♀) or a triangle (♂) in Figures 8-15; samples that caught 0 amphipods are not shown, but are included in the mean numbers/hour.

In the right component each tow is represented by a triangle. The base of the triangle encompasses the depth interval sampled; the apex shows the duration of the tow and is read from the abscissa. The numerals, displayed sequentially beyond the apices, indicate the numbers of *Themisto* collected during each tow.

Comparisons based on these graphs should be tempered by the lack of reliable information on volumes filtered, amount of net clogging, and patchiness. These factors must have contributed to the considerable variation in numbers of *Themisto* collected by replicate tows at the same depth interval. For example, the 3 replicate night tows at 0-25 m in the eastern eddy caught 7, 24, and 99 specimens (84, 720, and 1188 specimens/hour). The 5 replicate night tows in the western eddy at 101-125 m caught 0, 0, 0, 3, and 48 specimens (0, 0, 0, 36, and 720 specimens/hour).

**RESULTS AND DISCUSSION.**—A condensed summary of the sampling and results is given below.

	Eastern eddy		Western eddy	
	Day	Night	Day	Night
No. of samples	29	27	23	39
Total hrs. sampled	7.9	4.4	9.8	6.6
Av. and range of sampling time (min.)	16.4 (3-92)	9.85 (2-55)	24.6 (6-76)	10.2 (1.2-38)
Total <i>Themisto</i> caught	155	442	140	182
Mean <i>Themisto</i> /hr.	40.28	211.7	17.28	52.44

Greater numbers of *Themisto* were caught at night than during the day, especially in the eastern eddy. The mean catch/hour was about 5 times greater at night in the eastern eddy and 3 times greater in the western eddy. If almost the entire vertical range of the populations was sampled, as seems probable, it must be concluded

that net avoidance was greater during the day. Like most hyperiid amphipods of the infraorder Physocephalata, *Themisto* has very large compound eyes and may be able to detect daylight and moving objects at depths of several hundred meters, especially if the moving object stimulates bioluminescent flashes. The most sensitive known eyes, those of certain deep-sea fishes (Denton and Warren, 1957), may be able to detect some daylight down to about 1000 m (Clarke and Denton, 1962). While dip-netting with a night light from shipboard at night, it was found that very rapid sweeps were required to capture the hyperiid amphipod *Parapronoe crustulum*, a rapid-swimming species comparable in size to *T. gaudichaudii* (unpublished observations, T. E. Bowman). If *T. gaudichaudii* approaches *P. crustulum* in swimming speed, significant numbers would be expected to evade the IKMT in depths where the latter was visible.

The greatest numbers of *Themisto* were taken in shallow tows, with the majority of specimens being collected above 125 m. Thus at night 86% and 92% of the specimens in the eastern and western eddies, respectively, were caught between 125 m and the surface. (Percentages are based upon numbers/hour.) Only a small fraction of the population occurred below the 15°-16°C isothermal layer; in the eastern eddy 98% of the night specimens were collected between 300 m and the surface. About 1/3 of the eastern eddy night specimens (34%) occurred in the 0-25 m layer, above the isothermal layer.

Even though the population was concentrated in the upper layers, significant numbers were caught at the greatest depths sampled, e.g., a sample of 53 specimens (265/hr) in a 800-1000 m day tow in the eastern eddy. Stages 2, 3, and adults (both sexes) occurred from the shallowest (1-25) to the deepest (1205-1337 or 1425-1839 m) strata sampled. Stage 1 occurred from 1-25 m to 600-700 or 600-800.

Only 1 haul was taken deeper than 1400 m, a day trawl between 1839-1425 m, which caught 1 stage 2; this single specimen could easily have been a contaminant. Whether *Themisto* was pre-



sent deeper than 1426 m cannot be determined from the DWD-106 data.

Life history stages and sexes were not segregated by tows. In all tows catching at least 8 specimens, 3–8 of the 8 stages (4 male, 4 female) were caught per tow; in the 5 tows catching more than 30 specimens, 6–8 of the 8 stages were caught per tow.

In general *Themisto* was more abundant in the eastern eddy than in the western eddy. This difference in abundance was also reported for mesopelagic fishes by Krueger et al. (1977), who discussed 3 possible explanations. (1) Pollutants were dumped mainly at the western boundary of DWD-106, this being nearest to the coast. (2) Eddies have a stagnant core in which particles tend to be trapped and accumulate. Outside the core, which lies in the east eddy, the anticyclonic movement of the water tends to spin off particles. A contrary view, however, is that water is entrained at the outer edges of the eddy and is lost at the surface. (3) There is an inshore-offshore gradient in abundance, increasing from slope water to the east eddy.

It cannot be determined whether or not any of the above explanations were operative for *Themisto* abundance. Concerning pollutants, all 9 daytime tows between 151 and 600 m in the western eddy caught 0 *Themisto*, and 6 of these 9 tows were made near or even in the wakes of ships dumping industrial waste. But *Themisto* was caught in the other 4 tows taken near such dumping, i.e., the only 2 tows taken between 0–151 m and 2 of the 4 600–800 m tows.

The graphs (Figures 6–15) show differences in the details of vertical distribution between males and females and among the 4 growth stages. These differences are not related to known aspects of macro- or micro-behavioral patterns reported for pelagic amphipods, nor are they distinctive enough to suggest new interpretations.

Considering the total catch (Figure 16), the percentage of females, 47.5–63.2, was higher than that of males, 36.0–52.5. A possible explanation for the lower catch of males is that they are stronger swimmers and therefore more successful

in evading the net; however, we have no supporting evidence for this explanation. In some amphipods the apparent greater swimming ability of the males is reflected in the development of their pleopodal protopods, which are thicker than those of the females and contain larger muscles. Such differences are not evident in *Themisto*. The low numbers of stage 1 juveniles could be explained at least 2 ways: (1) the duration of this stage is short; (2) juvenile *Themisto* are much more likely than adults to be associated with salps or hydromedusae (Sheader and Evans, 1975; Madin and Harbison, 1977).

The small numbers of stage 3 females is puzzling. Our designation of growth stages to aid in analysis does not imply, however, that these stages are of equal duration. Figure 16 suggests that the duration of stage 3 may be shorter than that of stage 2.

The well-documented migration of *Themisto* upward at night and downward during the day in the upper 100–200 m is not apparent in the DWD-106 samples, perhaps because the day tows did not partition the upper layers finely enough, especially in the western eddy, where only 2 discrete-depth, day tows were made between the surface and 150 m.

The shallowest eddy samples may have been collected at temperatures close to the maximum normally experienced by *T. gaudichaudii*, 24°–26°C. Whether or not the amphipods were living at such temperatures is not known, since we do not know at what depths in the 0–25 m interval they were collected. If they were captured at 24–25 m their ambient temperature probably did not exceed 18°C. In any case, not only did substantial numbers of *T. gaudichaudii* survive and breed for about 1 month in the warm-core eddy, but the species was most abundant in the shallowest, warmest parts of the eddy.

Krueger et al. (1977) found that the presence of the eddy during cruise 2 increased markedly the proportion of the northern Sargasso Sea fish species over that normally present in DWD-106. Eddy-free samples of amphipods from DWD-106 have not been available for comparison, but the

composition of the amphipod fauna of the cruise 2 samples gives little evidence of an influx of the tropical species characteristic of the Gulf Stream or Sargasso Sea. *Themisto gaudichaudii* was by far the dominant species, followed by *Phronima sedentaria*, a widespread species that ranges in the Atlantic from about 50°S to about 45°N in the western Atlantic and the west coast of Ireland in the eastern Atlantic (Shih, 1969). Less common were species of *Vibilia* and *Scina*. In general the number of amphipod species was low, and there was a virtual absence of species known to be limited to tropical waters.

A possible explanation for the near absence of tropical amphipod species is suggested by Goulet and Hausknecht's (1977) statement that the eddy was "old and degenerate. It had lost much of its original warm core character in the upper 50 m and its original North Atlantic Central Water below 500 m had been mixed into Deep Slope Water."

An admirable review by Laval (1980) summarizes in detail the evidence that all hyperiids are associates of gelatinous zooplankters, at least in their early stages, and not "planktonic" in the sense that this term applies to calanoid copepods and euphausiids. Some hyperiids remain closely associated with gelatinous hosts throughout their lives; others, including *Themisto*, remain associated while juvenile but later become essentially free-living and pelagic, returning occasionally to rest or feed upon a host. We do not know how a post-juvenile *Themisto* apportions its time between a truly pelagic life and "a benthic-like existence on the pelagic substratum provided by gelatinous animals of the zooplankton" (Laval, 1980). Nor do we know whether the vertical migration of *Themisto* within the upper 200 m is performed actively by the amphipod or is due only to the migration of its hosts. Such questions cannot be answered by examination of plankton samples as in the present study, but require direct observations in the field or in laboratory aquaria.

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## Vertical Distribution Graphs

(for explanation of graphs see pp. 7, 8)

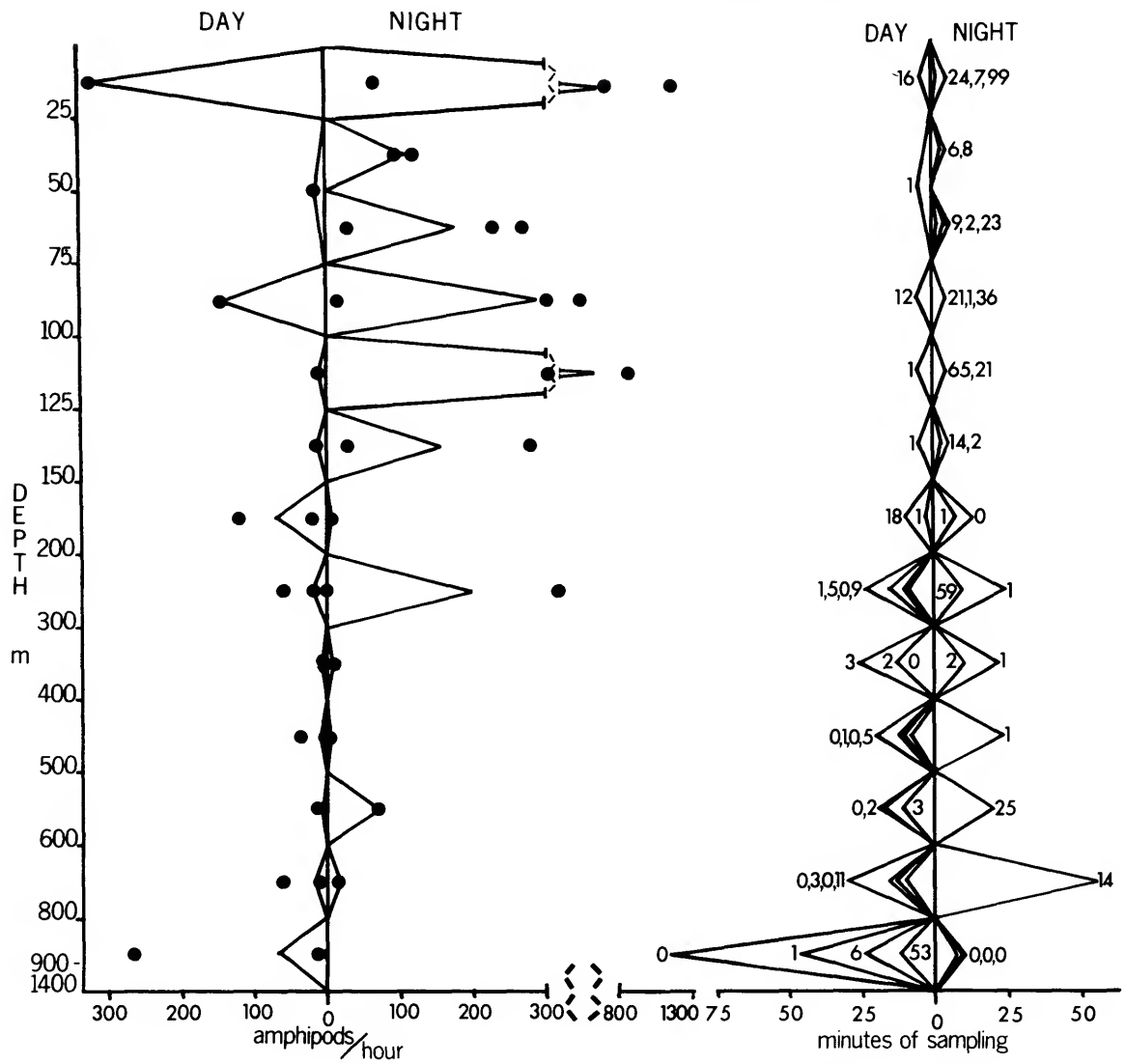


FIGURE 6.—Vertical distribution of *Themisto gaudichaudii*, eastern eddy, all stages and both sexes combined.



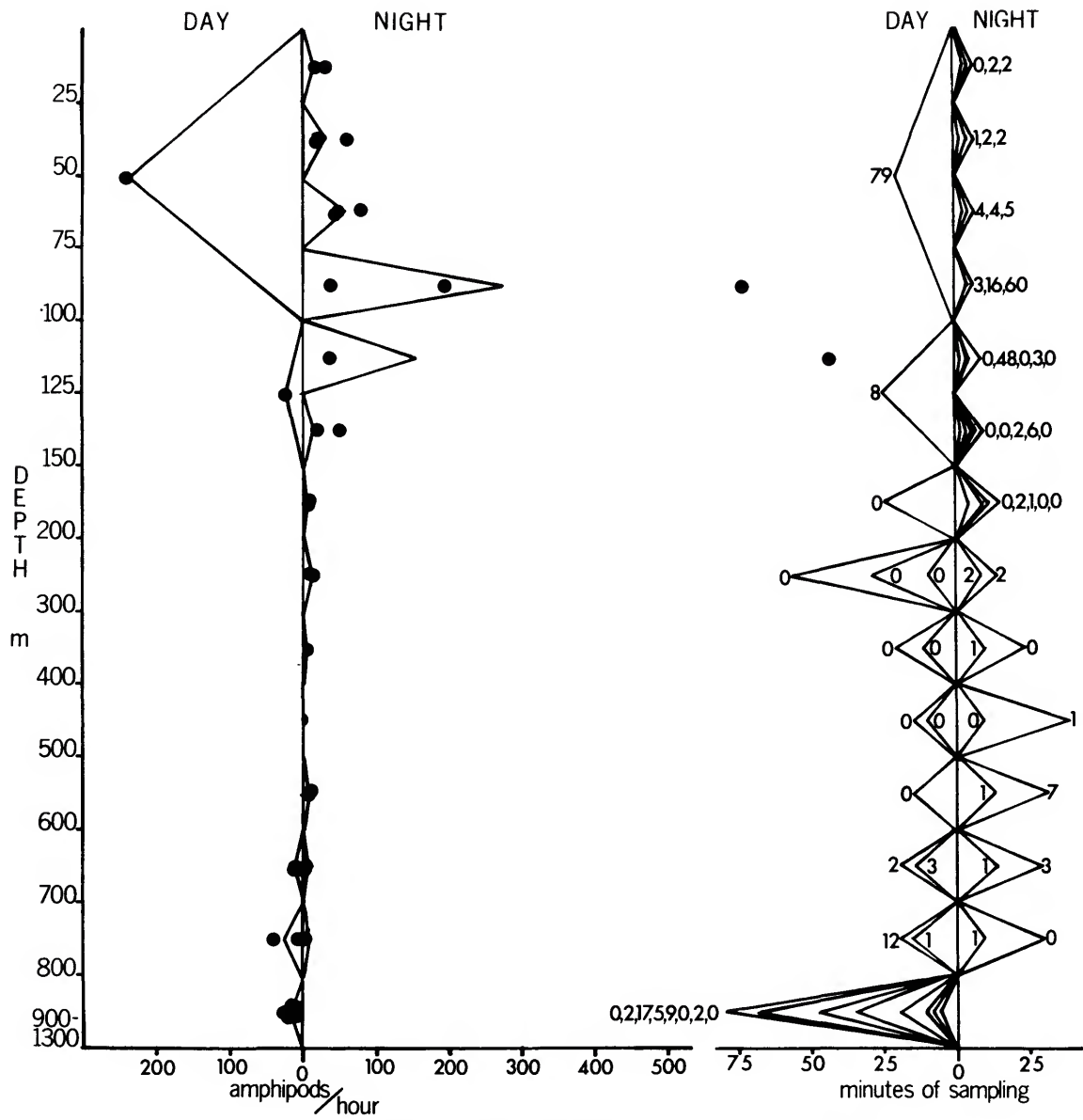


FIGURE 7.—Vertical distribution of *Themisto gaudichaudii*, western eddy, all stages and both sexes combined.

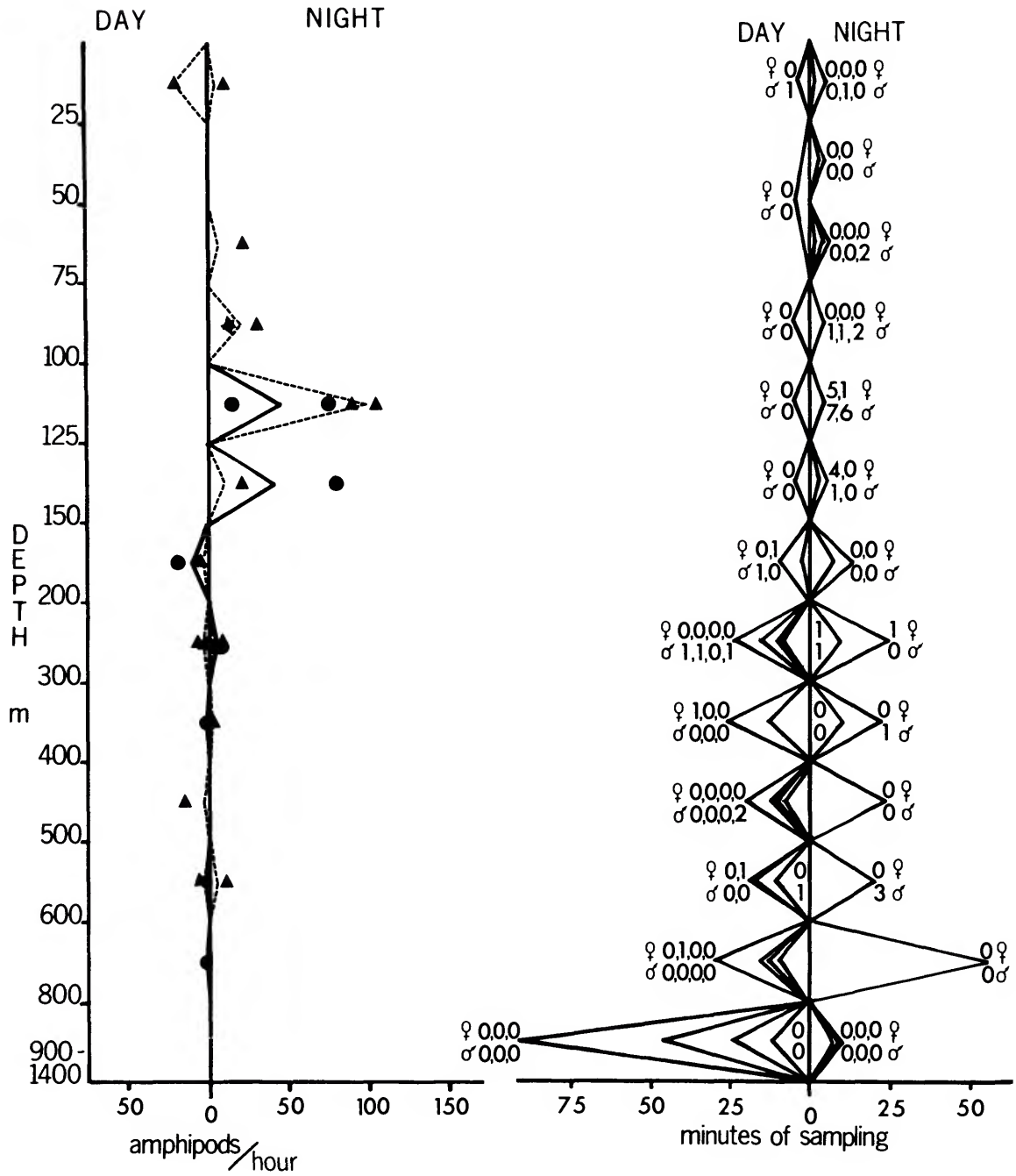


FIGURE 8.—Vertical distribution of *Themisto gaudichaudii*, eastern eddy, stage 1.

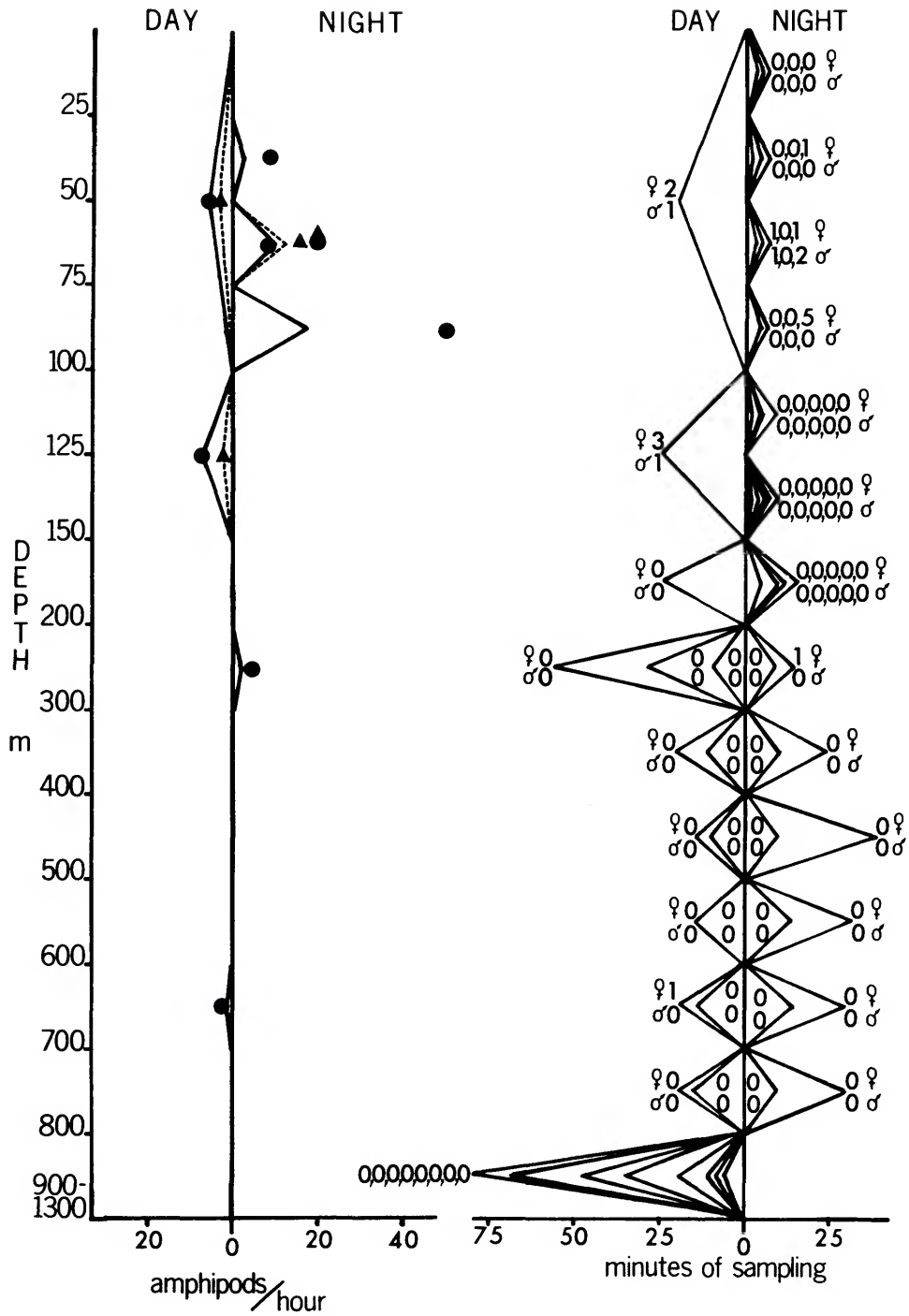


FIGURE 9.—Vertical distribution of *Themisto gaudichaudii*, western eddy, stage 1.

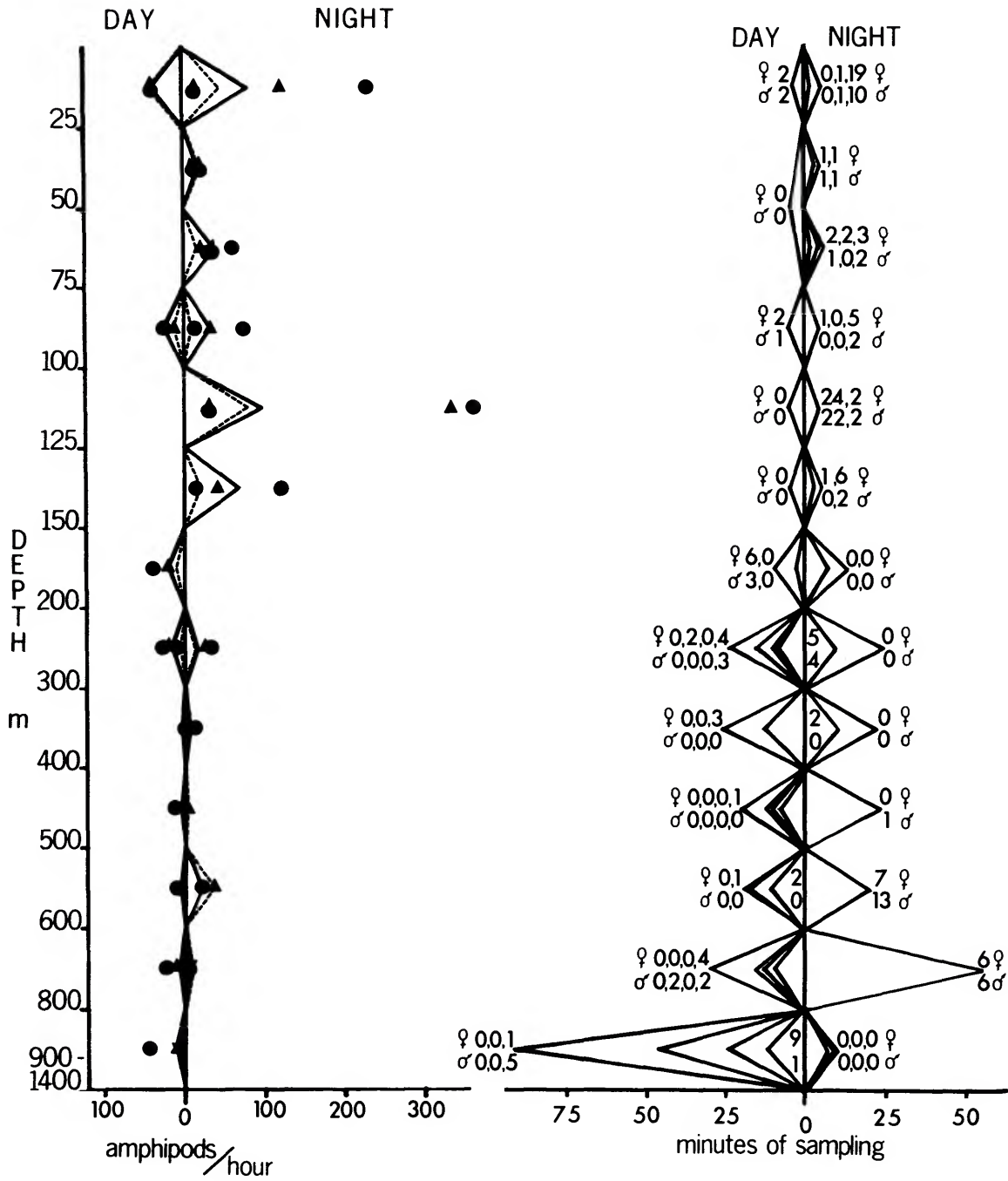


FIGURE 10.—Vertical distribution of *Themisto gaudichaudii*, eastern eddy, stage 2.

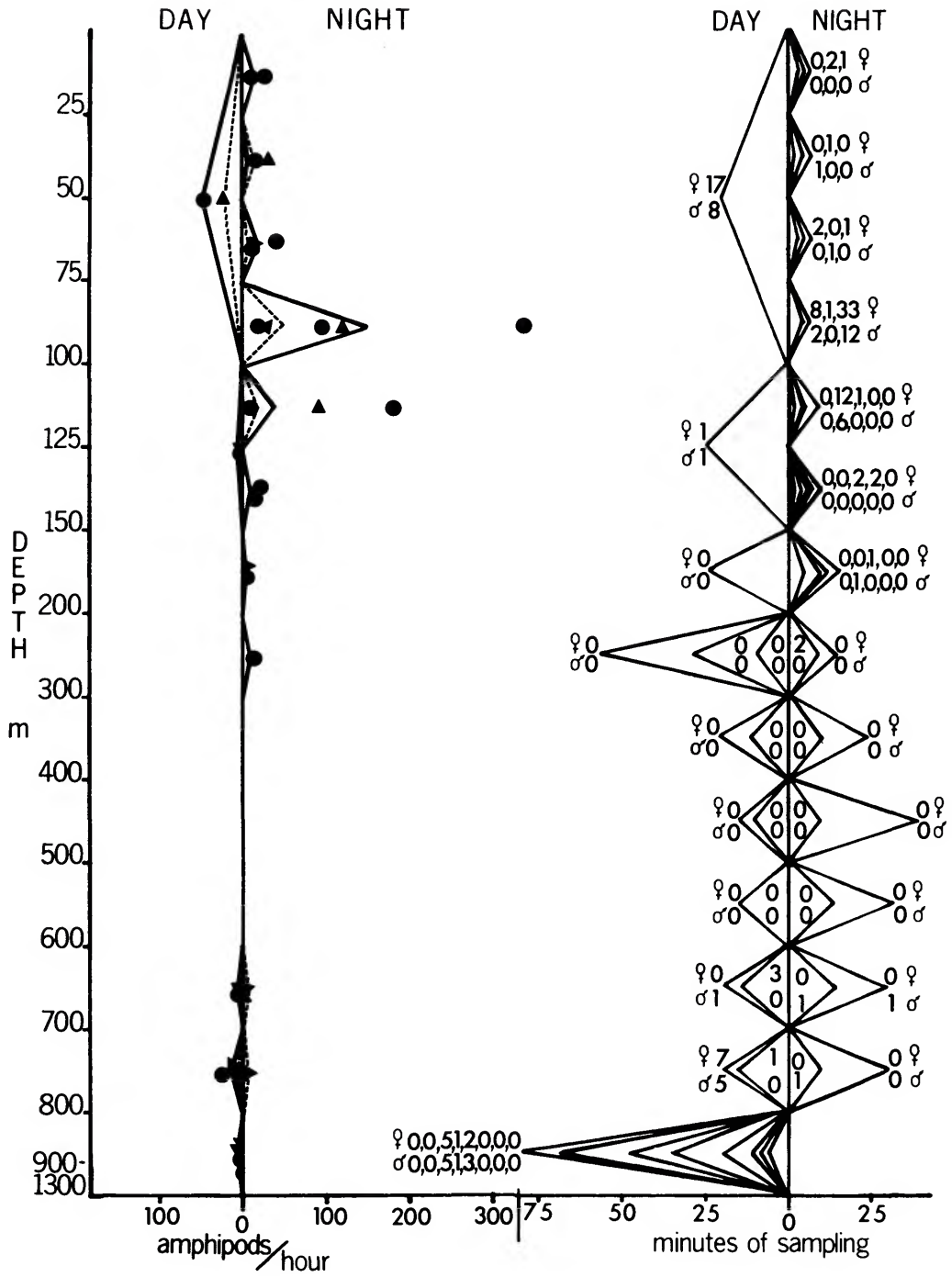


FIGURE 11.—Vertical distribution of *Themisto gaudichaudii*, western eddy, stage 2.

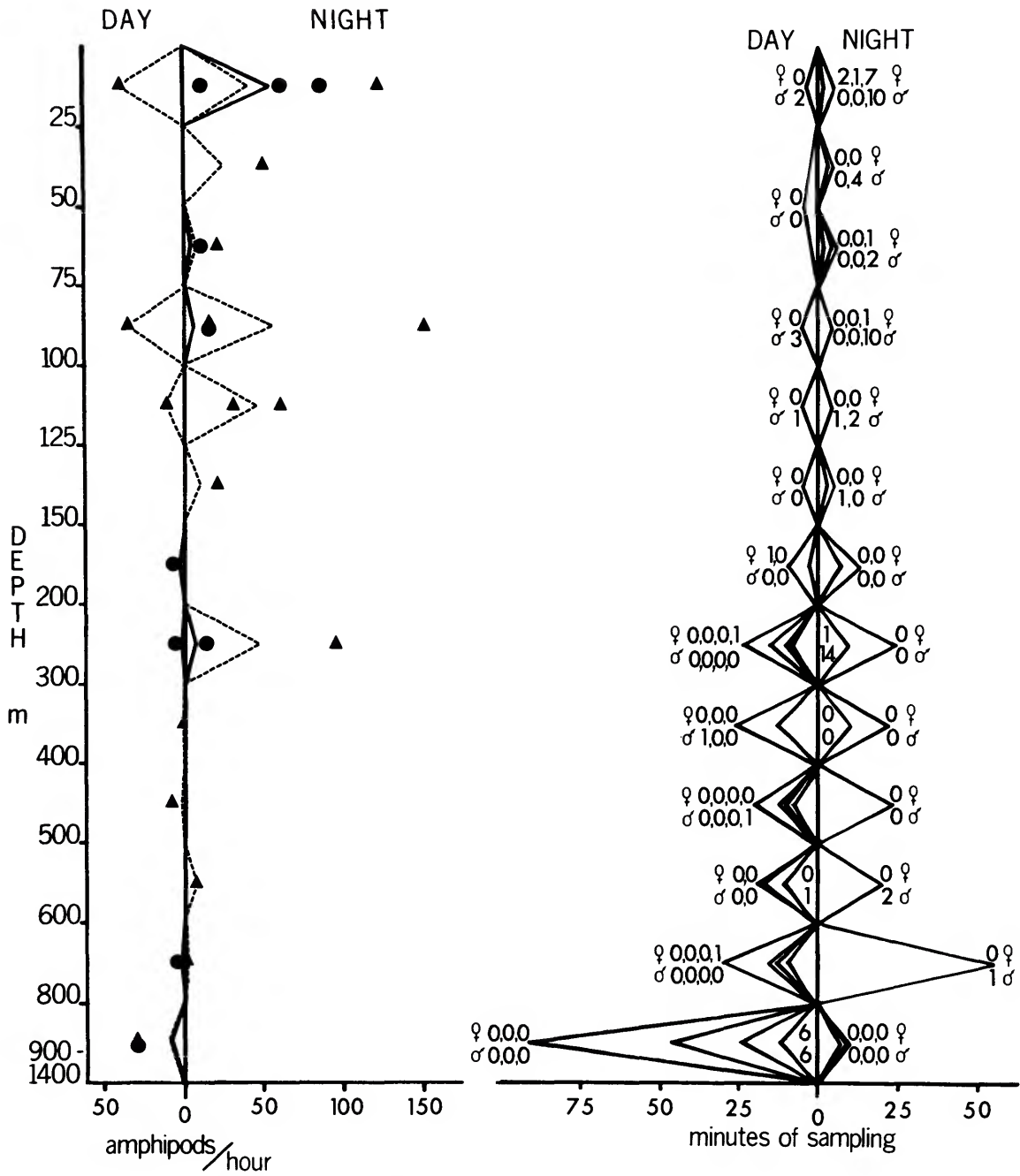


FIGURE 12.—Vertical distribution of *Themisto gaudichaudii*, eastern eddy, stage 3.



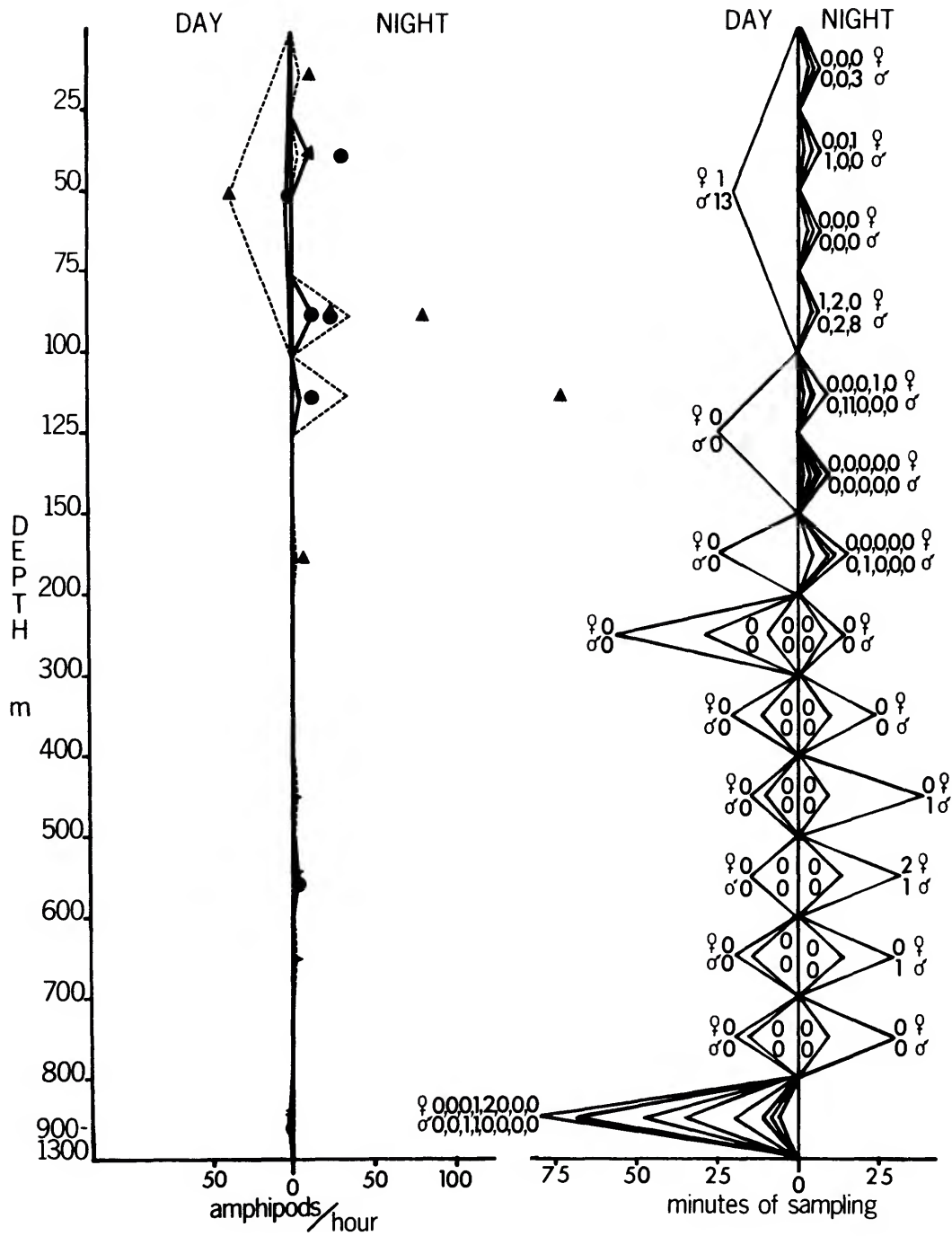


FIGURE 13.—Vertical distribution of *Themisto gaudichaudii*, western eddy, stage 3.

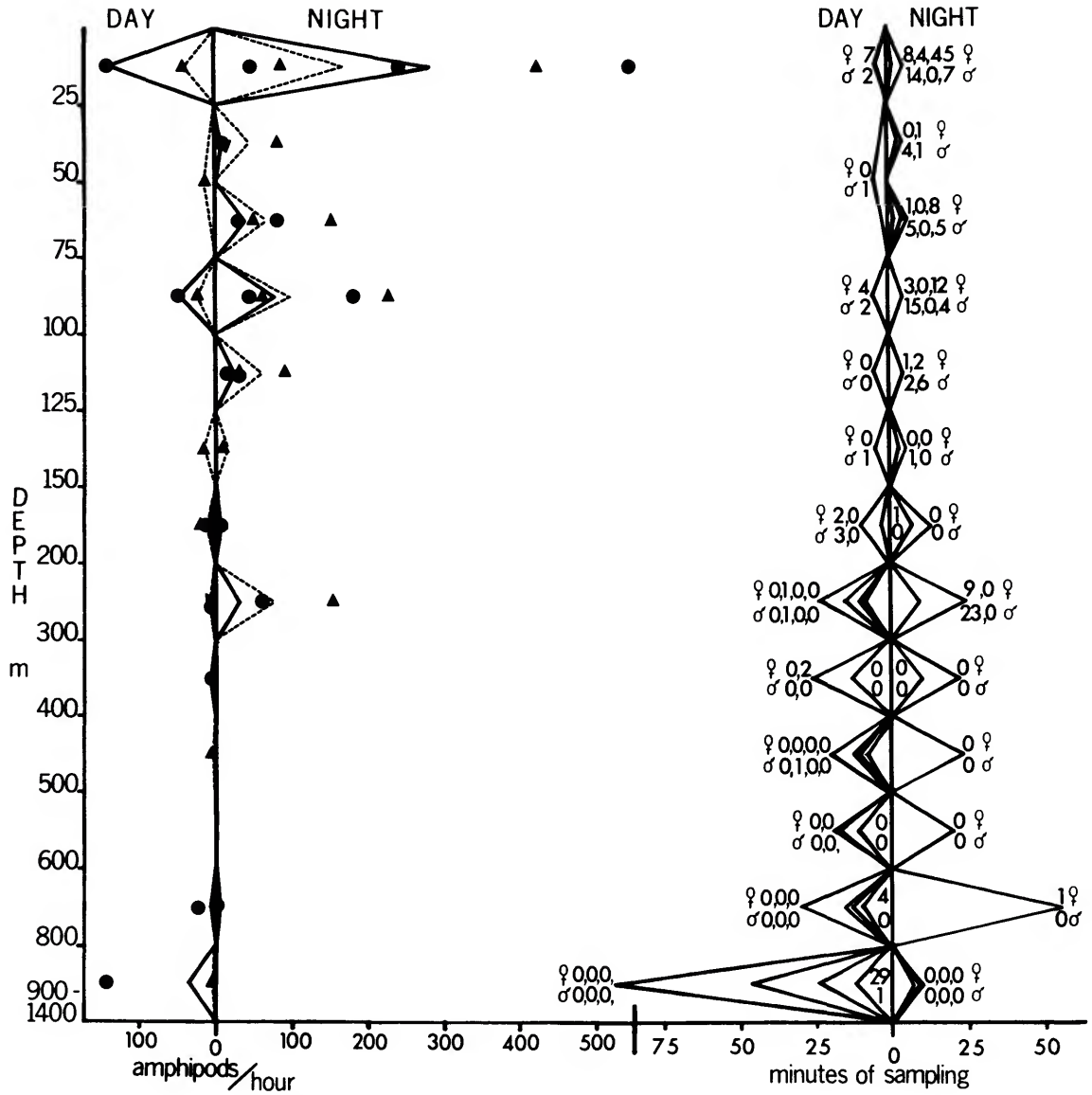


FIGURE 14.—Vertical distribution of *Themisto gaudichaudii*, eastern eddy, stage 4 (adults).

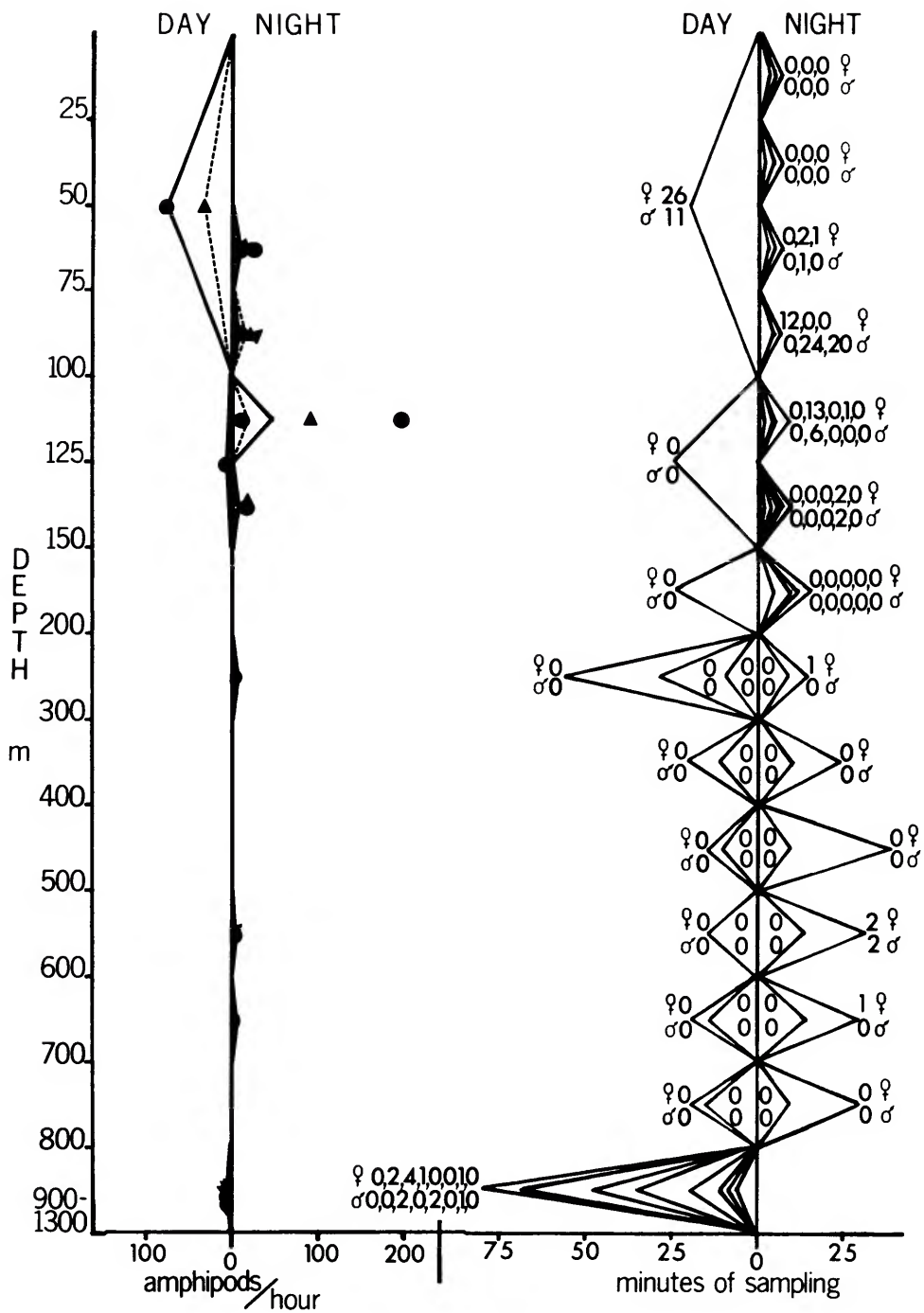


FIGURE 15.—Vertical distribution of *Themisto gaudichaudii*, western eddy, stage 4 (adults).

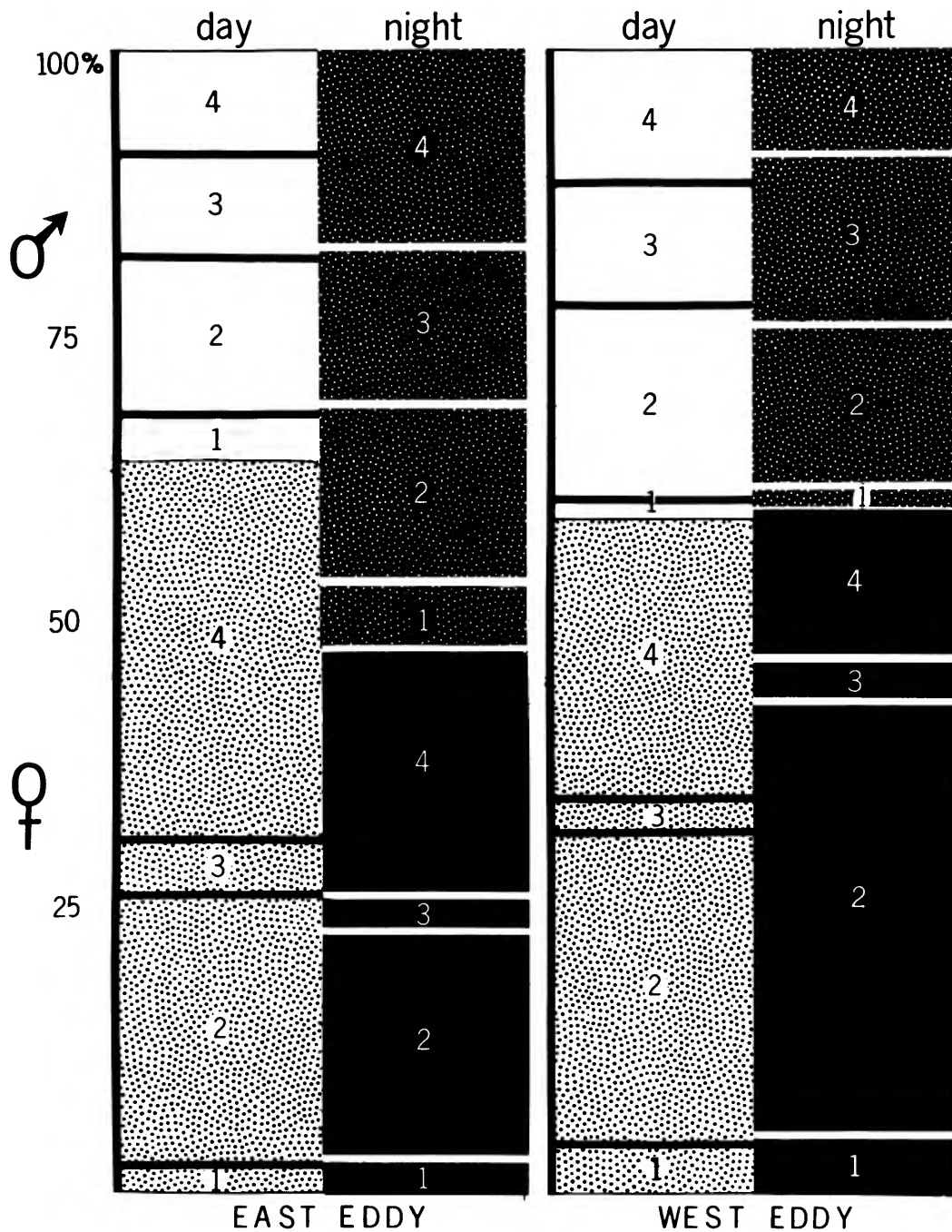


FIGURE 16.—*Themisto gaudichaudii*, growth stages in eastern and western eddies of DWD-106, in percentages of total specimens caught in cruise 2 (juveniles = stages 1-3, adults = stage 4).

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