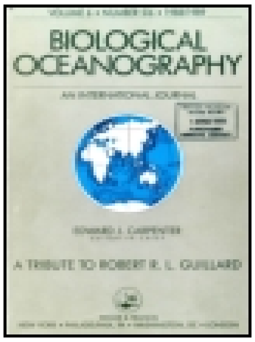

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Vertical Distributions of Continental Shelf Zooplankton in Stratified and Isothermal Waters

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Abstract Fine-scale vertical zooplankton distributions were compared in October 1978 on a cross-shelf transect south of Long Island, New York, at a time-series station south of Long Island, and at a time-series station on Georges Bank. Samples were collected at 5 to 10-m depth intervals with a pumping system and fine mesh (102 μm) nets. The waters south of Long Island were strongly stratified, whereas those of Georges Bank were isothermal. Juvenile or adult copepods accounted for a mean of 91% of the total number of animals collected. Of these, one species (*Oithona similis)* was overwhelmingly dominant, accounting for a mean of 50% of the total number of zooplankters collected. Comparison of our values for the abundance of *O.*

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similis with those obtained with coarser meshes of nets in previous investigations in these waters during the same season suggest that these previous studies may have underestimated the abundance of *O. similis* by at least a factor of 20.

Vertical distributions of some of the same dominant copepod species were markedly different in stratified (Long Island) and well-mixed (Georges Bank) waters. Further, there were distributional differences for different species under the same hydrographic conditions, or in one case for different sexes or developmental stages of the same species. There were few patterns suggestive of diel vertical migration in the stratified water, and these were not consistent. No patterns suggestive of migration were apparent in the isothermal water.

Due to the likely intrusion of offshore water over the New York shelf, which is known to occur in late summer and early autumn, approximately half of the copepod species collected were considered to be offshore warm water transients.

KEY WORDS: *Zooplankton, continental shelf, vertical distribution, New York Bight, Georges Bank.*

Introduction

Numerous studies, primarily in oceanic waters, have shown that zooplankton are distributed heterogeneously with depth (reviews by Russell, 1927; Banse, 1964; Vinogradov, 1970). The reasons for this include both active behavior of the animals themselves (i.e., vertical migration) as well as passive responses to changing hydrography.

Although there have been several seasonally and/or taxonomically comprehensive investigations of the zooplankton of the shelf systems of the New York Bight and Georges Bank (Bigelow and Sears, 1939; Riley et al., 1949; Grice and Hart, 1962; Wiebe et al., 1973; Judkins et al., 1980; Stepien et al., 1981), the samples for these studies were largely collected with vertical or oblique net tows. Thus, these studies reveal little on the vertical distributions of zooplankton in these waters. Further, all of these studies employed nets with meshes >202 μm, and substantial underestimation of the total zooplankton assemblage with nets of this mesh has been demonstrated for nearby estuarine waters (Turner, 1982).

In October of 1978 we had an opportunity to examine the vertical distributions of the same shelf zooplankton species under two different hydrographic situations. Samples were collected in stratified waters on a cross-shelf transect and at a time-series station south of Long Island, New York, and at a time-series station in isothermal water on the northeastern corner of Georges Bank. Further, by sampling with a pumping system combined with 102 μm mesh nets, we were able to define fine-scale vertical distributions of animals as small as copepod nauplii. Although our study was not as seasonally comprehensive as others employing net tows in these waters (Grice and Hart, 1962; Judkins et al., 1980; Dagg and Turner, 1982), since late summer to midautumn is a period when numerous transient species are known to occur in both estuarine (Turner, 1981) and shelf (Cox and Wiebe, 1979) waters of the mid-Atlantic region, the present study was performed during the period of the year when the zooplankton are most taxonomically diverse.

We will show that the vertical distributions of most, but not all, of the abundant copepod species were markedly different in the stratified and isothermal situations. Further, we found that the abundance of the dominant copepod species in our samples (*Oithona similis)* was much higher than levels recorded by previous studies of these waters during the same season based upon coarser meshes of nets. Finally, our data reveal substantial variability in the vertical distributions of different copepod species, or possibly for different sexes or developmental stages of the same species, in relation to hydrography and time.

Methods

Samples were collected during Cruise AN 104 of the *R/V Atlantis II* in October of 1978. The locations of the sampling sites south of Long Island are presented in Figure 1. In addition, locations, dates, and sampling times for the stations on the Long Island transect, Long Island time series, and Georges Bank time series are presented in Table 1.

Zooplankton was collected from discrete depths at 5 to 10-m intervals over most of the water column, using a pumping system

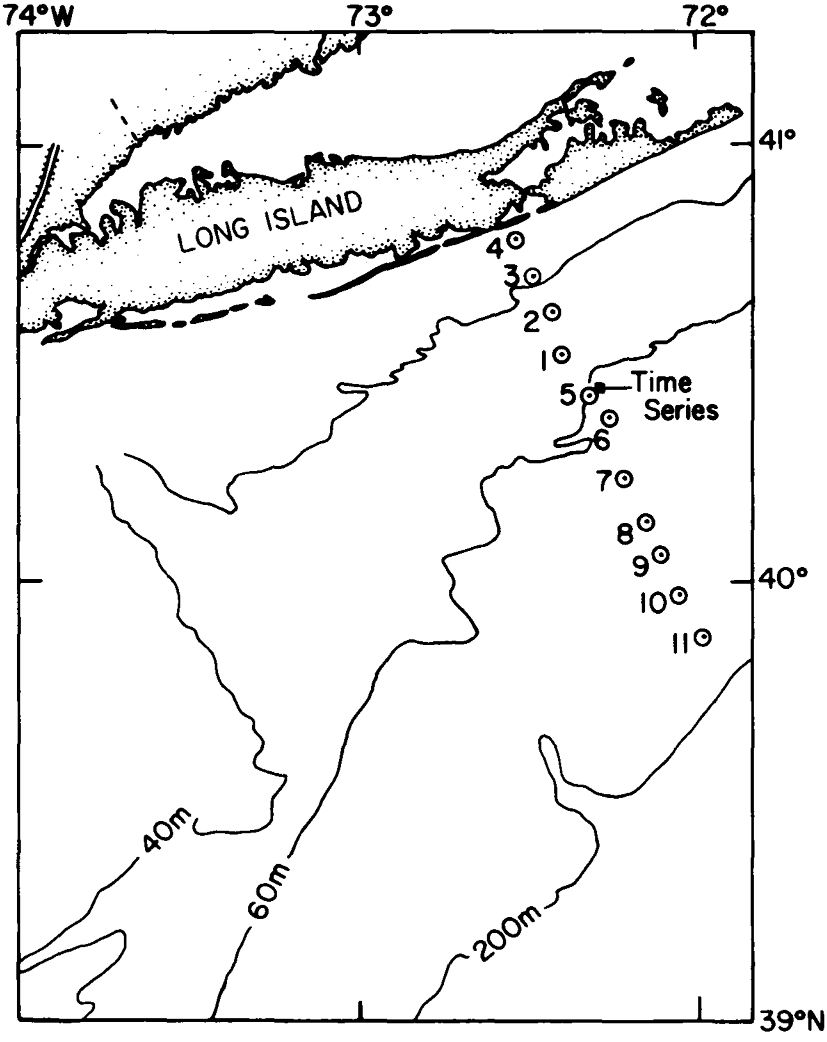

Figure 1. Locations of continental shelf stations occupied during the Long Island transect and time-series station.

Table 1
Locations, dates, and pumping times for the stations from which zooplankton and/or hydrographic data were collected.

Station	Latitude (N)	Longitude (W)	Date	Times of beginning and End of Pump Casts
LONG ISLAND TRANSECT				
1	40°31.8'	72°23.6'	10/12/78	0100-0155
2	40°37.4'	72°25.5'	"	---------
3	40°42.4'	72°28.7'	"	0637-0722
4	40°47.6'	72°31.6'	"	---------
5	40°26.2'	72°18.5'	"	1511-1610
6	40°21.1'	72°15.4'	"	---------
7	40°15.2'	72°12.5'	"	2053-22
		°06.0'	"	0353-0515
10	39°58.9'	72°02.9'	"	---------
11	39°53.2'	72°59.4'	"	1057-1220
LONG ISLAND TIME SERIES				
(40°26' N, 72°18' W)			10/14/78	0218-0317
			"	0500-0615
			"	0825-0941
			"	1208-1319
			"	1623-1740
			"	2016-2123
			10/15/78	0016-0123
			"	0442-0626
GEORGES BANK TIME SERIES				
(42°00' N, 66°40' W)			10/17/78	1620-1739
			"	2011-2120
			10/18/78	0021-0122
			"	0442-0607
			"	0822-0938
			"	1236-1345

described by Miller and Judkins (1981). Approximately 850 liters/min were drawn through a 10-cm internal diameter hose. At each depth this system was flushed for approximately 5 min and then 1,000 gal (3.7854 m^3) of seawater was pumped through a 102 μm mesh net on deck. A flow meter attached in line near the hose outflow measured the volume of water sampled, and a TSK time-depth recorder attached to the hose intake verified sampling depths. Samples were preserved in 15% formalin:seawater solutions.

In the laboratory, samples from the Long Island transect were reduced with a Folsom plankton splitter until aliquots of 406 to 1,374 ($\overline{X}$ = 609) animals each were obtained. All organisms in each aliquot were counted, and most were identified to species. Most of the copepods were distinguished further as to whether specimens were adult males, adult females, or copepodites. These distinctions were not made for *Oithona similis* and *Oithona atlantica;* thus the values reported here are for the totals of both sexes and all copepodites of these species. Copepod nauplii were counted but not identified. Specimens of holoplankters other than copepods and meroplankters were, for the most part, identified only to major group. Samples from the Long Island and Georges Bank time-series stations were reduced with a piston pipette, and five aliquots of approximately 300 animals each were removed. All copepods in each aliquot were counted, unless a taxonomic category contained more than 50 individuals, in which case the category was not counted in subsequent aliquots.

Pump casts were made every 4 hr at the Georges Bank time-series station, and every 3-4 hr at the Long Island time-series station (Table 1). On the Long Island transect pump casts were made at odd-numbered stations (Table 1).

Results

Long Island Transect

Hydrography

The period of sampling south of Long Island was prior to the autumn overturn. Temperature contours (Figure 2) reveal that the

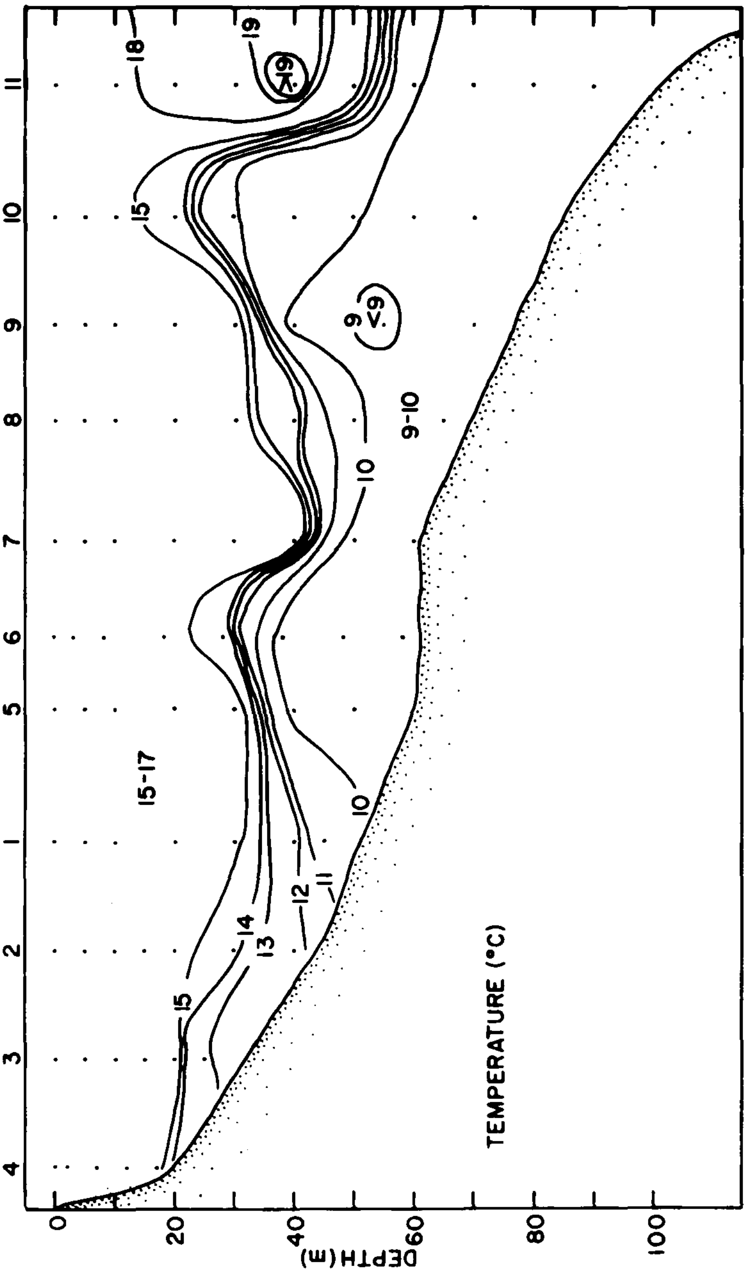

Figure 2. Vertical temperature structure during the Long Island transect.

water column was stratified with warm (15–17°C) water blanketing the upper 20 to 40 m over the entire width of the shelf. In addition, there was a tongue of warmer (18 to 10°C) water at intermediate depth near the shelf break. Below the warm water there was a sharp thermocline over the entire shelf, where temperatures dropped 5°C over vertical intervals of 10 to 20 m. Seaward of approximately the 50-m isobath the bottom was covered by colder (9 to 10°C) water, which corresponds to the "cold pool" or "remnant winter water" described by Ketchum and Corwin (1964).

Zooplankton Numbers

Total zooplankton numbers for Long Island transect samples ranged from 599 to 30,095/m^3 ($\bar{X}$ = 7,596/m^3). Of these, adult copepods, copepodites, and copepod nauplii were overwhelmingly predominant, accounting for 42 to 99% ($\bar{X}$ = 91%) of the total number of animals counted. Further, of the copepods, three species made a disproportionately large numerical contribution. The numbers of *Oithona similis* ranged from 82 to 23,298/m^3 ($\bar{X}$ = 3,845/m^3), and this species alone accounted for 6 to 88% ($\bar{X}$ = 50%) of the total number of zooplankters counted. In addition, adults and copepodites of *Centropages typicus* and *Paracalanus parvus* were recorded in numbers of up to 3,781/m^3 ($\bar{X}$ = 1,031/m^3) and 3,669/m^3 ($\bar{X}$ = 1,011/m^3), respectively. The combination of adults and copepodites of these three species accounted for 24 to 93% ($\bar{X}$ = 75%) of the total number of zooplankters recorded for the transect samples. Zooplankton were most abundant at the two nearshore stations and least abundant over the outer shelf (Figure 3).

*Vertical Distributions (*Oithona similis)

Oithona similis was distributed throughout the water column, and no consistent relationships with depth or time of day were apparent. Comparison of the vertical distributions of this species (Figure 4) with those of total zooplankton (Figure 3) reveals striking similarity of patterns and attests to the numerical predominance of this species.

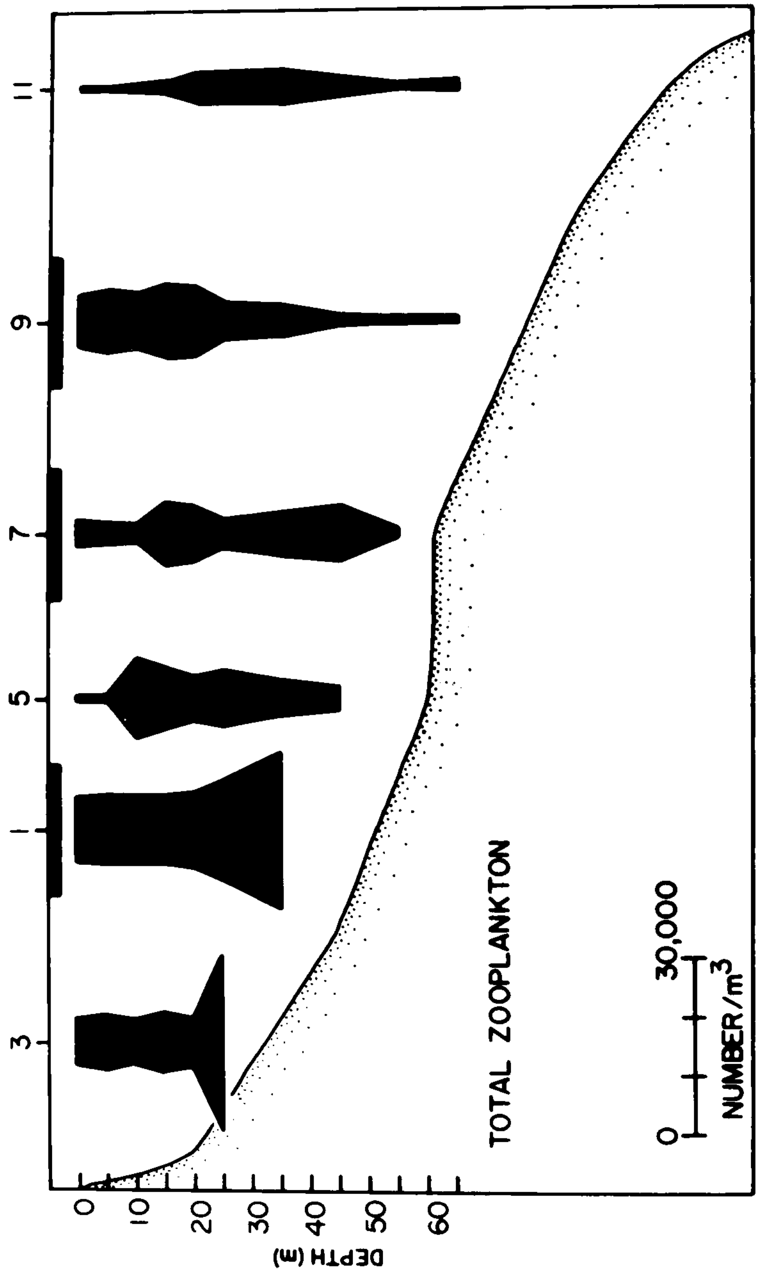

Figure 3. Vertical and inshore–offshore distributions of total zooplankton at pump stations on the Long Island transect. Station numbers are given on the top axis, and dark horizontal bars identify stations sampled at night.

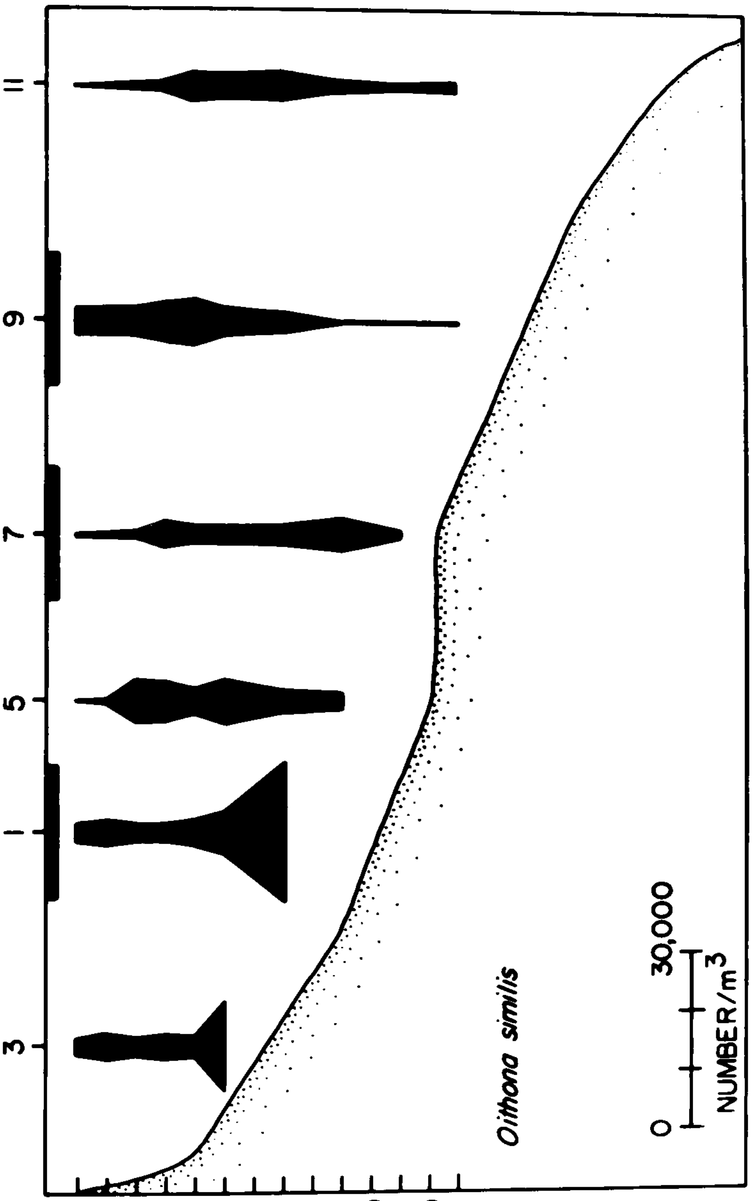

Figure 4. Vertical and inshore–offshore distributions of *Oithona similis* at pump stations on the Long Island transect. Station numbers are given on the top axis, and dark horizontal bars identify stations sampled at night.

*Vertical Distributions (*Centropages typicus)

The vertical distributions of *Centropages typicus* females (Figure 5, upper), males (Figure 5, middle), and copepodites (Figure 5, lower) were different from those of *Oithona similis. C. typicus* was collected largely from depths above the thermocline, and no consistent patterns indicative of vertical migration were apparent. *C. typicus* males and females were most abundant at Station 1 (approximately 37 km from shore), and they progressively declined in abundance in a seaward direction. Neither males nor females of this species were recorded from any depth at Station 11 (approximately 112 km from shore). Likewise, *C. typicus* copepodites were abundant at Station 1, but these abundance levels were approached or, at 15-m depth, exceeded at Station 9 (approximately 88 km from shore). Also, small numbers of *C. typicus* copepodites were collected at Station 11. Overall, *C. typicus* copepodites were at least five times as abundant as either male or female adults (compare scales in Figure 5).

*Vertical Distributions (*Paracalanus parvus)

The vertical distributions of *Paracalanus parvus* females (Figure 6, upper), males (Figure 6, middle), and copepodites (Figure 6, lower) revealed maximum levels of abundance above the thermocline. While males exhibited relatively even vertical distributions at all times, females were relatively more abundant near the surface during darkness (Stations 1, 7, and 9) than during daylight (Stations 5 and 11). While these patterns hint at vertical migration for females, the collection of maximum numbers of females at Station 3 at the surface during daylight suggests that either the bottom depth at Station 3 (32 m) was too shallow to allow migration, or more likely, that migration by females was intermittent. No suggestion of vertical migration was apparent from the distributions of copepodites. As with copepodites of *C. typicus,* those of *P. parvus* substantially outnumbered adults.

Vertical Distributions (Other Moderately Abundant Copepod Taxa)

While adults and late copepodites of *Pseudocalanus* sp. (the taxonomy of this organism is uncertain, Corkett and McLaren, 1978)

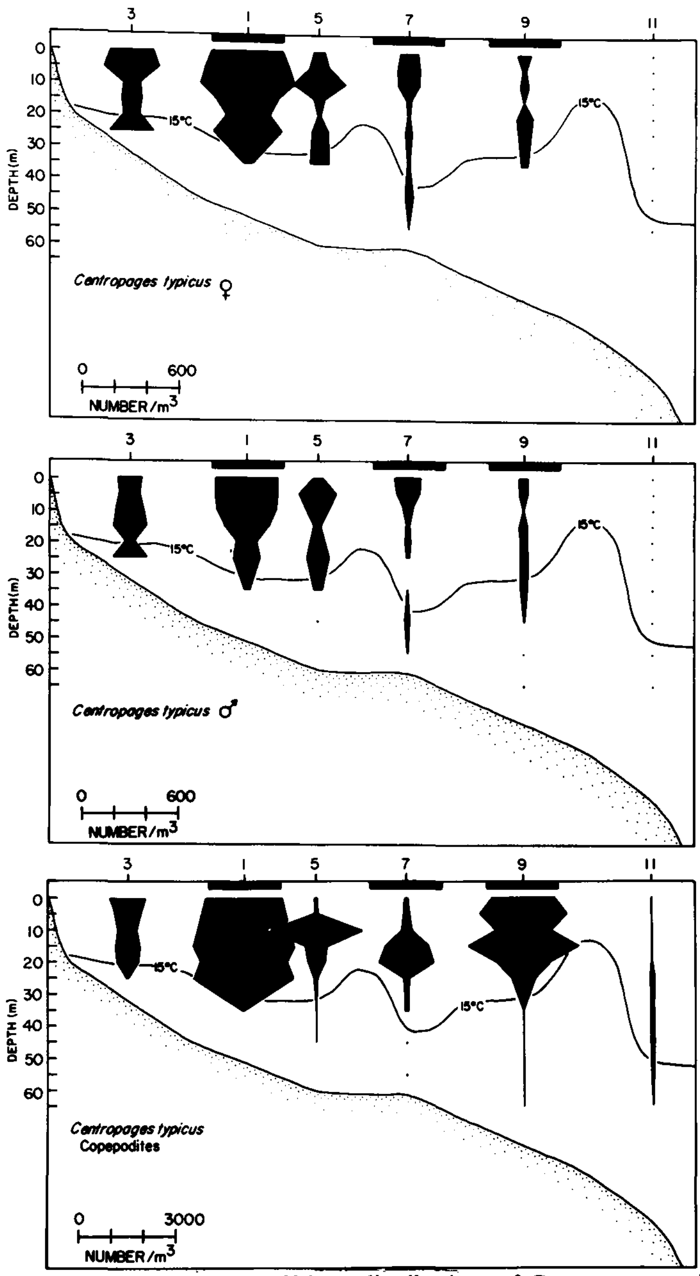

Figure 5. Vertical and inshore–offshore distributions of *Centropages typicus* females (upper), males (middle), and copepodites (lower) in relation to the 15°C isotherm at pump stations on the Long Island transect. Station numbers are given on the top axis, and dark horizontal bars identify stations sampled at night.

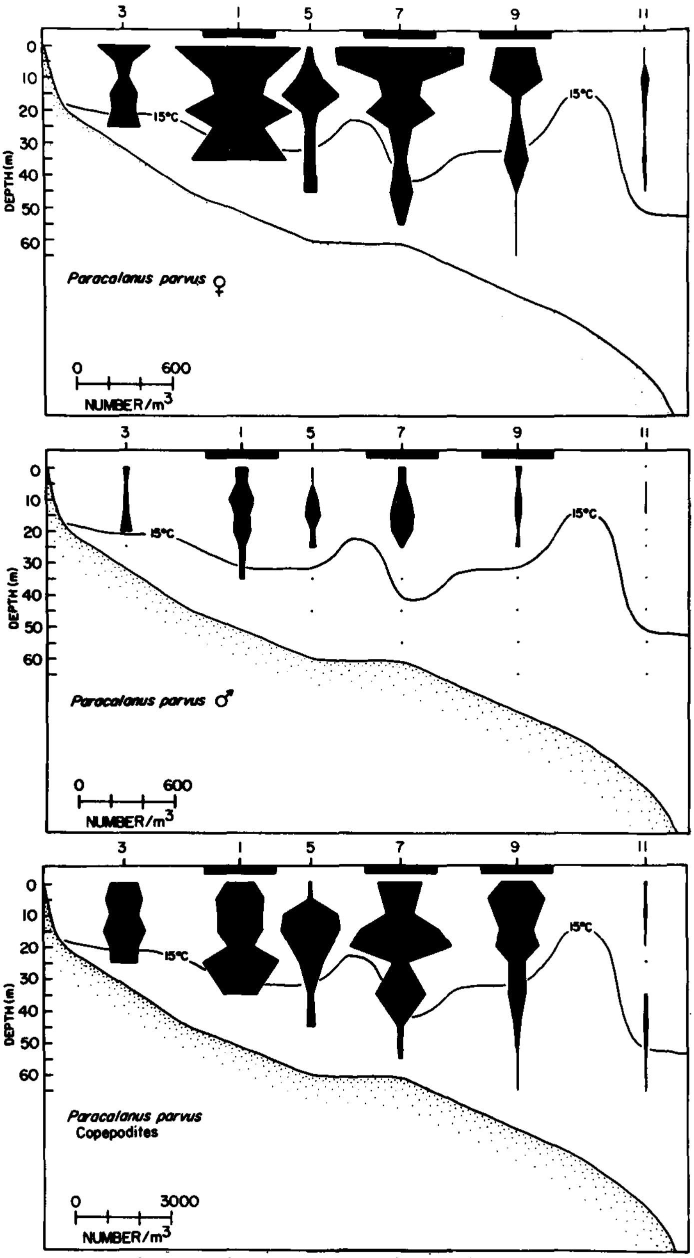

Figure 6. Vertical and inshore–offshore distributions of *Paracalanus parvus* females (upper), males (middle), and copepodites (lower) in relation to the 15°C isotherm at pump stations on the Long Island transect. Station numbers are given on the top axis, and dark horizontal bars identify stations sampled at night.

were collected in numbers < 150/m^3 during October, this species was a codominant with *Calanus finmarchicus* in the same area during colder periods of the year (Dagg and Turner, in press). While this suggests that *Pseudocalanus* might be confined to colder bottom waters in October, this proved not to be the case (Figure 7). At all stations where *Pseudocalanus* was present, except for Station 9, this species was collected mostly above the thermocline. At Station 9, however, this species was collected only below the thermocline. Further, since Stations 1 and 9 were both sampled during darkness, vertical migration cannot be implicated to explain these patterns.

Two additional species were, however, largely confined to cooler bottom waters. Adult and late copepodites of *Calanus finmarchicus* (Figure 8), and particularly *Oithona atlantica* (Figure 9), exhibited maximum levels of abundance in cold pool (< 10°C) or thermocline (10 to 15°C) water near the 60-m isobath at Station 7. A few *C. finmarchicus* adults and copepodites were collected in either surface or intermediate-depth waters at Stations 1 and 9, respectively. Since both of these pump casts were made at night, and *Calanus finmarchicus* is a reported vertical migrator (Marshall and Orr, 1955), these data may indicate vertical migration by a portion, but not all, of the population of this species.

In addition to identifiable adults and copepodites of the species discussed above, unidentified copepod nauplii, likely of numerous species, were abundant. The vertical distributions of nauplii (Figure 10) exhibited no consistent patterns of abundance in relation to position of the thermocline, time of day, or distance from shore.

Distributions of Rare Species and Patterns of Diversity

Due to examination of slightly larger aliquots and more complete taxonomic identifications, taxonomic coverage of the zooplankton assemblage was most complete for the Long Island transect. In addition to the copepod species discussed above, additional copepod species that were collected in low numbers (< 100/m^3) are listed in Table 2. Certain calanoids, such as *Acartia hudsonica, A. tonsa, Labidocera aestiva, Parvocalanus crassirostris, Temora*

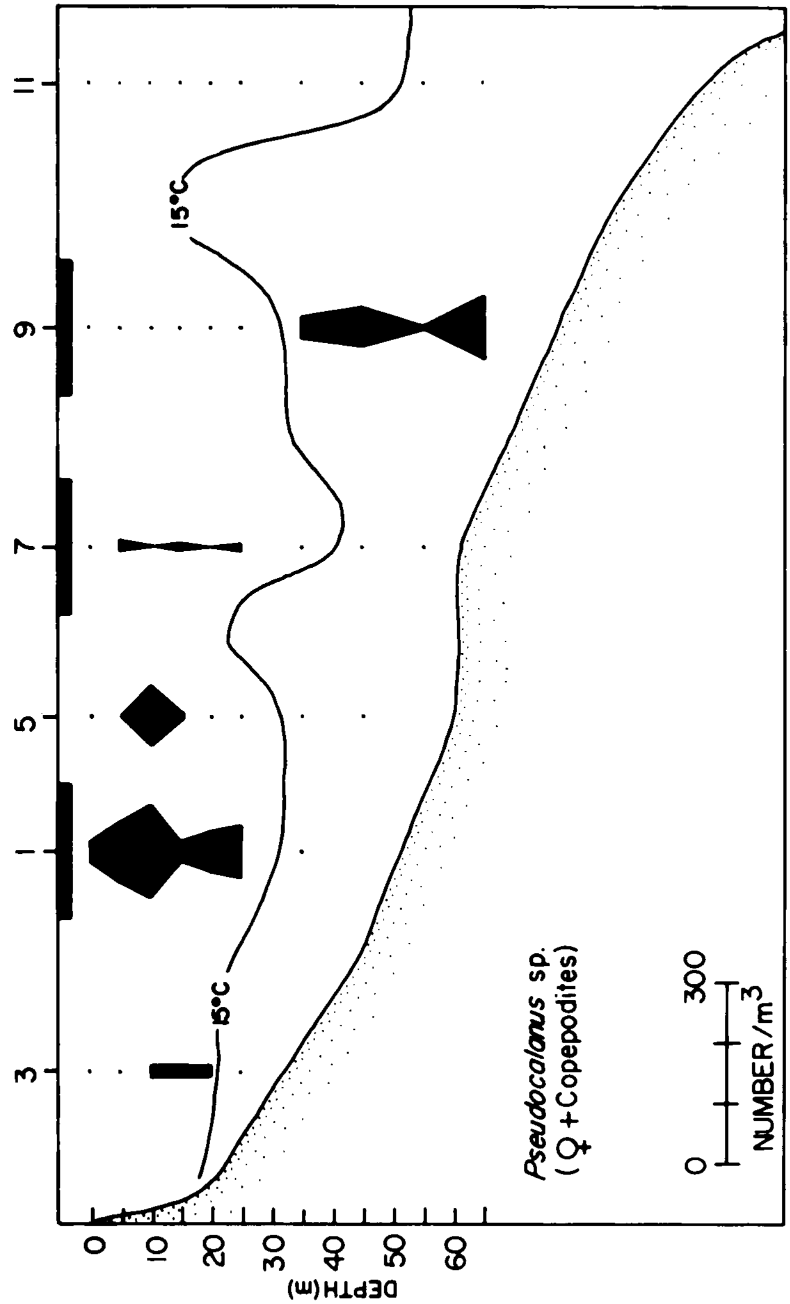

Figure 7. Vertical and inshore–offshore distributions of *Pseudocalanus* sp. in relation to the 15°C isotherm at pump stations on the Long Island transect. Station numbers are given on the top axis, and dark horizontal bars identify stations sampled at night.

Table 2
Occurrence by depth of rare copepod species collected in pump samples on the Long Island transect. Species include adults or positively identified copepodites; numbers refer to depths (in meters) of collection.

Species	Station 3	Station 1	Station 5	Station 7	Station 9	Station 11
CALANOIDA						
Acartia hudsonica	10	0,15	-----	-----	-----	-----
A. longiremis	0,5,10,15, 20,25	5,20,25	20,25,35, 45	0,5,15,20 25,35,45	0,5,10,15, 20,25,35	20,25,35,45, 55
A. tonsa	-----	0,10,25	-----	-----	-----	-----
Calocalanus pavo[a]	-----	-----	20	0,15,35, 45	5,10,20, 25	0,5,10,15,35, 45,55,65
Candacia armata[b]	10,15,20, 25	10,15,25	5,20,25, 35	0,5,10,25, 35,45	5,15,20,35	-----
Centropages bradyi[b]	-----	-----	15,20	10,20,25,35	25	55
C. velificatus	-----	-----	0,5	-----	-----	-----
Clausocalanus arcuicornis[a]	-----	5	-----	-----	-----	-----
C. furcatus[a,b]	0,5,10,15, 20	0,5,10,15, 25,35	0,45	0,5,10,15,20 25,35,45,55	0,5,10,15 25,35,45,55	-----
C. jobei[b]	-----	-----	0	-----	-----	-----
Labidocera aestiva	0,15,20	-----	5	-----	-----	-----
Mecynocera clausi[a]	15	0,5,10 25,35	10,15,20 25,35,45	10,15,10,25, 35,45,55	5,15,20,25, 35,45,55	15,20,35, 45,55
Metridia lucens	-----	-----	35,45	0,10,15,35, 45,55	0,5,10,20,25, 35,45,55,65	-----
Nannocalanus minor[a,b]	0,5,10,15, 20	15,25	10,15,25	0,5,10,15, 20,25	10,15,25,35,	10,35,45
Parvocalanus crassirostris	0,5,10,15, 20,25	0,5,10,15, 20,25,35	0,5,10,15,20, 25,35	0,5	-----	-----
Phaenna spinifera	-----	-----	-----	5	25	-----
Rhincalanus nasutus[b]	-----	-----	15	-----	-----	-----
Scolecethrix danae[b]	5	-----	-----	-----	-----	15
Temora longicornis	-----	0,10,15	-----	-----	-----	-----
T. stylifera[a,b]	0,10,15,20 25	0	-----	10	-----	0,5
T. turbinata		-----	0,5,15	0,5,10	-----	-----
Undinula vulgaris[a]	5,10,15	25	15,45	0,5,25	10,35	25
CYCLOPOIDA						
Corycaeus latus	-----	0,5	10	-----	-----	0,5
C. speciosus[b]	0,5,10,15, 20	0,5,10,15, 20,25,35	0,5,10,20, 25	0,5,10,15, 20,25	0,10,15,25	5,10,15,35

C. venustus	0,5,10,15,20	0	0,5,10,15,25	10	0	-----
Oncaea mediterranea	-----	5	-----	-----	-----	-----
O. venusta[b]	0,5,10,15, 20,25	0,5,10,15, 20,25,35	0,5,10,15,20, 25,35,45	0,5,10,15, 20,25,35	0,5,10,15,20, 25,35,55	10,15
Farranula gracilis	-----	-----	-----	-----	-----	0
HARPACTICOIDA						
Clytemnestra rostrata	0,10,15	15,20	35	0,5,10,15	-----	10,15,25,35
Macrosetella gracilis[a]	-----	-----	-----	-----	0,20	0,5,10,15
Microsetella norvegica	0,5,10,15, 20,25	5,15,20,25, 35	0,5,35,45	0,5,10,15, 35,45,55	0,10,20,35, 45,55,65	0,5,10,45, 55

[a]Grice and Hart (1962) and
[b]Judkins et al. (1980) found that these species typically inhabit slope and oceanic waters, and stated that their presence in shelf waters south of Long Island in autumn was probably related to shoreward drift of waters that had originated offshore.

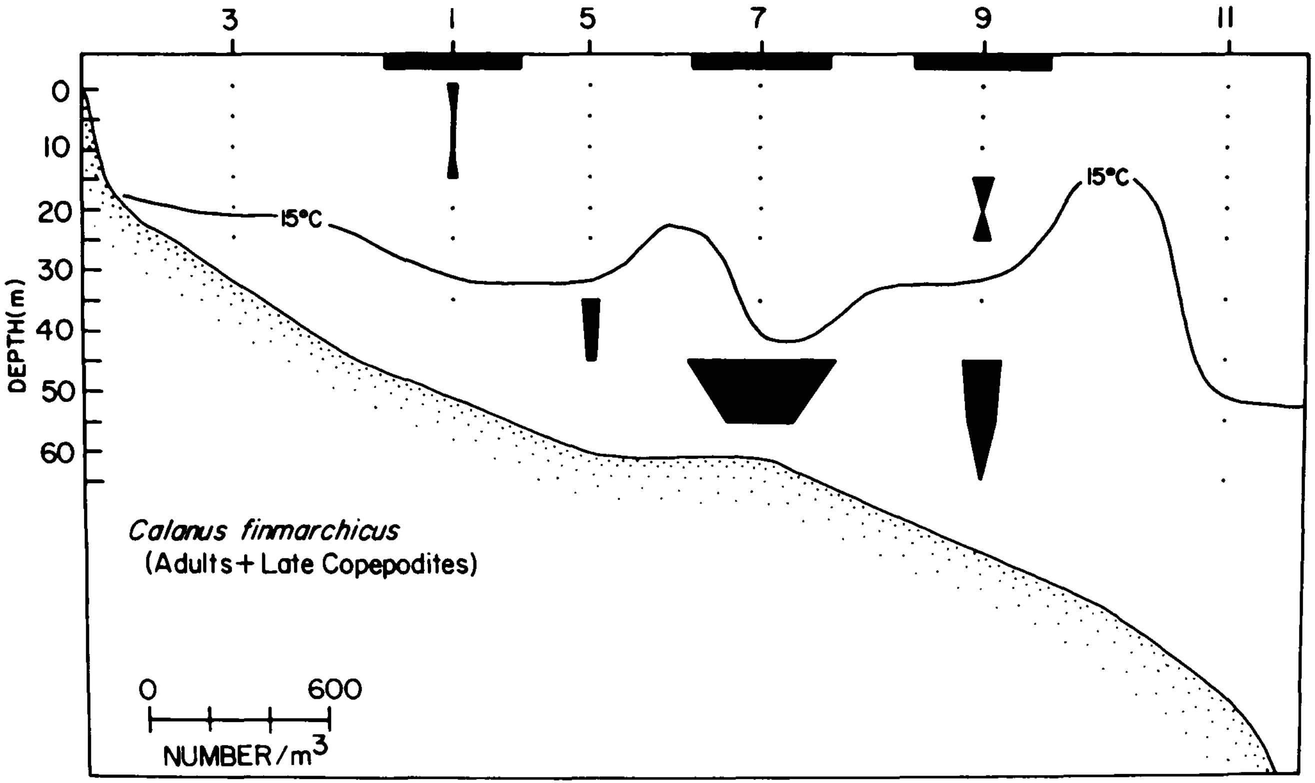

Figure 8. Vertical and inshore–offshore distributions of *Calanus finmarchicus* in relation to the 15°C isotherm at pump stations on the Long Island transect. Station numbers are given on the top axis, and dark horizontal bars identify stations sampled at night.

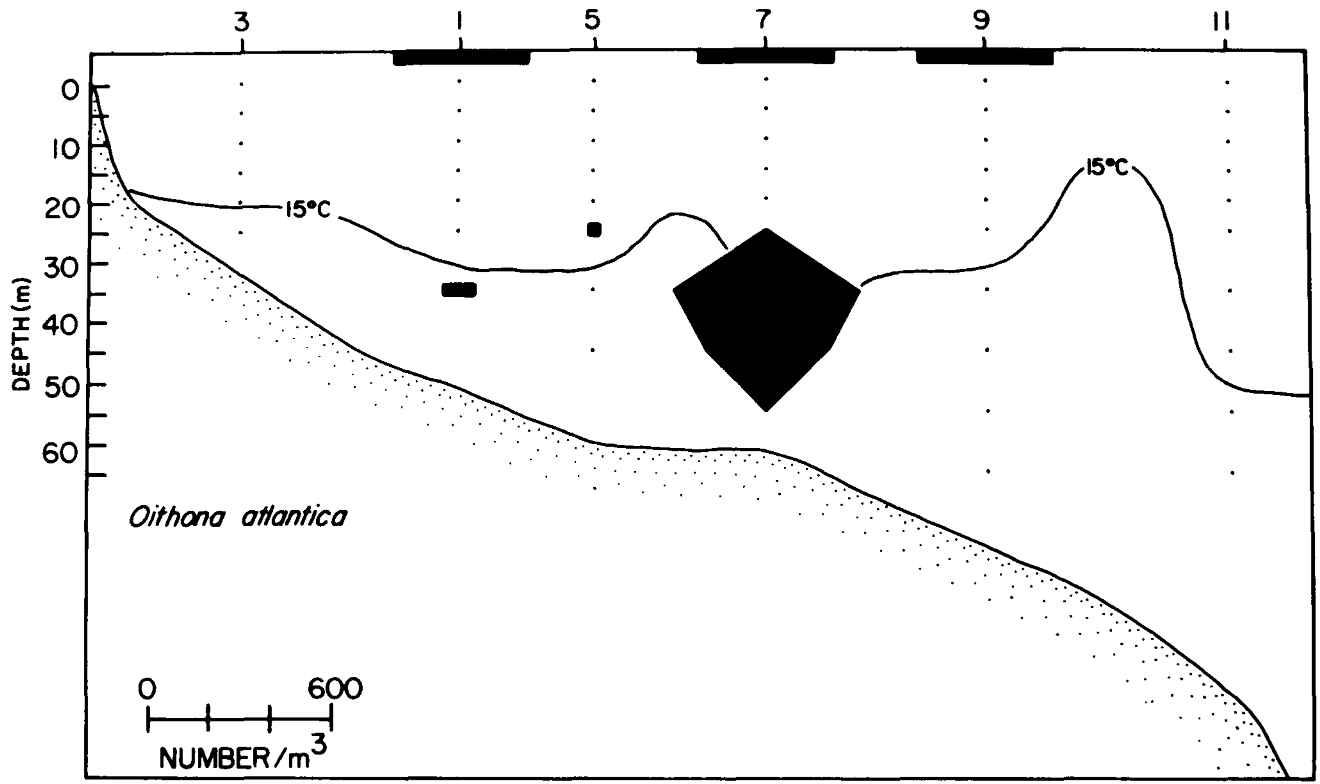

Figure 9. Vertical and inshore-offshore distributions of *Oithona atlantica* in relation to the 15°C isotherm at pump stations on the Long Island transect. Station numbers are given on the top axis, and dark horizontal bars identify stations sampled at night.

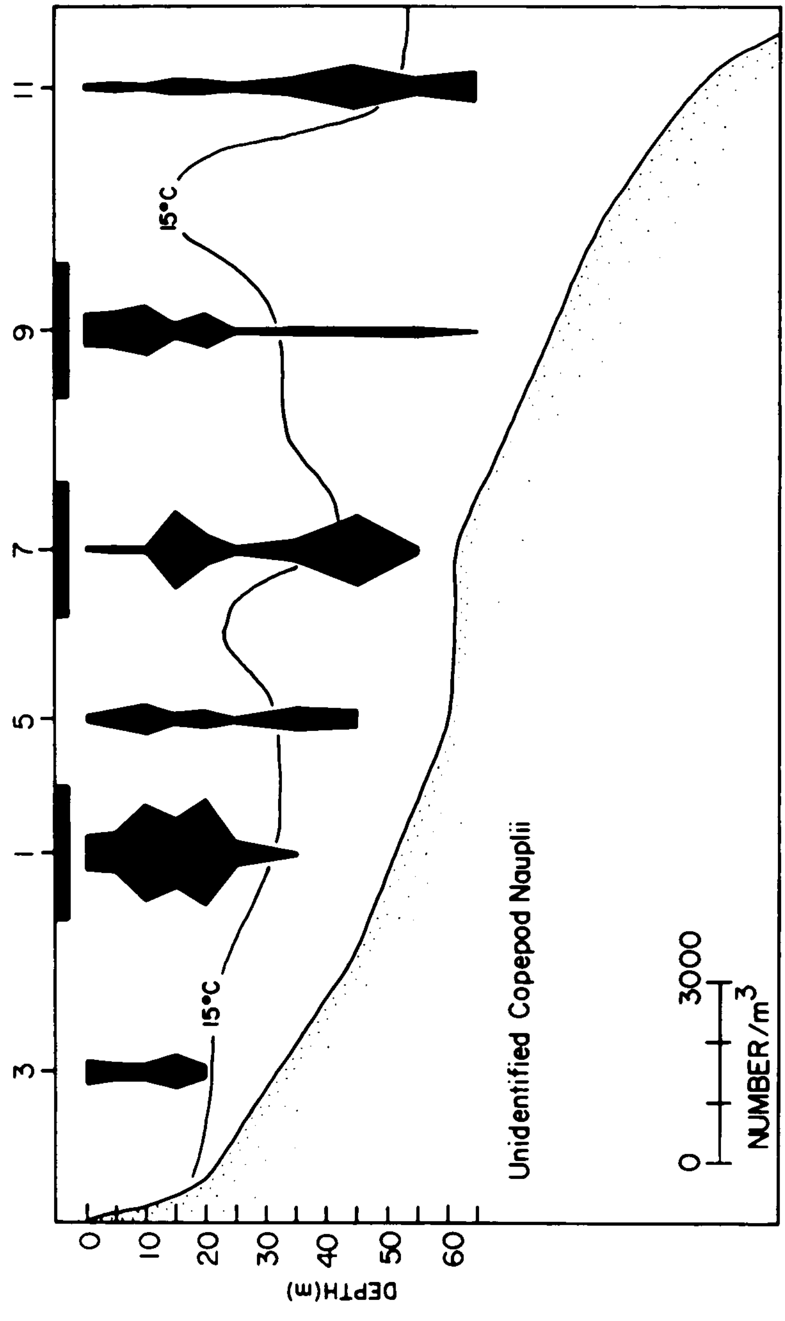

Figure 10. Vertical and inshore–offshore distributions of unidentified copepod nauplii in relation to the 15°C isotherm at pump stations on the Long Island transect. Station numbers are given on the top axis, and dark horizontal bars identify stations sampled at night.

longicornis and *T. turbinata,* were collected only at inshore stations. Other calanoids, such as *Calocalanus pavo, Centropages bradyi,* and *Metridia lucens,* were recorded mainly for offshore stations. Additional calanoids, such as *Acartia longiremis, Candacia armata, Clausocalanus furcatus, Mecynocera clausi, Nannocalanus minor, Temora stylifera,* and *Undinula vulgaris,* were collected over essentially the entire width of the shelf. No strong restriction to either shallow or deep waters was apparent for any of these species. Seven additional rare calanoids were collected, but never at more than three depths or at more than two stations. Three cyclopoid species (*Corycaeus speciosus, Corycaeus venustus,* and *Oncaea venusta*) and two harpacticoid species (*Clytemnestra rostrata* and *Microsetella norvegica*) were collected across most or all of the transect, but an additional harpacticoid (*Macrosetella gracilis*) was collected only at the two outermost stations. *C. rostrata* and *M. gracilis* appeared primarily limited to shallow depths, but no such trends were apparent for the other cyclopoids or harpacticoids. Of the 31 species of copepods recorded for the transect samples, 15 have been considered by previous investigators to be transients from offshore waters (Table 2).

The distributions of other noncopepod zooplankters, most of which were categorized only to major group, are presented in Table 3. Certain meroplankters, such as bivalve veligers and echinoderm plutei, were collected at most depths across the width of the shelf, while others such as crab and decapod zoeae were collected only inshore. Certain holoplankters, such as hyperiid and gammarid amphipods, chaetognaths, and salps, were collected across the entire shelf, but others such as *Oikopleura* sp. and *Penilia avirostris* were recorded for only the inner half of the shelf.

Long Island Time-Series Station

Vertical Distributions

The vertical distributions of *Oithona similis, Centropages typicus, Paracalanus parvus, Pseudocalanus* sp., and *Oithona atlantica* during the time series in some cases agreed with, but in others contradicted, the patterns recorded during the transect. The ver-

Table 3
Occurrence by depth of zooplankton taxa other than copepods collected in pump samples on the Long Island transect. Numbers refer to the depths (in meters) of collection.

Taxa	Station 3	Station 1	Station 5	Station 7	Station 9	Station 11
Bivalve veligers	0,5,10,15, 20,25	0,25,35	0,5,10,15,20, 25,35,45,	0,5,10,20,25, 35,45,55	10,15,25,35, 45,55,65	5,10,15,45, 55,65
Crab zoeae	15	15,20	15	-----	-----	-----
Decapod zoeae	0,15,20	10	-----	-----	-----	-----
Echinoderm plutei	5,10,15	-----	0,5,15	25,35	0,5,15,25 25,35,65	0,5,10,15
Euphausiid furcillae	-----	-----	-----	-----		-----
Fish eggs	-----	-----	5	-----	10,35	-----
25, Foraminifera	-----	-----	15,20,25, 35,45	5,10,15,20 25,35,45,55	0,5,10,15,20, 25,35,45,55,65	0,5,10,15,20, 35,45,55,65
Gammarid amphipods	-----	0	0,5,10	0	10,15,65	0,5,10,65
Gastrioid vekugers	-----	-----	20,35,45	0,5,10,15,20, 35,45,55	5,15,20,25, 35,45	0,5,10,15,20, 45,55,65
Hyperiid amphipods	5,10,20,25	10,15,20	0,5,20	0,5	5,20,25	10,20,55
Oikopleura sp.	0,5,10,15, 20	5	20	5,15	-----	-----
Ostracoda	-----	-----	-----	-----	5	-----
Penilia avirostris	0,15,10,15, 20,25	0,5,10,15, 20,25,35	0,5,10,15, 20	-----	-----	-----
Polychaete larvae	-----	-----	45	45,55	5,65	-----
Pteropods	-----	-----	-----	-----	-----	0,15,20,45, 55,65
Parvocalanus crassirostris	0,5,10,15, 20,25	0,5,10,15, 20,25,35	0,5,10,15,20, 25,35	0,5	-----	-----
Phaenna spinifera	-----	-----	-----	5	25	-----
Rhincalanus nasutus[b]	-----	-----	15	-----	-----	-----
Scolecethrix danae[b]	5	-----	-----	-----	-----	15
Temora longicornis	-----	0,10,15	-----	-----	-----	-----
T. stylifera[a,b]	0,10,15,20	0	-----	10	-----	0,5
T. turbinata	25	-----	0,5,15	0,5,10	-----	-----
Undinula vulgaris[a]	5,10,15	25	15,45	0,5,25	10,35	25
CYCLOPOIDA						
Corycaeus latus	-----	0,5	10	-----	-----	0,5
C. speciosus[b]	0,5,10,15, 20	0,5,10,15, 20,25,35	0,5,10,20, 25	0,5,10,15, 20,25	0,10,15,25	5,10,15,35
C. venustus	0,5,10,15,20	0	0,5,10,15,25	10	0	-----
Oncaea mediterranea	-----	5	-----	-----	-----	-----
O. venusta[b]	0,5,10,15, 20,25	0,5,10,15, 20,25,35	0,5,10,15,20, 25,35,45	0,5,10,15, 20,25,35	0,5,10,15,20, 25,35,55	10,15
Farranula gracilis	-----	-----	-----	-----	-----	0
HARPACTICOIDA						
Clytemnestra rostrata	0,10,15	15,20	35	0,5,10,15	-----	10,15,25,35
Macrosetella gracilis[a]	-----	-----	-----	-----	0,20	0,5,10,15
Microsetella norvegica	0,5,10,15, 20,25	5,15,20,25, 35	0,5,35,45	0,5,10,15, 35,45,55	0,10,20,35, 45,55,65	0,5,10,45, 55

tical distributions of *Oithona similis* (Figure 11) were similar to those of the transect in that this species was distributed throughout the water column, and no suggestion of vertical migration was apparent.

As on the transect, *Centropages typicus* females (Figure 12, upper), males (Figure 12, middle), and copepodites (Figure 12, lower) were almost exclusively collected from depths above the thermocline, and no migratory behavior was apparent. However, there were generally fewer copepodites than in the transect samples.

Paracalanus parvus females (Figure 13, upper), males (Figure 13, middle), and copepodites (Figure 13, lower) were collected mainly above the thermocline during the time series. Females were most abundant in the upper 10 m of the water column, irrespective of time of day. The distributions of copepodites may, however, reflect vertical migration. At 0600, 0900, and 1300 hr, copepodites were evenly distributed through the water column, but by 1700 the center of abundance was at 5-m depth. By 2100 copepodites were most abundant at the surface, but by 0100, the center of abundance was again at 5-m depth. By 0300 (on the previous night) the center of abundance was at 15-m depth, and by 0500 it had "sunk" (?) to 25 m. This suggestion of a late afternoon–early evening ascent to the surface, followed by a postmidnight return to deeper waters by *P. parvus* copepodites is supported by a somewhat similar pattern for males. If, indeed, these patterns represent active control of vertical position in the water column by the animals themselves, it appears that *P. parvus* copepodites and males were behaving differently from *P. parvus* females. However, the considerable differences in total abundance of *P. parvus* in the different pump casts suggest that a single patch was not being sampled throughout the time series. Thus, these patterns may be an artifact of advection, rather than indicative of migration.

The vertical distributions of combined females and late copepodites of *Pseudocalanus* sp. (Figure 14) during the time series were more confusing than those recorded for the transect. Small numbers of *Pseudocalanus* were recorded for samples in the upper 5 to 15 m in all casts, considerably larger numbers were recorded in the vicinity of or below the thermocline, and no specimens were

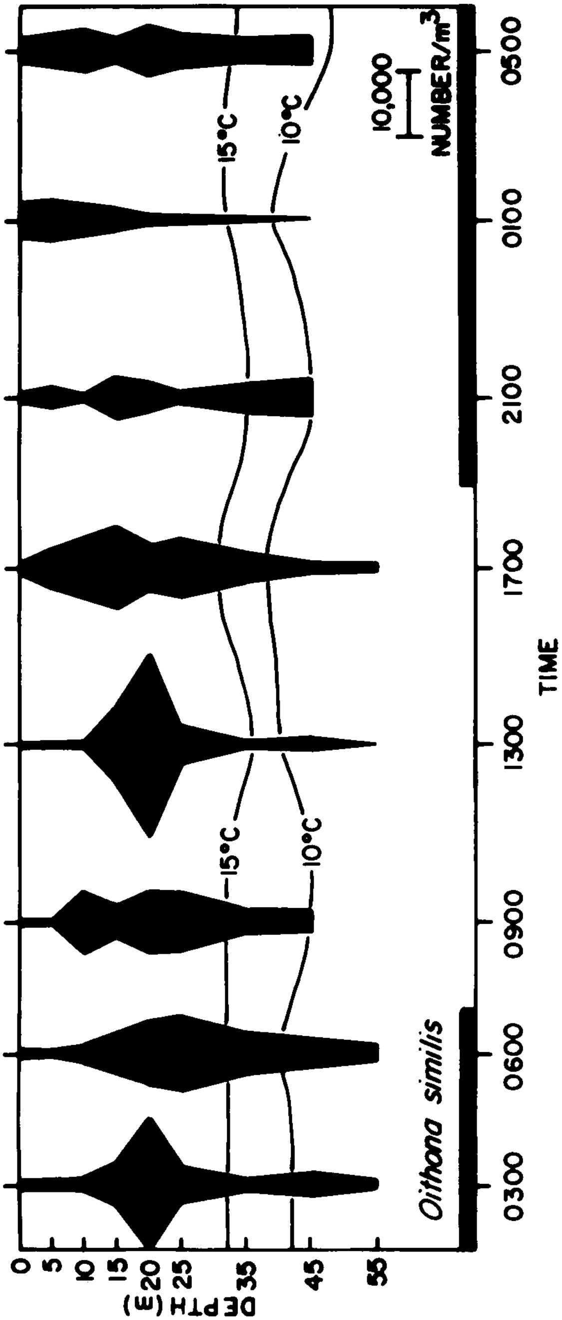

Figure 11. Vertical distributions of *Oithona similis* in relation to positions of the 15°C and 10°C water at the time of sampling during the Long Island time series. Sampling times are given on the bottom axis, and dark horizontal bars identify periods of darknesss.

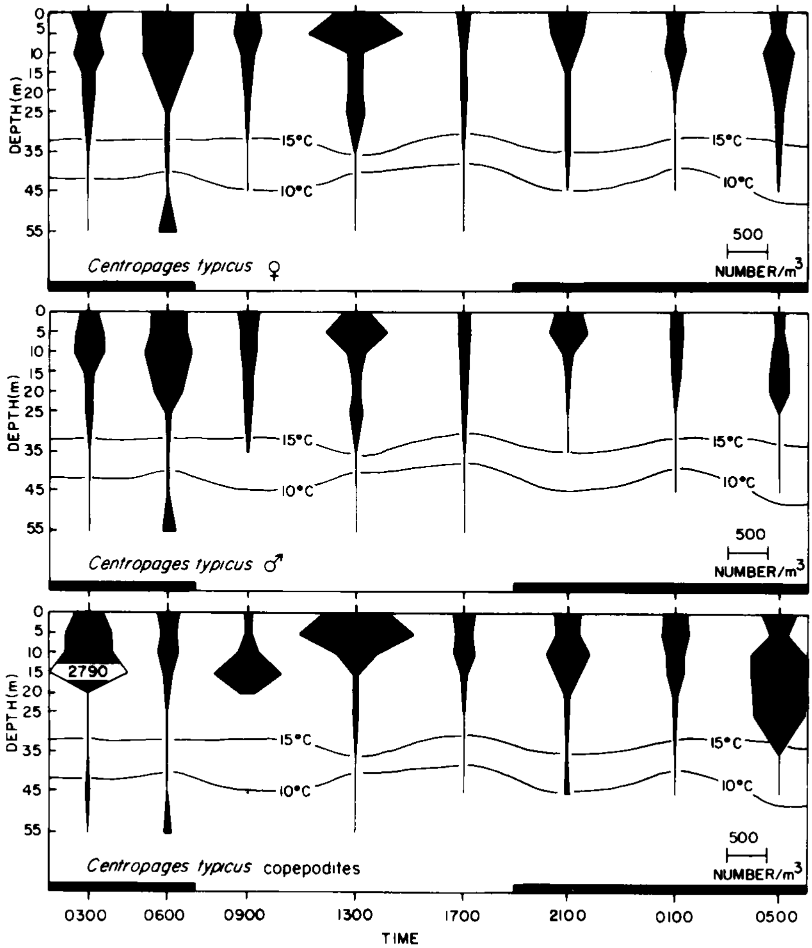

Figure 12. Vertical distributions of *Centropages typicus* females (upper), males (middle), and copepodites (lower) in relation to positions of the 15°C and 10°C water at the time of sampling during the Long Island time series. Sampling times are given on the bottom axis, and dark horizontal bars identify periods of darknesss.

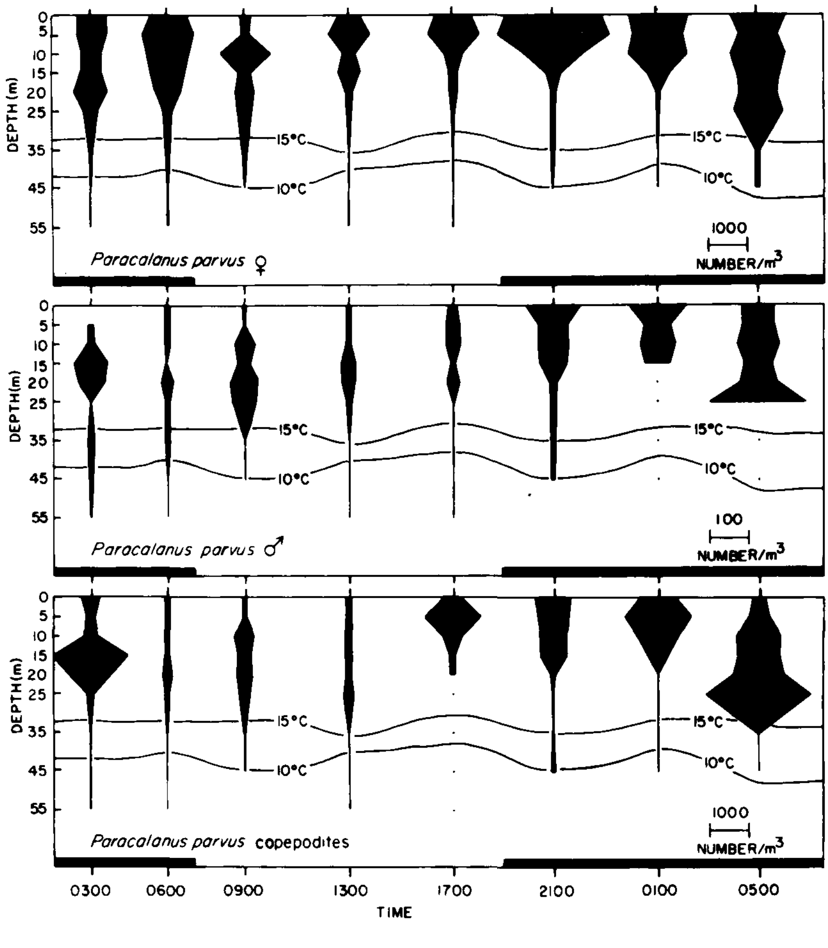

Figure 13. Vertical distributions of *Paracalanus parvus* females (upper), males (middle), and copepodites (lower) in relation to positions of the 15°C and 10°C water at the time of sampling during the Long Island time series. Sampling times are given on the bottom axis, and dark horizontal bars identify periods of darknesss.

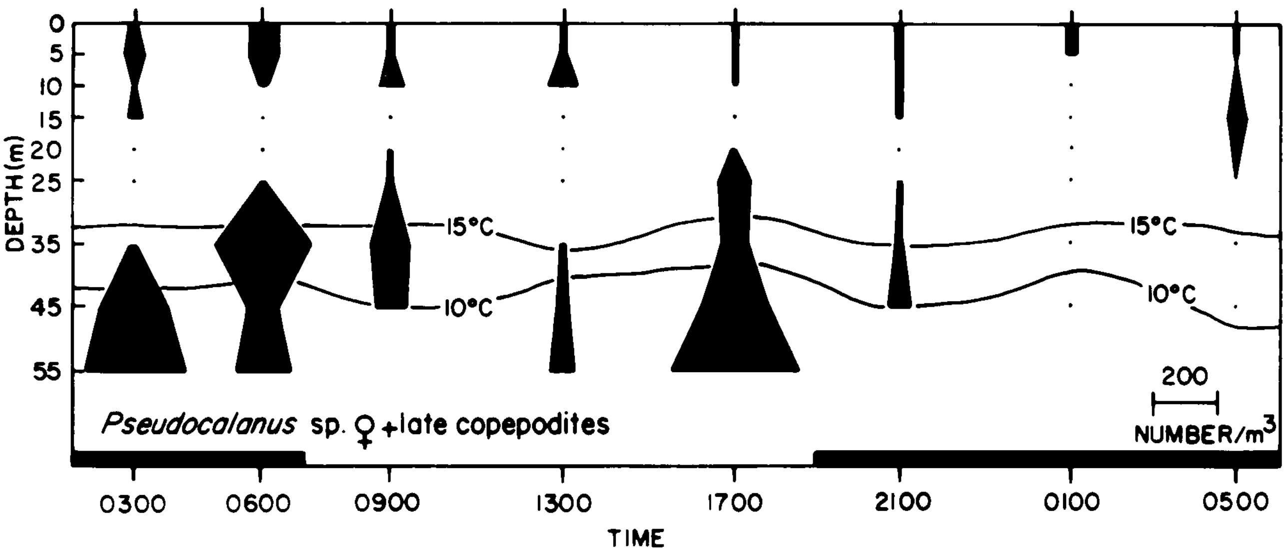

Figure 14. Vertical distribution of *Pseudocalanus* sp. in relation to positions of the 15°C and 10°C water at the time of sampling during the Long Island time series. Sampling times are given on the bottom axis, and dark horizontal bars identify periods of darknesss.

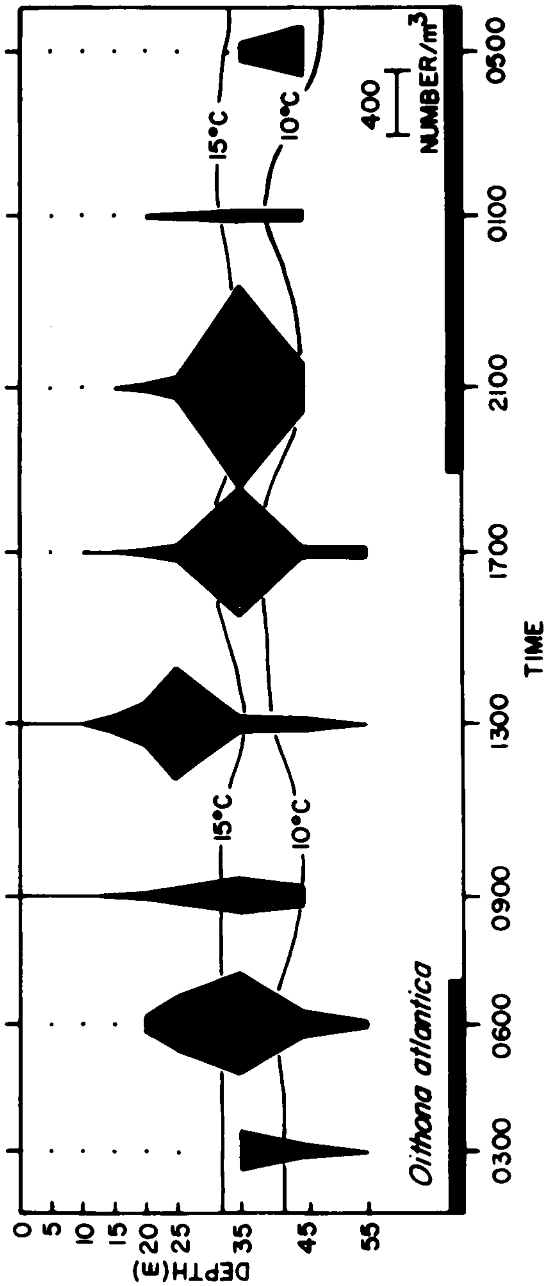

Figure 15. Vertical distribution of *Oithona atlantica* in relation to positions of the 15°C and 10°C water at the time of sampling during the Long Island time series. Sampling times are given on the bottom axis, and dark horizontal bars identify periods of darknesss.

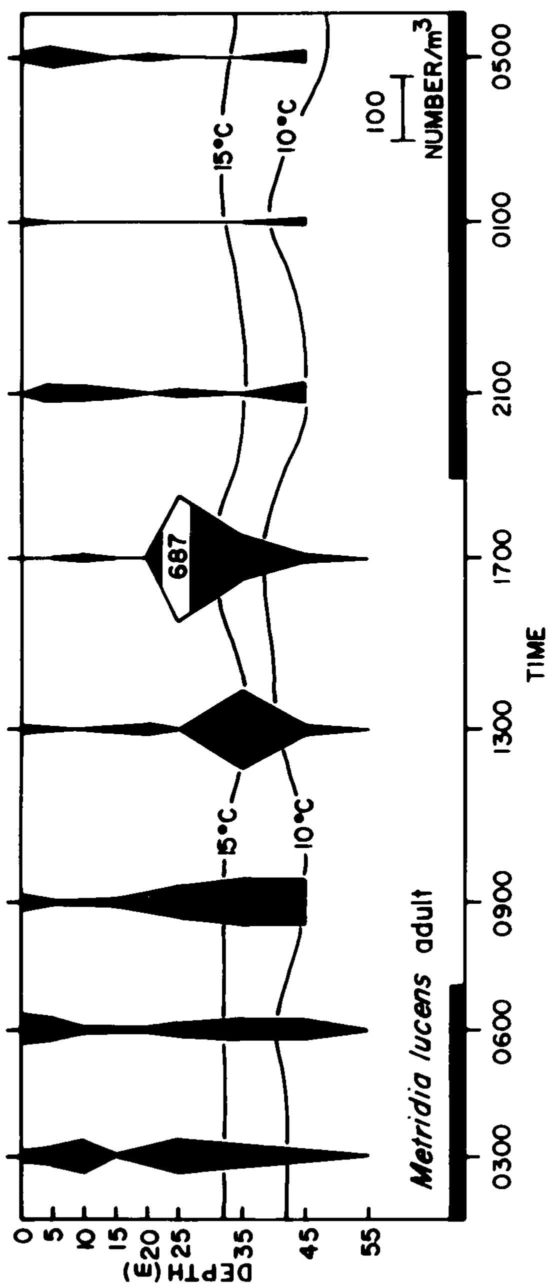

Figure 16. Vertical distribution of *Metridia lucens* adults in relation to positions of the 15°C and 10°C water at the time of sampling during the Long Island time series. Sampling times are given on the bottom axis, and dark horizontal bars identify periods of darknesss.

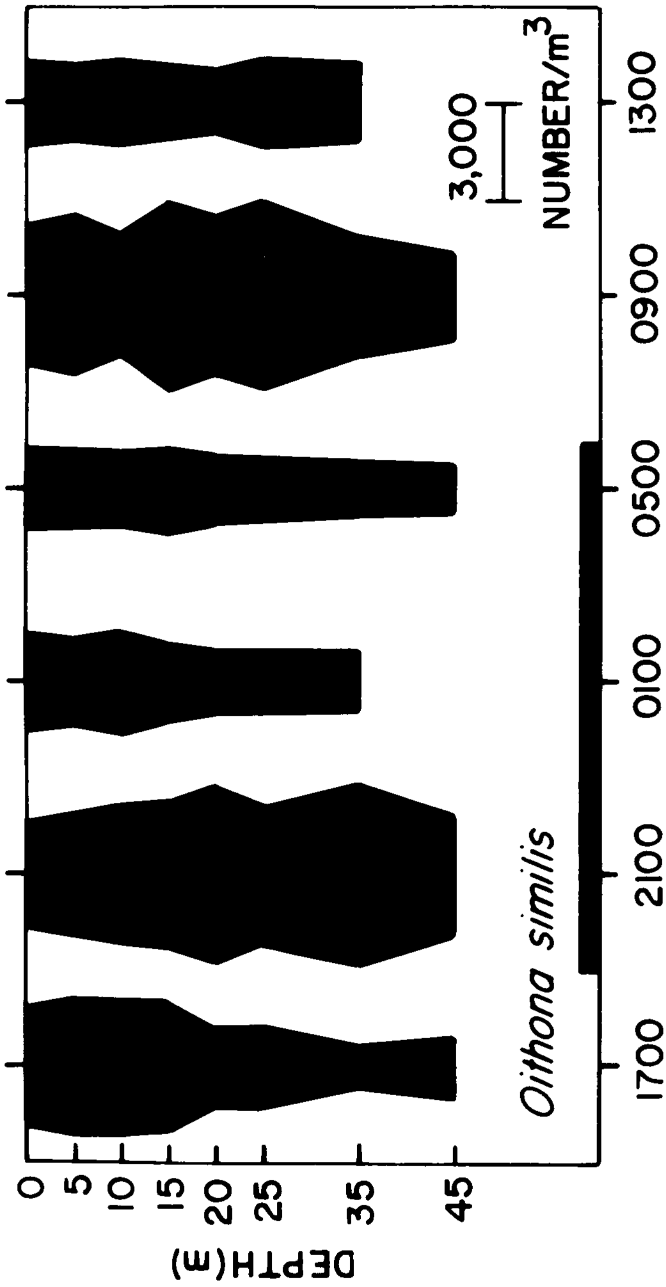

Figure 17. Vertical distribution of *Oithona similis* during the Georges Bank time series. Sampling times are given on the bottom axis, and the dark horizontal bar identifies the period of darkness.

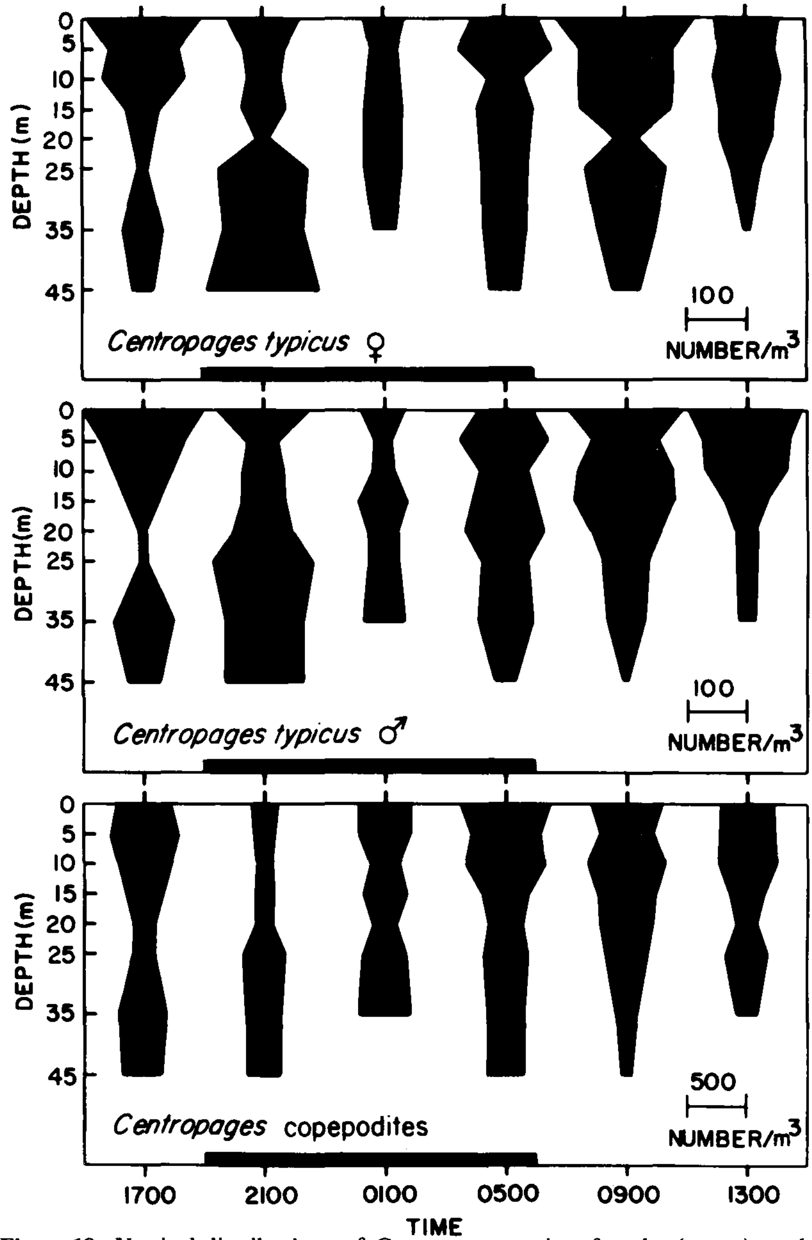

Figure 18. Vertical distributions of *Centropages typicus* females (upper), males (middle), and *Centropages* sp. copepodites (lower) during the Georges Bank time series. (*Centropages hamatus* adults comprised up to 1% of the total number of copepods counted ($\bar{x}$ = 0.18%) at the Georges Bank time series. Thus, a few of the *Centropages* copepodites included here were likely those of *C. hamatus.*) Sampling times are given on the bottom axis, and the dark horizontal bar identifies the period of darknesss.

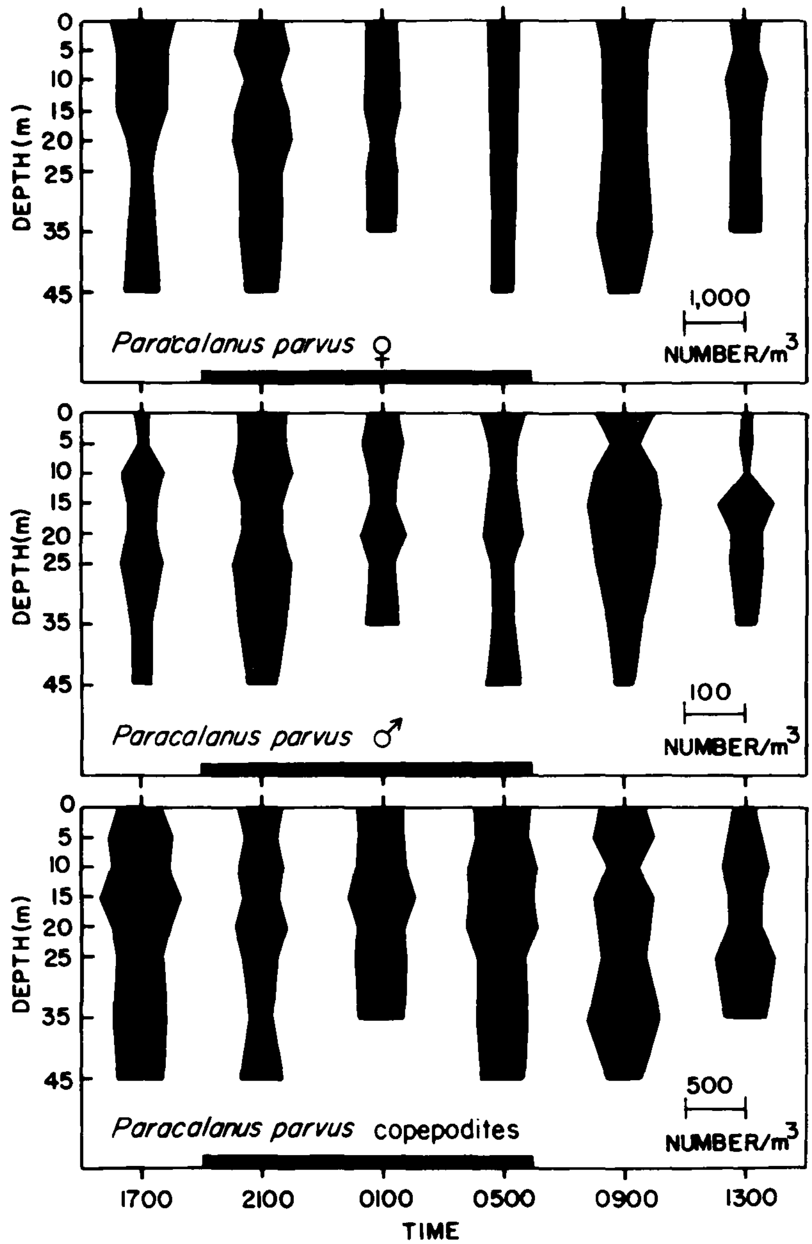

Figure 19. Vertical distributions of *Paracalanus parvus* females (upper), males (middle), and copepodites (lower) during the Georges Bank time series. Sampling times are given on the bottom axis, and the dark horizontal bar identifies the period of darknesss.

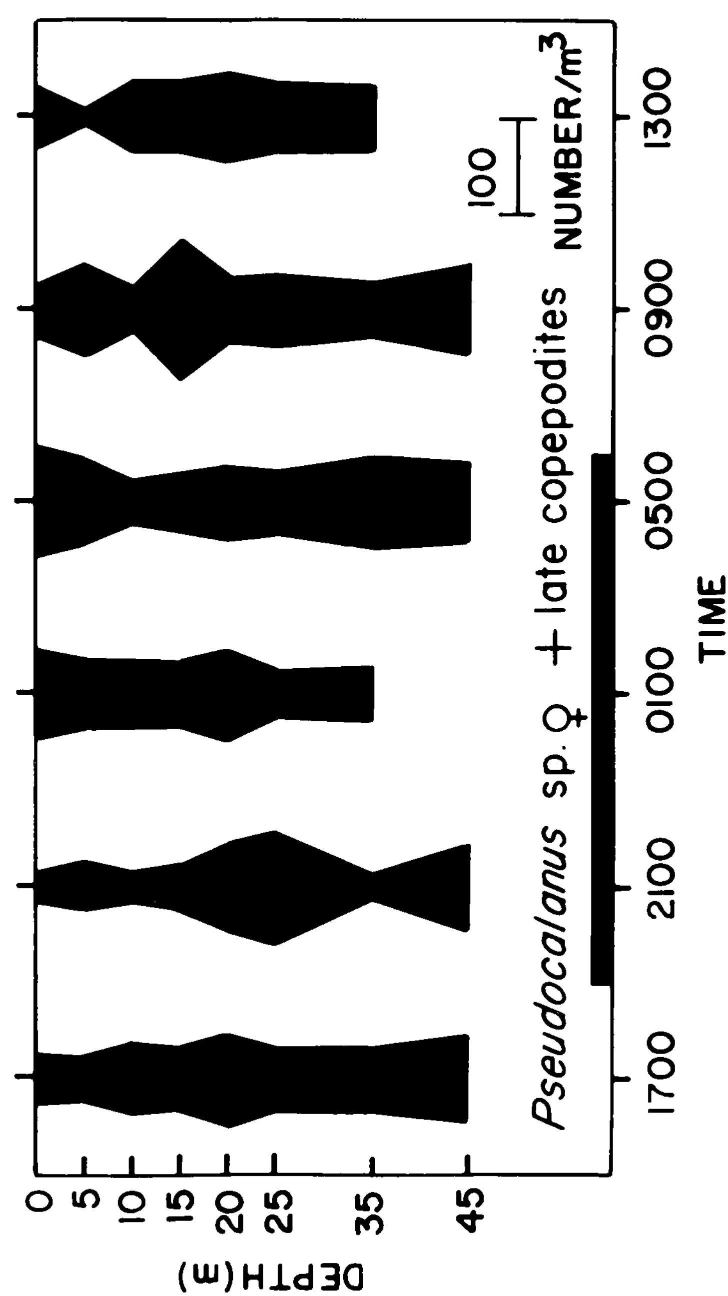

Figure 20. Vertical distribution of *Pseudocalanus* sp. during the Georges Bank time series. Sampling times are given on the bottom axis, and the dark horizontal bar identifies the period of darkness.

recorded for intermediate depths. These patterns were found in both daylight and darkness.

As in the transect samples, *Oithona atlantica* (Figure 15) exhibited maximum abundance in the vicinity of the thermocline during the time series. However, during daylight (0900 and 1300) *O. atlantica* was collected from the thermocline to the surface, and at 1300 this species exhibited a center of abundance 11 m above the thermocline. This pattern was different from that seen on the transect.

The vertical distribution of adults (mostly females) of *Metridia lucens* (Figure 16) is also of interest, since this species has been reported to undergo pronounced vertical migration in the Gulf of Maine (Clarke, 1933). During our time series, however, there was no consistent relationship between the vertical distribution of *M. lucens* and either time of day or position of the thermocline.

Georges Bank Time-Series Station

Vertical Distributions

During the Georges Bank time series, hydrographic conditions were markedly different from those found south of Long Island two days earlier. The water column was essentially isothermal (10.99–12.27°C). The vertical distributions of *Oithona similis* (Figure 17), *Centropages typicus* (Figure 18), *Paracalanus parvus* (Figure 19), and *Pseudocalanus* sp. (Figure 20) reveal fairly even vertical distributions regardless of time of day or developmental stage of the copepods. These distributions for *C. typicus* and *P. parvus* are in contrast to maximum levels of abundance for these species in the upper 25 m south of Long Island.

Discussion

Comparisons of the vertical distributions of the most abundant zooplankters recorded during the Long Island transect and the two hydrographically dissimilar time series reveal considerable differences. There are both agreement and disagreement between the patterns recorded for these three sample sets, as well as with observations made in previous studies.

In the stratified water south of Long Island *Oithona similis* was ubiquitously abundant over the entire water column, whereas adults and copepodites of *Centropages typicus* and *Paracalanus parvus* were collected mainly above the thermocline. Over Georges Bank all three species were evenly distributed with depth.

The presence of *Centropages typicus* mainly above the thermocline south of Long Island is in agreement with the pattern reported by Clarke (1933) for the same species in the Gulf of Maine in summer. The lack of evidence of vertical migration for this species during our sampling disagrees with the diel migration of *C. typicus* reported by White et al. (1979) off the mouth of Chesapeake Bay.

During the Long Island time series there was a suggestion that *Paracalanus parvus* males and copepodites underwent vertical migration, whereas during the transect they did not. In both the time series and transect samples from south of Long Island, *P. parvus* was collected mainly above the thermocline. At Georges Bank *P. parvus* was evenly distributed and nonmigratory. McLaren (1963) also found that *P. parvus* was typically nonmigratory, and both he and Bigelow (1926) stated that this species is usually found in warmer, near-surface waters.

Pseudocalanus was either collected above or below the thermocline south of Long Island, but was evenly distributed at Georges Bank. McLaren (1969) also found little evidence for vertical migration of *Pseudocalanus* in summer in a Canadian fjord.

Numerous studies (summarized by Marshall and Orr, 1955) have shown that the diel migration of *Calanus finmarchicus* is quite variable. In our Long Island transect samples this species was most abundant at or below the thermocline, although a small portion of the population may have migrated upward at night. *Metridia lucens* adults revealed no distributional relationships between hydrography and time of day during the Long Island time series, although Clarke (1933) found this species to be a pronounced vertical migrator in the Gulf of Maine. We are unware of any agreement with the pattern described by McLaren (1969).

Many previous studies of zooplankton vertical distributions have not distinguished between the distributions of different sexes or developmental stages of the same copepod species (examples include Deevey and Brooks, 1977; Roe, 1974; Roehr and Moore, 1965; White et al., 1979). Other studies that have done so (examples include Clarke, 1933; Gardiner, 1933; Longhurst and Williams, 1979; Nichols, 1933; Russell, 1928, 1934) have revealed that different sexes or developmental stages of the same species may be distributed differently with depth. Comparisons of the vertical distributions in waters south of Long Island of females, males, and copepodites of *Centropages typicus* reveal similar vertical distributions for all three, but the same comparison for *Paracalanus parvus* suggests possible differences.

Longhurst (1981) has proposed a general model for the vertical distribution of zooplankton based on numerous observations in oceanic waters. He found that a layer of abundant *epiplankton* near the surface lies above a *planktocline* across which zooplankton abundance declines substantially over a small depth interval. Below the planktocline is a *planktostad,* in which abundance is relatively low. Longhurst proposed that the planktocline is most developed in stratified waters, and that it coincides with the base of the thermocline. Longhurst stated that there is insufficient data from stratified shelf systems to indicate the applicability of the oceanic model. In our samples from south of Long Island, some species (*Centropages typicus* and *Paracalanus parvus)* had distributions that support the Longhurst prediction for vertical distributions in stratified waters. However, the distributions of *Oithona similis* did not fit the model, and because of the disproportionately high numerical contribution of this single species, the vertical distributions of total zooplankton numbers (Figure 3) do not conform to the Longhurst model.

The overwhelming numerical dominance of *Oithona similis* in our samples was a result that might be unexpected from previous zooplankton studies in the New York Bight. Table 4 reveals that the mean abundance of this species in our samples was over 20 times higher than the next highest mean value obtained in the New York Bight at the same general time of year. By comparison, our mean abundance for *Paracalanus parvus* was only higher than the next highest reported mean by a factor of 2. Our mean abundance for *Centropages typicus* was intermediate between previously reported means. The reasons for this are that previous studies with nets coarser than 202 μm quantitatively probably collected all copepodite stages of the relatively large *C. typicus* and all but the smallest copepodites of *P. parvus* collected by our system, but these studies seriously underestimated the abundance of the minute *O. similis.* The only abundance values for located *O. similis* in nonestuarine waters that approach ours are those of Fish (1936) for the central and western Gulf of Maine. Fish found mean values of 2,557 to 3,575 *O. similis* adults/m^3 in August of 1931 and 1932. His samples were also collected by pumping and a #10 (approximately 153 μm mesh) net.

Possibly due to the *O. similis* discrepancy, the inshore-offshore patterns of total zooplankton abundance revealed by our transect samples are different from the next most comparable previous data for the New York Bight at the same time of year. Grice and Hart (1962) found mean zooplankton numbers of 750/m^3, 1,600/m^3, and 3,300/m^3 at inner, middle, and outer shelf stations, respectively, in September of 1959 (their Figure 8). In contrast, our values (Figure 3) reveal a substantial decrease in total zooplankton number from inner to outer shelf waters.

Both Grice and Hart (1962) and Judkins et al. (1980) reported the presence of offshore warm water species on the New York shelf in autumn. This is apparently due to intrusion of Gulf Stream and/or slope water along isopycnals onto the shelf at this time of year (Gordon et al., 1976; Gordon and Aikman, 1981; Wright, 1976; Wright and Parker, 1976). While Judkins et al. (1980) recorded slope water (salinity 35°/oo-36°/oo) on the New York shelf in September of 1974, we did not detect salinities >35°/oo at any depth at Stations 1 to 11. However, the only salinities >34°/oo recorded at these stations were in the tongue of >18°C water immediately above the thermocline at Station 11 (Figure 2). This suggests that the presence of numerous transient copepod species on the shelf (Table 2) was likely due to intrusion of offshore water above the thermocline.

In summary, the vertical distributions of the same dominant copepod species in stratified (Long Island) and well-mixed (Georges Bank) waters revealed substantial variability. As in the study of Anraku (1975), the variability was on the scales of tens of meters. There were also distributional differences between species, and possibly between different sexes or developmental stages of the same species. There were no consistent patterns of diel vertical migration for any of the species examined. These patterns were in some cases contrary to those found in other investigations of the same species. It is clear that fine-scale vertical structure of zooplankton populations is variable, and that vertically discrete samples, such as those obtained with pumps and fine-mesh nets, reveal different patterns from those obtained with other gear. The major generalization to result from our study is that any vertical distribution "rules" followed by zooplankton are often different from those envisioned by zooplanktologists.

Acknowledgments

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