

Eastward Extension of the Distribution of the Marine Cladoceran (*Penilia avirostris*) in the Northwest Atlantic: a Case of Ecesis?*

J. B. Colton, Jr.

National Marine Fisheries Service, Northeast Fisheries Center
Narragansett Laboratory, Narragansett, Rhode Island, USA, 02882

Abstract

Data are presented on the distribution and abundance of *Penilia avirostris* Dana in continental shelf waters, Cape Hatteras to Nova Scotia, during 1980 and 1981. *Penilia* occurred in the plankton samples during approximately 6 months of the year (June–July to December). During periods of maximum abundance, *Penilia* occurred throughout the Middle Atlantic Bight and in isolated patches on Georges Bank, which represents an eastward extension of its previously-reported distribution. This eastward spread corresponds to the previously-documented direction of range expansion, but it is at variance with the westerly direction of residual drift. The absence of *Penilia* in the Gulf of Maine and seaward of the shelf break (outside 200-m isobath) indicates that some minimum level of bottom water temperature, which is necessary to initiate the development of resting eggs (~10°C), may be a determinant of the observed distributional patterns.

Introduction

Three genera and seven species of marine Cladocera occur in estuarine and neritic waters of the Northwest Atlantic: *Podon leuckarti* G. O. Sars, *P. intermedius* Lilljeborg, *P. polyphemoides* Leuckart, *Evadne tergestina* Claus, *E. nordmani* Loven, *E. spinifera* Muller, and *Penilia avirostris* Dana. *Penilia* is of special interest because it has an extremely sporadic and discontinuous distribution and is the only truly marine taxon among the many hundred species of filter-feeding Branchiopoda. *Penilia* has been recorded from the shores of every continent, frequently in tremendous numbers, but from widely separated locations and often only during a single season. As with other cladocerans, the periods of abundance are always associated with a high rate of ovoviviparous parthenogenesis. The populations of *Penilia* are renewed each year from benthic resting eggs which are produced in the autumn by sexual

reproduction. After the resting eggs develop in the spring, there are a number of generations with no males.

Zooplankton surveys of the Middle Atlantic Bight and the Gulf of Maine have been restricted, for the most part, to small geographic areas and to short periods of time, and consequently few data are available as to species abundance and distribution for extended time periods or areas. Published reports of occurrence of *Penilia* along the east coast of the United States are summarized in Table 1.

A striking case of the adventitious occurrence of *Penilia* is its sudden appearance in 1944 in the well-studied waters at Woods Hole, Massachusetts (Lochhead, 1954). The previous northern record for this species in the Northwest Atlantic was in Block Island

TABLE 1. Reported occurrences of *P. avirostris* off the Atlantic coast of the United States north of Cape Hatteras.

Location	Month and year	Reference
Beaufort, N. C.	June, 1898	Sudler (1899-1901)
Cape May and 60 km off Winterquarter, N. J.	October, 1931	Bigelow and Sears (1939)
Delaware Bay region	July–November, 1929–32	Deevey (1960)
Block Island Sound	August–November, 1943–45, 1949	Deevey (1952a, 1952b)
Woods Hole, Mass.	1944–53 to present	Lochhead (1954), N. Marcus ^a
Lower Chesapeake Bay	August–September, 1971–73	Bryan and Grant (1979)
New York Bight (<50 m)	August–November, 1974–75	Judkins <i>et al.</i> (1980)

^a Personal communication.

Sound which is about 90 km WSW of Woods Hole (Deevey, 1952a, 1952b). In the Northeast Atlantic, *Penilia* has been found at two isolated stations in the North Sea, 52° 22' N and 52° 09' N (Cattley and Hardy, 1949). In view of the restricted distribution of *Penilia* in both time and space, the extent and nature of its distribution, as revealed by recent plankton surveys of continental shelf waters between Cape Hatteras and Nova Scotia, are somewhat surprising. In this paper, data on the distribution and abundance of *Penilia* during bimonthly plankton surveys in 1980 and 1981 are presented, and an attempt is made to explain the observed distributional patterns in respect to hydrographic conditions.

Data Sources

Zooplankton samples were collected during plankton surveys (Table 2) of continental shelf waters between Cape Hatteras and Nova Scotia as part of the Marine Resources Monitoring, Assessment, and Prediction (MARMAP) Program of the U.S. National Marine Fisheries Service (Sherman, 1980). The area of coverage (shaded) during these surveys and the names of places referred to in the text are shown in Fig. 1. The sampling gear (61-cm bongo nets) and methodology (double oblique tows at 1.5–2.0 knots to a maximum depth of 200 m) were described by Smith and Richardson (1977) and Posgay and Marak (1980). Zooplankton taxa were identified and enumerated at the Morski Instytut Rybacki, Szczecin, Poland. Abundance estimates are based on samples from the 0.333-mm mesh nets that were deployed during the surveys.

Distribution of *Penilia* and Surface Temperature

In addition to the distribution of *Penilia* during the summer and autumn surveys, surface temperature distributions are also shown in Fig. 2 and 3, because it has been proposed that the distribution of *Penilia* is limited only by the need of a certain minimum surface water temperature in summer (Fuller, 1950; Lochhead, 1954). In 1980, *Penilia* first appeared in the samples during the July–August period (Fig. 2A), and the most extensive concentration occurred south of 40° N (Barnegat Inlet, New Jersey, to Cape Hatteras, North Carolina) and

extended offshore to the 100-m contour. The highest numbers of *Penilia* (>100,000/m²) were taken in a mid-shelf area (approximately 10,000 km²) southeast of Delaware Bay. Isolated patches of *Penilia* occurred in relatively shallow water (<50 m) in New York Bight and off central Long Island and Block Island. *Penilia* were not found east of Block Island (71° 35' W). The distribution of *Penilia*, for the most part, was restricted to areas where sea-surface temperatures were higher than 18° C, but *Penilia* did not occur in areas of the Gulf of Maine or along the southern edge of Georges Bank where surface temperatures were higher than 18° C.

The distribution of *Penilia* during September–October 1980 (Fig. 2B) was the most extensive of any that was encountered during the surveys. With the exception of a few offshore stations (>100 m) off southern New England and Long Island, the distribution of *Penilia* was continuous over the whole of the continental shelf from just west of Nantucket Shoals (70° 20' W) to Cape Hatteras. *Penilia* were not found in the vicinity of Nantucket Shoals, an area of upwelling as indicated by the 12° C surface isotherm, but three extensive, isolated concentrations were found over Georges Bank. The most easterly positive tow was made at 66° W. West of Nantucket Shoals, *Penilia* occurred only where surface temperatures were higher than 16° C. On Georges Bank, *Penilia* were found in areas where surface temperatures were slightly lower (14° to 15° C).

By November–December 1980 (Fig. 2C), both the abundance and the area of occurrence of *Penilia* had decreased appreciably. The highest numbers were in the range of 1,000–10,000/m², and the main concentration of *Penilia* was in the southern part of the Middle Atlantic Bight, extending from just south of Sandy Hook to just south of the entrance to Chesapeake Bay. The central part of this concentration extended offshore to the 1,000-m contour, but *Penilia* were restricted to midshelf and shallower waters at the northern and southern extremes. An isolated concentration (approximately 3,000 km²) occurred within midshelf waters eastward from the eastern end of Long Island. *Penilia* was not found east of 69° W and occurred for the most part at locations where surface temperatures ranged from 8° to 12° C.

Penilia did not occur in the samples again until June–July 1981 (Fig. 3A) and then only at isolated locations west of 72° W in the Middle Atlantic Bight and, unexpectedly, at a single station on the northeast part of Georges Bank. All positive tows in the Middle Atlantic Bight were made in areas where surface temperatures exceeded 20° C, whereas the surface temperature at the single positive station on Georges Bank was 16° C.

The area of occurrence and abundance of *Penilia* had increased markedly by August–September 1981

TABLE 2. Research vessels and dates of plankton surveys in 1980 and 1981.

1980		1981	
Vessel	Dates	Vessel	Dates
Albatross IV	28 Feb–04 Apr	Albatross IV	17 Feb–24 Mar
Evrika	14 Apr–15 May	Delaware II	07 Mar–14 May
Delaware II	21 May–12 Jun	Delaware II	21 May–17 Jun
Evrika	14 Jul–11 Aug	Delaware II	27 Jun–19 Jul
Albatross IV	24 Sep–30 Oct	Delaware II	} 04 Aug–02 Sep
Albatross IV	17 Nov–23 Dec	Albatross IV	
		Delaware II	
		Albatross IV	17 Sep–09 Nov

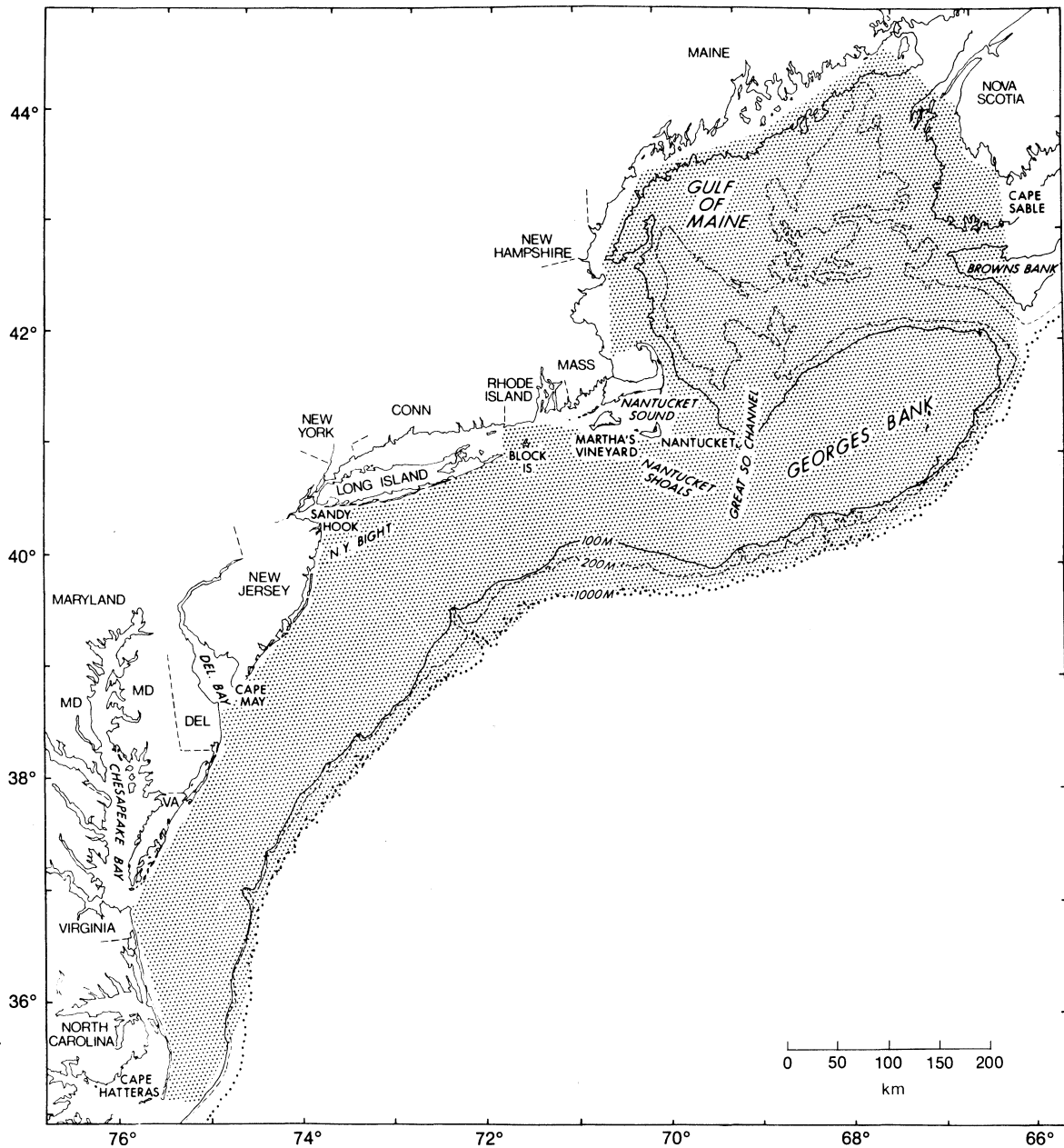


Fig. 1. Orientation map of the survey area (shaded) and place names mentioned in the text.

(Fig. 3B). The inshore distribution of *Penilia* was restricted to a narrow stretch of the New Jersey-Delaware coastline between 40°N and 38°N, whereas the offshore distribution extended from the eastern tip of Long Island to the southern extreme of the sampling area. Maximum abundance ($>100,000/m^2$) of *Penilia* occurred at nine stations running across the shelf from just south of the entrance to Delaware to the 100-m contour. The most easterly catches of *Penilia* were made at two isolated stations just south of Block Island. All positive tows were made in areas where surface temperatures were above 21°C.

Except for an isolated station on Nantucket Shoals, the distribution of *Penilia* during September-November 1981 (Fig. 3C) was restricted to areas west of Martha's Vineyard (69°W). Although *Penilia* was found throughout the Middle Atlantic Bight, its distribution was extremely patchy, which is perhaps a precursor to its impending seasonal demise from the plankton community. Concentrations of *Penilia* tended to be more extensive and spread further offshore in the southern than in the northern part of the Middle Atlantic Bight. With the exception of the isolated station on Nantucket Shoals where the surface

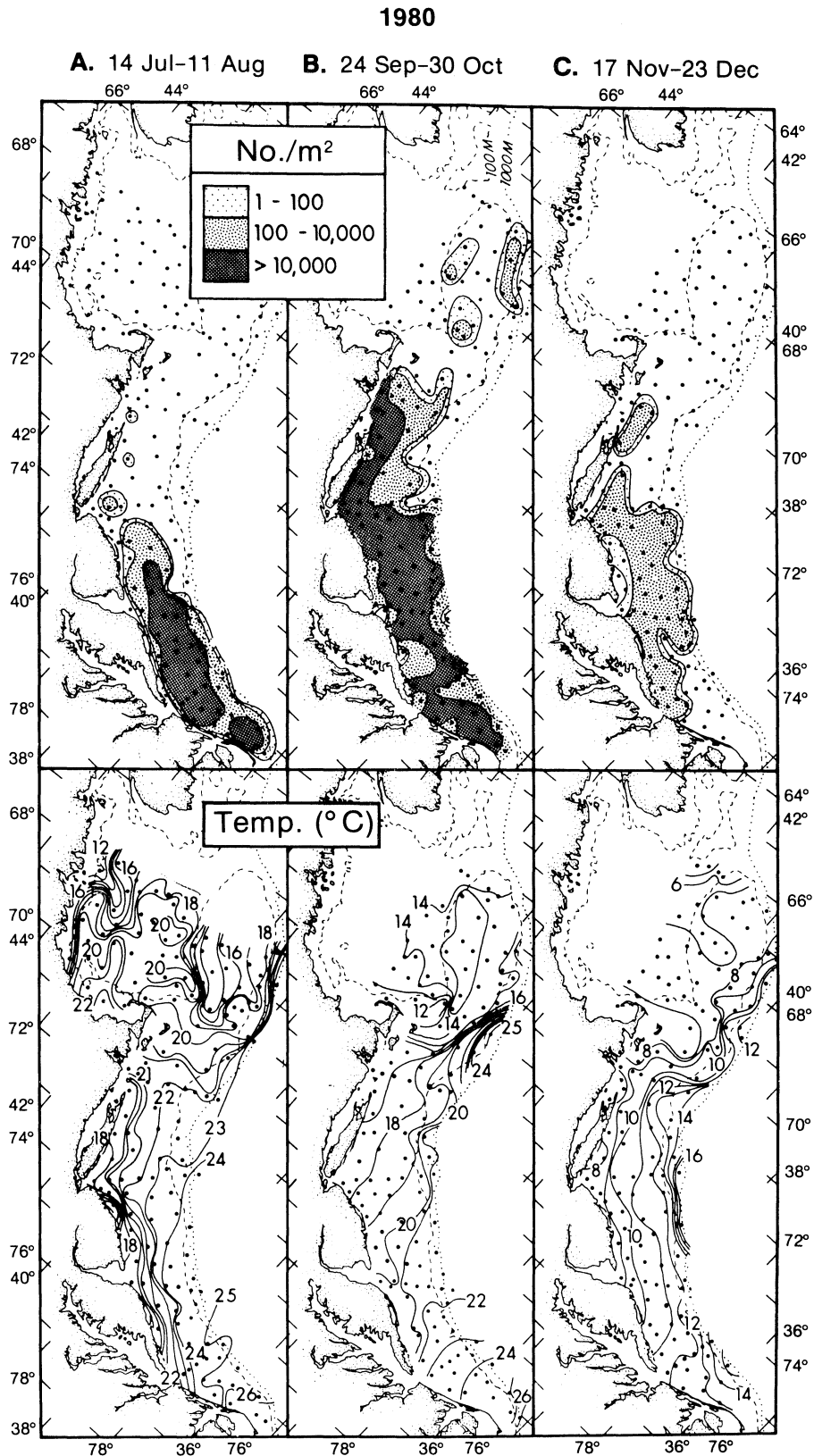


Fig. 2. Distribution and abundance of *P. avirostris* and surface temperatures, July-December 1980.

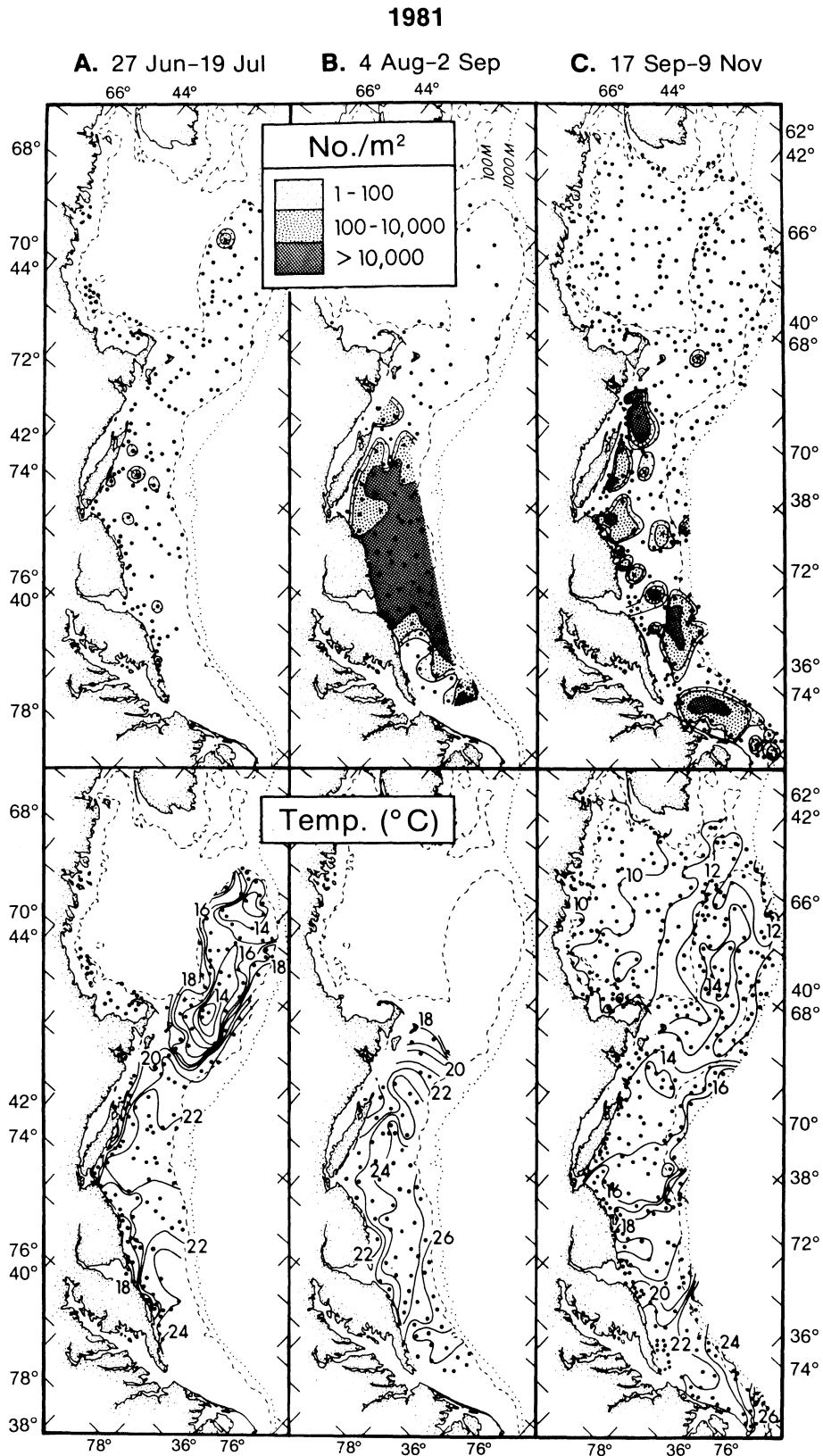


Fig. 3. Distribution and abundance of *P. avirostris* and surface temperatures, June–November 1981.

temperature was 12°C, the distribution of *Penilia* was restricted to areas where the surface temperatures were higher than 14°C.

Discussion

Apparently, sampling in the Gulf of Maine has been adequate enough in the past (e.g. Bigelow, 1926; Fish and Johnson, 1937) and during recent years (Sherman, 1980) to state unequivocally that *Penilia* does not occur in the Gulf of Maine. *Evadne* sp. and *Podon* sp. have been reported from scattered inshore stations throughout the Gulf of Maine (Bigelow, 1926; Fish and Johnson, 1937) and from as far north as the Grand Bank off Newfoundland (Gieskes, 1971; Semenova, 1964; Vladimirskaia, 1965). Up to the present time, survey coverage of the Georges Bank area has been infrequent and biased towards the spring months of the year, so that it cannot be said with any degree of certainty that *Penilia* did or did not occur on Georges Bank prior to 1980. This eastward extension of the distribution of *Penilia* corresponds to the direction of range expansion previously documented (Table 2) but is at variance with the direction of residual drift throughout the Middle Atlantic Bight, which is to the west and southwest (Bumpus, 1973; Butman *et al.*, 1982; Colton and Anderson, 1983). Therefore, the eastward dispersion of *Penilia* by surface drift must be ruled out as a causal factor.

Lochhead (1954) suggested that the sudden appearance of *Penilia* in new areas is perhaps a result of recently-laid resting eggs becoming caught up in wind-driven spray. However, this does not seem likely in the present case, because the distance from its former eastern distributional limit (Woods Hole) to Georges Bank is some 200 km or more. Lochhead (1954) ruled out the possibility of the transport of resting eggs after becoming attached to the feet (or feathers) of birds, as is often the case in freshwater Cladocera (and fish eggs and larvae). This may not be as remote a possibility as it first appears, because it is likely that some of the herring gulls (*Larus argentatus*) that breed and nest along the shores of Nantucket and Vineyard Sounds during late spring commute to Georges Bank in the summer (W. H. Drury, College of the Atlantic, Bar Harbor, Maine, pers. comm., 1985). Another likelihood is that *Penilia* are carried to Georges Bank in the salt-water cooling systems of many fishing vessels which travel to Georges Bank from southern New England ports via Nantucket Sound.

Regardless of how *Penilia* arrived on Georges Bank, a main point of interest is to determine why the distribution is completely isolated and restricted to Georges Bank itself and does not extend northward into the Gulf of Maine or westward across the Great

South Channel and Nantucket Shoals to connect with the apparent progenitor population. Because adult *Penilia* apparently always occur close to the surface (upper 20 m of the water column), investigators have resorted to surface temperature conditions (minimum temperature necessary for reproduction in summer) to account for the observed distributional patterns. Lochhead (1954), on the basis of observations at Woods Hole and a thorough review of the literature, concluded that adults can survive at temperatures below 9°C and can reproduce when temperatures are at and perhaps below 16°C, but that they do not become permanently established except where summer water temperatures exceed 21°C.

Maximum sea-surface temperatures of Slope Water along the edge of the shelf (seaward of 200-m isobath) always exceed 21°C (Colton and Stoddard, 1972), but *Penilia* does not occur in these waters (at least east of 70°W longitude). This implies that a factor or factors other than sea-surface temperature control the observed distributional patterns. Gieskes (1971) has suggested that, because Cladocera are daylight-feeding surface-water animals, they are restricted to shallow-water areas or to well-stratified deeper waters where vertical turbulence is limited and transport of animals to unfavorable environments cannot take place. This hypothesis could account for the confinement of *Penilia* to the shallow, although well-mixed, waters of Georges Bank. Another possible determinant is the necessity of a minimum bottom-water temperature to initiate the development of the resting eggs. Average long-term bottom-water temperatures in August, September and October and annual maximum bottom-water temperatures (Fig. 4) support this premise in that bottom-water temperatures at depths greater than 100 m in the warmest months were less than 10°C throughout the Gulf of Maine and 10°C or less along the shelf break (>200 m). Bottom-water temperatures over Georges Bank were as high as, and in some cases higher than, those in the Middle Atlantic Bight. A marked discontinuity in bottom-water temperatures occurred in the deeper parts of the Great South Channel. If sufficient numbers of viable resting eggs of *Penilia* could be obtained, verification of the hypothesis relating bottom-water temperature to survival would appear to be most amenable to laboratory study.

Regardless of whether the distribution of *Penilia* is limited by a minimum sea-surface temperature (necessary for sexual reproduction) or a minimum bottom-water temperature (necessary to initiate the development of resting eggs), long-term temperature observations (Colton and Stoddard, 1972, 1973) indicate that Georges Bank may constitute the eastern extreme of its range in the Northwest Atlantic. If sea-surface temperature is the primary controlling variable, the occurrence of *Penilia* on Georges Bank would be expected to be sporadic, because surface water of

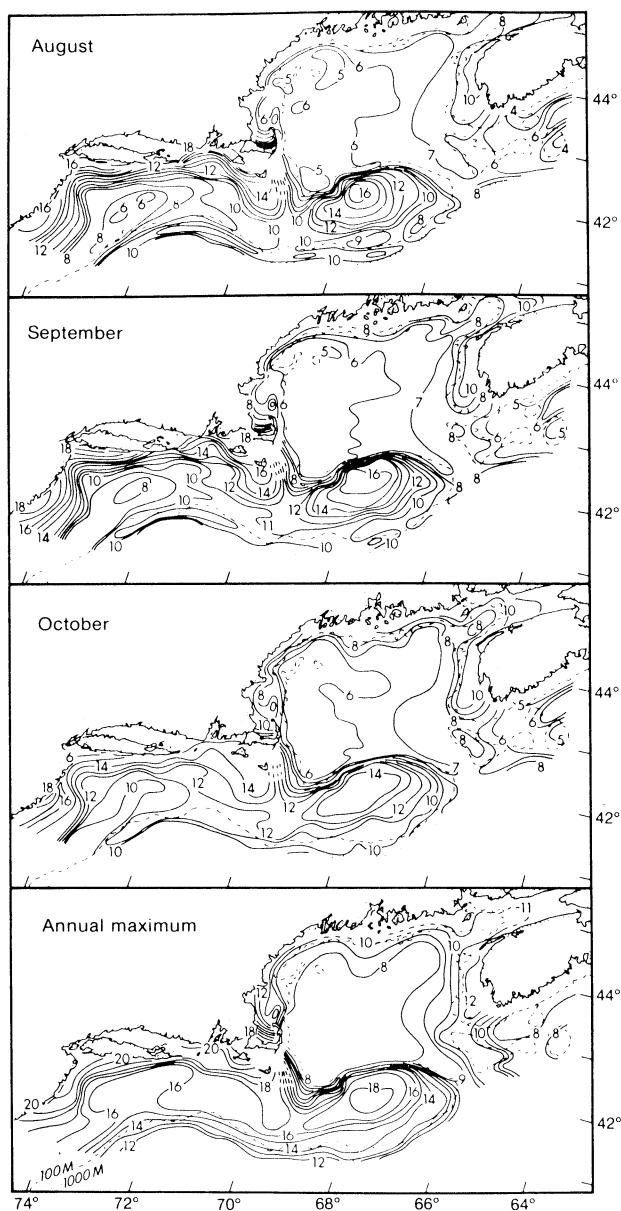


Fig. 4. Distribution of long-term average bottom water temperatures during August, September and October, and long-term annual maximum bottom temperatures (Colton and Stoddard, 1973).

21°C or higher is only found over Georges Bank irregularly. If, however, bottom-water temperature ($>10^{\circ}\text{C}$) is the primary determinant, *Penilia* would be expected to become permanently established on Georges Bank.

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