ZOOGEOGRAPHY OF THE GENUS *NEMATOSCELIS* (CRUSTACEA, EUPHAUSIACEA)

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ABSTRACT

The International Indian Ocean Expedition provided zooplankton samples to study the distribution and seasonal changes in numerical abundance of *Nematoscelis* in the Indian Ocean. Distributional boundaries of species of this genus in the Atlantic and Pacific oceans were determined mainly on the basis of mid-water trawls. All seven species of this genus occur in the Pacific, whereas only five species are present in the Indian and four in the Atlantic. Two forms ("old" and "new") of *N. gracilis*, considered to be ecophenotypes, but distinguished on the basis of morphological differences observed in the petasma, occupy the tropical Indo-Pacific subregion. The "old form" is most abundant in the oxygen-poor waters of the Arabian Sea, Bay of Bengal, and also in the eastern tropical Pacific. The "new form" is mostly confined to areas of the South Equatorial Current. The present study indicates that *N. gracilis* does not occupy the equatorial zone of the Atlantic Ocean, but "new forms" are transported from the Indian Ocean up to the southern tip of South Africa. *Nematoscelis atlantica* is distributed in the central water masses of the Pacific and Indian oceans, whereas in the Atlantic its distribution extends also to the equatorial zone. *Nematoscelis microps* and *N. tenalla* are warmwater species and are distributed between lat. 40°N and 40°S, although lacking in most areas of low oxygen water. *Nematoscelis lobata* has restricted distribution in the region of the Philippines. *Nematoscelis megalops* occupies the circumpolar transitional regions of the Southern Hemisphere and also the subarctic and transition subregions of the North Atlantic. *Nematoscelis difficilis* is endemic to the North Pacific transition zone. The basins of Timor and Banda Seas and their associated straits in the Indo-Australian Archipelago appear to allow inter-ocean gene flow among populations of *N. gracilis*, *N. Microps*, and *N. tenella*. A similar communication exists between Atlantic and Indian Ocean populations of these species through the oceanic waters around the tip of South Africa.

Zoogeography of the order Euphausiacea is reasonably well known for the Pacific Ocean (Brinton, 1962). The study on the distribution of euphausiids in the Indian Ocean is still in its preliminary phase. Available data from this ocean are adequate to make possible estimates of species ranges only. The role of the biological program during the International Indian Ocean Expedition (IIOE) (1960-65) was to provide materials from wide areas of the ocean to facilitate a better understanding of distributions of many zooplankton taxa in the Indian Ocean. Therefore, in the present study it was decided to put more effort into understanding the geographical distribution and seasonal abundance of Indian Ocean species of *Nematoscelis* than those from the Pacific and Atlantic oceans. Preliminary observations on the distribution of Euphausiacea as a whole were made by Gopalakrishnan and Brinton (1969). Subsequently, Brinton and Gopalakrishnan (1973) brought the distributional information up to date on the basis of IIOE samples studied up to that time.

Ocean-wide records of species of euphausiids in the Indian Ocean come from three major expeditions: the Percy Sladen Trust Expedition (Tattersall, 1912), the Deutsche Tiefsee Expedition (Illig, 1930), and the John Murray Expedition (Tattersall, 1939). Studies on the regional fauna are available for the eastern waters of South Africa (Boden, 1951), Red Sea, Arabian Sea, and Bay of Bengal (Ponomareva, 1964, 1968). Species of *Nematoscelis* of the southwest coast of India were provided by Sebastian (1966). Only four of the seven species of this genus have been reported from the Indian Ocean: *N. gracilis, N. megalops, N. microps,* and *N. tenella.* The present study confirms the presence of a fifth species, *N. atlantica,* in the southern Indian Ocean. *Nematoscelis megalops* was described by Boden (1951) from the southern African waters. Three females of this species were reported by Illig (1930) from southwest of Ceylon in the northern Indian Ocean. The present investigation does not confirm its distributional range in that region.

Nematoscelis difficilis is an endemic species of

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the transition zone in the North Pacific and is not reported from anywhere else. Previous studies on the distribution of all seven species of *Nematoscelis* in the Pacific Ocean are summarized by Brinton (1962).

Only four species of *Nematoscelis* have been reported from the Atlantic Ocean. Moore (1952) studied ocean-wide distributions of many euphausiids in the North Atlantic Ocean, including *N. microps* and *N. megalops*. Einarsson (1945) also reported *N. megalops* from the northeastern Atlantic. From the Mediterranean Sea *N. megalops, N. microps,* and *N. atlantica* were reported by Ruud (1936) and Casanova-Soulier (1968). Incorporating all previous records Mauchline and Fisher (1969) have provided a generalized picture of the distribution of *Nematoscelis* in the Atlantic Ocean. Gopalakrishnan (1973) examined the pattern of vertical distribution of *Nematoscelis* species of the Pacific Ocean.

METHODS AND MATERIALS

The Indian Ocean portion of the present study of *Nematoscelis* is based on samples collected during the IIOE. This expedition was a collaborative venture in which 10 countries participated and 16 vessels collected zooplankton samples as part of the biological program during 1960-65. The composite pattern of stations occupied during 70 cruises provided coverage of most geographical provinces of the Indian Ocean (Figure 1a, b). A standard procedure was followed by all participating vessels for collecting zooplankton samples. Accordingly, each sample was obtained by using the Indian Ocean Standard Net (IOSN) which was specially devised for the IIOE (Currie, 1963). It is a ring net with a mouth area of 1 m^2 and a length of 5 m. The straining surface is nylon gauze of 0.33-mm mesh. Hauls were as nearly vertical as possible, from approximately 200-m depth to the

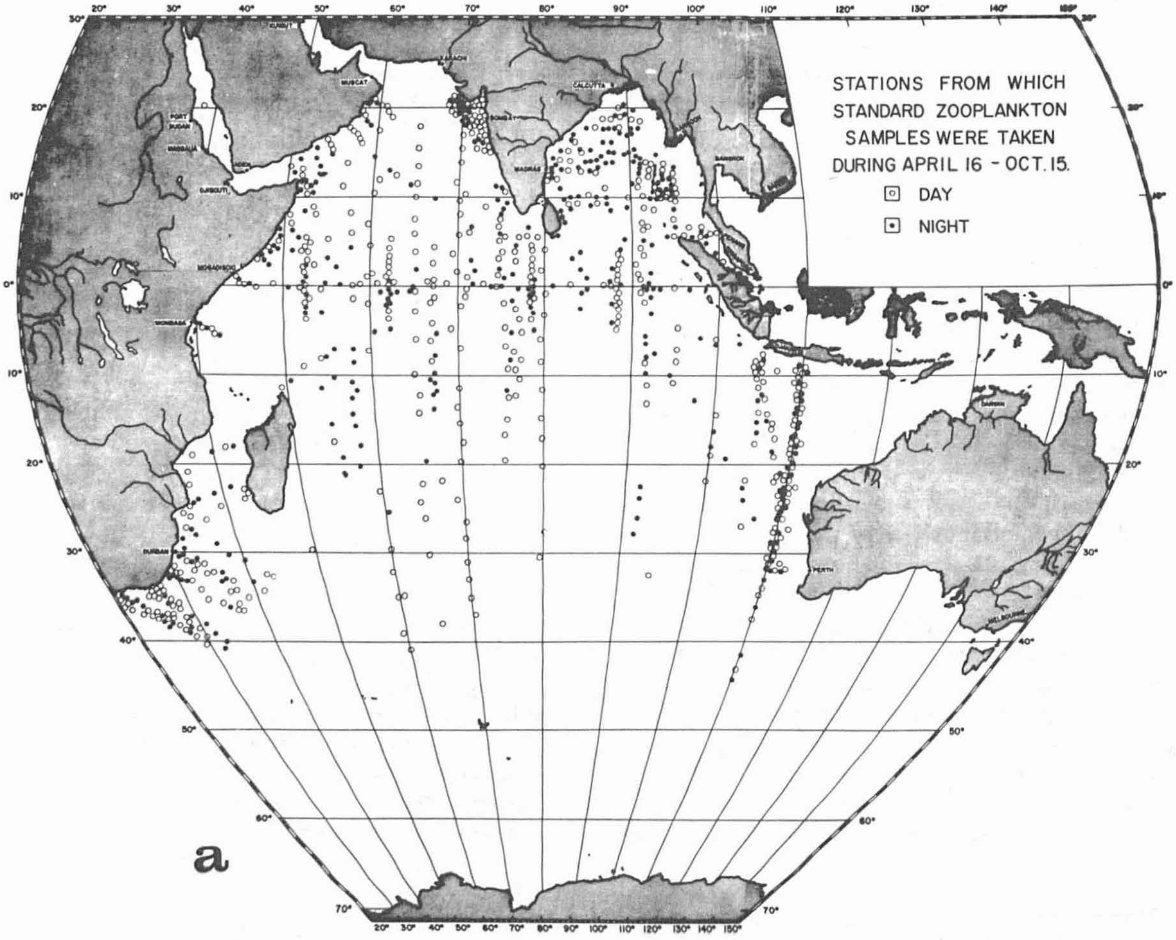


FIGURE 1.—Plankton samples examined for *Nematoscelis* of the Indian Ocean: a - SW Monsoon period.

surface. Assuming 0° wire angle the net would be expected to filter approximately 200 m^3 of water; but 0° wire angle was rarely attained at sea. Moreover, Tranter and Smith (1968) showed that the initial filtering efficiency of this net is 0.96; subsequent clogging does not reduce the filtering volume significantly.

Plankton samples collected according to these procedures are classified as "standard." In waters over the continental shelf where the depth was less than 200 m, the net was usually hauled up from within a few meters of the bottom; such collections were also treated as standard since the full water column was filtered. Samples collected from less than approximately 200-m depth in the open ocean, where the depth was far greater than 200 m, were designated as "nonstandard."

All samples were processed and sorted at the Indian Ocean Biological Centre situated in Cochin, India. The list of plankton samples processed at this center is included in a handbook to the international collections (Indian Ocean Biological Centre, 1969). The locality, time, and depth of haul at each station are given in this list, along with total displacement volume of the sample and fraction of each sample that was sorted into major taxa. At the sorting center a 3- to 4-ml portion of each sample was sorted into its constituent major taxa after removing large individuals from the sample. Individuals in each group were then counted to give an estimate of numbers in the whole sample. The sorted fractions ranged from 5% to 90% of the whole sample on the basis of the initial displacement volume of the sample. Further details of the sorting procedure were described by Hansen (1966). The unsorted portion (archive) of all samples were deposited at the Indian Ocean Biological Centre. About 215 of them were examined during the present study in order to check whether the fractionating proce-

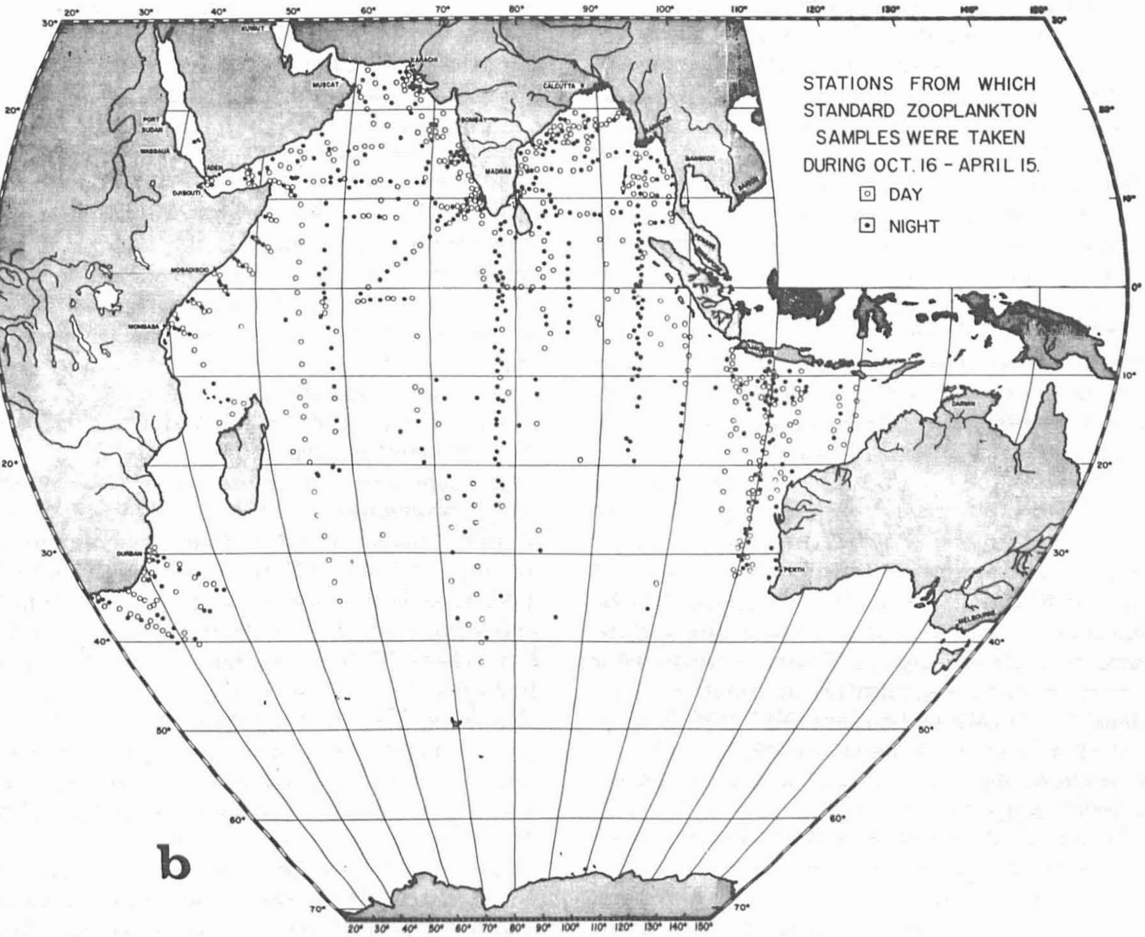


FIGURE 1.—Plankton samples examined for *Nematoscelis* of the Indian Ocean: b - NE Monsoon period.

dure was efficient enough to retain all species of *Nematoscelis* present in the whole sample. Only 26 archives were found to have contained one or more species not present in their subsamples. Therefore it is assumed that the subsampling procedure was usually adequate.

The wind system over the Indian Ocean is monsoonal. The two monsoon phases are designated as the Southwest (SW) and Northeast (NE) monsoons, indicating the predominant wind directions in the northern Indian Ocean during each phase. The bulk of the samples were grouped into two categories: those collected during 16 April to 15 October falling in the SW monsoon and those collected during 16 October to 15 April falling in the NE monsoon. The period 16 April to 15 October generally agrees with that of the wind regime of the SW monsoon (Wooster, Schaefer, and Robinson, 1967).

Of the 1,927 samples processed at the Indian Ocean Biological Centre, 1,732 samples were examined for the study of *Nematoscelis*. Of these, 879 samples were taken during the SW monsoon and 853 during the NE monsoon. Since a comparison of day and night catches of total euphausiids showed differences in day and night estimates (Gopalakrishnan and Brinton, 1969), it was decided to group day and night counts separately for each season. There were 401 night and 478 day samples for the SW monsoon period and 413 night and 440 day samples for the NE monsoon.

In order to fill gaps in certain geographical areas, some samples collected by using gear other than the IOSN have also been used in the preparation of charts. *Kistna* cruises 2 to 6 used an organdy net with 50-cm mouth diameter. *Natal* cruises 1 and 4 used the N-70 net with 70-cm mouth diameter. These samples were standardized for comparing with IOSN samples: the organdy net samples were multiplied by a factor of 5.1 and N-70 net samples by a factor of 2.6. In addition to these samples, 26 nonstandard surface samples taken during the *Patanela* cruise were also examined for qualitative information. *Argo* Monsoon Expedition stations 9-27 (ref. Snyder and Fleminger, 1972) have also been used in the preparation of present charts. These samples were collected using 1-m nets.

The observed differences between day and night catches of adult euphausiids are due to the fact that during day time many species either migrate to deeper layers or are able to dodge the net. Total euphausiids were 1.5-2.0 times more abundant in night samples than in day samples (Gopalakrishnan and Brinton, 1969). The mouth area of the IOSN is only 1 m^2 and it is probable that many large zooplankters can avoid the net. However, most samples taken at night contained many adult euphausiids, including some of the large thysanopods that migrated into the upper layer. All species of *Nematoscelis* are smaller than most *Thysanopoda* species. It is reasonable to believe that the IOSN tows taken at night would have been adequate to representatively sample adult species of *Nematoscelis*.

The present distributional study of *Nematoscelis* in the Indian Ocean is limited to the upper 200 m only. The geographical distribution of each species of this genus is compared with the pattern of water circulation in the upper layer. Larvae and juveniles of all *Nematoscelis* species are confined to the upper 200-m layer during both day and night, whereas adults undertake diurnal vertical migration (Gopalakrishnan, 1973). During daytime the distribution of adults extends from the upper 200-m layer to about 600-800 m; but at night, because of their upward migration, the range extends from the surface to about 400-600 m only, with the maximum above 200 m in most geographical regions. It is therefore probable that the IOSN would have caught adults better at night than during the day. For this reason only night samples were considered in charting the distribution of adults. However, a few trawls (Isaacs-Kidd Mid-water trawl) fished from depths greater than 200 m, were also used for examining overall geographical range. Station positions of these are included in Figures 7, 11, and 18. Most of these reached as deep as ca. 900-1,000 m, somewhat deeper than the lower limit of the vertical range of *Nematoscelis*. The geographical coverage of these trawls was not sufficient to examine the influence of deep circulation on the distribution of species. A total of 286 mid-water trawl samples were examined from the Pacific, Atlantic, and Indian oceans. [Collections from the Pacific and Indian oceans are located at the Scripps Institution of Oceanography. Collecting data regarding many of these appear in Clarke (1963).] The approximate boundaries of distribution of each species are shown on the basis of present evidence, including literature records.

The distributional ranges of species of *Nematoscelis* in the Atlantic Ocean were based on specimens sorted from fractions of plankton samples obtained by the Woods Hole Oceanographic

Institution. Most of the samples were from the North Atlantic. Charts were prepared for each species of *Nematoscelis*; but the abundance is expressed only as the percentage of the total *Nematoscelis* present in the aliquot, because the aliquot itself was an unknown quantitative fraction of the whole sample. *Atlantis II* and *Chain* cruises took samples using a 75-cm net from above 100 m; *Delaware* samples were also taken from similar depths, but by using 1-m nets. Lusiad VII cruise in the South Atlantic collected samples from 200 m to surface. In all, 217 plankton samples were examined from the Atlantic Ocean.

HYDROGRAPHY OF THE INDIAN OCEAN

In the upper strata of the sea, the general circulation may be related to the prevailing wind system. This wind-driven oceanic circulation affects and modifies the distribution of water masses in the upper strata; the wind-driven circulation penetrates into deeper layers and can be recognized at intermediate depths (Reid, 1965). The thermohaline circulation, caused by density differences in the ocean due to heat and water exchanges with the atmosphere, is thought to be responsible for formations of deepwater masses and the deep circulation (Neumann and Pierson, 1966). As a result of these types of circulations, properties such as temperature, salinity, oxygen, and nutrients show distinct features in their distributions in different oceanic areas, providing different characteristic habitat conditions for individual species or communities of organisms.

Since a major part of the present study deals with the seasonal distributions of Indian Ocean species of *Nematoscelis,* it is pertinent to provide a general background of the available information on the monsoonal seasons prevailing over the Indian Ocean. The surface currents of the Indian Ocean during the monsoon periods are described by Taft (1971) and for the present study I will follow his discussion of the wind and current patterns (see Neumann and Pierson, 1966, and Taft, 1971, for illustrations of surface currents of the Indian Ocean). Hydrographical changes associated with the monsoon are well documented for the Arabian Sea (Wooster et al., 1967). During the NE monsoon the northeast winds of the Northern Hemisphere cross the Equator into the Southern Hemisphere, there becoming northwesterly. This monsoon phase is established in November and persists through March; its maximum intensity is in January. During this phase a broad doldrum belt develops at about lat. 5°S to lat. 10°S between weak northerly winds and the southeast trade winds. In the SW monsoon, southeast trades from the Southern Hemisphere cross the Equator and gradually turn into southerly and southwesterly directions in the Northern Hemisphere. Winds are especially intense during this period near the African, Somali, and Arabian coasts. The SW monsoon is well established in May and persists through September. It is most intense in July.

The onset of monsoon periods in the Indian Ocean is found to be symmetrical in time (Wooster et al., 1967; Taft, 1971). Each period lasts for 5 mo; April and October are transition periods. Because of these short periods of transition in the monsoon system, it was decided to divide each April and October period into two halves and add the first half of April and the latter half of October to NE monsoon. The latter half of April and the first half of October were similarly added to the SW monsoon period. The overall winds and surface currents are far stronger in the SW monsoon than in the NE monsoon.

The surface circulation plays an important role in the distribution of planktonic animals in the ocean. In the Indian Ocean the surface circulation is subjected to a longer seasonal change than in other oceans. The outstanding features of the surface circulation are: 1) currents that follow in a more or less zonal direction far from the continents, and 2) currents near continental coasts. During the NE monsoon the North Equatorial and the South Equatorial currents flow westward and the Equatorial Countercurrent flows eastward between these two currents. Unlike those in the Pacific and Atlantic, the countercurrent in the Indian Ocean is situated in the Southern Hemisphere. This is related to the position of the doldrums south of the Equator. The South Equatorial Current, after reaching the African coast, contributes water to the Agulhas Current flowing southwest and also to the eastward flowing Countercurrent. During the NE monsoon the Somali Current, flowing southwest with a speed of about 100 cm/s, merges into the Mozambique Current (Neumann and Pierson, 1966), thereby bringing many tropical species as far south as lat. 35°-40°S along the coast of Africa. At this time the surface current off the southwest coast of India is also weak and flows in a southeast direction. In the Bay of Bengal the general circulation is counterclockwise. Unlike in the Pacific and Atlantic oceans, there is little evidence of an eastern boundary current in the Indian Ocean along the west coast of Australia. According to Wyrtki (1973), water movements in this region are weak and variable and most of the northward flow is situated farther offshore between long. 95°E and 105°E. In the Indian Ocean the Equatorial Undercurrent is also seasonal, being more pronounced during the NE monsoon than in the opposite season (Taft and Knauss, 1967; Taft, 1971).

At the onset of the SW monsoon the surface currents in the Indian Ocean change dramatically. The westward flowing North Equatorial Current is replaced by an eastward flowing Southwest Monsoon Current, thereby reversing the surface circulation in that region. Together with the Somali Current it is the outstanding current in these latitudes. The surface current north of lat. 5°S is then directed eastward and the Equatorial Countercurrent is not distinguishable as a separate flow. This is contrary to the conditions prevailing in other oceans where the intensity of the Countercurrent reaches a maximum during this period. The Somali Current, now flowing northeast as an intense western boundary current, extends to about lat. 8°N. The current transports southern forms into the Arabian Sea thereby serving to increase the faunal complexity of the region. In addition, enrichment of surface water north of the current produces zooplankton blooms. North of lat. 8°N the data suggest that this current leaves the coast and turns eastward (Taft, 1971). The South Equatorial Current becomes intensified in the western Indian Ocean; near the African coast it contributes to part of the northern flow. This brings species of the southern latitudes close to the Equator in the western Indian Ocean and even occasionally farther north to about lat. 10°N along the western boundary. During the SW monsoon the flow off the Arabian coast is toward the east and northeast but is much less intense than the Somali Current. This flow starts in April and is reported to persist until August. The southeastward flow off the southwest coast of India remains the same as in the NE monsoon. In this region the current flows northward only for 2 mo and it is essentially opposite to the prevailing wind stress. Taft (1971) pointed out that the circulation in the eastern Arabian Sea is therefore influenced by thermohaline processes.

During the SW monsoon three areas are prominent in the Arabian Sea for upwelling: off the Somali, Arabian, and southwest Indian coasts. There is evidence that the upwelling off the Arabian coast is wind driven; that off the Somali coast is partly wind driven and partly due to dynamic constraint on the current (Taft, 1971); and that off the coast of southwest India is due to the dynamic response which involves tilting of the thermocline up toward the coast (Darbyshire, 1967; Banse, 1968). The cool surface waters off the coasts of Arabia and Somalia during the SW monsoon are clear indication of intense upwelling (See Wyrtki, 1971:45). Along the western Indian Ocean Düing (1971) commented on the presence of many offshore anticyclonic and cyclonic vortices which are indicated by alternating highs and lows of dynamic height persisting through both monsoon phases. Taft (1971) singled out the importance of these vortices in the mixing processes of the near-surface waters which would increase the rate of nutrient enrichment of the surface layer. In the western Arabian Sea such enrichments are maximum during the June-August period (Table 1). High values of NO_3-N and SiO_3-Si persist for a longer period along the coast of Somalia than off the Arabian coast. The plankton atlas of the IIOE (Indian Ocean Biological Centre, 1968) shows that the maximum abundance of zooplankton is also associated with these upwelling areas.

The distribution of surface temperature during the NE monsoon indicates no cool surface water in

TABLE 1.—Surface nutrients at four coastal regions of the Arabian Sea. A = off the coast of Arabia, lat. 20°N; B = off the coast of India, lat. 20°N; C = off the coast of Somalia, lat. 10°N; D = off the coast of southwest India, lat. 10°N. All values are in μg-at/l. (Data from Wooster et al., 1967.)

	Dec.-Feb.				Mar.-May				June-Aug.				Sept.-Nov.			
Nutrients	A	B	C	D	A	B	C	D	A	B	C	D	A	B	C	D
PO_4-P	0.75	0.25	0.25	0.50	>0.25	0.25	0.25	0.25	>2.0	0.50	1.0	>0.25	>1.0	>0.25	1.0	0.25
NO_3-N		all values <2.5				all values <2.5			>25.0	2.50	>15.0	<2.5	<2.5	<2.5	15.0	<2.5
SiO_3-Si		all values 5.0				all values <5.0			>20.0	<5.0	>20.0	<5.0	10.0	<5.0	>15.0	<5.0

the Arabian Sea (see Wyrtki, 1971:38). Isotherms slope southwestward toward the African coast. During this period no upwelling is observed off the southwest coast of India, although the Ekman theory would predict upwelling in this area since the surface winds blow equatorward and parallel the coast. Taft (1971) suggested that this may be due to the low speed of the northeasterly wind.

In the Bay of Bengal upwelling has been reported to occur seasonally along the east coast of India and west coast of Burma (La Fond, 1954, 1957; Banse, 1960; La Fond and La Fond, 1968). During the early part of the NE monsoon, the northeasterly winds displace subsurface water offshore along the Burmese coast. Wyrtki (1961) also reported upwelling along the coast of Burma and Thailand during the December-February period. The general surface circulation of the Bay of Bengal is clockwise during January through July and it becomes counterclockwise from August to December (La Fond and La Fond, 1968). The southwesterly winds prevail over the northern Bay of Bengal in March and over the entire region in April. During these months an intense upwelling is noticed along the east coast of India (La Fond and La Fond, 1968). In this region, along with the nearshore occurrence of dense water, the average sea level also reaches a minimum height during this period (La Fond, 1954).

A remarkable feature of the Indian Ocean is the rapid attenuation of dissolved oxygen with depth; at 200 m values become 0.2 ml/l or less in the Arabian Sea and Bay of Bengal (Wyrtki, 1971). Vinogradov and Voronina (1961) and Vinogradov (1968) have discussed the association of low zooplankton biomass within the oxygen minimum layer in the Arabian Sea. North-south and east-west transects in the Arabian Sea indicate that oxygen values as low as 0.1 ml/l occur below 200 m during both seasons (Figure 2A, B). According to Wyrtki (1971) the concentrations of oxygen in the minumum layer do not vary seasonally, although the depth of this layer changes. The vertical profile at four north-south transects across the equatorial Indian Ocean show the occurrence of very low oxygen concentrations below 100 m (Figure 3). Since these profiles were taken during different months, it appears that this feature persists throughout the year.

The vertical distribution of temperature along four north-south transects (same transects as shown in Figure 3) indicates that the thermocline is situated between 75 and 100 m in the regions north of lat. 10°S. The South Equatorial Current

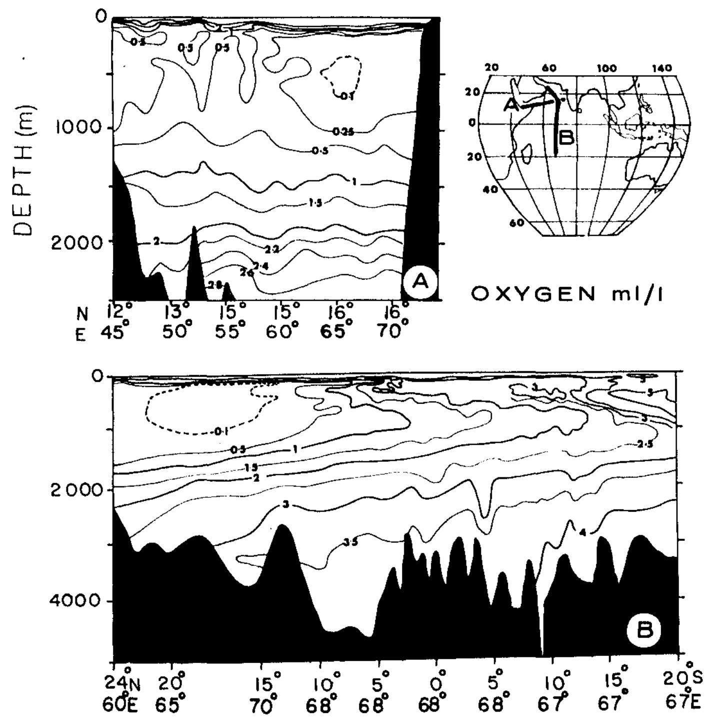


FIGURE 2.—Vertical distribution of oxygen in the Arabian Sea: A. East-west transect along lat. 11°N, long. 45°E to lat. 16°S, long. 72°E (July-August); B. North-south transect along lat. 24°N, long. 60°E to lat. 20°S, long. 67°E (November-May). (Charts reproduced from Wyrtki, 1971.)

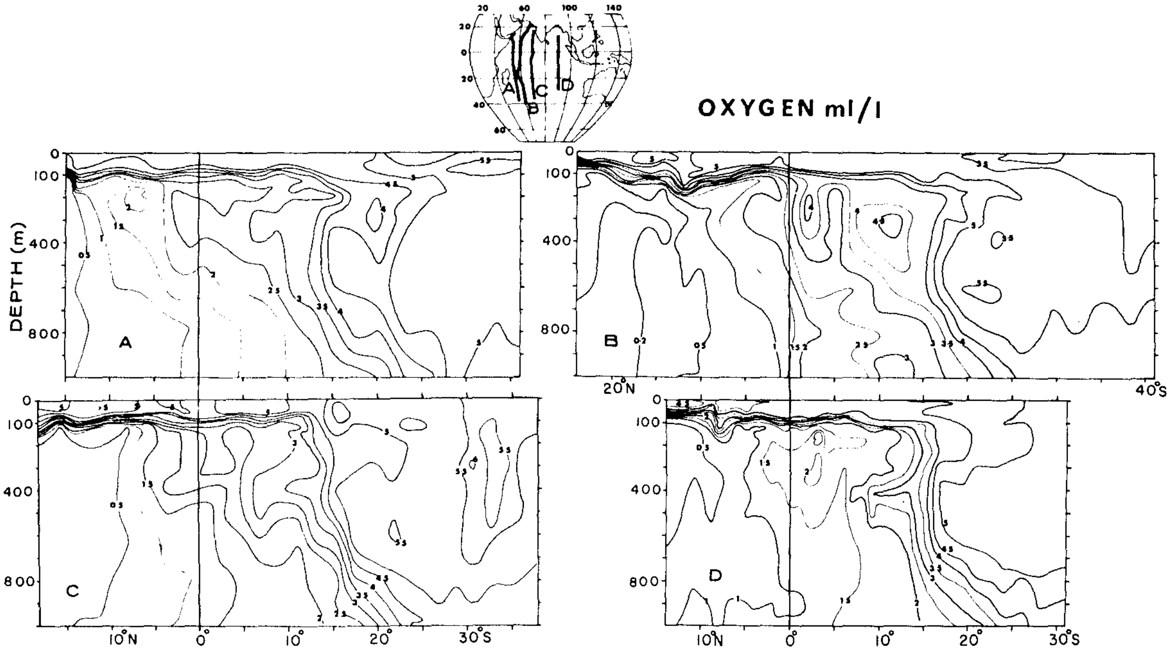


FIGURE 3.—Vertical distribution of oxygen along four north-south transects in the Indian Ocean: A - lat. 14°N to 36°S at long. 55°E (February-March); B - lat. 24°N to 41°S at long. 60°E (August-November); C - lat. 18°N to 37°S at long. 70°E (May-July); D - lat. 13°N to 30°S at long. 92°E (August-September). (Charts reproduced from Wyrtki, 1971.)

flows along the zone where the thermocline slopes upward toward the Equator between lat. 10°S and 20°S. The general distribution of subsurface isotherms is more or less similar across the full breadth of the equatorial region.

Wyrtki's figure (1971:38) indicates the presence of cold surface water in the northern part of the Bay of Bengal during the NE monsoon. Banse (1960) pointed out that the cold surface water in this region may not be attributed to upwelling, but to a high rate of evaporation caused by the dry air from the continent. The coasts of northwest Australia and Java are other regions reported to have seasonal upwelling. Wyrtki (1961) pointed out that there was intense upwelling in these two areas during the SW monsoon.

It is postulated that in the Indian Ocean wind-driven equatorial upwelling is less intense than in the Atlantic and Pacific oceans and may be totally absent (Taft, 1971). The absence of substantial peaks in the zooplankton biomass along the equatorial regions of the Indian Ocean is consistent with the idea of there being little equatorial upwelling, compared at least with the Pacific (King and Demond, 1953; Reid, 1962; Heinrich, 1968) and the Atlantic (Hentschel, 1933).

In the Indian Ocean seasonal changes in surface salinity are more pronounced in the Arabian Sea and the Bay of Bengal than in any other region (see Wyrtki, 1971). Throughout the year the surface salinity was greater in the Arabian Sea than in the Bay of Bengal. During the NE monsoon surface salinity becomes very low (30-33‰ in the Bay of Bengal; advection of low-salinity water occurs from the Bay of Bengal toward the western Indian Ocean. As the Monsoon Current develops during the SW monsoon, a tongue of high-salinity water flows eastward.

RESULTS

Geographical Distribution of *Nematoscelis gracilis*

Indian Ocean

Two forms considered to be ecophenotypes of *N. gracilis* are recognized to occur in the Indian Ocean: an "old form" which is identical in morphological character to the typical form described by Hansen (1910) from waters of the Indo-Australian Archipelago, and a "new form" which is distinguished from the typical form on the basis of the difference in dimension of the proximal process of the petasma. In the old form the proximal process does not reach the distal end of the median lobe, whereas in the new form it is extremely long, reaching far beyond the distal end of the median lobe. The proximal process of the old form is serrated at the distal end and that of the new form is without any serration. There is also an apparent size difference between the two forms; the body length of the old form is found to be significantly larger than that of the new form. Moreover, the upper lobe of the eye of the new form is narrower than that of the old form. Along the equatorial zone, where the distributions of the two forms overlap, another form, which is recognized to be "intermediate" of the old and new forms with regard to the length of the proximal process, is also encountered. All three forms are distinguishable only in mature adults: males on the basis of structural differences of the petasma and females on the basis of differences in the body lengths and eye shape. Further discussion of them will appear in a forthcoming taxonomic paper (manuscript).

Nematoscelis gracilis is by far the most abundant species of *Nematoscelis* in the tropical regions of the Indian Ocean, including the Arabian Sea and the Bay of Bengal (Figures 4, 5). Along the full extent of the ocean at the Equator this species was found to be distributed between lat. 20°N and 20°S. The southern limit extended farther south along the regions of the western and eastern boundary currents, the Mozambique Current, and the West Australian Current, respectively. Larvae and juveniles were caught year-round from all geographical areas within the distributional range of the species. Therefore, spawning apparently occurred everywhere within that range. Larvae consisted of metanauplii, calyptopes, and furcilias; metanauplii were undoubtedly underestimated since they (body length < 1 mm) could have been washed away through mesh apertures of the net.

During the NE monsoon maximum numbers of larvae and juveniles per sample were caught off the coast of southeast India (Figure 4a). For example, during *Kistna* cruise 26, 840 individuals were caught at station 704 (lat. 13°N, long. 81°E); and 764 individuals from station 705. Four stations had numbers exceeding 300 per sample from the same area. However, during the SW monsoon maximum abundance was in the western Indian Ocean north of the Equator (Figure 4b). Both larvae and juveniles were absent from the northern and northeastern Arabian Sea. There the oxygen concentration in the subsurface waters is as low as 0.1 ml/l (see Figure 2B). They were also absent to the north of lat. 10°N along the west coast of India; but during the NE monsoon they were caught as far north as lat. 15°N in the coastal waters of southwest India. The North Equatorial Current, flowing westward, has a northwestward component after passing the southern tip of India during the early part of the NE monsoon, bringing a spawning population of this species as far north as lat. 15°N. In the area of the Mozambique Current, larvae and juveniles were caught only as far south as lat. 30°S.

Adults of the old form are confined mostly to the Arabian Sea and the Bay of Bengal and the new form to areas of the Southwest Monsoon Current and the South Equatorial Current which is situated south of the Equator. During the NE monsoon old forms are frequently caught in the areas of the North Equatorial Current, whereas new forms occur only in the Equatorial Countercurrent and south of it. The two forms overlap in distribution along the northern boundary of the Countercurrent from east of long. 75°E. In the eastern Indian Ocean the distribution of old forms extends farther south (as far as lat. 14°S) (Figure 5a). "Intermediate forms" were encountered all along the overlapping zone. They were present along the western and eastern boundaries of the ocean. Most transport of the intermediate forms to the west is through the North Equatorial Current. In the South Equatorial Current it was found only at one station (*Koyo Maru* cruise 14, station 19: lat. 13°49′S, long. 94°16′E). In the western Indian Ocean there was no overlap in distribution of the forms, and the new forms did not occur north of the Equator. Moreover, during this period the Somali Current flows southwestward so that it brings the old form as far south as lat. 3°S. Therefore, the pattern of distribution of the two forms in the upper layer may be influenced by the direction of water flow in the equatorial current system which is subject to seasonal changes. During the NE monsoon no samples were taken from the Mozambique Current area north of lat. 30°S. However, mature adults of the new form were caught in one sample taken from the southeast coast of Africa (*Natal* cruise 6, day station 161: lat. 34°21′S, long. 26°21′E). Thus it appears likely that the Mozambique Current, which is stronger during the NE monsoon than in the opposite season (as judged

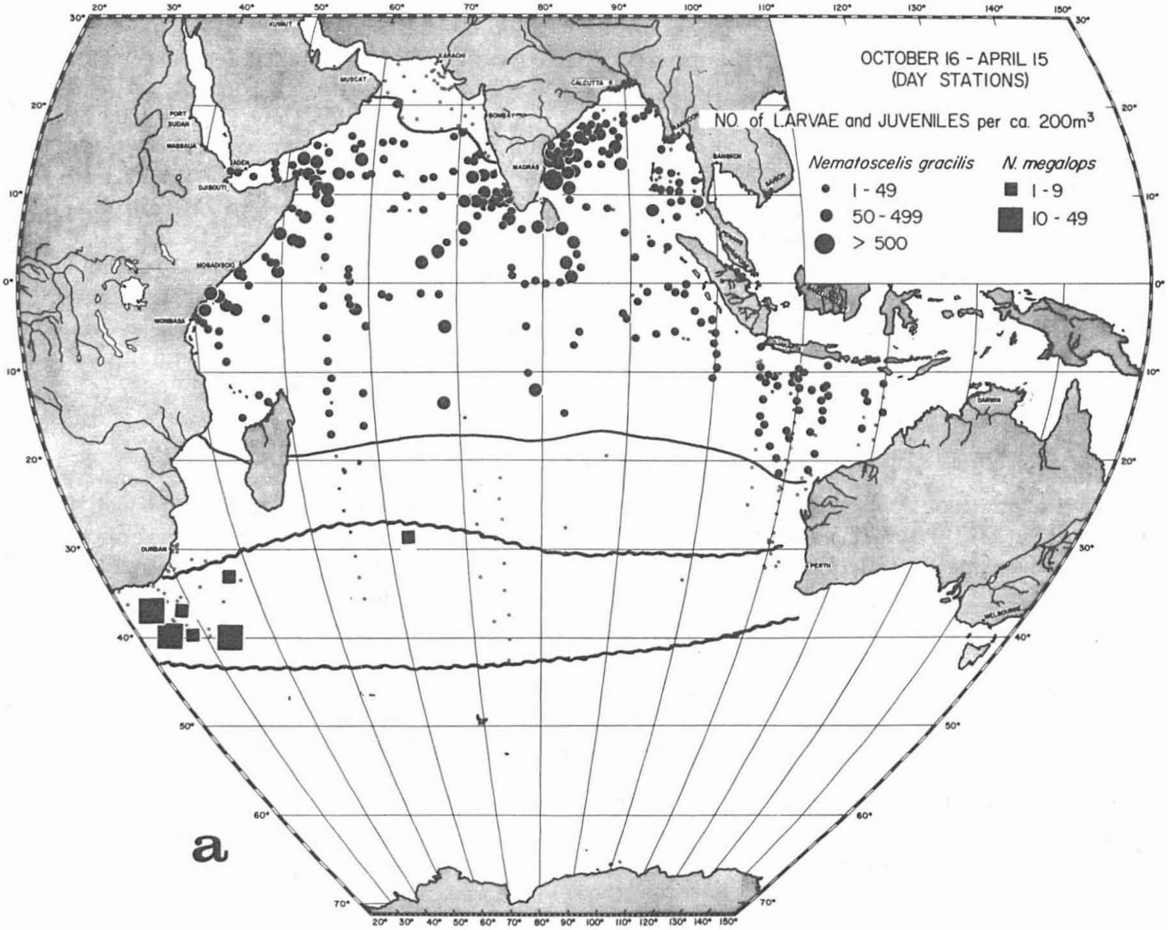


FIGURE 4.—Locality records and daytime abundance of larvae and juveniles of *Nematoscelis gracilis* and *N. megalops* in the Indian Ocean: a - NE Monsoon period. (Solid lines represent approximate distribution boundaries of *N. gracilis* and wavy lines represent those of *N. megalops*.)

from Figures 14.1 and 14.2 of Neumann and Pierson, 1966) and to which the South Equatorial Current contributes, transports some of the new forms to the south and the Agulhas Current transports them to the tip of South Africa.

During the SW monsoon the distribution of the new form is much broader in the west than in the east (Figure 5b). As the strong Somali Current begins to flow northeastward, a great deal of Southern Hemisphere water is brought to the north along the African coast. Thus the population of the new form is brought north of the Equator. It was caught as far north as lat. 8°N along the coast of Somalia; but it did not reach the upwelling areas of the Arabian coast. It has been suggested that the Somali Current turns eastward after reaching lat. 8°N and joins the Southwest Monsoon Current flowing east (Taft, 1971); the distribution of the new form in the upper layer follows the same pattern (Figure 5b). Except in the area of the Somali Current, the overlapping zone was confined to the eastern ocean. The intermediate forms were distributed across the equatorial ocean. In the region of the Mozambique Current new forms were found as far south as lat. 30°S.

Populations of the old form in the Bay of Bengal and the Arabian Sea show seasonal changes in the abundance of larvae and juveniles (Figure 6). All the available IIOE plankton samples from these two areas were used to prepare these monthly frequency distributions. In the Bay of Bengal the highest frequency of calyptopis larvae was observed in February, whereas in the Arabian Sea it

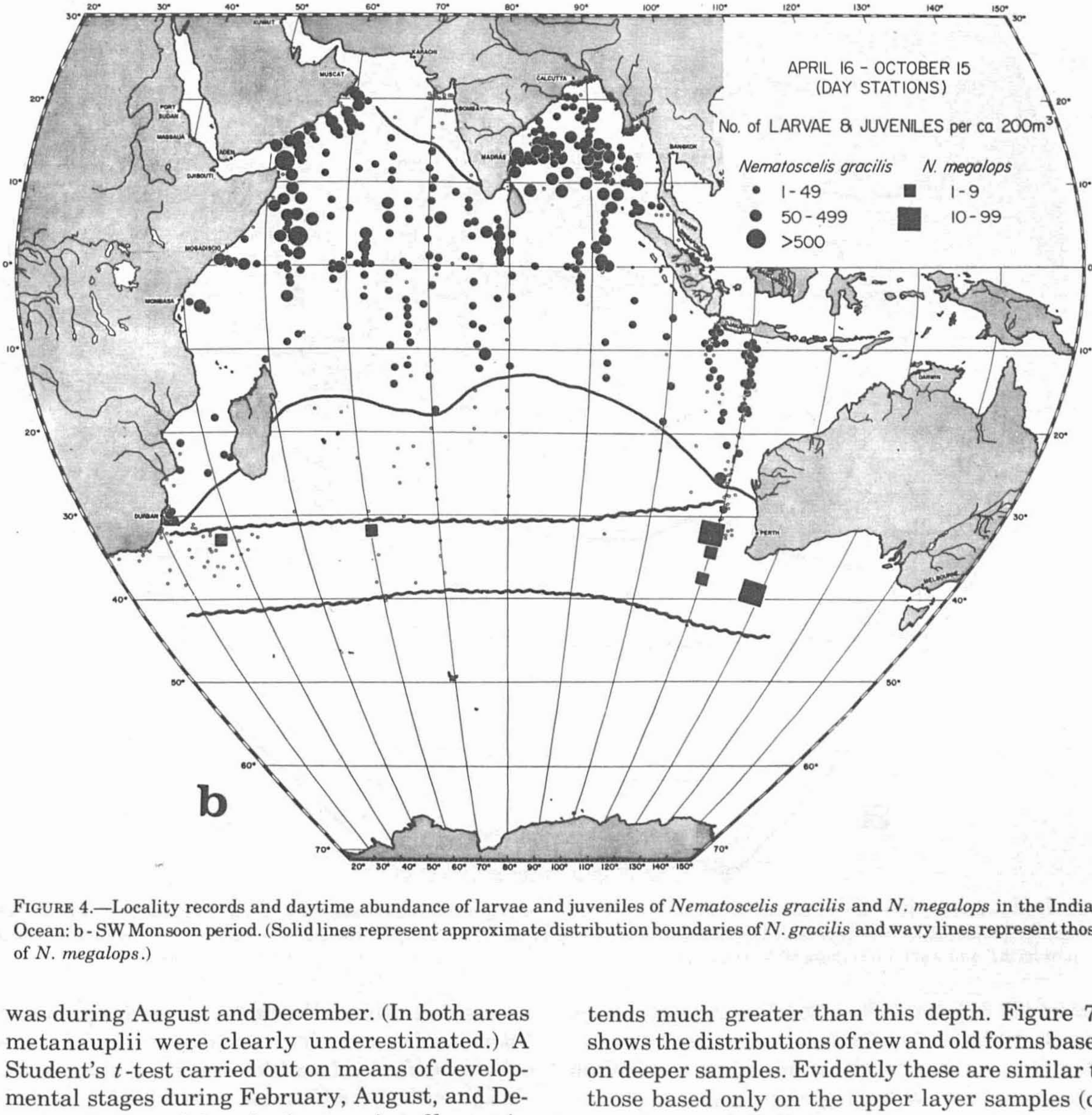


FIGURE 4.—Locality records and daytime abundance of larvae and juveniles of *Nematoscelis gracilis* and *N. megalops* in the Indian Ocean: b - SW Monsoon period. (Solid lines represent approximate distribution boundaries of *N. gracilis* and wavy lines represent those of *N. megalops*.)

was during August and December. (In both areas metanauplii were clearly underestimated.) A Student's t-test carried out on means of developmental stages during February, August, and December indicated that the frequencies of larvae in the Bay of Bengal were significantly different ($P < 0.01$) from those in the Arabian Sea during the same months. Frequencies during other months were not significantly different between the two populations. Since most of the developmental stages were caught each month, it appears that spawning is continuous; only the rate of production is subjected to seasonal changes.

The distributional patterns of the two forms of *N. gracilis* so far discussed are based on adults caught from the upper 200-m layer. As pointed out before, the vertical distribution of this species extends much greater than this depth. Figure 7a shows the distributions of new and old forms based on deeper samples. Evidently these are similar to those based only on the upper layer samples (cf. Figures 5, 7a). Both forms were caught from the same station only near the Equator, and intermediate forms were found only at the areas of overlap near the Equator.

Atlantic Ocean

Nematoscelis gracilis has not been reported from the tropical Atlantic Ocean, nor was it found in any collections examined during the present survey. The only record from the Atlantic Ocean was from the southwest coast of Africa (Lusiad VII-IKMT, station 63-539, lat. 33°47′S, long.

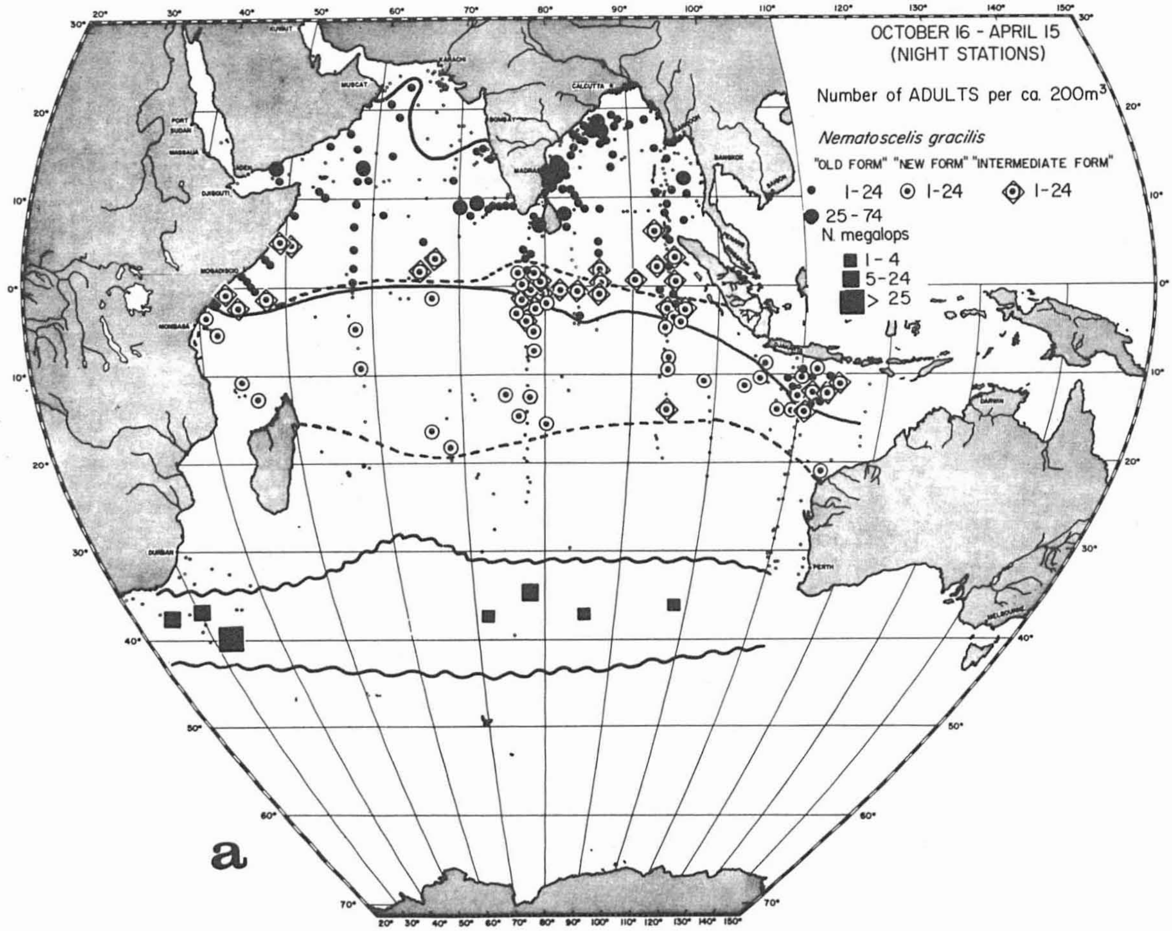


FIGURE 5.—Locality records and nighttime abundance of *Nematoscelis gracilis* and *N. megalops* adults in the Indian Ocean: a - NE Monsoon period. (Solid lines represent approximate boundaries of distribution of *N. gracilis* "old form," broken lines represent those of "new form," and wavy lines those of *N. megalops.*)

15°47′E, 5 June 1963). (See Figure 14b.) Three adult males and one female belonging to the new form were caught at this station, but no old form was found. Probably these new forms were transported westward by the Agulhas Current (Figure 7a).

Pacific Ocean

Nematoscelis gracilis is recorded from the equatorial zone of the Pacific (Brinton, 1962). Populations of this species were also shown to have been carried by the Kuroshio system to as far as lat. 40°N, east of Japan. The numerical density was found to be much higher in the east than in the west. In the present survey based on mid-water trawls from the Pacific, a similar pattern of distribution was observed (Figure 7a). The new forms were also found to occur in the Pacific, but only south of the Equator. There Reid (1965) recognized an eastward flow at about 400-800 m (on the basis of acceleration potentials at 125 cl/ton (lat. 2°-8°S) and 80 cl/ton (lat. 8° - 20°S) δ T). However, in the eastern Pacific the same latitudes are occupied by old forms where Reid (1965) and Love (1972) reported a narrow tongue of low oxygen, as low as 0.2-0.5 ml/l, extending westward. The contour of oxygen concentration of 0.5 ml/l extended as far west as long. 130°W between the Equator and lat. 10°S (at 160 cl/ton δ T surface, 150-200 m). This may account for the fact that new forms do not reach eastward to the coasts of Chile and Peru. The association of old forms with oxygen-poor

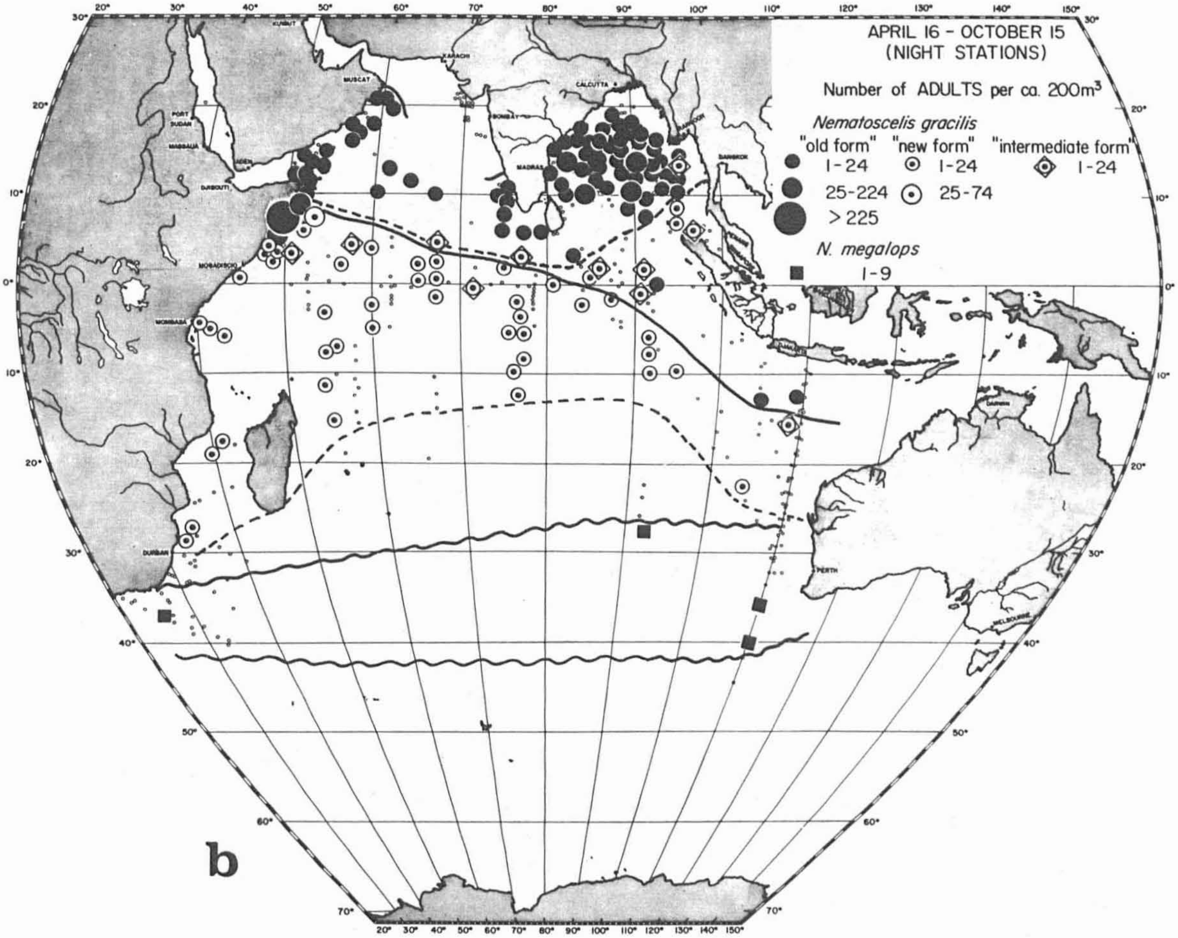


FIGURE 5.—Locality records and nighttime abundance of *Nematoscelis gracilis* and *N. megalops* adults in the Indian Ocean: b - SW Monsoon period. (Solid lines represent approximate boundaries of distribution of *N. gracilis* "old form," broken lines represent those of "new form," and wavy lines those of *N. megalops*.)

water is evident from these comparisons. *Nematoscelis gracilis* old form is the dominant *Nematoscelis* species occurring in the eastern tropical Pacific. Along the coasts of Peru and Chile this form is now known to be distributed as far south as lat. 33°S (personal observation in a sample collected by Antezana). Only old forms were found in the China Sea and in oceanic waters of the Kuroshio system. However, the new and old forms cooccurred in the Timor, Banda, Celebes, Halmahera, and Molucca seas. The Indian Ocean populations of both forms are therefore in continuity with those of the Pacific. In the Pacific the eastern and western populations of the species as a whole are linked along the equatorial zone between lat. 0° and 10°N (Brinton, 1962). Brinton has pointed out that the lat. 20°N-20°S range of *N. gracilis* in the east and the lat. 10°N-10°S range in the west corresponds reasonably well to the range of the equatorial water mass (Sverdrup, Johnson, and Fleming, 1942).

Geographical Distribution of *N. megalops*

Indian Ocean

Nematoscelis megalops was recorded during the IIOE between lat. 30°S and 45°S. This is the area of transition between subantarctic and Indian Central water (Sverdrup et al., 1942). The number of samples collected from this zone is too scanty to permit a seasonal study. Larvae, juveniles, and adults were caught during both seasons along the

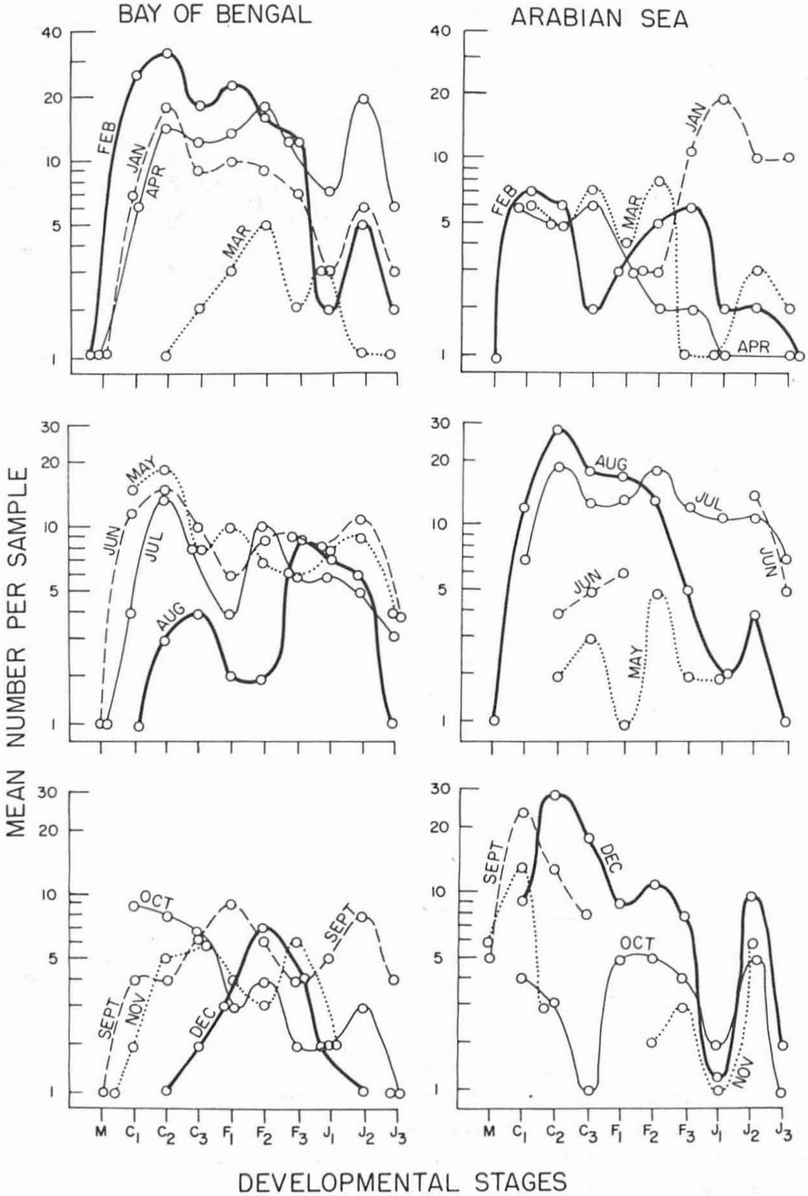


FIGURE 6.—Frequency distribution of developmental stages of *Nematoscelis gracilis* "old form" in the Bay of Bengal and the Arabian Sea. (Number of samples used to calculate monthly averages ranged from 11 to 18.)

full extent of the transition zone (Figures 4, 5). In the western Indian Ocean, the maximum number of larvae (as many as 280 larvae per sample) was caught during October 1962 (*Natal* cruise 5). In the east, *Diamantina* cruise 3/62 caught up to 90 larvae per sample during September 1962. Although Boden (1954) reported this species in the region of the Mozambique Current, I did not find it in meter-net samples or mid-water trawls taken north of lat. 34°S in waters of southeast Africa (Figure 7b). (Trawls were made during the October-November period.) However, the northern boundary of distribution appears to lie between lat. 28°S and 30°S. The northernmost record of this species was at lat. 28°18′S, long. 62°33′E (*Vitiaz* 36, station 5323).

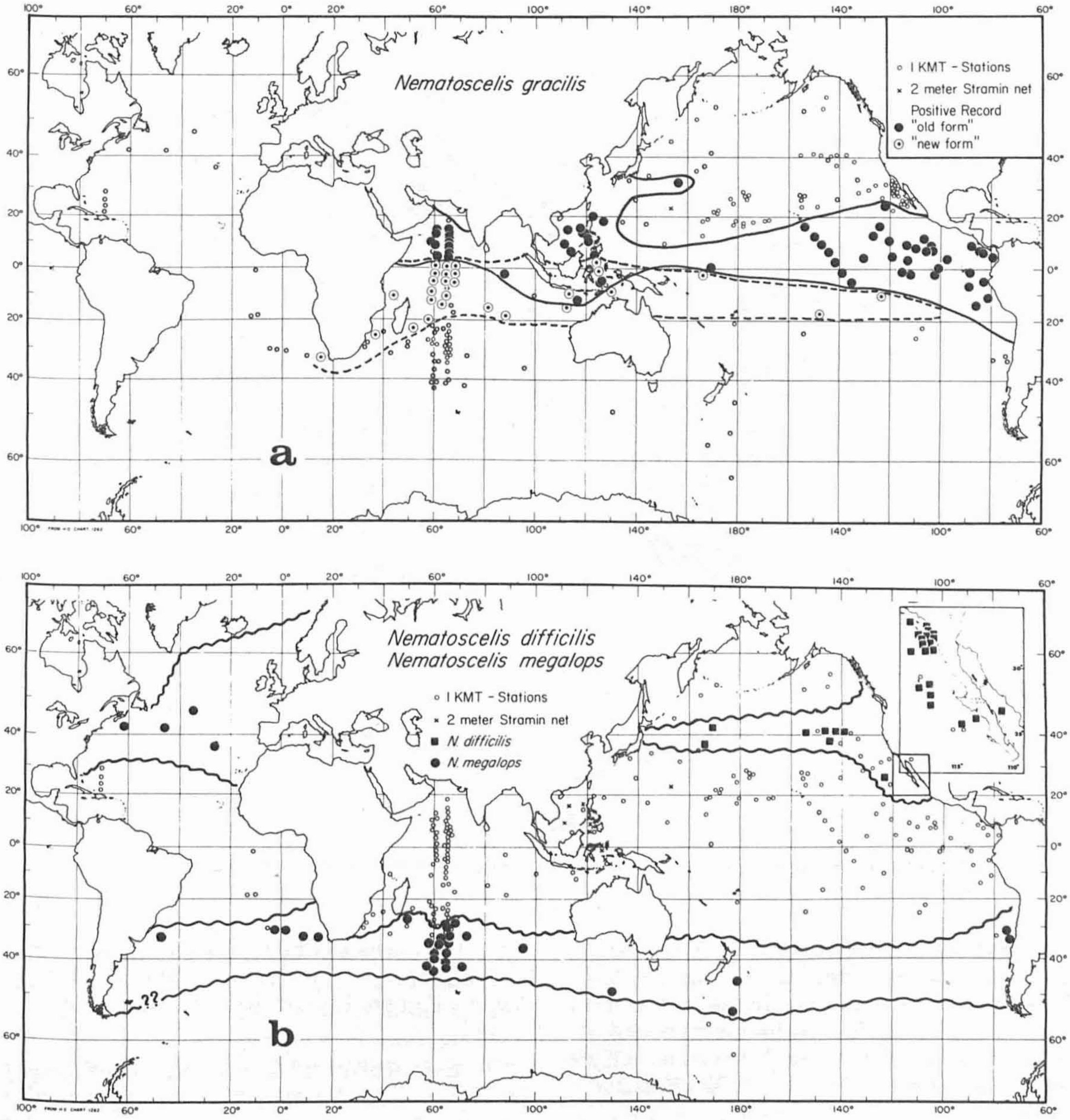


FIGURE 7.—Worldwide distribution of *Nematoscelis* based on mid-water trawls: a - *N. gracilis* "old" and "new" forms; b - *N. difficilis* and *N. megalops*. (Solid lines represent approximate boundaries of distribution of old form, broken lines represent those of new form, and wavy lines represent distributional boundaries of *N. difficilis* and *N. megalops*. Boundaries are based on literature records and present evidence.)

Atlantic Ocean

Nematoscelis megalops appears to have a wider north-south range in the Atlantic than in other oceans. The southernmost record in the North Atlantic was in the region of the Canary Current (Figure 8a). Larvae and juveniles were frequently caught between lat. 40°N and 53°N. Literature records of this species in the North Atlantic are as far north as lat. 68°N (Zelikman, 1964). Moore (1952) recorded this species from lat. 35°N to 55°N. It occurs in the Mediterranean Sea (Ruud, 1936). In the South Atlantic it was collected by the Lusiad Expedition between lat. 25°S and 30°S

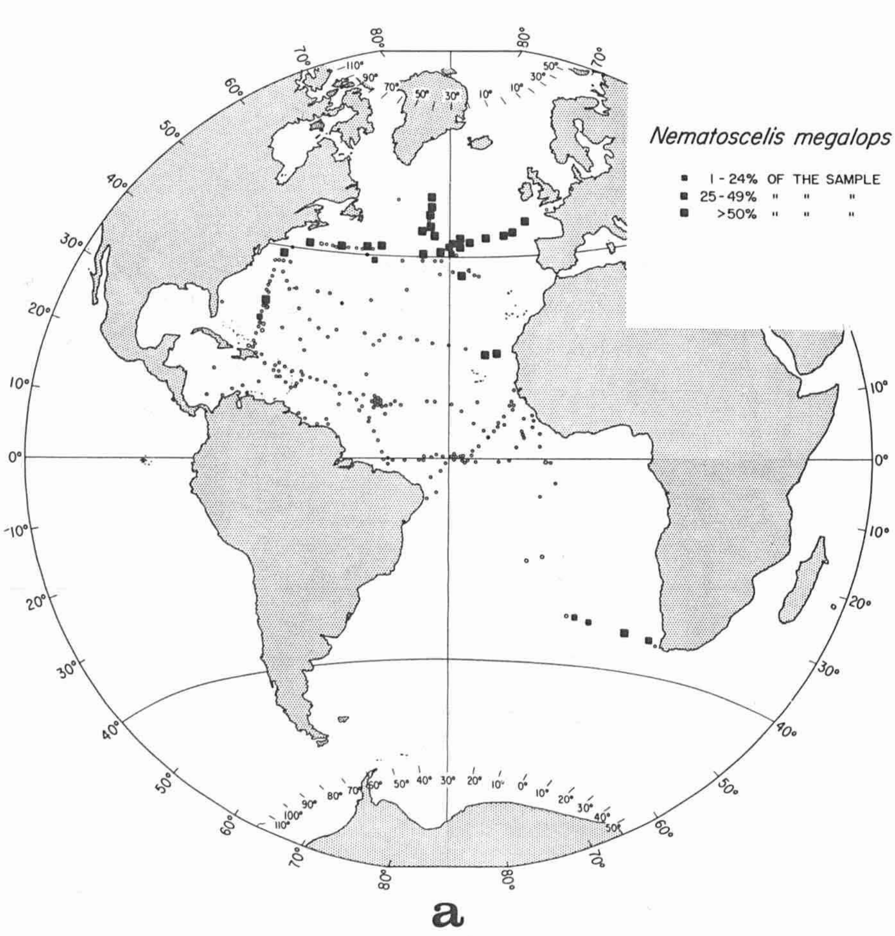


FIGURE 8.—Distribution of *Nematoscelis* in the Atlantic Ocean based on plankton samples: a - *N. megalops*.

(Figure 8a). Boden (1954) recorded this species from the Benguela Current as far north as lat. 22°S. From the western part of the South Atlantic no data is available. The only literature record is from the Brazil Current area, between lat. 45°S and 50°S and long. 62°W and 68°W (Ramirez, 1971).

Pacific Ocean

Nematoscelis megalops and *N. difficilis* are a recognized sibling species pair, occupying transoceanic belts of the transition zones of the South and North Pacific oceans respectively (Brinton, 1962). During the Downwind Expedition, Brinton found *N. megalops* distributed between lat. 33°S and 48°S in midocean. The Monsoon Expedition caught it as far south as lat. 54°21′S (Figure 7b). Along the coasts of Chile between lat. 30°S and 50°S this species was caught by MV-65 (*Anton Bruun*), Piquero III, and Scorpio I expeditions.

Geographical Distribution of *N. difficilis*

Nematoscelis difficilis is endemic to the North Pacific, occupying the North Pacific Drift and the California Current (Figure 7b). It was reported during Transpacific Expedition from seven stations located east of Japan (Brinton, 1962). In the present study it was found in mid-water trawls from near lat. 40°N between long. 130°W and 160°W. Along the North American coast, the distribution extends northward to lat. 51°N (Banner, 1949) and southward to lat. 20°N (Brinton, 1962). It is common in the cold water of the California

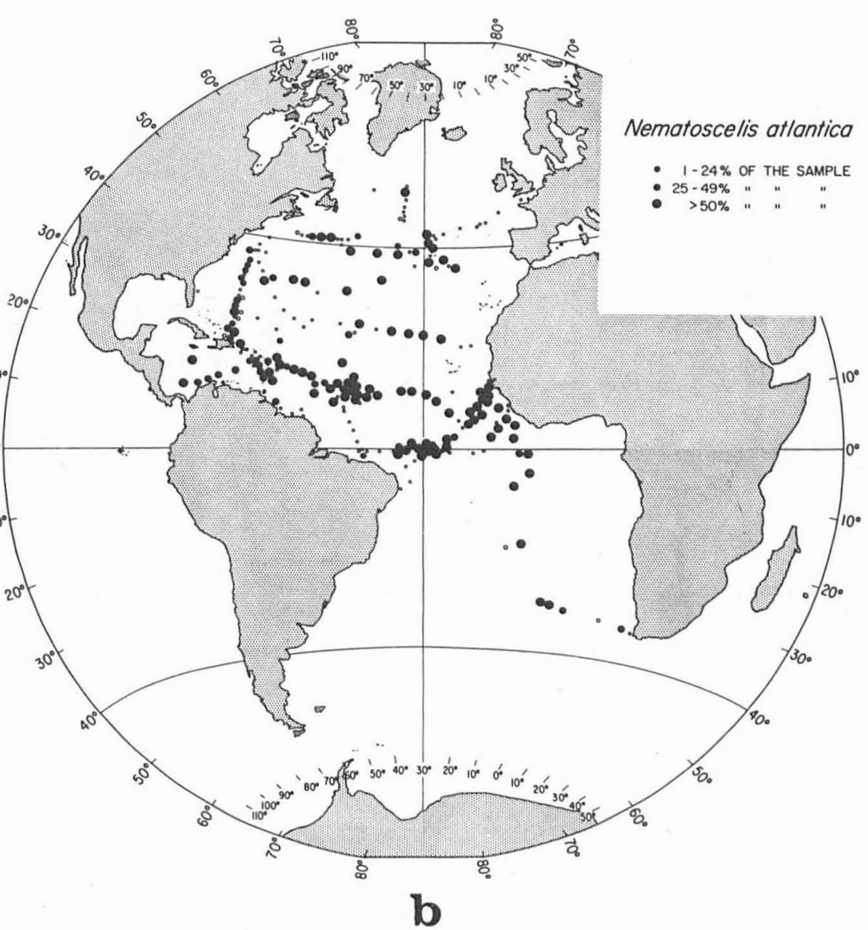


FIGURE 8.—Distribution of *Nematoscelis* in the Atlantic Ocean based on plankton samples: b - *N. atlantica*.

Current and caught frequently in mid-water trawls in the San Diego Trough area. This species was also caught in the Gulf of California by the Vermilion Sea Expedition; however, this population is believed to be separated, perhaps seasonally, from that on the west side of Baja California due to the influx of warm water from the south at the mouth of the Gulf (Brinton, 1962). Literature records and present evidence indicate that the ranges of *N. megalops* and *N. difficilis* do not overlap.

Geographical Distribution of *N. atlantica*

Indian Ocean

This species has not been reported previously from the Indian Ocean. In the IIOE collections there were frequent occurrences of this species, but only in the midlatitudes (lat. 15°-40°S) of the Southern Hemisphere (Figure 9a, b). *Nematoscelis atlantica* lives in the region of the Indian Ocean central water mass. Larvae and juveniles were caught from most stations occupied within the range of distribution of the species. Moreover, there were no obvious differences between seasonal distributions. IIOE samples included many adults from west of Australia and the Agulhas Current (Figure 10a, b). In the mid-water trawls it was caught between lat. 11°S and 42°S along long. 60°E (Figure 11a).

Atlantic Ocean

Nematoscelis atlantica was observed in many samples from the North Atlantic (Figure 8b). Un-

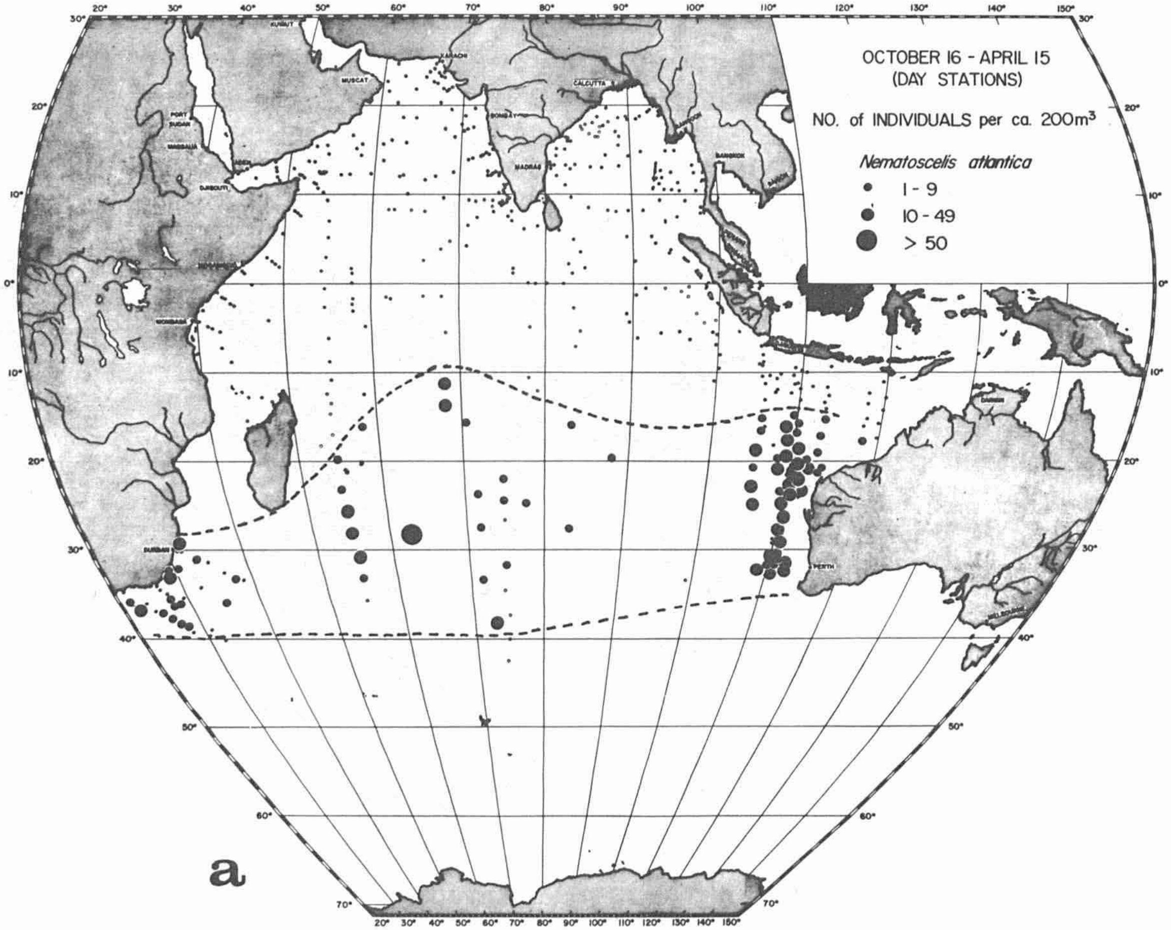


FIGURE 9.—Locality records and daytime abundance of larvae and juveniles of *Nematoscelis atlantica* in the Indian Ocean: a - NE Monsoon period.

like in the Pacific and Indian oceans, this species also occupies the Atlantic equatorial zone providing communication between North and South Atlantic populations. The German South Polar Expedition (Zimmer, 1914) first recorded the north-south continuity of *N. atlantica* in the Atlantic. In the eastern Atlantic between the Equator and lat. 40°N, *N. atlantica* constituted over 50% of the total *Nematoscelis* present in each sample. The northernmost record was at lat. 52°N (*Atlantis II*-9, station 371). This species was not reported previously from the North Atlantic central gyre (Mauchline and Fisher, 1969). In the present collection many larvae, juveniles, and mature adults were recorded from this area. Mediterranean Sea records come from Ruud (1936) and Casanova-Soulier (1968). In the South Atlantic it was present in the Lusiad collections (Figure 11a). Literature records in the South Atlantic show that it occurs in the Benguela Current, extending as far as lat. 40°S (Mauchline and Fisher, 1969). No samples were available from the areas of the Argentine Basin.

Pacific Ocean

In the Pacific, *N. atlantica* lives in the central water masses of both hemispheres (Figure 11a). The approximate boundaries of distribution are between lat. 13° and 38° in each hemisphere (Brinton, 1962). It was not caught in the Naga collections from the Indo-Australian Archipelago. The North Pacific population of this species appears to be separated from those of the South Pacific and Indian Ocean regions. It may be possible that communication exists between Indian and South Pacific populations through the oceanic waters south of Australia.

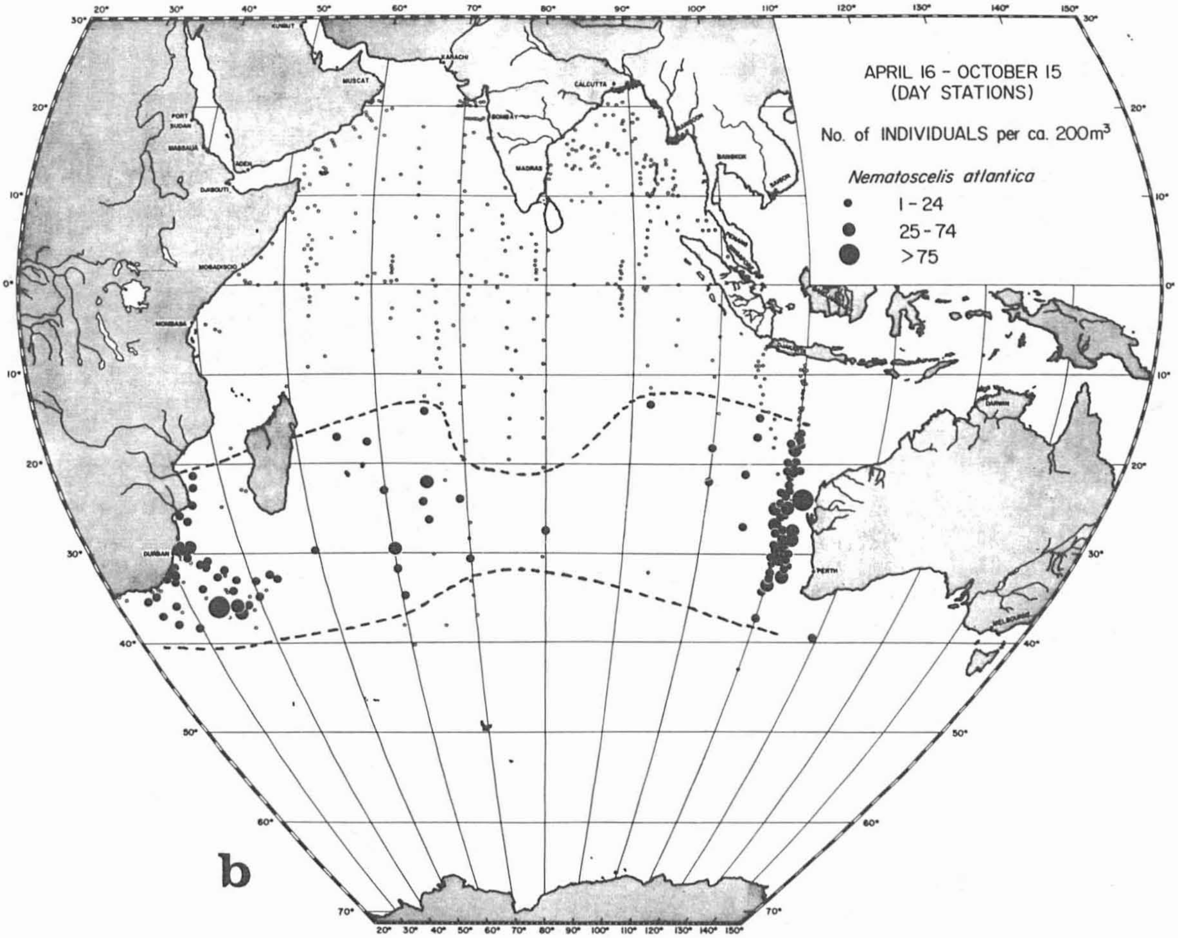


FIGURE 9.—Locality records and daytime abundance of larvae and juveniles of *Nematoscelis atlantica* in the Indian Ocean: b - SW Monsoon period.

Geographical Distribution of *N. microps*

Indian Ocean

Nematoscelis microps has wider ranges of distribution than *N. gracilis* and *N. atlantica*. This species penetrates the Arabian Sea and the Bay of Bengal only at their western and eastern sides respectively (Figure 12a, b). The northernmost record of this species in the western Arabian Sea was at lat. 14°N and that in the eastern side of the Bay of Bengal at lat. 19°N off the coast of Burma. It does not live in the poorly oxygenated subsurface waters of the Arabian Sea and Bay of Bengal. In midocean the northern boundary does not extend north of lat. 6°N and the southern boundary not beyond lat. 30°S. It was caught less frequently from the southern central gyre south of lat. 10°S. *Nematoscelis microps* is a predominant species of the South Equatorial Current and the West Australian area. The Agulhas Current apparently brings it around the tip of South Africa.

There was not much seasonal change in the distribution of this species in the Indian Ocean. Larvae and juveniles were present in the Somali Current area during both monsoon seasons but were carried as far north as lat. 14°N only during the SW monsoon. They were present throughout the year in the Andaman Sea area. During the NE monsoon adults were not caught in the Somali Current area north of the Equator, whereas they were present as far north as lat. 12°N during the opposite season when the flow is northeastward (Figure 13a, b). Adults occurred in the North Equatorial Current area during the NE monsoon

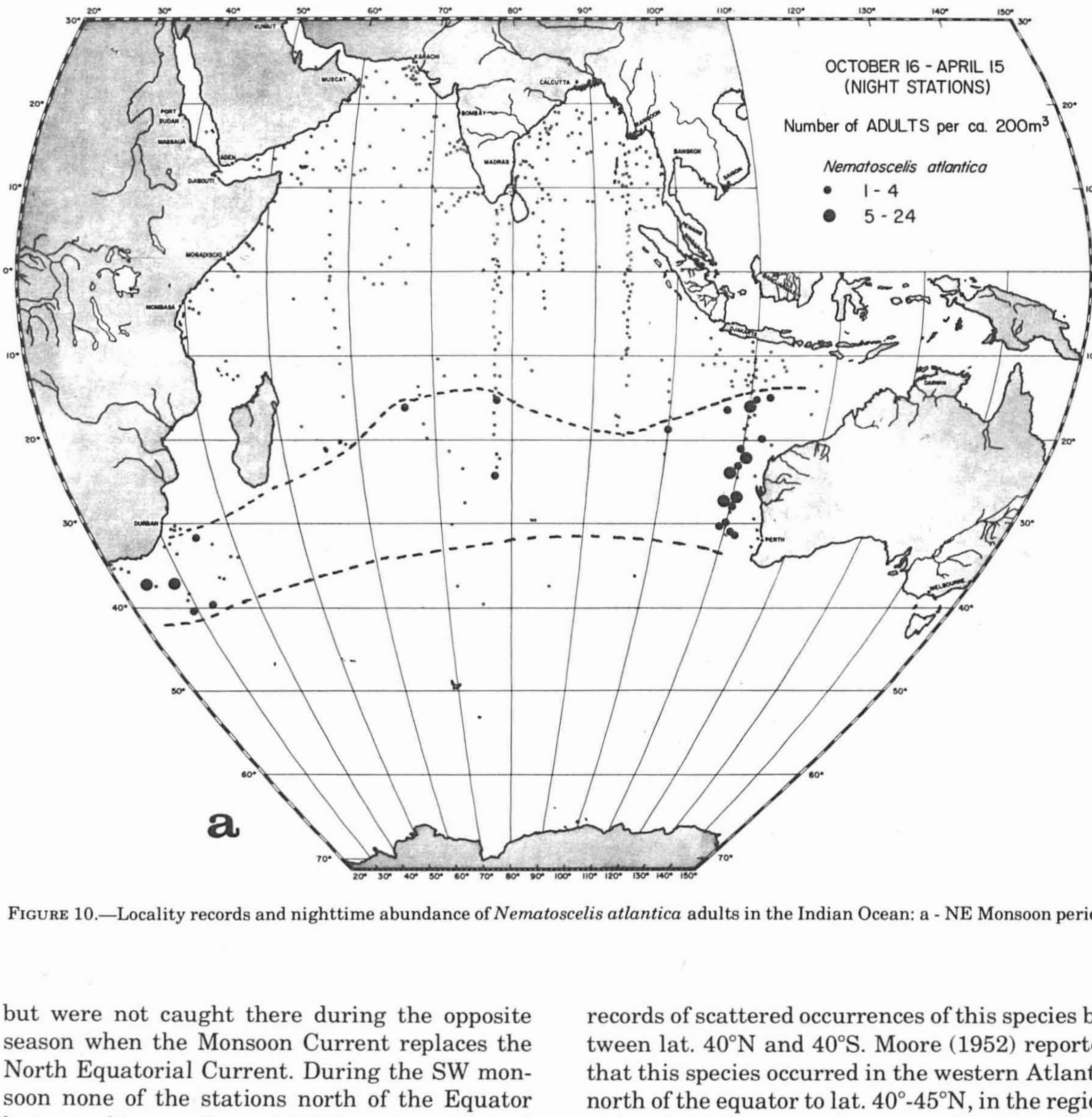


FIGURE 10.—Locality records and nighttime abundance of *Nematoscelis atlantica* adults in the Indian Ocean: a - NE Monsoon period.

but were not caught there during the opposite season when the Monsoon Current replaces the North Equatorial Current. During the SW monsoon none of the stations north of the Equator between long. 50°E and 90°E contained adult specimens (Figure 13b). Evidently this species does not reach the coast of India. In the mid-water trawls *N. microps* was caught between lat. 10°N and 41°S (Figure 11b), but north of lat. 2°N this species was caught from only one station (*Anton Bruun* cruise 3, station 146, lat. 10°09′N, long. 59°55′E).

Atlantic Ocean

From the Atlantic Ocean there are literature records of scattered occurrences of this species between lat. 40°N and 40°S. Moore (1952) reported that this species occurred in the western Atlantic north of the equator to lat. 40°-45°N, in the region of the Gulf Stream. The most northerly record in the eastern ocean was from lat. 59°39′N (Illig, 1930), although most other records lie south of lat. 40°N. In the present survey it was caught between the Equator and lat. 40°N and was relatively more abundant in the western ocean than in the east (Figure 14a). It was not present in many samples taken from the North Atlantic central gyre. There were a few doubtful records of this species from the Mediterranean Sea (Ruud, 1936; Bacescu and Mayer, 1961). In the South Atlantic it was caught by Lusiad and *Atlantis II* - 31 expeditions (Figure 11b).

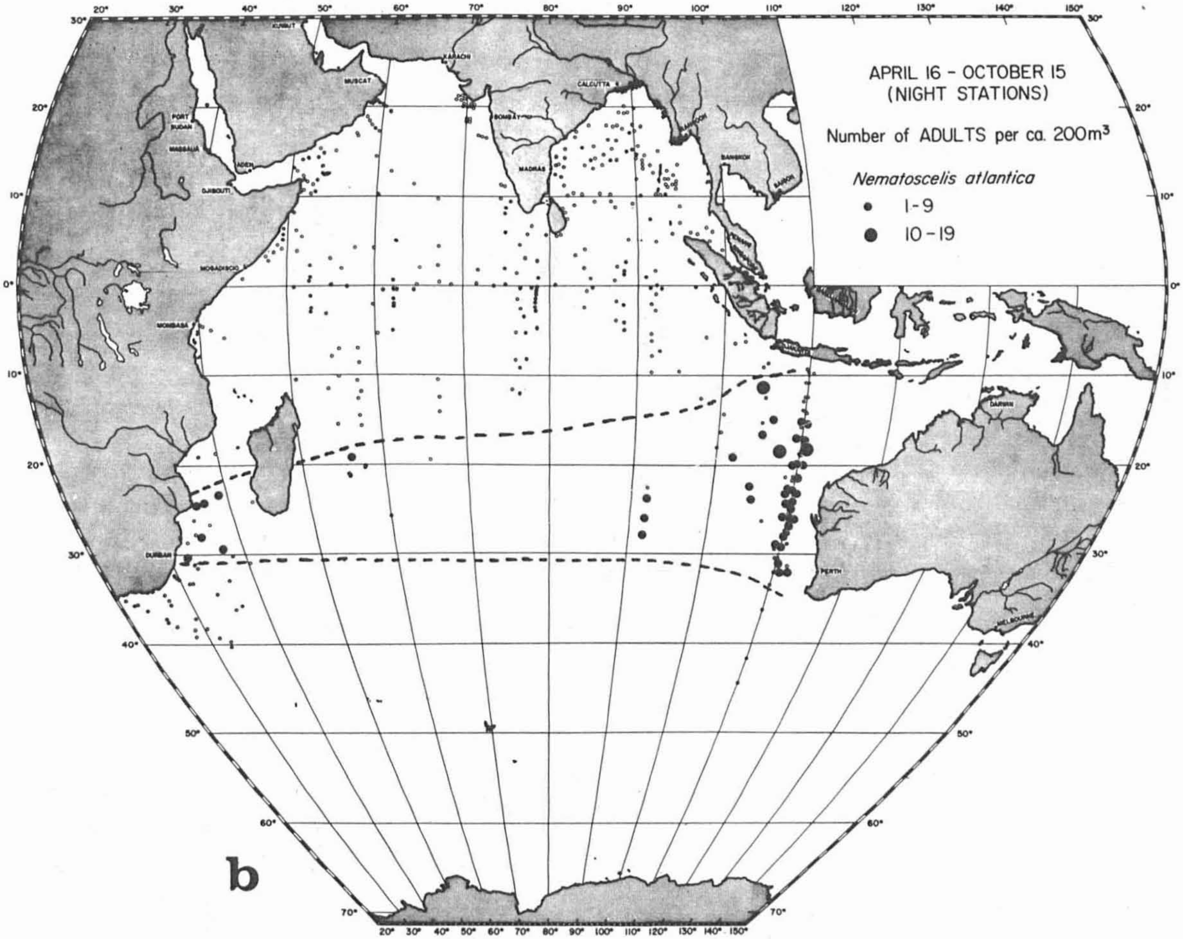


FIGURE 10.—Locality records and nighttime abundance of *Nematoscelis atlantica* adults in the Indian Ocean: b - SW Monsoon period.

Pacific Ocean

North and South Pacific populations of *N. microps* are in communication with each other across the western equatorial Pacific (Figure 11b). This species is absent along the eastern boundary currents (California Current and Peru Current) and also from the poorly oxygenated subsurface waters of the eastern tropical Pacific. *Nematoscelis microps* was also caught less frequently in the eastern North Pacific central water mass than in the western North Pacific central water mass. In the equatorial region this species is known to occur only west of long. 110°W (Brinton, 1962). It is also recorded from the China Sea and the regions of the Timor, Molucca, and Banda seas. The populations of the Indian and Pacific oceans are probably in communication with each other through the straits of Timor, Banda, Molucca, and Halmahera.

Geographical Distribution of *N. lobata*

Hansen (1916) described *N. lobata* from the Philippines. He found it at only two localities: lat. 13°43′N, long. 121°E and lat. 7°07′N, long. 125°40′E. *Nematoscelis lobata* appears to be endemic to the semi-isolated seas around the western side of the Philippines. In the present survey it was caught mostly from the Sulu Sea area (Naga Expedition) (Figure 15). At station S11B-205, five mature males and six females were caught in a 2-m-net collection, 0-500 m (lat. 6°35′N, long.

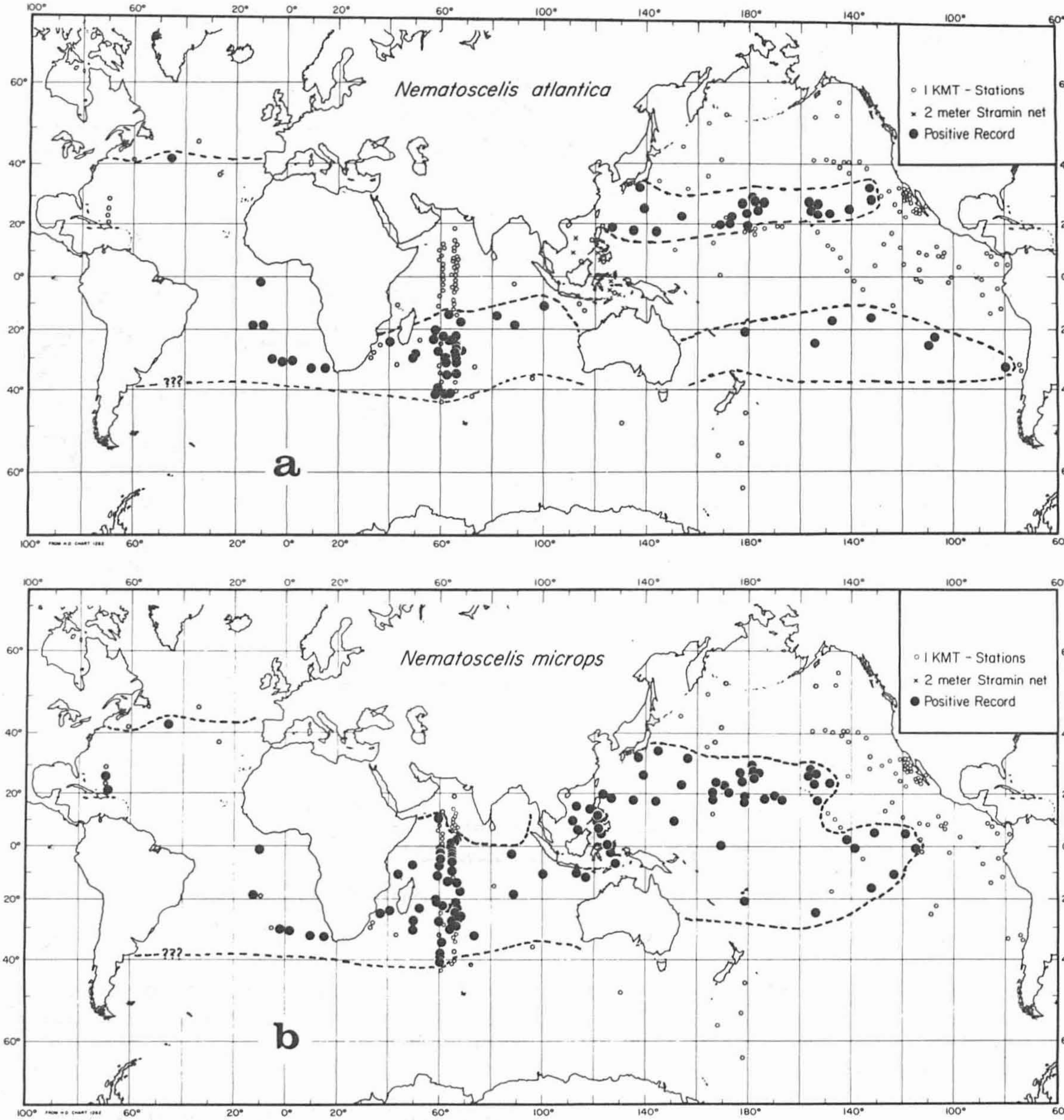


FIGURE 11.—Worldwide distribution of *Nematoscelis* based on mid-water trawls: a - *N. atlantica*; b - *N. microps*. (Broken lines represent approximate boundaries of distribution of the species based on literature records and present evidence.)

122°27′E; 29 April 1961). At six other stations only mature females were caught. The petasma, particularly the broad median lobe with its convex inner and outer margins, is an excellent diagnostic feature of this species. The shape of the keel on the carapace of both sexes is also different from other *Nematoscelis* species. *Nematoscelis lobata* is not reported from any other place, including the Siboga collections from the East Indian Archipelago and the Troll Expedition collections made along the eastern coast of the Philippines (Figure 15). This species appears to be absent from the South China Sea and the Gulf of Thailand (Brinton, manuscript).

Geographical Distribution of *N. tenella*

Indian Ocean

The geographical distribution of *N. tenella* is similar to that of *N. microps*. This species lives in the equatorial and central water masses of all oceans. In the Indian Ocean most records came from between lat. 7°N and 38°S except in the eastern and western boundary current areas (Figures 16a, b; 17a, b). It was most frequently caught in the equatorial zone and in the eastern ocean south of the Equator. Larvae and juveniles occurred throughout the range of distribution. There were no seasonal differences in the distribution of larvae and juveniles; however, in the western Indian Ocean north of the Equator they were more abundant during the SW monsoon than in the opposite season. This species penetrates into the Arabian Sea only in the western side. It is absent from the Bay of Bengal. The pattern of distribution of adults was like that of larvae and juveniles (Figure 17a, b). Mid-water trawls caught *N. tenella* between lat. 8°N and 40°S (Figure 18).

Atlantic Ocean

Illig (1930) recorded *N. tenella* from lat. 59°39′N, long. 8°49′W, but all other records are from lat. 35°N to 35°S. Lewis (1954) reported this species off southern Florida. In the present study larvae and juveniles were found to be more abundant in the western North Atlantic than on the eastern side (Figure 14b). Around lat. 40°N, its northern limit, it was caught in five plankton samples. It has not been reported from the Mediterranean Sea. In the South Atlantic this species was found in the Lusiad collections off South Africa. No samples were available from the western South Atlantic nor has it been reported from that region. It is also not known whether this species occurs in the Benguela Current.

Pacific Ocean

Nematoscelis tenella lives in both hemispheres of the Pacific, lat. 35°N-34°S. It does not occupy the more coastal areas of the California Current or its southward extension into the eastern equatorial region (Figure 18). It is also scarce in the region of the Peru Current (Brinton, 1962). In midocean, Brinton recorded it as far south as lat. 34°S. This species appears to be more abundant in the northern central gyre than in the south. It occurs farther east in the tropical belt than *N. microps*. The north-south range is continuous across the Equator. It is a common species in the South and East China seas and also in the Banda, Molucca, and Timor seas. Apparent communication exists between the Indian and Pacific populations.

Faunal Zones and Biogeography of *Nematoscelis*

Faunal regions of the oceanic environment are not as well defined as in the terrestrial habitats. The oceanic environment, as distinguished by Hedgpeth (1957), consists of a system of zonally oriented hydrographic provinces arranged in latitudinal succession within each ocean. In the Atlantic Ocean, Dahl (1894) recognized four epipelagic faunal regions: arctic, subarctic (temperate), subtropical, and tropical. Steuer (1933) described a similar system of classification but included the Pacific and Indian oceans. He recognized circumpolar arctic, circumequatorial tropical, and circumpolar antarctic on a global scale. The arctic region was subdivided into a circumpolar subregion as well as Atlantic and Pacific subarctic subregions. The antarctic region includes the circumpolar antarctic and subantarctic subregions. The tropical region was subdivided into Atlantic and Indo-Pacific provinces. A system of classification based on this and other subsequent works [for example: Deacon (1933, 1937); Radzikhovskaya (1965); Stepanov (1965); Frost (1969); McGowan (1971)] is adapted here and shown in Table 2. The division of the epipelagic environment into faunal zones agrees with the distributional patterns of many planktonic organisms [see McGowan (1971) for examples]. Species of *Nematoscelis* occupy one or more of the subregions (Table 3). As mentioned before, *N. difficilis* is endemic to a zone of transition between subarctic and central water in the North Pacific. Even though this zone (Johnson and Brinton, 1963) does not have as well defined a temperature-salinity envelope as other water masses, it maintains endemic species, as well as the densest part of the overall populations of some subarctic and central species. Evidence is accumulating for the existence of a unique water body in this zone with characteristic hydrographical and faunal properties (McGowan, 1971). The extent and location of an analogous transition zone in the North Atlantic, if such exists, is not

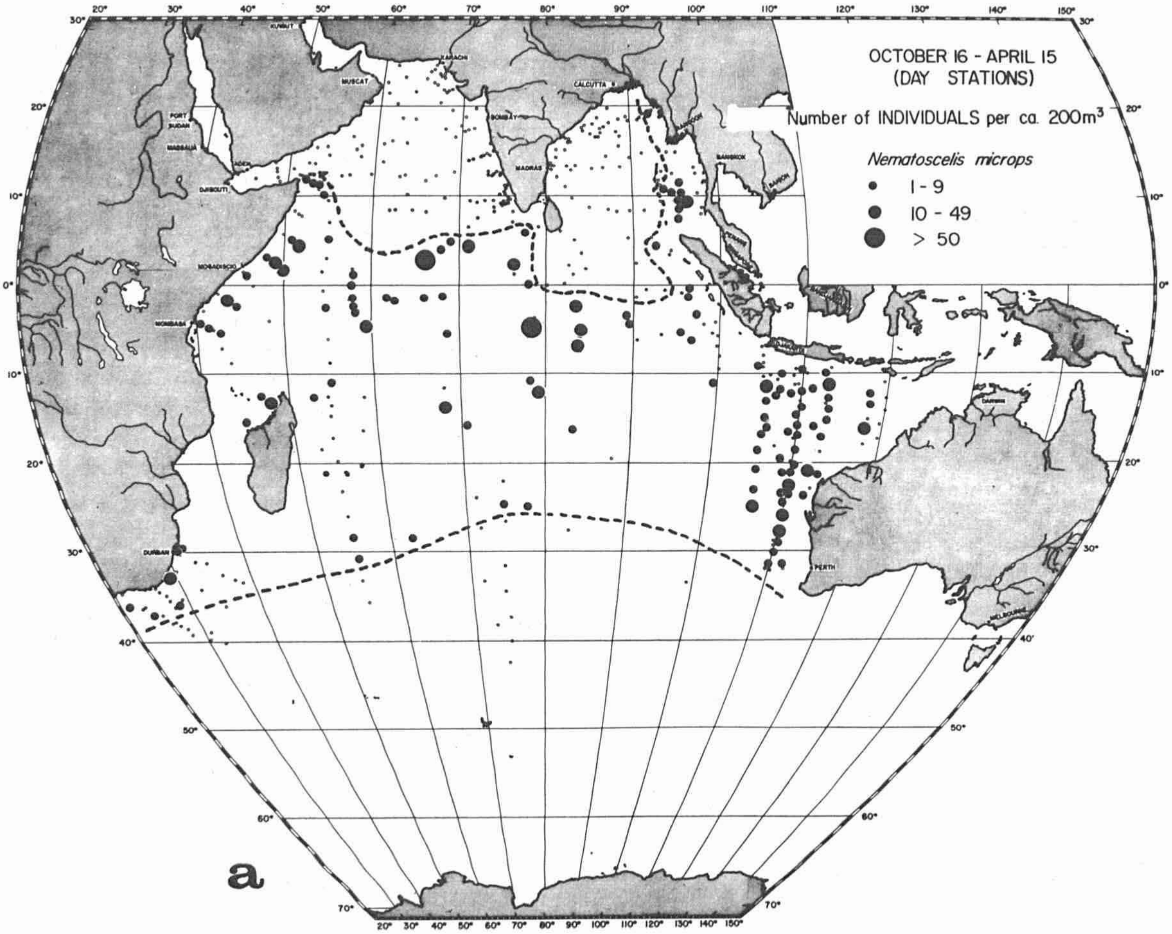


FIGURE 12.—Locality records and daytime abundance of larvae and juveniles of *Nematoscelis microps* in the Indian Ocean: a - NE Monsoon period.

TABLE 2.—Biogeographical zones of the oceanic environment.

Zones	Terminology (Regions)	Latitude (approximate)	Subregion
Northern Cold Water	Circumpolar Arctic	>67°N	Subarctic Atlantic
	Subarctic (Cold Temperate)	45°-67°N	Subarctic Pacific
Northern Transitional	————	35°-45°N	Transitional North Atlantic
			Transitional North Pacific
Warm Water	Northern Subtropical (Warm Temperate)	23°-35°N	Subtropical North Atlantic
			Subtropical North Pacific
	Tropical	23°S-23°N	Tropical Atlantic
			Tropical Indo-West Pacific
			Eastern Tropical Pacific
	Southern Subtropical (Warm Temperate)	23°-35°S	Subtropical South Atlantic
			Subtropical South Pacific
			Subtropical South Indian
Southern Transitional	————	35°-45°S	Circumpolar Transitional Region of the Southern Hemisphere
Southern Cold Water	Circumpolar Subantarctic (Cold Temperate)	45°-67°S	
	Circumpolar Antarctic	>67°S	

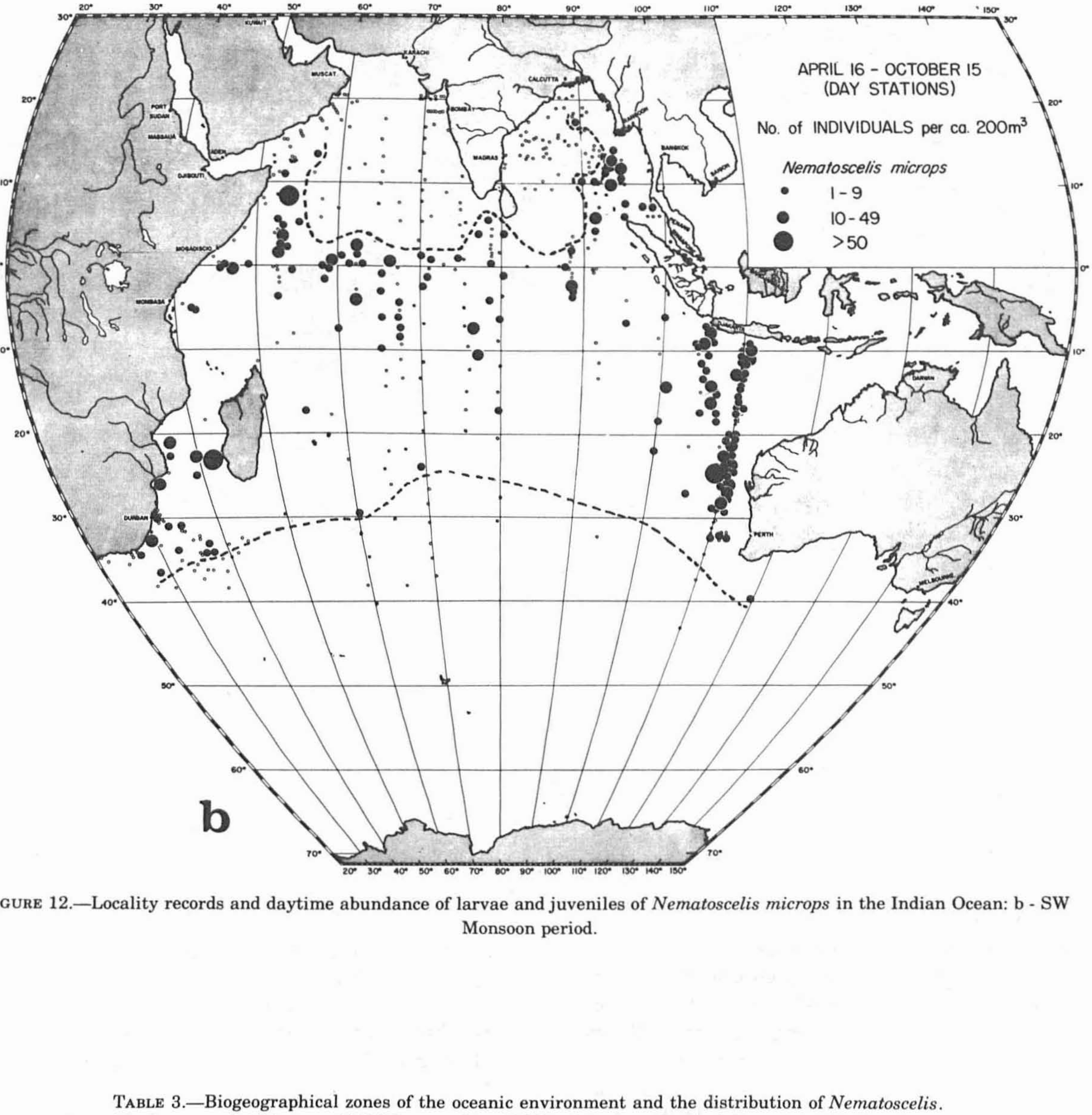


FIGURE 12.—Locality records and daytime abundance of larvae and juveniles of *Nematoscelis microps* in the Indian Ocean: b - SW Monsoon period.

TABLE 3.—Biogeographical zones of the oceanic environment and the distribution of *Nematoscelis*. *Both new and old forms. **Old forms only. ***New form expatriate adults only. ****New forms in Mozambique Current area only.

Subregions	*N. difficilis*	*N. megalops*	*N. atlantica*	*N. gracilis*	*N. microps*	*N. tenella*
Subarctic Atlantic		x				
Transitional North Atlantic		x				
Transitional North Pacific	x					
Subtropical North Atlantic		x	x		x	x
Subtropical North Pacific			x		x	x
Tropical Atlantic			x		x	x
Tropical Indo-West Pacific				x*	x	x
Eastern Tropical Pacific				x**		x
Subtropical South Atlantic			x	x***	x	x
Subtropical South Pacific			x		x	x
Subtropical South Indian			x	x****	x	x
Circumpolar Transitional Region of the Southern Hemisphere		x				

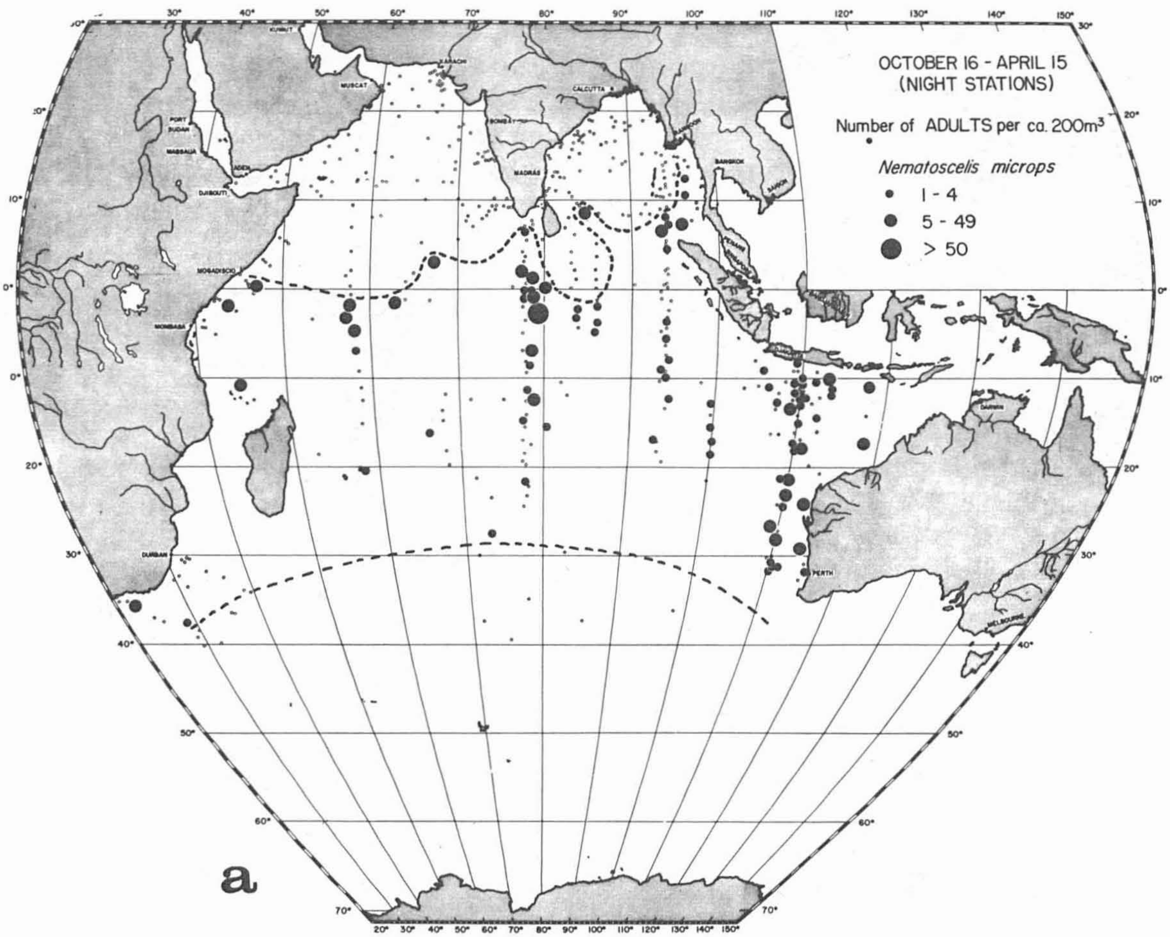


FIGURE 13.—Locality records and nighttime abundance of *Nematoscelis microps* adults in the Indian Ocean: a - NE Monsoon period.

clearly understood. However, lat. 35°-45°N, corresponding to the North Pacific transition, seems to be the extent of the region in the North Atlantic where *N. megalops* (instead of *N. difficilis*) is the most common *Nematoscelis*. *Nematoscelis atlantica, N. microps,* and *N. tenella* also appear in the transition zone of the North Atlantic but not in the corresponding zone in the North Pacific. The northeasterly North Atlantic Current carries warmwater species farther north into the transition zone or even beyond to the subarctic subregion. For example, the present survey recorded *N. atlantica* from lat. 52°N (*Atlantis II*-9, station 371). Outside of its main zone in the North Atlantic, *N. megalops* occasionally occurs in the subtropical and subarctic subregions. It is also the most common *Nematoscelis* species of the circumpolar transitional regions of the Southern Hemisphere, while *N. atlantica*, *N. microps*, and *N. tenella* also were occasionally caught there, from the Indian Ocean sector.

The eastern tropical Pacific Ocean is considered a subregion of the warmwater zone because of its characteristic hydrographical and faunal properties. *Nematoscelis gracilis* old form is part of that faunal assemblage. The Indo-West Pacific and eastern tropical Pacific subregions were considered separate from the Atlantic tropical subregion (Ekman, 1953). The distribution of *N. gracilis* and *N. atlantica* presents evidence for this. *Nematoscelis microps* and *N. tenella* are warmwater species, occupying both tropical and subtropical regions (Table 3). Many warmwater planktonic species are restricted to tropical latitudes, whereas others are found only outside of this region (examples in Bieri, 1959; Brinton, 1962; Alvariño, 1965; Baker, 1965; McGowan, 1971). In this respect *N. gracilis* is tropical and *N. atlantica*

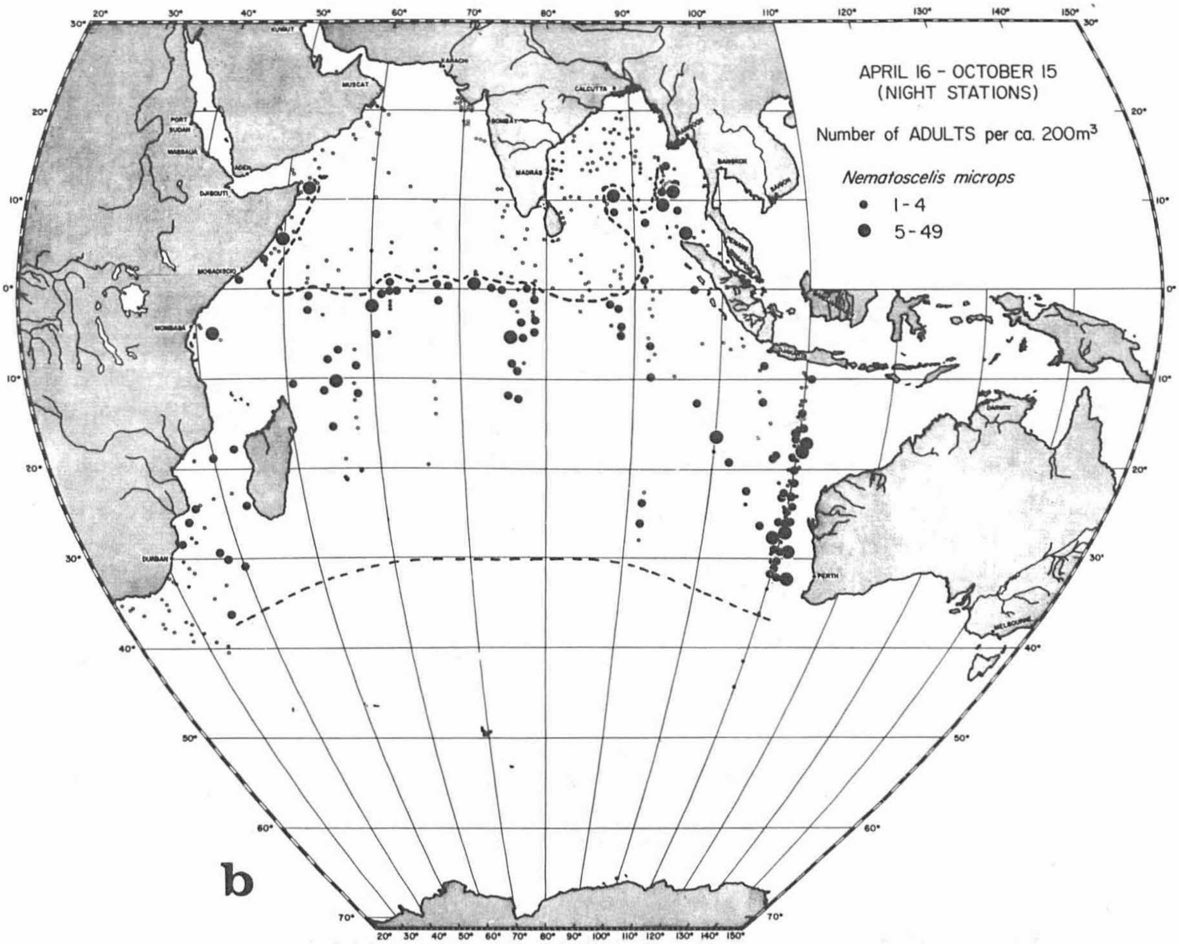


FIGURE 13.—Locality records and nighttime abundance of *Nematoscelis microps* adults in the Indian Ocean: b - SW Monsoon period.

is subtropical. Because the boundaries between the full breadth of tropical and subtropical regions are not well defined hydrographically, it is usually difficult to correlate species' distributional pattern to the hydrographical zones of these two areas.

DISCUSSION

The distributions of *Nematoscelis* species are associated with general hydrographical features in each ocean. In the Indian Ocean the seasonality in abundance of this genus is more pronounced in the Northern Hemisphere than in the south; and it is probably related to changes in monsoonal regimes. The hydrographical features of the Arabian Sea and Bay of Bengal limit the northern boundary of distribution of all species of *Nematoscelis* except *N. gracilis* old form. There appears to be a general break in the north-south midocean distribution of *N. microps* and *N. tenella* near the equatorial zone of the Indian Ocean. Their northern boundary of distribution corresponds to the approximate southern extent of oxygen-poor waters (<1 ml/l) of the Arabian Sea and the Bay of Bengal.

Wyrtki (1973) proposed a division of the Indian Ocean into three circulation systems: a seasonally changing monsoon gyre, a southern subtropical anticyclonic gyre, and the antarctic waters with the Circumpolar Current. One unique feature of the Indian Ocean is the persistence of a hydrochemical front at about lat. 10°S, separating the high-nutrient, low-oxygen content waters of the monsoon gyre from the low-nutrient, high-oxygen content waters of the subtropical gyre. The existence of such a front is very well reflected by the chemical characteristics of the subsurface water

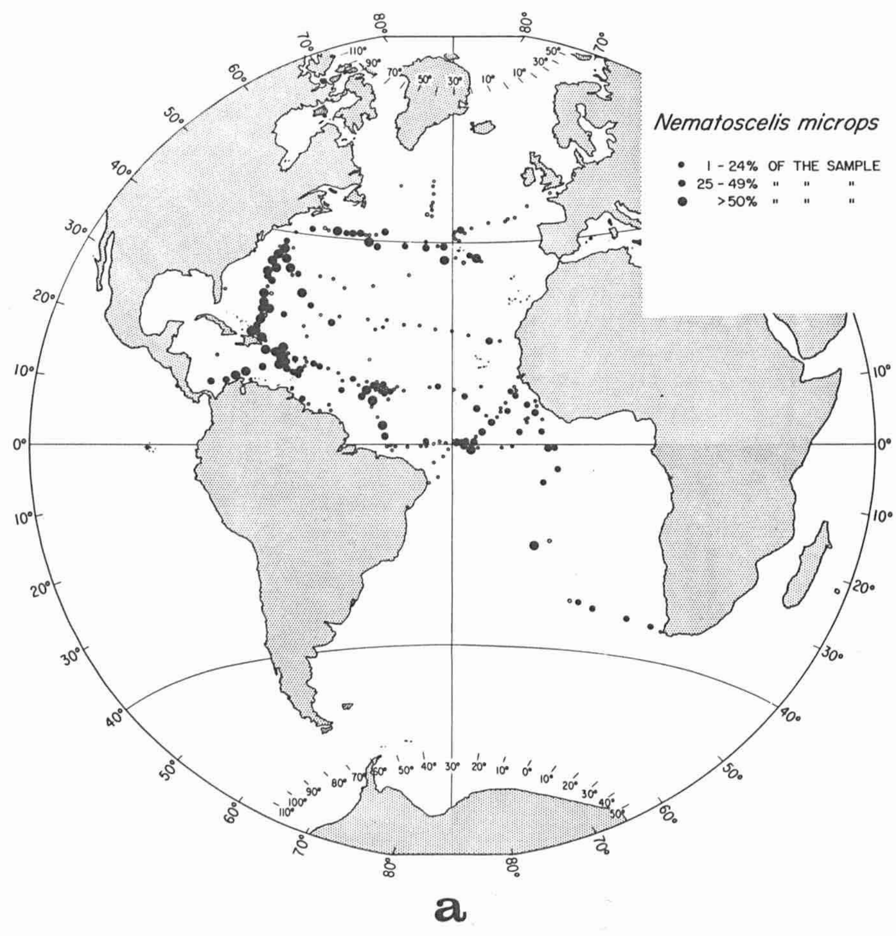
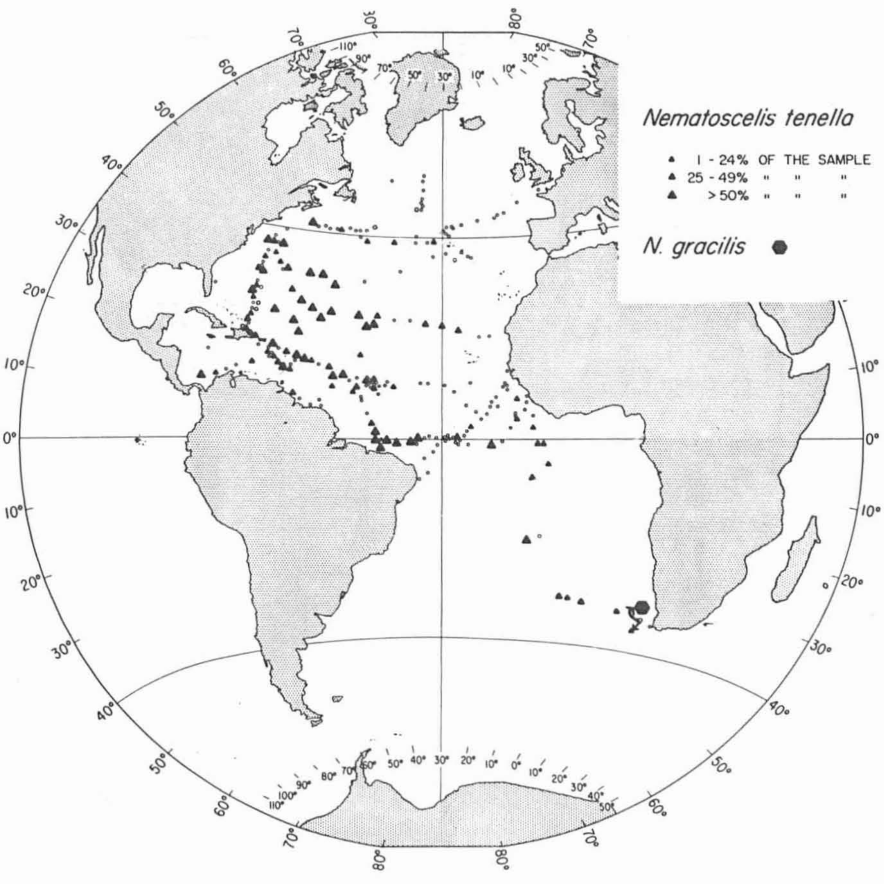


FIGURE 14.—Distribution of *Nematoscelis* in the Atlantic Ocean based on plankton samples: a - *N. microps*.

(Wyrtki, 1973). The boundaries of distribution of many zooplankton species appear to fall within this zonal band. This is also the area of the northern boundary of the subtropical species *N. atlantica*. Evidently the southern boundary of *N. gracilis* new form is not confined to this zone; since the South Equatorial Current carries it as far south as lat. 20°S. The subtropical convergence located at about lat. 40°-41°S separates the southern subtropical anticyclonic gyre and the antarctic circumpolar water. This is the region of the southern boundary of distribution of both the subtropical species *N. atlantica* and the warmwater species *N. microps* and *N. tenella*.

Brinton and Gopalakrishnan (1973) recognized different euphausiid faunal assemblages in the Indian Ocean, each of which is bounded mainly around lat. 10°N, 0°, 10°S, 25°-30°S. Latitude 10°N delimits the northern distribution of not only *N. microps* and *N. tenella* but also other euphausiid species such as *Euphausia tenera, Thysanopoda monacantha, T. tricuspidata, Nematobrachion flexipes, Stylocheiron abbreviatum,* and *S. longicorne* (Brinton and Gopalakrishnan, 1973). Therefore, the Arabian Sea and Bay of Bengal north of lat. 10°N contains large numbers of only *N. gracilis* old form along with *Stylocheiron indicum, S. carinatum, S. affine, Pseudeuphausia latifrons, Euphausia diomediae,* and *E. distinguenda*. In both the Arabian Sea and the Bay of Bengal a low level of oxygen (as low as 0.1 ml/l) persists year-round in the upper oxygen minimum layer (Wyrtki, 1971). However, temperature and salinity vary seasonally in these areas. The surface salinity ranges are 30-33‰ for the Bay of Bengal and 34-37‰ for the Arabian Sea. Biologi-



b

FIGURE 14.—Distribution of *Nematoscelis* in the Atlantic Ocean based on plankton samples: b - *N. tenella* and *N. gracilis*.

cal and oceanographical differences between these two parts of the Indian Ocean were discussed by Panikkar and Jayaraman (1966). Throughout the year *N. gracilis* old form maintains spawning populations in these two areas.

Nematoscelis gracilis new and old forms, *N. microps*, and *N. tenella* are part of the faunistic assemblage between lat. 0° and 10°S. The occurrence of *N. gracilis* new form in the mid-Pacific agrees with the distribution of *Euphausia pseudogibba* and *Thysanopoda subaequalis* in the zone lat. 10°-20°S (cf. Brinton, 1962:212). South of lat. 25°-30°S, *N. gracilis* is replaced by *N. atlantica*. Other species of this zone are *Euphausia brevis*, *E. mutica*, *Stylocheiron suhmii*, and *Thysanopoda subaequalis*. In the Indian Ocean all of these central species, including *N. atlantica*, occur only in the Southern Hemisphere.

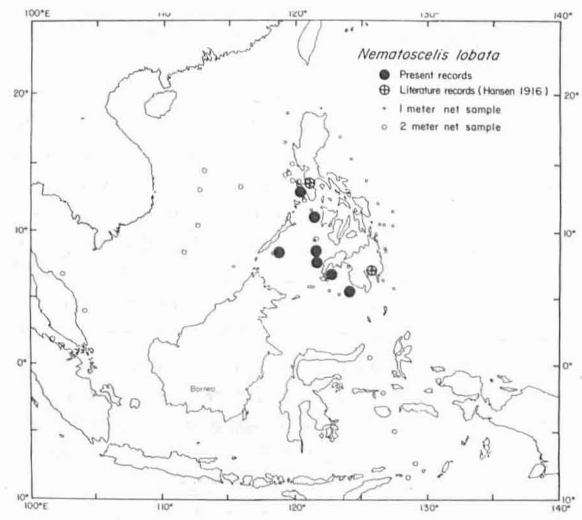


FIGURE 15.—All known records of *Nematoscelis lobata*.

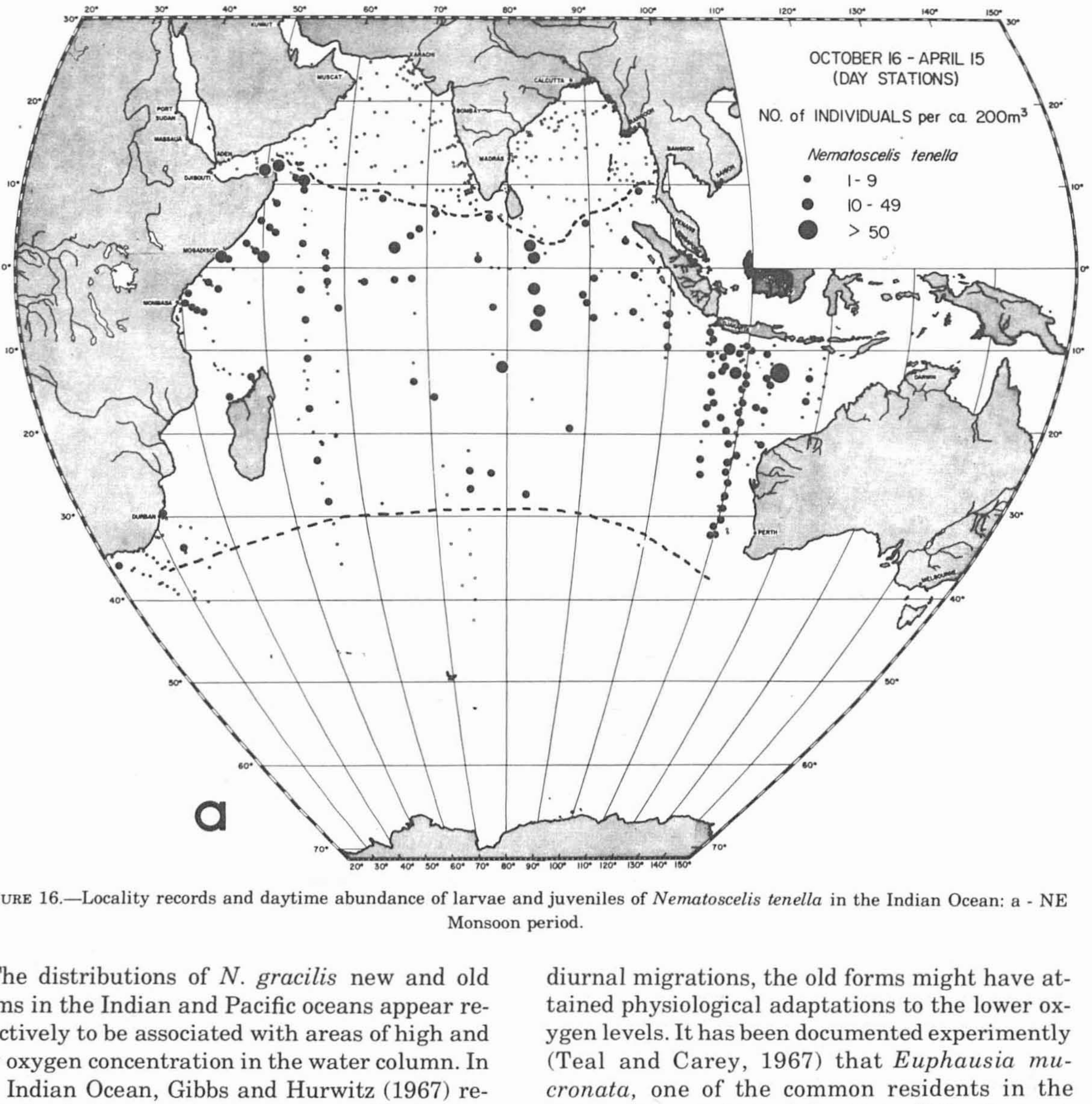


FIGURE 16.—Locality records and daytime abundance of larvae and juveniles of *Nematoscelis tenella* in the Indian Ocean: a - NE Monsoon period.

The distributions of *N. gracilis* new and old forms in the Indian and Pacific oceans appear respectively to be associated with areas of high and low oxygen concentration in the water column. In the Indian Ocean, Gibbs and Hurwitz (1967) reported a similar association of species distribution and oxygen concentration in the water column for two mesopelagic fish species, *Chauliodus pammelas* and *C. sloani*. Like *N. gracilis* old form, *C. pammelas* is only in the oxygen-poor waters of the Arabian Sea and the Bay of Bengal. The old form is largely confined to the tropical areas where the oxygen concentration in the upper minimum is less than 2 ml/l (Figure 3); whereas the new form occurs in those equatorial regions where the oxygen values in the upper minimum layer is never less than 1 ml/l. Since the adults have to pass through the oxygen minimum layer during their diurnal migrations, the old forms might have attained physiological adaptations to the lower oxygen levels. It has been documented experimently (Teal and Carey, 1967) that *Euphausia mucronata*, one of the common residents in the oxygen-poor waters of the Peru-Chile Current, can withstand the stress of oxygen pressure as low as that in the oxygen minimum layer.

Low oxygen values in the upper minimum layer of the tropical Indian and Pacific oceans reflect the presumed high productivity of the surface layers (Vinogradov and Voronina, 1961; Longhurst, 1967). Old forms occur in these areas of high zooplankton abundance, particularly in the eastern tropical Pacific, Arabian Sea, and Bay of Bengal. Reid (1962) plotted the distribution of zooplankton abundance in the Pacific. In the area of the North Equatorial Current the zooplankton biomass is

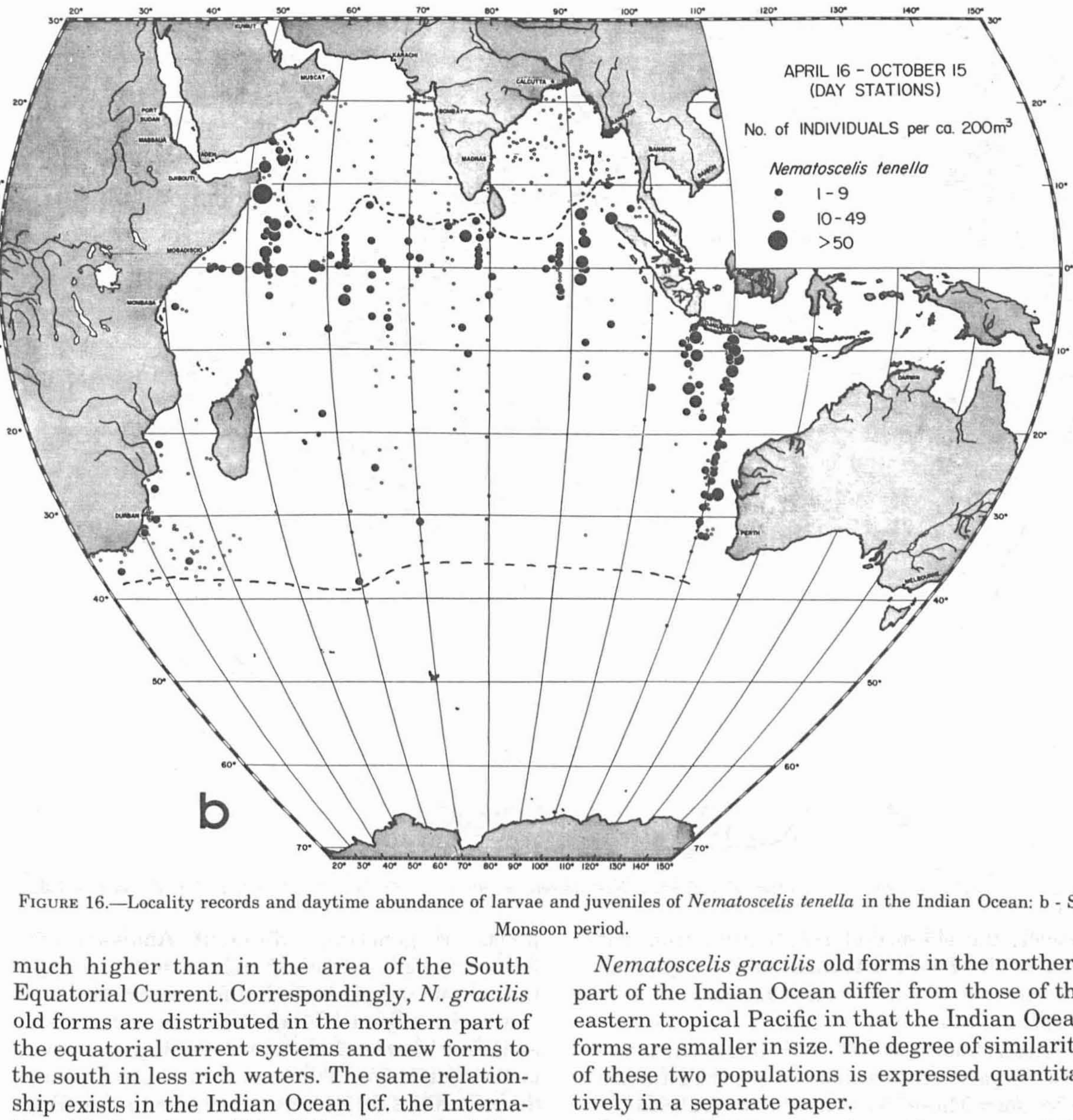


FIGURE 16.—Locality records and daytime abundance of larvae and juveniles of *Nematoscelis tenella* in the Indian Ocean: b - SW Monsoon period.

much higher than in the area of the South Equatorial Current. Correspondingly, *N. gracilis* old forms are distributed in the northern part of the equatorial current systems and new forms to the south in less rich waters. The same relationship exists in the Indian Ocean [cf. the International Indian Ocean Expedition Plankton Atlas. Indian Ocean Biological Centre (1968)].

Each form of *N. gracilis* is considered to be an ecophenotype. Mayr (1971) recognized ecophenotype as a nongenetic modification of the phenotype in response to an environmental condition. However, the observed morphological differences, associated with reproductive structures, suggest the possibility of genetic divergence of the two demes. The intergradation (intermediate forms) along the overlapping zones suggest incomplete genetic isolation.

Nematoscelis gracilis old forms in the northern part of the Indian Ocean differ from those of the eastern tropical Pacific in that the Indian Ocean forms are smaller in size. The degree of similarity of these two populations is expressed quantitatively in a separate paper.

Brinton (1962) pointed out that most of the inter-ocean waterways in the Indo-Australian Archipelago, (e.g., the Strait of Malacca, Sunda Strait, and Torres Strait) are too shallow (<100 m) to allow interoceanic transport of the oceanic euphausiid species. The deep pathway is through the straits of Molucca and Halmahera, and the Banda and Timor seas. Even central species like *Euphausia mutica* are found along this route. *Nematoscelis gracilis* new and old forms, *N. microps,* and *N. tenella* show similar communication between Pacific and Indian Ocean populations.

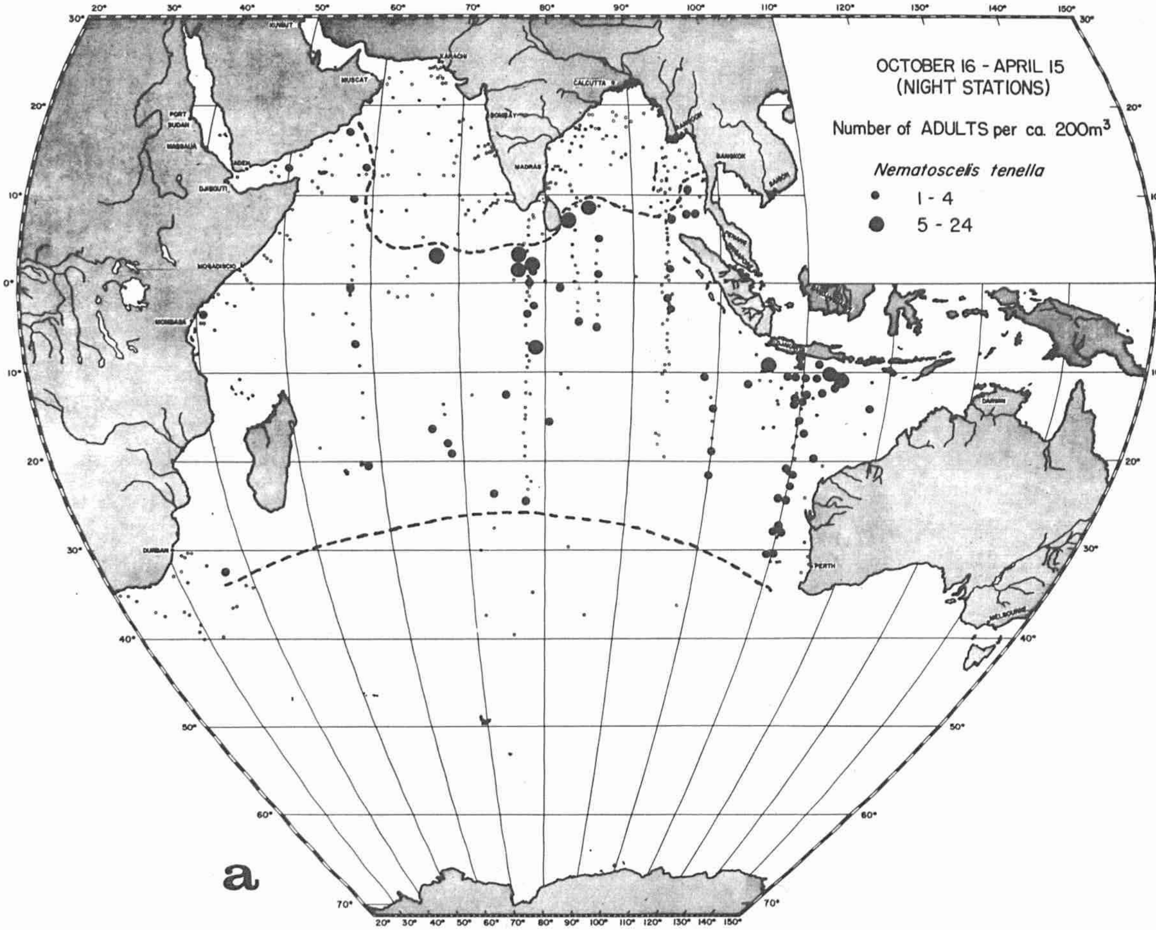


FIGURE 17.—Locality records and nighttime abundance of *Nematoscelis tenella* adults in the Indian Ocean: a - NE Monsoon period.

However, the absence of *N. atlantica* from the region of the Indo-Australian Archipelago suggests the lack of inter-ocean communication of this species. Moreover, *N. lobata,* which is morphologically most similar to *N. atlantica,* is endemic to a part of this region, mainly the Sulu and Celebes seas. These basins are connected with the open ocean by relatively shallow channels. This region is well known for its endemic species. Gilbert and Hubbs (1920) pointed out that the peculiar characteristics of the isolated basin of the Sulu Sea might have caused the evolution of many fish species. Because of morphological similarities and non-overlapping distribution (geographical isolation), *N. lobata* and *N. atlantica* may have derived from the same stock.

The North Pacific central population of *N. atlantica* is also isolated from its southern counterpart. However, it is not known whether the disjuncts are genetically different. Analyses performed by both numerical and conventional ways indicate no morphological differences.

Another region of importance in considering gene flow between Indian and Pacific populations is the South Australian Basin and the Tasman Sea. The Bass Strait between Australia and Tasmania is probably too shallow to allow passage of adult oceanic euphausiids. However, larvae and juveniles may be transported across this passage. The only route for adults is south of Tasmania, but this is almost certainly too far south for the tropical-subtropical species including *N. tenella, N. microps,* and *N. atlantica.* Evidence from south of Australia (Monsoon Expedition, long. 120°E-175°W) indicates that populations of *N. megalops* are in communication between the South Pacific and Indian oceans. The Pacific population evidently does not mix with the South At-

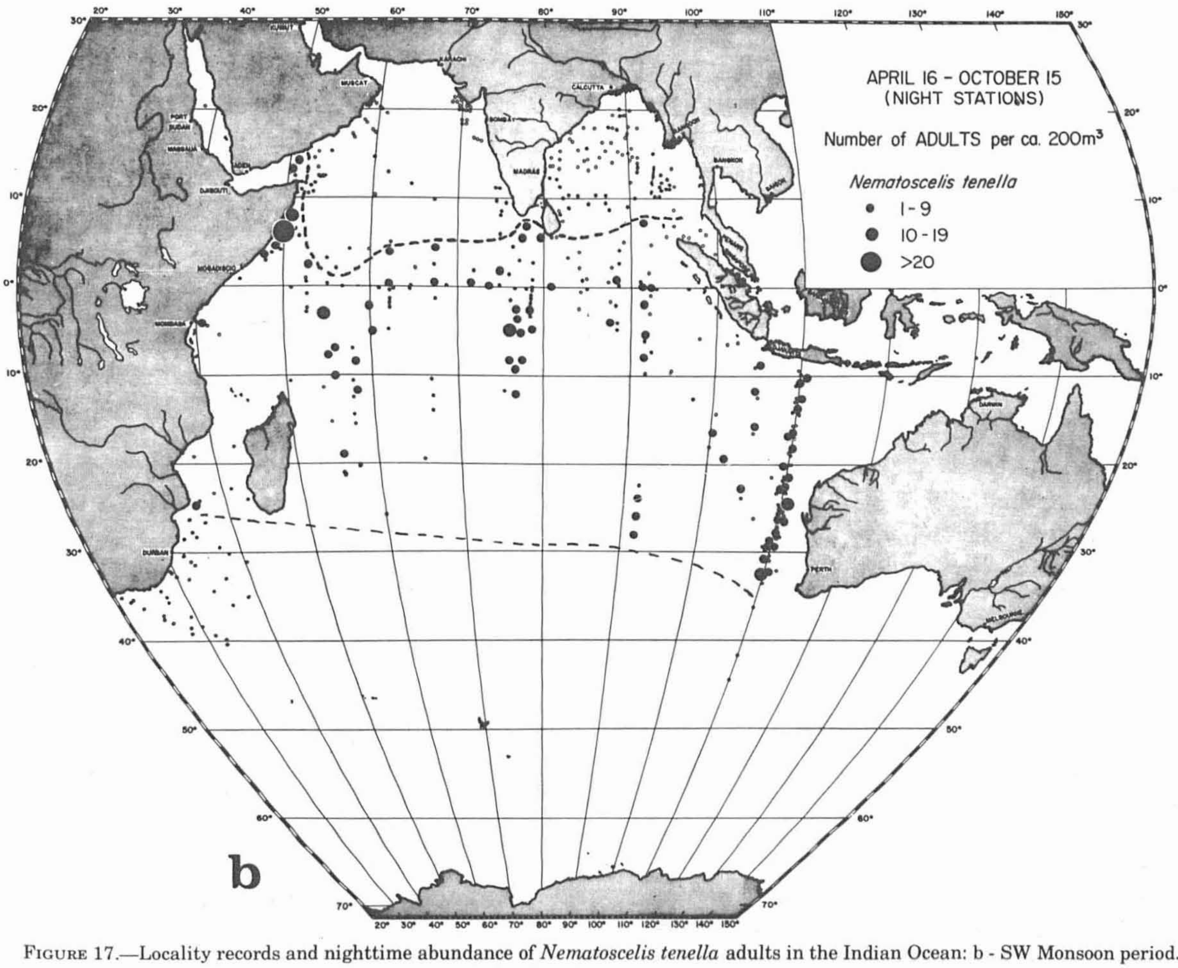


FIGURE 17.—Locality records and nighttime abundance of *Nematoscelis tenella* adults in the Indian Ocean: b - SW Monsoon period.

lantic counterpart at the Drake Passage (Antezana, manuscript). The morphological differences between *N. megalops* and *N. difficilis* already reflect presumed genetic differences.

Atlantic populations of *N. atlantica*, *N. microps*, and *N. tenella* are not in direct communication with their respective counterparts in the Pacific, but the North and South Atlantic populations are in communication at the Equator. It appears that the Atlantic and Indian Ocean populations of these species are in at least seasonal communication around the tip of South Africa.

A further aspect of the zoogeography of *Nematoscelis* in the Atlantic lies in the fact that *N. atlantica*, not *N. gracilis*, occupies the equatorial belt, permitting north-south continuity of the species. Atlantic expatriates of *N. gracilis* new form are found only off southwest Africa, probably transported by the Mozambique Current. The cool Benguela Current region may then limit northern transport of this tropical form, or the low oxygen (0.5 ml/l) in the minimum layer of the current, lat. 10°S and 15°S (Bubnov, 1966), might be a barrier to the new forms as it appears to be in the northern Indian Ocean.

There are similarities between distributions of species of *Nematoscelis* and those of other zooplankters. For example, the distribution of *N. megalops* is like that of a copepod, *Clausocalanus ingens* (Frost, 1969) and *Thysanoessa gregaria* (Brinton, 1962); horizontal boundaries of *N. microps* and *N. tenella* are like those of other tropical-subtropical species, *C. mastigophorus* and *Stylocheiron carinatum*. It is likely that both biological (species interaction) and physical [water mass, Sverdrup et al. (1942)] reasons are responsible for the numerous similarities.

McGowan (1971) classified the patterns of dis-

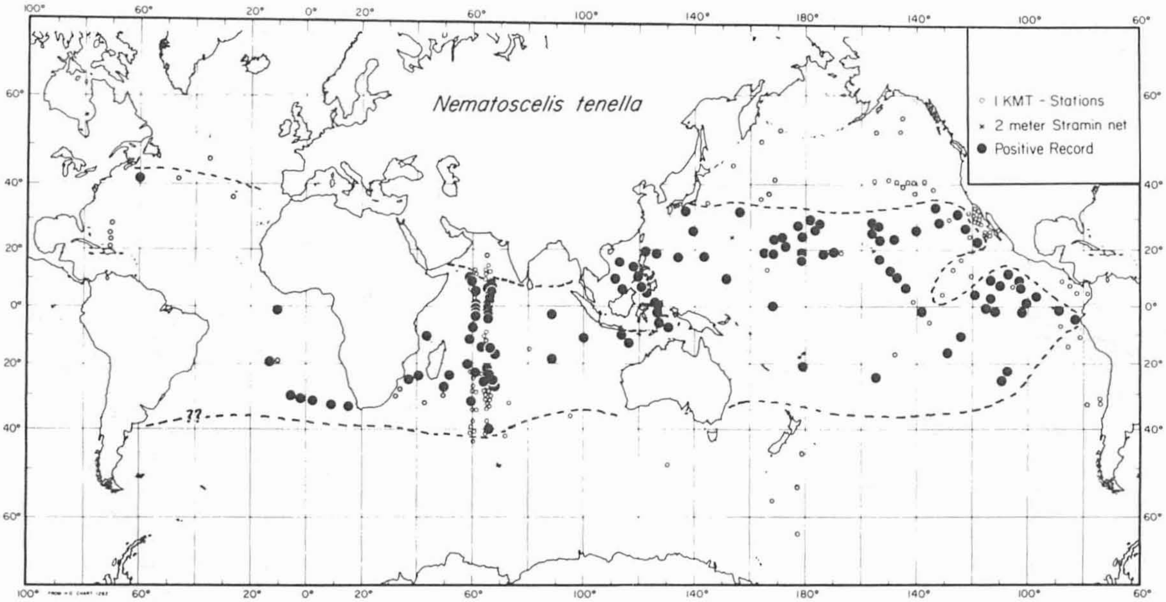


FIGURE 18.—Worldwide distribution of *Nematoscelis tenella* based on mid-water trawls. (Broken lines represent approximate boundaries of distribution of the species based on literature records and present evidence.)

tribution of many zooplankton species into four types on the basis of their association with water masses. They are: 1) species that show patterns of distribution whose boundaries are almost identical with the boundaries of the physical water masses; 2) species which have areas of highest levels of abundance within a water mass, but whose boundaries extend somewhat beyond the boundary of the water mass; 3) species that have distributions throughout several water masses; and 4) species having limited distributions in parts of some water masses. *Nematoscelis gracilis* and *N. atlantica* fall in the first category, *N. megalops* in the second, and *N. tenella* and *N. microps* in the third. *Nematoscelis difficilis* is restricted to the North Pacific transition zone whereas *N. megalops* is distributed in the central, transitional, and subarctic water masses of the Atlantic and in the southern transitional zones of the Indian and Pacific oceans.

ACKNOWLEDGMENTS

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