ON THE ECOLOGY OF BRAZILIAN MEDUSAE AT 25° LAT. S

(Received 19/3/63)

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1 — INTRODUCTION AND METHODS

The medusae present in plankton samples taken every fortnight at fixed stations off the coast of the State of São Paulo, Brazil, were totally counted and their abundance studied in relation to such ecological factors as temperature, salinity, season, other species present, depths, distance from the coast and vertical mixing.

Fluctuations of marine populations, whether they be intertidal (Hedgpeth 1957), planktonic (Margalef 1958, 1959; Glover 1961) nektonic (pelagic fisheries) or benthic (Thorson 1946) are an established fact. These fluctuations occur in space and time, are short term or long term, but only in few instances were they correlated to known factors in the study of the distribution and abundance of planktonic species.

Natural fluctuations occur in every ecosystem and because plankton is a highly complex system, oscillations should not be very intense. Since however they are much greater than might be expected, it is by considering only the average over a period

Publ. nº 182 do Inst. Ocean. da USP.

of years that we try to get around this difficulty. Periods longer than three years should be necessary and accordingly the collecting of data and samples proceeds.

Concerning the tropical and subtropical marine plankton knowledge is even more restricted than for the temperate and cold water plankton and problems such as standing stock, mortality, life span, rate of feeding and growth, seasonal cycles if any, minimum temperature for breeding and other factors affecting abundance, distribution, isolation and speciation remain almost unknown. Recently Margalef (1961a, 1961b) studied under these points of view the coastal plankton of Puerto Rico and elsewhere. However most of our knowledge on warm water plankton refers to the taxonomic and morphological aspects of the zooplankton species and their gross geographic distribution. This situation is a direct consequence of the manner in which warm water plankton was studied until recent times. Samples were usually taken during extensive oceanographic expeditions that inevitably collected over wide areas but in no continuous manner in any given one. We thus decided to establish fixed stations over a number of years in order to gain some knowledge on the mechanisms involved in the principal biological problems at action under warm water conditions. Information on the indicator value of different species for certain water masses in different regions has been gathered since the pioneer work by Russell (1935, 1936; also Fraser 1955a; 1955b).

New areas of study have recently been added, as for instance the eastern Pacific (Bieri 1959; Le Brasseur 1959 and Sund 1961).

Three fixed stations were established off Cananéia, State of São Paulo and were occupied every 15 days during three years, from January 1958 through December 1960. At each station the common hydrographical data were taken together with the plankton samples. The latter were taken by means of a Hensen net with flowmeter hauled vertically through the entire water column and by means of a Clarke-Bumpus plankton sampler, zooplankton mesh, hauled horizontally during fifteen minutes in the deepest layer about 2-3 m above the bottom.

A preliminary report of the total plankton volume was published recently (Vannucci 1962a, 1962b). The present paper refers only to the medusae present in the samples. All the Hensen net samples were totally counted for medusae and only about half of the Clarke-Bumpus ones. Of the latter only those that were considered interesting to count, for the purpose of the study of vertical distribution and relative abundance in different water masses when two different waters were present in the column, were counted.

The three fixed stations or points where samples were taken are as follows:

Pt. I — 25°7.9' S — 47°48.4' W — local depth 19 m; 5.6 miles offshore.

Pt. II — 25°8.4' S — 47°44.2' W — local depth 20 m; 9.5 miles offshore.

Pt. III — 25°9.5' S — 47°35.7' W — local depth 30 m; 17.2 miles offshore.

In the region under consideration the water mass present usually is the "coastal water mass" (Emilsson 1961) characterized by salinity lower than 35 ‰ and temperature usually higher than 20°C. Sometimes "shelf water" may be present in the lower layers at Pt. III, more rarely at Pt. II and only exceptionally at Pt. I, the latter being the nearest to the coast. The shelf water mass' salinity is 35-36 ‰ and the temperature not higher than 22°C. The distribution and volume of these water masses depends largely upon the strength and direction of the winds, amount of rainfall and land drainage and varies somewhat between winter and summer (dry and wet season), but it always was found to be very variable. The section studied extends 17.2 miles offshore at the exit of a vast mangrove bordered lagunar system. The quantitative contribution of this system both in volume of water and amount of nutrients is unpredictable until accurate measurements will be made, but appears to be considerable.

On account of reduced boat facilities, a grid of stations could not be established nor the section extended to the edge of the shelf which is 110 miles wide. The effect of the 200 m depth contour line on the distribution of the plankton could not be observed, but we were lucky in that the water masses that cover the wide continental shelf, for what concerns their origin may broadly be compared to the categories Glover (1961) calls oceanic, neritic and intermediate. These correspond to our tropical, shelf and coastal water masses. At our stations, tropical waters were practically absent, except as admixture to the shelf water mass.

This work was planned and directed by I. Emilsson for what concerns the physical part and by the author for the biological studies. While harboured at the Institute's station at Cananéia, the vessel "Emilia" was taken care of by the station's head Mr. V. Sadowsky. The plankton counts and the determinations were made by the author. A few samples were counted by Mrs. M. G. B. Soares Moreira; Miss T. Matsumura counted a few samples and helped with the graphs, Mr. J. Lupi curated the samples and Mr. C. Garcia made the final drawings. To all our thanks.

At each station water samples were taken with an isothermic water bottle at the surface and two (Pt. I & Pt. II) or three (Pt. III) constant depths. Temperature was read to the hundredth and water samples taken for salinity and dissolved oxygen determinations. Salinity was titrated in the laboratory in São Paulo; dissolved oxygen was precipitated on board and titrated in São Paulo by Winkler's method. Water density was computed in São Paulo.

The stations were supposedly worked on the 10th and 25th of every month, but due to bad weather some were delayed by one or more days. The whole series of data shows some gaps due once to loss of the single net we then had, other times due to repairs to the vessel or similar mishappens. Doubtful data were disregarded.

The density of the population is given in number of specimens per cubic metre of sea water. The number of specimens was obtained by the total count of the samples and the volume of water filtered by the net was obtained from the flowmetre data. It is a well known fact that flowmetres are not entirely reliable, therefore all data were compared with the evaluated volume of the water column filtered and all doubtful values were disregarded.

The plankton samples were labeled E_n; where E stands for the identification of the series and *n* refers to the serial number; the samples were numbered in succession from the beginning of the series. All the samples are stocked in the Plankton Section of this Institute for further studies, some are under way on the Chaetognatha, Appendicularia and Thaliacea.

The data on the number of specimens of each species for each sample were tabulated according to date, hour of day, salinity, temperature, wind, depth of haul and amount of water filtered by the net down to the accuracy that may be expected to obtain with a flowmetre. These data were used to assess some of the biological parametres of the species. From these tabulations graphs were drawn, a few of which are reproduced here. In this paper salinity and temperature are considered not only as ecological factors per se in relation with their limiting capacities but also as the factors that characterize the water masses present. They are thus used as the background against which the occurrence of the species may be projected in order to find out what is the better environment for each of them.

The station list with the hydrographical data will be published in the near future by the Physics branch of this Institute.

Altogether 247 samples were counted for the preparation of this paper. No new species were found, but three species are here recorded for the first time from this region; they are: *Eu-*

cheilota duodecimalis, Eucheilota paradoxica and *Amphogona apstein.* An undetermined specimen of *Octophialucium* sp. was taken at Pt. I (E_{81}) October 23, 1958, at 0737 a.m., with Hensen net, 31.82-32.99 ‰ salinity and 23.6-25°C in coastal waters. *Eucheilota duodecimalis* was previously known only from the New England coast down to Florida. *Eucheilota paradoxica* was previously known from Florida, Japan, Strait of Malacca, Bali. *Amphogona apsteini* was previously known from several localities in the Indian and Pacific Oceans, but in the Atlantic it was known only from the Gulf of Guinea; probably circumtropical and circumsubtropical.

For the geographical distribution of the species I refer to the complete paper by Kramp (1961).

2 — LIST OF SPECIES AND THEIR ABUNDANCE

Coastal Water Mass Indicators

1 — *Podocoryne minima* (Anthomedusae) — 20 specimens.
2 — *Bougainvillia ramosa* (Anthomedusae) — 833 specimens.
3 — *Stomotoca dinema* (Anthomedusae) — 238 specimens.
4 — *Laodicea minuscula* (Leptomedusae) — 33 specimens.
5 — *Obelia* spp. (Leptomedusae) — 301 specimens.
6 — *Eucheilota ventricularis* (Leptomedusae) — 173 specimens.
7 — *Eucheilota duodecimalis* (Leptomedusae) — 532 specimens.
8 — *Eucheilota paradoxica* (Leptomedusae) — 237 specimens.

Shelf Water Mass Indicators

9 — *Euphysora gracilis* (Anthomedusae) — 2,502 specimens.
10 — *Eucodonium brownei* (Anthomedusae) — 6 specimens.
11 — *Turritopsis nutricula* (Anthomedusae) — 11 specimens.
12 — *Proboscidactyla ornata* (Limnomedusae) — 1,486 specimens.
13 — *Amphogona apsteini* (Trachymedusae) — 2,306 specimens.
14 — *Cytaeis tetrastyla* (Anthomedusae) — 2,691 specimens.

Ubiquitous Species and Tropical Water Mass Indicators

15 — *Ectopleura dumortieri* (Anthomedusae) — 1,839 specimens.
16 — *Clytia cylindrica* (Leptomedusae) — 1,771 specimens.
17 — *Aglaura hemistoma* (Trachymedusae) — 774 specimens.

Graphs 1-9 show the distribution of the above species according to the point where taken, salinity and temperature. Three species are not shown on all the graphs because they are either undeterminable to species level (*Obelia* spp.) or were too scarce

(*Eucodonium brownei; Turritopsis nutricula*). Sometimes it is not possible to know precisely in what salinity or temperature layer the animals were living in when fished; such data were disregarded. Thus the numbers for each species plotted on graphs 4-9 are always smaller than the total number of specimens counted.

3 — COASTAL WATER MASS INDICATORS

1 — *Podocoryne minima* (Fig. 1), only 20 specimens of this species were found, seven of which were dead when taken. This species was previously (Vannucci 1957, pp. 49, 89) described as eurythermic preferring rather high temperatures and euryhaline preferring low salinity, inhabiting inshore and lagoon waters. The meager data at hand tend to confirm that this species, rare in plankton samples, probably liberates the medusae towards the end of winter or early summer; that the medusae live in waters with temperature above 20°C and salinity below 35 ‰; 85% of the specimens come from 34-35 ‰ salinity, while 84% of the specimens come from 26-28°C temperature. On the whole 89% of the specimens taken come from 24-28°C temperature associated to 33-35 ‰ salinity.

It is strictly coastal water mass indicator, and the specimens taken in waters with some admixture of shelf waters were dead or dying. Greatest density found was of 1.2 specimens/m^3.

This species was found associated to coastal water species such as *Bougainvillia ramosa, Eucheilota ventricularis, Sagitta friderici* and in waters where *Liriope tetraphylla* was very abundant. One specimen taken in sample E_{187} was found associated to shelf water species as well as coastal species, the reason of this is that the water at that station had undergone vertical mixing and was the result of the mixture of coastal and shelf waters. How long *Podocoryne minima* may survive in mixed waters is yet unknown.

2 — *Bougainvillia ramosa* (Fig. 2), 833 specimens were taken. This short-lived circumtropical and circumsubtropical species is usually stated to be only exceptionally taken in plankton hauls. This was found to be true also by the present author who never found it in plankton hauls taken during three years in the Gulf of Naples, although the species is common there and large hydroid colonies are known to produce vaste numbers of medusae, as may be checked with laboratory reared colonies. In the present collection it was surprisingly common and was found in every month of the year, in all developmental stages from newly liberated to mature.

The salinity range tolerated was now found to be 32.4 to 35.47 ‰ and the temperature limits were 19.3 to 27.7°C. Unpublished experiments by Petersen and Vannucci performed at the

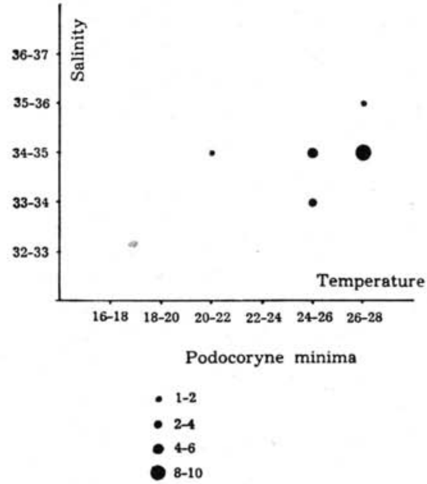


Fig. 1

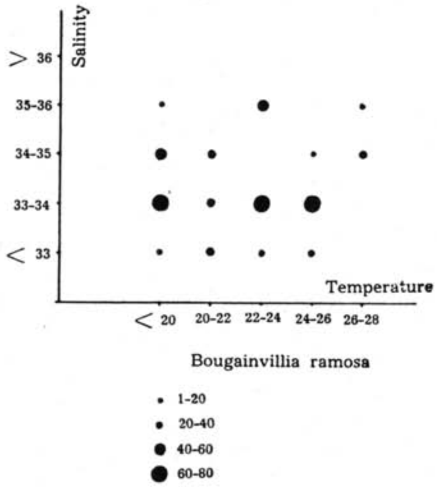


Fig. 2

Figs. 1-2 — Distribution of abundance in relation to temperature and salinity. Only those specimens are computed of which temperature and salinity conditions were known with certainty.

Naples Station, as well as scattered information in the literature indicate that this species may tolerate wider environmental variations, especially concerning temperature.

The distribution of the present specimens shows that in the region under consideration it is a good indicator of the coastal water mass. As a rule it was found to be almost exclusively present and most abundant at Pt. I or Pt. II. Even when a fair number of specimens was taken, it was rarely found to be present at two stations the same day and when it was taken at two stations, the bulk came from one and only a few specimens from the other, indicating that it forms only small patches. The greatest density was found at Pt. I where as many as 7.7 specimens per m^3 were taken, with 32.84 ‰ salinity and 25.1°C temperature, the next greatest abundance was 6.25 spec./m^3 in 35.47 ‰ salinity and 23.4°C temperature; 88% of the specimens come from coastal waters.

The present findings agree with earlier ones (Vannucci 1957, pp. 54, 89; Vannucci & Rees 1961, p. 82), except that it is now known to breed here all the year round.

The present data indicate that it may be found at any depth in the water column regardless of hour of day and water mass present, there being presumably no vertical migration; they also show it to be much more abundant near the coastline. This is due to the fact that the bottom off Cananéia is mainly sand, there being suitable substratum for the hydroid only in the lagoon region on the oyster growing on the roots of the mangrove trees and other hard objects and on the rocks of the offshore islands and coastline.

3 — *Stomotoca dinema* (Fig. 3), 238 specimens were found. Before this only four specimens had been taken along the Brazilian coast all in June-July (Vannucci 1957, pp. 55, 90). At that time it was listed as a rare although widely distributed species, to be found in coastal waters, euryhaline and eurythermic, probably preferring temperatures around 20-21°C. The present specimens come from 32.8 ‰ or lower up to 34.5 ‰ salinity and from 20.6 to 26.8°C temperature and thus confirm the above.

In the present collection this species was found from March to June 1958. One specimen was taken December 29, 1958 and one January 13, 1959, both immature. The peak of abundance was in June (88.5% of the total taken) when also mature specimens were caught. It seems likely that it is budded off and that it reproduces only in winter, water temperature from 20° to 21.8°C. The rare specimens taken in March and January indicate that this species may tolerate up to 26.5°C temperature. About 90% of the specimens were taken between 20.5 and 22°C.

This species was always taken in salinity lower than 35 ‰ and regularly avoided the lower layers when shelf waters were present while it was evenly distributed where coastal waters occupied the whole column; it thus appears as a good indicator of the coastal water mass; 69% of the specimens come from about 33.7 ‰ salinity and 90% of the specimens come from 33-34 ‰ salinity at 20-22°C temperature. The greatest density found was of about 7.6 spec./m^3.

When present it was usually so in fairly large numbers and patches were found to be large enough to include two stations.

4 — *Laodicea minuscula* (Fig. 4), only 33 specimens of this species were taken, all except one, in the coastal water mass. As previously supposed (Vannucci 1957, pp. 56, 95) it is a good indicator of the coastal water mass; over 75% of the specimens come from Pt. I. The salinity range for the species is 33.5 to 35.56 ‰, with a single specimen at salinity higher than 35 ‰; over 51% of the specimens come from 34-35 ‰ salinity. The temperature range is 19.8 to 27.3°C. The greatest density found was of about 1 spec./m^3.

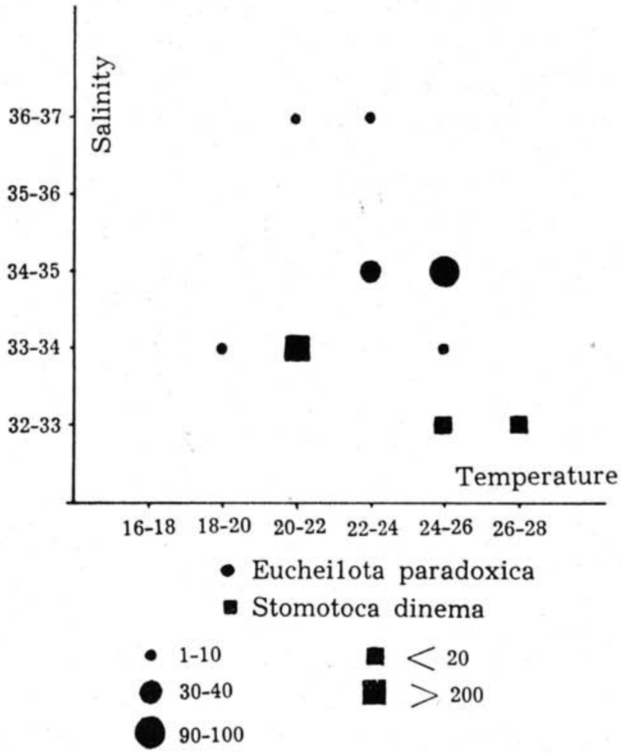


Fig. 3

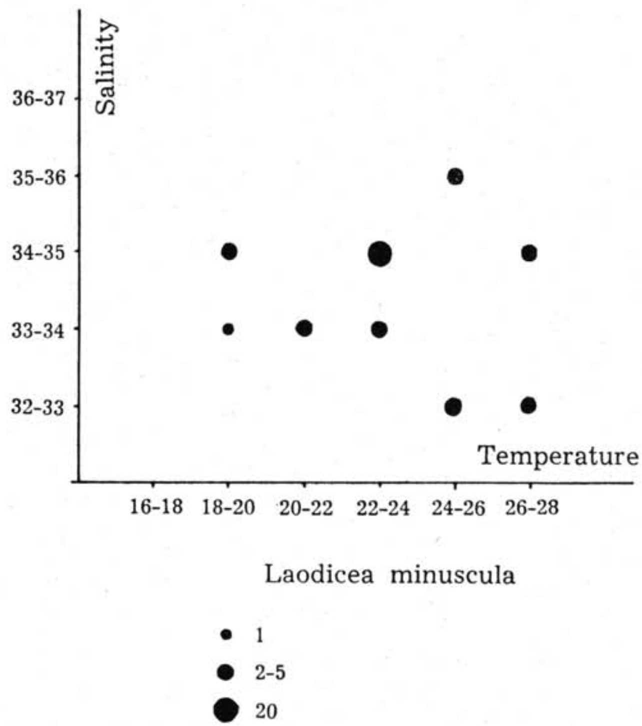


Fig. 4

Figs. 3-4 — Same as Figs. 1-2.

The medusae of this species are liberated and reproduce the year round; it is scarce and rare in plankton samples. Its life in the plankton is probably very short and this may explain its apparent scarcity. The hydroid is unknown and the species was recorded only from the coast of the State of São Paulo.

5 — *Obelia* spp. — 301 specimens belonging to this genus were taken. They do not belong to the same species but apparently they have a similar behaviour. The medusae of the genus *Obelia* may be considered here as indicators of the coastal water mass (90% of the specimens taken). The species are certainly eurythermic and euryhaline preferring high temperature and rather low salinity but may tolerate higher salinity and colder water, as is shown by their occasional presence in the shelf water mass.

These species were usually found scattered over the area, a patch having however been found at Pt. I, February 25, 1959 that extended over to Pt. II respectively with 10.3 and 4.4 spec./m^3. The patch lived in 30-34 ‰ salinity and 27°C temperature. Medusae are found the year round but tend to be more abundant in summer, they have a marked preference for surface layers where they tend to gather even when the water column is homogenous.

6 — *Eucheilota ventricularis* (Fig. 5), was represented by 173 specimens. The salinity range found in this series was 33.3 ‰ to 35.44 ‰; only 10% of the specimens come from salinity higher than 35 ‰ (shelf water mass). Precise data on specimens collected elsewhere are lacking, but in this region it had hitherto been taken in mangrove and coastal waters (Vannucci 1957, pp. 61, 91). The temperature range was found to be from 19.4 to 27.5°C. This species may thus be confirmed as euryhaline and eurythermic preferring salinities lower than 35 ‰ and temperatures higher than 26°C. It is here an indicator of the coastal water mass but may occasionally be found in shelf waters when mixing takes place. It is know with certainty that the hydroid lives in inshore waters with as low a salinity as 33 ‰ (Vannucci 1957, p. 62), how high a salinity they tolerate is still unknown. The present data show that medusae may be liberated in winter in temperature as low as 20°C and that they may attain maturity and reproduce at 19.8°C. However it is most abundant in the summer months. The life span of the medusa is probably shorter than fifteen days.

Figure 4, Graph 7 and frequency distribution curves suggest that this coastal water species has two reproductive periods, a principal one in summer and a secondary one in winter when the bottom temperature is about 24°C in summer and 20°C in winter. During each of these periods several successive batches of medusae are produced perhaps from the same hydroid stocks. Rearing experiments are highly desirable.

The greatest density was found in waters 34.56 ‰ salinity and 26.5°C in March when 9.3 spec./m³ were counted at 15 m depth. Densities higher than 3 spec./m³ were not uncommon.

Patches were found more than once always at Pt. I, the nearest to the coastline. They were always small and never lasted to the next station a fortnight later nor extended to the next station the same day. Usually the density was the same along the entire water column, except for once when all specimens appeared to be crowded in a narrow layer at about 15 m depth with 34.56 ‰ salinity and 26.5°C above the bottom layer, the salinity of which was 35.20 ‰ and temperature 26.4°C. This further indicates that this species tends to avoid shelf waters.

Eucheilota ventricularis was found associated to several others including the shelf water mass indicator species, further suggesting that it endures certain degree of mixture.

7 — A total of 532 specimens of *Eucheilota duodecimalis* (Fig. 6) was counted. All developmental stages were found. This species was first recorded from Brazil by Vannucci (1960) from specimens in this same series. It was found between 32.3 and 35.7 ‰ salinity and 19.6° and 27.8°C. It thus appears to be rather eurythermic thermophile and euryhaline and it lives in both the coastal and the shelf water mass. It may be considered a coastal water species that spreads into and tolerates higher salinity and colder waters as well as an indicator of the coastal water mass.

The species was previously known from Massachusetts to Florida. It is more abundant in the summer months; mature medusae were taken at all seasons indicating that both the hydroid and the short lived medusa reproduce all the year round. It is rather frequent and reasonably abundant, the greatest density found was of about 7 spec./m³, in 34.46 ‰ salinity and 26.1°C temperature. At another station more than 3 spec./m³ were found in salinity lower than 35 ‰ and 20°C. It forms small patches that rarely included more than two points. The distribution in the water column was fairly uniform, regardless of the water mass present. It probably does not have a life span greater than 15 days.

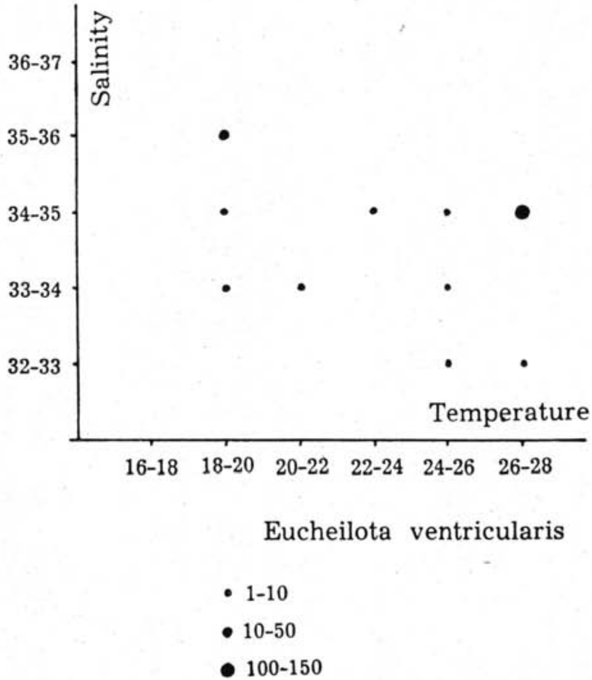


Fig. 5

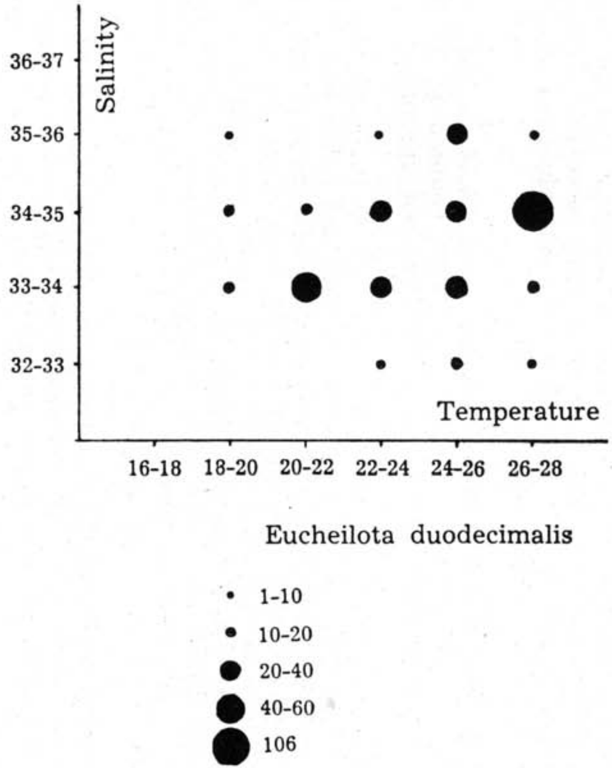


Fig. 6

Figs. 5-6 — Same as Figs. 1-2.

8 — *Eucheilota paradoxica* (Fig. 3), 237 specimens counted. The salinity interval was found to be from 34 to 36.3 ‰ and the temperature interval from 22.5 to 26.8°C. Over 84% of the specimens come from salinity between 34 and 35 ‰ and 86% come from 24-26°C temperature. The greatest density found was of about 5 spec./m^3 at 34.3-34.7 ‰ salinity and 26.8°C. Apparently a rather stenothermic and stenohaline warm water species preferring salinity between 34 and 35 ‰ and 24-26°C temperature. A coastal water mass species to be found where the salinity is higher in this area.

It was taken only from February through April (late summer) 1960 and then at almost every station. That was a year when there was a more restricted than usual amount of coastal water and salinity was higher. Both shelf water and tropical waters were found closer inshore and there was thus a greater admixture of these waters to the coastal water mass. This may be one of the reasons of the presence of this species in 1960 and its absence in previous years.

All developmental stages of the medusa were taken, from very young to mature. It has an intense vegetative reproduction and this may account for the fact that although rare, once having made its appearance it quickly became common. Its life span probably does not surpass fifteen days. Its distribution in the water column is independent of depth, salinity and temperature, provided the latter fall within the limits given above.

It was found to form patches large enough to include the three points sampled.

4 — SHELF WATER MASS INDICATORS

9 — *Euphysora gracilis* (Fig. 7), 2,502 specimens of this moderately large medusa were counted. Its life span may be of a few weeks and the hydroid is probably long lived and from deep waters. It was suggested earlier (Vannucci 1957, pp. 41, 85) that it is an eurythermic thermophile species whose temperature limits probably are between 14 and 22°C, the optimum unknown. This species was also shown to be stenohaline, the preferred range being 35-36 ‰ salinity. The present data confirm these findings in so far as 97% of the specimens counted come from samples taken when shelf water was present in the water column. The present data show that 86.8% of the specimens were found to be living in temperature not higher than 19°C and it is therefore only moderately thermophile. Only 3% of the total number captured was taken in waters with salinity lower than 35 ‰ and temperature higher than 19.5°C. These findings

associated to previous records of *Euphysora gracilis* from the South West Atlantic indicate that it is a good indicator species of the shelf water mass. Only 1.8% of the total number of specimens was taken in temperatures higher than 23°C, previously considered to be the higher limit of temperature tolerance for the species.

The small percentage of specimens taken in waters with salinity lower than 35 ‰ came almost entirely from a single haul at Pt. II, taken after a strong southeasterly wind and the presence of these specimens in diluted water is undoubtedly due to local mixing of shelf water with coastal low salinity and high temperature water. The data suggest it does not survive long in diluted waters.

This species is probably found the year round in the shelf water mass. Of the total number 96.6% was taken at Pt. II and III the same day, January 10, 1958, which suggests that this species may form large and dense patches. In Clarke-Bumpus samples from shelf waters, as many as 260 spec./m^3 were counted (Pt. III, January 10, 1958, at 10.00 a.m., 35.55 ‰ salinity and 16.87°C temperature at 25 m depth).

This species was taken almost exclusively at Pt. III, having been found at Pt. I (nearest to the coast) only twice after a strong southeasterly wind, that caused strong mixing of the water column. At Pt. II it also was found to be present only twice in the shelf water mass.

Comparing the Hensen net vertical samples with the Clarke-Bumpus horizontal deep layer samples, it may be confirmed that when the two water masses, the coastal and the shelf water mass were both present in the water column, *Euphysora gracilis* was living in the lower layer, i.e., the shelf water mass.

10 — *Eucodonium brownei,* only 6 specimens were found, all of them in sample E_{241}, taken at Pt. III, February 1960, temperature of the water column between 22.5 to 25.8°C and salinity from 34.78 to 36.29 ‰. There were 0.6 spec./m^3. No specimens were taken with the CB haul in the deepest layer at the same station, which suggests that the six specimens taken in the vertical Hensen net haul came from the intermediate or surface layers (about 35 ‰ salinity).

This species was discussed in an earlier paper (Vannucci 1957, pp. 44, 87) and the present information tends to support the view that it is a rare species living in small patches. The latter are probably produced by the property of the medusa to originate other medusae by budding on the manubrium. It may also be confirmed to inhabit the shelf water mass or mixed coastal and shelf waters. The narrow limits established previously: 21.2-22°C temperature and 35.4-35.85 ‰ salinity fall within the data of the water column as found here. Again the specimens were found in summer, as most of those previously collected. It here appears to be a thermophile species of rather high salinity, perhaps stenothermic and stenohaline.

11 — *Turritopsis nutricula,* only eleven specimens; two from samples E_{71} and E_{72} (September 26, 1958) and eight from samples E_{201} and E_{202} (October 27, 1959) both at Pt. III. Samples E_{71} (vertical Hensen net) and E_{72} (horizontal Clarke-Bumpus) were taken after strong southwesterly winds, the water column having been thoroughly stirred, the water was mixed shelf and coastal, salinity 34-34.78 ‰ and temperature 22.5-22.8°C; only two specimens were taken. The specimens from samples E_{201} and E_{292} were probably living in the shelf water bottom layer when taken.

This species was previously (Vannucci 1957, pp. 48, 88) found to live in waters with temperature between 19-21°C and 35.5 to 36.25 ‰ salinity, all specimens having been taken between June and November in depths varying between 41 and 142 m depth. It was at that time suggested that *Turritopsis nutricula* performs diurnal vertical migration, that it is a neritic shelf water species rather thermophile. The present findings tend to confirm the above information and this species may be considered a good indicator of the shelf water mass.

It having been taken only at Pt. III and here only in small numbers, together with previous data suggests that here it occurs mainly offshore.

The greatest density found was of 0.1 spec./m^3.

12 — *Proboscidactyla ornata* (Fig. 8), 1,486 specimens counted. The salinity interval in this series was 33.2 to 35.5 ‰. The known range of salinity for this species was between 35 and 36 ‰ (Vannucci 1957, pp. 68, 92); it was also found in the Gulf of Naples in salinity around 37 ‰ (Vannucci, unpublished); specimens from salinity lower than 34 ‰ were either dead or dying when taken.

The temperature interval in this series was 16.87°C to 28°C; 24.7% of the specimens were taken in waters with temperature higher than 22°C. The temperature interval known for the species was from 19°C to 22°C, some doubtful records from about 18°C.

The graphs concerning this species may be rather misleading since many data were disregarded because the net had fished

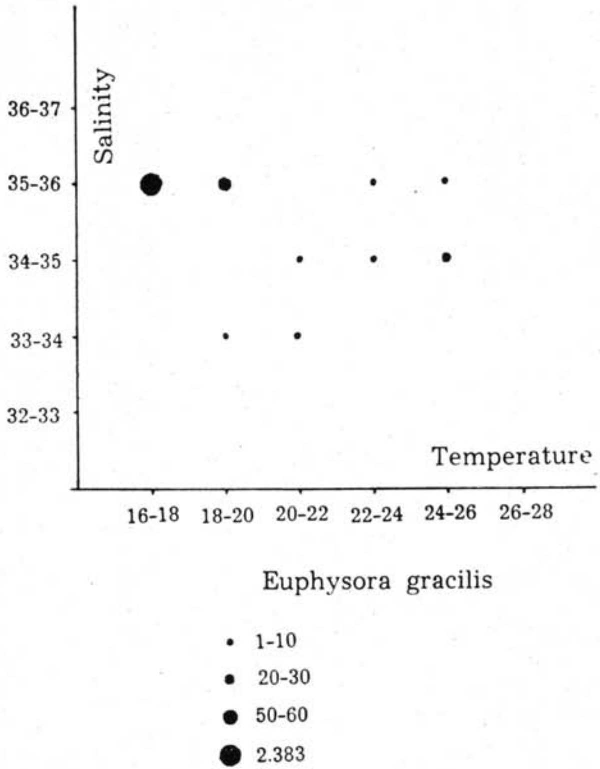


Fig. 7

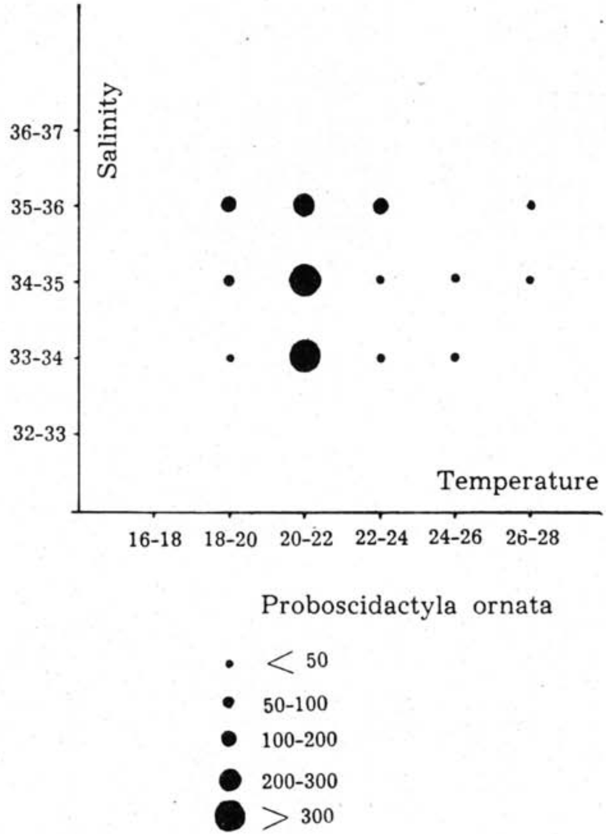


Fig. 8

Figs. 7-8 — Same as Figs. 1-2.

through different water layers. For this reason and because a vast majority of the samples in which *Proboscidactyla ornata* was present were mixed water samples, percentages of distribution per temperature or salinity were not computed. The greatest density for this species comes from mixed water samples; both the large number of such samples and the large number of specimens in each suggest that this species accumulates here were shelf water mixes with coastal water.

This species was previously considered (Vannucci, *l.c.*) to be a good indicator of the shelf water mass although it was also found in coastal waters and rather too high temperature. The present findings concerning this species are very interesting in that they show to what extent it can withstand the mixture of different water masses. *Proboscidactyla ornata* is undoubtedly a shelf water species as is shown by the fact that it always penetrates the area under study from Pt. III coastalwards and only spreads to Pt. II and then Pt. I when there has been a strong mixture of shelf and coastal waters due to strong winds or other causes. By following a patch in successive stations it may be established that the invader, a long lived species, comes from shelf waters and when present in low salinity water (down to 32.2 ‰, usually about 34 ‰) and high temperature (usually about 22°C, up to 28°C) mixed coastal and shelf water, may survive a month or more and may even produce a few buds but eventually it dies off. Dead or dying specimens are common on such occasions, specially in the lower layers. They were never taken in pure coastal waters.

This species may thus be considered a very good indicator of the presence of shelf waters, either pure or diluted.

Apparently this species is present and produces medusa buds the year round. It was found to be more abundant in the winter months. This is probably due to there being during this season a greater admixture of shelf waters at the points sampled, this and other facts, such as distribution of abundance in relation to temperature and salinity, indicate that lower salinity is better tolerated under lower temperature conditions, such as 20-21°C or lower.

It is much more abundant in the bottom layer when there is an invasion of shelf waters and stratification is well defined. Otherwise it is arranged irregularly in the water column, whether it is homogenous or not.

A density of 7.4 spec./m^3 was found in July in mixed waters with 20.5°C and 34.7 ‰ salinity (homogeneous water column).

In shelf waters extensive patches probably occur and the species must be both frequent and abundant, as may be judged by its frequency, abundance and extensive spread when it invades the coastal area.

13 — *Amphogona apsteini* (Fig. 9), 2,306 specimens counted. This species was found living in the following salinity interval in this series: 32.92 to 35.7 ‰.

Precise data from other sources are not available, but probably it may tolerate a wider salinity range. The optimum appears to be around 35 ‰.

The temperature interval was found to be in this series 19.3 to 25.4°C. No other precise data are available, however it may probably tolerate higher temperatures.

The indicator value of this species is closely related to that of *Proboscidactyla ornata*. It evidently lives in greater abundance in offshore waters and always comes into the area from Pt. III coastalwards. The bulk of the population probably lives in the shelf water mass and invades coastal water either by active diffusion of the population or by water movements mainly due to winds that cause vertical mixing. It tolerates dilution down to 32.9 ‰ and survived for 14 or 15 days in mixed coastal and shelf water with about 33.5-34.5 ‰ salinity. After a period of 15 to 20 days of lowered salinity they gradually begin to die off and dead medusae are abundant in great numbers.

The higher the salinity the longer the period of endurance; higher temperature is also better endured under high salinity conditions; the inverse relationship prevails with temperature, i.e, the lower the temperature the better it endures lowering in salinity.

Mature medusae are extremely rare in coastal water and very rare in mixed waters. When taken they are often dead or in otherwise bad conditions. This may indicate that adults die soon after spawning, however the relatively large number of dead medusae with incompletely mature gonads suggests that the young and immature specimens endure much better the lowering of salinity caused by admixture with low salinity waters. Fully mature adults appear to be restricted to the shelf water mass. Perhaps it does not reach maturity in salinity lower than 34.5 ‰. The young stages of this species are both frequent and abundant. It was present the year round.

The spatial distribution of this species in shelf water is unknown, however in the area studied it tends to be more abundant in the upper layers or to be uniformly distributed. Greatest densities were always found at Pt. III (Table I).

TABLE I

Sample Nº	Nº spec./m³	Salinity-average of column	Temperature (ºC) average of column	Date
E_{113}	9.2	34.35 ‰	19.9	10/9/60 10.32 a.m.
E_{179}	12.5	33.9 ‰	20.0	13/8/58 10.53 a.m.
E_{297}	29.5	35.7 ‰	24.0	13/4/60 10.29 a.m.

14 — *Cytaeis tetrastyla* (Fig. 10), 2,691 specimens counted. This species was reported previously as probably warm water, stenothermic and euryhaline to a certain degree, preferring high salinity. It was also reported as neritic off the southern Brazilian coast, living in the shelf water mass and rarely to be found in coastal waters (Vannucci 1957, pp. 89, 101). The present findings confirm the above conclusions except for temperature. We know that it is eurythermic, preferring warm waters. An indicator of shelf water or of mixed shelf and coastal waters.

Cytaeis tetrastyla was recorded for every month in the year both in the coastal and in the shelf water mass. Most of the specimens taken in this series come from waters the salinity of which falls within the limits given earlier, i.e. 33.5-35.9 ‰. In the present collection only 3% of the specimens were found in salinity lower than 35.5 ‰ but never lower than 33.21 ‰. All the specimens taken in salinity lower than usual were found there after strong south- or southwesterly winds that had caused a vertical mixing of the water column and thus it may be assumed that the medusae originally lived in the higher salinity waters of the lower layers. Mild salinity lowerings are well tolerated. As many as 16.4% of the total number of specimens were taken in water temperature lower than 20.5°-22.7°C but never lower than 19.4°C. About 78% of these were taken when a strong mixing of the water had taken place due to winds. The lower normal temperature limit for this species in this region is probably around 20°C. Three specimens come from 28°C and 24.2% of the total number taken certainly comes from temperature higher than 23°C.

Only two specimens were taken with medusa buds on the manubrium. Usually both large mature specimens and small ones are taken in the same haul the year round and nothing can be said on the duration of the different steps of the life cycle; probably it does not take more than 15 days to reach maturity as may be judged from successive hauls and by comparison with nearly related species reared in the laboratory.

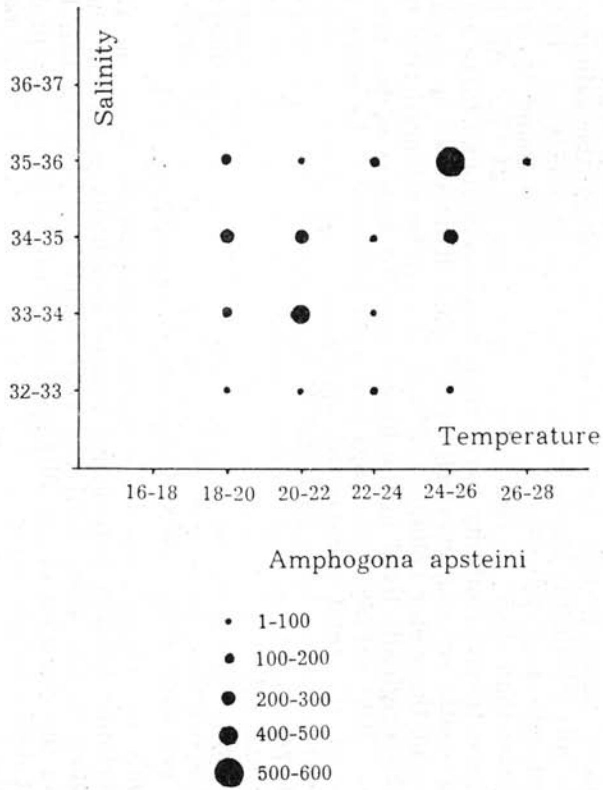


Fig. 9

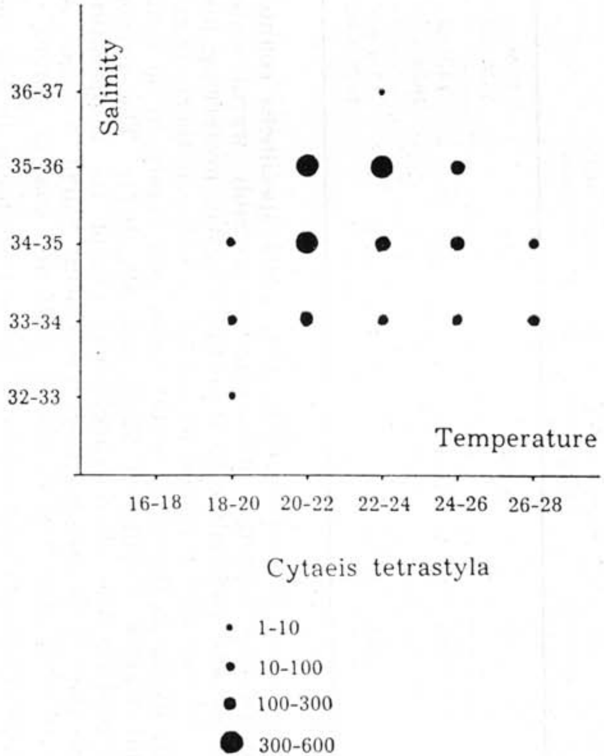


Fig. 10

Figs. 9-10 — Same as Figs. 1-2.

This species was present in 62% of the samples counted and is much more abundant at Pt. III indicating that it is not a coastal species but that it penetrates coastalwards coming from offshore waters.

The greatest density was of 11 spec./m^3 in 35.2 ‰ salinity and 22.5°C temperature.

Patchiness in distribution is not an outstanding feature for this species. Only five times a much greater concentration than usual was found, the distribution tends to be rather even. Patches were found once on February 12, 1958, when there were 132 specimens at Pt. III (5.7/m^3). Again on May 17, 1960, and May 25, 1960 there were 110 and 108 (7 and 6.1/m^3; evidently the same patch) at Pt. III; finally on June 27, 1960 at Pt. III, 142 specimens (4.2/spec./m^3) and on July 12, 1960, again at Pt. III there were 115 specimens (11 spec./m^3); the two latter catches probably belonged to the same patch.

Comparing the Hensen net vertical catches with the Clarke-Bumpus lower layer horizontal catches, it may be shown that when shelf waters are present near the bottom, the number of *Cytaeis tetrastyla* is greater in the lower layer. When the water column is homogeneous it is either evenly distributed or more abundant in the upper layers.

5 — UBIQUITOUS SPECIES AND TROPICAL WATER MASS INDICATORS

15 — *Ectopleura dumortieri* (Fig. 11), 1,839 specimens counted, including 1,483 medusae and 356 larvae. This species was already known to be euryhaline and presumably eurythermic preferring high temperatures (Vannucci 1957, pp. 40, 84). This is in agreement with its wide geographic distribution which is that of a tropical to temperate species that extends into southern boreal regions.

In the region now under consideration it may be found all year round. Russell (1953, p. 78) records it as taken singly or in small numbers along British coasts; according to Werner & Aurich (1955) it also is not abundant in the southern North Sea, where it is taken in the summer months. It may be found from March to December in southern Ireland; in May and September through November at Plymouth and in June at St. Andrews, Scotland. The different seasonal occurrence in temperate and warm waters is probably due to temperature conditions acting as limiting factor to survival and reproduction (liberation of actinulae and medusae) in colder waters.

The interesting life-cycle of this species was recently studied by Werner & Aurich (1955) who showed that the fertilized egg develops into a star-shaped proactinula with a variable number of tentacles, a mouth mounted on a short conical proboscis and a flattened aboral region. As development proceeds, the oro-aboral axis and the tentacles elongate, the latter will become the aboral whorl of tentacles of the actinula while the oral whorl develops later. When this happens and the larva has two whorls of tentacles it is called an actinula, the aboral region elongates and evolves into the future peduncle of the hydroid. The actinula settles and develops into the *Ectopleura dumortieri* polyp. According to Werner & Aurich the whole development from the egg to the fully developed actinula takes from 4 to 5 days at 17-19°C in the laboratory. The same authors found proactinulae from the North Sea to have 9-12 tentacles (22 specimens) and actinulae from 4 to 8 oral tentacles and 8 to 14 aboral tentacles (19 specimens). Our proactinulae were found to have 7-14 tentacles; the mean for 168 specimens was 10.8.

In the considerations below, proactinulae and actinulae were counted together and listed as *Ectopleura dumortieri* larvae.

In a general way the present data show *Ectopleura dumortieri* in this region to be an euryhaline species that prefers salinity above 35 ‰. The greatest abundance of specimens per cubic metre was found in salinity 35.4 ‰ where the density was 79.5 spec./m^3. Contrarily to what had been previously assumed (Vannucci 1957, p. 99) it is not exclusively present in lagoon waters, it may be found also in coastal waters and in the shelf water mass. It may endure dilution down to 32.15 ‰. It is eurythermic, but prefers temperatures lower than 20°C. The present data suggest that it is indifferently a coastal and shelf water species that may be found living actively in either water mass due to its euryhaline and eurythermic capacities. The high percentage of the specimens from shelf waters in the present series was always due to the presence of patches.

The actinulae tolerate a wider salinity range but a more restricted temperature interval than the medusae, they withstand lower salinity but not the lower temperatures. The figures indicate that there is no strict relationship between salinity and temperature.

What is known of the hydroid distribution, together with the distribution of the actinulae and displacement of the patches shows that the hydroid is euryhaline and lives better than the medusae in lower salinity and higher temperature conditions, accordingly it is abundant in bays, estuaries and mangrove outlets.

Both young and adult medusae as well as young and fully formed larvae are found in the plankton in any month of the year suggesting that the medusae are liberated and lay eggs year round. During three successive years of sampling the high peaks of frequency were in January 1958, November 1959 and July 1960, showing complete freedom from the salinity and temperature cycles. The high numbers found at these times are not due to sampling hazard since all the samples taken the same day showed strong increase in numbers, indicating that a dense patch was present at the moment. This is a rather short lived species and the hydroid is known to live in the area, therefore two factors may account for the occasional large numbers: a yet undetermined ecological factor inducing the budding and release of large numbers of medusae or currents such as to promote the formation of patches in the distribution of these poor swimmers. Further data will clear these points. The diagrams of frequency of medusa-produced larvae and hydroid-produced medusae, are roughly parallel which suggest that the two factors pointed above are probably concomitant and act in a similar way. Tidal currents and changes in salinity in the lagoon region might act as stimulating factors for medusa bud formation and actinula liberation.

The North Sea medusae produce a very small amount of eggs at a time, usually two, rarely more, the same appears to be the case here.

It is not known how often the medusa reproduces nor for how long a period, but if we admit that only four eggs are produced per medusa and that the sex ratio is 50%, the present data suggest a survival rate of about 8% of the larvae. Since the number of eggs laid must be greater than four, the survival rate of the larvae before they settle is probably smaller. The medusae have a very short life, probably 12-14 days, certainly not more than 15 days, as may be evaluated from the abundance of specimens at successive stations.

The greatest density of medusae plus larvae was found to be of 79.5 spec./m^3 at 35.44 ‰ salinity and 19.46°C. Large patches may include two or three stations, usually however a patch did not include more than one or two. When there are only small numbers present they do not aggregate in patches but rather are distributed uniformly at the three points within the area studied.

Comparing the numbers caught by the Clarke-Bumpus sampler and by the Hensen net per m^3, there are indications, that: 1 — there is a greater concentration of medusae in the lower layers when the sun is shining and around midday and 1 p.m., irrespective of the type of water in the bottom layer; neither higher salinity nor lower temperature prevent the species from migrating downwards; 2 — actinulae and proactinulae do not migrate to subsurface layers during daytime.

Table II shows the distribution of this species at the three stations worked the same day, January 1958. H = Hensen net vertical sample; CB = Clarke-Bumpus horizontal bottom layers sample.

TABLE II

Place	Sample	Net	No. spec./m^3	Time (h)	Depth	Salinity (°/₀₀)	Temperature (°C)
Pt. I	E_1	H	29.5	1350	0	34.47	27.51
	E_2	CB	79.5		7	35.43	19.70
					18	35.44	19.46
Pt. II	E_3	H	16.6	1200	0	34.11	27.10
	E_4	CB	18.8		7	34.70	25.07
					18	35.48	19.08
Pt. III	E_6	H	0.1	0945	0	34.79	26.49
	E_5	CB	1		10	35.08	24.20
					25	35.55	16.87

16 — A total of 1,771 medusae of *Clytia cylindrica* (Fig. 12) and 139 fragments of hydroid colonies of the same species, most of them still alive when taken, were counted.

The most astonishing fact about this species is the frequency of living fragments of hydroid colonies in the plankton. The hydranths look perfectly normal, they have food in the stomach and the gonophores when present, are in the process of actively budding off medusae. The stolon is reduced due to lack of substratum and the hydranths grow in a tuft. The presence of living hydroids of this species was reported earlier from the region of Fernando de Noronha at 3° S (Vannucci 1958, p. 9). Legaré (1961, p. 204) reported abundant hydroid fragments in the plankton from the region of Cariaco (Venezuela) and since Zoppi (1961, p. 179, fig. 5) recorded abundant *Phialidium hemisphericum* (presumably *Clytia cylindrica,* certainly genus *Clytia*) in the area, probably the hydroids belong to the same species.

Graph 3 shows the total number (hydroids plus medusae) of this species to decrease from Pt. I to Pt. III, this is also true for the medusae but not so for the hydroids, the numbers of which slightly increase away from the coast. This may be the effect of the relatively short life span of the medusa; the hydroid stands a better chance to be carried offshore and also contributes to spread the species.

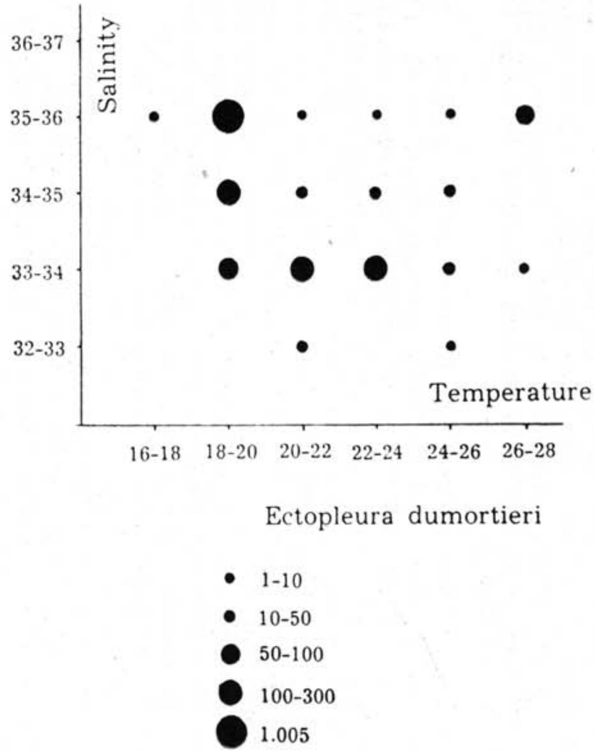


Fig. 11

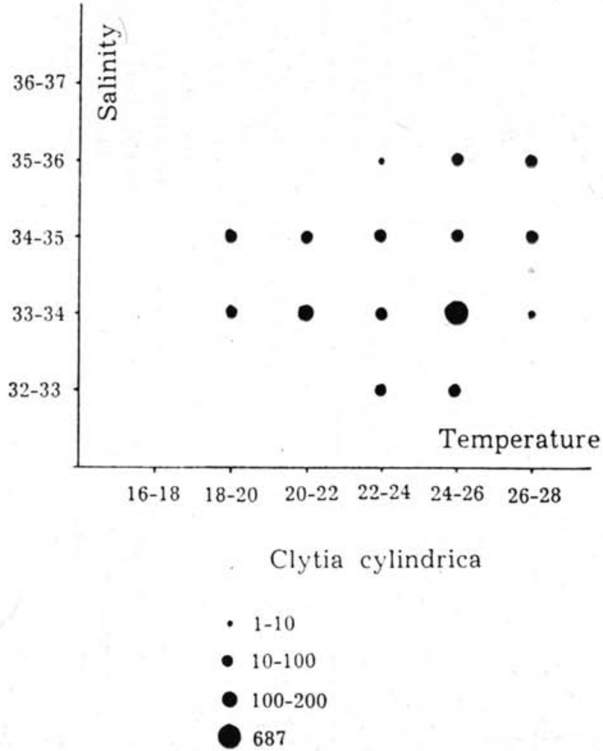


Fig. 12

Figs. 11-12 — Same as Figs. 1-2.

An eurythermic and euryhaline thermophile species, widely distributed. The medusae are present and reproduce the year round, but are more abundant in summer. As many as 15 spec./m^3 were found at 33-33.9 ‰ salinity and 24-24.6°C temperature. The salinity range was found to be from over 36 ‰ at Fernando de Noronha (Vannucci 1958, p. 9) down to 32 ‰. The temperature variation was from 26°C down to 19.5°C. Apparently the hydroid tends to prefer colder water of higher salinity. Although previously thought to be restricted to the coastal water mass, it was now found to be present in shelf and tropical waters as well. The medusae may be found in the plankton in any month of the year. Small patches are formed that rarely involved more than one point, and they were found to remain for 15 to about 40 days at the same place. Thus a patch found at Pt. I and Pt. II on Dec. 14, 1959, respectively with 14.9 and 12.6 spec./m^3 was still present at Pt. II on Dec. 28, with 9.5 spec./m^3. By then most specimens were old or in rather poor conditions and dying off. This agrees well with the experiments on rearing species of the genus *Clytia* in the laboratory (Vannucci, unpublished work done at the Naples Station), the medusae of which laid the first eggs when 15 days old and lived around 30-40 days (17°C temperature).

17 — Altogether 774 specimens of *Aglaura hemistoma* (Fig. 13) were counted. The salinity interval in which this species was taken in this series was 33.4 to 36.29 ‰. Previously recorded salinity interval was 33.5 to 36.9 ‰ (Vannucci 1957, p. 78). This species is known to be very abundant in areas where salinity is still higher.

The temperature interval was found to be 19° to 27.8°C. Previous records indicate 18.1 to 29°C, perhaps down to 15° (Thiel 1936, p. 15). In the western South Atlantic this species is known to be found in both tropical and shelf waters, being most abundant in the tropical water mass (Vannucci *l.c.*, p. 93). It is known to tolerate lowering of salinity and temperature to some extent. The present data confirm the close association between the tropical water mass and *Aglaura hemistoma*, its presence in shelf waters and its occasional survival in coastal waters as a temporary visitor. Anyhow, its presence is always a sure sign of admixture of tropical waters. It always entered the area studied from Pt. III coastalwards. It was taken almost exclusively from upper layers and this further supports the view that the specimens taken nearer to the coastline are not brought there by colder shelf waters but are the result of direct admixture of tropical waters. In this sense this species is a good indicator of tropical waters. It was found to be present in the bottom layers only after a thorough mixing of the water column had taken place.

It may survive 32 days in salinity as low as 33.6 ‰ and temperature between 20-20.5°C. Thus a large patch was present on June 25 at the three points, with a maximum density of 5.7 spec./m³ at Pt. III and a few mature specimens; on July 10 the same patch was present at the three points with a density of 4 spec./m³ and no mature specimens. On July 27 the same patch was present only at Pt. III and the density had fallen to 2.45 spec./m³ with only a few small and mature specimens and many large and dying ones. At this time the temperature had risen to 21.5°C while the salinity was still 33.6 ‰ on the average. Other patches were found to survive up to 38-40 days. Lowering of salinity is better tolerated when the temperature is also low, as may be seen by following patches in winter and in summer months.

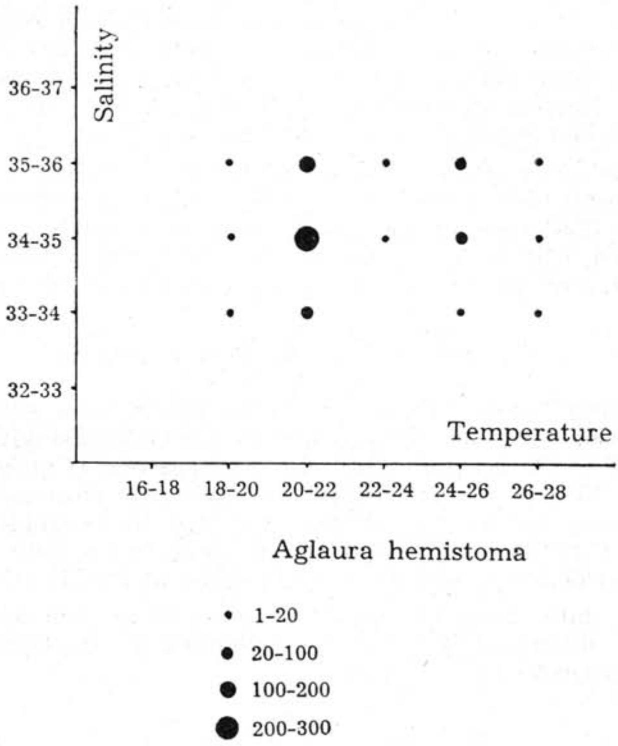


Fig. 13 — Same as Figs. 1-2.

Aglaura hemistoma may be found the year round and reproduces the year round in temperatures higher than 21°C.

Density was found to be as high as about 13 spec./m³ once in June in mixed waters with 33.38 to 34.59 ‰ salinity and 20.9°C temperature, all specimens small and immature.

6 — OTHER SPECIES

Besides the 17 species discussed above, there were other that will not be dealt with in this paper. Some were too scarce to allow for a detailed study. *Bougainvillia frondosa* (four specimens), probably a coastal and shelf water mass species; *Gastroblasta ovalis* (one specimen) is a species of doubtful validity and may be an abnormal *Clytia* sp., it has already been recorded from Brazil (Vannucci 1949, p. 225), it is here rare and coastal, although at times and elsewhere it has been found to be abundant (Gulf of Naples, unpublished). *Octophialucium* sp. (one specimen) was not determined down to species level.

Liriope tetraphylla (40,179 specimens), *Solmaris leucostyla* (1,148 specimens), *Cunina octonaria* (1,726 specimens) and *C. peregrina* (242 specimens) will be studied separately when more information will be available on the shelf water mass. *Liriope tetraphylla* was so far the only species present in every sample.

7 — SUMMARY AND CONCLUSIONS

The distribution in space, over the three years studied shows the following pattern. Seven species are decreasingly abundant from Pt. I to Pt. III and in all cases except one (*Clytia cylindrica* with only 45% at Pt. I) there were 57.5% or more specimens at Pt. I. Seven species are on the contrary increasingly abundant from Pt. I to Pt. III, two of them were taken only at Pt. III and at least 66.6% of the others were taken at Pt. III (Graphs 1-3).

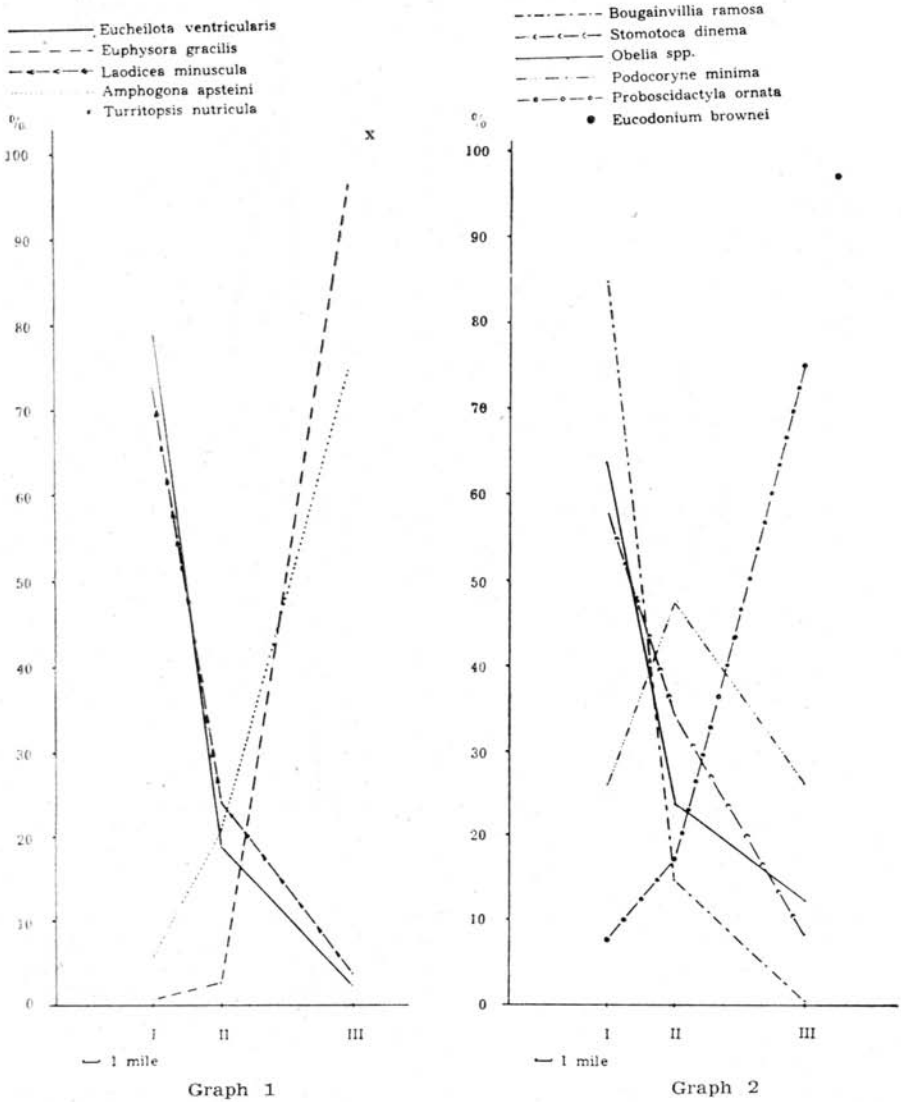
These data, those plotted on Graphs 4-9 as well as the points previously discussed indicate the following to be coastal species that may expand oceanwards:

Bougainvillia ramosa
Eucheilota ventricularis
Obelia spp.
Eucheilota duodecimalis
Stomotoca dinema
Clytia cylindrica

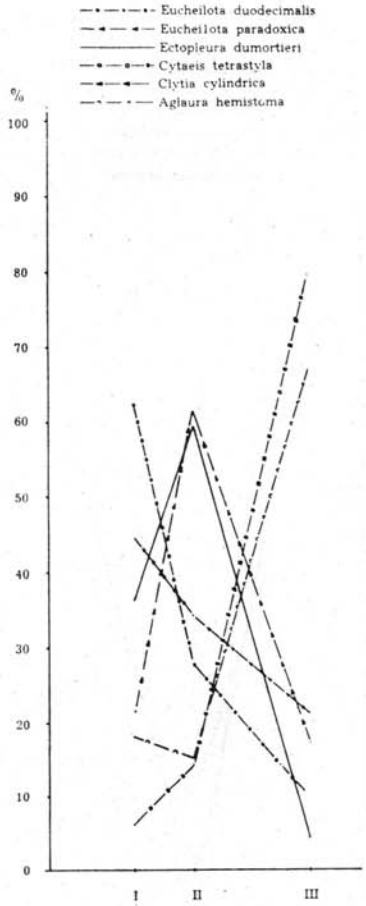
They are all coastal water mass indicators except for the last mentioned which is widely tolerant of environmental conditions such as salinity and temperature.

The following species are more abundant in offshore waters:

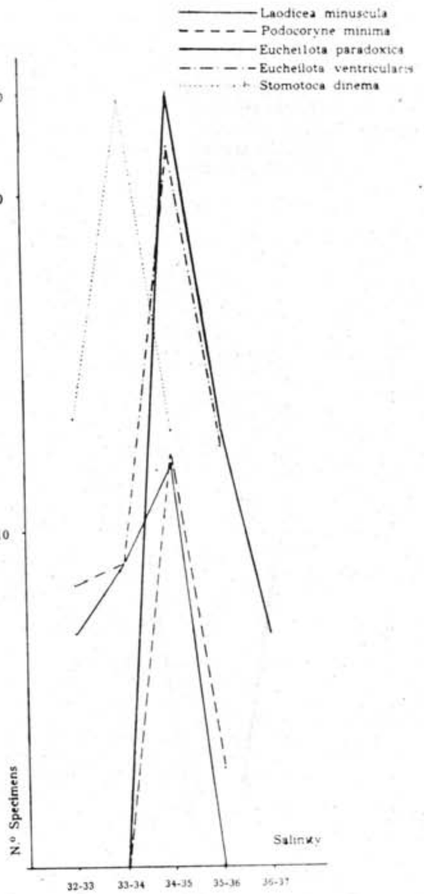
Turritopsis nutricula
Eucodonium brownei
Euphysora gracilis
Cytaeis tetrastyla
Amphogona apsteini
Proboscidactyla ornata
Aglaura hemistoma



Graphs 1-2 — Percentual distribution of specimens at each station in relation to distance from coast line. All specimens collected over the three years are entered in the graphs.



Graph 3 — Same as Graphs 1-2.

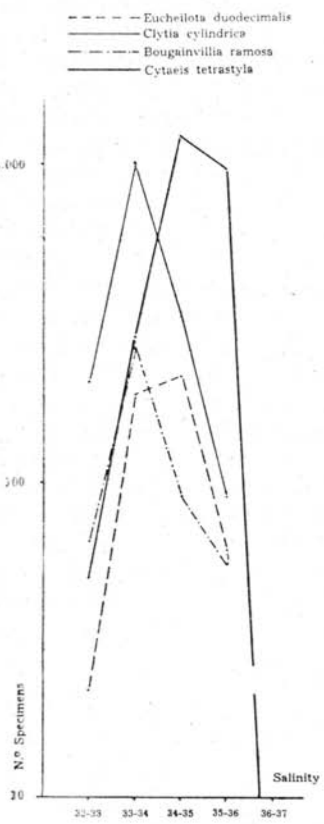


Graph 4 — Distribution in relation to salinity given in absolute figures. Only those specimens are computed of which living conditions were known with certainty. Monolog scale.

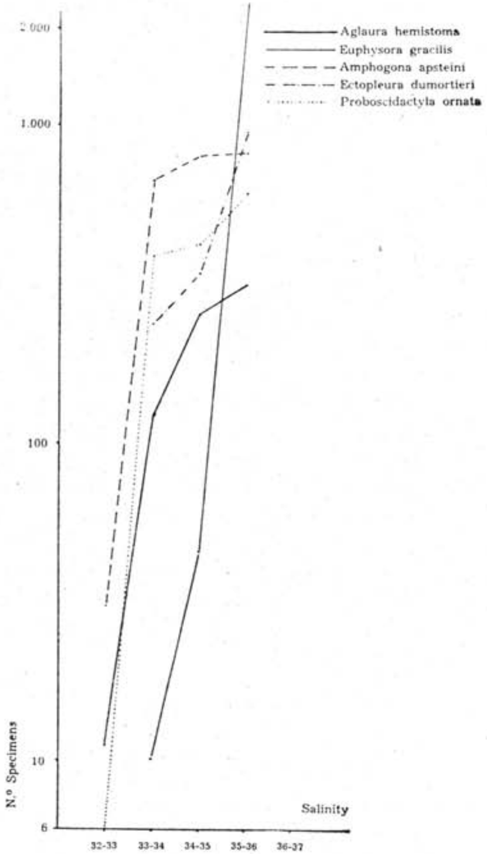
They are all shelf water mass indicators except for the last which is a tropical water mass species. The following species were more abundant at Pt. II, tending to be more abundant at Pt. I rather than at Pt. III and since according to their other properties, two of them may be good indicators of the coastal water mass, their greatest abundance at Pt. II (50% or about 60% of the total) may be due either to patchiness or to preference for mixed waters. They are:

Eucheilota paradoxica
Ectopleura dumortieri
Podocoryne minima

Two species that were taken only once will now be disregarded; they are *Turriptopsis nutricula* and *Eucodonium brownei*. Five species show increasing numbers with increasing salinity (Graph 6); they are: *Euphysora gracilis, Amphogona apsteini, Proboscidactyla ornata, Aglaura hemistoma* and *Ectopleura dumortieri*. These are evidently the species whose numbers decrease coastalwards, except for *Ectopleura dumortieri*, the maximum of



Graph 5



Graph 6

Graphs 5-6 — The same as Graph 4.

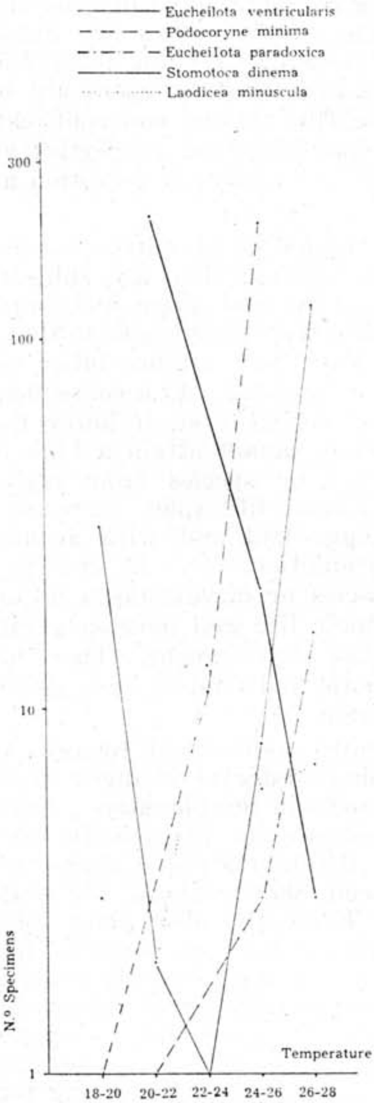
which was found at Pt. II. The remaining ten species have their peak of abundance within the salinity range studied here. Thus the principal factor for the species distribution in space appears to be salinity, which in this region agrees closely with the distribution of the water masses.

There are a few species which apparently have very similar salinity requirements, for instance *E. ventricularis, P. minima, L. minuscula* and *E. paradoxica* (Graphs 4, 5). *Stomotoca dinema, Bougainvillia ramosa* and *Clytia cylindrica* also have their peaks of abundance at the same salinity value. Comparing the temperature/frequency curves (Graphs 7-9) of the different species one with another and with the salinity-frequency curves (Graphs 4-6), one may be see that the ranges of temperature tolerated are much broader and that they differ more from species to species than do the ranges of salinity. Moreover, and this is the important fact, the species with similar salinity distribution curves are as a rule not those that have similar temperature distribution curves, and they show peaks at different values. Thus if they have similar salinity preferences, they have different temperature preferences and vice versa if they have similar temperature preferences they have different salinity. There are two groups of three species each that were found to have the same value both for the peaks for salinity and for temperature. They are *E. ventricularis, E. duodecimalis* and *P. minima* each of which had it peak of abundance at 20-22°C temperature and 33-34 ‰ salinity, but these curves are not similarly shaped or, when they are similar, they extend to different maximum or minimum value. *A. apsteini, P. ornata* and *A. hemistoma* likewise had they peaks of abundance at 20-22°C temperature but the salinity peak was at 35-36 ‰. The temperature curves of these species also were not similarly shaped in that the extreme values were different for each species. It is nevertheless true that these two groups of species have very similar requirements for salinity and temperature, and therefore they must have different requirements for some other ecological factor, for which at present there are no data. *Clytia cylindrica* and *Bougainvillia ramosa* have similarly shaped curves with the same peak of abundance for both salinity and temperature.

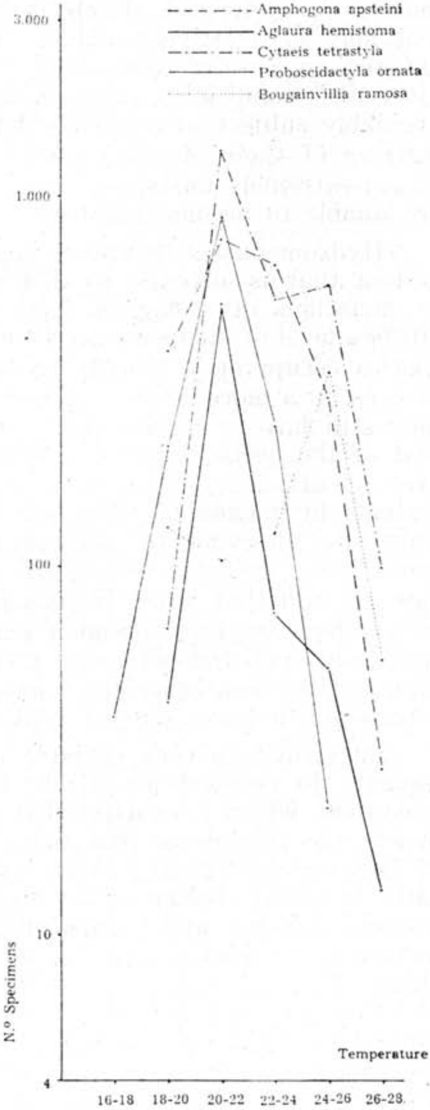
Margalef (1959, p. 226) discusses the gradual transformations that ecosystems not subjected to catastrophic changes undergo before reaching a certain degree of stability. The knowledge of the laws that govern this process allows one to recognize "juvenile" and "mature" systems even if their previous history is unknown. The terms "juvenile" and "mature" are used here in Margalef's sense. Plankton may be said to be, generally speaking, a juvenile type of ecosystem because of its usually changing conditions. However, different degrees of maturity may be recognized within a single planktonic environment, and also when different plankton or water masses are compared with each other; thus some are more juvenile and some less so. Old water masses may approach closely to being a mature type of ecosystem and may be relatively stable. Young water masses are usually exposed to greater variations and therefore remain in a more "juvenile" condition. Surface layers and coastal waters are unavoidably subject to relatively intense fluctuations and continuous shifting of their physical, chemical and biological properties and so are extremely unstable; they remain in a juvenile condition and are unable to become mature.

Hydromedusae occupy a high trophic level within an ecosystem that is juvenile to different degrees; they are subjected to variations of ecological factors in time and space and cannot attain a level of independence from the system comparable to that of species occupying a similar trophic level, for instance other carnivores, in a more stable and mature ecosystem. As a consequence they still have a high expenditure of energy even if lower than that of the herbivorous plankton. They cannot attain a high degree of efficiency such as is reached by species from mature systems by means of increased individual life span, increase of body size, decrease of number of eggs laid and with acquired brood care, decrease of oxygen consumption, etc. In general it may be said that when plankton species or larval stages acquire such capacities, they abandon planktonic life and develop greater efficiency and independence from the environment. They may even become homeothermic, homeosmotic and tend to have smaller broods and a lower oxygen consumption.

Survival in a very variable juvenile environment requires the capacity to respond adaptively to short interval changes of the ecosystem, which is exactly what happens in the plankton. Nevertheless the preference that many species show for specific levels of different ecological factors, often within restricted limits, prevails in many instances as has been shown above for water masses, salinity and temperature. Evidently also many other factors are important for the establishment of each species' ideal niche. The importance of each factor varies according to space and time for each species, for each of its different developmental stages, its different generations within the year and metagenesis when such occurs. Old water masses are ecologically a more mature environment than young water masses. They have long term and small amplitude variations and bear thus a more advanced type of community having the succession proceeded farther. A local example is the tropical water mass (Brazil Current) with scarce phytoplankton and relatively abundant carnivores, as may be seen by the tables of the plankton collected by Brazilian cruises



Graph 7



Graph 8

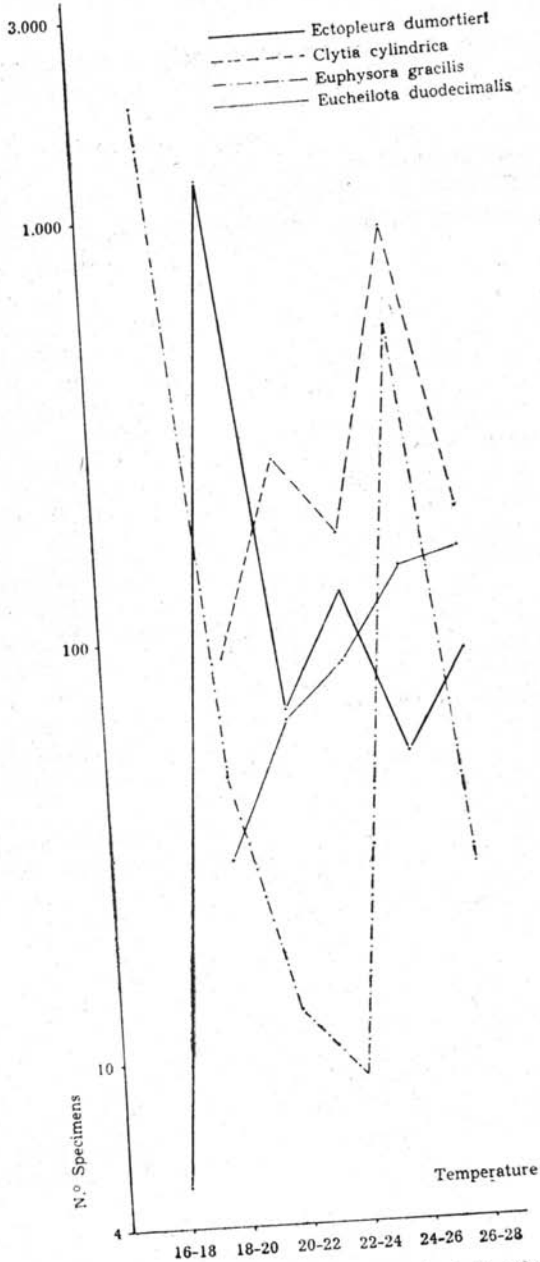
Graphs 7-8 — The same as Graph 4 in relation to temperature.

(Vannucci & Almeida Prado 1959; Vannucci 1961; Vannucci & Queiroz, under press).

Hydromedusae appear as extremely interesting subjects of study from the ecological point of view, they probably represent one of the highest levels of as mature as can possibly become a group of planktonic species. Chaetognatha are in the same position and this may account for the large number of indicator species in both these groups.

Some experimental facts suggest that very often there is a close relationship between temperature and salinity in the sense that tolerance to the variation of the two factors does not vary independently and that the lowering of temperature usually facilitates the tolerance for greater dilution. Vice versa higher temperatures are better tolerated under high salinity conditions. Kinne (1958) has recently shown experimentally this to be true for several different animals, including a hydroid: *Cordilophora*. It is also empirically very well known by any person who has endeavoured to rear plankton animals under laboratory conditions. It is practically impossible to keep such animals healthy when constant temperature rooms are not available and best results are obtained when the temperature is kept rather lower than normal. Figures 1-12 were partly drawn to show this relation. Petersen & Vannucci realized some experiments with *Koellikerina fasciculata* to the purpose (Petersen & Vannucci 1960). Andrewartha (1961, p. 82 and following) gives some examples of how the relation temperature/dryness of the air affects different animals, especially insects. It may be pointed out that in the sea, the relation temperature/salinity corresponds to the relation temperature/dryness of the air for the aerial environment.

Several authors have pointed out that animals reared in the laboratory show a much greater tolerance towards the variation of the different factors to which they are exposed, such as temperature, salinity, light intensity and others than those living in the natural environment. This may be explained by the fact that laboratory animals are presumably kept under optimum conditions for every factor except the one experimented upon, while in the natural environment all factors are subject to variations and there is a strong intra- and interspecific competition which is eliminated in the laboratory. Furthermore Brown & Wilson (1956) called "character displacement" the "situation in which, when two species of animals overlap geographically, the differences between them are accentuated in the zone of sympatry and weakened or lost entirely in the parts of their ranges outside this zone". Kohn & Orians (1962) have brought forth more information and they quote several examples in support of this view. This point may be stretched further to say that the greater degree of specialization necessary in the sympatric zone brought about by the necessity



Graph 9 — The same as Graph 4 in relation to temperature.

of occupying a single environment results in a greater uniformity of the species in the sympatric zone, which is unnecessary in cultures as well as in the zone where the species of close requirements are not sympatric. The authors quoted have shown that the closer the relationship with the other species present in the area of sympatry, the less variable each species appears to be. Variability under laboratory conditions may be very great within the same clone (Vannucci 1960) and is certainly greater between different clones and successive generations.

All the samples studied here come from rather shallow depths, therefore only species that have become adapted to an environment relatively variable in its biological as well as physical and chemical properties might be expected. Also a greater number of species and individuals will succumb to unfavourable environmental conditions and predators. It is for this reason that plankton specimens are to be found always living in conditions very near to their optimum and are thus good indicators, except for the very euryoecus ones. To a major extent ecological factors that govern the presence and abundance of species are the sole that may account for the patterns of distribution. As Andrewartha (1961, p. 17) points out, "there are four major categories which... influence an animal's chance to survive and multiply: (a) weather; (b) food; (c) other animals — and pathogens; (d) a place in which to live". Weather, for our present considerations must be translated into hydrographical conditions, both physical and chemical.

All the species from the present series of samples represented by 1,486 specimens or more are either shelf water or ubiquitous species (see § 2 — List of species and their abundance) while all the species represented by 833 specimens or less are coastal water mass species. We exclude from this context the two very rare *Turritopsis nutricula* and *Eucodonium brownei* and also *Aglaura hemistoma* that was not taken abundantly because it is a tropical water mass indicator and this water mass was only seldom sampled. This order of abundance may be due to greater productivity of the shelf water mass. Precise measurements of the standing stock of zooplankton of the coastal and shelf water masses are not yet available; preliminary results were not conclusive (Vannucci 1962, 1962a). The greater abundance of medusae in the shelf water mass also points to a higher degree of maturity of this ecosystem.

Summing up, the principal conclusions that may be drawn are:

1) Eight species are established as good indicators of the coastal water mass (p. 147).

2) Six species are established as good indicators of the shelf water mass (p. 147).

3) One species is a good indicator of tropical waters (*Aglaura hemistoma*). Two species are ubiquitous.

4) The distribution in space of the medusae agrees closely with the distribution of the water masses.

5) As a whole these medusae are more temperature than salinity tolerant; this may be due to the samples coming from shallow water and thus the species present are those that are usually subjected to and adapted to relatively wide temperature changes.

6) There are no two species with similar temperature and/or salinity curves, for peak of abundance and extremes. Species with similar salinity preferences have different temperature preferences and vice versa.

7) Plankton is a juvenile type of ecosystem that may be relatively more or less mature. The coastal water mass is subject to continuous changes and is the most juvenile of all those studied here, while the tropical mass (Brazil Current) is the relatively more mature (old water mass, with smaller variations and over longer periods). The shelf water mass is intermediate between the two.

8) Species or life stages occupying a high trophic level in a juvenile ecosystem cannot reach a high degree of independence and efficiency and thus in this case they either leave the plankton or adapt to their level and do not reach higher efficiency and stability.

9) There are some suggestions that some species tolerate lower than optimum salinity conditions better under lower temperature and vice versa higher than optimum salinity facilitates survival under higher temperatures. This is compared to the temperature/dryness of the air relation that has been shown to exist in some terrestrial animals.

10) Better endurance of a wider range of certain factors (salinity, temperature, etc.) under laboratory conditions is explained by greater inter- and intraspecific competition in the natural environment, as well as the unfavourable factor of sudden changes against protection from competition and best possible conditions for every ecological factor under control except for the one experimented upon, in laboratory rearing experiments where many specimens survive that would not in nature. This is also related to what has been described as "character displacement".

11) The shelf water mass species were much richer in number of specimens. This suggests higher standing stock in the shelf water mass or a higher degree of maturity of this system.

8 — RESUMO

A análise de 247 amostras quantitativas de plâncton coletadas durante três anos em três estações fixas ao largo de Cananéia, Estado de São Paulo, até 17,2 milhas ao largo e a 28 m de profundidade, revelaram a presença de 28 espécies de medusas, 17 das quais foram estudadas detalhadamente.

1) As oito espécies seguintes podem ser consideradas bons indicadores da massa de água costeira: *Podocoryne minima, Bougainvillia ramosa, Stomotoca dinema, Laodicea minuscula, Obelia* spp., *Eucheilota ventricularis, E. duodecimalis, E. paradoxica.*

2) As seis espécies seguintes são bons indicadores da massa de água da plataforma: *Euphysora gracilis, Eucodonium brownei, Turritopsis nutricula, Proboscidactyla ornata, Amphogona apsteini.*

3) Uma espécie é bom indicador de massa de água tropical: *Aglaura hemistoma,* além disso ocorrem duas espécies ubiquistas.

4) A distribuição das espécies no espaço acompanha de perto a das massas de água.

5) No conjunto essas medusas são mais tolerantes em relação à temperatura do que à salinidade. Isso pode ser devido à procedência das amostras, tôdas de águas de pequena profundidade e portanto com uma fauna adaptada e sujeita a variações relativamente intensas de temperatura.

6) Não há duas espécies que tenham curvas semelhantes em relação à freqüência/temperatura ou freqüência/salinidade, com os mesmos máximos ou com extremos comparáveis. Espécies com preferências semelhantes para salinidade, têm preferências diferentes para temperatura e vice-versa.

7) O plâncton é um tipo de ecosistema juvenil, que todavia pode ser relativamente mais ou menos maduro. A massa de água costeira, submetida a mudanças contínuas é a que se mantém em estado mais juvenil de tôdas as estudadas no presente trabalho, enquanto a massa de água tropical (Corrente do Brasil) é a relativamente mais madura, por ser u'a massa de água velha com variações de menor amplitude e de período mais longo. A massa de água costeira é intermediária entre as duas.

8) Espécies ou fases do ciclo específico que ocupam um alto nível trófico num ecosistema jovem não podem alcançar um nível de independência do ambiente e de eficiência muito altos e portanto ou abandonam a vida planctônica ou não alcançam um nível de eficiência e estabilidade mais altos.

9) Há indícios de que certas espécies toleram concentrações de salinidade inferiores ao ótimo em temperatura baixa e vice-versa salinidade mais alta do que o ótimo favorece a sobrevivência em temperatura mais alta. Êsse fato é comparado à relação temperatura/umidade do ar que foi demonstrada para certas espécies terrestres.

10) A tolerância de uma maior amplitude de variação, certos fatôres ecológicos como temperatura, salinidade, etc., em condições experimentais por parte de animais planctônicos, pode ser explicada pela existência de competição inter e intraspecífica no ambiente natural, enquanto que no laboratório todos os fatôres são mantidos no seu ótimo, afora aquêle experimentado. Êsse fato é relacionado também com o que tem sido chamado "character displacement" (deslocamento de caracteres).

11) As espécies de medusas da massa de água costeira apresentaram maior número de indivíduos, o que sugere maior produtividade dessa massa de água ou um mais alto nível de maturidade nesse ecosistema.

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