ZOOPLANCTON DE LA RÉGION DE NOSY-BÉ
X. THE BIOLOGY OF PLANKTONIC POLYCHAETA NEAR NOSY-BÉ, MADAGASCAR

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RÉSUMÉ

Sur la côte nord-ouest de Madagascar autour de Nosy-Bé, les fortes précipitations estivales (janvier à mars) et les apports des rivières et des lagunes entraînent une circulation marine du type estuarien.

Les eaux de surface à faible salinité formées pendant l'été dans les zones côtières passent au-dessus du plateau continental pendant l'automne. Trois zones peuvent donc être distinguées : néritique interne, néritique externe et océanique, auxquelles la distribution du plancton est reliée.

Nous avons analysé au total 307 échantillons de Polychètes planctoniques récoltés pendant 1 an, entre avril 1963 et mars 1964. Les 6 347 spécimens de Polychètes holoplanctoniques correspondaient à 31 espèces parmi lesquelles 3 sont nouvelles pour la région. Les 5 523 larves de Polychètes benthiques ont pu être classées par familles. Tous les échantillons ont été récoltés lors de traits horizontaux de 5 minutes exécutés à 2 mètres et 10 mètres de profondeur ; certains de jour, d'autres de nuit. Leur comparaison montre que chaque espèce varie dans sa distribution et dans ses migrations diurnes. Ces différences, auxquelles s'ajoutent des nombres inégaux d'échantillons, rendent nécessaire l'emploi d'une nouvelle méthode numérique pour simplifier les données avant d'essayer d'apprécier les changements saisonniers en abondance et distribution.

Pour chaque espèce les résultats sont présentés en même temps que l'amplitude de température et de salinité observée. Les larves benthiques prennent de l'importance au printemps et atteignent leur abondance maximale en été dans les zones néritiques. Les larves spionides sont en très grande majorité. Au moins 20 des 31 espèces holoplanctoniques sont océaniques et la majorité d'entre elles sont plus abondantes en hiver et au printemps.

Une espèce (Travisiopsis dubia) *semble être aussi abondante dans la zone néritique interne, dans la zone néritique externe et dans les eaux océaniques et ce, à toutes les saisons. Trois espèces* (Iospilus phalacroides, Phalacrophorus pictus *et* Tomopteris pacifica) *atteignent leur abondance maximale dans la zone néritique de février et mars. Elles dérivent ensuite au-dessus du plateau continental.* Plotohelmis capitata *est plus abondante sur le plateau externe en avril et mai.*

On peut penser que la concentration d'espèces néritiques vers l'intérieur pendant l'été et la concentration ultérieure vers l'extérieur du plateau en automne est liée à la dérive vers le large d'éléments nutritifs importants arrivant des mangroves.

ABSTRACT

In the seas around Nosy-Bé on the northwestern coast of Madagascar the heavy rains in summer (january to March) and the outflow from rivers and swamps produce an estuarine type of circulation. The low salinity surface waters formed in coastal areas in summer drift out over the continental shelf during the autumn. Three environmental areas may thus be distinguished namely the inner neritic, the outer neritic and the oceanic. The distribution of the plankton is related to this.

A total of 307 samples of planktonic polychaetes collected during the year April 1963 to March 1964 were analysed. Some 6347 specimens of holoplanktonic Polychaeta included 31 species of which three are new records. The 5523 larvae of benthic polychaetes were sorted to families.

All samples were collected in timed five minute horizontal tows at 2 m and 10 m, some by day and others by night. A comparison of these samples shows that each species differs in its distribution and diurnal migrations. These differences added to the unequal number of samples of each type made it necessary to devise a new numerical method to simplify the data before seasonal trends in abundance and distribution could be appreciated. The results for each species are presented together with the recorded range of temperature and salinity.

It is concluded that benthic larvae increase in spring and reach maximum abundance in summer in neritic waters. Spionid larvae dominate the collections. At least 20 of the 31 holoplanktonic species are oceanic and the majority of them are most abundant in winter or spring. One species (Travisiopsis dubia) *seems to be equally abundant in the inner neritic, outer neritic and oceanic waters in all seasons. Three species* (Iospilus phalacroides, Phalacrophorus pictus *and* Tomopteris pacifica) *reach maximal abundance in the inner neritic in February to March and then drift out over the outer shelf.* Plotohelmis capitata *is most abundant on the outer shelf in April and May. It is suggested that the concentration of neritic species in the inner shelf during the summer and the later concentration on the outer shelf in autumn is related to the outward drift of rich food supplies derived from the mangrove swamps.*

INTRODUCTION

From 1959 onwards Dr. Serge Frontier and his colleagues have investigated the zoo-plankton in the vicinity of Nosy-Bé off the northwest coast of Madagascar. The main aim was to determine the species composition in the western Indian Ocean, particularly in the Mocambique channel and to study changes in seasonal abundance on the continental shelf. The field work was organised from the "Centre O.R.S.T.O.M., de Nosy-Bé" and most of the results have been published in *Cahiers O.R.S.T.O.M., Océanographie*; this report on the planktonic Polychaeta is part of that series.

As the work proceeded it became evident that there are three fairly distinct planktonic populations around Nosy-Bé. These are an inner neritic population in bays where the salinity is low in summer, an outer neritic population on the open continental shelf where the salinity is higher and an oceanic population off the continental shelf. The distinction between neritic and oceanic plankton is well known but the distinction between the inner and outer neritic has not been so carefully studied before. It is particularly well marked in the Nosy-Bé area where most of the rain falls during the hot summer months with particularly heavy falls in January (Angot 1965). The precipitation on the sea surface added to the outflow from the large rivers into semi-enclosed bays results in the formation of a warm, low salinity surface layer. During February and March the salinity at 2 m falls below 29 ‰ (Binet and Dessier 1968, Frontier 1970). As mixing with the high salinity water of deeper levels proceeds, the surface layer deepens but the salinity within it rises to above 31.6 ‰. These surface waters gradually drift out of the bays over the outer continental shelf so that minimum salinities are recorded there a month later. Eventually the surface layers reach the deep ocean and minimum salinities are recorded there in April to May. During the winter months of July to September, cool high salinity oceanic water above 35 ‰ flows over the shelf as a subsurface current and eventually reaches the bays. The salinity maximum in Ambaro Bay is in October (Binet and Dessier 1968, Frontier 1970). As Frontier has said, the whole pattern of circulation is like that of an estuary with warm low salinity water flowing out at the surface and cool, high salinity water flowing in along the bottom.

Dr. Frontier and his colleagues have worked on several groups of zoo-plankton and shown how their distribution patterns, life histories and seasonal abundance are related to conditions in the inner shelf, the outer shelf and the open ocean. In this paper the reactions of the planktonic Polychaeta will be described.

MATERIAL AND METHODS

Dr. Frontier's assistants sorted the plankton collections to taxonomic groups and he entrusted two collections of planktonic Polychaeta to me. The first was a relatively small collection made between October and December 1960. A taxonomic account of this and other collections from the Mocambique channel, the Agulhas current, the south western Indian Ocean and the Benguela current was published in Day (1967). The second collection was much larger and more important. It consisted of 324 samples collected at fairly regular intervals through a whole year from April 1963 to March 1964. Some of the samples were collected with a coarse "000 net"

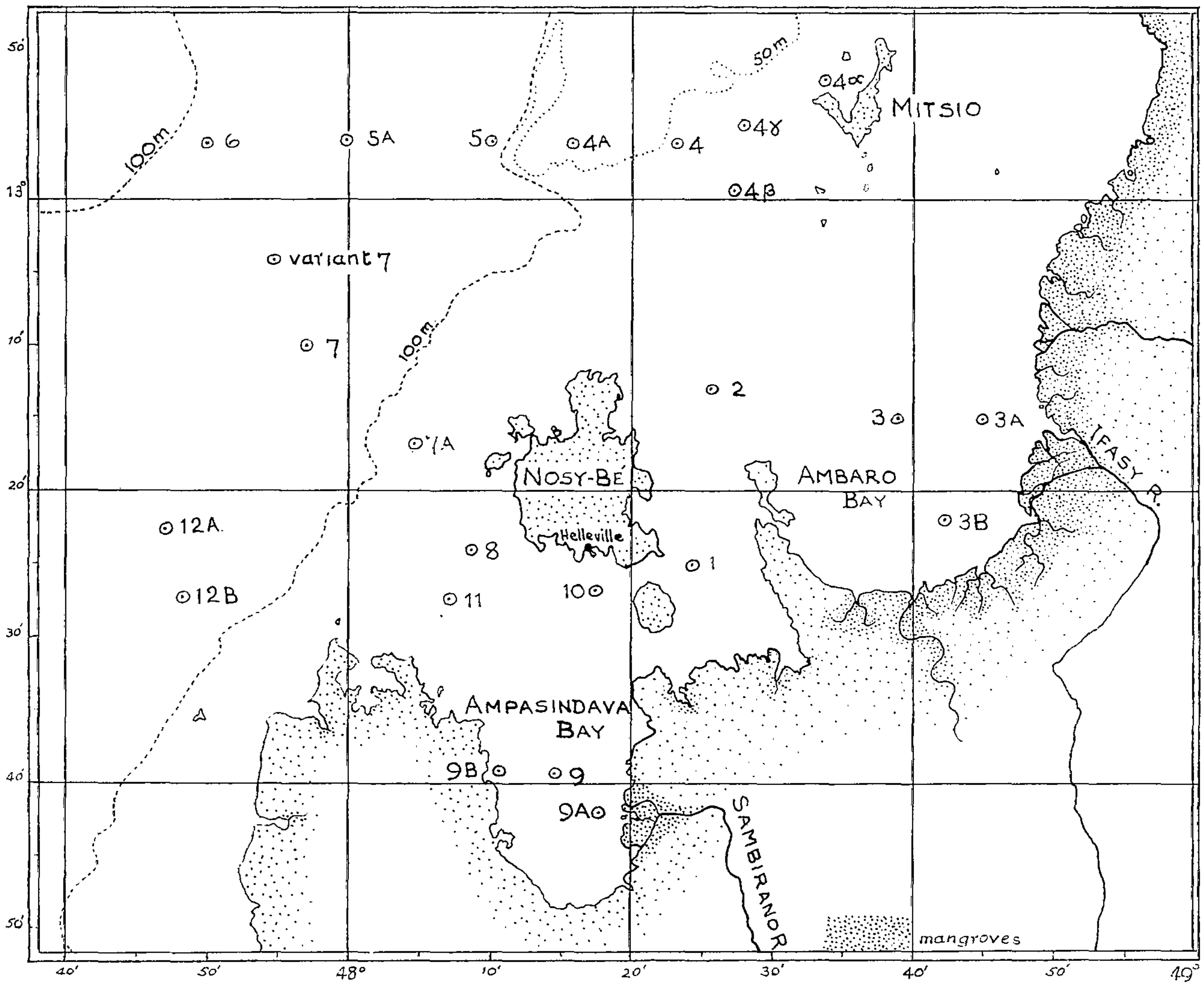

Fig. 1. — Location of plankton stations around Nosy-Bé occupied in 1963-64.

designed to catch fish eggs and not a representative sample of small polychaetes. These were omitted and one or two other samples were lost leaving a total of 307. These had all been taken in horizontal tows for five minutes with a "Tregouboff net". This net is fully described by TREGOUBOFF and ROSE (1957) and consists of a 4,5 m long net, 1 m in diameter at the mouth and includes four sections with mesh sizes of 81, 625, 1115 and 3500 meshes per cm². It obviously does not give absolute densities in numbers of organisms per m³ of water filtered but it does catch a wide range of planktonic organisms from large to very small and, as all the samples were taken with this net, they are comparable with one another.

The majority of the plankton samples were taken at principal stations. During the course of the year however a number of intermediate and variant stations were introduced so that the total number of stations is 24. The location of all these is shown in Figure 1.

TABLE 1

Numbers of samples collected in each area per month. (Day samples at 2 m and 10 m shown as D2 and D10; night samples at 2 m and 10 m shown as N2 and N10.)

Month	Inner Neritic			Outer Neritic				Oceanic				Monthly Totals
	D2	D10	N	D2	D10	N2	N10	D2	D10	N2	N10	
Apr. 1963	4	4	0	3	3	3	1	1	1	3	1	24
May	4	3	0	7	5	3	3	2	2	4	3	36
June	4	4	0	2	2	2	1	3	3	3	2	26
July	12	3	0	6	4	3	1	2	2	2	1	36
Aug	4	2	0	3	3	3	1	2	2	2	1	23
Sept	4	2	0	4	4	4	1	2	2	2	1	26
Oct	4	2	0	2	2	5	2	2	2	2	1	24
Nov	4	2	0	3	3	2	1	0	0	0	0	15
Dec	5	2	0	3	3	3	1	2	2	2	1	24
Jan 1964	8	1	0	3	3	3	1	2	2	2	1	27
Feb	4	2	0	3	3	0	0	0	0	0	0	12
Mar	6	2	0	2	2	7	2	4	4	4	2	35
Year's total.....	63	29	0	41	37	38	15	22	22	26	14	307

In this paper the stations are grouped as follows :

Inner Neritic	Stations 1, 2, 3, 3A, 9, 9A, 9B.
Outer Neritic	Stations 4, 4A, 4α, 4β, 4γ, Pt Mitsio, 7A, 8, 10, 11.
Oceanic	Stations 5, 5A, 5B, 6, 7, Variant 7, 12A, 12B.

This grouping is very similar to that adopted by FRONTIER but as he notes, the boundaries of the three planktonic populations are not sharply defined and shift with the seasons. Stations 1, 2 and 10 are in FRONTIER's transition zone between the inner and outer neritic. Stations 1 and 2 are not in bays but the surface salinities are rather low and the stations were seldom occupied. Station 10 has fairly high summer salinities and as its planktonic population is more similar to that at Stations 8 and 11 than that at station 9, 9A or 9B it was included in the outer neritic group. Station 5 is in the oceanic group but it is very close to the continental margin and appears to be affected at times by shelf water. The planktonic population there is very rich and further work may show that this due to "shelf edge water" in which upwelling occurs.

The plankton samples collected at these three groups of stations were all five minute horizontal tows some at 2 depth and some at 10 m. Some were collected during the day and some at night. Moreover due to bad weather and other reasons it was not always possible to collect the same number of day and night samples. Thus no samples from oceanic stations were collected in November or February and no night samples were collected at all from inner neritic stations. The monthly record of samples is shown in Table 1.

The planktonic polychaetes in each sample were identified to species and the numbers recorded. As was expected, the numbers from neighbouring stations varied due to "patchiness" and the numbers from day and night and from 2 m and 10 m tows varied due to diurnal vertical migrations. Thus a direct comparison of the numbers in different samples would lead to fallacious conclusions. Moreover as the aim of the whole analysis was to determine the seasonal changes in abundance from one area to another some simplification of the data necessary. As a first step it was decided that the numbers of each species from similar samples for all stations in each area should be summed season by season and expressed as the number of specimens divided by the number of samples. This reduced the data to a table of 40 bits of information and reduced the effect of patchiness. An example is shown in Table 2. From this the total number of specimens taken in the year in each type of sample was obtained and the ratios of specimens per sample type were calculated. These ratios immediately indicate the different densities at the 2 m and 10 m levels and the changes in concentration from day to night and from one area to another. But the data are still too complex to determine seasonal changes and they were simplified step by step. First the variability due to different numbers of samples in each season was eliminated by adjusting the numbers of specimens in each set to the number per 10 samples. The numbers from 2 m were then converted to the number from 10 m using the ratios that had been calculated. The sum of the original number at 10 m plus that calculated from the 2 m sample gave the number per 20 samples as shown in the middle of Table 2. Next the night samples were converted to day samples using the ratios calculated earlier and when these were added to the original day samples the number of specimens per 40 day samples was obtained. Finally as there were no night samples from the inner neritic, there were only 20 samples there as compared to 40 samples from outer neritic and oceanic areas; all values were therefore reduced to the number of specimens that would be obtained from 10 daylight samples at 10 m. All stages of the computation are shown in Table 2 and at the end it may be seen that the original table of 40 bits of information has been reduced to 12 bits. The seasonal changes in abundance from one area to another may now be deduced.

TABLE 2

Method of numerical analysis using the data of *Plotohelmis capitata*.

	Inner Neritic			*Outer Neritic*				*Oceanic*			
	D2	D10	N	D2	D10	N2	N10	D2	D10	N2	N10
Numbers of specimens / number of samples											
Aut.	114/12	82/11	—	10/12	128/10	48/2	21/5	7/6	0/6	28/10	11/6
Win.	24/20	92/7	—	87/13	97/11	12/10	3/3	4/6	4/6	30/6	19/3
Spr.	1/13	25/6	—	0/8	6/8	954/10	78/4	2/4	11/4	21/4	9/2
Sum.	1/18	3/5	—	102/8	53/8	220/10	11/3	0/6	0/6	9/6	4/3
Year's totals	140/63	202/29	—	199/41	266/37	1234/38	113/15	13/22	15/22	88/26	43/14
Ratios	2.22	6.96	—	4.85	7.19	32.5	7.53	0.59	0.68	3.38	3.07

Adjusting to number of specimens per 20 samples at 10 m.

Example 114 specimens in 12 samples at 2 m in inner neritic in autumn=95 in 10 samples.

Ratio of 2 m to 10 m samples is 2.22 : 6.96 ∴ 95 at 2 m=297.8 at 10 m

82 specimens in 11 samples at 10 m=74.5 in 10 samples.

Total specimens in 20 samples at 10 m=297.8+74.5=372.3

Similarly for all sets of data:

Aut.	372.3	140.4	55.8	13.4	43.8
Win.	169.1	171.0	12.8	14.4	108.7
Spr.	44.1	7.5	414.7	33.3	92.7
Sum.	10.8	255.3	87.3	0	27.0

Adjusting night to day samples and adding to give numbers of specimens per 40 samples.

Example 55.8 specimens per 20 night samples in outer neritic in autumn.

Ratio of night to day samples is 7.53:7.19 ∴ Number is $55.8/_{7.53} \times 7.19 = 53.3$

140.4 specimens recorded in 20 day samples ∴ total in 40 day samples=53.3+140.4=193.7

Reducing all values to numbers in 10 daylight samples.

(NB no night samples in inner neritic).

Aut.	186.2	48.4	5.8
Win.	84.6	45.8	9.6
Spr.	22.0	100.9	13.5
Sum.	5.2	84.7	1.5

It is obvious that this is not the only method of simplifying the data. It was suggested that an analysis of variance might be used to convert 2 m samples to 10 m samples but the data were too incomplete for this method to be used. It is also theoretically possible to use seasonal rather than yearly ratios for the conversions. But certain of the seasonal ratios are missing and for many species the numbers are too small to give reliable results. It is realised that the method has serious limitations and for this reason only qualitative and not numerical conclusions have been derived from the analyses. It will be ovious too that many bits of information contained in the original sample records have been lost by this method of grouping the data. However, where marked changes have occurred between seasons the monthly records were consulted and where appropriate, these have been included in the conclusions.

TAXONOMY

All the 31 species identified from the collections made by Dr. Frontier in 1960 and 1963-64 have been described by Day (1967) and all except three of them were recorded from the Mocambique Channel. The three new records are *Iospilus phalacroides*, *Vanadis formosa* and *Tomopteris pacifica*.

All of them are listed below and a reference to the description in Day (1967) is included for convenience. Further descriptions and synonymies will be found in Dales and Peter (1972) and Orensanz and Ramirez (1973).

Family Lopadorhynchidae

Lopadorhynchus (Prolopadorhynchus) henseni Reibisch 1893

Day 1967: 161, fig. 5.6.e-c.
Remarks: 13 specimens.

Lopadorhynchus krohnii (Claparède 1870)

Day 1967: 159, fig. 5.6. i-k.
Remarks: 43 specimens. Almost all of them are small juveniles which are not easily distinguished from *L. henseni* and some specimens may have been misidentified.

Lopadorhynchus nationalis Reibisch 1895

Day 1967: 162, fig. 5.7. a-c.
Remarks: 9 specimens.

Maupasia caeca Viguier 1886

Day 1967: 164, fig. 5.7. m-o.
Remarks: 37 specimens.

Maupasia gracilis (Reibisch 1895)

Day 1967: 164, fig. 5.7. j-i.
Remarks: 2 specimens.

Pedinosoma curtum Reibisch 1895

Day 1967: 158, fig. 5.6. a-c.
Remarks: 226 specimens.

Pelagobia longicirrata Greeff 1879

Day 1967: 163, fig. 5.7. f-i.
Remarks: 225 specimens.

Family Iospilidae

Iospilus phalacroides Viguier 1886

Day 1967: 170, fig. 6.1. e-h.
Remarks: 151 specimens. Orensanz and Ramirez (1973) distinguish three species in relation to the sizes of the anterior parapodia and the first appearance of dorsal and ventral cirri. The first few pairs of cirri are rudimentary and even under high power it is difficult to be certain whether they present or not on the first two feet. It is felt that this character alone is insufficient to distinguish *I. affinis* Viguier 1911 from *I. phalacroides* Viguier 1886. All the specimens reported here agree with the description in Day (1967) with the exception that the pigmentation on the dorsum is not in the form of four dark spots per segment but as a continuous black segmental bar.

Phalacrophorus pictus Greeff 1879

Day 1967: 171, fig. 6.1. n-o.
Remarks: 158 specimens.

Phalacrophorus uniformis Reibisch 1895

Day 1967: 171, fig. 6.1. i-m.
Remarks: 284 specimens. In some specimens the change from the first few rudimentary parapodia to the well developed parapodia behind segment 10 is very gradual. It is possible that such specimens have been confused with *P. pictus*.

Family Pontodoridae

Pontodora pelagica Greeff 1879

Day 1967: 167, fig. 6.1. a-d.
Remarks: Only one specimen of this very rare species was obtained. Although superficially similar to a Spionid larva, it is quite characteristic when carefully examined.

Family Alciopidae

Alciopina parasitica Claparède and Panceri 1867

Day 1967: 177, fig. 7.1. a-h.
Remarks: 103 specimens.

Krohnia lepidota (Krohn 1845)

Day 1957: 179, fig. 7.1. i-k.
Remarks: 2 specimens.

Plotohelmis alata (Chamberlin 1919)

Day 1967: 193, fig. 7.5. d-l.
Remarks: 2 specimens.

Plotohelmis capitata (Greeff 1876)

Day 1967: 195, fig. 7.5. j-l.
Remarks: 2432 specimens. This is the most common species in the Nosy-Bé area.

Plotohelmis tenuis (Apstein 1900)

Day 1967: 193, fig. 7.5. a-c.
Remarks : 3 specimens.

Rhynchonerella gracilis Costa 1862

DAY 1967: 189, fig. 7.4. a-d.
Remarks: 17 specimens.

Rhynchonerella petersii (Langerhans 1880)

DAY 1967: 189, fig. 7.3. g-l.
Remarks: 89 specimens.

Torrea candida Della Chiaje 1841.

DAY 1967: 188, fig. 7.3. d-f.
Remarks: 5 specimens.

Vanadis crystallina crystallina Greeff 1876

DAY 1967: 182, fig. 7.2. f-g.
Remarks: One specimen.

Vanadis formosa Claparède 1870

DAY 1967: 181, fig. 7.2. a-e.
Remarks: 7 specimens. This is a new record for the area.

Vanadis minuta Treadwell 1906

DAY 1967: 184, fig. 7.2. k-m.
Remarks: 166 specimens.

Vanadis studeri Apstein 1893

ORENSANZ & RAMIREZ 1873: 39, pl. 5, figs. 1-4.
(As) *Vanadis fuscapunctata*: DAY 1967: 184, fig. 7.2. i-j.
Remarks: 32 specimens. ORENSANZ & RAMIREZ state that *V. fuscapunctata* Treadwell 1906 is a synonym of *V. studeri*. I have not seen Apstein's original description, but that of Orensanz and Ramirez certainly fits the Nosy-Bé specimens.

FAMILY TOMOPTERIDAE

Tomopteris dunckeri Rosa 1908

DAY 1967: 201, fig. 8.1. k-l.
Remarks: 11 specimens.

Tomopteris elegans Chun 1888

DAY 1967: 205, fig. 8.2. c-k.
Remarks: 237 specimens.

Tomopteris nationalis Apstein 1900

DAY 1967: 198, fig. 8.1. a-e.
Remarks: 1 specimen and some doubtful juveniles.

Tomopteris pacifica Izuka 1914

DAY 1967: 199, fig. 8.1. i-j.
Remarks: 598 specimens.

Tomopteris sp.

Remarks: Many juvenile specimens were obtained which could not be assigned to any species with certainty.

FAMILY TYPHLOSCOLECIDAE

Sagitella kowalewskii Wagner 1872

DAY 1967: 212, fig. 9.1. j-i.
Remarks: 508 specimens.

Typhloscolex muelleri Busch 1851

DAY 1967: 208, fig. 9.1. a-b.
Remarks: 981 specimens. This species is neotenic with a general resemblance to a late trochophore stage. The form is very variable and it is possible that the larvae of other Typhloscolecidae may be included with *T. muelleri*. No definite specimens of *T. phyllodes* were identified.

Ecological notes on individual species

FAMILY LOPADORHYNCHIDAE

Lopadorhynchus henseni. No specimens were obtained from October to December 1960, but 13 were obtained in the year 1963-64. Nine were taken in the winter months, three in spring and one in summer. Ten were taken at oceanic stations and three in the outer neritic. All were taken at night. These few records suggest that this species is rare in the Nosy-Bé area. It is an oceanic species which only rises into the surface waters at night. The recorded temperature range was 24.8-29.4 °C and the salinity 33.5-35.2 ‰.

Distribution: tropical and warm N. and S. Atlantic; Agulhas current.

Lopadorhynchus krohnii. Thirty nine specimens were obtained in November 1960 and 5 in June and Septembrer 1963. It occurs in both outer neritic and oceanic areas and is almost restricted to night samples. Almost all the specimens were small juveniles which are not easily distinguished from *L. henseni* and there is some doubt that they are really *L. krohnii*. The recorded temperature range is 25.4-26.2 °C; salinity range 35.0-35.1 ‰.

Distribution: Mediterranean; tropical and S.E. Atlantic; Agulhas Current, S.W. Indian Ocean; Pacific off California.

Lopadorhynchus nationalis. No specimens were recorded from October to December 1960 and only 9 in the year 1963-64; most of these were taken at night in oceanic areas during December. This species is rare in the Nosy-Bé area; it is an oceanic species which occasionally strays into the outer neritic area. The recorded temperature range is 26.2-28.8 °C; salinity range 35.0-35.2 ‰.

Distribution: Mediterranean; tropical Atlantic; Mocambique and Agulhas currents; ? tropical Pacific.

Maupasia caeca. Seven specimens were recorded from October to December 1960, all from night samples in oceanic areas. In 1963-64 a total of 30 specimens were recorded, all except 3 at night and all from oceanic areas; 15 were taken in autumn, 6 in winter, 2 in spring and 7 in summer. This is obviously an oceanic species which is strongly photonegative. Small numbers are present throughout the year in the surface waters of the Nosy-Bé area and they are most common from March to June. The recorded temperature range is 24.8-29.6 °C and the salinity range is 34.1-35.1 ‰.

Distribution: Mediterranean; warm N.E., S.W. and S.E. Atlantic; warm deep current of Sub-antarctic; Mocambique current and S.W. Indian Ocean; N. Pacific.

Maupasia gracilis. No specimens were recorded from October to December 1960 and only two were found in December in oceanic samples during the year 1963-64. This species is very rare in the Nosy-Bé area and is known only from oceanic areas. The recorded temperature range is 28.7-29.1 °C and the salinity range is 35.0-35.2 ‰.

Distribution: Warm and tropical Atlantic; Mocambique and Agulhas currents; South Pacific.

Pedinosoma curtum. Two specimens were recorded at night from an oceanic station in November 1960. In the 1963-64 year 224 were recorded. These were analysed according to the methods described earlier with the following results.

TABLE 3

	Inner Neritic			*Outer Neritic*				*Oceanic*			
	D2	D10	N.	D2	D10	N2	N10	D2	D10	N2	N10
Specimens / Samples	0/63	0/29	—	0/41	1/37	17/38	0/15	5/22	0/22	120/26	81/14
Ratio	0	0	—	0	0.03	0.45	0	0.23	0	4.62	5.79
Numbers per 10 samples at 10 m in daylight.											
Aut.		0	—		0		0		0		70.1
Win.		0	—		0.5		15 at 2 m*		8 at 2 m*		54.5
Spr.		0	—		0		2 at 2 m*		0		92.6
Sum.		0	—		0		0		0		16.5

* No ratios available to convert these 2 m to 10 m values.

It is concluded that *P. curtum* is an oceanic species which occasionally strays into outer neritic waters. It is strongly photonegative and seldom occurs in the 2-10 m layer except at night. In the Nosy-Bé area it is rare in summer but increases rapidly in autumn. In winter it is carried by subsurface currents into the outer neritic but moves back to oceanic areas in spring and at this time it reaches its maximum numbers and then decreases to a minimum in summer. The recorded temperature range is 24.8-29.1 °C and the salinity range is 34.1-35.2 ‰.

Distribution: Mediterranean and warm N. and S. Atlantic; Mocambique and Agulhas currents; S.W. Indian ocean; N. Pacific.

Pelagobia longicirrata. There are no records for October to December 1960. In the year 1963-64, a total of 225 was recorded. An analysis gave the following results:

TABLE 4

	Inner Neritic			*Outer Neritic*				*Oceanic*			
	D2	D10	N	D2	D10	N2	N10	D2	D10	N2	N10
Specimens / Samples	0/63	2/29	—	9/41	9/37	6/38	1/15	31/22	27/22	91/26	68/14
Ratio	0	0.07	—	0.22	0.24	0.16	0.07	1.41	1.23	3.50	4.86
Numbers per 10 samples at 10 m in daylight.											
Aut.		0			0				19.5		
Win.		0			3.0				9.7		
Spr.		0			2.2				12.0		
Sum.		1.0			4.7				10.3		

It is concluded that *P. longicirrata* is an oceanic species but is occasionally found in neritic waters even reaching coastal areas. It occurs in the 2 m-10 m level during the day and night but is more common at the 10 m level and in oceanic areas it is two to three times more common at night. In the Nosy-Bé area it occurs throughout the year. In the autumn it is confined to oceanic waters but during the winter and spring it spreads into the outer neritic and occasional specimens even reach the inner neritic. There is no marked change in numbers through the year. Recorded temperature range 25.3-29.8 °C; salinity range 33.6-35.2 $^{0}/_{00}$.

Distribution: In all the world's oceans and very common in cold seas.

Family Iospilidae

Iospilus phalacroides. There are no records for October to December 1960. In the year 1963-64 a total of 151 was recorded. An analysis gave the following results:

Table 5

	Inner Neritic			*Outer Neritic*				*Oceanic*			
	D2	D10	N	D2	D10	N2	N10	D2	D10	N2	N10
Specimens / Samples	39/63	5/29	—	42/41	8/37	38/38	18/15	1/22	0/22	0/26	0/14
Ratios	0.62	0.17	—	1.02	0.22	1.00	1.20	0.05	0	0	0
Aut.		0			0.9				0		
Win.		0			0				0		
Spr.		0			0				0		
Sum.		7.95			10.15			0.50 (no conversion factor)			

It is concluded that *Iospilus phalacroides* is a neritic species. In the 2 m-10 m layers it is slightly more common at night than during the day. In the Nosy-Bé area it appears in inner neritic areas at the end of January, spreads over the continental shelf in February and reaches maximum density in March when a few drift into oceanic areas. There is a sharp decline in autumn and the species is not present in the surface layers during winter and spring. Recorded temperature range 27.6-31.5 °C; salinity range 19.8-34.7 $^{0}/_{00}$. The wide salinity tolerance is an obvious adaptation to inner neritic conditions.

Distribution: Mediterranean; S. Pacific, Agulhas Current and S. W. Indian Ocean, Benguela Current.

Phalacrophorus pictus. There are no records from October to December 1960. In the year 1963-64 a total of 158 specimens was recorded. An analysis gave the following results:

Table 6

	Inner Neritic			*Outer Neritic*				*Oceanic*			
	D2	D10	N	D2	D10	N2	N10	D2	D10	N2	N10
Specimens / Samples	21/63	17/29	—	25/41	21/37	36/38	13/15	8/22	10/22	5/26	2/14
Ratios	0.33	0.59	—	0.61	0.57	0.95	0.87	0.36	0.45	0.19	0.14
Numbers per 10 daylight samples at 10 m											
Aut.		0.8			2.2				2.0		
Win.		1.5			1.5				2.9		
Spr.		0			0.6				7.0		
Sum.		26.1			20.4				8.6		

It is concluded that *Phalacrophorus pictus* is more common in neritic than oceanic waters and in the 2 m to 10 m layer it is equally common by day and night. In the Nosy-Bé area small numbers are widely distributed in autumn and winter but in spring it is rare on the continental shelf but more common in oceanic waters. In summer maximal numbers are present in the inner and outer neritic areas. The recorded temperature range is 25.1-31.5 °C and the salinity range is 19.8-35.3 $^{0}/_{00}$. The wide salinity tolerance allows the species to live in an estuary type environment.

Distribution: Warm and temperate waters in all oceans.

Phalacrophorus uniformis. Four specimens were recorded in 1960, one in October and three in December, all of them at night. In the year 1963-64 the total was 277. An analysis of this total gave the following results:

TABLE 7

	Inner Neritic			Outer Neritic				Oceanic			
	D2	D10	N	D2	D10	N2	N10	D2	D10	N2	N10
Specimens / Samples	3/63	3/29	—	5/41	8/37	63/38	30/15	22/22	31/22	95/26	23/14
Ratios	0.05	0.10	—	0.12	0.22	1.66	2.00	1.00	1.41	3.65	1.64
Numbers per 10 daylight samples at 10 m.											
Aut.		0			0.4				13.1		
Win.		0			1.4				22.3		
Spr.		0			3.1				9.0		
Sum.		3.2			4.5				19.1		

It is concluded that this species is at least three times as abundant in oceanic waters as it is in neritic areas. It is also photonegative and at least twice as common in the 2 m-10 m layer at night than in daylight and in daylight it is more common at 10 m than 2 m. In the Nosy-Bé area it is present throughout the year. Fair numbers occur in autumn in oceanic areas. There is a considerable increase in winter but in spring oceanic samples show a sharp drop. Maximum concentrations are found in summer and at this time only the species penetrates close inshore. The temperature range is 24.8-30.6 °C and the salinity is 32.4-35.6 ‰. It will be noted that the salinity range is small which may account for its limited penetration into the inner neritic.

Distribution: Tropical and warm Atlantic; Agulhas and Mocambique currents; S.W. Indian Ocean; tropical and warm S. Pacific.

FAMILY PONTODORIDAE

Pontodora pelagica. Only as single specimen of this rare species was obtained. It occurred in December 1963 at 10 m in oceanic water at night. The temperature was 28.48 °C and the salinity was 35.21 ‰.

Distribution: Warm N. and S. Atlantic; Mocambique and Agulhas currents.

FAMILY ALCIOPIDAE

Alciopina parasitica. In 1960 a single specimen was obtained at night during October from the outer neritic area. In the year 1963-1964 a total of 102 specimens was recorded. An analysis of this total gave the following results:

TABLE 8

	Inner Neritic			Outer Neritic				Oceanic			
	D2	D10	N	D2	D10	N2	N10	D2	D10	N2	N10
Specimens / Samples	0/63	1/29	—	0/41	2/37	17/38	4/15	2/22	5/22	45/26	29/14
Ratios	0	0.03	—	0	0.05	0.40	0.27	0.09	0.23	1.73	2.07
Number per 10 dayligfft samples at 10 m.											
Aut.		0			0.3				1.8		
Wint.		0.7			0.3				2.2		
Spr.		0			0.1				0.8		
Sum.		0			0.9				3.8		

It is concluded that *A. parasitica* is an oceanic species but small numbers occur in neritic waters. It is strongly photonegative and is seldom taken in surface layers by day and then mainly by 10 m horizontal tows; at night however it rises to 2 m. In the Nosy-Bé area a few are found throughout the year. In autumn the numbers are lower than the mean for the year but in winter it is more common and a few individuals are carried by subsurface currents into the inner neritic. In spring there is a marked decline and the numbers remain very low until February. In March however there is a very rapid increase to the maximum for the year. The recorded temperature range is 24.7-29.6 °C and the salinity range is 34.1-35.2 °/₀₀.

Distribution: Warm N. and S.W. Atlantic and Mediterranean; tropical Indian Ocean, Mocambique and Agulhas currents to S.W. Indian Ocean; widespread in the Pacific but not along the California coast.

Krohnia lepidota. This species is rare in the surface layers around Nosy-Bé and only two specimens were obtained. One was taken off Hellville (Nosy-Bé) in October 1960 in the evening at 3 m and the other in the inner neritic in June 1963 in daylight at 2 m. The recorded temperature is 27.6° and the salinity 33.7 °/₀₀.

Distribution: Mediterranean; tropical and S.E. Atlantic; Mocambique and Agulhas currents to S.W. Indian Ocean; tropical and S. Pacific.

Ptotohelmis alata. This is a rare species; only two specimens were recorded around Nosy-Bé. One was taken off Hellville (Nosy-Bé) in October 1960 at night and the other in June 1963 at night in the oceanic area at 2 m. The recorded temperature is 26.2 °C and the salinity is 35.0 °/₀₀.

Distribution: Mocambique current; tropical and subtropical Pacific.

Ptotohelmis capitata. This is the most common species in the Nosy-Bé area. In 1960, 119 specimens were taken from October to December and in the year 1963-64 a total of 2313 was recorded. An analysis of the 1963-64 records gave the following results:

TABLE 9

	Inner Neritic			Outer Neritic				Oceanic			
	D2	D10	N	D2	D10	N2	N10	D2	D10	N2	N10
Specimens	140	202	—	199	266	1234	113	13	15	88	43
Samples	63	29		41	37	38	15	22	22	26	14
Ratios	2.22	6.96	—	4.85	7.19	32.47	7.53	0.59	0.68	3.38	3.07
Numbers per 10 daylight samples at 10 m.											
Aut.		186.2			48.4				5.8		
Win.		84.2			45.8				9.6		
Spr.		22.0			100.9				13.5		
Sum.		5.2			84.7				1.5		

It is concluded that *P. capitata* is primarily a neritic species which is common in surface waters even in daylight but is more common at 10 m than 2 m and even more common at the surface at night. In the Nosy-Bé area it is present throughout the year. Maximum numbers occur in autumn in the inner neritic zone but the concentration there declines in winter and in spring they drift into outer neritic where swarming and reproduction occurs. In summer there is a further decline in inner neritic and oceanic areas but fair concentrations remain in the outer neritic and it is possibly the inward drift of this population that gives rise to the concentration in coastal waters in the following autumn. The recorded temperature range is 24.8-29.8 °C and the salinity is 32.4-35.4 °/₀₀. Swarming occurred in December in the outer neritic in temperatures of 28.4°-28.6 °C and a salinity of 35.0-35.1 °/₀₀.

Distribution: Warm N. and S.W. Atlantic and Mediterranean; Mocambique and Agulhas current; S.W. Indian Ocean; ? Japan.

Ptotohelmis tenuis. Three specimens were obtained; one in November 1960 at night from the outer neritic at the surface, one in June 1963 during the day from the inner neritic at 10 m. The recorded temperature range is 25.8-27.6 °C and the salinity 33.7-35.1 °/₀₀.

Distribution: Tropical and subtropical S. Atlantic; Mediterranean; Mocambique and Agulhas currents; Pacific off California.

Rhynchonerella gracilis. No specimens were obtained during October to December 1960 and only 17 were recorded during the year 1963-64; 2 in May, 3 in June, 1 in August and 11 in September. Fourteen of the specimens were taken at night and all except one from oceanic stations. The recorded temperature range was 24.8-29.3 °C and the salinity was 34.8-35.1 °/₀₀.

Distribution: Warm N. and S.W. Atlantic; Mediterranean; Mocambique and Agulhas currents; S.W. Indian Ocean; Pacific off Japan.

Rhynchonerella moebii. One doubtful specimen was obtained in October 1960 and six were definitely identified in the year 1963-64, five in June at night and one in December in daylight at 10 m. All were obtained from oceanic areas. The recorded temperature range was 26.2-28.8 °C and the salinity was 35.0-35.1 °/₀₀.

Distribution: Warm N. Atlantic; Mediterranean; Mocambique and Agulhas currents; tropical and subtropical Pacific.

Rhynchonerella petersii. Five specimens were obtained from outer neritic and oceanic areas in October and November 1960 and a total of 84 was recorded in the year 1963-64. An analysis of the 1963-64 records gave the following results:

TABLE 10

	Inner Neritic			*Outer Neritic*				*Oceanic*			
	D2	D10	N	D2	D10	N2	N10	D2	D10	N2	N10
Specimens / Samples	0/63	0/29	—	0/41	0/37	3/38	4/15	0/22	0/22	37/26	40/14
Ratios	0	0	—	0	0	0.08	0.27	0	0	1.42	2.86
Numbers per 10 night samples at 10 m. (Note: no ratios are available to convert to daylight samples.)											
Aut.		0			0		2.1				15.1
Win.		0			0		10.0				47.6
Spr.		00			0		0				67.7
Sum.		0			0		0				6.7

It is concluded that *R. petersii* is strongly photonegative and is absent from the 2 m-10 m layers during the day; even at night it is less common at 2 m than 10 m. It is an oceanic species but at times a few stray over the outer shelf. In the Nosy-Bé area maximum numbers occur in spring in oceanic areas. There is sharp reduction to minimum numbers in summer and then a gradual increase in autumn and winter during which seasons the species spreads over the outer shelf. The recorded temperature range is 24.8-29.0 °C and the salinity range is 34.1-35.2 °/₀₀.

Distribution: Warm N. to S. Atlantic; Mediterranean; Mocambique and Agulhas currents; S.W. Indian Ocean; tropical W. Pacific.

Torrea candida. Only 5 specimens were obtained; one juvenile in October 1960, one in July 1963 and three in December 1963. All were obtained at oceanic stations, one at 10 m in daylight and 4 at night. The recorded temperature range is 25.6-28.5 °C and the salinity is 35.1-35.2 °/₀₀.

Distribution: Warm N. and S.W. Atlantic; Mediterranean; tropical Indian Ocean; Agulhas Current; warm N.W. Pacific from the China Sea and S. Japan.

Vanadis crystallina crystallina. Only one specimen was obtained in November 1960. It was taken in a surface tow at night in the outer neritic area.

Distribution: Mediterranean; warm and tropical Atlantic and Pacific oceans; Mocambique and Agulhas currents to S.W. Indian Ocean; Agulhas currents and S.W. Indian Ocean.

Vanadis formosa. No specimens were obtained in 1960 and only seven from July to October 1963. All were taken in oceanic areas, four at night and three in daylight at 10 m. The recorded temperatures ranged from 24.8-26.3 °C and the salinities from 35.0-35.2 °/₀₀.

Distribution: Mediterranean; tropical and subtropical Atlantic and Pacific Oceans.

Vanadis longissima. Five specimens were obtained in October and November 1960. All were obtained at night in the outer neritic area. During the year 1963-64 14 specimens were obtained at night, 13 at oceanic stations and one in the outer neritic. The records are spread all through the year indicating that there is a small but stable population around Nosy-Bé. The species is obviously photonegative. Recorded temperatures range from 25.4-28.7 °C and the salinities from 34.4-35.2 °/₀₀.

Distribution: Warm north to south Atlantic; tropical Indian Ocean and Agulhas currents; Pacific off California.

Vanadis minuta. Fourteen specimens were obtained at night in October and November 1960. All were from stations in the outer neritic. During the year 1963-64 a total of 152 was obtained. An analysis of these records gave the following results:

TABLE 11

	Inner Neritic			Outer Neritic				Oceanic			
	D2	D10	N	D2	D10	N2	N10	D2	D10	N2	N10
Specimens / Samples	0/63	0/29	—	0/41	2/37	20/38	5/15	7/22	4/22	88/26	26/14
Ratios	0	0	—	0	0.05	0.53	0.33	0.32	0.18	3.38	1.86
Numbers per 10 daylight samples at 10 m.											
Aut.		0			0.6				2.4		
Win.		0			0.7				2.5		
Spr.		0			0				1.0		
Sum.		0			0				0.5		

It is concluded that *V. minuta* is primarily an oceanic species but spreads into the outer neritic area at times. It is strongly photonegative and is about ten times more common in the surface layers at night than it is in daylight and then it does not reach the 2 m level. In the Nosy-Bé area the maximum concentrations occur in autumn and winter, mainly in oceanic areas. Numbers fall to less than half in spring and minimum numbers occur in summer. The recorded temperatures range from 24.8-29.6 °C and the salinities from 34.1-35.2 ‰.

Distribution: Tropical to subtropical S.W. Atlantic; Mocambique and Agulhas currents to the S.W. Indian Ocean; tropical Pacific off Hawaii and probably off S. California.

Vanadis studeri. Three specimens were recorded from October to December 1960 and 29 in 1963-64. All were obtained in night samples. About equal numbers were obtained from outer neritic and oceanic waters but none were recorded from the inner neritic. Only one specimen was obtained in summer, fair numbers appeared in autumn and reached a maximum in winter and thereafter numbers decreased in spring. It is concluded that *V. studeri* is primarily an oceanic species and rather rare in the surface waters of the Nosy-Bé area. It drifts into outer neritic areas with subsurface oceanic currents in autumn and decreases in spring and summer as the rainy season develops and the outflow of estuaries decreases the salinity. Recorded temperature range 24.8-29.5 °C; salinity 34.1-35.2 ‰.

Distribution: Tropical Pacific (Hawaii); off Argentina; Agulhas and Mocambique currents; off W. Australia.

FAMILY TOMOPTERIDAE

Tomopteris dunckeri. No specimens were obtained in October to December 1960 and only 11 in the year 1963-64. All of them were collected at night in oceanic waters. The few records were spread fairly evenly in all four seasons. This species appears to be exclusively oceanic and is rare in the surface layers near Nosy-Bé. Recorded temperature range 25.4 °C-29.3 °C; salinity range 34.6-35.1 ‰.

Distribution: Red Sea; tropical Indian Ocean; Mocambique and Agulhas currents.

Tomopteris elegans. A total of 21 specimens were recorded in November 1960 and a further 216 were recorded in the year 1963-64. An analysis of the 1963-64 records gave the following results:

TABLE 12

	Inner Neritic			Outer Neritic				Oceanic			
	D2	D10	N	D2	D10	N2	N10	D2	D10	N2	N10
Specimens / Samples	0/63	1/29	—	3/41	0/37	1/38	1/15	0/22	0/22	40/26	168/14
Ratios	0	0.03	—	0.07	0	0.03	0.07	0	0.09	1.54	12.0
Numbers per 10 daylignt samples at 10 m.											
Aut.		0.05			0				0.09		
Win.		0			?0.2				0.70		
Spr.		0			0				1.40		
Sum.		0			?1.0				0		

Note: The winter and summer values for the outer neritic are merely guesses since the ratios to convert day to night samples and 2 to 10 m samples are unknown in this area. It is evident that *T. elegans* is primarily an oceanic species which is only in the surface layers at night. It appears in small numbers in autumn, a few spread into the outer neritic in winter possibly with the inflow of oceanic water over the shelf at this time. In the spring it is restricted to oceanic areas but its numbers then increase to a maximum and then decrease to a minimum in summer. Recorded temperature range: 24.8-28.7 °C; salinity range 34.1-35.2 ‰.

Distribution: World-wide in temperate and tropical seas; temperate N. Atlantic to the subtropical convergence; Mediterranean; tropical Indian Ocean Mocambique and Agulhas currents; warm N. Pacific from Japan to California.

Tomopteris nationalis. Only one definite record taken at night from oceanic water in June 1963; recorded temperature 26.0 °C, salinity 35.07 ‰.

Distribution: Mediterranean; tropical and subtropical Atlantic; Mocambique and Agulhas currents; off S. California.

Tomopteris pacifica. In 1960 only 13 specimens were obtained, all from outer neritic areas, 11 in October and one each in November and December. In the year 1963-64, 585 specimens were recorded. An analysis of these records is shown below:

TABLE 13

	Inner Neritic			*Outer Neritic*				*Oceanic*			
	D2	D10	N	D2	D10	N2	N10	D2	D10	N2	N10
Specimens / Samples	95/63	79/29	—	125/41	176/37	43/38	42/15	0/22	3/22	16/26	6/14
Ratios	1.51	2.72	—	3.05	4.76	1.13	2.80	0	0.14	0.62	0.43
Numbers per 10 daylight samples from 10 m.											
Aut.		36.8			18.7				0.2		
Win.		8.1			1.8				1.9		
Spr.		28.3			11.0				1.5		
Sum.		41.5			179.4				1.3		

It is concluded that *T. pacifica* is a common neritic species although small numbers occur in oceanic waters throughout the year. In neritic areas it is evident that this species is more abundant in the surface layers in daylight than at night but it prefers the 10 m to the 2 m layer; in oceanic areas the reverse is true and it tends to come to the surface at night possibly due to the greater clarity of oceanic water. In winter there are only small numbers present and the main concentration is in the inner neritic; in spring there is a rapid increase and this continues into the summer. In February the main concentration starts to move offshore and by March (the end of summer) the maximum abundance is in the outer neritic. In autumn, numbers decrease rapidly in the outer neritic until the winter minimum is reached. Recorded temperature range 25.4-31.4 °C; salinity range 19.8-35.5 ‰.

Distribution: Japan and cool N. Pacific to California; Agulhas current.

FAMILY TYPHLOSCOLECIDAE

Sagitella kowalewskii. During October to December 1960, 24 specimens were taken at night in outer neritic and oceanic waters. In the year 1963-64 a total of 119 was recorded. These are analysed below:

TABLE 14

	Inner Neritic			*Outer Neritic*				*Oceanic*			
	D2	D10	N	D2	D10	N2	N10	D2	D10	N2	N10
Specimens / Samples	0/63	0/29	—	0/41	1/37	6/38	2/15	4/22	13/22	46/26	47/14
Ratios	0	0	—	0	0.03	0.16	0.13	0.18	0.59	1.77	3.36
Numbers per 10 daylight samples from 10 m											
Aut.		0			0.05				4.0		
Win.		0			0.1				4.2		
Spr.		0			0.4				20.4		
Sum.		0			0.3				0		

It is concluded that *S. kowalewskii* is primarily an oceanic species; a few specimens drift over the outer shelf but the species is absent from inner neritic waters. It is only common in the surface layers at night and always prefers the 10 m layer. Minimum numbers occur in summer; there is a marked increase in oceanic areas at the end of autumn (June) and numbers remain stable over the winter. They start increasing at the beginning of spring (October). No samples were taken in oceanic areas during November but the December samples show the maximum concentration for the whole year. The decline is equally abrupt and only a single specimen was found in the whole of summer. Recorded temperature range: 24.8-29.3 °C; salinity 34.8-35.2 °/oo.

Distribution: Temperate to tropical Atlantic and Pacific; Mediterranean; Mocambique and Agulhas currents to S.W. Indian Ocean.

Travisiopsis dubia. Five specimens were taken at night in outer neritic and oceanic waters in October to December 1960. In the year 1963-64 a total of 503 was recorded. These records are analysed below:

TABLE 15

	Inner Neritic			Outer Neritic				Oceanic			
	D2	D10	N	D2	D10	N2	N10	D2	D10	N2	N10
Specimens / Samples	44/63	75/29	---	79/41	67/37	133/38	49/15	12/22	45/22	68/26	31/14
Ratios	0.70	2.59	—	1.93	1.81	3.50	3.26	0.55	2.05	2.62	2.21
Numbers per 10 daylight samples from 10 m											
Aut.		14.5			6.6				22.9		
Win.		50.0			9.0				29.0		
Spr.		8.5			14.0				31.7		
Sum.		31.5			49.4				11.8		

It is concluded that *T. dubia* is a common species in the surface waters around Nosy-Bé and only slightly less common during the day than at night; in daylight it prefers the 10 m layer and at night it prefers the 2 m layer. It is equally common in all water masses from the inner neritic to the oceanic and there are no very marked seasonal changes but there are rather fewer in autumn. Numbers increase during winter with some dense patches in the inner neritic; in spring there is a decrease inshore but numbers continue to increase elsewhere and finally reach a maximum in late summer in the outer neritic. Recorded temperature range: 24.7-31.4 °C; salinity 19.8-35.6 °/oo.

Distribution: N. Atlantic; Mocambique and Agulhas currents to S.W. Indian Ocean; N. Pacific.

Typhloscolex muelleri. Ten specimens were obtained from October to December 1960; in the year 1963-64 a total of 971 was recorded. These records are analysed below:

TABLE 16

	Inner Neritic			Outer Neritic				Oceanic			
	D2	D10	N	D2	D10	N2	N10	D2	D10	N2	N10
Specimens / Samples	38/63	95/29	—	108/41	125/37	160/38	56/15	48/22	105/22	137/26	99/14
Ratios	0.60	3.28	—	2.63	3.38	4.21	3.73	2.18	4.77	5.27	7.07
Numbers per 10 daylight samples from 10 m											
Aut.		14.1			6.1				15.7		
Win.		83.3			20.2				100.8		
Spr.		21.0			41.5				79.8		
Sum.		15.2			74.9				17.7		

It is concluded that *T. muelleri* is a common species around Nosy-Bé. The largest concentrations are in oceanic waters but it is also common in neritic waters. It is more common in the surface layers at night and in daylight it is more common at 10 m than at 2 m. In all three areas the minimum numbers occur in autumn. In the inner neritic there is a marked increase during winter followed by a decline through spring and summer. In oceanic seas the sequence is similar but in the outer neritic the change is more gradual and the numbers rise progressively through winter and spring to a maximum in summer before falling sharply to the autumn minimum. The recorded temperature range is 24.8-30.6 °C and the salinity range is 31.8-35.6 °/oo.

Distribution: Cosmopolitan apart from the surface waters of the Arctic and Antarctic.

The planktonic larvae of benthic polychaeta

The larval stages in each sample were counted and over the year April 1963 to March 1964 a total of 5523 were recorded which is only slightly less than the 6347 holoplanktonic specimens. The larväe were distributed as shown below:

TABLE 17

	Inner Neritic			*Outer Neritic*				*Oceanic*			
	D2	D10	N	D2	D10	N2	N10	D2	D10	N2	N10
Specimens / Samples	1469	415	—	772	549	1144	251	197	249	372	104
	63	29		41	37	38	15	22	22	26	14
Ratios	23.3	14.3		18.9	14.8	30.1	16.7	8.95	11.3	14.3	7.43
Numbers per 10 daylight samples from 10 m											
Aut.		7.4			26.9				16.3		
Win.		10.1			14.3				62.3		
Spr.		107.4			99.3				100.5		
Sum.		518.9			532.3				306.8		

The ratios show that there is no marked difference between the numbers taken in daylight or night but the numbers at 2 m are larger than those at 10 m. It is possible that individual species of larvae may react differently in the same way as individual holoplanktonic species do but this is not apparent. The seasonal analysis shows the smallest numbers of larvae occur in the autumn; in winter there is an increase in oceanic samples but not in neritic samples. In spring there is a general increase in all three areas and the monthly records show that this is marked from late November. A three to five fold increase occurs in summer with maximum numbers in neritic areas. Monthly records show that this occurs in February and March.

Over the whole year from autumn to the following summer there is roughly a 30-fold increase in the number of benthic larvae in the surface layers. In contrast to this the numbers of holoplanktonic species are spread fairly evenly over all four seasons since different species reach their maximal density at different times. As shown, the larvae are mainly concentrated in neritic areas while holoplanktonic species predominate in oceanic waters. Exceptions to this general rule will be discussed later.

The identification of polychaete larvae to the species level is both laborious and uncertain particularly in the tropical Indian Ocean where the developmental stages of many species are unknown. No attempt was made to identify the species in the Nosy-Bé samples but the common and characteristic families were sorted. By the same token no elaborate numerical analysis was attempted. The ratios of the numbers of specimens to samples in each area during the whole year are shown in Table 18 and the changes from one season to the next in all areas is shown in Table 19.

TABLE 18

Distribution of the larvae of different families in the different areas

Family	Inner Neritic			Outer Neritic				Oceanic			
	D2	D10	N	D2	D10	N2	N10	D2	D10	N2	N10
Polynoidae	0.05	0.24	—	0.02	0.03	1.11	0.47	0.18	0.14	1.31	2.00
Phyllodocidae	0.03	0.24	—	0.34	0.16	0.34	0	1.14	1.64	1.38	0.57
Hesionidae	0.38	0.55	—	1.22	0.49	1.32	0.20	0.41	0.41	0.23	0
Spionidae	18.3	9.24	—	6.85	6.49	14.9	6.60	2.36	1.64	3.42	1.21
Poecilochaetidae	1.33	1.14	—	7.27	4.00	5.61	5.53	1.59	2.18	2.88	0.72
Chaetopteridae	0.06	0	—	0.39	0.62	2.74	1.60	1.00	1.50	0.23	0.43
Terebellidae	0.62	0.59	—	0.24	0.54	0.26	0.20	1.23	2.41	1.96	0.36
All other families	2.10	1.31	—	1.78	2.51	3.05	1.40	1.27	1.55	1.69	1.93

TABLE 19

Seasonal changes of the larvae of different families per sample (Samples of all areas combined)

Family	Autumn	Winter	Spring	Summer	Total larvae
Polynoidae	0.16	0.64	0.63	0.30	130
Phyllodocidae	0.16	0.20	0.73	0.91	147
Hesionidae	0.22	0.21	0.37	1.82	191
Spionidae	0.21	0.14	3.73	37.84	2800
Poecilochaetidae	1.30	0.59	2.81	9.31	1028
Chaetopteridae	0	0	0.21	3.04	238
Terebellidae	0	0.01	0	3.16	235
All other families	0.14	0.44	2.06	5.77	606
All benthic larvae	2.64	2.29	10.46	60.03	5523

It is interesting to see which families predominate in these surface plankton samples. Large numbers of larvae may theoretically be due to several different causes; thus the family may be very common in the area or its larvae may have a long planktonic phase so that they are found over a long period or they may congregate near the surface or produce numerous eggs and thus larvae. Present knowledge is insufficient to decide which factor is important but species with a prolonged larval phase would presumably be common over two or more seasons during which they would drift out from neritic to oceanic waters.

Among the 606 larvae of "all other families" in Table 19 were the sexual buds of Syllids and the larvae of Amphinomids, Nereids, Glycerids, Magelonids and Sabellids and others which were not recognised. None of these were common. Eunicid larvae were not seen at all and as adult Eunicids are common the larvae presumably have a very brief planktonic phase. The larvae of the Arenicolidae are very weak swimmers and would not be expected in surface plankton samples.

The total of 130 Polynoid larvae are spread fairly evenly over the year and tend to be more common in oceanic than neritic samples. The larvae of *Lepidasthenia* was often seen and it is suspected that this genus has a prolonged planktonic existence and often drifts into oceanic waters far from land.

Most of the 147 Phyllodocid larvae were found in spring and summer and they too were relatively common in oceanic waters. Many had a large mass of yolk protruding from the mouth.

The Hesionidae with 191 specimens were more numerous than was expected for the adults are not particularly common in benthic samples; possibly the main concentrations have not been discovered. The majority of the larvae occur in summer on the outer shelf.

The 2800 Spionid larvae form about half of the total larval population showing how abundant the Spionids are in benthic populations. The genus *Polydora* which burrows in coral was very common. About 90 % of the Spionid larvae occurred in summer samples (mainly March) indicating that many species have a restricted breeding season. Spionid larvae are far more common in neritic than oceanic waters.

The 1027 Poecilochaetid larvae represent almost a fifth of the total larval population. Yet adult Poecilochaetids are rare in benthic samples and the characteristic larva was known in European waters long before the adult was found. In these Nosy-Bé samples a wide range of developmental stages was seen in the summer samples but in autumn and winter the larvae were usually large. It is suggested that *Poecilochaetus* has a prolonged larval stage so that it drifts off the continental shelf and is found in oceanic waters far from land.

A total of 238 large and characteristic Chaetopterid larvae were recorded. There were none in autumn and winter, a few in spring and all the rest in summer mainly in outer neritic areas. It would seem that Chaetopterids lay large yolky eggs and have a short breeding season. BHAUD (1969) has shown that the larvae of *Mesochoetopterus sagittarius* are common near Nosy-Bé in February and April with smaller numbers in October. Samples taken at different depths over a 24 hour period show that they are concentrated at the surface during the day and sink down to 20 m or more during the night; further, that larger larvae sink to the deepest levels. He remarks that this downward migration at night is unusual but as shown earlier the means for all types of planktonic larvae indicate that diurnal vertical migrations are not marked. Table 18 shows that Chaetopterid larvae on the outer shelf were more common at night than in daylight but in oceanic waters the reverse was true. It should be noted that these figures include all Chaetopterid larvae and do not refer specifically to *Mesochaetopterus sagittarius*.

CONCLUSIONS

A total of 6347 specimens of holoplanktonic Polychaeta and 5523 larvae of benthic Polychaeta were obtained from 307 plankton tows giving an average of 20.7 holoplanktonic specimens and 18.0 larvae per five minute tow in 2 to 10 m. This confirms the well known fact that polychaetes do not predominate in plankton samples. Wide variations may occur; thus some of the tows contained no polychaetes at all but in others there were up to 532 holoplanktonic specimens or 1040 larvae. The larvae were not identified and the seasonal abundance of the dominant families has been discussed earlier.

There were 31 identified holoplanktonic species, some so rare that only one or two specimens were caught during the whole year and others relatively abundant such as *Plotohelmis capitata* with 2313 specimens, *Typhloscolex muelleri* with 971 and *Tomopteris pacifica* with 585. The 31 species recorded here include three species which were not recorded from the Mocambique Channel by DAY (1967) namely *Iospilus phalacroides*, *Vanadis formosa* and *Tomopteris pacifica* but four others namely *Naiades cantrainii*, *Tomopteris euchaeta*, *Tomopteris septentrionalis* and *Travisiopsis coniceps* which were recorded in the deep waters of the Mocambique current were not found in these shallow surface tows. Planktonic polychaetes like most planktonic organisms are very widely distributed in warm seas. All the species recorded here except *Plotohelmis alata* have been recorded by DAY (1967) from the Agulhas Current or the S.W. Indian Ocean south of Madagascar. *P. alata* appears to be restricted to the tropics and probably other tropical Indian Ocean species will be found near Nosy-Bé when the deeper waters are investigated.

As FRONTIER has shown, the greatest diversity of many zooplankton organisms occurs in oceanic waters and this is confirmed here for planktonic Polychaeta. All 31 species of holoplanktonic polychaetes were recorded in oceanic waters, 23 reached the outer shelf but only 12 were recorded on the inner shelf. Of the species which were sufficiently common to ascertain their centre of maximal abundance 20 were oceanic, one was equally common from the inner shelf to oceanic waters and 4 were most abundant in neritic waters. The six other species were possibly oceanic but their numbers are too small to be certain.

All except one of the species were more common in the surface waters at night but the relative numbers varied greatly, some being exclusively nocturnal while others were almost as common in daylight samples; *Tomopteris pacifica* was actually more common in daylight.

One of the main themes in the investigations which Dr. Frontier and his colleagues have made in the vicinity of Nosy-Bé is an analysis of seasonal changes between inner neritic, outer neritic and oceanic plankton populations. It is of interest to see whether an analysis of planktonic polychaetes agrees with the results obtained from other groups.

Distribution patterns and seasonal changes are obviously related to environmental changes. Most plankton samples are taken with vertical nets and even if the thermal structure and salinity changes in the whole water column is known (which is very seldom), it is impossible to state the exact temperature and salinity at which a particular planktonic species was living. One can merely state the maximum and minimum values in the water column. The great value of Dr. FRONTIER's horizontal plankton tows at 2 m and 10 m is that the salinities and temperatures at these levels were recorded. This has enabled me to state positively for the first time the salinity and temperature range which each species of planktonic polychaete can tolerate. This does not indicate limiting values for in these tropical waters the temperature range is small. All the species recorded here can tolerate tropical surface conditions with temperatures of 28-30 °C and salinities of 34-35 ‰. Many individual species have wider ranges than this. Oceanic species which do not penetrate to the inner neritic zone were only recorded at temperatures up to 29.6 °C and salinities down to 33.5 ‰. Inner neritic species show a wider range of tolerance with temperatures as high as 31.5 °C and salinities as low as 19.8 ‰.

A brief summary of hydrological conditions in the inner neritic, outer neritic and oceanic zones was compiled from the publications of Dr. FRONTIER and his colleagues and presented in the introduction. Recent correspondence with Dr. FRONTIER has provided further details of the bays of Ambaro and Ampasindava which comprise the main part of the inner neritic zone. Dr. FRONTIER states that there are dense mangrove swamps up to 5 km wide around the two large and many small estuaries which flow into Ambaro Bay and smaller swamps around the estuaries in Ampasindava Bay. Work in Florida by HEALD (1971) and LUGO & SNEDAKER (1974) has shown that mangroves are more than four times as productive as a similar area of open sea. The mangrove litter takes more than six months to decay completely and during this time the protein content at first falls as it is eaten by primary consumers and then rises again as the detritus is attacked by nitrogen fixing bacteria. Much of the detritus is carried out to sea and it is suggested that the low oxygen concentrations during March in Ampasindava Bay which were reported by ANGOT (1965) are due to the decay of mangrove detritus. If so, the low salinity surface waters provide a rich food supply for filter feeders during March. The same surface water is known to increase in salinity during April and May as it drifts out over the outer continental shelf into the deep ocean. The whole circulation from the bays to the ocean on the surface and the high salinity return current at deeper levels has been likened by Dr. Frontier to that of an estuary. It is now suggested that the mangroves between tide marks and the sea grasses in the shallows add greatly to the productivity of the system. If this suggestion is valid it could be expected that those filter feeders which can tolerate the low salinities of the inner neritic would reach maximum abundance in February or March while those restricted to the outer neritic would flourish later possibly in March or April.

Holoplanktonic polychaetes are not filter feeders and will be discussed later. The larvae of benthic polychaetes however *are* filter feeders and, as shown earlier, they increase in late November and reach maximal concentrations in March in neritic areas. The main family is the Spionidae whose highest concentration is in the inner neritic. The filter feeders of several other taxonomic groups have been analysed by Frontier and his colleagues. The accounts which deal with whole taxonomic groups are difficult to interpret for they show many irregular changes in abundance with the seasons. As in the case of holoplanktonic polychaetes it is probable that each species has its own environmental requirements and the sum of many species shows no clear spatio-temporal pattern. In contrast to such group analyses, the study of the copepod *Scottula ambariakae* by BINET and DESSIER (1968) shows clearly that it reaches maximum abundance in the inner neritic during February, in the outer neritic in April and in oceanic waters during May. It is tempting to correlate this sequence with the outward drift of the rich mangrove detritus.

Holoplanktonic polychaetes are apparently carnivorous. No plant materials or for that matter animal materials have been identified in their intestines and they are not provided with filter feeding organs. The genus *Phalacrophorus* in the Iospilidae is provided with pointed fangs and some of the Alciopid genera such as *Alciopa*, *Torrea* and *Vanadis* have an eversible pharynx equipped with a pair of prehensile lobes. These presumably catch relatively large prey but the other genera have no obvious prey-catching organs and possibly feed on microscopic prey or eggs in the plankton. As carnivores it would be expected that they would increase later in the season than their filter feeding prey.

The season of maximum abundance of each of the 31 holoplanktonic species was presented earlier and a summary is given below:

TABLE 20

	Season of maximum abundance				Total
	Autumn	Winter	Spring	Summer	
Rare species	Numbers too small to ascertain				6
Species equally common in all areas		doubtful			1
Oceanic species	2	8	8	2	20
Neritic species	1			3	4

No conclusions can be drawn from very rare species or those that are common in all areas. It would seem however that species which are mainly or entirely oceanic in distribution may reach maximum abundance in any season of the year although most of them are abundant in winter or spring. The one neritic species which is most abundant in autumn is *Plotohelmis capitata*. During this season the number of specimens per sample in the inner neritic is 17.6 in April, 7.67 in May and 1.63 in June; in the outer neritic the comparable numbers are 4.80 in April, 11.31 in May and 1.57 in June. Thus the maximum concentration is a month later in the outer neritic and in both areas the minimum numbers are in June.

The monthly records of the three neritic species which are most abundant in summer are summarised below:

TABLE 21

Mean number of specimens per sample

	Inner Neritic			Outer Neritic		
	Jan.	Feb.	Mar.	Jan.	Feb.	Mar.
Iospilus phalacroides...	0.67	1.67	3.50	0	0.33	6.31
Phalacrophorus pictus..	0.50	3.17	1.50	0	1.00	4.62
Tomopteris pacifica...	0.13	4.33	4.88	3.60	3.00	21.20

Iospilus phalacroides is most abundant in the outer neritic. In the inner neritic it is fairly rare in January but increases during February and March; in the outer neritic it first appears in February and reaches maximum abundance in March. *Phalacrophorus pictus* is most abundant in the inner neritic. In this case the main concentration is in February and the numbers decrease in March; in the outer neritic small numbers first appear in February and the sudden increase is in March. *Tomopteris pacifica* is most abundant in the outer neritic. In the inner neritic small numbers are present in January but they increase markedly in February and March. In the outer neritic fair concentrations are present in January and February but these increase to very large concentrations in March.

From all these data it is evident that these three neritic species show a progressive increase during the summer months in the inner neritic and that the main concentrations in the outer neritic appear later in the season. It it suggested that these changes are related to the outward drift of food supplies from the mangrove swamps along the coasts.

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