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Euphausiids of the equatorial and south tropical Pacific Ocean: Zoogeography, ecology, biology, and tropic relationships

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EUPHAUSIIDS OF THE EQUATORIAL AND SOUTH TROPICAL PACIFIC OCEAN : Zoogeography, Ecology, Biology and Trophic Relationships

Translation

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CHAPTER 2. COLLECTING AND RESEARCH TECHNIQUES

Methods applied in biological oceanography are of prime importance for they determine the general orientation of a research project. This fact is not arrived at by an intuitive approach but through experience alone. All samples collected at stations of the R.V. "CORIOLIS" were drawn by means of two nets made fast to the same rope: a 10-foot IKMT (4 and 1 mm mesh sizes) and 50-cm diameter plankton net (0.33 mm mesh size). Examination of the respective catches of each trawl towed simultaneously and for the same length of time was highly instructive: the samples were totally different (cf. also Banse, 1962; Barkley, 1964; Brinton, 1962a). Of less spectacular significance but nonetheless determining factors were the effects of the traction speed of the net, the laboratory sorting techniques, the amount of water squeezed from the biomass before examination, etc. (cf. Gehringer and Aron, 1968; Bourdillon, 1971).

The second reason why pelagic biology is highly dependent upon a sound methodology is the total impossibility of observing facts: biologists cannot make corrections through direct observations on an estimate that 100 individual Euphausiids are found per cubic metre at a depth of 600 metres in the Central Pacific (cf. Lamotte and Bourlière, 1971).

Given this two-fold evidence, namely the significant effect of methods upon results and the total absence of empirical verification, both the collecting and laboratory techniques must be described with utmost accuracy. Improving the techniques over the course of some 1500 sampling stations was attributable mainly to Messrs R. Grandperrin and A. Michel, biologist-oceanographers at the O.R.S.T.O.M. Centre at Numea, New Caledonia. We shall frequently refer to their work in this chapter.

A. COLLECTING TECHNIQUES

Figure 20 is a diagram of the sampling gear used at all stations of the R.V. "COLIOLIS".

1. SAMPLING GEAR

1.1. The <u>Isaacs-Kidd Midwater Trawl</u> was designed (Isaacs and Kidd, 1953), by its very size and design speed, for capturing macroplankton and 16 micronekton. The gear was approved without modifications by the UNESCO No. 4 Working Party (Fraser, 1966 and 1968).

With the exception of stations 10 to 39 on the "Alizé" expedition which made use of a 5-foot IKMT (mouth opening of approx. 2.2 m^2)[1] , a 10-foot model (mouth opening of approx. 8.5 m^2)[1] was used for all IKMT stations. The fore-net was in 4 mm mesh covering a length of some 9.5 m; the cod-end was an ordinary plankton net, 50 cm in diameter (1.80 m long) in 1 mm mesh (No. 000). The end of the entire net consisted in a very large plastic collector (20 cm ø , 60 cm long) with "windows" covered in No. 000 mesh. At the opening, the lower part of the net was equipped with a V-shaped metal depressor giving the gear its special feature (cf. below).

The 5-foot IKMT was identical, almost to scale, to the 10-foot model and had the same cod-end (plankton net, 50 cm ø, No. 000 mesh size); however, the depressor and forenet (4 mm mesh) were smaller and the mouth opening was approximately 2.2 m^2.

1.2. <u>Plankton Nets (FCO)</u>

Given their poor performance in collecting large Euphausiids, very little use was made of these nets during the course of this project.

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(1) As the opening of the IKMT is not retained within a rigid frame, its surface can vary by approximately 10% depending upon operating conditions.

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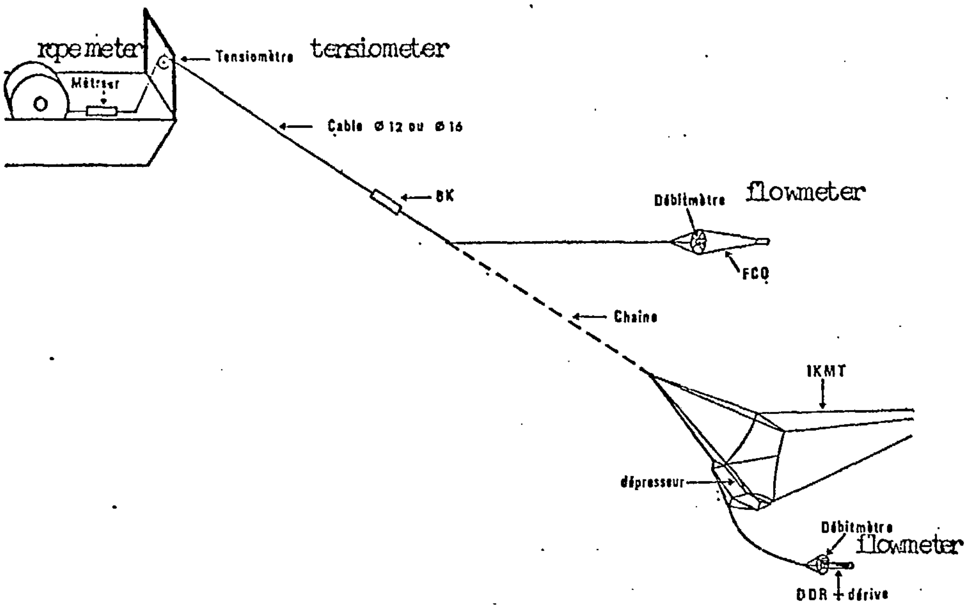

Fig. 20. — Engins utilisés pour les prélèvements de zooplancton-micronecton (BK : bathykymograph. FCO : filet conique ordinaire. IKMT : chalut pélagique Isaacs-Kidd. DDR : depth-distance-recorder).
Fig. 20. — Sampling gear used on board R. V. CORIOLIS for Plankton-Micronekton collections. *FCO:* Plankton net - *IKMT:* Isaacs-Kidd Midwater Trawl (10 foot) — *BK:* Bathykymograph. — *DDR:* Depth-Distance-Recorder.

17 In fact, only at the 10 stations of the "Bora" expedition were samples collected to compare the respective catches of a plankton net (FCO) and an IKMT 10 (Roger, 1968 a). The net, using 1 mm mesh, (No. 000) had a 1-meter diameter (opening to 0.8 m^2) and length of 3.60 m.

1.3. The <u>Neuston Net</u> (cf. David, 1965) is a net mounted on a frame and used to draw samples of the fauna found in the first few centimeters immediately below the surface. The gear was towed by a vessel travelling at a speed of approximately 5 knots, an asymetrical crowfoot keeping it away from the wake of the vessel. The Neuston net used on board the R.V. "CORIOLIS" was in a No. 2 mesh size (0.33 mm). Euphausiids from 35 samples drawn on the "Cyclone" I expedition were examined.

1.4. The <u>Larval Net</u> (L.N.) (Omori, 1965) is a closing net, 160 cm in diameter equipped with a double trigger system: the net is shot out closed, opens by means of one trigger device and closes by means of the other when the catch is completed, then hauled in. Two nets, one in 1 mm mesh ("Caride" III expedition), another in 0.33 mm mesh ("Maruru" expedition), were used to determine vertical distributions with greater accuracy than was possible by using the IKMT.

1.5. Accessory Gear: Part of the gear was strictly routine equipment, used either for sampling purposes or subsequently to identify certain definite characteristics.

- an OLYMPIC rope-meter to measure the length of rope paid out.
- a DILLON tensiometer to control rope tension during a station.
- T.S.K. flowmeters to estimate distances travelled in the water by the trawl. On the first few expeditions ("Alizé", "Bora"), the flowmeter was placed, in the case of the IKMT, at the mouth of the 50 cm ∅ plankton net serving as the cod-end. The turbulence occurring within the gear resulted in later placing the flowmeter outside the net, i.e., either directly under the IKMT depressor or, to provide better buffer, rigged independently within a circle 50 cm in diameter and fastened under the depressor (cf. Fig. 20). Given the fact that the IKMT is made in two different mesh sizes, one cannot, strictly-speaking, refer to a filtered volume, this volume being dependent upon the size of the animals (Aron, 1962a). Our objective was merely to measure the distance travelled by the net with respect to the water during each tow.

Intercalibration between readings on the flowmeter, placed either independently within the circle or under the depressor , or, in the cod-end, indicated that readings in the latter case were approximately 20% lower than in either of the two first cases.

- a Bathykymograph (BK) (Hester, Aasted and Gilkey, 1963), fastened to the towing cable of the trawl a few metres before the latter and recording the depth of the net in terms of time, was used on most expeditions. Towing depths given in the appendix were obtained from readings on that instrument. (Fig. 21). Values followed by an asterisk indicate theoretical estimates for stations during which the BK was out of order.

- On the "Caride" III expedition and subsequent expeditions, in addition to the instruments mentioned above, a Depth-Distance Recorder (D.D.R.) was rigged within the 50 cm circle next to the flowmeter. This instrument 18
recorded the distance travelled at each depth; the data obtained is shown on a curve (Fig. 22) plotted on a BT plotter. This curve gives an estimate of the volume of filtered water (or distance travelled) by a net at each given depth, as opposed to the BK which indicated only the immersion time and not whether the net had actually been working. Total readings on the BK and the DDR also gave for each depth the working speed of the trawl (DDR filtered volume/BK time), i.e., one of the basic parameters. The speed of the net in relation to the water can vary by a fraction of a knot while the net is being shot and by as much as 5 knots when the net is hauled in; the net obviously performs differently in either cases. Fig. 23 gives the course of the IKMT during a typical oblique tow, with indications of the mean working speeds of the net at various stages.

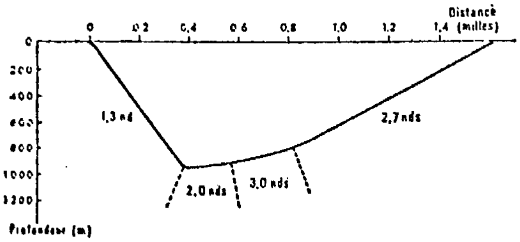

Fig. 23. — Profil d'un trait de chalut IKMT, avec indication des vitesses moyennes (en nœuds) du filet par rapport à l'eau au cours des différentes phases (d'après GRANDPERRIN et MICHEL, 1970).
Fig. 23. — Course of the IKMT during a typical oblique tow, with indications of the mean working speeds of the net during the different stages.

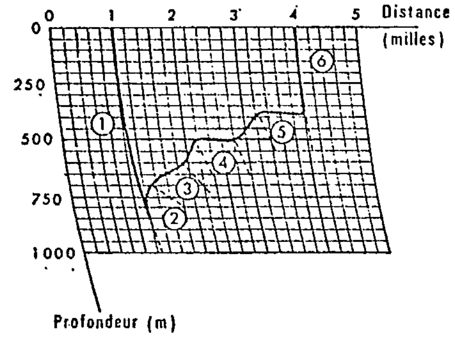

Fig. 24. — Tracé Profondeur-Distances parcourues d'un trait réalisé au filet ouvrant-fermant Larval Net (voir texte).
Fig. 24. — DDR graph of a tow carried out with the closing-opening Omori Larval Net — 1 : paying out, net closed. 2 to 5 : net working (open) with several successive horizontal stages. 6 : hauling in, net closed.

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2. SAMPLING METHOD

2.1. IKMT

We refer the reader to an excellent analysis by Grandperrin and Michel (1970) describing and commenting upon every detail of the operating techniques followed in using the IKMT on board the R.V. "CORIOLIS" from 1964 ("Alize" expedition) to 1969 ("Caride" IV expedition); we therefore consider it irrelevant at this point to repeat the details of the operations. The reasons for selecting this particular type of sampling method, i.e., the deep oblique tow, are given later in the chapter dealing with nychthemeral variations in catches.

Figures 21, 22 and 23 give a rough idea of the results obtained (cf. Aron et al, 1965; Backus and Hersey, 1956). In spite of successive improvements to the towing techniques, all had three inherent drawbacks attributable to the equipment itself:

- a definite, almost horizontal strata (cf. Fig. 21) at the greatest depth resulting in too many samples being drawn from that depth in comparison with other depths.

- irregular filtering speed (speed of net in relation to the water) (cf. Fig. 23) which, in extreme cases, varied from a few fractions of a knot 19
when the net was shot to as much as 5 knots or more when the net was hauled in (Aron and Collard, 1969).

- definite lack of accuracy concerning the maximum depth reached, known only subsequently from BK or DDR readings, the critical factor being the difficulty in controlling the speed of the vessel at speeds of less than 5 knots.

2.2. Larval Net (LN)

The operating technique of the Larval Net (cf. Omori, Marumo and Aizawa, 1965) is simpler, theoretically speaking at least, than that of the

IKMT. The closing-opening Larval Net operates only periodically; the actual towing time is therefore irrevelant as the net is opened only during a given period of total towing time.

Use of the Larval Net on board the R.V. "CORIOLIS" having been introduced at a later date, the basic sampling procedure, described hereunder and applied on the "Maruru" expedition, must therefore be considered as having served as a temporary measure.

- approximately 2/3 of the rope length estimated necessary at a given depth was paid out;
- the device for opening the net was triggered; the rope was no longer paid out so as to know when the net would open;
- once the net was opened, the remainder third of the rope was run out, progressively more slowly, in order to compensate for the sharp upsurge when the gear opened;
- the gear was left at three different horizontal levels within the strata to be investigated for some 5 to 15 minutes;
- the device for closing the net was triggered and the closed net was hauled in.

During the entire time, the vessel maintained a speed of 4-5 knots. Fig. 24 shows a DDR graph of a tow carried out with the Larval Net at depths of 800 to 380 metres: (1) paying out, net closed; (2) upsurge when net opens; (3) (4) (5) net working (open) at several successive horizontal levels; (6) hauling in, net closed.

Without instruments indicating the position of the net during the 20 tow, the greatest difficulty consisted in estimating the precise time when opening or closing should be triggered; the exact time could be known only subsequently from readings on the DDR.

3. ANALYSIS OF THE IKMT SAMPLINGS

We again refer the reader to the work of Michel and Grandperrin

(1970) giving an analysis of the theoretical and practical aspects of the selection made by the trawl in the populations investigated. We shall discuss only the salient points and special problems related to Euphausiids (Roger, 1968 a and b).

3.1. General Considerations

The IKMT is a type of gear designed for catching specific kinds of organisms given the fact that two different mesh sizes are used: 4 mm mesh for the forenet and 1 mm mesh for the cod-end. As Michel and Grandperrin (1970) demonstrated very clearly, a two-fold selection is therefore made: one by the 4 mm mesh, the other by the 1 mm mesh which further selects from the population previously selected by the forenet before reaching the cod-end. Two different samples are therefore obtained; however, given this essentially single procedure, care must be taken to avoid assigning the populations a false biological origin. Nonetheless, among available types of gear, no other better technique appears more satisfactory for capturing large varieties of organisms of the plankton and micronekton categories (cf. Aron, 1958 b). The first thought that comes to mind when considering an investigation of large quantities of organisms is the use of gear using a single mesh size. Michel and Grandperrin (1970) demonstrated that an IKMT made exclusively of 4 mm mesh would capture a much smaller variety of animals; on the other hand, a net made exclusively of 1 mm mesh offers considerable resistance to the water therefore requiring a slower towing speed and preventing large organisms from being captured. Conventional plankton nets are unsuitable for fast-swimming plankton (cf. Clutter and Anraku, 1968; Hopkins, 1966; Jerde, 1967; McGowan and Fraundorf, 1966; MacKintosh, 1934; Ponomareva, 1963) among which Euphausiids are included. Lasker (1966) noted that Euphausia pacifica was capable of swimming for a few seconds at

speeds of 18 cm/sec; assuming that a net moving at a speed of 4 knots could be detected from a distance of 5 metres by the animals, the latter are able to move 45 cm before being caught. The chapter on Vertical Distributions mentions how few Euphausiids larger than 2 cm were collected with a Larval Net having a diameter as great as 1.60 m and towed at a speed of approximately 5 knots. Michel and Grandperrin (1970) have also shown that an IKMT using two different mesh sizes collects a much larger number and larger variety in sizes of organisms, than the total sum captured by both nets working independently, i.e., an IKMT made exclusively of 4 mm mesh and a plankton net of 50 cm ∅, 1 mm mesh. Under these conditions, the IKMT appears as the best possible compromise given the types of gear available for collecting micronekton, the younger forms of these being included with plankton, i.e., Euphausiids are in this category. This observation agrees with that of the No. 4 Working Party (UNESCO-Zooplankton Sampling, 1968). 21
Researchers must therefore find newer and more satisfactory means and meanwhile, continue using the IKMT while recognizing its particular performances.

Researchers view certain observations as sheer enigmas, explanations of which become obvious only subsequently. For instance, we noted that the day/night ratio of the average number of individuals captured at each station for a given species was significantly smaller when the specimens were smaller in size. This fact is difficult to explain by conventional hypotheses: the animals could not possibly be found during the day at depths greater than that reached by the net (1200 m); furthermore, if the trawl was more easily detected by day than by night, it was nonetheless inconceivable that the smaller organisms systematically escaped the net more readily than larger ones. Michel and Grandperrin (1970) finally proposed a satisfactory explanation: the cod-end, made of finer mesh, offers strong resistance to the water and at the net opening, causes a pressure wall to form with associated back flow and turbulence; the animals avoid this area and whirl about the part of the net in 4 mm mesh during a good portion of total towing time, thus coming into contact with the sides more frequently as the duration of the station increases and eventually escape because of their smaller size. For instance, 10 mm specimens collected at night near the surface remain in the net for only a very short time before being hauled in; the same animals captured during the day at a depth of 600 m are largely lost when the net is hauled in. As their size increases, fewer animals are able to escape with only negligible numbers of the 25-30 mm specimens escaping through the 4 mm mesh. The day/night ratio therefore remains constant by reason of the very size of the organisms.

In spite of such serious drawbacks in using this type of gear for collecting a large number of specimens, there are still few other alternatives. Researchers must therefore estimate as accurately as possible the bias of the sample obtained in relation to the actual population. The basis of selection made by the IKMT is sufficiently complex that it is difficult to apply it directly to actual stocks. Instead, we preferred to deal with the problem by examining the facts. Two methods were successively suggested: a comparative analysis (cf. also Grandperrin, 1967; Friedl, 1971) between catches of an IKMT and that of another type of gear (i.e., a plankton net, 1 m diameter, 1 mm mesh size) used under identical conditions (Roger, 1968 a), and secondly, a correction of the populations by applying coefficients derived from biological considerations (Roger, 1968 a).

3.2. Comparative Analysis of Catches by a 10-foot IKMT and a 1-meter Plankton Net (FCO - 1 mm mesh size) (cf. Roger, 1968 a).

The comparison dealt with catches obtained on the "Bora" II expedition for 10 stations during which an IKMT tow was immediately followed by an identical tow with a plankton net (FCO). All stations were occupied at night between 2000 and 2300, oblique tows having been carried out between the surface and a depth of 300 metres.

The catches were divided into 6 size groups (from 0.9 to 3.0) according to the procedure described hereunder (cf. Roger and Wauthy, 1968). Two facts were particularly noticeable:

- the IKMT collected a greater number of Euphausiids than the plankton net (FCO), i.e., on the average, 984 per 5000 metres travelled as opposed to only 420;

- individual specimens captured with the IKMT were larger on the average, i.e., the ratio of the Number of individuals collected by the IKMT/Number 22 of individuals collected by the plankton net increased as the size of the organisms increased, as shown in Fig. 25. Also of importance was the two-fold selection made by the IKMT and the effectiveness of the plankton net in collecting smaller organisms (0,9 size group). The mean size index of each species (calculation described hereunder) indicates that the advantages of the IKMT over the plankton net are greater as the size of the organisms increases (fig. 26).

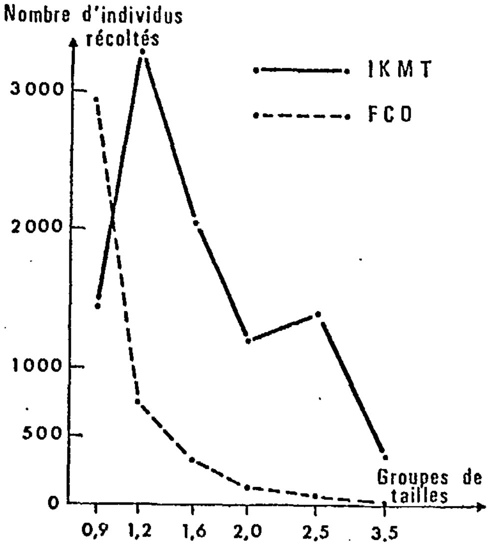

Fig. 25. — Nombres d'Euphausiacés récoltés au cours de 10 stations par un chalut IKMT 10 pieds et par un filet à plancton (FCO) de ⌀ 1 m, en fonction de la taille des organismes.

Fig. 25. — Numbers of Euphausiids collected during 10 stations by a 10-foot IKMT and a one meter plankton net (FCO), related to the size of the animals (0,9 to 3,5 = size groups = thoracic diameter of animals, in millimeters. Equivalence between size groups, mean individual length from the tip of the rostrum to the tip of the telson, and mean individual wet weight, is indicated in § 9.2 of the Summary).

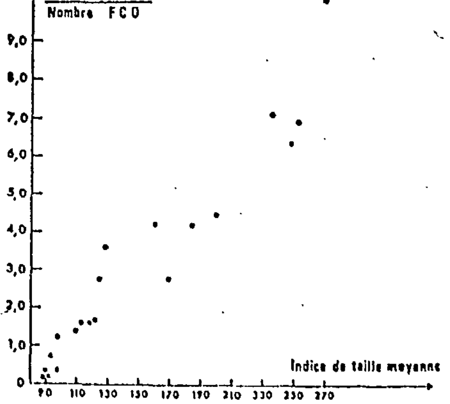

Fig. 26. — Rapports des nombres d'Euphausiacés capturés par le IKMT 10 et le FCO 1 m en fonction de la taille moyenne des organismes (1 point par espèce).

Fig. 26. — Ratio between the numbers of Euphausiids collected by the 10-foot IKMT and the one-meter plankton net, depending on the mean individual size of animals. 90 to 270 = mean size index of species. Each point represents one species.

These general principles having been set forth and taking into account the difficulty of estimating the bias for each catch from theoretical considerations, we might, when the purpose is to compare two different types of gear, merely intercalibrate them by towing them one alongside the other (Banse and Semon, 1963). In this case, the "useful" surface of the IKMT opening, made to vary according to the size of the given species, can be determined; large animals are captured as soon as they penetrate into the opening of the IKMT 23
("useful" surface: 8.5 m^2); very small animals which escape through the 4 mm mesh are captured only in the cod-end of 50 cm diameter and 1 mm mesh size ("useful" surface: approx. 0.25 m^2). Generally speaking, in relation to the 1-meter plankton net, the IKMT can be used to capture any species provided the "useful" surface of the gear is as follows:

$$Sm^2 = 0.8 \times \frac{\text{Number collected by IKMT}}{\text{Number collected by 1-m FCO}}$$

where .8 is the opening surface of the plankton net (1 m ∅) in m^2. Table I indicates different values of S for the main species of Euphausiids.

TABLE I

"Useful surface" of 10-foot IKMT in comparison with a 1-meter Plankton Net

Species	Number IKMT / Number FCO	"Useful surface" of IKMT in m^2
T. tricuspidata	37,5 (1)	(1)
T. pectinata	10,3	8,2
T. cristata	7,1	5,7
N. sexspinosus	7,0	5,6
T. monacantha	6,3	5,0
T. obtusifrons	4,5	3,6
T. orientalis	4,3	3,4
T. aequalis	4,3	3,4
N. tenella	3,6	2,9
N. microps	2,8	2,2
N. boopis	2,8	2,2
S. abbreviatum	1,6	1,3
E. paragibba	1,6	1,3
E. diomedae	1,6	1,3
N. gracilis	1,4	1,1
S. elongatum	1,2	1,0
E. brevis	0,8	0,6
S. carinatum	0,4	0,3
S. longicorne	0,4	0,3
S. affine	0,2	0,2
E. tenera	0,2	0,2

A comment is necessary at this point: the "useful surface" of the IKMT is determined according to the theoretical "useful surface" of the plankton net (0.8 m^2), i.e., that of the plankton is considered as being 100%, which is evidently inaccurate. The useful surface is therefore not the actual surface otherwise obtained by multiplying the useful surface by the efficiency of the plankton net, i.e., obtained not by using the value of 0.8 m^2 (opening surface of the 1-meter plankton net), but rather the section of the water column actually filtered by the 1-meter plankton net (0.64 m^2, for instance, in the case of a net efficiency of 80%).

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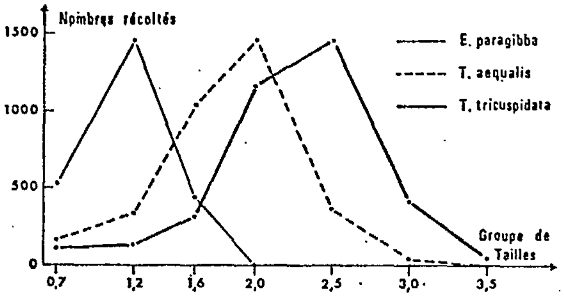
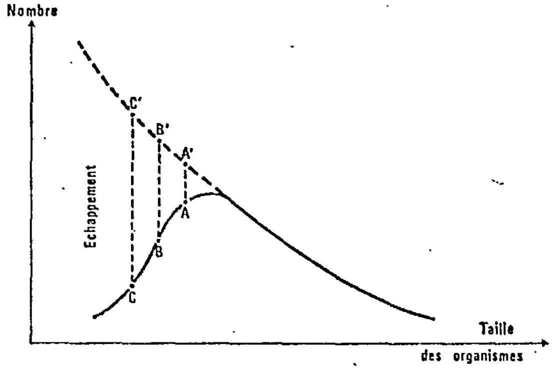


← **Fig. 27.** — Composition en tailles des échantillons IKMT pour des espèces de tailles moyennes différentes.

Fig. 27. — Size distribution of animals in the samples for 3 species having different mean individual sizes. (0.7 to 3.5 = size groups).

Fig. 28. — Artefacts introduits par la sélection du IKMT. —— composition en tailles de l'échantillon; — — — population réelle estimée ; - - - - - fraction de la population ayant échappé au travers des mailles. →

Fig. 28. — Bias introduced by the IKMT: — — — size distribution of animals in the actual population when the entire duration of the biological cycle of the species is considered. ——— size distribution of animals in the samples. - - - - - part of the population which escapes through the meshes. (escapement increasing as the animals size decreases). The evaluation of this parameter allows to calculate corrective factors to estimate the actual population.



3.3. Minimum estimate of actual population (cf. Roger, 1968 d)

On the "Cyclone" expeditions samples were drawn from the same region over a period of six months, all samples being collected by the same method. An examination of the samples collected from some 89 stations, all conducted under essentially identical conditions, demonstrated how the sampling gear definitely influenced the species being captured. Fig. 27 shows that the curve for animals of different size groups captured over the entire period

is essentially bell-shaped for each species, the bell curve leaning either
to the right or left according to the mean individual size of the species.
In an equatorial environment, six months is sufficiently long from a biological
standpoint to have met all phases of a biological cycle. We can therefore
assume that the curve for the total number of each species, for a given
period, was necessarily a fraction of a hyperbole with a negative slope,
given the fact that for an entire cycle there are naturally more larvae than
young, more young than adults, etc. We might therefore safely consider the
part of the curve located to the left of the mode as the reflection of a
bias due to the selective ability of the fishing gear (shown on Fig. 28):
A is in reality A', the fraction A-A' having escaped the net; likewise, B is
actually B'; B-B' having escaped, etc. For each size group, we are thus led
to estimate a minimum corrective factor based on the following reasoning: "C"
is at least as abundant as "A"; if the stock is half as plentiful, this means
that, at best, the sample is only half as representative, etc. According to
Fig. 28, it becomes immediately obvious that this reasoning can be pursued
further provided only one species is involved; on the other hand, if curves
are available for a range of different size groups, corrective estimates for 25
all size groups can be obtained by a step-by-step process. For instance
(cf. Fig. 27), <u>T. tricuspidata</u> would indicate that the 1.6 size group is, at
best, sampled 1200/300 or 4 times more poorly than the 2.0 size group; <u>T.
aequalis</u> would indicate that the 1.2 size group is sampled 1000/330 or 3
times more poorly than the 1.6 size group, etc. In practice, among the
sampled species, the one species providing the highest corrective factor between
two given size groups will be used to determine that corrective factor.
Table 2 and 3 give the minimum corrections applied to the various size groups
to compensate for bias in the sampling, established from specimens of 89
stations occupied on the "Cyclone" expeditions.

The drawbacks and limitations of this procedure are self-evident: the estimates are minimal, i.e., there is no possibility of obtaining accurate knowledge of actual stocks in any given location; only an estimate of the minimum population can be made. Furthermore, the basic assumption is that the largest size group is a 100% sample, which is of course inaccurate, although the error is minimal if the gear is capable of capturing animals of that particular size. Note also that no margin is allowed for the progressive increase in the percentage of losses in terms of time spent by the organisms in the net; e.g., the estimated 20% remaining in the net of the 2.0 size group represents the mean of the highest percentage of night catches (animals swimming near the surface are unable to escape) and the lowest percentage of daytime catches (animals captured at greater depths are more likely to escape as the net is hauled in).

The calculation of corrective factors requires very complete data, more particularly data on a period equivalent to at least a complete cycle; otherwise, the very basis of the method must be rejected because one could no longer claim that the actual population of any given location during the entire period can be shown as a curve decreasing progressively according to individual size. In addition, the stations must have investigated the entire vertical biotope of the species and not only those layers occupied by certain size groups. Finally, it is assumed that the species being examined are sufficiently related morphologically that even the size of the individual animals is reflected in the samplesdrawn from the net, as established earlier for Euphausiids (Fig. 26).

The advantages of this method are nevertheless significant: the corrective factors although calculated by a negative approach considerably reduce the possibility of underestimating the stocks as a result of poor sampling of smaller organisms, shown on Table 3. On the other hand, if the conditions necessary to determine those factors must be rather rigid, these factors are established once and for all for all given size groups and all types of gear. Finally, as the reasoning is based on actual observation and not on theoretical selection considerations, all contingencies unpredictable beforehand are automatically taken into account.

Finally, we must point out that the sampling procedure followed on the "Cyclone" expeditions did not meet all required conditions. In particular, only a six-month period was covered, which even in a tropical environment, is somewhat short; furthermore, for several species, only a few specimens were collected. The calculation described above is given more as an example than as an accurate method for determining corrections which must be applied to Euphausiid specimens captured with a 10-foot IKMT.

TABLE 2

Total number of Euphausiids, according to species and size, collected during 89 stations, and corrective factors (coeff.) calculated. Samples of less than 100 were disregarded (given in parentheses).

Species Espèces / Taille* Size	0,7 à 1,2	Coeff.	1,2 à 1,6	Coeff.	1,6 à 2,0	Coeff.	2,0 à 2,5	Coeff.	2,5 à 3,0	Coeff.	3,0 à 3,5	Coeff.	> 3,5
S. longicorne.......	374	—	150	—	(30)	—	(0)	—	(0)	—	(0)	—	(0)
E. diomedae........	9 979	1,15	11 507	—	5 972	—	378	—	(8)	—	(0)	—	(0)
E. paragibba......	535	*2,74*	1 468	—	452	—	(1)	—	(0)	—	(0)	—	(0)
N. tenella..........	845	2,70	2 276	—	1 712	—	241	—	(16)	—	(0)	—	(0)
T. aequalis........	153	2,28	347	*3,05*	1 060	1,36	1 438	—	383	—	(13)	—	(0)
N. boopis..........	(52)	—	145	1,95	283	1,62	459	—	374	—	166	—	(36)
T. tricuspidata.....	111	—	109	3,01	328	*3,63*	1 191	1,25	1 491	—	433	—	(22)
T. orientalis.......	(14)	—	(41)	—	106	1,25	132	*1,35*	178	1,39	247	—	143
T. monacantha.....	(7)	—	(29)	—	(85)	—	144	1,28	184	*2,21*	407	—	295
T. pectinata........	(1)	—	(14)	—	(38)	—	103	—	(76)	—	113	*1,71*	193
Coef.........		2,74		3,05		3,63		1,35		2,21	·	1,71	
Total coeff. applied.....	155		56		18,5		5,1		3,8		1,7		1,0 (hyp.)
Estimate of % captured.....	0,65 %		1,8 %		5,5 %		20 %		26 %		59 %		100 % (hyp.)

* Thoracic diameter in mm.

TABLE 3

Number of specimens (figures in parentheses) and estimated actual populations (total for 89 stations). Samples of less than 100 specimens were disregarded. The sign indicates categories used to calculate corrective factors.

Species Espèces / Tailles et % capturé size - % captured	0,7 à 1,2 0,65 %	1,2 à 1,6 1,8 %	1,6 à 2,0 5,4 %	2,0 à 2,5 20 %	2,5 à 3,0 26 %	3,0 à 3,5 59 %	> 3,5 100 % (hypothèse)
S. longicorne...........	58 000 (374)	8 400 (150)	— (30)	0	0	0	0
E. diomedae............	1 547 000 (9 979)	644 000 (11 507)	110 000 (5 972)	2 000 (378)	— (8)	0	0
E. paragibba...........	83 000 (535) =	83 000 (1 468)	8 400 (452)	— (1)	— (8)	0	0
N. tenella..............	131 000 (845)	127 000 (2 276)	32 000 (1 712)	1 200 (241)	— (16)	0	0
T. aequalis.............	24 000 (153)	19 500 (347) =	19 500 (1 060)	7 300 (1 438)	1 500 (383)	— (13)	0
N. boopis..............	— (52)	8 100 (145)	5 200 (283)	2 300 (459)	1 400 (374)	280 (166)	— (36)
T. tricuspidata..........	17 000 (111)	6 100 (109)	6 000 (328) =	6 000 (1 191)	5 700 (1 491)	740 (433)	— (22)
T. orientalis............	— (14)	— (41)	2 000 (106)	680 (132) =	680 (178)	620 (247)	143 (143)
T. monacantha..........	— (7)	— (29)	— (85)	730 (144)	700 (184) =	700 (407)	295 (295)
T. pectinata............	— (1)	— (14)	— (38)	525 (103)	— (76)	193 (113) =	193 (193)

B. LABORATORY METHODS

Given the wealth of material, it was necessary to develop new methods as the old ones were designed to handle only small amounts of material. A selection was necessary and, given our objectives, we considered that less information would be lost if a large amount of data were processed by means of less accurate techniques than by deliberately disregarding a major portion of the material and examining in detail only part of the catches.

We shall describe only briefly the methods for sorting the plankton, discussed in other sources (cf. Michel and Grandperrin, 1971), and only mention how the Euphausiids were treated prior to scientific examination. We shall discuss at greater length the procedure followed in examining the organisms.

1. SORTING THE PLANKTON

The general principle adopted in the laboratory sorting of the specimens was to mechanize the operation insofar as possible in order to minimize the workload of the sorters given the extensive volume of material. The catch was therefore run successively through a cylinder isolating categories of organism according to density, then through a series of sieves with parallel bars at the bottom, spaced at graduated distances, which separated the animals into a certain number of size groups. These sieves were like those designed to divideEuphausiids into size groups (cf. following paragraph; also Roger and Wauthy, 1968). For details of the operation, we refer the reader to Michel and Grandperrin (1971), the main points of which are given hereunder:

The haul was successively run through:

- a sieve with parallel bars spaced at 10 mm which collected the largest organisms, considered as having been captured by chance and not generally included in catches of the IKMT ("fraction A"). The following chapter will discuss how these sieves selected according to the smallest dimension of the animal: width in the case of fish, thoracic diameter in the case of crustaceans, etc., i.e., the sieves selected only very large animals. Euphausiids were never included among these, the largest being the giant species Thysanopoda cristata or T. egregia which never exceed 7 mm in thoracic diameter.

- a cylinder 1.60 m high, 20 cm in diameter, in which a rising current of water drew the animals upwards in such a way that animals with the lowest density were drawn to the upper levels; the organisms could thus be further sub-divided. The main purpose of this operation was to separate the gelatinous animals which considerably hampered manual sorting.

- a sieve with parallel bars spaced at 2.5 mm, selecting "fraction B" or organisms considered as having been adequately sampled by the IKMT;

- a sieve with parallel bars spaced at 1 mm, selecting "fraction C" or organisms of which many escaped through the mesh of the net. This part of the catch is referred to as "fraction D" or "remaining plankton" composed of very minute animals, only a small number of which remained in the net.

- each fraction was weighed as a total unit (wet weight after water was squeezed out for one minute at 56 g., (cf. Grandperrin and Michel, 1969a); fractions B and C were then sorted with pincers and separated into some twenty taxa.

2. TREATING THE EUPHAUSIIDS 28

For any one group, size classification strictly by means of the sorting procedure described above was obviously inadequate. A finer breakdown was necessary to subdivide the organisms into smaller size groups making it possible to roughly estimate (cf. Bargmann, 1945) the age of the populations (Kurata, 1962; Lasker, 1966; Ponomareva, 1963).

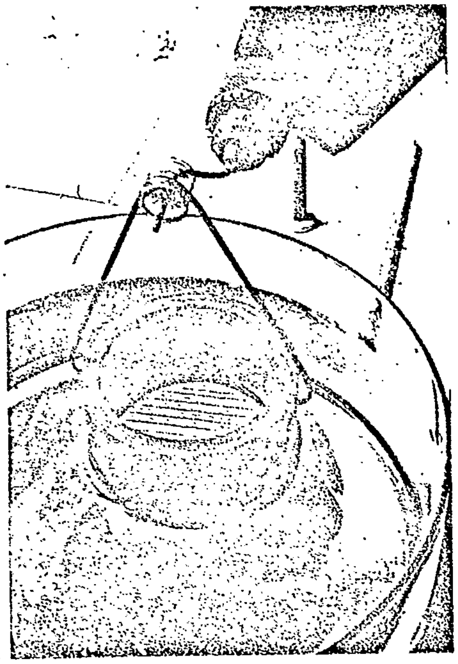
As mentioned earlier, the very volume of material led to mechanizing the operations as much as possible; in particular, special measures could be applied only to small sub-samples which, other than the difficulty in doing so with fairly large organisms, meant that an appreciable amount of data would be lost by having unreasonably small samples for several species.

The Euphausiids included in fractions B, C and D, selected as mentioned earlier, were all put through a series of sieves with glassrods spaced at 3.5/3.0/2.5/2.0/1.6/1.2/0.9/ 0.7 mm which successively selected the animals according to thoracic diameter. The sieves, 10 cm in diameter, could handle 400 to 500 individuals at once. The catch was introduced into electrically-driven shaking sieves rotating every 10 minutes (rotation of approx. 35 rpm) (cf. Photo A). Details of the operations and efficiency tests are described in Roger and Wauthy (1968). Photo B shows the 8 size groups (S.G.) in actual size.

The specimens within each size group were then identified even more specifically; these results are given in the form of a station sheet tabulating the animals according to species and size groups.

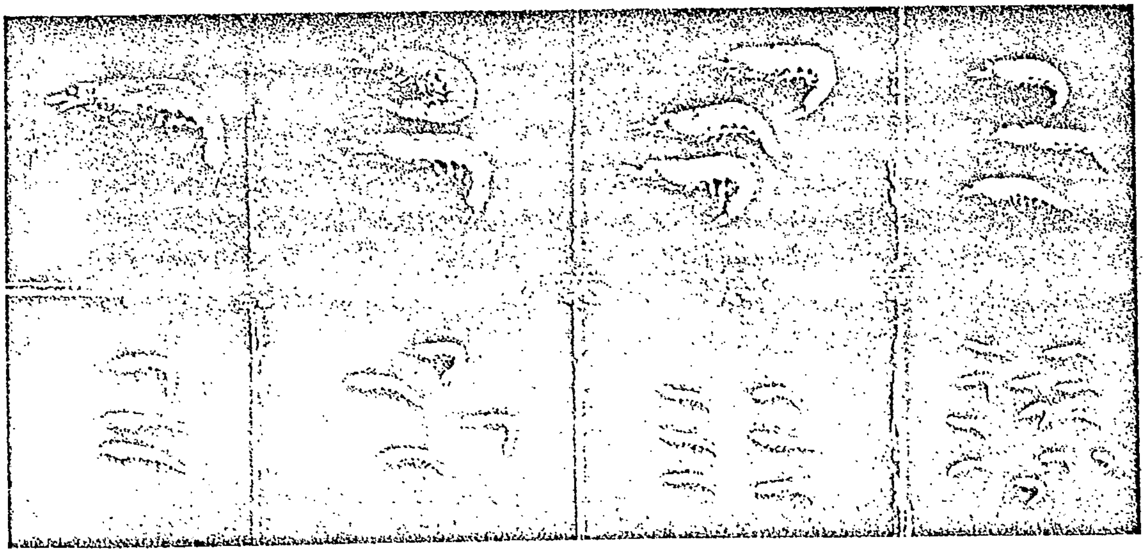
By this method, large samples could be handled quickly without any hand-sorting being necessary; i.e., results were easily obtainable. The major drawback was a sorting of organisms according to a single parameter (thoracic diameter), necessarily a limited one, such that the results were less accurate than if individual measurements had been taken. Table 4 gives, for various species, the relationship between size group and mean individual wet weight in mg (on formolized material: cf. Ahlstrom and Thrailkill, 1963; Grandperrin and Caboche, 1968)/length from tip of rostrum to tip of telson in mm. Variations noted between species depended naturally upon the individual morphology of the species, an "elongated" species being longer than a shorter species within the same size group. On the other hand, certain morphological characteristics sometimes altered measurements to some extent; for instance, mature ♀ (ovaries at stage IV) frequently causes swelling of the thoracic region with the result that these organisms were classified in a larger size group than that of immature ♂ or ♀ of the same length.

When Euphausiids were considered as a whole unit, we adopted a size and weight equivalence for each size group, i.e., the mean value for each species given on Table 4. The mean values are as follows:



A : appareillage utilisé pour la séparation des récoltes en groupes de tailles (8 tamis d'écartements décroissants).

1st Plate. — A : Device used to separate the samples into size groups (8 sifters which glass rods have respectively the following spacing : 0.7, 0.9, 1.2, 1.6, 2.0, 2.5, 3.0 and 3.5 mm).



B : les 8 groupes de tailles obtenus, grandeur réelle.
B : the 8 size groups, *actual size*.

TABLE 4 29

Relationship between size groups (S.G.), mean individual wet weight, in mg. (1st figure) and lengths, from tip of rostrum to tip of telson, in mm (2nd figure) for the different species. Each figure represents the average of a minimum of 10 measurements with the exception of figures indicated in parentheses.

Species G.T. Espèces S.G.	3,5	3,0	2,5	2,0	1,6	1,2	0,9	0,7
T. cristata..........	744/—	(181) —	95/—	(50)/—	(16)/—	—	—	—
T. tricuspidata......	—/33	116/30	85/26	65/21	38/17	17/(13)	5/10	—/9
T. orientalis........	421/(37)	209/33	127/—	63/—	36/—	(20)/—	(8)/—	(2)/—
T. monacantha......	287/35	196/30	100/24	59/19	35/(16)	—	(13)/(9)	—
T. pectinata........	377/34	240/(32)	130/25	72/20	(48)/18	—	—	—
T. obtusifrons.......	—	(171)/—	—	(79)/—	—	—	—	—
T. aequalis.........	—	—	70/20	53/18	34/16	18/13	6/9	(1)/(7)
T. egregia..........	(1162)/—	—	—	(54)/—	(28)/—	—	—	—
S. carinatum........	—	—	—	—	—	—	3/8	2/7
S. abbreviatum......	—	—	(44)/(19)	40/18	24/15	14/12	6/9	2/—
S. maximum........	238/—	153/(29)	95/24	56/21	32/18	15/13	(9)/(10)	—
S. *elongatum*........	—	—	—	—	—	11/(13)	7/—	(2)/—
S. longicorne........	—	—	—	—	(17)/—	12/(10)	6/9	2/(7)
S. affine............	—	—	—	—	—	4/—	3/7	2/7
E. diomedae........	—	—	(38)/(19)	35/18	29/16	19/13	9/9	3/7
E. paragibba.......	—	—	—	(28)/	26/17	18/14	8/10	(3)/(8)
E. tenera...........	—	—	—	—	—	(11)/—	4/9	3/8
E. gibboides........	—	—	—/25	—	—	—	—	—
N. tenella..........	—	—	(55)/24	40/23	31/19	20/16	9/14	3/—
N. microps.........	—	(90)/—	62/(23)	49/20	32/17	16/15	8/10	4/8
N. gracilis..........	—	—	—	—/17	23/16	14/14	9/12	—
N. flexipes.........	—	—	—/24	(65)/20	(30)/18	—/15	(8)/11	—
N. sexspinosus......	(305)/—	184/—	—	(36)/—	(34)/—	—	—	—
N. boopis..........	(201)/—	144/(27)	102/(23)	66/(20)	37/(18)	21/(13)	(9)/—	—
B. amblyops........	(218)/—	141/(24)	86/23	(58)/21	(36)/(17)	(19)/(13)	(10)/(11)	—

0.7 S.G. (mean values): 8 mm and 2 mg
limit ..... 9 mm and 4 mg
0.9 S.G. (mean values): 10 mm and 4 mg
limit ..... 12 mm and 11 mg
1.2 S.G. (mean values): 13 mm and 16 mg
limit ..... 15 mm and 20 mg
1.6 S.G. (mean values): 17 mm and 31 mg
limit ..... 18 mm and 37 mg
2.0 S.G. (mean values): 20 mm and 54 mg
limit ..... 22 mm and 65 mg
2.5 S.G. (mean values): 23 mm and 84 mg
limit ..... 26 mm and 120 mg
3.0 S.G. (mean values): 29 mm and 140 mg
limit ..... 33 mm and 220 mg
3.5 S.G. (mean values): 35 mm and 310 mg

By classifying the species into size groups, a "mean size index" could be quickly calculated by simply adding the products of each size group and the percentage of individuals within a given species. Thus, a species representing 30

8% of the 3.0 size group, 14% of the 2.5 G.S., 21% of the 2.0 S.G., 38% of the 1.6 S.G., 17% of the 1.2 S.G., 2% of the 0.9 S.G. will have a mean size index of : (3.0 x 8) + (2.5 x 14) + (2.0 x 21) + (1.6 x 38) + (1.2 x 17) + (0.9 x 2) = 184.

By using this index, not a rigidly accurate one, a species can be quickly located by the size of its individuals. However, this index does not qualify only the species being considered, but also the type of gear, i.e., the index is not based on actual populations, but rather on a biased image produced by the type of net being used.

Hauls with the IKMT (excluding specimens collected with the plankton net (FCO), Larval Net and Neuston Net), yielded over 400,000 specimens. Classification of this material according to genus, species and geographical origin will be discussed in detail in the chapter on Zoogeography.

CHAPTER 3 . Zoogeography, Characteristics of Distributions and Seasonal Variations

As we noted earlier, the major distribution patterns of various species inhabiting the Pacific are relatively well known (Brinton, 1962 b). One must bear in mind however the vastness of the zone investigated which, in comparison, makes the number of stations occupied to date seem ridiculously small. The material obtained from expeditions of the R.V. "CORIOLIS" represents a wealth of information unavailable until now on these regions and calls for a detailed study of distributions on a scale unattempted as yet.

In terms of zoogeography, the catches have made it possible to identify five major population zones (fig. 29):

- Zone A : Western Equatorial Pacific ("Cyclone" expeditions, northern section occupied on "Bora" expeditions, westernmost section on "Alizé" expedition) - 170°E -- 5°N to 5°S.
- Zone B : Southwest Tropical Pacific (southern section of "Bora" expeditions) - 170°E - 20°S to 5°S.
- Zone C : Central Equatorial Pacific ("Caride" expeditions, central section of "Alizé" expedition) -- 135°W to 155°W on the equator.
- Zone D : South Central Tropical Pacific ("Atoll" and "Brisants" expeditions) -- 130°W - 145°W/15°S - 25°S.
- Zone E : Eastern Equatorial Pacific (easternmost section of "Alizé" expedition) -- 92°W to 140°W on the equator.

The following points shall be successively discussed:

A. Use of statistical methods for analyzing the quantitative elements forming the basis of this part of the work.

B. Various species sampled, their relative abundance, measurements particularities influencing representative sampling of the catches.

C. Major population zones, density and specific compostion of each zone.

D. Some distribution characteristics of main species, especially swarmming and nycthemeral variations.

E. Seasonal variations.

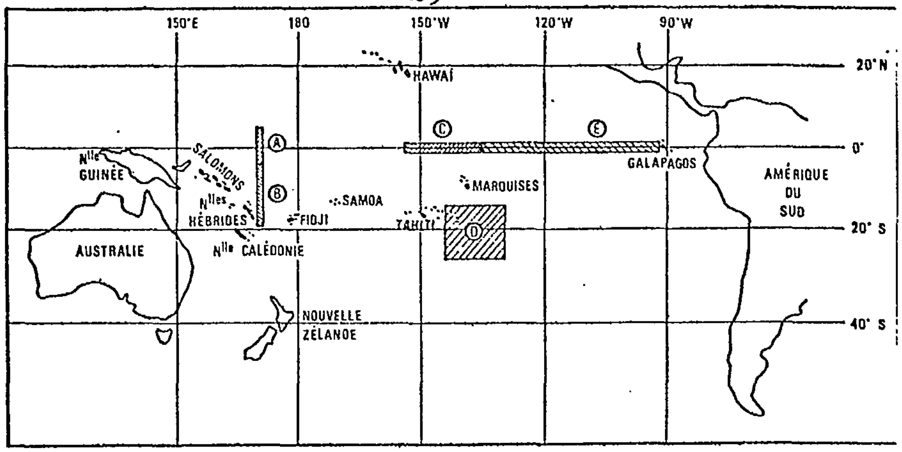


Fig. 29. — Les 5 régions étudiées.
Fig. 29. — The five areas investigated.

A. COMMENTS ON THE USE OF STATISTICAL TESTS

Colebrook (1969) observed, in a somewhat cynical manner, that to date researchers who did not apply statistical methods have contributed more to the knowledge of plankton than those who did make use of them. The fact is that plankton distributions do not fit within the "urn schemata" highly respected by statisticians; the researcher who observes such unusual distributions is therefore left completely at a loss. This author further mentions that planktonic populations are controlled by several factors (movements of masses of water, nutrition, reproduction, social behaviour patterns, migrations) governed by laws other than mere chance and to which conventional statistical methods cannot be applied any more than in the case of loaded dice or

We must further add that essentially random variables are considered and that the cause-effect relationship is obtainable only in exceptional cases and only if supported by assumptions other than statistical analysis; most frequently, the researcher must resign himself to simply observing facts.

The mathematical interpretation of phenomenon observed in planktology is in full development at the moment (cf. Daget, 1967; Ibanez, 1969; Frontier, 1971), but will not be considered in this project. We shall merely give very brief explanations of the following operations:

1. STANDARDIZATION OF DISTRIBUTIONS

1.1. Standardizing Transformations

The great majority of statistical tests assume that data to be processed will comply with normal frequency distributions and, in comparing two distributions, the variances will be essentially equal. However, this is seldom the case with planktonic samples. Distributions are generally far from the normal distribution pattern and variance increases with the number of samples. Consequently, if a hypothesis is to be supported with a statistical test, the actual distribution must invariably be transformed into a normal distribution. Standardization is performed by applying an arbitrary mathematical transformation selected solely for its ability to standardize: it is an expedient designed to temporarily modify the form of the distribution in order that tests may then be applied to it. The conclusions must therefore be drawn from the original data and not from the standardized values which have no real significance.

In practice, once it is known that the real distribution is not a normal one, the point is to find the transformation that will best bring about a standardization by testing the normal distribution of the series obtained (see following paragraph). The most commonly applied transformations are $y = \log x$, $y = \log (x+k)$, $y = \log^2 x$ and $y = \sqrt{x}$ (cf. Frontier, 1969).

1.2. Normal Distribution Tests

1.2.1. Graph Tests

A normal distribution can be quickly tested on a graph; the much more tedious calculated test is applied only if the normal distribution obtained seems rather dubious. The principle of the graph test is to transform the real curve into an S representative of the cumulative percentages, the characteristics of which are difficult to evaluate on a straight line (anamorphosis).

The most widely used method is the probit transformation which consists in plotting the cumulative percentages of the various types of samples on a probit ordinate graph on which any normal distribution, regardless of mean and variance, will result in a straight line, called Henry's Line. Inversely, any series of points which does not form a straight line will not give a normal distribution and will deviate from the normal distribution in as much as the curve differs from a straight line (see further on for Examples of applications). Another graph test can be applied on small samples ($N < 50$) if no special probit paper is available and is also more rapidly obtained than the probit transformation. This is the rankit test.

1.2.2. The Pearson χ^2 Test 34

When the points plotted on the probit or rankit graphs are rather doubtful, the distribution must be tested more accurately to determine whether or not it can be considered as a sufficient approximation of a normal distribution if the test is to be at all meaningful. This can be done by applying the Pearson χ^2 Test and comparing the distribution to the theoretical normal curve with the same mean and variance, the coordinates of which are calculated beforehand.

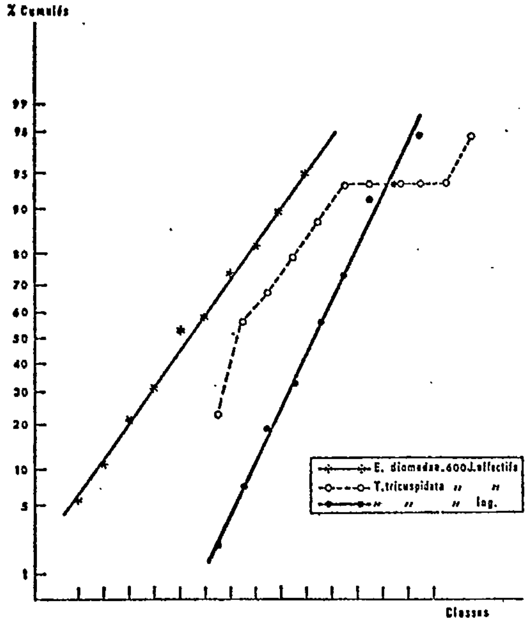


Fig. 30. — Test graphique de Normalité, échelle Probit.
Fig. 30. — Graphic tests of Normal distributions.

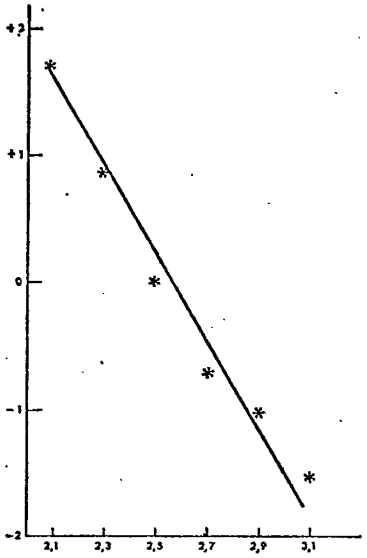


Fig. 31. — Test graphique de Normalité Rankit : log. des effectifs totaux d'Euphausiacés récoltés dans la région B.
Fig. 31. — Graphic test of Normal distributions.

1.3. Example of applications

We mentioned that the distribution of a series of planktonic samples seldom follows a normal distribution except by means of a transformation applied to the actual distribution. The case does occasionally occur however: fig. 30 shows that the specimens of E. diomedae drawn from 0-600 m daytime tows follow an almost straight line on probit coordinates. The same figure also shows that samples of T. tricuspidata drawn during the same tows deviate considerably from the normal curve: if statistical tests are applied to this series, the distribution must be standardized. As an example, we briefly explain how standardization is obtained:

- classify the specimens (in this case, 11 classes reduced to 6 after combining classes at either end of the range of which the theoretical number should be at least equal to 5 for calculating χ^2);
- verify the extent of deviation from the normal distribution according to the probit test (fig. 30);
- apply the standardizing transformations by testing the series obtained on the probit graph. In this case, the transformation y = log x provides a satisfactory standardization (fig. 30);

- if in spite of the probit transformation, there is still doubt about the quality of the standardized distribution, verify the latter by calculating the χ^2 between the series assumed as normal and the ordinates of the normal curve with the same mean and variance.

[Note that the highest ordinate of the theoretical normal curve is:

$$Yo = 0.39894\ N.C/S$$

where C is the class interval
N is the number of observations
S is the standard deviation.

The ordinate of each point on the curve is equal to a certain percentage of Yo, indicated by the table of ordinates of the normal curve in terms of the value of the ratio $(m - m_i)/S$.

where $m =$ the mean
$m_i =$ the ordinate of point i]

The normal distribution of the curve thus calculated can be verified by checking whether it can be plotted as a straight line in probit ordinates.

In our particular case, we obtain

$$\chi^2 = 2.05$$

As the χ^2 table indicates a limit of 11.07 at the 5% threshold for 5 d.d.l. (6 classes), we might conclude that the distribution of specimens of T. tricuspidata drawn from 0-600 night tows is essentially a normal log and that statistical tests can be applied to the logarithms.

We pointed out that, in the case of small samples, the rankit test was more useful than the probit test. Figure 31 shows the verification, by means of this test, of the normal distribution of the logarithms of the total number of Euphausiids captured during 23 stations occupied in region B (grouped into 6 classes).

2. COMPARISON OF MEANS AND VARIANCE ANALYSIS

In spite of the extreme caution which must be exercised when applying the tests, even simple tests of lesser importance, to series as statistically unusual as planktonic specimens, the point is nevertheless to attempt understanding certain results by means of these techniques. For instance, (cf. Table 8), the average number of Euphausiids captured per station in regions A to E was respectively 710, 450, 1032, 115 and 5446 or the number of Euphausiids captured at 2000, 0000 and 0400 hours on the "Caride" I expedition was 1334, 1213 and 1163 respectively on the average per station.

Are these differences significant? This question can be answered only by statistical analysis.

Before applying statistical tests to these series, one must ensure, by means of the methods described in the preceding paragraph, whether the distributions from which the means were drawn were normal, standardize them when necessary and verify whether the variances are not significantly different. An additional difficulty arises because the distributions which are compared against one another will necessarily be submitted to the same standardizing transformation. For instance, it seems rather difficult to apply a log transformation to specimens from the "Cyclone" II expedition and a $\sqrt{\ }$ transformation to those of "Cyclone" III in the hope of possibly finding seasonal variations. In this case, not only must the distributions be standardized or made to approach a normal distribution, but a procedure applicable to all distributions that will be compared must be found.

We briefly explain how such problems can be dealt with.

2.1. Average Number of Individuals Captured per Station in Regions A to E

Are the samples drawn from the 5 zones (710, 450, 1032, 115, 5446) significantly different? 36

- Having ascertained by the probit test that the distribution is not normal, a standardizing transformation must then be found;
- The transformation y = log x standardizes approximately 4 distributions (fig. 32). However, the rather doubtful standardization of the series for Zone C must be tested by the χ^2.

χ^2 = 13.93 for a limit of 16.9 at the 5% threshold.

The standardization is therefore acceptable.

We therefore obtain:

Region	A	B	C	D	E
Number of observations n	89	23	125	58	16
Mean $m_{\log}$	2,75	2,54	2,93	1,97	3,55
Variance $S^2_{\log}$	0,064	0,080	0,068	0,106	0,201

- test selection: a comparison of two means appears more interesting than a comparison of all means: in fact, geographical evidence would indicate that regions A and E, for example, have no direct relationship between one another and that the significant difference between these two means would be overshadowed, in an overall comparison, by the presence of an intermediate region C.

Likewise, the great difference between region D (mean: 115) and region E (mean: 5446) is sufficiently obvious to consider any statistical evidence unnecessary; furthermore, this difference would definitely alter the result of a general test. A more interesting point of view is to establish whether, in the western Pacific, the equatorial zone A (mean:710) is significantly more inhabited than tropical zone B (mean:450). We shall therefore compare the following couples which seem to bear some significance:

A-C / A-E / A-B / B-D / D-C / C-E

The test $F = S^2_A / S^2_B$ (where S^2_A is the value of the greatest variance) will enable us to verify whether the variances differ significantly at the 5% threshold if $F < Fs$ given in the table "point 2.5%" for the values $(n_A - 1)$ and $(n_B - 1)$:

	A-C	A-E	A-B	B-D	D-C	C-E
$F = \frac{S^2_A}{S^2_B}$	1,05	3,14	1,25	1,34	1,56	2,96
$n_A - 1$	124	15	22	57	57	15
$n_B - 1$	88	88	88	22	124	124
F_s	1,50	2,0	1,85	2,14	1,56	1,93

Note that the couples including region E do not meet the condition of equal variances. The means cannot therefore be compared statistically which, in practice, is of little importance. In spite of pronounced variability, region E (eastern Equatorial Pacific) is the only zone for which the number of specimens stands out among all the others to make any statistical analysis unnecessary. We are therefore left to compare the following couples:

A-C / A-B / B-D / D-C

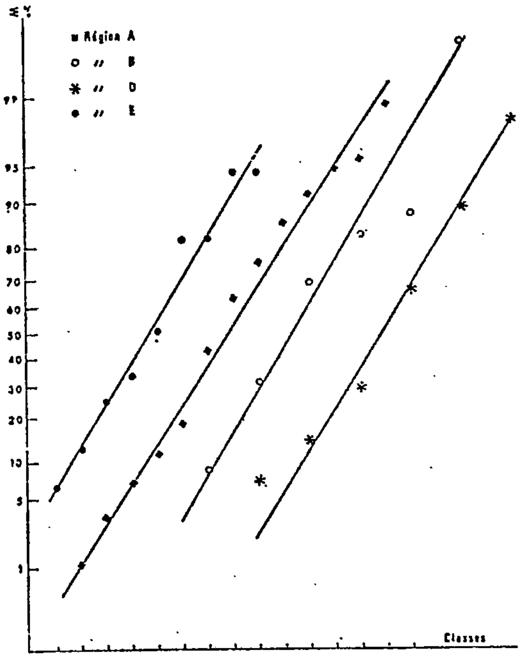


Fig. 32. — Test graphique de Normalité, échelle Probit : log. des effectifs capturés dans les différentes régions.
Fig. 32. — Graphic tests of Normal distributions.

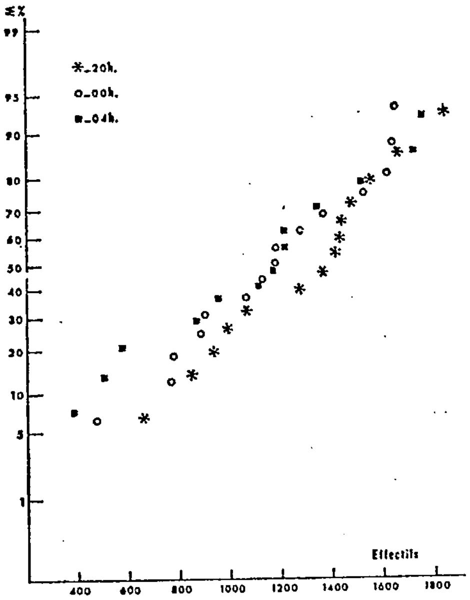


Fig. 33. — Test graphique de Normalité, échelle Probit : effectifs totaux récoltés à 20 h, 00 h, 04 h, pendant la croisière « Caride » I.
Fig. 33. — Graphic tests of Normal distributions.

As certain series of the pairs A-B and B-D include less than 30 measurements, test t must be applied :

$$t = \frac{m_A - m_B}{\sqrt{\frac{S^2}{n_A} + \frac{S^2}{n_B}}}$$

where S^2 is the variance common to both series, estimated according to the formula

$$S^2 = \frac{\Sigma (x-m_A)^2 + \Sigma (x-m_B)^2}{n_A + n_B - 2}$$

For couples A-C and D-C, on the contrary, all series include over 30 measurements and the normal deviate can therefore be applied

$$\epsilon = \frac{m_A - m_B}{\sqrt{\frac{S_A^2}{n_A} + \frac{S_B^2}{n_B}}}$$

According to Table 5, all the pairs are composed of significantly different means, in fact far beyond the 5% threshold. Disregarding the fact that we dealt with logarithms and not with the actual number of specimens, all distributions having been submitted to the same transformation, we might safely assume that the actual means are significantly different at a 5% risk.

TABLE 5 38

Comparison in terms of pairs of specimens drawn from Regions A to D

	A-C	A-B	B-D	D-C
$S^2 = \dfrac{\Sigma (x-m_A)^2 + \Sigma (x-m_B)^2}{n_A + n_B - 2}$	—	0,068	0,102	—
$t = \dfrac{m_A - m_B}{\sqrt{\dfrac{S^2}{n_A} + \dfrac{S^2}{n_B}}}$	—	3,44	7,12	—
limite $t_{n_A + n_B - 2}$ (à 5 %)	—	1,96	1,96	—
$\epsilon = \dfrac{m_A - m_B}{\sqrt{\dfrac{S_A^2}{n_A} + \dfrac{S_B^2}{n_B}}}$ (limite à 5 % : 1,96)	5,29	—	—	19,20

2.2. Can we assume that the catches of Euphausiids carried out by night at the average time of 2000, 0000 and 0400 hours on the "Caride" I expedition (respectively: 1334, 1213, 1163) can be directly compared against one another, or must a corrective factor be applied to take into account the time when the specimens were being drawn?

- According to fig. 33, the specimens in the three series are essentially distributed along a normal curve. The actual specimens can therefore be used.
- The variances are verified as being less than the limit F = 2.5.

$$\frac{F\ 00\ h}{F\ 20\ h} = 1.06 \qquad \frac{F\ 04\ h}{F\ 00\ h} = 1.44 \qquad \frac{F\ 04\ h}{F\ 20\ h} = 1.53$$

The distributions being fairly normal and the variances fairly close, the means can therefore be compared.

- selecting the test: Test F will be used to determine whether the overall means differ significantly:

$$F = \frac{\dfrac{\Sigma (T_i^2/n_i) - T_G/N}{C - 1}}{\dfrac{\Sigma x^2 - (T_i^2/n_i)}{N - C}}$$

where n_i — number of stations in series i
$N = \lesssim n_i$ = total number of stations
T_i — total specimens in series i
$TG = \lesssim T_i$ = total specimens
$\lesssim x^2$ = sum of the squares of specimens
C = number of series

The means will differ significantly as a whole at 5% risk if F exceeds the value F_{N-C}^{C-1} read in the table of F "point 5%" for the degrees of freedom (C-1) and (N-C).

By applying this formula, we determine that F # 0.001. This value is extremely low (table F point 1% gives a limit value of $F = 5.10$ for the degrees of freedom 2 and 42), which implies that the variance from series to series is negligible taking into account the variance within any of the given series. We might therefore quite safely conclude that the catches (total 39 number) obtained at 2000, 0000 and 0400 hours during the "Caride" I expedition do not significantly differ from one another.

3. COMPARISON OF NON-NORMAL DISTRIBUTIONS

Statistical methods are still lacking in this field and, most often, it is still necessary to follow the tedious standardization procedure previously described in order to apply the conventional tests. In spite of its limitations, we might mention one of the few tests which can be applied to non-normal distributions. This is the Wilcoxon rank test by which two distributions can be compared against one another without the use of the mean.

The test consists in classifying all measurements of both series in either increasing or decreasing order such that the lowest total rank order is obtained for the shortest series if the series are not of equal length. When two measurements have the same number of specimens, the mean of their rank order is used. Only the lowest total rank order is taken into consideration. If it is less than the value read in the Wilcoxon table for the number of values corresponding to both distributions, the difference between them is significant at the given threshold.

Example

i.e., Comparison of distributions of T. tricuspidata in the equatorial stations (0-3°S) of "Cyclone" II and III.

C II No. of Specimens	Classification (rank)		C III No. of Specimens
20	4	7,5	26
22	5	17	54
26	7,5	15,5	52
28	10	13,5	41
18	3	11	37
152	23	18	68
52	15,5	9	27
75	19	12	39
41	13,5	1	13
89	21	2	14
88	20	6	25
100	22		
$N_2 = 12$			$N_1 = 11$
Total of rank order TOTAL de rang.....	163,5	112,5	

Comparing $N_1 = 11$ and $N_2 = 12$ at the 5% threshold on the Wilcoxon table, we find the value 99.8. As our own value of 112.5 is greater, the distributions are not significantly different at the 5% threshold. The respective means of 59 and 36 were not taken into account.

4. COMMENTS ON MEASURING THE HETEROGENEITY OF DISTRIBUTIONS 40

This point will be discussed at greater length in the section on "Distribution Characteristics". However, it should be mentioned at this point to draw attention to the necessity of using, when examining the variability of planktonic specimens, a method for measuring heterogeneity which does not depend upon the number of specimens. It was generally noted that the variance S^2 increases as mean m increases. Therefore, the over-dispersion factor $C = S^2/m$ and the variation factor $V = S/m$, which cause the square of the deviations from the mean to enter into the calculation, increase as the value of m increases whenever over-dispersion ($S^2 > m$) occurs. On the other hand, the dispersion factor

$$a = \frac{S^2 - m}{m^2}$$

by being virtually independent of m, provides more information by stating whether or not there is over-dispersion and also evaluating its extent.

B. SPECIES SAMPLED

The 34 species collected from the total hauls are briefly commented upon in the following pages. A few words will suffice to situate them within the context of this study: excellent sources (cf. especially Boden, Johnson and Brinton, 1955) give a full description of each species; it is therefore redundant to do so here. We shall merely point out the number of specimens included in our samples, the major distribution patterns and characteristics which may have affected representative sampling. It is extremely important to have an idea of the average size of the species in order to estimate how the particular species was sampled: we noted that the percentage of animals entrapped in the net varied by approximately 65% for the 0.7/1.2 size groups and by as much as 100% (theoretical) for the 3.5 size group. Table 6 gives a size distribution for each species and the mean size index deduced according to the procedure described earlier. Figure 34 gives the mean size index of the species (70 to 270) and an evaluation of the mean percentage of the actual populations caught by the IKMT. This data serves only as a guide as the size of organisms within one species can vary slightly from one expedition to the other. The size distribution given hereunder was drawn after examining all hauls on the "Cyclone" expeditions, with the exception of N. flexipes samples drawn during the "Caride" I expedition. Closely related species of identical size were grouped together.

(T. orientalis, T. monacantha, T. pectinata / T. obtusifrons, T. aequalis, T. subaequalis / E. diomedae, E. brevis, E. mutica / N. tenella, N. microps, N. gracilis).

Only six genera are represented as no specimens of Nyctiphanes, Meganyctiphanes, Thysanoessa, Tessarabrachion or Pseudeuphausia inhabit the zone covered by our studies. In decreasing order of number of samples, the 400,000 individuals were classified as follows (fig. 35):

TABLE 6

Size distribution of various species and Mean size indices

Species Espèces — G.T. S.G.	0,7	0,9	1,2	1,6	2,0	2,5	3,0	3,5	Mean size index
T. tricuspidata	1 %	2 %	3 %	9 %	32 %	41 %	12 %	1 %	226
T. orientalis	1 %	1 %	3 %	9 %	15 %	17 %	30 %	25 %	269
T. monacantha									
T. pectinata									
T. aequalis	1 %	4 %	10 %	31 %	42 %	11 %	1 %		180
T. obtusifrons									
T. subaequalis									
S. carinatum	50 %	50 %							80
S. abbreviatum	3 %	20 %	60 %	17 %					120
S. maximum		6 %	16 %	24 %	32 %	14 %	6 %	2 %	187
S. elongatum	4 %	67 %	29 %						98
S. affine	60 %	40 %							78
S. longicorne	18 %	50 %	27 %	5 %					98
S. microphthalma	100 %								70
E. diomedae	7 %	29 %	41 %	21 %	2 %				118
E. brevis									
E. mutica									
E. paragibba	3 %	19 %	60 %	18 %					120
E. tenera	80 %	20 %							74
N. tenella	1 %	15 %	45 %	34 %	5 %	1 %			135
N. microps									
N. gracilis									
N. flexipes		4 %	15 %	40 %	20 %	18 %	3 %		172
N. boopis	1 %	3 %	10 %	19 %	30 %	25 %	11 %	2 %	208
B. amblyops		1 %	4 %	12 %	17 %	20 %	31 %	15 %	254

- the genus Euphausia, with its 261,000 representatives, was by far the largest sample (64% of total); among the 9 species, E. Diomedae in the west and E. eximia in the east were most abundant. Note that the minute size of certain most abundant animals (E. diomedae, E. tenera) resulted in highly under-estimating their actual numbers in the catches, such that the actual population of this genus is possibly even greater.

- the genus Thysanopoda comes in second place with 53,000 organisms (13%). The large size of most specimens and their deep-water habitat resulted in an excellent sampling of this genus which numerically occupies, in reality, only the 4th place following Euphausia, Stylocheiron and Nematoscelis. Among the 10 species of this genus, T. tricuspidata and T. aequalis were most common.

- the genus Nematoscelis, represented by only 3 main species (N. tenella, N. microps, N. gracilis), included 46,000 individuals (11%) of average size, moderately under-estimated according to the techniques used.

- the genus Stylocheiron (41,000 specimens or 10% of total catches) which, like the genus Euphausia, included many individuals but very minute in size (S. affine, S. carinatum, S. microphthalma), such that the population was grossly under-estimated. Only S. abbreviatum, which in fact displays amazing swarmming habits, was very abundant. Numerically-speaking, 42
this genus should with very little doubt occupy the second place immediately after the genus Euphausia.

- the genus Nematobrachion (8000 organisms or 2%) can be considered, as the genus Thysanopoda and for the same reasons (particularly the large size of animals), as having been well sampled: actual populations can reasonably be deducted directly from our data.

- the genus Bentheuphausia, including only one species B. amblyops, was well represented in our collections. We collected no less than 1200 specimens of this bathypelagic species considered as rare, or 3% of our total collections.

In conclusion, it might be interesting to compare the respective number of specimens in each genus, i.e., specimens collected and actual 43

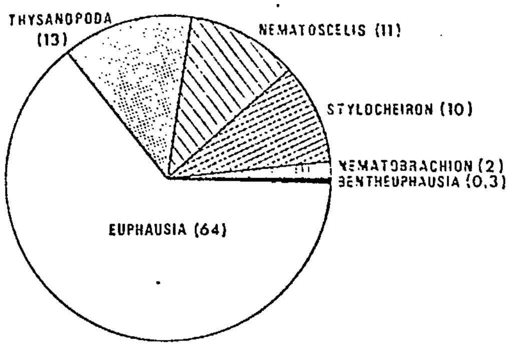


Fig. 35. — Composition moyenne des récoltes (en %).
Fig. 35. — Average composition of samples (%).

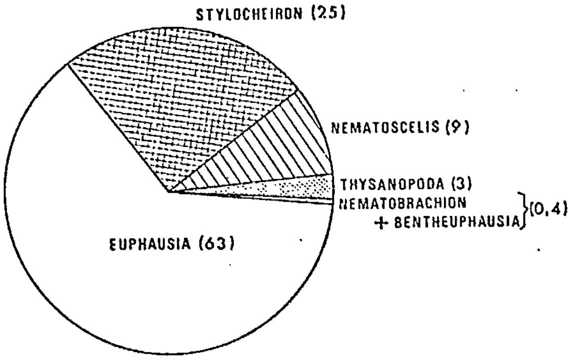


Fig. 36. — Composition estimée de la population réelle (en %) : moyenne des régions A à D.
Fig. 36. — Average composition of the estimated actual population (%) (Mean values for the 5 areas).

populations (Table 7 and fig. 35 and 36), estimated by applying to the number of specimens of each species/actually collected the factor calculated according to net efficiency for each species (Roger, 1968 d).

By making such comparison, the basic role of sampling and sampling bias introduced by each particular technique was brought out. This must be born in mind while reading the part dealing with the quantitative aspect of this study.

The total number of specimens collected as given for each species will in fact differ slightly from the actual count : the latter was corrected for the "Alizé" and "Atoll" expeditions to take the sampling gear into account. Stations occupied during the "Cyclone" I expedition and designed for a special programme were not considered. The figures quoted nevertheless give a highly adequate approximation of the number of specimens collected for each species (shown on fig. 37).

TABLE 7

Order of species according to number of specimens

Order	In hauls		In reality (estimate)*	
1	*Euphausia......*	64 %	*Euphausia......*	63 %
2	*Thysanopoda....*	13 %	*Stylocheiron.....*	25 %
3	*Nematoscelis.....*	11 %	*Nematoscelis.....*	9 %
4	*Stylocheiron.....*	10 %	*Thysanopoda....*	3 %
5	*Nematobrachion..*	2 %	*Nematobrachion..*	0,4 %
6	*Bentheuphausia..*	0,3 %	*Bentheuphausia..*	ϵ

* These percentages vary appreciably from one region to another throughout the zone investigated.

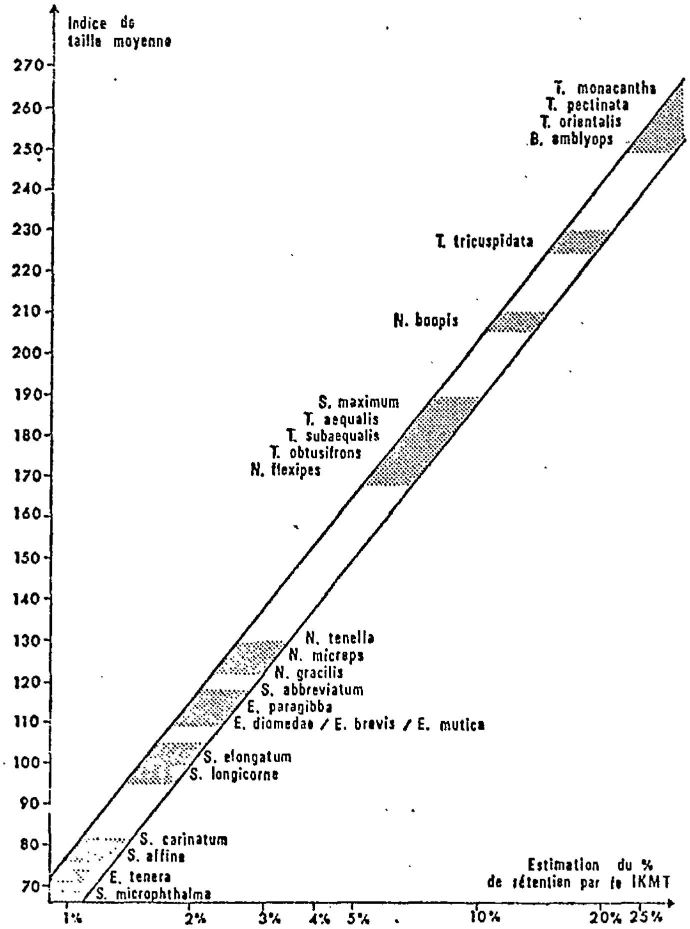


Fig. 34. — Indices de taille moyenne des espèces, et estimation de la fraction de la population réelle qui est retenue en moyenne par le IKMT 10.

Fig. 34. — Mean size index of species (70 to 270) and evaluation of the mean percentage of the actual population caught by the IKMT.

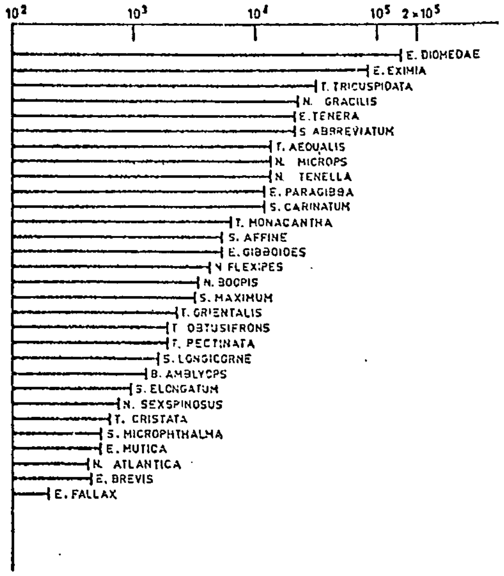


Fig. 37. — Nombres totaux d'individus récoltés (effectifs <100 non figurés).
Fig. 37. — Total numbers of specimens collected.

1. Thysanopoda cristata, G.O. Sars. Exceptionally large bathypelagic species. While Boden, Johnson and Brinton (1955) ascribed a maximum total length of 48 mm to this species, we collected even larger specimens, some of which were as long as 59.5 mm from tip of rostrum to tip of telson. (Roger, 1968 b). These measurements place this species somewhat beyond the range of size groups used for the other species as only the young of this species enter that range. Adult specimens were therefore classified in a special range including the 3.5/5.0 and 6.0 size groups. As a result of its deep-water habitat, the stocks were under-estimated for all tows at a depth of less than 600 m by night or 900-1000 m by day. Nevertheless, 626 individuals were collected on the "CORIOLIS" expeditions; this is a much larger sample than any other drawn to date. Brinton (1962 b) in describing the distribution of the species in the Pacific according to specimens of the Scripps Institution of Oceanography, had only 68 specimens, of which only 20 adults. In spite of its bathypelagic characteristics, which would lead one to assume that the species is widely distributed,

this species is not found in the eastern Pacific (Zone E); the specimen collected furthest to the east was captured at 143°09 W on the "Caride" I expedition.

2. Thysanopoda tricuspidata, Milne-Edwards. This species, one of the most widely sampled, is constantly found in relatively high numbers except in Zone E where it was considered scarce. Given a rather heterogeneous distribution, the species is sporadically found in large concentrations (Hansen, 1916). Its large size (adults: 20 - 30 mm) places it precisely within the range where the sampling gear works most efficiently (mean size index: 226). We collected approximately 28,000 specimens (general average: 70 per station). Although Boden, Johnson and Brinton (1955) had qualified this species as "essentially equatorial", we shall 45
question their statement in the chapter on Ecology.

3. Thysanopoda orientalis, Hansen. Adults measured as long as 40 mm (mean size index: 209) and the IKMT was therefore able to capture an adequate sample of this rather rare species: some 2000 specimens were captured or an average of 5 per station. The species is fairly evenly distributed although found less frequently in zones D and E. Brinton (1962 b) considered it as being closely related to T. monacantha and T. pectinata.

4. Thysanopoda monacantha, Ortmann. Resembling the preceding species very closely, this species was also well sampled with some 6000 individuals (average: 15 per station). It inhabits the entire zone investigated with a high density noted in the West and Central Equatorial Pacific (Zones A and C).

5. Thysanopoda pectinata, Ortmann. Closely related to the two

preceding species, T. pectinata was perhaps slightly less well sampled: 1600 organisms or an average of 4 per station.

6. Thysanopoda aequalis, Hansen, was oneof the species most commonly and most constantly found, i.e., over 12,000 specimens (again, to mention the abundance of our material, we might point out that Brinton (1962 b) established his charts for the entire Pacific on the basis of 614 individuals). On the average, 31 specimens were captured per station. The size of the species would indicate adequate sampling, perhaps slightly underestimated, by the IKMT (mean size index: 180).

7. Thysanopoda subaequalis, Boden. This species was only recently distinguished from the preceding by Boden and Brinton (1957). Their morphology is indeed practically identical with the only real difference being that, in the case of T. subaequalis, ♂ of the propodite of the 3rd pair of thoracic legs is transformed into a tail. Although according to Boden and Brinton (1957), other characteristics make it theoretically possible to differentiate both species, namely the shape of the rostrum, these criteria are highly uncertain in practice. Only adult males were counted separately, the young and females being included with T. aequalis. Such ambiguity does not alter estimates of T. aequalis stocks as T. subaequalis was found only in Zone B at the northern limit of 08°38 S and, furthermore, in very small numbers; i.e., only 54 males were collected. The species was totally absent in zone D (South Central Tropical Pacific) and throughout the Equatorial Pacific (Zones A, C and E). Its presence to the south of Zone B (15-20°S on 170°E) would extend the distribution charted by Brinton (1962 b).

8. Thysanopoda obtusifrons, G.O. Sars, is also part of the T. aequalis/

T. subaequalis group in which morphology and size are highly similar. *T. obtusifrons* is an antiequatorial species which Brinton (1962 b) considered as being totally absent from 5°N to 5°S. It appears, in fact, that there is some communication between the communities of the northern and southern hemispheres in the western Equatorial Pacific given the fact that specimens were collected on the equator on the "Bora" II and IV expeditions (170°E). No individuals having been captured further to the east on the equator, we might believe that the north and south distributions of the species are respectively inclined along NE-SW and SE-NW axes and join on the equator at the western boundary of the Pacific.

9. *Thysanopoda egregia*, Hansen, forms, with *T. cornuta*, Illig, and *T. spinicaudata*, Brinton, the group of giant bathypelagic Euphausiids. Adults are as long as 70 mm and their habitat barely rises above 1000 m. Thirty-three individuals were collected over the course of all expeditions; their bathypelagic nature would imply that their habitat covers a vast area. 46

10. *Thysanopoda cornuta*, Illig, is, it would appear, an inhabitant of even greater depths than *T. egregia*; distributed equally widely, only 3 specimens were collected which led us to assume that, either the species is very scarce or that more likely the adults are seldom found above 1200 m.

11. *Stylocheiron carinatum*, G.O. Sars, was one of the species least well sampled by the IKMT. Mean size index is 80 or generally a majority of individuals 8 mm long and 0.8 mm in thoracic diameter, i.e., most of the animals escapedthrough the meshes of the sampling gear. Very widely distributed throughout the Pacific from 40°N to 40°S, we collected no fewer than 11000 specimens (average: 26 per station) which likely accounted for only 1% of the population actually occupying the volume of water filtered

by the trawl.

12. Stylocheiron abbreviatum, G.O. Sars, is one of the four species displaying pronounced swarmming habits (cf. below), implying that caution must be exercised when giving a quantitative interpretation of their numbers. For instance, it was rather bewildering to note that of the total 11,000 individuals captured over the 89 stations of the "Bora" expeditions, 7,908 were collected only at station 16B on "Bora" II. Interpreting the means is rather critical in this case. Over 18,000 individuals were collected (average: 47 per station); the mean size index of 120 would lead one to assume that populations were rather grossly under-estimated.

It should also be noted that the identification of young individuals of S. abbreviatum frequently gave rise to difficulties due to their resemblance to S. maximum. An intermediate species, S. robustum (Brinton, 1962), was also recently identified further adding to the difficulty of recognizing juvenile stages. As this work has not yet been entered as systematic research, S. robustum was not considered and a certain percentage of uncertainty was accepted for the juvenile stages of S. abbreviatum and S. maximum.

13. Stylocheiron maximum, Hansen, is one of the rare species found from the Antarctic to the northern boundary of the Pacific. Due to its fairly large size (mean size index: 187), the species was well sampled by the IKMT. We collected over 3,000 individuals or an average of 8 per station. As in the case of the preceding species, identification of the juvenile stages was rather dubious.

14. Stylocheiron elongatum, G.O. Sars. Only 900 specimens of this species were collected which indicated that the species is indeed scarce and that only a small number was captured by the IKMT (mean size index: 98). The deep-water habitat resulted in under-estimating the species for

tows carried out at depths of less than 500 m. Practically no specimens were collected to the east of 140°W.

15. <u>Stylocheiron affine</u>, Hansen, is even smaller than the preceding species (mean size index: 78). The 5000 or more individuals captured in spite of techniques highly unsatisfactory for such minute animals would indicate that the populations are indeed great.

16. <u>Stylocheiron longicorne</u>, G.O. Sars, Only 1500 individuals were 47 collected, its small size (index: 98) rating the species among those least well sampled.

17. <u>Stylocheiron microphthalma</u>, Hansen, is the very smallest material which can be captured by an IKMT; all of the 500 specimens captured fall into the 0.7 size group (hence, by definition, a mean size index of 70) which makes this species the smallest of the 34 species collected. The ridiculously low proportion (in the orderof 1%) of the actual population captured by the IKMT left us with no other alternative than to mention its presence without any possibility of discussing its distribution.

18. <u>Euphausia gibboides</u>, Ortmann, is, with <u>E. eximia</u> and <u>E. distinguenda</u>, characteristic of the eastern Equatorial Pacific. Although Brinton (1962 b) had defined its limit to the west at 132°W on the equator, specimens were found on the "Alizé" expedition as far as 148°07 S (Roger 1967 a). We might therefore assume that this species, although definitely inhabiting the basin, can survive sporadically when drawn even into the Central Pacific. Specimens were collected much more frequently in zone E than in zone C, i.e., over 90% of the 5000 individuals originated from the eastern section of the "Alizé" expedition; the species was found regularly only to the east of 140°W.

19. Euphausia eximia, Hansen, as E. gibboides, is limited to the eastern Pacific; according to Brinton (1962 b) it is not found beyond 118°W on the equator. However, as in the case of the preceding species, isolated specimens were found on the "Alizé" expedition in the middle of the Central Pacific at 164°15W or nearly 2,700 miles to the west of the boundary considered until now as its distribution limit (Roger 1967 a). However such incursions remain quantitatively negligible; the species becomes common only to the east of 135°W where it forms over 80% of the Euphausiid fauna to the east of 110°W. In this latter zone, the species is found in considerable densities: on the "Alizé" expedition, 5000 m tows with the 10-foot IKMT produced as many as 6,000 specimens.

We were also brought to further specify a hitherto false diagnostic characteristic: according to Boden, Johnson and Brinton (1955), the inner protuberance of the 2nd segment of the antennal peduncle is bifid; however several of our specimens had a protuberance with 3 or even 4 spine-shaped denticules (Roger, 1967 a) (cf. photos C and D).

20. Euphausia diomedae, Ortmann, is the species numerically predominating throughout the Equatorial and Tropical Pacific with the exception of the eastern Equatorial Pacific where E. eximia is most common and of the south Central Tropical Pacific (Zone D) where it is outnumbered by E. brevis. Swarmming was observed, particularly on the "Bora" expeditions (Zones A and B). Almost 150,000 specimens were captured (average per station: 368) or 35% of the total specimens collected. Due to its relatively small size (mean size index: 118), the actual populations were seriously under-estimated by the type of gear used.

21. Euphausia brevis, Hansen, as E. mutica, is an antiequatorial

species collected only in regions B and D; Morphologically very similar to E. diomedae and of essentially identical size (mean size index: 118), it is however much less abundant; fewer than 400 individuals were captured. The northern boundary of the species was located in the vicinity of 9°13S ("Bora" I expedition).

22. Euphausia mutica, Hansen, presents the same type of antiequatorial distribution as the preceding species with a tendency to be more plentiful to the west rather than to the east. While E. brevis predominates in region D, E. mutica was more common in region B from where were drawn virtually all of the 500 individuals collected (northern boundary: 04°30S). The mean size index is essentially the same as that of E. diomedae and E. brevis (118). 48

23. Euphausia paragibba, Hansen, is a member of the "gibba group" (Hansen, 1910) and is essentially identical to the three other species. Consequently, as for the group S. maximum/S. abbreviatum and the group N. microps/N. gracilis, we accepted a certain percentage of uncertainty in determining distributions. As mentioned earlier, we deliberately chose to disregard closely observing very plentiful samples: individual dissection of male organs (which did not remove any uncertainty related to females or juveniles) is an example of a tedious operation which could not be applied to a great many specimens; we did not perform this dissection although it is the only criteria for definite identification. Furthermore, E. paragibba being the only species of that group found on the equator (Brinton, 1962 b), any possible confusion with one or the other of the "sister-species" could only occur with regions B or D. Nearly 11,000 individuals were collected in this category (average per station: 27); the mean size index was 120. 48

24. Euphausia tenera, Hansen, was the samllest species collected with the exception of S. microphthalma, its mean size index being only 74. The actual abundance of the species was therefore considerably under-estimated; Brinton (1962 b) considered the species as being almost constantly present on the equator, i.e., over 500 individuals per 1000 m^3. Our own estimates, assuming that barely 1% of the actual population was captured by the IKMT (Roger 1968 d), based on 20,000 specimens actually captured would indicate such an abundance (315 and 931 organisms per 1000 m^3 for Zones A and C respectively: cf. Table 9).

25. Euphausia distinguenda, Hansen, presents a distribution similar to that of E. exemia and E. gibboides, i.e., limited to the eastern section of the Equatorial Pacific. The animals being minute in size, identical or slightly larger than E. tenera, only 60 specimens were collected, exclusively during the first stations of the "Alizé" expedition (Zone E).

26. Euphausia fallax, Hansen, is similar to E. gibboides with the exception of the male copulative organ; however its distribution appears to be entirely different: The presence of E. fallax is as limited in the western Pacific as E. gibboides is in the eastern Pacific (Brinton, 1962 b). This distribution characteristic was the only one applied to identify both species; our findings can therefore be used neither to support further assumption of their separated biotopes, nor to further substantiate their specific validity. All 180 specimens collected originated from Zone B where they were found as far north as 08°28 S.

27. Nematoscelis tenella, G.O. Sars, was regularly collected on all expeditions. Given its mean size of 136, it was relatively well sampled by the IKMT; nearly 12,000 specimens were captured (average per station: 29).

28. Nematoscelis microps, G.O. Sars, was represented by over 12,000 individuals in our samples (average per station: 30). The mean size index was 135. This species was found inhabiting all five regions. Some confusion, particularly regarding juvenile stages, with N. gracilis resulted in some uncertainty in identifying individuals, without for that matter altering significantly any quantitative estimates: dubious cases account for only a small percentage of the specimens.

29. Nematoscelis gracilis, Hansen, is closely related to the preceding species in terms of both morphological (confusion of juvenile forms of both species; same mean size index: 135) and ecological aspects as N. gracilis was also captured very regularly on all expeditions. However, the habitat of N. gracilis appears to be somewhat deeper than that of N. microps. Over 21,000 specimens were collected (average per station: 53).

30. Nematoscelis atlantica, Hansen, is very difficult to differentiate from N. microps. The species is antiequatorial, however, and confusion could only arise at the southernmost sections of Zones E,D and only regarding a small number of specimens as only 400 individuals were collected. None were captured further north than 13°05 S.

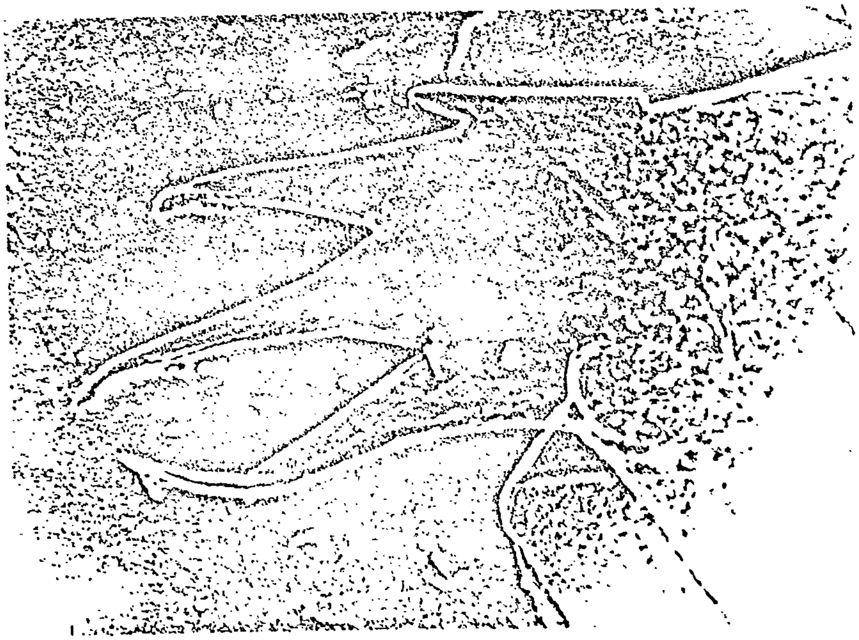
31. Nematobrachion flexipes, (Ortmann) Calman, was found in rather small numbers throughout all regions with a definite tendency to be more abundant in Zones C and E. The average size of 172 led us to assume that the 4000 specimens collected (average per station: 10) represented a fair proportion of total populations.

32. Nematobrachion sexspinosus, Hansen, was both more scarce and less ubiquitous than N. flexipes: Brinton (1962 b) confined its habitat on the equator to the west of 170°W and, in fact, none of the 700 organisms

PLANCHE II

C : *Euphausia eximia :* protubérance interne du second segment du pédoncule antennaire à 3 denticules (au-dessus, la protubérance externe à une seule pointe).

2nd Plate. — C : *Euphausia eximia* : protuberances of the distal end of the 2nd segment of the 1st antennal peduncle. *Foreground* : outer protuberance (simple). *Background* : inner protuberance (trifurcate). On the right, beginning of the dorsal keel of the 3rd segment.



D : id. : protubérance à 4 denticules.

D : id. : inner protuberance with 4 spine-shaped denticules.

were found in regions C and E. The mean size index, which could not be calculated, would be approximately 200, placing this species among the largest collected.

33. Nematobrachion boopis, Calman, was the most regularly distributed of the three species of that genus due likely to its deep-water habitat. Over 3000 specimens were collected (average per station: 8); the mean size index was established at 208. These organisms are generally fragile and a large percentage were injured when we collected them; the species was nevertheless very readily identified and was absent only towards the eastern boundary of the Pacific (Zone E).

34. Bentheuphausia amblyops, G.O. Sars, is considered scarce only because of its bathypelagic habitat seldom reached during routine sampling. Examination of the deep-water stations on our expeditions indicated that, on the contrary, the species is common in its biotope as over 1200 organisms were captured (mean size index: 254).

Note that Stylocheiron suhmii was not included among our samples although the species inhabits the Tropical Pacific (Brinton, 1962 b). However no specimens were retained in the sieve sorting the smallest size group considered in this study (0.7 mm thoracic ∅). A few individuals collected on recent expeditions will be used in examining vertical distributions (cf. Chap. IV).

C. MAJOR POPULATION ZONES

Although we had the relatively large number of 600 samplings to work with, they were concentrated in certain zones, very vast zones for that matter, and did not cover the entire Equatorial and South Tropical Pacific. If distribution charts cannot be established, the samplings can nevertheless be used to make a comparative study of the faunistic regions each one having been identified by a great many observations.

As mentioned earlier, we identified five major population zones, geographically defined earlier in this chapter. We shall also consider two special radials very clearly describing the transition between two or more faunas, namely:

- the entire area covered on the "Alizé" expedition, i.e., the Equatorial Pacific from the Galapagos to New Guinea (Zones A, C and E);
- the entire area covered on the "Bora" expeditions (20°S to 5°N on 170°E), which included Zones A and B, demonstrating in the western Pacific the transition between the tropical and equatorial zones.

The material used for the quantitative examination which follows originated from 311 stations occupied on the following expeditions:

Zone A : "Cyclone" II, III, IV, V, VI expeditions: 89 0-1200 m stations, 6 every 24 hours.

Zone B : southern sections covered on the "Bora" I, II, III, IV expeditions: eleven 0-350 m night stations, five 0-650 m night stations, seven 0-1200 night stations.

Zone C : "Caride" I, II, III, IV expeditions: ten 0-350 m night stations, eighty-four 0-500 to 0-1200 m night stations, thirty-one 0-500 to 0-1200 m day stations.

Zone D : "Atoll" and "Brisants" expeditions: forty-four 0-350 m night, fourteen 0-800 m day stations.

Zone E : eastern section of "Alizé" expedition: sixteen 0-350 m night stations.

A few remarks are in order at this point:

- all tows carried out by day at depths less than 500 m have not been considered as such depths are undeniably above the layers inhabited by the great majority of animals. For the remainder we deemed it preferable, given our intention to define each zone as a whole, to group a large number of samplings, although they might be somewhat unrelated. This approach resulted in appreciably over-estimating the populations of Zones B and E where only night stations were carried out, such stations always producing a much larger number of samples than day stations, even those at great depths.

- stations 10 to 39 on the "Alizé" expedition and all stations on the "Atoll" expedition having made use of a 5-foot IKMT, the number of specimens was multiplied by 4 to make them comparable to all other samplings drawn with a 10-foot IKMT.

- Euphausiids in Zones A and C were retained as specimens provided their thoracic diameter measured a minimum of 0.7 mm, in Zones B, D and E a minimum of 0.9 mm.

Another point may appear puzzling at first glance: approximately 30,000 m^3 of water are filtered during a 0-350 m station, 45,000 m^3 per 0-650 m tow, 70,000 m^3 per 0-900 m and 85,000 m^3 during a sampling at 0-1200 m. Yet, we shall directly compare the number of individuals captured per station without applying any corrective factor. The reason is as follows: 90% of the animals were collected by night in the 0-350 m layer; the 30,000 m^3 of water filtered in that layer for a 0-350 m station was, in reality, "efficient" filtering; on the other hand, during a 0-1200 m night station, 51 only the first 350 m were "efficient" (or the first 30,000 m^3), the remainder of the volume being in a zone that was practically deserted or lightly populated at that time. The same applied for 0-1200 m day tows which scanned the first 400 m unproductively. Therefore, as a first approximation, we might consider that all these samplings roughly correspond to a filtration of a similar volume of "populated" water in the order of

30,000 to 40,000 m^3.

- The "filtered" volume was defined earlier in Chapter II, i.e., the volume of water entering the 8.5 m^2 opening of the IKMT. Most of the minute organisms escaped through the 4 mm mesh of the forenet and a much smaller percentage was actually captured. However, as this fact was considered when estimating the percentage of animals collected by the IKMT in terms of size of animals, the final estimate of these small species, whatever their size,was related to the total volume of water entering the midwater trawl.

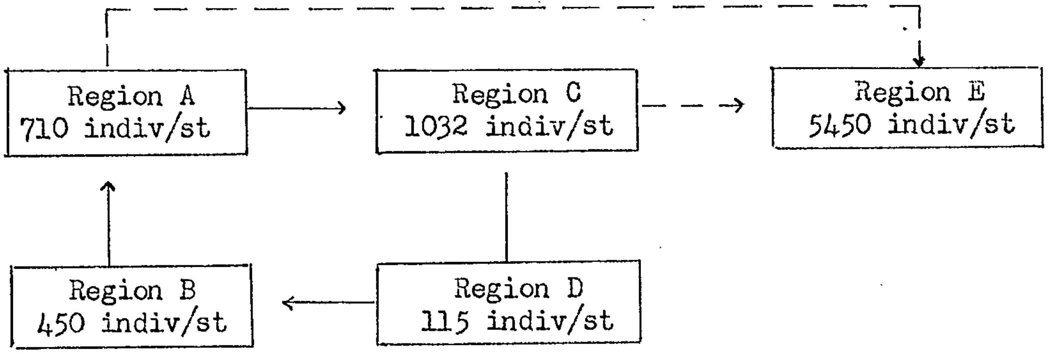
- Before examining the quantitative aspects of the distributions, we again bring to mind the fact that the fauna collected by means of the IKMT is actually involved and therefore likely bears little relationship, at least on a quantitative level, with a fauna which might have been captured in these same regions by means of a fine-mesh plankton net or a high-speed sampler with a small opening.

1. COMPARISON OF NUMBER OF SPECIMENS COLLECTED IN THE DIFFERENT REGIONS

Zone A : 710 individuals per station
Zone B : 450 " " "
Zone C : 1032 " " "
Zone D : 115 " " "
Zone E : 5450 " " "

The dearth of specimens drawn from Zone D (South Central Tropical Pacific) is immediately obvious. This zone appears to be a typical oligotrophic region contrasting sharply with the density of Zone E. The abundance of animals is in fact obvious throughout the equatorial zone as, on the same longitude, the figure increases from 450 to 710 individuals per station in the western Pacific and from 115 to 1032 in the Central Pacific. Note that the estimate of 450 individuals per station for Zone B is likely over-estimated as, contrary to other zones, specimens were drawn only during night stations when hauls were necessarily more abundant.

In the chapter dealing with the use of statistical tests, we mentioned that the five population zones were significantly different, quantitatively at a 5% threshold. The following diagram shows the variations in populations among the various zones: those adjacent to region E are indicated with a broken line to bring forth the fact, though evident, that it was not supported by the tests.



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Regions which do not seem to have been logically matched (A-D/D-E/B-C/B-E) were not compared.

In conclusion, a general look at the number of specimens collected indicated that the density of population in the five zones considered was highly dissimilar. By taking the mean, and arbitrarily applying the factor 1 to the least dense zone (Zone D), the following relative abundance indices were obtained:

Zone D (South Central Tropical Pacific) ...	1.0
Zone B (Southwest Tropical Pacific)	3.9
Zone A (Western Equatorial Pacific)	6.2
Zone C (Central Equatorial Pacific)	9.0
Zone E (Eastern Equatorial Pacific)	47.

2. SPECIFIC COMPOSITION OF THE FAUNA IN THE DIFFERENT REGIONS

Perhaps even more so than for giving a quantitative estimate of the populations, the influence of the sampling gear had certain repercussions on the specific distribution of the specimens: quite evidently, only approximately 1% of such minute species as *E. tenera* were sampled by the IKMT while some 80% of larger species such as *T. monacantha* were captured. We shall therefore firstly consider actual numbers of specimens and then attempt to estimate, from the estimated percentage of each size group captured by the IKMT (estimate obtained according to method described in Chapter II; see also Roger, 1968 d), the number of each species in the actual population.

On Table 8 this data is given for specimens collected by the IKMT for each zone and species. However, *S. microphthalma*, which virtually completely escaped the IKMT, as well as *T. egregia* and *T. cornuta*, both very scarce bathypelagic species, are not given; all three species were present only in negligible numbers.

Attention should be drawn to certain observations:

- Firstly, the number of species is essentially equal throughout the differant regions with a tendency to the species being slightly more numerous in the less abundant tropical zones (28 species for Zones B and D) than in the more abundant equatorial zones (25 species in Zones A and C). The fewer number of species found in Zone E is undoubtedly due, at least in part, to a less intensive programme having been pursued in that region. Among other considerations, the absence of the deep-water species *S. elongatum*, *N. boopis*, *T. cristata* and *B. amblyops* should not be considered significant as no tows were carried out at depths greater than 300 m. 53

- Secondly, only a few species predominate in number: *E. diomedae* representing 44% of total specimens for Zone A; 20% for Zone B and 36% for Zone C. The three species *T. aequalis*, *T. obtusifrons* and *T. tricuspidata* accounted for 68% of the specimens drawn from Zone D while *E. eximia* alone

TABLE 8

Specific composition of fauna in the various regions: average number per station and % of each species collected by the IKMT (The + sign indicates sporadic presence in very small numbers).

	Zone A		Zone B		Zone C		Zone D		Zone E	
T. cristata	2,7	0,4 %	1,3	0,3 %	0,4	—	1,0	0,9 %	—	
T. tricuspidata	41	5,8 %	75	16,7 %	78	7,6 %	22	19,1 %	15	0,2 %
T. orientalis	9,7	1,4 %	4,7	1,0 %	1,6	0,2 %	0,1	0,1 %	12	0,2 %
T. monacantha	13	1,8 %	7,1	1,6 %	23	2,2 %	0,4	0,3 %	1,5	—
T. pectinata	6,1	0,9 %	5,3	1,2 %	4,2	0,4 %	2,1	1,8 %	2,0	—
T. obtusifrons	+	—	13	2,9 %	—		23	19,7 %	—	
T. aequalis	38	5,4 %	22	4,9 %	28	2,7 %	33	28,8 %	5,3	0,1 %
T. subaequalis ♂	—		2,3	0,5 %	—		—		—	
S. carinatum	4,1	0,6 %	11	2,4 %	78	7,6 %	2,1	1,8 %	—	
S. abbreviatum	16	2,3 %	53	11,8 %	44	4,3 %	7,0	6,1 %	2,5	—
S. maximum	16	2,3 %	4,3	1,0 %	6,3	0,6 %	1,4	1,2 %	8,0	0,1 %
S. elongatum	3,2	0,5 %	8,7	1,9 %	0,3	—	0,9	0,8 %	—	
S. affine	11	1,5 %	3,3	0,7 %	33	3,2 %	—		—	
S. longicorne	6,1	0,9 %	6,0	1,3 %	4,3	0,4 %	0,7	0,6 %	—	
E. gibboides	—		—		1,9	0,2 %	—		298	5,5 %
E. eximia	—		—		0,2	—	—		4 804	88,2 %
E. diomedae	313	44,1 %	92	20,4 %	369	35,8 %	—		102	1,8 %
E. brevis	—		6,0	1,3 %	—		3,9	3,4 %	—	
E. mutica	—		21	4,7 %	—		+	—	—	
E. paragibba	28	3,9 %	29	6,4 %	44	4,3 %	0,2	0,2 %	3,0	—
E. tenera	43	6,1 %	1,8	0,4 %	127	12,3 %	+	—	—	
E. fallax	—		7,9	1,8 %	—		—		—	
E. distinguenda	—		—		—		—		3,7	—
N. tenella	57	8,0 %	15	3,3 %	17	1,7 %	1,2	1,0 %	66	1,2 %
N. microps	48	6,8 %	21	4,7 %	41	4,0 %	0,5	0,4 %	4,5	0,1 %
N. gracilis	31	4,4 %	5,2	1,2 %	115	11,2 %	0,1	—	78	1,4 %
N. atlantica	—		8,4	1,9 %	—		3,8	3,3 %	—	
N. flexipes	+	—	4,4	1,0 %	6,6	0,7 %	2,6	2,3 %	44	0,8 %
N. sexspinosus	1,2	0,2 %	6,7	1,5 %	—		6,5	5,7 %	—	
N. boopis	17	2,4 %	14	3,1 %	4,3	0,4 %	1,6	1,4 %	—	
B. amblyops	4,9	0,7 %	0,9	0,2 %	4,6	0,4 %	0,5	0,4 %	—	
TOTAL	710	—	450	—	1 032	—	115	—	5 446	

Note: T. egregia and T. cornuta, very scarce bathypelagic species, are not included in this table as well as S. microphthalma which virtually completely escaped the IKMT because of its very minute size.

3. ESTIMATES OF ACTUAL POPULATIONS

Estimates of actual populations will be deduced from this data by correcting the actual number of specimens by the percentage of specimens collected by the IKMT in terms of mean size of organisms. Thus, T. tricuspidata, for 54
example, which has a mean size index of 226, is considered to have been sampled at 20% (cf. fig. 34): the number of specimens collected of this species will therefore be multiplied by 5 to obtain an estimate of the

TABLE 9

Estimate of actual populations of main species throughout the various zones: number of individuals per 1000 m^3 and percentages (The + sign indicates sporadic presence of species in very small numbers).

	Zone A		Zone B		Zone C		Zone D		Moyenne	
T. tricuspidata	6,8	0,4 %	13	1,5 %	13	0,4 %	3,7	3,5 %	9,1	0,6 %
T. orientalis	1,3	0,1 %	0,6	0,1 %	0,2	—	+	—	0,5	—
T. pectinata	0,8	—	0,7	0,1 %	0,6	—	0,3	0,3 %	0,6	—
T. monacantha	1,7	0,1 %	0,9	0,1 %	3,1	0,1 %	+	—	1,4	0,1 %
T. aequalis	25	1,5 %	15	1,7 %	19	0,6 %	22	21,5 %	20	1,3 %
T. obtusifrons	+	—	8,7	1,0 %	—		15	13,9 %	5,9	0,4 %
T. subaequalis ♂	—		1,5	0,2 %	—		—		0,4	—
TOTAL *THYSANOPODA*	36	2,1 %	40	4,7 %	36	1,1 %	41	39,4 %	38	2,6 %
S. carinatum	22	1,3 %	59	6,9 %	416	13,0 %	11	10,6 %	127	8,6 %
S. abbreviatum	43	2,5 %	141	16,7 %	117	3,7 %	19	18,3 %	80	5,4 %
S. maximum	8,0	0,5 %	2,2	0,3 %	3,2	0,1 %	0,7	0,6 %	3,5	0,2 %
S. elongatum	16	0,9 %	43	5,1 %	1,5	—	4,3	4,2 %	16	1,1 %
S. affine	73	4,3 %	22	2,5 %	220	6,9 %	—		79	5,4 %
S. longicorne	31	1,8 %	30	3,5 %	22	0,7 %	3,5	3,3 %	22	1,5 %
TOTAL *STYLOCHEIRON*	193	11,2 %	297	35,0 %	780	24,4 %	39	37,0 %	327	22,2 %
E. diomedae	835	48,4 %	245	28,8 %	984	30,8 %	—		516	35,1 %
E. brevis	—		16	1,9 %	—		10	9,9 %	6,5	0,4 %
E. mutica	—		56	6,7 %	—		0,1	0,1 %	14	1,0 %
E. paragibba	75	4,3 %	77	9,0 %	117	3,7 %	0,5	0,5 %	67	4,6 %
E. tenera	315	18,2 %	13	1,5 %	931	29,1 %	0,2	0,2 %	315	21,4 %
TOTAL *EUPHAUSIA*	1 225	70,8 %	407	47,9 %	2 032	63,5 %	11	10,7 %	919	62,5 %
N. tenella	114	6,6 %	30	3,5 %	34	1,1 %	2,4	2,3 %	45	3,1 %
N. microps	96	5,6 %	42	4,9 %	82	2,6 %	1,0	1,0 %	55	3,7 %
N. gracilis	62	3,6 %	10	1,2 %	230	7,2 %	0,2	0,2 %	76	5,2 %
N. atlantica	—		17	2,0 %	—		7,6	7,2 %	6,2	0,4 %
TOTAL *NEMATOSCELIS*	272	15,7 %	99	11,7 %	346	10,8 %	11	10,7 %	182	12,4 %
N. flexipes	+	—	2,9	0,4 %	4,4	0,1 %	1,7	1,6 %	2,2	0,1 %
N. boopis	4,0	0,2 %	3,3	0,4 %	1,0	—	0,4	0,4 %	2,2	0,1 %
TOTAL *NEMATOBRACHION*	4,0	0,2 %	6,2	0,7 %	5,4	0,2 %	2,1	2,0 %	4,4	0,3 %
B. amblyops	0,7	—	0,1	—	0,6	—	0,1	0,1 %	0,4	—
TOTAL	1 731	—	849	—	3 200	—	104	—	1 471	—

actual density of *T. tricuspidata*. The figures thus obtained will then be brought to 1000 m^3 of water, by assuming (cf. earlier) that for each zone the "efficient" volume of water filtered was 30,000 m^3 per station.

In Table 9 the estimated density of individuals per 1000 m^3 of water is given for each species and zone.

Note:

- Size groups were not established for the "Alizé" expedition and therefore, no mean size index could be assigned to the species particular to Zone E (*E. eximia*, *E. gibboides*) and no estimate can be made of actual populations.
- Other species which do not appear in this table occurred only in very

limited numbers; their mean size index was difficult to determine and their absence virtually does not alter the estimate of actual populations.

The first observation is that the actual density of Zones A and D follows the same order indicated in § 1, but that the difference between the regions is more pronounced than could be established by merely examining the specimens collected; by again applying the arbitrary factor of 1.0 to Zone D, a relative density index of 8.2 is obtained for Zone B, 16.6 for Zone A and 30.8 for Zone C. This would indicate that our samplings underestimated actual populations even more when density was greater, i.e., the denser the population, the greater is the percentage of minute species. This fact could be expressed as follows: we shall calculate the percentage of the population, for each region, which makes up the species having a mean size index lower than 100 (S. carinatum, S. elongatum, S. affine, S. longicorne, E. tenera) and those having an index greater than 170 (all species of the genera Thysanopoda and Nematobrachion, in addition to S. maximum and B. amblyops).

By classifying the 4 zones in increasing order of density, the following results were obtained:

Increasing density →

	Zone D	Zone B	Zone A	Zone C
% index < 100 (= small species)	18,3 %	19,5 %	26,5 %	49,7 %
% index > 170 (= large species)	42,1 %	5,7 %	2,8 %	1,4 %

It is readily obvious that the proportion of small organisms increases as population density increases and that larger animals are more abundant in less dense zones. The significance of this fact will be outlined when the position of Euphausiids in the food chain will be discussed. Individuals 1 cm long or those 3 cm long are definitely not prey to the same predators and hence, the trophic definition of a given population depends to a certain extent on the size of its individuals.

It was rather interesting to compare our estimates of the density of species against those obtained by authors who had used other techniques. The point was not to verify figures as it is extremely difficult to accurately determine the actual density of a pelagic population. We believe that the estimates of other authors are, for other reasons related to methodology, as inaccurate as our own; we merely wished to check whether similar conclusions were reached by applying basically different methods and deductions. We applied data made available by Brinton (1962 b), given in the form of distribution charts; we compared our own results for Zone C against the charts for the central equatorial region for those species for which this author gave quantitative estimates. Figures indicate the number of individuals per 1000 m^3 (Table 10). Taking into account the inherently gross inaccuracies made in giving quantitative estimates of planktonic populations, 56
we noted that both series generally agreed with one another, except perhaps for the rather great disparity with respect to T. tricuspidata, this large species having been fairly well sampled by the IKMT. For his part, Ponomareva (1966) estimated a density of 100-500 Euphausiids per 1000 m^3 at a depth between 0 and 10 m in the Equatorial Pacific.

Figure 38 is a graph showing the estimated actual numbers of individuals per 1000 m^3 of water for the various species: the figures used were the means for Zones A to D. A comparison with fig. 37 will point out the influence of the sampling gear on the type of data made available. Taking into account only those species for which actual populations were estimated, Table 11 gives in numerical order both the number of specimens collected and actual populations.

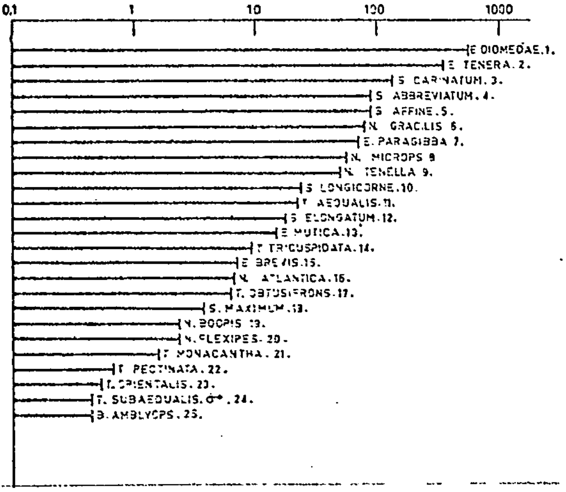

Fig. 38. — Nombres réels estimés d'individus par 1000 m³ d'eau (moyenne des régions A à D) et ordre d'importance numérique des espèces.
Fig. 38. — Estimated actual numbers of individuals per 1000 m³ of water (mean values for the 5 areas).

4. CHANGE IN FAUNA FROM EAST TO WEST IN ~~THE~~ EQUATORIAL PACIFIC

We established earlier that in the Equatorial Pacific, where populations were denser than in the tropical zone, density considerably decreased as one progressed from east to west (cf. also Desrosières, 1969, Voronina, 1964 b); furthermore, specific composition varied appreciably from Zone E to Zone C and to Zone A. These facts were established at the beginning of this chapter from data obtained on the various expeditions for each zone and selected on the basis of numerous and varied samplings required to properly establish satisfactory means. Nevertheless, one expedition carried out from the Galapagos to New Guinea over the full width of the Pacific was more likely to result in homogeneous samplings and in better observation of the transition from east to west. This was the purpose of the "Alizé" expedition carried out from November 1964 to March 1965 on the equator between 92°20W and 162°45E. Thirty-three IKMT stations were conducted, by night, between 0 and 350 m approximately (Roger, 1967 b). Examination of the specimens collected brought several facts to light:

- The great density of the Equatorial Pacific decreases progress- 58
ively as one moves westward, this fact confirming previous observations.
- A marked difference in specific compositions. Three well

TABLE 10

Number of individuals per 1000 m^3 calculated for Zone C and estimates given by Brinton (1962 b).

	Zone C	Brinton (1962 b)
T. tricuspidata	13	50 à 500
T. orientalis	0,2	« rare »
T. pectinata	0,6	« rare »
T. monacantha	3,1	« rare »
S. carinatum	416	50 à 500
S. abbreviatum	117	1 à 50
S. maximum	3,2	« rare »
S. elongatum	1,5	« rare »
S. affine	220	50 à 500
E. diomedae	984	50 à 500
E. paragibba	117	1 à 50
E. tenera	931	plus de 500
N. tenella	34	1 à 50
N. microps	82	1 à 50
N. gracilis	230	50 à 500
N. flexipes	4,4	1 à 50
N. boopis	1,0	« rare »

TABLE 11

Species in numerical order according to number of specimens, from IKMT hauls and estimates of actual populations, for the entire zone investigated. (Species for which no actual density could be estimated are not included).

	IKMT hauls	Estimated actual pop.
E. diomedae	1	1
T. tricuspidata	2	14
N. gracilis	3	6
E. tenera	4	2
S. abbreviatum	5	4
T. aequalis	6	11
N. microps	7	8
N. tenella	8	9
E. paragibba	9	7
S. carinatum	10	3
T. monacantha	11	21
S. affine	12	5
N. flexipes	13	20
N. boopis	14	19
S. maximum	15	18
T. orientalis	16	23
T. obtusifrons	17	17
T. pectinata	18	22
S. longicorne	19	10
B. amblyops	20	25
S. elongatum	21	12
E. mutica	22	13
N. atlantica	23	16
E. brevis	24	15
T. subaequalis ♂	25	24

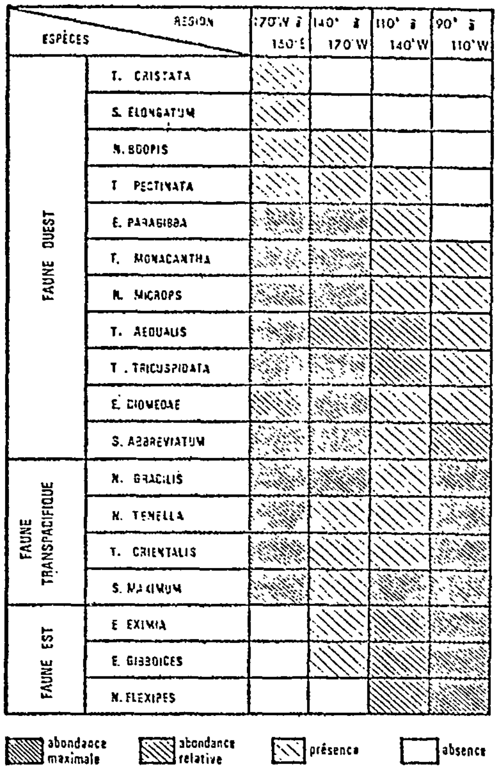

Fig. 39. — Évolution faunistique Est-Ouest dans le Pacifique équatorial.

Fig. 39. — East-West faunistic evolution on the equator, and definition of the Western, Transpacific and Eastern faunas.

differentiated faunas were identified:

. an eastern fauna, numerically very dense, including few main species seldom found to the west of 140°W (corresponding to Zone E defined earlier): E. eximia, E. gibboides, N. flexipes.

. a western fauna, less dense, including a greater number of species: T. cristata, S. elongatum, N. boopis, T. pectinata, E. paragibba, T. monacantha, N. microps, T. aequalis, T. tricuspidata, E. diomedae, S. abbreviatum.

. a trans-Pacific fauna, found throughout the whole length of the expedition, which tended to display a bimodal quantitative distribution, with fewer specimens being collected in the Central Pacific: N. gracilis, N. tenella, T. orientalis, S. maximum.

This faunistic distribution is shown on figure 39.

If the physical environment is characterized by a simple parameter outlining evolution along a longitude, e.g., depth of 15° isotherm (cf.

Chap. I), the quantitative distribution of the three faunas defined above follows a distinct pattern (fig. 40). This situation will be examined further in the chapter on Ecology by introducing diversity into the matter.

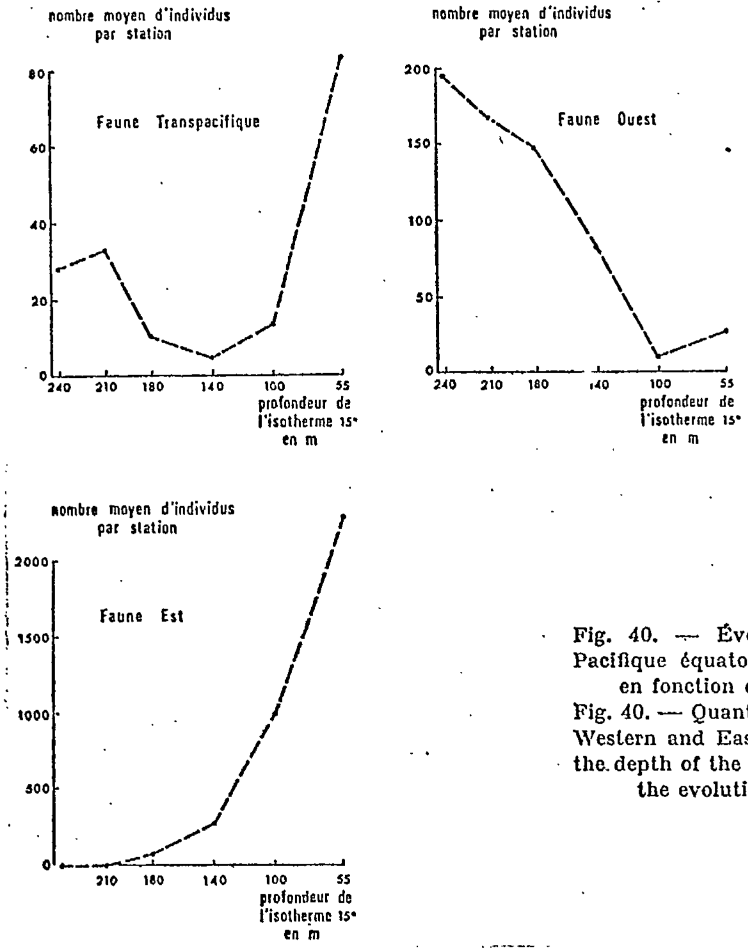

Fig. 40. — Évolution faunistique Est-Ouest dans le Pacifique équatorial : abondance des différentes faunes en fonction de la profondeur de l'isotherme 15°.
Fig. 40. — Quantitative distributions of the Transpacific, Western and Eastern faunas on the equator as regard to the depth of the 15 °C isotherm, choosen as to represent the evolution of the environment (see fig. 5).

5. CHANGE IN FAUNA FROM NORTH TO SOUTH IN THE WESTERN PACIFIC

Likewise, the transition from a tropical to an equatorial fauna in the western Pacific became obvious when examining specimens collected during the "Bora" expeditions which drew samples from 20°S to 4°N on 170°E (Zones A and B). There again, faunistic variations in terms of both numbers and species were extremely pronounced (Roger, 1968 b). The transition between the tropical zone (Zone B) and the equatorial zone (Zone A) occurred between 4 and 8°S and was characterized by three very definite conditions: a change in the specific composition of the faunas, a sharp increase in overall density (cf. also Le Bourhis and Wauthy, 1969) and different distribution characteristics.

5.1. Specific Composition of Fauna

As the expeditions progressed from south to north, the following species disappeared or became scarce: *T. obtusifrons*, *T. subaequalis*, *S. carinatum*, *E. fallax*, *E. brevis*, *E. mutica*, *N. atlantica*, *N. flexipes*, *N. sexspinosus*. These species are essentially or exclusively tropical. They were replaced by other species, fewer in number, but represented by a great many more individuals: *T. monacantha*, *E. diomedae*, *N. gracilis*, the tropical affinities of which are obvious. Figure 41 shows numerical variations in these tropical and equatorial faunas as a function of latitude. Other species were distributed somewhat more evenly throughout the region and tended to generally benefit from the greater density of the equatorial environment.

5.2. Comparative Density of Both Zones

Results agree with those established at the beginning of this chapter and indicate a considerable increase in the number of specimens collected as the expeditions progressed northward (fig. 42). Taking only night stations into account, an average of 510 individuals were collected per station between 20°S and 4°S and 1916 between 4°S and 4°N.

5.3. Distribution Characteristics 61

Examination of the number of individuals captured at each station indicated that the species sampled remained rather constant from one tow to another in the tropical zone, but that the samples were markedly less homogeneous, for certain species in any case, in the equatorial zone:

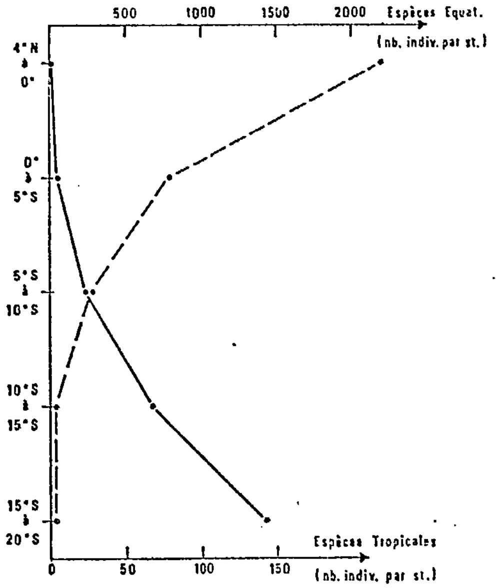

Fig. 41. — Évolution faunistique Nord-Sud dans le Pacifique ouest (170° E) : abondance des faunes tropicale (—) et équatoriale (- - - -) en fonction de la latitude.

Fig. 41. — Quantitative distributions of the Tropical (——) and Equatorial (- - -) faunas from 20° S to 4° N in the western Pacific (170° E). (Average numbers of animals per standard haul).

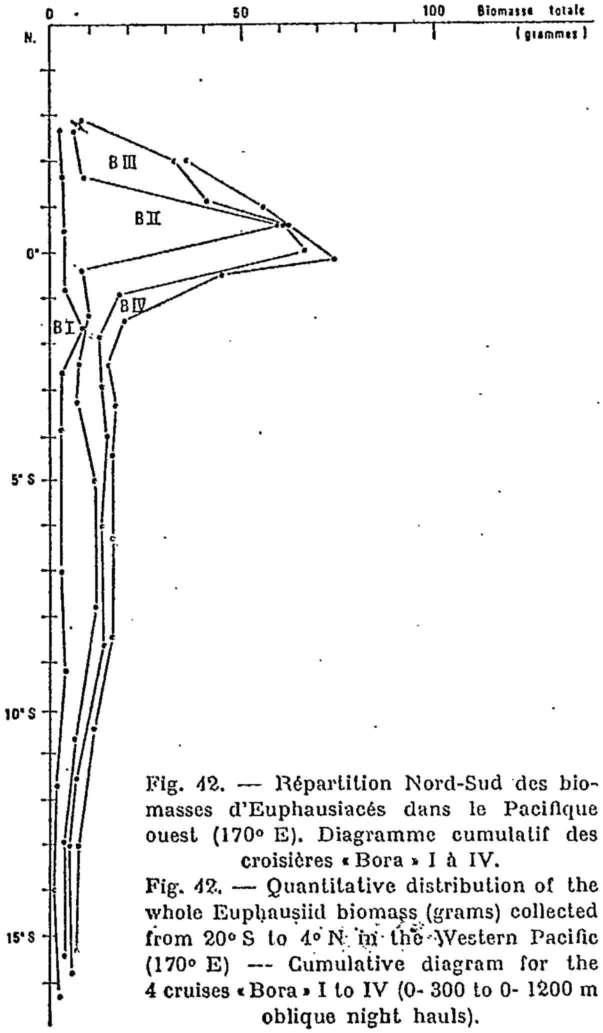

Fig. 42. — Répartition Nord-Sud des biomasses d'Euphausiacés dans le Pacifique ouest (170° E). Diagramme cumulatif des croisières « Bora » I à IV.

Fig. 42. — Quantitative distribution of the whole Euphausiid biomass (grams) collected from 20° S to 4° N in the Western Pacific (170° E) — Cumulative diagram for the 4 cruises « Bora » I to IV (0- 300 to 0- 1200 m oblique night hauls).

this was particularly the case for T. tricuspidata, E. diomedae, S. abbreviatum. We mention this fact at this point only as one of the characteristics distinguishing both regions: swarmming will be discussed in greater detail in the following section; the heterogeneity of distributions will be tested by applying a dispersion factor.

As with the east-west transition in the Equatorial Pacific, the north-south faunistic evolution in the western Pacific will again be examined in the chapter on Ecology in the light of data obtained by calculating a diversity index.

6. CHANGE IN FAUNA FROM NORTH TO SOUTH IN THE CENTRAL PACIFIC

We noted a very pronounced north-south gradient in the South Central Pacific between the very sparsely populated region D (15-25° S) and the much denser equatorial region C. Two research programmes were recently conducted by the R.V. "CORIOLIS" in the zone located between these two regions, essentially at 10° S and 142° W, some hundred miles off the Marquesas Islands. Initial examination of the data, processed insufficiently to be included in this study, definitely confirmed a north-south evolution in Euphausiid populations in terms of both overall density and specific distribution. The characteristics of this region, as compared with Zones C and D, are given in Table 12 hereunder.

Table 12

North-south faunistic evolution in the Central Pacific
(Change in fauna from north to south in the Central Pacific)

		Zone C (équateur)	Iles Marquises (10° Sud)	Zone D (15 à 25° S)
Mean number of individuals per station		1032	438	115
Estimate of actual pop.	Nombre total par 1000 m^3	3200	1000	104
	% *Thysanopoda*	1 %	11 %	39 %
	% *Euphausia*	64 %	44 %	11 %
	% *Stylocheiron*	24 %	37 %	37 %
	% *Nematoscelis*	11 %	7 %	11 %
	% *Nematobrachion*	0,2 %	1 %	2 %

There are striking faunistic similarities between this region and its homologue, the western Pacific (Zone B); it appears, however, that the abundance of species, due to equatorial divergence, becomes apparent further south in the Central Pacific than in the western Pacific. In comparison with Zone D, Euphausiids were definitely more plentiful at 10° S while in region B, abundance due to proximity to the equator was not noted before reaching 4° S (fig. 42). In other words, we confirmed that even in the case of macroplanktonic organisms, the latitudinal extension of the rich equatorial belt becomes sparser as one progresses westward.

In the chapter on trophic relationships, we shall mention that these particularly latitudes (10-20° S) are in fact major tuna (Thunnus alalunga) longline fishing zones.

D. DISTRIBUTION CHARACTERISTICS

In using the data forming the basis of this study, two characteristics have constantly interfered with the establishment of means. One of those factors introducing non-normal distributions was the heterogeneity of distributions, of which the swarmming habits displayed by certain species is an extreme case; nychthemeral variations constituted the other factor (cf. also Franqueville, 1970).

1. HETEROGENEITY OF DISTRIBUTIONS AND SWARMMING

The heterogeneity of distributions is a known constant of the planktonic world (Aron, 1958 a; Cushing, 1962; Griffiths, 1963; Hardy, 1955, Omaly, 1968; Wiebe, 1971...). More particularly in the case of Euphausiids, such distribution patterns are considered common (Brinton, 1962 a; Casanova-Soulier, 1968 and 1970; Einarsson, 1945; Fisher, Kon and Thompson, 1953; Forsyth and Jones, 1966; Komaki, 1967 b; MacKintosh, 1934, 1967 and 1968; Zelickman, 1959 and 1961...). Measuring the extent of the heterogeneity remains nevertheless a delicate procedure, the actual distribution being of course closely related to the methods that were applied. Although a major concentration of organisms observed visually near the surface of the water could be immediately recognized as a "swarm", it was much more difficult when processing data to detect whether swarmming had occurred as collecting the specimens had involved filtering millions of cubic metres of water; it was therefore extremely difficult, if not utterly impossible, to detect whether the sampling gear had at any given time passed through a particularly dense concentration of individuals.

Given those observations, what size of swarm were we likely to notice when we examined our data? Our sampling method was essentially the filtering of volumes of water at each station. If we assumed in first analysis that the distribution of individuals was a random selection (dispersion factor $a = (S^2 - m)/(m^2 = 0)$ both within a swarm and out of it, the danger of falsely arriving at a homogeneous distribution decreases as the volume of filtered water increases because the chances of encountering a swarm or completely by-passing one are considerably diminished (Aron, 1958 b). The inverse possibility does exist however, i.e., filtering a volume of water in proportion much more considerable than the size of the swarms. If we assume that a group of 500 individuals occurred in every 1000 m^3, a tow filtering 30,000 m^3 will include such extensive material that the heterogenity of the distribution will be entirely overlooked. However, if such a tow were carried out in a zone where a species is distributed on the basis of one large swarm of 5×10^5 individuals in every 10^6 m^3, the nature of the distribution will become apparent. We therefore readily admit that our results, obtained by filtering great volume of water, did not enable us to estimate the type of micro-distribution of species, but should, how- 63
ever, have made it possible to detect the presence of large swarms.

Our own definition of a "swarm" was both empirical and arbitrary insofar as it was related to our sampling method. We classified as "swarms" collections of specimens greater than $m+3$ S (where m is the mean of all values and S is the standard deviation) and greater than 10 m' (where m' is the mean of observations after elimination of values $> m+3$ S). In other terms, we considered as expressing possible swarmming phenomena only those values differing widely from the normal number of specimens collected for the given species ($> m + 3\ S$) and consisting in an inherently much greater abundance of specimens than those collected at other stations ($> 10\ m'$). Examination of Tables 14, 15 and 16 will indicate that these two quantities, namely $m + 3\ S$ and $10\ m'$, are independent values, one or the other being the greater depending upon the sampling series being considered. Hence, the importance of bearing in mind the extent of such phenomena: whenever we mention that "no swarms were encountered", the reader must assume that there were "no concentrations of individuals greater than $m + 3\ S$ or $10\ m'$" without for that matter implying that smaller concentrations did not exist.

After discussing the problem of swarmming, we shall attempt to determine how the organisms, other than those in swarms, were distributed. To do so, we shall consider only mean values for which coefficients of dispersion will be calculated; this will give an idea of the greater or lesser tendency of individuals to form groups according to species, time of day, depth, etc. Finally, we shall comment on the form of distributions.

Table 13 gives a summary of the data used to study the nature of distributions.

1.1. Swarmming

Examination of specimens revealed that only four species displayed swarmming habits, swarmming being understood as defined earlier: *E. eximia*, *E. diomedae*, *T. tricuspidata*, *S. abbreviatum*. Swarms of the first species were encountered only on the "Alizé" expedition and even then, the material was inadequate for a thorough study. We shall therefore examine the distributions of *L. diomedae*, *T. tricuspidata* and *S. abbreviatum* as obtained from several different tows: 0-350 m, 0-650 m, 0-900 m, 0-1200 m daytime tows and night tows at the identical depths (the few specimens collected during the 0-350 m daytime tow were disregarded). We could not reject an a priori hypothesis that a given species formed widely different groups depending upon time of day or depth and it was therefore necessary to examine each sample separately. Other factors such as age, sex, sexual maturity, etc. also came into play; however, too many categories would require examining samples too small to be representative. We might also point out that *E. fallax*, an important prey for surface bonito, very likely also forms into swarms; its limited geographical distribution (West Tropical Pacific) meant that we collected only a limited number of specimens and therefore, the behaviour patterns of that species will not be discussed at this point.

The distribution characteristics of *E. diomedae*, *T. tricuspidata* and *S. abbreviatum* are given in Tables 14, 15 and 16 for all 249 stations mentioned in Table 13.

E. diomedae

Considering night tows only, which appeared more heterogeneous, and taking into account the fact that the number of nocturnal observations was twice that for daytime stations, we recorded 6 swarms (defined by the two-fold requirement $> m + 3\ S$ and $> 10\ m'$) on a total of 165 observations. Assuming that each station represented some 30,000 m^3 of water being efficiently filtered, we concluded that a large swarm was present approximately every "inhabitated" $8 \times 10^5\ m^3$ for this species (by night). Given the mean percentage of *E. diomedae* captured by the IKMT (fig. 34), we might estimate the actual population at 4×10^6 organisms for every $5 \times 10^6\ m^3$ 66
inhabited, on the basis of the night hauls, or a density of 0.8 individual per cubic metre, broken down as:

TABLE 13

Stations used to examine Distribution Characteristics

	350 m nuit night	600 m jour day	600 m nuit night	900 m jour day	900 m nuit night	1 200 m jour day	1 200 m nuit night
BORA I	6.10.14. 18.22.25. 26.			9.13.17. 21.	7.11.15. 19.23.		
BORA II	7B.8B.10B. 11B.12B. 13B.14B. 16B.17B.		9B.	9A.10A. 11A.13A. 14A.			
BORA III		12.16.20. 24.28.37. 40.	10.14.18. 22.26.30. 34.42.	32.			
BORA IV				20.	21.23.	9.11.13. 15.18.22.	9.10.12. 14.16.17. 19.
CYCLONE II						3.4.9.10. 15.16.	1.6.7.12. 13.18.19.
CYCLONE III						3.4.9.10. 15.16.	1.6.7.12. 13.18.19.
CYCLONE IV						3.4.9.10.	1.6.7.12. 13.
CYCLONE V						1.6.7.12. 13.18.	3.4.9.10 15.16.
CYCLONE VI						3.4.9.10. 15.16.	1.6.7.12. 13.18.
CARIDE I	24.54.55. 63.61.88. 89.94.126. 127.128.	27.44.45. 46.64.65. 81.97.99. 116.117. 118.	31.32.48. 49.50.67. 68.69.83. 84.103.120. 121.122.	26.28.70. 71.98.	30.35.36. 73.74.75. 101.102. 107.108.	33.34.38. 39.40.72. 76.77.78. 104.105.106 110.111.112	41.42.43. 109.113. 114.115.
CARIDE II			38.39.40. 71.73.108. 109.		44.77.79. 113.115.		45.114.
CARIDE III			54.56.58. 102.104. 153.185. 189.		116.117. 118.150. 152.202.		68.69.70.
CARIDE IV			27.29.61. 63.65.97. 99.101.133. 137.		26.28.30. 62.64.66. 70.98.100 134.136.138		
Total no. of stations Nombre total de stations.......	27	19	48	16	40	49	50

TABLE 14

Particulars of E. diomedae Distributions (all values)

	0-350 m nuit	0-650 m jour	0-650 m nuit	0-900 m jour	0-900 m nuit	0-1 200 m jour	0-1 200 m nuit
Number of observations Nombre d'observations n	27	19	48	16	40	49	50
Effectif E. no. of specimens	10 605	2 701	46 824	1 996	19 272	9 411	24 601
Moyenne m Mean	393	142	975	125	482	192	492
Variance $S^2 = \frac{\Sigma e^2}{n-1}$	292 814	10 503	4 210 720	18 814	484 736	334 237	818 270
Écart type $S = \sqrt{\frac{\Sigma e^2}{n-1}}$ Standard deviation	541	102	2 052	137	696	578	905
m+3 S	2 016	548	7 131	536	2 570	1 926	3 207
10 m'	2 980	1 420	5 580	1 250	3 760	1 090	3 270
No. of swarms observed Nombre d'essaims observés > m+3 S et > 10 m'	1	0	2	0	1	1	2

TABLE 15

Particulars of T. tricuspidata Distributions (all values)

	0-350 m nuit	0-650 m jour	0-650 m nuit	0-900 m jour	0-900 m nuit	0-1 200 m jour	0-1 200 m nuit
No. of observations Nombre d'observations n	27	19	48	16	40	49	50
Effectif E. No. of specimens	7 192	1 528	3 183	1 810	3 540	1 618	3 019
Moyenne m Mean	266	80	66	113	89	33	60
Variance $S^2 = \frac{\Sigma e^2}{n-1}$	215 373	45 790	7 027	17 032	21 854	414	5 512
Standard deviation Écart type $S = \sqrt{\frac{\Sigma e^2}{n-1}}$	464	214	84	130	148	20	74
m+3 S	1 658	722	318	503	533	93	282
10 m'	1 860	300	560	847	703	320	526
No. of swarms observed Nombre d'essaims observés > m+3 S et > 10 m'	1	1	(1)	0	1	0	0

(1) Haul of 551 individuals

TABLE 16

Particulars of S. abbreviatum Distributions (all values)

	0-350 m nuit		0-650 m jour	0-650 m nuit	0-900 m jour	0-900 m nuit	0-1200 m jour	0-1200 m nuit
	(1)	(2)						
No. of observations Nombre d'observations n	27	26	19	48	16	40	49	50
Effectif E. No. of specimens	9 062	1 154	334	1 857	560	1 740	644	1 687
Moyenne m Mean	336	44	18	39	35	44	13	34
Variance $S^2 = \frac{\Sigma e^2}{n-1}$	2 207 207	1 862	294	1 899	4 243	4 500	285	1 816
Standard deviation Écart type $S = \sqrt{\frac{\Sigma e^2}{n-1}}$	1 490	43	17	44	65	67	17	43
m+3 S	4 806	173	69	171	230	245	64	163
10 m'	440	380	180	320	210	310	110	250
No. of swarms observed Nombre d'essaims observés > m+3 S et > 10 m'	1	0	0	0	1 (3)	1 (3)	0	0

(1) All values.
(2) After eliminating 7908.
(3) Low count, rather doubtful.

— 2.5. 10^6 specimens for 4.7 x 10^6 m^3 or 0.5 individual/m^3 for the zone where no swarms were supposedly encountered

— 1.5. 10^6 individuals for all six swarms which include some 40% of the population or an average of 250,000 individuals per swarm.

We were unable to estimate the size of these swarms on the basis of our data. Assuming that they were identical to those occurring in cold or temperate waters (cf. Burukovskiy, 1967; Hardy, 1965; Hardy and Gunther, 1939; Nemoto, Ishikawa and Kamada, 1969; Ozawa et al, 1968...), which still remains to be proven, i.e., the average volume of a swarm is in the order of 30 m^3, the density of the animals within the swarm would reach 10,000-16,000 individuals per cubic metre approximately. Although it may appear somewhat high, this estimate is rather conservative by certain evaluations and corresponds to a biomass of 150-250 grams per cubic metre: Nemoto (1966) estimated the biomass of E. superba in the Antarctic at 10-100 kg/m^3; Mauchline and Fisher (1969) estimated the density of swarms at 30,000 individuals/m^3. Swarms in equatorial zones are therefore both smaller and less dense than swarms inhabiting colder waters.

The above figures are of course only approximations and the reader must bear in mind the phenomena which we attempted to define: quite evidently, in addition to these large swarms, other smaller groups of varying sizes also occur; however, our techniques could not detect their presence. Furthermore, it is not entirely impossible that what appeared to be a single swarm was in reality the sum of several smaller groups : Burukovskiy (1967) and Zelickman (1961) noted the existence of such "swarm zones" no more than 67
a few metres in diameter.

T. tricuspidata

We shall apply to this species the same criteria and method of deduction to the data given in Table 15 as we did earlier for E. diomedae, but without developing these criteria.

Similarly to the preceding species, on the average night hauls appeared more irregular than daytime hauls (except for the 0-650 m tows) as we noted three presumed swarms among specimens collected at night against only one in the day stations. Here again, we shall consider only the nocturnal distribution which is the more heterogeneous. Swarms were encountered on the basis of one every 1.7 x 10^6 m^3 approximately (i.e., meeting the two-fold condition of m+3 S and 10 m' which we considered satisfactory for the methods we applied; use of a small net filtering some hundred cubic metres at each station would have resulted in our selecting an entirely different scale of reference and therefore in examining different phenomena and reaching different conclusions).

The estimated percentage of animals of this species captured by the IKMT being in the order of 20% (cf. fig. 34), the actual population would reach 85 x 10^3 organisms for every 5 x 10^6 m^3 or approximately 0.017 individual/m^3. As the zone where no swarms were encountered accounted for approximately 66 x 10^3 animals or 0.013 specimen/m^3, we arrived at an estimate of 19 x 10^3 individuals, or 20% of the population grouped into swarms each including approximately 6000 T. tricuspidata on the average; the very small number of organisms in the swarms would suggest that the swarms were rather small.

S. abbreviatum

The situation is much more definite (Table 16) in the case of this species than for the other two as only one swarm (7908 individuals at the "Bora" II station 16B) could be safely considered as such. Although values 273 (st. 17, "Bora" II) and 312 (st. 107, CA I) only slightly exceed their respective limits $m+3S$ and $10\ m'$, because they indicate only limited abundance, these values were rather doubtful and were not considered.

By applying to S. abbreviatum the same reasoning as to E. diomedae and T. tricuspidata, the following estimates were obtained; again, only figures for night hauls were examined. Only one swarm was noted during filtration of $5 \times 10^6\ m^3$, its population being estimated at 5.8×10^5 individuals or $0.12/m^3$ on the average, broken down as:

- swarms: 3.2×10^5 organisms
- single individuals : 2.6×10^5 individuals or an average of $0.05/m^3$.

Over half of the population appeared to be part of a swarm, a rather large swarm insofar as the available data enabled us to judge: such swarms were encountered so infrequently that their actual frequency could be accurately established only on the basis of data obtained from several hundred stations.

There is mention in the chapter "Nutrition" that S. abbreviatum is typically carnivorous; the occurrence of swarmming in this species would therefore contradict, at least for a tropical environment, the suggestions of Zelickman (1960) and Ponomareva (1963) that swarmming is due to a trophic stimulus proper to phytophagan.

Does swarmming actually occur under certain well defined conditions? 68

Burukovskiy (1967) examined all the hypotheses set forth to explain the formation of swarms and came to the conclusion that uncertainty prevailed: trophic stimuli (Zelickman, 1958 and 1961; Ponomareva, 1963), sexual stimuli (Ponomareva, 1959 a and 1963), passive accumulation due to currents (Rustad, 1930), or a combination of several of these factors (Naumov, 1962; Tonolli, 1958).

Table 17 indicates stations during which, among all 600 samplings, the presence of swarms was undeniably recorded. Numerous other probable cases were noted, but we preferred to restrict ourselves to observations of which we were certain. According to that table, it would appear that the season, depth (insofar as we could judge by using an open net) and weather conditions play no significant part in causing the formation of swarms. However, we noted the following:

1. All swarms were observed in the immediate vicinity of the equator and only in the western Pacific; no definite swarmming was noted during the 200 or so samplings carried out in the Central Pacific ("Caride" expeditions). The location of those swarms neither contradicts nor supports the hypothesis proposed by Zelickman (1961) who claimed that swarmming was particular to a highly stratified environment; all swarms were found in the Equatorial Pacific and not in a more homogeneous tropical environment and all were also found in the western Pacific which is less stratified than the eastern Pacific(1).

2. The great majority of swarms were noted during the night, only one during daytime. Contrary to a conventional hypothesis, it would appear that visual motivation is not a prime factor causing swarmming. There would therefore be greater justification in seeking a trophic, biological (reproduction) or ecological (cf. Casanova-Soulier, 1968) stimulus. Among the six stations during which the lunar phase was noted, for five of these the moonlight was very dim (LQ and NM); the only observation at a full moon phase occurred under heavily overcast skies.

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(1) However, although no swarms were noted among the 200 samples drawn in the Central Equatorial Pacific, during the 800 other tows that were not examined in detail a swarm of T. tricuspidata was observed during station 41 on the "Caride"III expedition (0-230 m, 1930 hours). Swarmming therefore does occur in the Central Equatorial Pacific but, it would appear, less frequently than in the Western Equatorial Pacific.

3. For 4 out of the 10 stations, strong currents were detected by a sudden pull on the towing cable of the net. Relating this observation to point 1, we might suggest the possible influence of dynamic factors in the formation of swarms, without attributing them a definite cause-and-effect relationship. Komaki (1967 b), Cassie (1959) also stressed the importance of the physical environment.

4. Independently of hauls carried out in the open sea, on several occasions we noted that a great number of Euphausiids had been run aground on the shores of the Isle of Pines (to the south of New Caledonia) and that swarms were noted nearby some 400 m above the ocean floor. These observations (points 1, 3 and 4) suggest a defense reaction of the organisms against a hostile environment or one different from their usual one and into which they were drawn.

70 5. All the foregoing observations suggest that swarms might be the result of complex stimuli, i.e., the response of organisms in a given biological state to certain environmental conditions. The "why" of this particular mode of behaviour nevertheless remains unknown: Mauchline and Fisher (1969) attributed to swarmming a major role in preserving the integrity of populations; Burukovskiy (1967) on the other hand considered that, rather than being beneficial, such behaviour contributed considerably to their being ready prey to predators. Applying the same reasoning, Ponomareva (1963) infered that only a sexual motivation would be strong enough to incite the organisms to adopt such a costly behavioural pattern; he also acknowledged the role of nutrition in causing this phenomena.

1.2. Heterogeneity of distributions

We described in the foregoing section the large concentrations of individuals commonly known as "swarms". To describe the distribution of

TABLE 17

Data pertaining to Stations during which Swarms were noted.

BORA I	23	7.12.65	00°28′ N	170° E	900	22 h 23	4 500		7/8-PL		*E. diomedae*	4 500
BORA II	12 B	15. 3.66	00°35′ N	170° E	440	20 h 42	4 500	200	2/8-DQ	Forts courants	*E. diomedae* *T. tricuspidata*	2 870 2 362
BORA II	16 B	24. 3.66	00°16′ S	180°	230	20 h 45	5 500	150	6/8-NL	Forts courants	*S. abbreviatum*	7 908
BORA III	26	22. 6.66	00°00	170° E	590	20 h 48	4 500				*E. diomedae*	11 703
BORA III	34	25. 6.66	02°01′ N	170° E	620	20 h 31	4 500		2/8		*E. diomedae*	9 450
BORA IV	17	5.10.66	00°09′ S	170° E	1 160	22 h 42	4 400	80 à 250	6/8-DQ	Forts courants	*E. diomedae*	5 322
BORA IV	19	6.10.66	00°57′ N	170° E	1 160	22 h 02	4 450	80 à 200	7/8-DQ	Forts courants	*E. diomedae*	3 594
CYCL. I	25	23.11.66	00°52′ S	170° E	160	02 h 18	4 300	170	5/8		*E. diomedae*	12 513
CYCL. I	N 26	23.11.66	00°52′ S	170° E	15′ en surface	23 h 05	4 300	80 à 180			*E. diomedae*	2 260
CYCL. II	9	30. 3.67	02°05′ S	170° E	1 200	09 h 36	4 200		3/8-DQ		*E. diomedae*	4 081

* Figure indicates maximum depth reached by the net, not depth at which the swarm was located.

individuals living outside such swarms, we shall now consider the mean values of distributions. We shall eliminate the most abundant hauls (16%) and examine 84% of the data obtained from the less abundant stations. This limit is based on the fact that, in a normal distribution, 84% of the values are less than m+ S (Fager and McGowan, 1963). The quantity m-S cannot be taken into consideration because it is negative in most cases.

First of all, two major preliminary questions must be answered.

The first consists in determining the measurable quantity that will be used for heterogeneity; if m is the arithmetic mean, S^2 the variance and S the standard deviation, the choice rests among three simple and commonly used coefficients:

— the coefficient of over-dispersion $C = S^2/m$ which expresses a random distribution if it approaches 1 (Poisson's Law), a sub-dispersion (distribution more regular than random) if it is significantly less than 1, an over-dispersion (tendency of animals to gather in groups) if it is significantly greater than 1. It is known that a population randomly distributed essentially falls into a Poisson distribution characterized by the mean and variance being equal ($S^2 = m$). The drawback of the C coefficient is obvious: if the population is randomly distributed, then $C \neq 1$ regardless of the number of individuals because, by definition, $S^2 = m$ in this case; however, there is always over-dispersion ($S^2 > m$). Under these conditions, the value C depends upon the number of individuals. In fact, in the formula $C = S^2/m$, the deviations from the mean affect the numerator by their squares with the result that, for an abundant species, S^2 becomes infinitely greater than m, while for a species including few individuals, S^2 remains very small (cf. Fager and McGowan, 1963). Therefore, the coefficient C can indicate only whether or not there is over-dispersion without measuring the over-dispersion if the number of individuals in the distributions to be compared are not the same. In the case of Euphausiids, where over-dispersion always occurs, calculating the coefficient C contributes little information.

— the coefficient of variation $V = S/m$, although applicable only to smaller values, presents the same drawbacks as the C coefficient: it is not independent of the number of individuals.

— we therefore chose to characterize heterogeneity by the dispersion factor $a = (S^2 - m)/m^2$ which, because the square of the mean enters into the calculation, is essentially independent of the number of individuals (cf. Cassie, 1959). For any value $a > 0$, over-dispersion occurs and the value of a increases in terms of heterogeneity.

71 The second question involves knowing whether the heterogeneity actually measured does indeed solely represent the distribution of the given populations. In Table 13 we indicated the total 249 stations used to study distributions. To work on rather homogeneous samples, we considered only samplings drawn from the equatorial zone (Zones A and C) by means of a IKMT 10, either by day or by night, and excluding dusk and dawn which are apparently periods when rapid vertical migrations occur.

We noted however that each category, defined according to time of day and depth of tow, included stations widely spread out in terms of both geographical and seasonal conditions. The obvious drawback of this method was to introduce "interference" due to variations in space and time. This was the only reasonable alternative, however, as it was necessary to have a fairly large number of observations which could not be obtained from a single expedition. To give an idea of such interfering variations, the average number of individuals per station for *E. diomedae* increased from 185 for "Cyclone" V to 476 for "Cyclone" IV (time variation) and from

313 for all "Cyclone" expeditions to 369 for all "Caride" expedition (geographical variations). The fact that all categories are represented by stations from several expeditions partly minimizes this drawback, the "interference" being the same for all; any doubt would affect absolute estimates of dispersion, not relative estimates. Under these conditions, the over-dispersion obtained can be "calibrated" only by analogy: we shall calculate, for instance, for 0-1200 m daytime tows having a rather low coefficient a, the over-dispersion noted for these same stations ("interference" will therefore be identical) for a population known through experience as being one of the most evenly distributed, in this case micronectonic fish. We shall select two of the most abundant species that we collected: Sternoptyx diaphana and Cyclothone pallida (identified by J. Rivaton, laboratory assistant).

Considering even extreme cases where the species are randomly distributed, the coefficient a would be a measurement of parasitic "interference" attributable to the methods applied and the geographical and seasonal spread of the hauls. As we might reasonably think that this is an ultimate hypothesis and that, in fact, the species are slightly over-dispersed, the coefficient a calculated for the species will express the maximum value of any possible bias: any value greater than a calculated for the Euphausiid population can be considered as expressing an actual over-dispersion of the population.

For thirty-six 0-1200 m daytime stations distributed over the "Bora" IV, "Cyclone" II, III, IV, V, VI and "Caride" I expeditions, we obtained the following values:

S. diaphana:

$n = 36$ $E = 750$ $m = 21$

$S^2 = 103$ $a = 0.19$

C. pallida:

$n = 36$ $E = 9.383$ $m = 261$
$S^2 = 9.327$ $a = 0.13$

According to these values of a, we estimated the highest value of the "interference" (= geographical and seasonal variations in the samples) at 0.20. Any value greater than a for any given species will therefore be considered as indicating a definite heterogeneity in the distribution. 72

In tables 18, 19 and 20 are given the distribution characteristics of E. diomedae, T. tricuspidata, S. abbreviatum, after elimination of 16% of the highest values for each species. Table 21 gives the distribution characteristics of T. aequalis, considered as being representative of the type of distribution particular to species which did not present swarmming habits; all values were used.

73 Note that, with the exception of one case, the coefficient a is always greater than 0.20. According to the maximum value of the interference estimated by calculating a for S. diaphana and C. pallida, we can state that, in the case of Euphausiids, there is always over-dispersion.

The values of a were plotted (fig. 43) for the four species examined and for various depths and time of day. Values for night hauls are not significantly greater than those for daytime hauls, a situation contrary to that noted in the case of swarmming.

TABLE 18

Particulars of E. diomedae distributions (all values)

	0-350 m nuit	0-650 m jour	0-650 m nuit	0-900 m jour	0-900 m nuit	0-1 200 m jour	0-1 200 m nuit
No. of observations Nombre d'observations n	23	16	40	13	34	41	42
Effectif E... No. of specimens	5 245	1 757	17 088	830	10 137	2 627	8 794
Moyenne m... Mean	228	110	427	64	298	64	209
Variance $S^2 = \frac{\Sigma e^2}{n-1}$	23 000	2 884	45 290	2 470	29 343	1 884	20 974
Dispersion factor Coeff. de dispersion $a = \frac{S^2 - m}{m^2}$	0,44	0,23	0,25	0,59	0,33	0,44	0,48
Over-dispersion factor Coeff. de surdispersion $C = \frac{S^2}{m}$	100	26	106	39	98	29	100
Standard deviation Ecart type $S = \sqrt{\frac{\Sigma e^2}{n-1}}$	152	54	213	50	171	43	145
Variation factor Coeff. de variation $V = \frac{S}{m}$	0,67	0,49	0,50	0,78	0,57	0,67	0,69
$m + 3S$	684	272	1 066	214	811	193	644

TABLE 19

Particulars of T. tricuspidata Distributions (84% of values).

	0-350 m nuit	0-650 m jour	0-650 m nuit	0-900 m jour	0-900 m nuit	0-1 200 m jour	0-1 200 m nuit
No. of observations Nombre d'observations n	23	16	40	13	34	41	42
Effectif E. No. of specimens	2 665	411	1 656	824	1 365	1 064	1 525
Moyenne m Mean	116	26	41	63	39	26	36
Variance $S^2 = \frac{\Sigma e^2}{n-1}$	4 749	210	578	2 435	1 073	127	581
Dispersion factor Coeff. de dispersion $a = \frac{S^2 - m}{m^2}$	0,34	0,27	0,32	0,69	0,68	0,15	0,42
Over-dispersion factor Coeff. de surdispersion $C = \frac{S^2}{m}$	41	8	14	39	28	5	16
Standard deviation Ecart type $S = \sqrt{\frac{\Sigma e^2}{n-1}}$	69	14	24	49	33	11	24
Variation factor Coeff. de variation $V = \frac{S}{m}$	0,59	0,54	0,59	0,78	0,85	0,42	0,67
m+3 S	323	68	113	210	138	59	108

TABLE 20

Particulars of S. abbreviatum Distributions (84% of values)

	0-350 m nuit	0-650 m jour	0-650 m nuit	0-900 m jour	0-900 m nuit	0-1 200 m jour	0-1 200 m nuit
No. of observations Nombre d'observations n	23	16	40	13	34	41	42
Effectif E. No. of specimens	727	187	880	163	655	284	739
Moyenne m Mean	42	12	22	13	19	7	18
Variance $S^2 = \frac{\Sigma e^2}{n-1}$	515	100	358	199	356	39	181
Dispersion factor Coeff. de dispersion $a = \frac{S^2 - m}{m^2}$	0,27	0,61	0,69	1,10	0,93	0,65	0,50
Over-dispersion factor Coeff. de surdispersion $C = \frac{S^2}{m}$	12	9	16	15	19	6	10
Standard deviation Ecart type $S = \sqrt{\frac{\Sigma e^2}{n-1}}$	23	10	19	14	19	6	13
Variation factor Coeff. de variation $V = \frac{S}{m}$	0,55	0,83	0,86	1,08	1,00	0,86	0,72
m+3 S	111	42	79	55	76	25	57

TABLE 21

Particulars of T. aequalis Distributions (all values)

	0-350 m nuit	0-650 m jour	0-650 m nuit	0-900 m jour	0-900 m nuit	0-1 200 m jour	0-1 200 m nuit
No. of observations Nombre d'observations n	27	19	48	16	40	49	50
Effectif E. No. of specimens	1 247	717	1 466	766	1 096	1 500	1 888
Moyenne m Mean	46	38	30	48	27	31	38
Variance $S^2 = \frac{\Sigma e^2}{n-1}$	678	722	497	1 423	529	429	439
Dispersion factor Coeff. de dispersion $a = \frac{S^2 - m}{m^2}$	0,30	0,47	0,52	0,60	0,69	0,41	0,28
Over-dispersion factor Coeff. de surdispersion $C = \frac{S^2}{m}$	15	19	17	30	20	14	12
Standard deviation Ecart type $S = \sqrt{\frac{\Sigma e^2}{n-1}}$	26	27	22	38	23	21	21
Variation factor Coeff. de variation $V = \frac{S}{m}$	0,57	0,71	0,73	0,79	0,85	0,68	0,55
m+3 S	124	119	96	162	96	94	101

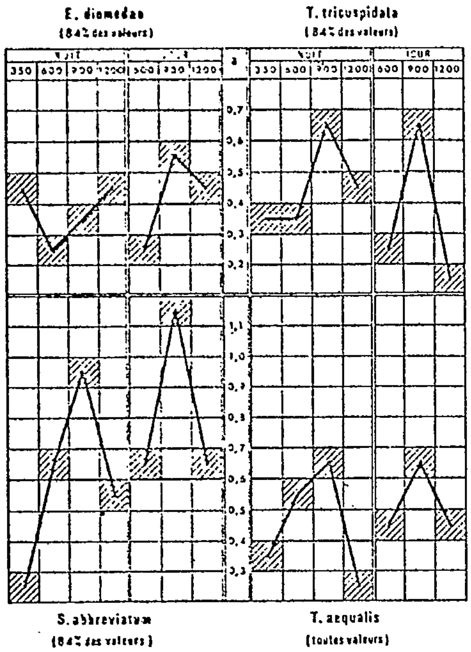


Fig. 43. — Valeurs du coefficient de dispersion a pour 4 espèces dans les différents types de prélèvements (traits 0-350 m à 0-1200 m, de jour et de nuit).
Fig. 43. — Values of the dispersion factor a for 4 species in the different categories of stations (0- 350 m to 0- 1200 m, day and night).

In 7 out of 8 cases, maximum values of a were recorded with the 900 m tows; as this fact can be verified for both daytime and night hauls, as well as for both migratory (T. aequalis) and sedentary (S. abbreviatum) species, we would suggest that it is likely due to the very nature of the towing technique rather than to a biological or ecological cause. It therefore bears limited significance.

There appears to be no definite relationship between a and m; i.e., it would appear that groups of individuals are not denser when the population is greater. This is true, however, in two cases which we shall point out in order to qualify their significance:

— when the coefficient $C = S^2/m$ is used to measure dispersion, there is a significantly positive relationship established with m. Such correlation, as we demonstrated earlier, results from a bias of the calculation inherent to the definition of the coefficient C, the latter being dependent upon the number of specimens.

— when all values are used, there is a positive correlation between a and m in the case of species displaying swarmming characteristics. This correlation is the expression of a definite fact: swarms, which represent an ultimate case of over-dispersion, result in 'a' having a high value, and the great number of specimens collected whenever swarms were encountered caused the value of m to increase considerably.

The significance of a possible correlation between population density and over-dispersion should therefore be carefully examined.

2. NYCHTHEMERAL VARIATIONS IN HAULS

It is well known that the greater majority of planktonic and micronectonic organisms migrate vertically within every twenty-four hour period with the result that the surface layers are virtually deserted during hours of sunshine except for very minute organisms which remain there.(cf. Vertical Distributions). 75 Consequently, samples drawn from those layers, by day and by night, were quite dissimilar and present nychthemeral variations reflecting the vertical displacements of the animals (cf. Aizawa and Marumo, 1967) or their greater or lesser ability to avoid the sampling gear if aided by the ambient lighting (Brinton, 1967 a and b; Taniguchi, 1969).

When planning an expedition, the fact that nychthemeral variations do occur must be contended with: if daytime and night hauls cannot be compared against one another, only one of these two categories must be used when examining data for a given programme (usually night stations for which tows need not be so deep). This implies that either there is a rather long time interval between two consecutive stations if the vessel travels during the day, or the expedition covers very little territory if the daily route is limited to the desired distance between two stations. To avoid such constraints, a sampling method must be found which minimizes or, if possible, eliminates the difference between daytime and night hauls. The first alternative consists in towing at progressively deeper depths so as to obtain a

Day/Night ratio = 1, where the net would pass through the entire vertical layer occupied by the animals, both by day and by night. This was the procedure followed on the "Bora" expeditions when both day and night stations were carried out at depths of 0-300 m and 0-900 m on "Bora" I and II, 0-600 m on "Bora" III and 0-1200 m on "Bora" IV.

Table 22 lists mean values of the Day/Night ratio of individuals from various species collected at various depths. In examining the data, we arrived at the following conclusions: nychthemeral variations are the result of a combination of biological conditions (daily vertical migration of organisms) 76 and methodological contingencies related to the sampling method. In fact, if we can provide explanations to the fact that the ratios are less than 1 for 0-600 m tows, because part of the population is found at greater depths during daytime, and if the frequency of ratios approximating 1 for 0-900 m tows confirms that this is the maximum depth inhabited by most species during daylightand also supports the fact that the initial reasoning was well founded, then why, in first analysis, would the very great majority of ratios be definitely less than 1 in the case of 0-1200 m tows? We noted that the ratio for 12 out of 17 species was included between 0.8 and 1.2 for the 0-900 m tows, for which only three species have a ratio of less than 0.8; on the other hand, 10 and 11 species had a ratio less than 0.8 for the 0-600 m and 0-1200 m tows, respectively (Roger, 1968 b).

What actually occurs? Two technical particularities of the sampling method are involved. We discussed earlier (cf. chapters on Methods) that during part of the station the net passes through a horizontal "level" when it reaches its greatest depth, i.e., 12 to 18% of total towing time, with the result that there is over-sampling at that particular depth. In addition, the cod-end (a plankton net in 1 mm mesh size) causes a pressure wall

TABLE 22

Day/Night ratio of mean number of individuals captured per station for the given towing depths (according to 40 stations on "Bora" I-III-IV).

Species Espèces	0-650 m	0-900 m	0-1 200 m
*T. tricuspidata**	0,40	0,58	0,49
T. aequalis	0,80	1,14	1,12
T. orientalis	1,76	1,00	1,07
T. monacantha	1,15	1,22	0,58
T. pectinata	1,29	1,14	0,80
*S. abbreviatum**	0,14	0,50	0,16
S. maximum	0,45	0,80	0,47
S. elongatum	0,30	1,00	0,42
S. longicorne	0,78	0,47	0,53
*E. diomedae**	0,11	0,91	0,20
E. paragibba	0,55	1,06	0,81
N. tenella	0,85	1,08	0,71
N. gracilis	0,65	1,06	0,60
N. microps	0,48	1,54	0,51
N. sexspinosus	0,66	1,00	0,29
N. boopis	0,77	1,17	1,14
B. amblyops	0,08	4,00	0,78

(1) Species displaying swarmming habits.

to form; after coming into contact with this wall, the organisms then whirl about the net before entering the finer-mesh cod-end. The animals tend to be progressively eliminated according to the time spent in the 4 mm mesh forenet. Given the foregoing, the situation is as follows:

— in the case of 0-600 m tows, night stations cover the entire vertical layer inhabited by the animals, while day stations do not reach the apparently great portion of the population found below that depth during hours of sunshine. Day/Night ratios equal to less than 1 are therefore most frequent.

— in the case of 0-900 m tows the horizontal level is located in the very zone where most of the organisms are found by day, which results in over-estimating the population and therefore compensating for the great number of animals escaping during the long hauling in procedure. The animals being closer to the surface at night, this level is therefore located in a deeper virtually deserted layer. However, as the organisms then occupy the upper layers, those which are captured spend less time in the net and fewer are able to escape. The combination of both factors results in the majority of D/N ratios being close to 1.

— in the case of 0-1200 m tows, both by day and by night this level is located at a greater depth than that inhabited by most organisms and there are no other factors compensating for the fact that, the animals being deeper down by day, a greater proportion escapes during hauling in than at night: D/N ratios are therefore usually considerably less than 1.

We wish to add three further remarks:

— organisms escaping the net, often considered as occurring more frequently during the daytime than at night, is generally held to be the prime factor causing differences between the number of specimens collected by day and by night (Brinton, 1966; Aizawa and Marumo, 1967...). This does not appear to be the case with Euphausiids-Midwater Trawls. If this were the case, we would obtain on the average, for any given species, a lower Day/Night 77
ratio for large organisms than for small ones. According to Table 23, the converse is generally true: this would indicate that the prime factor is indeed the fact that organisms escape through the net, more so in the case of minute animals. It is readily conceivable that, in the case of Euphausiids-Midwater Trawls, the organisms avoid the net no more by day than by night for the two reasons that very little light penetrates into their daytime deep-water habitat and that the very size and speed of the gear give them little opportunity to escape.

— the low Day/Night ratios obtained for species displaying swarmming habits do not necessarily imply a cause-and-effect relationship between the group behaviour of the organisms and the efficiency of the gear; this can more likely be attributed to the simple fact that swarming generally occurs at night.

— finally, it should be noted that results vary widely in spite of a relatively great amount of data having been examined. For instance, the Day/Night ratio for *T. monacantha* for the 0-1200 m tows was estimated at 0.58 according to "Bora" IV (Table 22) and at 1.34 according to results from the "Cyclone" expeditions (Table 23). Under these circumstances, only general facts can be stated.

In conclusion, we might assume that Day/Night ratios essentially 78
equal to 1 can be obtained under the following conditions:

(1) carrying out oblique tows for which the horizontal level is, both by day and by night, below the vertical layer occupied by the organisms.

(2) using a net of relatively fine mesh in order to prevent excessive losses while the gear is hauled in. In first approximation, we might assume that a mesh will retain 50% of animals of a size equal to the mesh size (cf. Saville, 1958); this percentage could vary considerably depending upon the morphology of the organisms and the time spent in the net. Use of a very fine mesh causes strong resistance requiring a slower towing speed which increases the possibility of large organisms escaping the net. The final option is in fact a compromise. In practice, once a given type of sampling gear is selected, the interpretation of data should bear only on animals sufficiently large that only a negligible number of them escape through the mesh.

E. SEASONAL VARIATIONS

In this section, we shall deal only briefly with an aspect that is surely a major subject in the biology of marine organisms; we shall only

TABLE 23

Day/Night ratios of mean number of individuals captured per station on "Cyclone" II to VI expeditions (0-1200 m tows) (28 day, 31 night stations)

Species Espèces	Effectif total No. of specimens	Taille des individus Size of individuals	Rapport J/N D/N ratio
T. tricuspidata............	2 372	small petits (G.T. 0,7 à 2,0)	— 0,60
		large grands (G.T. 2,0 à 3,5)	— 0,86
		Total....................................	0,73
T. monacantha............	698	small petits (G.T. 0,9 à 2,5)	— 1,28
		large grands (G.T. 3,0 à 3,5)	— 1,37
		Total....................................	1,34
T. aequalis................	2 417	small petits (G.T. 0,7 à 1,6)	— 0,79
		large grands (G.T. 2,0 à 3,0)	— 1,03
		Total....................................	0,92
*E. diomedae**.............	14 322	small petits (G.T. 0,7 à 1,2)	— 0,28
		large grands (G.T. 1,6 à 2,5)	— 0,24
		Total....................................	0,28
E. paragibba.............	1 650	small petits (G.T. 0,7 à 0,9)	— 0,88
		large grands (G.T. 1,2 à 2,0)	— 1,07
		Total....................................	1,03
N. tenella.................	3 504	small petits (G.T. 0,7 à 1,2)	— 0,77
		large grands (G.T. 1,6 à 2,5)	— 1,01
		Total....................................	0,85

* Swarm of 4081 individuals at station 9 on "Cyclone" II (day station) not included.

discuss the overall seasonal variations of various species: annual development in the biological characteristics of the population (size groups, ovarian stages) will be discussed in Chapter VI. This is indeed a fundamental point: seasonal variations affect the biology of the animals more than environmental features. In the same manner as the sequence of seasons is the prime motivator of biological phenomena particular to cold and temperate seas, the absence of consecutive seasons is responsible for the essential properties of tropical waters.

Numerous authors have pointed out how determining biological cycles in a tropical environment, where no or few seasonal variations occur, is difficult and virtually impossible: Blackburn (1966) claimed that quantitative variations of zooplankton in the eastern Tropical Pacific was not subject to pronounced seasonal changes; he stressed the importance of examining the species themselves when attempting to recognize biological cycles. During the expedition of the "SIBOGA", Hansen (1910) noted the presence of larvae of T. tricuspidata throughout the year and concluded that the species was in a permanent reproductive state. Brinton (1960), Heinrich (1961, 1962 a and b and 1963) observed that the age structure of Euphausiid and Copepod populations inhabiting warmer waters varied little, the result of continuous reproduction even when seasonal fluctuations occur in the physical environment (Brinton, 1963). Ponomareva (1969) reached the same conclusions regarding the Indian Ocean, King (1954) and King and Iversen (1962) for the Central Equatorial Pacific and King and Hida (1957 a) for Hawaii. Istoshin (1966) commented that, as the sun passed over the zenith twice during the year at the equator, from a climatic point of view there are "two summers and two winters"; for his part, Bogorov (1960) claimed that from a biological standpoint, there is no winter and that summer lasts for eight months. Vinogradov, Gitelzon and Sorokin (1970) admitted that seasonal variations in tropical seas are negligible and that factors causing population density (upwelling and divergences) are permanently present which is not the case in temperate waters where climatic fluctuations are the prime factor.

Certain authors have however introduced variants into an otherwise 79
monotonous theme : Ponomareva (1969), speaking about the tropical Indian Ocean, claimed that although reproduction was going on at all times throughout the population, such permanent state was due to the fact that the reproductive cycles of the individuals were not synchronous. The same idea was set forth by Drobysheva (1967) concerning Euphausiids in the Barents Sea during the summer and by Giese (1959) regarding marine invertebrates in general. Brinton (1962 b) claimed that in equatorial regions faunistic variations were due to movements within the bodies of water.

Upon closer examination, certain authors observed, in spite of very few variations occurring from year to year, a certain seasonal alternation related to tradewind patterns. Regarding the South Equatorial current with which we are concerned here (centered on 0°), milder winds from November to March (southern summer) cause equatorial divergence and consequently, an increase in planktonic life (Bogorov, 1941; King and Hida, 1957 b; Bogorov and Vinogradov, 1960); on the other hand, zooplankton is most abundant during the southern winter (July-November). However, equatorial divergence which is a seasonal occurrence in the western Pacific is essentially a permanent fact in the Central Pacific. Owen and Zeitzschel (1970) detected significant seasonal variations in the primary production in the eastern Tropical Pacific.

Any attempt to locate any variation affecting population density at any given time is of prime importance for the time factor is indispensable when examining growth patterns.

Our data concerns only the equatorial zone: firstly, because these are the populations examined from a biological point of view and secondly, because the tropical zone was investigated by means of ill-assorted techniques which may have failed to uncover minor biological changes. Our material was obtained as follows:

— at 170° E, stations from 0° to 3° S on the "Cyclone" II to VI expeditions, i.e., a total of 52 samplings centered on the following dates: March 30, May 5, June 14, July 20, September 3. Stations further to the south than 3° S were disregarded as they were too far away from the equatorial zone for purposes of this study. Only deep-water tows were carried out (0-1200 m), six within every twenty-four hour period.

— at 135-155° W, 0-500 m to 0-1200 m night stations on the "Caride" I to IV expeditions and fifteen 0-250 m to 0-950 m night stations on the "Caride" V expeditions, i.e., a total of 99 tows centered on the following dates: October 1, December 5, February 25, July 1, September 24.

In spite of the relatively great number of available stations and consistency in the methods applied, this material is still wanting : a six-month period was barely covered at 170° E, while at 135-155° W, where samplings were drawn over the course of a whole year, two consecutive expeditions were separated by a fairly long period of time due to the vast geographical area covered. Furthermore, as only one vessel was available to cover such an extensive programme, the samplings at 170° E were carried out in 1967, those at 135-155° W in 1968-69; in an equatorial environment subject to few noticeable seasonal cycles, such a time lapse can indeed be serious. We must not exclude the possibility under such conditions that aperiodic fluctuations may be the factors determining biological variations; if such is the case, it is then impossible to combine two series of observations carried out at different and more or less irregular dates. Such problems will stand out most prominently when we attempt to determine biological cycles. Regardless, in spite of inherent limitations, this data 80 represents to our knowledge the most coherent seasonal observations conducted as yet in these regions.

Results are shown on Tables 24 and 25, i.e., the mean number of individuals of each species captured per station during the various expeditions, those at 170° E and those at 135-155° W. For the "Caride" (CA) expeditions (135-155° W), the number of specimens collected was corrected according to flowmeter readings and adjusted for a tow of 10,000 metres; noticeable differences in towing procedures from one expedition to another resulted in an average tow of 8650 m per station for CA II and 2963 m for CA V, or a difference which can be expressed as the factor 2.9. On the "Cyclone" (C) expeditions, taking into account the fact that the flowmeter was placed in different positions during C II and C III on the onehand, and during C IV, C V AND C VI on the other (cf. Appendix), the mean difference in towing distance per station between two extreme cases does not exceed the factor 1.1 and no corrections were therefore applied to the number of specimens actually collected.

Table 26 gives the extent of seasonal variations for various species by giving for each species the ratio of specimens collected during the most successful expedition and those captured during the least successful one.

The following conclusions are reached upon examination of this data: there appears to be an inherent difference between variations observed at 170° E and those at 135-155° W:

— at 170° E, few variations were noticeable within the species 81
themselves, but the variations were synchronous such that their effects were cumulative and became apparent in the populations as a whole : a definite lower population density in May was noted for virtually all species: the

TABLE 24

Seasonal Variations at 170° E in the Equatorial Pacific. — Mean number of individuals collected per station.

	March mars 67 (C II)	May mai 67 (C III)	June juin 67 (C IV)	July juillet 67 (C V)	Sept sept. 67 (C VI)	Mean Moyenne (m)
T. cristata	2,3	2,0	2,1	2,0	1,4	2,0
T. tricuspidata	59	37	21	24	27	34
T. orientalis	8,9	11	9,8	14	13	11
T. monacantha	17	11	8,6	17	15	14
T. pectinata	5,2	3,2	3,2	5,3	5,2	4,4
T. aequalis	41	27	27	58	46	40
S. abbreviatum	17	2,5	17	10	25	14
S. elongatum	3,6	3,5	4,9	4,3	5,3	4,3
S. affine	13	6,3	14	10	17	12
S. longicorne	5,6	2,9	5,2	7,1	4,1	5,0
E. diomedae	574	344	418	303	374	403
E. paragibba	29	23	22	42	39	31
E. tenera	74	44	85	47	69	64
N. tenella	67	66	46	63	62	61
N. microps	68	35	31	40	63	47
N. gracilis	41	28	18	33	14	27
N. boopis	19	16	17	19	25	19
TOTAL	1 045	662	750	699	805	792
Number of species > m Nombre d'espèces > m	13	3	7	8	12	—

TAELE 25

Seasonal variations at 135-155° W in the Equatorial Pacific. — Mean number of individuals captured per 10000 m trawled.

	Oct. oct. 68 (CA I)	Dec. déc. 68 (CA II)	Feb. fév. 69 (CA III)	June juin 69 (CA IV)	Sept. sept. 69 (CA V)	Mean Moyenne (m)
T. cristata	1,0	0,3	0,1	0,1	0	0,3
T. tricuspidata	117	65	46	50	17	59
T. orientalis	1,9	2,0	1,6	2,1	2,7	2,1
T. monacantha	34	38	16	17	16	24
T. pectinata	4,5	7,4	4,5	7,3	2,2	5,2
T. aequalis	37	35	31	18	17	28
S. abbreviatum	110	15	31	18	6,5	36
S. elongatum	1,0	0,5	0,1	0,1	0	0,3
S. affine	26	69	82	45	14	47
S. longicorne	8,6	3,5	4,9	3,2	7,6	5,6
E. diomedae	434	727	657	511	728	611
E. paragibba	66	52	31	70	23	48
E. tenera	180	121	126	236	458	224
N. tenella	22	18	19	33	20	22
N. microps	62	64	40	36	8,5	42
N. gracilis	187	126	92	80	43	106
N. flexipes	3,9	29	14	3,8	3,4	11
N. boopis	5,8	3,6	4,9	4,2	1,7	4,0
TOTAL	1 302	1 376	1 201	1 135	1 369	1 277
Number of species > m Nombre d'espèces > m	12	12	5	5	5	—

total number of Euphausiids was twice as less as that recorded two months earlier. During C II, 13 species were more plentiful than their annual mean while only 3 species were present in greater numbers during C III. Population figures rose slowly during the course of C IV, C V and C VI during which 7.8 and 12 species respectively were more abundant than their annual mean.

In the western Pacific, an abrupt fall in population occurs during May likely due (cf. chapter on Ecology) to the intrusion of waters originating from the north of New Guinea; this ecological factor affects and synchronizes biological rhythms.

— at 135°- 155° W, on the contrary, quite paradoxically we noted rather pronounced seasonal variations within the species themselves and a remarkably constant overall population as the average number of individuals per standard tow of 10,000 m totalled 1302 (Oct. 68), 1376 (Dec. 68), 1201 (Feb. 69), 1135 (June 69) and 1369 (Sept. 69). This point confirms that this environment does not change as a function of time; furthermore, this fact gives no support to the statement whereby in this region, populations are denser from December to June than from July to November (Bogorov, 1941; King and Hida, 1957 b; Bogorov and Vinogradov, 1960). Without environmental fluctuations tending to synchronize cycles (suffice it to recall, however, that Owen and Zeitzschel, 1970, admitted that significant seasonal variations in primary production did occur), the various species seem to develop independently of one another, with peaks appearing in one season or another depending upon the given species.

Note that such rhythms can only be qualified as seasonal by analogy with the situation prevalent in temperate waters, without such rhythms following a seasonal chronology. We noted in particular that, during CA I, 12 species were more abundant than their annual mean, 8 of these being in their most plentiful numbers; on CA V, on the other hand, carried out the following year at the same date, 13 out of 18 species recorded their lowest population densities.

Whatever the case, taking into account major sampling discrepancies, it is readily noticeable that any attempt to determine changes in the Equatorial Pacific in terms of a time factor will result in uncertainty: the task would involve making several assumptions and looking for concordant series (e.g., size groups or ovarian maturity) before proposing a hypothesis which, under all circumstances, must be tested against facts.

TABLE 26

Extent of seasonal variations in the Equatorial Pacific (means of most abundant and least abundant expeditions).

Species Espèces	135-155° W	170° E
S. abbreviatum	17*	10*
N. flexipes	8,5	(absent)
N. microps	7,5	2,2
T. tricuspidata	6,9	2,8
S. affine	5,9	2,7
N. gracilis	4,3	2,9
E. tenera	3,8	1,9
T. pectinata	3,4	1,7
N. boopis	3,4	1,6
E. paragibba	3,0	1,9
S. longicorne	2,7	2,4
T. monacantha	2,4	2,0
T. aequalis	2,2	2,1
N. tenella	1,8	1,5
E. diomedae	1,7	1,9
T. orientalis	1,7	1,6
T. cristata	**	1,6
S. elongatum	**	1,5
TOTAL	1,2	1,6

* High values owing to widely varying distributions.
** Very few specimens.

CHAPTER 4 . VERTICAL DISTRIBUTIONS

1. THE PROBLEM

1.1. Extent and Significance of Vertical Distributions

The fact that nychthemeral movements have been associated with the great majority of planktonic organisms has been known ever since the initial studies in this field were undertaken during the last century. Such behaviour, virtually an ecological feat, brings the organisms daily through a series of different physical environments. The Equatorial Pacific which is highly stratified is the extreme of such diversified environments; figure 44 gives the vertical distribution of temperatures at 140° W and 170° E. Considering only the most easily measured parameter, this diagram indicates how an individual migrating only some 100 to 300 m will be subject within a few short hours to variations in temperature of ten degrees and more.

The vertical distribution of the organisms implies other important ramifications. Note that, according to figure 2, depending upon depth, the organisms are drawn into one direction or another by currents flowing in opposite directions at speeds frequently exceeding 3 knots. Therefore, if a certain stage, size group, sex, physiological state, etc. corresponds to a mean vertical level, all population distribution patterns are then possible in terms of biological parameters.

The trophic requirements of a species are also as dependent upon vertical distribution as size or nutritional value. Euphausiids are a prime example of this: an examination of the stomach contents of tuna fish (refer to chapter on Predators) indicated that Euphaussids are merely accessory food for these fish, contrary to Amphipoda for instance. It appears that one of major reasons can be attributed to the vertical distribution of the animals: tuna feed only during the day below the surface (0-400 m) while large Euphausiids, more likely prey, inhabit that layer only at night when the fish are not feeding.

On the basis of these few remarks, vertical distributions present major ecological and biological implications.

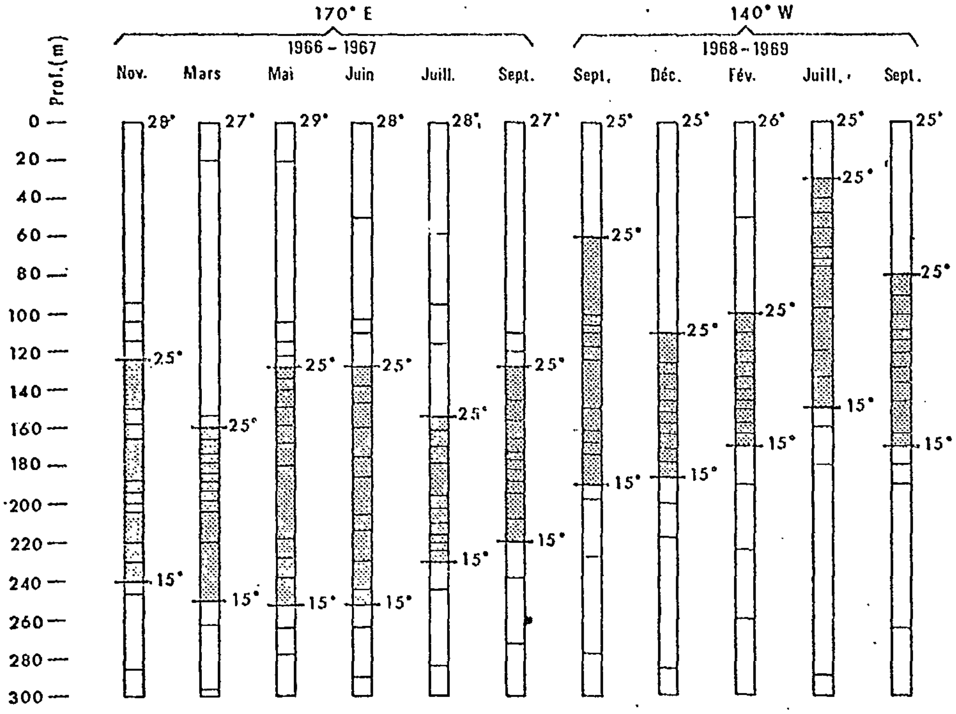


Fig. 44. — Stratification thermique dans le Pacifique équatorial ouest (170° E) et central (140° W).
Fig. 44. — Vertical distribution of temperature at different times of the year in the Western (170° E) and central (140° W) equatorial Pacific.

1.2. Papers relating to this subject

Establishing a bibliography on this subject is rather difficult due to the volume of publications as well as to their generally abstruse, vague and even contradictory contents. General principles can nevertheless be drawn from them.

1.2.1. Cause and Effects of Vertical Migrations

The influence of light is so obvious as to be generally regarded as the main direct cause of nychthemeral migrations : Boden and Kampa (1967),

Boden, Kampa and Abbot (1959 and 1961) noted that the DSL follows a given isophote; Backus, Clarke and Asa Wing (1965), Sherman and Honey (1970) observed a sudden rise of the organisms during an eclipse of the sun, similar behaviour having been noted when the skies became suddenly overcast (Grandperrin, 1969). Ringelberg (1961) claimed that DSL movements were controlled by variations (Δ I/I) in light intensity. Bogorov (1946) observed that in polar regions nychthemeral migrations occurred only during seasons when day and night alternated. Several authors have attempted to determine the optimum light conditions (Cushing, 1951; Itoh and Anaoka, 1968; Itoh, 1970) while the predominant influence of light, in combination with other factors, has been recognized by many: Clarke and Backus (1956 and 1964) agree that 85
factors other than light are also involved; Harris and Wolfe (1956) suggested that light intensity affects phototaxis; Foxon (1940), Ghidalia and Bourgois (1961), Harris (1953) suggested a geotaxis-phototaxis association; Lewis (1954) Moore (1952 and 1962), Moore et al (1953), Moore and Corwin (1956), Teal (1966), Teal and Carey (1967 a), Mauchline and Fisher (1969) stressed the joint action of light and temperature; Knight-Jones and Morgan (1966), Rice (1964) claimed that pressure played a certain role; this fact was rejected by Pearcy and Small (1968), Teal (1966), Teal and Carey (1967 a). Regarding pressure, Kazuo Sano (1959) observed that Bryozoans, *Mytilus* and Balanids survived a plunge of 3000 m while clinging to the hull of a bathyscaphe.

The deep-water habitat of certain migratory species does not appear to contradict the hypothesis of the definite action of light intensity : daylight has been detected at depths of 800 m and even at 1090 m in ocean areas where the water is clear (Waterman et al, 1939; Clarke, 1966; Clarke and Backus, 1964); Kampa (1965) noted that the eyes of Euphausiids are particularly well adapted to very low light, their greatest sensitivity corresponding to that part of the spectrum (blue-green) reaching such depths (Kampa, Boden and Abbot, 1959). McNaught and Hasler (1964) studying Daphnia, claimed that there was a linear relationship between activity and the light intensity logarithm, the slope of this curve being proportional to temperature.

Without necessarily causing such behaviour, other environmental characteristics appear to affect the vertical migrations of certain organisms which do indeed appear to be halted or slowed down by strong gradients, especially temperature gradients (Aron, 1962 a ; Hansen, 1951; Lance, 1962; Brinton, 1967 b); Harder (1968) noted that organisms accumulated in the interfaces, density being the determining factor. Lacroix (1961) established, for Euphausiids in Baie des Chaleurs, that the speed at which the organisms rise to the surface and the time during which they remain there are greater when there are fewer changes in temperature.

Although several authors attribute major causes to physical environmental factors, others rate endogenous rhythms as playing a significant part (Rudjakov, 1970) with the sequence of day and night only synchronizing the migrations (Enright and Hamner, 1967; Harris, 1963). Finally, others suggest that vertical displacements are merely a means by which individuals move about using the motion of currents to find a better environment (Woodmansee, 1966) or better food sources (Bainbridge, 1953). Whenever the various stages are not found at the same mean depth, the individuals are scattered and drawn even considerable distances away (Roger, 1967 b and c; Scheltema, 1966; Burukovskiy, 1967; Orr and Marshall, 1969). According to Voronina (1964 a), the great biomass of plankton and micronecton found at the equator is due to a combination of currents caused by equatorial divergence and the nychthemeral migrations of the organisms.

Due to the very size of the migratory populations and the extent of their vertical displacements, such behaviour accelerates the rate at which pigments synthesized in the subsurface and organic matter produced in the rich surface layers are brought into the deeper strata. (Jørgensen, 1966; Tchindonova, 1959; Vinogradov, 1961 and 1962).

The concept of a two-fold motivation has often been proposed, i.e., the animals rising to the upper layers by night and seeking refuge by day in 87
zones where predators are least likely found (Pearcy, 1970; Bainbridge in Waterman, 1960, etc.), thus benefitting from optimum conditions during the various physiological phases. By using mathematical models, McLaren (1963) demonstrated that feeding in high temperature areas and assimilating the food in low temperature areas gave the migratory species extra energy which increased as feeding temperature increased; the extra energy was used for other vital functions (growth, sexual maturation, etc.). Small, Hebard and McIntyre also expounded this idea.

Finally, the most direct result of vertical migrations is to submit the individuals to considerable environmental changes. We mentioned temperature levels earlier in this chapter; Longhurst (1967 a) noted that <u>E. eximia</u> in the eastern Pacific goes daily from an environment of 5 ml/l of oxygen to one of 0.2 ml/l. The effects of vertical displacements are felt differently by different species : according to Teal (1966) and Teal and Carey (1967 a), midwater species are capable of adapting to a deep-water habitat (the increase in pressure accelerates the breathing process slowed down by lower temperatures) while surface species are unable to do so. Childress (1971) demonstrated that deep-water organisms had a much slower breathing rate than surface organisms, such more "economical" metabolism enabling them to survive in a more impoverished environment.

TABLE 27 — Vertical Distributions (in metres)
The sign indicates a species considered as non-migratory)

*Auteurs Espèces	A	B	C	D	E	F	G	H	I	J	K	L	M	N
E. tenera.........	0-280			300-500	50	150-500	0-300		0-500	0-150 (1500-2100)	0-300	0-700		
E. gibboides......	0-700	300-500	0-200	200-400	0-200				0-500		100-500	25-100	300-500 (400-500)	50-250
E. eximia.........	0-700	200-600	0-20								0-500			
E. diomedae.......	0-700					150-300	0-150	0-200	0-2000	0-300 (700-1500)				
E. paragibba......									0-500					
T. tricuspidata....	0-700			400-700	0-400	400-1000	0-600		0-500	0-300 (700-2100)	200-1000	0-25		
T. acqualis ou *subacqualis*	0-700	350-700	0-250	500-700	100-400	200-800	0-300		0-2000		100-500	25-700	360-940 (380-620)	0-250
N. microps........	0-700			600-800	300-400	100-300	0-300		0-2000		Plus de 150	25-700	50-950 (470-610)	50-910 (170-460)
N. gracilis........	0-700					300-700	0-300		0-2000					
S. *affine*..........	0-700					0-500	0-400	400-800	0-500		Moins de 300	0-25	=0-500 (70-130)	=0-500 (70-130)
S. carinatum......	0-700	50-300	0-300	=0-300	=0-300	50-500	0-100	0-100	0-500	0-150 (700-1500)		0-100	0-40	0-700
S. abbreviatum....	0-700	=100-300	=100-300			0-600	0-500	0-100	0-500				85-410	100-500
N. flexipes........	0-700	=200-300	=200-300			150-700	0-300		0-500			100-300	90-600 (90-250)	100-250
S. *longicorne*......	140-700	=100-500	=100-500	=400-600	=200-500					150-700	100-500	25-700	=50-950 (100-280)	=50-800 (180-280)
S. elongatum......	140-1000	=Profond	=Profond	=300-500	=200-500	=150-1000	=150-1000	0-100				0-300	=150-590 (220-360)	=150-700 (240-380)
S. maximum......	140-1000								0-2000			300-700	250-570	220-580
N. tenella.........	140-1000	300-600	100-400	600-800	300-500	=150-1000	=150-1000		0-500		Plus de 200	25-700	200-900 (400-600)	50-580 (220-360)
T. orientalis.......	140-1000					500-4000	150-4000		0-500			25-300		
T. pectinata.......	140-1000					=300-3000	=300-3000					100-300		
T. monacantha....	140-1000			400-800	100-700	=150-3000	=150-3000							
N. boopis.........	140-1000	=300-600	=300-600			300-1000	150-1000				Plus de 400		=Plus de 360	=Plus de 360
N. sexspinosus.....	280-1000								0-2000			300-700	300-410	250-410
T. cristata........	280-1000					=300-3000	=300-3000							
B. amblyops.......	Plus de 1000					=500-4000	=500-4000		500-5000			700-2000		

A : Brinton (1962 b), Pacific.
B,C : Brinton (1967 b), California Current (B: Day; C: Night).
D,E : Mauchline & Fisher (1969), according to Lewis (1954) Florida Current (D: Day, E: Night).
F,G : Nemoto (1965), Duroshio (F: Day; G: Night).
H : Ponomareva (1968), Red Sea.
I : Ponomareva (1963), Pacific.
J : Le Reste (1969), Indian Ocean. Night stations (Values in parentheses indicate maximum secondary depth).
K : Boden (1961), Atlantic, 35° N to 10° S.
L : Leavitt (1935), Atlantic 35° N to 40° N.
M,N : Baker (1970), Canary Is. (M: Day; N: Night) (Values in parentheses indicate most populated layer).

1.2.2. Available Data

Disregarding possible errors and inaccurate methods of which available/data is not entirely free, it appears that vertical distributions within any given species are not similar in every region, either because individuals must adapt to special local conditions (Boden and Kampa, 1965) or because the water conditions differ; several authors have noted, for instance, that the organisms do not inhabit great depths in upwelling areas (Heinrich, 1960; Banse, 1964; Vinogradov and Voronina, 1966). Erratic fluctuations of very short duration may also occur as a result of essentially undetermined parameters causing changes in the vertical distributions of some one hundred metres from one day to another within a given species (Waterman et al, 1939). In conclusion, it seems somewhat hazardous to rely upon available data when looking for accuracy; insofar as possible, the study of vertical distributions should therefore be repeated for each particular study, the major reason being that results largely depend upon the methods applied : use of small nets, for example, will result in a great difference between the ability of organisms to escape the net by day and by night and will lead to making wrong estimates (Brinton, 1966 and 1967 b; Aizawa and Marumo, 1967).

In spite of the fact that the foregoing does not speak in support of generalizations, a few major characteristics might nevertheless be drawn. Firstly, it would appear that migratory populations remain at a given depth only for a few hours during the day and move about vertically during the remainder of the time (Grandperrin, 1969; Franqueville, 1970), but that, as a whole, migrating individuals represent only a fraction of the entire population: populations are most dense in the subsurface layers, regardless of sampling time, if we consider minute plankton. Johnston (1962) established that there was an almost linear relationship between depth and the logarithm of the number of animals; Banse (1964) estimated that 50% of the individuals captured in nets of 0.3 mm mesh size, and all smaller planktonic organisms, 80 never leave the euphotic zone; this fact was also supported by King and Hida (1955), Blackburn (1966) and Nakamura (1967). More and more authors agree that only part of the population migrates daily : as the larvae remain on the surface, migration accelerates with age (Brinton, 1962 b; Ponomareva, 1963; Baker, 1959...); even among adults, a great number appears to remain at the same depth during certain physiological phases (Herman, 1963; Baker, 1959; Mauchline, 1960; Ponomareva, 1963) associated mainly with sexual maturity. Certain authors have not given any evidence on differences in vertical displacements as a function of age or sexual state (Lacroix, 1961; Mauchline, 1966 b). Ponomareva (1963) believes that even individuals in a migratory phase do not move vertically every day, but rather at the most every other day when their nutritional requirements will force them to seek the upper layers where they are at the mercy of predators. In fact, it has frequently been noticed that, in the vertical distribution of a migratory species, the species is most dense in the upper layers and reaches the second greatest density level at the greatest depths where the proportion of older individuals is generally greater; between these high-density areas, there is a vast zone that is deserted or in any case less dense, including the thermocline which seems to be a particularly impoverished zone (Le Reste, 1969; Aizawa and Marumo, 1967; Angel, 1968; Baker, 1970; Leavitt, 1935 and 1938; Tregouboff, 1958).

With respect to Euphausiids in particular, it is often stated that they can be divided into two separate groups: the anatomically specialized non-migratory species (*Nematoscelis*, *Nematobrachion*, *Stylocheiron*), and the poorly specialized migratory species (*Euphausia*, *Thysanopoda*) (Baker, 1970;

Brinton, 1966 and 1967 b). The latter group is closely related to the DSL, composed essentially of Euphausiids in the upper layers and of micronectonic fish in the lower layers, both groups being linked by a predation relationship (Boden, Kampa and Abbot, 1959 and 1961). Note, with respect to this matter, that laboratory experiments and actual observations agree in giving the DSL and Euphausiids essentially similar vertical migration speeds (Waterman et al, 1939; Hardy and Bainbridge, 1954; Grandperrin, 1969). Direct observations in bathyscaphes as well as tows with midwater trawls have localized the greater proportion of Euphausiids at the level of the DSL, located by day at 400-600 metres, while only a few individuals reach much greater depths, at least 2000 metres (Aron, 1959; Bernard, 1955 and 1958; Peres, 1958; Tregouboff, 1958).

Figure 27 gives a summary of major observations by certain authors on the vertical distribution of species in the Equatorial and Tropical Pacific.

2. METHODS AND MATERIAL

2.1. Sampling Method

If the literature dealing with vertical distributions often appears to be rather confused, the fault lies both with inherently difficult sampling techniques and the very complexity of the subject matter itself. Although for small plankton, relatively simple vertical tows can determine 89
with relatively good accuracy the depth at which the organisms are found, this sampling method is entirely inadequate for capturing fast-swimming organisms; in the latter case, it it necessary to revert to horizontal or oblique tows which are less accurate, but which will capture the desired fauna.

The problem is further complicated when attempting to capture animals such as Euphausiids which readily escape the net; larger gear, for which no adequate closing device has yet been found, must be used, e.g., the Isaacs-Kidd Midwater Trawl. At the moment, proposals to make the latter a closing type gear suggest using a closing-opening device at the trawl cod-end, either a Catch Dividing Bucket (Foxton, 1963) or the/Be M.P.S. (Pearcy and Hubbard, 1964). We mentioned earlier (cf. chapter on Methods) that the cod-end causes a pressure wall to form at the opening; the animals are therefore held back, then whirl about during a good part of the trawl at this opening without entering it. We might therefore believe that the plankton does not enter the open cod-end immediately when it is captured, but is instead accumulated in the bellies and falls into the cod-end only when the gear is hauled in. An experiment was conducted at the Numea laboratory in 1967-68 by using a 30 cm Be net (1962) on its side as a cod-end. The results were very revealing: almost the entire haul, including deep-water species, was found in the surface net even during daylight hours at which time the surface layers explored by the conventional IKMT was almost void of micronectonic fauna.

Direct observation by means of bathyscaphes, other than being very difficult to achieve, leads to critical problems in identifying the animals and estimating the number of such minute forms (Bernard, 1955 and 1958; Peres, 1958; Tregouboff, 1958; Franqueville, 1970).

The material used to study the vertical distributions of Euphausiids in the Equatorial Pacific was obtained by means of three types of gear:

— the greatest portion of specimens was collected by means of an ordinary 10-foot IKMT, i,e., without a closing device (cf. above). As the subtractive method can be applied only to surface tows because of the variability of samplings, a fact which Leavitt recognized as early as 1935, this sampling method will make known only the highest limits of distributions.

— the Larval Net (Omori, 1965), an 160 cm diameter closing net, is perhaps one of the best compromises available at the moment : relatively reliable functioning, capable of being towed at high speeds are two of its major features; it collects small quantities of micronectonic organisms, less than the IKMT, but permits making good estimates of vertical distributions. Its use is unreliable in the case of deep tows (over 300 m) as a cable longer than 1000 m slows down the trigger mechanism causing it to function unsatisfactorily.

— the Neuston Net (David, 1965) was used to draw samples in the first few centimetres immediately below the surface.

Table 28 90

Gear used to examine vertical distributions (Number of stations examined).

Location and time	gear	IKMT highest limits only	Larval Net (closing-opening)	Neuston Net (surface)
Central Equatorial Pacific	day	7	—	—
	night	16	15	
Western Equatorial Pacific	day	24	—	6
	night	22	—	8
Southwest Tropical Pacific (24-hour series)		16	—	18

2.2. Available Material

Table 28 outlines the material used in the bathymetrical studies forming the basis of this chapter. To this must be added the initial results obtained from recent expeditions in the South Central Tropical

Pacific off the Marquesas Islands (10° S - 142° W), which will be briefly discussed (§ 3.2) so as to give an estimate of the upper vertical limits inhabited by the species during the day in these regions where longline tuna fishing is carried out; these elements will be required when examining trophic circuits (cf. Chap. VII).

This material is quite obviously wanting. We mentioned earlier that use of the IKMT resulted in obtaining knowledge of upper layers only, any estimate of populations inhabiting deeper layers, obtained by subtracting figures for the upper layers, being virtually impossible by reason of the great variations in samplings. The more reliable data obtained from samples drawn with the Larval Net originated from 15 stations only, all night stations and all from the same period; the possible effects of seasonal or cyclical factors (lunar phases especially) could not be detected. Finally, as no tows were carried out within the thermocline (100 to 160 m approx.), no estimates were made of populations inhabiting this supposedly deserted layer.

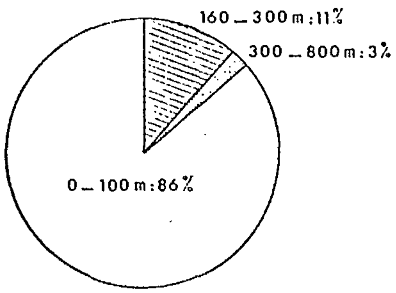
A further comment is necessary regarding samples drawn with the Larval Net. The material collected by means of a single fine net (0.33 mm mesh size) was sorted quite differently than that collected by the IKMT. As minute plankton was most abundant, Euphausiids were included only in fractions B and C, the smallest size corresponding essentially to the 1.2 size group. The 0.9 and 0.7 size groups were therefore not included among specimens collected with the Larval Net, contrary to IKMT specimens.

3. RESULTS

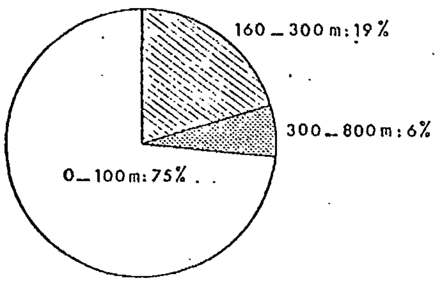
On the basis of the available data outlined above, the following points will be discussed:

— vertical distributions by night in the Central Equatorial Pacific

— upper vertical distribution limits by day in the South Central

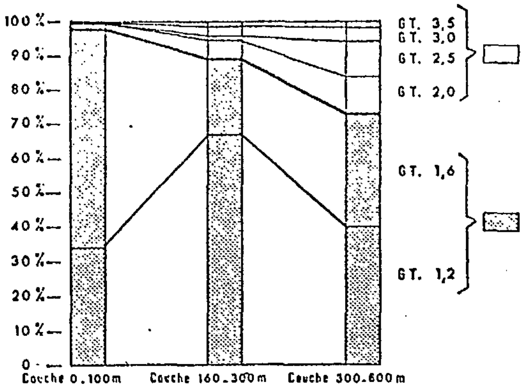


A) Pourcentage du nombre total d'Euphausiacés dans les différentes couches.

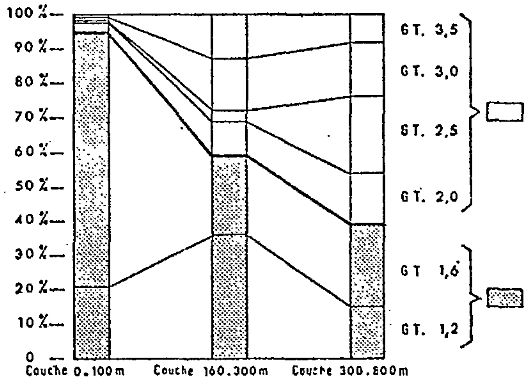


B) Pourcentage de la biomasse totale d'Euphausiacés dans les différentes couches.

Fig. 45. — Distributions verticales nocturnes dans le Pacifique équatorial central (150° W).
Fig. 45. — Vertical distribution of Euphausiids during the night in the central equatorial Pacific (150° W). A : percentages of the total number of animals in the different layers. B : percentages of the whole biomass in the different layers.



A) % en nombre



B) % en biomasse

Fig. 46. — Distributions verticales nocturnes des groupes de tailles dans le Pacifique équatorial central (150° W).
Fig. 46. — Percentages of the different size groups (GT) of Euphausiids in the water layers 0-100 m, 160-300 m, 300-800 m, during the night. A : numbers of animals. B : biomass.

Tropical Pacific

— comparison with the western Equatorial Pacific: surface, length of stay in subsurface layers during the night; differential vertical distributions among size groups; vertical distribution of minute plankton.

3.1. Vertical Distributions of Euphausiids by Night in the Central Equatorial Pacific

The relevant data was mostly obtained from hauls on the "Maruru" expedition (Larval Net) from which, we might recall, only individuals having a thoracic diameter equal to or greater than 1.2 mm were considered. IKMT samples were used as the control samples. Furthermore, when estimating populations in the various layers, the thickness of the layer was taken into account. For instance, if there were 10 individuals of one species per 1000 m^3 in both the 0-100 m layer and the 160-300 m layer, the population of the latter are considered as being 1.4 times greater than that in the 0-100 m layer.

3.1.1. Distribution in terms of Number

Figure 45.A is a diagram showing the bathymetrical distribution by night of the total Euphausiid populations. There is definite stratification as 86% of the individuals are found between 0 and 100 m, 11% between 160 and 300 m, 3% between 300 and 800 m. In terms of number of organisms per 1000 m^3, these percentages correspond to 163 for the 0-100 m layer, 22 for the 140-300 m, 1.5 for the 300-800 m layer. Note that no data is available for the 100-160 m layer which is the thermocline.

3.1.2. Distributions in terms of Size Groups

Figure 46.A gives the proportions of the various size groups making up the population of the various bathymetrical strata. There is a definite gradation, with the proportion of minute forms (e.g., 1.2 and 1.6 size groups), although still a sizeable portion, decreasing with depth; minute organisms represent 98% of the total number between 0 and 100 m, 89% between 160 and 300 m, 73% between 300 and 800 m. Expressed as a biomass, this tendency is of course further emphasized.

3.1.3. Vertical Distribution of Biomasses

By applying to the number of individuals within each size group a coefficient proportional to the mean individual weight of each size group, an estimate of the vertical distribution of the biomasses can be obtained (fig.45B). As the number of minute forms decreases with depth, the corollary follows that the biomass falls less abruptly with depth: 75% of the biomass is found (by night) between 0 and 100 m (against 86% in terms of numbers), 19% between 160 and 300 m (against 11%) and 6% between 300 and 800 m (against 3%). In mg/1000 m^3, these percentages correspond to 4494 for the 0-100 m strata, 699 for the 160-300 m and 68 for the 300-800 m strata.

3.1.4. Vertical Distribution of Species (Fig. 47)

In terms of species, hauls with the Larval Net gave us a fair idea of distributions by night, confirmed on the whole by data from IKMT specimens. We noted that in this region almost all Euphausiids were found in the upper 300 m during the night and that the most abundant species were those reaching the uppermost layers (*T. tricuspidata*, *E. diomedae*, *E. tenera*, *S. carinatum*); we did not exclude the possibility of a cause and effect relationship with the numerically predominating species being those having access to the most plentiful food sources concentrated in the subsurface. Beyond 300 m, there are very few Euphausiids found during the night.

3.1.5. Specific Composition of Different Layers 94

It is rather interesting to note what species are found at a given level to determine whether any of them play a definite part in a given biotope, i.e., are prey to a certain category of predators, for example.

Figure 48 gives in diagram form the specific compositions of the different layers at night. Positions are strongly marked: in the 0-100 m layer, *E. diomedae* alone accounts for 94% of total numbers; this species disappears entirely in deeper zones where it is replaced by *N. gracilis* which accounts for 62% of the total between 160 and 300 m and 50% between 300 and 600 m. Note also that the predominance of the main species is less pronounced at deeper levels than at the surface, progressively decreasing from 94% to 62% to 50%. At the 600-800 m depth, only two species, *B. amblyops* and *N. boopis*, occupy this biotope during the night.

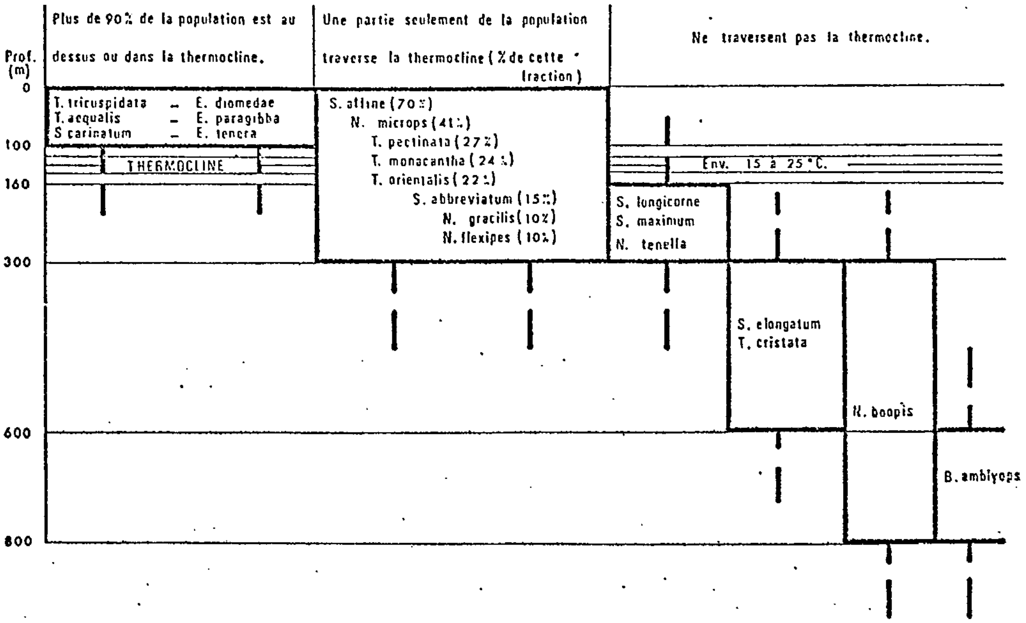


Fig. 47. — Distributions verticales nocturnes des espèces dans le Pacifique équatorial central (150° W).
Fig. 47. — Vertical distribution of species by night in the central equatorial Pacific (150° W). Percentages indicated in the second group represent the estimated fraction of the population crossing the thermocline at night.

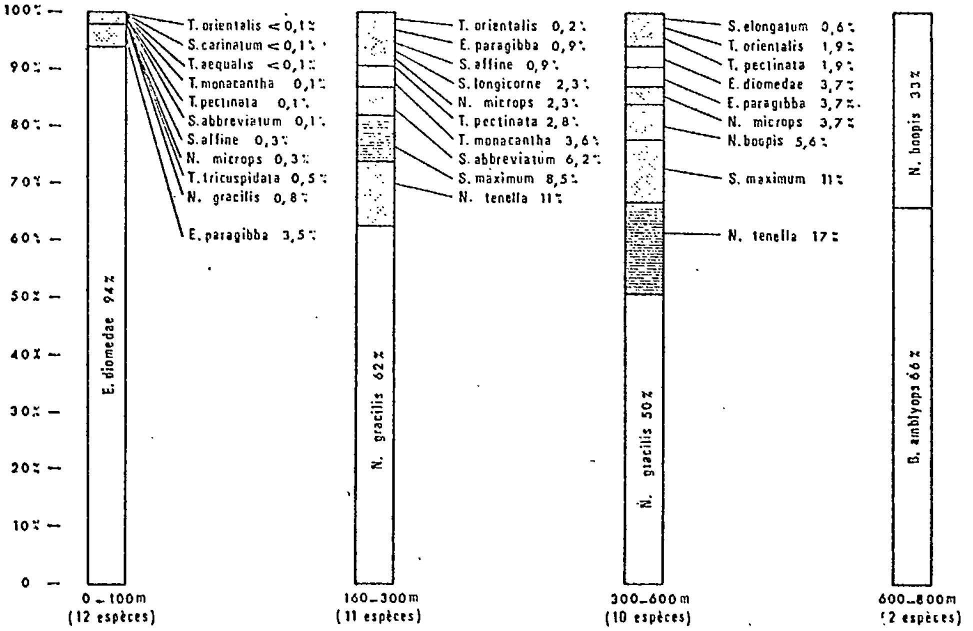


Fig. 48. — Distributions verticales nocturnes dans le Pacifique équatorial central (150° W) : composition spécifique de la population dans les différentes couches bathymétriques.
Fig. 48. — Specific composition of the populations inhabiting by night the different layers in the central equatorial Pacific (150° W).

3.2. Preliminary Data on Upper Vertical Limits of Distributions by Day in the South Central Tropical Pacific

Although these recent samplings have not yet been fully processed, some one hundred IKMT stations carried out at 10° S/142° W have madeit possible to outline the major daytime distribution patterns of the species, one of the factors determining the structure of trophic circuits (cf. Chap. VII). What species, biomasses and size groups are available to daytime predators at various bathymetrical levels is indeed a fundamental fact.

The most obvious situation is illustrated in figure 49: only minute organisms remain in the subsurface during the day, larger animals having left these levels. In the 100 uppermost metres, only individuals less than 15 mm/ 20 mg remain; from a depth of 200 m, 15-22 mm (20-65 mg) individuals appear while the largest organisms (over 22 mm and 65 mg) are found below 400 m. In terms of species, Table 29 indicates that only the small or average size species of the genus <u>Stylocheiron</u> are plentiful in the first 400 metres. All other genera are represented in these layers only by their juveniles and a few adults, the mass of the population being at greater depths.

It would appear that the organisms occupy deeper zones in these stable and impoverished regions where the water is very clear than do the species found in the equatorial zone. According to our estimates, animals in the latter area are some 50 to 150 metres closer to the surface.

3.3. Comparison with Data on the Western Equatorial Pacific

We were unable to note any striking differences in vertical distributions between the western and central Equatorial Pacific. Note however that no hauls were made with a closing net in the western Pacific and that therefore only IKMT figures were available, i.e., only major differences were brought to light. It is highly possible that minor differences between east and west, which may have considerable ecological or biological significance because the environment is highly stratified, may have been entirely overlooked. 95

3.4. Surface

Examination of 32 tows with the Neuston Net (dragnet for surface fishing) resulted in the data appearing in Table 30. Note that very few species reach the first few centimetres immediately below the surface. Juvenile and larval forms are most common, withdrawing further down only during midday; adults are found at this level only by night. The species occurring most frequently (E. paragibba, E. diomedae, E. brevis, E. tenera, S. carinatum) were captured only in small numbers, except for possible swarms (E. diomedae). T. tricuspidata was occasionally noticed. The presence of S. elongatum near the surface should be considered accidental as this species definitely prefers a deep-water habitat; in fact, only one specimen was collected with the Neuston Net. We noted also that, in terms of both numbers and frequency of occurrence, population density at the surface was greater in the tropical zone than in the equatorial zone.

3.5. Length of Stay in Subsurface Layers during the Night

Inasmuch as the two biotopes of the migratory species, subsurface by night and deep waters by day, differ fundamentally and affect the individuals in a completely different manner (environment, transportation, nutrition, predation), it is important to estimate the time spent in each biotope by the various species. Once again, our methods lacked sufficient accuracy and a first approximation was obtained by examining shallow tows carried out in 24-hour series. In this particular case, we used a series of samplings in the 0-200 m zone in the southwestern Tropical Pacific, the results of which are given in figure 50. The time at which the species arrived and left the 0-200 m layer, which generally includes the isotherm and thermocline, are clearly indicated. Several categories were identified according to time and length of stay in the subsurface.

(1) Species permanently present, little migration : *S. carinatum* *S. longicorne*.

(2) Species present throughout the night, from 1900 to 0600 hours, or approximately 11 hours: *T. aequalis*, *E. paragibba*, *N. microps*, *E. diomedae* *N. sexspinosus*, *N. flexipes*, *N. tenella* (the latter being most abundant in the late night)

(3) Species particularly abundant during the early hours of the night, from 1900 to 0100 hours approximately, or 6 hours: *S. abbreviatum*, *T. tricuspidata*, *T. obtusifrons*, *T. pectinata*, *N. atlantica*.

(4) Species present during the middle of the night:

T. cristata: 2200 to 0500 hours or 7 hours
T. monacantha: 2100 to 0100 hours or 4 hours
E. fallax: 2200 to 0100 hours or 3 hours
T. orientalis: 2300 to 0100 hours or 2 hours

(5) Species present in the late hours of the night:

N. gracilis: 0300 to 0500 hours or 2 hours
N. tenella similar to the preceding but occurring over a longer period of time.

(6) *S. affine* is in a category of its own as it appears to have an 98
entirely different migration pattern and disappears completely from 1800 to 0600 hours approximately.

As a whole, the occurrence of Euphausiids followed a regular curve with the peak at 2030 and 0030 hours. From 0600 to 1800 hours, they are found in negligible numbers in the 0-200 m strata.

Larval Net stations 52 and 54 on the "Maruru" expedition carried out in the 50-120 m level demonstrated in a most spectacular fashion the

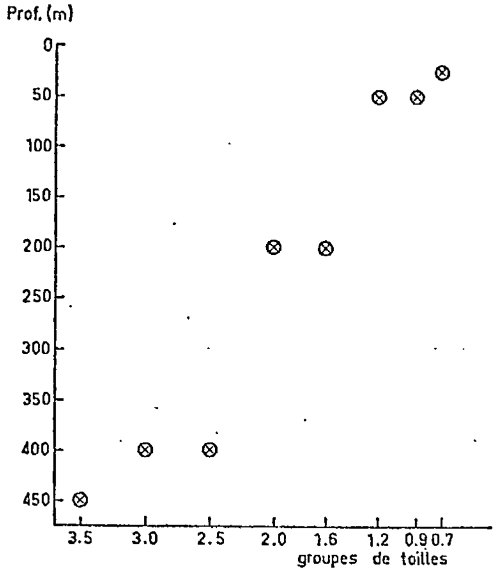


Fig. 49. — Limites supérieures diurnes de présence des Euphausiacés en fonction de leur taille, dans le Pacifique tropical sud central (10° S-142° W).

Fig. 49. — Upper vertical limit of occurrence of the different size groups during the daytime, in the central south tropical Pacific (10° S, 142° W).

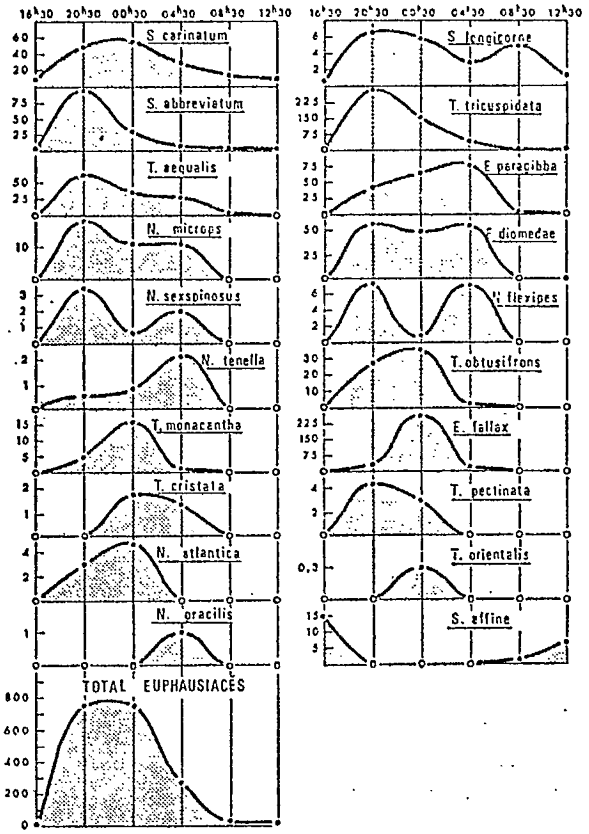


Fig. 50. — Évolution nycthémérale du peuplement des 200 premiers mètres dans le Pacifique tropical sud-ouest (170° E) : nombres d'individus récoltés par station (o : récolte nulle. • : récolte positive).

Fig. 50. — Species inhabiting the upper 200 m at the different times of the day in the southwestern tropical Pacific (170° E): numbers of individuals per station.

TABLE 29

Bathymetrical distributions of species by day in the South Central Tropical Pacific.

	0-200 m	200-400 m	> 400 m
Species found in great numbers (Espèces abondantes)	*S. carinatum* *S. microphthalma* *S. suhmii.*	*S. abbreviatum* *S. maximum* *S. affine* *S. longicorne*	*T. cristata* *T. tricuspidata* *T. monacantha* *T. pectinata* *T. obtusifrons* *T. aequalis* *S. elongatum* *E. diomedae* *E. paragibba* *E. tenera* *N. tenella* *N. microps* *N. gracilis* *N. flexipes* *N. sexspinosus* *N. boopis* *B. amblyops*
Species found only sporadically (Espèces présentes sporadiquement)	*S. longicorne* *E. diomedae* +JUVÉNILES of : *S. abbreviatum* *S. maximum* *N. microps* *T. tricuspidata* *T. monacantha*	*T. tricuspidata* *S. elongatum* *E. diomedae* *E. tenera* *N. tenella* *N. microps* +JUVÉNILES of : *T. cristata* *T. monacantha* *N. flexipes*	

TABLE 30

Neuston Net: frequency of species captured in surface hauls and mean number (m) of individuals per station. Western Pacific (170° E).

TROPICAL ZONE (20° S to 5° S), 18 stations :

	12 h	16 h	20 h	00 h	04 h	08 h
E. paragibba	0	0	3/5 m = 20	1/2 m = 12	1/2 m = 1,0	0
E. brevis	0	0	1/5 m = 3,0	2/2 m = 4,0	1/2 m = 0,5	0
E. tenera	0	0	0	1/2 m = 0,5	1/2 m = 1,5	0
S. carinatum	0	0	1/5 m = 0,6	2/2 m = 1,5	0	0
T. tricuspidata	0	0	1/5 m = 0,4	0	0	0
S. elongatum	0	0	1/5 m = 0,2	0	0	0
Larves et indéterminés Larvae and undetermined	0	1/3 m = 0,3	3/5 m = 10	2/2 m = 16	1/2 m = 4,0	3/3 m = 3,0
TOTAL	0	1/3 m = 0,3	4/5 m = 34	2/2 m = 34	1/2 m = 7,0	3/3 m = 3,0

EQUATORIAL ZONE, 14 stations

	20 h	23 h	02 h 30	12 h-14 h
E. tenera	0	1/4 m = 0,5	0	0
E. diomedae	0	1/4 *	2/3 m = 0,6	0
Larves et indéterminés Larvae and undetermined	0	1/4 m = 0,2	1/3 m = 1,0	1/6 m = 0,6

* 1 swarm of 2260 adult individuals.

"emptying" of the surface layer at dawn: at 0430 hours (station 52), 978 Euphausiids (including 944 E. diomedae) were captured over a short distance of 370 m. At 0730 hours (station 54), the net was towed over a distance of 1110 metres and no Euphausiids were collected.

Note that we were concerned here only with individuals longer than 10 mm or so. Smaller organisms (cf. § 3.7.) remain in the subsurface during the day.

Two further comments are necessary at this point:

- the situation described above was observed in the Southwest Pacific at a given time. It is highly probable that these same species behave quite differently in different regions. For instance, the inverse migration of S. affine was not noted in the Equatorial Pacific. This situation should therefore not be considered as a bathymetrical description of the species, but rather as an illustration of a particular situation.

. as the ordinates on figure 50 indicate the number of individuals collected between 0 and 200 metres at different hours, and not depths, the curves indicate the migration of animals. It is quite possible, for instance, that the entire population of *S. carinatum* is found at all hours above 200 metres : if by day, this species occurs between 100 and 200 metres, more individuals are lost as they rise than by night if the species is then concentrated between 0 and 100 metres, hence fewer individuals inhabiting there during the day.

3.6. Differential Vertical Distributions among Size Groups

We mentioned in § 3.1.2. and 3.2. that larger individuals were generally more numerous in deeper layers, without suggesting whether this was due to a difference in the specific composition of the population according to depth (larger species preferring deep-water habitats) or whether, within a given species, older organisms tended to dwell deeper down than young ones. Papers reviewed on this subject would indicate that several authors maintain the latter view which should indeed be further examined : this view would imply that the populations were scattered according to age groups whenever movements in the water were not consistent throughout the biotope.

Data on distributions by night obtained on the "Maruru" expedition led us to draw the following conclusions:

— 8 species (*T. tricuspidata*, *T. aequalis*, *S. carinatum*, *S. elongatum*, *S. affine*, *S. longicorne*, *E. diomedae*, *P. amblyops*) were represented by one single size group or occurred only in one layer, i.e., our samplings were carried out on too large a scale to permit detecting possible differences in size group distributions, these species being scattered over a limited vertical distance.

— among the 10 other species, only *H. tenella* seemed to show a

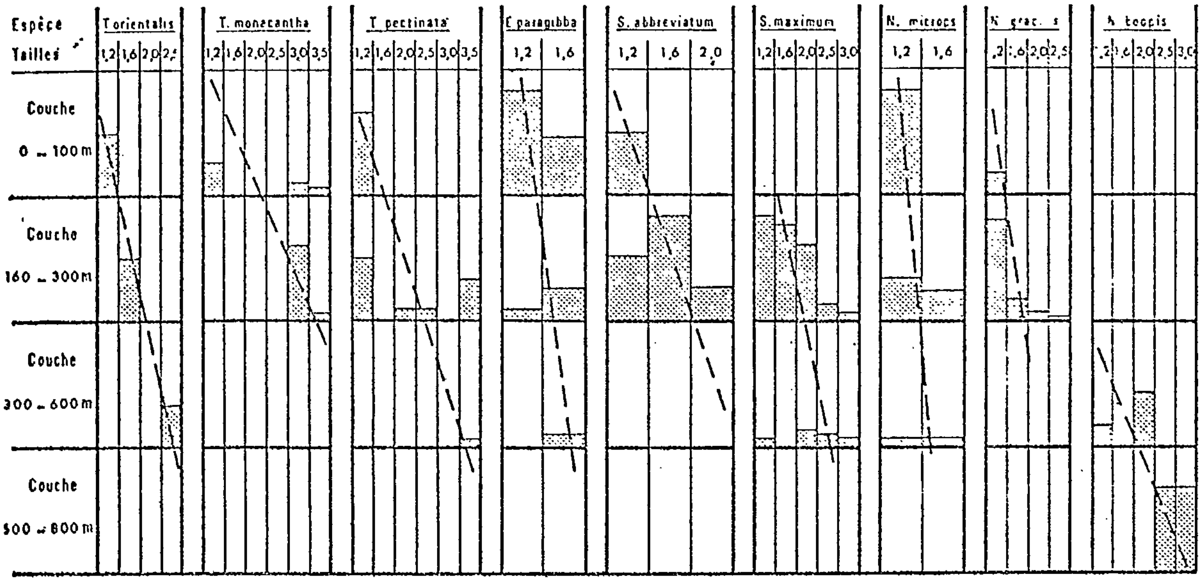


Fig. 51. — Distributions verticales nocturnes différentielles des groupes de tailles pour 9 espèces du Pacifique équatorial central.

Fig. 51. — Vertical distribution of size groups for 9 species of the central equatorial Pacific during the night, showing that older animals tend to dwell in deeper layers.

higher percentage of young individuals in the deeper layer; the 9 others (fig. 51) showed a tendency towards larger individuals being found deeper down. We might therefore assume that our data confirms the general opinion that, within a given species, there is a correlation between the age of the individuals and the depth at which they dwell. 99

The available data is too limited to allow us to determine whether differences in vertical distribution are also a function of sexual maturity. Accurate information can be obtained only by examining specimens captured with the Larval Net; however, this net captures very few individuals at the reproductive stage.

3.7. Vertical Distribution of Minute Plankton

This point must be discussed under a two-fold consideration. Firstly, approximately two-thirds of the largest organisms of this category, large individuals being generally from 4 to 10 mm long according to sorting of Larval Net material, are Euphausiids. These organisms are the larval and juvenile stages of the species discussed in detail in this study or representatives of very small species (E. tenera, S. suhmii, S. microphthalma). Secondly, the smallest among these, individuals 0.3 to 4 mm long, are likely what we might assume as being the food source of Euphausiids.

Table 31 gives the vertical distribution of the biomasses of both these categories in the Central Equatorial Pacific.

Note that the 0-100 m layer is by far the most plentiful where the density of minute plankton is 10 to 40 times greater than in deeper layers. Although our data on daytime phenomena in the subsurface is lacking, we might assume, given the absence of minute plankton deeper down during the day, that these small 100
individuals remain at the surface even during hours of sunlight.

We might therefore conclude that:

1. the juvenile or larval forms of Euphausiids never leave the euphotic zone and any vertical displacement is very minimal.

2. predatory Euphausiids, like the phytophaga, depend largely on the subsurface for food; species which do not migrate to the upper layers are very often detrivorous. Regarding this point, we in fact noted (Michel, comm. pers.) that specimens of minute plankton collected in the subsurface were generally in good condition, the animals being generally orange-pink; those collected in the 100-300 m layer were browner and rather damaged, more so than the length of their stay in the net would warrant; specimens from the 300-800 m depth varied from dark brown to grey in colour : the debris of dead organisms and animal wastes were most plentiful, the "flood of detritus" coming from the surface.

4. SUMMARY

According to the research outlined above and dealing with vertical distributions, the following can be established:

— the distribution of species during the night in the Central Equatorial Pacific, shown in figure 47, from which the following can be directly deduced:

- the type of tow required to capture a given species
- the ecological and dynamic conditions favourable to the various species in their nighttime biotope
- the food sources of nighttime predators (total biomass, specific composition, size of organisms) consisting of Euphausiids dwelling at different bathymetrical levels.

— the upper daytime limits of distributions. This point is fundamental as we shall later discuss when dealing with trophic relationships: in fact, the various species of Euphausiids are included in different food 101 chains depending upon whether they make themselves available to surface predators (0-400 m) which feed mostly during the day and are in turn eaten by the large tunas, or whether they escape the predators by inhabiting the deeper layers by day. According to our data, in this respect concerning mainly the South Central Tropical Pacific where longline tuna fishing is actively pursued, only the species of the genus Stylocheiron (with the exception of S. elongatum) remain plentiful during the day in the upper 400 metres. Other genera are represented only by their juveniles and a few adults (cf. Table 29). We might assume that the same situation occurs in the Equatorial Pacific (zone of divergence) but that the species are found some 50 to 150 metres deeper.

— a classification of species in terms of their vertical biotope and the extent of their nychthemeral migrations (given in Table 32).

TABLE 31

Vertical distribution of minute plankton: biomass in mg/1000 m^3

		Organisms 4 -10 mm long (approx. 30% Euphausiids)	Organisms 0.3 - 4 mm long (food source for Euphausiids)
Night Nuit......	0-100 m	25	30
	160-300 m	1,3	2,5
	300-800 m	0,7	1,0
Day Jour......	0-100 m	pas de données no data	
	160-300 m	0,5	1,0
	300-800 m	0,5	0,5

TABLE 32

Vertical biotope of species in the Central Pacific (*).

Type of Vertical Behaviour		Species	Equatorial Zone		Tropical Zone	
No or little migration (extent of migration less than 100 m). Except for S. elongatum and N. boopis, a large portion of the population remains in the upper 400 m during the day.	Surface	*S. suhmii*........	0-100 m		0-150 m	
		S. microphthalma.	0-100 m		0-150 m	
		S. carinatum.....	0-150 m		0-300 m	
		S. affine.........	50-150 m		50-300 m	
		S. abbreviatum...	50-300 m		50-300 m	
		S. longicorne.....	100-300 m		200-400 m	
	Midwater	*N. tenella*........	160-500 m		200-500 m	
		S. maximum.....	160-500 m		200-500 m	
	Deep-water	*S. elongatum*.....	250-600 m		300-600 m	
		N. boopis........	350-800 m		350-800 m	
			Day Jour	Night Nuit	Day Jour	Night Nuit
Migratory species (related more or less to the DSL).	Almost entire population concentrated by night above or in the thermocline...........	*E. tenera*......	200-500	0-160	350-800	0-200
		T. tricuspidata.	300-600	0-160	350-800	0-200
		E. diomedae...	300-600	0-160	400-800	0-200
		T. aequalis....	300-600	0-160	450-800	0-200
		E. paragibba..	350-600	0-160	450-800	0-200
	Large portion of population remains even at night below the thermocline..........	*N. microps*....	250-500	100-300	250-500	100-300
		T. monacantha.	350-600	50-300	450-800	50-300
		N. flexipes....	350-600	100-300	350-600	150-400
		N. gracilis.....	350-600	100-300	450-800	200-400
		T. pectinata...	350-600	100-300	450-800	200-400
		T. orientalis...	350-600	200-500	450-800	200-400
	Deep-water species	*T. cristata*.....	400-800	160-600	450-800	200-600
		B. amblyops....	600-1000	350-800	600-1000	350-800

(*) Depths indicate layers of maximum concentration; isolated specimens generally found closer to the surface, especially specimens of E. diomedae or T. tricuspidata found there during the day at approx. 100 m below the surface.

CHAPTER 5 . REGIONAL ECOLOGY AND INTERSPECIFIC ECOLOGICAL AFFINITIES

1. NATURE OF THE PELAGIC ECOLOGY

Relationships between the distribution of organisms and that of the physico-chemical parameters of the environment, in the case of animals near the top of a food chain (Euphausiids, for instance), are rather difficult to define clearly because of time and space factors. With this particular group, two other factors further hamper research into ecological considerations: firstly, extremely heterogeneous distributions impede the presentation of reliable data and the observance of rules in statistical analysis; secondly, these migratory or deep-water species, forming a large portion of our material, are rather cosmopolitan given the fact that the former must face great environmental changes within a very short period of time, which would imply a relative insensitivity to environmental conditions, and that the latter occupy a habitat that is very homogeneous throughout a vast area.

There are clear demonstrations of this in scientific literature: if, under well-defined local conditions, where widely different masses of water come into contact, species-environment relationships can be observed (Williamson, 1956; Furnestin, 1957, 1964 and 1970; Bary, 1959 a, b, c; Anraku, 1962 and 1964 a; Soulier, 1965; Thiriot, 1965), such relationships are generally applicable to a vast stretch of an ocean environment (Bary, 1970; Brodskiy, 1959; King and Demond, 1953; King and Doty, 1957; Bogorov, 1959 b; Aron, 1962 a; Beklemishev, 1966 a and b; Ebeling, 1967; Heinrich, 1968 a;

Lubny-Gertzyk, 1968; Bogorov and Vinogradov, 1971; Timonin, 1969) and therefore make it possible to outline the biotopes of various species (cf. Bieri, 1959 for Chaetognatha, Brinton, 1962 b for Euphausiids). Beklemishev (1959) noted that the uniformity of the oceanic habitat leads to very vast distribution zones, especially in the homogeneous tropical environment; Dimov (1962) further observed that marine currents formed very stable entities, i.e., masses of water remaining consistent over vast expanses and supporting the same planktonic life.

Hence, attempts to establish relationship between species and a given body of water over a smaller scale have invariably been fruitless (King and Hida, 1955 and 1957 a; Vinogradov and Voronina, 1966, Roger, 1968 b); with respect to Euphausiids, Chiba, Tsuruta and Maeda (1955) noted that *T. tricuspidata* 104 and *S. carinatum* did not vary significantly indensity according to any particular zone in equatorial waters. Furthermore, although surface organisms are to some extent sensitive to their environment (Baker, 1965), mid- or deep-water species are cosmopolitan and any knowledge of their ecology is therefore rather difficult to grasp (Ponomareva, 1963; Nemoto, 1969). Even when a relationship can be established between a certain species and a body of water, its significance is somewhat doubtful as the similarities between biological and physico-chemical distributions may have a common source, perhaps one of dynamic origin (Brinton, 1960).

Among environmental factors affecting distributions, temperature, salinity and oxygen content are most frequently mentioned (Drobysheva, 1963; Roger, 1966, etc.), the first two factors possibly causing osmotic effects on cells and tissues (Schlieper, 1959). However, many authors maintain that planktonic organisms are highly resistant to changes in their environment which they encounter daily during their vertical migrations; these same authors rather doubt that such changes affect distributions (Hopper, 1960;

Vinogradov and Voronina, 1961; Kinzer, 1966; Longhurst, 1967 a; Teal and Carey, 1967 b). We must bear in mind, however, that temperature, salinity and oxygen content are mentioned most frequently because these parameters are most easily measured; they are not necessarily more important than other more subtle ones (Rae, 1960; Furnestin, 1970). Among these, trophic conditions are often considered as being primarily responsible for distribution patterns (Vinogradov, Voronina and Sukhanova, 1961; Vinogradov, 1966; Vinogradov, Gitelzon and Sorokin, 1970; Timonin, 1971); other authors define conditions in a pelagic habitat in such vague terms as "sufficient food" or "tolerable temperature" (Johnson and Brinton, 1963).

Present ecological trends emphasize the importance, when examining relationships between organisms and environment, of considering smaller taxonomic units than the species, e.g., subspecies or geographic race (Brodskiy, 1965; Fleminger, comm. pers.), which implies extensive preparatory work.

In this chapter, we shall examine the ecological characteristics of the various regions investigated (regional ecology) and the ecological tendencies of the various species according to their response to the environment (specific ecology); finally, we shall attempt to group the species according to ecological affinities.

2. REGIONAL ECOLOGY AND DIVERSITY

2.1. Characteristics of the Different Regions and their Populations

The five regions defined in the chapter on Zoogeography each have fairly pronounced individual features, although some among them are related by a space factor (adjacent zones) or a time factor (the same masses of water successively cross Zones E, C, A). The area investigated has made it possible in particular to confirm the distinction between the populations of the stable, more impoverished zones (tropical waters) and those dwelling in waters benefitting from a source of abundance, upwelling or divergence (equatorial zone) (cf. Heinrich, 1962 b; Longhurst, 1967 b).

Zone E is biologically the "youngest" being closest to the source of the South Equatorial current, doubly enriched by the Peru current which 105 is one of the most productive regions on the globe and by intensive equatorial divergence; consequently, there is a very large planktonic biomass dominated by very abundant species (little diversity), mainly herbivorous species. The westward movement of the water and regular change in biological characteristics cause a depletion of the surface waters (according to a process described by Vinogradov, Gitelzon and Sorokin, 1970) and "aging" in population structures. From Zone E to Zone C to Zone A, the biomass gradually decreases in size while diversity and the proportion of carnivorous organisms increase.

A different type of transition occurs from north to south in the western Pacific between regions A and B where only distance comes into play, the fauna changing from tropical to equatorial species : there is no longer a succession of structures from east to west as in the Equatorial Pacific, only a transition from one environment to another, these environments being adjacent to one another without one being the biological evolution of the other. The contrast between Zone B, a homogeneous impoverished tropical environment, and the richer, less diversified Zone A does not bear the same meaning as the apparently similar phenomena observed between regions E, C and A.

The very isolated region D, located in the subtropical "gyral" of the Southeast Pacific, seems far removed from any enrichment phenomena (upwelling and divergence); an extremely stable stratification prevents nutritive salts from deeper layers from rising to the surface. This is therefore a typical oligotrophic tropical region with a highly diversified but very small planktonic biomass made up mainly of carnivorous species.

The trophic structure of the populations throughout the various zones will be further discussed in the chapter on nutrition.

2.2. Diversity

2.2.1. General Comments and Selection of an Index

Diversity and its significance were developed at great lengths by certain authors.(cf. especially to Margalef, 1957 and 1969; Timonin, 1971); any repetition would therefore be redundant. However, we must justify our choice of index, namely the Shannon-Wiener index:

$$I_s = -\sum p_i.\log_2 p_i \text{ (in bit/species)}$$

where $p_i = n_i/N$

n_i = number of individuals of given species

N = total number of individuals

The greatest diversity occurs when all species are represented by the same number of individuals; this will be expressed as:

$$I_{max} = \log_2 n$$

where n = number of species

Both the Shannon-Wiener index (I_s) and the Margalef index (I_m) take into account both the number of species and their distribution within the community, i.e., the abundance of each species. Gueredrat, Grandperrin and Roger (1972) demonstrated that I_s could be substituted for I_m whenever there were 106
large numbers of individuals (in practice, more than 100). Note that $I_m < I_s$ because, in calculating I_m, we took into account the signals (sic) taken for calculating the information given by the following (sic): the mean quantity of information per signaltherefore decreases regularly and equals zero for the last signal which is perfectly determined. When calculating I_s (its practical aspect being the use of Stirling's approximation for calculating

factorials), we assumed that each signal gave the same quantity of information regardless of preceding numbers (cf. Frontier, 1969): the deviation between I_m and I_s is greater when density is lower. As we collected over 100 specimens in most of our hauls, we thought I_s would be acceptable for measuring diversity.

2.2.2. Value of the Index of Specific Diversity according to Change in Geography

We mentioned in 2.1. that changes occurred from east to west in the case of regions E → C → A, and from north to south (different changes) in regions A-B. We shall examine these two series in terms of diversity and conclude by examining the oligotrophic tropical region D.

2.2.2.1. Changes from east to west in the Equatorial Pacific (cf. Gueredrat, Grandperrin and Roger, 1972)

We calculated the index of diversity for each of the 33 stations on the "Alizé" expedition, the greatest diversity and the ratio I_s/I_{max}; this data is given in Table 33. Figure 52 shows a graph of the distribution I_s, which is essentially identical to that of I_s/I_{max}. Note certain unusual measurements (stations 23, 27, 36, 38) expressed as a rather low index of diversity as compared with other stations; this was due to the appearance of swarms (E. diomedae) resulting in one species predominating, thus causing a drop in the value of the index.

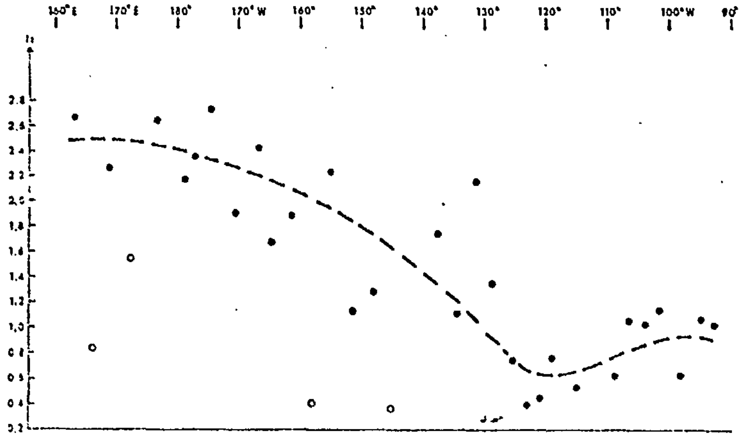


Fig. 52. — Évolution Est-Ouest de l'indice de diversité spécifique dans le Pacifique équatorial. o : Essaims de *E. diomedae*.

Fig. 52. — Values of the SHANNON-WIENER index of specific diversity (I_s) from East to West in the equatorial Pacific. (o: swarms of *E. diomedae*).

TABLE 33

Diversity along the equator ("Alizé" expedition).

Station	Longitude	I_s	I_s/I_{max}
2	92°20′ W	1,03	51 %
3	95°28′ W	1,07	43 %
4	98°18′ W	0,62	20 %
5	101°14′ W	1,15	35 %
6	103°48′ W	1,02	34 %
7	106°45′ W	1,06	33 %
8	109°10′ W	0,62	20 %
10	115°40′ W	0,54	16 %
11	118°27′ W	0,77	25 %
12	120°45′ W	0,45	17 %
13	123°35′ W	0,39	12 %
14	125°53′ W	0,77	23 %
15	128°26′ W	1,36	41 %
16	131°42′ W	2,17	72 %
17	134°46′ W	1,12	35 %
18	137°45′ W	1,74	49 %
23	145°06′ W	0,38*	13 %
24	148°07′ W	1,29	39 %
25	151°15′ W	1,13	68 %
26	154°38′ W	2,23	75 %
27	158°10′ W	0,41*	11 %
28	161°06′ W	1,89	53 %
29	164°15′ W	1,68	49 %
30	167°30′ W	2,42	76 %
31	170°30′ W	1,90	58 %
32	174°10′ W	2,74	73 %
33	177°30′ W	2,37	66 %
34	179°00′ E	2,17	66 %
35	176°06′ E	2,65	74 %
36	172°30′ E	1,54*	45 %
37	169°00′ E	2,28	60 %
38	166°00′ E	0,84*	24 %
39	162°45′ E	2,68	67 %

* abnormal, due to swarms of *E. diomedae*

Analysis of diversity distribution along the equator was developed by Gueredrat, Grandperrin and Roger (1972); we shall repeat only the main points. According to figure 52, there is:

(A) to the east, from 90° W to 125° W, little diversity, between 0.4 and 1.2.

(B) from 125° W to 180°, a regular increase in I_s, which runs from 0.4-0.6 to 2.2 to 2.7.

(C) to the west of 180°, great diversity (I_s 2.2 to 2.7).

The definite increase in the value of the index of specific diversity corresponds entirely to our description of the environment and the expected results of the latter upon the planktonic populations : the rich environment to the east (large biomass, little diversity) becomes progressively depleted as it progresses westward (smaller biomass, greater diversity). 108

We might conclude that, in introducing the notion of diversity, we obtained a very coherent description of the equatorial system by measuring population characteristics, changes from east to west in population structure being equated with changes in the environment.

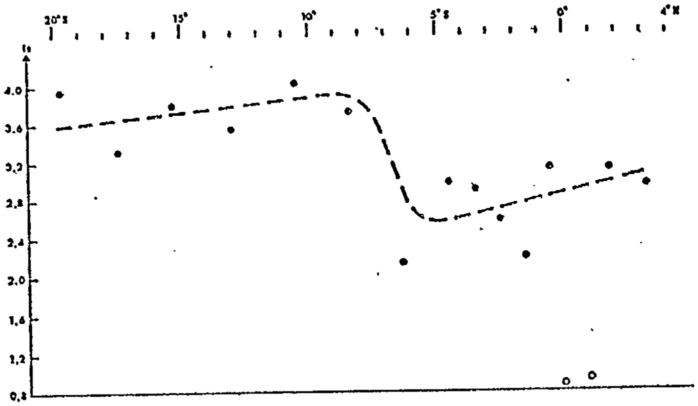


Fig. 53. — Évolution Nord-Sud de l'indice de diversité spécifique dans le Pacifique ouest (170° E). o : Essaims de *E. diomedae*.

Fig. 53. — Values of I_s from South to North in the Western Pacific (170° E) — (o : swarms of *E. diomedae*).

2.2.2.2. Changes from north to south in the western Pacific

The calculation of I_s for the sixteen 0-1200 m stations of the "Bora" IV expedition (from 20° S to 4° N on 170° E) was plotted on a diagram, shown as figure 53. Note:

(A) rather great diversity in the impoverished tropical zone (20° S - 7° S) : mean $I_s = 3.74$

(B) less diversity in the rich equatorial zone (7° S - 4° N): mean $I_s = 2.39$. These values agree entirely with those ($I_s = 2.2 - 2.6$) obtained for the same region on the "Alizé" expedition (cf. preceding § and fig. 52).

(C) a sudden drop in diversity caused by swarms (at 0° and 1° N).

As we pointed out earlier, the change in diversity from north to south differs from that observed from east to west: while the latter was a change

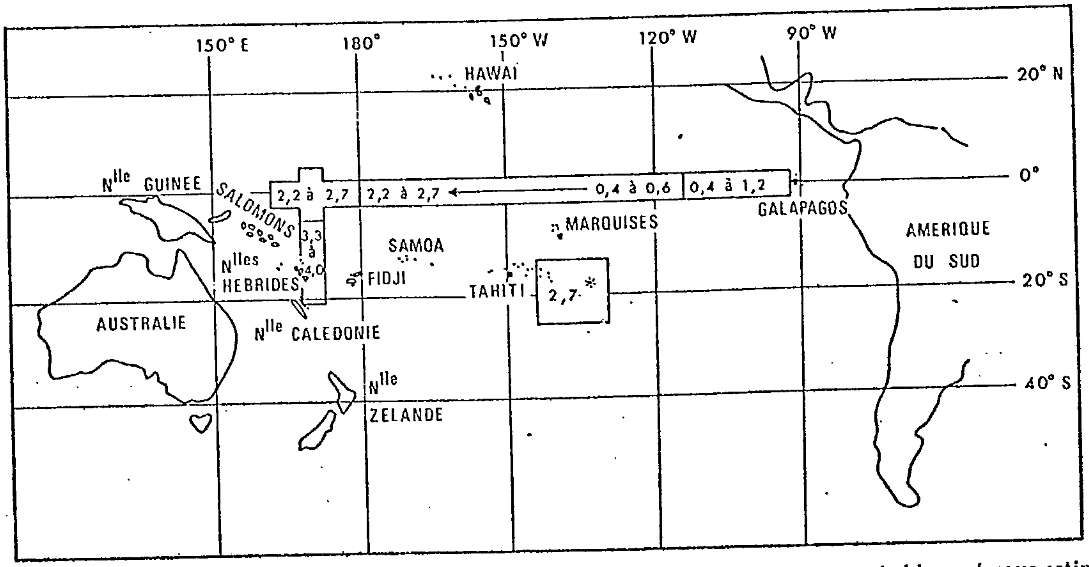


Fig. 54. — Distribution géographique de l'indice de diversité spécifique. * : valeur probablement sous-estimée en raison d'un échantillonnage défectueux.

Fig. 54. — Geographical distribution of I_s. (* : probably underestimated owing to insufficient data).

within an ecosystem, in this case the change occurs between two biotopes unrelated by any ecological succession. Note, in fact, on figure 53 the sudden drop at approximately 7° S (change from tropical to equatorial environment) and not the gradual change occurring from east to west at the equator (fig. 52).

2.2.2.3. Diversity in the South Central Pacific (Zone D)

We qualified this region as being a stable, oligotrophic tropical environment supporting a very small planktonic biomass. We can therefore expect to find a highly diversified population. In fact, the mean $I_S = 2.69$ for all 0-350 m night stations on the "Brisants" expedition, this value corresponding to the highest values noted for Zone A. The fact that there is less 109 diversity in Zone D than in Zone E might be questioned. This may be due to inadequate sampling during the "Brisants" expedition, especially a serious under-estimation of small organisms and therefore identification of fewer species than those actually present.

2.2.2.4. Conclusions on geographical variations of the index of specific diversity

Figure 54 summarizes the observations mentioned in the three preceding paragraphs. In particular, it points out:

(A) the contrast between the great diversity of tropical regions and low to average diversity of equatorial regions

(B) the increase in diversity from east to west at the equator.

Finally, we might again point out that these values of diversity agree remarkably well with the population structures we obtained in examining the distribution of biomasses (cf. chap III, § C).

3. SPECIFIC ECOLOGY

3.1. Environmental Influences on Species Distribution

We mentioned earlier in this chapter that Euphausiids have certain consistent characteristics (high trophic level, deep-water habitat or migratory habits) making it difficult to establish clear relationships between their distribution patterns and physico-chemical parameters, which in effect can be established only on a wide scale. Examination of our material definitely confirms this fact. Note:

— the obvious differences between the faunas of highly divergent 110
regions which are considerable distances apart (e.g., Zones A/E/D);

— the little influence (on a short term basis at least) exerted by environmental changes on the distribution of species. Our material contains two definite examples of this:

(A) In the Central Equatorial Pacific ("Caride" expeditions), the South Equatorial Current appears to meander semi-permanently, such that stations carried out during the middle of the expedition were located in a North body of water different from that where samples were drawn at the beginning and end of the expeditions. This was especially noticeable during "Caride" I (Hisard, comm. pers.). Although our hauls indicated a slight increase in the number of individuals for 4 out of 22 species and a decrease for one species during the middle of the course, none of these variations were significant and 17 species were collected in rather constant numbers along the entire radial.

(B) In the western Equatorial Pacific ("Cyclone" expeditions), there was a marked change, linked to the intrusion of waters originating from north of New Guinea, noted on the "Cyclone" III expedition.Although 12 out of 17 species were less abundant than their yearly average, for 10 of these this variation is not significant and there was no apparent radical change in the specific composition of the fauna.

3.2. Vertical Ecology

Knowledge of vertical distributions of both the organisms and environmental factors enables researchers to make approximations of the daytime and nighttime biotopes occupied by the organisms. This data is given in the chapter entitled "Vertical Distributions". It would be superfluous to list the various environmental factors when theiraction upon the animals remains unknown; for that reason, we have listed only temperature in Table 34 to give an idea of the degree of change to which the organisms are submitted within a 24-hour period, temperature being a parameter of great biological importance (cf. especially Fowler, Small and Keckes, 1971). These distributions apply to the equatorial zone; species migrating little were included with sedentary species; temperature estimates were deduced from data obtained during an expedition when heat conditions were considered average ("Caride" V). With respect to migratory species, we might believe that their length of stay in each biotope, daytime and nighttime, is in the order of 8 to 10 hours with the 2 to 4 hours remaining for each half-day spent on rapid descent or ascent.

In Table 34, note:

— the great difference between the living conditions of surface species surviving in temperatures of 16-25° C, and those of deep-water dwellers permanently submitted to temperatures of 5-12° C, with the probable ramifications of such contrasting environments on the biology of their respective inhabitants.

— secondly, temperature variations to which heavy migrators are subject daily reach 13 to 18°, implying an eurythermal behaviour.

TABLE 34

Biotopes occupied by different species.

(A) Sedentary species or species migrating little :

Espèces Species	Profondeur (m) Depth	Température Temperature
S. carinatum *S. microphthalma*	0-150	25-16°
S. affine	50-150	25-16°
S. abbreviatum *S. longicorne*	50-300	25-12°
S. maximum *N. tenella*	150-500	16-7°
S. elongatum	250-600	12-7°
N. boopis	350-800	11-5°

(B) Migratory species :

Species Espèces	JOUR DAY		NUIT NIGHT	
	Profondeur Depth	Température Temperature	Profondeur Depth	Température Temperature
E. diomedae *T. tricuspidata*	(100) 300-360	(23) 12-7°	0-160	25-16°
T. aequalis	300-600	12-7°	0-160	25-16°
E. paragibba	350-600	11-7°	0-160	25-16°
N. microps	250-500	12-7°	100-300	23-12°
T. monacantha	350-600	11-7°	50-300	25-12°
N. gracilis *N. flexipes*	350-600	11-7°	100-300	23-12°
E. gibboides	350-600	11-7°	160-300	16-12°
T. orientalis *T. pectinata*	350-600	11-7°	200-500	13-7°
T. cristata	400-800	10-5°	350-800	11-5°
B. amblyops	over plus de 600	less than moins de 7°	350-800	11-5°

3.3. Characteristics of the Different Species

The study of the zoogeographical and ecological aspects of our material being almost completed, we are now able to attribute certain characteristics to each species. In the preceding chapters, for each species we discussed the following:

— how each species was represented in our samples (Chap. 2 A.3);

— morphological characteristics (especially size) and major distribution patterns (Chap. 3.B);

— distribution in terms of number in the various zones investigated (Chap. 3.C).

— distribution characteristics (Chap. 3.D); 112

— the extent of seasonal variations (Chap. 3.E):

— vertical distributions and nychthemeral variations (Chap. 4), from which we deduced the nature of both the daytime and nighttime physico-chemical and dynamic environments.

4. INTERSPECIFIC AFFINITIES

Having described the quantitative distribution of the species throughout the various regions, we will now determine whether any of the species display similar ecological tendencies, i.e., whether any of them prefer the same regions.

4.1. Criteria Selection

The first criterion consisted in selecting a parameter expressing most satisfactorily the "prosperity" of organisms or the ecological "fitness" between species and environment. In practice, we could choose between the intrinsic abundance of the animals (e.g., mean number of individuals collected per 5000 m tow) and the percentage of the given species in comparison with the total population. The latter was selected on the basis of two major considerations:

(A) The abundance of the equatorial region as compared with that of tropical regions was such that most species were found in greater numbers there than in the other zones: although one species may have accounted for only a small fraction of the total population, because of the general richness of the environment, more specimens were collected than in an otherwise more impoverished zone where the species formed a major portion of the total population. In this case, considering the number of individuals would have falsely led to assuming that the equatorial environment was most favourable for most species.

(B) Independently of the first problem, it would appear more logical merely by intuition, to assess "fitness" between species and environment by estimating the total resources available to the given species. This is perfectly well expressed by use of the percentage of the species in terms of total population, the parameter which Moore qualified, as early as 1952, as indicating "prosperity" most satisfactorily.

According to the ecological criterion described above, we listed the species and for each one classified the regions in decreasing order according to percentage of the given species occupying each region.(Table 35). Species limited to a certain biotope were not considered, knowledge of their distribution patterns being unnecessary in this analysis: E. gibboides, E. exemia and E. distinguenda limited to the eastern Equatorial Pacific, T. obtusifrons, T. subaequalis, E. brevis, E. mutica, E. fallax and N. atlantica which are exclusively tropical species. The major criticism against this procedure, common to all rank-order tests, lies in the fact that all final values depend upon the signification of classifying regions by the "preferential" order shown by each species. For instance, T. tricuspidata accounted for 19.1% of the total population in Zone D and 16.7% in Zone E, the latter being classified after Zone D for this species; we therefore implicitely assume that 19.1% is significantly different from 16.7%. Determining the level of significance for all 600 stations investigated would have required 113 means of calculation which we did not have on hand; we resigned ourselves

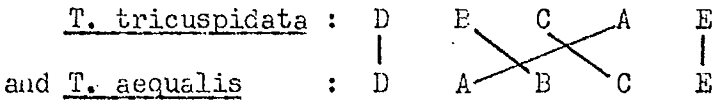
TABLE 35

Density of species in the different regions (as %, in decreasing order). The / sign separates two regions for which the same percentage was obtained for the given species.

Species	Regions (% decreasing)				
T. cristata	D	A	B	C	E
T. tricuspidata	D	B	C	A	E
T. orientalis	A	B	C /	E	D
T. monacantha	C	A	B	D	E
T. pectinata	D	B	A	C	E
T. aequalis	D	A	B	C	E
S. carinatum	C	B	D	A	E
S. abbreviatum	B	D	C	A	E
S. maximum	A	D	B	C	E
S. elongatum	B	D	A	C	E
S. affine	C	A	B	D /	E
S. longicorne	B	A	D	C	E
E. diomedae	A	C	B	E	D
E. paragibba	B	C	A	D	E
N. tenella	A	B	C	E	D
N microps	A	B	C	D	E
N. gracilis	C	A	E	B	D
N. flexipes	D	B	E	C	A
N. sexspinosus	D	B	A	C /	E
N. boopis	B	A	D	C	E

to checking whether our classification agreed with zoogeographical data in available papers.

Using Table 35, we expressed similarity and difference between distribution of species throughout the various regions by applying a very simple method which we called "Misfit Quotation". The method measured classification differences between two species according to the number of intersections obtained by joining homologous regions. Hence, between



there is a Misfit 2 (2 intersections).

Evidently, two species given the same classification, i.e., inhabiting the different regions in the same order of preference, will be rated Misfit 0 (no intersections):

T. orientalis : A B C E D

| | | | |

N. tenella : A B C E D

while the highest Misfit value (1), equal to 10 in the case of 5 regions, was obtained when two species had an inverse classification. The highest Misfit value we encountered was 9 (between _E. diomedae_: ACBED and _N. flexipes_ : DBECA). 114

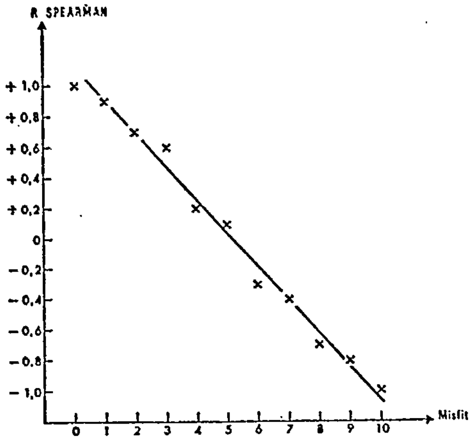


Fig. 55. — Relation entre la cotation MISFIT et le coefficient *R* de SPEARMAN.
Fig. 55. — Relationships between the Misfit Quotation and the Spearman's *R* index.

This method is extremely rapid for joining only a few points (approx. 8 points); when a longer series makes up the classification, a calculated test such as Spearman's may be more convenient. The Spearman method may in fact be applied to shorter series by altering the classification such that the difference in rank between two points does not take into account the absolute values of these points (inversion of the two regions must be measured by the same number regardless of the number of these regions, point A not having an intrinsically greater value than point B, for instance).

The Spearman R index is expressed as:

$$R = 1 - \frac{6\sum d^2}{n^3 - n}$$

where n is the number of points in the classification (in this case, 5 from which $n^3 - n = 120$) and d is the differences in rank.

Hence, in the couple _T. aequalis/T. tricuspidata_, the Spearman test gives

---

(1) The greatest misfit is equal to the sum of the (n-1) first whole numbers, where n is the number of points to be joined. $M_{max} = \frac{n(n-1)}{2}$

the following:

			D	A	B	C	E	
T. aequalis	— classification of regions:		D	A	B	C	E	
	—	rank:	1	2	3	4	5	
		d:	0	1	1	2	0	
T. tricuspidata	—	rank:	1	3	4	2	5	(with respect to T. aequalis)
	— classification of regions:		D	B	C	A	E	

$$\text{Hence } d^2 = (1)^2 + (1)^2 + (2)^2 = 6$$

$$\text{and } R = 1 - \frac{6 \times 6}{120} = 0.70$$

The advantage of this test is the possibility of calculating the level of significance, which is not the case with the Misfit Quotation which could only qualify this level as "low" from 0 to 3, "average" from 4 to 6 and "high" from 7 to 10 (when 5 points are being classified).

To test the validity of our Misfit Quotation, we also calculated the Spearman R index for 9 couples of species with Misfits ranging from 0 to 9. The Spearman/Misfit relationship is given in figure 55; the essentially 115 linear function led us to believe that our Misfit Quotation was valid and particularly convenient in our case because it could be used very rapidly.

TABLE 36

Misfit values for pairs of species.

	T. cristata	*T. tricuspidata*	*T. orientalis*	*T. monacantha*	*T. pectinata*	*T. aequalis*	*S. carinatum*	*S. abbreviatum*	*S. maximum*	*S. elongatum*	*S. affine*	*S. longicorne*	*E. diomedae*	*E. paragibba*	*N. tenella*	*N. microps*	*N. gracilis*	*N. flexipes*	*N. boopis*	*N. sexspinosus*
T. cristata		2	4	5	1	0	5	3	1	2	5	3	5	5	4	3	7	4	3	1
T. tricuspidata			6	5	1	2	3	1	3	2	5	3	7	3	6	5	7	2	3	1
T. orientalis				3	5	4	5	5	3	4	3	3	1	3	0	1	3	7	3	5
T. monacantha					6	5	2	4	4	5	0	4	2	2	3	2	2	7	4	6
T. pectinata						1	4	2	2	1	6	2	6	4	5	4	8	3	2	1
T. aequalis							5	3	1	2	5	3	5	5	4	3	7	4	3	1
S. carinatum								2	6	3	2	4	4	2	5	4	4	5	4	4
S. abbreviatum									4	1	4	2	6	2	5	4	6	3	2	2
S. maximum										3	4	2	4	4	3	2	6	5	2	2
S. elongatum											5	1	5	3	4	3	7	4	1	1
S. affine												4	1	2	2	2	1	7	4	6
S. longicorne													4	2	3	2	6	5	0	2
E. diomedae														4	1	2	2	9	4	6
E. paragibba															3	2	4	5	2	4
N. tenella																1	3	8	3	5
N. microps																	4	7	2	4
N. gracilis																		8	6	8
N. flexipes																			5	2
N. boopis																				2
N. sexspinosus																				

Table 36 gives Misfit values obtained for 20 species.

4.2. Ecological Groups

By grouping couples with a low Misfit value (0 to 3), we obtained ecological groups, each one made up of species inhabiting the same regions by preference (low intra-group misfits). We thereby obtained three ecological groups:

Group I : species most abundant in tropical waters, the biotope where they make use of most of the available resources. In the equatorial zone, they occur only in negligible numbers, but increase in numbers as they progress westward. 10 species: N. boopis, S. longicorne, S. maximum, S. elongatum, S. abbreviatum, T. cristata, T. tricuspidata, T. pectinata, T. aequalis, N. sexspinosus.

TABLE 37
Misfit values, within and between groups.

Group	Species	Misfit with species of Group I	Misfit with species of Group II
I	*T. pectinata*……………………	1.1.1.1.1.2.2.2.2.	5.5.6.6.6.8.
	N. sexspinosus……………………	1.1.1.1.1.2.2.2.2.	5.5.6.6.6.8.
	T. tricuspidata……………………	1.1.1.2.2.2.3.3.3.	5.5.6.6.7.7.
	T. aequalis……………………	0.1.1.1.2.2.3.3.3.	4.4.5.5.5.7.
	T. cristata……………………	0.1.1.1.2.2.3.3.3.	4.4.5.5.5.7.
	S. elongatum……………………	1.1.1.1.1.2.2.2.3.	4.4.5.5.5.7.
	S. abbreviatum……………………	1.1.2.2.2.2.3.3.4.	4.4.5.5.6.6.
Transition species Espèces de transition	*S. maximum*……………………	1.1.2.2.2.2.3.3.4.	3(a).3(b)4.4.4.6.
	N. boopis……………………	0.1.2.2.2.2.3.3.3.	3(a).3(b)4.4.4.6.
	S. longicorne……………………	0.1.2.2.2.2.3.3.3.	3(a).3(b)4.4.4.6.
	N. tenella……………………	3(c).3(d).3(e)4.4.4.5.5.5.6.	0.1.2.3.3.
	T. orientalis……………………	3(c).3(d).3(e)4.4.4.5.5.5.6.	0.1.3.3.3.
II	*T. monacantha*……………………	4.4.4.4.5.5.5.5.6.6.	0.2.2.3.3.
	E. diomedae……………………	4.4.4.5.5.5.6.6.6.7.	1.1.1.2.2.
	S. affine……………………	4.4.4.4.5.5.5.5.6.6.	0.1.1.2.3.
	N. gracilis……………………	6.6.6.6.7.7.7.7.8.8.	1.2.2.3.3.
III	*E. paragibba*……………………	2.2.2.3.3.4.4.4.5.5.	2.2.3.3.4.4.
	N. microps……………………	2.2.2.3.3.3.4.4.4.5.	1.1.2.2.2.4.
	S. carinatum……………………	2.3.3.4.4.4.4.5.5.6.	2.2.4.4.5.5.
—	*N. flexipes*……………………	2.2.3.3.4.4.4.5.5.5.	7.7.7.8.8.9.

(a) with N. tenella
(b) with T. orientalis
(c) with S. maximum
(d) with N. boopis
(e) with S. longicorne

GROUP II : species poorly adapted to oligotrophic tropical biotopes; thrive in the divergence, high productivity waters (equatorial zone). Six species: N. tenella, T. orientalis, T. monacantha, E. diomedae, S. affine, N. gracilis. 116

GROUP III : 3 species ranging between the two preceding groups, i.e., low Misfit values with certain species of Group I and with others of Group II: E. paragibba, N. microps, S. carinatum.

N. flexipes is an isolated case: linked only with the most typical species of Group I and separated from species of Group II by very high Misfit values.

Table 37 gives all Misfit values after species were grouped as described above. According to this table: .

— there are low (0 to 3) Misfit values within species of the same group (with the exception of S. maximum/S. abbreviatum rated a Misfit 4); 117
these species differ from others by high Misfit values, 4 to 9.

— Group III is indeed an intermediate group, having the same range of Misfit values as Groups I and II.

— N. flexipes is far removed from Group II (high Misfit values) and is related to Group I only by the most typical species of that group.

— finally, Groups I and II are joined to one another by links or average Misfit values with S. maximum, S. longicorne and N. boopis (Group I) forming the transition with Group II by rather low Misfit values (3) with N. tenella and T. orientalis.

These observations make it possible to show on a diagram the ecological trends applicable, according to our data, to all Euphausiids of the Equatorial and South Tropical Pacific (Fig. 56). This is only a general outline with errors possibly occurring as a result of difficult sampling

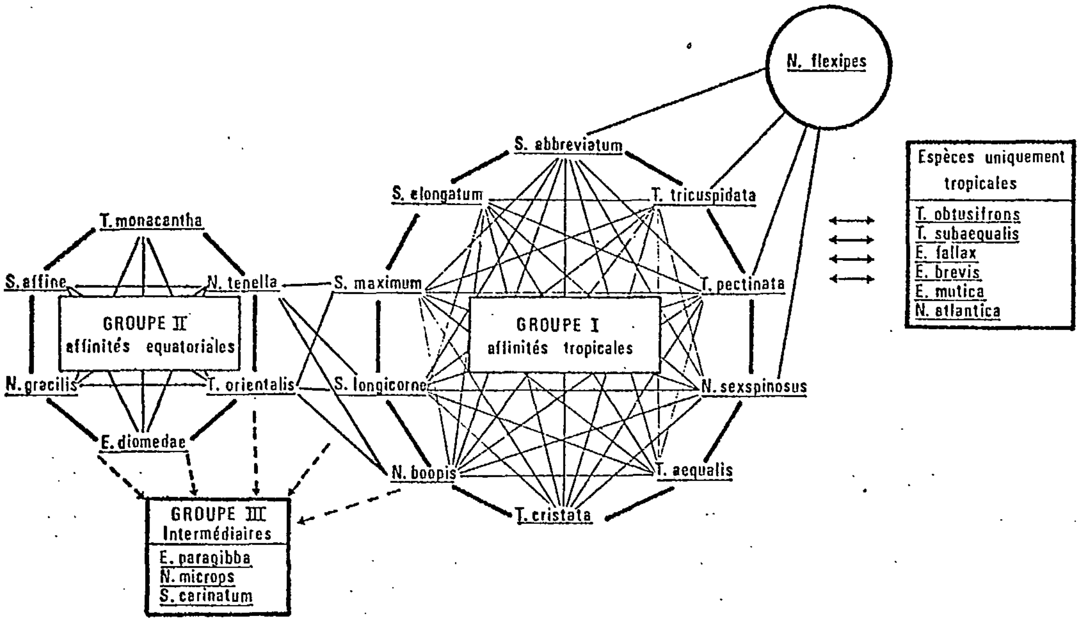


Fig. 56. — Groupement par tendances écologiques des espèces d'Euphausiacés du Pacifique équatorial et sud tropical.
Fig. 56. — Ecological affinities.

conditions; nevertheless, this diagram gives a fairly accurate idea of the ecological communities determining population structures.

CHAPTER . REPRODUCTION, GROWTH AND LIFE SPAN

I. INTRODUCTION

Researchers conducting studies on the biology of Euphausiids have met with serious difficulties drastically reducing the number of studies which might otherwise be available on the subject.

The initial problem involves following the movements of a pelagic population which escapes observation: a study of life cycles would imply that samples must be drawn from the same population of individuals at different seasons. However, in actual fact, reliability of sampling becomes hampered by great variations in hauls, long intervals of time between samplings, difficulties in capturing comparable quantities of individuals ranging from larva to adult, difficulties in estimating spawning periods because most organisms simply drop their eggs into the water. The above all create further impediments.

A further problem arises when hauls are examined to identify the organic development and sexual maturity of individuals in order to follow the rate of maturity and aging of a population. At this point, a compromise between accuracy and practical observation is imperative: it is quite impossible to carry out measurements on thousands of individuals, although this procedure would seem the only valid solution if significant data is to be obtained.

This is the extent of problems encountered when dealing with the populations of cold or temperate waters where the seasons are responsible for imparting a definite pattern to life cycles : spawning generally occurs in the spring or summer, is virtually interrupted during the winter; generations are therefore highly differentiated from one another and it is possible to follow their pattern of growth.

Not so in a tropical and equatorial environment where biological changes occur at an uninterrupted rate. According to samplings drawn from these waters, the same percentage of mature individuals is present at all seasons; likewise, the proportion of individuals forming each age group differs very little from one season to another: spawning is an almost semi-continuous process. At first glance, it would appear almost impossible to identify different generations and to follow their development.

120 These facts were well pointed out by Hansen (1910), Mauchline (1960 and 1968), Mauchline and Fisher (1969), Blackburn (1966) who recognized the continuous reproductive process of tropical species whereby it becomes difficult to identify biological phases and cycles; these authors nevertheless stressed the necessity of pursuing studies into the matter. For such obvious reasons as those mentioned above, available material on the biology of Euphausiids deals mainly with populations of colder regions where climatic variations are very pronounced, such regions being often protected seas limiting any possible migration of the organisms (North Sea, Barents Sea and Sea of Japan). Major research on biological cycles and reproduction was conducted by Zelickman (1958 and 1960), Drobysheva (1963), Ponomareva (1963), Komaki (1967 a) for the northwestern Pacific, the Sea of Japan and the Barents Sea; Smiles and Pearcy (1971) for the northeastern Pacific; Ruud (1932), Fraser (1936), Bargmann (1937 and 1945), Marr (1962), Baker (1959), Ivanov (1970) for the Antarctic; MacDonald (1928), Einarsson (1945), Adams (1966), Mauchline (1960, 1966 a, 1968), Jones (1969) for the North Sea and the North Atlantic.

Virtually no such research has been done for tropical waters due to the biological implications created by the lack of distinct climatic fluctuations; to date, the only studies available are those made by Ponomareva (1969) on Euphausiids in the Indian Ocean. Mauchline and Fisher (1969) commented that there were no estimates available of the growth curve of tropical species, still fewer of meso-pelagic species which have been captured only in very small numbers. In speaking about the Mediterranean, Casanova-Soulier (1968) noted that practically everything remained to be done on development cycles. However, since then, Franqueville (1971) has proposed a few diagrams illustrating the life cycles of major species found in the Mediterranean.

Certain authors view the apparent continuity of spawning in a tropical environment merely as the result of unsynchronized cycles: each individual ceases to spawn at certain periods, but as these periods do not occur at precisely the same time for all individuals, the proportion of larvae, juveniles, adults, reproducers remains essentially the same throughout the seasons (Giese, 1959). Ponomareva (1969) set forth a rather interesting finalist interpretation of the reproductive process of Euphausiids in the Indian Ocean: he claimed that the depleted tropical seas offer few resources such that, were spawning to occur at consistently the same period like in a temperate environment, a dearth of food and a high mortality rate among larvae would arise at the time of the phytoplanktonic bloom. If, on the other hand, spawning occurs throughout the year with the females releasing eggs at several different times, resources are better utilized. The author concluded that this process made it impossible to detect spawning periods in a tropical environment. Although certain authors (Giese, 1959) claimed that with reproduction going on continually it should be possible to detect periods of more intense activity, research into the life cycles of plankton inhabiting warm waters has met with very great difficulties.

2. APPRECIATION OF AVAILABLE MATERIAL

A two-fold criterion must be met when evaluating available data:

2.1. Sexual Characteristics of the Species 121

It is not necessary to know the life cycle of each different species to determine the number of eggs contained in a mature ovary (fecundity) or to know the size of the individual required before ovarian maturity can occur; any representative sampling should provide answers to such questions for a wide variety of species (cf. § 4).

2.2. Cycles

When attempting to determine biological cycles, on the other hand, the criteria for judging the sufficiency of the material will be much more restrictive for the very reason that there must be some consistency in both the time and location of samplings.

We mentioned earlier that one of the problems involved in examining the seasonal aspects of a pelagic population was precisely the difficulty of finding the same population over several successive samplings. No coherent description can be given of individuals of population A captured in January and individuals of population B collected in March; any interpretation will most likely be inaccurate. Currents in the Equatorial Pacific flow from east to west, with minor alterations unimportant at this point. That same direction must therefore be followed when drawing samples so as to remain within the same mass of water while covering a certain distance. Any other route might seriously distort the facts. This major point is outlined on figure 57: let us assume a population being drawn westward with individuals of various ages having been spread around by the action of the current such that the larger individuals become more concentrated to the east (plausible situation in equatorial currents). If samples are drawn along a north-south direction (1st case), a type of "stroboscopy" apparently accelerating the cycles will be noted: the first expedition records a maximum number of specimens in the 1.2 size group, this number becoming the 1.6 size group on the second expedition carried out further westward and class 2.0 is the one observed. We might falsely conclude that, between both observations, the 1.2 size group has become the 2.0 group, while in actual fact, it is the 1.6 size group, i.e., the individuals developed more slowly than anticipated. On the other hand, if in a similar situation, samplings follow the displacement of the water (2nd case), it becomes immediately obvious that the risk of error is considerably reduced.

On expeditions of the R.V. "CORIOLIS", the "Cyclone" and "Bora" (north-south) series were carried out according to the first instance, the "Caride" (east-west) according to the second. Only the data obtained from the latter will therefore be examined to determine biological cycles. Use of data obtained from gear trawled perpendicular to prevailing currents is useful only for identifying certain characteristics present at the time (e.g., percentage of mature females in a given age group, number of eggs in the ovaries, etc.), but must be definitely rejected for examination of the biological evolution of the populations. The material available to study life cycles is therefore limited to that obtained on the "Caride" I to V expeditions (135-155° W on 0°), respectively centered about the following dates: October 1, 1968; December 5, 1968; February 22, 1969; July 2, 1969 and September 24, 1969. Although an entire year was covered, the frequency of samplings remains unsatisfactory as the interval of time between two consecutive series of observations varied from 2 to 4 months. In an equatorial environment where one might expect cycles to succeed one another very rapidly, these conditions, due strictly to geographical distances, cannot be considered satisfactory

as major developmental changes may have gone entirely unnoticed between two 122
successive expeditions.

In terms of method, other than the inaccuracies mentioned in the chapter on Methods, changing certain towing techniques could result in considerably altering the type of specimens being collected. Aron and Collard (1969) demonstrated that increasing towing speed resulted in a greater number of large organisms being captured (fewer are able to escape) and fewer small ones (a greater number of these escape). When studying seasonal changes in population structure according to age groups, false conclusions
might be drawn if there are major technical disparities between one expedi- 123
tion and another.

In view of the foregoing, for this part of the work we selected material drawn from 109 stations of the "Caride" I to V expeditions, all of which were carried out during the night. Among these, 89 stations were carried out at a depth of at least 550 m; 20 other stations included between 250 and 550 m were disregarded in terms of deep-water species. The "Caride" I to IV expeditions covered the equatorial region from 135 to 155° W, "Caride" V at 140° W only and therefore having the same limitations mentioned in the case of the "Cyclone" expeditions (fig. 57, 1st case).

Finally, representative sampling was a further consideration, i.e., the number of specimens available for each species which further limited the number of species which could be examined to determine biological cycles. Species poorly represented in the zone selected for this part of the study, (species with tropical affinities or species confined to the eastern Pacific), species too minute to be adequately sampled by the IKMT, those for which the juvenile stage could not be properly identified (confusion between N. gracilis-N. microps and S. abbreviatum-S. maximum) were all rejected. Among remaining species, determining biological cycles required that several criteria had to be taken into consideration (establishing 8 size groups for each of the 5 expeditions resulted in 40 categories) such that only those species that were very well sampled had a sufficient number of individuals in each size group. On the basis of those requirements, only the 5 most abundant species were examined: T. tricuspidata (7013 specimens), T. monacantha (2031), T. aequalis (2747), E. diomedae (42740) and N. tenella (1806), to which we added, in spite of few specimens being available, two species of particular interest by reason of their deep-water habitat: B. amblyops (347) and N. boopis (318).

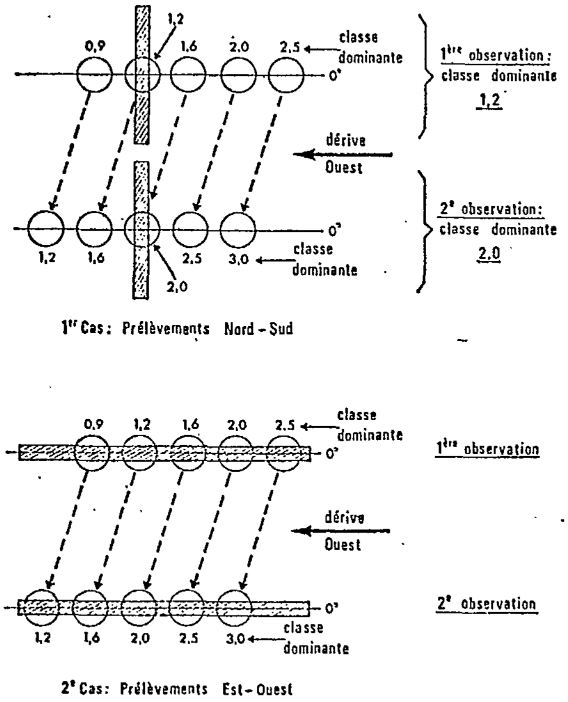


Fig. 57. — Influence du programme de prélèvement sur la validité des observations saisonnières.

Fig. 57. — Influence of the sampling program upon the validity of observations devoted to the seasonal evolution of the age (size) structures of the populations : in the East-West shifting equatorial zone, North-South sampling (1st case) results in an artificial apparent more rapid growth.

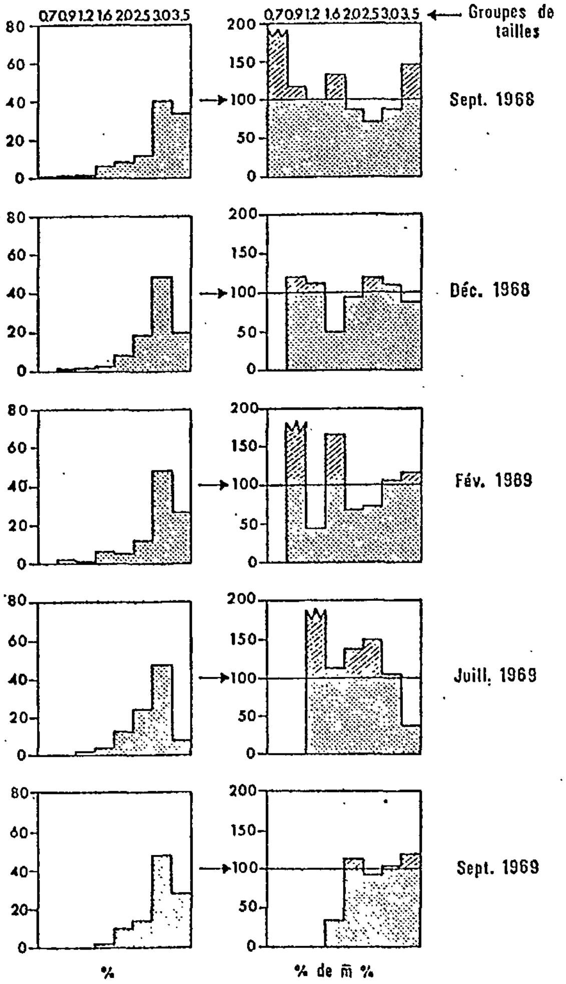


Fig. 58. — Répartition en tailles des *T. monacantha* dans les échantillons des différentes croisières dans le Pacifique équatorial central : pourcentages des différents groupes de tailles (à gauche) et leurs représentativités relatives (à droite).

Fig. 58. — Size structure of the populations of *T. monacantha* in the samples of successive seasonal cruises in the central equatorial Pacific : — on the left, percentages of the different size groups, relative abundances of which are principally determined by the selection of the net. — on the right, the percentage of each size group is expressed in terms of its mean annual value. Modal classes become obvious and allow to suggest a possible growth curve.

3. DESCRIPTION OF STUDY METHODS AND COMMENTARY

The determination of biological cycles is essentially based on the study of seasonal changes in the population structure in terms of age groups (i.e., size groups) and ovarian stages.

3.1. Size Groups

The procedure for establishing size groups was described in the chapter on Methods. We mentioned at that point that, although the technique selected was useful for sorting very productive hauls, the results were not as accurate as individual measurements would have otherwise given; uncertainty has therefore prevented us from accurately establishing growth curves for each species and from defining an equation of this growth. Although in the case of crustaceans, the size of the organisms is fairly indicative of their approximate age, the relationship between both parameters is not a rigid one: Mauchline (1960) noted differences in size and weight from one year to another; Bargmann (1945) claimed that size could only vaguely suggest age. For such reasons, we will limit ourselves to finding the salient features of biological cycles of which, we might recall, no parameters are known: contrary to many other studies, which might have further contributed to this study (cf. especially Garcia, Petit and Troadec, 1970), we were unable to refer to earlier re- 124
search and select plausible solutions among various hypotheses.

Nevertheless, for each expedition we prepared histograms giving size distributions for each species. For instance, the left portion of figure 58 are histograms for *T. monacantha* for all 5 "Caride" expeditions. It is immediately obvious that, throughout the year, the 3.0 size group is most highly represented in this species; from CA I to CA V, the five distributions are practically identical and, if we limit ourselves only to this data, we shall conclude that there is no evidence of seasonal changes, that reproduction is continuous and that a growth curve cannot be established for this species. The reason for this situation is obvious: due to the selection of certain size groups made by the sampling gear, minor seasonal fluctuations within the population become unnoticeable. As we cannot entirely do away with bias introduced by the methods applied, we must therefore examine relative abundance rather than the actual number of specimens. Thus, for instance, the 2.0 size group of T. monacantha over the 5 expeditions accounts respectively for 7.7%, 8.5%, 6.1%, 12.4% and 10.0% of total specimens, or an average of 8.9% for the whole year. In order to determine whether this size group undergoes significant seasonal variations, these percentages must be brought to their average of 8.9%. For the 5 expeditions, we therefore obtained relative abundances of 7.7/8.9 = 87, 8.5/8.9 = 96; 6.1/8.9 = 69; 12.4/8.9 = 139; 10.0/8.9 = 112 respectively. By proceeding in this manner for all size groups, possible seasonal fluctuations in size distributions are brought to light and compensation is made for biased selection by the sampling gear (fig. 58, right hand portion): determining biological cycles is therefore made possible by establishing relationships between modal classes.

The major drawback to this procedure is to consider all data as being equally reliable regardless of the actual number of specimens. In the case of T. monacantha, for example, the number of individuals in the 3.0 size group captured during the 5 expeditions was respectively 409, 223, 108, 115 and 33; these figures are fairly high and might therefore be considered as representative. For the smaller individuals, which largely escaped the IKMT, a much lower number of individuals was collected: for the 0.9 size group, for instance, we collected 7, 3, 4, 0 and 0 or 0.7%, 0.7%, 1.8%, 0% and 0% of total specimens on each respective expedition or an average of 0.6% of hauls over the entire year. By applying the mean percentage, the relative abundance for this group becomes 117, 117, 300, 0 and 0; there is nothing to indicate that these estimates are based on only 14 specimens having been collected for all samplings. When considering the validity of a relative value, it is therefore necessary to consider the actual number from which it was derived.

Evaluation of the reliability which might be granted to the proposed deductions will be discussed in § 6, Conclusions.

3.2. Ovarian Stages

Examination of the extent of ovarian maturity gives certain indications on the intensity of spawning activity at different seasons, i.e., confirms observations obtained from population structures established according to age groups.

We identified 4 stages of ovarian maturity which we shall describe in detail for one typical species, T. pectinata (photos E to K). Variations from this typical species will be pointed out when each species is considered 125 individually. Photo E shows the 4 stages given to scale and suggests the extent of ovary enlargement.

Stage I (photo H): the ovary is small, thin, contains very numerous transparent eggs, all of the same size.

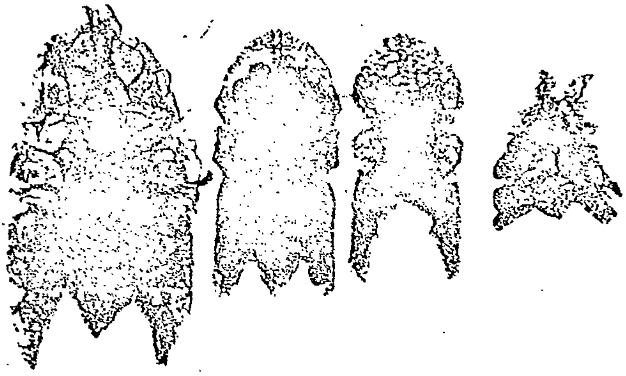
Stage II (photo I): The eggs at the centre of the ovary increase in size, but remain transparent. Those on the periphery (germinal layer) are unchanged from Stage I.

Stage III (photo J): The eggs at the centre of the ovary further increase in size, lose their transparency and become polygonal in shape due to their being closer together. At this stage, the ovary resembles an opaque mass surrounded by a fine germinal layer of small transparent eggs still at Stage I.

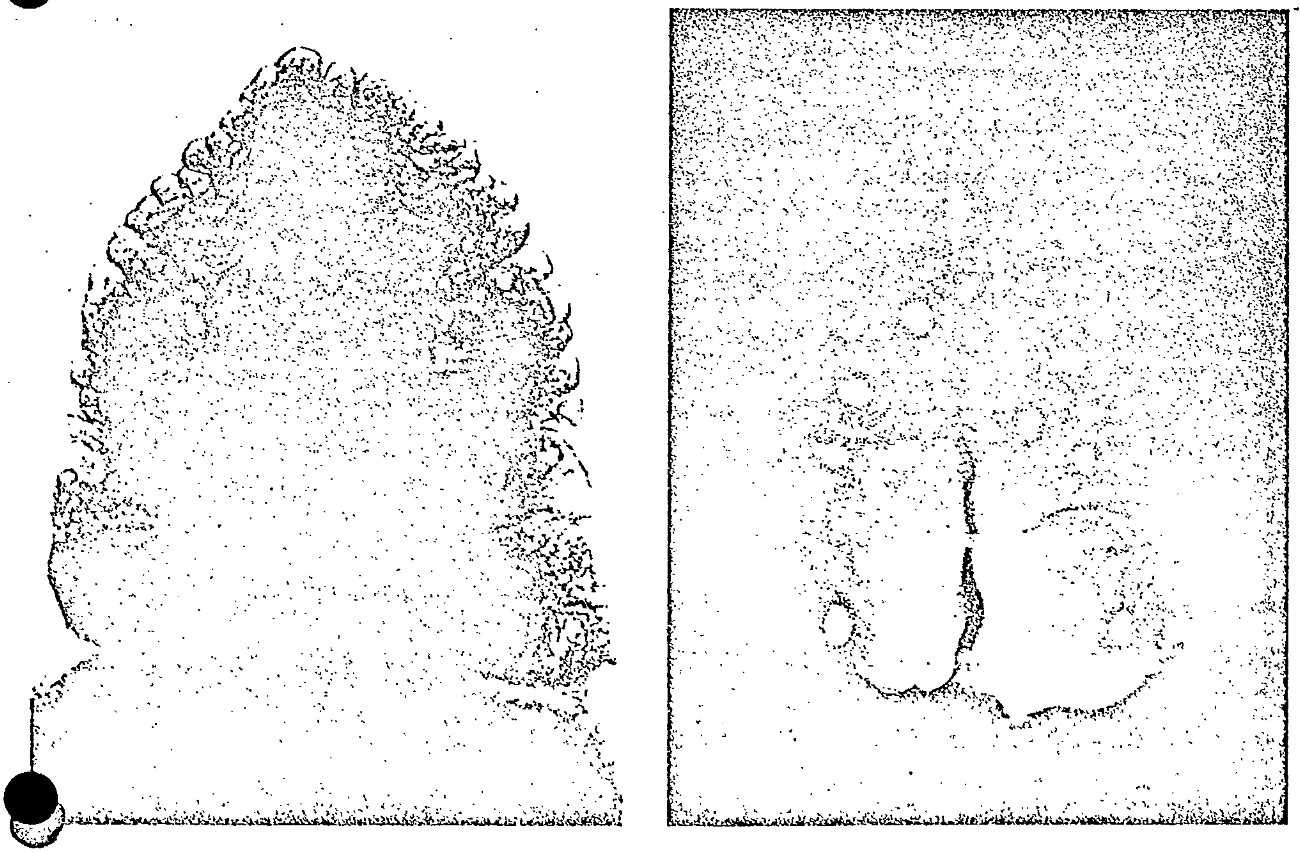
Stage IV (photos F, G, K): The largest eggs increase considerably in

OVAIRES DE *THYSANOPODA PECTINATA*

3rd and 4th Plates : ovaries of *Thysanopoda pectinata*

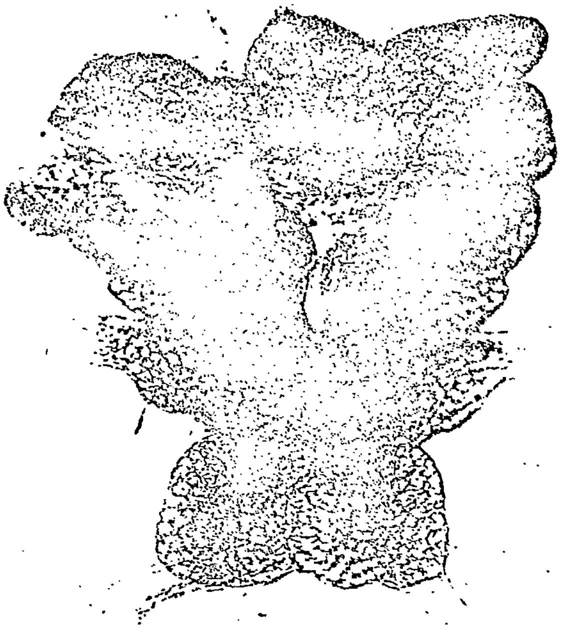


E : les 4 stades ovariens à la même échelle.
E : the four ovarian stages at the same scale.

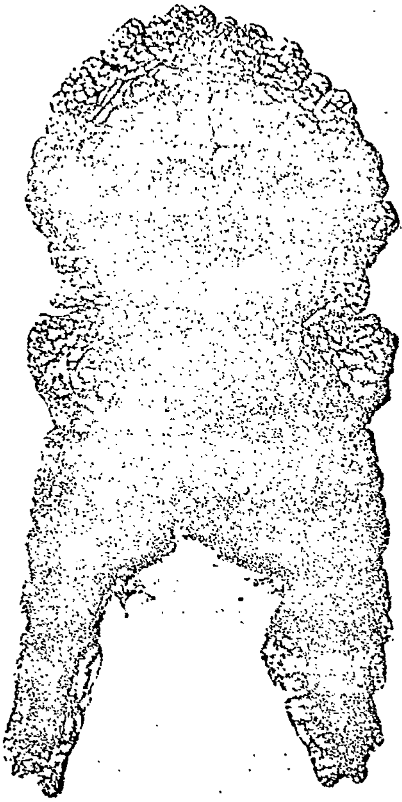


F et G : ovaire au stade IV (détail).
F and G : stage IV (detail).

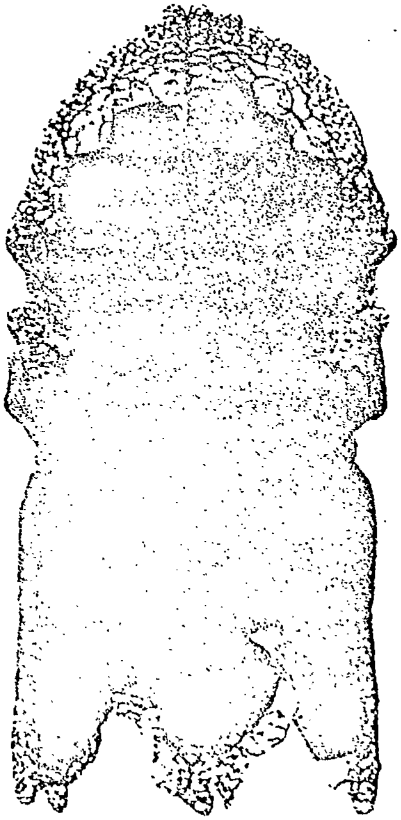
PLANCHE IV



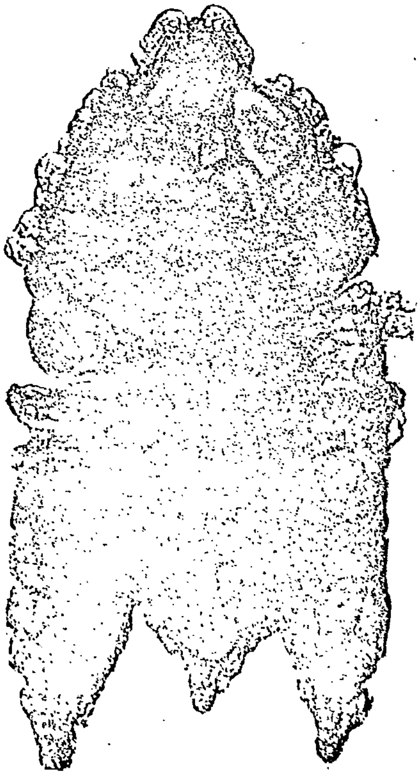
H : stade I.
H : stage I.



I : stade II.
I : stage II.



J : stade III.
J : stage III.



K : stade IV.
K : stage IV.

size, resume a sub-spherical shape and their cytoplasm becomes again transparent. The large opaque nuclei are perfectly visible. The smaller eggs on the periphery which remain unchanged are being reabsorbed. Very frequently, the entire thoracic area of the organism appears swollen and translucent.

This classification is essentially similar to that of other authors, with a few variations, however; in particular, the fact that the eggs again become transparent in Stage IV was seldom mentioned. Zelickman (1958) divided Stage IV into two phases, distinguishing the stage when a few eggs are ripe (St. IV) and when all the eggs are ripe (St. V), with the exception of the outer eggs which are being reabsorbed. Ponomareva (1963) described essentially the same classification. Ruud (1932) identified only 3 stages of maturation with Stage IV representing the empty ovary after spawning has occurred; we considered this state as being too difficult to separate from Stage II, the latter very closely resembling the state of the ovary a few weeks after spawning. According to our observations, the ovary does not return to Stage I after the ripe eggs are released: all females observed at that stage were smaller than those at Stages II, III or IV. The sequence is therefore as follows:

Stage I → St. II → St. III → St. IV → spawning → St. II → death or new maturation.

The distinction between "Stage II" and "the empty ovary" is considerably easier to make for organisms inhabiting cold or temperate seas for the simple reason that these stages occur at different times of the year, the first occurring before the spawning season, the second afterwards. In a tropical environment, spawning occurs throughout the year such that both stages are found at all times and cannot be identified on the basis of definite characteristics. It is likely relatively easy to identify an empty ovary immediately after spawning has occurred, but after a few weeks or months, it resumes the appearance of Stage II, hence the difficulty in differentiating either.

Granted, all the intermediate stages between the four major stages were also observed with the result that identification of a given stage is somewhat subjective. For that reason, it was very important to group the observations on a given species, thus avoiding that an ovarian structure identified as a Stage III on one expedition was not classified Stage II on the following expedition or vice versa: it was of prime importance to collect all the material and to examine ovarian development for one species only when 126 all sampling series, preferably for the entire year, could be examined without interruption.

4. CERTAIN SEXUAL CHARACTERISTICS OF MAJOR SPECIES

(The greater portion of this work was based on material obtained during the "Cyclone" expeditions; quantitative results may therefore differ slightly from those used for determining cycles (§ 5) which were obtained on the "Caride" expeditions).

4.1. Fecundity

Ponomareva (1963) defined the fecundity of a species by the average number of eggs contained in the ovary at Stage IV. As several authors pointed out, this results in greatly over-estimating fecundity as not all the eggs are released, a certain number of them being reabsorbed in the final process. Mauchline (1966 a, 1968) therefore proposed another means of measuring fecundity which consists in estimating the total volume of spawned eggs (= ovary at Stage IV — empty ovary after spawning) and estimating the number of these by dividing this value by the mean volume occupied by a ripe egg. Given the rather dubious identification of the "empty ovary" stage, we considered the method set forth by Mauchline rather difficult to apply. Furthermore, we considered that it was relatively easy to distinguish the very small outer eggs remaining unchanged, that will be ultimately reabsorbed, from the larger highly developed eggs which will certainly be spawned. By counting only the latter, a good estimate of fecundity is obtained.

Table 38 indicates the number of ripe eggs in the ovary at Stage IV for 11 different species, and the weight of the mature ovary in relation to the weight of the entire organism. Note that the fecundity of these tropical species is very low, the maximum number of eggs being in the order of 80 (*E. diomedae*, *N. tenella*); all species of the genus *Thysanopoda* present very similar fecundity (40 to 54 eggs depending upon the species), with the exception of *T. aequalis* (24). Fonomareva (1969) claimed that the small number of eggs spawned by tropical species displayed an adaptation to a particular environment, namely one having limited food supplies and few predators. Deep-water species (*N. boopis*, *B. amblyops*) seem particularly less productive. Note (column 1, figures in parentheses) that the observations remain relatively constant within a given species; Zelickman (1958) stated that *T. raschii* carried an average of 398 ripe eggs, but that this figure varied from 83 to 1185 depending upon individuals.

Numerous authors (Zelickman, 1958; Mauchline and Fisher, 1969; McLaren, 1963 and 1965; Jensen, 1958; Komaki, 1967 a; Nemoto, Kamada and Hara, 1972...) noted that the number of eggs spawned by a female of a given species increased considerably with the size of the animal: Zelickman (1958), for instance, claimed that a female of *T. raschii* of 28 mm spawned three times as many eggs as one of 22 mm. The situation is likely somewhat different in warmer seas: in a colder environment, a well defined spawning season spurs all females to release their eggs at approximately the same time; for example in the case of *T. raschii*, two-year old females (22 mm) as well as three-year old females (28 mm), each group has a rate of fecundity in proportion to its size. In

TABLE 38

Average number of ripe eggs contained in the ovary at Stage IV (minimum and maximum numbers observed are given in parentheses) and comparative weight of entire organism and ovary at Stage IV (wet weight in mg) for different species. All figures are the means obtained from at least 10 measurements, except for T. cristata and E. diomedae.

Species	Average number of ripe eggs in ovary IV	Weight of entire animal (mg)	Weight of ovary IV (mg)	% of ovary in weight
T. cristata	40 (20-76)	1 088	96,0	8,7 %
T. tricuspidata	40 (20-82)	97	5,3	5,4 %
T. orientalis	54 (38-74)	302	28,2	9,3 %
T. monacantha	54 (32-72)	240	22,7	9,5 %
T. pectinata	54 (30-82)	369	21,4	5,8 %
T. aequalis	24 (16-31)	55	4,6	8,5 %
N. flexipes	19 (12-39)	61	5,1	8,3 %
N. boopis	9 (4-12)	155	14,2	9,2 %
B. amblyops	3,5 (1-7)	113	9,8	8,7 %
E. diomedae	80 (estimé)	—	—	—
N. tenella:	Average number of eggs on the outside (estimate): 50-80. Average diameter of external egg : 0.50 mm.			

a warmer environment, no imperative circumstance compels the animals to spawn at a given period and, it would appear that, reproduction occurs only when the organism has reached a certain stage of development.

In any case, the degree of fecundity recorded for cold or temperate-water species is considerably higher than those we observed: 350 ripe eggs in the Stage IV ovary of T. raschii (Zelickman, 1960), 800 for E. superba (Mauchline, 1968), for instance. Very low fecundities were recorded for tropical species: 3 to 20 for the genus Stylocheiron according to Mauchline and Fisher (1969). However, the sexual characteristics of a given species may vary considerably depending upon the environment. Voronina (1964 b) claimed that reproductive activities for several species in the Equatorial Pacific differed greatly between the more abundant eastern section and the depleted western section. Mauchline (1968) attributed a fecundity of 170 to N. flexipes while our own findings for the warmer environment of the Equatorial Pacific indicated a fecundity of 19. Einarsson (1945) considered that cycles within a given species differed in the coldest and warmest regions of its habitat; this was also the opinion set forth by Allen (1966), Jensen (1958), Margalef (1967 a). Brinton (1969) pointed out that the reproductive periods of *N. difficilis* and *E. pacifica* were limited to the spring-summer season in the sub-arctic regions, while spawning occurred almost continually in the more stable environment of the California Current.

Regarding the size of the mature ovary in relation to thebody of the organism, our data (Table 38) gives values ranging from 5.4% to 9.5% of total body weight; these figures are somewhat lower than estimates of 8% to 12% suggested by Mauchline and Fisher (1969).

4.2. Level of Maturity among Females 128

Table 39 gives the percentage of females at each ovarian stage in terms of size groups for different species. In spite of certain inaccuracies attributable to the fact that we examined size groups rather than take individual measurements, these figures give an estimate of the maturity of individuals according to age. Note that figures are not available for all ovarian stages and for all species; Stage I (immature individuals) occurs mainly in organisms smaller than those used for this analysis. In the case of 129
E. diomedae, we could not identify a Stage IV corresponding to the description given in § 3.2. Note also that the percentage of individuals at each given stage varies from species to species. No intrinsic significance should be attached to this fact due entirely to the duration of the stage being considered. For instance, it would appear that the ovarian structure corresponding to our definition of Stage III is of very short duration for *N. flexipes*, while Stage IV which appears very long for *B. amblyops* seems very brief for *T. pectinata*.

This data will be discussed at greater length when each species is dealt with individually.

TABLE 39

Ovarian maturity according to size.

Species	Number of females examined	Size Groups	Stage of maturity			
			I	II	III	IV
T. cristata	84	3,5	89 %	9 %	2 %	0 %
		5,0	0	36 %	28 %	36 %
		6,0	0	8 %	21 %	71 %
T. tricuspidata	985	2,5	14 %	48 %	30 %	7 %
		3,0+3,5	0,4 %	42 %	43 %	15 %
T. orientalis	184	3,0	47 %	9 %	9 %	6 %
		3,5	3 %	15 %	18 %	62 %
T. monacantha	356	3,0	17 %	41 %	25 %	17 %
		3,5	3 %	30 %	28 %	38 %
T. pectinata	178	2,5	100 %	0	0	0
		3,0	63 %	11 %	24 %	0
		3,5	3 %	25 %	59 %	9 %
T. aequalis	678	2,0	—	61 %	18 %	20 %
		2,5+3,0	—	32 %	21 %	48 %
N. boopis	340	2,5	8 %	19 %	35 %	31 %
		3,0+3,5	7 %	11 %	29 %	53 %
E. diomedae	4 006	1,6	—	58 %	42 %	—
		2,0+2,5	—	33 %	67 %	—
N. tenella	1 077	1,6	—	75 %	15 %	10 %
		2,0+2,5	—	50 %	35 %	15 %
E. gibboides	200	2,0	—	29 %	62 %	10 %
		2,5	—	16 %	64 %	20 %
		3,0	—	40 %	22 %	38 %
N. flexipes	212	2,0	—	55 %	11 %	34 %
		2,5+3,0	—	33 %	8 %	59 %
B. amblyops	101	2,0	—	57 %	15 %	29 %
		2,5	—	17 %	4 %	79 %
		3,0+3,5	—	2 %	8 %	90 %

Nota: 1) For all species, observations dealt with material obtained on the "Cyclone" expeditions, except for E. gibboides, N. flexipes and B. amblyops, specimens of which originated from the "Caride" hauls. T. cristata, a species poorly sampled, was examined during both expeditions.

2) The sum of the percentages for all four ovarian stages does not equal 100% whenever the stage of certain females could not be identified.

3) For N. tenella, percentages in column "Stage IV" actually correspond to females bearing eggs externally.

4.3. Level of Fecundity among Females

Estimate of the percentage of impregnated females according to size, ovarian stage or season is relatively easy to establish for Euphausiids by counting females bearing one or more spermatophores. In a cold or temperate environment, the most intense reproductive periods can thus be determined:

Zelickman (1960) noted that, in the Barents Sea, the number of females bearing spermatophores depended upon the season and not on the ovarian stage. For a tropical or equatorial environment, the only observation was that sexual activity goes on at a constant rate throughout the year. Table 40 gives the percentage of females bearing spermatophores for different size groups, according to the entire material obtained on the "Cyclone" expeditions (89 stations carried out over a six-month period). Note that:

— females at Stages III and IV (late maturation) in all species had almost all been impregnated; this would confirm the continuous nature of reproduction, all mature females having been impregnated, regardless of the season. Locating any seasonal fluctuations in sexual activity must rest therefore on variations in the percentage of reproducing individuals (mature females) within the population, and not on the intensity of impregnation (% of females bearing spermatophores).

— the percentage of females bearing spermatophores is very high (70 to 99%) at the onset of ovarian maturity (Stage II), while the number of immature impregnated females (Stage I) is very low. This would imply:

* that sexual attraction is linked with ovarian development and is exhibited at the onset of maturity, or, that spermatophores can become attached only at such time (structure of the thelycum);

* that the permatozoa retain their impregnating ability for a long period of time, the eggs being fertilized only several weeks after spermatophores are introduced (Bargmann, 1937 and 1945; Zelickman, 1958; Mauchline and Fisher, 1969).

— in most cases, the proportion of impregnated females, which increases with ovarian maturity, also increases with the age of the female; for the same ovarian stage, the percentage of females bearing spermatophores

TABLE 40

Level of impregnation: percentage of females bearing spermatophores according to size group and ovarian stage (from material obtained on the "Cyclone" expeditions).

Species	Size Group	St. I	St. II	St. III	St. IV	Mean
T. cristata (*)	3,5	0 %	66 %	100 %	—	10 %
	5,0	—	75 %	100 %	100 %	92 %
	6,0	—	100 %	100 %	100 %	100 %
	Moyenne	0 %	78 %	100 %	100 %	—
T. tricuspidata	2,5	17 %	83 %	96 %	96 %	79 %
	3,0+3,5	—	98 %	99 %	100 %	99 %
	Moyenne	17 %	87 %	97 %	98 %	—
T. orientalis	3,0	0 %	33 %	100 %	100 %	22 %
	3,5	0 %	88 %	100 %	100 %	98 %
	Moyenne	0 %	73 %	100 %	100 %	—
T. monacantha	3,0	0 %	99 %	100 %	100 %	83 %
	3,5	0 %	100 %	100 %	100 %	97 %
	Moyenne	0 %	99 %	100 %	100 %	—
T. pectinata	2,5	0 %	—	—	—	0 %
	3,0	14 %	78 %	100 %	—	41 %
	3,5	50 %	95 %	98 %	100 %	96 %
	Moyenne	9 %	90 %	98 %	100 %	—
T. aequalis	2,0	—	99 %	99 %	100 %	99 %
	2,5+3,0	—	99 %	100 %	100 %	99 %
	Moyenne	—	99 %	99 %	100 %	—
N. boopis	2,5	0 %	81 %	91 %	100 %	84 %
	3,0+3,5	0 %	53 %	88 %	100 %	85 %
	Moyenne	0 %	70 %	90 %	100 %	—
E. diomedae	1,6	0 %	88 %	94 %	100 %	90 %
	2,0+2,5	—	100 %	100 %	100 %	100 %
	Moyenne	0 %	90 %	94 %	100 %	91 %

(*) Very few specimens.

was higher among older females.

4.4. Remarks on the Sex Ratio

Most authors having done research into the biology of pelagic crustaceans consider fluctuations in the sex ratio as having no obvious relationship with cyclical phases and, for that reason, are very difficult to 130
interpret (Ponomareva, 1963; Omori, 1969; Burukovskiy, 1967). In theory, there should be a drop in the sex ratio (males dying) after impregnation. and a rise (females dying) after spawning (Mauchline, 1960; Ponomareva, 1968; Mauchline and Fisher, 1969); in practice, this pattern has seldom been seen.

Our observations, obtained from hauls on the "Cyclone" expeditions, are given in Table 41. Note that the sex ratio (male/female ratio) does in

TABLE 41

Distribution of sexes according to size.

Species	Number of individuals examined	Size Group	Males	Females
T. cristata	197	3,5	54 %	46 %
		5,0	78 %	22 %
		6,0	25 %	75 %
T. tricuspidata	1 935	2,5	51 %	49 %
		3,0+3,5	34 %	66 %
T. orientalis	384	3,0	70 %	30 %
		3,5	22 %	78 %
T. monacantha	692	3,0	57 %	43 %
		3,5	37 %	63 %
T. pectinata	378	2,5	52 %	48 %
		3,0	57 %	43 %
		3,5	51 %	49 %
T. aequalis	1 073	2,0	45 %	55 %
		2,5+3,0	8 %	92 %
N. boopis	490	2,5	46 %	54 %
		3,0+3,5	6 %	94 %
E. diomedae	4 754	1,6	17 %	83 %
		2,0+2,5	1 %	99 %
N. tenella	1 117	1,6	4 %	96 %
		2,0+2,5	1 %	99 %
E. gibboides	365	2,0	52 %	48 %
		2,5	48 %	52 %
		3,0	29 %	71 %
N. flexipes	457	2,0	63 %	37 %
		2,5+3,0	45 %	55 %
B. amblyops	155	2,0	53 %	47 %
		2,5	37 %	63 %
		3,0+3,5	20 %	80 %

fact drop from the smallest to the larger size groups, except for *T. pectinata* where no apparent change is noticeable. We might conclude:

— that females reach a larger size than males (note, however, that our method for measuring size accentuates this feature, mature females displaying not infrequently a swelling of the thoracic region which places them in a larger size group than males of similar length)

— that the sex ratio obtained for a series of samples will depend upon the range of size groups collected: for a minute species of which only large individuals were collected, the percentage of females will be very 131
high (*E. diomedae*, *N. tenella*); for a larger species, on the contrary, the adults of which were well sampled, the sex ratio will be approximately

the same (T. cristata, T. tricuspidata, T. orientalis, T. monacantha).

4.5. Vertical Distributions according to Sex and Ovarian Stages

It is particularly important to locate any possible differences in the vertical distributions of individuals according to sex or sexual maturity, this being the only explanation to the distribution of a given species whose individuals are subject to different drifts. In the Equatorial Pacific in particular, the stratification of contrary currents causes a population spread that merely reflects displacements imposed upon the organisms by the usual depth of their habitat (Roger, 1967 c). A similar situation was described in several instances for E. superba in the Antarctic (Fraser, 132 1936; Burukovskiy, 1967; Orr and Marshall, 1969); Ponomareva (1963) claimed that reproducers ceased to migrate to the surface, while the larval and juvenile stages remained there; Margalef (1967 a) admitted that pelagic species relied on currents to move about horizontally, according to the cyclical phase of each individual.

Unfortunately, our data is insufficient to allow us to delve further into this matter: hauls with the closing Omori net, giving the only accurate material, produce too few specimens for separation into several categories (sex and ovarian stage). At this point, we shall only point out the two foregoing observations, namely that the depth of the habitat increasing with the age of the organisms (Chap. IV, § 3.6), and a higher percentage of mature females among larger organisms (Chap. VI, § 4.2) would indicate the likelihood of a mean vertical distribution closer to the surface for immature individuals than for reproducers.

5. STUDIES ON LIFE CYCLES

As mentioned in § 3, we shall attempt to determine, from data obtained during the "Caride" expeditions, whether the seasonal distribution of size groups (i.e., ovarian stages) cause certain categories to predominate thereby making it possible to follow their development. If so, firstly, periods of intense reproductive activity can be identified and secondly, a first approximation of growth curves of the species can be made. Beforehand, however, we shall repeat characteristics proper to each species (level of maturity and fecundity) or describe the ovarian stages whenever they differ from that of the typical species.

Suffice it to recall once again that no previous work on tropical and equatorial pelagic Euphausiids was available to us and therefore we could not select between two alternatives how modal classes should relate to one another. We adopted the following procedure: we selected the species for which the least confusion could arise and established its probable growth curve; using this estimate as reference and proceeding by analogy, we determined growth curves for the remaining species on the assumption that species belonging to a rather homogeneous family such as Euphausiids and occupying the same biotope would most likely follow a similar cycle. We selected T. tricuspidata as the standard species. Details of how we determined its growth cycle is outlined below, this being essentially the procedure followed for all other species.

5.1. Thysanopoda tricuspidata

5.1.1. Preliminary Notes

7013 individuals of this species, grouped according to size, were identified in the material collected over 109 stations. Out of this number, 6055 were included in the 3.5/3.0/2.5 mm size groups and used to establish the development towards ovarian maturity. No individual presented a particularly developed Stage IV, the most advanced stage showing a few large

TABLE 42

Number of specimens, percentages and relative representativity (% of m%) of age groups (size groups) for <u>T. tricuspidata</u> in the Central Equatorial Pacific.

Expedition Croisières	Tailles S.G.	3.5	3.0	2.5	2.0	1.6	1.2	0.9	0.7	Total
CA. I (Oct.)	Nb.	186	1 642	2 340	485	101	18	18	6	4 796
	%	3,9 %	34,2 %	48,8 %	10,1 %	2,1 %	0,4 %	0,4 %	0,1 %	—
	% $\overline{m}$ %	279	94	100	160	62	36	20	17	—
CA. II (déc.) (Dec.)	Nb.	10	224	442	39	21	7	30	12	785
	%	1,3 %	28,5 %	56,3 %	5,0 %	2,7 %	0,9 %	3,8 %	1,5 %	—
	% $\overline{m}$ %	93	79	115	79	79	82	190	250	—
CA. III (fév.) (Feb.)	Nb.	8	221	279	47	38	18	19	6	636
	%	1,3 %	34,4 %	43,9 %	7,4 %	6,0 %	2,8 %	3,0 %	0,9 %	—
	% $\overline{m}$ %	93	96	90	117	176	255	150	150	—
CA. IV (juill.) (July)	Nb.	4	134	497	25	27	10	21	4	722
	%	0,6 %	18,6 %	68,9 %	3,5 %	3,7 %	1,4 %	2,9 %	0,6 %	—
	% $\overline{m}$ %	43	51	141	56	109	127	145	100	—
CA. V (sept.) (Sept)	Nb.	0	48	20	4	2	0	0	0	74
	%	0	64,9 %	27,0 %	5,4 %	2,7 %	0	0	0	—
	% $\overline{m}$ %	0	179	55	86	79	0	0	0	—
Total......	Nb.	208	2 269	3 578	600	189	53	88	28	7 013
	% $\overline{m}$	1,4 %	36,2 %	49,0 %	6,3 %	3,4 %	1,1 %	2,0 %	0,6 %	—

TABLE 43

<u>T. tricuspidata: Sex ratio and ovarian stages (2.5/3.0/3.5 size</u> groups)

Expedition Croisières	♀ II	♀ III	♀ IV	Sex Ratio
CA. I (oct.) (Oct.).........	41 %	27 %	31 %	0,86
CA. II (déc.) (Dec.).........	41 %	42 %	17 %	1,04
CA. III (fév.) (Feb.).........	39 %	29 %	32 %	1,10
CA. IV (juill.) (July).........	77 %	15 %	7 %	1,42
CA. V (sept.) (Sept.).......	27 %	41 %	32 %	0,97

translucent eggs in the midst of a majority of eggs still at the opaque stage. Stages I, II and III seemingly conform with those given earlier. In fact, 133
according to Table 39, there were few individuals at the Stage IV level. Over the entire cycle, 37% of females 26-30 mm long were mature or in late maturation (Stages III and IV), this percentage increasing to 58% for females over 30 mm in length; practically all females having reached this stage had been fecundated (cf. Table 40). The number of specimens, percentages and mean representativity of size groups over the year are given in Table 42; figures on ovarian development and the sex ratio appear in Table 43.

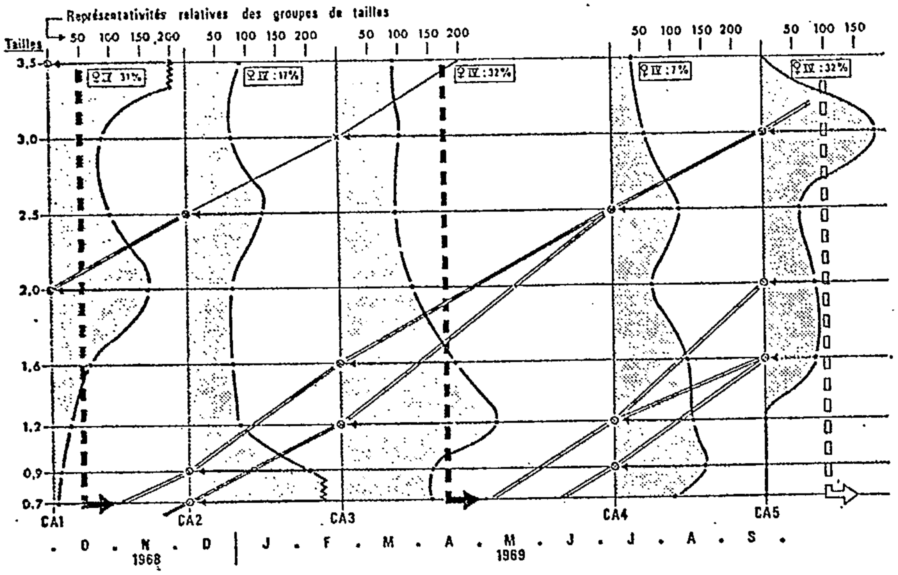


Fig. 59. — Évolution saisonnière de la structure d'âge (tailles) de la population de *T. tricuspidata* dans le Pacifique équatorial central, et filiation suggérée des classes modales. ▬ ▬ ▬ Ponte.

Fig. 59. — Seasonal age (size) structure of *T. tricuspidata* populations in the central equatorial Pacific, and suggested evolution of modal classes. ▬ ▬ ▬ : period of maximum spawning activity.

5.1.2. Determining the life cycle 134

We outlined earlier (cf. Fig. 58) the method applied to show possible fluctuations in percentages for each age group; similarly, from the data given in Table 42, seasonal changes in the age structure of the population can be pointed out by simply using the relative representativity of the different size groups over the 5 sampling series. By joining maximum values (the reliability of this operation will be discussed in § 5.1.3. and 6), we had an idea of the development of the dominant categories (fig. 59) from which the cycle of the species might be described as follows:

— early October 1968, we noted the presence of many large adult individuals (3.5 size group) among which were mature females (31% at Stage IV). We might therefore conclude that spawning was imminent or had begun only shortly as there were few young individuals (few in the 0.7-0.9 size groups). The presence of an intermediate generation (2.0 size) was also noted.

— early December 1968: A great number of juveniles confirmed the fact that spawning had indeed occurred during October and November. Reproductive activity had considerably slowed down, the number of adults, among which a low proportion of mature females (17% at Stage IV), having greatly dropped. The intermediate generation belongs roughly to the 2.5 size group.

— late February 1969: The two generations observed on the preceding
expedition now belong to the 1.2/1.6 and 3.0 size groups respectively. Al-
though the latter is less obvious, the total number of reproducers (sizes 3.0
and 3.5) is rather high with a high proportion of mature females (32% at 135
Stage IV); the development of this generation into the reproductive stage would
suggest that spawning is again imminent (April).

— early July 1969: The smallest specimens are in the 0.9-1.2 size groups, likely the new generation from the April spawning. The small number of reproducers (highest modal class is only 2.5) and the limited number of mature females (7% at Stage IV) indicate a decreased reproductive activity.

— late September 1969: A very high proportion of adults (3.0) and mature females (32% at Stage IV) forecasts another period of intense reproductive activity. The absence of small individuals would suggest that no major spawning period has occurred since April.

5.1.3. Comments on the Cycle of T. tricuspidata

The cycle described above was deduced from analysis of figure 59; the reliability of this operation rests on two postulates:

— the modes observed are accurate and do not originate from unusual variations in the sampling.

— the same population was investigated during the five expeditions (possiblesituation in equatorial currents) and consequently, these modes which follow a certain sequence can be related among one another.

Hence, there are two possibilities:

— either the actual sequence is the one described in figure 59

— or the cycle is a very rapid one and the modal classes observed on one expedition were already replaced by another generation on the following expedition.

The second alternative would imply that the entire cycle (from hatching of the egg to death) covers a six-month period, which seems very brief; we shall therefore assume that the cycle outlined in figure 59 is the most probable situation, without entirely rejecting the assumption that the cycle is half as long, the time between observations preventing us from observing such a situation.

Values of the sex ratio, given in Table 43, are not particularly indicative. At best, we noted that there were fewer males when spawning was in process (CA. I = October 1968: S.R. = 0.86) or imminent (CA. V = September 1969: S.R. = 0.97); the proportion of males was higher when spawning was not expected in the immediate future (CA. III = February 1969: S.R. = 1.10) or when reproductive activity had decreased (CA. II = December 1968: S.R. = 1.04; CA. IV = July 1969: S.R. = 1.42).

In terms of a horizontal distribution of size groups, we might expect, in a highly stratified environment with superimposed contrary currents, a certain spread of the population according to age groups if each group does not dwell normally at the same depth. In fact, we noted a definite tendency of the largest (3.0-3.5) and smallest (0.7-0.9-1.2-1.6) size groups to gather in the eastern portion of the region (around 140° W), which appeared to be the zone preferred for reproduction; intermediate sizes occurred more to the west. The horizontal distribution of modal classes is given in Figure 60. Again, the reason why samplings cannot be carried out perpendicular to the currents to determine biological cycles is made evident; expeditions in a north-south direction along 150° W, for instance, would have meant that we could not estimate the evolution of age groups over a period of time.

5.1.4. Conclusions on the Cycle of T. tricuspidata and Estimate of its Growth Curve 136

We therefore noted a period of intense spawning activity from October to April, with a certain drop occurring during January-February; on the other hand, reproductive activity appeared to be very low from May to September. The beginning and end of the cycle coincided particularly well as the situations observed in October 1968 (CA. I) and in September 1969 (CA. V) are very similar. Note that periods of intense spawning occurred at the end of seasons of maximum primary production, defined by Owen and Zeitzschel (1970): August-September and February-March. Although it is impossible to determine whether or not there is any significant coincidence, note that such synchronization has been previously pointed out (Einarsson, 1945; Zelickman, 1960; Ponomareva, 1963). Considering certain reservations as to the reliability of the situation actually observed, we might propose the following characteristics for the cycle of T. tricuspidata:

— spawning at approximately one year of age, followed very closely by death; the life-span would be from 13 to 14 months for females; judging by the small number of males included among large individuals (cf. Table 41), the life-span of males is no more than 12 months.

— the age of each size group, equivalent lengths and weights are given in Table 14.

TABLE 44

Growth of T. tricuspidata

Size Group	Age (months)	Length (mm)	Weight (mg)
0,7	1	9	~ (env. 2)
0,9	2	10	5
1,2	3,5	13	17
1,6	5	17	38
2,0	7	21	65
2,5	9	26	85
3,0	11,5	30	116
3,5	13	33	~ (env. 250)

From this data, we might directly infer the estimated growth curve of the species (fig. 61). Assumming an essentially linear function of size increase versus time, the average growth rate of *T. tricuspidata* is approximately 2 mm per month.

5.2. *Thysanopoda monacantha*

5.2.1. Preliminary Notes

For the entire 109 stations, the number of individuals collected of this species totalled 2031 organisms divided into 8 size groups (0.7 to 3.5). The 3.0 and 3.5 sizes (adults), the only ones considered to examine ovarian development and sex ratios, were represented by 1425 specimens. Ovarian stages corresponded to those described in § 3.2. According to Table 39, on 137
the average 42% of females 30-35 mm long were mature or in the late ovarian maturation stage (Stages III and IV); 66% for females longer than 35 mm. Table 40 indicates that 83% of females 30-35 mm long, and 97% of those over 35 mm were bearing one or several spermatophores, only immature females not having been fecundated. Number of specimens, percentages and relative representativity for each age group are given in Table 45; Table 46 gives the distribution of ovarian stages and the sex ratios for a one-year period.

5.2.2. Determining the Cycle

By proceeding as for *T. tricuspidata*, we established from the data given in Table 45, a growth pattern for the modal classes (fig. 62). We therefore inferred that the probable cycle of this species was the following:

— early October 1968: There were a very great many large individuals (3.5) among which females at Stage IV: it would appear that spawning was in progress. There was also a high proportion of very young individuals (0.7-0.9) indicating that a major spawning period had occurred a few weeks prior.

We therefore concluded that September and October 1968 were periods of active spawning. We also noted the presence of an intermediate generation (1.6 size group).

— early December 1968: Our observations suggested decreased spawning activity: the largest specimens (3.0), of uncertain origin, were immature (St. II) and spawned likely only in late December-early January. The smallest individuals, or the 0.9-1.2, were the 0.7-0.9 groups of October; the 2.0-2.5 groups were possibly from the 1.6 groups on the previous expedition; however, this development was uncertain.

— late February 1969: The peak number of individuals in the 0.9 size groups confirmed that intense spawning had occurred in January, as the situation described for CA. II had suggested. The largest individuals (3.0-3.5) were already sexually mature (St. IV) implying imminent spawning (March). 138
The 1.6 individuals were the 0.9-1.2 of December.

— early July 1969: The absence of juveniles (0.7-0.9) led us to believe that intense spawning had not recently occurred: the smallestsize group (1.2) most likely originated from the March spawning mentioned earlier. The largest organisms were not yet mature (St. III) indicating that intense spawning was not imminent.

— late September 1969: There were no individuals smaller than 2.0 suggesting that the last spawning period had occurred some time before, i.e., last March. Spawning may have occurred a few weeks earlier, but any such larvae and juveniles, which would be smaller than 0.7, were not captured by
the trawl. Another possibility was that the largest specimens had not yet 139
spawned and would do so only in October; however, most of them were not yet mature. Whatever the case, the presence of many large organisms (3.0-3.5) of reproductive ability implied that September-October 1969 would be a peak

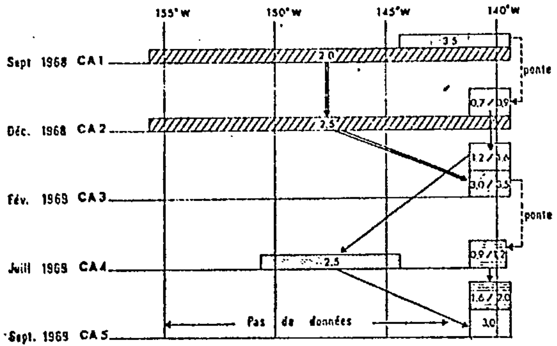


Fig. 60. — Distributions longitudinales des classes de tailles modales chez *T. tricuspidata* dans le Pacifique équatorial central et déplacements suggérés.

Fig. 60. — East-West distribution of modal size classes of *T. tricuspidata* in the central equatorial Pacific, and suggested shifting.

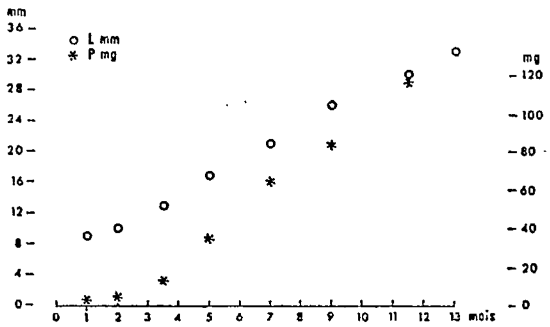


Fig. 61. — Croissance estimée de *T. tricuspidata* dans le Pacifique équatorial central (o : en longueur ; * : en poids).

Fig. 61. — Estimated growth of *T. tricuspidata* in the central equatorial Pacific (o : length. * : wet weight) (Longevity approx. 13 months).

TABLE 45

Number of specimens, percentage and relative representation (% of m%) of age groups (size groups) for T. monacantha in the Central Equatorial Pacific.

Croisières	Tailles	3.5	3.0	2.5	2.0	1.6	1.2	0.9	0.7	Total
CA. I (oct.)	Nb.	347	409	124	80	55	10	7	2	1 034
	%	33,6 %	39,6 %	12,0 %	7,7 %	5,3 %	1,0 %	0,7 %	0,2 %	—
	% m̄ %	146	86	74	87	133	100	117	500	—
CA. II (déc.)	Nb.	91	223	87	39	9	5	3	0	457
	%	19,9 %	48,8 %	19,0 %	8,5 %	2,0 %	1,1 %	0,7 %	0	—
	% m̄ %	87	106	117	96	50	110	117	0	—
CA. III (fév.)	Nb.	59	108	27	14	15	1	4	0	228
	%	25,9 %	47,4 %	11,8 %	6,1 %	6,6 %	0,4 %	1,8 %	0	—
	% m̄ %	113	103	72	69	165	40	300	0	—
CA. IV (juill.)	Nb.	21	115	59	30	11	6	0	0	242
	%	8,7 %	47,5 %	24,4 %	12,4 %	4,5 %	2,5 %	0	0	—
	% m̄ %	38	103	150	139	113	150	0	0	—
CA. V (sept.)	Nb.	19	33	10	7	1	0	0	0	70
	%	27,1 %	47,1 %	14,3 %	10,0 %	1,4 %	0	0	0	—
	% m̄ %	118	102	88	112	35	0	0	0	—
Total.....	Nb.	537	888	307	170	91	22	14	2	2 031
	% m̄	23,0 %	46,1 %	16,3 %	8,9 %	4,0 %	1,0 %	0,6 %	0,04 %	—

TABLE 46

T. monacantha: Sex ratio and ovarian stage (3.0 and 3.5 size groups).

Expedition	♀ II	♀ III	♀ IV	Sex Ratio
CA. I (oct.)..(Oct.).........	42 %	24 %	34 %	0,74
CA. II (déc.)..(Dec.).........	52 %	23 %	24 %	0,90
CA. III (fév.)..(Feb.).........	35 %	20 %	45 %	1,00
CA. IV (juill.).(July).........	41 %	35 %	24 %	0,96
CA. V (sept.).(Sept.)........	44 %	30 %	26 %	0,93

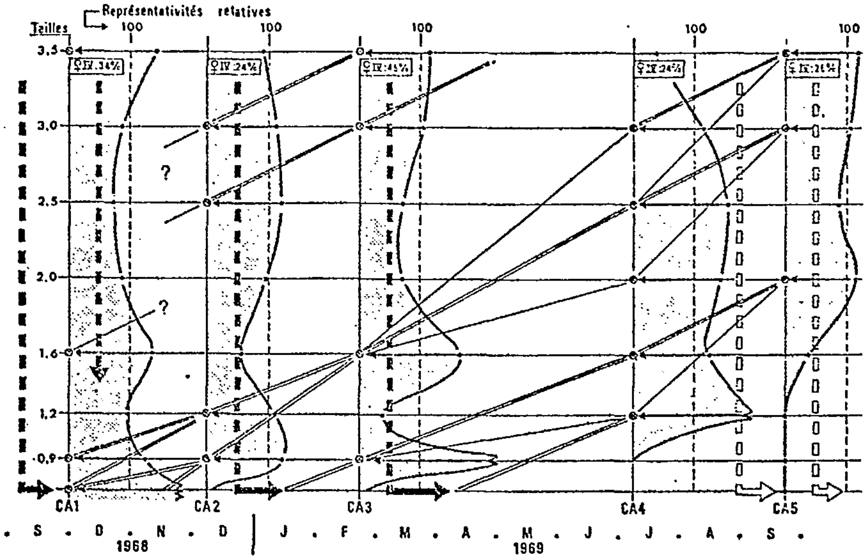


Fig. 62. — Évolution saisonnière de la structure d'âge (tailles) de la population de *T. monacantha* dans le Pacifique équatorial central, et filiation suggérée des classes modales. ▬ ▬ ▬ Ponte.
Fig. 62. — Seasonal age (size) structure of *T. monacantha* populations in the central equatorial Pacific, and suggested evolution of modal classes.

spawning period, imminent or in progress, as in the same months one year earlier. We might point out, however, that we inferred the situation of September 1969 only from samplings in one location, as "Caride" V was carried out at a stationary point and not along an east-west axis as on the other expeditions. Our comments regarding fig. 57 therefore apply in this case and there is some doubt as to how well the population was sampled: it is highly possible that juveniles (0.7-0.9) originated from a spawn during August-September, but that they were located further to the west or to the east.

5.2.3. Comments on the Cycle of T. monacantha

There is great similarity with the cycle of T. tricuspidata, in terms of both rate of growth and spawning periods. Taking into account the time intervals between expeditions, once again we cannot entirely disqualify the possibility of a very short cycle (6 months) of which the modal classes we

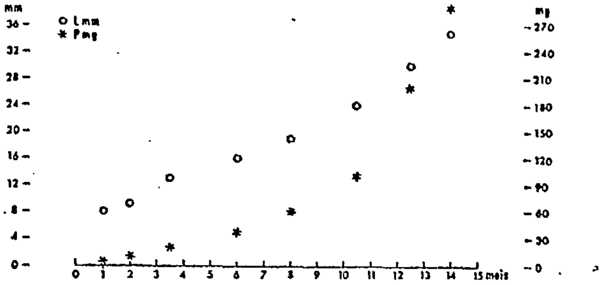


Fig. 63. — Croissance estimée de *T. monacantha* dans le Pacifique équatorial central (o : en longueur; * : en poids).
Fig. 63. — Estimated growth of *T. monacantha* in the central equatorial Pacific (Longevity approx. 15 months).

observed gave only a picture "in slow motion" caused by a stroboscopy effect.

Variations in the sex ratio (cf. Table 46) were not clear. Note, however, that the male/female ratio, with respect to reproducers (3.0-3.5 size groups), was 0.74 in October 1968, a period when spawning was in progress; for the other expeditions, all of which preceded intense spawning activity, the sex ratios were established at 0.90/1.00/0.96/0.93. This fact, without being definite, suggested that a high percentage of males die after the eggs have been fertilized.

As in the case of the species described previously, the various age 140
groups were found at different locations on the horizontal plane. For instance, the generation having originated from the spawn of September 1968 was found mainly to the east (135-142° W); in December 1968, most of this group (now the 0.9-1.2 groups) was found at the centre (142-147° W) and to the west (147-155° W); in July 1969, these same organisms having developed into 2.0/2.5/3.0 size groups showed a tendency to return to the eastern section where spawning would occur.

5.2.4. Conclusions on the Cycle of T. monacantha and Estimate of Growth Pattern

In the Central Equatorial Pacific, this species appears to have two particularly intense spawning periods (in fact, spawning occurs throughout the year, but to a greater or lesser extent): September-October and January-March, separated by a lessening of spawning activity during November and

December. There is a long period of less intense reproductive activity from April to August. The full cycle coincided very well with the beginning and end of the sampling series, as the situation encountered in September-October 1969 was highly similar to that of September-October 1968 (spawning imminent or in progress), with perhaps a slight delay of 1969 over 1968. Considering the generation originating from the spawn of September-October 1968, the following might be stated concerning T. monacantha:

— spawning occurs when the organisms are approximately one year old;

— the organisms likely die shortly afterwards, as the 3.5 group disappeared after spawning. The life-span of females was in the order of 15 months, of males no morethan 12 months;

— the growth curve of the organisms is essentially a straight line 141
(fig. 63) and amounts to 2 mm per month on the average. The age of the different size groups is given in Table 47.

TABLE 47

Growth pattern of T. monacantha

Size Group	Age (months)	Length (mm)	Weight (mg)
0,7	1	8	3
0,9	2	9	13
1,2	3,5	13	20
1,6	6	16	35
2,0	8	19	59
2,5	10,5	24	100
3,0	12,5	30	196
3,5	14	35	287

A linear growth curve would imply an exponential increase in weight (fig. 63), i.e., $\Delta p/p = \mathrm{Cte}$. From the size group/length/weight equivalences (cf. Table 4), we obtained the following weight increases:

$\frac{\Delta p}{p} = \frac{10}{8} = 1.25$ between 1 and 2 months

$= \frac{5}{16} = 0.31$ " 2 " 3.5 "

$= \frac{6}{27} = 0.22$ " 3.5 " 6 "

$$\frac{\Delta p}{p} = \frac{13}{47} = 0.28 \text{ between } 6 \text{ and } 8 \text{ months}$$

$$\frac{16}{80} = 0.20 \quad '' \quad 8 \quad '' \quad 10.5 \quad ''$$

$$\frac{48}{150} = 0.32 \quad '' \quad 10.5 \quad '' \quad 12.5$$

$$\frac{60}{240} = 0.25 \quad '' \quad 12.5 \quad '' \quad 14$$

We might therefore consider that, until approximately 2 months, the animal doubles its weight each month; then, for the remainder of its life, its weight increases by approximately 1/4 each month ($\Delta p/p \neq$ Cte. / 0.25).

5.3. Thysanopoda aequalis

5.3.1. Preliminary Notes

We collected a total of 2747 individuals of this species, of which 1033 were used to establish ovarian stages and the sex ratios (2.0 and 2.5 size groups). The ovarian stages were essentially identical to those of T. tricuspidata. However, we frequently noticed highly developed eggs that were not translucent, thereby implying that this criterion is not necessarily indicative of maturity for this species.

According to Tables 39 and 40, on the average for the entire cycle, 38% of females 18-20 mm long were in the late maturation stage (St. III and IV), this percentage increasing to 69% for females over 20 mm long; all were bearing spermatophores. Table 48 gives the data concerning the relative representation of size groups, Table 49 on ovarian stages and sex ratios.

5.3.2. Determining the Cycle

The available data is given in diagram form in figure 64. The situation is less defined than with the two precedingspecies; in particular, it is difficult to relate the situation of December 1968 to that observed in September (a certain gap was in fact noted for T. monacantha between "Caride"

TABLE 48

Number of specimens, percentages and relative representativity (% of $\bar{m}$%) of age groups (size groups) of <u>T. aequalis</u> in the Central Equatorial Pacific

Expedition Croisières	Tailles	2,5	2,0	1,6	1,2	0,9	0,7	Total
CA. I (Oct.) (Oct.)	Nb.	89	544	597	198	121	12	1 561
	%	5,7 %	34,8 %	38,2 %	12,7 %	7,8 %	0,8 %	—
	% $\bar{m}$ %	116	110	96	89	91	73	—
CA. II (déc.) (Dec.)	Nb.	10	140	172	59	32	7	420
	%	2,4 %	33,3 %	41,0 %	14,0 %	7,6 %	1,7 %	—
	% $\bar{m}$ %	49	105	104	99	88	155	—
CA. III (fév.) (Feb.)	Nb.	19	125	129	64	80	4	421
	%	4,5 %	29,7 %	30,6 %	15,2 %	19,0 %	1,0 %	—
	% $\bar{m}$ %	92	94	77	107	221	91	—
CA. IV (juill.) (July)	Nb.	3	69	122	49	23	5	271
	%	1,1 %	25,5 %	45,0 %	18,1 %	8,5 %	1,8 %	—
	% $\bar{m}$ %	22	80	114	127	99	164	—
CA. V (sept.) (Sept.)	Nb.	8	26	32	8	0	0	74
	%	10,8 %	35,1 %	43,2 %	10,8 %	0	0	—
	% $\bar{m}$ %	220	111	109	76	0	0	—
Total.........	Nb.	129	904	1 052	378	256	28	2 747
	% $\bar{m}$	4,9 %	31,7 %	39,6 %	14,2 %	8,6 %	1,1 %	—

TABLE 49

<u>T. aequalis</u>: sex ratio and ovarian stages (2.0 and 2.5 size groups)

Expedition	♀ II	♀ III	♀ IV	Sex Ratio
CA. I (oct.)...(Oct.)........	36 %	21 %	43 %	0,53
CA. II (déc.)..(Dec.)........	40 %	20 %	40 %	0,45
CA. III (fév.)...(Feb..)........	41 %	20 %	39 %	0,29
CA. IV (juill.)..(July)........	49 %	24 %	27 %	0,19
CA. V (sept.)..(Sept.)........	35 %	10 %	55 %	0,50

I and "Caride" II). The salient features are as follows:

— early October 1968: We mainly noted the presence of a high proportion of reproducers (2.0 and 2.5 size groups), among which most of the females were fully mature (43% at Stage IV). Active spawning was therefore in progress or imminent; a lesser peak of juveniles (0.9) indicated that 142
reproduction had begun a few weeks earlier.

— Early December 1968: The situation differed rather considerably from that encountered on the preceding expedition, except for the presence of juveniles (0.7) originating from the October-November spawn: the maximum size groups of 1.6-2.0 could not be foreseen in October. There were few

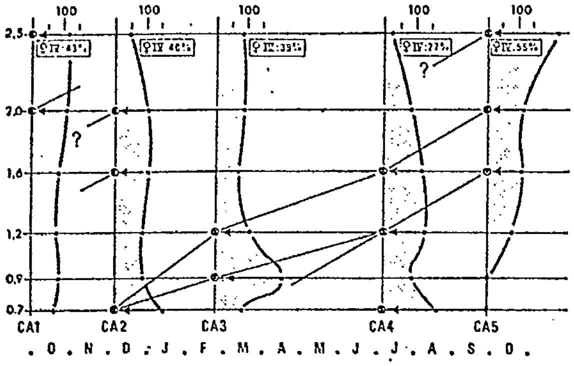


Fig. 64. — Évolution saisonnière de la structure d'âge (tailles) de la population de *T. aequalis* dans le Pacifique équatorial central, et filiation suggérée des classes modales.
Fig. 64. — Seasonal age (size) structure of *T. aequalis* populations in the central equatorial Pacific, and suggested evolution of modal classes.

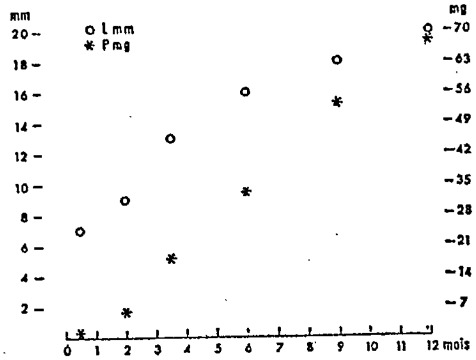


Fig. 65. — Croissance estimée de *T. aequalis* dans le Pacifique équatorial central (o : en longueur ; * : en poids).
Fig. 65. — Estimated growth of *T. aequalis* in the central equatorial Pacific (longevity approx. 12 months).

reproducers, although the very high percentage of mature individuals (40% at Stage IV) suggested that spawning was still in active process.

— February 1969: There was still a high proportion of adults; 39% of females were mature: there was no sign of any lessening in spawning activity. The largest group in terms of numbers was the 0.9-1.2 group, likely originating from the 0.7 individuals of December.

— early July 1969: Conversely, there was a low percentage of adults 143
very few among them being mature: this would indicate that spawning activity was definitely less intense than during the two previous periods. However, the slowdown was of recent date given the presence of very young organisms (0.7): we might assume that spawning proceeded until May-June. Modal classes corresponded to the mean size groups (1.2-1.6) originated from the recently ended very long spawning period and therefore, several generations were present: while the largest individuals originated from spawns in late 1968, the younger ones were the eggs which hatched in March-April 1969.

— late September 1969: A high proportion of mature adults (55% at Stage IV) implied that spawning was again in progress or would occur shortly.

The change in the large composite group of July (1.2-1.6 size group) created a confusing situation, slightly bimodal. The absence of small individuals (0.9-1.2), which should have been the 0.7 group of July, can be explained by the short geographical distance covered on the "Caride" V expedition.

5.3.3. Conclusions on the cycle of T. aequalis and Estimate of Growth Pattern

The situation is even less clear than for the preceding species, likely due to practically continuous spawning. In fact, we noted a slower reproductive activity only in July and August such that it would appear that active spawning occurs for 10 months of the year. Assuming that the species does not have a very brief cycle (5-6 months), which time intervals between expeditions would not have pointed out, the most likely situation, shown in figure 64, would lead us to attribute to T. aequalis a life-span of 10 to 12 months. Individuals would spawn when they have reached 9 or 10 months of age and would die a few weeks later. Growth in length appears to be slightly asymptotic (fig. 65) reaching an average of some 1.2 mm per month. Approximate size group/age/length equivalences are given in Table 50.

TABLE 50

Growth pattern of T. aequalis 144

Size group	Age (months)	Length (mm)	Weight (mg)
0,7	0,5	7	1
0,9	2	9	6
1,2	3,5	13	18
1,6	6	16	34
2,0	9	18	53
2,5	12	20	70

5.4. Nematoscelis tenella

5.4.1. Preliminary Notes

The 109 stations selected for this study resulted in 1806 individuals among which 930 from size groups 1.6 to 2.5 used to examine the sex and ovarian stage. Similarly to other species of this genus, N. tenella carries its eggs for a certain time after spawning, undoubtedly until hatching of the nauplii. This characteristic makes it possible to positively identify any spawning period, contrary to other species for which identification of Stage IV is partly a subjective process. We noted (Table 52) that the percentage of females bearing eggs remained rather constant throughout the year: we can therefore state that spawning occurs almost continually for this species. However, jolting during hauls caused most of the females to lose their eggs: seldom more than a dozen or so remained between the legs of the animal, thus contributing little to further knowledge on the fecundity of the species.

Females carrying eggs always presented a poorly developed ovary, corresponding to stages I-II described earlier; this provided further evidence to the fact that the ovary did indeed assume this structure after a spawn. The ovarian stages were essentially of the type described previously. Tables 51 and 52 give respective seasonal distributions for size groups and ovarian stages. Note very low values for the sex ratio, the number of males in the size groups examined appearing to be 4 to 5 times fewer than the number of females.

5.4.2. Determining the Cycle

Figure 66, established from data given in Table 51, does not express a definite situation, which we expected given virtually uninterrupted spawning activities (rather constant percentage of females carrying eggs). The result was rather confusing: in particular, it was difficult to determine the reproducers from which the juveniles (0.9-1.2) of December 1968 had originated, or those (0.7-0.9) of February 1969. However, the evolution of the modal classes was coherent: the 0.9-1.2 individuals of December 1968 could only develop into the 1.6 group by February (very few 1.2 and 2.0), then into 2.0-2.5 by July (again excluding the possibility of very rapid growth having

TABLE 51

Number of specimens, percentages and mean representativity (% $\overline{m}$%) of age groups (size groups) for N. tenella in the Central Equatorial Pacific.

Expedition Croisières	Tailles S.G.	2,5	2,0	1,6	1,2	0,9	0,7	Total
CA. I (oct.) (Oct.)	Nb.	25	105	208	296	125	8	767
	%	3,3 %	13,7 %	27,1 %	38,6 %	16,3 %	1,0 %	—
	% $\overline{m}$ %	66	70	84	125	144	100	—
CA. II (déc.) (Dec.)	Nb.	11	44	66	77	30	2	230
	%	4,8 %	19,1 %	28,7 %	33,5 %	13,0 %	0,9 %	—
	% $\overline{m}$ %	96	98	89	108	115	90	—
CA. III (fév.) (Feb.)	Nb.	17	40	86	64	35	5	247
	%	6,9 %	16,2 %	34,8 %	25,9 %	14,2 %	2,0 %	—
	% $\overline{m}$ %	138	83	107	84	126	200	—
CA. IV (juill.) (July)	Nb.	25	101	136	160	45	6	473
	%	5,3 %	21,4 %	28,8 %	33,8 %	9,5 %	1,3 %	—
	% $\overline{m}$ %	106	110	89	109	84	130	—
CA. V (sept.) (Sept.)	Nb.	4	24	38	20	3	0	89
	%	4,5 %	27,0 %	42,7 %	22,5 %	3,4 %	0	—
	% $\overline{m}$ %	90	138	132	73	30	0	—
Total.........	Nb.	82	314	534	617	238	21	1 806
	% $\overline{m}$	5,0 %	19,5 %	32,4 %	30,9 %	11,3 %	1,0 %	

TABLE 52

N. tenella: Sex ratio and ovarian stages (1.6 to 2.5 size groups).

Expedition	♀ II	♀ III	♀ IV		Sex Ratio
CA. I (oct.)..(Oct.)........	55 %	22 %	6 %	17 %	0,19
CA. II (déc.)..(Dec.)........	58 %	25 %	0	17 %	0,19
CA. III (fév.)..(Feb.)........	64 %	20 %	4 %	12 %	0,25
CA. IV (juill.).(July)........	54 %	18 %	4 %	24 %	0,18
CA. V (sept.).(Sept.).......	44 %	12 %	17 %	27 %	0,20

gone unnoticed owing to the time interval between observations). Judging by the development of that generation, we might estimate the growth pattern of the species.

5.4.3. Conclusions on the Cycle of N. tenella and Estimate of Growth Pattern 145

Considering the generation having hatched from the spawn of October 1968, we might attribute to N. tenella a life-span of approximately one year. As in the case of the other species, it appears likely that each female spawns only once and dies shortly thereafter. Table 53 indicates the size

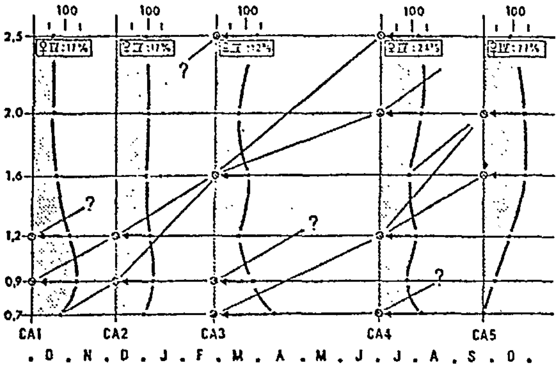


Fig. 66. — Évolution saisonnière de la structure d'âge (tailles) de la population de *N. tenella* dans le Pacifique équatorial central, et filiation suggérée des classes modales.

Fig. 66. — Seasonal age (size) structure of *N. tenella* populations in the central equatorial Pacific, and suggested evolution of modal classes.

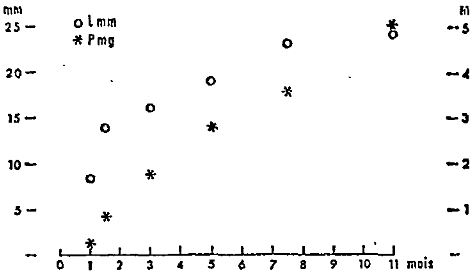


Fig. 67. — Croissance estimée de *N. tenella* dans le Pacifique équatorial central (o : en longueur ; * : en poids).

Fig. 67. — Estimated growth of *N. tenella* in the central equatorial Pacific (longevity approx. 12 months).

TABLE 53

Growth pattern of N. tenella

Size group	Age (months)	Length (mm)	Weight (mg)
0,7	1	8	3
0,9	1,5	14	9
1,2	3	16	20
1,6	5	19	31
2,0	7,5	23	40
2,5	11	24	55

group/age/length/weight relationships from which a growth curve can be inferred (fig. 67) which appears to be asymptotic for length. Over the entire cycle, the mean monthly growth amounts to 1.6 mm.

5.5. Euphausia diomedae 146

5.5.1. Preliminary Notes

Given the exceptional density of this species in the region investigated, we collected 42,740 specimens over the five expeditions, among which 7595 belonging to the 1.6 and 2.0 size groups examined (as sub-samples) for sex and ovarian stage. The sheer number of specimens would ensure reliable sampling.

The ovarian stages only slightly agreed with the description of the typical stages described earlier. In particular, the structure and transparency of the eggs did not appear to be strictly related to the degree of

TABLE 54

Number of specimens, percentages and relative representativity (% $\overline{m}$%) of age groups (size groups) of E. diomedae in the Central Equatorial Pacific

Expedition Croisières	Tailles S.S.	2,0	1,6	1,2	0,9	0,7	Total
CA. I (oct.) (Oct.)	Nb.	263	2 231	5 492	5 385	959	14 330
	%	1,8 %	15,6 %	38,3 %	37,6 %	6,7 %	—
	% $\overline{m}$ %	82	91	106	101	93	—
CA. II (déc.) (Dec.)	Nb.	369	1 335	3 173	3 211	721	8 809
	%	4,2 %	15,2 %	36,0 %	36,5 %	8,2 %	—
	% $\overline{m}$ %	191	89	99	98	114	—
CA. III (fév.) (Feb.)	Nb.	49	743	2 854	4 608	705	8 959
	%	0,6 %	8,3 %	31,9 %	51,4 %	7,9 %	—
	% $\overline{m}$ %	27	49	88	138	110	—
CA. IV (juill.) (July)	Nb.	137	1 546	3 095	2 017	605	7 400
	%	1,9 %	20,9 %	41,8 %	27,3 %	8,2 %	—
	% $\overline{m}$ %	86	122	115	73	114	—
CA. V (sept.) (Sept.)	Nb.	88	834	1 062	1 097	161	3 242
	%	2,7 %	25,7 %	32,8 %	33,8 %	5,0 %	—
	% $\overline{m}$ %	123	150	91	91	69	—
Total.........	Nb.	906	6 689	15 676	16 318	3 151	42 740
	% $\overline{m}$	2,2 %	17,1 %	36,2 %	37,3%	7,2 %	—

TABLE 55

E. diomedae: Sex ratio and ovarian stages (1.6 and 2.0 size groups).

Expedition	♀ II	♀ III	♀ IV	Sex Ratio
CA. I (oct.)..(Oct.).........	42 %	57 %	1 %	0,02
CA. II (déc.)..(Dec.).........	42 %	48 %	11 %	0
CA. III (fév.)..(Feb.).........	37 %	55 %	8 %	0,01
CA. IV (juill.)..(July).........	45 %	51 %	4 %	0,01
CA. V (sept.)..(Sept.).......	75 %	25 %	—	0,02

development. Under such circumstances, we had to be content with estimating the maturity of an individual according to the volume occupied by the ovary; however, the most mature individuals, i.e., having reached Stage IV, were distinguished by swelling of the thoracic region caused by the considerable size of the ovary. The seasonal distribution of size groups, ovarian stages and sex ratio appears in Tables 54 and 55. Note that, throughout the year, very few male specimens were collected. As suggested earlier, this was partly due to the fact that only females developed into the sizes which we examined for studying the sexual characteristics of the species.

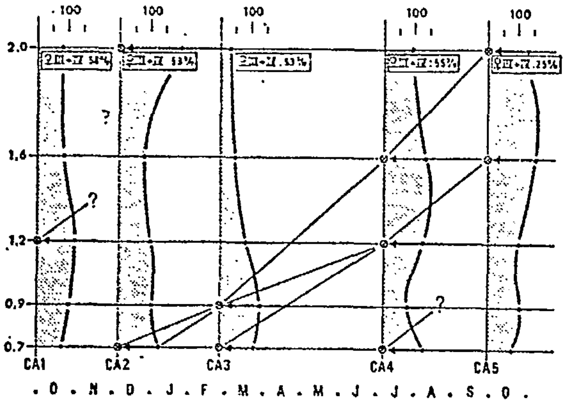


Fig. 68. — Évolution saisonnière de la structure d'âge (tailles) de la population de *E. diomedae* dans le Pacifique équatorial central, et filiation suggérée des classes modales.

Fig. 68. — Seasonal age (size) structure of *E. diomedae* populations in the central equatorial Pacific, and suggested evolution of modal classes.

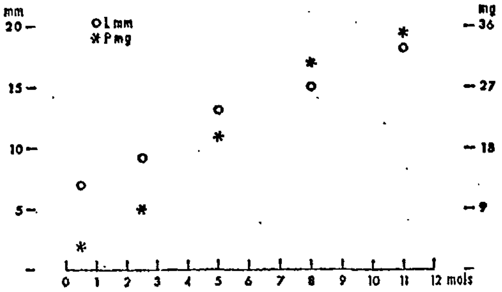


Fig. 69. — Croissance estimée de *E. diomedae* dans le Pacifique équatorial central (o : en longueur ; * : en poids).

Fig. 69. — Estimated growth of *E. diomedae* in the central equatorial Pacific (longevity approx. 11 months).

5.5.2. Determining the Cycle 147

Figure 68 was established from the data given in Tables 54 and 55.

Note:

— a consistent percentage of mature females or females in late maturation, except in September 1969 at which date the impending arrival of an abundant generation in the size groups of reproducers led us to assume that spawning would occur in the near future.

— the evolution of modal classes appeared to establish itself rather naturally as follows: 0.7 of December → 0.9 of February → 1.2/1.6 of July → 1.6/2.0 of September.

In addition, we noted two characteristics previously noticed for certain of the other species: 148

— a gap between "Caride" I and "Caride" II.

— very few small individuals collected on "Caride" V, a stationary station.

5.5.3. Conclusions on the Cycle of E. diomedae and Estimate of Growth Pattern

This species is almost in a permanent state of reproduction, with possibly a lessening of reproductive activity during August and September. According to the generation observed from December 1968 to September 1969, E. diomedae would have a life-span of approximately 12 months, with spawning occurring when the individuals are 10 to 12 months of age. Table 56 gives the size group/age/length/weight relationships from which we derived the growth pattern of the species (fig. 69). The mean individual growth in length does not exceed 1 mm per month.

TABLE 56

Growth Pattern of E. diomedae

Size group	Age (months)	Length (mm)	Weight (mg)
0,7	0,5	7	3
0,9	2,5	9	9
1,2	5	13	19
1,6	8	15	29
2,0	11	18	35

5.6. Nematobrachion boopis and Bentheuphausia amblyops 149

In spite of the very few specimens (318 and 347 respectively for all 109 stations) collected of these two species, it was rather interesting to study whether certain characteristics of their biology were related. In fact, with the exception of seldom collected giant bathypelagic species, they dwell at much greater depths than the species previously examined: in Chapter 4, we mentioned that most of them only on rare occasions rise above 300 m, even by night, such that their biotope, with temperatures always lower than 12-13°, differs considerably from that of the other species which rise to the subsurface at night (temperatures higher than 25°).

We might recall that these deep-water species have a very low fecundity (cf. Table 38) given the fact that the mature ovary of E. amblyops contained only 3.5 eggs on the average, and that of N. boopis only 9. For both

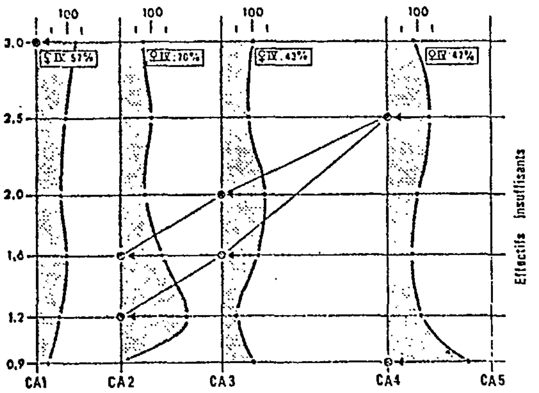


Fig. 70. — Évolution saisonnière de la structure d'âge (tailles) de la population de *N. boopis* dans le Pacifique équatorial central, et filiation suggérée des classes modales.

Fig. 70. — Seasonal age (size) structure of *N. boopis* populations in the central equatorial Pacific, and suggested evolution of modal classes.

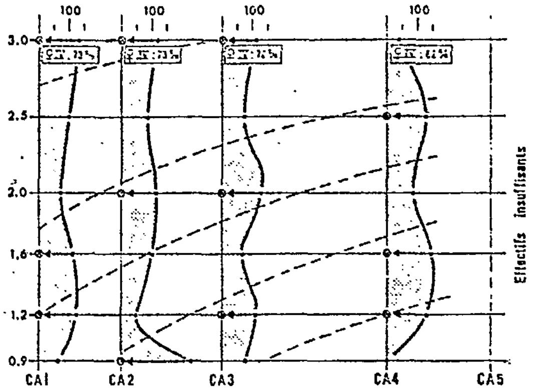


Fig. 71. — Évolution saisonnière de la structure d'âge (tailles) de la population de *B. amblyops* dans le Pacifique équatorial central, et filiation suggérée des classes modales.

Fig. 71. — Seasonal age (size) structure of *B. amblyops* populations in the central equatorial Pacific, and suggested evolution of modal classes.

species, Stage IV was readily identified; the ovarian structure of N. boopis agreed with that of T. pectinata while in the case of B. amblyops, the granular cytoplasm of the eggs was bright yellow in late maturation (the nucleii remained white) contrary to the eggs in Stages II and III which were white and opaque. B. amblyops displayed a very particular arrangement of the eggs in the ovary: two parallel rows with the ripest eggs in the middle. Figures 70 and 71 give the seasonal distributions of size groups for N. boopis and B. amblyops respectively, and the percentage of mature females which appears to remain constant in both cases. We might therefore assume that the intensity of reproduction does not significantly vary during the year.

Inasmuch as the number of specimens enabled us to obtain reliable figures, the situation for both species would be as follows:

— There is no basic difference between the cycle of N. boopis and 150
those of other species described earlier. In fact (cf. fig. 70), the most

probable modal development would mean that the 1.2 size group of December 1968 was the 2.5 group of July 1969, corresponding to an average growth of 1.4 mm/month over a 7-month period. Given the fact that this species grows from 9 mm to 30 mm during the course of its existence, this average rate of growth would give the species a life-span of approximately 15 months.

— In the case of E. amblyops, on the contrary, there are two possible alternatives:

* either this species has a very short cycle, with a rate of growth of 2 mm/month and a life-span of 8 months. This hypothesis seems unlikely in the case of a species permanently inhabiting a relatively cold environment.

* or the species has a very long cycle and the 25 mm increase in length would occur over a two-year period. Given the biotope of this species, the second interpretation appears to be the more reasonable.

6. CONCLUSIONS

6.1. Reliability of Observations

For the reasons mentioned at the beginning of this chapter, determining the life cycles of pelagic populations is rather difficult and many uncertainties therefore still prevail. Even with relatively well known species of colder environments where seasonal changes are well defined, there is still a possibility of error: Ivanov (1970) has questioned the life cycle of E. superba in the Antarctic, a species to which a dozen or so serious studies have been devoted over the last half-century; recent findings by Smiles and Pearcy (1971) on E. pacifica do not agree with those of Lasker (1966) and Ponomareva (1963).

In the case of tropical or equatorial populations, we demonstrated that the situation is even less well defined due to additional difficulties created by the unchanging quality of the environment as well as to the lack of previous research which might further contribute to the credibility of observations should they agree. For such reasons, we must emphasize the fact that the hypotheses set forth in this chapter must be viewed as an initial attempt at interpreting observations. This having been said, how reliable is our data? At the outset, the reader must assume two postulates:

1. Modal classes were actually observed and were not the product of erratic sampling fluctuations. In that respect, we might point out that the modes correspond, for a given expedition, to different sizes for different species; we might therefore believe that there were no inherent differences due to different methods having been applied from one expedition to another, except for "Caride" V, carried out at a stationary point and characterized by the consistent absence of small individuals.

2. The same population was sampled throughout the sampling series (plausible hypothesis given the stable east-west equatorial currents).

Under these conditions, the modes set forth follow from one another and may therefore be related to one another. Examination of the data for the 151 different species indicated that, in most cases, it was impossible to consider a longer cycle than the one suggested. However, we must admit that too infrequent observations has meant that we could not uncover cycles half as long. We can therefore state that the life cycles, all of which were one-year cycles (except for *E. amblyops*) are definitely not any longer; but, it is not entirely impossible that they are in fact twice as short and extend only over a six-month period. Only more frequent expeditions could prove this.

In conclusion, we wish to add two further comments:

— firstly, we noted in several instances a gap between two consecutive expeditions for certain species; the modes obtained on one expedition could not possibly have evolved from those of the previous expedition. This led us to believe, in certain cases at least, that the postulates established at the outset were not respected.

— secondly, the lack of accuracy in the methods applied (size groups) did not enable us to determine details for the growth curves, because the precise position of the modes was uncertain. It was generally impossible to state whether the growth pattern was linear or slightly asymptotic.

6.2. Summary of Observations

Our objective was to determine the salient features of the life cycles: life-span, average rate of growth, fecundity, spawning periods; we might recall that these parameters were hitherto unknown for equatorial Euphausiids, no research having so far been done to ascertain whether these organisms lived for a few months or a few years. These uncertainties implied that it was impossible to establish any energy balance whatsoever for such populations. We do not claim to have neither a definite, nor a complete answer, only indications of a certain probability.

Nevertheless, recalling again that the possibility of cycles twice as short cannot be rejected, the main characteristics of reproduction and growth for the species examined are summarized in Table 57. It would appear that females live through one spawn only, except perhaps for B. amblyops; with the exception of the latter, the life-span of the organisms is approximately 1 year, i.e., shorter than species of cold or temperate waters which live for 2 to 4 years (Zelickman, 1960; Ruud, 1932; Ponomareva, 1963; Mauchline, 1960 etc). However, most of the species we examined were rather large and preferred a midwater habitat. The smaller epipelagic species (E. tenera, S. affine, S. carinatum, etc.) permanently submitted to very high temperatures (20-25°) may well have even shorter cycles, from 4 to 6 months.

TABLE 57

Main characteristics of life cycles in the Central Equatorial Pacific.

Species	Estimated life-span (in months)	Growth rate (in mm/mo)	Peak spawning period
T. tricuspidata	12-14	2,0	October-December March-April
T. monacantha	13-15	2,0	September-October January -March
T. aequalis	10-12	1,2	continuous(perhaps slower in July-August)
N. tenella	11-13	1,6	continuous
E. diomedae	11-13	1,0	continuous (perhaps slower in August-Sept.)
N. boopis	15	1,4	continuous
B. amblyops	24	1,0	continuous

TABLE 58

Average growth rate of a few species of cold or temperate regions.

Author	Species	Location	Average growth rate (in mm/mo)
Zelickman, 1960	*T. raschii, T. inermis*	Barents	0,7
Ponomareva, 1963	*T. longipes* *E. pacifica*	Barents N. Pac.	1,25 0,83
Mauchline et Fisher, 1969	*T. aculifrons*	N. Atl.	1,46
Mauchline, 1960	*M. norvegica* (adults)	North Sea	1,0
Bargmann, 1945	*E. superba*	AA	1,88
Lasker, 1966	*E. pacifica* (juveniles) — (adults)	Calif. Current	1,5 0,5
Brinton, 1969	*N. difficilis* *E. pacifica*	Calif. Current	2,5
Smiles et Pearcy, 1971	*E. pacifica*	Oregon	2,0

Spawning undeniably occurs at all seasons. However, certain peak periods were noted for certain species (T. tricuspidata, T. monacantha); in such cases, intense spawning activity appeared to concide with the end of the seasons of maximum primary production, defined by Owen and Zeitzschel (1970). Fecundity is much lower than for species inhabiting cold or temperate regions (cf. Table 38). This is largely compensated by earlier sexual maturity reached by 8 to 12 months. Growth generally follows a linear pattern, perhaps faster for juveniles, although in certain cases the growth seems to take a slightly asymptotic pattern. Most authors have mentioned similar characteristics (Zelickman, 1960; Ruud, 1932; Ponomareva, 1963; Lasker, 1966; Mauchline, 1960; Bargmann, 1945), but in cold or temperate environments the growth rate tends to slow down during winter, thereby resulting in a curve resembling a flight of stairs; in a tropical or equatorial environment such fluctuations virtually do not occur and growth follows a generally linear pattern. Average monthly rates of growth (cf. Table 57) are on the whole somewhat higher than those of species of cold or temperate regions, estimates for the latter being given in Table 58.

153 Finally, we must point out that our data applies to the Central Equatorial Pacific and we do not exclude the possibility that these same species present different characteristics in other regions: several authors have pointed out the influence of environmental factors on the rate of growth, life-span, fecundity and maximum size (Lasker, 1960 and 1966; McLaren, 1963 and 1965; Allen, 1966; Margalef, 1967 a; Heinle, 1969; Regnault, 1969); Smiles and Pearcy (1971) recently suggested that E. pacifica, benefitting from more abundant resources off the coast of Oregon, apparently grows twice as fast than in the California waters. We might even conceive that future research might uncover significant disparities in the biology of one species between populations in the east and west of the Equatorial Pacific.

CHAPTER 7 . TROPHIC SITUATION

Trophic relationships form the prime factor of biological balance, the density of any population at any given location resulting from a particular nutrition-predation relationship (available food supplies/predation which a population is able to support). The ecology only defines for each species the range within which such balance is possible.

Only thorough knowledge of trophic relationships between the various parties occupying a given biotope could lead to a full understanding of pelagic biology. Any research in this field, even partial or inaccurate due to the great difficulties involved, will contribute some knowledge on the causes of the situations observed.

We shall attempt to give details on the following:

- the trophic level of the different species and conditions under which they feed (Chap. 7 A).
- the quantity of food which Euphausiids represent and the form under which it is available.(Chap. 7 B (I).
- major predators of the tropical and equatorial environment and their role in the economy of these regions (Chap. 7 B (II).

A. NUTRITION

1. Available Data

As in the case of many other groups of invertebrates, attempting to

determine the food sources of Euphausiids is indeed very difficult. We must necessarily examine stomach contents, the larger part of which is a shapeless mass without recognizable structure: food having been finely broken down before ingestion, any recognizable particle accounts for only a small fraction of the total mass. Furthermore, such particles do not necessarily form the greatest portion of ingested food, but shows only the most resistant organisms, which we therefore tend to over-estimate (Edmonson, 1957); 156
for instance, traces of diatoms (frustule remains) can certainly be seen for several hours in a stomach, while ingestion of a large quantity of flagellates will not be detected. Likewise, it appears that Euphausiids "suck in" Copepods through their oral parts, then cast off the empty shell (Mauchline and Fisher, 1969): few traces would therefore remain when the stomach contents were examined. In consequence, available data describes only the type of food ingested by Euphausiids, mostly in the form of lists stating which animals were present or absent in the stomach contents of a given species.

Mauchline and Fisher (1969) claim that phytoplankton is never their main source of food, except for E. superba in the Antarctic. Animal food sources most frequently quoted are Tintinnids, Radiolarians, Foraminifers, Globigerinae, Chaetognaths and Copepods (Fisher and Goldie, 1959; Lebour, 1924; MacDonald, 1927; Mauchline, 1960 and 1967; Nemoto, 1967; Ponomareva, 1963; Ponomareva, Naumov and Zernova, 1962; Tchindonova, 1959; Weigmann, 1970). Detritus is often mentioned as a nutritional source for certain species and cannibalism is considered to occur frequently in the event of famine (Fisher and Goldie, 1959). Several authors mentioned bacteria as a food source for zooplankton, particularly aggregates of bacteria (Seki, 1966; Pavlova, Petipa and Sorokin, 1971; Petipa et al, 1971; Ponomareva et al, 1971; Sorokin, 1971).

Simply stated, we generally agree with Mauchline (1967) that primitive Euphausiids (single pair of eyes, unextended legs, migratory, not carrying their eggs : Euphausia, Thysanopoda, Bentheuphausia) feed themselves through filtration and predation; more developed Euphausiids (double pair of eyes, one or two pairs of extended legs, non-migratory, carrying their eggs : Nematoscelis, Nematobrachion, Stylocheiron) are predatory and detrivorous, their ability for filtration being very limited.

Tropical Euphausiids are generally considered as being more carnivorous than temperate species (Marshall, 1954; Ponomareva, 1963 and 1971; Petipa et al, 1971), while in fact, lack of resources compels them to be somewhat euryphagous (Ponomareva, Naumov and Zernova, 1962; Timonin, 1969; Petipa, Pavlova and Sorokin, 1971; Pavlov, 1971): therefore, in principle, there are fewer trophic differences between species in a tropical environment and, although animal food predominates, almost all stomachs contained at least traces of phytophanktonic pigments, either chlorophyll "a" for surface feeders or broken down pigments for deep-water species (Nemoto, 1968 and 1970; Nemoto and Saijo, 1968); only strictly carnivorous species (e.g., Nematobrachion boopis) were completely void of any plant matter. In their trophic research, certain authors classified various species of tropical Euphausiids as being either "herbivorous" or "carnivorous" (Timonin, 1971) which appears as a rather gross approximation.

Nevertheless, our own knowledge in this field remains very fragmentary, even entirely lacking in terms of quantities. We considered it extremely important to specify the trophic level of the species; rather than establish, by painstaking analysis, another list of debris identified in stomach contents, we deemed it preferable to make an attempt at determining generally to what extent phytoplankton and zooplankton were the food sources for the adults of various species.

2. METHOD OF EXAMINATION

Each stomach content was the subject of a two-fold examination:

— fullness: 0 indicating an empty stomach, + a stomach half-full, ++ a stomach more than half-full;

— nature of contents: V if phytoplanktonic matter accounted for over 80% of total contents; A if animal matter was included in this percentage; VA if phytoplankton and zooplankton were present in comparable proportions.

Animal or vegetable matter in stomach contents was easily identified under the microscope, even under low magnification (x10 or x 20). Phytoplankton resembled a very recognizable greenish mass (verification under the microscope confirmed an abundance of plant debris); animal matter appeared as whitish aggregates or, much less frequently, blackish-brown matter. Determining the origin of stomach contents was therefore relatively simple, although assessing the proportion of each was necessarily inaccurate.

With respect to our method of examination, a major point must be pointed out. During the course of our work, we noticed by chance that the appearance of stomach contents changed with time, under the influence of Formol or light. With time, plant matter progressively lost its green color becoming whitish, thereby making it unidentifiable. According to our system, stomach contents had a greater proportion of animal matter increasing with the time having elapsed since the sampling. Consequently, we saw the importance of working on recent material, all species having been examined after a similar time interval.

This discrepancy appeared during our analysis of the nutritional habits of E. gibboides. Specimens collected on "Caride" I (October 1968) and examined in October 1969, i.e., after a one-year period, had 89% of their stomach contents rated as type V; a check carried out at the same time on specimens of the same species collected in 1964 indicated stomach contents of type V being only a few percent of the total mass. Given such obvious breaking down of stomach contents, we carried out systematic examinations on specimens of different ages for several species. We reached the conclusion that, under our conditions of work (specimens preserved in 10% Formol, kept away from direct light), stomach contents changed little during the first year; after 1 or 2 years, aging of the material leads to over-estimating by 10% the proportion of category A to the detriment of category V; discoloration accelerates thereafter and after 4 or 5 years, the original color has completely changed.

This situation led us to carefully select good specimens which had been collected within the previous 18 months; as shown in Table 59, this considerably limited the material available for certain species. On the other hand, stomach repletion which does not change with time was examined in a great many more specimens.

Finally, note that we examined only stomach content. Certain authors (Ponomareva, 1963) claimed that food being ingested should also be taken into consideration, e.g., food caught between the thoracic legs ("basket"); we agreed with Mauchline (1967) that such material could well be artificial food and could be merely debris caught by the animal during the haul while it was 158
entrapped in the net.

3. TROPHIC LEVELS

From the A/VA/V ratings established for the different species, we determined their respective trophic level which can be more conveniently expressed as a single number obtained by adding either: A+(VA/2)% or

TABLE 59

Trophic levels (species classified by decreasing order of proportion of animal matter present in stomach contents : A+(VA/2) % decreasing).

Species	Number of individuals examined	% empty stomachs	% A	% VA	% V	A+ (VA/2) %
T. aequalis	844 *	2 %	98 %	2 %	0	99 %
N. boopis	131	13 %	97 %	1 %	2 %	98 %
S. abbreviatum	14 **	(env. 50 %)	93 %	7 %	0	96 %
T. orientalis	51	10 %	87 %	13 %	0	93 %
N. gracilis	37 **	—	84 %	2 %	14 %	85 %
N. flexipes	57	21 %	78 %	4 %	18 %	80 %
T. monacantha	1 115 *	9 %	59 %	38 %	3 %	78 %
T. pectinata	110	3 %	53 %	40 %	7 %	73 %
T. cristata	36	44 %	65 %	0	35 %	65 %
N. microps	20 **	—	60 %	0	40 %	60 %
E. diomedae	989 *	1 %	37 %	40 %	23 %	57 %
N. tenella	542 *	35 %	50 %	4 %	46 %	52 %
T. tricuspidata	1 556 *	7 %	17 %	42 %	41 %	38 %
B. amblyops	66	8 %	7 %	31 %	62 %	22 %
E. paragibba	48 **	—	2 %	10 %	88 %	7 %
E. gibboides	199	4 %	4 %	7 %	89 %	7 %

* On sub-samples in the case of most abundant stations.
** Excluding empty stomachs.

V+(VA/2)%, both being complementary to one another, and stating the respective proportions of animal and vegetable matter.

The overall results are shown in Table 59 and figure 72. Analysis of this data led us to draw the following conclusions (suffice it to recall that this study dealt only with adult specimens):

— although most species are euryphagous, their feeding habits indicated a wide range of carnivorous and herbivorous species. Grouping the species into categories, we might therefore consider that:

- *T. aequalis*, *N. boopis*, *S. abbreviatum*, *T. orientalis* are strictly carnivorous.
- *N. gracilis*, *N. flexipes*, *T. monacantha*, *T. pectinata* appear to be mainly carnivorous, but complete their diet with plant matter.
- *T. cristata*, *N. microps*, *E. diomedae*, *N. tenella* are typically euryphagous, phytoplankton and zooplankton contributing equally to their nutritional requirements.

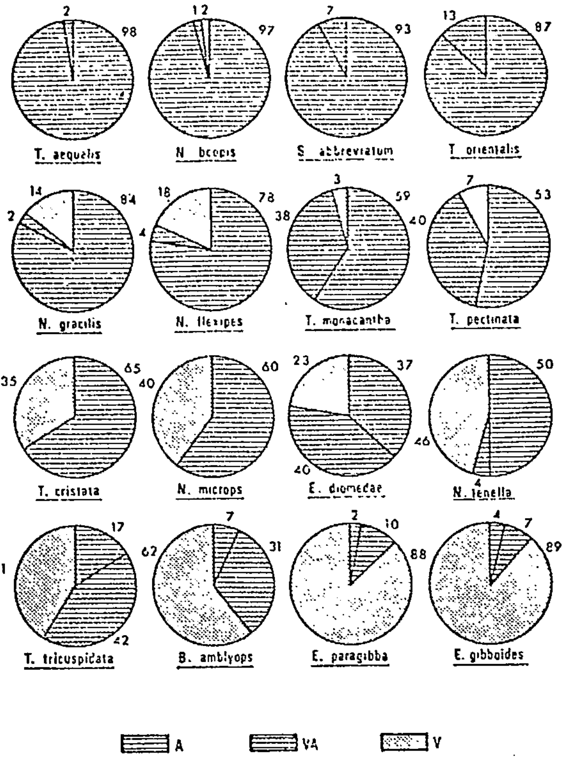


Fig. 72. — Niveaux trophiques des espèces (adultes) : pourcentages d'animaux dont le contenu stomacal est principalement de nature animale (A), végétale (V) ou mixte (VA).
Fig. 72. — Trophic levels of species (adults) : percentages of specimens whose stomach contains principally animal food (A), vegetal food (V) and mixed food (VA).

.• in T. tricuspidata and B. amblyops, plant matter was definitely more prominent, but zooplankton nevertheless accounted for 1/3 to 1/5 of the total food ingested. 159

• E. paragibba and E. gibboides are strictly herbivorous.

— Note that, on the whole, animal food sources are more prominent, 12 out of 16 species using them for more than half of their total nutritional requirements.

— Although included among the group of predatory Euphausiids, species of the genus Nematoscelis were far from being exclusively carnivorous, N. tenella in particular which depends upon phytoplankton for half of the food required for its subsistence. On the other hand, species of the genera Stylocheiron (S. abbreviatum) and Nematobrachion (N. boopis and N. flexipes) are definitely predatory.

— Note that certain animals had a high percentage of stomach contents rated VA, i.e., containing both animal and plant matter (T. tricuspidata,

T. monacantha, T. pectinata, E. diomedae, E. amblyops); others, on the contrary, had stomachs containing either animal or vegetable matter, seldom both (T. cristata, N. tenella, N. microps, N. flexipes). It is possible that these two types of euryphagous species have different feeding habits.

— Analysis of the stomach content of E. diomedae was particularly difficult: the constant texture and pale green color suggested that the species was highly euryphagous. Animal matter predominated, but always mixed with a small amount of phytoplankton.

— We noted no correlation between the trophic level of a species and the percentage of empty stomachs. In theory, predatory species should 160 have shown greater fluctuations in the repletion rating than phytophagous species, but in the case of Euphausiids, their trophic levels are undoubtedly too poorly developed to bring out this factor.

— Trophic levels did not appear to be strictly related to the biotope occupied by the species. We noted, in fact, that species rising to the surface layers at night, such as T. aequalis, can be carnivorous, while other bathypelagic species, such as B. amblyops, nourish themselves to a great extent on phytoplankton. Regarding this species, the presence of vegetable pigments in their stomach contents has frequently been mentioned, the authors finding it difficult to explain the compatibility between this type of nutrition and the deep-water habitat of the species. Nemoto (1968) and Nemoto and Saijo (1968) demonstrated that the pigments found in the stomachs of bathypelagic species were broken down and originated from the ingestion of/dead phytoplankton sinking to the bottom of the sea. In the case of surface species, on the contrary, pigments in stomach contents originated from living phytoplanktonic cells; analysis of the pigments contained in the stomach of T. tricuspidata (surface feeder) indicated a proportion of 10% chlorophyll "a"; this percentage dropped to 1.5% for T. monacantha, 0.8% for *N. gracilis* and 0.01% for *E. amblyops*. Hence, the importance of distinguishing several categories among herbivorous and euryphagous species becomes readily obvious.

— Although very few examinations were made to determine the origin of the food ingested, Copepod debris was frequently noticed in the stomachs of *N. boopis* and *T. cristata*, which also appear to be the usual predators of such organisms. Furthermore, as Marshall (1954) recorded for *T. acutifrons*, the large specimens of certain species very frequently carry fish scales in their basket. As we mentioned earlier, we believe that the basket contents are artificial and were caught by the animal entrapped in the net in which numerous fish scales whirl about. Nevertheless, we noted a very definite correlation between the size of the Euphausiids and the frequency at which fish scales were found in their basket (Table 60): this observation would to a certain extent support the possibility that Euphausiids are ichthyophagous.

TABLE 60

Percentage of individuals holding fish scales in their basket, on the basis of size of individual.

Species Espèces — Tailles S.J.	3,5	3,0	2,5
T. monacantha	57 %	38 %	—
T. tricuspidata	—	40 %	27 %
T. orientalis	52 %	27 %	—
T. pectinata	70 %	58 %	29 %

4. FEEDING CONDITIONS

The data resulting from analyses carried out for this part of the work enabled us to examine whether variations in stomach repletion and the nature of the stomach contents were related to any of the following parameters: time of haul, size (age) of organism, sex, ovarian stage and season.

4.1. Variations according to Time of Day in Stomach Fullness and Nature of Stomach Content

As a sizeable portion of the species carry out daily vertical migrations, to the upper layers during the night where phyto- and zooplankton are very plentiful while their deeper daytime habitat has much less to offer, one would logically expect to find a striking difference between stomach contents by day and by night in terms of both repletion and ingested food (Pavlov, 1971; Ponomareva, 1971). However, analysis of our own data partly contradicted this assumption.

An initial study was conducted on material obtained on the "Caride" expeditions by examining night hauls (2000 - 0400 hours) and daytime hauls (0700 - 1700 hours) separately. More intensive feeding at night was apparent only for T. tricuspidata, E. diomedae and N. flexipes, while we noted no significant difference in stomach repletion for T. monacantha, T. orientalis, T. pectinata, N. boopis, N. tenella, E. gibboides. In terms of type of food ingested, only N. tenella presented a definite difference between day and night (shown in Table 61). This lack of variation would confirm other research carried out on M. norvegica by Fisher and Goldie (1959) and on T. raschii by Mauchline (1966 b).

TABLE 61

Difference between day and night in nature of stomach content of N. tenella

	A	VA	V
Jour..... Day....	90 %	2 %	8 %
Nuit..... Night..	54 %	6 %	40 %

In fact, a more detailed analysis was carried out subsequently on material obtained on the "Cyclone" expeditions for which we had 6 samplings drawn within twenty-four hour periods, rather than only day and night hauls. It would appear that the peak feeding time for most species does not occur at night, such that the definite break between day and night does not coincide with feeding time. Unfortunately, these samples were examined only for stomach repletion and consequently, we did not/have sufficient data to determine any possible hourly fluctuations in the nature of stomach contents.

Figure 73 shows peak feeding time for different species. Note that variations in the percentage of empty stomachs (C S 0) and full stomachs (CS++), very obvious in most cases, take the form of a sinusoidal curve. Values of CS0 and CS++ were centered about their respective means; the extent of daily variations in the fullness factor [(max. fullness - min. fullness)/ mean fullness] is also shown. Considering that feeding is most intense between the time when the percentages of CS++ and CS0 respectively increase and decrease, and the time when the inverse occurs, we obtained the following peak feeding time for/each of the different species:

— <u>T. tricuspidata</u> : 1500 to 0600 hours 162
— <u>T. monacantha</u> : 2000 to 1000 hours
— <u>T. pectinata</u> : 1300 to 0600 hours
— <u>T. orientalis</u> : 2100 to 0600 hours
— <u>T. aequalis</u> : 1200 to 0000 hours
— <u>T. cristata</u> : 0800 to 2000 hours
— <u>N. boopis</u> : 1300 to 0000 hours
— <u>N. tenella</u> : 1300 to 0200 hours

These feeding periods are far from corresponding to strictly day or night hours and do not appear to be clearly related to trophic levels; note, however, that <u>T. cristata</u> feeds mostly during the day as its deep habitat is practically deserted at night.

The extent of variations in stomach fullness is rather minimal for these bathypelagic or mesopelagic migratory species. Maximum values were noted for predatory species feeding on relatively large prey (Copepods) : <u>T. cristata</u>, <u>N. boopis</u>. On the contrary, more phytophagous species or those feeding on animal matter composed essentially, it appears, of small organisms (Foraminifers, Radiolarians, Tintinnids...) vary less in terms of fullness of stomach.

On the whole, we might therefore conclude that the feeding intensity of these species follows a certain cycle, never very rigid and generally not in keeping with either day or night. The phases of such cycles do not appear to be related to trophic levels and do not imply (except perhaps for *N. tenella*) a change in the type of food ingested.

4.2. Variations in mean stomach fullness and nature of stomach contents in terms of size of organism

Larvae and juveniles were not examined and our data therefore bears only on adult specimens; consequently, we might expect only minor differences between various size groups.

No significant differences were noted in the mean stomach fullness for the following species:

T. monacantha: (3.0 and 3.5 size groups)
T. pectinata : (3.0 and 3.5 " ")
T. tricuspidata: (3.5/3.0 and 2.5 size groups)
N. tenella : (2.5/2.0 and 1.6 " ")
E. gibboides : (3.0 and 2.5 size groups)

Mean feeding intensity appears to increase with size for:

T. orientalis : (CS++ 71% for the 3.5 S.G.
48% for the 3.0 S.G.)
T. aequalis : (CS++ 79% for the 2.5 S.G.
63% for the 2.0 S.G.)
N. boopis : (CS++ 38% for the 3.5/3.0 S.G.
28% for the 2.5 S.G.)
E. diomedae : (CS++ 95% for the 2.5/2.0 S.G.
81% for the 1.6 S.G.)

We might therefore conclude that there is a positive correlation 163
betweem variations in feeding intensity and the size of the organism whenever such situation occurs.

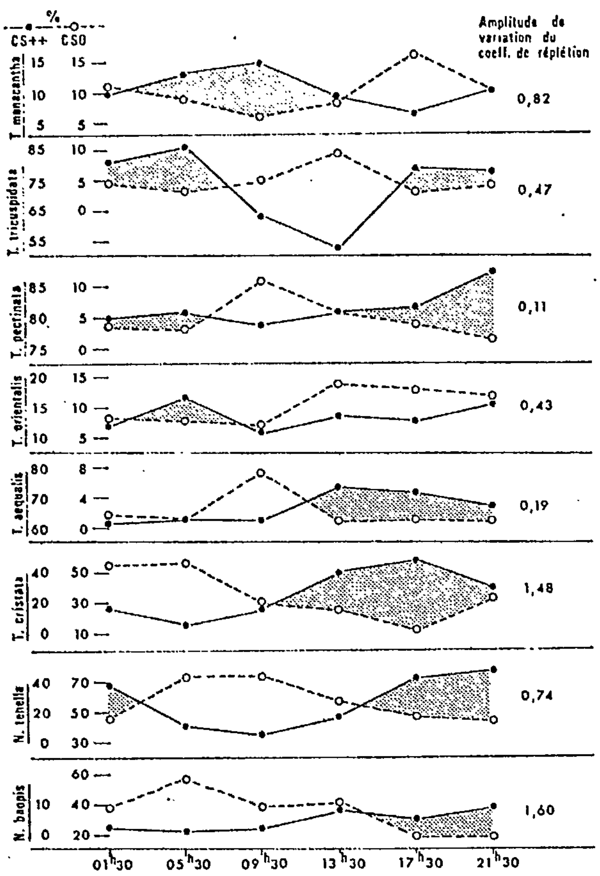


Fig. 73. — Variations nycthémérales du rythme nutritionnel : pourcentages d'estomacs vides (o : CSO) et plus de demi-pleins (• : CS++) aux différentes heures.
Fig. 73. — Fluctuations of the fullness of stomachs at the different times of the day : percentages of animals showing empty (—— o —— : CSO) and more than half-full (—— • —— : CS ++) stomachs.

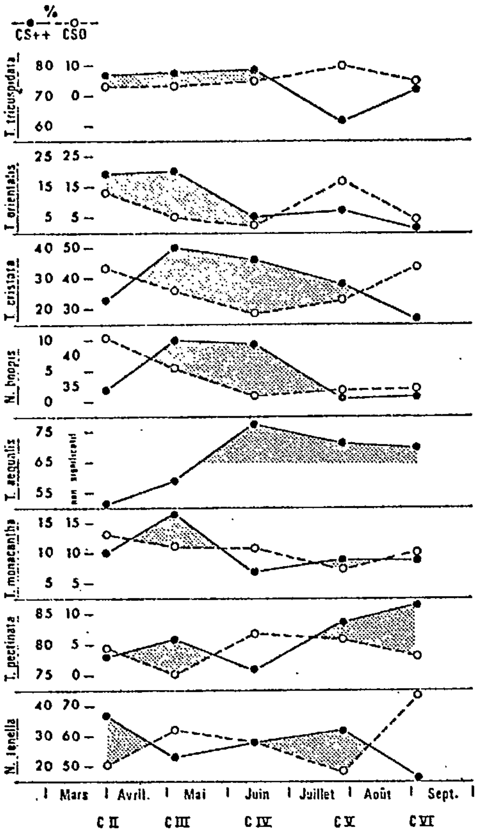


Fig. 74. — Variations saisonnières de la réplétion stomacale moyenne pour 8 espèces du Pacifique équatorial ouest (170° E) : pourcentages d'estomacs vides (o : CSO) et plus de demi-pleins (• : CS ++) aux différentes saisons.
Fig. 74. — Seasonal fluctuations of feeding intensity for 8 species of the western (170° E) equatorial Pacific : percentages of animals showing empty (—— o —— : CSO) and more than half-full (—— • —— : CS ++) stomachs at the different seasons.

Regarding the type of food ingested, we noted a slight increase in the amount of animal matter ingested as the size of the organism increased; this was true in the case of T. tricuspidata, E. diomedae and N. flexipes (although very few specimens were available for the latter) as Table 62 indicates.

Such difference might have been more pronounced had we also examined larvae and juveniles which likely depend more on phytoplankton as a source of food. The adults of other species examined did not show any appreciable change in their diet related to size; this fact was previously observed for M. norvegica (Fisher and Goldie, 1959) and T. raschii (Mauchline, 1966 b).

TABLE 62

Type of food ingested as related to size of organism

		A	VA	V
T. tricuspidata	3.5/3.0	23 %	51 %	26 %
	2.5	18 %	47 %	35 %
E. diomedae	2.5/2.0	42 %	35 %	23 %
	1.6	28 %	50 %	22 %
N. flexipes	2.5	92 %	8 %	0
	2.0	62 %	19 %	19 %

4.3. Variations in stomach fullness and nature of stomach contents in terms of sex and ovarian maturity

There was no obvious difference in the mean stomach fullness or in the nature of stomach contents between males and females. Any disparity noted occurred between the different species and changed according to the expedition being considered.

On the other hand, for all species we noted a very slight tendency to more intense feeding and increased preference for animal matter during ovarian maturation. However, the only obvious correlation was noted for N. tenella. Females of this species carry their eggs after spawning and it appears that this behaviour very seriously hampers them in their search for food. The following percentages, related to stomach fullness and shown in Table 63, were noted for the various stages of ovarian maturation:

TABLE 63

Mean stomach fullness as related to stage of ovarian maturation for N. tenella

	St I-II	St III-IV	Eggs being carried
CS O............	53 %	14 %	66 %
CS + +.........	28 %	70 %	14 %

Note the intensification of feeding during ovarian maturation, followed by a sharp drop after spawning when the females carry their eggs.

4.4. Seasonal variations in stomach fullness

Our data on seasonal variations was obtained only on the "Cyclone"
expeditions, as only CA I of the "Caride" series was used to study feeding
habits. Hence, only a six-month period was covered. Furthermore, as the 165
type of food ingested was not examined in the material drawn during the
"Cyclone" expeditions, the only available data concerns stomach fullness
(shown in figure 74). We noted a very definite, but very low, fluctuation
in stomach fullness for T. tricuspidata, T. orientalis, N. boopis, T. cristata and T. aequalis. The situation was rather confused in the case of T. monacantha, T. pectinata and N. tenella. On the whole for these 8 species, more intense feeding appears to occur from April to July than during March and August-September, as shown in Table 64.

TABLE 64

Seasonal variations in rate of stomach fullness for 8 species of the western Equatorial Pacific.

Month	Number of species having a higher rate of stomach fullness than the mean
March	3
April	6
May	7
June	6
July	6
August	4
September	2

Given the fact that the period considered was much too short, it is difficult to know whether these facts apply to the actual situation or to a random one.

5. SUMMARY OF FEEDING HABITS

We defined earlier (§ 3) the trophic levels of the species and therefore have a general idea of their source of food. We also discussed peak

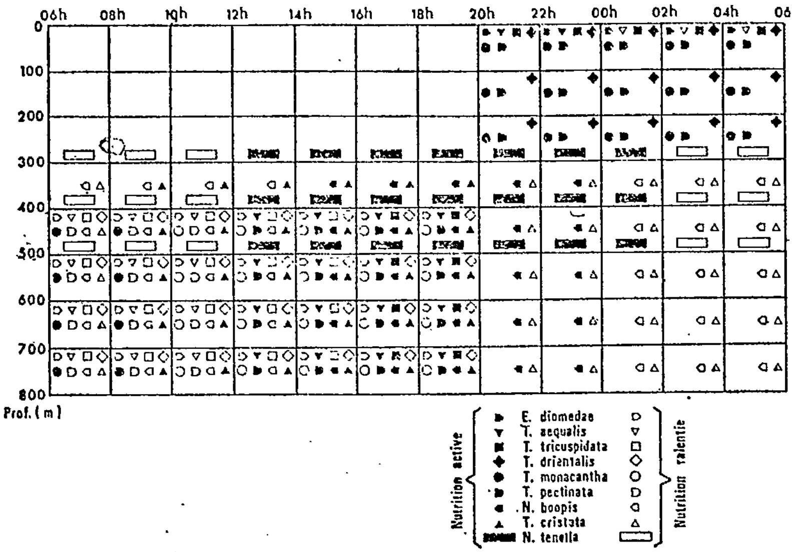


Fig. 75. — Schéma spatio-temporel de la nutrition pour 9 espèces du Pacifique équatorial ouest.
Fig. 75. — Depth-time nutritional diagram for 9 species of the western equatorial Pacific (black symbols : active feeding — White symbols : slackened feeding).

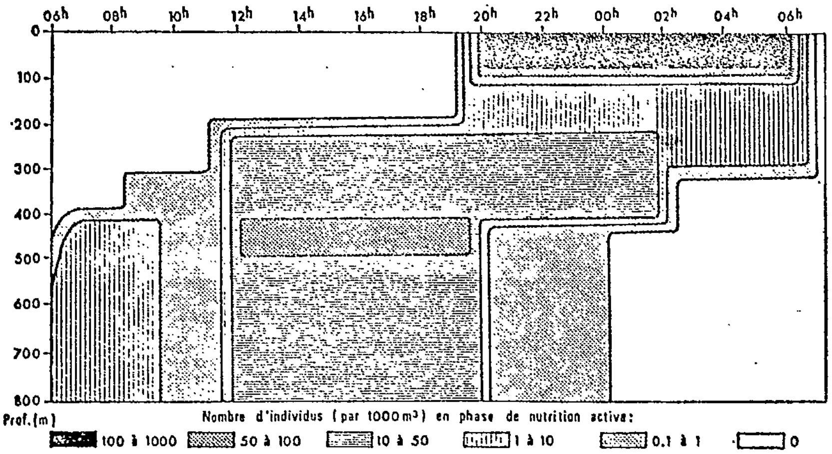


Fig. 76. — Intensité globale de la prédation exercée par les 9 espèces.
Fig. 76. — Depth-time diagram of the intensity of the predation exerted as a whole by the 9 species : numbers of individuals, per 1000 m³ of water, showing active feeding.

feeding times (§ 4.1.). Finally, in Chapter 4 (Vertical Distributions) we identified the habitat of each species. For 9 of the species, we now have all the information required to outline the space and time factors affecting their feeding habits (fig. 75). In order to evaluate the degree of predation carried out by all 9 species, the relative density of each species (shown in Table 9, Region C - Chap. 3) must also be taken into account:

E. diomedae, for example, represented by 984 individuals per 1000 m^3 forms a much larger group of predators than T. pectinata the density of which is only 0.6 individuals per 1000 m^3. Taking this factor into account, we may then estimate the amount of predation which populations can support within the different layers during the course of a day (fig. 76). Note two well defined preying periods: during the afternoon (1200 - 2000 hours) in the intermediate layers (300-600 m) and at the surface (0-100 m) during the night (2000 - 0600 hours); however, note also that predation during the night in the subsurface is ten times more intensive that that which populations found in the intermediate layers are subject to during the latter part of the day. 166
Few species are feeding, not only in the upper layers during the day (0-300 m; 0600 - 2000 hours) and at greater depths by night (300-800 m; 2200 - 0600 hours), which is logical as at such times these zones are relatively deserted, but also during the first part of the day (0600 - 1200 hours) in the deeper strata. We might recall that we are concerned here only with migratory species, whether mesopelagic or bathypelagic, and not with the smaller surface organisms (for instance, of the genus Stylocheiron) which perhaps have different feeding habits.

6. TROPHIC STRUCTURES OF POPULATIONS IN THE DIFFERENT GEOGRAPHICAL ZONES 167

The trophic level of the main species being known, it was then possible to specify that of the populations of Euphausiids observed in the various zones investigated, by determining for each one for example, the extent to which the total population preys upon minute zooplankton. This was done by adding the products of trophic levels for each species by the size of its population (in %) compared with the total population of the zone investigated. This amounted to somewhat estimating the percentage of carnivorous

TABLE 65

Trophic structures of populations
p = percentage in relation to total population

Species	Trophic Levels A+(VA/2)	p [A+(VA/2)]							
		Zone A		Zone B		Zone C		Zone D	
		p		p		p		p	
T. tricuspidata..........	38	0,4 %	15,2	1,5 %	57,0	0,4 %	15,2	3,5 %	133,0
T. orientalis............	93	0,1 %	9,3	0,1 %	9,3	—	—	—	—
T. pectinata............	73	—	—	0,1 %	7,3	—	—	0,3 %	21,9
T. monacantha..........	78	0,1 %	7,8	0,1 %	7,8	0,1 %	7,8	—	—
T. aequalis.............. *T. subaequalis*.......... *T. obtusifrons*...........	99	1,5 %	148,5	2,9 %	287,1	—	—	35,4 %	3 504,6
S. abbreviatum..........	96	2,5 %	240,0	16,7 %	1 603,2	3,7 %	355,2	18,3 %	1 756,8
E. diomedae............ *E. brevis*............... *E. mutica*...............	57	48,4 %	2 758,8	37,4 %	2 131,8	30,8 %	1 755,6	10,0 %	570,0
E. paragibba...........	7	4,3 %	30,1	9,0 %	63,0	3,7 %	25,9	0,5 %	3,5
N. tenella..............	52	6,6 %	343,2	3,5 %	182,0	1,1 %	57,2	2,3 %	119,6
N. microps............. *N. atlantica*............	60	5,6 %	336,0	6,9 %	414,0	2,6 %	156,0	8,6 %	516,0
N. gracilis.............	85	3,6 %	306,0	1,2 %	102,0	7,2 %	612,0	0,2 %	17,0
N. flexipes.............	80	—	—	0,4 %	32,0	0,1 %	8,0	1,6 %	128,0
N. boopis...............	98	0,2 %	19,6	0,4 %	39,2	—	—	0,4 %	39,2
B. amblyops............	22	—	—	—	—	—	—	0,1 %	2,2
TOTAL...............	—	73,3 %	*4 215*	80,2 %	*4 936*	49,7 %	*2 993*	80,8 %	*6 812*

species within the different populations. We used the data on the fauna of each zone given in Table 9 which indicates estimated actual populations. Results appear in Table 65. No estimates are available for Zone E because only one species E. eximia makes up 88% of the total population; the trophic level of this species is unknown. For other zones, we obtained trophic levels for:

73.3%	of	individuals	in	Zone A
80.2%	"	"	"	Zone B
49.7%	"	"	"	Zone C
80.8%	"	"	"	Zone D

The trophic levels of Zones A, B and D are well defined, while half 168
of that of the population inhabiting Zone C could not be determined. However, all the species from this region for which the trophic level remains unknown are very minute species: E. tenera, S. carinatum, S. affine, S. longicorne, and S. elongatum, and therefore, these species very likely feed mostly on

vegetable matter. According to calculations, the mean trophic level of these 5 species $\Sigma\,[A + (VA/2)]$ must be greater than 50 if the order in which regions A to D in Table 65 is to be altered. Considering this as an unlikely possibility, we assumed that the data given in Table 65 expresses the most probable situation. Therefore, for the entire Euphausiid population, the amount of animal food ingested decreases progressively from Zone D to Zone B to A to C; in other terms, the number of carnivores in the populations of these zones decreases according to the same order.

Our knowledge of trophic levels therefore completes and confirms our assumption discussed in the chapter dealing with zoogeography and further defined in our study on the ecology (Diversity). Zone D (Central Tropical Pacific) offers indeed the fewest resources and is inhabited by many species (high diversity) among which carnivorous species predominate; these characteristics are less pronounced in Zone B and are completely the reverse in the equatorial region which is much more plentiful and supports a few species of a low trophic level represented by numerous individuals. The density of the equatorial populations, their low diversity and low trophic level becomes more pronounced as one progresses from west (Zone A) to east (Zone C); it would appear logical to assume that these characteristics are even more pronounced in Zone E, i.e., that the most prominent species E. eximia is essentially phytophagous.

In any case, the zoogeography, ecology and trophic structures discussed in the foregoing pages give a very coherent description of Euphausiid populations in the Equatorial and South Tropical Pacific. In diagram form, a summary of the data can be expressed as follows:

Zones		D B A C E	
	−	Density of populations	+
	+	Diversity	−
	+	Mean trophic level	−

These results agree with recent research carried out in the tropical environment (Petipa, Pavlova and Sorokin, 1971; Timonin, 1971).

B. PREDATION

1. EUPHAUSIIDS AS A SOURCE OF FOOD

I. IMPORTANCE IN TERMS OF NUMBER

In certain oceans, Euphausiids may be considered as the vital organisms upon which rests the entire biological balance. The most obvious situation occurs in the Antarctic Ocean where Euphausia superba which feeds directly on phytoplankton, is the prime source of food for whales, seals, penguins, birds and very possibly for many fish (Ruud, 1932; Hardy and Gunther, 1939; Nenoto, 1966; Burukovskiy and Yagarov, 1967, etc.); due to the exceptional position of E. superba, all authors considered this species as the key organism in the Antarctic. To these predators may perhaps shortly be added the one predator who will prove to be most efficient of all: this species viewed as a phenomenally large biomass, of which apparently some 100 to 500 million tons could be commercially hauled in annually (as compared with the present annual world haul of 70 million tons), its high food value presented in the form of an economically profitable high-quality flour useful as livestock feed, has led man to closely study the possibility of directly using this resource (Burukovskiy, 1967; Sasaki, Inoue and Marsuike, 1968; Marty, 1969; Braxton, 1971).

Disregarding the ultimate situation existing in the Antarctic Ocean, Euphausiids are also considered as a prime source of food for many fish of commercial value such as herring and cod, as we shall discuss in the following chapter. Their commercial role in tropical and equatorial seas is much more difficult to define because considerably less investigation has been carried out in these environments and because pelagic fish are less sought in commercial fishing, their feeding habits therefore remaining relatively unknown. Although Knox (1970) claimed that the South Pacific undoubtedly contained the largest undeveloped reserves of the world oceans, nothing or very little is actually known about these pelagic populations (Clupeidae, Carangidae, etc.), with the exception of deep-sea tuna (Japanese and Korean fishing industry) and especially of anchovies found along the coasts of South America which alone provide 16% of world supplies (Kasahara, 1970).

Under these circumstances, no precise figures can be estimated, but it is nevertheless possible to determine fairly accurately the potential food source created by Euphausiids in these regions. Given the total amount of material collected during the "Cyclone" expeditions, for each 0-1200 m oblique IKMT tow, Euphausiids formed on the average 7.7% of the total biomass, the remainder being micronektonic fish (55%), other groups of crustaceans (22%) and other taxa (15%). The composition of IKMT hauls from this region is given in figure 77. Our estimate agrees closely with that of other authors (King and Demond, 1953; Blackburn, 1966 and 1968; Timonin, 1969). In terms of number, Ponomareva (1966) stated that, between 0 and 10 m, the density of Euphausiids per 1000 m^3 amounted to 100-500 in an equator- 170
ial zone, but was less than 100 in tropical zones; according to our own estimates for the entire 0-1200 m layer, there are 2465 and 476 Euphausiids per 1000 m^3 in the equatorial and tropical environments respectively (cf. Table 9, Chap. 3, mean for regions A-C and B-D). We might recall however that the greater productivity of warmer seas (rate of growth, virtually permanent and faster reproductive cycles) minimizes the differences in relative abundance between tropical and frigid zones, which appear considerable when considering only biomasses.

Whatever the case may be, density of population is only one of the parameters determining the position of an organism within its habitat: its value as a source of food and conditions whereby it is available or

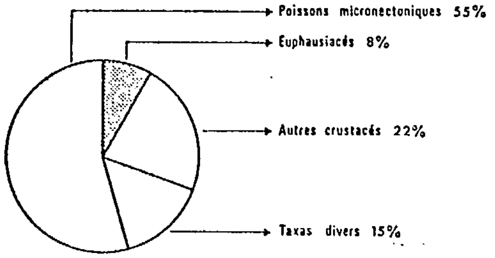


Fig. 77. — Composition moyenne des récoltes du chalut pélagique IKMT, en biomasse (organismes gélatineux non compris).
Fig. 77. — Average composition in biomass of IKMT samples (excluding gelatinous organisms).

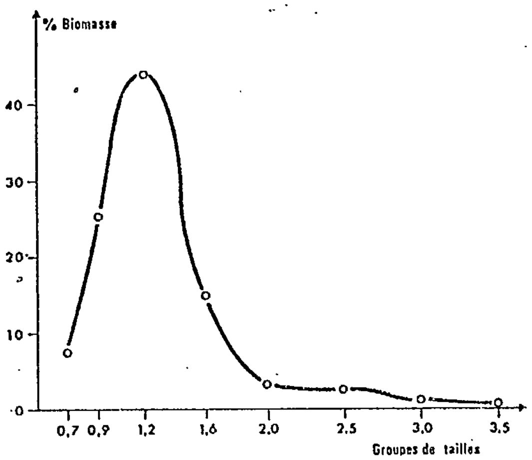


Fig. 78. — Répartition en tailles de la biomasse des Euphausiacés.
Fig. 78. — Size distribution of the biomass of Euphausiids (0.7 to 3.5 = Size groups).

unavailable to possible predators must also be taken into consideration.

2. IMPORTANCE IN TERMS OF FOOD VALUE

Recent studies by Soviet and Japanese scientists (Burukovskiy, 1967; Sasaki, Inoue and Marsuike, 1968; Marty, 1969) have demonstrated the high food value of "krill" which can be processed into a flour of excellent quality useful for feeding livestock. Human consomption does present a few problems, however, due to the amount of chitinous material; nevertheless, it has already been produced in the form of paste or powder (called "sea spice") which can provide a valuable source of protein in the human diet (Braxton, 1971). It has also been known for some time that Euphausiids are exceptionally rich in Vitamin A (Fisher, Kon and Thompson, 1953 and 1955) and Vitamin B_{12} (Hirano et al, 1964).

3. AVAILABILITY

Having discussed the quantities of Euphausiids available and their value as a source of food, the conditions under which they can be used by possible predators must be examined.

3.1. Size ratios

The relationship between the size of the predator and that of its prey is one of the prime factors required to establish trophic relationships. We shall discuss in the following chapter that it is indeed possible in most cases to draw a direct correlation between the length of the predator and the type or size of organism used as its source of food. It is therefore important to determine the distribution of the Euphausiid biomass throughout the various size groups in order to estimate which predators will prey upon each individual size group. We shall also mention which species are most abundant within each size group; i.e., important to a given type of predator.

3.1.1. Distribution of biomass within individual size groups

Table 66 gives the estimated biomass of Euphausiids per 1000 m^3,

TABLE 66

Estimated biomass per 1000 m^3 (in mg), from data obtained from 89 stations on the "Cyclone" expeditions (Zone A: western Equatorial Pacific).

Species Espèces / Tailles S.G.	3.5	3.0	2.5	2.0	1.6	1.2	0.9	0.7	Total	(1)
T. cristata.........	32	3	4	1	—	—	—	—	40	0,3 %
T. tricuspidata.....	1	24	138	110	63	29	11	3	379	2,9 %
T. orientalis.......	17	25	25	12	20	13	2	—	114	0,9 %
T. monacantha.....	24	39	19	12	16	10	2	—	122	0,9 %
T. pectinata.......	21	13	11	11	10	5	—	—	71	0,5 %
T. aequalis........	—	1	29	109	190	100	23	1	453	3,5 %
S. carinatum......	—	—	—	—	—	—	17	23	40	0,3 %
S. abbreviatum....	—	—	1	9	69	104	29	6	218	1,7 %
S. maximum......	12	28	36	27	19	10	3	—	135	1,0 %
S. elongatum......	—	—	—	—	—	13	37	1	51	0,4 %
S. affine..........	—	—	—	—	—	—	37	57	94	0,7 %
S. longicorne......	—	—	—	—	3	29	49	11	92	0,7 %
E. diomedae.......	—	—	—	19	914	3 504	2 086	320	6 843	52,9 %
E. paragibba......	—	—	—	—	63	416	74	11	564	4,4 %
E. tenera..........	—	—	—	—	—	—	271	543	814	6,3 %
N. tenella.........	—	—	1	13	280	736	200	11	1 241	9,6 %
N. microps........	—	—	8	60	175	256	254	40	793	6,1 %
N. gracilis.........	—	—	—	1	27	400	174	—	602	4,7 %
N. sexspinosus.....	5	3	1	—	1	1	—	—	11	0,1 %
N. boopis.........	2	12	41	43	53	48	11	1	211	1,6 %
B. amblyops.......	4	10	8	6	10	5	2	—	45	0,3 %
TOTAL.......	118	158	322	433	1 913	5 679	3 282	1 028	12 933	—
(2)..........	0,9 %	1,2 %	2,5 %	3,3 %	14,8 %	43,9 %	25,4 %	7,9 %	—	—

(1) Percentage of total biomass represented by each species.
(2) Percentage of total biomass represented by each size group.

according to species and size groups, obtained from material drawn during eighty-nine 0-1200 m stations on the "Cyclone" expeditions (Zone A). In terms of species, note that E. diomedae alone accounts for over one half of the total biomass. With respect to size distribution, note that 43.9% of the total Euphausiid biomass is composed of animals of the 1.2 size 172
group, i.e., 12 to 15 mm long and weighing 11 to 20 mg; 25.4% are organisms of the 0.9 size group (9 to 12 mm long and weighing 4 to 11 mg) and 14.8% belong to the 1.6 size group (15 to 18 mm long and weighing 20 to 37 mg). On the whole, Euphausiids ranging in length from 9 to 18 mm and weighing from 4 to 37 mg account for 84% of the Euphausiid biomass in this region of the Pacific.

The distribution of the species within the biomass is given in figure 78.

TABLE 67

% (in biomass) of each species within different size groups.

	3.5	3.0	2.5	2.0	1.6	1.2	0.9	0.7
T. cristata	*27,1*	1,9	0,1	—	—	—	—	—
T. pectinata	*17,8*	*8,2*	3,4	2,5	0,5	0,1	—	—
N. sexspinosus	*4,2*	*1,9*	0,1	—	—	—	—	—
T. orientalis	*14,4*	*15,8*	*7,8*	2,8	1,0	0,2	0,1	—
T. monacantha	*20,3*	*24,7*	*5,9*	2,8	0,8	0,2	0,1	—
S. maximum	*10,2*	*17,7*	*11,2*	*6,2*	1,0	0,2	0,1	—
B. amblyops	*3,4*	*6,3*	*2,5*	1,4	0,5	0,1	0,1	—
N. boopis	1 7	*7,6*	*12,7*	*9,9*	2,8	0,8	0,3	0,1
T. tricuspidata	0,8	*15,2*	*42,9*	*25,4*	3,3	0,5	0,3	0,3
T. aequalis	—	0,6	*9,0*	*25,2*	*9,9*	1,8	0,7	0,1
N. microps	—	—	2,5	*13,8*	*9,1*	*4,5*	*7,7*	3,9
S. abbreviatum	—	—	0,1	*2,1*	*3,6*	*1,8*	0,9	0,6
N. tenella	—	—	0,1	3,0	*14,6*	*13,0*	*6,1*	1,1
E. paragibba	—	—	—	—	*3,3*	*7,3*	*2,3*	1,1
N. gracilis	—	—	—	—	1,4	*7,0*	*5,3*	—
E. diomedae	—	—	0,1	4,4	*47,8*	*61,7*	*63,6*	*31,1*
S. elongatum	—	—	—	—	—	0,2	*1,1*	0,1
S. longicorne	—	—	—	—	0,2	0,5	*1,5*	*1,1*
S. carinatum	—	—	—	—	—	—	0,5	*2,2*
S. affine	—	—	—	—	—	—	1,1	*5,5*
E. tenera	—	—	—	—	—	—	8,3	*52.8*

3.1.2. Proportion of each species within each size group

Table 67 indicates, for each size group, the proportion of each species within the total biomass. Note that, depending upon the size of the organisms, a small number of species, in the order of 5, accounts for the greater portion of the total biomass. Figure 79 shows the distribution of the species according to size groups expressed as a percentage of the total biomass; depending upon the size of prey chosen by a given predator, the abundance of the different species for the particular predator can be determined. Note the two well defined groups: the genera Thysanopoda and Nematobrachion in addition to Stylocheiron maximum and Bentheuphausia amblyops which predominate among larger sizes up to the 2.0 size group. Beginning from the 1.6 size group among smaller species, note the predominance of the genera Euphausia, Nematoscelis and Stylocheiron (except for S. maximum).

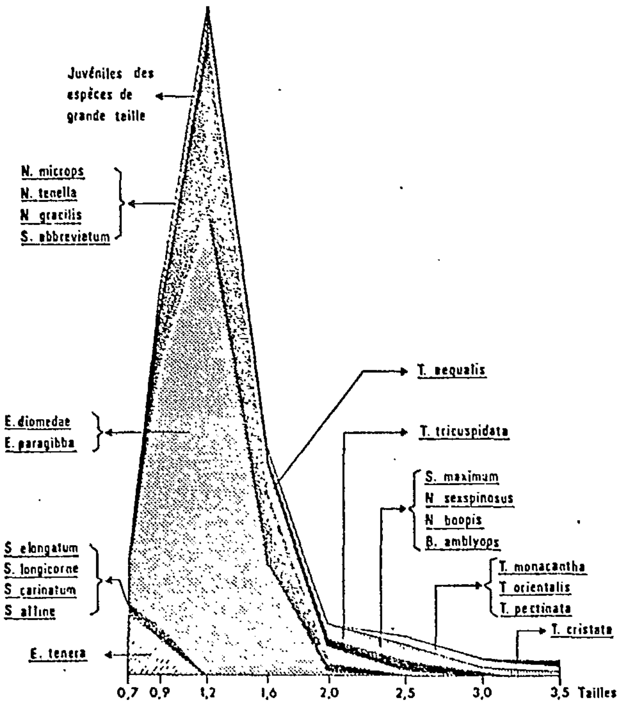


Fig. 79. — Importances relatives des espèces, en biomasse, dans les différents groupes de tailles.
Fig. 79. — Relative importance of species (in biomass) in the different size groups.

3.2. Biotope overlapping 173

The overlapping in time and location of the habitats of both predators and their prey is obviously a necessary condition to establishing predation relationships.

With respect to Euphausiids, Ponomareva (1963) noted that migratory species largely escape their most active potential predators: large planktivorous fish appear to locate their prey visually and therefore do not search for food in the deeper layers, nor during the night. Many species have thus only to contend with the less active preying of meso- or bathypelagic fish. According to studies being conducted at present at the Numea laboratory as well as to other studies dealing with the feeding habits of tunas (excluding perhaps _Euthynnus (Katsuwonus) pelamis_ or Skipjack), Euphausiids are very seldom found in their stomachs, while other organisms of similar morphology and size, Amphipods in particular, are found in large quantities. It would appear that this is due to the fact that tuna feed mainly in the subsurface layers (0-400 m) during the day at a time when large Euphausiids, seemingly a desirable prey, have deserted this zone (cf. Chap. 4, fig. 49). We shall also demonstrate in the following chapter that migratory species, dwelling by day at depths greater than 400 m (cf. Chap. 4, Table 29), escape surface feeders which are in turn eaten by tuna. Euphausiids therefore occupy an important position in food chains depending upon their vertical distribution during the day. 174

By referring to vertical distributions described earlier (cf. Chap. 4), an estimate of the species and Euphausiid biomass available during the night within each layer (Table 68) can be obtained. Note that 75% of the biomass is concentrated in the 0-160 m layer, 23% between 160 and 300 m; beyond 300 m, only 27% of the Euphausiid biomass remains at this depth during the night (note that these estimates, partly obtained from hauls on the 175

TABLE 68

Vertical distribution, according to species and size, of the biomass during the night in terms of depth (in mg per 1000 m^3).

		% présents	3.5	3.0	2.5	2.0	1.6	1.2	0,9	0,7	Total	%
Couche 0-160 m layer	*E. diomedae*....	100 %	—	—	—	19	914	3 504	2 086	320	6 843	71,0 %
	E. paragibba...	100 %	—	—	—	—	63	416	74	11	564	5,8 %
	E. tenera.......	100 %	—	—	—	—	—	—	271	543	814	8,4 %
	T. tricuspidata..	100 %	1	24	138	110	63	29	11	3	379	3,9 %
	T. aequalis.....	100 %	—	1	29	109	190	100	23	1	453	4,7 %
	S. carinatum...	100 %	—	—	—	—	—	—	17	23	40	0,4 %
	S. affine........	70 %	—	—	—	—	—	—	26	40	66	0,7 %
	N. microps.....	40 %	—	—	3	24	70	102	102	16	317	3,3 %
	T. monacantha..	25 %	6	10	5	3	4	3	—	—	31	0,3 %
	T. pectinata....	25 %	5	3	3	3	2	1	—	—	17	0,2 %
	T. orientalis....	25 %	4	6	6	3	5	3	—	—	27	0,3 %
	S. abbreviatum.	15 %	—	—	—	1	10	15	4	1	31	0,3 %
	N. gracilis......	10 %	—	—	—	—	3	40	17	—	60	0,6 %
	TOTAL. mg	—	16	44	184	272	1 324	4 213	2 631	958	9 642	75 %
	TOTAL. %	—	0,2 %	0,5 %	1,9 %	2,8 %	13,7 %	43,7 %	27,3 %	9,9 %	—	
Couche 160-300 m layer	*S. affine*........	30 %	—	—	—	—	—	—	11	17	28	1,0 %
	N. microps.....	60 %	—	—	5	36	105	154	153	24	477	16,3 %
	T. monacantha..	75 %	18	29	14	9	12	8	1	—	91	3,1 %
	T. pectinata....	75 %	16	10	8	8	8	4	—	—	54	1,8 %
	T. orientalis....	75 %	13	19	19	9	15	10	1	—	86	2,9 %
	S. abbreviatum.	85 %	—	—	1	8	59	88	25	5	186	6,3 %
	N. gracilis......	90 %	—	—	—	1	24	360	157	—	542	18,5 %
	S. longicorne...	100 %	—	—	—	—	3	29	49	11	92	3,1 %
	S. maximum....	100 %	12	28	30	27	19	10	3	—	135	4,6 %
	N. tenella.......	100 %	—	—	1	13	280	736	200	11	1 241	42,3 %
	TOTAL. mg		59	86	84	111	525	1 399	600	68	2 932	23 %
	TOTAL. %		2,0 %	2,9 %	2,9 %	3,8 %	17,9 %	47,7 %	20,5 %	2,3 %	—	
Couche 300-800 m layer	*S. elongatum*...	100 %	—	—	—	—	—	13	37	1	51	14,7 %
	T. cristata......	100 %	32	3	4	1	—	—	—	—	40	11,5 %
	N. boopis.......	100 %	2	12	41	43	53	48	11	1	211	60,8 %
	B. amblyops....	100 %	4	10	8	6	10	5	2	—	45	13,0 %
	TOTAL. mg		38	25	53	50	63	66	50	2	347	2,7 %
	TOTAL. %		11,0 %	7,2 %	15,3 %	14,4 %	18,2 %	19,0 %	14,4 %	0,6 %	—	

"Cyclone" expeditions carried out in the western Equatorial Pacific only slightly differ from those given in Chap. 4 obtained from material collected with the Larval Net in the Central Equatorial Pacific: our estimates were then 75%, 19% and 6% for each bathymetrical layer respectively). In the western Equatorial Pacific (Zone A), these percentages correspond approximately to 10 g/1000 m^3 (wet weight) between 0 and 160 m, 3 g/1000 m^3 between

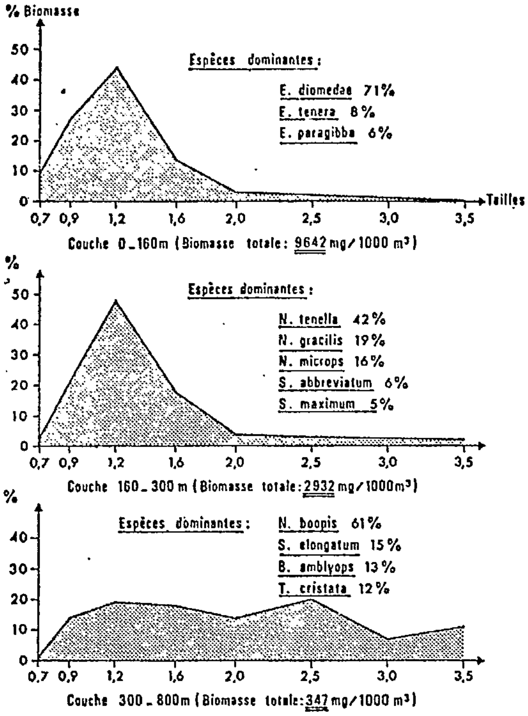


Fig. 80. — Répartition nocturne en tailles de la biomasse des Euphausiacés dans les différentes couches bathymétriques (en % de la biomasse de chaque couche) dans le Pacifique équatorial ouest (170° E).
Fig. 80. — Size distribution of the Euphausiid biomass occupying by night the different bathymetric layers (0-160 m, 160-300 m, 300-800 m) in the western equatorial Pacific, with indication of the dominant species and of the value of the whole Euphausiid biomass (in mg/1000 m³) in each layer.

160 and 300 m, and 0.3 g/1000 m^3 beyond 300 m. We noted furthermore that the most prominent species and the modal size groups differed according to depth: while the genus Euphausia accounted for 85.2% of the Euphausiid biomass between 0 and 160 m during the night (E. diomedae, E. tenera, E. paragibba), the genus Nematoscelis (N. tenella, N. gracilis, N. microps) forms 77.1% of the biomass in the 160-300 m layer; figure 80 gives the range, according to size groups, of these organisms available to predators in these three bathymetrical zones. This diagram might be compared against that shown in Chapter 4 (fig. 46B), established from samples drawn in the Central Equatorial Pacific among which individuals smaller than 1.2 were not included (hence, the absence of minute species such as N. tenera).

3.3. Distribution characteristics

Although less important than the two preceding factors, the type of distribution particular to a given species affects to an appreciable extent their potential use as a source of food: swarming species (E. diomedae,

T. tricuspidata, S. abbreviatum and possibly E. eximia and E. fallax) form a concentration of individuals encouraging fast and mass attacks by predators. To mention again the situation of the Antarctic Ocean, authors have 176
often pointed our that only large swarms of E. superba enable animals such as whales to find sufficient amounts of food; likewise, only such behaviour will enable man to capture these organisms under economically viable conditions.

A spread of individuals therefore results in less intensive predation while, on the same token, it minimizes the contribution of the species to the economy of their biotope.

II. MAJOR PREDATORS ON EUPHAUSIIDS IN THE EQUATORIAL AND SOUTH TROPICAL PACIFIC AND CONTRIBUTION OF EUPHAUSIIDS TO THE ECONOMY OF THESE REGIONS

In this last section we shall attempt to determine the contribution of Euphausiids to the economy of the Equatorial and Tropical Pacific, i.e., to define, in terms of both quantity and type of food, where Euphausiids belong in the food chains of pelagic species inhabiting these regions.

The difficulties involved in such research readily come to mind: there are hundreds, possibly thousands, of marine species likely to use Euphausiids as a source of food; even a brief analysis of their feeding habits would imply examining several dozens of stomach contents. Furthermore, these predators cover a wide range of organisms, from minute plankton such as Chaetognaths to large pelagic species such as Skipjack tuna Euthynnus (Katsuwonus) pelamis. It would therefore be difficult to cover the entire range. Our own material was adequate for organisms at either end of the range of potential predators: macroplankton-micronekton and the larger tuna and bonitos. There is a gap in our data for the intermediate fauna of cephalopods and fish 10 to 50 cm long, among which some would likely be collected by midwater trawls larger than an IKMT 10 and among which we might expect, by analogy with the situation described in papers on temperate seas, a high proportion of predators on Euphausiids.

Regardless, we shall proceed with our study of Euphausiids and their relationship to two important elements of food chains in the Equatorial and Tropical Pacific: micronekton and tuna, extending our study on the latter to include the feeding habits of fish upon which tuna themselves feed.

1. REVIEW OF PAPERS ON PREDATORS OF EUPHAUSIIDS

Similarly to the subject itself, literature on this topic is both very extensive and very scattered; in most cases, Euphausiids are mentioned only in a study on one of their predators and an appreciation of their own contribution can be obtained only by gathering a large amount of scattered and fragmentary information. We shall not mention either their relationship to whales, seals, penguins or birds of frigid zones or their potential use by man: we briefly mentioned these points earlier which, in fact, do not apply to the regions with which we are concerned.

1.1. Zooplankton to some extent feed upon Euphausiids; given their generally minute size, we might assume that such organisms only occasionally prey upon Euphausiids. Marshall (1954) and Fraser (1962) pointed out that Siphonophores, Ctenophoran and Chaetognaths feed upon Euphausiids; Bieri (1961) noted that their eggs and larvae form 12% of the food of Velella.

1.2. Micronekton use Euphausiids as a source of food even more extensively. Among them, three main categories of predators were identified:

— large decapod crustaceans, Sergestides and Carides, certain among which (Pandalus jordani, Pasiphaea pacifica, Sergestes similis) appear to use Euphausiids as one of their prime sources of food (Renfro and Pearcy, 1966;

Pearcy, 1970; Lagardère, 1971; Judkins and Fleminger, 1972).

— micronektonic fish (2-10 cm) the preying activity of which is extensive given their great numbers. Paxton (1967) examined the contents of 204 stomachs of Myctophids and concluded that 72% of the organisms ingested were Euphausiids; Collard (1970) noted that Euphausiids were present in 62% of the stomachs of 1087 mesopelagic fish belonging to 42 species, for 20% of these Euphausiids constituting the only food. Marshall (1954) mentioned them as a source of food for the micronektonic ichthyfauna; Beebe (1935) and Beebe and Crane (1936) considered them as one of the common prey of deep-dwelling Apodes. Several authors mentioned them as constituting the food of micronektonic fish eaten by tuna, thus indirectly contributing to the food source of the latter (Legendre, 1940; Dragovitch, 1970; Aloncle and Delaporte, 1970).

— Cephalopods are somewhat an enigma: they participate significantly in pelagic food chains (large portion of food for tuna), but virtually all escaped our sampling gear. Furthermore, they grind their prey so much that very few food particles are recognizable. However, it would appear that crustaceans, among which Euphausiids might be included, are a common source of food, at least for larger individuals (Marshall, 1954; Akimushkin, 1963; Voss, 1967). Other authors even consider Euphausiids as the main source of food for many species (Squires, 1957; Fields, 1965; Murata and Araya, 1970).

1.3. <u>Nekton</u>, which should also include certain Cephalopods, concerns mainly fish of commercial value caught in temperate and frigid waters; most of these are from 20 to 50 cm long and consider Euphausiids as one of their favourite prey: Gadids (Raitt, 1968 a and b; Alton and Nelson, 1970; Davies, 1949; Dexter, 1969; Kohler and Fitzgerald, 1969; Micheyev, 1967; Sidorenko, 1963; Zelickman, 1960); Clupeids (Berner, 1959; Frost, 1932; Hand and Berner, 1959; Hardy, 1924; Hickling, 1925; Kohler and Fitzgerald, 1969; Lebour, 1924; 178 Lewis, 1929; Ogilvie, 1934; Rudakova, 1959; Scott, 1924; Zelickman, 1960); Scombrids (Kramer, 1969; Lebour, 1924); Triglids (Holt and Tattersall, 1905; Taberly, 1949); Carangids (Carlisle, 1971; McGregor, 1966; Nepgen, 1957; Reuben, 1968); Gempylids (Blackburn, 1957; Mehl, 1969); salmon is considered as depending largely on Euphausiids (Bakkala, 1970; Allen and Aron, 1957; Manzer, 1969; Ueno, 1968; Okada and Taniguchi, 1971; Kanno and Hamai, 1971), as well as many other fish (Major and Shippen, 1970; Davies, 1949; Micheyev, 1967; Sheard, 1953, etc.) which led Lacroix (1961) to state that the main species of commercial fish depend at one time or another on the abundance of Euphausiids.

Finally, Euphausiids occupy a significant position in the food chain leading to tuna, the main pelagic resource of the inter-tropical Pacific at present. Although constituting a very secondary prey for the Yellowfin *Thunnus (Neothunnus) albacares* and the Albacore *Thunnus (Germo) alalunga* or the Bigeye *Thunnus (Parathunnus) obesus*, they form, as we shall mention later, a major source of food for fish eaten by these large predators (Dragovitch, 1970; Aloncle and Delaporte, 1970; Hiyama and Yasuda, 1957; Iversen, 1962; King and Ikehara, 1956; Legendre, 1940; McHugh, 1952; Reintjes and King, 1953; Rossignol, 1968; Kubota, 1971). Furthermore, certain tuna, among which the Bluefin tuna *Thunnus maccoyii* (Sheard, 1953), small tuna *Euthynnus affinis* (Williamson, 1970) and especially the Skipjack tuna (striped-bellied tuna) *Euthynnus (Katsuwonus) pelamis* (Alverson, 1963) directly consume large quantities of Euphausiids.

As we mentioned earlier in this chapter, our data enables us to specify the position of Euphausiids in the food chains of micronekton caught with the IKMT and of tuna.

2. PREDATORS OF MICRONEKTON CAPTURED WITH THE IKMT

2.1. Review of micronekton captured with the IKMT

We might briefly recall the composition of IKMT hauls because the abundance of each category must be borne in mind when establishing food sources. For instance, on an average expedition such as the 20 stations of the "Cyclone" III expedition, the total biomass (excluding gelatinous organisms) was generally divided as follows:

. fish and fish larvae	55%
. large crustaceans (Carides, Sergestides, Penaeids, Amphipods, Euphausiids, Mysidacids)	30%
. other groups	15%

Euphausiids alone formed one-quarter of the biomass of large crustaceans, or approximately 7.5% of the total biomass of a haul. Note that fish were by far the most abundant category and are, by their very size and swimming ability, most capable of preying upon Euphausiids. We shall therefore stress trophic relationships existing between these two groups and merely mention those existing with other potential predators. 179

2.2. Predators on micronekton other than fish

We mentioned that such predators were mainly Cephalopods and large crustaceans.

Although no traces of Euphausiids were noted in the very finely ground stomach contents of the former, we could not conclude that Euphausiids had not been ingested. During certain expeditions of the R.V. "CORIOLIS", we observed Cephalopods obviously chassing small swarms of Euphausiids which had gathered under the light during night fishing (Rancurel, pers. comm.).

Studies by Renfro and Pearcy (1966); Pearcy (1970), Lagardère (1971) and Judkins and Fleminger (1972) stressed the importance of Euphausiids as a source of food for Carides and Sergestides. We examined the stomach contents of 60 individuals (excluding those with empty stomachs) collected on the "Bora" I, II and III expeditions. Ten of these contained small fragments of Euphausiids accounting for only a small portion of the stomach contents. Our data does not confirm statements set forth by other authors as Euphausiids made up only 5% of the food ingested by the 60 individuals examined. There are very likely major differences between species and regions in the feeding habits of these organisms; only a study specifically dealing with this subject would clarify this point.

2.3. Fish included in the micronekton captured by the IKMT

2.3.1. Identification of the ichthyfauna captured by the IKMT

Table 69 indicates the average composition of the ichthyfauna captured by the IKMT on 282 stations carried out in the Equatorial Pacific; most of these fish were between 30 and 50 mm long.

The predominance of two families is immediately obvious: Gonostomidae and Myctophidae, which account for 97.3% of the total; the only other family represented to some extent was that of Sternoptychidae. Note the extraordinary abundance of the genus Cyclothone (61.8% of total) which creates certain problems of interpretation. In fact, the genus Cyclothone is distinguished from other genera by characteristics placing them somewhat aside from other micronektonic fish: they do not migrate and permanently remain at greater depths, beyond 400 m, and do not rise to the upper layers during the night like most other species. The proportion of such individuals in the hauls is therefore a direct function of the depth being investigated; their presence would have been virtually negligible had we established Table 69 on the basis

TABLE 69

Ichthyfauna captured by the IKMT. % in number. Percentages given in parentheses were obtained after excluding the genus Cyclothone.

FAMILIES, GENERA, SPECIES (*)			%	(%)
GONOSTOMIDAE				
Cyclothone			61,8	—
Vinciguerria			8,2	(21,3)
Gonostoma			0,7	(1,9)
Danaphos			1,0	(2,7)
MYCTOPHIDAE				
Lampanyctus			5,0	(13,5)
dont : *L. hubbsi*	2,3 %	(6,0 %)		
among which *L. niger*	2,2 %	(5,9 %)		
Diaphus			4,6	(12,1)
dont : *D. termophilus*	1,1 %	(3,0 %)		
among *D. regani*	0,8 %	(2,2 %)		
which: *D. lutkeni*	0,7 %	(1,9 %)		
D. fulgens	0,7 %	(1,9 %)		
D. theta	0,3 %	(0,9 %)		
D. schmidti	0,3 %	(0,9 %)		
D. lucidus *D. splendidus*	0,4 %	(1,1 %)		
Notolychnus			3,9	(10,2)
Triphoturus			3,4	(9,0)
Lepidophanes			3,1	(8,1)
Symbolophorus			1,7	(4,6)
Ceratoscopelus			1,4	(3,6)
Hygophum			1,3	(3,3)
Myctophum			0,6	(1,6)
dont : *M. affine*	0,3 %	(0,8 %)		
among which *M. aspersum*	0,2 %	(0,5 %)		
Diogenichthys			0,6	(1,6)
STERNOPTYCHIDAE				
Sternoptyx			1,7	(4,6)
CHAULIODIDAE				
Chauliodus			0,3	(0,8)
BREGMACEROTIDAE				
Bregmaceros			0,3	(0,8)
NEMICHTHYIDAE				
Nemichthys *Serrivomer* *Avocettina*			0,2	(0,5)
DIVERS..... Others			0,1	(0,2)

(*) Identified by J. Rivaton, laboratory technician, and J.R. Praxton, Curator of Fishes at the Sydney Museum.

of tows carried out between 0 and 300 metres, for example. In addition, these fish are never large; this fact restricts the size of their prey. For these reasons, we indicated in Table 69 the composition of the entire ichthyfauna (1st column) and percentages obtained after excluding the genus Cyclothone (2nd column). Note finally that, because of its relatively small size, Cyclothone as a biomass represents a smaller portion of the ichthyfauna, undoubtedly less than 40%.

The category "Others" includes a large number of species which appeared sporadically in the hauls, generally individuals larger than average. The 181 isolated specimens collected would very likely indicate that most of these organisms escape the gear and that our samples are not a true indication of their actual numbers. We therefore conducted a few observations on these large species (Melanostomiatidae, Evermannellidae, Malacosteidae, Stylophoridae, Astronesthidae, Paralepididae...) in order to gain some knowledge of a fauna which would undoubtedly be normally captured by a net larger than the IKMT 10.

On the whole, we noted that the ichthyfauna captured by midwater trawls were composed almost exclusively of migratory species (among others, Myctophidae) or bathypelagic species (Cyclothone, Sternoptyx); the fast-swimming surface species, on the contrary, are almost entirely absent while they form, as we shall discuss in the following section, virtually the entire micronektonic ichthyfauna found in the stomachs of tuna captured by longline fishing.

2.3.2. Food of micronektonic fish captured by the IKMT

2.3.2.1. Preliminary remarks

Identifying stomach contents being a rather difficult task, we cannot claim to have determined with great accuracy to what extent Euphausiids were ingested; we believe that 20% of the stomach contents we identified are rather doubtful. A particle of food well preserved in the stomach gives rise to yet another doubt: the food may have been "artificially" ingested while the animal was entrapped in the net. Wide variations in stomach contents can make it very difficult to interpret observations: for instance, 30 stomachs of *Vinciguerria nimbaria* may have been examined without having found a single trace of Euphausiids; then, in a series of 10 fish Euphausiids were found to form the sole type of food. Under such conditions, it would be difficult to assess to what extent *Vinciguerria* use Euphausiids as a source of food. An accurate estimate would imply examining a large amount of material, practically incompatible with a proper analysis of other species of the ichthyfauna that would also be required if the actual situation is to be known. The solution is to select specimens of each species originating from several different hauls thereby avoiding making generalizations from isolated bits of data.

2.3.2.2. Euphausiids as prey for micronektonic fish captured by the IKMT

Table 70 is a summary of all the observations conducted for this study. Note that the stomach contents of 1923 fish were examined; depending upon whether or not the genus *Cyclothone* is included, the percentage of the IKMT ichthyfauna whose diet was examined amounts to 95.9% or 90.3%. For the most numerous species, at least 60 stomach contents were examined. We shall therefore assume that our data was sufficient.

By adding the products of columns (3) and (6) or (4) and (6) in Table 70, an estimate of the extent to which Euphausiids constitute food for these fish can be obtained: considering all IKMT-collected fish, including *Cyclothone*, Euphausiids account for approximately 8% in volume of the food eaten by the ichthyfauna; excluding *Cyclothone*, their contribution rises to 183
21%, this figure representing fairly well their importance as a source of

TABLE 70

Euphausiids as source of food for micronektonic fish captured by a 10-foot IKMT

Fish	Number of stomachs examined (1)	Average length (mm) (2)	Number (%)		Euphausiids as food	
			(3)	(4)	occurrence (5)	importance (6)
Cyclothone sp	149	30	61,8	—	ε	ε
Vinciguerria nimbaria (13)	113	34	8,2	21,3	0 à 80 % (7)	20 %
Gonostoma rhodadenia	121	81	0,7	1,9	48 %	20 %
Tripholorus microchir	75	32	3,4	9,0	48 %	45 %
Lepidophanes phototborax	63	34	3,1	8,1	8 %	5 %
Lampanyctus hubbsi	75	35	2,3	6,0	73 %	60 %
Lampanyctus niger	88	47	2,2	5,9	47 %	25 %
Lampanyctus festivus (8)	15	87	0,4	1,1	64 %	50 %
Diaphus termophilus	62	37	1,1	3,0	42 %	25 %
Diaphus regani	73	55	0,8	2,2	41 %	15 %
Diaphus lutkeni	71	32	0,7	1,9	31 %	20 %
Diaphus fulgens	76	39	0,7	1,9	14 %	5 %
Diaphus theta (8)	12	51	0,3	0,9	50 %	20 %
Diaphus malayanus *Diaphus elucens* *Diaphus lucidus* *Diaphus splendidus* (8) (9)	30	64	0,7	1,9	74 %	35 %
Notolychnus valdiviae	71	19	3,9	10,2	5 %	ε
Symbolophorus evermanni (13)	100	32	1,7	4,6	61 %	50 %
Ceratoscopelus warmingi	89	26	1,4	3,6	11 %	5 %
Sternoptyx diaphana (13)	461	16	1,7	4,5	5 à 80 % (7)	25 %
Chauliodus sloanei (10)	7	120	0,3	0,9	0	0
Bregmaceros	23	67	0,3	0,7	78 %	75 %
Nemichthys *Serrivomer* *Avocettina* (8) (10)	5	262	0,2	0,5	(11)	
Melanostomias *Eustomias* *Leptostomias* *Flagellostomias* *Photonectes* *Echiostoma* MELANOSTOMIATIDAE (8) (10)	12	117				
Melamphaes (8)	7	52				
Evermannella (8)	7	76				
Malacosteus (8) (10)	12	100				
Stylophorus (8)	5	194				
Astronesthes (8)	3	156			(12)	
Paralepis *Macroparalepis* PARALEPIDIDAE (8)	14	120				
Collybus *Pteractis* *Taractes* BRAMIDAE (8)	56 15 13	42 51 30				
TOTAL	1 923	—	95,9	90,3	—	—

(1) excluding empty stomachs.

(2) suggested value, significance depending upon morphology of fish: A 30 mm Cyclothone can capture only prey smaller than a 16 mm Sternoptyx.

(3) for the entire IKMT-collected ichthyofauna.

(4) excluding the genus Cyclothone.

(Columns (3) and (4) were obtained from Table 69).

(5) percentage of stomachs containing Euphausiids, excluding empty stomachs.

(6) overall estimate of importance of Euphausiids as a source of

TABLE 70

(Notes - cont'd)

food for fish (% in volume of total food) = product obtained by % (mean) of stomach contents consisting in Euphausiids. This estimate is less than that obtained when considering weight.

(7) highly variable depending upon size of fish being considered.

(8) large individuals only.

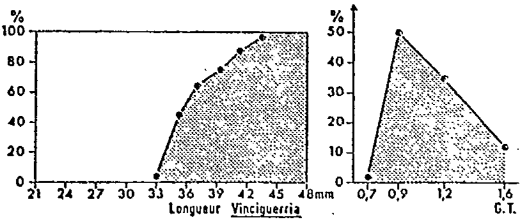
(9) related species, the description of which is under review.

(10) very high percentages of empty stomachs (60 to 85%).

(11) large fish most of which escape the IKMT; gives an idea of the fauna which might be captured by larger gear. Few stomachs being available for examination, no general statements can be made; refer to text for discussion.

(12) the few specimens collected by means of the IKMT were examined with those originating from stomachs of tuna and Alepisaurus (cf. § 3.1.3.).

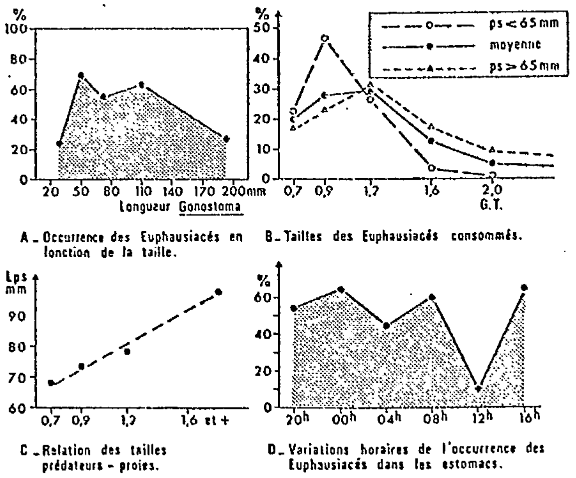
(13) these three species all being eaten by tuna, we added specimens found in stomachs of tuna to our own IKMT material.



A_ Occurrence des Euphausiacés en fonction de la taille.

B_ Tailles des Euphausiacés consommés.

Fig. 81. — Les Euphausiacés dans la nourriture de *Vinciguerria nimbaria* (G.T. : groupes de tailles). Fig. 81. — Euphausiids as food for *Vinciguerria nimbaria*. A : percentages of stomachs containing Euphausiids, depending on the size of fishes. B : sizes (GT : size groups) of Euphausiids ingested.



A_ Occurrence des Euphausiacés en fonction de la taille.

B_ Tailles des Euphausiacés consommés.

C_ Relation des tailles prédateurs - proies.

D_ Variations horaires de l'occurrence des Euphausiacés dans les estomacs.

Fig. 82. — Les Euphausiacés dans la nourriture de *Gonostoma rhodadenia* (ps : poissons. Lps : longueur des poissons). Fig. 82. — Euphausiids as food for *Gonostoma rhodadenia*. A : percentages of stomachs containing Euphausiids, depending on the size of fishes. B : Sizes of Euphausiids ingested by small (— — o — — : <65 mm) and large (- - - - Δ - - - - : > 65 mm) fishes. —— ● —— : average. C : relationships between the length of fishes (Lps) and that of their preys. D: percentages of stomachs containing Euphausiids at the different times of the day.

food for the genera Vinciguerria, Gonostoma, Triphoturus, Lepidophanes, Lampanyctus, Diaphus, Symbolophorus, Sternoptyx and Bregmaceros. In addition, for 6 species of fish, we actually weighed their various preys. This operation brought to light the fact that, in terms of weight, Euphausiids consist in a definitely larger proportion of their total food sources than an estimate of volume would indicate (cf. § 2.3.2.4.).

Euphausiids alone therefore account for nearly one-tenth, in volume, of the food resources for the ichthyfauna collected by the IKMT, and for many of the main genera, they account for one-quarter or one-fifth of the total food ingested, and even more if the amount is considered in terms of weight.

Depending upon the extent to which they consume Euphausiids, the species of fish can be divided into certain categories:

— Cyclothone sp., Notolychnus valdiviae and Chauliodus sloanei ingest hardly any: the first two because of their small size which brings them to prefer copepodophagous sources, the latter being essentially ichthyophagous because of its large size.

— for Lepidophanes phototthorax, Diaphus fulgens and Ceratoscopelus warmingi, Euphausiids form only an occasional source of food : approximately 5% of total volume ingested.

— Vinciguerria nimbaria (older individuals), Gonostoma rhodadenia, Lampanyctus niger, Diaphus termophilus, Diaphus regani, Diaphus lutkeni, Diaphus theta, Sternoptyx diaphana consider Euphausiids as an important prey i.e., 15 to 25% of the total volume of food ingested. Diaphus malayanus, D. elucens, D. lucidus, D. splendidus should also most likely be included in this category as the estimate of 35% for these species can be attributed to the fact that only large specimens were examined. In the following section, the discussion on how Euphausiids are preyed upon by various species will bring out the fact that these estimates are only approximations; in fact, in most cases, the proportion of Euphausiids included in the total food sources of micronektonic ichthyfauna increases with the size of the fish; in particular, juveniles of V. nimbaria and S. diaphana never or hardly ever eat Euphausiids, while older individuals consider them one of their favourite prey.

— finally, for Triphoturus microchir, Lampanyctus hubbsi, Lampanyctus festivus (large specimens only), Symbolophorus evermanni and Bregmaceros, sp., Euphausiids account for at least one half of the total volume of food ingested.

The predator-prey relationships existing between the various species should now be examined to determine their characteristics.

2.3.2.3. Predator-prey relationships existing between the main species of the IKMT-collected ichthyfauna and Euphausiids

For each given species of fish, we shall examine, whenever Euphausiids are considered as a source of food: their occurrence in terms of size of predator, quantity available to the species, size of Euphausiids ingested by various size of fish, species captured and the possibility of nychthemeral variations in predation (occurrence and specific distribution of prey). In 184 our opinion, this procedure is necessary to specify the general characteristics of predator-prey relationships; because it is a rather lengthy procedure, however, we limited ourselves to examining major predators of Euphausiids, others being studied only briefly.

. Vinciguerria nimbaria : we examined first of all 39 stomach contents (S.C.) of large Vinciguerria (average length: 37 mm) found in the stomachs of tuna; 80% of them contained Euphausiids. A second series of observations dealt with 52 smaller fish (average length: 30 mm) collected with the IKMT; only one of these had ingested Euphausiids. We therefore assumed that the frequency of Euphausiids being ingested was proportional to the size of the predator. To verify our assumption, we selected 22 fish collected with the IKMT, chosen among the largest collected (average length: 38 mm): Vinciguerria from 5 stations out of 8 had captured Euphausiids. In total, we had stomach contents of 113 fish of this species, covering a wide range of sizes.

43% of the total 113 stomachs contained Euphausiids. In fact, we noted a very definite correlation with the size of the predator:

occurrence of Euphausiids in Vinciguerria less than 32 mm long : 3%
" " " from 32 to 38 mm long : 47%
" " " over 38 mm long : 81%

The foregoing figures are shown in figure 81. It would appear that once the fish reaches a length of approximately 35 mm, its diet changes quite significantly. In terms of quantity, it was rather difficult to estimate the total proportion of Euphausiids found in V. nimbaria: none whatsoever for the smallest individuals and approximately 50% for individuals over 38 mm long. Therefore, this species generally considered as copepodophagous does in fact rely heavily upon Euphausiids, insofar as older individuals are 185
concerned; the latter are prey for tuna. All specimens had also ingested Amphipodes, Chaetognaths and various types of crustaceans. Ingested Euphausiids belonged mainly to the 0.9 and 1.2 size groups (fig. 81 B).

Although the presence of Euphausiids in the stomach of V. nimbaria is very definitely related to the size of the latter, as we have mentioned, the relationship between the length of the fish and the size of organism captured as prey is not definite. We obtained the following figures:

Euphausiid S.G. Length of fish	0,7	0,9	1,2	1,6
<36 mm................	3 %	58 %	26 %	13 %
36-40 mm................	2 %	51 %	41 %	6 %
> 40 mm................	0	43 %	24 %	33 %

We noted therefore only a tendency to a parallel increase in size of fish and prey.

The species of Euphausiids that were ingested appeared to vary. All Vinciguerria originating from tuna stomachs had captured Stylocheiron (26 S. longicorne, 14 S. abbreviatum). On the other hand, those collected with the IKMT contained only Euphausia diomedae. Although we had too few specimens to determine whether this was an actual or an accidental difference, we wish to propose the following explanation: almost all Vinciguerria collected with the IKMT were captured at night, at a time when this species is generally found between 50 and 300 metres (Legand, pers. comm.), a layer where E. diomedae also dwells. However, we shall discuss in section 3.1. that we have definite indications leading us to believe that, in the Tropical Pacific in any case, longline tuna feed mostly by day; under these circumstances, we might assume that the Vinciguerria found in their stomachs, distributed between 200 and 500 m during daytime, feed at such time on Stylocheiron which occupy the upper portion of those layers. Hence, it is not entirely impossible that V. nimbaria preys upon species of Euphausiids found near the surface during the night (Euphausia) and on those found in the intermediate layers during the day (S. abbreviatum).

. Gonostoma rhodadenia : We examined 121 fish collected during 62 IKMT stations. On the average, Euphausiids were found in 48% of the stomachs. Here again, we found appreciable differences depending upon the size of fish being considered (fig. 82 A): while Euphausiids accounted for 70, 55 and 62% of the food ingested by Gonostoma of average length of 50, 70 and 110 mm respectively, these percentages are only 24 and 27% for fish 30 and 190 mm long. It would then appear that Euphausiids are ingested mostly by individuals of average size; smaller individuals depend largely upon Copepods, larger ones upon other fish. The proportion of Euphausiids in the stomach contents of Gonostoma was rather difficult to estimate as the contents were composed mainly of debris; however, we estimated that they accounted for approximately 20% of the volume of food ingested by this species.

Figure 82 B gives a size distribution of ingested Euphausiids; in 186
addition, the relationship between the size of the predator and that of the Euphausiids it captures is particularly well defined (fig. 82 E).

Euphausiid G.S. Length of fish	0,7	0,9	1,2	1,6	2,0 et plus
< 48 mm	22 %	67 %	11 %	0	0
48 à 65 mm	23 %	27 %	41 %	9 %	0
65 à 82 mm	28 %	21 %	24 %	17 %	10 %
> 82 mm	9 %	26 %	30 %	17 %	17 %

This relationship can also be shown by calculating the average length of fish in which Euphausiids of different sizes were found; this correlation is very definite in the case of Gonostoma, as shown in figure 82 C.

Species of Euphausiids ingested were as follows:

Nematoscelis microps " gracilis	45%
Stylocheiron affine " longicorne	24%
" carinatum	4%
Euphausia diomedae " tenera	22%
Thysanopoda tricuspidata	5%

However, we noted appreciable differences according to the size of fish being considered: the smallest fish captured mostly Stylocheiron, the largest mainly Euphausia, Thysanopoda and Nematoscelis; the number of individuals found in stomach contents were as follows:

Length of fish Euphausiids	< 60 mm	60-80 mm	> 80 mm
Stylocheiron	11	4	4
Euphausia *Thysanopoda*	6	12	7
Nematoscelis	5	11	12

Examination of fluctuations in the feeding activities of Gonostoma indicated that the species fed much less during midday (fig. 82D). Furthermore, all specimens found in the stomachs of the fish caught between 1000 and 1400 hours were Nematoscelis; at other times, all species were present. With reference to fig. 82D, note that the fish prey again in late afternoon (1600 hours); it was earlier noted that Euphausiids are also feeding at this time.

. Triphoturus microchir : 75 full or partially full stomachs were 187
examined, originating from 19 different hauls. On the average, Euphausiids were found in 48% of stomachs, without any direct relationship seeming to exist between size of predator and size of prey:

Fish 26 to 28 mm long : 50%
" 29 to 31 mm long : 59%
" 32 to 34 mm long : 38%
" over 35 mm long : 56%

We therefore assumed that adult Triphoturus, 25 to 40 mm long, generally prey upon Euphausiids; whenever the latter were present, they normally formed approximately 45% in volume of total amount of food (72% in weight) ingested by the species which also preys upon Copepods and other small crustaceans.

Almost all ingested Euphausiids belonged to the smallest size groups (fig. 83A); however, in this case, there was a certain correlation between size of fish and size of prey (fig. 83A):

Euphausiid G.S. Length of fish	0,7	0,9	1,2	1,6 et plus
26-31 mm...............	*64* %	*36* %	0	0
32-34 mm...............	*45* %	*27* %	9 %	*18* %
> 35 mm...............	*31* %	*38* %	*15* %	*15* %

89% of the specimens ingested were of the genus Euphausia, divided somewhat equally between E. diomedae and E. tenera. The vertical distribution of *T. microchir*, 500-700 m by day and 50-200 m by night (Legand, pers. comm.) and its relatively constant preying activity which intensifies around midnight (fig. 83B), would indicate that this species follows the Euphausiids upon which it preys. The peak preying time during the middle of the night might coincide with the time when the fish meet the greatest density of these small organisms in the subsurface layers.

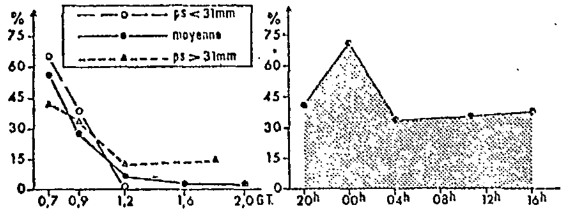
. *Lampanyctus hubbsi* : 75 full or partially full stomachs originating from 16 different stations contained on the average 73% Euphausiids. We noted a regular increase in the presence of Euphausiids related to the size of the fish, such increases tending to stabilize with fish 40 mm long (fig. 84A). We assumed that Euphausiids account for approximately 60% in volume (85% in weight) of all food ingested by *L. hubbsi*, which also feeds upon Copepods and other small crustaceans.

The sizes of Euphausiids ingested are shown in fig. 84B: there appears to be no definite relationship between size of predator andsize of prey; in fact, only fish over 40 mm long captured specimens of the 1.6 G.S. or larger, while all sizes of *L. hubbsi* ingested large quantities of the smallest individuals (0.7 and 0.9 G.S.), such that the average size of prey remains somewhat constant.

The genus *Euphausia* accounted for 94% of the Euphausiids found in the stomach contents (*E. diomedae*: 49%; *E. tenera*: 22%; undetermined *Euphausia*, very likely belonging to either of the preceding species: 23%).

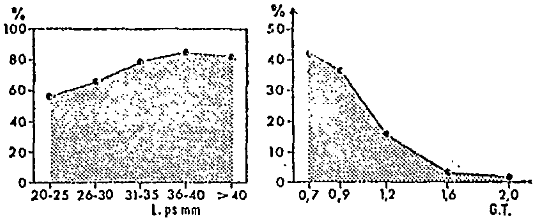
Analysis of hourly fluctuations in the occurrence of Euphausiids 188
in stomach contents indicated a rather remarkable invariability; unfortunately, we have no data for the 1000-1400 hours period and therefore could not establish whether therewas a drop in feeding activity in midday:

2000 h : 70%
0000 h : 71%
0400 h : 69%
0800 h : 83%
1200 h : no data available
1600 h : 77%



A - Tailles des Euphausiacés consommés.
B - Variations horaires de l'occurrence de Euphausiacés dans les estomacs.

Fig. 83. — Les Euphausiacés dans la nourriture de *Tripholurus microchir* (ps : poissons).
Fig. 83. — Euphausiids as food for *Tripholurus microchir.* A : sizes (GT) of Euphausiids ingested by small (— — o — — : < 31 mm) and large (- - - - △ - - - : > 31 mm) fishes. —— ● —— : average B : percentages of stomachs containing Euphausiids at the different times of the day



A - Occurrence des Euphausiacés en fonction de la taille.
B - Tailles des Euphausiacés consommés.

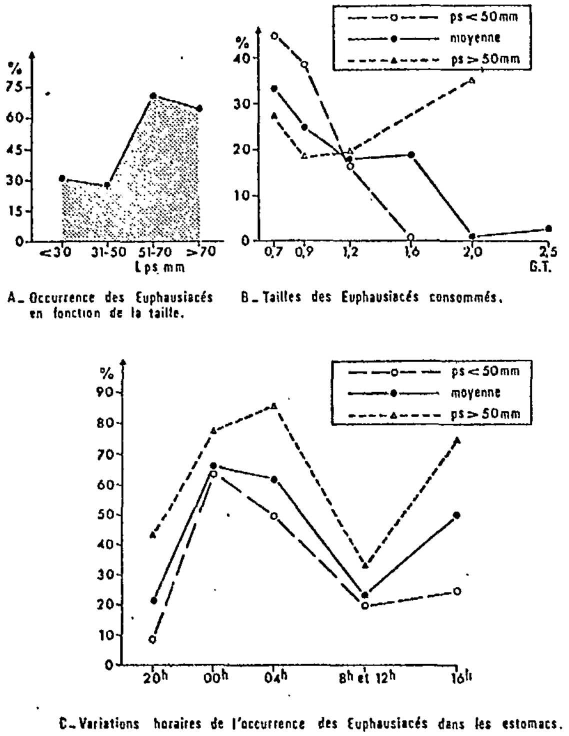
Fig. 84. — Les Euphausiacés dans la nourriture de *Lampanyctus hubbsi* (Lps : longueur des poissons).
Fig. 84. — Euphausiids a food for *Lampanyctus hubbsi.* A : percentages of stomachs containing Euphausiids, depending on the size (Lps) of fishes. B : sizes (GT) of Euphausiids ingested.

According to Legand (pers. comm.), L. hubbsi is found between 600 and 800 m by day and between 50 and 300 m by night; the species ingested (Euphausia) and a rather constant preying activity indicate feeding habits closely related to those of T. microchir, as regards Euphausiids in any case. We might suggest that both species follow the nychthemeral migrations of their prey and feed equally well in the subsurface layers during the night and at greater depths during the day.

• Lampanyctus niger : Examination of 88 full or partially full stomachs originating from 22 different stations led us to assume that, on the average, 47% of stomach contents were composed of Euphausiids and that the latter account for 25% of total volume of food ingested by the species, which also feeds upon Copepods, Amphipods and other small crustaceans. In terms of size of fish, we noted a much more frequent occurrence of Euphausiids among stomach contents of fish over 50 mm long (fig. 85A):

Fish < 30 mm : occurrence of Euphausiids - 31%
" 31-50 mm : " " - 28%
" 51-70 mm : " " - 71%
" > 70 mm : " " - 65%

This would indicate that feeding habits change when fish of this



A_ Occurrence des Euphausiacés en fonction de la taille.

B_ Tailles des Euphausiacés consommés.

C_ Variations horaires de l'occurrence des Euphausiacés dans les estomacs.

Fig. 85. — Les Euphausiacés dans la nourriture de *Lampanyctus niger* (ps : poissons. Lps : longueur des poissons).

Fig. 85. — Euphausiids as food for *Lampanyctus niger*. A : percentages of stomachs containing Euphausiids, depending on the size (Lps) of fishes. B : sizes (GT) of Euphausiids ingested by small (——o—— : < 50 mm) and large (- - - Δ - - - : > 50 mm) fishes. —— ● —— : average. C : percentages of stomachs containing Euphausiids at the different times of the day, in small (——o—— : < 50 mm) and large (- - - Δ - - - : > 50 mm) fishes. —— ● —— : average.

species reach a length of approximately 50 mm; other characteristics of the preying of L. niger upon Euphausiids would confirm this assumption. We noted in fact that the size distribution of ingested organisms (fig. 85B) was somewhat bimodal with the greatest proportion being the 0.7 (33%) and 0.9 (25%) size groups and the second greatest being the 1.2 (18%) and 1.6 189
(19%) size groups. By separately examining the various sizes of fish, we noted that this bimodal tendency was due to a direct correlation between the size of the predator and that of its prey; note in particular that fish less than 30 mm in length capture only Euphausiids in the 0.7 and 0.9 size groups, while only fish over 50 mm long ingest individuals of the 1.6 size group.

Euphausiid S.G. Length of fish	0,7	0,9	1,2	1,6 et plus
< 30 mm	*55 %*	*45 %*	0	0
31-50 mm	*33 %*	*33 %*	*33 %*	0
51-70 mm	*42 %*	*25 %*	8 %	*25 %*
> 70 mm	13 %	13 %	*30 %*	*44 %*

By calculating the average size of fish having ingested Euphausiids of the different size groups, the same distinction into two different lots was obtained:

Average size of fish having ingested individuals of 0.7 S.G. : 50 mm
" " " " " " 0.9 S.G. : 49 mm
" " " " " " 1.2 S.G. : 67 mm
" " " " " " 1.6 & over: 72 mm

This bimodal tendency was also noticeable in the particular species captured; the large variety of species of Euphausiids found in stomachs, 190
shown in the following table, was partly due to the fact that *L. niger* less than 50 mm in length feed mainly on *Stylocheiron* while those over 50 mm ingest mainly *Euphausia* and *Nematoscelis*.

Species	Number	%
N. microps-N. gracilis	9	27
S. affine	7	30
S. microphthalma	2	
S. longicorne	1	
E. diomedae	10	43
E. tenera	2	
T. aequalis	1	
T. tricuspidata	1	
T. monacantha	1	

Hourly fluctuations (fig. 85C) indicated a peak preying time around 0000 and 0400 hours (68% and 62%); feeding activities dropped during the day from 0800 to 1400 (25%) and resumed again more intensely in late afternoon (50% at 1600 hours). Another drop occurred around 2000 hours, at the time when both predators and prey rose to the surface. Again, there was a distinction between the two groups of *L. niger*, differentiated essentially by whether the fish were under or over a length of 50 mm, which displayed different feeding habits; hourly feeding activities of both groups were as follows:

Time Length of fish	20 h	00 h	04 h	08-12 h	16 h
<50 mm	9 %	66 %	50 %	20 %	25 %
>50 mm	43 %	78 %	86 %	33 %	75 %

Note that L. niger juveniles ingest large quantities of Euphausiids only at night (0000 to 0400 hours) in the subsurface, which is logical as the small Stylocheiron (0.7-0.9) upon which they feed do not migrate to deeper layers during the day. Those over 50 mm, on the other hand, which hunt larger prey (1.2 and 1.6 Euphausia and Nematoscelis) encounter them both by night in the subsurface and by day (1600 hours) in the intermediate and deeper layers, although in lesser quantities in the latter instance. For both groups of fish, however, preying activities considerably lessen in midday and also, but to a lesser extent, when the organisms rise to the surface (2000 hours).

- Diaphus termophilus : Examination of 62 stomachs selected from 22 different hauls led us to assume that Euphausiids were present in 42% of stomachs on the average; we also noted that the occurrence of Euphausiids was again a function of the size of the fish (fig. 86A) :

fish ≤ 25 mm : 27% occurrence 191
" 26-35 mm : 23% "
" 36-45 mm : 50% "
" > 45 mm : 58% "

We noted an appreciable difference between Diaphus less than 35 mm, among which only 25% had captured Euphausiids, and those over 35 mm for which this figure rises to 54% on the average. For the entire species, we believe that Euphausiids account for approximately 25% in volume (39% in weight) of total food ingested, which otherwise includes mainly Copepods. Figure 86B gives a size distribution of ingested organisms, centered about the 0.9 and 1.2 S.G.; note the tendency of larger fish to ingest larger prey:

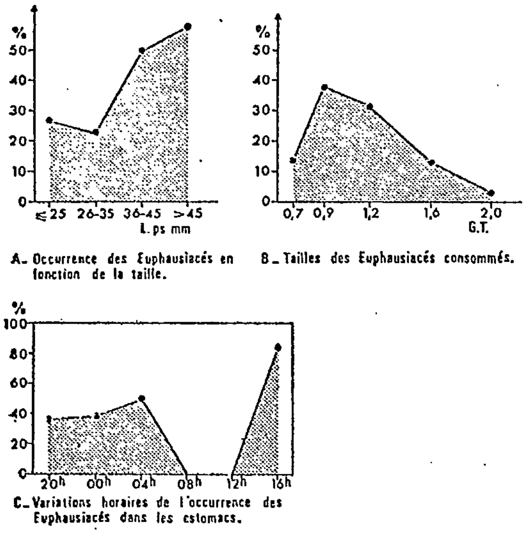
Euphausiid S.G. Length of fish	0,7	0,9	1,2	1,6	2,0
≤40 mm...............	22 %	44 %	22 %	11 %	0
>40 mm...............	11 %	37 %	37 %	10 %	5 %

Species	Number	%
Nematoscelis microps....................... *Nematoscelis gracilis*...................... *Nematoscelis tenella*.......................	10	45 %
Stylocheiron longicorne	2	23 %
Stylocheiron maximum.....................	1	
Stylocheiron affine.........................	1	
Stylocheiron indéterminé..................	1	
Euphausia diomedae......................	2	32 %
Euphausia tenera..........................	1	
Euphausia indéterminé....................	3	
Thysanopoda aequalis......................	1	

A wide range of species are ingested as the following table would indicate. Fish less than 45 mm indifferently consumed the various species while those over 45 mm prefer Nematoscelis almost exclusively.

Hourly variations (fig. 86C) indicated firstly, no preying activity upon Euphausiids during the entire first half of the day and secondly, a 192
pronounced increase in preying during the latter part of the day continuing throughout the night. Note the difference in the particular species being ingested: from 2000 to 0000 hours, Euphausia predominate, the fish being in the subsurface (100-200 m) at this time (Legand, pers. comm.); on the other hand, at either end of the active feeding period, 1600 hours and 0400 hours, there is a predominance of Nematoscelis which might be captured when Diaphus migrate from their daytime habitat (400-600 m) to their night-time environment or inversely.

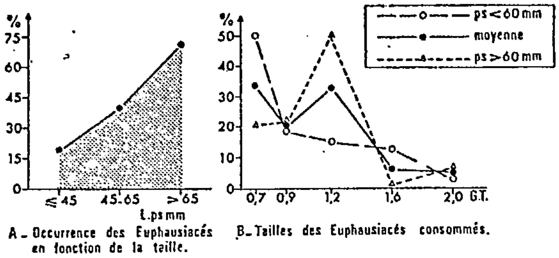
- Diaphus regani : Examination of 73 stomach contents originating from



A. Occurrence des Euphausiacés en fonction de la taille.

B. Tailles des Euphausiacés consommés.

C. Variations horaires de l'occurrence des Euphausiacés dans les estomacs.



A. Occurrence des Euphausiacés en fonction de la taille.

B. Tailles des Euphausiacés consommés.

Fig. 87. — Les Euphausiacés dans la nourriture de *Diaphus regani* (ps : poissons. Lps : longueur des poissons).

Fig. 87. — Euphausiids as food for *Diaphus regani*. A : percentages of stomachs containing Euphausiids, depending on the size (Lps) of fishes. B : sizes (GT) of Euphausiids ingested by small (— — o — — : < 60 mm) and large (- - - △ - - - : > 60 mm) fishes. —— ● —— : average.

Fig. 86. — Les Euphausiacés dans la nourriture de *Diaphus termophilus* (Lps : longueur des poissons).

Fig. 86. — Euphausiids as food for *Diaphus termophilus*. A : percentages of stomachs containing Euphausiids, depending on the size (Lps) of fishes. B : sizes (GT) of Euphausiids ingested. C : percentages of stomachs containing Euphausiids at the different times of the day.

23 different stations indicated 41% occurrence of Euphausiids or an average of 15% of total volume of food ingested by the species, other sources including Copepods, Amphipods and Sergestides.

As in the case of most other species, there was a correlation between the size of the fish and the occurrence of Euphausiids in their stomachs, in fact a very definite correlation (fig. 87 A):

fish $\leqslant$ 45 mm : 18% occurrence
" 46-65 mm : 38% "
" $>$ 65 mm : 71% "

The size distribution of specimens ingested showed a fairly pronounced bimodal tendency (fig. 87B) related, it would appear, to the relationship between size of prey and size of predator: fish less than 60 mm in length ingested mainly Euphausiids of the 0.7 S.G., those over 60 mm mainly those of the 1.2 S.G. This relationship expressed as the average length of fish having ingested organisms from each different size group indicated that individuals of the 0.7 and 0.9 S.G. were found in the stomachs of predators of 57 mm average length, while individuals of 1.2 were the prey of fish 70 mm long.

A large variety of species of Euphausiids were found in the stomach contents:

193

Species	Number	%
Euphausia diomedae	17	61 %
Euphausia tenera	3	
Euphausia paragibba	1	
Euphausia indéterminé	4	
Thysanopoda monacantha	1	
Nematoscelis microps *Nematoscelis gracilis*	3	12 %
Nematoscelis tenella	1	
Stylocheiron affine	11	27 %
Stylocheiron longicorne	1	

However, the particular species selected differed with the category of fish, as pointed out by calculating the average length of fish selecting a given species :

Average length of fish having ingested indiv. of Stylocheiron : 55 mm
" " " " " " Nematoscelis : 61 mm
" " " " " " Euphausia : 71 mm

Analysis of average preying activities gave the following results:

2000 hours : 50%
0000 hours : 47%
0400 and 0800 hours:: 44%
1200 and 1600 hours : 21%

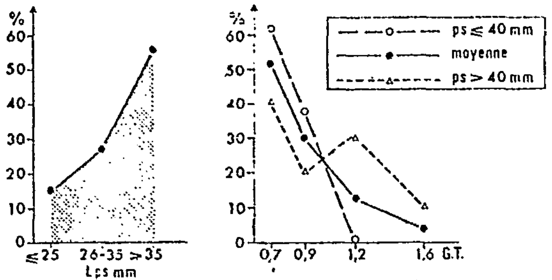
Note that this species of fish feeds upon Euphausiids mostly during the night. Note also that different species are captured depending upon time of day:

Species ingested	Night (20 - 04 h)	Day (08 0 16h)
Stylocheiron	11	1
Euphausia	17	9
Nematoscelis	4	1

The figures obtained for this species suggest that its feeding habits are similar to those of Lampanyctus niger: Diaphus regani juveniles which feed mostly on small Stylocheiron encounter this species only during the night in the subsurface, but not in the deeper habitat of the fish (400-600 m) during the day; the larger fish, however, share the same habitat with Euphausia upon which they feed, both by night in the subsurface and at greater depths by day with the result that hourly fluctuations in preying activites are less noticeable.

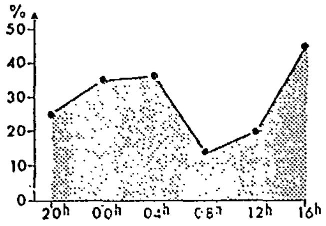
. Diaphus lutkeni : Among the 71 full or partially full stomachs 194
examined, originating from 22 different hauls, 22 contained Euphausiids or 31%. As is generally the case, the presence of Euphausiids was afunction of the size of the fish (fig. 88A):

fish ≤ 25 mm : 15% occurrence
" 26-35 mm : 27% "
" > 35 mm : 56% "



A - Occurrence des Euphausiacés en fonction de la taille.

B - Tailles des Euphausiacés consommés.



C - Variations horaires de l'occurrence des Euphausiacés dans les estomacs.

Fig. 88. — Les Euphausiacés dans la nourriture de *Diaphus lutkeni* (ps : poissons. Lps : longueur des poissons).
Fig. 88. — Euphausiids as food for *Diaphus lutkeni*. A : percentages of stomachs containing Euphausiids, depending on the size (Lps) of fishes. B : sizes (GT) of Euphausiids ingested by small (——o—— : <40 mm) and large (- - - △ - - - : > 40 mm) fishes. —— ● —— : average. C : percentages of stomachs containing Euphausiids at the different times of the day.

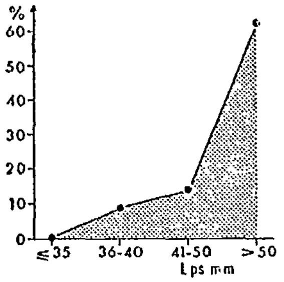


Fig. 89. — Occurrence des Euphausiacés dans les estomacs de *Diaphus fulgens* en fonction de la longueur (Lps) des poissons.
Fig. 89. — Percentages of stomachs of *Diaphus fulgens* containing Euphausiids, depending on the size (Lps) of fishes.

On the average, Euphausiids accounted for approximately 20% in volume (22% in weight) of the food ingested by the species, the remainder being made up mainly of Copepods. A size distribution of the specimens ingested (fig. 88 B) indicates the highest proportion belonged to the 0.7 and 0.9 S.G. However, size also varied with the size of the given predator (fig. 88 B):

Euphausiid S.G. / Length of fish	0,7	0,9	1,2	1,6
≤40 mm................	62 %	38 %	0	0
>40 mm................	40 %	20 %	30 %	10 %

Examination of the particular species ingested revealed a predominance of small organisms dwelling in the upper layers, belonging to the genus Stylocheiron (S. affine, S. longicorne, S. carinatum, S. microphthalma), captured during the night (2000, 0000, 0400 hours); during the latter part of the night (1600 hours), the genus Euphausia constituted the prime prey. Thus, preying follows the usual pattern (fig. 88C) : active preying upon small surface feeders (Stylocheiron) during the night, decreased feeding activity during the earlier part of the day (0800, 1200 hours) and intensified feeding in late afternoon (1600 hours) at the expense of species (Euphausia) dwelling in the deeper or intermediate layers during the day. 195

. Diaphus fulgens : Although 76 stomach contents of fish of this species were examined, Euphausiids were found in only 11 stomachs, i.e., 14%. This low proportion was due to the fact that small fish (less than 40 mm long) were examined, a stage when D. fulgens is essentially copepodophagous. Subsequently, fewer Copepods are found and more Euphausiids, the latter representing some 40% of total food sources of specimens over 50 mm in length; the curve showing the occurrence of Euphausiids (fig. 89) well shows this change, from 0 for fish less than 35 mm to 63% for those over 50 mm.

The small number of stomachs containing Euphausiids did not enable us to establish a relationship between size of predator and size of prey. However, we noted that fish less than 50 mm long had ingested only individuals of the 0.7 and 0.9 S.G., while individuals of the 1.2 and 1.6 size groups were most prominent in the stomachs of fish 50 mm and over. Various species appeared to be selected (N. microps: 3; S. abbreviatum: 3; E. diomedae: 3; E. tenera: 2; S. longicorne: 1; S. suhmii: 1), but here again, a detailed study was not possible for want of more specimens.

. Symbolophorus evermanni : We examined 100 stomach contents collected from 41 different stations. On the average, Euphausiids were found in 61% of stomachs and represented some 50% in volume (65% in weight) of food sources for the species, other sources including Copepods, Amphipods and various crustaceans.

The occurrence of Euphausiids in the stomachs as related to size of fish (fig. 90A) indicated a regular increase ranging from 44% for fish 20-25 mm to 52% for those 25-30 mm, then to 85% for those 30-40 mm and finally 75% of *S. evermanni* 40 to 70 mm long feeding upon Euphausiids. The size of organisms ingested was distributed as shown in figure 90B. The relationship between size of fish and size of Euphausiid ingested is clearly defined (fig. 90B) :

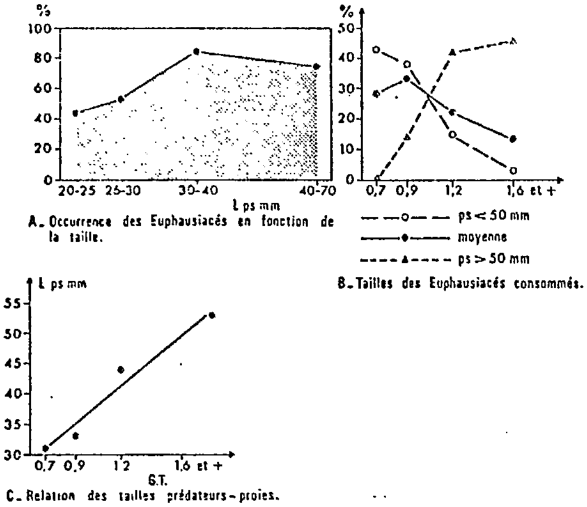
Euphausiid S.G. Length of fish	0,7	0,9	1,2	1,6 et plus
<25 mm................	53 %	33 %	14 %	0
25-50 mm..............	39 %	41 %	16 %	4 %
>50 mm................	0	14 %	41 %	45 %

This correlation can be equally well expressed by calculating the average length of the fish having ingested specimens from the various size groups (fig. 90C): the results are as follows:

Average length of fish having ingested indiv. of 0.7 S.G. : 31 mm
" " " " " " 0.9 S.G. : 33 mm
" " " " " " 1.2 S.G. : 44 mm
" " " " " " 1.6 & over: 53 mm

196 All individuals belonged to the genus *Euphausia*, especially *E. diomedae*. Given rather uninterrupted preying upon Euphausiids (at 2000 hours: 57%; 0000 hours: 59%; 0400 hours: 66%; 0800 hours and 1200 hours: 57%; 1600 hours: 83%), we might assume that *S. evermanni*, having a similar distribution to that of its prey (day: 600-800 m; night: 0-200 m), hunts *E. diomedae* in the subsurface by night as well as in the deeper layers during the day.

. *Sternoptyx diaphana* : A few comments are necessary concerning this particular species. Firstly, it was one of the few, together with *V. nimbaria* and *S. evermanni*, to have been collected in fairly large quantities, in both IKMT hauls and in the stomachs of large predators caught with the longline (tuna, *Alepisaurus*). Furthermore, *S. diaphana* does not migrate to the upper layers during the night; most individuals remain in the 400-800 m layer both by day and by night (Legand, pers. comm.); its behaviour is therefore



A. Occurrence des Euphausiacés en fonction de la taille.

B. Tailles des Euphausiacés consommés.

C. Relation des tailles prédateurs-proies.

Fig. 90. — Les Euphausiacés dans la nourriture de *Symbolophorus evermanni* (ps : poissons. Lps : longueur des poissons).

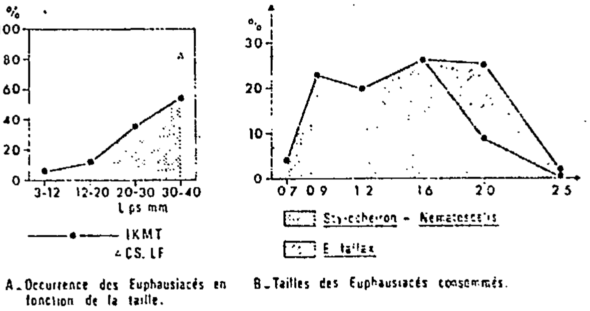
Fig. 90. — Euphausiids as food for *Symbolophorus evermanni*. A : percentages of stomachs containing Euphausiids, depending on the size (Lps) of fishes. B : sizes of Euphausiids ingested by small (- - o - - : <50 mm) and large (- - - △ - - - : > 50 mm) fishes. ——●—— : average. C : relationships between the length of fishes (Lps) and that of their preys.

different from that of the other species considered so far. In addition, its particular morphology (somewhat diamond-shaped, hence its name of "hatchet fish" or "hache d'argent") implies that "length" in this case bears a meaning different from that of other species; thus, a 30 mm Sternoptyx is a much larger fish generally than, for instance, a Cyclothone of similar length.

First of all, we examined the stomach contents of 82 large individuals (average length: 32 mm) found in the stomachs of 30 Alepisaurus (Lancet fish or LF) caught with the longline; for 82% of the fish, Euphausiids were the main food component. Secondly, we examined the stomachs of 379 much smaller specimens (average length: 12 mm) collected during 18 IKMT stations; Euphausiids were present in only 16% of the cases. Once again, we noted a very definite correlation between size of fish and the proportion of Euphausiids ingested (fig. 91A). Our results were as follows:

Fish 3 to 12 mm : 6% occurrence
" 12 to 20 mm : 12% "
" 20 to 30 mm : 36% "
" over 30 mm : 54% " { IKMT
82% " { CS.LF

Euphausiids are therefore very seldom included as a food source



A. Occurrence des Euphausiacés en fonction de la taille.

B. Tailles des Euphausiacés consommés.

Fig. 91. — Les Euphausiacés dans la nourriture de *Sternoptyx diaphana* (Lps : longueur des poissons. —•—: sur *Sternoptyx* pêchés au chalut IKMT. △ : sur *Sternoptyx* trouvés dans des estomacs d'*Alepisaurus*).

Fig. 91. — Euphausiids as food for *Sternoptyx diaphana*. A : percentages of stomachs containing Euphausiids, depending on the size (Lps) of fishes (——•——: fishes caught with IKMT trawl. △ : fishes found in *Alepisaurus* stomachs). B : sizes of Euphausiids ingested.

for individuals of S. diaphana less than 10 mm long, are ingested progressively more frequently as the fish increase in size and account for some 50% of the total volume for the largest individuals (30-50 mm); the remainder of food sources include Copepods, Amphipods, Carides, Annelids, fish larvae and Chaetognaths.

The size and species of Euphausiids used as food were examined only in large Sternoptyx found in the stomachs of LF where they were present in large amounts. Small IKMT specimens had ingested only very small prey (0.7 S.G.) among which E. tenera and E. diomedae were most prominent. From our examination of stomachs of Sternoptyx ingested by the LF, we drew the following conclusions: 73% of the stomachs containing Euphausiids included Stylocheiron, 27% Nematoscelis and 9% only Euphausia. In addition, while the two first genera were regularly present in the form of very few individuals belonging to the 0.9, 1.2 and 1.6 S.G., Euphausia appeared only in a few fish in the form of large swarms of large E. fallax (2.0 S.G.). The two cases must therefore be considered separately (fig. 91B):

Species	Size	Number
S. abbreviatum-S. maximum............	0,9/1,2/1,6	90
S. longicorne..........................		84
N. microps-N. gracilis..................		54
S. carinatum..........................		14
S. elongatum..........................		3
E. fallax..............................	2,0	56

We noted also that Stylocheiron and Nematoscelis were ingested mainly by fish 20 to 42 mm long; on the other hand, the much larger E. fallax were present only in fish 46 to 57 mm long. It would then appear that the very large S. diaphana prefer a different type of prey. Note also that the deep habitat (400-800 m) of this non-migratory species of fish offers it at all times of day, and particularly during daytime, stocks of Stylocheiron and Nematoscelis which are also sedentary or migrate little and remain mostly between 300 and 500 m; E. fallax which migrates to the upper layers during the night is likely the victim of night preying.

The material obtained from the stomachs of Alepisaurus did not make 198 it possible to specify hourly fluctuations in preying activities for the simple fact that we did not know at what time the LF had ingested the Sternoptyx. According to the IKMT hauls, variations in stomachs containing Euphausiids were as follows:

0000 hours : 52%
0400 hours : 38%
0800 hours : 33%
1200 and 1600 hours : 52%

We noted therefore that Sternoptyx ingested Euphausiids rather uninterruptedly, which would appear logical as the biotopes of predators and prey somewhat coincide; there was nevertheless a certain drop from 0400 to 1200 hours and the intensified preying activity noted time and again in late afternoon (1600 hours).

. Other species dependent upon Euphausiids : Isolated specimens of certain other species occasionally appeared in IKMT hauls, but their numbers did not justify a detailed study. We therefore attempted only to determine whether or not these species preyed upon Euphausiids.

The specimens were generally large; the number of stomach contents examined and the proportion of Euphausiids found in the contents are given in Table 70 for Diaphus theta, D. lucidus, D. splendidus, D. malayanus, D. elucens, Lampanyctus festivus and Bregmaceros sp.; we might also add the species *Melamphaes* from which 7 stomachs were examined. All were large consumers of Euphausiids; species of the genus *Diaphus* relied upon them for 20 to 35% (in volume) of their food. This figure would appear even higher for *Eregmaceros* and *Melamphaes*, their stomach contents showing Euphausiids as forming 75% of the total volume; this group was in fact 50% of the volume of food found in the stomachs of 15 *Lampanyctus festivus*.

Mention should be made of the large micronektonic species; we commented earlier (cf. Table 70, note 11) that the IKMT ichthyfauna included few large fish due, at least in part, to the fact that they easily escaped the sampling gear. In spite of their having been caught in few numbers, a study of them was rather interesting in that they provided certain information on the fauna immediately following, in terms of increasing size, that normally captured with the IKMT. *Paralepididae* and *Bramidae* are included among these, but will be discussed later as they form an important food for tuna.

We had a total of 51 full or partially full stomachs of which 30% contained Euphausiids; in fact, there was a high percentage of empty stomachs, from 50 to 85%, among these large species (cf. Table 70 for average length of fish) so that we actually examined 120 stomachs. Depending upon species, we noted highly different feeding habits:

* *Chauliodus* is strictly ichthyophagous; Euphausiids did not appear among their prey.

* *Stylophorus* appears to be exclusively copepodophagous.

* *Malacosteus* consumes Euphausiids as 3 out of 12 stomachs included some (*E. tenera*, *S. elongatum*): they also feed upon Copepods and fish.

* *Astronesthes*: one of the three stomachs examined was entirely filled with 3 large *E. diomedae* (2.0 S.[illegible].); the other two showed only fish debris.

* *Melanostomiatidae* (*Melanostomias*, *Eustomias*, *Leptostomias*, *Flagellostomias*,

Photonectes, Echiostoma) are mainly ichthyophagous; however, 4 out of 12 stomachs contained Euphausiids (E. diomedae: 1.2 to 2.0 S.G.) accounting for approximately 10% of total volume. A few Carides and Sergestides were also present.

* Evermannella also preys upon Euphausiids: 3 out of 7 stomachs examined were almost entirely filled with large E. diomedae (1.6 and 2.0 S.G.).

* Nemichthyidae (Nemichthys, Serrivomer, Avocettina) are major predators of Euphausiids (Beebe and Crane, 1936); however, 85% of the stomachs were empty and we had only 5 stomachs of which 4 were filled exclusively with large T. monacantha and T. orientalis (2.5 and 3.0 S.G.). These large prey are often thicker than their predators with Apodes having a diameter of only a few millimetres and a length of over 30 mm; the ingestion of a large crustacean (Euphausiid or Sergestide) causes distension of the stomach which explains why the fish often ruptured when the prey was being removed.

. Other fish of the micronektonic ichthyfauna : Other than Diaphus fulgens and certain other large micronektonic fish, which we mentioned earlier, only 4 species might be considered as relying little upon Euphausiids for food (cf. Table 70): Cyclothone sp. and Notolychnus valdiviae, both small fish, are mainly copepodophagous (however, small Euphausiids of the 0.7 S.G. such as E. tenera and S. longicorne form 6% in weight of the food of Notolychnus); Ceratoscopelus warmingi and Lepidophanes photothorax consider Euphausiids only as accessory to their food requirements.

2.3.2.4. Summary and general characteristics of IKMT-collected micronektonic fish preying upon Euphausiids.

We have just discussed the preying activities of the main species of migratory or deep-dwelling micronektonic fish (over 90% of IKMT-collected fish) and, at the beginning of this chapter, we estimated that Euphausiids accounted for approximately 8% in volume of the food sources of this fauna (21% if the genus *Cyclothone* is excluded). Furthermore, we might recall that if weight rather than volume is considered, Euphausiids form an even larger proportion of their food. We weighed the various components of the stomach contents of 6 species of fish and obtained the following figures:

200

Fish	Proportion of Euphausiids in relation to total food ingesta	
	In volume (estimate)	In weight
T. microchir....................	45 %	72 %
L. hubbsi.......................	60 %	85 %
D. termophilus..................	25 %	39 %
D. lutkeni......................	20 %	22 %
N. valdiviae....................	ε	6 %
S. evermanni....................	50 %	65 %

Having estimated the quantity of Euphausiids contributing to the food supplies of fish collected with the IKMT, the next step consists in giving a summary of the feeding relationships and pointing out the general features of the predation.

Table 71 gives a distribution of species and size of Euphausiids found in the 1 923 stomach contents which we examined. Note (fig. 92A) that the genus *Euphausia* (especially *E. diomedae* and *E. tenera*) provides 45% of the individuals ingested, the genus *Stylocheiron* 40% and the genus *Nematoscelis* 201 only 13%. Note also that specimens of the genus *Thysanopoda* are almost completely absent because their large size makes them undesirable for such small predators; specimens of *Nematobrachion* are absent for the same reason in addition to their being seldom in this environment. It was rather interesting to note that the order in which the various genera were found in stomach contents is identical to the order of their actual density (cf. chap. on Zoogeography, Table 7). Although predator-prey size ratio and the overlapping of their biotopes, whether or not vertical migrations

TABLE 71

Euphausiids as preyed upon by the IKMT-collected ichthyfauna : individual species and size of specimens found in stomachs.

(A) Species

Species	Number	%
E. diomedae *E. tenera*	296	33 %
*E. fallax**	56	6 %
Euphausia indéterminés	54	6 %
N. microps *N. gracilis* *N. tenella*	118	13 %
S. abbreviatum *S. maximum*	115	13 %
S. affine *S. longicorne*	159	18 %
S. carinatum *S. elongatum* *S. suhmii* *S. microphthalma*	29	3 %
Stylocheiron indéterminés. (undetermined)	54	6 %
Thysanopoda	20	2 %
TOTAL...............	901	—

(B) Size groups (S.G.)

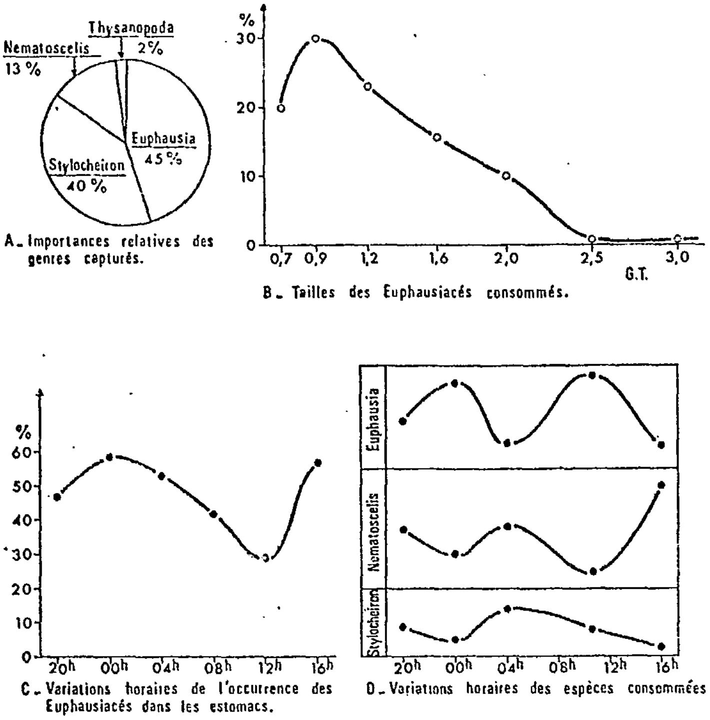
S.G.	Number	%
0,7	204	20 %
0,9	310	30 %
1,2	234	23 %
1,6	170	16 %
2,0*	99*	10 %*
2,5	8	0,8 %
3,0	6	0,6 %
3,5	0	0
TOTAL...	1 031**	—

* swarms of E. fallax (2.0 S.G.) captured by 3 Sternoptyx.

** among which 130 undetermined Euphausiids.

make such overlapping possible, are both factors determining predation, the density of the species in the environment ultimately determined their use as a source of food by the migratory or deep-dwelling ichthyfauna captured by the IKMT.

Examination of the size of Euphausiids ingested (fig. 92B) indicated that this ichthyfauna, generally fish from 30 to 50 mm long, captured individuals of the 0.7 - 1.6 S.G. (the apparently large number of the 2.0 S.G. is due to ingestion of a large number of E. fallax by 3 specimens of Sternoptyx), i.e., from 6 to 18 mm long. Larger Euphausiids are considerably less accessible to these fish. When examining each particular species of 202
fish, we demonstrated how a close relationship existed between the size of the predator and the occurrence and size of its prey; although it was



A. Importances relatives des genres capturés.

B. Tailles des Euphausiacés consommés.

C. Variations horaires de l'occurrence des Euphausiacés dans les estomacs.

D. Variations horaires des espèces consommées

Fig. 92. — Bilan de la prédation exercée vis-à-vis des Euphausiacés par les poissons micronectoniques migrateurs ou profonds capturés au chalut pélagique IKMT.

Fig. 92. — General features of the predation exerted toward Euphausiids by the migrating or deep-living micronektonic fishes caught with the Isaacs-Kidd midwater trawl. A : specific composition of Euphausiids ingested. B : sizes (GT) of Euphausiids ingested. C : percentages of stomachs containing Euphausiids at the different times of the day. D : fluctuations in the nature (genus) of Euphausiids ingested, depending on the time of the day.

generally the case, this fact could not be stated in actual figures because length held a different meaning when fish with very dissimilar morphologies were involved (for instance, a Cyclothone of 30 mm preys very little while a Sternoptyx of similar length can capture large prey).

Hourly fluctuations in the occurrence of Euphausiids in the stomachs of migratory or deep-dwelling micronektonic fish were highly indicative: figure 92C, established from examination of 800 full or partially full stomachs, shows three distinct phases:

— peak preying activity during the middle of the night (2200-0200 hours) progressively decreasing at 0400 and 0800 hours.

— general slump in preying activity during midday (1000-1400 hours).

— very definite increase in preying activity in late afternoon (1600 hours) occurring almost generally among both fish and Euphausiids (cf. Chap. 7 A). A slight drop around 2000 hours very likely coincides with the time when the organisms rise to the upper layers.

The species of Euphausiids ingested was also subject to hourly fluctuations (fig. 92D): note that *Euphausia* is attacked during the night in the upper layers and in the deeper layers by day. *Nematoscelis* is preyed upon most heavily when the fish migrate either upwards (2000 hours) or downwards (0400 hours); this species is also a prime victim in late afternoon when preying intensifies. The case of *Stylocheiron* is less clear, but we might assume that slight variations are due to the inconsistent habits displayed by the fish species. Too few specimens were collected to produce reliable data. It would appear that the smallest organisms (*S. affine*, *S. longicorne*, *S. carinatum*, *S. suhmii*, *S. microphthalma*) are ingested at the surface during the night, while the larger, deep-dwelling (200-500 m) species (*S. maximum*, *S. abbreviatum*) are attacked most heavily when the fish cross their biotope (2000 and 0400 hours).

As a conclusion to this study on the trophic relationships existing between Euphausiids and the migratory or deep-dwelling micronektonic ichthyfauna captured with the IKMT, we wish to point out the main features of their feeding patterns: small fish consume small organisms (0.7-0.9 S.G.) mostly by night in the upper layers (*S. carinatum*, *S. affine*, *S. longicorne*, *S. microphthalma*, *S. suhmii*, *E. tenera*); by day, very few Euphausiids are found in their deep habitat and therefore little preying activity goes on. Larger fish have a much wider choice of prey, from the migratory fauna (especially *E. diomedae*) found in the subsurface at night and at greater depths during the day, to the rather stationary species (*N. tenella*, *S. abbreviatum*, *S. maximum*) dwelling in the intermediate layers (200-500 m) which they encounter during

their migrations upwards (2000 hours) or downwards (0400 hours), as well as 203
in late afternoon (1600 hours). There were fewer hourly fluctuations in the occurrence of Euphausiids in stomach contents when the predator being considered was a large fish.

However, these general tendencies did not imply that they were always valid: for instance, the case of *T. microchir* and *L. photothorax* demonstrated that similar species may have dissimilar food preferences.

3. EUPHAUSIIDS IN THE FOOD CHAIN LEADING TO TUNA

Tuna are practically the only pelagic resource being exploited at present in the Tropical Pacific. We shall consider in turn the major species (Germon, Yellowfin...) captured by longline fishing as well as the bonitos caught by troll fishing along the coasts.

Given the confusion existing at the moment in the nomenclature of tuna (cf. Postel, 1966), we specify hereunder the terms we shall use in this study:

— Germon = *Thunnus (Germo) alalunga* (white tuna)
— Yellowfin = *Thunnus (Neothunnus) albacares* (yellow tuna)
— Bigeye = *Thunnus (Parathunnus) obesus* (obese tuna or Patudo)
— Bonito or Skipjack = *Euthynnus (Katsuwonus) pelamis* (striped-bellied tuna)

3.1. Fish caught by longline fishing

3.1.1. Identification of fish caught by longline fishing and general features of their feeding habits

As a guide, hereunder is a list of fish caught by longline fishing during the 26 stations of the "Calmar" I to V expeditions carried out by the R.V. "CORIOLIS" in the South Tropical Central Pacific (Polynesia):

* G =	Germon	116
* YF =	Yellowfin	37
* BE =	Bigeye	11
* SK =	Skipjack	5

* LF	(Lancet Fish) *Alepisaurus*	8
* PBM	(Pacific Blue Marlin) *Makaira nigricans*	6
* Other species	(*Scombrolabrax*, *Taractes*, *Xiphias*, *Tetrapterus*, *Acanthocybium*, etc.)	24

Note that tuna formed the greatest proportion of the hauls; however, the relative abundance of the two main species (G and YF) depended upon the depth of the fishing line, the latter species being found closer to the surface.

The species *Alepisaurus* merits a brief comment. Although these fish are of no commercial value, a study of them was extremely valuable for two reasons. Firstly, they appear to compete with tuna for the same prey 204 (Legand and Wauthy, 1961, Parin, 1968; Grandperrin and Legand, 1970; Fourmanoir, 1969) and are also a source of food for tuna which appear to consume large quantities of juvenile *Alepisaurus*. Secondly, while the stomach contents of tuna were generally highly digested making the identification of their prey very difficult, the stomach contents of *Alepisaurus* were always perfectly preserved; these fish are excellent collectors of micronekton and provided us with samples of food ingested by tuna in a state which made examination particularly easy. For these reasons, we used mainly the stomach contents of *Alepisaurus* for this part of our work.

TABLE 72

Food of fish captured by longline fishing (% in weight), from expeditions of the R.V. "CORIOLIS", 1956-69.

Predators Prey	G	YF	SK	LF	Others
Fish	50 %	70 %	2 %	53 %	49 %
Cephalopods	33 %	23 %	38 %	22 %	48 %
Crustaceans(1).........	7 %	3 %	50 % (3)	6 %	—
Others (2) and debris .	10 %	4 %	10 %	19 %	3 %

(1) Amphipods and Phronima, Carides, etc.
(2) Heteropods, Pteropods, etc.
(3) Only one stomach content containing a large number of Carides 30 to 40 mm long.

Table 72 indicates the type of food ingested by the main species caught by longline fishing. Note that, except for bonitos in occasional cases, fish and cephalopods account for two-thirds of the total; in order to specify the contribution of Euphausiids in this food chain, the feeding habits of these two groups must be examined.

We briefly mentioned earlier the food sources of Cephalopods. At the moment, the difficulties encountered in this research have not yet been overcome; we can merely point out that crustaceans, which include Euphausiids, are part of their food, at least at certain periods during their lifetime; but we could not ascribe definite figures to their contribution. Identifying the food of fish ingested by tuna was possible however; we shall examine these food sources after briefly discussing where Euphausiids belong among the direct prey of large predators captured by longline fishing.

3.1.2. Euphausiids as direct prey for tuna caught by longline fishing

Table 73 gives a list of Euphausiids found in the stomachs of 218 fish caught by Longline.

Note that Euphausiids are found very little in these large species, in 7 to 11% of tuna stomachs, none in stomachs of Alepisaurus; furthermore, Euphausiids consist in no more than a negligible fraction of the total volume of stomach contents and its direct contribution to the food of tuna can therefore be considered as insignificant, even though large individuals were 205

TABLE 73

Euphausiids found in the stomachs of fish caught by Longline on the "Calmar" I to V and "Diaphus" I and II expeditions.

Predators	No. of non-empty stomachs examined	Occurrence of Euphausiids	Species	S.G.
G.	107	7 %	*T. tricuspidata* *T. cristata*	2,0-2,5 3,5-5,0
YF.	49	8 %	*T. tricuspidata* *E. fallax* *T. cristata*	2,0-3,0 2,0-2,5 5,0
SK.	7	0	—	—
BE.	9	11 %	*T. cristata*	6,0
LF.	23	0	—	—
Divers.	23	4 %	*T. tricuspidata*	2,5

ingested (2.0-6.0 S.G.). However, we frequently found other crustaceans (Carides and Amphipods) similar in size to these large Euphausiids in the stomachs of tuna; we therefore assumed that Euphausiids and tuna do not share the same biotope when the latter are feeding. King and Iversen (1962), Parin (1968) claimed that tuna hunt only by day which unsuccessful nighttime fishing by the Numea laboratory would confirm. Parin (1968) also pointed out that tuna generally catch fish inhabiting the lower portion of the upper layers (*Paralepis*, *Chiasmodon*, *Alepisaurus*, *Bramidae*, *Gempylidae*...) but seldom those related to the DSL, which occupy nevertheless the same biotope during the night. Therefore, it appears very likely (cf. Legand et al, 1971 b) that tuna, distributed between 0 and 400 m, can prey only upon the species remaining at such depths during the day. As we mentioned earlier (cf. Chap. "Vertical Distributions"), large Euphausiids, especially those of the genus *Thysanopoda*, are located below 400 m during the day and reach the upper layers where tuna are found only at night when the latter are not feeding; the fact that their biotopes do not overlap must therefore be viewed as the prime reason why no preying relationship exists between both groups.

3.1.3. Euphausiids as a source of food for fish captured by tuna

Certain authors have often pointed out (cf. in particular King and Iversen, 1962; Legand et al, 1971 b) that the fish consumed by tuna bear practically no relationship with those captured by midwater trawl in the same regions. We have discussed above how the fact that the biotopes do not overlap partially accounts for this disparity; nets capture mostly the ichthyfauna related to the DSL which in fact shares the relatively superficial habitat of tuna during the night when the latter are not feeding; IKMT hauls did produce a few juveniles of species consumed by tuna; adults escaped the gear because of their swimming abilities. Another characteristics of fish consumed by tuna is their wide diversity ranging over some 100 species (Fourmanoir, 1971).

We examined the stomach contents of 299 fish caught by longline (107 G, 104 LF, 49 YF, 11 PBM, 9 BE, 7 SK and 12 others) in which we found 606 identifiable fish; to these 606 fish, we added 587 specimens of S. diaphana, V. nimbaria and S. evermanni collected with the IKMT in order to have more samples, bringing to 1 193 the total number of fish belonging to species ingested by tuna of which we examined the stomach contents. Table 74 lists the main species of these fish and indicates also the number of individuals of which the stomach contents were examined, their average length and their relative abundance in the ichthyfauna ingested by tuna, on the one hand, and by Alepisaurus, on the other.

Note that only 3 species, S. diaphana, V. nimbaria and S. evermanni, are common to both Longline and IKMT hauls (cf. Table 69), the latter collecting only juveniles of the other species and only in very small numbers. Note also that many fish are preyed upon by both tuna and Alepisaurus; however, the latter consumes a large quantity of a Gempylidae (Diplospinus multistriatus), a species which tuna do not seek particularly.

Figure 93 gives a size distribution of the fish. Note that tuna feed mainly upon small individuals (10 to 60 mm), similar in size to those collected with the IKMT, to which must be added larger prey (60 to 130 mm) in a proportion of approximately 10%. The size distribution of Diplospinus multistriatus is given separately; this species is consumed mostly by Alepisaurus which generally selects prey larger than that of the tuna; in fact, Diplospinus and Alepisaurus juveniles account for nearly 40% of the fish they ingest. 208

Table 74 also indicates the contribution of Euphausiids to the food supplies of fish preyed upon by Longline tuna and Alepisaurus; a general

TABLE 74

Fish ingested by Longline tuna and *Alepisaurus* : quantity ingested by their predators and contribution of Euphausiids to their food sources

Fish (identified by P. Fourmanoir)	Number of stomachs examined (1)	Average length mm (2)	Importance		Euphausiids as food	
			tuna (3)	LF (4)	occurrence (5)	importance (6)
GEMPYLIDAE						
Diplospinus multistriatus	134	114	*	28 %	80 %	50 %
Nealotus tripes	18	64	7 %	5 %	28 %	2 %
Lepidocybium flavobrunneum	3	68			(7)	(7)
Gempylus serpens	3	115			(7)	(7)
Promethycthys prometheus	3	95			(8)	(8)
Nesiarchus nasutus	0	—			—	—
NASIDAE : (*Naso*)	11	27	9 %	—	0	0
BRAMIDAE						
Collybus drachme	56	42	11 %	2 %	57 %	20 %
Taractes asper	13	30			33 %	15 %
Pteraclis carolinus	15	51			67 %	20 %
LATILIDAE (*Latilus, Caulolatilus, Hoplolatilus*)	20	31	11 %	—	0	0
OSTRACIONIDAE (*Lactoria diaphana, Ostracion, Rhinesomus*)	1	14	9 %	—	(8)	(8)
CHAETODONTIDAE (*Heniochus, Chaetodon, Centropyge*)	23	20	6 %	—	0	0
CAPROIDAE (*Antigonia*)	4	29	3 %	—	(8)	(8)
CHIASMODONTIDAE						
Chiasmodon	4	39	3 %	—	0	0
Pseudoscopelus	12	81				
PARALEPIDIDAE						
Paralepis et *Macroparalepis*	14	120	2 %	2 %	86 % (8)	70 % (8)
Stemonosudis	1	168				
Lestidiops	7	110				
ALEPISAURIDAE (*Alepisaurus* juvéniles)	24	101	2 %	12 %	8 %	2 %
ANOPLOGASTRIDAE (*Anoplogaster*)	23	28	2 %	5 %	4 %	2 %
GONOSTOMIDAE (*Vinciguerria*)	113 (9)	33	—	7 %	40 %	20 %
STERNOPTYCHIDAE (*Sternoptyx*)	461 (9)	16	12 %	16 %	28 %	25 %
MYCTOPHIDAE (*Symbolophorus*)	100 (9)	28	3 %	—	60 %	50 %
Autres espèces (10)	130	—	20 %	23 %	21 %	10 %
Other species TOTAL	1 193	—	100 %	100 %	—	—

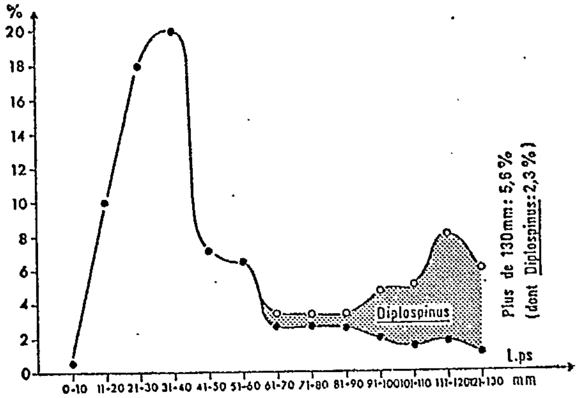


Fig. 93. — Répartition en tailles des poissons trouvés dans les estomacs des thons et des *Alepisaurus* (Lps : longueur des poissons). La répartition en tailles des *Diplospinus*, provenant presque uniquement des estomacs d'*Alepisaurus*, a été figurée séparément.

Fig. 93. — Size (Lps) of the fishes found in the stomachs of Long Line tunas and *Alepisaurus*. Size distribution of *Diplospinus* is shown separately (cumulative diagram) as these fishes originate almost uniquely from *Alepisaurus* stomachs.

NOTES to Table 74

* otoliths of *Diplospinus* were found in tuna stomachs; however, the highly digested stomach contents did not enable us specify any quantity.

(1) excluding empty stomachs.

(2) average length in mm.

(3) and (4) percentage of the various species in relation to the total number of fish ingested by tuna and *Alepisaurus* (Tuna = G, YF and BE).

(5) percentage of occurrence of Euphausiids in their stomachs.

(6) estimate of percentage of total food represented by Euphausiids (in volume). This estimate is lower than that obtained when considering weight.

(7) Too few specimens. Euphausiids present.

(8) Too few specimens. Euphausiids absent.

(9) including specimens captured with the IKMT.

(10) among these various species:

— we found Euphausiids in (number of stomachs containing Euphausiids/total number of full or partially full stomachs examined) :

Acropoma (1/1), *Actinoberyx* (1/2), *Anthias* (2/30), *Aphanopus* (2/3), *Benthodesmus* (3/3), *Beryx* (1/1), *Caranx* (1/2), *Cubiceps* (6/12), *Desmodema* (1/4), *Emmelichthys* (2/2), *Priacanthus* (1/2), *Pristipomoides* (2/3), *Scombrolabrax* (1/5), *Scopelarchus* (5/5), *Stolephorus* (1/2), *Synagrops* (1/2).

— we did not find Euphausiids in (number of empty stomachs examined):

Acanthurus (1), *Arethron* (2), *Balistes* (9), *Caristius* (4), Champsodon (1), *Decapterus* (1), *Diretmus* (3), *Etelis* (1), *Gephyroberyx* (1), *Grammatonutus* (1), *Idiacanthus* (1), *Lophius* (1), *Odontomacrurus* (3), *Phalacomacrurus* (1), *Pontinus* (1), *Pristigeynis* (1), *Psennes* (6), *Ranzania* (1), *Remora* (2), *Scombrosphyraena* (1), *Tetraodon* (2), *Trachichtodes* (1), *Uranoscopus* (1), *Uraspis* (1).

estimate of quantity is obtained by adding columns (3) and (6) or (4) and (6). When considering this sum, the reader must take into account the fact that Euphausiids were actually found more frequently in large Vinciguerria, Sternoptyx and Symbolophorus consumed by tuna than among specimens of these species most of which were small individuals collected with the IKMT.

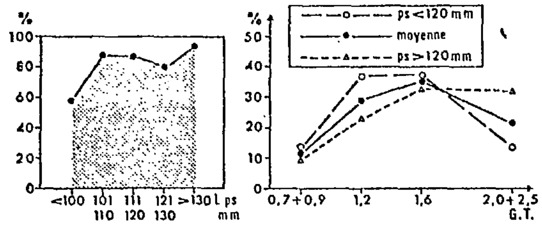
On the whole, the examination of 1 193 stomach contents led to the conclusion that Euphausiids form approximately 10% in volume of the food of fish upon which tuna feed; this amount increases to 20% for prey of Alepisaurus given their important contribution to the food sources of Diplospinus.

Among the ichthyfauna captured by tuna and Alepisaurus, the major predators of Euphausiids are: Diplospinus multistriatus, Bramidae (Collybus, Taractes, Pteraclis), Paralepididae (Paralepis, Macroparalepis), Vinciguerria, Sternoptyx and Symbolophorus. Other species (cf. note (10) in Table 74) also ingest Euphausiids, but in amounts too small to warrant a detailed study.

The preying habits of Vinciguerria, Sternoptyx and Symbolophorus having been examined earlier, those of Diplospinus, Bramidae and Paralepididae should now be considered.

- Diplospinus multistriatus : We had the stomach contents of 134 fish removed from the stomachs of 20 Alepisaurus; 108 among them contained Euphausiids or 80%, perhaps less frequently among Diplospinus less than 100 mm long (fig. 94A). On the average, we believe that Euphausiids account for some 50% in volume (70% in weight) of the food of this species which also feeds upon 209
Copepods, Amphipods, Cephalopods and fish. The size of the specimens ingested was distributed as shown in figure 94B; note also that the larger fish tend to prey upon the larger Euphausiids (fig. 94B):

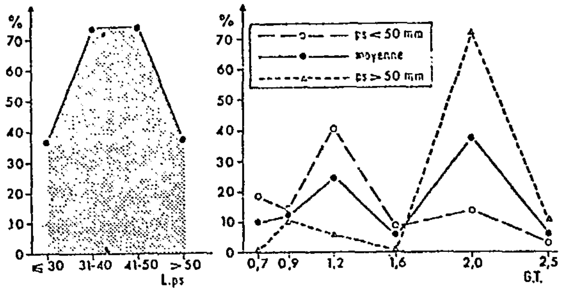
Euphausiid S.L. Length of fish	0,7+0,9	1,2	1,6	2,0+2,5
⩽100 mm...............	*20* %	44 %	*21* %	15 %
101-110 mm............	5 %	47 %	41 %	7 %
111-120 mm............	14 %	*19* %	48 %	*19* %
121-130 mm............	12 %	32 %	28 %	28 %
>130 mm...............	7 %	15 %	41 %	37 %



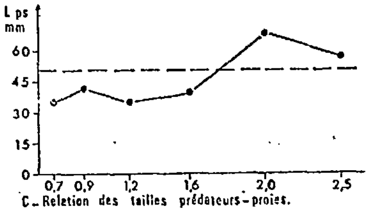
A. Occurrence des Euphausiacés en fonction de la taille. B. Tailles des Euphausiacés consommés.

Fig. 94. — Les Euphausiacés dans la nourriture de *Diplospinus multistriatus* (ps : poissons. Lps : longueur des poissons).

Fig. 94. — Euphausiids as food for *Diplospinus multistriatus*. A : percentages of stomachs containing Euphausiids, depending on the size (Lps) of fishes. B : Sizes (G.T.) of Euphausiids ingested by small (— — o — — : < 120 mm) and large (- - - △ - - - : > 120 mm) fishes. —— ● —— : Average.



A. Occurrence des Euphausiacés en fonction de la taille. B. Tailles des Euphausiacés consommés.



C. Relation des tailles prédateurs-proies.

Fig. 95. — Les Euphausiacés dans la nourriture des *Bramidae* (ps : poissons. Lps : longueur des poissons).

Fig. 95. — Euphausiids as food for the *Bramidae*. A : percentages of stomachs containing Euphausiids, depending on the size (Lps) of fishes. B : sizes (GT) of Euphausiids ingested by small (— — o — — : <50 mm) and large (- - - △ - - - : >50 mm) fishes. —— ● —— : average. C : relationships between the length of fishes (Lps) and that of their preys.

A closer look at the species ingested indicates that 95% of them belong to the genera Stylocheiron and Nematoscelis :

Species ingested	Number	%
S. abbreviatum-S. maximum	156	58 %
S. longicorne	25	9 %
S. carinatum	12	4 %
Stylocheiron indéterminés	9	3 %
N. microps-N. gracilis	56	21 %
E. fallax	7	3 %
E. diomedae	1	
T. tricuspidata	1	

In other words, Diplospinus feeds almost exclusively on species 210 migrating the least to deeper layers; this would suggest that they prey upon Euphausiids only during the day and in the uppermost 250 metres. In fact, by calculating the specific distribution of the fauna within the size range of prey selected by Diplospinus (Table 75), it becomes readily obvious that:

* all Euphausiids found in the stomachs of Diplospinus belonged to species inhabiting the uppermost 250 metres by day;

conversely, all Euphausiids dwelling by day in the uppermost 250 metres were preyed upon by <u>Diplospinus</u>, with the exception of <u>N. tenella</u> which may have been confused with <u>N. microps</u>, these specimens being at times difficult to differentiate in the stomach contents.

TABLE 75

Distribution of species of Euphausiids included in the size range of prey selected by <u>Diplospinus</u> (according to increasing depth by day).

Species	Upper vertical limit by day (m)	% in environment	% in S.C. of Diplospinus
S. carinatum	0	0,2 %	4 %
S. affine	50	0,5 %	ε
S. abbreviatum	50	5 %	58 %
S. maximum	200		
S. longicorne	200	0,6 %	9 %
N. tenella	200	10 %	0
N. microps	250	13 %	21 %
T. tricuspidata	100 à 350	7 %	ε
E. diomedae	100 à 400	43 %	ε
S. elongatum	300	0,3 %	0
E. tenera	350	1 %	0
N. boopis	350	3 %	0
T. aequalis	450	9 %	0
E. paragibba	450	4 %	0
T. monacantha	450	3 %	0
T. orientalis	450		
T. pectinata	450		
B. amblyops	600	0,5 %	0

• <u>Paralepididae</u> : The genera <u>Paralepis</u> and <u>Macroparalepis</u> of this family must definitely be considered as consuming large quantities of Euphausiids. However, the very small number of stomachs examined did not enable us to carry out a detailed study. Any of these fish over 80 mm long escaped the IKMT, such that we were able to examine only 14 specimens removed from tuna stomachs. 12 among them contained Euphausiids or approximately 80% in volume of the stomach contents; all belonged to the species <u>S. maximum</u>, <u>S. abbreviatum</u> and <u>N. microps-N. gracilis</u>. This led us to assume that, like <u>Diplospinus</u>, <u>Paralepis</u> and <u>Macroparalepis</u> prey mainly during the day in the uppermost 200 or 300 metres.

• Bramidae : Euphausiids form some 20% in volume (22% in weight) of the food of this important family; their contribution to the food sources of the 3 main genera Collybus, Taractes and Pteraclis is shown in Table 74. Given the few number of specimens, the data applies to all three genera as their preying action upon Euphausiids appeared to be highly similar. 211

We had a total of 84 stomachs of fish found in 44 stomachs of tuna and Alepisaurus caught by Longline fishing; 46% among them contained Euphausiids or an average of 55% with a higher frequency noted among average size predators (fig. 95A).

A size distribution of ingested organisms (fig. 95B) brings out a bimodal pattern with peaks centered about the 1.2 and 2.0 S.G. Examination of the size of the predators indicates that there is a relation between both distributions:

Euphausiid S.G. Length of fish	0,7	0,9	1,2	1,6	2,0	2,5 3,0
⩽30 mm...............	29 %	7 %	57 %	7 %		
31-40 mm...............	15 %	24 %	35 %	6 %	18 %	3 %
41-50 mm...............	12 %	12 %	30 %	15 %	23 %	8 %
>50 mm...............	0	12 %	6 %	0	72 %	10 %

By calculating the average length of fish having ingested Euphausiids of the different S.G. (fig. 95C), we also noted a change in the diet of fish longer than 50 mm :

Average length of fish having ingested Euphausiids of S.G. 0.7 : 34 mm
" " " " " " 0.9 : 43 mm
" " " " " " 1.2 : 35 mm
" " " " " " 1.6 : 39 mm
" " " " " " 2.0 : 70 mm
" " " " " " 2.5-3.0 : 56 mm

Examination of the species ingested confirmed this change in diet;

the table hereunder gives a distribution of all species of Euphausiids consumed:

Species	Number	%
S. suhmii, S. carinatum...................	20	36 %
S. affine, S. longicorne...................		
S. abbreviatum, S. maximum............	24	
N. microps, N. gracilis...................	12	10 %
T. tricuspidata..........................	57	54 %
T. monacantha..........................	2	
E. diomedae, E. tenera..................	5	
E. fallax................................	3	

However, we noted a definite difference between the small fish which 212 consumed mainly Stylocheiron and Nematoscelis and large fish which preyed upon the larger Thysanopoda :

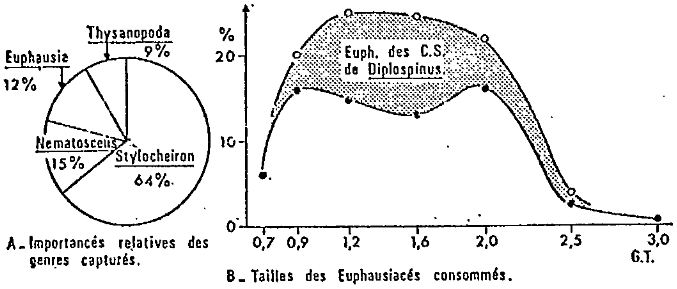
Length of fish Species ingested	⩽30 mm	31-40 mm	41-50 mm	>40 mm
Stylocheiron................ *Nematoscelis*................	64 %	63 %	69 %	15 %
Thysanopoda................ *Euphausia*.................	36 %	37 %	31 %	85 %

All the data on the predation by Bramidae upon Euphausiids tends to establish a distinction between fish less than 50 mm long, which hunt mainly Nematoscelis and Stylocheiron of the 0.7/0.9/1.2 S.G. as well as Copepods, Amphipods, Ostracods and other small crustaceans, and fish over 50 mm long which rely even more upon Euphausiids as a source of food, especially larger individuals of the genus Thysanopoda (T. tricuspidata).

3.1.4. Contribution of Euphausiids to the food sources of Longline tuna

In concluding this study, the species and numbers of Euphausiids contributing to the food chain leading to large pelagic tuna must be specified.

The 919 Euphausiids identified in the stomach contents of fish



A - Importancés relatives des genres capturés.

B - Tailles des Euphausiacés consommés.

Fig. 96. — Bilan de la prédation exercée vis-à-vis des Euphausiacés par les poissons micronectoniques trouvés dans les estomacs des thons et des *Alepisaurus*. Les Euphausiacés ingérés par les *Diplospinus*, qui proviennent presque uniquement des estomacs d'*Alepisaurus*, ont été figurés séparément (diagramme cumulatif).

Fig. 96. — General features of the predation exerted toward Euphausiids by the fishes found in the stomachs of Long Line tunas and *Alepisaurus*. A : specific composition of Euphausiids ingested. B : Sizes (GT) of Euphausiids ingested. Euphausiids found in the stomachs of *Diplospinus multistriatus*, which originate almost uniquely from *Alepisaurus* stomachs, are shown separately (cumulative diagram).

ingested by tuna and *Alepisaurus* were distributed as shown in Table 76. Note that (fig. 96A) the genus *Stylocheiron* was most prominent (64%), followed by the genus *Nematoscelis* (15%); *Euphausia* and *Thysanopoda* accounted for only 12% and 9% respectively. In other words, fish preyed upon by tuna hunt mainly organisms which remain near the surface during the day when 213 migratory species related to the DSL (*Euphausia* especially) are not accessible to them by reason of their deep habitat; this situation leads the fish to depend mainly upon carnivorous species (*Stylocheiron*) while the ichthyfauna related to the DSL feeds largely on omnivorous species (*Euphausia*).

A thorough analysis of Euphausiids consumed by micronektonic fish brings to light a certain independence between the food chains leading to Longline tuna and those of migratory micronekton responsible for the DSL: the former affect surface feeders feeding in the uppermost 300 or 400 metres and having little relation with the migratory fauna, captured by nets or midwater trawls, which dwells at greater depths during daytime.

A size distribution of these Euphausiids (fig. 96B) indicates a predominance of organisms 10 mm (0.9 G.G.) to 20 mm (2.0 G.G.) long. Larger individuals appear to be less accessible to the generally smaller fish (cf.

TABLE 76

Specific distribution of Euphausiids ingested by fish found in the stomachs of tuna and Alepisaurus.

Species	%
S. abbreviatum	35,3
S. maximum	3,2
S. longicorne	18,6
S. carinatum	4,4
S. suhmii	1,4
S. elongatum	0,6
S. affine	0,4
S. microphthalma	0,1
Total *Stylocheiron*	*64,0*
N. microps-N. gracilis	14,8
N. tenella	0,4
Total *Nematoscelis*	*15,2*
E. fallax	9,9
E. diomedae	1,5
E. tenera	0,6
Total *Euphausia*	*12,0*
T. tricuspidata	8,3
T. monacantha	0,4
Total *Thysanopoda*	*8,7*

fig. 93) consumed by tuna.

Figure 97 shows the quantity of Euphausiids contributing to the food chains leading to Longline tuna : although Euphausiids are only a negligible source of food for tuna(s), they account for some 50% in volume of the food of Diplospinus multistriatus which alone forms 15% of the prey 214 of Alepisaurus. We estimated that they form some 10% in volume of the total dietary resources of fish which are in turn captured by tuna, providing the latter with nearly one-half (45%) of their source of sustenance. Although Euphausiids contribute directly to only an insignificant proportion of the food of Longline tuna, they indirectly contribute an important part to the food chains leading to tuna.

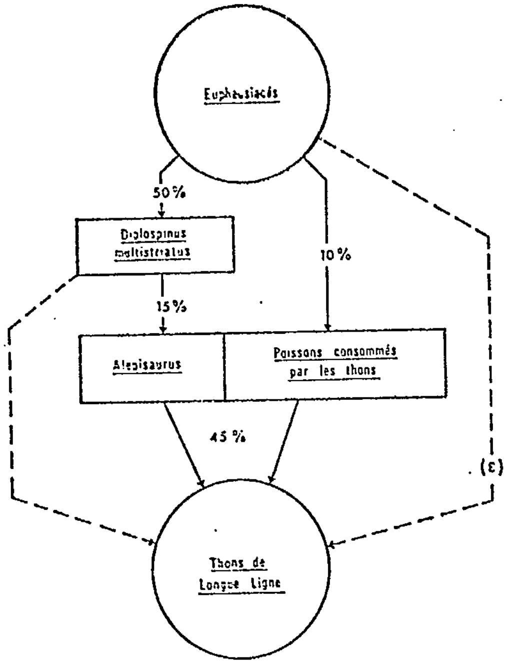


Fig. 97. — Bilan schématique de la position des Euphausiacés dans les chaînes alimentaires qui aboutissent aux grands thonidés pélagiques du Pacifique intertropical. Les pourcentages indiquent le montant de la participation d'un groupe à l'alimentation du maillon suivant.

Fig. 97. — Diagram tentatively suggesting the role of Euphausiids among the food webs leading to the large subsurface Long Line tunas. Percentages indicate the quantitative contribution of a group to the food resources of the following link.

3.2. Bonitos caught by trolling

Skipjacks, Euthynnus (Katsuwonus) pelamis, are one of the major resources of the Pacific and offer definite commercial prospects. In New Caledonia, bonito fishing is still poorly developed and is carried out only by a few bonito fishermen from Polynesia. Schools are found near the surface off the large reef (approximately 22° S-166° E) and are caught with fishing rods during the morning (0900 to 1200 hours). The fish in these schools are still in the initial stages of sexual maturity (Grandperrin, pers. comm.) and measure from 40 to 52 cm in length (weight: approximately 1.5 kg); they are appreciably younger than fish captured by Longline fishing (50-70 cm).

We examined the stomach contents of 407 bonitos caught during 7 fishing excursions carried out from 26/1 to 16/3/71 (Table 77). Significant differences appeared among the various samplings :

— excursions of 26/1 and 2/2 : The stomachs were very full (fig.

98B); little digestion had occurred. In section 1 (distal part), there were only Euphausiids; in 2 (mesial part), a mixture of Euphausiids, fish and Cephalopods; in 3 (proximal part), only the two latter groups. The stomach contents were being digested in 3, very little digested in 2 and still fresh in 1.

TABLE 77 215

Material used to study the feeding habits of bonitos

Date	Approximate time of beginning of fishing	Number of full or partially full stomachs examined	Euphausiids in S.C.	
			occurrence	importance (in weight)
26.1.71...........	09 h.	91	100 %	90 %
2.2.71...........	10 h.	86	100 %	66 %
9.2.71...........	12 h.	15 *	0	0
18.2.71...........	12 h.	23	39 %	2 %
24.2.71...........	11 h.	65	11 %	1 %
3.3.71...........	12 h.	60	8 %	1 %
16.3.71...........	12 h.	67	36 %	3 %
	83% of stomachs were empty			

On the whole, Euphausiids formed 90% and 66% respectively of the food ingested by the bonitos caught during these two samplings (in weight).

— excursions of 9/2, 18/2, 24/2, 3/3 and 16/3 : The stomachs were much less full (fig. 98D) and sections 1 and 2 which did not contain any food were constricted. Very well digested remains of food, mainly from fish and Cephalopods, were still in section 3. Euphausiids, present in the form of debris of eyes and legs, formed only from 1 to 3% of the total amount of food.

All Euphausiids found in bonito stomachs belonged to the species <u>E. fallax</u> and <u>T. tricuspidata</u>, of the 1.6 to 2.5 S.G. (average length: approximately 20 mm).

From our observations, we concluded that bonitos followed the following feeding pattern (in cooperation with R. Grandperrin; cf. fig. 98) : Euphausiids are ingested during the latter part of the night (around 0400

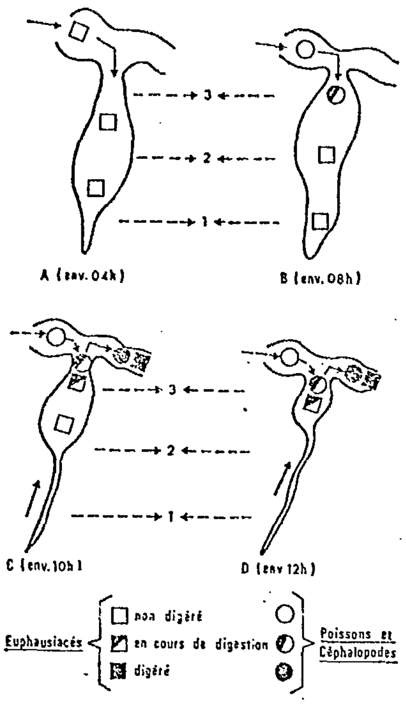


Fig. 98. — Schéma de la nutrition chez les bonites.
Fig. 98. — Diagram tentatively suggesting the feeding mechanisms in Skipjack tuna *(Euthynnus (Katsuwonus) pelamis).*

hours) before migrating to lower depths and are stocked in sections 1 and 2 (fig. 98A). After daybreak, prey still present in the subsurface (fish and Cephalopods) are accumulated in 2 and 3 (fig. 98B); this stage occurring from 0800-0900 hours was noted during our first two fishing excursions. As prey becomes more scarce, the rate of ingestion slows down and digestion of stored food intensifies, especially in section 3 (fig. 98C and D); the stomach contents then come up from the constriction in sections 1 and 2. During this stage, the few fish and Cephalopods which are captured are digested in 3 as they are ingested: this stage was noted during the last 5 excursions carried out at about 1100-1200 hours.

Differences in type of prey according to time of day can be explained by the rapid digestive process : Nakamura (1961) estimated that the intestinal transit of Skipjacks lasted 90 minutes. Euphausiids were found in the stomachs at 10 o'clock in the morning only because they had been stored; when digestion intensified because food was scarce, they disappeared very rapidly; around noon practically no traces of them were left.

We might therefore consider Euphausiids as being a prime source of food for bonitos which consume them in large quantities, especially during the latter part of the night, it would appear. Although an estimate of actual 216 quantities was difficult to obtain from our data, we believe that they account for 30 to 50% of the total food sources of these tuna, for individuals caught at present off the Great Caledonian Reef in any case.

4. CONTRIBUTION OF EUPHAUSIIDS TO OTHER COMMERCIAL SPECIES

As we mentioned earlier, the deep-sea resources of the South Pacific are still highly unexploited and, in most cases, the extent of these resources remains unknown. As a result the habits, especially feeding habits, of pelagic fish which could be of some commercial value are virtually unknown. The contribution of Euphausiids to these species cannot be specified accurately, but their contribution to the food sources of the counterparts of these fish inhabiting temperate waters (herring, cod, salmon, etc.) would imply that the Clupeids and Carangids of tropical seas also largely depend upon them for their subsistence.

Examination of data, unfortunately very limited, concerning the feeding habits of a Carangid caught in Polynesia, *Selar crumenophthalmus* (common Tahitian name depending upon stage: "ature" for individuals 15-21 cm; "aramea" from 21-29 cm; "orare" over 30 cm), confirmed our assumptions. Out of 26 full or partially full stomachs, 8 contained Euphausiids; from these 8 stomachs, we removed 500 large *T. tricuspidata* (1.6-2.0) as well as a few *E. diomedae*. Although no definite conclusions can be drawn from these observations, they nevertheless support the fact that Euphausiids occupy a certain position, probably an important one, in the food chains leading to certain fish of commercial value.

5. CONCLUSIONS ON THE PARTICIPATION OF EUPHAUSIIDS IN FOOD CHAINS IN THE EQUATORIAL AND TROPICAL PACIFIC

— *In terms of species*, the examination of Euphausiids found in the stomachs of fish led us to assume that, beginning with the relatively low trophic levels of zooplankton, there exists a certain independence between food chains affecting :

- firstly, the migratory (*Lampanyctus*, *Diaphus*, *Triphoturus*, *Lepidophanes*, *Symbolophorus*, etc.) or deep-dwelling (*Cyclothone*, *Sternoptyx*) micronektonic ichthyfauna providing almost all fish caught with the IKMT (total length generally between 3 and 5 cm), responsible for the deep scattering layer (DSL), which feeds equally upon migratory Euphausiids (especially *Euphausia*) found in deeper layers by day and near the surface by night and upon sedentary species (especially *S. abbreviatum*) encountered during vertical migrations; these fish prey mainly upon small organisms (0.7 to 1.6 S.G.). 217

- secondly, Longline tuna (Germon, Yellowfin, Bigeye) found between 0 and 400 metres, which directly consume only a negligible amount of Euphausiids because it appears that, in the Tropical Pacific, tuna feed mostly during the day, i.e., at a time when the large *Euphausia* or *Thysanopoda*, seemingly desirable prey, are located at greater depths. These tuna feed mainly on the ichthyfauna found near the surface (0-300 m), fast-swimming fish which escaped the IKMT. The *Gempylidae*, *Bramidae*, *Paralepididae*, etc. prey essentially during the day on sedentary species (mostly of the genus *Stylocheiron*) found nearer the surface by day than migratory species. These Euphausiids are of average size (0.9 to 2.0 S.G.).

Finally, large migratory Euphausiids (*Thysanopoda*, *Euphausia fallax*) of the 1.6 to 2.5 S.G., are consumed especially in the latter part of the night before they migrate to lower depths by predators ranging in size between the micronektonic fish (2-10 cm) and the large Longline tuna (over 60 cm): Bonitos, Carangids and undoubtedly other fish of commercial value not yet exploited.

— *In terms of quantity*, we demonstrated that Euphausiids accounted for :

- approximately 8% in volume (more when considering weight) of the total food resources of the micronektonic ichthyfauna of the deep scattering layer (DSL), captured by the IKMT. Other elements of the micronekton (Carides, Cephalopods) also depend upon them.
- approximately 10% in volume of the food of surface feeders which form over half of the prey of Longline tuna.
- from 30 to 50% of the food of bonitos caught by troll fishing.
- an undoubtedly important source of food for other fish of commercial value, Carangids among others.

GENERAL CONCLUSIONS

Very little is known about the biology and even the zoogeography of plankton inhabiting the Equatorial and South Tropical Pacific. The one hundred odd stations carried out during various expeditions using different samplings techniques are entirely insufficient. The expeditions of the R.V. "CORIOLIS" from the Numea ORSTOM Centre undertaken since 1964 have added considerably to the data available to date by their very number (some thirty major expeditions) as well as by a consistency in techniques, research programmes established on a permanent basis, the number of samplings and the great number of parameters obtained by methods ranging from physico-chemical measurements to tuna fishing.

From this wealth of material, we selected over 600 hauls of plankton and micronekton which we then used to examine the distribution and biology of one of the major groups, Euphausiids. These organisms are of particular interest because of their density (almost 10% of the total macroplanktonic biomass) and their contribution to the economy of equatorial and tropical regions.

Methods

Due to the difficulties involved in sampling a pelagic group belonging at once to both plankton and micronekton, we initially submitted our sampling methods to as critical an examination as possible. Once the sampling gear offering the best possible compromise was selected (a 10-foot Isaacs-Kidd midwater trawl or IKMT), we then :

— firstly, established with utmost accuracy the particular features of the stations, such as the depth reached (by means of a Bathykymograph), towing profile (by Depth-Distance Recorder), speed of filtration during various towing stages, etc.

— secondly, determined the sampling bias in relation to actual populations. To do so, we defined the selective process of the IKMT by making comparisons with hauls with conventional plankton nets and referring to theoretical biological considerations which enabled us to estimate corrective factors that were then applied to estimate actual populations. From this analysis, we concluded that although large Euphausiids were well sampled 220 by the IKMT, only a very small fraction of the smallest individuals (approximately 10 mm long), barely 1%, was collected; we estimated the percentage of each size group that was captured by the net.

In the laboratory, we devised a method for automatically determining size groups which gave us a clear idea of the size (age) structure of the populations; given the very abundant samplings, we could not possibly consider taking individual measurements of the organisms. This method enabled us to classify a wealth of material, i.e., over 400 000 specimens identified according to both species and size.

Examination of the samples pointed out that, in most cases, we were not dealing with normal distributions; it was therefore generally necessary to standardize the distributions before applying statistical tests.

Zoogeography

We identified a total of 34 species the distributions of which have been specified, although to date only in terms of major distribution patterns. Using the corrective factors mentioned earlier, we estimated the proportion of each species within the total population: Euphausia was by far the most prominent species (63%), followed by *Stylocheiron* (25%), *Nematoscelis* (9%), *Thysanopoda* (3%) and *Nematobrachion* (0.4%); the genus *Bentheuphausia* (*E. amblyops*), although our hauls produced 1 200 specimens, was only a minimal fraction of the entire group of organisms.

The classification of samples into size groups enabled us to calculate a mean size index for each species; this index was directly responsible for the mean percentage of individuals captured by the IKMT.

Using our material, we thoroughly examined the fauna of 5 major regions :

— western Equatorial Pacific (Region A) : 170° E
— southwest Tropical Pacific (Region B) : 170° E-15/25° S
— central Equatorial Pacific (Region C) : 135/155° W
— south central Tropical Pacific (Region D) : 130/145° W-15/25° S
— eastern Equatorial Pacific (Region E) : 92/140° W

We noted that more species inhabited the equatorial zone than the tropical regions; furthermore, we also noted that the density of the populations increased from east to west in the tropical zones, and from west to east along the equator. There was a striking contrast between the impoverished regions (Zone D: 115 individuals per station) and those benefitting from sources of enrichment such as equatorial divergence (Zone C: 1 032 individuals per station).

In terms of the species themselves, we noted a twofold change in the fauna :

— as we progressed from south to north, we noted that species with tropical affinities were gradually replaced by species characteristic of the equatorial system;

— along an east-west axis along the equator, the transition in the specific composition of the populations was sufficiently clear to enable us to identify a western fauna, an eastern fauna and a trans-Pacific fauna.

We also established that the proportion of small individuals was greatest when the region was most abundant in resources; this fact would 221 imply differences in the trophic levels of the various populations.

Heterogeneous Distributions

We defined two types of distributions :

— Firstly, we determined the nature of swarms formed by E. diomedae, S. abbreviatum and T. tricuspidata. The first two species appear to form very large groups, some hundreds of thousands of individuals which at certain time include almost one half of the total population. T. tricuspidata gathers into much smaller swarms, a few thousand individuals which never exceed one-fifth of the total population. E. eximia and E. fallax also form swarms, but our data concerning these species was inadequate. Other species follow more normal distribution patterns. However, our samplings techniques (filtering of large volumes of water) did not make it possible to specify the nature of the microdistribution.

Although the precise cause of the formation of swarms remains unknown, we encountered swarms generally at night, in a physically stratified (equatorial currents) or disturbed (along the coasts) environment. The fact that such carnivorous species as S. abbreviatum were observed in swarms would indicate that such behaviour is not peculiar to phytophagous species only.

— Secondly, an attempt to determine the distribution of means among our specimen populations demonstrated that, aside from the ultimate case presented by swarms, Euphausiids are always over-dispersed ($a = (S^2 - m)/m^2 = 0.15$ to 1.10).

Nychthemeral Variations in Hauls

The observation that hauls were consistently more abundant at night than during daytime, regardless of the towing depth, led us to determine the cause of this disparity. We concluded that this fact could be attributed to two different factors: the daily vertical migrations of the populations which dwell at much greater depths by day than by night and secondly, escapement of organisms through the mesh in the forepart of the net where the organisms whirl about during a major portion of sampling time. Escapement increased in proportion to the time spent by the organisms in the net; the percentage of losses was therefore greater during deep daytime hauls than during night tows carried out in the subsurface. Certain factors overshadowed these facts at times; in particular, the existence of a horizontal level at the greatest towing depth which resulted in over-sampling the organisms, compensated, whenever a densely populated layer was being sampled, for the loss of organisms while the net was hauled in. This analysis enabled us to determine the conditions under which nychthemeral variations in hauls would be void or minimal. We also demonstrated that, in the case of Euphausiids and the IKMT, the factor which introduced a bias sampling as compared with actual populations was the escapement of organisms through the mesh, while the avoidance of the trawl by larger organisms was undoubtedly of minor importance.

Seasonal Variations

Seasonal fluctuations in the density of populations are considerably 222
less pronounced in a tropical or equatorial environment because sharp climatic changes do not occur. Several authors consider any such fluctuations as being insignificant. Our observations of species nevertheless indicated that variations do occur, the extent of which could generally be assigned a

factor ranging from 1.5 to 8.0. In addition, we pointed out differences in variations observed in the eastern and western parts of the Equatorial Pacific:

— to the west (170° E), fluctuations in the density of each species were minimal, but synchronous, such that the curve showing overall density presented definite seasonal differences. A lower equatorial divergence and the intrusion of water originating from north of New Guinea, which appear during the austral summer, can be held responsible for the simultaneous development of the various species.

— to the east and at the centre, we noted a paradoxical situation: firstly, greater variations within each species and secondly, a remarkable constance in the curve of the overall population density. This apparent contradiction arises from the fact that the stable climatic environment does not cause changes within the overall population, only within each individual species as determined by its own biology. As the variations are not synchronized among the different species, the overall population density remains somewhat stable.

Vertical Distributions

In terms of vertical distributions, the nychthemeral migrations peculiar to most macroplanktonic organisms are of particular significance due to the very density of Euphausiids and the extent of their vertical movements and to their highly stratified environment (equatorial currents in the Pacific). Ramifications arising from such behaviour are particularly significant in two respects :

— the depth of immersion of the organisms conditions their distribution given the fact that they are submitted at different depths to currents flowing in opposite directions; whenever the age groups within a given population presented different mean vertical distributions, we noted that the generations were spread about differently; it was absolutely necessary to take this fact into account when interpretating biological phenomena.

— the trophic level of a species depends closely upon its vertical distribution, determining whether or not there exists a prey-predator relationship with other members of the food chain.

We demonstrated that in the Central Equatorial Pacific :

— by night, 75% of the Euphausiid biomass is concentrated between 0-100 (or 160) metres, 19% between 160-300 m, 6% beyond 300 m. The specific composition of each bathymetrical layer is clearly defined.

— by day, Euphausiids account for only a very small fraction of populations found near the surface; only the smallest species remain in the uppermost 200 or 300 metres.

The species were classified into certain well-defined groups : 223

— sedentary species or those migrating little

- epipelagic: inhabiting the first 300 metres (S. suhmii, S. microphthalma, S. carinatum, S. affine, S. abbreviatum, S. longicorne).
- mesopelagic: distributed between 160 and 500 metres (N. tenella, S. maximum).
- bathypelagic: located beyond 300 metres (S. elongatum, N. boopis).

— migratory species, generally related to the deep scattering layer (DSL) and found in great numbers during the day only beyond 300 or 400 metres. Certain species gather almost entirely above the thermocline during the night (E. tenera, T. tricuspidata, E. diomedae, T. aequalis, E. paragibba); part of the population of other species remain below the thermocline (N. microps, T. monacantha, N. flexipes,

N. gracilis, T. pectinata, T. orientalis); others do not rise above 200-300 metres, even at night (T. cristata, E. amblyops).

In the more stable, more depleted tropical zones where the water is clearer, vertical distributions appeared to be on the average from 50 to 150 metres deeper than in the divergence equatorial region.

We also demonstrated that the average size of the organisms increased with depth due to the fact that :

— firstly, within a given species older individuals dwelled at greater depths;

— secondly, most deep-dwelling species (T. cristata, N. boopis, E. amblyops) were larger than the surface dwellers (S. microphthalma, S. suhmii, S. affine, S. carinatum).

The major point brought forth during this study was the existence of two main categories defined by their vertical distribution during the day and having very different trophic relationships. Distinction must be made between :

— species which remain accessible during daytime to predators in the upper layer (0-300 m) which feed essentially by day and which are in turn consumed by large pelagic tuna. Species belonging to the food chain leading to tuna include all species of the genus Stylocheiron (except for S. elongatum) plus N. tenella, to which must be added the surface inhabitants of E. tenera, N. microps, E. diomedae, T. tricuspidata.

— migratory species related to the deep scattering layer (DSL) and located by day between 400 and 800 metres as well as deep-dwelling species, both of which are not accessible to surface feeders; they belong to other food chains, independent of those leading to Longline tuna. This group includes T. aequalis, E. paragibba, T. pectinata, T. monacantha, T. orientalis, *N. flexipes*, *N. gracilis*, *S. elongatum*, *N. boopis*, *T. cristata*, to which must be added the majority of *E. tenera*, *T. tricuspidata*, *E. diomedae* and *N. microps*.

Ecology

Examination of the distribution of the organisms in terms of environmental factors demonstrated that Euphausiids are largely independent of their environment, for three major reasons :

— with the exception of a few surface dwellers, they belong 224
either to species carrying out extensive vertical migrations which imply a relative indifference to the environment because they are subject to considerable differences in environmental conditions within a short period of time; e.g., a temperature drop from 13 to 18° C, or to mesopelagic or bathypelagic (over 300 m) species occupying a biotope where conditions remain stable over vast stretches;

— Euphausiids occupy a relatively high position in the food chain to which they belong and fluctuations in available resources affect them only indirectly, a drop in food sources having been minimized by lower members in the sequence;

— finally, the fact is now widely accepted that relationships between taxa and body of water generally appear only at a taxanomic level lower than the species (variety or geographic race).

An ecological analysis of the 5 regions outlined earlier was based on a calculation of specific diversity characterized by the Shannon-Wiener index :

$$Is = -\leq p_i . \log_2 p_i$$

Application of this index made it possible to define the characteristics of the various populations taking into account the deductions obtained from the study on zoogeography. The equatorial region is considered as being a coherent system progressively changing from east to west; the eastern region is biologically the youngest and benefits from enrichment sources such as the Peru Current and active divergence; there is a large biomass and a low diversity (0.4 to 1.2). Populations change to the west; the size of the biomass gradually drops and diversity gradually increases (Is = 1.2 to 2.2 between 125° W and 180°, 2.2 to 2.7 to the west of 180°).

Diversity is considerably higher in the tropical regions, reaching 3.7 in Zone E (western Tropical Pacific); the relatively low value of 2.7 obtained for Zone D (Central Tropical Pacific) was likely due to inadequate sampling.

We defined a rating, which we called the Misfit Quotation, describing whether or not the species preferred the same environment. By taking the percentage of the total population represented by each species in each different region, we classified the species according to decreasing order of preference; a comparison between the rank order of two species gave a Misfit Quotation the value of which was highest when the species occupied biotopes according to a different order.

An intercalibration of the Misfit Quotation and the Spearman R index gave an essentially linear relationship.

From the Misfit values obtained by comparing two species, we established ecological affinity groups such that species within the same group had low Misfit values, but high values if compared with species of another group. We thereby identified three ecological groups :

— species with equatorial affinities : *S. affine*, *N. gracilis*, *E. diomedae*, *T. monacantha*, *N. tenella*, *T. orientalis* (the latter two providing the transition with the following group);

— species with tropical affinities : *S. maximum*, *S. longicorne*, *N. boopis* (transition with the equatorial group); *T. pectinata*, *N. sexspinosus*, *T. tricuspidata*, *T. aequalis*, *S. abbreviatum*, *T. cristata*, *S. elongatum*. 225 To this group we added *N. flexipes*, *T. obtusifrons*, *T. subaequalis*, *E. fallax*, *E. brevis*, *E. mutica*, *N. atlantica* which are exclusively tropical species.

— intermediate species : *N. microps*, *E. paragibba*, *S. carinatum*.

Reproduction

No data was available until now on the reproductive cycles and the life-spans of planktonic organisms inhabiting the Equatorial Pacific. The lack of climatic fluctuations resulting in virtually uninterrupted biological activity, the vastness of the area and its remoteness from research centres limiting the possibility of frequent observations are all major obstacles to obtaining such information. Most authors, having had access to only fragmentary bits of information, concluded until now that reproductive activity was continuous, thus preventing any further examination being made of changes in the age structure of a population over a period of time.

We established first of all the sexual characteristics of the main species by describing ovarian development and dividing it into four major stages. Fecundity, measured by the number of ripe eggs contained in the ovary during Stage IV, was found to be much lower than that of species of cold or temperate regions : 80 for *E. diomedae* and *N. tenella*, 40 to 54 for all species of the genus *Thysanopoda* except for *T. aequalis* (24), less than 10 for the deep-dwelling species, *N. boopis* and *F. amblyops*. The maturity level of females was estimated by calculating the percentage of mature individuals within each different size group; we determined the period of impregnation (percentage of females bearing spermatophores) according to individual size and ovarian stage. Males being generally smaller than females, we noted that size was to be taken into account when determining sex ratios.

In attempting to determine life cycles, based on changes in the age structure of populations and the percentage of mature females at different periods, we encountered the same obstacle mentioned earlier, i.e., uninterrupted reproduction in the equatorial environment (females having reached ovarian maturity all bear spermatophores regardless of time of year). However, by altering the data (i.e., considering the percentage of each size group in relation to its average number of individuals over a one-year period), we were able to demonstrate that changes occurred over a period of time and to tentatively suggest a certain life cycle obtained by examining the development of modal classes.

T. tricuspidata, *T. monacantha*, *T. aequalis*, *N. tenella*, *E. diomedae* and *N. boopis* appeared to have a life-span of approximately 1 year (10 to 15 months); *E. amblyops* one of approximately 2 years. These life-spans are less than those of species of cold or temperate regions, most of which live from 2 to 3 years. Growth followed an essentially linear pattern, slightly asymptotic at times; the average monthly growth in length amounted to 1.0 mm for *E. diomedae* and *E. amblyops*, 1.2 mm for *T. aequalis*, 1.4 mm for *N. boopis*, 1.6 for *N. tenella* and 2.0 mm for *T. tricuspidata* and *T. monacantha*. These rates of growth are generally higher than those of temperate species (0.7 to 1.5 mm/month in general). Spawning occurred throughout the year with peaks having been noted for certain species from September to April; females appeared to spawn only once and to die shortly afterwards.

Trophic Situation

Trophic relationships are a prime factor of biological balance given the fact that the subsistence and density of a given population depend upon a particular food-predation element.

Food sources of Euphausiids

Major difficulties encountered in identifying stomach contents explain why the data available to date was limited to lists describing the type of debris found in the stomachs and representing only a minute fraction of the total food ingested. This data was totally insufficient for a study on trophic relationships; we therefore devised an arbitrary rating by which we estimated the proportion of material of animal (A) or vegetable (V) origin in the stomachs, the rating VA being used whenever both were found in equal proportions in stomach contents. Categories A and V were readily identified under the microscope provided fairly recent samples were examined: we demonstrated that, after the specimens had been preserved for 1 to 2 years, plant matter became discolored and could not be easily identified.

For each species we therefore had an estimate of the percentage of individuals with stomach contents of "A", "V" or "VA", i.e., we defined their trophic level identified by either of two complementary sums $\leq \left[A+(VA/2)\right]$ or $\lesssim \left[V+(VA/2)\right]$. After dissecting over 3 000 specimens, we established that :

— *T. aequalis*, *N. boopis*, *S. abbreviatum* and *T. orientalis* are strictly carnivorous; *N. gracilis*, *N. flexipes*, *T. monacantha* and *T. pectinata* appear to be essentially carnivorous, but complete their diets with plant matter; *T. cristata*, *N. microps*, *E. diomedae*, *N. tenella* are typically euryphagous consuming both phytoplankton and zooplankton in equal proportions; *T. tricuspidata* and *E. amblyops* ingest mainly vegetable matter (living phytoplankton in the case of T. tricuspidata and dead phytoplankton with broken down pigments in the case of E. amblyops), with zooplankton still accounting for 1/3 to 1/5 of their total food sources; E. paragibba and E. gibboides are strictly phytophagous.

— on the whole, we pointed out that Euphausiids ingested more animal matter than plant matter, as 12 out of 16 species relied upon animal sources for over one-half of their food requirements.

— the classification of more developed species having extended legs (Nematoscelis, Nematobrachion, Stylocheiron) as "predators" is a gross oversimplification. Although S. abbreviatum, N. boopis and N. flexipes are in fact carnivorous species, N. microps and especially N. tenella depend largely on phytoplankton. Likewise, many species belonging to less developed genera, considered as phytophaga obtaining their food by filtration, depend to a large extent on zooplankton (T. aequalis, T. monacantha, T. pectinata).

We also examined variations in stomach fullness in order to determine feeding habits and drew the following conclusions: the feeding pattern of most species did not coincide with the nychthemeral rhythm. In fact, we 227
frequently noted that feeding activity intensified in the second part of the day (1200-2000 hours) in the intermediate and deeper layers (300-600 m). By integrating the data obtained for 9 species, we outlined two peak feeding periods: one in the latter part of the day (1400-2000 hours) in the intermediate layers (300-600 m) and another at the surface during the night (0-100 m, 2000-0600 hours); however, the second peak period was subject to preying activity twice to ten times more intense than the first : from 100 to 1 000 individuals per 1 000 m^3 in active feeding being located there at such time as opposed to 50 to 100 in the first instance. No individuals were feeding during the day in the deserted subsurface zones (0-300 m;

0600-2000 hours), and very few in the deeper layers (300-800 m) both by night and during the forenoon (2200-1200 hours). We might recall at this point that we examined only migratory, mesopelagic and bathypelagic species and excluded the small surface dwellers (those belonging especially to the genus Stylocheiron) whose feeding habits are perhaps different.

With knowledge of the trophic levels of most species, we defined the trophic structure of populations within the different zones. We pointed out that the percentage of carnivorous species was inversely related to population density. Thus, feeding habits both confirm and complete the outline obtained in the study of zoogeographic populations and of the ecology (diversity) : in the order of regions E, C, A, B, D in the Equatorial and South Tropical Pacific, the populations become less and less dense, more and more diversified and have a higher and higher proportion of carnivorous species.

Euphausiids as a source of food

We determined precisely what Euphausiids represented as a source of food for their predators :

— in terms of value (source of Vitamins A and B_{12})

— in terms of quantity (8% of the total micronektonic biomass)

— and examined the form and conditions under which this resource was made accessible :

. given a definite relationship between size of predator and size of prey, we established the size distribution of the Euphausiid biomass. We demonstrated that 44% of the total Euphausiid biomass was formed of organisms belonging to the 1.2 size group (12-15 mm/11-20 mg), 25% to the 0.9 (9-12 mm/4-11 mg), 15% to the 1.6 S.G. (15-18/20-37 mg).

In terms of species, we noted that species of the genera Thysanopoda and Nematobrachion in addition to S. maximum and E. amblyops provided the majority of organisms over 18 mm long and weighing over 40 mg; smaller individuals belonged essentially to the genera Euphausia, Nematoscelis and Stylocheiron (with the exception of S. maximum):

. We demonstrated in the study on vertical distributions how these distributions determined whether or not Euphausiids were accessible to potential predators. As a source of food, Euphausiids form two major groups: those remaining accessible to surface feeders (0-300 m) during the day and participating in food chains leading to tuna and those dwelling at greater depths during daytime thus belonging to other food chains.

. Finally, we claimed that the formation of swarms by certain species promoted their potential use by predators; a spread of the organisms, on the contrary, protected the species but, by this very fact, limited its contribution to the economy of its biotope. 228

Major predators and participation in pelagic food chains in the Equatorial and Tropical Pacific

In analyzing the data required for this latter part of our work, we met with difficulties related to the very large variety of predators of Euphausiids which are included among large fish or in the plankton-micronekton category. Examination of stomach contents of Carangids (Selar crumenophthalmus) caught in Polynesia and especially those of bonitos (Euthynnus (Katsowonus) pelamis) caught by trolling off the coasts of New Caledonia specified the contribution of Euphausiids to species of commercial value; however, the type of available material led us to examine particularly: firstly, the position of Euphausiids in the food chains affecting micronektonic fish, generally migratory or deep-dwelling species captured with the midwater trawl, and secondly, their relation with respect to surface feeders (0-300 m) which escaped the trawl because of their swimming abilities but which consist in a source of food for the large tuna caught by Longline.

(1) Predators of the IKMT-collected micronekton

Aside from Cephalopods and large crustaceans (Carides, Sergestides) which also ingest a certain amount, we determined the quantity and species of Euphausiids contributing to the food sources of migratory or deep-dwelling micronektonic fish (generally 3-5 cm in length), forming the deep scattering layer (DSL) and over one half of total IKMT hauls. After examination of 1 923 stomach contents selected so as to represent from 90 to 95% of this particular ichthyfauna, we demonstrated that :

— Euphausiids providedsome 8% in volume (more in terms of weight) of the total food of these fish, 21% if the genus Cyclothone which forms a special category is excluded. They consist in one of the most common prey of Vinciguerria nimbaria (large individuals only), Gonostoma rhodadenia, Triphoturus microchir, Lampanyctus niger, L. hubbsi, L. festivus, Symbolophorus evermanni, Diaphus termophilus, D. regani, D. lutkeni, D. theta, D. elucens, D. malayanus, D. lucidus, D. splendidus, Sternoptyx diaphana and Eregmaceros sp.

— in terms of species, 45% of the Euphausiids ingested belonged to the genus Euphausia, 40% to the genus Stylocheiron and 13% to the genus Nematoscelis. The genera Thysanopoda, Nematobrachion and Bentheuphausia were practically absent, likely because of their larger size. We noted that over 90% of the Euphausiids consumed were of average length, from 6 to 18 mm.

We also determined the particular preying habits of these fish :

— we noted that for most species of fish there was generally a linear relationship between size of predator and occurrence and size of Euphausiids selected as prey;

— from our analysis of hourly variations, we observed three well 229
defined phases of preying activity :

. a peak occurrence of Euphausiids in stomachs during the night, from 2200 to 0200 hours, then a drop from 0200 to 0800 hours;

. the lowest occurrence at the beginning of the day and during midday, from 0800 to 1600 hours;

. a definite increase in preying activity during the latter part of the day (1600 to 1800 hours), followed by a slight drop coinciding with the vertical migration of the organisms to lower depths (2000 hours).

Furthermore, we noted that these fluctuations marked a change in the species being consumed : *Euphausia* was consumed both by night at the surface and at greater depths by day; small *Stylocheiron* ingested mainly by night at the surface; *Nematoscelis* and *S. abbreviatum* essentially during the upward (1600-2000 hours) and downward (0400 hours) vertical migrations of their predators.

Our overall observations led us to suggest the typical preying habits, as regards Euphausiids, displayed by migratory or deep-dwelling fish, generally related to the deep scattering layer (DSL) and captured by the IKMT :

— small fish (less than 40 mm long) consume the smallest Euphausiids almost exclusively (*Euphausia tenera*, *Stylocheiron carinatum*, *S. affine*, *S. longicorne*, *S. microphthalma*, *S. suhmii*) and capture them mainly by night in the subsurface.

— larger fish (over 40 mm long) are able to prey upon the larger migratory species (especially *Euphausia diomedae*) which they hunt both by night near the surface and by day at greater depths, as well as upon the species inhabiting the intermediate layers (*Stylocheiron abbreviatum* in particular) which they encounter during their vertical migrations.

(2) Euphausiids in the food chain leading to Longline tuna

Due to the fact that their biotopes do not overlap, Euphausiids form only a negligible food source for these large predators (Germon, Yellowfin) : it would appear that tuna in fact feed by day between 0 and 400 m where the large Euphausiids which they might possibly consume are not found. However, Euphausiids form an important portion of the food of fish ingested by tuna; these fish, slightly larger than those captured with the IKMT, belong to different species as only *V. nimbarria*, *S. evermanni* and *S. diaphana* were frequently found in both IKMT hauls and in tuna stomachs. While the IKMT-collected ichthyfauna included mainly migratory fish related more or less to the deep scattering layer or deep-dwelling species, tuna feed upon semi-sedentary species remaining in the uppermost 300 or 400 metres during daytime, most of the adults of which escaped the trawl. Examination of 1 193 stomach contents of specimens of this fauna led us to draw the following conclusions :

— Euphausiids account for approximately 10% in volume (more in terms of weight) of the food of fish ingested by tuna. Major predators are the *Bramidae* (*Collybus*, *Taractes*, *Pteraclis*), *Paralepididae* (*Paralepis*, *Macroparalepis*), *Vinciguerria*, *Symbolophorus* and *Sternoptyx*. To these must be added a *Gempylidae*, *Diplospinus multistriatus*, which forms the most com- 230
mon prey of *Alepisaurus*, the juveniles of which are eaten by tuna.

— in terms of species, these Euphausiids are somewhat larger than those selected by the IKMT-collected fish (9-20 mm long) and the species are distributed according to different proportions. We noted a predominance of the genus *Stylocheiron* (64%), while the *Nematoscelis* (15%), *Euphausia* (12%) and *Thysanopoda* (9%) were found only in small numbers.

Fish ingested by tuna therefore feed mainly upon sedentary Euphausiids (*Stylocheiron*) which are found nearest the surface during daytime, and not on migratory species (*Euphausia*) whose habitat is too deep during the day and which reach the subsurface only at night when tuna are not feeding; as a result, these fish depend mainly upon carnivorous species (*Stylocheiron*) while the ichthyfauna related to the deep scattering layer (DSL) prey more upon omnivorous species (*Euphausia*).

These results would indicate that, beginning with relatively low levels, there is a certain independence between the food chains affecting surface feeders (0-400 m), among which tuna are included, and the migratory or deep-dwelling fauna related to the deep scattering layer (DSL) and captured with the midwater trawl. In fact, if the migratory fauna draws its resources from the subsurface during the night (feeding activity of Euphausiids and IKMT-collected fish in the subsurface at night), thereby being prey for the deep-dwelling fauna during the diurnal phase, it would appear on the contrary that the surface feeders, including tuna, have little opportunity to utilize the migratory or deep-dwelling biomass because they feed mainly by day.

In other words, energy transfers operate effectively only along the surface-depth plane because the feeding habits of surface feeders do not allow this fauna to recuperate part of that energy from the migratory fauna.

On a broader basis, we hope to have successfully demonstrated during the course of this work that :

— the bathymetrical distributions of the faunas, their nychthemeral migrations and feeding habits, form in a pelagic environment the factors which determine the structure of food chains which, in turn, were to a large extent responsible for the situations we observed;

— an analytical approach to problems concerning a given taxonomic group is an effective means of identifying broader mechanisms affecting the entire pelagic world.

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