Biological Investigations of Some Important Species of Euphausiacea (Crustacea) from the Equatorial and South Tropical Pacific

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Abstract

Despite the misty picture obtained for the seasonal size structure of pelagic populations from warm water high sea regions, where reproductive processes are nearly permanent, some suggestions can be proposed about the life cycles of *Thysanopoda tricuspidata, T. monacantha, T. aequalis, Nematoscelis tenella,* and *Euphausia diomedae* inhabiting the Central Equatorial Pacific.

All these five species appear to have a longevity of 1 year approximately (10 to 15 months); sexual maturity is reached as soon as 8–10 months, but females seem to participate in only one spawning period and die soon after. The corresponding mean monthly growth in total length is 1 to 2 mm depending on species. The rapid cycle and early maturity are counterbalanced by a low fecundity, 24 to 80 according to species.

It is suggested that small epipelagic species, subjected permanently to very high temperatures (20–25°c), could present even more rapid cycles than the species here considered, which belong to the mesopelagic migrant type.

INTRODUCTION

Very little is known until now about the biological features which concern pelagic populations inhabiting warm waters. This lack of information appears to be due to the fact that tropical high sea regions are at once far away from research laboratories and need frequent investigation because of the very low magnitude of their temporal fluctuations.

With respect to Euphausiids from the intertropical Pacific, almost nothing is known about their growth rate, longevity, or fecundity.

MATERIAL AND METHODS

The research has been carried out in the equatorial currents of the Pacific, this system being a dynamic entity which provides a good probability to find again the same population during successive cruises.

The material comes from 109 stations occupied by the r.v. *Coriolis* from the Centre ORSTOM de Noumea (New Caledonia) during 5 cruises performed in October and December 1968, February, July, and September 1969. All the tows have been made at night with a 10-ft Isaacs-Kidd Midwater Trawl, obliquely from the surface to a depth of at least 250 m, 89 of them being deeper than 550 m. The location of the stations lies between 135° W and 155° W on the Equator.

The sexual characteristics of the different species will be defined for most of them, but the research on the biological cycles, which involves a large stock of animals, will concern only those satisfactorily sampled by the IKMT, namely:

Thysanopoda tricuspidata (7013 specimens).
Thysanopoda monacantha (2031 specimens).
Thysanopoda aequalis (2747 specimens).
Nematoscelis tenella (1806 specimens).
Euphausia diomedae (42,740 specimens).

The search for the vital cycles is based on the temporal evolution of the age (size) structure of the populations and that of the percentage of mature females.

Oceanography of the South Pacific 1972, comp. R. Fraser. New Zealand National Commission for UNESCO, Wellington: 1973.

TABLE 1. Equivalence between size groups, mean individual wet weight in mg (first number) and length from the tip of the rostrum to the tip of the telson in mm (second number). Each value represents the mean of the least 10 measures, except those placed between brackets.

Species	Size Groups 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)	..

The age distribution of the populations has been defined by dividing each sample into eight size groups obtained through the use of the method devised by Roger and Wauthy (1968), in which the animals are separated according to their thoracic diameter (in millimetres). The correspondence between size groups and individual mean length and wet weight is shown in table 1. It appeared that, for each species, the age histograms were almost similar for the five cruises, this being due to the fact that the selection of the net completely concealed the weak fluctuations of the size distributions.

To reveal the existence of these variations, the percentage of each size group in the different series must be referred to its mean annual percentage in the samples (here termed as "relative abundance" of the size groups), the modal size classes becoming then obvious.

The ovarian maturation has been described, and separated into four main stages (fig. 1):

Stage I: The ovary is thin, the numerous transparent tiny eggs being all of the same size;

Stage II: The eggs of the central part of the ovary become larger but remain transparent; the peripheric ones do not develop and are still at a stage I structure;

Stage III: The central eggs continue to grow, become polygonal in shape because of their packing, and lose their transparency. At this stage, the ovary looks like an opaque mass bounded by a fringe of small transparent undeveloped eggs;

Stage IV: The larger eggs attain a considerable volume, recover a subspheric shape, and become transparent again; their opaque nucleus is most perceptible. The thoracic part of the animal appears very often inflated because of the volume of the full grown ovary.

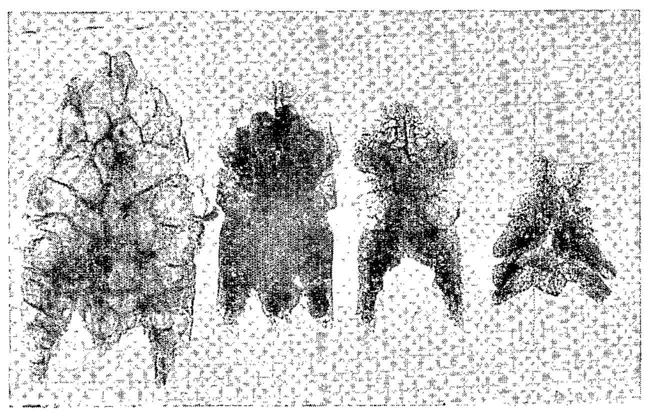


FIG. 1. Stages in ovarian maturation (I to IV, from right to left).

SEXUAL CHARACTERISTICS OF THE SPECIES

FECUNDITY

ripe eggs: this low fecundity is evidently counterbalanced

[redacted]

TABLE 2. Fecundity, after at least 10 measures for each species

Species	Number of Large Eggs in the Stage IV Ovary		Percentage of Stage IV Ovary Weight Related to Total Weight of Animal (wet weight)
	Mean (fecundity)	Extreme	
Thysanopoda cristata ..	40	20–76	8.7
T. tricuspidata	40	20–82	5.4
T. orientalis	54	38–74	9.3
T. monacantha	54	32–72	9.5
T. pectinata	54	30–82	5.8
T. aequalis	24	16–31	8.5
Nematobrachion flexipes ..	19	12–39	8.3
N. boopis	9	4–12	9.2
Bentheuphausia amblyops ..	3.5	1–7	8.7
Euphausia diomedae ..	80	..	..
Nematoscelis tenella ..	65	50–80	..

TABLE 3. Ovarian maturity for the different size groups

Species	Number of Specimens	Size Groups	Ovarian Stages			
			St. I	St. II	St. III	St. 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 ..	4006	1.6	..	58	42	..
		2.0+2.5	..	33	67	..
N. tenella	1077	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

NOTES—(1) The sum of the percentages for the ovarian stages is lower than 100% when the maturity of some individuals has not been determined.
(2) For *N. tenella*, "stage IV" corresponds here to the females carrying external eggs.

collected were immature (no stage I); for *E. diomedae*, no stage IV corresponding to the description previously established has been observed. With the aid of table 1, one can obtain an idea of the percentage of mature females of each species for the different size classes.

FECUNDATION

Fecundation is an almost permanent process in intertropical areas, as shown in table 4: at any season, nearly all the mature females (stage IV) carry one or two spermatophores. The ratio of impregnated females decreases toward the immature stages, but remains very high even for stages III and II. These facts confirm the continuity of reproduction in tropical zones.

SEX RATIO

The ratio males/females appears to be hardly connected with the life cycle, perhaps partly because of the

TABLE 4. Percentages of females carrying spermatophores in the different size groups and ovarian stages

Species	Size Groups	Ovarian Stages				Mean
		St. I	St. II	St. III	St. IV	
		%	%	%	%	%
T. cristata*	3.5	0	66	100	..	10
	5.0	..	75	100	100	92
	6.0	..	100	100	100	100
	Mean	0	78	100	100	..
T. tricuspidata	2.5	17	83	96	96	79
	3.0+3.5	..	98	99	100	99
	Mean	17	87	97	98	..
T. orientalis	3.0	0	33	100	100	22
	3.5	0	88	100	100	98
	Mean	0	73	100	100	..
T. monacantha	3.0	0	99	100	100	83
	3.5	0	100	100	100	97
	Mean	0	99	100	100	..
T. pectinata	2.5	0	..	..	..	0
	3.0	14	78	100	..	41
	3.5	50	95	98	100	96
	Mean	9	90	98	100	..
T. aequalis	2.0	..	99	99	100	99
	2.5+3.0	..	99	100	100	99
	Mean	..	99	99	100	..
N. boopis	2.5	0	81	91	100	84
	3.0+3.5	0	53	88	100	85
	Mean	0	70	90	100	..
E. diomedae	1.6	0	88	94	100	90
	2.0+2.5	..	100	100	100	100
	Mean	0	90	94	100	91

*Few specimens available.

TABLE 5. Male-female ratio according to size

Species	Number of Individuals	Size Groups	Males	Females
			%	%
T. cristata	197	3.5	54	46
		5.0	78	22
		6.0	25	75
T. tricuspidata	1935	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	1073	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	4754	1.6	17	83
		2.0+2.5	1	99
N. tenella	1117	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

failure of representative sampling. Table 5 indicates that, for Euphausiids, females reach a larger size than males, the sex ratio being higher in the smaller size groups. For the smaller species, the IKMT collects almost exclusively the females. This fact results in the necessity of taking into account the sizes of animals considered for the sex ratio analysis.

LIFE CYCLES OF SOME SPECIES

The data concerning the five selected species being treated in the same way, the details will be given only for the first one; for the other species, the results will be directly provided.

THYSANOPODA TRICUSPIDATA

The evolution of the size structure of the population between September 1968 and September 1969, represented by the relative abundance ("% m %") of the size groups at each season, is depicted in fig. 2, together with the percentage of mature females (ovarian stage IV).

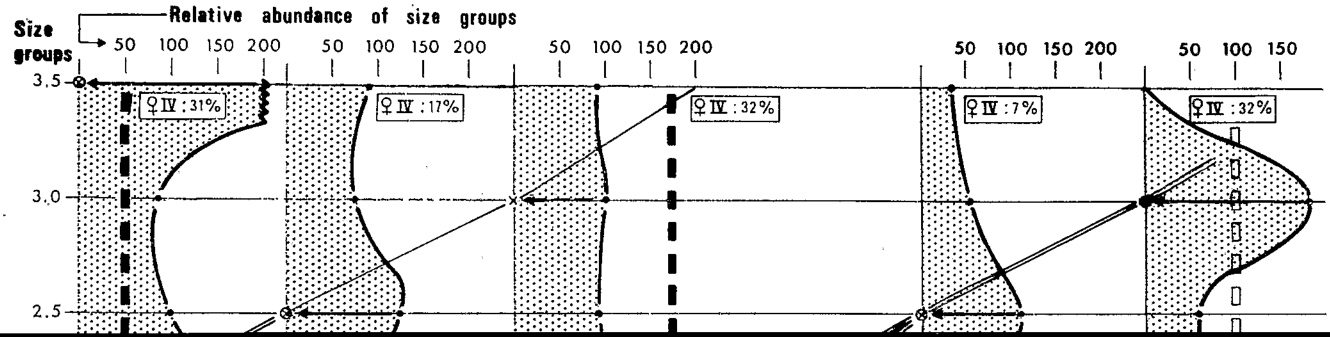
The way of connecting the modal classes from one season to the following one appears quite evident. The reproductive activity seems high between October 1968 and April 1969, except for a decline in January-February: the adult stock is abundant, with a noticeable proportion of mature females, and relatively large numbers of juveniles are present after December. These young specimens become mature by September-October 1969 and will participate to the next reproductive period. On the contrary, sexual activity remains comparatively

TABLE 7. Growth of *T. monacantha*

Size Groups	Age (months)	Total Length (mm)	Wet 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

THYSANOPODA AEQUALIS

The picture obtain for this species is much less clear than for the previous ones, this being due to an almost permanent reproductive activity resulting in the confusion of the successive modal classes. As far as it is possible to detect some of these, the longevity would be 10–12 months, corresponding to a mean monthly growth of 1.2 mm in total length. It appears probable that females become mature at 9–10 months and die soon after their single spawning period. Table 8 indicates the


Relative abundance of size groups
Size groups
50 100 150 200
50 100 150 200
50 100 150 200
50 100 150 200
50 100 150
3.5
3.0
2.5
♀IV : 31%
♀IV : 17%
♀IV : 32%
♀IV : 7%
♀IV : 32%

reproductive activity leads to a confusing picture in which it is hard to isolate the different generations. Yet a slight decrease in August–September allows to follow the growth of the next generation, from which one can suggest that the longevity would not exceed 12 months and the mean monthly increase of total length 1 mm. Sexual maturity of females would occur at the age of 10 months approximately. Table 10 indicates the equivalence between size, weight, and age.

TABLE 10. Growth of *E. diomedae*

Size Groups	Age (months)	Total Length (mm)	Wet 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

DISCUSSIONS AND CONCLUSIONS

The great difficulties encountered in the biological investigations performed in tropical areas arise mainly from the weakness of the fluctuations of the reproductive processes, considered as the consequence of a constant warm environment (Hansen 1910, Mauchline 1968, Mauchline and Fisher 1969) to which is added the problem of locating the same pelagic population during the successive sampling (Mauchline 1960). Most of the previous studies carried out until now on pelagic Euphausiids concern cold or temperate regions such as North Pacific, Japan Sea, and Barents Sea (Zelickman 1958 and 1960, Drobysheva 1963, Ponomareva 1963, Smiles and Pearcy 1971), Antarctic Ocean (Ruud 1932, Fraser 1936, Bargmann 1937 and 1945, Marr 1962, Baker 1959, Ivanov 1970) or North Sea and North Atlantic (McDonald 1928, Einarsson 1945, Adams 1966, Mauchline 1960, 1966, and 1968, Jones 1969). Some features of early development of tropical Euphausiids have still been proposed by Ponomareva (1969).

The schemes suggested in this paper for five tropical and equatorial species imply that:

(1) The modal classes observed are representative of the real age structure of the populations.

(2) The same population has been sampled in the course of the different cruises.

(3) The development of the individuals is sufficiently slow, so that a complete change of generation did not occur between two successive cruises.

If these conditions are fulfilled, one can propose for the five species studied the following features:

(1) Longevity is approximately 1 year (10 to 15 months).

(2) Sexual maturity is reached as soon as about 9 months.

(3) Each female participates in only one reproductive period, and dies soon after spawning (some weeks).

(4) For any species, the reproductive activity of the population as a whole appears almost permanent but can eventually present some fluctuations in intensity.

(5) The fecundity is low (24 to 80 ripe eggs in the stage IV ovary for the 5 species) but is counterbalanced by a more rapid cycle.

(6) Table 11 summarises the information obtained.

Finally, two remarks have to be made:

(1) The five species studied are all mesopelagic (Roger, 1971), their diurnal biotope being deeper than 300 m (temperature less than 10–12°C). It is likely that small epipelagic species (*E. tenera, Stylocheiron carinatum, S. affine*, etc.), inhabiting permanently warm subsurface layers (20–25°C), present more rapid cycles.

(2) As the characteristics of the environment influence the biology of the animals, the same species as those here considered may follow different cycles in other geographic areas.

TABLE 11. Characteristics of Reproduction, Growth, and Longevity of Five Species in the Equatorial Central Pacific

Species	Fecundity (number of ripe eggs in the stage IV ovary)	Period of Maximum Reproductive Activity	Mean Monthly Increment in Total Length (mm)	Longevity (months)
T. tricuspidata	40	October–December March–April	2.0	12–14
T. monacantha	54	September–October January–March	2.0	13–15
T. aequalis	24	Permanent, perhaps lower in July–August	1.2	10–12
N. tenella	65	Permanent	1.6	11–13
E. diomedae	80	Permanent, perhaps lower in August–September	1.0	11–13

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