DOCTOR OF PHILOSOPHY

Seasonal changes in the plankton of inshore waters with special reference to the life history of certate copepods

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SEASONAL CHANGES IN THE PLANKTON OF INSHORE WATERS WITH SPECIAL REFERENCE TO THE LIFE HISTORY OF CERTAIN COPEPODS

A thesis

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CONTENTS

General introduction

Purely qualitative investigations of the plankton of an area cannot provide sufficient information for the full understanding of the seasonal changes that occur nor of the interrelation of the various planktonic plants and animals. Quantitative data must be obtained before these can be properly described. Except for the qualitative records by Scott (1906, 1907) and Riddell (1914) the plankton of waters off the north coast of Wales, and of the Menai Straits in particular, has tended to be neglected. The unusual hydrographic conditions of the Menai Straits, which connect areas whose fauna and flora show considerable differences (Crisp & Knight-Jones, 1953), suggested such studies would be rewarding.

In describing the various populations the policy in the present work has been to give the details of the most numerous species of both plants and animals individually and to summarize the others in various groups. This simplifies the description and discussion of the dynamics of the population, which would be difficult to follow if all species were described in detail.

At an early stage in the investigations it became obvious that the plankton of these coastal waters differed considerably from that of the Irish Sea in general, which has been described by Williamson (1956). In particular the copepods Oithonina nana (Giesbrecht) and Euterpina acutifrons (Dana) were prominent species in the Menai Straits.

Euterpina acutifrons was found to have several points of interest. Firstly, dimorphism occurs in the male; this has received considerable attention and has been found to be of some significance in the biology of the species. Secondly, Euterpina is pelagic, while most other harpacticoid copepods are benthic or littoral. Investigations of its development (which was inadequately described by Tesch (1915)) in culture allowed a consideration of the adaptive modifications of Euterpina to a pelagic existence, of its rate of growth and development, and of the developmental aspects of dimorphism in the male. The latter has been a controversial subject in previous studies of copepod development (Sewell, 1912, 1929, 1940; Gurney, 1929; Coker, 1934). Thirdly, Euterpina has a world-wide distribution, mainly centered in the warmer seas. Consideration of this led to investigations of some aspects of the relationship between the environment and the development of the species and also to a comparison of its breeding season in the waters round Anglesey with those reported in other latitudes.

The present work also includes studies of the larval development of Oithonina nana, another warm water form. Despite its being a very common plankton animal, the larval development of this species has tended to be neglected.

In the work as now presented the studies of these species are given a considerable proportion of the total space, since the data provided on their development, growth and breeding illuminate the general study of the plankton which, in turn, forms a background to the detailed studies.

The form of presentation of this thesis may perhaps call for some explanation. The sections into which it is divided have been prepared in the form of separate papers intended for publication. This means that figures and tables are numbered consecutively within each section and not continuously throughout the thesis, and also that a separate bibliography will be found at the end of each section. It is hoped that this method of presentation will cause no inconvenience to the reader.

PART I

Seasonal abundance and variations in the plankton of the Menai Straits, 1957 and 1958

Contents

Introduction

Earlier investigations by Scott (1906, 1907), Herdman et al (1908-1921) and Riddell (1914) on the annual abundance of the plankton of the Irish Sea were made mainly in the central offshore region and around the southern end of the Isle of Man. Not much attention has been paid to the annual abundance along the North Wales coast, except for the qualitative records by Scott (1906, 1907) and Riddell (1914).

In addition to this, the unusual conditions of the Menai Straits suggested that a study of the composition and seasonal variations of the plankton in this area would be rewarding. This paper deals with the quantitative studies of the plankton made between March 1957 and December 1958. The weather was very different in the two years 1957 and 1958 and a comparison of their plankton populations has provided evidence for the relative importance of some environmental factors.

Hydrographical conditions

The Menai Straits run north-eastwards connecting Caernarvon Bay and Liverpool Bay (Fig. 1). High and low water at the north-eastern end of the Menai Straits occur about an hour later than at the south-western end, so that the water levels are different at either end through most of the tidal cycle. This leads to currents in the Straits flowing north-eastwards on the flood when the rising tide is higher at the Caernarvon end and south-west at the ebb. At certain stages of the tide, water flows in at both ends

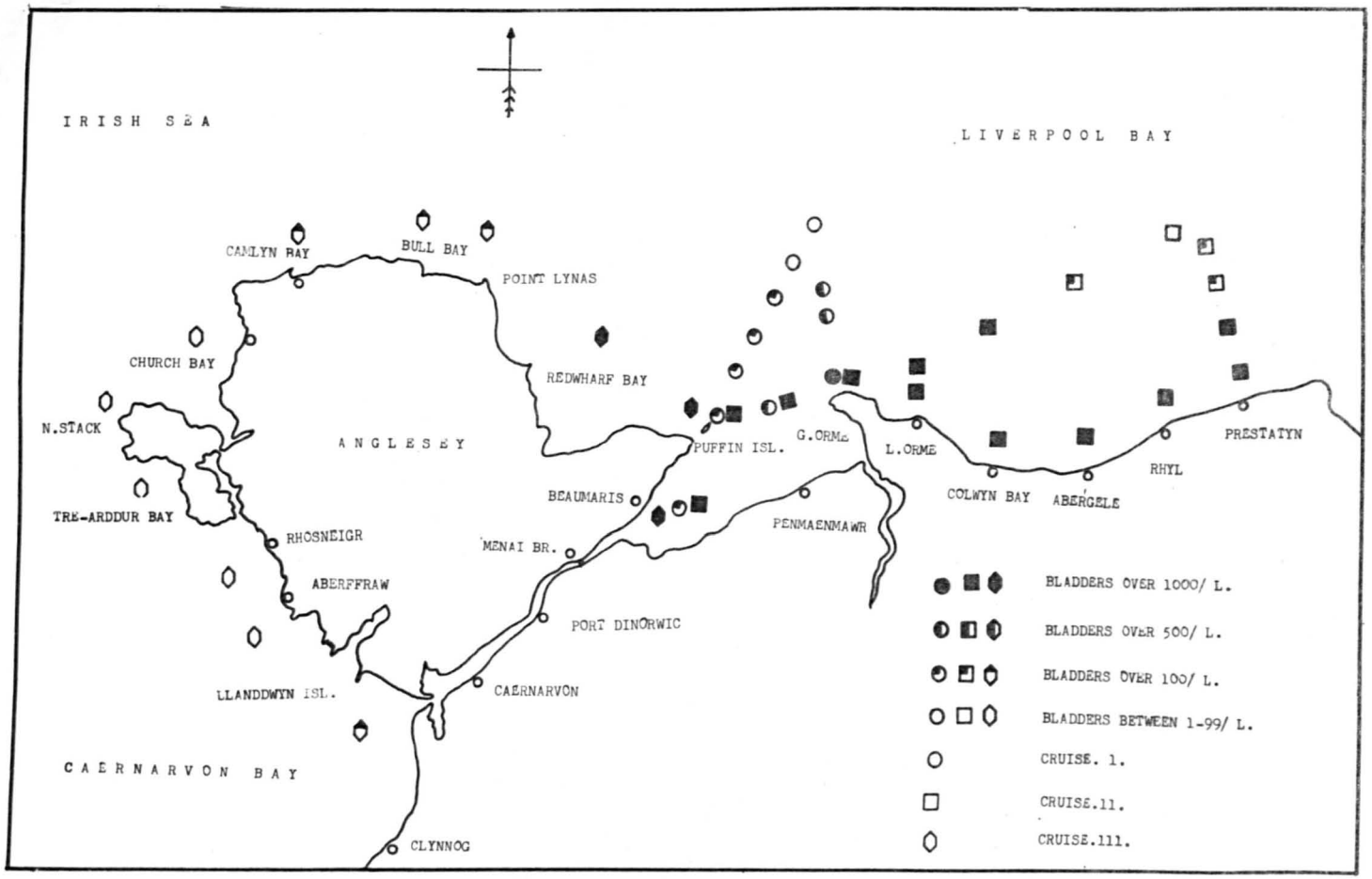


FIG. 1. DISTRIBUTION OF *PHAEOCYSTIS GLOBOSA* IN ADJACENT WATERS OF ANGLESEY(1958)

Table I. Distribution of *Phaeocystis globosa* in waters adjacent to Anglesey.
The number of bladders is the average of 5 per litre samples in each case.

Cruise I. 2.6.58		Cruise II. 5.6.58		Cruise III 11.6.58		Cruise 4.6.58	
Stations	Bladders/L	Stations	Bladders/L	Stations	Bladders/L	Stations	Bladders/L
Menai Bridge	25	Menai Bridge	1160	Menai Bridge Moorings	2660	Portdinorwic	350
Beaumaris	210	Beaumaris	1367	Portdinorwic	2360	Caernarvon	160
Puffin Island	328	Puffin Island	1712	Caernarvon	1180	Clynnog	-
2 miles due N.E. of Puffin	458	Between Puffin and Great Orme	1834	Caernarvon Bay	174		
4 miles " "	485	Off Great Orme	1690	Llanddwyn Island	6		
6 miles " "	294	Off Little Orme	1431	Rhosneigr	13		
8 miles " "	70	Off Colwyn Bay	2223	Trearddur Bay	10		
10 miles " "	30	Abergele	2520	North Stack	2		
3 miles due S.E. of Puffin	550	Rhyl	4420	Church Bay	35		
4 miles " "	724	Prestatyn	2800	Cemlyn Bay	202		
1 mile off Great Orme	1600	N. of "	1216	Bull Bay	250		
Between Great Orme and Puffin	632	N.W. of "	336	Point Lynas	374		
Puffin Island	466	N. of "	102	Red Wharf Bay	1543		
Friars Bay	288	N. of Rhyl	98	Puffin Island	3340		
Moorings	144	N. of Abergele	128	Moorings	2840		
		N. of Little Orme	1143				
		N. of Great Orme	1480				
		Between Great Orme and Puffin	1248				
		Beaumaris	872				
		Moorings	911				

of the Straits and at others outwards, the streams meeting and dividing in the region between Menai Bridge and Beaumaris.

Evidence obtained from experiments with drift bottles (Spencer, private communication) suggests that more water moves through the Straits with the south-west going streams than with the north-east going. The resultant flow is thus southward and the water of the Menai Straits might be expected to have characteristics similar to those of Liverpool Bay rather than Caernarvon Bay. This is borne out by the results of the present study.

An example of the close affinity of Liverpool Bay to the Straits was provided by studies of the distribution of Phaeocystis globosa (Scherffel), a colonial member of the Chryophyceae. A detailed study of this alga was made in the year 1958 when several surveys were made along the north coast of Wales, round Anglesey and into Caernarvon Bay. The courses followed in these surveys are shown in Fig. 1. The abundance of Phaeocystis was estimated by counting the number of bladders (colonies) per litre sample. In Table I the average values of 5 such samples in different surveys are given. They indicate that Phaeocystis flourished east of Point Lynas, decreased in number westward round the coast of Anglesey, and was absent further west in Caernarvon Bay.

The numbers of Phaeocystis colonies in the Menai Straits were similar to those found east of Point Lynas, indicating that the water of the Straits originated in Liverpool Bay. Additional evidence was provided by diatoms such as Eucampia zoodiacus and Guinardia flaccida, which also flourished

along the coast east of Point Lynas and whose abundance was much greater at the north-east entrance to the Straits and at Menai Bridge than near the south-west end.

Temperature of the sea water

The average weekly sea temperatures for the years 1957 and 1958 are given in Fig. 2. In 1957 a minimum temperature of 5·5°C was recorded in the third week of February and thereafter increased gradually, reaching about 16°C at the end of June. In 1958 a minimum temperature of 4·5°C was recorded in the third week of March. This was followed by a slow increase and a maximum of 16·5°C was reached in the third week of August. Thus the temperature rise was later during the early summer of 1958 than in 1957 and the maximum temperature was reached 6 to 7 weeks later.

Methods

(i) Phytoplankton

In the quantitative estimation of diatoms and other unicellular plants, use was made of the concentration methods described by Cole & Knight-Jones (1949) using a cellulose filter membrane having a pore diameter of 0·5μ. The efficiency of this method was tested by recovering Isochrysis, a flagellate measuring about 5 to 6μ in diameter, from a culture of known concentration. This concentration was first measured by means of a haemocytometer slide. A volume of this culture medium containing a known number of cells was then made up to 10 litres of sea water and shaken thoroughly. A 100 cc. sample of this was then filtered through the filter

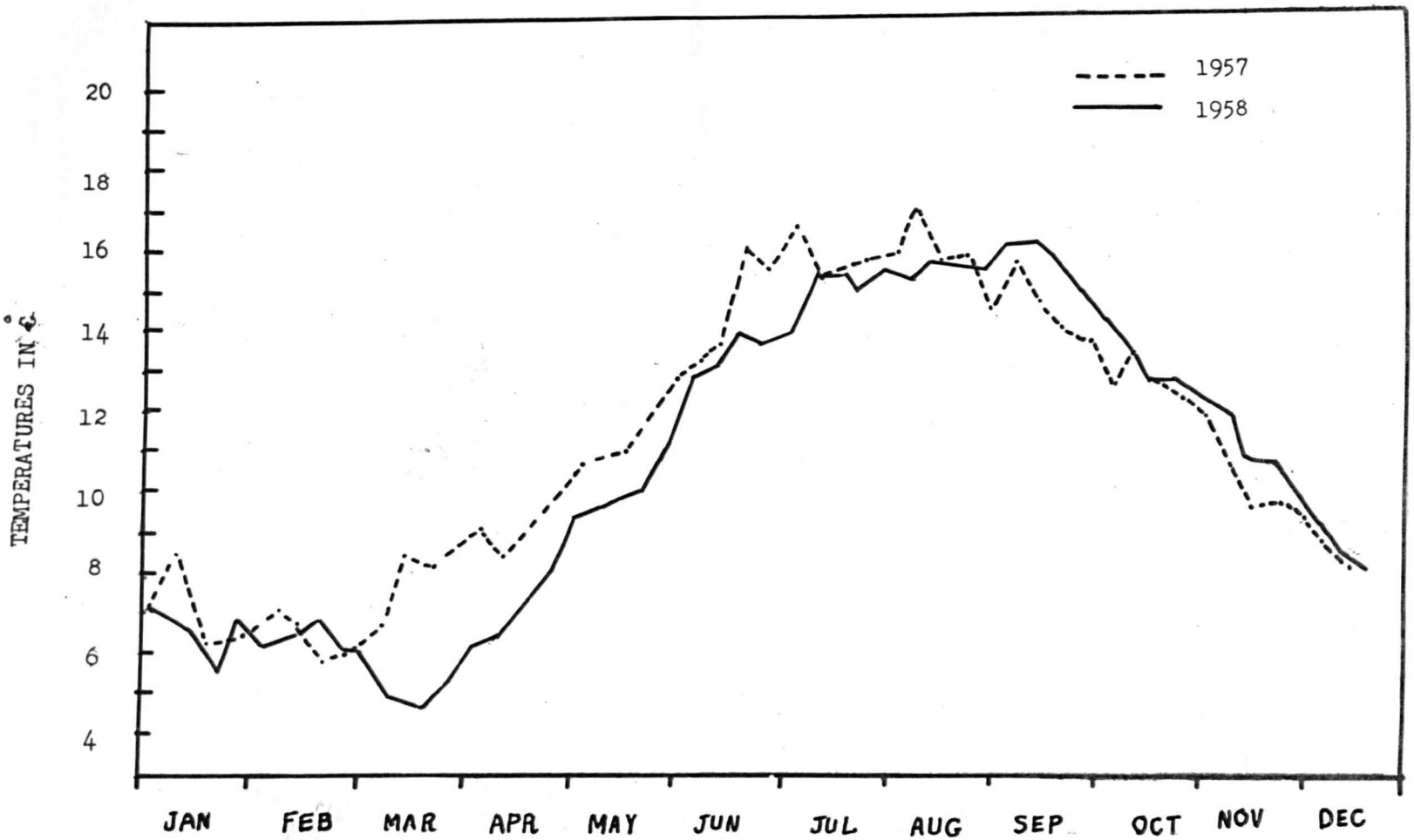


FIG.2.AVERAGE WEEKLY SEA WATER TEMPERATURE IN THE MENAI STRAITS DURING 1957 &1958.

membrane. The entire sample was not filtered through since, if this was allowed to happen, the cells adhered to the filter. Filtration was stopped when about 1 cc. remained and this volume was measured by means of a graduated pipette; after thorough stirring, portions of this sample were counted on a haemocytometer slide. The results of counts following ten such filtrations are given in Table II. These show that the average recovery was 84·5 per cent and that the method gave reasonably reliable results. Throughout the investigations samples of 500 cc. were taken from water bottles which were opened at a depth of 1 metre. Only during the occurrence of Phaeocystis globosa, when the bladders made filtration difficult, were smaller samples taken. These were never less than 200 cc. Using 500 cc. samples only those organisms whose numbers exceeded 2000 cells per litre could be counted with reasonable accuracy. The larger diatoms, which occurred in numbers smaller than this, were counted in the samples collected for the estimation of zooplankton, as described below.

In counting the nanoplankton a lower size limit of 2·5μ was adopted.

(ii) Zooplankton

Zooplankton was collected by means of a motor pump whose rate of discharge was checked, before and after the collection of each sample, by noting the time taken to fill a tank of 52 litres capacity. For all zooplankton samples a net of 200 mesh per inch was used, through which the discharge from the pump was passed. Each sample represented the zooplankton content of 500 to 900 litres of sea water, the volume depending on the time for which the pump ran. The fresh samples were immediately preserved in

Table II. Recovery of Isochrysis by filter membrane method. Dated 26th February 1957.

Initial concentration of Isochrysis cells in original culture medium = 2750 cells per mm^3.

100 cc. of culture medium containing $2{\cdot}75 \times 10^8$ cells were transferred to 10 litres of sea water, from which ten 100 cc. samples were taken. Each of these contained $2{\cdot}75 \times 10^6$ cells. Each sample was concentrated to 1 cc. by filtration and the concentration was estimated by counting fractions on a haemocytometer slide. The estimated concentrations were as follows:-

Samples	No. of cells per 100 cc.
1	$2{\cdot}40 \times 10^6$
2	$2{\cdot}27 \times 10^6$
3	$2{\cdot}70 \times 10^6$
4	$2{\cdot}25 \times 10^6$
5	$1{\cdot}98 \times 10^6$
6	$2{\cdot}55 \times 10^6$
7	$1{\cdot}80 \times 10^6$
8	$2{\cdot}65 \times 10^6$
9	$2{\cdot}35 \times 10^6$
10	$2{\cdot}20 \times 10^6$
Average No./100 cc.	$2{\cdot}32 \times 10^6$
Actual No. of cells/100 cc. in 10 litre sample	$2{\cdot}75 \times 10^6$
Percentage recovery	84·54 %

5 per cent neutral formalin sea water. Each sample was then concentrated to 100 cc. by decanting the supernatant water after the plankton had settled. Each 100 cc. concentrate was thoroughly mixed and a measured volume of it (10 - 15 cc.) was transferred to a perspex counting tray of the type described by Russel & Colman (1931). The sub sample examined represented about 30 to 70 litres of sea water, depending on the volume of the original sample, which was varied according to the abundance of the plankton. All individuals in each sub sample were counted.

Results of phytoplankton estimations

(i) Total diatoms

The total numbers of diatoms produced in 1957 and 1958 are shown in Fig. 3. The density of the diatom population differed in these years. In 1957 (Fig. 3.A) a gradual rise in the total number of diatoms began in March, reaching a maximum concentration of 510 x 10^3 cells per litre in mid April. A sharp decline followed towards the end of April. Thereafter the population fluctuated but remained generally low, reaching a minimum value of 25 x 10^3 cells per litre on 5th June. Numbers then increased and a second small peak of 350 x 10^3 cells per litre was reached at the end of July. A gradual decline followed with the onset of autumn and winter.

In 1958 (Fig. 3.B) a sharp increase in the diatoms was observed in the middle of March and a maximum of 870 x 10^3 cells per litre was reached on 2nd May. Higher numbers of diatoms were found during March and May than in the comparable period in 1957. There was a sharp decline at the end of May and a minimum concentration of 25 x 10^3 cells per litre occurred on

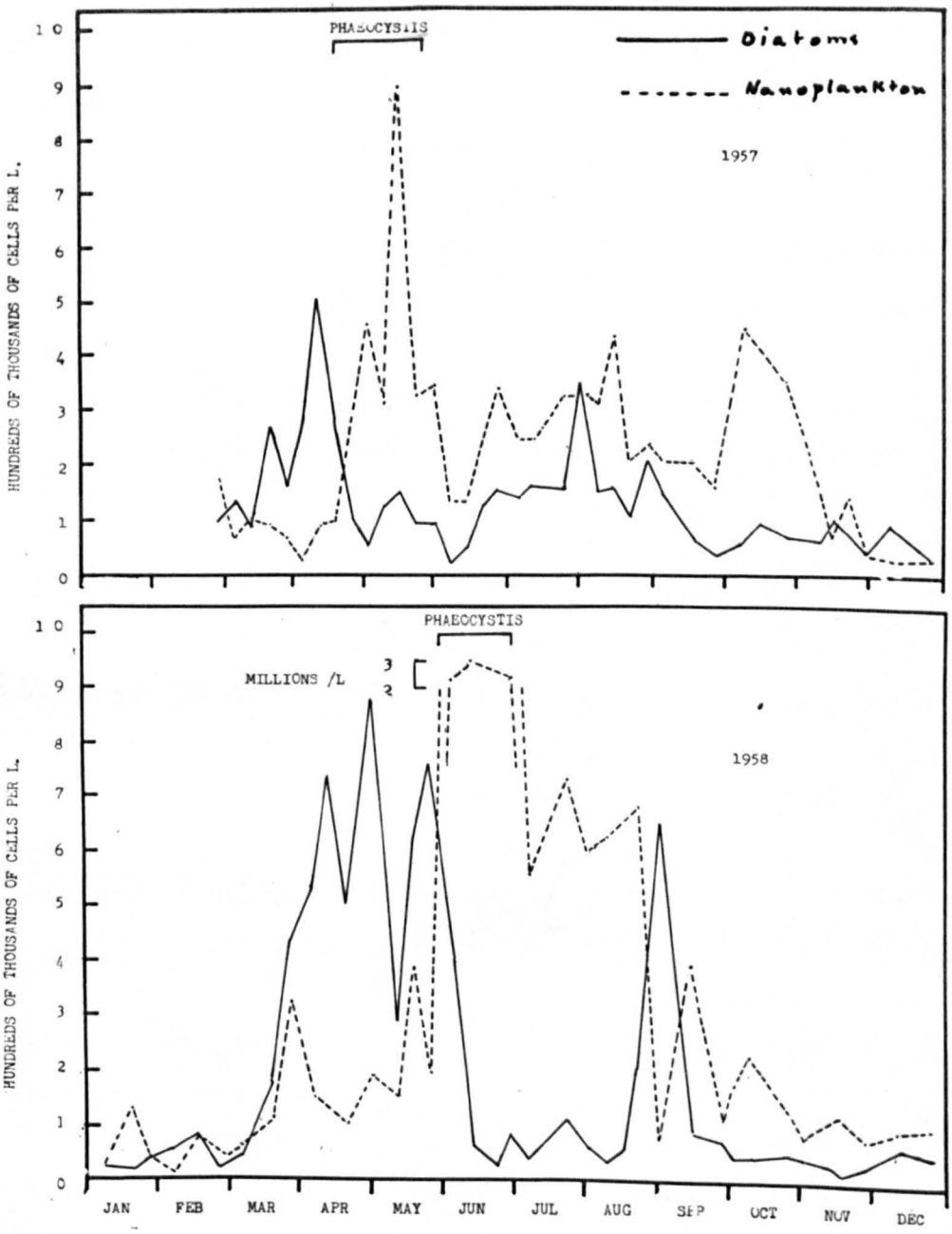


FIG. 3. SEASONAL ABUNDANCE OF TOTAL DIATOMS AND NANOPLANKTON IN THE MENAI STRAITS IN 1957 & 1958.

24th June. Numbers remained low until the middle of August when a sharp increase was observed. A maximum concentration of 650 x 10^3 cells per litre occurred on 2nd September. Thus the second diatom peak was delayed 4 to 5 weeks compared with 1957. The maximum number was higher in the 1958 autumn peak, while the population in the 1958 spring flowering was very much denser than in 1957 and also maintained these high numbers for much longer.

(ii) Other phytoplankton (mainly nanoplankton)

Under this heading organisms other than diatoms, (larger) than 2·5μ are described, including colourless chrysomonads, pigmented flagellates, silicoflagellates and palmelloid forms.

In both years the changes in nanoplankton numbers followed those of the diatoms. In 1957 (Fig. 3.A) a fall in the spring was followed by a rise, after the decline of the spring diatoms, which reached a maximum concentration of 850 x 10^3 cells per litre in mid May. The majority of these cells represented the palmelloid and motile stages of Phaeocystis. This was followed by a decline to a minimum of 135 x 10^3 cells per litre in early June. Numbers then increased, fluctuating through the later summer, and rising to a distinct peak on 9th October with a concentration of 400 x 10^3 cells per litre. This was followed by a gradual decline towards the winter months.

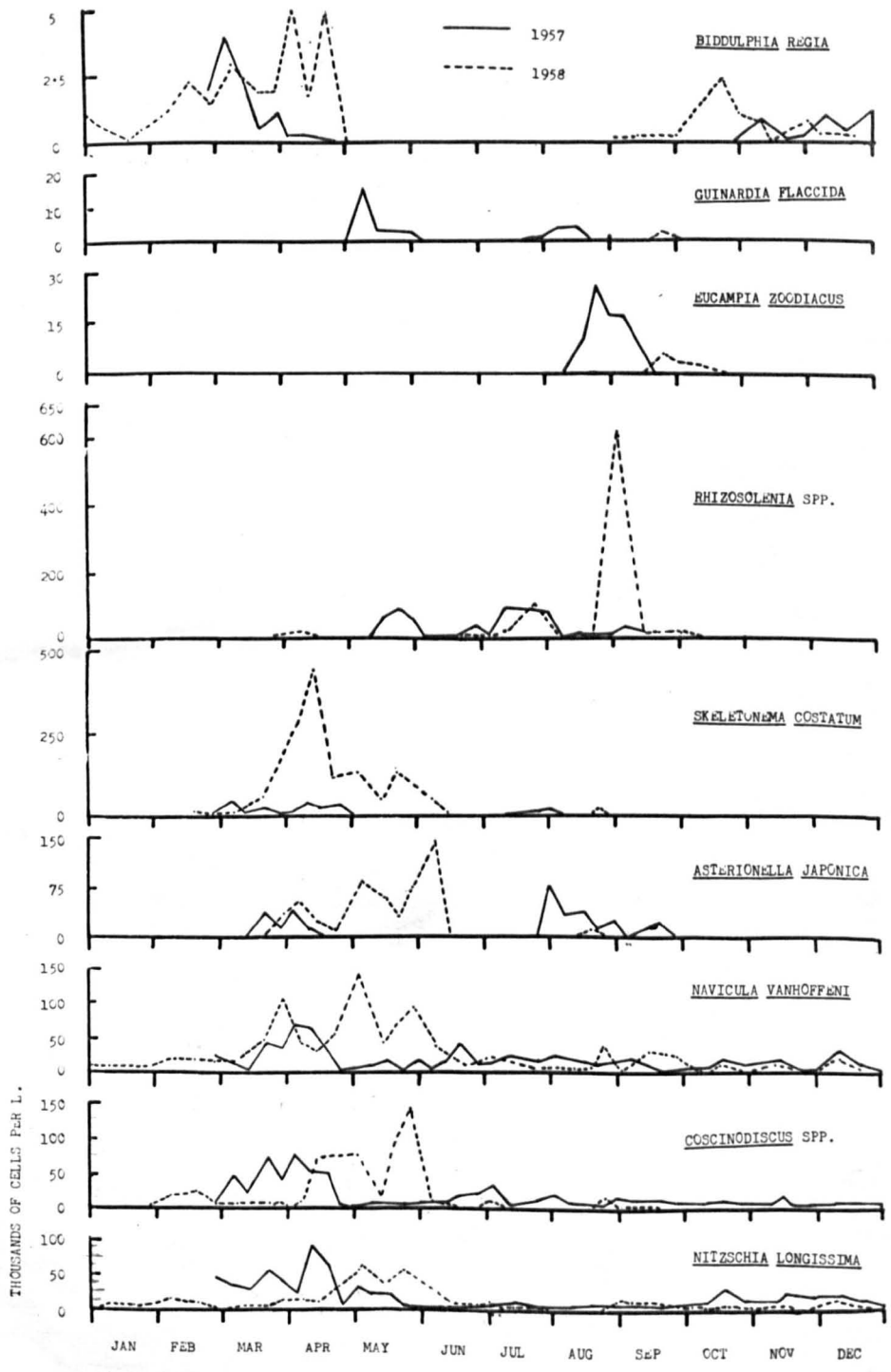
In 1958 (Fig. 3.B) a rise coincided with the subsiding of the spring burst of diatoms. A maximum concentration of about 3 x 10^6 cells per litre

was attained on 24th June. As in 1957 the majority of the cells at this time were the motile and palmelloid stages of Phaeocystis globosa. Subsequently the nanoplankton numbers remained much higher than those of the diatoms and also higher than in 1957. A sharp decline in late August coincided with the beginning of the autumn rise in diatom numbers. The numbers then fluctuated but showed a tendency to fall towards the winter months.

(iii) Seasonal abundance and succession of diatoms

The species of diatoms found to be dominant in different seasons are shown in Fig. 4. The commonest species, present all the year round, were Nitzschia longissima (de Breb) Ralfs ex Pritchard, Coscinodiscus spp. and Navicula vanahöffeni Gran which had intensive flowering periods during the spring months. Other species appeared temporarily and some became dominant for a time. For example, Skeletonema costatum (Grev.) Cleve and Asterionella japonica Cleve & Muller ex Gran were found to be the most abundant species in spring but also occurred in small numbers in early autumn. Among the late summer and early autumn dominants were Guinardia flaccida (Castr.) Perag. and Eucampia zoodiacus Ehrenberg which appeared in succession after June or July. Two common species of Rhizosolenia, R. delicatula Cleve and R. shrubsolei Cleve were abudnant in the late summer and early autumn. In 1958, the autumn peak was dominated by R. delicatula. Among the winter forms Biddulphia regia (Schultze) Ostenf. was the dominant species, having its maximum abundance in October to November and between February and April.

FIG. 4. SEASONAL ABUNDANCE OF MAJOR SPECIES OF DIATOMS IN THE MENAI STRAITS, 1957 AND 1958.



Other species which were important constituents of the plankton at times were:

Thalassiosira spp. (Cleve)

These species were much more abundant in 1957 than in 1958 and occurred during both the spring and autumn outbursts. In 1957 the highest concentrations of 86 x 10^3 cells per litre were recorded during August. In 1958 the highest concentrations, which occurred in April, were only 4 x 10^3 cells per litre.

Thalasiothrix nitzschiodes (Grun)

This was common in spring and autumn. The highest concentrations recorded were 14 x 10^3 cells per litre in March 1957 and 12 x 10^3 at the end of June 1958.

Fragilaria cylindrus (Grun)

In 1957 this species appeared irregularly during April, June and August with a maximum concentration (8 x 10^3 cells per litre) during April. In 1958 it appeared irregularly during June, November and December with the highest concentration (9 x 10^3 cells per litre) in December.

Laudaria spp. Cleve)

This occurred in spring (March - April) and early autumn (July - August). The highest concentrations recorded were 52 x 10^3 cells per litre at the end of July 1957 and 34·5 x 10^3 cells per litre at the end of October 1958.

Chaetoceros spp. (Ehrenberg)

These species appeared irregularly throughout the year. In 1957 the maximum concentration was 20 x 10^3 cells per litre in mid May. In 1958 the maximum concentration was only 3 x 10^3 cells per litre.

The species of diatoms described above were also recorded by Scott (1906, 1907) and Riddell (1914) with the exception of Nitzschia longissima. The absence of this, the commonest species, from their records may be due to its small size which would allow it to pass easily through their tow nets.

(iv) Phaeocystis globosa (Scherffel)

The colonies of Phaeocystis globosa are hollow gelatinous spheres or ovoids in which cells are embedded. The bladder-like colonies are easily seen with the naked eye. The numbers of cells vary according to the size of the bladders and a satisfactory estimation of the abundance of Phaeocystis cells was therefore difficult. In this study it has been expressed as the number of bladders per litre. This is a crude method but has proved useful in investigating the distribution of the species (p. 9).

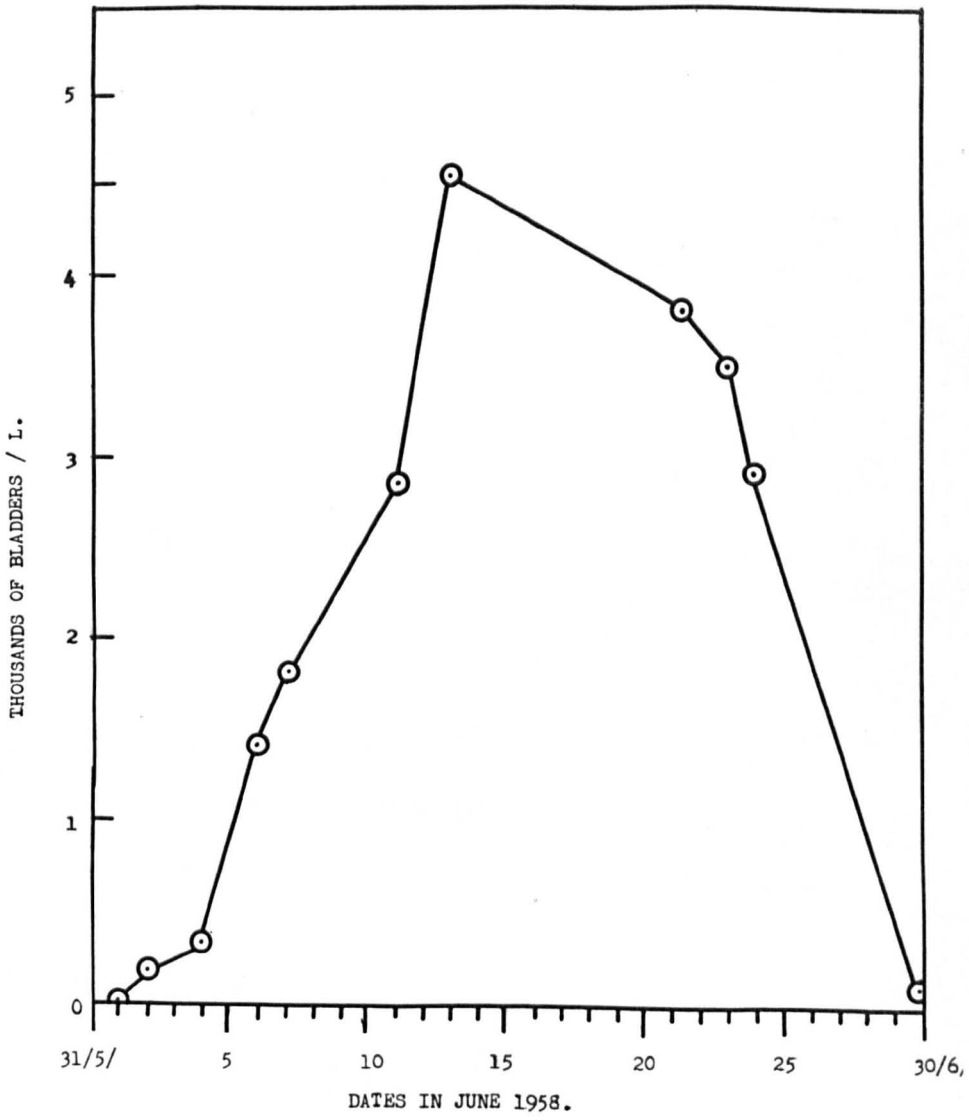
In 1957 no record of bladder numbers was made. The species first appeared in the plankton on 17th April and disappeared after 23rd May. In 1958 it appeared later in the year, on 1st June, and lasted until the end of the month.

Fig. 5 gives the number of bladders recorded in 1958. After reaching their maximum concentration on 13th June the colonies began disintegrating and motile cells were liberated. At times when free Phaeocystis cells are present in the plankton, their numbers may be so great that they can be counted directly from the sea water on a haemocytometer slide. In samples taken on 1st July 1958 at different places along the North Wales coast, the concentrations of cells by direct counts were found to be as follows:

Penmaenmawr: 193 x 10^6 per litre; Rhyl: 128 x 10^6 per litre;

Prestatyn: 141 x 10^6 per litre; Menai Straits: 28 x 10^6 per litre.

FIG. 5. ABUNDANCE OF PHAEOCYSTIS GLOBOSA IN THE MENAI STRAITS IN JUNE 1958.



Free Phaeocystis cells in high concentration may serve as a useful food for planktonic animals. Examination of the gut contents of Temora centropages in May 1957 showed the presence of Phaeocystis cells. These were also observed in undissected specimens of Oithonina nana. Labour (1922) also showed the presence of Phaeocystis cells in a large number of copepod species and also in other crustacean larvae. Nicholls (1935) in his studies on the feeding of adult Longepedia observed that colonies of Phaeocystis were generally broken down before they were ingested. The observations therefore do not agree with the idea of Harvey (1957) that planktonic animals find this plant inedible. Examination of the total zooplankton curves for 1957 shows that an increase occurred during the flowering of Phaeocystis (17th April - 23rd May) and a gradual fall occurred after the Phaeocystis disappeared. A similar correlation was seen in 1958. This is additional evidence that the zooplankton may live and thrive in the presence of Phaeocystis.

Results of zooplankton estimations

(i) Total zooplankton

Fig. 6 shows the total zooplankton in 1957 and 1958. In 1957 a gradual increase in the total zooplankton began in early April following the diatom maximum and reached a peak of 36 x 10^3 per M^3 in mid May. A sharp decline to a minimum in June then occurred, followed by a gradual rise throughout the late summer, reaching a maximum of 56 x 10^3 per M^3 at the beginning of October.

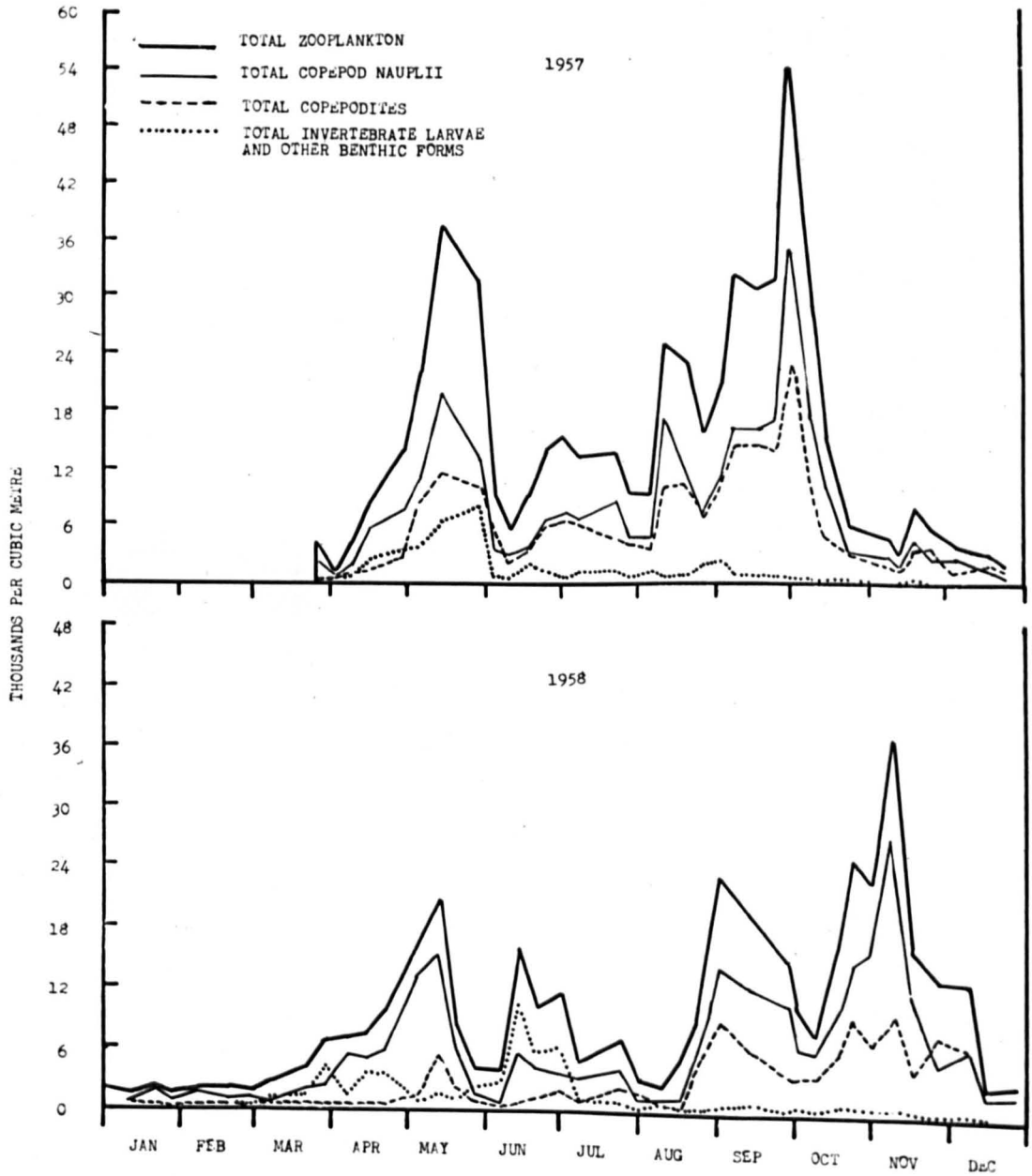


FIG. 6. COMPOSITION OF AND SEASONAL VARIATIONS IN THE TOTAL ZOOPLANKTON IN THE KENAI STRAITS, 1957 and 1958.

In 1958 the total zooplankton showed lower maxima than in 1957. A gradual increase began in March and a spring maximum of $18{\cdot}5 \times 10^3$ per M^3 was reached in early May. The autumn peak occurred later in the year than in 1957 with a maximum of $36{\cdot}8 \times 10^3$ per M^3 at the beginning of November.

At all times copepods and their nauplii formed the bulk of the zooplankton population. Their numbers and those of the planktonic larvae, which constituted most of the remainder of the population, are included in Fig. 6.

(ii) Seasonal abundance and succession of copepods

The seasonal abundance and succession of various copepod species are shown in Fig. 7.

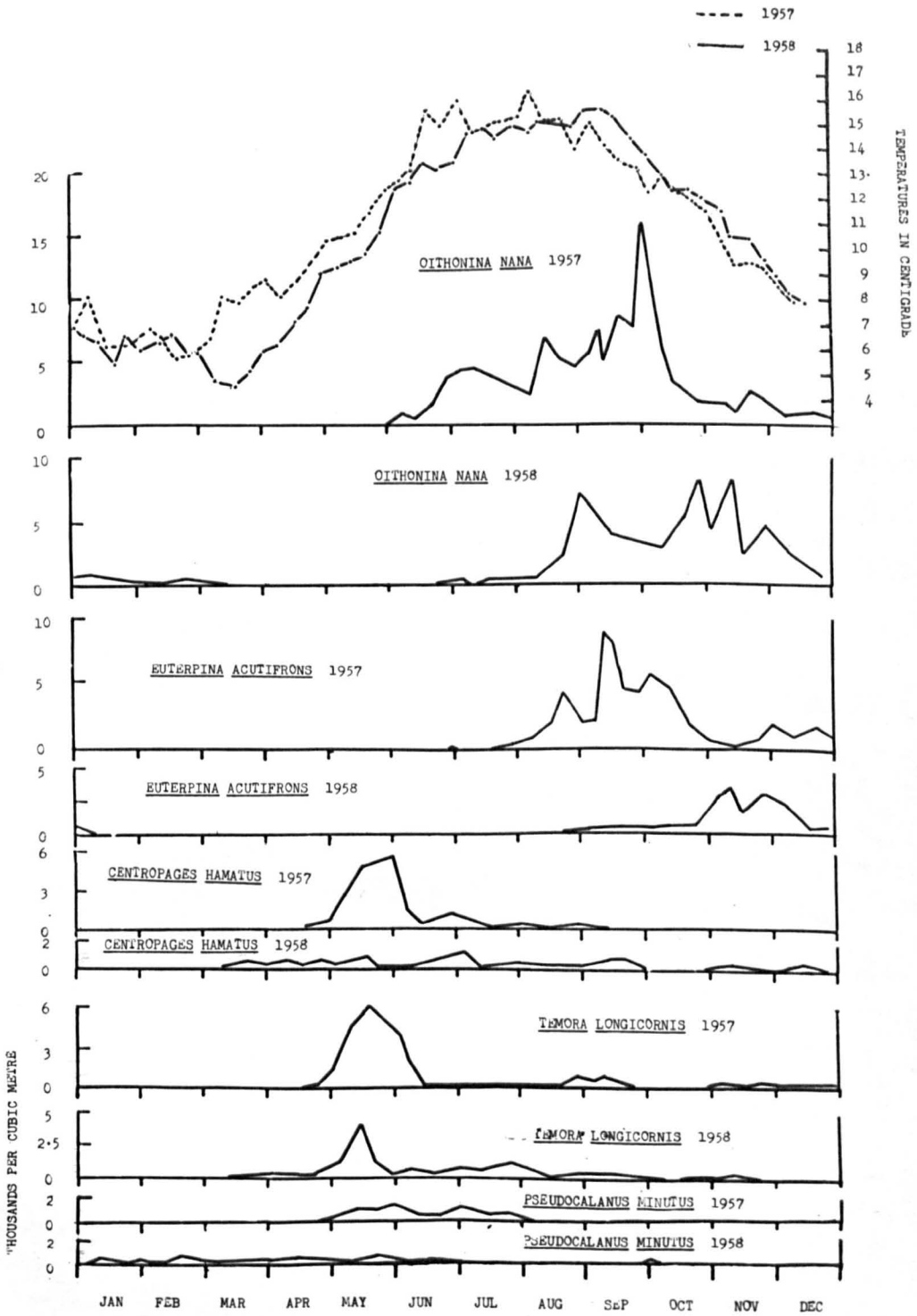
Temora longicornis (Müller)

This species occurred all the year round with intensive breeding in April and May. In 1957 a maximum of all copepodite stages was recorded in mid May after which numbers soon declined and, except for a slight increase during August and September, remained low. In 1958 the maximum was recorded in mid May at about the same time as the peak of 1957. The population then showed a similar decline.

Centropages hamatus (Lilljeborg)

This species has a similar breeding period to that of Temora. In 1957 the maximum abundance was recorded at the end of May. Except for a slight increase in September, numbers remained low for the rest of the year. In 1958 there was a marked difference in the abundance of this species. A

FIG. 7. SEASONAL ABUNDANCE AND SUCCESSION OF THE PLANKTONIC COPEPODS IN THE MENAI STRAITS, 1957 AND 1958



gradual increase began in March, reaching a maximum at the end of June which was much lower than that of 1957. In later months, except for a slight increase in September, numbers were low. The difference in population density in these two years suggests that this species may be sensitive to the sea temperatures which were lower in the first half of 1958 than in 1957.

Pseudocalanus minutus Krøyer

This species was most abundant between April and October. In 1957 the maximum numbers were recorded at the end of May. The species was rare after August. In 1958 the species was found from January onwards, reaching a maximum in mid May which was lower than that of 1957. After this numbers declined.

Oithonina nana (Giesbrecht)

This species was dominant in Autumn. In 1957 breeding started in May and the maximum numbers were recorded on 1st October. After this there was a gradual decline towards the colder months. In 1958 smaller numbers were recorded between January and April; the species was rare or absent for part of May and began to appear regularly from mid June, reaching its maximum in early November, after which numbers gradually fell.

Euterpina acutifrons (Dana)

A detailed consideration of the breeding of this species both in the laboratory and in the sea is made later in this work. In numbers it is second to Oithonina nana in the autumn plankton. In 1957 breeding started in July and the maximum numbers occurred in mid September. In 1958 breeding started much later, in the third week of August, and the maximum was not attained until early November.

Paracalanus parvus (Claus)

This species is commonest between July and December. In 1957 it appeared regularly from June onwards, reaching its maximum abundance of 400 per M^3 in early October. In 1958 its first appearance was in the third week of July and the maximum of 600 per M^3 occurred on 24th October.

Other species of copepods

Among other species of copepod which were found in very small numbers were Oithona similis Claus and Acartia clausi Giesbrecht. Oithona similis occurred between June and September. In 1957 the maximum abundance of 240 per M^3 was recorded on 10th July and in 1958 a maximum of 280 per M^3 on 1st September. Acartia clausi occurred between July and September. In 1957 a maximum of 400 per M^3 was recorded on 21st July and in 1958 a maximum of 216 per M^3 on 1st September.

The abundance of various species of copepods in the inshore waters of Conway Bay and the Menai Straits has been found to be different from that in offshore regions of the Irish Sea. The main difference is in the presence of large numbers of certain species, which seem to be characteristic of inshore conditions, while others are excluded. For example, Acartia clausi, Oithona similis and Isias claviceps Boeck, which are common in the Irish Sea (Williamson, 1956), are poorly represented in the Menai Straits. Similarly Oithonina nana and Euterpina acutifrons, which are dominant in the autumn plankton of the Straits, are found to be rare or absent in offshore waters (Williamson, 1956).

(iii) Seasonal abundance of larvae of benthic animals

The rest of the zooplankton is largely represented by the planktonic larvae of shore- and bottom-living animals. Fig. 8 shows the abundance of the major groups of invertebrate planktonic larvae in 1957 and 1958.

Polychaete larvae

The larvae of polychaetes are mainly those of Polydora ciliata (Johnston), P. caeca (Oersted) and Pectinaria koreni(Malmgren). The larvae of Polydora were found to be present all the year round with their maximum abundance during April and May. The larvae of Pectinaria koreni had their maximum abundance at the same time but were rare or absent early and late in the year.

Cirripede nauplii

The nauplii of cirripedes were found all the year round. At certain times their numbers were considerable. The species of barnacles most commonly found on shores in the Menai Straits and in Conway Bay are Balanus balanoides (L.), B. crenatus Bruguiere and Elminius modestus Darwin, and their nauplii presumably form the bulk of the population.

Veligers of Gastropoda

Among the veliger larvae whose numbers are shown in Fig. 7 the most common were those of lamellibranchs, but a few nudibranch veligers were also recorded. In 1957 the maximum abundance occurred at the end of May. In 1958 this was delayed until the middle of June.

The group termed miscellaneous in Fig. 8 represents the larvae of Polyzoa, echinoderms and other invertebrates. Cyphonantes of the Polyzoa were found all the year round with their greatest abundance between March and May and between July and September. In 1957 maxima of 130 per M^3 in

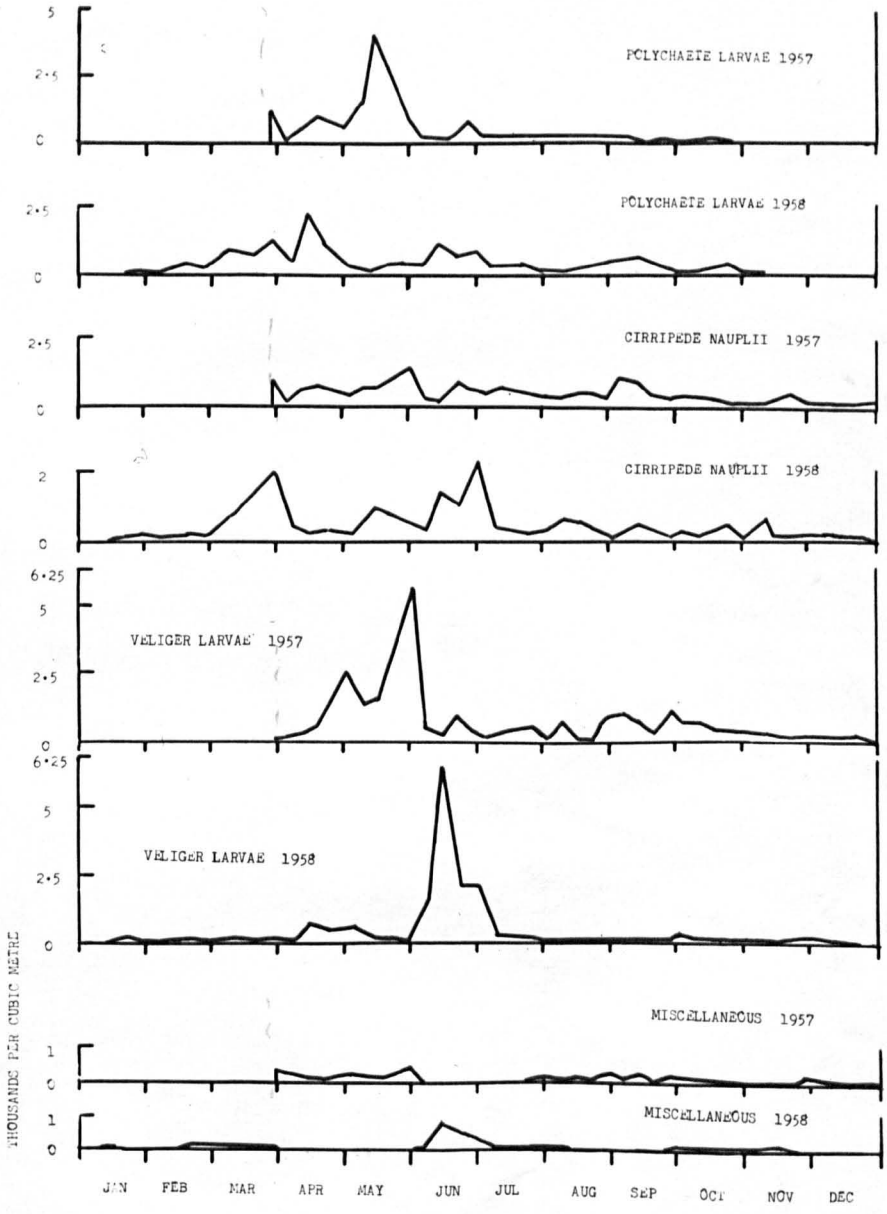


FIG. 8. SEASONAL ABUNDANCE OF LARVAE OF BENTHIC ANIMALS IN THE MENAI STRAITS, 1957 AND 1958.

May and of 240 per M^3 in September were recorded. In 1958 the maxima were 208 per M^3 in April and 115 per M^3 in October. Echinoderm larvae appeared only for a short period between May and August. In 1957 the maximum was 462 per M^3 in May and, in 1958, 665 per M^3 in June.

Among other invertebrate forms, represented in very small numbers, were the larvae of decapod Crustacea, actinula larvae (both present mainly in May), Sagitta (present during May and June) and free-living nematodes.

The influence of temperature on the breeding season of copepods and other planktonic organisms

The breeding seasons of the planktonic copepods mentioned above are similar to those described in other investigations in adjacent waters, as would be required by the generally accepted principle, suggested by Appellöf (1912) and Orton (1920), that a marine organism breeds at about the same time in all places where temperature conditions are similar. Temora longicornis, Centropages hamatus and Pseudocalanus minutus, which are mainly centred in northern waters (Wilson, 1932), start breeding at about the same time (February - March) in the Menai Straits as at Plymouth (Digby, 1950), (except that Centropages hamatus is not abundant and is replaced by the warmer-water form Centropages typicus) and also in Loch Striven (Marshall, 1949) and in Oslo Fjord (Wiborg, 1940). Similarly Paracalanus parvus and Oithonina nana, which are warm-water forms (Wilson, 1932; Sewell, 1940) breed in summer and their breeding seasons are the same in the localities mentioned above. Euterpina acutifrons, a species which extends into the tropics (Sewell, 1940), breeds in Anglesey at about the same time as in Plymouth (Digby, 1950) and in Dutch waters (Lucke, 1913).

On the other hand, differences in the temperature in these two years seem to have influenced not only the beginning of the breeding periods but also the population densities which are partly dependent upon the generation time which, in turn, depends upon temperature conditions (p. 10). The data available allowed comparison of the ~~summer~~ early and late summer populations. In 1958 the temperature in the first half of the year remained much lower than in 1957 and reached its maximum considerably later in the year. This coincided with the late appearance of Oithonina, Euterpina and Paracalanus in 1958. The temperature in the late summer of 1958 fell rapidly and this seems to have reduced the maximum numbers recorded compared with those of 1957. For example, in Euterpina acutifrons (as will be described in detail later) the breeding period in 1957 lasted for about 5 to 6 months and 4 to 5 generations were produced. In 1958 the breeding period lasted for only 3 to 4 months and only 2 generations were completed (p.127).

Comparison of the times at which the spring-breeding species first appeared in the two years is not possible, since records were not kept before April 17th in 1957. In 1958 the breeding of Temora and Centropages began in February when the temperature was about 6·5°C. The temperature then declined to 4·5°C in March and remained much lower than in the first half of 1957. The lower temperature in the spring months might be expected to reduce the development rate, in which case one would expect the maximum numbers to occur later than in 1957, as noticed in other copepods. In Temora, however, the peak in 1958 coincided with that of 1957, though the population was smaller in 1958. On the other hand, Centropages in 1958 did not show a distinct peak corresponding to that of 1957; its numbers were greatly reduced and spread

into the later summer months. It is possible that Centropages was much more influenced by the low temperature than Temora. Pseudocalanus minutus was also less abundant in 1958 than in 1957.

The temperature also seems to have influenced the succession of certain plants. For example, the first appearance of Phaeocystis globosa was about 6 weeks later in 1958 than in 1957. The general trend of the diatom curves in both these years also showed that various species reached their maximum numbers somewhat later in 1958. This is further supported by the shift of spring minimum values of dissolved phosphate content in 1958 (Fig. 9, P.G.W. Jones, personal communication)

The relationship between phytoplankton and zooplankton

The sequence of changes in both the phytoplankton and the zooplankton in 1957 and 1958 illustrates their inverse relationship (Fig. 38). In 1957 the spring peak of diatoms recorded in April was followed by a gradual increase in the total zooplankton. The peak of abundance of zooplankton in mid May coincided with that of other nanoplankton but declined as the latter fell. At the end of July a second outburst of diatoms, though with a small peak, was gradually followed by a rise in the zooplankton, reaching its maximum peak on 1st October. A peak in the nanoplankton was reached by the middle of October but no appreciable increase in the zooplankton followed. By this time the temperature had declined (Fig. 2) to 12°C and this may well have retarted very considerably development of further individuals in the zooplankton.

In 1958 the abundance figures of both diatoms and other phytoplankton and also the zooplankton were markedly different from those of 1957. The phytoplankton was more abundant through most of the year in 1958. The zooplankton, on the other hand, was present in much smaller numbers than in 1957.

The production of phytoplankton is largely dependent upon the supply of nutrients in the sea and the available light. Grazing by zooplankton has been suggested to play an important part in controlling the phytoplankton population (Harvey, 1934; Harvey et al, 1935; Nielsen, 1937; Riley, 1946). The greater abundance of phytoplankton in 1958 does not justify the conclusion that the rate of phytoplankton production was much higher than in 1957, since such a difference might well be due to differences in the grazing rate of the zooplankton between these two years. In this connection a comparison of the dissolved phosphate content (P.G.W. Jones, personal communication) of the sea water during phytoplankton production in 1957 and 1958 is interesting; this is shown in Fig. 9. In 1957 a sharp decline in the dissolved phosphate content was noticable from the middle of March, reaching a minimum in May which coincided with the greatest abundance of Phaeocystis globosa. In 1958 the dissolved phosphate content showed a gradual decline from March onwards and also tended to increase slightly between April and May. The phosphate then declined sharply by the end of May, which coincided with the maximum abundance of Phaeocystis. A sharp decline in phosphate in 1957 suggested that the rate of phytoplankton production was higher than in 1958. On the other hand, the population density of both diatoms and other phytoplankton was greater in 1958 than in 1957. This suggested that the rate at which the diatoms were grazed was higher in 1957 and this is supported by the figures for the total zooplankton population which in 1957 were considerably higher than in 1958.

A lower phytoplankton production in the autumn of 1957 is indicated by the higher values of dissolved phosphate in the sea water when compared

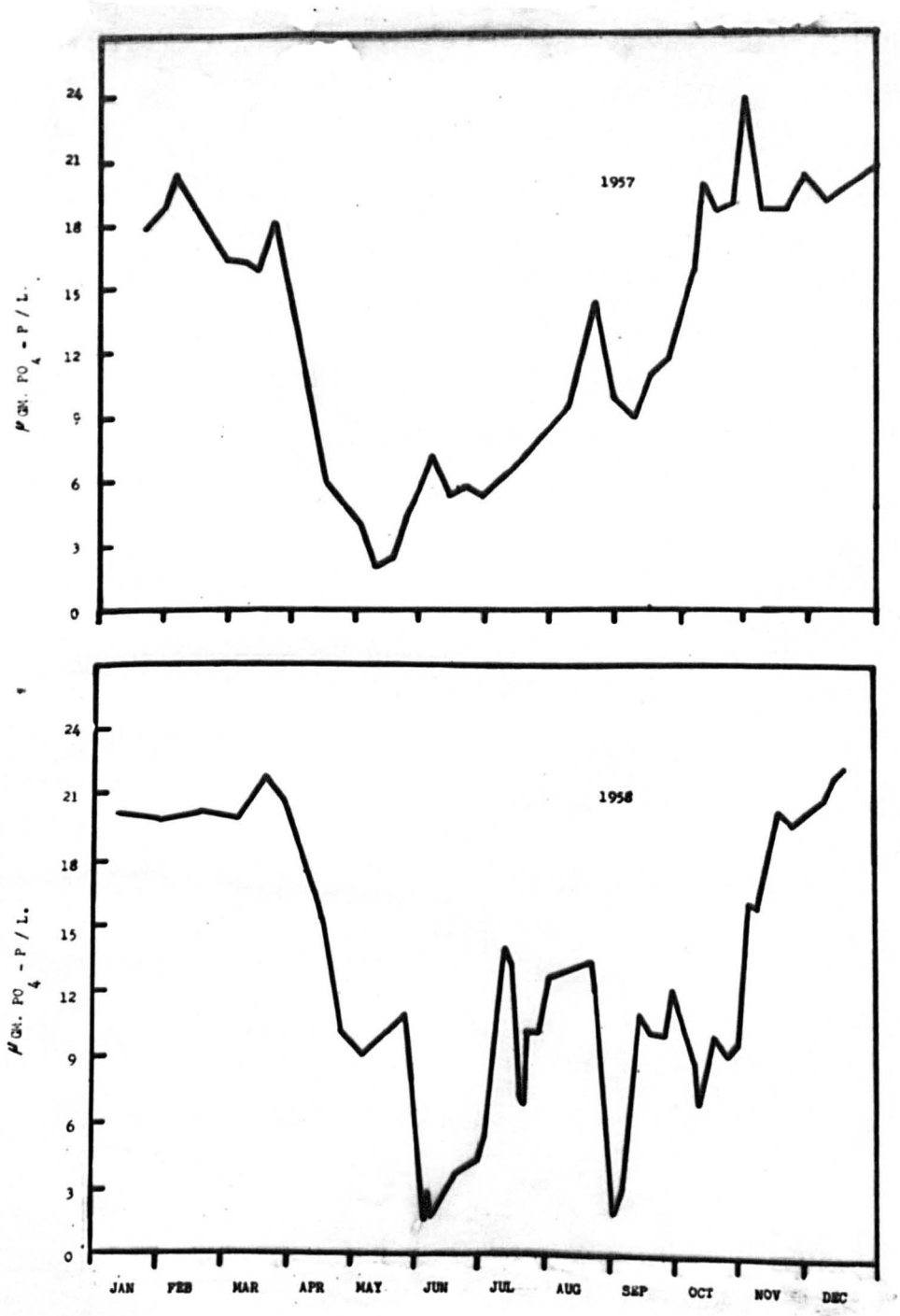


FIG.9.SEASONAL VARIATIONS IN THE DISSOLVED PHOSPHATE CONTENT OF SEA WATER IN THE MENAI STRAITS

1957 & 1958 (DATA PROVIDED BY MR. P.G.W.JONES.)

with those of the spring months. In 1958, however, a sharp decline in the phosphate (Fig. 9) at the end of August coincided with a sharp increase in the diatom population (Fig. 3) beyond the corresponding peak reached in 1957. From the end of August onwards, the phosphate tended to increase in both years. At the same time the total zooplankton also continued to increase (despite the decreased productivity of phytoplankton), reaching a value much higher than the spring peak. In 1957 the zooplankton peak was recorded on 1st October and in 1958 on 10th November, at which times the phytoplankton production was low. The lack of phytoplankton cannot be attributed to grazing, since the phosphate content of the sea water showed a sharp increase at the same time, indicating a reduced phytoplankton production. The zooplankton in the autumn months, as will be seen from Fig. 7, mainly represented Oithonina nana and Euterpina acutifrons. The increasing density of the populations of these species of copepod during September 1957 and October and November 1958, when the phytoplankton was low, is surprising. It is possible that these species, which are restricted to inshore waters, can obtain useful nutrient from organic particulate matter. This economy is in sharp contrast to that of the spring and early summer copepods whose grazing greatly depletes the phytoplankton.

The inverse relationship between the phytoplankton and the zooplankton has been explained by Hardy's animal exclusion hypothesis (Hardy & Gunter, 1935). This supposes that high concentrations of phytoplankton are in some way distasteful to the zooplankton and cause it to migrate vertically downwards away from the phytoplankton. At lower levels water currents may be different from those on the surface and carry the animals away from the

phytoplankton. In the present study Hardy's hypothesis does not appear to be applicable, since turbulent mixing of the water in the Menai Straits probably results in the population being more or less homogenous and nullifying the effect of vertical migration. The inverse relationship envisaged in this hypothesis involves the occurrence of the minimum zooplankton populations at times when the highest phytoplankton density occurs. The results of two years suggest that, rather than a relationship of this kind, the changes in the phytoplankton population in the Menai Straits were followed by similar changes in the zooplankton. No evidence of a high phytoplankton concentration having a harmful effect on zooplankton is provided in this work. For instance, the phytoplankton is most numerous during the Phaeocystis blooming; during this time some copepods, such as Temora and Centropages, could live and thrive.

The density of the zooplankton in 1958 was considerably lower than that of 1957. This may largely be attributed to low temperature conditions in 1958, which presumably had a marked influence on the development rate in various animals, and consequently affected the population density. This is in accordance with Nielson (1937) who considered the inverse relationship to be due to slower development of the zooplankton, although he accepted that the grazing effect may be the main factor.

Summary

The seasonal abundance and variations of the plankton of the Menai Straits has been studied from March 1957 to December 1958.

Comparison of the two years showed differences in the seasonal abundance and succession of various planktonic organisms. In 1957 the phytoplankton was less numerous than in 1958. On the other hand, the zooplankton population in 1957 was larger than in 1958. It is suggested that the comparative paucity of phytoplankton in 1957 was largely the result of grazing by a zooplankton population larger than that of 1958. It is also suggested that this larger zooplankton population in 1957 was mainly due to higher temperature conditions than those of 1958 and that the lower temperatures of 1958 resulted in the later appearance of many plants and animals.

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PART II

Development of *Euterpina acutifrons* (Dana) with special reference to dimorphism in the male sex

Contents

Introduction

Euterpina acutifrons Dana is one of the few pelagic harpacticoid copepods; the majority are benthic. It has a world wide distribution. In the waters round Anglesey it breeds as one of the dominant species of the zooplankton in late summer and autumn and it is this population that has provided the material for the present study.

The adult of Euterpina acutfrons was first described by Giesbrecht (1892) and his description has been amended by Sars (1921, Vol. VII). The development of the species (obtained from Haaks, Holland) was described by Tesch (1915), but his description was inaccurate and incomplete. According to him, there are five nauplius stages, an error resulting from a failure to distinguish between the fourth and fifth nauplii. He gave no illustration of the first nauplius and his description of it was deficient in some essential characteristics. His figures of later nauplii were also incorrect in some particulars, while his account of the posterior appendages gave rise to misleading conclusions which were criticized by Lang (1948, pp. 129-141). He gave a description of only the first two copepodite stages, which also required reinvestigation.

Thus an investigation of the development of the species seemed advisable, particularly since it exhibits the phenomenon of dimorphism in the males. The sequence of development in copepods where this occurs has been the subject of some controversy in the past. Sewell (1912, 1929), after studies on a number of calanoid copepods, put forward a rather complicated scheme of growth in species where dimorphism occurs in either sex. He postulated that a male at the end of the third copepodite stage

may moult into the fourth copepodite and thence into the 'high form' adult (omitting the fifth copepodite stage), or alternatively may moult directly into the fifth stage (omitting the fourth) and become sexually mature in this, the 'low form.' Thus in the line of development to either male dimorph, a copepodite stage is skipped. In the female he postulated that the two dimorphic adults are two successive stages and may be displayed in the same individual.

Gurney (1929), after working on fresh water calanoids, disagreed and suggested that all individuals must pass through the third, fourth and fifth copepodite, but that at the moult to the adult some would do so to become the 'low form' while a few, more vigorous than the others, would moult with a greater growth increment to the 'high form.' He also suggested that an additional moult of the 'low form' to the 'high' might occur. He referred to the 'low form' adult as the sixth copepodite stage and the 'high form' as the seventh.

Both Sewell and Gurney discounted the possibility of seasonal effects, but other workers have shown that minor differences in the structure and size may be conditioned by the environment. Hartmann (1917) observed minor differences in the fifth swimming leg of Cyclops straenus at different seasons. Coker (1933) demonstrated experimentally that temperature has a direct effect on the size of the individual in some species of Cyclops. Others have suggested that greater variability in mean size may be observed in successive broods (Marshall, 1933) or in broods segregated in different water masses (Russell, 1928b) or may result from the interbreeding of different varieties or races (Steuer, 1931).

It seemed desirable, in attempting to solve the problem of growth and development in dimorphic forms, to breed the animals under laboratory conditions so that the full course of development could be followed in single individuals. A complete explanation is unlikely to be attained by studies of the natural populations of plankton alone.

The morphology of the larval stages of a number of harpacticoid copepods has been described, notably by Chappuis (1916), Brian (1919, 1921), Gurney (1929) and Nicholls (1941), while complete studies of both larval and postlarval development have been made by Fraser (1936) and Shaw (1938) in Tigriopus fulvus; by Johnson & Olson (1948) in Tisbe furcata and by Krishnaswami (1951) in Macrosetella gracilis. Rearing the larvae has been attempted only seldom, however, and then with limited success. Nicholls (1935) reared the larvae of Longipedia corronata, L. scotti and L. minor sufficiently to demonstrate the specific characters, and the littoral species Tisbe furcata was reared by Johnson & Olson (1948). Battaglia (1957) succeeded in rearing Tisbe gracilis.

Description of the dimorphic males

The two adult males may be easily distinguished in natural populations by their marked differences in size and will be referred to as 'large' and 'small' male accordingly.

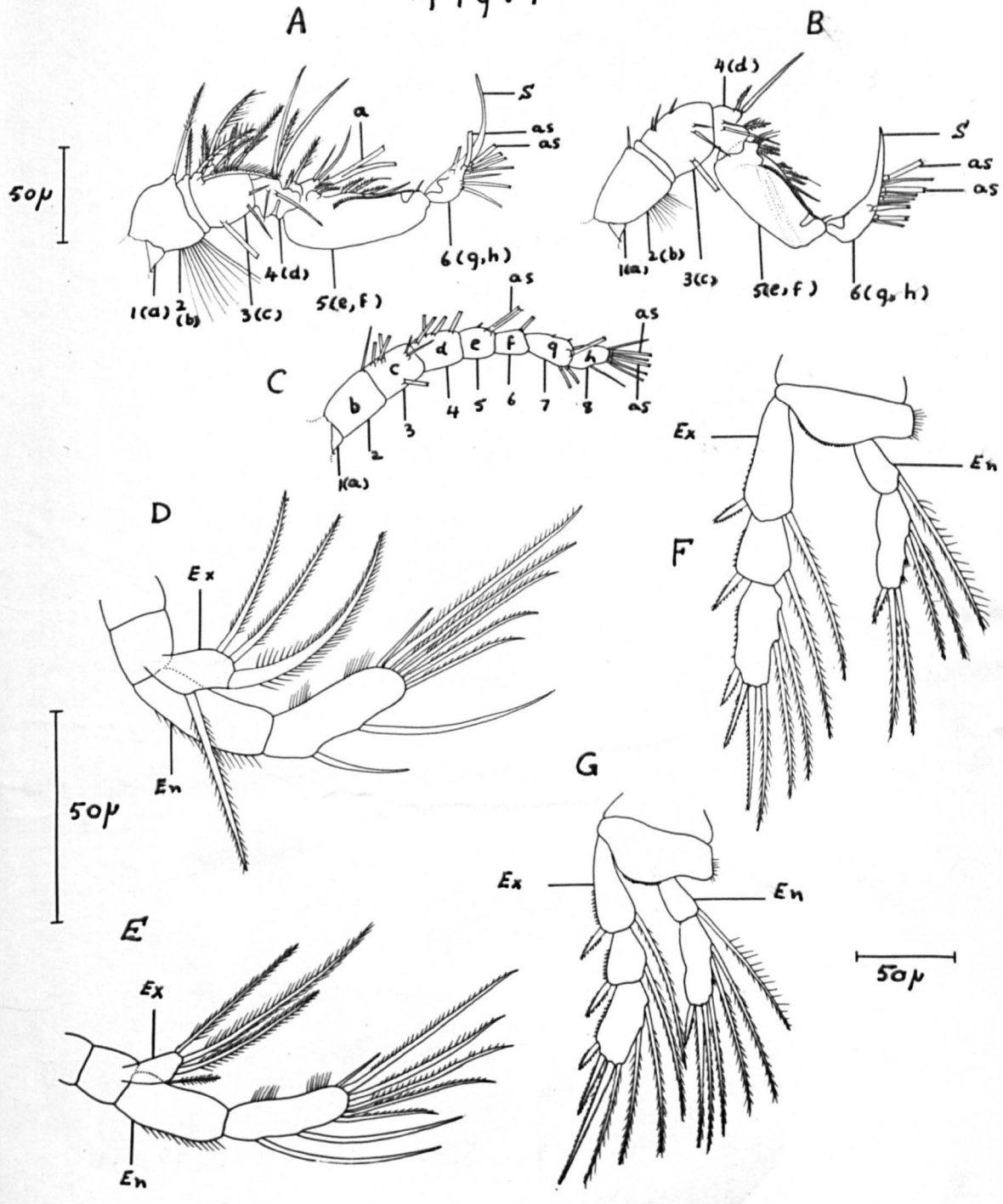
The large male in the typical form described by Giesbrecht (1892) measures about 0·65 to 0·70 mm. in length; the small male is about 0·525 to 0·60 mm. long. In addition to the difference in size, the two males show structural differences as follows:

Fig. 1. Appendages of the adults of Euterpina acutifrons showing dimorphism in the male sex.

A: Right antennule of the large male; B: Right antennule of the small male; C: Right antennule of the female; D: Left antenna of the large male; E: Left antenna of the small male; F: Right second swimming leg of the large male; G: Right second swimming leg of the small male.

1-8: antennular joints; as: aesthate seta; En: endopodite; Ex; Exopodite; S: spiny projection of last joint of antennule.

Fig. 1


A
B
C
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F
G
50μ
50μ
50μ
a
S
as
as
1(a)
2(b)
3(c)
4(d)
5(e,f)
6(g,h)
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c
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En

1. The antennules in both the males are strongly tumulated and resemble each other in general morphology, but differ markedly in the setation of the third joint. In the large male (Fig. 1,A) there are ten large setiferous setae and two small setae, whereas in the small male (Fig. 1,B) only one large and five small setae are found, as in the female (Fig. 1,C). The hinge joint (the fourth) in the large male also possesses one more seta in addition to those found in the small male. The second joint is markedly dilated in the large male but cylindrical in the small male.

2. The antennæ show differences in the setation. The proximal seta of the last joint of the endopodite is short and hook-like in the large male (Fig. 1,D) but is as long as the distal setae in the small (Fig. 1,E). The first seta of the exopodite in the large male is longer and the second is stouter than those of the small male. The antenna of the small male is similar to ~~the~~ that of female in all its characteristics.

3. There is a difference in the setation of the last joint of the endopodite of the second pair of legs. In the large male (Fig. 1,F) this possesses four setae (excluding an outer spine), whereas in the small male (Fig. 1,G) it has five.

Chappuis (1936) reported dimorphism in the second pair of legs in males collected from Racife (Brazil), as compared with specimens from Calicut (India) which resembled the typical form described by Giesbrecht (1892). He did not report the difference in the antennule and antenna

mentioned above. It is curious that the variation in Chappuis' material seems to be distinctly geographical and it would be interesting to investigate the extent of dimorphic variation in this species under different ecological conditions in different parts of the world.

Methods

In all the rearing experiments, culture dishes about 9 cm. in diameter and about 5 cm. deep were used, each containing about 150 ml. of unfiltered sea water. The larvae were fed on fresh cultures of Nitzschia closterium. The amount of food was limited to prevent more than a thin layer of diatom cells accumulating at the bottom of the culture dish. A serious mortality of nauplii was found to result from such an accumulation, presumably because of the tendency of the dead cells to clump together and stick to various parts of the bodies of the nauplii. Throughout the experiments the medium was unchanged and remained undisturbed except for occasional stirring.

Females carrying eggs were transferred to culture dishes. Here the eggs hatched and the larvae developed. Individual stages and the cast skins of the previous stages were picked out from the culture medium and studied in detail, using the Labgear-Harding microdissector.

In order to examine the inception of morphological differences between the dimorphic males and the female, the newly hatched larvae from a single egg mass were reared individually in Boveri dishes, each containing about 15 ml. of sea water which was changed on alternate days. After each moult the cast skin was examined. At the end of the experiment some

individuals had developed into large males, some into small males and some into females. No morphological differences could be seen until the moult of the third copepodite, but after this there were marked structural changes and the two males and the female could be distinguished in the fourth copepodite and subsequent stages.

Measurements of the whole body length in harpacticoid copepods does not give a reliable indication of size due to marked contractibility of the hyaline membrane between the body somites. To avoid this source of error the measurements of thoracic and abdominal somites were made separately and the total body length calculated. Measurements of the cephalothorax and the antennule were also recorded separately. The antennular measurement was taken from the proximal border of the second joint since the first joint in this species remains in a reduced form and is partly covered by the cephalothorax. All measurements were made at a magnification of x 600. All individuals were covered by a cover glass during measurement.

Larval development

Body shape and size

The body is oval shaped and in the early nauplius stages is completely covered by the dorsal cephalic shield (Fig. 2,A-E). In the fifth nauplius, and more noticably in the sixth nauplius (Fig. 2,E,F), the body extends beyond the posterior margin of the dorsal shield, thus changing the shape of the nauplius from oval to an oblong in the later stages.

The mean lengths and standard deviations of individual stages from the culture stock is given in Table I. The coefficients of variation show

Fig. 2. Larval stages of E. acutifrons.

A: Ventral view of the first nauplius showing associated structures. Only the right antennule, antenna and mandible are shown. B, C, D, E: Ventral view of the posterior half of the second to fifth nauplius stages, showing changes in the body. F: Ventral view showing changes in various appendages. Only the right antennule and mandible and the left antenna are shown.

A: antennule; An: antenna; P: blunt process; F: furcal seta; Fs: furcal spine; GP: mandibular gnathobase; La: labrum; Lr_1: rudiments of the first swimming leg; Lr_2: rudiments of the second swimming leg; M: rudiment of the maxillule; Ma: rudiment of the maxilla; Mn: mandible; MP: rudiment of the maxilliped; O_1: anterior fence, and O_2: posterior fence of stiff hairs; As_1: first row, and As_2: second row of abdominal spines. Other abbreviations as given earlier.

Fig. 2

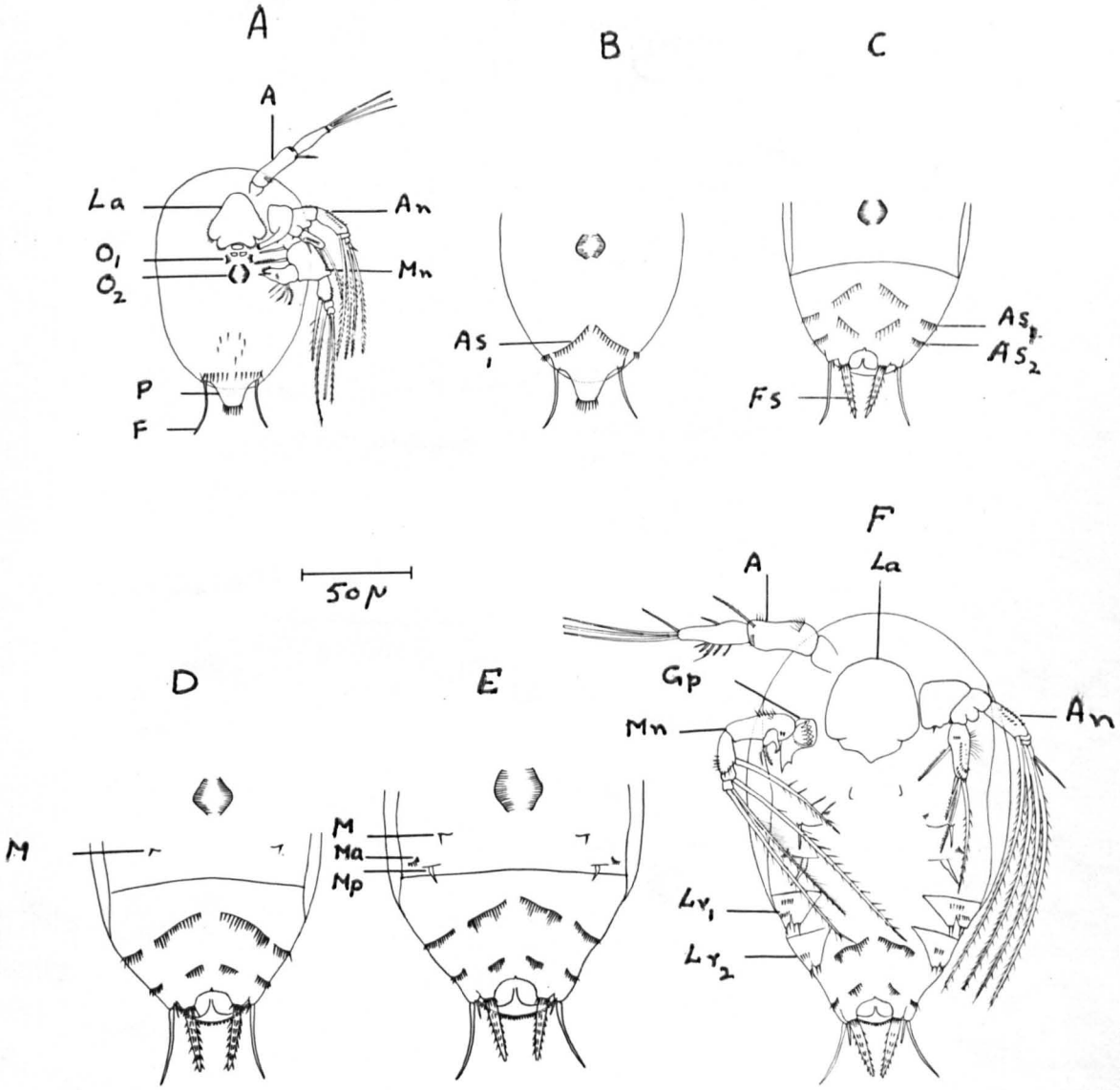

A
B
C
A
La
An
O1
O2
Mn
P
F
As1
Fs
As1
As2
50μ
F
A
La
Gp
Mn
An
Lv1
Lv2
D
E
M
M
Ma
Mp

Table I. Measurements of the larval stages of E. acutifrons reared under laboratory conditions. All measurements in microns. Mean values of all stages based on measurements of 36 individuals.

Growth factor = Mean length of one part ÷ mean length of that of the previous stage.
S.D. = Standard deviation. C.V. = Coefficient of variation.

Stages	Total body length				Length of antennule			
	Mean length	S.D.	C.V.	Growth factor	Mean length	S.D.	C.V.	Growth factor
Nauplius I	100 ± ·55	3·31	3·31	-	40 ± ·54	2·66	6·70	-
Nauplius II	117 ± ·55	3·31	2·83	1·17	44 ± ·23	1·41	3·21	1·1
Nauplius III	134 ± ·45	2·70	2·01	1·14	51 ± ·35	1·92	3·77	1·15
Nauplius IV	154 ± 1·07	6·47	4·19	1·14	57 ± ·26	1·58	2·77	1·11
Nauplius V	176 ± 1·22	7·35	4·17	1·14	64 ± ·54	3·25	5·08	1·12
Nauplius VI	194 ± 1·45	7·72	3·98	1·10	68 ± ·39	2·38	3·51	1·06

that no greater variability exists in the size of any one stage such as would indicate a sexual dimorphism, as Murphey (1923) considered might be the case in Oithonina nana. The growth factor, i.e. the ratio of the length of the stage following a moult to that of the stage before, is regularly about 1·14 at each moult, except that of the second and sixth n nauplii. This seems to be different from most other copepod nauplii, where the increase in the size of the nauplius varies considerably at each moult (Ogilvie, 1953; Johnson & Olson, 1948).

Associated structures of the ventral surface

The labrum (Fig. 2,A) of the larval Euterpina is characterized by the presence of distinct lobes on the posterior margin and is surrounded by a complex pattern of hairs. In the first five nauplius stages it remains unchanged, but at the sixth nauplius it loses its hairs and characteristic shape, becoming sac-like (Fig. 2,F). Just below the labrum there is a pair of vertical chitinous ridges. Behind these ridges there are two pairs of 'fences' of stiff hairs (Fig. 2,A. - O_1, O_2). The anterior pair, O_1, is small, while the posterior pair, O_2, is larger and extends antero-posteriorly in a semi-circular fashion. At the sixth nauplius these structures, which remain unchanged throughout the first five stages, disappear (Fig. 2,F). On the posterior half of the body there are spines which are irregularly arranged on the hind body in the first nauplius (Fig. 2,A). These ventral hind body spines undergo characteristic changes in their number and arrangement in the subsequent stages and provide diagnostic features by which the early naupliar stages may be separated. In the second nauplius they are

arranged in a convex line and consist of twelve medial and four lateral spines on either side of the mid line (Fig. 2,B. - AS_1). In the third nauplius there are two rows of these spines, AS_1 and AS_2. The first row is convex towards the front and is clearly split into four groups, two on either side of the mid line (Fig. 2,C), having about 10 to 12 medial and 7 to 9 lateral spines on either side. The second row is concave towards the front and is similarly split into four groups with 7 to 9 spines in each. In the fourth nauplius (Fig. 2,D) the two rows of hind body spines are parallel to each other. In the first row the medial group has 17 to 19 spines and the lateral 7 to 9 spines. The second row in both the groups has 7 to 9 spines. The arrangement of spines at the fifth nauplius differs from that of the fourth in having about 16 spines in the lateral group of the first row (Fig. 2,E). In the sixth nauplius the lateral group of the first row does not exist, the rudiment of the second pair of swimming legs appearing in its place (Fig. 2,F:Lr_2). The number of spines in the remaining groups is about the same as in the fifth nauplius.

In the third nauplius a segment line is visible in front of the abdominal spines (Fig. 2,C). This is also present in the fourth and the fifth nauplius, but becomes indistinct in the sixth.

The posterior end in the first two nauplius stages is extended to form a blunt process, (Fig. 2,A,B:P), bearing about 8 spinules on its tip. This disappears in the third nauplius (Fig. 2,C) and the posterior border becomes smooth. At the fourth nauplius this becomes fringed and remains so in subsequent stages.

Table II. Setation of the antennule of larval Euterpina.

Joint	Stages					
	first nauplius	second nauplius	third nauplius	fourth nauplius	fifth nauplius	sixth nauplius
1	0	0	0	0	0	0
2	1	1	1	1	1	1
3	0/1a1/0	0/1a1/1	2/1a1/1	3/1a1/1	4/1a1/1	6/1a1/2

In the third joint, the first figure represents the setae on the preaxial margin, and the last those on the postaxial. The centre group represents the terminal setae, as two figures on either side of the aesthate seta (a).

On each side of the blunt process in the first two nauplius stages there is one delicate furcal seta, F, arising from a protuberance, which is retained throughout the larval development. At the third nauplius a pair of strong dagger-shape furcal spines, FS, (Fig, 2,C-E) develop posteriorly on either side of the mid line and are retained in the subsequent stages.

Appendages and setations

Antennule

The antennule is three jointed throughout larval development. The first joint is very small and remains hairless at all stages. The second joint bears a long seta at its distal end and groups of hairs arranged in a characteristic pattern (Fig. 3,A-D). This joint also remains unchanged throughout larval development. In the early nauplius stages the second joint is longer than the others, but in the later stages the third, terminal joint becomes the longest. The third joint is slightly tapered and in the first nauplius bears only three terminal setae, of which the middle one is an aesthate (Fig. 2,A a). In the subsequent development there is an increase in the marginal setation of this joint (Fig. 3,A-D; Fig. 2,F), furnishing a useful diagnostic feature for the separating of the various larval stages. This increase in the setation is summarized in Table II. Characteristic changes of this kind in the antennule have not previously been reported in the group Harpacticoida. In this respect the species is similar to the Calanoida and Cyclopoida where characteristic changes in the setation of the terminal joint of the antennule occur in the nauplius stages.

Fig. 3.

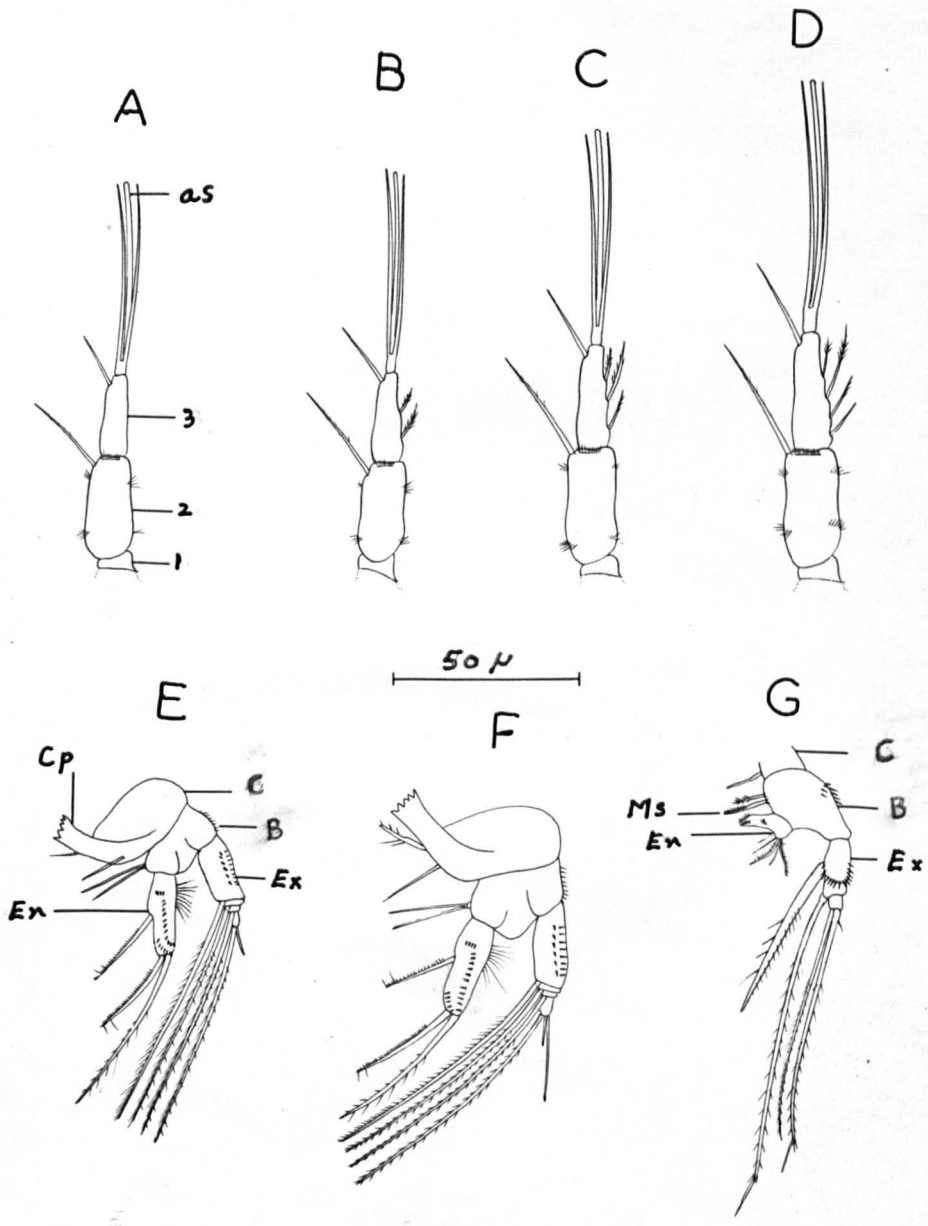
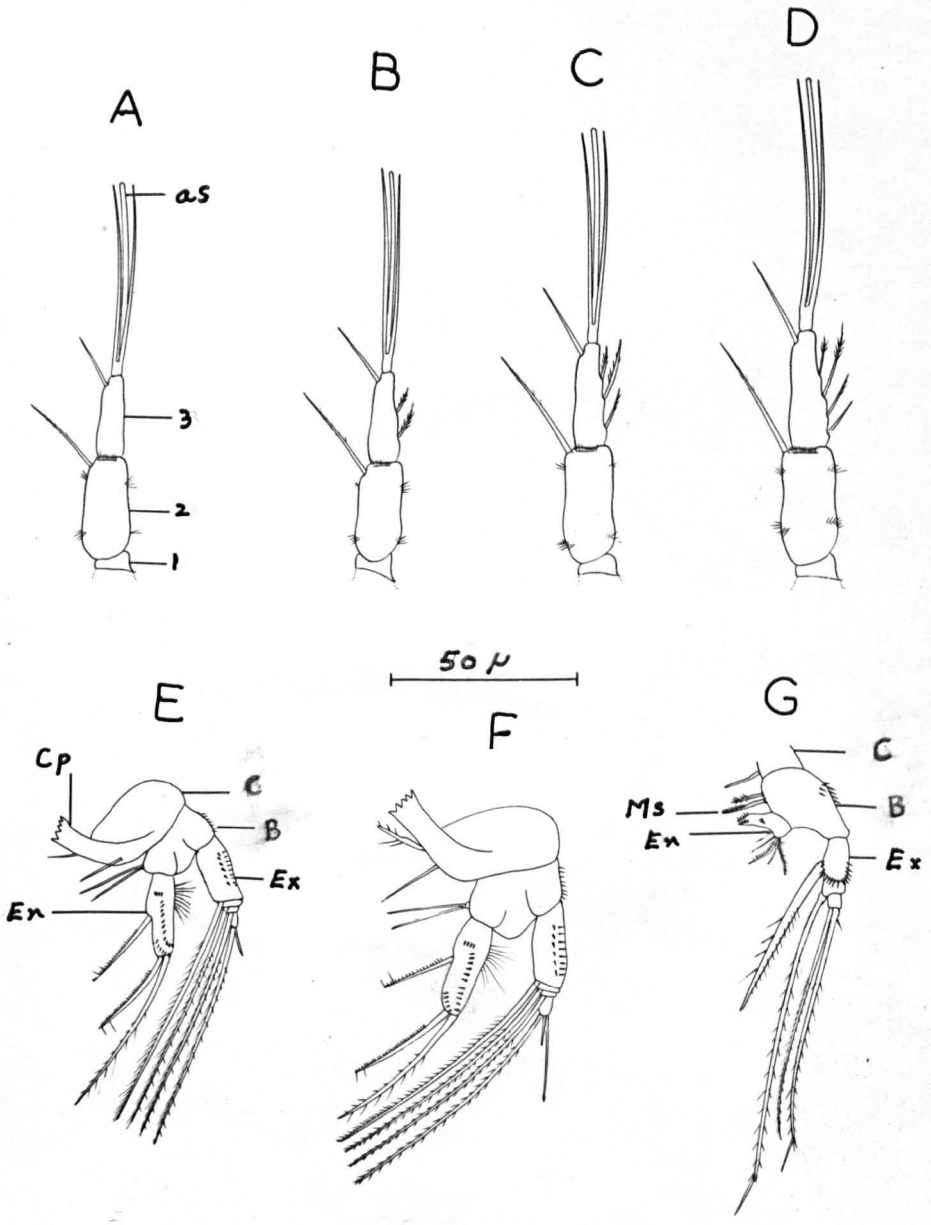


Fig. 3. Larval appendages of *E. acutifrons*.

A, B, C, D: Right antennule of the second, third, fourth and fifth nauplius. E, F: Right antenna of the second and third nauplius; G: Right mandible of the second nauplius.

B: basipodite; C: coxopodite; Cp: toothed coxal masticatory process of antenna; Ms: masticatory spine. Other abbreviations as given earlier.

Fig. 3.



The length of this appendage in each of the larval stages is given in Table I. There is a uniform increase in length at each moult except at the moult of the fifth nauplius when the increase is a little smaller. The increase in the length of this appendage is thus proportional to the uniform increment in the total body length (Fig. 6) at each stage.

Antenna

The antenna of the nauplius of Euterpina resembles in its main characteristics that of the typical harpacticoids (Gurney, 1931; Lang, 1948), but differs in certain details. Its endopodite has one joint (Fig. 3,E,F. - En), which bears one seta midway along and two delicate, curved, terminal setae, of which the smaller is highly mobile. In the first five nauplius stages the setation of the endopodite remains unchanged, but in the sixth nauplius there is an additional spine and a small seta at its distal end (Fig. 2,F).

The exopodite has four joints (Fig. 3,E,F. - Ex), the first being the longest, the second and third being annular, and the last thumb-like. Each joint bears a long feathery bristle, the last joint bearing a small spine in addition. The setation of this ramus, except for the addition of a small seta on the distal end of the last joint at the third nauplius (Fig. 3,F), remains unchanged from the first nauplius onwards. Both the endopodite and the exopodite of the antenna bear numerous small spinules arranged in a characteristic pattern. These spinules have not been reported in other harpacticoid nauplii.

Tesch (1915) reports that the larval antenna of Euterpina has a two jointed endopodite and a five jointed exopodite, but careful examination shows that the so-called first joint in each case is merely an extension of the basipodite which allows the rami a range of rotatory movement (Fig. 3.E,F:B).

The basipodite B (Fig. 3.E,F) is a folded plate, bearing two setae on its posterior margin, both arising from a common base. The coxopodite C (Fig. 3.E,F) is a large plate bearing a strongly toothed masticatory process Cp, as in other harpacticoids. The outer margin of this process bears a minute seta in the first nauplius. In the second nauplius a second blunt seta is also present; these setae remain unchanged up to the fifth nauplius. In the sixth nauplius the whole masticatory process and the setae on the basippdite are lost and are represented by spines (Fig. 2.F: An). There is no mention of this structure in the larval stages of Euterpina described by Tesch (1915) and no indication of it in his illustrations.

Mandible

The mandible (Fig. 3.G) has an exopodite of three joints which is longer in proportion to the appendage as a whole than that of other harpacticoid nauplii. On the postaxial margin of each of the first two joints is a very long bristle, the bristle on the first joint being slightly shorter and stouter than that on the second. The distal joint carries two very long bristles, of which the proximal is the more delicate (Fig. 3.G). The exopodite remains unchanged in form throughout the larval development.

The one-jointed endopodite is placed on the postaxial margin of the basipodite and is not so strongly prehensile as that described in all other harpacticoids. It is club-shaped and split distally into two halves each carrying fine, stiff hairs. The basal portion of this ramus extends alongside the basipodite and bears five small setae, of which two are feathery (Fig. 3.F:En). At the sixth nauplius this ramus becomes reduced and simplified, losing all its stiff hairs and the spines borne at its distal end (Fig. 2.F:Mn).

The basipodite of the mandible is a large square plate. A prominent masticatory spine arises from its postaxial margin in the first nauplius (Fig. 2.A:Ms). In the second nauplius a small masticatory spine is developed below the first long one (Fig. 3.G:Ms). These spines are retained up to the moult of the fifth nauplius and are represented by minute spines in the sixth nauplius (Fig. 2.F:Mn).

The coxopodite is a small plate with a smooth, delicate postaxial seta (Fig. 3.G:C). Its form remains unchanged in the first five nauplius. In the sixth nauplius, in place of the postaxial seta, the coxopodite develops a digital protuberance, beneath whose chitinous covering can be seen the toothed process of the gnathobase (Fig. 2.F:Gn). This early acquisition of the mandibular gnathobase (though it is non-functional at this stage) is not reported in other harpacticoid copepods.

The description of the mandible given by Tesch (1915) is incomplete. He did not distinguish between the endopodite and the exopodite of the appendage and his description of the former, in particular, is not clear and is vague in his illustration. There is no mention in his account of the

masticatory spines and coxal seta in the early stages nor of the precocious development of the gnathobase.

Rudiments of posterior appendages

The maxillule can first be distinguished in the fourth nauplius in the form of a single very small spine (about 4μ in length) arising from a ridge (Fig. 2.E:M) just behind the posterior fence of stiff hairs. In the fifth and sixth nauplii this spine is larger, but no other change is noticable (Fig. 2.E,F:M).

The maxilla first appears in the fifth nauplius in the form of a semi-circle of about five spines arising from a ridge behind the maxillule and further to the side of the body (Fig. 2.E:Ma). No radical change is noticable at the sixth nauplius. The maxilliped also appears in the fifth nauplius just in front of the segment line in the form of a small spine (Fig. 2.E:Mp). It is much more distinct in the sixth nauplius.

In the individuals of the sixth nauplius about to moult these appendages may be seen in a fully developed form below their respective larval sturctures. The rudiments of the first two pairs of legs, Lr_1 and Lr_2, appear in the sixth nauplius just above the level of the first row of hind body spines (Fig. 2.F).

The earlier account of the development of the posterior appendages given by Tesch (1915) is erroneous. He reports the appearance of the maxillule as early as the second nauplius, assigning this name to the posterior fence of stiff hairs in the oral region (Fig. 2.A-E:O_2). In fact this structure is also present in the first nauplius and disappears only in the sixth nauplius and therefore cannot be the maxillulary rudiment (Fig. 2.F).

Similarly he reports, as is clear from his illustrations, a row of hind body spines, just in front of the first segment line, as being the maxillipeds appearing for the first time in the second nauplius. Careful examination of their developmental stages and their casts does not show the presence of any spines of this kind either in the second or even in the third or fourth nauplius. In fact these spines appear in the fifth nauplius and represent the rudiment of the maxillae, whereas the maxillipeds appear in a digital form in the fifth nauplius as in other harpacticoids.

Tesch (loc-cit) also reports the rudiments of the first pair of legs appearing as early as the third nauplius and the second pair in the fourth or fifth nauplius, referring to the median groups of hind body spines (Fig. 2.D,E:As_1, As_2). In his illustration of the sixth nauplius, in addition to these hind body spines, there are indications of the rudiments of these legs in the same position as shown in Fig. 2.F:Lr_1, Lr_2), which he does not account for.

Feeding mechanism of the larvae

Some observations of the feeding mechanism in the fourth and fifth nauplius have been made. Observations were made under a microscope from preparations made both in a cavity slide and on an ordinary slide covered by a thin coverglass (no. 0). The food used was Nitzschia closterium.

The antennules do not take part in the collection of food. Both the antennae and, to a lesser extent, the mandibles are used in feeding. The antennae are highly mobile and capable of rotatory movement; they are the main feeding organs in the larva. The endopodite has terminal setae which

are more delicate than those of other harpacticoids. The smaller terminal seta is highly mobile and can be reflexed almost at a right angle to the axis of the appendage so that it can be placed on the mid-ventral surface of the body below the oral region. By the sweeping movements of the antennae and the continuous inward and outward movements of the smaller terminal seta on their endopodites, the food is brought to the oral region. The two toothed coxal masticatory processes of the antennae are placed underneath the labrum, each moving continuously against its counterpart. This action appears to crush the food before ingestion.

The mandible is mainly a swimming organ and is well adapted for this purpose, but also takes part in the collection of food. Its endopodite is smaller and less prehensile than that seen in other harpacticoids. The long feathery masticatory spine on its basipodite is directed inward and reaches very near the mouth. During the forward and backward movement of the mandibular exopodite, the food is gradually moved towards the oral region. This movement is clearly visible when the animal is seen from the dorsal side. Simultaneously, movements of the endopodite and of the long masticatory spine assists in pushing the food particles towards the mouth. The method by which food is ingested has not been observed.

Thus in Euterpina, as in other harpacticoids (Claus, 1858), both the antenna and the mandible take part in feeding. This seems to be different from the Calanoida and Cyclopoida (Gauld, 1959) where the mandible is the principal food collecting appendage. In cirripede nauplii, however, both the antenna and the mandible take part in feeding (Norris & Crisp, 1953).

Postlarval development

Body shape and size in postlarval stages

The body of the first copepodite resembles that of the adult in general form. It consists of a cephalothorax, four thoracic somites and one abdominal somite (Fig. 4.A). The anterior end of the cephalothorax has a beak-like projection, as in the adult. Posteriorly it completely covers the first thoracic segment, which is without a dorsal plate. The next three somites represent the second (Th_2), third (Th_3) and fourth (Th_4) thoracic somites. The last (posterior) somite represents the fifth thoracic and the rest of the abdominal somites and bears on its ventral surface two rows of spines which presumably correspond to the first two rows of hind body spines of the larvae. At its posterior end it has a fringed border, which corresponds to that of the larvae, and is retained throughout copepodite development. Each of the furcal rami bears three small spines on its dorsal surface and a long furcal seta at its subdivided tip. These structures are similar to those of the adult.

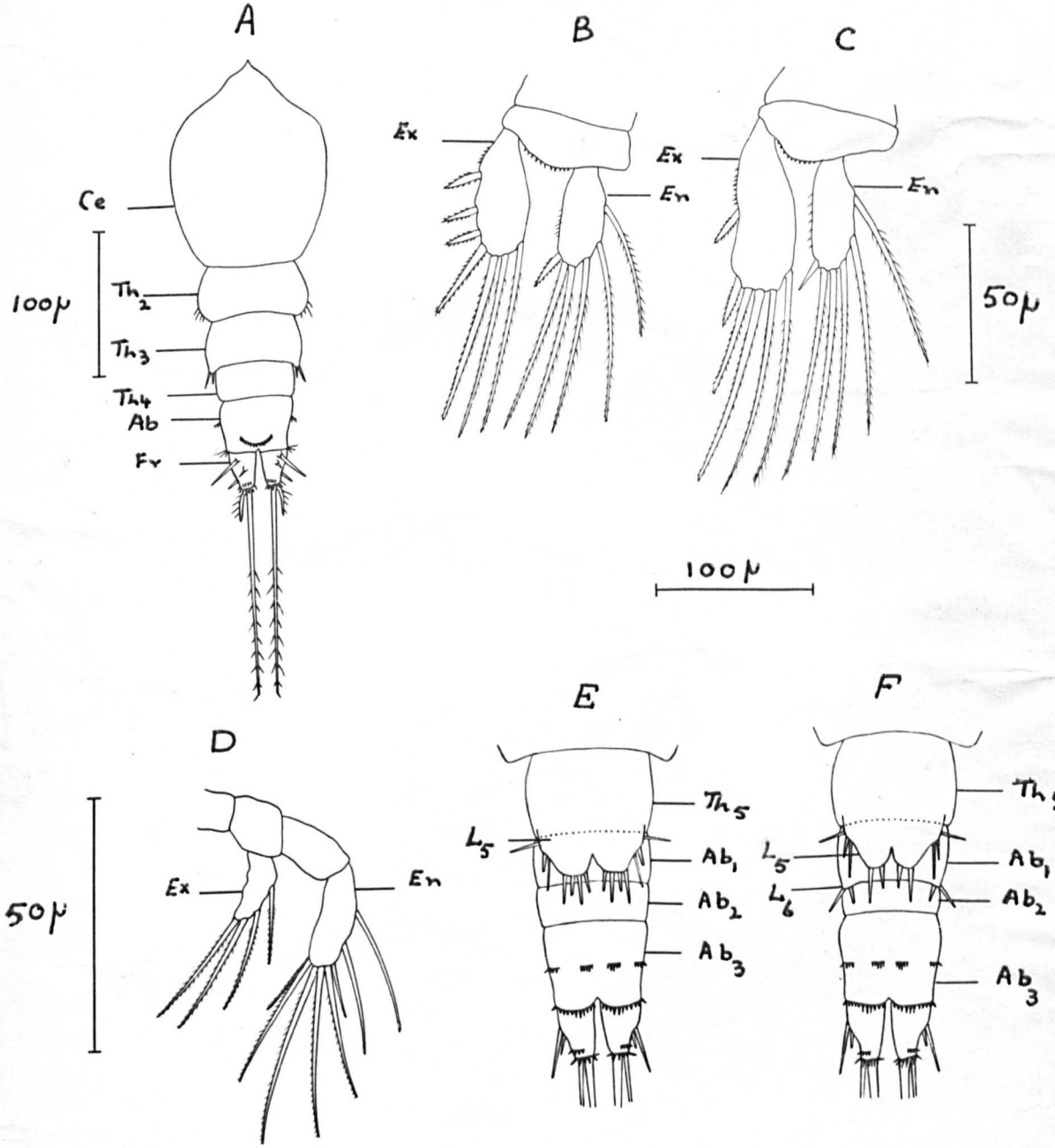
The addition of somites at each copepodite moult follows the general plan described in all other harpacticoid copepods (Gurney, 1932). At each moult one new somite is formed by the division of the last somite. Thus the fifth and last thoracic somite in the second copepodite is formed by the division of the fourth thoracic somite of the first copepodite. The first abdominal somite is formed at the moult of the second copepodite; the second at that of the third copepodite, and the third at that of the fourth. At the last moult in both the sexes the last somite divides to give rise to the fourth and the fifth abdominal somites of the adult. In the female, at the

Fig. 4. Copepodite I and its appendages, and the sex differentiation at copepodite IV.

A: Dorsal view of the entire body of copepodite I; B: Left first swimming leg, and C: left second swimming leg of copepodite I; D: Left antenna of copepodite I; E: Ventral view of the urosome of copepodite IV female; F: Ventral view of the urosome of copepodite IV large male, showing the sixth leg.

Ab: abdomen; Ab_1 - Ab_3: first, second and third abdominal somites; Th_2 - Th_4: second to fourth thoracic somites. Other abbreviations as given earlier.

Fig. 4


A
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Th4
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Ex
En
E
L5
Th5
Ab1
Ab2
Ab3
F
L5
L6
Th5
Ab1
Ab2
Ab3

last moult, as in other harpacticoid copepods, the first and second abdominal somites undergo fusion to form the genital somite.

In the larval stages the coefficients of variation show that the variability in size at any stage is not great enough to suggest a difference between the dimorphic males or between the sexes until the moult of the third copepodite, when the size range increases considerably. At this time sexual differentiation first occurs and the dimorphic males can also be distinguished both structurally and in size.

It will be seen from Table III that the total mean length in each of the two male forms differs considerably in the fourth copepodite and also in the subsequent stages. Until this time the growth factor has been uniform and about the same as that found during larval development. From the moult of the third copepodite onwards each dimorphic male has its own characteristic growth factor; 1·16 in the large male and 1·08 in the small. The total mean length of the female is much the same as that of the large male at each postlarval stage, so that the growth factors, except for a slight irregularity, are also about the same.

The two males show differences in the size of the cephalothorax from the fourth copepodite onward. No difference of this kind can be detected at earlier stages. In the small male the growth of the cephalothorax is retarded after the fourth copepodite in even more than proportion to the general reduction in growth rate of the body.

Table III. Measurement of the postlarval stages of E. acutifrons reared under laboratory conditions. All measurements in microns. Mean values of copepodite stages I ÷ V based on measurements of 30 individuals and adults on 35.

Growth factor = mean length of stage - mean length of previous stages.
S.D. = Standard deviation. C.V. = Coefficient of variation.

	Copepodite stages	Total body length				Length of cephalothorax				Length of antennule			
		Mean length	S.D.	C.V.	Growth factor	Mean length	S.D.	C.V.	Growth factor	Mean length	S.D.	C.V.	Growth factor
Small male	I	325 ± 1·58	8·62	2·65	1·67	157 ± ·71	3·91	2·49	-	70 ± ·30	2·68	3·83	1·02
	II	371 ± 1·42	7·78	2·09	1·14	167 ± ·54	2·97	1·77	1·06	81 ± ·42	3·74	4·61	1·15
	III	423 ± 1·31	7·14	1·68	1·14	174 ± ·87	4·75	2·73	1·03	93 ± ·44	3·82	4·10	1·14
	IV	459 ± 1·59	8·68	1·89	1·08	180 ± ·49	2·70	1·50	1·03	99 ± ·48	2·91	2·94	1·06
	V	488 ± 2·04	11·15	2·28	1·06	187 ± ·84	3·72	1·99	1·03	120 ± ·65	3·57	2·98	1·21
	VI	526 ± 1·86	11·06	2·10	1·07	190 ± ·30	1·81	·95	1·01	171 ± ·64	3·82	2·22	1·42
Large male	IV	490 ± 2·65	14·39	2·94	1·16	199 ± ·80	4·39	2·20	1·14	105 ± ·72	4·37	4·16	1·14
	V	569 ± 2·65	14·45	2·54	1·16	219 ± 1·30	7·11	3·24	1·10	138 ± ·59	3·27	2·44	1·31
	VI	678 ± 3·16	18·70	2·75	1·19	244 ± 1·18	7·02	2·87	1·11	206 ± 3·33	4·06	1·97	1·49
Female	IV	492 ± 1·91	10·46	1·12	1·16	198 ± ·92	5·02	2·53	1·13	105 ± ·88	5·29	5·03	1·12
	V	552 ± 2·60	14·21	2·57	1·12	219 ± ·92	5·05	2·31	1·10	116 ± ·61	4·79	4·13	1·10
	VI	674 ± 3·01	17·84	2·64	1·22	266 ± 1·38	8·17	3·07	1·21	147 ± ·74	4·40	2·99	1·26

The size of the cephalothorax is the same in the large male and the female at the fourth and fifth copepodite, but at the last moult that of the female grows longer than that of the large male. Despite the longer cephalothorax of the adult female, its total body length is the same as that of the large male, as the urosome is shorter.

Structural changes in the postlarval appendages

(i) Antennule

The development of the antennule in the postlarval stages of Euterpina acutifrons differs from that of typical harpacticoids (Gurney, 1931) in that the terminal joints of the adult (seventh and eighth in this species) are laid down at the moult of the sixth nauplius by the division of the terminal joint. In this respect this species agrees with the general plan of development presented by Oberg (1906) for the calanoids and cyclopoids.

In order to explain the course of development of the antennular joints each joint of the adult female antennule has been allocated a letter starting from the proximal joint (a) to the distal one (h). In Fig. 5 the joints of the appendage at earlier stages are shown with the same letters to indicate their relationship to the adult joints, e.g. the third joint of the antennule of the third copepodite (Fig. 5c) is lettered c-e, indicating that it will divide to give joints c, d and e, the third, fourth and fifth joints respectively of the adult female.

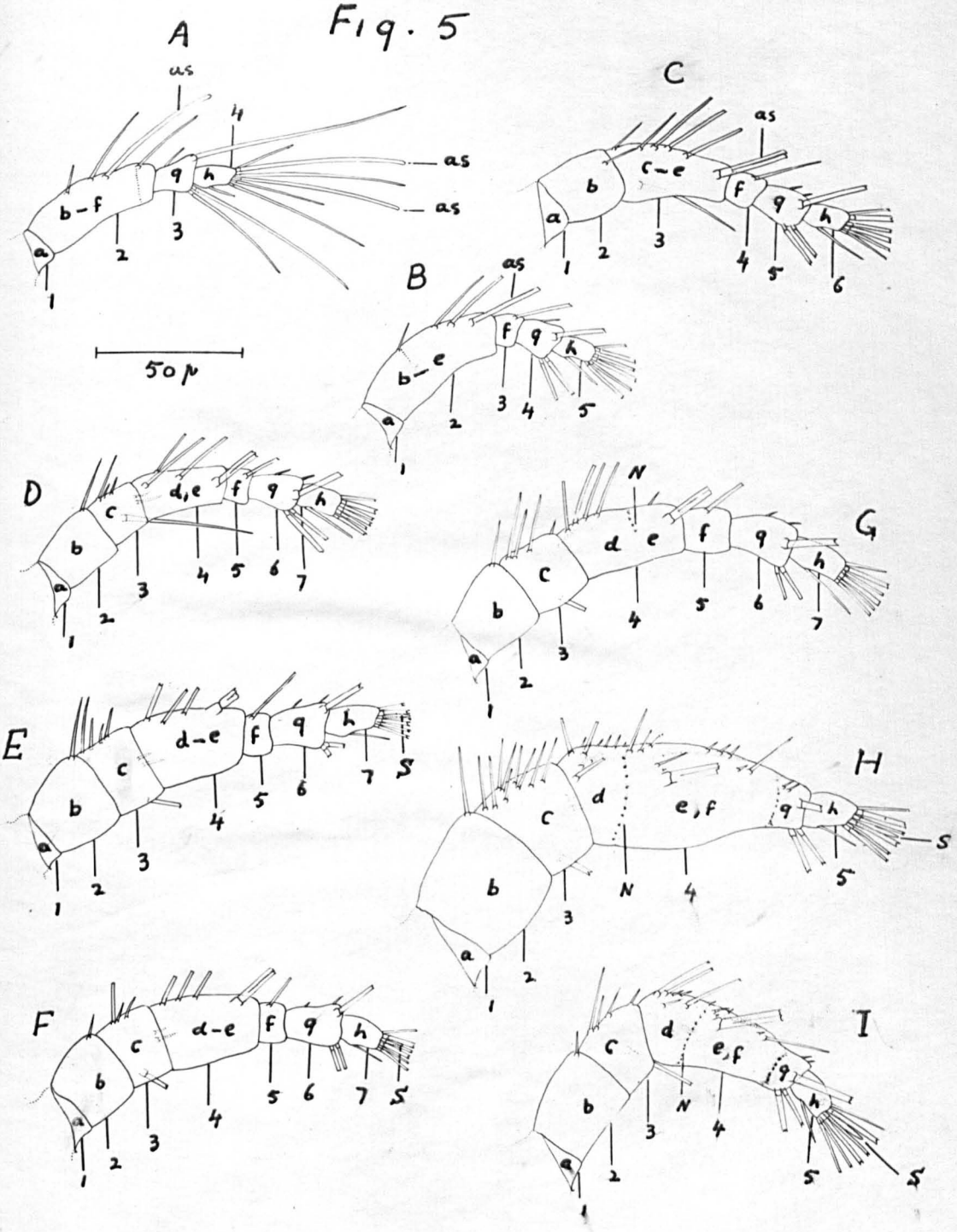
In the first copepodite the antennule is four jointed as a result of the division of the terminal joint of the larval antennule (Fig. 5.A). The two joints (g,h) thus formed at the distal end of the antennule remain unchanged throughout copepodite development and correspond to the last two

Fig. 5. Development of the antennule in the postlarval stages of *E. acutifrons*. In all stages only the right antennule is shown.

A, B, C: Antennule of first, second and third copepodite. D, E, F: Antennule of female, large male and small male respectively at copepodite IV. G, H, K: Antennule of female, large male and small male respectively at copepodite V.

N: furrow marking division line in the following moult. Other abbreviations as given earlier.

Fig. 5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joints (g,h) of the antennule in the adult female (Fig. 1.C).

The first joint of the larval antennule remains in a reduced form throughout postlarval development, and undergoes emargination in the later postlarval stages (Fig. 5.A-K).

The long second joint in the first copepodite has an incomplete furrow near the distal end (Fig. 5.A) which gives the appearance of a complete joint. This led Tesch (1915), who mistook the furrow for a complete division, to describe the antennule as five jointed. The first division of this joint occurs in the position of the furrow at the moult of the first copepodite, thus giving rise to a five jointed antennule (Fig. 5.B). The new joint (f) thus formed does not divide in subsequent development and corresponds to the sixth joint of the adult female. In both the third and fourth copepodite stages a new joint is added proximally by further divisions of the long joint (Fig. 5.C-F), thus giving rise to six and seven joints respectively in those stages. The new joints (b) and (c) correspond to the second and third joints in the adult. At the fourth copepodite the antennule shows differences between the sexes, and also between the two males. In the female the antennule (Fig. 5.D) is cylindrical and smooth, whereas in each male (Fig. 5.E,F) it is swollen. The males' antennules also differ from the female's in having their distal joints produced in the form of a sharp spine projecting beyond the base of the terminal setae (Fig. 5.E,F:S^1). The two males show differences in the setation of the third joint, there being seven setae in the large male and six in the small male.

At the moult of the fourth copepodite marked changes occur in the antennule. In the female it remains seven jointed, as in the fourth copepodite, but an increase in the setation of the fourth joint occurs (Fig. 5.G). The

fourth joint in the female also has a small furrow, N, in the distal half, which marks the future division line at the last moult (Fig. 5.G:N). In the males the antennule becomes swollen (Fig. 5.H,K). The fourth (d,e), fifth (f) and sixth (g) joints undergo fusion, but the sixth joint (g) still retains its individuality below the chitinous covering. In the proximal portion of the swollen joint in both the males an oblique furrow may be noticed (Fig. 5.H,K:n) which corresponds to that of the fourth joint in the female and marks the future division line of this joint in the adult. The sharp spine of the distal joint in the males extends well beyond the base of the terminal setae and is more prominent at this stage (Fig. 5.H,K:S^1). There are differences in the setation of the third joint which, in the large male, bears 10 large and 2 small setae (Fig. 5.H.3), as in the adult (Fig. 1.A.3), whereas in the small male the number remains unchanged (Fig. 5.K.3) as in the female (Fig. 5.G.3).

At the last moult the following changes take place to form the adult antennule:- In the female the antennule becomes eight jointed as a result of division of the fourth joint of the previous stage (Fig. 1.C). In the males the antennule becomes six jointed (Fig. 1.A,B), a new hinge joint (d) being formed between the tumulated fifth (e,f) joint and the third (c) by the division of the proximal part of the former (Fig. 5.H,K). This new fourth joint corresponds to the fourth joint (d) of the adult female. The tumulated joint of both the adult males corresponds to the fifth (e) and sixth (f) joints of the female.

It has been pointed out that the sixth joint of the antennule (g) of the fourth copepodite in the males (Fig. 5.E,F), though apparently fused with

the fourth (d-e) and fifth (f) to form the swollen fourth joint of the fifth copepodite (Fig. 5,H,K), in fact retains its individuality below the chitinous covering. At the last moult this joint fuses with the last joint (h) to form the sixth, distal joint (g,h) of the adult antennule (Table V; Fig. 1,A,B). This is also obvious if the setation of this joint in the adult males (Fig. 1,A,B) is compared with that of the last two joints of the previous stage. The sharp spine, projecting well beyond the base of the terminal setae in the previous stages in the males, now extends in a long curve tapering to a point (Fig. 1,A,B). This peculiar feature in the development of the male antennule has not been described in other species of harpacticoid copepod. The relatively longer antennule of the male with a hooked distal joint, which can be reflexed against the anterior side of the next segment, seems to be an adaptation to assist in holding the furcal setae of the female during copulation.

The difference between the antennules of the males may be seen in the third joint, as described earlier in the adults (Fig. 1,A,B). At the base of this joint in both the adult males a short annular ring may be noticed, giving the appearance of a separate joint. In fact this is a secondary feature and forms part of the joint.

The mean length of the antennule in each of the postlarval stages is given in Table III, and will be seen to vary considerably between the sexes and the dimorphic males. The males are marked by a longer antennule in the later stages. This is mainly due to the terminal spine on the distal joint, described above. The antennule of the small male is slightly longer relative to the total length of the body than that of the large male (Fig. 6). In

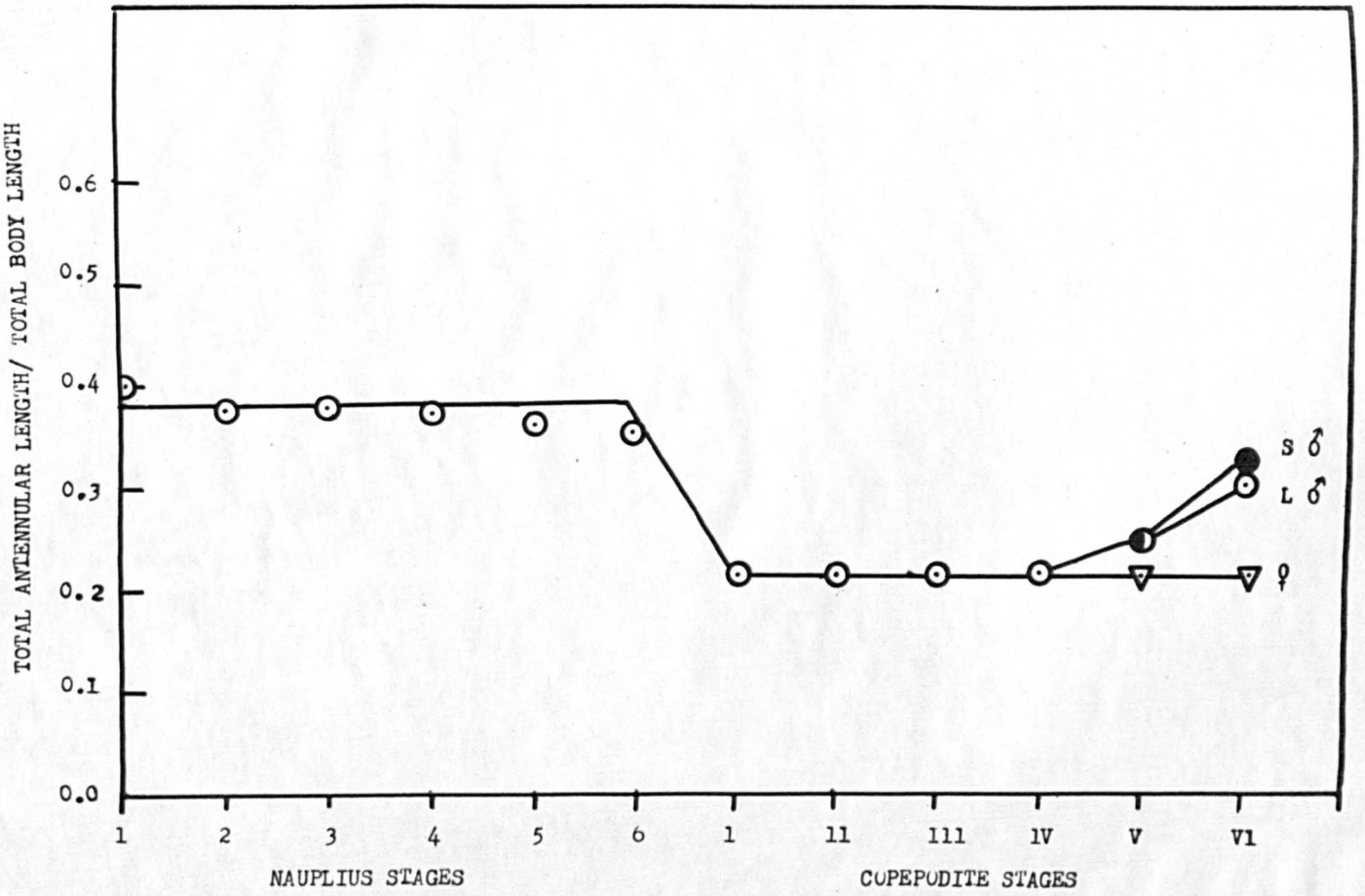

FIG. 6. RATIO OF THE LENGTH OF ANTENNULE AND TOTAL BODY LENGTH IN DEVELOPMENTAL STAGES OF *E. ACUTIFRONS*.

the female, where there is no terminal spine, the proportion between the body length and that of the antennule remains approximately the same in all the postlarval stages (Fig. 6). A similar relation has already been noted in the larval development.

It is important to note here that there are eight joints in the adult female antennule and six in the adult males instead of seven and five respectively, as described by previous workers (Giesbrecht, 1892; Sars, 1921). The first joint, which they neglected, remains in a reduced form throughout larval development and undergoes emargination in the later postlarval stages (Fig. 5,A-K). In the adult this joint is represented by a small chitinous plate (Fig. 1,A-C), the preaxial border of which is completely emarginated, and articulated about an extension from the ventral surface of the body. The second joint, which corresponds to the first joint of the earlier workers, is attached to the first and also directly to the same extension of the body wall.

(ii) Other appendages of the cephalothorax

The antenna (Fig. 4,B) in the first copepodite has a sub-divided protopodite. This agrees with the description of Sars (1921) of the adult, but disagrees with that of Giesbrecht (1892), who described the protopodite as having one joint only. The endopodite is two-jointed. The exopodite is very much reduced in size, losing all the four joints present in the larval stages but bearing annular ridges which probably represent the former divisions. The setation of both these rami corresponds to that of the adult.

The mandible, maxillule and maxilla are very small and therefore difficult to study. The maxilliped is as in the adult.

(iii) Swimming legs

The development of the swimming legs in the copepodite stages follows, in general, the same course as in the other harpacticoids (Gurney, 1932). In the first copepodite the first two pairs of swimming legs are present; in each leg the rami are one-segmented (Fig. 4,B,C); the third pair is rudimentary and is borne on the third thoracic somite (Fig. 3,A). Tesch (1915) incorrectly described these rami as being two-jointed in the first copepodite. A detailed description of the changes taking place in the setation and segmentation of the rami in each pair of swimming legs during copepodite development is given in Table IV.

At each succeeding moult a new pair of legs is formed, the rami of which at their first appearance are of one segment. They become two-segmented at the next moult and remain in this form until the moult of the fourth copepodite. At this moult the exopodite of the second, third and the fourth legs become three-segmented, whereas the endopodite becomes three-segmented only at the last moult. This is similar to the development reported by Gurney (1932) in Canthocamptus staphylinus. In Tisbe furcata, however, Johnson & Olson (1948) reported three-segmented endopodites as early as the fifth copepodite, as is common among the calanoids. In Euterpina acutifrons no difference appears between the second pair of swimming legs of the female and either dimorphic male until after the moult of the last copepodite.

The males differ from the female in the presence of a sixth pair of legs which appears for the first time at the moult of the third copepodite (Fig. 4,E,F) and remains rudimentary in the adult.

Table IV. Setation of the swimming legs during the postlarval development of Euterpina acutifrons.

Seg. = Segment of ramus; si = internal setae; st = terminal setae; sp = outer spines; * = one of the two terminal setae is setiferous.

Swimming legs	Stages	Endopodite			Exopodite		
		Seg.1	Seg.2	Seg.3	Seg.1	Seg.2	Seg.3
		si,st,sp	si,st,sp	si,st,sp	si,st,sp	si,st,sp	si,st,sp
1st swimming leg	Cop.I	3, 2, 1	-	-	1, 2, 4	-	-
	Cop.II	1, 0, 0,	2, 2, 1	-	0, 0, 1	2, 2, 3	-
	Cop.III	1, 0, 0	3, 2, 1	-	0, 0, 1	2, 2, 3	-
	Cop.IV-VI	1, 0, 0	3, 2, 1	-	0, 0, 1	2, 2, 3	-
2nd swimming leg	Cop.I	3, 2, 1	-	-	1, 1, 4	-	-
	Cop.II	1, 0, 0	2, 2, 1	-	0, 0, 1	2, 1, 3	-
	Cop.III	1, 0, 0	2, 2, 1	-	1, 0, 1	3, 1, 4	-
	Cop.IV	1, 0, 0	3, 2, 1	-	1, 0, 1	3, 1, 4	-
	Cop.V	1, 0, 0	4, 2, 1	-	1, 0, 1	1, 0, 1	2, 1, 3
	Cop.VI	1, 0, 0	2, 2, 0	2, 2, 1	1, 0, 1	1, 0, 1	2, 1, 3
	" "	1, 0, 0	2, 2, 1	-	1, 0, 1	1, 0, 1	2, 1, 3
	" "	1, 0, 0	3, 2, 1	-	1, 0, 1	1, 0, 1	2, 1, 3
3rd swimming leg	Cop.I	Rudimentary					
	Cop.II	3, 2, 1	-	-	1, 1, 4	-	-
	Cop.III	1, 0, 0	2, 2*, 1	-	0, 0, 1	2, 1, 3	-
	Cop.IV	1, 0, 0	4, 2*, 1	-	0, 0, 1	3, 1, 4	-
	Cop.V	1, 0, 0	4, 2*, 1	-	0, 0, 1	1, 0, 1	2, 1, 3
	Cop.VI	1, 0, 0	2, 0, 0	2, 2*, 1	0, 0, 1	1, 0, 1	2, 1, 3
4th swimming leg	Cop.I	Absent					
	Cop.II	Rudimentary					
	Cop.III	3, 2, 1	-	-	1, 1, 4	-	-
	Cop.IV	1, 0, 0	3, 2*, 1	-	0, 0, 1	3, 1, 4	-
	Cop.V	1, 0, 0	3, 2*, 1	-	1, 0, 1	1, 0, 1	1, 1, 3
	Cop.VI	1, 0, 0	2, 0, 0	2, 2*, 1	1, 0, 1	1, 0, 1	1, 1, 3
5th swimming leg	Cop.III	Rudimentary					
	Cop.IV-V	0, 4, 3	-	-	-	-	-
	Cop.IV-V	0, 2, 3	-	-	-	-	-

Influence of temperature on the size of dimorphs

In order to study whether the characteristic differences in size between the dimorphs are influenced by temperature changes, larvae from the same natural population were reared at temperatures of 10° and 25°C. The experiments were conducted in a cold cabinet and a thermostatic tank respectively, each with a temperature variation of ± 1°C. The larvae were fed as described above.

In Table V measurements of adults reared at these temperatures are given. This also includes measurements of adults reared at 16°C for comparison, although these were not of the same population. It may be seen that the individuals reared at 10°C grow to a larger size than those reared at 25°C. This is manifested both in the total length and the length of the cephalothorax. The results at 16°C fall into the same pattern. The experiment confirms that temperature has a direct effect on the size of the body, as demonstrated by Coker (1933), and shows that it influences different parts of the body similarly so that the characteristic differences between the dimorphic males and the female are not lost. On this basis it is reasonable to believe that, in the natural population, the effect of changing temperature should be parallel on both the growing dimorphs. This provides additional support for the view of Sewell (1912, 1929) and Gurney (1929) that the presence of two, and only two, kinds of adults in the same habitat, and at the same time, constitutes an example of dimorphism; it does not support the opinion of Coker (1934), who disagreed and suggested that the presence of two kinds of adults may be due to the dicyclic breeding reported in a number of freshwater cyclops.

Table V. Influence of temperature on the size of adult Euterpina. All measurements are in mm.

		Small male			Large male			Female		
		No. measured	Mean length	Range	No. measured	Mean length	Range	No. measured	Mean length	Range
10°C	Cephalothorax	20	·199	·188--·210	15	·254	·245--·265	20	·269	·255--·288
	Total body length	20	·557	·535--·595	15	·690	·660--·705	20	·716	·680--·770
16°C	Cephalothorax	35	·190	·188--·200	35	·244	·230--·255	35	·266	·250--·280
	Total body length	35	·526	·510--·550	35	·678	·645--·710	35	·674	·645--·710
25°C	Cephalothorax	20	·175	·170--·185	20	·225	·215--·235	20	·258	·250--·270
	Total body length	20	·490	·465--·520	20	·612	·590--·630	20	·658	·630--·675

Comparison with the development of other harpacticoid copepods

(i) Adaptive modifications in the larval phase

Despite a resemblance to other harpacticoid nauplii in general shape, in the marked symmetry of the body and in the presence of the well developed toothed masticatory process on the antenna, the larvae of Euterpina acutifrons show a number of striking differences which are as follows.

(i) The endopodite of the antenna is weakly prehensile as compared with the strongly prehensile endopodite of the other harpacticoids, including Tachidius (Gurney, 1932), which belongs to the same family (Tachiidae).

(ii) The mandibular exopodite consists of three joints, but is longer than that found in other harpacticoids. This seems to be an adaptation reflecting the pelagic life of Euterpina, as was suggested by Gurney (1929). The early acquisition of the coxal mandibular process in the sixth nauplius, though it is non-functional at this stage, is a feature not reported in other harpacticoids.

(iii) The maxillules appear in the fourth nauplius as compared with their earlier acquisition in the second nauplius in other harpacticoids, with the exception of Longipedia where they are present at the first nauplius (Gurney, 1929). The maxilla and maxilliped appear for the first time in the fifth nauplius, as in other harpacticoids.

(iv) Unlike most other harpacticoids, the ventral abdominal spines in the larval Euterpina assume a characteristic pattern in the early stages, but they show no relations to the origin of limbs as was suggested by Tesch (1915).

(v) The most unusual and perhaps unique feature of the development is the loss of structures, some of which are associated with the feeding mechanism of the larvae, at the moult of the fifth nauplius, i.e. before the end of the larval phase. The whole toothed coxal masticatory process of the antenna is lost. The mandible loses the two masticatory spines and its endopodite becomes greatly simplified, losing all its spines and hairs. This is accompanied by the complete disappearance of the vertical ridge and two posterior fences of stiff hairs in the oral region. These changes coincide with a precocious development of the mandibular gnathobase, although this is non-functional at this stage. There are also marked changes in the shape of the labrum. These changes are not reported at this stage in other harpacticoids.

The primary function of the antenna and the mandible (collecting, crushing and manipulation of food particles) has long been recognised in harpacticoid copepods (Claus, 1858). Specialization of these parts was necessary for the benthic and littoral habit that most harpacticoid copepods have adopted, and their consequent feeding on large pieces of organic matter. The changes taking place after the fifth nauplius in Euterpina suggest that the importance of these specialized feeding organs is reduced to a large extent because of the planktonic habit of the species, which in its pelagic life depends upon food that consists mainly of diatoms and other unicellular forms and fine organic particulate matter.

It is generally considered that most harpacticoid copepods, since their appendages are similar, have a similar feeding mechanism (Gauld, 1959). However, there seem to be deviations from the typical arrangement within the group. In some members primitive characters have been retained, while others

differ from the typical form because of further specialization. Well known examples of the first occur in the genus Longipedia (Gurney, 1929; Nicholls, 1935) where the larvae are pelagic and of the primitive form (Gurney, 1929), and resemble calanoid nauplii in most respects. The feeding mechanism in these larvae has not been studied, but the structure of the appendages suggests a close resemblance to the feeding of the calanoid copepods. On the other hand, the larvae of Thalestris rhadymeniae (Harding, 1954), parasitic on algae, provide an example of further specialization where the appendages are greatly reduced and adapted to a parasitic mode of life.

(ii) Earlier views on development of the dimorphs in copepods

The course of development in Euterpina, which has been described above, involves the establishment of structural dimorphism in the males at the same time as sexual differentiation (the moult of the third copepodite stage) with no suggestion of such differences at earlier stages.

This is in accordance with the view of Sewell (1929) that differentiation in the dimorphs takes place at the time when sexual differences first appear, but the course of development in the dimorphic males of Euterpina follows a simpler pattern than either of those put forward by Sewell (1912, 1929, 1940) or Gurney (1929). Both the males develop along two different parallel lines with different growth factors and pass through the fourth and fifth copepodite stages before becoming adult, thus excluding the possibility of skipping a stage (as was suggested by Sewell) or of undergoing an additional moult, as was suggested by both Sewell and Gurney. There is no evidence that the two forms represent successive stages in the development or that they can be displayed by the same individual, as was postulated by Sewell.

Summary

The eggs of Euterpina acutifrons were hatched and the larvae were reared successfully to the adults for the first time under laboratory conditions.

A detailed study of the larval and postlarval development has been made from these individuals.

The larvae of Euterpina acutifrons show striking differences from those of the other harpacticoids as follows.

(a) The antennular development during the larval phase is characterized by a marked increase in the marginal setation of the terminal joint, similar to that found in the Calanoida and Cyclopoida, and furnishing useful diagnostic features for the separation of the larval stages.

(b) The maxillule appears as late as the fourth nauplius, which is rare in the harpacticoids; the maxilla and the maxilliped appear in the fifth nauplius as in other harpacticoids.

(c) The ventral abdominal spines undergo characteristic changes in the pattern and serve as a diagnostic feature in separating the early larval stages.

(d) The presence of a blunt process on the posterior end of the body in the first two nauplii is a characteristic feature of Euterpina.

(e) A remarkable feature of the larval development is the retrogressive change which results in the loss of important larval structures associated with feeding before the end of the larval phase, probably an adaptation to pelagic life. The presence of a mandibular exopodite, which is longer, and an antennal endopodite, which is less prehensile

than those which are found in benthic species, are similar adaptations.

A detailed study of the antennular development of the postlarval stages shows the antennules to be eight jointed in the female and six jointed in the male. This contradicts Giesbrecht (1892) and Sars (1921), who described the antennule as seven jointed in the female and five jointed in the male.

Dimorphism in the male sex has been described in detail for the first time. The two males differ not only in size but also in the structure of the antennule, antenna and the second pair of legs. Both the males can be developed from one and the same batch of eggs. Both development and growth studies show that dimorphism can first be recognised at the fourth copepodite stage when sexual differentiation also occurs. The course of development and growth has been found to differ from those put forward by Sewell (1929) and Gurney (1931) in other copepods. The two males pass through the fourth and fifth copepodite with different growth factors before becoming adult. The two males do not represent successive stages of the development as has been postulated previously.

Temperature has a direct and parallel influence on the size of the dimorphs and the characteristic differences between them are not affected.

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P A R T III

Breeding of *Euterpina acutifrons* (Dana)

Contents

Introduction

Euterpina acutifrons is widely distributed between the latitudes 66°N and 40°S. Within these geographical limits it breeds at temperatures ranging from 8° to 30°C. Apellof (1912) and Orton (1920) suggested that marine organisms have characteristic temperature ranges within which breeding can occur and such limits control the geographical distribution of a species. Differences in the rate of development and growth, correlated with both seasonal and geographical variations of temperature, have been found by Fox (1936, 1938), Fox & Wingfield (1937), Runnstrom (1929) and Thorson (1946). Since the temperature range in any one habitat is normally narrower than the full range over which the breeding of Euterpina is possible, the determination of the latter must involve laboratory experiments on the species at various temperatures within and beyond the accustomed limits.

In marine copepods such studies have suffered in the past from the disadvantage that breeding them in the laboratory throughout the life cycle is difficult and has seldom been successful. A few attempts have been made to correlate the results of laboratory experiments with observations on natural populations (Raymont & Gross, 1942; Marshall & Orr, 1956). In the few cases where the difficulties of rearing and breeding have been overcome, the studies did not include work on temperature effects (Johnson & Olson, 1948; Shaw, 1938; Fraser, 1936).

Since no information is available on the breeding and the rate of development of Euterpina acutifrons, it was decided to investigate these aspects both under laboratory conditions and in the natural population

occurring in the waters round Anglesey, where the species breeds as one of the dominant autumn organisms.

Breeding under laboratory conditions

Experimental methods

Dark mature females, presumably fertilized, were collected from the plankton of the Menai Straits and were kept in the laboratory at the various temperatures at which their eggs were to be hatched and the larvae reared. At temperatures of 14°C or above, the laying of eggs took place from 2 hours to about 36 hours after collection, depending on the temperature and the state of maturity of the female. At 10°C laying took place from 2 to 5 days after the females were brought to the laboratory.

The eggs are laid in an egg sac, which can easily be seen with the naked eye. The number of eggs in each sac varies from 5 to 42. Each female with its freshly laid egg sac was transferred to a Boveri dish containing 10 to 15 cc. of sea water. These dishes were then kept at the required temperatures which were maintained throughout the subsequent hatching and development of larvae. All the experiments, except those at 10°C, which took place in a cold cabinet with a variation of ± 1°C, were conducted in thermostatic tanks in which the dishes were supported. The tanks, running at 14°, 18° and 20°C, were kept in a cold room where the temperature was constant to within ± 1°C so that the variation in each tank was within ± 0·5°C. Other tanks kept in the laboratory showed a variation of ± 1°C at 25°C and ± 1·5°C at 30°C.

The period of incubation of the egg mass from laying to hatching of the eggs was noted. The newly hatched nauplii were counted and transferred to a culture dish containing about 150 cc. of sea water with a fine smooth-ended pipette. Each dish was kept at the appropriate temperature for some time before receiving the larvae. The time involved in transferring the larvae was not more than 15 to 20 minutes and no appreciable change in the temperature of the culture medium during this time was noted. Evaporation was reduced by means of a glass plate placed over each dish.

The larvae were fed on fresh unialgal cultures of Nitzschia closterium. The amount of food given was never allowed to exceed a level at which a thin layer of diatom cells could be seen on the bottom of the dish. Preliminary experiments had indicated that too large a quantity of food resulted in a high mortality. In all the experiments the medium remained unchanged throughout and static, except for occasional stirring.

The duration of the larval phase from hatching to the moult of the sixth nauplius was noted at each temperature and that of the postlarval stages from this time until the moult to the adult. The number of larvae which successfully completed the larval and postlarval phases was also recorded. The total generation time was measured from the time of egg laying to the laying of eggs of the next generation.

Laying and hatching of eggs

Egg laying in Euterpina is similar to that of Calanus finmarchicus, as described by Raymont & Gross (1942), but differs in that the eggs of Euterpina are laid in an egg sac, whereas they are laid freely in Calanus.

The freshly fertilized eggs are flattened and arranged in four rows so that the whole egg sac appears more or less rectangular in shape. Within a few minutes of laying all the eggs swell into a spherical shape and, as they do so, they lose their regular arrangement and the whole egg sac assumes its final oval shape. Eggs which, owing to mechanical reasons, fail to enter the egg sac at the time of laying and are passed out into the culture dish soon decompose.

Freshly laid eggs are dark, but as they develop the colour changes to pink. The process of hatching was similar to that described in Tigriopus fulvus (Marshall & Orr, 1954). Hatching was observed in sea water on a slide covered by No. 0 coverglass. Before twitching was observed each egg measured 58μ in diameter and its volume was $102 \times 10^{-6} mm^3$. The egg moved jerkily inside the outer membrane and expanded to a diameter of 64·5μ so that its volume increased to $137 \times 10^{-6} mm^3$ before the outer membrane cracked. The increase in volume was very small compared with that found in Calanus (Marshall & Orr, 1954). The mandibular bristle of the nauplius could be seen projecting well out of the inner membrane as in Tigriopus fulvus and Oithona (Marshall & Orr, 1954). The nauplius then emerged suddenly, enclosed in a thin membrane but still attached to the outer membrane of the egg. A greater pressure was developed on the anterior margin until the inner membrane cracked and the nauplius was released, anterior end first, and began violent movements which eventually rid it of its attachment to the membranes. The total time taken for complete hatching was about 8 to 11 minutes, and the 20 eggs from one sac hatched in about 45 minutes at room temperature (17°C).

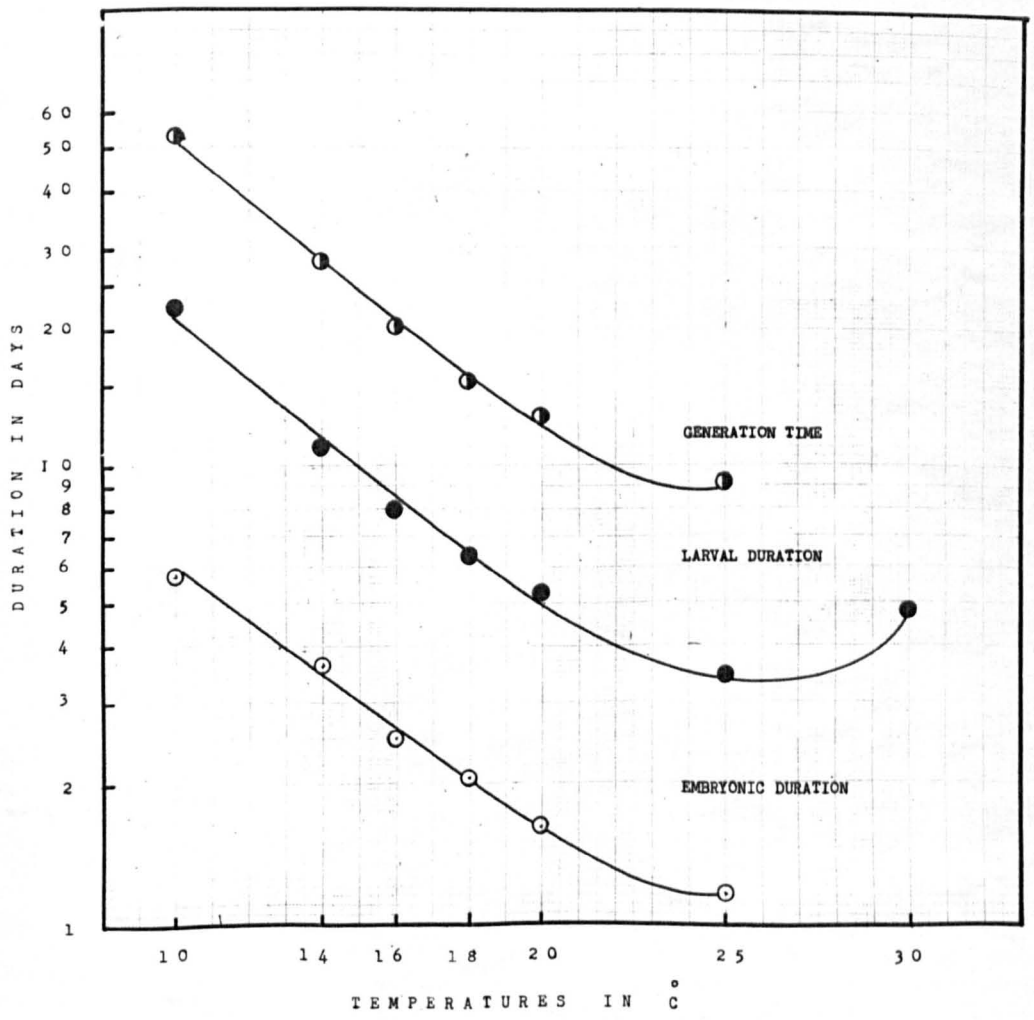
Rate of development

The eggs from a particular egg sac and the larvae hatched from them have the same parentage. These individuals, growing under any one set of experimental conditions, show marked similarity in their rates of development and have been found to complete the different phases at about the same time. Individuals where moulting was delayed for a considerable time failed to survive; these have not been included in results discussed here.

In Fig. 1 the duration of the embryonic and larval phases and the generation time at different temperatures is shown. Curve A indicates the duration of the embryonic phase. The duration fell exponentially as the temperature rose from 10° to 21°C. The Q_{10} value for this range was found to be 3·6. The maximum rate of development occurred at 25°C, but the Q_{10} between 20° and 25°C was 1·9, a much lower value than that between 10° and 20°C. At 25°C the development of the egg was affected; 15 per cent failed to hatch, compared with the successful hatching of almost all eggs at temperatures lower than this. At 30°C ± 1·5°C all eggs failed to hatch although a few gave indications of maturity. This suggests that a temperature of 30°C ± 1·5°C is lethal to the unhatched embryo.

Curve B of Fig. 1 shows the rate of development in the larval phase. The Q_{10} value is 4·2 between 10° and 20°C and 2·4 between 20° and 25°C, which shows a close agreement between the embryonic and larval phases. Some larvae hatched at 25°C were soon transferred to 30°C for rearing. The individuals which reached the first copepodite stage showed a decline in the rate of development from the maximum value found at 25°C.

FIG. 1. DURATION OF DIFFERENT PHASES OF DEVELOPMENT OF E. ACUTIFRONS AT VARIOUS TEMPERATURES



Curve C of Fig. 1 represents the generation time at different temperatures. The reduction in the generation time was uniform within the temperature range 10° to 20°C with a Q_{10} of 4·1, which was about the same as that of embryonic and larval development. At 10°C the generation time was found to be 52 to 55 days. This was reduced to 12 to 14 days at 20°C. The most rapid development was at 25°C, when the generation time was 9 days. The Q_{10} between 20° and 25°C was 2·0, which was markedly less than that between 10° and 20°C. This effect was similar to that seen in the embryonic and larval development.

The results of these observations show that the influence of temperature on various phases of development is uniform. This is in accordance with the observations of Loeb and Northrop (1917) who found that the Q_{10} was about the same for different phases in the life history of Drosophilla. The maximum Q_{10} value in Euterpina was found between 10° and 20°C, within which range the development was normal. The experiments did not precisely establish the upper limit, since no observations were made between 20° and 24°C. For temperatures lower than 10°C ± 1°C observations were made only at 5°C in a refrigerator. Most of those larvae newly hatched at 10°C which were transferred to 5°C died, but a few lived without moulting for 25 days. They remained inactive except when the temperature rose slightly during examination. They were apparently healthy when examined shortly before they died. On other occasions most of the nauplii at the sixth nauplius stage collected from the plankton died when transferred to a culture vessel at 5°C, but a few lived for about 20 days. One of these nauplii moulted into the first copepodite.

It seems that at 5°C the development was very slow but was not completely arrested. The difference in the rate of development between 5° and 10°C therefore seems to be very marked. When three pairs of adults, newly moulted from the fifth copepodite, were transferred to a culture at 5°C, no breeding was observed. They remained quiescent and died after 20 to 30 days. At higher temperatures similar adults were active and bred normally.

Throughout the series of experiments there was no indication of diapause at any stage of development in Euterpina of the kind which has been reported in freshwater copepods (Moore, 1939; Smyly, 1957; Elgmork, 1959).

The generation time is comparable to that of other species of harpacticoid copepods. In Tigriopus fulvus the generation time is about two months at Hull, according to Fraser (1936), and one month in California, according to Shaw (1938). In Tisbe furcata it is between 17 and 24 days at a temperature of 17° to 18°C (Johnson & Olson, 1948). Compared with species of copepods other than harpacticoids, the generation time of Euterpina acutifrons is short. For instance in Oithonina nana, a marine cyclopoid which is found in the same habitat as Euterpina, the generation time has been found to be 30 days at 18°C, twice as long as that of Euterpina under similar conditions (see p.184).

The duration of the post-embryonic stages

The time required for the completion of each stage has been studied in detail in larvae which were reared in small Boveri dishes at a temperature of 16°C. Fig. 2 shows the average value and the range of duration of each stage.

The first nauplius (Fig. 2) lasted for a period of two days before the first moult, but the duration of each of the subsequent stages up to the fourth copepodite was about one day. A prolonged first nauplius stage has also been reported in Tigriopus fulvus by Shaw (1938), although his observations of the duration of individual stages were made up to the fourth nauplius only. The duration at the fourth copepodite stage showed differences between the sexes, the female having a slightly longer duration than the males (Fig. 2). The duration of the female and the large male at the fifth copepodite was, however, approximately the same. The small male had a shorter duration both at the fourth and the fifth copepodite than that of the female. The total development time was longer in the female (14 days) than in the males and longer in the large male (13 days) than in the small (12 days). The shorter development times in the males of Euterpina seem to be in accordance with observations made in other copepods (Marshall & Orr, 1956).

Survival in the culture experiments

In the culture experiments it was not possible to determine survival at all stages of development under different culture conditions. The results were therefore confined to the percentage survival at the end of the larval and postlarval phases in each experiment, and are as shown in Table I.

The percentage survival at the end of the larval phase was calculated from the number of larvae at the beginning of the experiments and that of the postlarval phase from the total number which successfully completed the

FIG. 2. DURATION OF POSTEMBRYONIC STAGES IN E. ACUTIFRONS AT 16 °C.

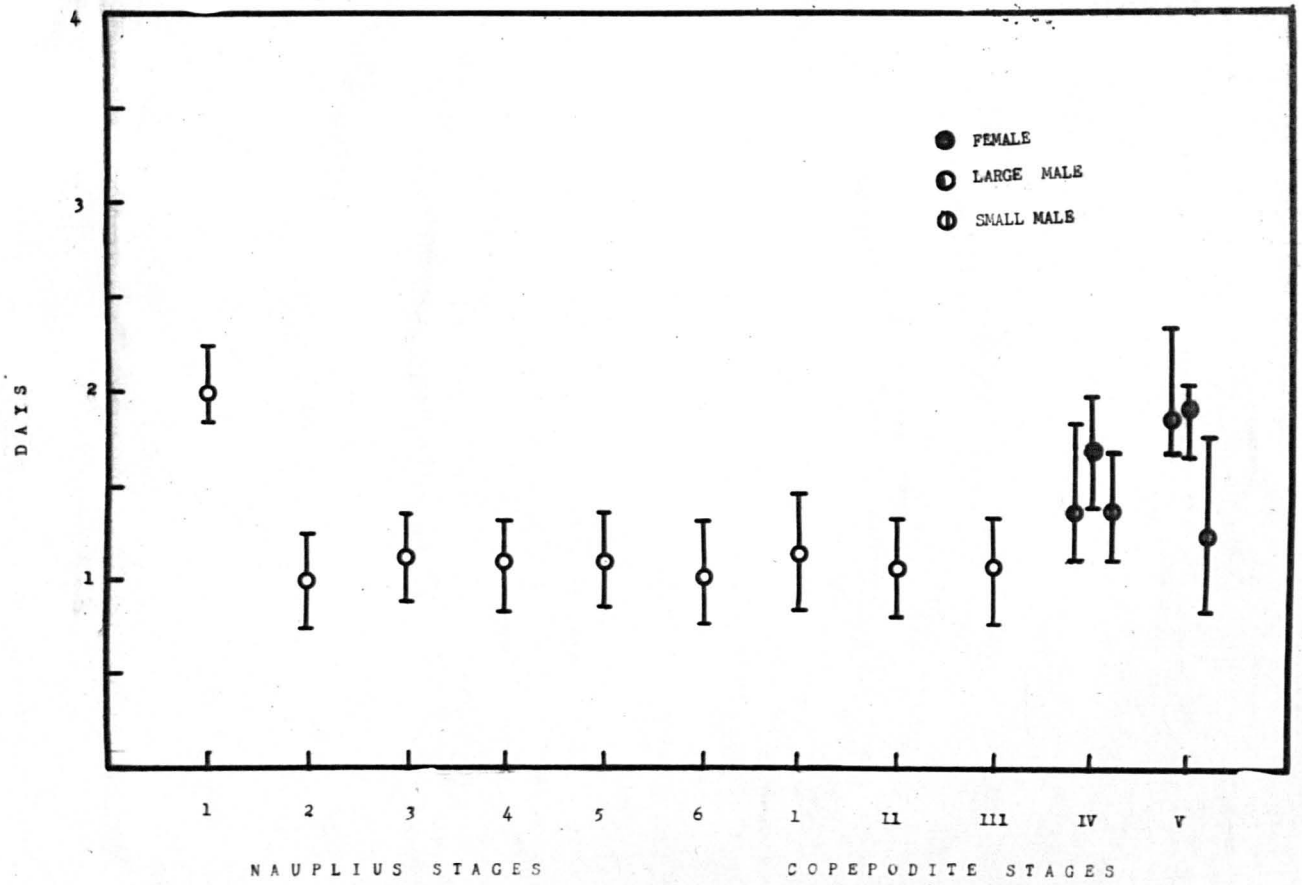


Table I. Survival of larval and postlarval stages of *E. acutifrons* reared under laboratory conditions.

L = larval phase; PL = postlarval phase.

Temperature	No. of experiments	Total No. hatched	No. completed L	% completed L	No. reached adults	% survival in PL	% reached adult	Minimum & maximum survival %
10°C	3	87	13	15	3	23	4	0-10
14°C	6	161	74	46	35	47	22	15-36
16°C	8	215	113	53	88	71	42	14-100
18°C	3	82	48	59	30	63	37	27-50
20°C	5	134	76	57	51	70	40	27-82
25°C	5	149	44	30	26	59	17	10-21
30°C	3	133	11	8	*	-	-	-

* Died at I - III copepodite after 6 - 8 days from hatching.

larval phase. The survival of larvae at temperatures between 14° and 20°C was about the same and was considerably higher than that at below 10° and above 25°C. The poor survival at 30°C suggests that this temperature was close to the lethal temperature.

Comparison of the percentage survival at the end of the larval and postlarval phases showed, on the whole, a better survival in the postlarval stages; at 25°C an average survival of 59 per cent was found in the post-larval stages compared with 29·5 per cent at the end of the larval phase. At 30°C a very small percentage survived up to the first, second or third copepodite stages, but none of them developed to the adult.

The best survivals to the adult stage were obtained at temperatures between 16° and 20°C. Between these temperatures the survival at the end of the experiment varied from a minimum of 14 per cent to a maximum of 100 per cent and the average survival reached a maximum of 42 per cent at 16°C. This value, when compared with that of other littoral species, is very low. For instance, in Tisbe furcata Johnson & Olson (1948) reported an average of 80 per cent survival under laboratory conditions. On the other hand the survival was very high compared with that of pelagic species of copepod. For instance, in Oithonina nana, which had been reared under similar conditions, only 23 per cent survived.

Sexual maturity in the males

In Table II the total time taken from hatching to the formation of the adults is shown at various temperatures. It will be seen that the large

Table II. Duration of the post-embryonic phase of *E. acutifrons* at different temperatures.

A = average duration in days; B = minimum and maximum duration;
C = number of observations.

Temperature	Female			Large male			Small male		
°C	A	B	C	A	B	C	A	B	C
10°	39·5	39–40	1	37·5	37–39	1	36	35–37	1
14°	20·6	19·5–22	13	19·2	18·5–20	6	18·7	17–19·5	16
16°	14·4	13·5–15	28	13·7	13–15	9	12·7	11·5–13·5	45
18°	10·6	10–11·5	14	10	9–11	6	9·3	9–11	10
20°	9·0	8–10	15	8·3	8–10	5	8·2	8–10	33
25°	6·5	6–7·5	7	5·7	5·5–6·5	4	5·7	5–6·5	15

male took longer to reach the adult stage than the small male. This difference was much more pronounced at lower temperatures (10° - 16°C) but tended to become less and less as the temperature rose (18° - 25°C). This was also shown in the observations made on the duration of the post-embryonic stages mentioned earlier.

The males are fully mature a very short time after the last moult and separate experiments were conducted to determine how long this maturation took. These observations were made at 16° and 20°C. A number of males of both dimorphic forms were separated at the fifth copepodite into small culture dishes in which they moulted into the adults. They were watched to see how soon the spermatophore was formed. After its first appearance, which may be recognized under a magnification of x 70 by its glistening surface in the male urosome, a virgin female was introduced into the dish and the time which elapsed before copulation took place was observed. The results are shown in Table III.

It will be seen that at 20°C the small male attained maturity less than 24 hours after the final moult into the adult. The time was probably longer at 16°C, but the interval between observations was too long to give a precise figure. Observations of the large male suggest that, while the spermatophore was formed at about the same time as in the small male, copulation took place a much longer time after its formation. This aspect of sexual behaviour in the two males will be considered later (see p. 111).

The spermatophore

In mature males the spermatophore can easily be squeezed out. The main body of the spermatophore is an elongated sac measuring about 70μ in

Table III. Sexual maturity in the males of Euterpina.

T = time.

Type of male	Temperature	T. of last moult	1st spermatophore appeared at	1st spermatophore time since last moult (hours)	1st copulation occurred at	1st copulation time since last moult (hours)	2nd spermatophore appeared at	2nd spermatophore time since last moult (hours)	2nd copulation occurred at	2nd copulation time since last moult (hours)
S (1)	20°C	10pm 8th – 8am 9th Dec.	2pm – 4pm 9th Dec.	8 - 20	6.30pm 9th Dec.	10 - 20	10am – 12am 10th Dec.	28 - 38	10am 11th Dec.	50 - 60
S (2)	"	" "	"	"	7.30pm 9th Dec.	13 - 21	-	-	-	-
S (3)	"	" "	"	"	9.30pm 9th Dec.	16 - 24	-	-	-	-
S (4)	16°C	10am – 4pm 11th Dec.	10pm 11th – 10am 12th Dec.	6 - 24	2pm 12th Dec.	22 - 26	-	-	-	-
S (5)	"	10pm – 11pm 12th Dec.	10pm 12th – 10am 13th Dec.	11 - 24	2pm – 3pm 2nd Oct.	23 - 27	-	-	-	-
L (1)	"	10pm 26th – 2pm 27th Sept.	10am – 6pm 28th Sept.	20 - 44	12am – 3pm 2nd Oct.	116 - 135	-	-	-	-
L (2)	"	10pm 1st – 10am 2nd Oct.	10pm 2nd – 10am 3rd Oct.	12 - 36	10pm – 4pm 5th Oct.	74 - 90	-	-	-	-
L (3)	Room temp.	8pm 13th – 8am 14th July	-	-	2pm 16th July	54 - 66	-	-	-	-

length and 20μ in breadth; the proximal end forms a very thin tube which is about 13μ long and 3μ broad. At the proximal end of the main body of the spermatophore there is a groove which is not reported in most other copepods. Despite a marked difference in the body size of the dimorphic males, the size of the spermatophore is about the same. Measurements of ten mature individuals of each dimorph and their extruded spermatophores have been given in Table IV.

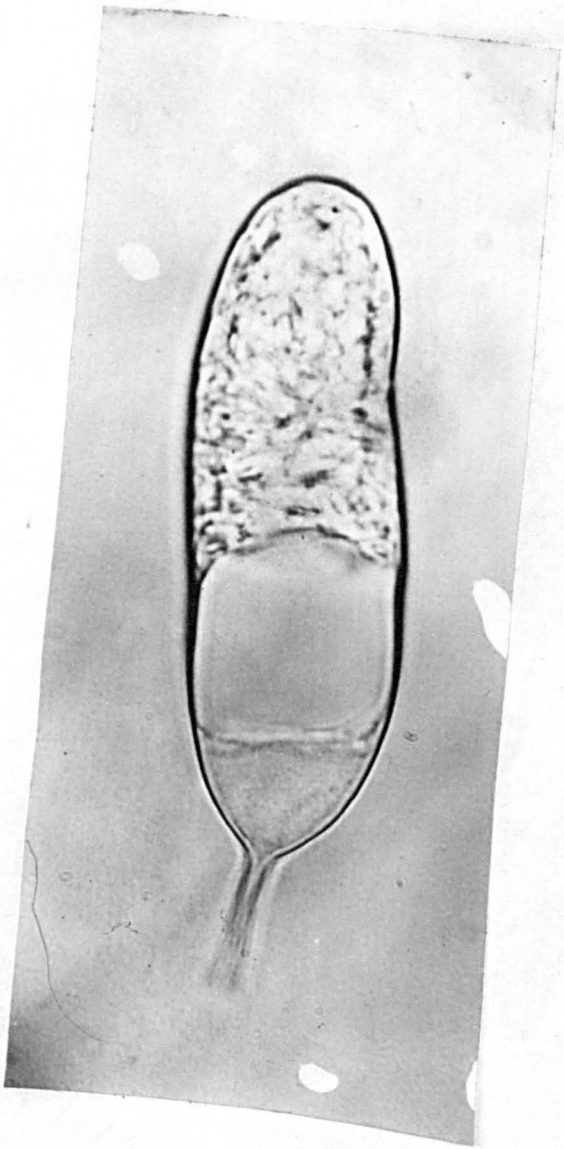
Table IV. Measurement of body size and spermatophore length in the dimorphic males of Euterpina.

	Total body length mean	Range	Total length of spermatophore	Range
Small male	526μ	510 - 544μ	68·4μ	63 - 73μ
Large male	681μ	645 - 670μ	70·6μ	68 - 75μ

No correlation between the total body length and the size of the spermatophore could be found. Thus the small male has a relatively larger spermatophore.

The spermatophore, as in Calanus (Marshall & Orr, 1954), has two functionally different halves which can be distinguished by a difference in their refractive indices (Fig. 3..). The transfer of spermatophore contents has been studied in detail. For this object a mature male was gently squeezed so that the spermatophore was extruded but remained connected by its thin tube to the body of the male. The main body of the spermatophore was in contact with the sea water. Soon the distal secretion of the spermatophore became swollen and gradually assumed a more globular form (Fig. 3.B). The contents of the proximal part were then gradually pushed out. In one of the specimens this was timed and found to occur about 45 minutes after the extrusion of the

Fig. 3. The spermatophore of *E. acutifrons*.



spermatophore. After passing through the thin tube the contents were deposited around the point where the spermatophore was in contact with the body, and soon became solidified as a result of contact with the sea water. Eventually the outward flow ceased.

Observations made soon after the spermatophores had been transferred to the females indicated that the complete transfer of the spermatophore contents took about 2 to 3 hours, the spermatophore becoming transparent towards the end of the process, its case dropping off the body of the female after a further period of 1 to 3 hours.

Copulation

Newly moulted females readily copulated. Virgin females kept separately for a long period were evidently less attractive since copulation was very seldom observed when males were given access to them. The course of copulation was as follows.

The male approached the female from the back and grasped the proximal portion of her furcal setae with his antennules. These are well adapted for this prupose. The last joint of the antennule in the males of this species is sharply tapered distally and can only be bent backwards along the ventral border of a tumulated joint, fitting a groove present on the distal end of the latter. The furcal setae of the female are held between this backwardly flexed joint and the ventral groove of the swollen joint. In other harpacticoids, where the antennule is not so specialized, the male holds the hind portion of

the female cephalothorax by his antennules (Williams, 1907). In calanoids, where only the right antennule is geniticulate, the male holds the female round the terminal somite of the urosome or the caudal rami and also by clasping her abdomen with his fifth pair of legs (Gauld, 1957).

The body of the male after its first grip was usually in line with to that of the female. In the actual act of copulation the male changed his grip twice to attain a position in a head-to-tail direction. He first released one antennule from its first position and brought it across to grip the furcal seta on the same side as the other antennule so that his body attained a position at right angles to that of the female. The grip of the second antennule was then changed swinging the body of the male through a further right angle so that the two animals were orientated in a head-to-tail direction. The male then moved round until the ventral body surfaces were opposed, and, bending his body, deposited the spermatophore on the female's genital somite. The actual act of copulation lasted only a few seconds. After deposition of the spermatophore the male reverted to its original position by reversing the two successive antennular grips. On most occasions the males deposited spermatophores as soon as they entered into copulation but held the female for a considerably longer period of from 30 minutes to 10 hours.

In none of the observations on copulation or in other breeding experiments was there any evidence that the actual transfer of the spermatophore was delayed until the female moulted. In Harpacticus uniremis, H. gracilis and Tisbe littoralis, Williams (1907) stated that "every successful copulation must be prolonged until the female moults." This does not seem to be true in Euterpina acutifrons. Males have only very rarely been observed

to clasp a female before her postlarval development was completed. In one case a fifth copepodite female was clasped by a male and a successful transfer of the spermatophore took place. The female did not moult into the adult until two days later. Johnson and Olson (1948) reported a male clasping on one occasion an immature female Tisbe furcata in the sixth copepodite stage, which moulted while being clasped. It is possible that moulting in this case might have occurred while the female was clasped quite by chance.

Sexual behaviour of dimorphic males

The two dimorphic males seem to differ in their sexual potency. In experiments on this aspect of behaviour the individuals used were collected at the fifth copepodite stage on the 3rd July 1959. All of them moulted into adults on the 4th July. The observations lasted from the 9th to the 12th July using 14 pairs each of one small and one large male. In each observation one small and one large male were placed in the same dish as virgin females which had been reared from immature stages in separate culture dishes.

The results show that out of 14 such observations only in one case was a large male the first to copulate (Table V(a)). The time taken for copulation after introduction, in the small males, varied between 5 and 60 minutes, showing that this dimorph very readily entered into copulation. The duration in copula varied from 40 minutes to 10 hours. No definite record of the time of the actual transfer of the spermatophore was made, but in most cases it took place a very short time after the start of copulation. The male remained in copula for a considerable period after the transfer of the spermatophore. In other experiments mature large males were almost

Table V(a). Sexual behaviour in the dimorphic males at room temperature (16° - 19°C), using one male of each kind in contact with a female.

Date	Type of male which copulated	Time before copulation	Duration in copula
9th July 1959	S	20 minutes	60 minutes
10th July 1959	S	35 minutes	-
"	S	30 minutes	-
"	S	50 minutes	-
"	S	35 minutes	-
"	S	60 minutes	-
11th July 1959	S	30 minutes	-
"	S	5 minutes	40 minutes
"	S	45 minutes	-
"	S	25 minutes	-
12th July 1959	L	60 minutes	2 hours
"	S	35 minutes	-
"	S	10 minutes	2 hours
"	S	5 minutes	12 hours

Table V(b). Frequency of copulations in the dimorphic males of *E. acutifrons*.

Number of days after last moult	Copulations										
	1st	2nd	3rd	4th	5th	6th	7th	8th	9th	10th	11th
Small male	2	4	6	8	9	9	10	11	13	14	15*
Large male	2·75	5	8·5	12·5†							

* Escaped next day.

† Died three days later.

invariably observed to take a longer time to enter into copulation, varying from a few hours to more than a day after they had access to a female.

A comparison was made of the frequency of copulation of a single small and a single large male. Each was allowed access to a virgin female in a separate dish. Observations were made every three hours between 9 a.m. and 6 p.m., or occasionally up to 9 p.m., each day, after which the observations were discontinued and the males were returned to their dishes. Each successful copulation was confirmed by the attachment of the spermatophore to the female. The results shown in Table V(b) indicate that the small male copulated 11 times in a period of 15 days, but unfortunately the specimen was lost after this. The large male copulated only 4 times in a period of 12·5 days and died after 16 days. In many other instances it has been observed that two, and sometimes three, small males were found to clasp a female or other males, and in one case a small male was seen to deposit a spermatophore on a large male.

All these observations point to the greater sexual potency of the small male.

Sexual maturity in the female

In Table II the average duration of the post-embryonic phase is given. This was found to be longer in the female than in the males. The difference was more obvious at temperatures between 10° and 14°C than at higher temperatures. The maximum duration, 39 to 40 days, occurred at 10°C and the minimum, 6 to 7·5 days, at 25°C.

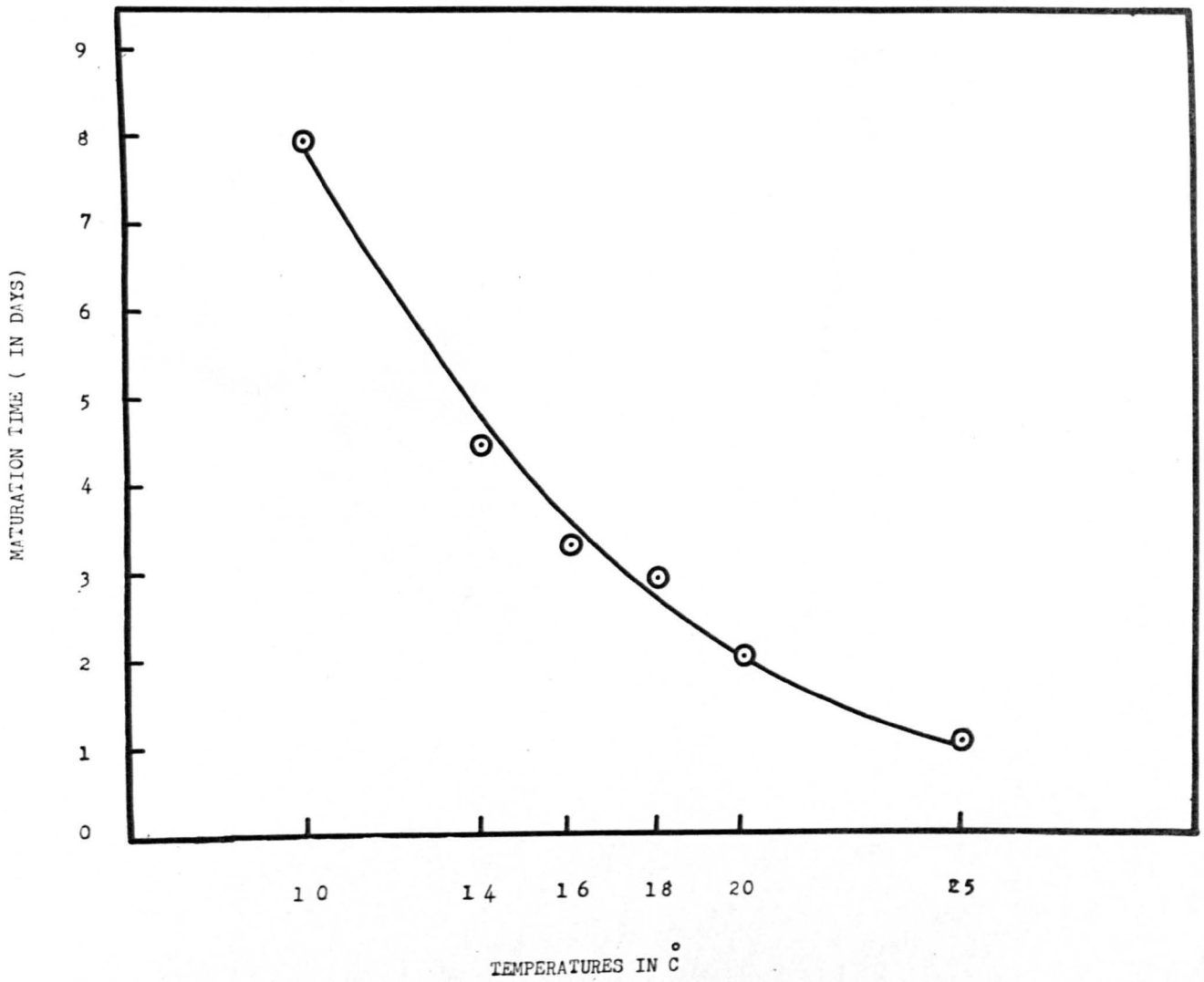
The time which the adult female took to reach maturity has been taken to be the time from the formation of the adult to the laying of eggs, which coincided with fertilization. In Fig. 4 an average value of this maturation time at different temperatures is given. These results indicate that the maturation time in the female is temperature dependent. At 10°C the females attained maturity about 8 days after the last moult and, as the temperature increased, the maturation time was reduced accordingly. At 25°C it was only about one day, but such an early maturation was followed by very poor egg production.

Egg production

Observations on the egg production under laboratory conditions were made on individuals fed with Nitzschia closterium. The laying of successive broods usually follows immediately, or within a few hours of, the hatching of the previous brood, but sometimes in the later broods a delay of as much as three days has been observed. The laying of the next brood did not take place until the previous brood matured and hatched. In a few cases where the egg sac was detached by mechanical action at an early stage of the development, the laying of the second brood was delayed till the time had elapsed which was required for incubation of the previous brood.

The number of eggs produced in a single brood varied from 3 to 38, depending on the brood. In the natural population a maximum of 42 eggs

FIG.4. AVERAGE MATURATION TIME OF THE ADULT FEMALE OF E. ACUTIFRONS AT DIFFERENT TEMPERATURES.



was recorded in August 1959. Under laboratory conditions the female was found to lay two or occasionally three broods. A maximum of five broods was produced by one female in a period of 8 to 9 days at a temperature of 20°C. In this case a total of 98 eggs was produced as a result of one copulation. This female was then allowed access to a few small males but no further egg production occurred and she died 8 days after the hatching of her last brood. Another female, bred at 16°C, laid 66 eggs in three successive broods in about the same time. This female also, despite the introduction of a few small males, produced no more eggs and died after 12 days. This suggests that one copulation is sufficient, at least under laboratory conditions, to fertilize all the eggs produced by a female, which agrees with observations in other copepods (Johnson & Olson, 1948).

It will be seen from Table VI that at any one temperature the numbers of eggs produced in the first two broods did not show any regular variations, but in later broods there was a marked decline in the number of eggs. At 20°C the number of eggs per batch was higher than in the corresponding broods at 16°C. It may also be seen that the time between the laying of successive broods was usually shorter at 20°C, corresponding to the shorter embryonic period at this temperature. Some further observations showed that at 10°C egg production was very much lower than at 16° and 20°C. These observations suggest that 20°C is the optimum temperature for egg production.

The optimal temperature for egg production in other northern species living at this latitude is lower. In Calanus finmarchicus this optimal temperature was found to be 8° to 10°C (Raymont & Gross, 1942) and egg

Table VI. Number of eggs produced in successive broods in E. acutifrons at different temperatures.

A = number of females; B = average number of eggs per brood;
C = average cumulative of eggs produced.

Broods	First		Second			Third			Fourth			Fifth		
Temperature in °C	A	B	A	B	C	A	B	C	A	B	C	A	B	C
10°	3	14·3	3	13·6	28	1	8	37*	-	-	-	-	-	-
16°	12	19·6	10	18	35·8	2	15	56*∓	-	-	-	-	-	-
20°	9	21·5	8	25·2	47·3	3	19	69·2*	1	16	88	1	10	98†
25°	5	9·4	4	4·9	13·25*	-	-	-	-	-				

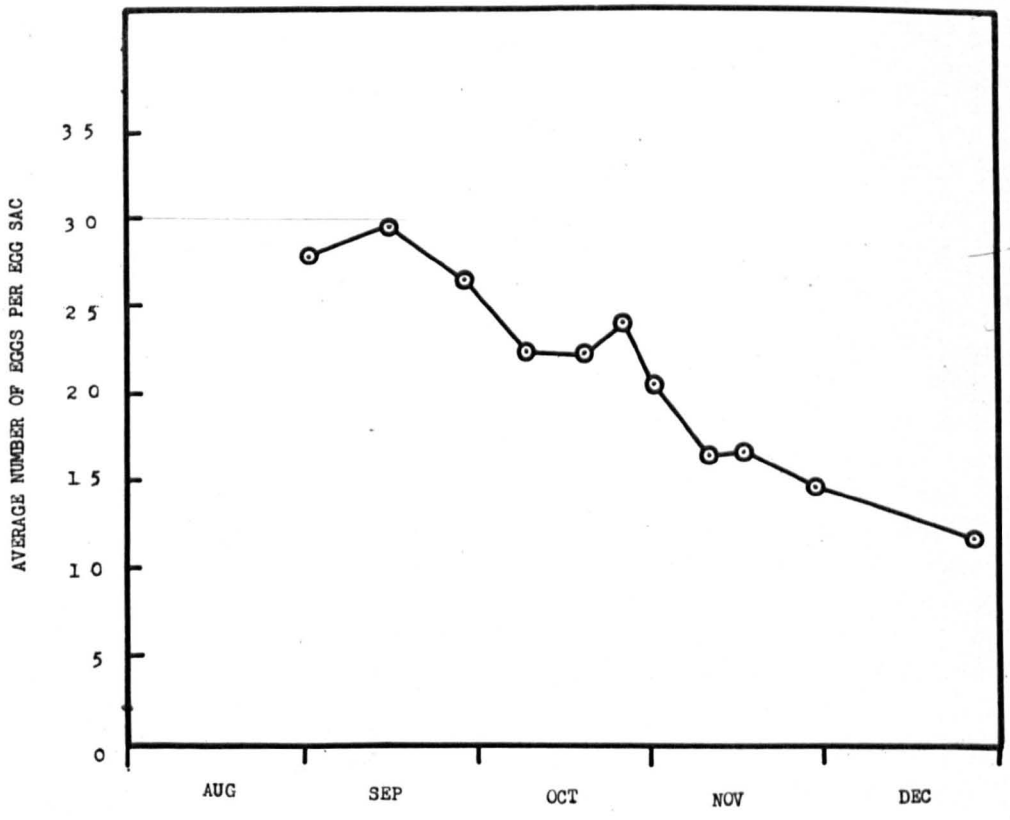
* Females were observed for 8 to 10 days after this but produced no more eggs.
† Died 8 days later.
∓ Includes one female which produced 66 eggs and died 12 days later.

production at 6° and 12°C was very low. This is perhaps due to the fact that Euterpina is a warm water and C. finmarchicus a cold water form.

Comparison shows that the number of eggs per brood is much higher in the natural population than in the laboratory. In Fig. 5 the numbers of eggs found per egg sac at different times during the breeding season of Euterpina in the year 1958 are given. In each sample 10 to 20 females were examined. The maximum average of 30 eggs per sac was observed about the middle of September when the sea surface temperature was between 15° and 16°C and the diatoms had shown a gradual decline from the autumn peak recorded at the beginning of the month (p. 14). Fewer eggs were found in later months and this may be correlated with the fall in the temperature and also with the decreasing food supply in the later autumn months

Both the laboratory and field observations show that the reproductive capacity of Euterpina, which is reflected in its egg production, differs considerably from that of the littoral and benthic species of harpacticoids when these breed under laboratory conditions. In Tigriopus fulvus the number of eggs per egg sac was found to vary from 30 to 93 with an average of 66 eggs per sac (Shaw, 1938). Similarly in Tisbe furcata the number of eggs per sac is reported to vary from 29 to 93 with an average of 57 eggs per sac (Johnson & Olson, 1948); this species is also reported to produce an average of 9 broods, a maximum of 12 and a total of 512 eggs in the whole life-time of a female. Nicholls (1935) in Longepedia coronata found that a female laid 11 broods after isolation from contact with males. Thus Euterpina

FIG. 5. SEASONAL VARIATIONS IN THE NUMBER OF EGGS PER EGG SAC IN FEMALE OF *E. ACUTIFRONS* IN THE MENAI STRAITS IN 1958.



acutifrons produces fewer eggs per brood and also fewer broods in the life-time of a female, and therefore a very much smaller total number of eggs.

Breeding under natural conditions

In copepods two types of breeding have been reported (Marshall, 1949). In one the broods are distinctly separated by periods when eggs and nauplii are scarce, as in Calanus (Marshall, 1949). In the other, which is commonly encountered in the smaller species of copepods, periods between successive broods are not distinct. This distinction implies that the maturation time of the female or of the broods or both is considerably longer in the first type than in the second. In Euterpina acutifrons it has been shown that the females attain maturity in a very short time and the duration between the successive broods is very short. In Euterpina such a feature seems to be reflected in natural populations, for often an increase in the number of adults coincides with an increase in the number of nauplii. Since the duration between successive broods is very short, it was not possible to determine the number of broods produced in various periods.

The data used in the breeding studies of Euterpina were collected from samples of zooplankton, taken at intervals of 8 to 14 days in the years 1957 to 1958. The details of sampling and method used in counting have been given elsewhere (p. 12).

In considering the number of generations produced in any one year the data have been expressed in two ways. In one the total numbers of nauplii, post larval stages and adults are given, and in the other their percentage

distribution. The graph indicating total numbers cannot, in the event of sharp fluctuations in the population, indicate whether a drop is due to mortality or to patchy distribution. The percentage graph gives a better indication of the changes in the proportions of different developmental stages in patchy conditions. On the other hand, it bears no relation to the actual numbers.

Breeding in 1957

Except for the occasional presence of a few adults at the end of June, the regular appearance of Euterpina was recorded in the first week of July, when a very high proportion of nauplii was noted in the plankton (Fig. 7a, 7b, C(1)). At this time the temperature of the sea had risen to about 16°C.

This first generation became adult at the beginning of August. In Fig. 6b, A(1) this is more conspicuous in the percentage curve and is not apparent in the abundance curve (Fig. 6a, A(1)) due to the small numbers. The sea temperature during July varied between 15° and 16·8°C.

From these adults a second burst of nauplii (Fig. 6a, 6b, C(2)) was produced by the end of the first week of August. The number of adults at the same time continued to increase as the later broods of the previous generations developed, and this was followed by a further rise in the number of nauplii.

In the third week of August, an increase in the postlarval stages, representing the earlier broods of the second generation, was followed by a second rise of adults in the last week of August (Fig. 6a, 6b, A(2)). During August the temperature of the sea remained above 15°C and so the development

FIG 6a

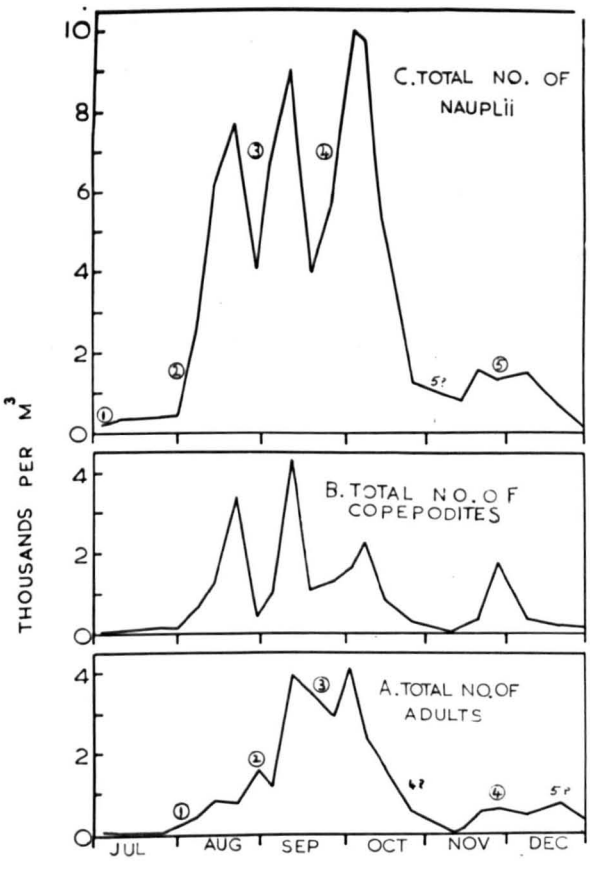


FIG. 6b.

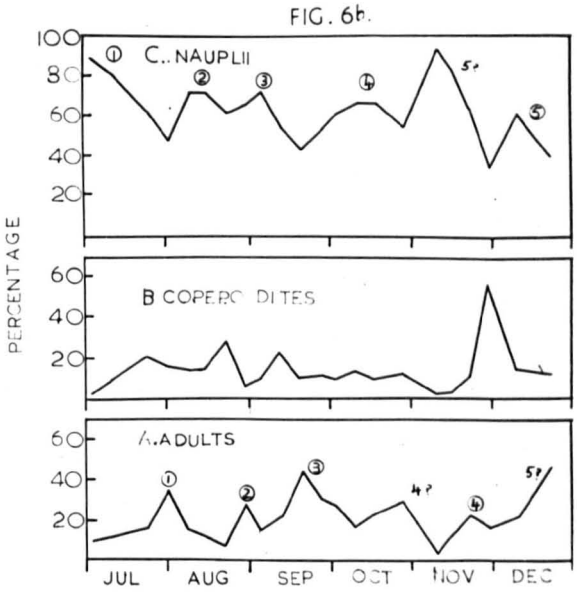


FIG.6a. ABUNDANCE OF E. ACUTIFRONS IN 1957

FIG.6b. PERCENTAGE DISTRIBUTION OF ADULTS COPEPODITES & NAUPLII OF E. ACUTIFRONS IN 1957

FIGUER THUS ① INDICATES SUCCESSIVE GENERATIONS OF ADULTS OR NAUPLII

time of the second generation was comparable to that of the first. From these adults a third generation of nauplii was produced in the last week of August (Fig. 6a, 6b, C(3)). The number of nauplii in the plankton continued to rise as more broods were liberated.

As the third generation developed, a rise in the postlarval stages was observed in the second week of September. From these individuals some from the earlier broods became adults in the third week of September, as shown by an increase in the proportion of adults in the percentage curve (Fig. 6b, A(3)). This was followed by a rise in the number of nauplii (the fourth generation) in the fourth week of September (Fig. 6a, 6b, C(4)). As breeding continued, more adults developed to maturity and more nauplii were liberated. A maximum number of adults was recorded in the first week of October (Fig. 6a, A), coinciding with the highest peak of nauplii produced in the season (Fig. 6a,C). The sea temperature fell during September from above 15°C to 13°C.

Most of these nauplii, representing the fourth generation, apparently did not survive. A rapid decline in the number of nauplii and also in the adults was noted towards the end of October (Fig. 6a). The temperature of the sea declined to 11·8°C by the end of October. It is possible that the mortality among the various stages might be due to this fall in the temperature.

The situation subsequently appeared more complicated and great difficulty was encountered in the separation of the generations. Although a continuous fall in the numbers of both nauplii and adults was noted, there was an indication of a small proportion of individuals becoming adult in the latter half of November after the peak of postlarval stages (presumably

representing the earlier broods of the fourth generation). This was more conspicuous in the percentage curve (Fig. 6b, 4?). In the abundance curve, however, due to the general fall in numbers, a separate peak for these freshly developed adults was not obvious. On the other hand, it is also possible that these adults represented survivors of the maximum number of adults recorded in the first week of October. The appearance of these adults was followed by an increase in the proportion of nauplii, and thus might represent the fifth generation.

During the second week in November there were very low numbers of adults and postlarval stages, and a similar, though less extreme, state in the nauplii (Fig. 6a). It is difficult to suggest a reason for this, but it is possible that the cause might be patchy distribution of the plankton.

By the end of November an increase in the number of adults was noted (Fig. 6a, A(4)). This was not supported by any preceding rise in the postlarval stages. It is possible that some individuals from the brood of the fourth generation might have survived, and a peak for postlarval stages was perhaps not apparent owing to patchy distribution. From these adults nauplii were produced, increasing their number in the plankton. At this time the temperature of the water had declined to about 9° to 8°C. This suggests that the breeding may be continued until the temperature falls to 8° ↔ 9°C, in accordance with the observations made in the laboratory.

A small peak in the postlarval stages at the end of November (Fig. 6a, B) suggests that they might have developed from the brood released in the early part of November (fourth or fifth generation). Some of these individuals became adult in the third week of December. No breeding occurred after this.

The sea temperature fell to about 6°C in the last days of December and this was accompanied by a marked decrease in the numbers of all stages.

Breeding in 1958

The temperatures recorded during 1958 showed marked differences from those of 1957. In 1958 the temperature remained low in the first half of the year, especially in the month of March, when the average temperature was more than 3 degrees lower. In the second half of the year the temperature remained slightly higher than in 1957.

Except for the occasional record of a few adults in late July, the first regular appearance of Euterpina was recorded in the third week of August, when numerous nauplii were recorded in the plankton (Fig. 7a, 7b, C(1)). Thus breeding began six weeks later than in 1957. The temperature of the sea surface at the time of breeding was a little above 16°C.

The number of nauplii continued to increase until the end of August as more broods were liberated. The earlier brood of the first generation, produced in the third week of August, presumably became adult by the middle of September, as suggested by the percentage graph (Fig. 7b, A(1)). The sea temperature remained between 15·5° and 16°C until mid September, but there was a sharp decline soon after this, which seems to have retarded the development rate of the subsequent broods of the first generation.

The individuals which became adult in mid September (Fig. 7a,7b, A(1)) liberated nauplii in the third week of September (Fig.7a,7b,C(2)). This may be seen in both the curves. Coinciding with this rise in the number of nauplii an increase in the postlarval stages occurred (Fig. 7a, B), representing the

FIG. 7a.

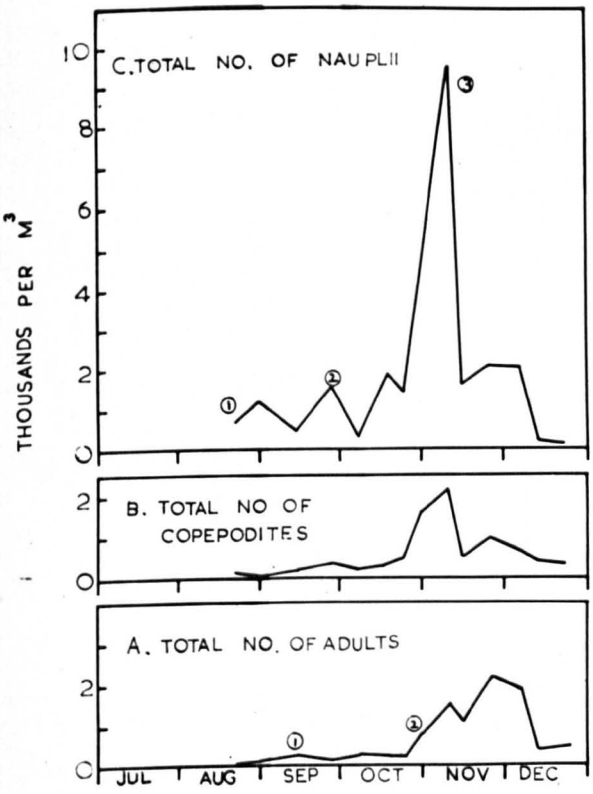


FIG. 7b.

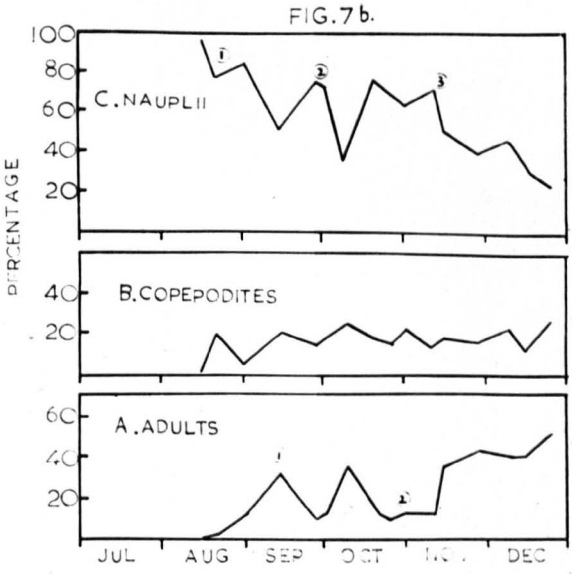


FIG. 7a. ABUNDANCE OF E. ACUTIFRONS IN 1958.

FIGUERS THUS ① INDICATES SUCESSIVE GENERATIONS OF ADULTS OR NAUPLII

FIG. 7b. PERCENTAGE DISTRIBUTION OF ADULTS, COPEPODITES & NAUPLII OF E. ACUTIFRONS IN 1958.

later broods of the first generation. This was gradually followed by an increase in the number of adults in the first week of October (Fig. 7a, b, A). On the other hand, it does not seem as likely as one might suppose from an inspection of the abundance curve that these adults represent broods of the second generation produced in the third week of September, since, under the prevailing conditions of low temperature, not enough time would have elapsed to allow their development.

In October a marked increase in the postlarval stages was followed by gradual increase in the number of adults towards the end of the month (Fig. 7a, A(2)). By this time the nauplii of the third generation were being produced by these adults.

The maximum number of nauplii was recorded at the end of the first week of November (Fig. 7a, C(3)). At this time the sea temperature had declined to about 12°C and this trend continued throughout the month.

The third generation did not survive and a sharp fall in the numbers of nauplii occurred in the middle of November. The number of adults increased as later broods of the second generation matured. From these more nauplii were produced but also failed to survive beyond the end of December. The number of adults also declined and the species disappeared in January.

Temperature influence on the breeding season

The delay of six weeks which occurred before the beginning of the breeding of Euterpina in 1958 coincides with sea temperatures which, in the first half of the year, remained lower than those of 1957, and reached a maximum considerably later in the year. In both years no larvae were recorded

until the temperature rose to between 15° and 16°C. In 1959 breeding began as early as the last week of June when the sea temperature rose above 16°C. It seems that the onset of breeding depends upon the attainment of a critical temperature of 16°C.

Temperature also seems to influence the ending of the breeding season. The two years' observations have shown that breeding ceased when the temperature fell below 8°C. A fall in temperature to 8° – 12°C adversely affected the survival of different stages in the natural population. These observations are in close agreement with the laboratory observations where survival below 9° – 11°C was poor and development was very slow.

Thus it seems that temperature has two effects: a rise above a critical value (16°C) stimulates breeding at the start of the season and the fall in winter to below 8°C so reduces the development rate and activity of the species that breeding virtually ceases. In 1957 the breeding season lasted for about 5 months, and in 1958 only three and a half months. The number of generations produced in these two years also differed in accordance with the length of the breeding period. In 1957 a total of four to five generations was produced, whereas in 1958 only two complete generations were produced and a third which apparently did not survive.

Food

A detailed consideration of the phytoplankton changes in the years 1957 and 1958 has been made (see p. 14), but reference will be made briefly to the conditions of the phytoplankton prevalent during the breeding season of Euterpina.

The phytoplankton during the breeding period of Euterpina shows slight differences between the two years. In 1957 a peak of diatoms was recorded at the end of July when the first generation of Euterpina matured. A gradual decline in diatoms followed. A peak in the nanopoankton occurred at the end of October, when the last generation was developing. In 1958 a peak of diatoms, much higher than that of 1957, was recorded at the beginning of September when the first generation of Euterpina was developing. This was followed by a sharp decline in the diatoms which thereafter remained at a lower level than that of 1957. The nanoplankton remained at a low level and no peak was recorded in the later months.

The main differences in the phytoplankton populations in 1957 and 1958 occurred in the first half of the year (p. 14); the differences in the second half were not so marked and appear to be insufficient to account for the considerable differences in the Euterpina populations in the two years.

Small males

Among other factors affecting the breeding of Euterpina in waters around Anglesey is the presence of small males in the natural population whose abundance seems to be related to the breeding activity of this species. A consideration of this aspect has been made in relation to sex ratio (see p. 142).

Breeding seasons of Euterpina in different parts of the world

Considering the important effects of temperature on breeding, it was thought of some importance to compare the breeding season of Euterpina in

different parts of its geographical range with the observations made in British waters. Unfortunately no records are available of the rate of development or range of temperature for normal breeding in different places. A few reports of its abundance at different seasons in different parts of the world allow only a limited comparison.

Although Euterpina has been reported from all the oceans of the world, except the Arctic and Antarctic, its distribution seems to be mainly centred in the warmer waters (Sewell, 1940; Lang, 1948). In the tropics the species is common round the southern coast of India (Indian Ocean), the Arabian Sea and the Red Sea. In temperate regions it is fairly common in the Mediterranean, and in the south on the south-east coast of Australia and New Zealand. In the north its distribution is recorded as far as the southern coast of Norway.

The results of the breeding experiments described above show that the temperature range at which the development of Euterpina is normal lies between 9° and 11°C (lower limit) and 20° and 24°C (upper limit) (Fig. 1). On the other hand, field observations in Anglesey waters suggest that the breeding of Euterpina does not commence until the temperature reaches 15° to 16°C. This is also found to be true in other northern regions. Lang (1948) quotes the observations of Tesch (1915) that this species is absent in the first half of the year in Dutch waters and starts breeding at the end of July at the time when the temperature rises above 16°C. Similar observations were made by Lücke (1912). Its maximum abundance occurs in September to October and falls quickly in November. Digby (1950), in his studies on the biology of planktonic copepods from Plymouth, reports the occurrence of

Euterpina as early as July, when the temperature rises to 16°C. His records of "juvenile adults" indicate the maximum abundance in September. It thus seems clear that the breeding season of this species towards the northern limits of its distribution starts at about the time when the temperature rises to 15° to 16°C.

Sewell (1940), after studying earlier records, found that 19 per cent of the species found in the Indian Ocean also occurred in the Arctic regions, and 15 per cent off the Norwegian coast, of which Euterpina acutifrons is one. The reasons why more of these species should be present in the Arctic region are not known, but the failure of Euterpina acutifrons to penetrate into the Arctic may be due to the fact that the sea temperature at the Arctic circle in the warmest season does not rise above 13°C. This is high enough for normal development but is below the critical temperature (15° to 16°C) at which breeding begins in northern waters.

In the southern part of Euterpina's range temperatures are higher. In the Mediterranean the average monthly sea temperature (W.A.S.S.T.*) rises from a minimum of 13°C in February to about 24°C in July and August, a range which corresponds to that found to allow normal development and breeding in the laboratory. Rose (1923, 1924, 1925) reports the continuous occurrence of this species in the years 1908 to 1910 in waters near Monaco. Unfortunately she does not report the seasonal abundance. In Sydney (Australia), where the sea water temperature rises from 16°C in the winter season to 24°C in the summer, breeding is reported to occur all the year round but with a maximum

* Temperatures recorded from World Atlas of Sea Surface Temperatures. H.O. No.225, Second Edition, 1944. Washington (1948 reprints).

abundance from June to September, when the temperature varies from 16° to 21°C (Dankin & Colefax, 1936).

In the tropics the temperatures at which the breeding of this species occurs seem to be outside the range so far found to be normal. Krishnaswamy (1953) reports the occurrence of Euterpina all the year round near the Madras coast with a maximum abundance in September at Krusadai, and in December at Madras. The average sea water temperatures for these months are about 25° and 21°C respectively. In the whole year the average monthly temperature varies between 25° and 30°C. The experiments already described show that the species, as it occurs round Anglesey, has a maximum rate of development at 24° to 26°C, but that survival is poor at this temperature and that a temperature of 28° to 31·5°C is lethal to the embryo and has an adverse effect on the development of later stages. It is therefore surprising that in the tropics the species breeds all the year round at temperatures above 25°C, unless different physiological races exist.

From the above account it may be seen that the breeding season of Euterpina in northern waters starts upon the attainment of a temperature of between 15° and 16°C, which approaches the summer maximum, and thus agrees with the generally accepted view that organisms living in the coldest parts of their geographical range breed in the warmest season (Appellöf, 1912; Orton, 1920; Runnström, 1929). The present observations, however, differ in part from their view that "marine organisms are restricted by the temperature prevailing during the breeding season." It has been shown that the minimum limit at which breeding can be carried on in the laboratory seems to have no influence on the start of the breeding season, although it may well control its close.

Further south, where the temperature falls within or above the laboratory limits for normal breeding, breeding is found to occur all the year round, with intense breeding in the colder months (Dankin & Colefax, 1933; Krishnaswamy, 1953). This differs from the view that breeding in the warmer waters should be continuous and without intensive breeding periods (Orton, 1920).

On the other hand, in the tropics, although intensive breeding is reported to occur in the colder months, the normal range of temperature for breeding seems to be much higher than that found in the species in British waters. This suggests that Euterpina has acquired a certain degree of local adaptation to temperature, but such a conclusion should remain tentative and requires further investigation.

Summary

The breeding of Euterpina has been studied both under laboratory conditions and in the natural population round Anglesey.

In the laboratory the rates of development increased uniformly between 10° and 20°C (Q_{10} = 3·6). At 25°C the maximum rate of development was between 20° and 25°C; the Q_{10} dropped to 1·9 at this stage. A temperature of 30° ± 1·5°C was found to be lethal to unhatched embryos and had an adverse effect on the larval development. The generation time at 10°C was about 53 days and about 9 days at 25°C. The Q_{10} values for embryonic and larval development were about the same as those for the generation time at any particular temperature range.

Both the dimorphic males were found to develop faster than the female; the small male had a shorter development time than the large. In each case the differences in development time are most obvious at lower temperatures and less so at higher.

The males reached maturity in a very short time after the last moult, particularly the small male, which matured in about 24 hours. The males also showed differences in sexual behaviour, the small male being more potent.

The time of maturation of the female was found to be temperature dependent. The maximum was 8 days at 10°C and the minimum 1 to 1·5 days at 25°C, but this was followed by poor egg production. The optimum temperature for egg production was found to be 20°C. The larvae reared at different temperatures showed better survival between 16° and 20°C. At 10° and 25°C the survival was very poor.

Temperature was found to have a limiting influence on the breeding period. Breeding began when the temperature reached 16°C, and stopped when it fell to 8°C.

The breeding of Euterpina in other parts of its geographic range has been compared with normal development exhibited under laboratory conditions.

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PART IV

Ratio of different sexes and dimorphic males of *Euterpina acutifrons* (Dana)

Contents

Introduction

Dimorphism in the males of Euterpina acutifrons inhabiting the waters off the north coast of Anglesey has already been described. These dimorphs differ in structure, in their development, and in their sexual behaviour.

Although dimorphism in one or the other sex has been reported in a number of copepods (Sewell, 1912, 1929, 1940; Thalawitz, 1916; Gurney, 1931) it has received very little attention in the past from an ecological point of view. In attempting to explain what factors are involved in the determination of these dimorphs, it was necessary to study in detail to what extent the dimorphic males of E. acutifrons occur in nature and whether the proportion of each was influenced by environmental factors only or by a combination of both environmental and genitical factors. This investigation involved both field observations and laboratory experiments.

Methods

Observations on the proportions of females and two dimorphic males in the plankton of the Menai Straits were made from samples collected at frequent intervals during 1957 and 1958. At the same time counts were made to determine the population density of the species. During the period in which Euterpina occurred, the number of individuals in each sample varied from 47 to 272, depending on the density of the population.

In addition to regular samples from the Menai Straits, further samples were taken from sea areas near the northern coast of Anglesey to study the proportion of sexes and dimorphs over a wide area.

Proportional changes in sexes and dimorphic males of E. acutifrons during breeding inside the Menai Straits

In 1957 breeding in this species started in the first week of July. The percentage of each type of adult during the breeding season is shown in Fig. 1a.A. Females outnumbered the males at all times. The proportion of the two males showed marked changes. At the beginning of the breeding season most males were of the large form and the small dimorph was very scarce. As the season progressed the proportion of small males increased and this dimorph remained dominant throughout the most intense breeding period from the middle of August to the end of October. A sharp decline in the proportion of small males was noted at the beginning of November and large males became dominant for a short while, but in the later months the numbers of the two dimorphs were about the same. Thus, as can be seen in Fig. 1a.B, the increase in the population coincided with the dominance of the small male and fell as it gave way to the large form.

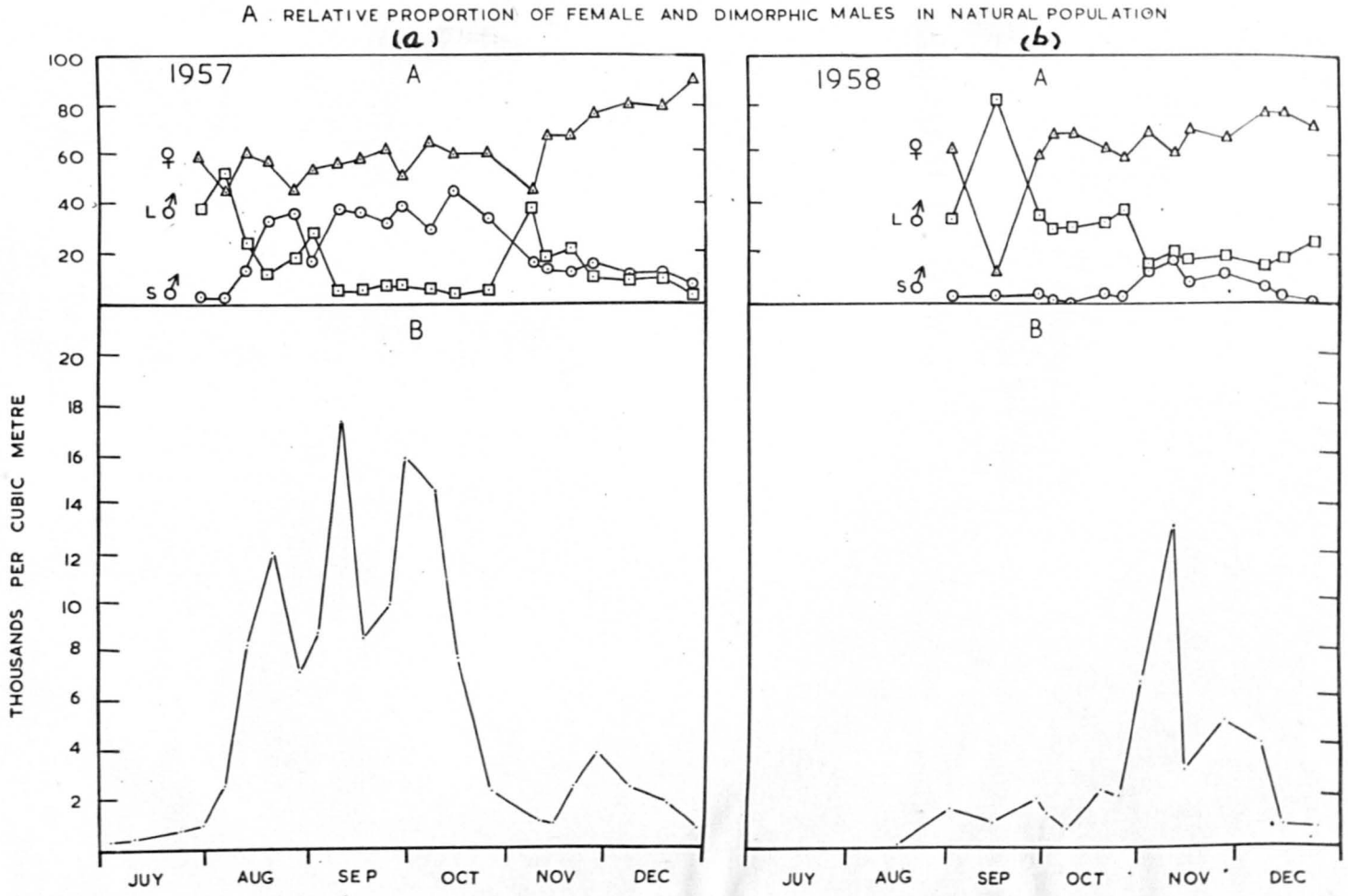
In 1958 the breeding period was shorter than in 1957. This may largely be attributed to differences in the temperature (p. 10). In Fig. 1b .A the proportions of the different adult forms during the breeding period is shown. The females were usually more numerous and were only once outnumbered by males. The proportions of dimorphic males were found to be altogether different from those of 1957. The large males remained dominant throughout. Small males were absent or very scarce during the early part of the breeding period but their relative numbers tended to increase in the later months, reaching a maximum in early November.

In addition to this a marked difference was noted in the total population recorded in these two years. The population in 1958 was smaller

Fig. 1. Proportional changes in sexes and dimorphic males during breeding in the Menai Straits.

a: 1957; b: 1958.

Fig. 1.


A . RELATIVE PROPORTION OF FEMALE AND DIMORPHIC MALES IN NATURAL POPULATION
(a)
(b)
1957
1958
A
B
♀
L ♂
S ♂
100
80
60
40
20
THOUSANDS PER CUBIC METRE
20
18
16
14
12
10
8
6
4
2
JUY
AUG
SEP
OCT
NOV
DEC
B . TOTAL POPULATION OF E.ACUTIFRONS .

than that of 1957, though in both years the highest peak in the population coincided with the highest proportion of the small males. In the later months of 1958 the population showed a rapid decline as the sea temperature fell (Fig.1b.B).

Distribution of sexes and dimorphs in the offshore region of the north coast of Anglesey

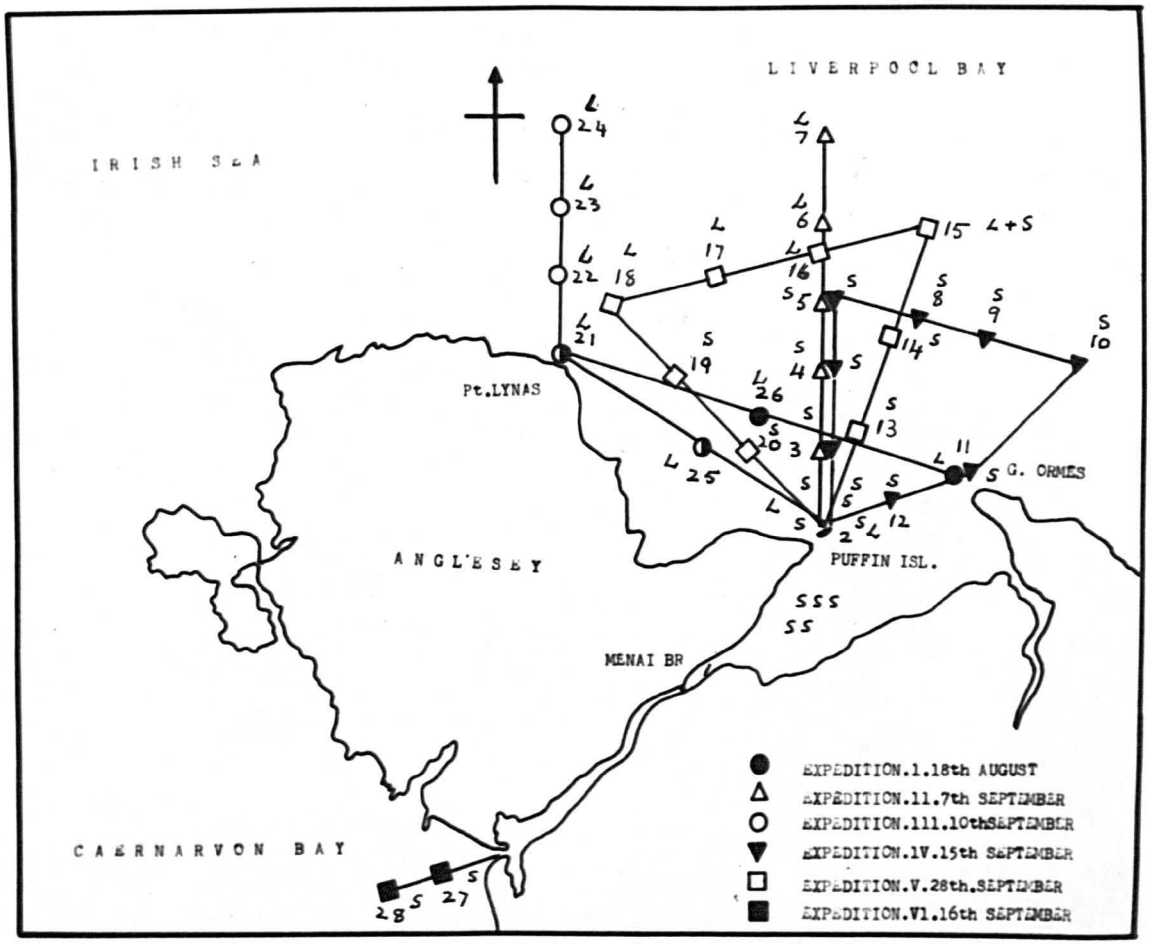
Observations in the Menai Straits showed that the greatest proportion of small males occurred during the most intensive breeding period. A number of similar observations were carried out in Liverpool Bay early in the breeding season of 1959. At the time marked changes in the population inside the Straits were noticed. The surveys were made in an area between a line 5 miles due north of the Great Orme and another 9 miles due north of Point Lynas. Each was planned after examination of the samples of the previous survey. The details of the course of each expedition and the stations chosen are given in Fig. 2. In each expedition samples were taken from the Straits (Mooring, Station I) and off Puffin Island (Station II), but the course was otherwise different. Altogether five expeditions were made into Liverpool Bay between 18th August and 28th September. At each station a 165 mesh to the inch plankton net was towed for 10 minutes.

While the expeditions were being made there were changes in the proportions of the dimorphs counted in the samples from the Menai Straits. The appearance of Euterpina was noted in June 1959, as in the previous two years. In a sample collected on 26th July the proportions of the adults were 28 per cent large males, 3 per cent small males and 78·5 per cent

Fig. 2. Distribution of dimorphic males in Anglesey waters. The stations are numbered.

L: Large male dominant; S: Small male dominant.

Fig. 2


LIVERPOOL BAY
IRISH SEA
Pt.LYNAS
ANGLESEY
G. ORMES
PUFFIN ISL.
MENAI BR
CAERNARVON BAY
EXPEDITION.I.18th AUGUST
EXPEDITION.II.7th SEPTEMBER
EXPEDITION.III.10thSEPTEMBER
EXPEDITION.IV.15th SEPTEMBER
EXPEDITION.V.28th.SEPTEMBER
EXPEDITION.VI.16th SEPTEMBER

females. On 15th August a sample contained 2·7 per cent of large males, 52·5 per cent of small males and 46·8 per cent of females. This change coincided with an increase in the population, a trend similar to that found in 1957. Details of the surveys are given in Table I.

In addition to the surveys summarized in the tables, observations were also made in Caernarvon Bay for about 4 to 6 miles south-west of Caernarvon Bar. In all these samples the small males were found to be dominant.

Interpretation of results of expeditions in 1959

At the time when the first expedition was made on 18th August the small males outnumbered the large in the Straits. Outside the Straits and adjacent areas the expeditions showed, at all stations, a preponderance of large males (Fig. 2). In the later surveys the small males became dominant in the inshore waters due north and north-east of Puffin Island. This was followed by a gradual decrease in the proportion of small males further offshore (Survey II, IV, V).

A marked difference was noticable, especially from expeditions carried out on 10th and 15th September, between the populations west and east of a line drawn northward from Puffin Island. East of the line, the small males were everywhere dominant, while west of the line the large males were usually dominant (Fig. 2). Successive expeditions showed a tendency for the eastern population, characterized by the dominance of small males, to shift westwards. This resulted in the dominance of small males in the inshore samples taken north-west of Puffin in Survey V (Fig. 2). A westerly

Table I. Distribution of different adults in the offshore region of Liverpool Bay, North of Anglesey.
Population densities expressed as D = dense; S = sparse; V.S. = very sparse.

Expedition I, 18th August

Stations	Number examined	Population density	%♀	%L♂	%S♂
1	178	D	47·1	14·6	38·2
2	124	"	38·8	53·3	8·8
11	172	S	41·9	37·1	20·8
21	144	"	37·5	37·5	25
25	106	"	45·2	45·2	9·4
26	151	V.S.	26·2	71·5	1·9

Expedition II, 7th September

Stations	Number examined	Population density	%♀	%L♂	%S♂
1	230	D	40·9	17·4	41·7
2	132	"	33·3	13·1	54·3
3	152	"	50	13·3	36·7
4	136	-	58·8	13·2	27·9
5	96*	-	33·3	43·7	22·9
6	104	S	9·6	88·5	1·9
7	188	"	35·1	46·7	18·1

Expedition III, 10th September

Stations	Number examined	Population density	%♀	%L♂	%S♂
1	118	D	56	8·4	35·6
2	160	-	36·3	62·5	1·2
21	146	-	52·1	30·1	17·8
22	131	S	21·3	76·3	2·3
23	130	V.S.	15·3	76·9	7·7
24	170	"	15·3	71·8	12·9
25	150	"	55	30	15

Expedition IV, 15th September

Stations	Number examined	Population density	%♀	%L♂	%S♂
1	140	D	62·7	9·3	27·9
2a	230	"	73·9	3·4	22·6
2b	186	"	64·5	11·8	23·6
3	198	"	68·6	3·1	28·2
4	235	"	67·2	7·2	25·5
5	205	"	73·2	3·4	23·4
8	160	"	61·2	5·6	33·1
9	272	"	56·2	19·8	23·0
10	296	"	54·0	20·9	25·0
11	180	"	65·6	3·3	31·1

Expedition V, 28th September

Stations	Number examined	Population density	%♀	%L♂	%S♂
1	149	D	57·7	16·8	25·5
2a	186	"	75·3	4·3	20·4
2b	100	"	62·0	4·0	34·0
13	88	"	54·5	9·1	37·4
14	216	"	70·4	7·4	22·2
15	68	S	44·1	27·9	27·9
16	68	V.S.	70·6	23·5	5·8
17	94	S	63·9	22·3	13·8
18	184	"	65·2	19·5	15·2
19	220	D	76·4	9·1	14·5

Expedition VI, 16th September (Caernarvon Bay)

Stations	Number examined	Population density	%♀	%L♂	%S♂
1	140	D	62·7	9·3	27·9
27	150	"	54·7	5·3	40·0
28	82	"	58·5	4·8	36·6

drift of population off the north coast of Anglesey was also noticed in earlier studies on the distribution of Phaeocystis globosa, so providing additional evidence of the west-going current off the North Wales coast (Crisp & Knight-Jones, 1954; Williamson, 1956).

Although in the 1959 investigations no quantitative hauls were taken, it is possible to give a rough estimate of population density since each haul in any one survey was made at the same depth and for the same time. The population of Euterpina tended to thin out in the waters furthest offshore in all surveys. There were few adults or nauplii in samples taken 9 miles due north of Point Lynas in which a predominance of large males were found. Conversely in the inshore region where the population was very dense, small males predominated. These differences in the population in different places also accord well with the seasonal changes observed in 1957 and 1958, when the maximum density of the population coincided with the dominance of the small males.

Early investigations made by Scott (1906) along the north coast of Wales also suggest that E. acutifrons is an inshore species. Dr. Williamson (private communication) in his investigations of the Irish Sea plankton during 1951-52 found the species in a number of samples, but it was seldom common and never a dominant form. His records of the occurrence of Euterpina north and due west of Holyhead (Anglesey), off Howath (Ireland), the Isle of Man and in Morecambe Bay show the species in these places to be much less common than off the north coast of Wales east of Point Lynas. Since the small male dimorph seems characteristic of rapidly increasing populations, it would be interesting to see whether it ever occurs in the thinly populated areas.

Ratio of different sexes and dimorphs under laboratory conditions

Some experiments have been conducted to study the proportion of different adults produced in breeding under laboratory conditions. Immature stages were collected from the plankton of the Menai Straits during November and December 1958 and reared under the conditions described earlier (p.93). The sexes were kept separately in culture dishes. Males of both dimorphic forms were crossed with virgin females. The eggs produced by each female were hatched and reared separately in culture dishes.

Table II, A & B gives the proportion of different forms produced from such crosses of each kind of male. It will be seen that in all crosses the progeny contained a higher proportion of small males than of large. There appears to be a tendency for the progeny of the small males to include more males than that of the large male, but this difference was not significant. Since there was an average survival of 78·7 per cent in experiments, the results seem unlikely to be significantly affected by differential mortality of one or the other form.

Of the progeny produced as a result of all the experimental crossings 50·5 per cent were small males and 8·7 per cent large. This is a very different ratio from that of the natural population at the same time, where the maximum proportion of small males (17·5 per cent), with ~~2·4~~ 20·1 per cent large males ~~were~~ recorded on 10th November. Also, the proportion of males as a whole (59·2 per cent) is higher under laboratory conditions than the maximum recorded in the natural population (38 per cent) at about the same time. This production of a greater proportion of males (and in particular

Table II.A. Sex ratio in small male cross in E. acutifrons under laboratory conditions.

Ref. & date 1958	Temperature	Number hatched	Number survived	♀	♂♂	L♂	S♂	♀%	♂♂%	L♂%	S♂%
ES.2. 10/11	16°C	19	11	3	8	1	7	27·2	72·7	9·0	63·3
ES.2. 12/11	"	7	7	1	6	0	6	14·2	85·7	0	85·7
ES.3. 14/11	"	14	14	10	4	0	4	27·2	72·7	9·0	63·3
ES.4.a. 14/11	"	22	14	0	14	2	12	0	100	14·2	85·7
ES.4.b. 17/11	"	27	24	0	24	6	18	0	100	25	75
ES.5.a. 15/11	"	20	15	8	7	0	7	53·3	46·7	0	46·7
ES.5.b. 18/11	20°C	20	16	8	8	0	8	50	50	0	50
ES.6. 11/11	"	18	11	3	8	7	1	27·2	72·7	63·3	9·0
ES.7. 11/11	"	26	24	2	22	0	22	8·3	91·7	0	91·7
ES.8. 15/11	"	16	8	1	7	0	7	12·5	87·5	0	87·5
Total		189	144	36	108	16	92	25	75	11·1	63·9

Table II.B. Sex ratio in large male cross in *E. acutifrons* under laboratory conditions.

Ref. & date 1958	Temperature	Number hatched	Number survived	♀	♂♂	L ♂	S ♂	♀ %	♂♂ %	L♂ %	S♂ %
EL.1. 1/11	16°C	12	11	8	3	0	3	72·7	27·3	0	27·3
EL.2. 5/11	"	18	18	15	3	0	3	83·3	16·6	0	16·6
EL.3.a. 8/11	"	17	14	14	0	0	0	100	0	0	0
EL.4.b. 6/11	"	18	14	0	14	0	14	0	100	0	100
EL.5. 14/11	"	14	10	4	6	0	6	40	60	0	60
EL.6.a. 30/11	"	16	12	4	8	5	3	33·3	66·6	41·6	25
EL.6.b. 3/12	"	14	11	6	5	1	4	54·5	45·4	9·09	36·3
EL.7.a. 1/12	"	15	11	9	2	2	0	81·8	18·1	18·1	0
EL.7.b. 3/12	"	11	7	5	2	1	1	71·4	28·5	14·2	14·2
EL.3.b. 10/11	20°C	19	14	14	0	0	0	100	0	0	0
EL.4.a. 3/11	"	18	18	0	18	0	18	0	100	0	100
Total		172	140	79	61	9	52	56·4	43·5	6·4	37·1

the small males) under laboratory conditions may be due to the temperatures at which they were bred (16° and 20°C) being higher than those recorded in the Straits (10° to 12°C). Comparison of the proportion of different adults produced from these crosses at temperatures of 16° and 20°C (Table III) shows the production of more males (and in particular the small males) at 20°C than at 16°C. The production of a high proportion of males under laboratory conditions has also been noticed in copepods and other crustaceans (Johnson & Olson, 1948; Takeda, 1950; Brown & Banta, 1932, 1935).

It seems that the relative proportions of sexes are much influenced by the environment. It is not so clear, however, whether or not production of the small male is also determined by genitical factors. Unfortunately studies of genetics in Euterpina suffer from the disadvantage that there is very high mortality in the inbred stock and also because one copulation only is sufficient to fertilize all eggs produced during the life of a female.

However, evidence of genitical influence has been obtained by comparing the proportions of females and male dimorphs produced in the successive broods laid by a single female. If these proportions are determined genitically they should be essentially the same in successive broods from the same mating, subject only to random variance. In Table IV two broods of sample matches of six such crosses are given. The results were compared by the "chi square" test.

The results show that the proportions of different sexes and dimorphic males produced by a single female in two successive broods do not differ significantly. When the proportions of different forms produced by different females were compared by the same test, they showed a highly significant difference.

Table III. Sex ratio of *E. acutifrons* at different temperatures in all crosses.

Temperature	Total hatched	Total survived	Percent survival	Percentage proportion of sexes			
				♀	♂♂	L♂	S♂
16°C	244	193	79·2	45·1	54·9	9·3	45·6
20°C	117	91	77·7	30·7	69·2	7·7	61·5
Total	361	284	78·6	40·7	59·2	8·7	50·5

Table IV. Comparison of two broods of sample matches from a single cross.

Exp. Cross		Temperature C	♀	L♂	S♂	Degrees of freedom	x^2	P
	a	16°	0	2	12			
ES.4						2	·6050	50–75%
	b	16°	0	6	18			
Small male			0	8	30			
	a	16°	8	0	7			
ES.5						2	·0335	97·5–99%
	b	20°	8	0	8			
			16	0	15			
	a	16°	14	0	0			
EL.3						2	0	100%
	b	20°	14	0	0			
			28	0	0			
	a	20°	0	0	18			
EL.4						2	0	100%
	b	16°	0	0	14			
Large male			0	0	32			
	a	16°	4	5	3			
EL.6						2	3·360	10–25%
	b	16°	6	1	4			
			10	6	7			
	a	16°	9	2	0			
EL.7						2	1·7150	25–50%
	b	16°	5	1	1			
			14	3	1			
Total						12	5·7135	90–95%
						10	127·1	0·1%

The observations also include three females transferred to different temperatures soon after the hatching of the first brood and before the laying of the second. The results show that changes in temperature before fertilization of the brood do not influence the proportion of different sexes and dimorphic males in the progeny.

Discussion

It is possible that environment alone may determine into which dimorphic form a male of E. acutifrons will develop. As shown earlier (p.79), this is unlikely to be the cause, since one would then expect a continuous range of variability rather than two distinct forms. There is no indication of intermediate forms in the plankton or in the laboratory experiments.

Among environmental factors food and crowding (Brown & Banta, 1932, 1935) have been considered to influence sex determination. The experiments on sex ratios described here were not designed to determine whether food supply had an influence on the relative numbers of male dimorphs. The abundance of phytoplankton in 1957 and 1958, explained earlier (p. 14), does not show any relation to the abundance of one or the other kind of male. In 1957 the small males first became dominant in the plankton on 21st August, following the diatom peak recorded on 1st August. These males presumably developed from parents which were well fed. In 1958 the maximum proportion of small males was noted on 10th November, although the large males were still dominant. The food conditions at this time were poor compared with those prevailing in August 1957.

The crowding effect has been suggested to cause male production in Cladocera (Brown & Banta, 1935). There seems to be no evidence that crowding of Euterpina affects the proportions of male dimorphs. In the experiments there was no correlation between the male production and the number of eggs in different batches, although each batch was reared in the same volume of culture medium and the degree of crowding varied greatly.

At higher temperatures a greater proportion of males was produced, as has also been shown in other copepods and crustaceans (Takeda, 1950; Brown & Banta, 1932). On the other hand, laboratory experiments have shown that the proportions of different sexes and of dimorphic males produced in two successive broods remain unaltered when the fertilized eggs develop at two different temperatures. It would appear that, if temperature is an important factor in deciding these ratios, it operates at the time of cell division to form eggs and sperms.

It seems probable that determination is by both environmental and genitical factors. This implies balanced polymorphism of the kind frequently encountered in insects (Ford, 1945). Observations spread over three years have shown that the proportion of dimorphic males changes progressively during the breeding period. In all these years the large males were found to be dominant at the onset of breeding, but as it continued the proportion of small males in the population tended to increase. In 1957 the breeding season lasted for 5 to 6 months and was marked by a high proportion of small males throughout the period of most intense breeding. In 1958 breeding started 6 weeks later, apparently being influenced by temperature conditions (p. 127). The breeding season lasted for 3 to 4 months and was marked by a sparse

population with a very low proportion of small males which increased to some extent in the later months. This suggests that the change to the production of small males is gradual, increasing as the breeding season progresses and that their proportion in the population is dependent on the length of the breeding period.

The evidence of the determination of different sexes and male dimorphs partly by genitical factors is in agreement with the result of the experimental study of successive broods in Tisbe gracilis by Battaglia (1958). He suggests that development into the male or female phenotype is conditioned by the heterozygosity of at least some of the genes more closely concerned with sex determination and also that the sex ratio in Tisbe is influenced partly by environemental and partly by genitical factors.

The same may well be true of Euterpina, which is closely related to Tisbe gracilis, and similar factors may be involved in the determination of the small males. It is noteworthy that structurally the small male resembles the female more closely than the large male. This suggests that the genes responsible for the characteristic structures in the large male may fail to express themselves. This failure may be influenced by environmental stimuli: a progressive change of some environmental factors during the breeding season might cause an increasing proportion of males to develop into the small form.

This problem is obviously one which merits further investigation, both of the environmental dependence and genitical basis of dimorphism.

Summary

Euterpina acutifrons produces two kinds of males in waters around Anglesey.

Observations spread over 1957 to 1959 showed that the small male production varied in different years. The large males were much more numerous than the small at the beginning of the breeding season, but when breeding became active the proportion of small males increased. During most of the long breeding season of 1957 the small males greatly outnumbered the large. In 1958 conditions were less favourable, and the breeding period was shorter than in 1957. The small males never outnumbered the large, although the proportion of small males increased when the population was densest.

Surveys off the north coast of Anglesey in 1959 showed that the production of small males began in the inshore population and then extended into offshore waters. The dominance of small males was most marked in the densest populations. This was true where the variation in density was geographical and also where the variation was seasonal.

Experiments under laboratory conditions suggest that the production of small males has a genitical basis; comparison with the proportions of large males and small males produced in the plankton at the same time suggests that environmental conditions also have an effect.

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PART V

Larval development of *Oithonina nana* (Giesbrecht)

Contents

Introduction

Our knowledge of development in the Cyclopoida results from the investigations of a number of workers whose studies have been mainly concerned with fresh water species (Claus, 1893; Dietrich, 1915; Amelina, 1927; Gurney, 1933; etc.) Very little work has been done on development in marine species. Among marine Cyclopoida the most satisfactory account of development has been given in the genus Oithona. Oberg (1906) described the larval development in Oithona similis. This species was reinvestigated by Gibbons and Ogilvie (1933) while studying the larval development of an allied species, O. spinirostris. The only account of the genus Oithonina, of which Oithonina nana is the only species, is that of Murphy (1923) who gave no morphological or anatomical description of the developmental stages. He illustrated only the first and the fifth nauplius, and these figures are too ambiguous to throw light on the structure and the specific characters of the nauplius.

Oithonina nana, a widely distributed planktonic copepod, has frequently been reported in natural populations together with an allied species, Oithona similis, which it closely resembles. In consequence the larval stages of these two species have been confused (Wiborg, 1940; Marshall, 1949; Digby, 1950). The failure to distinguish the larvae in the plankton has prevented a satisfactory interpretation of the breeding and biology of O. nana in different water masses. A study of the larval development of this species therefore seemed desirable.

Methods

Larvae which were believed to be developmental stages of this species were collected in plankton hauls from water around North Wales in 1958. These observations were later confirmed by examining developmental stages reared in small culture dishes containing about 150 ml. of sea water and fed on fresh cultures of Nitzschia closterium. Although some larvae were reared successfully through their entire life cycle by this method, the proportion that did so was small. The survival rate was sufficiently high to allow the verification of the course of development, and attempts to improve culture conditions were therefore not pursued.

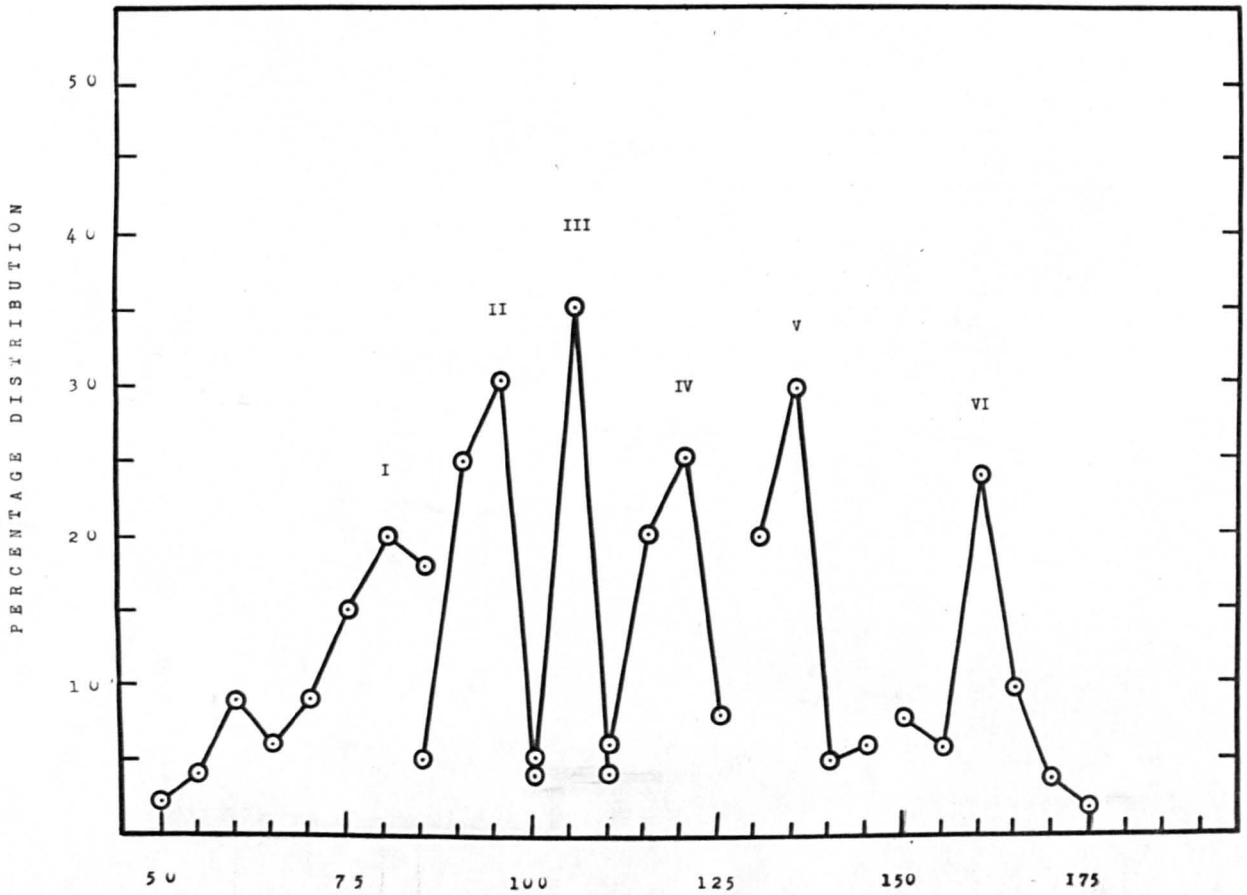
Measurements of all the stages were made under a microscope at a magnification of x 600, the individuals measured being covered by a cover glass.

General features of the larval stages

Size and shape

The percentage size distribution of each nauplius stage is shown in Fig. 1. The first nauplius measures from 65 to 85μ in length. Smaller individuals 50 to 60μ long are occasionally encountered in natural populations, thus accounting for the somewhat greater variability in size of this stage compared with that found in later stages. Under laboratory conditions the first nauplius is usually hatched at a stage of development similar to that observed in the natural population. Smaller individuals are very occasionally hatched prematurely; they are inactive and their appendages appear to adhere to the body without free mobility.

FIG . 1



PERCENTAGE SIZE DISTRIBUTION OF
LARVAL STAGES OF *O. NANA*.

Fig. 2 shows the body in ventral view. In the first nauplius (A) the broadest part of the body is about a quarter of its total length behind the slightly pointed anterior end. In the second (B) and the third (C) nauplius the body becomes elongated and its anterior end is rounded. In the fourth nauplius (D) it is oval. In the fifth (E) and the sixth (F) nauplius the body has its maximum breadth towards the rear, about two-thirds of its length from the anterior end.

Murphy (1923) reported that the sexes may be differentiated in Oithonina nana at the third nauplius stage. He separated the developmental stages on the basis of the size differences and the sexes by the anterior end of the body being 'square cut' in the case of the male and 'bluntly rounded' in the female. He have the sizes of each sex separately from the third nauplius onward.

In the present studies no morphological difference could be seen which might suggest sexual differentiation in the nauplii.

As it is clear from his account, Murphy (loc-cit) was relying entirely on the size differences in separating the various larval stages rather than on structural differences of the kind described later in this paper. It seems possible that he treated two succeeding stages as male and female. Gibbons and Ogilvie (1933) in their studies on the larval development of Oithona similis and O. spinirostris gave extensive measurements of the larval stages of both the species, but reported no sexual differences whatsoever in the early stages.

Fig. 2.

Larval stages of Oithonina nana shown in ventral view.

A = First nauplius with both antennules. Left antenna and right mandible articulated.

B, C = Second and third nauplius stages.

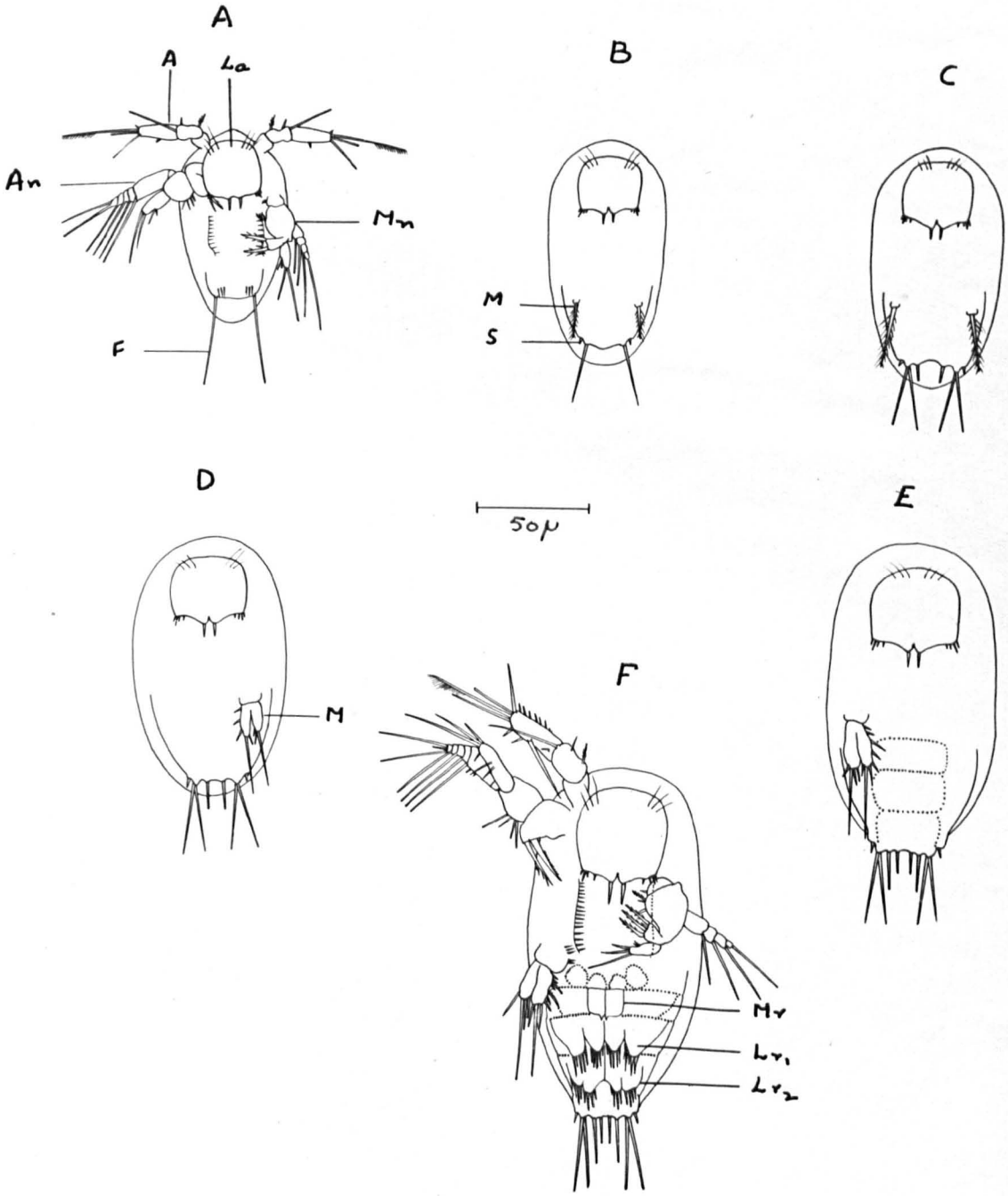
D = Fourth nauplius with right maxillule articulated.

E = Fifth nauplius with left maxillule articulated.

F = Sixth nauplius with left antennule, antenna and right mandible articulated.

A = antennule; An = antenna; F = furcal seta; La = labrum; Lr_1 & Lr_2 = rudiments of first and second swimming leg; M = maxillule; Mn = mandible; Mr = rudiment of the maxilliped; S = outer furcal spine.

Fig. 2.



Structures on the ventral surface

The most distinctly visible structure on the ventral surface is the labrum (Fig. 2: La). This has a characteristic shape; its anterior margin is rounded bearing three fine hairs on either side, and the lateral borders project posteriorly into four-spined points. On either side of the median groove on the posterior border of the labrum there is a single prominent spine which is a characteristic feature of the nauplius of this species. Behind the labrum a row of spines is present directed inwards on either side of the mid line, each arising from a ridge. These spines are also found in the closely related species Oithona similis and O. spinirostris. At the first nauplius stage, between the two delicate furcal setae (F) (Fig. 2.A), there are spines of similar shape to those on the ventral surface, but these are not to be found in the subsequent stages.

Marked changes in the furcal setae serve as useful diagnostic features in separating the naupliar stages. In the first nauplius (Fig. 2.A) there is only one pair of delicate setae emerging slightly above the posterior end of the dorsal cephalic shield. In the second nauplius (Fig. 2.B), on the outer side of each of the furcal setae, a small spine (s) is developed which becomes more distinct in the subsequent stages. The presence of this spine separates the nauplius of Oithonina nana from the nauplius of Oithona similis and O. spinirostris. The third nauplius (Fig. 2.C) has two more pairs of furcal setae on either side. In possessing three pairs of furcal setae the third nauplius in Oithonina nana differs from the related species Oithona similis and O. spinirostris which have two pairs only at this stage. In the fourth

nauplius (Fig. 2.D) the furcal armature remains the same as in the third. In the fifth nauplius (Fig. 2.E) a further inner pair of furcal setae is present, making a total of four pairs at this stage. The furcal armature in the sixth nauplius (Fig. 2.F) remains the same as in the fifth and is the same as that of the corresponding stages in Oithona similis and O. spinirostris.

The nauplius of Oithonina nana at later stages shows indications of segmentation within the body wall (Fig. 2.E,F), a feature not found in either of the related species.

Appendages and setation

Antennule

The antennule of Oithonina nana is three-jointed. The first joint (Fig. 3.A) is small and partly covered by the cephalic shield. The second joint is contracted in the middle and bears three setae, of which the distal-most is the longest. The third joint is the longest and in the first nauplius is furnished distally with three setae, of which the longest is feathery, the second a delicate aesthate (a) and the third is directed post-axially. In the first nauplius (Fig. 3.A) there are also two small rudimentary spines, one on the post-axial side and the other at the distal end. The third joint in the subsequent stages shows characteristic changes in its setation which furnish useful diagnostic features in separating the stages. The changes in the setation of this appendage, according to Ogilvie's (1953) method of formulation, is shown in Table I. The antennule at the fifth and sixth nauplii (Fig. 3.E,F) has the same setation but the sixth differs in that one of the setae of the post-axial margin is longer and backwardly-directed.

Fig. 3.

Antennule and antenna in the larval stages of

O. nana.

A - F = Right antennule of first to sixth nauplius.

G - I = Right antenna of first to third nauplius.

a = aesthate seta; b = basipodite; c = copepodite;

en = endopodite; ex = exopodite.

Fig. 3.

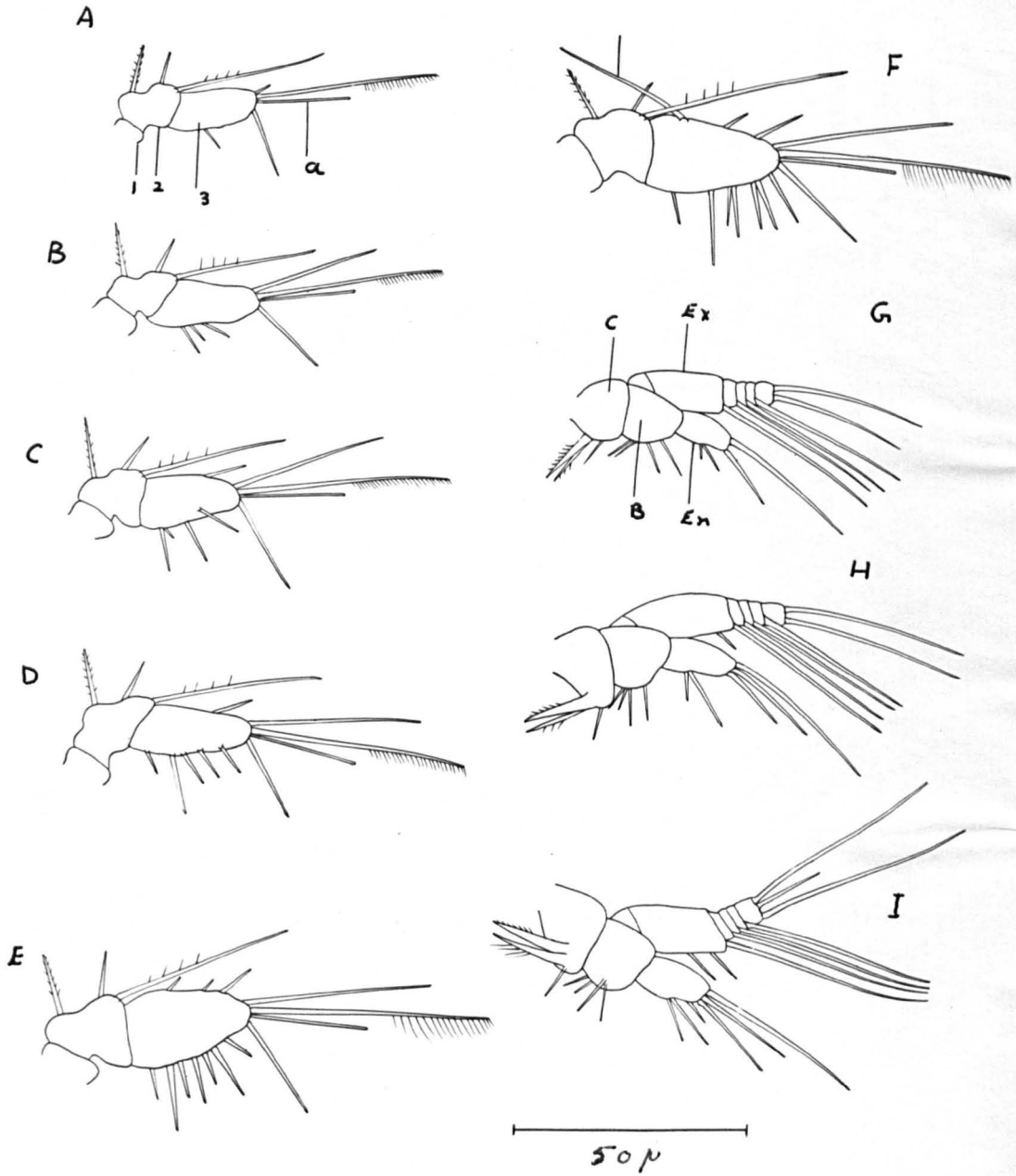


Table I. Setation of the antennule and maxillule in the larval stages of Oithonina nana.

		1st	2nd	3rd	4th	5th	6th
Antennule	1st joint	0	0	0	0	0	0
	2nd joint	3	3	3	3	3	3
	3rd joint	(2 a 2)	(2 a 4)	(3 a 5)	(3 a 6)	(5 a 8)	(5* a 8)
Maxillule	Endo.	-	spine	spine	se,st,si 0, 2, 3	se,st,si 0, 3, 5	se,st,si 0, 3, 7
	Exo.	-			0, 3, 0	1, 3, 0	1, 3, 0

The antennular formula for the 3rd joint is given round the aesthate seta; the number before the aesthate represents the setae on the ventral side and the number after represents those on the dorsal side.

a = aesthate seta; se = external setae; st = terminal setae; si = internal setae.

5* includes a backwardly-directed seta.

Examination of Oithona similis from the plankton showed that the increase in setation at each stage was similar to that described by Gibbons and Ogilvie (1933) but differs from the corresponding stages of Oithonina nana in the number of setae.

Antenna

The antenna resembles in all respects that of the related species. The coxopodite (c) (Fig. 3.G) bears a claw-shaped masticatory process as in other cyclopoid larvae (Gurney, 1933; Ewers, 1930). The basipodite (b) (Fig. 3.G) bears four fine setae. The endopodite has one joint and in the first nauplius (Fig. 3.G: En) bears two setae at the middle of the post-axial margin and two terminally. An additional terminal seta is developed on the endopodite in the second nauplius (Fig. 3.H: En) and a subterminal one in the third (Fig. 3.I: En).

The exopodite is six-jointed; the first joint is very small (Fig. 3. G-I: Ex) and may be seen only with difficulty. The second joint is the longest and bears one seta on the post-axial margin of the distal end at the second nauplius (Fig. 3.H: Ex) and two at the third (Fig. 3.I). The remaining joints of the exopodite bear one long post-axial seta, except the last one which possesses two (Fig. 3.G,H). At the third nauplius the last joint of the exopodite develops a small spine (Fig. 3.I) between the two long terminal setae. The structure of the antenna remains unchanged in the subsequent stages.

Fig. 4.

Mandible and maxillule of the larval stages of *O. nana*.

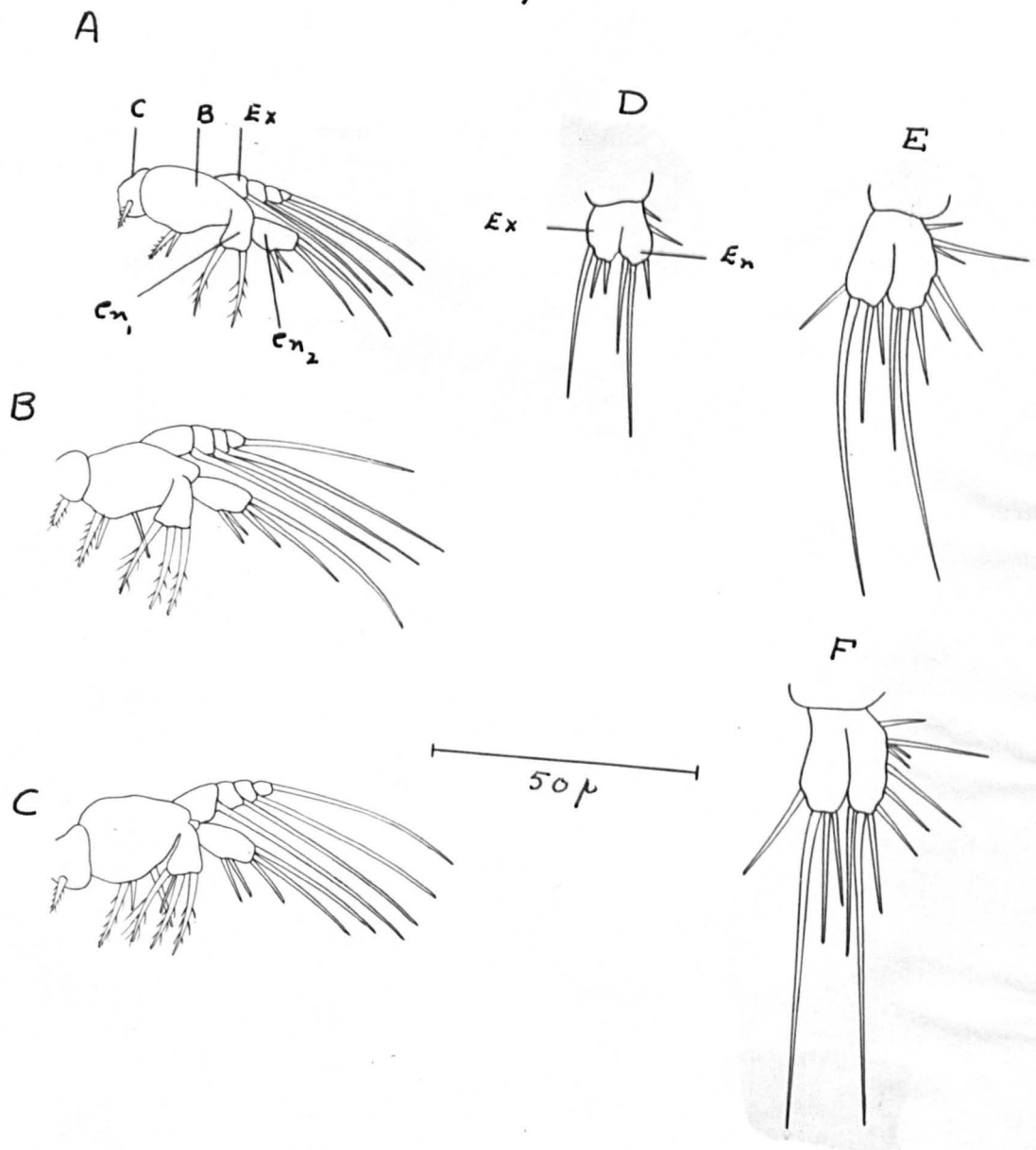
A - C = Right mandible of first, second and third nauplius.

D - F = Right maxillule of fourth, fifth and sixth nauplius stages.

en_1 = proximal joint, en_2 = distal joint of endopodite; P = masticatory process.

Other abbreviations as stated earlier.

Fig. 4.



Mandible

The mandible (Fig. 4.A-C), like the other appendages, resembles that of other cyclopoids. The coxopodite (c) bears a small bristle. The basipodite (b) has two setae in the first nauplius (Fig. 4.A), of which one is delicate and absent in the allied species. In the second nauplius (Fig. 4.B) a small seta is developed on the post-axial margin of the basipodite. The endopodite is two-jointed (Fig. 4.A-C), the proximal joint (En_1) being modified for clasping as in other cyclopoids (Gurney, 1933). In the first nauplius this joint bears two strong masticatory spines while the distal joint (En_2) bears two small post-axial and two terminal setae. In the second nauplius the proximal joint of the endopodite bears the third, median, spine of the clasping organ (Fig. 4.B) while the second joint now bears three terminal setae. At the third nauplius an additional delicate seta is borne in the middle of the masticatory spines of the first joint (Fig. 4.C).

Maxillule

The rudiments of the maxillules (Mr) appear for the first time in the second nauplius (Fig. 2.B) in the middle of the posterior half of the body in the form of a pair of feathery bristles, as in other cyclopoids. This remains unchanged in the third nauplius. In the fourth nauplius (Fig. 4.D) the maxillule (M) appears as two distinct lobes; the endopodite and the exopodite, which show an increase in the setation at the fifth and the sixth nauplius (Fig. 4.E,F) which are summarized in Table I. Examination of the later nauplius stages of Oithona similis showed the setation of the maxillule

to be different from that of Oithonina. The endopodite of the maxillule of Oithona similis at the fourth, fifth and the sixth nauplius stages possesses a long single terminal and three post-axial setae, whereas in Oithonina the setation of this ramus at the corresponding stages (Table I) is more complex and increases in the later stages.

Rudiments of other posterior appendages

In the sixth nauplius the rudiment of the maxilliped (Mp) (Fig. 2.F) may be seen in the middle of the body on the ventral surface resembling that of the last nauplius of other cyclopoids (Gurney, 1933). The rudiments of the maxilla cannot be seen in the sixth nauplius.

The sixth nauplius of Oithonina nana is also characterized by the presence of bilobed rudiments of the first two pairs of swimming legs (Lr_1, Lr_2) (Fig. 2.F). The rudiments of the maxilliped and the first two pairs of swimming legs are absent in the genus Oithona (Oberg, 1906; Gibbons & Ogilvie, 1933).

Copepodite I

The body (Fig. 5.A) consists of a cephalothorax, four thoracic somites and a long abdominal somite. Each of the furcal rami bears four long unequal setae and two outer spines. The total length is 260 to 290μ.

The antennule (Fig. 5.B) is six-jointed, as compared with the eight-jointed antennule of Oithona similis and O. spinirostris.

Fig. 5.

First copepodite of O. nana and its appendages.

A = Entire body of first copepodite seen from dorsal view.

B = Right antennule.

C = Right antenna.

D = Right mandible.

E = Right maxilla.

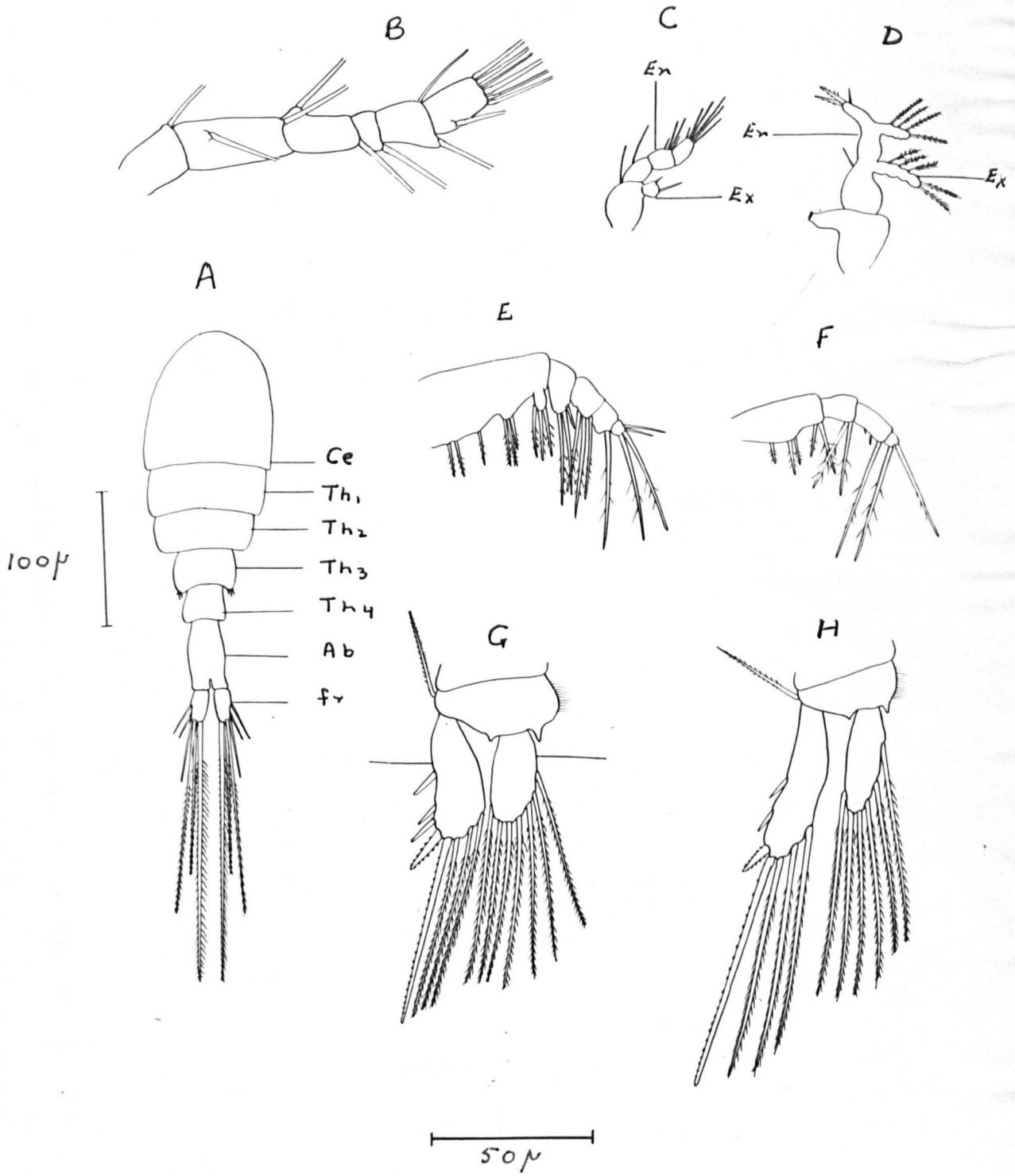
F = Right maxilliped.

G = Left first swimming leg.

H = Left second swimming leg.

Ab = abdominal somite; Ce = cephalothorax; fr = furcal ramus; Th_1 - Th_4 = first to fourth thoracic somites. Other abbreviations as stated earlier.

Fig. 5



The antenna (Fig. 5.C) is similar to that of the allied species . The basipodite (b) possesses a small seta. The exopodite (Ex) is much reduced in size and bears only two small spines. The endopodite (En) is three-jointed; the first joint bears one seta; the second four and the third bears six terminal setae of unequal length. In the allied species the endopodite is two-jointed.

The mandible (Fig. 5.D) is similar to that of the allied species. The coxopodite (c) bears a toothed masticatory process. The basipodite (b) is long and furnished with a median seta. The exopodite (Ex) appears to be four-jointed, each of the first three joints bearing a single seta, while the last one has two. The endopodite has a basal joint carrying four setae and a second joint with two stout spines and a small seta on its base, as in Oithona similis and O. spinirostris.

The maxilla (Fig. 5.E) is very stout. It consists of five joints and is similar to that of the allied species. The maxilliped (Fig. 5.F) is four-jointed and differs from that of the allied species in possessing only two long bristles on the last joint instead of three.

The first and the second pair of swimming legs (Fig. 5.G,H) each have one segmented rami and their setations differ from those of the first copepodite of Oithona similis in the presence of one additional outer spine on the exopodite of each leg, but resemble those of O. spinirostris (Gibbons & Ogilvie, 1933). The basipodite in each leg is furnished with a seta on the outer margin as in the allied species.

Life cycle

In order to investigate the time needed for the completion of the life cycle the larvae were hatched under laboratory conditions and reared at

11°, 18° and 20°C. The 11°C experiment was conducted in a cool cabinet with a variation of about ± 1°C and the 18° and 20°C experiments in a thermostatic tank with 0·5°C variation.

In Table II the results of rearing the larvae of O. nana are given. As has already been stated, the survival rate was low (50% at best), but reasonably constant results were obtained for the duration of various stages. At 20°C the species completed its life cycle in a period of 21 to 24 days. At 18°C this time increased to 28 to 31 days. At 11°C development was obtained only up to the earlier copepodite stages, but a comparison of rates of development of the larval phase showed that it required more than twice as long at 11°C as at 18°C with a Q_{10} of 3·06.

Murphy reported that under laboratory conditions O. nana completed its cycle in about ten weeks, a period which is considerably longer than that observed in the present investigations. Unfortunately, he did not mention the temperature at which his experiments were carried out. Therefore it is difficult to compare his results with mine. On the other hand the results are comparable to those reported in experiments on various species of fresh-water cyclopoids in which Ewers (1936) found that for 12 species under investigation the total development time varied from 8 to 50 days.

Comparison with other cyclopoid larvae

The larvae of Oithonina nana are very much smaller than those of other species of cyclopoids (Ewers, 1930; Gurney, 1933), including the closely related species Oithona similis and O. spinirostris. The measurement of

Table II. Duration of developmental phases of O. nana reared under laboratory conditions.

Date of hatching	Temperature	Number of larvae reared	Number reached copepodite I	Larval phase (days)	Number reached adult	Total time from hatching to egg laying (days)	Embryonic phase (days)	Generation time from hatching to hatching of next generation (days)
10.V.59	11°C	21	2	23	- *	-	-	-
11.VI.59	18°C	22	12	10 - 12	11 (6 + 5)	23 - 25	4 - 5	28 - 29
15.VI.59	18°C	15	5	9 - 11	4 (+ 3)	24 - 25	4 - 5	29 - 30
29.VII.59	20°C	6	4	7 - 9	3	18 - 20	2·5 - 3·5	22 - 23

* 2 reached 2nd copepodite stage

the larval stages of the latter species, together with those of O. nana, is given for comparison in Table III. The first, second and third nauplii of O. nana each measure less than the average size of the first nauplius of either of the allied species and may easily be separated on the size basis. The fourth, fifth and sixth nauplii of O. nana correspond in size to the first to fourth nauplii of the two allied species, but may be distinguished from them morphologically.

Although there is a marked resemblance in the general form and shape of the nauplii and their appendages, the larvae of O. nana show certain characteristic differences from those of Oithona spinirostris and O. similis:

1. The labrum of O. nana, though similar in its general shape, differs from those of the allied species in the presence of a single spine on the posterior border on either side of the median groove. In Oithona spp. this is supported by accessory spines.
2. The number of marginal setae of the terminal joint of the antennule at each larval stage differs considerably from those of Oithona spp. and can serve as a diagnostic feature in separating the various larval stages. The sixth nauplius of O. nana is also characterised by the presence of a backwardly directed seta on the ventral side of the last joint of the antennule.
3. The early nauplius stages of O. nana are also characterised by the presence of an outer spine (except in the first nauplius where this is not distinct) outside the furcal setae. The arrangement of the furcal setae in the later stages resembles that of Oithona similis. The maxillule shows considerable differences in its setation compared with those of the allied species.

Table III. Comparison of size of larval stages in O. nana and the allied species.* All measurements in microns.

	Oithona similis		*O. spinirostris*		*Oithonina nana*	
Larval stages	Modal length	Range	Modal length	Range	Modal length	Range
Nauplius I	115	100 - 125	130	120 - 140	080	50 - 85
Nauplius II	130	120 - 140	150	140 - 160	095	85 - 100
Nauplius III	140	125 - 155	170	155 - 185	105	100 - 110
Nauplius IV	165	155 - 180	200	190 - 210	120	110 - 125
Nauplius V	190	180 - 205	235	220 - 245	135	130 - 145
Nauplius VI	215	205 - 225	270	250 - 280	160	150 - 175

* Measurements reproduced from Gibbons & Ogilvie (1933)

4. A remarkable feature of O. nana is the presence of the rudiments of the first two pairs of legs and the traces of the maxilliped in the sixth nauplius, which is also synchronized with distinct segmentation of the body beneath the body wall. The early acquisition of these appendages in rudimentary form at the sixth nauplius stage, when they are absent in the allied genus Oithona and also other structural differences noted above, suggest an important taxonomic gap between these species and O. nana, and justifies Sars (1913, p.5) who separated the latter into the genus Oithonina as against Giesbrecht (1892) who described the species under the genus Oithona.

Both Oithonina and Oithona have six nauplius stages and therefore differ from other cyclopoids which are reported to have five by Amelina (1927), Dietrich (1915), Gelmini (1928), Gurney (1933) and others. Ewers (1930), however, described six stages in a number of American freshwater species of Cyclops. Ewer's (loc-cit) description of the larval development also differs from those of the previous workers as regards antennular joints of the larva. She describes a four jointed antennule while, according to others, it is three jointed. In Oithona and Oithonina my observations show that the antennule is three jointed, which confirms the description of larval Oithona by Oberg (1906) and Gibbons and Ogilvie (1933).

Summary

The larval development of Oithonina nana has been described in detail for the first time. There are six nauplius stages as in the allied genus Oithona.

The nauplii of O. nana, though resembling those of the allied species Oithona similis and O. spinirostris in general shape, differ from them in size, in the setation of the antennule and maxillule and also in the furcal armature. The spines of the labrum also show characteristic differences.

The salient feature of larval development in which the species differs from its allies is the early acquisition of the maxilliped and the rudiments of the first two pairs of legs.

The first copepodite of O. nana also shows differences in the antennular joints, the armature of the maxilliped and in the furcal setation.

Rearing under laboratory conditions has been accomplished. At 18°C the species completes its life cycle in about 28 to 30 days and at 20°C in about 21 to 24 days. Comparison of the duration of larval phases at these temperatures and also at 11°C shows that the rate of development is temperature dependent with a Q_{10} of 3·06.

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Key to the larval stages of Oithonina nana.

1. Only one pair of furcal setae present.

   (a) Maxillular rudiment absent.
   Antennular formula (2 a* 2) — Nauplius I.

   (b) Maxillular rudiment present in the form of feathery spine.
   Antennalur formula (2 a 4) — Nauplius II.

2. More than one pair of furcal setae present.

   (i) Three pairs of furcal setae present.

   (a) Maxillular rudiment in the form of feathery spine.
   Antennular formula (3 a 5) — Nauplius III.

   (b) Maxillular rudiment bilobed.
   Antennular formula (3 a 6) — Nauplius IV.

   (ii) Four pairs of furcal setae present.

   (a) Antennular formula (5 a 8) without backwardly directed spine on the last joint. Rudiments on the first two legs absent. — Nauplius V.

   (b) Antennular formula same as the fifth, but with a long backwardly directed seta on the last joint. Rudiments of the first two pairs of legs present. — Nauplius VI.

* a = aesthate seta. The number before the aesthate represents the setae on the ventral side and the number after represents those on the dorsal side.

General Summary and Conclusions

A study has been made of the plankton of the Menai Straits and nearby waters during 1957 and 1958. The phytoplankton population was, in general, smaller in 1957 but the evidence suggests that the phytoplankton production was in fact no greater in 1958 and that the different densities were the result of grazing by a larger zooplankton population in 1957. It is suggested that the difference in zooplankton numbers in the two years resulted from the influence of their different temperature conditions on the development of the zooplankton rather than from differences in the phytoplankton.

The composition of the plankton in the Menai Straits and the inshore waters at their northern end was found to be different from that in the waters further offshore. For example at certain times of the year Phaeocystis globosa is prominent inshore but comparatively scarce further out while Acartia clausi and Oithona similis, common in most of the Irish Sea, are scarce inshore where, instead, both Oithonina nana and Euterpina acutifrons are found.

Studies have been made, in culture, of the larval development of Oithonina nana which was found to differ materially from that of Oithona, so supporting the separation of Oithonina from that genus.

In Euterpina acutifrons dimorphism was found in the male and this has been related to an investigation of the development of the species. The development of the dimorphic males, as observed

in culture, was found to follow a simpler course than those suggested for other dimorphic copepods by previous workers.

The behaviour of the two male dimorphs was found to differ. The small males were more active, sexually more potent, and were found to be most numerous (relative to the large males) in the plankton when breeding was at its height and the population was densest.

Experiments have also shown that Euterpina from Anglesey waters had an optimum temperature range for breeding from about 10°C to about 20°C and that while development was faster at 25°C, mortality was greater. A temperature of 30°C was lethal to the earlier developmental stages and harmful to all.

Certain problems which arise from the present studies require further investigation.

(i) Some investigation of the factors which decide which dimorphic form will be manifested in a male has been attempted in this work and tentative suggestions have been made but this aspect requires further study. The approach may be cytological; this could be accompanied by breeding experiments under controlled conditions of temperature and food supply. Also, although conditions of crowding greater than those normal in the plankton had no effect on the sex and dimorph ratios in culture, further experiments in which these conditions are widely varied might possibly be instructive.

(ii) Euterpina breeds in regions nearer the tropics at temperature ranges higher than those which have been determined for the Anglesey population. Experiments on the rate of development of

Euterpina from populations in warmer waters should therefore be carried out. Similar studies might be possible on Oithonina nana which is also found in some warmer seas and whose development rate has also been investigated in the Menai Straits population.

(iii) Morphological differences between specimens of Euterpina from the Indian Ocean and others from the South Atlantic have been reported which are in part similar to the dimorphism which occurs off Anglesey. It would be interesting to see whether this phenomenon is a local characteristic and also whether the small male occurs in places other than those where the species is found in large numbers and breeds actively. An examination of collections of Euterpina from widely separated localities, taken in the breeding season, is suggested.

It is hoped that an attempt to solve the problems outlined above and others arising from them can be started on my return to Pakistan.

Further studies of the annual changes in the plankton of the Menai Straits and of the influence of temperature on the zooplankton production would also be useful. The conclusions put forward in the present study are based on investigations covering two years only and similar counts over a longer period would therefore be advisable.

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