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Growth, reproduction and vertical migration in *Clio pyramidata* Linné, 1767 forma *lanceolata* (Lesueur, 1813), with notes on some other Cavoliniidae (Mollusca, Pteropoda).

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ABSTRACT

Shell growth and size variation in populations of *Clio pyramidata*, *Cuvierina columnella*, *Diacria trispinosa* and *Cavolinia gibbosa* are studied. Attention is given to differences in the size variations of the four species caused by differences in their developmental biology. The reproductive cycle of *Clio pyramidata* forma *lanceolata* in the Bermuda Area is described and it is shown that there are more than one protandric hemaphrodite sexual cycles in one animal. The vertical migration of the four mentioned species is discussed.

INTRODUCTION

This is a preliminary paper on the biology of *Clio pyramidata* Linné, 1767, based on material collected during six cruises of the Bermuda Ocean Acre Program. Not all cruises in this project and not all samples from the cruises studied could be investigated at this time, but the results are so significant that publication seemed justified. The material studied was collected in spring, summer and winter in a relatively small oceanic area, 1° square, centered at 32°N 64°W southeast of Bermuda. With an Isaacs-Kidd Midwater Trawl, 153 discrete depth samples and 104 non-discrete samples were taken between 1500 metres and the surface. For full information on the cruises and samples one is referred to Gibbs *et al.*, (1971).

It is assumed that, notwithstanding the vertical migration, the entire population of *Clio pyramidata* forma *lanceolata* (Lesueur, 1813) lives above

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1500 metres, so that it is sampled completely. The forma *pyramidata* Linné, 1767, is not discussed here as it occurs only infrequently in the area during autumn. To demonstrate more clearly the biology of *Clio*, notes on *Diacria*, *Cavolinia* and *Cuvierina* are added. From the literature (Wormelle, 1962) it is known that diurnal vertical migration is found for this species in the Western Atlantic. For data on plankton production in the area one is referred to Deevey (1971) and Deevey & Brooks (1971) who described maximal plankton abundance in spring and peaks of abundance for pteropods and foraminifers in spring and autumn. A separate paper on the aberrant and skinny stages will be published, so these are not considered below. For terminology, anatomy and systematics one is referred to van der Spoel (1967).

ACKNOWLEDGMENTS

The author expresses his thanks to Dr. C. F. E. Roper from the National Museum of Natural History, Smithsonian Institution at Washington who made the material of the Bermuda Ocean Acre Program available and assisted in the interpretation of the computer countings used for the studies of the vertical migration. Special thanks are due to Mr. A. F. de Fluiter who did the serial sectioning of about 300 animals.

MATERIAL AND METHODS

For all specimens of *Clio pyramidata* forma *lanceolata* the shell length and width were determined. After measuring, the soft parts were taken out of the shells and sectioned histologically 5 μ thick. The sections were stained with Haematoxylin-Eosin. As the whole specimen was sectioned it was possible to study the development of the gonad as well as that of the accessory sexual organs: penis, accessory sexual gland, bursa seminis and receptaculum seminis. The stage of development of the accessory sexual organs was described by using the following code:

- 1 not present,
- 2 little developed (whole organ composed of interstitial cells),
- 3 little developed (besides interstitial cells also normally developed cells present),
- 4 developed (but not yet completely present),
- 5 developed (all structures present and partly functional but not all structures completely developed),
- 6 functional (without restrictions).

When determining the average development of an organ in a number of specimens the average of the code figures is determined. In the diagrams (fig. 5) these averages are given on the y axis (+ 1 axis) reduced by 1 as 1 means absent which in the graph should be 0. It should be mentioned that the average values expressed in figures in the graph cannot be translated like the original code could be. Development of the gonad is determined by

using three transverse sections, one through the anterior, one through the medial and one through the posterior part of the organ. For each section it was determined which percentage of the section is occupied by: unripe male (r), ripe male, spermatozoa (R), unripe female (e), and ripe female, ova (E) products, by undifferentiated germinal cells (D), and other structures or lumina (A).

The percentages are determined by putting a screen in the ocular of the microscope, the screen having meshes of about 0.01 mm² over the gonad section when working with an oil immersion objective. The number of meshes was counted in which a cell type occurs, and finally these data were converted into percentages.

The meristic data, percentages of sexual products and the code figures for development of organs are computerized. The vertical distribution and shell length variation discussed below are directly based on computer results, the other results are obtained without use of the computer, as programs are not yet available. All material was collected by the Bermuda Ocean Acre Program *).

SHELL GROWTH

Shell growth in *Clio pyramidata* forma *lanceolata* was already discussed by me (van der Spoel, 1969), using growth rings as an indication for daily growth. This study thus concerned only the growth rate of shells and not the age of shells. "*Clio pyramidata* forma *lanceolata* grows up to about 3.5 mm above the embryonic shell in a juvenile period of 4—6 days, during the skinny period (gonad of juvenile or male structure) about 6.5 mm is added in 11—12 days and about 8 mm is added in the adult period of about 0—24 days". The general conclusion was that this forma grows up to about 18 mm above the embryonic shell in about 52 days. A specimen hatched in April, as a consequence, measures about 10 mm in June and about 20 mm in July when growth is continuous, but it was assumed that growth was discontinuous (van der Spoel, l.c.) so that age and size cannot be correlated; what one can conclude from the shell is its growth and not the age of the shell. This is not comparable with the process found in species which shed their caudal spine, like *Diacria trispinosa* (Blainville, 1821) and *Cuvierina columnella* (Rang, 1827) or with the growth process found in species which develop through a minute stage, like *Cavolinia gibbosa* (d'Orbigny, 1836) (cf. van der Spoel, 1967, 1970).

A comparison with regard to the shell length variation in different seasons is made for *Clio pyramidata* forma *lanceolata*, *Cuvierina columnella* forma *atlantica* van der Spoel, 1970, *Diacria trispinosa* (Blainville, 1821), *D. major* (Boas, 1886) and *Cavolinia gibbosa*. For a more detailed description of the development in these species one is referred to van der Spoel (1967). The species status of *D. trispinosa* and *D. major* which were usually considered

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forms of one species is discussed in a paper in preparation. *Diacria major* (Boas, 1886) is infrequently found and rare in the winter period which is probably due to the more thermophilous character of this species which has its northern distributional border near Bermuda. *D. trispinosa* is much more tolerant and occurs also at more northern latitudes.

The size range, mean and estimated standard error given in the dicegram of figure 1 shows clearly the diverging type of size changes in the population of *Clio pyramidata* forma *lanceolata* in regard to the other three species.

Small specimens of 0 up to 2 mm, thus real juveniles, are never collected by the fact that the gear failed to collect them and by the fact that this stage has a very short duration of 1 up to 2 days so that its occurrence is of short duration and relatively rare.

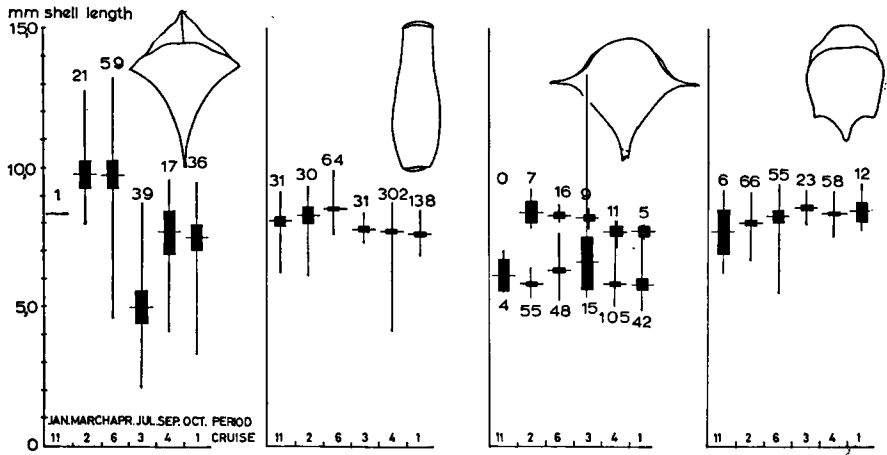


FIG. 1. Dicegrams for the shell length from the left to the right for *Clio pyramidata* forma *lanceolata*, *Cuvierina columnella* forma *atlantica*, *Diacria trispinosa* (*D. major* upper averages) and *Cavolinia gibbosa*. Shell length on y axis in mm, time scale in month, and Ocean Acre cruises along x axis. Vertical lines for size range, horizontal lines for mean, black bars for standard error, figures over verticals stand for number of specimens concerned.

There is no significant difference between the meristic data of the population when sampled in March and April or between these data when the population is sampled in September and October. When significant differences are mentioned these are based on "t" tests ($P < 0.05$). The mean shell length for the population in July differs significantly from that found in April and September. In July the mean shell length is about half that found for the population in April. Breeding in *Clio pyramidata* is found in all months of the year but there is a peak in reproduction during spring (the sexual cycle is discussed below). This explains the small specimens occurring in July; the juveniles do decrease the average and minimum shell length in this month. In figure 2 the same tendency is seen.

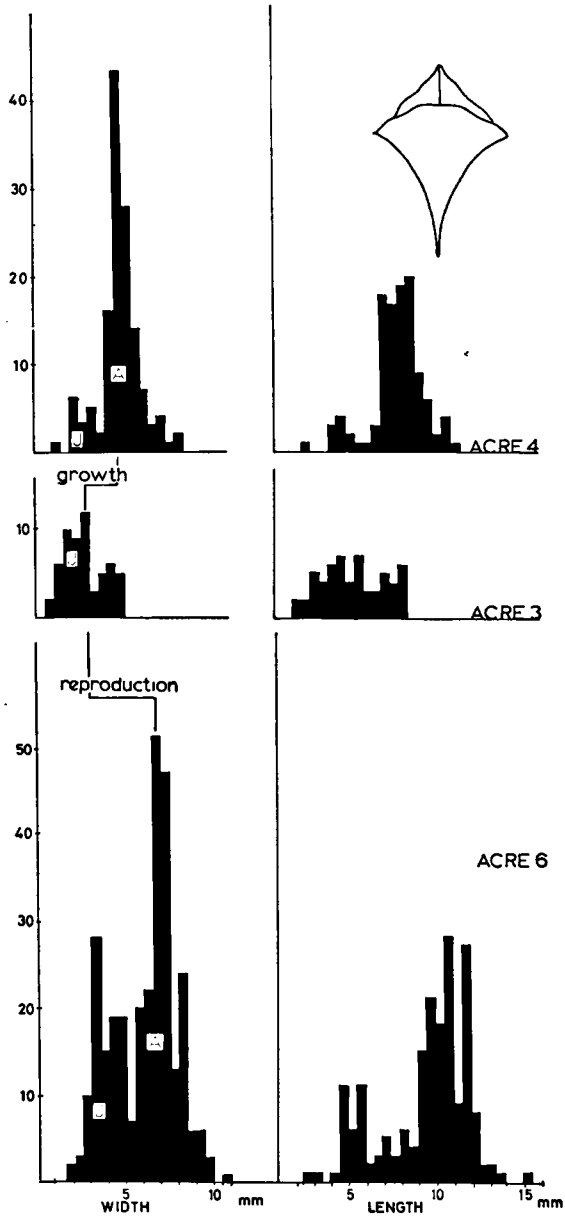


FIG. 2. Histogram for shell width and length on the x axis and number of specimens on the y axis for *Clio pyramidata* forma *lanceolata* in April (Acre 6), July (Acre 3) and September (Acre 4). A = Adults, J = Juveniles.

The dicegrams are based on shell length, the histograms of figure 2 represent shell width and shell length, separately. In *Clio pyramidata*, shell width is a more accurate parameter than shell length as the anterior projection and the posterior point of the shell are more frequently, and more invisibly, damaged than the lateral points. The lateral points determining shell width are not so fragile as they are supported by stronger lateral ribs.

From figure 2 it is clear that the April (Acre 6), July (Acre 3) and September (Acre 4) populations all comprise some juveniles. The juveniles indicated with "J" show shell width smaller than 5 mm. In the July population only juveniles and a few small older specimens are found as indicated in figure 2. Histological studies proved the July population to be composed chiefly by specimens with immature sexual organs.

The small drop of the average shell length of *Clio pyramidata* in the October population can also be correlated with an increase of young specimens. The dicegram for *Clio pyramidata* thus proves that this species shows maximal breeding activity in spring and autumn and it shows that the shell grows considerably during the development of the specimens.

Maximum shell length for the latitude under consideration is 13 mm (cf. van der Spoel, 1970, fig. 2). Specimens of maximal size are thus only found in March and April as shown in the dicegram. The maximal shell length in September and October is about 9.5 mm, which means that shells have reached a size common for the adult period but it shows also that there are no full grown shells in the autumn period. Considering minima and maxima in shell length it is clear that specimens with a shell length smaller than 3.5 mm common for the juvenile period are found only in July, while small adults between 3.5 and 10 mm occur in all months. Only in March and April full grown adults larger than 10 mm are found.

To conclude from shell growth: *Clio pyramidata* forma *lanceolata* reaches an age of one year and a maximum size of 13 mm in the Bermuda area, passing through the three growth stages as described by me (van der Spoel, 1969). That shell growth, taking about 52 days in total, is an interrupted process seems to be supported by the absence of statistical differences between shell length in the periods March and April and September and October. When juveniles smaller than 3 mm are not collected by failure of the gear, the above conclusion still stands as the growth up to 3.5 mm takes only some days so the percentage of such small animals in the population is very small only.

As the breeding pattern in *Cuvierina columnella* is in principle identical to that in *Clio pyramidata*, a resemblance between the dicegram for both species could be expected. However, the July population does not differ strongly from the other ones as it does in *Clio pyramidata*. The January, March and April populations do not differ significantly and the differences between the July, September and October populations are only small. A significant difference occurs between the April and July populations. As in *Clio pyramidata*, reproduction occurring in the April—July period influences

the length variation in the population of *Cuvierina columnella*. In the latter species the mean in July is 0.7 mm smaller than in April, but in *Clio pyramidata* this difference is 4.8 mm.

This discrepancy is explained by the fact that *Clio pyramidata* shows considerable growth of the permanent shell, while *Cuvierina columnella* grows quickly to its maximal size and then casts off its caudal spine (van der Spoel, 1970). The juvenile specimens of which the shell consists only of the caudal spine are not considered in the present study and specimens of which the shell is composed of caudal spine and permanent shell, or part of it, were not found among the material.

Thus shell increase in the measured *C. columnella* specimens is effected only by small additions to the permanent shell near its aperture. The two discussed dicegrams from figure 1 prove for the first time this difference in shell development in natural populations. After shell metamorphosis, *C. columnella* does not increase more than 0.7 mm in size. This increase in shell length can be correlated with the growth lines near the shell aperture. Usually two or sometimes three growth rings with mutual distances of about 0.4 mm are found. In my previous paper (van der Spoel, 1970) this small increase in length was considered normal.

The dicegram for *Diacria trispinosa* (figure 1) is similar to that of *C. columnella*; the July population shows significant differences with the April and September populations, while the January, March and April as well as the September and October populations as regards shell length are rather similar. The high value for shell length in the July population is explained by the presence of a few young specimens in which the adult shell is not yet full grown and which had not yet shed their caudal spines. The presence of these specimens points also to increased reproduction in the April—July period.

The dicegram for *Cavolinia gibbosa* shows significant differences between the populations as sampled in the six months, except for the January and March populations which show no statistical differences. The lowest minimum shell length for *C. gibbosa* is found in April which may prove more juveniles to be present in this month. The average shell length, however, increases from January up to July and it decreases in September. This gives the impression that breeding occurs also in September. A comparable tendency in the size fluctuation for the September—October period, indicating increased reproduction is also found for *Cuvierina columnella* and *Diacria trispinosa*, both show lower average and lower minimum size in this period.

Though there is no statistical difference between the means for shell length in September and October for *Clio pyramidata* it is striking that there is a drop in the mean and minimum shell length in this period too. Summarizing, it can be stated that growth in *Clio*, *Cuvierina* and *Diacria* and in *Cavolinia* is principally different and secondly it can be concluded from the size graphs that all four species reproduce in spring and autumn.

SEXUAL DEVELOPMENT

To study the sexual development, histological investigations were made and as a consequence the concepts “stages” and “functional” mean “morphological stages” and “anatomical functional”.

Concerning the aberrant and skinny stages, occurring sometimes in *Clio pyramidata*, nothing is dealt with as separate papers will give the results on these stages from the Ocean Acre cruises.

Out of the data from the anterior, medial and posterior sections through the gonad available only the data from the anterior and medial sections are used. This was possible as the differences between anterior and posterior gonad structure are not essential and only small. However, the difference with the medial sections are important, as formation of unripe female cells in the centre of the gonad is more intensive than it is in its extremities and as there are more lumina present which, in ripe gonads, give more space to ripe products in the middle part of the gonad. Figure 3 gives an impression of the difference between the three sections through the gonad.

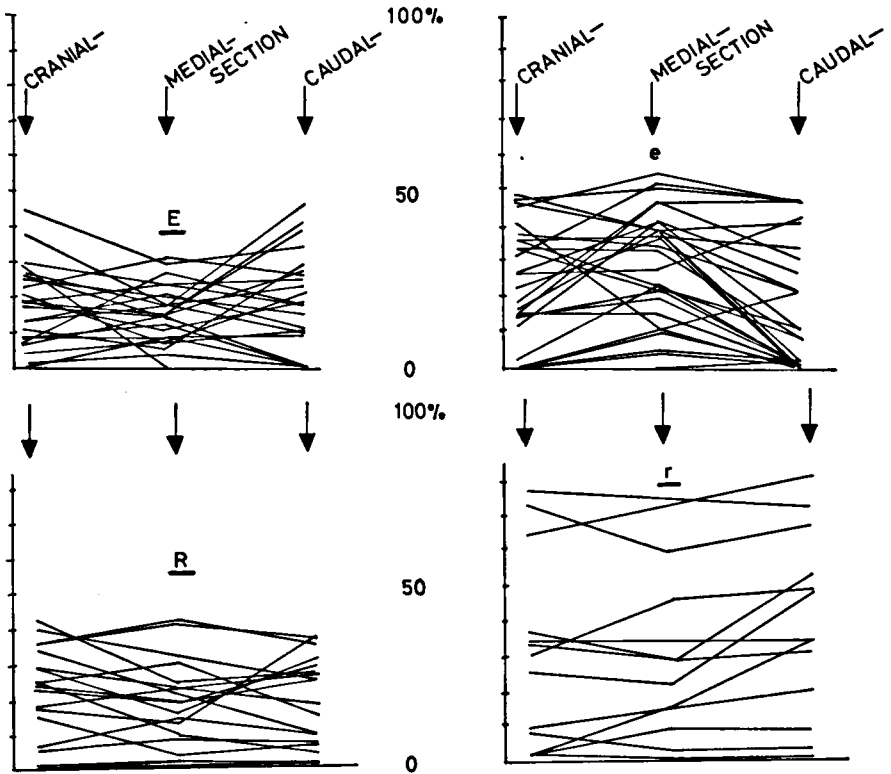


FIG. 3. Percentage (y axis) of ripe female (E), unripe female (e), ripe male (R) and unripe male (r) products in the cranial, medial and caudal part of the gonad of *Clio pyramidata* forma *lanceolata* in 28 specimens of different age. Values for each specimen are connected with lines.

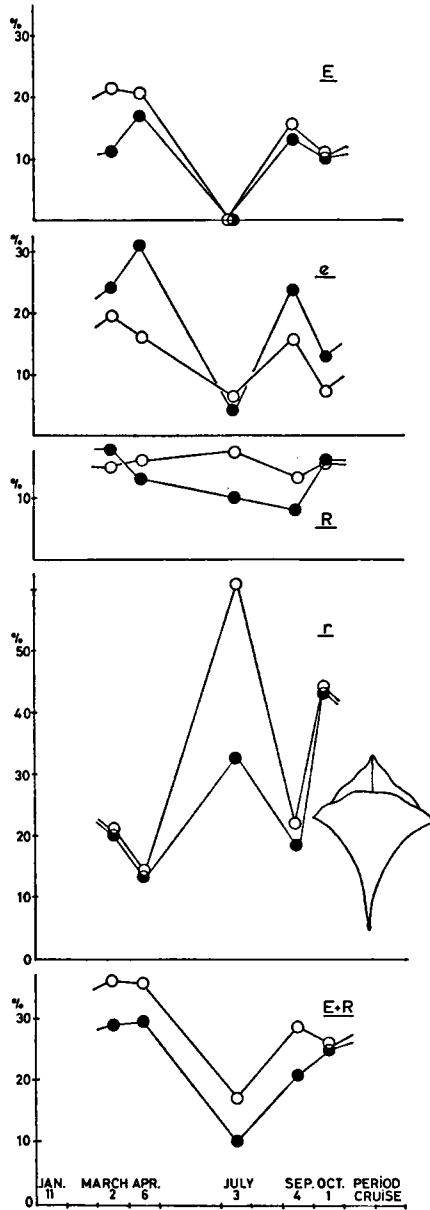


FIG. 4. Average percentage (y axis) of ripe female cells (E), unripe female cells (e), ripe male cells (R), unripe male cells (r) and ripe sexual products (E + R) per cruise in the cranial sections (open circles) and medial sections (black circles) for *Clio pyramidata* forma *lanceolata*.

In figure 4 the average percentages for the whole population of ripe sexual cells (E + R), unripe male cells (r), ripe male cells (R), unripe female cells (e) and ripe female cells (E) are given for the anterior (open circles) and medial sections (black circles) through the gonad.

From the last graph (fig. 4: E + R) it is clear that the sexual activity in the population is minimal in July and maximal in the March—April period. This confirms the idea that reproduction is maximal in the latter period and that the number of juveniles is maximal in July. The fluctuations in the quantity of ripe sperm in the gonad (fig. 4: R) is small. This means that male specimens are present throughout the year. Older, thus female, specimens are completely absent in July as in the whole population no egg is present in this month, unripe eggs are also rare (< 10%) then. The percentage of unripe male cells is maximal in July and it shows a second peak in October. The high percentage of unripe cells is caused by the high number of juveniles. In October a second breeding peak is thus reflected in these graphs. Ripe male products are more frequent while the percentage of female products distinctly drops in autumn.

Clio pyramidata is a protandric hermaphrodite and as a consequence the kind of sex products present can be correlated with age. But, up till now, it has always been considered that each specimen produces only once male gametes and female gametes at another time; this opinion becomes at least questionable when studying the activities of other sexual organs. In figure 5 the development of some accessory sexual organs is given. It was too complicated to correlate the development of these organs with actual developmental stages of the gonad. To make graphs better ordered only 13 developmental stages were recognized.

Along all the x axis in figure 5 these stages are given in which 1 stands for no sex products present, 2 for only unripe sperm present, 3 for only

FIG. 5. Development of gonad and accessory sexual organ in *Clio pyramidata* forma *lanceolata*.

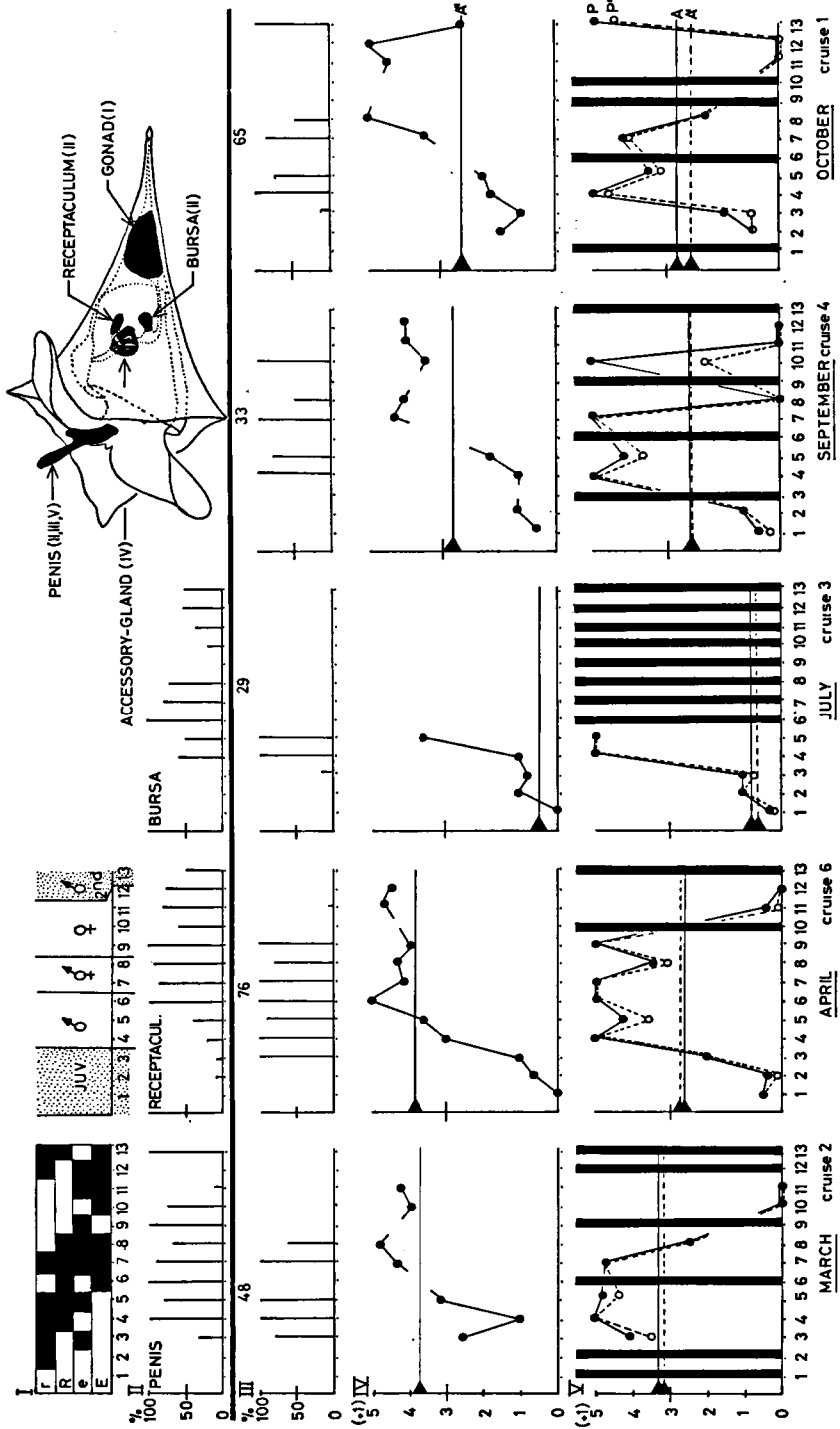
I, left graph, gonad stage recognized (presence of products represented by black); right graph, functional stages corresponding with the gonad stages represented on all the x axes in this figure.

II, left graph, for all cruises percentage of specimens with a penis; middle graph, for all cruises percentage of specimens with sperm in the receptaculum seminis; right graph, for all cruises percentage of specimens with sperm in the bursa seminis.

III, percentage of specimens with a penis for the separate cruises; the figures represent the number of specimens involved.

IV, development stage of the accessory sexual gland expressed as average for each stage of gonadial development; the horizontal line (A'') gives the average per cruise.

V, development stage of the penis (black circles, P) and penial stylets (open circles, P') expressed as averages for each stage of gonadial development; the horizontal lines (A and A') give the respective averages per cruise. For full explanation see text.



unripe male and female products present, 4 for only male products present, 5 for all products present except for ripe female cells, 6 for only ripe sexual products present, 7 for all kinds of products present, 8 for all products except for unripe males ones, 9 for only unripe female products present, 10 for only ripe female products present, 11 for only female products present, 12 for all but ripe male products present and 13 stands for all but unripe female products present; this is also represented in the left graph of row I in Fig. 5.

In the left graph of figure 5: II the percentage of specimens from all samples together, with a functional penis, is given. From this figure it is clear that young specimens (1 & 2) have not yet a penis and that two female stages (10 & 11) are losing the penis as the percentage of specimens with the copulatory organ decreases, the female stage 12 is represented entirely by specimens without penis. The fact the copulatory organ is lost in the female stage was hitherto only described for *Cuvierina columnella*, *Limacina helicoides* Jeffreys, 1877, and *Limacina bulimoides* d'Orbigny, 1836 and for one female specimen of *Clio pyramidata* forma *sulcata* Pfeffer, 1879 (cf. van der Spoel, 1967). This new find gives a better idea of the sexual cycle in euthecosomatous Cavoliniidae. A few specimens are found, however, in which the penis is completely absent but in which:

- a. production of male products has started and in which ripe female products were numerous;
- b. ripe males products were abundant;
- c. a few specimens with a functional penis and all cell types but unripe female cells in the gonad were found.

These finds induced me to accept the presence, at least in some specimens, of a second male phase. Though many combinations of gonadial activity and penis development may stay questionable, it seems absolutely sure that a gonad, in which ripe female products are found together with male cells but without unripe female cells, belongs to a specimen that has gone through a female phase before starting a new male phase. This second male phase of the gonad is represented by 13 on the x axis in figure 5. All specimens in "stage 13" are provided with a functional penis. The black bars in fig. 5: V stand for gonad stages not represented in the material of the successive cruises. In July, only juveniles and not yet fully developed males (1—5) are present. In September, males, hermaphrodites and females are present, the second male phase is, however, absent. Only in October representatives of the second male phase (13) are found. From figure 4 it was clear that the percentage of sperm significantly increases only in this month and from the dicegram in figure 1 it was concluded that a second increase in reproduction occurs, phenomena which may be correlated with the occurrence of the second male phase.

Besides the morphological evidence for a second male phase there is thus also an ecological reason for this stage. It is clear that the data available at this moment are too few to discover whether specimens hatched in spring of

the previous year or of the same year reach the second male phase in autumn; both situations are possible.

In figure 5: V the average development of the penis per cruise is given for the different stage of gonad development (black circles) and so is the development of the penial stylets (open circles); the total average for each cruise is given by a horizontal line. From these series of graphs it is clear that penial development is minimal in July and maximal in October. Concerning the development in regard to the gonad structures it can be stated that youngsters (1, 2 & 3) have always a penis in the first phase of development, that the males (4, 5 & 6) have always a well developed penis, that early hermaphrodites have always a well developed penis and that older hermaphrodites ($r = 0$) have sometimes no penis.

The fact that there is nearly no difference in the values for penes and penial stylets proves that the penis, when present in hermaphrodites shows full development as the penial stylets in developing penes are always less developed than the penes. The young females (9) have a penis but the older ones (10, 11, 12) have no penis except for those with a gonad development as represented by 10 which have a penis in September and those with a gonad development as represented by 11 which shows penial development in April. In these two occasions the penis is more developed than its stylets. This may indicate that penis development started in those female in which the female function of the gonad is coming to an end. Both stages mentioned have no kind of male cells in the gonad and though only three specimens are concerned the only explanation for this phenomenon can be that a second male phase is starting to develop here. As mentioned above the second male phase (13) based on penial and gonadial development, which is certainly correctly interpreted, occurs only in October.

In figure 5: IV the average development of the accessory sexual gland is given for the different stages of the gonad development per cruise, the total average per cruise is given by a horizontal line (A''). Though the different lobes of this gland fulfill different functions, the activity of the organ is considered as a whole, as it was impossible at this moment to detect which lobes could, in their activity, be correlated to which sexual stage of the specimen. The total averages show another change than those of the penial development, as it is less regularly fluctuating. The July value is low, the September and October values are of an average level and the March and April values are very high. The development and thus the activity of the accessory gland reaches its maximal level only in the beginning of the hermaphrodite stage and it stays very active during the female phase. The greater part of the gland or the major function of the gland is thus correlated with the female function of the gonad. And this may explain the different monthly averages. In July the gland is not yet really active as most specimens are juvenile. In summer and autumn, higher percentages of juveniles and males keep the average relatively low, while just before the great production increase in the March—April period the accessory gland reaches high levels

of activity correlated with egg production. The distinctly lower value of the gland activity during stage 13 should be mentioned here as during the second male phase the activity of the gland is of the same intensity as during the early first male phase. Thus all sexual activities show that the specimens grouped under 13 can be considered real young males though remains of egg cells are found in the gonad.

Fig. 5: III gives the percentage of specimens with a penis, which graphs support the conclusions made from the graphs below (fig. 5: V). A special note should be made concerning the activity of the receptaculum seminis and bursa seminis.

In fig. 5: II, middle and right graphs, the percentage of specimens which have sperm in the receptaculum and bursa respectively is given. It is striking that in some specimens the receptaculum already contains sperm, at a time when the bursa is still empty. Reception of sperm is thus executed earlier than deliverance. This phenomenon is also shown in males which have sperm in both but which cannot yet use the allosperm by absence of eggs. The receptaculum stays usually filled with sperm throughout life. The bursa seminis stays filled only till stage 8 though in the stage 10 up to 13 filled bursae are also found. Probably delivery of sperm is not always complete or in stage 13 new sperm may be brought in the bursa.

Summarizing it can be concluded that reproduction is maximal in spring, with a secondary increase in autumn. A second male phase follows in this species after the completion of the first protandric cycle and probably a complete second cycle is realized, which cannot yet be proved, however. The penis is usually lost during the female stage. The accessory sexual gland shows greatest activity during the female stage of the specimens and allosperm is accepted earlier than autosperm is delivered so specimens copulate usually at least twice.

DIURNAL VERTICAL MIGRATION

The vertical migration is studied for all samples together as there proved to be no differences between the migration in the different years or in the different month. It should be mentioned, however, that the number of samples was too small to detect possible very minute differences for the different month, but these differences, when present cannot affect the general conclusions made below. In this discussion not the actual number of specimens is used but the number of specimens per hour sampling effort.

The diurnal vertical migration in the four species of which shell growth is discussed differs remarkably. *Clio pyramidata* forma *lanceolata* (fig. 6) shows intense diurnal vertical migration. The average distance over which the specimens migrate is 330 metres and 74% of the specimens crosses the average depth level (= half of the sum of the average night and average day level of the population). The vertical range of the population is found between 50 and 550 metres at night and between 350 and 950 metres at

daytime. This shows that the maximal migration may be 900 m. As the difference between the number of specimens collected at night and daytime is too great it is not possible to discuss the migration of the bulk of the populations. Wormelle (1962) found that juvenile specimens live usually in distinctly deeper layers than the adults, which could not be demonstrated as the discrete depth samples with juvenile specimens were too few. The figures concerning migration mentioned above were found by comparing only data from discrete depth samples. In figure 6 the position of the population at different times of the day is given in black (as found by discrete depth samples) hatched (as found in N and P non discrete depth samples) and double hatched (as found in M non discrete depth samples). The use of the non discrete samples was only possible above the depth where the discrete depth samples found the species, above the upper limit given for the population no specimens were found.

Cuvierina columnella (fig. 7) seems to migrate less strongly but this is only partly true. The depth over which migration is effected is only 140 metres but 96% of the specimens crosses the average depth level. It should be mentioned that the results are based on nearly full grown specimens for *C. columnella* but for *Clio pyramidata* also young specimens are considered.

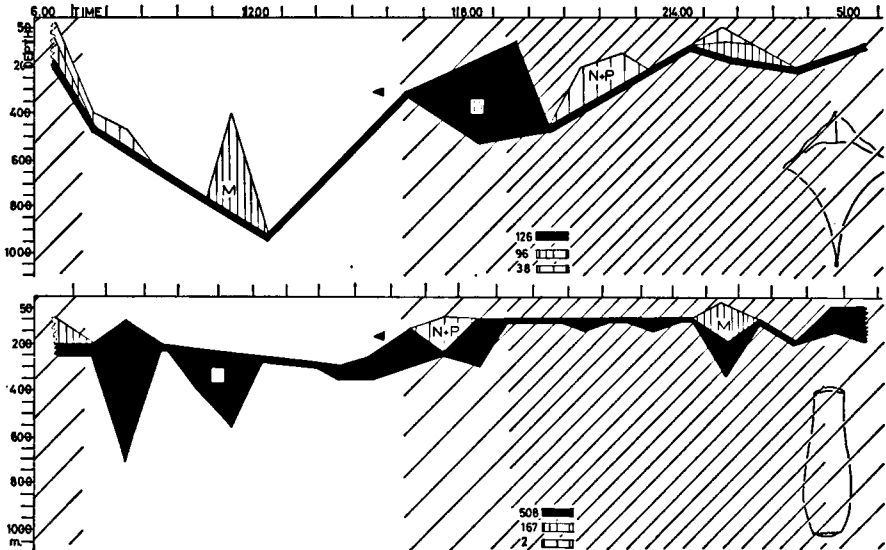


FIG. 6. Vertical migration of *Clio pyramidata* forma *lanceolata*, on the x axis time of the day in hours, on the y axis depth in metres, hatched is the twilight period and double hatched is the night period. The figures at the bottom of the graph represent the number of specimens collected in the different types of samples. D are discrete depth samples, N + P are oblique hauls and M are open net samples. The triangle indicates the average depth level.

FIG. 7. Vertical migration of *Cuvierina columnella* forma *atlantica* (for explanation see fig. 6).

This difference may result in partly incomparable results. Young specimens of *C. columnella* were not neglected in the research but they were rarely collected during the Acre Program due to their small size.

Though not all material could be used for the diagram of the figures 6 and 7 at this moment it seems already possible to compare the two species with regard to their vertical distribution during day and night-time.

Clio pyramidata shows during the whole day rather restricted "thickness" of the population; only in the evening a thicker layer of water is occupied by this species. *Cuvierina columnella* in contrast shows a "thicker" population which is pressed together in the first half of the night period. The latter tendency is probably also traceable in *Diacria trispinosa* (fig. 8). This species behaves also in regard to its diurnal vertical migration like *Cuvierina*

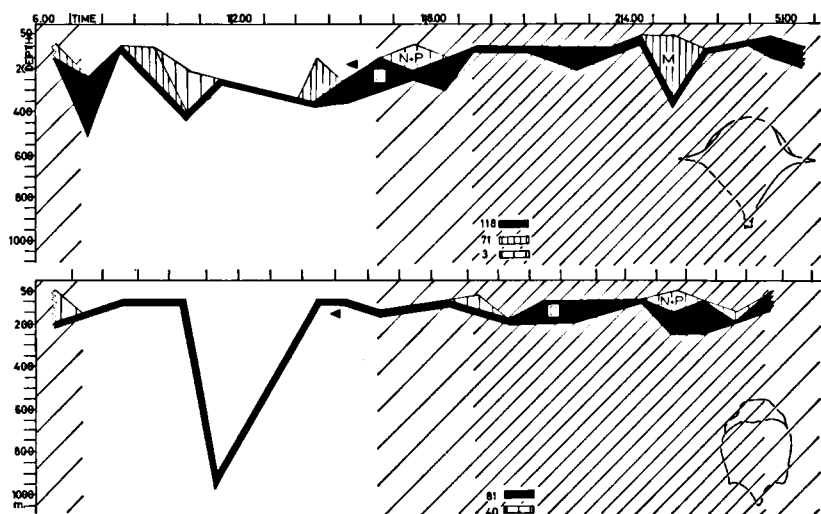


FIG. 8. Vertical migration of *Diacria trispinosa* (for explanation see fig. 6).

FIG. 9. Vertical migration of *Cavolinia gibbosa* (for explanation see fig. 6).

columnella. Migration is executed over a depth of 157 metres and 94% of the specimens crosses the average depth level.

Cavolinia gibbosa (fig. 9) shows a completely other picture, only 50% of the specimens are crossing the average depth level of the population and the average level of the population during day and night-time differs only by a few metres. The impression in figure 9 that there is evident migration at noon is a false impression due to a deep catch of a few specimens.

SUMMARY

Shell growth in *Clio pyramidata* forma *lanceolata* is compared with that in *Cuvierina columnella* forma *atlantica*, *Diacria trispinosa* and *Cavolinia*

gibbosa; it is proved that shell growth in *C. columnella* and *D. trispinosa* going through a shell metamorphosis gives another size variation in a natural population than the growth does in species which only go through a minute stage, and it is shown that the normal growth in *Clio* gives still another type of size fluctuation in the population. The study of the reproductive cycle of *Clio pyramidata* in combination with the data obtained from the shell growth and earlier finds (van der Spoel, 1967) made it possible to describe the biology of the species as follows.

Reproduction occurs throughout the year with a maximum in spring (April—June) and a lower maximum in autumn (October). The specimens reach an age of about one year. The sexual development is a protandric hermaphroditic one, which may result in one or two complete cycles as proved by the presence of specimens which developed for the second time into a male phase. Usually the penis is lost during the female phase and the highest activity of the accessory sexual gland is to be correlated with the female stage of the animal. The allosperm is received earlier, at least in some specimens, than the autosperm is delivered.

Concerning the vertical migration it is clear that *Clio pyramidata* shows intensive diurnal vertical migration, which is as intensive as in *Cuv. columnella* and *Diacria trispinosa*, but which extends over a much greater depth than in the latter two species. For *Cav. gibbosa* it turned out that diurnal vertical migration is nearly absent.

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