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Report of the Shrimp (*Pandalus borealis*) Ageing Workshop,

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and

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edited by

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As requested by the Scientific Council of NAFO at its November 1980 meeting, a shrimp ageing workshop was held in Quebec City at the Direction de la Recherche Scientifique et Technique, Direction Générale des Pêches Maritimes; results were summarized in a short preliminary report at the June 1981 NAFO Meeting (SCS Doc. 81/VI/14). The workshop was reconvened in Dartmouth at the Bedford Institute of Oceanography to complete the work begun in May. The present report is a more comprehensive version which elaborates on individual presentations and discussions and emphasizes consensus for various issues of the agenda.

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2. INTRODUCTION

For Pandalus borealis, as for all crustaceans, direct determination of age can not be made at present. Analysis of length frequency distributions and examination of sex-related characteristics permit some

interpretations, but procedures are very different from those commonly used for fish and molluscan species (otolith and scale reading, annuli on shells).

Analysis of size composition data has been the primary basis of ageing for P. borealis. Assumptions underlying age interpretations from such data are 1) that in a polymodal length frequency distribution (Fig. 1) modes correspond to cohorts (age groups) and 2) that within a given age group, growth rates are similar. In an ideal situation the first assumption may be closely met in practice, since many stocks exhibit an annual synchronous cycle of reproduction with a well-defined hatching time occurring in spring (Haynes and Wigley, 1969). Displacement of modal classes over time in sequential length frequency distributions, the underlying principle of Petersen's (1891) method, has been described for several different stocks of P. borealis (Balsiger, 1981). In other stocks, however, the hatching period may be more protracted and modes less well defined. The second assumption may not be met in many cases. Rasmussen (1969) observed fast and slow growing animals within the same age group, a phenomenon he attributed to sex inversion for part of the age group resulting in two modes of the same age. Other observations on shrimp growth also suggest that this species may not be amenable to the classical Petersen method of age determination (eg. Skuladottir, 1981). The problem is further complicated by selectivity and availability, especially for younger animals, and by the possibility of age class accumulation occurring in the last prominent female mode. The latter likely occurs due to a relative lengthy ovigerous period which considerably limits the time available for growth (Haynes and Wigley, 1969).

The objectives of the present report are 1) to review problems associated with sampling for length and stages of sexual development; 2) to examine the applications and limitations of graphical and analytical methods used for interpretation of ages; and, 3) to consider the utilization of the resulting data to estimate year-class strength, growth and mortality.

3. BIOLOGICAL REQUIREMENTS FOR AGEING

3.1 Sampling Techniques

3.1.1 Preservation of samples

Several methods of preservation have been used in shrimp sampling, the most accepted being freezing or fixation in 5-10% formalin. Ideally, fresh samples are recommended but, since this is not always possible, preservation by the above methods often must be employed. The group noted the necessity to conduct statistical evaluation of the effects of different preservation techniques on possible changes in weight and length of individuals and potential cumulative effects on age interpretation from the length frequencies. It was also pointed out that head roe deteriorates when shrimp are frozen. Therefore, prior sorting of animals in this condition is recommended.

3.1.2 Sample Size

For interpretation of age from length frequencies (Section 4), it was generally agreed that a minimum of 500 animals would be required. It was also felt that samples of this size would be large enough to provide representative data on stages of sexual development. Separation of normal components in a distribution mix requires a large number of length observations. Cohen (1966) suggested a minimum of 400 animals in mixtures of only two components and larger sample sizes when there are more than two for Hasselblad's (1966) separation methods. MacDonald and Pitcher (1979) recommended at least 50 individuals for each component which would require a large total sample if some components were poorly represented in a random sample.

3.1.3 Standardized Synoptic Surveys

Research surveys, synoptic over time, provide useful data for estimating biological parameters of mortality, growth and recruitment through age interpretation. These objectives can be accomplished through comparison of abundance indices at each age in successive years (see Section 6). Sequential commercial catch sampling could also provide these types of estimation.

3.2 Length Interval

The most universally accepted procedure for measuring individuals

of P. borealis is the oblique carapace length first described by Rasmussen (1953) and adopted by ICES in 1973. This is the distance measured from the posterior margin of the orbit to the posteriodorsal margin of the carapace. Intervals range from 1.0 mm to 0.1 mm with 0.5 being the most common.

For ageing purposes, the value of various length intervals (and subsequent combinations) was considered. A length frequency from a sample of shrimp from the Gulf of St. Lawrence measured to the nearest 0.1 mm generated too much noise and caused difficulties in the interpretation of modal groups (Fig. 2a). Combination in groups of 1.0 mm (Fig. 2b) resulted in the loss of detail especially on the extreme ends of the distribution. Although two modes were clearly represented, the interval of length was not considered precise enough to describe numerically the separation between groups, a necessity for statistical methods.

Combination to 0.3 and 0.5 mm (Fig. 2c & d) appeared to provide adequate separation of modes and allowed for finer definition of statistical inputs. The use of moving averages was also considered (Fig. 3). It is quite clear that the use of a moving averages of three significantly reduced the noise and provided a better picture to determine first estimates of the information on modal characteristics which serve as inputs for the statistical methods.

Discussions on length interval resulted in two general conclusions. Firstly, the use of any length interval may ultimately depend on the nature of the data, eg. the 0.5 mm interval may provide adequate separation of modes for some stocks but not for others. It was also recognized that since 0.5 has been the most commonly used interval, some of the historical data may not exist in any other form. Secondly, that to ensure sufficient precision in future data collections, it is advisable to measure the carapace length to the nearest 0.1 mm and subsequently combine the data to the optimum interval (eg. 0.3 or 0.5).

3.3 Determination of Stages in Sexual Development

Data were presented which showed that considerable information

on the age composition of shrimp samples could be gained by examining in some detail a breakdown of the various stages in sexual development. Males, transitionals and females are readily separated by examination of the endopod of the first pleopod (Rasmussen, 1953). Females can be further broken down into first year spawners and those which spawned at least once before on the basis of sternal spines (McCrary, 1971).

Separation by stages in sexual development is demonstrated in samples taken in the Cartwright Channel, off Labrador in July 1980 (Parsons, unpublished). From these distributions, three principal modes and the possibility of a fourth at 27 mm carapace length became apparent (Fig. 4). Separation by sex provided a good differentiation of male and female age groups. Separation by presence or absence of sternal spines showed two modes of females where one existed in the undifferentiated length data. It should also be noted that transitionals with head roe occurred at similar sizes as the less numerous female with sternal spines group and were considered to be a single cohort designated as ♀¹.

A great deal of information on the age composition of samples may be gained through supplementary observations on stages in sexual development. Theoretically, if only one age group of males is present and if transition takes place at the same age, age determinations could be made entirely by observing sex and spawning characteristics. However, this situation may not often occur. One age group of males can be expected only infrequently and it has been demonstrated that transition does not necessarily take place at a single age. Rasmussen (1953, 1969) showed that in the Norwegian shrimp stocks two transitional groups are often apparent simultaneously and the same situation exists in the Gulf of Maine (Fig. 5; Clarke, unpublished). In such cases, ageing must be attempted by separating modal groups rather than by stages in sexual development alone. Separation by these methods can also be used to check the accuracy of results obtained from statistical methods.

The separation of a single mode of females into two modes based on sternal spines can only be made prior to spawning since no ovigerous females will possess these spines. Table 1 shows changes in observations

on females by month in the Gulf of St. Lawrence (Fréchette, unpublished). It is apparent that the optimum time for observing females with sternal spines is prior to the onset of oviposition (ie. in this area summer or early fall).

It became evident through presentation of data from different areas that different interpretations can be made for the transitional stages based on condition of pleopods, sternal spines or gonads. The transitional group could be interpreted as first year females based on the presence of head roe and sternal spines. By the same token, first year females could be interpreted as transitionals based on the presence of male secondary sex characteristics on the pleopods. The potential diversity of stages in sexual development is well illustrated in Table 2 (Carlsson, unpublished). Although there was no attempt to standardize interpretation of these stages, the potential for ambiguity was recognized. Therefore, methodology concerning stages in sexual development should be stated unequivocally when such data are utilized.

3.4 Sources of Bias in the Interpretation of Length Frequency Distributions

3.4.1 Randomization of samples (from Carlsson)

Paragraph to be included later.

3.4.2 Stratification by Depth

It is generally accepted that average size, with the exception of migration of ovigerous females to shallower water (eg. Gulf of St. Lawrence, Gulf of Maine) increases with depth. This pattern of distribution is illustrated in Fig. 6 in length frequencies of shrimp from the Davis Strait sampled at 100 m intervals (Fréchette and Dupouy, 1979). For each modal age group, average size increased from shallow to deeper water (Table 3). Caution is advised if combination of samples from different depths is considered. Data given in Fig. 6 were combined over all depths and presented in Fig. 7. Although the three major peaks are still clearly identifiable, some information is lost especially concerning the possibility of bimodality in the second male and the third (female) components. Since the mean size of each age group generally increases with depth, it

is inevitable that some overlapping will occur when samples over a wide range of depth intervals are combined. If average length-at-age is required from such data, weighted averages must be computed over all depth intervals.

3.4.3 Selectivity and Availability

Codend mesh sizes in shrimp research trawls usually range between 30 and 40 mm (stretched). Small-meshed liners are also used to prevent the escape of the smallest animals, reducing the selectivity problem. Availability poses yet another problem eg. younger age groups may not be present in offshore situations and seasonal changes in availability also have been observed (Parsons et al., 1979; Atkinson et al., 1981).

It was recognized that both selectivity and availability may bias estimation of age group abundance by underestimating the younger animals. It was also recognized that mean length-at-age for partially recruited age groups will be over-estimated. Correction for selectivity can be achieved by applying a selectivity ogive (Fig. 8) which increases the number of smaller animals to the level expected if the trawl retained all shrimps which entered (Fr chet te and Labont e, 1981). However, it has also been shown that results of selectivity studies, themselves, are quite variable (Table 4; Sampson, 1980) even under strict standardization methods (viz. gear and mesh size). Correction for selectivity does not appear to account for availability since the proportion of the first modal group in Fig. 8 is not significantly increased. Some correction for availability is accomplished through stratification of the survey area by depth. The above problems are encountered to a much greater extent using commercial samples. Efficiency of trawls and mesh size often differ considerably; therefore caution was advised in the interpretation of mean length at age and year-class strength from such samples.

Data presented at the workshop demonstrated the potential for misinterpretation of the age of the first modal group probably due to effects of availability and selectivity. Two length frequencies from the Cartwright Channel off Labrador in July, 1980 (Fig. 4 and 18) showed differences in the mean size of male age groups. Two groups of males were

observed in the first sample with modes around 15 and 20 mm carapace length while the second showed three groups around 12, 17 and 20 mm. Since the 15 mm mode occupies a position which is intermediate in relation to modes shown in Fig. 18, the possibility for misinterpretation of ages based on Fig. 4 alone becomes apparent. There was also a general lack of agreement concerning the actual age of the 12 mm mode. Since effects of correction for selectivity are not well defined at these sizes and there is a lack of information on moult increments, it was recommended that additional work on this fundamental problem should be initiated.

3.4.4 Diel Variability

Evidence of diel vertical migration of P. borealis has been documented since the early 1900's (Allen, 1959). Studies on food and feeding have shown this migration to be associated with a pelagic phase of feeding directed at pelagic crustacea (eg. Horsted and Smidt, 1956; Barr, 1970). More recently, however, factors other than vertical migration have been considered inherent in diel variability including the effects of tidal currents on behaviour of shrimp and/or the sampling gear (Parsons and Sandeman, 1981).

Figure 9 presents size composition of shrimp observed in the first five meters off the bottom (Fréchette et al., 1981) and illustrates the problems encountered when sampling over a 24-hour period. Most obvious is the difference in catch rate between hours of daylight and darkness characteristic of many shrimp fisheries (Carlsson et al., 1978; Smidt, 1978; Jones and Parsons, 1978; Parsons and Sandeman, 1981). Also, the relative proportion of modal classes varies between day and night. Barr (1970) also showed that a greater proportion of larger shrimps in Kachemak Bay, Alaska occurred in bottom trawl catches at night. The same study showed that shrimp pots suspended vertically in the water column produced catches with greater proportions of small animals than those set on the bottom. Data from the Hopedale Channell off Labrador (Parsons, unpublished) showed that weighted mean size in the catch is smallest during the midday period and largest around midnight (Fig. 10). It has also been demonstrated that ovigerous females do not

undertake significant vertical migrations (eg. Appolonio and Dunton, 1969; Jones and Parsons, 1978).

Although patterns of diel variability in shrimp catches are difficult to model and correction factors equally difficult to derive, such behaviour should be considered when sampling. Every effort should be made to select samples at times when shrimp at all sizes are most available to the research gear, usually during daylight hours.

3.4.5 Weighted and Unweighted Size Distributions

It was recognized that before pooling samples it is advisable to weight them by numbers in the catch. This would give better representation of the age composition for the catch or stock especially in cases where density varies considerably by depth, time of day, etc... On the other hand, in areas where these sources of variability are not considered to cause problems of sufficient magnitude, weighting may not be necessary.

Weighting may be accomplished by any conventional method. In Alaska, for example, mean numbers of shrimp per trawl mile have been calculated in routine stock assessment surveys by sampling a standard proportion of the catch weight of each fishing set with subsequent pooling. Results of this procedure are presented in Fig. 11 where successive composite size distributions were plotted for several years (Jackson et al., 1981).

[Diel weighting (from Carlsson)
Paragraph to be included later.]

3.5 Additional sources of information

3.5.1 Shrimp discards

In shrimp fisheries, some discarding of small shrimp is known to occur, particularly in offshore fisheries. The utilization of sorting machines on large trawlers at times results in high rates of discard. Sampling the discards can complement the information obtained by sampling the total catch before sorting (Derible et al., 1980) as

younger age groups are more clearly represented (Fig. 12).

3.5.2 Weight frequency distribution

Interpretation of length frequency distributions is often difficult due to overlapping between modal groups. Data from the Scotian Shelf (Cormier, unpublished) show the male modal classes to be well-defined (Fig. 13, b). Severe overlapping appears to occur for the older individuals in the total composition (Fig. 13,a), especially for the females (Fig. 13,d).

By using the natural log of the weight measurements (g) and grouping them in intervals of 0.05 (Cormier and Labonté, 1980), the female mode became more obvious and was well separated from the transitional mode in the total size distribution (Fig. 14,a). While in this particular case the technique by itself seems to be no better than by length, it could be useful in providing additional information to separate modal classes should they not be apparent in the length frequency distribution. Investigations into the potential advantages of age group separation based on dry weights is presently in progress (Cormier, unpublished).

It was proposed that, in addition to weight and length, some other morphometric characteristics could be used for ageing purposes. Such data should be collected and treated using statistical techniques such as multivariate and discriminate function analyses.

4. YEAR-CLASS SEPARATION, BIO-STATISTICAL METHODS

4.1 Theoretical descriptions

4.1.1 Graphical methods

Most methods for ageing shrimp are expansions of the method of Petersen (1891) who suggested that the modes of a fish size-frequency distribution might represent age groups. Several graphical methods for separating polymodal distributions have been developed. The probability paper method of Cassie (1950, 1954), which has been widely used by fisheries biologists, assumes that fish size-at-age is normally distributed. The cumulative size-frequency distribution is plotted on probability paper and the parameters of the components of the mixture are estimated so that the theoretical cumulative distribution closely agrees with the observed

distribution. The Method of Successive Maxima (Gheno and Le Guen, 1968) is a somewhat simpler graphical method which only assumes that size-at-age is symmetrically distributed.

Additional graphical methods for separating mixtures of normal distributions include the method of Tanaka (1962), which is based on fitting parabolas to the natural logarithms of the size-frequencies, and the method of Bhattacharya (1967), which is based on fitting straight lines to the first finite differences of the natural logarithms of the size-frequencies.

Although graphical methods have the advantage that they can be completed without the aid of a high speed electronic computer, results are not generally reproducible and it is quite possible for different investigators to obtain very different results from the same data set.

4.1.2 Analytical methods

With the advent of high-speed computers the method of maximum likelihood has been used to separate mixtures of normal distributions. The FORTRAN program NORMSEP, (Abramson, 1971) based on the approximate maximum likelihood method of Hasselblad (1966), is probably the most commonly used by fisheries biologists for dissecting frequency distributions. The program produces estimates of the component means and standard deviations and of the number of observations from each component. Required inputs to the program are the estimated number of components in the mixture, their estimated "cut-off points" from which initial parameter estimates are derived, and estimated ranges for the means and standard deviation of each component.

MacDonald and Pitcher (1979) developed a more elaborate program for computing maximum likelihood estimates for the parameters of a mixture of normal distributions. The program requires input of the estimated number of components in the mixture and initial point estimates for their proportions, means and standard deviations. Like NORMSEP, it produces estimates of the component means and standard

deviations and of the number of observations from each component. Advantages of the MacDonald and Pitcher program are its availability in an interactive version and its versatility in constraining parameters.

Schnute and Fournier (1980) have extended the MacDonald and Pitcher program to constrain the estimates of mean size-at-age and the standard deviations to conform to the Von Bertalanffy growth model. They claim that such constraints are sometimes necessary to ensure that the final parameter estimates have biological meaning. All of the methods described employ a chi-square test for goodness-of-fit.

4.1.3 The deviation method

An entirely different approach to length frequency interpretation, that seems antithetical to Petersen-type analyses, was used first by Sund (1930) on cod and modified for use on shrimp by Skuladottir (1981). The method is based on the deviations formed when a mean length frequency distribution of a certain month (or any period where growth does not occur) is subtracted from a mean length frequency distribution of the same month for several years. For shrimp, positive deviations observed in successive millimeter length classes are considered to represent a strong year-class and negative deviations a poor year-class. Interpretation of age is therefore made by observation of the displacement of strong year-classes with time. This technique has been shown to reveal twice as many age classes in Icelandic samples as does the Petersen type methods.

4.2 Application of methods

4.2.1 Graphical methods

Among these methods, an application of the successive maxima method (Gheno and Le Guen, 1968) for the West Greenland stock (1979 survey on the French research vessel "La Thalassa") was presented. Figure 15 (from Dupouy, unpublished) illustrates the successive splitting of modal classes made from the left to the right side of the size distribution.

Results agree relatively well with those obtained from the same data by the application of the Cassie method (Fig. 16). This method was also applied by Minet et al. (1977) to data from the shrimp stock off Cumberland Sound and unlike the method of successive maxima provides statistical data on estimated parameters.

It was pointed out that these two methods are very sensitive to asymmetry in the first age groups, due to selectivity problem. When extensive overlap exists between age groups, graphical methods should be used with caution and reference should be made to available biological information on the stock. These methods need no computer assistance and therefore are useful when such facilities are lacking.

4.2.2 Analytical methods

4.2.2.1 Hasselblad method

Figure 17 presents an application of the Hasselblad method (NORMSEP) to a shrimp sample from the Gulf of St. Lawrence collected in July, 1979 (Fréchette and Parsons, 1981). Four modes assumed to correspond to age classes 1, 2, 3 and 4+, respectively were identified. The first two modes were shown to consist of males and the last two modes mostly females. Results (Table 5) include mean length and standard deviation of each age group and estimated numbers and proportion for each.

Number of female shrimp per age group estimated by NORMSEP can be compared to number at each stage in sexual development determined by presence or absence of sternal spines. Three different approaches were used: first, simple separation by stages in sexual development (sternal spines for females); second, separation of modes by NORMSEP using the total size distribution; and third, separation by sex and separation of modes by NORMSEP for each sex component (Table 6). The separation by stages in sexual development split the female group into two components but did not permit separation of male components. The utilization of NORMSEP on all data gives numbers of shrimp in each modal class which could be interpreted in this example as the absolute abundance of age groups in the

sample. The breakdown by sex before using NORMSEP shows that the third modal class is approximately 30% males indicating the possibility of a delay in transition. This result is well illustrated in Table 6 (NORMSEP used on males separately estimates 38 individuals). However, the addition of this male component (38) to the first female component (87) is similar to the actual number of this age group estimated by NORMSEP on all the data (121).

In addition, separation by sternal spines for females gives numbers of shrimp ($\bar{Q}^1 = 85, \bar{Q}^2 = 106$) which are quite similar to NORMSEP results when used separately for females ($\bar{Q}^1 = 87, \bar{Q}^2 = 104$). Assuming that NORMSEP in this particular case gives a good estimate of age group abundance, we can also conclude for these data that separation of females by sternal spines is sufficient to split the female mode into two age groups (3 and 4+). This fact is important since analytical methods may not give accurate separation when overlapping between modal classes is extreme.

Despite the overlapping, number of shrimp by age group given by the different techniques (Table 6) indicates a good agreement of results. This implies that the statistical and biological techniques may be used in conjunction, especially when reproductive evolution is not synchronous for all individuals of an age group.

Results indicate that ageing by stages in sexual development alone is the least reliable method because this breakdown only reflects age structure for females. A degree of uncertainty is also associated with the synchronism of reproductive evolution for all shrimp as mentioned before. Ageing by NORMSEP without observations on stages in sexual development gives better results but generates slight inaccuracy when overlapping is significant. It was the common suggestion of the participants that data on sexual development used in conjunction with NORMSEP can ameliorate results and that such data should be routinely investigated before using analytical methods such as NORMSEP.

4.2.2.2 MacDonald and Pitcher method

A shrimp sample from the Cartwright Channel off Labrador (July, 1980) was subjected to analysis by this method (Parsons, unpublished). Five age groups were interpreted from the length frequency (Fig. 18). Initial proportions, means and standard deviations were estimated and the program was run until a minimum chi-square value was obtained. Relatively low standard errors were associated with the final estimates (Table 7) and chi-square test failed to reject the null hypothesis ($0.10 < P < 0.25$). Use of NORMSEP on the same data set produced virtually identical results for both estimated means and proportions by age group (Table 8). Chi-square values indicating the goodness of fit were also similar. Such similarity can be expected since analytic processes are essentially the same.

4.2.3 The deviation method

Figure 19 presents some of the length frequency distributions plotted by month from 1961-77 for Arnarfjörður, Iceland. Appearance of modes and their relative strength indicate that, at least for this shrimp stock, recruitment is quite variable. This fact is especially evident when comparing abundance of the 1963 year-class with other year-classes. The deviation method in this case is very appropriate, since it is essentially based on tracking strong year-classes. Deviations (as described in Section 4.1.3) were analysed for the same period and are presented in Figure 20. As deviations move to greater lengths with time, growth can be detected. In pooling the data, great care must be taken to consider only individuals from the same stock. For this particular stock of Arnarfjörður, a cold threshold fjord in the north-west of Iceland, strong year-classes can be followed for up to 9 years (Fig. 19). For the estimation of mean length at age no complicated calculations are involved.

Considering the differences observed in the analysis of size composition between the deviation method and others presented, it was the consensus that the former method be tested and compared to others in using the same set of data.

5. APPLICATIONS OF BIO-STATISTICAL METHODS TO WORKSHOP SAMPLE

A sample of 414 shrimp from Anticosti Channel in the Gulf of St. Lawrence was used during the workshop to illustrate all the recognized procedures for ageing shrimp, from measurements and sex determination to the analysis of NORMSEP outputs. Because this sample was taken in July (1980), no transitionals were observed, this category having developed probably into female with sternal spines at that period in the Gulf of St. Lawrence (Table 1). Stages in sexual development (sternal spines for females) were determined and length of cephalothorax was measured to the nearest 0.1 mm using Vernier calipers. Individuals were separated into 3 categories: σ , φ^1 (females with sternal spines), φ^2 (females without sternal spines). Specimens were also weighed to the nearest 0.1 g (wet preserved weight).

The length interval of 0.1 was later combined to 0.3 mm and histograms constructed for each category (Fig. 21). Moving average of 3 was also employed to smooth the data (Fig. 22). Smoothing, in this case, appears to have been useful in reducing noise in the length frequency.

From size frequency distributions (Fig. 22), five modal classes were apparent, two of males (Fig. 22b) and three of females (Fig. 22c and d). The first mode of females was split into two by the examination of sternal spines. The weight frequency (Fig. 23) was also examined for additional information but failed to give extra details on age structure of the sample. No recombination of data by larger weight classes was applied to minimize observed frequency variation because of time limitations which also precluded the technique of log transformation (Section 3.4.4).

Mean length and cut-off points were then determined for each of the four modes evident in the total distribution (Fig. 22a). Table 9 presents the input parameters for the NORMSEP program. Results of NORMSEP and separation by stages in sexual development are given in Table 10.

Similarity in NORMSEP estimates of abundance of the first

two age groups (284) and actual numbers of males (289) indicate that the separation between males and females was well represented as normal distributions with little or no males forming part of the first female mode. A breakdown of females by sternal spines (Fig. 22) showed that the mode with sternal spines is not separated sufficiently to permit reliable separation by NORMSEP. Therefore, means and proportions for this age group were derived from the sternal spines breakdown (Table 10). In this case, separation made only by sternal spines is questionable since it was previously noted that synchronism of sex change for all individuals of a year class is not a general rule and different interpretations of age compositions can be made.

NORMSEP was also used with the smoothed data (0.3 mm, and a moving average of 3) to observe any changes in the means, proportions and/or chi-square value. The same input was used as for the unsmoothed data. Results indicated that proportions and mean length were similar for both treatments, however the chi-square value for smoothed data had no statistical meaning (Table 11).

Participants agreed that if the chi-square value is used, analytical methods should be used on unsmoothed data. It was also recognized that the relative goodness of fit is often heavily influenced by anomalous data and that the chi-square generated by any analytical method should not necessarily be considered as a critical value.

6. UTILISATION OF YEAR-CLASS SEPARATION METHODS TO ESTIMATE BIOLOGICAL PARAMETERS.

6.1 Year-class strength

Assuming that age class separation from samples adequately represents the age structure of the population, age class abundance can be determined by splitting any abundance index (direct biomass estimation, commercial catch rates) into its age components. The group advised caution in interpreting results for younger age classes due to availability and selectivity problems and age class accumulation in the final mode composed of older females.

Year-class abundance was estimated for a shrimp population of the Gulf of St. Lawrence using research vessel survey data from 1977 to 1980 collected by Fisheries and Oceans Canada, Newfoundland Region and Direction de la Recherche Scientifique et Technique, Québec (Fréchette and Parsons, 1981). Age groups were separated using NORMSEP in conjunction with maturity data for females. Before breaking down the female modes by sternal spines, the technique was tested using NORMSEP on the female distributions where two modes were obvious. The two methods gave similar results.

Table 12 presents the abundance at age obtained by relating density to age class separation. As pointed out previously age group 0 and 1 do not seem to be fully available to the sampling gear. It was also noted that, in spite of this problem, a strong year-class (possibly 1978) can clearly be observed which was more abundant than any other age group. Prediction of recruitment may therefore be possible based on repetitive surveys.

The same methodology was used for the stock in the Gulf of Maine to estimate catch-at-age from Maine summer research vessel surveys from 1972 to 1981 (Schick, 1981). Similar problems of availability and selectivity were encountered (Table 13), possibly associated with relatively low levels of sampling. Variability in abundance of a year-class between years excludes any inference about the presence of strong and weak year-classes. The major problem illustrated in Table 13 is the interpretation of sternal spines for ageing. Presence of two separate modes for transitionals in that area (Fig. 5) complicates the analysis and the separation of age groups by sternal spines may not be valid.

6.2 Growth

Much work has been done on growth of P. borealis based on Petersen's (1891) interpretation of length frequency distributions. However, other work has been conducted which does not require separation of normal components.

A method to estimate growth rates of inconspicuous year-classes from the sexual maturity of females was presented in conjunction with the growth of strong year-classes (Skuladottir, in prep.). By using the deviation method the growth of strong year-classes was detected. From this the mean length of 4 year olds was estimated in Fig. 20. The percentage of sexually mature females of eg. 4 year olds of the slow growing 1961 year-class was 3% as read from Fig. 24. The corresponding percentage of sexually mature 4 year old females of the fast growing 1969 year-class was 16% as indicated by the coordinates for the winters 1965-66 and 1973-74 respectively (Fig. 25). As sexual maturity of females seemed to occur earlier due to faster growth it seemed plausible to estimate the rate of growth of the intervening inconspicuous year-classes by assuming an even increase in the percentage of mature females at age 4, or the reverse with a delay in growth. Of the 1962 year-class about 5% would thus be spawning as 4 year olds about 7% of the 1963 year-class and so on. The lengths according to these percentages were then read from the graphs of percentage female maturity at length for the winters 4 years later. From the mean length of the presumed 4 year olds thus obtained, a growth curve is constructed which resembled the growth curves of the strong year-classes (Fig. 26).

This figure summarizes growth observed for several year-classes for the fjörd Arnarfjörður (Iceland) (from Skuladottir, unpublished). Growth rates vary dramatically within the different slow growing and fast growing age classes. The reasons for such a variation are not known.

Separation of age groups by any mathematical method could in fact be used the same way to estimate growth for fast and slow growing year-classes. Caution was, however, advised when combining different age classes in a common growth curve. Bias could be introduced if the presence of slow and fast growing groups is not only characteristic of Iceland shrimp stocks.

It was mentioned that a new method exists to estimate growth based on the von Bertalanffy growth equation that does not need initial

breakdown of length frequency distribution by age class (Pauly and David, 1980, Gaschutz et al., 1980). A computerized version of this method exists (ELEFAN I) (Pauly et al. 1980) and should be tried on Pandalid shrimp data.

The von Bertalanffy growth equation has often been used to represent growth of Pandalid shrimp. While this model may not be strictly applicable due to discontinuous growth patterns associated with moulting, it appears to provide reasonable approximations and, in the absence of more definitive biological data, can be considered useful. The group considered that use of this equation with length and weight-at-age data obtained from modal and sexual stage separations (described above) could provide useful parameter estimates but noted the potential for bias associated with incomplete recruitment of younger shrimp and the problem of assigning ages to older groups.

6.3 Mortality

The estimation of abundance by age group (Table 12 and 13) could be used to estimate instantaneous total mortality (Z) if adequate time series data are available. However, availability and selectivity may preclude estimates for the younger age groups. Mortality can be estimated for fully recruited animals, where abundance is not biased by selectivity, if age group separation is possible based on analytical methods and stages in sexual development.

Labonté (1979) illustrated the two hypotheses involved in estimating mortality for a shrimp population in the Gulf of St. Lawrence from estimates of abundance by age groups (Fig. 27). While the "A" hypothesis does not involve age class accumulation in the last female peak, the second "B" hypothesis does. This last hypothesis was preferred taking into account several indications of age-class accumulation (weight frequency distribution, occasional appearance of polymodality in the last female mode).

Natural mortality (M) was estimated (Fréchette and Parsons, 1981) using data from Table 12 and assuming that fishing mortality was very low

(North Anticosti stock). Other estimates were also produced for the Sept-Iles stock (Gulf of St. Lawrence) by calculating fishing mortality from commercial catches at age (Labonté, 1979; Fréchette and Labonté, 1981). For both studies, M was estimated in the range 0.5 - 0.8.

Several estimates were also presented for other stocks using different techniques. In Iceland, M was estimated for two stocks at 0.24 and 0.5 using cohort analysis and the catch curve method, respectively (Skuladottir, 1979). Andersen (1981) presents Z values from Pavlof Bay in Alaska that agree reasonably well with the above results (0.65), however, large variation was also observed. Because of the lack of certainty in the interpretation of age by modal analysis, estimates of mortality obtained from these methods must be viewed with caution.

It was suggested that predation by fishes is an important component in the natural mortality of shrimp. Among fish species, cod and Greenland Halibut feed heavily on shrimp. In Iceland, predation by cod has the effect to disperse shrimp (Skuladottir, unpublished). In Canadian waters abundance and distribution of shrimp and Greenland halibut seem to be related (Bowering and Parsons, 1981; Fréchette, 1981).

7. OTHER CONSIDERATIONS

7.1 Tagging

Few attempts have been made to tag *P. borealis*. Tagging activities were reported in Greenland but with very limited recoveries (Carlsson, unpublished). For other shrimp species there are several examples of tagging. The Penaeidae are routinely tagged using a vinyl streamer inserted through the abdominal muscle. In Iceland, a tagging program has been implemented using roughly the same technique. A recently exploited shrimp stock at East Greenland was identified as a source of potential for tagging experiments (NAFO, 1980).

7.2 Electronic measurement

Some information was presented concerning a new electronic caliper, permitting the direct accumulation of data through an interface

with a micro-computer. This feature could be very useful in that it eliminates the process of compiling the data. It was agreed that this information is very valuable for participants, and that much more information about this system should be circulated as soon as possible.

8. CONCLUSIONS

8.1 Age Interpretation

Several problem areas in the interpretation of shrimp ages became apparent. It was acknowledged that there is a general lack of information on growth increment through moulting and moulting frequency and that this information is needed if application of graphical and analytical methods are to have any real biological meaning. Data on larval growth and size during settling is also necessary to obtain a reliable estimate of the mean size of the young of the year occurring in the samples. Selectivity and availability also contribute to this problem causing discrepancies in the interpretation of the age of the first modal group. The interpretation of spawning characteristics is also unclear and it has been suggested that the females with sternal spines could constitute a separate age group, be combined with transitionals of similar size in a single age group, or be a slow or fast growing component of an adjacent modal group. If age groups do, indeed, have slow and fast growing components, bimodality within an age group is possible and may complicate the modal analysis to the point that it may be meaningless without a complete understanding of biological events. Problems lie not with the graphical or analytical methods of modal separation but with the interpretation of the modes themselves. This is the direction future research of ageing of Pandalid shrimp must take.

Age class accumulation in the last prominent mode of the length frequencies was generally accepted. Circumstantial evidence supporting this theory was obtained from examination of sternal spines and weight frequencies. Estimates of natural mortality for P. borealis used in prediction of yield often have been relatively high and assumed a heavy spawning mortality. If age class accumulation was not considered, these values may have been significantly over-estimated possibly affecting

estimates of potential yield by orders of magnitude. Prediction of recruitment and estimation of growth parameters are also important in shrimp stock assessment. Ageing the catch or stock can produce such information provided the techniques used give representative results.

8.2 Management Implications

Lack of reliable ageing technique for northern shrimp result in uncertainty in biological parameters estimated (eq. growth and mortality), thereby limiting the applicability of many traditional assessment methods. In particular, little information is available on natural mortality, and yet many techniques used to provide management advice are very sensitive to this parameter (eg., equilibrium yield models). The situation is further complicated by variability in M over the fishable life span and also by year-to-year variability associated with predation or other factors. Uncertainty with respect to M and other parameters has resulted in use of "reasonable" ranges of estimates and different techniques for corroborative purposes whenever possible, but results are nevertheless open to considerable latitude in interpretation in many cases and their use in formulating management decisions entails a degree of risk which could be avoided with more refined parameter estimates.

More intensive management of pandalid stocks will require detailed information on mortality, growth, and equilibrium yield, population size and age composition, and stock recruitment relationships. All of the above will in turn be contingent upon development of more accurate ageing procedures than are available at present. Since biologists are being increasingly challenged by managers and industry to provide such information, development of appropriate ageing techniques should be given the highest possible priority by agencies responsible for pandalid shrimp research and management.

Since no consensus was reached on the biological interpretation of modes in the length frequencies, the group advised that assessments based on preliminary ageing data be viewed with caution. It was agreed that work on these problems should begin immediately and that another workshop be convened along these lines in the near future (1983 or 1984).

9. SUMMARY OF CONSENSUS

Although every participant realized that the Workshop did not solve the ageing problems for P. borealis, several guidelines for age interpretation emerged and some consensus was achieved concerning the methods used and the research requirements needed.

It was generally agreed that:

- the minimum sample size required is 500 shrimps to permit the use of analytical methods or separation by stages in sexual development;
- it is advisable for ageing purposes to measure the carapace length to the nearest 0.1 mm to permit various subsequent combination as needed;
- problems of selectivity and availability in length frequency distributions produce bias in the mean size and proportion of the younger (male) age-groups;
- recruitment may be difficult to predict from length frequencies, however, relative strength of recruiting year-classes may in some cases be predicted in relation to abundance of cohorts in previous years;
- age composition data may be biased by differences in size distribution by depth and diel variability, requiring careful planning of surveys with respect to space and time;

- length frequency distributions should be weighted by catch in numbers before pooling;
- discards in commercial catches should be measured to obtain additional information concerning parameters of the younger age groups;
- weight frequency distribution data may contribute useful additional information when the interpretation of size composition is difficult; also other morphometric characteristics should be studied as potential aids to ageing;
- data on stages of sexual development used in conjunction with analytical methods can ameliorate results and in all cases these data should be routinely collected before using analytical methods, especially the separation of females by sternal spines;
- males, transitionals and females can be distinguished by observation of the first pleopod; first time spawners can be separated from multiple spawners by the presence of sternal spines;
- transitionals and first year females can be confused and the terms have been used synonymously; recommendations were expressed for standardization of sexual descriptions;
- sternal spines merely represent an aid to age class separation for females and may be interpreted to indicate the presence of single year-class (including transitionals of similar size) or slow growing members of a female component (in which case transitionals may be interpreted as fast growing members of the last male component);
- the deviation method should be tested on data where comparisons with results of other methods are possible;
- Hasselblad's technique or similar analytical procedures should be used on unsmoothed data if the chi-square is to be used to test for goodness of fit; however, initial smoothing can provide first estimates of input used to run these programmes;
- great care is needed when combining data from several years to estimate growth if the slow growing and fast growing age-groups which were observed in Iceland represent a general situation;

- although analytical methods provide objective separation of mixtures of normal distributions through accepted statistical procedures, they initially require subjective biological input concerning the number of components in the distribution;
- there is a paucity of information regarding the moulting sequence for P. borealis and that this process must be investigated further to gain a clear understanding of shrimp growth;
- mortality is perhaps the most important parameter in the assessment of shrimp stocks and in order to obtain reasonably accurate estimates, ageing techniques must be applied.

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Table 1. Proportion of females with sternal spines (♀) and berried females from Sept-Iles area, 1980 (Gulf of St-Lawrence).

Month	Number of samples	Number of females	♀ ¹ (%)	Berried Females (%)
April	3	577	-	72,1
May	3	663	3,6	50,0
June	3	230	19,6	0
July	1	145	45,5	0
August	2	259	48,5	0
September	5	738	10,4	2,0
October	3	396	43,0	53,7
November	3	496	0	100

Table 2. Sorting categories by sexual stages for *Pandalus borealis* used in Denmark for shrimp stocks off Greenland.

01	Juveniles
11	♂ Males
	12 US - Without ripe male gonad
	16 SS - With ripe male gonad and distended vasa deferentia
21	♂ Transitionals
	22 UR- No roe
	HR- Head roe
31	♀ Females
	32 UR - No roe
	3205 - specimens with female endopodite but with distinct ventral abdominal spines of male stage
	37 UR or HR - Females where presence or absence of head roe may not be decided
	42 HR - Head roe
	52 BR - Berried females
	53 No head roe, eggs not lost
	54 No head roe, eggs partially lost
	55 Head roe, eggs not lost or hatched
	56 Head roe, eggs partially lost or hatched
	57 BR and/or HBR - Berried females where presence or absence of head roe may not be decided (including females with partially lost or hatched eggs)
	62 HBR - Berried female with head roe (always head roe)
	63 HBR - Eggs not lost or hatched
	64 HBR - Eggs partially lost or hatched
	66 UR + EH - Females without roe, eggs setae present
	67 (UR + HR) + EH - Females where presence or absence of head roe may not be decided, egg setae present
	68 HR + EH - Females with head roe and egg setae
71	UR Specimens without roe
72	HR Specimens with head roe
73	BR Berried specimens (presence or absence of head roe not decided)
75	Loose head, no head roe
76	Loose head, head roe present
81	Juv. + ♂ - Juveniles and males
85	♂ UR + ♀ UR - Transitionals and females without roe
86	♂ +/- HR ♀ +/- HR - Transitionals and females where presence or absence of head roe may not be decided
87	♂ HR + ♀ (HR + EH) + ♀ HR - Transitionals and females with head roe, females may possess egg setae
89	Not sorted

Table 3. Estimated mean carapace length for each modal group (1,2 and 3+) and mean temperature by stratum and depth in NAFO, division 1B (Davis Strait). (From Fréchette and Dupouy, NAFO/SCR Doc. 79/X1/8.)

Stratum	Depth interval (m)	Mean modal length (mm)			Temperature (°C)
		1	2	3 +	
2	300-400	14	21	24,5	3,5
3	400+	-	22,2	26,1	3,85
4	300-400	15	22	26	3,45
6	200-300	15,9	21,3	26,1	2,9
9	200-300	16,8	21,3	26,3	3,8
11	300-400	17,1	22,2	27,3	4,05
12	400-600	17,3	22,5	27,6	4,4
13	200-300	17,3	21	26,5	3,7
15	200-300	16,5	21	25,3	2,1

Table 4. Maine shrimp survey gear* selectivity: 25, 50 and 75 percent dorsal carapace length (mm.) retention points estimated from Probit analyses of covered mesh tow data.

Date of tow	Percent retained by trawl		
	25%	50%	75%
1/5/73	15,2	18,0	20,9
1/5/73	13,5	18,0	22,6
9/25/74	16,0	18,3	20,5
9/25/74	16,2	18,6	20,9
1/5/78	9,7	15,6	21,5
1/23/78	12,8	15,6	18,5
3/16/78	12,8	15,5	18,3

* Covered mesh tows were conducted with a 16 foot headrope, 19 foot footrope semi-balloon otter trawl with a 1½ inch stretch mesh body and a 1½ inch stretch mesh cod-end with a ½ inch stretch mesh body cod-end liner. The entire bag was covered with a ½ inch stretch mesh bag.

Table 5. Results of NORMSEP application to a shrimp sample from the North Anticosti Channel, July 1979 (Gulf of St. Lawrence).

Age groups	Mean Carapace length (mm.)	Standard deviation	Proportion	Number of shrimps
1	14,5	1,15	42,3	380
2	18,4	1,27	49,0	255
3	21,8	0,91	13,7	121
4+	24,7	1,35	14,0	123

Table 6. Comparison between NORMSEP results (Table 5., Fig. 16) and separation by stages in sexual development for a sample in the Gulf of St. Lawrence.

Age groups	Sex	Number of shrimp		
		Separation by sexual stages	Separation by NORMSEP all data	Separation by sex and NORMSEP on ♂ and ♀
1	♂	688	380	346
2	♂		255	304
3	♂		121	38
4	♀ 1	85	123	104
	♀ 2	106		

total: 125

¹Females with sternal spines

²Females without sternal spines

Table 7. Results of the application of MacDonald and Pitcher method to a shrimp sample from the Cartwright Channel off Labrador, July 1980.

Age groups	Percent	Standard error	Mean	Standard error
1	3,9	0,8	12,2	0,16
2	23,7	5,3	16,2	0,30
3	29,1	8,1	20,1	0,28
4	40,7	4,4	24,4	0,14
5+	2,5	1,0	28,1	0,36

$\chi^2 = 30,6$, DF = 24

Table 8. Comparison of results using NORMSEP versus MacDonald and Pitcher methods for the sample from the Cartwright Channel, July 1980.

Age groups	NORMSEP (Hasselblad)		MacDonald and Pitcher	
	Mean length	Percent	Mean length	Percent
1	12,1	3,9	12,2	3,9
2	16,2	24,0	16,2	23,7
3	20,1	28,6	20,1	29,1
4	24,4	40,7	24,4	40,7
5+	28,0	2,9	28,1	2,5

$\chi^2 = 34,4$
DF = 24

$\chi^2 = 30,6$
DF = 24

Table 9. Input data to NORMSEP for total length distribution of the Workshop sample.

Cut-off points	Upper and lower bounds of means
15,35	12,2 - 15,2
22,25	15,7 - 21,0
25,85	21,5 - 25,5
	26,0 - 28,7

Table 10. Mean length and numbers by age class estimated by NORMSEP and by stages in sexual development.

Age groups	Mean length (mm)	Separation by NORMSEP (n)	Separation by Sexual stages(n)	Combined analysis (n)	(%)	
1	14,9	35	[289 54] [71]	35	8,5	
2	19,0	249		249	60,3	
3	23,2	[112 17]		54	13,1	
4	24,8			125	58	14,0
5+	27,1			17	17	4,1

Table 11. Results of NORMSEP for the Workshop sample. (Anticosti Channel, Gulf of St. Lawrence, 1979)

	Age groups								X ²	DF
	1		2		3		4 ⁺			
	Mean length	%	Mean length	%	Mean length	%	Mean length	%		
NORMSEP on total distribution (0,3 mm)	14,9	8,6	19,0	60,2	23,9	27,2	27,1	4,0	45,7	36
NORMSEP on total distribution (0,3 mm with a moving average of 3)	14,9	8,8	19,0	59,8	24,0	27,6	27,2	3,7	11,1	36

Table 12. Abundance (numbers x 10⁻⁶) by age class estimated by NORMSEP and sternal spines for a shrimp population of the Gulf of St. Lawrence. (From Fréchet and Parsons, 1981).

	0	I	II	III or III ⁺	IV ⁺
1977	53	486	653	545	-
1978	266	368	720	626	-
1979	90	731	579	517	337
1980	23	202	1230	597	344

Table 13. Maine August shrimp survey; average catch-at-age per half hour tow¹ based on sexual characteristics (A) and NORMSEP² results for a trimodal distribution (B).

Year caught	Assumed age			
	I	II	III	IV
1972	262	635	305	94
1973	1087	642	208	134
1974	542	337	157	72
1975	112	544	255	134
1976	462	206	118	78
1977	121	47	63	24
1978	270	121	40	82
1979	226	306	76	38
1980	332	66	48	21
1981	159	160	60	55

¹ Tows were conducted with a 25 foot headrope, 31 foot footrope semi-balloon otter trawl with a 1½ inch stretch mesh body and a 1½ inch stretch mesh cod-end with a ½ inch stretch mesh cod-end liner.

Year caught	Assumed age		
	I	II	III
1972	254	649	393
1973	1079	643	349
1974	566	302	241
1975	114	537	394
1976	454	233	178
1977	120	61	75
1978	271	127	115
1979	227	313	106
1980	334	72	62
1981	159	154	121

² It should be noted that none of the NORMSEP runs yielded non-significant chi-square values.

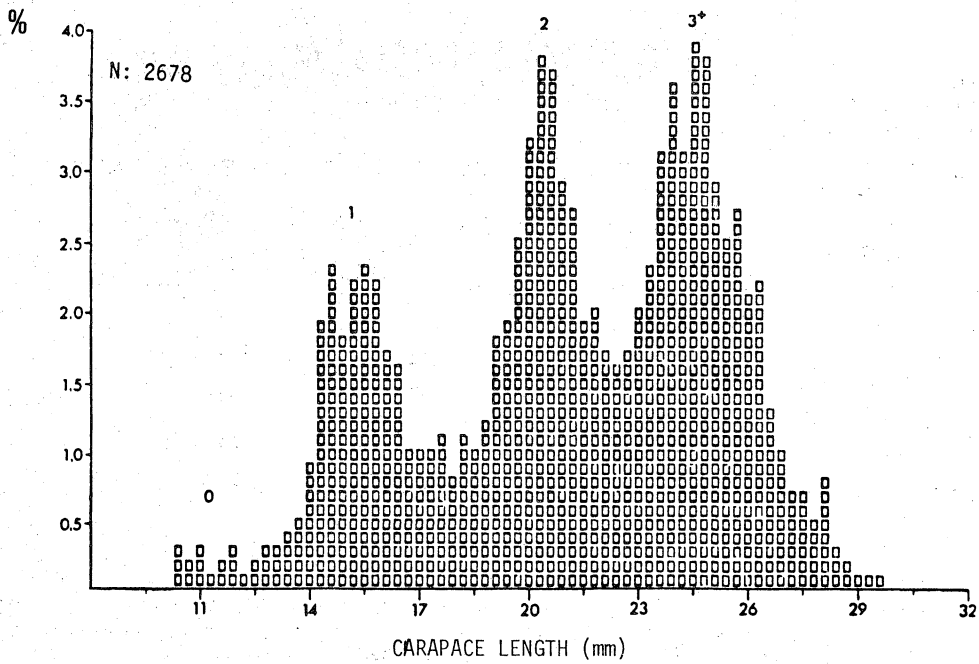


Fig. 1. Interpretation of age structure (0 to 3+) from shrimp size frequency distribution for a sample in the Gulf of St. Lawrence. (October 1977).

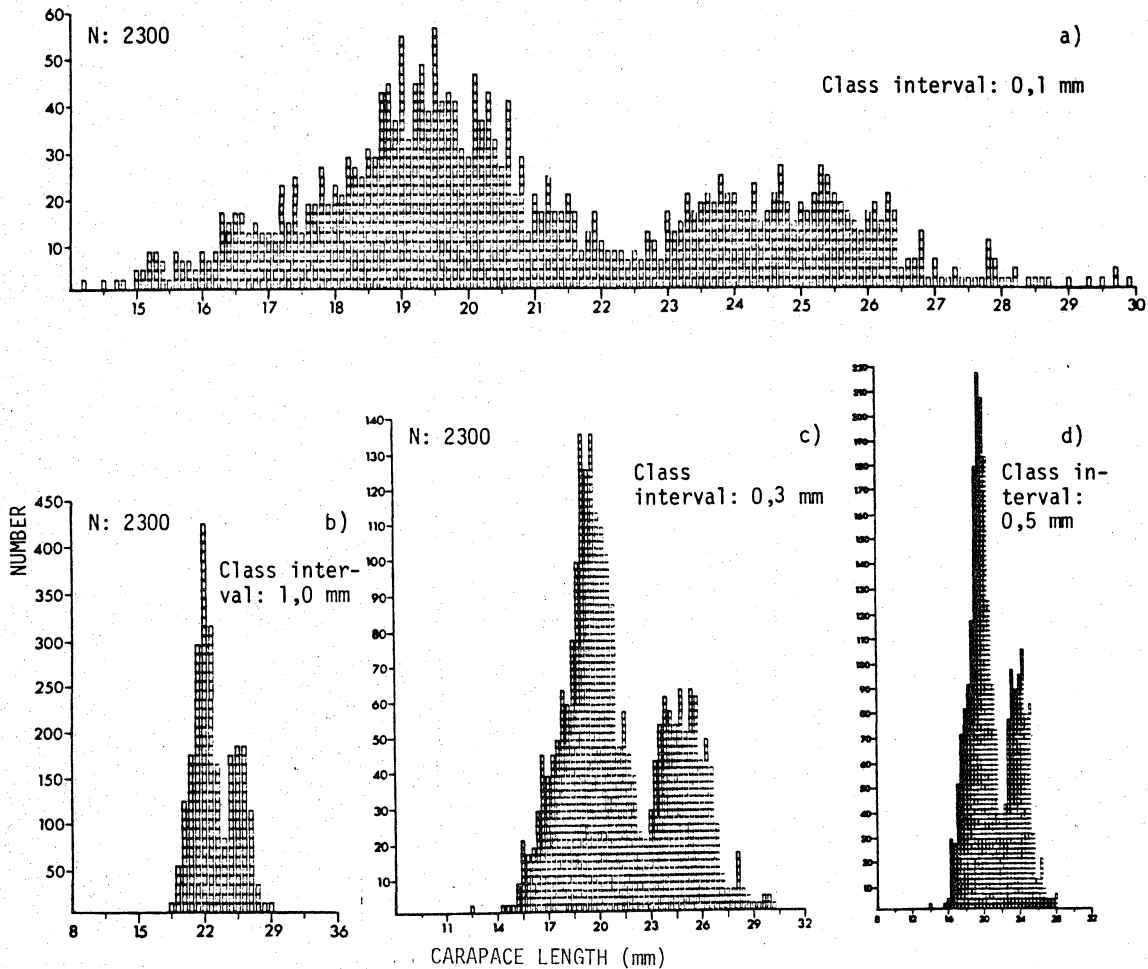


Fig. 2. Shrimp length frequency distributions using different class intervals for a commercial sample in the Gulf of St. Lawrence. (September 1980).

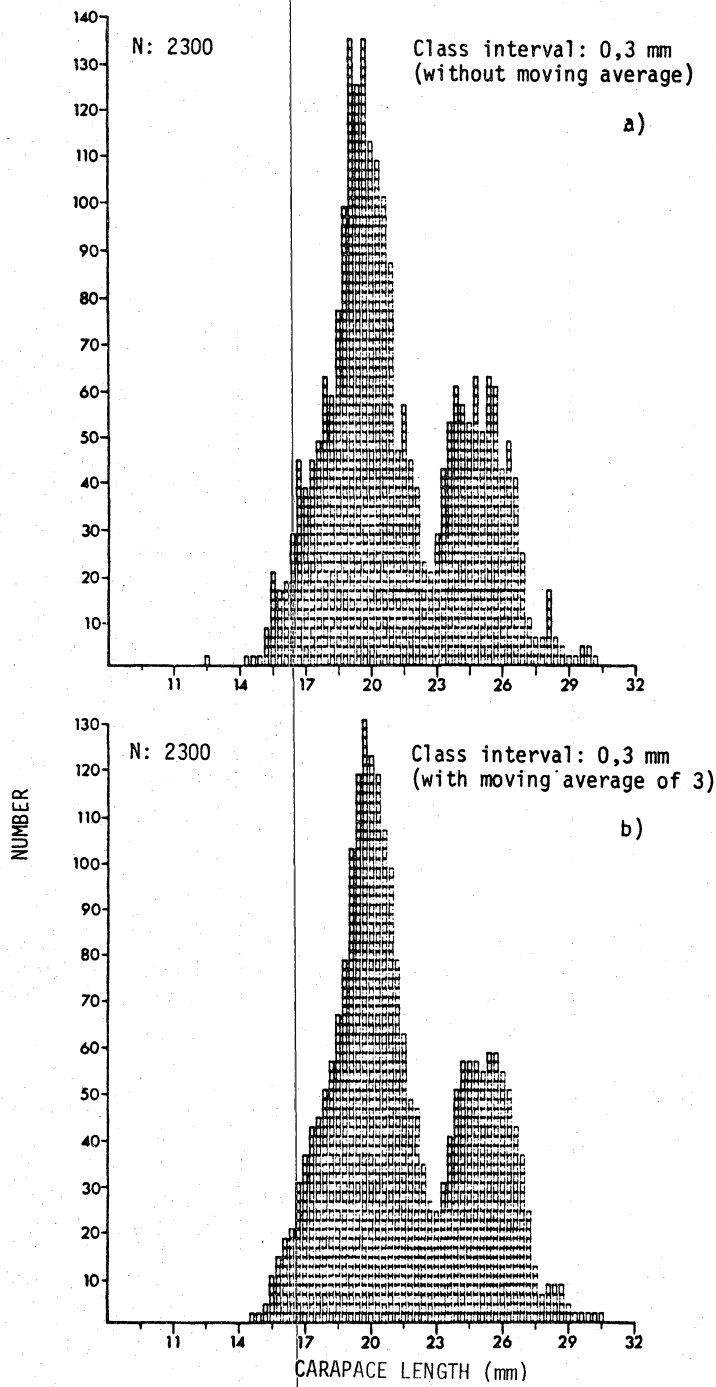


Fig. 3. Effect of a smoothing method on a shrimp length frequency distribution. (Commercial sample, September 1980, same as Fig. 2).

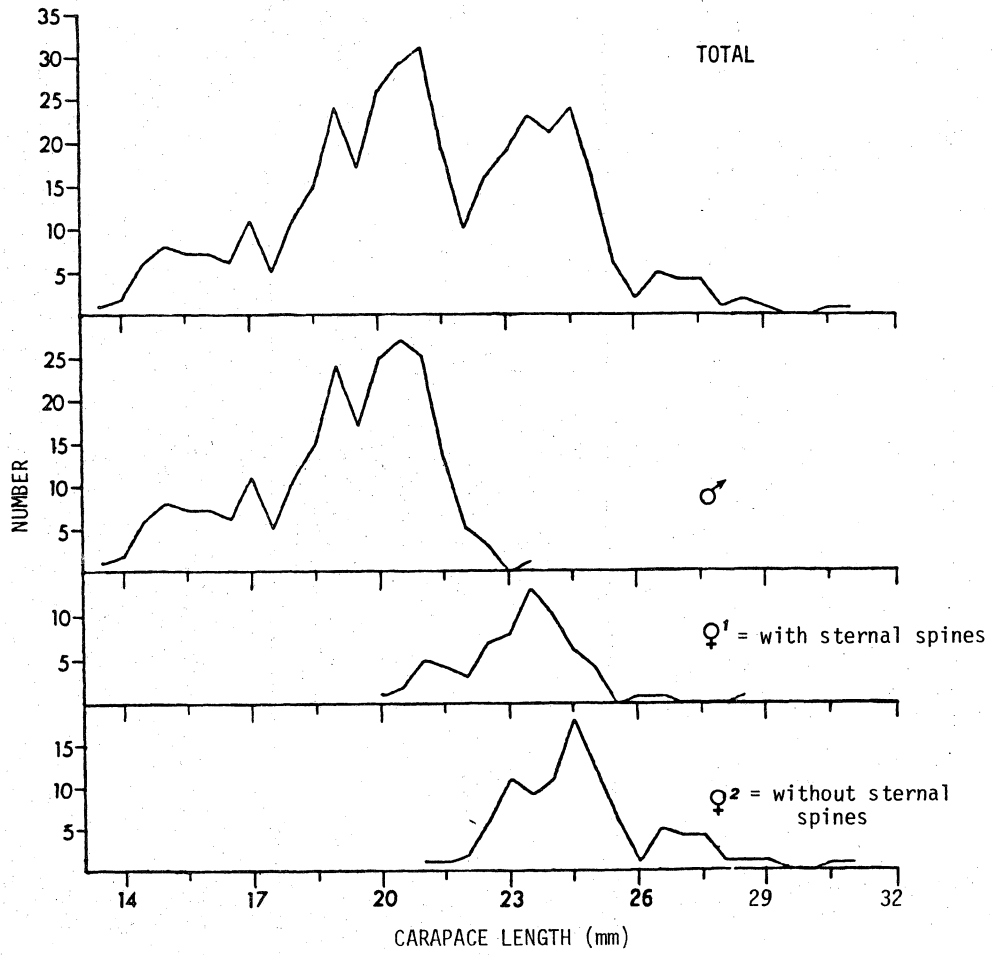


Fig. 4. Separation of a shrimp length frequency distribution by stages in sexual development. (Cartwright Channel, Labrador, July 1980).

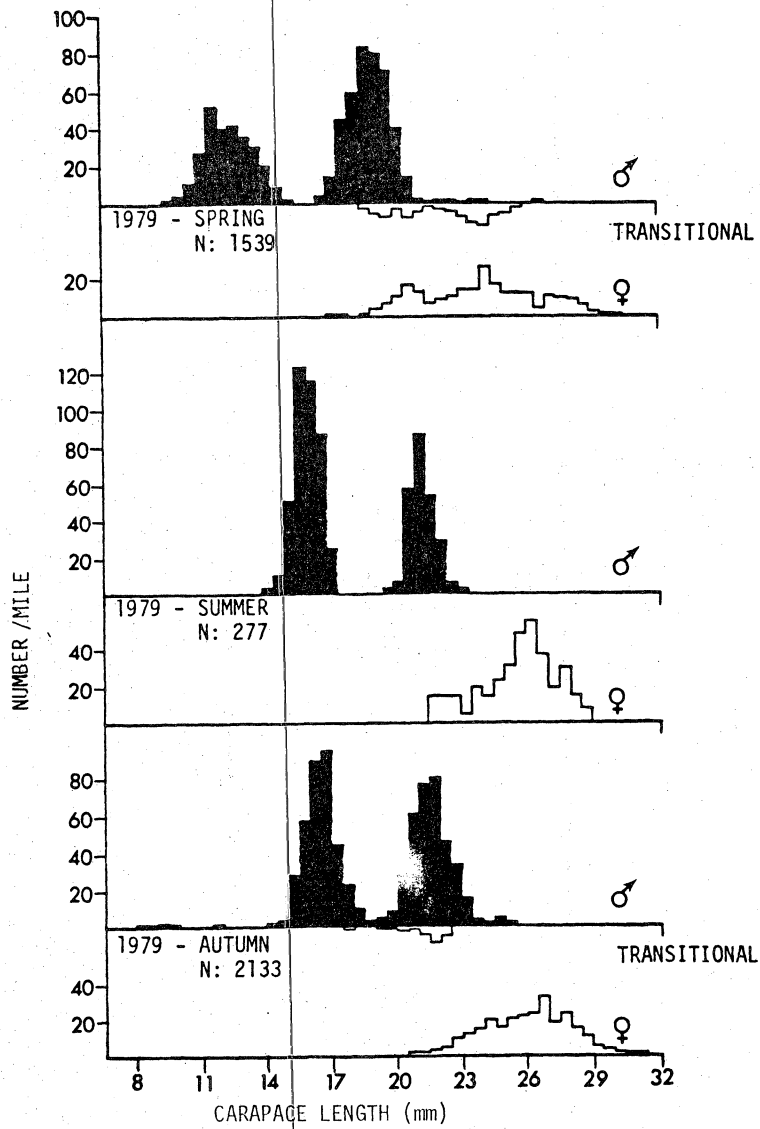


Fig. 5. Length frequency distributions of shrimp by sex in spring, summer and autumn bottom trawl surveys. (Gulf of Maine, 1979).

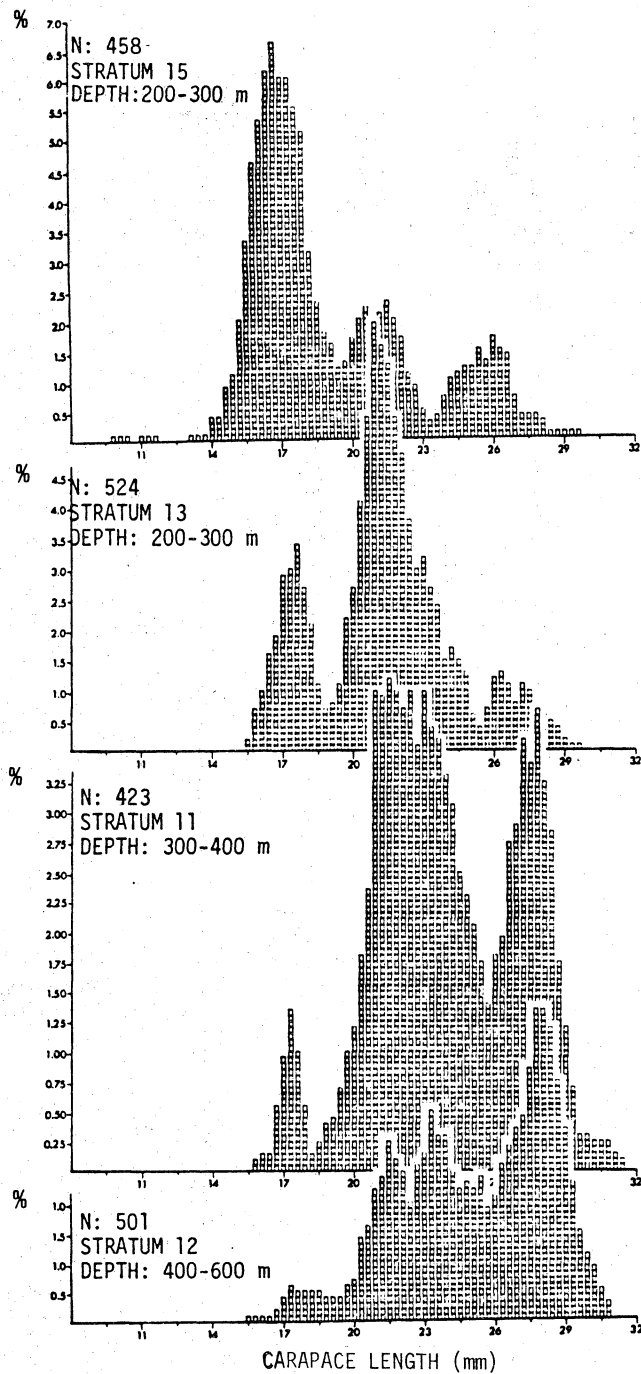


Fig. 6. Length frequency distributions of shrimp from different depth ranges for the southern part of division 1B, Davis Strait. (Extracted from Frechette and Dupouy, 1979).

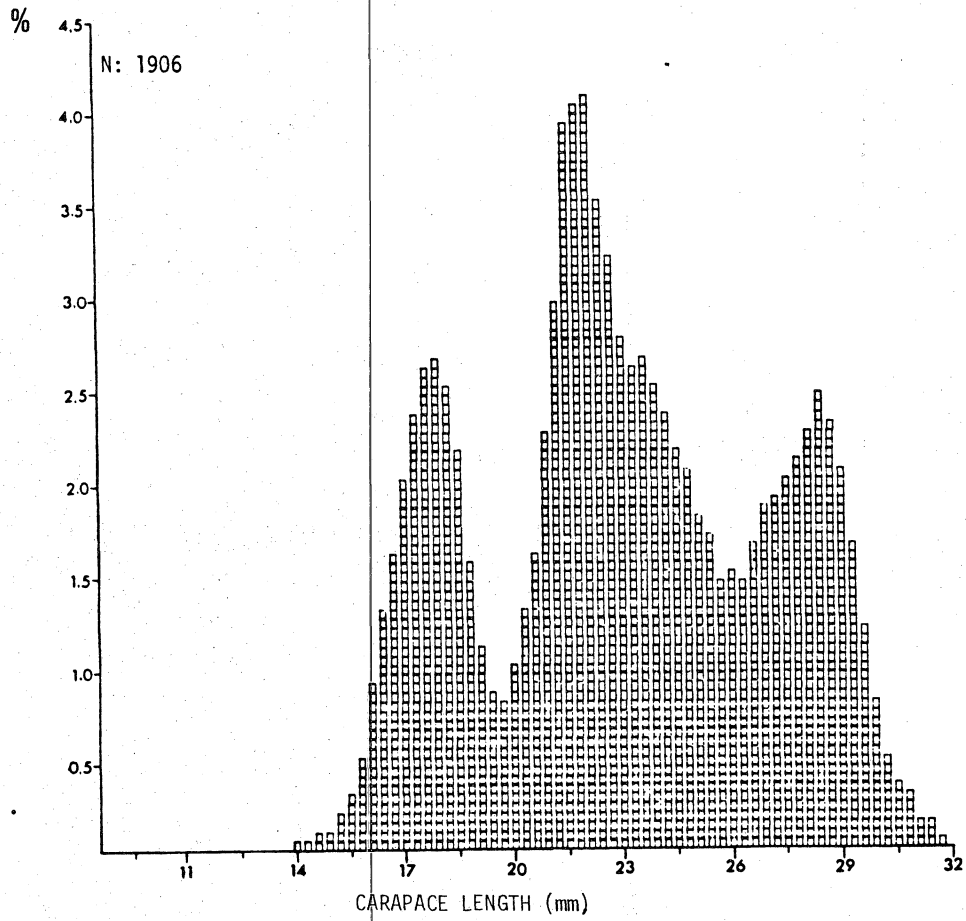


Fig. 7. Pooled length frequency distribution of shrimp from different depths. (Cumulated from data of Fig. 6., NAFO Division 1B, Davis Strait).

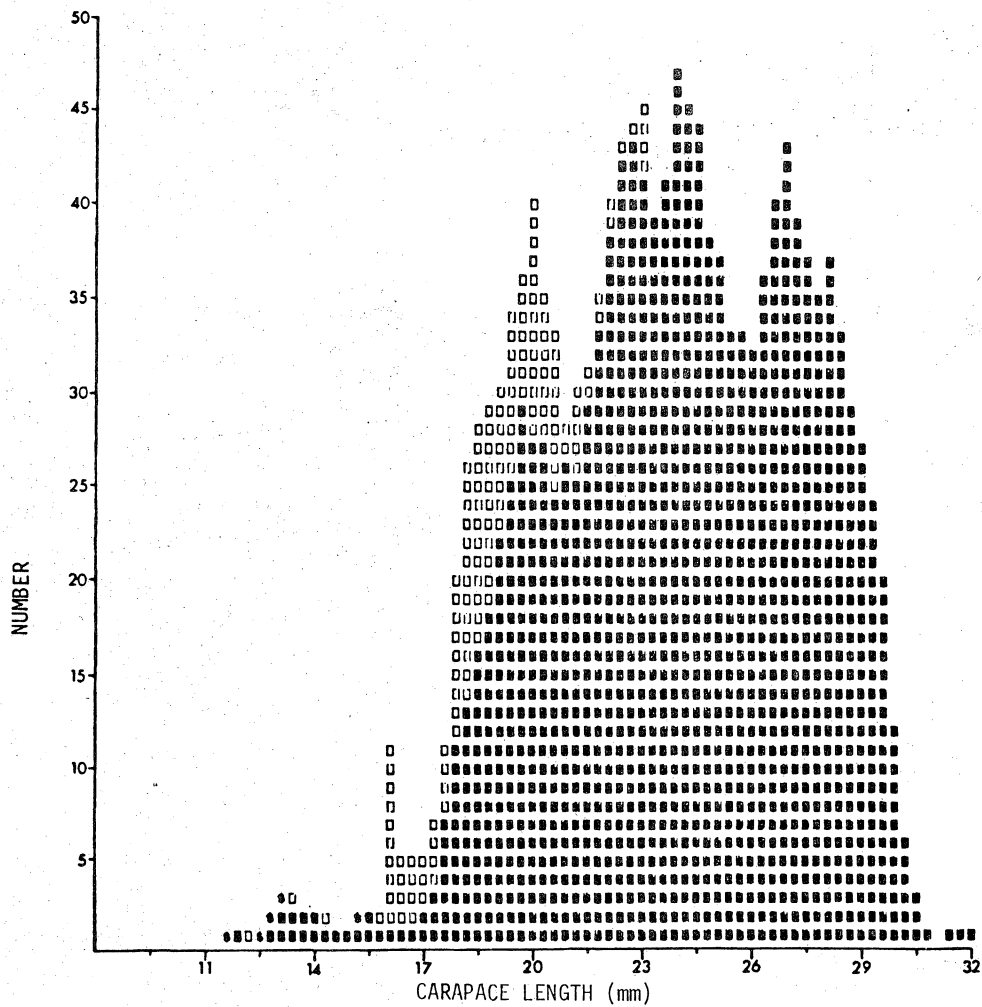


Fig. 8. Effect of correction in number of shrimps by the selective ogive (□) on a length frequency distribution (■). (Extracted from Fréchet and Labonté, 1981).

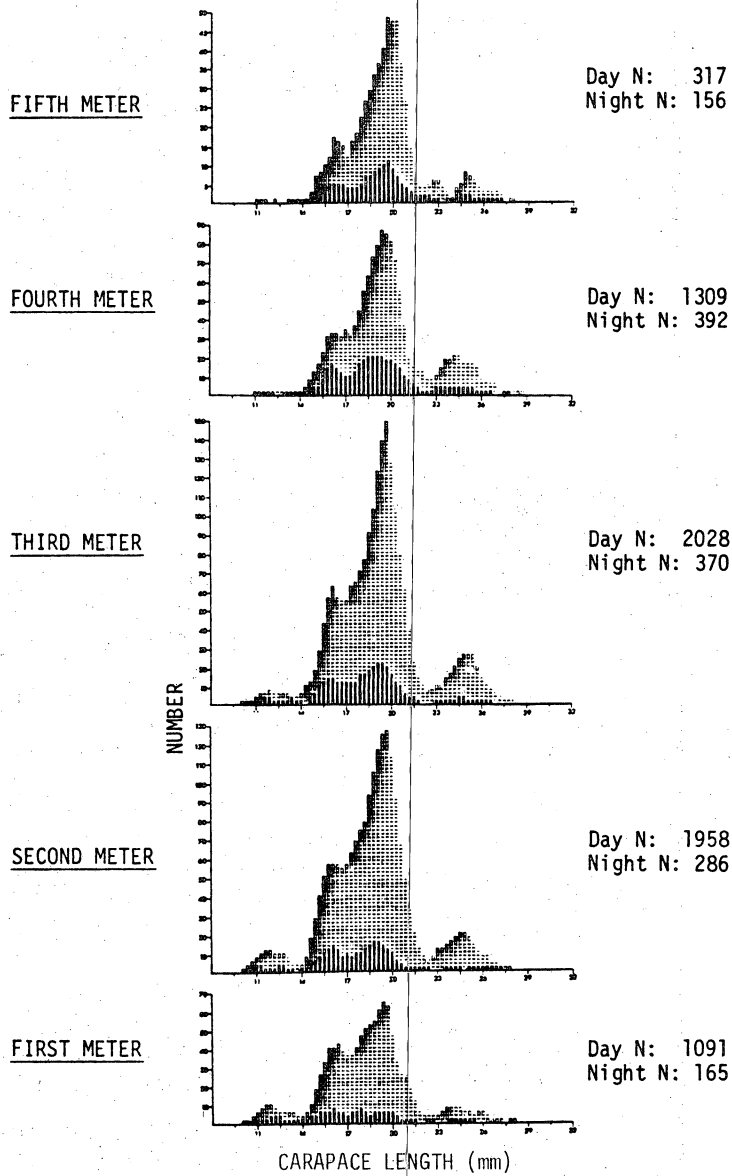


Fig. 9. Length composition of total shrimp catches at one meter intervals off the bottom during the day (□) and night (■), using a vertical sampler. (Gulf of St. Lawrence, 1980. Extracted from Fréchet et al., 1981).

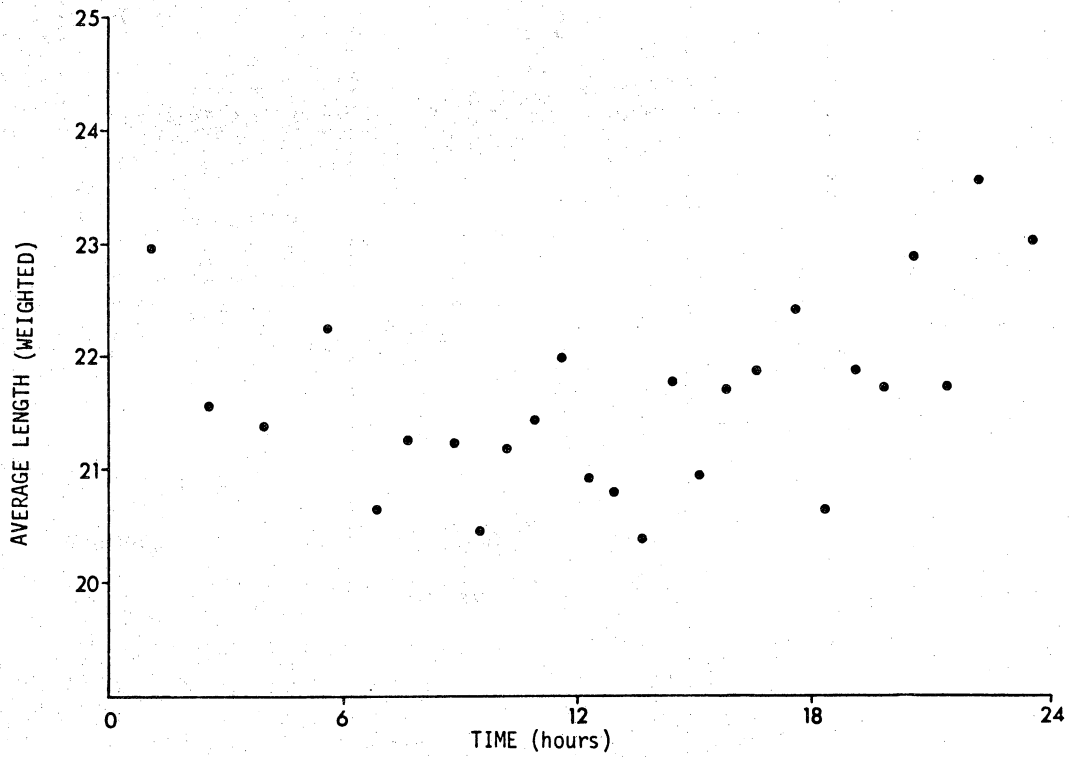


Fig. 10. Diel variation of size of shrimp in Hopedale Channel. (Labrador, July 1981)

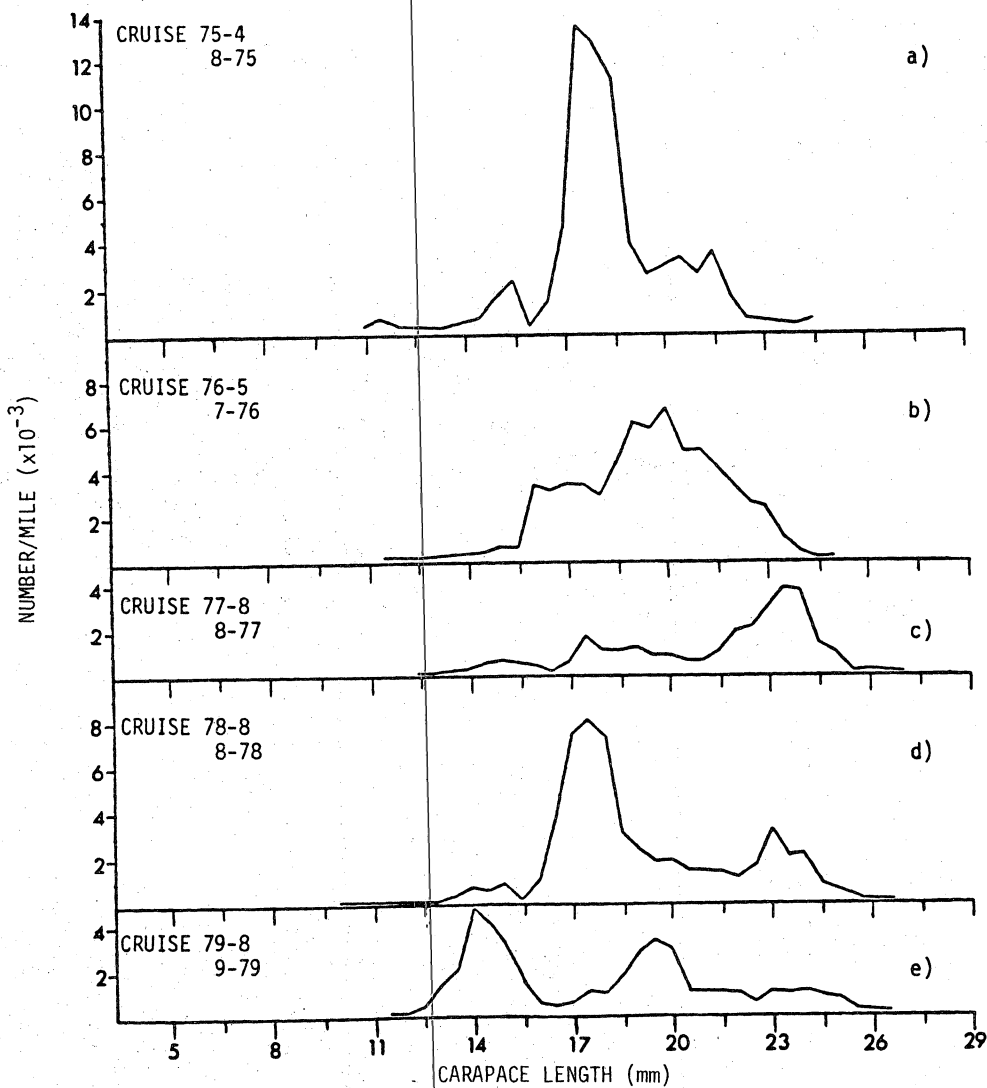


Fig. 11. Composite length frequencies of shrimp (*P. borealis*) from successive fall trawl surveys of the Alitak Bay section of the Kodiak District, Alaska, 1975-1979. (Extracted from Jackson et al., 1981.)

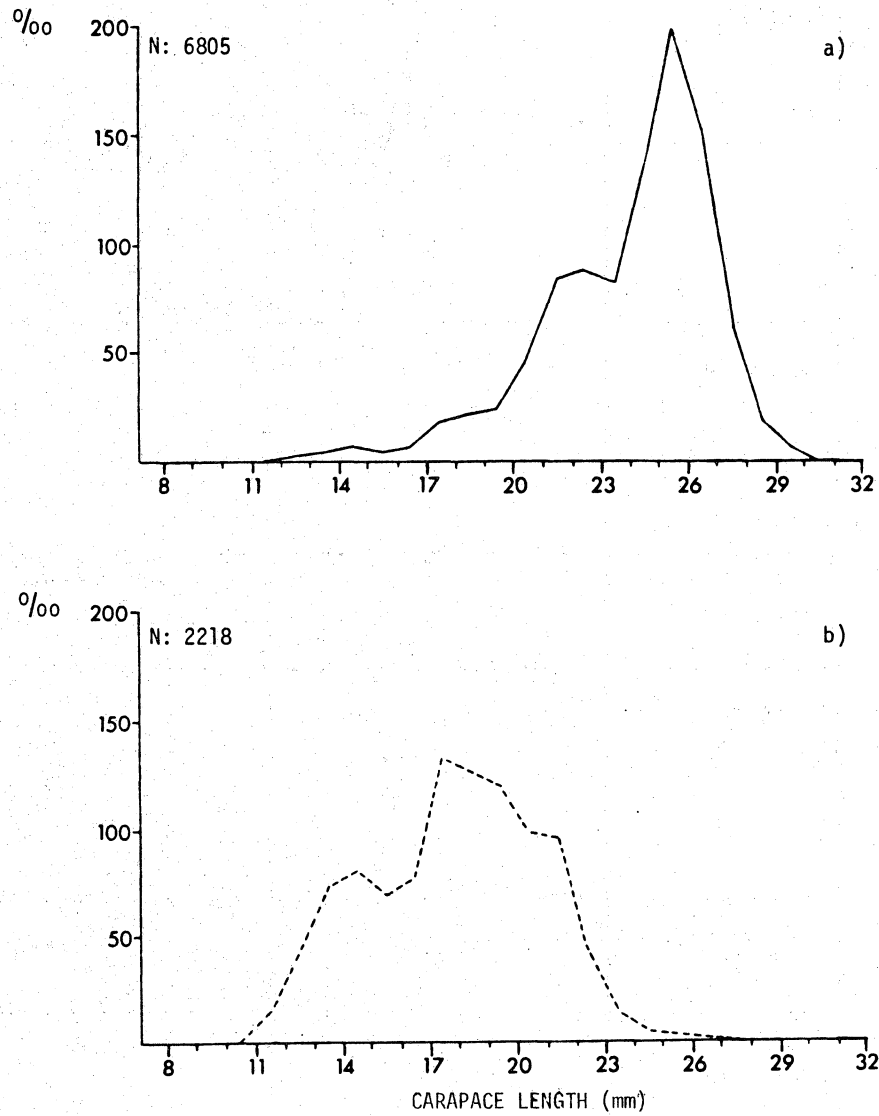


Fig. 12. Length frequency distributions obtained (a) from the total shrimp catch and (b) from the discarded shrimps. (Commercial sample, Davis Strait, July-August 1980. Extracted from Derible and al., 1980).

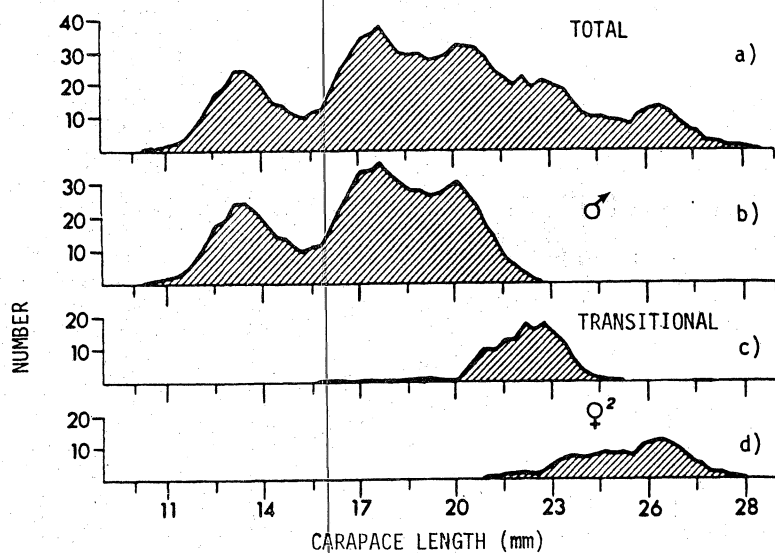


Fig. 13. Shrimp length frequency distributions by stages in sexual development. (Nova Scotia shelf, Canada).

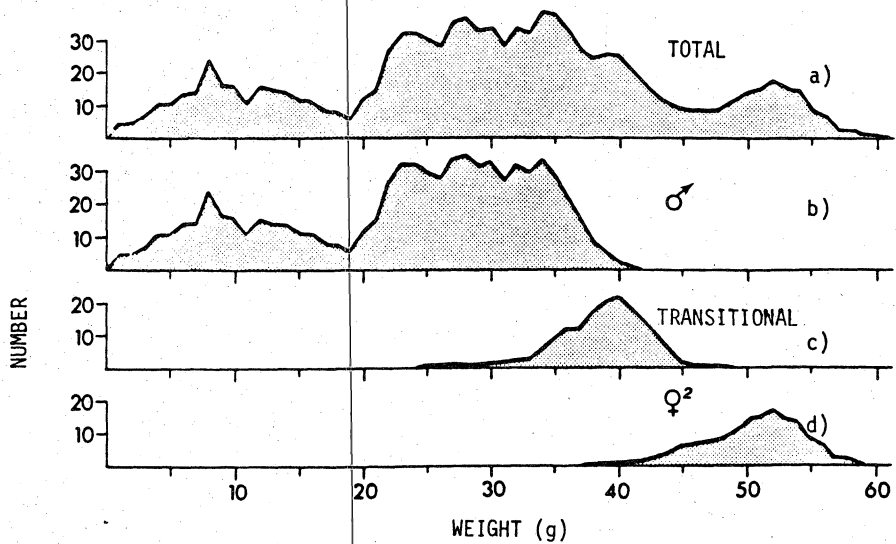


Fig. 14. Shrimp weight frequency distributions by stages in sexual development. (Nova Scotia shelf, Canada, same sample as Fig. 13).

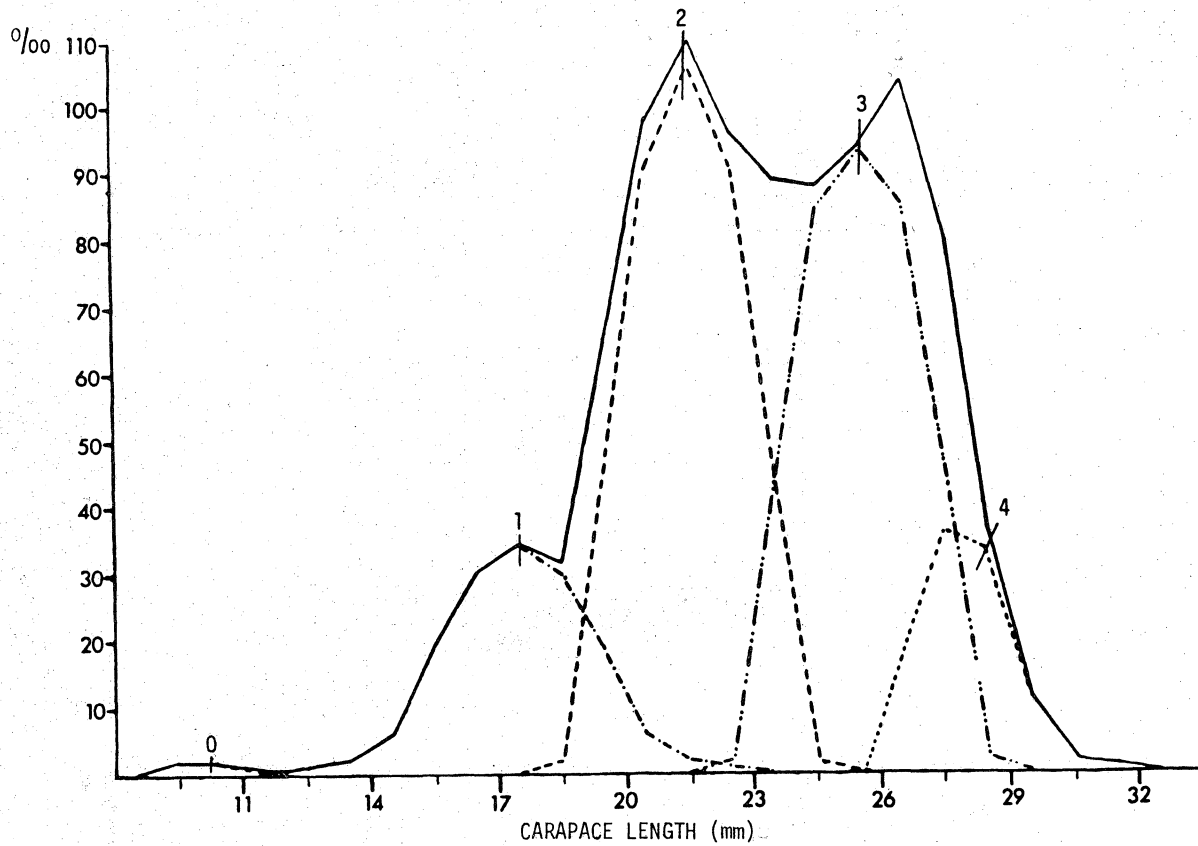


Fig. 15. Application of the successive maxima method (broken lines) on a total length frequency distribution of shrimp (solid line). (R/V Thalassa survey, Davis Strait, October 1979).

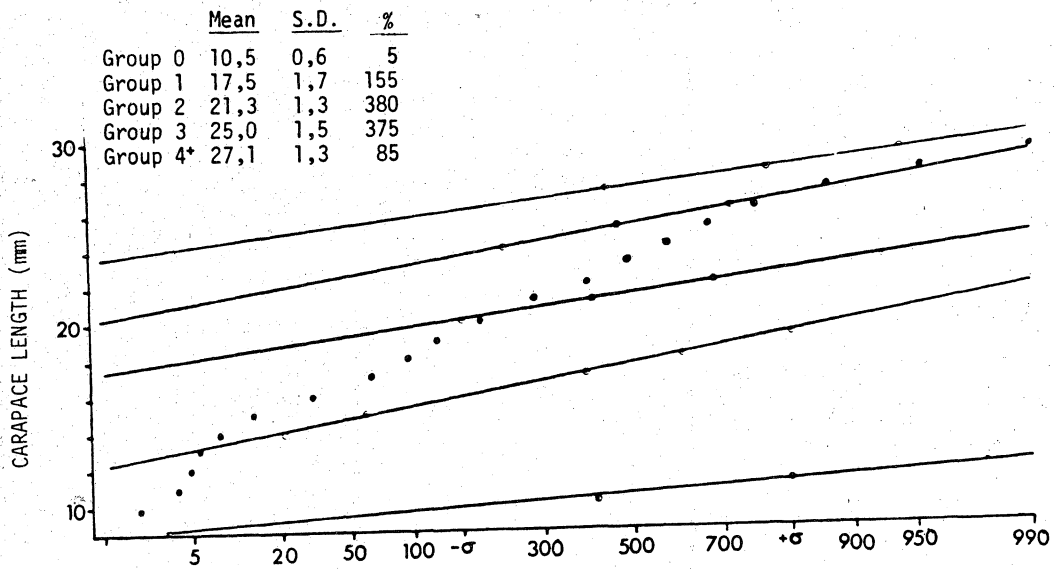


Fig. 16. Application of the Cassie (1950,1954) method on a total length frequency distribution of shrimp. (R/V Thalassa Survey, Davis Strait, October 1979).

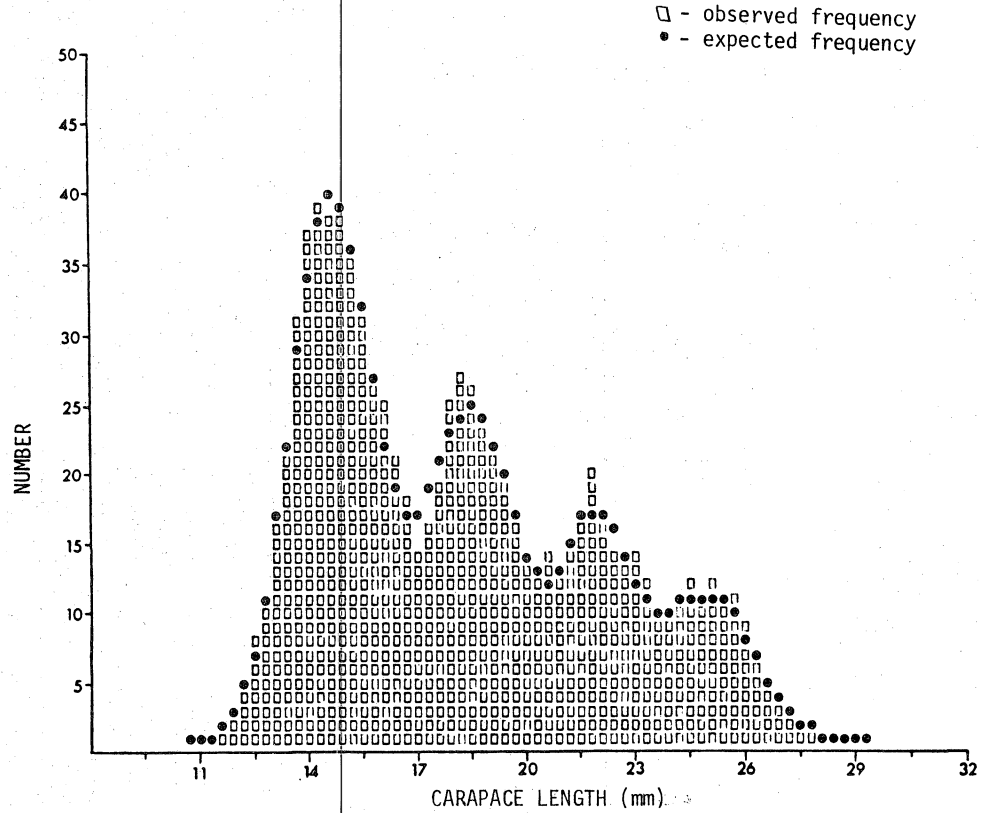


Fig. 17. Application of the Hasselblad (1966) method (NORMSEP) on a length frequency distribution of shrimp. (North Anticosti, Gulf of St. Lawrence, July 1979. Extracted from Fréchette and Parsons, 1981).

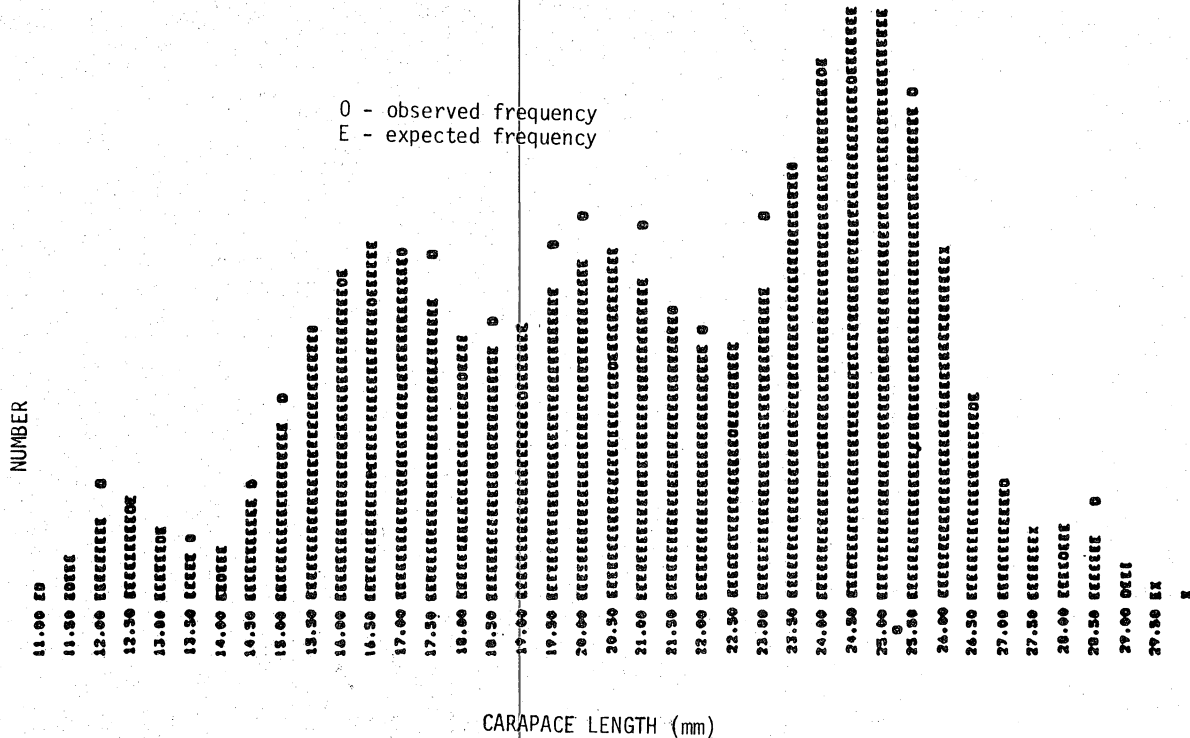


Fig. 18. Application of the MacDonald and Pitcher method to a length frequency distribution. (Cartwright Channel, Labrador, July 1980).

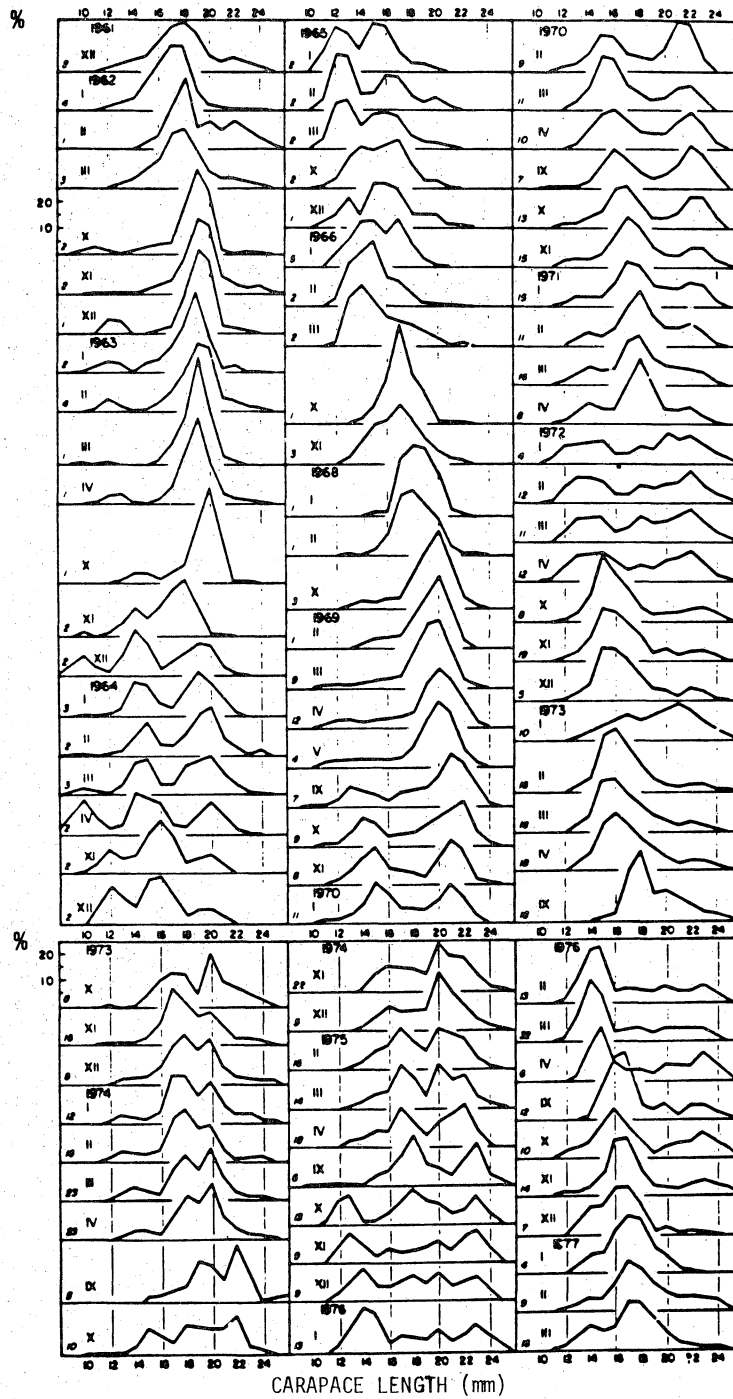


Fig. 19. Size frequency distributions plotted by month in Arnarfjörður, Iceland from 1961 to 1977. (Extracted from Skuladóttir, 1981).

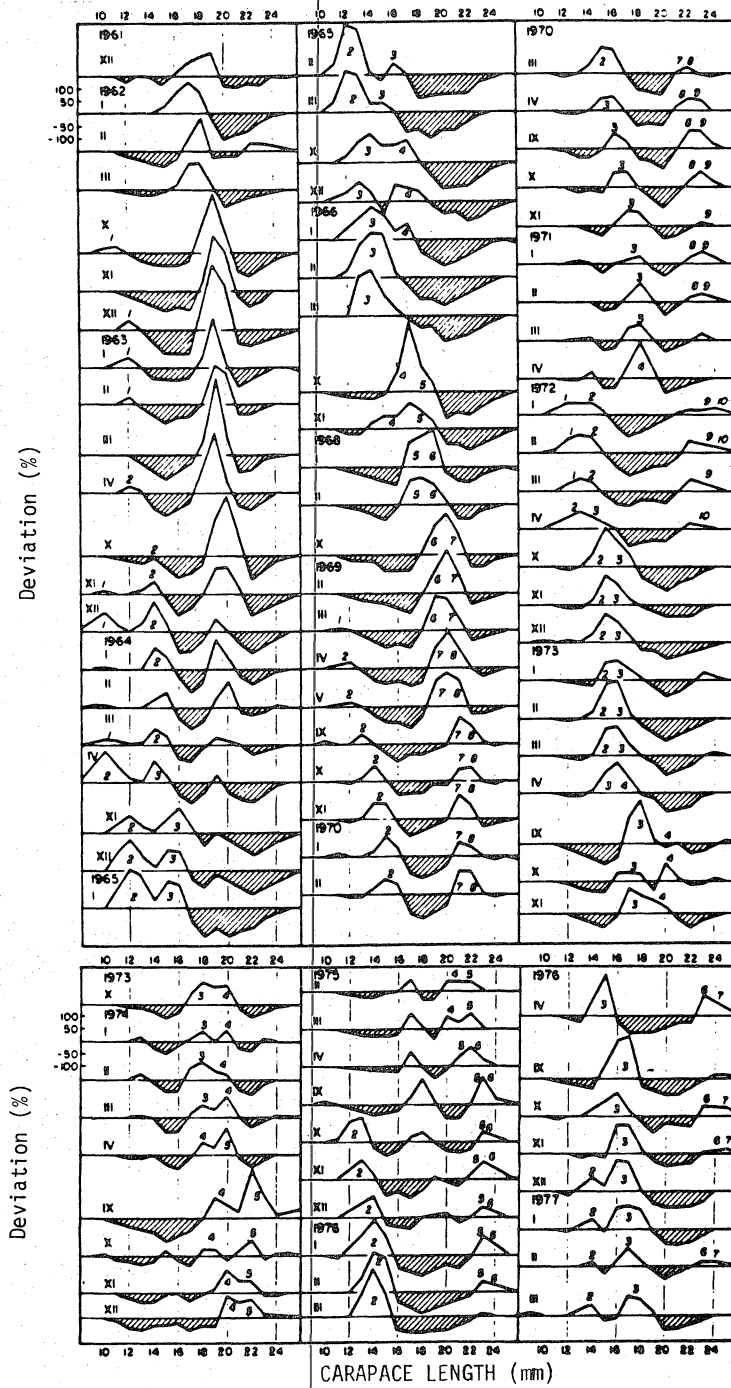


Fig. 20. Deviations of length frequency distributions from 1961 to 1977. (Extracted from Skúladóttir, 1981).

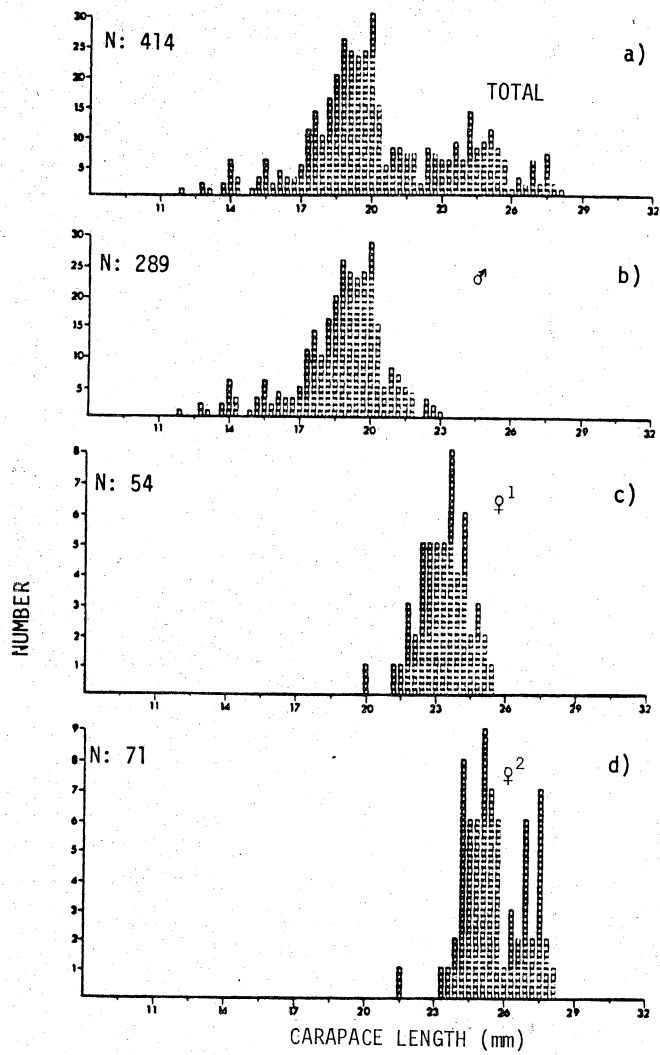


Fig. 21. Separation of a shrimp length frequency distribution by states in sexual development. (Workshop sample, Anticosti Channel, Gulf of St. Lawrence, July 1980).

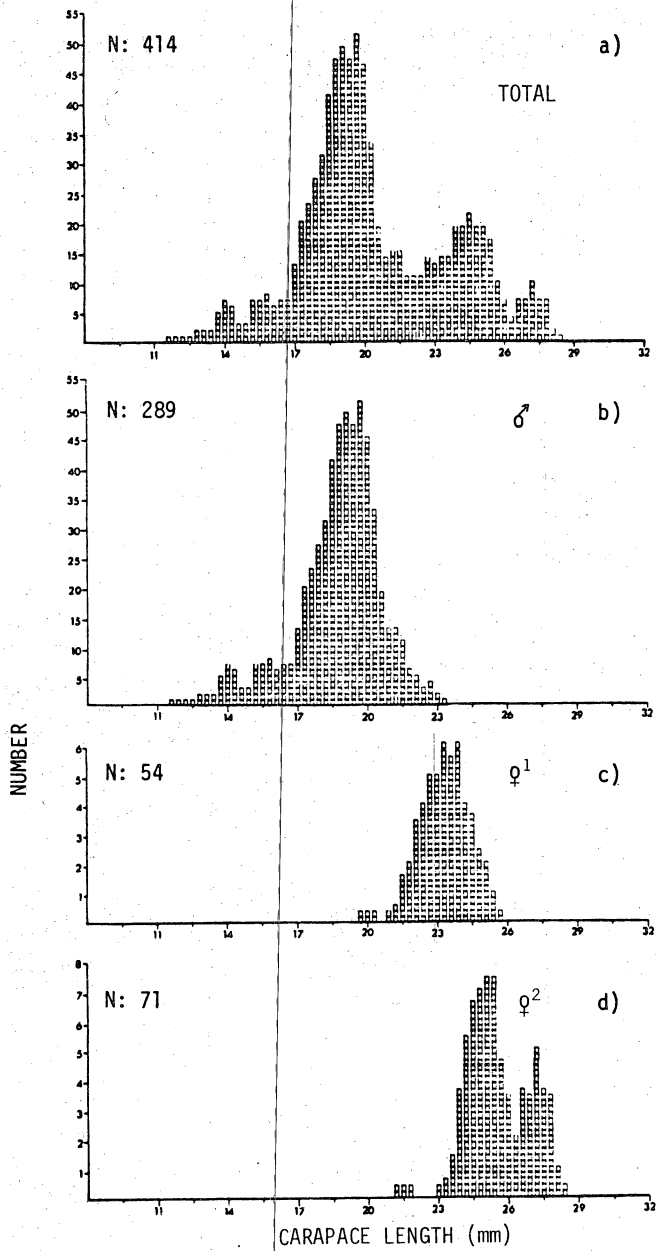


Fig. 22. Shrimp length frequency distributions by stages in sexual development using a moving average of three. (Workshop sample, Anticosti Channel, Gulf of St. Lawrence, July 1980).

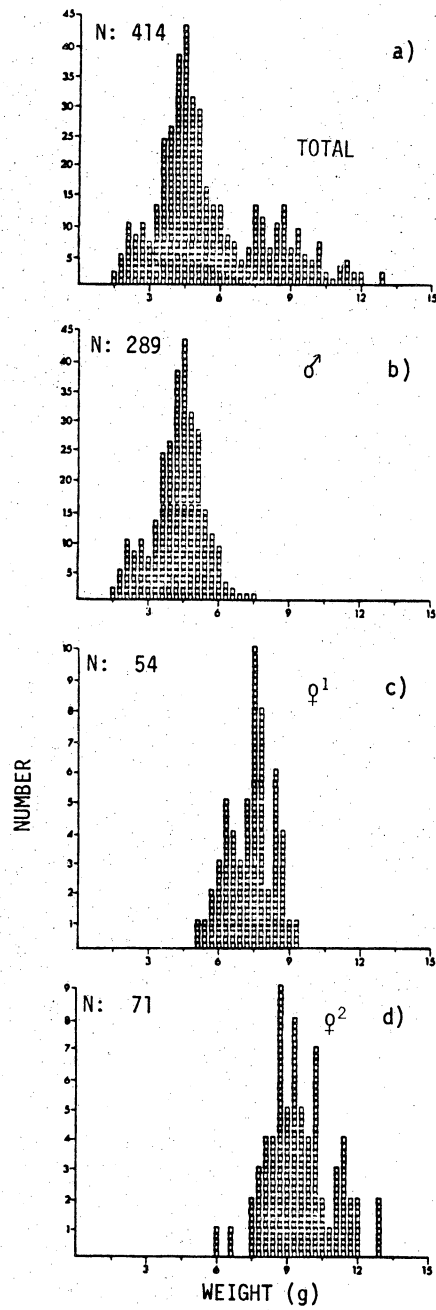


Fig. 23. Separation of a shrimp weight frequency distribution by stages in sexual development. (Workshop sample, Anticosti Channel, Gulf of St. Lawrence, July, 1980).

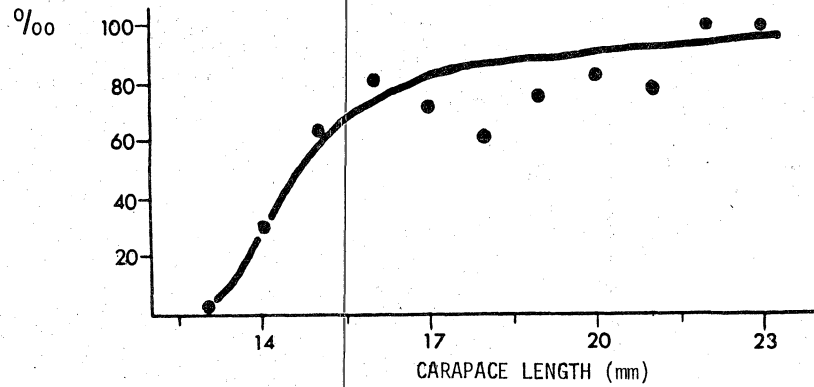


Fig. 24. Mean proportion of egg bearing female shrimp within mm length classes (12 samples, November-March 1965-1966, Arnarfjörður, Iceland).

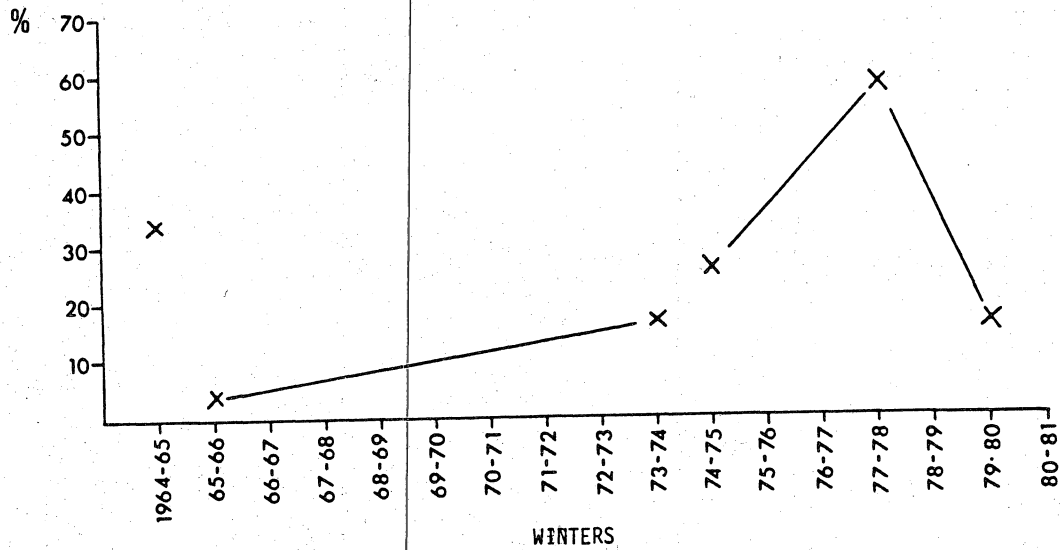


Fig. 25. Percentage of sexually mature female shrimp at the mean length at age 4 for six strong year-classes detected by the Deviation method.

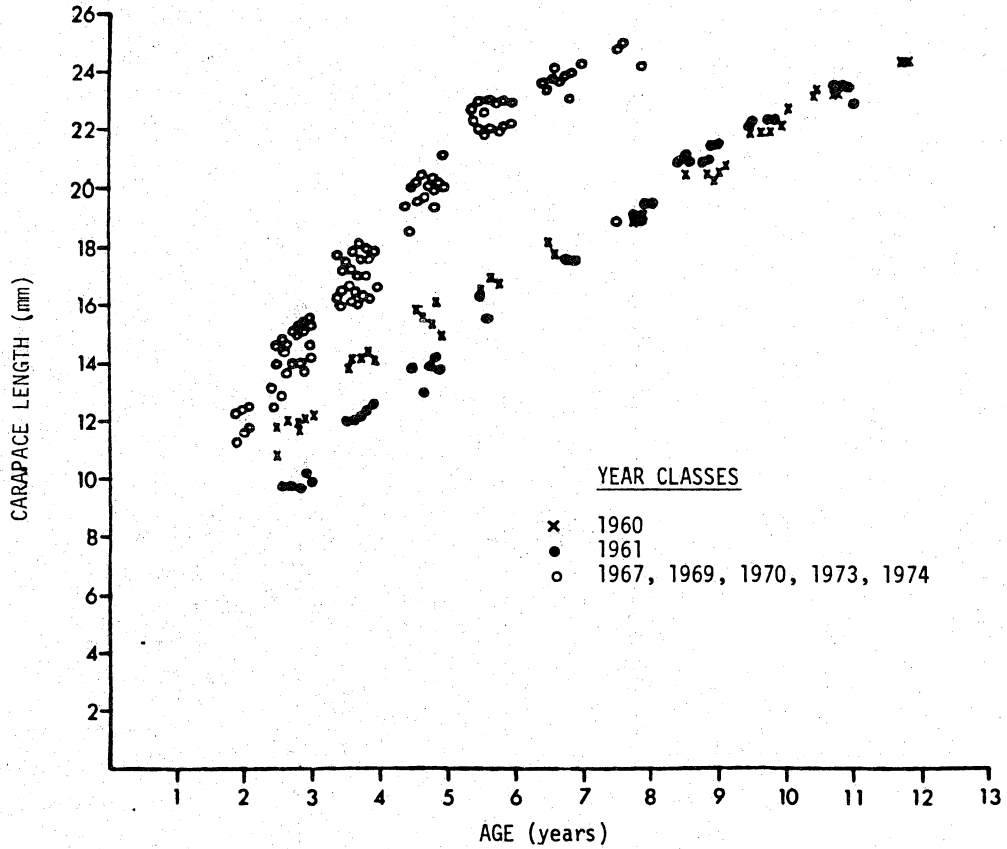


Fig. 26. Shrimp growth curves obtained by the Deviation method for two slow-growing year classes (1960, 1961) and five fast growing (1967, 1969, 1970, 1973, 1974). (Arnarfjördur, Iceland. Extracted from Skuladottir, 1981.)

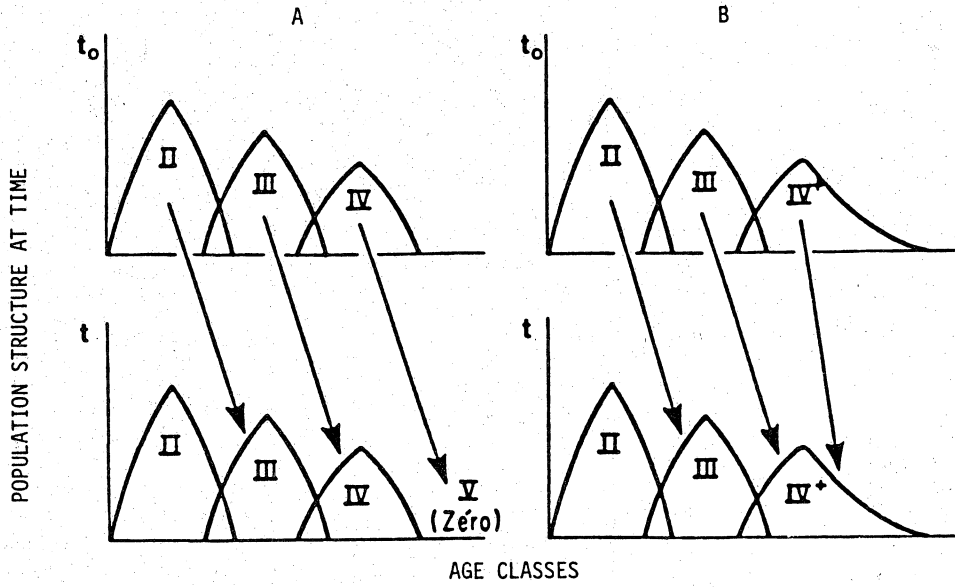


Fig. 27. Theoretical evolution of a shrimp population structure from $t_0 + t$ (1 year), assuming (A) that the last mode IV represents a single age class (B) that the last mode IV⁺ represents several year-classes. (Extracted from Labonti, 1979.)