

Report of Shrimp Ageing Workshop Held at Ste. Foy, Quebec, in May and at Dartmouth, Nova Scotia, in November 1981

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Abstract

A workshop on ageing northern shrimp, *Pandalus borealis*, sponsored by the Scientific Council of NAFO, was held in May and November 1981. Various aspects were considered, ranging from the collection of shrimp samples to treatment and analysis of the data. A general consensus was that a minimum of 500 shrimp per sample (frozen, or preferably fresh) is necessary for age interpretation. It was also considered advisable to measure the carapace length to the nearest 0.1 mm, with subsequent grouping into 0.3, 0.5 or 1.0 mm length intervals as desired. Standardized methods of collecting and combining samples is essential to minimize bias and provide representative length compositions of the populations. Such factors, as randomization of commercial samples, stratification of age-groups by depth, selectivity and availability problems for small shrimp, diel variability in distribution, weighting of length frequencies, and size composition of discards, must be taken into account.

Various graphical and analytical methods of determining age components (modal groups) in length frequencies were discussed, with emphasis being placed on analytical techniques employing computer programs. Application of such methodology to length distributions, supplemented by a breakdown of the samples by sex and reproductive stage, was considered useful in separating the modal components (age groups). Although the relative abundance of age-groups can be estimated from representative samples of the shrimp population, caution is advised in determining year-class strength unless sufficient data are available from repetitive surveys.

Growth and mortality may also be estimated from the modal analysis of length frequencies. Although growth of shrimp is discontinuous, the von Bertalanffy growth model provides a reasonable approximation. However, the presence of fast-growing and slow-growing year-classes in a population may create difficulties in deriving a representative growth curve. Few attempts have been made to estimate mortality rates, the available information indicating a wide range of natural mortality (0.2-0.8). Other problems in ageing shrimp were identified such as the lack of information on frequency of molting, larval growth, selectivity and availability, interpretation of spawning characteristics, and age-class accumulation in the modal group of females.

Because the estimation of almost all biological parameters used for resource management relies on representative ageing techniques, priority should be placed on improvements of existing methodology and development of new methods for ageing shrimp. The management implication of age-class accumulation of females is that natural mortality may be lower than the values previously used in estimating potential yield.

Introduction

Direct determination of age is not presently feasible for *Pandalus borealis*, as for all crustaceans. Analysis of length frequencies and examination of sex-related characteristics permit some interpretation, but these procedures are very different from those commonly used for fish (annuli in otoliths and scales) and molluscs (annuli on shells).

Analysis of size composition data has been the primary basis for ageing *P. borealis*. The assumptions underlying age interpretations from such data are that different modes correspond to different cohorts (age-groups) in a polymodal length distribution (Fig. 1) and

that growth is similar within a given age-group. The first assumption is often closely met, because many stocks exhibit an annual synchronous cycle of reproduction, with a well-defined hatching period in the spring (Haynes and Wigley, 1969). Displacement of modal classes over time in sequential length 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 the modes less well-defined. The second assumption may not be met in many cases. Rasmussen (1969) observed fast-growing and slow-growing shrimp within the same age-group, resulting in bimodality, which he attributed to sex reversal in some individuals.

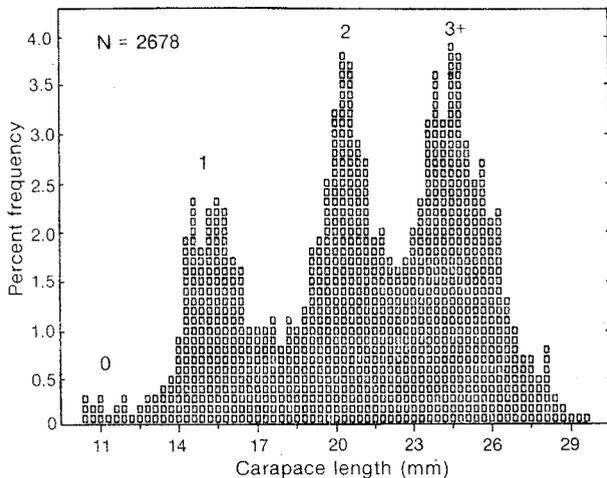


Fig. 1. Interpretation of the age structure (0 to 3+) of a *P. borealis* sample from the Gulf of St. Lawrence, October 1977.

Other observations on growth in shrimp also indicate that *P. borealis* length frequencies may not be amenable to the classical Petersen method of age determination (e.g. see Skúladóttir, 1981). The situation is further complicated by variation in selectivity of sampling devices and availability, especially for younger shrimp, and by the possibility of age-class accumulation within the last prominent modal group of females, the latter resulting mainly from a lengthly ovigerous period which limits the time available for growth (Haynes and Wigley, 1969).

This paper summarizes the proceedings of the workshop which was held at the Direction de la Recherche Scientifique et Technique, Ste. Foy, Quebec, during 11–14 May 1981 and was continued at the Bedford Institute of Oceanography, Dartmouth, Nova Scotia, during 20–21 November 1981, with the participation, at one or both meetings, of experts from Canada, Denmark, France, Greenland, Iceland, Norway and United States of America (Appendix I). J. Fréchette and D. G. Parsons were co-conveners for the sessions. The objectives of the workshop were to (a) review the problems associated with collecting data on size and sex of shrimp for age determination, (b) examine the applications and limitations of graphical and analytical methods used for interpretation of age-groups, and (c) consider the utilization of such data and methods for estimating year-class strength, growth and mortality.

Biological Requirements for Ageing

Sampling techniques

Several methods of preserving samples of shrimp have been used, the most common being freezing and

fixation in 5–10% formalin. The ideal situation would be the examination of fresh material, but this is often not possible. Whatever methods of preservation are used, their effects on length and weight of individuals and on age interpretation from the length frequencies should be evaluated statistically. Because head roe (maturing ovary) deteriorates when shrimp are frozen, sorting of individuals in this condition should be performed before freezing.

Separation of the normal components of a polymodal length distribution requires that the sample consist of a large number of observations. Cohen (1966) suggested a minimum of 400 animals in mixtures of only two components and larger samples when there are more than two, for application of Hasselblad's (1966) method of separating normal components. MacDonald and Pitcher (1979) recommended at least 50 individuals for each component. This obviously implies the need for a large random sample if some components are poorly represented. The participants in the workshop generally agreed that a minimum of 500 shrimp per sample should be sufficient for age interpretation and also provide representative data on stages of sexual development.

Standardized research vessel surveys, synoptic over time, can provide data for estimating such biological parameters as growth, mortality and recruitment, if the samples can be aged. These estimates can be obtained from comparison of abundance at each age in successive years. Sequential sampling of commercial catches also can provide the basis for such estimates.

Measuring methods and data summarization

The most universally-accepted procedure for measuring *P. borealis* is oblique carapace length which was described by Rasmussen (1953). This is the distance from the posterior margin of the orbit to the posterodorsal margin of the carapace. Measurements have been recorded in intervals of 0.1 mm, 0.5 mm or 1.0 mm by various investigators, but 0.5 mm is the most commonly used interval.

Grouping of length data by different intervals was examined. The presentation of data by 0.1 mm intervals, as illustrated by the shrimp sample from the Gulf of St. Lawrence (Fig. 2A), was considered to be too fine a breakdown because it tended to emphasize sampling variation and caused difficulty in interpretation of modal groups. On the other hand, combination of the same data by 1.0 mm length intervals (Fig. 2B) resulted in some loss of detail, especially at the ends of the distribution. Although two modal groups are clearly evident, the length interval used was not considered precise enough for statistical separation of the groups.

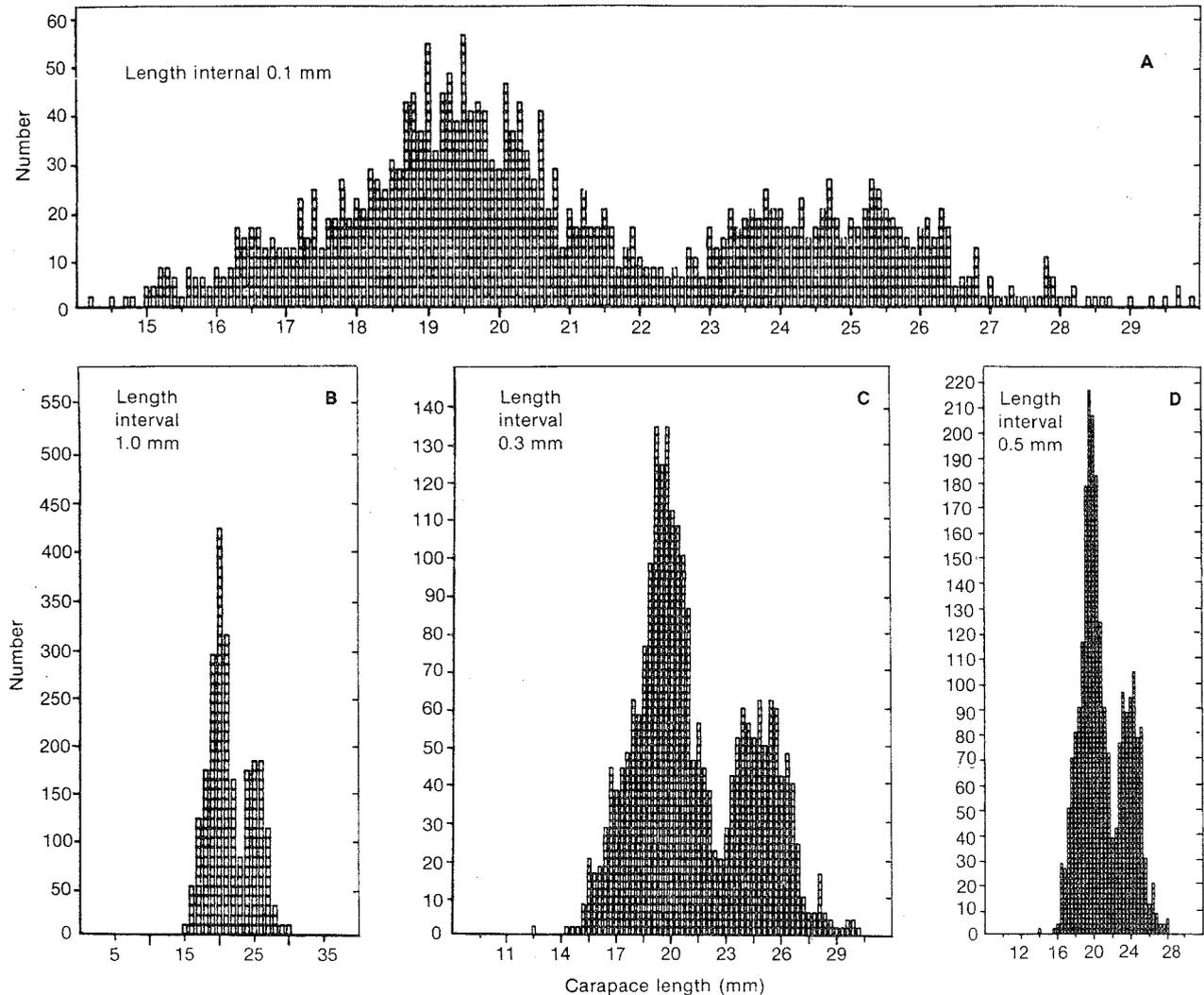


Fig. 2. Length distributions using different class intervals for a commercial sample ($N = 2,300$) of *P. borealis* from the Gulf of St. Lawrence, September 1980.

Combination of the data by 0.3 and 0.5 mm length intervals (Fig. 2C and 2D) appears to provide a better basis for definition of statistical parameters and separation of the modal groups. Use of moving averages (of three) significantly reduces the between-interval variation (Fig. 3) and provides further improvement.

Discussion of appropriate length intervals for measurement and data summarization resulted in two general conclusions. Firstly, the "optimal" length interval may depend on the nature of the investigation and vary from stock to stock (e.g. use of 0.5 mm interval may allow adequate separation of modal groups for some stocks but not for others). However, it was recognized that 0.5 mm has been the most commonly-used interval and that some of the historical data may not exist in any other form. Secondly, it is advisable to measure the carapace to the nearest 0.1 mm and subsequently combine the data to the preferred interval for analysis (e.g. 0.3 or 0.5 mm).

Stages of sexual development

Considerable information on age composition of shrimp samples can be gained by examining length frequency distributions of shrimp in different stages of sexual development. Males, transitionals and females can be readily separated by examining the endopod of the first pleopod (Rasmussen, 1953). According to McCrary (1971), females can be divided into first-time spawners (with sternal spines) and those which have spawned at least once previously (without sternal spines). Separation by stages of sexual development is demonstrated by a sample taken in Cartwright Channel off Labrador in July 1980 (Fig. 4). Three principal modal groups and the possibility of a fourth at 27 mm are apparent in these data. A breakdown of the sample by sex provides good differentiation of the male and female components, and separation of the females by presence or absence of sternal spines results in two modal groups which are not readily discernible in the overall length

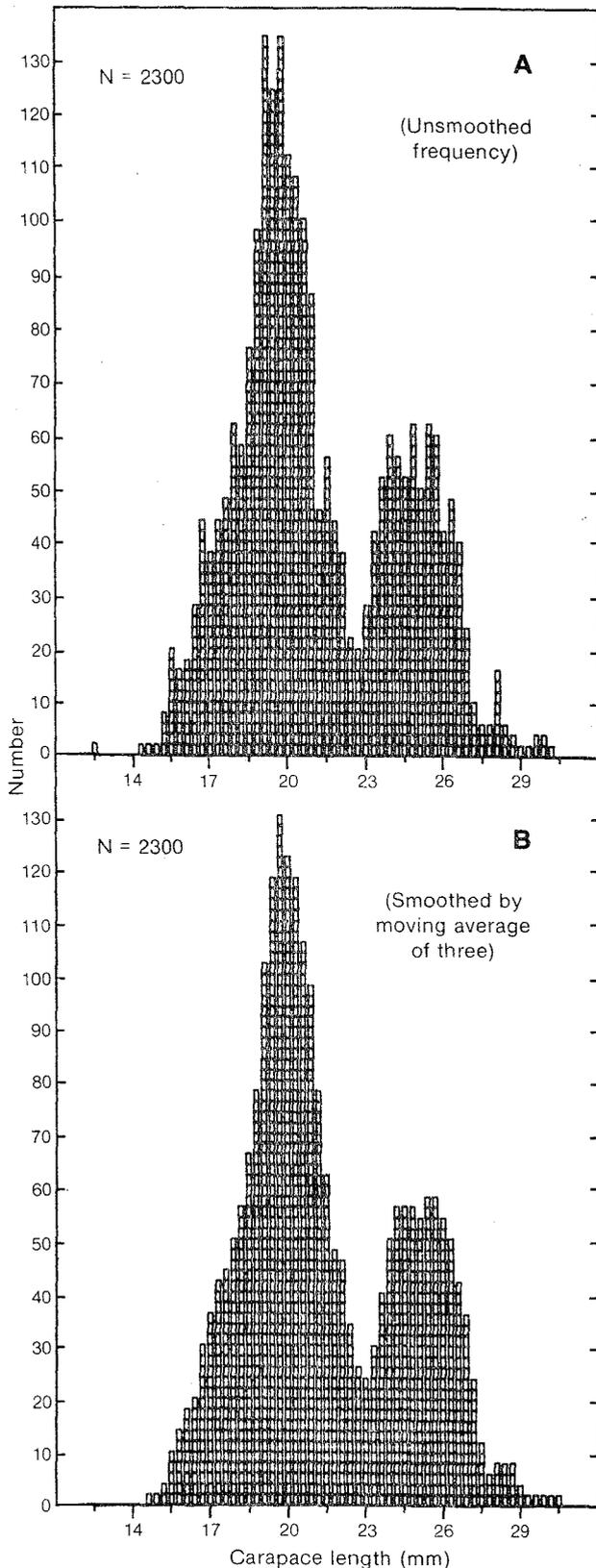


Fig. 3. Effect of smoothing (moving average of three) on a length distribution of *P. borealis* from the Gulf of St. Lawrence, September 1980. (Length interval = 0.3 mm.)

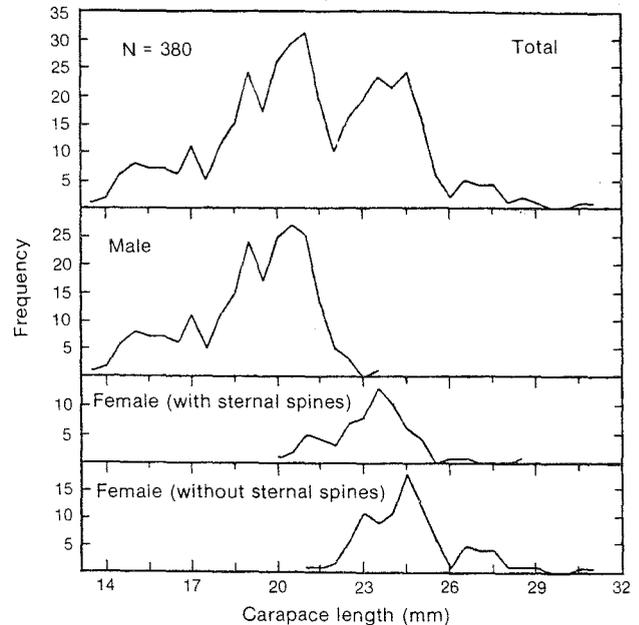


Fig. 4. Separation of the length distribution by stages of sexual development for a *P. borealis* sample from Cartwright Channel, Labrador, July 1980.

distribution. The size composition of transitionals with head roe was similar to that for females with sternal spines, and the two groups were considered to be a single cohort.

It is important, therefore, that the sampling process includes observations on stage of sexual development. Theoretically, if only one age-group of males is present and if transition of all individuals occurs at the same age, ages could be determined by observing sex and spawning characteristics alone. However, this situation may not occur often, as more than one age-group of males may be present and transition from male to female may occur over more than one age-group. Rasmussen (1953, 1969) reported that two modal length groups of transitionals often are present simultaneously in the Norwegian shrimp populations, and the same situation exists in the Gulf of Maine population (Fig. 5). In such cases, ageing should involve both the separation of modal groups statistically and data on stages of sexual development.

Because ovigerous females do not possess sternal spines, the separation of females into two groups by the presence or absence of these spines must be made prior to spawning. Data on the proportion of females with sternal spines from monthly sampling in the Gulf of St. Lawrence (Table 1) indicate that the best time for observing females with sternal spines is summer and early autumn in that area.

During discussion of data from shrimp populations in different areas, it became evident that there

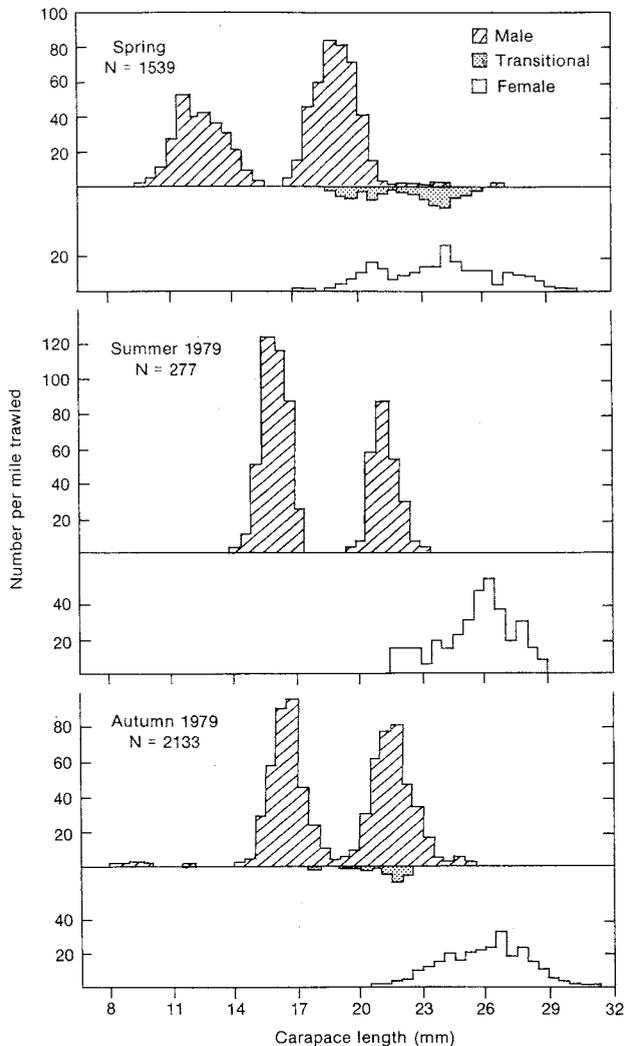


Fig. 5. Length distributions of *P. borealis* by sex from spring, summer and autumn bottom-trawl surveys in the Gulf of Maine, 1979. (S. H. Clark, Northeast Fisheries Center, Woods Hole, pers. comm.).

were differences in interpretation of the stages of sexual development based on condition of pleopods, sternal spines or gonads. For example, shrimp classified as transitionals by one investigator, based on the presence of secondary male characteristics on the pleopod, could be interpreted as first-year females by another researcher, based on the presence of head roe and sternal spines. The great diversity of items describing sexual development in shrimp is well illustrated by the classification scheme used by Danish scientists for shrimp off Greenland (Appendix II). No attempt was made to standardize interpretation of these stages, but the potential for ambiguity is clearly evident. It is important, therefore, that methodology used to evaluate sexual development stages in shrimp should be stated unequivocally when determinations are made.

TABLE 1. Percentage of female shrimp with sternal spines and berried females in samples from the Gulf of St. Lawrence in 1980.

Month	No. of samples	No. of females	Percent females	
			Spines	Berried
Apr	3	577	—	72.1
May	3	663	3.6	50.1
Jun	3	230	19.6	—
Jul	1	145	45.5	—
Aug	2	259	48.5	—
Sep	5	738	10.4	2.0
Oct	3	396	43.0	53.7
Nov	3	496	—	100.0

Sources of bias

Randomization of samples. Sampling methodology was considered to be very important in minimizing biases that are often associated with attempts to obtain representative length frequencies of the population. The most representative length frequencies are likely to be those obtained on board research vessels where samples may be taken directly from the trawl catches. Even in this situation, the shrimp may be segregated by size in the trawl codend, but the effect of this can be minimized by subsampling different parts of the catch.

On commercial fishing vessels, it is important that length frequencies be obtained from random samples of the catches, because samples taken at any time during the processing operation may not be representative of the actual catch due to sorting and discarding. Samples taken from landings of commercial vessels may be less useful than those taken at sea.

Stratification by depth. It is generally recognized that average size of shrimp increases with depth, except when ovigerous females migrate to shallow water (as in the Gulf of St. Lawrence and Gulf of Maine). This pattern of distribution is illustrated by length frequencies from three depth ranges in Davis Strait (Fig. 6) (Fréchet and Dupouy, MS 1979). Examination of the data by modal groups indicated a slight increase in average size with depth for each group (Table 2). However, an important consideration is the varying proportion of shrimp in the different modal groups. Consequently, the combination of samples from different depths should be considered with caution. Although the three major peaks are clearly evident when the data for all depth intervals are combined (Fig. 7), some information is lost, notably indications of bimodality in the second (male) and third (female) components (Fig. 6). If such data are used for average length-at-age determinations, weighted means should be computed over all depth intervals.

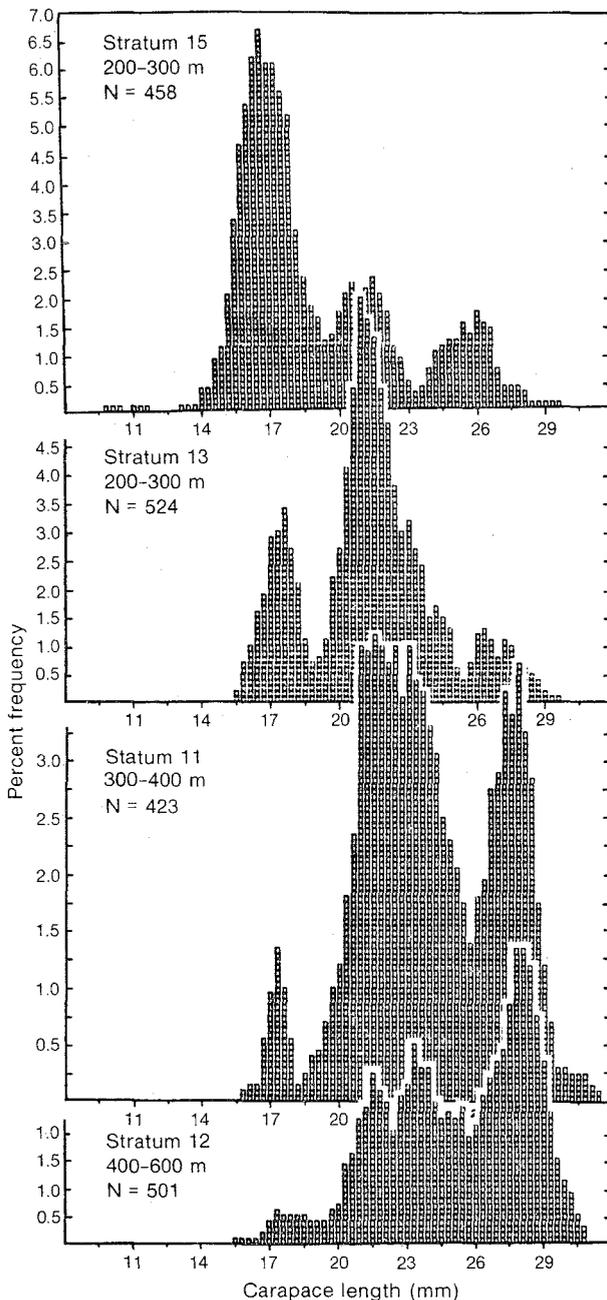


Fig. 6. Length distributions of *P. borealis* from different depth zones and strata in the southern part of NAFO Div. 1B in Davis Strait (from Fréchet and Dupouy, MS 1979).

Selectivity and availability. The mesh size in codends of shrimp research trawls usually range from 30 to 40 mm (stretched), and small-mesh codend liners are generally used in order to retain the smallest shrimp available in the fishing area. However, some escapement undoubtedly occurs through the large-meshed anterior parts of the trawl. Availability poses another problem in attempts to obtain representative samples of the population, because the youngest age-

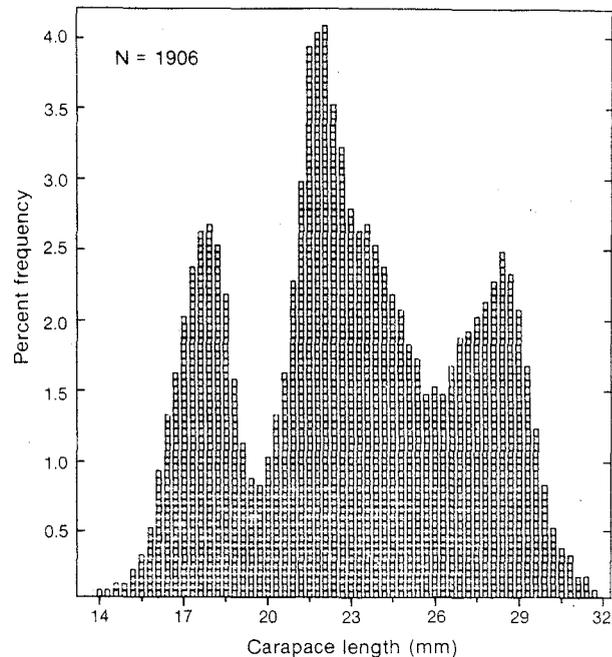


Fig. 7. Combined length distribution of *P. borealis* from various depths and strata in NAFO Div. 1B in Davis Strait (from Fig. 6).

TABLE 2. Mean carapace lengths for shrimp modal groups 1, 2 and 3+ and bottom temperature by depth and stratum off West Greenland (Div. 1B) in October 1979 (from Fréchet and Dupouy, MS 1979).

Depth (m)	Stratum No.	Mean length (mm)			Temp. (°C)
		1	2	3+	
200-300	6	15.9	21.3	26.1	2.9
	9	16.8	21.3	26.3	3.8
	13	17.3	21.0	26.5	3.7
	15	16.5	21.0	25.3	2.1
300-400	2	14.0	21.0	24.5	3.5
	4	15.0	22.0	26.0	3.5
	11	17.1	22.2	27.3	4.1
400-600	3	—	22.2	26.1	3.9
	12	17.3	22.5	27.6	4.4

groups may not be fully recruited to the surveyed fishing grounds. Extensive diurnal and seasonal changes in abundance have been reported for the Davis Strait population (Atkinson *et al.*, 1982). Consequently, estimates of shrimp abundance, particularly the youngest age-groups, may be underestimated, and estimates of mean length-at-age for the youngest age-groups may be biased upwards.

Correction for selectivity differences can be achieved by applying a selection ogive to increase the number of smaller animals to the level expected at full recruitment to the survey gear (Fig. 8). However, the results of selectivity studies can be quite variable

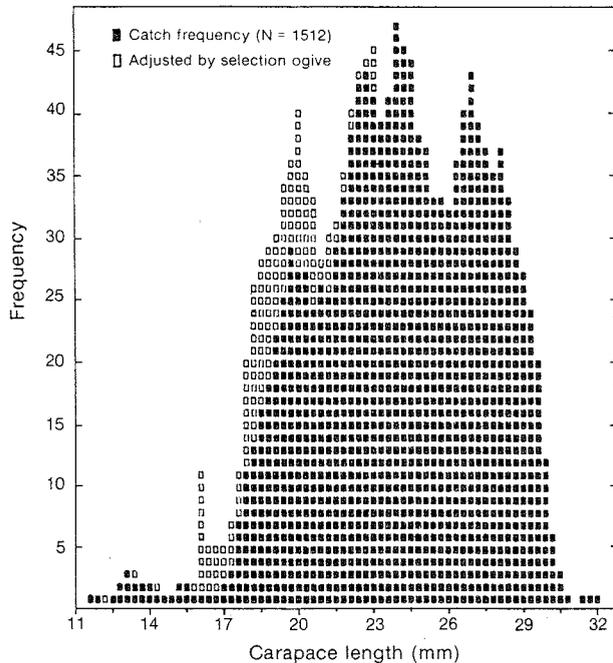


Fig. 8. Effect of adjusting a *P. borealis* length distribution by applying a selection ogive (from Fréchet and Labonté, 1981).

TABLE 3. Results of covered codend^a selection experiments for shrimp in the Gulf of Maine.

Year	Date	Retention lengths (mm) ^b		
		25%	50%	75%
1973	5 Jan	15.2	18.0	20.9
1973	5 Jan	13.5	18.0	22.6
1974	25 Sep	16.0	18.3	20.5
1974	25 Sep	16.2	18.6	20.9
1978	5 Jan	9.7	15.6	21.5
1978	23 Jan	12.8	15.6	18.5
1978	16 Mar	12.8	15.5	18.3

^a Covered codend tows were made with semiballoon otter trawl, with 5.8 m headrope, 6.9 m footrope, 38 mm mesh body, 31 mm mesh codend, and 12 mm mesh bag covering the codend.

^b Carapace lengths at 25%, 50% and 75% retention estimated from probit analysis of selection curves.

(Table 3), even in cases where gear, mesh size and experimental procedures have been carefully standardized (Sampson, MS 1979). Correction of selectivity differences cannot be expected to account for availability changes over time. Some correction for availability may be achieved through stratification of the survey area by depth. The above problems are encountered to a much greater extent when using samples of commercial catches, because of differences in mesh size and efficiency of trawls. Caution is therefore advised in determining year-class strength and mean length-at-age from such samples.

The potential for misinterpretation of the age of the first modal length group, due possibly to effects of availability or selectivity, is demonstrated in the length

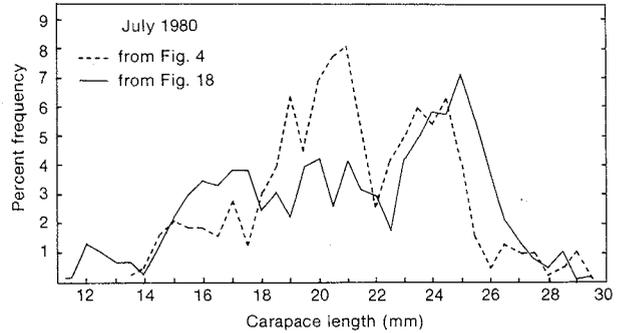


Fig. 9. Length compositions of two different samples of *P. borealis* from Cartwright Channel off Labrador, July 1980.

compositions of two samples from Cartwright Channel off Labrador in July 1980 (Fig. 9). Two groups of male shrimp are evident in one sample with modes around 15 and 20 mm carapace length, whereas three groups are evident in the other sample with modes around 12, 17 and 20 mm. In view of the differences in mean length of the modal groups of small shrimp, the possibility of misinterpretation of ages becomes apparent. Because the effect of selection by the gear is not well defined at these sizes of shrimp and information on early molting is lacking, the initiation of research on these problems is urgently required.

Diel variability. Evidence of diel vertical migration of *P. borealis* has been documented since the early 1900's (Allen, 1959). Such movement appears to be associated with pelagic feeding on various small crustaceans (Horsted and Smidt, 1956; Barr, 1970). However, other factors, such as the effects of tidal currents on the behaviour of shrimp and/or sampling gear, may also contribute to diel variation in catches (Parsons and Sandeman, 1981).

The problems encountered when sampling over 24-hr periods are evident from the length distributions illustrated in Fig. 10. Most obvious are the differences in numbers caught during periods of daylight and darkness, a phenomenon common to most shrimp fisheries (Carlsson *et al.*, 1978; Smidt, 1978; Jones and Parsons, MS 1978; Parsons and Sandeman, 1981). Also, the relative numbers in different modal groups vary from day to night. Barr (1970) found that the proportion of large shrimp in bottom trawl catches in Kachemak Bay, Alaska, increase at night, and that shrimp pots suspended vertically in the water column caught greater proportions of small shrimp than those set near the bottom. In samples of trawl catches from Hopedale Channel off Labrador, the average length of shrimp was smallest during daylight hours and largest around midnight (Fig. 11). Also, it has been demonstrated that ovigerous females do not undertake significant vertical migrations (Apollonio and Dunton, MS 1969; Jones and Parsons, MS 1978).

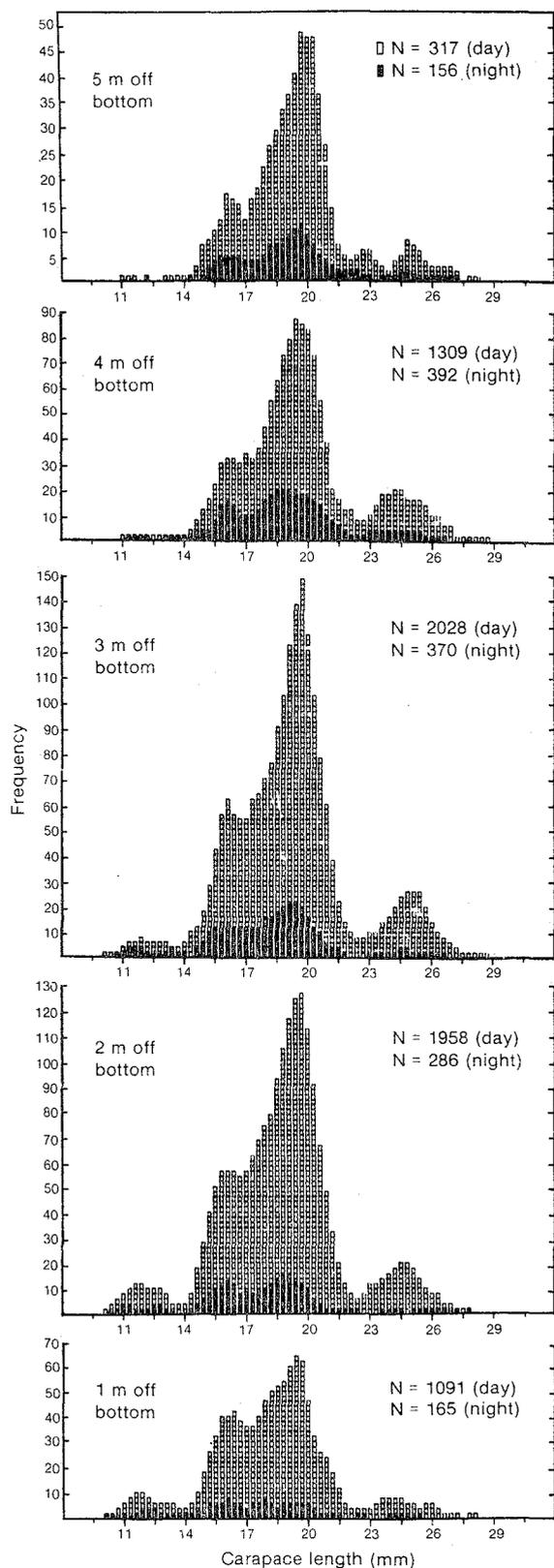


Fig. 10. Length compositions of *P. borealis* catches in a vertical sampler at 1-m intervals off the bottom during day and night sampling in the Gulf of St. Lawrence, 1980 (from Fr chet te *et al.*, 1981).

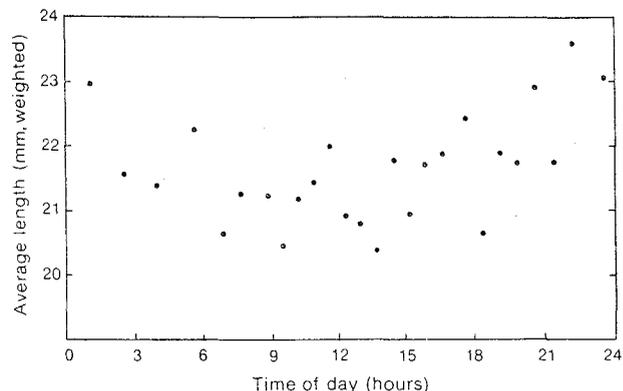


Fig. 11. Diel variation in average size of *P. borealis* from Hopedale Channel off Labrador, July 1981.

Although patterns of diel variation in shrimp catches are difficult to model and correction factors equally difficult to derive, such behavior should be considered when designing the sampling schemes. It is important that sampling be conducted at times when shrimp are most available to the research sampling gear, usually daylight hours.

Combination of length frequencies. Pooling of length frequencies, weighted by the numbers of shrimp caught, seems to provide the best representation of the size composition of the overall catch (or population), especially in cases where there is considerable variation in density by depth and time of day. However, such weighting may not be necessary for stocks in which these sources of variation are not considered important.

Weighting of length frequencies may be accomplished by any conventional method. In Alaska, for example, weighting was achieved initially by sampling a standard proportion of the catch by weight. Present sampling strategy involves weighting the length frequency of the sample from each trawl set by the number of shrimp caught, prior to pooling. Composite size distributions of shrimp in Alaskan waters, based on the latter procedure, are shown in Fig. 12 (Jackson *et al.*, 1981).

Additional considerations

Shrimp discards. Discarding of small shrimp generally occurs in all shrimp fisheries, particularly in offshore fisheries. The use of sorting machines on large trawlers sometimes results in high rates of discarding. Sampling the discarded shrimp often complements the information obtained from sampling catches before sorting (Derible *et al.*, MS 1980), because the younger age-groups may be more discernable (Fig. 13).

Weight frequencies. Interpretation of length frequencies is often difficult because of overlapping

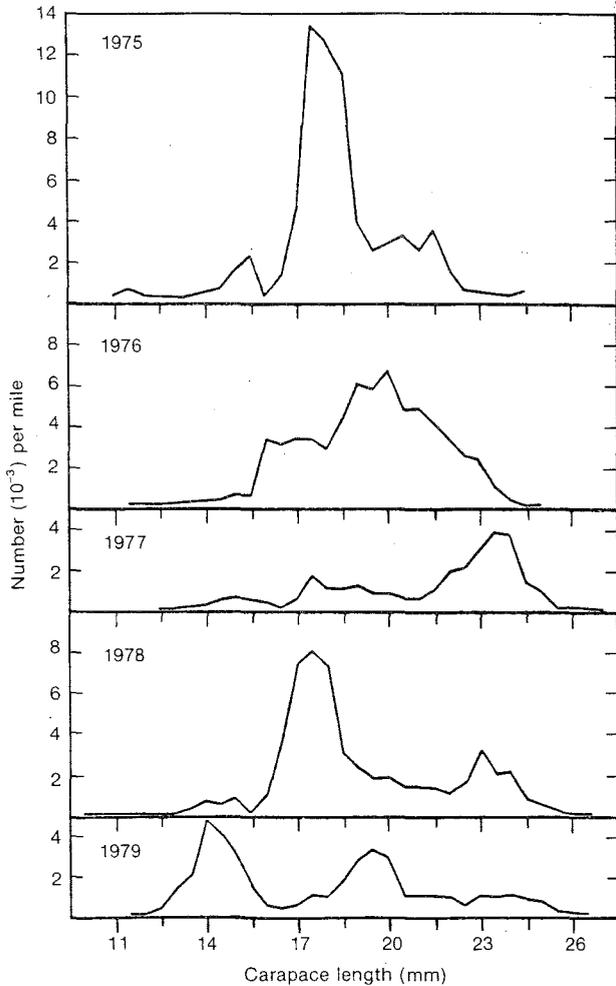


Fig. 12. Composite length frequencies of *P. borealis* from successive autumn trawl surveys of the Alitak Bay section of Kodiak District, Alaska, 1975-79 (from Jackson *et al.*, 1981).

modal groups, and weight frequencies may sometimes provide a clearer picture (Cormier and Labonté, MS 1980). Data for a shrimp sample from the Scotian Shelf are used to illustrate the size distributions by length and weight (\ln) intervals (Fig. 14) (R. J. Cormier, Marine Biological Research Centre, Moncton, New Brunswick, pers. comm.). The most obvious difference in the modal patterns is the lesser degree of overlap of the frequencies for transitionals and females in the weight frequencies. Although the results are not appreciably different in this case, the use of weight frequencies might be useful for separating modal groups in other situations. Investigation of the potential advantages of age-group separation based on dry weights is presently in progress.

In addition to length and weight, other morphometric characters could be collected with a view to their potential for age determination. Such data could be analyzed by appropriate statistical techniques, e.g. discriminant function analysis.

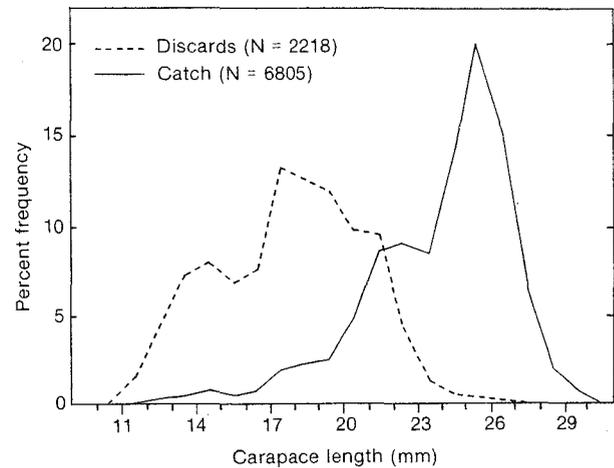


Fig. 13. Length frequencies of *P. borealis* in commercial samples of the total catch and the discarded portion of the catch in Davis Strait, July-August 1980 (from Derible *et al.*, MS 1980).

Separation of Modal Groups

Graphical methods

Most methods for ageing shrimp are expansions of the Petersen (1891) method which implies that the modes often present in length distributions represent different 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 fishery biologists, assumes that the size-at-age of animals is normally distributed. The cumulative size distribution is plotted on probability graph paper and the parameters of the modal groups are estimated so that the theoretical cumulative distribution closely agrees with the observed distribution.

The method of "successive maxima" (Gheno and LeGuen, 1968), which assumes only that the size at age is symmetrically distributed, is simpler than that of Cassie (1950, 1954). Other graphical methods include that of Tanaka (1962), which is based on fitting parabolas to 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 of analyzing data without the aid of high-speed computers, the results are not generally reproducible in that different analysts may obtain different results from the same set of data.

Application of the "successive maxima" method to data from a survey by the French research vessel *Thalassa* in Davis Strait in October 1979 is illustrated in Fig. 15. The resultant estimates of the parameters agree quite well with those obtained by applying Cassie's

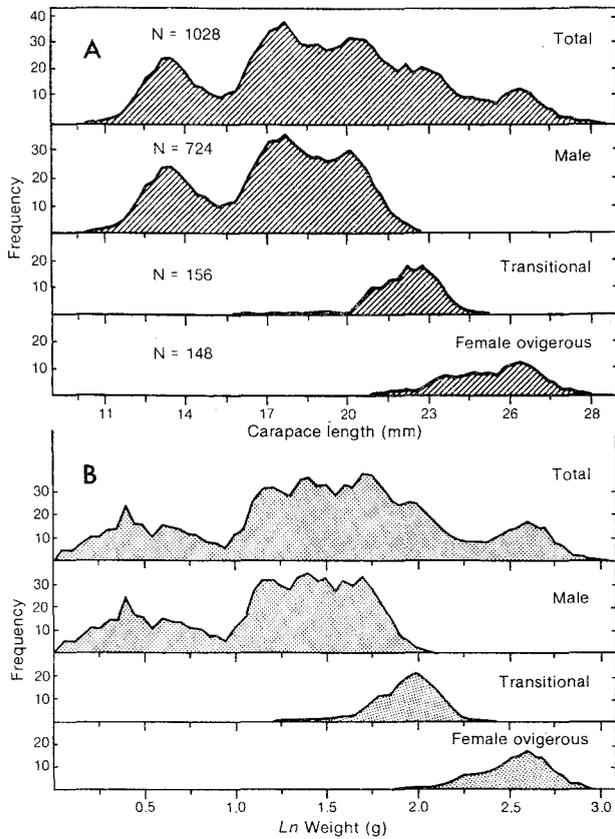


Fig. 14. Length (A) and weight (B) distributions by sexual maturity stages in a sample of *P. borealis* from the Scotian Shelf.

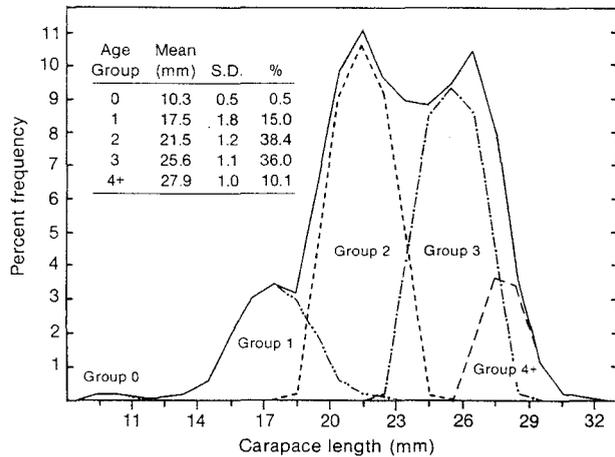


Fig. 15. Application of the "successive maxima" method (broken lines) to a length-frequency sample of *P. borealis* from the *Thalassa* survey in Davis Strait, October 1979.

method to the same set of data (Fig. 16). Cassie's method was also used by Minet *et al.* (1978) to separate modal groups and provide mean lengths of four age-groups of *P. borealis* sampled during a survey off Cumberland Sound, Baffin Island, in September–October 1977. Mean lengths and standard deviations can be readily calculated for the modal groups derived by both graphical methods. However, these methods are

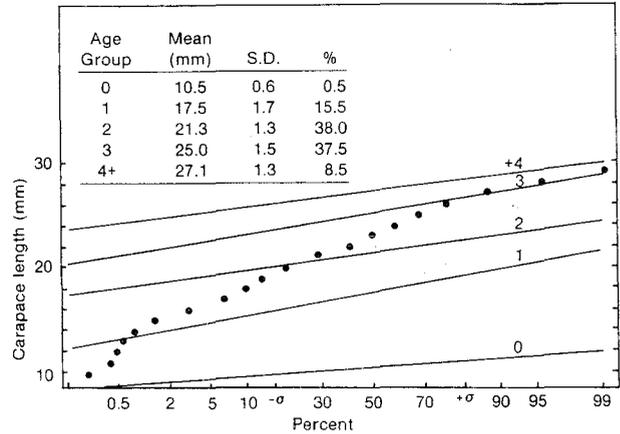


Fig. 16. Application of the Cassie (1950, 1954) method to the length-frequency sample of *P. borealis* shown in Fig. 15.

very sensitive to asymmetry of the youngest age-groups due to the selectivity problem, and they should be used with caution when there is considerable overlap of the age-groups.

Analytical methods

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

MacDonald and Pitcher (1979) developed a more elaborate program for computing maximum likelihood estimates of 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, estimates of the mean, standard deviation and number of individuals for each component are produced. Advantages of the MacDonald and Pitcher (1979) computer program are its versatility in constraining parameters and the availability of an interactive version.

Schnute and Fournier (1980) have expanded the MacDonald and Pitcher program to constrain the estimates of mean size-at-age and standard deviation 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.

An important feature of all three programs noted above is that they employ a chi-square test for goodness-of-fit.

Application of Hasselblad method. A shrimp sample from the Gulf of St. Lawrence in July 1979 was used to illustrate the application of this method using the NORMSEP computer program (Fig. 17). Four modal groups, assumed to be age-groups 1, 2, 3 and 4+, were identified, the first two groups consisting of males and the last two groups primarily of females. The resultant calculations include the mean length, standard deviation, and estimated number of individuals for each age-group (Table 4).

The use of biological characters (presence or absence of sternal spines, and sex) in conjunction with the separation of modal groups of NORMSEP provides a more refined breakdown of the length distribution. The analysis involved three steps: (a) simple separation of females into two components based on presence or absence of sternal spines; (b) separation of the overall length distribution in modal groups by NORMSEP; and (c) separation of the individuals by sex followed by separation of the modal groups by NORMSEP for each sexual component. The results of the analysis are given in Table 5. The breakdown by sex in the last step before applying NORMSEP indicates that the third modal group consists of approximately 30% males, implying a possible delay in transition. The application of NORMSEP only to the length distribution of males indicates that the third modal group consists of 38 individuals. The addition of this male component to the first female component (87 individuals) gives a number for this age-group which is similar to that (121) obtained by applying NORMSEP to the overall length distribution. In addition, separation of females by sternal spines gave numbers ($F_1 = 85$, $F_2 = 106$) which are very similar to the results obtained when NORMSEP was applied separately for females ($F_1 = 87$, $F_2 = 104$). These observations are important because they indicate that sternal spines may be used to separate females into two age-groups in cases where accurate separation of modal groups cannot be achieved by analytical methods due to extreme overlap of the groups.

TABLE 4. Results from application of NORMSEP to a shrimp length frequency from the Gulf of St. Lawrence, July 1979 (Fig. 17). (From Fréchet and Parsons, MS 1981).

Age-group (yr)	Mean length (mm)	Standard deviation	Percent	No. of shrimp
1	14.5	1.15	43.2	380
2	18.4	1.27	29.0	255
3	21.8	0.91	13.8	121
4+	24.7	1.35	14.0	123

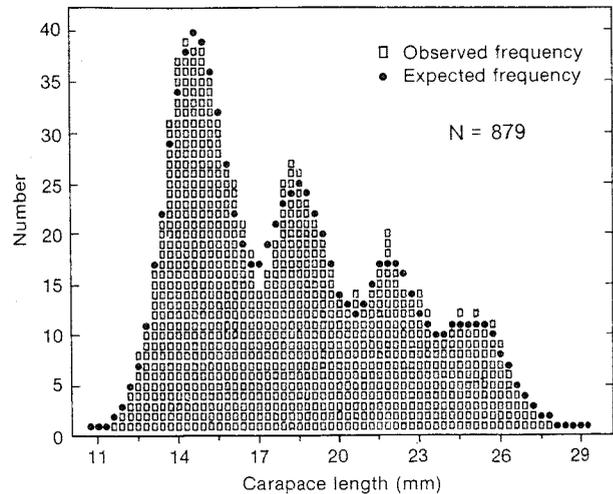


Fig. 17. Application of the Hasselblad (1966) method (NORMSEP) to a length-frequency sample of *P. borealis* from the Gulf of St. Lawrence, July 1979 (from Fréchet and Parsons, MS 1981).

The above analysis implies that statistical and biological techniques should be used conjunctively, especially in situations where reproductive evolution is not synchronous for all individuals. This approach often permits greater degree of resolution and more accurate interpretation of the population age structure. Therefore, data on sexual development should be collected routinely and used to complement investigations involving age determination of shrimp by analytical methods.

Application of MacDonald and Pitcher method.

This method was applied to a sample of shrimp taken in July 1980 from Cartwright Channel off Labrador, and five age-groups were interpreted from the length distributions (Fig. 18). Initial estimates of the proportions, mean lengths and standard deviations were used as input and the computer analysis proceeded until a minimum chi-square value was obtained. Application of NORMSEP to the same data produced essentially the same results in terms of mean length and proportion of shrimp constituting the modal groups (Table 6).

TABLE 5. Use of NORMSEP results and sexual development stages in separating modal groups of shrimp for the sample analyzed in Table 4. (M = males, F_1 = females with sternal spines, F_2 = females without sternal spines.)

Age-group (yr)	Sex	Separation by sexual stages	Separation by NORMSEP (all data)	Separation by sex and NORMSEP ^a
1	M	688	380	346
2	M		255	304
3	M	85	121	38
4+	F_2			106

^a NORMSEP was applied to males and females separately.

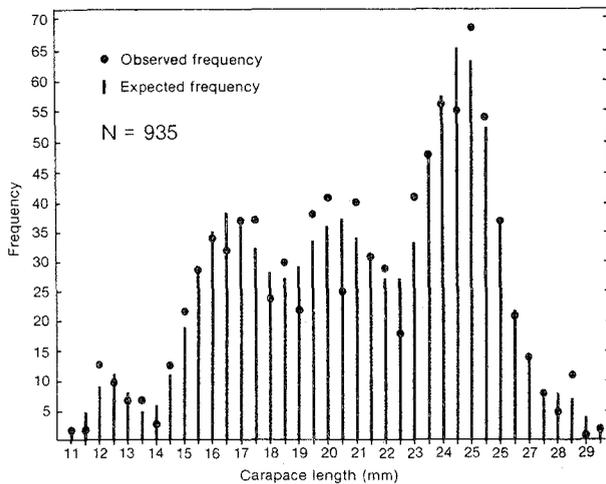


Fig. 18. Application of the MacDonald and Pitcher (1979) method to a length-frequency sample of *P. borealis* from Cartwright Channel, Labrador, July 1980.

Relatively small standard errors were associated with the final estimates by the MacDonald and Pitcher method, and the chi-square values for both methods indicated no significant difference between the observed and estimated parameters ($P > 0.05$). Similarity of results from the two methods can be expected because the analytical processes are essentially the same.

The deviation method

An entirely different approach to interpretation of length distributions, that seems antithetical to the Petersen-type analysis, was first used by Sund (1930) with cod length frequencies and modified for use with shrimp by Skúladóttir (1981). The method is based on the deviations formed when the length distribution in a certain month (or any period when growth does not occur) is subtracted from the mean length distribution in the same month over several years. For shrimp, positive deviations observed in successive millimeter length groups are considered to represent a strong year-class and negative deviations a weak year-class. Age interpretation 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 the Icelandic shrimp samples as the Petersen method.

Figure 19 illustrates monthly length distributions of shrimp sampled during 1961–77 in Arnarfjörður, a cold-water threshold fjord of northwest Iceland. Appearance of modal groups and their relative abundance indicates that recruitment is quite variable. This is especially evident when comparing abundance of the 1962 year-class (mode at 10 mm in April 1964) with other year-classes. The deviation method is very appropriate for analyzing such data, because it is based on tracking strong year-classes. Analysis of the

TABLE 6. Comparison of results from application of MacDonald and Pitcher and NORMSEP methods to a shrimp sample from Cartwright Channel off Labrador in July 1980 (see Fig. 18).

Age-group	MacDonald and Pitcher		NORMSEP	
	Mean length ± SE (mm)	Percent frequency ± SE	Mean length (mm)	Percent frequency
1	12.2 ± 0.16	3.9 ± 0.8	12.1	3.9
2	16.2 ± 0.30	23.7 ± 5.3	16.2	24.0
3	20.1 ± 0.28	29.1 ± 8.1	20.1	28.6
4	24.4 ± 0.14	40.7 ± 4.4	24.4	40.7
5+	28.1 ± 0.36	2.5 ± 1.0	28.0	2.9
		$\chi^2 = 30.6$ (df = 24)	$\chi^2 = 34.4$ (df = 24)	

deviations is shown in Fig. 20. The displacement of deviations along the horizontal (length) axis is indicative of growth. In this stock, strong year-classes can be followed up to 9 years (Fig. 20). No complex calculations are involved in estimation of mean length-at-age. Investigations contemplating the use of the deviation method for analysis of other shrimp stocks should carefully evaluate it on a trial basis relative to other methods.

Analysis of Workshop Sample

A sample of 414 shrimp from Anticosti Channel in the Gulf of St. Lawrence was analyzed in order to illustrate the procedures for measuring, sexing and ageing, as described above. Vernier calipers were used to measure carapace lengths to the nearest 0.1 mm, and weights of individuals were recorded to the nearest 0.1 g. The shrimp were separated into three categories according to stage of sexual development: males (M), females with sternal spines (F_1), and females without sternal spines (F_2). No transitionals were observed in this sample which was obtained in July 1980.

The data were grouped by 0.3 mm intervals and length frequencies were constructed for the three sexual stages without smoothing (Fig. 21A) and by moving average of three (Fig. 21B). The latter procedure reduced considerably the variation evident in the unsmoothed data. Cut-off points (15.35, 21.25 and 25.85 mm) and lower and upper bounds of means (12.2–15.2, 15.7–21.0, 21.5–25.5 and 26.0–28.7) were estimated for the four modal groups evident in the total smoothed data (Fig. 21B) and were used as input for the NORMSEP program which was applied to the unsmoothed data (Fig. 21A). The results of modal group separations by NORMSEP and by sexual maturity stage are given in Table 7. These data show that the number of males estimated by NORMSEP for the first two modal groups (284) is very similar to the actual number of males in the sample (289). The overlapping groups of females with and without sternal spines (designated as age-groups 3 and 4) could not be distinguished by NORMSEP, and means and deviations of

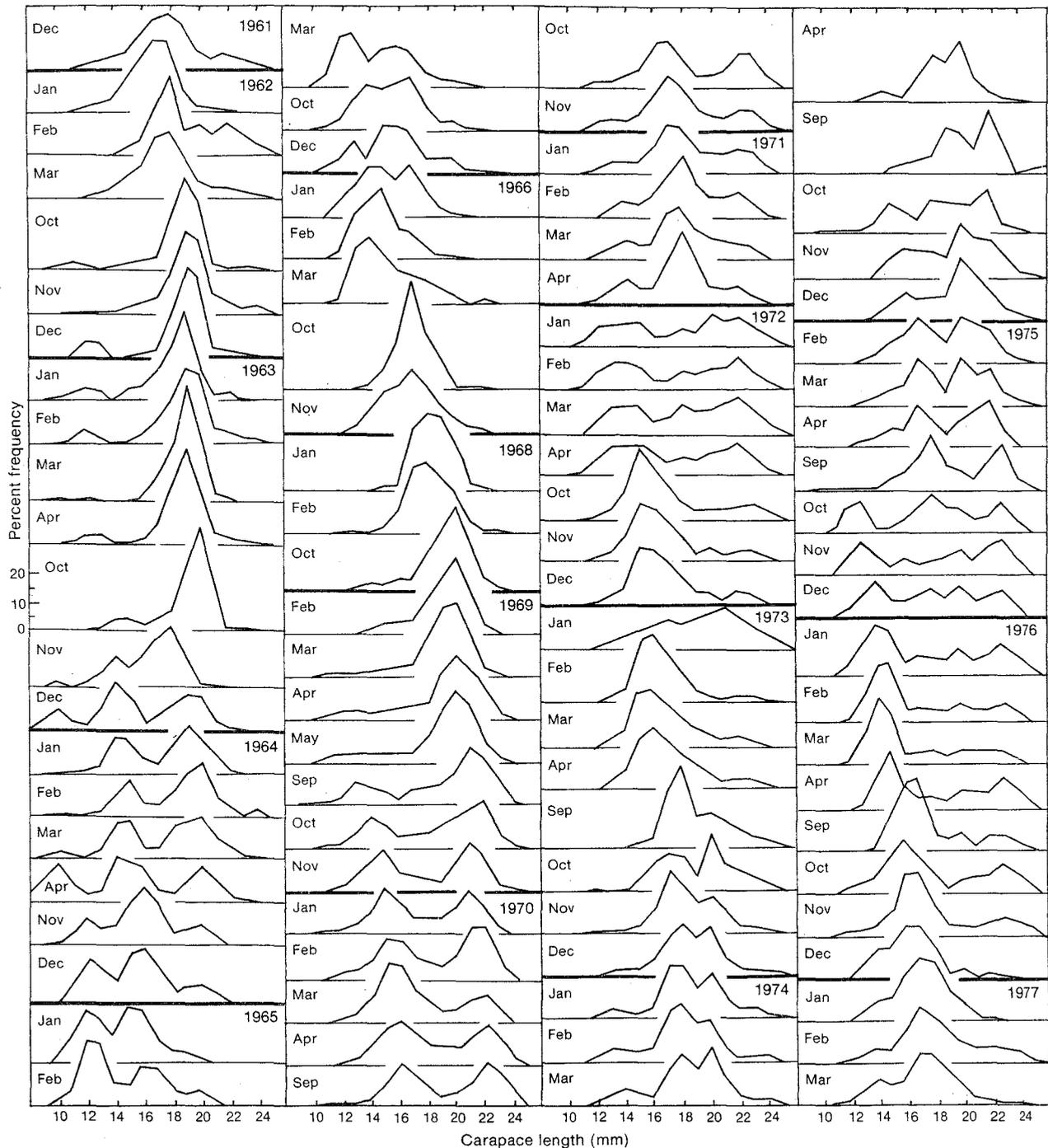


Fig. 19. Monthly length frequencies of *P. borealis* in Arnarfjörður, Iceland, 1961-77 (from Skúladóttir, 1981).

these groups were therefore derived from the biological observations. However, interpretation of the group with sternal spines as a year-class may be questionable in this case, because synchronism of sex change for all individuals of a year-class, may not be a general rule. Other interpretations of the data are also possible.

The NORMSEP program, with the same input parameters noted above, also was applied to the total smoothed (running average of three) length frequency (Fig. 21B) for comparison with the results from its application to the unsmoothed length frequency (Table 8). The biological observations on sexual devel-

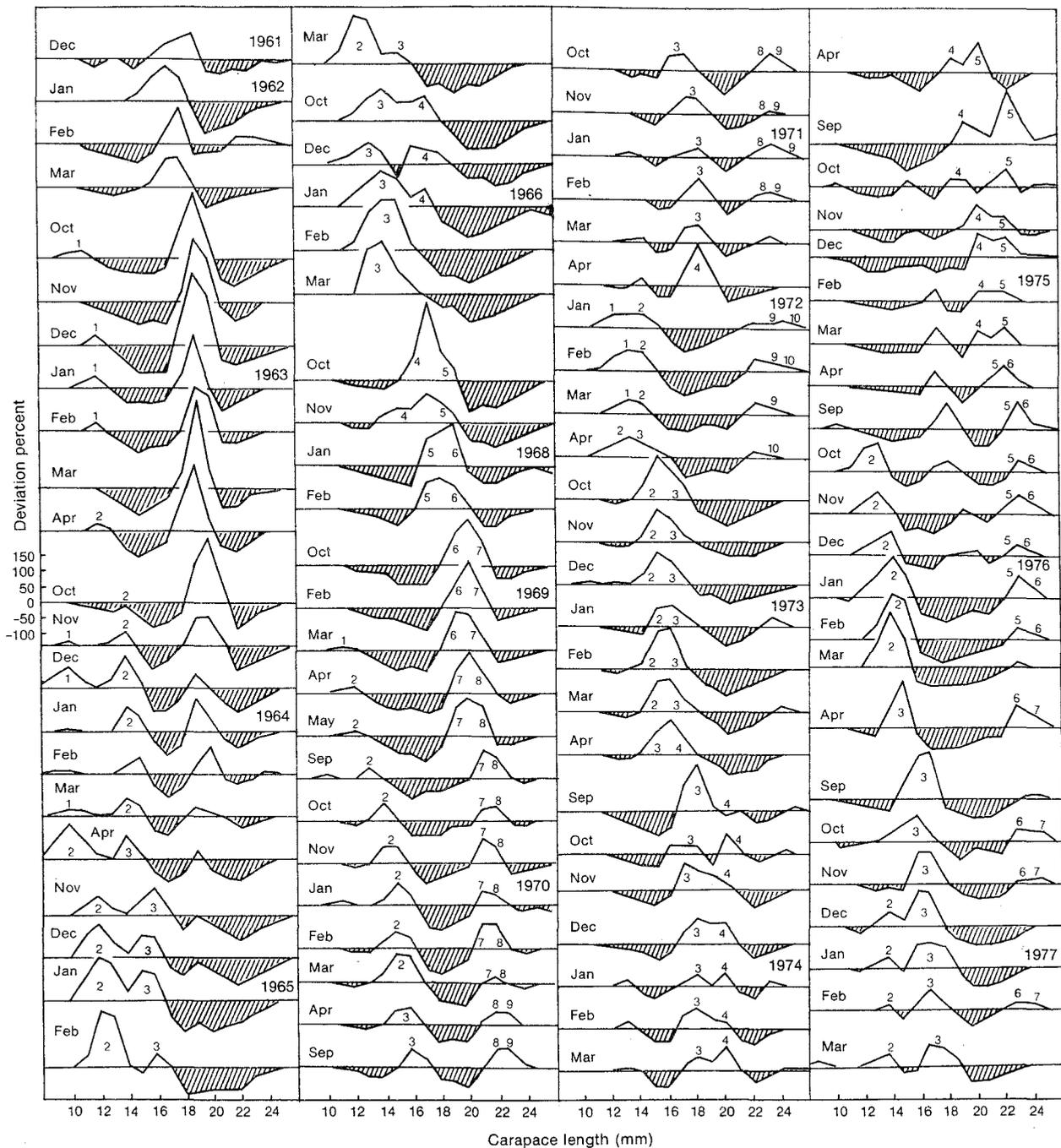


Fig. 20. Deviations of the monthly length frequencies of *P. borealis* illustrated in Fig. 19 (from Skúladóttir, 1981).

opment were not used for this comparison and consequently only four modal groups (not five) are compared. The mean lengths and proportions of these groups were very similar for both treatments, but the chi-square value for the smoothed data has no statistical meaning because the tabulated probability levels are not applicable. The workshop participants recognized that the goodness-of-fit, indicated by chi-square for unsmoothed data, may often be greatly influenced by anomalous data points and that the chi-square gen-

erated by analytical methods should not be necessarily considered as a critical value.

Examination of the weight (Fig. 22) did not provide any additional information about the age structure of the sample. Grouping of the data by larger weight increments to minimize frequency variation was not attempted due to time limitations, which also precluded the technique of log transformation (Cormier and Labonté, MS 1980).

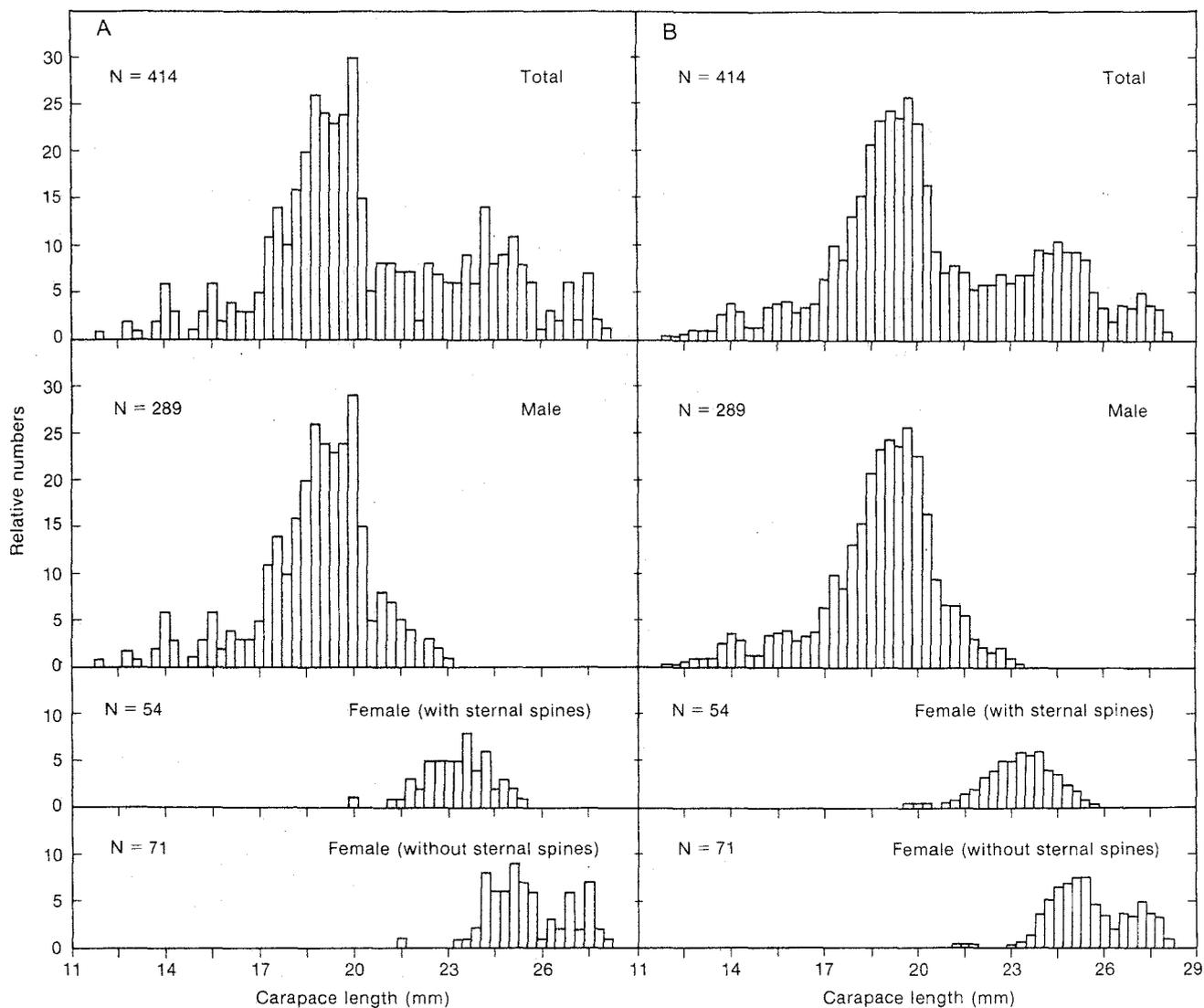


Fig. 21. Separation by sexual maturity stages of the workshop sample of *P. borealis* from Anticosti Channel in the Gulf of St. Lawrence, July 1980: **A**, actual length frequencies; **B**, smoothed by moving average of three.

TABLE 7. Number of shrimp and mean length by age-group based on application of NORMSEP and sexual development stages to the workshop sample from the Gulf of St. Lawrence in July 1980 (Fig. 21). (M = males, F₁ = females with sternal spines, F₂ = females without sternal spines.)

Age-group (yr)	Sex	Separation by NORMSEP method	Separation by sexual stages	Combined analysis		Mean length (mm)
				No.	%	
1	M	35	289	35	8.5	14.9
2	M	249		249	60.3	19.0
3	F ₁	112	54	54	13.1	23.2
4	F ₂			58	14.0	24.8
5+	F ₂	17	71	17	4.1	27.1

Estimation of Biological Parameters

Year-class strength

If the age composition of samples is assumed to adequately represent the age structure of the population, relative abundance by age-group can be deter-

mined by separating an abundance index into its respective components. However, caution must be used in interpreting the results for shrimp due to availability and selectivity of the younger age-groups and to age-class accumulation in the last modal group of large females.

TABLE 8. Result of NORMSEP application to unsmoothed and smoothed length frequencies for the workshop sample of shrimp from the Gulf of St. Lawrence, July 1980. (Data smoothed by running average of three; length interval is 0.3 mm; sexual development stages were not applied.)

Age-group (yr)	Unsmoothed data		Smoothed data	
	Mean length (mm)	Percent frequency	Mean length (mm)	Percent frequency
1	14.9	8.6	14.9	8.8
2	19.0	60.2	19.0	59.8
3	23.9	27.2	24.0	27.6
4+	27.1	4.0	27.2	3.7
$\chi^2 = 45.7$ (df = 36)		$\chi^2 = 11.1$ (df = 36)		

Year-class abundance was estimated for the shrimp population in the Gulf of St. Lawrence, based on data collected during surveys by Canadian research vessels in 1977-80 (Fr chet and Parsons, MS 1981). Age-groups were determined by using NORMSEP in conjunction with maturity data for females. In addition to separating two groups of females by sternal spines, NORMSEP was used to separate the female groups when two modes were obvious. Table 9 presents abundance by age-group, obtained by relating density to age-group separation in samples. As noted earlier, age-groups 0 and 1 may not have been fully available to the sampling gear. Despite this problem, however, the presumed 1978 year-class appears to have been more abundant during the surveys than any other year-class. Prediction of recruitment may therefore be possible from repetitive surveys.

The same methodology was used to estimate catch-at-age of the Gulf of Maine shrimp stock from data collected during research vessel surveys in the summers of 1972-81 (Schick *et al.*, MS 1981). Similar problems of availability and selectivity were encountered (Table 10), possibly associated with the low levels of sampling. Variability in year-class abundance precludes any inference about relative year-class strength. The major problem, associated with the data in Table 10, was the interpretation of ages by using sternal spines. The presence of two modal groups of transitionals in the Gulf of Maine (Fig. 5) complicates the analysis, and separation of age-groups by sternal spines may not be valid.

Growth

Much research has been done on growth of *P. borealis*, based on Petersen's (1891) method of interpreting length distributions. A new method of estimating growth of inconspicuous year-classes, by utilizing sexual maturity of females and data on growth of strong year-classes from the deviation method (Sk lad ttir, 1981), is presently being developed for Icelandic shrimp. The method assumes that sexual maturity of

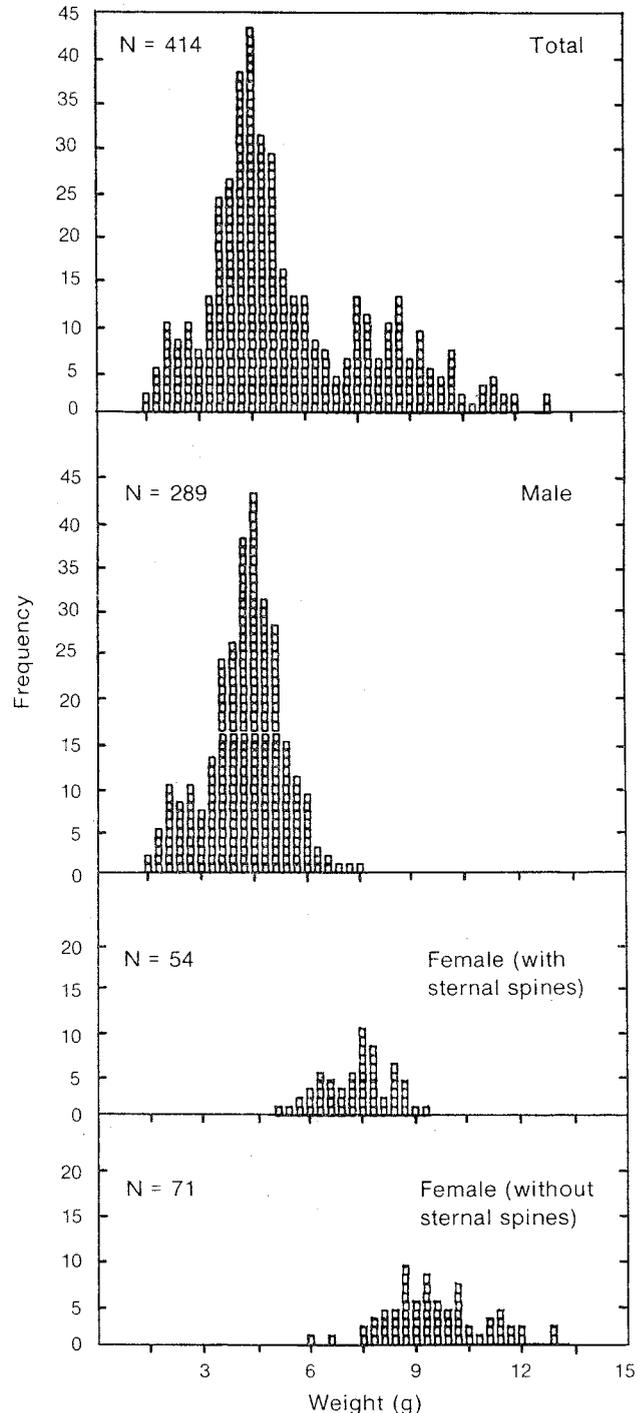


Fig. 22. Separation of sexual maturity stages of the weight frequency for the workshop sample of *P. borealis* from Anticosti Channel in the Gulf of St. Lawrence, July 1980.

females is related to growth, as observed for the strong year-classes. Growth patterns for some slow-growing and fast-growing year-classes at Arnarfj rdur, Iceland, are shown in Fig. 23. Growth varies considerably within the different slow-growing and fast-growing year-classes but the reason for such variation is unknown.

TABLE 9. Abundance estimates by age-group based on application of NORMSEP and sexual maturity stages to length composition data for a shrimp population in the Gulf of St. Lawrence. (From Fréchet and Parsons, MS 1981.)

Year	Numbers by age-group (millions)				
	0	1	2	3 or 3+	4+
1977	53	486	653	545	...
1978	266	368	720	626	...
1979	90	731	579	517	337
1980	23	202	1,230	597	344

Estimates of growth of fast-growing and slow-growing year-classes could be derived from the results of any method of age-group separation. However, the significant point is that bias may be introduced, if there is evidence of fast-growing and slow-growing groups in the population being studied and such data are combined to construct a general growth curve for the stock.

The von Bertalanffy growth equation often has been used to represent growth of shrimp. Although the model may not be strictly applicable due to the discontinuous growth pattern associated with molting, it appears to provide reasonable approximation. In the absence of more definitive biological data, use of the equation with length-at-age and weight-at-age data derived by the age-group separation methods described above is considered appropriate, although there exists the potential for bias associated with incomplete recruitment of the youngest age-groups and with the difficulty in assigning ages to the oldest shrimp.

A method of estimating von Bertalanffy growth parameters from analysis of length-frequency data has been developed (Pauly and David, 1980; Gaschütz *et al.*, MS 1980). A computerized version of this method termed "ELEFAN 1" exists (Pauly *et al.*, 1980) and it should be evaluated for analyzing growth in shrimp.

Mortality

The estimation of instantaneous mortality rates (Z) for shrimp is possible from abundance indices by

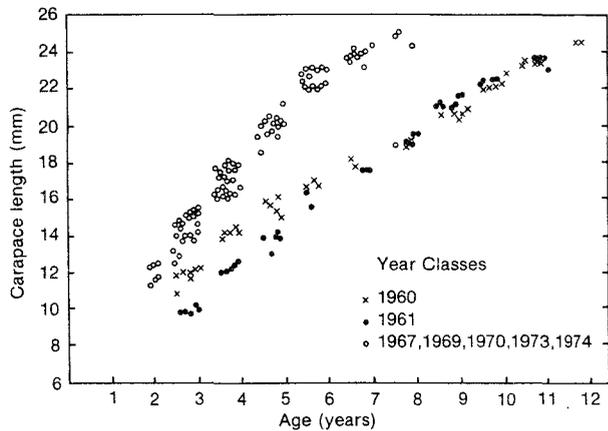


Fig. 23. Growth curves, derived by the Deviation Method, for two slow-growing year-classes (1960, 1961) and five fast-growing year-classes (1967, 1969, 1970, 1973, 1974) of *P. borealis* from Arnarfjörður, Iceland (from Skúladóttir, 1981).

age-groups (e.g. Tables 9 and 10), if an adequate time series of data is available. If abundance of the youngest age-groups is biased by selectivity and availability, total mortality estimates can be obtained for the fully recruited age-groups. Labonté (MS 1979) illustrated two hypotheses involved in estimating mortality for a shrimp population in the Gulf of St. Lawrence from estimates of abundance by age-groups (Fig. 24). The hypothesis, which takes into account the accumulation of age-classes in the last modal group of females (indicated by the occasional appearance of polymodality and by analysis of weight frequencies), was considered to be applicable to the northern shrimp stocks.

Several researchers have attempted to estimate instantaneous natural mortality (M) for *P. borealis*. Data for the stock north of Anticosti Island in the Gulf of St. Lawrence (Table 9) were used by Fréchet and Parsons (MS 1981) to estimate M under the assumption that fishing mortality (F) was very low. Other estimates were derived from research catch-at-age data for the Sept-Iles stock in the Gulf of St. Lawrence (Labonté, MS 1979; Fréchet and Labonté, MS 1981). In both

TABLE 10. Average catches (numbers) of shrimp per 30-min tow for August surveys in the Gulf of Maine, with separation by age (assumed) based on sexual characteristics and application of NORMSEP to trimodal length distributions. (Chi-squares were significant for all NORMSEP analyses.)

Year	Ages based on sexual stages				Ages based on NORMSEP		
	1	2	3	4	1	2	3+
1972	262	635	305	94	254	649	393
1973	1,087	642	208	134	1,079	643	349
1974	542	337	157	72	566	302	241
1975	112	544	255	134	114	537	394
1976	462	206	118	78	454	233	178
1977	121	47	63	24	120	61	75
1978	270	121	40	82	271	127	115
1979	226	306	76	38	227	313	106
1980	332	66	48	21	334	72	62
1981	159	160	60	55	159	154	121

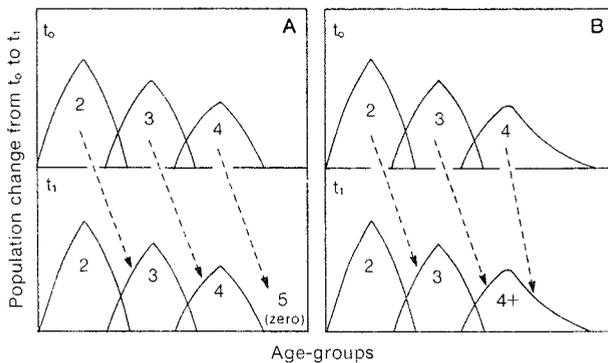


Fig. 24. Theoretical evolution of the age structure of a shrimp population from year t_0 to year t_1 , assuming (A) that the last modal group (IV) represents a single year-class, and (B) that the last modal group (IV+) represents several year-classes (from Labonté, MS 1979).

areas studied, M was estimated in the range of 0.5–0.8. For two stocks in Iceland waters, Skúladóttir (1979) estimated M at 0.24 and 0.50 by cohort analysis and catch curves respectively. Andersen (1981) reported a total mortality of 0.66 for a year-class of *P. borealis* in Pavlof Bay, Alaska, which adds some support to the above results, although large variation in the estimates was noted. Because of uncertainty in interpretation of age by modal analysis, estimates of mortality obtained by these methods must be considered with caution.

Predation on shrimp by various species of fish is considered an important component of natural mortality. In Iceland waters, predation by Atlantic cod has the effect of dispersing shrimp (U. Skúladóttir, Marine Research Institute, Reykjavik, Iceland, pers. comm.). In Canadian waters, abundance and distribution of shrimp and Greenland halibut seem to be related (Bowering and Parsons, MS 1981; Fréchette, MS 1982).

Other Considerations

Tagging

Few attempts have been made to tag *P. borealis*. Some tagging of this species has been carried out at West Greenland but the number of recoveries has been small. Other shrimp species have been marked successfully with a variety of tags. Penaeid shrimp are routinely tagged with a vinyl streamer inserted through the abdominal musculature. A tagging program using similar tags and techniques has been implemented by Icelandic scientists. The *P. borealis* stock of East Greenland has been proposed for the implementation of a tagging study to determine migration patterns of the various size-groups of shrimp (NAFO, 1981).

Length measurements by electronic devices

The workshop participants noted that electronic calipers have been developed, which allow direct

accumulation of measurements through an interface with a micro-computer (McAllister and Planck, 1981). Use of this device eliminates manual tabulation and subsequent key-punching of data for input to computers.

Conclusions

Age interpretation

Several problems concerning interpretation of ages of shrimp were identified. There is a general lack of information on molting frequency and associated implications with respect to growth. This information is needed if ageing by application of graphical and analytical methods is to have any real biological meaning. Data on larval growth and size when settling occurs is also necessary to supplement data on the size of the youngest age-group occurring in the samples. Selectivity and availability problems may also contribute to discrepancies in interpretation of the age of the first modal group. The interpretation of spawning characteristics differ among researchers, in that the observed modal group of females with sternal spines may sometimes include transitionals of similar size and be considered the same age or as slow-growing or fast-growing components of adjacent modal groups. If age-groups do, indeed, have slow-growing and fast-growing components, bimodality of an age-group will complicate the modal analysis to the point where it may be meaningless without complete understanding of biological events. The problems lie not so much with the graphical and analytical methods of analysis as with the interpretation of the modal groups, which is the direction that future research on ageing of pandalid shrimps must take.

Age-class accumulation in the last prominent modal group of observed length distributions is the generally-accepted hypothesis. Some evidence for this is provided by studies on the presence or absence of sternal spines and the polymodality of weight distributions of the female group. Natural mortality values used in predicting yields of *P. borealis* often have been relatively high under the assumption that spawning mortality is very high. In cases where age-class accumulation was not taken into consideration, natural mortality may have been significantly overestimated with consequent effects on the estimates of potential yield. Prediction of recruitment and estimation of growth parameters are also important for assessment of shrimp stocks. Such information can be derived from length and age compositions of the catches provided that the techniques used to collect and analyze these data are geared to give representative results.

Management implications

The uncertainty inherent in estimates of biological parameters for shrimp due to lack of reliable ageing

techniques greatly limits the applicability of traditional assessment methods. Little information is available on natural mortality, and yet the assessment techniques used to provide advice for management are very sensitive to changes in this parameter (e.g. equilibrium yield models). The situation is further complicated by variability in natural mortality over the fishable lifespan of the species and also by year-to-year variability associated with predation and other factors. Uncertainty with respect to natural mortality and other parameters has necessitated the use of "reasonable" ranges of estimates in assessment models, thus leaving the results of the analyses open to considerable latitude in interpretation when management decisions are being formulated. Such uncertainty could be avoided if more refined parameter estimates were available.

Proper assessment of the pandalid shrimp stocks requires detailed information on mortality, growth, population size and age composition, equilibrium yield, and stock-recruitment relationships. All of these are contingent on the development of more accurate ageing techniques than are presently available. The development of appropriate ageing techniques should be assigned the highest possible priority by research institutes responsible for research on shrimp and the provision of management advice. The workshop participants agreed that research on these problems should be intensified and that another workshop be held in 2-3 years to review progress.

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Appendix I

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* Attended November 1981 Meeting only.

Appendix II

Classification scheme (with numerical codes) used by Danish scientists for describing sexual stages of *Pandalus borealis* off Greenland

- | | |
|------|---|
| 01 | Juveniles |
| 11 | Males |
| 12 | US — without ripe male gonad. |
| 16 | SS — with ripe male gonad and extended vasa differentia. |
| 21 | Transitionals |
| 22 | UR — no head roe. |
| 26 | HR — with head roe. |
| 31 | Females |
| 32 | UR — no head roe. |
| 3205 | Specimens with female endopodite but with distinct ventral abdominal spines of male stage. |
| 37 | UR or HR — female 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 females with head roe. |
| 63 | HBR — eggs not lost or hatched. |
| 64 | HBR — eggs partially lost or hatched. |
| 66 | UR+EH — females without head roe, egg 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 head roe. |
| 72 | HR specimens with head roe. |
| 73 | BR specimens where presence or absence of head roe not decided. |
| 75 | Loose head, no head roe. |
| 76 | Loose head, head roe present. |
| 81 | Juveniles and males. |
| 85 | Transitionals and females without roe. |
| 86 | Transitionals and females where presence or absence of head roe may not be decided. |
| 87 | Transitionals and females with head roe, females may possess egg setae. |
| 89 | Not sorted. |