A Practical Assessment of the Performance of Shepherd's Length Composition Analysis (SRLCA): Application to Gulf of Maine Northern Shrimp *Pandalus borealis* Survey Data

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Abstract. – We applied Shepherd's length composition analysis (SRLCA) to research trawl survey catches of Gulf of Maine northern shrimp *Pandalus borealis* to test the efficiency of the method in interpreting the age structure of a length-frequency distribution incorporating significant variation in growth and recruitment rates. We evaluated the performance of the method by comparing the von Bertalanffy growth parameters provided by SRLCA and subsequently derived age frequencies and instantaneous total mortality rates with previously accepted results based on simple visual inspection of the annual length-frequency distributions.

In spite of the variable growth and recruitment rates exhibited by the stock, SRLCA yielded information providing a resolution of the length-frequency data close to *a priori* assumptions, although information external to the procedure was needed to select the best interpretation from among several locally optimal solutions.

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The analysis of length-frequency modes was the first method used by aquatic biologists to delineate successive cohorts in fish and invertebrate populations. Simple visual inspection of modes was developed first (e.g., the "Petersen" method [Petersen 1891]); this relies heavily on the intuition of the scientist for the correct separation of age groups. Later workers assumed a normal distribution underlying the observed length modes, and graphical methods using normal probability paper were used to resolve length distributions to cohorts by the successive identification and removal of suspected age groups. The method of Cassie (1954) is probably the best known of these graphical procedures, which rely to a large degree on subjective decisions of the scientist. Difficulty in defining modes for older age groups, problems in interpretation caused by variable growth rates and recruitment, and an inability to reproduce the interpretation of age groups from one worker to the next have limited the utility of these simple methods.

For most finfish stocks, the interpretation of growth intervals on hard body parts (e.g., scales, otoliths, spines, and vertebrae) has evolved as the ageing method of choice, replacing length-composition analysis methods. For many taxa, however, the interpretation of growth intervals from age structures is difficult, either due to problems in identifying periodic marks or because of the lack of suitable hard structure. For fast-growing, short-lived tropical finfish, and invertebrates such as lobsters, crabs, shrimps, and squids, the resolution to ages of modes in length-frequency distributions continues to be the primary method used to estimate growth and age structure of populations. Recently developed methods directed to interpreting length-frequency distributions generally fall into two categories. The first group treats the problem as one of statistically resolving a mixture of distributions, and usually assumes an underlying normal distribution for the components. The parameters resulting in the best match between the area under the theoretical distribution and the area under the observed length distribution are selected by employing chi-square or maximum likelihood methods. These distribution mixture methods require some prior constraint on the number of length modes and the bounds of the parameters to prevent biologically unrealistic results. The lineage of this approach includes the methods of Hasselblad (1966), Tomlinson (computer program

NORMSEP; 1971), Yong and Skillman (computer program ENORMSEP; 1975), McNew and Summerfelt (1978), and MacDonald and Pitcher (computer program MIX; 1979). The distribution mixture method of Schnute and Fournier (1980) uses a growth model to impose these constraints. A second category of procedures assumes a specific growth function (usually the von Bertalanffy) and attempts to match predicted length modes to those observed. Among these methods are the ELEFAN I procedure of Pauly and David (1981), and Shepherd's length composition analysis (1987).

The Shepherd length composition analysis method (SRLCA) (Shepherd 1987) relies on a goodness-of-fit score function which varies according to the correspondence of observed and predicted length-frequency modes for given pairs of von Bertalanffy growth parameters (L_{inf} and K), thus presumably constraining the indication of optimal parameters to within biologically realistic bounds. SRLCA has fewer subjective input requirements than the distribution mixture methods (Shepherd 1987). Basson et al. (1988) performed Monte Carlo tests of SRLCA and noted that although SRLCA provided biased results for simulated data with large variation in length-at-age, SRLCA generally performed better than ELEFAN I.

To test the performance of SRLCA on an observed, potentially difficult-to-interpret data set, as suggested by Shepherd (1987), we applied a version of SRLCA using the von Bertalanffy growth equation to research trawl survey data for Gulf of Maine northern shrimp *Pandalus borealis*, and compared our results with accepted interpretations of the data. Currently, simple visual inspection and information on sexual characteristics are used to resolve survey length frequency to age frequency, providing subsequent estimates of relative adult stock abundance, recruitment success, and total instantaneous mortality rates (Z) (McInnes 1986, NSTC 1987). Survey results reveal that this stock has experienced variable recruitment and growth during 1982 to 1988 (NSTC 1984, 1985, 1986, 1987, 1988). Although true ages for northern shrimp are not available for use as "ground truth" in this evaluation of SRLCA performance, we feel our assessment of the method is valuable since it is based on application to real data of the type which in practice might require the use of length-based assessment methodology.

Methods

Analysis

SRLCA compares the observed length-frequency distribution with that expected from the von Bertalanffy equation for given test pairs of L_{inf} and K by application of a continuous, periodic test function of the form:

$$T_i = ([\sin \pi \{t_{max} - t_{min}\}] / [\pi \{t_{max} - t_{min}\}]) \times (\cos 2\pi [t_{bar} - t_s])$$

where T_i is the value of the function for a given length interval i, t_{max} and t_{min} are ages at the upper and lower bounds of the interval for a given test set of growth parameters, t_{bar} is the average of t_{max} and t_{min}, and t_s is the date of observation, expressed as a fractional part of the age (e.g, annual) cycle (Shepherd 1987).

A measure of goodness-of-fit is then used to determine the best fitting set of growth parameters for the observed length-frequency distribution. This measure, the score function S, is given by:

$$S = \sum_i T_i N_i^{1/2}$$

where i indexes the length intervals, T is as indicated previously, and N is the number of animals in each interval. Taking the square root of N helps reduce the sensitivity of the score function to unusually large numbers of animals in a given length interval (e.g., in the event of exceptional recruitment; Shepherd 1987). Cumulative scores are large and positive when length modes predicted for a given pair of growth parameters are consistent with observed length-frequency modes, with negative scores indicating inconsistency. Shepherd (1987) suggested that regions of nearly constant scores within the K by L_{inf} score matrix may provide an indication of the shape of the confidence interval around pairs of parameters (e.g., Shepherd suggests a region equal to one-half of the maximum score might approximate the 95% confidence interval). Typically, several regions (hereafter called ridges) of high scores will be observed for each length-frequency distribution analyzed, with local maxima in each ridge that provide alternative interpretations of the data.

Length-frequency data

Gulf of Maine northern shrimp are protandric hermaphrodites, with the females the target of a valuable winter/spring fishery in the western Gulf of Maine (see McInnes 1986 for an overview of the fishery). A research vessel trawl survey was implemented in 1983 to provide a fisheries-independent source of data for the stock. A stratified random trawl survey is conducted annually during late July through mid-August aboard the Northeast Fisheries Center (NEFC) RV *Gloria Michelle* in the western Gulf of Maine (Fig. 1).

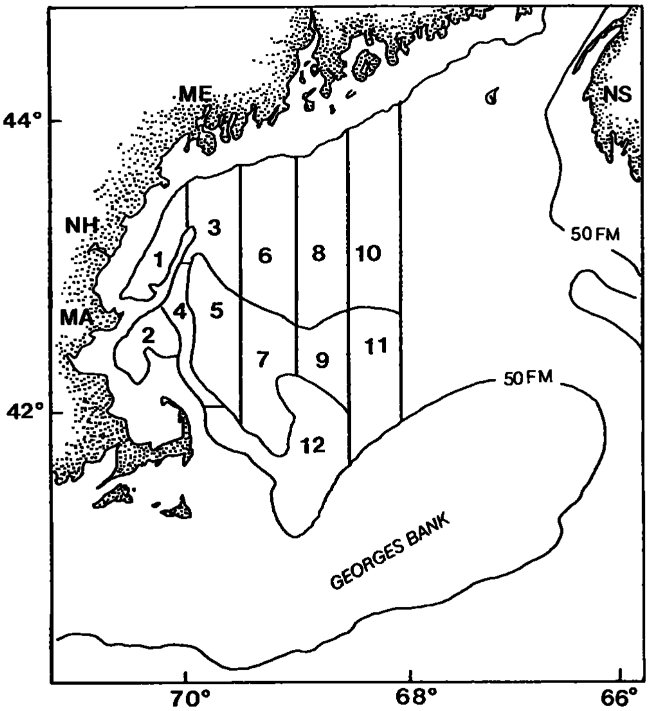

Figure 1

Western Gulf of Maine region with major bathymetric features and 50-fathom (100-m) isobath. Northern shrimp survey area extends from 68°W longitude to the 50-fathom isobath, except for stratum 2, where the sampled area extends to the 30-fathom (60-m) isobath.

Length-frequency data from identical sample strata sets (strata 1, 3, and 5–8) are available for 1984–88 (NSTC 1984, 1985, 1986, 1987, 1988). Trawl gear consists of a modified 4-seam commercial shrimp trawl with 35 mm (1.4 inch) stretched mesh in the body of the net and 32 mm (1.3 inch) stretched mesh in the extension and codend, with "rockhopper" ground gear to allow sampling over rough bottom (McInnes 1986). Samples (2 kg) of each tow are retained for length measurement and sex determination. All shrimp in the sample are measured, with mid-dorsal carapace lengths aggregated by 0.5-mm intervals (nearest 0.5 mm below that measured). A 1-kg subsample is retained for determination of sex and spawning stage.

To date, abundance and biomass indices from the RV *Gloria Michelle* survey (stratified mean number per tow, stratified mean weight [kg] per tow) have proven to be accurate predictors of year-class size and commercial fishery performance (total catch and catch-per-unit-effort; NSTC 1988). Coefficients of variation for stratified mean number and weight (kg) per tow, aggregated over all sample strata, have averaged (1984–88) about 13% and 12%, respectively, indicating relatively high precision.

A priori assumptions

Information is available from previous analyses of the Gulf of Maine northern shrimp length-frequency distributions to provide a baseline interpretation for evaluation of SRLCA results. The von Bertalanffy growth equation has been the accepted means of describing the growth of *P. borealis* (Frechette and Parsons 1983). For the Gulf of Maine stock, growth parameters were expected to be in the range of those previously estimated for this stock. These include (1) parameters derived here by nonlinear least-squares regression analysis of mean carapace length (CL) at age data summarized by Haynes and Wigley (1969; L_{inf} = 32 mm, K = 0.46, t_0 = −0.12), and (2) parameters derived from NEFC groundfish bottomtrawl survey data for northern shrimp (NEFC unpubl. data in McInnes 1986; L_{inf} = 35.2 mm, K = 0.36, t_0 = 0.06). In both of these studies, age was estimated by visual inspection of length-frequency distributions.

For Gulf of Maine northern shrimp survey data, a 1 March birthday was assumed (Apollonio et al. 1986), with an average catch date of 1 August (NSTC 1984, 1985, 1986, 1987, 1988); thus t_s was set equal to 0.42 for all SRLCA runs in this exercise. The usual presence of four age groups (ages 1–4) in the survey catch was suspected (McInnes 1986), with a maximum age of 5 years (Haynes and Wigley 1969, Apollonio et al. 1986), based on modes in length frequencies and sexual characteristics (Allen 1959, McCrary 1971). Northern shrimp in a length range of 13–18 mm CL are generally assumed to be of age-group 1, and mainly immature and mature males, while shrimp 18–22 mm CL are assumed to be age 2 and mostly mature males. Animals in the 22–25 mm CL interval are assumed age 3, usually females with no previous spawning history. Shrimp larger than 25 mm CL are assumed to be females of age-group 4, with possible age-group 5 female shrimp at CL greater than 29 mm. The survey samples northern shrimp in a CL range of 10–32 mm (Fig. 2), with animals assumed fully recruited to the gear at about 19–20 mm CL, or age 2 and older (Blott et al. 1983). Previous interpretations of survey results and commercial fishery performance suggest that the 1982 and 1987 year-classes (YC) of Gulf of Maine northern shrimp were strong, and the 1983 YC very weak, with the remaining cohorts (1984–86) of about equal strength (NSTC 1987, 1988).

Model evaluation

Exploratory runs were performed using L_{inf} values ranging from 20 to 50 mm, in 1-mm steps, and K values ranging from 0.20 to 0.50, in 0.01 steps, encompassing a very wide range of values (about ±50%) around

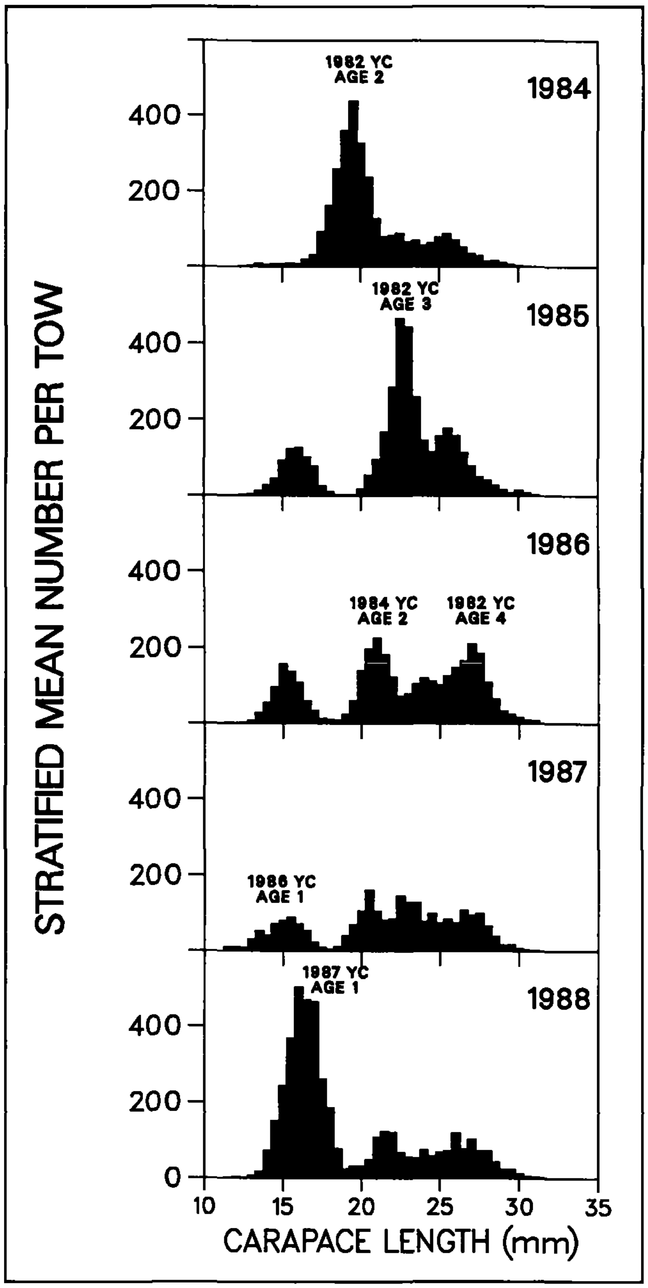

Figure 2

Length-frequency distributions (stratified mean number per tow) for *Pandalus borealis* collected in the western Gulf of Maine during the 1984–88 northern shrimp surveys aboard RV *Gloria Michelle*.

the growth parameters previously estimated for this stock of *P. borealis*, in order to adequately explore the high score ridges provided by the SRLCA score function. Preliminary evaluation of the highest scoring parameter values from each ridge, along with several local maxima (higher score than all eight nearest neighbors) within each ridge, indicated that parameter pairs within a given ridge tended to provide similar interpretations of the number of modes (assumed age groups) present in the observed length frequency, as expected from earlier testing of the method (Shepherd et al. 1987). Values of the optimum value of t_0 corresponding to K and L_{inf} parameter pairs are the decimal fraction part of t_0, and are indeterminate with respect to the addition or subtraction of any whole number of years (Shepherd 1987).

SRLCA results were examined in the context of previously developed parameter estimates and *a priori* assumptions, and alternative parameters were evaluated when the highest scoring values did not agree with prior interpretations of the number and position of modes (assumed age groups) expected. SRLCA was first applied to annual distributions independently, and then to distributions from 1984 to 1988 sequentially pooled in a single run. The annual distributions were analyzed primarily to evaluate interpretations provided by SRLCA given the variable patterns of growth and recruitment in the data. Growth parameters and subsequently resolved age frequencies from the final pooled analysis were used to estimate total mortality for comparison with rates estimated by visual resolution of the length-frequency data to age.

Shepherd (1987) noted that the number of older ages determined by decomposition of the length-frequency distribution according to the von Bertalanffy growth equation is dependent to a large degree on the value of L_{inf}, and suggested that parameters selected by SRLCA might be most appropriate for subsequent use in other length-based analyses, rather than to slice length frequencies to ages, unless additional data (e.g., knowledge of the expected number of cohorts) are available to select the ridge containing the "correct" parameter pair (see also Shepherd et al. 1987). In this exercise, we elected to proceed with resolution to cohorts, and subsequent age-based mortality estimation, both because of the apparently nonequilibrium nature of this northern shrimp population (thus limiting the utility of length-based methods which assume steady-state conditions), and to provide results comparable with those previously estimated (NSTC 1984, 1985, 1986, 1987, 1988).

Results

Annual length frequencies

1984 distribution This distribution is characterized by a dominant mode centered at 19.5 mm (Fig. 2). *A priori* interpretation suggested that the dominant mode at 19–20 mm should be age-group 2 shrimp (a strong 1982 YC), with shrimp 22–24 mm probably age-

Table 1

Von Bertalanffy growth parameter pairs and SRLCA score (S) for 1984 northern shrimp survey length-frequency distribution: primary and secondary ridge crests.

	L_{inf} (mm)	K	S
Primary ridge crest	35	0.50	47.0
	40	0.43	63.9
	45	0.36	64.4
	50	0.30	62.7
	39	0.50	67.7[1]
	41	0.43	65.8[2]
Secondary ridge crest	35	0.42	41.4[1]
	40	0.30	37.4
	36	0.37	40.3[2]*

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[1] High score parameters of ridge crest, on boundary of explored space.

[2] High score parameters of ridge crest, nonboundary maximum.

* Parameters selected for final evaluation.

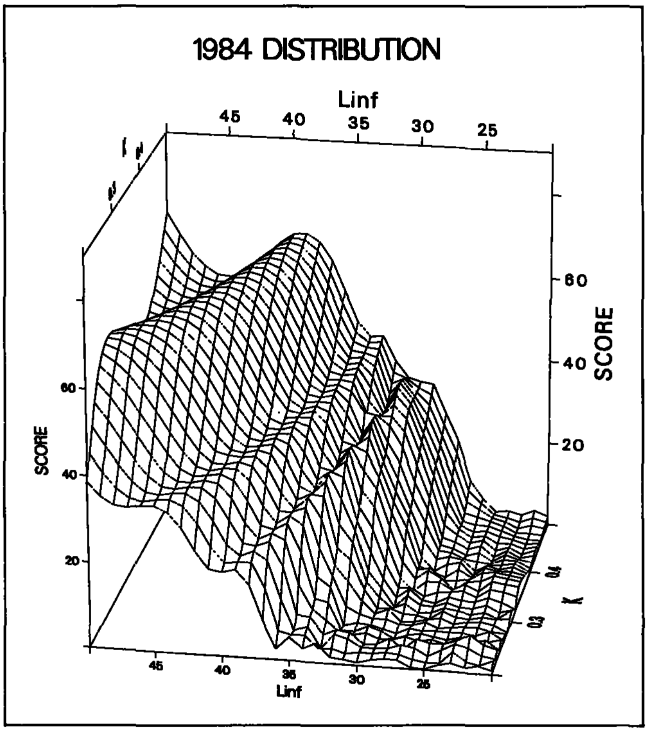

Figure 3

Response surface of the SRLCA score function for the northern shrimp survey 1984 length-frequency distribution.

group 3, and animals >25 mm defined as age 4+ (NSTC 1984). SRLCA scores exhibited a broad, primary (highest scores) ridge of scores within the explored parameter space ranging from a high score on the border of explored parameter space at $L_{inf} = 39$ mm, $K = 0.50$ to $L_{inf} = 50$ mm, $K = 0.30$, with a nonboundary local maximum at $L_{inf} = 41$ mm, $K = 0.43$ (Table 1, Fig. 3). Based on parameters in this ridge, the length frequency was interpreted as a single dominant mode (age-group 1), with the distribution to the right of the mode classified as two older age-groups, for a total of three cohorts present. A secondary ridge of scores, from $L_{inf} = 33$ mm, $K = 0.50$ to $L_{inf} = 38$ mm, $K = 0.30$, with a nonboundary local maximum at $L_{inf} = 36$ mm, $K = 0.37$ (Table 1, Fig. 3), classified four ages and defined the dominant mode as age 2, but did not interpret the small modes at 22.5 and 25.5 mm in accordance with prior assumptions (assumed age groups 3 and 4, respectively). However, this secondary ridge most closely matched the *a priori* interpretation, and represented the best performance of SRLCA for the 1984 data (Fig. 4). A tertiary ridge (a spur of the secondary) ranged from a nonboundary maximum at $L_{inf} = 31$ mm, $K = 0.46$ to $L_{inf} = 34$ mm, $K = 0.30$, and interpreted the length frequency in nearly the same manner as parameters from the secondary ridge.

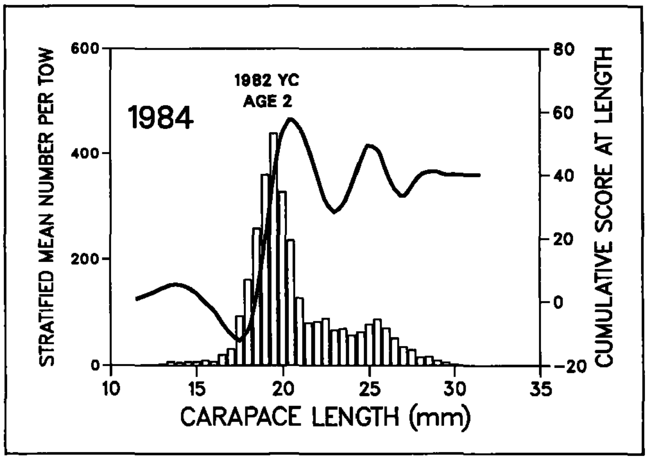

Figure 4

Northern shrimp survey 1984 length-frequency distribution (histogram) and pattern of SRLCA scores (solid curve) for growth parameters selected for final evaluation ($L_{inf} = 36$ mm, $K = 0.37$).

1985 distribution Previous work suggested that the first two modes of this distribution, 13–18 mm and 20–24 mm, should be interpreted as age groups 1 (1984 YC) and 3 (the strong 1982 YC), thus confronting SRLCA with a "missing cohort" situation (the weak 1983 YC; Fig. 2). Sex determinations further showed that shrimp in the 20–24 mm mode were not the expected first-year females, but mostly mature males that seemed not to have undergone transition during the previous winter (NSTC 1985). Inspection of the position of this age-3 mode, relative to the modal lengths

Table 2

Von Bertalanffy growth parameter pairs and SRLCA score (S) for 1985 northern shrimp survey length-frequency distribution: primary, secondary, and tertiary ridge crests.

	L_{inf} (mm)	K	S
Primary ridge crest	35	0.48	85.2[2]
	40	0.34	82.6
	45	0.26	78.7
	50	0.21	75.2
Secondary ridge crest	42	0.50	63.0
	46	0.41	69.7
	50	0.34	74.1[1]
Tertiary ridge crest	28	0.50	29.0[1]
	30	0.37	23.6
	32	0.30	22.5
	34	0.27	21.4
	36	0.23	23.4
	38	0.20	23.8
	29	0.42	25.3[2]*

[1] High score parameters of ridge crest, on boundary of explored space.

[2] High score parameters of ridge crest, nonboundary maximum.

*Parameters selected for final evaluation.

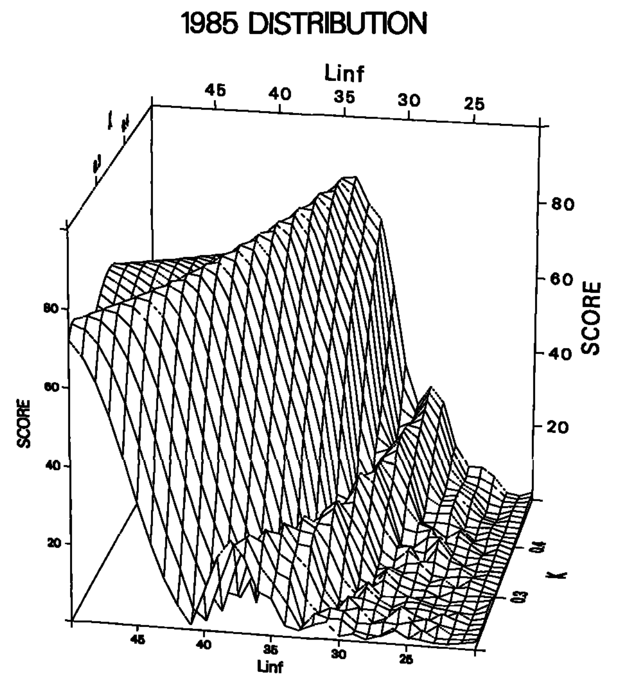

Figure 5

Response surface of the SRLCA score function for the northern shrimp survey 1985 length-frequency distribution.

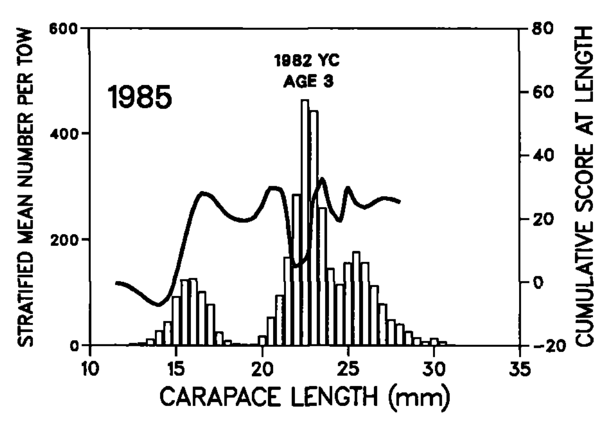

Figure 6

Northern shrimp survey 1985 length-frequency distribution (histogram) and pattern of SRLCA scores (solid curve) for growth parameters selected for final evaluation (L_{inf} = 29 mm, K = 0.42).

of assumed age-3 shrimp in the two subsequent years, suggests that the 1982 YC may also have experienced a slower growth rate between ages 2 and 3 than preceding cohorts.

The highest value in the SRLCA primary score ridge was at L_{inf} = 35 mm, K = 0.48, with the ridge then continuing to L_{inf} = 50 mm, K = 0.21. Parameters in this primary ridge classified the first two modes as successive cohorts, with three age groups total. A secondary ridge, from L_{inf} = 42 mm, K = 0.50 to a boundary maximum at L_{inf} = 50 mm, K = 0.34, resolved the distribution to only two age groups, with modal lengths of 17.0 and 26.5 mm for ages 1 and 2. It was necessary to explore a tertiary ridge, with a nonboundary local maximum at L_{inf} = 29 mm, K = 0.42, to successfully interpret the first two length modes as age groups 1 and 3, with shrimp >24.5 mm resolved to two main age-groups (Table 2; Fig. 5, 6).

1986 distribution This distribution is characterized by three clearly defined modes at 13–18 mm, 19–22 mm, and >25 mm, assumed to be ages 1, 2, and 4, and a small mode at 23 mm assumed to be either the 1983 cohort at age 3 or slow-growing shrimp from the 1982 cohort at age 4 (NSTC 1986; Fig. 2). Two ridges of comparable high scores were apparent from an initial SRLCA run, a primary ridge from L_{inf} = 35 mm, K = 0.49 to a boundary maximum at L_{inf} = 50 mm, K = 0.22, and a secondary ridge from L_{inf} = 32 mm, K = 0.47 to L_{inf} = 40 mm, K = 0.23 (Table 3, Fig. 7). The primary ridge identified three modal groups, matching the first observed mode well, but classifying shrimp between 18.5 and 24.5 mm as a single group, with the

Table 3

Von Bertalanffy growth parameter pairs and SRLCA score (S) for 1986 northern shrimp survey length-frequency distribution: primary and secondary ridge crests.

	L_{inf} (mm)	K	S
Primary ridge crest	35	0.49	65.5
	40	0.34	74.1
	45	0.26	78.0
	50	0.22	79.9[1]
Secondary ridge crest	32	0.47	65.1
	34	0.37	65.6
	36	0.31	63.1
	38	0.27	59.9
	40	0.23	55.7
	33	0.42	66.1[2]*

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[1] High score parameters of ridge crest, on boundary of explored space.

[2] High score parameters of ridge crest, nonboundary maximum.

*Parameters selected for final evaluation.

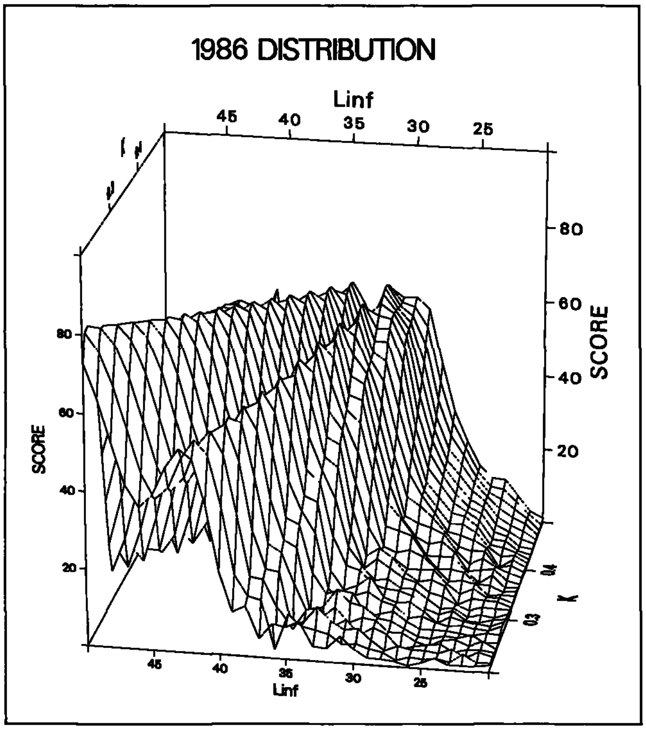

Figure 7

Response surface of the SRLCA score function for the northern shrimp survey 1986 length-frequency distribution.

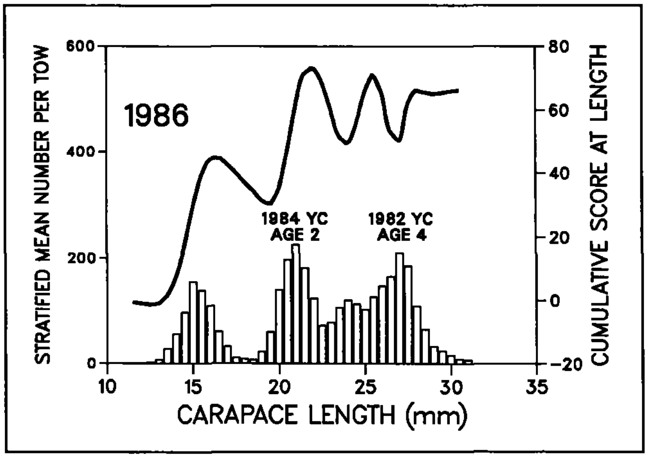

Figure 8

Northern shrimp survey 1986 length-frequency distribution (histogram) and pattern of SRLCA scores (solid curve) for growth parameters selected for final evaluation (L_{inf} = 33 mm, K = 0.42).

last mode interpreted as age-3 shrimp. The secondary ridge high-score parameters classified the first, second, and fourth observed modes fairly well, with the highest scoring parameters (L_{inf} = 33 mm, K = 0.42) falling in an interval between previously estimated von Bertalanffy parameters. SRLCA was thus able to match the *a priori* interpretation of the 1986 length-frequency distribution reasonably well, using parameters from the secondary ridge crest (Fig. 8).

1987 distribution The first mode of this distribution is fairly pronounced and has been interpreted as age 1, but the modes following are not well defined (NSTC 1987; Fig. 2). SRLCA indicated best fitting parameter pairs in a primary score ridge ranging from L_{inf} = 35 mm, K = 0.50 to L_{inf} = 50 mm, K = 0.23, with a maximum at L_{inf} = 40 mm, K = 0.36, and in a secondary ridge ranging from L_{inf} = 32 mm, K = 0.50 to L_{inf} = 40 mm, K = 0.24, with a nonboundary local maximum at L_{inf} = 33 mm, K = 0.43 (Table 4, Fig. 9). The primary ridge parameters defined three age groups, correctly classifying the first mode, lumping shrimp between 19.0 and 25.0 mm as a second group, and aggregating all shrimp >25 mm as a final group. The secondary ridge parameters resolved the distribution in a similar manner, but by splitting shrimp >23 mm into two groups (Fig. 10). Thus, neither set of parameters selected by SRLCA successfully resolved shrimp between 19.0 and 25.0 mm to distinct cohorts.

1988 distribution In the 1988 survey length frequency, the large mode between 13 and 19 mm was assumed to be age-1 shrimp. A smaller mode of 20–23 mm was interpreted as age 2, with shrimp >25 mm assumed, as usual, to be age-group 4+ (NSTC 1988; Fig. 2). SRLCA provided two ridges of high scoring parameters, a primary ridge extended from a boundary max-

Table 4

Von Bertalanffy growth parameter pairs and SRLCA score (S) for 1987 northern shrimp survey length-frequency distribution: primary and secondary ridge crests.

	L_{inf} (mm)	K	S
Primary ridge crest	35	0.50	55.0
	40	0.36	57.1[2]
	45	0.28	56.7
	50	0.23	55.9
Secondary ridge crest	32	0.50	42.5[1]
	34	0.39	40.1
	36	0.32	37.9
	38	0.28	35.5
	40	0.24	34.0
	33	0.43	41.3[2]*

[1] High score parameters of ridge crest, on boundary of explored space.

[2] High score parameters of ridge crest, nonboundary maximum.

*Parameters selected for final evaluation.

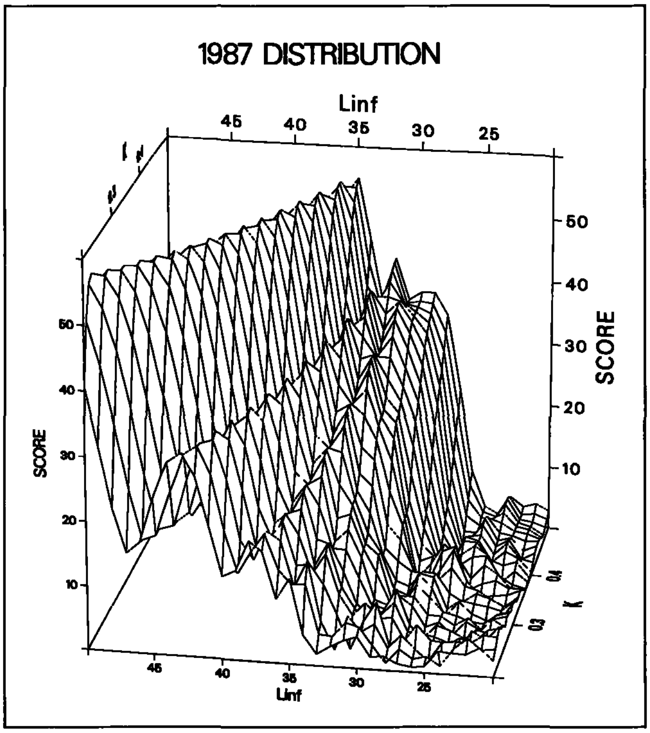

Figure 9

Response surface of the SRLCA score function for the northern shrimp survey 1987 length-frequency distribution.

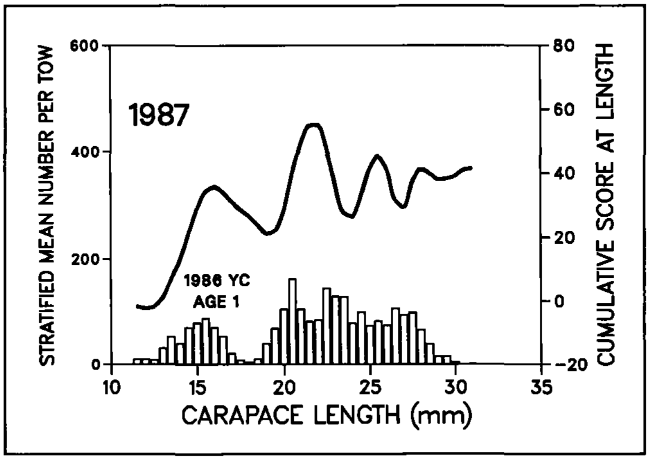

Figure 10

Northern shrimp survey 1987 length-frequency distribution (histogram) and pattern of SRLCA scores (solid curve) for growth parameters selected for final evaluation (L_{inf} = 33 mm, K = 0.43).

Table 5

Von Bertalanffy growth parameter pairs and SRLCA score (S) for 1988 northern shrimp survey length-frequency distribution: primary and secondary ridge crests.

	L_{inf} (mm)	K	S
Primary ridge crest	43	0.50	123.5[1]
	45	0.46	123.0[2]
	47	0.42	122.4
	49	0.39	121.9
Secondary ridge crest	35	0.47	93.3[2]*
	40	0.34	88.5
	45	0.25	85.0
	50	0.20	85.0

[1] High score parameters of ridge crest, on boundary of explored space.

[2] High score parameters of ridge crest, nonboundary maximum.

*Parameters selected for final evaluation.

imum at L_{inf} = 43 mm, K = 0.50 to L_{inf} = 49 mm, K = 0.39, while a secondary ridge ranged from L_{inf} = 35, K = 0.47 to L_{inf} = 50 mm, K = 0.20 (Table 5, Fig. 11).

Values from the primary ridge resolved shrimp 11–21.5 mm as a single cohort (age 1), with animals 22 mm and larger assigned to age 2. Values from the secondary ridge provided only a slightly improved interpretation, with shrimp 11–19.5 mm classified as age 1, 20–25 mm as age 2, and >25 mm as age 3. Clearly, the modes in this distribution were not sufficiently distinct to allow a reasonable interpretation using SRLCA (Fig. 12).

Pooled distribution: 1984–88 As with the annual distributions, an exploratory run was made with L_{inf} values ranging from 20–50 mm, in 1-mm steps, and K values of 0.20–0.50, in 0.01 steps. Two broad regions

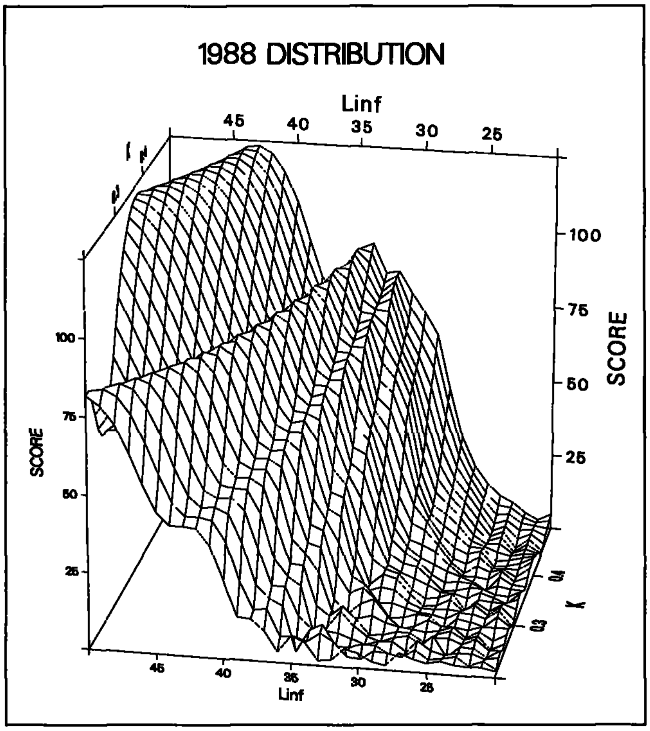

Figure 11
Response surface of the SRLCA score function for the northern shrimp survey 1988 length-frequency distribution.

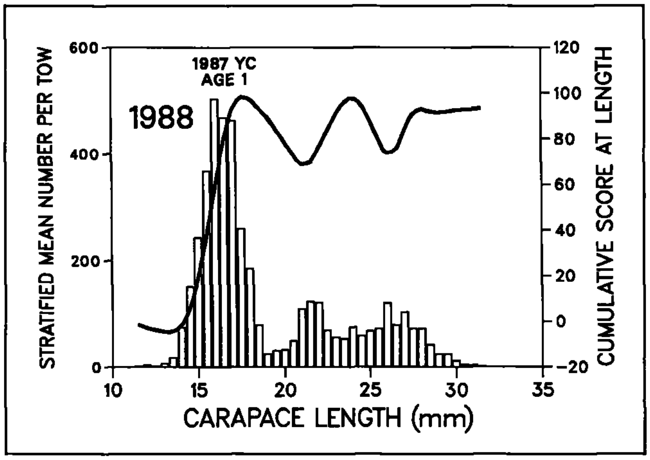

Figure 12
Northern shrimp survey 1988 length-frequency distribution (histogram) and pattern of SRLCA scores (solid curve) for growth parameters selected for final evaluation (L_{inf} = 35 mm, K = 0.47).

of parameters, with a primary ridge in one region and secondary, tertiary, and quaternary ridges in the other, were evaluated in an attempt to find parameters selected by the SRLCA test function that would interpret the 1984–1988 distributions in accordance with *a priori* assumptions.

Table 6
Von Bertalanffy growth parameter pairs and SRLCA score (S) for pooled 1984–88 northern shrimp survey length-frequency distribution: primary, secondary, tertiary, and quaternary ridge crests.

	L_{inf} (mm)	K	S
Primary ridge crest	43	0.50	244.0
	44	0.47	244.8
	46	0.43	245.7
	48	0.40	246.5[2]
	50	0.37	247.8[1]
Secondary ridge crest	35	0.50	219.2
	35	0.48	227.0
	36	0.44	230.3
	38	0.38	233.7
	40	0.34	234.0
	42	0.30	234.9[2]
	44	0.27	234.2
	46	0.25	233.4
	48	0.23	232.5
	50	0.21	232.1
Tertiary ridge crest	32	0.50	190.0
	32	0.49	191.4[2]
	33	0.43	175.0
	34	0.39	160.0
	35	0.35	147.3
	37	0.29	127.9
	40	0.23	108.9
	43	0.20	98.3
Quaternary ridge crest	33	0.33	101.5
	33	0.32	104.6[2]*
	34	0.29	94.8
	35	0.26	88.2
	36	0.24	80.7
	37	0.22	76.2
	38	0.20	73.3

[1] High score parameters of ridge crest, on boundary of explored space.
[2] High score parameters of ridge crest, nonboundary maximum.
*Parameters selected for final evaluation.

The primary ridge ranged from L_{inf} = 43 mm, K = 0.50 to a boundary maximum at L_{inf} = 50 mm, K = 0.37. The highest nonboundary score was at L_{inf} = 48.0 mm, K = 0.40. A secondary ridge ranged from L_{inf} = 35 mm, K = 0.50 to L_{inf} = 50, K = 0.21, with a nonboundary maximum score at L_{inf} = 42.0, K = 0.30. A tertiary ridge ranged from L_{inf} = 32 mm, K = 0.50 to L_{inf} = 43 mm, K = 0.20, with a nonboundary maximum at L_{inf} = 32 mm, K = 0.49. A quaternary ridge ranged from L_{inf} = 33 mm, K = 0.33 to L_{inf} = 38 mm, K = 0.20, with a nonboundary maximum score at L_{inf} = 33 mm, K = 0.32 (Table 6, Fig. 13).

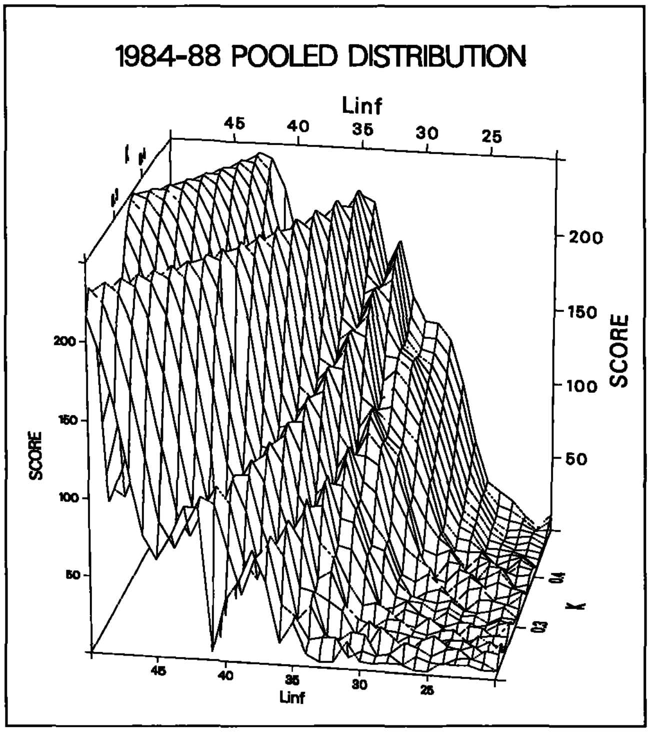

Figure 13
Response surface of the SRLCA score function for the northern shrimp survey 1984–88 length-frequency distribution.

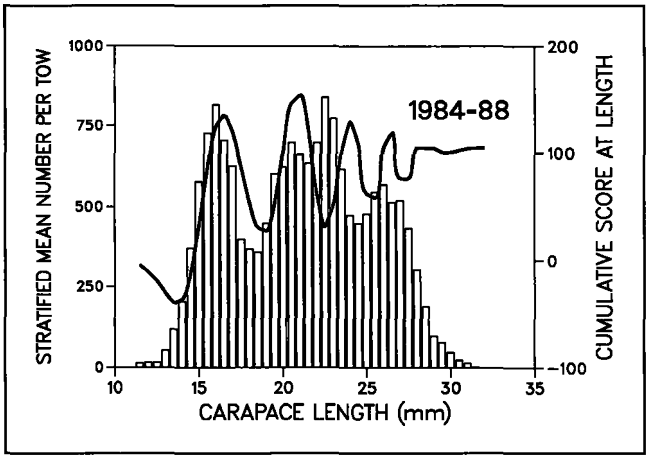

Figure 14
Northern shrimp survey 1984–88 pooled length-frequency distribution (histogram) and pattern of SRLCA scores (solid curve) for growth parameters selected for final evaluation (L_{inf} = 33 mm, K = 0.32).

Values from the primary ridge tended to treat the assumed first and second observed age-groups, up to 21 mm, as a single mode, with animals greater than 21.5 mm classified as age 2. Values from the secondary ridge accurately interpreted the assumed age-group 1, but lumped the assumed second and third age-groups as a single mode, with shrimp >25 mm classified as age 3. Values from the tertiary ridge also correctly characterized the first age group and failed to resolve the second and third modes to distinct age classes, but split shrimp >24 mm into age-groups 3 and 4. It is interesting to note that the two sets of previously derived von Bertalanffy parameters for this stock noted earlier (see Methods: *A Priori* Assumptions) fell within this tertiary ridge of scores. This indicated that growth rates based on those parameters were too fast to provide an interpretation of length distributions consistent with visual inspection of the length modes.

Quaternary ridge values successfully classified the first–fourth assumed age-groups in line with prior assumptions. These parameters also provided an age-group 5 for CL >27.5 mm. The quaternary ridge nonboundary maximum score parameters (L_{inf} = 33 mm, K = 0.32) were selected for final SRLCA evaluation of the pooled length frequency, as these values provided the characterization of the pooled distribution closest to the assumed age structure (Fig. 14). The growth curve defined by these parameters indicates a slower rate compared with previously estimated growth curves (data from Haynes and Wigley 1969, McInnes 1986), a result of the influence, or "bias," of the abundant, apparently slower-growing, 1982 cohort on the score function (Fig. 15).

We derived annual age frequencies by slicing annual length frequencies to age-groups according to the maximum-scoring growth parameters provided by the four score ridges of the pooled analysis (Table 6). Since shrimp of age-group 2 and older are assumed fully recruited to the survey trawl gear, total instantaneous mortality estimates (Z) were derived from:

$$Z =$$

$$\ln\left(\sum \text{age } 2+ \text{ for Year}_N \;/\; \sum \text{age } 3+ \text{ for Year}_{N+1}\right).$$

These values were then compared with previously calculated estimates of total mortality from the length-frequency data (NSTC 1985, 1986, 1987, 1988).

Table 7 shows the widely divergent age frequencies and subsequent Z estimates provided by the four different pairs of growth parameters, which again illustrate a necessity for some external source of information to interpret SRLCA results in a manner consistent with a priori assumptions. We note that for the 1987 distribution, the quaternary ridge parameters and NSTC visual inspection sliced the length-frequency distribution at the same length intervals, resulting in identical age frequencies for 1987. As expected, use of the quaternary SRLCA score ridge parameters to

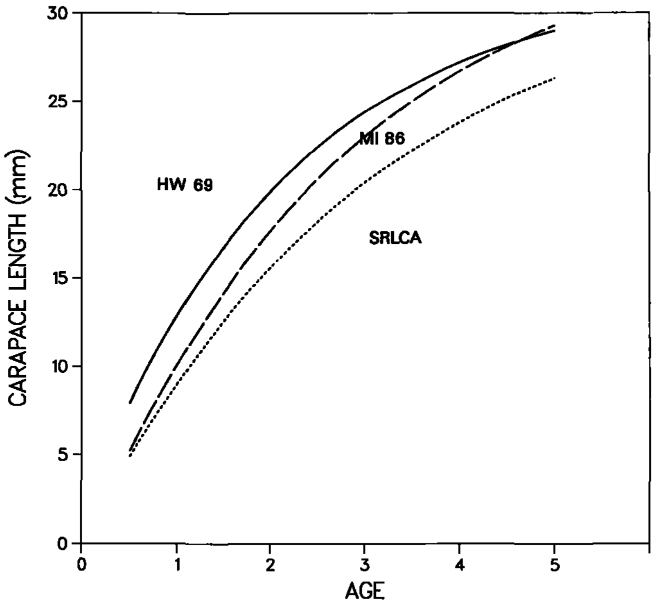

Figure 15

Von Bertalanffy growth curves for Gulf of Maine *Pandalus borealis*. Upper curve (solid line) is for parameters derived from age-length data in Haynes and Wigley (1969); center curve (large dashed line) is for growth parameters cited in McInnes (1986); lower curve (dot-dashed line) is for parameters derived by SRLCA for northern shrimp survey length-frequency data.

Table 7

Age-frequency matrices and instantaneous total mortality rates (Z) for age 2+ northern shrimp estimated by growth parameters from SRLCA high-score parameter ridges for the 1984–88 pooled distribution, compared with estimates using method of visual inspection of length modes (NSTC 1984, 1985, 1986, 1987, 1988).

Age	1984	1985	1986	1987	1988
SRLCA					
Primary score ridge					
1	2150	887	1489	1091	3192
2	856	2644	1872	1357	1136
3	0	0	0	0	0
4+	0	0	0	0	0
		Z_{85} = ---	Z_{86} = ---	Z_{87} = ---	Z_{88} = ---
Secondary score ridge					
1	633	660	753	575	2903
2	2001	2083	1504	1257	818
3	373	789	1104	620	604
4+	0	0	0	0	0
		$Z_{85} = 1.10$	$Z_{86} = 0.96$	$Z_{87} = 1.44$	$Z_{88} = 1.13$
Tertiary score ridge					
1	672	660	755	577	2906
2	1853	1849	1283	1088	693
3	410	876	857	545	504
4+	71	146	465	239	224
		$Z_{85} = 0.83$	$Z_{86} = 0.78$	$Z_{87} = 1.20$	$Z_{88} = 0.94$
Quaternary score ridge					
1	193	634	701	539	2564
2	1987	350	845	575	632
3	425	1710	615	663	433
4+	401	837	1200	671	699
		$Z_{85} = 0.10$	$Z_{86} = 0.47$	$Z_{87} = 0.69$	$Z_{88} = 0.52$
NSTC					
Visual inspection					
1	49	646	710	539	2828
2	2051	337	959	575	614
3	442	1596	491	663	187
4+	463	952	1200	671	699
		$Z_{85} = 0.15$	$Z_{86} = 0.53$	$Z_{87} = 0.69$	$Z_{88} = 0.77$

age the length frequencies provided mortality estimates consistent with those produced by visual inspection of length modes.

Discussion

We subjected SRLCA to a fairly stern test by attempting to interpret a data set exhibiting variable recruitment and growth patterns, and by using a broad initial parameter search space. As noted in the Monte Carlo tests of SRLCA by Basson et al. (1988), these variations in recruitment, and in mean length-at-age (presumed variable growth rate, especially for the abundant 1982 cohort) between cohorts, made interpretation of the northern shrimp length-frequency distributions difficult. The shape and proximity of the assumed age-2 and -3 modes frequently caused SRLCA to interpret these modes as a single age-group, resulting in highest scoring parameters that provided positively biased estimates of growth rate. This problem was most severe for the annual distributions and persisted in the pooled length frequency, although the increased amount of information in the pooled distribution did increase the effectiveness of the SRLCA approach, with a "correct" interpretation of the data available from the quaternary score ridge. Analysis of the pooled data in a truly sequential fashion, after the projection matrix approach of Rosenberg et al. (1986) and Basson et al. (1988), as a supplement to SRLCA might help in alleviating these problems.

This exercise demonstrated that the best objective fit obtained by SRLCA does not necessarily provide the best interpretation of the data, as with most of the existing length-frequency distribution analysis methods. Pragmatically, we could not rely on SRLCA to provide a single set (or even region) of growth parameters that yield both the highest parameter score and the "correct" interpretation of the data, unless supplemented by an external source of information. For SRLCA to be effective, the subjectivity required in the selection of input parameters for use with the family of distribution mixture methods (e.g., MacDonald and Pitcher 1979) must instead be applied to interpretation of the output of the procedure.

These problems are similar to those encountered by others in evaluating the ELEFAN I method of Pauly and David (1981). Testing of ELEFAN I has indicated it produces biased results unless the range of growth parameters considered for testing is relatively narrow, and that it is sensitive to increased variation in length-at-age or increased variation in recruitment timing (Rosenberg and Beddington 1987). Recent work by Morgan (1987), supplementing ELEFAN with age-length data, improved the performance of that method by allowing selection of the appropriate parameters from among several locally optimal solutions.

We are encouraged, however, that such external information requirements were moderate for SRLCA. For instance, with an expectation of age of the oldest cohort, we would have immediately selected the quaternary ridge of the pooled analysis as best. Or, had we limited the initial search space for L_{inf} to within 10% of the CL of the largest animal, and/or 10% of an "average" L_{inf} given previously derived parameters (e.g., 33 ± 2 mm), we again could have proceeded directly to selection of the appropriate score ridge.

Even given conditions of variable growth and recruitment, we were able to inspect the response surface of the test function and, using a moderate degree of subjectivity and a stepwise procedure of evaluation, select growth parameters from alternative high-score ridges that resolved the pooled distribution in a manner consistent with previous interpretations, and, more important, in a more satisfactory manner than previously derived von Bertalanffy growth parameters. Overall we found SRLCA to be a simple and generally effective tool for the estimation of growth parameters, and subsequently age frequencies, from length-frequency distributions for Gulf of Maine northern shrimp.

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