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

by

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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 ability of the method to interpret 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 was able to provide an interpretation of the data close to *a priori* assumptions, although some information external to the procedure was needed in order to select the best interpretation from among several locally optimal solutions.

INTRODUCTION

The analysis of length frequency modes was the first method used by fishery 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]), and relies 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 utilizing 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 the subjective decision of the scientist. Difficulty in defining modes for older age groups, problems in interpretation caused by variable growth rates and recruitment, and the inability to reproduce the interpretation of age groups from one worker to the next has 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 finish, 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 at 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), McNew and Summerfelt (1978), and MacDonald and Pitcher (1979). The distribution mixture method of Schnute and Fournier (1980) uses a growth model to impose these constraints. The 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 those of Pauly and David (1981) and Shepherd (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; Northern Shrimp Technical Committee MS 1987). Survey results reveal that this stock has experienced variable recruitment and growth during 1982 to 1987 (Northern Shrimp Technical Committee MS 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:

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

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:

$$S = \sum_i T_i (N^{1/2})_i$$

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) R/V Gloria Michelle in the western Gulf of Maine (Figure 1). Data from identical sample strata sets (strata 1, 3, and 5-8) are available for 1984 to 1988 (Northern Shrimp Technical Committee MS 1984; 1985; 1986; 1987; 1988). Trawl gear consists of a modified 4-seam commercial shrimp trawl with 35 mm (1.4 in) stretched mesh in the body of the net and 32 mm (1.3 in) stretched mesh in extension and codend, with "rockhopper" ground gear to allow sampling over rough bottom (McInnes 1986). Two kg samples 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 R/V Gloria Michelle survey (stratified mean number per tow, statified mean weight [kg] per tow) have proven to be accurate predictors of commercial fishery performance (total catch and catch per unit effort; Northern Shrimp Technical Committee MS 1988). Coefficients of variation for stratified mean number and weight (kg) per tow, aggregated over all sample strata, have averaged (1984-1988) about 13 and 12 percent, 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 is 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 (Appendix Table 1) by analysis of mean carapace length (CL) at age data summarized by Haynes and Wigley (1969; L_{inf} = 32 mm, K = 0.46, to = -0.12), and 2) parameters derived from NEFC groundfish bottom trawl survey data for northern shrimp (NEFC unpublished 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 (Northern Shrimp Technical Committee MS 1984; 1985; 1986; 1987; and 1988); thus t_s was set equal to 0.42 for all SRLCA runs in this exercise. The usual presence of 4 age groups (ages 1 to 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 to 18 mm CL are generally assumed to be of age group-1, and mainly immature and mature males, while shrimp from 18 to 22 mm CL are assumed of 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, with animals assumed fully recruited to the gear at about 19-20 mm CL, or age-2 and older (Fig. 2: 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 to 1986) of about equal strength (Northern Shrimp Technical Committee MS 1987; 1988; Figure 2).

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 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 (and range of the K*Linf product) tended to provide similar interpretations of the number of modes (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 (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 the 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) is 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 non-equilibrium nature of this northern shrimp population (thus limiting the utility of length-based methods which assume steady-state conditions), and to provide results comparable to those previously estimated (Northern Shrimp Technical Committee MS 1984; 1985; 1986; 1987; 1988).

RESULTS

Annual Length Frequencies

1984 Distribution

This distribution is characterized by a dominant mode centered at 19.5 mm. A priori interpretation suggested that the dominant mode at 19-20 mm should be age group-2 shrimp (a strong 1982 YC), with shrimp from 22 to 24 mm probably age group-3, and animals >25 mm defined as age 4+ (Northern Shrimp Technical Committee MS 1984; Figure 2). 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 Linf = 39 mm, K = 0.50 , to L_{inf} = 50 mm, K = 0.30, with a non-boundary local maximum at Linf = 41 mm, K = 0.43 (Table 1, Figure 3). Based on parameters in this ridge, the length frequency was interpreted as a single dominant mode (age group-1), with the tails defined as adjacent age groups, for a total of three cohorts present. A secondary ridge of scores, from Linf = 33 mm, K = 0.50 to Linf = 38 mm, K = 0.30, with a non-boundary local maximum at Linf = 36 mm, K = 0.37 (Table 1, Figure 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; Figure 4). Likewise, a tertiary ridge (a spur of the secondary) ranged from a non-boundary maximum at Linf = 31 mm, K = 0.46 to Linf = 34 mm, K= 0.30, and interpreted the length frequency in nearly the same manner as parameters from the secondary ridge (Table 1).

1985 Distribution

Previous work suggested that the first two modes of this distribution, from 13 to 18 mm and 20 to 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; Figure 2). Sex determinations further showed that shrimp in the 20 to 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 (Northern Shrimp Technical Committee MS 1985). Inspection of the position of this age-3 mode, relative to the modal lengths 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 Linf = 35 mm, K =

0.48, with the ridge then continuing to Linf = 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 Linf = 42 mm, K = 0.50 to a boundary maximum at Linf = 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 one and two. It was necessary to explore a tertiary ridge, with a non-boundary local maximum at Linf = 29 mm, K = 0.42, to successfully interpreted the first two length modes as age groups 1 and 3, with shrimp > 24.5 mm to two main age groups (Table 2, Figures 5 and 6).

1986 Distribution

This distribution is characterized by three clearly defined modes at 13 to 18 mm, 19 to 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 (Northern Shrimp Technical Committee MS 1986; Figure 2). Two ridges of comparable high scores were apparent from an initial SRLCA run, a primary ridge from Linf = 35 mm, K = 0.49 to a boundary maximum at Linf = 50 mm, K = 0.22, and a secondary ridge from Linf = 32 mm, K = 0.47 to Linf = 40 mm, K = 0.23 (Table 3, Figure 7). The primary ridge identified 3 modal groups, matching the first observed mode well, but classifying shrimp between 18.5 and 24.5 mm as a single group, with the 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 (Linf = 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 (Figure 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 (Northern Shrimp Technical Committee MS 1987; Figure 2). SRLCA indicated best fitting parameter pairs in a primary score ridge ranging from Linf = 35 mm, K = 0.50 to Linf = 50 mm, K = 0.23, with a maximum at Linf = 40 mm, K = 0.36, and in a secondary ridge ranging from Linf = 32 mm, K = 0.50 to Linf = 40 mm, K = 0.24, with a non-boundary local maximum at Linf= 33 mm, K= 0.43 (Table 4, Figure 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 (Figure 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 from 20 to 23 mm was interpreted as age 2, with shrimp > 25 mm assumed, as usual, to be age group-4+ (Northern Shrimp Technical Committee MS 1988; Figure 2). SRLCA provided two ridges of high scoring parameters, a primary ridge extended from a boundary maximum at Linf = 43 mm, K = 0.50, to Linf = 49 mm, K = 0.39, while a secondary ridge ranged from Linf = 35, K = 0.47, to Linf = 50 mm, K = 0.20 (Table 5, Figure 11).

Values from the primary ridge resolved shrimp from 11 to 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 to 19.5 mm classified as age-1, 20 to 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 (Figure 12).

Pooled Distribution: 1984-88

As with the annual distributions, an exploratory run was made with Linf 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. Two broad regions 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 to 1988 distributions in accordance with *a priori* assumptions.

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

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 a 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 through fourth assumed age groups in line with prior assumptions. These parameters also provided an age group-5 for CL greater than 27.5 mm. The quaternary ridge non-boundary maximum score parameters (Linf = 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 (Figure 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 (Figure 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:

$$Z = \ln(\Sigma \text{age } 2+ \text{ for Year}_N \;/\; \Sigma \text{age } 3+ \text{ for Year}_{N+1}).$$

These values were then compared with previously calculated estimates of total mortality from the length frequency data (Northern Shrimp Technical Committee MS 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 the neccessity of some external source of information to interpret SRLCA results in a manner consistent with a priori assumptions. As expected, use of the quaternary SRLCA score ridge parameters to age the length frequencies provided mortality estimates close to 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), Shepherd (1987), 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 a 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 mixure 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 encounted 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 were 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 Linf to within 10% of the CL of the largest animal, and/or 10% of an "average" Linf given previously derived parameters (e.g., 33 mm ± 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 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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Table 1. Von Bertalanffy growth parameter pairs and SRLCA score (S) for 1984 northern shrimp survey length frequency distribution: primary and secondary ridge crests.

Primary ridge crest

Linf(mm)	K	S
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

Linf(mm)	K	S
35	0.42	41.4[1]
40	0.30	37.4
36	0.37	40.3[2]*

1 - High score parameters of ridge crest, on boundary of explored space
2 - High score parameters of ridge crest, non-boundary maximum
* - Parameters selected for final evaluation

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.

Primary ridge crest

Linf(mm)	K	S
35	0.48	85.2[2]
40	0.34	82.6
45	0.26	78.7
50	0.21	75.2

Secondary ridge crest

Linf(mm)	K	S
42	0.50	63.0
46	0.41	69.7
50	0.34	74.1[1]

Tertiary ridge crest

Linf(mm)	K	S
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, non-boundary maximum
* - Parameters selected for final evaluation

Table 3. Von Bertalanffy growth parameter pairs and SRLCA score (S) for 1986 northern shrimp survey length frequency distribution: primary and secondary ridge crests.

Primary ridge crest

Linf(mm)	K	S
35	0.49	65.5
40	0.34	74.1
45	0.26	78.0
50	0.22	79.9[1]

Secondary ridge crest

Linf(mm)	K	S
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]*

1 - High score parameters of ridge crest, on boundary of explored space
2 - High score parameters of ridge crest, non-boundary maximum
* - Parameters selected for final evaluation

Table 4. Von Bertalanffy growth parameter pairs and SRLCA score (S) for 1987 northern shrimp survey length frequency distribution: primary and secondary ridge crests.

Primary ridge crest

Linf(mm)	K	S
35	0.50	55.0
40	0.36	57.1[2]
45	0.28	56.7
50	0.23	55.9

Secondary ridge crest

Linf(mm)	K	S
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, non-boundary maximum
* - Parameters selected for final evaluation

Table 5. Von Bertalanffy growth parameter pairs and SRLCA score (S) for 1988 northern shrimp survey length frequency distribution: primary and secondary ridge crests.

Primary ridge crest

Linf(mm)	K	S
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

Linf(mm)	K	S
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, non-boundary maximum
* - Parameters selected for final evaluation

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.

Primary ridge crest

Linf(mm)	K	S
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

Linf(mm)	K	S
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

1 - High score parameters of ridge crest, on boundary of explored space
2 - High score parameters of ridge crest, non-boundary maximum

Table 6 continued.

Tertiary ridge crest

Linf(mm)	K	S
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

Linf(mm)	K	S
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, non-boundary maximum
* - Parameters selected for final evaluation

Table 7. Age frequency matrices and instantaneous total mortality rates (Z) for northern shrimp estimated by growth parameters from SRLCA high score parameter ridges, compared with estimates using method of visual inspection of length modes (Northern Shrimp Technical Committee MS 1984; 1985; 1986; 1987; 1988; [NSTC]).

SRLCA

Primary score ridge

			Year		
Age	1984	1985	1986	1987	1988
1	2124	869	1421	1056	3111
2	845	2592	1787	1314	1107
3	0	0	0	0	0
4+	0	0	0	0	0

Z_{85}=---- Z_{86}=---- Z_{87}=---- Z_{88}=----

Secondary score ridge

			Year		
Age	1984	1985	1986	1987	1988
1	625	647	719	557	2829
2	1976	2042	1436	1217	797
3	368	773	1054	600	589
4+	0	0	0	0	0

Z_{85}=1.11 Z_{86}=0.98 Z_{87}=1.42 Z_{88}=1.13

Tertiary score ridge

			Year		
Age	1984	1985	1986	1987	1988
1	664	647	721	559	2832
2	1830	1812	1225	1053	675
3	405	859	818	528	491
4+	70	143	444	231	218

Z_{85}=0.83 Z_{86}=0.80 Z_{87}=1.32 Z_{88}=0.94

Quaternary score ridge

			Year		
Age	1984	1985	1986	1987	1988
1	246	637	704	540	2627
2	1970	478	898	613	625
3	415	1634	594	651	402
4+	337	712	1011	568	562

Z_{85}=0.15 Z_{86}=0.56 Z_{87}=0.72 Z_{88}=0.64

NSTC

Visual inspection

			Year		
Age	1984	1985	1986	1987	1988
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

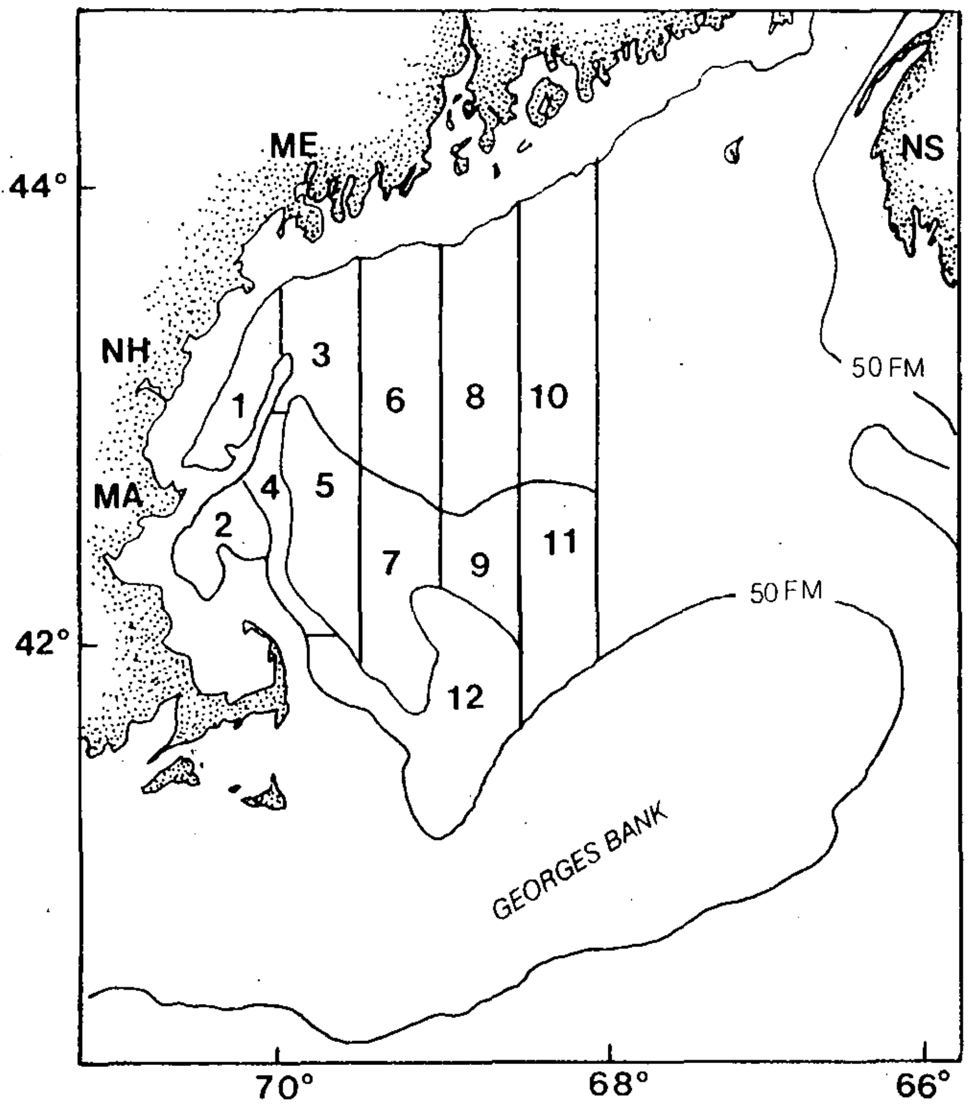

Figure 1. Western Gulf of Maine region with major bathymetric features and 50 fathom (100 m) isobath. Northern shrimp survey area extends from 68° W longitude to the 50 fathom isobath, except for stratum 2, where the sampled area extends to the 30 fathom (60 m) isobath.

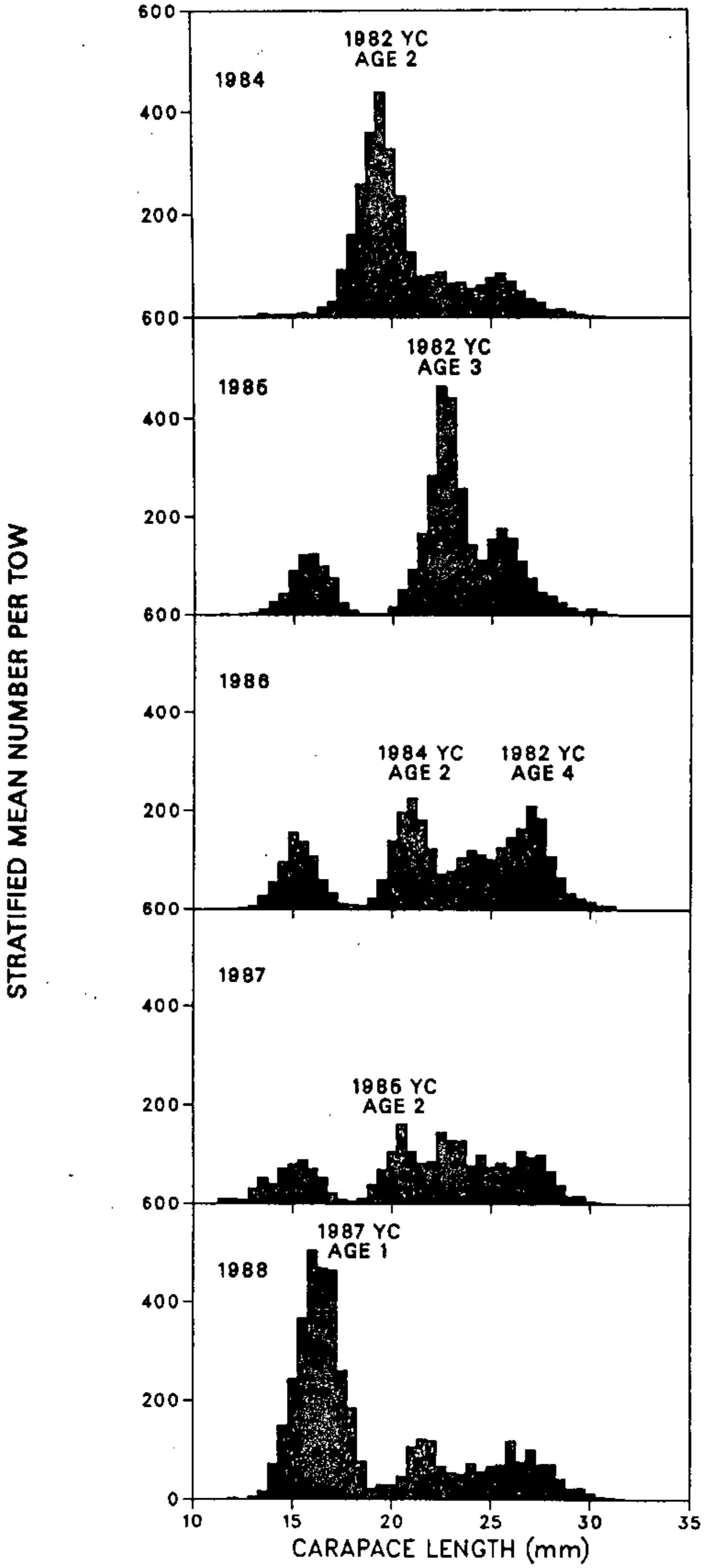

Figure 2. Length frequency distributions (stratified mean number per tow) for P. borealis collected in the western Gulf of Maine during the 1984-1988 northern shrimp surveys aboard R/V Gloria Michelle.

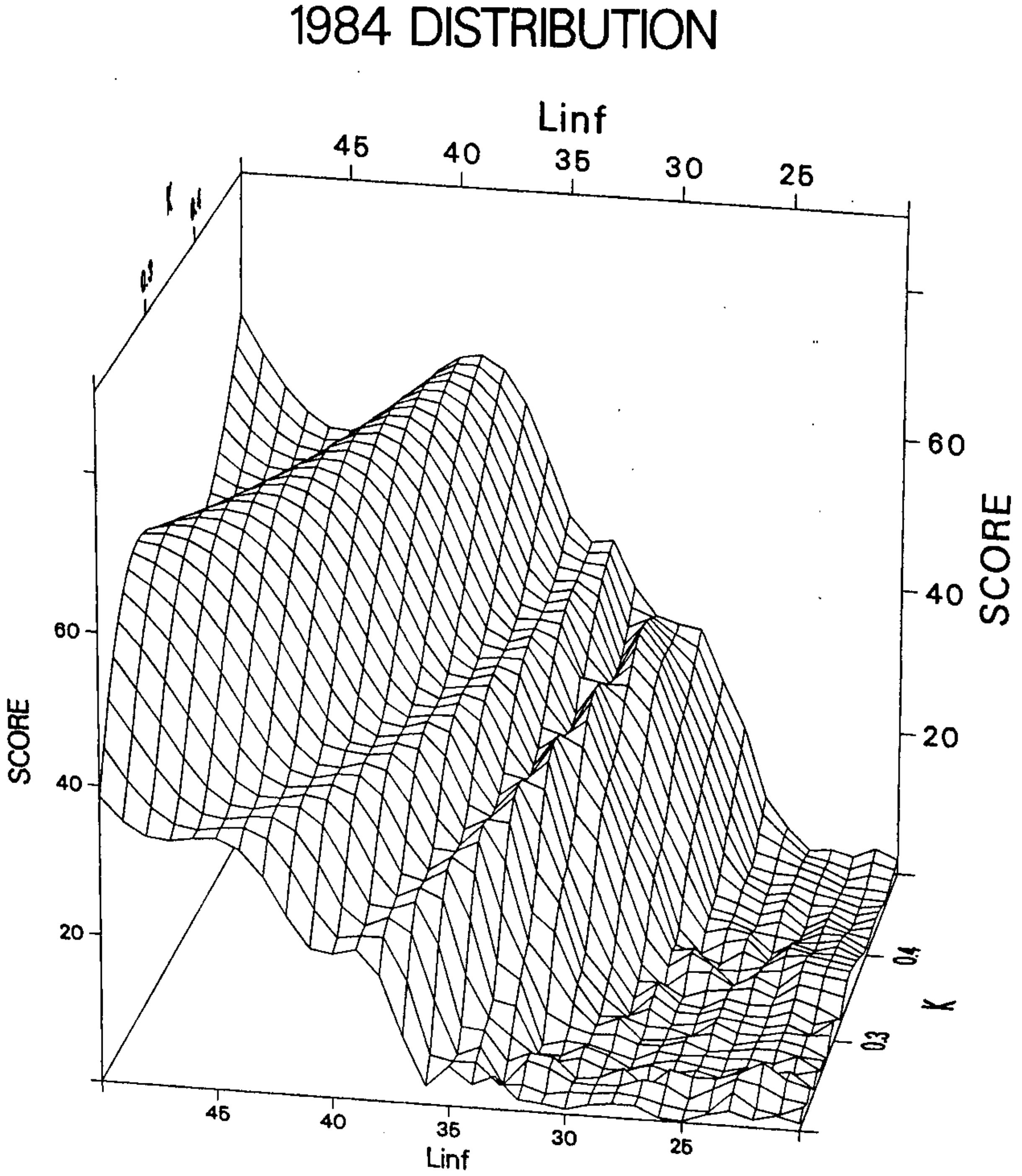

Figure 3. Response surface of the SRLCA score function for the Northern shrimp survey 1984 length frequency distribution.

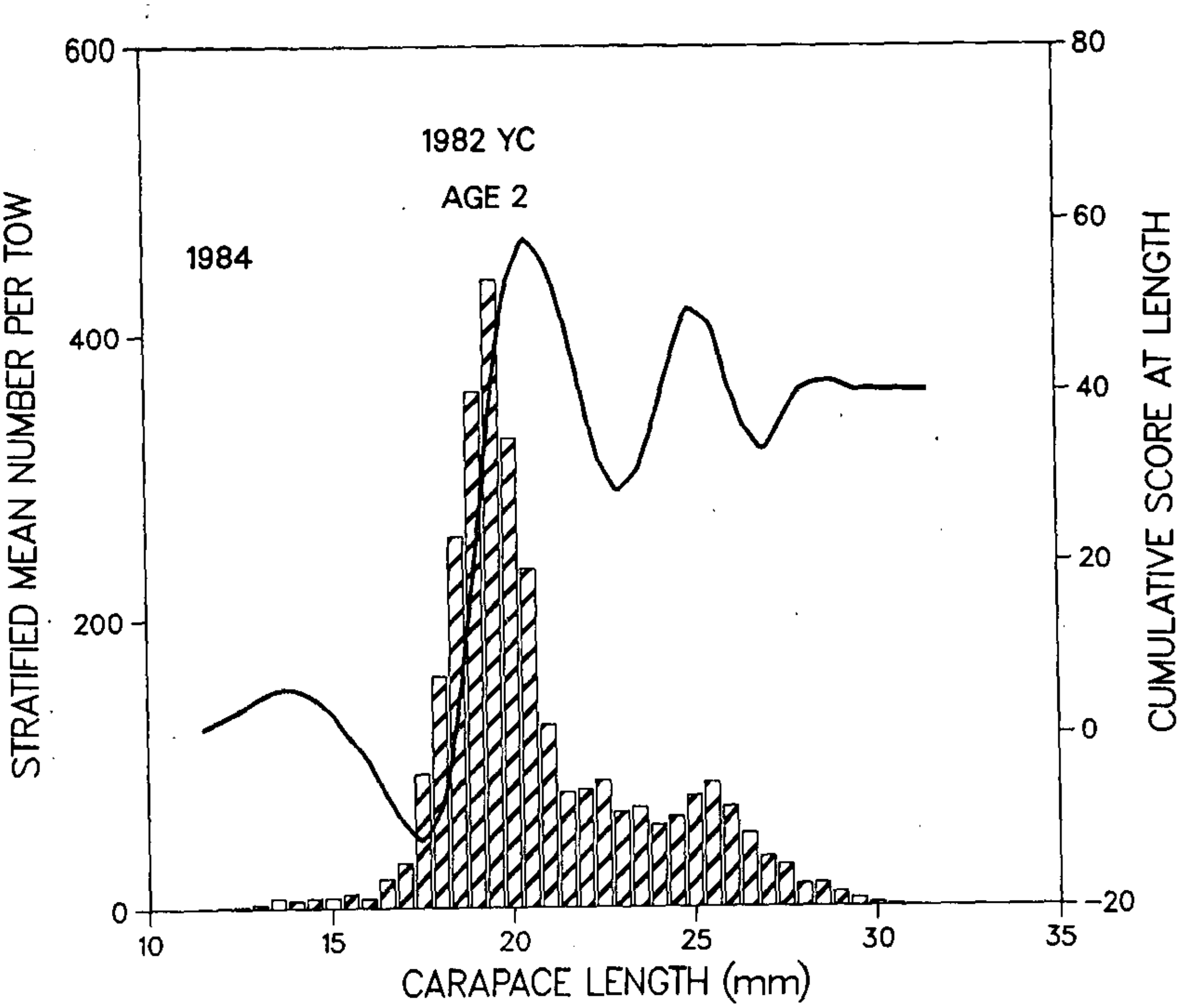

Figure 4. Northern shrimp survey 1984 length frequency distribution (histogram) and pattern of SRLCA scores (solid curve) for growth parameters selected for final evaluation (Linf = 36 mm, K = 0.37).

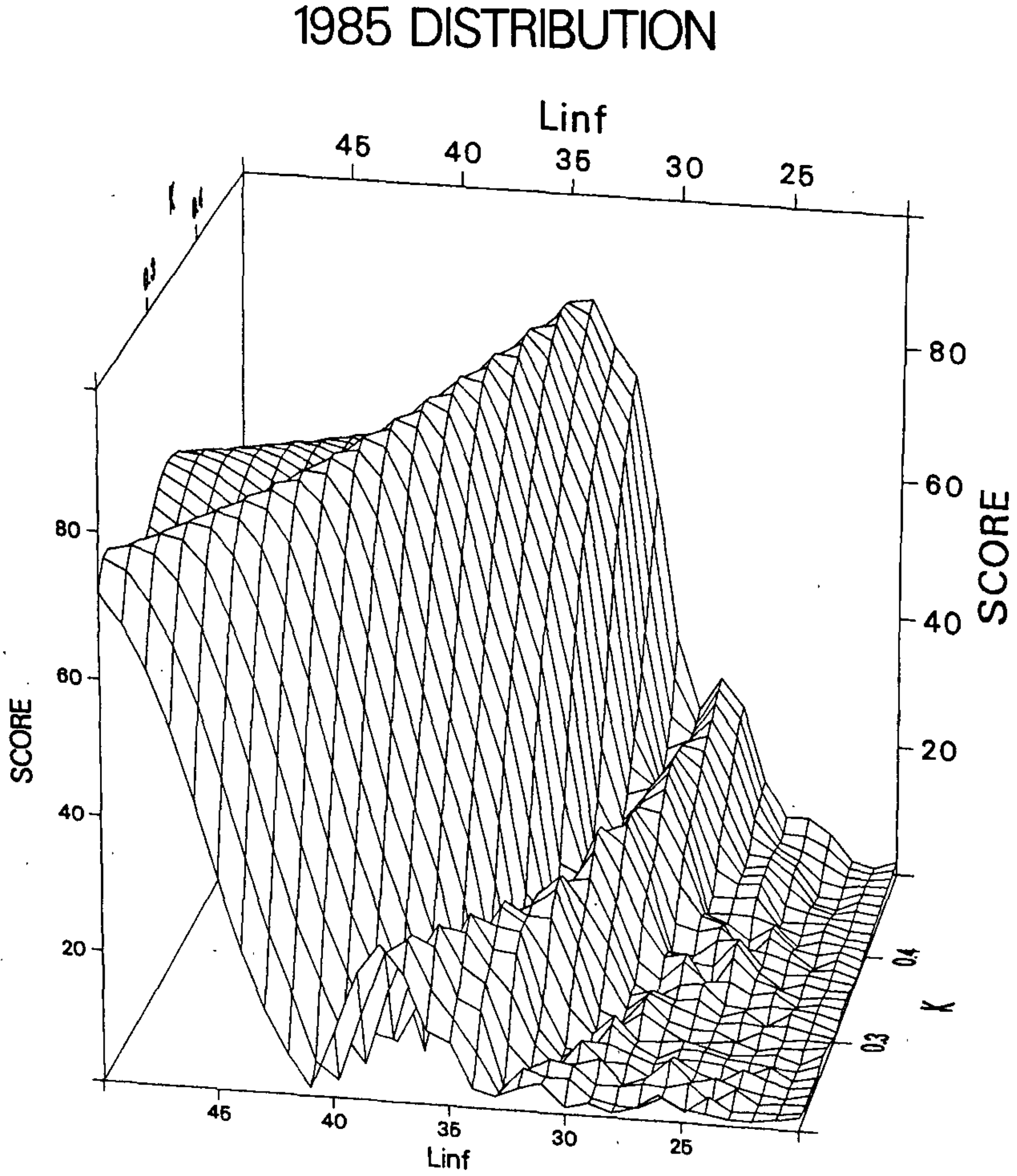

Figure 5. Response surface of the SRLCA score function for the Northern shrimp survey 1985 length frequency distribution.

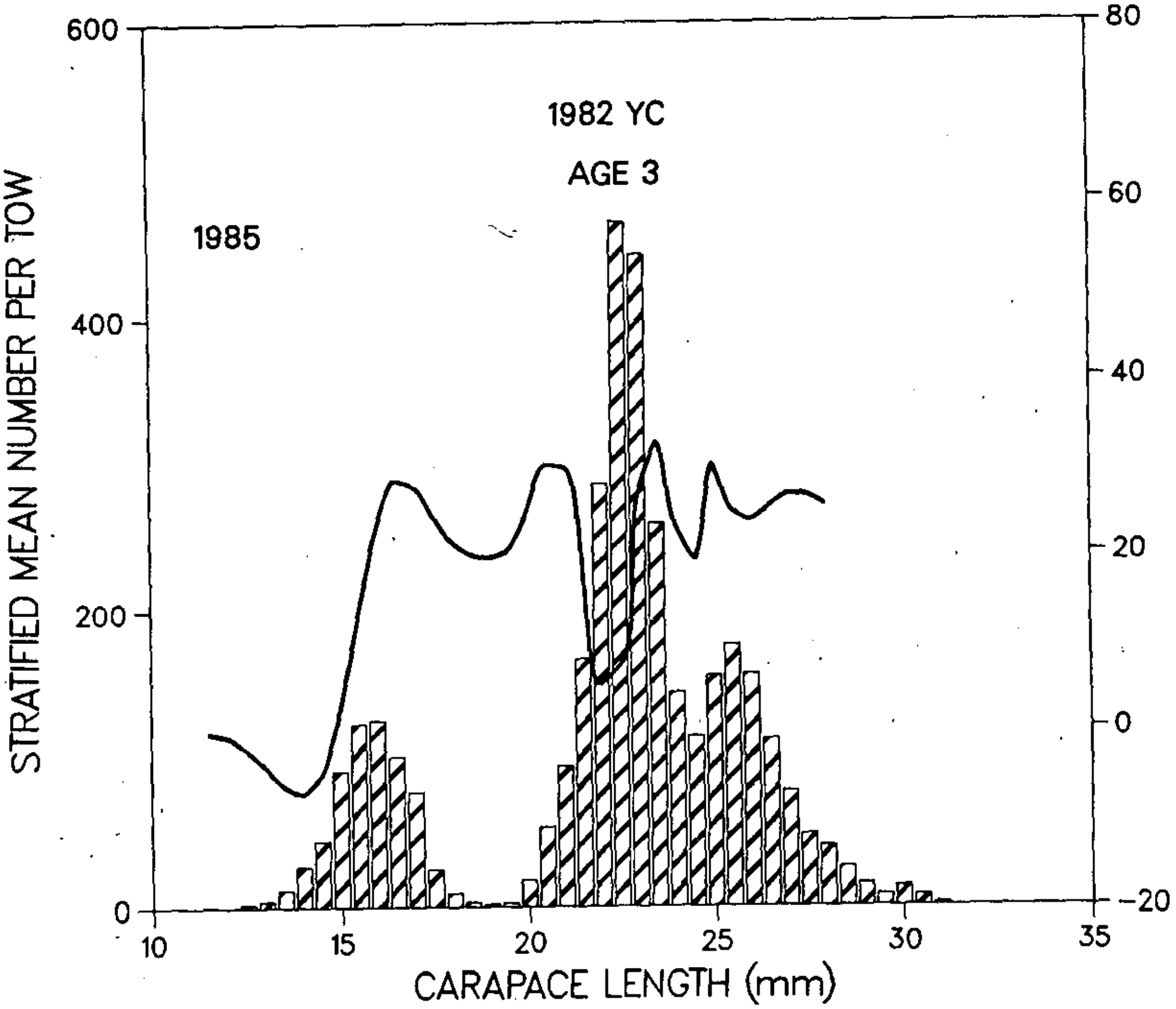

Figure 6. Northern shrimp survey 1985 length frequency distribution (histogram) and pattern of SRLCA scores (solid curve) for growth parameters selected for final evaluation (Linf = 29 mm, K = 0.42).

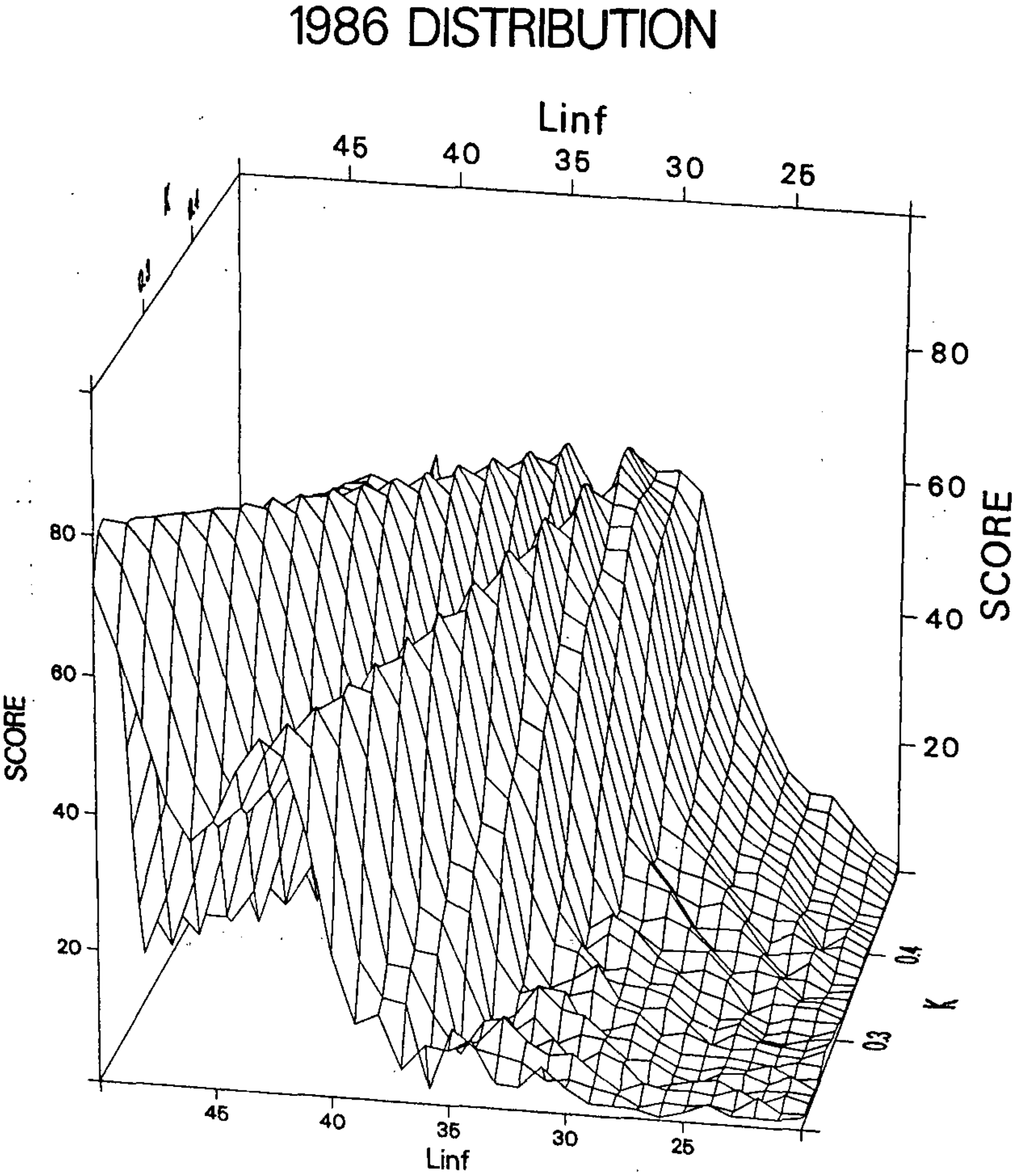

Figure 7. Response surface of the SRLCA score function for the Northern shrimp survey 1986 length frequency distribution.

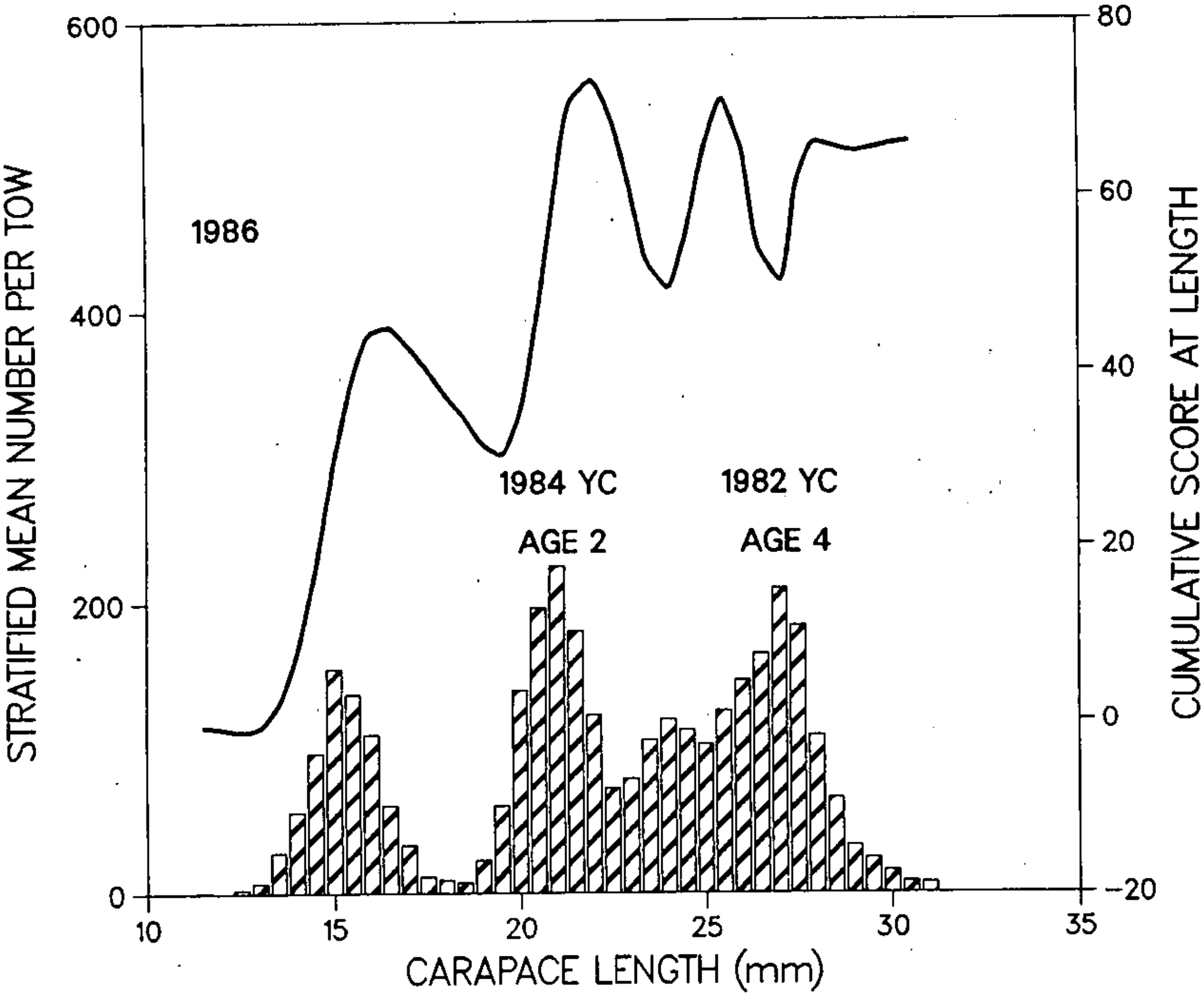

Figure 8. Northern shrimp survey 1986 length frequency distribution (histogram) and pattern of SRLCA scores (solid curve) for growth parameters selected for final evaluation (Linf = 33 mm, K = 0.42).

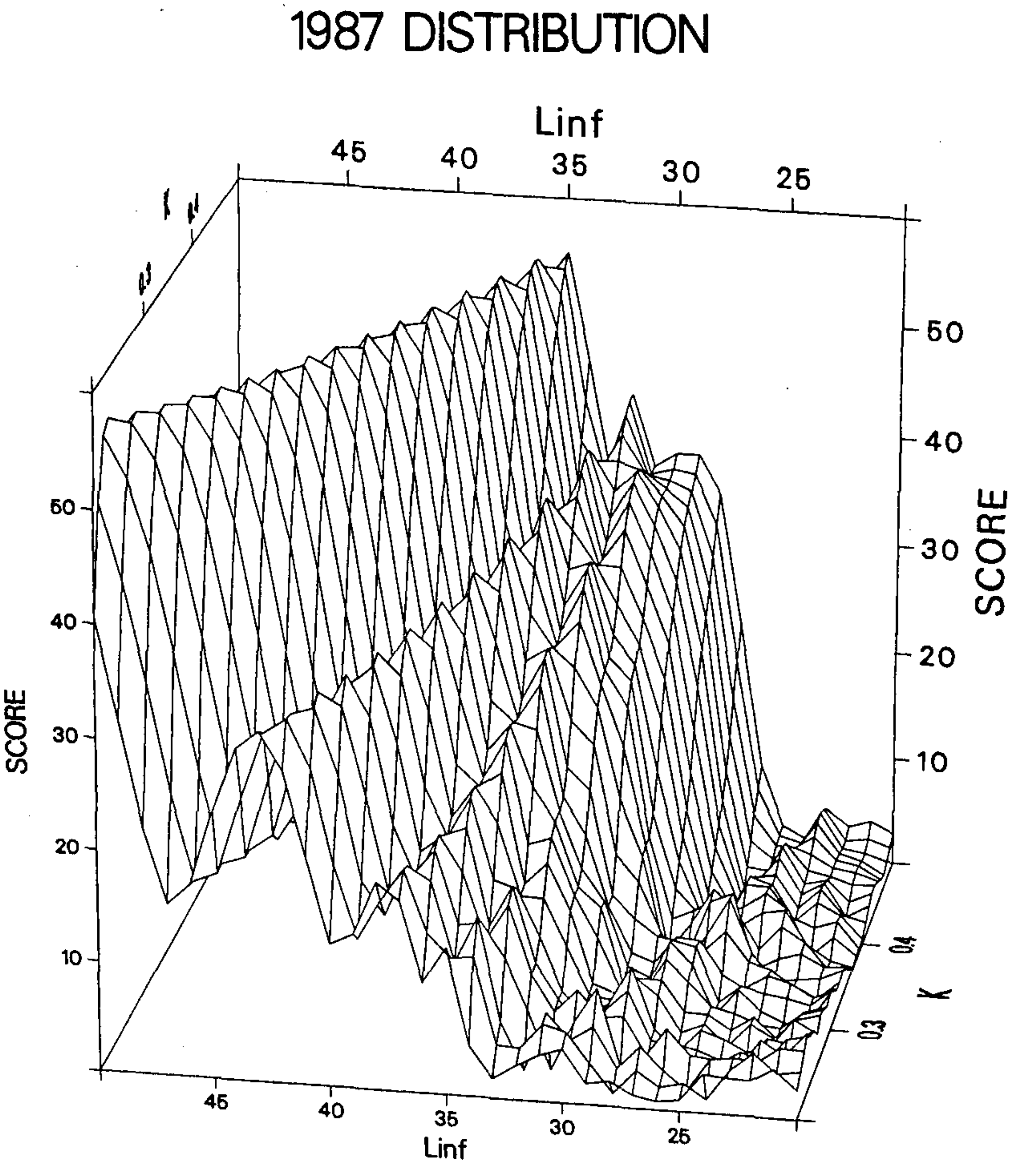

Figure 9. Response surface of the SRLCA score function for the Northern shrimp survey 1987 length frequency distribution.

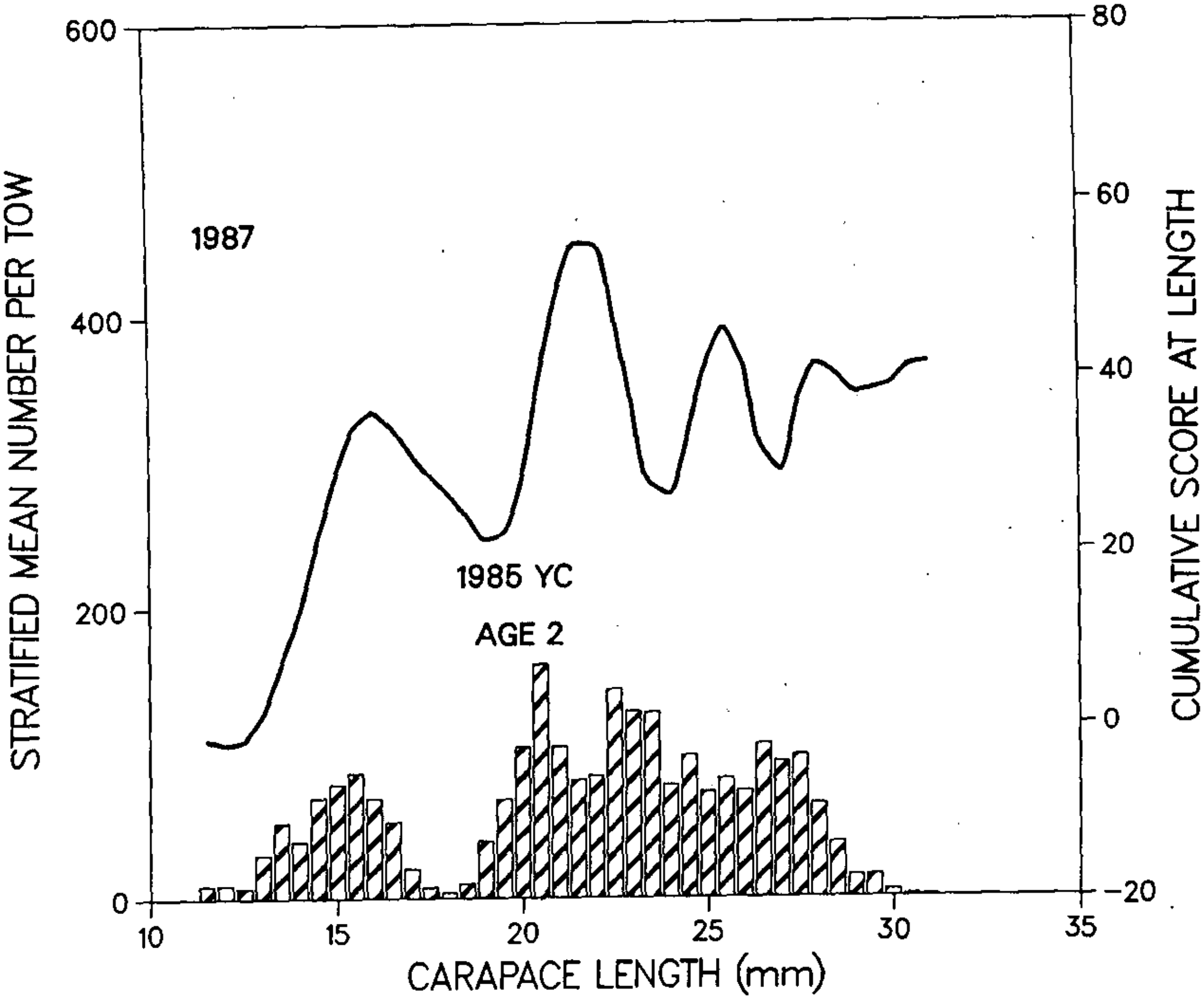

Figure 10. Northern shrimp survey 1987 length frequency distribution (histogram) and pattern of SRLCA scores (solid curve) for growth parameters selected for final evaluation (Linf = 33 mm, K = 0.43).

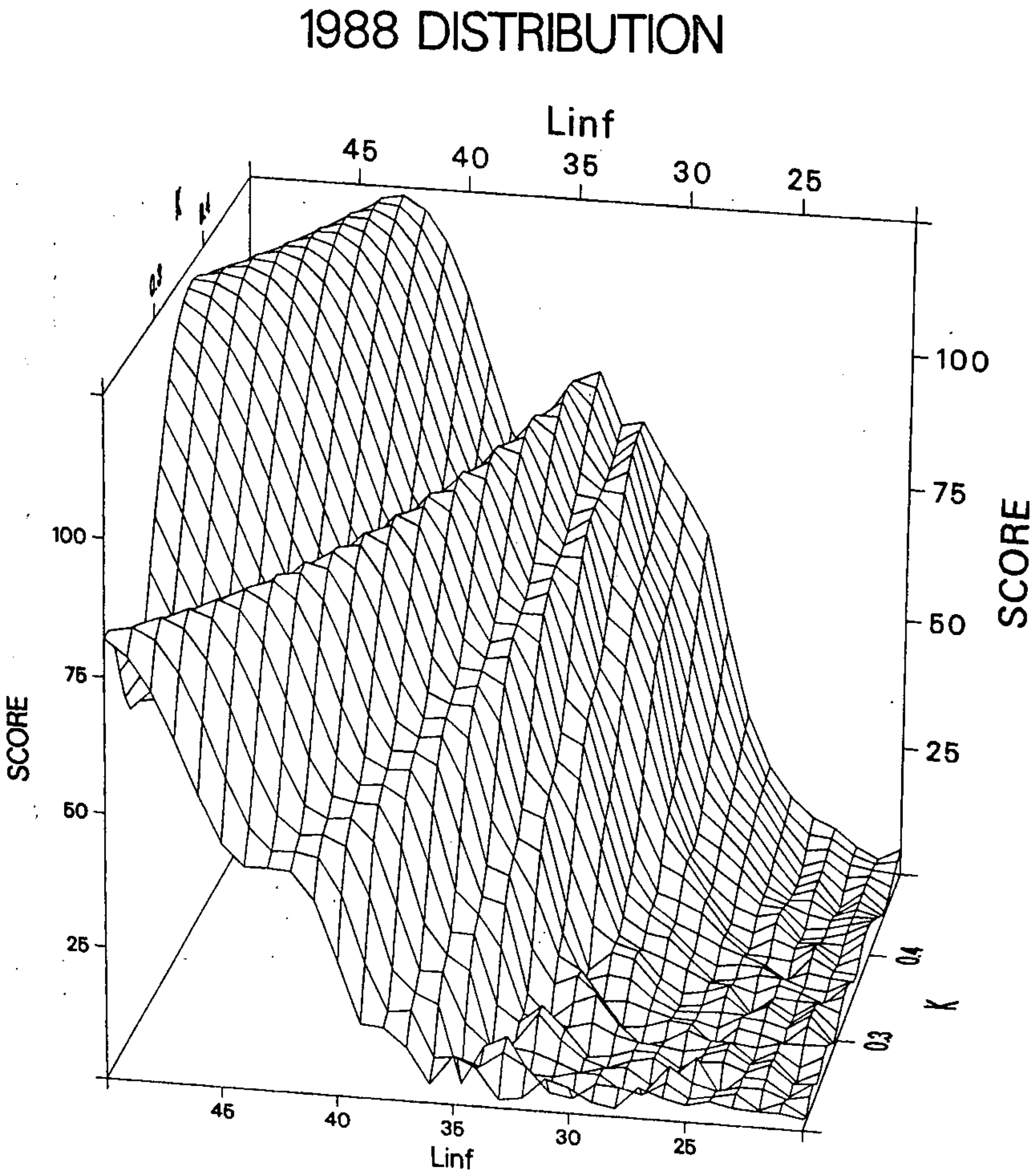

Figure 11. Response surface of the SRLCA score function for the Northern shrimp survey 1988 length frequency distribution.

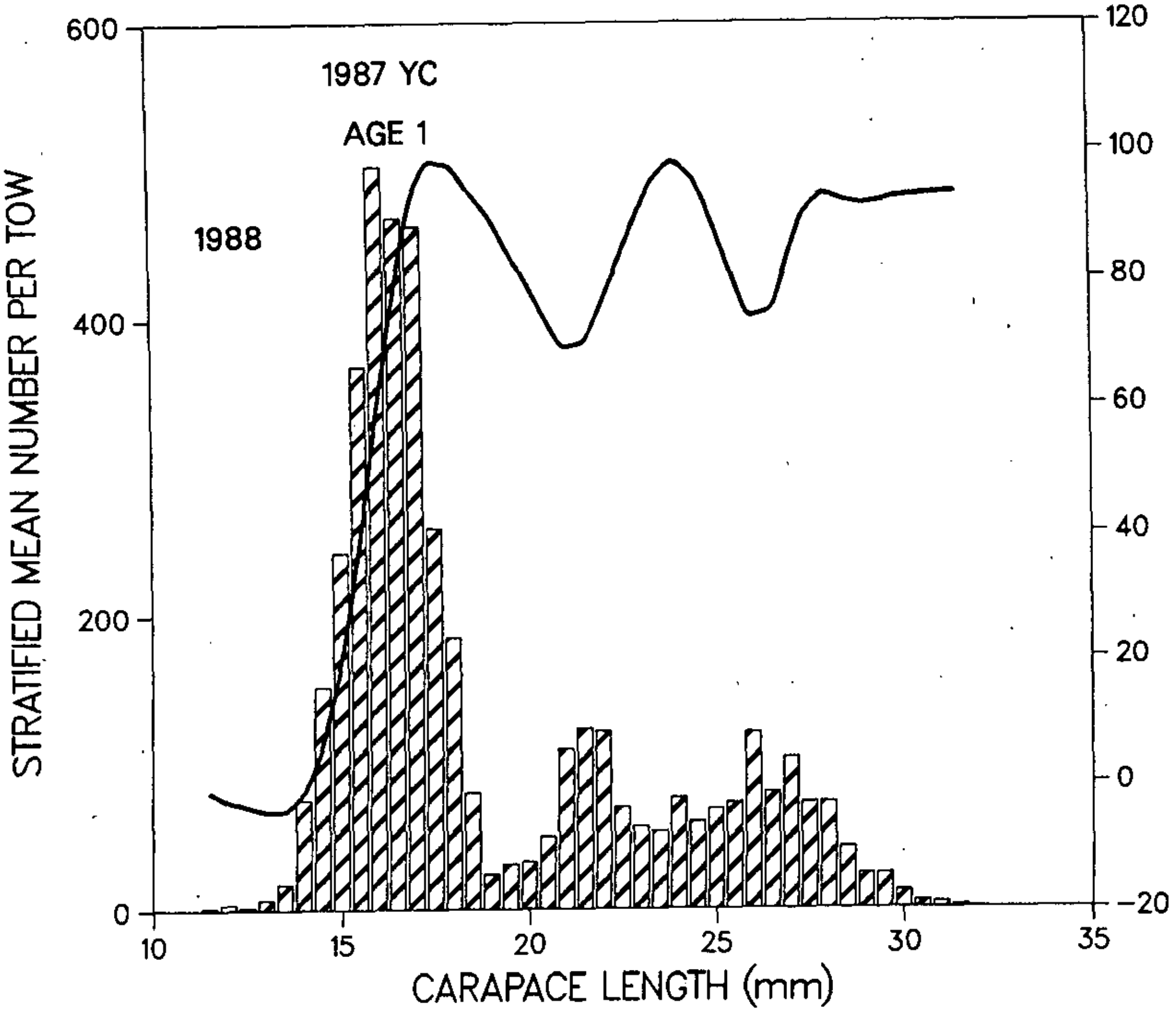

Figure 12. Northern shrimp survey 1988 length frequency distribution (histogram) and pattern of SRLCA scores (solid curve) for growth parameters selected for final evaluation (Linf = 35 mm, K = 0.47).

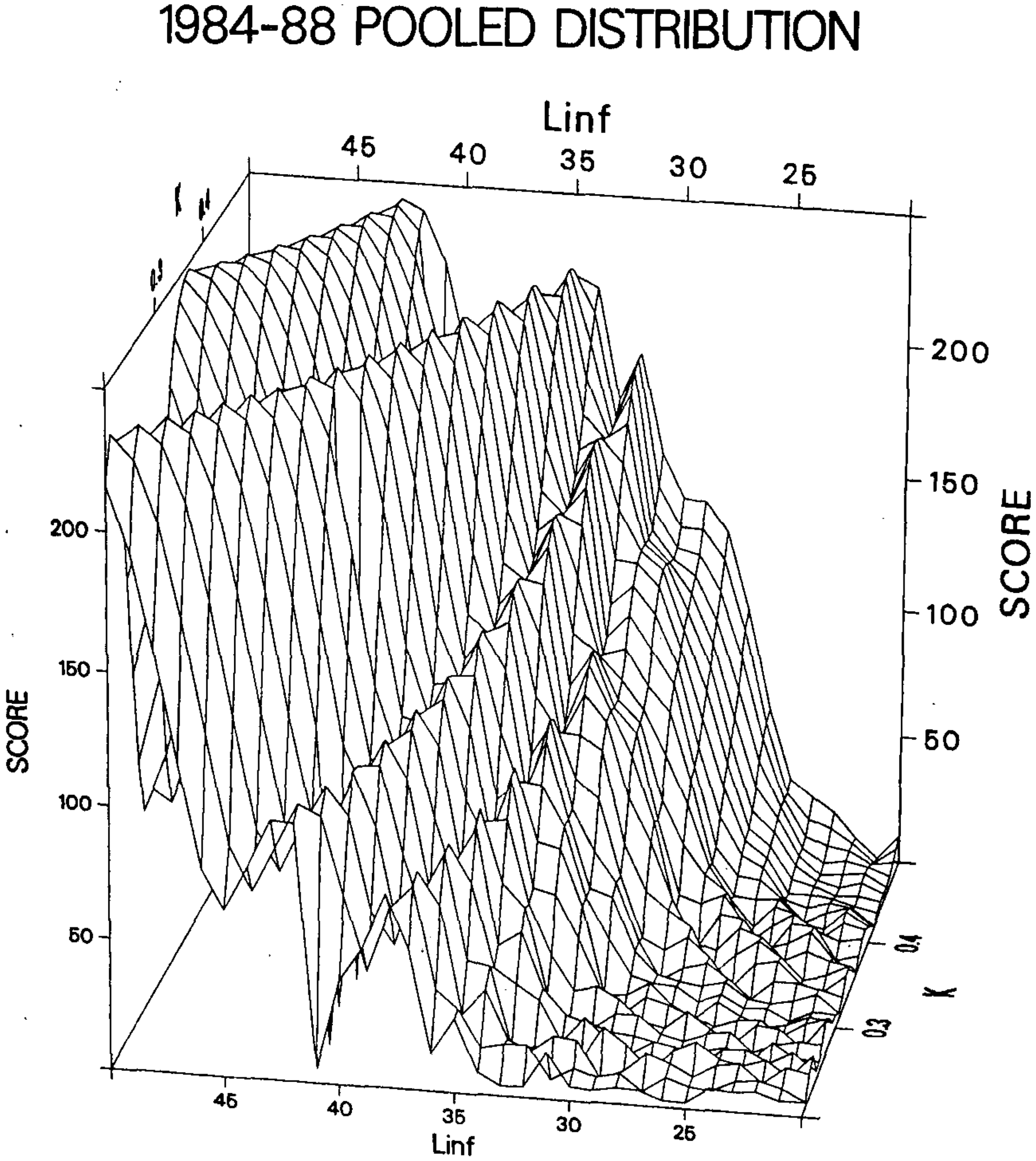

Figure 13. Response surface of the SRLCA score function for the Northern shrimp survey 1984-88 pooled length frequency distribution.

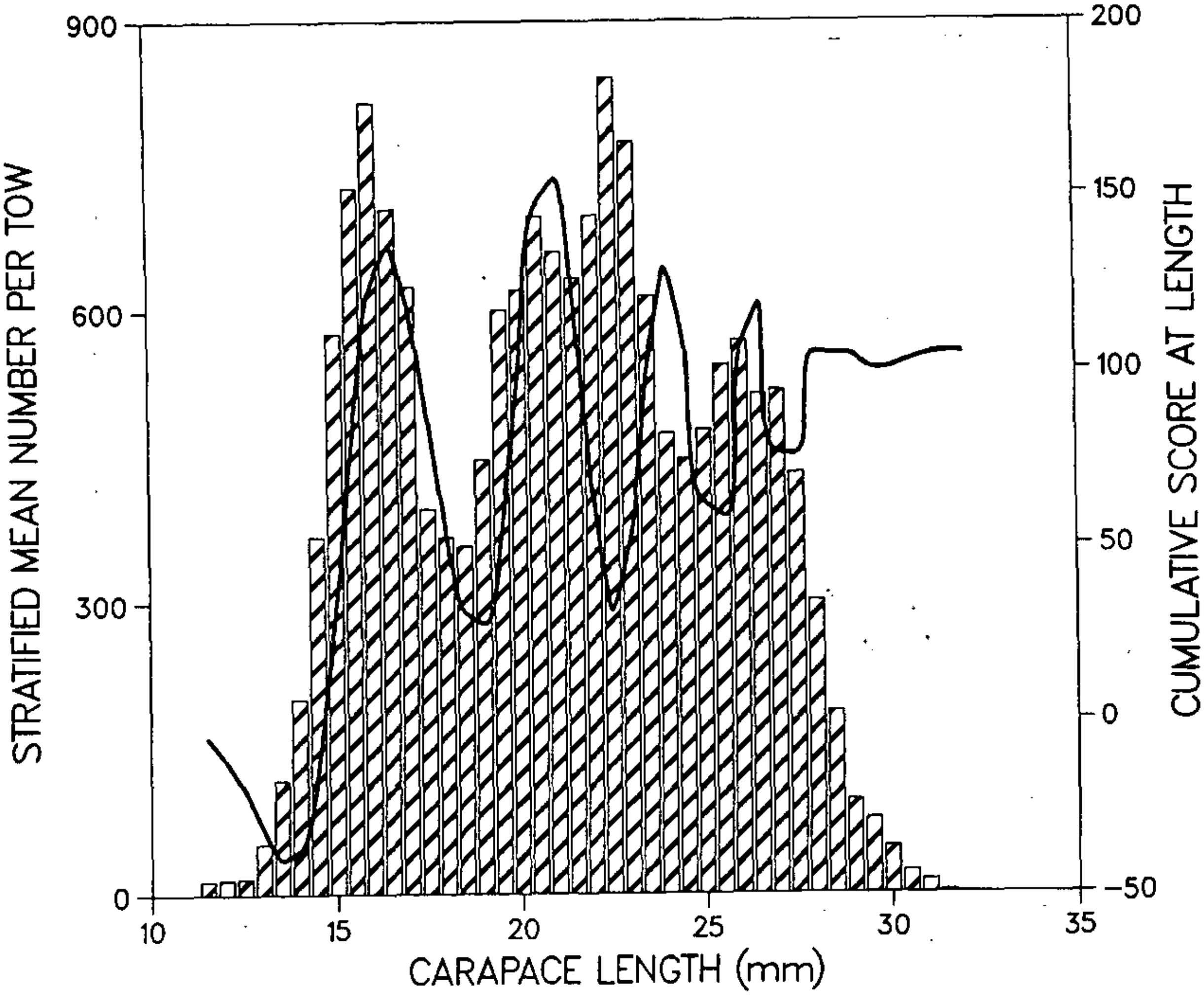

Figure 14. Northern shrimp survey 1984-88 pooled length frequency distribution (histogram) and pattern of SRLCA scores (solid curve) for growth parameters selected for final evaluation (Linf = 33 mm, K = 0.32).

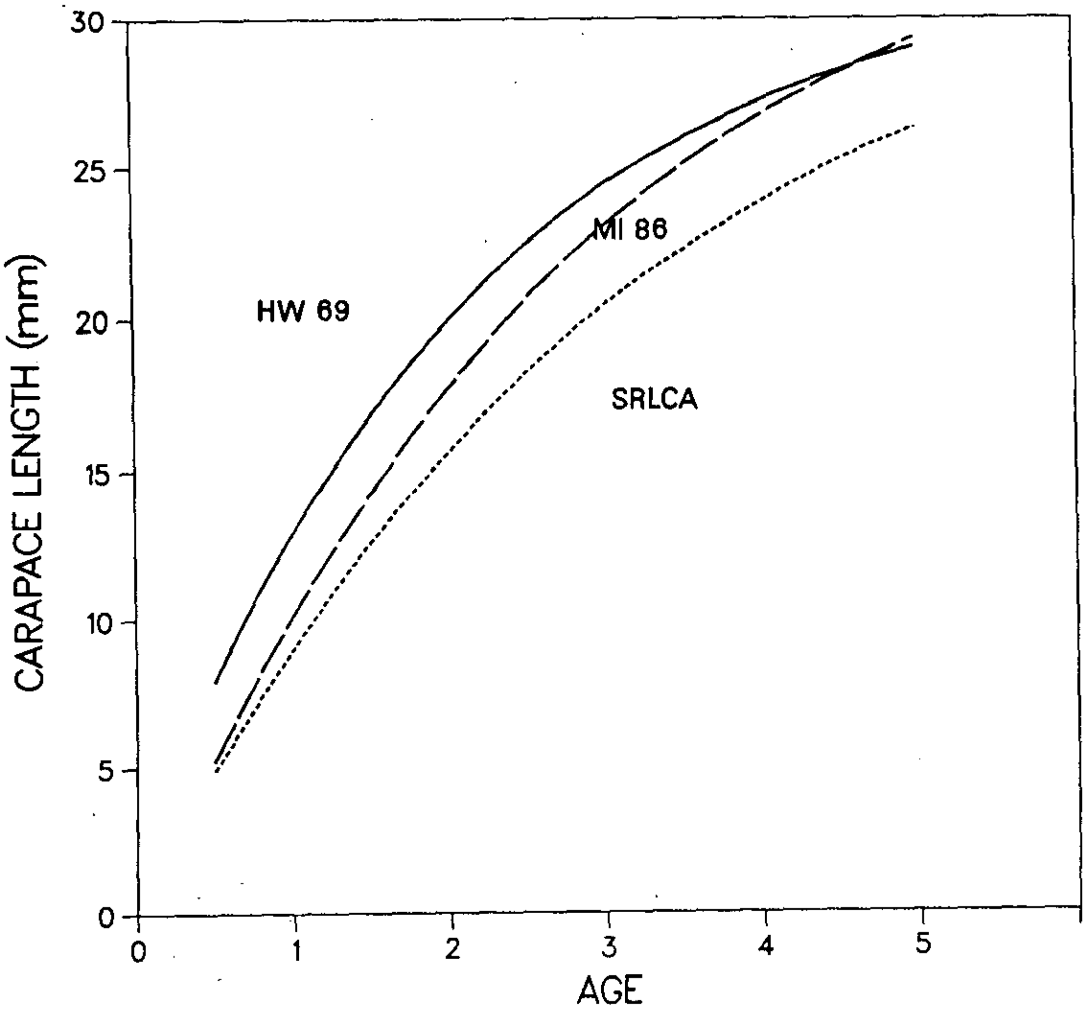

Figure 15. Von Bertalanffy growth curves for Gulf of Maine northern shrimp (P. borealis). Upper curve (solid line) is for parameters derived from age-length data in Haynes and Wigley (1969); center curve (large-dashed line) is for growth parameters cited in McInnes (1986); lower curve (small-dashed line) is for parameters derived by SRLCA for northern shrimp survey length frequency data.

Appendix Table 1. Derivation of von Bertalanffy growth parameters for Gulf of Maine northern shrimp, from data in Table 6 of Haynes and Wigley (1969): mean carapace length (mm) at age (years), by non-linear least squares procedure.

Age (years)	Mean mid-dorsal carapace length (mm)
0.50	8.1
0.83	11.2
1.17	14.0
1.50	16.7
1.83	19.0
2.17	20.8
2.50	22.4
2.83	23.8
3.17	24.9
3.50	25.8
3.83	26.6

ANOVA and statistics

Source	DF	SS	MS
Model	3	4520.82	1506.94
Error	8	0.17	0.02
Total	11	4520.99	
R-squared		0.99	

Parameter estimates

Parameter	Estimate
Linf	32 (mm)
K	0.46
t0	-0.12 (1/year)

Appendix Table 2. Length frequencies (stratified mean number per tow) for northern shrimp sampled in the western Gulf of Maine during northern shrimp survey, 1984-88 (survey strata 1,3, 5-8).

Mid-dorsal carapace length (mm)	Year				
	1984	1985	1986	1987	1988
11.5	0.6	0.7	0.8	9.7	2
12.0	0.9	0.2	0.2	9.5	4
12.5	1.5	2.2	2.6	7.9	2
13.0	2.9	4.3	7.1	30.4	7
13.5	7.1	11.9	28.0	52.7	18
14.0	5.5	27.0	56.0	39.7	74
14.5	6.9	44.6	96.7	70.2	151
15.0	6.9	91.4	156.0	79.1	243
15.5	9.6	122.9	138.3	87.5	368
16.0	6.6	125.7	109.7	69.6	503
16.5	20.1	100.8	61.1	53.4	469
17.0	31.1	77.4	33.0	20.9	463
17.5	92.8	25.0	11.6	8.0	260
18.0	160.7	9.3	9.3	4.2	185
18.5	258.5	3.0	7.6	10.4	79
19.0	359.7	2.0	22.5	39.5	24
19.5	438.8	2.7	60.4	68.5	31
20.0	327.2	17.6	140.6	104.7	32
20.5	235.3	53.6	197.2	161.2	49
21.0	126.7	94.4	225.4	105.0	109
21.5	79.9	167.0	181.7	81.7	123
22.0	82.2	285.7	123.6	84.6	121
22.5	88.4	464.5	72.8	144.3	69
23.0	66.1	442.3	79.1	129.1	56
23.5	69.1	259.2	106.0	128.1	53
24.0	56.7	144.1	120.2	78.2	75
24.5	62.5	114.4	112.9	98.9	59
25.0	77.5	155.6	103.1	73.6	68
25.5	86.6	176.9	126.6	82.5	72
26.0	69.6	156.7	147.7	74.3	120
26.5	51.0	112.4	165.8	106.2	79
27.0	34.9	77.2	210.1	94.1	103
27.5	29.2	48.1	185.1	98.7	72
28.0	15.9	40.2	109.1	65.3	72
28.5	16.6	25.8	65.7	38.4	42
29.0	10.0	14.7	32.7	15.5	24
29.5	5.9	7.5	23.8	15.5	24
30.0	2.2	13.2	15.2	5.0	12
30.5	1.3	7.2	8.1	1.3	5
31.0	0.0	1.7	7.1	0.9	4
31.5	0.1	0.0	0.0	0.0	2
32.0	0.0	0.0	0.0	0.0	0
Total	3004.9	3531.1	3360.5	2448.3	4328