

MULTIFAN-CL: a length-based, age-structured model for fisheries stock assessment, with application to South Pacific albacore, *Thunnus alalunga*

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Abstract: We introduce a length-based, age-structured model, MULTIFAN-CL, that provides an integrated method of estimating catch age composition, growth parameters, mortality rates, recruitment, and other parameters, from time series of fishery catch, effort, and length frequency data. The method incorporates Bayesian parameter estimation, estimation of confidence intervals for model parameters, and procedures for hypothesis testing to assist model development. We apply the method to South Pacific albacore (*Thunnus alalunga*) fishery data, and demonstrate the incorporation of model structure such as spatial heterogeneity, age-dependent natural mortality and movement rates, time series trends and seasonal variation in catchability, and density-dependent growth. Consistency of the results of the albacore analysis with various exogenous sets of biological and environmental data give credence to the model results.

Introduction

Age-structured models are now the method of choice for many fisheries stock assessments. Models range from simple deterministic methods, such as virtual population (or cohort) analysis (Megrey 1989), to statistical models, in which variability in the data and various population processes is acknowledged (Doubleday 1976; Paloheimo 1980; Fournier and Archibald 1982; Pope and Shepherd 1982; Dupont 1983; Deriso et al. 1985; Schnute and Richards 1995; McAllister and Ianelli 1997).

Statistical age-structured models are superior to deterministic models in that they permit the estimation of confidence intervals for the parameter estimates. This allows uncertainty in stock assessments to be incorporated into management advice through decision or risk analysis. Bayesian approaches to age-structured models (McAllister and Ianelli 1997; Punt

and Hilborn 1997) now provide a powerful framework for undertaking integrated analysis of fish stocks and for expressing the full range of uncertainty in the resulting advice given to fisheries management authorities.

A second advantage of statistical age-structured models is that they provide an objective means of comparing model hypotheses regarding alternative "states of nature". In a maximum-likelihood framework, the usual frequentist approach of testing nested models using likelihood-ratio tests can be applied. In the Bayesian framework, the posterior odds of competing models can be computed. In either case, statistical guidance can be obtained regarding an appropriate model structure for the case at hand.

Both deterministic and statistical catch-at-age models rely on catch-at-age data. These are sometimes derived from the analysis of annuli on various body parts of individual fish. Perhaps more commonly, age composition is derived from length frequency samples using an age-length relationship prior to the age-structured analysis taking place. In this type of sequential approach, the variability in length-at-age is often ignored. It would be preferable to estimate catch-at-age from the length frequency data and the parameters of the age-structured model simultaneously. In this way, parameter estimates would be conditioned on the length data rather than the catch-at-age estimates.

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In this paper, we describe an age-structured model that extends the MULTIFAN method of estimating catch age composition from length composition (Fournier et al. 1990). The new model is called MULTIFAN-CL (Catch at Length). The major extension concerns the parameterization of the proportions-at-age in the length frequency samples. In the original MULTIFAN, the proportions-at-age are free parameters. Fournier et al. (1991) extended the model using a “survey sample” parameterization, in which the length samples are assumed to be random samples of the population (with optional selectivity parameters for the initial age classes). In MULTIFAN-CL, we assume that the length samples are taken from the catch of an age-structured fish population; the proportions-at-age in the length samples are therefore constrained by the catch equations that express the age-structured population dynamics. The model is fully integrated – growth and catch-at-age structure are estimated simultaneously with recruitment, selectivity, catchability, natural mortality, and other parameters. Except for the parameterization of the proportions-at-age, the same likelihood function is employed for the length frequency data in all versions of the MULTIFAN model.

The Bayesian framework of the model is amenable to the formulation and testing of various hypotheses regarding the dynamics of the stock. Some of the model hypotheses that we formulate and test in this paper include spatial structuring of the population and fisheries, density-dependent growth, seasonal cycles in catchability, age-dependent rates of natural mortality, and age-dependent fish movement. The model is applied to catch, effort and length frequency data for South Pacific albacore, *Thunnus alalunga*.

Data structures

The fundamental data structure of the model is a “fishery”, which is defined as a collection of fishing units having similar catchability and selectivity characteristics with respect to the target species. Fisheries may be specific to geographical regions if spatial heterogeneity in the population and fisheries is to be modeled.

Each occurrence of a fishery at a particular time is termed a fishing incident. In reality, fishing is more or less continuous, so the data for each fishery need to be aggregated over appropriate time intervals. Each

fishing incident is associated with a data record, which is made up of an estimate of the total catch (in number of fish), the total effort and a length-frequency sample. Effort and the length-frequency sample may be missing for some fishing incidents.

The catch equations

The catch equations govern the dynamics of the exploited age-structured population. To demonstrate the addition of spatial structure, we assume a one-dimensional, three-region spatial configuration. More complicated spatial structure could be accommodated within the model framework, as warranted by the particular application. For simplicity of notation it is assumed that there is only one fishery operating in each region and that there is only one fishing incident per fishery per year. The model is easily generalized to accommodate a variable number of fisheries per region and fishing incidents per fishery per year.

The catch equations are as follows:

$$(1) \quad C_{ijk} = \frac{F_{ijk}}{Z_{ijk}} \left[1 - \exp(-Z_{ijk}) \right] N_{ijk} \quad 1 \leq i \leq n, \\ 1 \leq j \leq a, 1 \leq k \leq r$$

$$(2) \quad T_{i+1,j+1,k} = \exp(-Z_{ijk}) N_{ijk} \quad 1 \leq i \leq n, \\ 1 \leq j < a, 1 \leq k \leq r$$

$$(3) \quad T_{i+1,ak} = \exp(-Z_{i,a-1,k}) N_{i,a-1,k} + \\ \exp(-Z_{iak}) N_{iak} \quad 1 \leq i < n, 1 \leq k \leq r$$

$$(4) \quad T_{i1k} = \xi_k R_i \\ 1 \leq i < n, 1 \leq k \leq r, \sum_k \xi_k = 1, \xi_k \geq 0$$

$$(5) \quad N_{ijk} = \sum_l b_{jkl} T_{ijl} \\ 1 \leq i \leq n, 1 \leq j \leq a, 1 \leq k \leq r, 1 \leq l \leq r$$

$$(6) \quad Z_{ijk} = F_{ijk} + M_{ijk} \\ 1 \leq i \leq n, 1 \leq j \leq a, 1 \leq k \leq r$$

$$(7) \quad C_{i \cdot k} = \sum_j C_{ijk} \quad 1 \leq i \leq n, 1 \leq j \leq a, 1 \leq k \leq r$$

where i indexes year, j indexes age class, k indexes region, n is the number of years of fishing, a is the number of age classes in the population, r is the number of regions, C_{ijk} is the catch (in number of fish) of age class j fish in region k in year i , $C_{i\cdot k}$ is the total catch observed in region k in year i , F_{ijk} is the instantaneous fishing mortality rate of age class j fish in region k in year i , M_{ijk} is the instantaneous natural mortality rate of age class j fish in region k in year i , Z_{ijk} is the instantaneous total mortality rate for age class j fish in region k in year i , T_{ijk} is the number of age class j fish in the population in region k at the beginning of year i before movement has taken place, N_{ijk} is the number of age class j fish in the population in region k at the beginning of year i after movement has taken place, R_i is the recruitment at the beginning of year i , ξ_k is the proportion of recruitment occurring in region k , and \mathbf{b}_{kl} is a k by k diffusion matrix \mathbf{B}_j for age class j fish.

The cumulative age class (a) is designed to group fish above an age where they can be assumed to have insignificant growth (Fournier et al. 1991).

Movement hypothesis

The inclusion of spatial structure in the model requires the specification of a movement hypothesis. In the South Pacific albacore example, we use a one-dimensional diffusion model operating in three regions ($r=3$). In this case, the elements of \mathbf{B}_j are given by

$$(8) \quad \mathbf{B}_j = \begin{bmatrix} 1 + \mathbf{n}_j & -d_2 \mathbf{n}_j & 0 \\ -\mathbf{n}_j & 1 + 2d_2 \mathbf{n}_j & -d_3 \mathbf{n}_j \\ 0 & -d_2 \mathbf{n}_j & 1 + d_3 \mathbf{n}_j \end{bmatrix}^{-1}$$

where 1 , $d_2 > 0$ and $d_3 > 0$ specify the relative distribution of cohort abundance among regions at equilibrium and \mathbf{n}_j is the age-dependent diffusion rate. We employ a flexible parameterization of \mathbf{n}_j which can result in increasing, decreasing or constant diffusion rate with increasing age:

$$(9) \quad \mathbf{n}_j = \mathbf{f}_0 \exp \left\{ \mathbf{f}_1 \left[-(-\mathbf{k}_j)^{f_2} \right] \right\}$$

$$\mathbf{f}_0 \geq 0, \mathbf{f}_1 \geq 0, \mathbf{k}_j < 0$$

$$\mathbf{n}_j = \mathbf{f}_0 \exp \left\{ \mathbf{f}_1 \mathbf{k}_j^{f_2} \right\}$$

$$\mathbf{f}_0 \geq 0, \mathbf{f}_1 \geq 0, \mathbf{k}_j \geq 0$$

where $\mathbf{k}_j = \frac{2(j-1)}{a-1} - 1$, which expresses age scaled between -1 and 1.

Assumptions regarding constraints on natural and fishing mortality rates

A fundamental characteristic of statistical age-structured models is that they constrain the variation of mortality rates by age and time in a regular fashion. Constraints are placed separately on the variability of natural and fishing mortality rates.

Natural mortality

In the South Pacific albacore application, we assumed that the instantaneous natural mortality rate is independent of year and region, but may vary with age. Later, we show that this age dependency is supported by the data. For a given application, a range of more and less restrictive constraints on natural mortality can be tested.

Fishing mortality

We restrict the variation in the instantaneous fishing mortality rates F_{ijk} according to the ‘‘separability’’ assumption (Doubleday 1976; Paloheimo 1980; Fournier and Archibald 1982), which partitions F_{ijk} into an age-dependent effect (selectivity) and a time-dependent effect (catchability). Consider for simplicity an individual fishery (i.e., drop the k subscript). We assume that

$$(10) \quad \log(F_{ij}) = \log(s_j) + \log(q_i) + \log(E_i) + \mathbf{e}_i$$

$$(11) \quad \log(q_{i+1}) = \log(q_i) + \mathbf{h}_i$$

where s_j is the selectivity for age class j (assumed constant over time), q_i is the catchability in year i , E_i is the observed fishing effort in year i , \mathbf{e}_i are

normally distributed random variables representing large transient deviations in the effort–fishing mortality relationship (or simply, effort deviations), and h_i are normally distributed random variables representing small permanent changes in catchability.

Selectivity can be modeled as a function of age class, for example using a gamma function (Deriso et al. 1985). We have preferred to allow the s_j to be separate parameters but have applied a transformation that makes selectivity a length-based rather than an age-based concept (Appendix). The transformation ensures relatively small differences in s_j between adjacent age classes having large overlap of their length distributions, as would be expected where selectivity is fundamentally length-based.

Catchability is allowed to vary slowly over time. Following a concept introduced by Gudmundsson (1994), we assume that the q_i have the time series structure of a random walk (equation 11), which is the simplest statistical model of a slowly varying random quantity. We make the prior assumption that the variance of h_i is small compared to e_i .

Random walk steps can be taken at each successive fishing incident, or less frequently, as might be appropriate when multiple fishing incidents by one fishery occur within a year or fishing season. In the albacore analysis, random walk steps are taken annually for all fisheries.

Where the frequency of fishing incidents is greater than one per year, we may allow catchability within a year to vary with a regular seasonal pattern. Equation (10) then becomes

$$(12) \quad \log(F_{ij}) = \log(s_j) + \log(q_i) + \log(E_i) + c_1 \sin[24\mathbf{P}(m - c_2)] + e_i$$

where m is the month in which the fishing incident occurred and c_1 and c_2 are the seasonality parameters.

Assumptions regarding length-at-age

MULTIFAN-CL uses length data to estimate catch-at-age and therefore makes assumptions concerning the length distribution of the fish. These assumptions are identical to those used in Fournier et al. (1990), to which the reader is referred for details. The assumptions are (i) the lengths of the fish in each age

class are normally distributed, (ii) the mean lengths-at-age lie on (or near) a von Bertalanffy growth curve, and (iii) the standard deviations of the lengths for each age class are a linear function of the mean length-at-age.

We have introduced an additional, optional hypothesis concerning density-dependent growth, which can be incorporated into an analysis if warranted by the data. For many species it is suspected that individuals of weak cohorts may grow faster than those of more abundant cohorts (i.e., density-dependent growth). If true, this phenomenon could have a large effect on the conclusions drawn from a length-based stock assessment.

Let R_b be the normalized relative cohort strength for cohort b such that $R_b = (N_{bt} - \bar{R}) / s_R$, where \bar{R} and s_R are the mean and standard deviation of recruitment. The changes in mean length are effected by adjusting the apparent age (i.e., the age implied from the length using the inverse of the growth function) of the fish before the length-at-age is calculated. For fish of cohort b j years after recruitment, the adjusted age j' is

$$(13) \quad j' = j + 1.9 \left[\frac{1}{1 + \exp(-gR_b)} - 0.5 \right]$$

where g is a parameter determining the amount of density-dependent growth; if $g = 0$, $j' = j$. Since the standard deviation of R has been normalized to 1, the “generic” variation in R will be about -2 to 2. Thus the difference in j' between the strongest and weakest cohorts of any given age class will be approximately $1.9 \left[\frac{1}{1 + \exp(-2g)} - \frac{1}{1 + \exp(2g)} \right]$. For $g = -1.08$ (which is the estimate for the albacore data) this yields a generic variation of about -1.5 years, i.e. the adjusted age of the strongest cohort is about 1.5 years less than that of the weakest cohort.

Parameter estimation

Bayesian parameter estimation involves the computation of the mode of the posterior density function. We use the MPD (maximum of posterior distribution) method (Bard 1974), which involves maximizing the

sum of the log-likelihood of the data plus the log of the prior density function. We therefore maximize a function consisting of the sum of three components: the log-likelihood of length frequency data, the log-likelihood of total catch estimates and the log of the prior distribution for the effort-fishing mortality relationship.

Contribution of the length frequency data

Due to the large variability that often occurs in length frequency data, we employ a robust likelihood function. The motivation for using this procedure and its technicalities are described in Fournier et al. (1990). We shall not repeat this discussion here, but for convenient reference we briefly describe the form of the log-likelihood function employed.

Let \tilde{Q}_{ia} denote the observed proportion of fish in length frequency sample \mathbf{a} having a length lying in length interval i . If the \tilde{Q}_{ia} are derived from a random sample of size S_a , they would be random variables with means Q_{ia} and variances $(1 - Q_{ia})Q_{ia}/S_a$. Two modifications have been made to this formula. If $Q_{ia} = 0$ the formula implies that the variance of $\tilde{Q}_{ia} = 0$. To decrease the influence of areas where no observations are expected, we add a small number to the variance formula. To reduce the influence of very large sample sizes we have assumed that sample sizes $>1\ 000$ are no more accurate than sample sizes of $1\ 000$. Set $\mathbf{x}_{ia} = (1 - Q_{ia})Q_{ia}$ and $\mathbf{t}_a^2 = 1/\min(S_a, 1\ 000)$. Assume the variance of \tilde{Q}_{ia} is given by $(\mathbf{x}_{ia} + 0.1/I)\mathbf{t}_a^2$, where I is the number of length intervals in the length frequency samples. The likelihood function contribution for X length frequency samples is then

$$(14) \quad \prod_{\alpha=1}^X \prod_{i=1}^I \frac{1}{\sqrt{2\pi(\xi_{i\alpha} + 0.1/I)\tau_{\alpha}^2}} \left(\exp \left\{ -\frac{(\tilde{Q}_{i\alpha} - Q_{i\alpha})^2}{2(\xi_{i\alpha} + 0.1/I)\tau_{\alpha}^2} \right\} + 0.01 \right)$$

Taking the logarithm of expression (14) we obtain the log-likelihood function for the length frequency data:

$$(15) \quad -1/2 \sum_{\mathbf{a}=1}^X \sum_{i=1}^I \log \left[2\mathbf{P}(\mathbf{x}_{ia} + 0.1/I) \right] - \sum_{\mathbf{a}=1}^X I \log(\mathbf{t}_a) + \sum_{\mathbf{a}=1}^X \sum_{i=1}^I \log \left[\exp \left\{ -\frac{(\tilde{Q}_{ia} - Q_{ia})^2}{2(\mathbf{x}_{ia} + .1/I)\mathbf{t}_a^2} \right\} + 0.01 \right]$$

The addition of 0.01 in equations (14) and (15) improves the robustness of the estimator by reducing the influence of observations that are more than about three standard deviations from the mean (Fournier et al. 1990).

Contribution of the observed total catches

Assuming for simplicity that there is only one fishery per year, the contribution of the observed total catches is given by

$$(16) \quad -p_c \sum_i \left(\log(C_i^{obs}) - \log(C_i) \right)^2$$

where p_c is determined by the prior assumption made about the accuracy of the observed catch data. For the albacore analysis, we assumed $p_c = 200$, consistent with a coefficient of variation of about 0.07.

Contribution of the prior distribution for the effort-fishing mortality relationship

Given the random walk structure assumed to operate for time-series changes in catchability, it follows that the prior distribution for the \mathbf{h}_i is normal with zero mean. However, the prior distribution for \mathbf{e}_i is assumed to be a robustified normal distribution, i.e. the probability of events at the tails of the distribution is increased relative to a standard normal distribution. Then, the contribution of the Bayesian priors on the \mathbf{h}_i and \mathbf{e}_i (see equations 10 and 11) is given by

$$(17) \quad -p_{\eta} \sum_i \eta_i^2 + \sum_i \log \left[\exp(-p_{\epsilon} \epsilon_i^2) + 0.01 \right]$$

The size of the constants p_h and p_e are adjusted to reflect prior assumptions about the variances of \mathbf{h}_i and \mathbf{e}_i . For the albacore analysis, we assumed

$p_h = 25$ and $p_e = 10$, which is equivalent to assuming that the coefficients of variation of \mathbf{h}_i and \mathbf{e}_i are 0.14 and 0.22, respectively. Note that the second term of eq. 17 corresponds to an improper density. Therefore, the variance corresponding to the weight p_e cannot be estimated and must be specified.

Nonlinear optimization

The parameters of the model are estimated by maximizing the sum of expressions 15, 16, and 17. The maximization was performed by an efficient optimization using exact derivatives with respect to the model parameters. The derivatives were calculated using an extension of the technique known as automatic differentiation (Griewank and Corliss 1991), an approach especially useful for models with large numbers of parameters. It also provides quick and accurate estimates of the Hessian matrix at the mode of the posterior distribution, which can be used to obtain estimates of the covariance matrix and confidence limits for the parameters of interest.

Estimation of confidence intervals

Confidence limits for the parameter estimates are calculated by employing the usual second order approximation to the mode of the posterior distribution (Bard 1974). Let $\mathbf{q}_1, \dots, \mathbf{q}_n$ denote a minimal set of n model parameters from which all model parameters can be calculated, and let $p(\mathbf{q}_1, \dots, \mathbf{q}_n)$ be some parameter of interest, while $\ell(\mathbf{q}_1, \dots, \mathbf{q}_n)$ is the logarithm of the posterior distribution. The estimated standard deviation, p_s , for p is given by the square root of $\sum_{ij} \mathcal{I}p / \mathcal{I}q_i \mathcal{I}p / \mathcal{I}q_j \Lambda_{ij}$ where $\Lambda_{ij} = \left(\mathcal{I}^2 \ell / \mathcal{I}q_i \mathcal{I}q_j \right)^{-1}$, with the calculations carried out at the MPD. Then, 95% confidence limits for the p are given by $[p - 1.96p_s, p + 1.96p_s]$. These confidence limits are not invariant under reparameterization. To compensate somewhat for this, the confidence limits for parameters that must be positive, such as estimates of biomass, are calculated by computing the confidence limits for the logarithms of these parameters and then transforming the confidence limits. This yields the confidence limits $[p \exp(-1.96 p_s / p), p \exp(1.96 p_s / p)]$.

The above procedure provides approximate confidence intervals for the model parameters (initial cohort size, selectivity and catchability coefficients, natural mortality rates, growth parameters, etc). For stock assessment purposes, it may be desirable to have confidence intervals for quantities of interest, such as adult biomass, that are functions of the model parameters. The variances (and hence confidence intervals) for such quantities are determined using the delta method.

Hypothesis testing

It is frequently of interest in statistical modeling to add model structure in the form of a hypothesis concerning some process of interest, and to observe the resulting change in model performance. Let H_1 (with n_1 parameters) and H_2 (with n_2 parameters) denote alternative models to be tested. In a Bayesian framework, the support for H_2 over H_1 provided by the data D is measured by the posterior odds, which is the product of the ratio of the integrated likelihoods, known as the Bayes factor (Kass and Raftery 1994), and the prior odds for H_2 against H_1 :

$$(18) \quad \frac{p(H_2|D)}{p(H_1|D)} = \left[\frac{p(D|H_2)}{p(D|H_1)} \right] \left[\frac{p(H_2)}{p(H_1)} \right].$$

The Bayes factor is interpreted as the sample ‘‘weight of evidence’’ for H_2 over H_1 .

While appealing on theoretical grounds, there are two impediments to applying Bayes factors in practice. First, it is necessary to provide a Bayesian prior distribution for the parameters. For large problems the usual practice is to provide specific Bayesian priors for a small number of parameters of interest and to apply a locally uniform prior on the remaining parameters. This causes no problem when computing point estimates of the parameters. However, when computing Bayes factors, such diffuse priors lead to the well-known Lindley paradox (Aitken 1991), where, for point null hypotheses, the Bayes factor will tend to infinity as sample size tends to infinity.

A second difficulty is that evaluation of the Bayes factor involves integration of the likelihood functions over all model parameters. For large models (such as the albacore model), this may not be feasible because of limited computing power.

To avoid these problems, we have employed *posterior* Bayes factors (Aitkin 1991), which allow (but do not require) models to include priors with diffuse specifications. Posterior Bayes factors are generally applicable for arbitrary models and their use does not lead to the Lindley paradox (Aitkin 1991). The asymptotic form for the posterior Bayes factor for H_2 over H_1 is

$$(19) \quad A_{21} = \frac{L_2(\mathbf{q}_2)}{L_1(\mathbf{q}_1)} 2^{(n_1 - n_2)/2}.$$

This is a penalized version of the likelihood ratio, with the penalty based on the difference in the number of parameters of the two models. The A_{21} is then a measure of the weight of sample evidence in favor of H_2 over H_1 . We use Aitkin's calibration that values of A less than 0.05, 0.01 and 0.001 constitute "strong, very strong and overwhelming" sample evidence of one model over the other.

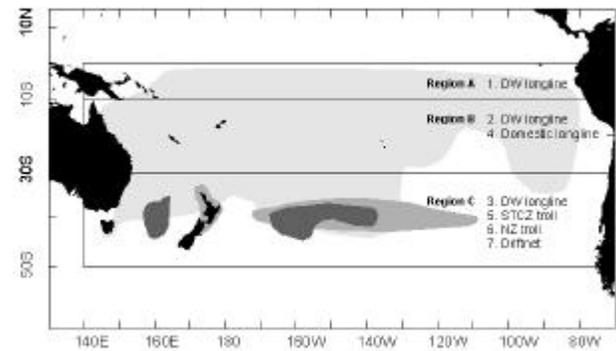
Application to South Pacific albacore

Background

Albacore comprise a discrete stock in the South Pacific Ocean (Murray 1994). Adults (larger than about 80 cm FL) spawn in tropical and sub-tropical waters between about 10°S and 25°S during the austral summer (Ramon and Bailey 1996), with juveniles recruiting to surface fisheries in New Zealand coastal waters and in the vicinity of the sub-tropical convergence zone (STCZ) in the central Pacific about two years later. Distant-water longline fleets of Japan, Korea and Taiwan, and domestic longline fleets of several Pacific Island countries catch primarily adult albacore virtually throughout their range. A troll fishery for juvenile albacore has occurred in New Zealand coastal waters since the 1960s and in the central Pacific in the region of the STCZ since the mid-1980s. Driftnet vessels from Japan and Taiwan targeted albacore in the central Tasman Sea and in the central Pacific near the STCZ during the 1980s. Surface fisheries are highly seasonal, occurring mainly during December to April, while longline fisheries operate throughout the year. Total annual catches have varied between 20 000 t and 52 000 t since the 1960s. Longline gear accounts for the majority of the catch, about 30 000 t per year on average. Troll

catches are relatively small, generally producing less than 10 000 t per year. The driftnet catch reached 22 000 t in 1989, but has since declined to zero following a United Nations moratorium on industrial-scale driftnetting. The approximate distribution of the fisheries is shown in Fig. 1.

Fig. 1. Distribution of longline (light shading), troll (medium shading) and driftnet (dark shading) fisheries for South Pacific albacore. The three rectangular zones define the model regions, which are used in the classification of fisheries and spatial stratification of the model.



Fisheries data

Catch, effort and size composition data have been routinely collected from the fisheries since the early 1960s. The data have inconsistent temporal resolution and include periods where effort, length frequency data, or both are missing. Length frequency sample sizes are highly variable. Such heterogeneous data, which are typical of many fisheries data sets, are readily handled by MULTIFAN-CL.

We defined fisheries on the basis of fishing method and region. Three regions are specified by the latitudinal bands 0–10°S (region A), 10°–30°S (region B) and 30°–50°S (region C) (Fig. 1). The distant-water longline fleets fishing in these regions are defined as separate fisheries by region, but are aggregated across nationality. The fleets of small-scale, domestic longliners that have developed in several Pacific Island countries (region B) in recent years are also defined as a fishery. Other fisheries are the troll fishery in New Zealand coastal waters, the troll fishery operating in the STCZ and the driftnet fishery (all region C).

For the longline fisheries, fishing incidents are aggregated by quarterly time periods (Jan-Mar, Apr-Jun, Jul-Sep, Oct-Dec). For the surface fisheries,

which tend to operate during the summer months only, fishing incidents are aggregated by month. With this data stratification, the albacore database for years 1962 through 1993 consists of 591 fishing incidents. Of these, 566 fishing incidents have a fishing effort estimate and 381 have a length frequency sample.

Constraints and model hypotheses

It is necessary to specify the number of age classes to be considered in the model. For the presentation of results below, we chose a model with eleven age classes, which is consistent with previous aging studies (Labelle et al. 1993). Trials with larger numbers of age classes did not significantly alter the results of the analysis.

We applied a one-dimensional diffusive movement hypothesis to the three-region spatial structure of the model. This hypothesis was considered to be a reasonable, albeit simple, representation of South Pacific albacore movement on the basis of qualitative examination of tagging data (Labelle 1993) and the variation in albacore size with latitude (smallest in the south, increasing towards the equator). Other movement hypotheses and/or spatial configurations could easily be incorporated into the model and tested. One such alternative hypothesis (spatial homogeneity) has been tested and is discussed below.

Several additional constraints on the model were necessary to produce stable behavior during parameter estimation. These include constraints that recruitment occurs only in region C (the southern-most region), recruitment varies log-normally among years, and selectivity coefficients are constant over time within fisheries.

The hypothesis testing procedure outlined earlier was used to test numerous alternative model structures, consisting of various combinations of the following model hypotheses (with the simpler alternative hypothesis in parentheses): spatial structuring of the population into three regions, as defined earlier (spatial homogeneity); age-dependent (age-independent) diffusion of fish among regions; age-dependent (age-independent) natural mortality rate; seasonal variability (constancy) in catchability for all fisheries; and density-dependent (density-independent) growth. The posterior Bayes factors indicated overwhelming support of the data for each of these hypotheses (Table 1). While these tests are by no means exhaustive,

they indicate how hypotheses that are supported by the data can be readily identified and incorporated into the analysis.

Table 1. Posterior Bayes factors (A_{i1}) for comparisons of model 1 with model i ($i=2,\dots,6$).

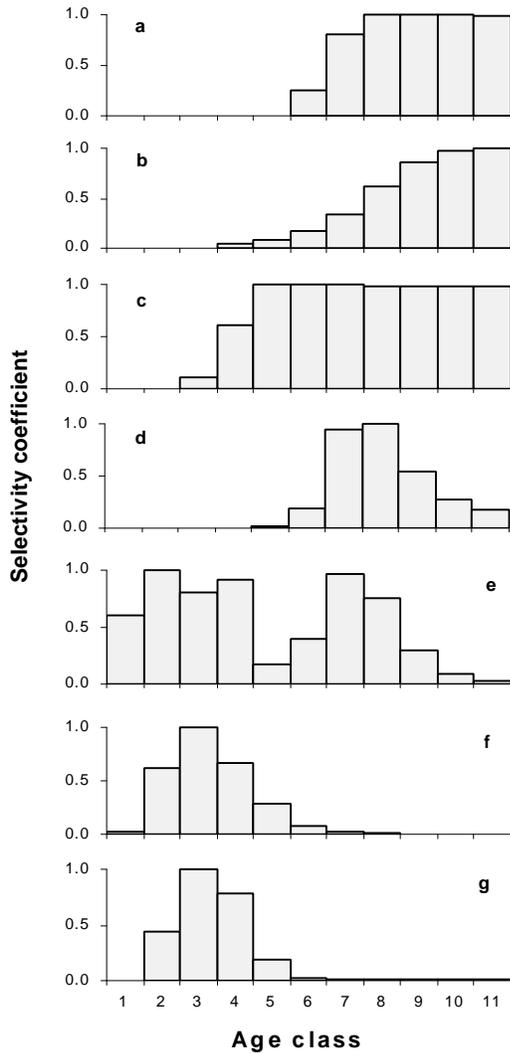
Model	Log-likelihood	Number of parameters	A_{i1}
1. Full model	57 543.7	901	
2. Model 1 without spatial structure	57 268.4	876	1.6E-116
3. Model 1 with age-independent diffusion	57 491.9	899	6.38E-23
4. Model 1 with age-independent natural mortality	57 519.7	892	8.54E-10
5. Model 1 without seasonal catchability for all fisheries	57 127.0	887	1.4E-179
6. Model 1 without density-dependent growth	57 430.3	900	7.97E-50

Some of the results of the South Pacific albacore analysis that illustrate the model features are given below.

Selectivity and catchability coefficients

Estimated selectivity coefficients (Fig. 2) broadly reflect differences in catch size composition among the fisheries. Most fisheries display a regular pattern of selectivity, either increasing with age class or unimodal over a restricted range of age classes. In contrast, the New Zealand troll fishery shows a bimodal selectivity pattern, probably reflecting some contamination of this data set with data from different fishing methods.

Fig. 2. Estimated South Pacific albacore selectivity coefficients. Panels a-g correspond to fisheries 1-7 as shown in Fig. 1.



Estimated catchability time series are plotted with effort deviations (e_i), by fishery, in Fig. 3. Strong trends in catchability are estimated for some of the fisheries. For the longline fisheries, this is likely to be due to changes in species targeting by the fleets concerned. Strong seasonal variation, which was a highly significant addition to the model (Table 1), is also evident for all fisheries. This seasonality is possibly related to changes in the vertical distribution of the albacore in response to seasonal temperature variation. After the removal of time-series trends and seasonal variation in catchability, the effort deviations are mostly evenly distributed about zero (Fig. 4), indicating that there is no further information in the data regarding catchability variation.

Fig. 3. Estimated South Pacific albacore catchability coefficients (normalized to the average for each fishery) (solid lines) and deviations from the effort-fishing mortality relationship (open circles). Panels a-g correspond to fisheries 1-7 as shown in Fig. 1.

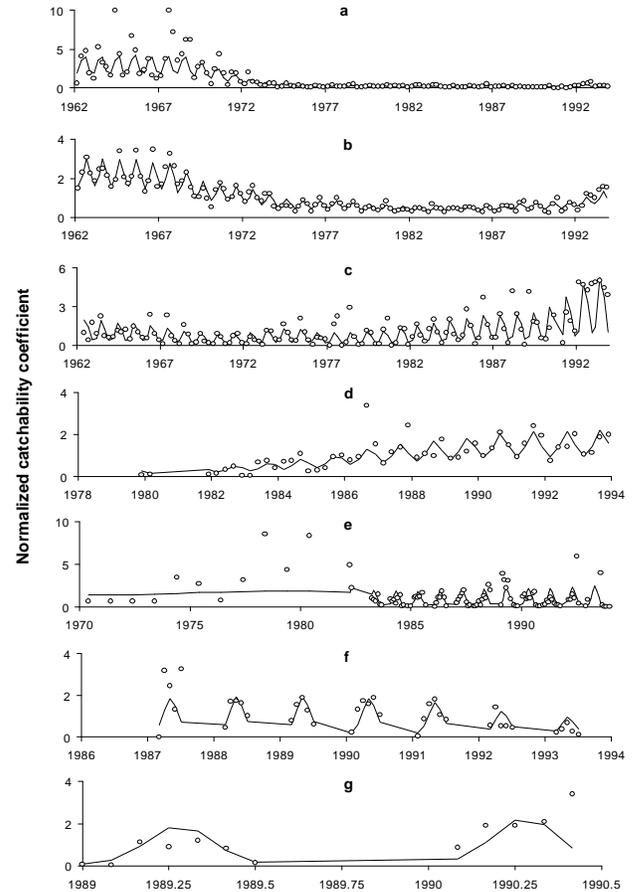
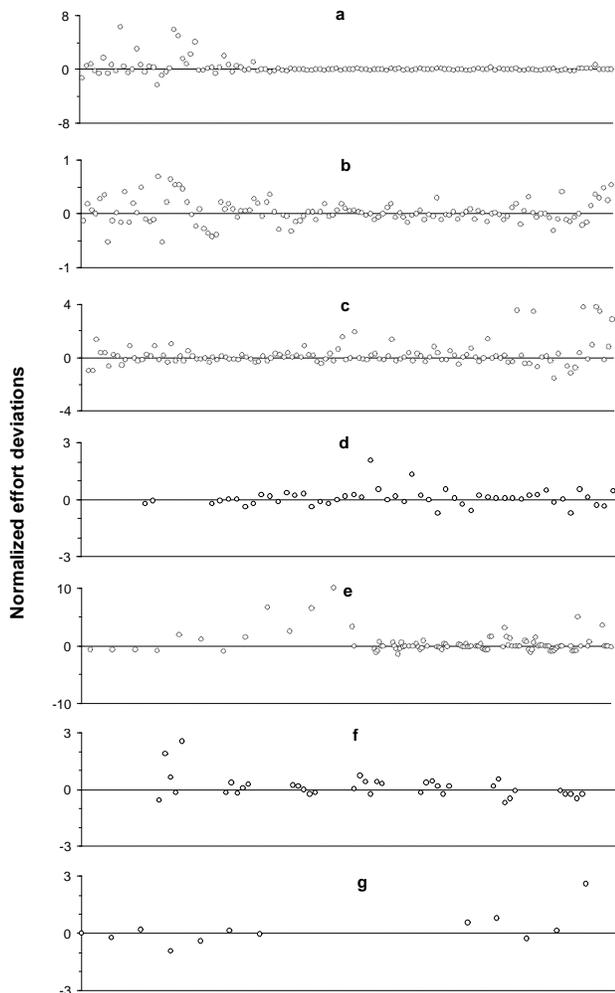


Fig. 4. Deviations from the effort-fishing mortality relationship after removal of time-series trends and seasonal variation in catchability. The deviations are normalized to the average catchability for each fishery. Panels a-g correspond to fisheries 1-7 as shown in Fig. 1.



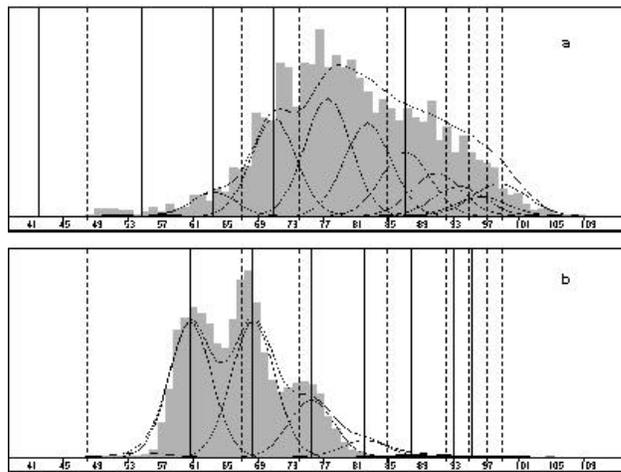
Growth parameters and catch age composition

The estimation of catch age composition from length composition assumes, amongst other things, that albacore exhibit von Bertalanffy growth. We use a parameterization such that growth is specified by three parameters - the mean length of the first age class (45.3 cm), the mean length of the last age class (100.9 cm), and growth coefficient K (0.190 yr^{-1}). These parameters can be transformed to provide the usual von Bertalanffy growth parameter L_{∞} (107.2 cm). Estimated growth rates over the range of exploited sizes are almost identical to estimates based on vertebral ring counts (Labelle et al. 1993).

There is good correspondence between estimated mean lengths-at-age and obvious modes in the length frequency samples for most of the fisheries. Examples of the fits to the length-frequency data are shown in Fig. 5.

The addition of density-dependent growth to the model makes the growth of individual cohorts dependent on their initial relative abundance. This effect appears to be quite strong in South Pacific albacore, with more abundant cohorts growing slower than less abundant cohorts - the difference in apparent age between the largest and smallest cohorts is about 1.5 years. The effect of density-dependent growth on the estimated mean lengths-at-age is shown in Fig. 5 by the differences between the solid and dashed vertical lines for each age class.

Fig. 5. Examples of fits (model 1 - Table 1) to the South Pacific albacore length-frequency data. The solid vertical lines indicate estimated mean lengths-at-age. The dashed vertical lines indicate mean lengths-at-age in the absence of density-dependent growth. Both the estimated aggregate (upper line) and age-class specific length distributions are shown. Panel (a) is a sample from the distant-water longline fishery in region C (2nd quarter, 1973); panel (b) is a sample from the sub-tropical convergence zone troll fishery in region C (March, 1990).

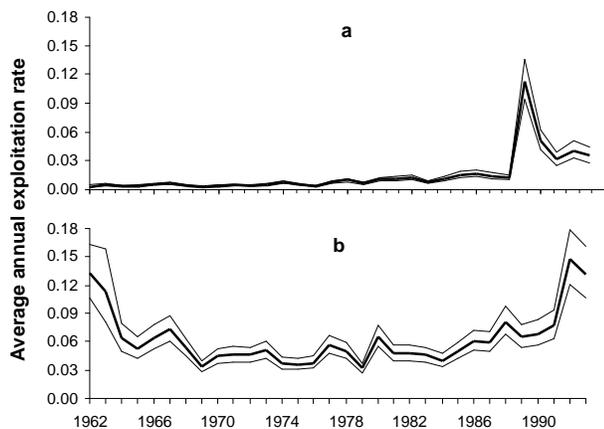


Exploitation rates

Exploitation rates (the proportion of the population harvested per year) and their 95% confidence intervals for two age groups, corresponding approximately to age classes 2-5 (primarily exploited by the surface fisheries) and 6-11 group (primarily exploited by the longline fisheries), have been computed (Fig.

6). This is an example of quantities of interest that are functions of other model parameters, with their confidence intervals estimated using the delta method.

Fig. 6. Estimated average annual exploitation rates (heavy lines) and their 95% confidence intervals (thin lines) for (a) combined age classes 2-5, and (b) combined age classes 6-11.



Natural mortality rates

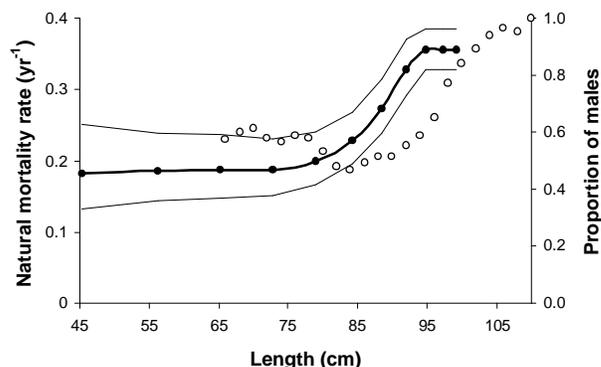
The inclusion of age-dependent M resulted in a highly significant improvement in model fit (Table 1). The M estimates are approximately 0.2 yr^{-1} for age classes 1-5, after which they increase to approximately 0.35 yr^{-1} by age class 9 (Fig. 7). The point at which M is estimated to increase (at about age class 6, or about 85 cm FL) corresponds well with the size at onset of female reproductive maturity (Ramon and Bailey 1996). At this point, the sex ratio of adult albacore also changes rapidly with increasing size to favor males (Fig. 7). This raises the possibility that M may be greater for older fish because of high female mortality associated with the physiological stress of spawning.

Movement parameters

The diffusion rate was estimated to be a decreasing function of age, declining from 0.35 yr^{-1} for age class 1 to less than 0.10 yr^{-1} for age classes 5 and older. The confidence intervals on the estimates are equivalent to coefficients of variation of about 0.7, suggesting that there is limited information the catch, effort and length frequency data on movement. Nevertheless, age-dependent diffusion was a significant model hypothesis (Table 1). Net movement of albacore occurs from south to north. The estimates of

population biomass indicate that most of the stock is located in regions B and C, with very little located in the northern-most region (Fig. 8). Ignoring spatial structure entirely resulted in a highly significant degradation in model fit (Table 1).

Fig. 7. Estimates of South Pacific albacore age-specific natural mortality rates (solid circles, thick line), their 95% confidence intervals (thin lines), and observed proportions of male albacore by 2-cm length classes (open circles).



Population biomass and recruitment

The time series of population biomass and recruitment are key outputs of the model from a stock assessment viewpoint. The biomass estimates (Fig. 8) show a strongly increasing trend up to the mid-1970s and a decreasing trend thereafter until about 1990. The trends are similar in the three regions.

The recruitment estimates (Fig. 9) are higher for the first half of the time series, and lower and more variable during the second half. This pattern drives the biomass trends observed in Fig. 8. Relatively low estimates of recruitment are obtained for 1980, 1985 and 1990. Assuming that the age of recruitment is approximately two years (consistent with the Labelle et al. (1993) vertebral ring count estimates), the spawning seasons corresponding to the low recruitments match well with the occurrence of *El Niño* episodes (negative values of the Southern Oscillation Index) in the Pacific Ocean (Fig. 9). The high recruitments in the second half of the time series also correspond to *La Niña* events (positive values of the Southern Oscillation Index) two years prior to recruitment. The relationship is not as good over the first half of the time series, probably because the absence of fisheries directed at small albacore during

this period results in less informative data for estimating recruitment variability.

Fig. 8. Estimated relative (scaled to the average) biomass of South Pacific albacore (thick lines) with 95% confidence intervals (thin lines) in (a) region A (0-10°S), (b) region B (10-30°S), and (c) region C (30-50°S).

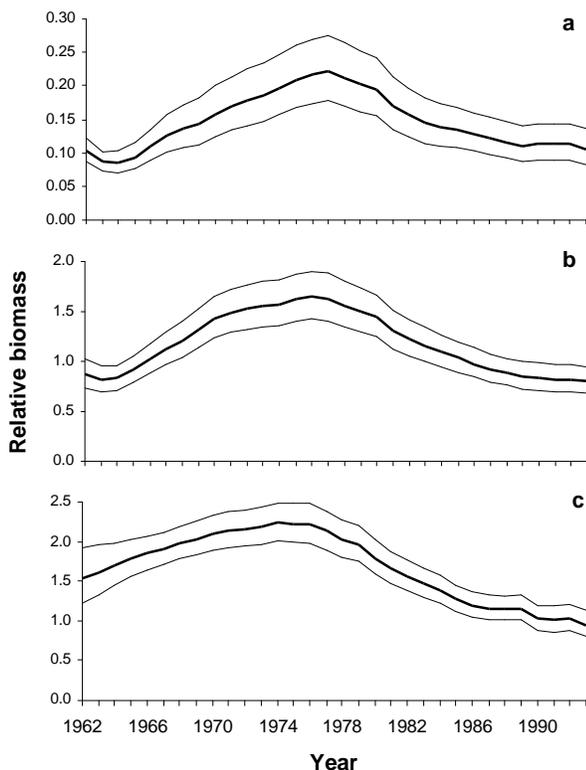
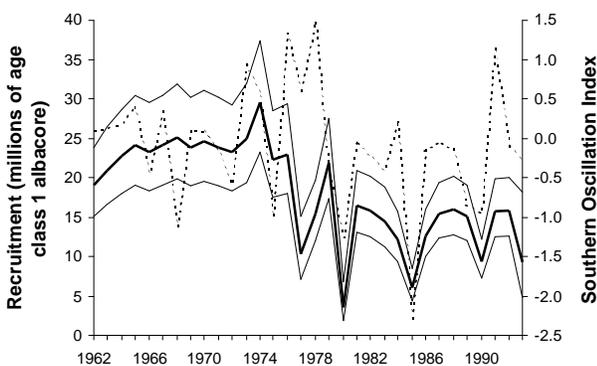


Fig. 9. Estimated South Pacific albacore relative recruitment (thick line), and 95% confidence intervals (thin lines) by year. The dashed line is the average annual Southern Oscillation Index (SOI) two years prior to recruitment. Negative values of the SOI indicate *El Niño* episodes and positive values indicate *La Niña* episodes.



Discussion

We have developed an integrated, age-structured model using length data that may, for many fisheries, be a viable alternative to sequential methods. Unlike most age-structured models that use length data to estimate catch-at-age, our approach fully integrates catch-at-age and growth parameter estimation with estimation of recruitment, mortality and related parameters of the age-structured model.

The model should be potentially applicable to fish stocks that exhibit an age-class signal in length frequency data. Extensive simulation trials during early model development indicated that, as expected, the precision of parameter estimates erodes as the variability of length-at-age increases. Where there is little information on catch-at-age in the length frequency data, the incorporation of independent age-length observations into the estimation as auxiliary data may help resolve catch-at-age estimation.

Simulation trials have also confirmed the obvious result that catchability trends will tend to be underestimated if the mean of the prior distribution for the h_i is zero. Nevertheless, model performance is much better than if constant catchability was assumed. In the case of the albacore analysis, the strong catchability trends estimated for the distant-water longline fisheries are suspected to be due at least in part to changes in targeting practices among the various national fleets. Further stratification of the longline data, or standardization to reduce the effects of targeting variability, may therefore be warranted.

The statistical approach to the age-structured model and Bayesian framework for parameter estimation and hypothesis testing offers the advantage of being able to objectively assess the information content of the data. This enables the construction of approximate confidence intervals on the parameters of interest. Because the model is fully integrated, such confidence intervals incorporate uncertainty arising from the estimation of catch-at-age from length data, as well as other sources of variability. The statistical approach also allows testing of alternative model hypotheses, using posterior Bayes factors, enabling sensible decisions to be made regarding model development.

We have adopted two variations on classical Bayesian methods regarding estimation of confidence intervals and hypothesis testing. First, we assume that

the posterior distribution is approximately normal in the vicinity of its mode, and that the covariance matrix is equal to the inverse of the Hessian. These assumptions are standard in maximum-likelihood estimation, and are reasonable in the Bayesian context for problems with largely non-informative priors (Bard 1974). Second, we use posterior Bayes factors rather than the posterior odds for hypothesis testing. In both cases, our objective was to avoid the necessity of numerically intensive, high-dimensional integration of the posterior density function. While Monte Carlo methods, such as the sampling-importance resampling (SIR) and the Monte Carlo Markov Chain (MCMC) algorithms provide efficient means for approximating such integrals (McAllister and Ianelli 1997), they are still not feasible for models the size of the albacore model presented in this paper.

Although further questions concerning the albacore analysis need exploration, the consistency of the model results with various exogenous data sets is encouraging. These include the consistency of MULTI-FAN-CL length-at-age estimates with those previously derived from vertebral ring counts; the consistency of age-dependent natural mortality rate estimates with changes in albacore sex ratio with size, and with the size at onset of female reproductive maturity; and the apparent relationship between variation in estimated recruitment and variation in the Southern Oscillation Index. While these relationships require further study, their persistence in ongoing analyses of updated albacore fisheries data would provide convincing validation of the model results. In this case, formal incorporation of such exogenous data into the model as auxiliary data could improve the precision and predictive power of the model.

The model could be a useful tool for management of the South Pacific albacore and other fisheries. Two key uses come readily to mind, and would require only minimal adaptation of the existing computer software. First, the results of the model could be cast in a form suitable for comparison with limit or target reference points, as envisaged by the recent United Nations agreement on straddling and highly migratory fish stocks (Levy and Schram 1996). This could be done by calculating the probability that a chosen reference point is violated by the present estimated population state, or by projected future population states estimated under a particular fishing regime. In the latter case, such forward projections would re-

quire a model for future recruitment (perhaps linked to large-scale environmental conditions such as indicated by the Southern Oscillation Index). This and other fishery performance measures provide a convenient framework for incorporating uncertainty in the assessment into management advice (Punt and Hilborn 1997). Second, forward projections could be a useful short-term forecasting tool for both the surface and longline fisheries, particularly if the predictability of recruitment from environmental variables is confirmed. Confidence intervals could be determined for the projections to capture the uncertainty in future recruitment and the current population state. Such forecasting could assist both industry and management decision-making.

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Appendix . Length-based selectivity coefficients

This appendix describes the transformation of age-based selectivity coefficients to coefficients that account for the degree of length overlap of age classes. The transformation is designed to make the selectivity coefficients reflect a length-based, rather than an age-based process. The following symbols are used in the derivation of the length-based selectivity coefficients: c_j is the “age-based” selectivity coefficient for age class j fish, s_j is the “length-based” or length-averaged selectivity for age class j fish, w_k are weights, determined from the normal distribution of length-at-age, k standard deviations from the mean, m_j is the mean length of age class j fish, s_j is the standard deviation of length of age class j fish, and L_1, L_a, r are the von Bertalanffy growth parameters.

Let $f(L_1, L_a, r)$ denote the von Bertalanffy growth function, so that $f^{-1}(m_j) = j$. Let

$\phi^{-1}(\mu_j + \delta_k \sigma_j) = i_{jk} + x_{jk}$, where i_{jk} is an integer, $0 \leq x_k < 1$ and d_k is the k th component of the vector $(-1, -0.5, -0.25, 0, 0.25, 0.5, 1)$. Then

$$(A1) \quad s_j = \sum_{k=-3}^3 w_{|k|} \left\{ c_{i_{jk}} (1 - x_{jk}) + c_{i_{jk}+1} x_{jk} \right\}$$

where $\mathbf{w}_k = w_k / (w_0 + 2w_1 + 2w_2 + 2w_3)$, $w_0 = 1$,
 $w_1 = \exp(-0.25^2/2)$, $w_2 = \exp(-0.5^2/2)$, and
 $w_3 = \exp(-1.0/2)$.