

HIERARCHICAL MODELS IMPROVE ABUNDANCE ESTIMATES: SPAWNING BIOMASS OF HOKI IN COOK STRAIT, NEW ZEALAND

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Abstract. It is often difficult to estimate abundance for a dynamic population, i.e., one that is moving through the survey area or in which birth or mortality rates are high. One approach is to estimate the proportion of animals present during each survey, using a model that estimates the dynamics of the survey proportion of the population. However, this can increase the uncertainty of the estimates if the dynamics parameters are not well estimated. Here we approached this problem by developing methods using hierarchical model structures, which allow us to share information on the dynamics parameters across years. We applied this modeling approach to the estimation of residence time and spawning biomass for New Zealand hoki (*Macruronus novaezelandiae*) in Cook Strait spawning grounds. By sharing parameters across years, we obtained better parameter estimates than by the traditional assumption that the dynamics in one year are independent of those of other years. By integrating the estimation of residence time into a dynamic model using simulated maximum likelihood methods, we also were able to calibrate acoustic estimates of spawning biomass for the fact that not all individuals are on the grounds at the time of the acoustic survey. We discuss alternative model formulations for the application of hierarchical methods to stage-structured data and the analysis of data from acoustic surveys of spawning fish.

Key words: abundance estimates; Cook Strait; hierarchical models; *Macruronus novaezelandiae*; New Zealand hoki; residence time; simulated likelihood; spawning biomass; spawning dynamics.

INTRODUCTION

An entire population may not always be available to be surveyed in one location because of migration, natality, or mortality. In these cases, the only option may be to estimate the proportion of individuals in the survey area at any one time. For example, seals often give birth over an extended period; hence, not all pups are present in a survey at the same time (Myers and Bowen 1989, Myers et al. 1997). It is possible to use stage composition of seal pups to estimate the distribution of births over time so that aerial surveys or mark-recapture data can be calibrated to estimate total abundance. Similar problems occur for stage composition of insects (Vogt and Morton 1991) and other taxa (Manly 1990). Here we develop an approach to adjust acoustic estimates of abundance of a spawning fish that migrates in and out of a survey area. Although the specific example is directed toward acoustic surveys of a spawning concentration of fish, the approach and problem are much more general.

In order to estimate total population size from the estimated population in the survey area, we model the dynamics using stage composition data. In our exam-

ple, the stages refer to spawning condition of the fish, but in other cases they could be ages (Myers and Bowen 1989). Stage-structured data and migration dynamics are often important for modeling population dynamics. Although stage composition data are very common in ecology, they are not always used effectively. Often we may have data for several time periods. Here we develop methods that allow the parameters that describe composition data to vary with time or among populations while still maintaining biologically reasonable constraints. We compare the traditional approach of independent analysis of data for each time period to hierarchical model structures that allow improved estimation of population abundance and dynamics parameters.

In this paper, we construct models to describe the spawning dynamics of New Zealand hoki, *Macruronus novaezelandiae*, also known as blue grenadier, and use these to estimate residence time and spawning biomass. The incorporation of the meta-analytic approach is in how the parameters describing spawning dynamics are treated. We demonstrate that it is possible to integrate the treatment of parameters as random effects into a nonlinear dynamic model. The models developed here take advantage of data collected over several years. This is critical, as we show that data for a single year are generally insufficient to reliably estimate the important parameters of these models.

First we review the biology of hoki that is needed for the model and compare it with similar species. Then

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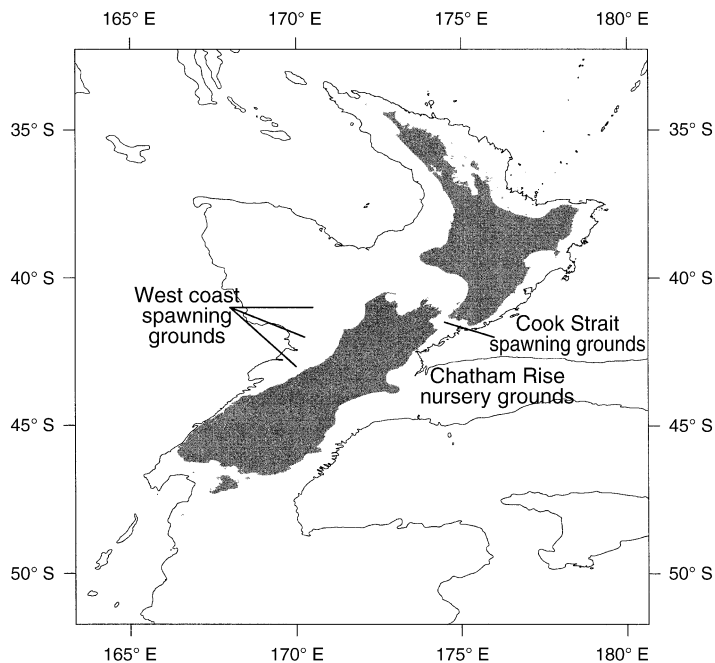


FIG. 1. Some areas of critical importance to New Zealand hoki. The solid line represents the 1000 m depth contour (adapted from Schofield and Livingston [1998]).

we develop a dynamic model for residence time for a single year, and develop hierarchical models that can be simultaneously used for several years. Finally, we test the robustness of the methods to violation of model assumptions.

New Zealand hoki

Hoki form New Zealand's largest commercial fishery, with landings of ~250 kt (1 kt = 1 Gg) per year since 1996–1997 (Annala et al. 2000). There are two main spawning populations of hoki around New Zealand (Fig. 1): the larger western stock spawns off the west coast of the South Island and the smaller eastern stock spawns in Cook Strait (Livingston 1990a, b). The nursery ground for both stocks, and the feeding ground for the eastern stock, is the Chatham Rise. The current stock assessment for hoki uses a dynamic model that incorporates many of the ecologically important processes, e.g., a two-stock model with separate feeding and spawning grounds (Ballara et al. 2002). Several types of data, such as catch-per-unit-effort indices, research trawl survey numbers-at-age, commercial catch-at-age, and acoustic biomass estimates for the spawning grounds, are fitted by the model.

If the abundance indices from the acoustic surveys could be used as absolute abundance indices, this could significantly reduce uncertainty in the current assessment. The two greatest problems that must be overcome to permit the use of acoustic indices as estimates of absolute abundance for spawning hoki are: (1) accurate determination of target strength for hoki; and (2) estimation of residence time for hoki on the spawning ground (Coombs and Cordue 1995). We address the second of these problems here.

Spawning of hoki and related species

Hoki are a member of the order Gadiformes, which includes hake (Family Merlucciidae), the grenadiers (Family Macrouridae), and the cods (Family Gadidae). The family Merlucciidae includes hoki and the true hakes (e.g., *Merluccius australis*).

Hoki appear to be determinant spawners, producing all eggs for a spawning season at once (Livingston et al. 1997, Schofield and Livingston 1998), but the eggs are released in several batches. Thus, individual hoki must undergo the final steps of maturation several times during a spawning season (M. Livingston, NIWA, Greta Point, Wellington, *personal communication*).

Hoki undertake long migrations to reach the spawning grounds (Gunn et al. 1989, Livingston 1990b), as do other Gadiformes, e.g., northeast Arctic cod (Godø 1984). It has been suggested that the onset of spawning for hoki is linked to water temperature in fall and early winter and also to lunar influences (Gunn et al. 1989). The link with water temperature also has been suggested for Atlantic cod, *Gadus morhua* (Hutchings and Myers 1993, Marteinsdóttir and Björnsson 1999).

The onset and duration of spawning have been shown to vary with age and size (Langley 1993, Hutchings and Myers 1994, Kjesbu et al. 1996, Marteinsdóttir and Björnsson 1999). Larger and older females tend to spawn earlier in the season and for a longer period than do smaller individuals. Most estimates of spawning duration have been for females, but there is some evidence that spawning duration could be longer for males than for females (Hutchings and Myers 1994). There is evidence for both Atlantic cod (Morgan and Trippel 1996) and hoki (Livingston et al. 2000) that males arrive at the spawning grounds before females.

The general approach to the estimation of spawning duration uses probit regression, in which the proportions of fish that are maturing, spawning, or spent are modeled over the spawning season (Hutchings and Myers 1994). For hoki there is the complication that they are observed only on the spawning grounds in commercial catches, rather than through a widespread survey encompassing all of the population (e.g., Hutchings and Myers 1993). Studies of captive fish also have been used to estimate spawning duration in cod (Kjesbu et al. 1996), but such studies have not been attempted for hoki.

METHODS

Data

Data used for this analysis consist mainly of biological data collected through port sampling of commercial landings. Random samples (within a landing) of fish were taken, aged, and measured, with females being assigned to one of five gonad stage categories: (1) immature/resting; (2) maturing; (3) mature/partially spent; (4) running ripe; and (5) spent.

In the model, stage-1 fish were not used, because few immature fish are found on the grounds and we have no basis to determine their residence. Stages 2 and 3 were combined. Length- and age-structured data were available, but were not used here because the addition of age structure to the models increased the number of parameters to be estimated without providing sufficient data with which to estimate them (Harley 2002). An estimate of the proportion of females in the catch was also available, as all fish that were measured were also sexed. All data were aggregated into two-week strata. Data were in the form of proportions at stage and sex, rather than absolute numbers, so there were no estimates of the true sample sizes. Because fish are not from a truly random sample, but rather a sampling of fish within trips, the total number of fish sampled may overestimate the effective sample size. The number of trips sampled in a two-week period was used as an index of relative sample size, and the sensitivity to scaling these sample sizes (4–16 trips) by a constant was examined. Commercial landings data were also available for these periods.

The final source of data was abundance estimates from the acoustic surveys of the spawning grounds. During the acoustic surveys, several snapshots (instantaneous biomass estimates), were obtained for the spawning ground over the season. Each snapshot was usually completed within 24 hours (Cordue et al. 1999). If target strength is determined correctly, each snapshot represents an estimate of the total abundance of hoki on the spawning ground at that time. Each snapshot estimate had a variance, calculated using stratified random sampling estimators. The coefficients of variation (cv) for the acoustic biomass estimates ranged from 20% to 80%. These cv values probably overestimate

the true precision of the acoustic surveys due to uncertainty in target strength and the composition of mixed-species aggregations.

Data were available for seven years (1993–1999). The gonad stage, sex ratio, and catch data were available for 5–6 two-week time strata for each year, whereas the acoustic snapshots were modeled using the day on which they were obtained.

Dynamic model

Our basic dynamic model is based upon our knowledge of the spawning dynamics of hoki and related species reviewed in previous sections, in particular, the observed changes in the sex ratios on spawning grounds during the season (Harley 2002: Figs. 3 and 4). In the model, females and males migrate to the spawning grounds over time, and then the females pass through a number of reproductive stages before leaving the grounds. The considerable notation required to describe the models has been summarized in Table 1.

We assume that (1) all fish do not have to be on the grounds at once; (2) females arrive and depart following a cumulative normal distribution that represents the simplest model consistent with the observed changes in sex ratios; and (3) male residence is a function of the female dynamics. Because gonad stage data are available only for females, it is not possible to estimate male residence time directly. Female arrival and residence time are estimated parameters, whereas male residence is derived from these parameters based on a number of assumptions. Data on male residence are the greatest gap in our model. Our model assumption represents the simplest of many alternative hypotheses that are likely to be consistent with the data.

It is important to distinguish the two groups that are modeled through the season. The first is the “total spawning population” that will migrate to the grounds in a given year. This is reduced throughout the year by fishing mortality (it is assumed that there is no natural mortality during the spawning season). The second is the numbers of “fish on the spawning grounds” at a given day of the season. This is a function of the immigration and emigration of fish with respect to the grounds, in addition to fishing mortality.

Considering a model for a single year (we will suppress the notation for year here), six parameters are estimated: the total number of fish in the spawning population (\tilde{N}), the mean of the arrival day distribution for females to the grounds (μ_a), the variance of the arrival-day distribution for females to the grounds (σ_a^2), and the three components that are summed to give female residence time (θ); the duration of the mature (θ_1) and running-ripe stages (θ_2), and time that spent fish spend on the grounds before leaving (θ_3). We pre-specify other model parameters for which lack of data or model structure do not allow estimation.

The number of females (\tilde{N}^f) and males (\tilde{N}^m) in the total spawning population is as follows:

TABLE 1. Summary of notation used in the two models.

Symbol	Description
Subscripts	
t, \dots, T	day of the year
i	subset of days on which biological samples were obtained
j	subset of days on which an acoustic snapshot was obtained
h, \dots, H	random samples used to approximate the integral
Estimated parameters	
\tilde{N}	total spawning population
μ_α	mean of the arrival-day distribution for females
α_α^2	variance of the arrival-day distribution
$\theta_1, \theta_2, \theta_3$	duration of mature, running-ripe, and spent stages
Derived parameters	
θ	residence time of a female on the grounds, $\theta_1 + \theta_2 + \theta_3$
ϑ	residence time of a male on the grounds
Θ	overall average residence time of hoki on the ground
μ_δ	mean of the departure day distribution for females, i.e., $\mu_\alpha + \theta$
$\Omega_{\text{start}}, \Omega_{\text{end}}$	days when 5% females have arrived and 95% of the females have departed
Ω_{length}	length of the spawning season (i.e., $S_{\text{end}} - S_{\text{start}}$)
\tilde{N}^f, \tilde{N}^m	total female and male spawning populations
$\tilde{N}_t^f, \tilde{N}_t^m$	number of females and males on the ground at day t
\tilde{B}	total spawning biomass
B_t	biomass on the ground at day t
α_t	proportion of \tilde{N}^f that has arrived on the ground
δ_t	proportion of \tilde{N}^f that has departed the ground
λ_t	proportion of \tilde{N}^f on the ground, i.e., $\alpha_t - \delta_t$
$\Phi_{2,t}, \Phi_{3,t}$	proportion of \tilde{N}^f that has reached the running-ripe, or spent stage
$P_{f,t}$	proportion of females on the ground, i.e., $N_t^f / (N_t^f + N_t^m)$
$P_{1,t}, P_{2,t}, P_{3,t}$	proportion of N_t^f that are mature, running-ripe, or spent
u_t	exploitation rate of fish on the ground
Assumed constants	
c_1	proportion of females in the total spawning population
c_2	constant proportion of the total male spawning population on the grounds
w_f, w_m	mean mass of females and males on the ground
ζ	proportion of running-ripe females back in the maturing/partially spent stage
Data related	
C_i	commercial catch
$p_{1,t}^{\text{obs}}, p_{2,t}^{\text{obs}}, p_{3,t}^{\text{obs}}$	observed proportion of N_t^f that are mature, running-ripe, or spent
S_i	assumed sample size for biological samples taken on day i
B_j^{obs}	acoustic biomass estimate for the ground on day j
σ_j^2	variance for acoustic biomass estimate

$$\tilde{N}^f = \tilde{N}c_1 \quad \tilde{N}^m = \tilde{N}(1 - c_1) \tag{1}$$

where c_1 is an assumed constant representing the proportion of females in the total spawning population, i.e., \tilde{N}^f/\tilde{N} . We fixed $c_1 = 0.6$ based on estimates of differential mortality and maturity (S. J. Harley, unpublished analysis). Using the estimated numbers and the approximate mean mass of female ($w_f = 1.36$ kg) and male ($w_m = 1.14$ kg) spawners (Harley 2002: Appendix 2), the total spawning biomass (\tilde{B}) in kilograms is given by

$$\tilde{B} = \tilde{N}^f w_f + \tilde{N}^m w_m. \tag{2}$$

The proportion of the total male spawning population that is on the grounds is assumed to be a constant, c_2 . As will be shown later, this constant is strongly related to male residence time. We fixed $c_2 = 0.4$ to provide ratios of male to female spawning duration consistent with observations for Atlantic cod (Hutchings and Myers 1993). Sensitivity to this assumption was tested.

The proportion of the total spawning female population that is on the grounds, γ_t , varies over the season (day t) as a function of the cumulative arrival proportion (α_t) and cumulative departure proportion (δ_t) for females to the grounds (Fig. 2):

$$\alpha_t = \Phi\left(\frac{t - \mu_\alpha}{\sigma_\alpha^2}\right) \quad \delta_t = \Phi\left(\frac{t - (\mu_\alpha + \theta)}{\sigma_\alpha^2}\right) \tag{3}$$

$$\gamma_t = \alpha_t - \delta_t$$

where the mean day of the departure distribution is $\mu_\delta = \mu_\alpha + \theta$, with the variance of the departure distribution equal to the arrival distribution, i.e., $\sigma_\delta^2 = \sigma_\alpha^2$, and $\Phi(\cdot)$ is the cumulative normal distribution function. The residence time of a female fish on the ground (θ) is assumed to be the same for all females. Female fish are assumed to be in the mature stage when they arrive on the ground. The cumulative proportion of females that have reached the running-ripe stage ($\Phi_{2,t}$), and the spent stage ($\Phi_{3,t}$), is given by the following:

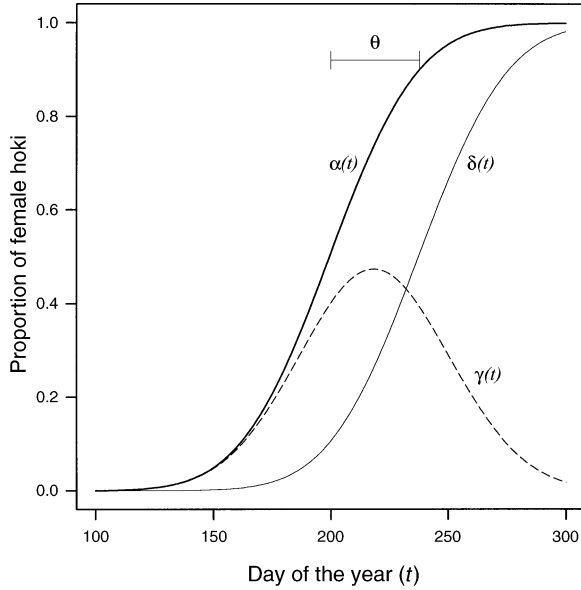


FIG. 2. Schematic of the curves used to structure the dynamic model. For females, the arrival cumulative proportion curve, $\alpha(t)$, plus the estimate of residence time, θ , is used to obtain the departure cumulative proportion curve, $\delta(t)$. The difference between the arrival and departure curves gives the proportion of the total population of spawning females that is on the grounds throughout the season, $\gamma(t)$. For day of the year (t), day 1 is 1 January.

$$\begin{aligned} \phi_{2,t} &= \Phi \left[\frac{t - (\mu_\alpha + \theta_1)}{\sigma_\alpha^2} \right] \\ \phi_{3,t} &= \Phi \left[\frac{t - (\mu_\alpha + \theta_1 + \theta_2)}{\sigma_\alpha^2} \right]. \end{aligned} \quad (4)$$

Using the arrival and departure curves, we have the proportion of the total female spawning population that is on the grounds (γ_t), and we now use the other curves to distribute the females across the different stages. The proportions of females on the ground that are mature ($p_{1,t}$), running ripe ($p_{2,t}$), and spent ($p_{3,t}$) are simply

$$\begin{aligned} p_{1,t} &= \phi_{2,t} - \alpha_t & p_{2,t} &= \phi_{3,t} - \phi_{2,t} \\ p_{3,t} &= \delta_t - \phi_{3,t}. \end{aligned} \quad (5)$$

One weakness of this model is that it ignores the cycling of hoki through the mature and running-ripe gonad stages during the season. An ad hoc fix to this problem is to assume that some proportion of fish, say ζ , that have reached the running-ripe stage at least once will be staged as maturing fish at day t . The sensitivity of the parameter estimates to the assumed value was assessed. With the addition of this parameter we get

$$\begin{aligned} p_{1,t} &= \frac{p'_{1,t} + (\zeta p'_{2,t})}{p'_{1,t} + p'_{2,t} + p'_{3,t}} & p_{2,t} &= \frac{p'_{2,t} - (\zeta p'_{2,t})}{p'_{1,t} + p'_{2,t} + p'_{3,t}} \\ p_{3,t} &= \frac{p'_{3,t}}{p'_{1,t} + p'_{2,t} + p'_{3,t}} \end{aligned} \quad (6)$$

where the prime symbol denotes the predicted value be-

fore the cycling parameter ζ was included (Eq. 5), and the denominator ensures that the proportions sum to 1.

The number of females and males on the grounds on the first day of the model ($t = 100$) is

$$N_{100}^f = \tilde{N}_{\gamma 100}^f \quad N_{100}^m = \tilde{N}^m c_2 \quad (7)$$

where the sum of these gives the total number of fish on the grounds. The total spawning population is reduced over the season by exploitation (u_t):

$$\tilde{N}_{t+1}^f = \tilde{N}_t^f - (N_t^f u_t) \quad \tilde{N}_{t+1}^m = \tilde{N}_t^m - (N_t^m u_t) \quad (8)$$

where $u_t = C_t/B_t$, C_t is the catch in mass at day t , and B_t is the biomass of fish on the grounds on day t , calculated from the numbers of fish and the mean mass just described.

As previously mentioned, it is not possible to directly estimate the residence time of male hoki, because no gonad stage data are available for them. In the model just described, female residence time is an estimated parameter, and a fixed proportion of males (c_2) is assumed to be on the grounds at all times. Given some estimate of the total spawning season, Ω_{length} , and assuming that all males spend equal time on the ground, male residence time ϑ , is given by

$$\vartheta = \Omega_{\text{length}} c_2. \quad (9)$$

It would be useful to define the total spawning season as some function of the time that female hoki are on the spawning grounds. Here we used the day when 5% of the females had arrived on the grounds as the start of the season, and the day when 95% of the females had left the grounds as the end of the season. Because arrival and departure of females are described by normal curves, we can calculate the start, end, and duration of the season, using the estimates of the mean and variance of the arrival day distribution, and female residence:

$$\begin{aligned} \Omega_{\text{start}} &= \mu_\alpha - (1.645\sqrt{\sigma_\alpha^2}) \\ \Omega_{\text{end}} &= \mu_\alpha + \theta + (1.645\sqrt{\sigma_\alpha^2}). \end{aligned} \quad (10)$$

Season length is then given by

$$\Omega_{\text{length}} = \theta + (3.29\sqrt{\sigma_\alpha^2}). \quad (11)$$

With female and male residence previously defined, the average residence of all individuals (male and female) is simply a weighted average:

$$\Theta = \theta c_1 + \vartheta(1 - c_1). \quad (12)$$

Likelihood functions

Here we use different likelihood functions for each data source to more appropriately model the sampling errors. The likelihood function for a single year y is as follows:

$$\begin{aligned}
 l_y(\text{data} | \mu_\alpha, \sigma_\alpha^2, \theta, \tilde{N}) &= \prod_{i \in t} \frac{S_i!}{P_{f,i}!(S_i - P_{f,i})!} (p_{f,i})^{P_{f,i}} (1 - p_{f,i})^{S_i - P_{f,i}} \\
 &\times \prod_{i \in t} \frac{S_i!}{P_{1,i}!P_{2,i}!P_{3,i}!} (p_{1,i})^{P_{1,i}} (p_{2,i})^{P_{2,i}} (p_{3,i})^{P_{3,i}} \\
 &\times \prod_{j \in t} \frac{1}{\sqrt{2\pi}\sigma_{y,j}^2} \exp\left\{-\frac{[\log(B_{y,j}) - \log(B_{y,j}^{\text{obs}})]^2}{2\sigma_{y,j}^2}\right\}
 \end{aligned}
 \tag{13}$$

where i and j denote days of the season for which estimates of gonad stage/sex ratio and biomass estimates, respectively, are available, S_i is the assumed sample size for sample i , $P_{f,i} = p_{f,i}^{\text{obs}}S_i$, $P_{1,i} = p_{1,i}^{\text{obs}}S_i$, $P_{2,i} = p_{2,i}^{\text{obs}}S_i$, and $P_{3,i} = p_{3,i}^{\text{obs}}S_i$.

The first row of Eq. 13 is the binomial likelihood that was assumed for the proportion of females on the spawning grounds (i.e., N_f^i/N_i), and the second is the multinomial likelihood assumed for the gonad stage data. The sample sizes used for the proportion of females and gonad stage data were the number of trips that were sampled over each two-week period. The last row of Eq. 13 is the lognormal likelihood used for the acoustic biomass estimates, where the variance term is that estimated for each individual snapshot biomass estimate.

The model was implemented with parameters for all years estimated together, although in the case for which years are treated independently, the results obtained are the same as those obtained from running the model with data for that year only. The objective function was the total likelihood over all of the Y years (i.e., the product of the individual likelihood):

$$L = \prod_{y=1}^Y l_y. \tag{14}$$

We consider several model structures with different assumptions about the relationship among years in spawning dynamics. In all models we treat annual spawning biomass as an independent variable, because there is no reason to believe that it necessarily will be closely related across years because recruitment, fishing mortality, and the proportion of mature fish that spawn each year vary annually.

Independent estimates.—The standard modeling approach for a problem such as this would be to estimate the residence time and spawning dynamics separately for each year. This represents a very weak and naive analysis, as it ignores the obvious fact that knowledge of the residence time in one year provides information about that in other years. This model will be referred to as Model 1.

Fixed parameters across models.—On a biological basis, it could be assumed that residence time and even arrival time should be similar from year to year. We

can summarize different hypotheses about the similarity in residence time across years with two models: Model 2 (arrival independent) with a single residence time, but separate (independent) arrival means for each year, i.e., the time of spawning can vary from year to year; and Model 3 (years constant), with a single residence time and arrival mean for all years.

Mixed-effects models.—A mixed-effects model is one in which some parameters are treated as fixed effects (same for all years), whereas others are treated as random effects (individual estimates assumed to come from a common distribution). Because previous researchers have reported that the timing of spawning for hoki can vary across years (Gunn et al. 1989), and because the peak of the spawning season is so critical to the plateau model, we allow mean arrival day μ_α to be a random effect in Model 4. We estimate a mean and variance for the distribution of mean arrival days across years, $\mu_{\alpha_y} \sim \mathcal{N}(\mu, \sigma^2)$. We treat the other spawning dynamics parameters as fixed effects, but still estimate biomass independently for each year.

If the estimated variance, σ^2 is greater than zero, this suggests that there are some variables, not included in the model (e.g., covariates), that are partially responsible for the observed differences. It is likely that environmental conditions and the age composition of the population both influence the onset of spawning and the length of the season. If this occurs, it is reasonable to assume that there will be interannual variation in the quantities describing spawning dynamics.

In the case for which a random effect is included, the likelihood becomes complicated because we need to integrate over the random effects:

$$l = \int_{\mu_{\alpha_y}} \prod_y l_y(\text{data} | \mu_{\alpha_y}, \sigma_{\alpha_y}^2, \theta_y, \tilde{N}_y) \eta(\mu_{\alpha_y} | \mu, \sigma^2) d\mu_{\alpha_y}. \tag{15}$$

This integral does not have a closed-form solution, and standard approximations, e.g., Laplace’s approximation, to the integral do not appear to be very accurate. Therefore we cannot use standard mixed-effects models. It is not feasible to use a Bayesian approach such as BUGS (Spiegelhalter et al. 1996), for this problem because the model is data intensive, and we have not found BUGS to be efficient for such models. Here we will use the method of maximum simulated likelihood (MSL), an approach used to estimate random-effects models in econometrics (Gourieroux and Monfort 1991). This involves approximating this integration through H random draws from $\eta(\mu_{\alpha_y})$, giving a more accurate approximation of the integral. The likelihood function for an individual year is now

$$l_y = \frac{1}{H} \sum_{h=1}^H l_y^h(\text{data} | \mu_{\alpha_y}^h, \sigma_{\alpha_y}^2, \theta_y, \tilde{N}_y). \tag{16}$$

The procedure for implementing the MSL approach is as follows:

TABLE 2. Summary of the assumptions about interannual variation in spawning dynamics for each model.

Parameter	Model 1	Model 2	Model 3	Model 4
Arrival mean (μ_{α_y})	I	I	F	R
Arrival variance ($\sigma_{\alpha_y}^2$)	I	F	F	F
Female residence (θ_y)	I	F	F	F
Population size (N_y)	I	I	I	I

Note: Key to abbreviations for table entries: I, parameter was estimated independently for each year; F, parameter was estimated to be a fixed effect across years; R, parameter was estimated to be a random effect across years from an estimated distribution.

1) Generate YH random normal deviates of mean zero and variance of unity that are kept throughout the estimation procedure, ε_y^h .

2) Provide starting values for all parameters including μ and σ^2 .

3) Generate $\mu_{\alpha_y}^h$ based on the current estimates of μ and σ^2 , and the random numbers from 1, i.e., $\mu_{\alpha_y}^h = \varepsilon_y^h \times \sigma + \mu$, and then calculate l_y^h .

4) Repeat Step 3 for all h .

5) Calculate the objective function.

6) Repeat the Steps 3–5 with new values for the parameters chosen by the nonlinear function minimizer until convergence is attained.

We have used the method of antithetic acceleration to improve the performance of the MSL approach (Arias and Cox 1999, Hajivassiliou 1999). For antithetic acceleration, we first generate $0.5YH$ random normal deviates. The second $0.5YH$ are simply the first half multiplied by -1 . The improvement occurs because more even sampling of the likelihood surface improves the accuracy of the integration.

As this method involves random sampling to approximate the integral, we must be aware of simulation error that occurs with the model converging at different solutions with different ε_y^h . To assess this, we ran the model for different seeds for the random number generator and different values for H . The final H was chosen to be one where the estimated random effect variance σ^2 did not vary greatly across runs with different seeds.

All four models were developed and implemented using AD Model Builder (ADMB), which allows fast maximization of the likelihoods of complex models because analytic derivatives are automatically calculated (Otter Research 2000). A summary of the structure assumed for each model is provided in Table 2. We can compare the fit of each of the models developed here using Akaike's Information Criteria, AIC (Akaike 1974), for which the model with the lowest AIC is the most parsimonious.

Note that for parameters modeled using a random-effects distribution, we estimate the distribution rather than getting individual values. If needed, empirical Bayes estimates of the predictions (i.e., estimates) of

the realized values can be obtained by standard methods (Robinson 1991).

RESULTS

We compared parameter estimates across the four model runs. We were interested in how both the estimated interannual variability in model parameters and the precision of the estimates change with different assumptions relating to interannual variation in spawning dynamics. Estimates (with standard errors) for the parameters describing the arrival distribution and residence time are provided in Fig. 3.

Parameters describing the migration to the spawning grounds were generally within reasonable bounds for all models. Estimates for Model 1 were the most uncertain, but this is not surprising, considering that 42 parameters were estimated in Model 1, as opposed to 18, 12, and 13 parameters for the other models (Table 3). The mean of the arrival-day distribution ranged from day 187 (in 1995) to day 219 (1999). When the residence time parameters and the variance of the arrival-day distributions were fixed (Model 2), the interannual variability in the mean of the arrival-day distribution was much less and the estimates were more precise. The mean of the arrival-day distribution for Model 3 and the estimated mean of the random-effect distribution for Model 4 were almost identical. The variance of the random-effect distribution for mean arrival day (Model 4) suggests that the timing of the spawning season can range by up to one month across years (95% limits for the random-effects distribution for the mean).

Combined residence time, as modeled here, is a direct function of five model parameters, but we consider only the final derived parameter here. Only Model 1 treated residence time as a parameter that can vary across years. The variation in the individual estimates was not large (38.4–49.3 days), however, and the random-effects analysis indicated no significant interannual variation. The other three models produced estimates (of the single residence time) within 0.2 days, 42.2–42.4 days. There is no evidence in the data (as modeled here) that residence time varies significantly across years.

The annual spawning biomass trajectories were similar for each of the four models, although Model 1 displayed the greatest reduction in spawning biomass over the time series (Fig. 4). The biomass estimates were associated with quite small standard errors, reflecting coefficients of variation from 8% to 20% across all models. All models showed a greater relative decline than that described by the indices used in the current assessment.

The model fit to the observed data was generally similar for all models. Models 3 and 4 gave fits that were visually indistinguishable. Models 3 and 4 did not fit well to the proportion of females in the catches for 1995 (Fig. 5), but fits were similar for all other years.

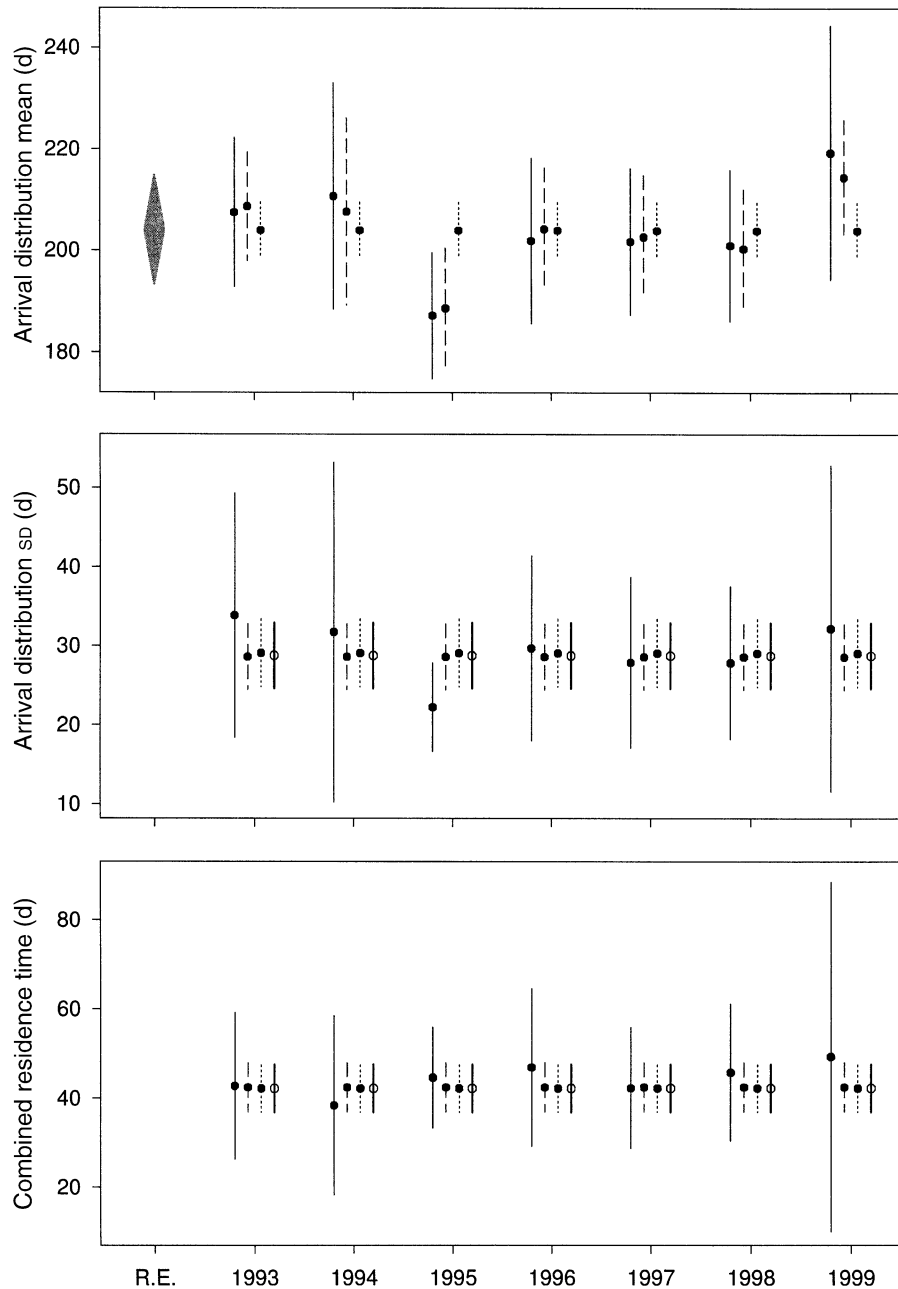


FIG. 3. Mean arrival day of females (μ_a), variance of the arrival day distribution (σ_a^2), and estimates of combined residence time (Θ) for each year and model: Model 1 (solid line, filled circle); Model 2 (long-dash line); Model 3 (dotted line); and Model 4 (solid line with open circle). Error bars indicate ± 2 SD. The estimated 95% bounds for the random effects distribution (R.E.) for mean arrival day from Model 4 is represented by the large gray diamond. Note that there are no annual estimates for mean arrival day for Model 4.

All models predicted similar trends in proportions in each of the three gonad stages through the spawning season (Fig. 6). The fit to the 1995 data was more variable, and none of the models could follow the steep decline in the proportion of mature (stage-1) fish in the catches. The predicted biomass on the spawning grounds always followed the acoustic estimates (Fig. 7). The assumption of sampling the plateau appears to

be met during 1995–1998, but there is fairly strong evidence that the peak spawning biomass was missed during 1993, 1994, and 1999. If true, this suggests that sample-based abundance estimates from the acoustic surveys, assuming sampling of the plateau, could be misleading.

Models 2, 3, and 4 were very similar in their fit to the data (as judged by the AIC) and were much lower

TABLE 3. Overall fit for each model.

Model	n	\mathcal{L}	AIC
1	42	1084	2252
2	18	1092	2219
3	12	1098	2220
4	13	1097	2219

Note: For the column headings, n is the number of parameters estimated; \mathcal{L} is the total negative log likelihood; and AIC is Akaike's Information Criterion (smaller is better), where $AIC = 2\mathcal{L} - 2n$.

than the fit for Model 1 (Table 3). We prefer the estimates from Model 4, as it provides a compromise between having the peak in arrival times all the same and having them estimated independently; there are good statistical reasons for believing that such an approach will give better estimates (Robinson 1991). There are also other criteria that can be used to compare the fit of alternative models (Burnham and Anderson 1998), but we have not considered these here.

Robustness and simulation testing

The robustness of the approach was tested by two methods. First, alternative models were fit by modifying the model structure, e.g., gamma errors, instead of lognormal errors, were assumed for the acoustic biomass estimates. Second, simulated data were generated from models with known parameter values, and we tested to see if we could recover these values. This second approach was considered only for Models 1–3 because the computational demands of Model 4 currently prohibit large numbers of simulations.

As the MSL approach is based on simulations using random numbers, there is a chance for extra variability in the results, i.e., obtaining different results with a different seed for the random number generator or a different number of simulations. For 20 simulations (as used for the results presented), a range of different seeds did not lead to differences of more than 10% in the estimate of the random-effects variance. This was not reduced when 40 samples were used. Because the 10% is less than the estimates of precision for the original estimates, the sample size of 20 appears to be adequate for this problem. When a sample size of 10 is used, however, performance is quite variable, with 50% of runs leading to estimates of close to zero for the random-effects variance. Inter-seed variation was reduced greatly by the use of antithetic acceleration.

Assuming gamma errors instead of lognormal errors made very little difference to the estimates (estimated spawner abundance changed less than 3%), probably because the cvs for acoustic estimates were relatively small. The relative weighting of the sex ratio and the gonad stage composition data to the acoustic estimates depends upon the effective sample size estimated from the sampling protocols. Estimating the effective sample size is inherently difficult because of the difficulty of

sampling at random from a commercial operation. When we halve the sample sizes, the model becomes unstable, as these data are critical to the estimation of the duration of the gonad stages. When the assumed effective sample size was doubled, the estimates of spawning biomass changed by less than 2%.

Estimates of spawner biomass and female residence time were most sensitive to the proportion of the total population of spawning males assumed to be on the grounds through the season (c_2). A 33% change in ϕ resulted in $\sim -15\%$ to 20% changes in estimates of spawning biomass and residence time, with a higher c_2 giving lower biomass. Estimates of biomass were quite insensitive to the cycle parameter ζ . This is most likely because it is confounded with the estimated duration of the mature and running-ripe stages θ_1 and θ_2 . Although the ratio of θ_1/θ_2 was sensitive to changes in ζ , their sum was not.

Simulation tests were used to confirm that we could recover the model parameters from the model, assuming the same model and sampling distributions as assumed to generate the simulated data. The simulations are also useful for testing model parsimony. Results of the simulations were assessed by the relative bias and relative root mean-squared error (RMSE) in the estimates of spawning biomass and average female residence time. We define bias and RMSE in terms of the true value, Z , and the estimate, \hat{Z} (Kendall et al. 1987):

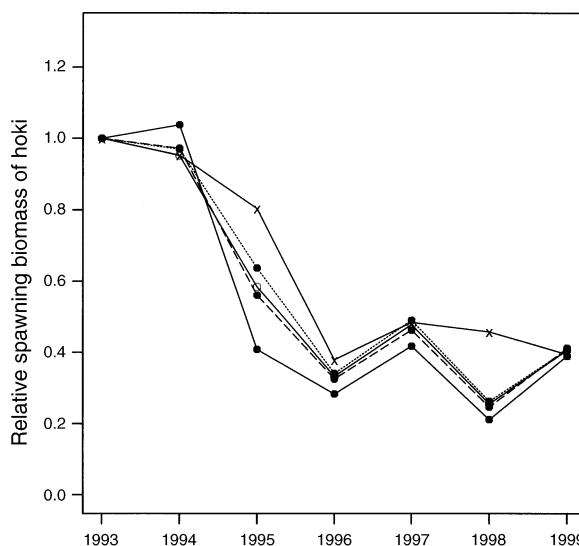


FIG. 4. Estimates of relative total spawning biomass (scaled to a value of 1.0 for 1993) on the Cook Strait spawning ground for each model: Model 1 (solid line, filled circles); Model 2 (long-dash line); Model 3 (dotted line); and Model 4 (solid line, open circles). Biomass estimates used in the current stock assessment model are also shown ("x" with the light solid line). The coefficients of variation for the biomass estimates were 0.15–0.20 (for Model 1), 0.09–0.18 (for Model 2), and 0.08–0.14 (for Models 3 and 4).

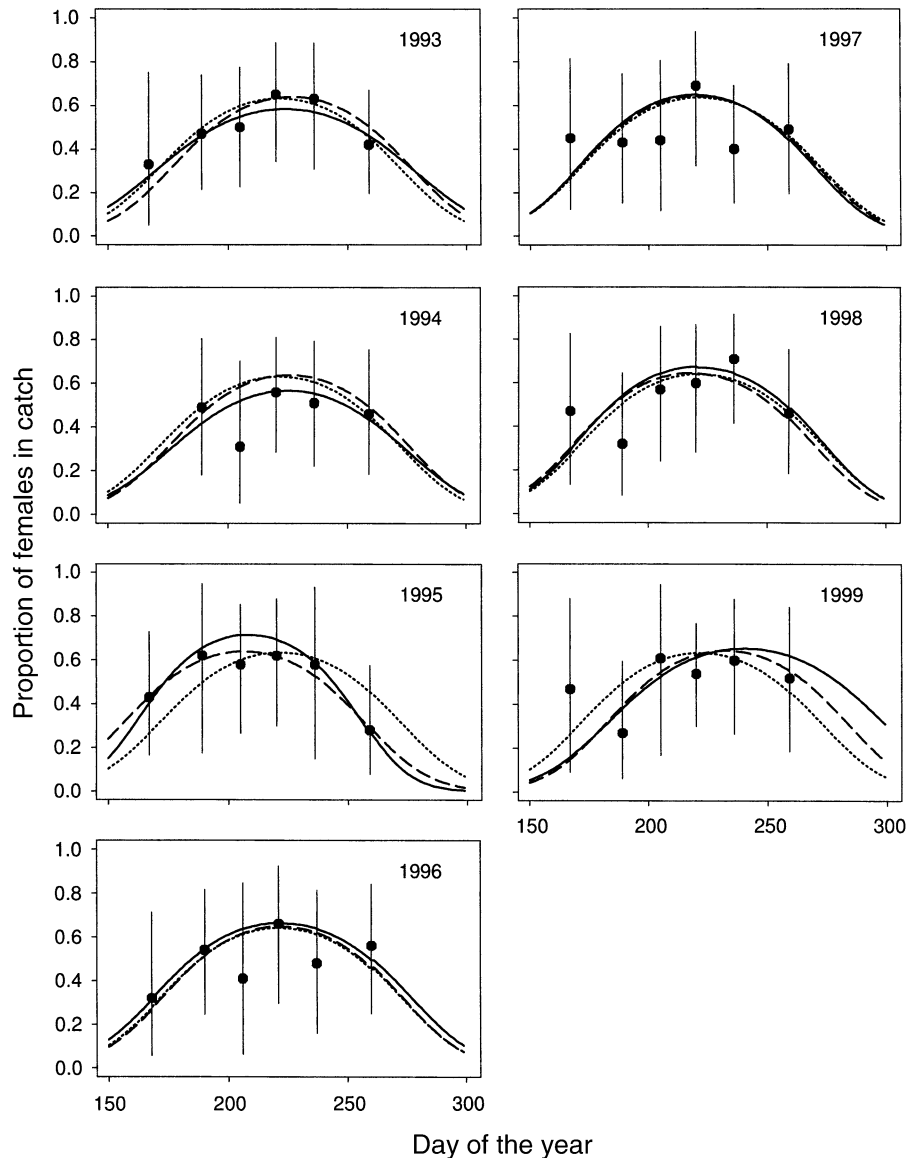


FIG. 5. Fit to the proportion of females on the Cook Strait spawning ground for Models 1 (solid line), 2 (long-dash line), and 3 (dotted line). The error bars represent the 95% likelihood-based confidence limits based on the assumed sample size and the estimated proportion.

$$\% \text{bias} = \{E[\hat{Z}|Z] - Z\} \frac{100}{Z} \quad (17)$$

$$\% \text{RMSE} = \{[b(\hat{Z})]^2 + \text{Var}(\hat{Z}|Z)\}^{1/2} \frac{100}{Z} \quad (18)$$

where $b(\hat{Z})$ is the bias in the estimates.

The parameter values used in the simulation were those estimated with each model. We report only the results for spawning biomass and residence time (Table 4), although the results for other parameters showed that the models were good at estimating mean arrival day (less than 2% bias for all simulations).

Spawning biomass.—When the true model had independent parameters (i.e., Model 1), the estimation

model with this assumption performed worst, whereas Model 2 had the lowest percentage bias (+1.5%) and Model 3 the lowest percentage RMSE (Table 4). In all simulations, there was a positive bias in the estimates of spawning biomass, although this was generally small (never greater than 1.5% for Model 2).

Average female residence time.—The models performed quite poorly in estimating average residence time, in terms of both bias and RMSE (Table 4). Estimates of bias were five times those for biomass, and RMSE was generally doubled. The high RMSE is not surprising, as average residence is the function of most of the parameters in the model, but the high (5.8–42.2%) and positive biases were a surprise. Estimates

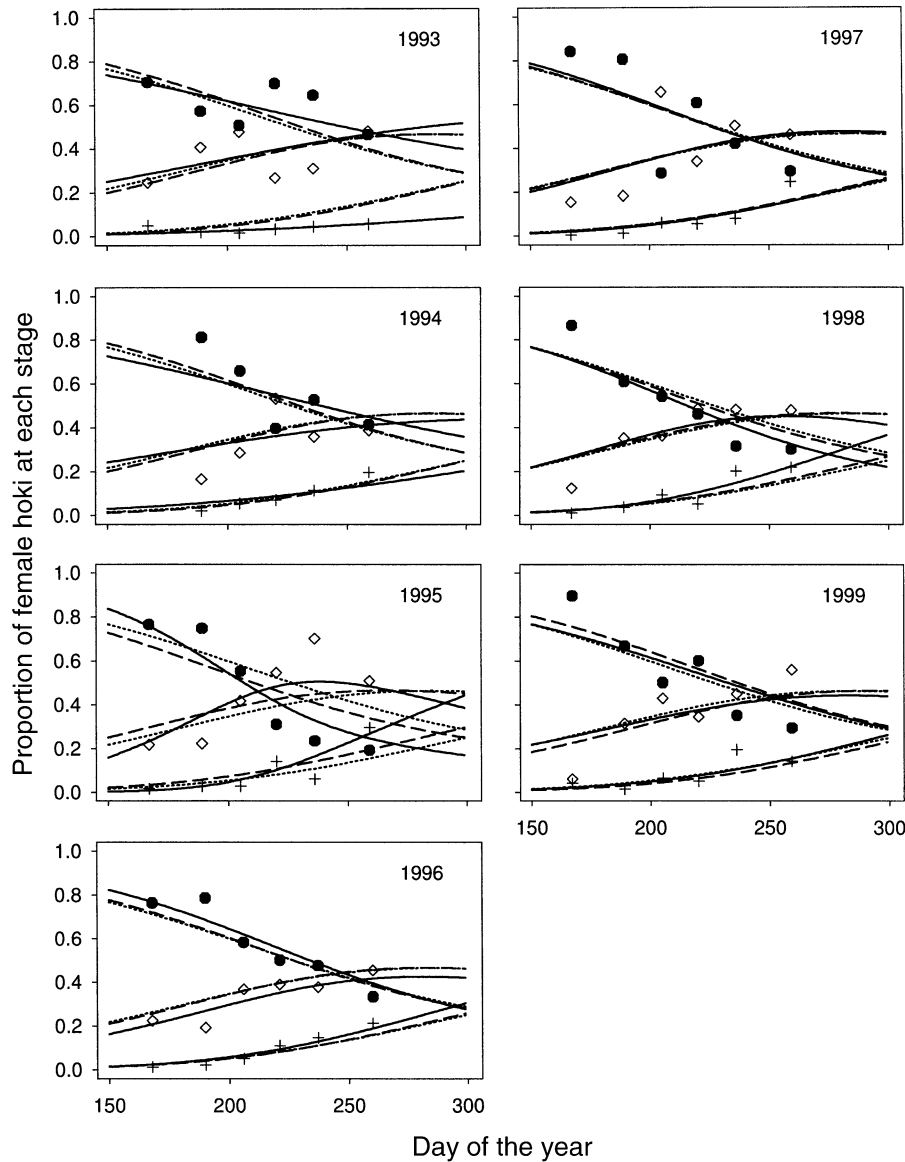


FIG. 6. Fit to the proportions at each gonad stage on the Cook Strait spawning ground for Models 1 (solid line), 2 (long-dash line), and 3 (dotted line): mature/maturing (solid circles), running ripe (open diamonds), and spent (+). To simplify this figure, we have not included error bars. The sample sizes are the same as those assumed for the sex ratio data.

of the spent duration contributed most of the bias to average residence time.

Model parsimony.—To determine overall model performance, we ranked each model in terms of its performance for each set of simulations. In terms of bias in the estimates of spawning biomass, Model 2 performed best, regardless of the true model, whereas Model 3 was slightly better than Model 2 in terms of RMSE. Overall, Model 3 most often had the lowest bias and RMSE for a given simulation and parameter. The superior performance of simpler models (even when they are not the true model) is not unusual (Hilborn and Mangal 1997).

DISCUSSION

A common problem when modeling population dynamics is that the dynamics (and therefore the models) are complex, but there are often insufficient data to reliably estimate the parameters of these models. This is particularly the case when modeling stage-structured data (Wood 1997), as we have done. Here we have demonstrated that it is possible to integrate a random-effects meta-analysis into a nonlinear dynamics model to overcome some of these problems.

A key feature of this model was that it integrated a variety of data. We combined gonad stage and biomass estimates to estimate the timing of spawning, residence

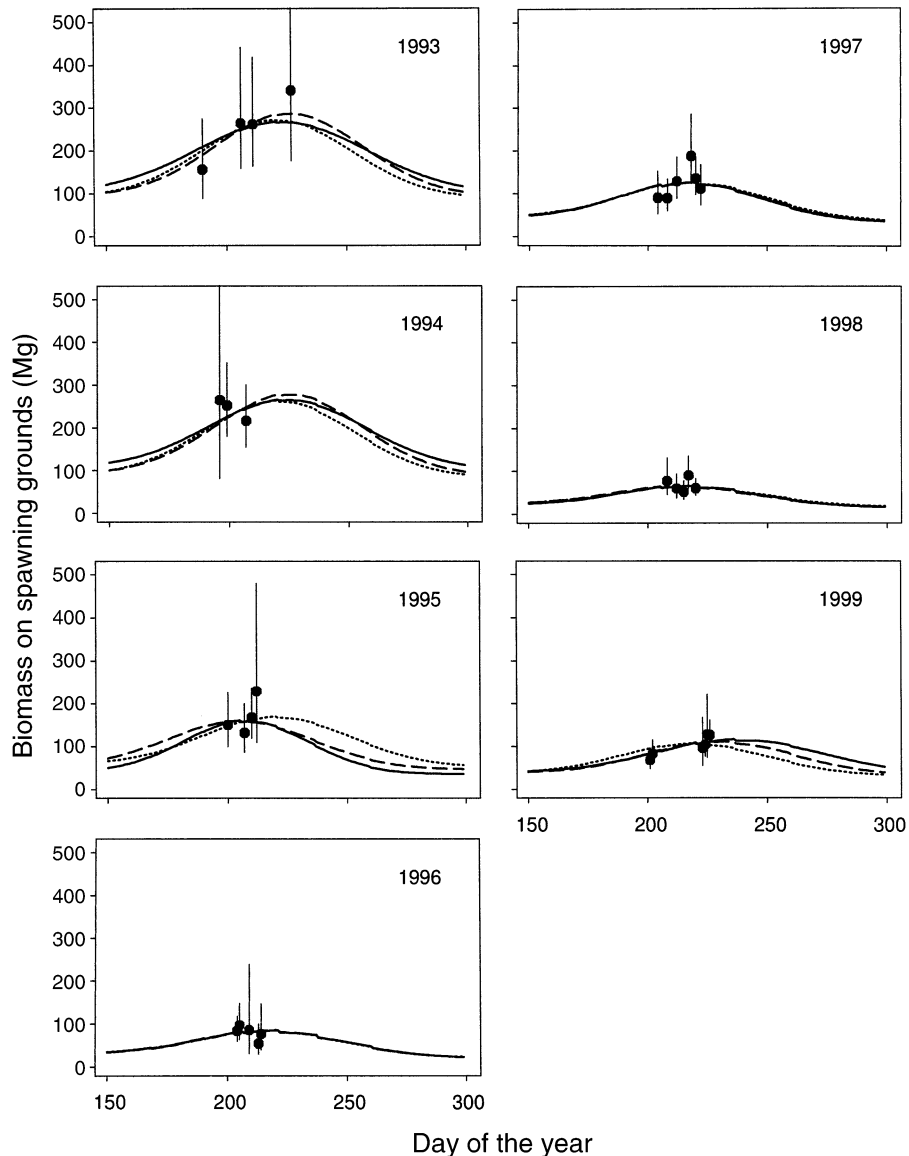


FIG. 7. Fit to the acoustic snapshot estimates on the Cook Strait spawning ground for Models 1 (solid line), 2 (long-dash line), and 3 (dotted line). The error bars represent the 95% confidence limits for the snapshot estimate assuming lognormal errors.

time, and total spawning biomass simultaneously. Earlier models of hoki spawning biomass (Coombs and Cordue 1995) assumed that the acoustic snapshots provided an estimate of biomass at the peak of the spawning season. In years during which the peak spawning was considered to be long after the acoustic surveys, ad hoc adjustments were made to biomass estimates (Annala et al. 2000).

Comparison of results

Here we estimated residence time of females on the spawning grounds. By accounting for the time that spent fish remain on the spawning grounds, we can compare our estimates of spawning duration to pre-

vious studies. The estimates of 32 days are greater than the range of 20–27 days found by Langley (1993) for hoki at the other major spawning ground. The estimates are slightly greater than the estimates for wild Atlantic cod (25.2 days; Hutchings and Myers 1993), but in the middle of the range of 22–48 days obtained for captive Atlantic cod (Kjesbu et al. 1996). Accounting for the positive bias found in the simulation study would make our estimates consistent with those of previous studies.

There is strong evidence for variability in the timing of spawning across years. This is consistent with other observations of spawning time for hoki (Gunn et al. 1989) and other Gadiformes, e.g., Atlantic cod (Hutchings and Myers 1993).

TABLE 4. Median percentage bias and percentage root mean-squared error (RMSE) for the estimates of spawning biomass and average female residence time (across years) for 200 simulated data sets. Bias and RMSE were divided by the true simulated value (and multiplied by 100) to give a relative measure comparable across models.

Estimation	Spawning biomass simulation			Average female residence (θ) simulation		
	Model 1	Model 2	Model 3	Model 1	Model 2	Model 3
Bias						
Model 1	4.4	10.3	10.3	34.7	33.8	42.2
Model 2	1.5	0.5	1.0	34.8	20.0	23.5
Model 3	1.9	1.5	3.6	5.8	12.2	11.4
RMSE						
Model 1	25.7	76.3	49.6	72.7	81.6	86.6
Model 2	19.8	17.9	26.2	61.2	34.0	44.0
Model 3	18.0	18.8	23.3	38.0	43.0	39.7

We compared estimates from all models with the biomass estimates used as indices of relative abundance in the current hoki stock assessment (Annala et al. 2000). Trends in relative abundance are again quite similar across models, but there is evidence of a greater decline in abundance over time for the models presented here than that suggested by the biomass estimates used in the present stock assessment.

Advantages of model-based estimation

The indices used in the stock assessment are generally based on the assumption that the acoustic snapshots were taken at the peak of the season (except for the last two years, for which the biomass estimates were scaled due to concerns that the survey missed the peak of the spawning season [Annala et al. 2000]). By incorporating biological data on the reproductive state of females with the acoustic biomass estimates inside a dynamic model, we were able to test whether the assumption of plateau sampling was likely to be met. Furthermore, the model-based approach allows us to estimate annual spawning biomass indices corrected for any potential sampling bias related to timing of the acoustic surveys.

It is difficult, however, to precisely estimate all of the model parameters using data for a single year. Estimated abundance indices are much less precise than indices based on combining acoustic snapshots. By simultaneously modeling data across years and treating model parameters in a biologically sensible, random-effect framework, we can estimate abundance indices with the same precision as sample-based indices without the potential bias introduced through the sampling process. We recommend that model-based approaches to estimating abundance from surveys be used in situations when population dynamics (e.g., migratory patterns) could introduce bias.

Comparisons to analyses of other taxa

The stage data used here allow for a much more precise model than would have been possible by using the acoustic survey alone. Vogt and Morton (1991) found that by incorporating age data to estimate survival and age-dependent vulnerability to capture, they were able to greatly improve the reliability of their estimates of population size in a mark-recapture model. Similarly, Myers et al. (1997) were able to use stage composition data to improve estimates of a grey seal, *Halichoerus grypus*, population from a mark-recapture study. Although these models are different from those used here, they show that using stage data along with abundance estimates can significantly improve estimates of population parameters. In addition to accommodating these features, our models allow stage data to be optimally incorporated over several years or over several populations.

The models developed here are very similar to those developed for estimating escapement in salmon (English et al. 1992, Hilborn et al. 1999, Su et al. 2001). Su et al. (2001) developed models of spawning pink salmon (*Oncorhynchus gorbuscha*) returns to Kadasan Creek in southeastern Alaska, where a hierarchical framework was used to share information across years.

Modeling approach

We have taken advantage of methods that allow sharing of information across years (or studies). In this analysis we have treated interannual variation in the mean arrival day in three ways: (1) independent from year to year; (2) fixed (constant) across years; and (3) as a random variable from an estimated distribution.

We found that the models that shared information performed much better than those that did not, even when there was considerable true variation across years. Adkison and Su (2001) also reported that their hierarchical estimators performed much better than the individual model estimates. A logical further step in this analysis would be to treat multiple parameters as random effects; this is possible using the approach described here. This was not warranted here, however, because the combination of estimates for residence time from Model 1 using simple random-effects models (Hardy and Thompson 1996) did not provide any evidence of significant interannual variation.

Here we used a maximum simulated likelihood approach to implement a random-effects analysis. This approach appears to provide the best way to implement computationally intensive nonlinear random-effects models. Alternatively, we could have used a Bayesian approach, which would have required the choice of priors for all model parameters. The simulated likelihood approach avoids the difficulties of choosing such priors.

By excluding the data for the proportion of females from the models, it was possible to determine the re-

liance of the models on these data. Interannual variability in all model parameters increased greatly with a number of “unlikely” results. With the current model and data structures, it does not appear possible to estimate residence time with gonad stage data alone. Various combinations of arrival and residence time can produce fits to the data that are equally likely.

There are several possible extensions for the sex- and stage-structured model presented here. First, it would be useful to introduce age structure (but not necessarily a category for each age) into the model. This was considered in the development of the current model, but was not considered further due to problems in estimating parameters with the very noisy age-disaggregated data. Using a hierarchical model, it could be possible to overcome many of the problems associated with the addition of age structure to the models. While the number of parameters being estimated increases, the use of constraints (i.e., treatment of parameters as fixed and random effects) assists parameter estimation. A further advantage of the hierarchical approach is that it may be possible to obtain better estimates of age-specific process (e.g., larger fish arriving on the grounds earlier) by sharing the information and constraining estimates of the relationship across years. We have used a similar approach here by constraining the arrival standard deviation to be the same across all years.

Recommendations for future research

One major concern for the reliability of our analysis is the dependence on fishery data for estimates of the sex and stage composition of the population on the spawning grounds; samples from commercial catches may not be representative of fish on the grounds, i.e., those fish sampled by the acoustic survey. The design of the acoustic survey incorporates a stratified random approach (Coombs and Cordue 1995), whereas the distribution of fishing effort is far from random with respect to the distribution of the fish. Fishers are likely to be targeting areas where they can achieve the highest catch rates or catches of hoki of a particular size. This strategy could vary across the fleet and change through the season (Langley 1993). The effect of this nonrandom approach on the representativeness of the samples is not clear. To best obtain representative samples of the spawning population, commercial samples should be either supplemented or replaced by fishery-independent sampling during the acoustic survey. The merging of the two sources would be difficult, but the use of a commercial “catching” vessel associated with the acoustic survey might provide representative samples (from both dense aggregations and less dense background “scatter” of hoki).

The data used for this analysis were aggregated across two-week strata. This is necessary because of the high inter-haul variability in the sex and gonad stage composition often associated with catches of

spawning Gadiformes (Langley 1993, Morgan and Trippel 1996). However, much of the spawning behavior occurs at shorter time frames. With female residence time of 30 days, a fish might be “represented” within only two observations of the spawning population from the grounds. The use of survey data could allow for the analysis of the gonad stage data on a finer scale.

Model-based estimation of residence time could be improved by laboratory-based studies of spawning behavior of hoki, providing useful estimates of the number of spawning batches and the length of time between batches. Any information on the behavior of male hoki on the spawning grounds, e.g., gonad stage, would help to overcome the biggest weakness in the current model, the definition of male residence time.

The model results suggest that the peak of the migration to the spawning grounds varies across years. Therefore, a short acoustic survey conducted during the same period every year could sample different stages of the spawning season each year. Gunn et al. (1989) proposed several environmental cues that may be important for the dynamics of hoki populations that spawn off southern Australia. It may be useful to investigate whether any of these factors (or others) can be used to predict the timing of spawning in a given year.

Finally, it would be possible to use the model and parameter estimates obtained here to investigate how the sampling strategy, e.g., the length and timing of the acoustic surveys, could be improved to allow for more reliable estimates. This was outside the scope of this paper, so all simulations were based on the historical sampling strategy. Adkison and Su (2001) used their model of pink salmon to investigate how run size could be estimated better by making additional counts. They found that the model estimates could be improved greatly if a single salmon count were conducted after the peak of the run. This type of analysis will be an important future step for those wishing to optimize future acoustic surveys.

Conclusions

We have shown that it is possible to improve survey estimates of abundance by hierarchical models in which the dynamical parameters are shared among years. Recent advances in estimation techniques, e.g., maximum simulated likelihood (as used here) and MCMC methods (Carlin and Louis 1996), allow for models that would have been impossible a short time ago. The type of model used here is particularly appropriate for stage composition data, which have often been used to improve estimates of abundance and population dynamics. In such models using stage composition data, it is often difficult to reliably estimate parameters of the models without assuming similarities in dynamics across years. The use of hierarchical models should improve estimates in these cases.

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