SPAWNER-RECRUIT PATTERNS AND INVESTIGATION OF ALLEE EFFECT IN PACIFIC SARDINE (*SARDINOPS SAGAX*) IN THE GULF OF CALIFORNIA, MEXICO

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ABSTRACT

We analyzed stock and recruitment data of Pacific sardine (*Sardinops sagax*) from the Gulf of California, México. We used the Shepherd and Ricker stock-recruitment (*S-R*) models and included a new parameter in the *S-R* function. The new parameter, associated with the Allee effect, was defined as λ, which permitted a non-zero intercept representing recruitment failure. The general model was $R_t = (S_t - \lambda)F(S_t - \lambda,\theta)$, where R_t is recruitment, S_t is spawning stock, and θ represents the parameters in the model. Parameters were estimated using a negative log-likelihood algorithm. The λ parameter was estimated to be 287 x 10^6 spawning adults in the Shepherd model and 1,569 x 106 spawning adults in the Ricker model, with these values representing the abundance of the adult stock with zero recruitment. We proposed using λ as a reference point in the fishery. Estimates of λ did not indicate an Allee effect in the sardine population in the Gulf of California, because when the parameters in this model were estimated, we observed that estimates of recruitment were not less than the reference value of 287 million individuals. We believe the fall of abundance during 1993 and 1994 is possibly associated with environmental factors. In these years, the Pacific sardine was far from the reference point estimated by our study, and we believe that the λ parameter is a good indicator of the minimum stock size necessary to maintain the fishery.

INTRODUCTION

The Pacific sardine (*Sardinops sagax*) population in the Gulf of California has been analyzed using two hypotheses. The first explains a relationship between the environment and fluctuations in abundance (De Anda et al. 1994; Cisneros-Mata et al. 1996a; Nevárez-Martínez et al. 1999; 2001), and the second proposes a density-dependent effect (Cisneros-Mata et al. 1995; 1996b). For the first hypothesis, there is evidence that environmental variability affects Pacific sardines. Baumgartner et al. (1992) showed a reconstruction of abundance changes of Pacific sardines and anchovy (*Engraulis mordax*) from the analysis of scales deposited in anaerobic sediments. Their analysis showed changes in sardine abundance over periods of 30 years. Lluch-Belda et al. (1989; 1991; 1992a; 1992b) explained the variability in abundance as changes in distribution along the California Current according to temperature and upwelling patterns. This change in distribution is more evident when an El Niño affects the California Current (Fiedler 1984; Hayward 1993; 2000; Lea and Rosenblatt 2000). El Niño causes a shift in distribution of Pacific sardines to the northern range of the California Current. During 1992, Hargreaves et al. (1994) observed *Sardinops sagax* along the British Columbia coast, and during 1997–98 the species was observed off Alaska (Wing et al. 2000).

When these changes in distribution and abundance are measured, the population dynamics of the sardine are affected, and an Allee effect could be observed in the stock. When a school falls below its critical level, any self-regenerating abilities are lost, and school rebuilding can only occur through mixing with other schools. Frank and Brickman (2000) explained that Allee effects have been demonstrated or hypothesized for the Pacific sardine. Allee affects can arise from a general ecological process (predation) under a variety of different combinations of functional and aggregative responses. Allee effects may thus be present in a broad spectrum of different taxa with different types of life history and not only in those taxa such as broadcast spawners and cooperative breeders (Gascoigne and Lipcius 2004). An increasing number of marine species are heavily exploited or threatened with collapse; consequently, there is a need to understand the performance of populations at low population density. The vulnerability of an animal population to overexploitation depends upon its reproductive behavior and mating system (Stoner and Ray-Culp 2000). Nevárez-Martínez et al. (2001) noted that the decline (1990–93) and recovery (1994–96) of sardines were due to the environment affecting the quality and quantity of primary productivity. Although the environmental effect is an important source of variability in Pacific sardine abundance, a management strategy for Pacific sardines in the Gulf of California needs to be determined so that we can develop management goals and reference points for the fishery. In this paper, we present an analysis of stock and recruitment data to inves-

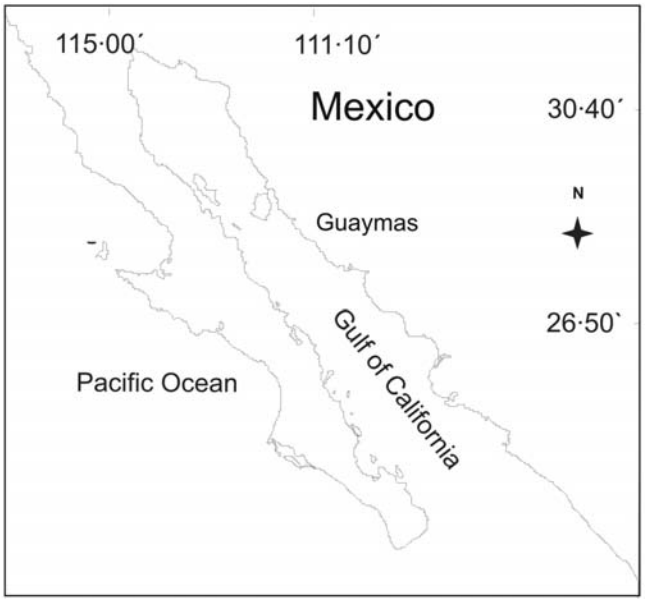

Figure 1. Study area of Pacific sardines (*Sardinops sagax*) in the Gulf of California, Mexico.

tigate the presence of an Allee effect and to identify a fishery reference point for Pacific sardines in the Gulf of California.

MATERIAL AND METHODS

Using biological and catch and effort data from the Pacific sardine fishery in the Gulf of California (fig. 1), the numbers of individuals-at-age in the sardine population were estimated using virtual population analysis (VPA) to estimate spawner and recruit abundance (Gulland 1965; Megrey 1989) from the 1971–72 through 1996–97 fishing seasons. The methods and assumptions were similar to those used by Cisneros-Mata et al. (1995) and Nevárez-Martínez et al. (1999). We used the VPA (sequential population analysis, SPA) module in FISHLAB (Darby and Flatman 1994). The number of recruits was estimated as the number of 0-age fish in each fishing season. Spawning-stock abundance was expressed as the sum of individuals from age 1 to the oldest age-group (Nevárez-Martínez et al. 1999).

Shepherd Model

We analyzed the stock-recruitment (*S-R*) relationship using a model described by Shepherd (1982) as

$$R_t = \frac{\alpha S_{t-1}}{1 + \left(S_{t-1}/\kappa\right)^{\beta}} e^{\varepsilon}, \tag{1}$$

where R_t is the recruitment size in year t, S_{t-1} is the parental stock size in the previous year, α is the maximum per capita recruitment, κ is the parental stock size above which density dependence dominates density-independent factors, and β measures the strength of density dependence (Cisneros-Mata et al. 1996b). The β parameter allows for a range of shapes in the stock-recruitment relationship. By changing β, the Shepherd model reflects (a) a dome-shaped relationship similar to a Ricker curve for $\beta = 2$ where a high abundance of spawners can reduce recruitment in future years, (b) a Beverton-Holt relationship for $\beta = 1$ where increasing the number of spawners eventually leads asymptotically to constant recruitment, or (c) a Cushing relationship for $\beta = 0.5$ where increasing spawners increases recruitment (Robb and Peterman 1998; Quinn II and Deriso 1999). The parameter ε is a normally-distributed, random-noise term with a mean = 0 and standard deviation = σ. The stock-recruitment data were analyzed in two different ways. We first excluded the period 1992–93 and 1993–94 because in those years the most important fall in Pacific sardine abundance was observed (Cisneros-Mata et al. 1995). Those authors assumed that the decline from 1989 to 1992 was an effect of overfishing, and during 1992–93 and 1993–94 the consequences were observed to be low abundance and an important fall in the landings. Additionally, during 1992 and 1993 the California Current was affected by El Niño conditions (Hayward 1993; Hayward et al. 1994), and during 1994 the California Current returned to a typical circulation pattern (Hayward et al. 1995). In our time series of *S-R* data, 1992–93 and 1993–94 showed the lowest values of spawning stock (fig. 2). In the second option, we analyzed the complete series of stock-recruitment data for 1971–72 to 1996–97 (fig. 2).

Frank and Brickman (2000) and Chen et al. (2002) proposed a natural extension of traditional *S-R* models where an Allee effect was incorporated. It is commonly known as "depensation" in fisheries (Liermann and Hilborn 2001). Despite the large number of studies supporting a depensatory mechanism, there is little evidence of depensation that is strong enough to be important in a population's dynamics (Liermann and Hilborn 1997; Myers et al. 1999; Myers 2001). However, because factors such as demographic and environmental variability make depensatory population dynamics difficult to detect, this lack of evidence should not be interpreted as evidence that depensatory dynamics are rare and unimportant (Liermann and Hilborn 2001). So the modified Shepherd model was then expressed as

$$R_t = \frac{\alpha (S_{t-1} - \lambda)}{1 + \left((S_{t-1} - \lambda)/\kappa\right)^{\beta}} e^{\varepsilon}, \tag{2}$$

where λ represents the Allee effect by permitting a non-zero intercept representing recruitment failure (Frank

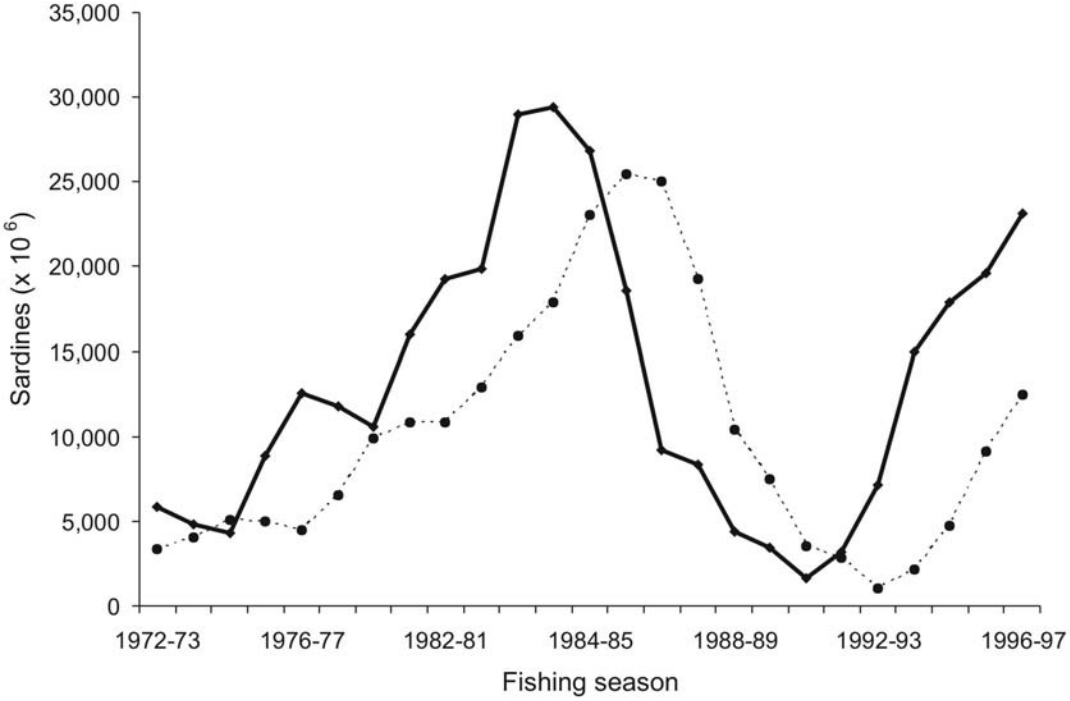

Figure 2. Time series of adult stock (dotted line) and recruitment (solid line) of the Pacific sardine (*Sardinops sagax*) in the Gulf of California, Mexico.

and Brickman 2000). Chen et al. (2002) explained that a model with depensatory-population dynamics may be used when the population is small, because then population growth declines as population density declines. A variety of processes can result in depensation at low abundance. Inbreeding may occur, spawning fish may not find mates, higher mortality may result from predator saturation or fishing, and poor conditioning of the spawning environment and low efficiency of food location may result. The evidence for a depensatory mechanism may be grouped according to four categories: (a) reduced probability of fertilization, (b) impaired group dynamics, (c) conditioning of the environment, and (d) predator saturation (Liermann and Hilborn 2001). When abundances are low, depensation will accelerate population declines and increase the probability of collapse. If we include depensatory effects, stock rebuilding could be delayed or prevented (Chen et al. 2002). In Pacific sardines, the decline observed in landings during 1992–93 and 1993–94 could have been a risk of collapse in this fishery. Cisneros-Mata et al. (1996b) noted that the intrusion of anomalous warm-water masses shortens the spawning season and forces adult distribution northward, and this mechanism probably increases cannibalism in the Pacific sardine in the Gulf of California.

The θ parameters in the modified Shepherd model (equation 2) were estimated using a negative log-likelihood estimator:

$$-\log L(\theta / data) = \sum_t \left[-\frac{1}{2} * \ln(2 * \pi) \right] - \left[\frac{1}{2} * \ln(\sigma^2) - \frac{(\ln R_O - 1\mathrm{n} R_E)^2}{2 * \sigma^2} \right], \qquad (3)$$

where *t* is brood year, and the θ parameters were α, β, κ, and λ. In this case, θ indicates the combination of hypothesized parameter values for the Shepherd model, R_O is the observed recruitment, and R_E is the estimated recruitment. For σ the analytical solution was proposed as

$$\sigma = \sqrt{\frac{1}{n} \sum_{t=1}^{n} (1\mathrm{n}R_O - 1\mathrm{n}R_E)^2}\ , \qquad (4)$$

where *n* is the number of years in the *S-R* data series (Hilborn and Walters 1992).

Confidence Intervals

To estimate the confidence intervals for the parameters in the modified Shepherd model, we used the likelihood profile (Venzon and Moolgavkor 1988; Hilborn and Mangel 1997) because it can be used to determine confidence intervals for the θ parameters either jointly or individually. The confidence intervals for the parameters were estimated based on the χ^2 distribution with *m* degrees of freedom (Zar 1974). For a single parameter *p*, the confidence interval was defined as all values of *p* that satisfy the inequality

$$2[L(Y|\ p_{est}) - L(Y|\ p)] < \chi^2_{1,1-\alpha}, \tag{5}$$

where $L(Y|\ p_{est})$ is the negative log-likelihood of the most likely value of p, and $\chi^2_{1,1-\alpha}$ gives the values of the χ^2 distribution with 1 degree of freedom at a confidence level of $1 - \alpha$. Thus, the 95% confidence interval for p encompasses all values of p that are twice the difference between the negative log-likelihood and the negative log-likelihood of the best estimate of p, which is less than 3.84 (Pawitan 2001).

Ricker Model

We also analyzed the data using a Ricker model $R_t = \alpha S_{t-1} e^{-\beta S_{t-1}} e^{\omega_t}$, where α is the parameter associated with density-independent mortality, β is the parameter associated with density-dependent mortality, and ω is the error normally distributed with a mean = 0 and a standard deviation = σ. Parameter values in the Ricker model were computed according to the negative log-likelihood estimator described in equation (3).

Where θ parameters were α and β, θ indicates the combination of hypothesized parameter values for the Ricker model. The standard deviation was computed with equation (4), and ω_t was estimated as

$$\omega_t = 1\mathrm{n}\left(\frac{R_t}{\alpha S_{t-1}}\right) + (\beta S_{t-1}). \tag{6}$$

When the λ parameter was incorporated into the Ricker equation, the *S-R* relationship was expressed as $R_t = \alpha(S_{t-1}-\lambda)e^{-\beta(S_{t-1}-\lambda)}e^{\omega_t}$. This equation was defined as the modified Ricker model (Chen et al. 2002). The parameters' values were estimated according to the negative log-likelihood estimator shown in equation (3), and the θ parameters were α, β, and λ.

For the Ricker model and the modified Ricker model, the parameters were estimated with a nonlinear fit using the Newton algorithm (Neter et al. 1996). Confidence intervals for parameters in these equations were computed from the likelihood profiles described in equation (5). Estimations of likelihood were computed as $L_i = \exp^{-\log L_i}$, where L denotes likelihood, and i means the modified Shepherd model, Ricker model, or modified Ricker model.

Akaike's Information Criterion

We compared the different model fits using Akaike's information criterion (AIC) $AIC = (2 \times - \log L) + (2 \times \theta)$, where $- \log L$ was the negative log-likelihood estimated in equation (5), and θ represents the number of parameters in each model. The smallest AIC is for the best model (Haddon 2001).

RESULTS

The parameters for the Shepherd and Ricker models are shown in Table 1, and the confidence intervals ($P < 0.05$) are shown in Table 2. The modified Shepherd model showed an estimation of the λ parameter lower than that estimated by the modified Ricker model. The non-zero intercept representing recruitment failure in the Shepherd model was 287 million spawners, whereas that of the Ricker model was 1,569 million spawners. The α and β parameters were similar in the modified and typical Ricker models. However, the modified Ricker model shows likelihood higher than that of the Ricker model (tab. 1). Likelihoods computed for the modified Shepherd model and modified Ricker model were similar. The observed value of recruitment fitted to the modified Shepherd model is shown in Figure 3. Estimates of spawners derived from virtual population analysis were not less than the reference value of 287 million individuals.

Estimations of the likelihood profiles and their confidence intervals ($\chi^2_{1,1-\alpha}$) for the modified Shepherd model are shown in Figures 3–6. The λ parameter (fig. 4) shows a likelihood profile with negative values. The trend

TABLE 1
Parameters and Likelihood Estimated for the Different Stock-recruitment Models. λ is Expressed in Millions of Individuals

	λ	α	κ	β	Likelihood
1) Modified Shepherd Model	287	1.4	23,339	5.43	1.87E-09
2) Ricker Model		2.3		5.1E-5	5.13E-12
3) Modified Ricker Model	1,569	2.55		5.4E-5	1.58E-09

TABLE 2
Confidence Intervals Estimated from Negative Log Likelihood Profiles ($P < 0.05$) for Parameters of the Different Stock-recruitment Models

	λ	α	κ	β
1) Modified Shepherd Model	–500 – 900	1.2 – 1.6	21,000 – 33,000	2.5 – 11.0
2) Ricker Model		1.8 – 2.8		3.0E-5 – 7.2E-5
3) Modified Ricker Model	240 – 2,280	2.0 – 3.2		3.4E-5 – 7.4E-5

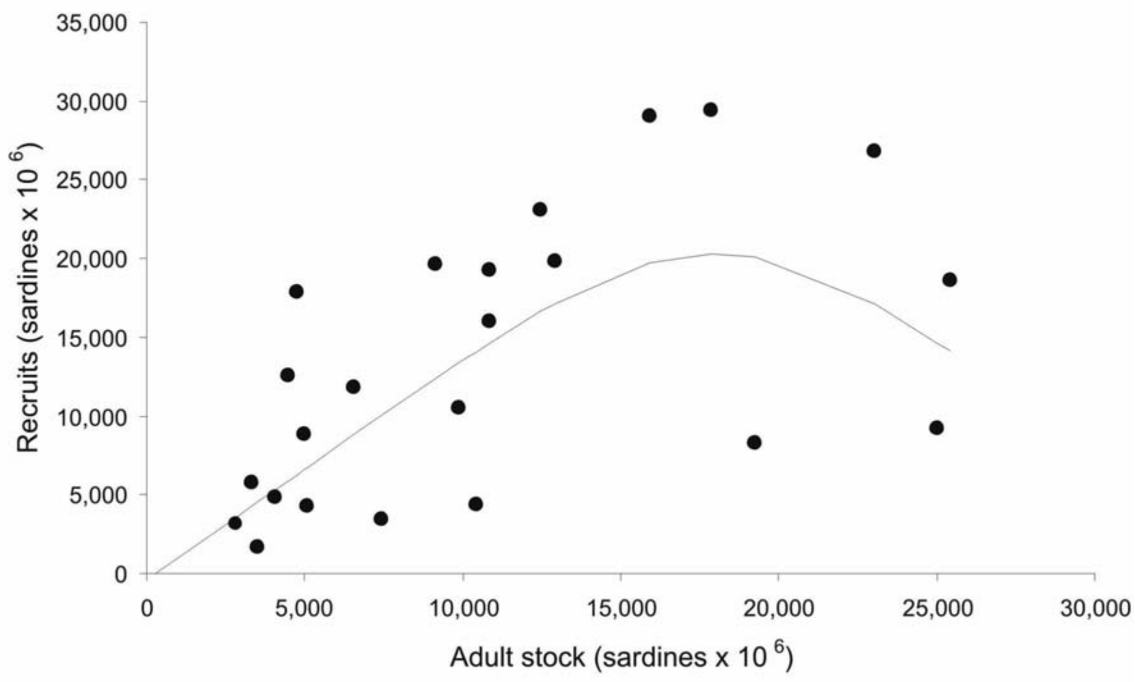

Figure 3. Recruitment of Pacific sardine (*Sardinops sagax*) estimated by the modified Shepherd model.

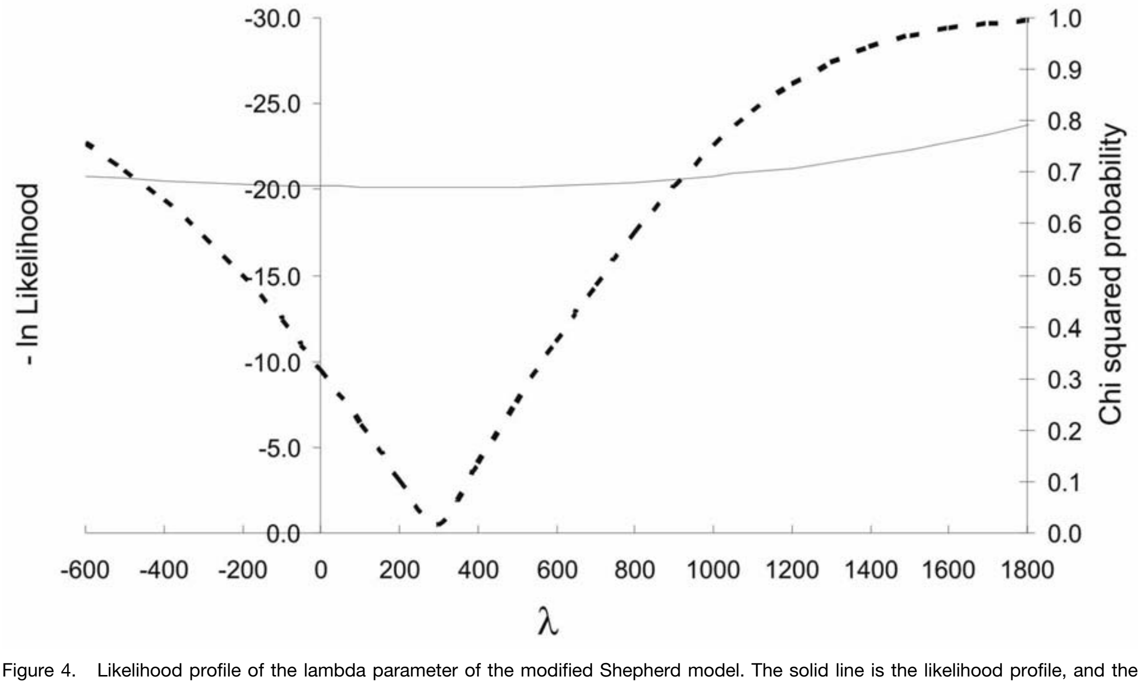

Figure 4. Likelihood profile of the lambda parameter of the modified Shepherd model. The solid line is the likelihood profile, and the dotted line is χ^2 probability.

of this parameter is not defined because the maximum likelihood is a flat line, and there are negative values for λ, and it does not explain the recruitment failures of the Pacific sardine from the Gulf of California. The α parameter shows a well-defined likelihood profile, and its confidence intervals were accurate (fig. 5). The κ and β parameters showed the same trend as λ, however it was possible to estimate confidence intervals for both parameters without computing negative values (fig. 6 and 7). The κ parameter was more accurate than β, and the likelihood profile of κ was similar to α.

The observed values of recruitment fitted for the Ricker model are shown in Figure 8. The likelihood profiles for parameters α (fig. 9) and β (fig. 10) showed that the α parameter had a better estimation of confidence intervals than the β parameter. Apparently, the

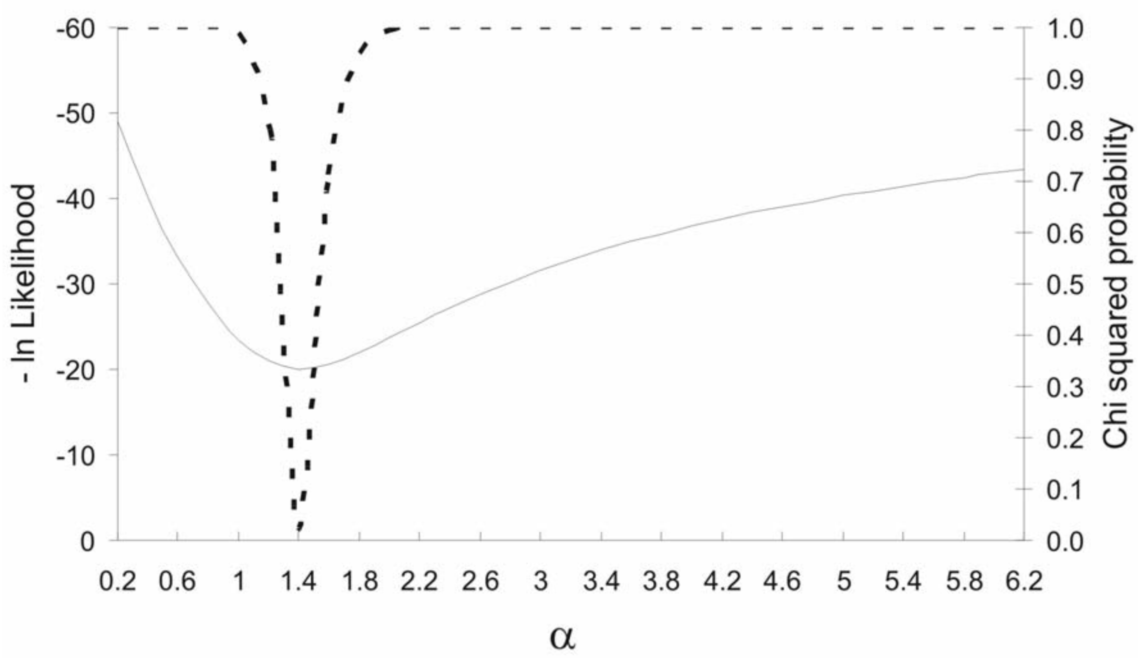

Figure 5. Likelihood profile of the alpha parameter of the modified Shepherd model. The solid line is the likelihood profile, and the dotted line is χ^2 probability.

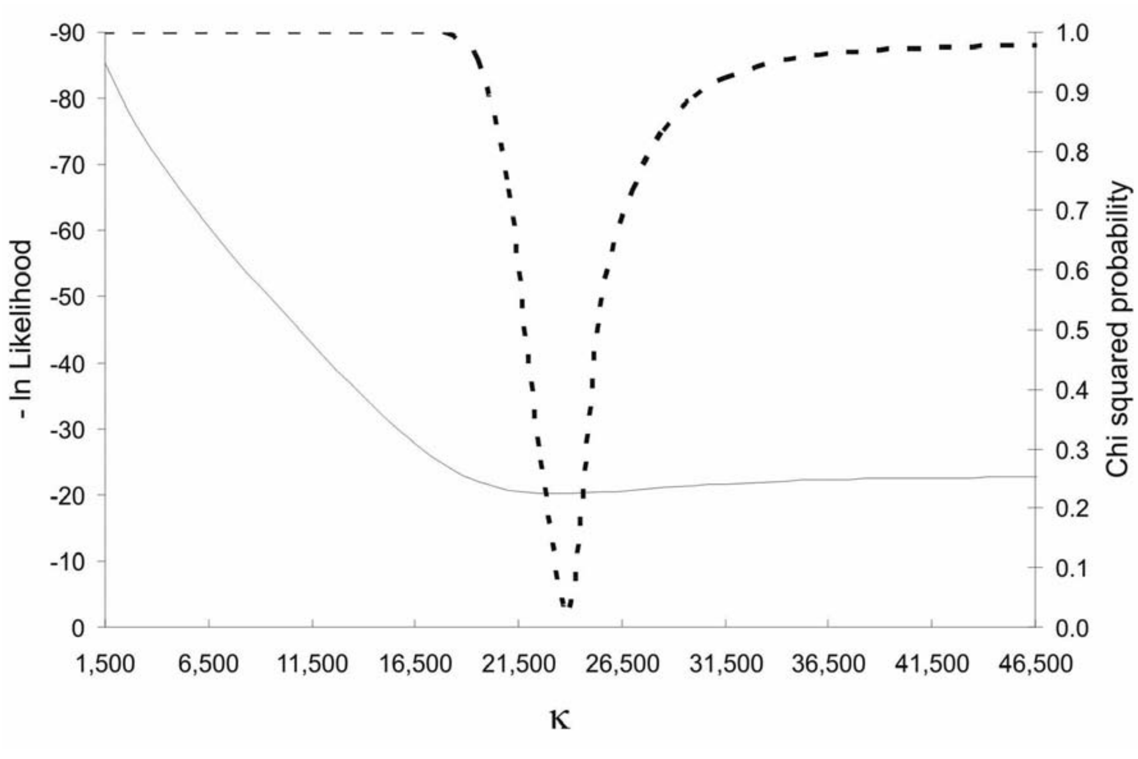

Figure 6. Likelihood profile of the kappa parameter of the modified Shepherd model. The solid line is the likelihood profile, and the dotted line is χ^2 probability.

likelihood profile of β is flat compared to α. When we compared the fits obtained with the Ricker model and modified Ricker model (fig. 11), the non-zero intercept (λ) (fig. 12) was estimated at 1,569 million spawners. This was five times greater than λ for the modified Shepherd model (tab. 1). The estimates of the number of spawners from the sequential population analysis were not lower than the value of the non-zero intercept,

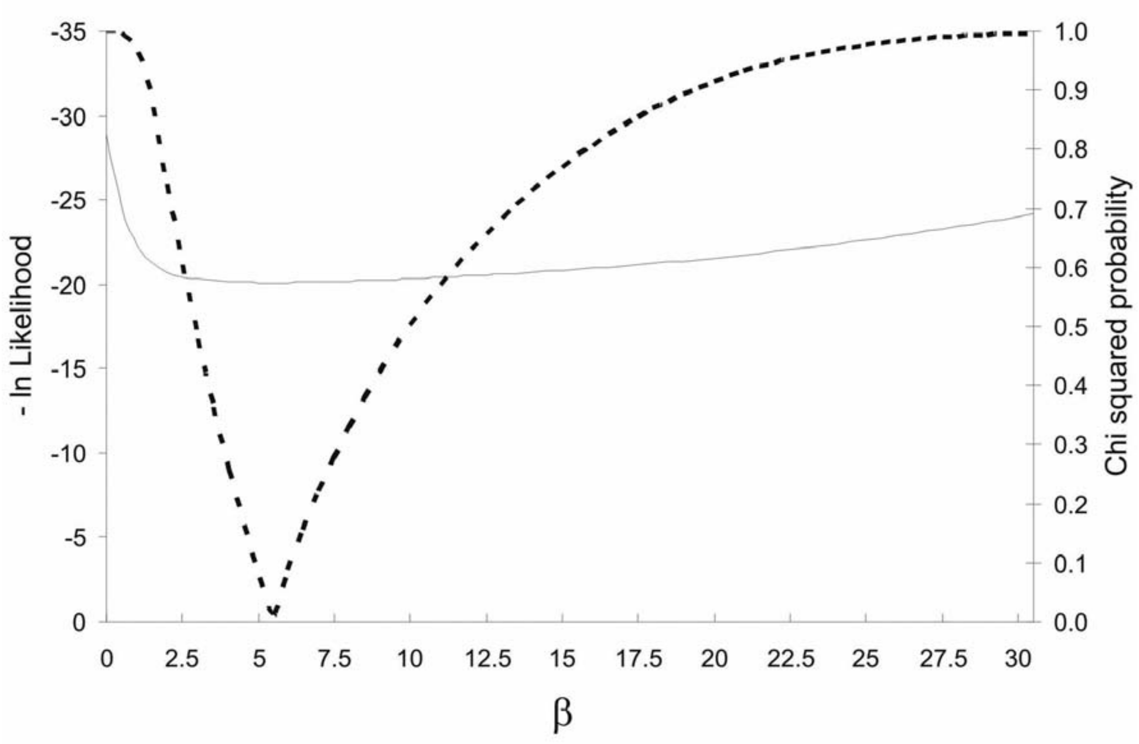

Figure 7. Likelihood profile of the beta parameter of the modified Shepherd model. The solid line is the likelihood profile, and the dotted line is χ^2 probability.

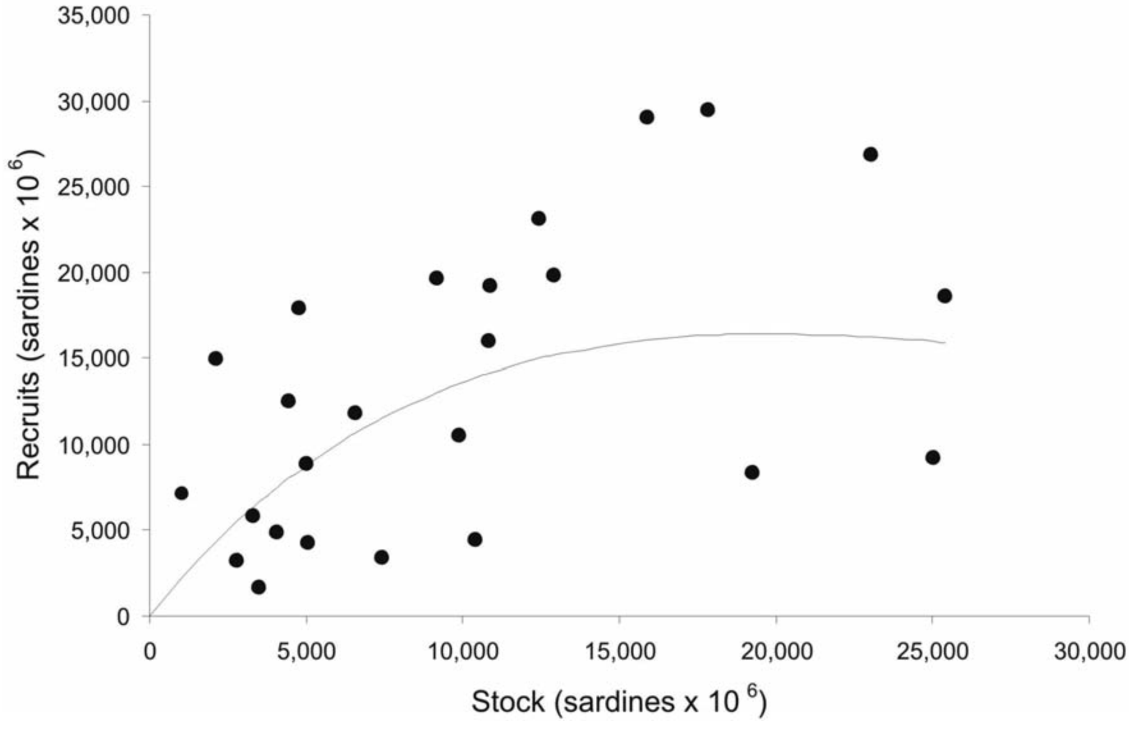

Figure 8. Recruitment of Pacific sardine (*Sardinops sagax*) estimated for a Ricker model.

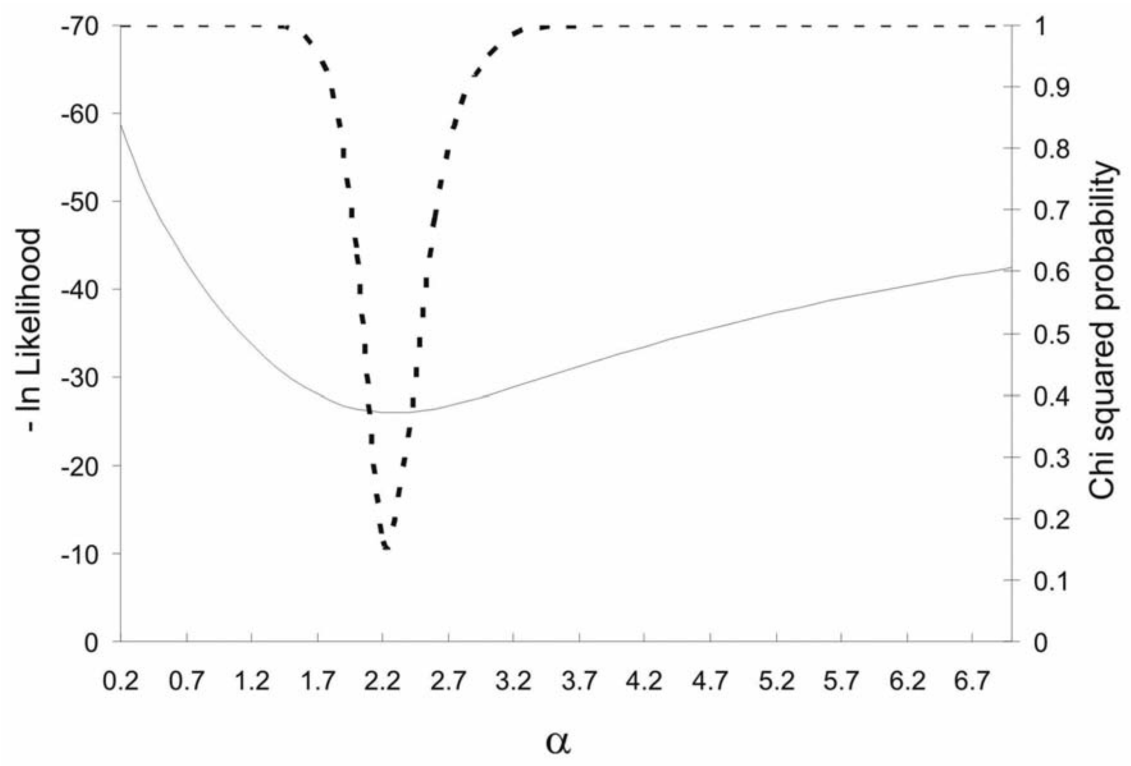

Figure 9. Likelihood profile of the alpha parameter of a Ricker model. The solid line is the likelihood profile, and the dotted line is χ^2 probability.

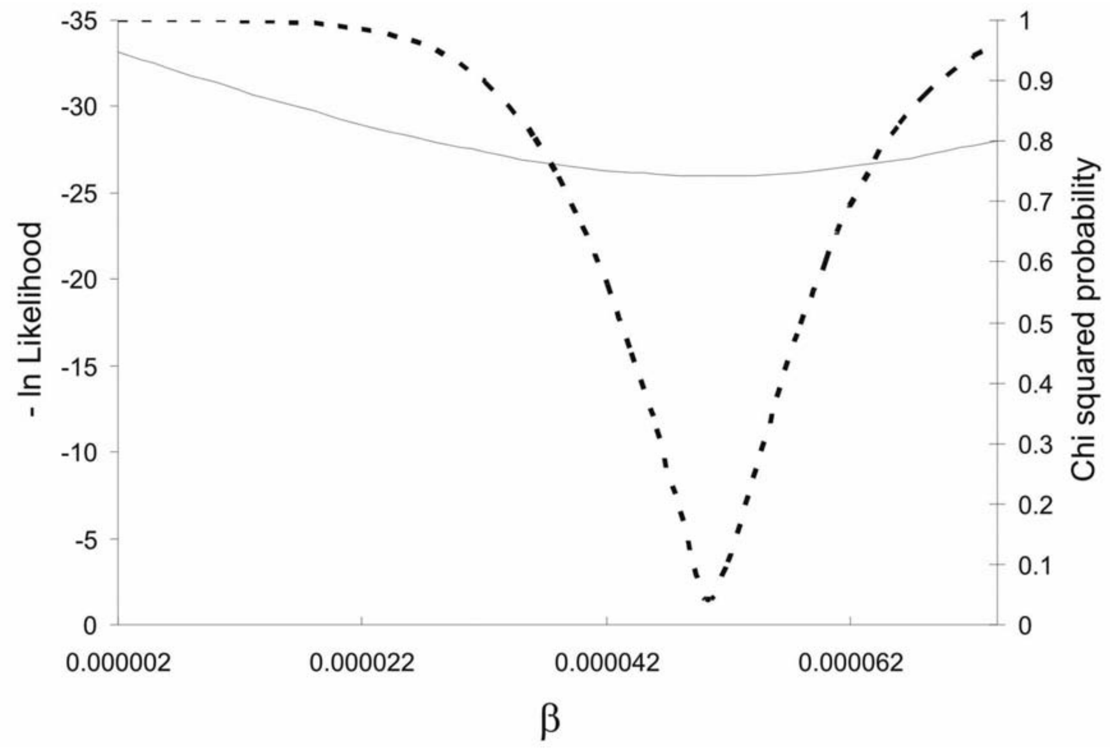

Figure 10. Likelihood profile of a beta parameter of a Ricker model. The solid line is the likelihood profile, and the dotted line is χ^2 probability.

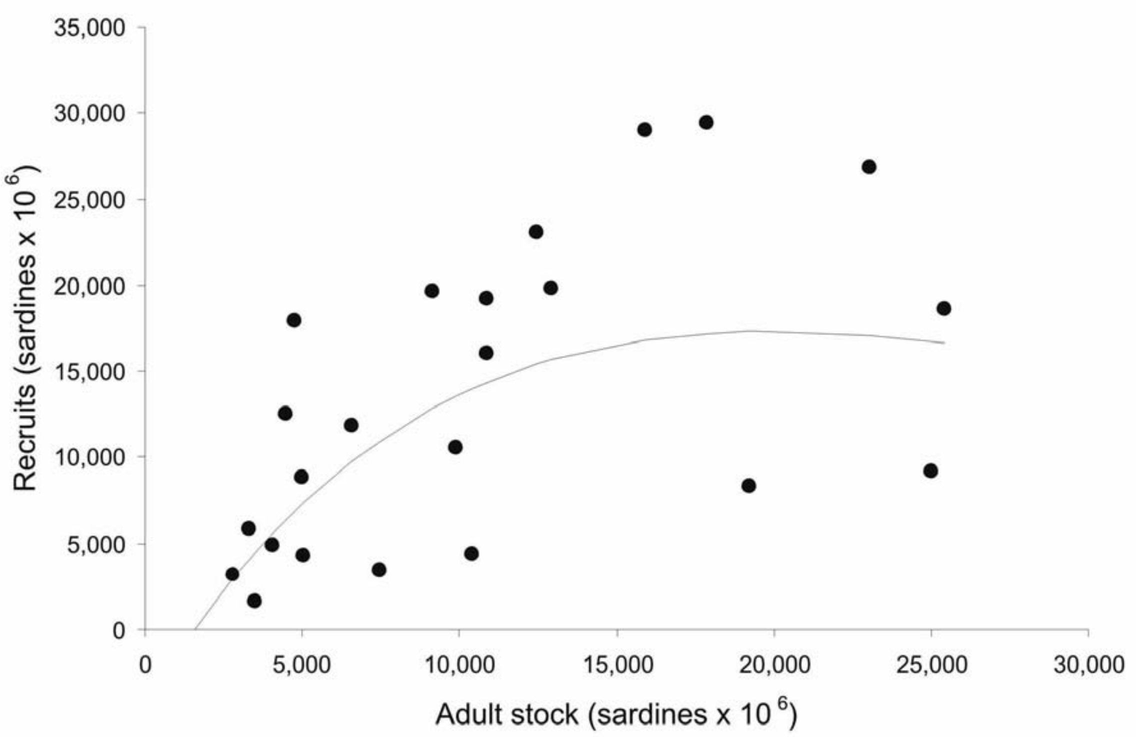

Figure 11. Recruitment of Pacific sardine (*Sardinops sagax*) estimated for a modified Ricker model.

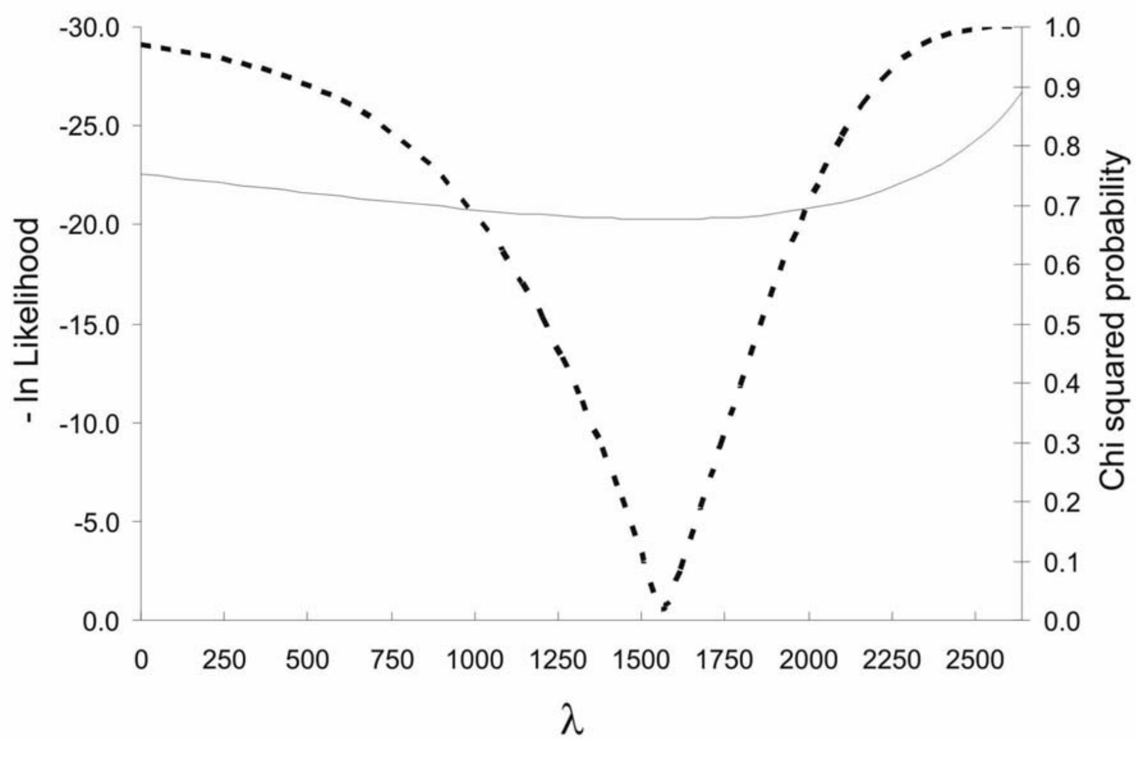

Figure 12. Likelihood profile of the lambda parameter of a modified Ricker model. The solid line is the likelihood profile, and the dotted line is χ^2 probability.

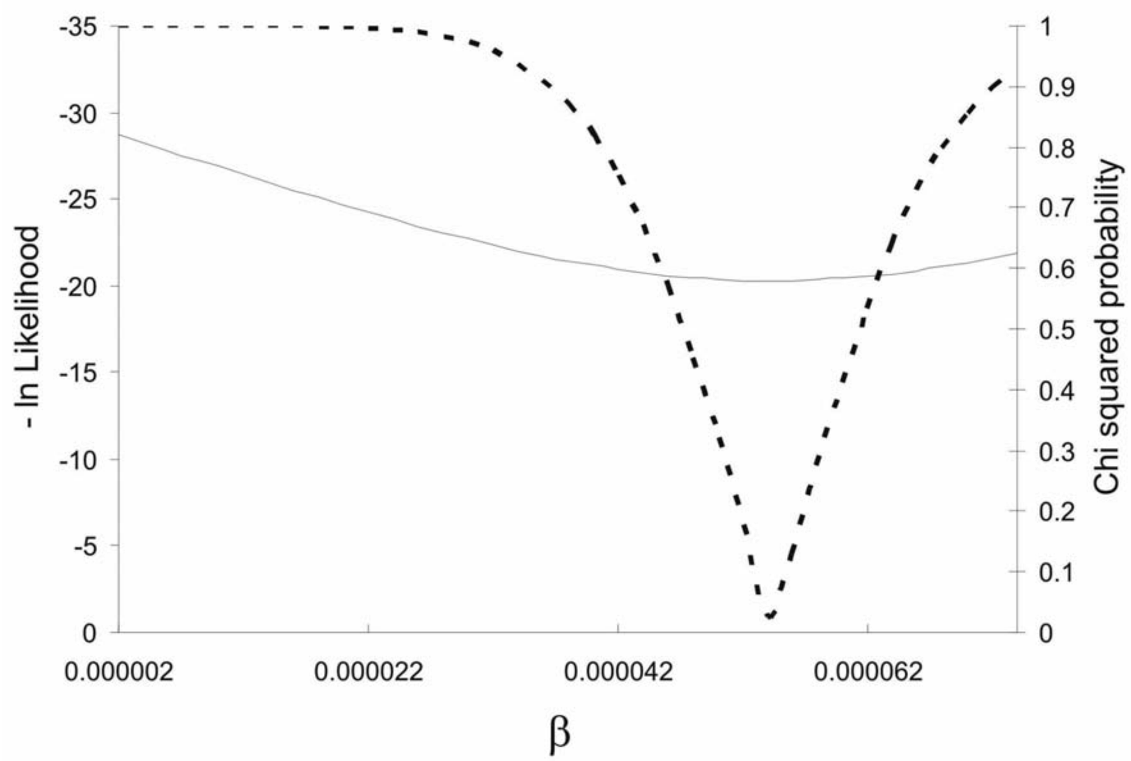

Figure 13. Likelihood profile of the beta parameter of a modified Ricker model. The solid line is the likelihood profile, and the dotted line is χ^2 probability.

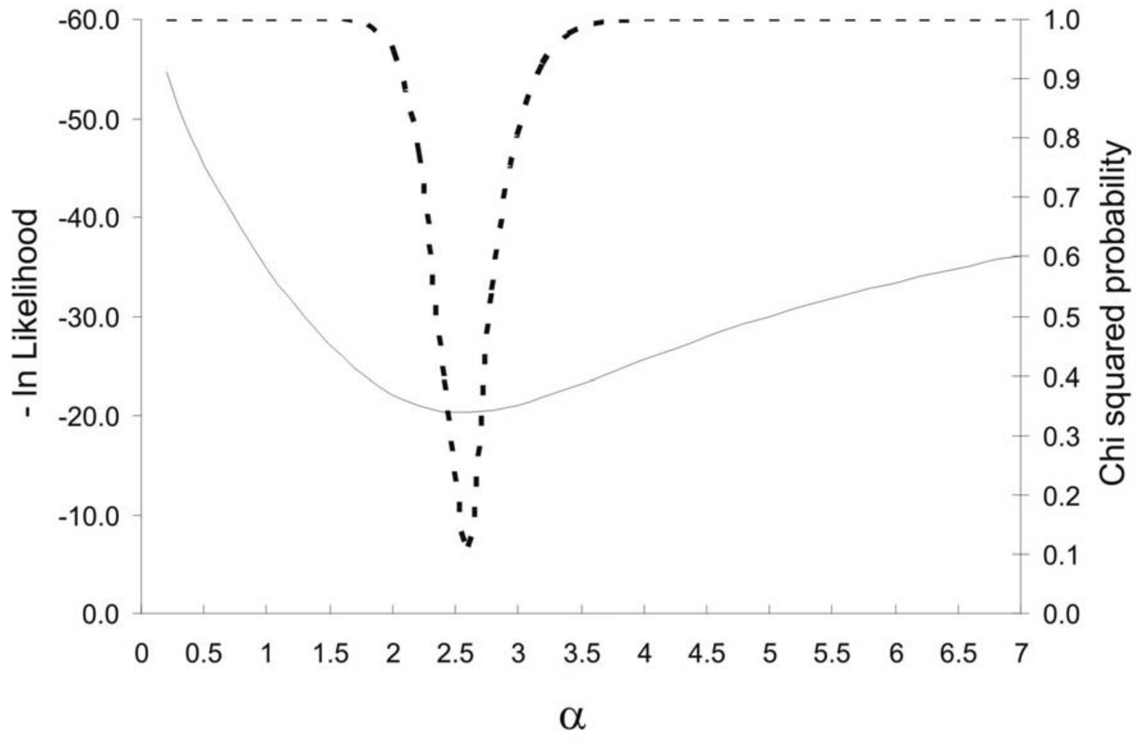

Figure 14. Likelihood profile of the alpha parameter of a modified Ricker model. The solid line is the likelihood profile, and the dotted line is χ^2 probability.

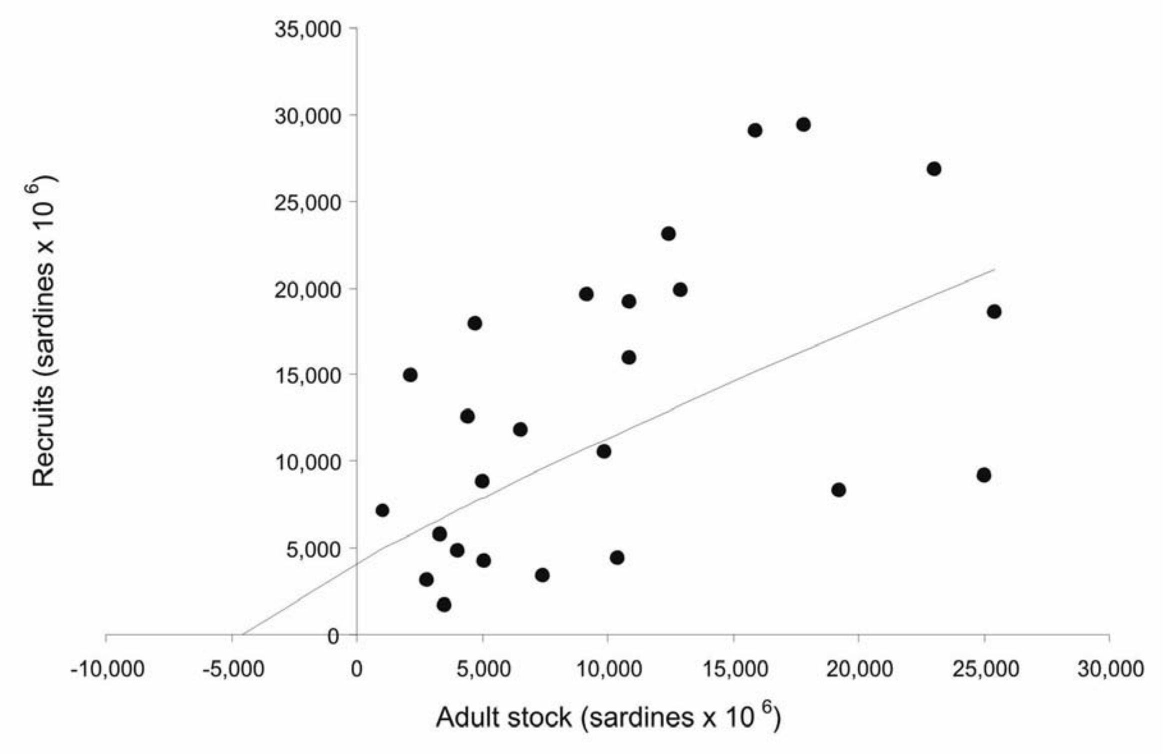

Figure 15. Stock-recruitment relationship of the Pacific sardine (*Sardinops sagax*) with a modified Shepherd model. This estimation includes complete time series of S-R data, from 1971 to 1997.

whereas β (fig. 13) and α (fig. 14) showed a trend similar to that of the Ricker model.

When the complete time series of *S-R* data were analyzed from 1971 to 1997, including 1993 and 1994, the estimates of λ in the modified Shepherd model were negative (fig. 15). The model showed an *S-R* relationship in which it was not possible to establish a reference point because the minimum stock size was negative, $\lambda = -4{,}558$, and the other parameters were $\alpha = 3.38$, $\kappa = 17.2$, and $\beta = 0.17$. This negative estimate of λ was observed as a consequence of variability in the stock and recruitment data.

Table 3 shows the results calculated for Akaike's information criterion. AIC values indicate that the best model was the modified Ricker model (46.52), for which the AIC was slightly less than for the modified Shepherd model (48.19). The AIC values of these models that included the λ parameter were better than that of the Ricker model (55.99). This result suggests that the inclusion of the λ parameter did not affect the performance of the model to fit stock-recruitment data. Although estimated AIC values for the modified Ricker model and modified Shepherd model were close, the main difference was the λ estimate, because the modified Ricker model computed 1,569 million spawners and the modified Shepherd model estimated 287 million spawners. This analysis shows there is no evidence of an Allee effect in the Pacific sardine in the Gulf of California. The number of spawners estimated with λ represents the reference point computed for stock recruitment data from the Gulf of California, and in our time-series of spawners they are greater than λ.

TABLE 3
Selection of the Best Model Based in AIC

	–log Likelihood	Number of Parameters	AIC
1) Modified Shepherd Model	–20.09	4	48.19
2) Ricker Model	–25.99	2	55.99
3) Modified Ricker Model	–20.26	3	46.52

DISCUSSION

The Pacific sardine population is characterized by high variability in abundance which affects the availability, distribution, production, and uncertainty in the fishery. It is important to maintain strong recruitment for the sardine fishery. Lasker (1985) mentioned that the solution to the stock-recruitment problem is to determine the minimum population for a species that ensures its recovery. However, it was also later noted that there was no definable minimum stock size for each species and stock, and this minimum stock size is necessary to understand the population dynamics (Watanabe et al. 1995). In this way, a reference point for populations under fishing pressure needs to be established. The reference point is defined as a conventional value derived from technical analysis, which represents a state of the fishery or population, and whose characteristics are believed to be useful for the management of the unit stock (Caddy and Mahon 1995).

In our results, we observed that the modified Shepherd model and modified Ricker model demonstrated good performance in estimating λ values. In both cases, λ represents a reference point for the stock-recruitment relationship. In the modified Shepherd model it was 287 million spawners, and in the modified Ricker model it was 1,569 million. Depensation could be observed if the sardine fishery exhibits low abundance (Liermann and Hilborn 2001). The changes in abundance of Pacific sardines in the Gulf of California were explained by Rodríguez-Sánchez et al. (2002) who illustrated that the population of *Sardinops sagax* changes its location within the ocean habitat. They suggested that the rise of a new sardine fishery inside the Gulf of California in the 1970s was the result of this population movement. Another example of this was illustrated by Hargreaves et al. (1994) and Wing et al. (2000) who found sardines in British Columbia and the Gulf of Alaska. We assume that during 1993–94 there were several factors (environment, population movement, and low spawning activity) that determined this particular shift in the population and catch (Nevárez-Martínez et al. 2001). This is because the California Current was affected by an El Niño in 1992 and 1993 (Hayward 1993; Hayward et al. 1994), and during 1994 the California Current returned to a typical circulation pattern (Hayward et al. 1995). The model performed poorly in estimating parameters when 1993 and 1994 were included in the complete time series of the *S-R*. The main effect was on the measurement of λ (fig. 15). Because 1993–94 is particularly anomalous, the approximation excluding this period could be an excellent approach for the Pacific sardine fishery. This reference point provides the primary mechanism by which the precautionary approach can be used. Our results did not show evidence of depensation in the Pacific sardines in the Gulf of California.

The λ value estimated with the modified Shepherd model is near the origin (see fig. 3), so the model implies that depensation is not present in the Pacific sardine. However, the modified Ricker model is far from the origin (see fig. 11), and there are points of stock-recruitment close to the λ value. Apparently, the modified Ricker model could indicate that the fishery needs an analysis of its management strategy to avoid depensation. Cisneros-Mata et al. (1995) believed that overfishing had an important role in the population decline of sardines in the Gulf of California from 1989 to 1992. The main risk to this sardine population is recruitment overfishing. This is understood to occur when spawning biomass is so low that recruitment decreases substantially and perhaps precipitously. In the context of our analysis, we define recruitment overfishing as a level of fishing pressure that reduces the spawning biomass produced by a year-class over its lifetime below the spawning biomass of its parents, on average (Sissenwine and Shepherd 1987). Our analysis is not focused to identify recruitment overfishing, because detecting it is complicated in most stocks by extreme recruitment variation due to factors other than spawning-stock size and by the unrepresentative sampling of *S-R* observations that occur when environmental effects are allowed to influence stock sizes over time (Walters 1990). Nevárez-Martínez et al. (2001) illustrated this when they analyzed survey research data and found a period of low relative abundance from 1990 to 1993 and one of high abundance between 1993 and 1996. In this study, the environment correlated successfully with upwelling and the sea surface temperature. As a consequence, the difference in λ estimates may be hidden because the resource-environment interaction was not measured in the modified Shepherd model (fig. 4) and modified Ricker model (fig. 12). The environment may be responsible for the "school trap" and possibly for the Allee effect for small pelagics. "School trap" was explained by Cury et al. (2000). They provided an empirical demonstration of the tendency for members of two or more pelagic schooling species of similar size and body shape to form mixed schools when abundance of one of the interacting species was low. The unfortunate outcome of this arrangement may be that the less abundant species would effectively be entrained into the life-history behavior of the more abundant species. This would put the less abundant species at risk with a critical disadvantage in growth, survival, and spawning success. We observed that λ for the modified Shepherd model estimated a confidence interval with negative values; evidently there is uncertainty in the parameter. We think that the critical-level stock must be higher, so we agree with the AIC; the Pacific sardine fishery was possibly far from the depensation effect during 1993–94.

An analysis is required to establish the reference point in the Pacific sardine, and we must evaluate the probability of the consequences of various management actions using the λ parameter as a reference point. That approach allows us to examine a stock complex consisting of numerous schools. This will show a stock-recruitment relationship that does not intercept the origin, but rather exhibits zero recruitment at some minimum stock size (Frank and Brickman 2000). We are interested in illustrating that the Pacific sardine in the Gulf of California has a minimum adult stock size. It is possible that when this adult stock is at low densities there is low egg fertilization (Allee effect). Cisneros-Mata et al. (1996b) commented that the existence of density-dependence in small pelagic fish has been questioned, probably because of the difficulty of finding convincingly supportive empirical data. Recruitment success in these species has been related to environmental indicators, such as plankton biomass or the annual sea temperature. A probable mechanism that results in increased cannibalism in the Gulf of California is the intrusion of anomalous warm-water masses that shorten the spawning season and force adult distribution northward (Cisneros-Mata et al. 1996a). Jacobson et al. (2001) analyzed eight anchovy and nine sardine stocks around the world. They showed that environmental effects are likely to contribute more variance to the annual surplus production and the instantaneous surplus production-rate than density-dependent effects for anchovy and sardine stock. This environment effect was also found by Morales-Bojórquez et al. (2003) who analyzed the stock-recruitment relationship to Pacific sardines along the southwest coast of the Baja California peninsula, Mexico and identified changes in the density-independent mortality associated with the sea surface temperature when it was >19.3°C.

The fall in Pacific sardine abundance may be explained from a process that is density-independent for environmental effects. Watanabe et al. (1995) suggested two explanations for a recruitment failure. One is low egg production from a reduced spawning biomass, or low spawning activity of adult fish, and the other is high mortality in the early life stages before recruitment to a fishing stock. Nevárez-Martínez et al. (2001) commented that the decline (1990–93) and recovery (1994–96) of sardines were due to the environment affecting the quality and quantity of primary productivity. In conclusion, we did not observe an Allee effect in the sardine population in the Gulf of California. The fall of abundance during 1993 and 1994 is possibly associated with environmental factors (Nevárez-Martínez et al. 1999; 2001). In those years, the Pacific sardine was far from the reference point estimated with our study, and we believe that the λ parameter is a good indicator of the minimum stock size necessary to maintain the fishery.

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